

# Functional diversity and identity effects on forest soil carbon stocks depend on climate contexts

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## Abstract

Soil carbon plays an important role in mediating global climate change and securing food production. Despite rapid declines in plant diversity worldwide, uncertainties remain concerning the relationships between tree diversity and soil carbon stock in natural forests, as well as the climatic factors that drive their directions and magnitudes. Using Canada's National Forest Inventory data, we tested the relationships between soil carbon stocks to tree functional diversity and identity, and how these relationships varied with stand age and climate gradients in the organic horizon, mineral horizon and entire soil profile. We found that the effects of functional diversity on soil carbon stocks were highly climate-dependent, shifting from negative in warm or moist climates to positive or null in cold and dry climates. In addition, tree species with acquisitive traits, such as high specific leaf area, leaf nitrogen content and phosphorus content, increased mineral soil carbon stocks in warmer sites, but decreased those in colder sites. Our results suggest that tree diversity effects on soil carbon are strongly dependent on climate context and promoting high functional diversity is important to increase soil carbon stocks of colder and drier sites in boreal and temperate forests.

## Introduction

Terrestrial soils store at least three times as much carbon (C) as found in either the atmosphere or in living plants (IPCC 2014). The storage of C in soils plays an important role in controlling soil fertility and agricultural production, and mediating global climate change (Lal 2004). Although the maximum soil C sink capacity is mainly determined by intrinsic abiotic soil properties (e.g. soil texture, Hassink 1997), soil C stock dynamics are also driven by biota and their interactions with climate (De Deyn et al. 2008; Chen et al. 2020). Biodiversity loss across multi-taxa is at an alarming rate globally (Butchart et al. 2010), with strong negative impacts on ecosystem functions and services (Cardinale et al. 2012). A meta-analysis of experimental studies, primarily from grasslands, shows the positive effects of plant diversity on soil C (Chen et al. 2020). Evidence is mounting that a functional trait-based approach (e.g., functional diversity and functional identity) will help to disentangle the underlying mechanisms of biodiversity-ecosystem functioning relationships (see Cornwell et al. 2008; De Deyn et al. 2008; Paquette & Messier 2011). However, previous regional studies have reported negligible (Alberti et al. 2017) or even negative (Conti & Diaz 2013; Carol Adair et al. 2018) responses of soil C stocks to tree functional diversity. It remains unclear whether the divergent findings result from context-dependent responses of ecosystem functioning to biodiversity (Kardol et al. 2018; Hisano & Chen 2020). Understanding the relationships between functional diversity and functional identity with soil C stocks at a large spatial scale (beyond regional), as well as the relative

contributions of climatic conditions in shaping these relationships, represents an important step forward to improve our ability to aid developing globally applicable strategies to meet international standards for C sequestration and mitigate the impacts of global climate change (Cardinale et al. 2012; Hisano et al. 2018).

Soil C stocks reflect the net balance between soil C inputs (e.g., plant litter production and root exudates) and losses (e.g., microbial decomposition and leaching of dissolved organic C) (Amundson 2001). Both recalcitrant plant litter components and the accumulation of microbial necromass during the degradation of litter contribute to the increase of soil C by promoting aggregate formation and protection within the mineral soil matrix by physiochemical processes (Cotrufo et al. 2015; Liang et al. 2017). It may be postulated that more diverse forests will have higher soil C stocks than less diverse forest as enhanced niche differentiation and total resource capture associated with high functional diversity may increase litterfall and root inputs into the soil due to increased tree production (Zhang et al. 2012). However, increased quantity of litter inputs with higher tree functional diversity may cause an increase in soil C loss *via* the ‘priming effect’, i.e. extra decomposition of existing, more stable soil C when microbes are stimulated by the energy released from the decomposition of fresh organic matter, which counters or even reverses the potential positive diversity effect of overstorey trees on soil C stocks (Fontaine et al. 2007; Chen & Chen 2018). Increased litter diversity in diverse forests can also increase litter decomposition due to more abundant and diverse soil decomposers (Meier & Bowman 2008; Chen et al. 2019).

Beyond functional diversity, the functional identity of trees can exert a strong influence on soil C stocks via both litter inputs and decomposition (De Deyn et al. 2008; Carol Adair et al. 2018). On the one hand, functional traits associated with large biomass stock and fast growth rate (resource acquisitive and exploitative traits, e.g. high leaf nitrogen concentration, leaf phosphorus concentration and specific leaf area, maximum tree height and low wood density, see Wright et al. 2004; Diaz et al. 2016) are expected to contribute to soil C pools through a large amount of plant litter inputs into soils (De Deyn et al. 2008). Despite higher decomposition rates, high-quality litter associated with resource acquisitive traits can be utilized more efficiently by microbes, resulting in higher accumulation of microbial necromass, which is the main source of physiochemically stabilized soil C (Cotrufo et al. 2013; Liang et al. 2019). On the other hand, functional traits associated with slow growth rate (resource conservative traits) are expected to contribute to soil C pools through the input of low-quality (recalcitrant) plant litter associated with slow decomposition rates (De Deyn et al. 2008; Faucon et al. 2017).

