



Intraspecific variations of adaptive strategies of native and invasive plant species along an elevational gradient

Hasigerili^{a,b}, Kun Guo^{a,b}, Miao-Miao Zheng^{a,b}, Rui-Ling Liu^{a,b}, Yan-Yan Wang^{a,b}, Yuan Gao^{a,b}, Li Shu^{a,b}, Xiao-Ran Wang^{a,b}, Jian Zhang^{a,b}, Wen-Yong Guo^{a,b,*}

^a Research Center for Global Change and Complex Ecosystems, School of Ecological and Environmental Sciences, East China Normal University, Shanghai, 200241, P.R. China

^b Zhejiang Tiantong Forest Ecosystem National Observation and Research Station, School of Ecological and Environmental Sciences, East China Normal University, Shanghai, 200241, P.R. China

ARTICLE INFO

Edited by Xiao-Tao Lü

Keywords:

Elevational gradient
Grime's plant adaptive strategies
Intraspecific trait variation
Mountain area
Plant invasions

ABSTRACT

The dispersal of invasive alien plant species (IAPS) into mountains has posed great threats to local native plant species. It has been assumed that high intraspecific trait variability contributes to the spread of invasive plant species, even along mountains. Although intraspecific variability of single trait was more often investigated, Grime's competitor, stress-tolerator, and ruderal (CSR) plant strategies, representing trade-offs among multiple functional characters, provides both theoretical and methodological frameworks to inspect plant species' adaptation to environments. Thus, considering Grime's CSR plant strategies with its intraspecific variation could improve the understanding of mechanisms of successful invasion by alien plant species. We estimated intraspecific variation of CSR plant strategies of five invasive and three native herb species and environmental characteristics (e.g., soil physiochemical variables) in their habitats along an elevational gradient ranging from 300 m to 1500 m a.s.l. We conducted linear mixed models to assess the variance explained by status (native vs. invasive), species identity and elevation, whereas linear regressions were used to link each of CSR scores of each species to elevation and environmental factors. The C- and R-score decreased, and the S-score increased along the elevational gradient, especially for invasive plant species. Species identity explained more proportion of the variation of CSR plant strategies. In addition, microhabitat variables like canopy cover and the ratio of soil ammonium nitrogen ($\text{NH}_4^+\text{-N}$) and nitrate nitrogen ($\text{NO}_3^-\text{-N}$) concentrations (NH_4/NO_3) rather than elevation better explained the variation of CSR plant strategies of four out of the eight examined species. Our results showed that the species-specific and microhabitat-dependent factors determined the intraspecific variation of CSR plant strategies of the eight species along the elevational gradient. Furthermore, our study stresses the importance of microenvironment, particularly soil characteristics, in shaping intraspecific variation of plant species, which is essential for plant species to survive on large environmental gradient.

1. Introduction

With the increasing globalization and climate change, more plant species are found in places where they would not appear and survive previously (Seebens et al., 2018, 2021), such as mountains or high elevation areas (Alexander et al., 2016; Larson et al., 2021). Formerly assumed relatively intact and away from invasive alien plant species (IAPS) (McDougall et al., 2011), mountain areas have been invaded globally, and many IAPS had reached relatively high elevations

(Pauchard et al., 2009; McDougall et al., 2011; Alexander et al., 2016), increasingly threatening native biodiversity (Gaertner et al., 2009; Hejda et al., 2009; Vilà et al., 2011). Thus, understanding the mechanisms and processes of invasion in mountain areas is of great importance, which can further provide insights into how plant species adapt to changing climate or how far species disperse along with environmental change.

There is increasing evidence that intraspecific trait variation (ITV) has significant effects on plant species properties and ecosystem

* Corresponding author: Research Center for Global Change and Complex Ecosystems & Zhejiang Tiantong Forest Ecosystem National Observation and Research Station, School of Ecological and Environmental Sciences, East China Normal University, Shanghai, 200241, P.R. China.

E-mail address: wgyuo@des.ecnu.edu.cn (W.-Y. Guo).

<https://doi.org/10.1016/j.flora.2023.152297>

Received 5 January 2023; Received in revised form 21 April 2023; Accepted 4 May 2023

Available online 7 May 2023

0367-2530/© 2023 Elsevier GmbH. All rights reserved.

functions and acts as a key predictor explaining the adaptation of species to varying environments and even invasion success (Albert et al., 2010; Violle et al., 2012; Siefert et al., 2015; Midolo et al., 2019). For example, Niu et al. (2020) found that the intraspecific trait variation for mature plant height, leaf dry matter content (LDMC), specific leaf area (SLA), leaf nitrogen (leaf N) and leaf phosphorus (leaf P) concentrations increased with the decline in soil resources, especially soil phosphorus (soil P) in the Tibetan alpine meadows. Kühn et al. (2021) found that the within-population variability of LDMC and SLA decreased with elevation for IAPS but increased for native plant species in Tenerife. Moreover, Westerband et al. (2021) reported that the ITV of IAPS was mostly explained by spatial heterogeneity in moisture, while solar energy explained more ITV of native plant species. Those studies mainly focused on individual functional traits, which may be insufficient to gain a comprehensive view of how plants' overall responses to changing environment. Therefore, trait syndromes, i.e., trade-off among multiple traits (Díaz et al., 2016), has been increasingly used in relevant studies and has shown great potential in exploring the trait-environment relationships (May et al., 2017; Giupponi 2020; Matos et al., 2021; Bricca et al., 2022) and explaining plant invasions (Guo et al., 2018; Tecco et al., 2010; Vedder et al., 2021; Zanzottera et al., 2021).

Comprised of three fundamentally different strategies, Grime' competitor (C), stress-tolerator (S), and ruderal (R) (CSR) plant strategies is one of such trait syndromes and reflects the trade-off of plant species in resource allocation in response to varying environmental conditions (Grime, 1974). Competitor (C-strategy) associates with low intensity of both stress and disturbance, stress-tolerator (S-strategy) relates to high intensity of stress and low intensity of disturbance, and ruderal (R-strategy) involves the low intensity of stress and high intensity of disturbance (Grime and Pierce 2012). The application of CSR plant strategies was largely hindered by its relatively "hard" method (Hodgson 1999; Pierce and Fridley 2021) until a strategy calculator tool (StrateFy) using three easy-measurable leaf traits, i.e., leaf area, SLA, and LDMC, was proposed and validated using a global dataset (Pierce et al., 2017). In the last years, CSR plant strategies are widely applied to explore the response of plant species to different environmental gradients (Pierce et al., 2007; Busch et al., 2019; Matos et al., 2021) and plant invasions (Dalle Fratte et al., 2019; Guo et al., 2022; Guo et al., 2018, 2019). For instance, Zhou et al. (2021) found that in an alpine meadow along a degradation gradient on the Tibetan Plateau, S-selected plant species were dominant in both non-degraded and severely degraded meadows; Bricca et al. (2022) found a dominance of the stress-tolerator (S-strategy) at both warmer and colder climatic conditions in the central Apennines, Italy. In addition, Guo et al. (2018, 2019) used CSR plant strategies to explain plant naturalization worldwide and found that species exhibiting C- or R-selection strategies are more likely to naturalize outside their native ranges.

