



# Species Asynchrony and Large Trees Jointly Drive Community Stability in a Montane Subtropical Forest

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## ABSTRACT

The relationships between biodiversity and community stability have been well-documented in grassland ecosystems, yet the diversity–stability relationship and the mechanisms driving community stability in forests remain poorly understood. In this study, we examined the community stability of a tropical montane forest in China over 10 years to explore the effect of multiple facets of biodiversity (that is, taxonomic, functional, and structural diversity). We further tested the relative importance of biodiversity, functional traits, species asynchrony, species stability, and abiotic factors (that is, soil nutrients) on community stability. We found that multiple facets of biodiversity had inconsistent effects on stability, including a neutral effect of species richness, and weak positive effects of functional diversity and structural diversity. Species asynchrony, rather than biodiversity, was the greatest predictor of community stability, fol-

lowed by the stability of large trees. Consistent with the mass-ratio hypothesis, the stability of dominant species also had an important direct effect on community stability. Although functional trait composition had no direct effect on stability, it regulated stability via species asynchrony, large tree stability, and dominant species stability. Similarly, soil nutrients conferred minor effects on community stability. Our results indicated that the insurance effect is the main mechanism driving community stability in this subtropical forest. Meanwhile, the mass-ratio hypothesis also played an important role, which suggested that the management and protection of forest ecosystem should not only focus on biodiversity but also the community structural attributes.

**Key words:** Biodiversity; Community stability; Dominant species stability; Ecosystem function; Functional traits; Species asynchrony; Subtropical forest.

Received 24 March 2022; accepted 11 September 2022

**Supplementary Information:** The online version contains supplementary material available at <https://doi.org/10.1007/s10021-022-00790-5>.

Authors Contributions: X.J.Q. and M.X.J. designed the research. T.Y.Z. and X.J.Q. conceived ideas, compiled and analyzed the data and led the writing of the manuscript. All authors did the field experiments and revised the drafts and gave final approval for publication.

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## HIGHLIGHTS

- Multiple facets of biodiversity had inconsistent

effects on community stability, including a neutral effect of species richness and weak positive effects of functional diversity and structural diversity.

- Species asynchrony was the key driver of community stability in this subtropical forest, followed by large tree stability and dominant species stability.
- Functional trait composition promoted community stability indirectly via asynchrony, large tree stability, and dominant species stability.
- Soil nutrients had only a minor effect on community stability.

## INTRODUCTION

Ecosystems can self-regulate to stabilize their services and functions in the face of environmental fluctuations (Grime 1998; Grman and others 2010; Ives and Hughes 2002). As the largest carbon sink of terrestrial ecosystems, the stability of forest ecosystems will be relevant to all aspects of human society (Albrich and others 2018). However, anthropogenic activities and intense environmental disturbances are threatening the ability of forests to self-regulate and altering the stability of this important ecosystem (Anderegg and others 2013). Therefore, a crucial step in preventing or minimizing damage to the sustainability of forest ecosystem services and functions is a more comprehensive understanding of the stabilizing mechanisms for forest ecosystems (Gamfeldt and others 2013; Morin and others 2014).

Both theoretical and empirical studies have verified the stabilizing effects of biodiversity on communities, and several mechanisms have been proposed to explain this phenomenon (Tilman 1996; Hector and others 2010; Loreau and de Mazancourt 2013). First, the sampling effect suggests that diverse communities tend to be more stable due to their more chances to contain the stabilizing species, especially those species with conservative functional traits, which has been verified in grassland ecosystems (Loreau and Hector 2001; Huang and others 2020). Second, complementarity in resource use suggests that plant species growing in mixture community perform better than in monoculture community due to the complementation in resource availability and use efficiency, and thus promoting community stability by increasing the mean ( $\mu$ ) relative to the variability ( $\sigma$ ) of ecosystem functions, since stability frequently was defined as ratio between  $\mu$  and  $\sigma$  (Hector and others 2010; Loreau and others 2021).

Third, the insurance effect, which depicts the species respond asynchronously to environmental fluctuations and thus reduce the variability at community-level by complementary dynamics among species, is regarded as the crucial factor to drive community stability (Loreau and others 2021). In order to quantify the insurance effect, species asynchrony, as a community structural attribute, is adopted in most ecosystem stability researches (Loreau and de Mazancourt 2013; Loreau and others 2021; Yachi and Loreau 1999). These three mechanisms and their relative importance have been explored extensively in grassland ecosystems (Tilman and Downing 1994; Shi and others 2016; Kigel and others 2021). However, to our knowledge, the relative contribution of each remains elusive, especially in high-diversity subtropical forests (Jucker and others 2014; Yuan and others 2019; Ouyang and others 2021).

