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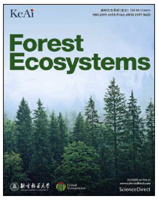

Dominant species stability outweighs species asynchrony and diversity in regulating temperate forest regeneration

Zhichao Xu[a,b], Meihui Zhu[a,b], Jonathan A. Myers[c], Lin Jiang[d], Fei Lin[a,b], Ji Ye[a,b], Shuai Fang[a,b], Zikun Mao[a,b], Xugao Wang[a,b,*]

[a] *CAS Key Laboratory of Forest Ecology and Silviculture, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, China*
[b] *Key Laboratory of Terrestrial Ecosystem Carbon Neutrality, Shenyang 110016, China*
[c] *Department of Biology, Washington University in St. Louis, St. Louis, MO 63130, USA*
[d] *School of Biological Sciences, Georgia Institute of Technology, Atlanta, GA 30332, USA*

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ABSTRACT

Climate change increasingly threatens forest regeneration by disrupting seedling dynamics, yet the stabilizing mechanisms underpinning these critical early life stages remain poorly understood. Using a 15-year seedling demographic dataset from a temperate forest in Northeast China, we quantified how vapor pressure deficit (VPD), snow depth, soil fertility, and neighboring tree density jointly influence the temporal stability of seedling survival and recruitment, and further disentangled the underlying stabilizing pathways mediated by dominant species stability, species asynchrony, and species richness. Our findings demonstrated that seedling temporal stability was associated more strongly with the degree of dominant species stability than with species asynchrony and richness. Seasonal drought (higher VPD) significantly reduced stability by weakening both dominant species stability and species asynchrony, while deeper snow enhanced stability by buffering climatic stress during winter. Dense neighborhood competition further decreased survival stability, whereas fertile soils suppressed asynchrony and reduced recruitment stability. These results indicate that the increasing seasonal drought in temperate forests may erode the compensatory mechanisms that maintain regeneration stability, while snowpack can serve as an important climatic buffer. Together, these findings highlight the pivotal role of dominant species in mitigating climate-induced stress during forest regeneration and underscore the importance of integrating stabilizing mechanisms into forest management and climate adaptation strategies.

1. Introduction

Stable ecosystems are fundamental for sustaining ecological functions and human well-being because they regulate variability, buffer environmental perturbations, and maintain functioning under increasingly variable climatic conditions (Oliver et al., 2015; Craven et al., 2018; Wang et al., 2025). In recent decades, temporal stability, the consistency of ecosystem structure and processes through time, has emerged as a central focus in ecological research, particularly in the context of intensifying climate extremes such as droughts and atmospheric aridity (Hector et al., 2010; Yuan et al., 2019; Valencia et al., 2020; McDowell et al., 2020; IPCC et al., 2021). Understanding the mechanisms that maintain the temporal stability of ecosystem functions is therefore critical for predicting ecosystem responses to future climate change and for informing effective conservation and management strategies.

A growing body of theory and empirical work has identified three non-mutually exclusive mechanisms that underpin temporal stability in ecological communities: diversity, asynchrony, and dominant species effects (Ives and Carpenter, 2007; Lisner et al., 2024; Segrestin et al., 2024). First, changes in biodiversity can lead to corresponding changes in the temporal stability of biomass (Tilman et al., 2006; Hautier et al., 2014). On the one hand, higher biodiversity may enhance biomass stability because more diverse communities are more likely to include species that are resistant to environmental fluctuations (the sampling effect, Craven et al., 2018). On the other hand, biodiversity can also

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[*] Corresponding author. CAS Key Laboratory of Forest Ecology and Silviculture, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, China.

E-mail address: wangxg@iae.ac.cn (X. Wang).

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increase biomass stability by promoting asynchronous population dynamics among species (Loreau and de Mazancourt, 2008; Muraina et al., 2021). Second, even in the absence of changes in biodiversity, variation in the degree of population asynchrony (stabilization due to temporal variations between species), driven by differences in abiotic and biotic conditions, can independently alter community biomass stability (Hautier et al., 2014; Wilcox et al., 2017; Leps et al., 2018). Third, community-level stability is often disproportionately influenced by a few highly abundant species, which typically rank among the most temporally stable members of the community, as frequently demonstrated by Taylor's power law (Taylor, 1961). However, this does not imply that community-level stability is equivalent to the stability of dominant species alone. When multiple dominant species exhibit divergent responses to environmental fluctuations, community stability may instead be more strongly regulated by species asynchrony or diversity. For instance, Ma et al. (2024) and Sheng et al. (2025) have reported that the association between dominant species stability and temporal biomass stability is weaker than that for species asynchrony and richness. Therefore, a key object of this study is to further explore the relative importance of these three mechanisms (i.e., dominant species stability, species asynchrony, and species richness) within forest communities, where long-lived species, complex size structures, and delayed demographic responses may fundamentally alter stability dynamics.

In forest ecosystems, climate variability is increasingly recognized as a key driver shaping community stability, yet its effects on stabilizing mechanisms remain incompletely understood (Uriarte et al., 2018). Environmental changes (e.g., elevated drought) are widely recognized to reduce the temporal stability of ecosystem functions by weakening both the stability of dominant species and the degree of species asynchrony (Hautier et al., 2015; Ma et al., 2024). Among different indicators of drought, vapor pressure deficit (VPD) has emerged as a particularly robust metric because it integrates atmospheric dryness and evaporative demand, providing a more direct link to plant physiological stress than precipitation or temperature alone (Tepley et al., 2017; McDowell et al., 2020). Elevated VPD increases transpirational water loss, intensifies hydraulic stress, and can amplify interannual fluctuations in survival and recruitment, thereby destabilizing forest demographic processes (McDowell et al., 2020). In contrast to growing-season drought stress, winter snowpack represents an important but often overlooked climatic buffer in temperate forests, substantially enhancing seedling survival by moderating winter microclimates and buffering against extreme low temperatures during the non-growing season (Guiden et al., 2018). Snowpack accumulation can also maintain soil moisture and nutrient availability during spring thaw, supporting early-season recovery (Augspurger, 2013). Our recent study showed that higher VPD significantly suppressed seedling survival, while snow cover significantly promoted it in the temperate forest of Northeast China (Xu et al., 2022b, 2025). Despite these opposing climatic influences, few studies have simultaneously evaluated how seasonal drought and winter snow regulate forest regeneration stability through their effects on dominant species stability, species asynchrony, and diversity. This limitation largely reflects the scarcity of long-term demographic datasets capable of linking interannual climate variability to stabilizing mechanisms in forest communities.

