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Multiple abiotic and biotic pathways shape biomass demographic processes in temperate forests

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Abstract. Forests play a key role in regulating the global carbon cycle, and yet the abiotic and biotic conditions that drive the demographic processes that underpin forest carbon dynamics remain poorly understood in natural ecosystems. To address this knowledge gap, we used repeat forest inventory data from 92,285 trees across four large permanent plots (4–25 ha in size) in temperate mixed forests in northeast China to ask the following questions: (1) How do soil conditions and stand age drive biomass demographic processes? (2) How do vegetation quality (i.e., functional trait diversity and composition) and quantity (i.e., initial biomass stocks) influence biomass demographic processes independently from soil conditions and stand age? (3) What is the relative contribution of growth, recruitment, and mortality to net biomass change? Using structural equation modeling, we showed that all three demographic processes were jointly constrained by multiple abiotic and biotic factors and that mortality was the strongest determinant on net biomass change over time. Growth and mortality, as well as functional trait diversity and the community-weighted mean of specific leaf area ($\mathrm{CWM}_{\mathrm{SLA}}$), declined with stand age. By contrast, high soil phosphorous concentrations were associated with greater functional diversity and faster dynamics (i.e., high growth and mortality rates), but associated with lower $\mathrm{CWM}_{\mathrm{SLA}}$ and initial biomass stock. More functionally diverse communities also had higher recruitment rates, but did not exhibit faster growth and mortality. Instead, initial biomass stocks and $\mathrm{CWM}_{\mathrm{SLA}}$ were stronger predictors of biomass growth and mortality, respectively. By integrating the full spectrum of abiotic and biotic drivers of forest biomass dynamics, our study provides critical system-level insights needed to predict the possible consequences of regional changes in forest diversity, composition, structure and function in the context of global change.

Key words: ecosystem functioning; functional diversity; growth; mortality; recruitment; soil nutrient; stand age; vegetation quality and quantity.

Introduction

By sequestering CO_2 from the atmosphere and storing it as wood, forests play a central role in regulating the terrestrial carbon cycle on a planetary scale (Pan et al. 2011). Underpinning this carbon sink is three key demographic processes that together shape the aboveground biomass dynamics of forests: the growth of mature trees, the recruitment of new individuals, and the biomass loss resulting from mortality (Chave et al. 2003). In recent years, a growing body of evidence has shown that diverse forest communities generally accumulate biomass more rapidly than species-poor ones (Jucker et al. 2014, Liang et al. 2016). Yet whether these patterns arise as a result of faster growth and/or reduced mortality remains unclear, as

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does the extent to which other biotic and abiotic conditions contribute to shaping these relationships (Poorter et al. 2017, van der Sande et al. 2017).

Species richness, as the simplest measure of biodiversity, has commonly been used as a metric to explore the relationship between diversity and productivity in forests (Zhang et al. 2012, Liang et al. 2016). However, species richness can fail to capture ecological differences or similarities among species that might be better characterized by their functional traits (Paquette and Messier 2011, Ali et al. 2017). Functional trait-based approaches focus on the ecophysiology, morphology and life-history strategies of organisms rather than their taxonomic identity, constituting a novel and promising tool to mechanistically link biodiversity and ecosystem functioning (Petchey and Gaston 2006, Ruiz-Benito et al. 2017a).

There are two complementary approaches to exploring the impacts of functional traits on ecosystem functioning at the community level: functional trait diversity and community-weighted mean (CWM) values of key functional traits (i.e., trait composition). Functional trait diversity quantifies the distance among species in a multidimensional trait space (Laliberté and Legendre 2010). In doing so it provides an opportunity to test the role of niche complementarity in driving biodiversity–ecosystem functioning relationships (Tilman 1997). The CWMs, on the other hand, capture the dominant functional trait value of a community (Ali et al. 2017). This allows the mass ratio effect to be tested, which assumes that ecosystem functions are primarily driven by the functional traits of dominant species in a given community (Grime 1998). For example, stands with higher CWM values of specific leaf area could result in higher photosynthetic and carbon sequestration rates due to the dominant role of fast-growing acquisitive trees (Poorter and Bongers 2006). By contrast, stands dominated by trees with high wood density (i.e., conservative strategy) may lead to higher stem construction costs per unit of wood volume and lower photosynthetic carbon gains (Chave et al. 2009).

