



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

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*Published in:*  
Ecosystems

*DOI:*  
[10.1007/s10021-016-9958-1](https://doi.org/10.1007/s10021-016-9958-1)

*Publication date:*  
2016

*Document version*  
Peer reviewed version

*Citation for published version (APA):*  
Dawud, S. M., Raulund-Rasmussen, K., Domisch, T., Finér, L., Jaroszewicz, B., & Vesterdal, L. (2016). Is Tree Species Diversity or Species Identity the More Important Driver of Soil Carbon Stocks, C/N Ratio, and pH? *Ecosystems*, 19, 645-660. <https://doi.org/10.1007/s10021-016-9958-1>

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

3

4 **Short title:** Tree species diversity and identity effects on soils

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<sup>1</sup> **Author contributions:** L. Vesterdal, K. Raulund-Rasmussen, L. Finér and B. Jaroszewicz designed the research; S.M. Dawud, T. Domisch, L. Vesterdal and K. Raulund-Rasmussen performed the research; S.M. Dawud analyzed the data; S.M. Dawud and L. Vesterdal wrote the paper with contributions from K. Raulund-Rasmussen, T. Domisch, L. Finér and B. Jaroszewicz.

22 *Abstract.* We explored tree species diversity effects on soil C stock, C/N ratio and pH as compared with  
23 effects of tree species identity. We sampled forest floors and mineral soil 0-40 cm in a diversity gradient of 1  
24 to 5 tree species composed of conifers and broadleaves in Białowieża Forest, Poland.  
25 Diversity was a weaker driver than identity of soil C stocks, C/N ratio and pH in the soil profile. However,  
26 there were significant non-additive effects of diversity and significant effects of identity on C stock and C/N  
27 ratio within different parts of the soil profile. More diverse forests had higher C stocks and C/N ratios in the  
28 20-40 cm layer whereas identity in terms of conifer proportion increased C stocks and C/N ratios only in  
29 forest floors. A positive relationship between C stocks and root biomass in the 30-40 cm layer suggested that  
30 belowground niche complementarity could be a driving mechanism for higher root carbon input and in turn a  
31 deeper distribution of C in diverse forests. Diversity and identity affected soil pH in topsoil with positive and  
32 negative impacts, respectively. More diverse forests would lead to higher soil nutrient status as reflected by  
33 higher topsoil pH, but there was a slight negative effect on N status as indicated by higher C/N ratios in the  
34 deeper layers. We conclude that tree species diversity increases soil C stocks and nutrient status to some  
35 extent, but tree species identity is a stronger driver of the studied soil properties, particularly in the topsoil.

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

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**43 1. Introduction**

44 Tree species are known to affect soils through addition of above-and below-ground litter, absorbing nutrients  
45 and water from different soil layers and by associations with various soil organisms (Prescott and Vesterdal,  
46 2013; Vesterdal et al., 2013). Whereas previous research has focused mainly on effects of the species identity  
47 based on studies within single species forests (Vesterdal et al., 2013) and two-species mixtures (Forrester et  
48 al., 2012; Laclau et al., 2013), the effect of wider gradients in tree species diversity on soils has been little  
49 studied. The current efforts to address functional implications of species diversity have only recently led to  
50 include soils in studies of forest ecosystem functioning as affected by species diversity (Gamfeldt et al.,  
51 2013; Scheibe et al., 2015). It is still not well known whether species diverse forests provide higher soil  
52 carbon stocks and soil nutrient status (Scherer-Lorenzen et al., 2007b; Nadrowski et al., 2010) and whether  
53 these functions increase with diversity or just level off within mixtures of two or three tree species (Schwartz  
54 et al., 2000; Scherer-Lorenzen et al., 2007b). Positive effects of tree species diversity were documented for  
55 productivity and above-ground C stocks (Paquette and Messier, 2011; Jucker et al., 2014). These effects  
56 were attributed to above- and below-ground niche differentiation resulting in increases in availability, uptake  
57 or use efficiency of light, water or nutrients (Forrester et al., 2013; Forrester, 2014). The question remains  
58 whether similar impacts on soil C stocks, C/N ratio and pH exist (Loreau and Hector, 2001; Hector et al.,  
59 2002). The above-ground mechanisms by which diversity influences these soil properties are related to litter  
60 production and litter quality (Scherer-Lorenzen et al., 2007a) while below-ground mechanisms include litter  
61 decomposition, vertical stratification of tree roots (Brassard et al., 2011), root litter inputs (Brassard et al.,  
62 2013), root turnover (Brassard et al., 2011; Lei et al., 2012), root exudates (Bardgett et al., 2005) and  
63 downward transportation of organic matter from topsoil layers to deeper layers by soil macro-fauna  
64 (Brussaard, 1997; Frouz et al., 2013).

65 Recent studies from temperate and boreal forests indicated different effects of diversity on soil C stocks,  
66 C/N ratio and pH in the forest floor and mineral soil layers, respectively. Diverse forests had lower forest  
67 floor C stocks (Guckland et al., 2009) but higher mineral soil C stocks and pH than the monocultures  
68 (Guckland et al., 2009; Gamfeldt et al., 2013; Schleuß et al., 2014). We found no consensus among previous  
69 studies of soil C/N ratios along tree species diversity gradients (Guckland et al., 2009; Schleuß et al., 2014)

70 but Schmidt et al. (2015) reported no effect of tree species diversity on N availability in the soil. However,  
71 there are studies that documented mixtures would increase the foliar N status of the component species  
72 (Rothe and Binkley, 2001) and tree species grown in mixtures extract nutrients and water from deeper soil  
73 layers and release base-cation rich litterfall into the soil (Guckland et al., 2009) but whether this would have  
74 an impact on the soil N status and pH has not yet been examined in mixtures of multiple tree species and  
75 functional groups. Some of the previous studies sampled only a shallow part of the soil profile (Vila et al.,  
76 2004), studying species dilution gradients rather than diversity gradients or including only broadleaved tree  
77 species rather than both broadleaf and conifer species (Guckland et al., 2009). Information is particularly  
78 lacking about the effect of diversity on mineral soil C stock, C/N ratio and pH deeper than 10 cm, and under  
79 conditions where the species mixtures include tree species with a range of functional traits. The studies by  
80 (Guckland et al., 2009; Schleuß et al., 2014) suggested effects on soil C and pH down to 30 cm, but these  
81 studies included only broadleaf mixtures that may have a more narrow range in functional characteristics.  
82 Information from single-species common gardens indicated that conifers and broadleaves have distinct and  
83 different biogeochemical signatures on soil C stock, C/N ratio and pH (Vesterdal et al., 2013; Augusto et al.,  
84 2015), and diversity effects may depend on the proportion of species from either group in mixtures. The  
85 current information might therefore be inadequate to understand the effects on characteristics of forest floors  
86 as well as mineral soil of tree species diverse forests incorporating both functional groups (broadleaves and  
87 conifers tree species).

