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The effect of biodiversity on tree productivity: from temperate to boreal forests

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ABSTRACT

Aim An important issue regarding biodiversity concerns its influence on ecosystem functioning. Experimental work has led to the proposal of mechanisms such as niche complementarity. However, few attempts have been made to confirm these in natural systems, especially in forests. Furthermore, one of the most interesting unresolved questions is whether the effects of complementarity on ecosystem functioning (EF) decrease in favour of competitive exclusions over an increasing productivity gradient. Using records from permanent forest plots, we asked the following questions. (1) Is tree productivity positively related to diversity? (2) Does the effect of diversity increase in less productive forests? (3) What metric of diversity (e.g. functional or phylogenetic diversity) better relates to tree productivity?

Location Temperate, mixed and boreal forests of eastern Canada.

Methods Over 12,000 permanent forest plots, from temperate to boreal forests, were used to test our hypotheses in two steps. (1) Stepwise regressions were used to identify the best explanatory variables for tree productivity. (2) The selected climatic and environmental variables, as well as density and biodiversity indices, were included in a structural equation model where links (paths) between covarying variables are made explicit, making structural equation modelling the best tool to explore such complicated causal networks.

Results This is the first large-scale demonstration of a strong, positive and significant effect of biodiversity on tree productivity with control for climatic and environmental conditions. Important differences were noted between the two forest biomes investigated.

Main conclusions We show for the first time that complementarity may be less important in temperate forests growing in a more stable and productive environment where competitive exclusion is the most probable outcome of species interactions, whereas in the more stressful environment of boreal forests, beneficial interactions between species may be more important. The present work is also a framework for the analysis of large datasets in biodiversity–ecosystem functioning (B-EF) research.

Keywords

Biodiversity and ecosystem functioning, boreal forests, Canada, ecosystem services, fertility gradient, forest biomes, functional diversity, phylogenetic diversity, temperate forests, tree productivity.

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INTRODUCTION

There is growing interest in evaluating the role of biodiversity in promoting ecosystem functions, services and resilience, and indeed the biodiversity–ecosystem functioning (B-EF) relation-

ship has been a subject of considerable interest and controversy during the last two decades (Symstad *et al.*, 2003; Reiss *et al.*, 2009). Two fundamental mechanisms have been proposed that could be responsible for generating positive biodiversity effects: (1) niche partitioning and facilitation – the

complementarity effect; and (2) selection of particular functional traits – the sampling effect (Loreau, 1998). Seminal experiments on which the theory was built have been criticized for being dominated by immature temperate grasslands and so the generality of their findings was questioned (Symstad *et al.*, 2003; Thompson *et al.*, 2005). Since then, however, two decades of research on diverse systems has mostly confirmed previous findings of a positive relationship between species richness and biomass increment (Balvanera *et al.*, 2006).

There is a strong and lasting debate over what element of biodiversity matters to ecosystem functioning (Diaz *et al.*, 2007; Mokany *et al.*, 2008) and how it should be quantified (Poos *et al.*, 2009; Laliberté & Legendre, 2010). Functional diversity indices, rather than species richness, were introduced as ways to tap into possible mechanisms to support the niche complementarity hypothesis by accounting for functional redundancy and acknowledging that some mixtures of species may be more 'diverse' than others, in which case species would compete less and make more extensive use of resources. Indeed, a simple prediction could be that ecosystem functions respond linearly to increasing functional diversity, whereas the relation with species richness saturates due to functional redundancy and niche overlap (Loreau *et al.*, 2001). Also, the use of phylogenies in community ecology is growing (Webb *et al.*, 2002), and evolutionary history has also been proposed as a better predictor of ecosystem functions than species richness (Cadotte *et al.*, 2008). Indeed phylogenetic diversity carries the same basic idea, that short evolutionary distances are found between functionally similar species, and vice versa.

One of the most interesting questions still being debated is whether the effects of complementarity (from either competition-driven niche partitioning or facilitation) on ecosystem functioning decrease in favour of competitive exclusions over an increasing productivity gradient (Warren *et al.*, 2009). In other words, is complementarity more important in less productive more stressful environments (i.e. would functionally different species increase the overall productivity of the system)? In contrast, dominant, highly productive species, would take over in more productive habitats, thus revealing the often reported hump-backed (unimodal) relationship between productivity and species richness.

B-EF research in natural systems has so far produced conflicting results (Jiang *et al.*, 2009), some studies even reporting negative relationships (e.g. Thompson *et al.*, 2005). Thus the debate around the outcome of plant interactions, namely along fertility and successional gradients, is ongoing (Warren *et al.*, 2009). Clearly, biodiversity effects need to be better understood in natural ecosystems in order to better manage them to provide as many ecological services as possible while maintaining their resilience, especially given the recent interest in ecosystem-based management (Puettmann *et al.*, 2009; Paquette & Messier, 2010). Strangely enough, given the importance of forests in the Earth's ecosystems, little work has so far been carried out in forests (Scherer-Lorenzen *et al.*, 2005), and large-scale investigations addressing the role of functional traits are also much needed (Loreau *et al.*, 2001; Symstad *et al.*, 2003; Reiss *et al.*,

2009). So far few studies have attempted to test B-EF relationships in natural forests, but most have reported overall positive results (Caspersen & Pacala, 2001; Vilà *et al.*, 2007; Lei *et al.*, 2009), although negative or insignificant results have also been reported (Vilà *et al.*, 2003). Some of these studies did not control for climate or environment, both strong determinants of productivity and species richness, and most used species numbers or functional groups for biodiversity assessment. Only Lei *et al.* (2009) included boreal species.

