Litter quality and the law of the most limiting: Opportunities for restoring nutrient cycles in acidified forest soils

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HIGHLIGHTS

- Rich litter (RL) is defined as leaf litter promoting fast soil nutrient turnover.
- In areas of high N deposition, N is no longer limiting.
- In this context base cations rather than C/N are determining litter quality.
- RL leads to increased earthworm biomass and topsoil base saturation.
- RL is functional as a restoration measure, even in poorly buffered sandy soils.

GRAPHICAL ABSTRACT
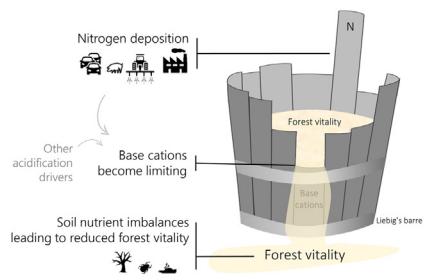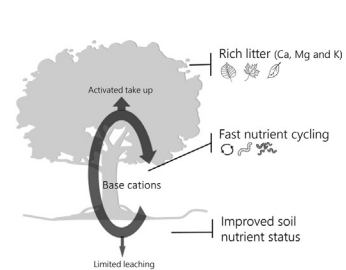
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ABSTRACT

The adverse effects of soil acidification are extensive and may result in hampered ecosystem functioning. Admixture of tree species with nutrient rich litter has been proposed to restore acidified forest soils and improve forest vitality, productivity and resilience. However, it is common belief that litter effects are insufficiently functional for restoration of poorly buffered sandy soils. Therefore we examined the effect of leaf litter on the forest floor, soil chemistry and soil biota in temperate forest stands along a range of sandy soil types in Belgium, the Netherlands and Germany. Specifically, we address: i) Which tree litter properties contribute most to the mitigation of soil acidification effects and ii) Do rich litter species have the potential to improve the belowground nutrient status of poorly buffered, sandy soils? Our analysis using structural equation modelling shows that litter base cation concentration is the decisive trait for the dominating soil buffering mechanism in forests that are heavily influenced by atmospheric nitrogen (N) deposition. This is in contrast with studies in which leaf litter quality is summarized by C/N ratio. We suggest that the concept of rich litter is context dependent and should consider Liebig's law of the most limiting: if N is not limiting in the ecosystem, litter C/N becomes of low importance, while base cations (calcium, magnesium, potassium) become determining. We further find that on poorly buffered soils, tree species with rich litter induce fast nutrient cycling, sustain higher earthworm biomass and keep topsoil base saturation above a threshold of 30%. Hence, rich litter can trigger a regime shift to the exchange buffer domain in

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sandy soils. This highlights that admixing tree species with litter rich in base cations is a promising measure to remediate soil properties on acidified sandy soils that receive, or have received, high inputs of N via deposition.

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1. Introduction

Nutrient cycling is one of the key ecosystem functions underpinning ecosystem services (Lavelle et al., 2003). A balanced return of nutrients to the forest soil is crucial in assuring stable production and vital ecosystems (Carnol and Bazgir, 2013). Yet, many temperate forests are characterized by disrupted element cycling and soil nutrient imbalances as a consequence of past and present human activity (Steffen et al., 2015). Particularly nutrient depletion by practices such as litter raking, plantation forestry using coniferous monocultures and atmospheric deposition of sulphur (S) and nitrogen (N) have led to widespread acidification of forest ecosystems (De Schrijver et al., 2006; Ulrich, 1991). Effects associated with acidification, including the loss of base cations (calcium (Ca), magnesium (Mg), potassium (K) and sodium (Na)) and mobilization of aluminum (Al), are adverse for numerous living organisms (Bowman et al., 2008; De Schrijver et al., 2012; Van Ranst et al., 2002). These disturbed nutrient cycles, alongside the lingering excess of N, jeopardize the potential diversity that forests can harbor (Emmer et al., 1998; Galloway et al., 2008; Maskell et al., 2010; Verstraeten et al., 2013) and have been linked to an overall reduced forest vitality (Lucassen et al., 2014; Tomlinson, 2003; Falkengren-Grerup and Lakkenborgkristensen, 1994; Hevia et al., 2019).

Several avenues have been explored in recent decades to curb forest soil acidification and its negative effects on tree vitality (Hüttl and Schneider, 1998). A first strategy focused on the abiotic soil compartment, augmenting soil pH by extensive application of lime to forest soils, yet most of these efforts failed (Kreutzer, 1995; Lundström et al., 2003; Hüttl and Schneider, 1998). Subsequently, multiple studies have theorized that the admixture of tree species with nutrient rich, easy degradable litter (further: rich litter species) may be a more successful strategy to reduce the effects of soil acidification and to restore nutrient cycles (Kooch and Bayranvand, 2017; Carnol and Bazgir, 2013; Emmer et al., 1998; Van Nevel et al., 2014; Hommel et al., 2007). Rich litter is the basis of fast nutrient turnover (Hommel et al., 2007). In this theory, tree species that produce rich litter, support a diverse belowground community that readily breaks down the input of organic material (OM). Subsequently this leads to enhanced incorporation and processing of fresh organic material, leading to an overall fast turnover of soil organic matter (SOM) and nutrients. This can finally result in augmented aboveground productivity, reduced nutrient limitations and feedback to the canopy as to further stimulate enhanced nutrient cycling (Prescott, 2002; Muys and Granval, 1997). In view of this theory, coniferous plantations and low tree diversity stands are actively converted to mixed broadleaved forests (Kint et al., 2009), yet results remain variable. This may be due to the fact that litter degradability and nutrient composition between species and even within species between sites may vary considerably (Berg and McClaugherty, 2008) and that site specific edaphic factors also affect decomposition dynamics (Brock et al., 2019; Verstraeten et al., 2018).

To date, studies on tree species litter quality and effects typically discuss the amount of recalcitrant carbon (C) compounds, such as lignin, in combination with the N content of the litter. Hence, litter decomposability is frequently summarized by the C/N ratio (Maes et al., 2018; Melillo et al., 1982; Moore et al., 2011; Satti et al., 2003; Wittich, 1953). This may be valid for forests where N availability typically is the prime limiting factor for growth (Fisher and Binkley, 2013). However, for a multitude of forests in industrialized regions, N availability has drastically increased due to anthropogenic factors. The atmospheric deposition of reactive N has more than doubled over the past century (Denman,

2007) and is expected to increase even further in many regions around the world (Galloway et al., 2004; Rockström et al., 2009). Moreover, many forests around the globe are located on marginal, often acidic soils and thus cycling of base cations may be an important limiting factor as well (Šantrůčková et al., 2019; Slessarev et al., 2016). Under such conditions, litter C/N ratio may therefore not be the most suitable indicator of tree species litter quality.

During acidification, aluminum in the soil solution increases drastically and the soil cation exchange complex (CEC) becomes loaded with aluminum ions that sorb more strongly to it compared to base cations (Chadwick and Chorover, 2001). As a result, soil restoration is challenging and becomes progressively difficult with increasing CEC of the soil (Desie et al., 2019; Verstraeten et al., 2018). For sandy soils, which are characterized by low CEC, this implies, however, that their predominant problem, i.e. the low CEC buffer capacity that has allowed them to rapidly degrade, also becomes their advantage, as there is less aluminum to compensate for and the soil can more easily escape from the negative spiral associated with soil acidification (Desie et al., 2019). Interestingly however, this potency seems to be partially missed in earlier studies as the potential of admixing rich litter for soil restoration focuses primarily on soils with a relative high CEC whereas for poorly buffered sandy soils rich litter is believed to have less or even no potential, with the same argument of having low buffering conditions (Hommel et al., 2007; Maes et al., 2018; Van Nevel et al., 2014).

Hence, in this study, we hypothesize that 'rich litter' is also functional in poorly buffered, sandy soils. For this purpose we aim at revisiting the concept of "rich litter" in a context of high N deposition. Therefore, this study targeted forests on sandy soils where we could explore the idea of admixing "rich litter" tree species as a measure for soil restoration. Specifically, we address the following research questions: i) Which litter traits have most effect on soil chemical properties, humus quality and burrowing soil fauna in forest on acidified sandy soils (i.e. what is 'rich litter' for this context?) and ii) Has the admixture of this rich litter species the potential to substantially improve the nutrient status of poorly buffered, sandy soils?

2. Materials and methods

2.1. Study region and sampling design

The study region is located on Pleistocene deposits of the West-European sand belt (Fig. 1) and stretches from Northern Belgium to the Netherlands and the border area with Germany. Characterized by a temperate climate, the mean annual precipitation (MAP) in the study region is circa 800 mm and the mean annual temperature (MAT) is 10.5 °C. Fourteen forest sites on sandy soils were selected and in each site, plots containing a tree species in monoculture were sampled. In total 50 of these monoculture-plots of 12 different tree species were sampled with variable numbers of replications ranging from 1 to 8. (Tables 1 and S1 for details of the plots and species sampled). Only for the species *Alnus incana* and *Prunus padus* no replicates could be sampled (Table 1). The confounding in tree species and site for these two plots was addressed by adding covariates to the model in order to account for site specific effects.

