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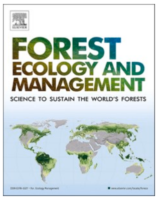

Impacts of tree mixtures on understory plant diversity in China

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ABSTRACT

Understory plants are one of the important components of forest biological diversity and play important roles in forest function. Although convincing evidence exists that mixed-species plantations are more conducive to increase the productivity and stability of forest ecosystems than monocultures, the effect of mixed-species plantations on the understory plant diversity (UPD) remains uncertain. This study conducted a *meta*-analysis based on 205 paired observations of plant species mixtures and corresponding monocultures from 76 peer-reviewed studies to assess the impact of tree mixtures on the UPD in China. The results showed that the UPD was on average 18.2 % higher in mixed-species plantations than in monocultures. This positive mixture effect increased over time, but it would take at least ten years for the effect size of UPD to change from negative to positive. In terms of different mixed forest types, tree-shrub mixtures were more beneficial to maintain the UPD than tree-tree mixtures, and this positive effect was more significant over time. In addition, the response ratio of UPD decreased with mean annual temperature (MAT) and precipitation (MAP), but this relationship was not significant. Therefore, our results suggested that planting mixed-species plantations was a more effective approach to enhance the UPD than monocultures in China. This study revealed the characteristics of UPD under different afforestation modes and could provide a scientific basis for forest management.

1. Introduction

Biodiversity is considered to be one of important factors of improved ecosystem productivity, stability, resilience and nutrient dynamics (Isbell et al., 2015; Carranza et al., 2020). Maintaining and enhancing biodiversity have become an important goal of sustainable forest management (Lindenmayer et al., 2000; Man and Bell, 2018). As an important component of forest ecosystems, understory plants play a vital role in maintaining forest biodiversity, nutrient cycles and energy flow and supplying many other forest products and ecosystem services (Nilsson and Wardle, 2005; Mestre et al., 2017; Wei et al., 2020). To meet the increasing demands of society for wood and fiber production, the total area of forest plantations globally has increased sharply from 167.5 million hectares in 1990 to 277.9 million hectares in 2015 (Bremer and Farley, 2010; Payn et al., 2015; Dai et al., 2017). However, due to limitations imposed by tree survival rates and human needs, most plantations are single species, which reduces biodiversity, soil fertility, and ecosystem stability (Lamb et al., 2005; Felton et al., 2010). In the face of climate change and resource scarcity, there is a growing interest in mixed-species plantations (Hulvey et al., 2013; Metz et al., 2016). Convincing evidence indicates that due to niche division and/or promotion processes, mixed forests can increase vegetation productivity, nutrient cycling rate, and resilience against biological stressors (e.g., pests or diseases) compared with monocultures (Pretzsch and Schutze, 2016; Coll et al., 2018; Liu et al., 2018). However, effects of mixed-species plantations on the understory plant diversity (UPD) remain uncertain (Houle, 2007; Butler et al., 2008; Molder et al., 2008).

The multi-species forest structure usually directly affects the type, composition, and biomass of understory vegetation by impacting the resource levels under the canopy (such as light, soil moisture and nutrients) (Barbier et al., 2008; Piwczynski et al., 2016). According to the niche complementarity hypothesis, the multi-species forest structure may promote the UPD as a result of increased resource heterogeneity and reduced interspecific competition (Bartels and Chen, 2013; Danescu et al., 2016; Yuan et al., 2018). Similarly, certain studies have shown that higher site tree heterogeneity in mixed forests increases the

