

Tree diversity increases decadal forest soil carbon and nitrogen accrual

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Increasing soil carbon and nitrogen storage can help mitigate climate change and sustain soil fertility^{1,2}. A large number of biodiversity-manipulation experiments collectively suggest that high plant diversity increases soil carbon and nitrogen stocks^{3,4}. It remains debated, however, whether such conclusions hold in natural ecosystems^{5–12}. Here we analyse Canada's National Forest Inventory (NFI) database with the help of structural equation modelling (SEM) to explore the relationship between tree diversity and soil carbon and nitrogen accumulation in natural forests. We find that greater tree diversity is associated with higher soil carbon and nitrogen accumulation, validating inferences from biodiversity-manipulation experiments. Specifically, on a decadal scale, increasing species evenness from its minimum to maximum value increases soil carbon and nitrogen in the organic horizon by 30% and 42%, whereas increasing functional diversity enhances soil carbon and nitrogen in the mineral horizon by 32% and 50%, respectively. Our results highlight that conserving and promoting functionally diverse forests could promote soil carbon and nitrogen storage, enhancing both carbon sink capacity and soil nitrogen fertility.

Forest soils play an important role in sequestering atmospheric CO₂, storing at least three times as much carbon (C) as found in living plants¹³. The C stock in forest soils is critical in sustaining soil fertility and mediating global climate change¹. Also, the soil nitrogen (N) stock is important in supporting soil N cycling and N availability, which drives C assimilation and plant growth in forest ecosystems². Plant diversity is rapidly declining globally, leading to the degradation of ecosystem function, including the function of soils^{3–5,14}. Local plant biodiversity (that is, at patch, neighbourhood or stand scales) has been shown to increase soil C and N stocks across several ecosystems in biodiversity-manipulation experiments, in which variation in factors other than biodiversity is minimal and species composition is randomly assembled and neutral within and among species richness levels^{3,4,14}. However, it remains unclear whether these positive relationships between plant diversity and stocks of soil C and N based on simplified biodiversity-manipulation experiments can be extrapolated to complex, non-experimental, natural forest ecosystems⁹.

In forests, soil C and N cycling are interactive and serve as both causes and consequences of tree diversity. At a macroecological scale, tree diversity, tree productivity and soil C and N accumulation are probably (co-)determined by drivers such as climatic factors^{5,15} (Fig. 1). For example, warm and humid environments are found to benefit tree diversity^{5,16}. By contrast, higher soil C and N stocks tend to occur more frequently in wetter and colder sites, because those conditions slow down decomposition and mineralization processes more than they decrease productivity^{5,6,17}. After accounting or standardizing for climate effects, diverse tree communities should have greater productivity

and lower soil N losses to groundwater because of enhanced niche complementarity^{3,18–20}. Furthermore, diversity-driven increases in C sequestration and N retention in tree biomass are expected to lead to greater accumulation of soil C and N over time (and thus enhanced soil fertility) from increases in both aboveground and belowground litter input^{3,5,14}. Complementarily, higher soil fertility should support more biomass production and more diverse communities because few species or functional groups can tolerate extremely low nutrient availabilities in natural forests¹⁵.

Previous studies have reported positive^{5,10,11}, negligible^{6,7,12} or even negative relationships⁸ between tree diversity and soil C stocks in non-experimental forests. These divergent empirical findings might be partly because of a potential mismatch between current versus historical forest composition and diversity attributes, as current soil C stocks may carry the imprint of historical plant species composition for centuries to millennia²¹. Compared with soil C and N storage (pools) that reflects long-term net accumulation over centuries, rates of changes in C and N stocks (net changes incorporating temporal losses and gains) during recent decades should better reflect the effects of current tree diversity and identity on net soil C and N cycling. However, large-scale assessments of plant diversity and identity effects on changes in soil C and N stocks have not yet been performed.

To determine whether positive relationships between tree diversity and soil C and N accumulation exist in natural forests while controlling for the influences of climate, soil condition, stand age and tree identity on soil C and N accumulation, as well as their possible downstream effects through changes in tree diversity and identity, we applied SEM²²

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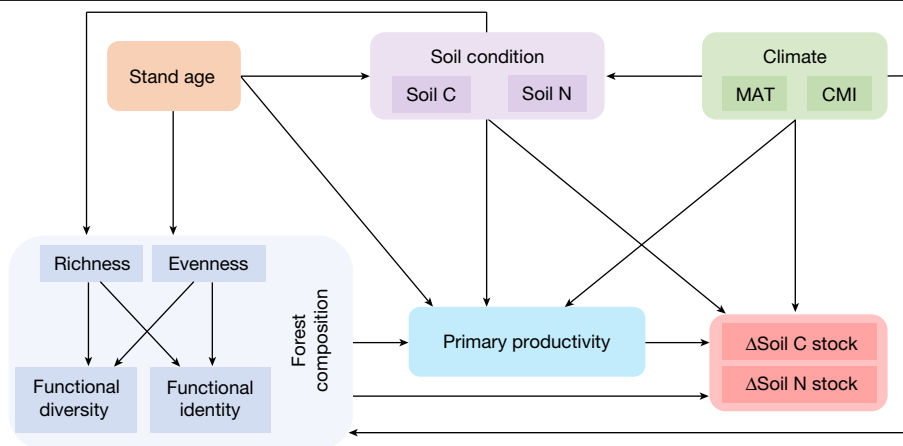


Fig. 1 | Suggested causal pathways of direct and indirect effects of tree diversity, identity, stand age, climate and background soil condition on tree productivity and changes in soil C and N stocks. Variables considered in the model include decadal changes in soil C and N stocks ($\Delta\text{Soil C stock}$ and

$\Delta\text{Soil N stock}$), aboveground primary productivity, tree species richness, evenness, functional diversity, CWM trait value, long-term averages of mean annual temperature (MAT), long-term averages of mean annual climate moisture index (CMI), stand age and initial soil C and N content.

on the basis of a priori causal pathways (Fig. 1) to the forest and soil data from the Canadian NFI programme. Although there are several different definitions of natural forests, both primary and naturally regenerated secondary forests are considered natural forests in our study. Tree diversity can be described by both species richness and evenness. Although species richness is the most common measure of tree diversity, species evenness, a measure of how equitably abundances are distributed across species in a community, has also been shown to substantially affect ecosystem functioning²³ (Fig. 1). Furthermore, increasing richness and evenness would, in theory, promote a high diversity of functional traits (that is, functional dispersion, hereafter functional diversity), which could reflect species complementarity in resource use and be associated with soil processes, such as litter or wood decomposition (see refs. 8, 24–26; Fig. 1). Tree functional identity is represented (at least in part) by the community-weighted mean (CWM) of trait values of all species, which is also interrelated with soil C and N pools^{6, 8, 27, 28} (Fig. 1). Specifically, we proposed that high tree diversity (species richness and evenness) would increase soil C and N accumulation in natural forests by means of increasing tree productivity, whereas tree diversity, productivity and soil C and N accumulation would also be affected by background climate, soil condition, site history and stochastic processes. Similar to previous studies⁶, tree identity was quantified as the first two principal components (CWM_{PC1} and CWM_{PC2}) derived from principal component analysis (PCA) of the CWMs of five functional traits, including leaf and plant economic traits (Extended Data Fig. 1). We used the first (2000–2006) and second (2008–2017) censuses data from NFI permanent sample plots to test these hypotheses. These successive NFIs make up a dataset of 406 plot inventories, covering much of the range of Canadian temperate and boreal forests (Extended Data Fig. 2).

The structural equation models for decadal changes in soil C and N stocks in the organic horizon (hereafter $\Delta\text{Soil C}_{\text{Organic}}$ and $\Delta\text{Soil N}_{\text{Organic}}$ stocks, respectively) conformed well to the data ($\Delta\text{Soil C}_{\text{Organic}}$ stock: goodness-of-fit index (GFI) = 0.991, standardized root mean square residual (SRMR) = 0.030, P = 0.188; $\Delta\text{Soil N}_{\text{Organic}}$ stock: GFI = 0.995, SRMR = 0.024, P = 0.900) and explained 45% and 38% of the variance in changes of soil C and N stocks, respectively (Fig. 2a,c). Both $\Delta\text{Soil C}_{\text{Organic}}$ and $\Delta\text{Soil N}_{\text{Organic}}$ stocks were positively associated with (standardized coefficient, r = 0.66 and 0.61, respectively) and most directly related to decadal changes in the thickness of the soil organic horizon ($\Delta\text{Thickness}$) (Fig. 2a,c). Although simple bivariate plots showed unsubstantial relationships between species evenness (or species richness, FD_{is}) with $\Delta\text{Soil C}_{\text{Organic}}$ and $\Delta\text{Soil N}_{\text{Organic}}$ stocks, $\Delta\text{Thickness}$ was

positively related to species evenness (Extended Data Figs. 3 and 4). The SEM showed that greater species evenness was indirectly associated with higher $\Delta\text{Soil C}_{\text{Organic}}$ and $\Delta\text{Soil N}_{\text{Organic}}$ stocks through the positive relationship with $\Delta\text{Thickness}$ (Fig. 2a,c) (r = 0.07 for both; see Table 1). On the basis of the SEM results, increasing species evenness from minimum to maximum value (Extended Data Table 1) increased $\Delta\text{Soil C}_{\text{Organic}}$ and $\Delta\text{Soil N}_{\text{Organic}}$ stocks by 1.16 and 0.05 kg m⁻² decade⁻¹, representing 30% and 42% increases in organic horizon soil C and N stocks, respectively (Table 1).

The structural equation models for decadal changes in soil C and N stocks in the mineral horizon (hereafter $\Delta\text{Soil C}_{\text{Mineral}}$ and $\Delta\text{Soil N}_{\text{Mineral}}$ stocks, respectively) also conformed well to the data ($\Delta\text{Soil C}_{\text{Mineral}}$ stock: GFI = 0.992, SRMR = 0.031, P = 0.491; $\Delta\text{Soil N}_{\text{Mineral}}$ stock: GFI = 0.992, SRMR = 0.032, P = 0.670) (Fig. 3a,c) and explained 25% and 39% of the variance in changes of soil C and N stocks, respectively (Fig. 3a,c). The simple bivariate plots showed that $\Delta\text{Soil C}_{\text{Mineral}}$ increased notably with FD_{is} but not with species richness and evenness, whereas $\Delta\text{Soil N}_{\text{Mineral}}$ increased with both species evenness and FD_{is} (Extended Data Fig. 5). The SEM indicated that greater FD_{is} was directly associated with higher $\Delta\text{Soil C}_{\text{Mineral}}$ and $\Delta\text{Soil N}_{\text{Mineral}}$ stocks (r = 0.15 and 0.21, respectively). At the same time, species richness and evenness were also indirectly positively related to $\Delta\text{Soil C}_{\text{Mineral}}$ and $\Delta\text{Soil N}_{\text{Mineral}}$ stocks through their positive relationship with FD_{is} (Fig. 3a,c). Increasing FD_{is} from minimum to maximum value (Extended Data Table 1) increased $\Delta\text{Soil C}_{\text{Mineral}}$ and $\Delta\text{Soil N}_{\text{Mineral}}$ stocks by 1.30 and 0.09 kg m⁻² decade⁻¹ (Table 2), representing 32% and 50% increases in mineral horizon soil C and N stocks, respectively.