Researchers are increasingly aware that multiple facets of diversity, besides species richness, lead to improved forest ecosystem stability (Craven and others 2018; Schnabel and others 2019). For example, (Ouyang and others 2021) reported that the direct effect of structural diversity mattered more than that of species richness on the community stability of subtropical forests. Similarly, one study of central European forests found that both functional diversity and species richness enhanced community stability (Morin and others 2014). However, the positive role of functional diversity on stability was absent in second-growth forests in northeast China (Yuan and others 2019). Moreover, these aforementioned inconsistent findings may imply that, on the one hand, the environmental heterogeneity may confuse the diversity-stability relationships, while on the other hand, the contrasting stabilization mechanisms can come from two communities with the same species richness, as they are composed of individuals with differences in spatial structure or functional characteristics (Grman and others 2010; Qiao and others 2021).

In contrast to the biodiversity effect, the mass-ratio hypothesis holds that ecosystem function is mainly determined by the functional trait composition or the dominant species (Grime 1998). Functional traits reflect the resource-use strategies and life histories of plants, which are expected to directly affect ecosystem functioning (Conti and Díaz 2013). Communities dominated by exploitative traits tend to have higher productivity, whereas communities with slow-growing conservative traits tend to be more stable under environmental stress (Craven and others 2018). In

addition, dominant species can regulate ecosystem functioning effectively, as demonstrated in grassland ecosystems (Hallett and others 2014; Grman and others 2010). At the same time, it also has been regarded to constrain the effect of biodiversity on ecosystem functions (Hillebrand and others 2008; Sasaki and Lauenroth 2011). In forests, questions remain about the influence of dominant tree species, as well as of large trees, on community stability. Large trees have low abundances, yet dominate the canopy and represent a large proportion of the community biomass. Meanwhile, growing evidence of the ability of large trees to acquire resources and resist disturbance has underscored their importance in ecological processes (Lutz and others 2018; Yuan and others 2020; Ali and others 2019).

Community stability can also be affected by abiotic factors, both directly and indirectly via modulating biotic effects and their relative importance. For example, the resource limitation caused by barren soil or low-light environments can reduce community stability by increasing mortality and reducing biodiversity (Yuan and others 2019; Ouyang and others 2021). In contrast, in resource-rich environments, competition can increase species asynchrony and thus improve community stability (del Rfo and others 2017). However, an alternative theory suggests that community stability can result from species' long-term adaptations and species selection in communities at local scales, even in suboptimal habitats or at low levels of biodiversity (Grman and others 2010; Thibaut and Connolly 2013; Roscher and others 2010). Therefore, a more comprehensive exploration in relationships between community stability, biotic factors and soil nutrients will optimize our understanding in the pattern of forest stability.

In this study, we analyzed forest stability using a large dataset spanning three censuses over ten years of a 25-ha subtropical forest in central China. Specially, we addressed the following two major questions: (1) Do different facets of biodiversity (that is, species richness, functional diversity, and structural diversity) have consistent effects on forest stability? (2) What is the relative importance of the various factors (that is, biodiversity, functional traits composition, species asynchrony, species stability and abiotic factors) that affect forest stability? Based on previous findings, we hypothesized that (1) multiple facets of biodiversity improve forest stability. Further, we anticipated that functional diversity has a stronger effect on stability than species richness, as it can reflect differences in plant growth strategies (Cadotte and

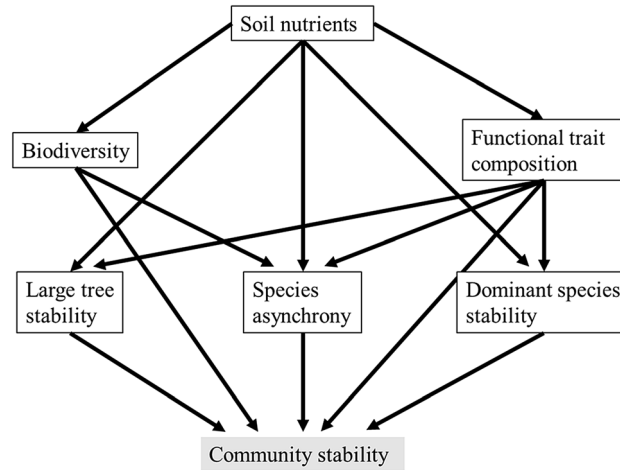
others 2013; Yuan and others 2019). Second, we hypothesized that (2) species asynchrony is the key driver of forest stability. In order to address these questions, we used structural equation model analysis according to a conceptual model (Figure 1). In particular, this model included both the direct and indirect effects of biodiversity, functional trait composition, and soil nutrients on community stability, and the direct effects of species asynchrony, large tree stability, and dominant species stability on community stability.

