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RESEARCH ARTICLE

Biomass temporal stability increases at two spatial scales during secondary succession

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Abstract

1. Ecological stability has long been considered to change over succession, but how secondary succession influences the relationship between diversity and temporal stability of biomass production at different spatial scales is poorly understood.
2. We studied changes in plant diversity, functional temporal stability (biomass production) and compositional temporal stability (the latter two are hereafter referred to as functional stability and compositional stability) and explored the stabilizing roles of plant diversity at two spatial scales (small plots of 0.25 m^2 and large transects of 1.25 m^2) during secondary succession in a subalpine meadow from 2003 to 2010.
3. Our results showed that both plant diversity and functional and compositional stability increased at the small plot scale and large transect scale during secondary succession. As secondary succession proceeded, higher average alpha diversity (i.e. species diversity at the plot scale) led to higher functional and compositional stability at the plot scale by mainly species stability, predominantly contributing to higher functional and compositional stability at the large transect scale. In addition, Simpson-based beta diversity (i.e. compositional dissimilarity among communities within the same transect), while unaffected by succession, contributed to functional stability at the large transect scale by promoting asynchronous dynamics among communities.
4. *Synthesis*. Our study highlights the stabilizing effects of plant diversity across the two spatial scales during secondary succession. Our findings provide the first empirical evidence that biodiversity-mediated effects on ecosystem temporal stability strengthen over successional time, suggesting that the stabilizing effects of biodiversity should be considered across spatial and temporal scales in the face of global changes and biodiversity loss.

KEYWORDS
beta diversity, ecosystem stability, old fields, spatial asynchrony, spatial scale, succession, temporal scale

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Wenjin Li and Xi Zhou authors contributed equally to this work as co-first authors.

1 | INTRODUCTION

Ecological stability is a multidimensional concept that can be quantified using various metrics, often including resistance, resilience, recovery and temporal stability (Donohue et al., 2013; Grimm & Wissel, 1997; Pimm, 1984; White et al., 2020). Temporal stability, which can be quantified using the inverse of the coefficient of variation, is the most common aspect among stability metrics (Donohue et al., 2016). Furthermore, most studies have focused on the temporal stability of biomass production (Donohue et al., 2016; Tilman et al., 2006; Wagg et al., 2022), which is more formally defined as the degree of biomass fluctuation over time (Tilman, 1996; Wagg et al., 2022) and calculated as the ratio of the mean of community biomass to its standard deviation in a given ecosystem (Tilman, 1996). The temporal stability of biomass production is also the measure of stability adopted in the present study because (i) it is an integrative measure of stability (Loreau, 2022), frequently used in ecology (Donohue et al., 2016; Tilman et al., 2006); (ii) it describes the combined effects of resistance and resilience on community dynamics over time (Clark et al., 2021) and (iii) it is also very useful when examining the stability of a community to sustain temporally stable biomass production across multiple years (Lehman & Tilman, 2000).

In the past two decades, many studies have emphasized the effects of global change, including nutrient addition, precipitation change, elevated CO_2 and warming (Su et al., 2022), and diversity change (Tilman et al., 2006), on the local temporal stability of biomass. However, predicting the relationships between biodiversity and ecological stability at different temporal and spatial scales remains challenging in ecology (Clark et al., 2021; Wang & Loreau, 2016). Theoretical and experimental research over the past decade has begun to explore ecosystem stability at larger spatial scales (Hautier et al., 2020; Liang et al., 2022; Wang et al., 2021; Wang & Loreau, 2014; Wilcox et al., 2017) and has revealed that ecosystem stability often increases with the spatial scale (Qiao et al., 2022; Wang et al., 2017). The theory predicts that ecosystem stability (γ stability) at a large spatial scale is driven by local community stability and asynchronous dynamics among local communities (spatial asynchrony; Wang et al., 2019; Wang & Loreau, 2014, 2016). For example, Wilcox et al. (2017) revealed that spatial asynchrony among local communities was an important predictor of stability at large spatial scales in global grasslands. Clark et al. (2021) showed that the joint stabilizing effects of both plant α and β diversity contribute to the stability of the grassland ecosystem at a large scale in North America and Europe. However, these empirical studies covered relatively short periods and mainly addressed the effects of spatial scale on ecosystem stability (Hautier et al., 2020; Liang et al., 2022). The studies did not examine the effects of temporal scale (e.g. duration of experiments), especially the successional stage (e.g. ecosystem development and land-use change), on ecosystem stability, which limits our understanding to longer-term, large-scale ecosystem management and conservation (Qiu & Cardinale, 2020). Indeed, ecosystem stability changes with the duration of experiments or observations (Luo et al., 2021; Pimm & Redfearn, 1988; Wagg et al., 2022). The duration of experiments can also change biodiversity–ecosystem functioning relationships (Meyer et al., 2016; Wagg et al., 2022). The plant diversity–productivity relationship often strengthens with the duration of artificially assembled biodiversity experiments (Meyer et al., 2016; Qiu & Cardinale, 2020). Species complementarity and asynchrony can take more than 10 years to play a strong role in stabilizing the effects of biodiversity on productivity in plant communities (Wagg et al., 2022). Thus, these results suggest that the duration of experiments or observations could modulate the effects of biodiversity on ecosystem stability (Wagg et al., 2022). However, to the best of our knowledge, the effects of successional change on ecosystem temporal stability via biodiversity across temporal and spatial scales remain largely unexplored.

The study of ecological succession is often regarded as a promising approach for addressing the temporal dynamics of ecosystem structure and functioning (Foster & Tilman, 2000; Prach & Walker, 2011; Walker & Wardle, 2014). Classic ecological succession studies indicate that population fluctuations and species turnover during succession depend on scales of time and space (Connell & Slatyer, 1977). The earliest synchronic chronosequence studies (Cowles, 1899; Oosting, 1942) and diachronic permanent plot studies (Foster & Tilman, 2000) have claimed that the rate of community change decreased during primary or secondary succession (Anderson, 2007; Li et al., 2016). Succession can also alter biodiversity and ecosystem functioning relationships (Lasky et al., 2014; Mori et al., 2017). One of the longest-running biodiversity experiments, conducted in Jena, Germany, has shown that the temporal stabilizing effect of species richness on plant productivity increased with community age at the local scale (Wagg et al., 2022). In recent years, with growing awareness of the spatial scale dependence of biodiversity and ecosystem functioning (Gonzalez et al., 2020; Isbell et al., 2018), β diversity has attracted increasing attention (Mori et al., 2018; Reu et al., 2022), and it has been determined that β diversity contributes to increasing ecosystem functioning (Mori et al., 2018) and ecosystem stability (Clark et al., 2021; Mellin et al., 2014) at large spatial scales. However, it is not clear whether β diversity consistently influences ecosystem stability at large spatial scales through spatially asynchronous dynamics among local communities during succession.

