Is Tree Species Diversity or Species Identity the More Important Driver of Soil Carbon Stocks, C/N Ratio, and pH?

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Is tree species diversity or species identity the more important driver of soil carbon stocks, C/N ratio and pH?

Short title: Tree species diversity and identity effects on soils

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Abstract. We explored tree species diversity effects on soil C stock, C/N ratio and pH as compared with effects of tree species identity. We sampled forest floors and mineral soil 0-40 cm in a diversity gradient of 1 to 5 tree species composed of conifers and broadleaves in Białowieża Forest, Poland.
Diversity was a weaker driver than identity of soil C stocks, C/N ratio and pH in the soil profile. However, there were significant non-additive effects of diversity and significant effects of identity on C stock and C/N ratio within different parts of the soil profile. More diverse forests had higher C stocks and C/N ratios in the 20-40 cm layer whereas identity in terms of conifer proportion increased C stocks and C/N ratios only in forest floors. A positive relationship between C stocks and root biomass in the 30-40 cm layer suggested that belowground niche complementarity could be a driving mechanism for higher root carbon input and in turn a deeper distribution of C in diverse forests. Diversity and identity affected soil pH in topsoil with positive and negative impacts, respectively. More diverse forests would lead to higher soil nutrient status as reflected by higher topsoil pH, but there was a slight negative effect on N status as indicated by higher C/N ratios in the deeper layers. We conclude that tree species diversity increases soil C stocks and nutrient status to some extent, but tree species identity is a stronger driver of the studied soil properties, particularly in the topsoil.

Key-words: forest ecosystem function, tree species diversity, tree species identity, soil carbon, soil pH, soil C/N ratio; niche differentiation

1. Introduction

Tree species are known to affect soils through addition of above-and below-ground litter, absorbing nutrients and water from different soil layers and by associations with various soil organisms (Prescott and Vesterdal, 2013; Vesterdal et al., 2013). Whereas previous research has focused mainly on effects of the species identity based on studies within single species forests (Vesterdal et al., 2013) and two-species mixtures (Forrester et al., 2012; Laclau et al., 2013), the effect of wider gradients in tree species diversity on soils has been little studied. The current efforts to address functional implications of species diversity have only recently led to include soils in studies of forest ecosystem functioning as affected by species diversity (Gamfeldt et al., 2013; Scheibe et al., 2015). It is still not well known whether species diverse forests provide higher soil carbon stocks and soil nutrient status (Scherer-Lorenzen et al., 2007b; Nadrowski et al., 2010) and whether these functions increase with diversity or just level off within mixtures of two or three tree species (Schwartz et al., 2000; Scherer-Lorenzen et al., 2007b). Positive effects of tree species diversity were documented for productivity and above-ground C stocks (Paquette and Messier, 2011; Jucker et al., 2014). These effects were attributed to above- and below-ground niche differentiation resulting in increases in availability, uptake or use efficiency of light, water or nutrients (Forrester et al., 2013; Forrester, 2014). The question remains whether similar impacts on soil C stocks, C/N ratio and pH exist (Loreau and Hector, 2001; Hector et al., 2002). The above-ground mechanisms by which diversity influences these soil properties are related to litter production and litter quality (Scherer-Lorenzen et al., 2007a) while below-ground mechanisms include litter decomposition, vertical stratification of tree roots (Brassard et al., 2011), root litter inputs (Brassard et al., 2013), root turnover (Brassard et al., 2011; Lei et al., 2012), root exudates (Bardgett et al., 2005) and downward transportation of organic matter from topsoil layers to deeper layers by soil macro-fauna (Brussaard, 1997; Frouz et al., 2013).

Recent studies from temperate and boreal forests indicated different effects of diversity on soil C stocks, C/N ratio and pH in the forest floor and mineral soil layers, respectively. Diverse forests had lower forest floor C stocks (Guckland et al., 2009) but higher mineral soil C stocks and pH than the monocultures (Guckland et al., 2009; Gamfeldt et al., 2013; Schleuß et al., 2014). We found no consensus among previous studies of soil C/N ratios along tree species diversity gradients (Guckland et al., 2009; Schleuß et al., 2014) but Schmidt et al. (2015) reported no effect of tree species diversity on N availability in the soil. However, there are studies that documented mixtures would increase the foliar N status of the component species (Rothe and Binkley, 2001) and tree species grown in mixtures extract nutrients and water from deeper soil layers and release base-cation rich litterfall into the soil (Guckland et al., 2009) but whether this would have an impact on the soil N status and pH has not yet been examined in mixtures of multiple tree species and functional groups. Some of the previous studies sampled only a shallow part of the soil profile (Vila et al., 2004), studying species dilution gradients rather than diversity gradients or including only broadleaved tree species rather than both broadleaf and conifer species (Guckland et al., 2009). Information is particularly lacking about the effect of diversity on mineral soil C stock, C/N ratio and pH deeper than 10 cm, and under conditions where the species mixtures include tree species with a range of functional traits. The studies by (Guckland et al., 2009; Schleuß et al., 2014) suggested effects on soil C and pH down to 30 cm, but these studies included only broadleaf mixtures that may have a more narrow range in functional characteristics. Information from single-species common gardens indicated that conifers and broadleaves have distinct and different biogeochemical signatures on soil C stock, C/N ratio and pH (Vesterdal et al., 2013; Augusto et al., 2015), and diversity effects may depend on the proportion of species from either group in mixtures. The current information might therefore be inadequate to understand the effects on characteristics of forest floors as well as mineral soil of tree species diverse forests incorporating both functional groups (broadleaves and conifers tree species).

Species identity (conifers or broadleaves) is an important driver of soil C stock, C/N ratio and pH particularly in the forest floor and top mineral soil layer (Vesterdal et al., 2008; Vesterdal et al., 2013; Augusto et al., 2015). However, it is not known whether diversity of tree species belonging to functionally different tree species groups would have non-additive influences on soil C stock, C/N ratio and pH relative to impacts expected from monocultures of the component species. It is also not yet documented whether tree species identity or diversity is the main driver of soil properties, and whether these two factors mainly influence topsoil or deeper layers. A few studies have recently reported that tree species identity effects dominated over diversity effects in the case of soil microbial communities (Cesarz et al., 2013; Scheibe et al., 2015), but the mutual importance of species identity and diversity remains to be determined for soil properties such as C stock, C/N ratio and pH.

In this study we explored species identity and tree species diversity effects on soil C stocks, C/N ratio and pH; and whether these effects were vertically stratified within the studied soil profiles, i.e. the forest floor and mineral soil down to 40cm. We tested the following hypotheses:

(i) Tree species identity influences the soil; in topsoil layers, conifers accumulate more carbon, have a higher C/N ratio and lower soil pH than the broadleaved species.

(ii) Forests with high tree species diversity accumulate more soil carbon compared to species poor forests.

(iii) Increasing tree species diversity decreases C/N ratio and increases soil pH

(iv) Tree species identity is a more important driver of soil C stock, C/N ratios and pH, compared to species diversity.

We studied a species diversity gradient of one to five species in the Polish exploratory platform of the FunDivEUROPE project (Baeten et al., 2013), which is composed of both conifers and broadleaves. We assessed diversity effects based on true Shannon diversity (Jost, 2006) and net diversity effects (NDE) which were calculated from the basal area proportions of individual species.

2.0 Materials and methods

2.1 Experimental design

The Polish exploratory platform of the FunDivEUROPE project included a total of 43 plots selected in mature stands (80-180 years old) of the Białowieża Forest consisting of pure coniferous, pure broadleaved, mixed coniferous, mixed broadleaves and mixed broadleaved-coniferous forests. The 43 plots were selected based on a range of criteria with a general idea to include plots that primarily differ in (stochastic or management driven) tree species diversity with special attention to community evenness while keeping the variation in confounding factors (topography, soil, disturbances) at a minimum. For more information, please see Baeten et al. (2013). The stands have comparable site conditions in terms of forest management, soil texture, topography and previous land use being forest land for a long period of time (Faliński, 1986; Baeten et al., 2013). The site is located at ca. 52.7ºN latitude and ca. 23.9ºE longitude with a mean annual temperature of 6.9ºC and a mean annual precipitation of 627mm. It has a flat terrain and an altitude of 135 to 185m above sea level. The selected 43 plots were located within an area of 30 km x 20 km and were located on well-drained Cambisols (21 plots) and Luvisols (22 plots). The tree species pool consisted of five species with 6,11,13,11 and 2 plots for the richness levels 1, 2, 3, 4, and 5, respectively. Tree species include conifers and broadleaves, namely *Pinus sylvestris* L., *Picea abies* (L.) Karst., *Betula pendula* Roth, *Carpinus betulus* L. and *Quercus robur* L.

