Forest conversion to conifers induces a regime shift in soil process domain affecting carbon stability

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B.M. designed the observational setup, K.Va. designed the geochemical and soil carbon components of the research, K. Va. and K.H. designed the microbial components and B.M. and K.Ve. designed the soil fauna and ecological components of the study. E.D. and J.H. collected the data and E.D. analyzed the data. All authors contributed to the interpretation of the results. E.D. and K.Va. contributed equally in compiling the manuscript.

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Highlights:

- Forest conversion can induce a shift in soil process domain (SPD)
- A shift in SPD impacts different functional compartments of the soil carbon cycle
- Topsoil total carbon concentrations increase after conversion to conifers
- Carbon is stored in less stable pools under coniferous forest in the Al-SPD
- Soil carbon stability is driven by the interplay of tree species and edaphics

Abstract

A substantial part of forests worldwide is located on acidic soils. Acidification processes are typically characterized by non-linear responses of soils to external drivers. Acid buffer ranges and thresholds in soils are widely acknowledged, yet these non-linearities are rarely incorporated into our understanding of soil carbon dynamics. Here we have studied the effect of conversion of broadleaved mixed forest to Norway spruce monocultures on different functional compartments of the belowground carbon cycle, i.e. litter layers, soil fauna and soil micro-organisms, and have examined how in turn they affect soil biochemical characteristics and ultimately, soil carbon stability. By studying this effect chain along a soil buffering gradient, we were able to evaluate the relative significance of forest management versus edaphic constraints on soil carbon processing. The effects of conversion are extensive and change trajectories are larger for forests that shifted from one buffering domain to another upon conversion. In the latter, conversion leads to a larger buildup of the litter layer, significantly stronger acidification, and a decrease in microbial functional diversity and earthworm biomass in the mineral soil, mirrored by a collapse of the base saturation. Although topsoil total carbon concentrations increased under spruce, this soil carbon is stored in less stable carbon pools compared to broadleaved forests. These are carbon pools where carbon is not occluded in aggregates or bound to soil minerals and therefore more vulnerable to environmental factors. Our findings show that changes in forest composition can, depending on the initial distance from a threshold in acid buffering, cascade through different compartments of the soil carbon cycle and eventually alter the way carbon is stored.

Key words

Tree species effect , Tree species composition , Forest management , Soil acidity , Soil carbon sequestration , Regime shift ; Soil process domains

1. Introduction

Climate-smart land management forms a principal chapter of the needed measures for decarbonization of the atmosphere (Law et al., 2018; Paustian et al., 2016; Rockström et al., 2017). Carbon sequestration in forest ecosystems is accordingly an ecosystem service of great importance (Lal, 2004; Minasny et al., 2017; Srivastava et al., 2012). More carbon can be sequestered in the soil than in living biomass, and with longer turn over times. Hence, sustainable management of forest soil carbon is of utmost importance in optimizing that service (Jandl et al., 2007). As the life cycle of a managed forest typically spans decades to centuries, the choice of tree species is one of the major long-term forest management decisions to be made (Seidl et al., 2008; Verheyen et al., 2016). But how this decision affects carbon storage in the soil and carbon stability remains little studied (Vesterdal et al., 2013). Recent efforts have been made by Angst et al. (2018) who find that tree species influence soil carbon stability independently from total carbon stocks, however the influence of the edaphic context remains unclear. There is accumulating evidence that edaphic constraints fundamentally affect soil carbon cycling (Angst et al., 2018; Schmidt and Schmidt, 2011). Changes in soil acidity, for example, may be a more important driver of soil organic matter behavior than climate, especially on longer time scales (Rasmussen et al., 2018). In addition, a great portion of the world's forests are located on acidic soils (Supporting information 1, Slessarev et al., 2016; FAO, 2015; IGBP-DIS, 1998). In this regard, a better understanding of carbon stability in relation to tree species - site interactions seems key to optimize forest management for carbon sequestration and to expand the concept of 'climate-smart' soils (sensu Paustian et al. (2016)) to forests.

Tree species composition determines the quantity and quality of organic matter added to the litter layer and the belowground compartment (Kögel-Knabner, 2017; De Schrijver et al., 2012; Reich et al., 2005). Most studies that discuss tree species effects focus on litter layer characteristics and their effect on nutrient cycling (Wang et al., 2016; Mueller et al., 2015; Reich et al., 2005), with little consideration for the influence of the edaphic component. Some studies also mention tree species effects on total carbon stocks or carbon composition (Quideau et al., 2001; Vancampenhout et al., 2010). The chemical quality of the organic input, largely determined by the forester's choice of overstory species, is however not regarded as relevant for long-term stabilization of organic carbon in the soil as compared to organo-mineral interactions and occlusion in aggregates (Lehmann and Kleber, 2015). Today, it is still unclear how these stabilization mechanisms interact with tree species effects or vary with soil type or depth (Angst et al., 2018; Jandl et al., 2007; Kögel-Knabner, 2017; Vesterdal et al., 2013). Moreover, the role of soil fauna in soil mass exchange remains largely overlooked (Filser et al., 2016; Mueller et al., 2015; Prescott, 2010).

Current ecological thinking increasingly focusses on the non-linear behavior of natural systems (Moore et al., 2009), yet successful application of such views are still scarce in soil carbon research (Vogel et al., 2018). The concepts of alternative stable states, tipping points and ecosystem collapse have all been applied to aboveground forest dynamics (Lindenmayer et al., 2016; Ghazoul et al., 2015; Suding et al., 2004) but remain largely unexplored for belowground processes. Many studies and models still assume linear relationships between carbon input and transformation to more stable forms (Jackson et al., 2017). Nevertheless, Muhs (1984), Ulrich (1991) and Vitousek and Chadwick (2013) have evidenced non-linearity in soil acidification processes. They introduced the concept of 'pedogenic thresholds' as "*points where soil properties change abruptly and/or nonlinearly with a small increment in environmental forcing*" (Chadwick and Chorover, 2001). The "*regions between thresholds where soils change much more gradually across a large range of environmental forcing*" are referred to as buffer ranges or soil process domains (Vitousek and Chadwick, 2013). In terms of acid buffering this is best illustrated by measured pH values, which do not respond instantaneously to the input of new hydrogen ions, but reflect the buffering by several concurrent or subsequent buffering mechanisms. The reactions at work in neutral and slightly acidic pH zones show narrow buffer ranges, where the soil process domains quickly substitute each other. These soils are therefore more susceptible to rapid change (Chadwick and Chorover, 2001). As the vast majority of the world's forests have acidic soils (FAO, 2015; IGBP-DIS, 1998), most forests soils are residing in this unstable region. Nevertheless, the effects of these biogeochemical thresholds on the dominant ecological feeding strategies of soil communities and the type of carbon stabilization mechanisms at work have up till now been largely neglected.

