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Structural equation modelling reveals plant-community drivers of carbon storage in boreal forest ecosystems

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Boreal forest ecosystems are important drivers of the global carbon (C) cycle by acting as both sinks and sources of atmospheric CO_2. While several factors have been proposed as determining the ability of boreal forest to function as C sinks, little is known about their relative importance. In this study, we applied structural equation modelling to a previously published dataset involving 30 boreal-forested islands that vary greatly in their historic fire regime, in order to explore the simultaneous influence of several factors believed to be important in influencing above-ground, below-ground and total ecosystem C accumulation. We found that wildfire was a major driver of ecosystem C sequestration, and exerted direct effects on below-ground C storage (presumably through humus combustion) and indirect effects on both above-ground and below-ground C storage through altering plant-community composition. By contrast, plant diversity influenced only below-ground C storage (and even then only weakly), while net primary productivity and decomposition had no detectable effect. Our results suggest that while boreal forests have great potential for storing significant amounts of C, traits of dominant plant species that promote below-ground C accumulation and the absence of wildfire are the most important drivers of C sequestration in these ecosystems.

Keywords: carbon sequestration; plant-community composition; plant diversity; wildfire; structural equation modelling

1. INTRODUCTION

Boreal forest ecosystems are important drivers of the global carbon (C) cycle (Goodale *et al.* 2002) and store more C on a global basis than any other forest biome (Anderson 1991). During the past decade, the potential of boreal forests to act as sinks for C has attracted increasing interest, because increased terrestrial C sequestration can potentially mitigate increasing atmospheric CO_2 concentrations and therefore influence global climate. To understand how forests influence the global C cycle and how they may function as sinks of atmospheric CO_2, it is important to understand the factors controlling the rate at which C is sequestered by forests and their relative importance (Schimel 2007). To date, wildfire regime, forest-stand age, net primary productivity (NPP), vegetation composition and functional traits of the dominant species, plant species diversity and litter decomposition have all been proposed as influencing C accumulation rates in forests (Wardle *et al.* 2003; Bunker *et al.* 2005; Luyssaert *et al.* 2008).

In boreal forests, wildfire is important in influencing C sequestration, both directly through combustion of above-ground and below-ground plant material, and indirectly through determining stand age, plant species composition, NPP and litter decomposition rates (Wardle *et al.* 2003). There may therefore be a suite of direct and indirect factors that simultaneously influence C sequestration in forest ecosystems, but their relative importance is little understood. Since wildfire suppression has reduced the importance of wildfire as a cause of C emissions in boreal forests throughout northern Europe, it is critical to understand how long-term suppression of wildfire may be influencing C storage in boreal forest ecosystems.

To investigate ecosystem dynamics over time periods beyond what is possible through experimental studies, observational studies and 'natural experiments' are essential (Fukami & Wardle 2005). For the present study, we used data collected from 30 boreal-forested lake islands that vary in time since the most recent fire 60 years ago to over 5000 years ago, with each island serving as an independent replicate (Wardle *et al.* 1997, 2003). The data for each island include the amount of C stored both above-ground and below-ground, and several factors that have been proposed as driving ecosystem C storage, including time since last major wildfire disturbance, plant species composition, plant diversity, NPP and litter decomposition. This dataset was organized into a path-relation network (figure 1) and subjected to structural equation modelling (SEM) (Malaeb *et al.* 2000; Grace *et al.* 2007). This enabled us to explore simultaneous influences of several potentially important drivers of C accumulation in forests that may be affected by fire regime, and thereby identify their relative importance to obtain a better understanding of forest ecosystems as sinks of atmospheric C.

