

# Species dominance rather than species asynchrony determines the temporal stability of productivity in four subtropical forests along 30 years of restoration



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## ABSTRACT

Understanding biodiversity and its relationship with ecosystem functioning along forest succession is extremely important to assessing dynamics of community stability and ecosystem integrity. Previous studies have revealed that increases in species richness, phylogenetic diversity (PD), species asynchrony and dominance can stabilize the temporal stability of community biomass in grasslands. However, how these determinants influence the stabilizing effect of biodiversity on forest productivity remains poorly understood. We analyzed the relationships between woody plant diversity and productivity stability along 30 years of restoration (1985–2015) in four types of subtropical forest: a mixed *Eucalyptus* plantation (EE), an *Acacia mangium* monoculture (AM), a mixed native species plantation (NS), and a mixed coniferous plantation (MC). Our results showed that community stability in three mixed species plantations (EE, NS, and MC) rather than the AM monoculture augmented remarkably as restoration proceeded. Both species richness and phylogenetic diversity significantly stabilized community productivity in the mixed species plantations instead of the monoculture during the 30-year restoration period. Species asynchrony was not a significant factor contributing to the forest productivity stability. Instead, community stability was mainly driven by that of the dominant tree species, and to a lesser extent, by the species richness. We demonstrated the more important role of species dominance in maintaining the temporal stability of forest productivity, which differs from that (species asynchrony) for grassland communities.

## 1. Introduction

Due to the increasing human disturbance and dramatic climate change, natural ecosystems have been suffering from severe destruction, including the reduction of biodiversity, degradation of ecosystem function and resultant ecosystem service loss (Jackson and Hobbs, 2009; Rey Benayas et al., 2009; Allan et al., 2015). Ecological restoration activities carried out in degraded regions at different spatial scales can improve ecosystem services such as carbon sequestration and biodiversity conservation (Stanturf et al., 2014; Deng et al., 2017). However, during the course of restoration, ecological communities are prone to environmental fluctuations, which may alter the abundance and distribution of species or even lead to local extinctions. Hence, the question of how species diversity influences community stability has

intrigued ecologists for several decades. An important finding is that diversity not only promotes ecosystem function but also serves to stabilize them as succession proceeds (Aussenac et al., 2017; Isbell et al., 2009; Hautier et al., 2014). Most previous studies on grasslands have revealed that species richness, phylogenetic diversity, species asynchrony, stability of dominant plant species and environmental changes impose significant impacts on the temporal stability of community productivity (Aussenac et al., 2019; Hillebrand et al., 2008; Xu et al., 2015; Duffy et al., 2017; Huang et al., 2018). However, few studies have been devoted to the understanding of how these determinants actually contribute to community stability in forests. Forest community productivity is both an important indicator of ecosystem functioning and a valuable ecosystem service (Gamfeldt et al., 2013). Identifying how diversity contributes to stabilizing community productivity during

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forest restoration could help to optimize future forest management and conservation strategies.

The temporal stability of community productivity defined as the ratio between mean community productivity ( $\mu$ ) and its variation in time ( $\sigma$ , SD of community productivity). The temporal stability of community productivity reflects how much community biomass fluctuates between years. Considering the fact that the stability of ecosystems is affected by different abiotic and biotic factors, there is still insufficient evidence to unravel the underlying mechanisms behind the diversity-stability relationship, especially in forests. There is a widespread viewpoint that ecological restoration will enhance biodiversity in the degraded ecosystems (Rey Benayas et al., 2009). Some large-scale experiments linking biodiversity with ecosystem functioning have also revealed that biodiversity had a significant effect on ecosystem productivity (Duffy et al., 2017; Huang et al., 2018). Diversity has two components, species richness and species evenness, which may augment the temporal stability of community productivity by increasing the mean of community productivity or by reducing summed variances of community productivity (Tilman, 1996). Traditionally, species richness has been served as the measure of diversity (Chiarucci et al., 2011; Gotelli and Colwell, 2001), and numerous studies have shown that more diverse communities tend to exhibit higher temporal stability (Campbell et al., 2011; Gross et al., 2014). Previous study has tested the effect of species richness (richness effect) on the community productivity by evaluating the variability in biomass production with a given species richness (McGrady-Steed et al. 1997). Specifically, “insurance hypothesis” indicated that species richness should ‘insure’ communities against reduction in their functioning (e.g. biomass production) because more species will provide a higher guarantee on maintaining functioning (Yachi & Loreau, 1999). In addition, to identify and disentangle different mechanisms behind diversity-stability relationship, Loreau & de Mazancourt (2013) proposed three main mechanisms associated with interspecific differences that may promote the stabilizing effect of diversity: (1) asynchronous dynamics across species to fluctuating environments, (2) species respond to disturbance with different speeds, (3) decrease in the intensity of species competition. However, to better understand the role of evolutionary history in forest successional process and its relationship with ecosystem service, ecologists have increasingly focused on phylogenetic diversity, which provided us insights into understanding the mechanisms regulating community assembly during the process of forest restoration (Gross et al., 2014). A few studies have examined the relationship between phylogenetic diversity and ecosystem function during succession in tropical and subtropical forests (Lasky et al., 2014; Ouyang et al., 2016), and the results have demonstrated that the relationships between biodiversity and ecosystem functioning were dynamic across succession. Moreover, this relationship can be strongly affected by abiotic and biotic factors as well as management practices.

Species asynchrony is the asynchronous dynamics across species to fluctuating environmental conditions, which is the consequence of niche differentiation (Loreau and de Mazancourt, 2008). Species asynchrony has been regarded as an important form of temporal complementarity among species and has been recognized as a key driver of stability in grasslands (Hector et al., 2010; Hautier et al., 2014; Xu et al., 2015). Recently, some studies also suggested that the asynchrony of tree species’ response to fluctuating environmental conditions drive the stabilizing effect of diversity. And the intraspecific variability of these responses regulated the stabilizing effect of species diversity (Aussenac et al., 2017; Aussenac et al., 2019). However, forests are quite different from grasslands, considering that the shifts in community composition occur much slowly in forests. The slower dynamism of forests is likely to influence the temporal stability of productivity in the larger scale.