If we accept non-linearity as a key feature of ecosystems (Moore et al., 2009), then why do we not extend these insights to belowground functioning and carbon cycling? In this study we therefore aim at evaluating the relative significance of tree species effects and soil process domains, sensu Vitousek & Chadwick (2013), on different functional compartments of the forest carbon cycle, i.e. the litter layer, soil fauna and soil micro-organisms. We moreover aim to assess how these compartments interplay with soil biogeochemical parameters and finally how they affect soil carbon storage and stability. By doing so, we want to verify if a change in overstory species can induce a geochemical shift in soil process domain. If so, does this change in litter quality cascade down into soil carbon dynamics? And finally, can this aboveground shift also induce a regime shift in soil carbon stability? The disentangling of biotic and edaphic drivers of soil carbon dynamics in forests is particularly difficult as long-term experiments are few and observational studies typically struggle to differentiate between co-varying factors or legacy effects. A major reason for this confounding is that mature forests where overstory species and edaphic conditions vary independently are extremely rare (Augusto et al., 2002; Binkley and Giardina, 1998). In this study, we benefit from a series of monocultural Norway spruce (*Picea abies*) stands, that were established ca. 70 years ago within a large, semi-natural broadleaved forest in the Gaume (southern Belgium). In this region, natural variations in marl content of the Jurassic parent material and variable addition of Quaternary eolian loess have created a natural gradient of soil properties, that span the pedogenic threshold between the exchange and the aluminium soil buffer domains. A twin-plot observational set-up was designed along this edaphic gradient, i.e. a series of pairs of a treated (converted to spruce) and an adjacent untreated plot (unconverted to spruce). The forest matrix was under the same ownership for centuries, with no previous agricultural use on record (sensu Hermy 1999), largely excluding land-use legacy effects. Altogether, the natural edaphic gradient, the synchronized forest conversion, and the paired sampling between converted and unconverted plots along the gradient form a unique design allowing the assessment of conversion effect in relation to Ulrich’s and Chadwick’s soil process domains.

2. Material and Methods

2.1 Study region

The study area is part of a 200 km^2 forested area in southern Belgium, the Gaume region (centre 49° 37′ N, 5° 33′ E) (Supporting information 2). This region contains one of the largest complexes of ancient forest in Belgium. We define ancient as being continuously forested since land use records began in Belgium in 1777 (Hermy et al., 1999). The deciduous forest matrix is uneven-aged, mixed and mostly dominated by *Quercus robur* L., *Fagus sylvatica* L. and *Carpinus betulus* L. Between 1960 and 1980 several patches, size 2-15ha, were clear-cut and replanted with Norway spruce monocultures. This particular land use history allows evaluating conversion effects while largely excluding other land use legacies, as the whole semi-natural forest matrix was managed as coppice with standards under the same ownership for centuries, and the spruce conversion happened a few decades ago in a relatively short lapse of time. The Gaume region is characterized by the intertwining of two geological formations (the Arlon and Luxembourg formation), which are both Jurassic calcareous sandstone (grès calcaire) with varying marl content (Supporting information 2). The landscape is part of a cuesta between the Ardennes and the Paris basin. A thin and discontinuous Quaternary aeolian loess deposition occurred on North-facing slopes. This range in parent materials has translated into a natural variation in soil properties in terms of intrinsic buffering capacity (in casu CEC_{clay}) and in reserve of weatherable bases. As a result, a range of soil pH values can be encountered, that spans the pedogenic threshold between the exchange and the aluminium soil buffer domains (Verstraeten et al., 2018). Soil texture varies from sand to loam and profiles can be classified as Luvisols, Alisols and Cambisols (IUSS Working Group WRB, 2015). The topsoils are characterized by relatively poor soil fertility as a consequence of the sandy substrate, a lack of free carbonates and a slow natural weathering to replenish base saturation (Bouezmarni et al., 2009).

Along the gradient in soil fertility a twin-plot design was established. For each Norway spruce plot (10m x 10m) situated in an island of coniferous forest amidst the mixed deciduous matrix, an adjacent mixed deciduous plot (10m x 10m) was established, with the plot centers about 30m from the edge between both patches and about 60m from each other, as a compromise between edaphic comparability and minimizing mutual tree influence (Fig. 1). In addition, all spruce plots have similar stand age, and have similar elevation and slope or orientation as the neighboring deciduous plot as to assure comparability in soil type, forest history and original tree species composition.

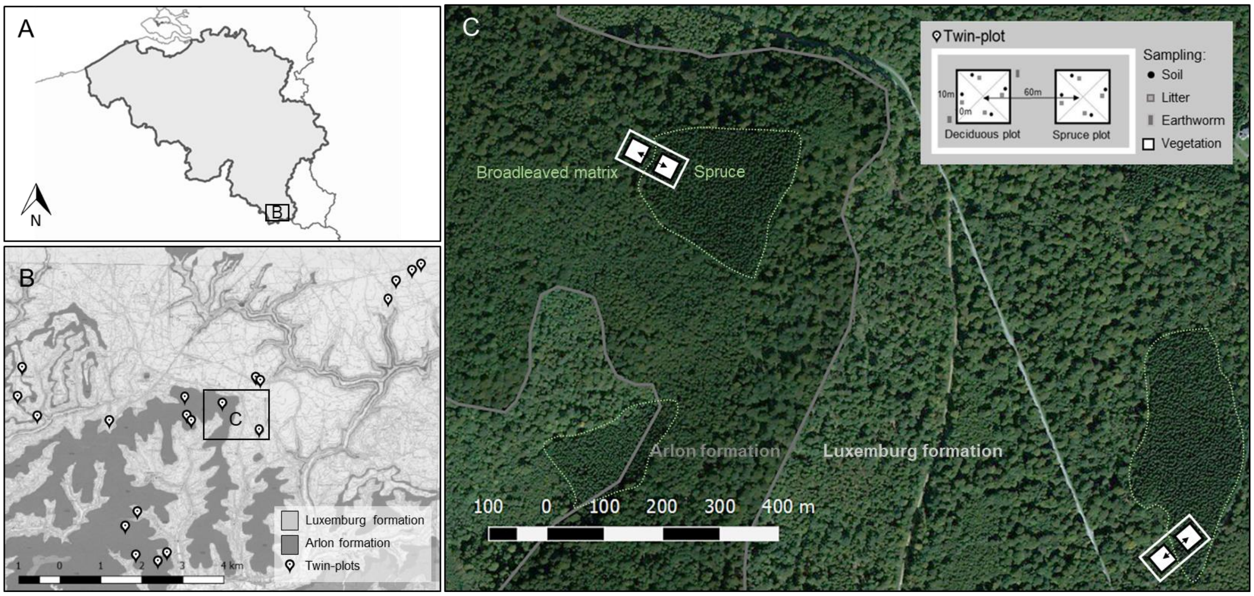

Figure 1: A) Geographical situation of study region in Belgium, B) Twin-plots (pins) on geological map of the study region with the Luxemburg formation (light grey) and the Arlon formation (dark grey), C) Cut-out showing two twin-plots located in the two different geological formations, and detailed sampling positions used per plot.