In addition to the functional trait diversity and composition of a community, another key aspect in shaping forest biomass dynamics is the total amount of standing biomass (i.e., vegetation quantity effect) (Lohbeck et al. 2015). Greater standing biomass generally equates to greater photosynthetically active leaf area, which in turn promotes greater productivity at the stand level (Coomes et al. 2012). However, stands with greater standing biomass are also expected to lose more biomass as a result of the mortality of large trees, while also exhibiting lower recruitment due to light-limitation in dense forests (Poorter et al. 2017). Recent studies have found that in natural forests productivity is more closely related to vegetation quantity (i.e., initial biomass stocks) rather than quality (i.e., functional trait diversity and composition) (Lohbeck et al. 2015, Yuan et al. 2018). Nevertheless, both vegetation quantity and quality are important for ecosystem functioning such as primary productivity and carbon storage, but their relative importance might depend on environmental conditions and successional stages (Paquette and Messier 2011, Vilà et al. 2013, Ali et al. 2017, Ruiz-Benito et al. 2017a). For instance, soil nutrients and stand age are the key drivers of species diversity, trait composition and standing biomass stocks at local and regional scales (Peña-Claros et al. 2012, Becknell and Powers 2014). High soil nutrient availability can promote niche differentiation (Coomes et al. 2009), which in turn leads to increased diversity, growth, and recruitment. But it could also promote competition, resulting in higher mortality and turnover rates and lower diversity (Quesada et al. 2012). Stand age can lead to a replacement of fast-growing, resource-acquisitive, and light-demanding species by slow-growing, resource-conservative, and shade-tolerant ones (Lasky et al. 2014), which in turn would strongly impact both productivity and mortality at the stand level (Becknell and Powers 2014, Ali et al. 2017).

Here, we use repeat-census data from four large permanent forest plots that capture the main vegetation types of temperate mixed forests in the Changbai region of northeast China to better understand the biotic and abiotic drivers that shape the biomass dynamics of these ecosystems. Using the conceptual model outlined in van der Sande et al. (2017) as a starting point (Fig. 1), we tested the following three questions. First, how do soil conditions and stand age drive biomass demographic processes? We hypothesize that stand age more than soil nutrients is the main driver of biomass dynamics because the former reflects the successional stage and disturbance history of the stand. Second, how do vegetation quality (i.e., functional diversity and trait composition) and quantity (i.e., standing biomass stocks) influence

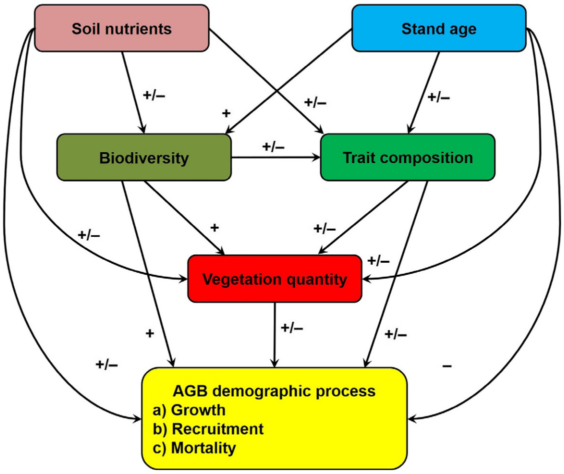

Fig. 1. A conceptual model revealing the expected links of abiotic factors (soil nutrients and stand age) and biotic factors (diversity, initial biomass, and trait composition) on biomass demographic processes (biomass recruitment, growth, and mortality). Hypothesized positive, negative, and unknown effects are indicated by +, –, and +/– signs.

demographic processes? We hypothesize that in addition to a strong effect of vegetation quantity on biomass dynamics, functional trait diversity and composition also play a key role in shaping growth, recruitment, and mortality. Third, what is the relative contribution of growth, recruitment, and mortality to biomass dynamics over time? We hypothesize that while, on average, net biomass change over time will be primarily driven by growth, biomass loss resulting from the mortality of mature trees will be the primary driver of fine-scale variation in biomass dynamics.

Materials and Methods

Study sites and forest inventory data

The study was conducted in Changbai Mountain National Natural Reserve in northeastern China (41°43′–42°26′ N, 127°42′–128°17′ E), near to the border between China and North Korea (Yang and Li 1985). The reserve covers an area of approximately 2,000 km^2 and is one of the largest protected temperate forests in the world (Yang and Li 1985, Hao et al. 2007). The region is characterized by a temperate continental climate, with long, cold winters and warm, rainy summer. The mean annual temperature is 2.8°C (mean temperature of the coldest and warmest months is −13.7°C and 19.6°C, respectively) and the mean annual precipitation is 700 mm, most of which falls during June and September (Yang and Li 1985, Hao et al. 2007).

In this study, we used forest inventory, functional trait, and soil data from four large forest dynamics plots ranging in size between 4 and 25 ha and representing forests at different successional stages (Table 1). These include poplar–birch forest (PBF), larch forest (LF), spruce–fir forest (SFF), and broad-leaved Korean pine (*Pinus koraiensis*) mixed forest (BKF). For each plot, stand age was determined by coring a subset of trees belonging to the dominant and/or codominant species in the stand (Wang et al. 1980, Xu et al. 2004). This work is also guided based on the Observation Methodology for Long term Forest Ecosystem Research of National Standards of the People's Republic of China (GB/T 33027-2016).

