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Context-Dependency of Agricultural Legacies in Temperate Forest Soils

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ABSTRACT

Anthropogenic activities have affected forests for centuries, leading to persistent legacies. Observations of agricultural legacies on forest soil properties have been site specific and contrasting. Sites and regions vary along gradients in intrinsic soil characteristics, phosphorus (P) management and nitrogen (N) deposition which could affect the magnitude of soil property responses to past cultivation. A single investigation along these gradients could reconcile contradictions and elucidate context-dependency in agricultural legacies. We analysed soil from 24 paired post-agricultural (established after approx. 1950) and ancient (in existence before 1850) forests in eight European regions. Post-agricultural forest soil had higher pH, higher P-concentration and lower carbon (C) to N ratio compared to ancient forest. Importantly, gradients of soil characteristics, regional P surplus and N deposition affected the magnitude of these legacies. First, we found that three soil groups, characterising inherent soil fertility, determined extractable base cations, pH and concentrations of total N, organic C and total P. Second, regions with greater current P surplus from agriculture correlated with the highest P legacy in post-agricultural forests. Finally, we found that N deposition lowered pH across forests and increased total N and organic C concentrations in post-agricultural forest. These results suggest that (1) legacies from cultivation consistently determine soil properties in post-agricultural forest and (2) these legacies depend on regional and environmental context, including soil characteristics, regional P surplus and N deposition. Identifying gradients that influence the magnitude of agricultural legacies is key to informing how, where and why forest ecosystems respond to contemporary environmental change.

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Key words: ancient forest; land-use history; nitrogen deposition; phosphorus; post-agricultural forest; soil carbon.

MANUSCRIPT HIGHLIGHTS

- Regional variables affect soil property responses to prior agriculture in forests.
- Accounting for regional context clarifies contrasting agricultural legacies in soils.
- Knowing the regional context of forest soils will help project ecosystem responses.

INTRODUCTION

Human activities have profoundly affected ecosystems and biodiversity on the long term (Waters and others 2016; Vellend and others 2017). Legacies of past anthropogenic disturbances can obscure ecosystem responses to current disturbance regimes due to time-lags (Bürgi and others 2017) and potentially interact with other global change drivers to steer ecosystem patterns and processes (Perring and others 2016). It is possible for numerous accounts of agricultural legacies in forest soil properties to be contrasting, and site specific when compared to each other (Baeten 2010). Combining observations of agricultural legacies in temperate forest within a single study across regions that vary in gradients of soil characteristics, intensity of agricultural use (phosphorus management) and nitrogen deposition offers the chance to reconcile contrasting findings (Verheyen and others 2017) and elucidate context-dependency in soil responses to agricultural legacy.

Key Soil Properties for Plant Growth Show Contrasting Agricultural Legacies

Legacy of agriculture is highly variable and depends on specific management practices that are followed during the agricultural period (McLauchlan 2006; Brudvig and others 2013). Agricultural practices can leave imprints in forest soil properties for centuries (Verheyen and others 1999) and even millennia (Dupouey and others 2002). We focus on five chemical soil properties that are of high importance for plant growth and where previous research has shown differences in the magnitude, or even in the direction, of their responses to prior agriculture in temperate forest: soil organic carbon (C), total nitrogen (N), base cations [calcium (Ca), magnesium (Mg), sodium (Na) and potassium (K)], pH and total and bio-available phosphorus (P).

Comparisons of concentrations of soil organic C and total N between post-agricultural and continuously forested land (ancient forest) are variable. A lower C concentration and C/N has been observed in post-agricultural forest (Verheyen and others 1999; Foote and Grogan 2010; Yesilonis and others 2016), as well as solely a lower C in post-agricultural forest (Falkengren-Grerup and others 2006; Leuschner and others 2014) and even no difference in C and C/N between post-agricultural forest and ancient forest (Koerner and others 1997; Compton and Boone 2000). Comparisons of base cation stocks are even more variable as they can differ within post-agricultural forest sites of single studies (Verheyen and others 1999; Flinn and others 2005), likely due to variations in spatial distribution of nutrients (Fraterrigo and others 2005) and bulk density (Bizzari and others 2015). Despite variable base cation concentrations, a consistently higher pH in post-agricultural forest occurs due to past fertilisation and liming in post-agricultural forests (Wall and Hytönen 2005), but the magnitude of the difference varies (Koerner and others 1997; Verheyen and others 1999; Falkengren-Grerup and others 2006; Grossmann and Mladenoff 2008; Yesilonis and others 2016). Aside from raising pH, past fertilisation also leads to a better retention of total phosphorus (P) in forest soils after tillage (Macdonald and others 2012) in contrast to other disturbance-types such as fires or clear-cutting (Grossmann and Mladenoff 2008; Bizzari and others 2015) and extensive pasture (Compton and Boone 2000).

Soil Characteristics, Phosphorus (P) Nutrient Management and Nitrogen (N) Deposition Could Alter Soil Responses to Agricultural Legacy

We identify three gradients that could influence comparisons between soils in post-agricultural and continuously forested sites across multiple regions and thus help explain contrasting site-specific responses.

Firstly, differences in soil characteristics between post-agricultural and continuously forested land (ancient forest) might occur as land for cultivation commonly occurs on the richer soils within a given region (Flinn and others 2005). Factors that would determine the suitability for agriculture are soil texture, wetness, slope, aspect, soil depth and underlying bedrock or parent material. Key topsoil processes are additionally affected by biotic components such as identity of tree species and litter quality in forest stands (Vesterdal and others 2008; De Schrijver and others 2012a; Cools and others 2014; Nitsch and others 2018). Both the abiotic suitability of the site for agriculture and soil-forming biotic processes are local-scale drivers that can cause variability among sites within regions unless explicitly controlled for in a study design, preferably with a paired approach. Furthermore, variations in soil characteristics between regions arise along large spatial gradients as nutrient availability generally decreases in temperate regions at higher latitudes and altitudes (De Frenne and others 2013).

Second, the intensity of past fertilisation and associated nutrient management will determine the magnitude of legacies' persistence in the forest ecosystem. Region-specific nutrient management practices can influence the magnitude of response in soil properties more than the actual agricultural land-use type. Macdonald and others (2012) illustrated this by showing that soil P legacies arose more prominently across regions than between types of agricultural land use practiced prior to abandonment within each region. The regional phosphorus balance could reflect how nutrient management of phosphorus occurs within sites at a regional level. This is because the region is a collection of local farms, where each farm reports its total amount of P applied on fields, as well as its total outflow from harvest and grazing (see the report to the European Commission by Bomans and others 2005). Farm practices in regions with a surplus of P have often included excessive manuring of fields and meadows (Ringeval and others 2017) leading to long-term accumulation of P with major consequences for the environment and global nutrient management (Sattari and others 2012; Rowe and others 2016; Bouwman and others 2017).