Since the effects of biodiversity loss on ecosystem function have gained broad attention, important tendencies for consequences of altered species dominance on ecosystem function emerged. The dynamics

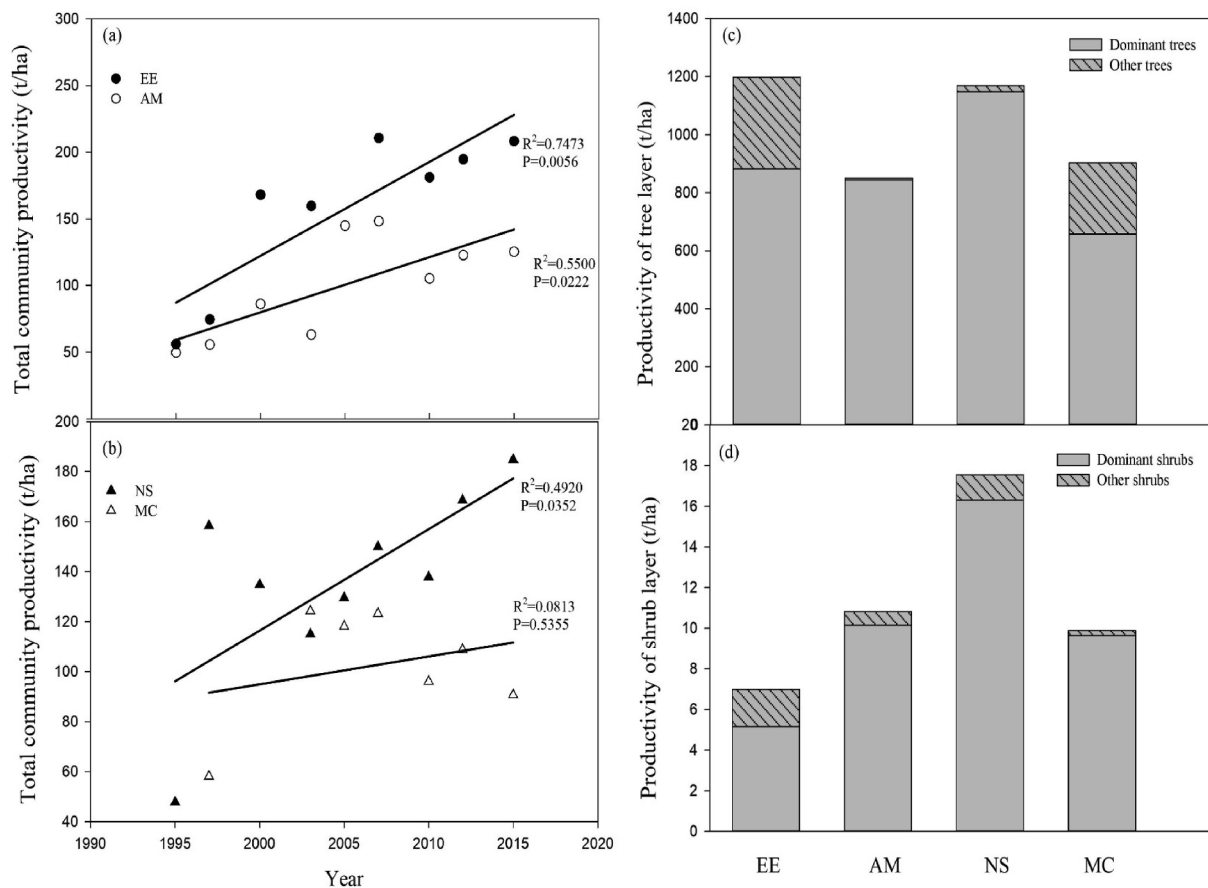
of a biotic community can not only be indicated by the changes in species richness but also the changes in species dominance or evenness. More importantly, evenness often responds more rapidly to human disturbance or dramatic climate change than the number of species (Smith and Knapp, 2003). Several studies also have revealed that dominant species could maintain ecosystem functioning with non-random species reduction (Smith and Knapp, 2003; Hillebrand et al., 2008; Yang et al., 2011). Previous review suggested that dominance influences species invasibility, ecosystem processes, and community stability (Hillebrand et al., 2008). When dominance is high (lower richness), most species contribute little to community biomass and the establishment or reduction of rare species has little effect on sum of variances (portfolio effect), therefore the summed covariance between species is largely determined by covariance between dominant species. Polley et al (2007) found that dominant species constrain the effect of species diversity on temporal stability of biomass production. Besides, one important finding from an experiment is that, diversity-stability mechanisms are altered in invaded ecosystems compared with native ones they replaced. In native ecosystems, stability was related to species asynchrony, whereas in the invaded ecosystems, stability was determined by the dominance of species (Wilsey et al., 2014).

In this study, to explore the diversity-stability relationship and its underlying mechanisms in restored forest ecosystem, we determined the effects of diversity (including species richness and phylogenetic diversity) on temporal stability of productivity across four plantation forests over 30 years of restoration. The four forests included a mixed Eucalyptus plantation (EE), an *Acacia mangium* monoculture (AM), a mixed native species plantation (NS), and a mixed coniferous plantation (MC). They are typical and representative of plantation forests in southern China (Duan et al., 2010). We expected that the stability would enhance during the course of the forest restoration, however the underlying mechanisms determining the stability would differ among the forest ecosystems. Specifically, we hypothesized that: (1) there are much stronger correlations between diversity and stability in mixed species plantation than monoculture, (2) the stability of dominant species will be the primary driver of community stability because of the greater contribution of dominant species to community productivity, (3) species asynchrony is not an important driver of stability in forests, due to their slower dynamism.

## 2. Materials and methods

### 2.1. Study site

The study area was situated in the Heshan National Field Research Station of Forest Ecosystem, Chinese Academy of Science (112°50'E, 22°34'N), Heshan City, Guangdong, South China. This area is characterized by a typical subtropical monsoon climate with a mean annual temperature of 21.7 °C and a mean annual rainfall of 1700 mm (Wang et al., 2010). Most rainfall occurs between May and September. The soil in this region is an Acrisol. Previously, the degradation of forests led to severe soil and water erosions. In 1984, to restore the degraded forest ecosystems in this region, four experimental plantations of various tree species were established at the station. The EE site (1.79 ha) was a mixed *Eucalyptus* plantation and the main established species were *Eucalyptus exserta*, *Eucalyptus citriodora*, and *Eucalyptus camaldulensis*. The AM site (4.58 ha) was a leguminous *Acacia mangium* monoculture. The MC site (3.17 ha) was a mixed-conifer plantation and the main established species were *Cunninghamia lanceolata* and *Pinus massoniana*. The NS site (2.68 ha) was a mixed-native species plantation and the main established species were *Schima superba* and *Schima wallichii*. The plantations were established with 1-year-old saplings spaced 2.5 m × 2.5 m apart. All four plantations had been left to grow naturally without anthropogenic disturbance.