The response of soil C to tree functional diversity and functional identity may also depend on abiotic factors because of contrasting mechanisms (inputs vs. decomposition) associated with tree diversity. Responses of soil C stocks to tree diversity may fluctuate with diverse abiotic conditions, as the positive diversity effects on productivity and the fate of subsequent C inputs may be strengthened in environments unfavourable for growth, since abiotic facilitation can increase with environmental stress (Maestre et al. 2009). For example, at large spatial scales, the positive effects of tree diversity on productivity are observed to be stronger in the drier (Ratcliffe et al. 2017; Garcia-Palacios et al. 2018) or colder (Paquette & Messier 2011; Mori 2018) climates than under more humid, warmer conditions. However, it is also possible that increasing temperature and water availability would accelerate the positive effects of functional diversity on plant productivity and associated C inputs due to more resources available for partitioning in benign environments (Hisano & Chen 2020). Additionally, functional identity effects on soil C stocks may also depend on abiotic conditions (De Deyn et al. 2008). For example, the relationship between resource acquisitive traits and plant productivity was more positive in drier, warmer sites, while negative in wetter, colder sites across Canada’s forests (Hisano & Chen 2020).

Here we used nationwide forest inventory data, a network of 589 permanent sample plots covering much of Canada’s forested landmass (Fig. 1), to investigate how the effects of functional diversity and functional identity on soil C stocks may depend on climate gradients in natural forests. We test the following hypotheses: (i) functional diversity increases soil C stocks due to higher C inputs, and this diversity effect will be stronger in drier/colder sites than humid/warmer sites; (ii) the directions and magnitudes of functional identity effects on soil C stocks are dependent on climates as observed for productivity (Hisano & Chen 2020), with

communities characterized by high resource acquisition having higher soil C stocks in drier/warmer sites, and communities characterized by high resource conservation having higher soil C stocks in wetter/colder sites.

## Method

### Study area and available data

In this study, we used the Canadian National Forest Inventory (NFI) database (<https://nfi.nfis.org>), a network of 589 permanent sample plots covering much of Canada’s forested landmass (Fig. 1). All plots were measured by Canadian provincial authorities between 2000 and 2006 using the same standard ground sampling guidelines (Canadian Forest Inventory Committee, 2004). Only plots located in unmanaged forest stands, with complete data coverage of forest canopy composition, stand age, and soil C stocks were selected. In total, 589 plots (43°48’–68°12’ N, 53°24’–139°12’ W), covering the entire range of forest ecosystems across Canada and wide climatic gradients (Fig. 1). Mean annual temperature and mean annual precipitation across plots varied between -12.2 °C and 9.0 °C, and 213 mm and 2,879 mm, respectively. Elevation ranged between 4 m and 1,940 m above sea level.

The standard plot design consisted of several sub-plots associated with specific vegetation layers, and a soil pit survey (Fig. S1). The vegetation inventory approach has been described in detail by Zhang et al. (2017). The canopy tree layer (all tree stems [?] 9.0 cm in diameter at breast height (DBH, 1.3m high)) and total canopy tree species were inventoried within a “large tree plot”, which varied in size from 125 to 500 m<sup>2</sup>, with the majority of plots being 400 m<sup>2</sup> with a radius of 11.28 m (Table S1). All canopy trees within the large tree plot were numbered, tagged, and measured by height and DBH for estimation of above-ground biomass. Biomass estimates of trees were calculated using a set of species-specific provincial allometric biomass equations (Boudewyn et al. 2007; Zhang et al. 2017).

Both organic and mineral horizon soils were sampled from each standard plot. Four 1 m<sup>2</sup> “microplots” were established outside of the large tree plot (but within a 15 m radius) (Fig. S1). Organic horizon soil samples, which include the litter, fibric, and humus horizons, and contain > 17% organic C by mass (British Columbia Ministry of Forests and Range and British Columbia Ministry of Environment 2010), were collected from each of the four microplots after all of the live vegetation had been removed. No mineral soil was included in the organic horizon soil sample. Mineral soil horizon samples, containing < 17% organic C by mass, were collected from an excavated soil pit in each NFI ground plot established outside of the large tree plot (but within a 25 m radius), that represented the overall conditions inside the plot, using a standard methodology (Gillis et al. 2005). When applicable, the minimum depth of the soil pit was dug to 60 cm in the mineral soil or 100 cm in organic soils. If necessary, an auger was used to probe deeper. For each soil sample, soil C concentration and bulk density were measured both in the organic horizon and mineral soil horizons, recorded by depth class, and analyzed in the laboratory according to standard protocols (Gillis et al. 2005). Soil C stock was calculated by multiplying soil bulk density, soil layer depth, and soil C concentration in both the organic horizon and mineral soil horizon. Total soil C was the sum of the C mass measured in the organic and mineral soil horizon C stocks.

