Litter quality, land-use history, and nitrogen deposition effects on topsoil conditions across European temperate deciduous forests

Running head: Driving variables of forest soils

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Abstract

Topsoil conditions in temperate forests are influenced by several soil-forming factors, such as canopy composition (e.g. through litter quality), land-use history, atmospheric deposition, and the parent material. Many studies have evaluated the effects of single factors on physicochemical topsoil conditions, but few have assessed the simultaneous effects of multiple drivers. Here, we evaluate the combined effects of litter quality, land-use history (past land cover as well as past forest management), and atmospheric deposition on several physicochemical topsoil conditions of European temperate deciduous forest soils: bulk density, proportion of exchangeable base cations, carbon/nitrogen ratio (C/N), litter mass, bio-available and total phosphorus, pH_{KCl} and soil organic matter. We collected mineral soil and litter layer samples, and measured site characteristics for 190 20x20 m European mixed forest plots across gradients of litter quality (derived from the canopy species composition) and atmospheric deposition, and for different categories of past land cover and past forest management. We accounted for the effects of parent material on topsoil conditions by clustering our plots into three soil type groups based on texture and carbonate concentration. We found that litter quality was a stronger driver of topsoil conditions compared to land-use history or atmospheric deposition, while the soil type also affected several topsoil conditions here. Plots with higher litter quality had soils with a higher proportion of exchangeable base cations, and total phosphorus, and lower C/N-ratios and litter mass. Furthermore, the observed litter quality effects on the topsoil were independent from the regional nitrogen deposition or the soil type, although the soil type likely (co)-determined canopy composition and thus litter quality to some extent in the investigated plots. Litter quality effects on topsoil phosphorus concentrations did interact with past land cover, highlighting the need to consider land-use history when evaluating canopy effects on soil conditions. We conclude that forest managers can use the canopy composition as an important tool for influencing topsoil conditions, although soil type remains an important factor to consider.

Highlights

- Litter quality strongly drives topsoil conditions in temperate deciduous European forests
- Litter quality was more important than land-use history or N deposition
- Litter quality effects were independent of regional N deposition or soil type
- Litter quality effects on topsoil P concentration depended on previous land cover

- Forest managers could influence topsoil conditions through the canopy composition

1. Introduction

Forest soils play a key role in global biogeochemical cycles, are important indicators of forest ecosystem health and productivity, and essential for maintenance of global biodiversity (Lukac and Godbold, 2011; Schoenholtz et al., 2000; Smith et al., 2015; Weil and Brady, 2016). Jenny (1941) proposed that soils develop through the interplay of five "soil-forming factors": three passive factors *time*, *parent material*, and *topography*, and two active factors *climate* (i.e. temperature and moisture), and *organisms* (i.e. microbes, vegetation, animals, man [sic]). The combined impact of these different factors determine the physical (e.g. bulk density) and chemical (e.g. pH) variables that characterize each forest soil (Jenny, 1941; Schoenholtz et al., 2000; Weil and Brady, 2016).

The relative importance of the different soil-forming factors remains debated (Cools et al., 2014; Cornwell et al., 2008). At the same time, some of the active factors are changing because of anthropogenic activities. Namely, European forests and thus their soils are not only undergoing *climatic* changes (Lindner et al., 2014), they have often undergone severe land-use changes, i.e. both in land cover (e.g. forests on previous agricultural land) and in forest management system or intensity (e.g. abandonment of coppice management) (i.e. *man* sensu Jenny (1941)) (Dupouey et al., 2002; Foster et al., 2003; Gimmi et al., 2013; Glatzel, 1999; McGrath et al., 2015). As part of these land-use changes, canopy composition (i.e. *vegetation*) in European forests has often changed markedly (Leuschner and Ellenberg, 2017; McGrath et al., 2015). For instance, a substantial share of the natural deciduous vegetation was replaced by coniferous tree species in the past centuries in Central Europe (McGrath et al., 2015). Finally, European forest soils have faced increased levels of atmospheric nitrogen and sulphur *deposition* during the 20^{th} century (Laubhann et al., 2009), which we consider here as an additional (active) soil-forming factor not yet considered by Jenny (1941).

These changes in climate, deposition, land use, and canopy composition can alter soil formation processes and thus the physicochemical soil conditions (Dupouey et al., 2002; Fraterrigo et al., 2005; Glatzel, 1991; Prévosto et al., 2004). Most of these factors are thought to affect mainly the uppermost part of soils (ca. 0-20 cm deep), further referred to as the "topsoil" here. Several studies have already investigated how these factors are individually affecting topsoil conditions in Europe. For instance, many studies attributed soil eutrophication and acidification effects to increased nitrogen and sulphur deposition across Europe (Hédl et al., 2011; Jandl et al., 2012). Other studies demonstrated that forest soils on previous agricultural land typically have a higher bulk density, pH, phosphorus levels and exchangeable base cations, and lower carbon stocks and C/N-ratios than ancient forest soils (Blondeel et al., 2018; Compton and Boone, 2000; Falkengren-Grerup et al., 2006; Holmes and Matlack, 2018; McLauchlan, 2006; Prévosto et al., 2004; Verheyen et al., 1999). Effects of (past) forest management on topsoil conditions might be more subtle and are less understood, with differing results across studies (Fraterrigo et al., 2005; Hölscher et al., 2001; Ringeval et al., 2017; Šrámek et al., 2015; Thiffault et al., 2011). Particularly interesting and still debated remains the question of how historically important management practices such as coppicing may have altered nutrient cycling and soil conditions (Buckley, 1992; Hédl and Rejšek, 2007; Hölscher et al., 2001; Šrámek et al., 2015). Finally, canopy composition, through its effects on light transmittance, the water balance, and nutrient availability through the leaf litter, can strongly affect soil conditions (Cools et al., 2014; Prescott and Vesterdal, 2013; Van Nevel et al., 2014; Vesterdal et al., 2008; Vesterdal and Raulund-Rasmussen, 1998). It can influence nutrient cycling and thus soil conditions directly through for example the variation in chemical composition of the litter (Bauters et al., 2017; Kooch, Samadzadeh, & Hosseini, 2017) or indirectly through for example effects on the size and composition of soil macro- and micro-fauna communities (e.g. earthworms: De Wandeler et al., 2018; Schelfhout et al., 2017).

These different factors alter soil conditions simultaneously, leading to the potential for interactive effects. For instance, Hédl et al. (2011) found that acidification effects attributed to atmospheric deposition varied depending on the canopy composition and altitude in a Czech mountain forest. Furthermore, some of these soil-forming factors are not independent from each other, hampering a correct assessment of their relative importance without potential confounding effects (Jenny, 1941). For instance, canopy composition does not unidirectionally affect topsoil conditions through litter quality or soil community effects, but is in itself determined by an interplay of other factors such as the parent material or climate (i.e. autecology of tree species), or man (i.e. forest managers can favor or disfavor certain species) (Dijkstra et al., 2003; Finzi et al., 1998; McGrath et al., 2015; van Breemen et al., 1997). Also, land-use legacies can not only affect soil conditions directly through e.g. ploughing/fertilization during agricultural use (Brasseur et al., 2018; McLauchlan, 2006), but indirect effects can occur through influencing climate (Lejeune et al., 2018; Pielke et al., 2002) or atmospheric deposition levels which in turn affect soil conditions (Foster et al., 2003).

If we want to be able to advise forest managers or policy makers correctly regarding how to maintain healthy and productive forests under global environmental change, and/or to achieve a desired state of soil fertility, we need to improve our understanding of the relative importance of these different factors on forest soils. Some studies have already taken into account multiple drivers to evaluate the combined effects of these factors on topsoil conditions (Augusto et al., 2002; Cools et al., 2014; Cornwell et al., 2008; De Schrijver et al., 2012; Thiffault et al., 2011). However, only a few of these studies covered large geographical areas, e.g. (sub)continental, and at the same time many of them comprise mostly experimental or meta-analysis studies and hence do not directly, and comparatively, measure *in situ* soil conditions.

In this study, we aim to address this knowledge gap by evaluating, *in situ*, the relative importance of atmospheric deposition, past land cover, (past) forest management, and canopy composition on fundamental physicochemical topsoil properties in temperate deciduous forests across Europe. The investigated topsoil properties reflect resources and conditions that determine plant growth (e.g. Olsen phosphorus) and nutrient cycling processes (e.g. C/N-ratio). To achieve our aim, we took topsoil samples in 190 forest plots across gradients of litter quality and nitrogen deposition, and for different categories of land-use history, i.e. both past land cover and past forest management such that we maximized differences in deposition between regions, while maximizing differences in land-use history within regions. Sampling 'across' these different gradients allows to evaluate the relative importance of, and several interactions, among these different factors through an orthogonal design (Verheyen et al., 2017).

Specifically, we wanted to assess here the effects and relative importance of different active (or dynamic) soil-forming factors that are important within temperate European forest soils. We chose to investigate deposition, land-use history, and litter quality because these factors are related to human activities and might thus be influenced by humans in the future. In particular, litter quality is determined by the occurring tree and shrub species (Kooch et al., 2017). For example, canopy composition can be an active choice of forest managers, and thus could be used to mitigate undesired changes in soil conditions caused by broad-scale environmental changes. We also tested the potential interaction between litter quality and soil type since previous studies have shown that the soils' parent material must be considered in determining tree species effects on topsoil conditions (Dijkstra et al., 2003). Overall, our study aims to further understanding of which active factors drive topsoil conditions in temperate deciduous forests, and better inform forest managers or policy makers on how tree species choice might affect these conditions in changing environments.

2. *Material and methods*

2.1. *Study regions*

We selected 19 regions along a spatial environmental gradient of atmospheric deposition and climatic conditions (temperature, precipitation) within the European temperate forest biome (**Fig. 1, Table 1**). This selection maximized differences in deposition, while including temperature and precipitation gradients in our procedure minimized potential biases between deposition and climate (e.g. all higher deposition regions being warmer). Mean annual temperature (MAT), total annual precipitation (TAP), and nitrogen deposition (Ndep) at the study regions ranged from 6.1 to 11.9 °C, from 526 to 1586 mm yr^{-1}, and from 7 to 30 kg ha^{-1} yr^{-1} respectively (**Fig. 1, Table 1 –** long-term average values from 1980-2015 for MAT and TAP, values for the year 2000 for Ndep). We tried to maximize differences in land-use history between plots (i.e. within regions, **Table A1**) by sampling in ancient vs. recent forest plots (i.e. past land cover), and in plots with different management histories (i.e. past forest management). We classified ancient forest (AF) plots here as plots that have been continuously forested since at least 1850, whereas recent forest (RF) plots have been (re)forested after 1850. We tried to minimize differences in parent material and topography (relief, elevation) between plots and regions. However, because the plots were selected as part of a vegetation resurvey project (ERC-project PASTFORWARD, http://www.pastforward.ugent.be/), ultimately there was quite some variation in parent material, hereafter referred to as "soil type". Furthermore, the presence of a prior understorey vegetation survey, and the availability of information on land-use history for the study regions were two additional important criteria to take into account during site selection, so that ultimately our selected regions were a trade-off between data availability and environmental gradient coverage. All forest regions comprised closed-canopy forests with a variable tree and shrub layer composition, but we focused on plots predominantly composed of broadleaved species that were representative for European deciduous forests encompassed by the investigated environmental gradients (San-Miguel-Ayanz et al., 2016). The canopies predominantly consisted of *Fagus sylvatica* (present in 65 of the 192 plots with mean tree layer cover of 58%), *Fraxinus excelsior* (64/192 plots, mean cover 22%), *Quercus robur* (60/192 plots, mean cover 35%), *Carpinus betulus* (52/192 plots, mean cover 40%), *Quercus petraea* (41/192 plots, mean cover 40%), and *Acer pseudoplatanus* (35/192 plots, mean cover 26%). Presence of coniferous species was kept at a minimum, but a higher prevalence in the easternmost regions with a more boreal climate (Białowieża (BI), Moricsala (MO) - see **Fig. 2**) was unavoidable.

