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Soil legacy effect of extreme precipitation on a tropical invader in different land use types

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ABSTRACT

Land use change and extreme precipitation are the main challenges for tropical forests, and numerous studies have indicated that these changes could affect soil ecology. However, it is not yet known whether the soil legacy effect of ongoing changes could influence the invasiveness of alien plants. Two mixtures of invader and native species (*Chromolaena odorata-Artemisia leucophylla* and *C. odorata-Desmodium sequax*) were transplanted to 18 soil treatments (3 forest types × 3 pre-water supply levels × 2 microorganism treatments). The results showed that the biomass of the invader was greater while its biomass fraction was lower in secondary forest soil than in primary and rubber forest soil; the soil legacy effect of drought was positive on both the biomass and biomass fraction of *C. odorata*. In rubber plantation soil, the biomass and biomass fraction of *C. odorata* were enhanced by the pre-increased water supply level. In primary and rubber forests, compared with normal precipitation, the sterilization treatment increased the biomass of the invader under drought and increased precipitation. The nutrient cycle and microorganisms both played a crucial role in this process. Overall, our study demonstrated the pronounced soil legacy effect of land use change, extreme precipitation and their interactions on the invasion success of *C. odorata*.

1. Introduction

It is widely accepted that the stronger biotic resistance to plant invasion is due to the fewer vacant niches in tropical Asia (van Kleunen et al., 2015). However, accelerating global change, characterized by land use change (Hansen et al., 2013) and extreme precipitation (Ge et al., 2021), has emerged as a challenge for tropical forests in Southeast Asia. Thus, more empty niches might be generated under the ongoing global scenarios mentioned above by altering soil conditions, such as water supply (Wu et al., 2011), nutrient availability (Lado-Monserrat et al., 2014) or microbial community composition (Kaisermann et al., 2017). Whether land use change and extreme precipitation influence plant invasiveness remains unknown in tropical forests.

Land use change, characterized by deforestation, plantation and urbanization, is a major global issue (Foley et al., 2005). Domenech et al. (2005) found that the distribution of the invader *Cortaderia selloana* could be related to historical land use change. Despite the fact that rubber plantations and deforestation are common phenomena in Southeast Asia (Hurni and Fox, 2018; Margono et al., 2014), few studies have evaluated their influence on plant invasion. In fact, the influence of land use change on soil properties might facilitate the invasion success of alien plants. For instance, Zhu et al. (2019) suggested that nutrient return was increased in secondary forests but decreased in rubber plantations relative to primary forests. A vast number of studies have elucidated that alien plants benefit more from nutrient fluctuations than native species (Davis et al., 2000; Parepa et al., 2013). Thus, experimental manipulations are still needed to test how land use change influences plant invasion.

Numerous studies have simulated the effect of extreme precipitation on invasive plants during the growth season (Gilgen et al., 2010; Duell et al., 2016). Indeed, extreme precipitation is also likely to occur in spring or winter (non-growing season) (Zhai et al., 2005). The soil legacy effect of changed precipitation before growth might play a crucial role in successful invasion. Whereas only a few studies have tested this hypothesis (Meisner et al., 2013), more studies are still needed to explore the influence of the abnormal water supply on plant invasion.

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Increasing research has begun to pay attention to plant invasion mediated by soil nutrient availability (Liu et al., 2017; Uddin and Robinson, 2018) and microorganisms (Mangla et al., 2008; Zhang et al., 2020) in recent decades. As mentioned above, land use change and extreme precipitation are known to affect soil nutrient availability and the microorganism community (Gionchetta et al., 2019; Faggioli et al., 2019), and there was also an interactive effect between the two factors (Moreno et al., 2019). Therefore, the analysis of the nutrient cycles and manipulations of microorganisms could further our understanding of associated mechanisms during the process of invasion.