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

96 2015), but the mutual importance of species identity and diversity remains to be determined for soil  
97 properties such as C stock, C/N ratio and pH.

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

- 101 (i) Tree species identity influences the soil; in topsoil layers, conifers accumulate more carbon, have a  
102 higher C/N ratio and lower soil pH than the broadleaved species.
- 103 (ii) Forests with high tree species diversity accumulate more soil carbon compared to species poor  
104 forests.
- 105 (iii) Increasing tree species diversity decreases C/N ratio and increases soil pH
- 106 (iv) Tree species identity is a more important driver of soil C stock, C/N ratios and pH, compared to  
107 species diversity.

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

112

## 113 **2.0 Materials and methods**

### 114 **2.1 Experimental design**

115 The Polish exploratory platform of the FunDivEUROPE project included a total of 43 plots selected in  
116 mature stands (80-180 years old) of the Białowieża Forest consisting of pure coniferous, pure broadleaved,  
117 mixed coniferous, mixed broadleaves and mixed broadleaved-coniferous forests. The 43 plots were selected  
118 based on a range of criteria with a general idea to include plots that primarily differ in (stochastic or  
119 management driven) tree species diversity with special attention to community evenness while keeping the  
120 variation in confounding factors (topography, soil, disturbances) at a minimum. For more information, please  
121 see Baeten et al. (2013). The stands have comparable site conditions in terms of forest management, soil  
122 texture, topography and previous land use being forest land for a long period of time (Faliński, 1986; Baeten

123 et al., 2013). The site is located at ca. 52.7°N latitude and ca. 23.9°E longitude with a mean annual  
124 temperature of 6.9°C and a mean annual precipitation of 627mm. It has a flat terrain and an altitude of 135 to  
125 185m above sea level. The selected 43 plots were located within an area of 30 km x 20 km and were located  
126 on well-drained Cambisols (21 plots) and Luvisols (22 plots). The tree species pool consisted of five species  
127 with 6,11,13,11 and 2 plots for the richness levels 1, 2, 3, 4, and 5, respectively. Tree species include  
128 conifers and broadleaves, namely *Pinus sylvestris* L., *Picea abies* (L.) Karst., *Betula pendula* Roth, *Carpinus*  
129 *betulus* L. and *Quercus robur* L.

130 Before World War I the forest was managed as hunting ground with minimal intervention. Therefore, we  
131 assume that all habitats of mixed deciduous forests of the (Tilio-Carpinetum type) were originally covered by  
132 stands consisting of tree species typical for such habitats. The original stands covering our research plots  
133 were clearcut probably in 1940s and then artificially regenerated by planting of desirable tree species (*P.*  
134 *sylvestris*, *P. abies* and *Q. robur*) whereas *B. pendula* and *C. betulus* probably established by natural  
135 regeneration. No documents from that period exist. The first management plans in the archives are from  
136 1950s but in the case of thinning they include only information on localization of activities and not on their  
137 intensity. During the second half of 20<sup>th</sup> century the stands were managed by regular thinning and harvesting  
138 operations, however detailed information on its intensity is not available. There are no good records of this  
139 back in time due to loss of some documents and the fact that stand delimitation could have changed several  
140 times. There was never any schematic approach to thinning, and in the past it was mainly based on individual  
141 skills of the local forest worker and varied in space depending on local neighbor context and tree density.  
142 All five focal tree species were represented by mature trees in each of the plots that were mainly even-aged,  
143 but as natural regeneration was frequent, the plots have trees of several age classes and sizes. Each plot  
144 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  
145 sampling took place within each of these subplots. The core plot was surrounded by a 20-m-wide buffer  
146 zone.

147

## 148 **2.2 Forest floor and mineral soil sampling**

149 We sampled forest floors using a 25 cm by 25 cm wooden frame and mineral soil with a soil corer (diameter  
150 3.6 cm). Nine forest floor samples and nine soil cores, one from each of the nine subplots per core plot, were  
151 taken. We weighed each of the 9 forest floor samples, and subsampled ca. 10% after pooling, and shipped  
152 one composite sample per plot to the laboratory. We cut each of the 9 soil cores per plot into fixed depths  
153 (i.e. 0-10 cm, 10-20 cm, 20-30 cm, and 30-40 cm) and pooled them into one composite sample by fixed  
154 depth per plot.

155

### 156 **2.3 Laboratory analysis**

157 The forest floor (FF) and the mineral soil samples were dried at 55°C to constant weight. After separating  
158 stones and mistakenly collected live moss fragments, we ground the forest floor samples first with a Heavy-  
159 Duty Model SM 2000 (Retsch, Germany) cutting mill. Subsamples were taken from this fine fraction and  
160 further ground into finer particles with a Planetary Ball Mill PM 400 (Retsch, Germany) for six minutes at  
161 280 rpm. After oven-drying, mineral soil samples were sieved with a 2mm diameter sieve in order to  
162 separate the coarse materials from the fine soils. The coarse material was then separated into stones and roots  
163 and weighed separately. Subsamples of the fine soil materials were also ground with Planetary Ball Mill PM  
164 400 for six minutes at 280 rpm into finer particles. Another batch of subsamples from both the forest floor  
165 and the fine mineral soil were oven-dried again to 105°C to determine moisture contents of the samples. We  
166 determined soil pH with 0.01M CaCl<sub>2</sub> solution at a ratio of 1:10 and 1:2.5 for organic material and mineral  
167 soil, respectively, using 827 pH lab (Metrohm AG, Herisau, Switzerland). The pH values of the soil samples  
168 were all lower than the threshold above which carbonate removal is recommended (Schumacher, 2002;  
169 Skjemstad and Baldock, 2007). The absence of carbonates was further confirmed using a fizz test with 4N  
170 HCl drops on subsamples (Schumacher, 2002). Thus, the soil carbon concentrations were considered to  
171 represent organic C. We analyzed C and total N with a FLASH 2000 Soil CN Analyzer (Thermo Fisher  
172 Scientific, Milan, Italy) based on the dry combustion method (Matejovic, 1993).