Within each plot, all free-standing individuals with a stem diameter at breast height (DBH) ≥ 1 cm were measured, mapped to a 20 × 20 m subplot and identified to species following the standard field protocol of the Center for Tropical Forest Science of the Smithsonian Institution (Hao et al. 2007). The plots were initially established between 2004 and 2010 (see Table 1 for details) and have since been re-inventoried every five years. The PBF and BKF plots have been resurveyed three times, while the LF and SFF plots have been resurveyed twice (Table 1).

Quantifying aboveground biomass and demographic processes

For each forest inventory period, the aboveground biomass of each individual stem was estimated from its DBH using locally calibrated allometric equations (Chen and Zhu 1989, Wang 2006, Li et al. 2010). By summing the aboveground biomass of all live trees recorded during the first census, we calculated the initial aboveground biomass stock (Mg ha^{-1}) of each 20 m × 20 m subplot (Chave et al. 2003). Net changes in aboveground biomass stocks, as well as biomass growth, recruitment and loss through mortality (all in Mg ha^{-1} yr^{-1}) were quantified at the 20 × 20 m subplot level using data from the first and last inventories in each subplot. Aboveground biomass recruitment (AGB$_\mathrm{R}$, Mg ha^{-1} yr^{-1}) is the annual biomass increase by trees recruited into the minimum diameter class (i.e., 1 cm) between the first and last inventory in each subplot. Aboveground biomass growth (AGB$_\mathrm{G}$, Mg ha^{-1} yr^{-1}) is the annual biomass accumulated by surviving trees between the first and last inventory. Aboveground biomass mortality (AGB$_\mathrm{M}$, Mg ha^{-1} yr^{-1}) is the annual biomass lost due to trees dying between the first and last inventory. Net aboveground biomass change (AGB$_\mathrm{N}$, Mg ha^{-1} yr^{-1}) is the

Table 1. Basic information of the study sites and forest demographic processes within each site in Changbai region.

Site names	Site size (ha) [dimension, m]	No. subplots	Elevation (m) [minimum, maximum]	Latitude, Longitude	Stand age (yr)	First/last census year (no. census)	Biomass (Mg ha^{-1} yr^{-1})			
							Recruitment	Growth	Mortality	Net change
PBF	4.8 [200 × 240]	120	801.5 [791.8, 809.5]	42°23′ N 128°05′ E	80	2005/2015 [3]	0.03 ± 0.02†	4.37 ± 1.02	1.82 ± 1.09	2.58 ± 1.48
LF	4 [200 × 200]	100	1430 [1425.6,1435]	42°04′ N 128°14′ E	240	2010/2015 [3]	0.06 ± 0.29	3.49 ± 0.84	0.85 ± 2.41	1.96 ± 2.58
SFF	4 [200 × 200]	100	1248 [1244.1,1248]	42°08′ N 128°08′ E	240	2010/2015 [2]	0.02 ± 0.05	2.64 ± 0.84	0.91 ± 1.33	2.60 ± 1.55
KBF	25 [500 × 500]	625	769.3 [788.5, 800.4]	42°22′ N 128°00′ E	280	2004/2014 [2]	0.02 ± 0.17	2.69 ± 1.41	0.95 ± 2.50	1.70 ± 2.99
Mean							0.03 ± 0.17	2.99 ± 1.41	1.05 ± 2.27	1.98 ± 2.67

† Mean ± SE.

annual net change in biomass between first and last inventory, and is equal to $AGB_R + AGB_G - AGB_M$ (Chave et al. 2003, van der Sande et al. 2017).

Functional trait composition and diversity

For each tree species recorded in forest inventory plots, we measured six functional traits that have been shown to strongly influence plant performance and ecological strategy (Pérez-Harguindeguy et al. 2013): maximum height (MH), wood density (WD), leaf nitrogen content (LNC), leaf phosphorus content (LPC), leaf area (LA), and leaf specific area (SLA). MH reflects variation in tree longevity, biomass accumulation potential and shade tolerance (Kunstler et al. 2016). WD captures a trade-off between fast growth and early reproduction vs. high survival rates and resistance to environmental and biotic stress (Chave et al. 2009, Kunstler et al. 2016). Leaf chemical traits such as LNC and LPC determine photosynthetic and growth capacity, whereas leaf physical traits such as LA and SLA reflect light interception ability and trade-offs between the construction cost and longevity of the plant tissues (Wright et al. 2004, Chave et al. 2009). Field methodologies used to measure the above traits are described in Yuan et al. (2016).

Functional diversity was quantified using a functional dispersion index (Laliberté and Legendre 2010), which has frequently been used in biodiversity–ecosystem functioning research (Paquette and Messier 2011, Ruiz-Benito et al. 2014, Chiang et al. 2016, Fotis et al. 2018). It measures the mean distance in multidimensional trait space of individual species to the centroid of all species, weighted according to the relative basal area of each species. Trait values were standardized to have a mean of 0 and a standard deviation of 1 before calculating both functional diversity and CWM values for each individual trait. All indices were calculated using the FD package (Laliberté and Legendre 2010) in R 3.4.3 (R Core Team 2017).

