



Nutrient fluctuation has different effects on a tropical invader in communities from the native and non-native range

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ABSTRACT

Invader success might depend on both nutrient availability and species richness of the resident community. Here, we combine these ideas in a single experiment, testing whether the Fluctuating resource and biotic resistance hypotheses might be contingent upon one another. The fluctuating resource hypothesis proposes that resource fluctuation might facilitate the successful invasion of exotic plants if invaders are better than natives at taking advantage of resource pulses. The biotic resistance hypothesis proposed that more species rich communities might be more resistant to invasion, due to greater competition for resources with greater native richness. Here, we use an experiment with the invader, *Chromolaena odorata* in 315 artificial communities with resident plants from native and non-native ranges. We found that resident origin, nutrient treatment and species richness of artificial community have significant effects on invasion success of *C. odorata*. The effect of nutrient fluctuation on invasion success was contingent on resident origin (native vs. non-native range), and this effect was weaker in more species rich communities. In addition, the invasion success of *C. odorata* was negatively related with biomass of resident plants, suggesting competition as a mechanism governing invader success. Our results suggest a novel twist on the fluctuating resource hypothesis: fluctuating resources may favor invaders more in species poor communities of non-native origin. This also suggests that competition for fluctuating resources may be one mechanism governing biotic resistance because the effects of richness were greater when resources were fluctuating. Our results suggest that the fluctuating resource hypothesis will apply only to resident communities with lower resource acquisition strategies, relative to the invader.

1. Introduction

Both nutrient environment and the composition of established (resident) or native plant communities might be expected to influence the success of invasive species. However, these factors have rarely been integrated into a single experiment to determine whether and how they interact (but see, e.g. Davis and Pelsor, 2001; Petchey et al., 2002; Thomsen et al., 2006). The fluctuating resource hypothesis is a popular theory that explains exotic plant invasion (Davis et al., 2000). This hypothesis suggests that resource fluctuation usually increases resource availability, which will provide invasion opportunities for non-native species, and the resident communities will be more susceptible to invasion (Davis et al., 2000; Li and Stevens, 2012). Some studies across multiple ecosystems provide supporting evidence that resource fluctuation is associated with invasion of non-native species (Leishman and

Thomson, 2005; Hobbs and Atkins, 2006; Radford, 2013). Davis et al. (2000) proposed that invasion of exotic species usually increased when resources were supplied as large-magnitude pulses rather than at continuous rates. Li and Stevens (2012) found nutrient fluctuation increased the invasion success of invasive species, and invaders had strong performance in resource fluctuation treatments. Nutrient fluctuation could increase the invasion status of Southern California's coastal sage scrub (Goldstein and Suding, 2014). In Germany, the invasion of several invaders was also increased by rainfall fluctuation (Kreyling et al., 2008). However, inconsistent evidence for the resource fluctuation hypothesis was also found. Walker et al. (2005) found fluctuation of water or nutrient resources did not increase the rate of invasion of the herbaceous perennial *Hieracium pilosella* (Asteraceae). The invasion of the annual grass *Schismus arabicus* (Poaceae) was also greater under continuous resource supply compared to fluctuating

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resource supply (James et al., 2006).

These apparent inconsistencies might be due in part to differences in how resident species respond to resource fluctuations. Different resident plants have different physiological requirements and ecological strategies (Li and Stevens, 2012). In our previous work, we demonstrated that plants from the native range of invasive plant *Chromolaena odorata* (Mexico) had faster relative growth rates than those from the non-native range (China) (Zheng et al., 2018; Burns et al., 2019). If greater relative growth rates correspond to a greater ability to utilize fluctuating resources (James and Richards, 2005; Keser et al., 2014), then species from *C. odorata*'s native range should be better at suppressing invader performance than those from the non-native range, especially when resource availability is fluctuating. Thus, we predict that the effects of fluctuating resource availability might be contingent on resident community composition, including the origin (native or introduced ranges) of the resident community.

Whether the influence of fluctuating resource availability are contingent on resident plant richness is also unclear. Species richness of resident communities plays an important role in resistance to invasion of non-native plants, as suggested by the biotic resistance hypothesis (Elton, 1958). Some studies found community richness was negatively related with the invasion of exotic plants (Maron and Marler, 2008; Zheng et al., 2018), consistent with this hypothesis. A few studies have proposed that resource fluctuation and richness have interactive effects on invasion of exotic plants (Davis and Pelsor, 2001; Petchey et al., 2002; Thomsen et al., 2006). High-richness communities usually have diverse ecological niches and complementary resource use patterns in time or space (Naeem et al., 2000), perhaps suggesting that high richness communities should be robust to resource fluctuations (Tredennick et al., 2017; Smeti et al., 2018). Therefore, we predict the effect of resource fluctuation on invasion should be greater in low-richness communities than in high-richness communities.