By evaluating previous land use based on historical maps and by soil auger descriptions (FAO, 2006) we ensured that all monoculture plots within a study site were located on a similar soil type and had comparable land use history. Monoculture plots were omitted from the study when differences in soil type or land use history within a site were
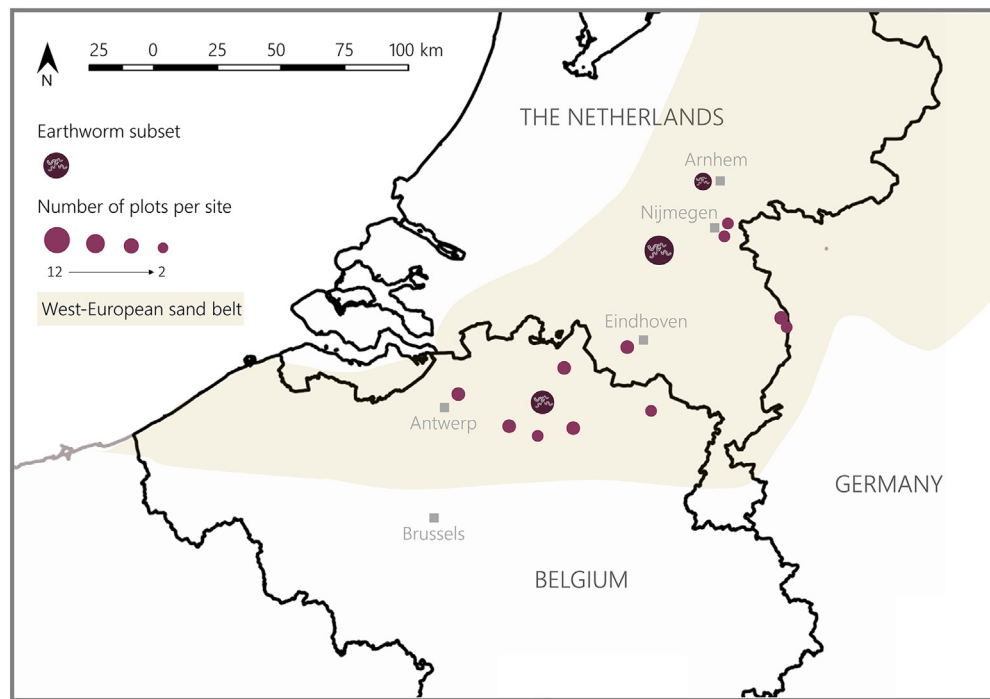
Fig. 1. Study region located over Belgium, the Netherlands and Western Germany. The West-European sand belt is the region where Pleistocene sands were deposited and is indicated by the yellow layer (based on Beerten et al. (2014)). Study sites are indicated by purple dots. The size of the dots indicates the amount of plots sampled per site (ranging from 1 to 12). N = 50. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

apparent. In order to minimize effects of non-plot species, our single species plots were established on sufficient distance from adjacent plots based on visual inspection of litter fall in autumn (ranging from 10 m to 600 m). For this study, only plots on sand or loamy sand were selected. Plots with a high loam or clay content (>40%) were discarded from the experiment. Soil type varied between sites including Arenosols, Cambisols, Podzols and Anthrosols. To account for the difference between anthropogenic influenced soil types and others, we corrected for land use legacy in the analysis (vide infra). This research was focused on pure rain-fed sandy soils, therefore plots that were found to be under influence of groundwater were excluded from further analysis.

In this study, we approached nutrient status of the forest belowground ecosystem by assessing nutrient concentrations in all compartments separately. We did not measure fluxes or turnover rates between individual compartments.

2.2. Sampling and laboratory analysis

In summer 2017, soil samples were collected in each plot (n = 50). Five mineral soil samples were randomly taken in each plot from two depths (0–10 cm and 20–30 cm) and merged in one composite sample per depth for chemical analysis. Mineral soil depths start under the forest floor layer and thus not at the surface (Zanella et al., 2014). We chose these depth intervals to assure we sample a topsoil layer under direct influence of tree species litter input and the subsoil layer which is less directly impacted by tree species but with possible indications of legacies. We determined organic matter content by weight loss-on-ignition (LOI) after burning samples at 550 °C for a minimum of 6 h. Soil pH, nitrate (NO_3^-), ammonium (NH_4^+) and available ion concentration were determined in salt extracts (after mixing fresh soil (17.5 g) with 50 ml 0.2 M NaCl solution). The pH of the solution was measured immediately using a combined pH electrode (radiometer and a

Table 1
Values of litter properties, forest floor characteristics and topsoil (0–10 cm) chemistry per tree species. Tree species are ranked based on the number of observations (#obs). Leaf litter cation contents are expressed as g/kg dry material and aluminum concentration as g/kg dry soil. Earthworms were sampled on a subset of 3 sites.

Tree species	#obs	Leaf litter quality			Forest floor		Topsoil chemistry			#obs	Earthworms	
		C/N ratio	Base cations g/kg	Calcium g/kg	Thickness O cm	Thickness OF + OH cm	BS %	pH-NaCl	Al^{3+} g/kg		Biomass g/m²	Count
Pinus sylvestris	8	40.6	9.1	5.2	7.4	6.9	25.2	3.3	1.6	2	1.8	11
Tilia cordata	8	29.1	25.0	11.9	4.3	1.0	39.6	3.5	1.2	3	14.9	57
Quercus robur	8	34.4	15.4	7.2	9.8	6.8	27.1	3.2	1.7	3	3.3	61
Prunus serotina	5	35.5	23.8	8.9	1.7	0.7	37.4	3.3	1.4	2	5.0	69
Acer pseudoplatanus	5	30.7	20.5	11.7	4.4	3.0	30.1	3.2	1.7	0		
Betula pendula	5	32.5	18.4	8.1	5.4	4.9	18.7	3.2	2.0	2	5.5	84
Fagus sylvatica	3	33.8	14.3	4.9	6.8	4.3	21.1	3.2	2.0	3	1.3	22
Prunus avium	2	43.4	34.2	13.0	2.9	0.0	71.1	4.2	0.1	0		
Pseudotsuga menziesii	2	22.6	11.7	6.5	3.3	1.8	19.3	3.3	1.6	1	0.0	0
Pinus nigra	2	34.6	8.1	5.0	4.1	1.8	27.4	3.2	1.0	1	1.3	48
Alnus incana	1	21.3	22.6	17.6	0.5	0.2	32.1	3.6	1.6	1	1.0	44
Prunus padus	1	23.2	29.6	20.8	0.4	0.0	60.8	3.6	0.7	1	8.5	36

TIM840 pH meter). Plant available phosphorus (P) was determined by bicarbonate extraction (3 g of dry soil shaken with 100 ml of 0.5 M NaHCO$_3$) (Olsen et al., 1954), and CEC and base saturation (BS) by mixing an amount of dry soil equivalent of 5 g fresh soil in 200 ml 0.2 M SrCl (Liu et al., 2001). Soil extracts were collected under vacuum conditions with Teflon pore water samplers (rhizon, Eijkelkamp Agrisearch Equipment, the Netherlands). In order to determine total element concentrations in soil material, 200 mg of ground, homogenized and dried sample was digested for 17 min with 4 ml 65% HNO$_3$ and 1 ml 30% H$_2$O$_2$ (Milestone Ethos D – Microwave Labstone) (Jin et al., 1999). Total concentrations of Ca, Mg, Al, iron (Fe), manganese (Mn), P, S, silicium (Si) and Zinc (Zn) were measured with an Inductively Coupled Plasma Spectrophotometer (ICP-OES, ICAP 6300 ARCOS MV, Spectro). NO$_3^-$, NH$_4^+$ and phosphate (PO$_4^{3-}$) concentrations were determined colorimetrically with a Seal auto-analyser III, using salicylate, hydrazin sulphate and ammoniummolybdate/ascorbic acid reagent, respectively. Chlorine (Cl$^-$) was determined colorimetrically with a Bran + Luebbe auto-analyser III system with mercuritiocynide. Na$^+$ and K$^+$ were determined with a flame spectrophotometer Sherwood Model 420 Flame Photometer (Technicon Corporation). Soil descriptions were executed on each site according to WRB guidelines (IUSS Working Group WRB, 2015). On each site an additional soil sample of the subsoil (C-horizon) was sampled and used for texture analysis (laser diffraction particle size analyzer - LS 13320).

In each plot the humus layer was described (n = 3) following the European humus reference base, Zanella et al., 2014). Thickness of the litter (OL), fragmentation (OF) and humic (OH) layers was measured and humus type was determined using the humus index (HI) (Ponge et al., 2002). Further analysis was based on the mean of the 3 replications (for HI the median).

In October 2017, fresh leaf litter was collected in every plot by catching 10 leaves falling from the canopy in the center of the plot. Leaf litter samples were oven dried at 60 °C and ground before chemical analysis. Total C and N content of the leaf litter were determined by combustion with a CN-elemental analyzer (total combustion at 900 °C, Flash 2000 series, Thermo Scientific). Total element contents (P, Ca, Mg, K, Na, Cu, Fe, Mn) of the leaf litter were determined after calcination (500 °C) and acid digest extraction in nitric acid, using ICP-OES analysis. The total base cation content was defined as the sum of Ca, Mg, K and Na content of the leaf litter.

Soil biota were sampled in November 2016 and 2017 on a subset of 19 plots located over three sites: Kasterlee (B), Heesch (NL) and Doorwerth (NL). Soil macrofauna was sampled in three pits (50 cm × 50 cm and 20 cm depth) per plot. The OL and OF layer were taken to the laboratory for hand-sorting. The OH-layer and mineral soil layer were hand sorted at location by spreading smaller volumes of OH material or mineral soil over a sieve into a tray. Macrofauna was preserved in 70% alcohol. In the lab, earthworms were identified to species level using Sims and Gerard (1999) and Sherlock (2018) and weighed (wet).

2.3. Data analysis

A principal components analysis (PCA) was executed based on subsoil variables; plant available phosphorus (P), total phosphorus (P$_{des}$), NH$_4^+$, NO$_3^-$, OM, sand (%), silt (%) and clay (%) to evaluate possible edaphic and land use variation present in the dataset (Fig. S1, Table S2). The PCA was based on the correlation matrix and no matrix rotation was performed. Principal component (PC) 1 corresponds with the variation in texture and PC 2 corresponds with differences in land use legacy. The plot scores on these two PC's were included in further analysis to account for texture and land use legacy respectively (Fig. S1, Table S2).

