



Impact of patch age and size on forest soil characteristics in European agricultural landscapes

Liping Wei^{a,b,*}, Jaan Liira^c, Steffen Ehrmann^d, Jonathan Lenoir^e, Guillaume Decocq^e, Jörg Brunet^f, Monika Wulf^g, Martin Diekmann^h, Tobias Naaf^g, Michael Scherer-Lorenzenⁱ, Karin Hansen^j, Pallieter De Smedt^b, Alicia Valdés^{k,l}, Kris Verheyen^b, Pieter De Frenne^b

^a Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China

^b Forest & Nature Lab, Ghent University, Gontrode, Belgium

^c Institute of Ecology and Earth Science, University of Tartu, Tartu, Estonia

^d German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstr. 4, 04103 Leipzig, Germany

^e UMR CNRS 7058 Ecologie et Dynamique des Systèmes Anthropisés (EDYSAN), Université de Picardie Jules Verne, 1 rue des Louvels, 80000 Amiens, France

^f Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, Box 190, 23422 Lomma, Sweden

^g Research Area 2, Leibniz Centre for Agricultural Landscape Research, ZALF, Eberswalder Straße 84, 15374 Müncheberg, Germany

^h Institute of Ecology, FB2, University of Bremen, Leobener Str. 5, 28359 Bremen, Germany

ⁱ Geobotany, Faculty of Biology, University of Freiburg, Schänzlestr. 1, 79104 Freiburg, Germany

^j The Swedish Environmental Protection Agency, Virkesvägen 2, 106 48 Stockholm, Sweden

^k Department of Ecology, Environment and Plant Sciences, Stockholm University, SE-106 91 Stockholm, Sweden

^l Bolin Centre for Climate Research, Stockholm University, Stockholm, Sweden

ARTICLE INFO

Editor: Manuel Esteban Lucas-Borja

Keywords:

Fragmentation
Forest land-use history
Land-use change
Macroclimate
Soil nutrient balance

ABSTRACT

Many landscapes worldwide are characterized by the presence of a mosaic of forest patches with contrasting age and size embedded in a matrix of agricultural land. However, our understanding of the effects of these key forest patch features on the soil nutrient status (in terms of nitrogen, carbon, and phosphorus) and soil pH is still limited due to a lack of large-scale data. To address this research gap, we analyzed 830 soil samples from nearly 200 forest patches varying in age (recent versus ancient forests) and size (small versus larger patches) along a 2500-km latitudinal gradient across Europe. We also considered environmental covariates at multiple scales to increase the generality of our research, including variation in macroclimate, nitrogen deposition rates, forest cover in a buffer zone, basal area and soil type. Multiple linear mixed-effects models were performed to test the combined effects of patch features and environmental covariates on soil nutrients and pH. Recent patches had higher total soil phosphorus concentrations and stocks in the mineral soil layer, along with a lower nitrogen to phosphorus ratio within that layer. Small patches generally had a higher mineral soil pH. Mineral soil nitrogen stocks were lower in forest patches with older age and larger size, as a result of a significant interactive effect. Additionally, environmental covariates had significant effects on soil nutrients, including carbon, nitrogen, phosphorus, and their stoichiometry, depending on the specific covariates. In some cases, the effect of patch age on mineral soil phosphorus stocks was greater than that of environmental covariates. Our findings underpin the important roles of forest patch age and size for the forest soil nutrient status. Long-term studies assessing edge effects and soil development in post-agricultural forests are needed, especially in a context of changing land use and climate.

1. Introduction

Forest soils play a key role in maintaining forest biogeochemical cycles of carbon (C) and nutrients, like nitrogen (N) and phosphorus (P)

(Lal, 2005; Maaroufi and de Long, 2020). However, forest soil nutrient concentrations and stocks are sensitive to land-use change and even slight changes in, for instance, their stoichiometry (e.g., C:N ratio, N:P ratios) can induce significant changes in forest community composition

* Corresponding author at: Ghent University, Belgium.

E-mail address: liping.wei@ugent.be (L. Wei).

<https://doi.org/10.1016/j.scitotenv.2023.165543>

Received 8 June 2023; Received in revised form 4 July 2023; Accepted 12 July 2023

Available online 13 July 2023

0048-9697/© 2023 Elsevier B.V. All rights reserved.

and dynamics (Wieder et al., 2015; Jakovac et al., 2016). Therefore, quantifying to what extent forest soil nutrients are affected by land-use change is critical for anticipating potential changes in biogeochemical cycles (Stevenson and Cole, 1999; Sattari et al., 2012; Bradford et al., 2016; Bouwman et al., 2017).

Forests throughout the world are strongly affected by habitat fragmentation, a process by which focal habitat gets divided into smaller and isolated patches due to various, typically anthropogenic activities such as land-use change, timber harvesting or construction of infrastructure. Unlike habitat loss per se, in which habitat is directly converted to another habitat type, such as from forest to agricultural land or urban cover, fragmentation refers to a change of the spatial configuration of habitat with increasingly smaller sizes for a given total amount of habitat (Fahrig et al., 2019). More than 70 % of the world's forest areas are within 1 km of a forest edge, with most forest patches embedded in artificial landscapes such as arable land (Haddad et al., 2015; Oduro Appiah and Agyemang-Duah, 2021). In Europe, the situation is even worse, with 40 % of the forest area situated within 100 m from the edge (Estreguil et al., 2012). Conversely, because of changing socio-economic conditions and policies, reforestation of post-agricultural sites is taking place at a large scale. In many countries in Europe, the reforestation of post-agricultural soils stands out as a significant land-use transformation (Wall and Hytönen, 2005; Olszewska and Smal, 2008; Wellock et al., 2011). At the landscape scale, this often leads to a mosaic comprised of forest patches of various age (ancient vs recent) and size since reforestation (Honnay et al., 2005; Ziter et al., 2013).

Both forest patch age and size are key features of forests that can affect soil characteristics. In terms of age, ancient forests are defined as forests that have not been cleared for agriculture for at least about 200 years, while more recently afforested lands occur on soils that may have been managed and cultivated in the past through agriculture treatment (e.g. fertilization, liming, pesticide addition). Many previous studies have assessed the difference in soil pH and nutrients between ancient and recent forests established on former agricultural land, arable land, pastures or abandoned settlements (Wilson et al., 1997; Graae et al., 2003; Vojta, 2007; Bergès et al., 2017; Abadie et al., 2018). Those studies often detected higher P concentrations, lower C:N ratios and reduced soil acidification in recent forest soils compared to ancient forest soils (Bergès et al., 2017; Brasseur et al., 2018), which can still be detected >100 to 150 years after afforestation (Verheyen et al., 1999; Perring et al., 2008; De Schrijver et al., 2012; Blondeel et al., 2019). Regarding patch size, smaller forest patches are more susceptible to edge effects due to their higher edge-to-core ratio. As a result, they experience higher drift of lime and nutrient inputs (such as nitrogen and phosphate fertilizers) from neighboring, potentially intensively used land, increased nitrogen deposition, higher irradiance and wind speeds, and warmer and drier microclimate conditions compared to larger forest patches (De Schrijver et al., 2007; Wuyts et al., 2008; Remy et al., 2016; Meeussen et al., 2021). Therefore, small forest patches with comparatively strong edge influences might, for instance, show elevated soil pH, N or P concentrations. Forest edges also tend to have higher structural and taxonomic plant diversity which can exert a facilitative effect on litter decomposition (e.g., due to litter mixing and accumulation) (Jastrow et al., 2007; Bueno and Llambí, 2015; Ramírez et al., 2015), thus higher nutrient cycling rates might be detected in small forest patches than in larger ones. However, due to a lack of data (Brzeziecki et al., 1993; Coudun and Gégout, 2006), few studies have focused on the concurrent impact of patch age and size on soil nutrients and acidity across large spatial extents, using consistent sampling and analytical methods. This is important since soil pH or nutrients are important drivers of forest community composition and forest ecosystem functioning (Salisbury, 1920; Brady and Weil, 1999; Pärtel, 2002). Patches of the same age but small vs large sizes may have different vegetation composition, litter quality, and soil microbial communities (Valdés et al., 2020), thereby influencing soil nutrient cycling processes. For example, smaller patches may have higher proportions of shade-

intolerant species, generalist species, or herbaceous species with higher leaf nutrient concentrations (Guirado et al., 2006). Contrasting patch sizes and the associated edge effects can also lead to distinct soil microbial communities, for instance resulting in a higher abundance of arbuscular mycorrhizal fungi closer to edges (Yang et al., 2022) which can then feed back to nutrient cycling. Examining the interactive effects of patch age and size thus bear both theoretical and practical significance.

The objective of this study was to fill the knowledge gap on the impact of forest patch age and size on soil nutrient status and pH in forest patches across agricultural landscapes of western Europe. We used a large-scale study design that covers forest patches varying in age (ancient vs recent) and size (large vs small) along a latitudinal gradient with variable macroclimate from central Sweden and Estonia to southern France. We focused on the concentrations and stocks of soil C, N and P and their stoichiometry in both forest floor (litter layer, fragmentation layer and humus layer) and mineral topsoil layer (0–10 cm), as these are biologically most relevant (e.g., for understory vegetation and forest-floor organisms) and have larger nutrient concentrations compared to deeper soil horizons. As different climates and vegetation types lead to soil types with distinct characteristics, we incorporated five additional ecological variables to increase the generality of our research. These variables capture variation in the data from the continental over the landscape to the patch level (macroclimate, N deposition, forest cover in a buffer zone, total tree basal area and soil type), to account for their potential confounding effects with forest patch age and size.

We hypothesized that: (1) recent forest patches have a higher pH, a lower soil C:N ratio and higher soil P concentrations and stocks compared to ancient forest patches; (2) small forest patches have a higher soil pH and higher concentrations and stocks of soil C, N and P than large patches, due to stronger edge deposition effects and a higher drift of lime and nutrient inputs from adjacent agricultural land. We used a sampling design from individual plots to patches, landscapes, and regions, allowing us to assess the relative importance of environmental factors for soil acidity and nutrient status across different spatial scales.