Finally, N deposition is a global change driver that varies regionally and originates from intensive agriculture (fertilisation and animal husbandry) and burning of fossil fuels (Bobbink and others 2010). Acidification and eutrophication are effects of reactive N that influence ecosystem composition and function (De Schrijver and others 2011) at an ecosystem-specific critical load (Bobbink and others 2015). Critical loads for different deciduous forest types range from 10 to 20 kg N ha^{-1} y^{-1} (Bobbink and others 2010, 2015; Simkin and others 2016). Exceedance of critical loads potentially leads to leaching of compounds following acidification (Bobbink and others 2010). Eutrophication of the soil occurs by an enrichment of N (Bobbink and others 2010), which can lead to nutrient imbalances in plants, e.g. chronic shortages of P (Tao and Hunter 2012) unless supply of P is enhanced through other mechanisms such as increased phosphatase activity (Perring and others 2008). Nitrogen enrichment is therefore expected to alter P dynamics and legacies of prior fertilisation in post-agricultural soils.

Hypothesis: Legacies of Prior Agriculture in Temperate Forest are Context Dependent

Based on the published literature, we expect legacies of prior agriculture for five chemical soil properties important for plant growth when combining measurements from paired sites of post-agricultural and continuously forested land (ancient forest). More precisely, we expect higher concentrations of P and base cations, higher pH, lower concentrations of C and lower C/N in post-agricultural forest. The magnitude of these legacies is expected to be affected by gradients of soil characteristics, agricultural intensity and N deposition thus exhibiting a context-dependency:

1. Inherent soil characteristics relate to texture and underlying parent material of soil deposits, but equally to other edaphic factors such as wetness, relief and exposure. We expect that several variable observations of soil legacies (such as responses of base cations) between pairs of sites and multiple regions are attributable to differences in soil characteristics.
2. The magnitude of the cultivation legacy in post-agricultural forest soil will for one be relative to prior fertilisation intensity and nutrient management on the regional level. Such intensity could be reflected in concentrations of P due to its biogeochemical properties and potential of prolonged adsorption in the soil. In the absence of historical data, we test whether contemporary regional P surplus is associated with a higher legacy in soil P-concentrations in post-agricultural forests compared to the regions' ancient forests.
3. N deposition varies widely on the regional level, where we expect that higher rates of deposition increase responses of acidification (pH) and eutrophication (N), with possible side effects on P availability dependent on the land-use history of the site.

MATERIALS AND METHODS

Selection of Regions Along Gradients of Soil Characteristics, Regional P-Balance and N Deposition

We selected eight regions across gradients of soil characteristics, regional P-balance (surplus of P) and N deposition within temperate Europe (Figure 1). These regions span from Pärnu county in the Lääne-Eesti department in Estonia (N 58°8′45.1″) to the Loiret department (N 47°50′10.05″) in France (Table 1). We define a region as a large-scaled area with homogeneous macro-climatic conditions (mean annual temperature and precipitation) and topography (Table 1). For this purpose, we adopt the third level of the *Nomenclature of Territorial Units for Statistics* (NUTS) by the European Union (2015) for our regional boundaries (Table 1). We aggregated multiple NUTS-III entities to one region where the administrative boundaries were too detailed or where forest patches were on the border of two neighbouring entities (Table 1).

Invariable soil characteristics such as texture and underlying parent material of soil deposits can differ between post-agricultural and ancient forest within and across regions. To isolate legacy effects of prior agriculture in our comparison of ancient and post-agricultural forest soils, rather than detecting that sites with agricultural history occur on richer soils, we utilised a paired-plot approach within regions (Foote and Grogan 2010; Brudvig and others 2013; Bizzari and others 2015). Thus, we attempted to ensure that local inherent soil characteristics varied minimally within a given pair (Table 1, WRB classifications) while simultaneously controlling for overstorey composition (de la Peña and others 2016, see Supplementary Table S1.3). Differences in inherent soil characteristics between pairs (landscape scale) and the regional scale allow analysing responses to agriculture's legacy in relation to gradients in inherent soil characteristics.

Agricultural intensity on the regional level is estimated by the nutrient balance for P from a report of the Soil Service of Belgium for the year 2003 to the European commission (Bomans and others 2005). This is calculated per region on NUTS-II and III-levels as the total inflow of P that farmers report to their local governments (fertilisation and manure production) subtracted with the