Similar as the increasing employment of CSR plant strategies in species-level studies, the intraspecific variations of adaptive strategies and how it changes along environmental gradient are attracting more attentions recently (Pierce et al., 2013). For example, either positive or negative correlation of temperature with S- or R-strategy was observed for *Arabidopsis thaliana* (May et al., 2017; Vasseur et al., 2018). Giupponi (2020) showed that stress-tolerant and competitive individuals of *Campanula elatinoidea* are more likely present at the lower elevation. Guo et al. (2023, unpublished) also found the CSR scores of a global collection of *Phragmites australis* showed significant latitudinal clines. They further found that the invasive populations showed a tendency of divergence with its source populations, indicating a post-introduction evolution of *P. australis*. These single-species studies have proven the nonnegligible magnitude of intraspecific CSR plant strategies variation and its unanimous relationship with environments, thus its importance in understanding plant species distribution and community assembly (Grime and Pierce 2012; Pierce et al., 2013). However, how intraspecific CSR plant strategies of multiple co-occurring species, particularly both native species and IAPS, vary along the same environmental gradient,

such as elevation, and how such intraspecific variation is related to microenvironmental factors (e.g., microclimate, fine-scale soil properties) are not well examined (Wang et al., 2018; Zhang and Wang 2021; Yu et al., 2022).

In this study, by estimating CSR scores of five invasive and three native herb species and environmental characteristics (e.g., soil physiochemical variables) in their habitats along an elevational gradient ranging from 300 m to 1500 m a.s.l., we aim to explore 1) how intraspecific variations of adaptive strategies of native species and IAPS change along the elevation, and 2) which factor(s) drive these variations and are they the same for native species and IAPS. Correspondingly, we hypothesized that 1) C-, and R-scores decrease, while S-scores increase for both native and invasive plant species along the elevation, due to the more stressful environments at high than low places; 2) factors affecting intraspecific variations of adaptive strategies differ between native and invasive plant species.

2. Methods

2.1. Study area

This study was conducted at the Mountain Tianmu National Nature Reserve (119°24'11"–119°27'11"E, 30°18'30"–30°21'37"N) that is located in the northwest of Lin'an District, Hangzhou, Zhejiang Province (Fig. S1). The reserve was established in 1986 and included as a member of the UNESCO International Man and the Biosphere Programme in 1996. The total area of the reserve is 42.84 km² with an elevation range of 300–1506 m a.s.l. Locating in the Pacific monsoon climate zone, the mean annual temperature at the foothill (300 m) and the top of the reserve is 14.8 °C (ranging between -13.1 and 38.2 °C) and 8.8 °C (ranging between -20.2 and 29.1 °C), respectively (Jiang and Zhang 1992). The vegetation cover ratio (the ratio of the vertical projection area of vegetation including leaves, stalks, and branches on the ground to the total vegetation area) of the Tianmu Mountain is over 95%, about 2000 vascular plant species belonging to 191 families and 858 genera are found in the reserve, among them, 307 are alien species.

2.2. Sampling design

In July 2022, sampling was carried out along the road from the foothill to the top of Mt. Tianmu with a vertical interval of approximately 100 m as long as IAPS were observed. In each elevation, one to five 1 m × 1 m plots were surveyed based on the space availability and in total 38 plots were surveyed. A mobile GPS (A8, Unistrong, China) with a 2-meter accuracy was used to record each plot's elevation, latitude, and longitude. Slope and canopy cover of the plots, respectively, were collected using a gradiometer and Canopeo (Patrignani and Ochsner 2015). Three sub-samples of topsoil (~10 cm in depth) were randomly collected using a soil drill in each plot, well-mixed and then brought to the laboratory for further measurements of soil physiochemical characteristics. Specifically, soil pH and electrical conductivity were measured using an Ultrameter-II pH meter (Myron L. Instruments, Malvern, UK). Concentrations of soil total carbon (TC) and total nitrogen (TN) were measured using Vario Max CN elemental analyzer (Elementar, Hanau, Germany). Ultraviolet and visible spectrophotometry (UV2700, SHIMADZU, Japan) was used to measure soil total phosphorus (TP) concentrations. SmartChem 2000 Discrete Auto Analyzer (WESTCO, USA) was used to measure soil ammonium nitrogen (NH₄⁺-N) and nitrate nitrogen (NO₃-N) concentrations, and their ratio was also calculated (NH₄/NO₃). Soil water content (WC) was calculated as the difference between sample weight before and after drying. Mastersizer-2000 laser diffraction-based particle size analyzer (Malvern Company, Worcestershire, England) was used to classify soil samples as sand (0.02–2 mm), silt (0.002–0.02 mm) or clay (<0.002 mm). iButton (iButtons DS1925L#F50, Maxim Integrated Products, Inc., TX) was buried at about 15 cm in depth at the center of each plot to measure soil

temperature for every two-hour during the grown season.

2.3. Functional trait measurement and csr estimation

At each plot, plant species were identified to species level and each species' vegetation cover was recorded. We then selected eight plant species exhibiting wide elevational ranges for further analysis. Based on the Checklist of the Alien Invasive Plants in China (Ma and Li 2018), five out of the eight plant species were classified as IAPS (Table 1). A total of 514 mature individuals were sampled for the eight plant species. Three fully expanded leaves per individual were collected and stored using zip-lock bags with saturated water, and then stored in a cooling box until back to laboratory. Leaves' fresh mass was measured via a digital analytical balance with a precision of 0.0001 g. Afterwards, those leaves were scanned with a scanner (CanoScan liDE 300, Cannon, China) and leaf area (LA) was calculated using R package *LeafArea* (Katabuchi 2019). Finally, leaves were dried at 72 °C for at least 48 h for dry mass determination. The ratio between leaf dry and fresh mass (leaf dry matter content, i.e., LDMC) and ratio between leaf area and leaf dry mass (specific leaf area, i.e., SLA) were then calculated according to Pérez-Harguindeguy et al. (2013). The CSR scores for each individual were calculated using the CSR calculator tool 'StrateFy' provided by Pierce et al. (2017).

2.4. Statistical analysis

All data analyses were performed in R v4.1.2 (R Core Team, 2021). The CSR scores of each plant species were plotted along the elevation in the CSR ternary space using the *ggtern* package (Hamilton and Ferry 2018). ANOVA and Tukey's post hoc test was used to compare the variation of each of the C-, S-, and R-score for the eight plant species, and the P value was adjusted by the Bonferroni Correction. To test which factors, i.e., invasion status (invasive or native), species, intraspecific trait variation within elevation (ITV_{within}) and between elevation (ITV_{between}), explain overall CSR plant strategies variations across all sampled individuals, we performed a linear mixed model to partition the variance in CSR plant strategies with each C-, S- and R-score as the dependent factor and only random effects ['elevation' nested in 'species' nested in 'status']. The remaining variance was explained by CSR differences between conspecific plants growing in different replicate plots at the same elevation (Weemstra et al., 2021). To avoid high collinearity among environmental variables, Pearson correlation analysis was performed and a threshold of $|r| < 0.7$ was used to select environment variables for further analyses. With such step, nine variables, i.e., electrical conductivity, NH4/NO3, pH, silt, TN, soil temperature, slope, vegetation cover, and canopy cover, were retained. For C-, S-, and R-score of each species, we conducted simple linear regressions relating them to elevation and the nine environmental variables. To include the non-linear relationships, we also conducted linear regressions with quadratic terms of the explanatory variables, and the best models were identified as the one with lower Akaike information criterions (AIC). When the difference of AIC between linear and quadratic models was less than 2 (Burnham and Anderson, 2002), linear models were selected (Table S3). We further used the Random Forest (RF, Breiman 2001)

algorithm to evaluate the relative importance of each environmental variable to C-, S- and R-score of each plant species.