## MATERIALS AND METHODS

### Study Area and Data Collection

We analyzed data from a 10-year forest dynamic monitoring plot (29°39'18"–29°49'48" N, 110°41'45"–110°09'50" E) established in a subtropical forest in 2011 at the Badagongshan (BDGS) National Nature Reserve in Hunan Province, China. The National Nature Reserve was established in 1986 to protect forest resources, endangered species, and biodiversity from anthropogenic disturbance. This region has a typical subtropical humid monsoon climate; the mean annual temperature is 11.5 °C, ranging from 0.1 in January to 22.8 °C in July, and the mean annual precipitation is 2,105 mm, with most rainfall between March and October.

In 2011, a permanent 25 ha (500 × 500 m) forest plot was established in the national nature reserve, divided into 625 subplots (20 × 20 m, each). The study plot is characterized by flat ridges and steep slopes, with elevation ranging 1354.7–1455.9 m above sea level, and contains typical paleudalfs soil (Zhou and others 2021). All woody plants with a diameter at breast height (DBH) at least 1 cm in the plot were measured, mapped, identified, and tagged. In the first census, the plot contained more than 186,000 stems of 232 species (93 evergreen and 139 deciduous), representing 53 families and 114 genera. This forest is dominated by *Cyclobalanopsis multinervis* and *Fagus lucida*. Other important species include *Betula insignis*, *Carpinus fargesii*, *Castanea seguinii*, *Sassafras tzumu*, *Litsea elongate*, *Cyclobalanopsis gracilis* and *Rhododendron stamineum*. The plot was censused again in 2016 and 2021 using the same methodology, and additional data on newly dead individuals was recorded. No acute natural disturbances occurred in the plot over the study period (Zhou and others 2021).



**Figure 1.** A conceptual model for structural equation model to test the direct or indirect effect of soil nutrients, biodiversity, functional trait composition, large tree stability, species asynchrony and dominant species stability on community stability in a montane subtropical forest. Solid arrows represent the direction of causal relationships.

## Community Stability

We defined community temporal stability (hereafter “community stability”) as the inverse of the coefficient of variance of aboveground biomass (AGB) through the three censuses (2011, 2016 and 2021) within each 20 m × 20 m subplot. First, we calculated the AGB of each individual with DBH at least 1 cm at each census, using a model that was fitted explicitly for use in this research area (Xu and others 2015). Then, we calculated the community stability within each subplot as Eq. 1 (Tilman 1999):

$$\text{Stability} = \frac{\mu}{\sigma} \quad (1)$$

where  $\mu$  and  $\sigma$  are the mean and standard deviation of AGB within each subplot over the 10 years, respectively.

## Community Structural Attributes

### Species asynchrony

Species asynchrony was defined following Loreau and de Mazancourt as Eq. 2 (2008):

$$\text{Species asynchrony} = 1 - \frac{\sigma^2}{(\sum_{i=1}^N \sigma_i)^2} \quad (2)$$

where  $\sigma^2$  is the variance of community (20 m × 20 m subplot) aboveground biomass, and  $\sigma_i$  is the standard deviation of aboveground biomass of species  $i$  in a community with  $N$  species over the years 2011–2021. Species asynchrony ranges between 0 (complete synchrony) and 1

(complete asynchrony) (Loreau and de Mazancourt 2008).

## Biodiversity

We selected three diversity indices to explore diversity–stability relationships. We recorded the number of alive tree species within each subplot in the first census (2011) as the species richness. We defined structural diversity as the coefficient of variance of DBH of alive trees within each subplot in the first census to reflect the vertical diversity of the forest as Eq. 3:

$$CV_d = SD_d \cdot / \hat{x}_d \quad (3)$$

where  $SD_d$  is the standard deviation of DBH at each subplot,  $\hat{x}_d$  is the mean DBH of each subplot (Schnabel and others 2019).

