

ORIGINAL ARTICLE

Temporal and spatial changes of ecological strategies of native and alien plant assemblages in response to chronic disturbances

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- **Background and Aims** Successional theory predicts directional shifts in plant community composition following disturbance. However, the long-term effects of chronic, recurring disturbances on plant ecological strategies at the community level in human-altered landscapes, and how they differ between the assemblages of native and alien species, remain poorly understood.
- **Methods** Using Grime's competitor, stress-tolerator, ruderal (CSR) framework, we examine temporal and spatial changes in plant strategies at the community level in the Three Gorges Reservoir Area, China. Based on repeated plant community surveys in 2012 and 2018 at the same localities, we assess the differences in the assemblages of native and alien strategies in response to chronic disturbances by extreme hydrological fluctuations and intense human activities over time and along a shoreline-to-upland disturbance gradient.
- **Key Results** Our results reveal a temporal shift in native assemblages, with a decline in R-score and an increase in C- and S-scores, while alien assemblages maintained a strong R-strategy. Spatial patterns show that native assemblages adopted a mid-elevation peak in C-strategy, with S- and R-strategies dominating at higher and lower elevations, respectively. In contrast, there is no spatial variation in the CSR strategies of alien plant assemblages.
- **Conclusions** Our findings demonstrate that chronic disturbances (e.g. water fluctuations and human activities) drive a spatiotemporal decoupling of the CSR strategies between native and alien plant assemblages. This divergence requires targeted management by prioritizing suppression of ruderal alien species and promoting competitive and stress-tolerant native species to guide succession dynamics.

Key words: Alien plants, community succession, CSR theory, Grime's adaptive strategy, hydrological fluctuation, plant invasions, Three Gorges Reservoir Area.

INTRODUCTION

Temporal shifts in plant communities reflect changes in species composition and abundance in response to environmental change, with implications for community succession and restoration (Funk *et al.*, 2008; Reich and Cornelissen, 2014; Meiners *et al.*, 2015). The magnitude of community shifts depends mainly on how the species respond to disturbance, on resource availability and on how interact with each other. The classical Grime's competitor, stress-tolerator, ruderal (CSR) scheme captures fundamental trade-offs in plant adaptation to resource availability and disturbance intensity (Grime, 1974). Specifically, competitors (C) dominate resource-rich habitats through rapid growth

and high biomass allocation, stress-tolerators (S) persist in low-resource environments via slow growth and resource storage, while ruderals (R) thrive under frequent disturbances by prioritizing rapid reproduction and short life cycles (Grime, 1977; Pierce *et al.*, 2017). These strategies represent key axes of plant adaptation, reflecting species' niches along resource–disturbance gradients (Radford, 2013; Díaz *et al.*, 2016). Thus, the CSR theory offers a robust framework for understanding how changes in plant ecological strategies scale-up at the community level in human-modified landscapes (Toffolo *et al.*, 2021; Sun *et al.*, 2023).

Grime's CSR theory elucidates transitions of plant communities during secondary succession (Grime, 1977, 2001). In early

successional stages, R-strategists dominate, characterized by rapid reproductive allocation through short life cycles and high dispersal capacity (Pierce *et al.*, 2017). The intermediate successional stage undergoes a dynamic reorganization favouring C-strategists, where species optimize resource interception through enhanced photosynthetic structures and spatial occupation (Huston and Smith, 1987; Pierce *et al.*, 2017). The magnitude of this competitive transition correlates positively with habitat productivity (Grime, 1977, 2001). Finally, late successional communities transition to S-strategists under stable, resource-limited conditions (Pierce *et al.*, 2017). These late successional species develop conservative metabolic regulation and long-term resource retention mechanisms, ultimately forming climax communities that are resilient to environmental constraints (Grime and Pierce, 2012). However, this theoretical directional trajectory may diverge under chronic or periodic disturbances, where successional advancement becomes arrested through selective filtering mechanisms (Catford and Jansson, 2014). Persistent and periodic disturbances can maintain non-equilibrium dynamics by periodically resetting community assembly, either through direct biomass removal or altered soil conditions. Such disturbance regimes (e.g. post-fire, post-flooding or post-grazing) detain vegetation succession in developmental states favouring R- or S-strategist species (Cramer *et al.*, 2008; Catford and Jansson, 2014; D'Antonio *et al.*, 2017; Wang *et al.*, 2018).