The invasion of exotic plants might also be influenced by global change factors, such as eutrophication and biodiversity loss. In the last 200 years, rapid development of industry has triggered unprecedented global environmental changes (Lei et al., 2012; USGCRP, 2018). Eutrophication and the addition of nitrogen deposition are two important components of environmental change (Zhang et al., 2016; Sinha et al., 2017; Walker et al., 2019), which induce greater nutrient fluctuation in the ecosystem, and might contribute to the successful invasion of exotic species. Meanwhile, with rapid economic development, human beings have modified the landscape, including through deforestation, grassland degradation, and desertification, which all of which can cause loss of biodiversity (Walther et al., 2002). In addition, disturbances, such as those caused by construction of motorway, railways, and reservoirs, may cause the fluctuation of some resources (Radford, 2013). Therefore, global change and biodiversity loss may interact to facilitate the invasion of exotic plants.

Exotic plants may either invade an already established resident community or exotic and resident species could arrive simultaneously, following a disturbance event. Most previous studies test fluctuating resource hypothesis in the first situation (Davis and Pelsor, 2001; Walker et al., 2005), or do not differentiate the colonization order between invasive and native species (Davis et al., 2000). However, successful invasion during simultaneous establishment is very important for exotic plants, and could be influenced by competition with "residents". When the exotic plants enter a new range, rapid population establishment is the critical step for successful invasion, which will support enough seeds (propagules) for further invasion. It is usually easier for the invader to establish in an open site (most residents were moved by disturbance) than the exotic plant invade an already established community. In this study, we use the invader *Chromolaena odorata* to experimentally test whether the fluctuating resource hypothesis is contingent on resident plant origin and species richness by planting the invader and resident species at the same time. This design is thus a conservative test of the biotic resistance hypothesis, because

natives are not given an establishment advantage.

Chromolaena odorata is an invasive plant in some tropical and sub-tropical areas; *Chromolaena odorata* can invade diverse habitats especially in disturbed environments (Raimundo et al., 2007; Zheng et al., 2018). If disturbance induces resource (light, water, or nutrient) fluctuations (Symstad, 2000; Gross et al., 2005; Radford, 2013; Seipel et al., 2018), the successful invasion of *C. odorata* might be due to differences between native and non-native resident plants response to resource fluctuation. In this study, in order to test how invasion is influenced by resource fluctuation, species range (native vs. non-native range), richness and their interactive effects, we created a series of artificial communities with resident plants from native (Mexico) and non-native (China) ranges. We replicated within and across 3 levels of species richness (1, 2 and 4 resident species communities) for a total of 315 experimental mesocosms.

We hypothesized that (1) invasion success will be suppressed in communities from the native range (Mexico), especially with fluctuating resource availability, if fast growing residents take advantage of fluctuating resource availability and suppress the growth of the invader, (2) the invasion success will be facilitated with fluctuating resources in communities from the non-native range (China), because these resident species are slower growing (Zheng et al., 2018) and less able to take advantage of resource pulses compared with the invader, and (3) high richness communities will be less influenced by resource fluctuation than low richness communities, if resource complementarity makes high richness communities more robust to perturbation.

2. Materials and methods

2.1. Study site

A common garden experiment was conducted at Xishuangbanna Tropical Botanical Garden of Chinese Academy of Sciences (XTBG-CAS) (21°56' N, 101°15'E) located in Mengla County, Yunnan Province, southwest China. 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 site is 1557 mm, with a dry period lasting from November to April (Zheng et al., 2015, 2018).

2.2. Study materials

Chromolaena odorata (L.) R. M. King and H. Robinson (Asteraceae) is a semi-lignified perennial subshrub, which is native to Latin America. In the middle of the 19th Century, *C. odorata* was introduced to some tropical areas as ornamental plants (Zheng et al., 2018). Over hundreds of years, it became one of the most seriously noxious invasive species in the world, and caused great threats to biodiversity and environments (Qin et al., 2013; Zheng et al., 2015, 2018).