Chromolaena odorata (Asteraceae), originating from North, Central and South America, is a semi lignified perennial subshrub and is a noxious plant worldwide (Galdini Raimundo et al., 2007). In the middle of the 19th century, *C. odorata* was first introduced to India and now has become one of the most invasive plants in southern China (Qin et al., 2013). A full factorial experiment was conducted to test the soil legacy effect of extreme precipitation and land use change on the absolute and relative biomass production. The invader *C. odorata* was mixed separately with two common co-occurring native species in the soil, exposed to three water supply levels (drought, normal, rainfall) and two soil microorganism treatments (ambient and sterile) collected from three forests (primary, rubber and secondary forests). The following hypotheses were proposed: (1) the soil legacy effect of extreme precipitation, forest type and their interaction would influence the absolute and relative biomass production of *C. odorata*, and (2) soil nutrients and microorganisms both played a crucial role during the invasion process.

2. Material and methods

2.1. Study site and species

This experiment was conducted in a greenhouse of Xishuangbanna Tropical Botanical Garden (21°56′ N, 101°15′ E), Yunnan Province, Southwest China. The average annual temperature is 21.7 °C; the hottest month is July (average temperature 25.3 °C), while the coolest month is January (average temperature 15.6 °C). The annual average precipitation is approximately 1557 mm, with a dry period lasting from November to April (Zheng et al., 2015).

2.1.1. Plant materials

The seeds of *C. odorata* and two native species (*Artemisia leucophylla* and *Desmodium sequax*) were collected from Xishuangbanna in 2019. The two residents are common co-occurring species with *C. odorata* at the collection site. In April 2020, seeds were mixed uniformly from different individuals and then germinated in a plastic tray (42 cm × 42 cm × 4 cm) filled with potting soil (Pindstrup, Danish).

2.2. Experimental design

The common garden experiment, consisting of three forest soil types (primary, rubber, secondary), three water supply levels (reduced, normal and increased precipitation) and two soil microbiome treatments (ambient and sterilized), was set as follows (Fig. 1). In May 2020, three types of forest soil were collected from the upper 20 cm in primary, rubber, and secondary forests. The sampled soil at each site was homogenized and then sieved through a 5-mm mesh to remove the plant residuals and coarse fragments. In terms of water supply treatments, no water (drought), normal water supply (control, 24 mm/2 day), and increased water supply (rainfall, 48 mm/1 day) were applied for 40 days (2020.5.9–2020.6.18). Since then, the soil was rewetted to normal moisture. Half of the pots were sterilized by applying dazomet (Aladdin, Shanghai, China).

In July 2020, two pairs of seedlings (*C. odorata-A. leucophylla* and *C. odorata-D. sequax*, approximately 10 cm in height) were transplanted into plastic pots (23 cm in diameter, 22 cm in height), and all pots were watered 24 mm/time. There were 288 pots in total, with 8 replicates of each treatment in two pairs.

2.3. Measurements

Before transplanting, the soil organic carbon (C) content and available nitrogen (N) and phosphorous (P) contents of the three forest types under the three water supply levels were determined using the routine methods described by Lu (1999) (N = 3). Of these, the soil organic C was determined by $K_2Cr_2O_7$-H_2SO_4 oxidation; available nitrogen was determined by the alkaline solution diffusion method; and available phosphorus was determined by the $NaHCO_3$ extraction colorimetric method. All plants were harvested in December 2020. For each individual, the total biomass was weighed after being dried at 60 °C (72 h). The biomass fraction was calculated as the total biomass of the invader/the total biomass of each pot (invader + paired native).

