

# Positive species diversity and above-ground biomass relationships are ubiquitous across forest strata despite interference from overstorey trees

Yu Zhang<sup>1</sup>, Han Y. H. Chen<sup>\*1</sup> and Anthony R. Taylor<sup>1,2</sup>

<sup>1</sup>Faculty of Natural Resources Management, Lakehead University, 955 Oliver Road, Thunder Bay, Ontario P7B 5E1, Canada; and <sup>2</sup>Atlantic Forestry Centre, Canadian Forest Service, Natural Resources Canada, 1350 Regent Street, Fredericton, New Brunswick E3B 5P7, Canada

## Summary

1. There is growing concern over rates of global species diversity loss and its implications on healthy ecosystem functioning. While positive relationships between tree species diversity and forest biomass production have been observed, forests are structurally complex, consisting of understorey vegetation layers that also contribute to ecosystem functioning as they often account for the majority of species richness. However, relationships between understorey vegetation diversity and function are largely unexplored. Further, few studies have simultaneously assessed how both overstorey and understorey vegetation interact and contribute to overall ecosystem function.

2. By analysing Canada's National Forest Inventory data base using structural equation modelling, we explored the relationships between species richness and above-ground biomass production across forest vegetation strata while accounting for potentially confounding factors, including climate, physical site characteristics and forest ageing.

3. We found positive relationships between species richness and biomass production across all forest vegetation layers, but the relationship was strongest for the overstorey layer. Species richness of the understorey tree, shrub and herb layers was positively related to overstorey species richness. However, overstorey biomass had a negative effect on the biomass production of all understorey layers.

4. Our results suggest that resource filtering by overstorey trees might have reduced the strength of the positive diversity–productivity relationships in the forest understorey, supporting previous hypotheses that the magnitude and direction of diversity–productivity relationships is context specific and dependent on the conditions of the surrounding environment. Further, heterogeneity in understorey resources, as affected by the overstorey, may promote niche complementarity as the main mechanism driving diversity–productivity relationships in understorey vegetation.

**Key-words:** biomass, diversity, ecosystem function, plant–plant interactions, productivity, species richness, understorey vegetation, vertical forest strata

## Introduction

Positive biodiversity and ecosystem functioning (BEF) relationships have been widely observed in natural and controlled environments, including forests, which are attributable to the use and retention of site resources by resource partitioning and reduced competition in species-rich communities (Hooper *et al.* 2005; Vilà *et al.* 2007, 2013; Paquette & Messier 2011; Zhang, Chen & Reich

2012; Forrester 2014; Jucker *et al.* 2014; Zhang & Chen 2015). However, most BEF studies in forests have focussed on the relationship between overstorey tree species diversity and productivity, with an emphasis on wood production (e.g. Vilà *et al.* 2007, 2013; Gamfeldt *et al.* 2013; Hulvey *et al.* 2013), for such reasons as economic considerations or limitations in data availability for other vegetation layers.

As important components of forest ecosystems, understorey trees, shrubs, herbs and bryophytes contribute

\*Correspondence author. E-mail: hchen1@lakeheadu.ca

greatly to the overall diversity and function of natural forests as they account for the majority of species richness, influence forest dynamics and affect forest soil carbon and nutrient pools (Nilsson & Wardle 2005; Gilliam 2007). However, BEF relationships in the understory tree, shrub, herb and bryophyte layers of forests have been largely overlooked in previous studies. Lack of consideration of all vegetative strata in forests may result in misleading conclusions concerning the magnitude and patterns of BEF in forest ecosystems (Fowler *et al.* 2012), leading to discrepancies between the aspect of biodiversity and ecosystem function being measured (Balvanera *et al.* 2014).

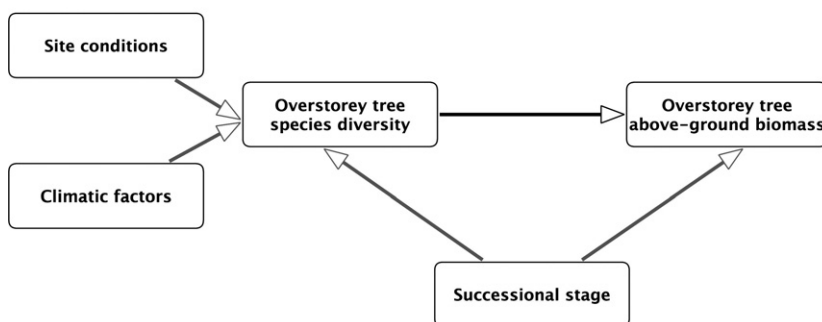
We hypothesize that positive species diversity and above-ground biomass relationships are ubiquitous across vegetation strata in forests (Fig. 1a,b), but the magnitude of the relationships may differ because local biotic interactions among strata shift resource availability for individual strata (Oberle, Grace & Chase 2009; Bartels & Chen 2013; Jonsson *et al.* 2015). For example, limited resource availability (e.g. light and throughfall), filtered by overstorey trees (Anderson, Loucks & Swain 1969; Bartels & Chen 2010), may reduce the strength of positive diversity and above-ground biomass relationships in understory strata because positive diversity effects are primarily the result of increased resource utilization (Hooper *et al.* 2005). We also hypothesize that overstorey tree species richness may increase understory species richness (e.g. Gamfeldt *et al.* 2013) (Fig. 1b), due to increased understory resource

heterogeneity associated with higher overstorey species richness, promoting higher species richness with reduced interspecific competition in the understory. Moreover, overstorey above-ground biomass may have a negative impact on understory above-ground biomass (Zhang, Chen & Taylor 2016a) and understory species richness due to increased interspecific competition following reduced resource availability (Fig. 1b).

