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Tree functional diversity influences belowground ecosystem functioning

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ABSTRACT

Many ecosystem processes in forest ecosystems are influenced by tree species richness and tree functional diversity (FD). Several studies, mainly in grasslands, have already underlined a positive effect of plant species richness on soil carbon (C) storage, but evidence for such a relationship for forests is scarce and not much is known about the role of FD. In this study, we investigated the impact of trees with contrasting functional litter traits on soil C and nitrogen (N) storage in a forest plantation on a former grassland. In addition, we also investigated the impact of increasing FD on six different soil enzymes, considered as proximate agents of potential microbial mineralization processes. We found synergistic effects of tree mixtures on soil enzymatic activities at the highest FD levels and an overall increase in soil mineralization potential with FD within tree mixtures. Moreover, we registered an overall decrease in soil C and N stocks 12 years after tree planting. Our results suggest that the selection of tree species and mixtures based on functional traits influencing soil C storage is fundamental for the success of climate change mitigation strategies employing tree plantations on abandoned pastures or grasslands.

1. Introduction

Experimental and theoretical evidence has demonstrated a strong link between the provision of ecosystem goods and services and biodiversity (Loreau et al., 2001; Cardinale et al., 2002; Hooper et al., 2005; Isbell et al., 2011). In the face of widespread global changes to the terrestrial carbon (C) cycle, C storage is considered one of the most important ecosystem functions and C sequestration in forest biomass and soil is being regarded as an important element of the strategies to mitigate rising atmospheric CO_2 (e.g. Ciais et al., 2008; Luyssaert et al., 2010; Pan et al., 2011). Soils store three times more C than standing terrestrial vegetation and for longer periods of time (Lal, 2005; Schimel et al., 2001). Nevertheless, this large C reservoir is not permanent, but is the result of a dynamic equilibrium between the C inputs entering the soil (i.e. aboveground litter, dead roots and root exudates) and their microbial decomposition and leaching. Therefore, such a balance is affected by changes in vegetation and plant growth (Vesterdal et al., 2013), harvesting and other disturbances (Jandl et al., 2007) and is sensitive to processes such as climate change (Davidson and Janssens, 2006) and nitrogen (N) deposition (Janssens et al., 2010).

Several studies have underlined the positive effects of plant species richness on soil processes (i.e. Hooper et al., 2005; De Deyn et al., 2009; Lange et al., 2015). However, detecting responses of the soil C pool to manipulated diversity is challenging, as C pools only change slowly (Smith, 2004), soil heterogeneity is large (Schrumpf et al., 2011), and the processes involved are complex (Cotrufo et al., 2015; Manzoni et al., 2012). However, as the activity of the soil microbial community drives soil C and N cycling through the action of extracellular enzymes (Sinsabaugh et al., 2002), enzyme activities can be used as proxies of potential microbial mineralization processes (Allison et al., 2007; Henry, 2013). Specifically, this includes the activities of C-degrading enzymes (i.e. α-glucosidase, β-glucosidase, cellulase), N-degrading enzymes (i.e. leucine aminopeptidase), and P-degrading enzymes (i.e. phosphatase and phosphodiesterase) (Allison et al., 2007; Henry, 2013). Changes in plant community composition may alter soil enzymatic activities and soil C storage directly, by modifying substrate avaliability and quality, or indirectly, through an effect on environmental drivers such as soil water content and temperature (Kreyling

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et al., 2008; Steinauer et al., 2015) or through affecting soil microbial communities (Pei et al., 2016). In this context, it has been suggested that changes in plant functional diversity (FD; Petchey and Gaston, 2006), i.e. 'the value, range, and relative abundance of plant functional traits in a given ecosystem' (Tilman, 2001), may have a stronger influence on decomposition and soil C and N than a simple change in species richness (Meier and Bowman, 2008). Litter quality is often species-specific (Eichenberg et al., 2015; Güsewell, 2004), and thus mixture of species with chemically different litters may significantly influence decomposition (Cornwell et al., 2008), soil microbial community (de Vries et al., 2012) and the overall biogeochemical cycling (Reich, 2014), even at the same level of plant species richness (Dawud et al., 2016). Moreover, as traits responsible for decomposability are correlated across leaves, stems and roots (Freschet et al., 2013), we expect that differences in the dynamics of labile organic matter measured between any two coexisting species aboveground are paralleled belowground.

Degradation of plant residues in soil occurs through the action of numerous extracellular soil enzymes (Sinsabaugh et al., 2008), six of which are the most frequent: α-glucosidase (AG), β-glucosidase (BG), cellulase (CEL), phosphatases (acid and alkaline; AP), phosphodiesterase (PDE) and leucine aminopeptidase (LAP). In particular, BG has been shown to be sensitive to changes in soil and residue management and may be an early indicator of changes in soil organic carbon (SOC), before these changes become apparent through changes in total soil organic C (Sinsabaugh et al., 2008). The activity of BG, which usually increases with increasing soil microbial biomass, reflects the rate at which plant residues decompose. The enzymes AP and PDE hydrolyze phosphomonoesters and phosphodiesters releasing mineral phosphate (Toor et al., 2003; Turner et al., 2002). Their activity has been widely used to monitor and evaluate the changes in P availability after fires, clear-cutting, scarification, and changes in management practices, as well as soil drying and rewetting. LAP hydrolyzes leucine and other hydrophobic amino-acids from the N terminus of polypeptides and its activity is broadly used as an indicator of potential peptide degradation (Sinsabaugh et al., 2008).

Despite the promise of extracellular enzyme analysis for early detection of the effects of plant functional diversity on soil processes, few if any studies have been conducted. Moreover, the connection between tree functional traits at community level and biogeochemical cycles has not been fully clarified yet. We therefore measured the activities of the above mentioned six hydrolytic extracellular enzymes, soil organic C and N, dissolved organic carbon (DOC), dissolved organic nitrogen (DON) and microbial biomass along a gradient in tree functional diversity within the BIOTREE-FD experiment (Scherer-Lorenzen et al., 2007a,b). We tested the hypothesis that the concomitant contribution of trees with contrasting functional litter traits (i.e. higher FD) increases soil enzymatic activities and decreases the overall soil C and N pools in the short/medium term.

2. Materials and methods

2.1. Study site and experimental setup

The BIOTREE-FD study site is located in Bechstedt, in the Thuringian basin (Germany; N 50°54′, E 11°05′) at an elevation of around 400–415 m a.s.l. Mean annual temperature at the site is 7.9 °C and mean annual precipitation is 553 mm. The bedrock consists of limestone, marl and clay beds of the Upper Muschelkalk formation (Ceratites layer, "Letten-Grenzschichten"), which belongs to the German Trias (pre-experimental soil characteristics are given in Table S1). The site was formerly used for pasture and was ploughed before tree planting.

In March 2003, in order to create a gradient of plot level tree community functional diversity (FD), 25 stands were planted with four tree species each, drawing from a pool of 16 tree species (Fig. S1; Table S2). These species represent several of the most abundant tree genera in Germany (Müller et al., 2015), they all occur, naturally or planted, in the region where the experimental site is located, on the same substrate and soil conditions, and reflect a wide range of forestry purposes (Kunz et al., 2016; Stark et al., 2015). FD for candidate species mixtures was calculated using information on species traits from the literature ($FD_{original}$), based on nine functional traits indicative of productivity, resource use and nutrient cycling of trees (i.e. leaf type, light requirements as adults, height growth vigor, mean annual increment growth, rooting vigor, crown architecture, root architecture, leaf N concentration, C:N ration of litter) (Scherer-Lorenzen et al., 2007a,b). $FD_{original}$ was calculated from the branch length of a dendrogram using Gower distances based on ordinal categories of the traits above (Petchey and Gaston, 2002).

Within each stand, trees were planted at a spacing of 1 m within rows and 2 m between rows (Fig. S1). As an alternative to randomly mixing individuals of the component species, clusters of 20 individuals (hereafter referred to as subplots) were planted in circular patches (area = 38.5 m^2) to prevent dramatic changes in the design (i.e. loss of a species in a stand) potentially arising from fast-growing species outcompeting slow-growing ones. More details on the BIOTREE-FD experimental design can be found in Scherer-Lorenzen et al. (2007a,b).