Soil nutrients

We collected soil samples in each plot using a regular 30-m sampling grid. To capture finer scale variations in soil nutrients, two additional points were sampled at each grid location at either 2, 5, or 15 m in a random compass direction from the grid point (Yuan et al. 2011). In total, we sampled 210, 192, 192, and 210 points in PBF, LF, SFF, and KBF sites, respectively. At each point, soil pH, soil organic matter content, total nitrogen (N), total phosphorus (P), and total potassium (K) were measured. Soil pH was analyzed by means of a Beckman pH meter in 1:1 soil-water solution. Soil organic matter content was determined by the acidified dichromate ($K_2Cr_2O_7$–$H2SO_4$) oxidation method. Total N was measured following the Kjeldahl method. Total P was obtained by molybdate colorimetry, after digestion in H_2SO_4–$HClO_4$. Total K was derived using atomic absorption spectrometry. We used spatial interpolation based on ordinary kriging as implemented in the geoR package in R (Ribeiro and Diggle 2001) to estimate soil variables for each 20 × 20 m subplot (for details, see Yuan et al. 2011).

Statistical analyses

Prior to analyses, the three demographic variables were log-transformed and all predictors were standardized to have a mean of 0 and a standard deviation of 1 in order to improve the interpretability of regression coefficients (Schielzeth 2010). Based on a priori expectations (Ruiz-Benito et al. 2017b, van der Sande et al. 2017), we constructed one structural equation model (SEM) for each of the three demographic processes as outlined in Fig. 1. We also consider the pathway between functional diversity and CWMs because we expected the higher probability of diverse forest communities to include higher productive species that will become dominant (Lohbeck et al. 2015, van der Sande et al. 2017), as the findings from manipulative BEF experiment (Loreau and Hector 2001). Although abiotic and biotic drivers are known to influence ecosystem process, it is less clear which combination of soil and trait composition variables is best for modeling biomass dynamics. To assess the relative importance of multiple predictors on demographic processes, we first used linear mixed-effects models to compare the explanatory power of different combinations of soil and CWM trait variables for predicting AGB_R, AGB_G, and AGB_M (Appendix S1: Table S1). Based on this preliminary analysis, we selected total soil P and CWM_{SLA} as predictors in all SEMs (Appendix S1: Table S2).

SEMs were fit using the sem function of the lavaan package in R (Rosseel 2012). The performances of the SEMs were evaluated using a combination of the chi-square statistic (where $\chi^2 \leq 2$ and $P > 0.05$ indicate a good fitting model), Bentler's comparative fit index (CFI, where $CFI \approx 1$ indicates a good fitting model), and the root mean square error of approximation (RMSEA; where $RMSEA \leq 0.05$ and $P > 0.1$ indicate a good fitting model). The indirect effects of the exogenous variables in the model (total soil P, stand age, functional diversity and CWM_{SLA}) were calculated by multiplying the coefficients of all paths linking the exogenous variables to each demographic process. Following the recommendation of Le Bagousse-Pinguet et al. (2017), the relative contribution of each predictor to the explained variance in the response variable (i.e., AGB_R, AGB_G, and AGB_M) was calculated as the ratio between the beta coefficient of a given predictor and the sum of beta coefficients of all predictors.

The relative importance of the three demographic processes (i.e., AGB_R, AGB_G, and AGB_M) to variation in AGB_N was calculated using the untransformed variables as described in (van der Sande et al. 2017):

$$\mathrm{Rel_G} = [var(\mathrm{AGB_G}) + cov(\mathrm{AGB_R}, \mathrm{AGB_G}) - cov(\mathrm{AGB_G}, \mathrm{AGB_M})]/var(\mathrm{AGB_N}) \quad (1)$$

$$\mathrm{Rel_R} = [var(\mathrm{AGB_R}) + cov(\mathrm{AGB_R}, \mathrm{AGB_G}) - cov(\mathrm{AGB_R}, \mathrm{AGB_M})]/var(\mathrm{AGB_N}) \quad (2)$$

$$\mathrm{Rel_M} = [var(\mathrm{AGB_M}) - cov(\mathrm{AGB_R}, \mathrm{AGB_M}) - cov(\mathrm{AGB_G}, \mathrm{AGB_M})]/var(\mathrm{AGB_N}) \quad (3)$$

where var($\mathrm{AGB_G}$), var($\mathrm{AGB_R}$), var($\mathrm{AGB_M}$), and var ($\mathrm{AGB_N}$) are the variances of AGB growth, recruitment, mortality, and net AGB change, respectively; while cov ($\mathrm{AGB_R}$, $\mathrm{AGB_G}$), cov($\mathrm{AGB_G}$, $\mathrm{AGB_M}$), cov($\mathrm{AGB_R}$, $\mathrm{AGB_G}$), and cov($\mathrm{AGB_R}$, $\mathrm{AGB_M}$) are the covariances between two demographic processes.

