



Effects of warming and nutrient fluctuation on invader *Chromolaena odorata* and natives in artificial communities

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Abstract There is increasing evidence that climate change and nutrient fluctuations can affect the invasion of alien plants. However, most studies have been performed in pairwise experiments between alien and native species, rather than in multispecies community experiments. In southwest China, a series of artificial multispecies communities containing one invasive species, *Chromolaena odorata*, and three co-occurring native species were constructed to test the effects of warming and nutrient fluctuations on the invasion success of *C. odorata*. We found that the invasion success of *C. odorata* was enhanced significantly

under warming but was not influenced by the nutrient fluctuation treatment. However, there was an interactive effect between the warming and nutrient fluctuation treatments on the aboveground biomass of the native plants. Further analysis revealed that the positive effect of warming on plant invasion could be explained by two factors: the enhancement of the invader and suppression of the native plants. Overall, strong warming but weak nutrient fluctuation effects on the invasion success of *C. odorata* were observed in this experiment.

Keywords *Chromolaena odorata* · Invasion success · Invasiveness · Native community · Warming · Nutrient fluctuation

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Introduction

Invasive alien plants, with exponential accumulation rates, pose serious threats to ecosystems and human health (Vila et al. 2011; Schaffner et al. 2020). Therefore, understanding the mechanisms that mediate invasion is crucial for their management and control. Despite the consensus that environmental changes, such as warming, fertilization, and industrial carbon dioxide emissions, could accelerate plant invasion (Blumenthal et al. 2013; Liu et al. 2017),

there is little evidence of this in multispecies communities.

It is widely accepted that invasive plants possess a high plasticity and broad stress tolerance, which might contribute to their survival in variable environments (Richards et al. 2006; Davidson et al. 2011). For instance, Filippou et al. (2014) provided biochemical evidence that the invasive plant *Ailanthus altissima* has a greater tolerance for drought and salinity than native plants. Moreover, previous studies have also found evidence that invasive plants might benefit from resource increases in an environment, such as nitrogen addition (Liu et al. 2018a) and CO₂ enrichment (Blumenthal et al. 2013), due to their greater resource utilization efficiency (Shen et al. 2011).

Ongoing environmental change has been considered a major driver of plant invasion (Dukes and Mooney 1999; Liu et al. 2017); however, many conclusions have been derived from single plant, monoculture, or pairwise experiments between natives and aliens (Baruch and Jackson 2005; Liu et al. 2018a). Multispecies community processes under environmental change are often more complex than those under two species systems. Species richness may play a crucial role in mediating invasions (Zheng et al. 2018). In addition, plant–plant interactions are key drivers of plant invasion (Brooker 2006; Zhang et al. 2020). Moreover, studies have revealed that the relative performance of invasive and native plants is species specific (Byun et al. 2013; Zhang and Kleunen 2019). Thus, the results of multispecies community experiments could be more credible and could reduce the potential bias from comparing only native species with an invasive species.

Numerous studies have illustrated that invasive plants benefit more from warming, a typical environmental change factor (IPCC 2013), than native plants (Liu et al. 2017). Recent studies have also found that elevated temperatures shift community composition and biomass production (Ma et al. 2017; Liu et al. 2018b), slightly increasing the vulnerability of native grasslands to invasion (Haeuser et al. 2017). Therefore, the effect of warming on invasion success could be realized by its influence on both the invader and the native plants.

Similarly, a great number of studies have revealed that nitrogen deposition promotes plant invasion; however, most studies have been carried out using constant nitrogen addition (Littschwager et al. 2010;

Liu et al. 2018a). In fact, invasive plants might benefit more from variable rather than constant nutrient addition (Parepa et al. 2013). The fluctuating resource hypothesis posits that fluctuating resources create empty niches, which will provide invasion opportunities for invasive plants; therefore, the native communities will be more susceptible to invasion (Davis et al. 2000). Given the higher variability in the nutrient utilization efficiency of invasive plants, nutrient fluctuations might both promote the invader and also inhibit the native plant community (Parepa et al. 2013; Liu and Kleunen 2017).

