INTRODUCTION

Ground-level ozone (O₃) is one of the most threatening components of global change that causes more damage to plants than any other air pollutant (Atkinson & Arey, 2003; IPCC, 2014; Krupa & Kickert, 1989). Ground-level O₃ concentration has increased from approximately 10 ppb in the late 1800s to greater than 40–50 ppb now (Brauer et al., 2016; Monks et al., 2015) mainly owing to the increased concentrations of nitrogen oxides, volatile organic compounds, and radical precursors responsible for its production (Atkinson & Arey, 2003; Tarasick et al., 2019; Yeung et al., 2019). The tropospheric O₃ concentration is increasing globally and is projected...
to reach 85 ppb by 2100 (IPCC, 2014). Consequently, research on the effects of O₃ pollution on ecosystems has garnered considerable interest in ecology.

Adverse effects of tropospheric O₃ on plants have been broadly documented (Agathokleous et al., 2020; Burkey et al., 2020; Grukle & Heath, 2020; Sicard et al., 2017). As plant leaves are most exposed to elevated O₃, they become the main places of phytotoxic effects of O₃ on plant. Ozone can enter into plant via the stomata and then react with unsaturated biomolecules to form reactive oxygen species initially causing programmed cell death and visible injury (Vainonen & Kangasjärvi, 2015). Such visible foliar O₃ injury is an unequivocal sign of phytotoxic O₃ levels (Paolletti et al., 2019), and is the only indicator of adverse effects of O₃ that can be used for routine field surveys (Sicard et al., 2016). Such injuries often appear as chlorosis, necrosis, spots and bronzing (Agathokleous et al., 2020). Some studies suggested that visible foliar injury could be associated with not only plant susceptibility (Bergmann et al., 2017; Davison & Barnes, 1998; Li et al., 2016) but also negative impacts on fitness traits (Marzuoli et al., 2019). In agricultural ecosystems, the influence of elevated O₃ on crop species has received much attention and is well understood, especially the effect on yield reduction (Ainsworth, 2017; Tai et al., 2014; Wilkinson et al., 2012). However, few studies have focused on studying the potential influence of O₃ on other important ecological processes that occur frequently in non-management regions, such as plant invasion.

Plant invasions, similar to O₃ pollution and many other components of global change (Steffen et al., 2011), have started to rapidly increase from the last century, and the number of naturalized alien species is still increasing (Seebens et al., 2017,2020). It is frequently assumed that plant invasion could interact with, and thus be affected by other components of environmental changes (Bradley et al., 2010; Dukes & Mooney, 1999; Liu et al., 2018). Indeed, a recent meta-analysis by Liu et al. (2017) showed that CO₂ enrichment and global warming increase the growth more strongly for invasive alien plants than for native species, and thus might promote plant invasion. On the other hand, many non-invasive alien plant species under current environmental conditions may become invasive with ongoing global changes (Dullinger et al., 2017; Haeuser et al., 2017; Speiβer et al., 2021; Walther et al., 2009). Therefore, given that the O₃ pollution varies across large scale (e.g. O₃ pollution in China; Figure S1), understanding its potential effects on plant invasion is important for the strategic management of increasing risks of such plant invasions in future.

Due to high phenotypic plasticity, invasive plants often exhibit broad environmental adaptation, and thus often show high fitness in altered environmental conditions (Davidson et al., 2011; Richards et al., 2006). Consequently, invasive species might be more adaptable to elevated O₃ than native species. Indeed, the very limited studies established in cropping systems showed that problematic weeds (i.e. Amaranthus tuberculatus, Amaranthus palmeri, and Cyperus esculentus) are more tolerant to elevated O₃ or can even benefit from elevated O₃ compared with co-occurring crop species. This suggests that increasing O₃ pollution can exacerbate these invasions in agricultural cropping systems (Grantz et al., 2019; Grantz & Shrestha, 2006; Paudel et al., 2016; Shrestha & Grantz, 2005). Nevertheless, based on the weed–crop experiments limited to agricultural systems, it is still difficult to determine the general pattern of elevated O₃ effects on alien plant invasion because agricultural systems are not natural plant communities and crop species are usually selected by high productivity. Moreover, some studies have found that O₃ has a greater effect on wild plants than on cultivated plants (Biswas et al., 2008). Thus, to rigorously test the responses of invasive and native species to elevated O₃, invasive species must be compared with their closely related and co-occurring native species from non-management systems. However, to the best of our knowledge, no such studies have been conducted.

