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## Research article

### Selective logging destabilizes the functioning and composition of forest ecosystems at multiple spatial scales

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Selective logging is one of the most prevalent land uses of forests worldwide, affecting biodiversity and ecosystem functioning. However, the effect of selective logging on the dual nature of temporal stability, and the scale dependence of this effect, remain to be elucidated. By conducting several decade-long experiments in temperate forest ecosystems, we tested the effects of selective logging on aggregate and compositional stability at multiple spatial scales. As expected, forest ecosystem stability at larger spatial scales was enhanced both by the stability of local scales (i.e.  $\alpha$  stability) and asynchronous dynamics among local communities (i.e. spatial asynchrony). We found that the negative effects of selective logging on both facets of forest stability propagated from local to larger spatial scales due to reduced  $\alpha$  stability and the biological insurance effects of  $\alpha$  diversity. However, both spatial aggregate and compositional asynchrony were not affected by selective logging. Interestingly, despite the selective logging,  $\alpha$  diversity still provided biological insurance effects for maintaining aggregate and compositional stability. Our results imply that selective logging may destabilize the aggregate ecosystem functioning and species composition of forest ecosystems at local and larger spatial scales. To our knowledge, this study provides the first evidence of the scale dependence of aggregate and compositional stability of forest ecosystems in response to selective logging. Our findings suggest that forest management should avoid excessive selective logging and strive to protect forest diversity to safeguard the sustainability of the functioning and composition of natural forest ecosystems at multiple spatial scales.

Keywords: aggregate stability, compositional stability, diversity, ecosystem functioning, spatial asynchrony, stability



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## Introduction

More than half of all tree species around the world are under threat from deforestation, forest degradation, and human-driven environmental change (Gibson et al. 2011, Liang et al. 2016). Aboveground biomass (AGB) and its production are both important functioning of forest ecosystems and play a key role in the maintenance of various environmental services (Luyssaert et al. 2008, Liang et al. 2016, Gadow et al. 2021). Therefore, the ability of forests to maintain essential functions over time (hereafter denoted as ‘stability’) has become a major focus of research (Jucker et al. 2014, Schnabel et al. 2021, Qiao et al. 2022). Stability is usually defined as the temporal invariability of ecosystem functioning, specifically the temporal mean of forest functioning divided by its standard deviation (Tilman et al. 2006, Isbell et al. 2009, Hautier et al. 2015). In the face of an increasing threat of forest degradation and fragmentation, a comprehensive understanding of the role of anthropogenic disturbances on forest stability is thus essential for the sustainable use of forest resources.

Selective logging, which refers to the selective harvest of specific tree species and sizes, is a common form of forest use in many parts of the world (Meijaard and Sheil 2007, Edwards et al. 2014). Selective logging has been recognized as a more sustainable method of forest management than clearcutting (Gibson et al. 2011). Large areas of forests around the world are being affected by selective logging, and logged areas in many forest regions now exceed those of unlogged areas (Edwards et al. 2014, Lesiv et al. 2022). By removing a limited number of individual trees while leaving the rest intact, selective logging may change the composition and relative abundance of species, resulting in an increase or decrease in species diversity (Martin et al. 2015, Geng et al. 2021). As some individuals are removed leading to sparse stands, selective logging may change the original forest microclimate, soil moisture and nutrient status, and thus lead to changes in the processes affecting tree biology (Oldén et al. 2019, Huang et al. 2020). A growing number of studies have shown that high logging intensities may reduce biodiversity, disrupt forest structure, and impair the functioning of ecosystems (Asner et al. 2004, Martin et al. 2015, Huang et al. 2020). However, there is still a lack of research linking selective logging, biodiversity, and stability of forest ecosystems. Moreover, studies on the effects of selective logging on forest ecosystems have mostly focused on local spatial scales, leaving the response of biodiversity and stability across spatial scales largely unknown.

A theoretical framework has been developed in recent years to integrate the processes affecting stability in ecosystem function at local and larger spatial scales, which makes it possible to quantify the processes that determine stability across spatial scales (Wang and Loreau 2014). The theory focuses on aggregate stability, which refers to the temporal stability of aggregate ecosystem functions. Stability at larger spatial scales (i.e.  $\gamma$  stability) can be partitioned into two multiplicative components, namely local scale stability (i.e.  $\alpha$  stability) and asynchronous dynamics among local communities

(i.e. spatial asynchrony; Wang and Loreau 2014).  $\gamma$  stability can be fully explained by  $\alpha$  stability and spatial asynchrony (Wang and Loreau 2014). The ‘local insurance hypothesis’ suggests that asynchronous dynamics among species within local communities (i.e. species asynchrony) can enhance  $\alpha$  stability, as declines in functioning in some species are compensated for by functioning increases in other species over time (Yachi and Loreau 1999, Loreau et al. 2003). The ‘spatial insurance hypothesis’ suggests that asynchronous dynamics among local communities can enhance  $\gamma$  stability, as declines in the functioning of some local communities are compensated for by increases in other communities over time (Wang and Loreau 2014). This theory has been further developed to link biodiversity and stability at local and larger spatial scales, and suggests that greater local diversity (i.e.  $\alpha$  diversity) and higher species turnover across space (i.e.  $\beta$  diversity) may enhance  $\gamma$  stability mainly by increasing  $\alpha$  stability and spatial asynchrony, respectively (Wang and Loreau 2016, Fig. 1).