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availability of growth-restricted resources, including light and soil nutrients, thereby increasing the diversity and biomass of understory species (Barbier et al., 2008; Gamfeldt et al., 2013; Jonsson et al., 2019). In contrast, mixed forests usually result in uneven resource distribution due to functional redundancy between species, leading to fierce competition between overstory and understory vegetation (Zhang et al., 2016; Sercu et al., 2017). For example, studies have shown that due to canopy overlap in mixed forests, the light utilization rate of the understory vegetation decreases, which in turn has a negative impact on the diversity of understory plants (Ligot et al., 2016; Ali and Yan, 2017; Forrester et al., 2018). In addition, divergent empirical findings of tree mixture effects on the UPD could also result from the type of plants, stand age, topographic conditions, soil physicochemical properties, and climatic conditions (Bartels and Chen, 2010; Chavez and Macdonald, 2010; Jin et al., 2019; Wang et al., 2019). Therefore, the quantitative synthesis of the results across multiple studies may help determine the overall effect of tree mixtures on the UPD and determine the source of variation (Gurevitch et al., 2018).

In the past two decades, the Chinese government has launched many ecological projects and implemented land-use policies to improve the environmental conditions and habitat quality of terrestrial ecosystems (Liu et al., 2003; Yuan et al., 2014; Deng et al., 2017), including the Grain for Green Project (GGP) and the Three North Shelterbelt Project (TNSP). Although these ecological projects have significantly increased vegetation coverage and effectively improved ecosystem services (e.g., carbon sequestration, soil and water retention) in China, most of the plantation forests are composed of a single tree species, which often have a negative impact on the ecological environment of the region (Cao et al., 2011; Sang et al., 2013). It is worth noting that afforestation of a single species usually severely consumes soil water and nutrients, which in turn results in lower species abundance and biomass under forests (Chen et al., 2005; Zhang et al., 2010; Wang and Cao, 2011). Compared with monocultures, mixed-species plantations usually have higher productivity and better soil quality, and the conversion of monocultures to mixed forests has become an important forest management approach (Lang et al., 2014; Yu et al., 2019). However, whether planting mixed-species plantations in China is conducive to increase the UPD is still unknown. In addition, although the factors affecting the UPD have been studied, these studies have focused on specific locations or vegetation types (Lu et al., 2011; Wang et al., 2019), and few studies have fully explored the differences in the UPD and their influencing factors between mixed-species plantations and monocultures in China.

In this study, we conducted a *meta*-analysis of 205 paired observations of plant monocultures and mixtures from 76 studies to investigate the effects of tree diversity on the UPD in China. Specifically, we want to address the following questions: (1) Are there differences in the UPD under different afforestation modes (monocultures and mixed-species plantations)? (2) How do mixed types, stand age and climate affect changes in UPD? This study provides a reference for the scientific management of forest ecosystems and biodiversity protection.

2. Materials and methods

2.1. Data collection

Peer-reviewed publications were searched and collected through online databases, including the Web of Science and China National Knowledge Infrastructure (CNKI). The search date was February 1, 2021. To include more research, we focused on the Shannon-Wiener diversity index as the response measure. This index effectively reflects species richness and species uniformity and has become a classic indicator of species diversity (Spellerberg and Fedor, 2003; Song et al., 2016). The following keywords were used: “mixed forest” or “mixed plantation” or “mixed species” or “afforestation” or “afforestation mode” or “forest management” or “shrub” or “monoculture” and “understory vegetation” or “diversity” or “understory species” or “understory plant” and “China”. To avoid publishing bias, we set the following criteria.

(1) The study reported the UPD in tree mixtures and had corresponding monocultures as control plots for comparison;

(2) Mixed-species plantations and the corresponding paired monocultures had the same initial climatic and soil properties;

(3) Only data from field monitoring studies were included, excluding laboratory control experiments; and

(4) The study focused only on artificial afforestation, excluding natural forests.

Finally, a total of 205 paired data points from 76 papers on the UPD under different afforestation modes were included in the study (Fig. 1; Supporting Information). The data were extracted from the tables in the literature or extracted through SigmaScanPro version 5.0 (Systat Software Inc., Point Richmond, CA, USA) if the data were displayed as graphic. We also extracted other information for each study, such as latitude, longitude, mean annual temperature (MAT), mean annual precipitation (MAP), sample size, stand age, and vegetation types. Additionally, the types of mixed-species plantations were divided into two categories: tree-tree mixtures and tree-shrub mixtures.