### Explanatory variables

We used five key functional traits that relate with growth and species competitive abilities (Reich 2014; Kunstler et al. 2016; Carol Adair et al. 2018): ‘leaf nitrogen content per leaf dry mass’ ( $N_{\text{mass}}$ , mg g<sup>-1</sup>), ‘leaf phosphorus content per leaf dry mass’ ( $P_{\text{mass}}$ , mg g<sup>-1</sup>), ‘specific leaf area’ (SLA, mm<sup>2</sup> mg<sup>-1</sup>; i.e., leaf area per leaf dry mass), ‘wood density’ (WD, g cm<sup>-3</sup>), and maximum height (MH, m) (Table S2). We obtained the  $N_{\text{mass}}$ ,  $P_{\text{mass}}$ , SLA, WD, and MH data for each tree species from the TRY Plant Trait Database (Kattge et al. 2011). Functional diversity ( $FD_{\text{is}}$ ) was calculated as functional dispersion, which

is the mean distance of each species to the centroid of all species in functional trait space, based on all five traits together (Laliberte & Legendre 2010). Functional identity was calculated as the community-weighted mean of trait values (CWM), weighted by basal area, based on each trait in each plot. Similar to previous studies (Ruiz-Benito et al. 2017), we performed a principal component analysis (PCA) using CWMs of the five traits to obtain a comprehensive functional identity to represent each trait as these values were highly correlated with one another (e.g.,  $CWM_{N_{mass}}$  with  $CWM_{P_{mass}}$  ( $r = 0.83$ ),  $CWM_{SLA}$  ( $r = 0.83$ ),  $CWM_{WD}$  ( $r = 0.31$ );  $CWM_{MH}$  with  $CWM_{P_{mass}}$  ( $r = 0.19$ )) (Fig. S2). We employed the first axis ( $CWM_{PC1}$ , which explained 55% of variation) and the second axis ( $CWM_{PC2}$ , 23% of the variation) of the PCA as variables of functional identity because  $CWM_{PC1}$  collectively represents traits associated with resource acquisition (Wright et al. 2004; Diaz et al. 2016), being strongly related with higher  $CWM_{SLA}$ ,  $CWM_{N_{mass}}$ ,  $CWM_{P_{mass}}$  and  $CWM_{WD}$ , while  $CWM_{PC2}$  collectively represents traits associated with lower resource exploitation, being strongly associated with lower  $CWM_{MH}$  (Diaz et al. 2016) (Fig. S2). The calculation of  $FD_{is}$  and CWM was conducted using the *FD* package (Laliberte & Legendre 2010) in the R statistical software (R Core Team 2019).

To account for the influence of the physical environment and other stand-level endogenous variables on soil C stocks, as well as their relationship with species diversity, and functional diversity and identity, we included climate (long-term average of mean annual temperature (degC) and climate moisture index (cm)), forest stand age (years), and site soil drainage classes in our analyses. The long-term average climate data for each plot were derived using the BioSIM software (<https://cfs.nrcan.gc.ca/projects/133>), which generates long-term (1951–2010), scale-free climate data from geographic coordinates (latitude, longitude and elevation) (Regniere & Saint-Amant 2008). Annual climate moisture index (CMI) was calculated as mean annual precipitation minus potential evapotranspiration (Hogg et al. 2017). Stand age (SA) for each plot was determined according to the last stand-replacing fire date, or by coring three dominant/co-dominant trees of each tree species inside or outside the plot at the time of plot establishment. With coring, SA was derived as the average ring count from tree species samples with the oldest age used as a conservative, minimum estimate of stand age (Senici et al. 2010). Soil drainage class (SD) was determined by field surveyors during the soil pit excavation, as a measure of local site conditions. SD classification considers multiple factors, including: topographic position, organic layer depth, soil permeability, soil texture, soil thickness and water table depth (British Columbia Ministry of Forests and Range and British Columbia Ministry of Environment 2010). Seven classes were employed, from 1 to 7, representing very rapidly, rapidly, well, moderately well, imperfectly, poorly and very poorly drained soils, respectively.

## Statistical analyses

Soil organic horizon C stock, mineral horizon C stock, and total soil C stock were considered our response variables and analyzed separately. To explore the relationships between functional diversity and identity with soil C stocks, and how these relationships varied across environmental gradients and stand age after accounting for the effect of soil drainage, we used the following linear model:

$$SC = \beta_0 + \beta_1 \cdot \log(MAT + 10) + \beta_2 \cdot CMI + \beta_3 \cdot SA + \beta_4 \cdot FD_{is} + \beta_5 \cdot CWM_{PC1} + \beta_6 \cdot \Omega_{M_{II}^2} + \beta_7 \cdot \log(MAT + 10) \times FD_{is} + \beta_8 \cdot \log(MAT + 10) \times CWM_{PC1} + \beta_9 \cdot \log(MAT + 10) \times CWM_{PC2} + B_{10} \cdot CMI \times FD_{is} + \beta_{11} \cdot CMI \times CWM_{PC1} + \beta_{12} \cdot CMI \times CWM_{PC2} + B_{13} \cdot SA \times FD_{is} + \beta_{14} \cdot SA \times CWM_{PC1} + \beta_{15} \cdot SA \times CWM_{PC2} + \beta_{16} \cdot SD + e \quad (1)$$

where  $\beta_i$  and  $e$  are the coefficients to be estimated and sampling error, respectively.  $FD_{is}$ ,  $CWM_{PC1}$  and  $CWM_{PC2}$  were functional diversity and CWM of the first and second dimensions of functional trait variation. MAT, CMI, SA and SD were the values of the long-term average of mean annual temperature, the long-term average of climate moisture index, stand age and soil drainage class. Based on AIC, the MAT was transformed by natural logarithmic functions ( $\log(MAT+10)$ ), as the minimum MAT across the study area was  $-9\text{ }^\circ\text{C}$ .