During the growing seasons (June to mid-September) from 2012 to 2015, we measured eight functional traits for a large proportion of species in our plot to calculate functional diversity and trait composition. Before measuring functional traits, we first sampled 10 individuals from each common species and 3 to 5 individuals from each rare species (less than one individual per ha). We then collected 10 to 20 healthy and mature leaves from each individual, for a total of 910 individuals from 129 common species and 33 rare species. The main information about functional traits of our plot can be represented by these sampled species since they covered more than 99% of individuals of the entire plot. Leaf thickness (LT, mm/m), leaf area (LA, m<sup>2</sup>), specific leaf area (SLA, cm<sup>2</sup>/g), leaf dry matter content (LDMC, g), leaf carbon content (LC, g/kg),

leaf nitrogen content (LN, g/kg), leaf phosphorus content (LP, g/kg), and leaf C/N ratio (LCN) were adopted in this study (Table S1). We used Deli DL3944 Vernier calipers (Deli Inc., Ningbo, Zhejiang, China) and a Canon CanoScan LiDE 110 portable electronic scanner (Canon Inc., Beijing, China) to measure LT and LA, respectively. LDMC was the ratio of the dry mass of a leaf to its saturated fresh mass and SLA was the ratio of LA to leaf dry mass. Stable isotope mass spectrometry was used to measure LC and LN, and LP was measured by the molybdenum antimony resistance spectrophotometric method (Zhang 2020). We then calculated LCN based on the measured LC and LN. Finally, we took species-level mean values for following analyses.

To assess functional diversity for the first census, we calculated the functional divergence (FDiv), functional richness (FRic), functional dispersion (Fdis), and Rao's quadratic entropy (RaoQ) within each subplot using the species-level mean value of functional traits (Laliberté and Legendre 2010; Morin and others 2014; Craven and others 2018).

## Functional Trait Composition

To explore the mass-ratio hypothesis of community stability, we calculated community-weighted means (CWMs) of each functional trait (CWM<sub>LT</sub>, CWM<sub>LA</sub>, CWM<sub>SLA</sub>, CWM<sub>LDMC</sub>, CWM<sub>LC</sub>, CWM<sub>LN</sub>, CWM<sub>LP</sub>, and CWM<sub>LCN</sub>, respectively), weighted according to the relative aboveground biomass of each species within each subplot. We calculated CWMs and functional diversity using the R package "FD" (Laliberté and Legendre 2010). To reduce the dimensionality of functional trait composition, we ran a principal component analysis (PCA) for the eight CWM traits. The first three PCA axes explained 79% of the total variation (Table S2), and these three axes were used in the statistical analysis. The first PC axis (TPC1) described low LN and LP, and high LC and LCN. The second PC axis (TPC2) described low LT and high SLA. The third PC axis (TPC3) reflected low LC (Table S2).

## Species Stability

### Dominant Species Stability

Dominant species were defined according to the relative basal area in the entire plot. Six species were considered dominant and accounted for 10.47% (*Fagus lucida*), 10.25% (*Quercus multinervis*), 5.73% (*Rhododendron stamineum*), 5.29% (*Cyclobalanopsis gracilis*), 4.97% (*Carpinus viminea*), and 5.11% (*Sassafras tzumu*) of the total AGB in the

plot in 2011 (Qin and others 2018). We combined these six species within each subplot and calculated their stability as the dominants, as mentioned above.

### Large Tree Stability

We defined large trees as the top about 1% of trees by DBH over the entire plot, as in previous studies (Yuan and others 2020; Ali and others 2019), resulting in a definition of large trees as those with DBH over 30 cm, which accounted for 1.16% of all alive trees in 2011. In subplots without large trees, we took large trees to be those in the top 1% of that respective subplot. The AGB of all large trees accounted for 39.36% of total AGB in 2011. We combined all large trees within each subplot and calculated their stability.

## Environmental Variables

To explore the effects of soil nutrients on temporal stability and diversity–stability relationships, we collected seven soil nutrients indexes, including soil organic carbon (%), soil total nitrogen (%), and available phosphorus (mg/kg) from the top (0–10 cm) and bottom (10–30 cm) soil layers, and soil pH. Details of soil sampling design and measurement of soil nutrients can be found in Appendix S1. In order to reduce the correlation among soil nutrients, we ran a PCA for the seven soil nutrients. The first three PCA axes accounted for 79% of the total variation (Table S2) and were used in the statistical analysis below. The first axis (SPC1) explained 45% of the variation, reflecting the soil organic carbon in both top and bottom soil layers and soil total nitrogen in the topsoil layer. The second axis (SPC2) explained 20% of the variation, describing soil pH. The third axis (SPC3) explained 14% of the variation, reflecting available phosphorus in the bottom soil layer (Table S2).