2.2. Meta-analysis

The response ratio (RR) of natural logarithmic transformation was used to quantify the response of UPD to tree mixtures (Hedges et al., 1999), as shown in Equation (1):

$$RR = ln\left(\frac{X_t}{X_c}\right) \tag{1}$$

where X_t and X_c are the UPD in mixed-species plantations and the corresponding monocultures in each study, respectively.

The calculation of effect size and subsequent inferences in a *meta*-analysis may depend on how individual observations are weighted (Chen et al., 2019; Zheng et al., 2021). However, in our dataset (Supporting Information), only ten studies reported the sampling variance of UPD. More importantly, weights based on sampling variance may assign extreme importance to some individual observations, which may cause the average RR to depend mainly on a small number of studies (Ma and Chen, 2016). Therefore, to better describe the characteristics of the data, we used the number of replications for weighting (Pittelkow et al., 2015; Chen et al., 2020). The weighting factor (W) for each study was calculated by Equation (2):

$$W = \frac{N_t \times N_c}{N_t + N_c} \tag{2}$$

where W represents the weight associated with each RR observation, and N_t and N_c are the number of replications in mixed-species plantations and the corresponding monocultures, respectively.

The mean value of the response ratio (MR) was estimated from the weighted average of the individual RR between the mixed-species plantations and the corresponding monocultures by Equation (3) (Zhou et al., 2018; Sun et al., 2020):

$$MR = \frac{\sum_{i=1}^{n} W_i \times RR_i}{\sum_{i=1}^{n} W_i} \tag{3}$$

The standard error of MR (SE_{MR}) was calculated by Equation (4) (Li et al., 2019):

$$SE_{MR} = \sqrt{\frac{1}{\sum_{i=1}^{n} W_i}} \tag{4}$$

where RR_i and W_i represent the response ratio and the weight of the ith observation, respectively. The 95% confidence interval (CI) is $MR \pm 1.96\, SE_{MR}$. If the 95% CI does not include zero, the observed effect size is considered to be significantly different from zero (Li et al., 2019; Kuang