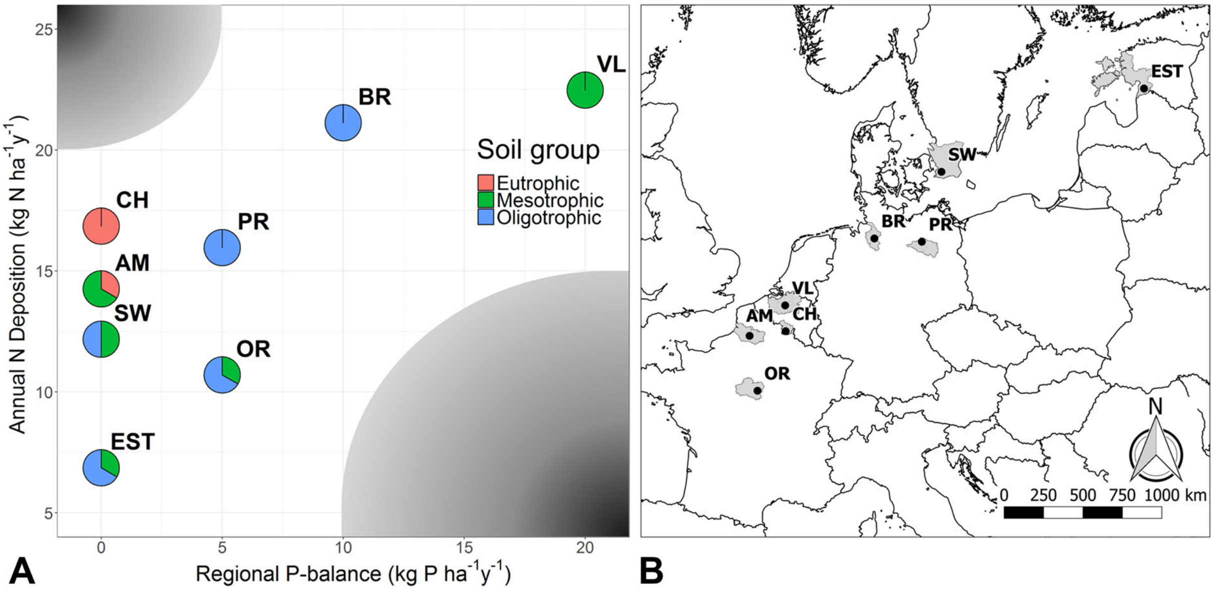

Figure 1. Design figure of region selection where three variables provide the context for soil property responses to prior agricultural land use. **A** Soil group, regional P-balance, N deposition provide the space for context in agricultural legacies. Soil group is a variable on the site level with three classes that group soil properties related to texture and underlying calcareous bedrock. Each of the pie charts represents the proportion of soil groups out of a total of six sites per region. N deposition and regional P-balance are continuous variables that vary on the regional level. Grey zones represent values that are deemed unlikely to occur in forest areas with agricultural history in Western Europe. **B** Locations of the eight regions with the following region codes: EST = Southern Estonia, SW = Southern Sweden, BR = Bremen (Germany), PR = Prignitz (Germany), VL = Vlaanderen (Belgium), CH = Chimay (Belgium), AM = Amiens (France), OR = Orléans (France). Corresponding NUTS codes for these regions are given in Table 1.

Table 1. Soil Samples and Their Main Attributes

Sample Code	NUTS-III	Land-use history	Forest area	Forest Age (y)	N deposition (kg N ha^{-1} y^{-1})	P-balance (kg P ha^{-1} y^{-1})	Long	Lat	Altitude (m)	MAT (°C)	MAP (mm)	Soil classification (WRB)
AM-A1	FR223—Somme	Ancient	Beaucamps-le-jeune	> 230	14.0	0	1.75718	49.82007	181	9.6	710	Eutric Cambisol
AM-A2	FR223—Somme	Ancient	Gentelles	> 230	13.9	0	2.43972	49.84222	120	10.0	658	Eutric Cambisol
AM-A3	FR223—Somme	Ancient	Mametz	> 230	14.9	0	2.7525	50.01992	128	9.8	676	Haplic Luvisol
AM-R1	FR223—Somme	Post-agricultural	Beaucamps-le-jeune	70	14.0	0	1.7405	49.82923	170	9.7	678	Calcaric Cambisol
AM-R2	FR223—Somme	Post-agricultural	Gentelles	70	13.9	0	2.42726	49.84303	86	10.1	652	Calcaric Cambisol
AM-R3	FR223—Somme	Post-agricultural	Mametz	70	14.9	0	2.75352	50.01988	120	9.8	676	Haplic Luvisol
BR-A1	DE937—Rotenburg	Ancient	Stellingdorf (Ge_W_O_03)	> 150	21.1	10	9.40361	53.34333	38	8.4	748	Gleyic Podzol
BR-A2	DE939—Stade	Ancient	Hohenhausen (Ge_W_O_14)	> 190	21.1	10	9.45906	53.3531	38	8.4	749	Gleyic Podzol
BR-A3	DE937—Rotenburg	Ancient	Weertzen (Ge_W_O_02)	> 130	21.1	10	9.396	53.32928	29	8.4	746	Gleyic Podzol
BR-R1	DE937—Rotenburg	Post-agricultural	Stellingdorf (Ge_W_O_08)	50	21.1	10	9.39556	53.33806	29	8.4	747	Gleyic Podzol
BR-R2	DE937—Rotenburg	Post-agricultural	Hohenhausen (Ge_W_O_01	20	21.1	10	9.45694	53.34667	36	8.4	749	Gleyic Podzol
BR-R3	DE937—Rotenburg	Post-agricultural	Weertzen (Ge_W_O_44)	60	21.1	10	9.41773	53.33144	34	8.4	752	Gleyic Podzol
CH-A1	BE326—Arr. Thuin	Ancient	Bois de Salles	> 240	16.9	0	4.25806	50.08051	233	9.4	933	Rendzic Leptosol
CH-A2	BE353—Arr. Philippeville	Ancient	Les réserves de Dailly	> 240	16.9	0	4.40258	50.05262	249	9.2	992	Rendzic Leptosol
CH-A3	BE353—Arr. Philippeville	Ancient	Gros tienne du Bi	> 240	16.9	0	4.44323	50.06725	199	9.6	922	Calcaric Cambisol
CH-R1	BE326—Arr. Thuin	Post-agricultural/intensive pasture	Monts trieu de l'air	50	16.9	0	4.25101	50.07163	226	9.3	935	Rendzic Leptosol
CH-R2	BE353—Arr. Philippeville	Post-agricultural/intensive pasture	Les réserves de Dailly	50	16.9	0	4.4045	50.05467	218	9.2	992	Rendzic Leptosol
CH-R3	BE353—Arr. Philippeville	Post-agricultural/intensive pasture	Gros tienne du bi	50	16.9	0	4.443	50.06801	179	9.6	922	Calcaric Cambisol
EST-A1	EE004—Lääne-Eesti	Ancient	Tali Reinu	> 120	6.9	0	24.68092	58.01923	76	5.4	664	Endogleyic Luvisol
EST-A2	EE004—Lääne-Eesti	Ancient	Laiksaare	> 120	6.9	0	24.81304	58.13339	47	5.4	663	Gleyic Luvisol
EST-A3	EE004—Lääne-Eesti	Ancient	Kikepera	> 120	6.8	0	24.85609	58.26674	37	5.5	665	Endogleyic Luvisol
EST-R1	EE004—Lääne-Eesti	Post-agricultural	Tali Reinu	60	6.9	0	24.72603	58.034	60	5.3	667	Endogleyic Luvisol
EST-R2	EE004—Lääne-Eesti	Post-agricultural	Laiksaare	60	6.9	0	24.7729	58.1205	47	5.4	665	Gleyic Luvisol
EST-R3	EE004—Lääne-Eesti	Post-agricultural	Kikepera	60	6.8	0	24.85907	58.30132	35	5.5	664	Epigleyic Podzol
OR-A1	FR246—Loiret	Ancient	Nogent North	> 170	10.7	5	2.75408	47.83968	152	11.0	679	Eutric Cambisol
OR-A2	FR246—Loiret	Ancient	Nogent Central	> 170	10.7	5	2.76104	47.83252	156	10.8	679	Eutric Cambisol
OR-A3	FR246—Loiret	Ancient	Nogent South	> 170	10.7	5	2.76411	47.83238	148	10.8	679	Eutric Cambsiol
OR-R1	FR246—Loiret	Post-agricultural	Nogent North	60	10.7	5	2.75408	47.84392	130	11.0	666	Calcaric Cambisol
OR-R2	FR246—Loiret	Post-agricultural	Nogent Central	60	10.7	5	2.76663	47.83518	129	11.0	672	Calcaric Cambisol