The objective of the present study was to investigate the nature of the relationship between biodiversity and ecosystem functioning over a large forest extent in north-eastern North America. The > 12,000 permanent 400-m² forest plots surveyed (Fig. 1; Table 1), including some 400,000 trees of over 50 species, are representative of the deciduous, mixed and boreal forests of North America, comprising some of Earth's most extensive ecosystems. From that dataset we computed tree biomass increments (hereafter 'productivity') and tested that against a number of explanatory variables to identify the major abiotic and biotic factors that affect productivity. Those were then used in structural equation models to test three hypotheses.

1. That productivity is generally positively related to biodiversity (even when covarying climatic and environmental determinants of productivity and species richness are considered).
2. That positive effects of biodiversity, possibly through complementarity, are more important in the more stressful, less diversified northern boreal forest.
3. That functional diversity (or phylogenetic diversity), is a better predictor of productivity than species richness alone.

METHODS

Dataset, tree productivity and environmental controls

We used the Québec (eastern Canada) forest survey dataset, dating back to 1970 and still in service today (Duchesne & Quimet, 2008). This forest sampling effort covers all of the province's public lands, thus including some of the most extensive ecosystems on Earth, from temperate forests to the vast boreal forests of the north (Fig. 1). New plots are added every year, while older ones are remeasured approximately every 10 years (mean 9.96 ± 3.21 years) (see Appendix S1 in Supporting Information for more details regarding the dataset). From that large dataset of over 36,000 plot measurements we selected pairs of surveys (two contiguous measures of the same plot) that met our criteria, namely that the plot had not been affected by a significant natural disturbance between the two censuses considered, or by human interventions of any kind, including plantations, for a total of 12,324 pairs for which we then computed the following.

1. Average total basal area for each of the species present. This was used as a matrix of species abundances and presence/absence for species, functional and phylogenetic diversity indices, as well as a proxy for competition intensity once all species are summed-up (total basal area).

