Species diversity and aboveground productivity relationships in forest ecosystems

BY

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ABSTRACT

Empirical and theoretical studies have attributed the observed positive diversity-productivity relationship (DPR) across various ecosystems to a complementarity effect through niche differentiation and/or facilitation among constituent species in more diverse communities, but such biological mechanisms have rarely been demonstrated in the published DPR studies. Moreover, a mechanistic understanding of a general framework on the multifaceted relationships between diversity, productivity, species coexistence, and their interactions with environmental gradient, has not been established, and calls for a novel multivariate approach. In forest ecosystems, studies focused on the above general framework are rare because of the complex temporal and spatial dynamics. The objectives of this thesis were to: (1) determine the relative influences of plant life-history traits, species diversity, biome, and stand origin on productivity, and (2) examine the multiple causal relationships between standing biomass and species diversity, variation in DBH within stand, stand age, and soil nutrient regime in boreal forests.

In a meta-analysis containing 53 studies in forest ecosystems, we used a trait-based approach to show the effects of species diversity, life-history variation, biomes, and stand origin (naturally established versus plantation) on productivity, which was calculated as effect size. Boosted regression tree analysis indicated that Shannon’s index had a 41.1% relative influence on effect size, life-history variation had a total of 41.3% relative influence with 27.2% for shade tolerance, 5.4% for leaf habit, 4.4% for growth habit, and 4.3% for nitrogen-fixing, whereas biome and stand origin had 16.2% and 1.38% relative influence, respectively. The effect size increased with Shannon's index and plateaued when diversity was high, and it was positive with presence of interspecific life-history variation. We conclude that a positive DPR occurs regardless of biome and stand origin when interspecific life-history variation is present among constituent species in polycultures, whereas an insignificant or negative DPR appears to dominate when interspecific life-history variation is absent.

Data from 448 sampling sites were used to examine the multivariate hypotheses based on theories and empirical studies by applying structural equation modeling (SEM). Bivariate relationships between variables were examined to facilitate the interpretation of the SEM results. The SEM model provided a strong fit to the data ($\chi^2 = 5.314$, df = 6, P = 0.504, CFI = 1.000, RMSEA < 0.001) and the set of hypotheses were supported by the data. Our results showed that tree size variation among individuals was the central mechanism linking resources availability, standing biomass, and species diversity. Standing biomass and Shannon’s species index were both positively correlated with DBH variation among individuals within stands.

Keywords

Boosted regression trees, effect size, life-history variation, meta-analysis, productivity, shade tolerance, Shannon's index, structural equation modeling, standing biomass, DBH variation

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NOTE

The chapter two and three were written separately according to varying publication requirements of selected peer-reviewed journals. Efforts have been made to integrate those chapters into this thesis with caution. As a result, the styles for writing and referencing may differ among chapters.

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1.0. GENERAL INTRODUCTION

Global warming and the degradation of forests have posted new challenges for ecologists to identify the key predictors to guide the efforts of restoring the functioning and services of forest ecosystems. In particular, biodiversity and ecosystem functioning (BEF) has been studied extensively during the last two decades. Both the selection hypothesis (Loreau & Hector 2001) and niche complementarity hypothesis (Tilman 1999;Loreau *et al.* 2001;Hooper *et al.* 2005) have received a great deal of empirical support, mostly in grassland systems. In addition, the stress-gradient hypothesis (SGH) has suggested that the diversity-productivity relationship (DPR) may vary greatly across a stress gradient in natural ecosystems, and may be affected by life-history traits of competing species (Maestre et al. 2009). However, BEF studies in forest ecosystems have been rare and the underlying mechanisms and their interrelationships are still not clear.

Moreover, it has been advocated that novel multivariate approaches, widely used in other disciplines such as in social sciences, be adopted by ecologists to study forest ecosystems from a realistic perspective (Reiss *et al.* 2009;Webb *et al.* 2010). Previous studies might be limited by the shortcomings of traditional statistical methods, such as GLM, because the relatively strict assumptions of parametric analysis may not be met when analyzing ecological data and the results may be misleading (Graham 2003;Grace 2006). In this thesis, I chose to use boosted regression trees and structural equation modelling to address the DPR in forest ecosystems by integrating multiple factors known to affect plant interactions, diversity, and productivity. The overall goal of this research was to establish a general framework consisting of multiple causal pathways between diversity, productivity, and their interactions with environmental factors.

The first and last chapters are general introduction and overall conclusions, respectively. The second chapter (meta-analysis) of the thesis focused on testing how the absence/presence of plant life-history traits affects DPRs in forest stands across tropical, temperate, and boreal biomes, using boosted regression trees. The third chapter of the thesis focuses on testing multiple mechanisms that influence standing biomass and maintenance of species diversity in the central boreal forest by linking species diversity, resource availability, stand age, and functional groups, using structural equation modelling.

In both the part 2 and part 3 of this research, we chose Shannon's index as the surrogate of species diversity instead of using species richness. We consider that the species richness more suitable for experiments in controlled environments, such as in grassland experiments, in which the relative abundance of constituent species are often equal or well controlled. However, stands with the same species richness may display high variability in proportions of basal areas for each constituent species in natural forest ecosystems, such as those in this research. The effects of such variability are not accounted for if we use species richness to study the DPR. In consistent with niche complementarity hypothesis, several studies conducted in tropical plantations, natural temperate forests, and grasslands, have demonstrated the combined influences of species richness and relative abundance on productivity by adopting Shannon's index as a surrogate of species diversity (e.g., Binkley *et al.* 2003;Forrester *et al.* 2004;Liang *et al.* 2007;Levine & HilleRisLambers 2009). Current syntheses about biodiversity and ecosystem functioning has suggested that local species richness may not be a good measure of biodiversity because the species richness does not represent functions of plants in local community (see Hillebrand & Matthiessen 2009;Hillebrand & Cardinale 2010).

2.0. DIVERSITY-PRODUCTIVITY RELATIONSHIPS AND LIFE-HISTORY TRAITS IN FOREST ECOSYSTEMS

2.1. INTRODUCTION

The diversity-productivity relationship (DPR) has received considerable attention during the past decade, largely because of the continuous loss of biodiversity from increased transformation of natural ecosystems globally (Chapin *et al.* 2000;Foley *et al.* 2005;Hooper *et al.* 2005). Positive DPR, i.e., increasing species diversity resulting in increased productivity at the community level (Tilman *et al.* 1996;Loreau *et al.* 2001), has been found in numerous empirical studies (Fornara & Tilman 2008;Stachowicz *et al.* 2008;Isbell *et al.* 2009a;Striebel *et al.* 2009;Wacker *et al.* 2009). This positive DPR occurs when polycultures have higher biomass production than the average production of monocultures, i.e., overyielding, also defined as net biodiversity effect (Loreau & Hector 2001;Schmid *et al.* 2008).

Two hypotheses have been proposed to explain the positive diversity effect on productivity. The first is the selection effect hypothesis (Loreau & Hector 2001), which argues that improved productivity in local competitive communities may be largely driven by the greater chance of including highly productive species in polycultures. The second is the niche complementarity hypothesis, which states that niche differences among species result in a positive DPR due to increased resource use and nutrient retention via niche differentiation or partitioning and interspecific facilitation (Tilman 1999;Loreau *et al.* 2001;Hooper *et al.* 2005;Maestre *et al.* 2009;van Ruijven & Berendse 2005). While both selection and niche complementarity tend to occur simultaneously (Cardinale *et al.* 2007;Fargione *et al.* 2007), the complementarity effect has been found to increase over time and to equal or exceed the selection effect (van Ruijven & Berendse 2005;Cardinale *et al.* 2007;Fargione *et al.* 2007;Schmid *et al.* 2008). However, it is rare in DPR experiments to directly demonstrate any form of niche partitioning or facilitative interactions among constituent species with only a few notable exceptions (e.g., phytoplankton communities) (e.g., Litchman *et al.* 2007;Striebel *et al.* 2009). Although selection and complementarity effects can be statistically quantified by the partitioning method (Loreau & Hector 2001), this method may not necessarily identify the underlying mechanisms since a complementarity effect may be an outcome of a large number of potential ecological and biological processes including niche differentiation, resource use efficiency and retention, and facilitative interactions. Accordingly, trait-based approaches have elicited much recent interest for predicting changes in community composition and ecological function (Coomes *et al.* 2009;Hillebrand & Matthiessen 2009;Reiss *et al.* 2009;Webb *et al.* 2010).

