

# Environmental and pedological factors influencing organic carbon storage in Italian forest soils

Anna Andreetta<sup>a,\*</sup>, Stefano Chelli<sup>b</sup>, Eleonora Bonifacio<sup>c</sup>, Roberto Canullo<sup>b</sup>, Guia Cecchini<sup>a</sup>, Stefano Carnicelli<sup>a</sup>

<sup>a</sup> Department of Earth Sciences, University of Florence, Piazzale delle Cascine 15, 50144 Firenze, Italy

<sup>b</sup> School of Biosciences and Veterinary Medicine, Plant Diversity and Ecosystems Management Unit, University of Camerino, Via Pontoni 5, I-62032 Camerino, MC, Italy

<sup>c</sup> University of Torino, Department of Agricultural, Forest and Food Sciences, Largo Braccini 2, 10095 Grugliasco, Italy

## ARTICLE INFO

### Keywords:

Soil organic carbon storage  
Plant traits  
Forest soils  
Reference soil groups  
Boosted regression trees  
Mediterranean  
Phosphorous  
Subsoil

## ABSTRACT

As a large and persistent carbon sink, forest soils have an essential role in the carbon cycle, thus performing valuable services to society. This paper aims to investigate the role of several environmental factors in driving soil organic carbon (SOC) storage variability in forest soils. The Italian ICP-Forests (International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests) dataset provides an excellent opportunity to analyse an extensive range of variables in a land spanning different ecological regions and climatic gradients, thus being a case of broad interest. We estimated SOC storage for mineral forest soils, considering the topsoil (0–20 cm; SOCM02) and the whole soil profile (0–80 cm; SOCM08). Boosted regression trees (BRTs) were applied to explore the relative influence of environmental predictors and to model SOC storage responses. The reference soil groups (RSG-WRB) and the total subsoil phosphorus (P) content were the factors with the highest performance in explaining SOC storage for both models (SOCM02-SOCM08). Parameters related to vegetation, such as tree species, biodiversity and plant traits, clearly influenced topsoil SOC storage, while their impact was reduced with depth. Climate directly controls SOC storage, but indirect influences via plant or soil characteristics were also identified. Interactions between different environmental factors were discussed to elucidate and analyse SOC responses evidenced by the models. Our results highlighted how soil types (RSGs) can be an effective environmental factor in explaining SOC storage variability, which would likely improve SOC models on national and global scales. Interactions between different environmental factors were seen to be most important, pointing out the strong links between SOC storage and the general ecological context.

## 1. Introduction

Soils support several ecosystem services fundamentals for life on our planet (Kopittke et al., 2021; McBratney et al., 2014) and contribute to most of the sustainable development goals (SDGs) of the United Nations. Within the complexity of the soil matrix, organic carbon (OC) plays a crucial role in soil functioning (Lal et al., 2018), and forest soils are considered effective carbon sinks, potentially stabilising a large amount of organic carbon (Pan et al., 2011), which depends on the balance between net primary production and soil C mineralization rate. Although in the past, the residence time of organic C in the soil was exclusively attributed to the inherent chemical recalcitrance to microbial degradation, over the last decades, it has become evident that this is a too simplified vision and that soil driven mechanisms contribute more

to organic residues stabilisation in soil (Schmidt et al., 2011; Castellano et al., 2015). Soil minerals and aggregates provide physico-chemical protection against decomposing organisms in the forms of occlusion in inaccessible microenvironments and the formation of organo-mineral complexes, promoting long-term SOM stabilisation (Torn et al., 1997; Baldock and Skjemstad, 2000; Kleber et al., 2021; Witzgall et al., 2021). Forest soils rich in clay minerals, nanocrystalline minerals, divalent cations and iron, aluminium and manganese oxides have a higher protective capacity than sandy and poorly developed soils (Oades, 1988; Hassink, 1997; Catoni et al., 2016; Schweizer et al., 2021). Furthermore, root- and mycorrhizal-derived carbon, having a much greater probability of physico-chemical interaction with soil particles, is retained and stabilised more efficiently than aboveground-derived carbon (Rasse et al., 2005; Schmidt et al., 2011).

\* Corresponding author.

E-mail address: [anna.andreetta@unifi.it](mailto:anna.andreetta@unifi.it) (A. Andreetta).

<https://doi.org/10.1016/j.geodrs.2023.e00605>

Received 16 August 2022; Received in revised form 6 December 2022; Accepted 6 January 2023

Available online 7 January 2023

2352-0094/© 2023 Elsevier B.V. All rights reserved.

Sparse information on SOC storage is reported in the literature for forest ecosystems in Italy. These studies are focused on specific topics, such as the potential of humus forms as indicators of carbon storage (Andreetta et al., 2011; Bonifacio et al., 2011), the effects of forest dynamics and management on SOC storage (De Marco et al., 2013; Ferré et al., 2014; Guidi et al., 2014; Pellis et al., 2019; Fino et al., 2020) and the relation between SOC storage, soil properties and landscape morphology (Conforti et al., 2016; Conforti et al., 2020; Oueslati et al., 2013). Most of these studies are based on local-scale research with no aim of capturing the complexity of the entire territory. At the national level, SOC stocks were estimated only for the first 30 cm depth in the National Forest Inventories (Gasparini and Di Cosmo, 2015) and related to vegetation cover. Thus, a comprehensive view of SOC in Italian forest soils and of the driving factors regulating its variability is missing. Italy spans different ecological patterns, with extensive climatic gradients, and hosts different types of soils and plant communities, thus offering the opportunity to obtain models that can be extended and be of broad interest. A recent study on N stocks (Rodeghiero et al., 2018), a soil property closely related to SOC, highlighted how the use of a few soil variables led to the low performance of the applied model. Furthermore, previous studies on the relationship between humus forms and environmental factors found that soil and forest species compete as the most important independent variables, highlighting that the distribution of forest species is not independent of soil characteristics (Andreetta et al., 2016, 2018). Thus, to better elucidate the roles of vegetation and soil as driving factors, we decided to include in the models soil properties and the Reference Soil Groups from IUSS Working Group WRB (RSG-WRB) as factors. The pool of variables related to vegetation was also enriched, by considering plant functional traits, which to our knowledge, are rarely included in models on SOC storage, despite their recognised effect on primary productivity, litter decomposability, and soil carbon and nutrient cycling (Cornwell et al., 2008; Buzzard et al., 2019).

In this paper, we aimed to investigate the factors that drive and explain SOC storage variability in forest soils, including subsoil OC, which is comparatively understudied. To reach this purpose, we used the data collected within the Italian ICP-Forests network, which is the branch of one of the International Cooperative Programme that was launched in 1985 under the Convention on Long-range Transboundary Air Pollution of the United Nations Economic Commission for Europe (UNECE). The main objective of the ICP-Forests is the assessment and monitoring of air pollution effects on forests. The Italian dataset is based on a systematic and probabilistic sampling design and is thus representative of the heterogeneity of Italian forests (Chiarucci et al., 2019). Sites were distributed across the three biogeographic regions of Italy, identified according to the EU policy for nature protection (ETC-BD European Topic Centre on Biological Diversity, 2006), namely Alpine, Continental and Mediterranean. The following objectives were addressed: 1) to estimate SOC storage for mineral forest soils, considering both topsoil (0–20 cm) and the 0–80 cm soil depth; 2) to point out the dominant explanatory factors and their influence on SOC using a statistical modelling approach.

## 2. Materials and methods

### 2.1. Sampling scheme and soil description

The survey area covers most of the Italian forests. Fig. 1 shows the geographical distribution of the large-scale soil survey (Level I) plots, belonging to the Italian branch of the ICP-Forests network ([www.ICPFoRESTS.net](http://www.ICPFoRESTS.net)). Plot location was established on a probabilistic method: a grid of 16 km × 16 km was superimposed onto the whole of Italy. Each corner was considered as a plot if a forest area larger than 1 ha was found. A total of 215 plots resulted from this process, was validated after a field check and used in this work. Sites were distributed across the three biogeographic regions of Italy, identified according to the EU policy for nature protection (ETC-BD 2006), namely Alpine, Continental and

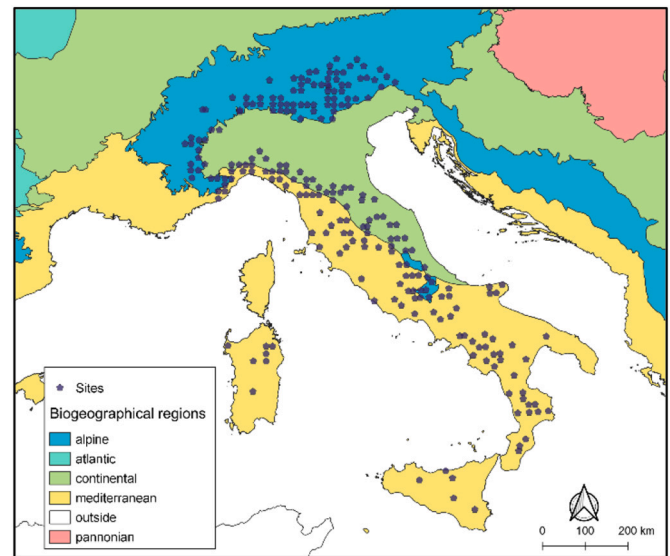


Fig. 1. Location of the study sites across different biogeographical regions (Alpine, Mediterranean and Continental). The Italian ICP-Forests sites were plotted on the map “Biogeographical regions in Europe” provided by the European Environment Agency (©EEA; <https://www.eea.europa.eu/legal/copyright>).

Mediterranean (Fig. 1).

Soil sampling was carried out according to standard ICP Forests procedures (FSCC, 2006). For each site, five sampling pits were opened within a circle of 25 m in diameter (Andreetta et al., 2018). Soil profiles were described according to FAO (FAO, 2006) and classified following the World Reference Base for Soil Resources (IUSS Working Group WRB, 2007, 2015). A national field excursion was organised for cross-calibration among soil surveyors. Furthermore, incremental depth sampling was applied to mineral soil profiles and fixed-depth samples were collected and defined as M01 (0–10 cm), M12 (10–20 cm), M24 (20–40 cm) and M48 (40–80 cm). During soil profile description, coarse fragments (CF) content was estimated as a percentage class (0–5–15–40–80) of total soil volume (FAO, 2006; FSCC, 2006). Bulk density (BD, g cm<sup>-3</sup>) was assessed on the fine earth (<2 mm), using cores of about 100 cm<sup>3</sup> volume.

### 2.2. Physical and chemical analyses

Physical and chemical parameters were analysed following the reference methods collected in the ICP-Forests Manual, part IIIa, sampling and analysis of soil (FSCC, 2006; ICP Forests, 2010). Soil samples were air-dried, macroscopic residues were removed and all mineral and organic soil materials passing a 2 mm sieve were analysed. OC concentration (g kg<sup>-1</sup>) was determined by dry combustion after correction for inorganic C, according to ISO 10694 (ISO, 1995a). Subsoil calcium (SubCa) and phosphorus (SubP) were analysed through aqua regia extraction by using hydrochloric acid followed by nitric acid, according to ISO 11466 (ISO, 1995b). Subsoil Ca and P start in the last available interval, usually the 40–80 cm depth interval. But when the soils were shallower, we used 20–40 cm depth (the layer more influenced by the parent material).