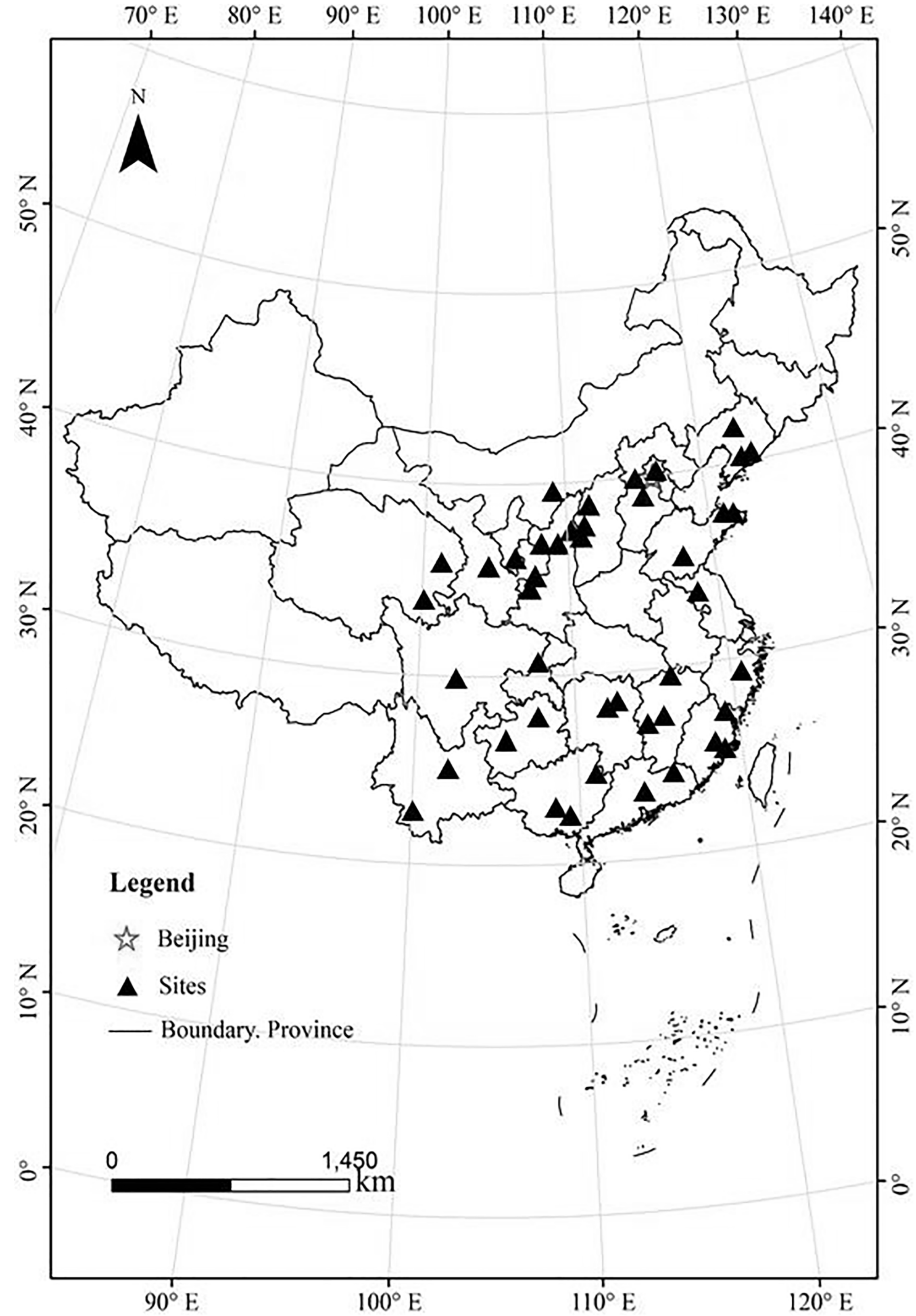

Fig. 1. Distribution of study sites reporting understory plant diversity included in this *meta*-analysis.

et al., 2021). We also calculated the percentage change of the response variable based on the formula (exp $^{(MR)}$ – 1) × 100% (Chen et al., 2020).

The following model (Equation (5)) was used to determine the overall effect of the mixed type (M) and stand age (A) and their interaction on the response ratio:

$$RR = \beta_0 + \beta_1 \bullet \mathrm{M} + \beta_2 \bullet \mathrm{A} + \beta_3 \bullet \mathrm{M} \times \mathrm{A} + \pi_{\mathrm{study}} + \varepsilon \tag{5}$$

where β , π_{study}, and ε are coefficients, the random effect factor of ‘study’, and sampling error, respectively. To verify the linear assumption of continuous predictors, the Akaike information criterion (AIC) was used to statistically compare linear and logarithmic functions, taking the predictor of interest as a fixed effect and “study” as a random effect (Chen et al., 2020). Furthermore, the maximum likelihood method with the *lme4* package was used to fit the mixed model, and *W* was used as the weight of each corresponding observation (Bates et al., 2015).

To further examine whether climatic factors affect RR, we tested the influence of MAT and MAP on RR by adding the terms of MAT and MAP to Equation (5). We also checked the AIC values of models with and without A × climate factor (MAT or MAP) and M × climate factor interaction terms. Since the model with no interaction term has the lowest AIC, we chose the model with no interaction between climate factors and A or M to avoid overfitting. All statistical analyses and graphical drawings were performed in R version 3.5.1 (R Core Team, 2018).