Following disturbances, alien species benefit from increased propagule pressure and resource availability, which impairs the establishment of native species (Hobbs and Huenneke, 1992). The CSR scheme has been used to investigate the mechanisms underpinning invasion by comparing the functional similarity of alien and native plant species (Radford, 2013; Cross *et al.*, 2015; Guo *et al.*, 2022). Comparative analyses demonstrate either significant CSR divergence between native and alien assemblages (Guo *et al.*, 2018) or substantial functional convergence (Cross *et al.*, 2015). These contradictions reflect the context-dependent invasion mechanisms, where the establishment of alien species hinges on both trait advantages and recipient ecosystem properties (Catford *et al.*, 2022). In addition, aliens can alter successional trajectories by suppressing natives (D'Antonio *et al.*, 2017). Although Grime's framework has been studied to compare native and alien plant traits, the temporal changes under chronic and periodic disturbances on the CSR strategies of alien and native assemblages at the community level remain scarce.

The Three Gorges Reservoir Area (TGRA) reached full impoundment in 2010 and is characterized by a pronounced 30-m seasonal hydrological fluctuation, driven by annual winter storage and summer discharge, and intensive utilization associated with urbanization and agricultural activities (Wu *et al.*, 2004; New and Xie, 2008; Zhang and Xie, 2021). In the reservoir riparian zones (i.e. the zones of water-level fluctuation), recurrent inundation creates an intermittent shift between herbaceous dominance and bare substrates, effectively suppressing natural succession trajectories (New and Xie, 2008; Zhang and Xie, 2021). In contrast, in the non-flooded upland areas, afforestation with monoculture plantations and cropland expansion also impede natural ecological succession (Zhong *et al.*, 2020). Notably, these disturbances facilitate invasion of alien plant species across the TGRA (Chen *et al.*, 2017; Le *et al.*, 2024a). A recent analysis revealed that the occurrence

of alien plants decreases with increasing distance from the hydrological network, reflecting the role of hydrological connectivity in mediating invasion processes (Le *et al.*, 2024a).

While Grime's CSR theory predicts directional shifts in the plant strategy spectra along disturbance gradients, the spatial scaling of CSR strategy redistribution across hydrological-terrestrial disturbance gradients remains unexamined. Here, utilizing a 6-year dataset spanning post-impoundment phases (2012–2018) in the TGRA, we aim to address the following questions: (1) How do the CSR strategies at the community level shift over 6 years of chronic disturbance? (2) Do the assemblages of alien species exhibit distinct CSR strategies compared to natives under chronic disturbances? (3) How do the CSR strategies at the community level shift along the shoreline–upland gradient? We hypothesize that: (1) plant communities would converge toward R- and S-strategies over time, reflecting filtering by recurring disturbances; (2) alien assemblages would consistently exhibit greater C- and R-scores compared to native assemblages, due to their advantage in exploiting fluctuating resources in disturbed habitats (Davis *et al.*, 2000; Turner, 2010; Guo *et al.*, 2018); and finally (3) on average, community strategies would vary spatially with disturbance intensity, transitioning from S- and R-strategies in frequently flooded lowlands to a C-strategy in less disturbed upland zones, mirroring the hydrological connectivity gradient (Le *et al.*, 2024a).

MATERIALS AND METHODS

The TGRA, spanning over 58 000 km², is located in the southwestern region of China (Wu *et al.*, 2004). The TGRA achieved its first full impoundment in 2010. The water level of the reservoir riparian zones changes from 175 m above sea level (m a.s.l.) in winter to 145 m a.s.l. in summer. Before the dam was built, there was no difference in plant species composition between the reservoir riparian zones and non-flooded upland zones (Wang *et al.*, 2002). However, the dramatic fluctuations in water level, coupled with the resettlement of over 2 million people, has significantly altered the region's plant community structure, creating numerous opportunities for the invasion of alien species and consequently threatening the region's plant community composition (Wu *et al.*, 2004; New and Xie, 2008).

To detect changes in species' CSR strategy across the TGRA, we compiled a broad-scale repeated-sampling dataset based on 2-year field surveys in 2012 and 2018, respectively. Sampling was conducted during the mid-growing season (either July or August) by selecting 22 transects along both the south bank and the north bank (145–350 m a.s.l.) of the Yangtze River in 2012 and resampled in 2018 (Supplementary Data Fig. S1). The elevational gradient (145–350 m a.s.l.) in the TGRA was selected as a surrogate environmental gradient, integrating covarying abiotic and anthropogenic drivers. Elevation here correlates with inundation duration and frequency (Le *et al.*, 2024a), soil chemical properties (Fig. S2) and land-use intensity (Huang *et al.*, 2024), collectively shaping plant community assembly. In each transect, eight grassland plots of 2 × 2 m² were randomly placed in the reservoir riparian zone and adjacent upland. In each plot, identification and abundance for all native and alien plants were recorded. Species abundance in each plot was estimated by the Braun–Blanquet method. Determination of alien plant species was made with reference to Ma and Li

(2018). In 2018, due to practical constraints (e.g. road rebuilding and human disturbance), only 126 out of the 176 grass-dominated communities sampled in 2012 could be resurveyed.