3. Results

3.1. CSR plant strategies of native and invasive plant species

Two out of the three native plant species (*Aster trinervius* and *Boehmeria japonica*) were C-selected (mean of C-scores% were 44.48 and 40.75, respectively), with *Lophatherum gracile* as a S-selected (mean of S-score% was 44.27). In contrast, four out of the five IAPS were R-selected, with *Solidago canadensis*, as a S-selected (mean of S-score% was 37.33; Table S1). Overall, IAPS tended to be R-selected while native plant species tended to be C- or S-selected (Fig. 1). In addition, all plant species showed remarkably intraspecific strategy variations along the elevation, i.e., their coefficient of variation (CV) of C-, S- and R-scores, respectively, ranged from 0.14 to 0.43, from 0.20 to 1.86, and from 0.21 to 0.39 (Table S1).

3.2. Intraspecific CSR variations along elevation

Results of mixed model showed that variation of C-score across all sampled plant individuals was mostly explained by species identity followed by elevation (within and between elevation, correspondingly, explained 19.80% and 17.30%), whereas invasion status explained none of the variation. Similar pattern was also observed for S-score, and explained variation of species identity, between and within elevation were 39.30%, 19.60%, and 39.10%, respectively. As for R-score, most of the variation was explained by ITV_{within} (Figs. 2 and 3).

Many species show relatively large intraspecific CSR variations, and certain species' intraspecific CSR show some relations with elevation (Fig. 3). For example, the C-score of invasive *Bidens frondosa* decreased with elevation while its S-score increased; on the contrary, the individuals of invasive *S. canadensis* generally clustered at the center of the CSR triangle and showed no change with elevation (Figs. 3 and 4). Regressions analysis revealed several response patterns, i.e., no relation, decreasing or increasing linear relation, bell-shaped relation, and U-shaped relation, between CSR scores and elevation (Fig. 4; Table S3). These response patterns were species- and strategy-dependent, i.e., for a single plant species, different patterns were observed for C-, S-, and R-scores. For example, the C-score of invasive plant species *E. annuus* and *E. canadensis* were significantly related to elevation ($P < 0.001$), showing a weak bell-shaped relationship with elevation (Fig. 4; Table S3). Four out of the eight plant species showed a significant relationship between S-score and elevation, with both native *B. japonica* and invasive *E. annuus* showing weak U-shaped, invasive *C. crepidioides* positive, and invasive *B. frondosa* weak bell-shaped associations with increasing elevation (Fig. 4; Table S3). For R-score, invasive *C. crepidioides* decreased, and invasive *E. annuus* showed a weak bell-shaped pattern with increasing elevation (Fig. 4; Table S3).

3.3. Factors driving intraspecific CSR variations

The relationships between each selected environmental variable and

Table 1
Taxonomic information, life form, growth form, status, and elevational range of the eight focused plant species in this study.

Species	Family	Life form	Growth form	Status	Elevational range(m)
<i>Aster trinervius</i>	Compositae	Perennial	Forb	Native	300–1500
<i>Boehmeria japonica</i>	Urticaceae	Perennial	Forb	Native	500–1500
<i>Lophatherum gracile</i>	Poaceae	Perennial	Grass	Native	400–1500
<i>Bidens frondosa</i>	Compositae	Annual	Forb	Invasive	400–1500
<i>Crassocephalum crepidioides</i>	Compositae	Annual	Forb	Invasive	300–1300
<i>Erigeron annuus</i>	Compositae	Annual/Perennial	Forb	Invasive	300–1500
<i>Erigeron canadensis</i>	Compositae	Annual	Forb	Invasive	400–1400
<i>Solidago canadensis</i>	Compositae	Perennial	Forb	Invasive	300–1500

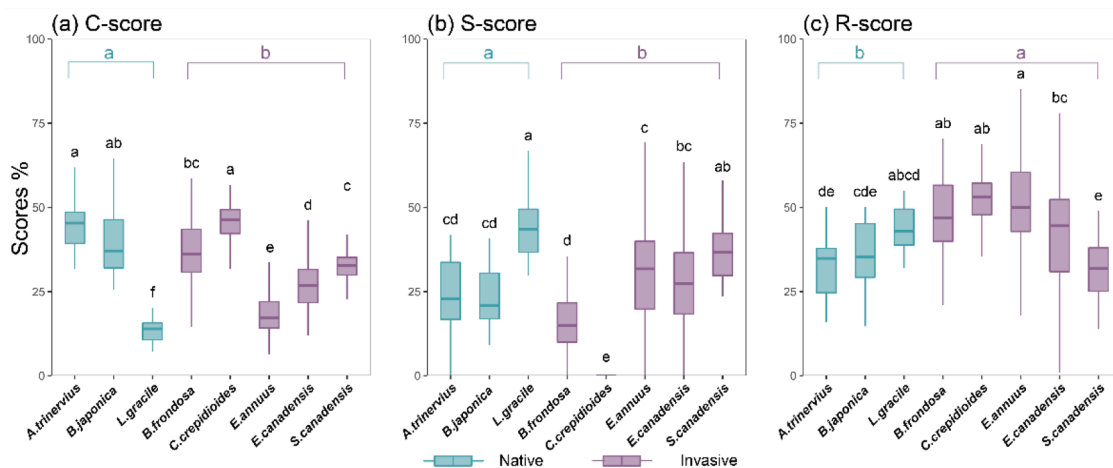


Fig. 1. Statistical tests of the C-, S-, and R-score for the eight plant species. Different letters indicate significant difference at the $P < 0.05$ level as determined by ANOVA and Tukey’s multiple post hoc test (For (a), F-ratio = 102.10, $df = 7$, $P < 0.001$; for (b), F-ratio = 31.22, $df = 7$, $P < 0.001$; for (c), F-ratio = 19.40, $df = 7$, $P < 0.001$).