Several recent studies have tested the effects of various drivers, including anthropogenic factors, abiotic and biotic factors, on aggregate stability at local and larger spatial scales (Hautier et al. 2020, Wang et al. 2021, Qiao et al. 2022). However, while aggregate stability is an important facet of temporal stability, the latter also includes compositional stability (Micheli et al. 1999, Hillebrand et al. 2018, Lamy et al. 2021). Compositional stability refers to the temporal stability of the relative frequencies of component species, and is completely different from aggregate stability (Lamy et al. 2021). Although the importance of the dual nature of temporal stability is well recognized, most previous studies have focused solely on aggregate stability, while the analysis of compositional stability has been restricted to research at local spatial scales (Micheli et al. 1999). Recently a theoretical framework was proposed to evaluate compositional stability across scales (Lamy et al. 2021, Fig. 1), suggesting that complementary insights into the mechanisms controlling stability can be gained by simultaneously considering both facets of ecosystem stability, aggregate and compositional (Hillebrand et al. 2018). For instance, the same community may be classified as having low or high stability, depending on whether the focus is on compositional or aggregate stability (Micheli et al. 1999). Yet, both facets of temporal stability have hardly been investigated simultaneously in long-term empirical studies (Lamy et al. 2021). Selective logging is a widespread anthropogenic disturbance that has the potential to simultaneously affect both species composition and aggregate functioning of forest ecosystems. Therefore, in this study, we explore selective logging effects considering both aggregate and compositional stability simultaneously and across scales.

Selective logging may affect the links between biodiversity and stability at local and larger spatial scales in several ways. At local spatial scales, selective logging may alter species composition and relative species frequencies and thus affect  $\alpha$  diversity (Geng et al. 2021). Selective logging may destabilize local-scale forest functioning, since anthropogenic environmental changes affect ecosystem stability (Hautier et al. 2015). However, the understanding of whether the negative

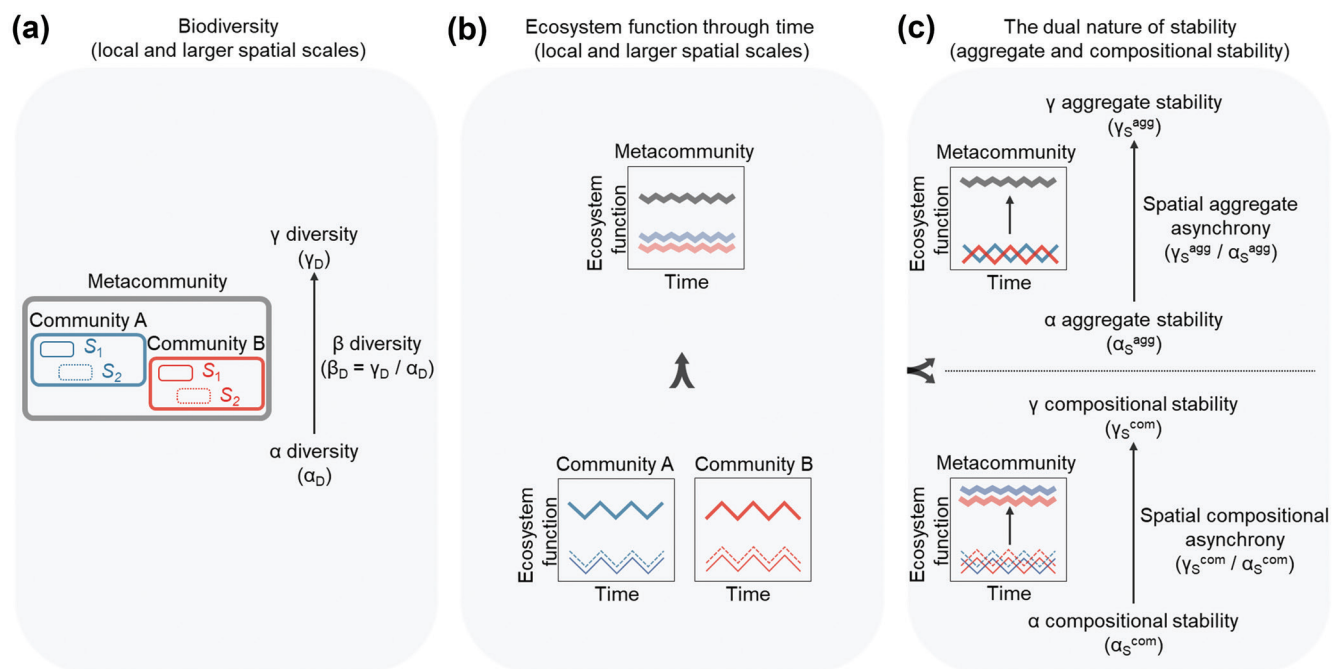


Figure 1. Conceptual figure showing biodiversity and stability at local and larger spatial scales. (a) Biodiversity, (b) ecosystem function through time, and (c) aggregate and compositional stability. In (a and b), the thinner dashed and continuous lines indicate different species ( $S_1$  and  $S_2$ ). The thicker blue and red lines represent different local communities (community A and community B). The grey lines represent the larger spatial scale, here refer to as the metacommunity. In (c), aggregate stability refers to the temporal stability of aggregate ecosystem functions, and compositional stability refers to the temporal stability of the relative frequencies of component species. Stability at larger spatial scales (i.e.  $\gamma$  stability) can be partitioned into two multiplicative components, namely local scale stability (i.e.  $\alpha$  stability) and asynchronous dynamics among local communities (i.e. spatial asynchrony).  $\gamma$  stability is always fully explained by  $\alpha$  stability and spatial asynchrony (Wang and Loreau 2016, Lamy et al. 2021).

effect of selective logging on  $\alpha$  stability further reduces  $\gamma$  stability, as reported in recent studies in grasslands, is still lacking regarding forest ecosystems (Zhang et al. 2019, Hautier et al. 2020, Liang et al. 2021). At larger spatial scales, there is uncertainty about whether and how selective logging affects spatial asynchrony, which leads to more uncertainty about the link between selective logging and  $\gamma$  stability. Selective logging may change the abiotic and biotic factors in forests and thus lead to reduced environmental heterogeneity among local communities, which may decrease spatial asynchrony as a consequence of synchronized local communities responding to similar environments (Wilcox et al. 2017, Qiao et al. 2022). In addition, if pioneer species have higher dispersal ability and become dominant after selective logging, this should reduce  $\beta$  diversity (Yano et al. 2021), and thus decrease spatial asynchrony. Alternatively, spatial asynchrony may not be directly affected by selective logging, and thus spatial asynchrony may be able to enhance ecosystem stability at larger spatial scales, even in the face of anthropogenic environmental changes (Zhang et al. 2019).