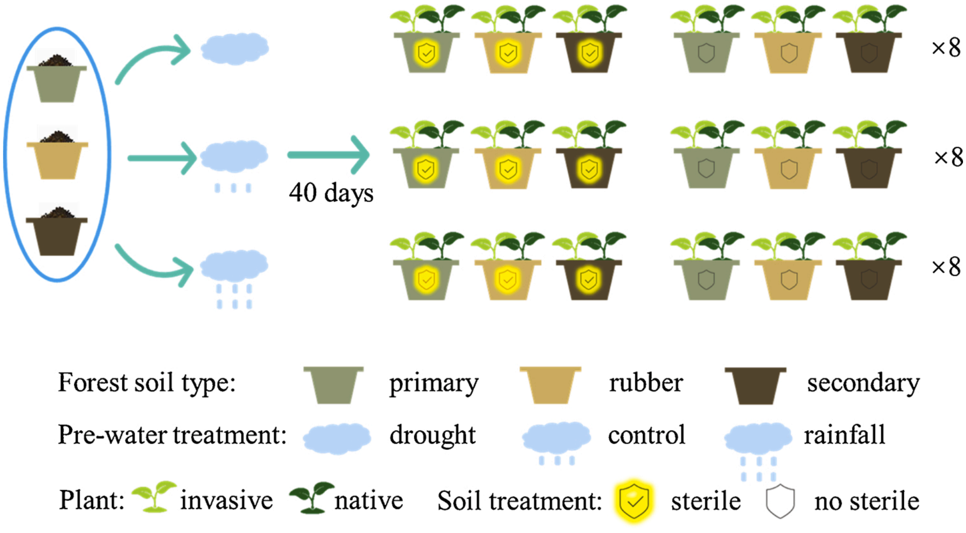

Fig. 1. Graphical illustration of the experimental design. The common garden experiment consisted of three types of forest soil (primary, rubber, secondary forests), three water supply treatments (drought, control, rainfall), and two treatments for soil microorganisms (with or without dazomet). There were 288 pots in total with 8 replicates of each treatment in two combinations (*C. odorata* vs. *A. leucophylla*; *C. odorata* vs. *D. sequax*).

2.4. Statistical analysis

All statistical analyses were conducted in R version 4.0.4 (R Core Team, 2021). Two-way ANOVAs were used to test for the effects of forest soil type, pre-water supply and their interaction on soil organic carbon (C) content, available nitrogen (N) and phosphorous (P) content. Tukey's HSD tests were used for multiple comparisons when the ANOVA results were significant. To test the soil legacy effect of forest type, extreme precipitation was applied to the biomass production of *C. odorata*. Two linear mixed models, in which total biomass and biomass fraction were response variables were implemented in the study, forest soil types, precipitation patterns, sterile treatments and their interaction effect were treated as fixed factors, and the combination (*C. odorata* - *A. leucophylla*; *C. odorata* - *D. sequax*) was treated as a random factor. Total biomass was square root transformed to improve the normality of residuals. Analysis was carried out using the lme function in the nlme package (version 3.1–152) (Pinheiro et al., 2021). Post hoc tests for multiple comparisons of biomass production across different levels of each factor were carried out in the emmeans package (version 1.5.4) (Russell, 2021).

3. Results

Averaged across all water supply treatments, the soil organic carbon content and available phosphorous content were both highest in secondary forest among the three forest types (Fig. 2a and b). Compared with the normal water supply, the pre-drought treatment increased the available phosphorous content (16.0 %) (Fig. 2c) but reduced the available nitrogen content (-11.2 %) (Fig. S1); however, the effect of the pre-rainfall treatment on phosphorous and nitrogen availability was not significant (Figs. 2c and S1).

The forest soil type ($P < 0.01$), precipitation ($P < 0.01$), sterile treatment ($P < 0.01$), and the interactions of forest × sterile ($P < 0.01$) and forest × precipitation ($P < 0.05$) had significant effects on the absolute and relative biomass of the invader (Table 1). However, sterile × precipitation ($P = 0.0559$) and forest × sterile × precipitation ($P = 0.0533$) had marginally significant effects on the biomass of *C. odorata* and had no significant influence ($P > 0.1$) on its biomass fraction (Table 1).

Chromolaena odorata had a greater total biomass (10.3 %) but a lower biomass fraction (-24.7 %) in secondary forest soil than in primary forest and rubber plantation soil (Fig. 3a, d). Compared with the normal water supply treatment, pre-drought significantly increased the total biomass (12.9 %) and biomass fraction (14.8 %) of the invader, whereas pre-rainfall had no significant influence on these values (Fig. 3b, e). On average, sterilization significantly increased the biomass (21.1 %) and biomass fraction (9.1 %) of the invader (Fig. 3c, f).

