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Multiple biotic factors mediate the invasion success of Chromolaena odorata

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Abstract

Community resistance plays a crucial role in the successful invasion of alien plants. However, our understanding of how the soil legacy effects of native species richness, parasitic plants, competition and soil microbes contribute to shaping community resistance has not been achieved. In this study, we grew *Chromolaena odorata* and two co-occurring native plants from three soil sources (native richness gradient, i.e., heavily invaded moderately invaded and lightly invaded). We then implemented treatments containing parasitism (*Cuscuta chinensis*), competition and sterilization. Overall, our research indicated that *C. odorata* outperformed two other native species (in terms of height and biomass). However, our findings also revealed that both the soil legacy effects of native plant richness and competition negatively impact the growth of *C. odorata*, and native plants tend to produce more biomass in soils with greater diversity and under competitive conditions (5.0%). Interestingly, *C. chinensis* parasitism had asymmetric negative effects on alien (-11.1%) and native plants (-39.9%). Furthermore, *C. odorata* did not experience limitations from parasitism in sterilized soil, as indicated by a slight increase in biomass of 2.3%. This study underscores that community resistance to *C. odorata* is governed by an interplay of multiple biotic factors, both individually and in combination.

1. Introduction

With the exponential rate of trade and globalization, alien plants invasion has attracted the attention of governments, scientists, environmentalists and biodiversity conservationists with regard to ecosystem imbalance and diversity loss, as well as economic loss (Bajwa et al. 2016; Pyšek et al. 2020; Schaffner et al. 2020; Vila et al. 2011). Previous studies have revealed that numerous biotic factors (e.g., parasitism, competition, microorganisms and species richness) influence the invasion success of alien plants (Li et al. 2012; Omer et al. 2022; Reinhart and Callaway, 2006; Zhang et al. 2020). However, as few studies integrate these factors to study this issue, our understanding of all the factors that interactively affect invasion is still limited.

It is inevitable that alien plants will compete for resources with native plants when they reach their non-native range. Elton proposed that alien plants had greater competitive ability than native plants, and numerous studies supported it (Elton, 1958; Ragan and Erik, 2000). For instance, a previous meta-analysis revealed that alien species possess greater suppressive and tolerance abilities when they coexisted with natives (Golivets and Wallin, 2018; Kuebbing and Nunez, 2016). Therefore, competition has been regarded as a crucial factor in determining plant resistance and is recognized as a fundamental mechanism underlying the successful invasion of alien species (Callaway and Aschehoug, 2000; Inderjit and Van Der Putten, 2010).

Apart from direct competition, the biotic resistance hypothesis postulates that communities with higher native plant richness maintain greater community stability and resistance to prevent alien invasion (Elton, 1958; Levine et al. 2004; Wang et al. 2020). Perhaps communities with higher native richness have narrow niches or accumulate more native-range pathogens to prevent the naturalization of alien plants

(Zhang et al. 2020). Anthropogenic activities have created empty niches for alien plants through trade and construction, providing opportunities for entry. Moreover, the soil legacy effect of native richness has been overlooked. We predict that the soil legacy effect of richness may also inhibit alien plant invasion (Kuťáková et al. 2023).

Community resistance can also be regulated by the soil biota, but this topic is still unclear. The enemy release hypothesis predicts that alien species are not suppressed by pathogens due to the limited coevolutionary history of these organisms. Mitchell and Power (2003) found that invasive plants were actually released from fungal and viral pathogens in their non-native range. However, aliens would also be inhibited compared to native plants due to the limited number of mutualists, as confirmed by the *Pinaceae* invasion of Isla Victoria (Nuñez et al. 2009). Therefore, after the invasion of aliens, it remains unclear whether the soil microbial effects mentioned earlier is positive or negative.

Beyond soil microorganisms, the presence of aboveground parasitic plants may also play a crucial role in this process. Parasitic plants are widely occurred that extract nutrients, carbon and water from the host's roots or stems, which can have direct negative impacts on the growth, reproduction and survival of host plants (Bardgett et al. 2008; Brunel et al. 2020). Numerous studies have revealed that parasitism can indirectly increase biotic resistance to invasive plants through host plants (Dunn et al. 2012; Prider et al. 2009; Těšitel et al. 2020). Thus, parasitism also influences the community resistance of alien plants.