Table 1. continued

Sample Code	NUTS-III	Land-use history	Forest area	Forest Age (y)	N deposition (kg N ha^{-1} y^{-1})	P-balance (kg P ha^{-1} y^{-1})	Long	Lat	Altitude (m)	MAT (°C)	MAP (mm)	Soil classification (WRB)
OR-R3	FR246—Loiret	Post-agricultural	Nogent South	60	10.7	5	2.7664	47.83307	134	10.8	679	Calcaric Cambisol
PR-A1	DE40D—Ostprignitz-Ruppin	Ancient	1.7 km Maulbeerwalde	> 230	15.7	5	12.37876	53.17829	111	8.2	584	Haplic Albeluvisol
PR-A2	DE40F—Prignitz	Ancient	2.5 km nne Pritzwalk	> 230	15.7	5	12.19625	53.17175	75	8.3	575	Haplic Albeluvisol
PR-A3	DE40F—Prignitz	Ancient	3.1 km sw Meyenburg	> 230	15.4	5	12.20848	53.28882	108	8.1	590	Haplic Albeluvisol
PR-R1	DE40F—Prignitz	Post-agricultural	2.5 km sw Putlitz	70	16.5	5	11.96965	53.232	66	8.5	582	Gleyic Albeluvisol
PR-R2	DE40F—Prignitz	Post-agricultural	2.0 km se Putlitz	80	16.2	5	12.05946	53.23826	69	8.4	577	Haplic Albeluvisol
PR-R3	DE40F—Prignitz	Post-agricultural	1 km SW Sagast	70	16.5	5	11.9375	53.25991	79	8.4	581	Haplic Albeluvisol
SW-A1	SE224—Skåne län	Ancient	Torup (250)	> 210	12.2	0	13.20699	55.55432	65	7.7	647	Dystric Cambisol
SW-A2	SE224—Skåne län	Ancient	Skabersjö (58a)	> 170	12.2	0	13.19563	55.54342	50	7.8	640	Dystric Cambisol
SW-A3	SE224—Skåne län	Ancient	Skabersjö (74b)	> 170	12.2	0	13.30391	55.5577	61	7.7	660	Dystric Cambisol
SW-R1	SE224—Skåne län	Post-agricultural	Torup (251)	80	12.2	0	13.20736	55.5517	71	7.7	647	Dystric Cambisol
SW-R2	SE224—Skåne län	Post-agricultural	Skabersjö (62a)	60	12.2	0	13.20175	55.54378	57	7.7	648	Dystric Cambisol
SW-R3	SE224—Skåne län	Post-agricultural	Skabersjö (84 l)	70	12.2	0	13.33121	55.54688	63	7.7	669	Dystric Cambisol
VL-A1	BE234—Arr. Gent	Ancient	Aelmoeseneiebos (5 l)	> 240	24.3	20	3.80259	50.97501	24	10.2	758	Haplic Albeluvisol
VL-A2	BE242—Arr. Leuven	Ancient	Doode Bemde (Langerodebos)	> 240	19.9	20	4.63983	50.82343	36	10.2	786	Eutric Cambisol
VL-A3	BE211—Arr. Antwerpen	Ancient	Muizenbos	> 240	23.3	20	4.57108	51.19906	20	10.0	781	Gleyic Albeluvisol
VL-R1	BE234—Arr. Gent	Post-agricultural/intensive pasture	Aelmoeseneiebos (5 m)	40	24.3	20	3.80207	50.97549	21	10.2	758	Haplic Albeluvisol
VL-R2	BE242—Arr. Leuven	Post-agricultural	Doode Bemde (Langerodevijver)	50	19.9	20	4.64174	50.82799	28	10.2	781	Eutric Cambisol
VL-R3	BE211—Arr. Antwerpen	Post-agricultural	Muizenbos	50	23.3	20	4.57092	51.19965	17	10.0	781	Gleyic Albeluvisol

The sample code consists of concatenated information on the region, the land-use history and the pair number. AM = Amiens (France), BR = Bremen (Germany), CH = Chimay (Belgium), EST = Southern Estonia, OR = Orléans (France), PR = Prignitz (Germany), SW = Southern Sweden, VL = Vlaanderen (Belgium). The letters ''A'' and ''R'' separated by the hyphen, respectively, symbolise ancient or recent post-agricultural land-use history and ends with the pair number. NUTS-III codes are administrative regions according to the Nomenclature of Territorial Units for Statistics (NUTS) by the European Union (2015). Forest area is the name of either the forest, or the closest village centre. Forest age is based on the historical information in Supplementary information Table S1.2. N deposition is data extracted from the EMEP database. The phosphorus balance (P-balance) is calculated per region as the total inflow of P (fertilisation and manure production) subtracted with the total outflow (harvest and grazing) and expressed per area of agricultural land (kg P ha^{-1}). Coordinates are given as longitudes and latitudes, altitude in metres. Mean annual temperature (MAT) and mean annual precipitation (MAP) are extracted from the WorldClim database (http://www.worldclim.org/). The soil classification is in the taxonomy of the World Reference Base for Soil Resources (WRB) and is given in the last column for information. We classified our soil samples using local site descriptions and local forestry maps or regional soil maps.

total outflow (harvest and grazing), formulating a regional nutrient balance when expressed per area of agricultural land (kg P ha^{-1}). A positive balance (surplus) indicates an excess of P with potential risk of accumulation and eutrophication by leaching. A negative or zero balance indicates a potential depletion of nutrients. In the absence of historical data for P nutrient balances in European regions, we resort to the use of the contemporary values for the P nutrient management in these areas (Bomans and others 2005). We expect that the relative differences of the P-balance between the regions would still hold when using contemporary values for a historical context, i.e. we assume that regions with the highest current surplus likely also had the highest P surplus during the mid-twentieth century. This assumption would be worthy of further investigation.

