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RESEARCH ARTICLE

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The effects of forest thinning on understory diversity in China: A meta-analysis

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Abstract

Forest management has been widely used to maintain and improve multiple ecosystem services. However, large-scale synthesis of the effects of forest management on understory diversity, especially regarding the effects of thinning, has not been well represented in China. Therefore, we synthesized 146 peer-reviewed publications and conducted a meta-analysis to evaluate the response of understory diversity (species richness) and seven related variables to forest thinning in China. Overall, forest thinning significantly increased shrub diversity by 28% and herb diversity by 24%. Unthinned diversity and recovery time were the two most important drivers of understory diversity. When the unthinned diversity was low, a decline of understory species richness in managed stands could occur, which may be related to the size of the regional species pool. Rather than the recovery time of 1–2 years after forest thinning, the period of 3–5 years after thinning found the greatest diversity improvement. The northern arid and semiarid ecological domains observed the greatest diversity improvement, which may be due to the specific characteristics in this ecological domain. The coniferous forest was more favorable for understory improvement than in the broadleaved forest. Specific mechanisms on how disturbance (thinning intensity) affect understory diversity need to be further explored. No significant influences of stand stage or sampling quadrat area could be identified. Our study provides a synthetic review of the effects of forest thinning on understory diversity in China and may benefit forest management strategies. Future studies should address changes in compositional or functional diversity after thinning.

KEYWORDS
forest thinning, meta-analysis, understory diversity, unthinned diversity

1 | INTRODUCTION

Forests cover roughly a third of the global land surface and are home to much of the planet's biodiversity (Keenan et al., 2015; Pan et al., 2011). Although the quality timber production was the main objective of forest management in the last decades, nowadays, much attention of multiple ecosystem services of forests have been introduced in the face of climate change (i.e., addressing plant biodiversity, reductions in carbon emissions, and forest production) (Ruiz-Peinado, Bravo-Oviedo, Lopez-Senespleda, Bravo, & del Rio, 2017). Understory vegetation, as an important component of forests, not only accounts for much of the biodiversity in forests and plays essential role in soil cycling and carbon stocks but also provides many nontimber forest products and other ecosystem services and functioning (Chen, Chen, Chen, & Huang, 2019; Liu, Wu, Zhou, Lin, & Fu, 2012; Nilsson & Wardle, 2005). However, we still lack a complete understanding of the response of understory vegetation dynamics to forest management.

As a widely applied forest management strategy worldwide, forest thinning has resulted in a variety of ecological responses in understory vegetation. Forest thinning can increase understory species richness by increasing the available resources and allowing a greater number of understory species to persist. Alternatively, forest thinning might reduce understory diversity as a result of the increased dominance of one or a few understory species (Alaback & Herman, 1988). Besides these two general arguments for interpretation of diversity change after forest thinning, other factors were also reported to affect the response (magnitude and direction) of understory diversity to forest thinning, such as the thinning intensity (Ares, Neill, & Puettmann, 2010; Seiwa, Eto, Hishita, & Masaka, 2012), forest type (Barbier, Gosselin, & Balandier, 2008), stand stage (Juodvalkis, Kairiukstis, & Vasiliauskas, 2005; Zhou et al., 2016), and time since disturbance (Duguid & Ashton, 2013). Therefore, it is reasonable that positive (Ares et al., 2010; Dang, Gao, Liu, Yu, & Zhao, 2018), negative (Abella & Springer, 2015; Taki et al., 2010), and neutral (Lei et al., 2007) responses of understory diversity to forest thinning have been reported quantitatively at the plot scale.

Diverse results have also been reported in previous quantitative reviews at the regional scale, including positive (Abella & Springer, 2015; Verschuyl, Riffell, Miller, & Wigley, 2011; Wilims, Bartuszevige, Schwilk, & Kennedy, 2017) and neutral responses (Dieler et al., 2017; Duguid & Ashton, 2013). However, these quantitative reviews overlooked some factors, such as unthinned understory diversity and the spatial scale, which have both been indicated as important predictors of changes in vegetation diversity after thinning treatments in recent studies (Dodson & Peterson, 2010; Rossman et al., 2018). In addition, the impacts of characteristics of distinctive geographic region (site-specific resource availability and heterogeneity, and climatic factors) on understory species richness have not been well researched. Therefore, given that the knowledge about the effects of forest thinning on understory diversity is still fragmented, quantitative reviews involving more impactful factors are necessary to interpret the response of understory diversity to forest thinning.

China has been ignored or sparsely represented in previous quantitative reviews on understory vegetation diversity and forest management. Thus, there is a need to fill this gap in knowledge not only because China has been undergoing large-scale afforestation and has many forest areas but also because of the many serious ecological problems that have emerged in the forest, such as low species richness, reduced biological diversity, loss of water, and changes to nutrient exchange (Zhou et al., 2016). A better understanding of the effects of forest thinning on understory diversity may help to improve forest management strategies. Moreover, an increasing number of studies reporting data on species richness of understory vegetation in response to forest management have become available for China, thereby enabling analyses for this region.

In this paper, we conducted a meta-analysis to reveal the general responses of understory diversity to forest thinning treatments. We aimed to (a) identify the major effect of forest thinning on understory diversity in China and (b) explore the effects of unthinned diversity, recovery time since thinning, ecological domain, thinning intensity, forest type, stand stage, and sampling quadrat area on the response of forests to thinning.

2 | METHODS AND MATERIALS

2.1 | Data selection

We reviewed the literature for case-studies focusing on the topic of understory vegetation diversity in unthinned and thinned forest stands by searching the online databases Web of Science and China National Knowledge Infrastructure (http://www.cnki.net/) with no restriction on publication year before January 2019. For simplicity, we focused on species richness as the response measure. We analyzed woody (shrub) and herbaceous species separately because they are sampled in different types of sampling quadrats. We used the following combination of terms: '(thin*) AND (*diversity) AND (China).' We also substituted 'richness' for diversity and 'harvest' and 'forest management' for thin*. This resulted in a list of 646 references at the very beginning. To identify studies that were not retrieved from this search but also satisfying our criteria, we reviewed the reference lists of the retrieved papers to obtain the potential study candidates.

The following criteria were used to select the papers for the meta-analysis: (a) The study was conducted in a forest ecosystem in China; (b) measures of understory vegetation diversity (richness) in unthinned forests and thinned forests were included; (c) the forest thinning intensity was provided or can be calculated by the density of trees, or an indicative word, such as light, middle, or strong, was used to describe the forest thinning intensity; (d) the growth phase of the thinned forest stand when receiving the thinning treatment or the specific stand age, which helps to describe the growth phase of the forest, was included; and (e) the recovery time, which is the time since forest thinning (after the last forest thinning treatment if the stands received multiple thinning treatments), was included.

After this exhaustive literature search, we obtained a list of 146 articles that were included in our meta-analysis (Table S1), with sites spanning across China (Figure 1).