Overall, our dataset had 281 native and 43 alien plant species. For each species, we collected three leaf traits used for CSR ordination: leaf area (LA), leaf dry mass content (LDMC) and specific leaf area (SLA). These traits were obtained from the TRY plant traits database (Kattge *et al.*, 2020) and the BIEN database (Enquist *et al.*, 2016). We filtered for trait values with an error risk <4 according to the TRY database criterion. In instances where identification was ambiguous at the species level, or where specific trait data were unavailable in the TRY database, we used the traits from congeneric relatives. Throughout our analysis, we used mean trait values for each species. LA, LDMC and SLA records were available for 96.3, 97.8 and 99.4 % of the species, respectively. We imputed missing values using multivariate imputation by random forest using the R package ‘mice’ (van Buuren and Groothuis-Oudshoorn, 2011).

Building upon the three key leaf traits (LA, LDMC and SLA) that encapsulate the fundamental functional spectrum of plants, we utilized the ‘Stratefy’ tool developed by Pierce *et al.* (2017) to quantify Grime’s CSR strategies for each species. To document shifts in community-level CSR strategies over succession, we calculated the community-weighted mean (CWM) of CSR scores for each plot at two surveys (Garnier *et al.*, 2004). The CWM of C-, S- and R-scores of a plot were calculated as follows:

$$\text{CWM} = \sum_{i=1}^n P_i * S_i$$

where P_i is the relative cover of species i across all plots, S_i is each strategy score of species i and n is the number of species in the field. To compare the CSR strategies of alien and native species through time, we separately calculated the CWM values of CSR scores for alien and native species within each plot.

To test whether the CSR strategies of the whole community, alien and native assemblages within the community changed across time, we used linear mixed-effects models, including sampling year as a fixed predictor, elevation and its interaction with sampling year as covariates, and plot nested with transect as a random effect. All statistical analyses were conducted using the R package ‘lme4’ (Bates *et al.*, 2015). We used the ‘glht’ function from the R package ‘multcomp’ (Hothorn *et al.*, 2008), applying Tukey’s all-pair comparisons with Bonferroni correction to assess differences in CSR scores between sampling years or species status (alien vs. native).

To further assess whether the temporal shifts in plant CSR strategies varied between native and alien assemblages, we conducted a two-way repeated measures ANOVA. This analysis employed CSR scores as the dependent variable, with the sampling year as the repeated measure and species status (native vs. alien) as the grouping factor. Significant interaction between year and species status would indicate that the shifts in CSR strategies differed between alien and native assemblages.

Then, for each sampling year, we used linear mixed-effects models to assess how the CSR scores of the community-level, alien and native assemblages changed along the elevational gradient. In the models, we included elevation as a fixed effect and plot nested in the transect as a random effect. To capture the potential non-linear relationship between elevation and CSR

scores, we also incorporated a quadratic term of elevation into the fixed effects. The model with the lower Akaike information criterion (AIC) was selected as the best-fitting model. To assess marginal and conditional R^2 , we used the ‘rsquaredGLMM’ function of the R package ‘MuMIn’ (Bartoń, 2023).

RESULTS

Initially, following the impoundment of the Three Gorges Reservoir, the area was dominated by species exhibiting an R-strategy (Fig. 1; Supplementary Data Table S1). However, as frequent flooding and agricultural activities continued throughout the TGRA, a significant temporal shift in community CSR strategy was observed, characterized by a significant increase in the mean CWM of C- and S-scores and a concomitant decrease in R-scores across the reservoir region (Fig. 1; Table S1).

A notable statistical divergence emerged in the CSR scores of native and alien assemblages over time as indicated by a significant interaction between species status and time on the CSR scores (Supplementary Data Table S2). According to Stratefy’s standard, both native and alien assemblages initially exhibited R-strategies. The alien assemblages maintained an R-strategy, reflected in their non-significant difference in CSR scores over time (Fig. 2; Table S3). In contrast, native assemblages demonstrated a significant shift towards a more balanced strategy, characterized by increased C-scores and decreased R-scores (Fig. 2; Table S4). Although alien assemblages initially displayed higher C-scores compared to native species, this advantage disappeared over time (Fig. 2; Table S6). Alien assemblages consistently outperformed native species in terms of R-characteristics, while native assemblages maintained a persistent advantage in S-characteristics (Fig. 2).

At the community level, the CWM of C-score showed a hump-shaped pattern along elevation and peaked at 250–300 m a.s.l. (Fig. 3A). In contrast, CWMs of S- and R-scores exhibited opposing elevation patterns, with higher values at low and high elevations, respectively, and lower values at mid-elevations (Fig. 3B, C). Regarding species status, the CWMs of CSR scores for alien assemblages exhibited no significant changes across elevation, whereas native assemblages showed clear shifts that aligned with community-level patterns (Fig. 4).

