Ecosystem context illuminates conflicting roles of plant diversity in carbon storage

Abstract

Plant diversity can increase biomass production in plot-scale studies, but applying these results to ecosystem carbon (C) storage at larger spatial and temporal scales remains problematic. Other ecosystem controls interact with diversity and plant production, and may influence soil pools differently from plant pools. We integrated diversity with the state-factor framework, which identifies key controls, or ‘state factors’, over ecosystem properties and services such as C storage. We used this framework to assess the effects of diversity, plant traits and state factors (climate, topography, time) on live tree, standing dead, organic horizon and total C in Quebec forests. Four patterns emerged: (1) while state factors were usually the most important model predictors, models with both state and biotic factors (mean plant traits and diversity) better predicted C pools; (2) mean plant traits were better predictors than diversity; (3) diversity increased live tree C but reduced organic horizon C; (4) different C pools responded to different traits and diversity metrics. These results suggest that, where ecosystem properties result from multiple processes, no simple relationship may exist with any one organismal factor. Integrating biodiversity into ecosystem ecology and assessing both traits and diversity improves our mechanistic understanding of biotic effects on ecosystems.

Keywords

biodiversity, community-weighted mean, ecosystem functioning, ecosystem services, functional diversity, functional traits, interactive factors, phylogenetic diversity, species richness, state factors.

INTRODUCTION

Decades of research have established that biodiversity influences ecosystem properties (Schulze & Mooney 1993; Chapin et al. 2000; Tilman et al. 2014) and services (Naeem et al. 2009; Cardinale et al. 2012; Isbell et al. 2017b). This research generated its own subdiscipline – biodiversity and ecosystem functioning (BEF). To isolate the influence of diversity from co-varying factors, much BEF research has occurred at small scales in communities where biodiversity is manipulated experimentally (Hooper et al. 2005; Cardinale et al. 2012). While this work provides strong evidence for isolated effects of altered species richness, genetic diversity and functional diversity, interactions with other drivers may confound extrapolating these effects to landscape scales (Srivastava & Vellend 2005; Wardle et al. 2011; Wardle 2016). A more recent approach explores diversity effects across broad geographic gradients, controlling for environmental variation through multiple regression or structural equation modeling. To date, few studies (but see, Diaz et al. 2007; Poorter et al. 2017) have integrated diversity with all the ecosystem drivers, known as ‘state factors’ in ecosystem ecology (Vitousek 2004; Chapin et al. 2011), typically used to model ecosystem processes at large scales. However, this progress suggests BEF is ripe for more complete integration with ecosystem ecology (Chapin et al. 2000).

Integrating plant diversity with other ecosystem drivers will help merge biodiversity research with ecosystem ecology and clarify diversity effects at large spatial scales. Organisms are an integral component of ecosystem ecology’s state-factor framework (Jenny 1980; Vitousek 2004; Chapin et al. 2011), but it has focused on dominant species or mean plant traits (Grime 1998), rather than diversity (but see Chapin et al. 2000). In the state-factor framework, climate, organisms (regional species pool), topography, geological substrate and
time since disturbance are independent state factors driving all ecosystem properties (Fig. 1). These distal drivers interact to influence proximal drivers (‘interactive factors’): microclimate, resource availability, organismal functional traits and disturbance regimes (Chapin et al. 2011). Although the relative strengths of plant functional traits and diversity as biotic drivers affecting ecosystem properties have been compared and contrasted (Grime 1998; Winfree et al. 2015; Finerty et al. 2016), an alternative approach integrates both, recognising the different axes of influence by which organisms affect ecosystem properties (see also, Díaz et al. 2007). In that spirit, we suggest incorporating diversity into the state-factor paradigm by broadening the interactive ‘organismal functional traits’ factor to ‘interactive biotic factors’, within which both mean traits and diversity warrant consideration (Fig. 1 and Fig. S1).

Although integrating diversity with environmental drivers has progressed in the past several years, the development and use of a cohesive theoretical framework is needed. The major ecosystem models (e.g. CENTURY, TEM, BIOME-BGC) currently do not incorporate diversity as a driver of carbon and nitrogen cycling, perhaps because of the lack of information on how diversity effects and interactions play out at landscape scales. Recent studies assessing diversity effects in combination with different environmental factors have found significant influences at broad geographic scales, including on algal biomass (Zimmerman & Cardinale 2014), primary production (Paquette & Messier 2011; Cavanaugh et al. 2014; Poorter et al. 2017), or multifunctionality in ecosystem properties (Maestre et al. 2012) or services (Gamfeldt et al. 2013; Liang et al. 2016; Duffy et al. 2017; Oehri et al. 2017). One study even structured some analyses on the state-factor framework, but their interpretations instead focused on diversity effects (Jing et al. 2015). Most, however, have assessed diversity as the only biotic predictor, ignoring concurrent impacts of important plant traits (but see Poorter et al. 2017). Fewer still also structured their analyses to reflect the key relationships among state factors, interactive factors and the processes of interest. A key component of the state-factor framework is whether ecosystem drivers are functionally outside (state factors) or inside (interactive factors) the realm of internal ecosystem feedbacks (Chapin et al. 2011). This distinction helps direct the structure of measurements and analyses assessing effects of different ecosystem drivers (Fig. 1 and Fig. S1).

What is the strength of plant traits and diversity, as interactive factors, on landscape-scale ecosystem properties and services after accounting for state factors? Mean functional traits and organismal diversity both have demonstrable mechanisms that should influence ecosystem properties at the landscape scale.