In our study, a chronosequence of five old fields (1, 3, 5, 15 and 30 years since abandonment) and one natural meadow (without agricultural land use for approximately 100 years) in a subalpine meadow was employed to assess how secondary succession influences the relationship between the diversity and stability of biomass production at two spatial scales and the underlying mechanisms. We quantified temporal stability from functional (biomass) and structural (composition) perspectives to reflect ecosystem and community dynamics. The following hypotheses were specifically tested:

(i) Plant diversity and functional and compositional stability at the plot and transect scales increase over succession because community change rates generally decline over the course of succession (Anderson, 2007).

(ii) This increase in functional and compositional stability at two spatial scales is driven by increasing plant diversity over succession. Because increased average α plant diversity at the plot scale during succession (Li et al., 2017) induces greater α functional and compositional stability at the plot scale and a decline in β diversity over succession, resulting in lower asynchronous dynamics among local communities (Wang & Loreau, 2014, 2016), the relative contribution of α diversity to functional and compositional stability at the large transect scale is greater than that of β diversity.

2 | MATERIALS AND METHODS

2.1 | Study sites and experimental design

The study site was located at the Gannan Grassland Ecosystem National Observation and Research Station and established on a subalpine meadow on the eastern Qinghai-Tibetan Plateau, China (N34°55′, E102°53′). Using a space-for-time substitution approach, we selected different stages of secondary succession consisting of five old fields (1, 3, 5, 15 and 30 years since abandonment) and one natural meadow (without agricultural land use for approximately 100 years) by referring to the historical data of local land use and interviewing the local herdsmen. We also considered that the early-stage plant communities were dominated by annual or biennial weeds and herbs, such as *Aconitum gymnandrum*, *Poa annua* and *Potentilla sp*., and that the later stage plant communities were dominated by perennial species, such as *Elymus nutan*, *Kobresia humilis* and *Roegneria nutans* (Li et al., 2009). All sites share similar substrate, topographic position and historic cultivation conditions (Li et al., 2017). The only agricultural practice in this alpine region is rotational cultivation of oat (*Avena sativa*)—fallow—and rapeseed (*Brassica napus*) in the last century (Li et al., 2009). After the cessation of cultivation, these abandoned meadows were grazed by livestock until 2003. Afterward, large herbivores were excluded using a wire fence. The area of these study meadows is small, ranging from 0.10 to 0.20 ha, located within an area of 10 km^2 at a similar elevation (from 2926 to 3000 m above sea level) and at least 300 m apart. The annual mean temperature is 3.2°C, ranging from 9.9°C in January to 12.8°C in July. The mean annual rainfall was 540 mm from 2000 to 2010, with 86% of the precipitation concentrated during the growing season. The natural vegetation in this region is typical subalpine meadow, which is dominated by *Agrostis hugoniana* Rendle, *Stipa aliena* Keng, and *Kobresia humilis* (C. A. Mey.) Serg and *Polygonum viviparum* L. In some patches, a shrub, sea buckthorn (*Hippophae rhamnoides*), is also present, but not in our study sites.

In July 2003, two parallel transects (A and B) were established at each old field site and at the control meadow, and 10 permanent 50 × 50 cm sampling plots were established along the two transects inside each field. The distance between the two parallel transects ranged from 5 to 8 m; both transects were located at least 5 m from the edge. The interval between two adjacent plots within each transect was 3.5 m. The plots in each old field were sampled annually every August from 2003 to 2010 (with the exception of 2005, when no sampling was conducted). All above-ground biomass was estimated by clipping the above-ground plant parts at the 1 cm soil surface level. All clipped plants were sorted into individual species and litter and then dried to a constant mass at 60°C. Species diversity is quantified as species richness (i.e. number of species in the plot or transect), and plant biomass is quantified as the weight of aboveground dry materials per m^2.

2.2 | Alpha, beta and gamma diversity

Species diversity and temporal stability of biomass were considered at both the plot scale (0.25 m^2 area) and transect scale (1.25 m^2 area). Each 0.25 m^2 plot was treated as the small plot scale, and the combination of the five replicated plots along a transect was classified as the large transect scale. The Simpson-based diversity index can best explain ecosystem stability at different spatial scales (Wang & Loreau, 2016). Therefore, we calculated the Simpson index $D_k = \sum_i^S {p_{ik}}^2$, where p_{ik} is the relative biomass of species i and S is the number of species within community k. Thus, we applied the inverse of the Simpson index as α diversity (α_{simp}). The γ diversity was calculated as $\gamma_{\text{simp}} = 1 / \sum_i^S {p_{iM}}^2$, where p_{iM} is the relative biomass of species i and S is the number of species at the transect scale. As alpha diversity is measured at the plot scale and gamma diversity is measured at the transect scale, multiplicative beta diversity at the transect scale is the ratio of gamma diversity to mean alpha diversity. Multiplication-based β diversity (β_{simp}) was calculated as the ratio of γ_{simp} to α_{simp} (Wang & Loreau, 2016), which represents the turnover of species among local communities.

To quantify different aspects of the change in plant composition at the plot level in the 7-year sampling, we used the 'species exchange ratio' (SER) approach (Hillebrand, Blasius, et al., 2018) to measure the proportional exchange of species or relative abundances of species between an earlier sampling and later sampling in a time series at the plot level (the caption of Figure S1 in the Supplementary Material provides detailed information on the calculation of SER). We found that the richness-based species exchange ratio (SERr) and abundance-based species exchange ratio (SERa) at most sites (with the exception of one or two sites) did not significantly change with sampling year. Thus, we quantified average species diversity per plot by averaging species diversity in the same plot over a 7-year period to examine plant diversity effects on temporal stability across two spatial scales (Tilman, 1996; Wagg et al., 2022).