All the explanatory variables were centered and scaled (mean = 0, SD = 1) before the analysis to permit

an easier comparison of the resulting model coefficients. To prevent overfitting (Johnson & Omland 2004), we selected the most parsimonious model based on the lowest AIC among all alternatives by using the ‘*dredge*’ function of the *muMIn* package (Barton 2018), for the organic layer, mineral soil and the whole soil profile, respectively (Table 1). Collinearity among explanatory variables was tested by VIF; no evidence of multicollinearity was found in the most parsimonious models. To control for potential influences of variation in plot size (Chisholm et al. 2013), we also included plot size (PS) as a covariate, which yielded qualitatively similar estimates and trends as the most parsimonious models (Table S3). Thus, below we report results for the most parsimonious models. As an alternative to functional diversity, we also investigated how relationships between soil C stocks and species diversity were associated with the environmental context, by replacing functional diversity ( $FD_{is}$ ) in the most parsimonious models with species richness ( $S$ ). Across the study area, we found qualitatively similar estimates and trends for species richness and functional diversity (Table S4, Fig. S3).

To illustrate, graphically, how tree functional diversity and functional identity affected soil C stocks, as influenced by CMI and MAT, we used the method described by Cohen et al. (2013) to estimate tree functional diversity and functional identity effects at CMI of 15, 50, 100, 200 cm, and MAT of -5, 0, 5, 10°C, respectively. All statistical analyses were performed in R 3.6.1 (R Core Team 2019).

## Results

Across all study plots, soil C stocks averaged 41.2 Mg·ha<sup>-1</sup> in the organic horizon, 120.1 Mg·ha<sup>-1</sup> in the mineral horizon and 158.2 Mg·ha<sup>-1</sup> for the entire soil profile (Table 1). Soil C stocks were strongly related to the climate variables (i.e., CMI and MAT) and soil drainage class (Table 1). Soil C stocks increased with both CMI (herein referred to as water availability) and soil drainage class significantly ( $P < 0.05$ ) and/or marginally ( $P < 0.10$ ), while temperature had a greater negative effect on soil C stocks in all soil horizons, as indicated by the greater sums of squares for mean annual temperature (Table 1, Fig. 2). With increasing stand age, organic soil horizon C stocks increased, but stand age was excluded in the most parsimonious models for the mineral soil horizon and the entire profile C stocks (Table 1, Fig. S4).

The effects of functional diversity and functional identity on soil C stocks were dependent on climate, as indicated by significant interactions between functional diversity and functional identity with climate variables (Table 1). The effects of  $FD_{is}$  on the organic soil horizon C stocks were not significant, on average, but shifted from positive in drier sites to negative in wetter sites (Fig. 3A). Mineral soil horizon and whole profile soil C stocks decreased with  $FD_{is}$  on average, with more pronounced decreases in warmer and wetter sites, respectively (Fig. 3B, C). Soil C stocks did not change with the values of resource acquisition traits ( $CWM_{PC1}$ , positively related with  $CWM_{SLA}$ ,  $CWM_{Nmass}$ ,  $CWM_{Pmass}$  and  $CWM_{WD}$ ) on average across all soil horizons, but the effects of  $CWM_{PC1}$  on mineral horizon soil C stocks changed with temperature, shifting from negative in colder sites to positive in warmer sites (Fig. 3A, B, C). Organic horizon soil C stocks did not change with  $CWM_{PC2}$  (negatively related to  $CWM_{MH}$ ) on average, but significantly decreased with it in wetter climates (Fig. 4D). Mineral horizon and whole profile soil C stocks decreased with  $CWM_{PC2}$  on average, and the relationships between mineral horizon soil C stocks with  $CWM_{PC2}$  shifted from negative in drier sites to positive in wetter sites (Fig. 4E, F).

## Discussion

Our study provides the first large scale evidence that the relationship between soil C stocks and tree functional diversity and functional identity is dependent on climate context. Our results revealed several new insights into the ongoing debate regarding biodiversity-ecosystem functioning relationships. First, our results indicate that the effects of functional diversity on soil C stock became more positive (or less negative)

with decreasing temperature or water availability (i.e., increasing environmental harshness), which corroborates those relationships between plant productivity and diversity along climate gradients (Paquette & Messier 2011; Mori 2018) and, to some extent, extends the debate of the stress gradient hypothesis beyond biodiversity-productivity relationships (Maestre et al. 2009). Second, tree species with acquisitive traits increased mineral soil C stocks in warmer sites, but decreased those in colder sites. Furthermore, different responses of soil C stocks to tree functional diversity and functional identity were observed between the organic and mineral soil horizons, indicating tree functional diversity and functional identity may affect not only soil C stocks but also soil C distribution across soil layers.