2. Material and methods

2.1. Study sites

This study was carried out in eight regions along a 2500 km-long macroclimatic gradient in Europe, from central Sweden and Estonia to south France (Fig. 1). The broad geographical extent of the study area covers a gradient in macroclimate, and variations in N deposition and forest community composition (Table 1). In each of the eight regions, two 5 km by 5 km landscape windows with predominant agricultural use were selected. Within each window, eleven to sixteen forest patches were chosen to be representative of the variation of patch age (ancient vs recent) and size (large vs small). A total of 199 patches were sampled, about half of the patches were large and half were small, and within each of these two size categories, half of the patches were ancient and half were recent. The mean size for large and small patches was 8.4 ± 8.7 ha and 1.1 ± 0.9 ha, respectively; the mean age for ancient and recent patches was 140.3 ± 72.8 year and 31.1 ± 25.1 year, respectively (see detailed summary statistics with mean and range of patch age and size for each region in Table SM. 1 in Supplementary material). The patches are dominated by broadleaved tree species (95.76 ± 13.38 % cover across regions, see Table SM. 2 for the proportion in each region). The six most dominant tree genera were *Quercus*, *Alnus*, *Populus*, *Fraxinus*, *Fagus*, and *Betula*, and the detailed information on their relative proportions per region can be found in Table SM. 3 in the Supplementary material.

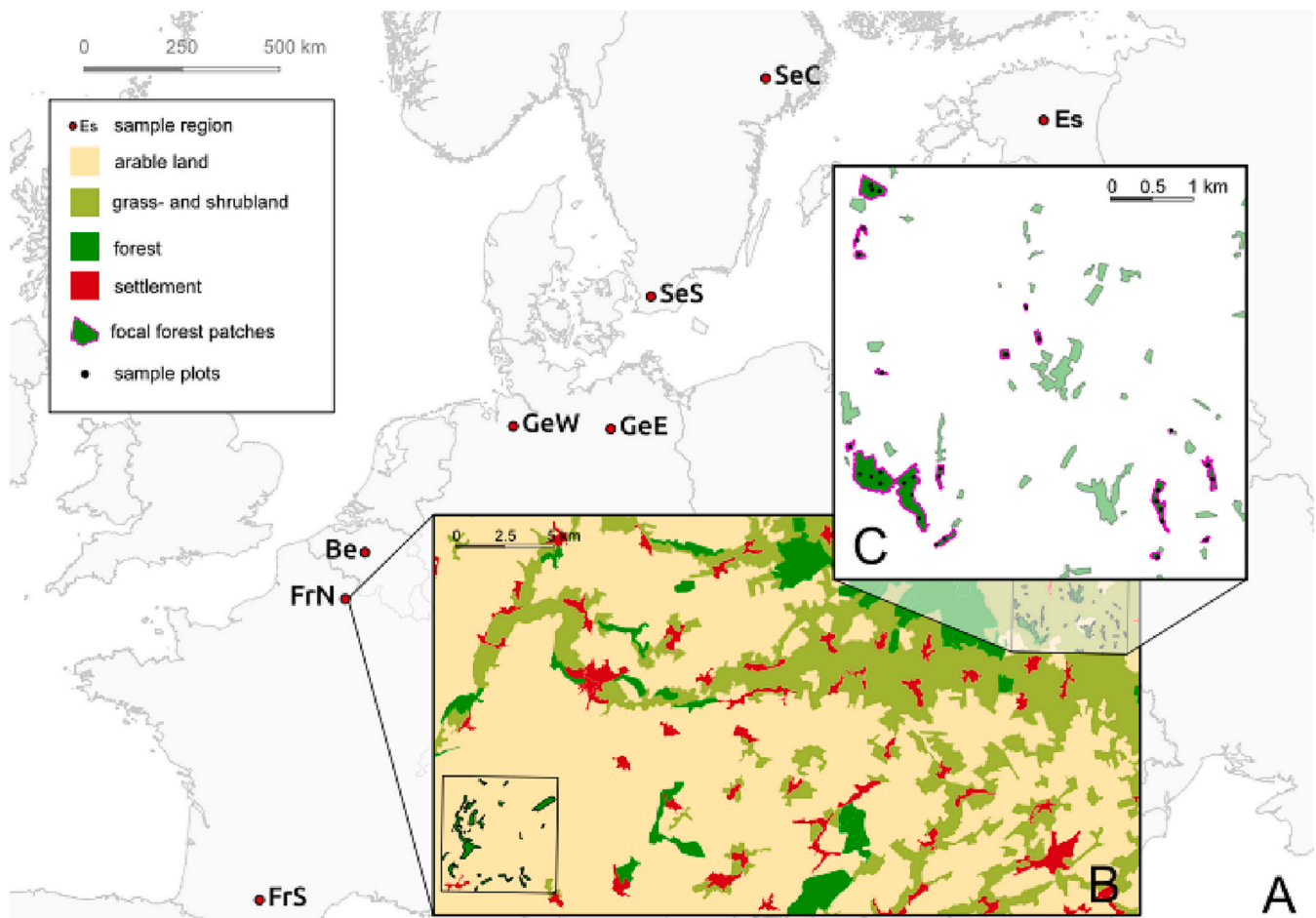


Fig. 1. Sampling design. (A) Location of the eight study regions along a macroclimatic gradient in Europe (Es, Estonia; SeC, central Sweden; SeS, south Sweden; FrN, north France; FrS, south France; Be, Belgium; GeW, west Germany; GeE, east Germany). (B) Detail of the forest patches and the surrounding land uses in northern France. (C) Soil sampling plots in selected forest patches.

2.2. Data collection

2.2.1. Soil sampling and laboratory analysis

Soil samples for chemical analyses were taken during the period from August to October 2012 before leaves were shed. For each patch, we sampled soil evenly along parallel transect lines located 100-m apart from each other. In the smallest patches (<1000 m²), a total of 3–5 soil samples were taken and subsequently pooled. In larger patches, the number of soil samples was related to patch size, ranging from 5 to 31 soil samples per patch. A square wooden frame of 25 cm × 25 cm was used to collect the forest floor samples following the method by [Vestdal and Raulund-Rasmussen \(1998\)](#). Living plant parts were cut at the base and removed, and leaf litter, fragmented litter and humus were collected by hand for forest floor samples. Great care was taken to ensure that the forest floor and mineral soil samples were not mixed. After removing forest floor, one upper mineral soil sample (0–10 cm) was taken inside the wooden frame using a metal core sampler (Ø4.2 cm). A total of 830 samples (forest floor and mineral soil) were collected from 415 sampling locations, placed in marked paper bags and stored dark pending analyses at Forest & Nature laboratory at Ghent University in Belgium.

All soil samples were dried at 40 °C for analyzing soil C, N and P, and weighed for calculating bulk density. To separate the fine earth and coarse soil fraction, the mineral soil samples were sieved through a 2 mm sieve. The fraction >2 mm which contained roots, small stones, and gravel was removed ([Homann et al., 1995](#)). We analyzed soil pH, C and N for both forest floor and homogenized mineral soil samples, and soil P

for mineral soil samples. To determine soil pH (CaCl₂), a soil/CaCl₂ (0.01 M) mixture with a ratio of 1:5 was shaken for 5 min at 300 rpm. The pH was then measured using a pH meter (Orion 920A) with pH electrode model Ross sure-flow 8172 BNWP (Thermo Scientific Orion, Massachusetts, USA). The C and N concentrations were determined using an elemental analyzer (Vario MACRO cube CNS, Elementar, Langensfeld, Germany) through high temperature combustion at 1150 °C. Total P concentration was measured after complete destruction with HClO₄ (65 %), HNO₃ (70 %) and H₂SO₄ (98 %) in Teflon bombs for 4 h at 150 °C. Phosphorus and Olsen P concentrations were measured according to the malachite green procedure at 700 nm (Varian, Cary 50 UV-Vis Spectrophotometer, Agilent, Victoria, Australia) ([Lajtha et al., 1999](#); [Frossard et al., 2000](#)). Given that soil pH values are lower than 7 in our study (except for one pH data point that falls between 7 and 8), the total carbon measured in our study predominantly represents organic carbon ([Ulrich, 1991](#); [Wetzel and Likens, 1991](#)). To check this hypothesis, we plotted the relationship between mineral soil total carbon and total nitrogen by pH group (two groups: low/high pH groups with pH < 5 and pH ≥ 5, respectively) (Fig. SM. 1 in Supplementary material). We found that for the same total N concentration, soil samples with high pH had lower total carbon concentration than those with low pH. This indicates that soil total carbon is more related to organic carbon than to increasing soil inorganic carbon.

For the forest floor, soil bulk density (BD) was calculated as its dry weight divided by the multiplication of depth and area of the sampling square (25 cm × 25 cm). The C, N and P stocks at this layer were calculated by multiplying the concentrations of C, N and P with BD and

Table 1
Mean, SD and range of predictor and response variables used in the LMM models.

	Abbreviation	Explanation	Unit	Mean	SD	Range
Predictor variables	Region	Estonia, central Sweden, south Sweden, west Germany, east Germany, Belgium, north France, South France, used as random effect	–	–	–	–
	Window	Landscape window	–	–	–	–
	MAT	Mean annual temperature	°C	8.5	3.1	3.6–14.7
	MAP	Mean annual precipitation	mm	677.7	85.3	55.5–820.0
	N _{deposit}	Annual 2012 N deposition	kg N ha ⁻¹ yr ⁻¹	12.8	5.1	4.8–24.9
	Forest. buffer500	Proportion of forest in a 500 m buffer around the patch	%	12.8	15.8	0.0–99.9
	Age	Patch age (weighted by size)	years	110.4	81.9	12.0–326.3
	Size	Patch size	ha	9.3	10.3	0.1–44.1
	Clay	Percentage of clay (from SoilGrids)	%	19.3	9.1	5.4–35.8
	BA	Total tree basal area	m ² ha ⁻¹	30.0	23.0	5.0–200.6
Response variables	pH _{ff}	pH in the forest floor	–	5.1	0.7	3.2–7.9
	C _{ff}	Carbon concentration in the forest floor	g kg ⁻¹	449.0	54.6	150.9–536.8
	N _{ff}	Nitrogen concentration in the forest floor	g kg ⁻¹	15.2	4.0	6.8–29.7
	C:N _{ff}	Carbon to nitrogen ratio in the forest floor	–	31.7	9.8	15.4–73.8
	C _{ff} stocks	Carbon stocks in the forest floor	Mg ha ⁻¹	4.7	6.1	0.0–73.7
	N _{ff} stocks	Nitrogen stocks in the forest floor	Mg ha ⁻¹	0.2	0.3	0.0–3.8
	pH _{ms}	pH in the mineral soil	–	4.4	1.0	2.8–6.9
	C _{ms}	Carbon concentration in the mineral soil	g kg ⁻¹	60.0	36.6	12.0–195.9
	N _{ms}	Nitrogen concentration in the mineral soil	g kg ⁻¹	4.8	2.4	1.3–16.4
	P _{ms}	Phosphorus concentration in the mineral soil	mg kg ⁻¹	514.8	302.9	77.2–2848.7
	P _{Olsen} _{ms}	Olsen phosphorus concentration in the mineral soil	mg kg ⁻¹	24.6	19.1	0.2–188.8
	C:N _{ms}	Carbon to nitrogen ratio in the mineral soil	–	12.1	2.8	7.8–32.6
	N:P _{ms}	Nitrogen to phosphorus ratio in the mineral soil	–	10.7	5.3	1.9–45.8
	C _{ms} stocks	Carbon stocks in the mineral soil	Mg ha ⁻¹	40.3	16.5	1.2–146.2
	N _{ms} stocks	Nitrogen stocks in the mineral soil	Mg ha ⁻¹	3.3	1.1	0.1–8.6
	P _{ms} stocks	Phosphorus stocks in the mineral soil	kg ha ⁻¹	373.9	195.2	11.1–1365.8
	P _{Olsen} _{ms} stocks	Olsen phosphorus stocks in the mineral soil	kg ha ⁻¹	17.1	19.1	0.2–132.0