2.3 | Stability and asynchrony across two spatial scales

Following previous work (Wang et al., 2019), species temporal stability (hereafter referred to as species stability) was defined as the weighted average of local population stability across species and plots. We utilized total above-ground biomass to quantify functional temporal stability. Following previous work (Tilman, 1999), functional temporal stability was defined as μ_T/σ_T, where μ_T and σ_T are the interannual mean and standard deviation, respectively, of community biomass over the 7 years (2003–2010, with the exception for 2005). α functional stability at the plot scale was defined as the biomass-weighted average of the temporal stability of each plot, and γ functional stability at the transect scale was defined as the temporal stability of the total community biomass of the 5 plots along a transect (Wang et al., 2019). The α compositional stability at the plot scale was quantified by one minus the mean Euclidean distance from each plot in each year to its centroid over 7 years (2003–2010, with the exception of 2005), with the distance calculated based on the Bray–Curtis dissimilarity between two communities of the same plot in each year and then averaged at the transect level (Xu et al., 2022). γ compositional stability at the transect scale was quantified by one minus the mean Euclidean distance from each transect in each year to its 7-year (2003–2010, with the exception of 2005) transect centroid, with distance calculated based on the Bray–Curtis dissimilarity among communities of the same transect.

In addition, functional stability at two spatial scales was also determined after detrending to eliminate potentially confounding effects of directional biomass change on temporal stability (Lepš et al., 2019; Valencia et al., 2020). Specifically, we replaced σ in the stability definition as the standard deviation of the residuals of the linear regression between aboveground biomass and the sampling year (Tilman et al., 2006). Here, the detrended functional α and γ stability was applied.

The previous framework for partitioning ecosystem stability (see, e.g. Wang et al., 2019; Wang & Loreau, 2014, 2016) demonstrated that local α stability can be partitioned into species stability and species synchrony (see also Thibaut & Connolly, 2013). Therefore, species asynchrony indicates that the dynamics of asynchronous species within local communities respond to environmental fluctuations, which is defined as the ratio of α stability to species stability (Wang et al., 2021). Similarly, spatial asynchrony is calculated as the ratio of γ stability to α stability, which indicates the asynchronous community dynamics among local communities in response to environmental fluctuations. More details on the asynchrony index equations are provided in Wang et al. (2019).

2.4 | Statistical analysis

To improve normality and linear relationships, diversity, stability, and asynchrony measures and successional year (as a continuous variable) were log10 transformed before analyses. First, linear mixed-effects models (LMMs) were performed using the R package NLME (Pinheiro et al., 2021) to assess the effects of successional time on diversity, stability, and asynchrony at two different spatial scales, where the sites were treated as random factors. Similarly, we employed LMMs to test the diversity–asynchrony–stability relationships at the two spatial scales during succession. We calculated the marginal R^2 (R^2_m) and conditional R^2 (R^2_c) using the package MuMIn to evaluate the model performance (Nakagawa & Schielzeth, 2013). Specifically, the marginal R^2 (R^2_m) and conditional R^2 $(R^2_c)^2$ correspond to '*fixed effects*' and 'fixed + *random effects*', respectively.

We used the R package 'piecewise structural equation model (SEM)' (Lefcheck, 2016) to conduct a stepwise selection of a piecewise structural equation model to quantify the relative contribution of α and β diversity to γ stability during succession. An initial model based on theory (see, e.g. Wang et al., 2019; Wang & Loreau, 2014, 2016) was established (Table S1 and Figure S2), with site as a random factor. In the SEM, all diversity, stability and asynchrony metrics were log10 transformed, and Shipley's d-separation test was conducted to ensure all possible paths. Next, the non-significant paths were iteratively removed. Lastly, the final model that had the most simplified path and the lowest AIC was chosen. All analyses were performed using R 3.6.3 (R Core Team, 2019).

3 | RESULTS

3.1 | Changes in diversity, stability and asynchrony across two spatial scales during succession

We found that the annual α diversity did not strongly vary with the sampling year, with the exception of the control and 5-year sites ($p < 0.05$; Figure 1a), and that the annual β diversity did not change with sampling year, with the exception of the 1-year and 5-year sites ($p < 0.05$; Figure 1b). During succession, both the average α diversity at the plot scale (Simpson-based, ${R_m}^2 = 0.69$, $p < 0.05$; richness based, ${R_m}^2 = 0.79$, $p < 0.01$) and γ diversity at the transect scale (Simpson based, ${R_m}^2 = 0.61$, $p < 0.05$; richness based, $R^2 = 0.60$, $p < 0.05$) consistently increased over time (Figure 1c and Figure S3c, Tables S2 and S3). Simpson-based β diversity did not show a significant trend with succession time (${R_m}^2 = 0.53$, $p > 0.05$; Figure 1c and Table S2), but richness-based β diversity (${R_m}^2 = 0.71$, $p < 0.05$) decreased during succession (Figure S3c and Table S3). Likewise, there were consistent increases in species stability (${R_m}^2 = 0.60$, $p = 0.04$), α functional stability (${R_m}^2 = 0.67$, $p = 0.03$) and γ functional stability (${R_m}^2 = 0.57$, $p = 0.05$) over successional time (Figure 2a and Table S2). Both α compositional stability (${R_m}^2 = 0.73$, $p = 0.01$) at the plot scale and γ compositional stability (${R_m}^2 = 0.68$, $p = 0.02$) at the transect scale also increased with successional time (Figure 2b and Table S2). In contrast, neither species asynchrony (${R_m}^2 = 0.002$, $p > 0.05$) nor spatial asynchrony (${R_m}^2 = 0.012$, $p > 0.05$) significantly changed with successional time (Figure S4a,b and Table S3).