In forest ecosystems, DPR research is greatly lagging behind compared with other ecosystems (e.g., temperate grasslands) due to the longevity and large size of trees, and the complexity of forest ecosystems (Leuschner *et al.* 2009). Previous empirical studies testing the DPR in forest ecosystems, mostly observational comparisons of naturally established stands, have reported positive (Amoroso & Turnblom 2006;Garber & Maguire 2004;MacPherson *et al.* 2001;Pretzsch & Schutze 2009), negative or insignificant (Edgar & Burk 2001;Chen & Klinka 2003;Legaré *et al.* 2005) effects of species diversity on productivity. While data from long-term and large scale biodiversity experiments are not available, the accumulation of the DPR studies lends itself to a synthesis to explore the DPRs across habitats with a focus on plant identity and functional diversity (Naeem *et al.* 2009). Differences in life-history traits in polycultures are known to influence spatial (fast vs. slow growing, shade-intolerant vs. tolerant) and temporal (evergreen vs. deciduous) niche occupancy and resource availability (N-fixation) within a site (Man & Lieffers 1999;Wang *et al.* 2002;Binkley 2003). Recent studies support that the range of shade tolerance and growth rate between constituent species within a stand affect DPRs through improved light and nutrient use efficiency and nutrient cycling due to complementary niches in temperate natural stands and tropical plantations (Coomes *et al.* 2009;Richards & Schmidt 2010). Can the positive vs. negative DPRs be attributable to the presence or absence of life-history variation such as contrasting shade tolerance, growth rate, leaf habit, and nitrogen (N) fixation among constituent species in polycultures at the global scale?

Stand origin, i.e., natural established stands and artificial plantations, may also be an important factor influencing DPR in forest ecosystems (Leps 2004). Experiments under highly controlled homogeneous environments may allow for a mechanistic understanding of DPR, but findings may not reflect processes in unmanipulated communities (Leps 2004;Nadrowski *et al.* 2010). The results from observational studies that often involve a high degree of spatial and resource heterogeneity and extend over a long time frame arguably provide a greater inference (Stachowicz *et al.* 2008;Tylianakis *et al.* 2008;Griffin *et al.* 2009). Differences in spatial and resource heterogeneity and time span among studies may partially explain different outcomes in previous DPR studies (van Ruijven & Berendse 2005;Stachowicz *et al.* 2008;Duffy 2009). These differences may be more pronounced in forest ecosystems because of the long-term dynamics associated with tree establishment, competition, and mortality (Wardle *et al.* 2004;Hart & Chen 2008). Compared with experimental plantations that are established to test DPR, natural stands with variations in stand age, density, disturbance history, and habitat homogeneity may exhibit a different DPR pattern. Furthermore, DPR patterns may differ among biomes because of their differences in productivity, attributable to environmental resources, evolutionary histories of tree species, and species interactions (Pärtel *et al.* 2007;Pärtel *et al.* 2008;Maestre *et al.* 2009).

We conducted a meta-analysis of 53 DPR studies in forest ecosystems to test the following hypotheses: (i) the observed positive or negative DPRs are dependent on whether life-history variation, such as contrasting shade tolerance, growth rate, leaf habit, and nitrogen (N) fixation, exists among constituent species in polycultures; (ii) DPRs differ with stand origin, i.e., plantations established in homogeneous environments and natural stands with highly variable natural conditions; (iii) DPRs vary across biomes.

Our meta-analysis contributes to the ever-evolving debate in DPR in the following ways. First, to our knowledge, it is the first observational confirmation of DPR experiments in forest ecosystems at the global scale. Second, we implemented a trait-based approach (Hillebrand & Matthiessen 2009) by directly testing the impact of interspecific life-history variation on DPR at the stand level, which can be a more realistic evaluation on the effect of species loss (Hillebrand & Matthiessen 2009;Reiss *et al.* 2009).

2.2. METHODS

2.2.1. *Data collection*

We conducted an extensive literature search for studies concerning DPRs in forest ecosystems using ISI Web of Science, Forest Science Database, and Google Scholar. Different combinations of key words such as basal area, volume, biomass, productivity, forest, tree, species richness, plantation, diversity, biodiversity, pure, mixed-species, single-species, boreal, temperate, and tropical were used for the search.

We retrieved over 200 studies based on the above search terms. We excluded studies where it was impossible to isolate the effect of tree species diversity, thus, resulting in 53 studies in the meta-analysis. We extracted aboveground productivity measurements, climate, geographical location, species diversity, and life-history traits from the original papers. For studies with multiple sampling dates, only the latest data of productivity and species diversity measurements were included in our analysis. When more than one paper reported on the same study, we included the data only once to avoid duplication. All included studies were at stem exclusion or canopy transition stage of stand development where full site occupancy has occurred (Chen & Popadiouk 2002;Franklin *et al.* 2002). Where the means and standard deviations or standard errors were reported graphically, we used SigmaScan® Pro version 5 (Systat Software Inc., Point Richmond, CA, USA) to extract data from figures digitally. Although a weighted meta-analysis considering both variance and replication size in each study is preferred for its statistical power and accuracy, we used an unweighted meta-analysis in order to avoid the loss of information (Gurevitch & Hedges 1999), since the variance or replicate size was missing in more than half of the 53 studies.

Shannon's (or Shannon–Wiener's) index (Shannon 1948) was calculated as a measure of species diversity based on species' proportions by stand basal area ($n = 494$). When basal area was not reported in the original papers, we calculated Shannon's index by crown cover ($n = 5$) or stem density ($n = 16$), and by assuming equal abundance of each tree species ($n = 49$) within the stand. In most grassland experiments where all constituent species are sowed equally, species richness is adequate to represent diversity. In forest ecosystems, however, many DPR studies are conducted by sampling naturally established stands and typically using large sample plots because of the large stature of trees. As a result, "pure" stands may include a minor component of other species. As such, Shannon's index allowed us to represent both species richness and the evenness of individual stands (Magurran 1988).

We adopted a trait-based approach (Hillebrand & Matthiessen 2009) by using the extent of life-history variation, selected a priori, as a measure of functional trait dissimilarity. A trait-based approach has more strength to predict ecosystem functioning than species taxonomic richness, as both complementarity and selection effects are considered, based on the differences in species traits (Hillebrand & Matthiessen 2009). By accounting for the distances between traits and their proportional abundance (Wacker et al. 2009), a continuous measure of functional trait diversity may have an advantage in avoiding assumptions when selecting functional traits non-objectively (Wright *et al.* 2006). However, the best metric for measuring functional diversity is still in debate, and should depend on the specific objectives of an individual study (Reiss et al. 2009). Life-history variation in our study was qualified as discrete variables, because the traits we were interested in were qualitatively classified in the literature. Similar to our metric, life-history variation, qualified as non-objectively chosen a priori, has been found to be one of the best predictors to explain productivity in grassland experiments (Cadotte *et al.* 2009;Marquard *et al.* 2009).

The classification of presence/absence of life-history variation was based on the explicit description in original papers. When the description of interspecific differences in life-history traits was not presented in the original paper, we obtained these life-history traits from the USDA plant database (http://plants.usda.gov/). This approach is practical because trait information on individual species is usually available for plants (Statzner *et al.* 2007). The presence of life-history variation within a stand was defined a priori as the presence or absence of the following four contrasting traits: shade tolerant versus shade intolerant (246 observations for presence and 318 for absence), fast versus slow growing (247 for presence and 317 for absence), N-fixing versus non-fixing (133 for presence and 431 for absence), and deciduous versus evergreen (109 for presence and 455 for absence). The number of contrasting traits was assigned in an individual study based on the number of traits associated with its constituent species in the study. Biome was identified as boreal, temperate, and tropical. Stand origin was determined based on site description in original studies, as either plantations or naturally established stands. The citations and summary of the 53 studies were included in Appendix I.

2.2.2. *Data analysis*

Effect size was used as a standardized measure for productivity within each study, calculated using a response ratio:

$$[1] \qquad NE_{ij} = \frac{P_{ij}}{\bar{M}_i}$$

where *NE* ($i = 1, 2, \ldots 53; j = 1, 2, \ldots 564$) is effect size of *j*th observation in *i*th study, P_{ij} is the observed yield of *j*th observation in *i*th study, and $\bar{M}_i$ *is* the mean productivity of all monocultures within each study. Consistent with most observational studies, monocultures were defined as one single species comprising 80% or more basal area of the stand. For the studies that examined the DPRs across different stand ages and site conditions, the effect size was calculated by using stands with the same age and site condition. The productivity measures were chosen in the order of preference from biomass, volume, and basal area from original studies when multiple measurements were reported as surrogate of aboveground productivity.

In order to partition independent influences and to examine the patterns of marginal effects of presence/absence of life-history variation in all selected traits, Shannon's index, stand origin, and biomes on ln(NE), we used boosted regression trees (BRT). The BRT is an advanced form of machine learning method based on classification and regression trees, and is ideal for complex data with unidentified distributions (De'ath & Fabricius 2000;De'ath 2007).