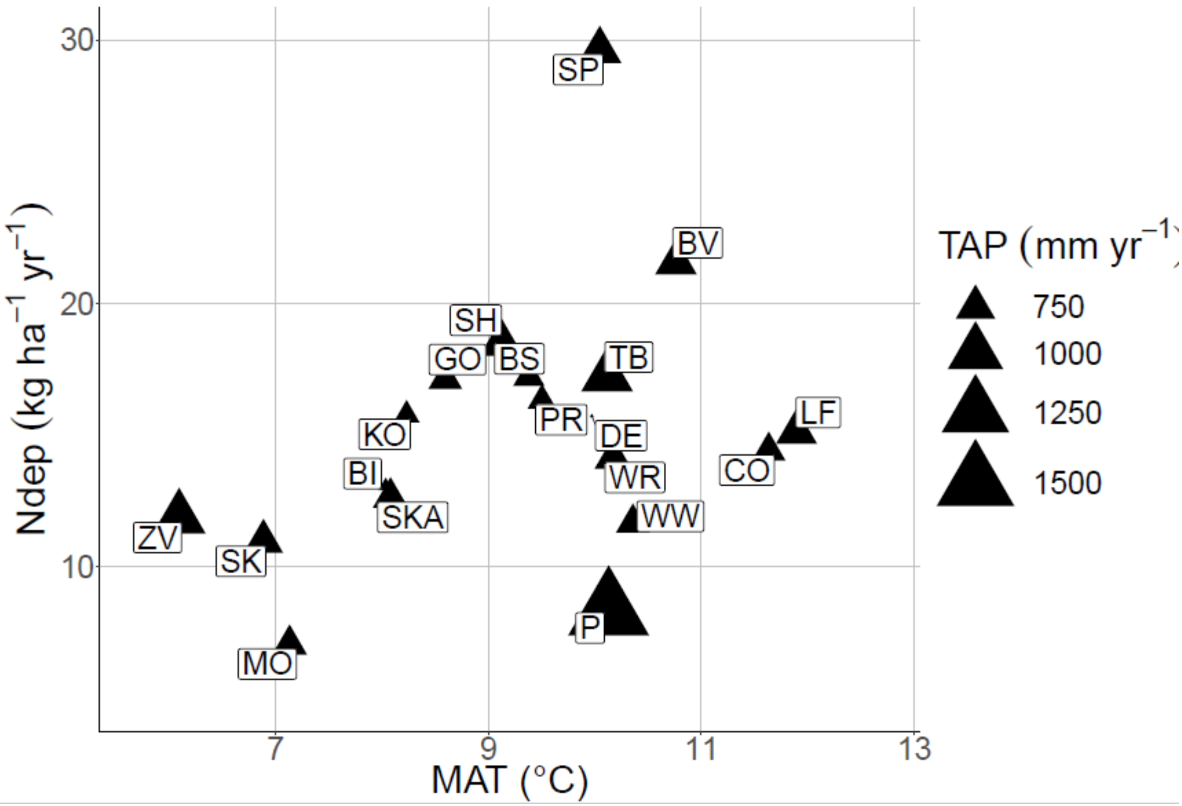


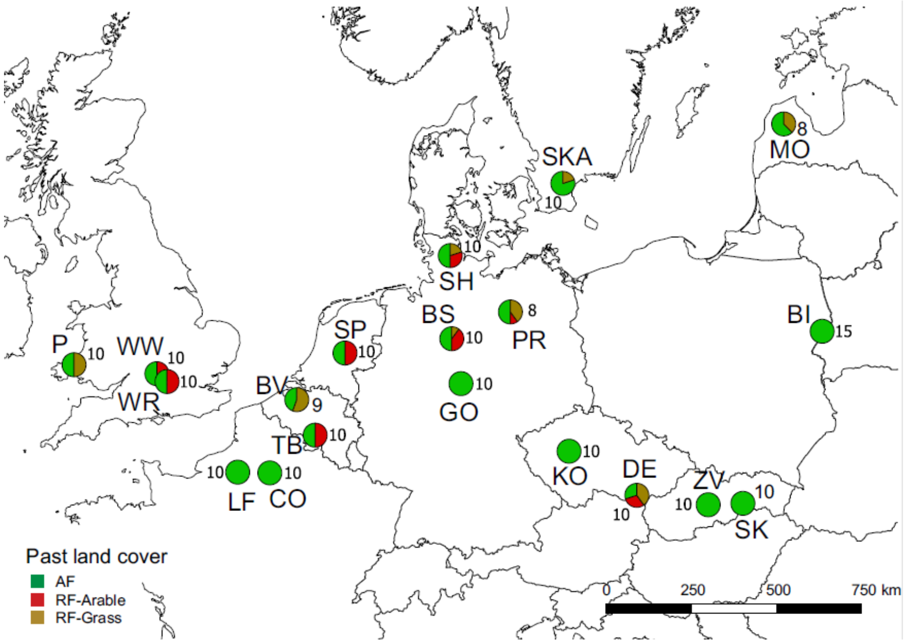
Figure 1. Environmental gradients covered by the 19 forest regions where plots were sampled: mean annual temperature (MAT – °C) and nitrogen deposition (Ndep – kg ha^{-1} yr^{-1}) are plotted, with the symbol size reflecting the total annual precipitation (TAP – mm yr^{-1}) in that region. Values from the year 2000 were used for Ndep, and average values for 1980-2015 were used for MAT and TAP. Region codes: see **Table 1**.

Table 1. Location and characteristics of the 19 forest regions where plots were visited in November 2014 and Spring 2015 and 2016. For each region, the following characteristics are shown: month and year of sampling (*Month-Year*), number of plots visited (*No plots*), mean coordinates in decimal degrees (*Mean coord* - DD), elevation in meters above sea level (*Elevation* - masl), litter quality score (*LQ*), soil types (*Soil Type:* 1=*Clay Carbonate*, 2=*Clay No Carbonate*, 3=*Sand*), number of ancient (*AF*) vs. recent forest (RF) plots with an arable (*RF-Arable*) or grassland/heathland (*RF-Grass)* past land use, number of non-coppiced (0) vs. coppiced (1) plots between 1850-2015, mean annual temperature (*MAT* - °C), total annual precipitation (*TAP* - mm yr^{-1}), and nitrogen deposition (*Ndep* - kg ha^{-1} yr^{-1}). Either a minimum-maximum range of values (e.g. Elevation), or one value (e.g. MAT) is presented. Values from the year 2000 were used for Ndep, and average values for 1980-2015 were used for MAT and TAP. Note that coppiced plots were only found in ancient forest, and none of the plots is currently undergoing coppice management.

Region ID	Region, country code	Month-Year	No plots	Mean coord (DD)	Elevation (m.a.s.l.)	LQ	Soil Type*	Past land cover (AF – RF_Grass – RF_Arable)	CoppHist (0 – 1)	MAT (°C)	TAP (mm yr^{-1})	Ndep (kg ha^{-1} yr^{-1})
BI	**Białowieża, PL**	06-2016	15	52.71 °N – 23.77 °E	160 – 176	1.3 – 3.5	3	15 – 0 – 0	15 – 0	8.0	546	13.1
BS	**Braunschweig, GE**	06-2015	10	52.45 °N – 10.14 °E	55 – 80	1.0 – 2.7	3	5 – 1 – 4	0 – 5	9.4	661	17.2
BV	**Binnen-Vlaanderen, BE**	05-2015	9	51.11 °N – 3.45 °E	1 – 17	2.3 – 4.1	1, 3	4 – 5 – 0	2 – 2	10.8	780	21.6
CO	**Compiègne, FR**	05-2016	10	49.39 °N – 2.91 °E	56 – 110	1.0 – 2.1	3	10 – 0 – 0	10 – 0	11.6	682	14.4
DE	**Děvín Wood, CZ**	06-2015	10	48.86 °N – 16.65 °E	327 – 439	1.5 – 5.0	1, 2	3 – 4 – 3	0 – 3	10.0	526	15.7
GO	**Göttingen, GE**	06-2015	10	51.55 °N – 10.04 °E	197 – 436	1.0 – 3.2	1, 2	10 – 0 – 0	0 – 10	8.6	684	17.1
KO	**Koda Wood, CZ**	06-2015	10	49.93 °N – 14.11 °E	335 – 385	1.5 – 3.0	1, 2	10 – 0 – 0	3 – 7	8.2	613	15.8
LF	**Lyons-la-Forêt, FR**	05-2015	10	49.44 °N – 1.48 °E	130 – 224	1.0 – 1.4	2, 3	10 – 0 – 0	10 – 0	11.9	769	15.1
MO	**Moricsala, LTV**	06-2016	8	57.19 °N – 22.15 °E	22 – 28	1.5 – 2.8	2, 3	5 – 3 – 0	5 – 0	7.1	695	7.1
P	**Pembrokeshire, UK**	05-2016	10	51.97 °N to -4.77 °E	7 – 273	1.3 – 4.2	2	5 – 5 – 0	0 – 5	10.1	1586	8.3
PR	**Prignitz, GE**	06-2015	8	53.24 °N – 11.96 °E	33 – 90	0.9 – 4.9	3	5 – 2 – 1	5 – 0	9.5	634	16.3
SH	**Schleswig-Holstein, GE**	06-2016	10	54.43 °N – 9.83 °E	13 – 80	1.0 – 2.4	3	5 – 2 – 3	5 – 0	9.1	805	18.5
SK	**Slovak Karst, SLK**	06-2015	10	48.61 °N – 20.57 °E	542 – 663	1.5 – 2.8	2	10 – 0 – 0	0 – 10	6.9	748	12.6
SKA	**Skåne, SW**	11-2014	10	55.81 °N – 13.58 °E	41 – 111	1.0 – 3.2	2, 3	8 – 2 – 0	8 – 0	8.1	704	11.0
SP	**Speulderbos, NL**	05-2016	10	52.26 °N – 5.68 °E	50 – 66	1.0 – 1.4	3	5 – 0 – 5	2 – 3	10.0	799	29.6
TB	**Tournibus, BE**	05-2015	10	50.32 °N – 4.58 °E	244 – 260	1.3 – 3.6	2	5 – 0 – 5	0 – 5	10.1	932	17.2
WR	**Warburg Reserve, UK**	05-2015	10	51.59 °N to -0.97 °E	147	1.7 – 4.9	1, 2	5 – 0 – 5	0 – 5	10.2	721	14.1
WW	**Wytham Woods, UK**	05-2015	10	51.77 °N to -1.34 °E	70 – 111	2.5 – 4.9	2, 3	5 – 0 – 5	0 – 5	10.4	684	11.7
ZV	**Zvolen, SLK**	05-2015	10	48.63 °N – 19.32 °E	476 – 587	1.3 – 1.9	2	10 – 0 – 0	2 – 8	6.1	957	11.9
All Regions		11-2014 – 06-2016	190	48.61 – 57.19 °N -4.77 – 23.77°E	1 – 663	0.89 – 5.0	1/2/3	135 – 24 – 31	67 – 68	6.1 – 11.9	526 – 1586	7.1 – 29.6

*1 = Clay Carbonate, 2 = Clay No Carbonate, 3 = Sand

a)



b)

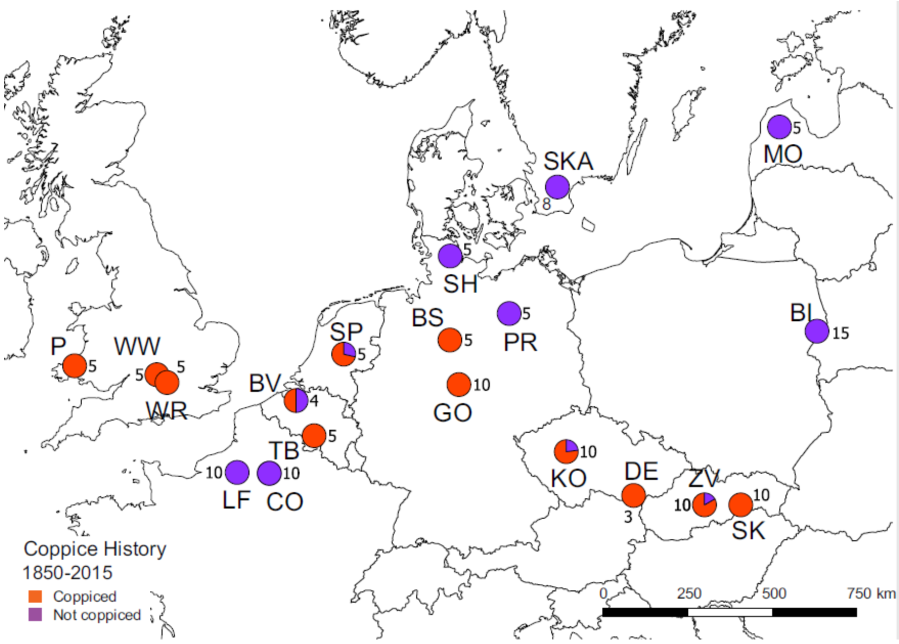


Figure 2. Distribution of the plots used for the analysis of past land cover (**a**), and for the analysis of coppice history (**b,** only ancient plots). Each pie chart visualizes **a)** the proportion of ancient forest (AF: green) vs. recent forest plots with past arable land use (RF-Arable: red) vs. recent plots with past heathland/grassland as past land use (RF-Grass: brown) per region, or **b)** the formerly coppiced (orange) vs. non-coppiced (purple) forest plots. The Region code and total number of plots used per region is indicated next to the pie charts. Region codes: see **Table 1**.

2.2. Data collection

In each region, we selected ten 400 m² forest plots (except for 8 plots in Moricsala, 9 plots in Binnen-Vlaanderen, and 15 plots in Białowieża. Each 400 m² plot contained a nested 100 m² plot. In this smaller plot, we sampled the mineral topsoil (0-20 cm) and organic forest floor layer. In the larger plot, we measured the diameter-at-breast-height (DBH) and recorded the individuals of all tree and shrub species within the plot with DBH > 7.5 cm.

Mineral soil samples for chemical analyses were collected at two intervals (0-10, and 10-20 cm depth) as mixed-soil samples from five locations in each smaller plot (four corners + center) after removing the organic litter (OL), fragmentation (OF), and humus (OH) layers. We also collected a soil sample of the 0-10 cm interval with Kopecky rings at the center of each plot to determine the whole-soil bulk density. To characterize the forest floor, we sampled the organic layer (OL+OF+OH) with a 20 x 20 cm wooden frame at two locations along a plot diagonal. After drying the samples for 24 hours at 65 °C, we recorded the dry weight of the organic layer as the litter mass (g).

2.3. Soil analysis

The mineral topsoil samples (0-10, 10-20 cm) were sieved with a 2 mm sieve and dried at 40 °C for 24 hours before analyzing i) the 0-10 cm samples for pH_{KCl}, proportion of exchangeable base cations (*EBC*), total and Olsen phosphorus concentration (*TotP*, *OlsenP* – mg/kg), organic and inorganic carbon and total nitrogen concentration (*C, N* – %), and soil organic matter (*SOM* – %), and ii) the 10-20 cm samples for soil texture (*% Clay, % Silt, % Sand*).
Samples were analysed for pH_{KCl} by shaking a 1:5 ratio soil/KCl (1M) mixture for 5 min at 300 rpm and measuring with a pH meter Orion 920A with pH electrode model Ross sure-flow 8172 BNWP, Thermo Scientific Orion, USA. Extraction of exchangeable K^+, Ca^{2+}, Mg^{2+}, Na^+ and Al^{3+} concentrations were measured by atomic absorption spectrophotometry (AA240FS, Fast Sequential AAS) after extraction in 0.1 M $BaCl_2$ (NEN 5738:1996). The proportion of exchangeable base cations was calculated by converting the values from mg/kg to meq/kg so that charge of the cations is included, and then taking the ratio of the sum of K^+, Ca^{2+}, Mg^{2+} and Na^+ over the sum of K^+, Ca^{2+}, Mg^{2+}, Na^+ and Al^{3+} (Cools and De Vos, 2010). All P-concentrations were measured colorimetrically according to the malachite green procedure (Lajtha et al., 1999). Total P was extracted after complete destruction of the soil samples with HClO4 (65%), HNO3 (70%) and H2SO4 (98%) in teflon bombs for 4 h at 150°C. Bioavailable or Olsen P, which is available for plants within one growing season (Gilbert et al., 2009), was extracted in NaHCO3 (POlsen; according to ISO 195 11263:1994(E)). Total C (%) and N (%)

concentration was quantified by combusting samples at 1200°C which releases all C and N and then measuring the combustion gases for thermal conductivity in a CNS elemental analyser (vario Macro Cube, Elementar, Germany). Next, 1 g of dry soil was ashed for 4 hours at 450°C by gradually increasing temperature, which removes the organic C and leaves only inorganic (mineral) C in the ashes (i.e. dry ashing procedure – cfr. Wäldchen, Schulze, Schöning, Schrumpf, & Sierra, 2013). Inorganic C concentration (%) was then measured using the CNS elemental analyser as above for total C and N, and organic C (%) was calculated by subtracting inorganic C from total C (cfr. Wäldchen et al., 2013). This organic C metric was used to calculate the C:N ratio by taking the ratio of organic C to total N (Cools and De Vos, 2010). Also from the dry ashing procedure, the mass of organic matter (Mo) was calculated as the difference between the dry soil mass (Md) and the ashed soil mass (Ma), which gives us soil organic matter (SOM) as (Mo/Md)*100 (Cools and De Vos, 2010).