Tree species litter effects were tested by mixed models with site as a random effect using nlme in R, followed by a post hoc Tukey test of the multcomp package (Fig. S2). We assessed the normality and homoscedasticity of the residuals and found no violations of the assumptions.

Fig. 2 shows both the raw data and the predictions (of the above described mixed models) per tree species for C/N ratio and base cation concentrations. Correlations between litter properties were tested using spearman correlation and significance values were reported in the text. We considered relations significant if P values were lower than 0.05 and indicated the level of significance (*P < 0.05, **P < 0.01, ***P < 0.001). Relations with P values between 0.05 and 0.1 were described as marginally significant in the text but are not indicated in any figures.

The effects of litter base cation concentration and litter C/N ratio on the thickness of the forest floor layer and topsoil chemistry were evaluated by mixed models including land use legacy and texture as covariates, and site as a random effect (Table 1). Partial correlations between litter quality (base cations and C/N) and soil properties were evaluated by spearman correlation tests using the ppcor package in R, and if significant the significance level was added to the linear relations plots (Fig. 3). All additional correlations between litter and soil variables were tested and illustrated with the Corrplot package in R (Fig. S5).

To gain a better understanding of the underlying mechanisms and to analyze causal relationships, a structural equation model (SEM) was constructed using the PiecewiseSEM package (Lefcheck, 2016) (Fig. 5). The a priori model included the effects of leaf litter base concentrations and C/N ratio on the thickness of the OF and OH layer, which in turn affected topsoil pH and base saturation. All variables were standardized (to a mean of zero and standard deviation of 1), and site was included as a random effect.

3. Results

3.1. Soil properties

Although a considerable amount of variation between sites was detected (Table S2), all sampled sites which were included in further analyses could be classified as acidic to acid, sandy soils (with a mean pH of 3.3). The percentage sand in the soil ranged from 63% to 95% with a mean of 80% (standard deviation of 7%) providing a good coverage of sandy soil types in the 50 plots. Tree species did not significantly explain variation in texture or any of the individual components of this variable (% sand, % silt, % clay) indicating that there is no confounding effect between tree species and site quality in terms of texture (see Section 2.3). Soil types varied within the study region in relation to former land use. Soil types varied between sites from soils with no agricultural land use legacy, such as Arenosols, Cambisols and Podzols, to those with agricultural legacy, i.e. Anthrosols. Again tree species is not a significant factor of influence on the encompassing variable land use legacy (see Section 2.3). In terms of leaf litter properties, C/N ratio is correlated with land use legacy (P = 0.02). There were no significant correlations between other litter properties, such as P, and land use legacy or texture. However, land use legacy was linked to topsoil base saturation and topsoil available Al concentration (Table 2).

3.2. Litter quality

Leaf litter C/N ratio ranges from 20 (observation of *Pseudotsuga menziesii*) to 47 (observation of *Pinus sylvestris*). Based on the predictions of a mixed model, the sampled tree species could be ranked with decreasing C/N: *Prunus avium* > *Pinus sylvestris* > *Prunus serotina* > *Pinus nigra* > *Quercus robur* > *Fagus sylvatica* > *Betula penduna* > *Acer pseudoplatanus* > *Tilia cordata* > *Prunus padus* > *Alnus incana* > *Pseudotsuga menziesi*. The C/N ratio differed significantly between tree species (P < 0.001) and subsequent multiple comparison test illustrated that the C/N ratio of *Pinus sylvestris* is significantly higher than the C/N ratio of *Tilia cordata* (P < 0.001), *Pseudotsuga menziesii* (P = 0.001) and *Acer pseudoplatanus* (P = 0.003) (Fig. S2).

Cumulative base cation concentration range from 6.9 g/kg dry weight (DW) (*Pinus sylvestris*) to 41.3 g/kg DW (*Tilia cordata*) and tree
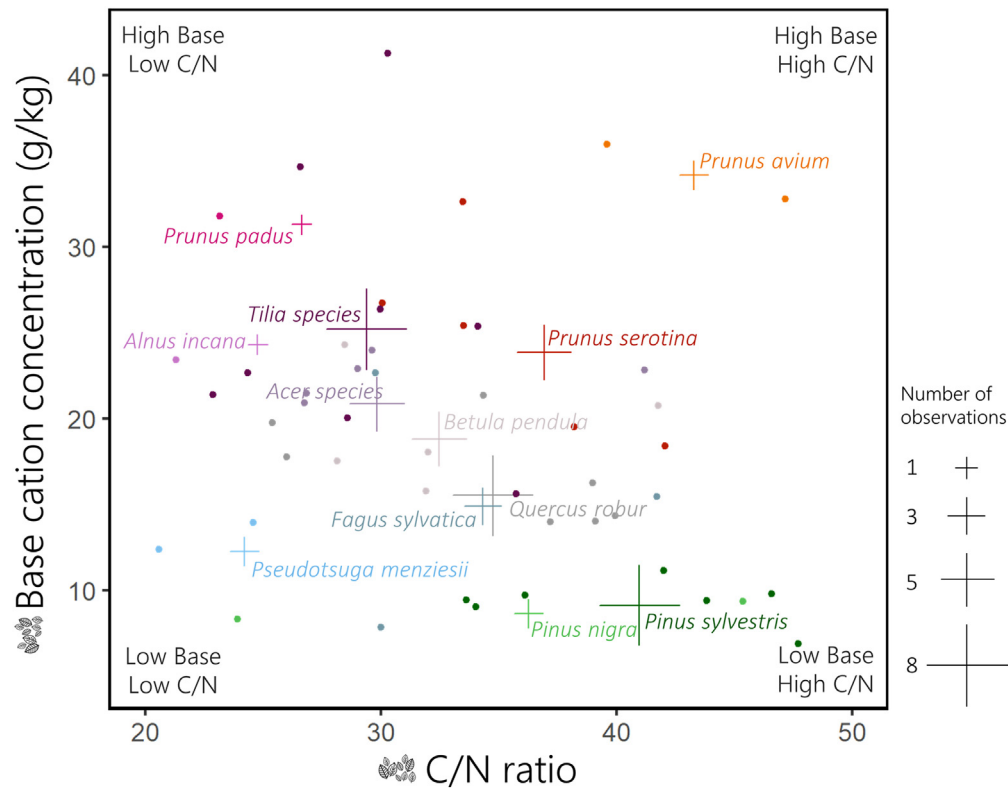
Fig. 2. Leaf litter base cation concentration and C/N ratio per tree species. Raw data are indicated by dots. The predictions for each tree species of a mixed model that incorporates site as a random effect are indicated by the +'s. The number of observations per tree species is indicated by the size of the +.

species could be ordered according to decreasing leaf litter base cation concentrations: *Prunus avium* > *Prunus padus* > *Tilia cordata* > *Alnus incana* > *Prunus serotina* > *Acer pseudoplatanus* > *Betula pendula* > *Quercus robur* > *Fagus sylvatica* > *Pseudotsuga menziesi* > *Pinus sylvestris* > *Pinus nigra* based on the predictions of a mixed model with *Prunus* species, Tilia and *Acer* significantly different from *Pinus sylvestris* (see Fig. S2 for all significant differences in between tree species).

There is only a marginally significant correlation between litter C/N ratio and litter total base cation concentrations ($r = -0.27$, $P = 0.06$). There are, however, significant negative correlations between litter C content and litter base cation concentrations (total base concentration ($r = -0.42$, $P = 0.003$), Ca ($r = -0.38$, $P = 0.007$) and Mg ($r = -0.30$, $P = 0.03$)). When tree species litter C/N is plotted against litter base cation concentration there is an overall significant negative linear relation ($P = 0.01$), however, there are some tree species that do not follow this trend: *Prunus avium* and *Prunus serotina* are tree species with high base cation concentration (mostly Mg – Fig. S4) but simultaneously high C/N ratio, and inversely *Pseudotsuga menziesii* has low base cation concentration, but also low C/N ratio (Fig. 2).

3.3. Effect of litter quality on forest floor layer, soil chemistry and soil macrofauna

With mixed models the impact of litter quality and specific site properties on forest floor and topsoil chemical properties was tested (Table 1). Litter base cation concentration was negatively related to the thickness of the forest floor, the humus index and aluminum concentrations of the topsoil. In contrast, litter base cation concentration was positively related to topsoil pH, base saturation, and available Ca. Litter C/N ratio and soil texture are not significant predictors for any of the tested variables (Tables 1, S3 and Fig. 5). Additionally, partial correlation coefficients were calculated for the above discussed relations (Table S3). These analyses indicate the same trend as the mixed models above described.

Litter base cation concentration is positively correlated with earthworm biomass (g/m^2) ($r = 0.53$, $P = 0.02$) whereas no significant correlation was found for litter C/N ratio and earthworm biomass (Fig. 4).

The tested structural equation model (Fig. 5) fitted the data well (fisher.c = 10.23, df = 8, $P = 0.24$) and shows significant pathways from leaf base concentration directly to topsoil base saturation (0.47, $P = 0.003$) and the thickness of the OF and OH layer (-0.51, $P < 0.001$) and from there further to topsoil pH (-0.27, $P = 0.05$). There was no significant pathway ($P = 0.21$) from leaf litter C/N ratio to the forest floor layer nor from the forest floor layer to topsoil base saturation ($P = 0.57$).