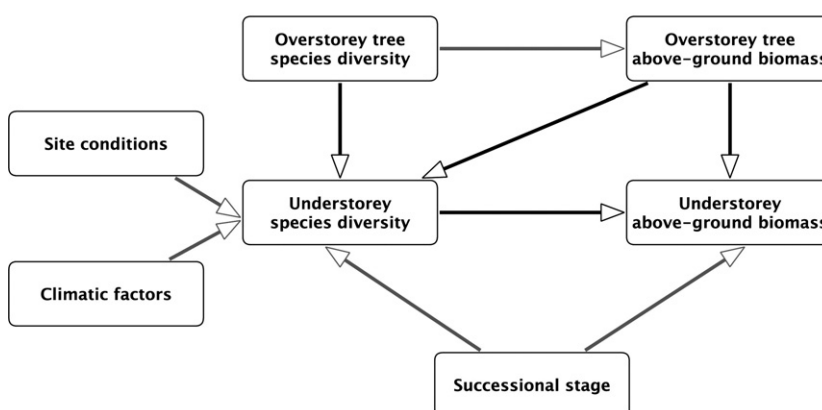
Studies on BEF conducted in forest ecosystems have often been criticized for failing to account for environmental drivers and endogenous forest stand ageing that may be important in influencing functions in natural forests (Flombaum & Sala 2008; Duffy 2009; Willig 2011). For instance, climatic variation is known to affect biomass accumulation and wood production (Michaletz *et al.* 2014; Pretzsch *et al.* 2014); local soil conditions that determine nutrient and water availability may strongly influence ecosystem functions such as net primary productivity and forest carbon storage (Wang, Bond-Lamberty & Gower 2003) and may affect BEF through complex plant–soil feedback loops (van der Putten *et al.* 2013) (Fig. 1a,b). Furthermore, stand age is known to influence plant community structure, standing biomass and productivity (Michaletz *et al.* 2014; Pretzsch *et al.* 2014; Taylor *et al.* 2014) (Fig. 1a,b).

To assist in addressing gaps in our knowledge of BEF in natural forests, we examined species richness and above-ground biomass relationships across forest vegetation

### (a) Overstorey trees



### (b) Understorey layers



**Fig. 1.** Concept diagram summarizing the current consensus on the biodiversity–ecosystem functioning relationship based on numerous studies from the past two decades. The bold paths show the hypothesized causal relationships: positive species diversity and above-ground biomass relationships across forest strata and the negative impact of overstorey trees on understory above-ground biomass. (a) Overstorey trees. (b) Understorey vegetation: understory trees, shrubs, herbs and bryophytes. The grey paths show the effects of covariates.

strata, including the overstorey tree, understorey tree, shrub, herb and bryophyte layers, while accounting for the influences of climate, local site conditions and forest stand age. In the cases of understorey strata, we also accounted for the effects of overstorey tree species richness and above-ground biomass on understorey species richness and above-ground biomass. Based on the above-described multiple agents of causation, we summarize two theoretical frameworks in Fig. 1 for stand-level relationships of the overstorey layer (a) and the understorey layers (b), respectively. We used above-ground biomass stocks to approximate productivity because productivity is strongly correlated with biomass in forest ecosystems after accounting for the effects of stand age (Chisholm *et al.* 2013; Michaletz *et al.* 2014; Jenkins 2015).

## Materials and methods

### STUDY AREA AND AVAILABLE DATA

We used the Canadian National Forest Inventory (NFI) data base, including 987 permanent ground sample plots, to study the entire range of forested ecosystems across Canada (Figs S1 and S2, Supporting information). The study areas covered by these ground plots were between 53°25'W and 134°46'W longitude and 42°37'N and 68°14'N latitude, spanning Canadian temperate and boreal forests. Elevations ranged from 4 to 2170 m above sea level, with mean annual precipitation ranging from 200 to 3100 mm, and mean annual temperature between -11.2 °C and 9.3 °C. The ground plots were randomly distributed over a 20 × 20 km grid of photoplots, which were systematically selected to encompass a full coverage of Canadian forests. The measurement of ground plots was carried out by various provincial agencies using similar ground sampling guidelines (Canadian Forest Inventory Committee, 2004). Overall, the NFI data set consists of only a single measurement of all plots, which was conducted between 2000 and 2006. Plots without tree cover present or plots that were established and measured inconsistently between jurisdictions that interfered with the integrity of our analysis were excluded through our NFI data validation process. The full NFI data base may be accessed by contacting NFI program staff through the NFI website (<https://nfi.nfis.org>) and requesting a data sharing agreement.

For each ground plot, forest vegetation was quantified based on vertical strata and plant growth forms. Specifically, vegetation within each stand was classified as either part of overstorey tree, understorey tree, shrub, herb or bryophyte layer. The overstorey tree layer included all trees with a diameter at breast height (dbh)  $\geq 9.0$  cm; the understorey tree layer included all trees with a dbh  $< 9.0$  cm, but  $\geq 1.3$  m in height and shrubs  $\geq 1.3$  m in height. The shrub layer included all woody plants (shrubs and trees)  $< 1.3$  m in height, whereas the herb layer included all non-woody vascular plants such as ferns, graminoids and saprophytes. The bryophyte layer encompassed all ground-growing non-vascular plants such as mosses, liverworts and lichens (note: lichens are composite organisms that often exhibit plant-like growth morphologies and photosynthetic capacities). Moreover, the definitions for the shrub layer were slightly different between provinces, that is  $< 1.3$  m in height in Alberta, Manitoba, Nova Scotia and Northwest Territories ( $n = 274$ ) and  $< 2.0$  m in height for the remaining provinces.

