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Temporal stability of aboveground biomass is governed by species asynchrony in temperate forests☆

Zuoqiang Yuan[a,*], Arshad Ali[b], Shaopeng Wang[c], Xugao Wang[a], Fei Lin[a], Yunyun Wang[d], Shuai Fang[a], Zhanqing Hao[a,e,*], Michel Loreau[f], Lin Jiang[g]

[a] CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110164, China
[b] Department of Forest Resources Management, College of Forestry, Nanjing Forestry University, Nanjing 210037, Jiangsu, China
[c] Department of Ecology, College of Urban and Environmental Science, and Key Laboratory for Earth Surface Processes of the Ministry of Education, Peking University, 100871 Beijing, China
[d] National Engineering Laboratory for Applied Technology of Forestry & Ecology in South China, Central South University of Forestry and Technology, Changsha 410004, China
[e] Research Center for Ecology and Environmental Sciences, Northernwest Polytechnical University, China
[f] Centre for Biodiversity Theory and Modelling, Theoretical and Experimental Ecology Station, CNRS and Paul Sabatier University, 09200 Moulis, France
[g] School of Biology, Georgia Institute of Technology, Atlanta, GA 30332, USA

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ABSTRACT

Understanding the effects of plant species diversity and trait composition on aboveground biomass is a central focus of ecology and has important implications for biodiversity conservation. However, the simultaneous direct and indirect effects of soil nutrients, species asynchrony, functional trait diversity, and trait composition for explaining the community temporal stability of aboveground biomass remain underrepresented in natural forests. Here, we hypothesized that species asynchrony relative to soil nutrients, functional trait diversity, and trait composition plays a central role in stabilizing the community temporal stability of natural forests. We tested this hypothesis using a structural equation model based on 10-year continuous monitoring data (i.e., three-time repeated forest inventories) in both second-growth and old-growth temperate forests in northeast China. Our results showed that the community temporal stability of aboveground biomass was driven by a strong direct positive effect of species asynchrony in both second-growth and old-growth temperate forests, whereas functional trait diversity and composition (i.e. community-weighted mean of leaf nitrogen content) were of additional importance in an old-growth forest only. Functional trait diversity decreased community-weighted mean of leaf nitrogen content in an old-growth forest, whereas this relationship was non-significant in a second-growth forest. Soil nutrients had non-significant effects on the community temporal stability of both second-growth and old-growth forests. Species asynchrony was the direct determinant of the community temporal stability of aboveground biomass in temperate forests. The direct effect of species asynchrony increased with forest succession, implying that temporal niche differentiation and facilitation increase over time. This study suggests that managing forests with mixtures of both early and late successional species or shade intolerant and tolerant species, not only species diversity, is important for maintaining forest stability in a changing environment. We argue that the species asynchrony effect is crucial to understand the underlying ecological mechanisms for a diversity-biomass relationship in natural forests.

1. Introduction

Understanding the effects of plant species diversity and trait composition on aboveground biomass is a central focus of ecology and has important implications for biodiversity conservation (Duffy, 2009; Tilman, 1997). Widespread studies have suggested that species (taxonomic, functional trait, and phylogenetic) diversity generally promotes aboveground biomass in natural forests, even though diversity-biomass

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* Corresponding authors at: CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110164, China (Z. Hao).

E-mail address: hzq@iae.ac.cn (Z. Hao).

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relationship is strongly context-dependent (Ali et al., 2017; Poorter et al., 2017; Ratcliffe et al., 2017; Yuan et al., 2016). Yet, four main research aspects are crucial to improve our understanding of diversity-biomass relationships in natural forests (del Río et al., 2017; Grossman et al., 2017; Jucker et al., 2014; Morin et al., 2014): 1) considering the community temporal stability of aboveground biomass (i.e. measured over repeated forest inventories) rather than aboveground biomass stock (i.e. measured over a single forest inventory); 2) evaluating the effects of soil nutrients on species asynchrony, diversity, and trait composition, and then finally on community temporal stability; 3) considering the effects of multiple indices of functional trait diversity and trait composition, rather species richness only, on community temporal stability; and 4) evaluating diversity-temporal stability relationships across second-growth and old-growth forests.

Ecological theories predict and empirical studies show that community stability is due to the combination of species asynchrony, species interactions, the stability of dominant species and overyielding (del Río et al., 2017; Loreau and de Mazancourt, 2013; Sasaki and Lauenroth, 2011; Xu et al., 2015). Stability can be the resistance, resilience, persistence, and temporal stability of community properties (Griffin et al., 2009). For example, community temporal stability, measured as the ratio of the mean (μ) to its temporal standard deviation (σ) of community properties in a given community (i.e. plot) (Lehman and Tilman, 2000), has attracted much attention from both empirical (del Río et al., 2017; Gross et al., 2013; Jucker et al., 2014) and theoretical (Loreau and de Mazancourt, 2013; Wang and Loreau, 2016) perspectives. Biological mechanisms suggest that biodiversity could promote temporal stability through species asynchrony and overyielding (Loreau and de Mazancourt, 2008; Loreau et al., 2001). Species asynchrony represents the intrinsic differences in species' response to disturbances and natural fluctuations (Loreau and de Mazancourt, 2013), which has been suggested as a key driver for community temporal stability by decreasing the variability in constituents at the community level (Loreau and de Mazancourt, 2008). Overyielding (hence higher functioning) occurs in species mixtures than in monocultures caused by facilitation and/or competition reduction among interspecific neighbours (Loreau and Hector, 2001), which could generate a stabilizing influence through a faster increase in the mean relative to the variance in communities (Lehman and Tilman, 2000). However, changes in species composition of forests are relatively slow and might be decoupled from interannual variations in climate, because of the longevity of trees and no regeneration of the bulk of their aboveground biomass per year (Stephenson and van Mantgem, 2005). Thus, species asynchrony is difficult to be detected in forests at the short term, implying that the extent to which forests can express compensatory dynamics among species may be limited compared to grasslands ecosystems (Jucker et al., 2014; Xu et al., 2015).

Functional traits are expected to provide the most direct relationship between biodiversity and ecosystem functioning (Lohbeck et al., 2015), therefore we consider the functional trait diversity and composition to quantify the effects of biodiversity properties on community temporal stability. For example, functional trait diversity frequently performs better than species richness in predicting aboveground biomass or productivity in forest ecosystems, probably resulting from greater niche differentiation or complementarity among functionally-diverse species within a community (Ali et al., 2017; Paquette and Messier, 2011; Prado-Junior et al., 2016; Yuan et al., 2016). Alternatively, diverse communities could sustain ecosystem functioning consistently probably due to the fact that they contain key species with temporally stable functioning (Grman et al., 2010). For example, the temporal stability of dominant species, but not species diversity, may strongly influence community temporal stability (Sasaki and Lauenroth, 2011; Xu et al., 2015), coined as the ‘mass ratio effect’ (Grime, 1998). This effect can be also represented by functional trait composition, measured via community-weighted mean (CWM) of trait values (Díaz et al., 2007). Moreover, species asynchrony has a strong positive effect compared to the mass ratio effect, species diversity and overyielding on stability of community stability, suggesting that species mixtures can maintain consistent rates of productivity across a wide range of abiotic conditions compared to monocultures (Jucker et al., 2014; Xu et al., 2015).

Previous studies have suggested that soil nutrients are the key abiotic factors of forest diversity, structure and functioning (Ali and Yan, 2017; Prado-Junior et al., 2016), which may affect community temporal stability directly or indirectly via species asynchrony, functional trait diversity and composition (Xu et al., 2015). For example, fertile soils could directly relieve tree species growth from limited resources, leading to biomass accumulation less affected through their variations over time (i.e. stronger stability). Alternatively, greater resource availability may cause weaker stability if it causes greater interspecific competition resulting in higher mortality and turnover rates (Quesada et al., 2012; Russo et al., 2005). Moreover, dominant species are often acquisitive in nature as they have a higher requirement for available resources (Nepstad et al., 1994), implying that larger trees might be strongly limited by resource availability (Ali et al., 2018; van der Sande et al., 2015). As such, variations in soil fertility could cause a difference in the responses of species adaptation to environmental changes, which may, in turn, affect community temporal stability through altering the degree of species asynchrony (Hautier et al., 2014; Xu et al., 2015).