RESULTS

Across the four forest plots, mean $\mathrm{AGB_R}$ was 0.03 ± 0.17 Mg $\mathrm{ha^{-1}}$ $\mathrm{yr^{-1}}$, $\mathrm{AGB_G}$ was 2.99 ± 1.41 Mg $\mathrm{ha^{-1}}$ $\mathrm{yr^{-1}}$, $\mathrm{AGB_M}$ was 1.05 ± 2.27 Mg $\mathrm{ha^{-1}}$ $\mathrm{yr^{-1}}$, and $\mathrm{AGB_N}$ change was 1.98 ± 2.67 Mg $\mathrm{ha^{-1}}$ $\mathrm{yr^{-1}}$ (Table 1).

Bivariate analyses showed that all demographic processes significantly increased with functional trait diversity (Appendix S2). Aboveground biomass growth significantly increased with CWM of leaf area, total phosphorus and initial biomass. Recruitment increased with CWM of wood density, leaf phosphorus content, specific leaf area, soil organic matter, and total nitrogen but decreased with CWM of leaf area, pH value, soil total potassium and initial biomass. Aboveground biomass mortality increased with CWM of leaf traits (i.e., leaf nitrogen content, leaf area, and specific leaf area) and soil total phosphorus, but decreased with initial biomass and CWM of maximum height and LPC (Appendix S2).

The SEM for $\mathrm{AGB_G}$ revealed that productivity was directly affected by stand age (β = −0.55), initial biomass stocks (β = 0.44) and total soil P (β = 0.23; Fig. 2a). Stand age also enhanced $\mathrm{AGB_G}$ indirectly as older stands tended to have greater initial standing biomass stocks, while stands with higher soil P tended to have lower initial biomass stocks thus partially limiting the net effect of soil P on $\mathrm{AGB_G}$ (Fig. 2a). $\mathrm{CWM_{SLA}}$ and functional trait diversity did not have a significant direct effect on $\mathrm{AGB_G}$, but they did indirectly affect productivity via their association with initial biomass stocks (Fig. 2a and Appendix S3: Table S1).

The SEM for $\mathrm{AGB_R}$ revealed that functional diversity had the strongest positive direct effect on recruitment (β = 0.42, Fig. 2b). $\mathrm{CWM_{SLA}}$ was also positively associated with $\mathrm{AGB_R}$ (β = 0.14), whereas initial biomass stocks had a negative effect on recruitment (β = −0.11). While soil P and stand age did not have a significant direct effect on $\mathrm{AGB_R}$, both indirectly impacted recruitment as a result of their negative association with functional diversity and (in the case of stand age) the negative correlation with initial biomass stocks and $\mathrm{CWM_{SLA}}$ (Fig. 2b and Appendix S3:Table S2).

The SEM for $\mathrm{AGB_M}$ highlighted how biomass loss as a result of tree mortality was directly influenced by stand age (β = −0.35), soil P (β = 0.28), and $\mathrm{CWM_{SLA}}$ (β = 0.19; Fig. 2c). Soil P and functional diversity and stand age also had an indirect effect on $\mathrm{AGB_M}$ via their negative association with $\mathrm{CWM_{SLA}}$ (Fig. 2c, Appendix S3: Table S3). Of the three demographic processes, $\mathrm{AGB_M}$ explained most of the variation in net aboveground biomass change, followed by $\mathrm{AGB_G}$ and $\mathrm{AGB_R}$ (Fig. 2). Fig. 3 summarizes the