soil depth. For the mineral soil layer, BD is the weight of the fine earth fraction (<2 mm) divided by the sampling volume after correcting for the presence of stones (>2 mm) and roots (Dawud et al., 2016). Stone volume was estimated by dividing the coarse fraction weight by 2.65 g cm⁻³ (density of common minerals). The volume of roots was estimated in a similar way, i.e., by dividing the weight of roots by the root density. A value of 0.56 g cm⁻³ was used for all sites and tree species to represent the root density of broadleaved tree species (Moltesen, 1988). In general, the presence of stones and roots was low. The nutrient stocks for mineral soil were calculated as the concentration of C, N and P multiplied by the fine earth BD and the depth of the soil layer.

Finally, because actual soil texture analyses were not feasible on this large amount of soil samples, we extracted the soil texture (clay, sand, and silt contents of 5–15 cm) per patch from the European soil database (<https://soilgrids.org/>) to have comparable data for all windows. The spatial resolution of this database is 1:250.

2.2.2. Tree stand inventory

During the growing seasons of 2012 and 2013, trees were selected in every sampled plot according to the point-centre quarter method (Cottam and Curtis, 1956). Sampling was restricted to a 20 m radius from the central point, to avoid sampling the same trees twice in nearby locations. For each selected tree, we measured and recorded its diameter at breast height (DBH), azimuth direction and distance towards the centre of the plot.

2.2.3. Landscape and patch features

At landscape scale, we estimated the proportion of forest in a 500 m buffer ring around each focal patch (Donald and Evans, 2006). We assumed that a larger forest cover can hinder human disturbances and mitigate agricultural fertilizer pollution (Martino, 2001; Andersson and Nordberg, 2017), which might decrease soil nutrient stocks (Cardinale et al., 2012; Vellend et al., 2013). Using a geographic information system (GIS, specifically ArcGIS 9.3 by ESRI), patch size and historical age were determined at the patch scale. This involved analyzing

contemporary and historical maps depicting the landscape windows, including recent aerial photographs taken after 2000, as well as maps from the 18th, 19th, and 20th centuries. The calculation of patch size entailed the utilization of digitized polygons representing forest patches within each window. To determine the historical age of the patches, we digitized all forest patches from historical maps and estimated their age based on the date of the oldest map in which a focal forest patch was identified. Considering that a patch may consist of a mosaic of patches having different ages, we computed a size-weighted average of the age for all fragments within an isolated patch.

2.2.4. Macroclimate and nitrogen deposition

We extracted the long-term climatology for mean annual temperature (MAT) and mean annual precipitation (MAP) covering the period 1970–2000 from the WorldClim global geodatabase (1-km resolution, <http://www.worldclim.org/>) and averaged the variables for each forest patch using all 1-km² pixels intersecting it. The N deposition was the sum of nitrate (NO₃⁻-N) and ammonium (NH₄⁺-N), which was derived from the MSC-W model developed within the European Monitoring and Evaluation Program (EMEP) (Simpson et al., 2012) using recalculated emission values. Gridded (50 km × 50 km) data between 1990 and 2012 was used to cover a period of high deposition (1990) and the lower deposition loads close to the soil sampling event (2012). The model was run by meteorological parameters derived from the European Center of Medium-Range Weather Forecasts (ECMWF). The spatial resolution of both the climate and deposition data often exceeds the distance between the forest patches. Therefore, the calculated values refer to entire landscape windows within regions. Since the macroclimate and N deposition variation within the same landscape of 5 × 5 km² is expected to be quite limited, we used these variables to differentiate between different regions rather than focusing on different patches within the same landscape.

2.3. Data analysis

Our study included six categories of predictor variables (Table 1). The first and key predictor variables were patch features with patch age and size for testing our two hypotheses. Although we had the classification of ancient vs recent and large vs small to represent patch age and size categories, for data analysis we used the actual estimated numerical value of age and size rather than the categorical variables. To increase the generality of our research, we then included five more categories of variables across patch, landscape, regional and continental scales as covariates, which are often studied and considered as important indicators of forest soil nutrients and soil pH (Martino, 2001; Lal, 2005; Pregitzer et al., 2008; Hou et al., 2018): (1) macroclimate with annual mean temperature (MAT) and precipitation (MAP); (2) N deposition rate (N_{deposit}); (3) forest proportion in a 500 m buffer ring around each focal patch (Forest.buffer500); (4) total tree basal area (BA); and (5) soil texture with clay content (Clay). The response variables were soil pH, the concentration and stocks of soil C, N, P and Olsen P, and the stoichiometric ratios of C:N and N:P (Table 1). The response variables were the same for both forest floor and mineral soil layers, except for soil P related variables that were measured only in mineral soil. Each variable had 415 values corresponding to the total number of soil sampling locations, and data was analyzed at the sampling location level. Linear mixed-effects models (LMMs) were applied for each soil response variable, using region and window ID (nested within region) as random intercept terms. Before running the models, we log-transformed some predictor variables (Age, Size, Forest.buffer500 and BA) and response variables (C_{ff} , N_{ms} , P_{ms} , $P_{\text{Olsen}_{\text{ms}}}$, $C:N_{\text{ms}}$, $N:P_{\text{ms}}$, and C_{ff} stocks, N_{ff} stocks and $P_{\text{Olsen}_{\text{ms}}}$ stocks), and scaled all predictor variables. The LMMs had the following structure: Soil variable \sim Age \times Size + MAT + MAP + N_{deposit} + Forest.buffer500 + BA + Clay + (1 | region/window ID). We used variance inflation factors (VIF) to test for multicollinearity of all LMMs. VIFs for most predictor variables was below 2, except for MAP and N_{deposit} which were between 2 and 3. We therefore kept all predictor variables for each soil variable. Data analysis was performed in R 4.1.1 (R Core Team, 2021). The lme function from the lme4 package (Bates and Maechler, 2016) was applied.

3. Results

Higher concentration and stocks of mineral soil P (P_{ms} and P_{ms} stocks) were found in more recent than in more ancient forest patches

Table 2

Relationships between forest patch age and size, environmental covariates and the forest floor and mineral soil properties (soil pH and nutrients concentrations and stocks in the forest floor and mineral soil layers). Values are standardized parameter estimates from general LMM with region and landscape type as random effect.

Soil layer	Predictor variable	Patch features variables			Environmental covariates					
		Age	Size	Age \times size	MAT	MAP	N_{deposit}	Forest.buffer500	BA	Clay
Forest floor	pH_{ff}	-0.08	-0.05	0.05	0.14	0.12	-0.30	-0.11	0.06	0.12
	C_{ff}	-0.09	0.02	-0.05	-0.28	0.29	-0.33	-0.01	0.02	-0.27
	N_{ff}	-0.07	-0.03	-0.03	0.03	0.18	0.03	0.00	-0.02	-0.42***
	$C:N_{\text{ff}}$	-0.04	0.07	-0.03	-0.23	0.00	-0.24	0.05	0.01	0.05
	C_{ff} stocks	0.11	-0.08	-0.02	0.40***	-0.25	0.14	0.07	-0.02	-0.06
	N_{ff} stocks	0.10	-0.08	-0.02	0.41***	-0.20	0.16	0.05	-0.02	-0.13
Mineral soil	pH_{ms}	-0.07	-0.10*	0.01	0.20	0.11	-0.34	-0.02	0.05	0.09
	C_{ms}	0.04	0.02	0.00	-0.33*	0.00	0.20	-0.01	-0.05	-0.19
	N_{ms}	0.05	-0.04	-0.04	-0.36*	0.14	0.00	-0.05	-0.03	-0.28*
	P_{ms}	-0.13*	-0.03	-0.05	-0.31	-0.05	-0.06	-0.07	0.06	0.01
	$P_{\text{Olsen}_{\text{ms}}}$	-0.03	0.02	0.03	-0.39	-0.40	0.59*	0.01	-0.07	0.00
	$C:N_{\text{ms}}$	0.12	0.07	0.08	-0.25	-0.22	0.39	0.13*	-0.12***	0.02
	$N:P_{\text{ms}}$	0.20***	-0.01	0.02	-0.08	0.29	0.02	0.02	-0.10*	-0.39*
	C_{ms} stocks	0.01	-0.05	-0.06	-0.12	-0.16	0.11	0.00	-0.08	-0.17
	N_{ms} stocks	-0.05	-0.08	-0.14*	-0.09	0.02	-0.14	-0.09	-0.02	-0.13
	P_{ms} stocks	-0.31***	0.00	-0.09	0.00	-0.22	-0.06	-0.07	0.08	0.23
	$P_{\text{Olsen}_{\text{ms}}}$ stocks	-0.05	0.01	0.01	-0.27	-0.47	0.59*	0.03	-0.07	0.15

The variable abbreviations and explanations are mentioned in Table 1.

*** $P < 0.001$.

* $P < 0.05$.

(Table 2 and Fig. 2). A standardized unit change in age caused 0.13 standardized unit decrease of P_{ms} , 0.31 standardized unit decrease of P_{ms} stocks, and 0.20 standardized unit increase of $N:P_{\text{ms}}$. Patch age did not have any effects on soil pH, C:N or the concentration or stocks of soil C and N in both forest floor and mineral soil layers.

Smaller patches showed higher pH_{ms} than larger forest patches (Table 2 and Fig. 3). A standardized unit change in patch size caused 0.10 standardized unit decrease of pH_{ms} . Patch size did not have significant effects on pH_{ff} , the concentration or stocks of soil C, N, and P, or their ratios ($C:N_{\text{ff}}$, $C:N_{\text{ms}}$ and $N:P_{\text{ms}}$) in both the forest floor and mineral soil layers. For the interactive effect of patch age and size, lower mineral soil N stocks in patches with older age and larger size was detected (Table 2).