2.2 Data collection

Data was collected during subsequent field campaigns in 2009 (earthworms and litter layers), 2013 (biogeochemistry and microbiota) and 2015 (soil carbon). Earthworm communities were sampled in opposite corners of each plot (Figure 1 – top right) (Verstraeten et al., 2018) by subsequent sampling and hand sorting the forest floor, mustard extraction on the same surface of the mineral soil (surface of 0.5 m^2, earthworms were collected directly after coming to the surface) and by hand sorting a soil core taken within the mustard treated area (0.1m^2, 20cm deep) (De Wandeler et al., 2018; Valckx et al., 2011). All earthworms were killed and preserved in 95% ethanol and afterwards fixed in 5% formalin solution. They were identified at species level following Sims and Gerard (1999). Earthworm biomass was expressed as g/m^2 ethanol preserved mass. The forest floor was collected in a separate square of 20x20cm^2, separated in fresh litter layer (L), fermentation layer (F) and humus layer (H). The litter samples were dried at 70°C until constant mass and weighed. The total forest floor mass equals the sum of the three separate layers. Vegetation and humus types were described according to Braun-Blanquet (1964) and Zanella et al. (2014) respectively. Composite soil samples, consisting of 4 sampling points randomly chosen in each quadrant of the plot, were collected at three depth intervals (0-5cm, 10-20cm, 25-35cm) using a soil corer. Soil samples were dried at 40°C until constant mass. Soil texture was measured by laser granulometry (Malvern Mastersizer S) after pretreatment for removal of organic material. Soil pH-KCl (extraction in 1M KCL, 1:5 suspension, ion specific electrode: ISRIC and FAO 2002) was measured for all depths. Cation exchange capacity (CEC) and base saturation (BS) were determined by extraction with cobalt hexamine (Ciesielski et al., 1997) and pH-water was measured (1:5 suspension, ion specific electrode: ISRIC) for the topsoil (0-5 cm) and subsoil (25-30 cm) layer. The soil for microbial analysis was sampled according to Muys et al. (2013) and microbial functional diversity was determined using Biolog EcoPlates after preparation of the soil samples (Gaublomme et al., 2006). Due to the time consuming carbon fractionation procedure the carbon research was executed on a subset of 10 twin-plots that spans the variation within the original dataset (Supporting information 2). The chemical carbon fractionation was executed based on the Zimmerman protocol (Zimmermann et al., 2007). All soil samples were divided into 4 separate fractions: sand and stable aggregates (S+A), silt and clay (s+c), particulate organic matter (POM) and dissolved organic carbon (DOC). For each of those fractions, in addition to the total soil sample, carbon contents were measured by dry combustion (900°C Shimadzu

5050A element analyzer). The division of carbon over stable (S+A and s+c) and labile (POM and DOC) carbon pools serves as a proxy for carbon stability (Zimmermann et al., 2007).

2.3 Data analysis

To evaluate the edaphic context of the study site, a K-means clustering analysis was executed on the deciduous plots based on variables indicative of soil buffering capacity and dominating soil process domain (Chadwick and Chorover (2001) and Vitousek and Chadwick (2013)): i.e. soil texture (sand content, clay content) and CEC, BS, exchangeable Al concentration and exchangeable calcium concentration measured at 25-30 cm. This analysis (Supporting information 4) separates the deciduous plots into two distinct clusters, with variable values that correspond to respectively the exchange buffer domain and the aluminium buffer domain (hereafter exchange domain and Al domain; according to Chadwick and Chorover (2001) and Vitousek and Chadwick (2013)).

To evaluate the effect of conversion on soil variables, including variables indicating for the edaphic gradient in the study site, a principal components analysis was executed including both deciduous and spruce plots (Fig. 2). On top of the variables sand content, subsoil CEC and subsoil exchangeable Al, also topsoil pH, topsoil base saturation, topsoil exchangeable Al, earthworm biomass and litter and subsoil functional diversity (MBD litter and MBD sub) were included. The factor map of the variables was plotted rescaled but with true inter-distances and contributions behind the factor map of the individuals. In the factor map, the deciduous and spruce plot of every twin-plot are connected with a line to show the their change trajectory along the variable factor map (Fig. 2). The visualized difference in conversion effect between soil process domains (based on previously identified clusters, *vide supra*) was then further tested by means of mixed models with site of the twin-plot as a random factor. The results of a post-hoc multiple comparison test are indicated in the boxplots. All statistical analyses were performed with R 3.3.2.

3. Results

3.1 Conversion effects on soil process domains

We first examined how natural variations in the Jurassic and Quaternary parent material of the study site have determined soil acidity and site conditions independently from conversion to spruce. Hence, we allocated the deciduous plots to the exchange domain or the Al domain based on K-means clustering on variables indicative of soil buffering capacity and ions on the exchange complex in the deciduous plots (see 2.3 and Supporting information 4). Deciduous forest plots allocated to the exchange domain typically have a base saturation above the 30% threshold (Chadwick and Chorover, 2001) and range up to 80%, with a mean of 62%. Aluminum concentrations are below 0.11 g Al^{3+}/kg soil whereas deciduous forest plots in the Al domain have base saturation values always below 30% and aluminum concentrations up to 0.21 g Al^{3+}/kg soil. Next, we evaluated the impact of overstory conversion relative to the initial soil process domain by a principal components analysis on deciduous and spruce plots (Fig. 2; plots belonging to the same twin are connected by a line). Principal component (PC) 1 explained 46.16% of the variation within the dataset and PC 2 explained 14.81% respectively. This analysis illustrates the large natural range in site conditions under a deciduous overstory (Fig. 2: circles) while the converted plots (Fig. 2: triangles) show a more narrow range. All converted plots show a shift to the right, which corresponds to a decrease in topsoil pH and BS and an increase in topsoil Al^{3+}, and can be allocated to the Al domain. Moreover, conversions of deciduous plots initially in the exchange domain (Fig. 2: light blue circles) to spruce are characterized by larger trajectories along PC1 compared to conversions of twins that were already within the aluminium domain prior to conversion, which corresponds to a larger change in belowground ecosystem functioning.