Fig. 1 Relationship among state factors, interactive factors, and ecosystem carbon pools. Diversity, in bold, and the arrows emanating from it, show our proposed modification of the state factor approach. The circle indicates whether ecosystem drivers are functionally outside (state factors; outside the circle) or inside (interactive factors; inside the circle) the realm of internal ecosystem feedbacks. Grey text indicates lack of data in this study to include these factors. We aimed to determine the impact of biotic factors on C pools, so we did not include feedbacks from C pools to biotic factors. Variables used for different state factors are in parentheses (MAT = mean annual temperature, MAP = mean annual precipitation). Dashed arrows indicate fluxes between different ecosystem C pools and atmospheric CO2 to emphasise that these components of total ecosystem C storage respond differently to the different ecosystem state and interactive factors. Dark blue arrows indicate that interactive factors result from interactions among state factors. Light blue arrows are positive relationships, and red arrows are negative relationships of biotic factors on ecosystem C pools. Adapted from Chapin et al. 2011.
scale. For example, mean traits along the leaf economic spectrum affect productivity (Díaz et al. 1999; Wright et al. 2004; Reich 2014), litter quality, decomposition and plant-soil productivity feedbacks (van der Putten et al. 2013; Hobbie 2015). Trait diversity can increase resource capture and productivity via complementarity or facilitation (Vandermeer et al. 2002; Cardinale et al. 2011; Tilman et al. 2014). Diversity may also stabilise services by incorporating environmentally tolerant species or allowing asynchronous responses to environmental fluctuations (Walker et al. 1999; Yachi & Loreau 1999; Bald vanera et al. 2006; Isbell et al. 2009; Cardinale et al. 2013; Wang & Loreau 2016). We argue that studies should incorporate both mean traits and diversity as biotic drivers to better understand when and where they have strong impacts. Many ecosystem services are combinations of properties (Cardinale et al. 2012) that may respond independently to altered diversity. Thus, understanding mechanisms will require considering the component properties rather than the single aggregated service. For example, total ecosystem C storage reflects imbalances between C inputs from primary production and losses from decomposition (Fig. 1). Decomposition is typically more sensitive to temperature and high soil moisture than production, so that soil C increases at colder, higher latitudes (Díaz et al. 2009a) and in waterlogged soils (Schuur et al. 2001; Mack et al. 2008; Grosse et al. 2011). At the same time, production and decomposition are maximised by high nitrogen, low lignin leaves (Hobbie 1992; Wright et al. 2004; Reich 2014; Hobbie 2015; Cornelissen et al. 1999), and shifts in these traits may have little net effect on soil C.

Production appears to be more sensitive to changes in diversity than decomposition (Srivastava et al. 2009; Hooper et al. 2012; Jewell et al. 2017), but whether this translates into greater ecosystem C storage remains unclear. Generally, diversity increases plant production and plant C (e.g. Cardinale et al. 2011; Paquette & Messier 2011; Gamfeldt et al. 2013; Ruiz-Benito et al. 2014; Liang et al. 2016; Duffy et al. 2017; Poorter et al. 2017), but diversity effects on decomposition and soil C show mixed effects (Hattenschwiler et al. 2005; Fornara & Tilman 2008; Srivastava et al. 2009; Reid et al. 2012; Gamfeldt et al. 2013; Hungate et al. 2017). Greater plant and detritivore diversity can accelerate decomposition (Nielsen et al. 2011; Handa et al. 2014), which should decrease C storage. Thus, C storage is an aggregate property of production, decomposition and disturbance – processes that respond independently to environmental and biotic changes, including changes in diversity. The state-factor framework offers structure for evaluating these interacting influences simultaneously.

We investigated diversity effects on ecosystem C storage using the state-factor framework with climate, topography and stand age, and the interactive factor of mean organismal traits. We selected variables representative of these state factors based on well-supported ecosystem science (e.g. Chapin et al. 2011) and recent studies in our focal ecosystem (Paquete & Messrier 2011). Our goal was to illustrate how integrating biodiversity with other ecosystem controls leads to mechanistic insights that may be lost when this framework is not used, when key drivers are not accounted for, or when emphasis is solely on whether biodiversity is significant or not. We used Québec Forest Survey data to evaluate these effects on C in live trees, standing dead trees, the soil organic horizon, and their sum, total ecosystem C. We asked: 1. How does geographic variation in interactive biotic factors (plant traits and diversity) affect C storage when accounting for variation in state factors across broad geographic regions? What are the relative strengths of mean traits and diversity effects? We used structural equation modeling (SEM) to reflect direct effects of state factors (those outside the realm of internal ecosystem feedbacks) on C storage, as well as indirect effects via interactive biotic factors (mean plant traits and diversity), consistent with the state-factor framework (Fig. 1 and Fig. S1). This structure also allowed us to compare relative effects of mean traits and diversity. Debate continues about which functional traits and diversity components (phylogenetic diversity, functional diversity, or species richness) have greatest effects on ecosystem properties (e.g. Cadotte 2015; Cardinale et al. 2015; Venail et al. 2015; Naeem et al. 2016). We therefore evaluated a variety of traits and diversity metrics to better understand which provide the most explanatory power when combined with state factors in this framework. 2. Is there evidence that different biotic mechanisms control various C pools? Ecosystem theory and evidence suggest this likelihood (Chapin et al. 2011), with production traits driving live tree C and decomposition traits driving organic horizon C. We hypothesised that explaining variation in landscape C storage requires mechanistic linkages among C pools and different functional traits or diversity metrics. Because we expected that state and interactive biotic factors would affect C pools with varying strengths (Díaz et al. 2009b), we assessed whether models of total C would perform as well as those investigating individual pools: is it sufficient to lump contributing properties into a single ecosystem service, or should they be separate? Although we focused on ecosystem C, we anticipate this approach will clarify organisal effects on other ecosystem services as well.