For annual mean temperature (MAT) and precipitation (MAP), N deposition (N_{deposit}), forest proportion in 500 m buffer zone (Forest.buffer500), total tree basal area (BA) and soil texture (Clay), we found inconsistent responses of soil C and N between forest floor and mineral soil to MAT. More specifically, C_{ms} and N_{ms} decreased, while C_{ff} stocks and N_{ff} stocks increased with increasing MAT (Table 2 and Fig. SM.2 in Supplementary material). MAP did not show significant effects on soil variables (Table 2 and Fig. SM.3 in Supplementary material). The $P_{\text{Olsen}_{\text{ms}}}$ and $P_{\text{Olsen}_{\text{ms}}}$ stocks increased with increasing N_{deposit} (Fig. SM.4 in Supplementary material). Forest.buffer500 showed a positive effect on $C:N_{\text{ms}}$ and the BA had a negative effect on $C:N_{\text{ms}}$ and $N:P_{\text{ms}}$ (Figs. SM.5 & SM.6 in Supplementary material). Furthermore, decreased N_{ff} , N_{ms} and $N:P_{\text{ms}}$ with increasing clay content were found (Fig. SM.7 in Supplementary material).

Finally, the effect of patch age on P_{ms} stocks was sometimes much stronger than N_{deposit} or BA (Table 2). For example, a standardized unit change in patch age had an almost five times higher impact than N_{deposit} , or a four times higher impact than BA on P_{ms} stocks.

4. Discussion

4.1. Effects of patch age and size on soil nutrients and pH

Since soils of more recent forest patches had higher mineral soil P concentration and stocks than soils of more ancient forest patches, we detect an important role of past land-use history and fertilization legacy on soil nutrients in forests across a latitudinal gradient in Europe. More recently afforested lands have been previously managed and cultivated through agricultural management, which could result in a higher soil P

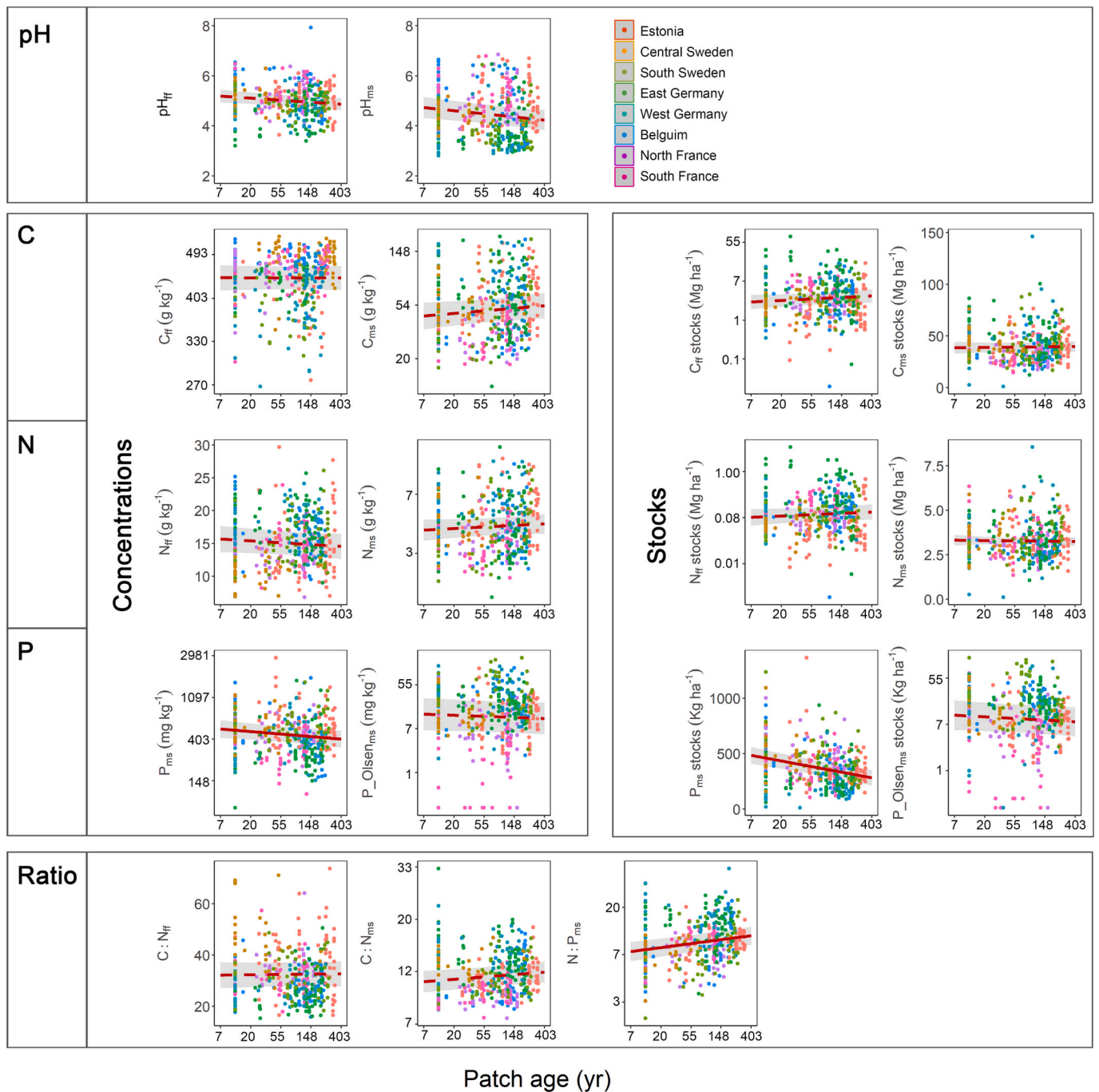


Fig. 2. The relationships between forest patch age (in years, the X axis was log transformed) and soil variables including soil pH and the concentrations and stocks of soil C, N and P and their ratios for both forest floor and mineral soil layers. The abbreviations and explanations for the variables are in Table 1. The soil variables of C_{ff} , N_{ms} , P_{ms} , P_Olsen_{ms} , $C:N_{ms}$, $N:P_{ms}$, C_{ff} stocks, N_{ff} stocks and P_Olsen_{ms} stocks are log transformed. The solid red lines represent the significant trends ($P < 0.05$) and dashed red lines represent non-significant trends ($P > 0.05$). The shaded area represents 95 % confidence intervals.

concentration or stocks. For instance, the application of P-based fertilizers, along with the use of livestock manure and organic waste as natural fertilizers, introduces P to agricultural fields (Almeida et al., 2019; Bindraban et al., 2020). Over time, these inputs can lead to the accumulation of forest soil P. Previous studies also found a higher P concentration (few studies tested P stocks as we did) in post-agricultural forest soils compared to ancient forest soils (Verheyen et al., 1999; De Schrijver et al., 2012; Blondeel et al., 2019). Those studies showed that the legacies of soil P can persist for decades, indicating that the geochemical mechanisms associated with soil P availability operate over long time-scales (Walker and Syers, 1976; Vitousek and Farrington,

1997; McDowell et al., 2001; Dupouey et al., 2002; De Schrijver et al., 2012). For example, in previous local studies on similar forest soil layers (0 to 30 cm), Verheyen et al. (1999) and Honnay et al. (1999) showed that mixed hardwood forests with a history of agricultural land use experienced a significant increase in soil phosphate, especially in the twentieth century. Likewise, Bergès et al. (2017) and Blondeel et al. (2019) found that post-agricultural forests, even after afforestation for several decades or centuries, still had higher P concentration compared to ancient forests. Some studies also observed variations in different soil P fractions. For example, De Schrijver et al. (2012) demonstrated that as forests age, labile and slowly cycling inorganic soil phosphorus fractions