More importantly, the above four factors, both above- and belowground, might interactively affect communities. For instance, soil microbes might influence diversity-invasibility (Zhang et al. 2020), plant–plant interactions (Yan et al. 2022), and host-parasite interactions (Cai et al. 2023). Additionally, the competition between alien and native plants might also be influenced by factors such as parasitism (Mellado and Zamora, 2020) and soil legacy effects attributed to native plant richness (Li et al. 2023). Overall, further exploration is needed to understand how these four factors collectively shape community resistance.

Chromolaena odorata, a perennial herb, is a notorious invasive species in tropical and subtropical areas and has severely disrupted ecosystem biodiversity and integrity in China (Muniappan et al. 2009; Zheng et al. 2018). *Cuscuta chinensis* is a common holoparasite plant that obtains nutrients, water and other resources via the host stem and connected tissue from numerous wild or cultivated species (Donnapee et al. 2014; Jayasinghe et al. 2004). Some scientists have wanted to utilize *C. chinensis* to control its invasion and restrain its growth (Wan et al. 2010). We also observed that *C. odorta* was parasitized by *C. chinensis* in nature.

Here, we conducted a full factorial common garden experiment with *C. odorta* and two native plants (*Artemisia leucophylla and Desmodium sequax*) to address the following question: How do these four factors shape community resistance individually and interactively? We aim to explore whether the complex interactions within the community can successfully resist the invasion of alien plants. Simultaneously, this study contributes to a theoretical foundation for understanding the invasion of *C. odorta*.

2. Materials and methods

A greenhouse experiment was conducted at the Xishuangbanna Tropical Botanic Garden (21°56'N, 101°15'E), Yunnan Province, in China (Zheng et al. 2018). The experiment consisted of two phases, the details of which are described in Fig. 1.

2.1 Preparing and experimental set-up

2.1.1. Preparing phase

We constructed a field artificial community to condition soil with six species (*C. odorata* and five co-occurring native species) before the start of the experiment. The artificial community lasted three years (from 2019 to 2021) and consisted of three richness gradients in which *C. odorata* had invaded individually (heavily invaded), *C. odorata* with three native plants (moderately invaded), and *C. odorata* with five native plants (lightly invaded) (Yu et al. 2005). The richness of artificial community species was negatively related to invasion degree. The area of each community plot was 3 m × 3 m, with three replicate treatments. We collected topsoil (0–20 cm) from the various plots and sieved it with a 5 cm sieve. Then, half of the soil was sterilized by gamma rays, which could eliminate any living microbes, and the remaining half of the soil was kept with live microbes.

2.1.2. Experimental design

For the test species, we chose *C. odorata* and two co-occurring native species (*A. leucophylla* and *D. sequax*) as the study materials. In addition, we evaluated four factors: parasitism (parasite vs. non-parasite), soil resources with gradient richness (i.e., heavily, moderately, lightly), soil microbes (live vs. sterile), and competition (alone vs. together). The combinations of these treatments are shown in Fig. 1. For the competition treatment, one *C. odorata* and one native (*A. leucophylla* and *D. sequax*, respectively) seedlings were transplanted into plastic pots (diameter: 15 cm, height: 25 cm) at each richness gradient. After one month, the seedlings were in a stable growth phase, and we used *C. chinensis* to cultivate parasitism. The above treatments had four replicates, accounting for 240 pots in total.

Plant height was measured with a tape at mid-growth. All the aboveground branches and roots of the plants were harvested after six months and subsequently dried at 70°C for 72 h (DHG-9620A, Shanghai, China). We weighed the biomass with an electronic scale (ME2002E, Mettler-Toledo, CH) with an accuracy of 0.01 g.

2.2 Statistical analysis

To test the effects of soil microbes (live vs. sterile), parasitism (parasite vs. non-parasite), soil sources (richness gradient of the invaded community), and competition among species (alone vs. together), we constructed linear mixed effect models with the "*lme*" functions in the *nlme* package to analyze total biomass and plant height (Pinheiro et al. 2023). To improve the normality of the residuals of the models, total biomass and plant height were squared root and logit transformed, respectively. We included all the

main factors (microbes, soil source, parasitism, competition type, origin) and their interactions as fixed factors, and competition combinations were included as a random factor.