Although functional diversity decreased total soil C stocks in forests across Canada, especially in the mineral soil horizon, we showed that the effects of functional diversity on the soil C stocks were dependent on climate. The effects of functional diversity on organic horizon soil C stocks shifted from positive in drier sites to negative in wetter sites. This decline of organic horizon soil C stocks with functional diversity in wetter conditions might have been the result of the positive effects of litter functional diversity on litter decomposition (Meier & Bowman 2008), which decreased organic horizon C stocks via mineralization by soil fauna and microbes, as well as via leaching of dissolved organic C (Mueller et al. 2015). The positive effects of litter functional diversity on litter decomposition might be higher in wetter sites due to increases of abundance and diversity of decomposers with water availability (Phillips et al. 2019; van den Hoogen et al. 2019), which provide a larger pool of decomposer species for niche partitioning. Functional diversity decreased mineral horizon soil C stocks on average, but decreasing temperature shifted this negative functional diversity effect to null. While the mechanism is unclear, the negative functional diversity effects on soil C stocks of the mineral soil horizon might have been attributable to the rhizosphere priming effect, which is stronger in higher temperatures (Zhu & Cheng 2011).

Our results also showed that the relationships between soil C stocks and functional identity ( $CWM_{PC1}$ ,  $CWM_{PC2}$ ) were also dependent on climate conditions. Tree communities with higher values of resource acquisition identity ( $CWM_{PC1}$ ) showed higher C stocks in the mineral horizon than those with lower  $CWM_{PC1}$  in warmer sites, whereas colder sites had opposite trends. Moreover, the relationship between tree maximum height and soil C stocks in the mineral horizon was more positive in drier sites, while it was rather negative in wetter sites. These temperature- and water availability-dependent responses in soil mineral horizon C stocks were consistent with those of tree productivity reported in a previous study based on the forest inventory network across Canada (Hisano & Chen 2020). Together, these trends emphasize the essential role of tree litter inputs in the accumulation of soil C stocks in the mineral soil horizon (Cotrufo et al. 2015).

However, we found that the responses of soil C stocks to functional identity differ among soil horizons. The relationship between tree maximum height and soil C stocks of the organic horizon was more negative in drier sites, while it was rather positive in wetter sites. This might be partly attributable to different regulatory mechanisms for C accumulation in organic and mineral soil horizons (Vesterdal et al. 2013). Contrary to mineral soils, whose C stocks were less determined by C output processes (decomposition), due to greater stability and less accessibility to microbes and exoenzymes, the main regulatory mechanism of C accumulation in the organic soil horizon is C losses (Hobbie et al. 2007). Larger tree species, which are generally associated with low wood strength, would produce more easily decomposable wood litter (Pietsch et al. 2014), resulting in smaller organic horizon soil C stocks (Vesterdal et al. 2008), and this effect may be stronger in wetter sites due to the higher abundance and diversity of decomposers (Phillips et al. 2019; van den Hoogen et al. 2019).

In conclusion, our analysis demonstrates that higher tree diversity is not always of benefit to C stocks. Importantly, tree functional diversity and functional identity effects on soil C stocks are highly climate-dependent. We find that the effects of tree functional diversity on soil C stocks increase under lower water availability and temperatures, which indicates that promoting high functional diversity is important to increase soil C stocks of colder and drier sites in boreal and temperate forests. Further, our results show different responses of soil C stocks to functional diversity and functional identity between the organic and mineral soil horizons, which highlights the need to incorporate the distribution of C stocks in projecting

diversity loss on soil C stocks.

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**Table 1.** Effects of tree functional diversity (*FD*), functional identity (*CWM*), stand age (*SA*), soil drainage, long-term averages of mean annual temperature (MAT) and climate moisture index (CMI) on the soil C stocks.

Fixed effects	Coefficients	Sum
<b>Organic horizon soil C (<math>R^2 = 0.230</math>, AIC = 5609)</b> (Intercept)	<b>Organic horizon soil C (<math>R^2 = 0.230</math>, AIC = 5609)</b> 41.2	<b>Org</b> 898.