The main aim of this study is to evaluate the effects of soil nutrients, species asynchrony, functional trait diversity, and trait composition on the community temporal stability of aboveground biomass, thereby to test the importance of the soil fertility, niche complementarity and mass ratio effects in natural second-growth and old-growth temperate forests. We ask the following specific research questions, using three-time repeated forest inventory data from second-growth and old-growth temperate forests in northeast China: 1) How do soil nutrients, functional trait diversity, species asynchrony and trait composition affect community temporal stability? 2) How do soil nutrients affect community temporal stability indirectly via species asynchrony, functional trait diversity and composition? 3) How does functional trait diversity affect community temporal stability indirectly via species asynchrony and trait composition? We hypothesize that species asynchrony, relative to soil nutrients, functional trait diversity and composition, plays a central role in stabilizing the community temporal stability of natural forests. We also expect that the relative effects of soil nutrients, species asynchrony, functional trait diversity and composition on community temporal stability will change along with forest succession stages (i.e. second-growth and old-growth forests).

2. Materials and methods

2.1. Study area, forest plots and repeated forest inventory

This study was conducted in temperate forests on the Changbai Mountain Natural Reserve, located in northeastern China, which is one of the biggest protected temperate forests across the world (Hao et al., 2007). This region (∼200,000 ha area) belongs to a temperate continental climate with warm summers and long, cold winters, and has an average annual temperature of 2.8 °C. The average temperature in the warmest months is 19.6 °C and the coldest month is −13.7 °C (Hao et al., 2007). The mean annual precipitation is about 700 mm, most of which happens between June and September; Annual evaporation is about 1251 mm and annual relative humidity is 72%. This area was the legendary birthplace of the imperial family during the Qing Dynasty and changed into a natural reserve in the 1960s. The study area is dominated by old-growth forests, famous for its high species diversity and unique community composition among temperate forests (Stone, 2006). The soil is a dark brown soil developed from volcanic ash (Albic Luvisol). Parts of this forest area have been disturbed by windthrow or timber harvest and hence second-growth forests also exist (Xu et al., 2004).

In this study, we selected a second-growth forest (i.e. poplar-birch forest; PBF) and an old-growth forest (i.e. broad-leaved Korean pine (*Pinus koraiensis*) mixed forest; BKF), in order to test the effects of soil nutrients, species asynchrony, functional trait diversity, and trait composition on the community temporal stability of aboveground biomass across forest succession. The stand age of a second-growth and an old-growth forest was approximately 80 and 280 years, respectively, according to the references and official records of local Forestry Bureau (Wang et al., 1980; Xu et al., 2004; Yan et al., 2012). The two studied forest plots had been strictly protected from human activities for at least 20 years since the beginning of China's Natural Forest Protection Project in 1998.

In a second-growth (42°22′N, 128°00′E) and an old-growth forest (42°23′N, 128°05′E), 120 contiguous subplots (20 × 20 m) within 4.8 ha plot, for each forest type, were established during 2004–2005, i.e., a total of 240 subplots (Fig. S1 in Appendix A). During the first forest inventory, which was conducted at different inventory periods for two different forest types (T_0, 2004 for old-growth and 2005 for second-growth forest), all individual trees having a stem diameter at breast height (DBH) ≥ 1 cm were mapped, measured, and identified to the species level following a standard field protocol (Hao et al., 2007). Based on the first inventory data, a total of 59,138 individuals were recorded and measured, belonging to 42 species, 30 genera and 16 families in an old-growth forest, whereas a total of 20,101 individuals were measured, belonging to 56 species, 30 genera and 17 families in a second-growth forest. In total, there were 36 species common between two forest types (see Table S1 in Appendix A). The stand density of the second-growth and the old-growth forest was 4187 ± 881 and 2102.3 ± 350 stems ha^{-1}, respectively. In the second and third forest inventories, with five-year intervals for each forest (T_1, 2009 and 2010; T_2, 2014 and 2015 for an old-growth and a second-growth forest, respectively), all living individual stems were re-measured, and recruitment rates, growth and mortality were assessed for the accurate the temporal variability of individuals. For each forest inventory data, aboveground biomass of each individual stem was estimated based on tree DBH (cm) using species-specific available allometric equations which covered all dominant and abundant species in the study area. For some missing species, we used the generic allometric equation or family values (Chen and Zhu, 1989; Wang, 2006) (see Table S2 in Appendix A). This work is also guided based on the "Observation Methodology for Long term Forest Ecosystem Research of National Standards of the People's Republic of China (GB/T 33027-2016)".

2.2. Quantification of community temporal stability and species asynchrony

The community temporal stability (TS) of aboveground biomass within each 20 × 20 m subplot was quantified using an intuitive and classically accepted approach: $TS = \mu/\sigma$ (Jucker et al., 2014; Lehman and Tilman, 2000; Wang and Loreau, 2016), where μ and σ are the mean and the standard deviation of the aboveground biomass of the three-time repeated inventories data (2004, 2009 and 2014 for BKF plot while 2005, 2010 and 2015 for BKF plot). Approximately one-quarter of the subplots showed a significant ($P < 0.05$) temporal trend in community aboveground biomass (evaluated by regressing aboveground biomass against inventory years for each subplot) during the study period (see Fig. S2 in Appendix A). A detrending procedure was applied in those subplots by subtracting the mean fitted aboveground biomass value of the linear regression against the inventory years as suggested by Tilman et al. (2006). The detrended community temporal stability (TS_d) of aboveground biomass was expressed as: $TS_d = \mu/\sigma_d$, where σ_d is the standard deviation of residuals for regression.

There are many ways to define and measure species synchrony in multi-species communities, of which the average temporal correlation coefficient has been commonly used as a standardized measure of synchrony between species at the community level (Loreau and de Mazancourt, 2008). Species asynchrony (Eq. (1)) was calculated for each subplot in order to understand how the aboveground biomass of multiple species differentially fluctuates in time (Loreau and de Mazancourt, 2008):

$$1 - \varphi x = 1 - \sigma^2 \Big/ \left(\sum_{i=1}^{s} \sigma_i \right)^2 \tag{1}$$

where φ_x is the species synchrony, σ^2 is the temporal variance of aboveground biomass in the given subplot, and σ_i is the standard deviation of aboveground biomass of the *i*th species in the subplot with S species over the ten years. For the above-mentioned subplots existing significant ($P < 0.05$) temporal trend in community aboveground biomass, the species asynchrony was calculated using detrended population data accordingly for further analysis. The species asynchrony values vary between 0 (perfect synchrony) and 1 (perfect asynchrony). A significant positive relationship between temporal stability and species asynchrony indicates that species asynchrony may enhance stability (Loreau and de Mazancourt, 2013).

2.3. Quantification of functional trait diversity and composition

In each 20 × 20 m subplot, functional trait diversity and composition indices were measured using six functional traits which were assumed to be tightly linked to tree life-history strategies and aboveground biomass production (Conti et al., 2013; Petchey and Gaston, 2006), i.e., leaf phosphorus content (LPC), leaf nitrogen content (LNC), maximum tree height (MH), wood density (WD), mean leaf area (LA) and specific leaf area (SLA). Functional trait diversity (FD_{com}) was quantified using a multi-trait functional dispersion index (Laliberté and Legendre, 2010), which measures the mean distance in multidimensional trait space of individual trees to the centroid of all species, weighted according to the relative basal area of each species. To determine the influences of the mass ratio effect on the community temporal stability, functional trait composition, i.e., community-weighted mean (CWM) of a single trait values, was calculated as the average trait value (CWM_{MH}, CWM_{WD} , CWM_{LPC}, CWM_{LNC}, CWM_{LA} and CWM_{SLA}) of component species within each subplot, weighted by its relative basal area (Garnier et al., 2004). The species' relative basal area was applied to weight the traits of species within each subplot because it scales properly with the photosynthetically active leaf area of trees (Ali and Yan, 2017; Prado-Junior et al., 2016).