3. Results

Overall, mixed-species plantations had a 18.2% (95% CI: 12.7%–23.8%) higher UPD than monocultures (Fig. 2a). For different types of mixed forest types, the UPD of tree-tree mixtures and tree-shrub mixtures was 16.0 % (95% CI: 9.4%–22.7%) and 21.8 % (95 %CI: 12.4%-31.2%) higher than that of monocultures, respectively (Fig. 2b). In addition, the improvement in UPD for tree-shrub mixtures was significantly higher than that for tree-tree mixtures ($P = 0.04$, Fig. 2b).

The mixture effect on the UPD increased significantly with the increase of stand age, similarly among different mixed types (Fig. 3, $P < 0.001$). Specifically, this mixture effect on the UPD shifted from negative to positive approximately ten years after stand establishment ($P < 0.001$) (Fig. 3a). For different mixed types, this positive effect increased more obviously over time in tree-shrub mixtures (Fig. 3b; $P = 0.001$).

The response ratio of the UPD decreased with the increase of MAT and MAP (Fig. 4). However, there was no significant difference in this relationship (MAT, $P = 0.54$; MAP, $P = 0.49$; Fig. 4), indicating that the UPD response to tree mixtures was consistent across climatic gradients.

4. Discussion

Our results showed that the UPD of mixed-species plantations was significantly higher than that of monocultures in China (Fig. 2). Similarly, Vockenhuber et al. (2011) also found that a positive association between tree diversity and herb species richness in central German deciduous stands. Marialigeti et al. (2016) observed that forest stands with high tree diversity usually featured higher herb species richness in Hungary. Generally, due to the differentiation of the niche and the differences in rotation periods, the multi-species forest structure often affects the UPD by influencing the light, water and nutrient use efficiency and the heterogeneity among forests (Zhang and Chen, 2015; Danescu et al., 2016). Firstly, multi-species forest structure usually leads to heterogeneity of light in forest, resulting in the coexistence of both shade-intolerant and shade-tolerant species, thereby increasing the diversity of understory plants (Yu and Sun, 2013; Ligot et al., 2016; Tinya and Odor, 2016). Secondly, mixed forests may affect soil moisture by adjusting rainfall redistribution and root characteristics (Breshears et al., 1997; Zhao et al., 2018). For example, the multi-species forest structure can increase the soil moisture content and hydraulic conductivity by increasing the buffer and retention capacity of the forest canopy and litter layer (Robichaud 2000; Jin et al., 2011). In addition, the differences in the growth period and the distribution of root systems of multiple species lead to a reduction in overall competition for water (Schwendenmann et al. 2015). Thirdly, mixed forests can increase soil nutrients by increasing the decomposition rate of litter and the root turnover rate, which are beneficial to the growth of understory species (Gartner and Cardon, 2004; Gong et al., 2020a).

Our findings showed that the response ratio of UPD increased with planting age (Fig. 3). Previous studies have shown that multi-species would tend to have a positive impact on ecosystem function through increased mixing effects and environmental heterogeneity over time (van Ruijven and Berendse, 2005; Cardinale et al., 2007). Moreover, this *meta*-analysis found that it would take at least ten years for mixed-species plantations to significantly improve the UPD (Fig. 3). This result may be due to mixed plantations usually consuming more resources (such as light and soil water) than monocultures, while the positive impact of tree diversity on nutrient cycling and energy flow between forests is lagging. Ampoorter et al. (2015) indicated that plant mixtures did not significantly influence herb layer species richness in the early stage. In addition, two experimental studies from tropical regions concluded that mixed forests with young trees have higher light interception than any monoculture (le Maire et al., 2013; Sapijanskas et al., 2014), which may reduce the diversity and biomass of understory plants. Overall, these findings indicate that the study duration needs to be long enough (based on Fig. 3 > 10 years) to correctly estimate the impact of tree diversity on the UPD.