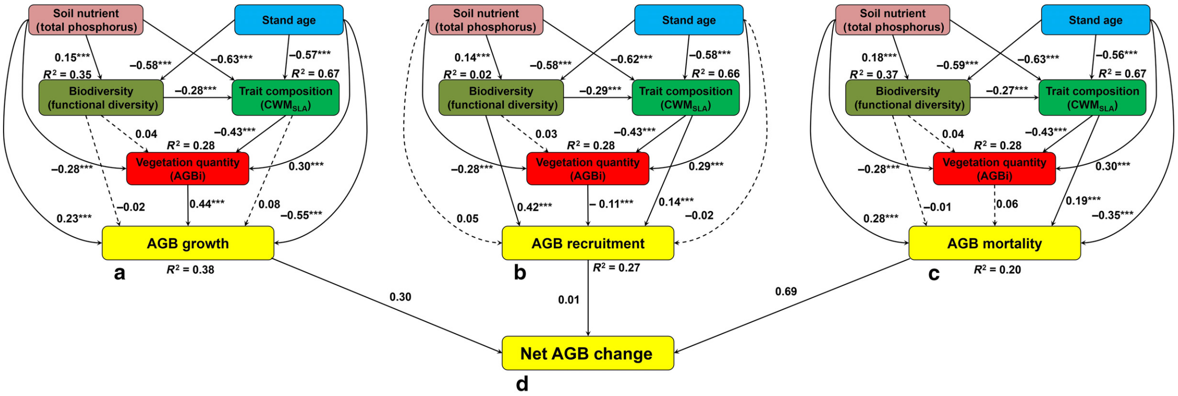

FIG. 2. Results for the effects of abiotic factors (soil and stand age) and biotic factors (diversity, trait composition, and initial biomass) on three demographic processes (a, biomass growth; b, biomass recruitment; and c, biomass mortality), which underlie (d) net aboveground biomass change. The upper part of panels a–c is tested with three separate structural equation models. The lower part (panel d) could not statistically be tested, but it shows the relative contributions of demographic processes to variation in net biomass change across plots. Black arrows represent significant effects and dashed arrows represent non-significant effects. For all paths, standardized regression coefficients and significance are given (*<0.05, ***<0.001). Abbreviations are $\mathrm{CWM_{SLA}}$, community-weighted means of specific leaf area; AGBi, initial aboveground biomass stock. Model fit statistics are provided in Appendix S1, whereas direct, indirect, and total effects are provided in Appendix S3.

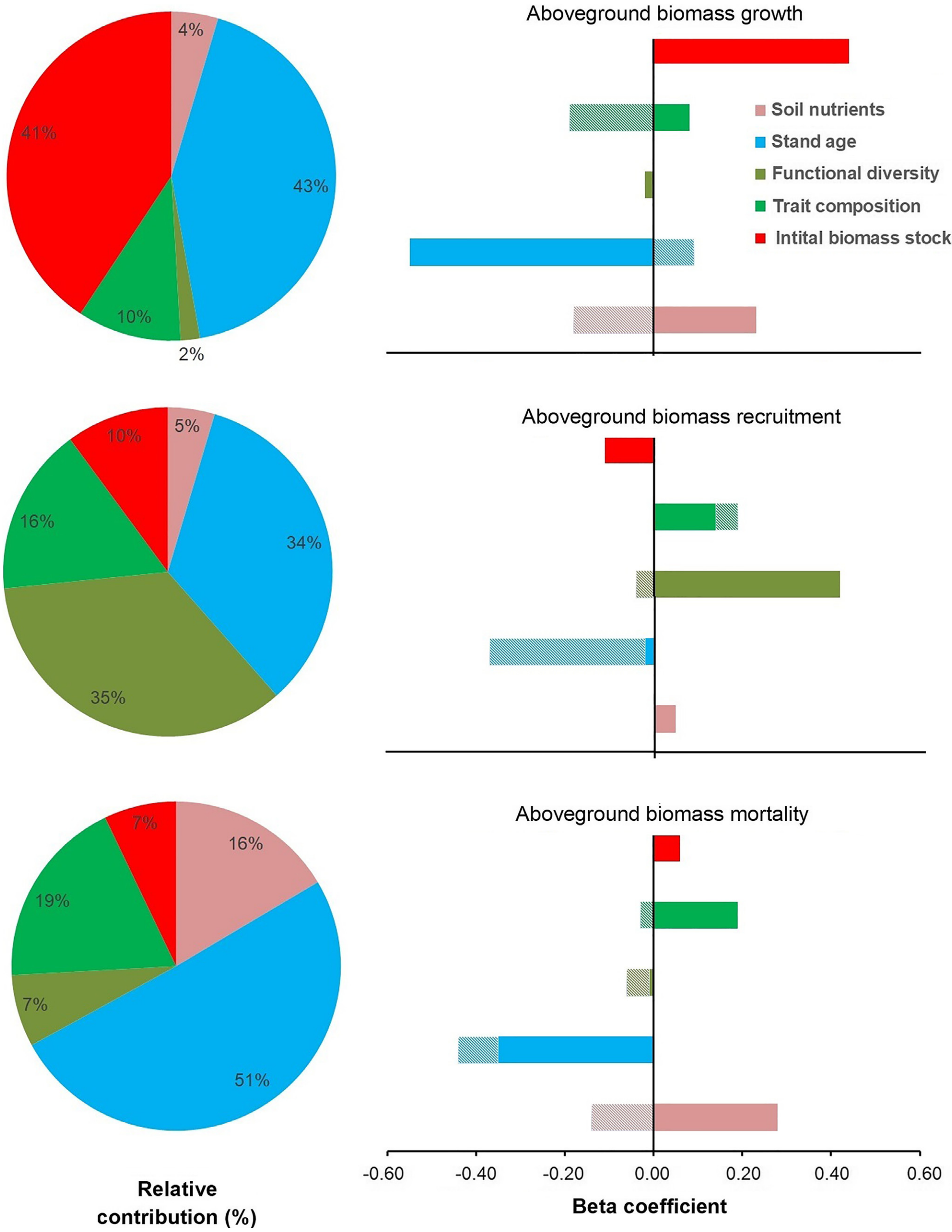

FIG. 3. Beta coefficients and the relative contribution of abiotic and biotic factors on demographic processes: aboveground biomass growth, recruitment, and mortality. The filled bars indicate the direct effect and the striped bars indicate the indirect effect of abiotic and biotic factors on biomass demographic processes. The pies show the relative importance of each predictor on forest demographic processes.

relative contribution of each abiotic and biotic driver to AGB_R, AGB_G and AGB_M.