CWM_{PC1} (which represents the higher value of acquisitive strategy traits, that is, high leaf N and phosphorus (P) concentrations and high specific leaf area) was not related to changes in soil C and N stocks in either organic or mineral horizons, whereas CWM_{PC2} (which represents the lower maximum height and higher wood density) was related to changes in soil C and N both directly and indirectly (Figs. 2 and 3). The $\Delta\text{Soil C}_{\text{Organic}}$ stock was positively associated with the relative abundance of species with high CWM_{PC2} (particularly *Acer* spp. and *Betula* spp.; see Extended Data Table 2) indirectly by means of changes in $\Delta\text{Thickness}$ (Fig. 2a) (r = 0.07; see Table 1). Furthermore, both $\Delta\text{Soil C}_{\text{Mineral}}$ and $\Delta\text{Soil N}_{\text{Mineral}}$ stocks have direct positive associations with the relative abundance of species with high CWM_{PC2} (r = 0.13 and 0.15, respectively) (Fig. 3a,c).

Soil conditions were the most important predictors for changes in soil C and N stocks when considering direct and indirect effects (Figs. 2b,d and 3b,d). The $\Delta\text{Soil C}_{\text{Organic}}$ and $\Delta\text{Soil N}_{\text{Organic}}$ stocks were

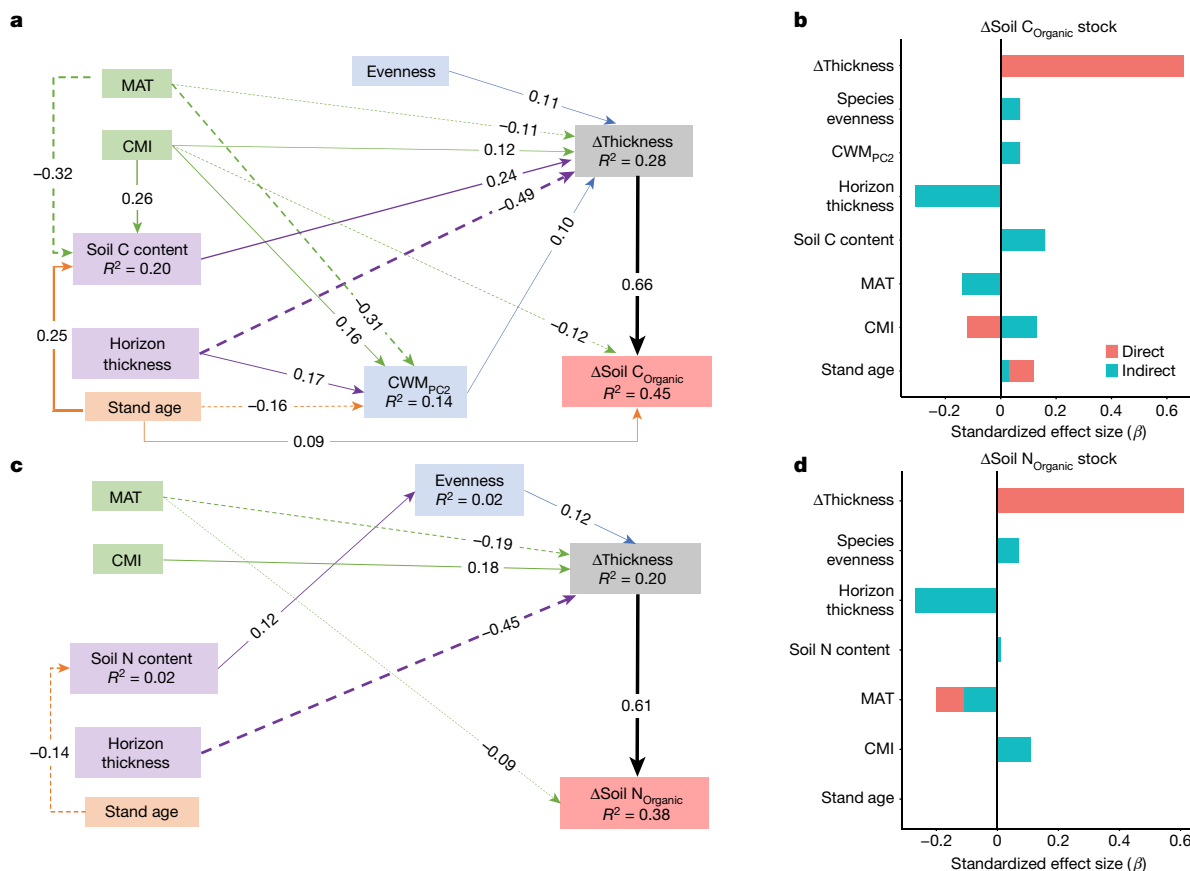


Fig. 2 | Structural equation model showing the effects of tree diversity and climatic and soil conditions on decadal changes in soil C and N stocks in the organic soil horizon ($N = 361$). **a, c**, Path diagrams of factors influencing changes in soil C and N stocks. **b, d** Summed direct and indirect effects. Numbers adjacent to arrows are standardized path coefficients, analogous to relative regression weights. Solid and dashed arrows represent positive and negative relationships, respectively. Only significant pathways are shown ($P < 0.05$). The goodness-of-fit statistics for panels **a** and **c** are GFI = 0.991, SRMR = 0.030,

$P = 0.188$ and GFI = 0.995, SRMR = 0.024, $P = 0.900$, respectively, indicating close model-data fit. Δ Soil C_{Organic} and Δ Soil N_{Organic} represent decadal changes in soil C and N stocks in organic soil horizons, respectively. Δ Thickness, decadal changes in soil organic horizon thickness; CMI, the long-term averages of mean annual climate moisture index; CWM_{PC2}, community-weighted mean of trait values; Horizon thickness, initial organic horizon thickness; MAT, the long-term average of mean annual temperature. Higher CWM_{PC2} values indicate traits associated with lower tree maximum height (see Extended Data Fig. 1).

inversely related to the initial organic horizon thickness indirectly by means of changes in Δ Thickness (Fig. 2a,c) ($r = -0.31$ and -0.27 , respectively; see Table 1). The initial organic horizon soil C content was positively related to Δ Soil C_{Organic} stock through a positive relationship with Δ Thickness (Fig. 2a) ($r = 0.16$; see Table 1), whereas Δ Soil C_{Mineral} and Δ Soil N_{Mineral} stocks were inversely related to initial mineral horizon soil C and N content, respectively ($r = -0.48$ and -0.55 , respectively) (Fig. 3a,c).

Species richness, evenness and FD_{is} were higher but CWM_{PC2} was lower in warmer sites (that is, higher MAT), whereas FD_{is} was lower but CWM_{PC2} was higher in more humid sites (that is, higher CMI) (Figs. 2a,c and 3a,c). Organic horizon Δ Thickness and soil C content were inversely related to MAT but positively related to CMI (Fig. 2a,c). The Δ Soil C_{Organic} and Δ Soil N_{Organic} stocks were inversely related to MAT both directly and indirectly (Fig. 2a,c) ($r = -0.14$ and -0.20 , respectively; see Table 1). Although there was a direct negative association between CMI and Δ Soil C_{Organic} stock ($r = -0.12$), the positive indirect association between them through the relationships with Δ Thickness, CWM_{PC2} and C content offsets the direct negative association, resulting in a very weak overall association (Fig. 2a,b) ($r = 0.01$; see Table 1). The Δ Soil N_{Organic} stock was positively related to CMI indirectly by means of changes in Δ Thickness (Fig. 2c,d) ($r = 0.11$; see Table 1). The MAT was negatively ($r = -0.07$ and -0.14 , respectively) but CMI was positively ($r = 0.16$ for both) related to Δ Soil C_{Mineral} and Δ Soil N_{Mineral} stocks when taking into consideration direct and indirect associations (Fig. 3; see Table 2). Stand age had

negligible effects on decadal changes in soil C and N stocks in both the organic and mineral horizons except for Δ Soil C_{Organic} stock, which was positively associated with stand age both directly and indirectly (Figs. 2 and 3) ($r = 0.12$; see Table 1).

Our findings provided new evidence that higher tree diversity was associated with greater soil C and N accrual in natural forests when background climatic and soil conditions were statistically controlled. Specifically, we found strong evidence that soil C and N accumulation was greater in forests with higher species evenness and functional diversity. This finding underscores the importance of considering measures of biodiversity other than species richness in biodiversity–ecosystem functioning relationships. Further, we showed that the linkages between background climatic conditions and soil C and N accumulation rates were mediated by tree diversity and identity, suggesting that tree composition plays a key role in controlling climate–soil interactions.

Our results showed that higher tree functional diversity was associated with greater soil C and N accumulation in the mineral soil horizon, whereas forests with higher species evenness had larger organic horizon soil thickness and larger increases in associated C and N stocks. Those findings suggest that equitable distribution of functional traits drives soil C and N sequestration, as functional diversity and species evenness better reflect contributions to the function of an ecosystem by minimizing the influence of dominant species or functional traits²⁹. Aboveground primary productivity increased with species richness, species evenness and functional diversity (Extended Data Fig. 6);

Table 1 | Standardized effect sizes, net decadal increase/decrease (in kg m⁻² decade⁻¹) and changes (% decade⁻¹) across the range of values for each predictor for the decadal changes in organic horizon soil C and N stocks based on structural equation models