Soil texture (*% Clay* or 0.4-6 µm, *% Silt* or 6-63 µm, and *% Sand* or 63 µm-2 mm) was analysed with laser diffraction (Coulter Laser LS 13 320 (SIP-050D2) with auto-sampler (Beckman Coulter, 2011)) after removal of organic material with H_2O_2 (28.5%) and dispersing the sample with Sodium polyphosphate (6%). Sample preparation followed standard ISO procedure 11277 (2002), and laser measurements ISO 13320 (2009). This method allows large numbers of samples to be measured in a feasible amount of time, but we should keep in mind that it may cause a measurement bias, such as an underestimation of the fine fractions compared with other methods e.g. standard pipette method (Buurman et al., 2001; Taubner et al., 2009).

The Kopecky samples were dried at 105 °C for 24h, after which we calculated the whole-soil bulk density (*BD* – g/cm³) as the weight of dry soil divided by the total soil volume of the Kopecky rings with a 5 cm radius and 10 cm height. We did not exclude >2 mm fractions (e.g. small stones), in order to collect samples that were representative for the specific soil and consistently collected across all our study sites. We should keep in mind that this "whole-earth bulk density" can deviate from the "fine-earth" bulk density (Baetens et al., 2009; Cools and De Vos, 2010; Vincent and Chadwick, 1994).

2.4. Litter quality

We calculated a plot-scale average litter quality score (LQ) as the weighted average (by basal area) of ordinal litter quality indices of individual canopy species (with DBH > 7.5 cm) present within the plot, originally determined by Hermy (1985) (original notation: "STR"). This index was calculated for important tree/shrub species across Flemish forests. The LQ score approximates the rate of leaf litter decomposition for different species (Hermy, 1985). We used the individual scores from studies that built further upon this original ordinal scoring, depending on the species occurrence within each of the literature sources (i.e. Baeten et al., 2009; Hermy, 1985; Van Calster et al., 2008; Verheyen et al., 2012 - details see **Table A3**). The LQ scores range between 1 (very low) and 5 (very high decomposition rate), and the median and mean plot LQ scores were 1.8 and 2.2. See **Figure 3** for a summary of the occurring tree/shrub genera with their LQ scores in the dataset. Note that we did not include tree species diversity as a predictor here, because our design did not allow to disentangle tree identity from diversity effects (e.g. *FunDivEurope* platform: Baeten et al. (2013), Dawud et al. (2017), Joly et al. (2017)), and we were not interested in the (direct) effects of tree species diversity on topsoil conditions, but on the effects that the canopy layer can have through the litter quality.

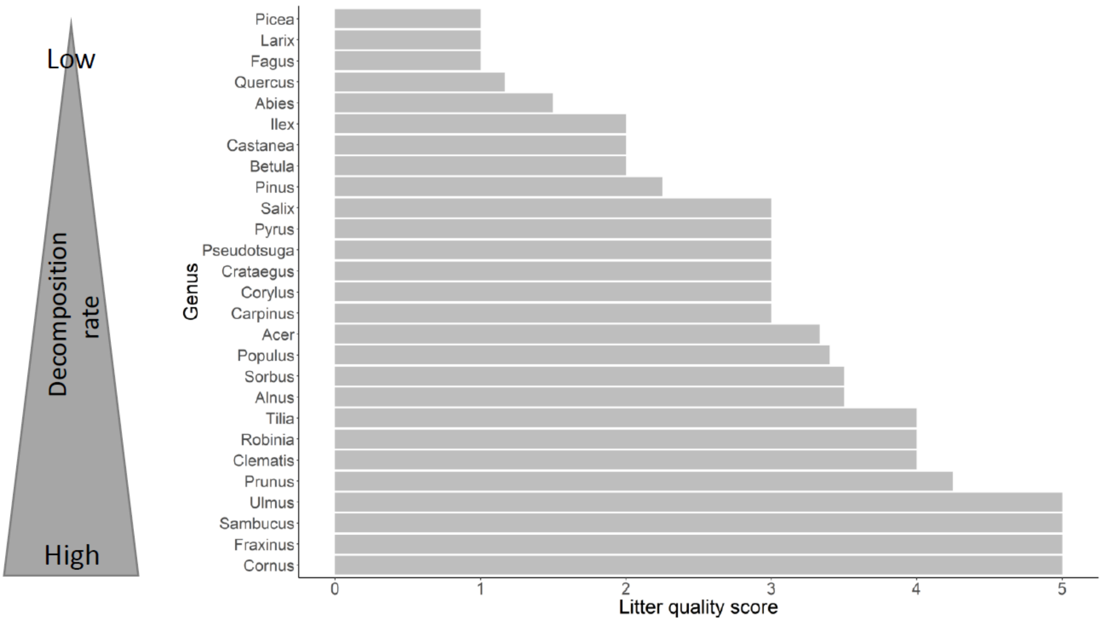


Figure 3. Litter quality scores (1-5) per tree/shrub genus that occurred within our plots, reflecting a gradient of low (lower LQ score) to high (higher LQ score) decomposition rate. If only one species of a genus occurred within the dataset, the value represents the LQ score for that species. See appendix **Table A3** for individual species names, scores and literature references, and **Table 1** for a summary of the plot average LQ scores per region.

2.5. Atmospheric deposition

We tried to disentangle potentially eutrophying from acidifying effects of increased deposition by including atmospheric nitrogen deposition (*Ndep*, kg ha^{-1} yr^{-1}) in the year 2000 as a measure of eutrophication (**Table 1**), and acidification rate in the year 2000 (*AcidRate*, keq/ha yr) as a measure of acidification (**Table A4**). Therefore, we extracted total nitrogen deposition (NH_3 +

NO_x) and sulphur deposition (SO_x) for the year 2000 based on interpolated model results from the European Monitoring and Evaluation Programme (version 2013, http://www.emep.int/) and calculated the acidification rate based on nitrogen and sulphur deposition as (cfr. Verheyen et al., 2012):

$$AcidRate = \frac{N_{dep}}{14} + 2 * \frac{S_{dep}}{32.06}$$

Because we define a region as a large-scale area with homogeneous macroclimatic conditions (i.e. climate and deposition), we extracted deposition and acidification values at the plot level, and used the mean of all plots for each region. The critical load of deposition in temperate forests above which nitrogen saturation generally occurs is thought to be 18 kg ha^{-1} yr^{-1} (Bobbink et al., 2017). We tried to encompass this ecological variation by sampling along a gradient of nitrogen deposition of 7 to 30 kg ha^{-1} yr^{-1}, including regions that are likely still limited by nitrogen (e.g. Pembrokeshire, UK: 8 kg ha^{-1} yr^{-1}), as well as regions (e.g. Speulderbos, NL: 30 kg ha^{-1} yr^{-1}) that are likely nitrogen-saturated (Aber, 1992; **Fig. 1, Table 1**). We used *Ndep* and *AcidRate* from the year 2000 as a proxy for cumulative amounts of deposition and acidification, which may influence topsoil conditions. Cumulative deposition values would have been based on backcasting from deposition patterns for the year 2000 (as in Duprè et al. 2010), and thus highly correlated with the 2000 values, leading to high similarity in model results (Henrys et al., 2011). To minimize the number of assumptions in our analysis, we used 2000 values rather than estimated cumulative deposition. Finally, it should be noted that deposition data provided by EMEP represents open-field deposition, whereas deposition on forests, above and below the canopy, can differ as a result of canopy exchange processes (Kahle et al., 2008; Lövblad et al., 1995). However, several studies comparing modelled deposition values of sulphur and nitrogen with observed values in European forests generally conclude that the EMEP model performs rather well in reproducing patterns of sulphur and nitrogen deposition across regions to European forests (Simpson et al., 2006; van Dobben and de Vries, 2017).

2.6. Land-use history reconstruction

We reconstructed the land-use history of each plot between 1850 and 2015 in a standardized way based on a combination of expert knowledge of our local contact person in each region, a thorough search of site-specific maps and literature (e.g. management plans), and oral interviews. We tried to maximize differences both in past land cover, as well as in past forest management within the regions. Because of other plot criteria that had to be fulfilled in the

PASTFORWARD project (e.g. presence of a prior vegetation survey), it was not always possible to find a perfectly even distribution of land-use categories within each region.

For the difference in past land cover, we distinguished between 'ancient forest (AF) plots' (sample size = 135), i.e. plots that have been continuously forested since at least 1850, vs. 'recent forest (RF) plots' (sample size = 57), i.e. plots that were (re)forested after *around* 1850 (i.e. majority reforested after 1850, with several 'recent forest plots' that were (re)forested between 1800-1850 – **Table A1**). For the recent forest plots, the previous land cover categories were heathland (3), grassland (23), and arable land (31). The recent forest plots transitioned into forest between 1810 and 1970 (heathland plots: 1810-1900; grassland plots: 1860-1912; arable plots: 1820-1970, **Table A1**). Assuming that the past land cover of the recent forest plots may have influenced current soil conditions differently, we distinguished between the 31 post-arable recent forest plots on the one hand, and the 23 post-grassland + 3 post-heathland plots on the other hand. We assumed that nutrient-enrichment practices such as fertilization and liming and soil disturbance practices in the form of soil tilling or ploughing likely took place in the post-arable plots, which may severely alter soil fertility and microbial communities (Buckley and Schmidt, 2001; Fichtner et al., 2014; Matson et al., 1997). We grouped the post-grassland and heathland plots, assuming that no such practices occurred in these plots during the grassland/heathland period. Rather, more nutrient-depleting management practices typically occur on pastured grassland (e.g. grazing) or on heathland sites (e.g. sod-cutting), such that physicochemical conditions in post grass- or heathland forest soils can be differently affected than in post-arable forest soils (e.g. Holmes & Matlack, 2017). Thus, for the analysis of past land cover, we ended up with three categories: ancient forest plots (AF), recent post-arable plots (RF-Arable), and recent post-grassland/heathland plots (RF-Grass) (**Fig. 2a**). In addition, the past forest management histories between 1850-2015 comprised three management types: Coppice or Coppice-With-Standards – C(WS), High Forest – HF, and Zero Management – ZM. We classified the plots as belonging to one of seven management histories: C(WS) throughout, HF throughout, ZM throughout, C(WS) to HF, C(WS) to ZM, HF to ZM, and C(WS) to HF to ZM (Details: **Table A1**) (see Perring et al., 2018). Because we hypothesize that coppicing in the past may have influenced current soil conditions, we also derived a categorical variable 'Coppice History' to characterize the management histories of our plots as either 0 or 1, i.e. respectively no coppicing vs. coppicing between 1850-2015 (**Fig. 2b, Table A1**). For the analysis of coppice history, we only included ancient forest plots since coppiced plots were only found in ancient forest. Note that none of the plots is currently undergoing coppice management, but coppiced plots were denoted as such if coppicing had occurred at some point in their recorded land-use history.

2.7. Data analysis

2.3.1. Cluster analysis

To take into account the potentially confounding effects of the parent material on topsoil conditions, we clustered our plots in three "soil type" groups based on soil texture *(% Clay*, *% Silt*, *% Sand*), and *carbonate* or *inorganic carbon concentration (%)* using the *hclust* function in R (*stats* package, ward.D method, Euclidian distances, R Core Team, 2017; **Fig. A1**). All cluster variables required a transformation to achieve normality of their distribution: *inorganic C* (log), *% Clay* (sqrt), *% Silt* (sqrt), *% Sand* (log). The three resulting clusters from this analysis were used as a categorical variable *Soil type* in the statistical analyses, referring to them as 'ClayCarbonate', 'ClayNoCarbonate', and 'Sand' soils hereafter. We performed two principal component analyses (PCA) on these clusters to allow for an ecological interpretation: i) on the abovementioned cluster variables (**Fig. A2a**), and ii) on the other available soil variables (**Fig. A2b**).

The first PCA shows that the *ClayCarbonate* soils (22 plots) represent silty-clay-carbonate soils with high inorganic carbon concentration, whereas the *ClayNoCarbonate* soils (82 plots) represent silty-clay soils without the presence of carbonates (low inorganic carbon concentration), and the *Sand* soils (88 plots) represent sandy soils with a low inorganic carbon concentration (**Fig. A2a**). The second PCA shows the alignment of the *ClayCarbonate* soils with a high proportion of exchangeable base cations and pH_{KCl}, but low C/N-ratio and litter mass (i.e. a faster mineralization), confirming the calcareous and richer properties of this group. The PCA also confirms the poorer, sandy properties of the *Sand* soils, since these align with higher bulk density, C/N-ratios and litter mass reflecting higher acidity and lower nutrient concentration. The *ClayNoCarbonate* soils adopt an intermediate position in soil properties (**Fig. A2b**).

2.3.2. Response and predictor variables

We evaluated the following physicochemical response variables that characterize topsoil conditions: bulk density (*BD*), proportion of exchangeable base cations (*EBC*), organic carbon/nitrogen ratio (*C/N*), litter mass, bio-available phosphorus (*OlsenP*), total phosphorus (*TotP*), pH_{KCl} and soil organic matter (*SOM)* (mean values see **Table A2**). As predictor variables, we included the plot-scale litter quality score (LQ) to reflect how tree species composition may influence topsoil conditions through their litter quality. Furthermore, we included either *Ndep* or *AcidRate* as predictors reflecting potential eutrophication and acidification respectively. To assess the influence of the past land cover, we used a plot categorical variable with three levels indicating whether it was an ancient forest plot (*AF),* a recent post-arable forest plot (*RF-Arable)* or a recent post-grassland or heathland plot (*RF-Grass*). To assess the influence of the past forest management, or more specifically the coppice history, we used a plot categorical variable with two levels indicating whether the plot had been coppiced between 1850-2015 (*1*) or not (*0*). Lastly, we included the categorical variable *Soil type* with three levels (see *Cluster analysis*).