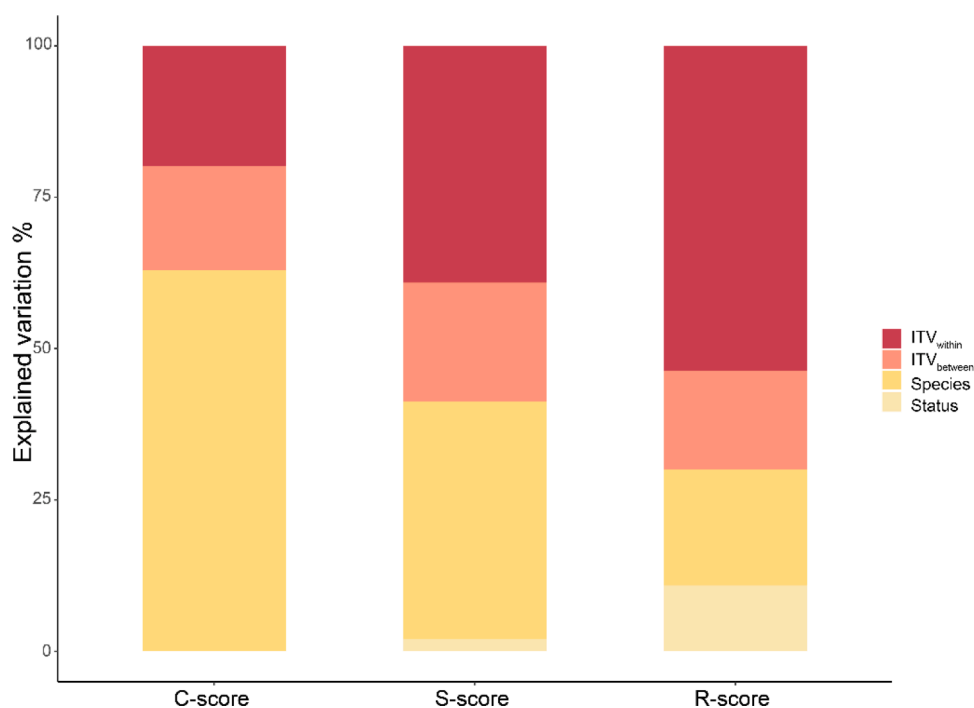


Fig. 2. Percentage of C- (Competitor), S- (Stress-tolerator), and R- (Ruderal) score variations explained by intraspecific trait variation within elevation (ITV_{within}) and between elevation (ITV_{between}), between species, and between invasion status (native and invasive).

species’ intraspecific C-, S-, or R-score differed among score types and species, and showed no consensus within either native or IAPS (Fig. 5; Table S3). Among the tested variables, soil NH₄/NO₃ was the most important contributor to C-score, and negatively related to the native *A. trinervius* and a bell-shaped relationship with invasive *E. canadensis* ($P < 0.05$, Fig. 5a; Table S3; Fig. S4). For the S-score variation, canopy cover was the most significantly negative contributor to native *B. japonica*, besides a U-shaped relationship with invasive *E. annuus* ($P < 0.05$, Fig. 5b; Table S3; Fig. S4). Canopy cover was the dominantly positive contributor to the R-score variations of native *A. trinervius*, invasive *E. canadensis* and *S. canadensis* ($P < 0.05$, Fig. 5c; Table S3; Fig. S4).

4. Discussion

Our study explored how intraspecific variation in ecological adaptive strategies of native and IAPS change along an elevational gradient and identified key regulators of these variations. Surprisingly, our results showed that a relatively large proportion of variations in intraspecific adaptive strategies were explained by species identity, rather than invasion status, which always explained the least variations among the four tested biologically hierarchical levels (i.e., invasion status, species identity, variations within and between elevations). Besides, we found that microenvironment in each plot, e.g., canopy cover, was the key regulator of the variations in adaptive strategies of most plant species, highlighting the importance of microhabitat in driving species’ adaptive strategy variations along the elevation gradient.

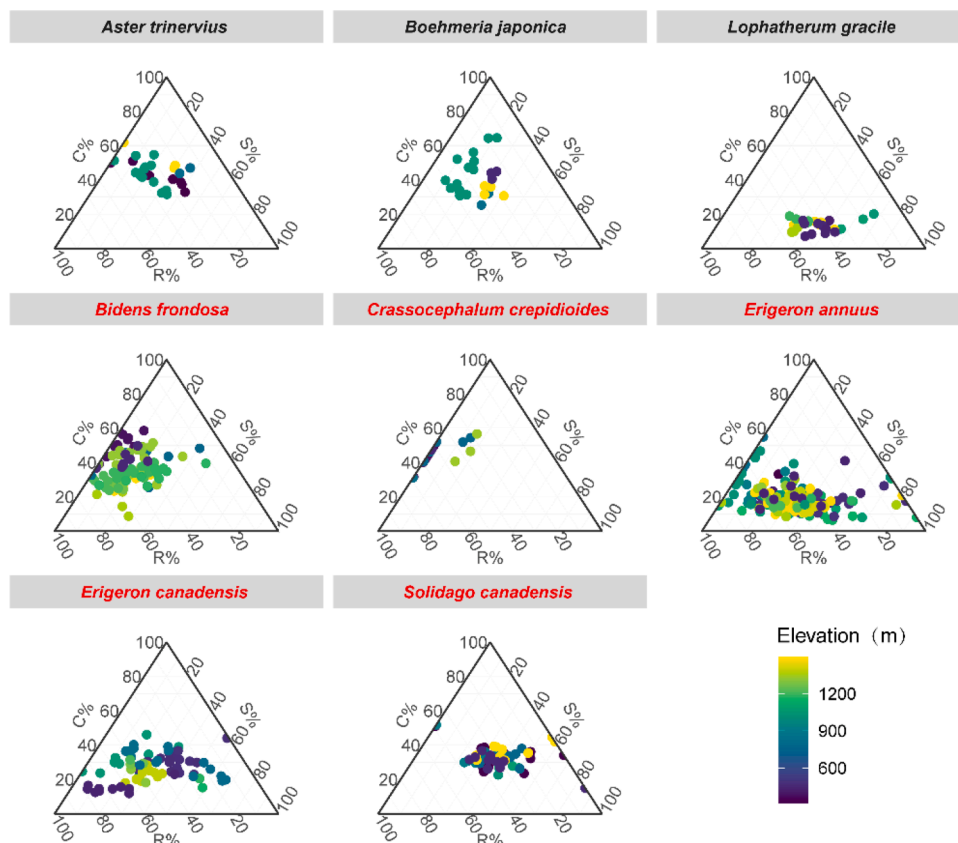


Fig. 3. Ternary space plot showing the CSR-score variation along elevation for the eight plant species. Species name in black and red, respectively, represent native and invasive alien plant species.

The intraspecific trait variation within elevation explained more proportion of the R-score variation, and species identity and intraspecific trait variation within elevation explained the S-score variation equally, indicating that the variation of CSR plant strategies along the elevation gradient is species-specific and plot-dependent (i.e., microhabitat). Similarly, a previous study also found those kinds of context-dependent patterns for certain traits along elevation, such as the intraspecific variation of root traits along elevation was mostly explained by species identity and the variation within elevation (i.e., ITV_{within} ; Weemstra et al., 2021). There is evidence manifested that intraspecific trait variation results from phenotypic plasticity, which plays a key role in plant populations experiencing large environmental variations (Nicotra et al., 2010). Especially for R-selected plant species, most of the ITV were attributed to within elevation variation, suggesting the high phenotypic plasticity and rapid responses of ruderals to environmental changes.