To test the effects of selective logging on aggregate and compositional stability across spatial scales and identify the associated mechanisms, we conducted a series of 10-year selective logging experiments in temperate forests in north-eastern China. In our analysis, we consider two facets of temporal stability, aggregate and compositional stability

across scales. To our knowledge, this is the first attempt to examine the scale dependence of selective logging effects on aggregate and compositional stability of forest ecosystems. We specifically analyze 1) the effects of selective logging on biodiversity across spatial scales at different measurement years; 2) the effect of selective logging intensity on aggregate and compositional stability across spatial scales; and 3) the links between selective logging, biodiversity and ecosystem stability across scales.

## Material and methods

### Study site and experimental design

The study sites are located in the experimental forest sites (43°58'N, 127°44'E) of the Jiaohe Management Bureau in Jilin Province, China (Supporting information). The region is characterized by a temperate continental climate influenced by a monsoon season (Yuan et al. 2019). The annual average temperature is 3.8°C and the annual average precipitation is 695.9 mm. Our experimental forests is a typical Korean pine and broadleaf mixed community. The dominant tree species are *Pinus koraiensis*, *Acer mono*, *Tilia amurense*, *Juglans mandshurica*, *Fraxinus mandshurica*, and a few pioneer species (*Populus davidiana* and *Betula platyphylla*).

Following the standard protocol proposed by Condit (1998), hundreds of permanent square forest plots (10 × 10 m) were established in six sites in 2009, 2010 and 2011 (Supporting information). The distance between any two plots is greater than 10 m. Within the plots, all individual woody stems with a diameter at breast height (DBH) ≥ 1 cm were marked, measured, identified, and stem-mapped before selective logging. A total of 20 992 individuals belonging to 32 species from 14 distinct families were present in our permanent forest plots during the study period (Supporting information). The ‘target tree silviculture method’ was used to select the trees to be harvested (Lu 2006), which is common in the region. Target trees are identified based on the prioritization of factors such as tree vigor, quality, rarity, commercial value. Trees that are defective, unhealthy, or competing with the target tree are removed. This logging method is thus beneficial for improving the quality and growth of the remaining target trees. It is worth noting that selective logging is not biased towards specific species and that the intensity of harvesting is similar for different diameters at breast height classes (Geng et al. 2021). Directional felling of trees was done with chainsaws, and all harvested material was concentrated on both sides of a skidding road, and transported away by bullock carts and tractors. Particular care was taken to extract the harvested material to avoid damage to the roots of live trees and saplings. Logging activities were carried out in each 10 × 10 m plot. The logging intensity in the four 5 × 5 m subplots was more or less the same, as far as possible. After logging, we quantified the logging intensity of each plot using percentage reduction in basal area (m<sup>2</sup> ha<sup>-1</sup>) and assigned these plots to one of the following four logging categories: ‘int1’, < 10% of basal area removed; ‘int2’, 10% ≤ and < 20% of basal area removed; ‘int3’, 20% ≤ and < 30% of basal area removed; ‘int4’, ≥ 30% of basal area removed. The number of four logging categories in each site is the same. All trees were measured before and immediately after the selective logging activities and were re-measured at least 2 times ten years after logging. AGB was estimated based on a set of regional- and species-specific allometric models with DBH as the independent variable (Supporting information). We calculated forest productivity as the increase in biomass per ha between consecutive years (i.e. kg ha<sup>-1</sup> year<sup>-1</sup>). When a temporal trend in forest biomass and biomass productivity was detected (by regressing the biomass and productivity, normalized to annual values, for each inventory interval against time) we applied a detrending procedure (Tilman et al. 2006, Yuan et al. 2019).

### Stability across scales

Investigating stability across spatial scales requires defining a local (α) scale and a larger (γ) spatial scale (Zhang et al. 2019, Hautier et al. 2020). In the study of forest ecosystems, different spatial grains are commonly used to define spatial scales (Chisholm et al. 2013, Qiao et al. 2021b, Reu et al. 2022). In our study, each 10 × 10 m larger quadrat represents the larger (γ) spatial scale, and each of the

four non-overlapping 5 × 5 m local quadrats represents the local (α) spatial scale (Supporting information). We then quantified aggregated and compositional stability of forest ecosystem functioning (i.e. biomass and biomass productivity) across spatial scales (Lamy et al. 2021, Wang et al. 2021). These stability metrics indicate the temporal stability of forests in fluctuating environments and have been used as proxies for the temporal stability of forest ecosystem functioning (Jucker et al. 2014, Yuan et al. 2019, Ouyang et al. 2021). We defined aggregate stability at larger spatial scales (γ aggregate stability,  $\gamma_S^{\text{agg}}$ ) as the reciprocal of the square coefficient of temporal variation of the ecosystem functioning of the larger quadrats. We defined aggregate stability at local spatial scales (α aggregate stability,  $\alpha_S^{\text{agg}}$ ) as the reciprocal of the weighted average of the squared coefficients of temporal variation in ecosystem functioning across the four local quadrats. Spatial aggregate asynchrony ( $\varphi^{\text{agg}}$ ) was defined as the ratio between γ aggregate stability to α aggregate stability as follows:

$$\varphi^{\text{agg}} = \left( \sum_i^4 \sigma_{Ti} / \sigma_{TT} \right)^2 \quad (1)$$

where  $\sigma_{TT}$  denotes the temporal standard deviation of the total ecosystem functioning at larger spatial scales,  $\sigma_{Ti}$  denotes the temporal standard deviation of ecosystem functioning in local quadrat  $i$ , and  $\mu_{TT}$  denotes the temporal mean of the total ecosystem functioning in the bigger quadrat.