The standard plot design consisted of several plots associated with the vegetation layers. An overstorey tree plot, which varied in size from 125 to 500 m<sup>2</sup>, with the majority of plots being 400 m<sup>2</sup> with a radius of 11.20 m, was used for measuring

attributes of the overstorey tree layer. Despite the variability in plot size, we found negligible effects of plot size on species diversity and above-ground biomass, which did not affect model integrity (Zhang, Chen & Taylor 2014, 2016a). Within the overstorey tree plot, an understorey tree layer plot with a radius of 3.99 m (50 m<sup>2</sup>) was used for measuring the above-ground biomass of the understorey tree layer, accompanied by a 314-m<sup>2</sup> plot for surveying species presence. Four 1-m<sup>2</sup> microplots were used for measuring the biomass of low shrubs and trees ( $< 1.3$  m in height), herbs and bryophytes, accompanied by a 100-m<sup>2</sup> plot for surveying species presence. A soil pit was excavated outside of the overstorey tree plot, but within a 25-m radius, for measuring soil attributes. Whenever applicable, the minimum depth of the soil pit was 60 cm into the mineral soil or 100 cm into the organic soils.

### ABOVE-GROUND BIOMASS

We used the above-ground biomass (Mg ha<sup>-1</sup>) that had accumulated since stand establishment to represent forest above-ground biomass production (Fig. S3). Overstorey trees within the large tree plots were numbered, tagged and measured by height and diameter at breast height (DBH, 1.3 m above root collar) for estimation of above-ground biomass. Similarly, DBH and mid-point heights were measured for understorey trees and tall shrubs within understorey tree layer plots. Biomass estimates of overstorey and understorey trees, as well as tall shrubs, were calculated using a set of species-specific provincial allometric biomass equations (Boudewyn *et al.* 2007).

In each microplot, biomass samples of all above-ground vegetation from the shrub, herb and bryophyte layers were separately collected, oven-dried and weighed. A plant was included in the sample when the main root system was within the plot. For large clumps of graminoids, the portions that resided within the plot boundaries were clipped. For bryophyte biomass, live and photosynthetic active tissues were collected while the brown portions of the bryophytes were considered as part of the forest floor. In addition, whenever applicable, slime moulds and mushrooms were included with the bryophyte samples. To facilitate the bagging of the material, plant samples were cut into smaller pieces. All bagged samples were oven-dried in a forced-air drying oven at 70 °C for 72 h and weighed to the nearest 0.1 g.

### EXPLANATORY VARIABLES

The genus and species of vegetation within the sample plots, including trees, shrubs, herbs and bryophytes, were identified in the field. For species that were unidentifiable in the field, adequate representative samples of the unknown species, that is flowers, cones, bark and branches, were collected, bagged and labelled for later identification by specialists in the laboratory.

Species richness for the overstorey tree layer (OTR) was determined as the number of species counted in the overstorey tree plot. Species richness for the understorey tree layer (UTR) was the number of tree and tall shrub species found in the 314-m<sup>2</sup> species-presence plot. Species richness for shrub (SR), herb (HR) and bryophyte (BR) layers was the number of species counted for each layer in the 100-m<sup>2</sup> species-presence plot. However, understorey strata were not measured in 170 plots within Quebec, Prince Edward Island and New Brunswick. For those plots, species richness for respective understorey layers was treated as absent in the analysis.

To account for the influence of the environment and stand development on above-ground biomass, we included climate, soil drainage class and stand age as covariates in our analyses. Climate data for each plot were derived from BioSIM (<https://cfs.nrcan.gc.ca/projects/133>), which generated long-term (1951–2010)

scale-free climate data from geographic coordinates (latitude, longitude and elevation) (Régnière & Saint-Amant 2008). Specifically, for climate data, we used growing degree-days (GDD, °C, yearly summation of the mean of daily maximum and minimum temperature minus 5 °C) as a measure of the overall energy available for plant growth, and climate moisture index (CMI, cm, annual precipitation minus annual potential evapotranspiration) to represent climate moisture availability, where higher CMI values represent higher water availability for plants (Hogg 1997). We used soil drainage class (SDC), determined by field surveys involving soil pit excavations, as a measure of local site conditions. Similar to soil moisture regimes and nutrient regime classifications (Chen, Krestov & Klinka 2002), SDC classification considers multiple factors, including topographic position, organic layer depth, soil permeability, soil texture, soil thickness and water-table depth (Taylor *et al.* 2000). Seven classes were employed, from A to G, representing very rapidly, rapidly, well, moderately well, imperfectly, poorly and very poorly drained soils, respectively. Stand age (SA, years) for each plot was determined according to the last stand-replacing fire date, or by coring three dominant/co-dominant trees of each tree species inside or outside the plot at the time of plot establishment. With coring, SA was derived as the average ring count from tree species samples with the oldest age and used as a conservative, minimum estimate of stand age (Senici *et al.* 2010).

#### STATISTICAL ANALYSES

We used structural equation models (SEMs) to examine the relationships between above-ground biomass and species richness within each layer, while simultaneously accounting for the effects of covariates such as GDD, CMI, SDC and SA, as well as the effects of the overstorey tree layer, in the cases for understorey layers. As recommended (Grace *et al.* 2012, 2016), we specified a meta-model based on known theoretical multivariate causes of plant diversity and ecosystem function in natural forests (Fig. 1). To validate the specification of SEM and aid in interpretation of the SEM results (Grace *et al.* 2012, 2016), we examined the bivariate relationships representing each directional causal path according to the hypotheses in Fig. 1, using correlation and regression analysis. The complementary bivariate relationships to the SEM models of overstorey tree, understorey tree, shrub, herb and bryophyte layers are shown in Table S2 and Figs S4–S8, respectively.