173

### 174 **2.4 Calculation of response and explanatory variables**



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

183 We evaluated the effect of tree species diversity on soil properties (C stock, C/N ratio and soil pH) using the  
 184 Shannon diversity index (Shannon, 1948) and the net diversity effect (NDE). First we used the proportional  
 185 basal area contributions of individual trees of the respective species and calculated the Shannon diversity  
 186 index. We converted the calculated Shannon index into effective numbers of species (true Shannon diversity)  
 187 using the conversion formula by (Jost, 2006). Second we characterized whether diversity effects were  
 188 additive (NDE = 0), positive non-additive (i.e. synergistic or NDE > 0) or negative non-additive (i.e.  
 189 antagonistic or NDE < 0) relative to the expected values based on the corresponding monocultures. The net  
 190 diversity effect is defined as the proportional deviation between the observed values of mixtures and the  
 191 values expected from the corresponding monocultures based on weighting the contribution of each species  
 192 by its basal area proportion in the mixture (Wardle et al., 1997; Hector et al., 2002; Scherer-Lorenzen et al.,  
 193 2007a) i.e.  $\frac{\text{Observed} - \text{Expected}}{\text{Expected}}$ . The analyses of NDE were performed for each richness level in the mixed  
 194 stands (2 to 5 species).

195

## 196 **2.5 Explanatory variables and statistical analysis**

197 We used the basal area proportion of each tree species and the soil type (indicator of possible variation in soil  
 198 fertility within the experimental site) as explanatory variable to test species-specific effects on soil C stock,  
 199 C/N ratio and pH in a linear model using analysis of covariance. Based on this analysis we analyzed the  
 200 relative impacts of species identity and diversity by including coniferous basal area proportion in all models

201 as covariate to represent species identity. Tree species diversity in terms of true Shannon diversity, and tree  
202 species identity in terms of conifer proportion based on basal area was analyzed in a linear model that also  
203 included soil type (Cambisols and Luvisols) as explanatory variable. We tested for possible effects induced  
204 by the different species composition in the mixtures by using the species composition as grouping variable in  
205 a random effect structure of a linear mixed model (Pinheiro and Bates, 2000; Bates, 2010). Inclusion of  
206 species composition as grouping variable resulted in a variance component equivalent to zero which  
207 indicated the variability between the different species combinations was not adequate to warrant  
208 incorporating random effects in the models (Bates, 2010). We then used linear models (multiple regressions)  
209 without random effect structure. We checked pairwise interaction effects of the explanatory variables on  
210 each response variable and found only significant main effects. We thus excluded interaction terms and  
211 tested only for main effects (Crawley, 2012).

212 To avoid the risk of including highly correlated explanatory variables, we calculated variance inflation  
213 factors (VIF) to assess multicollinearity and found VIF less than 5 in all models which indicates no  
214 collinearity effects (Chatterjee and Hadi, 2006). We partitioned the  $R^2$  to the proportions of explained  
215 variance by each of the explanatory variables using the *calc.relimp* function from the *relaimpo* package  
216 (Grömping, 2006). We used the *lmg* metric which partitioned  $R^2$  by averaging over orders (Lindeman et al.,  
217 1980; Grömping, 2006).

218 We investigated the response of the C stock and C/N ratio in the studied soil profile (forest floor plus mineral  
219 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  
220 overview of the basic data see Table S1. The dependent variables were log transformed when needed to fit  
221 model assumptions.

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

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

227 All data analysis were carried using the R statistical package version 3.1.0 (R Core Team, 2014). We used  
228 *visreg* (Breheny and Burchett, 2013) and (*Grapher<sup>TM</sup> 11 Golden Software LLC*) to plot and visualize effects  
229 and relationships graphically.

230

### 231 **3.0 Results**

#### 232 **3.1 Overview of soil C, N, C/N ratio and pH**

233 The soil C stock of the examined profile (FF+0-40 cm) within the studied 43 plots in Białowieża (Table S2)  
234 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).  
235 The average C/N ratio of the examined soil profile was 17.3 (range 13.5-23.1). The average forest floor pH  
236 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  
237 (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  
238 C stocks (P=0.053) and had higher C/N ratios (P=0.002) than the Luvisols in the studied soil profile. There  
239 was no significant effect of soil type on pH.

240

##### 241 **3.1.1 Tree species-specific influences on soil properties**

242 Species-specific influences on soil C stock, C/N ratio and pH were observed mainly in the top soil layers  
243 (Table 1). Forest floor C stock significantly increased with the share (basal area proportion) of *Picea abies*  
244 and marginally significantly with that of *Pinus sylvestris*. Forest floor C stocks significantly decreased with  
245 the share of *Carpinus betulus* and did not show any relationship with that of *Betula pendula* or *Quercus*  
246 *robur*. In the mineral soil layers there were no significant relationships between C stock and the share of any  
247 tree species other than the significantly decreasing C stock in the 30-40cm layer with the share of *C. betulus*.  
248 Forest floor C/N ratio significantly decreased with increasing share of *Q. robur*, increased with that of *P.*  
249 *sylvestris* and had no relationship with shares of the other species. In the 0-10cm layer, an increased share of  
250 the broadleaves *B. pendula* and *C. betulus* marginally significantly reduced the C/N ratio. In the deeper  
251 layers, the C/N ratio increased in the 10-20cm layer with increasing share of *Picea abies* and decreased in the  
252 30-40 cm layers with increasing share of *C. betulus* and *P. sylvestris*. Soil pH was significantly related to the  
253 share of certain tree species only in the forest floor and 0-10 cm layer. Three relationships were identified:

254 increasing proportions of *B. pendula* and *C. betulus* were associated with increasing pH; dominance of the  
255 conifers was associated with a decrease in pH, whereas the relative share of *Q. robur* was unrelated to pH.  
256