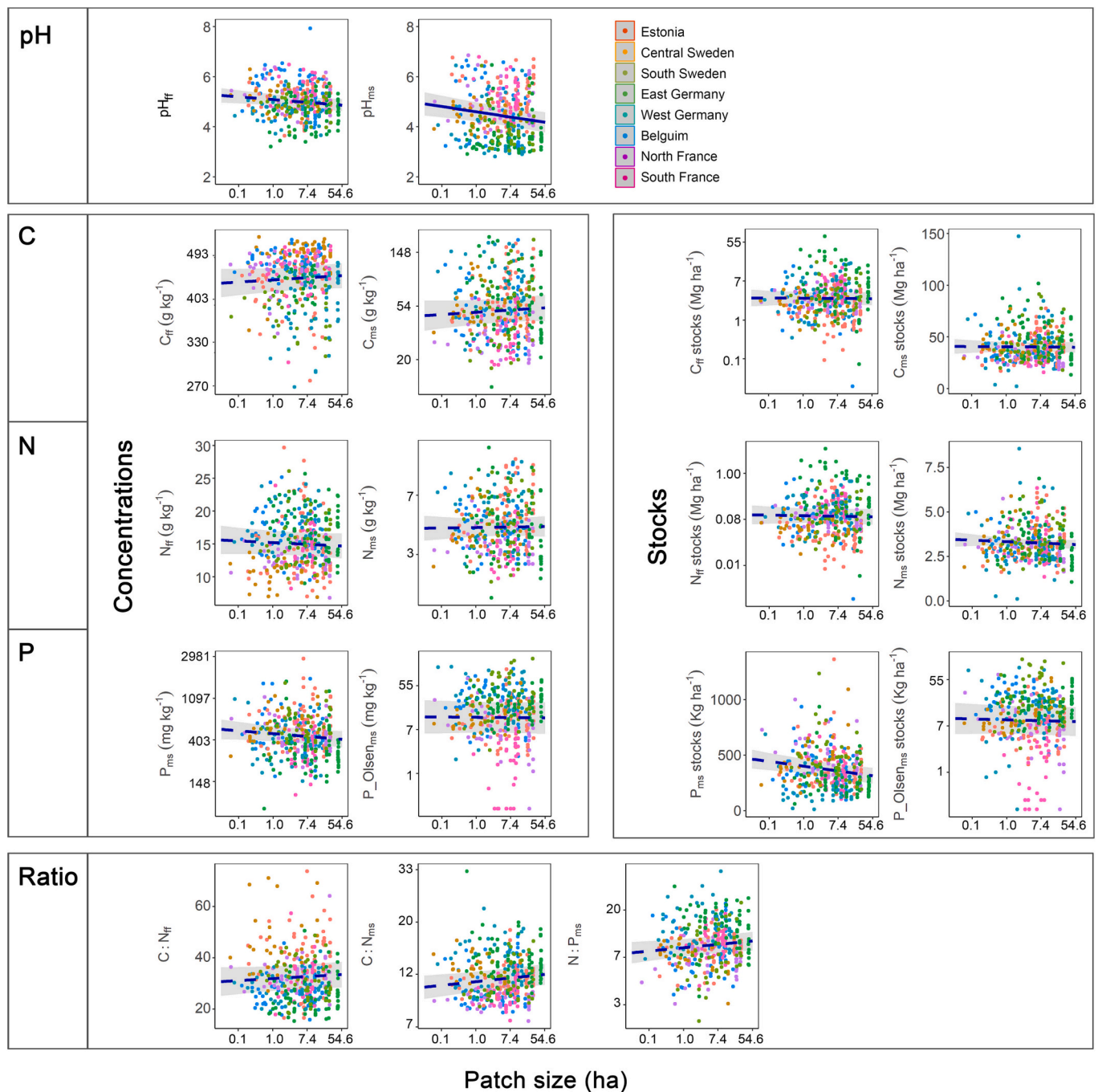


Fig. 3. The relationships between forest patch size (in hectares, the X axis was log transformed) and soil variables including soil pH and the concentrations and stocks of soil C, N and P and their ratios for both forest floor and mineral soil layers. The abbreviations and explanations for the variables are in Table 1. The soil variables of C_{ff} , N_{ms} , P_{ms} , P_Olsen_{ms} , $C:N_{ms}$, $N:P_{ms}$, C_{ff} stocks, N_{ff} stocks and P_Olsen_{ms} stocks are log transformed. The solid blue lines represent the significant trends ($P < 0.05$) and dashed blue lines represent non-significant trends ($P > 0.05$). The shaded area represents 95 % confidence intervals.

decrease, while organic fractions exhibit a significant increase. In our study, we did not detect a change in Olsen P with patch age. In addition, some of the studies that reported higher soil P levels also observed higher pH values (e.g., Honnay et al., 1999; Blondeel et al., 2019). However, we did not find changes in soil pH with patch age. Yet, there are also studies showing that soil pH remains relatively unchanged in the upper soil layer, for instance in northern hardwood forests in the U.S. (Goodale and Aber, 2001), reforested forests in Spain (Hevia et al., 2014), and former agricultural land in Belgian forests (Bossuyt et al., 1999).

However, consistent with our hypothesis, smaller forest patches had

a higher pH in the mineral soil than larger forest patches. This indicated potentially higher drift of K^+ , Ca^{2+} and Mg^{2+} into forest edges from nearby agricultural soil particles (Valdés et al., 2015), which reduces soil acidity. Previous studies have reported elevated pH values and higher concentrations of K^+ , Ca^{2+} and Mg^{2+} in the organic layer or mineral soil at the edges of deciduous and coniferous forests (Honnay et al., 2002; Malmivaara-Lämsä et al., 2008; Govaert et al., 2020; Meeussen et al., 2021). These studies have attributed the observed differences to factors such as increased base cation input through throughfall and litterfall, or increased leaching of ions, dry deposition, due to the edge effects, which could also counteract or outweigh the soil

acidification effect caused by higher levels of acidifying deposition at the edge (Lovett and Reiners, 1986; Beier and Gundersen, 1989; Devlaeminck et al., 2005). Therefore, patches with small size are probably more affected by surrounding agricultural practices due to edge effects, while patch age effects on soil P, are the result of the agricultural legacy in afforested, post-agricultural forests.

Our study also suggested that patch features may not be the determinants of soil C and N in the upper soil layer, since we did not observe any significant effects of forest patch age or size on the concentrations and stocks of soil C and N in the forest floor and mineral soil layers. Similar to our results, Von Oheimb et al. (2008) showed no significant differences in mineral soil C and N concentrations with the land-use conversion from agricultural land to forest over 150 years. Mund and Schulze (2006) found no forest age effect on the mineral soil C stocks of beech forests. Nitsch et al. (2018) concluded that, the studies that did not detect changes in soil C or N were because only the uppermost soil layers down to a depth of 10–15 cm were considered. Significant difference in pH or soil nutrients were previously only detected deeper, up to about 30 cm, rather than at the forest floor or top of the mineral soil layer (Wulf, 2022). Leuschner et al. (2014) and Nitsch et al. (2018) showed that decades or centuries of former land use have reduced the C and nutrient storage of the subsoil. This might be because the organic and mineral soil layers accumulate C more rapidly than the subsoil, allowing for the rebuilding of C stocks characteristic of the organic layer or mineral soil layer in continuously forested sites. New equilibrium at these two layers is typically reached after several decades or 50–130 years of forest development (Jandl et al., 2007; Leuschner et al., 2014). On the contrary, the recovery of C stocks in the deeper soil is a much slower process, driven by inputs of fine litter, dead roots, root fragments, as well as the accumulation of dead microbial and soil animal biomass in the soil profile (Gregorich et al., 1998; Pregitzer and Euskirchen, 2004). The absence of effect of patch size on soil C or N was contrary to a study by Remy et al. (2016) in temperate forests, who found strong interior-to-edge trends for the mineral C and N stocks. This may also suggest that higher soil C and N levels can only be detected at the soil point strictly located at the forest edge compared to the forest interior. Yet, our study is consistent with Meeussen et al. (2021) at the European scale who found no interior-to-edge variation of soil C stocks for the mineral topsoil. Schedlbauer and Miller (2022) showed that edge effects altered soil C cycling by increasing soil respiration rates but with non-significant difference in soil C pools between forest edge and the interior. Finally, it was only when estimating the interactive effects of patch age and size that the variation in soil N could be detected. Specifically, we observed lower mineral N stocks in patches with older age and larger size.

4.2. Effects of other predictor variables on soil nutrients and pH

Contrasting to previous local studies that solely focused on patch features, our study also assessed the impact of other environmental factors across different scales on soil nutrients. The response direction and magnitude of patch-scale soil nutrients to the other predictor variables (MAT, MAP, N_{deposit} , Forest.buffer500, BA and Clay) were generally consistent with previous findings at regional/continental or at local levels. High temperatures facilitate rapid immobilization and mineralization (Wallenstein et al., 2011; Hou et al., 2018), which could speed up the natural processes of forest soil nutrient loss at a continental or global extent (Singh et al., 2022). High-latitude temperate regions are expected to experience a temperature rise that surpasses the average global increase (IPCC, 2022). We found decreased soil C and N concentrations in mineral soil layers with increasing MAT along the latitudinal gradient. Similarly, in a comprehensive analysis by Crowther et al. (2015), significantly lower soil C stocks were observed in high-latitude areas across North America, Europe, and Asia. Although high precipitation was found to generally increase nutrient levels, in our case, precipitation did not affect soil pH or nutrient stocks. On the other hand, high temperature and high N deposition may increase plant productivity (if no

other resources are limiting) and the accumulation of surface litter and soil organic matter (Lützow et al., 2006; Paul, 2016), which might contribute to the increased soil C and N stocks in the forest floor or increased mineral soil Olsen P as we found (Berg and Matzner, 1997; Hinsinger, 2001; Pregitzer et al., 2008). Both the studies by Zhang et al. (2014) and by Tian et al. (2015) also showed that N addition significantly increased the Olsen P concentration in grassland soils. The decrease in soil pH caused by N addition led to a reduction in exchangeable cations, thereby resulting in decreased soil P resorption to cations. Our findings also suggested a potential link between increasing nitrogen deposition and a decrease in soil pH, although the decrease was not statistically significant. This might explain our results because we also found a decrease in soil pH (though not statistically significant) with increasing N deposition.

Moreover, at landscape scale, the role of Forest.buffer500 generally had a weak effect on soil nutrients, with only a positive effect on C:N_{ms}. For the effect of BA, stands with high BA might represent highly productive stands and thus induce high organic matter (e.g. high plant leaf and root residues) input into the soil (Li et al., 2010; Lal, 2005; Paul, 2016; Rasse et al., 2005; Mooshammer et al., 2014), i.e., low C:N, or N:P ratios of mineral soil in our study. The result that increasing clay content decreased soil N in both forest floor and mineral soil or N:P in mineral soil suggested that soils with higher clay content have higher cation exchange capacity, which decreased N concentrations by increasing biological activity, and N mainly forms in the organic rather than in the clay (Pepper and Brusseau, 2019). The relatively stronger effect of patch age on soil P stocks than macroclimate (MAT or N_{deposit}) also highlighted the importance of forest fragmentation effect when predicting forest soil nutrient status.

5. Conclusions

Despite the global concerns on the impact of forest fragmentation on forest ecosystems, there is still a research gap in our overall understanding of the relationship between forest patch features and the soil nutrient status. Our study addressed this gap by using a large-scale sampling design to assess how the age and size of forest patches affect soil nutrients at the continental extent of Europe. We highlighted that recent and small forest patches, respectively, have higher P concentration and stocks in soils and a less acidic soil. Moreover, considering multi-scale environmental factors allowed for these key findings general and applicable for ecologists and forest managers. Our intensive sampling design could not detect the effects of age or size on other soil nutrients in addition to soil P, as found in some case studies. With increasing climate and land-use changes, long-term studies on assessing edge effects on soil nutrients and soil system recovery (including subsoil layer) of forest patches are needed for better predicting forest soil health in a habitat fragmentation background.

CRedit authorship contribution statement

Liping Wei: Conceptualization, Methodology, Data curation, Formal analysis, Writing – original draft. **Jaana Liira:** Data curation, Writing – review & editing. **Steffen Ehrmann:** Data curation, Writing – review & editing. **Jonathan Lenoir:** Data curation, Writing – review & editing. **Guillaume Decocq:** Data curation, Writing – review & editing. **Jörg Brunet:** Data curation, Writing – review & editing. **Monika Wulf:** Data curation, Writing – review & editing. **Martin Diekmann:** Data curation, Writing – review & editing. **Tobias Naaf:** Data curation, Writing – review & editing. **Michael Scherer-Lorenzen:** Data curation, Writing – review & editing. **Karin Hansen:** Data curation, Writing – review & editing. **Pallieter De Smedt:** Data curation, Writing – review & editing. **Alicia Valdés:** Data curation, Writing – review & editing. **Kris Verheyen:** Conceptualization, Methodology, Data curation, Formal analysis, Writing – original draft. **Pieter De Frenne:** Conceptualization, Formal analysis, Methodology, Writing – original draft.

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

The raw data is available on Figshare: https://figshare.com/articles/dataset/smallforest-soil_data_xlsx/22220593.