Trait values were rescaled to a mean of 0 with a standard deviation of 1 before the calculations of functional trait diversity and CWM indices. All indices were obtained using the FD package (Laliberté and Legendre, 2010) in R 3.3.3 (R Development Core Team, 2017). For a detailed description of functional traits measurements, and calculations of functional trait diversity and composition, please see Yuan et al. (2016,2018). Functional trait diversity and trait composition indices, for each forest inventory, were calculated separately, and then averaged to get the mean values for each plot (Table S3 in Appendix A).

2.4. Measurement of soil nutrients

In order to cover the entire plots and capture fine-scale variations in soil physicochemical properties, soil samples were sampled in a second-growth forest and an old-growth using regular and random sampling approaches according to the standard sampling protocol of the 50-ha BCI (Barro Colorado Island) plot soil survey (John et al., 2007). All the soils were taken at a depth of 10 cm and air-dried at ambient laboratory temperature and then sieved through a 2-mm mesh to remove roots and stones. Soil pH was analyzed by means of a Beckman pH meter in 1:1 soil-water solution. Soil organic matter content was determined by the acidified dichromate ($K_2Cr_2O_7$–H2SO$_4$) oxidation method. Total N was measured following the Kjeldahl method. Total P was obtained by molybdate colorimetry, after digestion in H_2SO_4–$HClO_4$. Total K was

Table 1

Summary of the variables used in this study across second-growth (PBF) and old-growth (BKF) temperate forests.

Variables	Unit	Second-growth forest (n = 120)		Old-growth forest (n = 120)	
		Mean	Min.–Max.	Mean	Min.–Max.
Vegetation properties					
Temporal stability of aboveground biomass (TS of AGB)	–	28.3^{a}	4.9–418.0	44.8^{b}	3.2–359.6
Species asynchrony	–	0.80^{b}	0.001–0.99	0.36^{a}	0.003–0.99
Functional trait diversity (FD_{com})	–	0.17^{b}	0.11–0.21	0.13^{a}	0.10–0.20
Community-weighted mean of maximum height (CWM_{MH})	m	20.8^{a}	12.7–25.3	26.8^{b}	22.4–30.8
Community-weighted mean of wood density (CWM_{WD})	g cm^{-3}	0.52^{b}	0.49–0.55	0.49^{a}	0.41–0.56
Community-weighted mean of leaf phosphorus content (CWM_{LPC})	%	1.78^{b}	1.65–1.91	1.72^{a}	1.51–1.93
Community-weighted mean of leaf nitrogen content (CWM_{LNC})	%	2.26^{b}	2.07–2.46	2.00^{a}	1.69–2.21
Community-weighted mean of mean leaf area (CWM_{LA})	cm^{2}	42.1^{b}	23.3–65.2	30.9^{a}	15.5–44.5
Community-weighted mean of specific leaf area (CWM_{SLA})	cm^{2} g^{-1}	243.6^{b}	195.5–326.5	194.8^{a}	132.2–246.6
Soil properties					
pH value	–	5.40^{a}	4.88–5.79	5.51^{a}	4.78–6.89
Organic matter (OM)	g kg^{-1}	200.6^{a}	110.8–372.3	201.8^{a}	64.7–422.6
Total nitrogen (TN)	g kg^{-1}	7.1^{a}	2.4–12.4	7.2^{a}	2.54–12.1
Total phosphorus (TP)	g kg^{-1}	1.13^{a}	0.53–2.23	1.37^{b}	0.7–1.94
Total potassium (TK)	g kg^{-1}	13.8^{a}	10.1–16.6	16.3^{b}	7.99–21.2

Different letters represent significant differences (Kruskal-Wallis test, $P < 0.05$) between two forest types.

derived using atomic absorption spectrometry. We used spatial interpolation based on ordinary kriging as implemented in the *geoR* package in R (Ribeiro and Diggle, 2001) to estimate soil variables for each 20 × 20 m subplot (for details see Yuan et al. (2011).

In order to reduce the correlation among soil properties, principal component analyses (PCA) was used for a second-growth and an old-growth forest, separately. The PCA showed that first axis (PC1), explained 41.7% of the variation, reflected a gradient with infertile to fertile soil, while second axis (PC2) accounted for 20.1% of the variation, mainly described high total potassium and nitrogen in a second-growth forest (Appendix S5). In an old-growth forest, PC1 explained 61.8% of the variation and described a gradient with infertile to fertile soil with an exception of total potassium, whereas soil PC2 accounted for 21.3% of the variation, mainly reflected a gradient with high to low acidic sites with high total phosphorous. We used PC1 axis for soil nutrients in the statistical analysis (Table S4 in Appendix A).

2.5. Statistical analyses

According to the known theoretical multivariate causes for ecosystem functioning and community temporal stability (van der Sande et al., 2017; Xu et al., 2015), we constructed one identical structural equation model (SEM) to relate soil nutrients, species asynchrony, functional trait diversity and composition, and the community temporal stability of aboveground biomass in a second-growth and an old-growth forest, separately. Here, we used the partially confirmatory model because the structure of the SEM is fixed because we assumed soil nutrients, species asynchrony and functional trait diversity could influence community temporal stability, but we did not know the role of functional trait composition in driving community temporal stability. Therefore, we used all subsets of multiple regressions to pre-select the best index of functional trait composition by evaluating all possible combinations of six CWM of trait values (Ali and Yan, 2017; van der Sande et al., 2017). We selected the best model that has the lowest Akaike's information criterion corrected for small sample sizes (AICc) (Burnham and Anderson, 2004). Models were considered equally important when the difference in AICc was less than two units. If models were equally supported, we calculated the relative importance values for each variable by model averaging of all subset models where the specific variable occurred (conditional average) (Barton, 2012). The CWM of leaf nitrogen content (CWM_{LNC}) was selected as a final representative variable for functional trait composition in SEM because it had the highest relative importance value (Table S5 in Appendix A). The model fit of SEM was critically evaluated based on the Chi-square (χ^2) test (i.e., P-value > 0.05), Bentler's Comparative Fit Index and Goodness of Fit Index (i.e., CFI and GFI > 0.90), standardized root mean square residual (SRMR ≤ 0.05), lowest AIC value and coefficient of determination (R^2) (Table S6 in Appendix A). Finally, we obtained the standardized direct, indirect and total effects (and associated P-values), from SEM analysis, in order to address their relative effect to the explained variation in the community temporal stability of aboveground biomass. All subsets of multiple linear regressions and model averaging were evaluated using the *dredge* function and the *model.avg* function, respectively, of the *MuMIn* package (Barton, 2012). The analysis of SEM was conducted in *lavaan* package (Rosseel, 2012).

In order to complement the results from SEM, we then conducted the bivariate analysis for all hypothesized paths, using simple linear regressions without considering spatial autocorrelation. However, we also tested the spatial autocorrelation in the community temporal stability of aboveground biomass using generalized least-squares models, which is an appropriate method for assessing whether subplots are independent of each other within a large forest plot (Yuan et al., 2016). Here, we fitted linear models with and without spherical autocorrelation structure for each hypothesized path in the SEM, and then compared these two type of models with Akaike Information Criterion (AIC) (Zuur et al., 2009). We did not find any strong evidence for the spatial autocorrelation because the models without spherical autocorrelation structures always showed the lower AIC values compared to spherical autocorrelation models (Table S7 in Appendix A).