Light is a limited aboveground resource in plant communities (Craine and Dybzinski 2013), particularly in tropical forests. If invaders benefit from the environmental factors mentioned above (warming and nutrient fluctuations), more energy might be invested in leaf construction for light competition (Huang et al. 2016; Wei et al. 2020). For instance, Huang et al. (2016) found that increased specific leaf area (SLA) improved the performance of two invasive plants under nutrient addition conditions. Therefore, a higher plasticity of leaf functional traits of invaders may be an important strategy to increase their irradiance utilization efficiency, further suppressing natives.

Chromolaena odorata, originating from North, Central, and South America, was introduced to tropical areas of Asia in the middle of the nineteenth century (Qin et al. 2013). It is one of the most noxious plant species globally posing severe threats to invaded ecosystems (Zheng et al. 2015). Previous studies have mainly focused on its competitive ability, such as high plasticity and resource utilization efficiency in response to environmental change (Liao et al. 2019), strong allelopathy (Zheng et al. 2015), and negative soil biota legacy effect for native plants (Mangla et al. 2008). Zheng et al. (2018) also found that its invasion success was negatively related to the native community biomass. Therefore, this species was selected as the focal species of our study.

We conducted an artificial community experiment to test the effects of warming and nutrient fluctuations on the performance of the invader *C. odorata* and the native community. According to our field observations in Southwest China, three co-occurring perennial native species were selected to construct the native community (*Desmodium sequax*, *Laggera pterodonta*, and *Pennisetum alopecuroides*). We proposed that increased invasion success could be classified into

three scenarios: a, increased invasiveness (invader productivity) and stable native community productivity; b, increased invasiveness and decreased native community productivity; and c, stable invasiveness and decreased native community productivity. The following questions were proposed. (1) Do warming, nutrient fluctuations, and their interaction facilitate the invasion success of *C. odorata*? (2) If so, was the increased invasion success due to increased invasiveness and decreased native community productivity (scenario b)?

Methods

This study was conducted in two walk-in rooms of the phytotron at the Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences. In this area, the mean annual temperature is 21.7 °C. In July, the hottest month, the mean temperature is 25.3 °C and in January, the coolest month, the mean temperature is 15.6 °C. The average annual precipitation of this area is 1557 mm, with a dry period lasting from November to April. The seeds of four species were collected in 2018 in Xishuangbanna and Puer, China, and all three natives (*D. sequax*, *L. pterodonta*, and *Pennisetum alopecuroides*) have sympatric distribution with *C. odorata*. In June 2018, the seeds were germinated in the seedbed in greenhouse (a simple plastic greenhouse). On August 5, 2018, artificial communities consisting one of three native species and one invasive species (*C. odorata*) were constructed in square plastic pots (60 × 40 × 25 cm) filled with mixed soil (topsoil: sand: peat = 2:2:1). We transplanted four similar-sized individuals (approximately 6 cm in height) of each species into each artificial community. Thus, there were 16 individuals in each artificial community (pot). The experiment included 10 replicates of four treatments: (1) control, (2) warming, (3) nutrient fluctuation, and (4) warming plus nutrient fluctuation (details are shown in Fig S1).

Half of the pots were placed in an ambient temperature chamber (25 °C from 7:00 to 19:00, 22 °C from 19:00 to 7:00), while the others were placed in heated chambers (30 °C from 7:00 to 19:00, 27 °C from 19:00 to 7:00). The communities within each walk-in room were randomized weekly to minimize potential position effects. All pots were supplied with a liquid fertilizer (Cuikang Seniphos,

Yara International ASA, UK) during the entire experimental period. For the constant nutrient treatment, the pots received 0.072 g N weekly (10 times). For the nutrient fluctuation treatment, the pots received a random amount of nitrogen weekly (the same total amount of N; details are in Table S1).

Two months after transplanting, the aboveground parts of all plants were harvested. The stems and leaves of each individual were dried at 60 °C for 72 h and then measured. Before drying, the leaf area of each individual was measured using a leaf area meter (Li-3000A, Li-Cor, Lincoln, NE, USA). The specific leaf area (SLA) was calculated as the leaf area/leaf biomass. Invasion success was evaluated by the biomass fraction of *C. odorata*, which was calculated as the biomass of *C. odorata* divided by total biomass of all plants (both natives and *C. odorata*) in the community. Changes in SLA, leaf mass, and aboveground biomass of the four species were calculated as follows: $(\text{Treatment2} - \text{Treatment1}) / \text{Treatment1} \times 100\%$, where Treatment1 was the control treatment and Treatment2 was either the warming, nutrient fluctuation, or warming plus nutrient fluctuation treatment.