## 257 **3.2 Tree species diversity versus species identity effects on soil properties**

### 258 **3.2.1 Soil C stock**

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

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

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

280

### 281 3.2.2 Soil C/N ratio

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

286 The C/N ratio in the two deepest layers was significantly positively related to diversity (Table 2, Fig. 2B).

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

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

295

### 296 3.2.3 Soil pH

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

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

305

## 306 4.0 Discussion

### 307 4.1 Soil organic carbon stocks

308 Our results indicated that tree species diversity and identity influenced soil C stocks, but their impacts  
309 differed and were vertically separated within the soil profile. Neither of the two potential drivers had a strong  
310 influence on total C stocks in the sampled soil profile, but tree species identity explained slightly more of the  
311 variability than diversity (Fig. 1). Our hypotheses that soil carbon stocks would be higher under diverse  
312 forests and under conifer-dominated forests were thus only partly supported. In fact, species diversity and  
313 identity appeared to have a greater influence on distribution of C within the soil profile. High tree species  
314 diversity was associated with higher C stock in the deeper soil layers (20-30 cm and 30-40 cm) while tree  
315 species identity (measured as proportion of conifers) more strongly influenced C stock in the forest floors.  
316 The higher C stock in deeper layers with increasing diversity supports the hypothesis that soil C stock would  
317 be higher under diverse forests. This deeper layer C accumulation could be related to belowground niche  
318 complementarity (Loreau and Hector, 2001), i.e. stratification of roots of different tree species to top- and  
319 subsoil in diverse stands (Brassard et al., 2013; Laclau et al., 2013). For example, compared with pure  
320 stands, Norway spruce was reported to root more shallowly when mixed with beech (*Fagus sylvatica* L.) and  
321 beech rooted more deeply in mixtures with spruce (Rothe and Binkley, 2001). More intensive exploitation of  
322 the soil profile by root development in deeper soil layers under mixed stands would lead to higher root litter  
323 inputs into those layers. Greater inputs of root litter and exudates would cause higher accumulation of soil  
324 carbon stocks (Bardgett et al., 2005; Brassard et al., 2013). Root biomass indeed increased with tree species  
325 diversity in the 30-40 cm layer in which soil C stocks were most closely related to tree species diversity (Fig.  
326 5A). Moreover, C stock in the 30-40 cm layer was significantly and positively related to fine root biomass of  
327 trees (Fig. 5B), indicating that higher fine-root turnover probably contributes to a higher soil C stock in tree-  
328 species-diverse stands. Schleuß et al. (2014) also found increasing C stocks along a diversity gradient from 1  
329 to 5 broadleaf species in Germany and attributed this to increased fine root biomass and turnover which is an  
330 important source for mineral soil C (Rumpel and Kögel-Knabner, 2011). The tree species included in our  
331 study were reported to have vertically stratified root distributions, and this stratification could be enhanced in  
332 mixed stands (Rothe and Binkley, 2001). *Picea abies* is shallow-rooted with its roots mostly concentrated in  
333 the top (0–11 cm) soil (Göransson et al., 2006) or with approximately 80% of its fine roots found in the top  
334 20-25 cm (Rosengren et al., 2006). On the other hand, *Quercus robur* is deep-rooted and has 80% of its roots

335 down to 60 cm soil depth (Rosengren et al., 2006). The rooting depth of *P. sylvestris* was reported to be  
336 intermediate between *P. abies* and *Q. robur* with 80% of its roots within the top 25-30 cm (Rosengren et al.,  
337 2006).

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

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

360 The slightly stronger effect of tree species identity than tree species diversity on soil C stock supported our  
361 hypothesis regarding their strength as drivers of C stock, but the vertical separation between diversity and

362 identity effects was most notable. Conifer proportion was used as a proxy for species identity based on the  
363 clear separation between the two functional groups in the direction of linear relationships (Table 1). As  
364 hypothesized, an increasing conifer proportion increased forest floor C stock in agreement with expectations  
365 from previous studies of single-species forests (Vesterdal and Raulund-Rasmussen, 1998; Vesterdal et al.,  
366 2008; Augusto et al., 2015). The higher forest floor C stock under conifer-dominated forests could be  
367 attributed to slower decomposition rates since litterfall rates in coniferous and deciduous tree species are  
368 relatively similar within this region (Reich et al., 2005; Vesterdal et al., 2008; Hansen et al., 2009).  
369 There was a marked gradient in species-specific identity effects on forest floor C stock that spanned from a  
370 positive effect of basal area proportion of the conifers *P. abies* and *P. sylvestris* over no relationship with the  
371 share of the broadleaves *Q. robur* and *B. pendula* to a negative influence on C stock of increasing share of *C.*  
372 *betulus* basal area. These relationships are consistent with reports from many studies that *P. abies* and *P.*  
373 *sylvestris* had lower rates of decomposition than *B. pendula* which led to higher forest floor C stocks (Saetre  
374 et al., 1999; Hansson et al., 2013; Vesterdal et al., 2013). In contrast, the foliar litter of *C. betulus* has a high  
375 nutrient content and low lignin to N ratio which makes it decompose faster in the forest floor or it is quickly  
376 incorporated into the mineral soil by earthworms (Kooijman, 2010), thereby facilitating deeper distribution  
377 of SOC. *Quercus robur* proportion was not related to forest floor C stock which corresponds to its  
378 intermediate status in terms of litter quality decomposition rates and earthworm abundance among the  
379 studied species (Reich et al., 2005; Vesterdal et al., 2008; Vesterdal et al., 2012).

380

#### 381 **4.2 Soil C/N ratio**

382 The increasing C/N ratio with true Shannon diversity in deeper layers as well as the synergistic effect on C/N  
383 ratio in forest floor and 20-40 cm (NDE>0) was contrary to our hypothesis that higher species diversity  
384 would lead to lower C/N ratio, i.e. higher N status. As N stocks were unaffected by diversity, the change in  
385 C/N ratio was driven by increased C stocks, i.e. a “dilution” of N in organic matter. This higher C/N ratio  
386 could be caused by higher retranslocation of N by the above- and below-ground biomass before litterfall as a  
387 result of competition for N as reported from other studies of mixtures and monocultures (Vogt et al., 1989;  
388 Oelmann et al., 2010; Vergutz et al., 2012). The higher C/N ratios in 20-40 cm layers under diverse stands



389 could be attributed to ectomycorrhiza mining the N in soil organic matter to a greater extent in mixed stands  
390 as a result of increased competition (Lang and Polle, 2011; Phillips et al., 2013). However, it remains a  
391 question whether the exact mechanism behind the stable soil N stocks and increased C stocks should be  
392 sought above- or belowground.

393 The positive effect of conifer proportion on forest floor C/N ratio supported our hypothesis with regard to  
394 species identity impacts. The main contribution of species identity is likely associated with higher foliar C/N  
395 ratio in conifers than in broadleaves (Yang and Luo, 2011), and species identity effects on soil C/N ratio is  
396 often controlled by tree species-specific identities through variation in foliar litter C/N ratio (Vesterdal et al.  
397 2008). The tree species specific identity effect on soil C/N ratio was detectable from the lower forest floor  
398 C/N ratio with increasing basal area proportion of *Q. robur* as opposed to the higher C/N ratio with that of *P.*  
399 *sylvestris*. These results at local level are even consistent with effects of oak and pine on topsoil C/N ratio at  
400 European level (Cools et al., 2014).

401

### 402 4.3 Soil pH

403 The positive influence of tree species diversity on forest floor pH and the decrease in topsoil pH with  
404 increase in conifer proportion supported our hypotheses that pH would increase with diversity and decrease  
405 with conifer dominance. However, tree species diversity was inferior to species identity in explaining the  
406 variability in topsoil pH. Contrary to the effects observed on C stock and C/N ratio, the effects on pH of  
407 diversity and species identity were not vertically stratified but were confined to the forest floor and the 0-  
408 10cm layer. The positive synergistic effects of diversity on forest floor pH (Table 2, Fig.2C and Fig.3C)  
409 suggested higher base cation saturation in mixtures than that expected from the corresponding monocultures.  
410 This could be attributed to higher concentration or strength of the organic acids in pure stands or stands in  
411 the low end of the diversity gradient. Alternatively, the higher fine-root biomass in deeper layers of more  
412 diverse stands (Fig. 5A) could sustain a “base pump effect” (Guckland et al., 2009), i.e. a higher capacity to  
413 exploit nutrients in deeper layers thereby increasing the circulation of base cations and the pH of topsoil in  
414 more diverse stands. The influence of species diversity on topsoil pH was indeed weaker than that of identity  
415 but the mechanisms behind diversity effects deserves to be fully disentangled.