We also calculated the interspecific neighbor effect (NE_{inter}, ln response ratio). This index quantifies the influence of neighboring plants on a target plant and is calculated by the following formula:

$$NE_{inter} = \ln \frac{Mass_{inter\_k}}{Mass_{alone\_k}}$$

Where $Mass_{inter\_k}$ represents the biomass of the target plant under treatment k with competition and $Mass_{alone\_k}$ represents the biomass of the target plant under treatment k without competition (Mangla et al. 2011). Similarly, to further explain the interactions between different species under multiple factors, NE_{inter} was selected as the response variable, microbes, parasitism, plant origin, soil resources and their interactions were included as fixed factors, and competition combinations were used as random factors. We conducted post hoc multiple comparisons for model values among variables via the "*emmeans*" package (Lenth et al. 2023). An effect was considered significant if $P < 0.05$. In our study, we conducted all the statistical analyses and data visualization with R version 4.2.3 (R Core Team, 2023).

3. Results

3.1 Alien plants exhibit greater performance

Overall, we found that all the main factors (i.e., origin, richness, competition, parasitism and soil microbes) had significant influences on total biomass and plant height (Table S1). Alien plants tended to produce more total biomass than did native plants (+ 128.4%, Fig. 2a); the same trend was also found for plant height (+ 56.4%, Fig. 2b). However, when the plants were grown together, the inhibitory ability of the native plants on *C. odorata* was significantly greater than that of the alien plants on the native plants (Fig. S1, Table S2).

3.2 Individual effects of four factors on *C. odorata* invasion

In communities with soils of varying native richness that were invaded, we observed divergent biomass and height patterns between the alien and native plants (Fig. 3a, b). Both the biomass and height of the native plants exhibited a progressive rise with increasing species richness. Conversely, *C. odorata* had the weakest effect (on both biomass and height) on the soils with the highest richness gradient, as illustrated in Fig. 3a, b. Sterilization treatment significantly increased alien growth in terms of both biomass and height, while it had no significant influence on the native plants (Fig. 3c, d). Parasitism and competition significantly reduced the total biomass (-25.3%, -39.1%, Table S1 and Fig. 3e, f). Furtherly, parasitism treatment did not significantly affect the total biomass of the alien plants, whereas parasitism resulted in a notably reduced biomass of the native plants (Fig. 3e). Additionally, competition resulted in varying degrees of reduction in the biomass of alien (-30.2%) and native plants (-21%, Fig. 3f).

3.3 Interactive effects influence on *C. odorata* invasion

We also observed significant interactions of origin × microbes × parasitism and origin × competition × richness (Fig. 4, Table S1). We found that parasitism no longer led to a reduction in the biomass of alien plants when they were grown in sterile soil (alien: +2.3%, Fig. 4a). Although alien plants generally produced more biomass than native plants did, this advantage diminished when alien plants were grown in soil from the highest richness with competition (Fig. 4b).

3.4 Responses to the interactive effects of parasitism and soil resources, microbes and competition on plants

Additionally, there were other interactive effects for the above factors (parasitism × richness on both biomass and height, microbes × richness and microbes × richness on biomass) on both plants regardless of origin (Table S1, Fig. 5). Parasitism significantly suppressed plant growth in moderately and lightly invaded soil, while had significant influences on plant biomass and height in the heavily invaded soil treatment (Fig. 5a). Although plant height exhibited the same decreasing trend with biomass, soils with lower richness invasion were more susceptible to parasitic suppression (Fig. 5b). Additionally, although sterilization promoted plant growth regardless of the soil source, the positive effect was significantly greater in heavily invaded soil than in the other soils (Fig. 5c). While sterilized soils promoted plant growth but also were influenced by competition, monoculture plants (alone) produced more biomass (17.3%) than mixed plants (grown together) after sterilization (10.8%, Fig. 5d). For neighbor effects analysis, we noted that there were significant interactions involving four key variables: microbes, parasitism, origin, and native species richness (Fig. S2). There was a significant difference for aliens and natives in specific conditions (live soil and non-parasitic, sterilized and parasitic) in relatively high-rich soil. These phenomena revealed that the competitive advantage of native plants is amplified with an increasing in native richness within the soil. However, this effect was also influenced by the presence of the above parasitism and microbes (Fig. S2). However, further research is still needed to explore the underlying mechanism of these interactions.

4. Discussion

4.1 Individual effects on alien plant invasion

In our study, we found that *C. odorata* has greater growth performance, which could explain why it was listed as among the 100 worst invasive species (Daehler, 2003; Lowe et al. 2000) and why it was successful in China (Zheng et al. 2015).