We defined compositional stability at larger spatial scales (γ compositional stability,  $\gamma_S^{\text{com}}$ ) as the reciprocal of the compositional variability of the bigger quadrat. At local spatial scales, we defined α compositional stability ( $\alpha_S^{\text{com}}$ ) as the reciprocal of the weighted average of the compositional variability across the four local quadrats. In both cases, compositional variability was measured as β diversity based on the Hellinger distance. Spatial compositional synchrony ( $\varphi^{\text{com}}$ ) was defined as the ratio between γ compositional stability to α compositional stability, as follows:

$$\varphi^{\text{com}} = \sum_i^4 \frac{X_{i..}}{X_{...}} \sum_j^s v_{ij}^b / \sum_j^s v_{Tj}^b \quad (2)$$

where  $v_{Tj}^b$  denotes the temporal variation of the Hellinger-transformed biomass/productivity of species  $j$  at larger spatial scales,  $v_{ij}^b$  denotes the temporal variance of the Hellinger-transformed ecosystem functioning of species  $j$  in local quadrat  $i$ .  $X_{i..}$  denotes the total ecosystem functioning of local quadrat community  $i$ , while  $X_{...}$  denotes total ecosystem functioning of the bigger quadrat. The above metrics were calculated using the *metacommunity\_variability* function from the ‘ltmc’ package which was developed by Lamy et al. (2021). In order to test the robustness of our results, we also calculated the stability based on forest biomass and forest productivity respectively, which yielded similar results (refer to Supporting information).

## Biodiversity across scales

Theory suggests that Simpson-based diversity metrics, which take into account both the number of species and the evenness of species abundance, best explain ecosystem stability at different spatial scales (de Mazancourt et al. 2013, Wang et al. 2021). In addition, the inverse of the Simpson concentration index is a true diversity index (i.e. diversity of order 2), and as such provides an effective number of species (Jost 2006). Therefore, we quantified species diversity using the inverse of the Simpson concentration index,  $1/\sum_i p_i^2$ , where  $p_i$  is the observed relative abundance of species  $i$ . Specifically,  $\alpha$  diversity ( $\alpha_D$ ) was measured as the inverse of a weighted average of local quadrats-level Simpson indices, weighted by the relative forest biomass stock of local quadrats in the year of the remeasurement.  $\gamma$  diversity ( $\gamma_D$ ) was measured as the inverse of the Simpson index at the bigger quadrats.  $\beta$  diversity ( $\beta_D$ ) was defined following a multiplicative framework as the ratio between  $\gamma$  diversity and  $\alpha$  diversity. In order to test the robustness of our results, we also calculated species diversity based on species richness (refer to Supporting information).

## Statistical analysis

All analyses were conducted using the R software unless specified otherwise (www.r-project.org, ver. 4.1.0). Linear mixed-effects models (LMM) were used to test the effects of selective logging on  $\alpha$ ,  $\beta$  and  $\gamma$  diversity at each measurement year, and the effects of selective logging intensity on spatial asynchrony,  $\alpha$  stability and  $\gamma$  stability, using the *lme* function of the 'nlme' package (Pinheiro et al. 2013). The fixed effect in these models was *selective logging intensity* with *site* as the random effect. One-way analysis of variance (ANOVA) and Tukey's post hoc test were used to test any significant differences in species diversity and stability across the four logging intensity categories. This method was also applied to test for significant differences in the basal area of the different treatments pre- and post-logging. To ensure that plots are independent of each other (Dormann et al. 2007, Chisholm et al. 2013), we used generalized least-square models (GLS) to estimate spatial autocorrelation based on the location coordinates (X and Y coordinates) of each plot. No spatial autocorrelation was detected in our study, which is consistent with several other studies in broadleaved Korean pine forests (Yuan et al. 2016, Hao et al. 2019). Before performing the statistical analysis, the diversity and stability variables were naturally log-transformed to meet the normality requirements of the data analysis (Wang et al. 2021).

LMM was used to test the biodiversity-stability relationship (BSR) to investigate how biodiversity and stability across spatial scales respond to selective logging. Piecewise structural equation modeling (SEM) was then used to illustrate the different pathways by which selective logging affected  $\gamma$  aggregate and compositional stability. We developed a SEM framework based on prior knowledge of the mechanisms driving biodiversity and stability across spatial scales, to examine

potential pathways of selective logging intensity effects on biodiversity and stability at both local and larger spatial scales (Supporting information). The SEM was estimated using the 'piecewise' package (Lefcheck 2016). Fisher's C statistics and AIC were used to evaluate the overall fitness of SEM, that is, when the model had a Fisher's C statistic with  $p > 0.05$ , we assume that the model provides an adequate fit (Shipley 2009). To obtain standardized path coefficients, all explanatory variables were standardized (average=0 and SD=1) prior to the SEM analysis.