In this study, in order to test whether the effect of resource fluctuation on invasion success of *C. odorata* was different between native and non-native origin communities, in March 2017, we established a series of artificial communities in the common garden using resident plants from Mexico (native range) and China (non-native range) (Table S1). Each community included 16 individuals of Mexican or Chinese resident species and nine individuals of *C. odorata*. According to our field investigation, this ratio (16:9) is about the median value in the field for *C. odorata* in its introduced range. Three types of artificial communities were used: one resident species, two resident species (eight individuals per species) and four resident species (four individuals per species) (Fig. S1). The seeds of resident species from Mexico (Morelos and Veracruz) and China (Xishuangbanna and Pu'er) were collected in 2011, 2012, 2014. The seeds of *Chromolaena odorata* were collected from Xishuangbanna in 2012. These species were selected because they were common and have sympatric distributions

with *C. odorata* at each collection site. Seeds of each species were collected from more than 10 individuals, spaced at least 20 m apart and mixed uniformly in paper bags. These seeds were germinated, and seedlings were planted in a common garden at XTBG-CAS. To reduce maternal effects, we used the seeds of each species from this common garden for our experiments. According to our previous study, the performance of the Mexican species growing in China was similar as their performance in the field in Mexico (Zheng et al., 2018).

2.3. Construction of artificial communities

There were 8 Chinese resident species and 7 Mexican resident species to construct artificial communities with 1, 2, 4 resident species respectively. If we used all the possibilities of species combination, the number of artificial communities would be more than 1500, and the workload would be very heavy. In addition, the requirement of seed amount would also be high for each species. Therefore, we randomly chose 18 species combinations (8, 7 and 3 combinations with one, two and four resident species respectively) for artificial communities with resident species from China, and 17 combinations (7, 7 and 3 combinations with one, two and four resident species respectively) for artificial communities with resident species from Mexico (Table S1). The rule of species combination was that the species in each combination had to have sympatric distributions in the field. The size of each experimental community was 2 m × 2 m, and each community was 1 m apart from neighboring communities. Each species combination had nine community replicates, for a total number of 315 experimental communities. Communities of each combination were randomly arranged in the common garden.

In March 2017, the seeds of each species were germinated in a greenhouse in XTBG-CAS, and in June 2017, similar sized seedlings were transplanted into the artificial communities. The seedlings of resident and invasive plants were planted to the communities at the same time. During the first 15 days, the seedlings were watered daily at a rate of 30 L per artificial community. Then seedlings were grown under natural conditions. Weeds were removed carefully when necessary.

2.4. Nutrient treatments

During July to November, artificial communities received nutrient treatments with Germany Lion Horse Compound Fertilizer (nitrogen: phosphorus: potassium 21:8:11). For each species, three artificial communities received a continuous nutrient (Each time, 0.2 g fertilizer per individual. One time per month, for a total of 5 times), another three artificial communities received a fluctuated nutrient treatment (In September, 1 g fertilizer per individual). Thus, the two nutrient treatments (continuous and fluctuating) received the same total amount of fertilizer. The last three artificial communities did not receive any nutrient as control.

2.5. Biomass harvesting and calculation of invasion success

In December 2017, we harvested the aboveground parts of all plants, and oven-dried them at 100 °C for 72 h. Then the weight of each individual was measured.

We used the proportion of *C. odorata* biomass to represent invasion success of this period, which was calculated as the equation: invasion success = (the biomass of *C. odorata*) / (biomass of all plants in the artificial community). A high proportion of *C. odorata* biomass indicated that the invasion success was great, which meant the community was easily invaded by *C. odorata*.

2.6. Statistical analysis

The effects of range (resident species origin), nutrient treatment and richness on invasion success were tested by a linear mixed-effects

Table 1

Effects of range, nutrient treatment, richness and their interactions on invasion success according to a linear mixed model. Range, Treatment and Richness as fixed factors, and community nested within range as a random factor. Data was log transformed.

Source	Sum Square	d.f.	F-value	P-value
Range	0.0979	1	11.6224	< 0.01
Treatment	0.0731	2	4.3380	< 0.05
Richness	0.1013	2	6.0111	< 0.01
Range × Treatment	0.3048	2	18.086	< 0.001
Range × Richness	0.0464	2	2.7556	0.0802
Treatment × Richness	0.0229	4	0.6782	0.6076
Range × Treatment × Richness	0.1606	4	4.763	< 0.001

The bold value indicate the source effect is significant ($P < 0.05$).

model. Range, nutrient treatment and richness were treated as fixed factors, and artificial community (species combination) nested within range was treated as a random factor. Data was log10 transformed to improve normality of residuals. Analysis was carried out using the lmer function in the lmerTest package (version 3.1–128) in R version 3.5.1 (R Core Team, 2018). EMMEANS (version 1.3.0) post hoc tests were used for multiple comparisons of invasion success across different nutrient treatments. Differences in nutrient treatments were carried out within each species richness levels and within each range respectively.