As a recommended practice with BRT (De'ath 2007;Elith *et al.* 2008), we fit the models to a randomly selected 50% of the observations (bagging fraction of 0.5), reserving 50% for model validation. This partitioning, termed 'cross-validation', was repeated 10 times. The final model was fitted based on the balance between the goodness-of-fit and predictive performance, i.e., the data is well described while avoiding overfitting (Elith *et al.* 2008;Leathwick *et al.* 2008). This technique tends to minimize the bias introduced in unweighted meta-analyses via the randomness from bagging (De'ath 2007).

The predictive deviance, expressed as a percentage of the null deviance, for each model was calculated as a measure of goodness-of-fit (Leathwick *et al.* 2008). For individual regression trees, relative influence of predictor variables was estimated by the number of times a variable was used for splitting, weighted by the squared improvement to the model at each split (Friedman 2001). In the boosted model, the value of relative influence was the average of all trees in a BRT model (Friedman & Meulman 2003). The relative influence of predictors on the dependent variable was scaled to a sum of 100. The partial dependence plot illustrates the marginal effect of the individual predictor on the response variable while accounting for the average effects of other variables in the model (De'ath 2007;Elith *et al.* 2008). All statistical analyses were carried out in R (R Development Core Team 2009) using the "gbm" package (Ridgeway 2007), and supplemental functions (De'ath 2007;Elith *et al.* 2008). Graphs were done using SigmaPlot software (SPSS, Chicago, Illinois, USA).

To compliment the BRT, we used a full-two factorial general linear model (GLM) to examine whether the response of natural log effect size [Y=ln(NE)] to Shannon's index (H′) differed with the number of contrasting life-history traits in each individual study. Because only one study with three observations involved four contrasting traits, the study was pooled with those having three traits in the GLM analysis. Based on our hypotheses, we expected that the presence of life-history traits would be equally important as Shannon's index in explaining the variation in effect size. Further, the extent of life-history variation would be a necessity in order to have positive DPRs in forest ecosystems, i.e., a strong interaction between contrasting life-history traits and Shannon's index were expected.

2.3. RESULTS

The BRT model explained 19.04% of the predictive deviance in ln(NE). Shannon's index had a 41.1% relative influence on ln(NE) (Fig. 2.1). With other factors averaged, ln(NE) showed a general increasing trend with Shannon's index; it was positive when Shannon's index was ≥ 1.3, but negative when Shannon's index was < 1.3 (Fig. 2.2A). The marginal effect of Shannon's index increased rapidly between1.1 to 1.5, but remained constant when Shannon's index exceeded 1.8 (Fig. 2.2A).

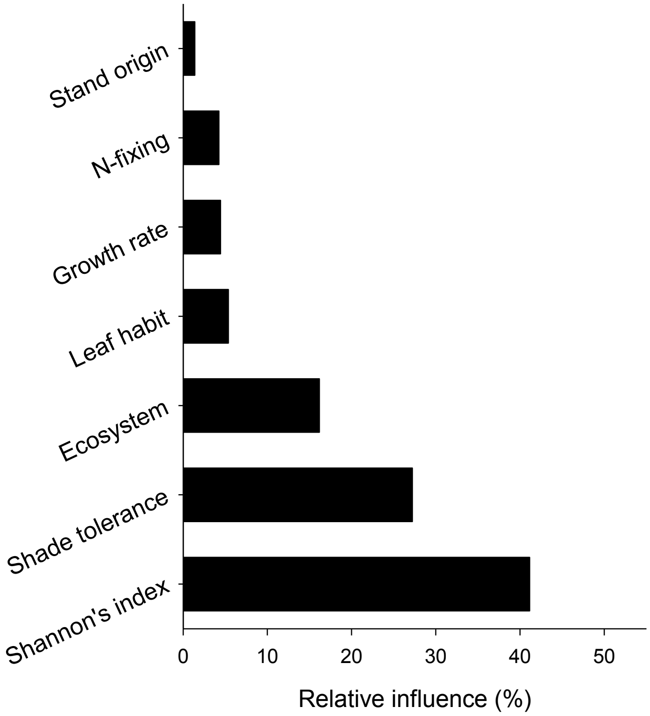

Figure 2.1. Results from the boosted regression trees showing the relative influences of predictors on productivity (natural log transformed effect size, see eq. 1 for definition)

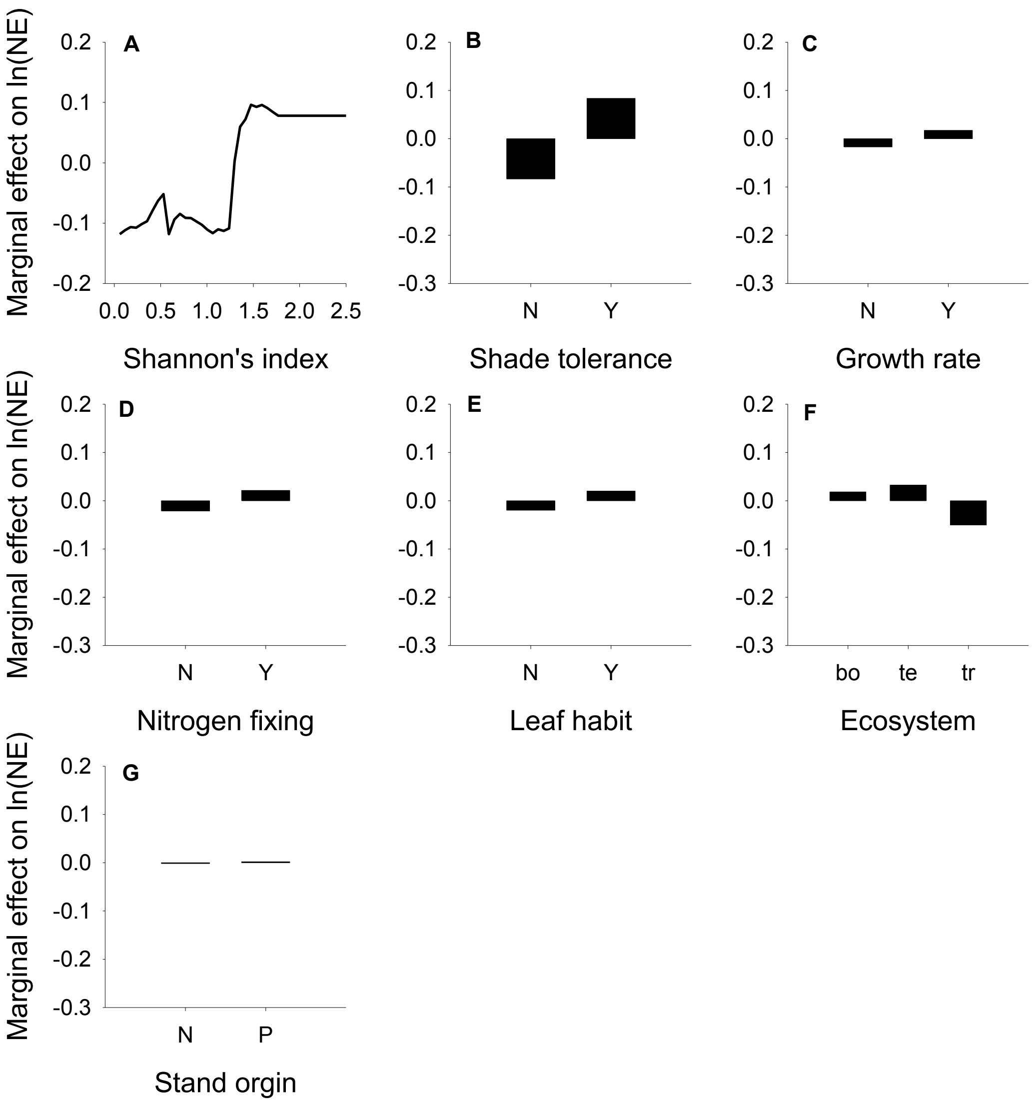

Figure 2.2. Marginal effects of Shannon's index, presence (Y) or absence (N) of contrasting shade tolerance, growth habit, nitrogen fixing, and leaf habit, biome (bo = boreal, te = temperate, and tr = tropical), and stand origin (N = naturally established, P = plantation) on natural log transformed effect size (*n* =564).

The GLM showed an overall positive effect of Shannon's index and a significant interaction of Shannon's index and number of contrasting traits on ln(NE) across biomes (Table 2.1; Fig. 2.3). ln(NE) from studies without contrasting trait among constituent species decreased with Shannon's index (Fig. 2.3A), whereas ln(NE) from studies with 1, 2, or 3 and 4 contrasting traits among constituent species increased with Shannon's index (Figs. 2.3B-D). However, the regression slopes did not differ significantly for studies with different numbers of contrasting traits involved.

Table 2.1. Summary of the analysis of Shannon's index (H´) and the number of contrasting traits (T) on natural log transformed effect size.