## Results

Over the 10-year period selective logging significantly decreased both  $\alpha$  diversity ( $F_{1,1663}=197.68$ ,  $p < 0.001$ ) and  $\gamma$  diversity ( $F_{1,1663}=141.71$ ,  $p < 0.001$ ), but was not significantly associated with  $\beta$  diversity ( $F_{1,1663}=2.20$ ,  $p > 0.05$ ). The effect of selective logging on diversity across scales appears to be changing over time (Fig. 2, Supporting information). In the first few years after logging,  $\alpha$  and  $\gamma$  diversity were negatively related to selective logging ( $p < 0.001$ ). However, in the tenth year after logging, selective logging was no longer significantly associated with diversity across spatial scales ( $p > 0.05$ ). We also assessed the relationship between selective logging and richness-based metrics of  $\alpha$ ,  $\beta$  and  $\gamma$  diversity, obtaining qualitatively similar results (Supporting information). At local spatial scales, increasing selective logging intensity decreased  $\alpha$  aggregate ( $F_{1,501}=140.71$ ,  $p < 0.001$ ) and compositional ( $F_{1,501}=171.01$ ,  $p < 0.001$ ) stability (Fig. 3a). Negative effects thus propagated to larger scales and lead to a lower  $\gamma$  aggregate ( $F_{1,501}=100.37$ ,  $p < 0.001$ ) and compositional ( $F_{1,501}=163.29$ ,  $p < 0.001$ ) stability (Fig. 3b). Selective logging intensity had no significant effect on spatial aggregate and compositional asynchrony ( $F_{1,501}=3.29$ ,  $p > 0.05$ ;  $F_{1,501}=2.22$ ,  $p > 0.05$ ; Fig. 3c).  $\alpha$  stability and  $\gamma$  stability of the *int4* were significantly lower than those of the other treatments ( $p < 0.05$ ; Supporting information).

We found evidence of positive BSRs both at local and larger spatial scales, when considering both aggregate and compositional stability (Fig. 4a,c,d,f). However, BSRs were not significant when considering the relationship between  $\beta$  diversity and spatial asynchrony, whether considering aggregate or compositional stability (Fig. 4b,e). The magnitude and direction of BSRs greatly varied across treatments (Fig. 4). Results based on species richness were similar to those based on the Simpson-based diversity metric (Supporting information). Our final SEM showed that selective logging decreased  $\gamma$  stability mainly by reducing  $\alpha$  stability at local spatial scales (Fig. 5, Supporting information). Selective logging had a negative effect on  $\alpha$  diversity but no significant effect on  $\beta$  diversity and spatial asynchrony.  $\alpha$  diversity promoted  $\alpha$  aggregate and compositional stability. The effect of  $\beta$  diversity on both spatial compositional and aggregate asynchrony was not significant.

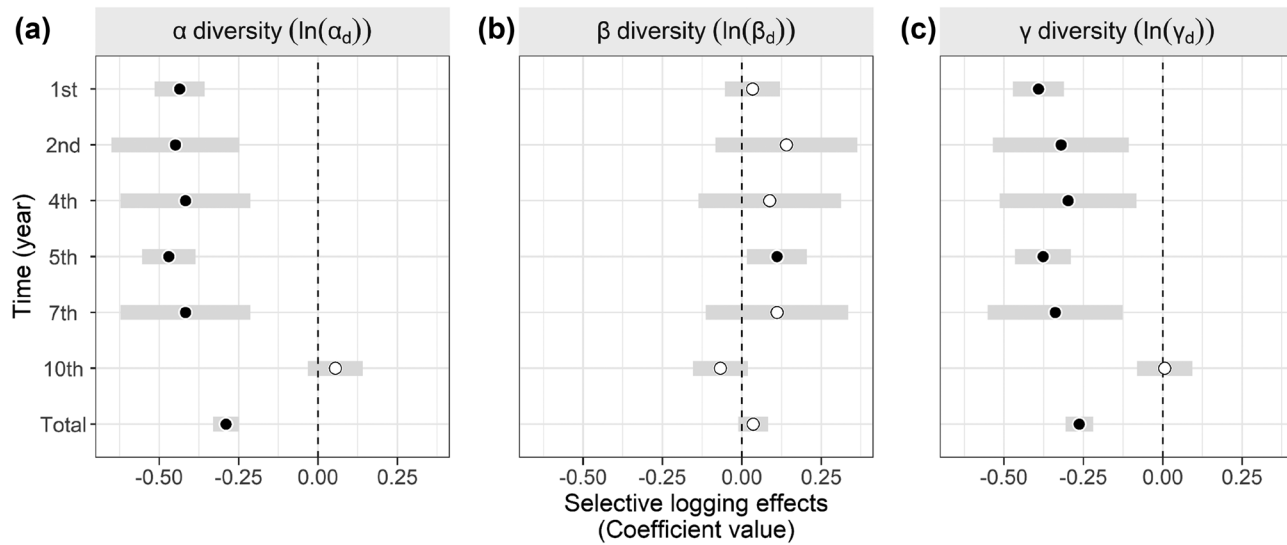


Figure 2. Effects of selective logging on biodiversity across spatial scales. (a)  $\alpha$  diversity; (b)  $\beta$  diversity; and (c)  $\gamma$  diversity. The points and shades represent the estimated mean and confidence interval (95%) of the model, respectively. Confidence intervals not overlapping with the dashed line ( $x=0$ ) indicate statistical significance ( $p < 0.05$ ). Solid symbols indicate statistical significance ( $p < 0.05$ ) and hollow symbols indicate no statistical significance ( $p > 0.05$ ).

## Discussion

This study provides a comprehensive analysis of the long-term effects of selective logging on the stability of our temperate forests across scales. Our results show that selective logging had a negative effect on biodiversity and stability across spatial scales, and provide empirical evidence for the scale-dependent effects of selective logging on forest aggregate and compositional stability. Interestingly, spatial asynchrony among local communities promoted forest stability at

larger spatial scales and was not directly affected by selective logging, when considering both aggregate and compositional stability. Our findings highlight the importance of considering the dual nature of ecosystem stability to obtain a comprehensive understanding of ecological stability in natural and complex forested landscapes in response to anthropogenic disturbance.