4. Discussion

4.1. Soil properties

Studies evaluating tree species litter effects are often executed in common gardens or adjacent forest stands of different tree species, planted for comparative purposes on a homogeneous site. Such set-ups minimize confounding effects between tree species performance and environmental factors (Augusto et al., 2002), and have contributed greatly to our current knowledge on tree species effects on soils (Angst et al., 2018; Augusto et al., 2002; Mueller et al., 2015; Muys et al., 1992; Reich et al., 2005). A drawback, however, is that experimental common gardens seldom incorporate tree species other than the most commonly used in forestry or that existing common gardens are often young stands in which tree species effects are accordingly less developed (Vesterdal et al., 2013). This current study evaluates tree litter effects in adjacent forest stands located at multiple sites. Such set-up allows the incorporation of less frequently used tree species (Vesterdal et al., 2013), in this case the evaluation of tree species with assumed remediating litter effects. As an additional benefit, our study covers a variety of sandy soil types and land-use legacies, which are too often considered as one and the same poor substrate or not considered at all. Our
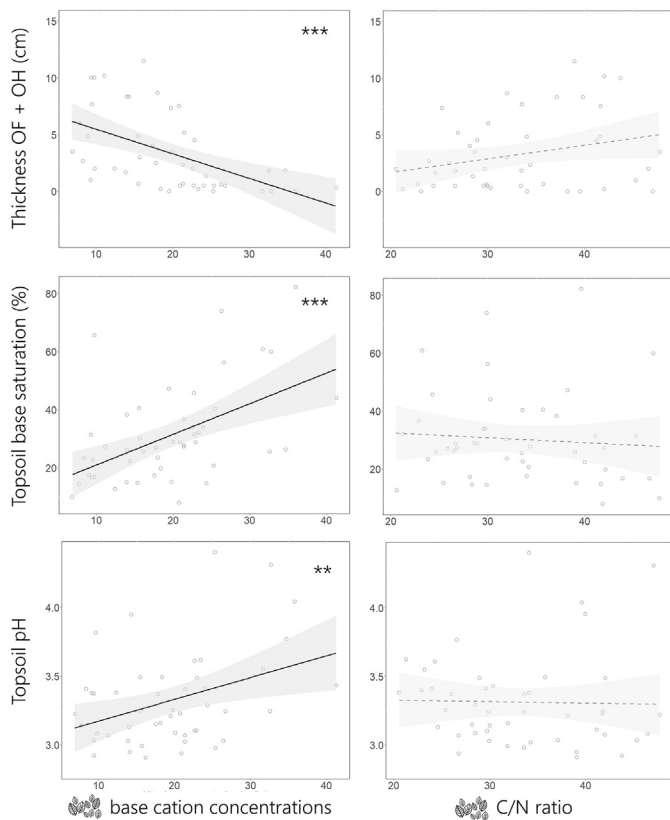
Fig. 3. Relation between litter base cation concentration (left) and litter C/N ratio (right) with thickness of the OF and OH layer (top), topsoil base saturation (middle) and topsoil pH (bottom). All observations are indicated by grey dots. Significant correlations are indicated by full lines whereas correlations that are not significant are indicated by dotted lines. The 95% confidence interval is indicated by a grey area along the regression line. Significance level of the correlation is indicated by ** for P < 0.01 and *** for P < 0.001 in the top right corners.

analyses indicate that texture only impacts litter K content and that land use legacy only affects litter C/N ratio and no other litter properties. Although there are correlations with litter properties and topsoil variables (Fig. S5), we argue that this is mostly in the direction of leaf litter impacting topsoil conditions. It could be that improved topsoil conditions feedback into improved nutrient availability in the plant leaves, however we consider this enforcing feedback as part of the tree species litter effect. We assured that all tree species in the same site were sampled on the same soil type with the same land use history, as to assure that any measured difference in topsoil quality can be attributed to tree species effects. With this set-up, we can thus evaluate litter effects on the topsoil independent from intrinsic soil quality, also by addressing potential confounding with site or land-use history using co-variates in the analysis.
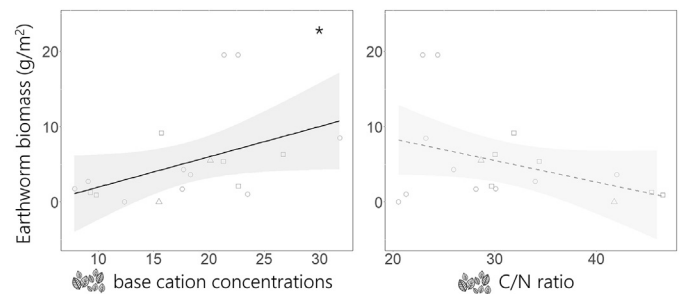

Fig. 4. Relation between leaf litter base cation concentration (left) and C/N ratio (right) with earthworm biomass. All observations are indicated in grey in the plot. This analysis is based on a subset (N = 19) of 3 sites indicated by shape (circle = Heesch, square = Kasterlee and triangle = Doorwerth). Significant correlations are indicated by full lines whereas correlations that are not significant are indicated by dotted lines. The 95% confidence interval is indicated by a grey area along the regression line. Significance level of the correlation is indicated by *P<0.05 in the top right corner.

4.2. Leaf litter quality spectrum

Our study proves that tree litter quality is the most important driver of forest belowground ecosystem functioning in comparison to land use legacy and soil texture for the considered range in soil properties. This is congruent with Maes et al. (2018), who report litter quality as a stronger driver of topsoil conditions compared to land-use history and atmospheric N deposition across European temperate deciduous forests. Base cation concentrations and C/N ratio are key leaf litter traits that contribute considerably to the variation within tree species and are prominent drivers of litter quality, sometimes extended by leaf litter lignin content (Reich et al., 2005; Zhang et al., 2008).

Based on leaf litter base cation concentration, we rank tree species from rich litter broadleaved species (*Prunus*, *Alnus*, *Tilia*, *Acer* and *Betula*) over broadleaved species with a more conservative resource use strategy (*Quercus* and *Fagus*) to coniferous species (*Pseudotsuga* and *Pinus*). This rank corresponds with Ponge's (2003) theory of ecosystem strategies, i.e. how tree species capture and use resources. In terms of C/N ratio the ranking of tree species is less evident. In correspondence to other studies (Hobbie et al., 2006; Schelfhout et al., 2017), our results show a low leaf litter C/N ratio for tree species *Tilia cordata*, *Acer pseudoplatanus*, *Prunus padus* and *Alnus incana*. Remarkably, *Prunus serotina* and *Prunus avium* have very high C/N ratios, comparable to *Pinus sylvestris* and *Pinus nigra*, but combined with high base concentrations (Fig. S2). Hence not all rich litter species meet both norms of low C/N and high base cations and follow the linear gradient (Fig. 2). A multivariate representation of litter quality (Fig. 2) seems necessary if we want to correctly define litter quality differences between tree species. The importance of Ca for litter decomposition has been reported earlier (Reich et al., 2005; Hobbie et al., 2006). In our study, Ca contributes almost 50% to the total amount of base cations in leaf litter, followed by K 40% and Mg 10%, yet the variation in Mg shows the most interesting trend. *Prunus serotina* and *Prunus avium*, two tree species that combine high C/N ratios with high base cation concentrations, have mostly high

Table 2
Effects of litter variables, land use legacy and soil texture on forest floor and topsoil (0–10 cm) variables. Standardized coefficients with standard deviations and significance levels of fixed effects (intercept, litter base cations, litter C/N, land use legacy and texture) of mixed models including site as a random factor. Significance levels are indicated by ** for P < 0.01 and *** for P < 0.001.

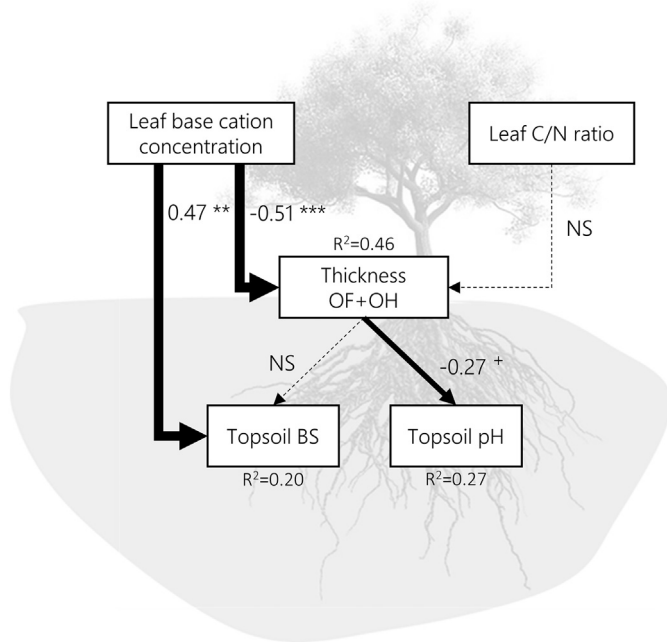| Response variable	Intercept	Litter base cations	Litter C/N	Land use legacy	Texture
Total O layer	6.03 (±0.85) ***	−2.36 (±0.57) ***	−0.29 (±0.57)	−0.39 (±0.66)	−0.02 (±0.74)
OF + OH layer	3.85 (±0.55) ***	−1.73 (±0.43) ***	−0.05 (±0.42)	−0.83 (±0.47)	−0.14 (±0.54)
Humus index	5.44 (±0.37) ***	−1.85 (±0.31) ***	−0.02 (±0.30)	−0.35 (±0.33)	−0.41 (±0.38)
Topsoil BS	29.89 (±1.68) ***	9.87 (±1.86) ***	2.42 (±7.78)	5.54 (±1.74) **	3.28 (±1.99)
Topsoil pH	3.28 (±0.06) ***	0.15 (±0.05) **	0.06 (±0.05)	0.02 (±0.05)	−0.01 (±0.06)
Topsoil Al	1.52 (±0.07) ***	−0.23 (±0.07) **	−0.08 (±0.07)	−0.40 (±0.07) ***	0.03 (±0.08)
Topsoil Ca	2.96 (±0.53) ***	1.12 (±0.33) **	−0.03 (±0.33)	0.33 (±0.34)	0.36 (±0.38)

Fig. 5. Piecewise structural equation model capturing the causal pathway from litter quality to topsoil chemistry. Arrow width is proportional to the size of the standardized model coefficients. $^+$P $= 0.05$, *P < 0.05, **P < 0.01, ***P < 0.001 and dashed lines represent non-significant (NS) effects. Number below the endogenous variables indicate the percentage of variation explained (R^2 conditional). Abbreviations: base saturation (BS).