### 2.3. Model building (BRT - Boosted regression trees)

Boosted regression trees (BRT) were used to explore the relative influence of different environmental drivers on SOC storage. Individual BRT models were built for two mineral soil depth intervals, M02 (0–20 cm) and M08 (0–80 cm). BRT modelling is a machine learning technique and a further development of classification and regression tree models. A

BRT-model splits the data set of the response variable into groups of predictor variables, where each group represented a branch of a regression tree. This modelling step was repeated multiple times (at least 1000 trees are built in a BRT; Elith et al., 2008). Each of the trees combines a set of predictor variables that explains SOC storage. BRTs are characterised by their effective predictive performance and can effectively describe non-linear relationships between factors. They can accommodate any type of variable (continuous, categorical, nominal), missing, non-independent data and automatically incorporate interactions between variables. Therefore, BRTs are recommended modelling approaches for comprehensive and differently scaled datasets (Elith et al., 2008). Additionally, a BRT model allows the derivation of partial dependence plots, which indicate how the response is affected by a certain predictor after accounting for the average effects of all other predictors in the model; thus, these plots can be used for model interpretation (Elith et al., 2008).

The predictive performance of BRT is influenced by three parameters: the learning rate controls the fractions of the data that are modelled in each tree, tree complexity determines the interaction depth within the BRT model and the bag fraction represents the fraction of training data that was randomly selected in each modelling step. After testing various combinations of the parameters, the most effective parameters for our data were 0.5 for bag fraction, 0.002 for the learning rate and 4 for the tree complexity. Cross-validation was performed to estimate the optimal number of trees producing the best predictive performance, which was evaluated by predictive deviance. Parameterisation of BRTs was conducted within the R-environment (R Core Team, 2021), using the *gbm.step* function in “dismo” packages (Hijmans et al., 2021). For each model, 20 bootstrapped BRT model runs were performed. Percent deviance of the response variable was used to assess model fit.

We evaluated the role of different environmental factors in driving SOC storage within each soil depth interval based on the relative influence and shapes of partial-dependence plots. We first constructed preliminary BRT models with 14 predictors (Table 1). The preliminary models' predictors with low relative influence (RI < 5%; Table 1) were removed to obtain more effective final models.

**Table 1**

Variables included in the preliminary models and the selected variables used to optimize the BRT models for SOC storage: SOCM02 ( $\text{kg m}^{-2}$ ) 0–20 cm of mineral soil depth and SOCM08 ( $\text{kg m}^{-2}$ ) 0–80 cm; BIO16: precipitation of the wettest quarter of the year (mm); PET: potential evapotranspiration (mm); Tree: dominant tree species; Richness: plant species richness; SLA: specific leaf area ( $\text{cm}^2 \text{g}^{-1}$ ); LDMC: leaf dry matter content ( $\text{mg g}^{-1}$ ); RSG-WRB: References Soil Groups; HUMUS: mull-moder-amphi; SubCa: subsoil extractable Ca ( $\text{mg kg}^{-1}$ ); SubP: subsoil total P ( $\text{mg kg}^{-1}$ ).

	Variables for the preliminary models	Selected variables for the optimized models SOCM02	Selected variables for the optimized models SOCM08
Climatic factors	BIO16	BIO16	BIO16
Vegetation factors	PET		PET
	Tree	Tree	Tree
Soil factors	Richness	Richness	
	SLA	SLA	
	LDMC	LDMC	
	Canopy height		
	RSG-WRB	RSG-WRB	RSG-WRB
	HUMUS		
	SubCa	SubCa	SubCa
Terrain factors	SubP	SubP	SubP
	pH		
	Elevation		
	Slope		Slope

## 2.4. Explanatory variables

An extensive set of explanatory variables relating to climate, vegetation and soil, was considered.

### 2.4.1. Climate

Climate parameters were downloaded from the WorldClim global database (version 1; Hijmans et al., 2005, period 1970–2000). Before launching the BRT model, we decided to reduce the number of climate variables, thus we applied Boruta, an all-relevant variable selection algorithm, which works as a wrapper algorithm around Random Forest, and can cope with redundancy and collinearity between variables (Xiong et al., 2014; Kursa and Rudnicki, 2020). Following this method, the precipitation of the wettest quarter (BIO16) was identified as the climate factor relevant for SOC storage and was then included in the BRT models for both topsoil and whole mineral soil. To run the Boruta algorithm, we applied the “Boruta” package (R version 4.0.5 (2021–03–31)). Potential evapotranspiration (PET) was also used in the BRT models.

### 2.4.2. Dominant tree species

The “Tree” factor was based on the dominant tree species, as recorded in the ICP-Forests crown condition survey (Lorenz et al., 2004). *Picea abies* (Pabi), *Fagus sylvatica* (Fsyl), *Castanea sativa* (Csat), *Quercus cerris* (Qcer), *Quercus pubescens* (Qpub) and *Larix decidua* (Lardec) were the most frequent species and each of them represented a group. Qpub was dominated by *Quercus pubescens* and included all strictly deciduous oaks, except *Q. cerris*. Other species were grouped according to physiological and ecological similarities: Conif included all conifers except *P. abies* and *L. decidua*; “Other” grouped all broadleaved trees except *F. sylvatica*, *C. sativa* and oaks. Med grouped all sclerophyll oaks, mostly *Quercus ilex* and also included other Mediterranean species such as *Pinus halepensis* and *Eucalyptus* spp.

### 2.4.3. Richness

The vegetation survey was performed at the community level in 400 m<sup>2</sup> plots. In this study, only data on species presence/absence were used. A National Reference Manual was prepared to facilitate uniform team methodology, defining the procedural and technical standards. The ICP-Forests program guidelines, which stress the necessity of using Quality Assurance procedures, were adopted (Allegrini et al., 2009). The resulting species lists have been used to estimate the “plant species richness”.

### 2.4.4. Plant functional traits

We measured these plant functional traits for the understorey layer, which is an important, but still neglected, component of forest ecosystem functioning (Landuyt et al., 2019). We selected two key plant functional traits of the Leaf–Height–Seed traits (LHS) scheme (Westoby, 1998) that are independent of each other and represent the major axes of plant strategies. They are specific leaf area (SLA), a proxy of plant growth rate, related to leaf economics and lifespan, and plant height (H), related to competitive ability, aboveground biomass and access to the vertical light gradient (Weiher et al., 1999). Additionally, we included in this study the leaf dry matter content (LDMC), related to leaf structural characteristics. Both SLA and LDMC are included in the Leaf Economics Spectrum and are informative of litter quality and decomposability (Rawlik et al., 2022). Considering that the trait values of the dominant species of the understorey have a proportionally greater effect than those of less abundant ones (biomass-ratio hypothesis; Grime, 1998; Wasof et al., 2018), we (a) selected from each plot all the understorey species contributing to reach a relative cumulative coverage of 80% at the plot level; (b) attributed trait values to these species; and (c) weighted trait values according to understorey species coverage at the plot level, in order to obtain community-weighted mean (CWM) values for each trait (Garnier et al., 2004). Trait values were extracted from Chelli et al.

(2019).

#### 2.4.5. Soil

In the models, we included soil pH, subsoil acid extractable-Ca (SubCa) and total P (SubP), which are indicative of the properties inherited from the parent material. These parameters were obtained from the deepest samples. Soil type (RSG-WRB; IUSS Working Group 2015) was also included as the product of soil genesis, and humus form (HUMUS), as an indicator of nutrient turnover and soil nutrient strategies (Ponge et al., 2002;). The diagnostic properties that are key to reference soil groups are not directly related to OC content, except for RSGs for which the presence of a *Mollic* or *Umbric* diagnostic horizon is a prerequisite. The amount of OC necessary to classify a soil horizon as a *Mollic* or *Umbric* horizon is, however,  $\geq 0.6\%$  (IUSS WRB, 2015). In the Italian ICP-Forests dataset, all the OC values are higher than this threshold. This allows us to consider the RSG-WRB as independent factors in the built models.

Although BRTs do not require prior data transformation, SubCa, SubP and SLA were included in the model after being log-transformed to improve the readability of the partial dependence plots.

### 3. Results

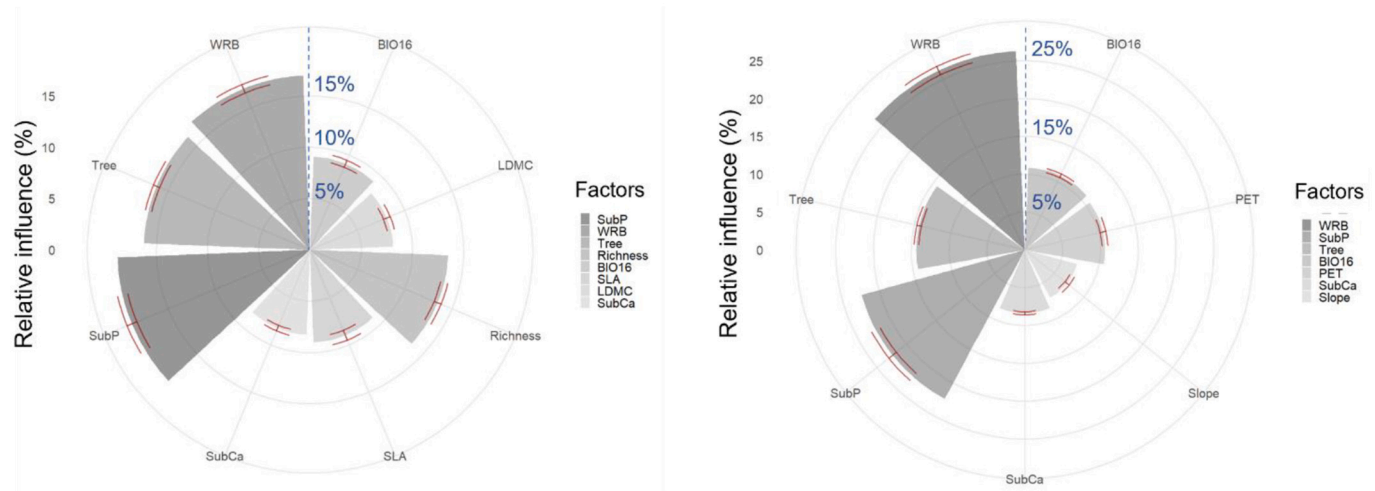
#### 3.1. Model building and factor impact on SOC storage

Several variables such as Humus form, soil pH, Canopy height and elevation contributed little to the SOC preliminary models (Table 1) for both soil depth intervals; they were thus not included in the final models. The factors with relative influence (RI) higher than 5% in the preliminary models were selected and included in the final models (Table 1). The RI scores for each variable are reported in Fig. 2, while the relationships between SOC and each factor are shown in Figs. 3 and 4. Models performed well at both depth intervals and explained 65% and 54% of the variation for SOCM02 and SOCM08, respectively. Summary statistics of dependent (SOCM02 and SOCM08) and independent variables are reported in Table 2, to show their range of values for the analysed forest sites.