As recommended in SEM fitting for alleviating departure from normality, the standard in most ecological data (Grace *et al.* 2010; Hoyle 2012), all numerical variables including GDD, CMI, SA and above-ground biomass and species richness across forest vegetation strata were transformed to the natural log scale, centred by the mean and scaled by one standard deviation to allow comparisons among multiple predictors and models (Zuur *et al.* 2009). As SDC was an ordinal, categorical variable (coded as 1–7) and considered a strict exogenous variable in our SEMs, it was treated as a numeric covariate as recommended (Hoyle 2012; Rosseel 2012). Due to jurisdictional sampling discrepancies, some data of exogenous and endogenous variables were missing; in these cases, plots were excluded from our SEM analysis. The number of plots included for each layer in the SEM models is shown in the captions of Figs S4–S8.

We use two common index methods to evaluate the goodness-of-fit of SEMs, standardized root mean square residual (SRMR) and goodness-of-fit index (GFI), as recommended (Hoyle 2012), because the chi-square test is not reliable due to excessive Type I errors for data larger than 200 cases (Kenny, Kaniskan & McCoach 2015). Although the goodness-of-fit indices for some models marginally exceeded the recommended cut-off values, that is >0.95 for GFI and <0.08 for SRMR (Hoyle 2012), we specified

identical SEM models throughout all understorey layers to facilitate interpretation.

In our fitted SEMs, directional paths with solid and dashed single-headed arrows indicate statistically significant ( $P < 0.05$ ) and insignificant ( $P \geq 0.05$ ) causal relationships, respectively. The value of path coefficients, standardized for comparison between pathways, represents measures of sensitivity of the response variable to the explanatory variable (Grace & Bollen 2005). The total effects, combining the direct and indirect standardized effects (Grace & Bollen 2005; Grace *et al.* 2016), of a given exogenous variable on above-ground biomass were also calculated to enhance the interpretation of our SEM results. It is worth noting that the hypothesized causal relationships in SEM may be consistent with our theoretical framework but does not necessarily exclude alternative causality between variables. The SEM was implemented using the *lavaan* package (Rosseel 2012) in R 3.2.2 (R Development Core Team 2015).

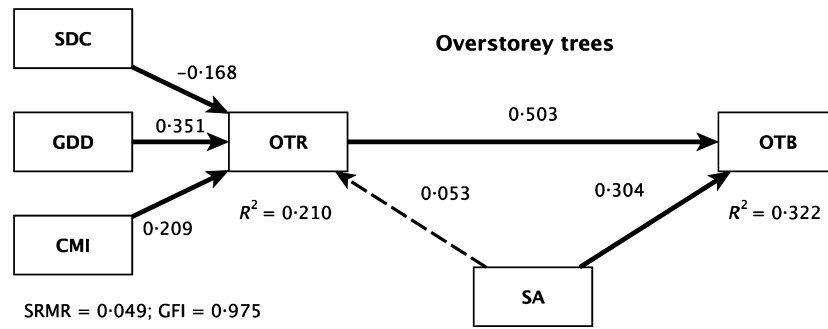
#### Results

The SEM for the overstorey tree layer conformed well to the data (SRMR = 0.049; GFI = 0.975), with overstorey tree species richness and stand age accounting for 32.2% of the variation in overstorey tree above-ground biomass (Fig. 2). Our results suggest that overstorey tree species richness had a positive direct effect on overstorey tree above-ground biomass (standardized coefficient,  $r = 0.503$ ), and overstorey tree above-ground biomass increased with stand age ( $r = 0.304$ ) (Fig. 2, Table S1). Growing degree-days and climate moisture index had positive indirect effects on overstorey tree above-ground biomass through their positive direct effects on overstorey tree species richness, whereas overstorey tree above-ground biomass decreased with soil drainage class (Table S1).