The specific logging activities significantly reduced biodiversity at the local and larger spatial scale (Fig. 2). Several previous studies have evaluated the direction and strength of

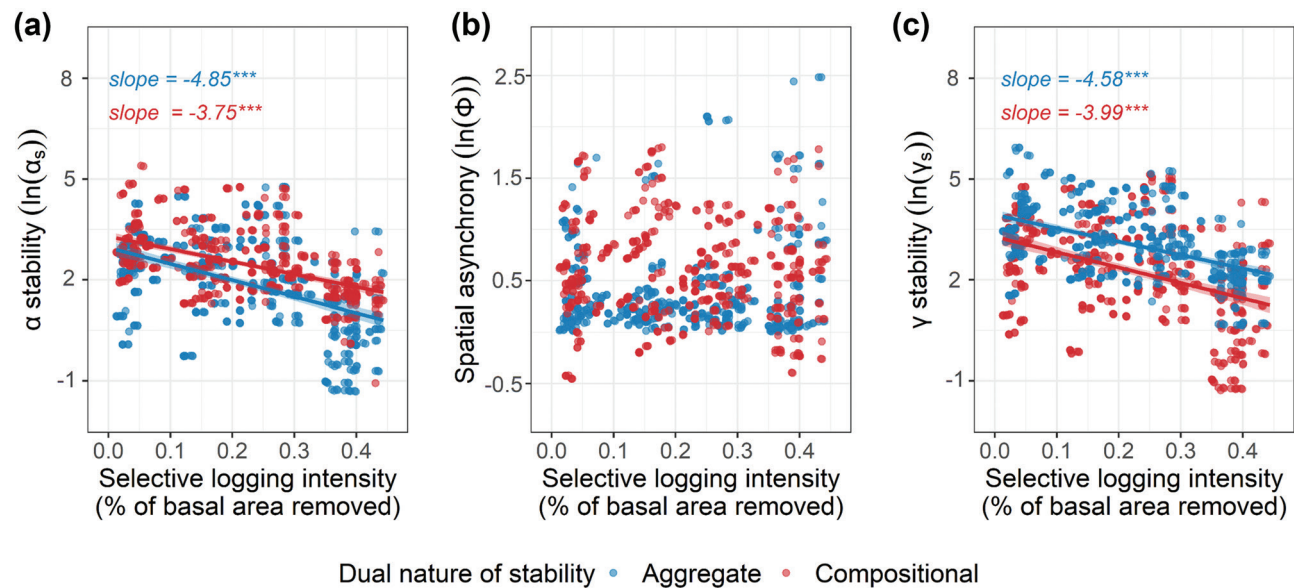


Figure 3. Effect of different selective logging intensities on compositional and aggregate stability at local to larger spatial scales. Relationships between selective logging and (a)  $\alpha$  stability, (b) spatial asynchrony and (c)  $\gamma$  stability. Fitted regression is significant at  $p < 0.05$ , and the relationships without fitted lines are non-significant at  $p > 0.05$ .