Competition is considered one of the most important processes that determine the likelihood of alien plant invasion (Baker, 1965; Bishop & Cook, 1981; Roy, 1990). Competition can often interact with other abiotic factors ( Larson et al., 2018; Low-Décarie et al., 2011) and is affected by elevated O₃ concentration (McDonald et al., 2002; Scebba et al., 2006). Moreover, invasive weeds in weed–crop experiments are more tolerant to O₃, thereby resulting in greater competitive success of specific crop species (Grantz et al., 2006,2008,2019; Paudel et al., 2016; Shrestha & Grantz, 2005). Therefore, it is important to consider the potential interaction between competition and O₃ when assessing plant invasiveness.

In this study, we performed an open-top chamber (OTC) experiment with multiple species to test whether responses to elevated O₃ differ between invasive and native species. This is of particular interest to understand whether O₃ pollution can promote or suppress plant invasion. As the degree of susceptibility to O₃ stress can differ among species (Van Goethem et al., 2013), we selected six congeneric pairs of invasive and native species and grew them with and without competition under ambient and elevated O₃ conditions. We measured the aboveground biomass and the number of leaves damaged by O₃, and addressed (1) whether invasive species are more tolerant to O₃ than their co-occurring native species and (2) whether there is an interactive effect between O₃ and plant competition, and if so, whether it differs between invasive and native species.

## METHODS

### 2.1 Study species and cultivation

To test for differences in plant responses to elevated O₃ between invasive and native species with and without competition, we selected 12 herbaceous species. To control for phylogenetic relatedness, we used congeneric pairs, that is six congeneric pairs of invasive and native species (Table S1). In each pair, one species is alien invasive in China, and the other is native co-occurring with the invader in natural habitats. We classified the species as invasive or native to China based on the information available in the databases of Invasive Alien Species in China (www.chinaias.cn) and Flora of China (www.efloras.org). The plant materials used in this experiment were derived
from ramets that were collected in natural habitats (Dai et al., 2016; Wang et al., 2017) or acquired from commercial seed companies (Table S1).

From 13 to 26 May 2020, we used seeds or stolon/rhizome fragments from maternal plants to obtain seedlings/plantlets for the experiment. For species with clonal reproduction, we selected healthy, strong stolons (for the stoloniferous species) and rhizomes (for the rhizomatous species) from original plants, cut them into single-node/bud fragments per species into trays. For species with sexual reproduction, we sowed approximately 200 seeds per species into trays. The cultivation substrate was potting soil (Pindstrup Plus, Pindstrup Mosebrug A/S, Denmark; pH: 6; 120.0 mg/L N; 12.0 mg/L P; 400.0 mg/L K; 28.0 mg/L Mg; 0.4 mg/L B; 2.0 mg/L Mo; 1.7 mg/L Cu; 2.9 mg/L Mn; 0.9 mg/L Zn; 8.4 mg/L Fe), and all trays were randomly assigned to positions on a bench in a greenhouse. The temperature in the greenhouse ranged between 22°C and 28°C with no additional lighting, and the humidity was approximately 60%.

2.2 | Experimental setup

To assess the performance of invasive and native species in response to elevated O₃ concentration, we conducted an OTC experiment at the Northeast Institute of Geography and Agroecology of the Chinese Academy of Sciences (43°59'49''N, 125°24'3''E). On 25 June 2020, we selected 192 similar-sized seedlings/plantlets from 12 species (24 seedlings/plantlets per species) for transplanting. First, 192 circular 2.5 L plastic pots were filled with a substrate (1:1 mixture of sand and fine vermiculite) mixed with 7 g of slow-release fertilizer (Osmocote Exact Standard; 15.00% N + 9.00% phosphorus pentoxide +12.00% potassium oxide +2.00% magnesium oxide +0.02% B +0.05% Cu +0.45% Fe +0.09% chelated by EDTA +0.06% Mn +0.02% Mo +0.015% Zn; Evriess International B.V., Geldermalsen, The Netherlands). From each species, eight seedlings/plantlets were planted alone as control (i.e. in eight separate pots), eight seedlings/plantlets were planted as target plants to compete with a seedling/plantlet from the other species of the pair (resulting in eight pots with two seedlings of different statuses: invasive vs. native), and the remaining eight seedlings/plantlets served as competitors for a target plant (Figure S2a). After transplanting, we randomly assigned 192 pots (12 species x [8 alone +8 competition]) to positions on one greenhouse bench for one week (temperature: 22–28°C; humidity: approximately 60%; no additional lighting) and watered them regularly.