Prior to statistical analysis, the community temporal stability of aboveground biomass was natural-log transformed for the aim to meet the assumptions of linearity and normality. One-way analysis of variance (ANOVA) was applied to compare the difference in community temporal stability of aboveground biomass, soil nutrients, species asynchrony, functional trait diversity and composition between second-growth and old-growth forests (see Table 1 for the summary of variables used in SEMs).

3. Results

The SEM for a second-growth forest showed that the community temporal stability of aboveground biomass was directly influenced by species asynchrony ($ß = 0.29$, $P < 0.01$), but not directly influenced by soil nutrients, functional trait diversity and composition (CWM_{LNC}) (Fig. 1a). Functional trait diversity had non-significant indirect effects on the community temporal stability of aboveground biomass via

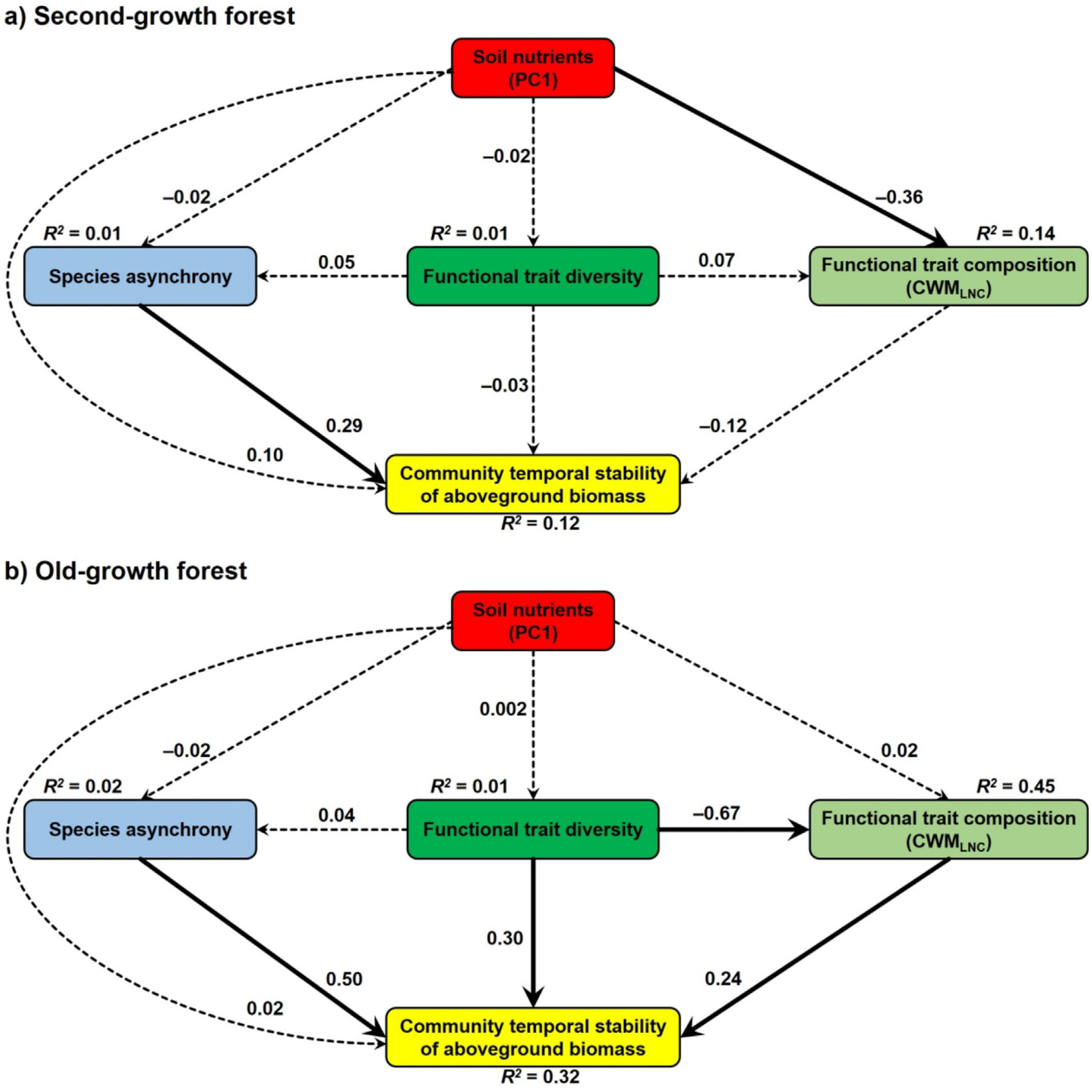

Fig. 1. Structural equation models for testing the relative effects of soil nutrients, species asynchrony, functional trait diversity and composition for explaining community temporal stability in natural second-growth (a) and old-growth (b) temperate forests. Solid arrows represent significant paths and dashed arrows represent non-significant paths. For each path, the standardized regression coefficient is shown. R^2 indicates the total variation in a dependent variable that is explained by the combined independent variables. The model-fit statistics summary is provided in Table S6 in Appendix A. Direct, indirect and total effects for second-growth and old-growth forests are provided in Tables S8 and S9 in Appendix A.

species asynchrony and functional trait composition (Fig. 2; Table S8 in Appendix A). Soil nutrients (i.e. soil PC1) had non-significant indirect effects on the community temporal stability of aboveground biomass via species asynchrony, functional trait diversity and composition (i.e. $\mathrm{CWM_{LNC}}$), and hence a non-significant total effect (Fig. 2; Table S8 in Appendix A). These results indicated that species asynchrony was the direct determinant of the community temporal stability in a second-growth forest. Bivariate relationships for supporting the second-growth SEM results are presented in Fig. 3.

The SEM for an old-growth forest showed that species asynchrony had the strongest direct positive effect on community temporal stability ($ß = 0.50$, $P < 0.01$), followed by functional trait diversity ($ß = 0.30$, $P < 0.01$) and composition ($\mathrm{CWM_{LNC}}$; $ß = 0.24$, $P = 0.02$) (Fig. 1b). Functional trait diversity had an indirect negative effect via trait composition ($ß = -0.16$, $P = 0.02$), but resulted in a positive total effect on the community temporal stability of aboveground biomass ($ß = 0.16$, $P = 0.08$) (Fig. 2; Table S9 in Appendix A). Soil nutrients (i.e. soil PC1) had non-significant indirect effects on the community temporal stability of aboveground biomass via species asynchrony, functional trait diversity and composition, and hence a non-significant total effect (Fig. 2; Table S9 in Appendix A). These results indicated that species asynchrony was the direct determinant of the community temporal stability, while functional trait diversity and composition were also of additional importance for maintaining stability in an old-growth forest. Bivariate relationships for supporting the old-growth forest SEM is presented in Fig. 4.

4. Discussion

Whether biologically-diverse communities tend to be more stable has fascinated scientists for more than six decades (Cardinale et al., 2012; MacArthur, 1955). We assessed the relative effects of soil nutrients, species asynchrony, functional trait diversity and composition on the community temporal stability of aboveground biomass across forest succession stages (i.e. second-growth and old-growth forests), and found strong support for the role of species asynchrony in stabilizing forest communities. Species asynchrony was the main determinant of community temporal stability in both second-growth and old-