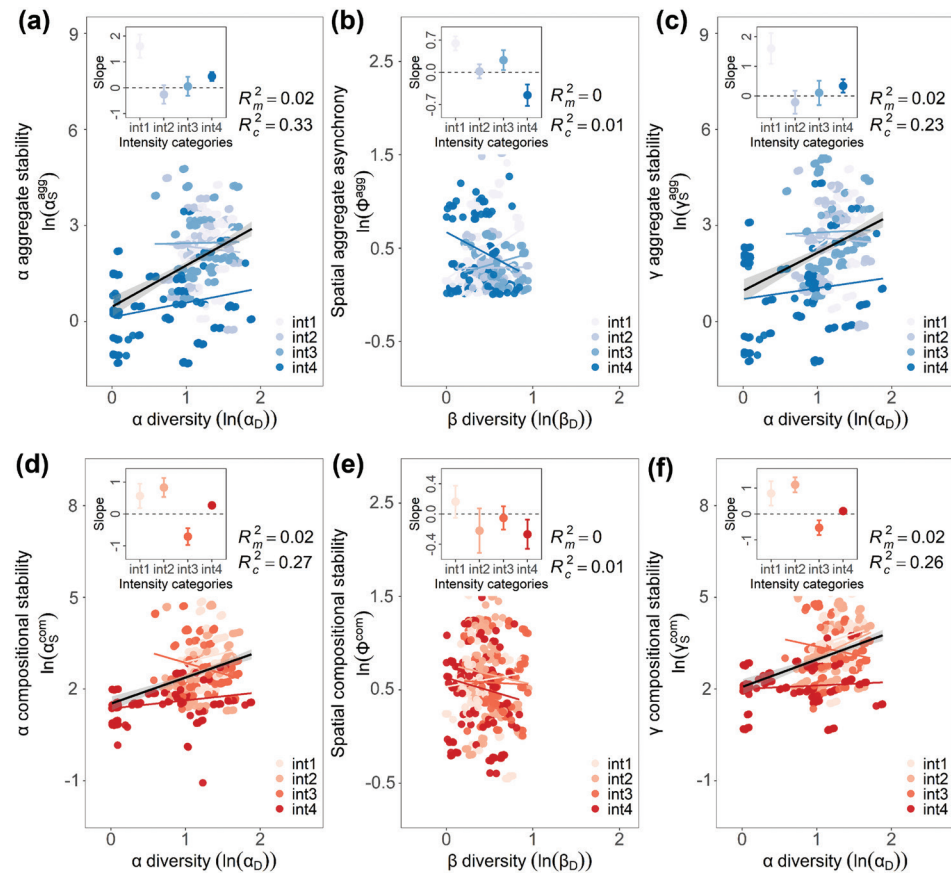


Figure 4. Relationships between biodiversity and stability at local and larger spatial scales. Relationship between: (a)  $\alpha$  diversity and  $\alpha$  aggregate stability; (b)  $\alpha$  diversity and  $\gamma$  aggregate stability; (c)  $\beta$  diversity and spatial aggregate asynchrony; (d)  $\alpha$  diversity and  $\alpha$  compositional stability; (e)  $\alpha$  diversity and  $\gamma$  compositional stability; and (f)  $\beta$  diversity and spatial compositional asynchrony, respectively. The insets in the figure represent the slope of the BSR at four logging intensity categories: int1, < 10% of basal area removed; int2, 10% ≤ and < 20% of basal area removed; int3, 20% ≤ and < 30% of basal area removed; int4, ≥ 30% of basal area removed. The fitted regression is significant at  $p < 0.05$ , and the relationships without fitted lines are non-significant at  $p > 0.05$ . The black lines represent the overall relationship (fixed effect), and the respective bands represent the 95% confidence intervals. Abbreviations:  $R_m^2$ , marginal  $R^2$ ;  $R_c^2$ , conditional  $R^2$ .

selective logging effects on biodiversity, but the results were inconsistent or even contradictory (Martin et al. 2015). The inconsistency of these results was attributed to the fact that different studies may have used different logging intensities, diversity metrics, and taxonomic groupings. Our 10-year empirical studies of the effects of selective logging on species diversity includes six-time steps corresponding to the 1st, 2nd, 4th, 5th, 7th, and 10th year following logging. We found that selective logging significantly reduced  $\alpha$  and  $\gamma$  diversity up to 7 years (in 1st, 2nd, 5th and 7th re-measurement), and recovered to the pre-logging diversity after 10 years. Therefore, the time span following logging might explain discrepancies among previous studies regarding the direction and strength of selective logging on biodiversity.

Selective logging had negative impacts on both aggregate and compositional stability at local spatial scales. This negative impact on forest stability propagates from local to larger spatial scales, as  $\alpha$  stability is the major driver of  $\gamma$  stability (Fig. 5). Several studies on the impact of human disturbance on community aggregate stability in grassland ecosystems

reported similar results. For example, both grazing and nitrogen addition indirectly reduced  $\gamma$  aggregate stability by reducing  $\alpha$  aggregate stability (Zhang et al. 2019, Liang et al. 2021). It should be noted, however, that human disturbances in grassland ecosystems differ from selective logging disturbances in forest ecosystems (Hautier et al. 2015, Geng et al. 2021). Indeed, grazing and nitrogen application in grasslands are usually carried out annually or even monthly, whereas logging in forests occurs at longer intervals (Asner et al. 2004). The negative impact of selective logging on  $\gamma$  stability is lower than that of  $\alpha$  stability, since asynchronous responses among local communities to environmental fluctuations provide spatial insurance effects for maintaining ecosystem stability at larger spatial scales (Loreau et al. 2003, Wang et al. 2021, Qiao et al. 2022).

The theory of the dual nature of metacommunity variability assumes that aggregate variability and compositional variability are independent of each other. The two facets of temporal stability at multiple scales thus require different interpretations.  $\alpha$  diversity affects  $\alpha$  aggregate and

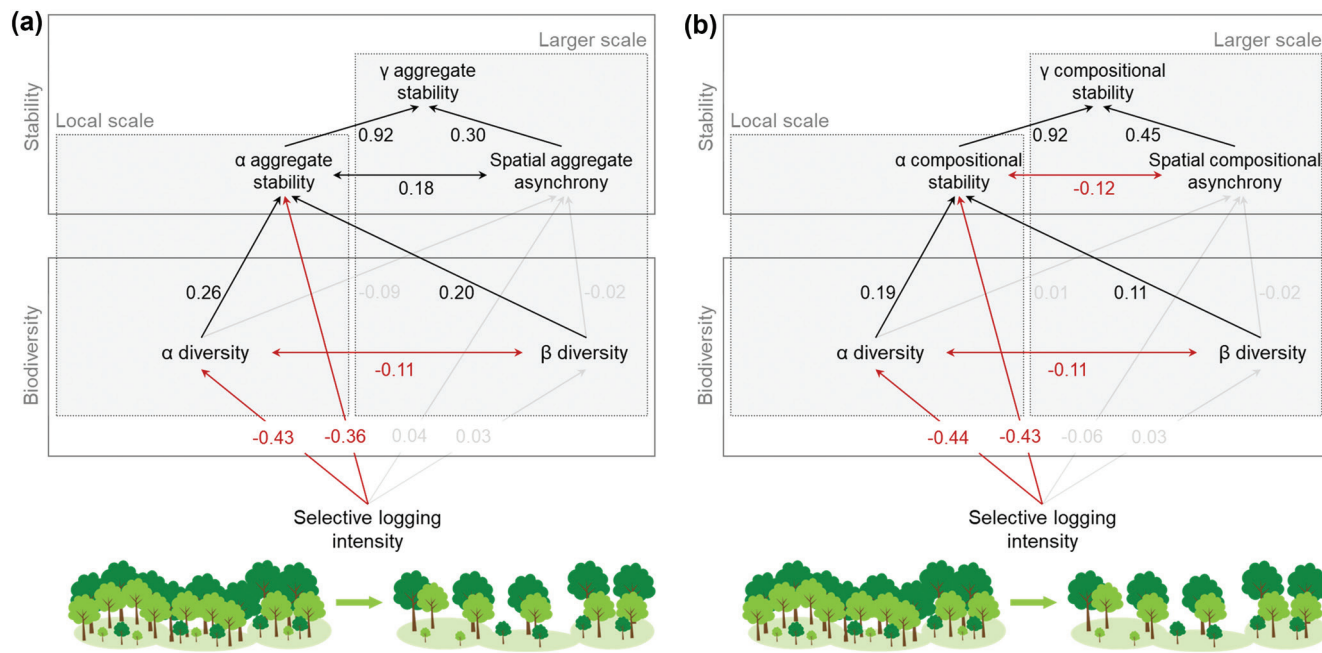


Figure 5. Piecewise structural equation modeling (SEM) depicting the direct and indirect effects of selective logging on biodiversity and stability across scales. (a) Aggregate stability across scales; (b) compositional stability across scales. Results of the final model fitting: (a) Fisher's  $C = 2.906$ ,  $p = 0.821$ ,  $AIC = 52.906$ ; (b) Fisher's  $C = 5.605$ ,  $p = 0.469$ ,  $AIC = 55.605$ . Single-headed arrows represent causal pathways while double-headed arrows correspond to co-varying variables. Black and red solid arrows indicate significant positive and negative coefficients ( $p < 0.05$ ), respectively. Grey lines arrows indicate non-significant ( $p > 0.05$ ) coefficients. Numbers next to the arrow correspond to standardized effect size.