2.2. Soil sampling

Soil sampling was performed in September 2015. From the 25 experimental stands, we selected three stands representing the lowest, the highest and a medium $FD_{original}$ (Table S3). Within each of them, monospecific and mixture samples were defined based on neighbourhood tree diversity (Fig. S1). These two types of samples were defined as follows. First, samples collected at the center of tree species patches were treated as effective monospecific plots (at the neighbourhood scale). For each tree species, four of these monospecific planting patches were randomly selected (4 replicates x 12 subplots = 48 samples). Second, samples collected at the midpoint where three adjacent plots border each other were treated as three species mixtures. All of these 3-species combinations within each selected stand were sampled (mixture patches; 4 replicates x 12 mixtures = 48 samples). At each sampling point, one 377 cm^3 soil core (0–30 cm) was collected using a petrol driven pneumatic auger (Eijkelkamp, the Netherlands). Each core was then divided in two depths (0–15 and 15–30 cm) and stored at 4 °C until analyzed.

2.3. Soil analysis

Soil pH – A sieved (2 mm) subsample of soil was taken from each core (0–15 and 15–30 cm) and soil pH was determined in 1 M KCl.

Total organic carbon and nitrogen (g kg^{-1}) were measured for each single sampling point and depth interval using a CHN Elemental Analyser (Carlo Erba Instruments, mod 1500 series 2). Prior to analyses, soil samples were treated with HCl to eliminate carbonates (Harris et al., 2001).

Dissolved organic carbon and nitrogen – Dissolved organic carbon (DOC; mg g^{-1}) and dissolved organic nitrogen (DON; mg g^{-1}) were determined on extracts obtained by shaking 5 g of soil (dry weight) with 20 ml of 0.5 M K_2SO_4 for 30 min. After centrifugation (5 min at 1000*g*), supernatants were filtered using 0.7 μm glass filters (Whatman GF-F). Soluble C and N were determined with a Shimadzu TOC-V analyzer (Shimadzu Corp., Kyoto, Japan) equipped with a TNM-1 module for N determination.

dsDNA – Extraction of double stranded deoxyribonucleic acids (dsDNA; μg g^{-1}) from soil was performed with a 0.12 M, pH 8 Na_2HPO_4 buffer and bead beating. The dsDNA content was quantified in the crude extract without further purification using PicoGreen (Fornasier et al., 2014).

Soil enzymatic activities (EAs). EAs were determined in soil extracts

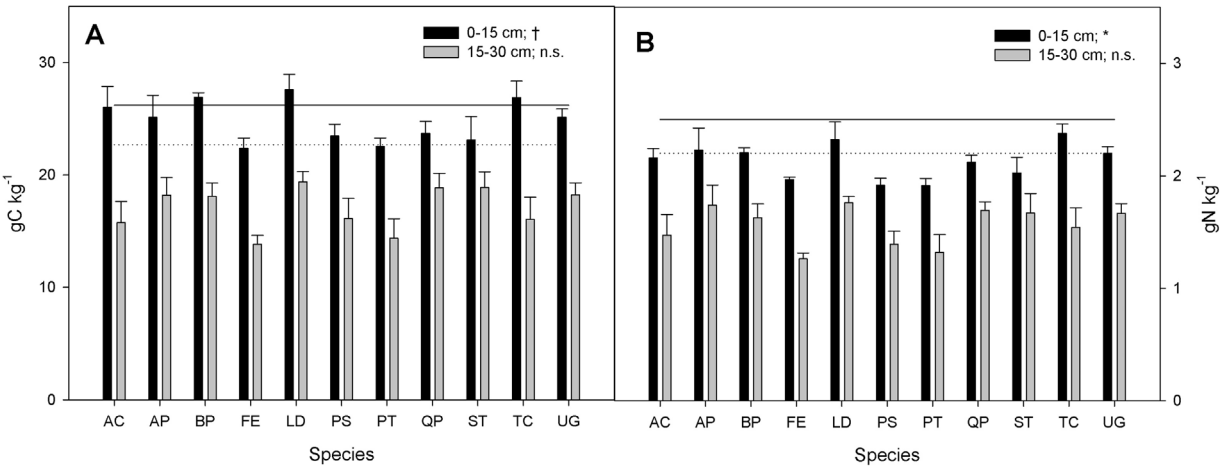

Fig. 1. Soil organic carbon (A) and nitrogen content (B) in the upper (0–15 cm) and lower (15–30 cm) soil layers for the eleven tree species (monospecific plots). Horizontal solid and dashed lines represent the original contents at 0–15 and 15–30 cm soil depth, respectively, before trees were planted in 2003–2004 (Table S1). Vertical bars indicate standard error (n = 4 for all species; n = 8 for *Quercus petraea*). Species code: AC = *Acer campestre*; AP = *Acer platanoides*; BP = *Betula pendula*; FE = *Fraxinus excelsior*; LD = *Larix decidua*; PS = *Pinus sylvestris*; PT = *Populus tremula*; QP = *Quercus petraea*; ST = *Sorbus torminalis*; TC = *Tilia cordata*; UG = *Ulmus glabra*. ANOVA results among tree species: * $p < 0.05$; † $p < 0.10$; n.s., not significant.

as described by Cowie et al. (2013). Briefly, 0.5 g dry soil was put in a 2-ml Eppendorf tube together with 1.25 ml of a solution containing 4% bovine serum albumin and Triton X-100 and glass beads. The contents of the tubes were subjected to bead-milling at 30 strokes s^{-1} for 3 min and then centrifuged at 20.000*g* for 2 min. Supernatants, containing desorbed enzymes, were dispensed in well microplates with appropriate buffers to determine enzymatic activities using specific fluorescent, 4-methyl-umbelliferyl substrates. Because of their strong covariance with soil organic matter, extracellular enzyme activity potentials were expressed as specific enzymatic activities (nmol of 4-methylumbelliferone $h^{-1}\,g\,C^{-1}$) to easily analyse and compare the dynamics of decomposition (Sinsabaugh et al., 2008).

2.4. Data analysis

Mathematically, functional diversity can be expressed using several approaches and indices (Laliberté and Legendre, 2010; Mason et al., 2005; Petchey and Gaston, 2006, 2002; Villéger et al., 2008). The determination of site-specific trait data in previous studies at the site and recent conceptual developments in functional diversity indices permitted the re-calculation of functional diversity for the planted mixtures. This re-calculation was also appropriate, as some of the original functional traits used to calculate $FD_{original}$ were unlikely to be predictive for the soil C storage and the potential acquisition of readily available nutrients expressed by the enzymatic activities. Thus, functional diversity was recomputed using three physical (specific leaf area, SLA; leaf thickness; leaf toughness) and five chemical traits (C and N content; C:N ratio; total phenolics and tannin content), measured on leaves collected at the site (Hantsch et al., 2014). Among all possible available indices, we expressed functional diversity in terms of functional dispersion (FDis), i.e. the mean distance in a multidimensional trait space of individual species to the centroid of all species, weighted by their relative abundances (Laliberté and Legendre, 2010). In our case, species distance was weighted by the mean tree diameter of each species within the mixure and FDis was computed using the R-package FD (R Development Core Team 2008 (Laliberté and Shipley, 2011). Weighting by diameter was used to reflect the different sizes that tree species reached after 12 years of growth. It has been suggested that communities with only one species should have FDis = 0, but there is no upper limit for this index.

All measured data were log-transformed before performing the statistical analysis to meet the requirements for parametric statistical tests. Soil variables (i.e. organic C, N, pH, DON, DOC), microbial biomass (dsDNA) and specific enzymatic activities of monospecific subplots were compared among tree species by one-way ANOVA, separately by soil depth (0–15 and 15–30 cm). The importance of each individual leaf trait on measured variables was assessed using a Spearman's correlation matrix based on the monospecific plots only.

We tested for an effect of the functional diversity gradient (mixtures) on measured variables using linear mixed models with original experimental plot as a random factor to account for nesting of sampled mixtures within plots (Table S3). To asess model fit, we calculated marginal R^2 values – the proportion of variance explained by the fixed factor(s) alone (Nakagawa and Schielzeth, 2013). For that purpose, we used the function sem.model.fits from the piecewiseSEM R package (Lefcheck, 2016).

We also evaluated the effect of species mixures on soil enzyme activities by quantifying the net diversity effect (NDE) 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 mean diameter in the mixture (Dawud et al., 2016; Hector et al., 2002), that is $\frac{(Observed - Expected)}{Expected}$. The diversity effect can be additive (NDE = 0), synergistic (NDE > 0) or antagonistic (NDE < 0).

Statistical analysis were carried out with R and figures were created using SigmaPlot 11 (©Systat Software, Germany).