Before World War I the forest was managed as hunting ground with minimal intervention. Therefore, we assume that all habitats of mixed deciduous forests of the (Tilio-Carpinetum type) were originally covered by stands consisting of tree species typical for such habitats. The original stands covering our research plots were clearcut probably in 1940s and then artificially regenerated by planting of desirable tree species (*P. sylvestris*, *P. abies* and *Q. robur*) whereas *B. pendula and C. betulus* probably established by natural regeneration. No documents from that period exist. The first management plans in the archives are from 1950s but in the case of thinning they include only information on localization of activities and not on their intensity. During the second half of 20th century the stands were managed by regular thinning and harvesting operations, however detailed information on its intensity is not available. There are no good records of this back in time due to loss of some documents and the fact that stand delimitation could have changed several times. There was never any schematic approach to thinning, and in the past it was mainly based on individual skills of the local forest worker and varied in space depending on local neighbor context and tree density.

All five focal tree species were represented by mature trees in each of the plots that were mainly even-aged, but as natural regeneration was frequent, the plots have trees of several age classes and sizes. Each plot consisted of a core plot of 30 m x 30 m which was divided into 9 subplots of 10 m x 10 m area. Soil sampling took place within each of these subplots. The core plot was surrounded by a 20-m-wide buffer zone.

2.2 Forest floor and mineral soil sampling

We sampled forest floors using a 25 cm by 25 cm wooden frame and mineral soil with a soil corer (diameter 3.6 cm). Nine forest floor samples and nine soil cores, one from each of the nine subplots per core plot, were taken. We weighed each of the 9 forest floor samples, and subsampled ca. 10% after pooling, and shipped one composite sample per plot to the laboratory. We cut each of the 9 soil cores per plot into fixed depths (i.e. 0-10 cm, 10-20 cm, 20-30 cm, and 30-40 cm) and pooled them into one composite sample by fixed depth per plot.

2.3 Laboratory analysis

The forest floor (FF) and the mineral soil samples were dried at 55°C to constant weight. After separating stones and mistakenly collected live moss fragments, we ground the forest floor samples first with a Heavy-Duty Model SM 2000 (Retsch, Germany) cutting mill. Subsamples were taken from this fine fraction and further ground into finer particles with a Planetary Ball Mill PM 400 (Retsch, Germany) for six minutes at 280 rpm. After oven-drying, mineral soil samples were sieved with a 2mm diameter sieve in order to separate the coarse materials from the fine soils. The coarse material was then separated into stones and roots and weighed separately. Subsamples of the fine soil materials were also ground with Planetary Ball Mill PM 400 for six minutes at 280 rpm into finer particles. Another batch of subsamples from both the forest floor and the fine mineral soil were oven-dried again to 105°C to determine moisture contents of the samples. We determined soil pH with 0.01M $CaCl_2$ solution at a ratio of 1:10 and 1:2.5 for organic material and mineral soil, respectively, using 827 pH lab (Metrohm AG, Herisau, Switzerland). The pH values of the soil samples were all lower than the threshold above which carbonate removal is recommended (Schumacher, 2002; Skjemstad and Baldock, 2007). The absence of carbonates was further confirmed using a fizz test with 4N HCl drops on subsamples (Schumacher, 2002). Thus, the soil carbon concentrations were considered to represent organic C. We analyzed C and total N with a FLASH 2000 Soil CN Analyzer (Thermo Fisher Scientific, Milan, Italy) based on the dry combustion method (Matejovic, 1993).

2.4 Calculation of response and explanatory variables

We determined the soil bulk density by dividing the oven-dried fine soil mass by the fine soil volume estimated from the difference between volume of the soil corer and volume of stones and roots. Stone volume was estimated from density of particles ($2.65 g/cm^3$) and root volumes were estimated from root densities and dry root mass. Stocks of C were estimated by multiplying soil bulk density, concentrations of C, depth of soil layer and relative volume of stones and roots (Vesterdal et al., 2008). Living fine roots (diameter ≤ 2 mm) were separated from the soil core samples by hand and sorted into tree roots and ground vegetation roots. After separation, the roots were washed with water to remove adhering soil. Subsequently, the roots were dried at 40°C until constant mass and weighed for estimation of root biomass.

We evaluated the effect of tree species diversity on soil properties (C stock, C/N ratio and soil pH) using the Shannon diversity index (Shannon, 1948) and the net diversity effect (NDE). First we used the proportional basal area contributions of individual trees of the respective species and calculated the Shannon diversity index. We converted the calculated Shannon index into effective numbers of species (true Shannon diversity) using the conversion formula by (Jost, 2006). Second we characterized whether diversity effects were additive (NDE = 0), positive non-additive (i.e. synergistic or NDE > 0) or negative non-additive (i.e. antagonistic or NDE < 0) relative to the expected values based on the corresponding monocultures. The net diversity effect is defined as the proportional deviation between the observed values of mixtures and the values expected from the corresponding monocultures based on weighting the contribution of each species by its basal area proportion in the mixture (Wardle et al., 1997; Hector et al., 2002; Scherer-Lorenzen et al., 2007a) i.e. $\frac{Observed\ \ Expected}{Expected}$. The analyses of NDE were performed for each richness level in the mixed stands (2 to 5 species).

2.5 Explanatory variables and statistical analysis

We used the basal area proportion of each tree species and the soil type (indicator of possible variation in soil fertility within the experimental site) as explanatory variable to test species-specific effects on soil C stock, C/N ratio and pH in a linear model using analysis of covariance. Based on this analysis we analyzed the relative impacts of species identity and diversity by including coniferous basal area proportion in all models as covariate to represent species identity. Tree species diversity in terms of true Shannon diversity, and tree species identity in terms of conifer proportion based on basal area was analyzed in a linear model that also included soil type (Cambisols and Luvisols) as explanatory variable. We tested for possible effects induced by the different species composition in the mixtures by using the species composition as grouping variable in a random effect structure of a linear mixed model (Pinheiro and Bates, 2000; Bates, 2010). Inclusion of species composition as grouping variable resulted in a variance component equivalent to zero which indicated the variability between the different species combinations was not adequate to warrant incorporating random effects in the models (Bates, 2010). We then used linear models (multiple regressions) without random effect structure. We checked pairwise interaction effects of the explanatory variables on each response variable and found only significant main effects. We thus excluded interaction terms and tested only for main effects (Crawley, 2012).

To avoid the risk of including highly correlated explanatory variables, we calculated variance inflation factors (VIF) to assess multicollinearity and found VIF less than 5 in all models which indicates no collinearity effects (Chatterjee and Hadi, 2006). We partitioned the R^2 to the proportions of explained variance by each of the explanatory variables using the *calc.relimp* function from the *relaimpo* package (Grömping, 2006). We used the *lmg* metric which partitioned R^2 by averaging over orders (Lindeman et al., 1980; Grömping, 2006).

We investigated the response of the C stock and C/N ratio in the studied soil profile (forest floor plus mineral soil down to 40cm depth, i.e. FF + 0-40cm) as well as C stock, C/N ratio and pH in each soil layer. For an overview of the basic data see Table S1. The dependent variables were log transformed when needed to fit model assumptions.

To characterize whether NDEs for soil properties were equal to zero (NDE=0), we performed a single factor t-test for each richness level in the mixtures (2 to 5 species).

The correlations between fine root biomass and C stock in different soil layers were tested using the cor.test function (Pearson's product moment correlation) from the stats package in base R. Whereas the relationship between fine root biomass of tree species and diversity was tested using linear regression.

All data analysis were carried using the R statistical package version 3.1.0 (R Core Team, 2014). We used *visreg* (Breheny and Burchett, 2013) and *(Grapher^{TM} 11 Golden Software LLC)* to plot and visualize effects and relationships graphically.

3.0 Results

3.1 Overview of soil C, N, C/N ratio and pH

The soil C stock of the examined profile (FF+0-40 cm) within the studied 43 plots in Białowieża (Table S2) averaged 68.4 Mg/ha (range 49.0-111.0 Mg/ha). The soil N stock averaged 3.9 Mg/ha (range 3.3-6.3 Mg/ha). The average C/N ratio of the examined soil profile was 17.3 (range 13.5-23.1). The average forest floor pH was 4.9 (range 3.4-5.5). In the mineral soil, pH increased with depth from 3.8 (range 3.1-4.5) in the topsoil (0-10 cm) layer to 4.5 (range 4.2-5.3) in the deepest layer (30-40 cm). The Cambisols tended to have higher C stocks (P=0.053) and had higher C/N ratios (P=0.002) than the Luvisols in the studied soil profile. There was no significant effect of soil type on pH.