2.3.3. Modelling

Several response variables required a transformation prior to the analysis to achieve a normal distribution*: litter mass* (sqrt), *OlsenP* (log), *TotP* (sqrt), *EBC* (asin(sqrt)). We checked for potential confounding and collinearity issues between the predictor variables by means of boxplots and correlograms. Nitrogen deposition and acidification rate were highly correlated, therefore separate models were built using one or the other. Litter quality and soil type were also slightly confounded, with higher litter quality values for the plots with clay-carbonate soils (mean = 2.9, median = 2.7) than for the plots with sandy soils or clay-no-carbonate soils (in both cases, mean = 2.1, median = 1.7). We excluded two post-grassland plots (RF-: PR196, PR197, **Table A1**) because they were outliers with regard to soil organic matter (79% and 72% compared to a mean 13% organic matter), suggesting that these plots had peat/fen (organic) rather than mineral soils. For the analysis of past land cover, we compared the ancient forest plots with the two groups of recent forest plots (i.e. RF-Arable and RF-Grass). Since for the analysis of coppice history only ancient forest plots were included, we investigated the effects of past land cover and past forest management separately. Ultimately, in both datasets, we had an adequate balance of the remaining plot groups across the three soil types, although overall we had more ancient than recent plots available (**Fig. A3**). Finally, all continuous predictors were standardized (scaled and centered) prior to analysis to enable comparison of their effect sizes.

We built four models to assess our research questions. Model 1 considered the effects of the past land cover (AFRF: AF/RF-Arable/RF-Grass) of the plots, whereas model 2 considered the effects of the past forest management, i.e. coppice history (CoppHist: 0/1) of the (ancient forest) plots. Both models were then built with either nitrogen deposition or acidification included in the model. Because the results of the acidification models largely overlap with the results of the nitrogen deposition models, we report them in the Supporting Information (**Table A5**), and only highlight new results compared to the deposition models in the main text.

For each of the four models, we built a global model including three predictors – i.e. the three soil-forming factors of interest: *LQ*, *Ndep/AcidRate,* and *AFRF/CoppHist.* We included the interactions *LQ x Ndep/AcidRate, LQ x AFRF/CoppHist*, to test whether the litter quality effect on topsoil conditions depended on the regional deposition/acidification load, or on the existing land-use legacies of a former land cover (*AFRF*) or management type (*CoppHist*). We included the additional predictor *Soil type* because we expected it to influence topsoil conditions. Although some soil types had a slightly higher mean LQ than others, we also tested whether there was any evidence for the effect size of LQ depending on soil type by fitting the interaction term *LQ x SoilType*. We did not include the interaction *Ndep x AFRF/CoppHist* because of inadequate gradients of deposition in the separate past land cover and coppice history categories.

We adopted an AIC-based multi-model inference approach to evaluate these effects for the soil responses. We weighted and ranked all possible models based on a small-sample information criterion (AICc), and derived 'full' average parameter estimates and 95% confidence intervals ('zero-method' *sensu* Grueber, Nakagawa, Laws, & Jamieson, 2011) based on a reduced set of models with good empirical support (ΔAICc $\leq$ 3 from lowest AICc model; (Burnham and Anderson, 2002). Models were run using the MuMIn package in R (Barton, 2017). To take into account the hierarchical structure of our data (plots within regions), we included the random intercept *Region* in the models.

We focused on the average model results rather than a selection of the 'best-ranked models' because we were interested to see the relative importance of the effects, and did not want to exclude small, yet important effects (Burnham & Anderson, 2002). We discuss an effect if zero was not included in the 95% CI of its parameter estimate (Burnham & Anderson, 2002). We evaluated the global and selected models' performance graphically by looking at plots of the residuals vs. fitted values, and of the fitted vs. observed values (i.e. 'goodness of fit'). We also calculated the marginal and conditional R^2 (proportion of variance explained by fixed factors – R^2_m, and by both fixed and random factors – R^2_c) of the global and selected models following Nakagawa & Schielzeth (2013). All statistical analyses were performed in R (version 3.3.3: R

Core Team, 2017) with the packages ‘stats’, ‘MuMIn, ‘nlme’, and ‘ggplot2’ (Barton, 2017; Pinheiro et al., 2016; Wickham, 2009).

3. Results

We did not find any evidence that the regional variables, i.e. N deposition or acidification rate, influenced topsoil conditions in our plots, either as a main effect or via an interaction with litter quality (**Table 2, Table A5**). We did find effects of the plot-specific variables, i.e. litter quality and land-use history, as well as soil type, on topsoil conditions, with evidence of an interaction between litter quality and land-use history for topsoil phosphorus concentration. The R^2 values (R^2_m up to 73%) suggested that much of the variation in response variables could be explained by the predictors. However, variation explained for Olsen P (R^2_m = 0.01%) in the past forest management dataset was low (**Table 2**).

Litter quality affected several of the topsoil conditions in our plots: proportion of exchangeable base cations and total phosphorus increased with an increasing plot litter quality score, whereas the litter mass and the C/N-ratio decreased with an increasing litter quality score (**Table 2, Fig. 4a-d**).

When analyzing the effects of past land cover, the post-arable plots had higher bioavailable (Olsen) phosphorus concentration compared to ancient forest plots or post-grassland/heathland plots (**Table 2a**, **Fig. A4a**). Finally, bulk density, C/N-ratio, total phosphorus, pH_{KCl} and soil organic matter differed between the soil type groups in both datasets (**Table 2a-b, Fig. A4b**). Namely, bulk density and C/N-ratios increased, while total phosphorus, pH_{KCl}, and soil organic matter decreased from the richer clay-carbonate soils to the intermediate clay-no-carbonate soils to the poorer sandy soils (**Table 2a-b, Fig. A4b**).

When assessing the relative importance of the different predictors for the topsoil conditions by comparing effect sizes, litter quality showed the largest effect sizes relative to the other factors for proportion of exchangeable base cations, and litter mass, and large effect sizes relative to the other factors excluding soil type for bulk density, C/N-ratio, total phosphorus and pH_{KCl} (**Table 2a**). Past land cover, or more specifically the contrast between post-arable vs. ancient forest plots, was most important for Olsen phosphorus (**Table 2a**). At the same time, past land cover also seemed relatively important for C/N-ratio, total phosphorus, and soil organic matter. Coppice history, although it did not significantly affect any of the topsoil conditions, did seem relatively important for litter mass, Olsen and total phosphorus, and soil organic matter (**Table 2b –** large effect sizes compared to other predictors). Soil type was an important predictor for several of the topsoil conditions (**Table 2**). Finally, although no clear effects were detected (i.e. confidence intervals included zero for all response variables), nitrogen deposition did seem relatively important (compared to other predictors) for C/N-ratio, pH_{KCl} and organic matter concentration (**Table 2**).

Besides main effects, we observed two interactions between litter quality and past land cover for both Olsen as well as total phosphorus concentration in the topsoil (**Table 2a:** LQ:AFRF). Namely, litter quality affected phosphorus content differently in ancient (no strong trend) vs. post-grassland/heathland plots (increase) vs. post-arable plots (no strong trend/decrease) (**Table 2**, **Fig. A5**). We did not find interactions between litter quality and any of the other factors (i.e. past forest management, nitrogen deposition/acidification rate, soil type). However, although a "significant" interaction between litter quality and soil type was not observed, we did additionally test and visualize main effects of litter quality for EBC for each of the three soil types separately, because **Figure 4a** suggested a differential response of the clay-carbonate soils to litter quality than the clay-no-carbonate or sandy soils.

Table 2: Effect sizes and directions of the main and interactive effects in the average models for the soil response variables (top row) in the ancient-recent forest dataset (**a**, 190 plots) and coppice history dataset (**b**, 135 plots). The last four rows in a) and b) provide information on the selected models that make up the average model: the maximum R^2 explained with the models by fixed factors only (R^2_m), and by fixed and random factors (R^2c), the relative weight of the "best-ranked" model based on the AICcutoff of 3 (*max weight*), and the number of models included. The response variables *BD, EBC, C/N, litter mass, OlsenP, TotP, and SOM* respectively refer to bulk density, proportion of exchangeable base cations, carbon/nitrogen ratio, litter mass, bioavailable Olsen phosphorus, total phosphorus, and soil organic matter. The predictor variables (first column) *LQ, Ndep, SoilType[ClayNoCarb], SoilType[Sand], AFRF[RF-Grass]*, and *AFRF[RF-Arable]* refer to the litter quality score, nitrogen deposition, clayey soils without carbonate, sandy soils, recent post-arable forest plots and post-grassland/heathland forest plots respectively. ↑ or ↓ is used to indicate whether the response variable increases or decreases with an increasing predictor. Effect sizes are in **bold** if the 95% confidence intervals do not include zero, and these are discussed in the manuscript.

a)	**BD**	**EBC**	**C/N**	**Litter mass**	**OlsenP**	**TotP**	**pHKCl**	**SOM**
(Intercept)	0.795	1.137	12.501	3.646	2.905	28.179	5.884	18.8
LQ	-0.014↓	**0.073↑**	**-0.915↓**	**-0.984↓**	0.075↑	**2.472↑**	0.164↑	0.130↑
Ndep	0.0003↑	-0.017↓	0.466↑	-0.141↓	0.068↑	-0.03↓	0.032↑	0.108↑
SoilType[ClayNoCarb]	**0.137↑**	-0.035↓	**1.808↑**	0.346↑	NA	**-4.479↓**	**-1.372↓**	**-3.335↓**
SoilType[Sand]	**0.221↑**	-0.066↓	**1.771↑**	0.861↑	NA	**-8.94↓**	**-1.858↓**	**-9.912↓**
AFRF[RF-Grass]	0.006↑	-0.009↓	0.042↑	NA	0.077↑	1.054↑	NA	-0.026↓
AFRF[RF-Arable]	0.008↑	0.003↑	-0.826↓	NA	**0.292↑**	1.172↑	NA	-0.242↓
LQ:Ndep	NA	0.003	0.008	-0.009	-0.002	NA	0.021	0.092
LQ:SoilType[ClayNoCarb]	NA	0.01	0.172	0.121	NA	-0.739	0.159	NA
LQ:SoilType[Sand]	NA	0.008	-0.286	0.065	NA	-0.517	0.118	NA
LQ:AFRF[RF-Grass]	NA	0.003	NA	NA	**0.271**	**3.48**	NA	NA
LQ:AFRF[RF-Arable]	NA	-0.005	NA	NA	**-0.274**	**-2.042**	NA	NA
Max R^2m	0.19	0.42	0.39	0.38	0.12	0.47	0.73	0.34
Max R^2c	0.59	0.77	0.69	0.63	0.45	0.77	0.87	0.60
Max weight	0.32	0.28	0.22	0.27	0.49	0.51	0.30	0.41
No models	6	8	8	7	3	3	6	5

b)	**BD**	**EBC**	**C/N**	**Litter mass**	**OlsenP**	**TotP**	**pHKCl**	**SOM**
(Intercept)	0.769	1.097	11.618	4.455	2.88	27.821	5.732	17.611
LQ	-0.003↓	**0.102↑**	-0.824↓	**-0.852↓**	0.006↑	**1.596↑**	0.21↑	0.008↑
Ndep	0.003↑	-0.034↓	0.246↑	-0.081↓	0.022↑	-0.038↓	0.066↑	-0.113↓
SoilType[ClayNoCarb]	**0.198↑**	NA	**2.064↑**	-0.07↓	NA	**-5.299↓**	**-1.288↓**	-2.85↓
SoilType[Sand]	**0.262↑**	NA	**3.463↑**	0.225↑	NA	**-10.777↓**	**-1.789↓**	**-8.209↓**
CoppHist[1]	-0.059↓	-0.004↓	0.11↑	-0.387↓	0.038↑	2.629↑	0.032↑	0.785↑
LQ:Ndep	NA	0.053	-0.008	NA	NA	NA	0.054	NA
LQ:SoilType[ClayNoCarb]	NA	NA	0.007	NA	NA	NA	0.177	NA
LQ:SoilType[Sand]	NA	NA	-0.426	NA	NA	NA	0.084	NA
LQ:CoppHist[1]	NA	NA	0.048	-0.07	NA	-0.012	NA	NA
Max R^2m	0.21	0.25	0.44	0.35	0.01	0.53	0.65	0.33
Max R^2c	0.59	0.71	0.67	0.53	0.36	0.79	0.84	0.62
Max weight	0.34	0.50	0.16	0.20	0.38	0.53	0.22	0.34
No models	6	4	12	10	5	4	9	6