3.2 | Biodiversity-mediated effects of successional time on asynchrony and stability across two spatial scales

During succession, the average α diversity was consistently positively associated with α functional stability (Simpson based, ${R_m}^2 = 0.88$,

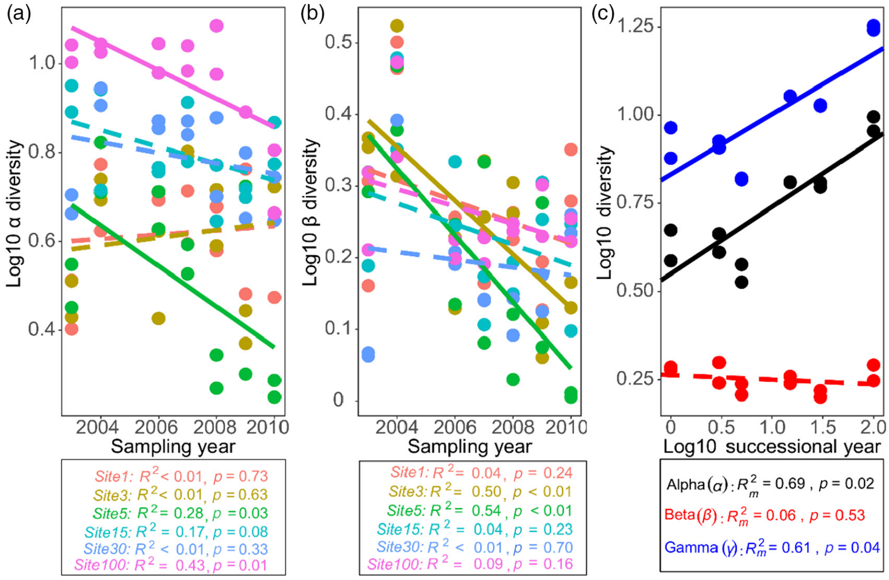

FIGURE 1 Temporal changes in annual α diversity (Simpson) at the plot scale (a) and annual β diversity (Simpson) at the transect scale (b) at each old field site with sampling year. (c) Changes in the average 7-year diversity (Simpson) at both the plot and transect scales during secondary succession. These diversity metrics are based on biomass. Solid lines represent the significant relationships from the linear models (a and b) and the linear mixed-effects model (c) at $p < 0.05$, and the dashed lines represent the non-significant relationships at $p > 0.05$. The marginal (R^2_m) r-squared represents '*fixed effects*' explanation. Details of the models can be found in Table S2.

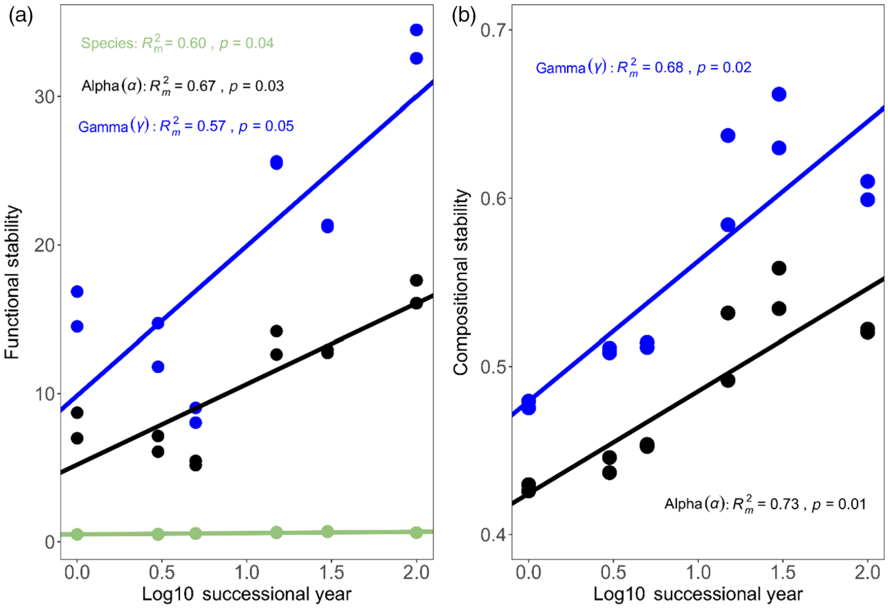

FIGURE 2 Changes in functional (a) and compositional (b) stability at both plot and transect scales during secondary succession. These functional stability metrics are based on biomass. The solid lines represent the significant relationships from linear mixed-effects models at $p \le 0.05$. The marginal (R^2_m) r-squared represents '*fixed effects*' explanation. The details of the models can be found in Table S2.

$p < 0.001$; richness based, $R_m^2 = 0.69$, $p < 0.05$) and γ functional stability (Simpson based, $R_m^2 = 0.83$, $p < 0.01$; richness based, $R_m^2 = 0.63$, $p < 0.05$; Figure 3a,c, Figure S5a,c and Table S2). The α and γ compositional stabilities at the two spatial scales were also positively correlated with the average α diversity (compositional α stability, Simpson based, $R_m^2 = 0.39$, $p < 0.1$; richness based, $R_m^2 = 0.58$, $p < 0.05$ and compositional γ stability, Simpson based, $R_m^2 = 0.37$, $p < 0.1$; richness based, $R_m^2 = 0.62$, $p < 0.05$; Figure 3b,d, Figure S5b,d and Table S2). The average α diversity was not significantly positively correlated with species stability (Simpson based, $R_m^2 = 0.14$, $p > 0.05$; richness based, $R_m^2 = 0.11$, $p > 0.05$) or species asynchrony (Simpson based, $R_m^2 = 0.04$, $p > 0.05$; richness based, $R_m^2 = 0.01$, $p > 0.05$; Figure S6 and Table S4). Simpson-based β diversity was positively associated with spatial asynchrony ($R_m^2 = 0.78$, $p < 0.01$; Figure 3g and Table S2) and γ functional stability ($R_m^2 = 0.03$, $p < 0.1$; Figure 3e and Table S2), but Simpson-based β diversity was not associated with γ compositional stability ($R_m^2 < 0.01$, $p = 0.77$; Figure 3f and Table S2). Richness-based β diversity was not correlated with spatial asynchrony ($R_m^2 = 0.05$, $p = 0.55$; Figure S5g and Table S3) but was positively related to γ functional stability ($R_m^2 = 0.05$, $p < 0.1$; Figure S5e and Table S3) and negatively related to γ compositional stability ($R_m^2 = 0.43$, $p = 0.05$; Figure S5f and Table S3).