The magnitude of N deposition between 1990 and 2010 has proven to be an important determinant of the adverse effects of reactive N in forest ecosystems (Dirnböck and others 2017). Interpolated values of model results from the EMEP database (version 2013, http://www.emep.int/) for the year 2000 were therefore used as the annual nitrogen deposition variable. The critical load concept highlights that we have robustly covered ecologically important variation in our choice of sites. For instance, two regions (OR, EST) are found below typical critical load exceedances, while, at the other extreme, two regions (VL, BR) have N deposition well in excess of a temperate forest understorey threshold of 18 kg N ha^{-1} y^{-1} (Bobbink and others 2015; Simkin and others 2016).

Selection of Forest Patches and Determining Their Land-Use History

We searched for three pairs of ancient and post-agricultural broadleaved forests in each of the eight regions, leading to 48 forest patches included in the study. These pairs consisted of forest patches that are nearby in a landscape context, with the median distance between two pairs being 760 m (supplementary information, Table S1.1). This paired approach allows for minimising differences in site characteristics such as texture, aspect and wetness and allows for isolating the legacies of previous land management rather than inherent differences of post-agricultural and ancient forest sites (Flinn and others 2005; Brudvig and others 2013). Forest types were mainly mesophytic with fresh deep soils and sandy to loamy soil textures (see Soil World Reference Base in Table 1).

The land-use history of these forest patches was determined by use of historical land-use maps (see Supplementary information Table S1.2), which predated 1850 for most regions. Forests that have been continuously present on land-use maps since the earliest reliable recording are considered as ancient, while reforestations on abandoned fields during mid-twentieth century are considered post-agricultural (Peterken 1996). This ''binary'' approach (Bürgi and others 2017) for classifying land-use history types (or land-cover types) has the drawback that subtleties in land management transitions might be missed, potentially leading to contrasting legacies of past agriculture. We minimised this issue by confining the period of cultivation abandonment to around 1950 (Cramer and others 2008) and by gathering data from multiple regions (Macdonald and others 2012; Verheyen and others 2017).

Canopy composition within paired forest patches was ideally as similar as possible and sharing multiple tree species (supplementary information, Table S1.3). The forest canopy often consisted of *Quercus robur/petraea*, *Fraxinus excelsior*, *Acer pseudoplatanus* and *Fagus sylvatica*. Patches with the presence of *Alnus* sp. were avoided due to unwanted confounding of N fixation effects, as well as being an indicator for high soil moisture content (idem with *Salix*). The presence of coniferous species was kept at a minimum, but a higher incidence in the northernmost region (EST) was unavoidable.

Soil Collection and Physicochemical Analyses

We collected a large volume of soil (ca 0.1 m^3) in each forest patch from a pit with a depth of 15 cm and surface of 70 × 100 cm. Roots, drainage lines and wet depressions were avoided as a location for sampling in the forest stands. The field campaign ran from October 2015 until February 2016, and its primary purpose was to provide material for a large mesocosm experiment, necessitating the collection strategy used even though composited samples could have been more representative for the entire forest patch. All 48 bulk soil samples were separately sieved (4 mm mesh, 5 mm for heavy soils) for homogenisation and removing of coarse organic material. We subsampled 500 ml from the 0.1 m^3 of homogenised soil and processed this through a 1-mm sieve for chemical analysis. Prior to chemical analysis, soil was dried to constant weight at 40°C for 48 h.

We analysed samples for pH-H_2O by shaking a 1:5 ratio soil/H_2O mixture for 5 min at 300 rpm and measuring with a pH metre Orion 920A with a pH electrode model Ross sure-flow 8172 BNWP, Thermo Scientific Orion, USA (Norm: ISO 10390:199). Total C (%) and N (%) concentrations were 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). Inorganic C content was measured after 1 g of dry soil was ashed for 4 h at 450°C by gradually increasing temperature. This procedure drives off organic C leaving only mineral carbon in the ashes, which were measured using a CNS elemental analyser. Subtracting inorganic C from total C gives the organic C (%). This organic C metric was used to calculate the C/N ratio by taking the ratio of organic C to total N.

Extraction of mobile soil cations (Ca, K, Mg, Na, and Al) was performed by extracting soil samples with a 1:5 soil/extractant ratio with ammonium lactate which consisted of lactic acid (88%), acetic acid (99%) and ammonium acetate (25%) at pH 3.74. The cations were measured using atomic absorption spectrophotometry. 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 $K^{+,}$ Ca^{2+}, Mg^{2+} and Na^+ over the sum of K^+, Ca^{2+}, Mg^{2+}, Na^+ and Al^{3+}. Total Ca and Fe concentration was measured by atomic absorption spectrophotometry (AA240FS, Fast Sequential AAS) after complete digestion of the soil samples with $HClO_4$ (65%), HNO_3 (70%) and H_2SO_4 (98%) in Teflon bombs for 4 h at 150°C. All P-concentrations were measured colorimetrically according to the malachite green procedure (Lajtha and others 1999). Total P was extracted after complete digestion of the soil samples with $HClO_4$ (65%), HNO_3 (70%) and H_2SO_4 (98%) in Teflon bombs for 4 h at 150°C. Soluble and readily soluble P was extracted in $CaCl_2$ (P_{CaCl2}; Simonis and Setatou 1996). Bio-available P, which is available for plants within one growing season (Gilbert and others 2009), was extracted in NaHCO3 (P_{Olsen}; according to ISO 11263:1994(E)).

Soil texture (% clay, % sand % silt,) was analysed with laser diffraction (Coulter Laser LS 13 320 (SIP-050D2) with auto-sampler) after removal of organic material with H_2O_2 (28.5%) and dispersing the sample with Sodium polyphosphate (6%).

Data Analysis

All data analyses and handling was performed in R (R Core Team 2017). Firstly, we clustered data on invariable soil properties related to soil texture and properties of calcareous bedrock (clay, silt, sand and concentrations of total Ca, total Fe and inorganic C, Supplementary information Figure S2.1) using the *hclust* function in R (R Core Team 2017). The three resulting clusters from this analysis were used as a categorical variable ''*Soil group*'' in the statistical analyses. The results from the cluster analysis were subsequently analysed for principal components to check how the soil groups from the cluster analysis align with all centred and scaled continuous variables to aid in interpretation (Supplementary information Figure S2.2). In addition, we calculated correlations between all soil variables with Spearman's rank correlation coefficients (Supplementary information Figure S2.3) to aid the interpretation of the soil clustering procedure, the principal component analysis and our a priori selection of response variables. We apply the relative terms ''Eutrophic'', ''Mesotrophic'' and ''Oligotrophic'' to our soil groups as they reflect major differences in soil fertility between our study forests (as in Hirst and others 2005; Balkovič and others 2012). Principal component analysis (Supplementary information Figure S2.2) shows that alignment of the Eutrophic soil group with concentrations of inorganic C and total Ca indicate the calcareous properties of these soils, resulting in higher pH and proportion of extractable base cations (BC). Mesotrophic soils adopt an overall intermediate position in soil properties, which is visualised in their position around the origin of the principal component analysis. Oligotrophic soils align with high Sand and a high C/N which both correlate with high acidity and lower nutrient concentration (Supplementary information Figure S2.3).