3.1.1 Tree species-specific influences on soil properties

Species-specific influences on soil C stock, C/N ratio and pH were observed mainly in the top soil layers (Table 1). Forest floor C stock significantly increased with the share (basal area proportion) of *Picea abies* and marginally significantly with that of *Pinus sylvestris.* Forest floor C stocks significantly decreased with the share of *Carpinus betulus* and did not show any relationship with that of *Betula pendula* or *Quercus robur*. In the mineral soil layers there were no significant relationships between C stock and the share of any tree species other than the significantly decreasing C stock in the 30-40cm layer with the share of *C. betulus*. Forest floor C/N ratio significantly decreased with increasing share of *Q. robur*, increased with that of *P. sylvestris* and had no relationship with shares of the other species. In the 0-10cm layer, an increased share of the broadleaves *B. pendula* and *C. betulus* marginally significantly reduced the C/N ratio. In the deeper layers, the C/N ratio increased in the 10-20cm layer with increasing share of *Picea abies* and decreased in the 30-40 cm layers with increasing share of *C. betulus and P. sylvestris*. Soil pH was significantly related to the share of certain tree species only in the forest floor and 0-10 cm layer. Three relationships were identified:

increasing proportions of *B. pendula* and *C. betulus* were associated with increasing pH; dominance of the conifers was associated with a decrease in pH, whereas the relative share of *Q. robur* was unrelated to pH.

3.2 Tree species diversity versus species identity effects on soil properties

3.2.1 Soil C stock

The total C stock (FF+0-40 cm) was not significantly related to true Shannon diversity, and diversity accounted for only 3% of the variability. The total C stock was closer, but not quite significantly (P=0.076), related to conifer proportion that explained 11% of the variance (Fig.1, Table S3). True Shannon diversity and conifer proportion had vertically stratified associations with soil C stocks within the sampled profile (Figs. 2A and D). The C stock in the 20-30cm layer was almost significantly positively related to true Shannon diversity (P=0.057), and C stocks in the 30-40cm layer were significantly positively related to diversity (Table 2, Fig. 2A). This vertically stratified influence of true Shannon diversity was further supported by a significantly positive net diversity effect (NDE<0) in the 30-40 cm layer in three-, four- and five-species mixtures indicating synergistic diversity effects (Fig. 3A). The forest floor C stock in 2-5 species mixtures was generally lower than that expected from the corresponding monocultures (i.e. NDE < 0 or antagonistic effects, Fig. 3A). However, NDE was only significant for the three-species mixtures (P=0.015) and there was no indication of a consistent influence of true Shannon diversity on forest floor C (P=0.802, Table 2, Fig. 2A).

In contrast, species identity strongly influenced the topsoil C stocks. As much as 42% of the variability in forest floor C stocks was explained by the positive relationship with the proportion of conifers in the stands (Table 2, Fig. 2D). Species identity had no significant effect on the mineral soil C stock in the sampled layers but there was a trend of increasing C stocks with the proportion of conifers in the 0-10 cm layer.

The fine root biomass of trees in the 30-40 cm layer was positively but not quite significantly (P=0.08) related to the true Shannon diversity (Fig. 5A) and fine root biomass was also positively and significantly associated with the soil C stock of the 30-40 cm layer (Fig. 5B). There were no relationships between fine root biomass and tree species diversity in other soil layers (data not shown).

3.2.2 Soil C/N ratio

The C/N ratio calculated from the total C and N stocks (FF+ 0-40 cm) was positively related to true Shannon diversity but the relationship was not quite significant and explained only 5% of the variance (Fig. 4, Table S4). Conifer proportion was significantly positively related to the C/N ratio and explained 17% of the variability.

The C/N ratio in the two deepest layers was significantly positively related to diversity (Table 2, Fig. 2B). The vertically stratified relationship with true Shannon diversity was consistent with the presence of net diversity effects on C/N ratio except for a synergistic effect on forest floor C/N ratio in four-species mixtures (P=0.049, Fig. 3B). The most consistently positive net diversity effects were observed in three-, four- and five-species mixtures in the 30-40 cm (i.e. NDE>0, P=0.019, 0.001 and 0.037, respectively, Fig. 3B) along with a positive NDE in the 20-30 cm layer of two-species mixtures (P=0.011).

Tree species identity (in terms of conifer proportion) was associated with increasing C/N ratio in the forest floor (Table 2, Fig. 2E). There was no significant relationship with C/N ratio in the mineral soil layers, but C/N ratios tended to be higher in stands with a high proportion of conifers.

3.2.3 Soil pH

Forest floor pH was significantly positively related to true Shannon diversity, but mineral soil pH was unrelated to diversity (Table 2, Fig. 2C). The diversity effect on forest floor pH (Fig. 3C) was synergistic in three- and four-species mixtures (NDE >0, P=0.018 and P=0.038, respectively), and the same species richness levels had NDE>0 in the 0-10 cm layer (P=0.002 and P=0.052, respectively) although there was no general relationship between pH and true Shannon diversity in this layer (P=0.167, Table 2).

Species identity was a more important explanatory factor than species diversity for pH in the topsoil. Conifer proportion was significantly negatively related to pH in the forest floor and 0-10 cm layer and explained as much as 40-47% of the variability (Table 2, Fig. 2F).

4.0 Discussion

4.1 Soil organic carbon stocks

Our results indicated that tree species diversity and identity influenced soil C stocks, but their impacts differed and were vertically separated within the soil profile. Neither of the two potential drivers had a strong influence on total C stocks in the sampled soil profile, but tree species identity explained slightly more of the variability than diversity (Fig. 1). Our hypotheses that soil carbon stocks would be higher under diverse forests and under conifer-dominated forests were thus only partly supported. In fact, species diversity and identity appeared to have a greater influence on distribution of C within the soil profile. High tree species diversity was associated with higher C stock in the deeper soil layers (20-30 cm and 30-40 cm) while tree species identity (measured as proportion of conifers) more strongly influenced C stock in the forest floors. The higher C stock in deeper layers with increasing diversity supports the hypothesis that soil C stock would be higher under diverse forests. This deeper layer C accumulation could be related to belowground niche complementarity (Loreau and Hector, 2001), i.e. stratification of roots of different tree species to top- and subsoil in diverse stands (Brassard et al., 2013; Laclau et al., 2013). For example, compared with pure stands, Norway spruce was reported to root more shallowly when mixed with beech (*Fagus sylvatica* L.) and beech rooted more deeply in mixtures with spruce (Rothe and Binkley, 2001). More intensive exploitation of the soil profile by root development in deeper soil layers under mixed stands would lead to higher root litter inputs into those layers. Greater inputs of root litter and exudates would cause higher accumulation of soil carbon stocks (Bardgett et al., 2005; Brassard et al., 2013). Root biomass indeed increased with tree species diversity in the 30-40 cm layer in which soil C stocks were most closely related to tree species diversity (Fig. 5A). Moreover, C stock in the 30-40 cm layer was significantly and positively related to fine root biomass of trees (Fig. 5B), indicating that higher fine-root turnover probably contributes to a higher soil C stock in tree-species-diverse stands. Schleuß et al. (2014) also found increasing C stocks along a diversity gradient from 1 to 5 broadleaf species in Germany and attributed this to increased fine root biomass and turnover which is an important source for mineral soil C (Rumpel and Kögel-Knabner, 2011). The tree species included in our study were reported to have vertically stratified root distributions, and this stratification could be enhanced in mixed stands (Rothe and Binkley, 2001). *Picea abies* is shallow-rooted with its roots mostly concentrated in the top (0–11 cm) soil (Göransson et al., 2006) or with approximately 80% of its fine roots found in the top 20-25 cm (Rosengren et al., 2006). On the other hand, *Quercus robur* is deep-rooted and has 80% of its roots down to 60 cm soil depth (Rosengren et al., 2006). The rooting depth of *P. sylvestris* was reported to be intermediate between *P. abies* and *Q. robur* with 80% of its roots within the top 25-30 cm (Rosengren et al., 2006).

Factors other than root dynamics could also be responsible for deeper distribution of soil C. Macro-fauna species such as earthworms are important engineers for deeper storage of C (Frouz et al., 2013) and could be stimulated by litter diversity (Hättenschwiler and Gasser, 2005). However, Schwarz et al. (2015) found no effect of diversity but only a strong effect of species identity on earthworm communities in ca. 10-year-old experimental plots of *P. sylvestris*, *P. abies*, *Q. robur* and *Larix decidua*. In grassland ecosystems, increasing soil C stocks with increasing plant species richness was driven by higher root litter inputs into the microbial community rather than by reduced rates of C mineralization (Lange et al., 2015). Further studies are needed in forest ecosystems to unravel whether sequestration of C in stable forms in mineral soil occur mainly through greater root litter input or by stimulation of macro-faunal activity (Vesterdal et al., 2013).