DISCUSSION

We investigated the shifts in plant CSR strategies at the community level in response to chronic and periodic disturbances in the TGRA, focusing on 324 plant species, including both alien and native taxa. The Three Gorges Project’s flooding and subsequent human-induced disturbances have disrupted the vegetation (Wu *et al.*, 2004), triggering a shift in CSR strategies at the community level from predominantly ruderal (R-strategy) to a more balanced distribution of CSR strategies. Initially, both alien and native assemblages followed an R-strategy. However, this pattern has diverged over time, with alien assemblages maintaining an R-strategy, while native species assemblages have decreased in R-score and increased in C-score. Furthermore, the CSR scores of alien and native assemblages exhibited different patterns along the elevational gradient. These findings highlight the complex interplay between

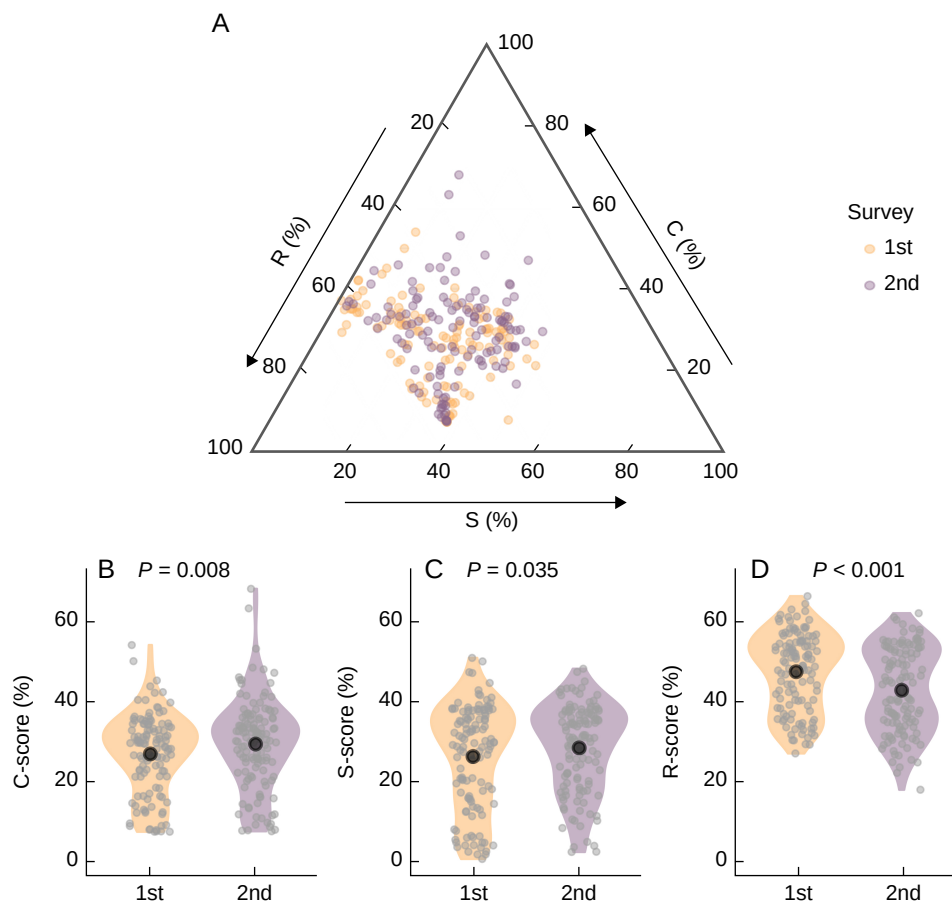


FIG. 1. Temporal shifts of plant ecological strategies at the community level. Ternary plot of the CSR (competitive, stress-tolerant, ruderal) strategy (A), showing the mean community-weighted means (CWMs) of CSR scores for each plot across surveys. Temporal shifts of plant communities for C-score (B), S-score (B) and R-score (C). Violin plots represent the distribution of the data. Black circles represent the mean CWM CSR scores, with error bars indicating standard errors.

anthropogenic disturbance, species status and ecological strategies in shaping plant community dynamics, with implications for biodiversity conservation and ecosystem restoration in disturbed landscapes.