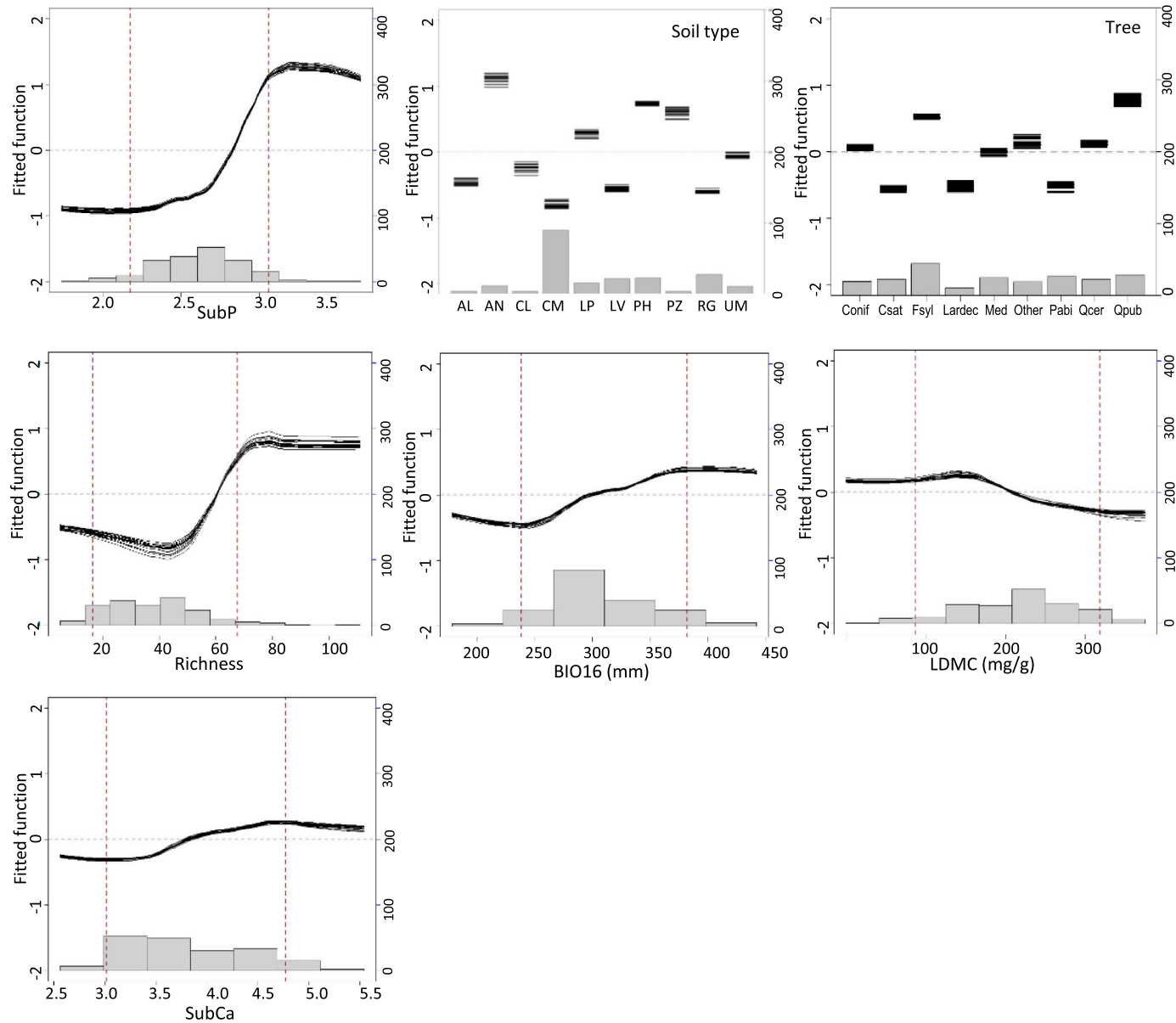
Soil type (RGS-WRB) was one of the dominant variables for both models, with a relative influence (RI) of  $17\% \pm 0.4$  for SOCM02 and  $22\% \pm 0.6$  for SOCM08 (Fig. 2). The partial dependency plots showed that Andosols (AN) are most positively associated with both topsoil and subsoil SOC, followed by Phaeozems (PH) and Podzols (PZ). In contrast,

Cambisols (CM), Luvisols (LV) and Regosols (RG) showed a negative association (Figs. 3 and 4). Leptosols (LP) and Umbrisols (UM) showed different depth patterns, Leptosols influencing positively SOCM02 and negatively SOCM08, while Umbrisol influence is close to neutrality for topsoil SOC variability and positive for the whole soil profile (Fig. 3 and Fig. 4). SubP was a major driver with a RI of  $19\% \pm 0.5$  and  $16\% \pm 0.6$  for SOCM02 and SOCM08, respectively and showed a positive effect on SOC storage. The impact of SubCa was less marked, although positive (Fig. 2, Fig. 3 and Fig. 4). The role of dominant vegetation on soil organic carbon stock reaches a high score of relative influence but is second to soil reference group and subsoil P content for both models (Fig. 2). Tree factor reached values close to those of RGS-WRB for SOCM02 ( $16\% \pm 0.3$ ), while Tree influence was significantly lower for the SOCM08 model ( $14\% \pm 0.3$ ). The BRT models showed a positive effect of *Fagus sylvatica* (Fysl), *Quercus pubescens* (Qpub) and Other, and a negative effect of *Castanea sativa* (Csat), *Larix decidua* (Lardec) and *Picea abies* (Pabi) on SOC storage for both models (Fig. 3 and Fig. 4). The climate variable BIO16, which represents the precipitation of the wettest quarter of the year, explained part of the variation in SOC storage (RI =  $9\% \pm 0.4$  and  $11\% \pm 0.4$  for SOCM02 and SOCM08, respectively) and was positively associated with SOC. The potential evapotranspiration (PET) and terrestrial-derived factors, such as the terrain slope, significantly explained the variation of SOC stocks for the whole soil profile, but they did not when considering only the topsoil. They both negatively affected SOC storage. Richness and plant traits (LDMC and SLA) showed high performance in accounting for variability in topsoil SOC stocks (Fig. 2). At the same time, their influence was less marked for the SOCM08 models (RI < 5% for all these variables in the preliminary model). The shape of the partial dependence plots showed that Richness has not a linear influence on SOCM02, with negative effects at low values and positive impact at values higher than 40 (Fig. 3). Regarding plant functional traits, leaf dry matter content (LDMC) negatively influenced SOCM02, while the shape of specific leaf area (SLA) fitted function presented several small oscillations, which made the interpretation difficult.

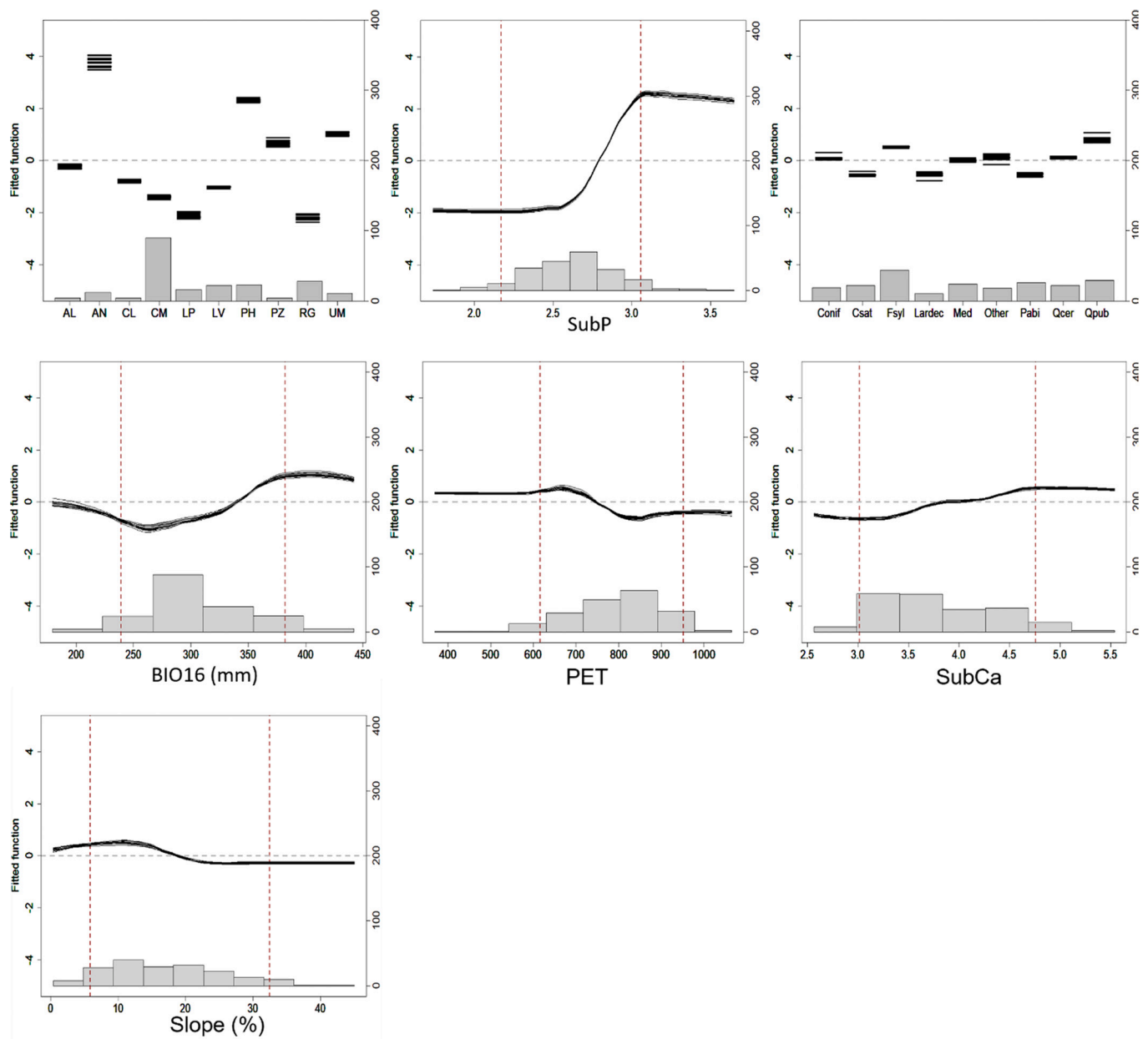
The distribution of SOC stored at each depth interval (0–10 cm, 10–20 cm, 20–40 cm and 40–80 cm) was represented in Fig. 5 and showed the highest variability between soil types (Fig. 5a) than among tree species (Fig. 5 b). The largest amount of organic carbon was stored in Andosols (AN) for all the soil intervals, followed by Phaeozems and Umbrisols (Fig. 5a). *Fagus sylvatica* (Fysl) exhibited the highest value of SOC storage, while the lowest was observed for *Castanea sativa* (Csat)



**Fig. 2.** Rotate plots representing the variability across 20 model runs of the **relative influence** values for the selected predictors of the regression tree (BRT) models for SOC storage: (A) topsoil SOCM02 ( $\text{kg m}^{-2}$ ) 0–20 cm mineral soil depth; (B) whole the analysed soil profile: SOCM08 ( $\text{kg m}^{-2}$ ) 0–80 cm mineral soil depth. BIO16: precipitation of the wettest quarter of the year (mm); PET: potential evapotranspiration; Tree: dominant tree species; Richness: plant species richness; SLA: specific leaf area; LDMC: leaf dry matter content; RSG-WRB: References Soil Groups; HUMUS: mull-moder-amphi; SubCa: subsoil Ca; SubP: subsoil total P.



**Fig. 3.** Partial dependency plots showing the marginal influence of each predictor variable on soil organic carbon storage (SOCM02 kg m<sup>-2</sup>; 0–20 cm soil depth; y axes); the effect of each predictor on soil organic carbon storage (SOCM02), given the average effects of all other predictors in the model. Each plot includes 20 black lines representing individual model runs. Histograms show distributions of predictors across sites and the red vertical dashed lines are the 5th and 95th percentiles of each predictor. BIO16: precipitation of the wettest quarter of the year (mm); Richness: plant species richness; LDMC: leaf dry matter content (mg g<sup>-1</sup>); SubP: subsoil total P SubCa: subsoil extractable Ca (Subsoil P and Ca are log-transformed values). Soil types (RSG-WRB: AL – Alisols, AN – Andosols, CL – Calcisols, CM – Cambisols, LP – Leptosols, LV–Luvisols, PH – Phaeozem, PZ – Podzols, RG – Regosols, UM – Umbrisols).