Predictor	Effect	Standardized <i>r</i>	Net decadal increase or decrease (kg m ⁻² decade ⁻¹)	Decadal percentage change (% decade ⁻¹)
Decadal change in soil C stock in the organic horizon				
ΔThickness	Direct	0.66	21.06	550
Evenness	Indirect → ΔThickness	0.07	1.16	30
CWM _{PC2}	Indirect → ΔThickness	0.07	1.57	41
Horizon thickness	Indirect → ΔThickness	-0.32	-5.84	-152
	Indirect → CWM _{PC2}	0.01	0.21	5
	Total	-0.31	-5.63	-147
Soil C content	Indirect → ΔThickness	0.16	3.02	79
MAT	Indirect → ΔThickness	-0.07	-1.30	-34
	Indirect → CWM _{PC2}	-0.02	-0.37	-10
	Indirect → Soil total C	-0.05	-0.89	-23
	Total	-0.14	-2.56	-67
CMI	Direct	-0.12	-2.96	-77
	Indirect → ΔThickness	0.08	1.89	49
	Indirect → CWM _{PC2}	0.01	0.26	7
	Indirect → Soil total C	0.04	1.01	26
	Total	0.01	0.20	5
Stand age	Direct	0.09	2.77	72
	Indirect → CWM _{PC2}	-0.01	-0.33	-9
	Indirect → Soil total C	0.04	1.21	32
	Total	0.12	3.65	95
Decadal change in soil N stock in the organic horizon				
ΔThickness	Direct	0.61	0.82	683
Evenness	Indirect → ΔThickness	0.07	0.05	42
Horizon thickness	Indirect → ΔThickness	-0.27	-0.21	-170
Soil N content	Indirect → Evenness	0.01	0.007	6
MAT	Direct	-0.09	-0.07	-58
	Indirect → ΔThickness	-0.11	-0.08	-67
	Total	-0.20	-0.15	-125
CMI	Indirect → ΔThickness	0.11	0.11	92
Stand age	Indirect → Soil total N	-0.001	-0.002	-2

ΔThickness, decadal changes in soil organic horizon thickness; CMI, the long-term averages of mean annual climate moisture index; CWM_{PC2}, community-weighted mean of trait values; Horizon thickness, initial organic horizon thickness; MAT, the long-term average of mean annual temperature. Higher CWM_{PC2} values indicate traits associated with lower tree maximum height (see Extended Data Fig. 1).

however, in contrast to our expectation, soil C and N accumulation did not change with aboveground primary productivity (Extended Data Figs. 3–5). It is possible that tree species evenness and functional diversity contribute to soil C and N accumulation mainly through enhancing root turnover and rhizodeposition^{5,14}, which are approximately five times more efficient in stabilizing soil C than aboveground litter inputs³⁰. Alternatively or additionally, the higher soil C and N accumulation might be because of the slowing down of soil organic matter decomposition and mineralization in more diverse forests, although plant diversity is generally expected to increase the decomposition and mineralization rates¹⁴. The lack of positive relationships between changes in soil C stock with that in net aboveground biomass was also reported in Chinese forests⁵, which was attributable to soil C losses induced by microbial respiration owing to the priming effect associated with further aboveground litter input³¹. Furthermore, tree diversity is expected to reduce soil N leaching loss owing to the more complete exploitation of the soil N and, in so doing, increase plant productivity

and ecosystem N retention³; however, the soil N stock might not track aboveground productivity because soil N is progressively locked up in aboveground biomass.

Our results also showed that tree communities with a higher wood density and a lower maximum tree height (CWM_{PC2}) would possess greater organic horizon thickness and, therefore, soil C accumulation. This suggests that tree species with high wood density (for example, *Acer* spp. and *Betula* spp.) might produce more recalcitrant wood and bark litter^{32,33}, resulting in more litter C accumulation in the organic horizon. Alternatively, in this dataset, such impacts could largely be related to tree identity, either specifically to the main *Acer* and *Betula* species (as these had the largest contrasts among taxa in height and wood density) or because of differences between angiosperm and gymnosperm species. Previously, both positive and neutral relationships between wood density and wood decomposition rate have been reported^{26,34}, indicating that further wood traits (for example, wood N and P concentrations) and decomposition data might need to be

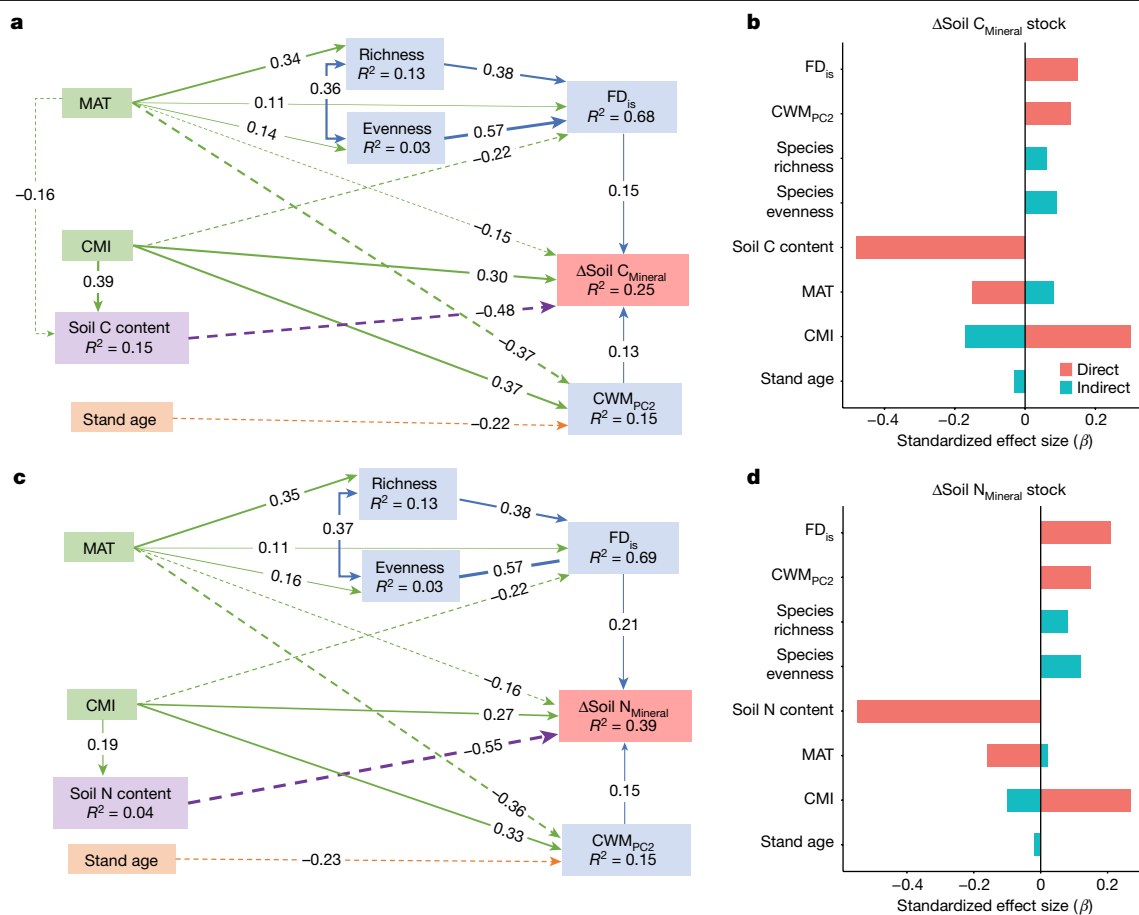


Fig. 3 | Structural equation model showing the effects of tree diversity and climatic and soil conditions on decadal changes in soil C and N stocks in the mineral soil horizon ($N = 245$). **a,c**, Path diagrams of factors influencing changes in soil C and N stocks. **b,d** Summed direct and indirect effects. Numbers adjacent to arrows are standardized path coefficients, analogous to relative regression weights. Solid and dashed arrows represent positive and negative relationships, respectively. Only significant pathways are shown ($P < 0.05$). The proportion of variance explained (R^2) appears alongside every response variable in the model. The goodness-of-fit statistics for panels **a** and **c** are

GFI = 0.992, SRMR = 0.031, $P = 0.491$ and GFI = 0.992, SRMR = 0.032, $P = 0.670$, respectively, indicating close model-data fit. $\Delta\text{Soil C}_{\text{Mineral}}$ and $\Delta\text{Soil N}_{\text{Mineral}}$ represent decadal changes in soil C and N stocks of the mineral horizon, respectively. CMI, the long-term averages of mean annual climate moisture index; CWM_{PC2} , community-weighted mean of trait values; FD_{is} , functional diversity; MAT, the long-term average of mean annual temperature. Higher CWM_{PC2} values indicate traits associated with lower tree maximum height (see Extended Data Fig. 1).

collected to better explore the relationships between wood traits and soil C and N accumulation²⁶ and, in any case, be more easily tested in systems with greater species richness. Also, soil C and N accumulation in the surface mineral horizon was also higher in tree communities with higher wood density and lower maximum tree height, probably because of higher root litter inputs in the surface soil. Compared with the organic soil horizon, the primary source of C and N accumulation in the mineral soil horizon is through root litter inputs³⁰. The shallow root systems of tree species with lower maximum tree height³⁵ might contribute more C to the surface than to the deeper soils. Compared with the notable effects of CWM_{PC2} on soil C and N accumulation, we find that aboveground primary productivity substantially increased, but soil C and N accumulation did not change, with leaf traits (that is, CWM_{PCL}) (Extended Data Fig. 6), which could result from the opposing effects of high-quantity litter versus low-quality litter cancelling the leaf litter influence on soil organic matter formation²⁴. Our results indicate that wood traits should be considered in predicting forest soil C and N changes.

Background soil condition played a dominant role in controlling soil C and N accumulation. Stands with higher initial organic horizon thickness probably have subsequent smaller increases (or even decreases) in organic horizon thickness and, therefore, less accumulation of soil

C and N in the organic horizon, which could be attributed, in part, to greater soil organic matter mineralization in thicker organic horizons³⁶; the thickness of the organic horizon can then reach an equilibrium³⁷. Moreover, we found that soil C and N accumulation in the mineral horizon was lower in stands with higher background mineral horizon C and N content, respectively, suggesting that the saturation effect influenced mineral horizon soil C and N accumulation³⁸. The accumulation of soil C and N could be dependent on initial soil C and N contents, with greater soil C and N losses in sites with higher background soil C and N (Extended Data Fig. 7), as the capacity of soils to store and stabilize C and N is limited³⁸. Furthermore, the greater species evenness in stands with higher soil N content in the organic horizon suggests that high N availability promoted a more equitable distribution of tree species in the studied temperate and boreal forests, which—overall—tends to be limited by low N availability² (although higher evenness could in return also promote high organic horizon soil N content). It is important to posit that lack of soil microbial population size and root productivity data in our dataset might have contributed to the relatively low predictive power shown in this study because they play important roles in controlling soil C and N dynamics^{5,14,39}. Nonetheless, low predictive power at the level of individual samples should not be associated with a lack of substantial relationships; in cases

Table 2 | Standardized effect sizes, net decadal increase/decrease (in kg m⁻² decade⁻¹) and changes (% decade⁻¹) across the range of values for each predictor for the decadal changes in mineral horizon soil C and N stocks based on structural equation models