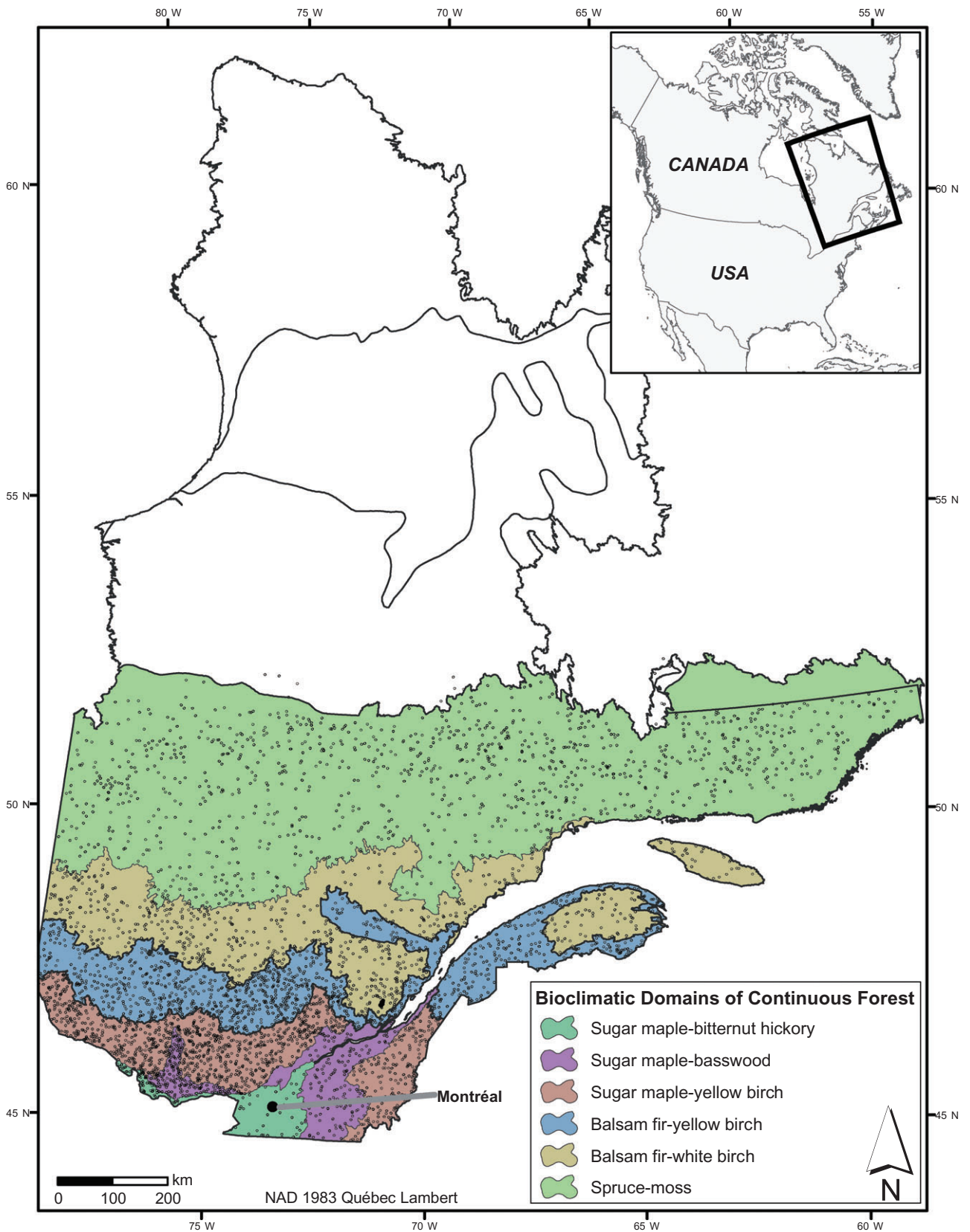


Figure 1 Map of plots used in this study and their distribution across all bioclimatic domains of continuous forest in Québec, Canada.

Table 1 Basic description of the dataset under study per biome.

	Temperate	Boreal
Bioclimatic domains included (Fig. 1)	Sugar maple–bitternut hickory Sugar maple–basswood Sugar maple–yellow birch	Balsam fir–yellow birch Balsam fir–white birch Spruce–moss
Number of plots	4466	7858
Dominant species (in order of dominance)	<i>Acer saccharum</i> <i>Abies balsamea</i> <i>Acer rubrum</i> <i>Betula alleghaniensis</i>	<i>Picea mariana</i> <i>Abies balsamea</i> <i>Betula papyrifera</i> <i>Populus tremuloides</i>
Basal area (m ² ha ⁻¹)*	23 ± 8.3 (7.8–41)	19 ± 9.4 (2.9–38)
Species richness	5.5 ± 2.1 (1–13)	3.3 ± 1.7 (1–11)
Monocultures/low SR†	1.6%/18%	12%/61%
Functional diversity‡	1.04 ± 0.29 (0–1.8)	0.59 ± 0.34 (0–1.7)
Mean growth (tons ha ⁻¹ year ⁻¹)§	2.6 ± 1.1 (0.58–4.9)	1.4 ± 1.1 (0.02–3.8)

Mean ± 1 SD are provided for continuous variables, followed by the range.

*Values were scaled to 1 ha from the original plot size (400 m²), and ranges are 2.5 and 97.5 percentiles.

†Low species richness (SR) plots have fewer than four species (one to three).

‡FDis₃ index.

§Aboveground biomass increment of trees; range = 2.5 and 97.5 percentiles.

2. Tree productivity, specifically annual aboveground biomass increments, computed using tree diameter at breast height (d.b.h.) and the following equation:

$$Y = \frac{\sum_{i=1}^n b_{i-t_2} - b_{i-t_1}}{t_2 - t_1} \quad (1)$$

where Y is the yearly increment of total aboveground biomass of live trees between a pair of measurements at times t_1 and t_2 for a given plot, and b is the biomass of tree i present at both sampling times (recruits and dead trees are thus excluded; see Appendix S1). Individual biomasses b of trees were computed using d.b.h. and published equations for aboveground stem and branch biomass (Lambert *et al.*, 2005).

A number of continuous environmental descriptors (log-transformed when necessary) were used to control for environmental conditions: drainage class, slope and the pH and depth of the organic horizons (Appendix S1). To control for climate we used plot coordinates to compute climatic variables using ANUSPLIN interpolation of 30-year normals from all available weather stations (Hutchinson, 1995; Milewska *et al.*, 2005).

Quantification of functional and phylogenetic diversity

Although there is growing consensus on the fact that ecosystem functioning (EF) is related to the diversity of plant communities, little is known about the importance of different components of diversity (Cadotte *et al.*, 2008), the appropriate way to account for diversity and the relative role and importance of particular plant traits (Petchey & Gaston, 2006; Mokany *et al.*, 2008). Like others before we used both a priori knowledge and a