Table 1
Results from the linear mixed model (species pair as a random factor) presenting the effects of forest soil type, soil microorganism and precipitation treatment on the total biomass and biomass fraction (square root scale) of *Chromolaena odorata*. Bold values indicate that these effects are significant ($P < 0.05$), and underlined values are marginally significant ($P < 0.1$).

Source	df	Total biomass of *C. odorata*		Biomass fraction of *C. odorata*	
		F	*P*	*F*	*P*
Forest	2	9.491	**0.0001**	53.269	**<0.0001**
Sterile	1	87.262	**<0.0001**	11.790	**0.0005**
Precipitation	2	17.223	**<0.0001**	7.295	**0.0003**
Forest × Sterile	2	17.749	**<0.0001**	8.255	**0.0008**
Forest × Precipitation	4	4.512	**0.0015**	2.689	**0.0259**
Sterile × Precipitation	2	2.916	0.0559	0.427	0.6579
Forest × Sterile × Precipitation	4	2.366	0.0533	0.636	0.5084

In the secondary forest soil, the invader produced more total biomass (21.9 %) and biomass fraction (10.1 %) in response to pre-drought treatment than the primary forest soil (Fig. 4a, b). In the rubber plantation soil, the pre-rainfall treatment increased the biomass (14.4 %) and biomass fraction (15.4 %) of the invader relative to normal precipitation (Fig. 4a, b). Furthermore, *C. odorata* tended to increase its biomass (10 %) under the drought treatment, while its biomass fraction was not affected in rubber plantation soil (Fig. 4a, b).

In the rubber plantation soil, sterilization increased biomass production for the invader (15.1 %) but did not influence its biomass fraction (Fig. 5a, b). The sterilization of secondary forest soils resulted in 40.7 % and 31.4 % increases in the biomass and biomass fractions of *C. odorata,* respectively (Fig. 5a, b). Further analysis revealed that in the secondary forest soil, sterilization increased the total biomass of *C. odorata* irrespective of the water supply level, while its biomass was not affected by sterilization under extreme precipitation (drought or rainfall) in primary and rubber forests (Fig. 6a–c).

4. Discussion

It has been frequently suggested that secondary forests might be susceptible areas due to the fluctuating resource hypothesis (Davis et al., 2000). In contrast, we found a higher biomass but lower biomass fraction of *C. odorata* in the secondary forest soil (Fig. 3a and d). A higher soil organic carbon content and available phosphorous were found in the secondary forest (Fig. 2a and b), and both the biomass and biomass proportion were increased by sterilization in this kind of soil (Fig. 5a and b). Therefore, higher nutrient availability could benefit both invaders and native species in secondary forests, while the invader was