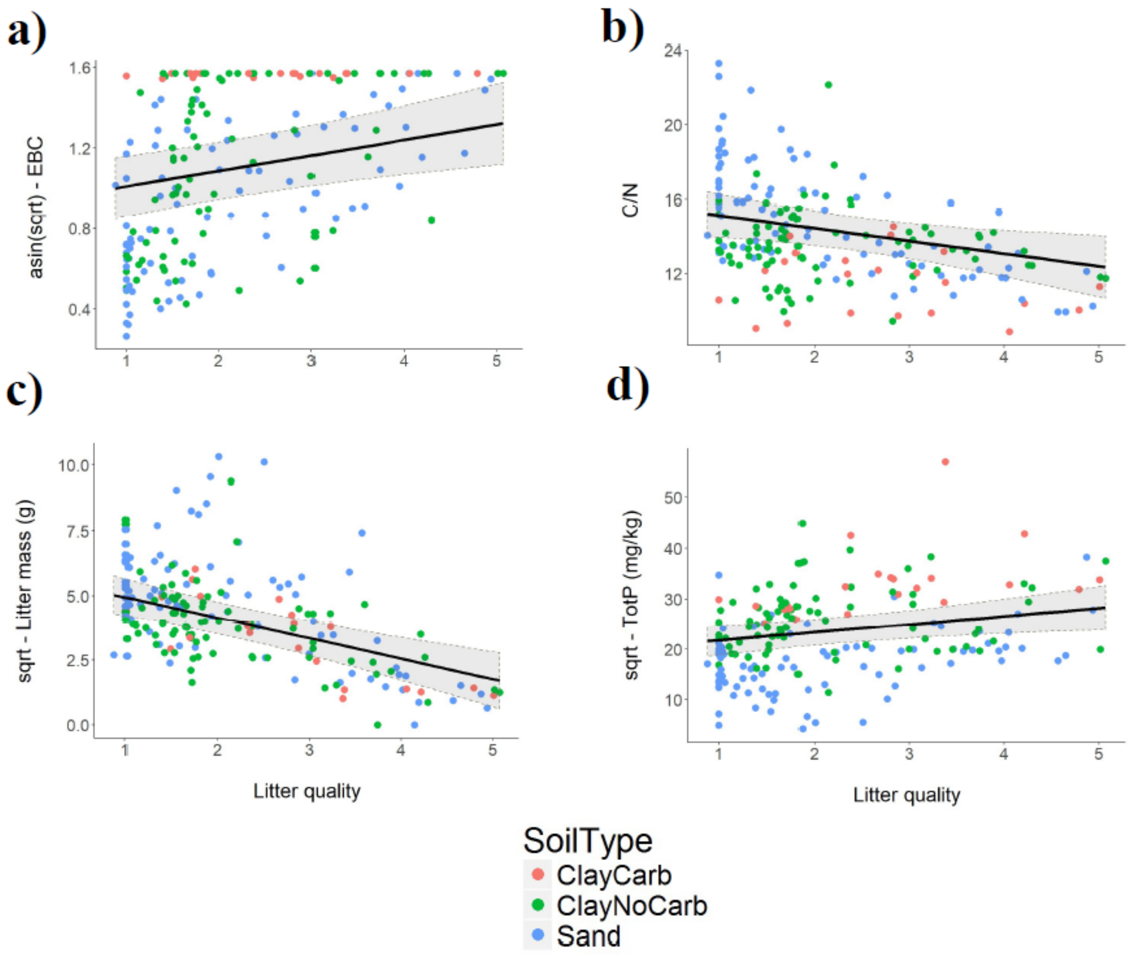


Figure 4. Main effects of litter quality plot score (LQ) on **a)** proportion of exchangeable base cations (EBC), **b)** C/N-ratio (C/N), **c)** litter mass (g), and **d)** total phosphorus concentration (TotP – mg/kg). Actual data points (*dots*) and average model estimates of the effects (*full lines with 95% confidence intervals*), in which the values of the other continuous variables were set at their observed mean, are shown.

4. Discussion

4.1. Driving variables of topsoil conditions

4.1.1. Litter quality

Out of the potential variables affecting topsoil conditions across European temperate forests investigated here, litter quality was a key explanatory variable for several soil conditions (**Table 2, Fig. 4**). The proportion of exchangeable base cations, and total phosphorus concentration were higher, while C/N-ratios were lower in the mineral topsoil of plots with higher litter quality. At the same time, plots with higher litter quality also had less organic material built-up on their forest floor (lower litter mass). Taken together, these findings suggest that mineralization and nutrient cycling processes were faster in plots with higher litter quality originating from the canopy. Even when litter quality was not a "significant" predictor (i.e. confidence intervals included zero), e.g. for bulk density, Olsen phosphorus, pH_{KCl}, and soil organic matter, it still affected these conditions to a similar, or larger extent than the past land cover or N deposition/acidification rate.This dominant effect of the litter quality on topsoil conditions supports many other studies that show that tree species, through the chemical composition of the litter, can exert a large influence on the humus layer and its biological activity, as well as on the mineral soil (Augusto et al., 2003; Cools et al., 2014; De Wandeler et al., 2018; Langenbruch et al., 2012; Leuschner and Ellenberg, 2017; Macdonald et al., 2012; Vesterdal et al., 2008; Vesterdal and Raulund-Rasmussen, 1998). Litter decomposition rates, as well as the microbial community structure and abundance that performs the decomposition process, are mainly controlled by the concentration of easily degradable organic compounds in the litter, and its nitrogen concentration (with high lignin and low N litter decomposing more slowly) (Aubert et al., 2005; Cornwell et al., 2008; Djukic et al., 2018; Leuschner and Ellenberg, 2017; Ponge, 1999).

Importantly however, the current canopy composition is in the first place already determined by an interplay of other factors such as the parent material's influence on soil type, or tree species choice by forest managers (Dijkstra et al., 2003; Finzi et al., 1998; McGrath et al., 2015; van Breemen et al., 1997). Previous studies have stressed the need to differentiate between possible (confounding) effects of litter quality and parent material in studies investigating topsoil properties (e.g. Langenbruch, Helfrich, & Flessa, 2012; Prévosto, Dambrine, Moares, & Curt, 2004). Indeed, plots on clay-carbonate soils had a median LQ value one unit higher (LQ=2.7) than those on other soil types (LQ=1.7), suggesting that parent material (co)-determined canopy composition to some extent in the investigated plots.

Nevertheless, we found a similar range of LQ in the different soil types, and we found an overruling main effect of litter quality on topsoil conditions across the different contexts and interdependencies. Furthermore, we did not detect any interactions between litter quality and deposition or soil type here. This suggests that the litter quality effects on topsoil were independent of the context of regional deposition, and of the soil type, at least within the gradients covered here (cfr. Cools et al., 2014; Gurmesa, Schmidt, Gundersen, & Vesterdal, 2013). In contrast, we did find an interaction between past land cover and litter quality on bio-available (or “Olsen”) and total phosphorus concentration, suggesting that the context shaped by previous land use can alter tree species effects on topsoil conditions, as shown here for phosphorus levels. Finding this effect for phosphorus is not surprising, since P legacies are generally the most persistent land-use effects observed in current forest soils (see also 4.1.2.; Dupouey et al., 2002; Grossmann & Mladenoff, 2008; McLauchlan, 2006).

These litter quality results agree with other studies that demonstrate the key role that litter quality has for decomposition processes that ultimately determine many of the topsoil conditions in forests (Cools et al., 2014; Djukic et al., 2018; Schelfhout et al., 2017). Temperate forest soils receive large amounts of litterfall year after year (e.g. ca. 4000±2000 kg ha^{-1} yr^{-1} litterfall for broadleaf forests), transferring nutrient amounts of around 45 kg N ha^{-1} yr^{-1}, 3.2 kg P ha^{-1} yr^{-1}, and 10.5 kg K ha^{-1} yr^{-1} to the forest floor (Bray and Gorham, 1964; Liu et al., 2004; Neumann et al., 2018). This litterfall nutrient input is equivalent to applying about 80 kg of NPK fertilizer with 16% N, 4% P, and 8% K per hectare each year (Neumann et al., 2018). From this, it is not surprising that these “natural” nutrient cycling and decomposition processes driven by litter with different characteristics might have a greater impact on topsoil conditions than other variables that can influence the topsoil (e.g. nitrogen deposition or land-use history) (Neumann et al., 2018).

4.1.2. Land-use history

In terms of past land cover, post-arable plots had higher bioavailable phosphorus concentration compared to ancient forest plots (**Table 2**, **Fig. A4a**). Furthermore, although non-significant, we noticed that the topsoil of post-arable plots showed lower C/N-ratios and soil organic matter. This is in agreement with many other studies demonstrating similar long-term soil legacies in post-agricultural forests (Compton et al., 1998; Foote and Grogan, 2010; Jussy et al., 2002; Mausolf et al., 2018; Prévosto et al., 2004; Verheyen et al., 1999; Yesilonis et al., 2016). The elevated bio-available phosphorus levels in post-agricultural forest soils are likely due to organic amendments in the form of manure or other fertilizers that can lead to long-lasting P enrichment (Compton and Boone, 2000; Dupouey et al., 2002; Koerner et al., 1997). Lower C/N-ratios in post-arable plots probably result from simultaneous cultivation of crops (i.e. organic C and N removal) and increased nitrification potentially triggered by deforestation, tillage, and N fertilization during agricultural land use (Compton and Boone, 2000; Jussy et al., 2002). Regarding the past forest management, we did not find clear differences in topsoil conditions between plots that have a history of coppicing between 1850-2015 vs. plots that were not coppiced (**Table 2**). C/N-ratio

The effects of coppice history on topsoil conditions might be less pronounced than those of other explanatory variables here because coppicing took place in the past (we did not explore actively coppiced plots – **Table A1**), and forest management effects are likely more subtle than differences in land cover which usually involve much more severe soil disturbances (e.g. clearcut/ploughing). Furthermore, since the canopy composition is often a direct relict of forest management, there may be a potential confounding effect between litter quality and coppice history. Certain tree species suitable for coppicing (e.g. *Quercus spp*., *Carpinus betulus*, *Fraxinus excelsior*, *Tilia* spp., *Corylus avellana* – **Table A3**) might have been favored in coppiced plots, as well as other tree species (e.g. *Fagus sylvatica*) might have been excluded (Buckley, 1992; Müllerová et al., 2015). Thus the effect of coppicing might be confounded by a litter quality effect from these different tree species (Hölscher et al., 2001). We do not think this actually applies here because (i) the current litter quality scores for plots that were coppiced in the past were only slightly higher than for those that were not coppiced (**Fig. A6**), (ii) coppice history did not significantly affect litter quality (**Table A6**), and (iii) we had a lot of formerly coppiced plots with *Quercus* in the canopy (51 of the 79 coppiced plots, mean cover 47%), a species which is on the poor side of the litter quality spectrum (**Fig. 3**).

4.1.3. Parent material

Parent material drives topsoil conditions, which we took into account here by considering soil type as an additional predictor in our analyses. As expected, we detected several gradients in topsoil conditions between the different soil groups, i.e. increasing bulk density and C/N-ratios, and decreasing total phosphorus, pH, and soil organic matter contents from the richer clay-carbonate soils to the intermediate clay-no-carbonate soils to the poorer sandy soils (**Table 2a-b, Fig. A4b**). Since we did not detect interactive effects between soil type and litter quality here, this suggests that an overruling effect of litter quality, independent of the soil type, took place in our plots. Although a “significant” interaction between litter quality and soil type was not observed through our modelling approach, we did find indications that the Clay Carbonate soils responded differently to litter quality than the Clay No Carbonate / Sandy soils (see **Fig. A7**).

4.1.4. Deposition

We had expected to find eutrophication or acidification effects from increased nitrogen deposition on European topsoil conditions (Brumme et al., 2009; Hédl and Rejšek, 2007; Jandl et al., 2012). However, nitrogen deposition and acidification rates did not explain any of the topsoil conditions in our plots, although they did appear in all the models, with a low importance compared to other predictors. Other studies also found that nitrogen deposition was not a strong driver of topsoil conditions when compared to other explanatory variables (Cools et al., 2014; Watmough, 2010). Furthermore, nitrogen deposition effects vary greatly between studies due to context-dependencies (Bertills et al., 2000). Thus, since Ndep and AcidRate remained in all models, even while not significantly explaining topsoil conditions, they should not be ignored as a potential driver of soil changes. Rather, further studies should aim to clarify under which contexts increased deposition has the potential to alter certain soil conditions through eutrophication or acidification effects. We should also consider the possibility that the lack of (direct) effects from deposition here might be because the regional EMEP deposition values that we used deviate from actual local nitrogen input to the forest plots because of (i) canopy exchange processes (compared to the open-field estimates that EMEP provides), as well as (ii) smaller-scale plot variability due to specific stand properties such as stand height, distance to forest edge and/or to local N-emission sources. Finally, we should consider that N deposition might have had an indirect effect on topsoil conditions through influencing the canopy composition hence the litter quality score over time (Suding et al., 2008). However, we cannot investigate such changes over time here, as our dataset represents a snapshot of the plot conditions.

4.2. Relevance for forest management

Litter quality determined by the canopy composition was an important driver of topsoil conditions, and seemed to affect the topsoil in our mixed deciduous forest plots consistently across different contexts of nitrogen deposition, land-use history and soil type. This reconfirms the idea that forest managers – wanting to maintain, ameliorate, or restore topsoil conditions on existing or degraded forest sites – could actively influence the canopy composition so as to achieve their desired state of soil fertility/productivity (e.g. improving pH and buffer capacity, increase mineralization rates and nutrient cycling; (Aubert et al., 2006, 2004; Katzur and Haubold-Rosar, 1996; Kooch et al., 2017; Vesterdal and Raulund-Rasmussen, 1998). Our plots covered a gradient of litter quality originating from the different mixtures of tree and shrub species in the canopy, each with individual litter characteristics and reflective of nutrient cycling traits and thus decomposition rates (**Table 1, Figure 3, Table A3**). These litter quality scores differed between the broadleaved tree species and the conifers (e.g. **Fig. 3**: poor-litter *Picea* vs. richer-litter *Acer*), but also within the broadleaved species (e.g. poor-litter *Fagus* vs. richer-litter *Acer*). Forest managers working in temperate forests should thus consider these differences in litter quality and decomposition rates during the process of selecting appropriate tree species to plant or favor in their forests when their aim is e.g. to ameliorate soil productivity. If their aim is rather to maintain or achieve for instance understorey species diversity, and soil fertility improvements could hamper this, they should also consider canopy choice, but perhaps in the opposite direction (e.g. by avoiding tree species with richer litter).

However, soil type and potential land-use legacies should also be taken into account in management plans as these factors may interfere with litter quality effects. Even though there was no interaction between soil type and litter quality (i.e. the same effect of litter quality regardless of soil type), it is likely that some soil types have inherently low nutrient conditions. The three soil types still showed strong gradients in several topsoil conditions (pH, total P, C/N: **Table A2**, **Fig. A4b**) despite sites being chosen to reflect mesotrophic conditions. Litter quality effects in soils with lower nutrient conditions than those investigated here may therefore differ from our findings. Other authors have already put forward that a litter quality effect may only be “successful” in improving soil fertility within a range of “intermediate” (moderately poor) sites (Prescott and Vesterdal, 2013; Van Nevel et al., 2014). Our poorest soil type group, i.e. the sandy plots, were still relatively rich sandy soils (e.g. mean loam content of 38%), so they might still be susceptible to litter quality effects. In this regard, we should also consider that by using the laser diffraction method to determine particle size here, this may have underestimated the finer fractions (e.g. clay - Yang et al., 2015), so that our poorest soils may have belonged to even finer standard soil texture classes than classified here. We also focused on deciduous tree species and avoided conifer stands. Further research should extend to other tree species and soil types on a European scale, to determine if in nutrient-poor (conifer) dominated forests, soils are (as) susceptible to litter quality effects. In a study in sandy podzol forest soils in north-east Belgium, for instance, nutrient-richer litter species did not significantly improve soil conditions (Van Nevel et al., 2014). This might be due to the lack of important macrofauna such as earthworms which are of major importance for decomposition (Prescott and Vesterdal, 2013; Van Nevel et al., 2014). Given the key role that the belowground community plays in decomposition processes (e.g. mycorrhizae – Craig et al., 2018, soil invertebrates – Lavelle et al., 2006), future studies should also investigate the effects of litter quality (and other driving factors) on these belowground communities, i.e. something that was not considered here. By extension, belowground effects of the canopy composition, i.e. through root input and dynamics, or microclimatic effects were not considered here as well, but could influence topsoil conditions as well.