posteriori identification of the most promising set of explanatory variables and functional traits (Diaz *et al.*, 2007; Mokany *et al.*, 2008). First, a table of functional traits was assembled from published sources for the 51 tree and large shrub species present in our dataset: maximum height, growth rate, leaf size, longevity, mass per area and nitrogen content, wood density and decay resistance, vegetative reproduction, seed mass, pollination vector, shade, drought and water-logging tolerance and mycorrhizal infection type (see Appendix S2 for details). Dummy variables and weights were used for some categorical traits (mycorrhizal infection and pollination vector) for which more than one state is possible for a given species (Petchey & Gaston, 2006). Functional diversity (FD) indices were then computed using an index called functional dispersion (FDis) (Laliberté & Legendre, 2010). We also computed functional redundancy (FR) within plots which can be expressed as the difference between the potential and realized FD. We adapted the de Bello *et al.* (2007) FR index to species richness (SR) minus FDis and plotted it over mean temperatures to test whether redundancy increased along a climatic gradient. We also computed the ratio of realized over potential diversity [(FD + 1)/SR] as a measure of the average contribution of a single species to the community FD. Finally, phylogenetic diversity (PD) indices were computed using a molecular phylogeny of our tree species based on chloroplastic genes (see Appendices S2 & S3). The classic Faith (1992) PD index and the more recent phylogenetic species variability (PSV) index (Helmus *et al.*, 2007), which quantifies how phylogenetic relatedness decreases the variance of a hypothetical unselected or neutral trait shared by all species in a community, were compared. Plots comprising a single species were assigned FD and PD values of zero (see Appendix S1 for further details regarding functional traits and the computation of FD and PD indices).

Analyses

Once we had gathered all data and biodiversity indices, analyses were carried out in two main steps. First, using the log-transformed annual aboveground biomass increment of trees as a response variable, we proceeded to identify the most promising explanatory variables using stepwise procedures. Second, we used the selected variables, including controls for climate and the environment as well as for competition intensity, in a general model using structural equation modelling (SEM). The first stage was carried out in logical independent steps to identify abiotic and biotic drivers of productivity (Diaz *et al.*, 2007): (1) abiotic factors (local environmental and climatic conditions); (2) stand basal area (BA) as proxy for competition intensity; (3) biodiversity. We first tested FDis indices based on all (weighted) available traits. More FD indices were then built on groups of traits based on a priori knowledge using seed mass, wood density and maximum height, as well as leaf mass per area (LMA) and leaf nitrogen content. Because of the many variables available and possible loss of interpretable information with insignificant increases in variance explained, we used Mallows' C_p to help retain only those variables that contributed the most.

In the second step, the above-selected abiotic and biotic variables were then used to test our hypotheses through SEM. This method was deemed appropriate given the obvious causal links between productivity and other explanatory variables such as climate. Moreover, biodiversity potentially shares some of these causes with productivity which would be masked in a regression model. Finally, there is a well-documented link between diversity and productivity going in the opposite direction, with productivity being the driver of diversity (Waide *et al.*, 1999; Loreau *et al.*, 2001; Grace *et al.*, 2007). The often used chi-square test for SEM model fit is dependent on sample-size and becomes very powerful at detecting trivial deviations that may not be of interest in large sample sizes (e.g. > 500) (Shipley, 2000). Given the very large dataset used here, Bentler's comparative fit index (CFI) was used instead because it standardizes for sample size (Bentler, 1990). In SEM, multisample analysis can be used to ask whether the dataset is taken from a single homogeneous population or from two or more populations with possibly different causal relations (Shipley, 2000). We used that feature to test for differences between bioclimatic zones. Two groups (biomes) were thus compared (for simplicity, following prior analyses using all six bioclimatic domains): the temperate forests of the south, comprising the three southernmost bioclimatic zones dominated by deciduous species (Fig. 1, $n = 4466$), and the mixed and coniferous boreal forests to the north ($n = 7858$) (see Appendix S1 for technical details regarding SEM analysis).

RESULTS

Abiotic and biotic determinants of tree productivity

Following stepwise selection of the most important explanatory variables, mean annual temperatures and depth of the organic horizons were significant in explaining tree productivity, as was

Table 2 Results of the stepwise procedure for the selection of the most important explanatory variables from each group of abiotic and biotic drivers of tree productivity for further, combined analyses using structural equation modelling (SEM).

Variable	R^2_a
Abiotic variables*	
Mean temperature	0.42
Organic layer depth	0.23
Competition intensity	
Stand basal area (BA)	0.37
Biodiversity indices	
Functional diversity (FDis_3)	0.36
Phylogenetic diversity (Faith's PD)	0.29
Functional diversity (FDis_5)	0.15
Species richness (SR)	0.30
Phylogenetic species variability (PSV)	0.16

Variables within each group are listed in order of selection. All variables listed were significant ($P < 0.0001$; $n = 12,324$). Adjusted R^2_a are given for each variable taken alone.

*More abiotic variables were significant in the stepwise procedure but were not retained due to very small increases in variance explained.