**METHODS**

**Datasets and carbon pools**

We used three state factors – climate, topography and time since disturbance – plus mean plant traits and diversity as facets of the interactive biotic factor (Table I and Table S1; Fig. 1 and Fig. S1; Appendix 2) to assess ecosystem controls on C pools in temperate and boreal forests of Québec (Fig. 2; Paquette & Messier 2011): live tree, standing dead, soil organic horizon, and total C (their sum). Data at each site were collected in 400 m² circular plots as part of the Québec Forest Survey (MRNFQ 2006; summarised by Paquette & Messier 2011, Appendix 1; Table S1). Sites were sampled every decade; we selected the most recent measurement for sites with a recorded age. Data were insufficient to estimate coarse woody debris C and did not include mineral soil C or measurements of nutrient availability.

We expected effects of topography (drainage) on C pools would overwhelm other factors in fast (dry) and slow (wet) draining sites, so we performed analyses on full \((n = 2624)\) and moderately drained datasets (drainage rating 2–4,
n = 2323), where we expected biotic factors would play a stronger role in C accumulation. Temperate forests were restricted to a relatively limited climatic range that may not represent the breadth of environmental conditions in this biome, challenging our ability to test for distinct relationships in temperate vs. boreal systems; we therefore grouped these forests together for analyses.

At each site, all trees > 9.1 cm DBH were measured, identified, and counted. Live tree biomass was the sum of stem wood, bark, branches, leaves and roots using species-specific allometric equations for aboveground pools (Lambert et al. 2005) and coarser deciduous and conifer allometries for roots (Li et al. 2003). Dead tree biomass was the sum of dead wood, bark, branches and roots. Live and standing dead biomass were converted to carbon (C) content using C = 0.5 * biomass. Although the C content of conifer and hardwood temperate trees ranges from 43 to 55% C (Lamplom & Savidge 2003; Thomas & Martin 2012), we chose 50% as a mid-point value because we did not have data on all species encountered. We estimated organic horizon C using site measurements of soil group and organic layer depth, combined with soil great group bulk density and C content (Shaw et al. 2008). Organic horizon C = bulk density * organic layer depth * %C. Total C was the sum of live, standing dead and organic horizon C. All values are Mg C ha⁻¹.

### Plant traits and diversity metrics

Site-level species richness was assessed for each 400 m² site. We assembled trait data for the species in the dataset from published sources (Tables 1, S1, S2) (Paquette & Messier 2011), focusing on traits we hypothesised would affect C pool sizes either via trait means or diversity. To represent the traditional ecosystem approach, we calculated community-weighted means (CWM) for each functional trait at each site, per Lavorel et al. (2008), weighted by species basal area. For ordered traits, CWM calculations return the value of the dominant class (Tables S1, S2). We investigated three types of diversity metrics: species richness, functional diversity and phylogenetic diversity. We used species richness (SR) to represent the dominant BEF approach. We computed functional dispersion (FDIs), which provides the average multivariate distance of individual species from the centroid of all species in functional trait space, weighted by basal area (Laliberté & Legendre 2010; Paquette & Messier 2011) (Table 1). We calculated twelve FDIs metrics, using either single or multiple traits, for traits we hypothesised could influence C pools via diversity (Tables 1 and S1). While many studies using FDIs include a wide variety of traits, we were concerned that, in such an approach, variation in less relevant traits could obscure effects of more relevant traits (Bernhardt-Römermann et al. 2008). Our limited number of multiple trait FDIs metrics were intended to capture a variety of explicit mechanisms by which species might contribute to complementary resource use or tolerance to abiotic conditions (Table 1). We chose FDIs a measure of functional diversity because it computes for plots with only two species (FDIs = 0 when SR = 1) and is not strongly correlated with SR for theoretical communities (Laliberté & Legendre 2010). In practice, SR and FDIs metrics were moderately correlated across our datasets (Pearson’s r = 0.39–0.70), but were never used together to predict C pools. For phylogenetic diversity, we calculated Phylogenetic Species Variability (PSV), using a molecular phylogeny of our species based on chloroplast genes (Paquette & Messier 2011). PSV quantifies how phylogenetic relatedness decreases variance of a hypothetical trait shared by species in a community and is mathematically independent of SR (Helmus et al. 2007). Although PSV was moderately correlated with SR across the dataset (r = 0.51), they were never used together to predict C pools. We computed CWM and FDIs using the ‘FD’ package (Laliberté & Shipley 2011) and PSV using the ‘picante’ package for R (Kemel & Legde 2010; R Core Team 2011).

All metrics were calculated using a priori species traits rather than plot-based measurements. While this certainly missed some within-species variability resulting from genetic effects and phenotypic plasticity, it is a common approach in
broad-scale geographic studies, was essential given our large number of sites, and avoided circular logic for some functional traits. For example, maximum tree height was an *a priori* species trait taken from the literature and was not also used to calculate live tree C in individual plots. Thus, correlation between maximum height and plot-based measurements such as basal area was very low ($r = 0.05$).