Mg concentrations and relatively low Ca concentrations in their litter contrary to tree species such as *Tilia* and *Acer* with low C/N ratios (Fig. S4). It has previously been suggested that Mg fulfills a role comparable to Ca due to its similar chemical characteristics (Cesarz et al., 2016; Schelfhout et al., 2017; Wittich, 1948). Therefore the total amount of base cations present in the leaf litter may be a better predictor for litter effects to soil ecosystem functioning than Ca concentration alone. Both total bases as C/N ratio were subsequently linked to litter layer characteristics, soil fauna and soil chemistry.

4.3. Impact on belowground ecosystem compartment

4.3.1. Earthworms and the forest floor

Earthworm biomass increases markedly with litter base concentrations, whereas no correlation with C/N ratio could be reported, indicating again the negligible influence of C/N in the functioning of our systems. From medium to high litter base cation concentrations (>18 mg/kg DW) onwards all three functional groups of earthworms (i.e. epigeics, endogeics and epi-ancecics) are present, suggesting higher functional diversity in these plots. These results correspond with Neirynck et al. (2000) and Schelfhout et al. (2017) who found more diverse earthworm community under rich litter species (Tilia, Acer and Fraxinus) compared to poor litter (Quercus, Fagus or Picea). A true anecic species such as *Lumbricus terrestris* was not found in our study sites. Muys and Granval (1997), Reich et al. (2005) and Valckx et al. (2010) have shown close relationships between the quality of its living environment (in terms of pH and Ca concentrations) and the occurrence density of these species. Soil pH values in our sites are below 4.4 and calcium concentrations were below 9.7 mg/g DW and therefore too low to allow occurrence of real anecic species like *Lumbricus terrestris*.

Accordingly, higher leaf litter base cation concentrations lead to significantly reduced thickness of the forest floor layer (Fig. 3). The high Ca and/or Mg concentrations in rich litter support a higher earthworm abundance, directly through the high requirement of such elements for the calciferous glands of earthworms (Piearce, 1972) and indirectly by increasing the soil pH and creating a more favorable environment.

As a result, this leads to enhanced bioturbation and incorporation of litter material in the mineral soil so that less material can accumulate on top in the forest floor and less aggressive organic acids are formed, resulting in mull humus types. No significant correlation is observed between litter C/N ratio and the thickness of the forest floor layer, suggesting the low impact of C/N in comparison to base cations as a predictor of litter decomposition. In terms of litter accumulation *Pseudotsuga menziesii* shows an opposite trend: despite the low base cation concentrations in its needles, C/N ratio is low and the thickness of the forest floor layer is limited. Our study did only include two observations of *Pseudotsuga menziesii*, which bids some caution when interpreting the trend. Nonetheless, this result corresponds with multiple other field observations of moder to even mull humus types under *Pseudotsuga menziesii*. This suggests that if litter base cation concentrations are high, C/N ratio has low importance, yet for medium or low concentrations of base cations, litter C/N ratio does play a role in forest floor decomposition and prevailing humus type. Also lignin content may play a role in the accumulation of organic material on top of the soil. Thomas and Prescott (2000) already linked the low lignin content of *Pseudotsuga menziesii* to its faster litter turnover. Although lignin content plays an important role in terms of microbial decomposition, the contrast in lignin content between broadleaved species remains limited (Brock et al., 2019; Satti et al., 2003) and with earthworms as the drivers of the so called nutrient pump, leaf litter lignin is less determinant for forest floor turnover than leaf litter base cation content (Hobbie et al., 2006). Finally, unlike previously assumed (Muys and Lust, 1992; Ponge, 2003) our results indicate that mull humus types can occur on poor sandy soils when leaf litter quality is high enough (in terms of base cation concentrations) to sustain an earthworm population and corresponding fast nutrient cycling.

4.3.2. Soil chemistry

When leaf litter base cation concentrations are low, organic matter accumulates in the forest floor leading to moder/mor humus types and the production and leaching of strong organic acids. These acids increase the hydrogen load on the soil's exchange complex and may subsequently induce and shift of the soil to the aluminum buffer domain (Muys et al., 1992; de Vries et al., 1995; Vitousek and Chadwick, 2013). What follows is a vertical decoupling of nutrient cycles: the absence of earthworms implies poor vertical distribution of organic matter and nutrients, soil pH is below the threshold of 4 (Muys and Granval, 1997) and soil base saturation below 30% (Chadwick and Chorover, 2001; Desie et al., 2019). Contrary, for tree species with the highest litter base cation concentrations we find base saturation values above the 30% threshold, which is substantial for sandy forest soils with a history of acidification due to land use changes and atmospheric deposition, and sufficient to push the system out of the Al buffer domain and back into the more favorable exchange domain where acidity is buffered by base cations on the exchange complex, supply of base cations to plants is adequate and aluminum toxicity is relieved (Ulrich and Sumner, 1991; Vitousek and Chadwick, 2013; Desie et al., 2019).

When leaf litter traits are linked to soil chemistry and soil biota, litter base cation concentration is consistently a significant predictor for topsoil chemistry (Table 1). Contrary, C/N ratio is never a significant predictor for topsoil pH or topsoil base saturation. Previous works have repeatedly emphasized the importance of C/N ratio in terms of litter quality (Kooch et al., 2017), promoting it as the most appropriate measure to summarize tree species litter quality (Maes et al., 2018; Melillo et al., 1982; Moore et al., 2011; Wittich, 1953). In contrast, our result suggest a negligible impact of C/N ratio on the belowground functioning of forests on poor sandy soils compared to litter base cation content. Hence, in line with the proposed theory of fast nutrient cycling (Hommel et al., 2007), we found that litter quality indeed drives ecosystem functioning of forests on sandy soils mainly through base cation concentrations. Tree species with high concentrations of base cations in their litter drive the nutrient cycle by promoting higher abundance

of earthworms with burrowing capacities, which in turn positively impact soil chemistry via increased organic matter incorporation.

4.3.3. Nutrient imbalanced soils

The specific context of West-European Pleistocene sandy soils may explain the dominance of litter base cation concentration over the other litter traits (i.e. C/N ratio). Acidification as a consequence of land use changes along with N and S deposition, induced leaching of base cations. Simultaneously, past and continued N deposition have caused a lingering overload of N in all compartments of natural ecosystems. The combination of both acidification and eutrophication has resulted in a limiting amount of macronutrients available for growth (Perakis and Sinkhorn, 2011; Perakis et al., 2006). This shortage of nutrients is a consequence of the above described mechanisms concerning macro fauna that lead to reduced incorporation of nutrients but also because high N deposition impedes microbial litter decomposition as the lignin/N ratio is drastically affected (Aerts, 1997; Prescott et al., 2004). The reduced decomposition due to higher N inputs, however, also promotes SOM accumulation. The results discussed above are a reminder of the broad validity of Liebig's law "*the availability of the most abundant nutrient in the soil is only as good as the availability of the least abundant one*". Leaf litter C/N ratios in our study are lower compared to C/N ratios reported in studies where eutrophication was no significant factor (Fassnacht and Gowerr, 1999; Satti et al., 2003; Thomas and Prescott, 2000; Wittich, 1953). Muys (1995) already suggested that the low C/N ratios he observed in Belgium, which are comparable to our results, must be a consequence of high N-deposition in the region and in time. Therefore, the lower importance of C/N found in this study is, potentially, specifically related to the context of nutrient imbalanced sandy soils. Similarly, other studies already reported the decreasing value of C/N ratio as an indicator due to with N saturation in plant tissue of lichens and mosses as a consequence of N enrichment (Fritz et al., 2014; Lamers et al., 2000; Remke, 2010). In Europe the largest N deposition is concentrated in the Western part (de Vries et al., 2014), with multiple studies in Belgium (Carnol and Bazgir, 2013; Muys and Lust, 1993), the Netherlands and Denmark (Schelfhout et al., 2017) reporting similar low C/N ratios, yet the ever increasing loads of N in natural systems due to human activity is a continental and even global problem (Galloway et al., 2004; Rockström et al., 2009). Since there are many other forest sites around the globe facing identical threats of acidification and eutrophication (Schwede et al., 2018), our findings have broad implications.

4.4. Management implications for restoration of acidified sandy soils

It is commonly assumed that poor sandy soils drastically limit the options in tree species choice for forest managers as well as the performance in terms of forest floor dynamics (e.g. mull humus is not possible) which determines the herb layer to a great extent and in terms of productivity (Maes et al., 2018; Muys et al., 1992; Ponge, 2003; Van Nevel et al., 2014). For that reason, alongside historical land-use legacies, many of Western Europe's sandy soils have been converted from heathlands into homogenous, even-aged plantations of coniferous species or broadleaved species such as oak and beech with similar low litter quality (Augusto et al., 2002). Although many forest managers in the region have moved away from production oriented monocultures to more close-to-nature systems (Kint et al., 2009) allowing birch to codominate oak stands, the current forest composition of oak and birch proves insufficient to restore degraded soils and performs below-average in terms of multifunctionality and productivity (Baeten et al., 2018). This is in line with our study as *Betula pendula* did not produce high quality litter in our study (intermediate between *Acer pseudoplatanus* and *Quercus robur*).