**Fig. 4.** Partial-dependence plots showing the marginal influence on soil organic carbon storage (SOCM08 kg m<sup>-2</sup>; 0–80 cm soil depth, y axes) of boosted regression tree model predictors. Each plot includes 20 black lines representing individual model runs. Histograms show distributions of predictors across sites and the red vertical dashed lines are the 5th and 95th percentiles of each predictor. BIO16: precipitation of the wettest quarter of the year (mm); PET: potential evapotranspiration (mm); Richness: plant species richness; SubP: subsoil total P and SubCa: subsoil extractable Ca (Subsoil P and Ca are log-transformed values). Soil types (RSG-WRB: AL – Alisols, AN – Andosols, CL – Calcisols, CM – Cambisols, LP – Leptosols, LV-Luvisols, PH – Phaeozem, PZ – Podzols, RG – Regosols, UM – Umbrisols).

and *Larix decidua* (Lardec), especially for the deepest layers (20–40 cm and 40–80 cm; Fig. 5b).

Given the high weight of soil types as a driving factor for SOC storage, density plots were used to visualise the distribution of the other variable in relation to each soil group as a tool to better discuss the results. The peaks of the Density Plot help display where values are concentrated over the interval (Fig. 6).

## 4. Discussion

### 4.1. The influence of soil type and forming processes on SOC storage

The evident weight of the soil type on OC storage is likely due to soil-forming processes that, while generating primarily specific soil types,

also modulate the distribution of OC in mineral horizons. Andosols, Phaeozems and Podzols have distinctive physical, chemical and mineralogical properties that guarantee the effectiveness of the OC protection mechanisms.

Andosols' colloidal fraction is dominated by nanocrystalline minerals, which are extremely effective in binding organic matter (OM), because of their large surface area (Kleber et al., 2005). SOM is further stabilised into metallorganic complexes by high solution activities of metals, especially aluminium (Dahlgren et al., 2004; Tonnejck et al., 2010), hampering enzymatic activity. Carbon accumulation in mineral soil can be further amplified by a somewhat acidic environment that reduces the activity of pedofauna and microorganisms. Radiocarbon ages and mean residence times for OM are usually high in Andosol (Aran et al., 2001; Marin-Spiotta et al., 2011; Mathieu et al., 2015). Finally,

**Table 2**

Summary statistics of SOC storage and environmental factors at the sampling sites. SOCM02: Soil organic carbon storage for 0–20 cm of mineral soil depth; SOCM08: soil organic carbon storage for 0–80 cm; BIO16: precipitation of the wettest quarter; PET: potential evapotranspiration; Richness: plant species richness; SLA: specific leaf area; LDMC: leaf dry matter content; SubCa: subsoil extractable Ca; SubP: subsoil total P.

	1st Qu.	Median	Mean	3rd Qu.
SOCM02 (kg m <sup>-2</sup> )	4.54	5.83	6.48	8.18
SOCM08 (kg m <sup>-2</sup> )	7.32	10.05	11.53	13.80
BIO16 (mm)	264	283	293	322
PET (mm)	717	807	790	878
Slope (%)	11.4	18.1	18.8	25.9
Richness	23.8	37.0	38.2	49.0
LDMC (mg g <sup>-1</sup> )	150.4	217.4	209.3	263.4
SLA (cm <sup>2</sup> g <sup>-1</sup> )	20.3	25.9	37.0	34.9
SubCa (mg kg <sup>-1</sup> )	2441	6227	29,054	31,902
SubP (mg kg <sup>-1</sup> )	258	430	537	645

stabilisation of OM in Andosols often occurs by topsoil burial by repeated additions of fresh volcanic ejecta (Taboada et al., 2019). All the mechanisms mentioned above, plus the high net primary productivity due to favourable physical conditions, help to explain the remarkable capacity of Andosol to sequester OC (Fig. 5).

Phaeozems (PH) have high base saturation with polyvalent cations such as Ca<sup>2+</sup> and Mg<sup>2+</sup>, which act as bridging agents between OM and clay (IUSS Working Group WRB, 2015). The relationship between Phaeozem (PH) and Ca content is also evident in the empirical density plot of subsoil Ca (SubCa) for RSG-WRB (Fig. 6). OC stabilisation in Phaeozems might be also due to biological ped formation, promoted by microbial activity and primarily by pedofauna mixing and burrowing (krotovinas) in the lower topsoil and subsoil, with OC incorporation into thick black Mollic A horizons (Wilkinson et al., 2009). Phaeozems were always associated with mull or amphi humus forms in the analysed dataset. The high fertility of these soils and consequently high primary productivity also likely promotes abundant root-derived C inputs (Feng and Simpson, 2007), favouring the incorporation of OM in the mineral soil matrix.

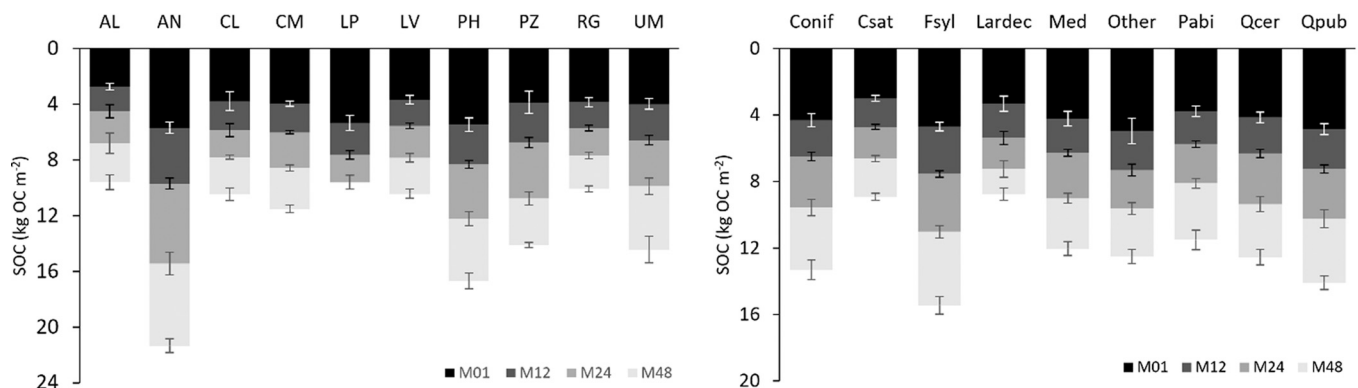
In Italy, Podzols (PZ) occur at high elevations. Their positive influence is evident for the SOCM02 model, while for SOCM08 it is moderate, as Podzols in the database are relatively shallow, with a mean of 58 ± 13.4 cm depth. This capacity to sequester high amounts of carbon can be explained by specific mechanisms of SOM mobilisation, translocation and stabilisation linked to the processes of podzolisation (Sauer et al., 2007). Specific processes can also be observed for each type of horizon. Organic horizons in Podzols account for a limited fraction of SOC compared to the mineral soils (Grand and Lavkulich, 2011). In our

database, E horizons are very thin and poorly contribute to topsoil OC stock, while within the first 20 cm of mineral soils, spodic horizons of all types (Bms, Bhs, Bs) are present. Accumulation of OM in Spodic horizons is caused by the illuviation of colloids, followed by their immobilisation due to combined increases in pH and colloid metal loading (Al + Fe/C ratio; Bazilevskaya et al., 2018). Fe oxides and nanocrystalline Al-silicates with high surface area and microporosity might play a key role in the formation of organo-mineral associations (Eusterhues et al., 2005). The association between metals and OM further promotes soil structure in the Spodic horizon, improving OC stabilisation through OM-Me-mineral interactions (Bonifacio et al., 2013; Cornelis et al., 2018).

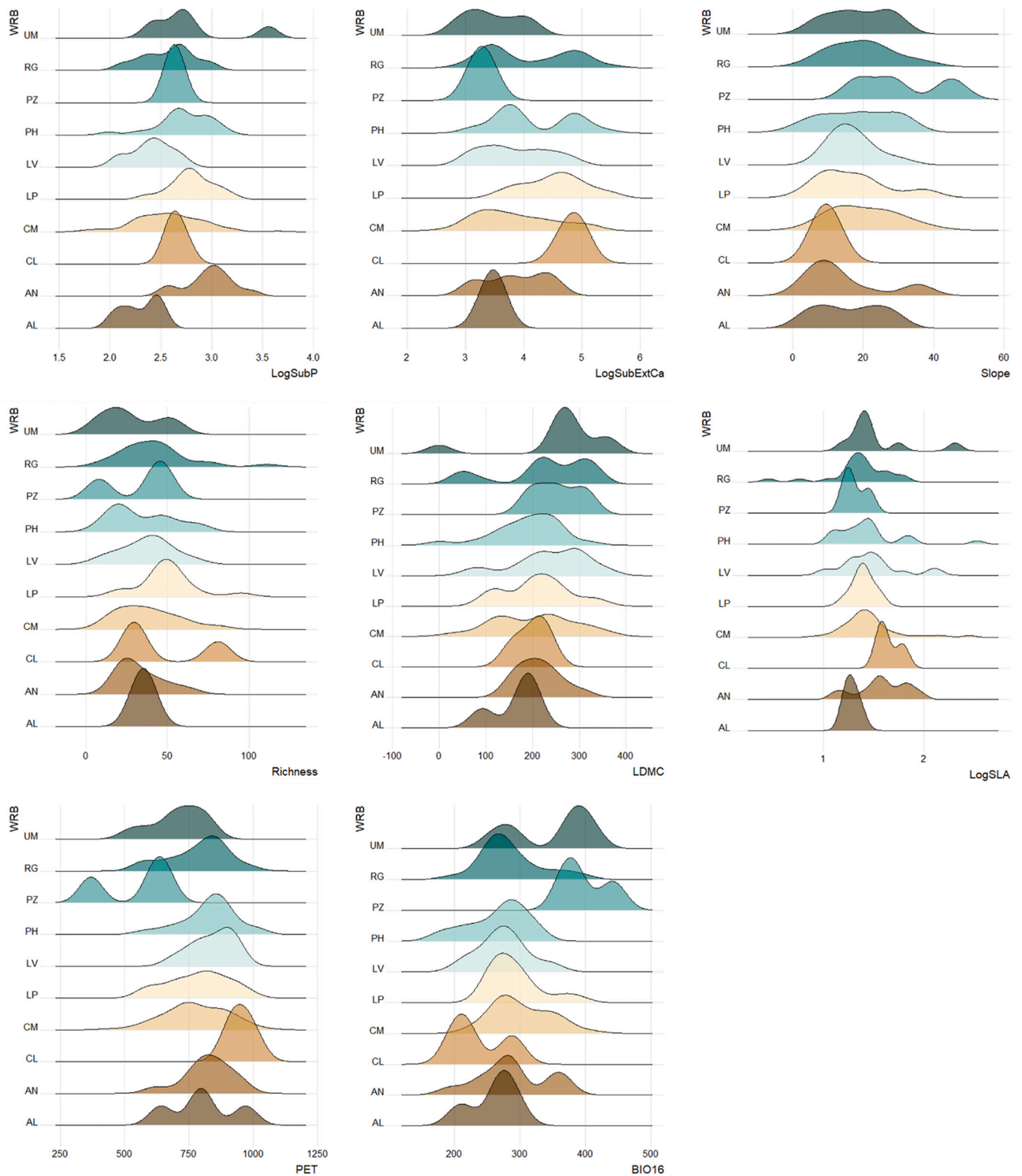
#### 4.2. Subsoil P and Ca contents as proxies of parent material influence

Subsoil P was among the most important predictors for both models (Fig. 2), pointing out its great ecological significance (Walker, 1964). Subsoil total P was selected as proxies of the parent material. Porder and Ramachandran (2013) found that the variation in P concentration among common rock types mirrors the changes in total soil P and that the P concentration of rocks explained 42% of the variance in total soil P, with higher explanatory power (≥70%) among sites with a similar climate. Also, for the present dataset, topsoil phosphorus content was more related to soil parent material and geochemical evolution than P litter content (Andretta et al., 2016, 2018). P might represent a limiting element for plant productivity in a wide variety of terrestrial ecosystems (Vitousek et al., 2010); Walker and Syers (1976) suggested that even minimal P losses cannot readily be replenished. The soil-substrate age hypothesis (Walker and Syers, 1976) is also the basis of the plant trait hypothesis for nutrient availability (Buzzard et al., 2019); soil nutrient contents likely change with soil age because of weathering and leaching. The high performance of subsoil P in predicting SOC storage can also be explained by other mechanisms. Rock type may exert a strong control on pedogenesis and resulting soil characteristics, which can influence OC accumulation and stabilisation, as discussed above. Furthermore, rock type impacts ecosystem nutrient status, in turn influencing plant growth and the quantity and quality of organic matter that reaches the soils. P addition can also increase the belowground NPP and root turnover rates in low-P availability forests (Ostertag, 2001).