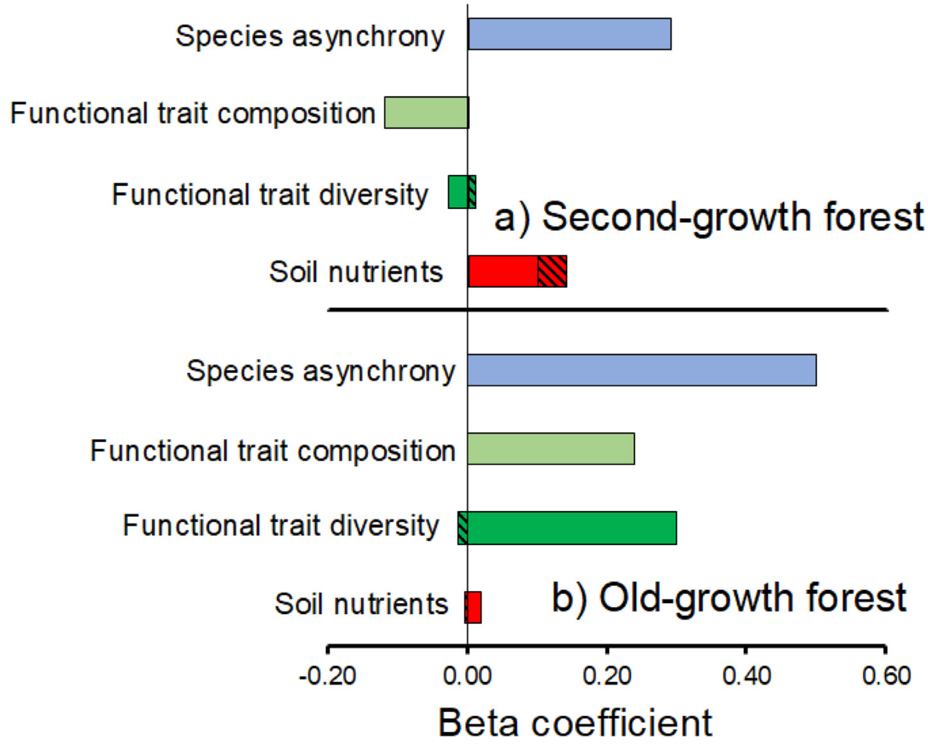

Fig. 2. Comparison of direct and indirect effects of soil nutrients, species asynchrony, functional trait diversity and composition on the community temporal stability of aboveground biomass in second-growth and old-growth forests. The filled bars indicate the direct effects whereas the streak filled bars indicate the indirect effects.

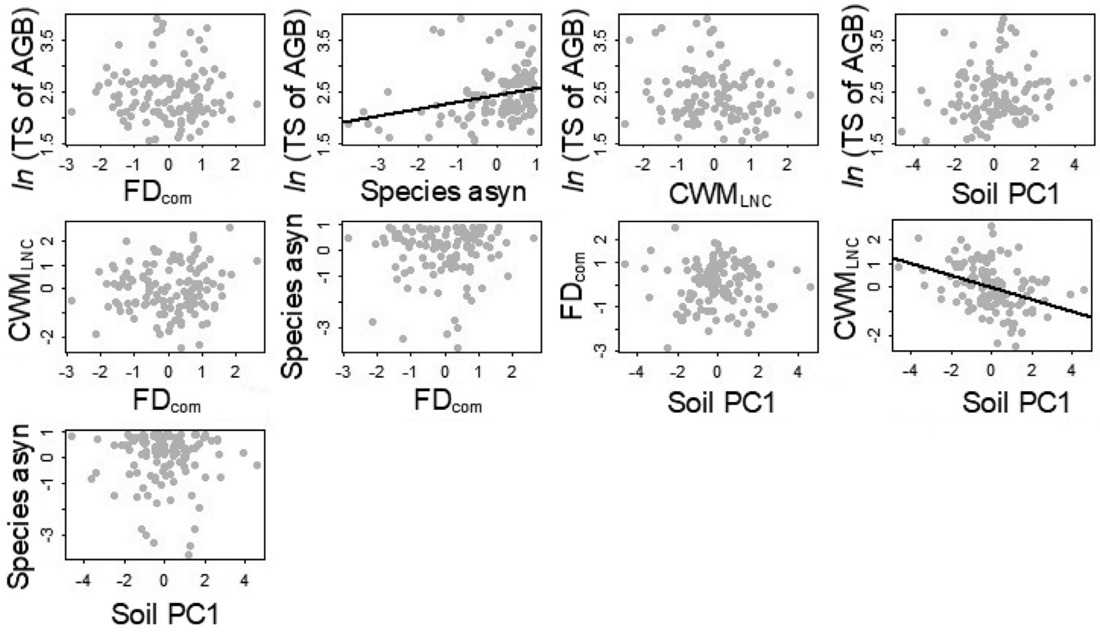

Fig. 3. Bivariate relationships between exogenous and endogenous variables used in the structural equation model of a second -growth forest.

growth forests, while functional trait diversity and composition were only of additional importance for promoting stability in an old-growth forest. Our results suggest that species asynchrony overrides the effects of functional trait diversity and composition in explaining community temporal stability, particularly in a second-growth forest. These results are in partial agreement with the previous findings from virtual herbaceous (Isbell et al., 2009; Tilman et al., 2006) and forest communities (Jucker et al., 2014; Morin et al., 2014).

According to the theory (Loreau and de Mazancourt, 2013), species asynchronous responses to changing environmental conditions as a result of temporal niche differentiation among species, which could be induced by external environmental forcing, endogenous species interactions or a combination of both (Gonzalez and Loreau, 2009). In natural forests, biomass dynamics are frequently driven by small disturbances like the death of large individuals, leading to canopy gap and greater variations in light availability (Feeley et al., 2007). If a stand with coexisting species having greater asynchrony, then it is expected that new canopy gaps will be filled more quickly than in stands with lower species asynchrony, resulting in an optimisation of canopy occupancy (Morin et al., 2014). Consequently, our results highlight the

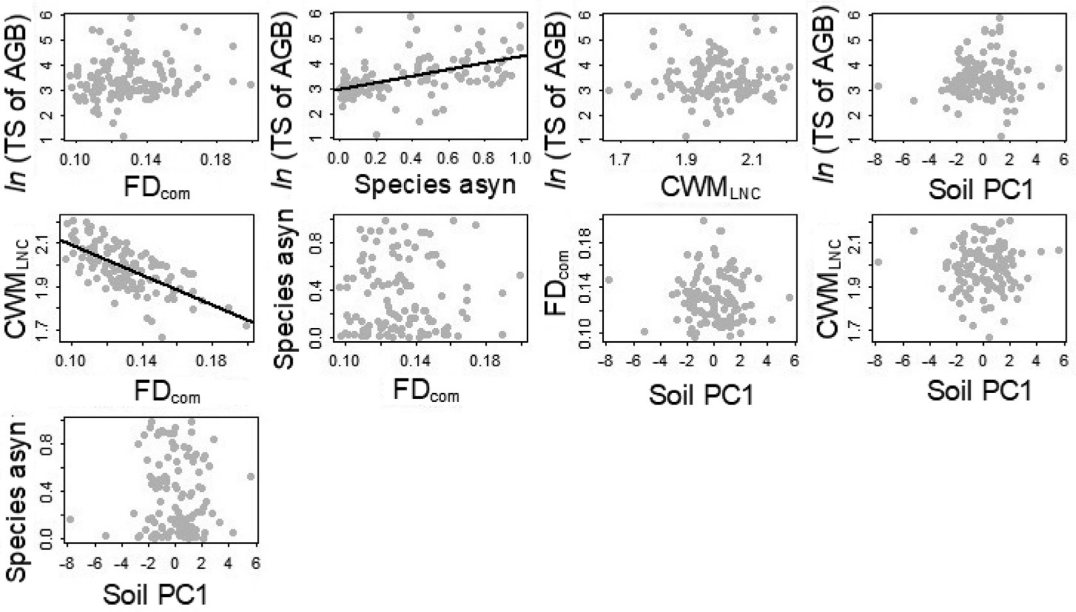

Fig. 4. Bivariate relationships between exogenous and endogenous variables used in the structural equation model of an old-growth forest.

key role of species asynchrony in stabilizing the temporal stability of aboveground biomass in natural temperate forests, in accordance with the previous empirical studies from European forests (del Río et al., 2017; Jucker et al., 2014). This mechanism might have happened due to the fact that communities composing of different shade tolerance strategies might have greater ability to quickly respond to local small-scale disturbances and sustaining the stability of biomass (del Río et al., 2017; Pretzsch, 2014).

