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RESEARCH ARTICLE

Native Plant Species Are More Resistant Than Invasive Aliens to Escalating Environmental Change Factors

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ABSTRACT

The interplay between invasive alien plant species and various environmental change factors can lead to unpredictable ecosystem impacts. Existing research predominantly examines isolated or specific environmental factors, leaving the effects of complex, multifaceted environmental changes on the growth of both invasive alien and native plant species inadequately explored. Here, we investigated the biomass responses of ten confamilial pairs of invasive and native species to six individual and combined environmental change factors. Our results revealed a significant reduction in biomass for both invasive and native species as the number of environmental change factors increased, with invasive species demonstrating heightened sensitivity. Notably, drought and salinity exhibited particularly severe negative effects across different environmental combinations, highlighting their critical role in driving these effects. Our findings underscore the importance of understanding and predicting how intensified environmental changes impact plant invasions and overall ecosystem stability.

1 | Introduction

The proliferation of invasive alien plant species poses a significant threat to global biodiversity and incurs substantial economic costs, garnering widespread international concern (Dawson et al. 2012; Seebens, Bacher, et al. 2021; Seebens, Blackburn, et al. 2021; Soto et al. 2024; van Kleunen et al. 2015; Vellend et al. 2017). This issue has been intensifying worldwide, with anticipated further increases in the rates of introduction (Essl et al. 2019; Liu et al. 2024; Seebens, Bacher, et al. 2021; Seebens, Blackburn, et al. 2021; van Kleunen et al. 2015). Therefore, understanding the mechanisms of invasive species invasion is crucial for controlling their spread.

Moreover, the ongoing amplification of environmental changes is expected to further augment the proliferation and impacts of these invasive species (IPBES 2023). Several types of typical environmental change factors can influence plant growth and reproduction. These encompass not only extreme and variable weather events driven by climate change (such as heat wave, salinity, and droughts), but also the global increase in temperature with varying intensities depending on the climatic region, and changes in precipitation patterns (Bai et al. 2023; Parmesan and Yohe 2003). Additionally, sea-level rise, which can lead to increased salinity in coastal areas, should be considered as an indirect effect of global change, further impacting plant growth and reproduction (Rillig et al. 2019; Zandalinas, Fritschi, et al. 2021, Zandalinas, Sengupta, et al. 2021). Various anthropogenic factors (including herbicides, microplastics, and eutrophication) also play significant roles in these changes (Zandalinas, Fritschi, et al. 2021, Zandalinas, Sengupta, et al. 2021). Due to disparities in evolutionary history

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and adaptive abilities, native and invasive species may exhibit distinct responses to environmental change factors (Bajwa et al. 2016; Smith et al. 2012; Tecco et al. 2010; Turner et al. 2015; Zhao et al. 2023). The hypothesis that invasive species often benefit more from global environmental changes than native species, first proposed by Dukes and Mooney (1999) and Davidson et al. (2011), has been extensively tested through experiments and meta-analysis (Liu et al. 2017; Parepa et al. 2013; Song et al. 2019). Song et al. (2010) found that extreme high temperatures had less inhibitory effects on the relative growth rate and biomass production of the invasive *Wedelia trilobata* compared to the native *W. chinensis* (Table 1). Previous studies revealed that invasive species with greater salt tolerance may gain a competitive edge over native species and thus have higher invasion potential in high-salt environments (Bollen et al. 2016; Guo et al. 2023; Liu et al. 2019). Similarly, microplastics had a greater impact on native plants than on invasive ones, suggesting that invasive species may exhibit stronger resistance to microplastic pollution, potentially enhancing their invasion success (Deng et al. 2022; Li et al. 2024; Zhang et al. 2024). However, the response differences of invasive and native species to environmental change factors might depend on life history. Under drought conditions, invasive annual species responded more negatively compared to native species (Copeland et al. 2016; LaForgia et al. 2018; Valliere et al. 2019). Similarly, native perennial species frequently outcompete invasive species in growth under nutrient-rich conditions (Xiao et al. 2019). Herbicide reduced the abundance of the alien biennial herb *Alliaria petiolata* without negatively affecting native species (Carlson and Gorchov 2004). Therefore, the growth advantage of plant species under various environmental change factors may hinge not only on their origin but also on diverse life history strategies (Aoyama et al. 2023; Chiuffo et al. 2022; Valliere 2019).