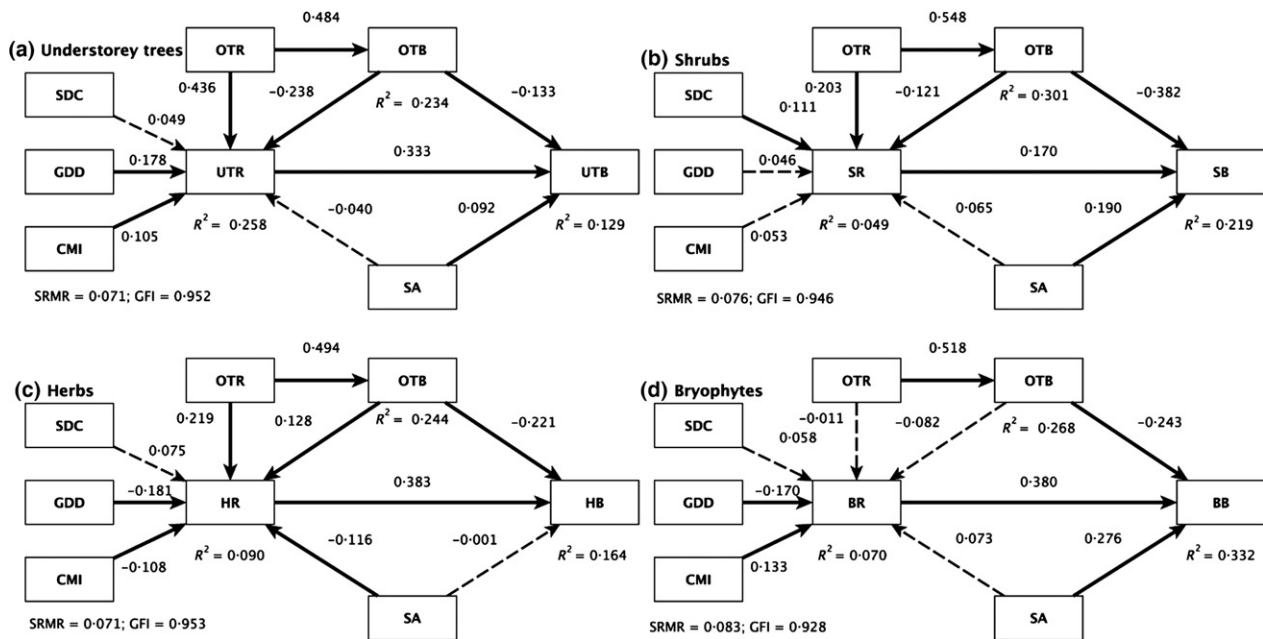
The SEMs for understorey layers also conformed well to the data (Fig. 3). Model results imply that understorey tree species richness had a positive direct effect on understorey tree above-ground biomass ( $r = 0.333$ ), and understorey tree above-ground biomass increased with stand age. Overstorey above-ground biomass had a negative direct effect ( $r = -0.133$ ) and a negative indirect effect via understorey tree species richness ( $r = -0.079$ ) on understorey tree above-ground biomass (Fig. 3a, Table S1). Overstorey tree species richness had a positive direct effect on understorey tree species richness and had a positive total indirect effect ( $r = 0.081$ ) on understorey tree above-ground biomass via its positive effect on understorey tree species richness ( $r = 0.145$ ), but a negative indirect effect via overstorey above-ground biomass ( $r = -0.064$ ) (Fig. 3a, Table S1). The overstorey tree layer had a negative total effect on understorey tree above-ground biomass ( $r = -0.131$ ). Similar to the overstorey layer, growing degree-days and climate moisture index had positive indirect effects on understorey tree above-ground biomass, but the effect of soil drainage on understorey tree above-ground biomass was insignificant (Fig. 3a, Table S1).

Shrub species richness had a positive direct effect on shrub above-ground biomass ( $r = 0.170$ ). Shrub above-ground biomass increased with stand age, but was





**Fig. 2.** Structural equation models linking above-ground biomass (OTB) and species diversity (OTR) of overstorey trees, with the effects of climate, soil and stand age accounted for. The coefficients are standardized for each causal path. Solid lines represent significant paths ( $P < 0.05$ ) and dashed lines non-significant paths ( $P \geq 0.05$ ). OTB, overstorey tree biomass; OTR, overstorey tree richness; SDC, soil drainage class; GDD, growing degree-days (yearly summation of the mean of daily maximum and minimum temperature minus 5 °C); CMI, climate moisture index (cm); SA, stand age (years); SRMR, standardized root mean square residual; GFI, goodness-of-fit index. See Table S1 for the total effects of explanatory variables on OTB by combining direct and all the indirect paths in the model.



**Fig. 3.** Structural equation models linking above-ground biomass and species diversity of the understorey tree (a), shrub (b), herb (c) and bryophyte (d) layers. UTR, SR, HR and BR are species richness for the understorey tree, shrub, herb and bryophyte layers, respectively; UTB, SB, HB and BB are above-ground biomass for the understorey tree, shrub, herb and bryophyte layers, respectively. Other abbreviations are explained in Fig. 2.

negatively affected by overstorey above-ground biomass directly ( $r = -0.382$ ) and indirectly via shrub species richness ( $r = -0.021$ ) (Fig. 3b, Table S1). Overstorey tree species richness had a positive direct effect on shrub species richness, but had a negative total indirect effect ( $r = -0.175$ ) on shrub above-ground biomass as the sum of its positive indirect effect via shrub species richness ( $r = 0.035$ ) and the negative indirect effect via overstorey above-ground biomass ( $r = -0.209$ ) (Table S1). Similar to the understorey tree layer, shrub above-ground biomass was negatively affected by overstorey trees via overstorey tree species richness and above-ground biomass ( $r = -0.578$ ) (Table S1). Growing degree-days and climate moisture index did not significantly affect shrub above-

ground biomass, whereas shrub above-ground biomass increased with soil drainage class.

The SEMs for the herb and bryophyte layers showed similar positive species richness effects on the above-ground biomass of each respective layer (Fig. 3c,d, Table S1). The overstorey tree layer had a negative total effect on herb layer above-ground biomass ( $r = -0.197$ ) from its above-ground biomass ( $r = -0.172$ ) and species richness ( $r = -0.025$ ) (Table S1). The overstorey tree layer also had a negative total effect on bryophyte above-ground biomass ( $r = -0.404$ ) via overstorey species richness ( $r = -0.130$ ) and overstorey above-ground biomass ( $r = -0.274$ ) (Table S1). Stand age had a positive effect on bryophyte above-ground biomass, but had no effect on

herb above-ground biomass. Herb layer above-ground biomass was negatively affected by growing degree-days and climate moisture index and was unaffected by soil drainage. Bryophyte above-ground biomass decreased with growing degree-days but increased with climate moisture index, with no effect by soil drainage.