stand BA which was used as a proxy for competition intensity (Table 2). These variables explained 49% (both abiotic variables taken together) and 37% (BA for competition) of the variance in tree productivity. Mean temperature is a strong determinant of growth, whereas the depth of the organic horizons is commonly used as a proxy for soil microbial activity. Where the latter is low, the organic horizons tend to grow thicker and are associated with low decomposition rates and nutrient turnover. The same method was applied to select the best explanatory indices of diversity. Although it was significant and explained a large fraction of the variance in productivity when taken alone, FD based on all available functional traits was outperformed by all other variables we tested. The single best diversity index tested (FDis_3) was based on seed mass, which relates to reproductive strategy, wood density (reproductive strategy and growth rate) and maximum height (dominance and structural diversity), all traits often used in the B-EF literature (Ackerly & Cornwell, 2007; Chave *et al.*, 2009; Lei *et al.*, 2009) (Table 2). A second index (FDis_5) that added leaf mass per area (LMA) and leaf N content, well-known ecosystem drivers (Diaz *et al.*, 2004), was also significant but was surpassed by phylogenetic diversity (PD) which came second. Indeed, leaf traits are often cited as 'ecosystem drivers' whereby EF is related to their weighted community mean, rather than to their variance. Species richness (SR) was also significant, as well as phylogenetic species variability (PSV), an alternative to Faith's PD (which is much dependent on SR). Once PD and SR were removed, PSV came second after FDis_3, thus revealing some true effect of phylogenetic distances that was not captured by FD. Together, functional diversity (FDis_3) and PSV, both independent of SR, explained about 37% of variance in tree productivity. All significant biodiversity indices taken together explained about 40%.

Towards a general model of tree productivity

The above variables were then included in a general model of tree productivity using SEM. Climate (mean annual temperatures), the environment (depth of the organic horizons), stand BA, SR and FD still contributed enough explanatory power to be retained in a general model that included all plots (all coefficients significant, CFI = 0.949, R^2 for productivity = 0.65). That model was therefore retained for multisample analysis (Fig. 2a, b). It includes a retroactive loop for the effect of productivity on SR. It hypothesizes that climate and the environment have direct effects on SR (as well as on productivity and stand BA), but that the effect of biodiversity on productivity is mediated through FD.

Following multisample analysis comparing temperate and boreal biomes, Lagrange multipliers revealed that all constraints between biomes could be relaxed (i.e. that all paths between the two groups were different) based on significant ($P < 0.05$) chi-square increments. Again the increased power of the chi-square test statistic with large sample sizes might have revealed differences that are in fact ecologically trivial. We therefore only noted the constraints that, if released, contributed an overwhelming majority of chi-square increments in the model. Three important differences between the boreal and temperate forest biomes were thus revealed (Fig. 2a, b, asterisks): the SR → FD, FD → productivity and climate → environment paths. With few exceptions, all paths in the boreal biome were stronger than in the temperate. Consequently, response variables were also better explained by the model as expressed by larger R^2 coefficients. The model for boreal forests was well supported by the data (CFI = 0.987), whereas the fit was poorer for temperate forests (CFI = 0.933). Overall, close to 70% of the variance in tree productivity could be explained by the model for the boreal biome, and less than 25% for the temperate. The model for temperate forests could be improved by removing non-significant paths for parsimony, and by allowing quadratic relationships for the effect of competition (BA) on productivity and SR. We tested that by adding an additional factor in the model, BA^2 , which further improved the fit to CFI = 0.982 and R^2 for productivity to 0.297 (Fig. 2c). No such improvement could be obtained in the boreal biome.

DISCUSSION

The extensive dataset used enabled us to detect a significant and positive effect of biodiversity on tree productivity, thus confirming our first hypothesis. As expected, this effect was somewhat smaller than that of other known determinants of tree growth such as climate and the environment. The amount of variance explained by biodiversity alone (approximately 37%) was still much greater than that found in other studies done in forests (e.g. Vilà *et al.*, 2007, 4.7%), and comparable to that of Mokany *et al.* (2008) in grasslands. Moreover, the effect of biodiversity remained significant when all other factors were also included in structural equation models (Fig. 2). Indeed, this is the first large-scale demonstration of a strong, positive and significant effect of

biodiversity on forest ecosystem processes with control for climatic and environmental conditions.

Factors driving productivity between contrasting forest types

Even with extensive coverage of local environmental and climatic conditions, we noted a strong effect of bioclimatic zones over the partitioning of variance components used in our study (Fig. 2). The effects of biodiversity and climate on productivity were barely significant within the southerly, more stable and more productive temperate biome that is dominated by sugar maple (*Acer saccharum*; Table 1), but became highly significant in the northern, more stressful and less productive and diversified boreal biome. Within the temperate biome, tree productivity was determined mostly by the intensity of competition, which was made even more obvious with the improved model allowing quadratic relationships with basal area (Fig. 2c). The same was observed for species richness, which was also strongly determined by competition intensity. In this biome, as stands develop into forests dominated by sugar maple (in the absence of major disturbance), the growth of older living trees declines as the stand enters a period of relative stability in which late-successional stages are maintained through localized mortality. The effect of competition intensity on ecosystem functioning, through changes in the intensity of species dynamics, was also investigated in other ecosystems (e.g. Griffin *et al.*, 2008), and follows the often proposed unimodal relationship between diversity and density along a successional gradient (Guo, 2003). This is illustrated in temperate forests by an increase in both stand biomass and diversity during early succession (Fig. 2c, positive BA → SR path), followed by a decline in diversity as the ecosystem reaches the high standing biomass typical of the more stable late-successional states (negative BA^2 → SR path). Evidently, competitive exclusions and selection effects seem to play a large role in the less disturbed and more productive temperate forests of north-eastern North America, a phenomenon often observed in herbaceous communities (Grace, 1999). This increased competition in species-rich communities is thought to promote stability through statistical averaging (Doak *et al.*, 1998).