2.2 | Data extraction and structure

We recorded the following data for each study:

1. basic information regarding the study sites (latitude and longitude, mean annual temperature, and mean annual precipitation);
2. thinning intensity (control [C], light thinning [<35% of the trees removed], moderate thinning [>35% and <55% of the trees removed], and heavy thinning [>55% of the trees removed]);

FIGURE 1 Geographic distribution of data sources

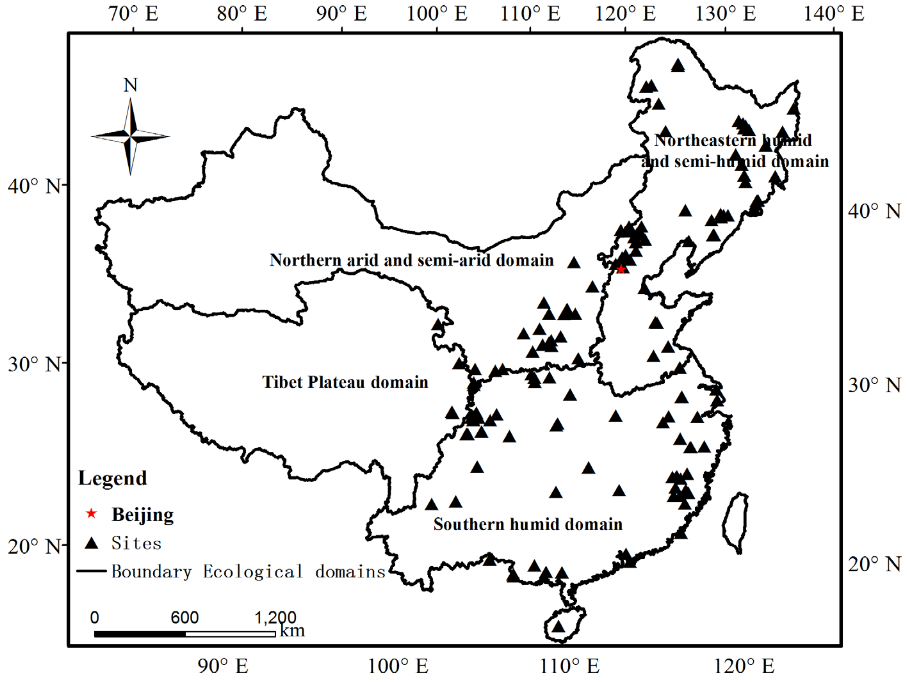


TABLE 1 Categorical variables used to interpret the response values of understory species richness to forest thinning

Thinning intensity	Forest type	Forest stage	Recovery time (yr)	Sampling quadrat (m^2)	Ecological domain
Light (<35%)	Plantation versus natural	Young	1–2	1 × 1	Southern humid
Moderate (35–55%)	Pure versus mixed	Half-mature	3–5	2 × 2	Northeastern humid and semihumid
Heavy (>55%)	Coniferous versus broadleaved	Near-mature	6–10	5 × 5	Northern arid and semiarid
		Mature	11–20		Tibetan plateau
			>20		

3. stand growth stage (young stand stage, half-mature stage, near-mature stage, mature stage, and over-mature stage);
4. forest type (plantation vs. natural stand, pure forest vs. mixed stand, and conifer vs. broadleaved);
5. recovery time (1–2, 3–5, 6–10, 11–20, and >20 years);
6. area of sampling quadrat (1 × 1, 2 × 2, and 5 × 5 m^2); and
7. geographic region; the geographic region was represented by four ecological domains: northern arid and semiarid domains, northeastern humid and semihumid domains, Tibetan Plateau domain, and southern humid domain, which were proposed by Xie et al. (2012) based on climate, topography, and ecosystem characteristics.

The classification of these factors and data structure are presented in Table 1. Data regarding the measured variables were extracted from the tables, figures, and main text in the selected articles. For data expressed in figures, EGAUGE DIGITIZER 4.1 was used to obtain the exact values. The stand stages were identified by a combination of tree species, stand age, and location, based on 'Regulations for age-class and age-group division of the main tree-species' (Regulatory document from the Chinese government, 2017, ICS 65.020 B60 LY, LY/T 2908—2017). Some studies do not provide the exact thinning intensity, stand age, or recovery time; in these cases, we attempted to collect the relevant information across studies or filled the blanks with the closest estimate.

2.3 | Response ratio calculation and meta-analysis

Data from thinned and control forests were compared for woody species and herbaceous species separately. The size of the effect in each investigation was calculated as the response ratio (r) = Xt/Xc, where Xt and Xc represent posttreatment the mean species richness for the treatment and control group, respectively. The result was back-transformed to a percentage change, (r – 1)*100%, to represent the relative differences in understory diversity between the thinned and unthinned forest. The values of effect size outside three standard deviations of the mean were considered outliers and discarded according to the Pauta criterion (Shi et al., 2016). An unweighted meta-analysis was used because not all studies reported a measure of variance, which is needed to weight a meta-analysis, and the sample size differed among the studies (Adams, Gurevitch, & Rosenberg, 1997; Deng et al., 2017). The mean effect size, 95% confidence interval (CI) and between-group variance (Q_b) and its *P* values were obtained by bootstrapping (9,999 interactions) using MetaWin 2.1 (Rosenberg et al., 2000). Mean effect sizes were significantly different from one another if their 95% CIs did not overlap. The significantly positive or negative effects could be affirmed if their 95% CIs did not overlap zero .

To quantify the importance of different predictors in determining the response of richness to the forest thinning treatment, we used the machine learning technique 'random forest' with the package 'random Forest,' which was used to determine variable importance (Hapfelmeier, Hothorn, Ulm, & Strobl, 2014). Unthinned diversity, ecological domain, forest type (conifer vs. broadleaved, plantation vs. natural forest, and pure vs. mixed forest), thinning intensity, recovery time, sampling quadrat area, and stand growth stage were evaluated in terms of their importance. *Z* scores were calculated for standardized values of unthinned diversity and posttreatment diversity; original values of thinning intensity and recovery time were evaluated; ecological domain, forest type, stand growth stage, and sampling quadrat area were considered according to the indicative grouping variable (for instance, 1 and 0 were used to refer to conifer and broadleaved). These statistical analyses were performed in R v3.5.2 (R Development Core Team).

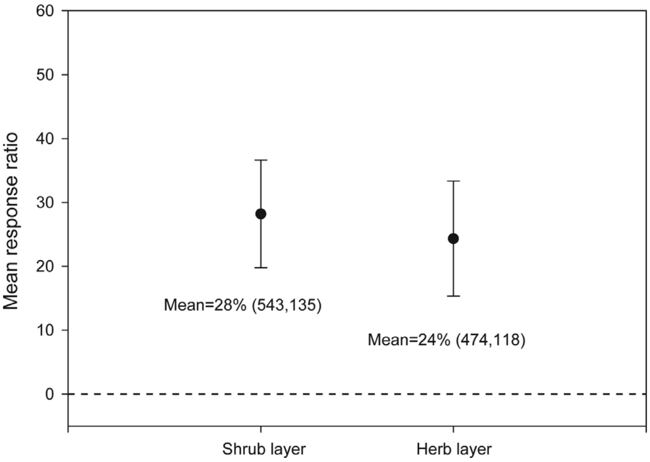


FIGURE 2 .Overall mean response ratios of richness at shrub layer and herb layer in comparison of unthinned and thinned forests. Error bars represent 95% confidence intervals. The dotted line means no significant difference between unthinned and thinned forests. Labels show the means (number of response values and number of studies)

3 | RESULTS

3.1 | Overall effect of forest thinning on understory diversity

Irrespective of the affecting factors, forest thinning significantly increased understory plant diversity (Figure 2). The response ratio indicates an increase in species richness of 28% (*n* = 543; 95% CI [20%, 36%]) in the shrub layer and an increase of 24% (*n* = 474; 95% CI [15%, 33%]) in the herb layer under forest thinning in comparison to the unmanaged forests.