Furthermore, our findings indicated that each of the four factors significantly mediated community resistance. The soil legacy effects of richness, competition, and microbes enhanced the community's resistance to *C. odorata*. In contrast, the parasitic plant *C. chinensis* appeared to facilitate the invasion of alien plants. Consistent with the biotic resistance hypothesis, we found that the soil legacy effects of native plants richness negatively impacted alien plants while simultaneously conferring benefits to native plants, which was consistent with the findings of previous research (Chen and Van Kleunen, 2022; Zhang

et al. 2020). This also highlights that while disturbances (such as logging and fire) may create aboveground vacant niches for alien plants, species richness still offers community resistance to these invasions through belowground mechanisms. In addition, our findings suggested that alien plants benefited more from sterilization than did native plants (Fig. 5a, b), and Cai et al. (2023) also found the similar results for *Alternanthera philoxeroides*. In our study, we speculated that sterilization might eliminate some specific soil pathogens for *C. odorata*, then they could capture more sunlight, water, nutrients and other resources due to their greater intrinsic growth rate, which was consistent with the findings of previous studies (Zhang et al. 2020). Moreover, our research indicated that competition remains a potent mechanism for preventing the spread of *C. odorata*. Although the evolution of increased competitive ability (EICA) hypothesis posits that alien species may evolve to become competitive after introduction (Oduor et al. 2017). Our findings suggested that controlling their spread was still effective when co-occurring natives were selected. In terms of parasitism, our study results exerted a more detrimental impact on native plants than on alien plants, which was consistent with Prider et al. (2009). There have also been studies examining the effects of parasitism on other invasive plants. For instance, Li et al. (2015) found that *C. australis* decreased the total biomass of *Bidens pilosa*, a pattern similarly observed in both *Mikania micrantha* and *Wedelia trilobata*. This disparity could be attributed to two key factors. First, parasitic plants may more readily extract nutrients from native species, which have a longer co-evolutionary history (Walder et al. 2018). Second, invasive species exhibit a relatively high intrinsic growth rate, rendering *C. chinensis* less effective at suppressing its growth (Yu et al. 2011). These insights shed light on the complex interactions between parasitic plants and their hosts, underlining the unique challenges posed by invasive species.

4.2. Interactive effects influence alien plant invasion

Furthermore, our study revealed that soil microbes could maintain their coexistence between *C. odorata* and native plants under parasitic pressure, while sterilization will tip their balance (Fig. 4a). The elimination of soil pathogens could no longer limit the capture ability for resources, this may help *C. odorata* alleviate parasitic pressure (Cai et al. 2023). Therefore, we hypothesize that the extensive use of fungicides in agriculture may inadvertently facilitate the spread of alien species under the pressure of *C. chinensis* in the future (Zubrod et al. 2019).

We also observed that the soil legacy effects of native plant richness on *C. odorata* was greater when *C. odorata* was grown with natives (competition), and there was no significant interaction between microbes and richness. Therefore, we speculated that soil characterized by a greater diversity of native plants may develop physical and chemical properties that were more beneficial to native vegetation. In exploring the biotic resistance hypothesis, previous researches have focused predominantly on how soil legacy effects, associated with species richness, impact the growth of alien plants and native species separately (Chen and van Kleunen, 2022; Li et al. 2023; Zhang et al. 2020). Our study provided insight into the context of competition between alien and native plants. Overall, our results suggested that combining soil from diverse plant communities with native flora might be a more effective strategy in curbing the invasion of alien plants.

4.3. Effects of complex interactions on plant performance

Additionally, we also found several other interactions that affected plant growth regardless of plant origin. There were significant interactions: richness × parasitism, richness × microorganism, and microorganism × competition. Generally, the parasitic plant *C. chinensis* suppressed host growth (biomass and plant height) at each richness level, while the results showed that parasitism had a negative effect on plants at higher richness levels than on those in soil from the *C. odorata* monoculture (Fig. 5a, b). A previous study elucidated that *C. odorata* could produce a potent allelochemical that had a strong negative effect on plant growth (Zheng et al. 2015). Based on these findings, we inferred that plants from *C. odorata* monocultures were suppressed mainly by allelochemicals rather than by parasitism. Our findings also indicated that sterilization had a more positive impact on biomass in monoculture soil than in monoculture soil, which suggested the possibility of accumulated pathogens resulting from the dense growth of *C. odorata* in monoculture conditions; these findings are also consistent with previous studies (Mangla and Callaway, 2008). Finally, our research revealed that sterilization promoted plant growth more when plants were grown alone than when grown under competitive conditions. This could be attributed to the fact that the soil resources in the pots were more abundant when grown as a single species compared to mixture.