416 The significantly decreasing topsoil pH with conifer-dominance is linked to common traits of conifers litter  
417 recalcitrance, decomposition rate and associated activities of the soil biota (Augusto et al., 2015). As  
418 recorded in many studies (de Schrijver et al., 2012; Mueller et al., 2012), conifers have lower forest floor and  
419 top mineral soil pH compared to broadleaves. The slow decomposition of forest floor materials under  
420 coniferous forests would delay the time for recycling of buffering cations, and increase organic acid  
421 production (Miles, 1986 ; Kuiters, 1990; de Schrijver et al., 2012). We observed significant effects of the  
422 admixture of individual tree species on pH. The tree species displayed a distinct signature where some  
423 showed positive effects (*C. betulus* and *B. pendula*) or negative effects (*P. abies* and *P. sylvestris*) on pH in  
424 the forest floor and 0-10 cm layers whereas *Q. robur* admixture was unrelated to pH throughout the soil  
425 layers. These trends were in line with reports of other studies from pure species stands (de Schrijver et al.,  
426 2012; Mueller et al., 2012). *Betula pendula* stands had higher base saturation and concentration of calcium  
427 and magnesium in forest floors than *P. abies* forests in Finland (Lindroos et al., 2011) which indicates birch  
428 forests have better buffering capacity and higher soil pH which provides a more suitable environment for a  
429 wider range of soil fauna and microorganisms, thereby promoting forest floor decomposition (Saetre et al.,  
430 1999). Furthermore, litterfall fluxes of base cations under *B. pendula*, *Q. robur* and *P. sylvestris* differed  
431 significantly with highest inputs under *B. pendula* (Van Nevel et al., 2013). Based on a common garden  
432 experiment in Poland, it was reported that forest floor pH decreased in the order *B. pendula* > *Q. robur* > *C.*  
433 *betulus* > *P. abies* > *P. sylvestris* (Reich et al., 2005). This is quite consistent with our results on influence of  
434 species proportions in mixed stands with the exception of *Q. robur* admixtures.

435

#### 436 **4.4 Tree species diversity effects on soil C distribution and nutrient status**

437 The exploratory platform design in mature forests enabled us to detect diversity impacts on soils with  
438 minimum risk of confounding effects of climate, management, stand age and species dilution (Nadrowski et  
439 al., 2010; Baeten et al., 2013). As we worked on an exploratory platform and not in a specifically designed  
440 common garden experiment, we cannot completely eliminate factors other than species diversity and  
441 identity, such as variable management over time and between plots that could have had some small  
442 influence. However, the careful, well-documented selection procedure of the exploratory platform (Baeten et

443 al., 2013) supports that potential influences of other factors on our results would be of negligible and more  
444 random nature across the studied forest area.

445 Our study suggested that conversion of species-poor to more species-diverse forests leads to a small increase  
446 in the pool of soil C. While the magnitude of this effect was smaller than that of species identity, the  
447 influence on soil C stocks in deeper layers suggest that we may influence more stable soil C pools through  
448 diversity than through species identity. Increasing coniferous admixture led to more C in topsoil, but C  
449 stored mainly in the forest floor is also more vulnerable to changes in management or climate (Jandl et al.,  
450 2007; Cotrufo et al., 2013). In contrast, the C stored in deeper layers via root-mediated processes could be  
451 protected by more close association with mineral soil particles in aggregates (Jastrow et al., 1998; Cotrufo et  
452 al., 2013). In addition to aggregate formation, further protection would be provided by the moderated  
453 environment in subsoils compared to topsoil (Rumpel and Kögel-Knabner, 2011). Higher subsoil C stocks  
454 would also have a positive feedback on productivity through increased water holding capacity and higher  
455 CEC in case of the sandy soils of our study site.

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

466

## 467 **5. Conclusion**

468 Tree species diversity was a weaker driver than species identity for soil C stocks, C/N ratio and pH in the  
469 entire sampled soil profile. However, there were significant and non-additive effects of diversity as well as

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

483

## 484 **6. Acknowledgements**

485 The FunDivEUROPE project received funding from the European Union's Seventh Framework Program for  
486 research, technological development and demonstration under grant agreement No [265171]. We thank  
487 Dawid Zielinski, Izabela Sondej and Jakub Zaremba for establishing the study plots and for logistical help  
488 during field data collection. We also thank the two anonymous reviewers for the comments and constructive  
489 feedbacks.

490 Conflict of Interest: The authors declared that they have no conflict of interest.

491

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

Depth	Tree Species	C stock (Mg/ha)			C/N ratio			pH		
		Slope*	R <sup>2</sup>	P-value	Slope	R <sup>2</sup>	P-value	Slope	R <sup>2</sup>	P-value
Forest Floor	Betula pendula	-0.058	0.15	0.130	-0.042	0.02	0.280	<b>0.014</b>	<b>0.32</b>	<b>0.005</b>
	Carpinus betulus	<b>-0.045</b>	<b>0.17</b>	<b>0.009</b>	-0.028	0.03	0.240	<b>0.005</b>	<b>0.11</b>	<b>0.044</b>
	Quercus robur	-0.017	0.04	0.330	<b>-0.055</b>	<b>0.14</b>	<b>0.041</b>	0.001	0.01	0.640
	Picea abies	<b>0.045</b>	<b>0.15</b>	<b>0.025</b>	-0.019	0.03	0.380	<b>-0.007</b>	<b>0.22</b>	<b>0.006</b>
	Pinus sylvestris	0.043	0.17	0.064	<b>0.049</b>	<b>0.18</b>	<b>0.021</b>	<b>-0.007</b>	<b>0.29</b>	<b>0.010</b>
0-10cm	Betula pendula	-0.128	0.08	0.180	-0.045	0.18	0.077	<b>0.010</b>	<b>0.22</b>	<b>0.026</b>
	Carpinus betulus	-0.085	0.07	0.120	-0.027	0.08	0.094	<b>0.005</b>	<b>0.15</b>	<b>0.019</b>
	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	<b>-0.006</b>	<b>0.24</b>	<b>0.003</b>
	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	<b>0.051</b>	<b>0.15</b>	<b>0.024</b>	-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	<b>-0.027</b>	<b>0.11</b>	<b>0.046</b>	<b>-0.041</b>	<b>0.10</b>	<b>0.040</b>	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	<b>-0.049</b>	<b>0.12</b>	<b>0.022</b>	0.000	0.00	0.780