**Fig. 1.** Temporal variation trend of total community productivity (a-b) and productivity of dominant and non-dominant species (c-d) in the four subtropical plantation forests over 30 years of restoration. In the left panel (a-b), solid and open dots represent the mixed *Eucalyptus* plantation (EE) and *Acacia mangium* monoculture (AM), respectively; solid and open triangles represent the mixed native species plantation (NS) and mixed coniferous plantation (MC), respectively. In the right panel (c-d), blank bars represent dominant tree or shrub species, while black bars represent non-dominant tree or shrub species.

## 2.2. Inventory of plant biomass

Community inventories have been carried out 9 times every 2–3 years since 1995. From 1995 to 2000, sixteen 5 m × 5 m plots were randomly established in each plantation and inventoried, after which the sixteen plots were combined and enlarged to 9 plots of 10 m × 10 m due to the gradually growth of the trees (a list of species is provided in Table A1). To assess the relative importance of overstory plants and understory plants in determining the community-level diversity-stability relationship, individuals were divided into tree layer (height > 3 m), shrub layer (all other woody plants) and herbaceous layer at each inventory. We measured the height of each individual, tree diameter at breast height (DBH), and the basal diameter of all shrubs, and all individuals with a DBH > 1 cm were recorded. The allometric equations based on the DBH and height were applied to calculate biomass for trees and shrubs in each plantation (Chen et al., 2015). The equations and summary statistics are provided in Table A2.

## 2.3. Community phylogenetic tree

We estimated phylogenetic relationships of all recorded species of each plantation since the beginning of monitoring. We used a recently published plant phylogeny (Yu et al., 2019), which (Fig. A1) was derived from DNA sequencing data, including chloroplast (rbcL, matK, psbA-trnH) and nuclear (ITS) regions. All genetic sequences were collected from NCBI GenBank (Benson et al., 2008) and are listed in Table A3. We aligned all sequences using Clustal X2.1 (Larkin et al., 2007) and edited gene fragments in Geneious 7.1.4 (Kearse et al., 2012). We

defined *Amborella trichopoda* as the outgroup species for each phylogeny as it was believed to be representative of early divergence in plant evolution. We estimated a maximum likelihood phylogeny using RAxML software (Stamatakis, 2006), along with rapid bootstrap analysis and search for the best-scoring tree using 1000 runs.

## 2.4. Community stability

We defined the community temporal stability as  $\mu/\sigma$  (Lehman and Tilman, 2000), where  $\mu$  and  $\sigma$  represent the inter-annual mean and standard deviation of community productivity for every sampling year, respectively. To determine the role of dominant species (trees and shrubs) (Table A4) for community stability, we selected the species based on its relative abundance and biomass, and calculated their temporal stability in the same way.

## 2.5. Species asynchrony

Species asynchrony was quantified as  $1 - \frac{\sigma^2}{(\sum_1^N \sigma_i^2)}$  (Loreau and Mazancourt, 2008), where  $\sigma^2$  is the inter-annual variance of community productivity and  $\sigma_i$  is the inter-annual standard deviation of productivity of species  $i$  in a community with  $N$  species. Species asynchrony reflects that the asynchronous dynamics across species to environmental fluctuation or disturbances.

## 2.6. Statistical analysis

We defined species richness (SR) as the total number of species

recorded in plots at each inventory. To estimate the evolutionary relatedness among species, we used phylogenetic diversity (PD), which is defined as the total phylogenetic distance among species. The related analysis was conducted in R package “picante” (Kembel et al., 2010). Ordinary least squares (OLS) regression analysis was used to examine the relationships of time with community productivity, community stability, community diversity and species asynchrony. Repeated measures ANOVA was used to test differences in productivity, species richness, phylogenetic diversity, community stability and species asynchrony among four forests in SPSS18.0 (SPSS Inc., Chicago, IL, USA).

Drawing upon previous literatures, we developed a multivariate hypothesis about the drivers of community stability in a conceptual model (Fig. A2). Structural equation modeling (SEM) (Wilsey et al., 2014) was employed to estimate the direct and indirect effects species richness, phylogenetic diversity and dominant species stability through species asynchrony on community stability. Adequacy of the model was determined using a Chi-squared test, the root-square-mean errors of approximation (RMSEA), and Akaike Information Criterion (AIC) values. Adequate model fits were indicated by a nonsignificant chi-squared test ( $P > 0.05$ ), low RMSEA ( $< 0.08$ ) and low AIC. SEM analyses were performed using AMOS 22.0 (Amos Development Co., Greene, Maine, USA).

### 3. Results

#### 3.1. Community productivity

Although the total productivity of each plantation fluctuated during restoration process, the generally rising trends were detected (Fig. 1a, b). And the increasing trend was statistically significant in EE ( $R^2 = 0.7473$ ,  $P = 0.0056$ ), AM ( $R^2 = 0.4920$ ,  $P = 0.0352$ ) and NS ( $R^2 = 0.5500$ ,  $P = 0.0222$ ), but not in MC ( $R^2 = 0.0813$ ,  $P = 0.5355$ ). The productivity of the dominant species exhibited the main contribution to total community productivity in both the tree and shrub layers across the four plantations (Fig. 1c).

#### 3.2. Community diversity

Species richness and phylogenetic diversity across all plantations also increased over time (Fig. 2a, b). Species richness in the four plantations augmented significantly as succession proceeded (EE,  $R^2 = 0.9134$ ,  $P = 0.008$ ; AM,  $R^2 = 0.7703$ ,  $P = 0.0042$ ; NS,  $R^2 = 0.8533$ ,  $P = 0.0010$ ; MC,  $R^2 = 0.9394$ ,  $P = 0.003$ ; respectively). PD also augmented remarkably with time in EE, NS, and MC (EE,  $R^2 = 0.8588$ ,  $P = 0.0027$ ; NS,  $R^2 = 0.6911$ ,  $P = 0.0105$ ; MC,  $R^2 = 0.9589$ ,  $P < 0.0001$ ; respectively), but no obvious trend of increasing PD was detected in AM ( $R^2 = 0.1946$ ,  $P = 0.2741$ ). PD in MC was significantly higher than those in EE and AM (Fig. 2d, EE,  $P = 0.006$ ; AM,  $P = 0.003$ ).

#### 3.3. Community stability

Community stability increased obviously over time in EE, NS and MC, but no significant trend was detected in AM (Fig. 3a, b;  $R^2 = 0.2350$ ,  $P = 0.2703$ ). Community stability of NS and AM were significantly higher than that of MC (NS,  $P = 0.014$ ; AM,  $P = 0.008$ ), while there was no significant difference of community stability between MC and EE (Fig. 3c).