5. Conclusion

In conclusion, our study revealed that the soil legacy effects of native plant richness, competition, microbes and parasitism each individually and interactively influence the invasion success of *C. odorata*. Notably, we discovered that native plants could thwart the invasion of *C. odorata* when the native soil legacy had a relatively high native diversity. Furthermore, we observed that alien plants might gain an advantage through parasitism, especially when soil microbes were absent. These findings underscore that the interplay of aboveground and belowground biotic factors is crucial in determining the success of invasive species. It is practical to further explore how different biological factors collaborate to shape a community's resistance to invasive species.

Declarations

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Author contributions

Mingbo Chen: Data curation, Writing- Original draft preparation. **WeiTao Li**: Conceptualization, Methodology, Data curation, Writing- Original draft preparation. **YuLong Zheng**: Visualization, Investigation, Writing- Reviewing and Editing.

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Competing Interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Figures

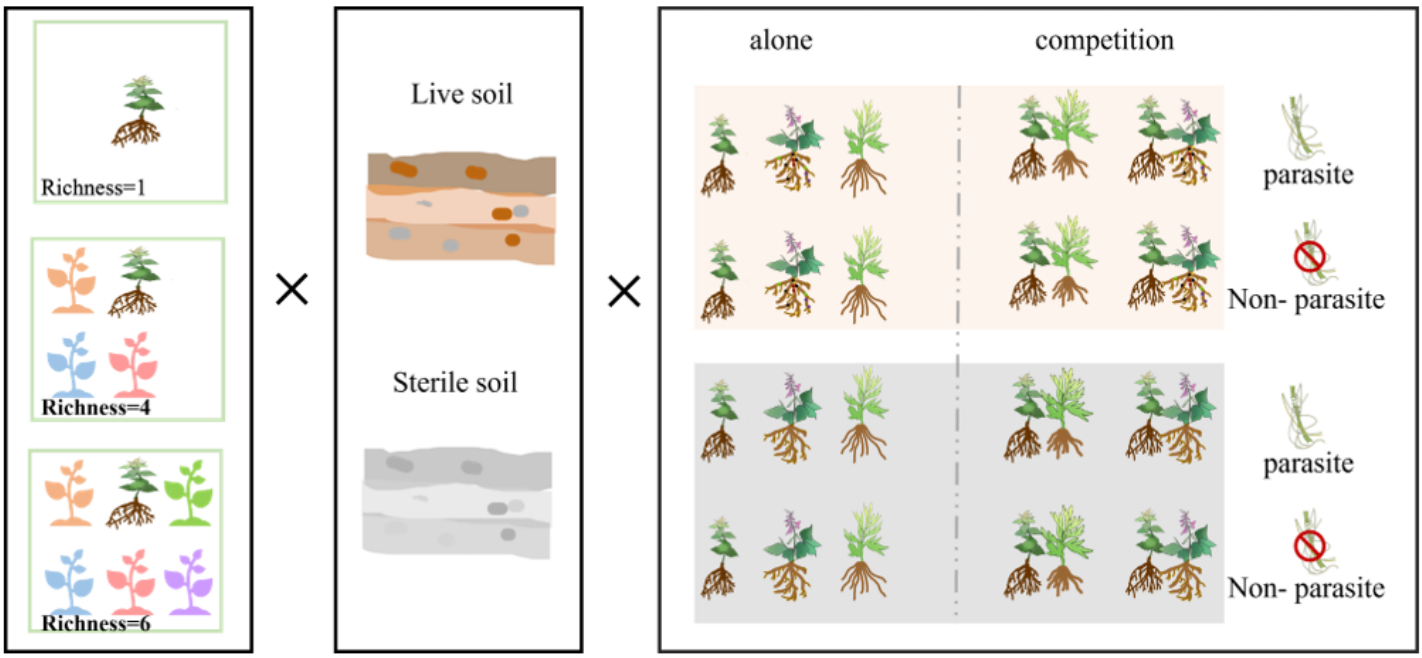

Figure 1

Conceptual diagram of the experimental design. Fully crossed factorial combinations of richness (i.e., heavily, moderately, lightly), microbes (live vs. sterile), parasitism (non-parasite vs. parasite) treatments were used within each plot that lived alone or lived together (competition).