Interestingly, we also found that the increase in UPD under tree-shrub mixtures was significantly higher than that under tree-tree mixtures, and this positive effect was more significant over time (Fig. 2b and Fig. 3b), which might be attributed to the more obvious niche differentiation and heterogeneity of tree-shrub mixtures, thereby leading to the overstory and understory vegetation having more resources to share in horizontal and vertical spaces (Kovacs et al., 2017; Gong et al., 2020b). For example, the shrub layer can slow evaporation by reducing the wind speed, resulting in a more even temperature gradient and higher humidity in the forest (Unterseher and Tal, 2006; Bigelow and North, 2012). In addition, the complementary shrub layer can increase the light transmittance of the forest floor and soil nutrient content (England et al., 2016; Sercu et al., 2017), thereby increasing the UPD.

We also found that the response ratio of UPD decreased with MAT and MAP (Fig. 4). This phenomenon is consistent with the stress gradient hypothesis (SGH); that is, when the environment is restricted, the complementary effects between species may increase (Bertness and Callaway, 1994; Brooker et al., 2008). Because of the limitation of hydrothermal conditions in arid and semiarid areas, afforestation usually causes the consumption of soil moisture, which directly causes a decline in vegetation diversity (Hiers et al., 2007; Cao, 2011). In contrast, due to the division of the niche in mixed-species plantations, the hydrothermal

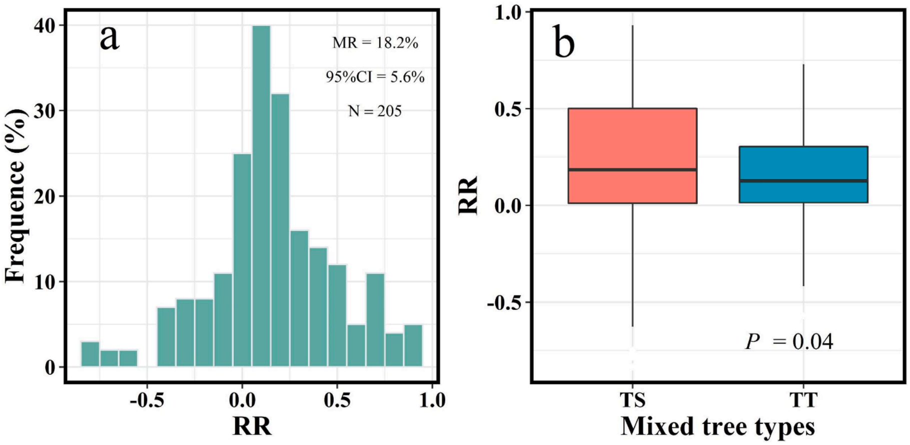

Fig. 2. Effects of different afforestation modes and mixed tree types on the changes in understory plant diversity. **Note:** TS: tree-shrub mixtures; TT: tree-tree mixtures; RR: log response ratio. MR: mean value of log response ratio; N: number of observations.

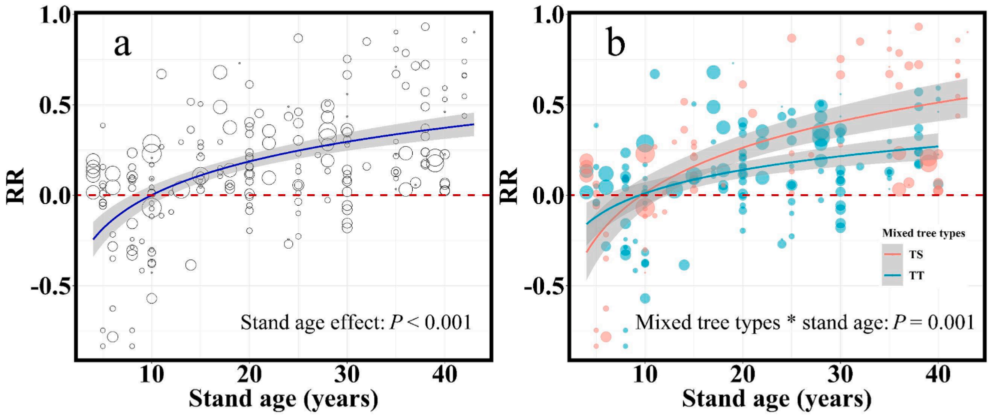

Fig. 3. Effects of stand age on the changes in understory plant diversity. **Note:** TS: tree-shrub mixtures; TT: tree-tree mixtures; RR: log response ratio. The 95% confidence intervals (CIs) are shaded in gray. The sizes of the circles represent the relative weights of corresponding observations. The red dashed line represents the log response ratio = 0. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