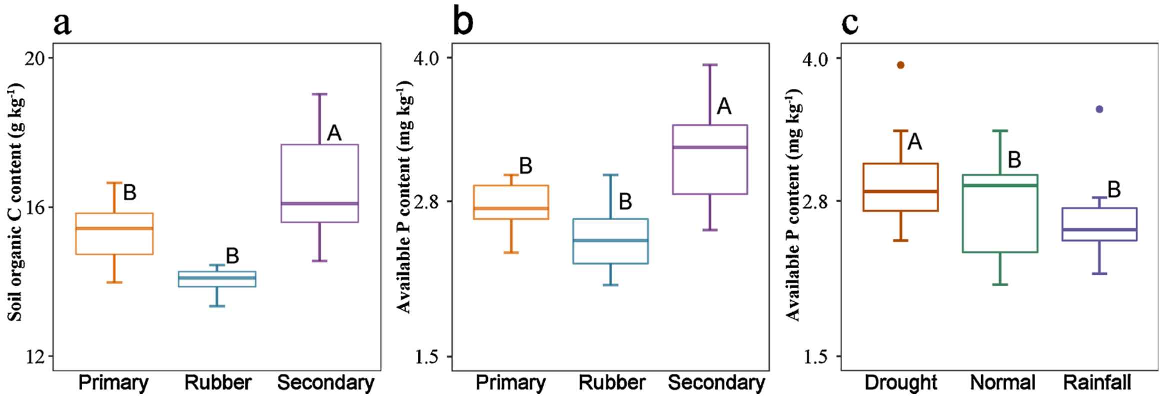

Fig. 2. Box plot of averaged soil organic C (carbon) content and averaged available P (phosphorous) content under three types of forest soil (a, b) and averaged available P content of three water supply levels (c). Letters indicate significant differences ($P < 0.05$). In the box plots, the upper boundary of each box indicates the 25th percentile, the horizontal line inside each box marks the median, and the lower boundary of the box indicates the 75th percentile.

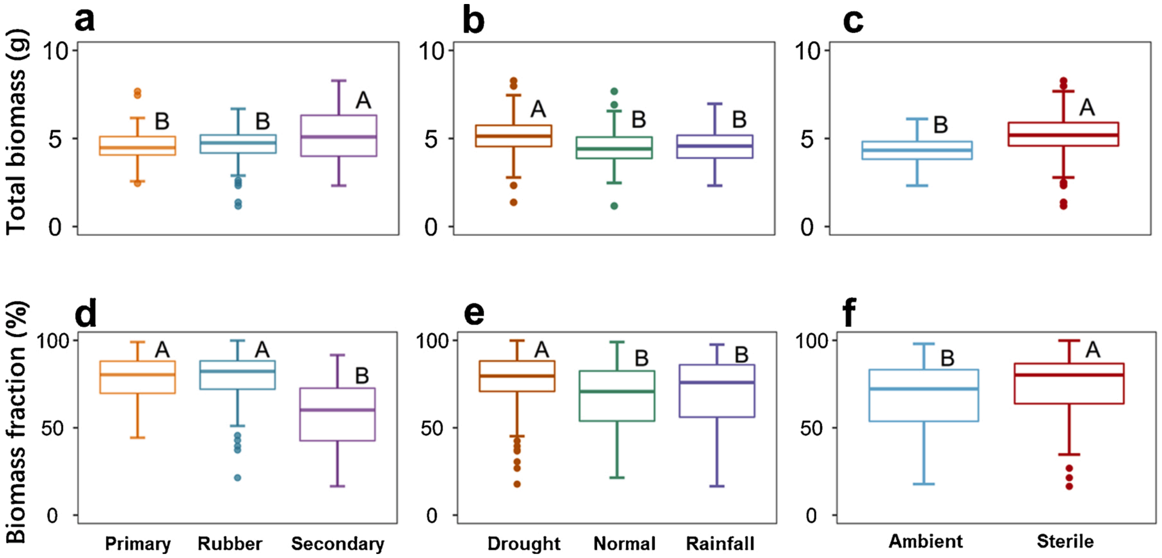

Fig. 3. Box plot of averaged total biomass and its fraction of *C. odorata* under three types of forest soil (a, d), precipitation (b, e) and two soil treatments (c, f). Letters indicate significant differences ($P < 0.05$). In the box plots, the upper boundary of each box indicates the 25th percentile, the horizontal line inside each box marks the median, and the lower boundary of the box indicates the 75th percentile.