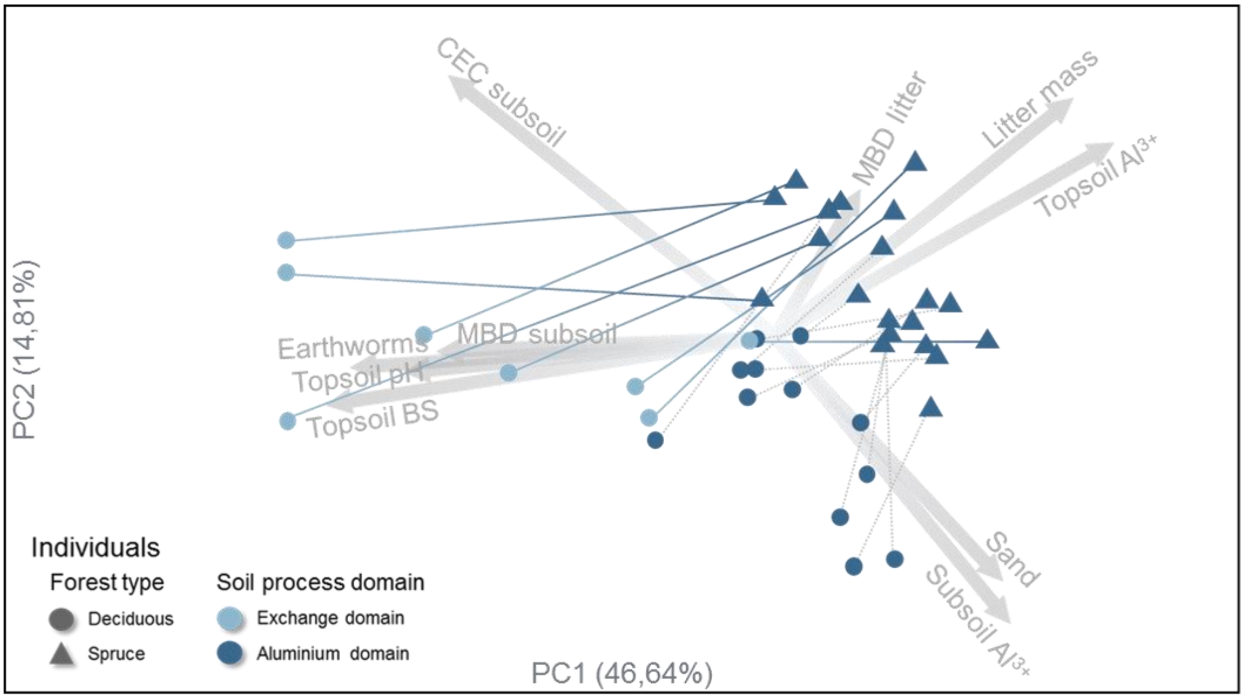

Figure 2: Principal components analysis on deciduous forest plots and plots converted to spruce. Deciduous plots are indicated by dots whereas spruce monocultures by triangles. Plots belonging to the same twin are linked by a line. A distinction is made (based on a K means cluster analysis (Supporting information 4)) between deciduous plots located in the exchange domain before conversion (light blue) and plots that were already in the Al domain prior to conversion (dark blue). The first PC corresponds mostly with the overstory conversion effects whereas the soil process domain of the deciduous plots is a function of both first and second PC. Deciduous forest plots initially located in the exchange domain show larger trajectories along the first axis upon conversion than deciduous forest plots already in the Al domain. Abbreviations in the figure: microbial diversity (MBD) and cation exchange capacity (CEC). (N=40).

3.2 Conversion effects on litter layers, decomposer communities and soil biogeochemistry

Overall, we found significant changes in soil biotic communities and soil biogeochemistry after overstory conversion. Accumulation of organic matter in the litter layer is double under spruce compared to mixed broadleaved forest (Fig. 3: A and B). Additionally, our results indicate that initial soil process domain and conversion both affect the earthworm biomass, which is significantly reduced from the exchange domain to the Al domain, and upon conversion (Fig. 3: C). Although the biomass of burrowing earthworms is drastically lower in the Al domain (with average values of 2g/m^2 in contrast to 40g/m^2 in the exchange domain), some rather acid tolerant burrowing earthworm species, e.g. *Aporrectodea caliginosa* and *Lumbricus rubellus* (Muys and Granval, 1997), are still present in the Al domain under deciduous vegetation (Supporting information 6), while after conversion to spruce, only strict acid tolerant litter dwelling earthworm species without burrowing capacities survive (Supporting information 6). Functional microbial catabolic diversity is well distributed over the litter-soil horizons in deciduous plots in the exchange domain, and somewhat shifted towards the upper compartments in deciduous plots in the Al domain (Fig. 3: D). Conversion induces a sharp discontinuity in the microbial catabolic functioning between litter and soil (Fig. 3: D). In terms of soil biogeochemistry, soil acidity and soil base saturation (BS) increase significantly from the exchange domain to the Al domain and even more with conversion to spruce (Fig. 3: E, G and H). The drop in pH and BS is larger for sites where conversion induces a shift from one soil process domain to another. For these sites pH drops from 5.1 to 4.1 and BS shifts from 62% to 16% in the topsoil and 48% to 8% in the subsoil. Moreover, the higher clay content of these sites (Verstraeten et al., 2018) leads to a larger potential to build up toxic aluminium cations on the exchange complex (Fig. 3: F).

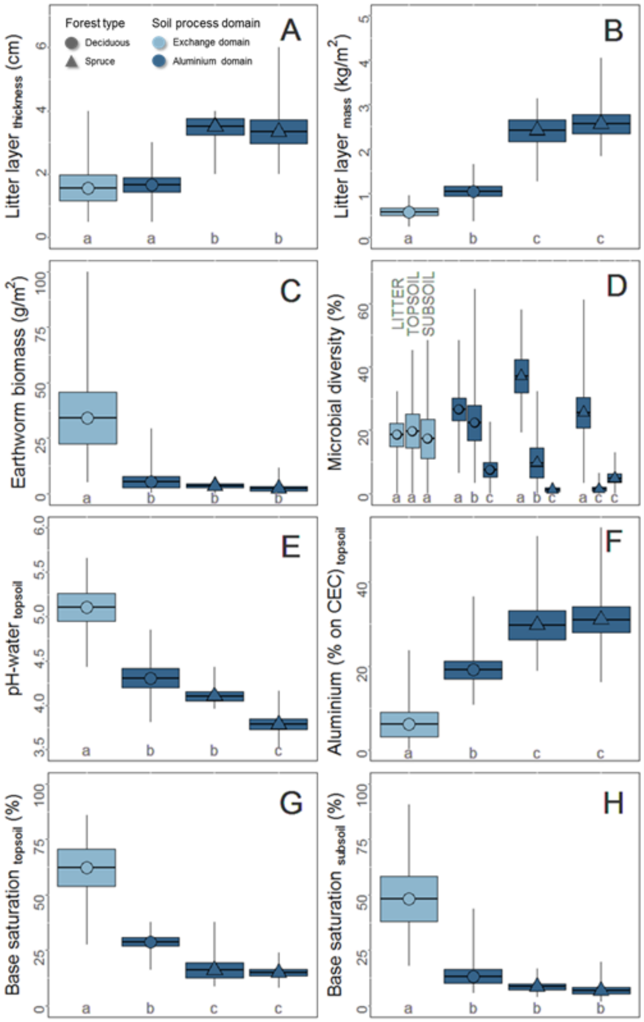

Figure 3: Values (range, standard error and mean) per forest type and per initial soil process domain for litter layer thickness (A), litter layer mass (B), earthworm biomass (C), functional microbial diversity (D), topsoil pH (E) topsoil aluminium on the CEC (F), topsoil and subsoil base saturation (G and H). A distinction is made between deciduous plots initially in the exchange domain (light blue) or in the Al domain (dark blue). Results of a post hoc multiple comparison test (α<0.05) are indicated below the boxes: different letters indicate a significant difference between the mean of two boxes. (N=40).