Statistical analyses

**Strategy and conceptual framework**

Our primary goal was to build on the wealth of the knowledge from ecosystem and community ecology about drivers of C storage and biotic composition to develop ecologically relevant SEMs, based on the state-factor framework (Fig. 1), that would evaluate the role of both plant functional traits and diversity at landscape extents. To this end, we developed full and simplified meta-models (Grace *et al.* 2016) to guide our analysis (Fig. S1). However, given the large range of theoretically and empirically supported potential relationships among state and interactive factors and of potential relationships between these factors and different C pools, we first aimed to find the best descriptors for each state and interactive factor using multi-model inference and *a priori* ecological knowledge. The goal for this step was to minimise the likelihood of dismissing conceptually important explanatory variables solely because we had not used an appropriate statistical relationship or had arbitrarily used a particular metric that strongly covaried with another metric. Based on our simplified meta-model (Fig. S1), we then selected variables to build SEMs. We describe these steps in more detail below and in Appendix 2.

**Multi-model inference: state and biotic interactive factor selection**

We first identified the best variables or function shape for effects on different C pools for each state factor: climate, topography and time since disturbance. Because previous studies found strong correlations among various temperature and precipitation predictors at these sites, we used the simplest estimators: mean annual temperature (MAT) and mean annual precipitation (MAP) (Paquette & Messier 2011). Based
on those results and abundant previous research on ecosystem C controls (e.g. Chapin et al. 2011; Taylor et al. 2017), we expected MAT, MAP, and their interaction would affect all pools, so we included them in all state factor models. Plot coordinates and elevation were used to compute MAT and MAP using interpolation of 30-year normals from all available weather stations (as in Paquette & Messier 2011).

Drainage represented the topography state factor, and ranged from 0 to 6 in 0.5 increments: 0-1.5 are rapidly draining, dry soils; 2-4 are moderately draining soils; 4.5–6 are slowly draining, wet soils. We tested for linear, exponential, or unimodal relationships between C pools and drainage. Stand age, representing time since disturbance, was estimated by coring from the five trees with the largest DBH at each site (MRNFQ 2006). We tested for linear, exponential, unimodal or lognormal (saturating) relationships between C pools and age. We used multi-model inference (MMI), including model averaged parameters, sums of weights (SW; Burnham & Anderson 2002), and standardised effect sizes (Galipaud et al. 2014; Galipaud et al. 2017; Cade 2015), to select the best relationships between each variable and C pool combination (Table 2; see Appendix 2 and Tables S3 and S4 for detailed methods and results).

We then selected variables for the interactive biotic factors using MMI to identify the trait mean and diversity metric that added the most explanatory power to the selected state factor models for each C pool. We did so by including only a single trait mean or diversity metric at a time, or one trait mean plus a diversity metric, in addition to the state factors. Selection of biotic factors was almost fully balanced across the candidate models; correcting for potential bias caused by the slight imbalance did not alter results (Appendix 2; Fig. S2). We chose this approach, rather than examining the effects of biotic factors on C pools in a fully factorial model set with abiotic factors, because the latter would allow models consisting of only biotic factors - not ecologically realistic given known drivers of C pools (Chapin et al. 2011; Liang et al. 2016; Oehri et al. 2017). Even so, we repeated the above analysis including models that contained only biotic factors (one trait, one diversity, or one trait + one diversity), but selected models were identical (Appendix 2). For live tree C, MMI clearly selected potential maximum height and PSV as the best predictors for CWM and diversity metrics in both datasets (Table 2, Fig. S3). Leaf mass per area was the clear selection for the CWM variable for organic horizon C. Diversity of LMA was the best predictor of organic horizon C, though more strongly in the moderately drained than full dataset. MaxH and FDis of wood density were the strongest biotic predictors for total C, though with less clear predominance than in the individual C pools (Table 2, Fig. S3). See Appendix 2 for detailed methods and Tables S5 and S6 for detailed results. Before constructing the SEMs, we used MMI to identify the shape of the relationships among state factors and the selected trait mean and diversity metrics for each C pool in each dataset, using the same process described above for the selection of state and interactive factors (Appendix 2; Tables S7-S8).

**Structural equation model**

For each C pool within each dataset, we constructed SEMs based on our simplified meta-model (Fig. S1, Appendix 2) using the selected state and interactive biotic factors for that pool (package ‘lavaan’ in R) (Rosseel 2012). Each SEM accounted for the direct state and interactive biotic factor effects on a given C pool and indirect state factor effects via diversity and mean plant traits. Each also allowed for potential correlations among state factors (not shown) and between mean trait and diversity metrics. Because the impact of diversity on ecosystem properties often saturates at high diversities, we used AICc to compare SEMs with untransformed and ln-transformed diversity. If there was no best model, the simpler linear model was selected. To understand the predictive impact of including plant traits and diversity with state factors, we compared the C pool $R^2$ from the complete SEM to the R’s from an SEM without plant traits (state and diversity factors only) and one with only state factors.

**RESULTS**

**Pool size distributions**

Across all sites, the distribution of total C was skewed. On average, sites contained 150 Mg C ha$^{-1}$ (median = 130 Mg C ha$^{-1}$), but the distribution tail reached 766 Mg C ha$^{-1}$ (Fig. 3, Table S2). The tail was largely driven by organic horizon C (OHC), which increased exponentially with drainage (Fig. 3c); OHC as a percentage of total C increased with drainage from fast (< 2, 15–30%) to slow (>4, 70–90%; Fig. 3g). Live tree C, as a percent of total C, followed the opposite pattern (Fig. 3e). While standing dead C reached 25–35% of total C in some sites, in most it was <5% (median = 0.73%; Fig. 3b and f).