3.2 | Factors affecting the response ratios of understory diversity after forest thinning

By adopting the random forest machine learning technique, we determined the importance of the assessed factors. Unthinned diversity and recovery time were the two most important predictors of response ratios in the shrub and herb layers (Table 2). Although the unthinned diversity ranked the most important predictor for the herb layer, the recovery time was the most significant factor for the shrub layer, which means that the shrub layer and the herb layer had different sensitivities to the influencing factors. By analyzing the between-group variance (Q_b) and *P* values for the categorical variables, significant differences among ecological domains and forest

TABLE 2 %INcMSE (increase in mean squared error) of variable contributing to the difference in species richness between thinned and unthinned forest

	Shrub richness		Herb richness	
Rank	Variable	%IncMSE	Variable	%IncMSE
1	Recovery time	40.01497	Unthinned diversity	62.88238
2	Unthinned diversity	36.84887	Recovery time	43.62494
3	Conifer versus broadleaf	32.10564	Ecological domains	33.88009
4	Ecological domains	29.97035	Sampling quadrat	23.98716
5	Sampling quadrat	20.44283	Stand stage	23.47608
6	Stand stage	19.54684	Thinning intensity	21.58269
7	Pure versus mixed	17.1759	Pure versus mixed	21.13336
8	Plantation versus natural	16.62858	Conifer versus broadleaf	20.08451
9	Thinning intensity	13.88468	Plantation versus natural	19.66893

Note: Numbers are predictors variable importance estimated based on the given variable, using the random forest analysis.

TABLE 3 Categorical variables and total number of case studies used to quantify understory richness after thinning treatment and the test of heterogeneity between groups (Q_b) using meta-analysis

	Number of case					*P* value of Q_b					
Variable	Paper	Total	+	–	0	Thinning intensity	Forest type	Stand stage	Recovery time (yr)	Sampling quadrat (m^2)	Ecological domain
Richness[a]	135	543	341	159	43	0.18654	0.00773	0.95614	0.02691	0.60181	0.05502
Richness[b]	118	474	314	128	32	0.26492	0.1035	0.9781	0.87131	0.77004	0.00914

Notes: *P* values of Q_b were obtained in MetaWin. We only represented the values of forest types one kind of forest classification (conifer and broadleaf) because it was rather a more important one forest classification as compared with others. The symbols +, –, and 0 represent increase, decrease, and unchanged, respectively.

[a] Shrub richness.

[b] Herb richness.

types were found, because both had particularly low *P* values in the Q_b test (Table 3).

3.2.1 | Unthinned diversity

Unthinned understory diversity was one of the most important predictors of the response values of understory diversity after thinning (Table 2). When the values of unthinned species richness and the corresponding response ratios were standardized, scatters were less likely to assemble in such a way as to indicate positive synergy (Figure 3), which means that there was a low chance of diversity improvement after forest thinning when the unthinned diversity was high. In contrast, when the unthinned diversity was low, a decline in understory diversity after forest thinning could also occur, because the scatters also assembled in such a way as to indicate negative synergy. In addition, the response ratios of shrub diversity after forest thinning were more variable than those observed among herbs, as a greater number of scatters observed for shrubs indicated both positive and negative synergy.

3.2.2 | Recovery time

Recovery time was another important predictor of the understory species richness response values after forest thinning (Table 2). Diversity improvement varied in magnitude in accordance with the recovery time intervals (Figure 4). Specifically, understory diversity increased by 22% and 27% in the shrub and herb layers 1–2 years after thinning, respectively, and increased by 40% and 25% after 3–5 years, respectively. After that, in 6–10 years, a lower level of diversity improvement occurred after forest thinning for shrub diversity (21%) and nonsignificant diversity improvement was observed in the herb layer (14%). Diversity improvement was not significant in the shrub layer in 10–20 years (14%) after thinning. In the herb layer, the value was 27%, which was quite similar to that 3–5 years after thinning. These results indicate the different responses of diversity with recovery time between the shrub and herb layers. However, no significant differences were found among the recovery periods we grouped.

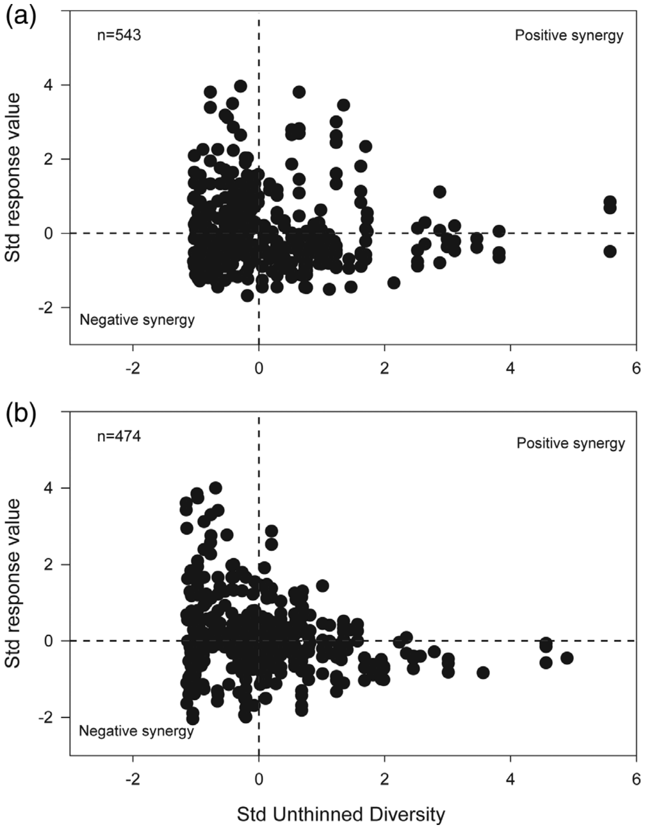


FIGURE 3 Distribution of standardized mean response ratios of richness and corresponding standardized unthinned richness at shrub layer (a) and herb layer (b) after forest thinning

3.2.3 | Ecological domain

Diversity in both the shrub layer and the herb layer showed the greatest improvement after forest thinning in the northern arid and semiarid domains (56% and 49%, respectively), followed by the southern humid domain (28% and 37%, respectively), and the northeastern humid and semihumid domains (22% and 11%, respectively; Figure 5). No significant differences were found between the thinned and unthinned forests in the Tibetan Plateau domain. Although richness increased in both the shrub layer and the herb layer in the three-mentioned ecological domains, significant differences were found only