In accordance with the first hypothesis, we found that C- and R-score decreased, while S-score increased with the increasing elevation, particularly for the IAPS, and nor did find for native plant species (Fig. 4). Similar pattern between S-score and elevation was also observed for the invasive *Arabidopsis thaliana* (Vasseur et al., 2018). For mountain plant invaders, most of them were initially introduced to lowland areas of relatively strong disturbance whilst high productivity (Lembrechts et al., 2016; Dainese et al., 2017). In contrast, species experience harsher environment (e.g., low temperatures, shortage of nutrients) with the increasing elevation, thus reallocating more nutrients to defense rather than growth and/or reproduction and becoming more conservative. Thus, our results indicated that C- and R-selected plant species are more likely to occur at lower elevation, while plant species with high S-score are more likely to occur at higher elevation areas (e.g., more stressful), which is consistent with Grime (1974).

Our results showed that variations of CSR plant strategies were

explained by different microenvironmental variables, canopy cover and soil properties were mainly affecting factors, which was consistent with our second hypothesis. We found that R-score increased and S-score decreased with increasing canopy cover, which reflects the light availability as a key factor that could impact species' strategy. A previous study also found that the CSR plant strategies of herb communities were associated with tree layer shade-casting ability (a proxy for light availability in the understory layer), and C strategy increased and S strategy decreased with tree layer shade-casting ability (Kermavnar et al., 2022). Moreover, each plant species responds differently to environmental variables, highlighting the species-specific responses to environmental changes. For instance, NH_4/NO_3 was the key positive regulator affecting the variation of R strategy of invasive *E. annuus*. Soil temperature, which is negatively related to elevation ($R_{adj}^2 = 0.75, P < 0.001$; Table S4 & Fig S3), was the important factor affecting the variation of S strategy of invasive *C. crepidioides*. Probable explanation is that *C. crepidioides* is a temperature-sensitive plant (Chen et al., 2009) and IAPS are generally distributed in warm and resource-rich environments (Huenneke et al., 1990; Pattison et al., 1998). Overall, canopy cover and soil properties (i.e., NH_4/NO_3) were the most important factors affecting the variation of ecological adaptive strategies of these plant species (Fig. 5).

Our result showed that four of the five IAPS are R-selected, which was consistent with previous studies, like Dainese & Bragazza (2012) found that a higher proportion of IAPS with CR-R strategy compared to native plant species, and Guo et al. (2018, 2019, 2022) found that R-selected plant species are more often related to naturalization. With increasing climate change and human activities, IAPS grow in open habitats or along roadsides (Vorstenbosch et al., 2020), where usually have low intensity of stress and high disturbance and be suitable for IAPS, especially for the ruderals (R-strategy) (Grime and Pierce 2012). However, Zanzottera et al. (2021) found that alien woody species were

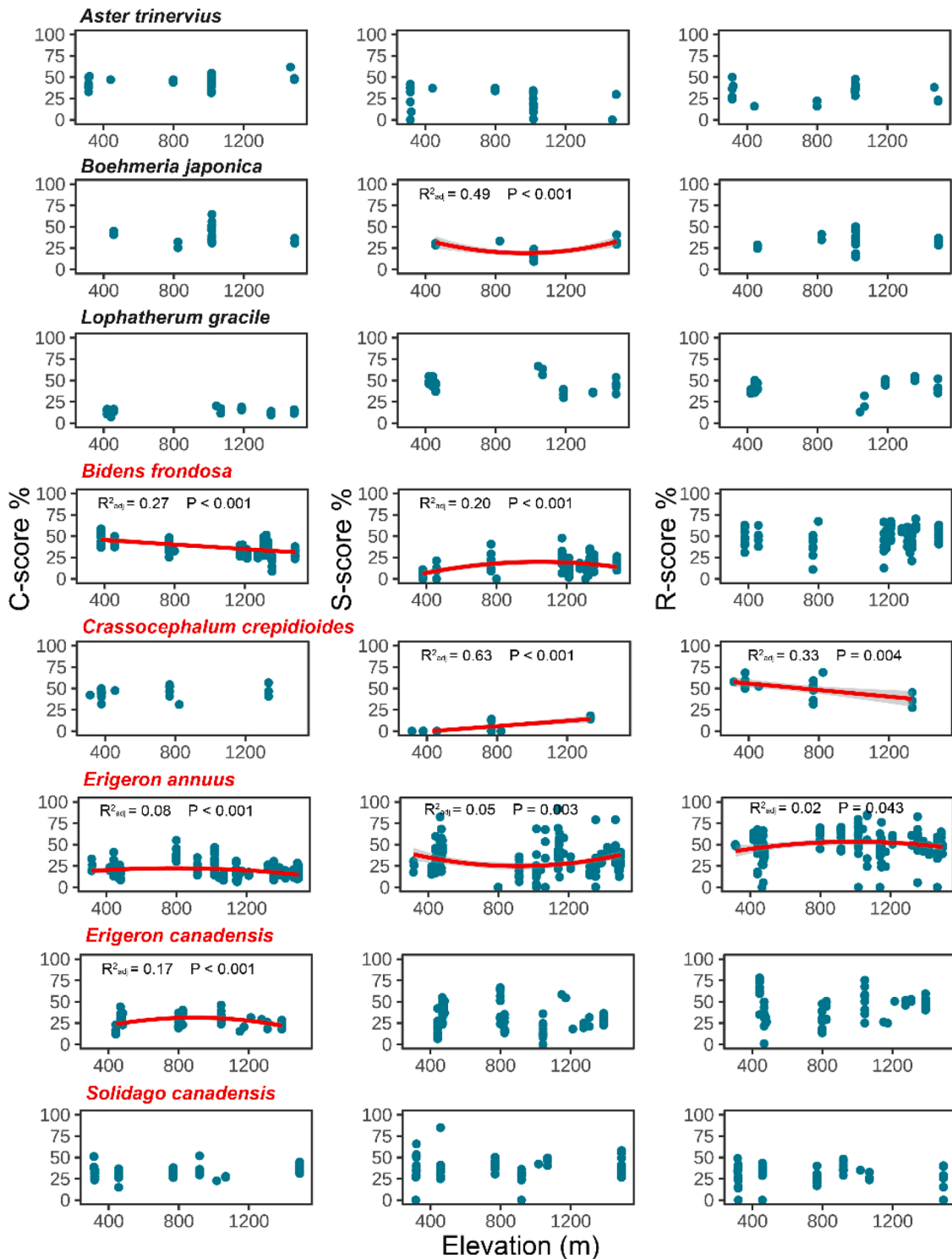


Fig. 4. The relationships between each of CSR scores of the eight plant species and elevation. Significant relationships ($P < 0.05$) are illustrated by a red line. Model statistics are presented in Table S3. Species name in black and red, respectively, represent native and invasive alien plant species.