3.3 Conversion effects on soil carbon sequestration

Mineral topsoil total carbon concentrations increase from 3% to 4% with a conversion to spruce regardless the initial soil process domain (Fig. 4: A). However under spruce less carbon is stored in the sand and stable aggregates (S+A) fraction and more in the labile fraction particulate organic matter (POM) and stable fraction silt and clay fraction (s+c) as defined by Zimmermann et al. (2007) . The relative storage of carbon over such stable and labile pools is lower under spruce than under deciduous forest (Fig. 4: E). This effect becomes particularly distinct when data are split into soil process domains: in the Al domain a smaller proportion of topsoil carbon is stored in stable aggregates (S+A), whereas a larger fraction of topsoil carbon is stored as more labile particulate organic matter (POM) (Fig. 4: D and F).

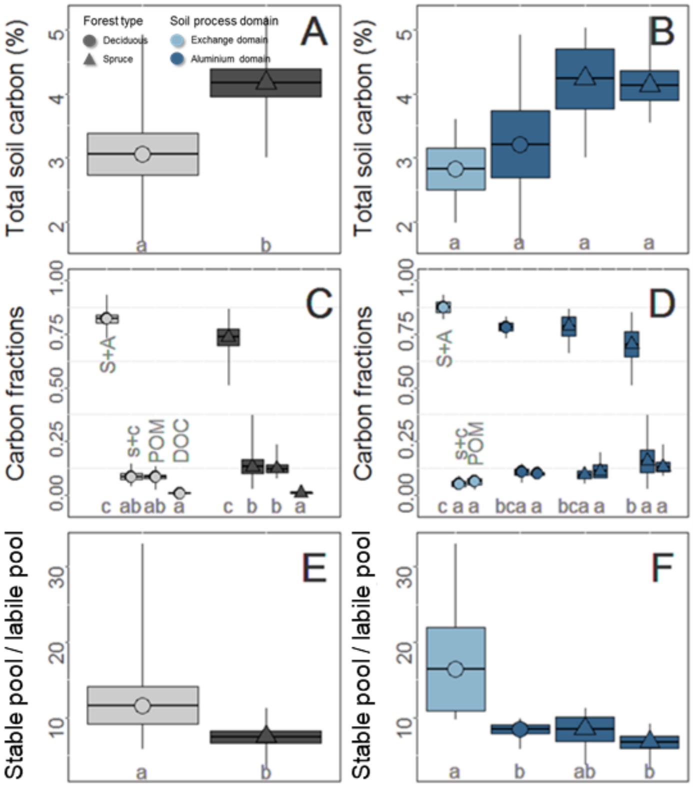

Figure 4: Values (range, standard error and mean) for total carbon stocks (A and B), carbon fractions (sand and stable aggregates – S+A, silt and clay – s+c, particulate organic matter – POM and dissolved organic carbon – DOC) (C and D) and the division of carbon over stable and labile pools (E and F) respectively for forest type (left graphs: light grey for deciduous versus dark grey for

spruce) and per initial soil process domain (right graphs: light blue for the exchange domain and dark blue for the Al domain). In the analyses per soil process domain carbon stored in the DOC fraction showed no variation and was therefore not included in the graph. Results of a post hoc multipe comparison test (α<0.1) are indicated under the boxplot. (N=20).

4. Discussion

4.1 Can a change in litter quality induce a shift in soil process domain?

Comparison of the deciduous plots along the edaphic gradient showed contrasting values in terms of soil acidity and soil base saturation that support the idea that our study site is indeed a system residing either closely above or below a pedogenic threshold in soil process domain. Therefore, our twin setup of conifer conversion along a gradient is particularly suitable for evaluating whether management-induced non-linearities in acid buffering can also affect the broader dynamics of belowground functioning. Our results confirm the adverse impact of Norway spruce effects on soil quality described in literature: accumulation of organic material in the litter layer is higher, earthworm biomass is reduced, soil acidity and aluminium saturation are higher and base saturation lower under spruce compared to mixed deciduous forest (Vesterdal et al. 2008; Reich et al. 2005; Hagen-Thorn et al. 2004; Augusto et al. 2002; Binkley & Valentine 1991). Additionally, our results show that the initial soil process domain determines the trajectory upon conversion, with conversion effects being more pronounced in deciduous plots originally located in the exchange domain. This seems counterintuitive, but is in line with Verstraeten et al. (2018) who found for the same sites that the most dramatic impact of conversion on soil geochemistry occurs in the richest plots, i.e. the plots that were still in the exchange domain prior to conversion to conifers. Indeed, after conversion, all plots resided in the more acid Al domain, which substantiates the hypothesis that for the edaphic situation of the Gaume forest, an increment in acid load induced by the change in litter quality is enough to deplete the remaining base cations left on the exchange complex and topple the soil system from the exchange domain into the Al domain.

4.2 How far does a change in litter quality cascades down into soil carbon dynamics?

The adverse effects of low quality spruce litter on the belowground ecosystem are no novelty (Augusto et al. 2002; Reich et al. 2005; Vesterdal et al. 2008), yet the distinct behavior of the conversion trajectories per initial soil process domain is striking. Although the thickness of the litter layer seems to reveal little difference between process domains, a shift in ecological functionality becomes evident when studying the soil organisms. As a consequence of the decrease in earthworm biomass, the incorporation of organic material into the mineral soil is hampered, leading to a vertical decoupling of material flows between the litter layer and the soil, and between soil horizons (Muys et al., 1992). Besides the redistribution of nutrients and carbon in the mineral soil by bioturbation, earthworms also improve litter palatability for micro-organisms by fragmenting larger organic matter particles and by their gut passage (Brown et al., 2000). The functional change in soil fauna therefore co-occurs with a fundamental change in microbial communities. There is an abrupt decoupling of microbial catabolic diversity between the soil and the litter layer, with most functionality now in the forest floor layers where organic substrates are more plentiful. Catabolic diversity in the soil itself becomes particularly low, illustrating the harsh soil conditions in the Al domain. Hence, our findings are in line with an observed increase in the activity of bacterial stress genes as a reaction to soil acidity reported in literature (Song et al., 2017). The implications of this fundamental change in decomposer functionality moreover becomes obvious in the soils' biogeochemistry: the increased production of acids as intermediate decomposition products in accumulating litter layers is known to affect the soil pH (de Vries et al., 1995), yet our data show that a shift in carbon cycles from the soil to the litter layer not only increases acid load but also triggers a collapse of base cation concentrations in the subsoil as decomposer activity becomes more superficial.