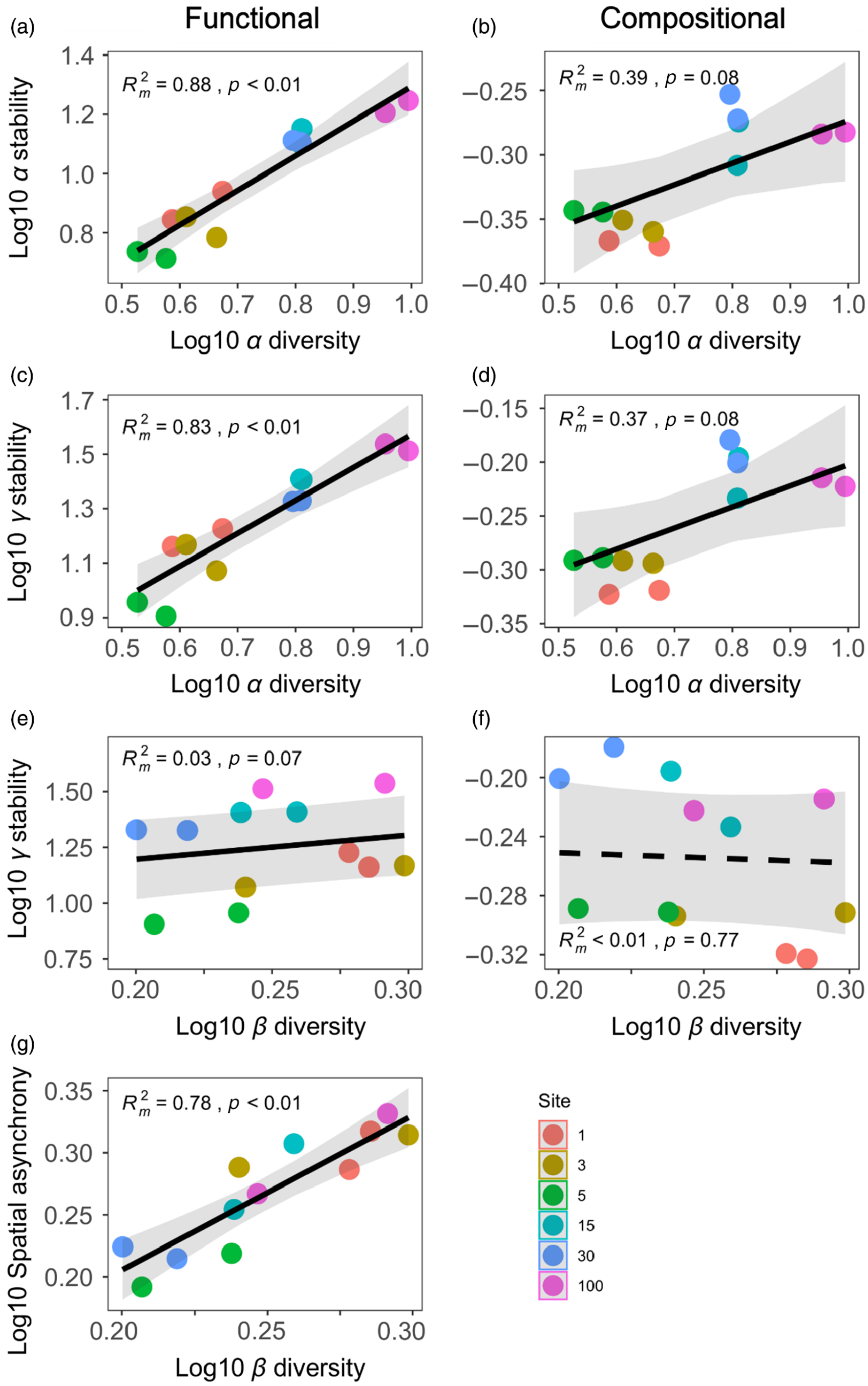

FIGURE 3 The diversity–synchrony–stability relationships at both plot and transect scales during secondary succession. These diversity, asynchrony and stability metrics are based on biomass. Species diversity is measured using Simpson-based metrics. Relationships between alpha diversity and functional stability at plot (a) and larger transect (c) scales; relationships between alpha diversity and compositional stability at plot (b) and larger transect (d) scales; relationships between beta diversity and gamma (e: functional; f: compositional) stability; relationships between beta diversity and spatial asynchrony (g). The colour of the dots represents the different old field sites. Solid lines represent the overall significant relationships from a linear mixed effects model at $p<0.1$, and the dashed line represents a nonsignificant relationship at $p>0.1$. The shaded areas are the error bands and denote 95% confidence intervals. The marginal ($R^2{}_m$) *r*-squared represents '*fixed effects*' explanation. The details of the models can be found in Table S2.

The SEM demonstrated that successional time positively affected functional stability and compositional stability at the two spatial scales mainly through increased average α diversity (Figure 4a,b). During succession, the average α diversity significantly increased with time (direct effect: 0.87) and further enhanced γ functional and compositional stability at the transect scale by increasing α functional and compositional stability at the plot scale, respectively (Figure 4a,b). Average α diversity had stronger positive impacts on α functional stability than on α compositional stability. β diversity was not affected by succession but significantly increased spatial asynchrony (direct effect: 0.88), thus also increasing γ functional stability (indirect effect of β diversity: 0.88*0.23 = 0.20; Figure 4). However, β diversity did not increase γ compositional stability via increased spatial asynchrony (Figure 4b). We obtained qualitatively similar results when analysing the relationships of α and β diversity based on species richness with functional stability and compositional stability at the two spatial scales (Figure S7a,b). Although β diversity was negatively affected by succession, it did not significantly increase spatial asynchrony. Therefore, plant diversity at the two spatial scales promoted γ functional and compositional stability at the transect scale during succession, and there were stronger stabilizing