Linear (communities with one and four non-native species) or nonlinear regression was used to analyze the relationship of invasion success of *C. odorata* with resident plant biomass. We selected the linear or non-linear (power function) model according to the following rule, first, the P value for the predictor variable-resident biomass should be less than 0.05, then the model with a higher R value was preferred between models, if both models included a significant predictor.

3. Results

Range ($P < 0.01$), nutrient treatment ($P < 0.05$) and richness ($P < 0.01$) had significant effects on invasion success (Table 1). The interactions of Range × Treatment ($P < 0.001$) and Range × Treatment × Richness ($P < 0.001$) had significant effects on invasion success, whereas Range × Richness ($P = 0.0802$) and Treatment × Richness ($P = 0.6076$) had no significant effects on invasion success (Table 1). The invasion success was higher for communities with resident species from non-native range (China) than those from native range (Mexico) (Fig. S2).

For communities with one resident species from non-native range, those that received continuous nutrients had significantly higher (13.75 %) invasion success than control, but lower invasion success (14.74 %) than those that received fluctuated nutrients (Fig. 1). For communities with one resident species from native range, those that received continuous (11.23 %) and fluctuated nutrients (15.15 %) had significantly lower invasion success than control (Fig. 1). A similar pattern was found in communities with two resident species, however control and continuous treatments did not differ for communities from the non-native range, and continuous and fluctuation treatments did not differ for communities from the native range (Fig. 2). For communities with four resident species from China or Mexico, there were no significant differences among communities in the continuous nutrient, fluctuated nutrient and control treatments (Fig. 3).

For communities with resident species from China and Mexico, invasion success was significantly and negatively related with biomass of resident plants (Fig. 4). However, at the same biomass of resident plants, invasion success of *C. odorata* was higher for communities with non-native species than communities with native species (Fig. 4). For non-native communities, the relationships were nonlinear (Fig. 4). For native communities, the relationship was linear in communities with one and four native species, and nonlinear in communities with two

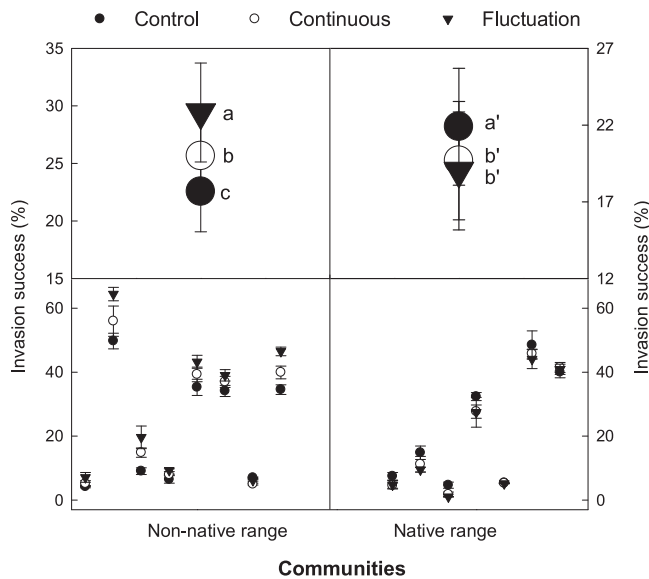


Fig. 1. Invasion success of *C. odorata* in communities with one species from non-native range and native range at different nutrient treatments. Big points in above part depict the mean $\pm$ SE for artificial communities with species from non-native range (China) and native range (Mexico) respectively, and small points in below part indicate the mean $\pm$ SE for each species combination. Different letters indicate there are significant differences among treatments.

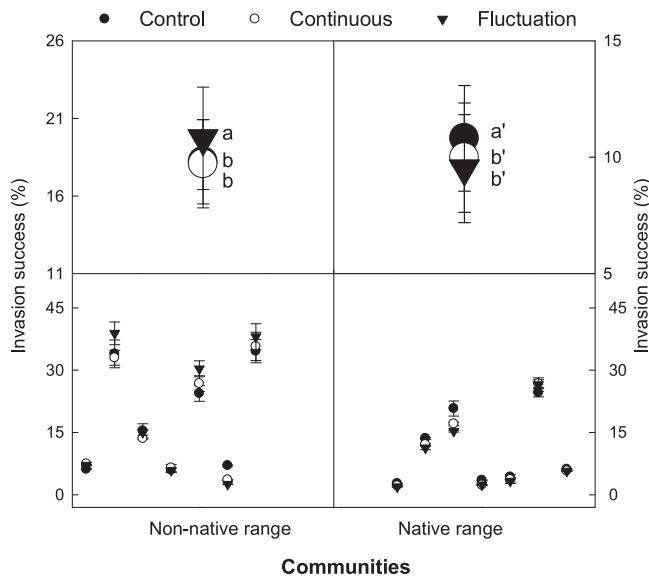


Fig. 2. Invasion success of *C. odorata* in communities with two species from non-native range and native range at different nutrient treatments. Big points in above part depict the mean $\pm$ SE for artificial communities with species from non-native range (China) and native range (Mexico) respectively, and small points in below part indicate the mean $\pm$ SE for each species combination. Different letters indicate there are significant differences among treatments.

native species (Fig. 4).