Predictor	Effect	Standardized <i>r</i>	Net decadal increase or decrease (kg m ⁻² decade ⁻¹)	Decadal percentage change (% decade ⁻¹)
Decadal change in soil C stock in the mineral horizon				
FD _{is}	Direct	0.15	1.30	32
CWM _{PC2}	Direct	0.13	1.61	39
Richness	Indirect → FD _{is}	0.06	0.65	16
Evenness	Indirect → FD _{is}	0.09	0.78	19
Soil C content	Direct	-0.48	-6.30	-153
MAT	Direct	-0.15	-1.48	-36
	Indirect → FD _{is}	0.02	0.16	4
	Indirect → CWM _{PC2}	-0.05	-0.46	-11
	Indirect → Richness	0.02	0.19	5
	Indirect → Evenness	0.01	0.12	3
	Indirect → Soil C content	0.08	0.74	18
	Total	-0.07	-0.73	-18
CMI	Direct	0.30	4.12	100
	Indirect → FD _{is}	-0.03	-0.45	-11
	Indirect → CWM _{PC2}	0.05	0.63	15
	Indirect → Soil C content	-0.19	-2.56	-62
	Total	0.16	1.74	42
Stand age	Indirect → CWM _{PC2}	-0.03	-0.55	-13
Decadal change in soil N stock in the mineral horizon				
FD _{is}	Direct	0.21	0.09	50
CWM _{PC2}	Direct	0.15	0.10	56
Richness	Indirect → FD _{is}	0.08	0.05	28
Evenness	Indirect → FD _{is}	0.12	0.06	33
Soil N content	Direct	-0.55	-0.58	-322
MAT	Direct	-0.16	-0.08	-44
	Indirect → FD _{is}	0.02	0.01	6
	Indirect → CWM _{PC2}	-0.05	-0.03	-17
	Indirect → Richness	0.03	0.01	6
	Indirect → Evenness	0.02	0.01	6
	Total	-0.14	-0.08	-44
CMI	Direct	0.27	0.19	105
	Indirect → FD _{is}	-0.05	-0.03	-17
	Indirect → CWM _{PC2}	0.05	0.04	22
	Indirect → Soil N content	-0.11	-0.07	-39
	Total	0.16	0.13	72
Stand age	Indirect → CWM _{PC2}	-0.02	-0.04	-22

CMI, the long-term averages of mean annual climate moisture index; CWM_{PC2}, community-weighted mean of trait values; FD_{is}, functional diversity; MAT, the long-term average of mean annual temperature. Higher CWM_{PC2} values indicate traits associated with lower tree maximum height (see Extended Data Fig. 1).

such as this, many of other (poorly quantified) drivers contribute to low explanatory power in an analysis that identifies several notable key drivers.

Soil C and N accumulations were higher in colder and more humid sites. Higher temperature is generally associated with greater microbial activity, which enhances microbial decomposition and, in turn, decreases soil C and N accumulation, as well as organic horizon thickness²⁸. High water availability would increase soil moisture content and, in turn, increase the accumulation of soil C and N, as well as organic horizon thickness owing to the low decomposition rate in anaerobic environments⁴⁰, although a large amount of precipitation might also

reduce C accumulation in the organic horizon owing to leaching loss of dissolved organic C (ref. 41). Different from previous findings in which large-scale patterns of soil C and N stocks are controlled predominantly by climatic conditions^{5,17}, we found that MAT and CMI play less important roles in regulating short-term changes in soil C and N stocks, similarly ranked to tree diversity and identity. This is in line with experimental findings that increasing plant diversity has much larger effects than enhancing soil N availability, or continuing climate change effects, on grassland soil C stocks⁴². Our results collectively suggest that biodiversity loss might serve as a main driver of soil C and N change in the future.

We also showed that high temperature may promote tree richness, evenness and functional diversity, consistent with previous reports^{16,28}. However, functional diversity was lower in more humid sites, which is largely because of diverse, yet functionally similar, coniferous forests on the humid west coast of Canada⁴³ (Extended Data Fig. 2). Tree communities with species exhibiting overlapping functional traits would decrease the effectiveness of niche complementarity²⁵ and, in turn, soil C and N inputs. Promoting mixedwood forests that include both broadleaf and coniferous species can increase functional diversity and improve ecosystem function⁴⁴. Furthermore, tree communities with high maximum height and low wood density were observed on warmer sites, probably because of the greater risk of freeze embolism for taller trees in cold regions⁴⁵ and the stronger water transport capacity for coping with high-temperature-induced drought stress²⁷. After accounting for the temperature effect, tree communities with high wood density were found in more humid sites, which could have resulted from the greater abundance of tree species with higher wood density (that is, *Acer* spp. and *Betula* spp.) in the more humid Great Lakes forest region⁴⁶ (Extended Data Fig. 2). Background climatic and soil conditions could also affect soil C and N accumulation in organic and mineral horizons through changes in tree functional diversity and functional identity, indicating the need for incorporating tree diversity and composition into Earth system models⁴⁷ to more accurately predict the responses of C and N dynamics to climate change.

In summary, our findings demonstrate that soil C and N accumulation in both organic and mineral horizons can be substantially enhanced by fostering tree evenness and functional diversity (for example, mixedwood forests that include both broadleaf and coniferous species). These findings, to some extent, demonstrate the validity of inferences from biodiversity-manipulation experiments^{3,4} and collectively support the conclusion that biodiversity plays an important role in sustaining the functioning of Earth's ecosystems. Given that soil C and N are critical to the mitigation of climate change and ecosystem production, and have declined globally substantially^{30,48}, our results highlight that promoting tree functional diversity not only increases aboveground functioning but also mitigates global climate change and reduces soil degradation. Our results are of notable importance in demonstrating the long-term effect of tree diversity on soil C and N accumulation on a large spatial scale for the first time and in guiding the growing efforts to use forests for C and N sequestration. Tree-planting efforts with the goal of aboveground and belowground C sequestration, for example, should also consider species diversity to better improve soil C and N sequestration.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41586-023-05941-9>.

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Study area and available data

In this study, we used the NFI database (<https://nfi.nfis.org>), which is based on a network of plots covering much of Canada's forested landmass on a multiple-biome scale. All plots were established and monitored by Canadian provincial authorities; the plots were first measured between 2000 and 2006 and were remeasured between 2008 and 2017 (second measurement) using the same standard ground sampling guidelines⁴⁹. Only plots located in unmanaged forest stands (during the intervals between samplings) that had been measured twice, with complete data coverage of forest canopy composition, stand age and soil C and N stocks, were selected. In total, 406 plots (44° 00'–64° 24' N, 53° 24'–128° 36' W) met these criteria (Extended Data Fig. 2). Most of these plots were established in natural-disturbance-driven ecosystems (310 plots), whereas others were harvested (73 plots) or stands with unknown origin (23 plots).

The standard plot design consisted of several subplots associated with specific vegetation layers (Extended Data Fig. 2h). The vegetation inventory approach has been described in detail by Zhang et al.¹⁶. The tree canopy layer (all tree stems ≥ 9.0 cm in diameter at breast height (DBH, at 1.3 m height)) and all canopy tree species were inventoried in a 'large tree plot', which has a radius of 11.28 m and an area of 400 m² (0.04 ha) (Extended Data Fig. 2h). All canopy trees in the large tree plot were numbered, tagged and measured for height and DBH. Biomass of trees was calculated using published Canadian national species-specific DBH-based tree aboveground biomass equations⁵⁰. The decadal aboveground net primary productivity (kg m⁻² decade⁻¹) was calculated as the decadal increment of the biomass of living trees plus the biomass of the recruited trees between the two consecutive censuses⁵¹. Four 1-m² 'microplots' were established outside the large tree plot (but within a 15-m radius) (Extended Data Fig. 2h). Both organic and mineral horizon soil samples were collected from each of the four microplots after removing all existing vegetation in 20 × 20-cm (inside dimensions) aluminium sampling frames. In each sampling frame, an organic horizon soil sample that includes the litter, fibric and humus layers that contained >17% organic C by mass⁵² was collected and the depth of each sample collected was then measured. Seven mineral soil horizon samples that contained <17% organic C by mass were collected at fixed depths (0–15 cm) in each NFI microplot using a 10-cm-diameter auger⁵³. The organic and mineral horizon soil samples were oven dried (at 70 °C) and sieved with 8-mm and 2-mm screens to remove gravel and roots, respectively. After excluding missing values for each horizon, 361 plots for organic soil horizon samples and 245 plots for 0–15-cm mineral soil horizon samples were included in the statistical analyses. For each soil sample from both the organic and mineral soil horizons, soil C and N content and bulk density were measured in the laboratory according to standard protocols⁵³. The soil C and N stocks were calculated as follows⁵⁴:

$$\text{Soil C stock (kg m}^{-2}\text{)} = \text{BD} \times d \times C \times 100 \quad (1)$$

$$\text{Soil N stock (kg m}^{-2}\text{)} = \text{BD} \times d \times N \times 100 \quad (2)$$

in which BD is bulk density (g cm⁻³), d is soil depth (cm) and C and N are C and N contents, respectively, in the soil (g kg⁻¹). We calculated $\Delta\text{Soil C}_{\text{Organic}}$, $\Delta\text{Soil N}_{\text{Organic}}$, $\Delta\text{Soil C}_{\text{Mineral}}$ and $\Delta\text{Soil N}_{\text{Mineral}}$ stocks (kg m⁻² decade⁻¹) in each microplot as the difference in soil C and N stocks between two consecutive censuses divided by the census length in decades. Organic horizon thicknesses (depths) can change temporally and directly affect changes in organic C and N stocks. We calculated the $\Delta\text{Thickness}$ (cm decade⁻¹) as the difference in organic soil horizon thicknesses divided by the year intervals between the two inventories.

Tree species richness, evenness, functional diversity and functional identity

We determined tree species richness as the number of tree species in each 400-m² plot. Species evenness was estimated using Pielou's index (J') and weighted by the basal area of constituent tree species in each plot⁵⁵. We used five key functional traits to describe functional diversity and identity: 'leaf nitrogen content per leaf dry mass' (N_{mass} , mg g⁻¹), 'leaf phosphorus content per leaf dry mass' (P_{mass} , mg g⁻¹), 'specific leaf area' (SLA, mm² mg⁻¹; that is, leaf area per leaf dry mass), 'wood density' (WD, g cm⁻³) and maximum height (MH, m) (Extended Data Table 2). These traits are expected to be related to growth and species competitive abilities across temperature and water-availability gradients^{56–58}. The SLA is related to plant growth rate, leaf life span, resource uptake and use efficiency, whereas N_{mass} and P_{mass} are related to growth and photosynthetic capacity of plants^{56,59}. The WD and MH are related to capacity of sustained access to light, plant fecundity, tolerance or resistance to disturbances and storage of C (refs. 57,60). We obtained the mean trait values of N_{mass} , P_{mass} , SLA, WD and MH using all available measurements for each tree species from the TRY Plant Trait Database⁶¹. Functional diversity was calculated as functional dispersion (FD_{is}), which is the mean distance of each species to the basal-area-weighted centroid of all species in functional trait space, based on all five traits together⁶².