In addition to regional climate variability, local habitat conditions can further mediate how stabilizing mechanisms operate during forest regeneration (Johnson et al., 2017; Xia et al., 2019; Yao et al., 2020). Variations in soil fertility can alter competitive hierarchies and resource allocation strategies, leading to differential demographic responses among species. For instance, soil fertilization has been shown to destabilize plant communities by weakening species asynchrony and enhancing dominance effects (Zhang et al., 2019). Similarly, neighborhood crowding intensifies both above- and belowground competition for light, water, and nutrients, which can increase interannual variability in seedling survival and recruitment (Fortunel et al., 2018; Muscarella et al., 2018). Because climate stress and local habitat conditions often interact, their combined effects may either amplify or dampen stabilizing mechanisms, depending on resource availability and biotic context. However, how these local factors jointly regulate the temporal stability of forest regeneration, and through which stabilizing pathways they operate, remains poorly understood, particularly at the seedling stage where demographic sensitivity to environmental variability is highest.

While ecosystem temporal stability has traditionally been examined using aggregate ecosystem functions such as biomass or productivity, the temporal stability of forest regeneration has received far less attention. Regeneration represents a critical demographic bottleneck in forest dynamics, as seedling survival and recruitment determine whether species can persist, colonize gaps, and ultimately contribute to future community structure and ecosystem functioning (Beckage et al., 2005; Hanbury-Brown et al., 2022). Importantly, mean regeneration rates alone do not fully capture regeneration success under variable environments. Even high average survival or recruitment can fail to sustain forest regeneration if these processes fluctuate strongly among years, leading to cohort failure during unfavorable climatic periods. Temporal stability of regeneration, therefore, represents an emergent ecological property that reflects the resistance and buffering capacity of seedling communities to interannual environmental variability (Schnabel et al., 2021). Reduced temporal fluctuations in seedling survival or recruitment indicate more predictable demographic outcomes, lower extinction risk of early life stages, and greater resilience of forest regeneration under climatic extremes. In this sense, regeneration stability provides a mechanistic link between short-term climatic variability and long-term forest persistence.

In this study, we integrated 15 years of seedling demographic and environmental data from a temperate forest in Northeast China to address two overarching questions:

(1) How do the temporal stability of seedling dynamics and their underlying stabilizing mechanisms respond to climate—specifically vapor pressure deficit (VPD) and snow depth—and to local habitat conditions, including soil nutrient availability and neighboring tree crowding? We hypothesize that seasonal drought stress, reflected by elevated VPD, decreases the temporal stability of seedling survival and recruitment by intensifying physiological water limitations and demographic fluctuations, whereas deeper snowpacks act as natural climatic buffers with opposing effects (Guiden et al., 2018; Xu et al., 2025). Moreover, higher neighborhood tree density and lower soil nutrient availability are expected to exacerbate competitive stress, forcing seedlings to rely on sporadic resource pulses such as rainfall and canopy gaps (Muscarella et al., 2018), thereby reducing the stability of seedling demographic rates.

(2) Through what ecological pathways do climate and habitat conditions influence the temporal stability of seedling dynamics? We propose two complementary assumptions: (i) Species diversity, dominant species stability, and species asynchrony jointly enhance the temporal stability of seedling survival and recruitment; and (ii) Climate and local habitat factors regulate these stabilizing effects by modifying physiological constraints and interaction strengths among species. Specifically, we expect that the stability of dominant species will exert the greatest influence on seedling community stability, owing to their adaptive advantages in water-use efficiency and nutrient acquisition (Yang et al., 2011). These adaptive traits promote the persistence of dominant species under environmental variability, thereby enhancing overall community-level stability.

2. Materials and methods

2.1. Study site

The field site is located at the ChangBaiShan (CBS) Nature Reserve (41°43′–42°26′ N, 127°42′–128°17′ E) in Jilin Province of Northeast China. This region has a temperate continental climate with warm summers and long, cold winters, and has an average annual temperature of 2.8 °C. The average temperature in the warmest months is 19.6 °C, and the coldest month is −13.7 °C. The mean annual precipitation is about 700 mm, most of which occurs between June and September (Hao et al., 2007). The study area is dominated by old-growth temperate forests, with high species diversity and unique composition, growing in dark-brown soil developed from volcanic ash.

To conduct long-term forest biodiversity monitoring and research, a 25-ha temperate forest dynamic plot at CBS (hereafter CBS plot) was established in 2004, which was the first plot in the Chinese Forest Biodiversity Monitoring Network, with an altitude of 791.8–809.5 m. All free-standing woody stems in the plot with at least 1 cm in diameter at breast height (DBH; 1.3 m above ground) were tagged, measured, mapped, and identified to species following the Forest Global Earth Observatory protocols (ForestGEO, http://www.forestgeo.si.edu, Davies et al., 2021).

2.2. Seedling recruitment and survival

To investigate seedling dynamics (survival and recruitment), a total of 150 sample plots were selected for establishing seedling subplots (Fig. S1a). We set up one seedling subplot at a distance of 2 m from the center of each sample plot in the west, north, and east directions in 2004 (a total of 450 seedling subplots; Fig. S1b). Every year since 2005, seedlings (defined as woody plants <1 cm DBH, including trees, shrubs, and lianas) were tagged and identified to species from June 25 to July 15 at each seedling plot. Seedling survival was defined as the number of previously recorded seedlings that remained alive in the subsequent census, whereas seedling recruitment was defined as the number of newly emerged seedlings recorded during that census. In this study, we used annual seedling census data collected from 2008 to 2022, which include a total of 61,411 seedlings belonging to 47 species, 31 genera, and 20 families. It should be noted that as individuals grow, those reaching 1 cm (DBH) will be removed from our analysis.