#### 3.4. Species asynchrony

Overall, the asynchrony of tree species augmented non-significantly with time when all plantations were combined (Fig. 4a;  $R^2 = 0.0486$ ,  $P = 0.2416$ ), whereas a significant trend of decreasing asynchrony of shrub species across all plantations was observed (Fig. 4b;  $R^2 = 0.4232$ ,

$P < 0.0001$ ). Asynchrony of tree species increased remarkably with time in EE and MC (EE,  $R^2 = 0.6918$ ,  $P = 0.0203$ ; MC,  $R^2 = 0.7415$ ,  $P = 0.0128$ ) while asynchrony of shrub species decreased prominently with time in AM ( $R^2 = 0.6801$ ,  $P = 0.0118$ ). Species asynchrony of EE, NS and MC in the tree layer were higher than that in the shrub layer, while the species asynchrony of AM in the shrub layer was much higher than that in the tree layer (Fig. 4c). Besides, the species asynchrony of AM in the tree layer was significantly lower than that of other plantations ( $P < 0.0001$ ).

#### 3.5. Factors influencing community stability

Community stability was significantly positively correlated with phylogenetic diversity and species richness (Fig. 5a, b, c, d) in EE, NS and MC rather than in AM. The stability of dominant tree biomass was remarkably positively related to community stability in EE, AM and NS rather than MC (Fig. 5e, f), while community stability was unaffected by the stability of dominant shrub biomass in each plantation (Fig. A3). Regression analyses showed that community stability firstly decreased and then increased with the asynchrony of tree species in EE, AM and NS. However, an opposite pattern of relationship between community stability and asynchrony of shrub species was observed in each plantation (Fig. A4). Community stability of EE and MC were positively related to the asynchrony of tree species, while community stability of EE, AM and NS first increased then decreased with the asynchrony of shrub species. Species richness and phylogenetic diversity were positively correlated with asynchrony of tree species across in MC (Fig. 6), but negatively related to asynchrony of shrub species in NS and MC (Fig. A5). We found no significant relationship between phylogenetic diversity and asynchrony of tree species in EE, AM and NS. The asynchrony of tree species in EE, AM and NS was also unaffected by species richness. Similarly, there was no significant correlation of asynchrony of shrub species in EE and AM with species richness and phylogenetic diversity.

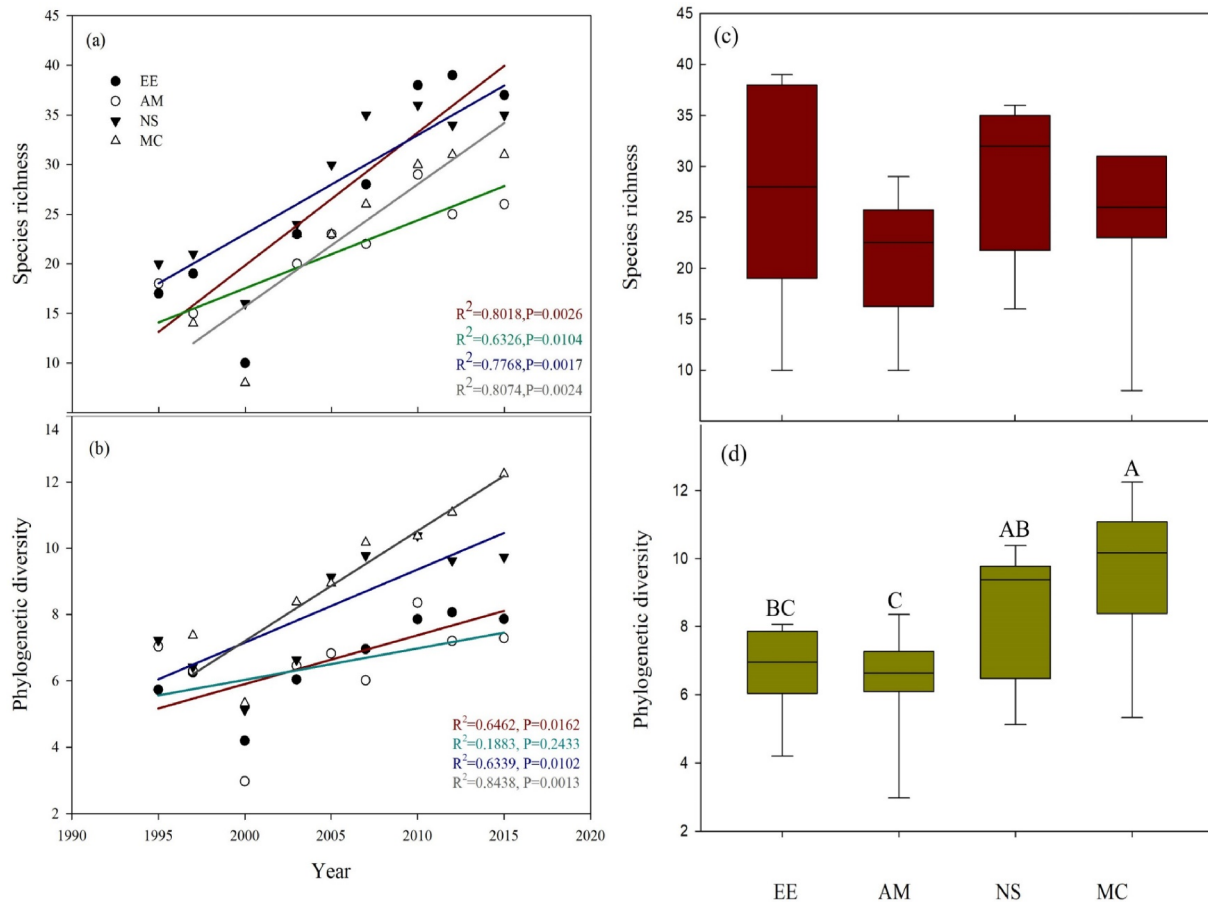
Structural equation modelling (SEM) revealed that both stability of dominant tree biomass and species richness had significant and direct influence on community stability (Fig. 7). Community stability was unaffected by species richness and phylogenetic diversity indirectly, through changing species asynchrony. Species asynchrony of tree layer was negatively related to community stability, which was not a significant factor in the SEM. In contrast to species richness, the stability of dominant tree species was the most important variable which directly influenced community stability.

### 4. Discussion

Consistent with our hypothesis, we found that both species richness and phylogenetic diversity significantly stabilize community biomass in mixed species plantation rather than *Acacia mangium* monoculture over the 30-year succession period. Species asynchrony was not a significant factor that contributing to stabilizing community biomass. Overall, the studied forest community stability was mainly determined by that of dominant tree species, and to a lesser extent, by the species richness.