## Statistical Analysis

Community stability, dominant species stability, and large tree stability were all log-transformed to meet normality assumptions prior to all analyses. Due to many of species asynchrony close to one within the 0–1 interval, we also used the angular transformation ( $\arcsin(\sqrt{\text{asynchrony}})$ ) to meet normality assumptions (Bongers and others 2021). We used ordinary least squares (OLS) regression to examine bivariate relationships between community stability and the facets of diversity (that is, species richness, structural diversity, and functional diversity metrics). Be-

cause only functional dispersion (FDis) had a significant relationship with community stability (Table S3), we selected it as the functional diversity in the following analyses.

We used structural equation modeling (SEM) to investigate the relative importance of the predictors (biodiversity, species asynchrony, large tree stability, dominant species stability, functional trait composition, and soil nutrients) on community stability. First, we constructed a conceptual model (Figure 1). This model included direct paths from biodiversity, species asynchrony, dominant species stability, large tree stability, functional traits, and soil nutrients to community stability (Yuan and others 2019; Ouyang and others 2021; Morin and others 2014), and indirect paths from biodiversity, soil nutrients, and functional traits composition to community stability via species asynchrony, large tree stability, and dominant species stability (Ma and others 2020; Craven and others 2018; Kigel and others 2021; Schnabel and others 2021). To explore the variation in the stabilizing effects of multiple facets of diversity, we used species richness, functional diversity (FDis), and structural diversity in this conceptual model. We used a directed separation test to examine whether missing paths should be added based on the probability of two variables being independent. The two variables with significantly nonzero coefficients ( $P < 0.05$ ) were adopted to the SEM model as the correlated relationship to improve the SEM model (Shipley 2000). We then estimated global model fit according to Fisher's C statistic ( $P > 0.05$ ) and Akaike's information criterion (AICc) (Shipley 2009). The SEM analysis was performed using the R package "piecewiseSEM" (Lefcheck 2016). All the above-mentioned analyses were performed in R v.3.6.0 (R Core Team 2019).

## RESULTS

### The Stabilizing Effect of Multiple Facets of Biodiversity

Ordinary least squares regression analysis indicated that there was no significant relationship between species richness and stability (Figure 2A). However, there were significantly positive relationships between stability and functional diversity ( $P < 0.01$ ,  $R^2 = 0.01$ , Figure 2B), and stability and structural diversity ( $P < 0.01$ ,  $R^2 = 0.02$ , Figure 2C), despite their small effects.

### The Relative Importance of Predictors On Community Stability

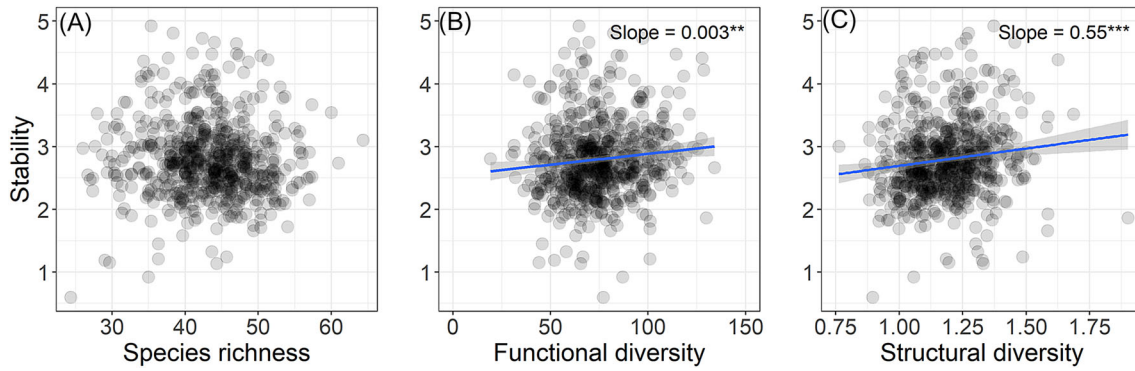
The three SEM models showed that all predictors explained a total of 75% of the variance in community stability for each metric of biodiversity (Figure 3). Using species richness as the biodiversity metric (model A), species asynchrony was the most important factor (standardized path coefficient: 0.63,  $P < 0.001$ , Figure 3A and Figure 4), followed by large tree stability (standardized path coefficient: 0.33,  $P < 0.001$ , Figure 3A and Figure 4), and dominant species stability (standardized path coefficient: 0.15,  $P < 0.001$ , Figure 3A and Figure 4). Functional traits had an indirect positive effect on community stability via large tree stability, species asynchrony, and dominant species stability (Figure 3A). Soil nutrients had an indirect effect on community stability via large tree stability and functional traits, albeit weakly (Figure 3A and Figure 4). However, species richness itself had a non-significant effect on stability (Figure 3A and Figure 4).