Two-way ANOVAs were used to test for the effects of warming, nutrient fluctuations, and their interaction on invasion success and the aboveground biomass of invader and native plants in the community. One-way ANOVAs were used to determine differences in the change in aboveground biomass (nutrient fluctuation vs. control), as well as SLA and leaf mass (warming vs. control) among the four species. Tukey's HSD tests were used for multiple comparisons when the results of the ANOVAs were significant. Before analysis, all data were tested for normality and homogeneity of variance (Levene's test). All statistical analyses were carried out in R version 4.0.4 (R Core Team 2021).

Results

On average, the invasion success of *C. odorata* was enhanced significantly by warming (+ 9.6%, $P = 0.02$, Fig. 1a) but was not affected by the nutrient fluctuation treatment ($P = 0.61$, Fig. 1a). The aboveground biomass of *C. odorata* was also enhanced by warming (+ 21.76%, $P = 0.01$; Fig. 1b) but not by the nutrient fluctuation treatment ($P = 0.59$). Moreover, warming tended to reduce the aboveground biomass of

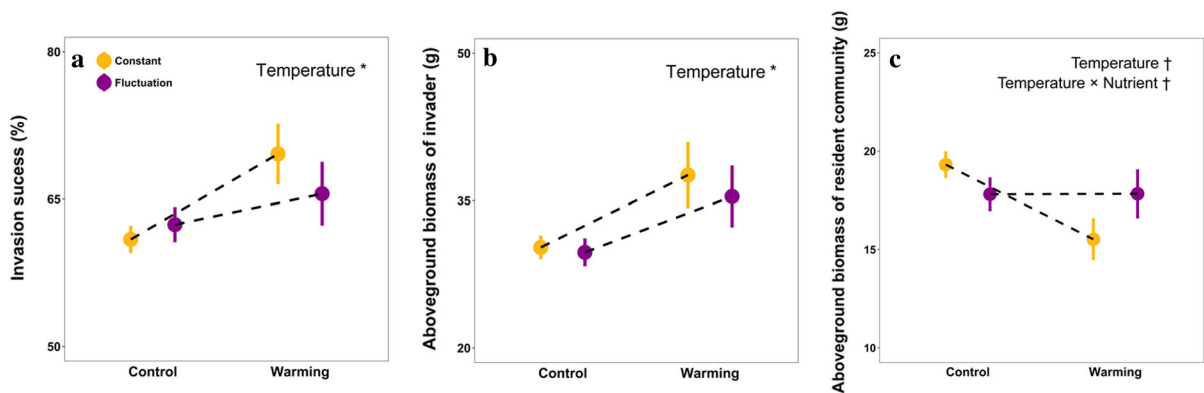


Fig. 1 Effects of warming, nutrient fluctuations, and their interaction on invasion success (a) and the aboveground biomass of the invader *Chromolaena odorata* (b) and the native

community (c). $N = 10$. Error bars (SEM). Significant effects ($P < 0.05$) are marked with an asterisk (*), and marginally significant effects ($0.05 < P < 0.1$) are marked with daggers (†)

the native community (-10.15% , $P = 0.06$; Fig. 1c), and there was a slightly significant interactive effect of nutrient fluctuations and warming on native community aboveground biomass ($P = 0.06$; Fig. 1c).

The change in aboveground biomass, SLA, and leaf mass of *C. odorata* was greater than native plants between the control and the warming treatments ($P < 0.05$; Fig. 2a, d, and g). For the nutrient fluctuation vs. control treatment comparison, changes in all indexes did not differ significantly between the invader and the three native species (Fig. 2b, e, and h). For the warming plus nutrient addition vs. control treatment comparison, the change in aboveground biomass of the invader species was not different from that of the native *L. pterodonta*, but significantly higher than that of the other two native species (Fig. 2c) and the changes in SLA and leaf mass for the invader were higher than those of the three native species (Fig. 2f and i).

Discussion

Overall, warming facilitated the invasion success of *C. odorata*, which is consistent with prior studies on other invasive species (Fridley 2012; Liu et al. 2017). An increase in *C. odorata* biomass and decrease in biomass of the native community occurred simultaneously, consistent with scenario b. The results revealed that warming is a double-edged sword for *C. odorata* invasion (i.e., one edge affects the invasive species, the other affects the native species.).