## Discussion

We found positive relationships between species richness and above-ground biomass across all vegetation strata, regardless of whether the confounding effects of climate, local site conditions and stand age were controlled for in our analysis. Our results suggest that the positive relationships reported in previous studies between overstorey tree species diversity and biomass production in forest ecosystems (e.g. Paquette & Messier 2011; Zhang, Chen & Reich 2012; Zhang & Chen 2015) may be extended to include all forest vegetation strata. Although we did not test for specific underlying causal mechanisms, the positive relationships we observed between species richness and biomass production may be attributable to several known hypothesized mechanisms, including: ‘niche complementarity’, which leads to reduced interspecies competition and greater site resource utilization; ‘facilitation’, where some species may alter the environment in such a way that it favours the fitness of other species; or ‘negative density dependence’, in which communities with greater abundance of conspecific species tend to be more susceptible to host-specific pathogens. Alternatively, it is suggested that selection effects (a.k.a. sampling effects) is the only real mechanism linking biodiversity and ecosystem function since higher species richness increases the likelihood that plant communities will contain more productive species with specific functional traits that permit greater site resource exploitation, including increasing the likelihood of positive complementarity and facilitation interactions (Fridley 2001; Hooper *et al.* 2005; Forrester 2014; Ruiz-Benito *et al.* 2014).

We found that the strength of the effect of species diversity on above-ground biomass production in the understorey tree, shrub, herbaceous and bryophyte layers was weaker than that observed for overstorey trees. This supports the general hypothesis that the magnitude and direction of diversity–productivity relationships is context dependent and influenced by the conditions and available resources in the surrounding environment (Diaz & Cabido 2001; Fridley 2002). Overstorey trees impose competitive constraints on understorey vegetation because of their size, altering above- and below-ground resource availability such as light, water and space, especially for the shrub and herbaceous layers (Gilliam, Turrill & Adams 1995; Gilliam 2007; Mason *et al.* 2011). This was evident by the ubiquitously negative effects of overstorey tree above-ground biomass on the understorey layers we observed in our analysis. Resource filtering, caused by the overstorey (Anderson, Loucks & Swain 1969; Bartels & Chen 2013),

likely reduced the strength of the effect of species diversity on increased resource utilization in the resource-limited understorey environment (Hooper *et al.* 2005). This was not only true for species groups with overlapping niches, such as woody plants (Mason *et al.* 2011), but also for herbaceous and non-vascular plants in our analysis.

The positive relationships we observed between overstorey species richness and the richness of understorey vascular plants are consistent with previous studies (Gamfeldt *et al.* 2013), but overstorey tree species richness had no observable effect on bryophyte species richness. The positive associations of species richness among vascular plants across vertical vegetation strata may have resulted from their similar responses to climate, soil and stand development (Zhang, Chen & Taylor 2014), but could also be a result of increasing understorey resource heterogeneity and availability through light penetration and litterfall feedback under a more diverse overstorey (Bartels & Chen 2010, 2013). Indeed, this might suggest that niche complementarity plays an important role as a mechanism driving the observed positive diversity–productivity relationships among understorey vascular plants since complementarity is likely to play a more prominent role when resources are spatially and temporally heterogeneous (Fridley 2001; Hooper *et al.* 2005). The lack of an effect of overstorey species richness on that of bryophytes may be because bryophytes possess divergent life-history traits compared with vascular plants (Jonsson *et al.* 2015).

The effects of climatic factors, local site conditions and stand age on above-ground biomass and species richness varied in magnitude and direction, depending on the vertical position and life form within the forest. The response of overstorey tree above-ground biomass to climatic factors, local site conditions and stand age are consistent with previous reports (Michaletz *et al.* 2014; Pretzsch *et al.* 2014; Zhang & Chen 2015; Zhang, Chen & Taylor 2016a). We note that the responses of the understorey layers to environmental drivers and stand age were generally weaker or even in an opposite direction. These results suggest that the resource filtering by the overstorey did not only influence the strength of the relationships between diversity and above-ground biomass, but also affected the responses of understorey layer species richness to climate, soil and stand development (Zhang, Chen & Taylor 2014). The modulating effect of the overstorey and the environment on understorey diversity–productivity relationships supports the notion that no single, universal relationship between diversity and productivity exists, but rather that the magnitude and direction of these relationships is highly dependent on environmental context (Diaz & Cabido 2001; Fridley 2002).

Our results show that positive species diversity and above-ground biomass production relationships are ubiquitous across forest vegetation strata, but that the relationship is stronger for the overstorey layer than for the understorey tree, shrub, herb and bryophyte layers. Although species richness of overstorey tree, understorey tree, shrub and herb layers was positively correlated,

overstorey tree above-ground biomass had ubiquitously negative effects on the understorey layers. Resource filtering by overstorey trees has likely reduced the strength of the positive diversity–productivity relationships in understorey layers since positive diversity effects are primarily a result of increased resource utilization (Hooper *et al.* 2005), supporting the general hypothesis that the strength and direction of diversity–productivity relationships is context dependent and influenced by the surrounding environment. Further, heterogeneity in understorey resources, as affected by overstorey trees, likely promotes niche complementarity as the main mechanism driving the diversity–productivity relationships in the understorey.

## Acknowledgements

We thank the Canadian Forest Service for sharing the National Forest Inventory data base and E.H. (Ted) Hogg for sharing climatic data. Financial support from the Natural Sciences and Engineering Research Council of Canada (RGPIN-2014-0418), Lakehead University Research Chair program and the Canadian Forest Service are gratefully acknowledged.

## Author contributions

Y.Z., H.Y.H.C. and A.R.T. conceived the research; Y.Z. compiled and analysed data; Y.Z., H.Y.H.C. and A.R.T. wrote the paper.

## Conflict of interest

The authors declare no conflict of interest.

## Data accessibility

Data available from the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.g529s> (Zhang, Chen & Taylor 2016b).