Functional identity was calculated as the CWM of trait values, in which weights reflected basal area, based on each trait in each plot. Similar to previous studies^{6,63,64}, we performed PCA using CWMs of the five traits to obtain a composite functional identity, as individual trait values were correlated, sometimes highly, with one another (for example, $\text{CWM}_{N_{\text{mass}}}$ with $\text{CWM}_{P_{\text{mass}}}$ ($r = 0.88$), CWM_{SLA} ($r = 0.49$), CWM_{WD} ($r = 0.25$) and CWM_{MH} ($r = -0.15$)) (Extended Data Fig. 1). We used the first axis (CWM_{PC1} , which explained 47% of the variation) and the second axis (CWM_{PC2} , 23% of the variation) of the PCA as variables of functional identity. CWM_{PC1} represents traits associated with resource acquisitive versus conservative functions^{56,60,65} and is strongly related to higher CWM_{SLA} , $\text{CWM}_{N_{\text{mass}}}$ and $\text{CWM}_{P_{\text{mass}}}$. CWM_{PC2} is related negatively to maximum height (CWM_{MH}) and positively to wood density (CWM_{WD}) (Extended Data Fig. 1). An assemblage of species characterized by fast growth rate (higher CWM_{PC1}) and large biomass stock (lower CWM_{PC2}) is expected to increase plant productivity and N retention and, therefore, soil C and N pools through increased plant litter inputs^{8,66}. On the other hand, resource-conservative traits, such as low specific leaf area and leaf N and P concentrations, are also expected to contribute to soil C and N accumulation through the input of low-quality (recalcitrant) plant litter associated with slow decomposition rates^{24,32}. The calculation of FD_{is} and CWM was conducted using the FD package⁶². Because species richness, species evenness, FD_{is} and CWM varied during the first and second measurements, we used their mean values of two measurements as proxies for tree diversity and identity⁵⁸.

Local climate, soil condition and stand age

Similar to previous studies⁶⁴, we calculated the long-term mean annual temperature (MAT, °C) and mean annual climate moisture index (CMI, mm) using the BioSIM software (<https://cfs.nrcan.gc.ca/projects/133>), which generates long-term (2002–2018), scale-free climate data from geographic coordinates (latitude, longitude and elevation)⁶⁷. Annual CMI was calculated as the mean annual precipitation minus potential evapotranspiration⁶⁸. We also used mean annual growing degree-days (GDD, °C, yearly summation of the mean of daily maximum and minimum temperature minus 5 °C) and mean annual precipitation in the growing season (APG, mm) as alternative temperature and precipitation indices to explore important climate–forest composition relationships. We found that both groups of temperature and precipitation indices (MAT and CMI versus GDD and APG) yield similar explanatory powers and estimates (Figs. 1 and 2 and Extended Data Fig. 8). For simplicity, we chose to report structural equation models that include MAT and CMI in the main text.

We used the corresponding initial soil C and N contents and organic horizon thickness (first measurement) in each plot as background soil conditions for assessing decadal changes in soil C and N stocks for a specific horizon. Stand age 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 and remeasurement. Stand age was determined with coring, and the average of ring counts from the tree-ring samples of the species with the oldest age was used as a conservative estimate of stand age⁶⁹. We used the middle stand age between the first and second NFIs to represent the stand age.

Statistical analyses

Similar to previous studies^{22,28}, we used SEM to examine the multivariate relationships between species richness, FD_{is} , CWM_{PC1} , CWM_{PC2} , aboveground primary productivity and $\Delta Soil\ C_{Mineral}$ and $\Delta Soil\ N_{Mineral}$ stocks (or $\Delta Thickness$ and $\Delta Soil\ C_{Organic}$ and $\Delta Soil\ N_{Organic}$ stocks), while simultaneously accounting for the effects of covariates such as MAT, CMI, stand age, soil C content, soil N content, as well as initial soil thickness (only for $\Delta Soil\ C_{Organic}$ and $\Delta Soil\ N_{Organic}$ stocks). We first examined the bivariate relationships between MAT, CMI, stand age, species richness, FD_{is} , CWM_{PC1} , CWM_{PC2} , aboveground primary productivity, organic horizon soil N content, $\Delta Thickness$ and $\Delta Soil\ C_{Organic}$ and $\Delta Soil\ N_{Organic}$ stocks (Extended Data Figs. 3 and 4). We also examined the bivariate relationships between MAT, CMI, stand age, species richness, FD_{is} , CWM_{PC1} , CWM_{PC2} , aboveground primary productivity, mineral horizon soil N content and $\Delta Soil\ C_{Mineral}$ and $\Delta Soil\ N_{Mineral}$ stocks (Extended Data Fig. 5). Similar to a previous study²⁸, we calculated the total C and N gain/loss across the measured range of a given variable (for example, functional diversity) by multiplying the unstandardized effect size in SEM results by the range of the given variable shown in Extended Data Table 1.

We implemented the SEM using the lavaan 0.6-9 package⁷⁰ along with the lavaan.survey 1.1.3.1 package⁷¹ based on the suggested effects and relationships between the key drivers (Fig. 1). We started with the most complete model and eliminated from the model variables that did not contribute substantial information. The final models among several alternatives were selected on the basis of the goodness-of-fit statistics and Akaike information criterion (AIC). Aboveground primary productivity and CWM_{PC1} were excluded in the final model for both organic and mineral horizons. We used three common indices to evaluate the goodness-of-fit of structural equation models, SRMR (SRMR < 0.08 indicates a good model fit), GFI (GFI > 0.95 indicates a good model fit) and chi-squared test ($P > 0.05$ for a satisfactory fit), as recommended⁷². We also calculated relative soil C and N changes in the mineral horizon as the ratio of the accumulation in soil C and N stocks to the initial soil C and N stocks. Then we identified the saturation soil C and N contents in the mineral horizon based on the relationship between relative soil C and N changes with the initial soil C and N contents (Extended Data Fig. 7). All statistical analyses were performed in R 4.2.1 (ref. 73).

Inclusion and ethics

For this research, local researchers were included throughout the research process, including study design, study implementation, data ownership and authorship. Contributors who do not meet all criteria for authorship have been listed in the Acknowledgements section. All roles and responsibilities were agreed on among collaborators ahead of the research. We have considered local and regional research relevant to our study in the citations. This study does not involve human research participants or animals and does not require approval by a local ethics review committee.

Data availability

The source data underlying Figs. 2 and 3 are provided as source data files and all data used in this study are archived in Figshare (<https://doi.org/10.6084/m9.figshare.20988187.v2>).

doi.org/10.6084/m9.figshare.20988187.v2). Source data are provided with this paper.

Code availability

The R scripts needed to reproduce the analysis are archived in Figshare (<https://doi.org/10.6084/m9.figshare.20988187.v2>).

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Competing interests The authors declare no competing interests.

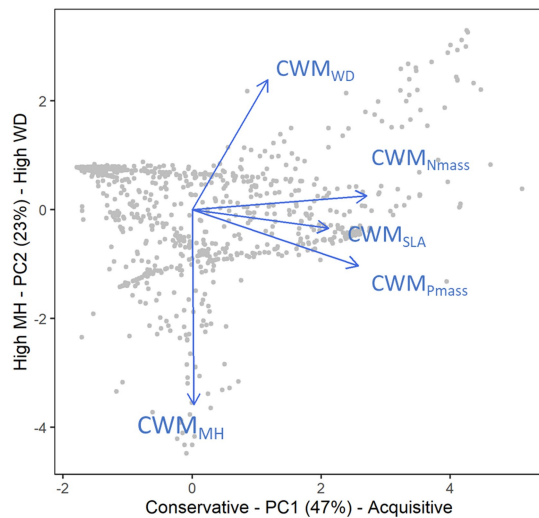
Additional information

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41586-023-05941-9>.