Also, subsoil acid extractable-Ca exerted a positive influence on SOC (Fig. 3 and Fig. 4). Soil calcium originates from rock weathering (Dijkstra et al., 2003), decomposition of Ca<sup>2+</sup>-rich organic materials (Ranjbar and Jalali, 2012) and atmospheric dust deposition (Cecchini et al., 2019, 2021). A positive correlation between Ca-bearing minerals and total Ca concentration in the surface soil was previously found (Dijkstra et al., 2003). Chemical modelling indicates that Ca<sup>2+</sup> can readily create both inner- and outer-sphere complexes with organic functional groups, playing an active role in SOC stabilisation (Rowley et al., 2018).



**Fig. 5.** Distribution of average SOC stored at each soil depth interval (M01 = 0–10 cm, M12 = 10–20 cm, M24 = 20–40 cm, M48 = 40–80 cm) among soil types (RGS-IUSS) and dominant tree species. Soil types (RSG-WRB): AL – Alisols, AN – Andosols, CL – Calcisols, CM – Cambisols, LP – Leptosols, LV – Luvisols, PH – Phaeozem, PZ – Podzols, RG – Regosols, UM – Umbrisols).



**Fig. 6.** Empirical density plots of the environmental variables for RSG-WRB (AL – Alisols, AN – Andosols, CL – Calcisols, CM – Cambisols, LP – Leptosols, LV-Luvisols, PH – Phaeozem, PZ – Podzols, RG – Regosols, UM – Umbrisols). SubP: subsoil total P SubCa: subsoil extractable Ca (Subsoil P and Ca are log-transformed values); Slope (%); Richness: plant species richness; LDMC: leaf dry matter content ( $\text{mg g}^{-1}$ ); LogSLA: specific leaf area (log-transformed values); BIO16: precipitation of the wettest quarter of the year (mm); PET: potential evapotranspiration (mm).



However, the relative influence (RI%) of SubCa as a driving factor in SOC storage variability was not very high (Fig. 2). The soil groups with higher subsoil Ca are Calcisols (CL), Leptosols (LP), Regosols (RG) and Phaeozems (PH; Fig. 6). These soil groups, except Phaeozems, also show a negative association with SOC storage. The positive influence of Ca on SOC storage through soil fertility and SOC stabilisation appears to be contrasted by other factors, which could also involve the presence of paedogenic carbonates in the deeper soil layers, adding variability to the contents provided by the parent material. Calcisols are associated with high PET and low precipitation (Fig. 6). Water shortage might affect these soils, negatively impacting primary productivity. Leptosols are either shallow or extremely gravelly soils (IUSS-WRB, 2015). They show a positive association with SOCM02 but, expectedly, not with SOCM08 (Fig. 3 and Fig. 4), as deeper horizons are either missing or too stony to store SOC. Regosols are weakly developed mineral soils on unconsolidated parent material, widespread in eroding lands, semi-arid areas, or mountains. All the factors that negatively impact and slow down soil development, such as soil erosion and drought, also likely constrain OC accumulation and stabilisation, explaining the lowest values of SOC storage, even in the topsoil (Fig. 3 and Fig. 5)

#### 4.3. Dominant tree species

When the Italian forest soils were grouped according to stand type (Fig. 5b), SOC storage was significantly lower under *Castanea sativa* (Csat) and *Larix decidua* (Lardec); this may be due to either a large proportion of OC stored in the organic layers compared to mineral soil, especially for *L. decidua*, or to a relatively sparse vegetation cover. However, SOC stock variability was too high to draw practical and management indications. The data available for Italy (National Inventory of Forests and Forest Carbon Tanks) confirm that there are no significant differences in SOC topsoil (0–30 cm) storage between dominant tree species (Gasparini and Di Cosmo, 2015). However, the BRT models (Fig. 3 and Fig. 4) showed different effects on SOC storage among species.

Dominant tree species can affect soil organic carbon content through net primary productivity (NPP) and litter composition. A dependence between tree species and SOC storage, through litter quality, might explain the predictive performance of the tree factor. In a previous study within the same dataset (Andreetta et al., 2016), various soil and litter properties were analysed in relation to tree species, to discover potential interactions leading to high weights of tree species as predictors for humus form differentiation. Some of the reported results can be reconsidered and analysed for SOC storage. Species groups, such as spruce and chestnut, with the lowest litter Ca content (see table 5 in Andreetta et al., 2016), showed a negative effect on SOC storage (Fig. 3 and Fig. 4), while species with high litter Ca content, such as “Other” and “Qpub” showed a positive effect.

Although the comparison between species evidenced specific plant effects, tree-site interactions must also be considered. Chestnut tends to be found on acid soils with low subsoil Ca and P (See Table 8 in Andreetta et al., 2016); litter's low Ca and P content may then be partly attributed to low-subsoil Ca and P. On the other hand, “Other” tree species thrive on subsoils with high Ca and P, associated with similar litter properties. *Q. pubescens* showed a stronger positive effect than *Q. cerris*, although there is no significant correspondence between tree species and other predictor variables. Beech forests exhibited the highest value of SOC storage at both soil depth intervals (Fig. 5). The positive effect of beech forests on SOC storage can be ascribed to factors other than Ca litter content. Despite intermediate values of litter Ca, beech shows high litter P content (Andreetta et al., 2016) and is associated with high subsoil P (Table 8; Andreetta et al., 2016). Further, Andosols (AN) are often associated with *F. sylvatica*; 41.7% of Andosols, acknowledged to have a high available water capacity, were found under beech forests within our dataset. Beyond that, Southern European beech can also cope with drought through rapid responses to environmental

stressors' variability. Fine roots in Mediterranean beech forests were found to represent a functional carbon sink during the dry season when sinks in other tissues are reduced (Scartazza et al., 2015). This points out the crucial role of carbon allocation by plants in soil carbon dynamics. It could be hypothesised that in Italy, especially in Mediterranean environments, the high solar radiation and the water shortage can favour carbon allocation to the roots, turning out in a carbon source that is efficiently retained in soils (Schmidt et al., 2011).

Parent material likely influences tree distribution which in turn modulates the fertility of soils. However, it is not always easy to distinguish whether trees or soil play a major role. These results agree with previous studies (Van Breemen et al., 1997; Finzi et al., 1998; Dijkstra et al., 2003) that, trying to separate the effects of tree species from the effects of parent material, concluded that the parent material and its impact on tree distribution must be considered in determining tree species effects on soil properties. The high fertility of soils improves the net primary productivity with a consequently high input of organic matter to the soil.

#### 4.4. Climate, biodiversity and plant traits

The precipitation of the wettest quarter of the year (BIO16) was positively associated with SOC, while PET was negatively associated (Fig. 3 and Fig. 4). This is consistent with previous findings by studies covering a wide range of geographical regions, from semi-arid areas (Wynn et al., 2006) to Tibetan (Yang et al., 2008) and permafrost regions (Wu et al., 2022). Climate can, directly and indirectly, impact SOC storage variability. Precipitation effectively stimulates vegetation growth, and NPP is sensitive to climate (Schuur, 2003; Wynn et al., 2006). High vegetation cover and productivity imply higher C input through plant residues, resulting in higher SOC stocks. Precipitation influences the water and C cycle by regulating aboveground and belowground biomass (Campo and Merino, 2016). Decomposition of dead plant material is an important process in OC and nutrient cycling. Both the average decomposition rate and the ratio of above- to below-ground decay were found to increase with annual precipitation (Powers et al., 2009). Droughts, by decreasing the decomposition rate of organic matter, favour high OC accumulation in the forest floor and prevent the concomitant CO<sub>2</sub> release in the atmosphere, thus functioning as a strategy to maintain a pool of nutrients; on the other hand, decomposed plant residues accumulate in the form of particulate organic matter without being associated and stabilised in the mineral soil (Cuevas et al., 2013; Roa-Fuentes et al., 2013), thus preventing long-term OC persistence in the soil. Furthermore, the effect of precipitation and PET on other factors, such as the presence of calcium carbonates, appears to indirectly modulate carbon storage variability, as we have pointed out when discussing climate interactions with other drivers.

Although at the small-catchment scale, topographic factors (e.g., slope gradient) heavily influence the SOC storage (Conforti et al., 2016; Oueslati et al., 2013), slope, as an explaining factor, achieves a low relative influence score at the national-scale (Fig. 2). Slope impact is evident only considering the whole soil profile (SOCM08; Fig. 4). Decreased SOC storage with increasing slope values may be explained by changes in soil depth according to topography, with shallow soils on steep slopes and deeper soils in flat areas. Furthermore, continuous and undisturbed OM input can favour OC accumulation in areas on stable topography with gentle slopes, which are often associated with dense vegetation and a low degree of soil erosion.

Other factors related to vegetation, such as Richness, leaf dry matter content (LDMC) and specific leaf area (SLA), showed a relevant influence on SOC storage only for the topsoil (SOCM02, Fig. 2), highlighting the decreased impact of the biota in the deepest soil layers. The Richness impact on SOC storage, could be ascribed to the widely recognised role of feedback in biodiversity-ecosystem functioning relationships (Qiu et al., 2018). Biodiversity favours interspecific complementarity, better use of limiting resources, and nutrient-cycling feedback, thus enhancing

the ability of ecosystems to sustain multiple functions, such as carbon storage, productivity, and the increase of nutrient pools (Maestre et al., 2012; Tilman et al., 2014). Several studies, mainly focused on grassland biodiversity, show that high-diversity mixtures are more productive than monocultures of the same species, favouring SOC storage (De Deyn et al., 2011; Marquard et al., 2009). However, the shape of the fitted functions for Richness shows a more complex response (Fig. 3). This can be related to two aspects. First, we used a variable that does not include species abundance (and, consequently, neglects the role played by each species) nor considers the proportion of different functional groups. Second, Richness can be affected by climate. We further explored this second aspect, but no significant relationships were found between species richness and climate variables, such as precipitation (BIO16) and PET. However, significant trends within some groups were identified by stratifying the population according to dominant vegetation or soil type (Supplementary Fig.S1 and Fig.S2). This is according to the contrasting results obtained by other researchers. For example, Chen et al. (2018) found that favourable climate conditions, particularly high precipitation, increased species richness and belowground biomass, positively affecting SOC storage in forests, shrublands, and grasslands. On the other hand, Roach et al. (2021) found how herbaceous species richness increased with decreasing precipitation and increasing aridity in Douglas-fir forests. In dry sites, open stand conditions promote higher herb richness than closed canopies in moist and productive climates, where low light levels are unfavourable to understory plant communities (Burton et al., 2013). These results point out the complex interrelationships between biodiversity, climate, soil type and SOC storage, and explain the initial decreasing SOC trend with increasing richness followed by a subsequent increasing trend.