Changes in CSR strategies over time

Partially contrary to our hypothesis, after 8 years of post-dam full operation, plant communities have increased in both C- and S-scores but decreased in R-scores, suggesting an ecological transition from a disturbance-dominated to a stress-mediated community assembly. This pattern resonates with the stress-gradient hypothesis, where increasing environmental harshness (e.g. prolonged inundation at lower elevations) favours stress-tolerant species (He *et al.*, 2013; Sun *et al.*, 2023). Specifically, plant communities within the riparian zones exhibited a gradual shift towards increased stress tolerance in response to the flood–dry–flood cycle patterns, while their competitive ability remained relatively stable over time (Supplementary Data Fig. S3), consistent with the reduced importance of interspecific competition under intense disturbance regimes (Grime, 1977; Shea and Chesson, 2002). In contrast, the non-fluctuation zones, characterized by intensive agricultural activities, including monocultures and the

liberal use of chemical and fertilizer inputs (Violle *et al.*, 2010; Zhong *et al.*, 2020; Huang *et al.*, 2024), drive plant communities towards higher levels of stress tolerance and competition for soil resources. A decline in ruderal characteristics of plant communities over time is expected in ecological successions.

Our comparative analysis of native and alien assemblages revealed distinct responses in their C- and S-strategies during a 6-year period. Alien assemblages predominantly clustered along the C–R axis, while native assemblages aggregated along the S–R edge. Alien species, such as *Sesbania cannabina* and *Talinum paniculatum*, displayed a more pronounced competitive advantage over native species, aligning with the general observation that successful invaders often possess traits associated with resource acquisition and competitive dominance (Funk and Vitousek, 2007; Richardson and Pysek, 2012; Fridley *et al.*, 2022). Unexpectedly, in the second survey, alien assemblages had no competitive advantage over native assemblages, which contradicts both our initial hypothesis and the prevailing view that alien species possess an inherent competitive advantage over natives. This is because the frequency of native C-strategists has increased substantially over time compared to aliens. These native species assemblages have occupied more ecological niches, gradually expanded their proportion within the plant community and in turn enhanced the

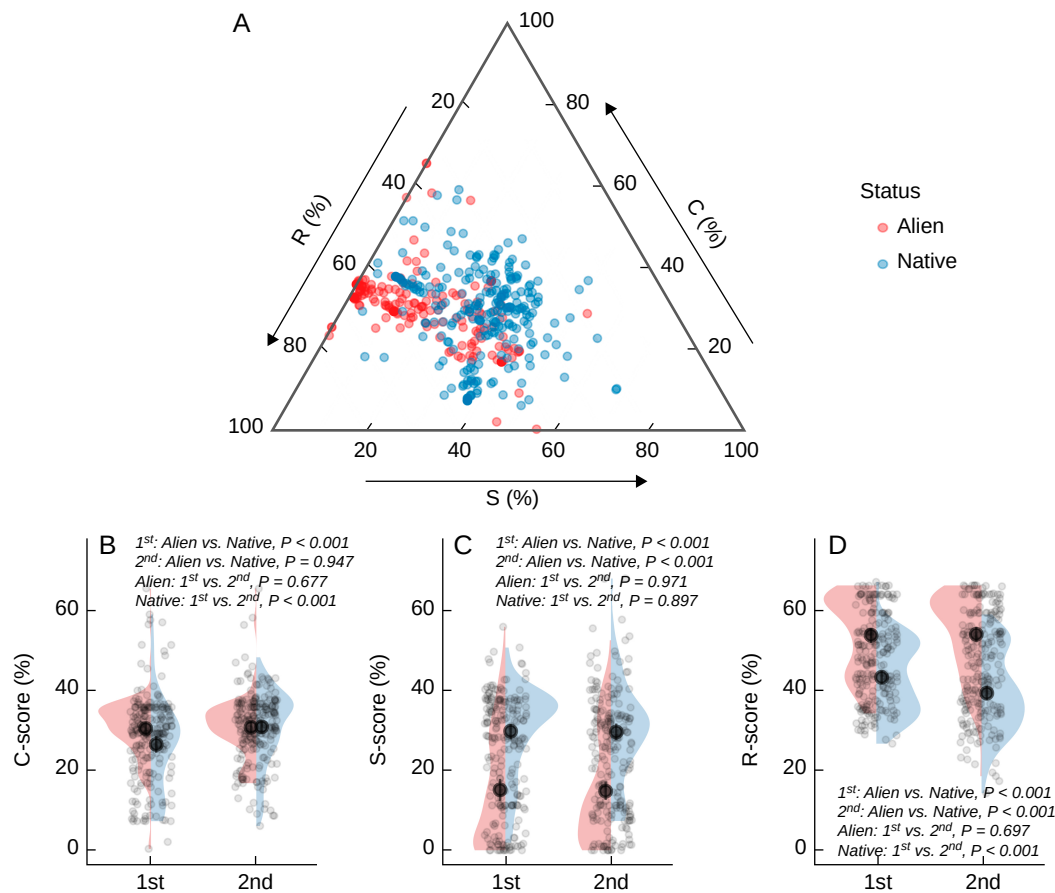


FIG. 2. Temporal shifts in CSR (competitive, stress-tolerant, ruderal) strategies of alien and native species assemblages. Ternary plot of alien and native assemblages within the mean community-weighted means (CWMs) of CSR scores for each plot across surveys (A). Temporal shifts of alien and native species assemblages for C-score (B), S-score (B) and R-score (C). Violin plots represent the distribution of the data. Black circles represent the mean CWM CSR scores, with error bars indicating standard errors.