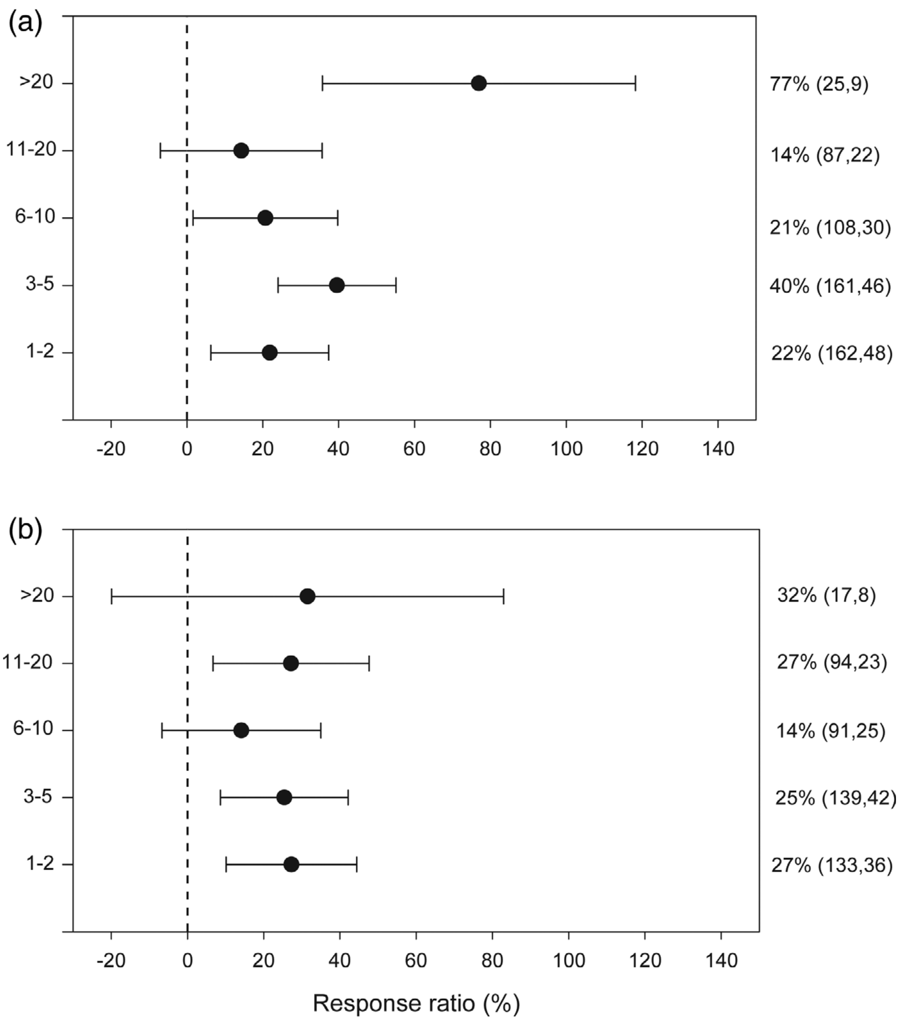


FIGURE 4 Mean response ratios for different recovery times at the shrub layer (a) and the herb layer (b) in comparison of unthinned and thinned forests. Error bars represent 95% confidence intervals. Right side labels show the means (number of response values and number of studies)

between the northern arid and semiarid domains and the northeastern humid and semihumid domains. To further explore how geographic regions affect the responses of understory diversity, we also presented the standardized unthinned diversity in all four ecological domains (Figure S1), and we found that the northern arid and semiarid ecological domains had a relatively low unthinned diversity and the southern humid domain had the highest unthinned diversity among ecological domains.

3.2.4 | Forest type

Among all three classifying methods, the responses of shrub and herb diversity to forest thinning both found higher in plantation, natural forest, and coniferous forest than their counterparts (Figure 6). To be more precise, the highest shrub diversity improvements after forest thinning was found in the coniferous forest (37%), followed by pure (34%), and plantation (32%), whereas their counterparts (broadleaved, mixed, and natural forests) figures were close to a nonsignificant 15%. The herb diversity in all three higher ones increased significantly by around 30%, which well doubled the number of the improvement in the broadleaved forest (14%) and tripped in natural (10%) and mixed forest (10%).

3.2.5 | Thinning intensity

Thinning intensity had limited effects on understory diversity (Table 2). We found a relatively small diversity improvement in both the shrub layer (21%) and the herb layer (18%) when the stands received a light-intensity thinning treatment (Figure 7). The responses of the understory diversity to moderate and heavy thinning intensity were similar in the herb layer, with heavy thinning 32% and moderate thinning 33%. In the shrub layer, the heavy thinning leveled up diversity improvement by 40%, and the figure for moderate thinning was 34%. To further explore the effects of thinning intensity on diversity improvement, we considered the response ratios at different forest thinning intensities with relation to recovery time (Figure S2). In the shrub layer, higher diversity improvement was found under moderate thinning than under light and heavy thinning in the first 5 years after forest thinning. However, in the herb layer, diversity improvement showed the following order: heavy thinning intensity > moderate thinning intensity > light thinning intensity.

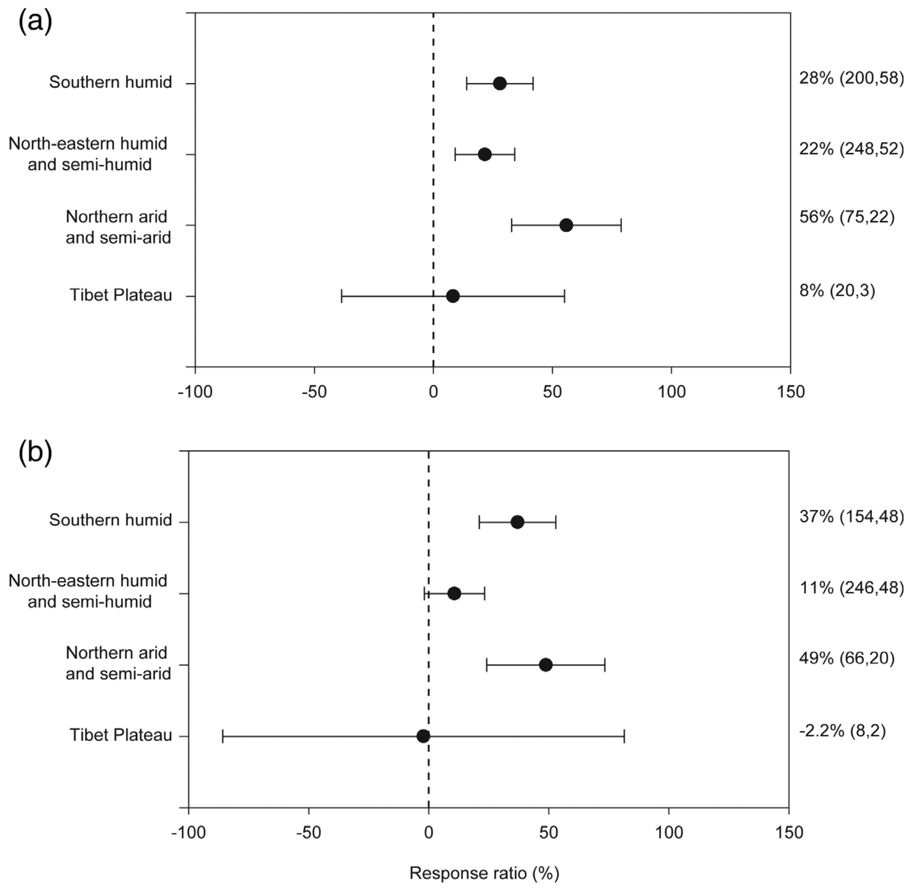


FIGURE 5 Mean response ratios for different ecological domains at the shrub layer (a) and the herb layer (b) in comparison of unthinned and thinned forests. Error bars represent 95% confidence intervals. Right side labels show the means (number of response values and number of studies)