Specific leaf area (SLA) and leaf dry matter content (LDMC; Kazakou et al., 2006) were reported as traits affecting decomposition rates. Thus, LDMC and SLA influence on topsoil SOC (Fig. 2) is clearly due to their function in regulating litter quality. The understory was reported to produce high biomass that can reach values comparable to the biomass of leaves produced by the overstory (Landuyt et al., 2019). This highlights the significant contribution of the herbaceous layer to the litter and can explain the relative influence of the understory leaf traits as a driver of topsoil SOC storage. Rawlik et al. (2022) correlated functional traits of herbaceous leaves with their decomposition, and the best predictor for decomposition rates was LDMC, before SLA. SOCM02 decreases with increasing values of LDMC (Fig. 3), which might be due to the relatively slow decomposition rate of species with conservative strategies mirrored by high LDMC (i.e., implying slow nutrient use and photosynthetic capacity and long-lived leaves; Aponte et al., 2012; Cortez et al., 2007; Chelli et al., 2022).

## 5. Conclusion

We assessed SOC storage based on field measured data for forest soils in Italy. The BRTs models show that dominant predictors for SOC storage variability are the reference soil groups (RSG) and subsoil P content for topsoil and the whole mineral soil profile, pointing out the importance of soil properties in driving OC accumulation and stabilisation processes. The crucial role of vegetation is evident for the topsoil; the relative influence of dominant tree species is comparable to the RI of RSG, and other vegetation factors such as biodiversity and plant traits by modulating litter and root input and decomposition rate also exert their control on C cycle.

Overall, the high weight of factors influencing primary productivity could well be expected, but, among these factors, the importance of P content appears to be greater than usually considered. On the other hand, the major weight of soil factors influencing SOC stabilisation, either through interactions with highly reactive mineral components or through specific soil biota actions, represents an important finding. Indeed, although soil classification keys are mostly not based on organic carbon content, RSGs exhibit different and specific pedogenic OM

stabilisation processes. Our results suggest that including pedogenic soil types in SOC storage models can improve the prediction of forest SOC stock, especially for the subsoil where the influence of plant-related processes is reduced and the power of other factors in driving SOC accumulation and stabilisation is less marked. The way in which different pathways lead to SOC accumulation and the weights of interactions between predictors highlight that the variability of SOC stocks depends on the ecological context; often, the interaction between several factors, triggering positive feedback, is decisive in favouring high content and long persistence of soil organic carbon.

## 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.

## Data availability

Data will be made available on request.

## Acknowledgements

Data were gathered within the Italian ICP Forests - CON.ECO.FOR. network, managed by the Carabinieri Command for the Protection of Biodiversity and Parks - Studies and Projects Office (CUFAA). Financial support for data collection was co-funded by the European Commission within the Demonstration Project BioSoil, following Forest Focus Regulation (EC) No. 2152/2003 concerning monitoring of forests and environmental interaction in the community (Forest Focus Regulation). Statistical analysis of data was supported by LIFE+ 2013 SMART4Action Project, ENV-IT 000813.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.geoder.2023.e00605>.

## References

- Allegrini, M.-C., Canullo, R., Campetella, G., 2009. ICP-Forests (international co-operative programme on assessment and monitoring of air pollution effects on Forests): quality assurance procedure in plant diversity monitoring. *J. Environ. Monit.* 11, 782–787. <https://doi.org/10.1039/B818170P>.
- Andreetta, A., Ciampalini, R., Moretti, P., Vingiani, S., Poggio, G., Matteucci, G., Tesconi, F., Carnicelli, S., 2011. Forest humus forms as potential indicators of soil carbon storage in Mediterranean environments. *Biol. Fertil. Soils* 47, 31–40. <https://doi.org/10.1007/s00374-010-0499-z>.
- Andreetta, A., Cecchini, G., Bonifacio, E., Comolli, R., Vingiani, S., Carnicelli, S., 2016. Tree or soil? Factors influencing humus form differentiation in Italian forests. *Geoderma* 264, 195–204. <https://doi.org/10.1016/j.geoderma.2015.11.002>.
- Andreetta, A., Cecchini, G., Carnicelli, S., 2018. Forest humus forms in Italy: a research approach. *Appl. Soil Ecol.* 123, 384–390. <https://doi.org/10.1016/j.apsoil.2017.09.029>.
- Aponte, C., García, L.V., Marañón, T., 2012. Tree species effect on litter decomposition and nutrient release in Mediterranean oak forests changes over time. *Ecosystems* 15, 1204–1218.
- Aran, D., Gury, M., Jeanroy, E., 2001. Organo-metallic complexes in an andosol: a comparative study with a Cambisol and a Podzol. *Geoderma* 99, 65–79. [https://doi.org/10.1016/S0166-7061\(00\)00064-1](https://doi.org/10.1016/S0166-7061(00)00064-1).
- Baldock, J.A., Skjemstad, J.O., 2000. Role of the soil matrix and minerals in protecting natural organic materials against biological attack. *Org. Geochem.* 31, 697–710. [https://doi.org/10.1016/S0146-6380\(00\)00049-8](https://doi.org/10.1016/S0146-6380(00)00049-8).
- Bazilevskaya, E., Archibald, D.D., Martínez, C.E., 2018. Mineral colloids mediate organic carbon accumulation in a temperate forest Spodosol: depth-wise changes in pore water chemistry. *Biogeochemistry* 141, 75–94. <https://doi.org/10.1007/s10533-018-0504-4>.
- Bonifacio, E., Falsone, G., Petrillo, M., 2011. Humus forms, organic matter stocks and carbon fractions in forest soils of northwestern Italy. *Biol. Fertil. Soils* 47, 555–566. <https://doi.org/10.1007/s00374-011-0568-y>.
- Bonifacio, E., Catoni, M., Falsone, G., Pullicino, D.-S., Celi, L., 2013. Evolution of surface properties and organic matter stabilisation in podzolic B horizons as assessed by nitrogen and phosphate sorption. *Biol. Fertil. Soils* 49, 505–516.