Climate and environmental effects were much stronger in the boreal biome than in temperate forests, whereas the effect of competition intensity was lessened and linear (Fig. 2b). Biodiversity effects were also far more important in that biome. Productivity tended to increase species richness via feedback mechanisms which are still unclear, as shown by the many hypotheses that have been proposed, but are known to occur essentially across sites or latitudinal gradients (Waide *et al.*, 1999; Loreau *et al.*, 2001; Symstad *et al.*, 2003). Productivity was increased by the functional diversity of the tree species present thus demonstrating a positive effect of biodiversity on ecosystem processes. This result supports the idea that complementarity may also operate in natural communities (not only under controlled experiments), especially in communities of long-living organisms such as forests (Cardinale *et al.*, 2007). More-

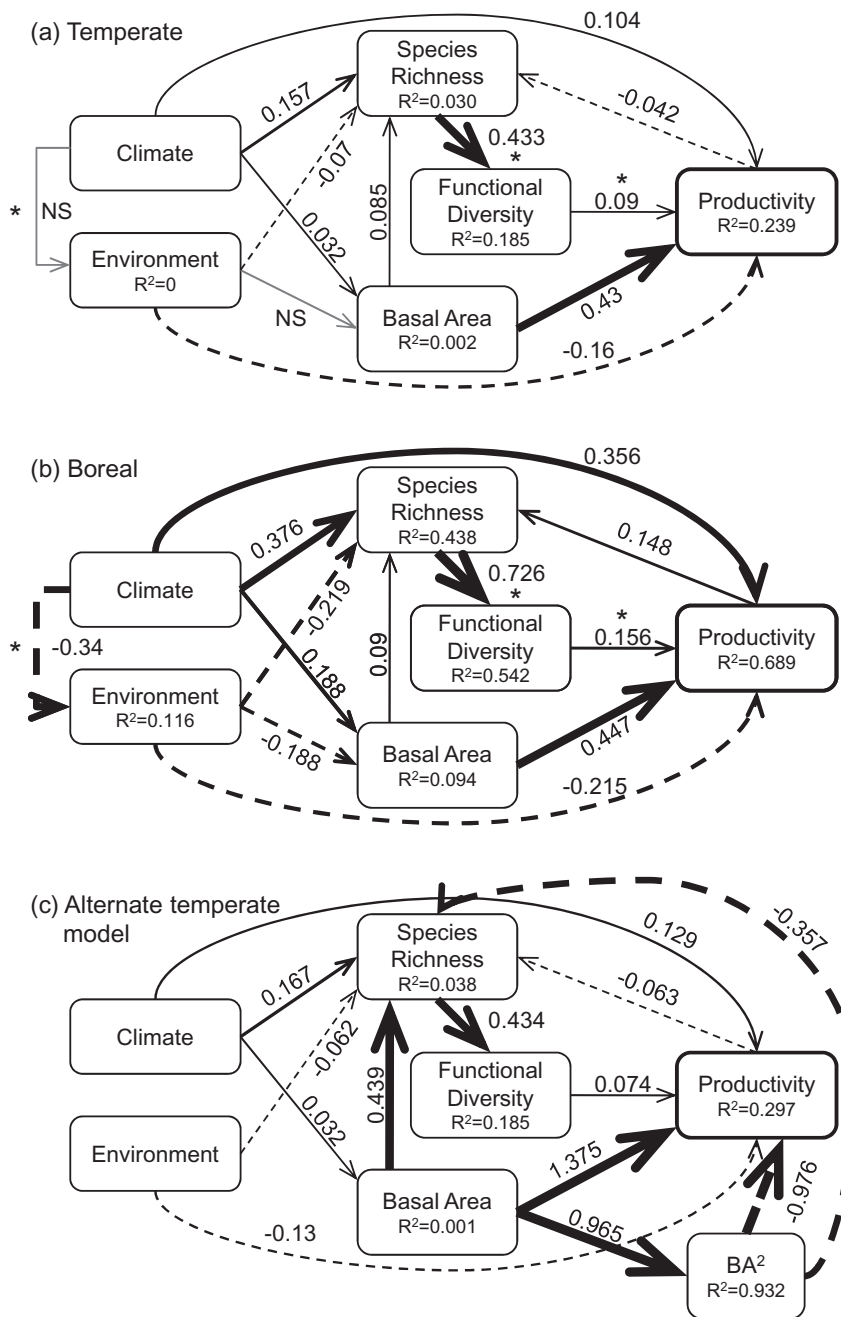


Figure 2 Results of the multisample structural equation modelling (SEM) analysis for (a) temperate and (b) boreal forest biomes. Single arrows represent causal paths (error paths are not presented for clarity). Printed standardized coefficients are significant ($P < 0.05$; robust statistics). Arrow thickness is proportional to path coefficient (solid, positive; dashed, negative; grey, not significant). All coefficients were significantly different between biomes but only those that contributed the most in chi-square increments are shown by asterisks. The amount of variance explained for each dependent variable in the model is shown inside their respective box. The model's robust comparative fit indices (CFI) were 0.933 and 0.987, respectively, for the temperate and boreal biomes. Climate = mean temperature; environment = organic layer depth. (c) Alternate SEM analysis for the temperate biome allowing for asymptotic productivity and species richness responses to stand density through the addition of a quadratic factor (BA^2 = basal area squared). The model's robust CFI was 0.983.