We found no consistent trend between tree species diversity and forest-floor C stock (Table 2, Fig. 2A), and forest-floor C stocks were only significantly lower than expected from the respective monocultures in three-species mixtures (Fig. 3A). This provides limited support of an antagonistic effect on C stocks in topsoil of more diverse forests. We attribute such a negative non-additive effect to faster forest floor decomposition rather than reduced litter production. Aboveground productivity as well as basal area in the studied plots were unaffected by diversity (Jucker et al., 2014; Jucker et al., 2015), so we expect litterfall would have been unchanged along the diversity gradient. Similar or even higher litter production was also reported in diverse compared to pure stands (Scherer-Lorenzen et al., 2007a). Higher forest floor decomposition rates can be a result of higher variety of litter substrates to decomposers and thereby higher activities of soil organisms in diverse forests (Bardgett et al., 2005; Wardle et al., 2006), but it remains to be further documented whether higher decomposition rates in litter mixtures (Ball et al., 2014) is the main cause of a non-additive effect on forest floor C in diverse stands. Our results suggested that tree species diversity positively influenced soil C stocks through increased subsoil C stocks rather than negatively via reduced forest floor C stocks.

The slightly stronger effect of tree species identity than tree species diversity on soil C stock supported our hypothesis regarding their strength as drivers of C stock, but the vertical separation between diversity and identity effects was most notable. Conifer proportion was used as a proxy for species identity based on the clear separation between the two functional groups in the direction of linear relationships (Table 1). As hypothesized, an increasing conifer proportion increased forest floor C stock in agreement with expectations from previous studies of single-species forests (Vesterdal and Raulund-Rasmussen, 1998; Vesterdal et al., 2008; Augusto et al., 2015). The higher forest floor C stock under conifer-dominated forests could be attributed to slower decomposition rates since litterfall rates in coniferous and deciduous tree species are relatively similar within this region (Reich et al., 2005; Vesterdal et al., 2008; Hansen et al., 2009). There was a marked gradient in species-specific identity effects on forest floor C stock that spanned from a positive effect of basal area proportion of the conifers *P. abies* and *P. sylvestris* over no relationship with the share of the broadleaves *Q. robur* and *B. pendula* to a negative influence on C stock of increasing share of *C. betulus* basal area. These relationships are consistent with reports from many studies that *P. abies* and *P. sylvestris* had lower rates of decomposition than *B. pendula* which led to higher forest floor C stocks (Saetre et al., 1999; Hansson et al., 2013; Vesterdal et al., 2013). In contrast, the foliar litter of *C. betulus* has a high nutrient content and low lignin to N ratio which makes it decompose faster in the forest floor or it is quickly incorporated into the mineral soil by earthworms (Kooijman, 2010), thereby facilitating deeper distribution of SOC. *Quercus robur* proportion was not related to forest floor C stock which corresponds to its intermediate status in terms of litter quality decomposition rates and earthworm abundance among the studied species (Reich et al., 2005; Vesterdal et al., 2008; Vesterdal et al., 2012).

4.2 Soil C/N ratio

The increasing C/N ratio with true Shannon diversity in deeper layers as well as the synergistic effect on C/N ratio in forest floor and 20-40 cm (NDE>0) was contrary to our hypothesis that higher species diversity would lead to lower C/N ratio, i.e. higher N status. As N stocks were unaffected by diversity, the change in C/N ratio was driven by increased C stocks, i.e. a “dilution” of N in organic matter. This higher C/N ratio could be caused by higher retranslocation of N by the above- and below-ground biomass before litterfall as a result of competition for N as reported from other studies of mixtures and monocultures (Vogt et al., 1989; Oelmann et al., 2010; Vergutz et al., 2012). The higher C/N ratios in 20-40 cm layers under diverse stands could be attributed to ectomycorrhiza mining the N in soil organic matter to a greater extent in mixed stands as a result of increased competition (Lang and Polle, 2011; Phillips et al., 2013). However, it remains a question whether the exact mechanism behind the stable soil N stocks and increased C stocks should be sought above- or belowground.

The positive effect of conifer proportion on forest floor C/N ratio supported our hypothesis with regard to species identity impacts. The main contribution of species identity is likely associated with higher foliar C/N ratio in conifers than in broadleaves (Yang and Luo, 2011), and species identity effects on soil C/N ratio is often controlled by tree species-specific identities through variation in foliar litter C/N ratio (Vesterdal et al. 2008). The tree species specific identity effect on soil C/N ratio was detectable from the lower forest floor C/N ratio with increasing basal area proportion of *Q. robur* as opposed to the higher C/N ratio with that of *P. sylvestris.* These results at local level are even consistent with effects of oak and pine on topsoil C/N ratio at European level (Cools et al., 2014).

4.3 Soil pH

The positive influence of tree species diversity on forest floor pH and the decrease in topsoil pH with increase in conifer proportion supported our hypotheses that pH would increase with diversity and decrease with conifer dominance. However, tree species diversity was inferior to species identity in explaining the variability in topsoil pH. Contrary to the effects observed on C stock and C/N ratio, the effects on pH of diversity and species identity were not vertically stratified but were confined to the forest floor and the 0-10cm layer. The positive synergistic effects of diversity on forest floor pH (Table 2, Fig.2C and Fig.3C) suggested higher base cation saturation in mixtures than that expected from the corresponding monocultures. This could be attributed to higher concentration or strength of the organic acids in pure stands or stands in the low end of the diversity gradient. Alternatively, the higher fine-root biomass in deeper layers of more diverse stands (Fig. 5A) could sustain a “base pump effect” (Guckland et al., 2009), i.e. a higher capacity to exploit nutrients in deeper layers thereby increasing the circulation of base cations and the pH of topsoil in more diverse stands. The influence of species diversity on topsoil pH was indeed weaker than that of identity but the mechanisms behind diversity effects deserves to be fully disentangled.

The significantly decreasing topsoil pH with conifer-dominance is linked to common traits of conifers litter recalcitrance, decomposition rate and associated activities of the soil biota (Augusto et al., 2015). As recorded in many studies (de Schrijver et al., 2012; Mueller et al., 2012), conifers have lower forest floor and top mineral soil pH compared to broadleaves. The slow decomposition of forest floor materials under coniferous forests would delay the time for recycling of buffering cations, and increase organic acid production (Miles, 1986 ; Kuiters, 1990; de Schrijver et al., 2012). We observed significant effects of the admixture of individual tree species on pH. The tree species displayed a distinct signature where some showed positive effects (C. *betulus* and *B. pendula*) or negative effects (*P. abies* and *P. sylvestris*) on pH in the forest floor and 0-10 cm layers whereas *Q. robur* admixture was unrelated to pH throughout the soil layers. These trends were in line with reports of other studies from pure species stands (de Schrijver et al., 2012; Mueller et al., 2012). *Betula pendula* stands had higher base saturation and concentration of calcium and magnesium in forest floors than *P. abies* forests in Finland (Lindroos et al., 2011) which indicates birch forests have better buffering capacity and higher soil pH which provides a more suitable environment for a wider range of soil fauna and microorganisms, thereby promoting forest floor decomposition (Saetre et al., 1999). Furthermore, litterfall fluxes of base cations under *B. pendula*, *Q. robur* and *P. sylvestris* differed significantly with highest inputs under *B. pendula* (Van Nevel et al., 2013). Based on a common garden experiment in Poland, it was reported that forest floor pH decreased in the order *B. pendula* > *Q. robur* > C. *betulus* > *P. abies* > *P. sylvestris* (Reich et al., 2005). This is quite consistent with our results on influence of species proportions in mixed stands with the exception of *Q. robur* admixtures.

4.4 Tree species diversity effects on soil C distribution and nutrient status

The exploratory platform design in mature forests enabled us to detect diversity impacts on soils with minimum risk of confounding effects of climate, management, stand age and species dilution (Nadrowski et al., 2010; Baeten et al., 2013). As we worked on an exploratory platform and not in a specifically designed common garden experiment, we cannot completely eliminate factors other than species diversity and identity, such as variable management over time and between plots that could have had some small influence. However, the careful, well-documented selection procedure of the exploratory platform (Baeten et al., 2013) supports that potential influences of other factors on our results would be of negligible and more random nature across the studied forest area.

Our study suggested that conversion of species-poor to more species-diverse forests leads to a small increase in the pool of soil C. While the magnitude of this effect was smaller than that of species identity, the influence on soil C stocks in deeper layers suggest that we may influence more stable soil C pools through diversity than through species identity. Increasing coniferous admixture led to more C in topsoil, but C stored mainly in the forest floor is also more vulnerable to changes in management or climate (Jandl et al., 2007; Cotrufo et al., 2013). In contrast, the C stored in deeper layers via root-mediated processes could be protected by more close association with mineral soil particles in aggregates (Jastrow et al., 1998; Cotrufo et al., 2013). In addition to aggregate formation, further protection would be provided by the moderated environment in subsoils compared to topsoil (Rumpel and Kögel-Knabner, 2011). Higher subsoil C stocks would also have a positive feedback on productivity through increased water holding capacity and higher CEC in case of the sandy soils of our study site.