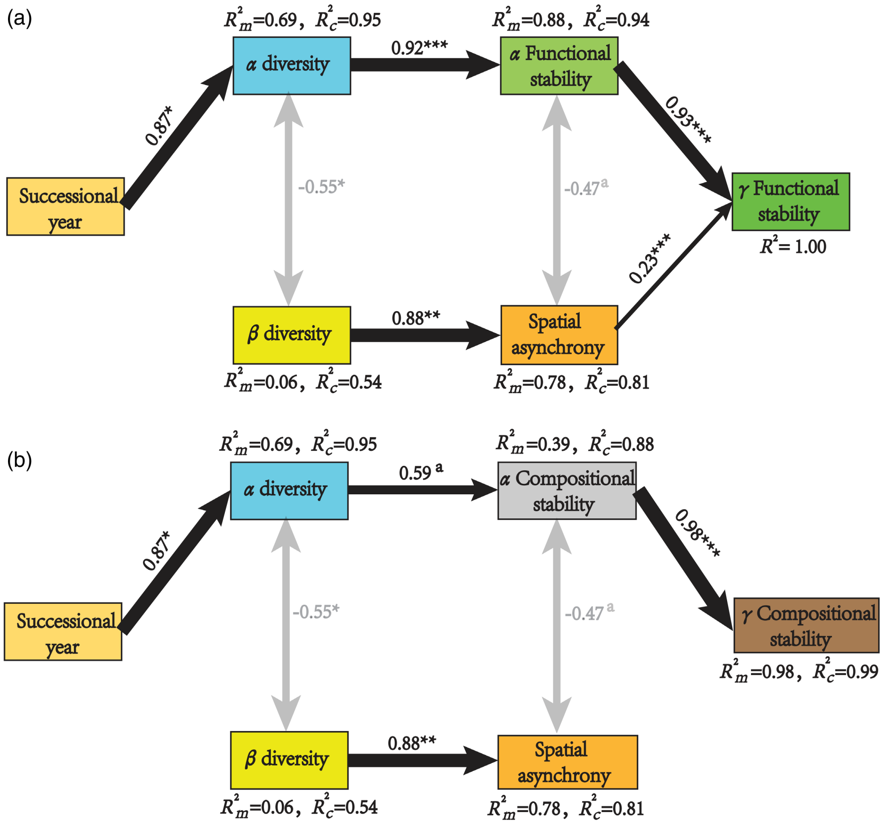

FIGURE 4 Structural equation models (SEM) describing the relative effects of alpha and beta diversity on gamma stability (a: functional; b: compositional), through alpha stability (a: functional; b: compositional) and spatial synchrony at two spatial scales. In both SEMs, the average species diversity is measured by Simpson-based metrics. (a) Fisher's $C = 24.495$, $p = 0.079$, $df = 16$, AIC = 64.495. (b) Fisher's $C = 16.343$, $p = 0.293$, $df = 14$, AIC = 58. 343. The solid arrows represent positive relationships and the light-grey (bidirectional) arrows represent a correlation between variables. All the lines marked are significant effects (the significance levels of each predictor are $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, a: $0.05 < p < 0.1$). For each response variable, marginal (R^2_m) values showing the variance explained by fixed effects and conditional (R^2_c) values indicating the variance explained by the whole model are provided. The widths of each arrows are relative to the standardized path coefficients.

effects of average α diversity on γ functional stability and compositional stability at the transect scale than on β diversity during succession.

4 | DISCUSSION

To the best of our knowledge, our study provided the first assessment of how succession influences functional and compositional stability and their relationships with plant diversity at two different spatial scales. Our results were consistent with the classic notion that plant diversity and ecosystem stability at the small plot scale increased over the course of succession (Odum, 1969). Our study also extended plant diversity and ecosystem stability from the small plot scale to the large transect spatial scale during succession, supporting our hypothesis that there is a stronger stabilizing effect of average α diversity than β diversity at the large transect scale during succession. We also discovered that β diversity could improve functional stability at the large transect scale by increasing spatial asynchrony among local communities without altering compositional stability at the large transect scale during natural succession. Our results highlight that multiple spatial scales should be considered to fully understand the stabilizing effects of biodiversity during succession.

4.1 | α diversity and α stability during succession

We found that although succession did not affect species asynchrony, species stability significantly increased over successional time (Figure 2a and Table S2). Both species stability and species synchrony strongly positively affected α functional stability (Figure S8a,b and Table S4), while only species stability strongly enhanced α compositional stability (Figure S8c and Table S4). This result is consistent with previous studies that show that local ecosystem stability can be driven by both species stability and species synchrony (Li et al., 2022; Wilcox et al., 2017; Xu et al., 2021). In our study, species stability had a relatively stronger effect on functional and compositional stability than species asynchrony at the plot scale (Figure S8 and Table S4). However, during forest succession, the direct effect of species asynchrony on local ecosystem stability increased with time. Other findings have also reported the important role of species asynchrony in stabilizing local community dynamics (Wilcox et al., 2017; Xu et al., 2021). The increase in species asynchrony compensates for the decline in species stability (Xu et al., 2021). During succession, increasing α diversity over time weakly increased species stability and species asynchrony (Figure S6), but the increase in species stability surpasses the increase in species asynchrony, both resulting in enhanced local ecosystem stability.

Although diversity and stability at the two spatial scales demonstrated an overall significant increase over secondary succession, we also observed that alpha and gamma diversity and functional stability decreased at the early stage of succession (between 1 year and 5 years) and then increased at the late stage of succession (between 5 years and 100 years). Explanations for this trend are presented as follows: (1) a confounding site-specific effect because there was no replication of sites with the same successional time in our experiment and (2) the disappearance of pioneer weed species such as *Aconitum gymnandrum* and *Galium aparine* prior to the establishment of late-successional species such as *Elymus nutans*, *Roegneria nutans* and *Kobresia humilis* (Li et al., 2009).