Over 98% of current scholarly research has focused on examining interactions between single or dual components of environmental change (Rillig et al. 2019). Yet, there is growing recognition of the complex interactions among multiple factors (Rillig et al. 2023; Zandalinas, Fritschi, et al. 2021, Zandalinas, Sengupta, et al. 2021; Zhang et al. 2022), and the accumulation of multiple stressors markedly diminishes plant and soil biodiversity and ecosystem functionality (Cheng et al. 2024; Rillig et al. 2023; Speißer et al. 2022), potentially interacting in synergistic, additive, or antagonistic ways (Rillig et al. 2019; Zandalinas, Fritschi, et al. 2021, Zandalinas, Sengupta, et al. 2021). Additive effects are observed when the combined influence of multiple factors equals the sum of their individual contributions (Shi et al. 2025). Conversely, synergistic or antagonistic interactions occur when the observed combined effect deviates significantly from this additive expectation (Crain et al. 2008; Yang, Cui, et al. 2022; Yang, Ryo, et al. 2022). For example, recent research has unveiled that when microplastics and drought interact concurrently, drought-induced reductions in aboveground and belowground biomass are mitigated by microfibers at the community level (Lozano and Rillig 2020). The combined treatment of high temperature and salinity significantly mitigated the adverse effects of salinity on tomato plants (Rivero et al. 2014). Furthermore, polyester fiber-microplastics, UV-B radiation, drought, and their synergistic interactions have been shown to profoundly influence the functional traits of plant communities (Deng et al. 2022). Despite recent studies emphasizing the negative impacts of multiple environmental change factors on plant species, communities, or ecosystems (Rillig et al. 2021; Song et al. 2019; Yang, Cui, et al. 2022; Yang, Ryo, et al. 2022; Yang et al. 2021; Zandalinas, Fritschi, et al. 2021; Zandalinas, Sengupta, et al. 2021), most research has investigated no more than three factors concurrently (but see (Rillig et al. 2019)). Furthermore, there remains limited understanding of how species of different origins respond to these factors and which specific environmental change factors have the most pronounced effects.

Here, we selected ten congeneric pairs of invasive species and native species with divergent life history traits (Table S1) to investigate the effects of six typical environmental change

TABLE 1 | Summary of the effects of the six examined environmental change factors on different plant species origins. Downward arrows represent negative impacts, upward arrows denote positive impacts, and horizontal lines indicate no impact. Two arrows signify a greater impact than that of one arrow.

Environmental change factors	Summary	Impact	
		Invasive	**Native**
Drought	Drought had a greater negative impact on the growth and reproductive traits of invasive compared to native species (Valliere et al. 2019).	⇊	↓
Salinity	Invasive species were more tolerant to soil salinity than native species (Liu et al. 2019).	⇊	↓
Eutrophication	Under eutrophication, native species outcompeted invasive species in growth (Xiao et al. 2019).	↑	⇈
Heat wave	Heat wave had less inhibitory effects on the relative growth rate and biomass of invasive compared to native species (Song et al. 2010).	↓	⇊
Microplastic	Microplastic exerted a more pronounced impact on native than invasive species (Li et al. 2024).	↓	⇊
Herbicide	Herbicide reduced invasive species abundance without affecting native species (Carlson and Gorchov 2004).	↓	—

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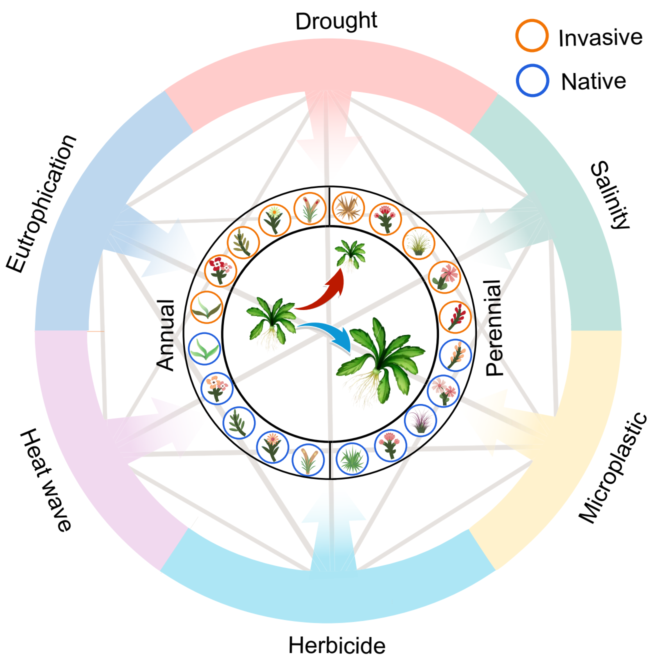

FIGURE 1 | Schematic diagram of the experimental design. Different colors in the outer circle denote the six environmental change factors, with arrows indicating their impacts on the examined plant species. The lines crossed in the bottom gray show the different combinations of factors (one, two, four, and six). For the inner circle, colors around the plant symbols signify species origins: Orange for invasive, blue for native, and annuals and perennials are divided by solid lines. The plant pointed with the red arrow in the innermost circle denote potential negative effects from various environmental change factors, whereas that pointed with the blue arrow denote potential positive effect. Icons representing different plants were adapted from free vectors of Freepik and Vecteezy (www.freepik.com, www.vecteezy.com).

factors: heat wave, drought, eutrophication, herbicide pollution, microplastic pollution, and salinity. These factors were tested individually and in combinations of two, four, and all six, resulting in a total of 38 treatment combinations and 1460 experimental pots (Figure 1). We primarily addressed three key questions: (1) Do invasive and native species differ in their susceptibility to the adverse effects of increasing environmental factors? (2) Does the response between invasive/native species will differ depending on the life history (annual or perennial)? and (3) Do variations in key factors drive the emergence of interactions (synergistic or antagonistic) between different combinations of global environmental change factors, such as drought and/or salinity?