Our hypothesis of a higher soil nutrient status in species diverse stands was only partly supported. The higher pH in combination with higher organic matter stocks (i.e., also higher CEC) would indicate a higher availability of base cations in more diverse stands (Van Nevel et al., 2011). This supports evidence from studies of beech dilution gradients (Guckland et al., 2009) that tree species diversity *per se* has a positive influence on soil pH and base saturation. However, N stocks did not follow the increase in C stocks, as reflected by higher C/N ratios, suggesting lower availability of N in more diverse stands. More direct studies of N transformation processes in soils and studies of litter N reabsorption would be required to address whether the apparent negative effect of species diversity on soil N availability is driven by more N-poor organic matter inputs or a more efficient uptake of N from soil organic matter, e.g. via belowground niche complementarity of roots and associated mycorrhiza.

5. Conclusion

Tree species diversity was a weaker driver than species identity for soil C stocks, C/N ratio and pH in the entire sampled soil profile. However, there were significant and non-additive effects of diversity as well as species identity on C stock and C/N ratio within distinct parts of the soil profile. More diverse forests had higher C stocks and C/N ratios in the 20-30 cm and 30-40 cm layers whereas species identity (in terms of conifer proportion) increased C stocks and C/N ratios of forest floors. A positive relationship between soil carbon stocks and root biomass in the 30-40 cm layer suggested that belowground niche complementarity could be a driving mechanism for higher root carbon input and in turn a deeper distribution of soil carbon in tree-species-diverse forests. Tree species diversity and identity affected pH only on the topsoil with positive effects of diversity and negative effect of conifer proportion. More diverse forests might lead to higher soil nutrient status as reflected by higher topsoil pH, but on the other hand there was a negative effect on N status as indicated by higher C/N ratios in the deeper layers. It remains to be explored whether the latter effect is driven by more N-poor organic matter inputs in these deeper layers or a more efficient uptake of N from soil organic matter in diverse stands. We conclude that tree species diversity may have increased soil C stocks, C/N ratios and pH, but tree species identity was a stronger driver of the studied soil properties, particularly in the topsoil.

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TABLE 1. Tree species-specific effects on C stock, C/N ratio and pH by soil layers*.

		C stock (Mg/ha)			**C/N ratio**			**pH**		
Depth	**Tree Species**	**Slope****	**R^2**	**P-value**	**Slope**	**R^2**	**P-value**	**Slope**	**R^2**	**P-value**
Forest Floor	Betula pendula	-0.058	0.15	0.130	-0.042	0.02	0.280	**0.014**	**0.32**	**0.005**
	Carpinus betulus	**-0.045**	**0.17**	**0.009**	-0.028	0.03	0.240	**0.005**	**0.11**	**0.044**
	Quercus robur	-0.017	0.04	0.330	**-0.055**	**0.14**	**0.041**	0.001	0.01	0.640
	Picea abies	**0.045**	**0.15**	**0.025**	-0.019	0.03	0.380	**-0.007**	**0.22**	**0.006**
	Pinus sylvestris	0.043	0.17	0.064	**0.049**	**0.18**	**0.021**	**-0.007**	**0.29**	**0.010**
0-10cm	Betula pendula	-0.128	0.08	0.180	-0.045	0.18	0.077	**0.010**	**0.22**	**0.026**
	Carpinus betulus	-0.085	0.07	0.120	-0.027	0.08	0.094	**0.005**	**0.15**	**0.019**
	Quercus robur	0.049	0.02	0.420	0.015	0.02	0.470	0.001	0.01	0.720
	Picea abies	0.017	0.01	0.730	0.017	0.05	0.260	**-0.006**	**0.24**	**0.003**
	Pinus sylvestris	-0.019	0.00	0.800	-0.011	0.01	0.570	-0.005	0.14	0.078
10-20cm	Betula pendula	0.001	0.01	0.990	-0.020	0.04	0.680	0.001	0.01	0.640
	Carpinus betulus	-0.030	0.01	0.560	-0.014	0.02	0.550	0.003	0.08	0.077
	Quercus robur	0.031	0.01	0.480	-0.021	0.02	0.480	-0.001	0.01	0.550
	Picea abies	0.033	0.04	0.300	**0.051**	**0.15**	**0.024**	-0.002	0.08	0.100
	Pinus sylvestris	-0.011	0.00	0.750	-0.022	0.02	0.450	-0.001	0.01	0.560
20-30cm	Betula pendula	-0.005	0.04	0.880	-0.012	0.03	0.790	-0.001	0.00	0.740
	Carpinus betulus	-0.019	0.04	0.360	-0.037	0.07	0.150	0.001	0.01	0.660
	Quercus robur	0.003	0.00	0.890	-0.040	0.06	0.140	0.000	0.00	0.890
	Picea abies	-0.004	0.00	0.820	0.005	0.01	0.850	-0.001	0.01	0.660
	Pinus sylvestris	-0.017	0.01	0.570	-0.028	0.01	0.470	0.000	0.01	0.680
30-40cm	Betula pendula	0.017	0.02	0.400	0.019	0.04	0.630	-0.001	0.00	0.640
	Carpinus betulus	**-0.027**	**0.11**	**0.046**	**-0.041**	**0.10**	**0.040**	0.001	0.01	0.590
	Quercus robur	0.001	0.00	0.940	-0.035	0.06	0.130	0.001	0.02	0.530
	Picea abies	-0.004	0.00	0.740	-0.025	0.01	0.190	-0.001	0.02	0.420
	Pinus sylvestris	-0.021	0.06	0.210	**-0.049**	**0.12**	**0.022**	0.000	0.00	0.780

* Significant effects are highlighted as bold, ** slope indicates the regression coefficients

TABLE 2. Vertically stratified effects of true Shannon diversity and conifer proportion on soil properties *.

Explanatory variables	Depth	C stock (Mg/ha) Slope**	R^2	P-value	C/N ratio Slope	R^2	P-value	pH Slope	R^2	P-value
Conifer proportion	Forest Floor	**0.0087**	**0.42**	**<0.001**	**0.042**	**0.11**	**0.012**	**-0.009**	**0.47**	**<0.001**
	0-10cm	0.0018	0.06	0.128	0.001	0.09	0.124	**-0.007**	**0.41**	**<0.001**
	10-20cm	-0.0001	0.01	0.967	0.001	0.06	0.334	-0.001	0.04	0.235
	20-30cm	0.0000	0.02	0.984	0.001	0.06	0.273	0.000	0.00	0.928
	30-40cm	0.0006	0.02	0.715	0.019	0.09	0.142	0.000	0.02	0.418
True Shannon diversity	Forest Floor	-0.0109	0.00	0.802	0.586	0.03	0.170	**0.078**	**0.05**	**0.045**
	0-10cm	0.0399	0.04	0.212	0.020	0.03	0.265	0.052	0.03	0.167
	10-20cm	-0.0157	0.00	0.691	0.006	0.00	0.824	0.031	0.03	0.259
	20-30cm	**0.0729**	**0.08**	**0.057**	**0.062**	**0.10**	**0.030**	0.019	0.01	0.478
	30-40cm	**0.1322**	**0.18**	**0.003**	**1.467**	**0.21**	**<0.001**	0.002	0.00	0.800

* Significant effects are highlighted as bold, **slope indicates the regression coefficients

Fig.1. Effect of true Shannon diversity and conifer proportion on the pooled C stock (Mg/ha) forest floor down to 40cm depth. The band is 95% confidence interval and the points are partial residuals. Effect of a single explanatory variable was constructed under the condition that the other two variables were held constant at their median values or at the most common categorical variable i.e. conifer proportion at 46.7%, soil types at Luvisols and true Shannon diversity at 3.1.

Fig.2. Effects of True Shannon diversity (A to C) and conifer proportion (D to F) on soil C stock, C/N ratio and pH across the examined soil profile. The plot was constructed by taking values from two true Shannon diversity levels (1.5 and 4.5 represented by the dashed and the solid lines, respectively) and two conifer proportions (10% and 90% represented by the dashed and the solid lines, respectively) which were extracted from model outputs that display effects. Effects of a single explanatory variable was constructed under the condition that the other two variables were held constant at their median values or at the most common categorical variable i.e. conifer proportion at 46.7%, soil types at Luvisols and true Shannon diversity at 3.10. Strongly significant effects are marked with asterisk.