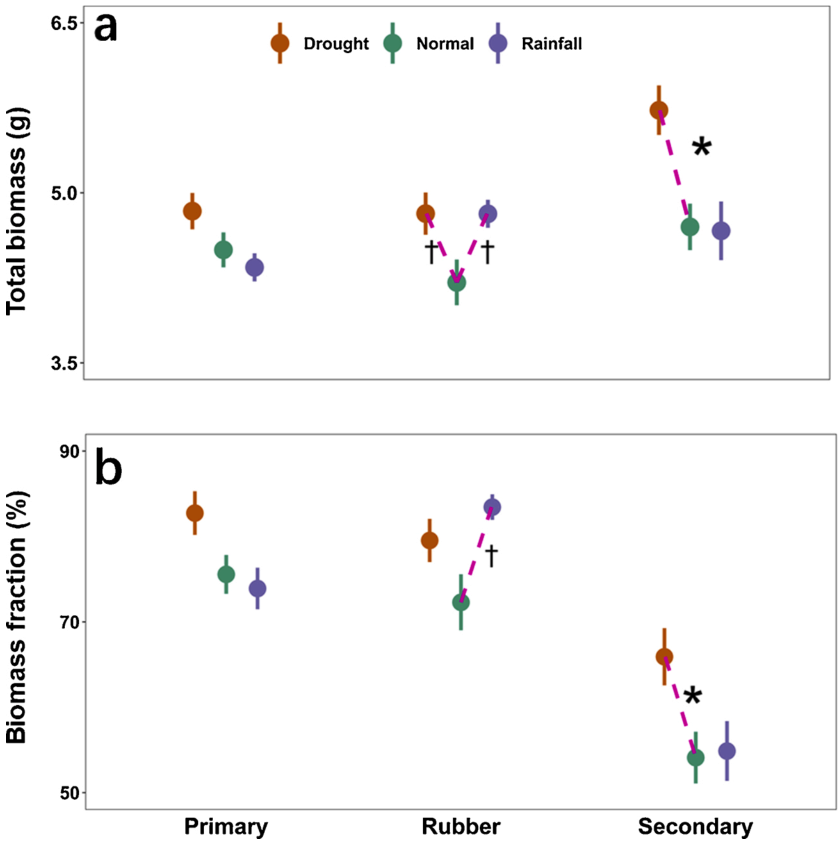

Fig. 4. Mean values of averaged total biomass of *C. odorata* under three precipitation patterns in three forest soil types (a). Mean values of the averaged biomass fraction of *C. odorata* under three precipitation patterns in three forest soil types (b). Error bars (SEM). The significant effects ($P < 0.05$) are marked with an asterisk, and marginally significant effects ($0.05 \le P < 0.1$) are marked with a dagger according to *post hoc* tests.

suppressed by microorganisms more than native species were, which could explain this interesting phenomenon. Thus, microorganisms in secondary forest soil might be a key factor mediating the coexistence of invaders and native species, and more studies are still needed to test the associated mechanism.

In terms of the soil legacy effect of extreme precipitation, sterilization increased the total biomass of the invader regardless of the water supply (Fig. S2), and there was also no significant interactive effect of precipitation × sterilization on the biomass fraction (Table 1). One potential explanation is that the legacy effect altered nutrient availability. Most studies focused on the influence on the nitrogen cycle (Meisner et al., 2013; Yang et al., 2020). Unlike these studies, our study