#### 4.1. Dynamics of community productivity, species diversity and asynchrony

To assess the relative importance of diversity-stability relationship in overstory and understory plants, we measured both the canopy tree and understory shrub productivity across four plantation forests. Our results showed that productivity of the dominant species in the tree layer contribute substantially to the total community productivity of each plantation, this is consistent with that of previous studies (Whittaker, 1965; Grime, 1998; Geider et al., 2001). During 30 years of restoration, we found that the total productivity of each plantation fluctuated. One possible interpretation is that some trees die from typhoons and pests (Kauffman and Cole, 2010; Boyd et al., 2013). And



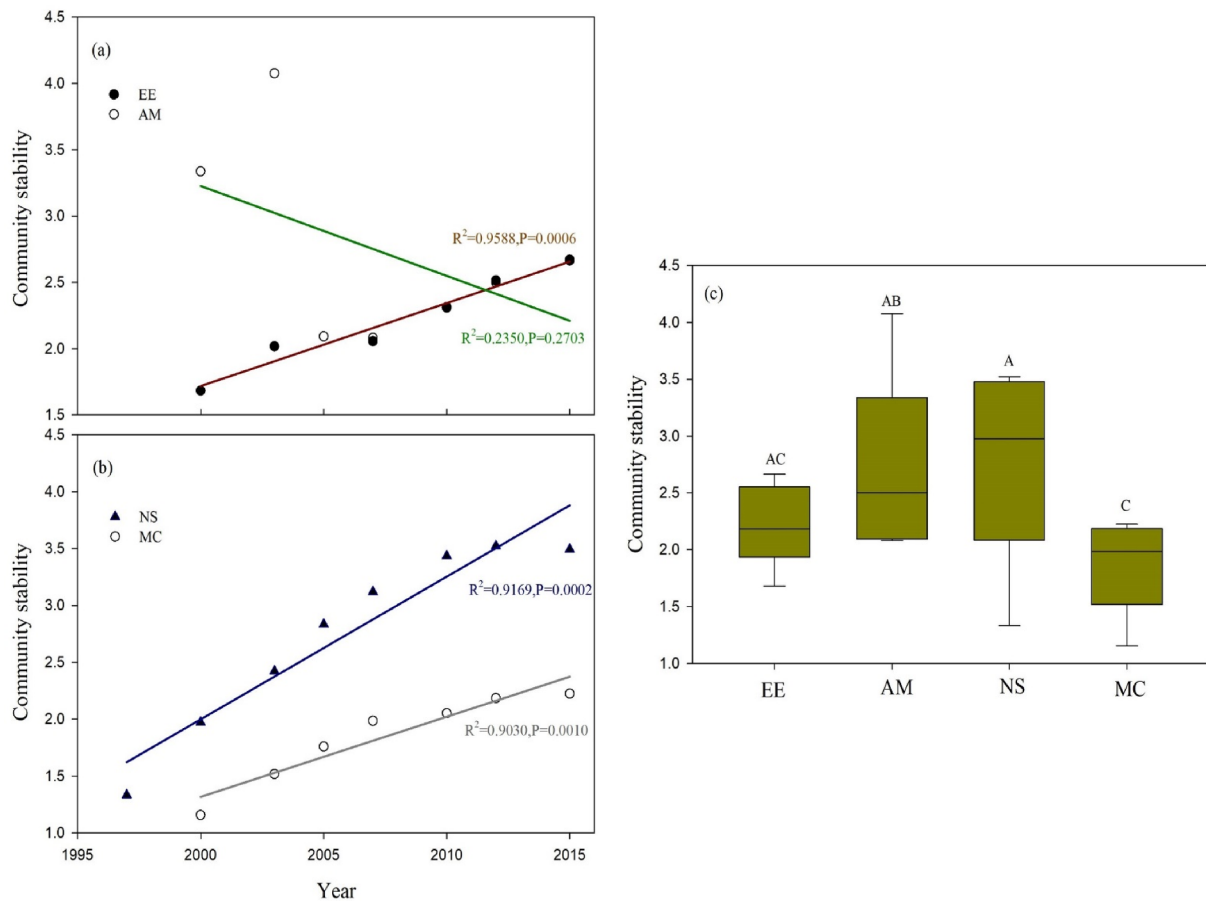
**Fig. 2.** Temporal variation trend (a-b) and average species richness and phylogenetic diversity (c-d) of four subtropical forests over 30 years of restoration. In the left panel (a-b), solid and open dots represent the mixed *Eucalyptus* plantation (EE) and *Acacia mangium* monoculture (AM), respectively; solid and open triangles represent the mixed native species plantation (NS) and mixed coniferous plantation (MC), respectively. Shared letters in the right panel (c-d) indicate that are not significantly different from each other (significance level of 0.05).

sampling errors may also account for the fluctuating biomass. The total productivity across four plantations increased with time, but no obvious trend was detected in MC (Fig. 1b). This could be explained by that the main established species *Cunninghamia lanceolata* and *Pinus massoniana* are fast-growing during 1995–2003, subsequently these dominant species began to degenerate.

Species richness and phylogenetic diversity across all types of plantation increased over time, indicating that biodiversity in the plantations were gradually recovering as expected. Besides, species richness in NS and EE were higher than that in AM and MC, while PD in NS and MC were higher than that in EE and AM. One possible explanation is that the main established tree species of EE and AM are fast-growing, as well as progressively degenerated. However, the mixed-species plantations recruited more understory vegetations than monoculture (Duan et al., 2010). Hence, plantations consisting of mixed native species are preferable for enhancing taxonomic and phylogenetic diversity, given the fact that native species are more adaptable to local environmental conditions than are exotic species (Duan et al., 2010).

Temporal variation in species asynchrony in the tree layer and shrub layer were found to be opposite when all plantations were put together. Besides species asynchrony of all plantations except AM in the tree layer were higher than that in the shrub layer. Species richness and phylogenetic diversity were markedly positively correlated with species asynchrony of tree layer in MC, but significantly negatively related to species asynchrony of shrub layer in NS and MC. In general, community

composition is highly affected by several different factors including environmental conditions (especially the light environment), the structural characteristics of the planted species, litter production, decomposition rates, and the availability of critical nutrients (Duan et al., 2010). For overstory plants, the established species not only occupied the niches in advance and they were also highly competitive for available resources. Under this circumstance, the species asynchrony in the tree layer were higher than that in the shrub layer. Besides, the species asynchrony in the tree layer across all plantations augmented with time, whereas a significant trend of decreasing species asynchrony in the shrub layer was observed (Fig. 4). However, the lower species asynchrony in the tree layer of *Acacia mangium* plantation may result from the accumulation of litter, which is not decomposing rapidly, and might be serving as a physical barrier to seed germination and sapling growth of woody species (Parrotta, 1995; Duan et al., 2010). Above all, niche differentiation among mixed species plantation may result in asynchronous responses of species to changeable environments (Loreau and de Mazancourt, 2008). The positive diversity-asynchrony relationship was reported in previous studies (Xu et al., 2015; Zhang et al., 2018;), but in our analysis, a positive relationship between diversity and asynchrony of tree species was determined only in MC, and negative relationship between diversity and asynchrony of shrub species was found in NS and MC. This may explained by that, MC not only has higher phylogenetic diversity, but also the tree species of MC respond to changing environments more faster and stronger than that of species in other forests.