Similar to species richness, the SEM models that included functional diversity (model B) or structural diversity (model C) showed similar stabilizing effect of species asynchrony, large tree stability, dominant species stability, and functional traits (Figure 3B and C). Moreover, functional diversity had an indirect positive effect on community stability via species asynchrony, and structural diversity had a direct positive effect on stability, although these effects were both small (Figure 3B and C, Figure 4). Soil nutrients had a positive effect on stability via functional diversity, its stabilizing effect was still small (Figure 3B and C, Figure 4). Soil nutrients had also a negative effect on stability via structural diversity (Figure 3C).

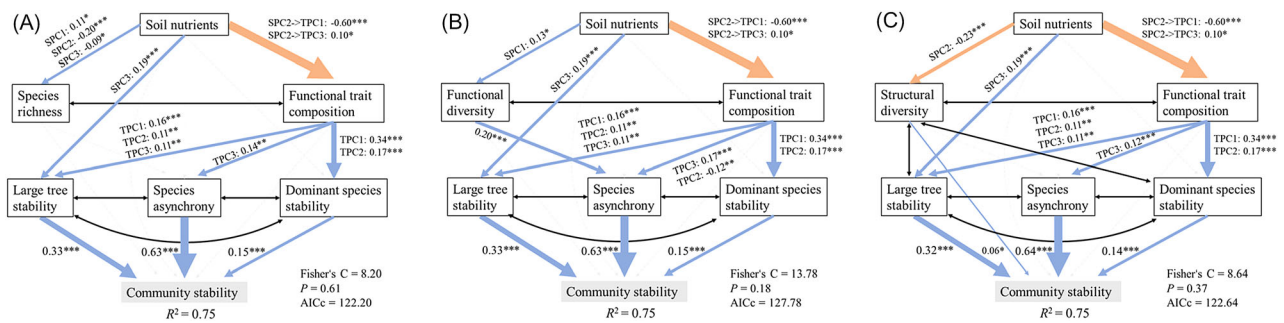
## DISCUSSION

### Inconsistent Stabilizing Effect of Multiple Facets of Biodiversity

Results from our 10-year study showed that multiple facets of biodiversity had inconsistent effects on the community stability of a montane subtropical forest, which did not support our first hypothesis (Figures 2, 3). First, we found that species richness had a neutral effect on stability. Although positive diversity–stability relationships have been demonstrated in numerous theoretical



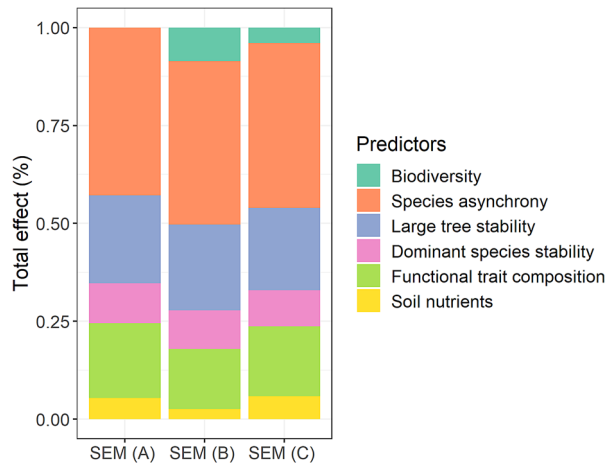
**Figure 2.** Relationships between multiple facets of biodiversity and community stability. Shown are (A) species richness, (B) functional diversity ( $P < 0.01$ ) and (C) structural diversity ( $P < 0.001$ ). Solid lines represent significant regression lines; gray bands represent 95% confidence intervals; each dot represents a subplot ( $n = 625$ ).