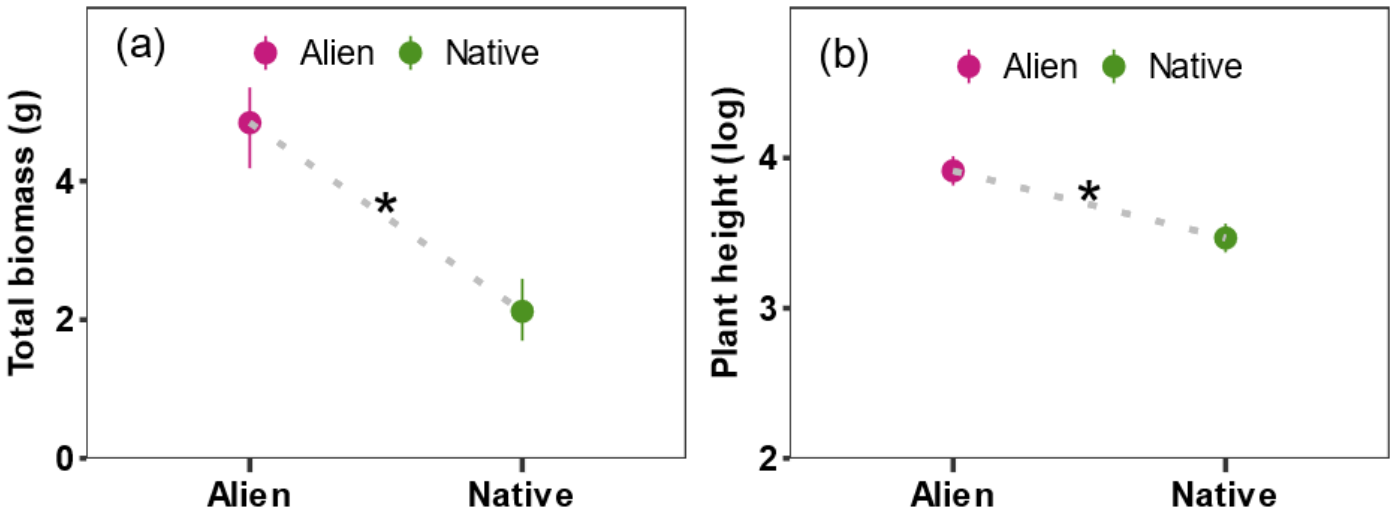

Figure 2

Different growth performances of alien plants and native plants. The panels show the effects of A, total biomass of alien and native species; B, plant height (log values) of alien and native species. The error

bars represent the means ± SE. (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.01$).