We then tested whether land-use history's (LUH) effect on *pH*, organic carbon (org C), total nitrogen (tot N), C/N, proportion of extractable base cations (BC), total phosphorus (P_{total}) and bio-available phosphorus (P_{Olsen}) was context dependent by considering the gradients of invariable soil characteristics (soil group), nitrogen deposition (N_{dep}) and P nutrient management (P-balance). The land-use history of the forest is a categorical variable with two levels indicating whether a forest is continuously forested since at least 1850 (*Ancient*) or whether a forest has been established around 1950 on abandoned arable land (*post-agricultural*). Soil group is a categorical variable with three levels that reflects the inherent soil fertility, as the variable is a product of the cluster analysis on soil properties that relate to texture and calcareous bedrock. To test whether legacies of prior agriculture depend on the soil group, an interaction of LUH*Soil group was added in the explanatory models along with the constituent main effects (hypothesis 1). Testing the dependence of agricultural legacies in soil properties along the nitrogen deposition gradient was conducted by adding an interaction term of LUH*N_{dep} (hypothesis 3). These two interaction terms and their main effects formed the fixed factors of the base model (Eq. 1). The interaction of N_{dep} and soil group was not included in this model due to a limited spread of one soil group (eutrophic) along the N deposition gradient. To test whether total and bio-available phosphorus concentrations in post-agricultural forest are higher in regions with greater P surplus (hypothesis 2), we add in an extra interaction term between LUH*P-balance to model responses of total phosphorus (P_{total}) and bio-available phosphorus (P_{Olsen}). The phosphorus balance could also interact with nitrogen deposition to determine responses of P_{total} and P_{Olsen} (hypothesis 3) so a final term of N_{dep}*P-balance was added to the model structure of these properties (Eq. 2). We adopted the use of hierarchical mixed-effects models to test these effects, using the *lme4* package and the function *lmer* (Bates and others 2014) with *Pair* within *Region* incorporated as a nested random effect. We used maximum likelihood estimation to allow the calculation of a likelihood ratio test when comparing between models.

Equation 1: base model

$$\text{Response variable} \sim \text{LUH} + \text{Soil group} + N_{\text{dep}} + \text{LUH} * \text{Soil group} + \text{LUH} * N_{\text{dep}} + (1|\text{Region}/\text{Pair}) \tag{1}$$

Equation 2: Expanded base model with P-balance as an additional interactive term to test responses of soil P

$$P \sim \text{base model} + \text{P}-\text{balance} + \text{LUH} * \text{P}-\text{balance} + N_{\text{dep}} * \text{P}-\text{balance} + (1|\text{Region}/\text{Pair}) \tag{2}$$

We then found the most parsimonious models for explaining variation in each response variable using stepwise backwards model selection and a *Chi-squared* test in the *drop1* function (R Core Team 2017) for calculation of p values on the likelihood ratio statistic. We consider $p < 0.05$ as significant and $p < 0.1$ as supporting minor evidence for an effect. Nonsignificant interactions with the highest p values were left out of the models first, prior to testing the constituent main effects. Main effects were retained, even if nonsignificant, if they appeared in interaction terms. Normality of the residuals in the final model was controlled by performing a Shapiro–Wilk test with the *shapiro.test* function (R Core Team 2017). If normality in the residuals could not be assumed, a log transformation of the response variable was performed for right-tailed response variables and a squared transformation with left-tailed response variables. Goodness-of-fit (R^2 values) for linear mixed-effects models were calculated using the *r.squaredGLMM* function from the *MuMIn* package (Barton 2017), which lists both the marginal R^2 (variance explained by fixed factors only) and the conditional R^2 [variance explained by both fixed and random effects, Nakagawa and Schielzeth 2013)].

RESULTS

Post-agricultural forest had significantly ($p < 0.05$) higher pH, higher phosphorus concentration (P_{Olsen} and P_{total}) and lower C/N compared to ancient forest (Figure 2 and Table 2). Soil group affected responses of pH, proportion of extractable base cations and total P-concentration ($p < 0.05$) as main effects, with the highest values of these three variables in rich ''eutrophic'' soils and the lowest values in the poor ''oligotrophic'' soils, with ''mesotrophic'' soil having intermediate means. Higher N deposition is associated with lower pH ($p < 0.05$) across all forest sites as a main effect. Crucially, we found that gradients of soil characteristics, P nutrient management and N deposition affected the magnitudes of organic C, total N, bio-available Olsen P and total P-concentrations in interaction with the forests' land-use history (Figure 2, Table 2).

Firstly, we found minor evidence for a dependence of total N concentration on the land-use history between soil groups ($p < 0.1$), as lower total N concentrations in post-agricultural forest only occurred in mesotrophic and oligotrophic soils (Table 2).

Secondly, we found that the magnitude of phosphorus (P) legacy in post-agricultural forest is dependent on the regions' phosphorus balance, with higher P-concentrations in regions with greater surplus of P. The interaction term for land-use history and P-balance (which we assume is a proxy for nutrient management intensity of past agriculture) is significant for modelling responses of P_{total} ($p < 0.05$) but only with minor evidence for P_{Olsen} ($p < 0.1$).