over, this effect may in fact be more important in less productive environments (Warren *et al.*, 2009). Incidentally, one of the few documented facilitation effects among forest trees, possibly leading to complementarity and enhanced ecosystem function-

ing (Cardinale *et al.*, 2002), is that of aspen (*Populus tremuloides*), a common pioneer species of the boreal forest, on spruce (*Picea glauca* and *Picea mariana*) (Légaré *et al.*, 2005; Comeau *et al.*, 2009). Facilitation is indeed often associated with less

productive habitats (Callaway *et al.*, 2002; Gómez-Aparicio *et al.*, 2004). This observation appears to contradict results obtained in experiments where fertility was manipulated (e.g. Fridley, 2003; Weigelt *et al.*, 2009) in which the biodiversity effect is often found to be increasing with fertility, not the reverse. However, that evidence came from short-term experiments (most lasting only one growing season) which may have prevented dominance hierarchies (and competitive exclusions) from developing in high-fertility plots (Dimitrakopoulos & Schmid, 2004).

The effects of biodiversity on productivity may therefore be less important in temperate forests growing on rich deep soils under more favourable climates where competitive exclusion is the most probable outcome of species interactions. In the more stressful environment of the boreal forest, where resources are scarcer, the climate is harsher and forest dynamics are mostly through stand-replacing disturbances (e.g. fire), beneficial complementary interactions between species may become more important. Our results and those of Lei *et al.* (2009) in similar forests thus tend to support our second hypothesis that complementarity effects are more important to ecosystem processes in nutrient-poor and/or harsh climates, whereas competitive exclusions tend to favour few dominant, highly productive species in more productive conditions. Such an effect was theoretically predicted (Warren *et al.*, 2009) and has been found in other natural systems (Guo, 2003).

If verified, this would translate into a slightly different general B-EF relationship along fertility gradients than theoretically proposed by Loreau *et al.* (2001, p. 806). Within the space defined by the diversity–productivity unimodal relationship, favourable forest habitats (in our case temperate forests) would show a mostly flat relationship (weak productivity increases with increases in diversity) but a proportionally larger intercept, i.e. a greater productivity at low diversity (Fig. 3). A completely different picture was found in our less favourable forest habitat (boreal forests), showing less productivity on average, as expected, but a much stronger, mostly linear response to diversity. Furthermore, we hypothesize that the negative relationship often found in very fertile or ruderal habitats, for which at least three possible causes have been proposed and are still debated (recent human activity, e.g. agriculture, and competitive exclusions, and evolutionary constraints imposing either a restricted species pool or a sampling/size effect where plant size increases as fertility rises, thus squeezing out species at the local scale) (see Warren *et al.*, 2009), would fill the upper part of the graph showing high productivity at low levels of diversity and a decreasing trend.

We see another possible mechanism for the lack of a strong biodiversity effect in the more favourable temperate forests: a reduced functional diversity span that would make the detection of its effect difficult. Species-rich temperate forests may indeed be composed of functionally similar species, interchangeable with little to no effect on ecosystem functioning. This is known as functional redundancy (FR) (de Bello *et al.*, 2007), and would translate into an SR → FD relationship that reaches a plateau at high levels of species richness following an asymptotic curve.

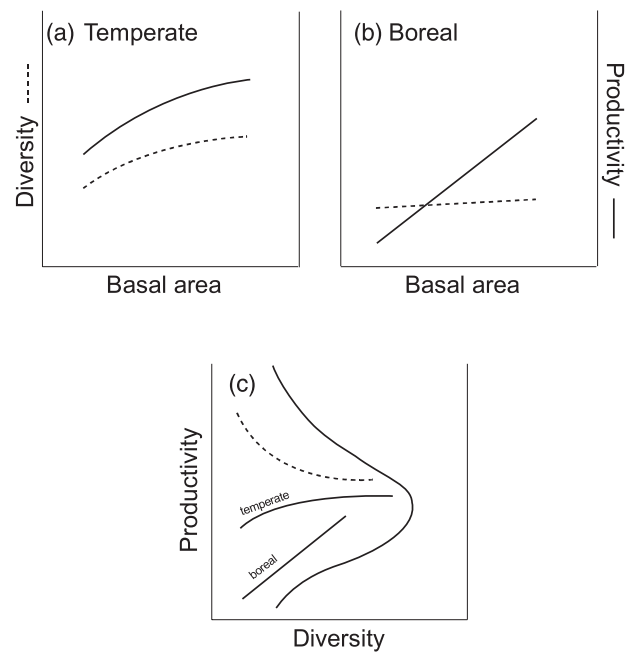


Figure 3 Schematic representation of the study results and hypothesized integration in the larger productivity–diversity debate. (a), (b) The diversity and productivity relations with stand basal area (here used as a proxy for competition intensity) for the temperate and boreal biomes, respectively. Whereas in the temperate forest both follow a regular asymptotic curve, in the boreal forest diversity and productivity follow diverging paths. This translates in (c) and in structural equation modelling (SEM) analyses (Fig. 2) into very different productivity–diversity relationships for both forest types once climate and environment are factored in. Both relations are included within the space defined by the unimodal response of biodiversity to productivity (bell curve). The often reported negative productivity–diversity relationship in very fertile and ruderal habitats would be found in the upper area of the graph (dash line). Adapted from Loreau *et al.* (2001).