C-selected species. Given that our study considered only herbaceous species, it is presumable that the strategies adopted by different life forms could be different. Thus, comparative studies with a high number of woody and non-woody IAPS are needed. Besides, we also found that invasive *S. canadensis* was a CSR species, as the three scores were rather similar, indicating its strong flexibility to different environments, thus high invasion potential, which has been evidenced by its wide distribution worldwide (Lu et al., 2007). In addition, each of the CSR score of *S. canadensis* was not related to elevation. Recently, a study found that

the latitudes range of *S. canadensis* in China has a wide ecological niche, spanning from 25° to 50° N (Lu et al., 2007), and would be less influenced by climate change in the future. Although we found no significant relationship between *S. canadensis* and elevation, the soil NH₄/NO₃ was the relatively important factor. This is consistent with other studies which reported that soil properties had a directly positive effect on *S. canadensis* and N addition would make the invaded habitat more suitable for the growth of invasive *S. canadensis* (Dong and He, 2019; Ren et al., 2020). Moreover, *S. canadensis* prefers to grow in acidic,

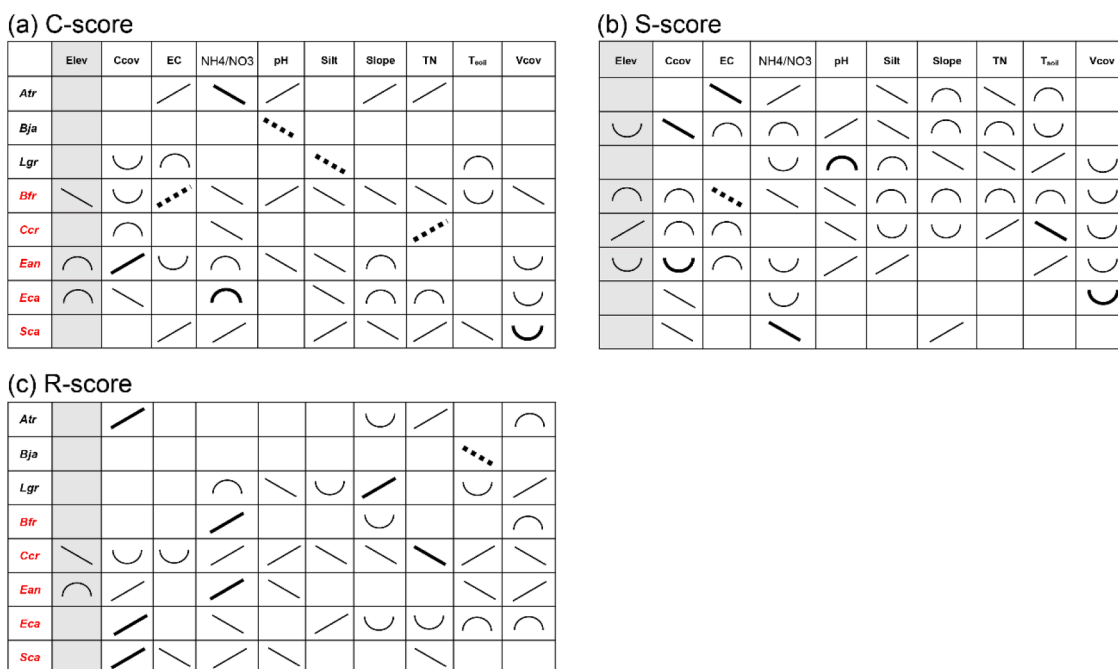


Fig. 5. Relationships between environmental variable and intraspecific C-, S-, and R-scores of the eight plant species. Line represents the best fitted models (linear or quadratic relationships). Thick line indicates variables with high contributions in the Random Forest analysis, while thick dotted line is variables showing relatively high contribution in the RF analysis, but the relationship is not significant ($P > 0.05$) in linear regressions. Species name in black and red, respectively, represent native and invasive alien plant species. Detailed model statistics are presented in Table S4. *Atr*, *Aster trinervius*; *Bja*, *Boehmeria japonica*; *Lgr*, *Lophatherum gracile*; *Bfr*, *Bidens frondosa*; *Ccr*, *Crassocephalum crepidioides*; *Ean*, *Erigeron annuus*; *Eca*, *Erigeron canadensis*; *Sca*, *Solidago canadensis*. Elev, elevation; Ccov, canopy cover; EC, soil electrical conductivity; NH4/NO3, ratio of soil ammonium nitrogen ($\text{NH}_4^+\text{-N}$) concentration and soil nitrate nitrogen ($\text{NO}_3^-\text{-N}$) concentration; pH, soil pH; Silt, soil silt content; Slope, plot slope; TN, soil total nitrogen concentration; T_{soil}, soil temperature; Vcov, plot vegetation cover.

low-salinity sandy loam and loam soils (Guo and Fang 2003) and has relatively high shade- and drought-tolerance (Dong et al., 2006). Therefore, the habitat with a high degree of disturbance and fertile soil is most suitable for the growth of *S. canadensis*, and we need to reduce the increasing interference and prevent the intensification of malignant invasion of *S. canadensis*.

5. Conclusions

It is predicted that mountain ecosystems are facing intensifying invasion pressures under increasing climatic variation and human activities (such as tourism and trade; Bellard et al., 2013; Diagne et al., 2021; Irl et al., 2021). Therefore, understanding which factors determine the success of alien invasive plant species' expansion to high elevation areas is of vital importance to theoretical and practical invasion ecology. In this study, we found that both native species and IAPS showed relatively large, yet species-specific and microhabitat-dependent responses of intraspecific variation in CSR plant strategies to an elevational gradient. Our results highlight the importance of microenvironment, particularly soil characteristics, in shaping plant species' intraspecific variation, which is central to species' survival along large environmental gradient.

CRedit authorship contribution statement

: Conceptualization, Data curation, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Kun Guo**: Data curation, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Miao-Miao Zheng**: Data curation, Writing – review & editing. **Rui-Ling Liu**: Data curation, Writing – review & editing. **Yan-Yan Wang**: Data curation, Writing – review & editing. **Yuan Gao**: Data curation, Writing – review & editing. **Li Shu**: Data curation, Writing – review & editing. **Xiao-Ran Wang**: Data curation, Writing – review & editing. **Jian Zhang**: Supervision, Writing – review

& editing. **Wen-Yong Guo**: Conceptualization, Project administration, Funding acquisition, Supervision, Writing – original draft, Writing – review & editing.

Declaration of Competing 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.

Data availability

Data that support the findings of this study will be openly available in Supporting Information.

Sources of funding

The project was supported by Shanghai Pujiang Program (21PJ1402700) and the Natural Science Foundation of China (32171588). This is a part of work based on BEST (Biodiversity along Elevational gradients: Shifts and Transitions) cooperation network.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.flora.2023.152297](https://doi.org/10.1016/j.flora.2023.152297).

References

Albert, C.H., Thuiller, W., Yoccoz, N.G., Douzet, R., Aubert, S., Lavorel, S., 2010. A multi-trait approach reveals the structure and the relative importance of intra- vs. interspecific variability in plant traits. *Funct. Ecol* 24, 1192–1201.