**Fig. 3.** Temporal variation trend (a-b) and mean community stability (c) of four subtropical forests during 30 years of restoration. Solid and open dots represent the mixed *Eucalyptus* plantation (EE) and *Acacia mangium* monoculture (AM), respectively; solid and open triangles represent the mixed native species plantation (NS) and mixed coniferous plantation (MC), respectively. Shared letters in (c) indicate that are not significantly different from each other (significance level of 0.05).

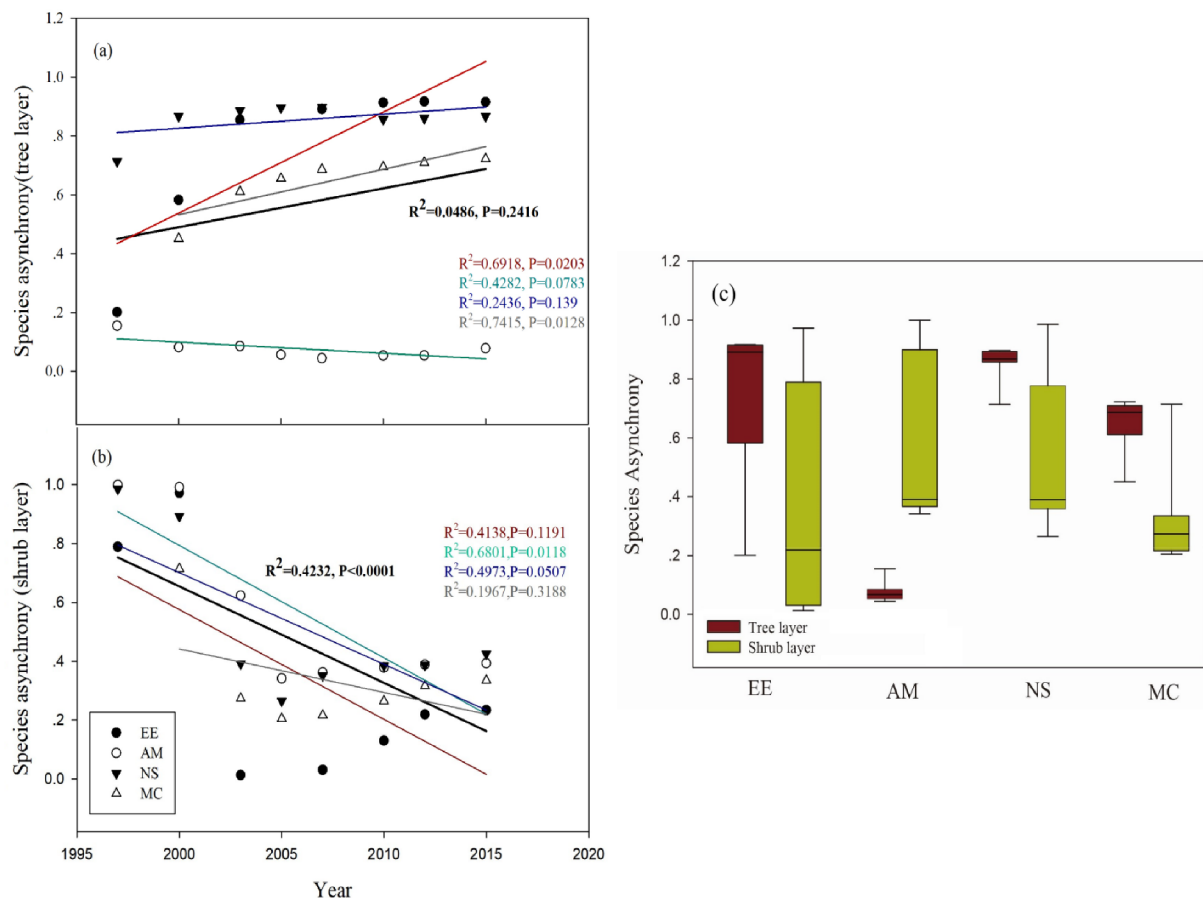
#### 4.2. Relating structural attributes to community stability

Overall, community stability of each plantation augmented as succession proceeded. Community stability increased obviously over time in EE, NS and MC, but no significant trend was observed in AM (Fig. 3). Many studies in grasslands and forests have shown that diverse communities have more temporally stable biomass production than less diverse communities (Campbell et al., 2011; Jucker et al., 2014; Ouyang et al., 2016), and our results show that mixed species plantations have more significantly stable biomass production than monoculture. The study results of relationship between diversity and stability are quite different in grasslands. Most of case studies have shown that species richness is a key driver of stabilizing the biomass (Campbell et al., 2011; Gross et al., 2014). Moreover, results from 16 grassland biodiversity studies revealed that species richness rather than phylogenetic diversity affected temporal stability (Venail et al., 2015). However, another three case studies also revealed the influence of phylogenetic diversity on stability of plant biomass: positive (Cadotte et al., 2009), negative (Venail et al., 2013) and nonlinear (Pu et al., 2014) relationship between phylogenetic diversity and stability, respectively. In our study, community stability was significantly positively correlated with phylogenetic diversity and species richness in mixed species plantation rather than monoculture. In view of the fact that species maximize fitness under different environmental conditions has significant implications for diversity-stability relationships. This signifies that mixed forests remain productive than monoculture under a wide range of environmental conditions (Tilman, 1999).

Consequently, mixed species forests will tend to stabilize productivity. Our results support findings of previous forest studies (Jucker et al., 2014; Morin et al., 2014; Ouyang et al., 2016).

Previous studies have also suggested that species asynchrony is a key driver of stability in grasslands (Hector et al., 2010; Xu et al., 2015; Sasaki et al., 2019). However, regression analyses indicated an insignificant relationship between tree species asynchrony and community stability in EE and NS. Moreover, asynchrony of tree species was not a significant factor in the SEM when combining all plantations during 30 years of restoration (Fig. 7). Due to the long life span of trees, the inability of forests to instantly adjust their species compositions to accommodate fluctuating environments that weaken the importance of species asynchrony as a promoter of stability. But, some recent studies have revealed that the asynchrony of tree species drove the stabilizing effect of diversity in a small time scale, (Aussenac et al., 2017; Aussenac et al., 2019). Therefore, whether the species asynchrony is an important determinant in forest systems remains to test at a sufficiently long time scale. A recent research revealed the scale-dependence of the mechanisms of stability, through developing a partitioning framework that bridged the variability and synchrony measures across spatial scales and organizational levels (Wang et al., 2019). And this framework will provide a useful toolbox for future empirical studies of community productivity stability across scales in natural ecosystems.