3. Results

3.1. Monocultures

Tree species displayed differences in the surface soil layer (0–15 cm) for the following soil properties: pH ($p = 0.017$), organic C ($p = 0.081$; Fig. 1a), soil N ($p = 0.026$; Fig. 1b) and DOC ($p = 0.027$). When compared to initial soil C and N contents before tree planting (Table S1), the monospecific plots showed an average decrease of −5% and −15%, respectively, with important differences among tree species. In fact, soil under *Larix decidua* showed the highest soil organic C concentration (27.6 g C kg^{-1}; +5%) followed by *Betula pendula* and *Tilia cordata* (26.9 g C kg^{-1}; +3%), while the lowest concentration was found under *Fraxinus excelsior* (22.4 g C kg^{-1}; −15%) and under *Populus tremula* (22.6 g C kg^{-1}, −14%) (Fig. 1a). All species showed a decrease in soil N content in comparison to the pre-planting situation as well (Fig. 1b), with the greatest reduction for *Populus tremula* (1.91 kg N kg^{-1}; −24%) and the smallest reduction for *Tilia cordata* (2.38 kg N kg^{-1}; −5%). All six specific enzymatic activities were also

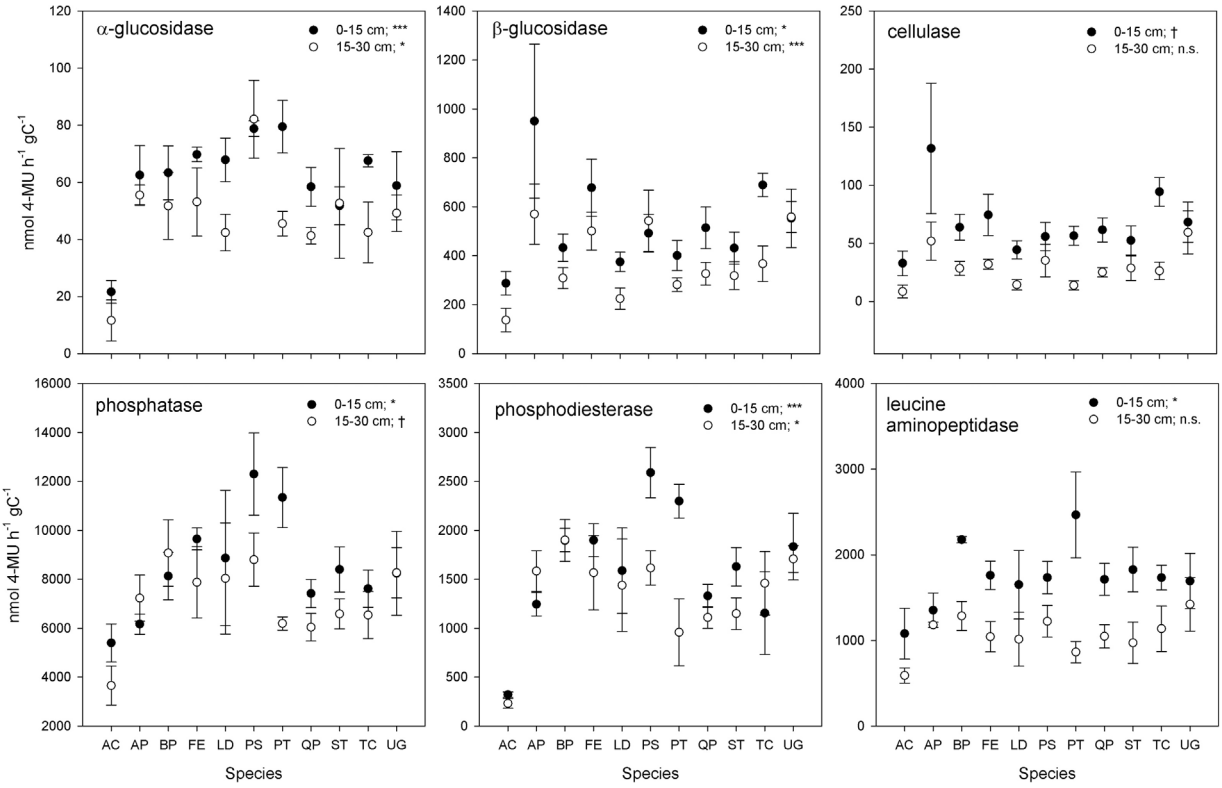

Fig. 2. Specific activities of extracellular enzymes (nmol of 4-MU h^{-1} g C^{-1}) at 0–15 cm and at 15–30 cm for the 11 sampled species. Vertical bars indicate standard error (n = 8 for *Quercus petraea;* n = 4 for all the other species). Species code: AC = *Acer campestre*; AP = *Acer platanoides*; BP = *Betula pendula*; FE = *Fraxinus excelsior*; LD = *Larix decidua*; PS = *Pinus sylvestris*; PT = *Populus tremula*; QP = *Quercus petraea*; ST = *Sorbus torminalis*; TC = *Tilia cordata*; UG = *Ulmus glabra*. ANOVA results among tree species: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; † $p < 0.10$; n.s., not significant.

significantly different among the considered tree species (Fig. 2). On the contrary, no differences in DON ($p = 0.281$) and in microbial biomass ($p = 0.129$), as expressed by the soil's dsDNA content, were detected. Testing the importance of leaf litter traits in a multiple regression analysis (Table S4) revealed that dsDNA content was positively influenced by leaf N ($p = 0.027$), soil organic C ($p = 0.063$), soil N ($p = 0.036$) and negatively by the leaf C:N ratio ($p = 0.021$) and leaf toughness ($p = 0.002$). Moreover, higher leaf phenolics and tannin contents reduced α-glucosidase (AG; $p = 0.038$ and $p = 0.040$), phosphatases (AP; $p < 0.001$ and $p < 0.001$), phosphodiesterase (PDE; $p < 0.001$ and $p < 0.001$) and leucine aminopeptidase (LAP; $p = 0.010$ and $p = 0.005$) specific activities. Leaf phenolics and tannin accumulation also decreased soil pH ($p = 0.053$ and $p = 0.084$ for phenolics and tannin content, respectively). Both soil organic C and total N were positively influenced by leaf phenolics ($p = 0.084$ and $p = 0.067$) and tannin content ($p = 0.084$ and 0.05) and negatively by leaf toughness ($p = 0.069$ and $p = 0.054$).

In the deeper soil layer (15–30 cm), all soil properties did not differ among species, with the exception of DOC ($p = 0.005$) and pH ($p = 0.022$). A significant difference was detected only for β-glucosidase (BG), AP and PDE activities ($p < 0.001$, $p = 0.054$ and $p = 0.015$, respectively). Soil C and N contents were always lower than the concentrations measured in 2003, before tree planting (-25% and −29% on average, respectively; Fig. 1a and b).

3.2. Functional diversity

FDis of the twelve considered tree mixtures ranged between 1.03 and 3.07 (Table 1). Mixtures showed a mean soil C content of 24.7 and 16.8 g C kg^{-1} at 0–15 cm and 15–30 cm, respectively, corresponding to an overall decrease of −6% and −26% in comparison to the pre-planting conditions (Table S1). Similarly, we measured a soil N content of 2.16 and 1.57 g N kg^{-1} at the two depths, corresponding to an overall decrease of −14% and −28%.

Table 1
The twelve considered mixtures ordered according to their increasing functional diversity level, as expressed by functional dispersion (FDis; Laliberté and Legendre, 2010). Species code: AC = *Acer campestre*; AP = *Acer platanoides*; BP = *Betula pendula*; FE = *Fraxinus excelsior*; LD = *Larix decidua*; PS = *Pinus sylvestris*; PT = *Populus tremula*; QP = *Quercus petraea*; ST = *Sorbus torminalis*; TC = *Tilia cordata*; UG = *Ulmus glabra*.

Mixture	FDis
BP-LD-QP	1.03
BP-LD-ST	1.56
AP-QP-TC	1.92
AC-FE-PT	1.96
BP-QP-ST	1.99
QP-TC-UG	2.08
AP-QP-UG	2.11
LD-QP-ST	2.12
AP-TC-UG	2.45
FE-PS-PT	2.70
AC-PS-PT	3.06
AC-FE-PS	3.07

Regarding the effects of functional diversity on soil variables, we did not detect any significant change in soil C and N, pH, DOC, DON with FDis (Fig. S2; Table S5). On the contrary, at 15–30 cm, microbial biomass, as expressed by dsDNA, decreased significantly with FDis ($p = 0.01$; Fig. S2). Moreover, specific activities of AG, BG and CEL significantly increased with functional diversity at 0–15 cm ($p < 0.05$; Fig. 3), while AP, PDE and LAP did not show any significant trend.