2. MATERIAL AND METHODS

(a) *Study system*

We used data collected from each of 30 lake islands in the boreal forest of northern Sweden (65°55′ N to 66°09′ N; 17°43′ E to 17°55′ E); these islands vary greatly in fire history but with all other extrinsic driving factors being constant (Wardle *et al.* 1997, 2003). This fire regime gradient leads to well-characterized gradients in several community and ecosystem properties both above-ground and below-ground, with large increases in below-ground C storage and decreases in above-ground C storage with increasing time since fire (Wardle *et al.* 1997, 2003). Here, we used previously published data on time since fire, vascular plant diversity (Shannon–Weiner index), plant species composition, NPP, litter decomposition, and above-ground and below-ground C storage, in order to investigate drivers of above-ground, below-ground and total C storage. Our C-storage data represent a time-integrated measure over a lengthy timeframe, while our measurements of NPP, decomposition and plant-community variables are one-off measurements; we assume that these one-off measurements are reliable surrogates of time-integrated measures of them (Wardle *et al.* 1997, 2003). This dataset in total provides unique

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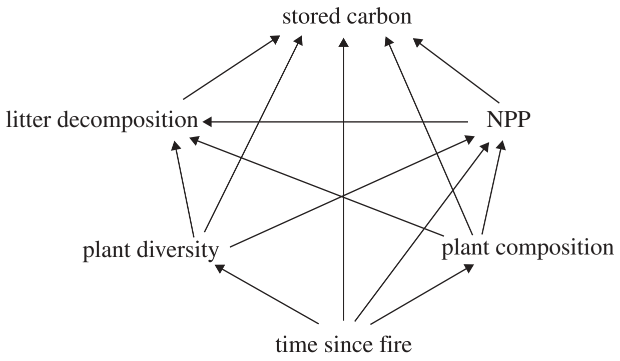

Figure 1. Illustration of all plausible interaction pathways in the study system.

opportunities for evaluating the mechanisms underlying how fire suppression in the order of centuries to millennia may directly or indirectly determine ecosystem C sequestration.

(b) *Statistical methods*

For all analyses, SEM (MPLUS software, version 5.2; Muthén & Muthén 1998–2007) was used for determining the combination of factors that best predicted above-ground and below-ground C storage. SEM is an advanced and robust multivariate statistical method that allows for hypotheses testing of complex path-relation networks (Malaeb *et al.* 2000; Grace *et al.* 2007). Here, we used step-wise procedures, guided by Akaike values, to obtain the most parsimonious set of predictors, starting off with all plausible interaction paths among the data variables obtained from the study system (figure 1) and removing those that did not improve the model. Several tests were used to assess model fit, i.e. the χ^2-test, comparative fit index (CFI), root square mean error of approximation (RMSEA) and standardized mean square error of approximation (SRMR). SEM assumes linear relationships between variables in the model. In our study system, factors that were hypothesized to drive C storage were significantly linearly related to both above-ground and below-ground C, with the exception of the relationships between above-ground C and plant diversity and time since fire, which were marginally non-significant. (A more detailed description of the study system and statistical methods is outlined in the electronic supplementary material, appendix A.)

3. RESULTS

(a) *Above-ground C*

The most parsimonious model for predicting above-ground C was obtained when plant composition, plant diversity and litter decomposition were the variables with hypothesized effects (figure 2*a*). The χ^2-test of model fit ($\chi^2 = 0.738$, d.f. $= 5$, $p = 0.981$), CFI (1.000), RMSEA (<0.001) and SRMR (0.033) all indicated that the model was of excellent fit. Further, the model showed that time since fire had significant effects on both plant species composition ($p = 0.005$) and plant diversity ($p = 0.001$), and that plant species composition affected both NPP ($p < 0.001$) and above-ground C storage ($p < 0.001$). There was also a significant negative effect of plant diversity on litter decomposition ($p = 0.023$). The amounts of variance explained by the model for all dependent variables except plant species composition were statistically significant at $p = 0.05$ (figure 2*a*). Since the direct influence of fire was not included in this model, the indirect effects of time since fire in relation to direct effects could not be investigated.