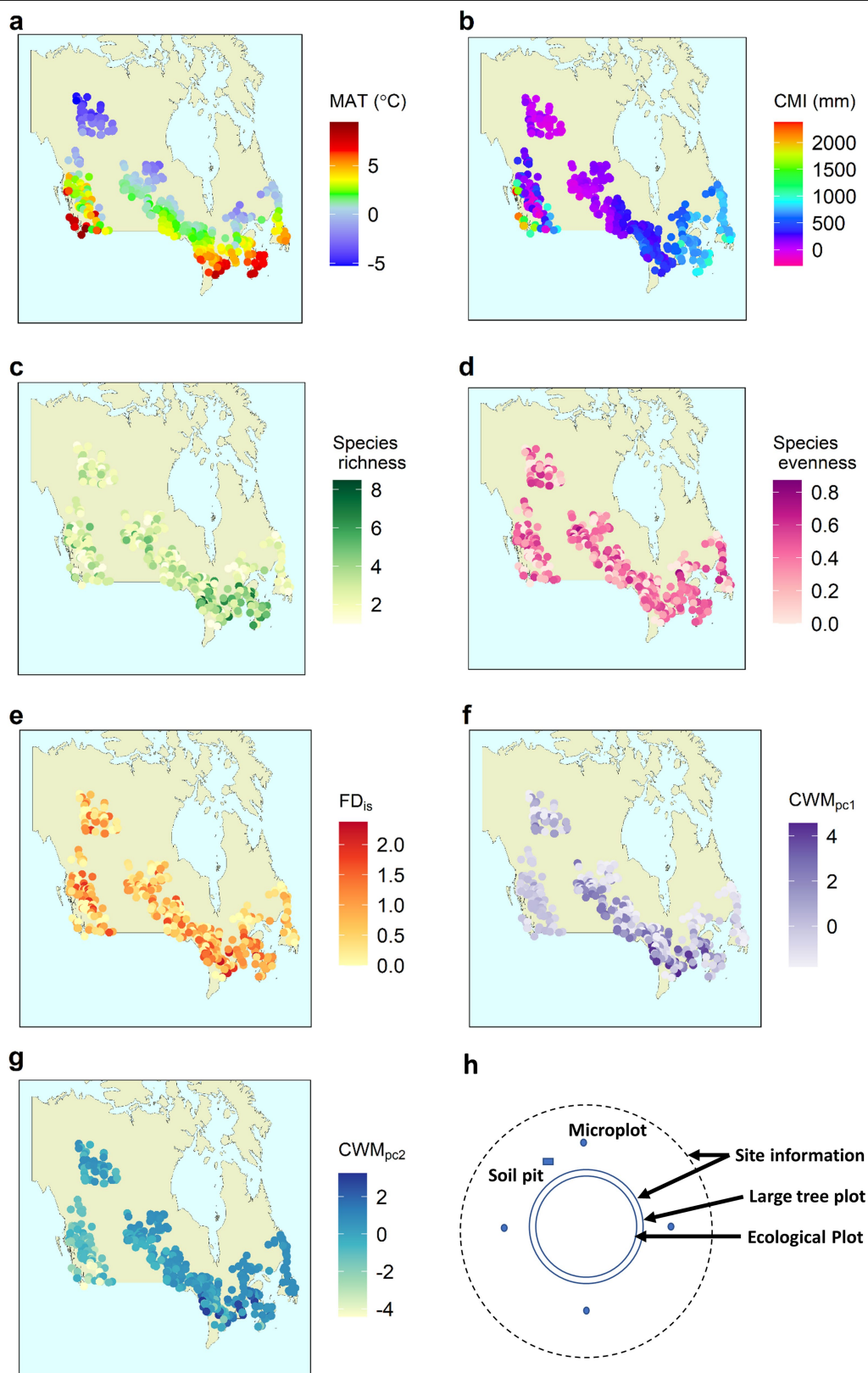
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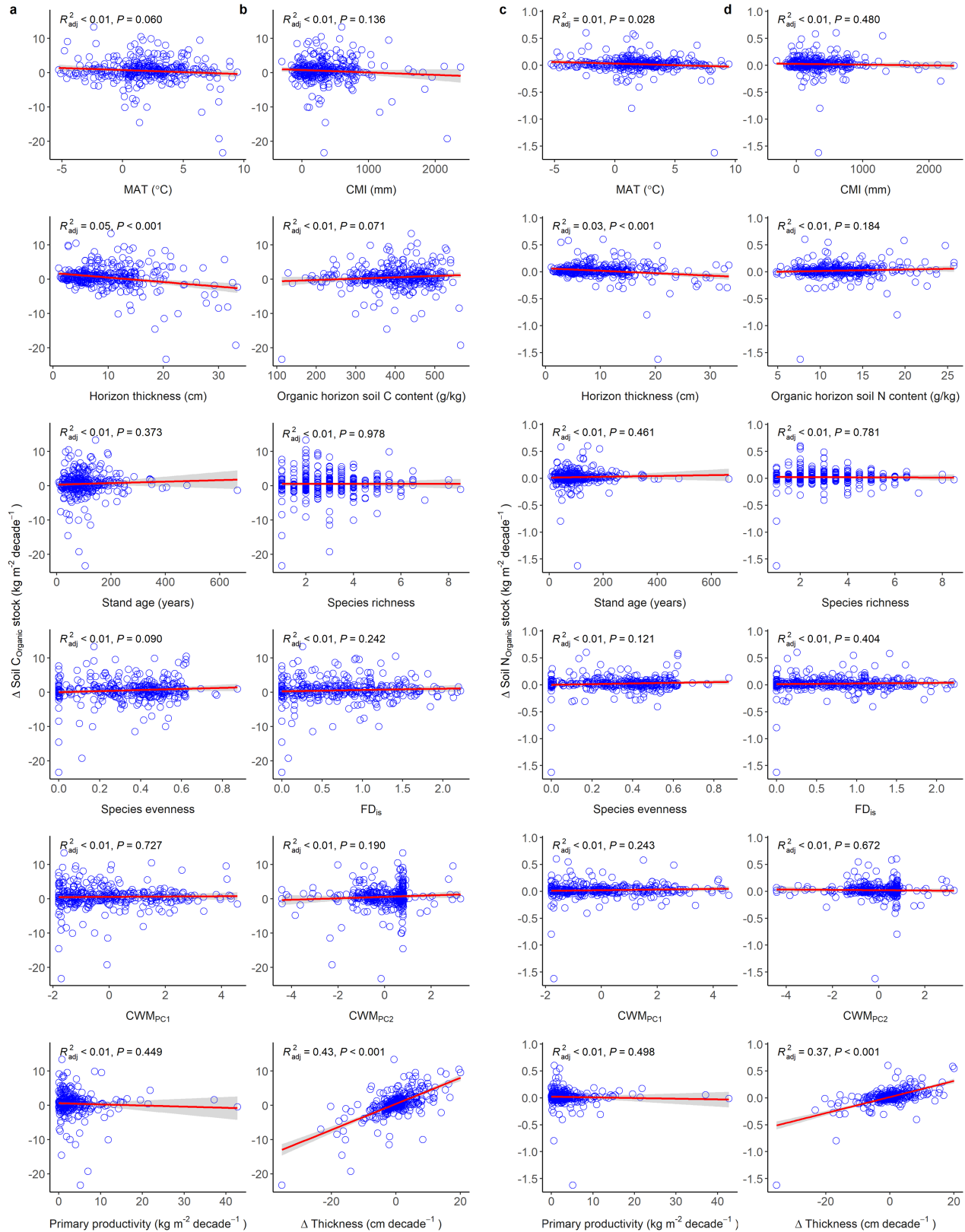


Extended Data Fig. 1 | The result of PCA showing permanent sampling plots and each functional identity. CWM, community-weighted mean of trait value; CWM_{Nmass} , CWM of nitrogen content per leaf mass; CWM_{Pmass} , CWM of phosphorus content per leaf mass; CWM_{SLA} , CWM of specific leaf area; CWM_{WD} , CWM of wood density; CWM_{MH} , CWM of maximum height. The first axis (PC1) represents traits associated with acquisitive versus conservative strategies, whereas the second axis (PC2) refers to traits associated with wood density (WD) versus the maximum height (MH) of trees.



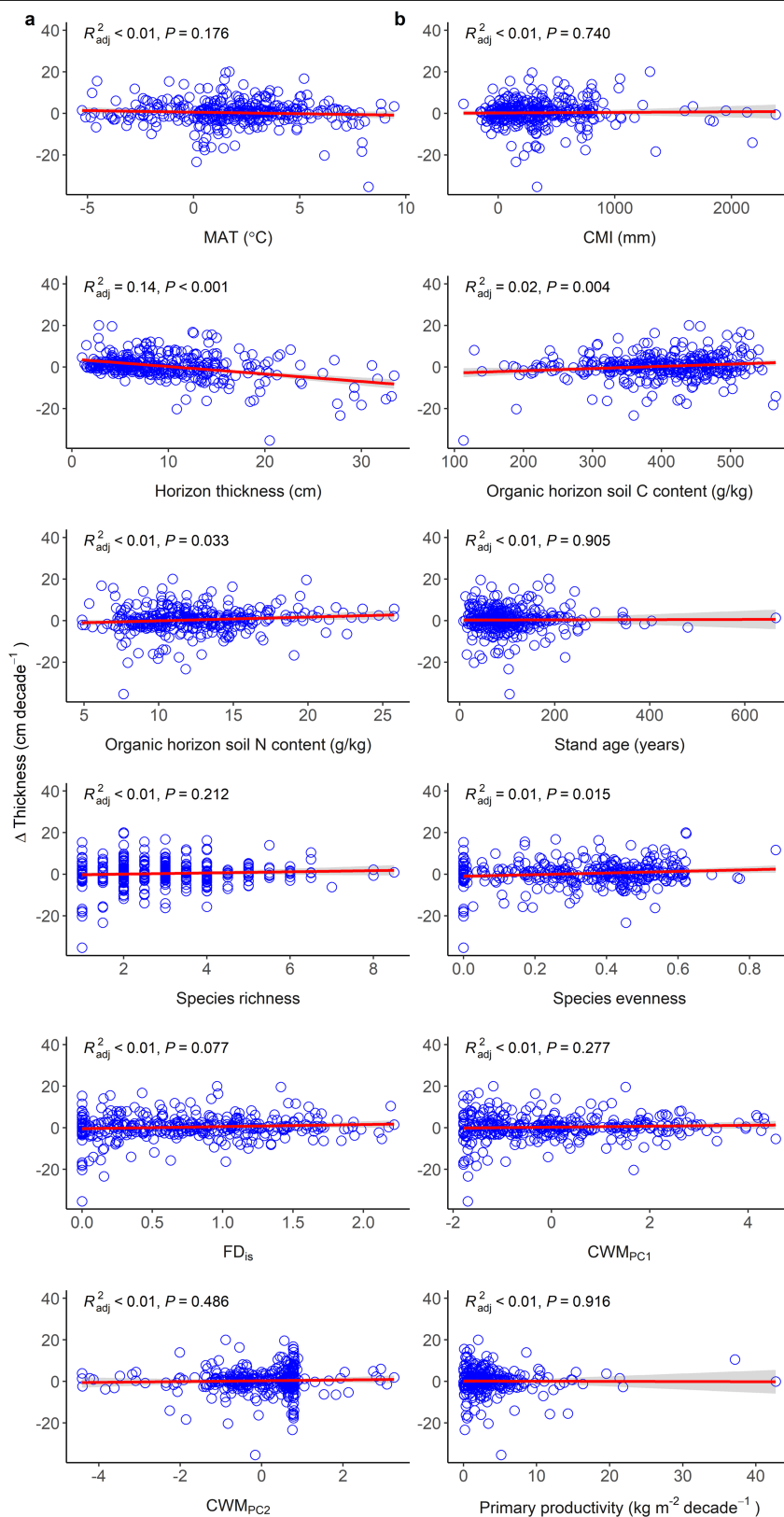
Extended Data Fig. 2 | The distributions of 406 ground plots from the Canadian NFI with climate and plant community characteristics information. a, Long-term averages of mean annual temperature (MAT).

b, Long-term averages of mean annual climate moisture index (CMI). c, Species richness. d, Species evenness. e, Functional diversity (FD_{IS}). f, g, CWM of trait value (CWM_{PC1} , CWM_{PC2}). h, Schematic diagram of the NFI ground plot.