Furthermore, consideration of future climate scenarios, and actual experimental tests in the field should additionally guide adaptive forest management plans since climatic changes are causing tree species to shift their distributions already. Furthermore, decomposition rates in the field could still be influenced by other confounding factors such as litter quantity, as well as belowground decomposer community composition (Prescott, Zabek, Staley, & Kabzems, 2000). Finally, in this study, we used an (approximative) litter quality score that was derived from current canopy composition, and the individual species scores were originally based on litter decomposition rates from Flemish forest sites. Actual litter quality values may differ from these scores as individual species and their litter quality may vary over space and time. Future studies should consider this and also measure litter quality in the field and/or take into account changes in canopy composition when assessing these effects.

Our results add to the growing body of evidence on the importance of litter decomposition for topsoil conditions, and the fact that canopy composition is recognized as a strong driver of litter decomposition rates (Prescott and Vesterdal, 2013). However, our understanding of the realistic potential of such strategies and experiments to promote forest floor and soil quality in a certain direction remains limited (Kooch and Bayranvand, 2017). Amongst other things, this is likely due to the many interdependencies of different soil-forming factors, and the long-term time frame needed to evaluate such strategies in the field. In the context of adaptive forest management with regard to global environmental changes, biodiversity loss, as well as many forests worldwide being in a degraded state, we recommend that future studies should focus on further disentangling these soil-forming factors, and use observational and experimental datasets covering multiple gradients of these factors. An increased understanding of the relative importance of these factors for specific forest types, combined with actual long-term field observations will hopefully allow to build realistic strategies for keeping forest soils worldwide healthy and productive.

4.3. Conclusion

We found that litter quality was a strong driver of topsoil conditions across temperate deciduous European forests, while land-use history and nitrogen deposition or acidification rates were less important. The investigated gradient of atmospheric deposition did not affect any of the soil conditions, while the potentially confounding factor soil type, determined in part by the underlying parent material, significantly influenced topsoil conditions here. Furthermore, the observed litter quality effects were independent of the context of regional nitrogen deposition or the studied plot-level soil type. However, litter quality effects on topsoil P concentration depended on previous land cover. Overall, our results suggest that manipulation of canopy composition by planting or promoting certain tree or understory shrub species can be an important tool for forest managers in maintaining or ameliorating certain topsoil conditions, at least in temperate deciduous European forests. More generally, we have shown that topsoil sampling on a larger geographical scale, and across gradients of specific factors of interest (here litter quality, land-use history and nitrogen deposition), can help in disentangling the effects of these factors on topsoil conditions.

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Conflict of interest

The authors have no conflicts of interest to declare.

References

Aber, J.D., 1992. Nitrogen cycling and nitrogen saturation in temperate forest ecosystems. Trends Ecol. Evol. 7, 220–224. https://doi.org/10.1016/0169-5347(92)90048-G

Aubert, M., Bureau, F., Alard, D., Bardat, J., 2004. Effect of tree mixture on the humic epipedon and vegetation diversity in managed beech forests (Normandy, France). Can. J. For. Res. 34, 233–248. https://doi.org/10.1139/x03-205

Aubert, M., Bureau, F., Vinceslas-Akpa, M., 2005. Sources of spatial and temporal variability of inorganic nitrogen in pure and mixed deciduous temperate forests. Soil Biol. Biochem. 37, 67–79. https://doi.org/10.1016/j.soilbio.2004.07.025

Aubert, M., Margerie, P., Ernoult, A., Decaëns, T., Bureau, F., 2006. Variability and heterogeneity of humus forms at stand level: Comparison between pure beech and mixed beech-hornbeam. Ann. For. Sci. 63, 177–188. https://doi.org/10.1051/forest

Augusto, L., Dupouey, J.-L., Ranger, J., 2003. Effects of tree species on understory vegetation and environmental conditions in temperate forests. Ann. For. Sci. 60, 823–831. https://doi.org/https://doi.org/10.1051/forest:2003077

Augusto, L., Ranger, J., Binkley, D., Rothe, A., 2002. Impact of several common tree species of European temperate forests on soil fertility Laurent. Ann. For. Sci. 233–253. https://doi.org/10.1051/forest

Baeten, L., Bauwens, B., De Schrijver, A., De Keersmaeker, L., Van Calster, H., Vandekerkhove, K., Roelandt, B., Beeckman, H., Verheyen, K., 2009. Herb layer changes (1954-2000) related to the conversion of coppice-with-standards forest and soil acidification. Appl. Veg. Sci. 12, 187–197. https://doi.org/10.1111/j.1654-109X.2009.01013.x

Baeten, L., Verheyen, K., Wirth, C., Bruelheide, H., Bussotti, F., Finér, L., Jaroszewicz, B., Selvi, F., Valladares, F., Allan, E., Ampoorter, E., Auge, H., Avăcăriei, D., Barbaro, L., Bărnoaiea, I., Bastias, C.C., Bauhus, J., Beinhoff, C., Benavides, R., Benneter, A., Berger, S., Berthold, F., Boberg, J., Bonal, D., Brüggemann, W., Carnol, M., Castagneyrol, B., Charbonnier, Y., Chećko, E., Coomes, D., Coppi, A., Dalmaris, E., Dănilă, G., Dawud, S.M., de Vries, W., De Wandeler, H., Deconchat, M., Domisch, T., Duduman, G., Fischer, M., Fotelli, M., Gessler, A., Gimeno, T.E., Granier, A., Grossiord, C., Guyot, V., Hantsch, L., Hättenschwiler, S., Hector, A., Hermy, M., Holland, V., Jactel, H., Joly, F.X., Jucker, T., Kolb, S., Koricheva, J., Lexer, M.J., Liebergesell, M., Milligan, H., Müller, S., Muys, B., Nguyen, D., Nichiforel, L., Pollastrini, M., Proulx, R., Rabasa, S., Radoglou, K., Ratcliffe, S., Raulund-Rasmussen, K., Seiferling, I., Stenlid, J., Vesterdal, L., von Wilpert, K., Zavala, M.A., Zielinski, D., Scherer-Lorenzen, M., 2013. A novel comparative research platform designed to determine the functional significance of tree species diversity in European forests. Perspect. Plant Ecol. Evol. Syst. 15, 281–291. https://doi.org/10.1016/j.ppees.2013.07.002

Baetens, J.M., Verbist, K., Cornells, W.M., Gabriels, D., Soto, G., 2009. On the influence of coarse fragments on soil water retention. Water Resour. Res. 45, 1–14. https://doi.org/10.1029/2008WR007402

Barton, K., 2017. MuMIn: Multi-model Inference. [WWW Document]. URL https://cranr-project.org/package=MuMIn.

Bauters, M., Verbeeck, H., Doetterl, S., Ampoorter, E., Baert, G., Vermeir, P., Verheyen, K., Boeckx, P., 2017. Functional Composition of Tree Communities Changed Topsoil Properties in an Old Experimental Tropical Plantation. Ecosystems 20, 861–871. https://doi.org/10.1007/s10021-016-0081-0

Beckman Coulter, I., 2011. LS 13 320 Laser diffraction particle size analyzer. Instruction for use.

Bertills, U., Näsholm, T., Lövblad, G., Bertills, U., Näsholm, T., 2000. Effects of Nitrogen Deposition on Forest Ecosystems. Stockholm, Sweden.

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., 2018. Context-Dependency of Agricultural Legacies in Temperate Forest Soils. Ecosystems. https://doi.org/10.1007/s10021-018-0302-9

Bobbink, R., Ashmore, M.R., Braun, S., Flückiger, W., Van den Wyngaert, I.J.J., 2017. Empirical nitrogen critical loads for natural and semi-natural ecosystems: 2002 update.

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? L. Degrad. Dev. 1–11.

https://doi.org/10.1002/ldr.3065

Bray, J.R., Gorham, E., 1964. Litter Production in Forests of the World. Adv. Ecol. Res. 2, 101–157. https://doi.org/10.1016/S0065-2504(08)60331-1

Brumme, R., Meesenburg, H., Bredemeier, M., Jacobsen, C., Schönfelder, E., Meiwes, K.J., Eichhorn, J., 2009. Changes in Soil Solution Chemistry, Seepage Losses, and Input–Output Budgets at Three Beech Forests in Response to Atmospheric Depositions. Ecol. Stud. 208, 303–336. https://doi.org/10.1007/978

Buckley, 1992. Ecology and Management of coppice woodlands. Springer Science, London.

Buckley, D.H., Schmidt, T.M., 2001. The Structure of Microbial Communities in Soil and the Lasting Impact of Cultivation. Microb. Ecol. 42, 11–21. https://doi.org/10.1007/s00248-004-0202-8

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference, Book. https://doi.org/10.1007/978-3-319-02868-2_3

Buurman, P., Pape, T., Reijneveld, J.A., de Jong, F., van Gelder, E., 2001. Laser-diffraction and pipette-method grain sizing of Dutch sediments: Correlations for fine fractions of marine, fluvial, and loess samples. Geol. en Mijnbouw/Netherlands J. Geosci. 80, 49–57. https://doi.org/10.1017/s0016774600022319

Compton, J.E., Boone, R.D., 2000. Long-term impacts of agriculture on soil carbon and nitrogen in New England forests. Ecology 81, 2314–2330. https://doi.org/10.1890/0012-9658(2000)081[2314:LTIOAO]2.0.CO;2

Compton, J.E., Boone, R.D., Motzkin, G., Foster, D.R., 1998. Soil carbon and nitrogen in a pine-oak sand plain in central Massachusetts: Role of vegetation and land-use history. Oecologia 116, 536–542. https://doi.org/10.1007/s004420050619

Cools, N., De Vos, B., 2010. Manual on methods and criteria for harmonized sampling, assessment, monitoring and analysis of the effects of air pollution on forests, in: Manual on Methods and Criteria for Harmonized Sampling, Assessment, Monitoring and Analysis of the Effects of Air Pollution on Forests. UNECE, ICP Forests, Hamburg, p. 208. https://doi.org/10.1007/s13157-010-0025-y

Cools, N., Vesterdal, L., De Vos, B., Vanguelova, E., Hansen, K., 2014. Tree species is the major factor explaining C:N ratios in European forest soils. For. Ecol. Manage. 311, 3–16. https://doi.org/10.1016/j.foreco.2013.06.047

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, I.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

Craig, M.E., Turner, B.L., Liang, C., Clay, K., Johnson, D.J., Phillips, R.P., 2018. Tree mycorrhizal type predicts within-site variability in the storage and distribution of soil organic matter. Glob. Chang. Biol. 24, 3317–3330. https://doi.org/10.1111/gcb.14132

Dawud, S.M., Raulund-Rasmussen, K., Ratcliffe, S., Domisch, T., Finér, L., Joly, F.X., Hättenschwiler, S., Vesterdal, L., 2017. Tree species functional group is a more important driver of soil properties than tree species diversity across major European forest types. Funct. Ecol. 31, 1153–1162. https://doi.org/10.1111/1365-2435.12821

De Schrijver, A., De Frenne, P., Staelens, J., Verstraeten, G., Muys, B., Vesterdal, L., Wuyts, K., van Nevel, L., Schelfhout, S., De Neve, S., Verheyen, K., 2012. Tree species traits cause divergence in soil acidification during four decades of postagricultural forest development. Glob. Chang. Biol. 18, 1127–1140. https://doi.org/10.1111/j.1365-2486.2011.02572.x

De Wandeler, H., Bruelheide, H., Dawud, S.M., Dănilă, G., Domisch, T., Finér, L., Hermy, M., Jaroszewicz, B., Joly, F.X., Müller, S., Ratcliffe, S., Raulund-Rasmussen, K., Rota, E., Van Meerbeek, K., Vesterdal, L., Muys, B., 2018. Tree identity rather than tree diversity drives earthworm communities in European forests. Pedobiologia (Jena). 67, 16–25. https://doi.org/10.1016/j.pedobi.2018.01.003