The described change in belowground communities and mass exchange further affects the way carbon is stored in the mineral soil. Similar to the observed accumulation of non-stabilized organic material in the forest floor layer, mineral topsoil total carbon concentrations increase with a conversion to spruce regardless the initial soil process domain. However, not all carbon stored in the topsoil is equally well protected from microbial decay. Occlusion in aggregates (S+A carbon fraction) and interaction between organic molecules and soil minerals (s+c carbon fraction) make organic components inaccessible to microbes as compared to non-protected carbon present as particles (POM carbon fraction) or in solution (DOC carbon fraction) (Zimmermann et al., 2007) where it is much more susceptible to disturbances and decomposition. Our results indicate that with a shift in soil process domain from the exchange domain to the Al domain, also topsoil carbon processing is altered. Although more carbon is stored, it accumulates partly in more labile fractions, mostly as POM, and thus the stability of this carbon storage decreases. The here mentioned POM fraction is based on a chemical fractionation described by Zimmermann et al. (2007) and corresponds with the “large” POM fraction reported by Angst et al. (2018), who also define it as a labile SOC fraction, contrary to their “small” POM fraction. Hence, even on the relatively short time span of a few decades, there is a trade-off between topsoil carbon storage and carbon stability between soil process domains. With progressing time, this trade-off is expected to increase. Our results support the idea of Prescott (2010) and Liang et al. (2017): rather than slowing down the carbon cycle by planting species with more recalcitrant litter, it is a more sustainable climate mitigation strategy to divert litter into decomposition pathways with more active entombing of soil carbon in the stable fraction by soil fauna or anabolic processes. Moreover, low quality litter implies a potential threat to tree health and productivity, as our data evidences important knock-on effects in terms of acidity, availability of nutrients and accumulation of toxic exchangeable aluminium.

Some studies have suggested a trade-off between forest floor layers, topsoil and subsoil carbon sequestration (Vesterdal et al., 2013) and have emphasized the importance of deep soil carbon (Li et al., 2012; Rumpel and Kögel-Knabner, 2011). As our main focus was soil biota and the link with soil edaphics and carbon processing, we limited the study to the first 35 cm. Also in that regard, we do not research the impact of root litter input on carbon sequestration as well as root exudates on soil acidity. Moreover, turnover time generally increases with depth and the spruce stands are relatively young (ca. 70 yrs), therefore we focused on the more rapidly evolving leaf litter pathway. Nevertheless, further research of tree species effects on deep soil carbon is necessary as the contribution of subsoils to the total soil carbon budget cannot be neglected (Rumpel and Kögel-Knabner, 2011). The effect of habitat continuity, or the lack of it due to a clear cut and forest conversion, on carbon dynamics also needs further attention (Leuschner et al., 2013; Nitsch et al., 2018).

4.3 Can tree species conversion induce a regime shift?

An essential question towards management is now whether the observed non-linearity in our dataset is merely a threshold, or whether it represents a regime shift between stable states, sensu Scheffer et al. (2001). In case of a regime shift, simply changing overstory species in the next rotation back to deciduous will be insufficient to shift the degraded soil back to a more favorable process domain, and hence more effort will be required for a complete restoration. Although it was not possible to study reverse trajectories in our in-field setup, several observations indicate that hysteresis may be considerable which is one of the key characteristics of regime shifts in ecosystems. First, the cascade of effects from decomposer communities to the soils' biogeochemistry and carbon cycling, described above, strongly suggests the existence of a substrate-soil-biota positive feedback loop, complicating the reversibility of the process. In addition, the slow recolonization speed of earthworms (Valckx et al., 2010) impedes fast return of soil faunal communities to the previous state. Recent publications moreover suggest that regaining lost functional pathways in soil microbial communities may also be slower than previously assumed (Morriën et al., 2017), and it is evident from our results that edaphic properties and faunal activity are closely mirrored in the microbial functional diversity. Managing soil fauna may therefore be necessary upon restoration, and may be the most promising avenue to steer soil microbial cycles in support of carbon sequestration and other forest ecosystem services (Cotrufo et al., 2013; Singh et al., 2010). Second, the strong retention of aluminium on the soils' exchange complex in comparison to base cations is a potential cause of hysteresis, thus making restoration of pH and base saturation more difficult after crossing a pedogenic threshold, and this effect becomes more pronounced with increasing CEC (Chadwick and Chorover, 2001).

In addition, although it seems counterintuitive that deciduous plots with higher initial buffering capacity experience more extreme adverse effects from overstory conversion, such longer trajectories are typical for ecosystems that undergo a regime shift (Fig. 1 and Fig. 5: trajectory A->B compared to trajectory A'->B'). Along with the above described positive feedback mechanisms it is a strong argument for the existence of acidity-mediated stable states in the forest's belowground ecosystem.

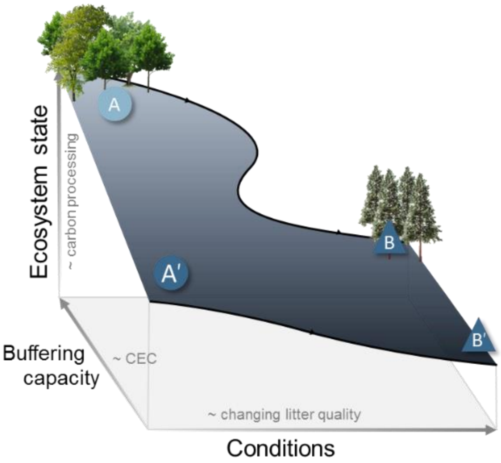

Figure 5: Conceptual representation of pedogenic regime shifts in temperate forests following tree species conversion from broadleaved (A and A') to spruce (B and B'). The belowground ecosystem state is affected by a change in litter quality (conditions) and this response is modulated by the CEC (acid buffering capacity) of the site. A site initially located in the exchange domain (A) undergoes a regime shift when litter quality is changed by overstory conversion, whereas sites that are already in the Al domain (A') under deciduous vegetation (circles) have a smaller more gradual response to the change in litter quality (triangle).

In general, the restoration of all natural systems showing stable states may require large efforts and involve high costs for society, or at worst may even be unfeasible (Steffen et al., 2018). For this reason, avoiding regime shifts is key in the management of natural systems (Ghazoul et al., 2015; Lindenmayer et al., 2016; Scheffer et al., 2001), certainly in a context of climate change mitigation. In forestry and agricultural systems where humans as ecosystem engineers directly interfere in the species composition for their own benefit, i.e. the selection of a certain crop or tree species and the choice for a mixture or monoculture, caution is always necessary. However, this also reveals a great management opportunity: near pedogenic thresholds the impact of management is largest, so by identifying sites in that condition, conservation measures can be targeted to where they will be most effective. This also emphasizes that soil boundary conditions can no longer be overlooked when studying tree species effects and in the process of making forest management decisions, especially with carbon sequestration and climate-smart soil management in mind.