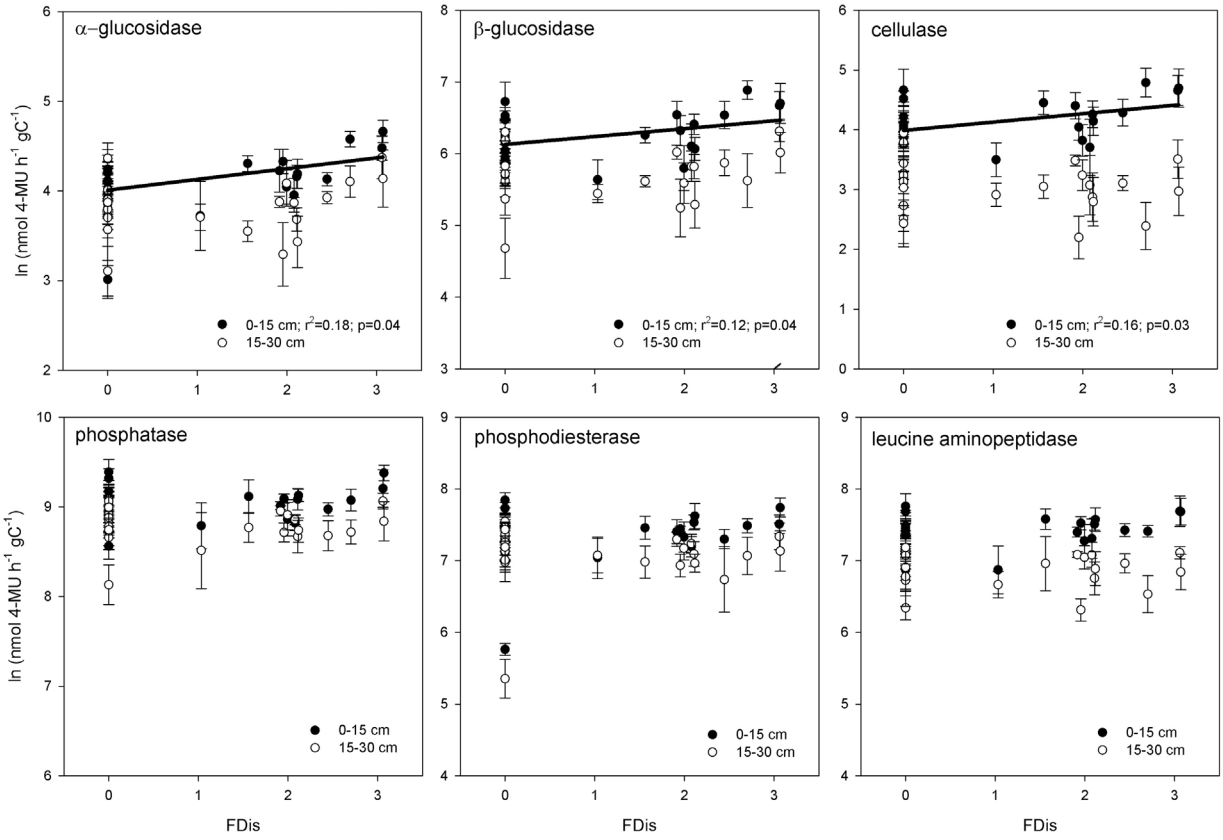

Fig. 3. Variation in the natural logarithm of specific activities of extracellular enzymes (nmol of 4-MU h^{-1} g C^{-1}) at 0–15 (closed symbols) and 0–30 cm (open symbols) with tree species functional diversity, as expressed by functional dispersion (FDis). FDis = 0 values correspond to monospecific plots. Vertical bars indicate standard error (n = 8 for *Quercus petraea;* n = 4 for all the other species and mixtures), bold and dashed lines are the effect of FD predicted from a linear mixed model for 0–15 and 15–30 cm, respectively. Predicted effect of FD, marginal R^2 and p-value for the effect of FD are shown when $p < 0.10$.

Similarly, at 15–30 cm depth, we did not find any significant correlation between all specific enzymatic activities and FDis (Fig. 3; Table S5).

At both depths, a synergistic mixture effect (NDE > 0) was found for most of the enzyme activities at the highest FDis levels. In fact, all the mixtures in which *Pinus sylvestris* was present generally showed positive NDE values (Fig. 4). An additive, or even antagonistic, effect was instead generally detected at the lowest FDis values (i.e. birch-larch-oak mixture). AG, BG, CEL and LAP activities showed a significant linear increase in NDE with FDis at 0–15 cm, while AP and PDE at 15–30 cm (Fig. 4). Soil C and N, DOC, DON did not show any significant trend in NDE at both depths. On the contrary, dsDNA showed an increase in NDE with FDis at 0–15 cm (Fig. 5).

4. Discussion

Our results showed an overall decrease in soil C and N contents in monospecific plots at both 0–15 cm and 15–30 cm depths in comparison to pre-planting conditions. Guo and Gifford (2002), in their comprehensive meta-analysis on soil C stocks and land use changes, reported an average 10% decline in soil C stocks when shifting from pasture to plantation, mainly because of site preparation at tree planting (i.e. soil disturbance) and the change in the C input (i.e. quantity and quality). Similarly, Poeplau and Don (2013) studying secondary forests on abandoned grasslands measured an increase in forest floor C, but a significant decrease in soil C stocks in the topsoil (0–30 cm depth). However, while there is a strong evidence for higher forest floor C stocks under coniferous than under broadleaved trees, tree species effects on mineral soil C stocks are less consistent (Vesterdal et al., 2013, 2008). In any case, such a decline has been generally reported to be limited to the first 10 years after the plantation and soil C stocks have been reported to recover thereafter (Paul et al., 2003). In our study, twelve years after the land use change, the soil under some of the tree species (monospecific plots) has either been maintained at or already returned to the pre-planting soil C level at 0–15 cm, with a proportional difference between the highest and the lowest soil C concentration of 7.38 g C kg^{-1}. On the contrary, all the species still showed a lower soil C concentration at the deepest soil horizon (15–30 cm). The different soil C concentrations measured among the tree species may be related to both differences in the amount of C entering the soil through litter and rhizo-depositions and in the quality of such an input (De Deyn et al., 2008). In fact, even if trees with a higher basal area, wood production and leaf area index have been shown to have a larger litter production (Vilà et al., 2004), the detected differences in the specific soil enzymatic activities among the tree species support the idea that litter chemical traits are important drivers as well. This has been also shown by Meier and Bowman (2008) who found that key soil processes are influenced by interactions between plant litter chemical traits and the microbial enzymes that catalyze the decomposition reactions. Previous experiments have identified foliar litter concentration of calcium (Reich et al., 2005), N or C:N ratio (Vesterdal et al., 2012, 2008), lignin (Hobbie et al., 2006) or lignin:N ratio as the most important factors influencing litter decomposition and forest floor dynamics. In our case, microbial biomass, as expressed by dsDNA, was positively influenced by leaf N content and negatively by leaf C:N ratio and leaf toughness. Similarly, all specific soil enzymatic activities were negatively, even though not significantly, influenced by leaf C:N ratio. Moreover, phenolics and tannin concentrations seem to strongly control AP and PDE activities and soil organic C, probably because tannins bind to N-containing substrates, limiting their mineralization (Fierer et al., 2001; Kraus et al., 2004). However, no relationship between leaf litter C:N and soil organic C was detected, as previously reported by