2 | Materials and Methods

2.1 | Species Selection and Cultivation

We chose 10 pairs of phylogenetically related plant species, with each pair consisting of an invasive species and a native species to China. Within the ten pairs of species, five pairs are annual and the other five are perennial (Table S1). Species in each pair are widespread in the wild and coexist in natural habitats of China (Table S1). To increase generalizability, pairs of species were selected from six families (i.e., Asteraceae, Poaceae, Amaranthaceae, Brassicaceae, Portulacaceae, and Onagraceae). Species information regarding origin, native range, and life history was obtained from the Invasive Alien Species of China (IASC) (www.iplant.cn/ias) and Flora of China (www.efloras.org) databases. Classification of species as invasive or native to China followed criteria established by Ma and Li (2018).

The seeds of the test species used in this experiment were acquired from Shanghai Chenshan Botanical Garden. Clonal fragments were collected from Hubei, Zhejiang, and Guangdong Province (Table S1). The collected seeds or clonal fragments were cultivated in greenhouses at Huazhong Agricultural University in Wuhan, Hubei Province, P.R. China (30°28′48″ N, 114°21′43″ E). To synchronize seedling development, species with varying germination times were sown on different dates. Plant seeds were individually sown or ramets were cultivated in plastic trays filled with potting soil (GB-Pindstrup Substrates; Ryomgaard, Denmark). Seedlings were acclimatized outdoors 2 days before transplantation. After 3 weeks, 80 seedlings or ramets per species (average initial height is 4.38 ± 0.42 cm, mean ± SE, $n = 40$) of similar size were selected for transplantation. Species were chosen based on uniform root size and height from cultivated seedlings.

2.2 | Experimental Set-Up

2.2.1 | Experimental Treatment

We first filled 2 L pots (diameter = 16.4 cm, height = 12.5 cm) with a 3:3:2 (v/v/v) soil mixture of river sand, vermiculite, and yellow-brown soil. The initial soil mixture contained a total N of 0.19 ± 0.04 g kg^{-1} and a total P of 0.20 ± 0.05 g kg^{-1} (mean ± SE, $n = 6$). Seedlings were transplanted into the pots on 2 September 2021, with only one seedling of either alien or native species placed centrally in each pot. In cases where transplanted species did not survive, replacements were introduced within 3 weeks.

On September 23, 2021, 3 weeks after transplanting the seedlings, treatments commenced involving six environmental change factors: heat wave, eutrophication, drought, microplastic pollution, soil salinization, and herbicide accumulation. These six environmental change factors were selected due to their prevalence and urgency, as they are expected to intensify with ongoing climate change and human activities. They are also suitable for experimental manipulation, allowing for controlled assessment of their individual and combined effects on plant performance. A greenhouse experiment was designed to evaluate the effects of these factors, individually and in combination, on plant growth.

2.2.2 | Environmental Change Factors Treatments

To test the effects of environmental change factors on both invasive and native species, we subjected them to specific treatments as follows. Specifically, (1) Drought treatment: imposed by reducing water availability to 30%–40% of the average ambient precipitation during the growing season (Knapp et al. 2017; Wade et al. 2017), mimicking the precipitation patterns observed in the experimental site (i.e., Wuhan) from 2007 to 2016. This treatment involved supplying 30 mL of water to each pot every 4 days, resulting in a

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soil water content of 8.8% (±1.1) (Figure S2). The drought control treatment involved regularly watering 100 mL of water to maintain soil moisture levels around 25%–30% throughout the experiment. (2) Heat wave treatment: we conducted experiments in two distinct greenhouses—one ventilated and one sealed—maintaining the temperature increases of 5°C–10°C above ambient levels and lasting 7–10 days of the experiment (Figure S3), in accordance with the average duration of such events (Jagadish et al. 2021). (3) Eutrophication treatment: we applied 0.21 g of water-soluble fertilizer (20% N, 20% P_2O_5, 20% K_2O, w/w; Peters Professional, Scotts, Geldermalsen, the Netherlands) per pot at an interval of once every 2 weeks, totaling five applications and resulting in a cumulative amount of 1.05 g. This amount equates to a nitrogen application of $10\,g\,N\,m^{-2}$, aligning with the global nitrogen deposition rate of $100\,kg\,N\,ha^{-1}$ (Galloway et al. 2008). In the eutrophication control treatment, each pot received a uniform application of 0.21 g of water-soluble fertilizer to provide essential nutrients. (4) Microplastic pollution treatment: we used small non-degradable polypropylene fibers (PP), representative of common environmental pollutants (Zhou et al. 2018). In soil microplastic treatments, the concentration was set at $2\,g\,kg^{-1}$ per pot, within observed ranges found in natural soils (Khalid et al. 2020; Pignattelli et al. 2020). (5) Salinity treatment: soils are classified as saline when the electrical conductivity of the saturation extract (ECe) reaches 4 dS m^{-1} or higher, roughly equivalent to 40 mM NaCl (Munns and Tester 2008). In our experiment, soil salinization was induced by adding a 68 mM NaCl solution, as determined in preliminary trials. (6) Herbicide treatment: glyphosate, a commonly used herbicide, was applied as a foliar spray 3 weeks after seedling transplantation. The spray concentration was determined based on preliminary tests to be an effective ingredient rate of $10\,mg\,m^{-2}$, which corresponds to 5% of the sublethal concentration (Boutin et al. 2019). For the microplastic pollution, salinity, and herbicide control treatment, all plants were subjected to no microplastics, salt, and herbicides. We had three replicates in each of six single-factor treatments, with the control treatment consisting of fifteen replicates.