Source	*df*	*MS*	*F*	*P*
H´	1	2.094	9.246	0.0025
T	3	0.311	1.375	0.2496
H´×T	3	0.920	4.060	0.0070
Residual	556	0.078		

T was defined as presence of 0, 1, 2, and 3 or all of the following four contrasting traits: shade-intolerant *vs.* intolerant, fast *vs.* slow growing, deciduous *vs.* evergreen, and N-fixing *vs.* non-N-fixing involved in each study.

The extent of life-history variation had a total of 41.3% relative influence on ln(NE) with 27.2% for shade tolerance, 5.4% for leaf habit, 4.4% for growth habit, and 4.3% for N-fixing, respectively (Fig. 2.1). The presence of variations in shade tolerance, leaf habit, growth habit, and N-fixing had a marginal effect of 0.083, 0.020, 0.017, and 0.021, respectively (Figs. 2.2B-E).

Biome had a 16.2% relative influence on ln(NE) (Fig. 1). The marginal effect of ecosystem type in BRT was 0.018, 0.032, and 0.050 for boreal, temperate, and tropical forest ecosystems, respectively (Fig. 2.2F). Stand origin had only a 1.38 % relative influence on ln(NE) (Fig. 2.1). The marginal effect of stand origin was -0.0019 and 0.0019 in natural stands and plantations, respectively (Fig. 2.2G).

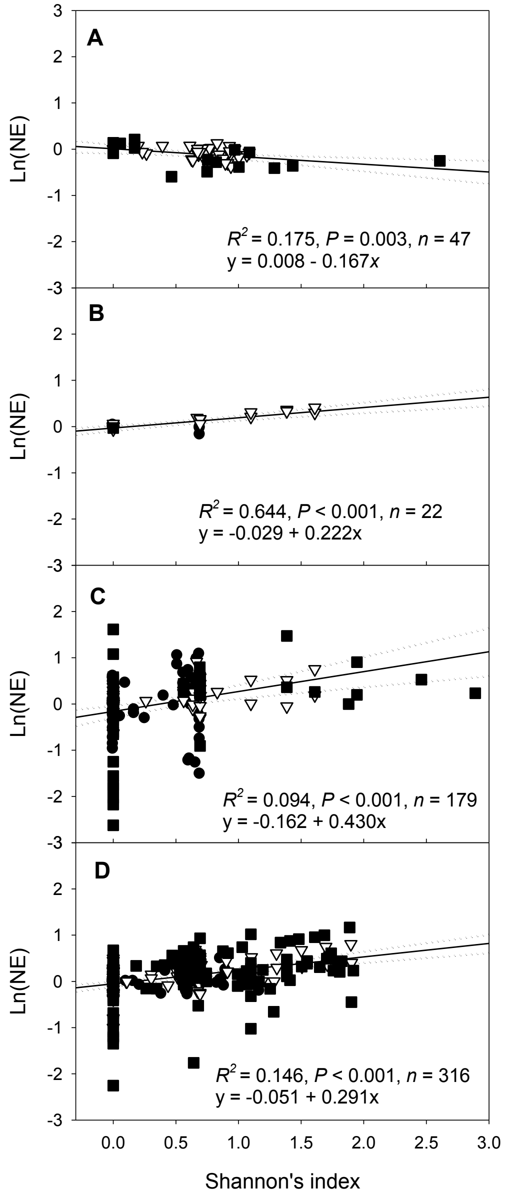

Figure 2.3. The relationship between natural log transformed effect size [ln(NE)] and Shannon's index with presence of: (A) 0, (B) 1, (C) 2, and (D) 3 or all of the following four contrasting traits: shade-intolerant *vs.* intolerant, fast *vs.* slow growing, deciduous *vs.* evergreen, and N-fixing *vs.* non-N-fixing involved in each study. Dotted lines are 95% confidence intervals for fitted regressions. Ecosystem types are labeled as boreal (✸), temperate (▽), and tropical (■).

2.4. DISCUSSION

We found that Shannon’s index had a 41.1% relative influence on ln(NE) in the BRT. When accounting for the average effects of other variables, the BRT shows that the marginal effect of diversity increased from negative to positive, and stayed constant from low, intermediate, and high ranges of Shannon's index. The negative marginal effect at the low range of Shannon's index indicates no or minimum effect of diversity on productivity at this range of diversity. This result appears to support that the species complementarity effect may not be strong enough to offset the negative sampling effect when species diversity is low (Loreau & Hector 2001;Fargione *et al.* 2007;Wacker *et al.* 2009). The higher marginal effect of diversity is consistent with previous findings that greater overyielding is achieved with higher species diversity in non-forest ecosystems (Isbell *et al.* 2009a;Marquard *et al.* 2009). The stabilized marginal effect size at the high range of Shannon’s index appears to provide support for the hypothesis that “ceiling” of productivity gain may occur at high level of species diversity due to functional redundancy of species (Naeem *et al.* 2009). In addition, since stands with Shannon's index > 1.7 are mostly from tropical forests, the stabilized marginal effect size appears to be coupled with the biome effect.

The life-history variation had a total of 41.3% relative influence on ln(NE) shade tolerance, accounting for the largest relative influence . Their positive marginal effects (Figs. 2B-D) appear to be attributable to better nutrient, light, and space exploitation and complementary uses of resources in polycultures with contrasting traits of shade tolerance and fast-slow growth habits (Amoroso & Turnblom 2006;Liang *et al.* 2007;Coomes *et al.* 2009;Pretzsch & Schutze 2009;von Felten *et al.* 2009). For example, shade-tolerant and intolerant species within a stand may occupy different niches in light interception, since shade-intolerant species have advantages in height growth, and prefer direct irradiances, while the shade-tolerant species can perform equally under diffuse and direct light due to greater light use efficiency under diffuse light (Chen & Klinka 1997;Brodersen *et al.* 2008;Almeras *et al.* 2009); shade tolerance and growth habit may also reflect niche differentiation in belowground, e.g., fast-growing species tend to be deep rooted while slow-growing species tend to be shallow rooted in polycultures (Wang et al. 2002).

Despite the relatively weak contribution of biome to DPR after the effects of diversity and species traits are averaged, the marginal effect was positive in boreal and temperate forests and negative in tropical forests. In both the BRT and GLM analyses, the diversity effect was analyzed by assuming common DPRs, a machine-learnt curvilinear DPR in the BRT and a linear DPR in the GLM, across biomes. The negative marginal effect of tropical forests appears to be a result of overestimating the diversity effect at the very high levels of diversity, i.e., Shannon's index > 1.7 when a global DPR is assumed across biomes. This finding provides support for the "ceiling" hypothesis of diversity on productivity (Naeem *et al.* 2009).

We found a limited influence of stand origin on net biodiversity effects. It is commonly believed that DPR is stronger in highly manipulated experiments than observational studies under natural conditions (Balvanera *et al.* 2006), but argued otherwise by Duffy (2009). Recent empirical studies have demonstrated that the intrinsic resource and spatial heterogeneity in natural environments may enhance the expression of niche differentiation (Stachowicz *et al.* 2008;Tylianakis *et al.* 2008;Griffin *et al.* 2009). Intuitively, we may expect a greater degree of resources and space exploitation from contrasting niche requirements of tree species when more niches exist due to the resource heterogeneity in natural environments. Conversely, the results of an algal diversity experiment with no effects of spatial heterogeneity demonstrated that environmental heterogeneity alone may not warrant stronger biodiversity effects (Weis *et al.*

2008). Our analysis is the first to demonstrate that DPRs are consistent between manipulated experiments and observational studies in forest ecosystems at the global scale.

We found significant positive DPRs of similar slopes for studies with 1 or more contrasting traits and a negative DPR for studies without contrasting traits among constituent species. Trait-based studies in grassland experiments have demonstrated that life-history variation results in positive DPRs (Tilman *et al.* 1997;Fornara & Tilman 2008;Marquard *et al.* 2009;Cadotte *et al.* 2009). The observed positive DPR may be attributable to niche differentiation and/or facilitation caused by the differences or divergence of tree species functioning within polycultures, because life-history variation can affect the performance of species in resource uptake and utilization (Man & Lieffers 1999;Wang *et al.* 2002;Binkley 2003;Coomes *et al.* 2009;Potvin & Dutilleul 2009;Richards & Schmidt 2010). The similar DPR slopes for studies with 1 or more contrasting traits are attributable to the strongest influence of shade tolerance among traits found in this study.