**Figure 3.** Structural equation models (SEM) exploring the effects of multiple facets of biodiversity ((A), species richness; (B), functional diversity; (C), structural diversity), soil nutrients (SPC1, SPC2, SPC3 are the first, second and third axis of PCA for soil nutrients, respectively), functional trait composition (TPC1, TPC2, TPC3 are the first, second and third axis of PCA for functional trait composition, respectively), large tree stability, species asynchrony and dominant species stability on community stability. For (A), the model fit the data well (Fisher'  $C = 8.20$ ,  $P = 0.61$ ,  $AICc = 122.20$ ), as was the case for (B) (Fisher'  $C = 13.78$ ,  $P = 0.18$ ,  $AICc = 127.78$ ), and (C) (Fisher'  $C = 8.64$ ,  $P = 0.37$ ,  $AICc = 122.64$ ). The solid lines represent significant positive (blue) and negative (orange) paths; asterisks indicate significance ( $* P < 0.05$ ,  $** P < 0.01$ ,  $*** P < 0.001$ ). Dashed lines represent non-significant paths ( $P > 0.05$ ). Arrow thickness indicates the strength of the causal relationships with a standardized path coefficient. Black bidirectional arrows indicate the significant partial correlations between variables.

and empirical studies (Ives and Carpenter 2007; Jucker and others 2014; Morin and others 2014), neutral and even negative effects have also been reported (Roscher and others 2011; Houlahan and others 2018). For example, one study spanning multiple ecosystem types found positive diversity–stability relationships in only 29% of study plots, and this unexpected result may stem from species richness covarying with other factors (Valencia and others 2020). Species richness is often taken to represent the diversity of plant life histories, morphologies, and physiologies (Carven and others 2018). The neutral effect of species richness on community stability in this study may be attributed to two probable reasons. On the one hand, although different species may have varying response mechanisms to environmental change, the

long-term adaption of plants will result in similar responses to less stressful environment (Roscher and others 2011; Jucker and others 2014; Valencia and others 2020). This is confirmed by the neutral effect of species richness on species asynchrony in our study (Figure 3A) and similar phenomena were also found in grasslands (Liu and others 2019). On the other hand, previous studies indicated that disturbance type is an important factor driving the diversity–stability relationship (Radchuk and others 2019). Theoretically, fluctuating environmental conditions lead to variation in species richness, and thus change community stability and the relationship between them (Tredennick and others 2017; Ratcliffe and others 2017). That no major disturbance occurred in our plot during



**Figure 4.** Total effects of multiple facets of biodiversity (SEM (A): species richness; SEM (B): functional diversity; SEM (C): structural diversity), soil nutrients, functional trait composition, large tree stability, species asynchrony and dominant species stability on community stability.

the observation period might limit the effects of species richness (Zhou and others 2021).

Second, we further found a significant positive relationship between functional diversity and community stability, albeit a weak one (Figure 2B). A similarly weak stabilizing effect of functional diversity was also found in temperate forest (Yuan and others 2019) and planted subtropical forest (Schnabel and others 2021). However, this result does not mean that functional diversity is not important for stability. Indeed, one recent study showed that the effect of functional diversity on ecosystem function (that is, productivity) increased with temporal scale (Bongers and others 2021). The relatively small temporal scale of our study may limit understanding of the stabilizing effects of functional diversity. Furthermore, given that some unmeasured functional traits, such as root or hydraulic traits, were considered to regulate the community stability efficiently (Schnabel and others 2021), the stabilizing effect of functional diversity in this study may be underestimated since it was calculated by only eight traits. When accounting for other factors, we found no direct effect of functional diversity on stability (Figure 3B). However, functional diversity increased stability indirectly via species asynchrony, which supported the complementary effect.

Third, we found structural diversity directly improved community stability (Figure 3 and Figure 4). Higher light capture and utilization efficiency in a more complex forest stand structure could explain this stabilizing effect of structural diversity (Forrester and others 2019; Ouyang and

others 2021). As such, forest conservation policies should be designed to take full account of the benefits offered by structural diversity in future.

## The Relative Importance of the Factors Affecting Ecosystem Stability

We found that the most important driver of forest stability was species asynchrony rather than biodiversity (Figures 3 and 4). Our result was consistent with the insurance effect and previous experimental research reporting that the effect of species asynchrony on community stability matters more than that of species richness (Blüthgen and others 2016; Valencia and others 2020). Our results also verified that the local community stability of natural forest ecosystems can be divided into species stability and species asynchrony (Thibaut and Connolly 2013). Contrary to previous analyses, our study showed that the stabilizing effect of species asynchrony was independent of biodiversity (Figure 3, Liu and others 2019; Valencia and others 2020). As we noted, long-term adaption of different species populations to their habitat may result in a similar response to environmental fluctuation, thus masking the positive relationship between species richness and asynchrony.