- Burton, J.I., Ares, A., Olson, D.H., Puettmann, K.J., 2013. Management trade-off between aboveground carbon storage and understory plant species richness in temperate forests. *Ecol. Appl.* 23, 1297–1310.
- Buzzard, V., Michaletz, S.T., Deng, Y., He, Z., Ning, D., Shen, L., Tu, Q., Van Nostrand, J.D., Voordeckers, J.W., Wang, J., Weiser, M.D., Kaspari, M., Waide, R.B., Zhou, J., Enquist, B.J., 2019. Continental scale structuring of forest and soil diversity via functional traits. *Nat. Ecol. Evolut.* 3, 1298–1308.
- Campo, J., Merino, A., 2016. Variations in soil carbon sequestration and their determinants along a precipitation gradient in seasonally dry tropical forest ecosystems. *Glob. Chang. Biol.* 22, 1942–1956. <https://doi.org/10.1111/gcb.13244>.
- Castellano, M.J., Mueller, K.E., Olk, D.C., Sawyer, J.E., Six, J., 2015. Integrating plant litter quality, soil organic matter stabilization, and the carbon saturation concept. *Glob. Chang. Biol.* 21, 3200–3209. <https://doi.org/10.1111/gcb.12982>.
- Catoni, M., D'Amico, M.E., Zanini, E., Bonifacio, E., 2016. Effect of pedogenic processes and formation factors on organic matter stabilization in alpine forest soils. *Geoderma* 263, 151–160. <https://doi.org/10.1016/j.geoderma.2015.09.005>.
- Cecchini, G., Andreetta, A., Marchetto, A., Carnicelli, S., 2019. Atmospheric deposition control of soil acidification in Central Italy. *Catena* 182, 104102. <https://doi.org/10.1016/j.catena.2019.104102>.
- Cecchini, G., Andreetta, A., Marchetto, A., Carnicelli, S., 2021. Soil solution fluxes and composition trends reveal risks of nitrate leaching from forest soils of Italy. *Catena* 200, 105175. <https://doi.org/10.1016/j.catena.2021.105175>.
- Chelli, S., Simonetti, E., Wellstein, C., Campetella, G., Carnicelli, S., Andreetta, A., Giorgini, D., Puletti, N., Bartha, S., Canullo, R., 2019. Effects of climate, soil, forest structure and land use on the functional composition of the understory in Italian forests. *J. Veg. Sci.* 30, 1110–1121. <https://doi.org/10.1111/jvs.12792>.
- Chelli, S., Ottaviani, G., Tsakalos, J.L., Campetella, G., Simonetti, E., Wellstein, C., Bartha, S., Cervellini, M., Canullo, R., 2022. Intra- and inter-specific leaf trait responses of understory species to changes in forest maturity. *For. Ecol. Man.* 506, 119977. <https://doi.org/10.1111/plb.13199>.
- Chen, S., Wang, W., Xu, W., Wang, Y., Wan, H., Chen, D., Tang, Z., Tang, X., Zhou, G., Xie, Z., Zhou, D., Shanguan, Z., Huang, J., He, J.-S., Wang, Y., Sheng, J., Tang, L., Li, X., Dong, M., Wu, Y., Wang, Q., Wang, Z., Wu, J., Stuart Chapin, F., Bai, Y., 2018. Plant diversity enhances productivity and soil carbon storage. *Proc. Natl. Acad. Sci. U. S. A.* 115, 4027–4032. <https://doi.org/10.1073/pnas.1700298114>.
- Chiarucci, A., Nascimbene, J., Campetella, G., Chelli, S., Dainese, M., Giorgini, D., Landi, S., Lelli, C., Canullo, R., 2019. Exploring patterns of beta-diversity to test the consistency of biogeographical boundaries: a case study across forest plant communities of Italy. *Ecol. Evol.* 9, 11716–11723. <https://doi.org/10.1002/ece3.5669>.
- Conforti, M., Lucà, F., Scarciaglia, F., Matteucci, G., Buttafuoco, G., 2016. Soil carbon stock in relation to soil properties and landscape position in a forest ecosystem of southern Italy (Calabria region). *CATENA* 144, 23–33. <https://doi.org/10.1016/j.catena.2016.04.023>.
- Conforti, M., Longobucco, T., Scarciaglia, F., Niceforo, G., Matteucci, G., Buttafuoco, G., 2020. Interplay between soil formation and geomorphic processes along a soil catena in a Mediterranean mountain landscape: an integrated pedological and geophysical approach. *Environ. Earth Sci.* 79, 59. <https://doi.org/10.1007/s12665-019-8802-2>.
- Cornelis, J.-T., Delvaux, B., Van Ranst, E., Rouxhet, P.G., 2018. Sub-micrometer distribution of Fe oxides and organic matter in Podzol horizons. *Geoderma* 323, 126–135. <https://doi.org/10.1016/j.geoderma.2018.02.043>.
- Cornwell, W.K., Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., Hobbie, S.E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H.M., Santiago, L.S., Wardle, D.A., Wright, J.J., Aerts, R., Allison, S.D., Van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T.V., Díaz, S., Garnier, E., Gurvich, D.E., Kazakou, E., Klein, J.A., Read, J., Reich, P.B., Soudzilovskaia, N.A., Vaieretti, M.V., Westoby, M., 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecol. Lett.* 11, 1065–1071. <https://doi.org/10.1111/j.1461-0248.2008.01219.x>.
- Cortez, J., Garnier, E., Pérez-Harguindeguy, N., Debussche, M., Gillon, D., 2007. Plant traits, litter quality and decomposition in a Mediterranean old-field succession. *Plant Soil* 296, 19–34. <https://doi.org/10.1007/s11104-007-9285-6>.
- Cuevas, R.M., Hidalgo, C., Payán, F., Etchevers, J.D., Campo, J., 2013. Precipitation influences on active fractions of soil organic matter in seasonally dry tropical forests of the Yucatan: regional and seasonal patterns. *Eur. J. For. Res.* 132, 667–677.
- Dahlgren, R.A., Saigusa, M., Ugolini, F.C., 2004. The nature, properties and management of volcanic soils. *Adv. Agron.* 82, 113–182. [https://doi.org/10.1016/S0065-2113\(03\)82003-5](https://doi.org/10.1016/S0065-2113(03)82003-5).
- De Deyn, G.B., Shiel, R.S., Ostle, N.J., McNamara, N.P., Oakley, S., Young, I., Freeman, C., Fenner, N., Quirk, H., Bardgett, R.D., 2011. Additional carbon sequestration benefits of grassland diversity restoration. *J. Appl. Ecol.* 48, 600–608. <https://doi.org/10.1111/j.1365-2664.2010.01925.x>.
- De Marco, A., Esposito, F., Berg, B., Giordano, M., Virzo De Santo, A., 2013. Soil C and N sequestration in organic and mineral layers of two coeval forest stands implanted on pyroclastic material (Mount Vesuvius, South Italy). *Geoderma* 209–210, 128–135. <https://doi.org/10.1016/j.geoderma.2013.06.011>.
- Dijkstra, F.A., Van Breemen, N., Jongmans, A.G., Davies, G.R., Likens, G.E., 2003. Calcium weathering in forested soils and the effect of different tree species. *Biogeochemistry* 62, 253–275. <https://doi.org/10.1023/A:1021132132199>.
- Elith, J., Leathwick, J.R., Hastie, T., 2008. A working guide to boosted regression trees. *J. Anim. Ecol.* 77, 802–813. <https://doi.org/10.1111/j.1365-2656.2008.01390.x>.
- ETC-BD (European Topic Centre on Biological Diversity), 2006. The indicative map of European biogeographical regions: Methodology and development. Paris, France: ETC-BD.
- Eusterhues, K., Rumpel, C., Kögel-Knabner, I., 2005. Organo-mineral associations in sandy acid forest soils: importance of specific surface area, iron oxides and micropores. *Eur. J. Soil Sci.* 56, 753–763. <https://doi.org/10.1111/j.1365-2389.2005.00710.x>.
- FAO, 2006. Guidelines for Soil Profile Description and Classification, 4th edition. Food and Agriculture Organisation, Rome.
- Feng, X.J., Simpson, M.J., 2007. The distribution and degradation of biomarkers in Alberta grassland soil profiles. *Org. Geochem.* 38, 1558–1570. <https://doi.org/10.1016/j.orggeochem.2007.05.001>.
- Ferré, C., Comolli, R., Leip, A., Seufert, G., 2014. Forest conversion to poplar plantation in a Lombardy floodplain (Italy): effects on soil organic carbon stock. *Biogeosciences* 11, 6483–6493. <https://doi.org/10.5194/bg-11-6483-2014>.
- Fino, E., Blasi, E., Perugini, L., Pellis, G., Valentini, R., Chiti, T., 2020. Is soil contributing to climate change mitigation during woody encroachment? A case study on the Italian alps. *Forests* 11, 887. <https://doi.org/10.3390/f11080887>.
- Finzi, A.C., Canham, C.D., van Breemen, N., 1998. Canopy tree–soil interactions within temperate forests: species effects on pH and cations. *Ecol. Appl.* 8, 447–454. <https://doi.org/10.2307/2641084>.
- FSCC, 2006. Manual IIIa: Sampling and Analysis of Soil. ICP Forests, 2006: Manual on Methods and Criteria for Harmonized Sampling, Assessment, Monitoring and Analysis of the Effects of Air Pollution on Forests. UN/ECE ICP Forests Programme Co-ordinating Centre, Hamburg (130 pp.).
- Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., Toussaint, J.-P., 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85, 2630–2637. <https://doi.org/10.1890/03-0799>.
- Gasparini, P., Di Cosmo, L., 2015. Forest carbon in Italian forests: stocks, inherent variability and predictability using NFI data. *For. Ecol. Man.* 337, 186–195. <https://doi.org/10.1016/j.foreco.2014.11.012>.
- Grand, S., Lavkulich, L.M., 2011. Depth distribution and predictors of soil organic carbon in podzols of a forested watershed in southwestern Canada. *Soil Sci.* 176, 164–174. <https://doi.org/10.1097/SS.0b013e3182128671>.
- Grime, J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* 86, 902–910. <https://doi.org/10.1046/j.1365-2745.1998.00306.x>.
- Guidi, C., Vesterdal, L., Gianelle, D., Rodeghiero, M., 2014. Changes in soil organic carbon and nitrogen following forest expansion on grassland in the Southern Alps. *For. Ecol. Man.* 328, 103–116. <https://doi.org/10.1016/j.foreco.2014.05.025>.
- Hassink, J., 1997. The capacity of soils to preserve organic C and N by their association with clay and silt particles. *Plant Soil* 191, 77–87. <https://doi.org/10.1023/A:1004213929699>.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25, 1965–1978. <https://doi.org/10.1002/joc.1276>.
- Hijmans, R.J., Phillips, S., Leathwick, J., Elith, J., 2021. dismo: Species Distribution Modeling. R Package Version 1.3–5. Available at: <http://CRAN.R-project.org/package=dismo>.
- ICP Forests, 2010. Manual on Methods and Criteria for Harmonized Sampling, Assessment, Monitoring and Analysis of the Effects of Air Pollution on Forests, of Air Pollution on Forests. UNECE, ICP Forests, Hamburg. <http://icp-forests.net/page/icp-forestsmanual>.
- ISO, 1995a. ISO 10694. Soil Quality — Determination of Organic and Total Carbon After Dry Combustion (Elementary Analysis). International Organization for Standardization, Geneva, Switzerland, p. 7 (available at [www.iso.ch](http://www.iso.ch)).
- ISO, 1995b. ISO 11466. Soil Quality – Extraction of Trace Elements Soluble in Aqua Regia. International Organization for Standardization, Geneva, Switzerland, p. 6 (available at [www.iso.ch](http://www.iso.ch)).
- IUSS Working Group WRB, 2007. World Reference Base for Soil Resources 2006, first update 2007. World soil resources Reports 103. FAO, Rome, pp. 128–pp.
- IUSS Working Group WRB, 2015. World reference base for soil resources 2014, update 2015. In: International soil classification system for naming soils and creating legends for soil maps. World Soil Resources Reports No. 106. FAO, Rome.
- Kazakou, E., Vile, D., Shipley, B., Gallet, C., Garnier, E., 2006. Co-variations in litter decomposition, leaf traits and plant growth in species from a Mediterranean old-field succession. *Funct. Ecol.* 20, 21–30. <https://doi.org/10.1111/j.1365-2435.2006.01080.x>.
- Kleber, M., Mikutta, R., Torn, M.S., Jahn, R., 2005. Poorly crystalline mineral phases protect organic matter in acid subsoil horizons. *Eur. J. Soil Sci.* 56, 717–725. <https://doi.org/10.1111/j.1365-2389.2005.00706.x>.
- Kleber, M., Bourg, I.C., Coward, E.K., Hansel, C.M., Myneni, S.C.B., Nunan, N., 2021. Dynamic interactions at the mineral–organic matter interface. *Nat. Rev. Earth Environ.* 2, 402–421. <https://doi.org/10.1038/s43017-021-00162-y>.
- Kopittke, P.M., Berhe, A.A., Carrillo, Y., Cavagnaro, T.R., Chen, D., Chen, Q.-L., Román Dobarco, M., Dijkstra, F.A., Field, D.J., Grundy, M.J., He, J.-Z., Hoyle, F.C., Kögel-Knabner, I., Lam, S.K., Marschner, P., Martinez, C., McBratney, A.B., McDonnell-Madden, E., Menzies, N.W., Mosley, L.M., Mueller, C.W., Murphy, D.V., Nielsen, U. N., O'Donnell, A.G., Pendall, E., Pett-Ridge, J., Rumpel, C., Young, I.M., Minasny, B., 2021. Ensuring planetary survival: the centrality of organic carbon in balancing the multifunctional nature of soils. *Crit. Rev. Environ. Sci. Technol.* 4308–4324. <https://doi.org/10.1080/10643389.2021.2024484>.
- Kursa, M.B., Rudnicki, W.R., 2020. Wrapper Algorithm for All Relevant Feature Selection. <https://cran.r-project.org/web/packages/Boruta/Boruta.pdf>.
- Lal, R., Smith, P., Jungkunst, H.F., Mitsch, W.J., Lehmann, J., Ramachandran Nair, P.K., McBratney, A.B., De Moraes Sá, J.C., Schneider, J., Zinn, Y.L., Skorupa, A.L.A., Zhang, H.-L., Minasny, B., Srinivasrao, C., Ravindranath, N.H., 2018. The carbon sequestration potential of terrestrial ecosystems. *J. Soil Water Conserv.* 73, 145A–152A. <https://doi.org/10.2489/jswc.73.6.145A>.
- Landuyt, D., De Lombaerde, E., Perring, M.P., Hertzog, L.R., Ampoorter, E., Maes, S.L., De Frenne, P., Ma, S., Proesmans, W., Blondeel, H., Sercu, B.K., Wang, B., Wasof, S.,