For studies without contrasting traits among constituent species, however, decreasing productivity with increasing species diversity is unexpected since it is commonly believed that competition is stronger within than between species as a key mechanism for stable coexistence (Chesson 2000). However, the variation of individuals within a species in responses to competition may be greater than average differences among species (Clark 2010). The negative DPR is typically attributed to negative selection effect due to dominance by species of low productivity in polycultures when diversity is expressed as species richness (Loreau & Hector 2001), but this is not the case in our analysis as Shannon's index has incorporated the species proportions. Alternatively, negative DPRs may be a result of negative interactions between species that have similar competitive or stress-tolerant life histories (Maestre et al. 2009). A close examination of the three original studies without contrasting traits among constituent species shows one study with a negative DPR (i.e., Firn et al. 2007) and the other two with an insignificant DPR (i.e., Chen & Klinka 2003;Rouhi-Moghaddam *et al.* 2008). While an insignificant DPR for studies without contrasting traits among constituent species supports our trait-based hypothesis, the negative DPR in Firn *et al*. (2007) appears to be a result of that the monocultures of planted trees consisted of species with high productivity and polycultures consisted of both planted trees and natural in-growth with the latter being regenerated later than the planted trees and less productive.

Our meta-analysis consolidated previous observations about the importance of life-history variation and species diversity on DPR in forest ecosystems. Our findings provide a generalized DPR prediction: interspecific life-history variation leads to a positive productivity gain in polycultures. This finding can provide a broad guide for forest management that desires higher per-unit-area productivity. Our analysis did not test whether interspecific niche differentiation or facilitative interaction is the underlying mechanism for a complementarity effect at the global scale since such mechanism-driven studies are rare in forest ecosystems. We speculate that the mechanisms that can lead to positive DPRs may include niche differentiation or partitioning, resource use efficiency, and a large number of facilitative interactions among species in polycultures (Callaway 1995). The relative importance of these mechanisms may differ with ecosystem type, site condition, species composition, and stand disturbance history (Maestre et al. 2009).

3.0. LINKING BIODIVERSITY, PRODUCTIVITY, AND RESOURCE AVAILABILITY OF BOREAL FORESTS IN CENTRAL CANADA

3.1. INTRODUCTION

The continuing extinction of species raises concerns about the sustainability of current ecosystem functioning and services important to human wellbeing (Naeem et al. 2009). Consequently, biodiversity and ecosystem functioning (BEF), namely diversity and productivity relationship (DPR) in local communities across ecosystems, has been studied extensively during the last two decades. Recent empirical studies across taxa and habitats, mostly in grasslands, have observed positive complementarity effects of species diversity on productivity (Fornara & Tilman 2008;Stachowicz *et al.* 2008;Isbell *et al.* 2009a;Striebel *et al.* 2009;Wacker *et al.* 2009). The observed positive diversity-productivity relationship (i.e., polycultures produce more biomass than monoculture) has been attributed to the complementarity effects from interspecific facilitation and/or niche complementarity (Cardinale *et al.* 2007;Fargione *et al.* 2007). The variation in size of trees among individuals within a community may be another mechanism for positive DPR through neighbourhood effects (Potvin & Dutilleul 2009). Further, theoretical simulation and grassland experiments have supported that facilitation and/or niche differentiation may be the mechanism for the maintenance of species diversity (Gross 2008;Isbell *et al.* 2009b;Levine & HilleRisLambers 2009). In forest ecosystem, a new study has shown that the niche differentiation, represented by strong variation among individuals in responses to environment, may occur due to contrasting plant life-history traits (e.g., stress tolerance) when the variation on average at species-level does not differ (Clark 2010).

The observed positive DPRs have been attributed to plant functional diversity, e.g., number of functional groups within a community (e.g.,Cadotte *et al.* 2009;Marquard *et al.*

2009;Wacker *et al.* 2009). Using trait-based approaches, functional trait dissimilarity or divergence between species is considered the key to explain the causation of the observed effects of facilitation and/or niche differentiation on productivity and coexistence of competitors in local competitive communities (Hillebrand & Matthiessen 2009). However, the actual biological processes as underlying mechanism for positive DPR remain unclear. This uncertainty in the mechanisms of DPR has been linked to the metric selection of biodiversity, e.g., species richness (species count), non-objectively grouping (number of non-objectively classified functional group), and functional diversity index (continuous variable) (Hillebrand & Matthiessen 2009). For example, the singular hypothesis (Naeem et al. 2002) suggests that each plant species contribute to ecosystem functioning uniquely (e.g.,Meinen *et al.* 2009;Eisenhauer *et al.* 2010) in contrast to the previous belief that there is a high degree of redundancy in plant functions in stable ecosystems.

Previous DPR studies have mostly been done in controlled environments, the applicability of those findings to natural ecosystems has been questioned, because experiments in controlled environments are oversimplified and may fail to account for the complexity of natural ecosystems (Duffy 2009;Hillebrand & Matthiessen 2009;Reiss *et al.* 2009). Abiotic factors may influence the observed patterns of relationships between species diversity and productivity through their impacts on plant interactions (Callaway & Walker 1997). The different functional trait characteristics of species in polycultures have been proposed to affect their responses to stress, e.g., the polyculture of competitive species and stress-tolerant species facilitate with each other in stressed condition (Maestre et al. 2009). Thus, the relationship between plant interactions and environmental gradients must be considered to understand plant community dynamics (Brooker *et al.* 2008;Mitchell *et al.* 2009). Further, the spatial and resource heterogeneity combined with the time frame of an experiment arguably have important influences on DPR in natural ecosystems (Stachowicz *et al.* 2008;Tylianakis *et al.* 2008;Griffin *et al.* 2009).

Moreover, a mechanistic understanding of a general framework on the multifaceted relationships between diversity, productivity, species coexistence, and their interactions with environmental factors, has not been established, and calls for a novel multivariate approach (Hillebrand & Matthiessen 2009;Reiss *et al.* 2009;Webb *et al.* 2010) because previous studies mostly have focused on individual process of ecosystem using univariate analyses and may omit the reciprocal interactions and feedbacks between response and independent variables (Grace 2006). In forest ecosystems, studies focused on the above general framework are rare because of the complex temporal and spatial dynamics (Wardle *et al.* 2004;Hart & Chen 2008).

In this study, we conducted a careful dissection of the overall relationship between species diversity, variation in DBH among individuals within a stand, standing biomass, stand age, and stand nutrient regime in boreal forests via structural equation modeling (SEM) in boreal forests. Specifically, we hypothesize that (1) the relationship between species diversity and standing biomass is mediated through variation among individuals within stands, (2) variation among individuals is mediated by the number of functional groups, (3) resource availability limits the overall standing biomass and variation among individuals, and (4) variation among individuals mediates species diversity as a mechanism for species coexistence. Given that stand age mediates standing biomass and species succession (Chen & Popadiouk 2002), we further hypothesize that stand age mediates interrelationships between standing biomass, variation among individuals, and species diversity.

3.2. METHODS

3.2.1. *Forest sampling plot data*

The data used in this study were from the permanent sample plot (PSP) data of boreal forests collected in Saskatchewan, Canada, provided by the Timberline Natural Resource Group under a user agreement. The data was part of the Growth and Yield Survey (Frey 1981), which aimed to provide appropriate guidance for the sustainable management of forested areas in Saskatchewan. The majority of plots sampled were located in moderate-aged to mature, naturally established, and undisturbed stands within the boreal forest region, commonly consisting of *Pinus banksiana* Lamb., *Picea mariana* (Mill.) B.S.P., *Picea glauca* (Moench) Voss, *Abies balsamea* (L.) Mill., *Larix laricina* (Du Roi) K. Koch, *Populus tremuloides* Michx., *Populus balsamifera* L., and *Betula papyrifera* Marsh (Beckingham et al. 1996).

All plots were selected within forest management areas of Prince Albert and Pasquia-Porcupine and adjacent areas prior to the sampling (Timberline Forest Inventory Consultants 2005). Efforts were made to ensure the validity of the data for academic purposes during the original data collection and consequent data consolidations (Frey 1981;Timberline Forest Inventory Consultants 2005): (1) all plots were not established in systematic random sampling in order to cover as extensive ranges of stand ages and site types as possible, and to achieve spatial and temporal dispersion between plots, (2) all plots were located in well-stocked and even-aged stands with a sufficient distance from openings and roads, (3) plots were considered unsuitable for remeasurement if major disturbance (e.g., fire, blowdown, and entomological infestation) had occurred after the last measurement, (4) measures were taken to ensure data were collected with sufficient accuracy and precision by following appropriate procedures set prior to actual sampling, and (5) all data were carefully examined and consolidated in 2005, and the subset of data collected using incompatible procedures was marked and converted when applicable, because the whole dataset were collected over a long period of time through various agencies.

To further restrict the potential errors in the data, we only selected the 448 PSP plots (819m^2 per plot), measured under consistent measuring standard after 1958 with measurement of soil nutrient regime in conformity with Saskatchewan's ecosystem classification guidelines (Beckingham et al. 1996), from total 2187 plots to examine the multivariate relationships between stand productivity and tree species diversity across a extensive range of soil nutrient regime and stand ages.