**Structural equation models: integrating state and interactive biotic factors**

For all C pools, including biotic interactive factors with state factors in the SEMs better predicted forest C pools,
particularly for live tree C (Table 3). In most models, abiotic state factors were the most important factors with the largest impacts on C pools (Table 4). The exception was for live tree C, where interactive biotic variables had equally large impacts compared to state factors (Table 4; Fig. 4–6). For all pools except organic horizon and total C in the full dataset, diversity effects did not saturate; the best SEMs used untransformed diversity (Figs 4–6; Tables 3, S9).

Temperature and age had the greatest effects of individual state factors on live tree C, with similar effects in both datasets (Fig. 4). Across both datasets, the strongest individual direct effect on live tree C was from a biotic factor, the CWM of maximum potential tree height (MaxH; Fig. 4; Table 4). However, variation in state factors drove up to 40% of the variation in MaxH (Fig. 4), indicating substantial species turnover responding to environmental conditions. After accounting for indirect and direct state factor effects, the effect of MaxH on live tree C was comparable to effects of temperature and age. Increasing temperature and MaxH from their minimum to maximum value across each dataset increased live tree C by 80 Mg C ha$^{-1}$ in both datasets. Increasing age, holding other factors constant, initially increased live tree C to a maximum at c. 150 years, but decreased it by 15–19 Mg C ha$^{-1}$ in the oldest sites (unimodal relationship; Fig. 4; Table 4). PSV responded less strongly to environmental variation and had smaller impacts on live tree C.

![Graphs](image-url) Fig. 3 Carbon pool sizes (a–d) and percent of total C (e–g) for live tree C (a and e), standing dead C (b and f), organic horizon C (c and g), and total C (d) for the full dataset. $N = 2624$ sites, with 149 sites poorly drained (D>4). Lines are loess smoothers with 95% confidence intervals (shaded areas).

Table 3 Comparison of the full SEM containing state factors, best community-weighted mean plant trait (CWM) and best diversity (Div) metric, with the state-factor-only and state factor plus diversity SEMs

<table>
<thead>
<tr>
<th>C pool</th>
<th>Dataset</th>
<th>CWM</th>
<th>Diversity</th>
<th>Best Div</th>
<th>dAICc (between best and next best full SEM)</th>
<th>Full SEM R$^2$</th>
<th>State factor SEM R$^2$, C pool</th>
<th>State Factor + Diversity SEM R$^2$, C pool</th>
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<td>WDR</td>
<td>FDis.TolS</td>
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</table>

CWM and diversity metric abbreviations as in Table 1. Full = all sites ($n = 2624$). Mod. Drain = Moderately drained sites, drainage classes 2–4 ($n = 2323$). LTC = Live Tree Carbon. SDC = Standing Dead Carbon. OHC = Organic Horizon Carbon. TC = Total Carbon. A comparative fit index (CFI) > 0.9 indicates a good fit. dAICc was used to compare SEMs with linear and nonlinear diversity.
weak direct effects on organic horizon C in the full and moderately drained datasets respectively. After accounting for indirect temperature and precipitation effects on organic horizon C via interactive biotic factors, the temperature by precipitation interaction remained significant only in the moderately drained sites (Fig. 5). For the full set, direct climate effects disappeared; they were mediated through biotic factors, with strong negative temperature effects on mean LMA. Similarly, direct age effects on organic horizon C were minor in the moderately drained or insignificant in the full datasets (Table 3, Fig. 5). Again, age effects were moderated by interactive biotic factors, resulting in positive indirect age effects in both datasets (Fig. 5).

Biotic factors had significant but smaller effects on organic horizon C than live tree C. Increasing LMA across the range of values in both datasets increased organic horizon C by 30-35 Mg C ha\(^{-1}\), but in the moderate drainage dataset, this was
one of the dominant effects, on par with the magnitude of temperature and drainage impacts (Table 4). Again, plant trait effects were stronger than those of diversity. Although mean LMA increased organic horizon C, FDis of LMA decreased organic horizon C by a maximum of 12–13 Mg C ha$^{-1}$ (Table 4).

Drivers of total C reflected the most important variables affecting live tree and organic horizon C. As with organic horizon C, drainage had the largest effect in the full dataset: reducing drainage from fast to slow increased total C by 420 Mg C ha$^{-1}$ (Fig. 6; Table 4). It had a smaller impact in the moderately drained sites, increasing total C by only 39 Mg C ha$^{-1}$ (Table 4). Climate, age and mean plant trait (MaxH) effects on total C were similar in direction to live tree C. However, path coefficients were muted compared to live tree C (Figs 4–6): increasing maximum tree height from its minimum to maximum value increased total C by 39 Mg C ha$^{-1}$ in both datasets, roughly half of the increase for live tree C.

Diversity effects — both variables and direction — differed between live tree C and total C. In full and moderately drained sites, increasing the FDis of wood density across the full range of values decreased total C by 12 and 15 Mg C ha$^{-1}$ respectively (Fig. 6), similar to negative diversity effects on organic horizon C.