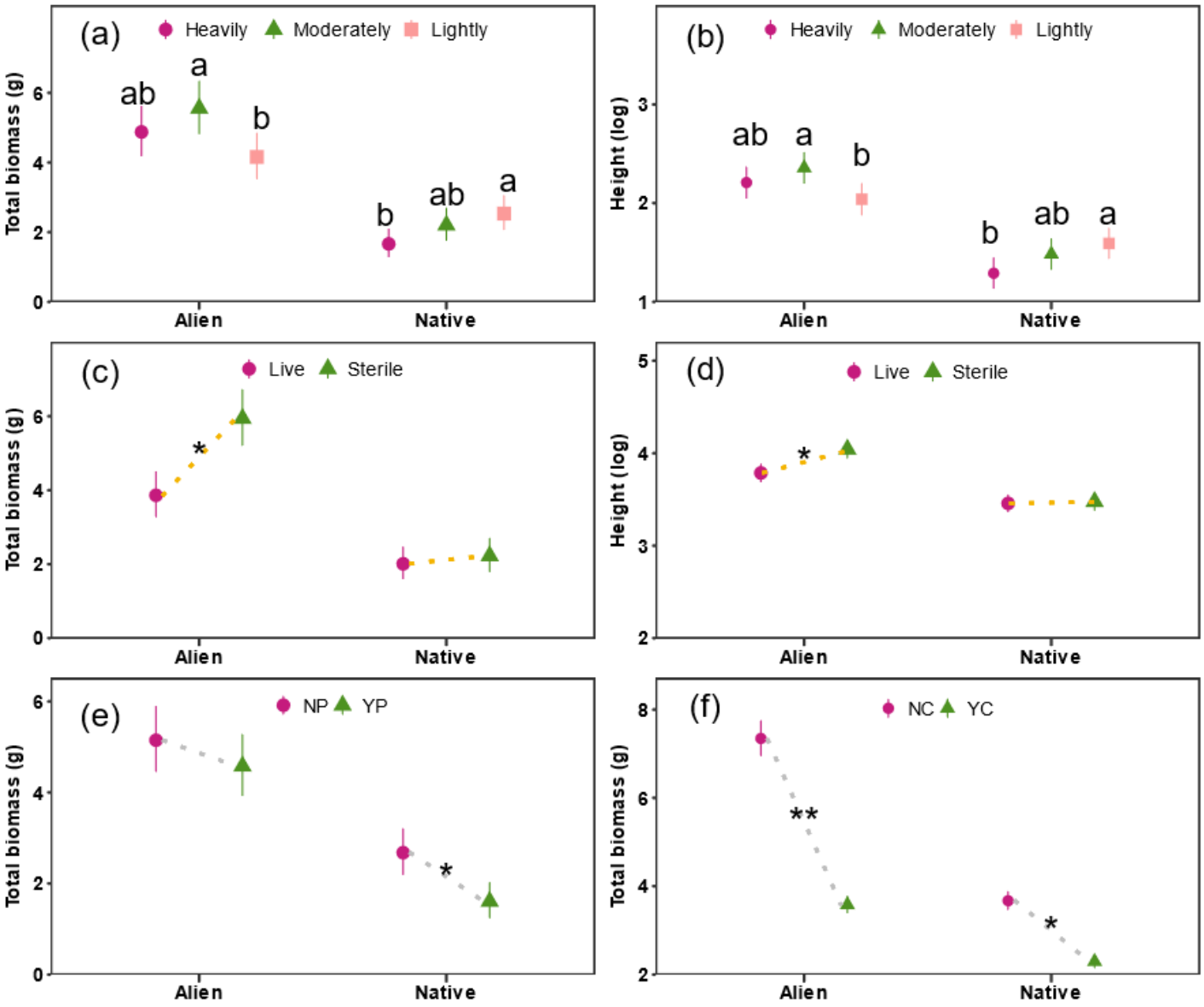

Figure 3

Total biomass and plant height (log values) of alien and native species under different richness levels (i.e., heavily, moderately, lightly), microbes (live vs. sterile), parasitism (NP: non-parasite, YP: parasite) and competition (NC: alone, YC: together). The panels show the effects of A, total biomass and richness; B, plant height and richness; C, total biomass and microbes; D, plant height and microbes; E, total biomass and parasitism; and F, total biomass and planting status. (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$).

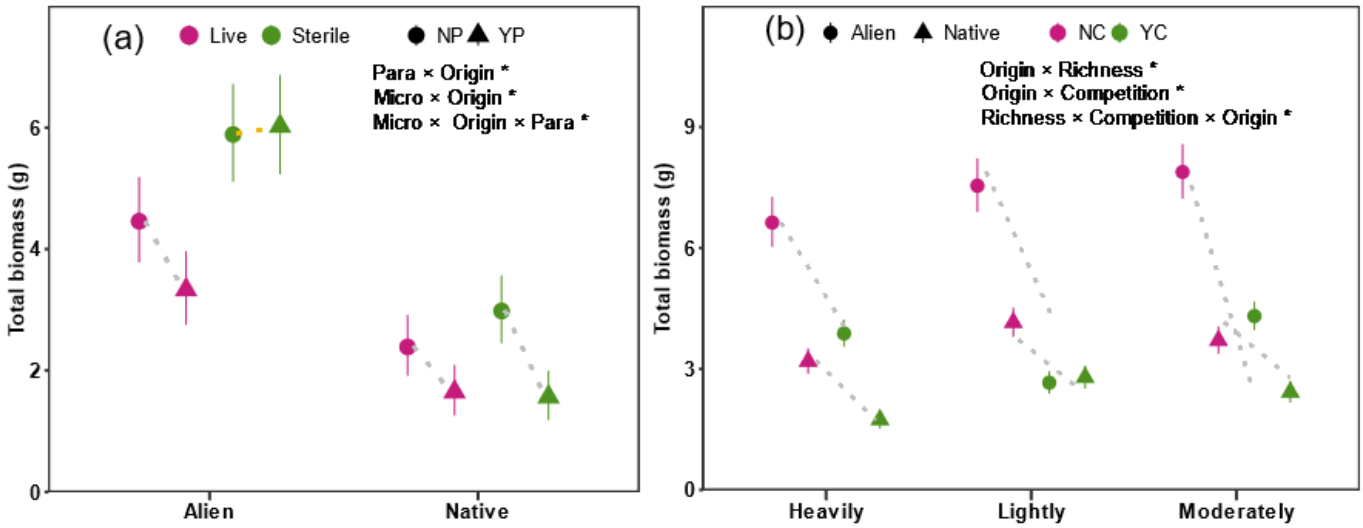

Figure 4

Total biomass of alien and native species under interactions of different richness (i.e., heavily, moderately, lightly), origin (native, alien) and competition (NC: alone, YC: together) treatments. The panels show the effects of A, origin, parasitism and microbes; B, origin, richness and competition.