According to the results of regression analyses and SEM, the stability of dominant tree species had primary influence on community stability, which were consistent with results of previous studies (Smith and Knapp, 2003; Hillebrand et al., 2008; Yang et al., 2011). The



**Fig. 4.** Temporal variation trend (a-b) and mean species asynchrony (c) in the tree and shrub layers of four subtropical forests over 30 years of restoration. Solid and open dots represent the mixed *Eucalyptus* plantation (EE) and *Acacia mangium* monoculture (AM), respectively; solid and open triangles represent the mixed native species plantation (NS) and mixed coniferous plantation (MC), respectively. Dark red regression indicate EE, dark green regression indicate AM, dark blue regression indicate NS, and dark grey regression indicate MC; the black regression the four plantations combined. The dark red in (c) is the tree layer; dark yellow is the shrub layer. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

portfolio effect is particularly important for communities that exhibit high species evenness when biomass is evenly distributed among species (Hillebrand et al., 2008; Yang et al., 2011). But when communities are dominated by several species, the temporal change of these dominant species is likely to be a more important promoter of community stability. Because evenness often responds more rapidly to altered environment than other ecosystem property like species richness, which might lead to rapid responses in ecosystem functions (Chapin et al., 2000). In additional, changes in population stability in response to changes of environmental conditions may convert into changes in stability at the community level, especially when communities are dominated by a small number of species (Polley et al., 2007; Xu et al., 2015).

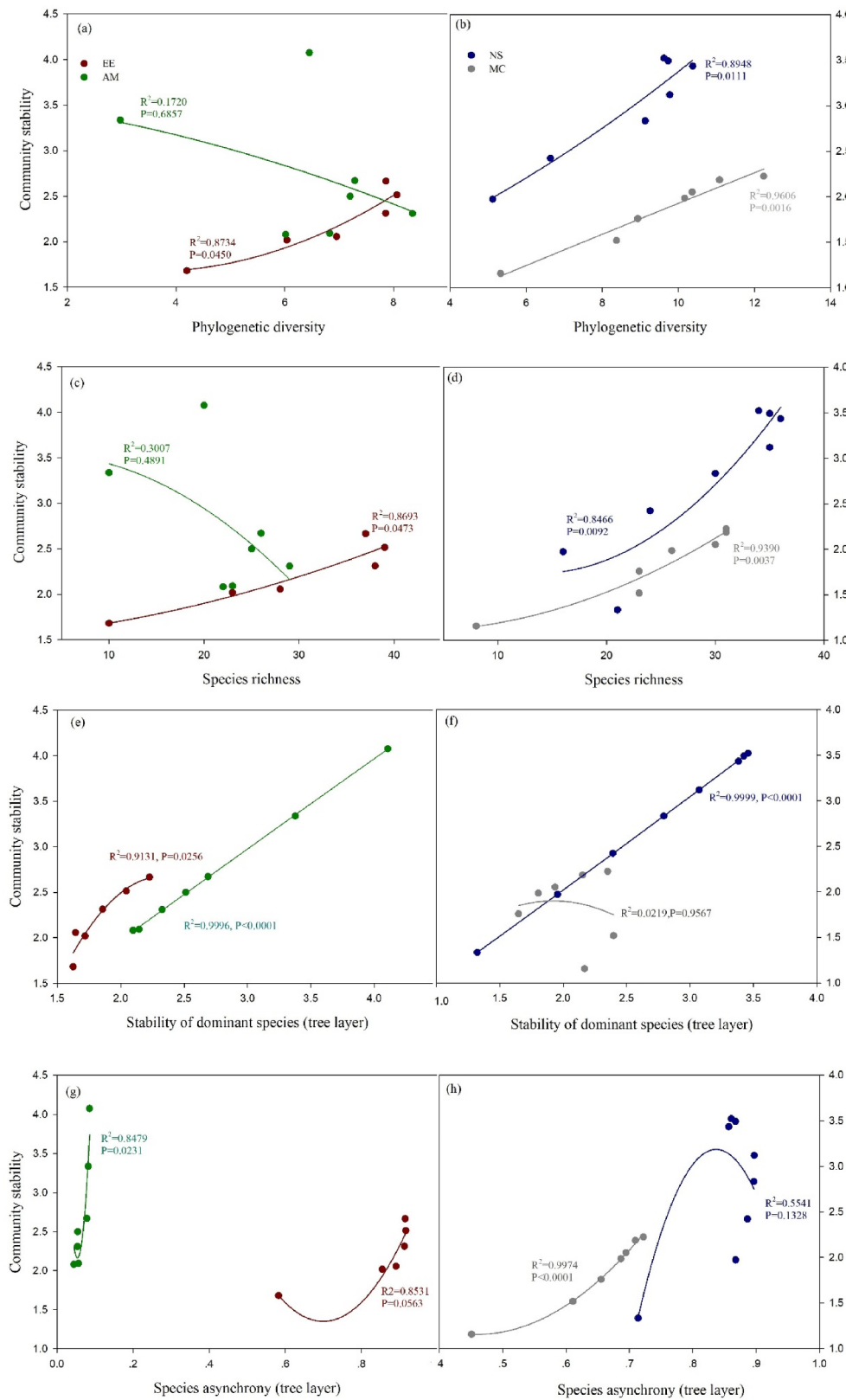
#### 4.3. Implications for forest management and conservation

There is an increasing concern that if biodiversity loss continues, which will have important influences on ecosystem functions and human well-being (Cardinale, 2012). Traditionally, managing forests with the goals of promoting diversity has been recognized as largely incompatible with the requirements of forests production (Seidl et al., 2014). However, both species richness and phylogenetic diversity have significantly positive effects on stability of biomass in our study, supporting the idea that diverse forests have more stable biomass production than monoculture. With the objective of enhancing taxonomic and phylogenetic diversity, plantations consisting of mixed native species are preferable. It is worthy to point out that the stability of dominant tree species was the primary factor which directly influences

community stability. Thereby, we suggest policy makers paying more attentions to overstory dominant species when developing new forest management strategies.