DISCUSSION

Our study provides one of the first comprehensive tests of how abiotic and biotic processes interact to shape the biomass dynamics of temperate forest ecosystems. Using a structural equation modeling framework, we show that stand age and soil P content play a central role in constraining the functional composition, diversity and packing density of temperate forests. In turn, these compositional and structural attributes were key to explaining fine-scale variation in growth and mortality within and among stands (Fig. 2). Below, we expand on these results and attempt to put them in context with the three underlying questions outlined in the introduction.

Biomass growth, mortality, and recruitment decline with stand age but increases with soil nutrient availability

We found that after having accounted for differences in standing biomass stocks, which, as expected, tended to increase with stand age, older stands were generally less productive than younger ones (i.e., biomass increment per unit of biomass declines with stand age). This supports the notion of age-related declines in tree growth (Gower et al. 1996). Mature trees may exhibit decreased canopy carbon gains and photosynthetic efficiency, as well as shifts in biomass allocation to belowground and greater canopy respiration (Ryan et al. 2004). As stems become taller with age, they have a higher evaporative demand and suffer hydraulic constraints due to increased difficulties in supplying water and nutrients to leaves (Ryan and Yoder 1997, Baret et al. 2018). Additionally, they may also become increasingly dependent on deep groundwater, especially during the dry season (Nepstad et al. 1994).

Stand age was also a strong predictor of biomass loss through the mortality of mature trees. In particular, we found that during stand development community composition tended to shift away from species with resource-acquisitive traits (e.g., $\mathrm{CWM}_{\mathrm{SLA}}$ declined with stand age) and that this, in turn, coincided with decreased mortality (Fig. 2c). This suggests that lower mortality rates in older stands may result from these becoming increasingly dominated by species with conservative life-history strategies (Wright et al. 2004, Chave et al. 2009). Pioneer species characterized by resource-acquisitive traits such as high SLA typically tend to decline in abundance during stand succession as they are slowly outcompeted by late-successional species that have intrinsically lower mortality rates (Lepš 2004, Reich 2014). This pattern is very similar to that observed in old-growth Neotropical forests, where early-successional light-demanding species with high SLA and low WD are outcompeted by late-successional shade-tolerant species characterized by more conservative functional trait portfolios (Van der Sande et al. 2016).

In addition to stand age, our results also suggest that soil P content is another key driver of forest biomass dynamics in these temperate forest ecosystems (Fig. 2). This contrasts in part with the traditional view that temperate forests are primarily limited by N availability (LeBauer and Treseder 2008, Bobbink et al. 2010). Previous studies have suggested that N availability should be a stronger limiting factor to growth than P in temperate regions, due to slow N mineralization and low plant N use efficiency, while recent glaciations have resulted in soils rich in P (Alvarez-Clare et al. 2013). And yet recent evidence supports the idea that P limitation is a key driver of forest succession in the Changbai region (Yaosheng et al. 2014). One possible explanation for this is that available organic P that is not absorbed by organisms eventually becomes immobilized by forming Al or Fe hydrous oxides, rendering the phosphorus largely unavailable to the biota (Crews et al. 1995). Another plausible cause might be nutrient limitation changes during ecosystem development (Menge et al. 2012). For example, young forests might be N limited as mineral soils are N poor and litterfall remains low, while old-growth forests might be P limited because the majority of P has weathered from soils (Bobbink et al. 2010).

Vegetation quantity enhances growth, functional diversity promotes recruitment while trait composition increases mortality

Our results suggest that initial standing biomass stocks were the second most important predictor of stand-level biomass growth (see Figs. 2a and 3). The effect of vegetation quantity on biomass growth (i.e., $\beta = 0.44$; relative contribution = 40.7%) was greater than the effect of vegetation quality (i.e., functional diversity $\beta = -0.02$; relative contribution = 1.9%) and trait composition (i.e., $\mathrm{CWM}_{\mathrm{SLA}}$ $\beta = 0.08$; relative contribution = 10.2%), leading support to the vegetation quantity hypothesis (Lohbeck et al. 2015). One explanation for this pattern is that more mature stands with higher standing biomass also have a higher proportion of large trees, which are known to disproportionately contribute to stand-level productivity (Stephenson et al. 2014). Additionally, stands with a greater basal area (a key correlate of aboveground biomass stocks) generally also have greater a leaf area index, allowing them to intercept more light and sequester greater amounts of carbon via photosynthesis (Coomes et al. 2012, Michaletz et al. 2014). These results are consistent with those of a number of studies that have shown that basal area is a stronger driver of productivity than tree diversity in European and North American forests (Paquette and Messier 2011, Vilà et al. 2013).