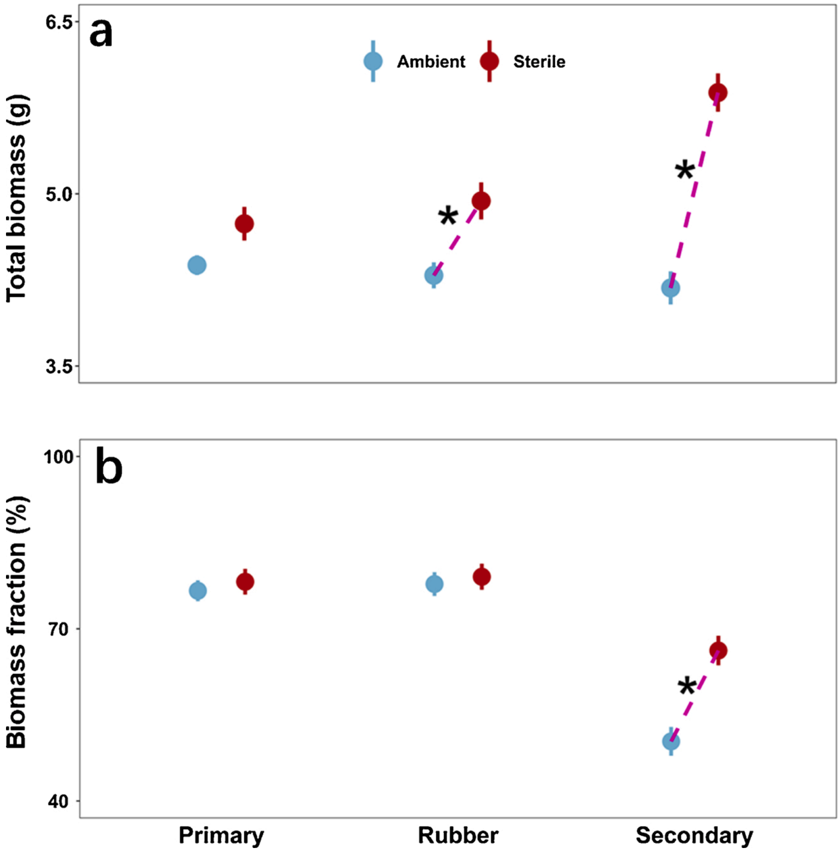

Fig. 5. Mean values of averaged total biomass of *C. odorata* under two soil treatments in three forest soil types (a). Mean values of the averaged biomass fraction of *C. odorata* under the two soil treatments in the three forest soil types (b). Error bars (SEM). The significant effects ($P < 0.05$) are marked with an asterisk according to *post hoc* tests.

found increased phosphorous availability in response to pre-drought treatment, which could explain the greater biomass and biomass fraction of *C. odorata* in response to pre-drought treatment (Fig. 3b and e). First, phosphorous is a stronger limiting factor in tropical forests than the nitrogen content (Vitousek et al., 2010), and a previous study also found that the competitive advantage of *C. odorata* was enhanced when phosphorous availability was increased (Wang et al., 2006). More importantly, pervasive phosphorus limitation has been suggested in natural terrestrial ecosystems (Hou et al., 2020). Thus, the soil legacy effect of abnormal precipitation on an altered phosphorous cycle might play a crucial role in alien plant invasion, and this complex process might be mediated by microbial activities, such as microbial biomass phosphorous and microbial respiration under drought stress (Bagheri-Novair et al., 2020). However, the further studies are still required.

Meanwhile, we found that the legacy effect of extreme precipitation affects the biomass and biomass fractions of the three types of forest soil differently (Table 1, Fig. 4). In the rubber plantation, the biomass and biomass fraction of *C. odorata* under rainfall was greater than that under the control treatment (Fig. 4). However, there were no significant interactive effects of forest × precipitation on soil nutrients and forest × precipitation × sterile on invader biomass (Table 1 and S1), meaning that nutrients and microorganisms may not be the main drivers explaining the interactive effect of precipitation and forest soils. Based on this, there might be other ways to mediate invasion under extreme rainfall in rubber plantations, such as altered soil acidity (Ding et al., 2019) and soil aggregate stability (Liu et al., 2021). *C. odorata* produced higher biomass but an unsignificant biomass fraction difference in rubber plantations (Fig. 4), suggesting that resident species took a similar advantage from the legacy effect of drought in rubber plantation soils.

On average, we found that sterilization enhanced the higher biomass and biomass fraction of the invader (Fig. 3c and f), suggesting that the overall effect of microorganisms was more negative for the growth of the invader in the mixture. This could be due to pathogens′ direct effects on plants by reducing their productivity (Hodge and Fitter, 2013). Further analysis revealed that the biomass of *C. odorata* increased significantly via sterilization under the two extreme precipitation treatments in the secondary forest but not in the two other forests (Fig. 6). This suggested the weak resistance and resilience of soil microorganisms to extreme precipitation in primary and rubber forests. Despite the lack of direct evidence for this phenomenon, we speculated that the higher nutrient availability (Fig. 2) and plant richness might contribute to the higher microbial community stability in secondary forests than in the two other forests (Royer-Tardif et al., 2010; Hueso et al., 2012). Thus, in the future, we need to analyse and compare the microbial community among different forest soil types.