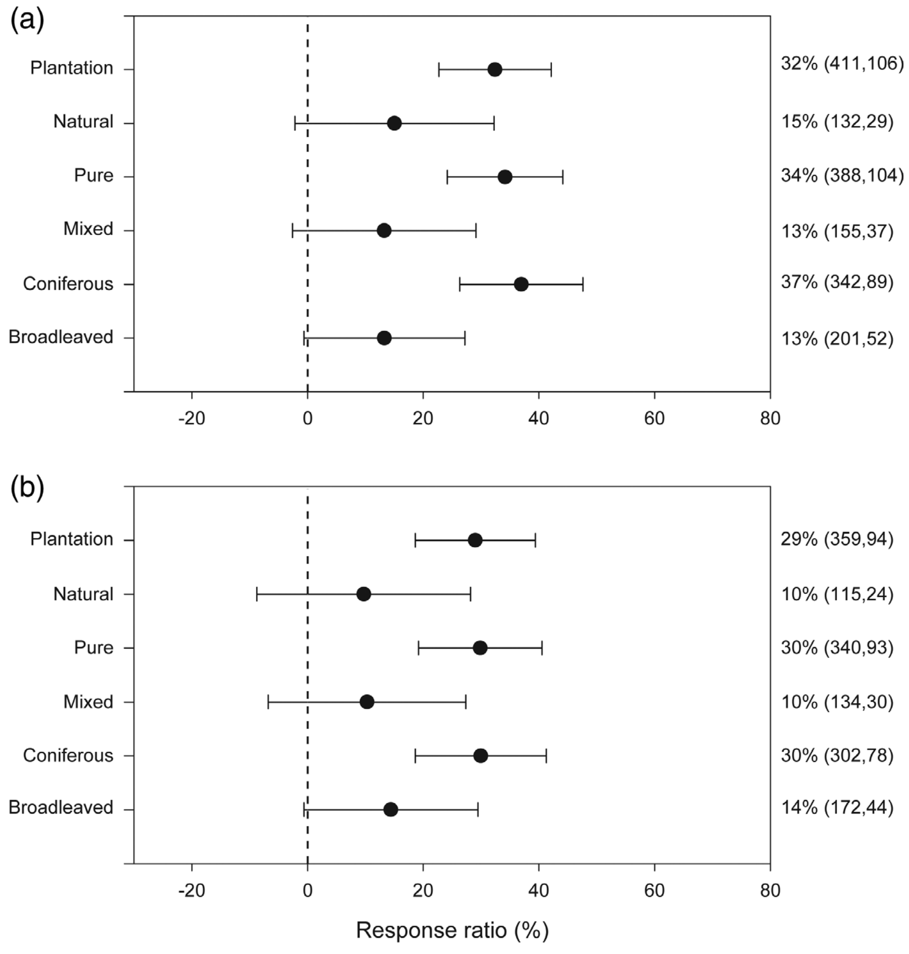


FIGURE 6 Mean response ratios for different forest types at the shrub layer (a) and the herb layer (b) in comparison of unthinned and thinned forests. Error bars represent 95% confidence intervals. Right side labels show the means (number of response values and number of studies)

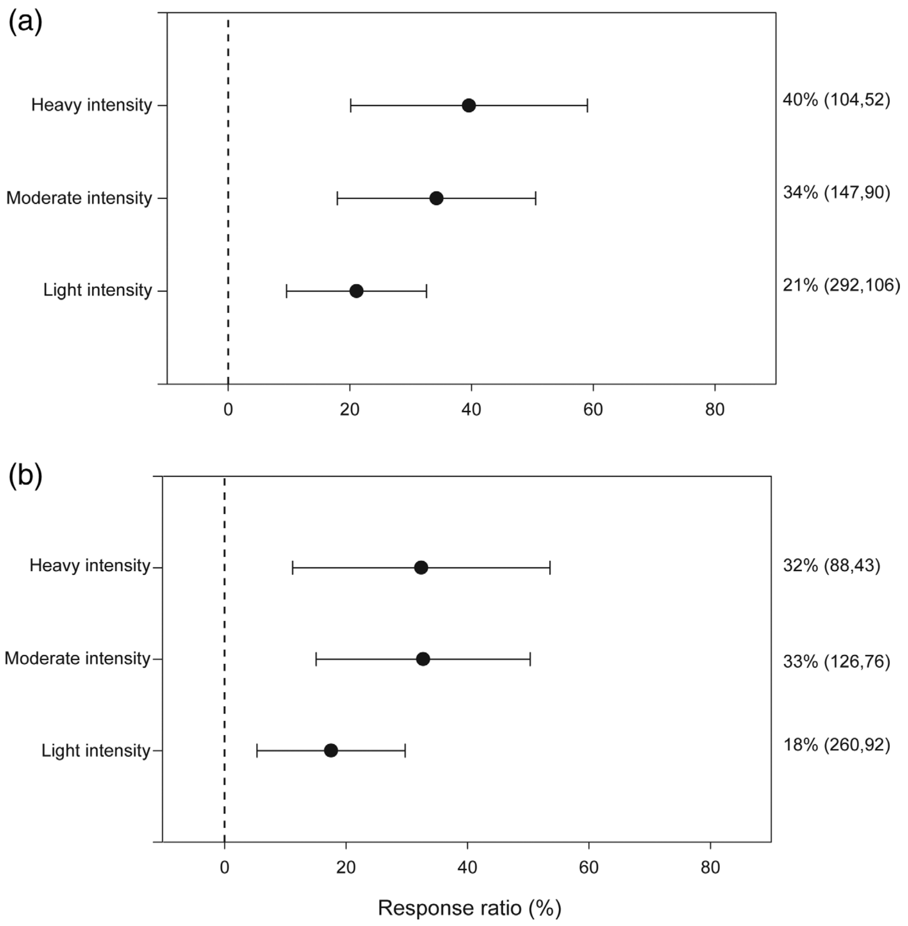


FIGURE 7 Mean response ratios for different thinning intensities at the shrub layer (a) and the herb layer (b) in comparison of unthinned and thinned forests. Error bars represent 95% confidence intervals. Right side labels show the means (number of response values and number of studies)

3.2.6 | Stand stage

The magnitude of diversity improvement was quite similar among the different stand stages after forest thinning (Figure 8). In the shrub layer, the highest diversity improvement was found in the half-mature forest (31%), and this was higher than that in the young stage (27%) and near-mature forest (26%). Besides, a nonsignificant improvement was observed in the mature forest (37%). The herb layer represented a similar amount of diversity improvement as the shrub layer when the stand was at the young stage (27%) and near-mature stage (25%). Unlike at the shrub layer, the lowest diversity improvement after forest thinning was found in half-mature stand at the herb layer (21%). We do not present the results for over-mature forest due to the limited data collected in the shrub layer (11 response values from four studies) and the herb layer (three response values from two studies) and the huge 95% CIs (67% and 248%).

3.2.7 | Sampling quadrat area

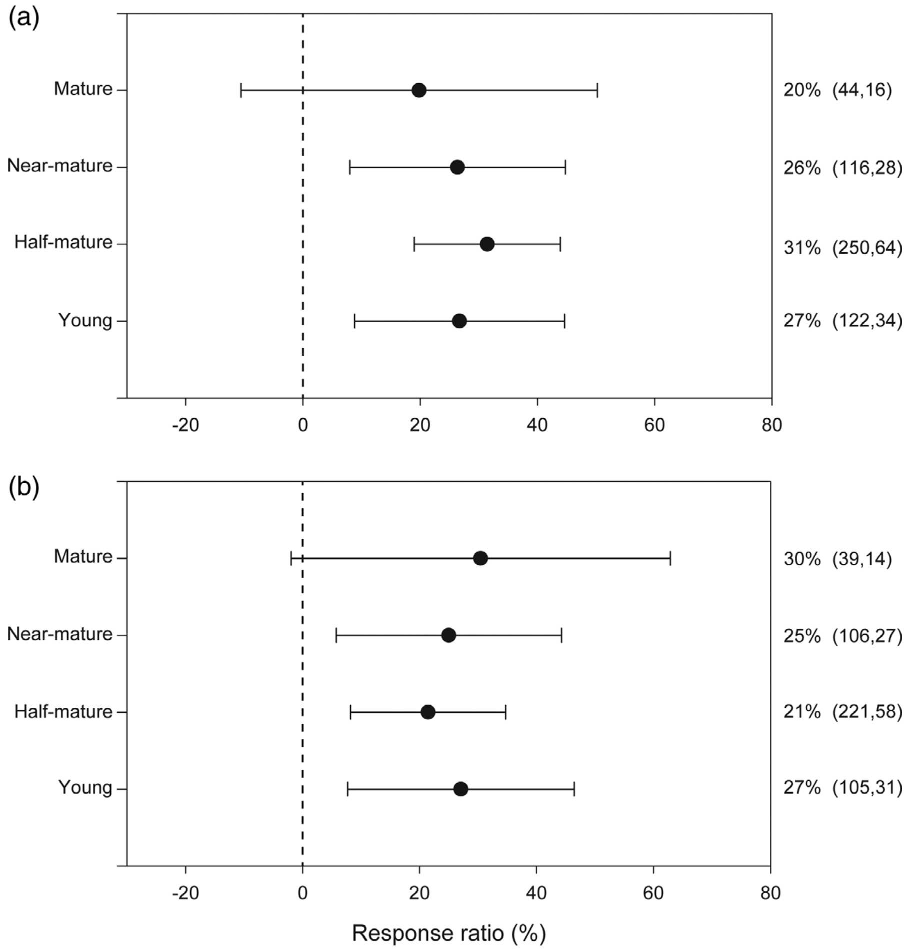
The response ratios of understory diversity varied across sampling quadrat areas and the shrub and herb layers (Figure 9). In the shrub layer, richness improvement was lower in 5×5 m^2 (25%) than in 2×2 m^2 sampling quadrats (34%), and both of these sampling quadrat areas showed a significant improvement in richness. In the herb layer, richness improvement was only significant in the sampling quadrats of 1×1 m^2 (26%). The improvement in richness was also lower in the 5×5 m^2 sampling quadrats (15%) than in the 2×2 m^2 sampling quadrats (21%), although no significant differences were found between these sampling areas.