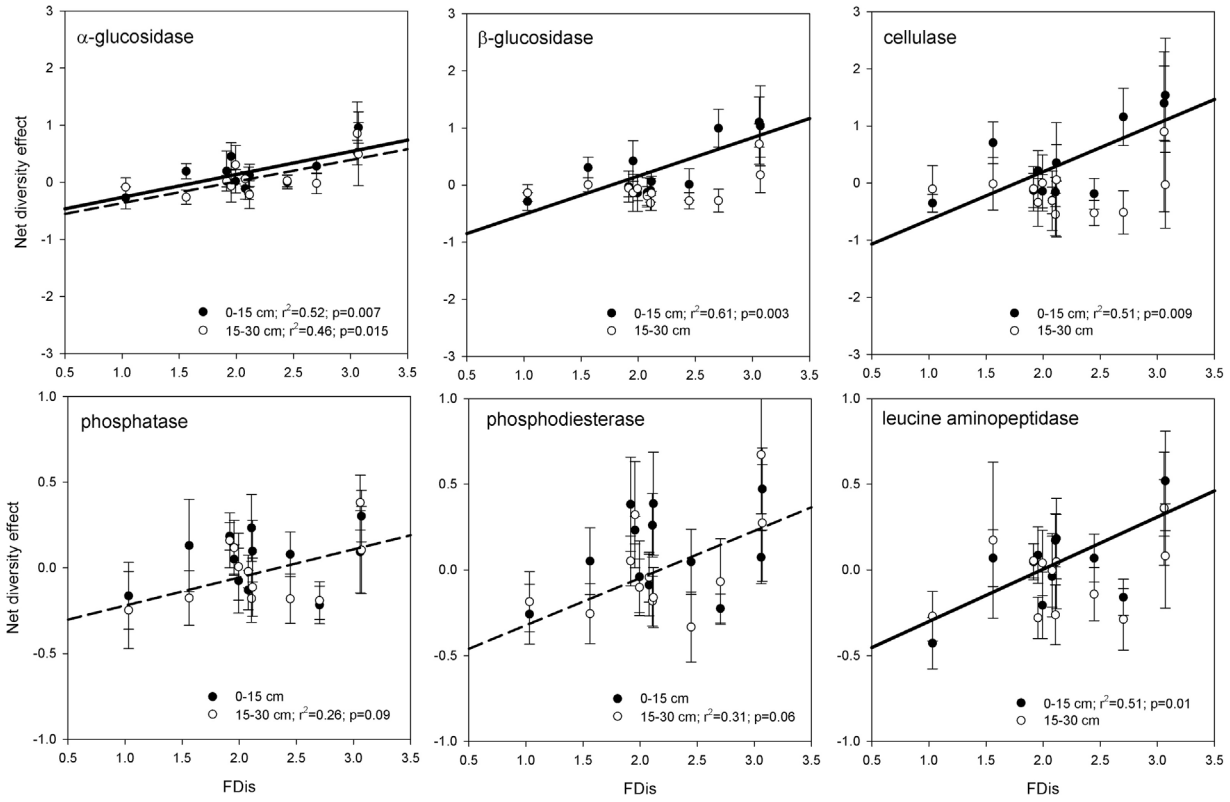

Fig. 4. Net diversity effects (NDE) for α-glucosidase, β-glucosidase, cellulase, phosphatases, phosphodiesterase and leucine aminopeptidase (nmol of 4-MU h^{-1} g C^{-1}) at 0–15 cm (closed symbols) and 15–30 cm (open symbols). Vertical bars indicate standard error (n = 4), bold and dashed lines are the regression lines for 0–15 and 15–30 cm, respectively. Simple linear regression lines, R^2 and p-value are shown when $p < 0.10$.

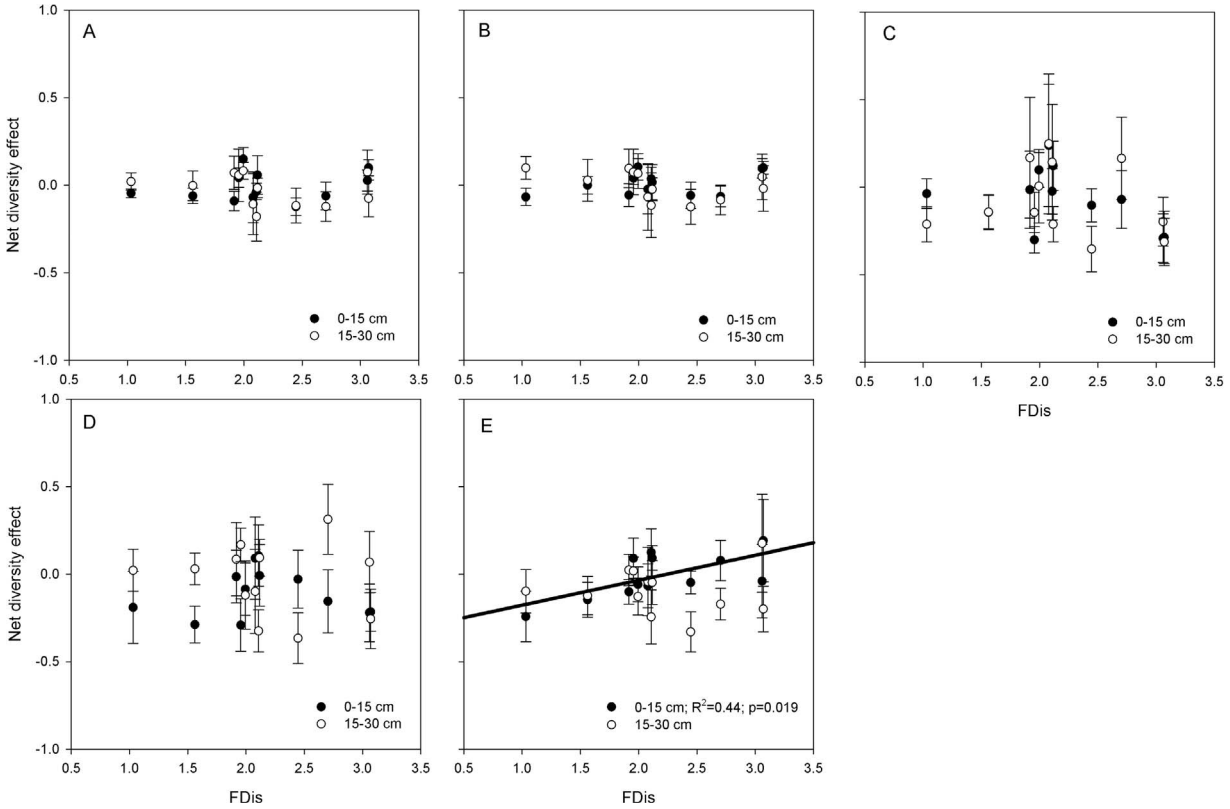

Fig. 5. Net diversity effect (NDE) for soil organic carbon content (A; g C kg^{-1}), soil nitrogen (B; g N kg^{-1}), dissolved organic carbon (C; mg g^{-1}), dissolved organic nitrogen (D; mg g^{-1}) and dsDNA (E; μg g^{-1}) at 0–15 cm (closed symbols) and 15–30 cm (open symbols) by functional diversity level, as expressed by functional dispersion (FDis). Vertical bars indicate standard error (n = 4), bold and dashed lines are the regression lines for 0–15 and 15–30 cm, respectively. Simple linear regression lines, R^2 and p-value are shown when $p < 0.10$.

Vesterdal et al. (2008).

At the ecosystem scale, Dawud et al. (2016) have recently shown that species identity (i.e. conifer proportion in the mixtures) is a stronger driver for soil C stocks, C:N ratio and pH than tree species diversity. Moreover, Vilà et al. (2004) and Scherer-Lorenzen et al. (2007a) have already reported that litter pools are larger in tree mixtures than in monocultures. As microbial growth and potential enzymatic activities are ultimately limited by the availability of organic matter (Sinsabaugh et al., 2014), we normalized each activity by soil C, to easily analyse and compare the dynamics of decomposition (Sinsabaugh et al., 2008). Thus, when comparing mixed with monospecific situations, we were able to highlight synergistic effects (NDE $>$ 0) for the six studied enzymes in plots where *Pinus sylvestris* was present and mostly additive (NDE = 0) or even antagonistic (NDE $<$ 0) effects in broadleaf dominated mixtures with low FDis value. These results may be again related to litter traits as a higher diversity in litter composition may have influenced soil C and N mineralization directly or indirectly through reactions among different chemical groups and between these and soil microbes. This is even more evident when looking at functional diversity, as also reported in previous studies in grassland ecosystems (Chung et al., 2007; Meier and Bowman, 2008; Steinauer et al., 2015). In fact, increasing the functional diversity led to an overall increase in specific enzyme activities of AG, BG and CEL, with a corresponding increase in soil organic matter mineralization potential and decrease in soil C because of a stronger decline in soil organic matter from the former pasture. However, as said before, this decrease in soil C should be a transient effect which should be compensated by a higher litter input in the long term.

In conclusion, to our knowledge, this was the first investigation of the impact of functional diversity on C and N stocks in combination with soil microbial activities in tree mixtures. Our results clearly show strong synergistic effects of tree mixtures characterized by a high litter functional diversity on soil enzymatic activities and an overall increase in soil mineralization potential (i.e. AG, BG and CEL activities) with functional diversity within tree mixtures. This can have important implications for climate change mitigation strategies employing tree plantations on abandoned pastures or grasslands, as more attention should be paid on the selection of tree species and mixtures based on functional traits that may influence soil C storage. More investigations on belowground inputs are, however, needed to better understand the possible impacts of quantity and quality of fine-root material and root exudates on microbial and extracellular enzymatic activities. Moreover, the use of metagenomics will allow deeper insight into soil bacterial abundances and community composition (i.e. Jenkins et al., 2016; Smets et al., 2016) and their links with plant functional diversity and how biodiversity at different ecological levels may influence ecosystem multifunctionality (Soliveres et al., 2016).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.apsoil.2017.07.038.