5. Conclusions

Our study on tree species conversion from broadleaved forest to spruce monocultures along a natural edaphic gradient shows the strong effect of overstory species and its leaf litter quality on belowground forest ecosystem processes, but also emphasizes the existence and prominent role of a pedogenic threshold in acid buffering modulating the change trajectory upon this conversion. This means that depending on the initial distance from a pedogenic threshold, effects of tree species conversion on the soil functioning and the way soil carbon is stored may either translate in small changes or in a true regime shift. Sites belonging to the exchange buffer domain but closely located to the threshold with the aluminium buffer domain show a more extreme response in terms of change in acidity, base saturation, earthworm biomass and carbon stability compared to forests already residing in the Al buffer domain. From a practical forest management perspective, we showed that slowing down decomposition by the promotion of tree species with more recalcitrant litter is not a good strategy to optimize carbon sequestration. Although recalcitrant litter input leads to a higher carbon concentration in forest floor and topsoil, this carbon is stored in less stable pools and thus more exposed to disturbances. As pedogenic thresholds occur in many forms and many places around the world, taking into account such non-linearities in the belowground ecosystem when considering forest management decisions is crucial.

Acknowledgements

We thank the municipal councils of Virton and Etalle and ir. B. Van Doren of the Cantonnement de Virton of the Walloon Department of Nature and Forest for permission to access the forest and for providing information on the local forest management. We would like to acknowledge the support of Dr. Gorik Verstraeten, Jeroen Buelens, Dries Martens, Michaël Van Raemdonck and Olaf Brock in the data collection and the help of Kim Vekemans, Dr. Tim De Clercq and Dr. Bart Kerré during the laboratory analysis. Also we would like to thank Dr. Ana Rita Sousa-Silva and Dr. Koenraad Van Meerbeek for their feedback on the manuscript. E.D. holds a SB-doctoral fellowship of the Research Foundation Flanders (FWO).

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6. Supporting information

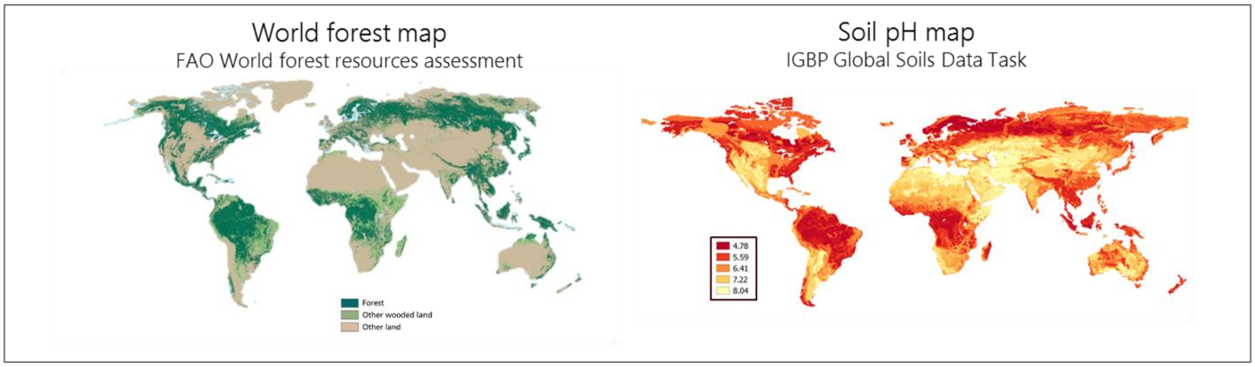

Fig. S1. Left: world forest map adapted from (FAO, 2015). Right: World acidity map (soil pH) adapted from (IGBP-DIS, 1998).

Table. S2. Overview of dataset and carbon subset. Plots are ranked based on clay content.

Twin-plot	Geology	Clay content (%)	Soil process domain (deciduous plot)	Carbon dataset
22	Luxembourg	4.70046	Aluminium	
36	Luxembourg	4.8264	Aluminium	x
8	Luxembourg	5.49994	Aluminium	x
12	Luxembourg	6.31643	Exchange	x
15	Luxembourg	6.47122	Aluminium	
16	Luxembourg	6.83493	Aluminium	
13	Luxembourg	7.46528	Aluminium	
11	Luxembourg	7.74801	Aluminium	x
2	Luxembourg	8.39291	Aluminium	x
21	Luxembourg	9.273	Aluminium	x
17	Arlon	10.39184	Exchange	x
29	Arlon	10.4122	Exchange	
19	Arlon	10.52302	Aluminium	
9	Arlon	10.55077	Aluminium	
27	Arlon	11.11994	Exchange	x
26	Luxembourg	11.55765	Aluminium	x
5	Arlon	11.99477	Exchange	
25	Arlon	12.21832	Exchange	x
30	Arlon	12.26116	Exchange	
1	Arlon	12.3779	Exchange	

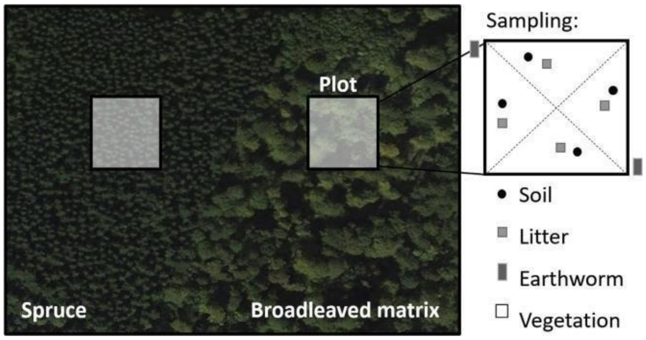

Fig. S3. Scheme of twin-plot set-up in the Gaume forest. (Verstraeten et al., 2018)

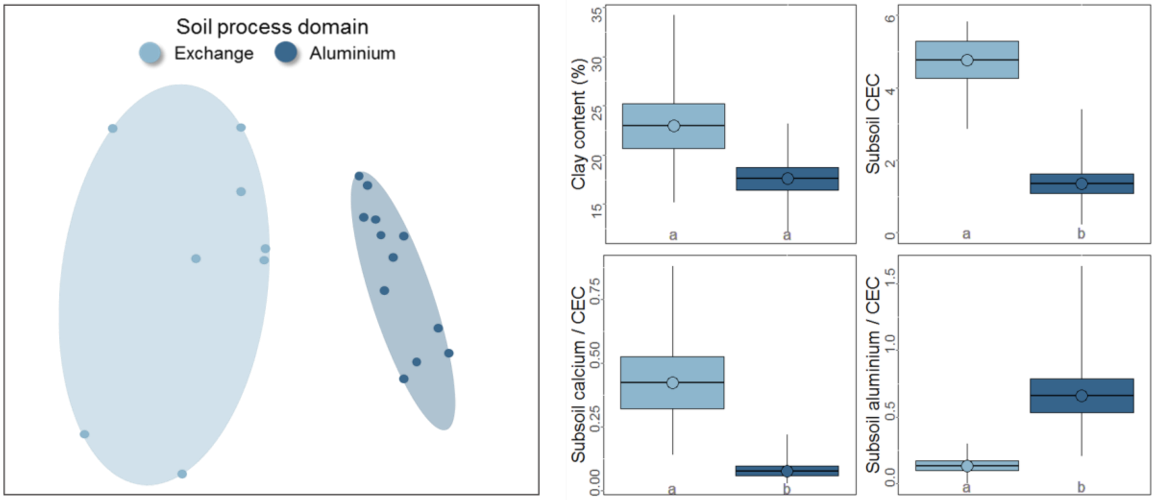

Fig. S4. Left: K-mean cluster analysis of deciduous plots based on variables texture, subsoil CEC, subsoil exchangeable aluminium and exchangeable calcium. The two resulting components explain 79.16% of the point variability. Right: boxplots of above mentioned variables for deciduous plots located in the exchange domain and for deciduous plots located in the Al domain. Results of a post hoc multiple comparison test (α<0.05) are indicated below the boxes: different letters indicate a significant difference between the mean of two boxes.