The fact we did not find a clear relationship between functional diversity and productivity contrasts with the results of a number of recent studies that have highlighted positive diversity-productivity relationships in both managed (Forrester and Bauhus 2016) and natural forests (Liang et al. 2016). One explanation for this could be our choice of functional traits used to estimate functional trait diversity (Chiang et al. 2016, Ali et al. 2017), as we may have simply failed to measure the relevant axes of trait variation that promote niche complementarity in this study system (Kunstler et al. 2016). In support of this hypothesis is the fact that preliminary analyses conducted with our data highlighted the fact that the effects of functional diversity and trait composition on biomass productivity were largely dependent on which traits were selected (Appendix S4). For instance, functional diversity was found to promote biomass growth when modeled in combination with $\mathrm{CWM}_{\mathrm{LA}}$, whereas the opposite was true for $\mathrm{CWM}_{\mathrm{WD}}$ (Appendix S4). These additional analyses support the findings of Yang et al. (2018), which suggest that trait–demographic-rate relationships in tree communities are generally weak and hard to predict (Yang et al. 2018).

Recruitment rates were generally lower in high standing biomass forests, which could be caused by lower light availability in the understory (van der Sande et al. 2017). The negligible effect of total P on biomass recruitment (Fig. 2b) suggests that the light availability, more so than soil nutrients, is the primary limiting factor driver of sapling survival and growth in these forests (Danescu et al. 2016). In addition to this, seedlings and understory plants in high biomass forests may experience higher mortality as a result of large tree and branch falls (McDowell et al. 2018), as our results highlighting a positive link between trait composition and mortality would suggest (Fig. 2c).

In contrast to growth and mortality, our results do suggest that functional diversity positively influences sapling recruitment rates (Ruiz-Benito et al. 2017a). We estimated functional diversity based on maximum tree height, wood density, and four leaf traits, which have been identified as critical indicators of life-history strategies and plant performance (Wright et al. 2004, Chave et al. 2009). Previous studies have reported similar patterns in other forest type. For instance, Ruiz-Benito et al. (2017a) found that the abundance of saplings in conifer-dominated and Mediterranean broad-leaved forests was promoted by a coexistence of functionally diverse species. Within this context, soils and stand development stage therefore likely play an important indirect role in shaping recruitment through their influence on functional diversity. Fertile soils will generally support more diverse forest communities by providing a greater range of niches and by imposing less stringent ecological limitations to growth (Lepš 2004, Coomes et al. 2009). Similarly, functional diversity and composition will generally tend to change during stand development as late-successional species characterized by more conservative life-history strategies come to dominate the community in the absence of major disturbances (Van der Sande et al. 2016).

Biomass mortality determines net biomass change

We found that biomass loss resulting from the mortality of mature trees accounted for most of the fine-scale variation in net biomass change in our plots, thus supporting recent studies that have found mortality to be a key driver of aboveground biomass dynamics in natural forests (Delbart et al. 2010, Poorter et al. 2017, Ruiz-Benito et al. 2017b). In contrast to previous empirical studies (Poorter et al. 2017, van der Sande et al. 2017), our results suggest that biomass mortality in our region can be adequately predicted using the combination of biotic and abiotic variables we selected (Fig. 2c). One explanation for this is that the forests we studied did not suffer any major anthropogenic and/or natural disturbance events (e.g., fire, wind damage) during the period captured by our study. This contrasts with most previous studies in the tropics or in European forests, which have been subjected to logging or other natural disturbances (Poorter et al. 2017, Ruiz-Benito et al. 2017b, van der Sande et al. 2017). For instance, tree mortality (both natural and as a result of logging) has played a key role in driving recent changes in the functional composition of European forests (Ruiz-Benito et al. 2017a, b). These, in turn, would likely alter the relationship between functional diversity and ecosystem functioning in these ecosystems.

CONCLUSIONS

Our study highlights how multiple abiotic and biotic drivers interact to shape the biomass dynamics of temperate forest ecosystems over relatively short times scales. Fine-scale spatial variation in net biomass change was strongly determined by biomass loss arising as a result of the mortality of large, mature trees. As has been reported previously, we found that forest productivity and turnover tended to decline with stand age, whereas higher soil P concentrations were associated with faster rates of growth and mortality. Dense forests generally had faster rates of biomass growth, but lower recruitment of saplings. The relative importance of niche complementarity and mass ratio effects varied among the three demographic processes studies here, with a strong effect of functional diversity on recruitment emerging from out models. The lack of a clear relationship between diversity and productivity seems to depend, in part, on which functional traits are included in the analysis, and we, therefore, recommend that future research explore this choice more carefully. Our study provides a more complete picture of the biomass dynamics of temperate forests, which is key to predicting the response of these ecosystems to global change.

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