References

Allison, S.D., Gartner, T., Holland, K., Weintraub, M., Sinsabaugh, R., 2007. Soil enzymes: linking proteomics and ecological processes. In: Hurst, C., Crawford, R., Garland, J., Lipson, D., Mills, A., Stetzenbach, L. (Eds.), Manual of Environmental Microbiology. ASMscience, pp. 704–711.

Cardinale, B.J., Palmer, M.a, Collins, S.L., 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. Nature 415, 426–429. http://dx.doi.org/10.1038/415426a.

Chung, H., Zak, D.R., Reich, P.B., Ellsworth, D.S., 2007. Plant species richness, elevated CO_2, and atmospheric nitrogen deposition alter soil microbial community composition and function. Glob. Change Biol. 13, 980–989. http://dx.doi.org/10.1111/j.1365-2486.2007.01313.x.

Ciais, P., Schelhass, M.J., Zaehle, S., Piao, S.L., Cescatti, A., Liski, J., Luyssaert, S., Schulze, E., Bouriaud, O., Freibauer, A., Valentini, R., Yvette, G., Ecosystemen, C., Moldovenesc, C., 2008. Carbon accumulation in European forests. Nat. Geosci. 1, 425–429.

Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., Hobbie, S.E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H.M., Santiago, L.S., Wardle, D.A., Wright, I.J., Aerts, R., Allison, S.D., van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T.V., Díaz, S., Garnier, E., Gurvich, D.E., Kazakou, E., Klein, J.A., Read, J., Reich, P.B., Soudzilovskaia, N.A., Vaieretti, M.V., Westoby, M., 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecol. Lett. 11, 1065–1071. http://dx.doi.org/10.1111/j.1461-0248.2008.01219.x.

Cotrufo, M.F., Soong, J.L., Horton, A.J., Campbell, E.E., Haddix, M.L., Wall, D.H., Parton, W.J., 2015. Formation of soil organic matter via biochemical and physical pathways of litter mass loss. Nat. Geosci. 8, 776–779. http://dx.doi.org/10.1038/ngeo2520.

Cowie, A.L., Lonergan, V.E., Rabbi, S.M.F., Fornasier, F., Macdonald, C., Harden, S., Kawasaki, A., Singh, B.K., Anderson, T., Domsch, K., Anderson, T.-H., Domsch, K., Anderson, T.-H., Domsch, K., Anderson, T., Joergensen, R., Ascher, J., Ceccherini, M., Pantani, O., Agnelli, A., Borgogni, F., Guerri, G., Nannipieri, P., Pietramellara, G., Baldock, J., Skjemstad, J., Bandick, A., Dick, R., Batjes, N., Blagodatskaya, E., Blagodatskii, S., Anderson, T., Campbell, C., Chapman, S., Cameron, C., Davidson, M., Potts, J., Chan, K., Oates, A., Li, G., Conyers, M., Prangnell, R., Poile, G., Liu, D., Barchia, I., Chan, K., Conyers, M., Li, G., Helyar, K., Poile, G., Oates, A., Barchia, I., Conant, R., Paustian, K., Conant, R., Paustian, K., Elliott, E., Cookson, W., Abaye, D., Marschner, P., Murphy, D., Stockdale, E., Goulding, K., Dalal, R., Dalal, R., Chan, K., Dick, W., Duiker, S., Lal, R., Fierer, N., Jackson, J., Vilgalys, R., Jackson, R., Fierer, N., Bradford, M., Jackson, R., Fornasier, F., Margon, A., Gangneux, C., Akpa-Vinceslas, M., Sauvage, H., Desaire, S., Houot, S., Laval, K., Gattinger, A., Muller, A., Haeni, M., Skinner, C., Fliessbach, A., Buchmann, N., Mader, P., Stolze, M., Smith, P., Scialabba, N., Niggli, U., Guggenberger, G., Elliott, E., Frey, S., Six, J., Paustian, K., et al., 2013. Impact of carbon farming practices on soil carbon in northern New South Wales. Soil Res. 51, 707. http://dx.doi.org/10.1071/SR13043.

Davidson, E.a., Janssens, I.a., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440, 165–173. http://dx.doi.org/10.1038/nature04514.

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. http://dx.doi.org/10.1007/s10021-016-9958-1.

De Deyn, G.B., Cornelissen, J.H.C., Bardgett, R.D., 2008. Plant functional traits and soil carbon sequestration in contrasting biomes. Ecol. Lett. 11, 516–531. http://dx.doi.org/10.1111/j.1461-0248.2008.01164x.

De Deyn, G.B., Quirk, H., Yi, Z., Oakley, S., Ostle, N.J., Bardgett, R.D., 2009. Vegetation composition promotes carbon and nitrogen storage in model grassland communities of contrasting soil fertility. J. Ecol. 97, 864–875. http://dx.doi.org/10.1111/j.1365-2745.2009.01536.x.

de Vries, F.T., Manning, P., Tallowin, J.R.B., Mortimer, S.R., Pilgrim, E.S., Harrison, K.A., Hobbs, P.J., Quirk, H., Shipley, B., Cornelissen, J.H.C., Kattge, J., Bardgett, R.D., 2012. Abiotic drivers and plant traits explain landscape-scale patterns in soil microbial communities. Ecol. Lett. 15, 1230–1239. http://dx.doi.org/10.1111/j.1461-0248.2012.01844.x.

Eichenberg, D., Purschke, O., Ristok, C., Wessjohann, L., Bruelheide, H., 2015. Trade-offs between physical and chemical carbon-based leaf defence: of intraspecific variation and trait evolution. J. Ecol. 103, 1667–1679. http://dx.doi.org/10.1111/1365-2745.12475.

Fierer, N., Schimel, J.P., Cates, R.G., Zou, J., 2001. Influence of balsam poplar tannin fractions on carbon and nitrogen dynamics in Alaskan taiga floodplain soils. Soil Biol. Biochem. 33, 1827–1839. http://dx.doi.org/10.1016/S0038-0717(01)00111-0.

Fornasier, F., Ascher, J., Ceccherini, M.T., Tomat, E., Pietramellara, G., 2014. A simplified rapid, low-cost and versatile DNA-based assessment of soil microbial biomass. Ecol. Indic. 45, 75–82. http://dx.doi.org/10.1016/j.ecolind.2014.03.028.

Freschet, G.T., Cornwell, W.K., Wardle, D.A., Elumeeva, T.G., Liu, W., Jackson, B.G., Onipchenko, V.G., Soudzilovskaia, N.A., Tao, J., Cornelissen, J.H.C., 2013. Linking litter decomposition of above- and below-ground organs to plant-soil feedbacks worldwide. J. Ecol. 101, 943–952. http://dx.doi.org/10.1111/1365-2745.12092.

Güsewell, S., 2004. N:P ratios in terrestrial plants: variation and functional significance. New Phytol. 164, 243–266. http://dx.doi.org/10.1111/j.1469-8137.2004.01192.x.

Guo, L.B., Gifford, R.M., 2002. Soil carbon stocks and land use change: a meta analysis. Glob. Change Biol. 8, 345–360.

Hantsch, L., Braun, U., Haase, J., Purschke, O., Scherer-Lorenzen, M., Bruelheide, H., 2014. No plant functional diversity effects on foliar fungal pathogens in experimental tree communities. Fungal Divers. 66, 139–151. http://dx.doi.org/10.1007/s13225-013-0273-2.

Harris, D., Horwáth, W.R., van Kessel, C., 2001. Acid fumigation of soils to remove carbonates prior to total organic carbon or CARBON-13 isotopic analysis. Soil Sci. Soc. Am. J. 65, 1853. http://dx.doi.org/10.2136/sssaj2001.1853.