4.2 | α stability and γ stability during succession

Metacommunity stability theory has clarified the close link between stability at a small spatial scale and stability at a large spatial scale (Wang et al., 2019; Wang & Loreau, 2014, 2016). Using the SEM, we discovered that increased α diversity over time promoted α functional and compositional stability at the plot scale, which predominantly contributed to functional and compositional γ stability at the large transect scale during succession. This finding also showed agreement with a recent finding of Wang et al. (2021), who also reported stronger effects of α diversity on γ stability than of β diversity on γ stability in long-term grassland observation studies. The stronger stabilizing effect of α diversity during succession emerged presumably because increasing α diversity over time enhanced local α stability by a combination of species stability and species asynchrony, supporting previous findings that α diversity is a key driving mechanism for local ecosystem stability (Tilman et al., 2006; Xu et al., 2021). Our study also provides evidence that α diversity is a primary contributor to ecosystem stability via local α stability at a larger spatial scale.

4.3 | Stabilizing effects of β diversity during succession

Theoretical studies (Wang et al., 2019; Wang & Loreau, 2014, 2016) and several experimental studies (Clark et al., 2021; Patrick et al., 2021) suggest that β diversity can increase ecosystem stability via spatial asynchrony among communities at larger spatial scales due to an increase in dissimilarity in the local community structure leading to greater differences in community dynamics (Wang & Loreau, 2014, 2016). However, to the best of our knowledge, few studies have examined the stabilizing effects of β diversity by spatial asynchrony during succession. Previous succession studies have shown that β diversity declines with successional time (Anderson, 2007; Li et al., 2016), implying that the magnitude of the stabilizing effect of β diversity via spatial asynchrony may decline over time (Mori et al., 2018). However, our SEM showed that β diversity did not change with successional time but significantly increased spatial asynchrony, thus increasing functional stability at the large transect scale (Figure 3). Our results support the prediction that spatial asynchrony among localities was enhanced by β diversity, although β diversity contributed to a smaller stabilizing effect than α diversity. In contrast, some studies have also shown that β diversity is not related to spatial asynchrony (Wilcox et al., 2017), probably because the relatively small sampling size and homogeneous environmental conditions in these studies could weaken the stabilizing effect of β diversity. Two recent studies, conducted with a larger spatial extent, provided robust evidence for the stronger contribution of β diversity than α diversity to ecosystem stability at large spatial scales (Liang et al., 2022; Qiao et al., 2022). The responses of spatial asynchrony among communities to environmental variations provide a spatial insurance effect to stabilize ecosystem function at large spatial scales (Loreau et al., 2003; Wang & Loreau, 2014).

4.4 | Caveats

One caveat is that we utilized a space-for-time approach to analysing the natural succession of plant communities (Foster & Tilman, 2000; Johnson & Miyanishi, 2008; Walker et al., 2010). Although this approach is often criticized due to reaching false ecological patterns and temporal dynamics (Johnson & Miyanishi, 2008), it can still be a useful tool for analysing successional trajectories if it is judiciously utilized (Walker et al., 2010). In this study, the combination of the chronosequence approach with the long-term study of permanent plots could better predict successional trajectories (Foster & Tilman, 2000, Johnson & Miyanishi, 2008, Walker et al., 2010) and ecosystem stability. Furthermore, we acknowledge that pseudoreplication (i.e. no replication in our study sites of the same successional age) could affect the outcomes and generalizability of our study, although site identity as a random effect was included in LMMs. In this region, natural grasslands are dominant, and old field sites are rare. It is difficult to identify multiple sites that share similar successional stages. Another caveat is that our experiment was conducted in a relatively small spatial area at each field site. Therefore, our result must be queried to determine whether it can be generalized to large spatial scales where β diversity may contribute to ecosystem stability at regional scales and spatial asynchrony among local communities (Liang et al., 2022; Wang & Loreau, 2016). In our study, we focused on the temporal stability of both ecosystem function and community composition. We discovered that functional stability was significantly positively correlated with compositional stability at the plot scale but not at the transect scale (Figure S9). However, no single facet of stability can sufficiently reflect the overall ecosystem stability (Donohue et al., 2013; Hillebrand, Langenheder, et al., 2018), thus preventing generalizable conclusions regarding overall stability across ecosystems. Therefore, in the future, it is necessary to conduct more successional experiments on different ecosystem types to verify how succession influences the relationships between diversity and multidimensional ecosystem stability at large spatial scales.

5 | CONCLUSIONS

Our study demonstrates that ecological succession increases plant diversity and functional and compositional stability at spatiotemporal scales. α diversity and β diversity provide stabilizing effects for a large spatial scale by local α stability and spatial asynchrony, respectively, during succession. The effect of α stability on γ stability is greater than that of spatial asynchrony on γ stability during succession, regardless of functional and compositional stability. These findings have the following important implications: (i) the positive effects of biodiversity (α, γ and β) on ecosystem stability in natural systems are spatially and temporally dependent. The effects of biodiversity are not only important on short term, small local scales but also become even stronger in long term, large-scale landscapes. (ii) Findings on biodiversity stabilizing mechanisms at local spatial scales from short-term studies (e.g. Hautier et al., 2020; Wang et al., 2021; Wilcox et al., 2017; Zhang et al., 2019) are likely to underestimate the temporal impacts of biodiversity change in real-world ecosystems (Qiu & Cardinale, 2020), and their effects could strengthen over longer periods (Wagg et al., 2022), particularly across successional stages. (iii) In the context of ongoing biodiversity loss, it is vital to restore multiple components of biodiversity at multiple spatial scales (such as local, regional and habitat) to stabilize ecosystem functions, especially macrosystem stability (Patrick et al., 2021). Temporal or successional changes should be considered, if possible, for a more comprehensive understanding of the effects of biodiversity on ecosystem functioning in a given ecological system (Lasky et al., 2014; Wagg et al., 2022).

AUTHOR CONTRIBUTIONS

Wenjin Li and Xi Zhou developed and framed research questions and drafted the manuscript, Jinhua Li designed the experiment and contributed to paper writing, Shaopeng Wang, Michel Loreau and Lin Jiang revised the manuscript, Xi Zhou and Zhiqiang Xiang contributed to data analyses, Wenjin Li and Jinhua Li carried out the fieldwork and collected the data. All authors contributed substantially to manuscript writing and revisions. Wenjin Li and Xi Zhou contributed equally to this work.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data are archived with Dryad https://doi.org/10.5061/dryad.qv9s4mwkq. (Li et al., 2023).