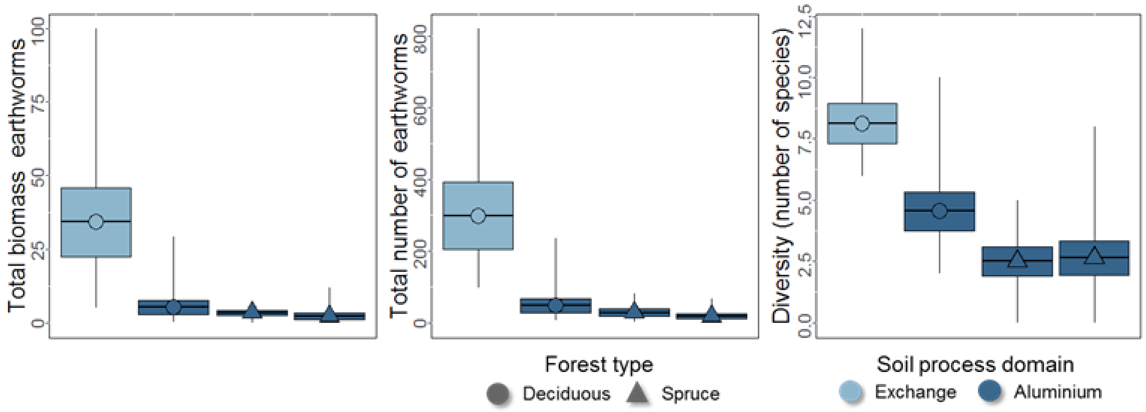

Fig. S5. Values (range, standard error and mean) before and after conversion and per initial soil process domain for total earthworm biomass (g/m^2) (left), total number of earthworms (middle) and total number of earthworm species (right). A distinction is made between deciduous plots initially in the exchange domain (light blue) or in the Al domain (dark blue).

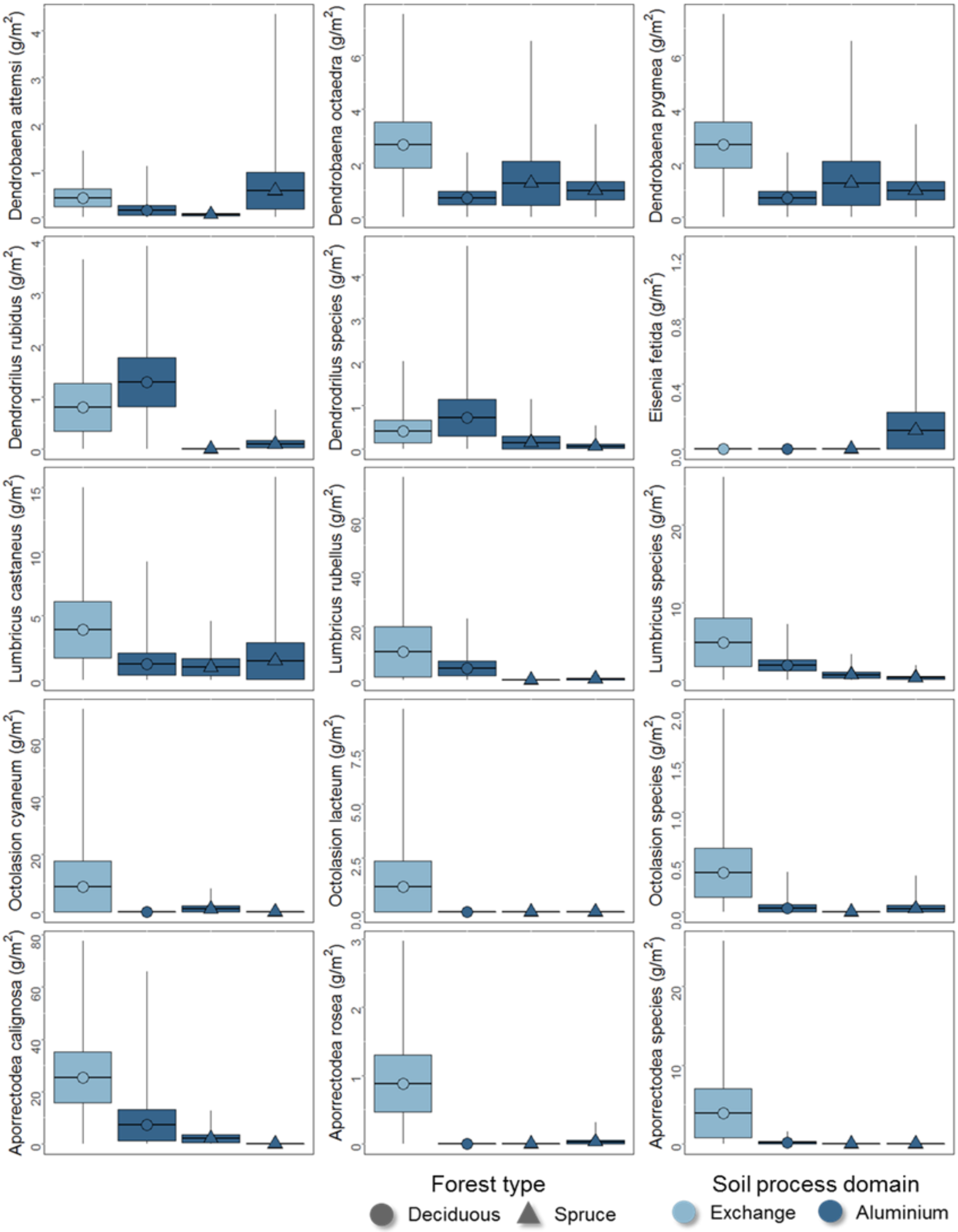

Fig. S6. Biomass (g/m^2) values (range, standard error and mean) before and after conversion and per initial soil process domain for different earthworm species. A distinction is made between deciduous plots initially in the exchange domain (light blue) or in the Al domain (dark blue).