2.3. Climate and local habitat variables

Monthly VPD and snow depth data were acquired from the automated meteorological data collection system located 4 km from the CBS plot. Average VPD was calculated with air temperature and relative humidity from May to September (Will et al., 2013), and maximum snow depth (SNOW) was calculated with the daily values from October to April (Xu et al., 2022b). There were five soil variables in our soil dataset: pH, organic matter, total nitrogen (N), total phosphorus (P), and total potassium (K). These soil properties were used to characterize the soil fertility gradient in the CBS plot. Because these soil variables might be correlated with each other, we performed a principal component analysis (PCA) that included the five variables. Only the first principal component (PC1), which described 83.8% of the total soil variation, was used to represent soil fertility of each seedling plot (Xu et al., 2022b). Topographical conditions such as elevation and convexity have not been included in our study. This is because previous analyses in this plot have shown that, compared to local habitat conditions like neighborhood density and soil nutrients, topography exerts the weakest influence on seedling survival (Xu et al., 2022b).

To quantify local biotic neighborhood, we used total basal area of all stems surrounding each seedling plot to calculate neighbor tree crowding (neighboring density) as Eq. 1 (Wang et al., 2012):

$$\text{Neighboring density} = \sum\nolimits_{i}^{N} \text{BA}_i / \text{Distance}_i \tag{1}$$

where i is an individual tree; BA_i is basal area of an individual tree. Neighborhood density was calculated using a 30 m radius, as prior analyses demonstrated that biotic interactions at this scale exert the strongest inhibitory effect on seedling survival and provide the best model performance compared with smaller radii (Xu et al., 2022b, 2025). Consistently, research from other plots has shown that direct neighborhood interactions generally occur within a 30 m radius (Stoll and Newbery, 2005; Liang et al., 2016). To account for stem turnover (both gains and losses) over the 15-year period, we applied a "nearest point principle" to align seedling dynamics with census data (i.e., 2009, 2014, 2019, and 2024). For instance, stem data from 2014 were used to calculate neighborhood density corresponding to seedling dynamics observed from 2012 to 2016 (Xu et al., 2022b).

2.4. Statistical analysis

We quantified temporal stability of seedling survival (survival stability) and recruitment (recruitment stability) as the ratio of mean seedling dynamics (i.e., survival and recruitment (μ)) to their temporal standard deviation (σ) in each seedling plot, as in many other studies (Hautier et al., 2014; Ma et al., 2017). Specifically, temporal stability of seedling survival (hereafter survival stability) and recruitment (hereafter recruitment stability) were calculated as the ratio of the temporal mean to the temporal standard deviation (μ/σ) over time, following established stability frameworks. This metric captures the resistance of demographic processes to interannual fluctuations, with higher values indicating more consistent and predictable regeneration dynamics under variable environmental conditions. In this study, survival stability and recruitment stability were analyzed separately because they represent distinct but complementary ecological processes. Survival stability reflects the persistence and stress resistance of established seedling cohorts, whereas recruitment stability reflects the consistency of new individual and species inputs into the community. Jointly, these two components determine the buffering capacity and resilience of forest regeneration to climatic variability and local habitat heterogeneity.

Seedling richness in survival and recruitment stability analysis was calculated as the total number of species (species richness (total)) and the number of new species (species richness (new)) in each seedling plot each year, respectively. We quantified the community-wide species asynchrony (species asynchrony) in seedling survival and recruitment over time as (Loreau and de Mazancourt, 2008):

$$1-\varphi_x = 1-\sigma^2 \Big/ \left(\sum\nolimits_{i=1}^{S}\sigma_i\right)^2 \tag{2}$$

where φ_x is species synchrony, σ^2 is the variance of seedling survival or recruitment, and σ_i is the standard deviation of survival or recruitment of species i in a plot with S species. This index attains one when species fluctuations are completely asynchronized, and zero when they are perfectly synchronized.

According to their relative abundance, species were further classified into three species groups: dominant (>5%), subordinate (1%–5%), and rare (<1%) species (Thibaut and Connolly, 2013; Xu et al., 2022a). For survival stability analysis, the three groups consisted of 3 (*Fraxinus mandshurica*, *Tilia amurensis*, *Syringa reticulata*), 8, and 36 species, and accounted for 75.4%, 15.7%, and 8.9% of community abundance, respectively (Fig. S2a). For recruitment stability analysis, the three groups consisted of 2 (*F. mandshurica*, *T. amurensis*), 3, and 36 species, and accounted for 89.2%, 7.1%, and 3.7% of community abundance (Fig. S2b), respectively. These three dominant species are common woody species in temperate forests of northern China. *F. mandshurica* is a light-demanding, fast-growing canopy tree preferring moist and fertile soils. *T. amurensis* is a shade-tolerant, long-lived broadleaf species that regenerates well under closed canopies and contributes to late-successional forest structure. *S. reticulata* is a small tree or shrub mainly occurring in the understory or forest edges, enhancing structural and functional diversity during forest regeneration (Chen et al., 2000).

We employed generalized linear mixed models to assess the effects of climate variables (VPD and SNOW) and local habitat factors (neighboring density and soil fertility) on two aspects of seedling temporal stability (survival and recruitment) and three stabilizing mechanisms (dominant species stability, species asynchrony, and species richness (total/new)). Local conditions (i.e., soil fertility and neighboring tree density) were measured at the plot level. In contrast, climate variables (i.e., VPD and SNOW) were available at the interannual scale. Therefore, we calculated mean values of the climate variables over the corresponding time window, which were uniformly applied to all seedling subplots. Finally, VPD, SNOW, neighboring tree crowding, and soil fertility were treated as continuous fixed effects, while seedling plot was included as a random effect. The significance threshold was set at $\alpha = 0.05$.