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SUPPORTING INFORMATION

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

Table S1. Rationales of the priori structural equation model were developed to test the direct and indirect effects of successional year through plant diversity on stability at the plot and larger transect spatial scales.

Table S2. The results of linear mixed-effects models (LMMs) from Figure 1 to Figure 3; the marginal (R^2_m) and conditional (R^2_c) *r*-squared represent "*fixed effects*" and "*fixed+random effects*" explanations, respectively.

Table S3. The results of linear mixed-effects models (LMMs) from Figure S3 to Figure S5, with "*site*" as random effect. The marginal (R^2_m) and conditional (R^2_c) r-squared represent "*fixed effects*" and "*fixed + random effects*" explanations, respectively.

Table S4. The results of linear mixed-effects models (LMMs) from Figure S6 to Figure S10 (except for Figure S7), with "*site*" as random effect. The marginal (R^2_m) and conditional (R^2_c) r-squared represent "*fixed effects*" and "*fixed + random effects*" explanations, respectively.

Figure S1. Temporal changes in $\mathrm{SER_a}$ and $\mathrm{SER_r}$ at the plot level in each old field site with sampling year. This richness-based species-exchange ratio($\mathrm{SER_r}$), is quantified as $\mathrm{SER_r} = \frac{S_{imm}+S_{ext}}{S_{tot}}$, where S_{imm} is the number of species immigrating (newly recorded in the later sample), S_{ext} is the number of species extinct (lost from the previous sample) and S_{tot} is the total number of species across both samples. $\mathrm{SER_a}$ as a measure of turnover by changes in species proportional abundances, $\mathrm{SER_a} = \frac{\sum_i (p_i - p\prime_i)^2}{\sum p_i^2 + \sum p\prime_i^2 - \sum p_i p\prime_i}$, p_i and $p\prime_i$ represent the proportional abundances of species i in the first (time 1, i.e. in 2004) and second (time 2, i.e. in 2005) communities, respectively. The solid lines represent the significant relationships from linear models at $p < 0.05$, and the dash lines represent the non-significant relationships at $p > 0.05$.

Figure S2. A initial structural equation modeling (SEM) for predicting successional year on ecosystem temporal stability via plant diversity at two spatial scales, please see the rationales in the Table S1.

Figure S3. Temporal changes in α diversity (richness) (a) and β diversity (richness) (b) in each old field site with sampling year. (c) Changes in seven-year average diversity (richness) at both plot and transect scales during secondary succession. These diversity metrics are based on biomass. The solid lines represent the significant relationships from linear models (a and b) or linear mixed-effects model (c) at $p < 0.05$, and the dash lines represent the non-significant relationships at $p > 0.05$. The marginal (R^2_m) r-squared represents "*fixed effects*" explanation. The details of the models can be found in Table S3.

Figure S4. The effects of successional year on species asynchrony and spatial asynchrony. The color of the dots represents the different old field sites. The dash lines represent the non-significant relationships from a linear mixed- effects model at $p > 0.05$. The shaded areas are the error bands and denote 95% confidence intervals. The marginal (R^2_m) r-squared represents '*fixed effects*' explanation. The details of the model can be found in Table S3.

Figure S5. The diversity–asynchrony-stability relationships at both plot and transect scales during secondary succession. These diversity, asynchrony and stability metrics are based on biomass. Species diversity is measured by richness-based metrics. Relationships between alpha diversity and functional stability at plot (a) and larger transect (c) scales; relationships between alpha diversity and compositional stability at plot (b) and larger transect (d) scales; relationships between beta diversity and gamma (e: functional; f: compositional) stability; relationships between beta diversity and spatial asynchrony (g). The color of the dots represents the different old field sites. The black lines represent the significant relationships from a linear mixed-effects model at $p < 0.1$, and the dash line represent a non-significant relationship at $p > 0.1$. The shaded areas are the error bands and denote 95% confidence intervals. The marginal (R^2_m) r-squared represents "*fixed effects*" explanation. The detail of the models can be found in Table S3.

Figure S6. Relationships between alpha diversity and species stability, species asynchrony. The color of the dots represents the different old field sites. The dash lines represent non-significant relationships at $p > 0.1$. The shaded areas are the error bands and denote 95% confidence intervals. The marginal (R^2_m) r-squared represents "*fixed effects*" explanation. The details of the model can be found in Table S4.

Figure S7. Structural equation model (SEM) describing the relative effects of alpha and beta diversity on gamma (a: Functional; b: Compositional) stability, through alpha (a: Functional; b: Compositional) stability and spatial asynchrony at two spatial scales. In this SEM, species diversity is measured by richness-based metrics. (a) Fisher's $C = 16.537$, $p = 0.555$, $df = 18$, AIC = 56.537. (b) Fisher's $C = 16.33$, $p = 0.43$, $df = 16$, AIC = 58. 33. The black and red arrows represent positive and negative relationships, respectively. The light-grey (bidirectional) arrows represent a correlation between variables. All of the lines marked are significant effects (significance levels of each predictor are $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$). For each response variable, marginal (R^2_m) values showing the variance explained by the fixed effects and conditional (R^2_c) values indicating the variance explained by the whole model are provided. The width of each arrows is relative to the standardized path coefficients.

Figure S8. Relationships between alpha functional stability and compositional stability and species stability, species asynchrony. The color of the dots represents the different old field sites. The black lines represent the overall significant relationships from a linear mixed-effects model at $p < 0.05$, and the dash line represent a non-significant relationship at $p > 0.05$. The shaded areas are the error bands and denote 95% confidence intervals. The marginal (R^2_m) r-squared represents "*fixed effects*" explanation. The details of the model can be found in Table S4.

Figure S9. Relationships between compositional stability and functional stability at two spatial scales. The color of the dots represents the different old field sites. The black lines represent the overall significant relationships from a linear mixed-effects model at $p < 0.05$, and the dash line represent a non-significant relationship at $p > 0.05$. The shaded areas are the error bands and denote 95% confidence intervals. The marginal (R^2_m) r-squared represents "*fixed effects*" explanation. The detail of the models can be found in Table S4.

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