3.2.2. *Variables used in analysis*

In this study, we calculated aboveground standing biomass per plot area (tonne.ha^{-1}) as a surrogate of productivity. We estimated standing biomass of live trees for each PSP plot by using published species-specific allometric equations using tree DBH as the predictor (Lambert et al. 2005). Species diversity was measured in three levels: species functional groups, DBH variations among all species (size inequity) (Potvin & Dutilleul 2009), and Shannon's index to test their influences on DPRs. Species richness, a species count within plot, was widely used in DPR studies in grassland experiments. However, because boreal forests have limited number of tree species (e.g., 85% of 448 plots consist of less than 5 tree species) and large variability in species compositions, Shannon's index was used as a more realistic measurement of species diversity in natural forests (Magurran 1988).

Life-history trait-based grouping of species as implemented in previous studies (Hector *et al.* 1999;Roscher *et al.* 2004;Fornara & Tilman 2008) was adopted in this study. We used characteristics of shade tolerance and leaf habit to classify tree species into 4 groups: deciduous intolerant, evergreen intolerant, deciduous tolerant and evergreen tolerant. Presumably, differences in leaf habit and shade tolerance can influence spatial niche occupancy, light use efficiency, and nutrient cycling within a site (Man & Lieffers 1999;Wang *et al.* 2002), thereby playing an important role in shaping DPRs. Recent studies support that the differences in shade tolerance between constituent species within a stand resulted in positive DPRs (Coomes *et al.* 2009;Richards & Schmidt 2010). We adopted shade tolerance rating for the studied species following Spurr et al. (1980). The number of groups for each plot was counted.

Stand age for each measurement was determined as the time period between the year of stand origin and the year of the particular survey. The nutrient regime as indicator of the nutrient availability of each site was determined mainly based on humus form and type of A horizon using methods described in Klinka et al. (Klinka et al. 1981). The nutrient regime among the study sites ranged from very poor, poor, medium, to rich (Beckingham et al. 1996). We defined DBH variation of all trees within each plot to represent the size inequity (see Chu et al. 2009). The dataset used in analysis was summarized in Table 3.1.

Table 3.1. Summary of endogenous (dependent) and exogenous (independent) variables (n=448) used in developing the structural equation model of species diversity and productivity relationships.

Conceptual category	Variable name*	Scale (units)	Mean± SD (range)‡
Species diversity	Shannon's index	Continuous (unitless)	0.56 ± 0.34 (0.00-1.58)
Productivity	log10 (Standing biomass)	Continuous (tonne ha^{-1})	2.1 ± 0.19 (1.14-2.43)
Functional diversity	number of functional groups	Ordinal (ranks)	2 (1-4)
Variation among individuals	log 10 (DBH variation)	Continuous (unitless)	2.1 ± 0.19 (-0.18-0.85)
Resources availability	Nutrient regime	Ordinal (ranks)	2 (1-4)§
Succession stage	Stand age	Continuous (year)	86.7 ± 27.3 (33-189)

*Variables are listed under the related conceptual category.

‡ Median and range are used instead of mean and SD for ordinal variables.

§The nutrient regime is defined as very poor (1), poor (2), medium (3), and rich (4).

3.2.3. *Data analysis*

We used structural equation modeling (SEM; Amos v. 8, SPSS, Chicago, Illinois, USA) to examine whether the proposed multivariate hypotheses based on current knowledge and theory, is consistent with the covariance matrix that describes the actual data. As a combination of modern path analysis and confirmatory factor analysis, SEM can test consistency between the hypothesized multiple relationships and the observed data in a multivariate space (Kline 2005;Grace 2006).

As recommended (Grace & Bollen 2005;Grace & Bollen 2008;Grace *et al.* 2010), we used pertinent predictor variables to build the SEM model according to the hypothesized multivariate hypotheses. The DBH variation and standing biomass were log-transformed to mitigate departure from normality and linearity. Model evaluation was based on maximum likelihood. The goodness-of-fit of the SEM model was evaluated by Chi-square test, Comparative Fit Index (CFI), and root mean square error of approximation (RMSEA) (Byrne 2010). The distributions of individual variables were checked (Appendix II: Fig. S3.1). The multivariate kurtosis was examined to evaluate a departure from multivariate normality by comparing to the recommended critical ration of multivariate kurtosis (i.e., it suggests non-normally distributed if larger than 5) (Bentler 2005). To relieve from violation of multivariate normality, an asymptotic distribution-free (ADF) estimation of the SEM model was conducted, provided that the sample size (n=448) was ten times greater than the freely estimated parameters (n=15) in the SEM model (Raykov & Marcoulides 2000). Regressions were used to show important causal relationships predicted in the SEM mode. In addition, autocorrelation was well controlled because (1) the site conditions and stand ages were purposely dispersed over as wide ranges as possible, (2) nutrient regime and stand age were included in the model.

We expected that the deviation of the covariance structures between the SEM model and the data was not significant in order to support our proposed set of hypotheses. The regression coefficients representing the proposed causal relationships would be statistically significant and positive in order to support our hypotheses. Further, the above relationships examined in univariate space would be positively significant in conformity with the regression coefficients in SEM model.

3.3. RESULTS

Overall, we found a non-linear relationship between Shannon's species index and standing biomass: coefficients for linear and quadratic terms (H' and H'^2) were significant (P<0.001) (Fig. 3.1). However, the amount of variation explained (R^2=0.049) in log transformed biomass suggested that other factors may affect DPR. This non-linear relationship between Shannon's index and standing biomass is consistent with the proposed SEM model (Fig. 3.2). The bivariate relationships between DBH variation and standing biomass, stand age and standing biomass, DBH variation and Shannon's index, and age and DBH variation were positive and significant (Fig. 3.3), and consistent with the result of the SEM (Fig. 3.2).

The results of Chi-square test (χ^2 = 5.314, df=6, P = 0.504) of the SEM model (Fig. 3.2) suggested that the deviation between the proposed model and the data was not significant. The values of other recommended model fitting criteria (CFI = 1.000, RMSEA < 0.001) further confirmed that the SEM model was appropriate and could not be rejected (Hu & Bentler 1999). All hypothesized paths between variables in our model were significant except correlation between age and Shannon's index (P = 0.218). Since this study was done in a confirmatory manner based on current knowledge from previous BEF studies, we retained this path in the SEM model. Nutrient regime positively affects standing biomass and DBH variation among individual trees within a stand. The results found in multivariate space (Fig. 3.2) were partially confirmed by results in bivariate space (Fig. 3.1 and Fig. 3.3) as well.

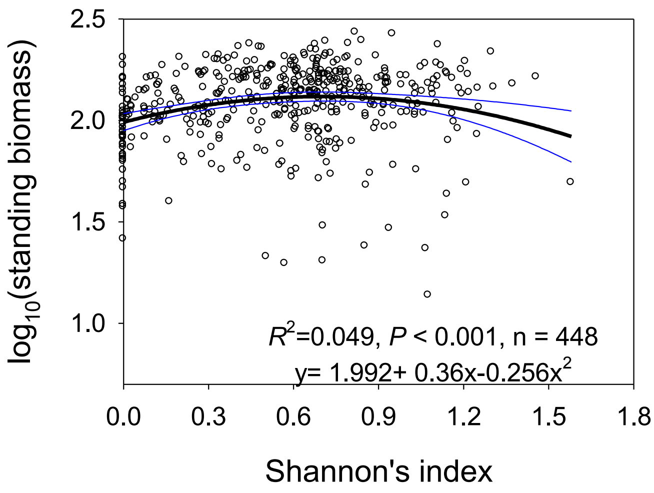

Figure 3.1. Non-linear relationship between Shannon's species index and stand biomass.