Fixed effects	Coefficients	Sum
<i>CMI</i>	7.8	11.3
$\ln(\text{MAT}+10)$	-10.0	35.0
<i>SA</i>	6.1	14.2
<i>Soil drainage</i>	7.5	27.8
$FD_{is}$	1.7	1.3
$CWM_{PC1}$	-1.4	0.9
$CWM_{PC2}$	1.3	0.9
$CMI \times FD_{is}$	-5.3	6.9
$CMI \times CWM_{PC2}$	-5.5	13.8
<b>Mineral horizon soil C (<math>R^2 = 0.110</math>, AIC = 4992)</b>	<b>Mineral horizon soil C (<math>R^2 = 0.110</math>, AIC = 4992)</b>	<b>Min</b>
(Intercept)	120.1	5039
<i>CMI</i>	20.4	66.1
$\ln(\text{MAT}+10)$	-21.8	105.
<i>Soil drainage</i>	8.8	28.3
$FD_{is}$	-11.7	41.0
$CWM_{PC1}$	1.2	0.4
$CWM_{PC2}$	-17.7	118.
$\ln(\text{MAT}+10) \times CWM_{PC1}$	25.7	105.
$CMI \times CWM_{PC2}$	11.6	49.5
$\ln(\text{MAT}+10) \times FD_{is}$	-14.5	51.9
<b>Entire soil horizon (<math>R^2 = 0.159</math>, AIC = 4759)</b>	<b>Entire soil horizon (<math>R^2 = 0.159</math>, AIC = 4759)</b>	<b>Ent</b>
(Intercept)	158.2	8504
<i>CMI</i>	25.7	156.
$\ln(\text{MAT}+10)$	-29.2	195.
<i>Soil drainage</i>	18.6	119.
$FD_{is}$	-13.7	52.4
$CWM_{PC1}$	1.1	0.3
$CWM_{PC2}$	-16.5	100.
$\ln(\text{MAT}+10) \times CWM_{PC1}$	13.0	30.3
$CMI \times FD_{is}$	-16.5	49.9

$P$  and  $R^2$  are the significance of the model and the variance explained by the model, respectively.  $P < 0.05$  are bolded.

Figure captions

**Figure 1. The distributions of 589 national forest inventory ground plots with climatic information.** A, long-term averages of mean annual temperature (MAT); B, long-term averages of climate moisture index (CMI).

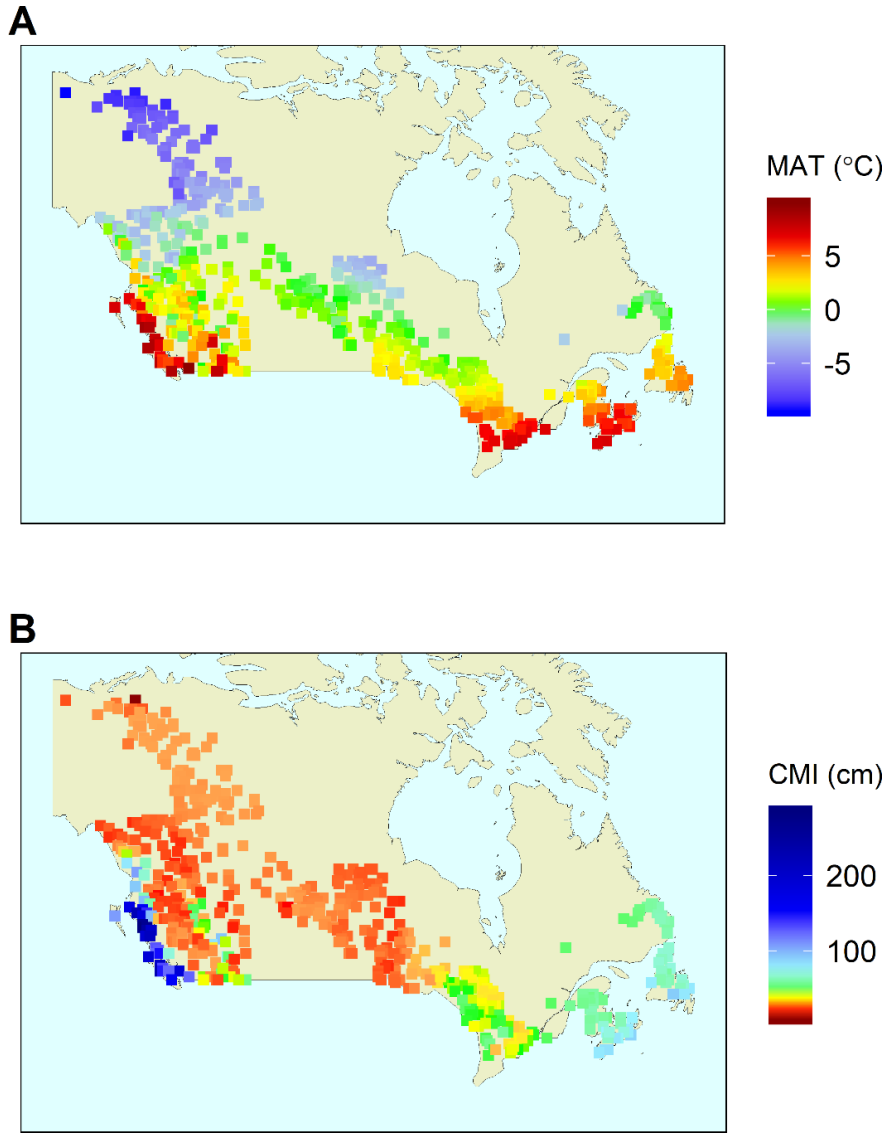
**Figure 2. The soil C stocks in relation to mean annual temperature, climate moisture index and soil drainage after accounting for the effects of all other explanatory variables in the model.** A, soil organic horizon; B, soil mineral horizon; C, entire soil horizon. The black line and grey shaded areas represent the fitted regression and its bootstrapped 95% confidence intervals. Points represent the values predicted by partial regressions for each explanatory variable. The significance (P) is presented for each term tested with solid and dashed lines respectively for significant and insignificant effects at  $\alpha = 0.05$ . CMI: the long-term average of climate moisture index (for each plot); MAT: the long-term average of mean annual temperature (for each plot).