(b) *Below-ground C*

The most parsimonious model for predicting below-ground C was one in which plant composition, plant diversity and time since fire were the variables with hypothesized effects (figure 2*b*). The model had a high fit according to the chi-square test ($\chi^2 = 1.924$, d.f. $= 4$, $p = 0.750$), CFI (1.000), RMSEA (<0.001) and SRMR (0.041). Below-ground C was significantly influenced by plant species composition ($p < 0.001$), time since fire ($p = 0.004$) and plant diversity ($p = 0.012$). The other statistically significant relationships were the same as for the model predicting above-ground C (figure 2*a*). The amounts of variance explained by each variable for figure 2*b* were the same as for figure 2*a*, except that the amount of variance explained for below-ground C (75%) was considerably higher than for above-ground C (47%). In analyses of the indirect effects, the paths from time since fire via plant species composition and plant diversity were both significant ($p = 0.014$ and $p = 0.043$, respectively).

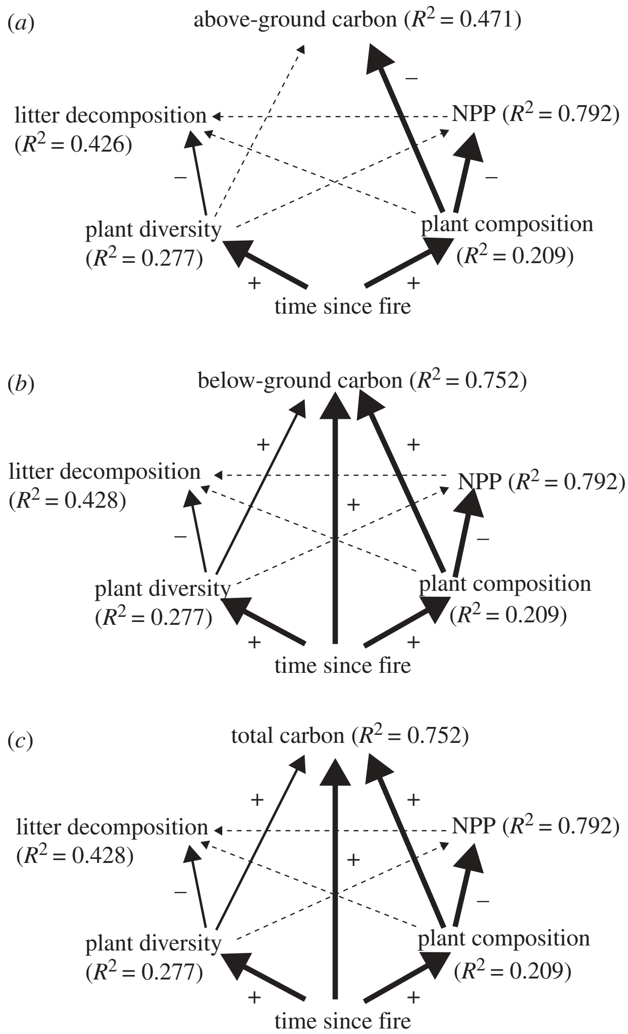

Figure 2. Results from SEM on the drivers of (*a*) above-ground C, (*b*) below-ground C and (*c*) total C. Bold arrows indicate statistically significant paths at $p = 0.05$ (thick bold arrows indicate $p < 0.01$). Dashed arrows indicate non-significant paths that were necessary to include in order to obtain the most parsimonious model. Signs ('+' or '−') indicate direction of relationships.

(c) *Total C*

The most parsimonious model for predicting total C stored included plant composition, plant diversity and time since fire as hypothesized drivers (figure 2*c*). The model also had a high fit according to the χ^2-test ($\chi^2 = 1.994$, d.f. = 4, $p = 0.737$), CFI (1.000), RMSEA (<0.001) and SRMR (0.041). Total C was influenced by plant species composition ($p < 0.001$), time since fire ($p = 0.004$) and plant diversity ($p = 0.023$). The other statistically significant relationships were the same as for the model predicting below-ground C (figure 2*b*). The amounts of variance explained for each variable in figure 2*c* were the same as for figure 2*a*,*b*, except that the amount of variance explained for total C (72%) was close to that explained for below-ground C (75%). The indirect influence of time since fire on total C via plant species composition was significant ($p = 0.018$), while the indirect effect via plant diversity was marginally non-significant ($p = 0.059$).