4. Discussion

Consistent with our hypothesis, nutrient fluctuation had different effects on invasion success of *C. odorata* in communities with species from native and non-native ranges (Table 1, Figs. 1–3). For communities with one and two species, resource fluctuation increased invasion success in non-native origin communities (China) but added nutrients decreased invasion success in native origin communities (Mexico)

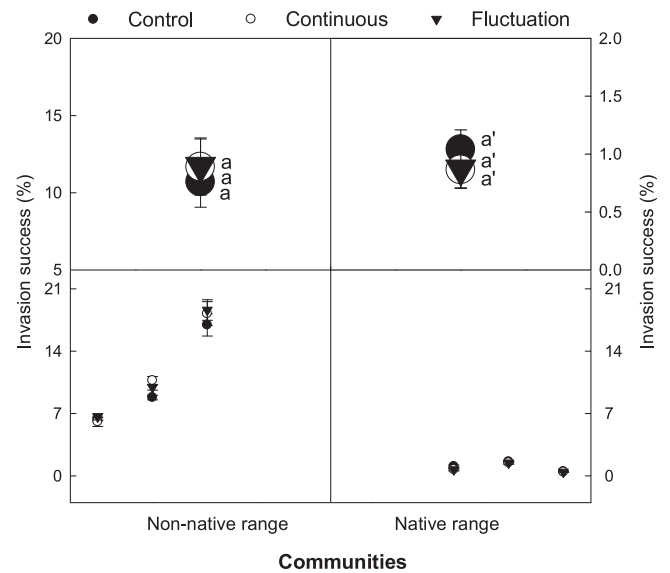


Fig. 3. Invasion success of *C. odorata* in communities with four species from non-native range and native range at different nutrient treatments. Big points in above part depict the mean $\pm$ SE for artificial communities with species from non-native range (China) and native range (Mexico) respectively, and small points in below part indicate the mean $\pm$ SE for each species combination. Different letters indicate there are significant differences among treatments.

(Figs. 1, 2). Because these resident plants from native range had faster relative growth rates (Zheng et al., 2018; Burns et al., 2019), we expect that they used the added nutrients efficiently and suppressed invader growth. This expectation is also consistent with the negative correlation we observed between invasion success and resident biomass (Fig. 4). The relatively slower growing residents from the non-native range (Zheng et al., 2018; Burns et al., 2019) may be less efficient in taking advantage of these resource additions, leading to greater invasion success in non-native communities, especially when resources were fluctuating. Further, resource fluctuation had no effect on invasion in more species richness communities (Fig. 3). We speculate that richness diminishes the effect of resource fluctuation, because high-richness communities usually have diverse ecological niches and complementary resource use patterns (Naeem et al., 2000; Ptacnik et al., 2008), such that fluctuating resources will be used more thoroughly in high than in low richness communities.

Invaders have long been thought to be exceptionally good at resource acquisition, having high growth rates and opportunism in the face of high nutrient availability (Qin et al., 2013) or nutrient pulses due to disturbance (Davis et al., 2000; Burns and Winn, 2006). A large number of functional trait studies are consistent with this prediction, finding especially that invaders often have high relative growth rates (e.g. Burns, 2006; Grotkopp and Rejmanek, 2007; Dawson et al., 2011). Thus, invaders often have a more opportunistic resource use strategy than their competitors in the non-native range (e.g. Burns and Winn, 2006). Our previous study demonstrated that most resident species in *C. odorata*'s native range have a faster resource acquisition strategy (relative growth rate) than the invader, but most residents in non-native range have slower resource use efficiency than the invader (Zheng et al., 2018). Thus our results here could explain why tests of the fluctuating resource hypothesis generate inconsistent results. As we demonstrate, invader success in response to nutrient fluctuation was contingent on the resident community's origin (native vs. non-native range), and thus its resource acquisition strategy (see also Zheng et al., 2018; Burns et al., 2019), suggesting that the fluctuating resource hypothesis will apply only to resident communities with lower resource acquisition strategies, relative to the invader.