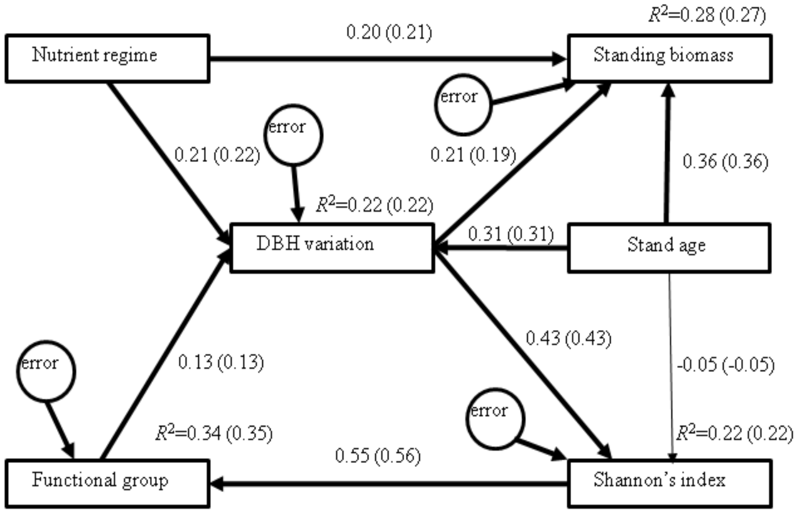

Figure 3.2. Results of the structural equations model used to test whether covariance among variables measured in the boreal forest permanent sampling plots conform to predictions of the set of hypothesized pathways proposed in this study. The standardized coefficients, the standard deviation change in dependent variable given a standard deviation change in predictor variable, are shown beside the arrow. R^2 (amount of variation explained by the model) for each endogenous (dependent) variables are shown at the left, top corner of each boxes. Measures of

overall model fit are given. The goodness-of-fit results ($\chi^2 = 5.314$, df=6, P = 0.504, CFI = 1.000, RMSEA < 0.001) suggested that this model is consistent with the data. To account for the slight departure from multivariate normality (critical ratio = 7.213), the results of standard coefficients from asymptotic distribution-free (ADF) estimation were given in the brackets. The validity of the current model was confirmed by ADF ($\chi^2 = 5.687$, df=6, P = 0.459, CFI = 1.000, RMSEA < 0.001).

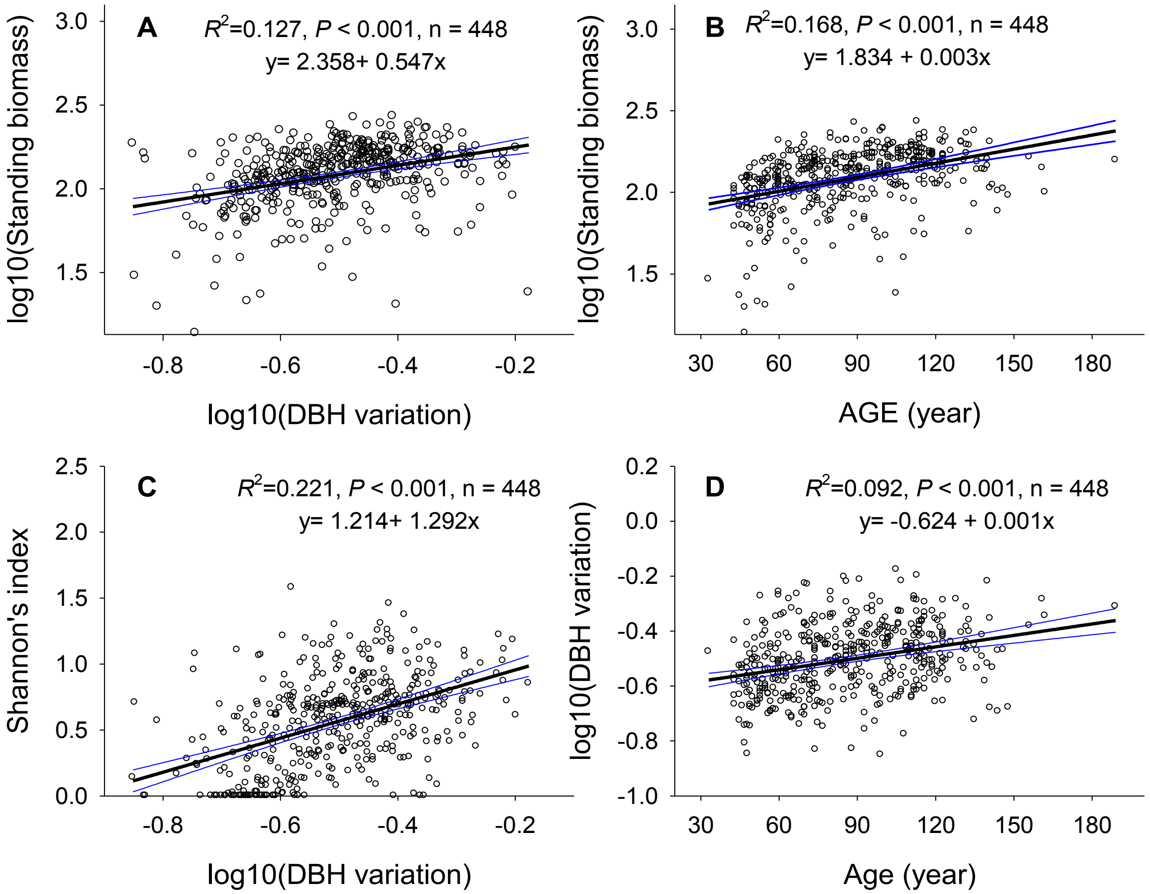

Figure 3.3. Bivariate relationships between variables of the multivariate hypotheses in the structural equation model (Fig. 1). (A) Stand biomass as a function of the tree DBH variation. Bold line is the regression between 95% confidence intervals. (B) Stand biomass as a function of the stand age. (C) Shannon's species index as a function of tree DBH variation. (D) Tree DBH variation as a function of the stand age.

3.4. DISCUSSION

We found an overall quadratic relationship between Shannon's index and standing biomass. The non-linear DPR is not consistent with results from previous studies conducted in grasslands

(Fornara & Tilman 2008;Isbell *et al.* 2009a;Wacker *et al.* 2009). The non-linear DPR supports the SEM assumption that species diversity may influence standing biomass of forest stands through multiple causal relationships, which are mediated by other factors. The multivariate nature of DPRs in natural forest stands may explain the negative DPR found in forest ecosystems analyzed in univariate space (e.g., Firn et al. 2007). The goodness-of-fit of our SEM model (Fig. 3-2) compared with the well-accepted cutoff criteria of fit indexes (Hu & Bentler 1999) and those significant bivariate relationships (Fig. 3-3A-D) further confirmed that numerous causal pathways and interrelated factors influence DPR and species coexistence simultaneously and plant responses to multiple stimuli in a non-additive manner (Bai *et al.* 2010;Cahill *et al.* 2010).

The SEM results support that the DBH variation among individuals may be the link between species diversity and productivity. Consistent with the niche complementarity hypothesis, the DBH variation as the manifestation of tree size asymmetry may represent niche differentiations in the occupation of the canopy in polycultures through contrasting shade tolerance and leaf habit. Thus, the positive correlations between the number of functional groups, DBH variation, and standing biomass can be expected through improved light use efficiency. However, the correlation ($r = 0.13$) between functional groups and DBH variation was relatively weak. This may be partially due to many other life-history traits (e.g., drought tolerance) that were not used for grouping in this study to influence plant responses to the environment.

Moreover, the two causal relationships from DBH variation to Shannon’s index and standing biomass ($r = 0.43$ and 0.21, respectively) in the SEM model suggested that maintenance of species diversity and positive DPR may be driven by the same mechanism in accordance with classic theory (Chesson 2000). Isbell et al. (2009a;2009b) have demonstrated that complementarity effects from niche differentiation and/or facilitation are responsible for positive

DPR and stability of plant species diversity concurrently. The population growth rate of rare species increases greater than relative abundant species driven by niche differentiation (Levine & HilleRisLambers 2009). Although it is not safe to conclude that variation among individuals are equivalent to niche complementarity between species, our findings do support that maintenance of species diversity and positive DPR may share the same ecological processes. Further, the niche differences at the species level may be difficult to detect, e.g., in our case, the niche differences at the individual level, or DBH variation among individuals, can result in similar response of niche differentiation at the species level predicted by coexistence theory (Chesson 2000) in responses to environment gradient for coexistence of competitors in a community (Clark 2010).

The SEM model showed that nutrient regime as an index of resources quantity within stands controls standing biomass directly and indirectly via DBH variation among individuals. Despite the debate about effects of resources availability and heterogeneity (Cardinale et al. 2009b), resources availability has been found more potent to influence plant community dynamics than resources heterogeneity in natural ecosystems (Stevens & Carson 2002;Bartels & Chen 2010). Moreover, the nutrient regime also affects Shannon's index indirectly through DBH variation among individuals. The individual variation may be attributed to the different responses of species with contrasting functional traits to nutrient regime. Our findings are partially consistent with predictions of the multivariate productivity-diversity (MPD) hypothesis stating that resources supply directly confines standing biomass of primary producers, and affects standing biomass indirectly through influences on species diversity, supported by an empirical experiment conducted in an algal community (Cardinale et al. 2009a). Contrasting to the MPD hypothesis, we have included the potential underlying mechanism, DBH variation, explicitly in the SEM model. The limitation of nutrient regime on standing biomass and species diversity also supports the species energy theory (Wright 1983).