- Verheyen, K., 2019. The functional role of temperate forest understorey vegetation in a changing world. *Glob. Chang. Biol.* 25, 3625–3641. <https://doi.org/10.1111/gcb.14756>.
- Lorenz, M., Becher, G., Mues, V., Fischer, R., Ulrich, E., Dobbertin, M., Stofer, S., 2004. *Forest Condition in Europe. 2004. Technical Report of ICP Forests. Institute of World Forestry, Hamburg*, p. 96.
- Maestre, F.T., Quero, J.L., Gotelli, N.J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M., García-Gómez, M., Bowker, M.A., Soliveres, S., Escolar, C., García-Palacios, P., Berdugo, M., Valencia, E., Gzozalo, B., Gallardo, A., Aguilera, L., Arredondo, T., Blones, J., Boeken, B., Bran, D., Conceição, A.A., Cabrera, O., Chaieb, M., Derak, M., Eldridge, D.J., Espinosa, C.I., Florentino, A., Gaitán, J., Gabriel Gatica, M., Ghiloufi, W., Gómez-González, S., Gutiérrez, J.R., Hernández, R.M., Huang, X., Huber-Sannwald, E., Jankju, M., Miriti, M., Moneris, J., Mau, R.L., Morici, E., Naseri, K., Ospina, A., Polo, V., Prina, A., Pucheta, E., Ramírez-Collantes, D.A., Romão, R., Tighe, M., Torres-Díaz, C., Val, J., Veiga, J.P., Wang, D., Zaady, E., 2012. Plant species richness and ecosystem multifunctionality in global drylands. *Science* 335, 214–218. <https://doi.org/10.1126/science.1215442>.
- Marin-Spiotta, E., Chadwick, O.A., Kramer, M., Carbone, M.S., 2011. Carbon delivery to deep mineral horizons in Hawaiian rainforest soils. *J. Geophys. Res.* 116, G03011. <https://doi.org/10.1029/2010JG001587>.
- Marquard, E., Weigelt, A., Temperton, V.M., Roscher, C., Schumacher, J., Buchmann, N., Fischer, M., Weisser, W.W., Schmid, B., 2009. Plant species richness and functional composition drive overyielding in a six-year grassland experiment. *Ecology* 90, 3290–3302.
- Mathieu, J.A., Hatt'e, C., Balesdent, J., Parent, E., 2015. Deep soil carbon dynamics are driven more by soil type than by climate: a worldwide meta-analysis of radiocarbon profiles. *Glob. Chang. Biol.* 21, 4278–4292.
- McBratney, A., Field, D.J., Koch, A., 2014. The dimensions of soil security. *Geoderma* 213, 203–213. <https://doi.org/10.1016/j.geoderma.2013.08.013>.
- Oades, J.M., 1988. The retention of organic matter in soils. *Biogeochemistry* 5, 35–70. <https://doi.org/10.1007/BF02180317>.
- Ostertag, R., 2001. Effects of nitrogen and phosphorus availability on fine-root dynamics in Hawaiian montane forests. *Ecology* 82, 485–499. [https://doi.org/10.1890/00129658\(2001\)082\[0485:EONAPA\]2.0.CO;2](https://doi.org/10.1890/00129658(2001)082[0485:EONAPA]2.0.CO;2).
- Oueslati, I., Allamano, P., Bonifacio, E., Claps, P., 2013. Vegetation and topographic control on spatial variability of soil organic carbon. *Pedosphere* 23, 48–58. [https://doi.org/10.1016/S1002-0160\(12\)60079-4](https://doi.org/10.1016/S1002-0160(12)60079-4).
- Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A large and persistent carbon sink in the world's forests. *Science* 333, 988–993. <https://doi.org/10.1126/science.1201609>.
- Pellis, G., Chiti, T., Rey, A., Curiel Yuste, J., Trotta, C., Papale, D., 2019. The ecosystem carbon sink implications of mountain forest expansion into abandoned grazing land: the role of subsoil and climatic factors. *Sci. Total Environ.* 672, 106–120. <https://doi.org/10.1016/j.scitotenv.2019.03.329>.
- Ponge, J.-F., Chevalier, R., Loussot, P., 2002. Humus index: an integrated tool for the assessment of forest floor and topsoil properties. *Soil Sci. Soc. Am. J.* 66, 1996–2001. <https://doi.org/10.2136/sssaj2002.1996>.
- Porder, S., Ramachandran, S., 2013. The phosphorus concentration of common rocks—a potential driver of ecosystem P status. *Plant Soil* 367, 41–55. <https://doi.org/10.1007/s11104-012-1490-2>.
- Powers, J.S., Montgomery, R.A., Adair, E.C., Brearley, F.Q., DeWalt, S.J., Castanho, C.T., Chave, J., Deinert, E., Ganzhorn, J.U., Gilbert, M.E., González-Iturbe, J.A., Bunyavejchewin, S., Grau, H.R., Harms, K.E., Hiremath, A., Iriarte-Vivar, S., Manzano, E., De Oliveira, A.A., Poorter, L., Ramanamanjato, J.-B., Salk, C., Varela, A., Weiblen, G.D., Lerdaun, M.T., 2009. Decomposition in tropical forests: a pan-tropical study of the effects of litter type, litter placement and mesofaunal exclusion across a precipitation gradient. *J. Ecol.* 97, 801–811. <https://doi.org/10.1111/j.1365-2745.2009.01515.x>.
- Qiu, K., Xie, Y., Xu, D., Pott, R., 2018. Ecosystem functions including soil organic carbon, total nitrogen and available potassium are crucial for vegetation recovery. *Sci. Rep.* 8, 7607.
- R Core Team, 2021. *R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria*.
- Ranjbar, F., Jalali, M., 2012. Calcium, magnesium, sodium, and potassium release during decomposition of some organic residues. *Commun. Soil Sci. Plant Anal.* 43, 645–659.
- Rasse, D.P., Rumpel, C., Dignac, M.F., 2005. Is soil carbon mostly root carbon? Mechanisms for a specific stabilization. *Plant Soil* 269, 341–356. <https://doi.org/10.1007/s11104-004-0907-y>.
- Rawlik, K., Kasprowicz, M., Nowiński, M., Jagodziński, A.M., 2022. The afterlife of herbaceous plant species: a litter decomposition experiment in a temperate oak-hornbeam forest. *For. Ecol. Man.* 507, 120008 <https://doi.org/10.1016/j.foreco.2022.120008>.
- Roach, W.J., Simard, S.W., Defrenne, C.E., Pickles, B.J., Lavkulich, L.M., Ryan, T.L., 2021. Tree diversity, site index, and carbon storage decrease with aridity in Douglas fir Forests in Western Canada. *Front. For. Glob. Change* 4. <https://doi.org/10.3389/ffgc.2021.682076>.
- Roa-Fuentes, L.L., Hidalgo, C., Etchevers, J.D., Campo, J., 2013. The effects of precipitation regime on soil carbon pools on the Yucatan peninsula. *J. Trop. Ecol.* 29, 463–466. <https://doi.org/10.1017/S0266467413000552>.
- Rodeghiero, M., Vesterdal, L., Marcolla, B., Vescovo, L., Aertsen, W., Martinez, C., Di Cosmo, L., Gasparini, P., Gianelle, D., 2018. Soil nitrogen explanatory factors across a range of forest ecosystems and climatic conditions in Italy. *For. Ecol. Man.* 408, 25–35. <https://doi.org/10.1016/j.foreco.2017.10.039>.
- Rowley, M.C., Grand, S., Verrecchia, É.P., 2018. Calcium-mediated stabilisation of soil organic carbon. *Biogeochemistry* 137, 27–49. <https://doi.org/10.1007/s10533-017-0410-1>.
- Sauer, D., Sponagel, H., Sommer, M., Glani, L., Jahn, R., Stahr, K., 2007. Podzol: soil of the year 2007. A review on its genesis, occurrence and functions. *J. Plant Nutr. Soil Sci.* 170, 1–17. <https://doi.org/10.1002/JPLN.200700135>.
- Scartazza, A., Moscatello, S., Matteucci, G., Battistelli, A., Brugnoli, E., 2015. Combining stable isotope and carbohydrate analyses in phloem sap and fine roots to study seasonal changes of source–sink relationships in a Mediterranean beech forest. *Tree Physiol.* 35, 829–839. <https://doi.org/10.1093/treephys/tpv048>.
- Schmidt, M.W.I., Torn, M.S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I.A., Kleber, M., Kögel-Knabner, I., Lehmann, J., Manning, D.A.C., Nannipieri, P., Rasse, D.P., Weiner, S., Trumbore, S.E., 2011. Persistence of soil organic matter as an ecosystem property. *Nature* 478, 49–56. <https://doi.org/10.1038/nature10386>.
- Schuur, E.A.G., 2003. Productivity and global climate revisited: the sensitivity of tropical forest growth to precipitation. *Ecology* 84, 1165–1170. [https://doi.org/10.1890/0012-9658\(2003\)084\[1165:PAGCRT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[1165:PAGCRT]2.0.CO;2).
- Schweizer, S.A., Mueller, C.W., Höschen, C., Kögel-Knabner, I., 2021. The role of clay content and mineral surface area for soil organic carbon storage in an arable toposequence. *Biogeochemistry* 156, 401–420. <https://doi.org/10.1007/s10533-021-00850-3>.
- Taboada, T., Ferro-Vazquez, C., Stoops, G., Martínez-Cortizas, A., Rodríguez-Flores, R., Rodríguez-La, L., 2019. Secondary aluminium, iron and silica phases across a volcanic soil climosequence. Galapagos Islands Eur. J. Soil. Sci. 70, 540–549. <https://doi.org/10.1111/ejss.12788>.
- Tilman, D., Isbell, F., Cowles, J.M., 2014. Biodiversity and ecosystem functioning. *Annu. Rev. Ecol. Evol. Syst.* 45, 471–493. <https://doi.org/10.1146/annurev-ecolsys-120213-091917>.
- Tonneijck, F.H., Jansen, B., Nierop, K.G.J., Verstraten, M., Sevink, J., De Lange, L., 2010. Towards understanding of carbon stocks and stabilization in volcanic ash soils in natural Andean ecosystems of northern Ecuador. *Eur. J. Soil Sci.* 61, 392–405. <https://doi.org/10.1111/j.1365-2389.2010.01241.x>.
- Torn, M.S., Trumbore, S.E., Chadwick, O.A., Vitousek, P.M., Hendricks, D.M., 1997. Mineral control of soil organic carbon storage and turnover. *Nature* 389, 170–173. <https://doi.org/10.1038/38260>.
- Van Breemen, N., Finzi, A.C., Canham, C.D., 1997. Canopy tree-soil interactions within temperate forests: effects of fine-scale variation in soil texture and elemental composition on species distributions. *Can. J. For. Res.* 27, 1110–1116. <https://doi.org/10.1139/x97-06>.
- Vitousek, P.M., Porder, S., Houlton, B.Z., Chadwick, O.A., 2010. Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen–phosphorus interactions. *Ecol. Appl.* 20, 5–15. <https://doi.org/10.1890/08-0127.1>.
- Walker, T.W., 1964. The significance of phosphorus in pedogenesis. In: Hallsworth, E.G., Crawford, D.V. (Eds.), *Experimental Pedology. Butterworths, London*, pp. 295–315.
- Walker, T.W., Syers, J.K., 1976. The fate of phosphorus during pedogenesis. *Geoderma* 15, 1–19. [https://doi.org/10.1016/0016-7061\(76\)90066-5](https://doi.org/10.1016/0016-7061(76)90066-5).
- Wasof, S., Lenoir, J., Hattab, T., Jamoneau, A., Gallet-Moron, E., Ampoorter, E., Saguez, R., Bennisadek, L., Bertrand, R., Valdès, A., Verheyen, K., Decocq, G., 2018. Dominance of individual plant species is more important than diversity in explaining plant biomass in the forest understorey. *J. Veg. Sci.* 29, 521–531. <https://doi.org/10.1111/jvs.12624>.
- Weier, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E., Eriksson, O., 1999. Challenging Theophrastus: a common core list of plant traits for functional ecology. *J. Veg. Sci.* 10, 609–620. <https://doi.org/10.2307/3237076>.
- Westoby, M., 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant Soil* 199, 213–227.
- Wilkinson, M.T., Richards, P.J., Humphreys, G.S., 2009. Breaking ground: pedological, geological, and ecological implications of soil bioturbation. *Earth Sci. Rev.* 97, 257–272. <https://doi.org/10.1016/j.earscirev.2009.09.005>.
- Witzgall, K., Vidal, A., Schubert, D.I., Höschen, C., Schweizer, S.A., Buegger, F., Pouteau, V., Chenu, C., Mueller, C.W., 2021. Particulate organic matter as a functional soil component for persistent soil organic carbon. *Nat. Commun.* 12, 4115. <https://doi.org/10.1038/s41467-021-24192-8>.
- Wu, T., Wang, D., Mu, C., Zhang, W., Zhu, X., Zhao, L., Li, R., Hu, G., Zou, D., Chen, J., Wei, X., Wen, A., Shang, C., La, Y., Lou, P., Ma, X., Wu, X., 2022. Storage, patterns, and environmental controls of soil organic carbon stocks in the permafrost regions of the Northern Hemisphere. *Sci. Total Environ.* 828.
- Wynn, J.G., Bird, M.I., Vellen, L., Grand-Clement, E., Carter, J., Berry, S.L., 2006. Continental-scale measurement of the soil organic carbon pool with climatic, edaphic, and biotic controls. *Glob. Biogeochem. Cycles* 20, GB1007. <https://doi.org/10.1029/2005GB002576>.
- Xiong, X., Grunwald, S., Myers, D.B., Kim, J., Harris, W.G., Comerford, N.B., 2014. Holistic environmental soil-landscape modeling of soil organic carbon. *Environ. Model. Softw.* 57, 202–215. <https://doi.org/10.1016/j.envsoft.2014.03.004>.
- Yang, Y., Fang, J., Tang, Y., Ji, C., Zheng, C., He, J., Zhu, B., 2008. Storage, patterns and controls of soil organic carbon in the Tibetan grasslands. *Glob. Chang. Biol.* 14, 1592–1599. <https://doi.org/10.1111/j.1365-2486.2008.01591.x>.