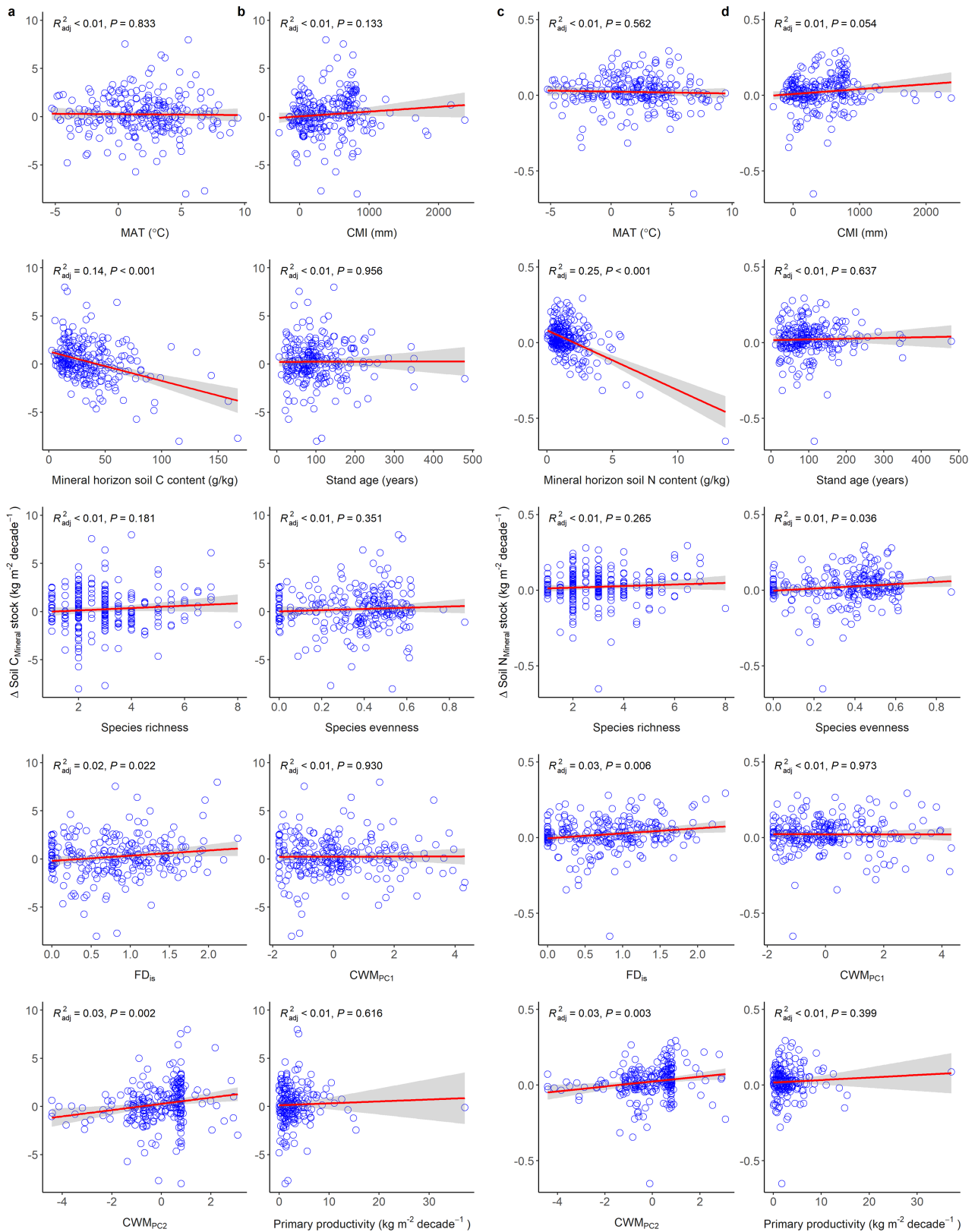
Extended Data Fig. 3 | The bivariate relationships between decadal changes in soil C and N stocks in the organic horizon (Δ Soil C_{organic} stock and Δ Soil N_{organic} stock) and explanatory variables ($n = 361$) for all proposed causal paths in the structural equation model. MAT, the long-term average of mean annual temperature; CMI, the long-term average of mean annual climate moisture index; FD_{is}, functional diversity; Horizon thickness, initial organic

horizon thickness; Δ Thickness, decadal organic horizon soil thickness change. Higher CWM_{PC1} values indicate traits associated with acquisitive strategy, whereas lower values indicate conservative strategy. Higher CWM_{PC2} values indicate traits associated with lower tree maximum height (see Extended Data Fig. 1).



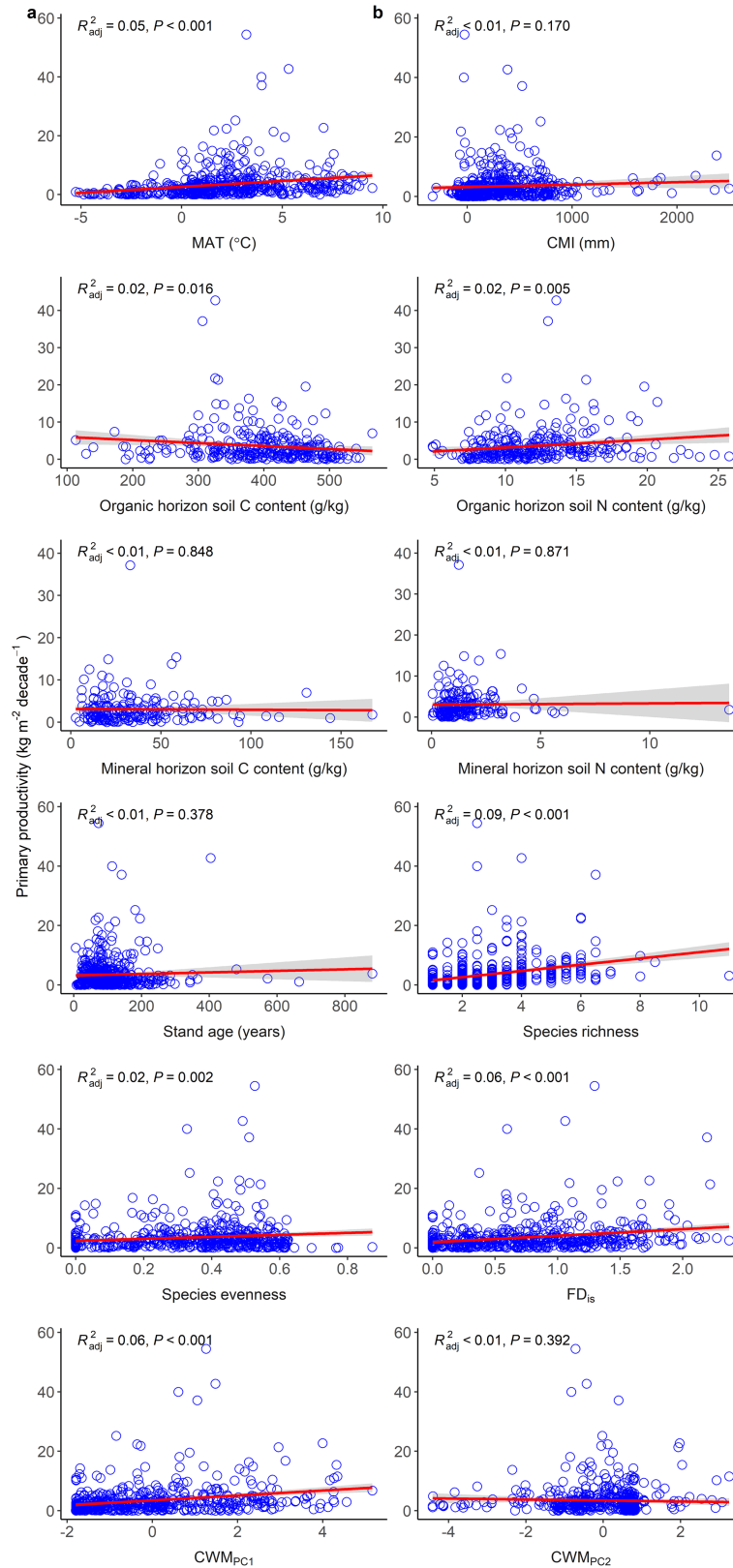
Extended Data Fig. 4 | The bivariate relationships between decadal changes in soil thickness in the organic horizon (Δ Thickness) and explanatory variables ($n = 361$) for all proposed causal paths in the structural equation model. All fitted regressions are significant at $P < 0.05$. MAT, the long-term average of mean annual temperature; CMI, the long-term average of mean

annual climate moisture index; FD_{is}, functional diversity; Horizon thickness, initial organic horizon thickness. Higher CWM_{PC1} values indicate traits associated with acquisitive strategy, whereas lower values indicate conservative strategy. Higher CWM_{PC2} values indicate traits associated with lower tree maximum height (see Extended Data Fig. 1).



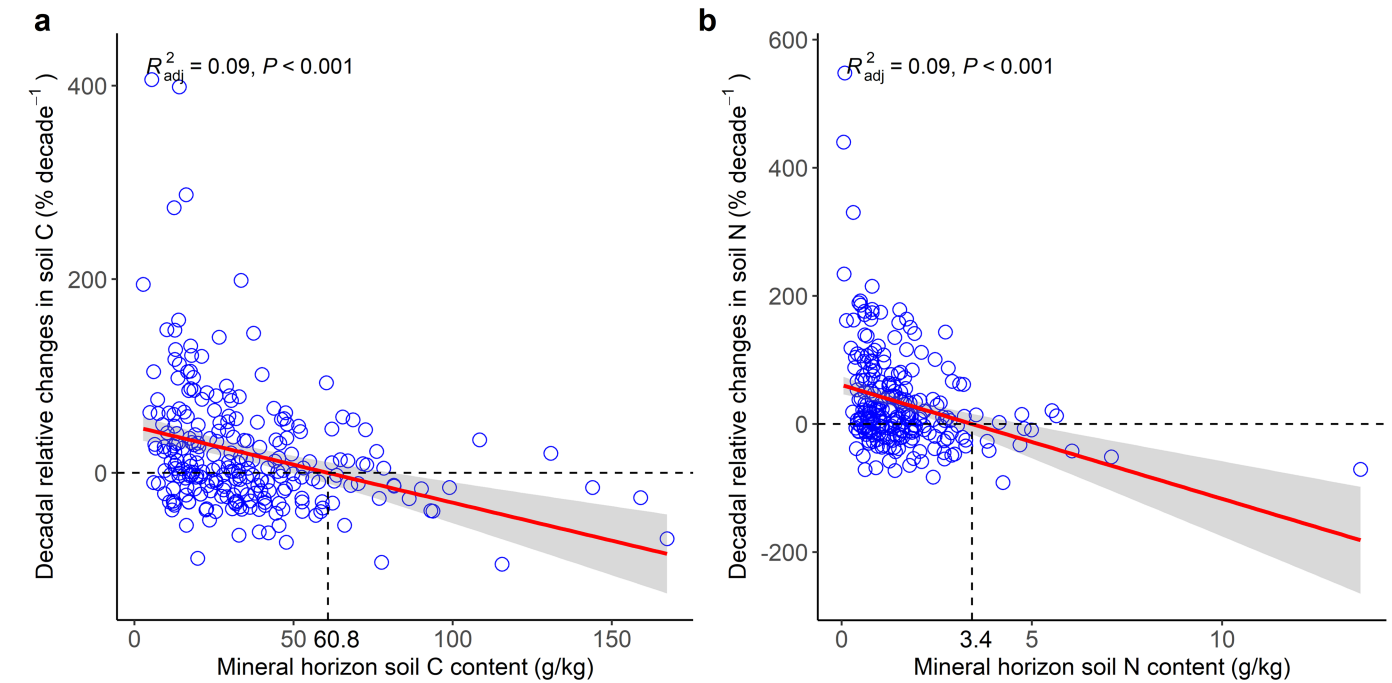
Extended Data Fig. 5 | The bivariate relationships between decadal changes in soil C and N stocks in the mineral horizon ($\Delta\text{Soil } C_{\text{Mineral}}$ stock and $\Delta\text{Soil } N_{\text{Mineral}}$ stock) and explanatory variables ($n = 245$) for all proposed causal paths in the structural equation model. All fitted regressions are significant at $P < 0.05$. MAT, the long-term average of mean annual temperature; CMI, the

long-term average of mean annual climate moisture index; FD_{is} , functional diversity. Higher CWM_{PC1} values indicate traits associated with acquisitive strategy, whereas lower values indicate conservative strategy. Higher CWM_{PC2} values indicate traits associated with lower tree maximum height (see Extended Data Fig. 1).