compositional stability positively (Fig. 5). Yachi and Loreau (1999) proposed the biological insurance hypothesis to explain the positive effects of biodiversity on aggregate stability at local spatial scales. Biodiversity can promote the functioning of ecosystems in fluctuating environments through 1) 'buffering effects', i.e. increased temporal stability in ecosystem properties due to different responses of species to environmental variations; and 2) a 'performance-enhancing effect', i.e. an increase in the mean level of the functioning of ecosystems when the best performing species are favored in every environmental condition (Yachi and Loreau 1999, Loreau and Way 2010). We found that in the case of our selective logging,  $\alpha$  diversity may still provide biological insurance to maintain aggregate and compositional stability. This means that plots with more species on average display a more stable species composition (i.e. relative frequencies of the different species) and aggregate ecosystem functions (i.e. biomass and productivity) through time. Changes in species composition could be attributed to several factors including different responses of species to environmental change (Lamy et al. 2021). These results may indicate that both performance-enhancing effects and buffering effects play important role in the positive (BSR) affected by selective logging disturbances. In addition, we found that  $\beta$  diversity was not significantly associated with spatial aggregate asynchrony. Most theoretical and empirical studies have reported positive relationships between  $\beta$  diversity and spatial aggregate asynchrony (Hautier et al. 2020, Wang et al. 2021, Qiao et al. 2022). However, non-significant relationships have also been

reported (Wilcox et al. 2017, Zhang et al. 2019). This may be due to differences in spatial extent and grain size of the plots. Several studies have shown that the  $\beta$  diversity-spatial asynchrony relationship may vary with the spatial extent and the grain size used in the analysis (Wang and Loreau 2016, Qiao et al. 2022). The same results were obtained for the biodiversity-functioning relationship (Chisholm et al. 2013, Qiao et al. 2021a, Reu et al. 2022).

As suggested by theory (Wang and Loreau 2014, Lamy et al. 2021), we found a positive effect of spatial asynchrony on  $\gamma$  stability when considering both aggregate and compositional facets of temporal stability. Asynchronous responses across local communities, notably in response to environmental fluctuations, allow for compensatory changes across space, thus buffering temporal fluctuations in aggregate ecosystem functions at larger spatial scales (Loreau et al. 2003, Wang and Loreau 2014). Several theoretical and empirical studies report that spatial aggregate asynchrony can provide spatial insurance effects for maintaining aggregate stability at larger spatial scales (Wang and Loreau 2016, Liang et al. 2021, Qiao et al. 2022). In our study neither spatial aggregate asynchrony nor spatial compositional asynchrony were affected by selective logging. Such spatial asynchrony among local communities may help to stabilize forest ecosystems at larger spatial scales, despite selective logging disturbances.

We acknowledge that there are some limitations to this study, although our experimental unit is extensive compared with several other smaller selective logging experiments (Martin et al. 2015, Huang et al. 2020). According to the



experience gained in previous studies, (BSRs) are affected by the spatial extent and grain size (Zhang et al. 2018). The effects of forest logging activities are usually assessed at the landscape level (Gibson et al. 2011). Although our study area is large, the scale of our  $\gamma$  diversity is smaller than that of a large natural forest landscape. Nevertheless, our results provide a systematic basis for the assessment of scale dependent effects of selective logging in natural forests that may guide future studies. Landscape-level selective logging experiments may provide additional evidence of landscape-level processes of community assembly and the potential impact on ecological restoration. The effect of anthropogenic disturbance on compositional stability at the local scale has been receiving greater attention in other ecosystems (such as grasslands) (Xu et al. 2022, Li et al. 2023). Based on our results, embracing the dual nature of ecosystem stability across spatial scales in different taxa will contribute to a better understanding of the overall stability of ecosystems in the future.

## Conclusions

This study presents evidence about the long-term effects of selective logging on ecosystem stability at different spatial scales in natural temperate forests. Selective logging had a negative effect on stability across spatial scales and these effects propagated from local to larger spatial scales. Selective logging reduced diversity at the local and larger spatial scales. Interestingly,  $\alpha$  diversity still provided biological insurance effects for maintaining aggregate and compositional stability despite the selective logging. We found a positive contribution of spatial asynchrony in stabilizing forest productivity at larger spatial scales. Neither spatial aggregate asynchrony nor spatial compositional asynchrony was directly affected by the selective logging. Based on these results, we suggest that it is important to maintain local tree species diversity during selective logging to safeguard forest stability at different spatial scales. Asynchronous dynamics among local communities contribute to stabilizing the functioning and composition of forest ecosystems, despite disturbances caused by selective logging. Future research may find our multiscale approach helpful in designing and analyzing other logging experiments, and thus provide a scientific basis for sustainable management of complex natural forests.

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## Data availability statement

Data are available from the Figshare Digital Repository: <https://doi.org/10.6084/m9.figshare.23683395> (Qiao et al. 2023).

## Supporting information

The Supporting information associated with this article is available with the online version.

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