As mentioned above, due to the higher stress tolerance, plasticity, and resource utilization efficiency, invasive plants might benefit more from warming through increased photosynthesis (Blumenthal et al. 2013), a longer growth period (Fridley 2012), and increased survivorship (Walther et al. 2007) compared with native species. In this study, the increased biomass of *C. odorata* could be related to the adjustment of SLA and leaf mass in response to warming. We found that the changes in SLA and leaf mass of *C. odorata* were significantly higher than those of the three native species under the warming and the warming plus nutrient fluctuation treatments (Fig. 2d, f, g, and i). The greater change in SLA indicated a more effective irradiance utilization efficiency (Perez-Harguindeguy et al. 2013) and the increase in leaf mass and SLA (more leaf area) meant that more irradiance could be captured by the invader. Generally, plants are unlikely to adjust their biomass to alter organ morphology (Poorter et al. 2012). The simultaneous adjustment of SLA and leaf mass indicates that *C. odorata* could optimize its irradiance utilization efficiency more effectively than the native species (Perez-Harguindeguy et al. 2013).

In contrast, previous studies revealed that warming has a negative influence on native plants (Haeuser et al. 2017; Ma et al. 2017). We propose two explanations for the decrease in aboveground biomass of the native community in this study. First, warming might have had a direct negative effect on the native species. For instance, a previous study found that elevated temperatures had a negative influence on undisturbed native communities (Haeuser et al. 2017).