2.2.3 | Multiple Combinations of Environmental Change Factors Treatments

To assess the impacts of varying numbers and combinations of environmental change factors on both invasive and native species, we exposed them to combinations of two, four, and six treatments including heat wave, eutrophication, drought, microplastic pollution, soil salinization, and herbicide accumulation. Multiple combinations were used, and we obtained 15 two-factor, 15 four-factor, and 1 six-factor treatments. Therefore, all experimental treatments resulted in a total of 1460 pots. We re-randomized the pots within blocks every 4 weeks. During the experiment, the mean temperature in the control treatment greenhouse was 18.0°C, and the heat wave treatment greenhouse was 18.7°C (measured with TR-74Ui-S, T&D Corporation, Nagano, Japan). The experiment lasted 86 days and ended on November 26, 2021.

2.3 | Measurements

At the end of the experiment, we harvested the aboveground and belowground biomass of each plant in each pot. The biomass was dried at 80°C until reaching a constant weight, after which the dry biomass was measured using a balance with 1/1000 accuracy.

2.4 | Data Analysis

All statistical analyses were conducted in R 4.1.1 (R Core Team 2022). Our two-step analytical approach (i.e., first treating the number of environmental change factors as a continuous variable, followed by analyses of individual factors) was intended to address two complementary research questions: (1) how cumulative environmental change factors impact plant responses, and (2) how specific factors contribute individually to those responses.

To examine whether the growth of invasive and native species with different life histories responded differently to a single environmental change factor and their factorial combinations, we utilized linear mixed-effects models with the *lme* function in the *nlme* package (version 3.1-122) (Pinheiro et al. 2022). In these models, total biomass per individual plant was specified as a response variable. To meet the assumption of normality, this variable was square-root transformed. We included plant species origins (invasive vs. native), life histories (annual vs. perennial), numbers of environmental change factors (zero vs. one, two, four and six), and their interactions were treated as fixed-effect independent variables in all models. To account for the non-independence of individuals of the same plant species and for the phylogenetic relatedness of the species, species, family, and environmental change factor combinations were included as random terms. Loglikelihood ratios were employed to assess significant differences between fixed factors (Zuur et al. 2009). For cases exhibiting significant interaction among fixed-effect variables, we conducted post hoc multiple comparisons of estimated marginal means (emmeans) across various treatment combinations, utilizing the *emmeans* function in the *emmeans* package (version 1.7.4-1) (Lenth et al. 2022). To mitigate potentially inflation of Type I error rates, the Bonferroni correction was applied to all post hoc comparisons, ensuring a conservative threshold for statistical significance.

To analyze the primary drivers among environmental change factors, we classified the various combinations of these factors into distinct groups. Combinations incorporating factor *A* were designated as "with *A*". Those without any treatments served as the "control" group. Lastly, combinations excluding factor *A* from all environmental change factors were labeled "without *A*". We employed linear mixed models of the form (y ~ origins × life histories × groups) to analyze the fixed factors, including plant origins, life histories, different environmental change factor groupings (control vs. with *A* vs. without *A*), and their interactions. We incorporated species, family, and environmental change factor combinations as random terms in the model. Consequently, we constructed a total of six linear mixed models to evaluate the effects of environmental change factors and their interactions on the response variable.

We calculated the effect size to assess specific individual and combined impacts of various environmental change factors on the total biomass of species, using the natural log of the response ratio (Borenstein et al. 2009):

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$$\text{Effect size} = \ln\left(X_t / X_c\right)$$

where (X_t) and (X_c) represent the treatment and control means, respectively. Positive values of effect size indicate that different combinations of global environmental change factors enhance the growth of plant species, whereas negative values indicate the opposite. Values indicate the means with 95% confidence intervals (CIs), and a significant positive effect is where the CI is greater than 0 and a negative effect is where the CI is less than 0.

To evaluate the interactive effects of two different environmental factors on biomass, we employed an analytical framework based on additive, antagonistic, and synergistic effects (Crain et al. 2008). First, we calculated the mean biomass of the control group (M_{ck}). Next, we quantified the effects of six single-factor treatments. For each treatment (M_a), we calculated the single-factor effect (E_a) by comparing the mean biomass of the treatment group to that of the control group:

$$\mathrm{E_a} = \mathrm{M_{ck}} - \mathrm{M_a}$$

For two-factor treatments (M_{ab}), we calculated the actual additive effect (A_{ab}) by comparing the mean biomass of the two-factor combination to the control group:

$$\mathrm{A_{ab}} = \mathrm{Y_{ab}} - \mathrm{E_a}$$

The expected additive effect ($A_{expected}$) was derived by summing the single-factor effects of the two constituent factors:

$$\mathrm{A_{expected}} = \mathrm{E_a} + \mathrm{E_b}$$

The interaction effect (I_{ab}) was then determined as the difference between the actual and expected additive effects:

$$\mathrm{I_{ab}} = \mathrm{A_{ab}} - \mathrm{A_{expected}}$$

Based on the interaction effect (I_{ab}), the two-factor treatments were classified as synergistic if $I_{ab} > 0$, antagonistic if $I_{ab} < 0$, and additive if $I_{ab} = 0$.