Finally, we found interactions of N deposition and land-use history on concentrations of organic C ($p < 0.05$) but with minor evidence on total N

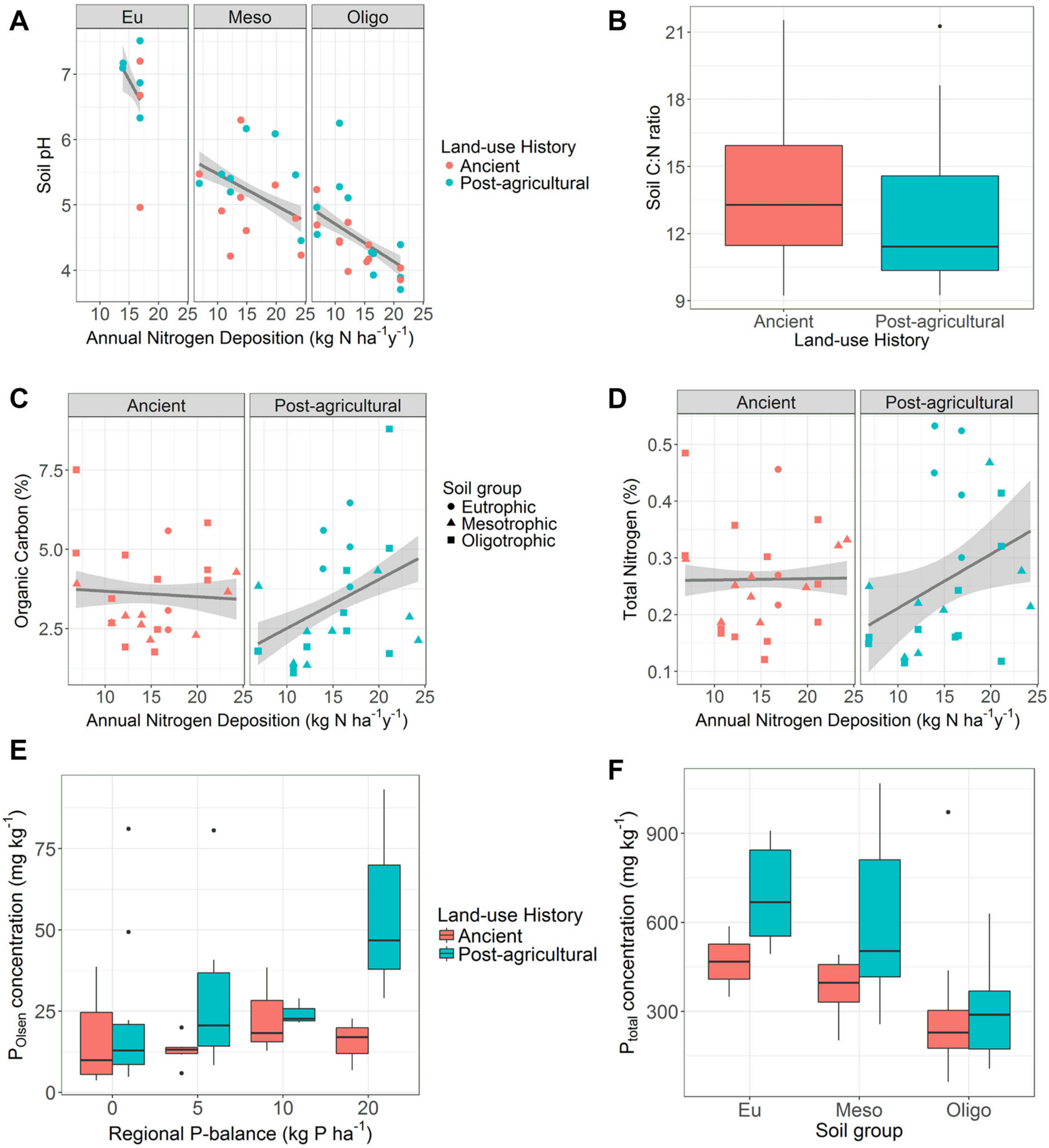

Figure 2. Context-dependent legacies commonly shape soil properties in post-agricultural forests. **A** Soil pH as a function of nitrogen deposition within each soil group, with post-agricultural forest soils having a higher pH on average ($p < 0.05$) and a 95% confidence interval on the computed means. **B** Boxplot of C/N ratio showing lower values in post-agricultural forest ($p < 0.05$). **C** Organic C (%) increases in post-agricultural forest with increasing N deposition, but no N deposition effect occurs in ancient forest with a 95% confidence interval on the computed means ($p < 0.05$). **D** Organic N (%) increases in post-agricultural under higher N deposition, but no N deposition effect occurs in ancient forest with a 95% confidence interval on the computed means ($p < 0.1$). **E** The difference in Olsen P of post-agricultural forest soils compared to ancient forest soil increases with regional P-balance ($p < 0.1$). **F** Difference in concentrations of total P between ancient and post-agricultural forest is dependent on soil group ($p < 0.05$). The sorption of P is highest in eutrophic clay and carbonate rich soil, reflecting its biogeochemical nature.

Table 2. Regression Coefficients and Likelihood ratio Tests (LRT) of Predictors on Soil Chemical Responses

Response	Mean intercept	LUH	Soil group	N_{dep}	LUH*Soil group	LU* N_{dep}	P-balance	LUH*P-balance	N_{dep}*P-balance	R^2_m	R^2_c
pH	7.35	*Coefficient* Post-ag. **+ 0.405** *LRT* **6.56***	*Coefficients* Meso **− 1.49** Oligo **− 2.31** *LRT* **25.48*****	*Coefficient* **− 0.054** *LRT* **8.61****	–	–				0.74	0.74
log(C/N)	2.61	*Coefficient* Post-ag. **− 0.10** *LRT* **5.54***	–	–	–	–				0.05	0.59
Org C	5.27	*Coefficient* Post-ag. − 3.08 *LRT* *0.45*	*Coefficients* Meso **− 1.88** Oligo **− 1.21** *LRT* **6.87***	− 0.025	–	*Coefficient* Post-ag*N_{dep} **0.176** *LRT* **4.55***				0.26	0.33
Tot N	0.341	*Coefficient* Post-ag. − 0.013 *LRT* 0.005	*Coefficients* Meso **− 0.077** Oligo **− 0.075** *LRT* **13.32****	*Coefficient* − 0.001 *LRT* 0.805	*Coefficients* Post-ag.*-Meso − 0.14 Post-ag.*Oligo − 0.17° *LRT* 5.53°	*Coefficient* Post-ag. 0.009° LRT 3.06°				0.45	0.5
BC^2	0.886	–	*Coefficients* Meso **− 0.229** Oligo **− 0.456** *LRT* **14.19*****	–	–	–				0.40	0.49

Table 2. continued

Response	Mean intercept	LUH	Soil group	N_{dep}	LUH*Soil group	LU* N_{dep}	P-balance	LUH*P-balance	N_{dep}*P-balance	R_m^2	R_c^2
		Coefficient					*Coefficients*	*Coefficients*			
$\log(P_{Olsen})$	2.42	Post-ag. **+ 0.293**	–	–			0.019	Post-ag. 0.039	–	0.25	0.55
		LRT **8.06****					*LRT 2.59*	*LRT* 2.89°			
		Coefficient	*Coefficients*				*Coefficients*	*Coefficient*			
$\log(P_{total})$	6.43	Post-ag. **+ 0.047**	Meso **− 0.599**	–			− 0.020	Post-ag. **0.037**	–	0.26	0.61
			Oligo **− 0.801**								
		LRT **5.25***	*LRT* **6.94***				*LRT 0.264*	*LRT* **4.16***			