Our study confirms the importance of leaf litter quality in shaping topsoil conditions and this impact is even more crucial in sandy soils given their low acid buffering capacity. In poorly buffered soils, litter effects are not only more pronounced in terms of soil chemistry (Desie et al., 2019; Verstraeten et al., 2018), but also on soil biota (Cesarz et al., 2016): endogeic earthworms become more dependent on litter quality when soils are poor in organic matter and switch feeding behaviour accordingly from humified organic matter to litter input, which consequently affects the food source for several microbial communities (Cesarz et al., 2016; Brown et al., 2000). Unlike previously assumed this highlights great opportunity for managers as the impact of overstory tree species composition, and thus the foresters' choice, is substantial in such sandy soils.

Our results highlight the potential of certain tree species to aid in soil and ecosystem restoration. We identify tree species with medium to high base cation concentration in their leaf litter, i.e. *Tilia cordata*, *Acer pseudoplatanus*, *Alnus incana* and *Prunus species*, as potential candidate species for restoring nutrient imbalanced soils. Previous studies also mention *Acer pseudoplatanus* and *Prunus serotina* as tree species with soil ameliorative capacities and additionally suggested the potential of *Sorbus aucuparia* and *Carpinus betula* (Carnol and Bazgir, 2013; Kooch and Bayranvand, 2017; Van Nevel et al., 2014). Once these mature rich-litter tree species occupy the canopy and produce sufficient quantities of rich litter, they can fundamentally impact the belowground ecosystem functioning by shifting the soil buffer domain at work. The establishment of tree species on acidified sandy soils may be challenging, therefore integrated soil restoration methods combining tree species conversion with nutrient replenishment and inoculation of soil biota should be further explored (Muys et al., 2003).

Keeping forest production and multifunctionality in mind, managers often opt to mix tree species with different strategies, and thus in practice also rich and poor litter species (Nickmans et al., 2019). Here we focused on the effects of rich litter species in monocultures and hence we cannot predict how much recalcitrant litter may be admixed to a rich litter matrix to remain in the exchange buffer domain. Van Nevel et al. (2014) found that a dense shrub layer (of up to 90% cover) of *Prunus serotina* under dominant pine or oak canopies only contributes up to 17% of the total litterfall, which was insufficient to significantly improve topsoil conditions in pine and oak stands on poor sandy Podzols. This suggests that a high proportion of rich litter input is necessary to improve soil conditions in acidified sandy soils. On the other hand, there are studies which report that mixtures of different litters support more divers forest floor communities throughout the year and have positive effects on decomposition (Hättenschwiler et al., 2005; Gartner and Cardon, 2004; Forrester and Bauhus, 2016). Further research may identify the ideal species composition and specifically the share of rich litter needed in a mixture for specific soil contexts, to have a comparable beneficial remediating effect as the monocultures reported in this study (but see Nickmans et al., 2019; Baeten et al., 2018). Moreover, future studies should research the economic potential of rich litter tree species as a source of high quality wood in the context of multifunctional forest management.

5. Conclusion

Our study of tree species litter effects on acidified sandy soils across Belgium, the Netherlands and Western Germany shows that high quality litter (rich litter) positively impacts topsoil pH and base saturation, as well as earthworm biomass and density. Leaf litter base cations concentrations, mainly Ca and Mg, are consistently well correlated with soil chemistry and soil biota whereas no significant correlation with litter C/N ratio is found, indicating the more prominent impact of litter base cation concentrations in comparison to litter C/N ratio on belowground ecosystem functioning. This allows defining "rich litter" as litter with high base cation concentrations (>20 g/kg DW) which promotes nutrient cycling via biological processes such as mechanisms where burrowing earthworms play a key role. Accordingly, the importance of C/N ratio as an indicator for litter quality decreases. This definition of rich litter and reported effects should be seen in the context of nutrient

imbalanced, sandy soils that are characterized by past and present N-deposition and high acidity that has led to base cation leaching. This study focused on monocultures and should stimulate further research determining the impact of rich litter in tree species mixtures and to ultimately determine optimal tree species compositions. Nonetheless, our results show the potential of the management intervention "admixing rich litter species" for restoring degraded soil systems and suggest the restorative capacities of rich litter are not limited to only fine textured soils, i.e. also poorly buffered sandy soils can benefit from rich litter input.

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Declaration of Competing Interest

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

Author contributions

ED, BM, KVC, BN, LVDB, JDO designed the study; ED, MW, GVD collected the data; ED and KVM analyzed the data; All authors contributed to the interpretation of the results; ED compiled the manuscript; All authors contributed critically to the drafts and gave final approval for publication.

References

Aerts, R., 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos 79, 439. https://doi.org/10.2307/3546886.
Angst, G., Mueller, K.E., Eissenstat, D.M., Trumbore, S., Freeman, K.H., Hobbie, S.E., Chorover, J., Oleksyn, J., Reich, P.B., Mueller, C.W., 2018. Soil organic carbon stability in forests: distinct effects of tree species identity and traits. Glob. Chang. Biol. gcb. 14548. https://doi.org/10.1111/gcb.14548.
Augusto, L., Ranger, J., Binkley, D., Rothe, A., 2002. Impact of several common tree species of European temperate forests on soil fertility. Ann. For. Sci. 59, 233–253. https://doi.org/10.1051/forest:2002020.
Baeten, L., Bruelheide, H., van der Plas, F., Kambach, S., Ratcliffe, S., Jucker, T., Allan, E., Ampoorter, E., Barbaro, L., Bastias, C.C., Bauhus, J., Benavides, R., Bonal, D., Bouriaud, O., Bussotti, F., Carnol, M., Castagneyrol, B., Charbonnier, Y., Chećko, E., Coomes, D.A., Dahlgren, J., Dawud, S.M., De Wandeler, H., Domisch, T., Finér, L., Fischer, M., Fotelli, M., Gessler, A., Grossiord, C., Guyot, V., Hättenschwiler, S., Jactel, H., Jaroszewicz, B., Joly, F.-X., Koricheva, J., Lehtonen, A., Müller, S., Muys, B., Nguyen, D., Pollastrini, M., Radoglou, K., Raulund-Rasmussen, K., Ruiz-Benito, P., Selvi, F., Stenlid, J., Valladares, F., Vesterdal, L., Verheyen, K., Wirth, C., Zavala, M.A., Scherer-Lorenzen, M., 2018. Identifying the tree species compositions that maximize ecosystem functioning in European forests. J. Appl. Ecol. https://doi.org/10.1111/1365-2664.13308.
Beerten, K., Vandersmissen, N., Deforce, K., Vandenberghe, N., 2014. Late Quaternary (15 ka to present) development of a sandy landscape in the Mol area, Campine region, north-east Belgium. J. Quat. Sci. 29, 433–444. https://doi.org/10.1002/jqs.2713.
Berg, B., McClaugherty, C., 2008. Plant Litter: Decomposition, Humus Formation, Carbon Sequestration. Springer-Verlag, Berlin, Germany, pp. 1–10.
Bowman, W.D., Cleveland, C.C., Halada, Ĺ., Hreško, J., Baron, J.S., 2008. Negative impact of nitrogen deposition on soil buffering capacity. Nat. Geosci. 1, 767–770. https://doi.org/10.1038/ngeo339.