**DISCUSSION**

**Overview**

The state-factor paradigm provided a clear conceptual framework to integrate BEF with ecosystem ecology. Our intent was to integrate diversity with known controls on ecosystem properties by asking: what does including diversity as a control add to our knowledge of ecosystem C storage? Our results suggest that diversity effects on ecosystem processes are an important second dimension of organismal traits as an interactive factor (Fig. 1) (Diaz et al. 2007; Chapin et al. 2011). Diversity and mean traits both responded to external state factors and directly influenced C pools in SEMs. That said, diversity per se (richness, phylogenetic, or functional) generally had substantially less impact on C pools than mean traits, and state factors together had a similar or stronger impact than interactive biotic factors. Our conclusions differ somewhat from recent studies (Liang et al. 2016; Duffy et al. 2017; Oehri et al. 2017): while those studies emphasised significant diversity effects and similar ranking to some individual abiotic variables in landscape-scale studies, we found that diversity had significant, but small, impacts on forest C storage. Our approach is conceptually consistent with recent studies of diversity effects on ecosystem properties at landscape scales (Grace et al. 2007; Grace et al. 2016; Cavanaugh et al. 2014; Poorter et al. 2017), but explicitly differentiated between state and interactive factors, included mean traits and diversity as drivers, and included both live and detrital C storage. Our findings are also consistent with studies that found diversity to have relatively small impacts on ecosystem processes across broad geographic gradients in dryland (Maestre 2012), tropical (Poorter et al. 2017), and grassland (Grace et al. 2007) ecosystems. However, we do not propose that this will always hold, either across ecosystems or across processes, depending both on ecological differences among ecosystems (see, for example, Paquette & Messier 2011; Liang et al. 2016) and the range of variability in key drivers within any given study (as we saw in comparing our two datasets). Within
tropical forests, some studies show stronger effects of diversity than mean traits and environmental variables (e.g. Cavanaugh et al. 2014) and others show the opposite (Poorter et al. 2017). More importantly, we argue that evaluating drivers together using common metrics (e.g. actual changes in ecosystem services) and integrating them within the state-factor framework will paint a more complete picture of mechanisms affecting C storage, or other ecosystem services, than opportunistic subsets of drivers alone. The approach we advocate will also guide consistent data collection for future studies aiming to refine and test within- and cross-system comparisons.

Our results emphasise the importance of modeling processes independently when assessing complex ecosystem services. When we assessed total C, rather than independent pools, biotic effects were masked, obscuring underlying mechanisms. While some complex processes (Caliman et al. 2013) or suites of positively correlated processes (Maestre et al. 2012) may show stronger diversity effects, the pattern we saw is likely whenever contributing processes exhibit different responses to environmental drivers. Furthermore, quantifying responses of individual processes to diversity allowed us to compare positive and negative diversity effects on a similar scale (i.e. Mg C ha\textsuperscript{-1}) and to evaluate the net impact on the ecosystem service of C storage. This has not been possible with previous multifunctionality studies (Zavaleta et al. 2010; Maestre et al. 2012; Byrnes et al. 2014). Understanding how complex 'bundles' of ecosystem services will respond to changing environmental conditions and management (Raudsepp-Hearne et al. 2010; Balvanera et al. 2014; Cavender-Bares et al. 2015) will require understanding the relationships among state and interactive factors – both abiotic and biotic – and the processes that contribute to specific ecosystem services.

**Relative impacts of mean traits and diversity on C storage at landscape extents**

Across C pools, interactive biotic factors had the strongest effect on live tree C. Increasing from minimum to maximum diversity and plant trait values added 16 and 78 Mg live tree C ha\textsuperscript{-1} respectively, an amount comparable to the direct increase in live tree C across the full range of temperatures. The consistently positive diversity effects on live tree C agree with other studies that assessed diversity effects on live tree biomass and productivity (e.g. Paquette & Messier 2011; Gamfeldt et al. 2013; Liang et al. 2016; Oehri et al. 2017). Our results further suggest that mean plant traits and diversity influenced C pools independently. Plot experiments frequently show diversity effects on plant biomass via complementarity, facilitation and insurance effects (Cardinale et al. 2011; Tilman et al. 2014), in addition to the effects of particular species (sampling effects) (Loreau & Hector 2001). Similarly, the consistent significance of both mean traits and diversity in our models suggests that some diversity effects occur orthogonally to mean traits (Cavanaugh et al. 2014; Ruiz-Benito et al. 2014; Poorter et al. 2017).

For organic horizon C, drainage was the dominant driver. Despite this, total biotic effects across the range of values in these sites were still half the size of their effects on live tree C. Mean functional traits increased organic horizon C by a maximum of 34 Mg C ha\textsuperscript{-1} and diversity decreased it by a maximum of 12–13 Mg C ha\textsuperscript{-1}. Negative effects of FDis of LMA on organic horizon C stocks in our dataset align with recent
estimates of positive effects of litter mixing on decomposition rates (e.g. Handa et al. 2014), which leads to smaller soil C pools. As discussed below, however, among-study variability indicates that we still have much to learn about the mechanisms driving such responses (Gessner et al. 2010).

Despite the importance and independence of diversity in our results, it ranked well below mean functional traits as a biotic predictor of C storage (Table 4, Figs 4–6). Díaz et al. (2007) also found stronger mean trait than diversity influences for various ecosystem services. In our study, diversity always had low standardised effect sizes (< 0.15) and accounted for C gains or losses of ≤ 16 Mg C ha⁻¹. These effects were lowest for non-living pools, where C stored often greatly exceeded that in live trees. These findings contrast with recent analyses that found diversity effects to be as strong as the most important abiotic variables across landscapes (Liang et al. 2016; Duffy et al. 2017; Oehri et al. 2017). Few other studies have assessed plant diversity effects on non-living pools at these scales, but those that have also found weak (although positive) effects of tree richness on soil C pools (Gamfeldt et al. 2013) and other belowground properties (Maestre et al. 2012). Additional analyses that explicitly incorporate the state-factor framework will help assess whether our results about the relative effect sizes of diversity on C storage are general.