Fig.3. Net diversity effects for C stock (A), soil C/N ratio (B) and pH (C) across the soil layers and tree species richness levels. The error bars are mean ±SEM. Significant NDE for C stock, soil C/N ratio and pH are coded as: '***' 0.001, '**' 0.01, '*' 0.05, '▪' 0.1. NDE bars without the asterisk (*) sign show non-significant effects, i.e. NDE =0.

Fig.4. Effect of true Shannon diversity and conifer proportion on C/N ratio calculated based on the total C and N stocks (Mg/ha) from the forest floor down to 40cm depth. The band is 95% confidence interval and the points are partial residuals. Effects of a single explanatory variable was constructed under the condition that the other two variables were held constant at their median values or at the most common categorical variable i.e. conifer proportion at 46.7%, soil types at Luvisols and true Shannon diversity at 3.1.

Fig. 5. Relationship between true Shannon diversity and fine root biomass of trees in the 30-40 cm layer (A) and relationship between fine root biomass of trees and soil C stock in the 30-40 cm layer (B) with linear fits.

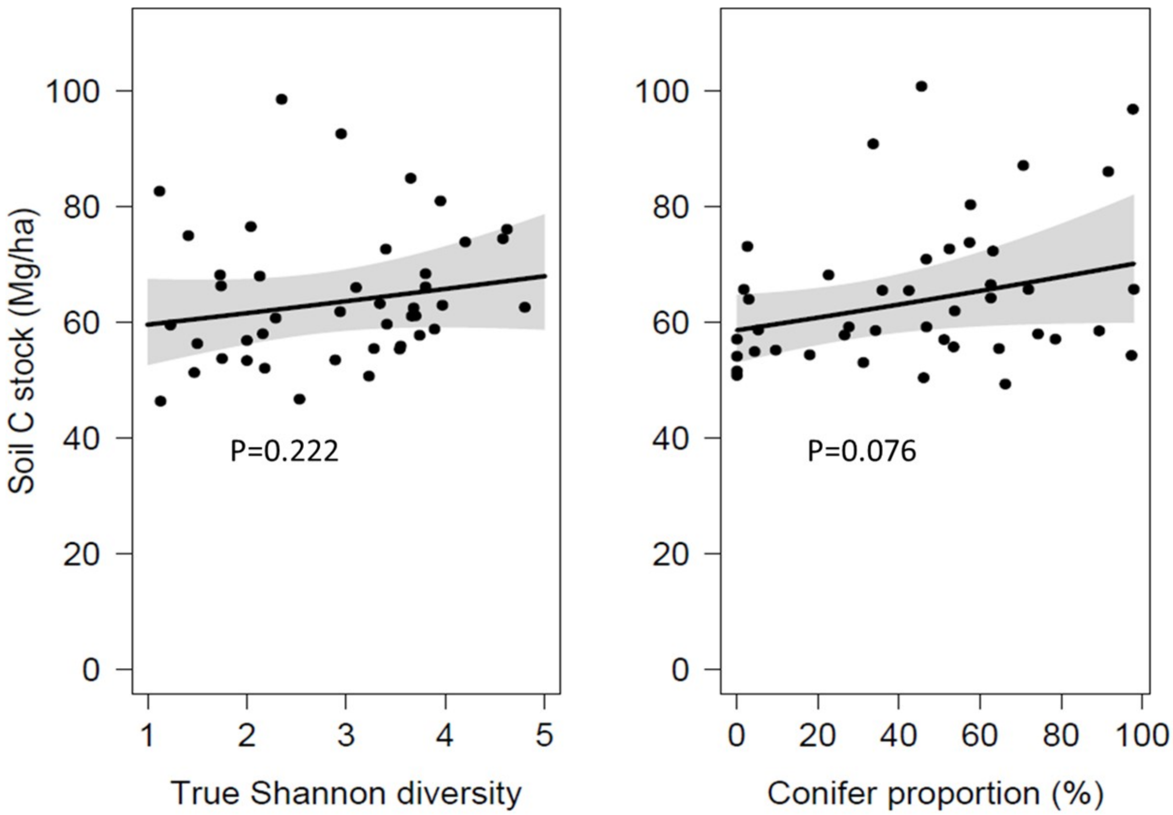
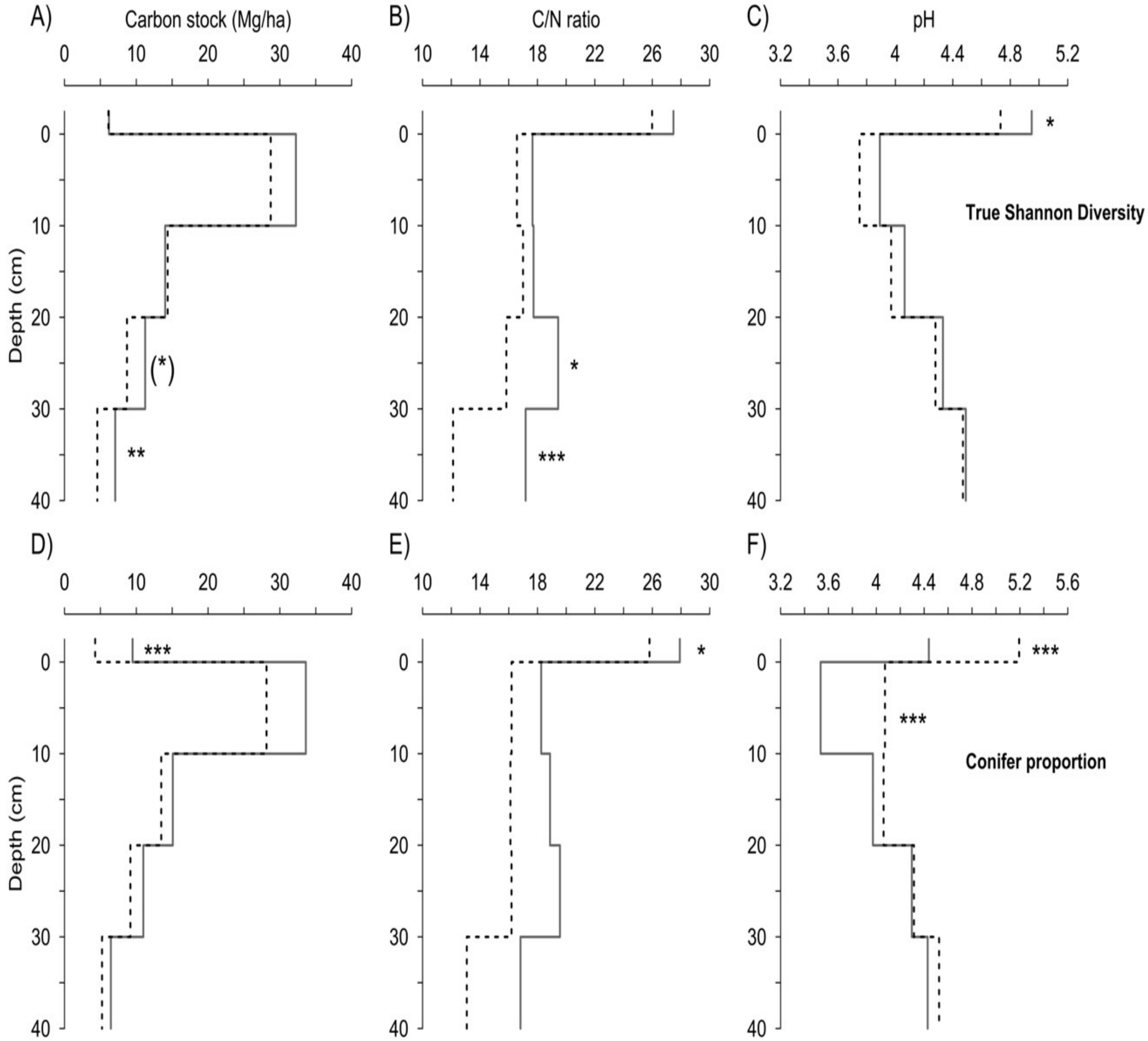
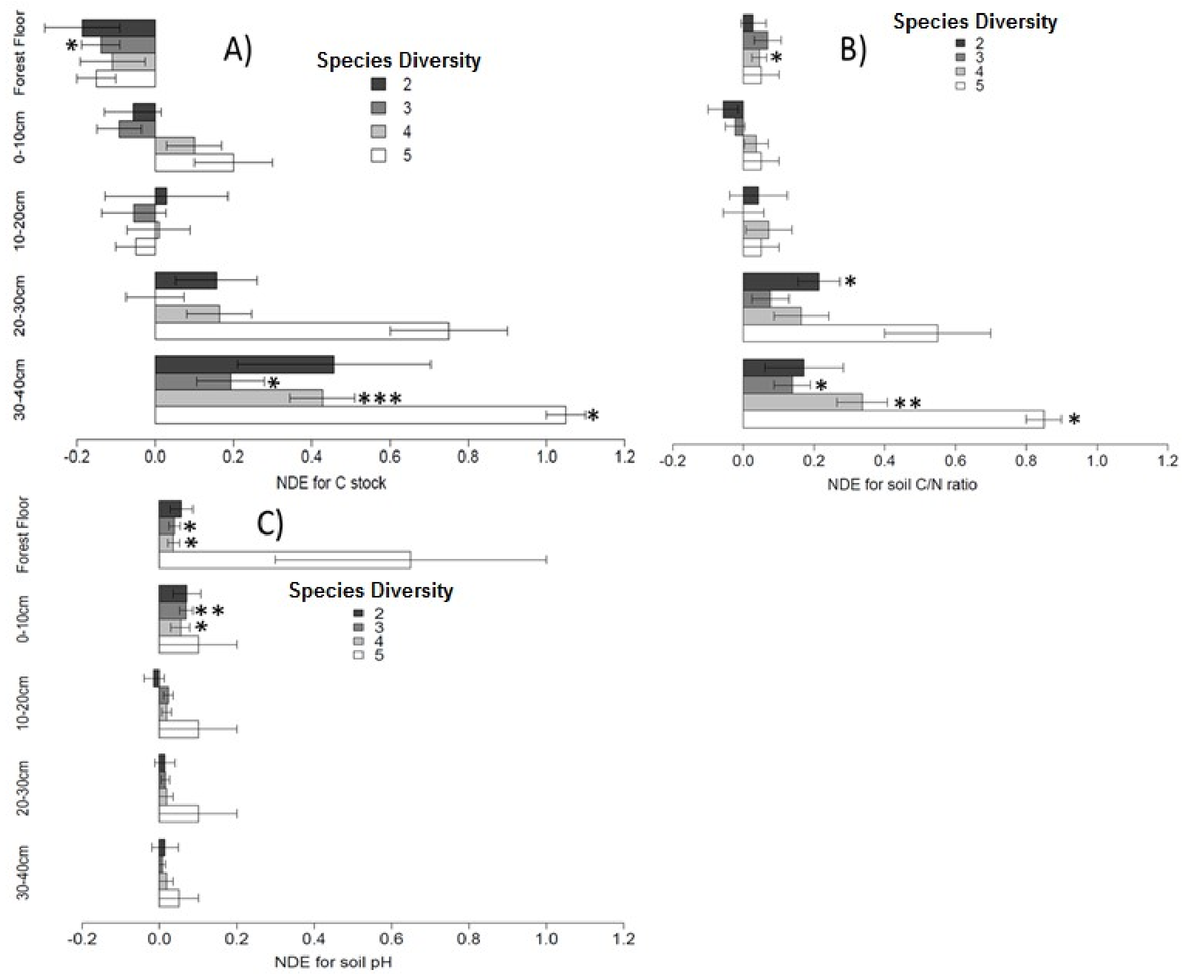