competitive capacity of native assemblages (Supplementary Data Table S7). This result suggests that, in harsh environments, competitive native species can outcompete less-tolerant aliens by capitalizing on their superior ability to withstand resource scarcity and other stressors (Shea and Chesson, 2002). Disturbances, serving as environmental filters, selectively facilitate the coexistence of functionally similar species (Le et al., 2024b), such that competition is not the primary driver of the invasion of alien plants in these disturbed environments (Le et al., 2024a).

In the early stage, both alien (e.g. *Erigeron sumatrensis*) and native species (e.g. *Cynodon dactylon*, *Cyperus rotundus* and *Senecio scandens*) exhibited a tendency towards R-strategies, characterized by rapid growth and reproduction. However, native plant assemblages tended to adopt a more uniform strategy over time, balancing competitive and stress-tolerant traits to face resource-limited environments. Conversely, alien assemblages maintained an R-strategy, suggesting their ability to exploit disturbance-created opportunities and complete their life cycle before successional processes limit their growth. Specifically, alien R-strategist species have maintained their ruderal characteristics by increasing in occurrence frequency while decreasing in their relative abundance (Table S7). Meanwhile, the occurrence

frequency of native R-strategists has declined substantially (Table S7). This shift has resulted in alien assemblages retaining a competitive advantage over native assemblages in terms of R-scores. Notably, the emerging statistical divergence in CSR scores implies temporal niche partitioning, potentially reducing competitive exclusion between native and alien assemblages (MacDougall et al., 2009). This finding supports the notion that many invaders are opportunistic species that can thrive in dynamic environments (Catford and Jansson, 2014; Le et al., 2024a).

Native assemblages consistently exhibited greater stress tolerance compared to alien assemblages. Native species, such as *Xanthium strumarium* and *Miscanthus floridulus*, with high S-scores possess traits such as long life spans, robust foliage, slow growth rates and limited reproductive output (Grime and Pierce, 2012). These adaptations enable them to persist in environments with chronically or seasonally constrained productivity (Pierce et al., 2017). Previous studies have demonstrated that native ruderal species exhibited remarkable adaptability to local conditions, rendering them resilient to a range of disturbances, including droughts, floods and anthropogenic perturbations (Dlugosch et al., 2015; Khattak et al., 2024). A recent meta-analysis also indicated that native species possess greater adaptive advantages in high-stress environments than alien species

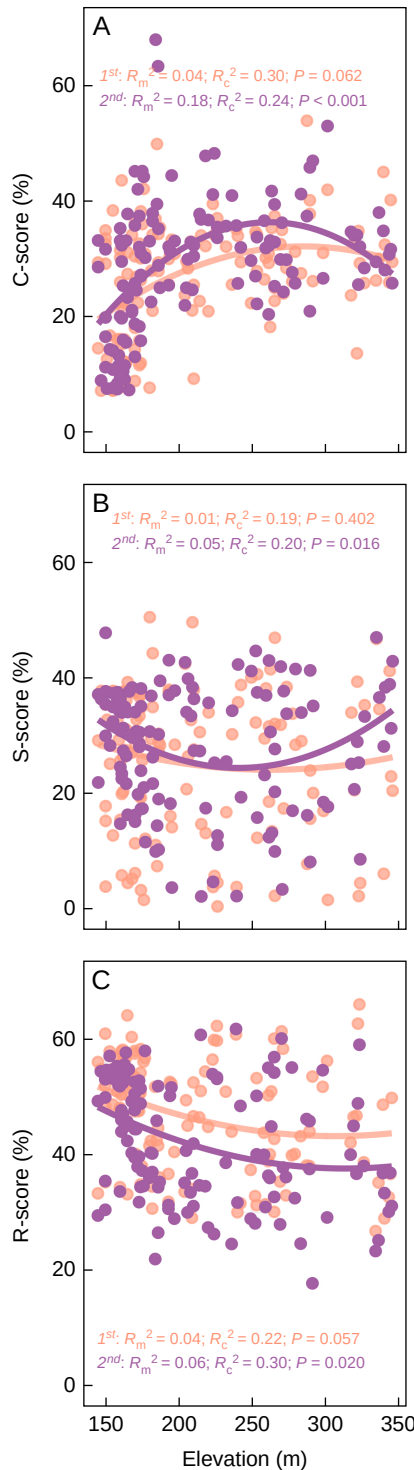


FIG. 3. Generalized linear mixed models were used to test the relationships between elevation and the community-weighted means (CWMs) of CSR scores of plant communities across surveys. (A) C-score; (B) S-score; (C) R-score. R_m^2 represents marginal R^2 and R_c^2 represents conditional R^2 .