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

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

Explanatory variables	Depth	C stock (Mg/ha)			C/N ratio			pH		
		Slope**	R <sup>2</sup>	P-value	Slope	R <sup>2</sup>	P-value	Slope	R <sup>2</sup>	P-value
Conifer proportion	Forest Floor	<b>0.0087</b>	<b>0.42</b>	<b>&lt;0.001</b>	<b>0.042</b>	<b>0.11</b>	<b>0.012</b>	<b>-0.009</b>	<b>0.47</b>	<b>&lt;0.001</b>
	0-10cm	0.0018	0.06	0.128	0.001	0.09	0.124	<b>-0.007</b>	<b>0.41</b>	<b>&lt;0.001</b>
	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	<b>0.078</b>	<b>0.05</b>	<b>0.045</b>
	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	<b>0.0729</b>	<b>0.08</b>	<b>0.057</b>	<b>0.062</b>	<b>0.10</b>	<b>0.030</b>	0.019	0.01	0.478
	30-40cm	<b>0.1322</b>	<b>0.18</b>	<b>0.003</b>	<b>1.467</b>	<b>0.21</b>	<b>&lt;0.001</b>	0.002	0.00	0.800

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

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

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

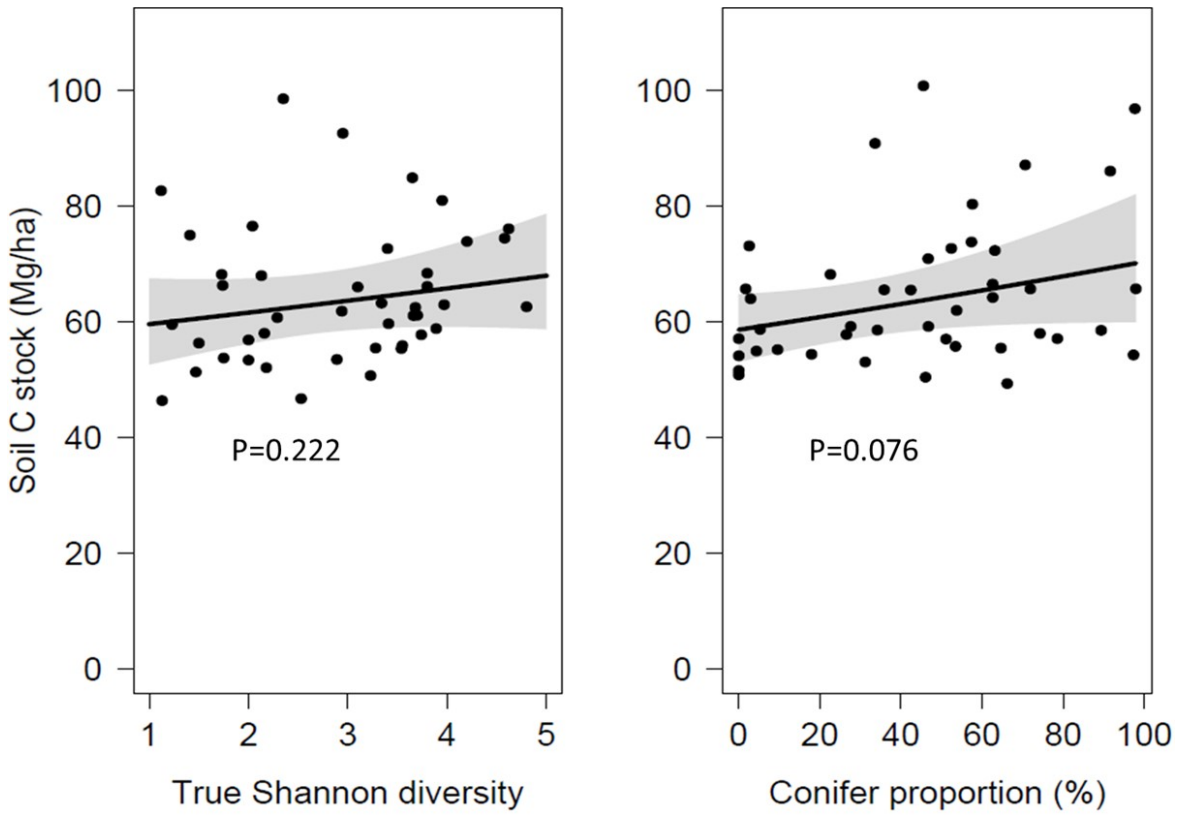
752 **Fig.3.** Net diversity effects for C stock (A), soil C/N ratio (B) and pH (C) across the soil layers and tree  
 753 species richness levels. The error bars are mean  $\pm$ SEM. Significant NDE for C stock, soil C/N ratio and pH  
 754 are coded as: '\*\*\*\*' 0.001, '\*\*\*' 0.01, '\*\*' 0.05,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