- Alexander, J.M., Lembrechts, J.J., Cavieres, L.A., Daehler, C., Haider, S., Kueffer, C., et al., 2016. Plant invasions into mountains and alpine ecosystems: current status and future challenges. *Alp. Bot* 126, 89–103.
- Bellard, C., Thuiller, W., Leroy, B., Genovesi, P., Bakkenes, M., Courchamp, F., 2013. Will climate change promote future invasions? *Glob. Chang. Biol* 19, 3740–3748.
- Breiman, L., 2001. Random forests. *Mach. Learn* 542–545.
- Bricca, A., Musciano, M.di, Ferrara, A., Theurillat, J.-P., Cutini, M., 2022. Community assembly along climatic gradient: contrasting pattern between- and within- species. *Perspect. Plant. Ecol. Evol. Syst* 56, 125675.
- Burnham, K.P., & Anderson, D.R. (2002). *Model selection and multimodel inference*.
 Busch, V., Klaus, V.H., Schäfer, D., Prati, D., Boch, S., Müller, J., et al., 2019. Will I stay or will I go? Plant species-specific response and tolerance to high land-use intensity in temperate grassland ecosystems. *Journal. of. Vegetation. Science* 30, 674–686.
- Chen, G.Q., Guo, S.L., Huang, Q.S., 2009. Invasiveness evaluation of fireweed (*crassocephalum crepidioides*) based on its seed germination features. *Weed. Biol. Manag* 9, 123–128.
- Dainese, M., Aikio, S., Hulme, P.E., Bertolli, A., Prosser, F., Marini, L., 2017. Human disturbance and upward expansion of plants in a warming climate. *Nat. Clim. Chang* 7, 577–580.
- Dainese, M., Bragazza, L., 2012. Plant traits across different habitats of the Italian Alps: a comparative analysis between native and alien species. *Alp. Bot* 122, 11–21.
- Dalle Fratte, M., Bolpagni, R., Brusa, G., Caccianiga, M., Pierce, S., Zanzottera, M., Cerabolini, B.E.L., 2019. Alien plant species invade by occupying similar functional spaces to native species. *Flora: morphology, Distribution. Functional. Ecology. of. Plants* 257.
- Diagne, C., Leroy, B., Vaissière, A.C., Gozlan, R.E., Roiz, D., Jarić, I., et al., 2021. High and rising economic costs of biological invasions worldwide. *Nature* 592, 571–576.
- Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., et al., 2016. The global spectrum of plant form and function. *Nature* 529, 167–171.
- Dong, L.J., He, W.M., 2019. The relative contributions of climate, soil, diversity and interactions to leaf trait variation and spectrum of invasive *Solidago canadensis*. *BMC. Ecol* 19, 1–9.
- Dong, M., Lu, J.Z., Zhang, W.J., Chen, J.K., Li, B., 2006. Canada goldenrod (*Solidago canadensis*): an invasive alien weed rapidly spreading in China. *Acta. Phytotaxonomica. Sinica* 44, 72–85.
- Gaertner, M., Breyen, A.den, Hui, C., Richardson, D.M., 2009. Impacts of alien plant invasions on species richness in mediterranean-type ecosystems: a meta-analysis. *Prog. Phys. Geogr* 33, 319–338.
- Giupponi, L., 2020. Intraspecific variation in functional strategy and leaf shape of *Campanula elatinoidea* reveals adaptation to climate. *Flora* 268, 151605.
- Grime, J.P., 1974. Vegetation classification by reference to strategies. *Nature* 250, 26–31.
- Grime, J.P., Pierce, S., 2012. *The Evolutionary Strategies That Shape Eco-Systems*. John Wiley & Sons, Ltd. <https://doi.org/10.1002/9781118223246>.
- Guo, S.L., Fang, F., 2003. Physiological adaptation of the invasive plant *Solidago canadensis* to environments. *Acta. Phytocool. Sinica* 27, 47–52.
- Guo, K., Pyšek, P., Chytrý, M., Divišek, J., Lososová, Z., van Kleunen, M., et al., 2022. Ruderals naturalize, competitors invade: varying roles of plant adaptive strategies along the invasion continuum. *Funct. Ecol* 36, 2469–2479.
- Guo, W.Y., Čuda, J., Skálová, H., Lambertini, C., Pierce, S., Lučanová, M., Hasigerili, Brix, H., Meyerson, L.A., Pyšek, P., 2023. Genome size and climate shape the intraspecific variation in ecological adaptive strategies of a cosmopolitan grass species. *Under. Review*.
- Guo, W.Y., van Kleunen, M., Pierce, S., Dawson, W., Essl, F., Kreft, H., et al., 2019. Domestic gardens play a dominant role in selecting alien species with adaptive strategies that facilitate naturalization. *Global Ecol. Biogeogr.* 28, 628–639.
- Guo, W.Y., van Kleunen, M., Winter, M., Weigelt, P., Stein, A., Pierce, S., et al., 2018. The role of adaptive strategies in plant naturalization. *Ecol. Lett* 21, 1380–1389.
- Hamilton, N.E., Ferry, M., 2018. Ggtern: ternary diagrams using ggplot2. *J. Stat. Softw* 87.
- Hejda, M., Pyšek, P., Jarošík, V., 2009. Impact of invasive plants on the species richness, diversity and composition of invaded communities. *J. Ecol.* 97, 393–403.
- Hodgson, J.G., 1999. Allocating C-S-R plant functional types: a soft approach to a hard problem. *Oikos* 85, 282–294.
- Huenneke, L.F., Hamburg, S.P., Koide, R., Mooney, H.A., Vitousek, P.M., 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology* 71, 478–491.
- Irl, S.D.H., Schweiger, A.H., Steinbauer, M.J., Ah-Peng, C., Arévalo, J.R., Beierkuhnlein, C., et al., 2021. Human impact, climate and dispersal strategies determine plant invasion on islands. *J. Biogeogr* 48, 1889–1903.
- Jiang, X.Q., Zhang, X.J., 1992. Forest meteorological features of Tianmu Mountain Nature Reserve. *Mt. Tianmu Nature Sanctuary Comprehensive Investigation Report On Natural Resource of Tianmu Mountain Nature Reserve*. Zhejiang Science and Technology, Press, Hangzhou, China, pp. 39–54.
- Katabuchi, M.M., 2019. Package “LeafArea” Type Package Title Rapid Digital Image Analysis of Leaf Area.
- Kermavnavar, J., Kutnar, L., Marinšek, A., 2022. Variation in floristic and trait composition along environmental gradients in the herb layer of temperate forests in the transition zone between Central and SE Europe. *Plant. Ecol* 223, 229–242.
- Kühn, P., Ratier Backes, A., Römermann, C., Bruelheide, H., Haider, S., 2021. Contrasting patterns of intraspecific trait variability in native and non-native plant species along an elevational gradient on Tenerife, Canary Islands. *Ann. Bot* 127, 565–576.
- Larson, C.D., Pollnac, F.W., Schmitz, K., Rew, L.J., 2021. Climate change and micro-topography are facilitating the mountain invasion by a non-native perennial plant species. *NeoBiota* 65, 23–45.
- Lembrechts, J.J., Pauchard, A., Lenoir, J., Nuñez, M.A., Geron, C., Ven, A., et al., 2016. Disturbance is the key to plant invasions in cold environments. *Proc. Natl. Acad. Sci. U. S. A* 113, 14061–14066.
- Lu, J.Z., Weng, E.S., Wu, X.W., Weber, E., Zhao, B., Li, B., 2007. Potential distribution of *Solidago canadensis* in China. *Acta. Phytotaxonomica. Sinica* 45, 670–674.