**Figure 3. Abiotic context-dependent response of soil C stocks to functional diversity ( $FD_{is}$ ).**

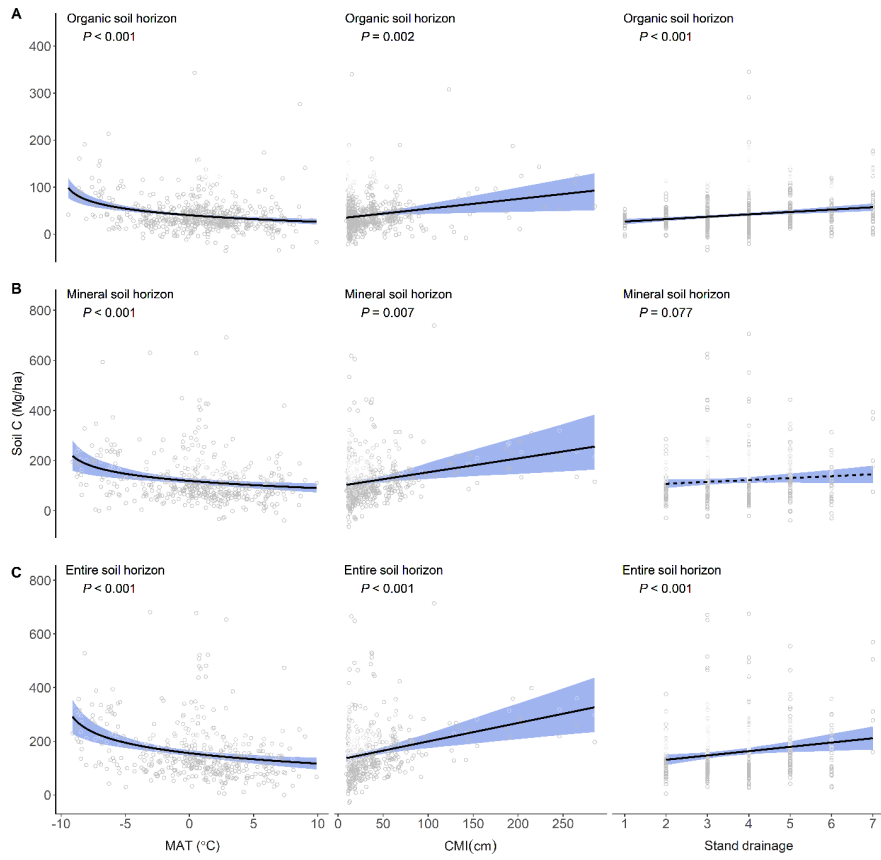
A, soil organic horizon; B, soil mineral horizon; C, entire soil horizon. Black and coloured lines represent the average and MAT- and CMI-specific responses, respectively, with their bootstrapped 95% confidence intervals shaded. Points represent the values predicted by partial regressions for each explanatory variable. The colors of the points indicate the different MAT or CMI of corresponding observations. The significance (P) is presented for each term tested with solid and dashed lines respectively for significant and insignificant effects at  $\alpha = 0.05$ . CMI: the long-term average of climate moisture index (for each plot); MAT: the long-term average of mean annual temperature (for each plot).

**Figure 4. Abiotic context-dependent response of soil C stocks to functional identity (community-weighted mean,  $CWM_{PC1}$ ,  $CWM_{PC2}$ ).** A, response of soil C stocks to  $CWM_{PC1}$  in the organic horizon; B, CMI-dependent response of soil C stocks to  $CWM_{PC2}$  in the organic horizon; C, MAT-dependent response of soil C stocks to  $CWM_{PC1}$  in the mineral horizon; D, CMI-dependent response of soil C stocks to  $CWM_{PC2}$  in the mineral horizon; E, MAT-dependent response of soil C stocks to  $CWM_{PC1}$  in the entire soil horizon; F, response of soil C stocks to  $CWM_{PC2}$  in the entire soil horizon. Black and coloured lines represent the average and MAT- and CMI-specific responses, respectively, with their bootstrapped 95% confidence intervals shaded. Points represent the values predicted by partial regressions for each explanatory variable. The colors of the points indicate the different MAT or CMI of corresponding observations. The significance (P) is presented for each term tested with solid and dashed lines respectively for significant and insignificant effects at  $\alpha = 0.05$ . CMI: the long-term average of climate moisture index (for each plot); MAT: the long-term average of mean annual temperature (for each plot).