## References

- Anderson, R.C., Loucks, O.L. & Swain, A.M. (1969) Herbaceous response to canopy cover, light intensity, and throughfall precipitation in coniferous forests. *Ecology*, **50**, 255–263.
- Balvanera, P., Siddique, I., Dee, L., Paquette, A., Isbell, F., Gonzalez, A. *et al.* (2014) Linking biodiversity and ecosystem services: current uncertainties and the necessary next steps. *BioScience*, **64**, 49–57.
- Bartels, S.F. & Chen, H.Y.H. (2010) Is understorey plant species diversity driven by resource quantity or resource heterogeneity? *Ecology*, **91**, 1931–1938.
- Bartels, S.F. & Chen, H.Y.H. (2013) Interactions between overstorey and understorey vegetation along an overstorey compositional gradient. *Journal of Vegetation Science*, **24**, 543–552.
- Boudewyn, P., Song, X., Magnussen, S. & Gillis, M. (2007) *Model-Based, Volume-to-Biomass Conversion for Forested and Vegetated Land in Canada*. Pacific Forestry Centre, Victoria, BC, Canada.
- Canadian Forest Inventory Committee (2004) *Canada's National Forest Inventory: Design Overview*. Canadian Forest Service, Ottawa, Ontario, Canada.
- Chen, H.Y.H., Krestov, P.V. & Klinka, K. (2002) Trembling aspen site index in relation to environmental measures of site quality at two spatial scales. *Canadian Journal of Forest Research*, **32**, 112–119.
- Chisholm, R.A., Muller-Landau, H.C., Abdul Rahman, K., Bebbler, D.P., Bin, Y., Bohlman, S.A. *et al.* (2013) Scale-dependent relationships between tree species richness and ecosystem function in forests. *Journal of Ecology*, **101**, 1214–1224.
- Diaz, S. & Cabido, M. (2001) Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution*, **16**, 646–655.
- Duffy, J.E. (2009) Why biodiversity is important to the functioning of real-world ecosystems. *Frontiers in Ecology and the Environment*, **7**, 437–444.
- Flombaum, P. & Sala, O.E. (2008) Higher effect of plant species diversity on productivity in natural than artificial ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 6087–6090.
- Forrester, D.I. (2014) The spatial and temporal dynamics of species interactions in mixed-species forests: from pattern to process. *Forest Ecology and Management*, **312**, 282–292.
- Fowler, M.S., Laakso, J., Kaitala, V., Ruokolainen, L., Ranta, E. & Post, D. (2012) Species dynamics alter community diversity-biomass stability relationships. *Ecology Letters*, **15**, 1387–1396.
- Fridley, J.D. (2001) The influence of species diversity on ecosystem productivity: how, where, and why? *Oikos*, **93**, 514–526.
- Fridley, J.D. (2002) Resource availability dominates and alters the relationship between species diversity and ecosystem productivity in experimental plant communities. *Oecologia*, **132**, 271–277.
- Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P. *et al.* (2013) Higher levels of multiple ecosystem services are found in forests with more tree species. *Nature Communications*, **4**, 1340.
- Gilliam, F.S. (2007) The ecological significance of the herbaceous layer in temperate forest ecosystems. *BioScience*, **57**, 845–858.
- Gilliam, F.S., Turrill, N.L. & Adams, M.B. (1995) Herbaceous-layer and overstorey species in clear-cut and mature central Appalachian hardwood forests. *Ecological Applications*, **5**, 947–955.
- Grace, J.B. & Bollen, K.A. (2005) Interpreting the results from multiple regression and structural equation models. *Bulletin of the Ecological Society of America*, **86**, 283–295.
- Grace, J.B., Anderson, T.M., Olf, H. & Scheiner, S.M. (2010) On the specification of structural equation models for ecological systems. *Ecological Monographs*, **80**, 67–87.
- Grace, J.B., Schoolmaster, D.R., Guntenspergen, G.R., Little, A.M., Mitchell, B.R., Miller, K.M. *et al.* (2012) Guidelines for a graph-theoretic implementation of structural equation modeling. *Ecosphere*, **3**, art73.
- Grace, J.B., Anderson, T.M., Seabloom, E.W., Borer, E.T., Adler, P.B., Harpole, W.S. *et al.* (2016) Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature*, **529**, 390–393.
- Hogg, E.H. (1997) Temporal scaling of moisture and the forest-grassland boundary in western Canada. *Agricultural and Forest Meteorology*, **84**, 115–122.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S. *et al.* (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.
- Hoyle, R.H. (2012) *Handbook of Structural Equation Modeling*. Guilford Press, New York City, New York, NY, USA.
- Hulvey, K.B., Hobbs, R.J., Standish, R.J., Lindenmayer, D.B., Lach, L. & Perring, M.P. (2013) Benefits of tree mixes in carbon plantings. *Nature Climate Change*, **3**, 869–874.
- Jenkins, D. (2015) Estimating ecological production from biomass. *Ecosphere*, **6**, art49.
- Jonsson, M., Kardol, P., Gundale, M.J., Bansal, S., Nilsson, M.C., Metcalfe, D.B. *et al.* (2015) Direct and indirect drivers of moss community structure, function, and associated microfauna across a successional gradient. *Ecosystems*, **18**, 154–169.
- Jucker, T., Bouriaud, O., Avacaritei, D., Danila, I., Duduman, G., Valldares, F. *et al.* (2014) Competition for light and water play contrasting roles in driving diversity-productivity relationships in Iberian forests. *Journal of Ecology*, **102**, 1202–1213.
- Kenny, D.A., Kaniskan, B. & McCoach, D.B. (2015) The performance of RMSEA in models with small degrees of freedom. *Sociological Methods & Research*, **44**, 486–507.
- Mason, N.W.H., de Bello, F., Doležal, J. & Lepš, J. (2011) Niche overlap reveals the effects of competition, disturbance and contrasting assembly processes in experimental grassland communities. *Journal of Ecology*, **99**, 788–796.
- Michaletz, S.T., Cheng, D., Kerkhoff, A.J. & Enquist, B.J. (2014) Convergence of terrestrial plant production across global climate gradients. *Nature*, **512**, 39–43.
- Nilsson, M.C. & Wardle, D.A. (2005) Understorey vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. *Frontiers in Ecology and the Environment*, **3**, 421–428.
- Oberle, B., Grace, J.B. & Chase, J.M. (2009) Beneath the veil: plant growth form influences the strength of species richness-productivity relationships in forests. *Global Ecology and Biogeography*, **18**, 416–425.