To maximize sample size while ensuring model robustness, we analyzed 6-year rolling windows spanning 2008–2022 (Meng et al., 2023), calculating the temporal mean and standard deviation of seedling survival and recruitment for each plot within each window. We further evaluated temporal stability using alternative window lengths (3-year, 9-year rolling windows, and a 15-year timescale) to test the robustness of our models, finding consistent positive relationships between temporal stability and the three stabilizing mechanisms across all window lengths (Fig. S4 and S5). We also used three non-overlapping time windows (3 years, 5 years, and 7 years) to test the relationships between dominant species stability/species asynchrony/species richness and regeneration stability (i.e., seedling survival and recruitment), and the results showed that their relationship remains solid (Fig. S6 and S7). Subsequently, simple linear regressions were conducted to examine the relationships between dominant species stability, species asynchrony, and seedling richness with the temporal stability of seedling survival and recruitment. We fitted piecewise structural equation models (pSEM) to test direct effects of the above three stabilizing mechanisms on temporal stability of seedling survival and recruitment, as well as indirect effects of climate and local habitat variables through the stabilizing mechanisms. In the pSEM, we used a random effect with seedling plot. We first considered a full model that included all possible pathways, and then sequentially eliminated nonsignificant pathways until we attained the final model. Models were selected based on Fisher's C statistic ($P > 0.05$), which follows a x^2 distribution. We standardized all variables by subtracting the mean and dividing by the standard deviation across the whole dataset. All analyses were conducted in R 4.2.2 (R Development Core Team; http://r-project.org), with the “lme4” package for fitting generalized linear mixed models (Bates et al., 2015).), the “ggplot2” package for plotting all histograms and regression figures (Wickham, 2016), and the “piecewiseSEM” package for fitting pSEM (Lefcheck, 2016).

3. Results

3.1. Climate and local habitat condition impacts on seedling stability

Temporal stability of seedling survival and recruitment was influenced by both climate and local habitat conditions, as revealed by linear mixed-effects models (Fig. 1). Among climate variables, survival and recruitment stability decreased with increasing VPD (Fig. 1a and e), but increased with higher SNOW levels (Fig. 1b and f). Regarding local habitat factors, survival stability declined with increasing neighborhood tree crowding (Fig. 1c), whereas recruitment stability tended to increase with neighboring density, although this relationship was only marginally significant (Fig. 1g). In contrast, soil fertility had no significant effect on either survival or recruitment stability (Fig. 1d and h). Furthermore, the inhibitory effect of higher VPD on survival stability was amplified in more fertile plots (Fig. S8b). In contrast, the positive relationship between SNOW and survival stability was weakened under conditions of higher neighborhood density and elevated soil nutrients (Fig. S8c and S8d).

3.2. The effects of climate and local habitat conditions on stabilizing mechanisms

Climate and local habitat conditions generally influenced species asynchrony, species richness, and the stability of dominant species (Fig. 2). Specifically, species asynchrony and dominant species stability for both seedling survival and recruitment exhibited negative

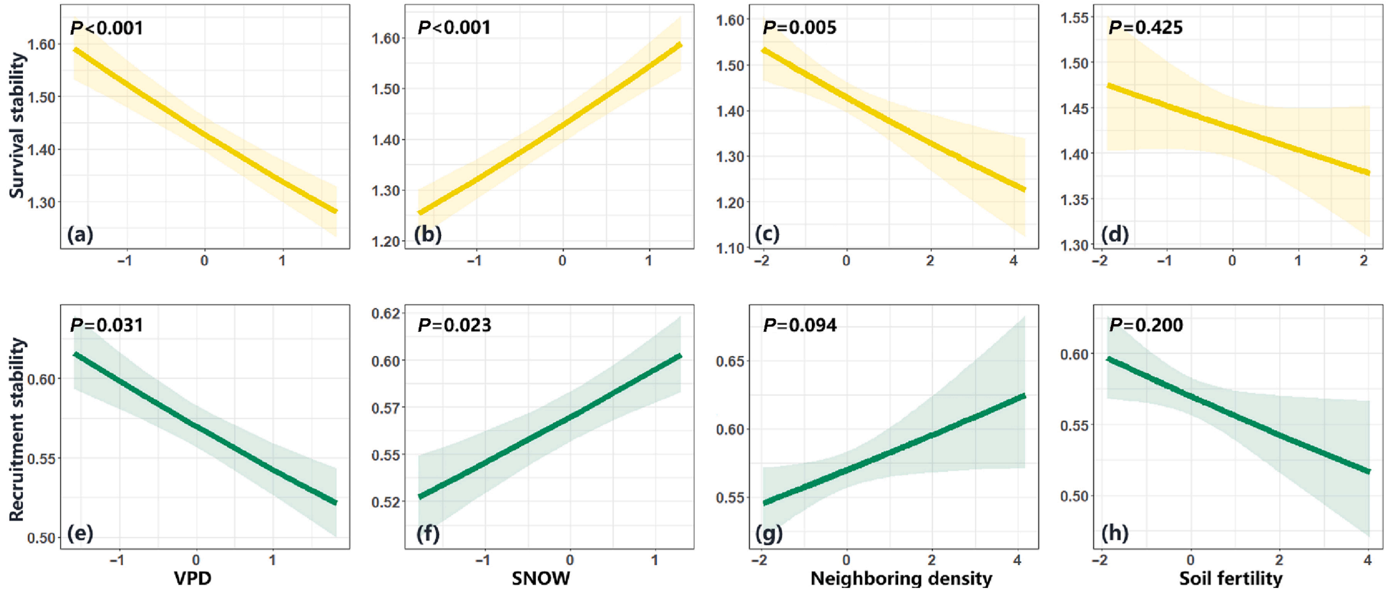

Fig. 1. Effects of climate (VPD and SNOW) and local habitat conditions on temporal stability of seedling survival and recruitment. Neighboring density: neighboring tree crowding; Soil fertility: soil nutrients calculated using the PC1 of five soil variables (pH, organic matter, total N, total P, and total K). Lines and shading indicate the linear-mixed model (LMM) predictions and their 95% confidence intervals.