Acknowledgments

This research was funded by the ERA-Net BiodivERsA project smallFOREST, with the national funders ANR (France), MINECO (Spain), FORMAS (Sweden), ETAG (funding continuation under the grant PRG1223, Estonia), DFG/DLR (Germany) and BELSPO (Belgium) as part of the 2011 BiodivERsA call for research proposals. This research was also funded by the international mobility project of National Natural Science Foundation of China - Research Foundation Flanders (NSFC-FWO, No. 32211530482). The Forest & Nature laboratory at Ghent University is acknowledged for chemical analysis work.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.165543>.

References

- Abadie, J., Avon, C., Dupouey, J.L., Lopez, J.M., Taton, T., Bergès, L., 2018. Land use legacies on forest understory vegetation and soils in the Mediterranean region: should we use historical maps or in situ land use remnants? *For. Ecol. Manag.* 427, 17–25. <https://doi.org/10.1016/j.foreco.2018.05.050>.
- Almeida, R.F., Queiroz, I.D.S., Mikhael, J.E.R., Oliveira, R.C., Borges, E.N., 2019. Enriched animal manure as a source of phosphorus in sustainable agriculture. *Int. J. Recycl. Org. Waste Agric.* 8 (Suppl. 1), 203–210. <https://doi.org/10.1007/s40093-019-00291-x>.
- Andersson, J., Nordberg, Å., 2017. Biogas upgrading using ash from combustion of wood fuels: laboratory experiments. *Energy Environ. Res.* 7, 38–47. <https://doi.org/10.5539/eer.v7n1p38>.
- Bates, D., Maechler, M., 2016. Matrix: sparse and dense matrix classes and methods. R package version 1.2-6. <https://CRAN.R-project.org/package=Matrix>.
- Beier, C., Gundersen, P., 1989. Atmospheric deposition to the edge of a spruce forest in Denmark. *Environ. Pollut.* 60 (3–4), 257–271. [https://doi.org/10.1016/0269-7491\(89\)90108-5](https://doi.org/10.1016/0269-7491(89)90108-5).
- Berg, B., Matzner, E., 1997. Effect of N deposition on decomposition of plant litter and soil organic matter in forest systems. *Environ. Rev.* 5, 1–25. <https://doi.org/10.1139/a96-017>.
- Bergès, L., Feiss, T., Avon, C., Martin, H., Rochel, X., Dauffy-Richard, E., Cordonnier, T., Dupouey, J.L., 2017. Response of understory plant communities and traits to past land use and coniferous plantation. *Appl. Veg. Sci.* 20, 468–481. <https://doi.org/10.1111/avsc.12296>.
- Bindraban, P.S., Dimkpa, C.O., Pandey, R., 2020. Exploring phosphorus fertilizers and fertilization strategies for improved human and environmental health. *Biol. Fertil. Soils* 56, 299–317. <https://doi.org/10.1007/s00374-019-01430-2>.
- Blondeel, H., Perring, M.P., Bergès, L., Brunet, J., Decocq, G., Depauw, L., Diekmann, M., Landuyt, D., Liira, J., Maes, S.L., Vanhellemont, M., Wulf, M., Verheyen, K., 2019. Context-dependency of agricultural legacies in temperate forest soils. *Ecosystems* 22, 781–795. <https://doi.org/10.1007/s10021-018-0302-9>.
- Bossuyt, B., Deckers, J., Hermy, M., 1999. A field methodology for assessing man-made disturbance in forest soils developed in loess. *Soil Use Manag.* 15, 14–20. <https://doi.org/10.1111/j.1475-2743.1999.tb00056.x>.
- Bouwman, A.F., Beusen, A.H.W., Lassaletta, L., van Apeldoorn, D.F., van Grinsven, H.J.M., Zhang, J., Ittersum Van, M.K., 2017. Lessons from temporal and spatial patterns in global use of N and P fertilizer on cropland. *Sci. Rep.* 7, 40366. <https://doi.org/10.1038/srep40366>.
- Bradford, M.A., Wieder, W.R., Bonan, G.B., Fierer, N., Raymond, P.A., Crowther, T.W., 2016. Managing uncertainty in soil carbon feedbacks to climate change. *Nat. Clim. Chang.* 6, 751–758. <https://doi.org/10.1038/nclimate3071>.
- Brady, N.C., Weil, R.R., 1999. *The Nature and Properties of Soils*, 12th edition. Prentice Hall, Publications Office.
- Brasseur, B., Spicher, F., Lenoir, J., Gallet-Moron, E., Buridant, J., Horen, H., 2018. What deep-soil profiles can teach us on deep-time pH dynamics after land use change? *Land Degrad. Dev.* 29, 2951–2961. <https://doi.org/10.1002/ldr.3065>.
- Brzeziecki, B., Kienast, F., Wildi, O., 1993. A simulated map of the potential natural forest vegetation of Switzerland. *J. Veg. Sci.* 4, 499–508. <https://doi.org/10.2307/3236077>.
- Bueno, A., Llambí, L.D., 2015. Facilitation and edge effects influence vegetation regeneration in old-fields at the tropical Andean forest line. *Appl. Veg. Sci.* 18, 613–623. <https://doi.org/10.1111/avsc.12186>.
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., MacE, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. *Nature* 486, 59–67. <https://doi.org/10.1038/nature11448>.
- Cottam, G., Curtis, J.T., 1956. The use of distance measures in phytosociological sampling. *Ecology* 37, 451–460. <https://doi.org/10.2307/1930167>.
- Coudun, C., Gégout, J.C., 2006. The derivation of species response curves with Gaussian logistic regression is sensitive to sampling intensity and curve characteristics. *Ecol. Model.* 199, 164–175. <https://doi.org/10.1016/j.ecolmodel.2006.05.024>.
- Crowther, T., Glick, H., Covey, K., Bettigole, C., Maynard, D., Thomas, S., Smith, J., Hintler, G., Duguid, M., Amatulli, G., Tuanmu, M., Jetz, W., Salas, C., Stam, C., Piotta, D., Tavani, R., Green, S., Bruce, G., Williams, S., Wiser, S., Huber, M., Hengeveld, G., Nabuurs, G., Tikhonova, E., Bradford, M., 2015. Mapping tree density at a global scale. *Nature* 525, 201–205. <https://doi.org/10.1038/nature14967>.
- Dawud, S.M., Raulund-Rasmussen, K., Domisch, T., Finer, L., Jaroszewicz, B., Vesterdal, L., 2016. Is tree species diversity or species identity the more important driver of soil carbon stocks, C/N ratio, and pH? *Ecosystems* 19, 645–660. <https://doi.org/10.1007/s10021-016-9958-1>.
- De Schrijver, A., Devlaemincq, R., Mertens, J., Wuyts, K., Hermy, M., Verheyen, K., 2007. On the importance of incorporating forest edge deposition for evaluating exceedance of critical pollutant loads. *Appl. Veg. Sci.* 10, 293–298. <https://doi.org/10.1111/j.1654-109X.2007.tb00529.x>.
- De Schrijver, A., Vesterdal, L., Hansen, K., de Frenne, P., Augusto, L., Achat, D.L., Staelens, J., Baeten, L., de Keersmaecker, L., de Neve, S., Verheyen, K., 2012. Four decades of post-agricultural forest development have caused major redistributions of soil phosphorus fractions. *Oecologia* 169, 221–234. <https://doi.org/10.1007/s00442-011-2185-8>.
- Devlaemincq, R., Bossuyt, B., Hermy, M., 2005. Inflow of seeds through the forest edge: evidence from seed bank and vegetation patterns. *Plant Ecol.* 176, 1–17. <https://doi.org/10.1007/s11258-004-0008-2>.
- Donald, P.F., Evans, A.D., 2006. Habitat connectivity and matrix restoration: the wider implications of agri-environment schemes. *J. Appl. Ecol.* 43, 209–218. <https://doi.org/10.1111/j.1365-2664.2006.01146.x>.
- Dupouey, J.L., Dambrine, E., Laffite, J.D., Moares, C., 2002. Irreversible impact of past land use on forest soils and biodiversity. *Ecology* 83, 2978–2984. <https://doi.org/10.2307/3071833>.
- Estreguil, C., Caudullo, G., De Rigo, D., San-Miguel-Ayanz, J., 2012. *Forest Landscape in Europe: Pattern, Fragmentation and Connectivity*. EUR 25717. Publications Office of the European Union, Luxembourg (Luxembourg) (2012).
- Fahrig, L., Arroyo-Rodríguez, V., Bennett, J.R., Boucher-Lalonde, V., Cazetta, E., Currie, D.J., Eigenbrod, F., Ford, A.T., Harrison, S.P., Jaeger, J.A.G., Koper, N., Martin, A.E., Martin, J.L., Metzger, J.P., Morrison, P., Rhodes, J.R., Saunders, D.A., Simberloff, D., Smith, A.C., Tischendorf, L., Vellend, M., Watling, J.L., 2019. Is habitat fragmentation bad for biodiversity? *Biol. Conserv.* 230, 179–186. <https://doi.org/10.1016/j.biocon.2018.12.026>.
- Frossard, E., Condron, L.M., Oberson, A., Sinaj, S., Fardeau, J.C., 2000. Processes governing phosphorus availability in temperate soils. *J. Environ. Qual.* 29, 15–23. <https://doi.org/10.2134/jeq2000.00472425002900010003x>.
- Goodale, C.L., Aber, J.D., 2001. The long-term effects of land-use history on nitrogen cycling in northern hardwood forests. *Ecol. Appl.* 11 (1), 253–267. [https://doi.org/10.1890/1051-0761\(2001\)011\[0253:TLTEOL\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2001)011[0253:TLTEOL]2.0.CO;2).
- Govaert, S., Meeussen, C., Vanneste, T., Bollmann, K., Brunet, J., Cousins, S.A.O., Diekmann, M., Graae, B.J., Hedwall, P.O., Heinken, T., Iacopetti, G., Lenoir, J., Lindmo, S., Orzechowska, A., Perring, M.P., Ponette, Q., Plue, J., Selvi, F., Spicher, F., Tolosano, M., Vermeir, P., Zellweger, F., Verheyen, K., Vangansbeke, P., De Frenne, P., 2020. Edge influence on understory plant communities depends on forest management. *J. Veg. Sci.* 31, 281–292. <https://doi.org/10.1111/jvs.12844>.
- Graae, B.J., Sunde, P.B., Fritzbøger, B., 2003. Vegetation and soil differences in ancient opposed to new forests. *For. Ecol. Manag.* 177, 179–190. [https://doi.org/10.1016/S0378-1127\(02\)00438-3](https://doi.org/10.1016/S0378-1127(02)00438-3).
- Gregorich, E.G., Greer, K.J., Anderson, D.W., Liang, B.C., 1998. Carbon distribution and losses: erosion and deposition effects. *Soil Tillage Res.* 47 (3–4), 291–302. [https://doi.org/10.1016/S0167-1987\(98\)00117-2](https://doi.org/10.1016/S0167-1987(98)00117-2).
- Guirado, M., Pino, J., Rodà, F., 2006. Understorey plant species richness and composition in metropolitan forest archipelagos: effects of forest size, adjacent land use and distance to the edge. *Glob. Ecol. Biogeogr.* 15, 50–62. <https://doi.org/10.1111/j.1466-822X.2006.00197.x>.
- Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.X., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* 1, e1500052. <https://doi.org/10.1126/sciadv.1500052>.
- Hevia, J.N., de Aratijo, J.C., Manso, J.M., 2014. Assessment of 80 years of ancient-badlands restoration in Saldaña, Spain. *Earth Surf. Process. Landf.* 39 (12), 1563–1575. <https://doi.org/10.1002/esp.3541>.
- Hinsinger, P., 2001. Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: a review. *Plant Soil* 237, 173–195. <https://doi.org/10.1023/A:1013351617532>.