Regression coefficients are provided in units of the response variable per unit of predictor variable. Response variables include pH, organic C (org C, %), total N (%), C/N, proportion of extractable base cations (BS), Olsen P-concentration (P_{Olsen}, mg kg^{-1}) and total P-concentration (P_{total}, mg kg^{-1}). Explanatory variables are land-use history (LUH, Ancient or post-agricultural), soil group (Eutrophic, Mesotrophic, Oligotrophic), N deposition (N_{dep}, kg N ha^{-1} y^{-1}) and P-balance (kg P ha^{-1}). Regression coefficients and likelihood ratio test statistics for main effects and interaction terms of the most parsimonious model are listed with significant terms ($p < 0.05$) in bold. p values of these terms are represented as significance levels (0.1°, 0.05, 0.01**, 0.001***). Effects on $p < 0.1$ are not listed in bold and only bear the ''°'' marker to show that there is minor support for evidence of the effect. Regression coefficients for categorical variables are relative to the intercept, which is ''Ancient'' for LUH and ''Eutrophic'' for soil group. Continuous variables (N_{dep}, P-balance) have slope coefficients. Random intercept terms for Pair within Region were calculated with mean intercept values being listed here. The goodness-of-fit is given as a marginal R^2 (includes only fixed effects) and a categorical R^2 (includes random effects).*

($p < 0.1$) We found higher total N and organic C concentrations in post-agricultural forest with increasing N deposition, while total N and organic C concentrations in ancient forest remained unchanged (Table 2 and Figure 2).

DISCUSSION

Combining soil data from 24 paired sites of ancient and post-agricultural forests across eight European regions successfully elucidated consistent legacies of past land use. As expected, we observed an overall higher P-concentration, higher pH and lower C/N ratio in post-agricultural forest compared to ancient forest. The magnitude of these legacies was affected by gradients of soil characteristics, P nutrient management on the regional level and N deposition thus exhibiting a context-dependency. First, we found that three soil groups characterised the inherent fertility of the soils and determined the proportion of extractable base cations, pH and concentrations of total N, organic C and total P. Second, regions with greater current surplus of P from agriculture experienced the highest P legacy in post-agricultural forests. Finally, we found that increasing N deposition coincided with a lower pH across forests and increasing total N and organic C concentrations in post-agricultural forest. These results suggest that (1) land-use legacies from cultivation consistently determine soil property responses in post-agricultural forest and (2) differences in the magnitude of response to land-use history can relate to the regional and environmental context, including soil characteristics, regional surplus of P and nitrogen deposition.

Inherent soil characteristics are important when comparing legacies of prior agriculture between regions and sites as portrayed in the difference in the proportion of extractable base cations, pH and agricultural phosphorus legacies that we observed between the three soil groups (hypothesis 1). Forests on abandoned fields with carbonate and clay-rich soils exhibited the highest total P-concentrations (694 mg P/kg), likely due to strong retention of P after cultivation (von Wandruszka 2006). This result was in contrast to ancient forest on sandy oligotrophic soil (292 mg/kg), as these soils are capable of retaining P only by adsorption with Fe/Al oxides which is generally lower than sorption by clay minerals (Gérard 2016). The large regional differences in soil characteristics consequently determined the P legacy effect.

The magnitude of phosphorus legacy in post-agricultural forest was furthermore affected by the P-balance in the regions (hypothesis 2). Post-agricultural forests had higher total P-concentrations (P_{total}, $p < 0.05$) and bio-available P (P_{Olsen}, $p < 0.1$) concentrations in regions with greater surplus of P, where fields and meadows are prone to intensive fertilisation (Ringeval and others 2017). Since P is particularly persistent in soils (Fisher and Binkley 2000), concentrations of P_{total} are excellent indicators of prior cumulative fertilisation. P_{Olsen} reflects the labile P pool, which is thought to be available for immediate biological uptake (Gilbert and others 2009), and consists of phosphate in the soil solution or phosphate that can rapidly desorb or mineralise from inorganic or organic soil compounds (De Schrijver and others 2012b). In Flanders (Belgium), a region with a 20-kg surplus of P per ha of agricultural land, P_{Olsen} in post-agricultural forest was on average 56.3 mg/kg, which was more than triple the 15.5 mg/kg in paired ancient forests. A biological consequence of this dependence of P legacy on regional P-balance is that typical forest plants recruit poorly in post-agricultural forest under high nutrient stocks (Honnay and others 2002; Baeten and others 2010) and are therefore likely less inhibited in areas with a lower P-balance (Brunet and others 2012).

Study regions with higher N deposition exhibited responses of acidification and eutrophication in, respectively, pH and concentration of total N as hypothesised (hypothesis 3). The pH was 0.56 units lower across soil groups for each 10 kg N ha^{-1} y^{-1} of deposition. This acidifying response magnifies the risk that Fe/Al oxides leach in poorly buffered oligotrophic soils (Lukac and Godbold 2011), underlining that these systems are most susceptible to acidification (Bobbink and others 2015). Aside from acidification, greater N deposition is associated with increased organic C and total N concentration but only in post-agricultural forest. We identify two possible explanations why we found signals of an accumulation of soil organic matter in post-agricultural forest under high N deposition. First, decomposer communities of post-agricultural forests may be less adapted to decomposition in high acidity than decomposer communities of ancient forest (Fichtner and others 2014; Tardy and others 2015). Second, it is likely that N deposition has stimulated an acceleration in forest growth and C storage in young temperate deciduous forests (Pretzsch and others 2014; Fowler and others 2015). This dependence of N deposition on forest land-use history on responses of organic C and total N could reveal why responses of eutrophication by N deposition were found to be less clear in temperate forests as opposed to other ecosystems such as grassland and heathland (Bobbink and others 2010; De Schrijver and others 2011; Verheyen and others 2012, but see Dirnböck and others 2014).

Legacies of prior agriculture can be important drivers of global change (Foster and others 2003) in temperate forest in interaction with other environmental changes (Perring and others 2016). With our results, we show that agricultural legacies across temperate forest sites are elucidated when considering differing soil characteristics, regional phosphorus nutrient management and nitrogen deposition on a regional level. Identifying gradients that have influenced the magnitude of agricultural legacies is key to informing how, where and why forest ecosystems respond to contemporary environmental change.

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