(Wan *et al.*, 2024). Given the prevalence of periodic droughts, floods and agricultural activities within the region (New and Xie, 2008; Le *et al.*, 2024a), we posit that the stress-tolerant strategies exhibited by native plant assemblages represent adaptations to recurrent disturbances.

Changes in CSR strategies along the elevational gradient

Inconsistent with our initial hypothesis, the C-score at the community level exhibited a hump-shaped pattern along the elevational gradient, while the lowest S-score occurred at mid-elevations. The CSR strategy of native plant assemblages aligns with this pattern, as they constitute the majority of the communities. In contrast, alien plant assemblages exhibited consistent CSR scores along the elevational gradient, suggesting their strategies are less sensitive to local abiotic filters compared to natives. The spatial conservatism of alien species' strategies may reflect their generalist adaptation strategy, which offsets environmental heterogeneity challenges by maintaining high reproduction, consistent with the 'jack-of-all-trades' nature of alien species (Davidson *et al.*, 2011).

Grime suggested that the importance of C-strategists depends on habitat productivity (Grime, 1997, 2001). The humpback distribution of the C-score supports the hypothesis that moderate disturbance prevents competitive exclusion (Connell, 1978). Prolonged inundation at lower elevations resulted in soil hypoxia and nutrient loss, hindering root growth and favouring stress tolerance (Catford and Jansson, 2014). In the non-flooded upland areas, reduced disturbance and stress generally improve soil conditions and enhance competitive ability (Supplementary Data Fig. S2). A notable shift occurs in C- and S-scores between 250 and 350 m, potentially due to intense human activity, including agriculture and urbanization (Zhong *et al.*, 2020; Huang *et al.*, 2024), which disrupts the resource acquisition and competitive dominance required for C-strategists. As a result, competitive ability ceases to be the dominant filter for community assembly. Species survival depends more on tolerance to frequent disruption (favouring stress-tolerant S-strategists or ruderal R-strategists) rather than competitive superiority. In this context, the use of agrochemicals and frequent human movements in these areas impose additional stressors, potentially amplifying the selective pressure for stress tolerance and pushing native species assemblages toward more S-oriented strategies. The first survey, however, did not reveal significant changes in stress tolerance of native assemblages, suggesting a strong influence of historical land use on successional trajectories.

Consistent with our expectations, we found a decline in R-scores of plant communities and native assemblages along the elevational gradient. The most pronounced variation occurred between 145 and 175 m, driven by the severe hydrological regime imposed by the reservoir. The dynamic water level fluctuations further promoted the abundance of native ruderal species, such as *Cynodon dactylon* and *Cyperus rotundus*, which are well adapted to exploit disturbance-induced opportunities. Competitive species were relatively scarce, with only a few dominant competitors (e.g. *Xanthium strumarium* and *Persicaria hydropiper*). This reflects the inability of competitive species to tolerate intensified riparian zones, especially in those with annual and seasonal regulations, due to prolonged inundation, soil saturation, drying and nutrient leaching (Nilsson and Berggren, 2000; New and Xie, 2008; Catford and Jansson, 2014). The downward trend of R-scores slows down in the 250–350 m range (areas with dense human activities), which reflects the maintenance effect of human disturbances on R-strategy species. This is because agricultural activities (e.g. tillage, fertilization and weeding) create frequent small-scale disturbances (e.g. soil turning and crop rotation), which are conducive to the