Brock, O., Kooijman, A., Nierop, K.G.J., Muys, B., Vancampenhout, K., Jansen, B., 2019. Disentangling the effects of parent material and litter input chemistry on molecular soil organic matter composition in converted forests in Western Europe. Org. Geochem. 134, 66–76. https://doi.org/10.1016/J.ORGGEOCHEM.2019.05.006.
Brown, G.G., Barois, I., Lavelle, P., 2000. Regulation of soil organic matter dynamics and microbial activity in the drilosphere and the role of interactions with other edaphic functional domains. Eur. J. Soil Biol. 36, 177–198. https://doi.org/10.1016/S1164-5563(00)01062-1.
Carnol, M., Bazgir, M., 2013. Nutrient return to the forest floor through litter and throughfall under 7 forest species after conversion from Norway spruce. For. Ecol. Manag. 309, 66–75. https://doi.org/10.1016/j.foreco.2013.04.008.
Cesarz, S., Craven, D., Dietrich, C., Eisenhauer, N., 2016. Effects of soil and leaf litter quality on the biomass of two endogeic earthworm species. Eur. J. Soil Biol. 77, 9–16. https://doi.org/10.1016/J.EJSOBI.2016.09.002.
Chadwick, O.A., Chorover, J., 2001. The chemistry of pedogenic thresholds. Geoderma 100, 321–353. https://doi.org/10.1016/S0016-7061(01)00027-1.
De Schrijver, A., Mertens, J., Geudens, G., Staelens, J., Campforts, E., Luyssaert, S., De Temmerman, L., De Keersmaeker, L., De Neve, S., Verheyen, K., 2006. Acidification of forested podzols in North Belgium during the period 1950–2000. Sci. Total Environ. 361, 189–195. https://doi.org/10.1016/J.SCITOTENV.2005.06.015.
De Schrijver, A., De Frenne, P., Staelens, J., Verstraeten, G., Muys, B., Vesterdal, L., Wuyts, K., Van Nevel, L., Schelfhout, 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.
de Vries, W., Kros, J., van der Salm, C., 1995. Modelling the impact of acid deposition and nutrient cycling on forest soils. Ecol. Model. 79, 231–254. https://doi.org/10.1016/0304-3800(93)E0121-I.
de Vries, W., Dobbertin, M.H., Solberg, S., van Dobben, H.F., Schaub, M., 2014. Impacts of acid deposition, ozone exposure and weather conditions on forest ecosystems in Europe: an overview. Plant Soil 380, 1–45. https://doi.org/10.1007/s11104-014-2056-2.
Denman, K., 2007. IPCC Climate Change 2007: The Physical Science Basis. Cambridge Univ. Press.
Desie, E., Vancampenhout, K., Heyens, K., Hlava, J., Verheyen, K., Muys, B., 2019. Forest conversion to conifers induces a regime shift in soil process domain affecting carbon stability. Soil Biol. Biochem. 136, 107540. https://doi.org/10.1016/J.SOILBIO.2019.107540.
Emmer, I.M., Fanta, J., Kobus, A.T., Kooijman, A., Sevink, J., 1998. Reversing borealization as a means to restore biodiversity in Central-European mountain forests - an example from the Krkonose Mountains, Czech Republic. Biodivers. Conserv. 7, 229–247.
Falkengren-Grerup, U., Lakkenborgkristensen, H., 1994. Importance of ammonium and nitrate to the performance of herb-layer species from deciduous forests in Southern Sweden. Environ. Exp. Bot. 34, 31–38. https://doi.org/10.1016/0098-8472(94)90006-x.
FAO, 2006. Guidelines for Soil Description. 4th ed. (Rome).
Fassnacht, K.S., Gowerr, S.T., 1999. Comparison of the litterfall and forest floor organic matter and nitrogen dynamics of upland forest ecosystems in north central Wisconsin. Biogeochemistry 45, 265–284.
Fisher, B., Binkley, D., 2013. Chapter 14: nutrition management. Ecology and Management of Forest Soils, Fourth edition John Wiley & Sons, Ltd.
Forrester, D.I., Bauhus, J., 2016. A review of processes behind diversity–productivity relationships in forests. Curr. For. Reports 2, 45–61. https://doi.org/10.1007/s40725-016-0031-2.
Fritz, C., Lamers, L.P.M., Riaz, M., van den Berg, L.J.L., Elzenga, T.J.T.M., 2014. Sphagnum mosses - masters of efficient N-uptake while avoiding intoxication. PLoS One 9. https://doi.org/10.1371/journal.pone.0079991.
Galloway, J.N., Dentener, F.J., Capone, D.G., Boyer, E.W., Howarth, R.W., Seitzinger, S.P., Asner, G.P., Cleveland, C.C., Green, P.A., Holland, E.A., Karl, D.M., Michaels, A.F., Porter, J.H., Townsend, A.R., Vorosmarty, C.J., 2004. Nitrogen cycles: past, present, and future. Biogeochemistry 70, 153–226. https://doi.org/10.1007/s10533-004-0370-0.
Galloway, J.N., Townsend, A.R., Erisman, J.W., Bekunda, M., Cai, Z., Freney, J.R., Martinelli, L.A., Seitzinger, S.P., Sutton, M.A., 2008. Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. Science 320, 889 (80-.).
Gartner, T.B., Cardon, Z.G., 2004. Decomposition dynamics in mixed-species leaf litter. Oikos 104, 230–246. https://doi.org/10.1111/j.0030-1299.2004.12738.x.
Hättenschwiler, S., Tiunov, A.V., Scheu, S., 2005. Biodiversity and litter decomposition in terrestrial ecosystems. Annu. Rev. Ecol. Evol. Syst. 36, 191–218. https://doi.org/10.1146/annurev.ecolsys.36.112904.151932.
Hevia, A., Sánchez-Salguero, R., Camarero, J.J., Querejeta, J.I., Sangüesa-Barreda, G., Gazol, A., 2019. Long-term nutrient imbalances linked to drought-triggered forest dieback. Sci. Total Environ. https://doi.org/10.1016/J.SCITOTENV.2019.06.515.
Hobbie, S.E., Ogdahl, M., Reich, P.B., Oleksyn, J., Hale, C., Zytkowiak, R., Karolewski, P., 2006. Tree species effects on decomposition and forest floor dynamics in a common garden. Ecology 87, 2288–2297. https://doi.org/10.1890/0012-9658(2006)87[2288:TSEODA]2.0.CO;2.
Hommel, P., de Waal, R., de Muys, B., den Ouden, J., Spek, T., 2007. Terug naar het lindewoud: strooiselkwaliteit als basis voor ecologisch bosbeheer. KNNV Uitgeverij, Zeist.
Hüttl, R.F., Schneider, B.U., 1998. Forest ecosystem degradation and rehabilitation. Ecol. Eng. 10, 19–31. https://doi.org/10.1016/S0925-8574(97)10023-4.
IUSS Working Group WRB, 2015. World Reference Base for Soil Resources 2014, Update 2015 International Soil Classification System for Naming Soils and Creating Legends for Soil Maps (Rome).
Jin, Q., Liang, F., Zhang, H., Zhao, L., Huan, Y., Song, D., 1999. Application of microwave techniques inanalytical chemistry. Trends Anal. Chem. 18, 479–484.

Kint, V., Lasch, P., Lindner, M., Muys, B., 2009. Multipurpose conversion management of scots pine towards mixed oak-birch stands-a long-term simulation approach. For. Ecol. Manag. 257, 199–214. https://doi.org/10.1016/j.foreco.2008.08.031.

Kooch, Y., Bayranvand, M., 2017. Composition of tree species can mediate spatial variability of C and N cycles in mixed beech forests. For. Ecol. Manag. 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.

Kreutzer, K., 1995. Effects of forest liming on soil processes. Nutrient Uptake and Cycling in Forest Ecosystems. Springer Netherlands, Dordrecht, pp. 447–470 https://doi.org/10.1007/978-94-011-0455-5_51.

Lamers, L.P.M., Bobbink, R., Roelofs, J.G.M., 2000. Natural nitrogen filter fails in polluted raised bogs. Glob. Chang. Biol. 6, 583–586.

Lavelle, P., Dugdale, R., Scholes, R., Asefaw Berhe, A., Carpenter, E., Codispoti, L., Izac, A.-M., Lemoalle, J., Luizao, F., Scholes, M., Tréguer, P., Ward, B., 2003. Ecosystems and Human Well-being: Chapter 12 Nutrient Cycling, a Report of the Millennium Ecosystem Assessment.

Lefcheck, J., 2016. PIECEWISESEM: piecewise structural equation modelling in R for ecology, evolution and systematics. Methods Ecol. Evol. 7, 573–579.

Liu, C.L., Wang, M.K., Yang, C.C., 2001. Determination of cation exchange capacity by one-step soil leaching column method. Commun. Soil Sci. Plant Anal. 32 (15–16). https://doi.org/10.1081/CSS-120000378.

Lucassen, E., Van den Berg, L., Ralf Aben, F., Smolders, J., Bobbink, R., Bobbink, R., 2014. Bodemverzuring en achteruitgang Zomereik.

Lundström, U.S., Bain, D.C., Taylor, A.F.S., van Hees, P.A.W., 2003. Effects of acidification and its mitigation with lime and wood ash on forest soil processes: a review. Water, Air, Soil Pollut. Focus 3, 5–28. https://doi.org/10.1023/A:1024115111377.

Maes, S.L., Blondeel, H., Perring, M.P., Depauw, L., Brūmelis, G., Brunet, J., Decocq, G., Den Ouden, J., Härdtle, W., Hédl, R., Heinken, T., Heinrichs, S., Jaroszewicz, B., Kirby, K., Kopecký, M., Máliš, F., Wulf, M., Verheyen, K., 2018. Litter quality, land-use history, and nitrogen deposition effects on topsoil conditions across European temperate deciduous forests. For. Ecol. Manag. 433, 405–418. https://doi.org/10.1016/j.foreco.2018.10.056.

Maskell, L.C., Smart, S.M., Bullock, J.M., Thompson, K., Stevens, C.J., 2010. Nitrogen deposition causes widespread loss of species richness in British habitats. Glob. Chang. Biol. 16, 671–679. https://doi.org/10.1111/j.1365-2486.2009.02022.x.

Melillo, J.M., Aber, J.D., Muratore, J.F., 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63 (3), 621–626. https://doi.org/10.1111/j.1365-2486.2009.02022.x.

Moore, T.R., Trofymow, J.A., Prescott, C.E., Titus, B.D., 2011. Nature and nurture in the dynamics of C, N and P during litter decomposition in Canadian forests. Plant Soil, 163–175 https://doi.org/10.1007/s11104-010-0563-3.

Mueller, K.E., Hobbie, S.E., Chorover, J., Reich, P.B., Eisenhauer, N., Castellano, M.J., Chadwick, O.A., Dobies, T., Hale, C.M., Jagodziński, A.M., Kałucka, I., Kieliszewska-Rokicka, B., Modrzyński, J., Rożen, A., Skorupski, M., Sobczyk, Ł., Stasińska, M., Trocha, L.K., Weiner, J., Wierzbicka, A., Oleksyn, J., 2015. Effects of litter traits, soil biota, and soil chemistry on soil carbon stocks at a common garden with 14 tree species. Biogeochemistry 123, 313–327. https://doi.org/10.1007/s10533-015-0083-6.

Muys, B., 1995. The influence of tree species on humus quality and nutrient availability on a regional scale (Flanders, Belgium). Nutrient Uptake and Cycling in Forest Ecosystems. Springer Netherlands, Dordrecht, pp. 649–660 https://doi.org/10.1007/978-94-011-0455-5_72.

Muys, B., Granval, P., 1997. Earthworms as bio-indicators of forest site quality. Soil Biol. Biochem. 29, 323–328. https://doi.org/10.1016/S0038-0717(96)00047-8.

Muys, B., Lust, N., 1992. Inventory of the earthworm communities and the state of litter decomposition in the forests of Flanders, Belgium, and its implications for forest management. Soil Biol. Biochem. Biochem 24, 1677–1681.

Muys, B., Lust, N., 1993. Synecologische evaluatie van regenwormactiviteit en strooiselafbraak in de bossen van het vlaamse gewest als bijdrage tot een duurzaam bosbeheer Phd. p. 335.

Muys, B., Lust, N., Granval, P., 1992. Effects of grassland afforestation with different tree species on earthworm communities, litter decomposition and nutrient status. Soil Biol. Biochem. 24, 1459–1466. https://doi.org/10.1016/0038-0717(92)90133-I.