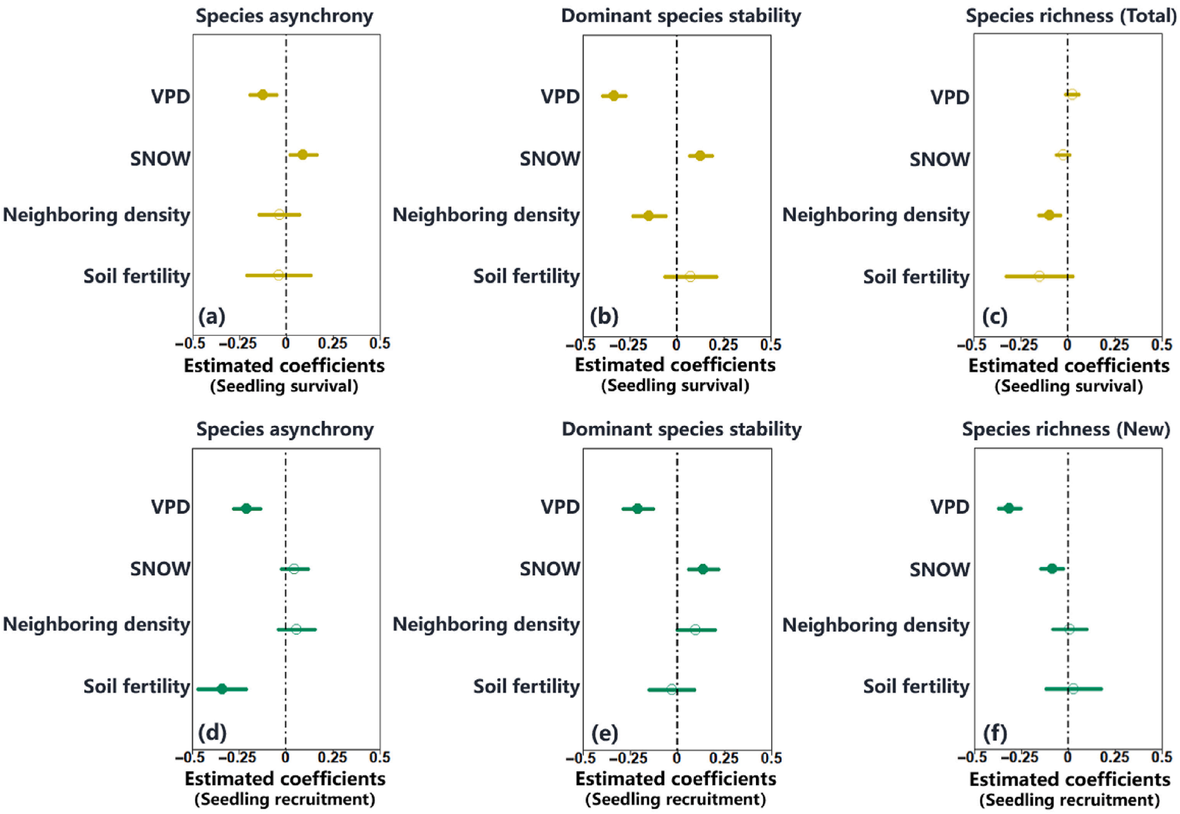

Fig. 2. Effects of climate and local habitat conditions on species asynchrony, dominant species stability, and seedling richness (species richness). **(a–c)** show results for survival stability, and **(d–f)** show results for recruitment stability. Climate and local habitat variables are defined in Fig. 1. Solid circles indicate significant effects (95% confidence interval does not overlap zero) and open circles indicate non-significant effects.

relationships with VPD (Fig. 2a and d, b and e). In contrast, species asynchrony and dominant species stability of survival (Fig. 2a and d) and dominant species stability of recruitment (Fig. 2e) were positively associated with SNOW. Total seedling richness was not significantly related to climate (Fig. 2c), whereas richness of seedling recruitment declined with increasing VPD and SNOW (Fig. 2f). Regarding local habitat factors, both the stability of dominant species in survival and total seedling richness decreased with higher neighborhood tree crowding (Fig. 2b and c). Additionally, species asynchrony in recruitment declined with increasing soil fertility (Fig. 2d).

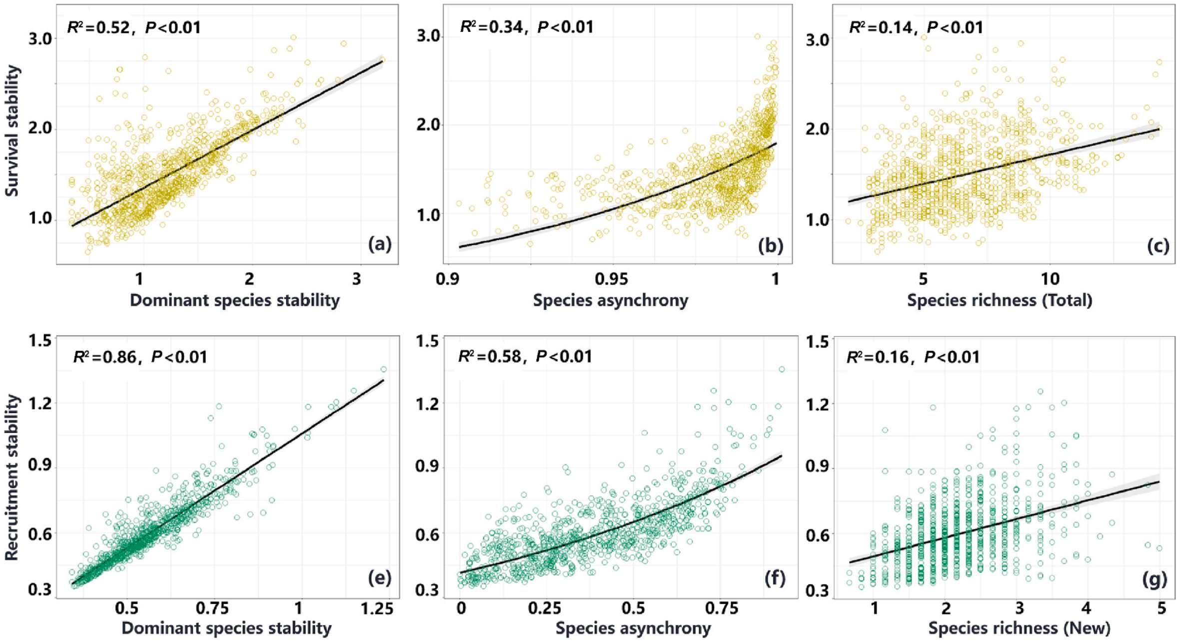

Fig. 3. Relationships of seedling survival stability and recruitment stability with **(a, e)** dominant species stability, **(b, f)** species asynchrony, and **(c, g)** seedling richness. The corresponding shaded area represents 95% confidence intervals.