We found that higher richness resident communities are less

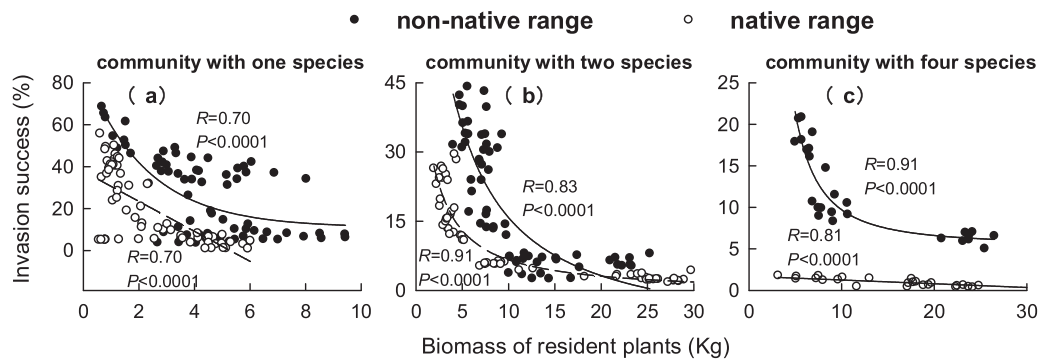


Fig. 4. The relationship between invasion success of *C. odorata* and biomass of resident plants.

invasion overall, and the invasion success was not influenced by fluctuating resources in these communities, which is generally consistent with the biotic resistance hypothesis (Elton, 1958; Beaury et al., 2020) and with studies demonstrating that higher richness communities are more resilient (Naeem et al., 2000; Allan et al., 2011). In particular, experimental studies often find that more species rich resident communities are more resistant to invasions (e.g. Levine, 2000), and recent large-scale studies find similar patterns (Beaury et al., 2020). It had been suggested that resource complementarity might govern the greater resiliency of more diverse communities (Allan et al., 2011). Though we did not test for complementary resource use here, the negative correlation between invasion success and resident biomass is consistent with resource competition as a possible mechanism influencing the interaction between resident richness and fluctuating resources. Interestingly, this suggests that competition for fluctuating resources may be one mechanism governing the biotic resistance hypothesis, at least in this study system.

Eutrophication and the addition of nitrogen deposition are two important factors of global change (Sinha et al., 2017; Zhang et al., 2016; Walker et al., 2019), which could induce great nutrient fluctuation in the ecosystem. Meanwhile, land utilization change (deforestation, major projects construction, etc) usually causes loss of biodiversity (Walther et al., 2002) and the fluctuation of some resources (Radford, 2013). According to our results (Figs. 1–3), in non-native range, biodiversity loss and resource fluctuation may further facilitate the invasion of exotic plants (MacDougall et al., 2009; Maron et al., 2014), though studies replicated across multiple native and non-native ranges would be useful to test the generality of this idea.

In conclusion, nutrient fluctuation had different effects on invasion success of *C. odorata* in communities from the native and non-native ranges for low richness communities. Functional differences between species from the native (Mexico) and non-native (China) ranges, such as differences in relative growth rate (Zheng et al., 2018) might contribute to this pattern. Thus, we found that the fluctuating resource hypothesis explains some variation in the success of the invader, *C. odorata*, and that this effect was contingent on resident plant origin (native vs. introduced range) and species richness of the resident community. Thus we combined the biotic resistance and fluctuating resource hypotheses, and report the novel finding that these mechanisms can interact to influence invader performance. Lower richness communities were generally more vulnerable to invasion, especially when resources were fluctuating, as might be expected with disturbance (Symstad, 2000; Gross et al., 2005; Radford, 2013; Seipel et al., 2018). In future, biodiversity loss and increasing disturbance could interact to exacerbate the invasion of exotic plants.

Author contributions

Y.L.Z. designed the research. Y.L.Z. and L.L. performed the research. Y.L.Z., J.H.B. and Z.Y.L. analyzed the data. Y.L.Z., J.H.B., Z.Y.L. W.T.L.

wrote and revised the paper.

Declaration of Competing Interest

We declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.envexpbot.2020.104193>.