4 | DISCUSSION

4.1 | General impacts of forest thinning on understory diversity

Although diverse results have been reported in other countries, China has not been well represented with respect to the response of understory diversity to forest management. Our results showed significant increases in diversity in both the shrub (28%) and the herb layers (24%) after forest thinning in China, which is in general agreement with previous studies in other regions (Abella & Springer, 2015; Willms et al., 2017). Thinning can decrease canopy density and improve the microclimate, including light, soil water, and nutrient availability, which affect resource availability and heterogeneity and drive increases in understory diversity. Despite the vague response of understory diversity to forest management in other regions (Duguid & Ashton, 2013; Paillet et al., 2010), the significant improvement found in China was likely related to relative low unthinned diversity in

FIGURE 8 Mean response ratios for different stand stages at the shrub layer (a) and the herb layer (b) in comparison of unthinned and thinned forests. Error bars represent 95% confidence intervals. Right side labels show the means (number of response values and number of studies)



China. This mainly because a high planting density in the young stage, a feature of Chinese activities in China for seeding survival, may introduce a low understory diversity, which in turn contributes the significant understory improvement after forest thinning in China. This assertion was supported by the conceptual model of Roberts and Gilliam (1995).

The higher variable importance of recovery time than unthinned diversity in predicting shrub diversity after forest thinning was mainly attributable to the features of local thinning treatments, which often involve the complete removal of the shrub understory. In contrast, recovery time was a less important predictor than unthinned diversity in the herb layer due to the speedy recovery to its previous state. These differences suggest that the dynamics of herb diversity and shrub diversity to forest thinning are not exactly the same. In fact, shrub layer with a high density, for instance, can lead to a low herb layer diversity due to shade effect (Sabatini, Jiménez-Alfaro, Burrascano, & Blasi, 2014) but could potentially increase herb species richness by increasing soil nutrient availability and light heterogeneity as a result of increasing shrub layer. In addition, these results indicate that separating shrubs and herbs layers may be a better choice in reflecting understory diversity dynamics as a response to forest thinning. After all, the dynamics of the shrub layer and the herb were diverse in at different stands (Yılmaz, Yılmaz, & Akyüz, 2018).

4.2 | Factors affecting the response ratios of understory diversity after forest thinning

The higher unthinned diversity is indicative of local resource conditions that are conducive to posttreatment establishment (e.g., greater soil moisture or N availability; Rossman et al., 2018), which means the amount of species which are able to grow in specific ecological conditions and therefore to affect the performance of vegetation establishment after forest thinning (Sams, Hao, Bonser, Vesk, & Mayfield, 2017). However, unthinned diversity had been rarely included in previous quantitative reviews. Our results highlighted the importance of unthinned richness in predicting posttreatment richness after forest thinning. Specifically, this study found that a relatively high diversity understory improvement was hard to be observed after forest thinning when the unthinned richness species was high (Figure 3). This is reasonable because the plot scale diversity is subjected to the regional species pool (Zobel et al., 2011), and some specialist species, which are dependent on a restricted range of resources or habitats and are more frequent in homogeneous environments, may get lost after disturbance (Devictor et al., 2010). After all, high heterogeneity levels may lead to habitat patch fragmentation with negative consequences for specialist (Zelený & Chytrý, 2010).

An interesting result in our study was that a decline in understory diversity could also occur even when the unthinned diversity is low at

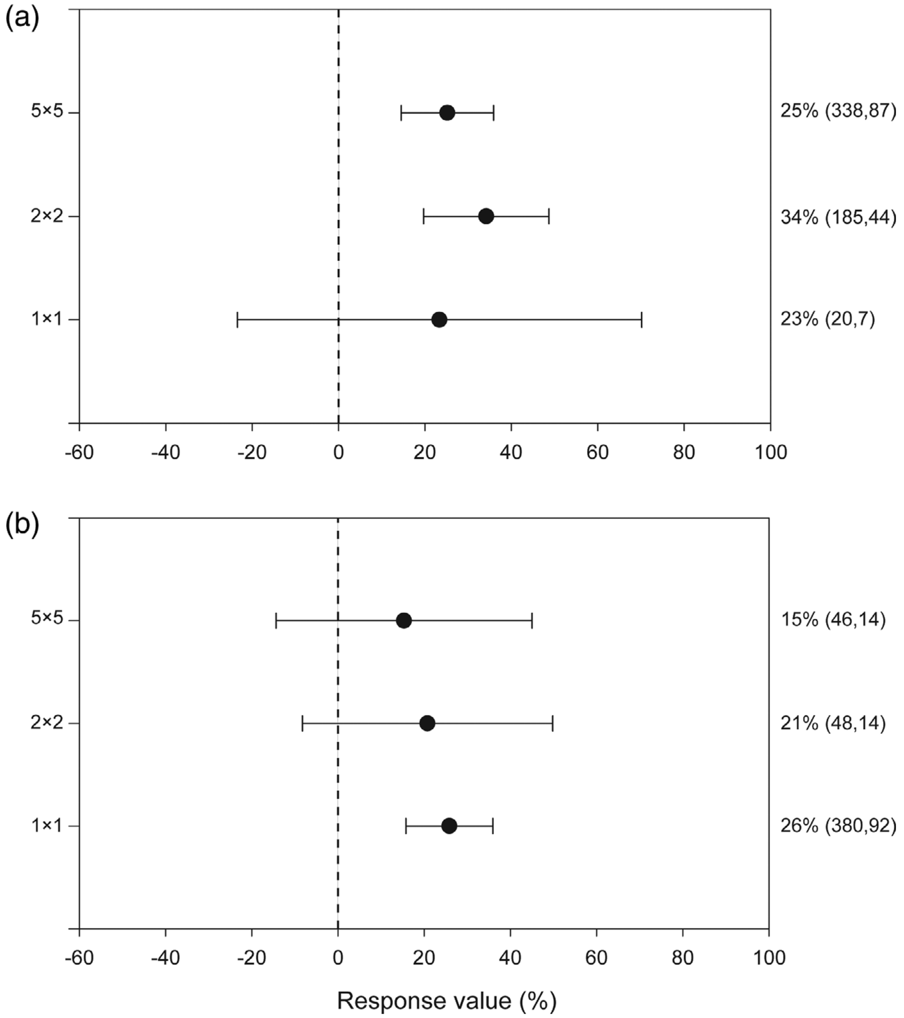


FIGURE 9 Mean response ratios for sampling quadrate areas at the shrub layer (a) and the herb layer (b) in comparison of unthinned and thinned forests. Error bars represent 95% confidence intervals. Right side labels show the means (number of response values and number of studies)

the local scale. A low unthinned density may suggest poor local resources. Besides that some specialist species would disappear due to the limited size of regional species pool as we mentioned above, we assumed that this decline was related to the general competitive pressure of overstory on the understory through resource competition (Ujházy et al., 2017). Understory diversity should reduce when intense competition occurred after forest thinning, as the seedlings and sprouts of regenerating overstory species compete with resident species (e.g., perennial herbs) for aboveground and belowground resources before they pass through this layer to create a new overstory (Gilliam, 2007). These results suggest that forest thinning may not always be a good choice for diversity improvement when the local understory diversity is low. For these reasons, we supported the study of Martín-Queller that emphasized that the diversity of forest communities in the landscape should be put much attention (Martín-Queller & Saura, 2013), which may be more informative about the regional species pool, especially the objective of forest management including diversity improvement.