This study also shows that the direct effect of species asynchrony on the community temporal stability of aboveground biomass becomes stronger in an old-growth forest compared to second-growth forest, supporting the general notion that niche differentiation and facilitation due to tree size variations increase over time (Ali et al., 2016; Reich et al., 2012). In forest ecosystems, light availability but not soil nutrient is the key limiting abiotic factor for plant growth (Pretzsch, 2014), which could be partly confirmed by the negligible effects of soil nutrients on community temporal stability in the studied forests. The ability to optimize light capture seems to contribute to the asynchrony of species dynamics via a diversity of tree shade tolerances (Ali et al., 2016; Danescu et al., 2016; Valladares and Niinemets, 2008). Second-growth forests, dominated by pioneer or shade-intolerant trees, usually grow fast and have a quick response to environmental fluctuations, leading to unstable ecosystem properties if they face deteriorating environment since their dynamics largely depend on disturbances (Bazzaz, 1979). In this study, *Betula platyphylla*, a pioneer and fast-growing tree species, was the sole dominant species at the early forest successional stage (Hao et al., 2008). At this stage, trees experience strong environment filtering and hence the selection of specific functional traits is important (van der Sande et al., 2016), as also indicated in our SEM result (i.e. the significant soil nutrients → $\mathrm{CWM_{LNC}}$ path in Fig. 1a). As forest developing, long-living and slow-growing trees, such as *Tilia amurensis* and *Fraxinus mandschurica* in this study, tended to be advantageous in unfavourable periods owing to resources maintained from the previous more favourable periods (Reich, 2014; Wright et al., 2004). These species will become the local survivors and regulate community stability (i.e. the positive $\mathrm{CWM_{LNC}}$ → temporal stability path in Fig. 1b), underlining the importance of mass ratio effect in temperate forests (Fotis et al., 2017). By building complex vertical forest structure, old-growth forests with various light foraging strategies species enable shade-tolerant trees to maintain longer crowns with denser foliage (Valladares and Niinemets, 2008), as well as allow understory trees to capture and use more light and hence enhance high stand-level biomass than homogeneity forests (Parker, 1997). Consequently, a stronger asynchrony in species' respond to changes in the light regime lead forest stands to respond quickly to small canopy gaps and to have larger and more stable biomass accumulation rates, which results in greater temporal stability in old-growth forests (Morin et al., 2014).

Interestingly, but not surprisingly, this study shows the weak or nonsignificant relationships of functional trait diversity and composition with community temporal stability in second-growth forest. This result supports the findings of previous studies where they found a non-significant or negative diversity-stability relationship in natural forests (del Río et al., 2017; Sasaki and Lauenroth, 2011). One possible reason for such type of relationship might be the presence of higher functional redundancy species which may undervalue the biodiversity effect on ecosystem functioning (Loreau et al., 2001). Under this reason, it is also clear that studied second-growth forest has higher species richness with lower functional trait diversity relating to plant maximum height, wood density and leaf phosphorus content compared to an old-growth forest (Yuan et al., 2018). Another possible reason is that species or functional trait diversity is not a major driver of forest functioning (Lohbeck et al., 2015; Yuan et al., 2018) and hence also for community temporal stability in highly stochastic systems (Sasaki and Lauenroth, 2011), where the death of early successional species during stand thinning may overwhelm growth effects (Lasky et al., 2014; Poorter et al., 2017).

Lastly, it is worth to note that we studied the temporal stability of aboveground biomass rather than productivity over time due to limited forest inventories data. More specifically, calculating the community temporal stability of forest productivity (measured in $\mathrm{Mg\,ha^{-1}\,yr^{-1}}$) rather than aboveground biomass (measured in $\mathrm{Mg\,ha^{-1}}$) requires at least four repeated forest inventories data. However, aboveground biomass (used in this study) is also frequently used as an important forest function regarding biodiversity – forest functioning studies (Conti et al., 2013), and hence an ideal proxy for biomass productivity in natural forests (Lohbeck et al., 2015; Yuan et al., 2018). It is also clear that aboveground biomass and productivity are positively related at all spatial scales in natural forests (Chisholm et al., 2013). Yet, further studies may need to elucidate and confirm these complex path relationships using the community temporal stability of forest productivity. Nevertheless, this study advances our understanding regarding diversity-biomass relationships over time, thereby contributing to the understanding of soil fertility, niche complementarity and mass ratio effects on community temporal stability of aboveground biomass in natural forests over succession.

5. Conclusions

This study provides one of the first comprehensive analyses of how soil nutrients, species asynchrony, functional trait diversity and composition interact to shape the community temporal stability of temperate forests. We demonstrate that the 'species asynchrony effect' overrules the effects of functional trait diversity and composition on the community temporal stability of aboveground biomass in second-growth forest, whereas functional trait diversity and composition are of additional important for driving temporal stability of an old-growth temperate forest. We also show that the species asynchrony effect increases with forest developing, indicating that niche differentiation and facilitation increase over time. We argue that the effect of species asynchrony on the community temporal stability of aboveground biomass should be tested for better understanding the underlying ecological mechanisms by which soil nutrients, functional trait diversity and composition drive forest functioning and stability. This study suggests that managing forests with mixtures of both early and late successional species or shade intolerant and tolerant species, not only species diversity, is important for maintaining forest stability in a changing environment.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.105661.

References

Ali, A., Yan, E.-R., Chen, H.Y.H., Chang, X.S., Zhao, Y.-T., Yang, X.-D., Xu, M.-S., 2016. Stand structural diversity rather than species diversity enhances aboveground carbon storage in secondary subtropical forests in Eastern China. Biogeosciences 13, 4627–4635.

Ali, A., Yan, E.-R., Chang, S.X., Cheng, J.-Y., Liu, X.-Y., 2017. Community-weighted mean of leaf traits and divergence of wood traits predict aboveground biomass in secondary subtropical forests. Sci. Total Environ. 574, 654–662.

Ali, A., Lohbeck, M., Yan, E.-R., 2018. Forest strata-dependent functional evenness explains whole-community aboveground biomass through opposing mechanisms. For. Ecol. Manage. 424, 439–447.

Ali, A., Yan, E.-R., 2017. Functional identity of overstorey tree height and understorey conservative traits drive aboveground biomass in a subtropical forest. Ecol. Ind. 83, 158–168.

Barton, K., 2012. MuMIn: multi-model inference. R package version 1.7.11.

Bazzaz, F., 1979. The physiological ecology of plant succession. Annu. Rev. Ecol. Syst. 10, 351–371.

Burnham, K.P., Anderson, D.R., 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociol. Methods Res. 33, 261–304.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. Nature 486, 59–67.

Chen, C., Zhu, J., 1989. Biomass Manual of Main Trees in Northeastern China. China Forestry Press, Beijing.

Chisholm, R.A., Muller-Landau, H.C., Abdul Rahman, K., Bebber, D.P., Bin, Y., Bohlman, S.A., Bourg, N.A., Brinks, J., Bunyavejchewin, S., Butt, N., Cao, H., Cao, M., Cárdenas, D., Chang, L.-W., Chiang, J.-M., Chuyong, G., Condit, R., Dattaraja, H.S., Davies, S., Duque, A., Fletcher, C., Gunatilleke, N., Gunatilleke, S., Hao, Z., Harrison, R.D., Howe, R., Hsieh, C.-F., Hubbell, S.P., Itoh, A., Kenfack, D., Kiratiprayoon, S., Larson, A.J., Lian, J., Lin, D., Liu, H., Lutz, J.A., Ma, K., Malhi, Y., McMahon, S., McShea, W., Meegaskumbura, M., Razman, S. Mohd., Morecroft, M.D., Nytch, C.J., Oliveira, A., Parker, G.G., Pulla, S., Punchi-Manage, R., Romero-Saltos, H., Sang, W., Schurman, J., Su, S.-H., Sukumar, R., Sun, I.F., Suresh, H.S., Tan, S., Thomas, D., Thomas, S., Thompson, J., Valencia, R., Wolf, A., Yap, S., Ye, W., Yuan, Z., Zimmerman, J.K., 2013. Scale-dependent relationships between tree species richness and ecosystem function in forests. J. Ecol. 101, 1214–1224.