The stability of both dominant species and large trees promoted community stability at our site (Figure 3), supporting the mass-ratio hypothesis. The effect of species stability on community stability is well understood in grassland ecosystems (Hallett and others 2014; Grman and others 2010; Kigel and others 2021), but, to our knowledge, it is still poorly explored in forests (Jucker and others 2014), whereas our result provided robust evidence to emphasize its importance on forest ecosystem stability. Most studies of grassland ecosystems attribute the effects of dominant species stability on community stability to the sampling effect of biodiversity (Romanuk and others 2006; Huang and others 2020), but the lack of a relationship between species richness and dominant species stability or community stability in our study did not support this opinion (Figure 3A). Large trees are central to many ecological processes, such as community productivity and carbon sequestration (Lutz and others 2018; Yuan and others 2020; Ali and others 2019). For instance, from the same subtropical forest plot, Xu and others (2015) reported that large trees played a main role in determining the distribution of biomass. Similarly, Yuan and others (2020) demonstrated the importance of large trees for the dynamics and stocks of biomass in temperate forest. Our work, however, emphasizes the



major role of large trees for forest stability (Figures 3 and 4). Despite their low abundance, large trees such as *Fagus lucida*, *Quercus multinervis*, and *Sassafras tzumu*, make up a large proportion of aboveground biomass in our plot, acquire resources rapidly, and effectively buffer against environmental fluctuations (Yuan and others 2020; Valencia and others 2020). Thus, more attention should be paid to large trees in forest management and policy formulation (Zhou and others 2021).

It has been reported that communities dominated by conservative traits (for example, higher leaf carbon content, leaf thickness, and leaf dry matter content) are more stable than those with explorative traits (for example, higher leaf phosphorus, leaf area, and specific leaf area) under environmental disturbance (Polley and others 2013; García-Palacios and others 2018). Unexpectedly, our study did not provide evidence to support this opinion. It is worth noting that community stability was affected by functional trait composition indirectly via large tree stability, dominant species stability, and asynchrony, which offers partial support to the mass-ratio hypothesis (Figures 3 and 4). However, Dolezal and others (2020) reported that trait composition directly affected stability and that there was no indirect effect of functional traits on community stability via asynchrony in temperate forest. These inconsistent results suggest that it is important to consider the differences among forest types in future studies (Ouyang and others 2021). In line with our trait composition results, soil nutrients also did not have a direct effect on stability, in contrast to a previous study that found that soil nutrients affect plant growth, species composition, and turnover, and thus stability (Yuan and others 2019). Moreover, one study conducted in European temperate forest suggested that intensified species interaction stem from the improvement of soil fertility increased species asynchrony and thus stability (Morin and others 2014). However, we did not find evidence for this stabilizing mechanism in our study. Although soil nutrients promoted stability via large tree stability, structural diversity, functional trait diversity and composition, it had little effect on community stability (Figure 4).

## CONCLUSION

Despite growing evidence for the stabilizing effects of biodiversity, we found a neutral effect of species richness and weak positive effects of functional diversity and structural diversity on subtropical montane forest stability. Instead, community sta-

bility was driven by species asynchrony, supporting the insurance effect. Furthermore, we also found the important role of dominant species stability and large tree stability in driving community stability. Although the functional trait composition had no significant direct effect on stability, it did improve stability indirectly via asynchrony, large tree stability and dominant species stability. Finally, we found that soil nutrients had weak effects on stability. Our study highlighted the central role of species asynchrony, large tree stability, and dominant species stability in driving forest stability, and suggested that not only biodiversity but also the structural attributes of forests should be considered in future forest management and policy formulation.

## ACKNOWLEDGEMENTS

This work was financially supported by the Strategic Priority Research Program of Chinese Academy of Sciences (XDB31000000), National Natural Science Foundation of China (32171536 and 31670441) and China Scholarship Council (202104910379). We acknowledge the Chinese Forest Biodiversity Monitoring Network (CForBio) for supporting the BDGS plot, and all the field technicians and students who helped us. We also thank the anonymous reviewers who provided useful suggestions that improved the manuscript.

## DATA AVAILABILITY

Data is available from the corresponding author (Xiujuan Qiao, email: xjqiao@wbgcas.cn).

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