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

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

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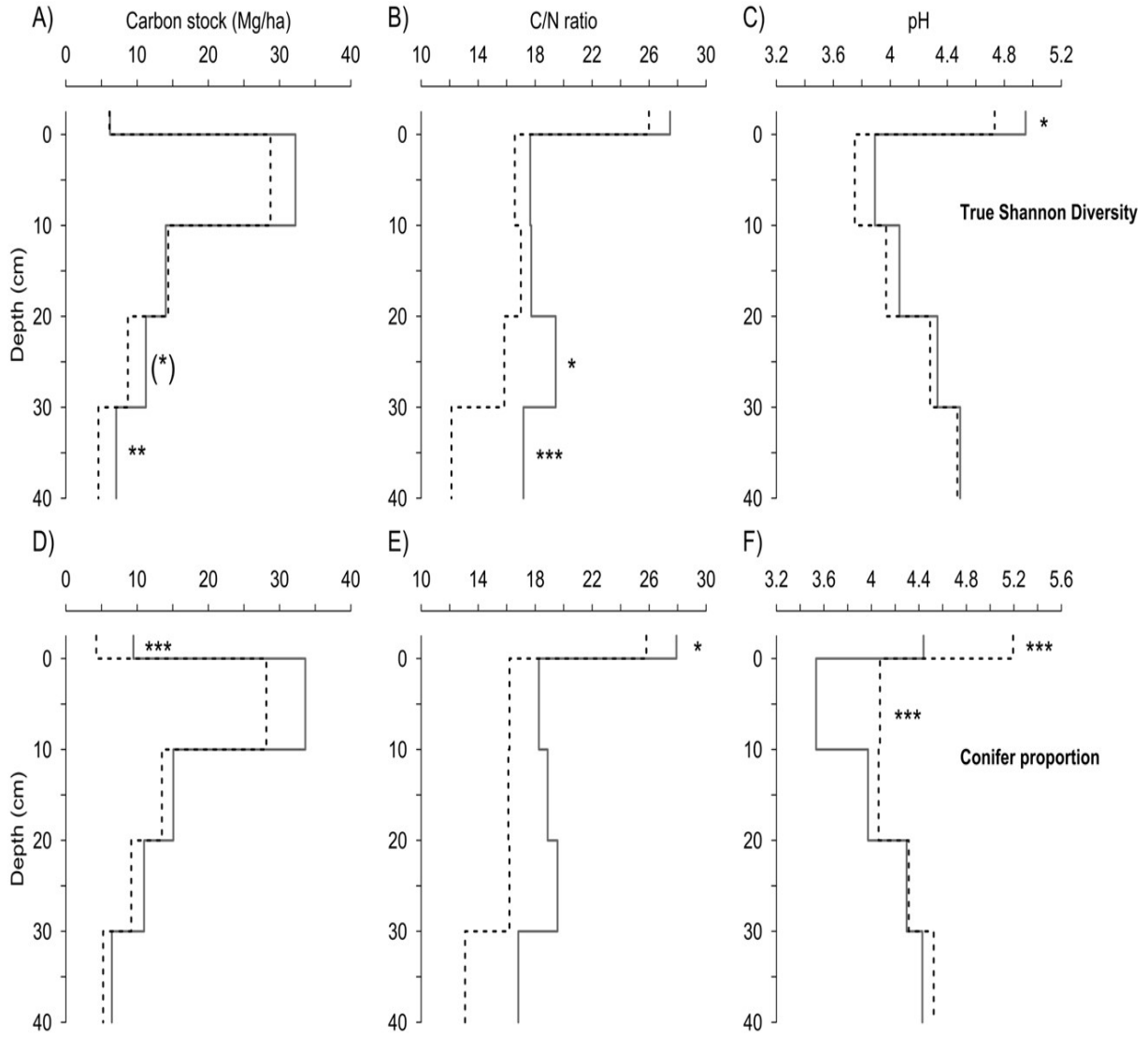
767 **Figure 1**

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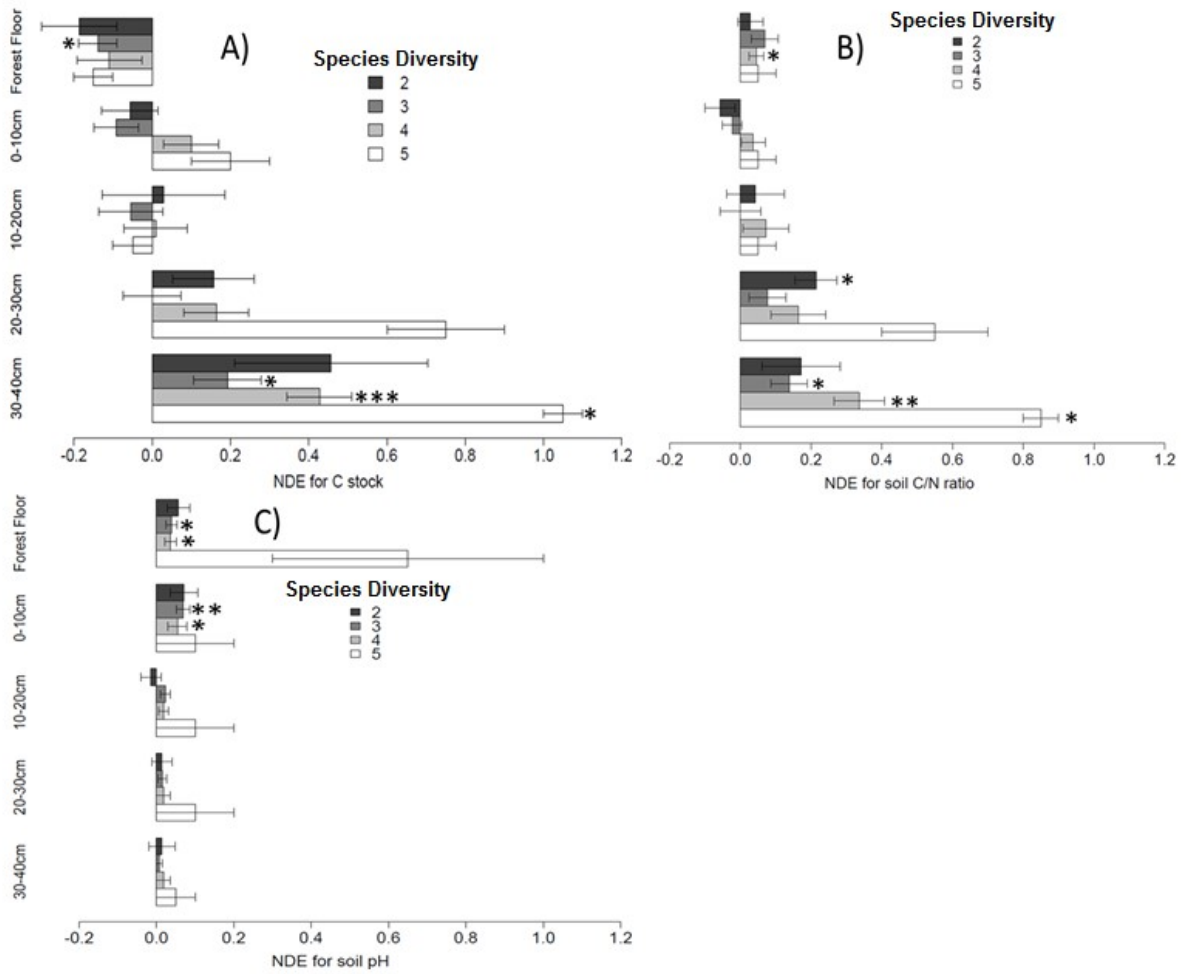
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**Figure 3**