5. Conclusions

Our study highlighted that pre-drought could increase the available phosphorus content in phosphorus-limited soil, which could be a driver of plant invasion, especially in secondary forests, while increased precipitation could promote invasion in rubber plantations. The biotic legacy effects of extreme precipitation events decreased the invasiveness of *C. odorata* in secondary forest soil; however, this effect was alleviated in primary forest and rubber forest soils. The mechanisms related to microbial communities, nutrient cycling, and other soil processes remain to be tested in the future.

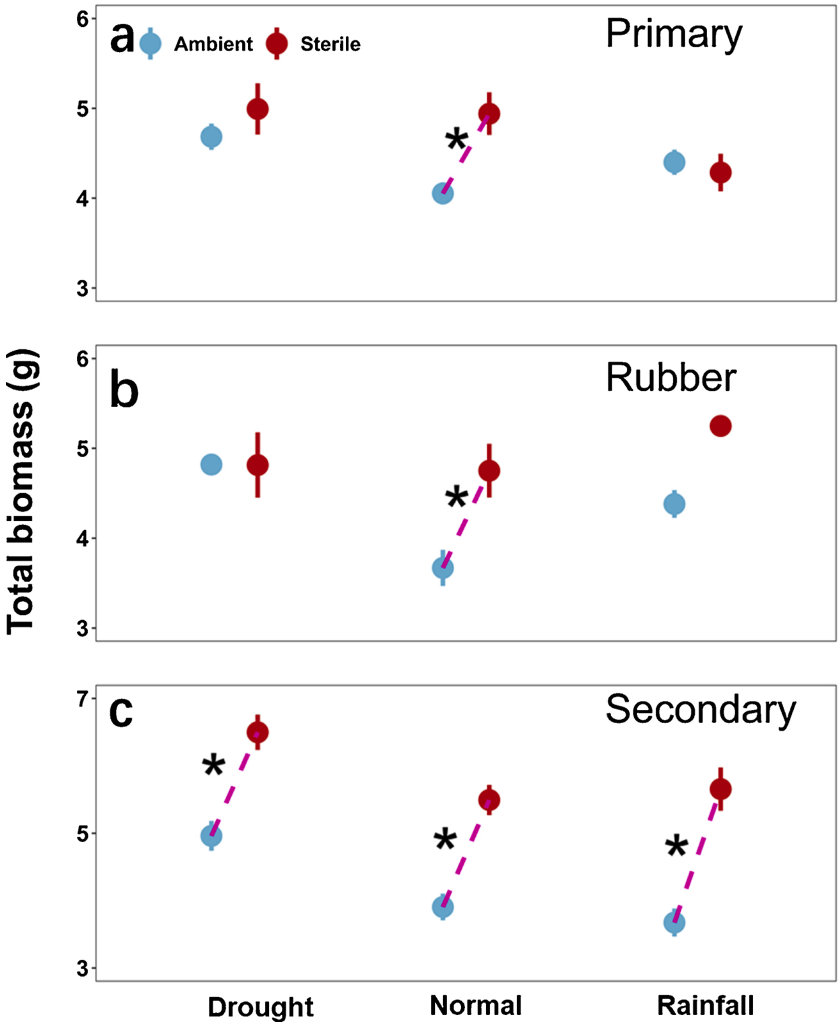

Fig. 6. Mean values of averaged total biomass of *C. odorata* of two soil treatments under three precipitation patterns in primary forest (a), rubber plantation (b) and secondary forest (c). Error bars (SEM). The significant effects ($P < 0.05$) are marked with an asterisk according to *post hoc* tests.

Author statement

Xiong Shi: Data curation, Writing- Original draft preparation. **Wei Tao Li**: Conceptualization, Methodology, Software. **Yu Long Zheng**: Visualization, Investigation, Writing- Reviewing and Editing.

Declaration of Competing Interest

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

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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.2021.104625.

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