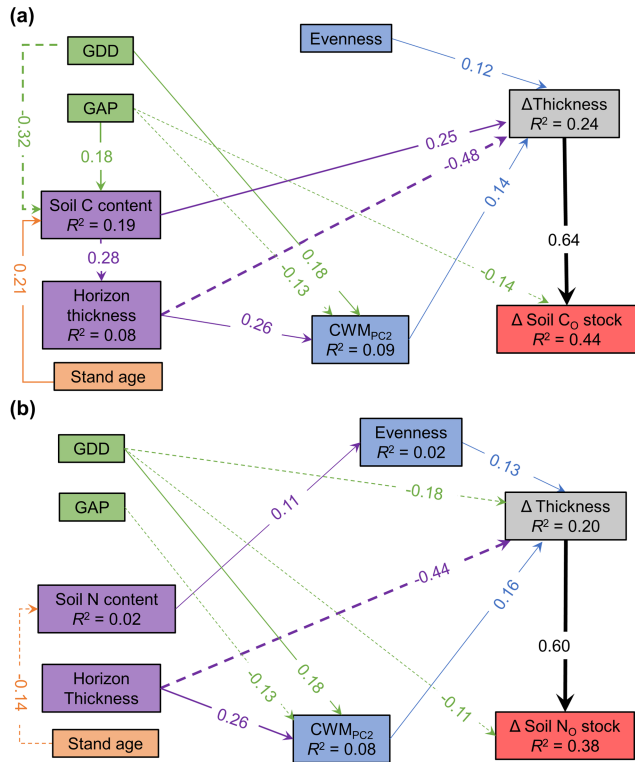
Extended Data Fig. 6 | The bivariate relationships between decadal aboveground primary productivity and explanatory variables for all proposed causal paths in the structural equation model. All fitted regressions are significant at $P < 0.05$. MAT, the long-term average of mean annual temperature; CMI, the long-term average of mean annual climate moisture

index; FD_{is} , functional diversity. Higher CWM_{pc1} values indicate traits associated with acquisitive strategy, whereas lower values indicate conservative strategy. Higher CWM_{pc2} values indicate traits associated with lower tree maximum height (see Extended Data Fig. 1).

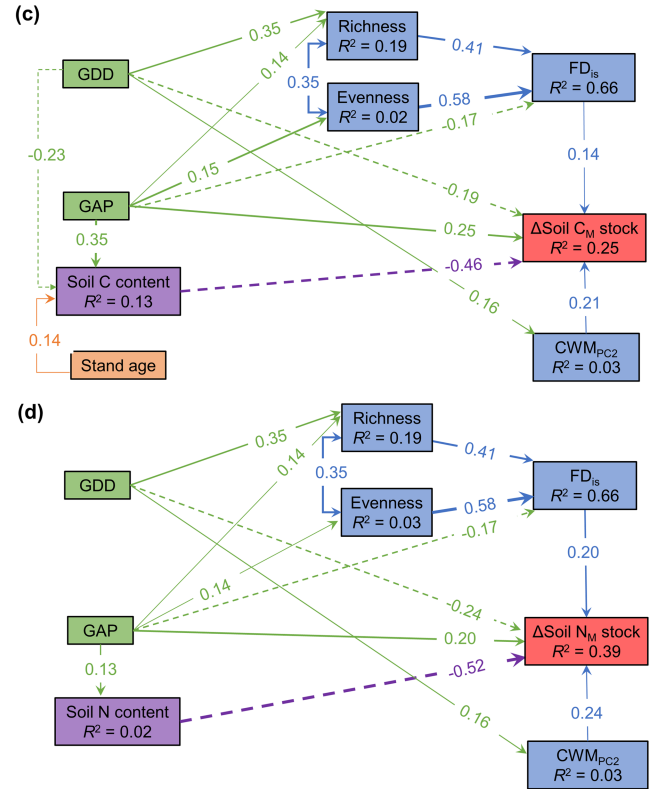


Extended Data Fig. 7 | The bivariate relationships between decadal relative changes in soil C and N stocks in the mineral horizon and mineral horizon soil C and N content, respectively. All fitted regressions are significant at

$P < 0.05$. Dotted vertical line represents the soil C or N content when relative changes in soil C and N stocks began to shift from positive to negative.



Extended Data Fig. 8 | Structural equation models showing the effects of tree diversity, alternative climatic factors and soil conditions on decadal changes in soil C and N stocks. a, b, Path diagrams of factors influencing changes in soil C and N stocks in the organic horizon ($n = 361$). **b, d** Path diagrams of factors influencing changes in soil C and N stocks in the mineral horizon ($n = 245$). Numbers adjacent to arrows are standardized path coefficients, analogous to relative regression weights. Solid and dashed arrows represent positive and negative relationships, respectively. Different colours represent different types of explanatory variable (see Fig. 1). Only significant pathways are shown ($P < 0.05$). The goodness-of-fit statistics for panels **a–d** are: GFI = 0.988, SRMR = 0.032, $P = 0.249$; GFI = 0.991, SRMR = 0.029, $P = 0.477$;



GFI = 0.987, SRMR = 0.033, $P = 0.367$; and GFI = 0.986, SRMR = 0.038, $P = 0.391$, respectively, indicating close model-data fit. Δ Soil C_{Organic} and Δ Soil N_{Organic} represent decadal changes in soil C and N stocks of the organic soil horizons, respectively. Δ Soil C_{Mineral} and Δ Soil N_{Mineral} represent decadal changes in soil C and N stocks of the mineral soil horizons, respectively. GDD, mean annual growing degree-days; AGP, mean annual precipitation at the growing season; FD_{is}, functional diversity; Δ Thickness, decadal changes in soil organic horizon thickness; CWM_{PC2}, community-weighted mean of trait values; Horizon thickness, initial organic horizon thickness. Higher CWM_{PC2} values indicate traits associated with lower tree maximum height (see Extended Data Fig. 1).

Extended Data Table 1 | Summary statistics (mean, s.d. and range) of the permanent sample plots across Canada (2002–2018)

Attribute	Unit	Mean	SD	Range
Average number of live trees per plot across two measurements	ha ⁻¹	943	657	25 – 4080
Average stand basal area per plot across two measurements	m ² ha ⁻¹	24.3	18.4	0.2 – 99.3
Stand age	years	100.5	71.6	6 – 665
Long-term average of mean annual climate moisture index (CMI)	mm	361	379	-297 – 2378
Long-term average of mean annual temperature (MAT)	°C	2.0	2.9	-5.3 – 9.5
Species richness	unitless	3.0	1.5	1 – 9
Species evenness	unitless	0.34	0.19	0 – 0.87
Functional diversity (functional dispersion, FD _{is})	unitless	0.75	0.56	0.00 – 2.37
Community weighted mean of leaf nitrogen content per leaf dry mass (CWM _{N_{mass}})	mg g ⁻¹	14.83	4.32	9.92 – 25.97
Community weighted mean of leaf phosphorus content per leaf dry mass (CWM _{P_{mass}})	mg g ⁻¹	1.46	0.32	0.98 – 3.04
Community weighted mean of specific leaf area (CWM _{SLA})	mm ² mg ⁻¹	13.41	7.29	3.33 – 36.80
Community weighted mean of wood density (CWM _{WD})	g cm ⁻³	0.46	0.08	0.32 – 1.00
Community weighted mean of maximum height (CWM _{MH})	m	43.41	14.67	11.43 – 119.80
Community weighted mean of resource acquisition traits (CWM _{PC1})	unitless	0.08	1.52	-1.79 – 4.56
Community weighted mean of resource colonization traits (CWM _{PC2})	unitless	0.01	1.11	-4.42 – 3.26
Measurement interval	years	9.7	2.9	3.0 – 15.2
Decadal Soil C stock change in organic horizon	kg m ⁻² decade ⁻¹	0.56	3.43	-23.32 – 13.34
Decadal Soil C stock change in 0-15 cm mineral horizon	kg m ⁻² decade ⁻¹	0.24	2.08	-8.02 – 7.97
Decadal Soil N stock change in organic horizon	kg m ⁻² decade ⁻¹	0.02	0.14	-1.62 – 0.60
Decadal Soil N stock change in 0-15 cm mineral horizon	kg m ⁻² decade ⁻¹	0.02	0.11	-0.65 – 0.29
Background soil C content in organic horizon	g kg ⁻¹	399.1	83.0	113.1 – 565.4
Background soil C content in 0-15 cm mineral horizon	g kg ⁻¹	35.26	25.83	2.73 – 167.36
Background soil N content in organic horizon	g kg ⁻¹	12.31	3.70	4.87 – 25.77
Background soil N content in 0-15 cm mineral horizon	g kg ⁻¹	1.54	1.35	0.05 – 13.64
Background soil C stock in organic horizon	kg m ⁻²	3.83	3.08	0.24 – 26.38
Background soil C stock in 0-15 cm mineral horizon	kg m ⁻²	4.11	2.08	0.72 – 15.03
Background soil N stock in organic horizon	kg m ⁻²	0.12	0.11	0.01 – 0.84
Background soil N stock in 0-15 cm mineral horizon	kg m ⁻²	0.18	0.12	0.01 – 0.92

Extended Data Table 2 | Functional trait values of major tree genus (>5% of the total basal area across all plots during the entire census) occurred from all the provinces

Genus	SLA (mm ² mg ⁻¹)	Nmass (mg g ⁻¹)	Pmass (mg g ⁻¹)	WD (g cm ⁻³)	MH (m)
<i>Abies</i>	14.10	13.76	1.35	0.35	49.21
<i>Acer</i>	29.50	23.30	2.21	0.62	28.28
<i>Betula</i>	24.19	23.70	1.89	0.60	23.79
<i>Picea</i>	7.57	11.64	1.38	0.42	56.60
<i>Pinus</i>	10.46	12.74	1.27	0.42	56.97
<i>Populus</i>	15.72	21.98	2.12	0.39	41.00
<i>Thuja</i>	6.57	12.83	1.51	0.39	57.50
<i>Tsuga</i>	10.38	12.33	1.55	0.44	52.53

Values of each species were averaged to obtain genus-level values to aid our interpretation of the results (see main text). Note that, for the analysis, we used species-level trait values but not those of the genus level (see Methods).
SLA, specific leaf area; N_{mass} , leaf nitrogen content per leaf dry mass; P_{mass} , leaf phosphorus content per leaf dry mass; WD, wood density; MH, maximum height.