Hector, A., Bazeley-White, E., Loreau, M., Otway, S., Schmid, B., 2002. Overyielding in grassland communities: testing the sampling effect hypothesis with replicated

biodiversity experiments. Ecol. Lett. 5, 502–511. http://dx.doi.org/10.1046/j.1461-0248.2002.00337.x.
Henry, H.A.L., 2013. Reprint of Soil extracellular enzyme dynamics in a changing climate. Soil Biol. Biochem. 56, 53–59. http://dx.doi.org/10.1016/j.soilbio.2012.10.022.
Hobbie, S.E., Reich, P.B., Oleksyn, J., Ogdahl, M., Zytkowiak, R., Hale, C., Karolewski, P., 2006. Tree species effects on decomposition and forest floor dynamics in a common garden. Ecology 87, 2288–2297. http://dx.doi.org/10.1890/0012-9658(2006)87[2288:TSEODA]2.0.CO;2.
Hooper, D., Chapin, F.I., Evel, J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J., Lodge, D., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, J., Vandermeer, J., Wardle, D., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knwoledge. Ecol. Monogr. 75, 3–35.
Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W.S., Reich, P.B., Scherer-Lorenzen, M., Schmid, B., Tilman, D., van Ruijven, J., Weigelt, A., Wilsey, B.J., Zavaleta, E.S., Loreau, M., 2011. High plant diversity is needed to maintain ecosystem services. Nature 477, 199–202. http://dx.doi.org/10.1038/nature10282.
Jandl, R., Lindner, M., Vesterdal, L., Bauwens, B., Baritz, R., Hagedorn, F., Johnson, D.W., Minkkinen, K., Byrne, K.a., 2007. How strongly can forest management influence soil carbon sequestration? Geoderma 137, 253–268. http://dx.doi.org/10.1016/j.geoderma.2006.09.003.
Janssens, I. a., Dieleman, W., Luyssaert, S., Subke, J., Reichstein, M., Ceulemans, R., Ciais, P., Dolman, a.J., Grace, J., Matteucci, G., Papale, D., Piao, S.L., Schulze, E.-D., Tang, J., Law, B.E., 2010. Reduction of forest soil respiration in response to nitrogen deposition. Nat. Geosci. 3, 315–322. http://dx.doi.org/10.1038/ngeo844.
Jenkins, J.R., Viger, M., Arnold, E.C., Harris, Z.M., Ventura, M., Miglietta, F., Girardin, C., Edwards, R.J., Rumpel, C., Fornasier, F., Zavalloni, C., Tonon, G., Alberti, G., Taylor, G., 2016. Biochar alters the soil microbiome and soil function: results of next generation amplicon sequencing across Europe. GCB Bioenergy 9, 591–612. http://dx.doi.org/10.1111/gcbb.12371.
Kraus, T.E.C., Zasoski, R.J., Dahlgren, R.A., Horwath, W.R., Preston, C.M., 2004. Carbon and nitrogen dynamics in a forest soil amended with purified tannins from different plant species. Soil Biol. Biochem. 36, 309–321. http://dx.doi.org/10.1016/j.soilbio.2003.10.006.
Kreyling, J., Beierkuhnlein, C., Elmer, M., Pritsch, K., Radovski, M., Schloter, M., Wöllecke, J., Jentsch, A., 2008. Soil biotic processes remain remarkably stable after 100-year extreme weather events in experimental grassland and heath. Plant Soil 308, 175–188. http://dx.doi.org/10.1007/s11104-008-9617-1.
Kunz, J., Räder, A., Bauhus, J., 2016. Effects of drought and rewetting on growth and gas exchange of minor european broadleaved tree species. Forests 7, 239. http://dx.doi.org/10.3390/f7100239.
Lal, R., 2005. Forest soils and carbon sequestration. For. Ecol. Manage. 220, 242–258. http://dx.doi.org/10.1016/j.foreco.2005.08.015.
Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91, 299–305. http://dx.doi.org/10.1890/08-2244.1.
Laliberté, E., Shipley, B., 2011. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R Package Version 1. pp. 0–11.
Lange, M., Eisenhauer, N., Sierra, C.A., Bessler, H., Engels, C., Griffiths, R.I., Mellado-Vázquez, P.G., Malik, A.A., Roy, J., Scheu, S., Steinbeiss, S., Thomson, B.C., Trumbore, S.E., Gleixner, G., 2015. Plant diversity increases soil microbial activity and soil carbon storage. Nat. Commun. 6, 6707. http://dx.doi.org/10.1038/ncomms7707.
Lefcheck, J.S., 2016. piecewiseSEM: piecewise structural equation modelling in r for ecology, evolution, and systematics. Methods Ecol. Evol. 7, 573–579. http://dx.doi.org/10.1111/2041-210X.12512.
Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, a., Hooper, D.U., Huston, M.a., Raffaelli, D., Schmid, B., Tilman, D., Wardle, D.a., 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294, 804–808. http://dx.doi.org/10.1126/science.1064088.
Luyssaert, S., Ciais, P., Piao, S.L., Schulze, E.-D., Jung, M., Zaehle, S., Schelhaas, M.J., Reichstein, M., Churkina, G., Papale, D., Abril, G., Beer, C., Grace, J., Loustau, D., Matteucci, G., Magnani, F., Nabuurs, G.J., Verbeeck, H., Sulkava, M., van der WERF, G.R., Janssens, I.a., 2010. The european carbon balance. Part 3: forests. Glob. Change Biol. 16, 1429–1450. http://dx.doi.org/10.1111/j.1365-2486.2009.02056.x.
Müller, J., Wende, B., Strobl, C., Eugster, M., Gallenberger, I., Floren, A., Steffan-Dewenter, I., Linsenmair, K.E., Weisser, W.W., Gossner, M.M., 2015. Forest management and regional tree composition drive the host preference of saproxylic beetle communities. J. Appl. Ecol. 52, 753–762. http://dx.doi.org/10.1111/1365-2664.12421.
Manzoni, S., Taylor, P., Richter, A., Porporato, A., Agren, G.I., 2012. Environmental and stoichiometric controls on microbial carbon-use efficiency in soils. New Phytol. 196, 79–91. http://dx.doi.org/10.1111/j.1469-8137.2012.04225.x.
Mason, N.W.H., Mouillot, D., Lee, W.G., Wilson, J.B., 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111, 112–118. http://dx.doi.org/10.1111/j.0030-1299.2005.13886.x.
Meier, C.L., Bowman, W.D., 2008. Links between plant litter chemistry, species diversity, and below-ground ecosystem function. Proc. Natl. Acad. Sci. U. S. A. 105, 19780–19785. http://dx.doi.org/10.1073/pnas.0805600105.
Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods Ecol. Evol. 4, 133–142. http://dx.doi.org/10.1111/j.2041-210x.2012.00261.x.
Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., Canadell, J.G., Khatiwala, S., Primeau, F., Hall, T., Quéré Le, C., Dixon, R.K., Kauppi, P.E., Kurz, W.A., Stinson, G., Rampley, G.J., Dymond, C.C., Neilson, E.T., Stinson, G., Birdsey, R., Pregitzer, K., Lucier, A., Kauppi, P.E., Pan, Y., Pan, Y., Birdsey, R., Hom, J., McCullough, K., Mantgem, P.J., van Breshears, D.D., Ciais, P., Fang, J., Chen, A., Peng, C., Zhao, S., Ci, L., Lewis, S.L., Phillips, O.L., Gloor, M., Lewis, S.L., Lloyd, J., Sitch, S., Mitchard, E.T.A., Laurance, W.F., Houghton, R.A., Friedlingstein, P., Tarnocai, C., Hooijer, A., Page, S.E., Rieley, J.O., Banks, C.J., McGuire, A.D., Goodale, C.L., Sarmiento, J.L., Schulze, E.D., Pacala, S.W., Phillips, O.L., Metsaranta, J.M., Kurz, W.A., Neilson, E.T., Stinson, G., Zhao, M., Running, S.W., Houghton, R.A., 2011. A large and persistent carbon sink in the worldés forests. Science 93. http://dx.doi.org/10.1126/science.1201609.
Paul, K.I., Polglase, P.J., Richards, G.P., 2003. Sensitivity analysis of predicted change in soil carbon following afforestation. Ecol. Modell. 164, 137–152. http://dx.doi.org/10.1016/S0304-3800(03)00027-9.
Pei, Z., Eichenberg, D., Bruelheide, H., Kröber, W., Kühn, P., Li, Y., von Oheimb, G., Purschke, O., Scholten, T., Buscot, F., Gutknecht, J.L.M., 2016. Soil and tree species traits both shape soil microbial communities during early growth of Chinese subtropical forests. Soil Biol. Biochem. 96, 180–190. http://dx.doi.org/10.1016/j.soilbio.2016.02.004.
Petchey, O.L., Gaston, K.J., 2002. Functional diversity (FD), species richness and community composition. Ecol. Lett. 5, 402–411. http://dx.doi.org/10.1046/j.1461-0248.2002.00339.x.
Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. Ecol. Lett. 9, 741–758. http://dx.doi.org/10.1111/j.1461-0248.2006.00924.x.
Poeplau, C., Don, A., 2013. Sensitivity of soil organic carbon stocks and fractions to different land-use changes across Europe. Geoderma 192, 189–201. http://dx.doi.org/10.1016/j.geoderma.2012.08.003.
Reich, P.B., Oleksyn, J., Modrzynski, J., Mrozinski, P., Hobbie, S.E., Eissenstat, D.M., Chorover, J., Chadwick, O.A., Hale, C.M., Tjoelker, M.G., 2005. Linking litter calcium, earthworms and soil properties: a common garden test with 14 tree species. Ecol. Lett. 8, 811–818. http://dx.doi.org/10.1111/j.1461-0248.2005.00779.x.
Reich, P.B., 2014. The world-wide fast-slow plant economics spectrum: a traits manifesto. J. Ecol. 102, 275–301. http://dx.doi.org/10.1111/1365-2745.12211.
Scherer-Lorenzen, M., Luis Bonilla, J., Potvin, C., 2007a. Tree species richness affects litter production and decomposition rates in a tropical biodiversity experiment. Oikos 116, 2108–2124. http://dx.doi.org/10.1111/j.2007.0030-1299.16065.x.
Scherer-Lorenzen, M., Schulze, E., Don, A., Schumacher, J., Weller, E., 2007b. Exploring the functional significance of forest diversity: a new long-term experiment with temperate tree species (BIOTREE). Perspect. Plant Ecol. Evol. Syst. 9, 53–70. http://dx.doi.org/10.1016/j.ppees.2007.08.002.
Schimel, D.S., House, J.I., Hibbard, K.A., Bousquet, P., Ciais, P., Peylin, P., Braswell, B.H., Apps, M.J., Baker, D., Bondeau, A., Canadell, J., Churkina, G., Cramer, W., Denning, A.S., Field, C.B., Friedlingstein, P., Goodale, C., Heimann, M., Houghton, R.A., Melillo, J.M., Murdiyarso, D., Noble, I., Pacala, S.W., Prentice, I.C., Raupach, M.R., Rayner, P.J., Scholes, R.J., Steffen, W.L., Wirth, C., Moore, B., Murdiyarso, D., Noble, I., Pacala, S.W., Prentice, I.C., Raupach, M.R., Rayner, P.J., Scholes, R.J., Steffen, W.L., Wirth, C., 2001. Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. Nature 414, 169–172. http://dx.doi.org/10.1038/35102500.
Schrumpf, M., Schulze, E.D., Kaiser, K., Schumacher, J., 2011. How accurately can soil organic carbon stocks and stock changes be quantified by soil inventories? Biogeosciences 8, 1193–1212. http://dx.doi.org/10.5194/bg-8-1193-2011.
Sinsabaugh, R.L., Carreiro, M.M., Repert, D.A., 2002. Allocation of extracellular enzymatic activity in relation to litter composition, N deposition, and mass loss. Biogeochemistry 60, 1–24. http://dx.doi.org/10.1023/A:1016541114786.
Sinsabaugh, R.L., Lauber, C.L., Weintraub, M.N., Ahmed, B., Allison, S.D., Crenshaw, C., Contosta, A.R., Cusack, D., Frey, S., Gallo, M.E., Gartner, T.B., Hobbie, S.E., Holland, K., Keeler, B.L., Powers, J.S., Stursova, M., Takacs-Vesbach, C., Waldrop, M.P., Wallenstein, M.D., Zak, D.R., Zeglin, L.H., 2008. Stoichiometry of soil enzyme activity at global scale. Ecol. Lett. 11, 1252–1264. http://dx.doi.org/10.1111/j.1461-0248.2008.01245.x.
Sinsabaugh, R.L., Belnap, J., Findlay, S.G., Shah, J.J.F., Hill, B.H., Kuehn, K.a., Kuske, C.R., Litvak, M.E., Martinez, N.G., Moorhead, D.L., Warnock, D.D., 2014. Extracellular enzyme kinetics scale with resource availability. Biogeochemistry 121, 287–304. http://dx.doi.org/10.1007/s10533-014-0030-y.
Smets, W., Leff, J.W., Bradford, M.A., McCulley, R.L., Lebeer, S., Fierer, N., 2016. A method for simultaneous measurement of soil bacterial abundances and community composition via 16S rRNA gene sequencing. Soil Biol. Biochem. 96, 145–151. http://dx.doi.org/10.1016/j.soilbio.2016.02.003.
Smith, P., 2004. How long before a change in soil organic carbon can be detected? Glob. Change Biol. 10, 1878–1883. http://dx.doi.org/10.1111/j.1365-2486.2004.00854.x.
Soliveres, S., van der Plas, F., Manning, P., Prati, D., Gossner, M.M., Renner, S.C., Alt, F., Arndt, H., Baumgartner, V., Binkenstein, J., Birkhofer, K., Blaser, S., Blüthgen, N., Boch, S., Böhm, S., Börschig, C., Buscot, F., Diekötter, T., Heinze, J., Hölzel, N., Jung, K., Klaus, V.H., Kleinebecker, T., Klemmer, S., Krauss, J., Lange, M., Morris, E.K., Müller, J., Oelmann, Y., Overmann, J., Pašalić, E., Rillig, M.C., Schaefer, H.M., Schloter, M., Schmitt, B., Schöning, I., Schrumpf, M., Sikorski, J., Socher, S.A., Solly, E.F., Sonnemann, I., Sorkau, E., Steckel, J., Steffan-Dewenter, I., Stempfhuber, B., Tschapka, M., Türke, M., Venter, P.C., Weiner, C.N., Weisser, W.W., Werner, M., Westphal, C., Wilcke, W., Wolters, V., Wubet, T., Wurst, S., Fischer, M., Allan, E., 2016. Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. Nature 536, 456–459. http://dx.doi.org/10.1038/nature19092.
Stark, H., Nothdurft, A., Block, J., Bauhus, J., 2015. Forest restoration with Betula ssp. and Populus ssp. nurse crops increases productivity and soil fertility. For. Ecol. Manage. 339, 57–70. http://dx.doi.org/10.1016/j.foreco.2014.12.003.
Steinauer, K., Tilman, D., Wragg, P.D., Cesarz, S., Cowles, J.M., Pritsch, K., Reich, P.B., Weisser, W.W., Eisenhauer, N., 2015. Plant diversity effects on soil microbial functions and enzymes are stronger than warming in a grassland experiment. Ecology 96,