3 | Results

3.1 | The More, the Worse: Intensified Negative Effects With the Increasing Number of Environmental Factors

Overall, the total biomass of both invasive and native species significantly decreased with the number of environmental change factors increasing from one to six ($\chi^2 = 105.543$, $p < 0.001$; Figure 2a; Table S2), and the detrimental effects experienced by invasive species were significantly more pronounced than those observed in native species ($\alpha_{IA} = -2.37$, $\alpha_{IP} = -2.25$, $\alpha_{NA} = -0.84$, $\alpha_{NP} = -1.82$). Progressively increasing environmental change factors had significant negative effects on both perennial and annual species ($\chi^2 = 9.457$, $p < 0.05$), with invasive annual species showing the most severe effects. The differentiation between native and invasive annual species was more pronounced when fewer environmental factors were present, whereas this disparity gradually decreased with increasing factor complexity. Notably, the examined species exhibited relatively minor within-group variations, with the exception of the invasive perennial species *Pennisetum purpureum*, which showed little sensitivity to treatment quantity (Figure 2b).

3.2 | The Decisively Detrimental Effects of Salinity and Drought on Plant Growth

The growth of both native and invasive species exhibited similar negative effects depending on the varying strengths of the main environmental change factors. In contrast to perennial species, which displayed no significant differences, annual species exhibited marked variations in their responses. Drought and salinity treatments exhibited comparable patterns in their effects on both native and invasive species, resulting in significant negative impacts (Figure 3a,b; Tables S8 and S9). In contrast, eutrophication significantly ameliorated the biomass reduction initiated by the combined treatment of all other factors, particularly for native annual and invasive perennial species (Figure 3c). For heat wave, microplastic, and herbicide treatments, the presence or absence of each did not significantly alter the total biomass of native and invasive species (Figure 3d–f).

4 | Discussion

Recent studies indicate that plant invasions risk increases with global environmental change, yet existing investigations primarily focus on the effects of limited change factors (Bradley et al. 2010; Liu et al. 2017; Yang, Cui, et al. 2022; Yang, Ryo, et al. 2022). Here, by investigating the combined effects of six major environmental change factors on plant growth from different origins, our results revealed that as the number of environmental change factors increases, the total biomass of both invasive and native species progressively decreases. Specifically, invasive species experience significantly stronger negative effects compared to native congeneric species. Furthermore, we found that different combinations of environmental change factors exert varying degrees of negative effects on plants from different origins, with drought and salinity as the two dominantly detrimental ones.

Our results revealed that a higher number of environmental change factors led to more severe negative impacts on invasive species compared to native species (Figure 2; Tables S2 and S4). This contrasts with previous findings that invasive species might outperform natives under global change factors (Davidson et al. 2011; Liu et al. 2017; van Kleunen et al. 2010). The discrepancy may arise from those studies examining fewer environmental change factors than ours (Speißer et al. 2022). These findings support the hypothesis that abiotic resistance mechanisms suppress invasions in extreme or multifactorial stress environments due to physiological constraints such as resource scarcity (Alpert et al. 2000). The success of native versus invasive species depends on the intensity of environmental stress, aligning with previous observations that environmental pressure influences invasion outcomes (Zefferman et al. 2015). Native species, with their broader niche breadth, evolved through long-term adaptation to local climatic variations, exhibit superior resistance