3.3. *Impacting pathways of climate and local habitat conditions on seedling stability*

Bivariate regressions showed that both survival stability and recruitment stability were positively associated with dominant species stability ($R^2_{\text{survival}} = 0.53$, $P_{\text{survival}} < 0.001$;$R^2_{\text{recruitment}} = 0.85$, $P_{\text{recruitment}} < 0.001$; Fig. 3a and e), species asynchrony ($R^2_{\text{survival}} = 0.30$, $P_{\text{survival}} < 0.001$; $R^2_{\text{recruitment}} = 0.52$, $P_{\text{recruitment}} < 0.001$; Fig. 3b and f), and seedling richness ($R^2_{\text{survival}} = 0.12$, $P_{\text{survival}} < 0.001$; $R^2_{\text{recruitment}} = 0.14$, $P_{\text{recruitment}} < 0.001$; Fig. 3c and g). Furthermore, seedling richness positively influenced species asynchrony, dominant species stability, and the temporal stability of both seedling survival and recruitment (Fig. 4), indicating a positive diversity-stability relationship within seedling communities.

Climate and local habitat conditions also modulated the effects of stabilizing mechanisms on temporal stability. Specifically, VPD exerted an indirect negative effect on survival stability by reducing species asynchrony and dominant species stability (Fig. 4a), and it similarly decreased recruitment stability by suppressing species asynchrony and seedling recruit richness (Fig. 4b). In contrast, SNOW positively affected survival and recruitment stability by enhancing species asynchrony and dominant species stability (Fig. 4a). Neighborhood tree crowding indirectly reduced survival stability by decreasing total seedling richness and dominant species stability (Fig. 4a), whereas soil fertility indirectly influenced recruitment stability by promoting dominant species stability while simultaneously reducing species asynchrony (Fig. 4b).

4. Discussion

Beyond describing the demographic rates, the temporal stability of regeneration provides critical insight into how forest communities buffer environmental variability during early life stages. Through a novel integration of longitudinal demographic monitoring dataset (15

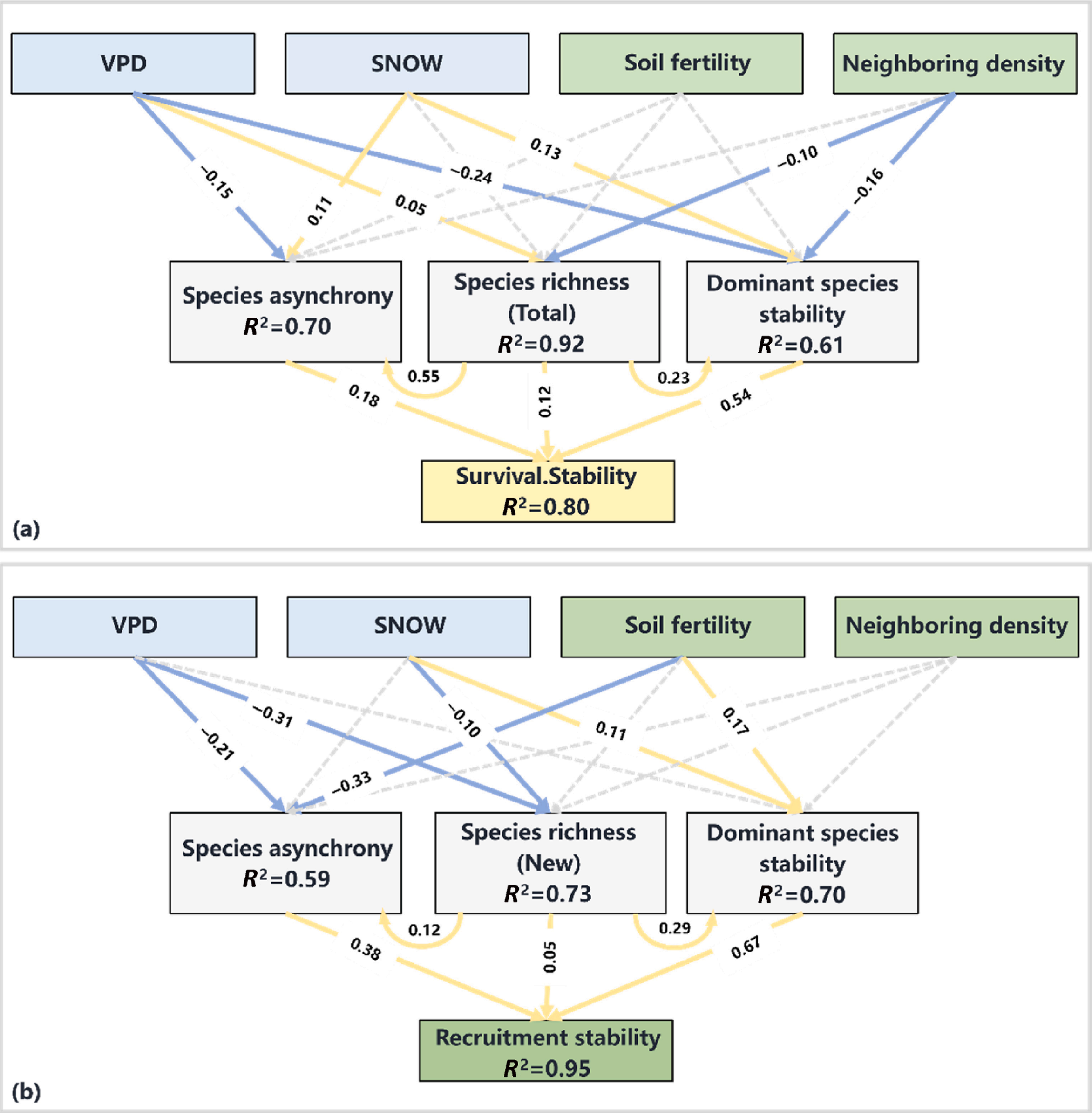

Fig. 4. The results of final piecewise structural equation modeling showing the causal relationships among climate and local habitat conditions, species asynchrony, species richness, and dominant species stability to temporal stability of **(a)** seedling survival and **(b)** recruitment. Blue and yellow arrows represent negative and positive relationships, respectively. Dashed grey arrows represent non-significant effects. The final models adequately fitted the data: (a) Fisher's C = 13.502, *df* = 14, *P* value = 0.487; (b) Fisher's C = 11.513, *df* = 16, *P* value = 0.777.