On 3 July 2020, we divided these 192 pots into eight groups and moved them into eight separate OTCs (Figure S2b). Each OTC included 24 pots, that is two pots per target species with one pot with the target species growing alone and one pot with the target species growing under competition with the other species of the pair. We randomly assigned the 24 pots to positions in each OTC and re-randomized them in the fourth week after transplantation. To test the effects of elevated O₃ concentration on invasive and native species, we treated the plants growing under elevated O₃ conditions in four OTCs (i.e. O1, O2, O3 and O4; Figure S2b) and treated those growing under ambient O₃ conditions in the other four OTCs (i.e. C1, C2, C3 and C4; Figure S2b).

2.3 | Ozone fumigation

To simulate O₃ enrichment, we supplied extra O₃ to four of the eight OTCs (O1–O4). O₃ was generated by an O₃ generator (FH- CYJ1910A-Y, Fogha) and delivered to these four OTCs by a blower (XGB-370W/220V) through pipelines (Figure S2b). O₃ was applied from 8:00 to 18:00 every day of the experiment, except when the plants were wet from fog, dew or rain events. For the other four OTCs (C1–C4), we delivered air instead of O₃ by a blower during the experiment as a control. We monitored the O₃ concentration in each OTC using an O₃ analyser (Aeroqual Series 200) for at least five days, three times per day. The average O₃ concentration ranged from 87.1 ppb to 90.6 ppb in the elevated O₃ chambers and from 42.8 ppb to 44.0 ppb in the ambient O₃ chambers (Table S2).

2.4 | Measurements

We concluded the experiment on 6 August 2020, 43 days after the start of the experiment. We recorded the number of total leaves and the number of damaged leaves under elevated O₃ treatment and harvested the aboveground parts of all the plants. As three plants died during the experiment, the number of final harvested plants was 189 instead of 192. All the plant materials were dried at 65°C for at least 72 h and then weighed with an accuracy of 0.001 g.

2.5 | Statistical analyses

To test for differences in biomass production between invasive and native species in response to elevated O₃, we fitted a linear mixed-effects model in R 3.0.2 (R Core Team, 2013) using the lme function in the nlme package (Pinheiro et al., 2013). As the aboveground biomass analysis model had a Gaussian error distribution, we square-root-transformed the data prior to analysis to improve the normality and homogeneity of the residuals. The fixed part of the model included status (invasive vs. native), O₃ (elevated vs. ambient O₃ concentration), competition (with vs. without) and all their interactions. To account for heterogeneity of variance (i.e. differences in variance between the different species), the model also included a variance structure using the varIdent function in the nlme package, which allowed each level of the factor "species" to have a different variance. To test for differences in the number of total leaves and the number of damaged leaves between the invasive and native species under elevated O₃ treatment, we fitted generalized linear mixed-effects models using the glmer function in the lme4 package (Bates et al., 2015). For both models with negative binomial error
terms, we used the bobyqa optimizer with a maximum of 10,000 iterations to fit these models. The fixed part of the model included status (invasive vs. native), competition (with vs. without) and their two-way interaction. To account for non-independence of plants from the same species, non-independence of species from the same genus, and non-independence of plants from the same OTC, all three models included genus, species (nested within genus) and OTC as random effects. In the (generalized) linear mixed-effect models described above, we assessed the significance of the main fixed-effect terms (i.e. status, competition and O₃) and their interactions using likelihood-ratio tests (Zuur et al., 2009).