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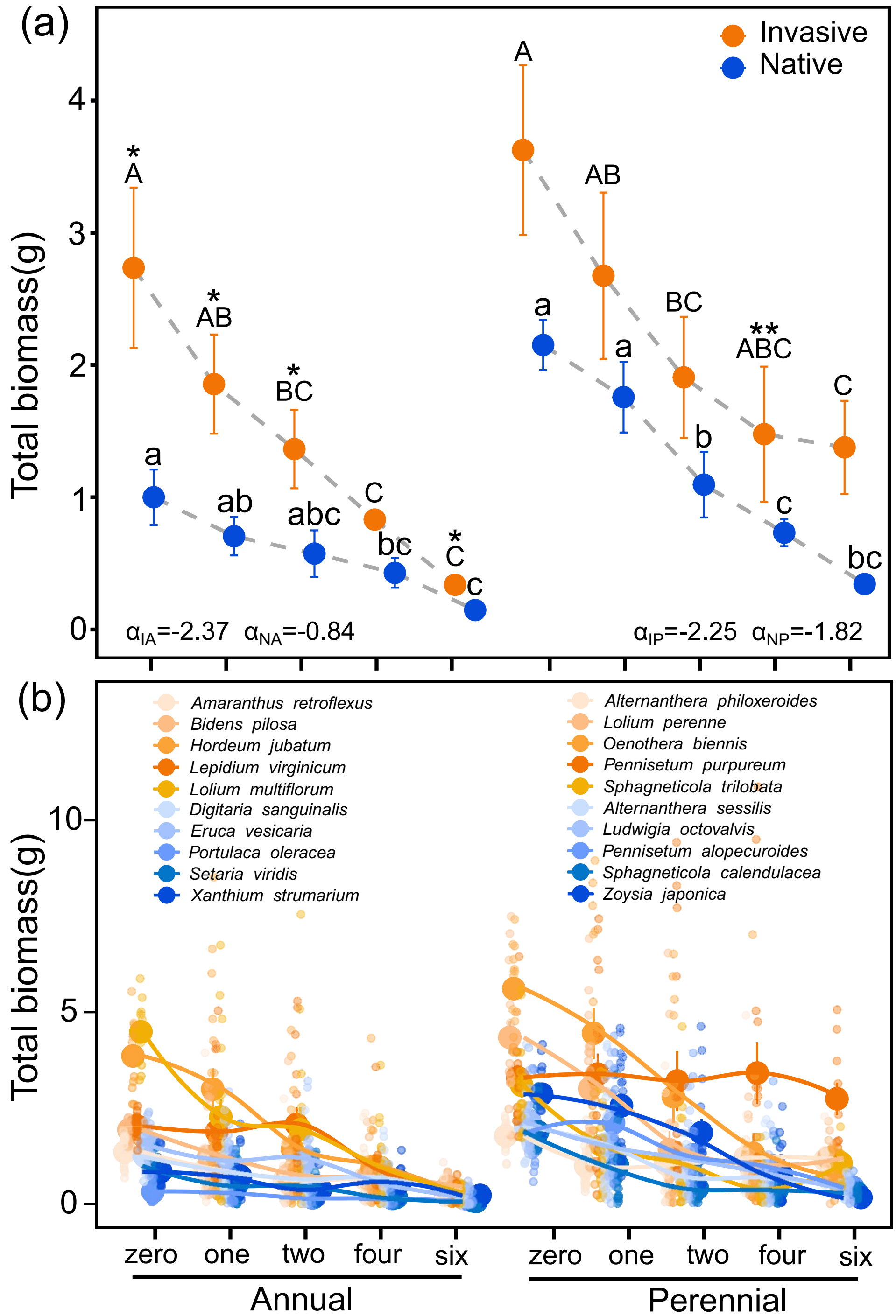

FIGURE 2 | Effects of the number of environmental change factors on plant growth. (a) Total biomass under different species origins (invasive vs. native) and life histories (annual vs. perennial) in response to different numbers of environmental change factor treatments. Means (±SE) are shown. Symbols (*$p<0.05$ and **$p<0.01$) represent significant differences between different species life histories of the native and invasive species under the same numbers of environmental change factor treatments. Capital letters indicate significant differences among different numbers of environmental change factor treatments for invasive annual or perennial species, and lowercase letters represent significant differences of different numbers of environmental change factor treatments for native annual or perennial species (*Tukey* post hoc comparisons, $p<0.05$). The symbols α_{IA}, α_{IP}, α_{NA}, and α_{NP} represent the slopes for invasive annuals, invasive perennials, native annuals, and native perennials, respectively. (b) Total biomass of 10 congeneric pairs of different species origins (invasive vs. native) and life histories (annual vs. perennial) under different number of environmental change factor treatments.

under multifactorial changes. This resistance is facilitated by their ability to tolerate diverse moisture and soil gradients, employ phenotypic plasticity (e.g., stomatal regulation, antioxidant systems), and adopt "stress resistance-first" strategies such as deep root systems, secondary metabolite accumulation, and symbiotic microbial networks (Dawson et al. 2012). In contrast, invasive species typically adopt a "rapid resource acquisition" strategy, focusing on narrow but efficient niches (e.g., high light/