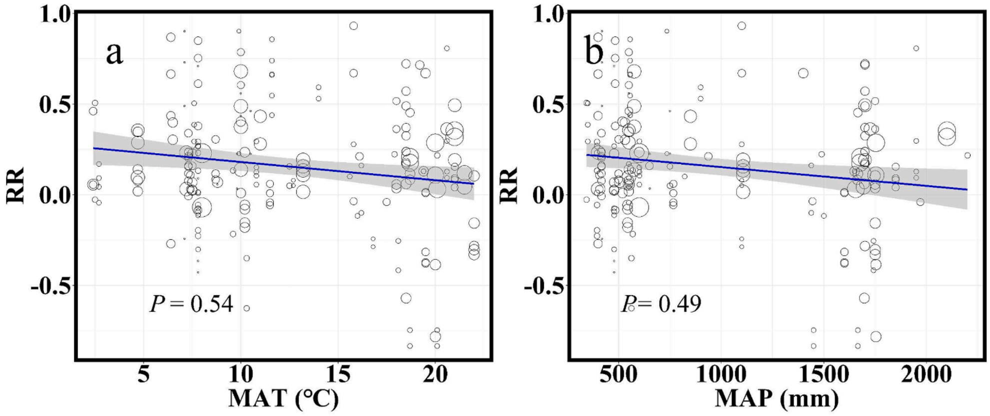

Fig. 4. Effects of climate on the changes in understory plant diversity. **Note:** MAT: mean annual temperature; MAP: mean annual precipitation; RR: log response ratio. The 95% confidence intervals (CIs) are shaded in gray. The sizes of the circles represent the relative weights of corresponding observations.

conditions in the area might be improved by adjusting the microclimate between the forests, which is more conducive to the growth of understory plants (Cavanaugh et al., 2011; Edwards et al., 2014). Similarly, Wang et al. (2019) indicated that due to sufficient water and light conditions in humid areas, the relationship between the overstory and understory vegetation was more likely to be a mutual relationship rather than a competitive relationship. However, we also found that the response of MAT and MAP to tree mixtures was not statistically significant (Fig. 4), similar to the reported effects of species mixtures on aboveground and underground productivity (Zhang et al., 2012), soil respiration and soil microbes (Chen et al., 2019), and soil carbon (Chen et al., 2020). In addition, previous research showed that the development of understory plant communities was not driven by the macroclimate (MAT and MAP) change rate (Zellweger et al., 2020).

5. Conclusion

Mixed-species plantations, especially tree-shrub mixtures, lead to greater UPD in China than monocultures. In addition, stand age and climate (MAT and MAP) will also affect the response of UPD to tree mixtures. In particular, this positive effect on the UPD increases over time, and is strongly dependent on mixed types. These results provide references for scientifically based plantation management. In the context of climate change and frequent droughts, planting mixed-species plantations is an effective measure to increase the UPD. In addition, to better understand the impact of tree mixtures, more long-term observations are needed in the future to study the characteristics of UPD changes with recovery time.

CRediT authorship contribution statement

Chen Gong: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing - original draft, Writing-review & editing. **Qingyue Tan:** Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing-review & editing. **Guobin Liu:** Formal Analysis, Software, Supervision, Validation, Project administration, Writing-review & editing. **Mingxiang Xu:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Investigation, Supervision, Validation, Writing-review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author contributions

C.G., Q. T., and M.X., conceived the study. Q. T., G.L., and M.X., designed the study. C.G., and M.X., analyzed the data, all authors wrote and edited the manuscript.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119545.

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