years) with high-resolution climate (VPD, snow depth) and habitat (soil fertility, neighborhood competition) parameters, we demonstrate that seasonal drought—reflected by elevated VPD—was negatively associated with the temporal stability of both seedling survival and recruitment, whereas increased snowfall was positively associated with stability. High neighborhood tree crowding decreased survival stability but, interestingly, enhanced recruitment stability, likely through seed-source and microsite effects. Consistent with our expectations, dominant species stability matters more than species asynchrony and species diversity in maintaining the temporal stability of seedling dynamics. Elevated VPD and neighborhood crowding were associated with lower survival stability, with these relationships being linked to declines in dominant species stability, while greater snow depth and higher soil fertility indirectly enhanced recruitment stability through positive effects on dominant species persistence. These findings highlight the pivotal role of dominant species in buffering climatic variability during early successional stages and emphasize their disproportionate contribution to overall community stability. Moreover, the negative correlations between VPD, species asynchrony, and dominant species stability suggest that increasing atmospheric aridity may be associated with weaker compensatory population dynamics, which is consistent with lower regeneration stability. Collectively, these results highlight the vulnerability of temperate forest regeneration to progressive drying and underscore the value of incorporating species-level stabilizing mechanisms into dynamic forest–climate models to better predict regeneration stability and ecosystem resilience.

4.1. Climate has strong effects on temporal stability of seedling dynamics

As anticipated, increased seasonal drought markedly reduced the temporal stability of seedling survival and recruitment, whereas snowfall had the opposite effect. The divergent responses of demographic stability to climate likely arise from contrasting changes in the temporal mean versus the standard deviation of survival and recruitment. Elevated VPD was associated with lower temporal means of seedling survival and recruitment, as high VPD induces stomatal closure, thereby limiting photosynthesis, reducing growth, increasing mortality, and impairing regeneration (Tepley et al., 2017). Concurrently, higher VPD decreased the standard deviation of seedling survival but had no significant effect on the standard deviation of recruitment (Fig. S10a and S10b), ultimately leading to declines in both survival and recruitment stability.

Additionally, increased snow depth not only reduced the standard deviations of both survival and recruitment but also enhanced mean survival (Fig. S10), which was associated with greater temporal stability. Thick snowpacks act as a natural buffer by insulating soil and seedlings from air temperature fluctuations, protecting seedlings from damage caused by frequent freeze-thaw cycles and deep freezing, and maintaining nutrient cycling, ultimately contributing to greater stability in seedling dynamics (Guiden et al., 2018). Contrary to our initial expectations, neighborhood tree crowding negatively affected survival stability but positively influenced recruitment stability. In crowded environments, trees compete intensely for light, water, and nutrients, which intensifies both interspecific and intraspecific competition among seedlings (Muscarella et al., 2018). As a result, seedlings in resource-limited conditions rely more on unstable resource pulses, exacerbating interannual variation in survival (Sayer, 2006). Conversely, high local tree density is often associated with stronger seed-source effects (Clark et al., 1998), which can buffer interannual fluctuations in seed production at the community level, thereby enhancing recruitment stability.

Overall, reduced interannual fluctuations in seedling survival and recruitment indicate greater demographic predictability and a lower risk of regeneration failure under unfavorable climatic conditions. Such stability reflects the capacity of seedling communities to maintain continuous regeneration despite year-to-year variation in atmospheric aridity (e.g., higher VPD), winter severity (e.g., less snowpack), or habitat constraints (e.g., stronger local competition) across the spatial scale. From a demographic perspective, stable regeneration (e.g., seedling survival and recruitment) enhances the likelihood that at least part of each cohort survives climatic extremes, thereby sustaining population persistence and community continuity over time.

4.2. Dominant species contribute the most to seedling dynamic stability

Our findings revealed that dominant species stability exhibited a stronger positive relationship with the temporal stability of seedling dynamics than either species asynchrony or diversity, consistent with patterns previously reported in grassland ecosystems (Ma et al., 2017). This result can be largely explained by the pivotal role of dominant species in community dynamics, as articulated by Grime's mass ratio hypothesis (Quan et al., 2021). In our study, three species (*S. reticulata*, *F. mandshurica*, and *T. amurensis*) accounted for 75.4% of individuals in the temporal survival analysis, while two species (*F. mandshurica*, and *T. amurensis*) contributed 89.2% in the recruitment analysis. Although the remaining species comprised over 90% of total richness, they contributed less than 25% to community abundance. We found that dominant species exhibited higher stability than subordinate and rare species populations, both in terms of seedling survival stability and recruitment stability (Fig. S11a and S11b). Furthermore, we confirmed that dominant species play a more critical role in promoting the stability of seedling communities compared to subordinate and rare species (Fig. S12a and S12b). These results highlight the strong association between dominant species stability and forest ecosystem stability, and extend Grime's mass ratio hypothesis to the early stages of forest regeneration. To our knowledge, this study provides the first empirical evidence from a seedling perspective, highlighting the critical stabilizing influence of dominant species in maintaining forest temporal stability under global change.

Temporal asynchrony among populations of individual species is recognized as a key mechanism for maintaining community stability (Craven et al., 2018; Lisner et al., 2024). Typically, populations that fluctuate synchronously are closely linked to abiotic conditions (Leps et al., 2018), performing well during favorable periods but declining under unfavorable ones. In contrast, asynchronous population responses, which deviate from perfect synchrony, often arise from biotic interactions—particularly interspecific competition—or from species-specific differences in responses to abiotic factors (Tilman, 1996). A notable finding of this study is that seasonal drought reduced species asynchrony, thereby diminishing the temporal stability of seedling communities (i.e., survival and recruitment) under drought conditions—a phenomenon that has been largely overlooked in forest ecosystems.