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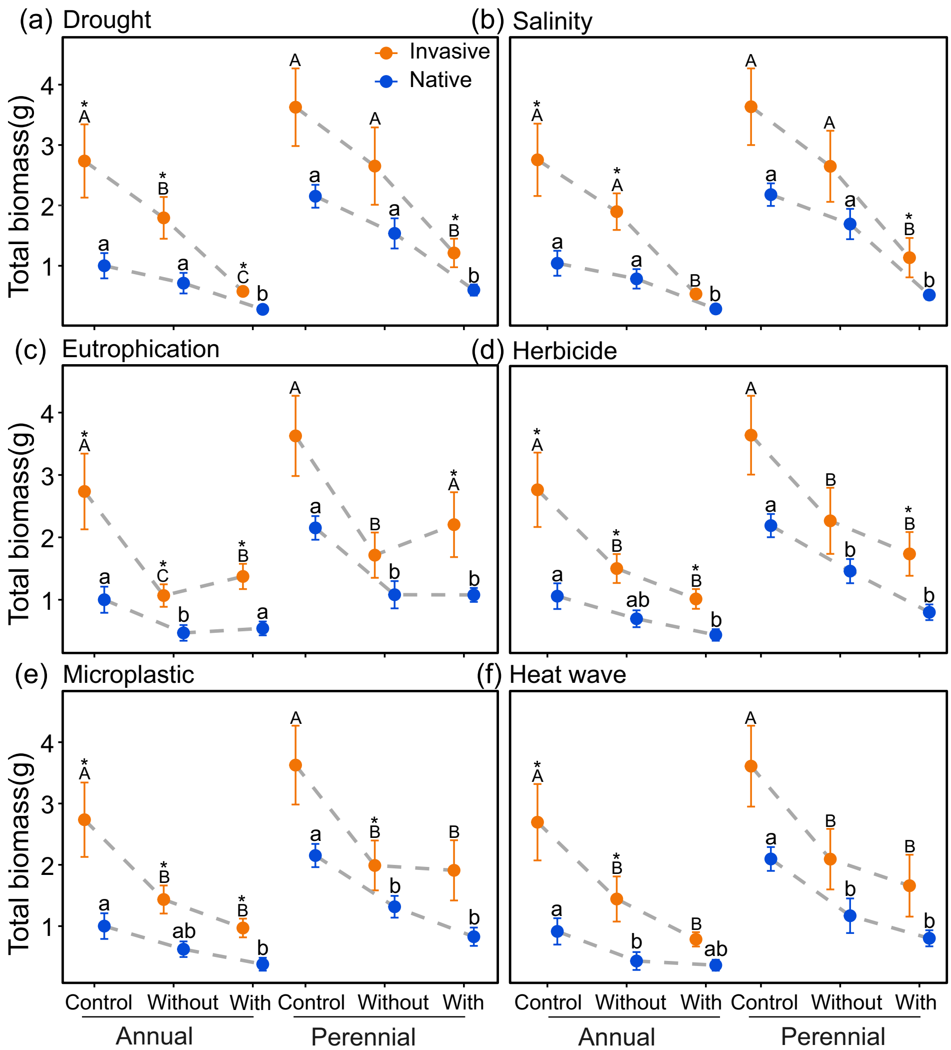

FIGURE 3 | Relative strength of each environmental change factor on plant growth. (a) Drought, (b) Salinity, (c) Eutrophication, (d) Herbicide, (e) Microplastic, and (f) Heat wave. Means (±SE) are shown. Symbols (*$p<0.05$) represent significant differences between different species life histories of the native and invasive species under the same environmental change factor treatments. Capital letters indicate significant differences among different environmental change factor combination treatments for invasive species, and lowercase letters represent significant differences of different environmental change factor combination treatments for native species (*Tukey* post hoc comparisons, $p<0.05$). "With" indicates the presence of a specific environmental factor within the combination. "Without" means that the specific factor is absent, but all others (and their combinations) are present. "Control" refers to a treatment where no environmental change factors are applied.

nutrient use efficiency) at the expense of stress tolerance (Guo et al. 2022). This supports the "opportunity window hypothesis," suggesting that while phenotypic plasticity may provide short-term advantages under fluctuating conditions, the long-term resilience of invasive species remains uncertain (Johnstone 1986).

Furthermore, we found that increasing environmental change factors exhibited the most pronounced negative effects on invasive annual species (Table S5). This is in line with previous research showing that invasive annual species responded more negatively to drought compared to native species (Copeland et al. 2016; LaForgia et al. 2018; Valliere et al. 2019). Conversely, invasive perennial species experienced fewer negative effects (Table S6), suggesting that while annual invasives often have "acquisitive" life strategies, their success may heavily depend on seedling establishment (Funk et al. 2016; Grime 1974). Perennials, with their usually "conservative" strategies, largely depend on stored resources (James et al. 2011; Leffler et al. 2011). Therefore, species with different life history strategies may exhibit varying resource tolerance and acquisition under different environmental conditions (Balachowski and Volaire 2018; Valliere et al. 2022). However, whether this difference between annual and perennial species persists across multiple generations remains to be explored. Research indicated that annual species, with their shorter generation time, higher rates of genetic recombination, and greater population turnover, may adapt more rapidly to changing environments through standing genetic variation or de novo mutations (Friedman 2020). In contrast, long-lived perennials, with their extended generation time and lower population turnover, are likely to exhibit more pronounced adaptive lag (Li, Lathe, et al. 2022; Li, Li, et al. 2022). Interestingly, apart from *P. purpureum*, we did not observe species-specific responses to escalating environmental factors (Figure 2b). The possible reason is that invasive perennial

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species *P. purpureum* may survive harsh conditions by leveraging its deep root system and capacity to absorb moisture at low soil water potentials (Li, Lathe, et al. 2022; Li, Li, et al. 2022; Monção et al. 2020).

Our results support the notion that simultaneous global change factors can lead to novel effects, such as antagonistic or synergistic interactions, on plant growth (Figures S1 and S4), which is consistent with the majority of the literature (Rillig et al. 2019; Yang, Cui, et al. 2022; Yang, Ryo, et al. 2022; Zandalinas and Mittler 2022). Drought, when combined with most other treatments, typically exhibited a synergistic effect, suggesting it may be a primary driver of negative outcomes from such environmental factor combinations (Yang, Cui, et al. 2022, Yang, Ryo, et al. 2022). Salinity and drought treatments showed similar impacts, and their combination led to synergistic negative effects, potentially aiding in resisting plant invasions. Conversely, eutrophication combined with other treatments predominantly resulted in antagonistic effects. The similar trends observed in our study and that of (Shi et al. 2025) imply that global environmental change factors that enhance resource availability may increase the risk of plant invasion. Additionally, environmental factor combinations differentially affect invasive and native species. For example, intensified drought and eutrophication showed synergistic effects on perennial invasives but antagonistic effects on natives, likely due to species-specific ecological differences (Valliere et al. 2017).