- Paquette, A. & Messier, C. (2011) The effect of biodiversity on tree productivity: from temperate to boreal forests. *Global Ecology and Biogeography*, **20**, 170–180.
- Pretzsch, H., Biber, P., Schütze, G., Uhl, E. & Rotzer, T. (2014) Forest stand growth dynamics in Central Europe have accelerated since 1870. *Nature Communications*, **5**, 4967.
- van der Putten, W.H., Bardgett, R.D., Bever, J.D., Bezemer, T.M., Casper, B.B., Fukami, T. *et al.* (2013) Plant-soil feedbacks: the past, the present and future challenges. *Journal of Ecology*, **101**, 265–276.
- R Development Core Team (2015) *R Version 3.2.2*. R Foundation for Statistical Computing, Vienna, Austria.
- Régnière, J. & Saint-Amant, R. (2008) *BioSIM 9 – User's Manual*. Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, Québec City, QC, Canada.
- Rosseel, Y. (2012) lavaan: an R package for structural equation modeling. *Journal of Statistical Software*, **48**, 1–36.
- Ruiz-Benito, P., Gómez-Aparicio, L., Paquette, A., Messier, C., Kattge, J. & Zavala, M.A. (2014) Diversity increases carbon storage and tree productivity in Spanish forests. *Global Ecology and Biogeography*, **23**, 311–322.
- Senici, D., Chen, H.Y.H., Bergeron, Y. & Cyr, D. (2010) Spatiotemporal variations of fire frequency in Central Boreal forest. *Ecosystems*, **13**, 1227–1238.
- Taylor, K.C., Arnup, R.W., Meredith, M.P., Parton, W.J. & Nieppola, J. (2000) *A Field Guide to Forest Ecosystems of Northeastern Ontario*. NEST Field Guide FG-01, Northeast Science and Technology, Ontario Ministry of Natural Resources, Timmins, Ontario, Canada.
- Taylor, A.R., Seedre, M., Brassard, B.W. & Chen, H.Y.H. (2014) Decline in net ecosystem productivity following canopy transition to late-succession forests. *Ecosystems*, **17**, 778–791.
- Vilà, M., Vayreda, J., Comas, L., Ibanez, J.J., Mata, T. & Obon, B. (2007) Species richness and wood production: a positive association in Mediterranean forests. *Ecology Letters*, **10**, 241–250.
- Vilà, M., Carrillo-Gavilan, A., Vayreda, J., Bugmann, H., Fridman, J., Grodzki, W. *et al.* (2013) Disentangling biodiversity and climatic determinants of wood production. *PLoS ONE*, **8**, e53530.
- Wang, C.K., Bond-Lamberty, B. & Gower, S.T. (2003) Carbon distribution of a well- and poorly-drained black spruce fire chronosequence. *Global Change Biology*, **9**, 1066–1079.
- Willig, M.R. (2011) Biodiversity and productivity. *Science*, **333**, 1709–1710.
- Zhang, Y. & Chen, H.Y.H. (2015) Individual size inequality links forest diversity and above-ground biomass. *Journal of Ecology*, **103**, 1245–1252.
- Zhang, Y., Chen, H.Y.H. & Reich, P.B. (2012) Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. *Journal of Ecology*, **100**, 742–749.
- Zhang, Y., Chen, H.Y.H. & Taylor, A. (2014) Multiple drivers of plant diversity in forest ecosystems. *Global Ecology and Biogeography*, **23**, 885–893.
- Zhang, Y., Chen, H.Y.H. & Taylor, A.R. (2016a) Aboveground biomass of understorey vegetation has a negligible or negative association with overstorey tree species diversity in natural forests. *Global Ecology and Biogeography*, **25**, 141–150.
- Zhang, Y., Chen, H.Y.H. & Taylor, A.R. (2016b) Data from: Positive species diversity and above-ground biomass relationships are ubiquitous across forest strata despite interference from overstorey trees. *Dryad Digital Repository*, <http://dx.doi.org/10.5061/dryad.g529s>
- Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York City, New York, NY, USA.

Received 3 February 2016; accepted 1 June 2016

Handling Editor: Rebecca Ostertag

## Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

**Table S1.** Direct, indirect and total standardized effects on the above-ground biomass.

**Table S2.** Pearson's correlation coefficients between variables.

**Fig. S1.** The distributions of national forest inventory ground plots.

**Fig. S2.** The stand age distributions of national forest inventory ground plots.

**Fig. S3.** The summary of above-ground biomass and species richness by strata.

**Fig. S4.** The bivariate relationships for overstorey tree layer.

**Fig. S5.** The bivariate relationships for understorey tree layer.

**Fig. S6.** The bivariate relationships for shrub layer.

**Fig. S7.** The bivariate relationships for herb layer.

**Fig. S8.** The bivariate relationships for bryophyte layer.