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

Djukic, I., Kepfer-Rojas, S., Schmidt, I.K., Larsen, K.S., Beier, C., Berg, B., Verheyen, K., Caliman, A., Paquette, A., Gutiérrez-Girón, A., Humber, A., Valdecantos, A., Petraglia, A., Alexander, H., Augustaitis, A., Saillard, A., Fernández, A.C.R., Sousa, A.I., Lillebø, A.I., da Rocha Gripp, A., Francez, A.-J., Fischer, A., Bohner, A., Malyshev, A., Andrić, A., Smith, A., Stanisci, A., Seres, A., Schmidt, A., Avila, A., Probst, A., Ouin, A., Khuroo, A.A., Verstraeten, A., Palabral-Aguilera, A.N., Stefanski, A., Gaxiola, A., Muys, B., Bosman, B., Ahrends, B., Parker, B., Sattler, B., Yang, B., Juráni, B., Erschbamer, B., Ortiz, C.E.R., Christiansen, C.T., Carol Adair, E., Meredieu, C., Mony, C., Nock, C.A., Chen, C.-L., Wang, C.-P., Baum, C., Rixen, C., Delire, C., Piscart, C., Andrews, C., Rebmann, C., Branquinho, C., Polyanskaya, D., Delgado, D.F., Wundram, D., Radeideh, D., Ordóñez-Regil, E., Crawford, E., Preda, E., Tropina, E., Groner, E., Lucot, E., Hornung, E., Gacia, E., Lévesque, E., Benedito, E., Davydov, E.A., Ampoorter, E., Bolzan, F.P., Varela, F., Kristöfel, F., Maestre, F.T., Maunoury-Danger, F., Hofhansl, F., Kitz, F., Sutter, F., Cuesta, F., de Almeida Lobo, F., de Souza, F.L., Berninger, F., Zehetner, F., Wohlfahrt, G., Vourlitis, G., Carreño-Rocabado, G., Arena, G., Pinha, G.D., González, G., Canut, G., Lee, H., Verbeeck, H., Auge, H., Pauli, H., Nacro, H.B., Bahamonde, H.A., Feldhaar, H., Jäger, H., Serrano, H.C., Verheyden, H., Bruelheide, H., Meesenburg, H., Jungkunst, H., Jactel, H., Shibata, H., Kurokawa, H., Rosas, H.L., Rojas Villalobos, H.L., Yesilonis, I., Melece, I., Van Halder, I., Quirós, I.G., Makelele, I., Senou, I., Fekete, I., Mihal, I., Ostonen, I., Borovská, J., Roales, J., Shoqeir, J., Lata, J.-C., Theurillat, J.-P., Probst, J.-L., Zimmerman, J., Vijayanathan, J., Tang, J., Thompson, J., Doležal, J., Sanchez-Cabeza, J.-A., Merlet, J., Henschel, J., Neirynck, J., Knops, J., Loehr, J., von Oppen, J., Þorláksdóttir, J.S., Löffler, J., Cardoso-Mohedano, J.-G., Benito-Alonso, J.-L., Torezan, J.M., Morina, J.C., Jiménez, J.J., Quinde, J.D., Alatalo, J., Seeber, J., Stadler, J., Kriiska, K., Coulibaly, K., Fukuzawa, K., Szlavecz, K., Gerhátová, K., Lajtha, K., Käppeler, K., Jennings, K.A., Tielbörger, K., Hoshizaki, K., Green, K., Yé, L., Pazianoto, L.H.R., Dienstbach, L., Williams, L., Yahdjian, L., Brigham, L.M., van den Brink, L., Rustad, L., Zhang, L., Morillas, L., Xiankai, L., Carneiro, L.S., Di Martino, L., Villar, L., Bader, M.Y., Morley, M., Lebouvier, M., Tomaselli, M., Sternberg, M., Schaub, M., Santos-Reis, M., Glushkova, M., Torres, M.G.A., Giroux, M.-A., de Graaff, M.-A., Pons, M.-N., Bauters, M., Mazón, M., Frenzel, M., Didion, M., Wagner, M., Hamid, M., Lopes, M.L., Apple, M., Schädler, M., Weih, M., Gualmini, M., Vadeboncoeur, M.A., Bierbaumer, M., Danger, M., Liddell, M., Mirtl, M., Scherer-Lorenzen, M., Růžek, M., Carbognani, M., Di Musciano, M., Matsushita, M., Zhiyanski, M., Pușcaș, M., Barna, M., Ataka, M., Jiangming, M., Alsafran, M., Carnol, M., Barsoum, N., Tokuchi, N., Eisenhauer, N., Lecomte, N., Filippova, N., Hölzel, N., Ferlian, O., Romero, O., Pinto, O.B., Peri, P., Weber, P., Vittoz, P., Turtureanu, P.D., Fleischer, P., Macreadie, P., Haase, P., Reich, P., Petřík, P., Choler, P., Marmonier, P., Muriel, P., Ponette, Q., Guariento, R.D., Canessa, R., Kiese, R., Hewitt, R., Rønn, R., Adrian, R., Kanka, R., Weigel, R., Gatti, R.C., Martins, R.L., Georges, R., Meneses, R.I., Gavilán, R.G., Dasgupta, S., Wittlinger, S., Puijalon, S., Freda, S., Suzuki, S., Charles, S., Gogo, S., Drollinger, S., Mereu, S., Wipf, S., Trevathan-Tackett, S., Löfgren, S., Stoll, S., Trogisch, S., Hoeber, S., Seitz, S., Glatzel, S., Milton, S.J., Dousset, S., Mori, T., Sato, T., Ise, T., Hishi, T., Kenta, T., Nakaji, T., Michelan, T.S., Camboulive, T., Mozdzer, T.J., Scholten, T., Spiegelberger, T., Zechmeister, T., Kleinebecker, T., Hiura, T., Enoki, T., Ursu, T.-M., di Cella, U.M., Hamer, U., Klaus, V.H., Rêgo, V.M., Di Cecco, V., Busch, V., Fontana, V., Piscová, V., Carbonell, V., Ochoa, V., Bretagnolle, V., Maire, V., Farjalla, V., Zhou, W., Luo, W., McDowell, W.H., Hu, Y., Utsumi, Y., Kominami, Y., Zaika, Y., Rozhkov, Y., Kotroczó, Z., Tóth, Z., 2018. Early stage litter decomposition across biomes. Sci. Total Environ. 628–629, 1369–1394. https://doi.org/10.1016/j.scitotenv.2018.01.012

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.

Duprè, C., Stevens, C.J., Ranke, T., Bleekers, A., Peppler-Lisbach, C., Gowing, D.J.G., Dise, N.B., Dorland, E., Bobbink, R., Diekmann, M., 2010. Changes in species richness and composition in European acidic grasslands over the past 70 years : the contribution of cumulative atmospheric nitrogen deposition. Glob. Chang. Biol. 16, 344–357. https://doi.org/10.1111/j.1365-2486.2009.01982.x

Eugster, W., Haeni, M., 2013. Nutrients or pollutants? Nitrogen deposition to european forests. Dev. Environ. Sci. 13, 37–56. https://doi.org/10.1016/B978-0-08-098349-3.00003-7

Falkengren-Grerup, U., ten Brink, D.-J., Brunet, J., 2006. Land use effects on soil N, P, C and pH persist over 40 – 80 years of forest growth on agricultural soils. For. Ecol. Manage. 225, 74–81. https://doi.org/10.1016/j.foreco.2005.12.027

Fichtner, A., von Oheimb, G., Härdtle, W., Wilken, C., Gutknecht, J.L.M.M., 2014. Effects of anthropogenic disturbances on soil microbial communities in oak forests persist for more than 100 years. Soil Biol. Biochem. 70, 79–87. https://doi.org/10.1016/j.soilbio.2013.12.015

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

Foote, R.L., Grogan, P., 2010. Soil carbon accumulation during temperate forest succession on abandoned low productivity agricultural lands. Ecosystems 13, 795–812. https://doi.org/10.1007/s10021-010-9355-0

Foster, D., Swanson, F., Aber, J., Burke, I., Brokaw, N., Tilman, D., Knapp, A., 2003. The Importance of Land-Use Legacies to Ecology and Conservation. Bioscience 53, 77–88. https://doi.org/10.1641/0006-3568(2003)053[0077:TIOLUL]2.0.CO;2

Fraterrigo, J.M., Turner, M., Pearson, S.M., Dixon, P., 2005. Effects of past land use on spatial heterogeneity of soil nutrients in southern appalachian forests. Ecol. Monogr. 75, 215–230. https://doi.org/10.1890/03-0475

Gilbert, J., Gowing, D., Wallace, H., 2009. Available soil phosphorus in semi-natural grasslands: Assessment methods and community tolerances. Biol. Conserv. 142, 1074–1083. https://doi.org/10.1016/j.biocon.2009.01.018

Gimmi, U., Poulter, B., Wolf, A., Portner, H., Weber, P., Bürgi, M., 2013. Soil carbon pools in Swiss forests show legacy effects from historic forest litter raking. Landsc. Ecol. 28, 835–846. https://doi.org/10.1007/s10980-012-9778-4

Glatzel, G., 1999. Historic forest use and its possible implication to recently accelerated tree growth in Central Europe. Causes consequences Accel. tree growth Eur. 27, 65–74.

Glatzel, G., 1991. the Impact of Historic Land-Use and Modern Forestry on Nutrient Relations of Central-European Forest Ecosystems. Fertil. Res. 27, 1–8. https://doi.org/10.1007/BF01048603

Grossmann, E.B., Mladenoff, D.J., 2008. Farms, fires, and forestry: Disturbance legacies in the soils of the Northwest Wisconsin (USA) Sand Plain. For. Ecol. Manage. 256, 827–836. https://doi.org/10.1016/j.foreco.2008.05.048

Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: Challenges and solutions. J. Evol. Biol. 24, 699–711. https://doi.org/10.1111/j.1420-9101.2010.02210.x

Gurmesa, G.A., Schmidt, I.K., Gundersen, P., Vesterdal, L., 2013. Soil carbon accumulation and nitrogen retention traits of four tree species grown in common gardens. For. Ecol. Manage. 309, 47–57. https://doi.org/10.1016/j.foreco.2013.02.015

Hédl, R., Petřík, P., Boublík, K., 2011. Long-term patterns in soil acidification due to pollution in forests of the Eastern Sudetes Mountains. Environ. Pollut. 159, 2586–2593. https://doi.org/10.1016/j.envpol.2011.06.014

Hédl, Rejšek, 2007. Soil changes after forty years of succession in an abandoned coppice in the Czech republic. Acta Agron. Hungarica 55, 453–474.

Henrys, P.A., Stevens, C.J., Smart, S.M., Maskell, L.C., Walker, K.J., Preston, C.D., Crowe, A., Rowe, E.C., Gowing, D.J., Emmett, B.A., 2011. Impacts of nitrogen deposition on vascular plants in Britain: An analysis of two national observation networks. Biogeosciences 8, 3501–3518. https://doi.org/10.5194/bg-8-3501-2011

Hermy, M., 1985. Ecologie en fytosociologie van oude en jonge bossen in binnen-Vlaanderen. University of Ghent.

Holmes, M.A., Matlack, G.R., 2018. Assembling the forest herb community after abandonment from agriculture: long-term successional dynamics differ with land-use history. J. Ecol. 0–2. https://doi.org/10.1111/1365-2745.12970

Holmes, M.A., Matlack, G.R., 2017. Forest micro-environment develops through time: Changes in physical and structural heterogeneity follow abandonment from two forms of agriculture. For. Ecol. Manage. 404, 55–64. https://doi.org/10.1016/j.foreco.2017.08.034

Hölscher, D., Schade, E., Leuschner, C., 2001. Effects of coppicing in temperate deciduous forests on ecosystem nutrient pools and soil fertility. Basic Appl. Ecol. 2, 155–164. https://doi.org/10.1078/1439-1791-00046

Jandl, R., Smidt, S., Mutsch, F., Fürst, A., Zechmeister, H., Bauer, H., Dirnböck, T., 2012. Acidification and nitrogen eutrophication of Austrian forest soils. Appl. Environ. Soil Sci. 2012. https://doi.org/10.1155/2012/632602

Jenny, H., 1941. Factors of Soil Formation. A system of quantitative pedology. Mc Graw-Hill Book Company, Inc. New York and London.

Joly, F.X., Milcu, A., Scherer-Lorenzen, M., Jean, L.K., Bussotti, F., Dawud, S.M., Müller, S., Pollastrini, M., Raulund-Rasmussen, K., Vesterdal, L., Hättenschwiler, S., 2017. Tree species diversity affects decomposition through modified micro-environmental conditions across European forests. New Phytol. 214, 1281–1293. https://doi.org/10.1111/nph.14452

Jones, L., Provins, A., Holland, M., Mills, G., Hayes, F., Emmett, B., Hall, J., Sheppard, L., Smith, R., Sutton, M., Hicks, K., Ashmore, M., Haines-Young, R., Harper-Simmonds, L., 2014. A review and application of the evidence for nitrogen impacts on ecosystem services. Ecosyst. Serv. 7, 76–88. https://doi.org/10.1016/j.ecoser.2013.09.001

Jussy, J.H., Koerner, W., Dambrine, E., Dupouey, J.L., Benoit, M., 2002. Influence of former agricultural land use on net nitrate production in forest soils. Eur. J. Soil Sci. 53, 367–374. https://doi.org/10.1046/j.1365-2389.2002.00468.x

Kahle, H.-P., Karjalainen, T., Schuck, A., Ågren, G., Kellomäki, S., Mellert, K., Prietzel, J., Rehfuess, K.-E., Spiecker, H., 2008. Causes and consequences of forest growth trends in Europe. European Forest Institute Research Report 21 Results of the RECOGNITION Project. Koninklijke Brill NV, Leiden, The Netherlands.

Katzur, J., Haubold-Rosar, M., 1996. Amelioration and reforestation of sulfurous mine soils in Lusatia (Eastern Germany). Water, Air, Soil Pollut. 91, 17–32.

Koerner, A.W., Dupouey, J.L., Dambrine, E., Benoit, M., 1997. Influence of Past Land Use on the Vegetation and Soils of Present Day Forest in the Vosges. Society 85, 351–358.

Kooch, Y., Bayranvand, M., 2017. Composition of tree species can mediate spatial variability of C and N cycles in mixed beech forests. For. Ecol. Manage. 401, 55–64. https://doi.org/10.1016/j.foreco.2017.07.001

Kooch, Y., Samadzadeh, B., Hosseini, S.M., 2017. The effects of broad-leaved tree species on litter quality and soil properties in a plain forest stand. Catena 150, 223–229. https://doi.org/10.1016/j.catena.2016.11.023

Lajtha, K., Driscoll, C.T., Jarrell, W.M., Elliott, E.T., 1999. Standard soil methods for long-term ecological research., in: Standard Soil Methods for Long Term Ecological Research. Oxford University Press, New York, pp. 115–143.

Langenbruch, C., Helfrich, M., Flessa, H., 2012. Effects of beech (Fagus sylvatica), ash (Fraxinus excelsior) and lime (Tilia spec.) on soil chemical properties in a mixed deciduous forest. Plant Soil 352, 389–403. https://doi.org/10.1007/s11104-011-1004-7

Laubhann, D., Sterba, H., Reinds, G.-J., de Vries, W., 2009. The impact of atmospheric deposition and climate on forest growth in European monitoring plots : An individual tree growth model. For. Ecol. Manage. 258, 1751–1761. https://doi.org/10.1016/j.foreco.2008.09.050

Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P., Rossi, J.P., 2006. Soil invertebrates and ecosystem services. Eur. J. Soil Biol. 42, S3–S15. https://doi.org/10.1016/j.ejsobi.2006.10.002

Lejeune, Q., Davin, E.L., Gudmundsson, L., Winckler, J., Seneviratne, S.I., 2018. Historical deforestation locally increased the intensity of hot days in northern mid-latitudes. Nat. Clim. Chang. 8, 386–390. https://doi.org/10.1038/s41558-018-0131-z

Leuschner, C., Ellenberg, H., 2017. Ecology of Central European Forests: Vegetation Ecology of Central Europe, 1st ed. Springer International Publishing Switzerland. https://doi.org/10.1007/978-3-319-43042-3

Lindner, M., Fitzgerald, J.B., Zimmermann, N.E., Reyer, C., Delzon, S., van der Maaten, E., Schelhaas, M.J., Lasch, P., Eggers, J., van der Maaten-Theunissen, M., Suckow, F., Psomas, A., Poulter, B., Hanewinkel, M., 2014. Climate change and European forests: What do we know, what are the uncertainties, and what are the implications for forest management? J. Environ. Manage. 146, 69–83. https://doi.org/10.1016/j.jenvman.2014.07.030

Liu, C., Westman, C.J., Berg, B., Kutsch, W., Wang, G.Z., Man, R., Ilvesniemi, H., 2004. Variation in litterfall-climate relationships between coniferous and broadleaf forests in Eurasia. Glob. Ecol. Biogeogr. 13, 105–114. https://doi.org/10.1111/j.1466-882X.2004.00072.x

Lövblad, G., Kindbom, K., Grennfelt, P., Hultberg, H., Westling, O., 1995. Deposition of Acidifying Substances in Sweden. Ecol. Bull. 44, 17–34.