**Fig 1**



**Fig 2**



**Fig 3**

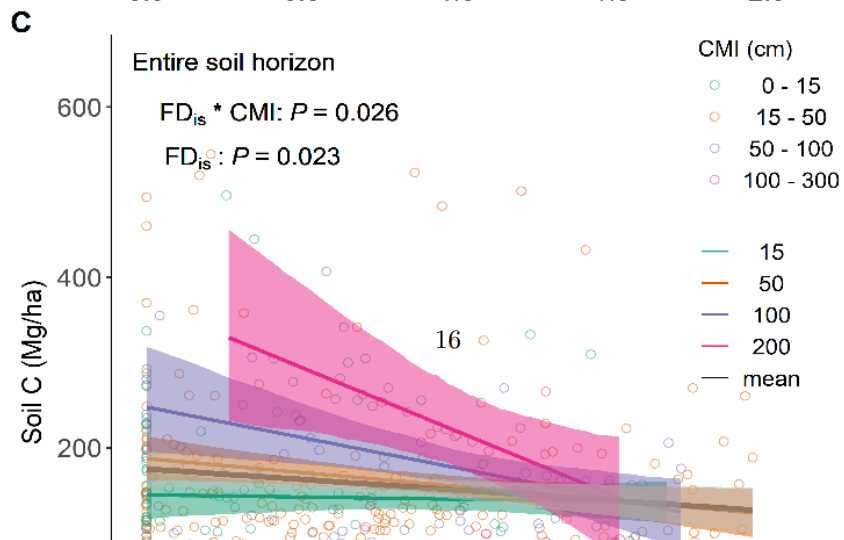
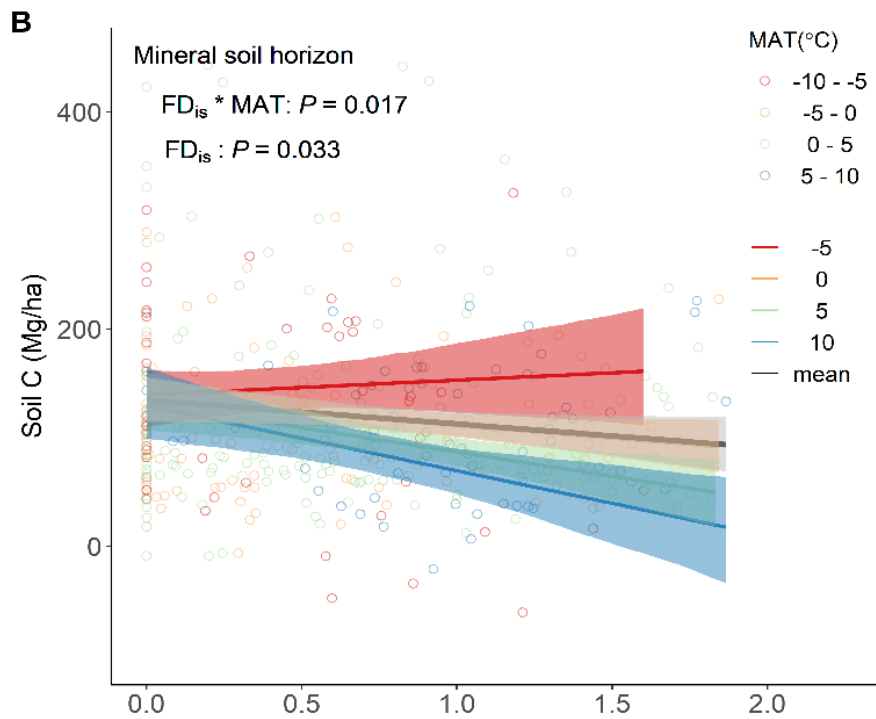
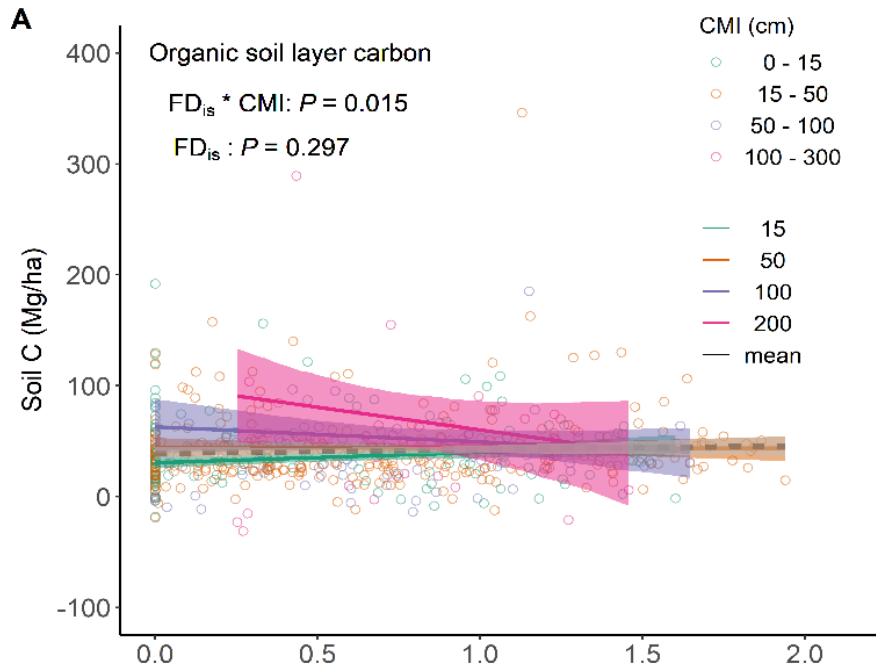




Fig 4