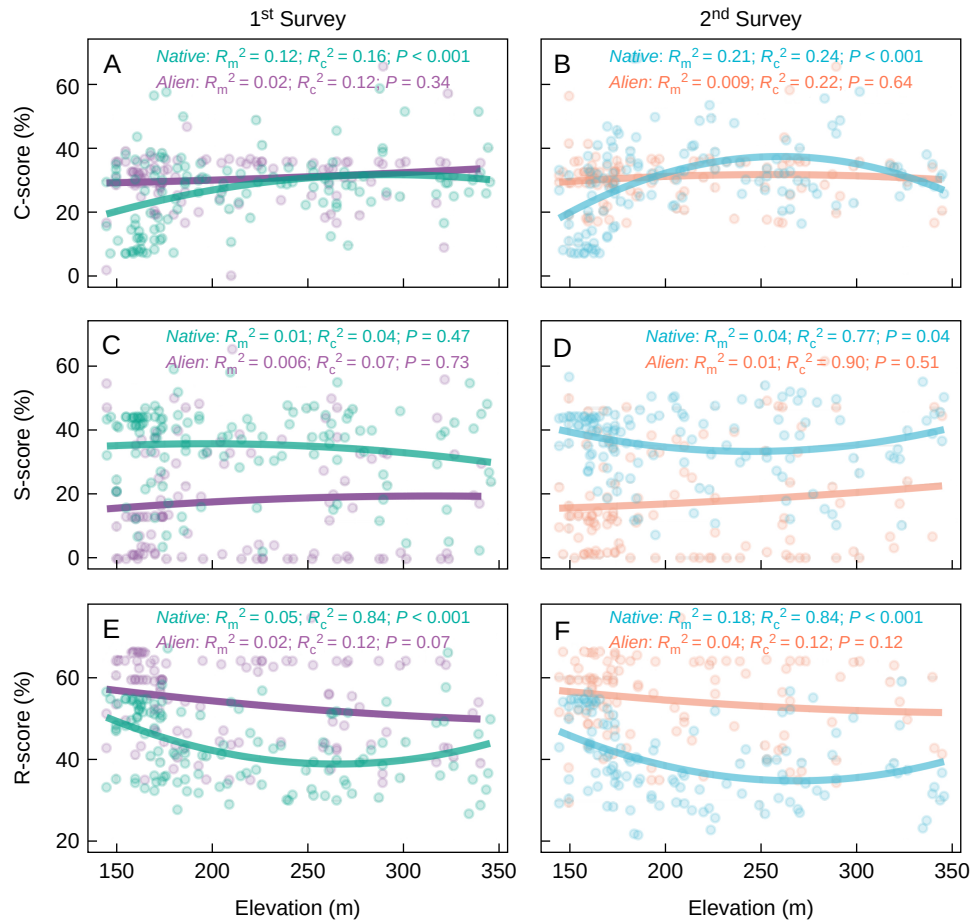


FIG. 4. Generalized linear mixed models were used to test the relationships between elevation and the community-weighted means (CWMs) of CSR scores of alien and native assemblages across surveys. (A, B) C-score; (C, D) S-score; (E, F) R-score. R_m^2 represents marginal R^2 and R_c^2 represents conditional R^2 . Left and right panels display results from the first and second surveys, respectively.

survival of fast-growing and short-life-cycle R-strategists in the fields. Human activities such as roads and buildings increased soil disturbance, forming empty ecological niches that allow R-strategists to continuously occupy these temporary habitats (Grime, 2001; Le *et al.*, 2024a).

Our work provides targeted implications for conserving and managing plant communities in disturbed riparian ecosystems, in response to the CSR strategy shifts observed in response to dam-induced environmental changes. In low-elevation riparian zones, where post-dam flooding intensifies and native communities show enhanced dominance of S-strategy species, conservation should focus on protecting these stress-tolerant assemblages and on avoiding additional disturbances that could reduce their resilience. Concurrently, restoring soil conditions in these lowlands (e.g. improving drainage or organic matter content) directly might support the persistence of S-strategists (Zhang *et al.*, 2024). In upland areas, where native C-strategists remain prevalent, management should minimize resource competition, particularly by controlling overgrowth of aggressive alien C-strategists.

For alien species, management must account for their CSR patterns across time and elevation, which is probably sustained by a balance between R-strategy and C-strategy. R-strategy aliens thriving in frequently disturbed microhabitats require timed

physical removal during dormant periods (e.g. post-flooding) to limit dispersal, while C-strategy aliens in less disturbed upland demand early warning systems to detect shifts in abundance. Managers could implement targeted shading interventions by establishing fast-growing native trees and shrubs to form dense canopy cover, thereby limiting the establishment of alien plants requiring high-light environments (Song *et al.*, 2017).

CONCLUSIONS

Our findings indicate that plant CSR strategies at the community level, under chronic and periodic disturbance regimes, showed temporal shifts that depend on species' status. Our findings demonstrate a temporal divergence and spatial decoupling in ecological strategies between native and alien species assemblages. Native species assemblages shifted from R- toward CS-strategy over time, while alien species assemblages persistently maintained an R-strategy. Along the elevational gradient, native assemblages exhibited clear CSR shifts, whereas alien assemblages showed no elevation-dependent strategy variation. This contrast underscores how the native and alien species assemblages distinctively in response to dynamic disturbance regimes.

SUPPLEMENTARY DATA

Supplementary data are available at *Annals of Botany* online.

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AUTHOR CONTRIBUTIONS

Z.X., W.X., M.V. and H.L. conceived the ideas and designed the research. C.Z., G.X. and H.L. collected the data. H.L. performed the analyses. H.L. wrote the first draft of the manuscript with major contributions from M.V. and Z.X. All authors contributed substantially to draft revisions.

CONFLICT OF INTEREST

The authors declare they have no conflict of interest.

DATA AVAILABILITY

The data that support the findings of this study are available in Figshare at: <https://doi.org/10.6084/m9.figshare.28735751.v1>.

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