**Impacts of different state and interactive biotic factor controls on C pools**

**Direct and indirect state factor controls**

The strength and direction of state factors and interactive biotic drivers varied by C pool. State factor SEMs explained 30–34% of variation in live tree C, 19–66% in organic horizon C, and 10–60% in total C, but very little variation in standing dead C (≤ 2%). Live tree C responses to state factors were consistent with known biogeochemical and successional drivers of plant production and biomass, such as positive interactions between temperature and precipitation (Fig. S5), unimodal effects of drainage, and unimodal relationships with age (Díaz et al. 2009a; Chapin et al. 2011). Similarly, responses for organic horizon C were consistent with the positive effects of temperature and precipitation on decomposition rates (Fig. S5), negative effects of anaerobic conditions on decomposition, and accumulation of C in soil and litter layers over successional time (Díaz et al. 2009a; Chapin et al. 2011).

However, substantial effects of abiotic state factors on C pools also occurred as indirect effects via interactive biotic factors. For example, MaxH increased with stand age, temperature, and precipitation, and diversity increased with temperature, while also having positive direct effects on live tree C. Such interactive effects are well known in ecosystem ecology, when indirect abiotic effects via plant traits can outweigh direct abiotic effects on decomposition (e.g. Van Cleve et al. 1991; Vitousek et al. 1994) and production (e.g. Lauenroth & Sala 1992; Hooper & Johnson 1999). In our datasets, changes in mean functional traits across sites resulted from changing relative abundances and species turnover due to changing abiotic conditions. The strength of these effects, particularly for live tree C, suggests that species turnover across sites (beta diversity) may be more important in driving ecosystem properties across broad geographic extents than alpha diversity within sites (e.g. Wintz et al. 2015).
Different interactive biotic factor controls on component C pools

Mean functional traits differentially affected the various pools, with strongest effects on live tree C. MaxH had the strongest direct effects on live tree C and was correlated with several other traits (positive with leaf N, wood density, and leaf size; negative with leaf longevity and LMA; Table S11). These traits are consistent with late successional forest growth, light-competitive life history traits (Grime 2001), and faster growth on the leaf economic spectrum (Hobbie 2019; Wright et al. 2004; Reich 2014), which predominate in locations with high resource availability and long disturbance intervals. Therefore, the strong effects of maximum height may reflect species’ natural associations with soil fertility (i.e. larger species in high fertility sites), for which we did not have a direct measure.

Mean functional traits had weaker effects on organic horizon C than live tree C. The principal trait affecting this pool reflected previous understanding from ecosystem ecology: positive correlation of LMA with organic horizon C, consistent with its negative effects on decomposition rates (Table 4, Fig. 5; Diaz et al. 2009). LMA was also negatively correlated with leaf N (Table S11), which could further explain the impact of LMA on organic horizon C, as declining N content reduces decomposition rates (Hobbie 2015) and increases landscape-scale soil C (Diaz et al. 2007; Gamfeldt et al. 2013).

Diversity had its strongest impact on live tree C via PSV. The independence of this effect from trait means suggests diversity increased resource uptake or environmental tolerances of the entire community, increasing productivity and live tree C. The importance of PSV over functional diversity metrics suggests that the diversity of unmeasured traits affected this pool, though which and how requires further study (Paquette et al. 2015). On the other hand, where diversity was significant for organic horizon C, its effects were negative. Increasing FDis of LMA decreased organic horizon C. Mechanisms driving this relationship remain unclear, as decomposition rates show variable responses to aboveground diversity: litter mixtures can show increases, decreases, or no effects on decomposition compared to single-species litter (Srivastava et al. 2009; Handa et al. 2014; Jewell et al. 2015, 2017) and sparse literature shows inconsistent diversity effects on soil and litter pools (Diaz et al. 2007; Fornara & Tilman 2008; Gamfeldt et al. 2013; Lange et al. 2015; Isbell et al. 2017). However, observations from forests generally support increased decomposition with increasing diversity (Nadowski et al. 2010), potentially via priming effects or decomposer complementarity, facilitation, and decomposer interactions (Gessner et al. 2010; Cardinale et al. 2011). We found comparatively poor performance of FDis combinations of multiple traits. Our results suggest that combining many functional traits into one metric may obscure mechanisms affecting C pools (Bernhardt-Römermann et al. 2008). In addition, while we have confidence in the traits selected by our statistical procedures, selecting a priori among many potential traits for use in functional diversity metrics remains a vexing problem (Petchey & Gaston 2006; Laliberté & Legendre 2010; Mouchet et al. 2010).

Assessing total C pools: relationship to complex ecosystem services

Combining C pools reduced the predictive power of state and interactive biotic factors. Responses of total C to drainage followed relationships found for soil organic horizon C, but the remaining abiotic state factors followed patterns found in live tree C. Combining component pools into total C greatly reduced the importance of biotic variables. For example, maximum tree height was among the strongest effects on live tree C, and diversity (PSV) also made significant contributions. However, when assessing total C, mean trait and diversity effects greatly decreased. This suggests that combining pools into total C obscured the importance of biotic variables and the underlying mechanisms driving C accumulation (see also Gamfeldt et al. 2013).