Soil C stock (Mg/ha)
0
20
40
60
80
100
P=0.222
1
2
3
4
5
True Shannon diversity
P=0.076
0
20
40
60
80
100
Conifer proportion (%)

Figure 1



A)
Carbon stock (Mg/ha)
B)
C/N ratio
C)
pH
True Shannon Diversity
D)
E)
F)
Conifer proportion
Depth (cm)
(*)
**
*
***
*
***
*
***
***

Figure 2



A)
B)
C)
Species Diversity
2
3
4
5
Forest Floor
0-10cm
10-20cm
20-30cm
30-40cm
NDE for C stock
NDE for soil C/N ratio
NDE for soil pH
-0.2
0.0
0.2
0.4
0.6
0.8
1.0
1.2

Figure 3

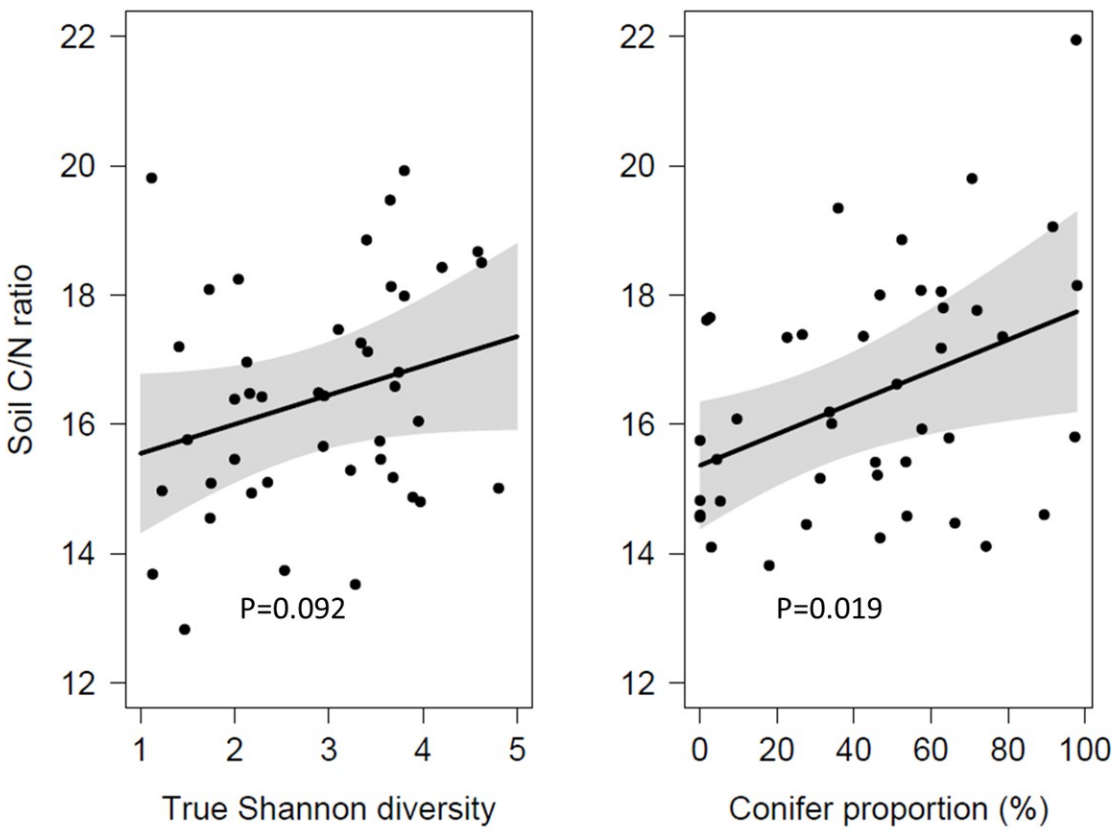

Soil C/N ratio
22
20
18
16
14
12
P=0.092
1
2
3
4
5
True Shannon diversity
P=0.019
0
20
40
60
80
100
Conifer proportion (%)