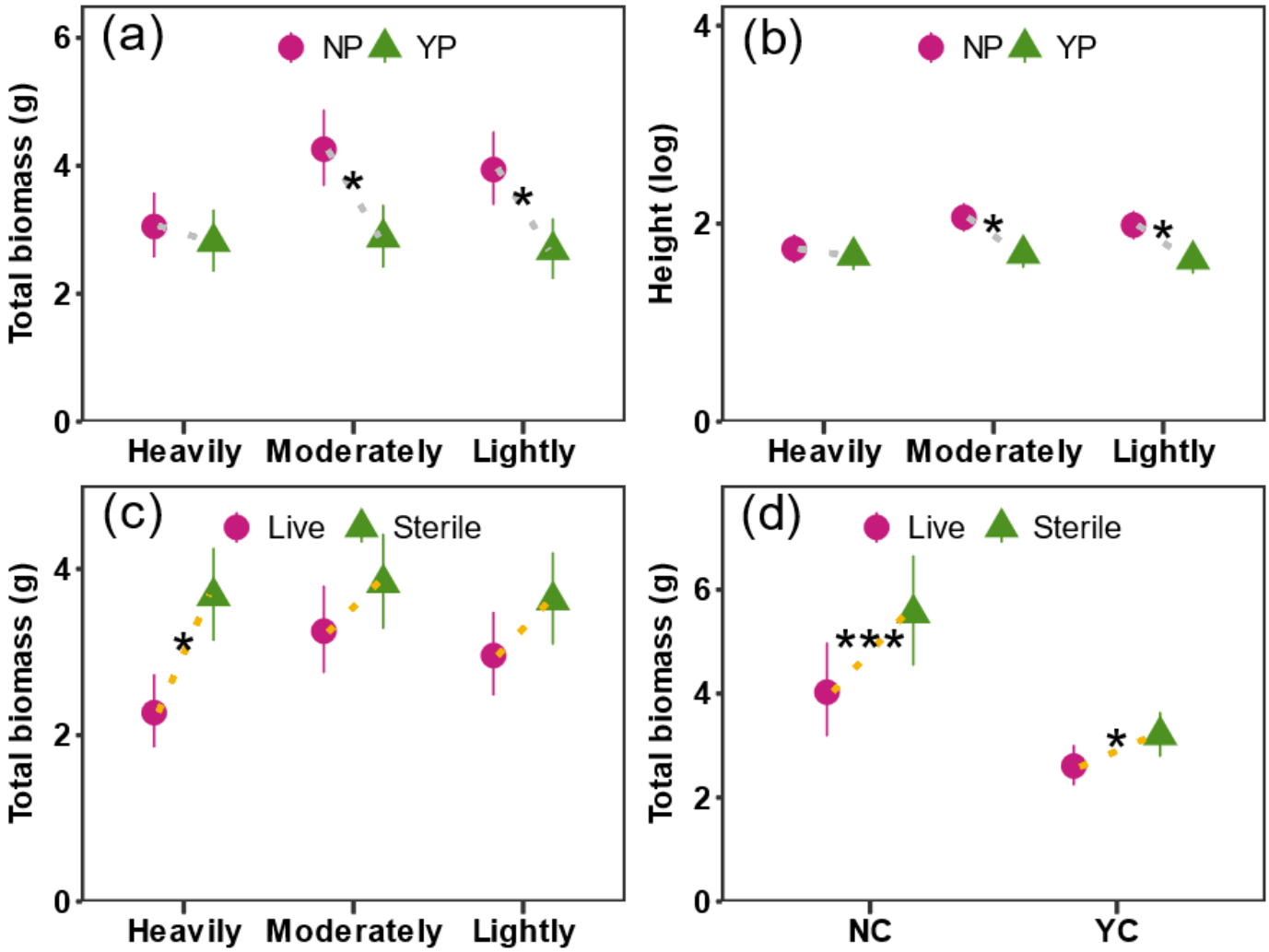

Figure 5

Total biomass of plants under richness (i.e., heavily, moderately, lightly)and parasitism (NP: non-parasite, YP: parasite), microbes (live vs. sterile) and competition (NC: alone, YC: together) treatments. The panels show the effects of A, the interaction of richness and parasitism; B, the interaction of richness and parasitism on plant height; C, the interaction of richness and microbes; and D, the interaction of microorganism and competition. (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$).

Supplementary Files

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