Our study confirmed that drought and salinity significantly reduce growth in both native and invasive species (Figure S1). Consistent with our hypothesis, drought is a major driver that adversely affects plant species (Figure 3a). Numerous studies showed that drought exacerbates negative impacts when combined with other environmental factors, reducing plant biomass and limiting nutrient uptake, thereby suppressing growth and photosynthetic efficiency (He and Dijkstra 2014; Lozano and Rillig 2020; Vile et al. 2012; Zandalinas et al. 2018). Similarly, salinity, in conjunction with other environmental factors, significantly reduced plant biomass (Figure 3b). This is consistent with previous research indicating its inhibitory effects on invasive species establishment and growth (Qi et al. 2017). Elevated salt levels can impair nutrient and water absorption, though evidence on salinity's role in facilitating invasive species remains conflicting (Infante-Izquierdo et al. 2019; King et al. 2022; Mao et al. 2016).

Eutrophication mitigated the impact of other environmental treatments on biomass, especially affecting native annuals and invasive perennials (Figure 3c; Tables S8 and S9), probably because nutrient enrichment can enhance water use efficiency under drought conditions (Gessler et al. 2017). Invasive perennials responded more strongly to eutrophication than native species (Table S7), likely due to higher photosynthetic efficiency, growth rates, and phenotypic plasticity in nitrogen-rich environments (Davidson et al. 2011; Liu et al. 2017; van Kleunen et al. 2010). However, invasive perennials did not benefit more than invasive and even native annuals from eutrophication (Figure 3c). This discrepancy may stem from varying life history strategies that affect how species respond to environmental change (Rajnoch et al. 2020; Valliere et al. 2019), and studies indicate that biomass allocation varies with resource availability and life history strategies, leading to species-specific responses to nutrient enrichment (Garnier 1992; Grime 1977; Roumet et al. 2006).

Heat wave, microplastics, and herbicide treatments significantly reduced total biomass across species, but their individual presence or absence did not produce notable differences in biomass (Figure 3d–f), indicating these factors may not be the primary drivers when combined with other environmental change factors. Although herbicides are shown to reduce belowground biomass and delay flowering (Carpenter et al. 2013; Rotchés-Ribalta et al. 2015), our study found no significant biomass difference between herbicide-treated and untreated conditions (Figure 3d; Tables S8 and S9). This may be due to the sub-lethal herbicide concentration utilized, which spanned multiple plant families and minimized biomass variation between treated and untreated conditions, despite an overall biomass reduction. High herbicide doses can severely inhibit growth, while low doses may induce resistance, as seen with glyphosate resistance in 38 weed species (Heap and Duke 2018). Microplastics, which have shown mixed effects on plant growth (de Souza Machado et al. 2018; Fu et al. 2024), had minimal impact in our study (Figure 3e; Tables S8 and S9). Consistent with previous findings, microplastics mitigated drought's negative effects by increasing shoot and root biomass (Lozano and Rillig 2020). This benefit likely resulted from improved soil aeration, water retention, and enhanced root growth (de Souza Machado et al. 2019; Zheng et al. 2016). Although heat wave generally decreases plant survival and growth (Teskey et al. 2015; Wei et al. 2023), it was not the primary factor driving biomass changes in our study (Figure 3f; Tables S8 and S9). This relatively modest effect may be due to differences in heat wave duration and intensity, as longer, more extreme heat exposures tend to cause great harm (Colombo and Timmer 1992). Shorter heat wave, on the other hand, can promote resilience and induce heat tolerance (Jagadish et al. 2021; Ruehr et al. 2016; Shi et al. 2015). Studies have found that heat wave treatment initially enhances arctic plant growth, but later stages are adversely affected, potentially due to decreased cold tolerance of those species (Marchand et al. 2005). Thus, the exact effects of heat wave probably depend on stress intensity, plant developmental stage, and species characteristics (Giri et al. 2017; Vescio et al. 2021).

Our study reveals that increased global environmental change factors significantly reduce the total biomass of both native and invasive species, with invasive species experiencing more pronounced negative effects. Specifically, drought and salinity dominate the interactions (synergistic or antagonistic) among various combinations of global environmental change factors. Our findings emphasize the critical importance of a holistic approach in studying global environmental changes, emphasizing how multiple interacting factors can drive complex and pronounced effects on biodiversity. This complexity calls for integrative research strategies to fully capture the breadth of environmental changes and their consequences for plant survival, ecosystem resilience, and overall biodiversity.

Author Contributions

Yang Zhao: data curation, visualization, writing – original draft. **Yu-Han Xu:** formal analysis, writing – review and editing. **Kun Guo:**

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writing – review and editing. **Wen-Yong Guo:** writing – review and editing. **Yong-Jian Wang:** conceptualization, funding acquisition, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and R code that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.q2bvq83w1.

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