Diversity did not simultaneously maximise all C pools. Indeed, assessing diversity effects only on live tree C would have missed contrasting effects on organic horizon C, one of the largest ecosystem carbon pools. Similar cancelling effects muted responses of forest C dynamics to diversity in the tropics: tree species richness increased both growth of surviving trees and biomass loss by mortality, with no significant effect on net change in aboveground biomass (Poorter et al. 2017). Multifunctionality studies indicate that such tradeoffs are common (Zavaleta et al. 2010; Byrnes et al. 2014), such that conditions that maximise one ecosystem service may not maximise others (e.g. the well-known tradeoffs between production and regulation services; Cavender-Bares et al. 2015). On the other hand, some ecosystem processes or services may be positively associated with one another, or may depend on different traits of different species, leading, for example, to greater effects of diversity on multiple or more complex functions (e.g. Hooper & Vitousek 1998; Bracken & Stachowicz 2006; Isbell et al. 2011; Maestre et al. 2012; Caliman et al. 2013; Barnes et al. 2018). In our C storage example, however,
contrasting effects of diversity and effects of different functional traits on different C pools meant that explicitly modeling the drivers of each property provided the clearest path toward understanding the underlying responses of C storage (Gamfeldt et al. 2013; Ricketts et al. 2016).

Conclusions: The merger of BEF and ecosystem ecology?

Using the well-established state-factor framework of ecosystem ecology provided insights into abiotic state factor and interactive biotic controls of C storage and helped reveal underlying mechanisms. We used SEMs to test this framework, but they are not in themselves a panacea for merging BEF and ecosystem ecology. First, SEMs can only assess effects of biotic variables if they have unshared variance with abiotic drivers. If biotic factors are so highly correlated with abiotic state factors that their effects are indistinguishable (e.g. MAP, taxon richness, and plant and soil nutrient content across precipitation gradients in dryland ecosystems; Jing et al. 2015), only experimental approaches can tease apart interactive effects (e.g. Van Cleve et al. 1983; Lauenroth & Sala 1992; Hooper & Johnson 1999). However, the state-factor framework can and should inform interpretation of covariance among abiotic factors, diversity, functional traits, and ecosystem properties, rather than attributing the effects of shared variance to diversity alone (e.g. Jing et al. 2015). Thus, there is a need for complementary experimental approaches for better understanding how ecosystem properties might change with species gain or loss at multiple sites across environmental gradients (Wardle et al. 2011; Hooper et al. 2012; Craven et al. 2016).

Because of strong collinearity among potential biotic predictors, we restricted our work to identifying the best single predictors among mean trait and diversity metrics. Greater predictability may be achieved using multiple traits or diversity metrics (Díaz et al. 2007; Villéger et al. 2008; Naem et al. 2016), incorporating individual species or functional type effects (Nadrowski et al. 2010; Gamfeldt et al. 2013), or assessing interactions and feedbacks among traits, diversity and abiotic variables (Grace et al. 2016). For example, we did not include non-recursive SEM feedbacks of C storage (biomass) on diversity, as in Grace et al. (2016). While a feedback from biomass to diversity is plausible in temperate and boreal forests, its influence is likely small, as diversity typically responds to changes in broad climatic and topographic gradients and successional status (Mittelbach et al. 2001), as captured in our analyses. While our results provide clues about C storage mechanisms, they should be tested directly and mechanisms driving the strong relationship with PSV determined.

Our approach emphasises a shift in perspective when applying BEF results at the landscape scale for ecosystem management. The catchall term ‘biodiversity’ continues to cause confusion (Hooper et al. 2005). Often, ‘biodiversity effects’ are cited when what is meant is ‘the effects of traits, or presence/absence of particular species,’ rather than effects of diversity per se, as clarified by Cardinale et al. (2012). It makes more sense – and would cause less confusion – to refer to diversity as a subset of interactive biotic factors. Doing so more explicitly integrates BEF studies into the powerful state-factor paradigm of ecosystem ecology. Rather than merely assessing diversity effects to assert that ‘diversity matters,’ this perspective emphasises mechanistic understanding of when, where, why and how much it matters, in combination with other known state and interactive (e.g. mean plant traits) factors. These questions are much more relevant to ecosystem services management than such vague (and common) statements as ‘biodiversity increases ecosystem functioning’. The ecosystem perspective argues that, rather than existing as its own subdiscipline, BEF becomes more relevant by explicitly integrating diversity with other controls on ecosystem properties in the state-factor framework.

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AUTHOR CONTRIBUTIONS

ECA and DUH contributed equally to the writing of this manuscript. AP, with help from all authors, developed the working dataset from the original data provided by the Ministère des Forêts, de la Faune et des Parcs du Québec (Canada), including synthesis of plant trait data, and calculating diversity metrics, community-weighted mean plant traits, and carbon pool sizes. All authors contributed to developing the candidate model sets. ECA performed the model comparisons, model averaging analyses, and the structural equation modeling. DUH performed principle component analyses. All authors contributed substantially to interpretation of results and manuscript revisions.

DATA ACCESSIBILITY STATEMENT

The working data are archived on Dryad, https://doi.org/10.5061/dryad.4hj00fr. The original dataset is publically available from the Ministère des Forêts, de la Faune et des Parcs du Québec (Canada): http://mffp.gouv.qc.ca/le-ministere/accuesaux-donnees-gratuites/

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