Also, examples of very low species richness and monospecific stands are fewer in the temperate than the boreal biomes (Table 1), further reducing our capacity to detect the effects of FD on productivity. Monocultures and low species richness stands in the temperate forest did not, however, show lower productivity when compared with the remaining plots (one-sided *t*-tests; $P < t = 0.53$ and 0.91 , respectively), as opposed to the same stands in the boreal forest (both tests $P < 0.0001$). This further supports the hypothesis of competitive exclusion in favour of sugar maple, the dominant species in the temperate biome and the species most often found in monospecific stands.

Although mean functional diversity in temperate forests was almost double that of boreal forests, the overall span and variance did not differ by much (Table 1). On the other hand, species-rich temperate forests did show strong FR. For instance the SR → FD path was significantly stronger in the boreal biome than in the temperate (Fig. 2). FR was indeed determined by climate as shown by a strong positive relation to mean tempera-

ture over the entire dataset ($\text{adj}R^2 = 0.37$, $P < 0.0001$). Furthermore, the contribution of FD per unit species (ratio of realized over potential diversity) was much greater in boreal forests (0.45 on average, almost double that of temperate forests, 0.26). Both these results tend to confirm our hypothesis that the much weaker FD \rightarrow productivity link found in temperate forests was due to functional redundancy in these forests, not to an artefact of the dataset. Redundancy would increase competitive exclusion between similar species, as opposed to FD which is expected to promote complementarity.

Biodiversity effects on ecosystem functions: what diversity?

Although two of the diversity indices tested (FDis and phylogenetic species variability) are conceptually free of species richness, both naturally showed strong correlations with it (0.70 and 0.51, respectively), which was still less than with Faith's PD index (0.82). Without an experimental system specifically designed for that purpose (yet to be established), it is not possible to distinguish such closely related variables. We could only notice whether some index performed better in terms of variance explained. The single best predictor of tree productivity in our dataset was FDis based on three traits associated with reproduction, growth and successional status (FDis_3). Faith's PD did explain slightly more variance than did PSV, but actually less than SR alone (Table 2). More importantly, Faith's PD is not independent of species numbers and thus includes that effect, probably making PSV a better estimate of the true contribution of evolutionary history to ecosystem processes. It could be that tree species that evolved from distant ancestors have independently developed similar strategies in response to their environment (forest canopy), such as shade tolerance, often using different mechanisms or traits to achieve similar adaptive capabilities (Valladares & Niinemets, 2008). In that respect, even distant tree species probably have more in common than do herbaceous species, belonging to a much larger pool of functional types (as illustrated by Raunkiaer life-forms), which would explain the different results obtained by Cadotte *et al.* (2008) using Faith's PD. Interestingly, Laanisto *et al.* (2008) report that most unimodal SR–productivity relationships are found in herbaceous communities whereas forests would show positive linear relations. They propose that this is due the lack of clonal abilities (which limits the number of species able to colonize productive sites) in temperate trees and to niche conservatism (most temperate tree species having evolved from tropical species adapted to high productivity). This concurs with our own findings synthesized in Fig. 3: we could only find linear or asymptotic relations in both forested biomes studied, not unimodal.

Despite our best efforts to obtain traits from published sources, we could only find data in sufficient numbers for common traits such as leaf economics, reproductive and morphological descriptors. Data on belowground traits could only be found for much fewer than half of our species and therefore could not be used. As belowground interactions are expected to

be important factors in forest dynamics and for the complementary use of resources (Fargione *et al.*, 2007), we expect that even stronger results could have been obtained using FD indices with a more complete coverage of species functional traits and better knowledge of the relative importance of the different traits involved (Petchey & Gaston, 2006).

Although not formally demonstrating causal links as within controlled experiments, our study adds much needed support from natural forest ecosystems to the current hypothesis that ecosystem functioning is enhanced through niche complementarity. Furthermore, it adds to our understanding of the nature of plant relationships, in that competitive exclusions are most likely to occur under more favourable habitats, whereas complementary interactions may be more important under harsher, less favourable conditions. These results provide much needed insights into the functioning of forest ecosystems that could better guide world-wide conservation efforts, especially in support of sustainable forest management based on complexity theory for Earth's most diverse and important terrestrial ecosystems, the forests.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Further details regarding the dataset and methods used.

Appendix S2 Lists of species names, functional traits and their specific values, as well as GenBank references used in this study.

Appendix S3 Bayesian molecular phylogeny of tree species.

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