References

- Allan, E., Weisser, W., Weigelt, A., Roscher, C., Fischer, M., Hillebrand, H., 2011. More diverse plant communities have higher functioning over time due to turnover in complementary dominant species. *Proc. Natl. Acad. Sci. U. S. A.* 108, 17034–17039.
- Beaury, E.M., Finn, J.T., Corbin, J.D., Barr, V., Bradley, B.A., 2020. Biotic resistance to invasion is ubiquitous across ecosystems of the United States. *Ecol. Lett.* 23, 476–482.
- Burns, J.H., 2006. Relatedness and environment affect traits associated with invasive and noninvasive introduced commelinaceae. *Ecol. Appl.* 16, 1367–1376.
- Burns, J.H., Winn, A.A., 2006. A comparison of plastic responses to competition by invasive and noninvasive congeners in the Commelinaceae. *Biol. Invasions* 8, 797–807.
- Burns, J.H., Jennifer, E.M., Zheng, Y.L., 2019. Tests of alternative evolutionary models are needed to enhance our understanding of biological invasions. *New Phytol.* 222, 701–707.
- Davis, M.A., Pelsor, M., 2001. Experimental support for a resource-based mechanistic model of invasibility. *Ecol. Lett.* 4, 421–428.
- Davis, M.A., Grime, J.P., Thompson, K., 2000. Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.* 88, 528–534.
- Dawson, W., Fischer, M., van Kleunen, M., 2011. The maximum relative growth rate of common UK plant species is positively associated with their global invasiveness. *Glob. Ecol. Biogeogr.* 20, 299–306.
- Elton, C.S., 1958. *The Ecology of Invasions by Animals and Plants*. Chapman & Hall, New York, NY.
- Goldstein, L., Suding, K., 2014. Applying competition theory to invasion: resource impacts indicate invasion mechanisms in California shrublands. *Biol. Invasions* 16, 191–203.
- Gross, K.L., Mittelbach, G.G., Reynolds, H.L., 2005. Grassland invasibility and diversity: responses to nutrients, seed input, and disturbance. *Ecology* 86, 476–486.
- Grotkopp, E., Rejmanek, M., 2007. High seedling relative growth rate and specific leaf area are traits of invasive species: phylogenetically independent contrasts of woody angiosperms. *Am. J. Bot.* 94, 526–532.
- Hobbs, R.J., Atkins, L., 2006. Effect of disturbance and nutrient addition on native and introduced annuals in plant communities in the Western Australian wheatbelt. *Austral Ecol.* 13, 171–179.
- James, J.J., Richards, J.H., 2005. Plant N capture from pulses: effects of pulse size, growth rate, and other soil resources. *Oecologia* 145, 113–122.
- James, J.J., Caird, M.A., Drenovsky, R.E., Sheley, R.L., 2006. Influence of resource pulses and perennial neighbors on the establishment of an invasive annual grass in the Mojave Desert. *J. Arid Environ.* 67, 528–534.
- Keser, L.H., Dawson, W., Song, Y.B., Yu, F.H., Fischer, M., 2014. Invasive clonal plant