3.5. CONCLUSIONS

Our results showed that tree size variation among individuals is the central mechanism linking resources availability, biomass of primary producers, and species diversity. Species diversity alone may not result in polycultures yielding greater biomass than monocultures in natural forest ecosystems. Resource availability controls species diversity, and species diversity affects biomass production indirectly through functional diversity. We argue that study on any single process may be difficult to develop a mechanistic understating of BEF and it is necessary to examine natural ecosystems in multivariate space because the interactions of multiple factors shape the overall picture of community dynamics. This study is unique by integrating multiple ecological processes concurrently as the way they happen in real world based on historical theory and latest empirical studies.

4.0. SUMMARY

The meta-analysis support that life-history variation among species may be the mechanism mitigating the species diversity effects on stand productivity in forest ecosystems, which is consistent with previous reported findings in grassland experiments. The BRT results suggest that interspecific life-history variation results in positive DPRs. The findings in further consolidate the importance of tree size variation that is significantly affected by functional diversity based on life-history traits of constituent species within stands. The tree size variation may be the mechanism for mitigating DPR and species coexistence. The soil nutrient availability limits the standing biomass directly and indirectly via tree size variation among individuals, possibly through different responses of species to site conditions based on contrasting life-history traits. We found that the variation among individuals is the center piece, which linking species diversity and standing biomass. However, we could not attribute the causal relationships we found to one mechanism exclusively. Likely, niche differentiation and neiboughing effects might be the underlying mechanisms to explain the SEM model.

The belowground ecological processes were not accounted in the SEM model. Although studied to a much lesser extent, the belowground and aboveground inter-relationships have been found to play an essential role in shifting plant interactions between facilitation and competition. Further, Janzen-Connell effects have been found to be important in the maintenance of species diversity in both forest and grassland ecosystems. Therefore, future studies on BEF may include both the aboveground and underground interactions in a multivariate space.

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APPENDIX I. Summary of data and references of studies used in meta-analysis (part two)

Reference	Biome	Stand Origin	Number of traits per study	Number of observations
Amoroso & Turnblom (2006)	temperate	plantation	2	9
Ares and Fownes (2001)	tropical	plantation	2	4
Austin *et al*. (1997)	tropical	plantation	2	7
Bauhus *et al*. (2004)	tropical	plantation	2	10
Binkley (2003)	temperate	plantation	3	5
Binkley *et al*. (1992)	tropical	plantation	3	7
Binkley *et al*. (2003)	tropical	plantation	3	7
Burleigh and Yamoah (1997)	tropical	plantation	2	6
Cavard *et al*. (2010)	boreal	natural	3	9
Chen and Klinka (2003)	temperate	natural	0	27
Chen *et al*. (2003)	boreal	natural	1 and 2	5
da Gama-Rodrigues *et al*. (2007)	tropical	natural	2	2
Debell (1985)	tropical	plantation	3	3
DeClerck *et al*. (2006)	temperate	natural	2	3
Dickmann *et al*. (1985)	temperate	plantation	2	3
Edgar and Burk (2001)	boreal	natural	3	4
Erskine *et al*. (2006)	tropical	plantation	3	53
Firn *et al*. (2007)	tropical	natural/plantation	0	15
Forrester (2004)	temperate	plantation	3	10
Forrester *et al*. (2006)	tropical	plantation	2	11
Forrester *et al*. (2007)	temperate	plantation	2 and 3	10
Garber and Maguire (2004)	temperate	plantation	1 and 2	6
Hunt *et al*. (1999)	tropical	plantation	3	21
Kaye *et al*. (2000)	tropical	plantation	3	6
Kelty (1989)	temperate	natural	3	4
Khanna (1997)	tropical	plantation	3	8
Klang and Eko (1999)	boreal	plantation	2 and 3	12
Legare and Bergeron (2005)	boreal	natural	3	3
Liang *et al*. (2007)	temperate	natural	3	20
Linden and Agestam (2003)	boreal	plantation	2	8
Longpré *et al*. (1994)	boreal	natural	1	3
Luis and Monteiro (1998)	temperate	plantation	2	7
Lygis *et al*. (2004)	boreal	plantation	3	5
MacPherson *et al*. (2001)	boreal	natural	3	58

Mard (1996)	boreal	natural	3	2
Menalled *et al*. (1998)	tropical	plantation	2	5
Montagnini (2000)	tropical	plantation	3	10
Montagnini *et al*. (1995)	tropical	plantation	3	5
Parrotta (1999)	tropical	plantation	2	6
Petit and Montagnini (2006)	tropical	plantation	3	13
Piotto *et al*. (2003)	tropical	plantation	3	13
Piotto *et al*. (2004)	tropical	plantation	2	16
Pretzsch and Schutze (2009)	temperate	natural	3	27
Pukkala *et al*. (1994)	boreal	natural	2	48
Rouhi-Moghaddam *et al*. (2008)	temperate	plantation	0	5
Sayyad *et al*. (2006)	temperate	plantation	2	5
Son *et al*. (2007)	temperate	plantation	3	3
Tripathi *et al*. (2004)	tropical	plantation	2	3
Vila *et al*. (2003)	temperate	natural	2	10
Vila *et al*. (2007)	temperate	natural	1	10
Vogel and Gower (1998)	boreal	natural	3	4
Wierman (1979)	temperate	natural	1	3
Zhang *et al*. (2007)	temperate	plantation	2	5

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APPENDIX II. Histograms showing univariate distributions of variables used in structural equation modeling (part three)

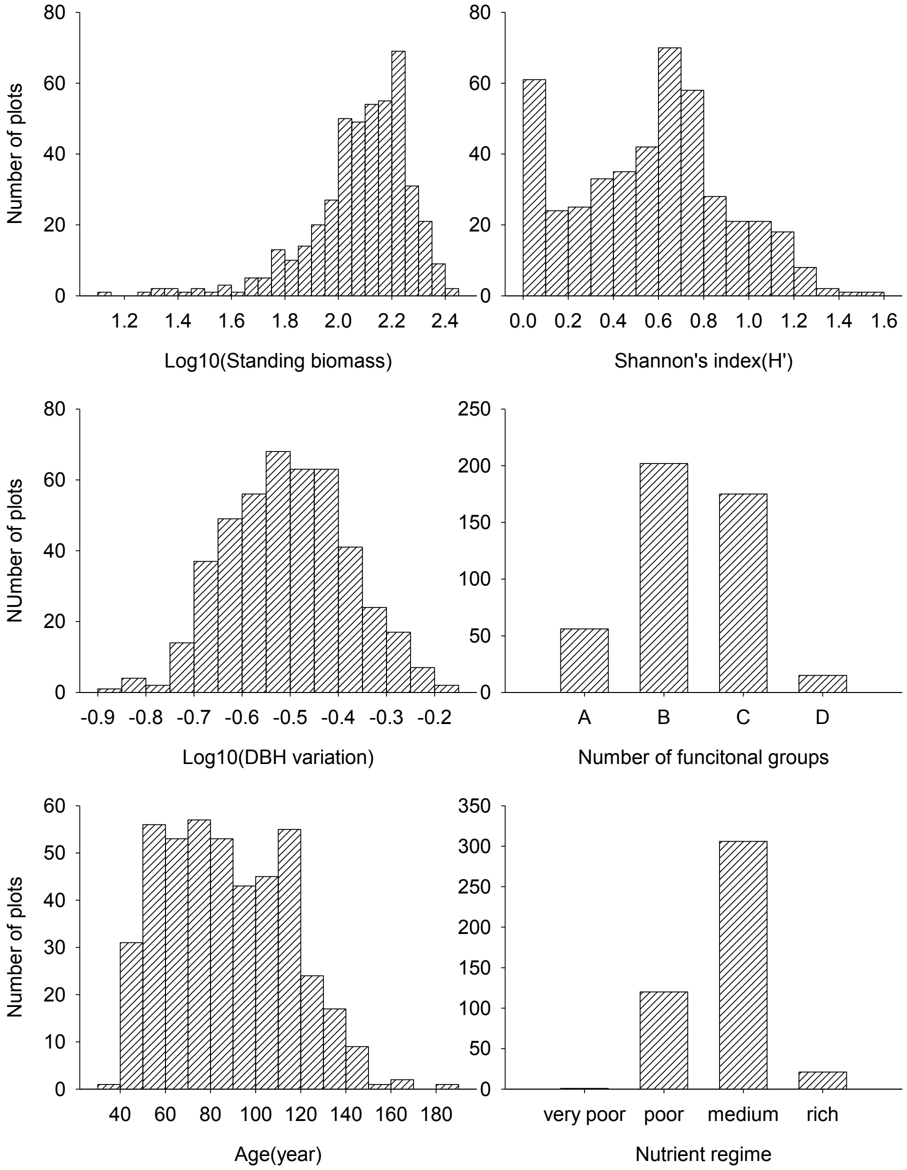

Figure S3.1. Distributions of the variables used in structural equation modeling.