Muys, B., Beckers, G., Nachtergale, L., Lust, N., Merckx, R., Granval, P., 2003. Medium-term evaluation of a forest soil restoration trial combining tree species change, fertilisation and tree species introduction: the 7th international symposium on earthworm ecology·Cardiff·Wales·2002. Pedobiologia (Jena) 47, 772–783.

Neirynck, J., Mirtcheva, S., Sioen, G., Lust, N., 2000. Impact of Tilia platyphyllos Scop., Fraxinus excelsior L., Acer pseudoplatanus L., Quercus robur L. and Fagus sylvatica L. on earthworm biomass and physico-chemical properties of a loamy topsoil. For. Ecol. Manag. 133, 275–286.

Nickmans, H., Jonard, M., Verheyen, K., Ponette, Q., 2019. Modelling leaf dispersal and nutrient return in tree species mixtures. For. Ecol. Manag. 436, 68–78. https://doi.org/10.1016/J.FORECO.2019.01.001.

Olsen, S., Cole, C., Watanabe, F., Dean, L., 1954. Estimation of Available Phosphorus in Soils by Extraction With Sodium Bicarbonate. USDA Circular, Washington, D.C.

Perakis, S.S., Sinkhorn, E.R., 2011. Biogeochemistry of a temperate forest nitrogen gradient. Ecology 92, 1481–1491. https://doi.org/10.1890/10-1642.1.

Perakis, S.S., Maguire, D.A., Bullen, T.D., Cromack, K., Waring, R.H., Boyle, J.R., 2006. Coupled nitrogen and calcium cycles in forests of the Oregon coast range. Ecosystems 9, 63–74. https://doi.org/10.1007/s10021-004-0039-5.

Piearce, T.G., 1972. Acid intolerant and ubiquitous lumbricidae in selected habitats in North Wales. J. Anim. Ecol. 41, 397–410.

Ponge, J.F., 2003. Humus forms in terrestrial ecosystems: a framework to biodiversity. Soil Biol. Biochem. 35, 935–945. https://doi.org/10.1016/S0038-0717(03)00149-4.

Ponge, J.-F., Chevalier, R., Loussot, P., 2002. Humus index: an integrated tool for the assessment of forest floor and topsoil properties. Soil Sci. Soc. Am. J. 66 (1996). https://doi.org/10.2136/sssaj2002.1996.

Prescott, C.E., 2002. The influence of the forest canopy on nutrient cycling. Tree Physiol. 22, 1193–1200. https://doi.org/10.1093/treephys/22.15-16.1193.

Prescott, C.E., Vesterdal, L., Preston, C.M., Simard, S.W., 2004. Influence of initial chemistry on decomposition of foliar litter in contrasting forest types in British Columbia. Can. J. For. Res. 34, 1714–1729. https://doi.org/10.1139/x04-040.

Reich, P.B., Oleksyn, J., Modrzynski, J., Mrozinski, P., Hobbie, S.E., Eissenstat, D.M., Chorover, J., Chadwick, O.a., Hale, C.M., Tjoelker, M.G., 2005. Linking litter calcium, earthworms and soil properties: a common garden test with 14 tree species. Ecol. Lett. 8, 811–818. https://doi.org/10.1111/j.1461-0248.2005.00779.x.

Remke, E., 2010. Impact of Atmospheric Nitrogen Deposition on Lichen-Rich, Coastal Dune Grasslands. Radboud University Nijmegen.

Rockström, J., Steffen, W., Noone, K., Persson, Å., Chapin, F.S., Lambin, E.F., Lenton, T.M., Scheffer, M., Folke, C., Schellnhuber, H.J., Nykvist, B., de Wit, C.A., Hughes, T., van der Leeuw, S., Rodhe, H., Sörlin, S., Snyder, P.K., Costanza, R., Svedin, U., Falkenmark, M., Karlberg, L., Corell, R.W., Fabry, V.J., Hansen, J., Walker, B., Liverman, D., Richardson, K., Crutzen, P., Foley, J.A., 2009. A safe operating space for humanity. Nature 461, 472–475. https://doi.org/10.1038/461472a.

Šantrůčková, H., Cienciala, E., Kaňa, J., Kopáček, J., 2019. The chemical composition of forest soils and their degree of acidity in Central Europe. Sci. Total Environ. 687, 96–103. https://doi.org/10.1016/J.SCITOTENV.2019.06.078.

Satti, P., Mazzarino, M.J., Gobbi, M., Funes, F., Roselli, L., Fernandez, H., 2003. Soil N dynamics in relation to leaf litter quality and soil fertility in north-western Patagonian forests. J. Ecol. 91, 173–181. https://doi.org/10.1046/j.1365-2745.2003.00756.x.

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.

Schwede, D.B., Simpson, D., Tan, J., Fu, J.S., Dentener, F., Du, E., deVries, W., 2018. Spatial variation of modelled total, dry and wet nitrogen deposition to forests at global scale. Environ. Pollut. 243, 1287–1301. https://doi.org/10.1016/J.ENVPOL.2018.09.084.

Sherlock, E., 2018. Key to the earthworms of the UK and Ireland. Editorial: Field Studies Council, 2nd edition.

Sims, R.W., Gerard, B.M., 1999. Earthworms: notes for the identification of British species. In: Barnes, R.S.K., Crothers, J.H. (Eds.), Synopses of the British Fauna (New Series). Field Studies Council, Shrewsbury.

Slessarev, E.W., Lin, Y., Bingham, N.L., Johnson, J.E., Dai, Y., Schimel, J.P., Chadwick, O.A., 2016. Water balance creates a threshold in soil pH at the global scale. Nat. Publ. Gr. 540. https://doi.org/10.1038/nature20139.

Steffen, W., Richardson, K., Rockström, J., Cornell, S.E., Fetzer, I., Bennett, E.M., Biggs, R., Carpenter, S.R., De Vries, W., De Wit, C.A., Folke, C., Gerten, D., Heinke, J., Mace, G.M., Persson, L.M., Ramanathan, V., Reyers, B., Sörlin, S., 2015. Planetary boundaries: guiding human development on a changing planet. Science 347. https://doi.org/10.1126/science.1259855 (80-.).

Thomas, K.D., Prescott, C.E., 2000. Nitrogen availability in forest floors of three tree species on the same site: the role of litter quality. Can. J. For. Res. 30, 1698–1706. https://doi.org/10.1139/x00-101.

Tomlinson, G.H., 2003. Acidic deposition, nutrient leaching and forest growth. Biogeochemistry 65, 51–81. https://doi.org/10.1023/A:1026069927380.

Ulrich, B., 1991. An ecosystem approach to soil acidification. Soil Acidity. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 28–79 https://doi.org/10.1007/978-3-642-74442-6_3.

Ulrich, B., Sumner, M.E. (Eds.), 1991. Soil Acidity. Springer Berlin Heidelberg, Berlin, Heidelberg https://doi.org/10.1007/978-3-642-74442-6.

Valckx, J., Pennings, A., Leroy, T., El Berckmans, D., Govers, G., Hermy, M., Muys, B., 2010. Automated observation and analysis of earthworm surface behaviour under experimental habitat quality and availability conditions. Pedobiologia (Jena) 53, 259–263. https://doi.org/10.1016/j.pedobi.2009.12.005.

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. Manag. 330, 38–45. https://doi.org/10.1016/j.foreco.2014.07.002.

Van Ranst, E., De Coninck, F., Roskams, P., Vindevogel, N., 2002. Acid-neutralizing capacity of forest floor and mineral topsoil in Flemish forests (North Belgium). For. Ecol. Manag. 166, 45–53. https://doi.org/10.1016/S0378-1127(01)00677-6.

Verstraeten, G., Baeten, L., De Frenne, P., Vanhellemont, M., Thomaes, A., Boonen, W., Muys, B., Verheyen, K., 2013. Understorey vegetation shifts following the conversion of temperate deciduous forest to spruce plantation. For. Ecol. Manag. 289, 363–370. https://doi.org/10.1016/j.foreco.2012.10.049.

Verstraeten, G., Vancampenhout, K., Desie, E., De Schrijver, A., Hlava, J., Schelfhout, S., Verheyen, K., Muys, B., 2018. Tree species effects are amplified by clay content in acidic soils. Soil Biol. Biochem. 121, 43–49. https://doi.org/10.1016/j.soilbio.2018.02.021.

Vesterdal, L., Clarke, N., Sigurdsson, B.D., Gundersen, P., 2013. Do tree species influence soil carbon stocks in temperate and boreal forests? For. Ecol. Manag. 309, 4–18. https://doi.org/10.1016/j.foreco.2013.01.017.

Vitousek, P.M., Chadwick, O.A., 2013. Pedogenic thresholds and soil process domains in basalt-derived soils. Ecosystems 16, 1379–1395. https://doi.org/10.1007/s10021-013-9690-z.

Wittich, W., 1948. Die heutigen Grundlagen der Holzartenwahl (Hannover).

Wittich, W., 1953. Untersuchungen über den Verlauf der Streuzersetzung auf einem Boden mit starker Regenwurmtätigkeit. Forstl. Fak. Göttingen 9.

Zanella, A., Jabiol, B., Ponge, J.F., Sartori, G., De Waal, R., Van Delft, B., Graefe, U., Cools, N., Katzensteiner, K., Hager, H., Englisch, M., Brethes, A., Broll, G., Gobat, J.M., Brun, J.J., Milbert, G., Kolb, E., Wolf, U., Frizzera, L., Galvan, P., Koll, R., Baritz, R., Kemmers, R.,

Vacca, A., Serra, G., Banas, D., Garlato, A., Chersich, S., Klimo, E., Langohr, R., 2014. European Humus Forms Reference Base.

Zhang, D., Hui, D., Luo, Y., Zhou, G., 2008. Rates of litter decomposition in terrestrial eco-systems: global patterns and controlling factors. J. Plant Ecol. 1, 85–93. https://doi.org/10.1093/jpe/rtn002.