- Homann, P.S., Sollins, P., Chappell, H.N., Stangenberger, A.G., 1995. Soil organic carbon in a mountainous, forested region: relation to site characteristics. *Soil Sci. Soc. Am. J.* 59, 1468–1475. <https://doi.org/10.2136/sssaj1995.03615995005900050037x>.
- Honnay, O., Hermy, M., Coppin, A.P., 1999. Effects of area, age and diversity of forest patches in Belgium on plant species richness, and implications for conservation and reforestation. *Biol. Conserv.* 87 (1), 73–84. [https://doi.org/10.1016/S0006-3207\(98\)00038-X](https://doi.org/10.1016/S0006-3207(98)00038-X).
- Honnay, O., Verheyen, K., Hermy, M., 2002. Permeability of ancient forest edges for woody plant species invasion. *Forest Ecol. Manag.* 161, 109–122. [https://doi.org/10.1016/S0378-1127\(01\)00490-X](https://doi.org/10.1016/S0378-1127(01)00490-X).
- Honnay, O., Jacquemyn, H., Bossuyt, B., Hermy, M., 2005. Forest fragmentation effects on patch occupancy and population viability of herbaceous plant species. *New Phytol.* 166, 723–736. <https://doi.org/10.1111/j.1469-8137.2005.01352.x>.
- Hou, E., Chen, C., Luo, Y., Zhou, G., Kuang, Y., Zhang, Y., Heenan, M., Lu, X., Wen, D., 2018. Effects of climate on soil phosphorus cycle and availability in natural terrestrial ecosystems. *Glob. Chang. Biol.* 24, 3344–3356. <https://doi.org/10.1111/gcb.14093>.
- IPCC, 2022. In: Pörtner, H.-O., Roberts, D.C., Tignor, M., Poloczanska, E.S., Mintenbeck, K., Alegria, A., Craig, M., Langsdorf, S., Löschke, S., Möller, V., Okem, A., Rama, B. (Eds.), *Climate Change 2022: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK and New York, NY, USA. <https://doi.org/10.1017/9781009325844> (3056 pp.).
- Jakovac, C.C., Bongers, F., Kuyper, T.W., Mesquita, R.C.G., Peña-Claros, M., 2016. Land use as a filter for species composition in Amazonian secondary forests. *J. Veg. Sci.* 27, 1104–1116. <https://doi.org/10.1111/jvs.12457>.
- Jandl, R., Lindner, M., Vesterdal, L., Bauwens, B., Baritz, R., Hagedorn, F., Johnson, D., Minkinen, K., Byrne, K.A., 2007. How strongly can forest management influence soil carbon sequestration? *Geoderma* 137 (3–4), 253–268. <https://doi.org/10.1016/j.geoderma.2006.09.003>.
- Jastrow, J.D., Amonette, J.E., Bailey, V.L., 2007. Mechanisms controlling soil carbon turnover and their potential application for enhancing carbon sequestration. *Clim. Chang.* 80, 5–23. <https://doi.org/10.1007/s10584-006-9178-3>.
- Lajtha, K., Driscoll, C.T., Jarrell, W.M., Elliott, E.T., 1999. Soil phosphorus: characterization and total element analysis. In: Robertson, G.P., Coleman, D.C., Bledsoe, C.S., Sollins, P. (Eds.), *Standard Soil Methods for Long-term Ecological Research*. Oxford University Press, New York, pp. 115–142.
- Lal, R., 2005. Forest soils and carbon sequestration. *For. Ecol. Manag.* 220, 242–258. <https://doi.org/10.1016/j.foreco.2005.08.015>.
- Leuschner, C., Wulf, M., Bächler, P., Hertel, D., 2014. Forest continuity as a key determinant of soil carbon and nutrient storage in beech forests on sandy soils in northern Germany. *Ecosystems* 17, 497–511. <https://doi.org/10.1007/s10021-013-9738-0>.
- Li, P., Wang, Q., Endo, T., Zhao, X., Kakubari, Y., 2010. Soil organic carbon stock is closely related to aboveground vegetation properties in cold-temperate mountainous forests. *Geoderma* 154, 407–415. <https://doi.org/10.1016/j.geoderma.2009.11.023>.
- Lovett, G.M., Reiners, W.A., 1986. Canopy structure and cloud water deposition in subalpine coniferous forests. *Tellus Ser. B Chem. Phys. Meteorol.* 38 (5), 319–327. <https://doi.org/10.3402/tellusb.v38i5.15140>.
- Lützw, M.v., Kögel-Knabner, I., Ekschmitt, K., Matzner, E., Guggenberger, G., Marschner, B., Flessa, H., 2006. Stabilization of organic matter in temperate soils: mechanisms and their relevance under different soil conditions – a review. *Eur. J. Soil Sci.* 57, 426–445. <https://doi.org/10.1111/j.1365-2389.2006.00809.x>.
- Maaroufi, N.I., de Long, J.R., 2020. Global change impacts on forest soils: linkage between soil biota and carbon-nitrogen-phosphorus stoichiometry. *Front. For. Glob. Change* 3, 16. <https://doi.org/10.3389/ffgc.2020.00016>.
- Malmivaara-Lämsä, M., Hamberg, L., Haapamäki, E., Liski, J., Kotze, D.J., Lehvävirta, S., Fritze, H., 2008. Edge effects and trampling in boreal urban forest fragments—impacts on the soil microbial community. *Soil Biol. Biochem.* 40 (7), 1612–1621. <https://doi.org/10.1016/j.soilbio.2008.01.013>.
- Martino, D., 2001. Buffer zones around protected areas: a brief literature review. *Electron. Green J.* 15. <https://doi.org/10.5070/g311510434>.
- McDowall, R., Sharpley, A., Condon, L., Haygarth, P., Brookes, P., 2001. Processes controlling soil phosphorus release to runoff and implications for agricultural management. *Nutr. Cycl. Agroecosyst.* 59, 269–284. <https://doi.org/10.1023/A:1014419206761>.
- Meeussen, C., Govaert, S., Vanneste, T., Bollmann, K., Brunet, J., Calders, K., Cousins, S.A.O., de Pauw, K., Diekmann, M., Gasperini, C., Hedwall, P.O., Hylander, K., Iacopetti, G., Lenoir, J., Lindmo, S., Orszewska, A., Ponette, Q., Plue, J., Sanczuk, P., Selvi, F., Spicher, F., Verbeeck, H., Zellweger, F., Verheyen, K., Vangansbeke, P., de Frenne, P., 2021. Microclimatic edge-to-interior gradients of European deciduous forests. *Agric. For. Meteorol.* 311, 108699. <https://doi.org/10.1016/j.agrformet.2021.108699>.
- Moltesen, P., 1988. *Skovtræernes ved og dets anvendelse*. Tech. rep. Skovteknisk Institut, Frederiksberg, Copenhagen, p. 132.
- Mooshammer, M., Wanek, W., Hämmerle, L., Fuchslueger, L., Hofhansl, F., Knoltsch, A., Richter, A., 2014. Adjustment of microbial nitrogen use efficiency to carbon: nitrogen imbalances regulates soil nitrogen cycling. *Nat. Commun.* 5 (1), 3694. <https://doi.org/10.1038/ncomms4694>.
- Mund, M., Schulze, E., 2006. Impacts of forest management on the carbon budget of European beech (*Fagus sylvatica*) forests. *Allg. Forst. Jagdztg.* 177 (3/4), 47. <https://doi.org/10.1007/s10457-005-0589-3>.
- Nitsch, P., Kaupenjohann, M., Wulf, M., 2018. Forest continuity, soil depth and tree species are important parameters for SOC stocks in an old forest (Templiner Buchheide, northeast Germany). *Geoderma* 310, 65–76. <https://doi.org/10.1016/j.geoderma.2017.08.041>.
- Oduro Appiah, J., Agyemang-Duah, W., 2021. Identifying spatially-explicit land use factors associated with forest patch sizes in a forest reserve in Ghana. *Land Use Policy* 101, 105135. <https://doi.org/10.1016/j.landusepol.2020.105135>.
- Olszewska, M., Smal, H., 2008. The effect of afforestation with Scots pine (*Pinus silvestris* L.) of sandy post-arable soils on their selected properties. I. Physical and sorptive properties. *Plant Soil* 305, 157–169. <https://doi.org/10.1007/s11104-008-9537-0>.
- Pärtel, M., 2002. Local plant diversity patterns and evolutionary history at the regional scale. *Ecology* 83, 2361–2366. [https://doi.org/10.1890/0012-9658\(2002\)083\[2361:LPDPAE\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2361:LPDPAE]2.0.CO;2).
- Paul, E.A., 2016. The nature and dynamics of soil organic matter: plant inputs, microbial transformations, and organic matter stabilization. *Soil Biol. Biochem.* 98, 109–126. <https://doi.org/10.1016/j.soilbio.2016.04.001>.
- Pepper, I.L., Brusseau, M.L., 2019. Physical-chemical characteristics of soils and the subsurface. In: Brusseau, M.L., Pepper, I.L., Gerba, C.P. (Eds.), *Environmental and Pollution Science*, 3rd edition. Academic Press, pp. 9–22. <https://doi.org/10.1016/b978-0-12-814719-1.00002-1>.
- Perring, M.P., Hedin, L.O., Levin, S.A., McGroddy, M., de Mazancourt, C., 2008. Increased plant growth from nitrogen addition should conserve phosphorus in terrestrial ecosystems. *Proc. Natl. Acad. Sci. U. S. A.* 105, 1971–1976. <https://doi.org/10.1073/pnas.0711618105>.
- Pregitzer, K.S., Euskirchen, E.S., 2004. Carbon cycling and storage in world forests: biome patterns related to forest age. *Glob. Chang. Biol.* 10, 2052–2077. <https://doi.org/10.1111/j.1365-2486.2004.00866.x>.
- Pregitzer, K.S., Burton, A.J., Zak, D.R., Talhelm, A.F., 2008. Simulated chronic nitrogen deposition increases carbon storage in Northern Temperate forests. *Glob. Chang. Biol.* 14, 142–153. <https://doi.org/10.1111/j.1365-2486.2007.01465.x>.
- R Core Team, 2021. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Ramírez, L.A., Rada, F., Llambí, L.D., 2015. Linking patterns and processes through ecosystem engineering: effects of shrubs on microhabitat and water status of associated plants in the high tropical Andes. *Plant Ecol.* 216, 213–225. <https://doi.org/10.1007/s11258-014-0429-5>.
- Rasse, D.P., Rumpel, C., Dignac, M.F., 2005. Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. *Plant Soil* 269, 341–356. <https://doi.org/10.1007/s11104-004-0907-y>.
- Remy, E., Wuyts, K., Boeckx, P., Ginzburg, S., Gundersen, P., Demeijer, A., van den Bulcke, J., van Acker, J., Verheyen, K., 2016. Strong gradients in nitrogen and carbon stocks at temperate forest edges. *For. Ecol. Manag.* 376, 45–58. <https://doi.org/10.1016/j.foreco.2016.05.040>.
- Salisbury, E.J., 1920. The significance of the calcicolous habitat. *J. Ecol.* 8, 202–215. <https://doi.org/10.1093/ajph/10.2307/2255613>.
- Sattari, S.Z., Bouwman, A.F., Giller, K.E., van Ittersum, M.K., 2012. Residual soil phosphorus as the missing piece in the global phosphorus crisis puzzle. *Proc. Natl. Acad. Sci. U. S. A.* 109, 6348–6353. <https://doi.org/10.1073/pnas.1113675109>.
- Schedlbauer, J.L., Miller, J., 2022. Edge effects increase soil respiration without altering soil carbon stocks in temperate broadleaf forests. *Ecosphere* 13 (6), 1–12. <https://doi.org/10.1002/ecs2.4092>.
- Simpson, D., Benedictow, A., Berge, H., Bergström, J.E., Emberson, L.D., Fagerli, H., Flechard, C.R., Hayman, G.D., Gauss, M., Jonson, J.E., Jenkin, M.E., Nyíri, A., Richter, C., Semeena, V.S., Tsyro, S., Tuovinen, J.P., Valdebenito, A., Wind, P., 2012. The EMEP MSC-W chemical transport model – technical description. *Atmos. Chem. Phys.* 12, 7825–7865. <https://doi.org/10.5194/acp-12-7825-2012>.
- Singh, J., Ashfaq, M., Skinner, C.B., Anderson, W.B., Mishra, V., Singh, D., 2022. Enhanced risk of concurrent regional droughts with increased ENSO variability and warming. *Nat. Clim. Chang.* 12, 163–170. <https://doi.org/10.1038/s41558-021-01276-3>.
- Stevenson, F.J., Cole, M.A., 1999. *Cycles of Soils: Carbon, Nitrogen, Phosphorus, Sulfur, Micronutrients, second ed.* John Wiley & Sons.
- Tian, Q.Y., Liu, N.N., Bai, W.M., Li, L.H., Zhang, W.H., 2015. Disruption of metal ion homeostasis in soils is associated with nitrogen deposition-induced species loss in an Inner Mongolia steppe. *Biogeosciences* 12 (11), 3499–3512. <https://doi.org/10.5194/bg-12-3499-2015>.
- Ulrich, B., 1991. *An ecosystem approach to soil acidification*. In: Ulrich, B., Sumner, M.E. (Eds.), *Soil Acidity*. Springer Verlag, New York, pp. 28–79.
- Valdés, A., Lenoir, J., Gallet-Moron, E., Andrieu, E., Brunet, J., Chabrierie, O., Closset-Kopp, D., Cousins, S.A.O., Deconchat, M., de Frenne, P., de Smedt, P., Diekmann, M., Hansen, K., Hermy, M., Kolb, A., Liira, J., Lindgren, J., Naaf, T., Paal, T., Prokofieva, I., Scherer-Lorenzen, M., Wulf, M., Verheyen, K., Decocq, G., 2015. The contribution of patch-scale conditions is greater than that of macroclimate in explaining local plant diversity in fragmented forests across Europe. *Glob. Ecol. Biogeogr.* 24, 1094–1105. <https://doi.org/10.1111/gcb.12345>.
- Valdés, A., Lenoir, J., De Frenne, P., Andrieu, E., Brunet, J., Chabrierie, O., Cousins, S.A.O., Deconchat, M., De Smedt, P., Diekmann, M., Ehrmann, S., Gallet-Moron, E., Gärtner, S., Giffard, B., Hansen, K., Hermy, M., Kolb, A., Le Roux, V., Liira, J., Lindgren, J., Martin, L., Naaf, T., Paal, T., Proesmans, W., Scherer-Lorenzen, M., Wulf, M., Verheyen, K., Decocq, G., 2020. High ecosystem service delivery potential of small woodlands in agricultural landscapes. *J. Appl. Ecol.* 57, 4–16. <https://doi.org/10.1111/1365-2664.13537>.
- Vellend, M., Baeten, L., Myers-Smith, I.H., Elmendorf, S.C., Beauséjour, R., Brown, C.D., de Frenne, P., Verheyen, K., Wipf, S., 2013. Global meta-analysis reveals no net change in local-scale plant biodiversity over time. *Proc. Natl. Acad. Sci. U. S. A.* 110, 19456–19459. <https://doi.org/10.1073/pnas.1312779110>.
- Verheyen, K., Bossuyt, B., Hermy, M., Tack, G., 1999. The land use history (1278–1990) of a mixed hardwood forest in western Belgium and its relationship with chemical