Recovery time has been shown as an indispensable factors when evaluating the vegetation diversity responses to disturbance (Cole, Bhagwat, & Willis, 2014; Crouzeilles et al., 2016; Duguid & Ashton, 2013; Liu et al., 2019), Our study identified the importance of recovery time among the factors that potentially affect understory diversity after thinning, but no significant differences were found among the different recovery time intervals. This was in line with previous studies (Dieler et al., 2017; Liu et al., 2019). One possible reason for this was that the complied data involved too many forest types, which may mediate the significant difference between different recovery intervals. Another one may be accounted for species turnover because species richness can increase with pioneer species and then decrease because of competition during coexistence (Chesson, 2000; Dornelas et al., 2014).

It had been reported that temporal understory development was tightly related to overstory tree density, mainly because it expresses a general level of tree competition and its temporal development and controls the dynamics of understory vascular-plant diversity (Ujházy et al., 2017). Our study found a significant increase in diversity after 1–2 years. This phenomenon could be well explained by high productivity of plant species (including herbs and shrubs), complex food webs, large nutrient fluxes, and high structural and spatial complexity, as tree canopies do not dominate the forest site in this stage (Swanson et al., 2011). After 3–5 years, even higher diversity improvement was found than in the 1–2 years. This is attributed to a time lag for vegetation establishment after forest thinning. For instance, the advantageous change of microorganisms for more vegetation establishment may delay due to the accumulation of dead plant materials needed (Martín-Queller & Saura, 2013). The time lag may be the very reason why there is a richness decline over the first 2 years following a disturbance in other studies (Abella & Springer, 2015; Taki et al., 2010). Over time, stands become more homogeneous in structure and more uniformly limiting in terms of shade and microhabitats, excluding early successional shade-intolerant species and thus lowering plant diversity over time (Bartels & Chen, 2010). This assertion is also supported by figures of diversity improvement in the shrub layer after 6–10 years, which is the half as much in relative terms than that of 3–5 years. Although we found a new peak in understory diversity improvement during the last recovery time interval (>20 years), we maintained a conservative viewpoint regarding its implications because of the limited supporting data (nine studies) and relatively short (<40 years) recovery time. These results highlighted that whether understory diversity ultimately undergoes a small decrease or reaches a new peak still requires more studies with long-term observations and the changes of species composition in the stands after forest management.

Based on four geographic regions with different climate, topography, and ecosystem characteristics, the response of understory diversity to forest thinning differed significantly across ecological domains (Table 2). The greatest improvement in richness was observed in the northern arid and semiarid ecological domains. One possible reason is that in this area, the local species pool is already adapted to relatively warm, dry, and well light conditions, especially there are natural vegetation of grasslands, forest-grassland mosaics, or forests with open canopies in this ecological domain. When forest thinning happens, these species can establish in the forests as forests become more open (Erdős et al., 2018). Another reason may be that the improved hydrothermal conditions may occur after forest thinning, for instance, warmer, lighter, and drier in this ecological domain may well facilitate understory species richness and negative effects on understory diversity due to water deficiency may not take place (Gillman, Wright, & Ladle, 2014). A recent study also found that soil temperature significantly increased after forest thinning (Zhang et al., 2018). The third one was possibly related to the reduction of biotic competition for resources after forest thinning; it is possible the soil nutrient in the shallow soil layer would support more understory species. Meanwhile, the existence of deep-rooted plants in arid and semiarid regions grown up in the dry soil continue drives the plant roots to extend deeply for water and nutrients utilization in deep soil layer (Zhang, Chen, & Jiang, 2014). Besides those favorable conditions for understory establishment, we assumed that the relatively low unthinned diversity should another primary reason for the highest diversity improvement in this ecological domains. Overall, our study suggests that after forest thinning, stands in the northern arid and semiarid ecological domains are the best candidates for improvements in terms of understory diversity.

Based on the ecological domains, this study also supports that climatic factors (rainfall and average temperature) were an indispensable factor in determining species diversity (Amissah, Mohren, Bongers, Hawthorne, & Poorter, 2014; Gillman et al., 2014; Wang et al., 2009). Temperature affects primary production and metabolic rates, evolutionary processes, and the occurrence of species coexistence (Fuhrman et al., 2008), and it has been reported that species richness increases exponentially with increasing environmental temperature (Wang et al., 2009). Our study observed that the southern humid ecological domain maintained a high unthinned diversity (Figure S1), which supports that high rainfall is more favorable to high understory richness, mainly due to their greater forest structure and heterogeneity (Khaine et al., 2017). In addition, the northern arid and semiarid ecological domains had a lower unthinned diversity, which is related to the climatic condition in this ecological domain with relatively low precipitation and temperature. This is maybe the very first reason why there is large difference between the response of the understory diversity to forest thinning in these two ecological domains, northeastern humid and semihumid domains, which also increased the difference in the response of diversity to forest thinning in these two ecological domains. However, it was hard for us to detect impacts of climatic conditions, and future studies should focus on this topic when interpreting the responses of understory diversity to forest thinning (Liu et al., 2019).

Understory vegetation is influenced by overstory composition and structure through the modification of resource availability (light, water, and soil nutrients) and other effects, such as the physical characteristics of the litter layer (Barbier et al., 2008; Bartels & Chen, 2010; Hakkenberg, Song, Peet, & White, 2016; Thomsen, Svenning, & Balslev, 2005). In general, the deciduous forest is considered to be more favorable to understory diversity than conifer forest. A higher broadleaved percentage in the overstory can promote the cover and richness of the shrub and herb layers, which mainly because of that it leads to greater resource availability for the understory vegetation (Bartels & Chen, 2013). However, understory diversity to forest thinning was significantly lower in the broadleaved forest than in the coniferous forest, which can be explained as follows. The first explanation may be that conifers (e.g., Chinese pine) are a type of plant with short root length in the upper soil layer, and this root pattern shows a good capability of avoiding competition with adjacent individuals for resources (Zhang et al., 2014). The second explanation was likely related to the enhancement of coniferous litter decomposition reduced the litter thickness and increased the soil nutrients, with the former be more obvious among conifers than broadleaved trees after forest thinning. This is reasonable because the increase in soil temperature after forest thinning was found to be more pronounced in coniferous forest than broadleaved forest (Zhang et al., 2018). A third explanation may be related to the significantly increased soil respiration in the broadleaved forest but not in coniferous forest microclimates after forest thinning (Zhang et al., 2018), so that the difference in understory diversity was difficult to detect over the short duration over which the microclimate changed. The fast growth rates and tall stature of the broadleaved forest may also influence the understory vegetation by shading or reducing the availability of nutrients and water (Bartels & Chen, 2013). Based on these results, we suggest that the thinning of the coniferous forest is a better choice for biodiversity improvement.