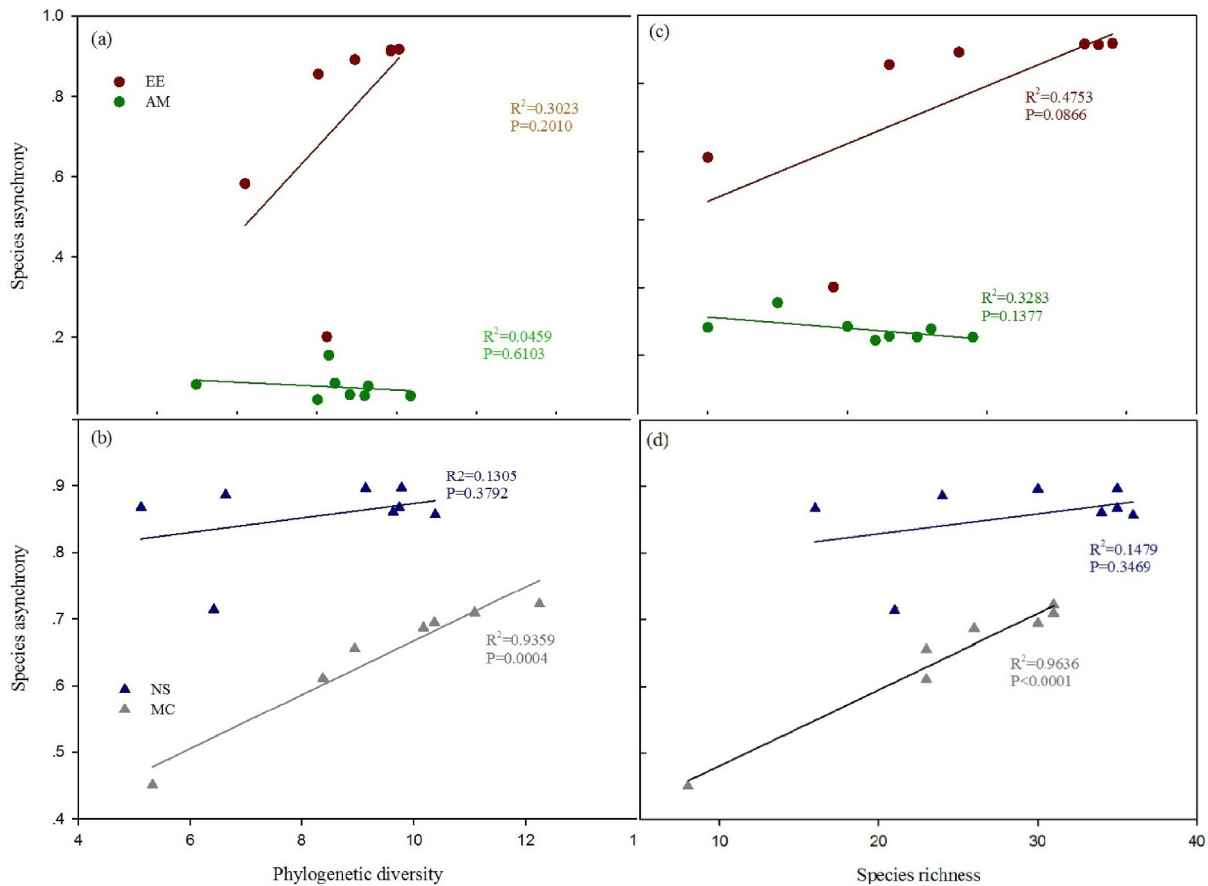
#### 5. Conclusion

Here, we analyzed the relationships between woody plant diversity and productivity stability along 30 years of restoration (1985–2015) in four types of subtropical forest. Our results showed that both species richness and phylogenetic diversity significantly stabilized community productivity in the mixed species plantations instead of the monoculture during the 30-year restoration period. Notably, species asynchrony was not a significant factor contributing to the forest productivity stability. Instead, community stability was mainly driven by that of dominant tree species, and to a lesser extent, by the species richness. We highlight the important role of dominant tree species instead of species asynchrony in maintaining forest ecosystems productivity during the course of the 30-year restoration. The relationship between diversity and stability has interested ecologists for decades due to its complicity problem. Much of the complexity results from the different definitions of diversity and stability, as well as the context in which an ecosystem is disturbed. Besides, anthropogenic changes also impact stability and diversity simultaneously, diversity-stability relationships cannot be understood outside the context of the changing environment. In short, we can not expect a general conclusion about the diversity-stability relationship, but we need to explore the exact and comprehensive mechanisms behind different study contexts in the future.

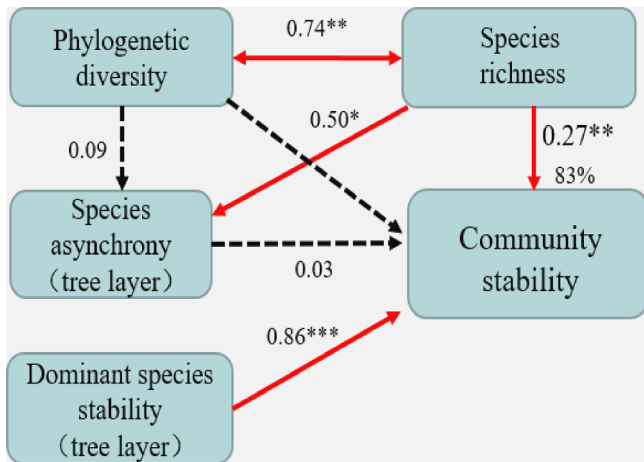


**Fig. 5.** Relationships between community stability and phylogenetic diversity (a-b), species richness (c-d), and species asynchrony of tree (c-d) and shrub (e-f) layers of four subtropical forests in the tree layer during 30 years of restoration. Solid and open dots represent the mixed *Eucalyptus* plantation (EE) and *Acacia mangium* monoculture (AM), respectively; solid and open triangles represent the mixed native species plantation (NS) and mixed coniferous plantation (MC), respectively. Dark red, EE; dark green, AM; dark blue, NS; dark grey, MC. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)





**Fig. 6.** The relationships between species asynchrony and phylogenetic diversity (a-b) and species richness (c-d) in the tree layer of four subtropical forests. Dark red, EE; dark green, AM; dark blue, NS; dark grey, MC. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 7.** Structural equation modelling analysis relating phylogenetic diversity, species asynchrony, dominant species stability and species richness to community stability. Numbers adjacent to arrows are standardized path coefficients and indicate the effect size of the relationship. Arrows indicate positive (red solid) and negative (black dashed) relationships. Percentage close to response variable indicate the variance explained by the model ( $R^2$ ). Goodness-fit statistics for model are shown below the model. \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ .  $\chi^2 = 2.906$ ,  $P = 0.406$ , d.f. = 3; RMSEA = 0.000, AIC = 26.906. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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**Appendix A. Supplementary data**

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2019.117687>.

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