- soil characteristics. *J. Biogeogr.* 26, 1115–1128. <https://doi.org/10.1046/j.1365-2699.1999.00340.x>.
- Vesterdal, L., Raulund-Rasmussen, K., 1998. Forest floor chemistry under seven tree species along a soil fertility gradient. *Can. J. For. Res.* 28, 1636–1647. <https://doi.org/10.1139/x98-140>.
- Vitousek, P.M., Farrington, H., 1997. Nutrient limitation and soil development: experimental test of a biogeochemical theory. *Biogeochemistry*. 37, 63–75. <https://doi.org/10.1023/A:1005757218475>.
- Vojta, J., 2007. Relative importance of historical and natural factors influencing vegetation of secondary forests in abandoned villages. *Preslia*. 79, 223–244.
- Von Oheimb, G., Härdtle, W., Naumann, P.S., Westphal, C., Assmann, T., Meyer, H., 2008. Long-term effects of historical heathland farming on soil properties of forest ecosystems. *Forest Ecol. Manag.* 255 (5–6), 1984–1993. <https://doi.org/10.1016/j.foreco.2007.12.021>.
- 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).
- Wall, A., Hytönen, J., 2005. Soil fertility of afforested arable land compared to continuously forested sites. *Plant Soil* 275, 247–260. <https://doi.org/10.1007/s11104-005-1869-4>.
- Wallenstein, M., Allison, S.D., Ernakovich, J., Steinweg, J.M., Sinsabaugh, R., 2011. Controls on the temperature sensitivity of soil enzymes: a key driver of in situ enzyme activity rates. *Soil Biol.* 245–258. https://doi.org/10.1007/978-3-642-14225-3_13.
- Wellock, M.L., LaPerle, C.M., Kiely, G., 2011. What is the impact of afforestation on the carbon stocks of Irish mineral soils? *For. Ecol. Manag.* 262, 1589–1596. <https://doi.org/10.1016/j.foreco.2011.07.007>.
- Wetzel, R.G., Likens, G.E., 1991. The inorganic carbon complex: alkalinity, acidity, CO₂, pH, total inorganic carbon, hardness. In: *Limnological Analyses*. Springer, New York, NY. https://doi.org/10.1007/978-1-4757-4098-1_8.
- Wieder, W.R., Cleveland, C.C., Smith, W.K., Todd-Brown, K., 2015. Future productivity and carbon storage limited by terrestrial nutrient availability. *Nat. Geosci.* 8, 441–444. <https://doi.org/10.1038/NGEO2413>.
- Wilson, B.R., Moffat, A.J., Nortcliff, S., 1997. The nature of three ancient woodland soils in southern England. *J. Biogeogr.* 24, 633–646. <https://doi.org/10.1111/j.1365-2699.1997.tb00074.x>.
- Wulf, M., 2022. Legacies of human land use impacts in central European forests. In: Lüttge, U., Cánovas, F.M., Risueño, M.C., Leuschner, C., Pretzsch, H. (Eds.), *Progress in Botany*, vol. 83. Springer, Cham. https://doi.org/10.1007/124_2021_56.
- Wuyts, K., De Schrijver, A., Staelens, J., Gielis, L., Vandenbruwane, J., Verheyen, K., 2008. Comparison of forest edge effects on throughfall deposition in different forest types. *Environ. Pollut.* 156, 854–861. <https://doi.org/10.1016/j.envpol.2008.05.018>.
- Yang, J., Blondeel, H., Meeussen, C., Govaert, S., Vangansbeke, P., Boeckx, P., Lenoir, J., Orzechowska, A., Ponette, Q., Hedwall, P.O., Iacopetti, G., Brunet, J., de Frenne, P., Verheyen, K., 2022. Forest density and edge effects on soil microbial communities in deciduous forests across Europe. *Appl. Soil Ecol.* 179, 104586. <https://doi.org/10.1016/j.apsoil.2022.104586>.
- Zhang, G.N., Chen, Z.H., Zhang, A.M., Chen, L.J., Wu, Z.J., 2014. Influence of climate warming and nitrogen deposition on soil phosphorus composition and phosphorus availability in a temperate grassland, China. *J. Arid Land.* 6, 156–163. <https://doi.org/10.1007/s40333-013-0241-4>.
- Ziter, C., Bennett, E.M., Gonzalez, A., 2013. Functional diversity and management mediate aboveground carbon stocks in small forest fragments. *Ecosphere*. 4, 85. <https://doi.org/10.1890/ES13-00135.1>.