4. DISCUSSION

Our results highlight that increasing time since fire (resulting from fire suppression) promotes below-ground and total ecosystem C storage, both directly through accumulation of humus and indirectly through altering composition of the plant community (figure 2*b*,*c*). They also indicate that plant-community composition is an important driver of C accumulation in forest ecosystems, and that composition influences above-ground C storage in the opposite direction to below-ground and total C storage (figure 2*a*–*c*). Further, they support previous findings that absence of fire, and thus increased forest age, positively affects below-ground and total ecosystem C accumulation (Wardle *et al.* 2003; Luyssaert *et al.* 2008). By contrast, we found no evidence of NPP (i.e. ecosystem C gain) or decomposition (i.e. ecosystem C loss) in directly affecting C storage. In reaching these conclusions, we recognize that our measurements of NPP, decomposition and plant-community variables are one-off measurements, while our C-storage data represent a time-integrated measure over a much longer period. Like all studies of this type, it is necessary to assume that these one-off measures are related to time-integrated measures of them (Wardle *et al.* 1997, 2003).

The strong importance of plant-community composition on C storage that we found most likely reflects the importance of functional traits of the dominant plant species (Bunker *et al.* 2005). Previous work on this study system shows that with increasing time since fire, islands become increasingly dominated by slow-growing species that have well-defended tissues that impair soil-microbial activity and organic-matter breakdown, and should therefore contribute to accumulation of humus and below-ground C (Wardle *et al.* 1997, 2003). Communities dominated by such species are represented by high ordination scores in our analyses, and high ordination scores are in turn related to high C sequestration (figure 2*b*,*c*). By contrast, recently burnt islands are dominated by species that grow faster and promote microbial activity, leading to soil C loss. Thus, although early successional species store more C above-ground, this is more than offset by their negative effect on C storage below-ground, leading to less total C storage. A potential direction forward for this type of study would be to use weighted trait averages as predictors of processes relevant to C storage, as has been recently used for herbaceous communities using leaf trait data (e.g. Fortunel *et al.* 2009). However, there are challenges in applying such an approach to forests, for which leaves represent a relatively small proportion of total plant productivity.

Increasing plant species diversity has been proposed as contributing to greater ecosystem C sequestration (Fornara & Tilman 2008; Saha *et al.* 2009). We found a significant though relatively weak effect of plant diversity on below-ground and total C storage, which was considerably less than the direct effects of fire and plant species composition. This is most likely explained by diverse plant communities in our study system having a greater probability of including species with traits that promote below-ground C accumulation (Wardle *et al.* 1997). Our results are in agreement with previous observational studies using SEM (Grace *et al.* 2007) in revealing that the ecological impact of species diversity can be minor relative to the over-riding effects of plant species composition and abiotic disturbances.

In total, our results highlight the fact that C accumulation in boreal forests to a large extent is determined by wildfire frequency exerting both direct effects and indirect effects through influencing plant-community composition (and composition of plant traits) rather than plant diversity, NPP and litter decomposition rates. Thus, in addition to wildfire suppression, human activities, such as forest harvesting, that lead to plant compositional changes may greatly influence the ability of boreal forests to function as sinks of atmospheric CO_2 (Bunker *et al.* 2005; Luyssaert *et al.* 2008). Consequently, boreal forests that would most efficiently mitigate increases in atmospheric CO_2 are those containing particular (notably late-successional) plant species that promote below-ground C accumulation and those in which wildfires are suppressed.

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