99–112. http://dx.doi.org/10.1890/14-0088.1.
Tilman, D., 2001. Functional diversity. In: Levin, S.A. (Ed.), Encyclopedia of Biodiversity. Academic Press, pp. 109–120.
Toor, G.S., Condron, L.M., Di, H.J., Cameron, K.C., Cade-Menun, B.J., 2003. Characterization of organic phosphorus in leachate from a grassland soil. Soil Biol. Biochem. 35, 1317–1323. http://dx.doi.org/10.1016/S0038-0717(03)00202-5.
Turner, B.L., McKelvie, I.D., Haygarth, P.M., 2002. Characterisation of water-extractable soil organic phosphorus by phosphatase hydrolysis. Soil Biol. Biochem. 34, 27–35. http://dx.doi.org/10.1016/S0038-0717(01)00144-4.
Vesterdal, L., Schmidt, I.K., Callesen, I., Nilsson, L.O., Gundersen, P., 2008. Carbon and nitrogen in forest floor and mineral soil under six common European tree species. For. Ecol. Manage. 255, 35–48. http://dx.doi.org/10.1016/j.foreco.2007.08.015.
Vesterdal, L., Elberling, B., Christiansen, J.R., Callesen, I., Schmidt, I.K., 2012. Soil respiration and rates of soil carbon turnover differ among six common European tree species. For. Ecol. Manage. 264, 185–196. http://dx.doi.org/10.1016/j.foreco.2011.10.009.
Vesterdal, L., Clarke, N., Sigurdsson, B.D., Gundersen, P., 2013. Do tree species influence soil carbon stocks in temperate and boreal forests? For. Ecol. Manage. 309, 4–18. http://dx.doi.org/10.1016/j.foreco.2013.01.017.
Vilà, M., Vayreda, J., Gracia, C., Ibáñez, J., 2004. Biodiversity correlates with regional patterns of forest litter pools. Oecologia 139, 641–646. http://dx.doi.org/10.1007/s00442-004-1546-y.
Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New dimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89, 2290–2301. http://dx.doi.org/10.1890/07-1206.1.