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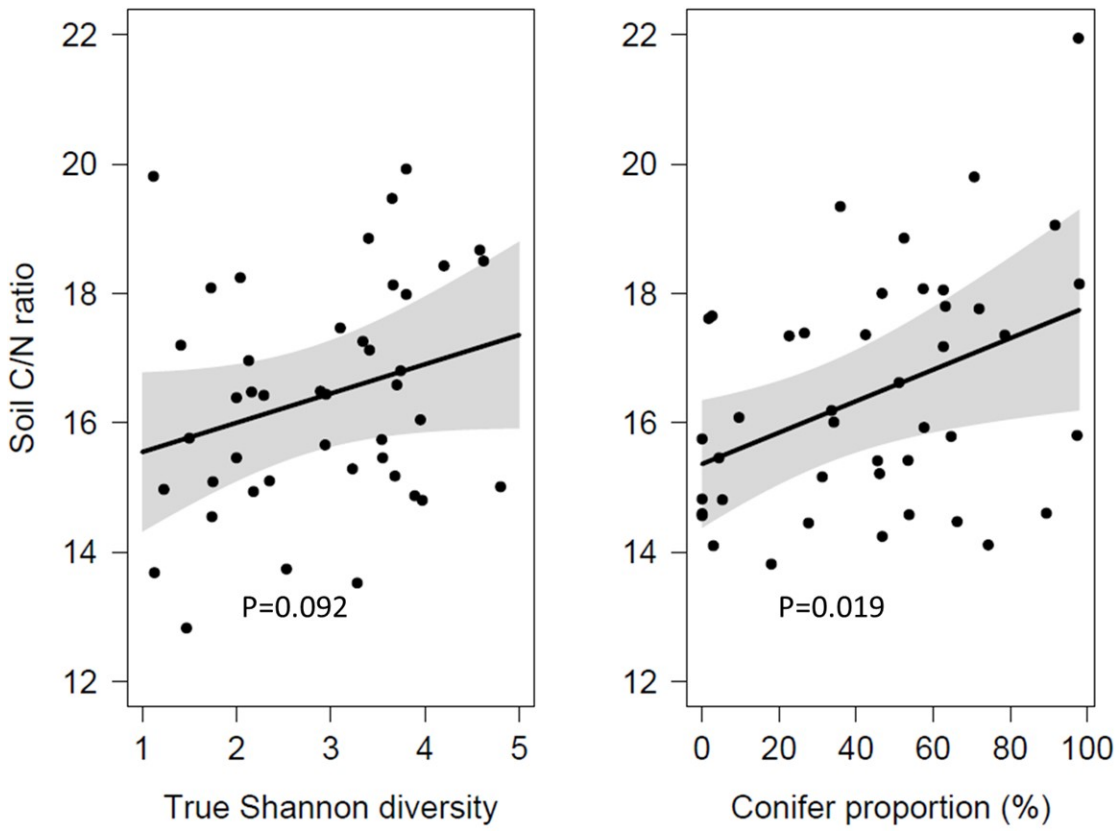
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797 **Figure 4**

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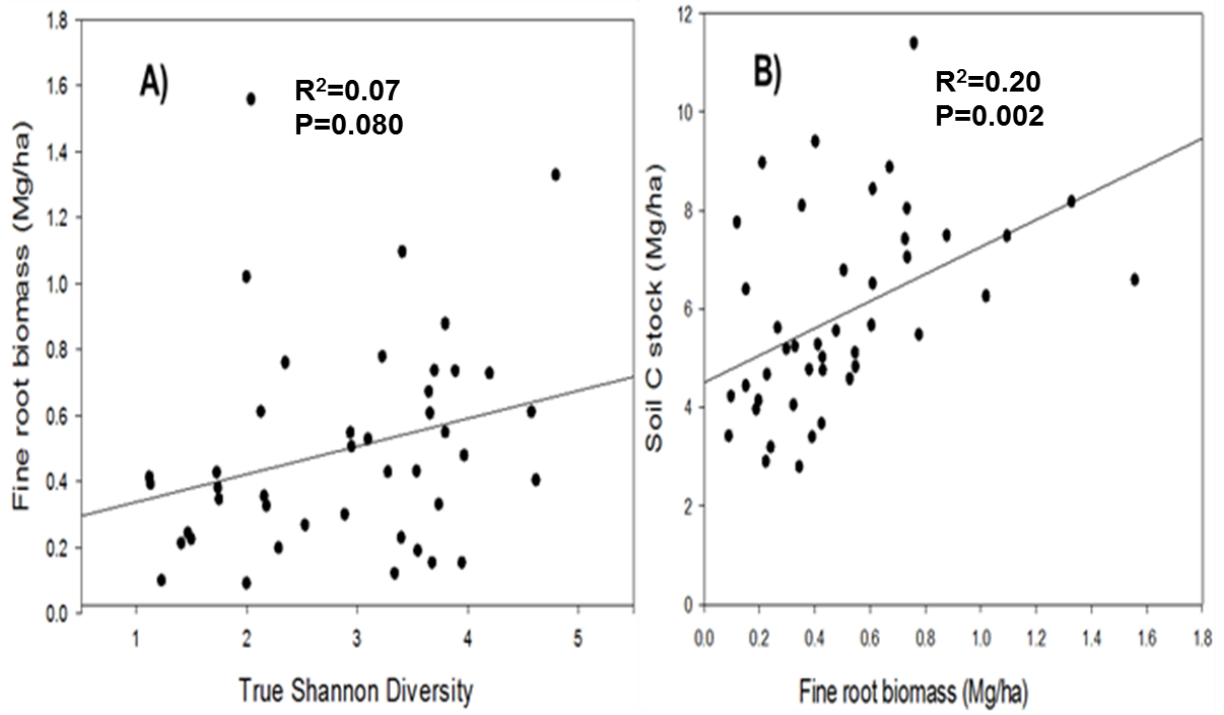
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812 **Figure 5**

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829 **8. Supporting information**

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831 **TABLE S1.** Plot characteristics, C stocks, C/N ratio and pH for each of the 43 plots in  
832 Białowieża.  
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Species composition	TShann	CP	C stock <sub>FF</sub> (Mg ha <sup>-1</sup> )	Total C stock (Mg ha <sup>-1</sup> )	Total C/N ratio	C/N <sub>FF</sub>	pH <sub>FF</sub>	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

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

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849 **TABLE S2.** Mean  $\pm$  standard error of the examined soil properties by layer.  
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Depth	N	C stock (Mg/ha)		N stock		C/N ratio		pH	
		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		

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893 **TABLE S3.** Model outputs for C stock in the forest floor plus 0-40cm (FF+0-40cm) layer\*+.  
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Parameters	Slope	Std. Error	t-value	P-value	Partitioned R <sup>2</sup>
(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

895 \* See above for abbreviated words

896 + **lm(log(Cstock) ~ TShann + CP + Soil types, data= depthname)** was the linear regression model used.

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936 **TABLE S4.** Model outputs for C/N ratio calculated from the total C stock and N stock from the  
 937 forest floor plus 0-40cm (FF +0-40cm) layer \*+.  
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<b>Parameters</b>	<b>Slope</b>	<b>Std. Error</b>	<b>t-value</b>	<b>P-value</b>	<b>Partioned R<sup>2</sup></b>
(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

939 \* See above for abbreviated words  
 940 + **lm(C/N ratio ~ TShann + CP + Soil types, data= depthname)** was the linear regression model used.

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