- species have a greater root-foraging plasticity than non-invasive ones. *Oecologia* 174, 1055–1064.
- Kreyling, J., Beierkuhnlein, C., Ellis, L., Jentsch, A., 2008. Invasibility of grassland and heath communities exposed to extreme weather events additive effects of diversity resistance and fluctuating physical environment. *Oikos* 117, 1542–1554.
- Lei, Y.B., Wang, W.B., Feng, Y.L., Zheng, Y.L., Gong, H.D., 2012. Synergistic interactions of CO₂ enrichment and nitrogen deposition promote growth and ecophysiological advantages of invading *Eupatorium adenophorum* in Southwest China. *Planta* 236, 1205–1213.
- Leishman, M.R., Thomson, V.P., 2005. Experimental evidence for the effects of additional water, nutrients and physical disturbance on invasive plants in low fertility Hawkesbury Sandstone soils, Sydney, Australia. *J. Ecol.* 93, 38–49.
- Levine, J.M., 2000. Species diversity and biological invasions: relating local process to community pattern. *Science* 288, 852–854.
- Li, W., Stevens, M.H.H., 2012. Fluctuating resource availability increases invasibility in microbial microcosms. *Oikos* 121, 435–441.
- MacDougall, A.S., Gilbert, B., Levine, J.M., 2009. Plant invasions and the niche. *J. Ecol.* 97, 609–615.
- Maron, J.L., Marler, M., 2008. Effects of native species diversity and resource additions on invader impact. *Am. Nat.* 172, S18–S33.
- Maron, J.L., Auge, H., Pearson, D.E., Korell, L., Hensen, I., Suding, K.N., Stein, C., 2014. Staged invasions across disparate grasslands: effects of seed provenance, consumers and disturbance on productivity and species richness. *Ecol. Lett.* 17, 499–507.
- Naeem, S., Knops, J.M.H., Tilman, D., Howe, K.M., Kennedy, T., Gale, S., 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* 91, 97–108.
- Petchey, O.L., Casey, T., Jiang, L., McPhearson, P.T., Price, J., 2002. Species richness, environmental fluctuations, and temporal change in total community biomass. *Oikos* 99, 231–240.
- Ptácnik, R., Solimini, A.G., Andersen, T., Tamminen, T., Brettum, P., Lepistö, L., Willén, E., Rekolainen, S., 2008. Diversity predicts stability and resource use efficiency in natural phytoplankton communities. *Proc. Natl. Acad. Sci. U. S. A.* 105, 5134–5138.
- Qin, R.M., Zheng, Y.L., Valiente-Banuet, A., Callaway, R.M., Barclay, G.F., Silva-Pereyra, C., Feng, Y.L., 2013. The evolution of increased competitive ability, innate competitive advantage, and novel biochemical weapons act in concert to promote invasion for a tropical invader. *New Phytol.* 197, 979–988.
- R Core Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Radford, I.J., 2013. Fluctuating resources, disturbance and plant strategies: diverse mechanisms underlying plant invasions. *J. Arid Land* 5, 284–297.
- Raimundo, R.L.G., Fonseca, R.L., Schachetti-Pereira, R., Peterson, A.T., Lewinsohn, T.M., 2007. Native and exotic distributions of Siamweed (*Chromolaena odorata*) modeled using the genetic algorithm for rule-set production. *Weed Sci.* 55, 41–48.
- Seipel, T., Rew, L.J., Davis, K.T., Maxwell, B.D., Lehnhoff, E.A., 2018. Disturbance type influences plant community resilience and resistance to *Bromus tectorum* invasion in the sagebrush steppe. *Appl. Veg. Sci.* 21, 385–394.
- Sinha, E., Michalak, A.M., Balaji, V., 2017. Eutrophication will increase during the 21st century as a result of precipitation changes. *Science* 357, 405–408.
- Smeti, E., Roelke, D.L., Tsirtsis, G., Spatharis, S., 2018. Species extinctions strengthen the relationship between biodiversity and resource use efficiency. *Ecol. Model.* 384, 75–86.
- Symstad, A.J., 2000. A test of the effects of functional group richness and composition on grassland invasibility. *Ecology* 81, 99–109.
- Thomsen, M.A., D'Antonio, C.M., Suttle, K.B., Sousa, W.P., 2006. Ecological resistance, seed density and their interactions determine patterns of invasion in a California coastal grassland. *Ecol. Lett.* 9, 160–170.
- Tredennick, A.T., Adler, P.B., Adler, F.R., 2017. The relationship between species richness and ecosystem variability is shaped by the mechanism of coexistence. *Ecol. Lett.* 20, 958–968.
- USGCRP, 2018. Impacts, risks, and adaptation in the United States: fourth national climate assessment, volume II. In: Reidmiller, D.R., Avery, C.W., Easterling, D.R., Kunkel, K.E., Lewis, K.L.M., Maycock, T.K., Stewart, B.C. (Eds.), U.S. Global Change Research Program, Washington, DC, USA, <https://doi.org/10.7930/nca4.2018>. 1515 pp. doi: 10.7930/NCA4.2018.
- Walker, S., Wilson, J.B., Lee, W.G., 2005. Does fluctuating resource availability increase invasibility? Evidence from field experiments in New Zealand short tussock grassland. *Biol. Invasions* 7, 195–211.
- Walker, J., Bell, M.D., Schwede, D., Cole, A., Beachley, G., Lear, G., Wu, Z.Y., 2019. Aspects of uncertainty in total reactive nitrogen deposition estimates for North American critical load applications. *Sci. Total Environ.* 690, 1005–1018.
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. *Nature* 416, 389–395.
- Zhang, Y.H., Loreau, M., Lü, X.T., He, N.P., Zhang, G.M., Han, X.G., 2016. Nitrogen enrichment weakens ecosystem stability through decreased species asynchrony and population stability in a temperate grassland. *Glob. Change Biol.* 22, 1445–1455.
- Zheng, Y.L., Feng, Y.L., Zhang, L.K., Callaway, R.M., Valiente-Banuet, A., Luo, D.Q., Liao, Z.Y., Lei, Y.B., Barclay, G.F., Silva-Pereyra, C., 2015. Integrating novel chemical weapons and evolutionarily increased competitive ability in success of a tropical invader. *New Phytol.* 205, 1350–1359.
- Zheng, Y.L., Burns, J.H., Liao, Z.Y., Li, Y.P., Yang, J., Chen, Y.J., Zhang, J.L., Zheng, Y.G., 2018. Species composition, functional and phylogenetic distances correlate with success of invasive *Chromolaena odorata* in an experimental test. *Ecol. Lett.* 21, 1211–1220.