Conti, G., Díaz, S., Lavorel, S., 2013. Plant functional diversity and carbon storage – an empirical test in semi-arid forest ecosystems. J. Ecol. 101, 18–28.

Danescu, A., Albrecht, A.T., Bauhus, J., 2016. Structural diversity promotes productivity of mixed, uneven-aged forests in southwestern Germany. Oecologia 182, 319–333.

del Río, M., Pretzsch, H., Ruíz-Peinado, R., Ampoorter, E., Annighöfer, P., Barbeito, I., Bielak, K., Brazaitis, G., Coll, L., Drössler, L., Fabrika, M., Forrester, D.I., Heym, M., Hurt, V., Kurylyak, V., Löf, M., Lombardi, F., Madrickiene, E., Matović, B., Mohren, F., Motta, R., den Ouden, J., Pach, M., Ponette, Q., Schütze, G., Skrzyszewski, J., Sramek, V., Sterba, H., Stojanović, D., Svoboda, M., Zlatanov, T.M., Bravo-Oviedo, A., Hector, A., 2017. Species interactions increase the temporal stability of community productivity in Pinus sylvestris-Fagus sylvatica mixtures across Europe. J. Ecol. 105, 1032–1043.

Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K., Robson, T.M., 2007. Incorporating plant functional diversity effects in ecosystem service assessments. Proc. Natl. Acad. Sci. 104, 20684–20689.

Duffy, J.E., 2009. Why biodiversity is important to the functioning of real-world ecosystems. Front. Ecol. Environ. 7, 437–444.

Feeley, K.J., Davies, S.J., Ashton, P.S., Bunyavejchewin, S., Nur Supardi, M., Kassim, A.R., Tan, S., Chave, J.M., 2007. The role of gap phase processes in the biomass dynamics of tropical forests. Proc. R. Soc. B: Biol. Sci. 274, 2857–2864.

Fotis, A.T., Murphy, S.J., Ricart, R.D., Krishnadas, M., Whitacre, J., Wenzel, J.W., Queenborough, S.A., Comita, L.S., Hector, A., 2017. Above-ground biomass is driven by mass-ratio effects and stand structural attributes in a temperate deciduous forest. J. Ecol.

Garnier, E., Cortez, J., Billes, G., Navas, M.L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., Toussaint, J.P., 2004. Plant functional markers capture ecosystem properties during secondary succession. Ecology 85, 2630–2637.

Gonzalez, A., Loreau, M., 2009. The causes and consequences of compensatory dynamics in ecological communities. Annu. Rev. Ecol. Evol. Syst. 40, 393–414.

Griffin, J.N., O'Gorman, E.J., Emmerson, M.C., Jenkins, S.R., Klein, A.-M., Loreau, M., Symstad, A., 2009. In: Biodiversity and the stability of ecosystem functioning Biodiversity, Ecosystem Functioning, and Human Wellbeing–an Ecological and Economic Perspective, pp. 78–93.

Grime, J., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J. Ecol. 86, 902–910.

Grman, E., Lau, J.A., Schoolmaster, D.R., Gross, K.L., 2010. Mechanisms contributing to stability in ecosystem function depend on the environmental context. Ecol. Lett. 13, 1400–1410.

Gross, K., Cardinale, B.J., Fox, J.W., Gonzalez, A., Loreau, M., Wayne Polley, H., Reich, P.B., Van Ruijven, J., 2013. Species richness and the temporal stability of biomass production: a new analysis of recent biodiversity experiments. Am. Nat. 183, 1–12.

Grossman, J.J., Cavender-Bares, J., Hobbie, S.E., Reich, P.B., Montgomery, R.A., 2017. Species richness and traits predict overyielding in stem growth in an early-successional tree diversity experiment. Ecology.

Hao, Z.Q., Zhang, J., Song, B., Ye, J., Li, B.H., 2007. Vertical structure and spatial associations of dominant tree species in an old-growth temperate forest. For. Ecol. Manage. 252, 1–11.

Hao, Z., Zhang, J., Li, B., Ye, J., Wang, X., Yao, X., 2008. Natural secondary poplar-birch forest in Changbai Mountain: species composition and community structure. J. Plant. Ecol. 32, 251–261.

Hautier, Y., Seabloom, E.W., Borer, E.T., Adler, P.B., Harpole, W.S., Hillebrand, H., Lind, E.M., MacDougall, A.S., Stevens, C.J., Bakker, J.D., 2014. Eutrophication weakens stabilizing effects of diversity in natural grasslands. Nature 508, 521–525.

Isbell, F.I., Polley, H.W., Wilsey, B.J., 2009. Biodiversity, productivity and the temporal stability of productivity: patterns and processes. Ecol. Lett. 12, 443–451.

John, R., Dalling, J.W., Harms, K.E., Yavitt, J.B., Stallard, R.F., Mirabello, M., Hubbell, S.P., Valencia, R., Navarrete, H., Vallejo, M., 2007. Soil nutrients influence spatial distributions of tropical tree species. Proc. Natl. Acad. Sci. 104, 864–869.

Jucker, T., Bouriaud, O., Avacaritei, D., Coomes, D.A., 2014. Stabilizing effects of diversity on aboveground wood production in forest ecosystems: linking patterns and processes. Ecol. Lett. 17, 1560–1569.

Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91, 299–305.

Lasky, J.R., Uriarte, M., Boukili, V.K., Erickson, D.L., John Kress, W., Chazdon, R.L., 2014. The relationship between tree biodiversity and biomass dynamics changes with tropical forest succession. Ecol. Lett. 17, 1158–1167.

Lehman, C.L., Tilman, D., 2000. Biodiversity, stability, and productivity in competitive communities. Am. Nat. 156, 534–552.

Lohbeck, M., Poorter, L., Martinez-Ramos, M., Bongers, F., 2015. Biomass is the main driver of changes in ecosystem process rates during tropical forest succession. Ecology 96, 1242–1252.

Loreau, M., de Mazancourt, C., 2008. Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. Am. Nat. 172, E48–66.

Loreau, M., de Mazancourt, C., 2013. Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. Ecol. Lett. 16, 106–115.

Loreau, M., Hector, A., 2001. Partitioning selection and complementarity in biodiversity experiments. Nature 412, 72–76.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D., Wardle, D.A., 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294, 804–808.

MacArthur, R., 1955. Fluctuations of animal populations and a measure of community stability. Ecology 36, 533–536.

Morin, X., Fahse, L., de Mazancourt, C., Scherer-Lorenzen, M., Bugmann, H., 2014. Temporal stability in forest productivity increases with tree diversity due to asynchrony in species dynamics. Ecol. Lett. 17, 1526–1535.

Nepstad, D.C., de Carvalho, C.R., Davidson, E.A., Jipp, P.H., Lefebvre, P.A., Negreiros, G.H., da Silva, E.D., Stone, T.A., Trumbore, S.E., Vieira, S., 1994. The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. Nature 372, 666.

Paquette, A., Messier, C., 2011. The effect of biodiversity on tree productivity: from temperate to boreal forests. Glob. Ecol. Biogeogr. 20, 170–180.

Parker, G.G., 1997. Canopy Structure and Light Environment of an Old-growth Douglas-fir/Western Hemlock Forest.

Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. Ecol. Lett. 9, 741–758.

Poorter, L., van der Sande, M.T., Arets, E.J.M.M., Ascarrunz, N., Enquist, B., Finegan, B., Licona, J.C., Martínez-Ramos, M., Mazzei, L., Meave, J.A., Muñoz, R., Nytch, C.J., de Oliveira, A.A., Pérez-García, E.A., Prado-Junior, J., Rodríguez-Velázques, J., Ruschel, A.R., Salgado-Negret, B., Schiavini, I., Swenson, N.G., Tenorio, E.A., Thompson, J., Toledo, M., Uriarte, M., Hout, P.v.d., Zimmerman, J.K., Peña-Claros, M., 2017. Biodiversity and climate determine the functioning of Neotropical forests. Glob. Ecol. Biogeogr. 26, 1423–1434.

