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

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ARTICLE INFO
Keywords: Biodiversity Forest stability Mass ratio effect Soil nutrients Species asynchrony Temporal niche complementarity

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
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 (Lobbeck 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 (Grifﬁn 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 (Diaz 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.,
by Tilman et al. (2006). The detrended community temporal stability value of the linear regression against the inventory years as suggested the subplots showed a significant 2005, 2010 and 2015 for BKF plot). Approximately one-quarter of three-time repeated inventories data (2004, 2009 and 2014 for BKF plot). The stand density of the aboveground biomass of the species level following a standard deviation of the aboveground biomass of the mean and the standard deviation of the aboveground biomass of the second-growth forest, whereas a total of 20,101 individuals belonging to 56 species, 30 genera and 17 families in a 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 (T₁, 2009 and 2010; T₂, 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 = μ/σ (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 (TSd) of aboveground biomass was expressed as: TSd = μ/σd, where σd 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):

$$1 - \varphi x = 1 - \sigma_x^2 \left( \sum_{i=1}^{S} \sigma_i^2 \right)^{-1}$$

where $\varphi_x$ is the species synchrony, $\sigma^2_x$ is the temporal variance of aboveground biomass in the given subplot, and $\sigma_i^2$ is the standard deviation of aboveground biomass of the ith 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 phosphorous 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 (FDcom) was quantified using a multi-trait functional dispersion index (LaLiberté and Legendre, 2010), which measures the mean distance in multi-dimensional 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_SLAA) 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 (K₂Cr₂O₇-H₂SO₄) oxidation method. Total N was measured following the Kjeldahl method. Total P was obtained by molybdate colorimetry, after digestion in H₂SO₄-HClO₄. Total K was

had the highest relative importance value (Table S5 in Appendix A). Presentative variable for functional trait composition in SEM because it caused the structure of the SEM is significant. Therefore, we used all subsets of multiple regressions to pre-select the important variables for the SEM (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 used evaluating the dredge function and the model.sel 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 AICc values compared to spherical autocorrelation models (Table S7 in Appendix A).

### 3. Results

The SEM for a second-growth forest showed that the community temporal stability of aboveground biomass was directly influenced by species asynchrony ($\beta = 0.29$, $P < 0.01$), 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
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. 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 community temporal stability in a second-growth forest. Bivariate relationships for supporting the second-growth forest SEM results are presented in Fig. 3.

For an old-growth forest (Fig. 1b), species asynchrony had the strongest direct positive effect on community temporal stability ($\beta = 0.50$, $P < 0.01$), followed by functional trait diversity ($\beta = 0.30$, $P < 0.01$) and composition ($\beta = 0.24$, $P = 0.02$). Functional trait diversity had an indirect negative effect via trait composition ($\beta = -0.16$, $P = 0.02$), but resulted in a positive total effect on the community temporal stability of aboveground biomass ($\beta = 0.16$, $P = 0.08$) (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-
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
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 composed 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 $\rightarrow$ CWM$_{INC}$ path in Fig. 1a). As forest developing, long-living and slow-growing trees, such as Tilia amurensis and Fraxinus mandshurica 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 CWM$_{INC} \rightarrow$ temporal stability path in Fig. 1b), underlining the importance of mass ratio effect in temperate forests (Potis 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 nonsignificant 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 Mg ha$^{-1}$ yr$^{-1}$) rather than aboveground biomass (measured in 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 forests, whereas functional trait diversity and composition are of additional importance 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.

Acknowledgements

This study was funded by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB13000000), National Natural Science Foundation of China (31730015, 41671050, 31570432), Youth Innovation Promotion Association CAS (2017241), and LiaoNing Revitalization Talents Program (LYCX1807093). This work is supported by CFERN & BEIJING TECHNO SOLUTIONS Award Funds on Excellent academic achievements. AA is supported by the Metasequoia Faculty Research Startup Funding at Nanjing Forestry University (Grant No. 163010230). ML is supported by the TULIP Laboratory of Excellence (ANR-10-LABX-41) and by the BIOSTASES Advanced Grant, funded by the European Research Council under the European Union’s Horizon 2020 research and innovation programme (Grant No. 666971).

Appendix A. Supplementary data

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

References