Figure 4

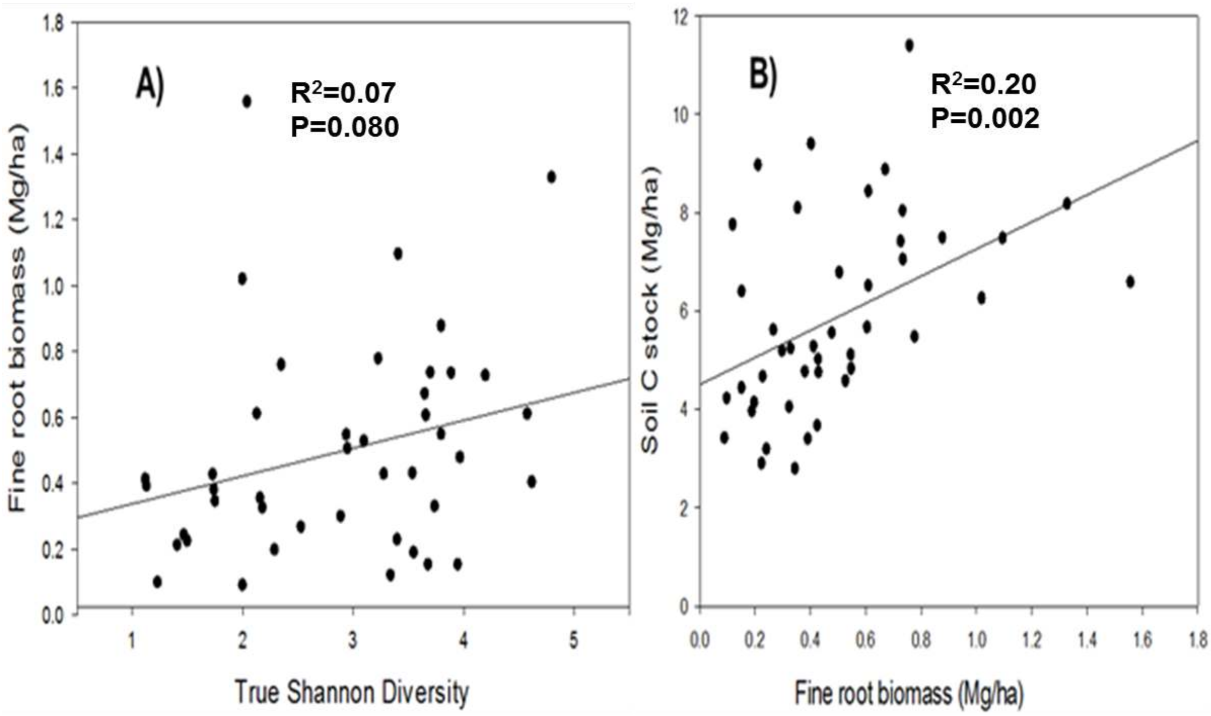

A)
R²=0.07
P=0.080
Fine root biomass (Mg/ha)
True Shannon Diversity
B)
R²=0.20
P=0.002
Soil C stock (Mg/ha)
Fine root biomass (Mg/ha)

Figure 5

8. Supporting information

TABLE S1. Plot characterististics, C stocks, C/N ratio and pH for each of the 43 plots in Białowieża.

Species composition	TShann	CP	C stock$_{FF}$ (Mg ha^{-1})	Total C stock (Mg ha^{-1})	Total C/N ratio	C/N$_{FF}$	pH$_{FF}$	Soil types
Pa	1.1	0.98	18.7	102.4	23	24	3.4	Cambisols
Cb	1.5	0.04	5.5	52.1	15	21	4.9	Luvisols
Pa	1.1	0.97	5.8	57.4	17	23	4.6	Cambisols
Cb	1.2	0.05	3.0	55.2	14	31	5.3	Luvisols
Ps	1.4	0.92	9.0	91.8	20	29	4.5	Cambisols
Ps	1.5	0.89	11.5	62.6	16	28	4.3	Cambisols
Cb,Qr	2	0.00	5.1	58.9	17	24	5.0	Cambisols
Bp,Cb	2	0.00	3.0	49.0	14	24	5.3	Luvisols
Cb,Pa	2.2	0.65	3.1	53.8	15	25	5.0	Luvisols
Cb,Qr	1.7	0.03	6.8	61.2	13	23	5.0	Luvisols
Bp,Cb	1.8	0.00	3.0	49.3	14	25	5.5	Luvisols
Pa,Qr	2.4	0.46	6.6	111.0	17	24	4.5	Cambisols
Pa,Ps	2.2	0.98	11.6	71.9	20	28	4.4	Cambisols
Cb,Qr	1.7	0.02	3.4	62.8	17	24	5.0	Luvisols
Cb,Ps	2.1	0.63	6.9	79.0	19	27	4.9	Cambisols
Bp,Cb	2	0.03	4.0	70.6	17	29	5.1	Luvisols
Bp,Pa	2.3	0.63	7.6	62.5	17	29	5.1	Luvisols
Bp,Pa,Qr	3.7	0.27	5.9	66.4	20	22	5.4	Cambisols
Bp,Cb,Pa	3.1	0.42	4.9	65.5	17	30	5.0	Luvisols
Bp,Cb,Qr	2.9	0.00	3.8	56.8	15	21	5.3	Luvisols
Cb,Pa,Qr	3	0.34	4.4	90.4	16	22	5.0	Luvisols
Cb,Ps,Qr	3.2	0.46	5.6	57.1	17	28	4.6	Cambisols
Pa,Ps,Qr	3.3	0.72	11.2	66.2	18	27	4.3	Luvisols

Cb,Pa,Ps,	2.9	0.79	12.0	64.0	19	28	4.7	Cambisols
Cb,Ps,Qr	3.5	0.31	6.4	60.7	17	29	4.8	Cambisols
Bp,Ps,Qr	3.6	0.53	5.4	56.6	16	30	4.9	Luvisols
Bp,Cb,Ps	3.4	0.52	5.6	73.4	19	34	4.7	Luvisols
Bp,Cb,Qr	3.4	0.10	3.5	55.8	16	27	5.2	Luvisols
Bp,Cb,Ps	2.5	0.66	8.3	54.6	16	29	4.7	Cambisols
Pa,Ps,Qr	3.3	0.74	7.2	58.3	14	32	4.8	Luvisols
Bp,Cb,Pa,Qr	3.8	0.36	7.9	67.1	20	29	4.9	Luvisols
Cb,Pa,Ps,Qr	3.7	0.71	9.2	100.1	22	24	4.2	Cambisols
Bp,Cb,Ps,Pa	4	0.58	7.1	82.6	16	27	4.8	Luvisols
Cb,Pa,Ps,Qr	3.7	0.51	5.6	58.2	17	28	4.8	Luvisols
Bp,Cb,Ps,Pa	3.8	0.63	10.8	76.8	20	25	4.4	Cambisols
Bp,Cb,Pa,Qr	3.7	0.28	3.1	60.4	15	27	4.9	Luvisols
Bp,Pa,Ps,Qr	4.6	0.47	4.2	84.0	21	26	5.0	Cambisols
Bp,Cb,Ps,Qr	3.9	0.18	6.3	63.0	16	27	5.2	Cambisols
Bp,Cb,Ps,Qr	4.2	0.23	6.3	79.8	20	27	5.2	Cambisols
Bp,Pa,Ps,Qr	3.7	0.34	4.7	59.8	16	25	5.3	Luvisols
Bp,Cb,Pa,Ps,	4	0.54	6.0	71.9	17	29	5.0	Cambisols
Bp,Cb,Pa,Ps,Qr	4.8	0.47	6.0	70.6	17	24	5.1	Cambisols
Bp,Cb,Pa,Ps,Qr	4.6	0.57	6.5	87.5	21	26	4.9	Cambisols

*Keys for abbreviated species names: Pa = Picea abies, Cb= Carpinus betulus, Bp=Betula pendula , Qr=Quercus robur, Ps= Pinus sylvestris. CP= Conifer proportion based on basal area proportion of tree species, TShann= true Shannon diversity, FF= Forest floor, Total= FF + 0-40cm mineral soil layers, C $stock_{FF}$ = Forest floor C stock, pH_{FF} = Forest floor pH, C/N_{FF} = Forest floor C/N ratio, Total C stock and Total C/N ratio are the C stock and the C/N ratio for the examined soil profile (FF+0-40cm), respectively.

TABLE S2. Mean ± standard error of the examined soil properties by layer.

		C stock (Mg/ha)		N stock		C/N ratio		pH	
Depth	**N**	**mean**	**se**	**mean**	**se**	**mean**	**se**	**mean**	**se**
Forest Floor	43	6.6	0.47	0.2	0.02	26.6	0.45	4.9	0.06
0-10cm	43	30.9	1.05	1.8	0.05	17.0	0.34	3.8	0.05
10-20cm	43	14.7	0.68	0.9	0.03	17.2	0.53	4.0	0.03
20-30cm	43	10.2	0.46	0.6	0.02	17.4	0.58	4.3	0.03
30-40cm	43	5.9	0.30	0.4	0.01	14.3	0.54	4.5	0.03
FF+0-40cm	43	68.4	2.25	3.9	0.09	17.3	0.35		

TABLE S3. Model outputs for C stock in the forest floor plus 0-40cm (FF+0-40cm) layer*+.

Parameters	Slope	Std. Error	t-value	P-value	Partitioned R^2
(Intercept)	4.09	0.11	37.59	< 0.001	
TShann	0.03	0.03	1.24	0.222	0.03
CP	0.002	0.001	1.82	0.076	0.11
Soil.typeLuvisols	-0.12	0.06	-1.99	0.053	0.13

* See above for abbrevated words
+ lm(log(Cstock) ~ TShann + CP + Soil types, data= depthname) was the linear regression model used.

TABLE S4. Model outputs for C/N ratio calculated from the total C stock and N stock from the forest floor plus 0-40cm (FF +0-40cm) layer ***+.**

Parameters	Slope	Std. Error	t-value	P-value	Partioned R^2
(Intercept)	16.00	1.08	14.87	< 0.001	
TShann	0.45	0.26	1.73	0.092	0.05
CP	0.02	0.01	2.45	0.019	0.17
Soil.typeLuvisols	-2.03	0.60	-3.40	0.002	0.26

* See above for abbrevated words

+ lm(C/N ratio ~ TShann + CP + Soil types, data= depthname) was the linear regression model used.