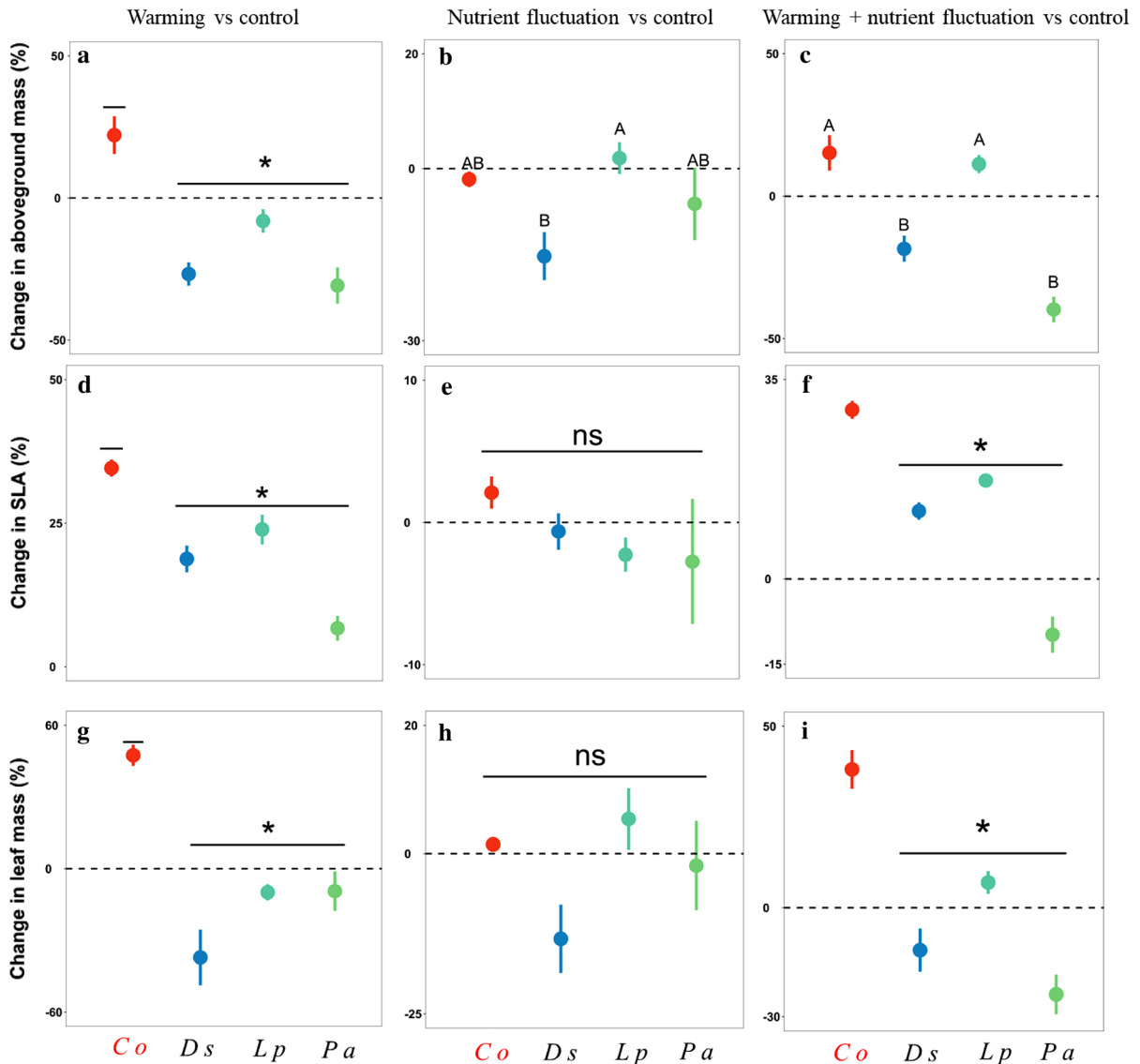


Fig. 2 Change in aboveground biomass (a, b, c), specific leaf area (SLA) (d, e, f), leaf mass (g, h, i), and of the invader *Chromolaena odorata* (*C. o*) and native species *Desmodium sequax* (*D. s*), *Laggera pterodonta* (*L. p*), and *Pennisetum alopecuroides* (*P. a*) between treatments (treatment

comparisons indicated above graphs). $N = 10$. Error bars (SEM). Asterisks indicate significant differences between invader and native species ($P < 0.05$). Different capital letters indicate significant differences among the four species ($P < 0.05$)

Second, the competitive effect of the invader might have increased under warming. *Chromolaena odorata* might be more efficient at competing for available resources (e.g., irradiance, water, and nutrients), which renders a higher competitive advantage to the invader over the native plants. In other words, the native community was vulnerable to invasions under warming, thus providing a relative advantage to the invasive plant. A previous meta-analysis revealed that

warming had no influence on native plants (Liu et al. 2017), which might due to lack multispecies experiments.

Inconsistent with our hypothesis, the results demonstrated that nutrient fluctuations had a weaker effect on both the invader and the native species. However, there is evidence that nutrient fluctuations have a positive effect on plant invasion (Parepa et al. 2013; Li and Stevens 2012). In our previous study with

C. odorata, we also found a weaker effect of nutrient fluctuations on its invasion success in multispecies communities (Zheng et al. 2020). In general, diverse ecological niches and efficient complementary resource patterns are more likely to occur in multi-species communities (Ptacnik et al. 2008) and species richness might diminish the effects of nutrient fluctuations in this study.

Interestingly, we found a slightly significant interactive effect of warming and nutrient fluctuations on native community productivity. Similarly, a previous study revealed that the effect of resource pulses was influenced by seasonal timing, and fluctuating nutrients could be better utilized by the native *Atriplex parryi* during mid-spring than early spring (James et al. 2006). We found that the aboveground biomass, SLA, and leaf mass of native *L. pterodonta* increased under the warming plus nutrient fluctuation treatment (Fig. 2c, f, and i). More importantly, the change in aboveground biomass for *L. pterodonta* was lower in the warming vs control but equal to that of *C. odorata* in the nutrient fluctuation vs. control comparison and warming plus nutrient fluctuation vs. control comparisons (Fig. 2a, b, and c). Therefore, we could infer that the native *L. pterodonta* benefited more from nutrient fluctuations. Thus, in this study, nutrient fluctuations might compensate for the negative effect of elevated temperature on native plants due to their greater variability in nutrient utilization efficiency under both warming and nutrient fluctuations.

Conclusion

Our results demonstrate that warming can facilitate the invasion success of *C. odorata* by enhancing its invasiveness and decreasing the productivity of the native community. While nutrient fluctuations had no influence on either the invader or native community, there was a slight interactive effect between warming and nutrient fluctuations on the native community. More multispecies community experiments in field conditions are needed to strengthen our understanding of plant invasion.

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Author contributions YLZ and ZYL designed the research. YLZ performed the research. XS analyzed the data. XS, YLZ, and ZYL wrote and revised the paper.

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Data availability Data are available as the electronic supplementary material.

Code availability Code are available as the electronic supplementary material.

Declarations

Conflict of interest We have no conflict of interest to declare.

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