Lukac, M., Godbold, D.L., 2011. Soil Ecology in Northern Forests: A Belowground View of a Changing World. Cambridge University Press, Cambridge and New York.

Macdonald, G.K., Bennett, E.M., Taranu, Z.E., 2012. The influence of time, soil characteristics, and land-use history on soil phosphorus legacies: A global meta-analysis. Glob. Chang. Biol. 18, 1904–1917.

https://doi.org/10.1111/j.1365-2486.2012.02653.x

Matson, P.A., Parton, W.J., Power, A.G., Swift, M.J., 1997. Agricultural intensification and ecosystem properties. Science (80-.). 277, 504–509. https://doi.org/10.1126/science.277.5325.504

Mausolf, K., Härdtle, W., Jansen, K., Delory, B.M., Hertel, D., Leuschner, C., Temperton, V.M., von Oheimb, G., Fichtner, A., 2018. Legacy effects of land-use modulate tree growth responses to climate extremes. Oecologia 1–13. https://doi.org/10.1007/s00442-018-4156-9

McGrath, M.J., Luyssaert, S., Meyfroidt, P., Kaplan, J.O., Bürgi, M., Chen, Y., Erb, K., Gimmi, U., McInerney, D., Naudts, K., Otto, J., Pasztor, F., Ryder, J., Schelhaas, M.J., Valade, A., 2015. Reconstructing European forest management from 1600 to 2010. Biogeosciences 12, 4291–4316. https://doi.org/10.5194/bg-12-4291-2015

McLauchlan, K., 2006. The nature and longevity of agricultural impacts on soil carbon and nutrients: A review. Ecosystems 9, 1364–1382. https://doi.org/10.1007/s10021-005-0135-1

Müllerová, J., Hédl, R., Szabó, P., 2015. Coppice abandonment and its implications for species diversity in forest vegetation. For. Ecol. Manage. 343, 88–100. https://doi.org/10.1016/j.foreco.2015.02.003

Nakagawa, S., Schielzeth, H., 2013. A General and Simple Method for Obtaining R2 from Generalized Linear Mixed-Effects Models A general and simple method for obtaining R 2 from generalized linear mixed-effects models. Methods Ecol. Evol. 4, 133–142. https://doi.org/10.1111/J.2041-210x.2012.00261.X

Neumann, M., Ukonmaanaho, L., Johnson, J., Benham, S., Vesterdal, L., Novotný, R., Verstraeten, A., Lundin, L., Thimonier, A., Michopoulos, P., Hasenauer, H., 2018. Quantifying Carbon and Nutrient Input From Litterfall in European Forests Using Field Observations and Modeling. Global Biogeochem. Cycles 32, 784–798. https://doi.org/10.1029/2017GB005825

Pastforward-team, 2018. PASTFORWARD [WWW Document]. URL http://www.pastforward.ugent.be/

Perring, M.P.M.P., Bernhardt-Römermann, M., Baeten, L., Midolo, G., Blondeel, H., Depauw, L., Landuyt, D., Maes, S.L.S.L., De Lombaerde, E., Carón, M.M.M.M., Vellend, M., Brunet, J., Chudomelová, M., Decocq, G., Diekmann, M., Dirnböck, T., Dörfler, I., Durak, T., De Frenne, P., Gilliam, F.S.F.S., Hédl, R., Heinken, T., Hommel, P., Jaroszewicz, B., Kirby, K.J.K.J., Kopecký, M., Lenoir, J., Li, D., Máliš, F., Mitchell, F.J.F.J.G., Naaf, T., Newman, M., Petřík, P., Reczyńska, K., Schmidt, W., Standovár, T., Świerkosz, K., Van Calster, H., Vild, O., Wagner, E.R.E.R., Wulf, M., Verheyen, K., 2018. Global environmental change effects on plant community composition trajectories depend upon management legacies. Glob. Chang. Biol. 24, 1722–1740. https://doi.org/10.1111/gcb.14030

Pielke, R.A., Marland, G., Betts, R.A., Chase, T.N., Eastman, J.L., Niles, J.O., Niyogi, D., Running, S., 2002. The influence of land-use change and landscape dynamics on the climate system- relevance to climate change policy beyond the radiative effect of greenhouse gases. Philos. Trans. R. Soc. A 360, 1705–1719.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., 2016. {nlme}: Linear and Nonlinear Mixed Effects Models} R package.

Ponge, J., 1999. Interaction between soil fauna and their environment., in: Going Underground: Ecological Studies in Forest Soils. Research Signpost, pp. 45–76.

Prescott, C.E., Vesterdal, L., 2013. Tree species effects on soils in temperate and boreal forests: Emerging themes and research needs. For. Ecol. Manage. 309, 1–3. https://doi.org/10.1016/j.foreco.2013.06.042

Prescott, C.E., Zabek, L.M., Staley, C.L., Kabzems, R., 2000. Decomposition of broadleaf and needle litter in forests of British Columbia: influences of litter type, forest type, and litter mixtures. Can. J. For. Res. 30, 1742–1750. https://doi.org/10.1139/cjfr-30-11-1742

Prévosto, B., Dambrine, E., Moares, C., Curt, T., 2004. Effects of volcanic ash chemistry and former agricultural use on the soils and vegetation of naturally regenerated woodlands in the Massif Central, France. Catena 56, 239–261. https://doi.org/10.1016/j.catena.2003.10.014

R Core Team, 2017. R: A language and environment for statistical computing.

Ringeval, B., Augusto, L., Monod, H., van Apeldoorn, D., Bouwman, L., Yang, X., Achat, D.L., Chini, L.P., Van Oost, K., Guenet, B., Wang, R., Decharme, B., Nesme, T., Pellerin, S., 2017. Phosphorus in agricultural soils: drivers of its distribution at the global scale. Glob. Chang. Biol. 23, 3418–3432. https://doi.org/10.1111/gcb.13618

San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A. (eds. ., 2016. European Atlas of Forest Tree Species. European Commission. Publication Office of the European Union, Luxembourg. https://doi.org/10.2788/4251

Schelfhout, S., Mertens, J., Verheyen, K., Vesterdal, L., Baeten, L., Muys, B., De Schrijver, A., 2017. Tree species identity shapes earthworm communities. Forests 8, 1–20. https://doi.org/10.3390/f8030085

Schoenholtz, S.H., Van Miegroet, H., Burger, J.A., 2000. A review of chemical and physical properties as indicators of forest soil quality: challenges and opportunities. For. Ecol. Manage. 138, 335–356. https://doi.org/10.1016/S0378-1127(00)00423-0

Simpson, D., Fagerli, H., Hellsten, S., Knulst, J.C., Westling, O., 2006. Comparison of modelled and monitored deposition fluxes of sulphur and nitrogen to ICP-forest sites in Europe. Biogeosciences 3, 337–355. https://doi.org/10.5194/bg-3-337-2006

Smith, P., Cotrufo, M.F., Rumpel, C., Paustian, K., Kuikman, P.J., Elliott, J.A., McDowell, R., Griffiths, R.I., Asakawa, S., Bustamante, M., House, J.I., Sobocká, J., Harper, R., Pan, G., West, P.C., Gerber, J.S., Clark, J.M., Adhya, T., Scholes, R.J., Scholes, M.C., 2015. Biogeochemical cycles and biodiversity as key drivers of ecosystem services provided by soils. Soil 1, 665–685. https://doi.org/10.5194/soil-1-665-2015

Šrámek, M., Volařík, D., Ertas, A., Matula, R., 2015. The effect of coppice management on the structure, tree growth and soil nutrients in temperate Turkey. J. For. Sci. 61, 27–34. https://doi.org/10.17221/91/2014-JFS

Suding, K.N., Lavorel, S., Chapin, F.S., Cornelissen, J.H.C., Diaz, S., Garnier, E., Goldberg, D., Hooper, D.U., Jackson, S.T., Navas, M.-L., 2008. Scaling environmental change through the framework for plants. Glob. Chang. Biol. 14, 1125–1140. https://doi.org/10.1111/j.1365-2486.2008.01557.x

Taubner, H., Roth, B., Tippkötter, R., 2009. Determination of soil texture: Comparison of the sedimentation method and the laser-diffraction analysis. J. Plant Nutr. Soil Sci. 172, 161–171. https://doi.org/10.1002/jpln.200800085

Thiffault, E., Hannam, K.D., Paré, D., Titus, B.D., Hazlett, P.W., Maynard, D.G., Brais, S., 2011. Effects of forest biomass harvesting on soil productivity in boreal and temperate forests — A review. Environ. Rev. 19, 278–309. https://doi.org/10.1139/a11-009

van Breemen, N., Finzi, A.C., Canham, C.D., 1997. Canopy tree-soil interactions within temperate forests: effects of soil elemental composition and texture on species distributions. Can. J. For. Res. 27, 1110–1116. https://doi.org/10.1139/x97-061.

Van Calster, H., Baeten, L., Verheyen, K., De Keersmaeker, L., Dekeyser, S., Rogister, J.E., Hermy, M., 2008. Diverging effects of overstorey conversion scenarios on the understorey vegetation in a former coppice-with-standards forest. For. Ecol. Manage. 256, 519–528. https://doi.org/10.1016/j.foreco.2008.04.042

van Dobben, H.F., de Vries, W., 2017. The contribution of nitrogen deposition to the eutrophication signal in understorey plant communities of European forests. Ecol. Evol. 7. https://doi.org/10.1002/ece3.2485

Van Nevel, L., Mertens, J., De Schrijver, A., De Neve, S., Verheyen, K., 2014. Can shrub species with higher litter quality mitigate soil acidification in pine and oak forests on poor sandy soils? For. Ecol. Manage. 330, 38–45. https://doi.org/10.1016/j.foreco.2014.07.002

Verheyen, K., Baeten, L., De Frenne, P., Bernhardt-Römermann, M., Brunet, J., Cornelis, J., Decocq, G., Dierschke, H., Eriksson, O., Hédl, R., Heinken, T., Hermy, M., Hommel, P., Kirby, K., Naaf, T., Peterken, G., Petřík, P., Pfadenhauer, J., Van Calster, H., Walther, G.R., Wulf, M., Verstraeten, G., 2012. Driving factors behind the eutrophication signal in understorey plant communities of deciduous temperate forests. J. Ecol. 100, 352–365. https://doi.org/10.1111/j.1365-2745.2011.01928.x

Verheyen, K., Bossuyt, B., Hermy, M., 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.

Verheyen, K., De Frenne, P., Baeten, L., Waller, D.M., Hédl, R., Perring, M.P., Blondeel, H., Brunet, J., Chudomelová, M., Decocq, G., De Lombaerde, E., Depauw, L., Dirnböck, T., Durak, T., Eriksson, O., Gilliam, F.S., Heinken, T., Heinrichs, S., Hermy, M., Jaroszewicz, B., Jenkins, M.A., Johnson, S.E., Kirby, K.J., Kopecký, M., Landuyt, D., Lenoir, J., Li, D., Macek, M., Maes, S.L., Máliš, F., Mitchell, F.J.G., Naaf, T., Peterken, G., Petřík, P., Reczyńska, K., Rogers, D.A., Schei, F.H., Schmidt, W., Standovár, T., Świerkosz, K., Ujházy, K., Van Calster, H., Vellend, M., Vild, O., Woods, K., Wulf, M., Bernhardt-Römermann, M., 2017. Combining biodiversity resurveys across regions to advance global change research. Bioscience 67, 73–83. https://doi.org/10.1093/biosci/biw150

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

Vesterdal, L., Schmidt, I.K., Callesen, I., Nilsson, L.O., Gundersen, P., 2008. Carbon and nitrogen in forest floor and mineral soil under six common European tree species. For. Ecol. Manage. 255, 35–48. https://doi.org/10.1016/j.foreco.2007.08.015

Vincent, K.R., Chadwick, O.A., 1994. Synthesizing bulk density for soils with abundant rock fragments. Soil Sci. Soc. Am. J. 58, 455–464. https://doi.org/10.2136/sssaj1994.03615995005800020030x

Wäldchen, J., Schulze, E.-D., Schöning, I., Schrumpf, M., Sierra, C., 2013. The influence of changes in forest management over the past 200years on present soil organic carbon stocks. For. Ecol. Manage. 289, 243–254. https://doi.org/10.1016/j.foreco.2012.10.014

Watmough, S.A., 2010. An assessment of the relationship between potential chemical indices of nitrogen saturation and nitrogen deposition in hardwood forests in southern Ontario. Environ. Monit. Assess. 164, 9–20. https://doi.org/10.1007/s10661-009-0870-4

Weil, R.R., Brady, N.C., 2016. The nature and properties of soils., Fifteenth edition. Pearson Education Limited, Harlow, United Kingdom.

Wickham, H., 2009. ggplot2: Elegant graphics for data analysis.

Yang, X., Zhang, Q., Li, X., Jia, X., Wei, X., Shao, M., 2015. Determination of Soil Texture by Laser Diffraction Method. Soil Sci. Soc. Am. J. 79, 1556–1566. https://doi.org/10.2136/sssaj2015.04.0164

Yesilonis, I., Szlavecz, K., Pouyat, R., Whigham, D., Xia, L., 2016. Historical land use and stand age effects on forest soil properties in the Mid-Atlantic US. For. Ecol. Manage. 370, 83–92. https://doi.org/10.1016/j.foreco.2016.03.046