The definition of thinning intensity varied across tree species, which increased the difficulty in interpreting the effect of thinning intensity on understory diversity. Our study adopted the frequently used classification of thinning intensities based on the percentage of tree removal. Our study found that compared with the light thinning intensity, the moderate and heavy thinning intensities both had a higher effect on understory diversity, which seems to contradict the intermediate disturbance hypothesis that richness should show a unimodal relationship to disturbance, such that richness is maximal at moderate extents of disturbance (Connell, 1978). Previous studies also found forest recovery was more successful when stands received a less intense disturbance, and even at intermediate levels of disturbance and stress, the highest species richness would not occur (Crouzeilles et al., 2016; Dolezal, Hara, & Toshihiko, 2013). Three reasons may well account for inconsistencies of these studies with intermediate disturbance hypothesis. The first one may be that disturbance actually contains multiple components (i.e., disturbance frequency, intensity, or extent) and operate interactively so that diverse response diversity to disturbance may occur in terrestrial landscapes (Miller, Roxburgh, & Shea, 2011). Species richness peaks at intermediate frequency after both high and intermediate disturbance intensities, but the richness–frequency relationship differed between intensity classes (Yeboah & Chen, 2015). The second reason may related to the species pool size at the local landscape (Karger et al., 2011), which means that the impact of a particular disturbance on a community's species richness may depend on the composition of the surrounding communities and the degree of connection with them (Bengtsson, Nilsson, Franc, & Menozzi, 2000). The third one that should be taken into account is the interaction of disturbance intensity with recovery time (Duguid & Ashton, 2013). Our study identified that the response of understory diversity to different forest thinning intensity was diverse along with recovery time. These results support the view that the effect of thinning intensity on understory diversity cannot be completely separated from the recovery time. Overall, these result implies high flexibility in terms of forest thinning at intensities over 35%, allowing the forest manager to place greater emphasis on other ecosystem functions, such as tree growth and stand structure (Del Río, Bravo-Oviedo, Pretzsch, Löf, & Ruiz-Peinado, 2017), carbon stock storage and dynamics (Zhang et al., 2018), soil microbial communities (Dang et al., 2018), and other ecosystem functions, such as drought mitigation (Sohn, Saha, & Bauhus, 2016). However, the specific mechanisms of how thinning intensity or disturbance impacts on understory diversity need to be further explored.

At different stands stages, understory diversity should differ due to the differences in community structure and tree species composition (Pesola et al., 2017). Early succession is the only period during which tree canopies do not dominate at forest sites, so this stage can be characterized by high productivity among plant species (Swanson et al., 2011). However, with a further increase in age, the closed overstory canopy generally reduces the resources available to understory plants (Reich, Frelich, Voldseth, Bakken, & Adair, 2012), thereby decreasing the cover and species richness of species that established during the stand initiation stage. Our study found that there are no significant differences in the responses of understory diversity to forest thinning across the different stand development stages. However, we still found that the response of shrubs was higher in stands of middle age than in those that were young. One reason for this result was that the tree at the young stage has an advantageous position in soil nutrient acquisition than the understory vegetation, and the competition is not so intense in the middle forest age. Another reason may be that the structural diversity was higher in the middle-aged stands than in young stands, which increases the resource availability and heterogeneity (Liu, Wang, & Nan, 2017) and favors species coexistence. A previous study also found that structural diversity could be enhanced by forest thinning (Dieler et al., 2017). A recent study that favors the view that intraspecific competition is stronger than the interspecific competition also supports our results (Adler et al., 2018); otherwise, the strong interspecific competition for resources after forest thinning in the middle-aged stands will limit the establishment of shrubs.

Previous studies have indicated that diversity is spatial scale dependent (Dodson & Peterson, 2010; Rossman et al., 2018). At small scales, dispersal and competition for resources may limit the number of species and the ability of new species to establish, whereas larger forests can support a greater diversity of species because they can encompass greater habitat heterogeneity and resource (niche) diversity. In this study, we focused on the effect of sampling quadrat area. We found that greater shrub diversity improvement was observed when the sampling quadrats were 2×2 m^2 than when they were 5×5 m^2. In addition, we found that significant diversity improvement was only observed with sampling quadrats of 1×1 m^2. These results were not contradictory to our hypothesis that a larger spatial scale tends to show higher understory richness improvement after forest thinning (Dodson & Peterson, 2010) because the sampling quadrat areas in our database were all at the small scale. Indeed, the results indicate the importance of sampling area when measuring differences in understory diversity between thinned and unthinned forests. We suggest that diversity measurements in the shrub layer should be undertaken at a 5×5 m^2 area rather than a 2×2 m^2 area because the surveys conducted at 5×5 m^2 were more representative of the real vegetation conditions and prone to fewer accidental errors than those that occur in smaller sampling quadrats.

5 | UNCERTAINTIES

As with many other meta-analyses, our study also showed some uncertainties. Understory diversity can also be affected by factors other than those addressed in this study. Topography can also significantly alter microclimates and resource availability under the tree canopy (Hart & Chen, 2006). Previous studies also found that topographic variables had higher explanatory power than site conditions in terms of understory plant distributions, which were primarily affected by elevation and aspect (Huo, Feng, & Su, 2014). Potential solar radiation, which is a compound variable derived from slope, aspect, and latitude, has been identified as the most important driver of herb diversity (Ellum, Ashton, & Siccama, 2010; Sabatini et al., 2014). In addition, soil properties, such as nutrients, pH, and litter properties, are also likely to affect understory diversity (Ellsworth, Harrington, & Fownes, 2004; Yu & Sun, 2013). However, inadequate data regarding these variables were reported in the relevant publications. Although some of these factors were included in the factor 'ecological domains,' our study also suggested that the effects of these factors remain uncertain, and the interactions among them also increase the difficulty in terms of explaining the changes in understory diversity.

As with many other meta-analyses, we did not study the confounding effects of various factors by analyzing their interactions, which can help us to determine whether the role of some factors was mediated by those of others (Paul, Polglase, Nyakuengama, & Khanna, 2002). However, both of the important predictors, unthinned diversity and recovery time, were continuous variables. Without clear separation, the interpretation of the confounding effects by analyzing interactions with other factors could be difficult. Indeed, our study suggests that confounding effects should be well researched with reasonable ecological models or equations, which can be used to discover new findings. As a component of biodiversity, functional diversity generally concerns the range of things that organisms do in communities and ecosystems, and these roles are thus more similar to ecosystem services than to richness or abundance (Cadotte, Carscadden, & Mirotchnick, 2011; Petchey & Gaston, 2010). Moving forward, research that seeks to draw broader conclusions should include measures such as compositional or functional diversity after forest thinning (Duguid & Ashton, 2013).

6 | CONCLUSIONS

In general, based on 148 recent publications, our study indicates that forest thinning in China has had a positive effect on understory diversity and that shrub and herb diversity had different responses to forest thinning. Unthinned diversity and recovery time were the two most important drivers in understory diversity after forest thinning. Diversity improvement was not easily detected when the unthinned diversity was high, but a decline in diversity can occur when the unthinned diversity is low, which suggested careful consideration should be introduced when the objective is to increase diversity. No significant difference was found in different recovery times, but we found a long-lasting diversity improvement over the period after 1–2 years after forest thinning and 3–5 years after thinning. Our study found that the effect of forest thinning on understory diversity differed among the ecological domains. The northern arid and semi-arid ecological domains showed the largest understory improvement, which may relate to the characteristics of this ecological domain. As compared with the broadleaved forest, forest thinning in the coniferous forest is a better choice for diversity sustainability. The moderate and heavy thinning intensity had similar effects on understory diversity, which may imply greater flexibility than that observed under light forest thinning, allowing the forest manager to place greater emphasis on other ecosystem functions, but how disturbance impacts the understory diversity need to be further explored. Stand stage or sampling quadrat areas plays a minor role in determining understory diversity. Whether there are confounding effects or not still relies on other statistics method. Overall, this study provides a systematic review of the effects of forest thinning on understory diversity in China, which may provide useful suggestions for forest management strategies. Future studies should pay much attention to the dynamics of compositional or functional diversity after forest thinning, so as to further understand the dynamics of understory diversity to forest thinning.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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