Prado-Junior, J.A., Schiavini, I., Vale, V.S., Arantes, C.S., Sande, M.T., Lohbeck, M., Poorter, L., 2016. Conservative species drive biomass productivity in tropical dry forests. J. Ecol. 104, 817–827.

Pretzsch, H., 2014. Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. For. Ecol. Manage. 327, 251–264.

Quesada, C.A., Phillips, O.L., Schwarz, M., Czimczik, C.I., Baker, T.R., Patiño, S., Fyllas, N.M., Hodnett, M.G., Herrera, R., Almeida, S., Alvarez DÃ¡vila, E., Arneth, A., Arroyo, L., Chao, K.J., Dezzeo, N., Erwin, T., di Fiore, A., Higuchi, N., Honorio Coronado, E., Jimenez, E.M., Killeen, T., Lezama, A.T., Lloyd, G., López-González, G., Luizão, F.J., Malhi, Y., Monteagudo, A., Neill, D.A., Núñez Vargas, P., Paiva, R., Peacock, J., Peñuela, M.C., Peña Cruz, A., Pitman, N., Priante Filho, N., Prieto, A., Ramírez, H., Rudas, A., Salomão, R., Santos, A.J.B., Schmerler, J., Silva, N., Silveira, M., Vásquez, R., Vieira, I., Terborgh, J., Lloyd, J., 2012. Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. Biogeosciences 9, 2203–2246.

R Core Team, 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Ratcliffe, S., Wirth, C., Jucker, T., der Plas, F., Scherer-Lorenzen, M., Verheyen, K., Allan, E., Benavides, R., Bruelheide, H., Ohse, B., Paquette, A., Ampoorter, E., Bastias, C.C., Bauhus, J., Bonal, D., Bouriaud, O., Bussotti, F., Carnol, M., Castagneyrol, B., Chećko, E., Dawud, S.M., Wandeler, H.D., Domisch, T., Finér, L., Fischer, M., Fotelli, M., Gessler, A., Granier, A., Grossiord, C., Guyot, V., Haase, J., Hättenschwiler, S., Jactel, H., Jaroszewicz, B., Joly, F.-X., Kambach, S., Kolb, S., Koricheva, J., Liebersgesell, M., Milligan, H., Müller, S., Muys, B., Nguyen, D., Nock, C., Pollastrini, M., Purschke, O., Radoglou, K., Raulund-Rasmussen, K., Roger, F., Ruiz-Benito, P., Seidl, R., Selvi, F., Seiferling, I., Stenlid, J., Valladares, F., Vesterdal, L., Baeten, L., 2017. Biodiversity and ecosystem functioning relations in European forests depend on environmental context. Ecol. Lett. 20, 1414–1426.

Reich, P.B., 2014. The world-wide ‘fast–slow’plant economics spectrum: a traits manifesto. J. Ecol. 102, 275–301.

Reich, P.B., Tilman, D., Isbell, F., Mueller, K., Hobbie, S.E., Flynn, D.F., Eisenhauer, N., 2012. Impacts of biodiversity loss escalate through time as redundancy fades. Science 336, 589–592.

Ribeiro Jr, P.J., Diggle, P.J., 2001. geoR: a package for geostatistical analysis. R News 1, 14–18.

Rosseel, Y., 2012. lavaan: An R Package for Structural Equation Modeling. J. Stat. Softw. 48, 1–36.

Russo, S.E., Davies, S.J., King, D.A., Tan, S., 2005. Soil-related performance variation and distributions of tree species in a Bornean rain forest. J. Ecol. 93, 879–889.

Sasaki, T., Lauenroth, W.K., 2011. Dominant species, rather than diversity, regulates temporal stability of plant communities. Oecologia 166, 761–768.

Stephenson, N.L., van Mantgem, P.J., 2005. Forest turnover rates follow global and regional patterns of productivity. Ecol. Lett. 8, 524–531.

Stone, R., 2006. A threatened nature reserve breaks down Asian borders. Science 313, 1379–1380.

Tilman, D., 1997. The influence of functional diversity and composition on ecosystem processes. Science 277, 1300–1302.

Tilman, D., Reich, P.B., Knops, M.H., 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. Nature 441 (7093), 629–632. https://doi.org/10.1038/nature04742.

Valladares, F., Niinemets, Ü., 2008. Shade tolerance, a key plant feature of complex nature and consequences. Ann. Rev. Ecol., Evol., Syst. 39, 237–257.

van der Sande, M.T., Zuidema, P.A., Sterck, F., 2015. Explaining biomass growth of tropical canopy trees: the importance of sapwood. Oecologia 177, 1145–1155.

van der Sande, M.T., Arets, E.J., Peña-Claros, M., de Avila, A.L., Roopsind, A., Mazzei, L., Ascarrunz, N., Finegan, B., Alarcón, A., Cáceres-Siani, Y., 2016. Old-growth Neotropical forests are shifting in species and trait composition. Ecol. Monogr. 86, 228–243.

van der Sande, M.T., Peña-Claros, M., Ascarrunz, N., Arets, E.J.M.M., Licona, J.C., Toledo, M., Poorter, L., Hector, A., 2017. Abiotic and biotic drivers of biomass change in a Neotropical forest. J. Ecol. 105, 1223–1234.

Wang, C., 2006. Biomass allometric equations for 10 co-occurring tree species in Chinese temperate forests. For. Ecol. Manage. 222, 9–16.

Wang, S., Loreau, M., 2016. Biodiversity and ecosystem stability across scales in metacommunities. Ecol. Lett. 19, 510–518.

Wang, Z., Xu, X., Li, X., 1980. The main forest types and their features of community structure in northern slope of Changbai Mountain. Res. J. For. 1, 25–42.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., 2004. The worldwide leaf economics spectrum. Nature 428, 821.

Xu, W., He, X., Chen, W., Liu, C., 2004. Characteristics and succession rules of vegetation types in Changbai Mountain. Chin. J. Ecol. 23, 162–174.

Xu, Z., Ren, H., Li, M.-H., van Ruijven, J., Han, X., Wan, S., Li, H., Yu, Q., Jiang, Y., Jiang, L., MacDougall, A., 2015. Environmental changes drive the temporal stability of semi-arid natural grasslands through altering species asynchrony. J. Ecol. 103, 1308–1316.

Yan, Y., Zhang, C., Zhao, X., 2012. Species-abundance distribution patterns at different successional stages of conifer and broad-leaved mixed forest communities in Changbai Mountains, China. Chin. J. Plant Ecol. 36, 923–934.

Yuan, Z., Gazol, A., Wang, X., Lin, F., Ye, J., Bai, X., Li, B., Hao, Z., 2011. Scale specific determinants of tree diversity in an old growth temperate forest in China. Basic Appl. Ecol. 12, 488–495.

Yuan, Z., Wang, S., Gazol, A., Mellard, J., Lin, F., Ye, J., Hao, Z., Wang, X., Loreau, M., 2016. Multiple metrics of diversity have different effects on temperate forest functioning over succession. Oecologia 182, 1175–1185.

Yuan, Z., Ali, A., Wang, S., Gazol, A., Freckleton, R., Wang, X., Lin, F., Ye, J., Zhou, L., Hao, Z., Loreau, M., 2018. Abiotic and biotic determinants of coarse woody productivity in temperate mixed forests. Sci. Total Environ. 630, 422–431.

Zuur, A., Ieno, E., Walker, N., Saveliev, A., Smith, G., 2009. Mixed Effects Models and Extensions in Ecology with R. Spring Science and Business Media, New York, NY.