Theoretical and empirical studies have consistently shown that the temporal stability of biomass production in plant communities increases with species richness (Xu et al., 2021). This is because species diversity acts as an insurance mechanism against environmental fluctuations, sustaining more stable community dynamics—such as primary productivity and species abundance—over time (Tilman et al., 2006; Isbell et al., 2017). Consistent with this concept, we observed significant positive relationships between seedling temporal stability and species richness in a temperate forest ecosystem. Species richness was positively associated with species asynchrony, thereby enhancing seedling community stability. Differences in species' responses to environmental changes—such as variation in seedling survival and recruitment—can generate asynchronous population dynamics, where declines in some species are offset by increases in others. This compensatory effect helps stabilize overall community density over time (Hautier et al., 2014). However, such compensatory effects are expected to weaken in species-poor or functionally homogeneous communities (Loreau and de Mazancourt, 2008). Furthermore, the significant positive correlation between species richness and the temporal stability of dominant species aligns with previous findings that species diversity can facilitate resource competition and utilization by dominant species (Dolezal et al., 2019). It should be noted that the positive relationship between diversity and temporal stability gradually strengthened as the temporal scale increased (Fig. S4 and S5), which was not documented in previous research. Therefore, future studies should further explore the relationship between these three key mechanisms and seedling temporal stability across different temporal scales to avoid underestimating or overestimating the relative importance of stability mechanisms due to excessively long- or short-time scales.

4.3. Climate and local habitat conditions regulate the stabilizing mechanisms of seedling dynamics

Climate and local habitat conditions are associated with variations in the relationships between dominant species stability, species asynchrony, and species richness with the temporal stability of seedling dynamics. Notably, drought and snowfall strongly affected dominant species stability, likely because tree seedlings are particularly sensitive to climate fluctuations due to their limited stored resources and relatively underdeveloped root systems (Hanbury-Brown et al., 2022). Higher neighborhood densities were associated with lower survival stability, which co-occurred with lower dominant species stability. This finding is consistent with the Janzen–Connell hypothesis, which posits that common species are more susceptible to conspecific negative density dependence driven by the accumulation of natural enemies (e.g., herbivores, pathogens) (Janzen, 1970; Connell, 1971), thereby promoting local species diversity (Harms et al., 2000).

Specifically, we found that seasonal drought was associated with lower temporal stability of seedling dynamics, with this relationship being linked to reduced species asynchrony and dominant species stability (Muraina et al., 2021; Ma et al., 2024). In contrast, snowfall during the non-growing season had the opposite effect, reinforcing the role of species asynchrony in maintaining community stability under climate change (Segrestin et al., 2024). Moreover, drought and snowpack can alter water and nutrient availability, leading to the loss or proliferation of specific species (e.g., drought-intolerant or cold-resistant species) (Guiden et al., 2018; Ma et al., 2024). Previous studies have shown that extreme drought favors deep-rooted species, resulting in a more homogeneous community composition and consequently lower temporal stability (Ma et al., 2024). Beyond interspecific differences in environmental preferences, another key driver of asynchrony is the variability in the frequency and intensity of plant–plant interactions (competition and facilitation) under changing environmental conditions (Lopez-Angulo et al., 2023). In this context, species do not fluctuate independently in response to environmental changes; instead, compensatory dynamics are often driven by asymmetric competition (Leps et al., 2018). For example, harsh conditions such as drought may intensify facilitative interactions among species according to the stress-gradient hypothesis (Mulder et al., 2001), forcing species to fluctuate more synchronously and thereby reducing seedling stability (Ma et al., 2024). Conversely, benign conditions, such as winter snowfall, may promote hierarchical competitive interactions, increasing temporal asynchrony (Tilman et al., 1998). Thus, shifts in positive and negative plant interactions associated with climate variation can modulate temporal stability by either amplifying or diminishing species asynchrony (Lopez-Angulo et al., 2023).

Seasonal drought reduced the species diversity of new recruits in this study plot, consistent with previous findings from both forest and grassland ecosystems (Ma et al., 2017, 2024; McDowell et al., 2020). This drought-induced decline in diversity likely contributes to reduced ecosystem stability under warming and drying conditions (McDowell et al., 2020; Schnabel et al., 2021). Although previous studies in temperate forests have shown that deep snowpacks can enhance seedling survival by inducing dormancy and providing protective insulation (Xu et al., 2022b), our results revealed a negative relationship between snow depth and the species richness of new recruits, thereby weakening recruitment stability. While snowfall generally offers favorable protection that promotes seedling survival (Guiden et al., 2018), excessive snow accumulation may inhibit seed germination due to increased prevalence of snow molds, which can impair seed viability and germination (Smull et al., 2019).

5. Conclusions

Our 15-year analysis demonstrates that climatic variability exerts a strong influence on the temporal stability of seedling dynamics by regulating three stabilizing effects and interacting with local habitat within regenerating communities. Seasonal drought, indicated by elevated VPD, destabilizes seedling communities through reductions in species asynchrony and dominant species stability, whereas deeper snowpack mitigates these impacts by alleviating winter stress and promoting consistent recruitment. Among the stabilizing mechanisms evaluated, dominant species stability emerged as the strongest contributor to regeneration stability, followed by species asynchrony and species richness. These results emphasize the crucial role of dominant species in buffering climate-induced fluctuations and maintaining demographic resilience during the early stages of forest succession. From an eco-meteorological perspective, this study provides a process-based framework linking short-term climatic variability to long-term ecological stability in forest regeneration. Incorporating such stabilizing mechanisms into forest–climate models will enhance predictions of regeneration success, carbon sequestration, and vegetation resilience under future climate extremes. Furthermore, management strategies that promote snow retention and conserve functionally diverse dominant species are likely to be vital for sustaining temperate forest stability in an increasingly arid and variable climate.

CRediT authorship contribution statement

Zhichao Xu: Writing – review & editing, Writing – original draft, Methodology, Funding acquisition, Data curation, Conceptualization. **Meihui Zhu:** Writing – review & editing, Software, Funding acquisition, Formal analysis. **Jonathan A. Myers:** Writing – review & editing. **Lin Jiang:** Writing – review & editing. **Fei Lin:** Writing – review & editing. **Ji Ye:** Writing – review & editing. **Shuai Fang:** Writing – review & editing. **Zikun Mao:** Writing – review & editing. **Xugao Wang:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Data curation, Conceptualization.

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Data availability

The data that support the findings of this study are openly available via Zenodo at: https://zenodo.org/records/15209295.

Conflict of interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fecs.2026.100433.

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