- Ma, J.S., Li, H.R., 2018. *The Checklist of the Alien Invasive Plants in China*. Higher Education Press, Beijing, China.
- Matos, I.S., Eller, C.B., Oliveras, I., Mantuano, D., Rosado, B.H.P., 2021. Three eco-physiological strategies of response to drought maintain the form and function of a tropical montane grassland. *Journal. of. Ecology* 109, 327–341.
- May, R.L., Warner, S., Wingler, A., 2017. Classification of intra-specific variation in plant functional strategies reveals adaptation to climate. *Ann. Bot* 119, 1343–1352.
- McDougall, K.L., Khuroo, A.A., Loope, L.L., Parks, C.G., Pauchard, A., Reshi, Z.A., et al., 2011. Plant invasions in mountains: global lessons for better management. *Mt. Res. Dev* 31, 380–387.
- Midolo, G., de Frenne, P., Hölzel, N., Wellstein, C., 2019. Global patterns of intraspecific leaf trait responses to elevation. *Glob. Chang. Biol* 25, 2485–2498.
- Nicotra, A.B., Atkin, O.K., Bonser, S.P., Davidson, A.M., Finnegan, E.J., Mathesius, U., et al., 2010. Plant phenotypic plasticity in a changing climate. *Trends. Plant. Sci* 15, 684–692.
- Niu, K., Zhang, S., Lechowicz, M.J., 2020. Harsh environmental regimes increase the functional significance of intraspecific variation in plant communities. *Funct. Ecol* 34, 1666–1677.
- Patrignani, A., Ochsner, T.E., 2015. Canopeo: a powerful new tool for measuring fractional green canopy cover. *Agron. J* 107, 2312–2320.
- Pattison, R.R., Goldstein, G., Ares, A., 1998. Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. *Oecologia* 117, 449–459.
- Pauchard, A., Kueffer, C., Dietz, H., Daehler, C.C., Alexander, J., Edwards, P.J., et al., 2009. Ain't no mountain high enough: plant invasions reaching new elevations. *Front. Ecol. Environ* 7, 479–486.
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., et al., 2013. New handbook for standardised measurement of plant functional traits worldwide. *Aust. J. Bot* 61, 167–234.
- Pierce, S., Luzzaro, A., Caccianiga, M., Ceriani, R.M., Cerabolini, B., 2007. Disturbance is the principal α -scale filter determining niche differentiation, coexistence and biodiversity in an alpine community. *J. Ecol* 95, 698–706.
- Pierce, S., Brusa, G., Vagge, I., Cerabolini, B.E.L., 2013. Allocating CSR plant functional types: the use of leaf economics and size traits to classify woody and herbaceous vascular plants. *Funct. Ecol* 27, 1002–1010.
- Pierce, S., Fridley, J.D., 2021. John Philip Grime, 30 April 1935 — 19 April 2021. In: *Biograph. Memoirs. Fellows Royal. Soc.*, 71, pp. 249–270.
- Pierce, S., Negreiros, D., Cerabolini, B.E.L., Kattge, J., Díaz, S., Kleyer, M., et al., 2017. A global method for calculating plant CSR ecological strategies applied across biomes world-wide. *Funct. Ecol* 31, 444–457.
- R. Core Team (2021). R: a language and environment for statistical computing. R Foundation for Statistical Computing.**
- Ren, G.Q., Yang, H.Y., Li, J., Prabakaran, K., Dai, Z.C., Wang, X.P., et al., 2020. The effect of nitrogen and temperature changes on *Solidago canadensis* phenotypic plasticity and fitness. *Plant. Species. Biol* 35, 283–299.
- Seebens, H., Blackburn, T.M., Dyer, E.E., Genovesi, P., Hulme, P.E., Jeschke, J.M., et al., 2018. Global rise in emerging alien species results from increased accessibility of new source pools. *Proc. Natl. Acad. Sci. U. S. A* 115, E2264–E2273.
- Seebens, H., Blackburn, T.M., Hulme, P.E., van Kleunen, M., Liebhold, A.M., Orlova-Bienkowskaja, M., et al., 2021. Around the world in 500 years: inter-regional spread of alien species over recent centuries. *Global. Ecology. and. Biogeography* 30, 1621–1632.
- Siefert, A., Violle, C., Chalmandrier, L., Albert, C.H., Taudiere, A., Fajardo, A., et al., 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecol. Lett* 18, 1406–1419.
- Tecco, P.A., Díaz, S., Cabido, M., Urcelay, C., 2010. Functional traits of alien plants across contrasting climatic and land-use regimes: do aliens join the locals or try harder than them? *J. Ecol.* 98, 17–27.
- Vasseur, F., Sartori, K., Baron, E., Fort, F., Kazakou, E., Segrestin, J., et al., 2018. Climate as a driver of adaptive variations in ecological strategies in *Arabidopsis thaliana*. *Ann. Bot* 122, 935–945.
- Vedder, D., Leidinger, L., Sarmento Cabral, J., 2021. Propagule pressure and an invasion syndrome determine invasion success in a plant community model. *Ecol. Evol* 11, 17106–17116.
- Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., et al., 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol. Lett* 4, 702–708.
- Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., et al., 2012. The return of the variance: intraspecific variability in community ecology. *Trends. Ecol. Evol* 27, 244–252.
- Vorstenbosch, T., Essl, F., Lenzner, B., 2020. An uphill battle? The elevational distribution of alien plant species along rivers and roads in the Austrian Alps. *NeoBiota* 63, 1–24.
- Wang, J., Zhang, C., Yang, H., Mou, C., Mo, L., Luo, P., 2018. Plant community ecological strategy assembly response to yak grazing in an alpine meadow on the eastern Tibetan Plateau. *Land. Degrad. Dev* 29, 2920–2931.
- Weemstra, M., Freschet, G.T., Stokes, A., Roumet, C., 2021. Patterns in intraspecific variation in root traits are species-specific along an elevation gradient. *Funct. Ecol* 35, 342–356.

- Westerband, A.C., Knight, T.M., Barton, K.E., 2021. Intraspecific trait variation and reversals of trait strategies across key climate gradients in native Hawaiian plants and non-native invaders. *Ann. Bot.* 127, 553–564.
- Yu, J., Hou, G., Zhou, T., Shi, P., Zong, N., Sun, J., 2022. Variation of plant CSR strategies across a precipitation gradient in the alpine grasslands on the northern Tibet Plateau. *Sci. Total Environ.* 838, 156512.
- Zanzottera, M., Dalle Fratte, M., Caccianiga, M., Pierce, S., Cerabolini, B., 2021. Towards a functional phytosociology: the functional ecology of woody diagnostic species and their vegetation classes in Northern Italy. *IForest* 14, 522–530.
- Zhang, X., Wang, S., 2021. Joint control of plant ecological strategy by climate, regeneration mode, and ontogeny in Northeastern Chinese forests. *Ecol. Evol.* 11, 6703–6715.
- Zhou, T., Hou, G., Sun, J., Zong, N., Shi, P., 2021. Degradation shifts plant communities from S- to R-strategy in an alpine meadow, Tibetan Plateau. *Sci. Total Environ.* 800, 149572.