3 | RESULTS

Elevated O₃ concentration had a significant negative effect on aboveground biomass (6.9 g vs. 5.1 g; Table 1; Figure 1). In particular, elevated O₃ treatment reduced the aboveground biomass of invasive species (−33.2%) significantly more than that of native species (−17.6%) (Significant interaction of status × O₃, Table 1; Figure 1). Competition and its interactions with other factors did not show any significant effects on aboveground biomass (Table 1; Figure 1). All plants in the 95 pots growing under elevated O₃ treatment experienced leaf damage, whereas none of the plant leaves were damaged when they grew under ambient O₃ conditions. Under elevated O₃ treatment, the total number of leaves produced did not significantly differ between invasive and native species (Table 2; Figure 2). However, the number of damaged leaves was significantly higher for invasive species than for native species (25.8 vs. 10.8; Table 2; Figure 2). Competition and its interaction with elevated O₃ increased leaf damage (Table 1; Figure 1). Moreover, O₃ treatment resulted in higher degree of leaf damage in invasive species than in native species. These results indicate that elevated O₃ may reduce the competitive advantage of invasive species in natural systems, and thus invasive species might expand their distribution more easily to the area with lower O₃ pollution.

Moreover, O₃ stress reduced the aboveground biomass of invasive species significantly more than that of native species. These results indicate that elevated O₃ may reduce the competitive advantage of invasive species in natural systems, and thus invasive species might expand their distribution more easily to the area with lower O₃ pollution.

4 | DISCUSSION

In this study, we found although there was no significant differ on the production of aboveground biomass between invasive and native species, invasive species reduced significantly more aboveground biomass than native species in response to elevated O₃. Moreover, O₃ treatment resulted in higher degree of leaf damage in invasive species than in native species. These results indicate that elevated O₃ may reduce the competitive advantage of invasive species in natural systems, and thus invasive species might expand their distribution more easily to the area with lower O₃ pollution.

Plant growth was significantly inhibited under elevated O₃ conditions (approximately 89 ppb) compared with that under ambient O₃ conditions (approximately 43 ppb) for both aboveground and belowground biomass (Figure S3). Our study provides more evidence to support the previous findings that exposure to elevated O₃ can result in suppressed photosynthesis, accelerated senescence and decreased growth in plants (Ashmore, 2005; Burkey et al., 2020; Gruelke & Heath, 2020). However, in weed–crop study systems, it was found that invasive weeds often suffer less from O₃ stress than specific crop species (Grantz & Shrestha, 2006; Shrestha & Grantz, 2005). Contrarily, we found that O₃ stress reduced the aboveground biomass of invasive species significantly more than that of native species Moreover, similar pattern is found in most native–invasive species pairs (Figure S4). This indicates that in general, elevated O₃ has a stronger adverse effect on invasive species than on native species.

Ozone can damage plant leaves, and visible foliar injury is an accurate indicator of plant susceptibility to O₃ (Li et al., 2016). We compared the numbers of total leaves and O₃-induced damaged leaves between invasive and native plants and found that invasive plants had significantly more damaged leaves than native plants, whereas the number of total leaves did not differ. Moreover, similar pattern is found in most native–invasive species pairs (Figure S5). That indicates in general invasive species had higher foliar injury rates under O₃ stress. Given that the degree of foliar injury is closely related with photosynthesis (Marzuoli et al., 2019; Vainonen & Kangasjärvi, 2015), the most likely explanation for the higher growth suppression of invasive species than of native species is the greater photosynthesis suppression due to higher foliar injury in invasive species.

However, some studies on invasive weeds versus crops in agricultural systems found that invasive species are more tolerant to elevated O₃ concentration than crops (Grantz et al., 2008, 2019; Grantz & Shrestha, 2006; Paudel et al., 2016; Shrestha & Grantz, 2005). Therefore, our results highlight that the effects of elevated O₃ concentration on alien plant invasions may differ between natural and agricultural systems. A plausible explanation is that crop species are not really equivalent to native species from non-management systems. The strong selection for crop species to grow fast and be
productive under relatively good conditions could result in their relatively poor performance under stressful conditions. On the other hand, natural selection for tolerance to O₃ may occur in native species rather than invasive species from natural systems, because most invasive species originate in South America, which has less O₃ pollution than China (Cooper et al., 2014). The populations of some species have been demonstrated to differ in O₃ sensitivity/tolerance, and these differences were statistically related primarily to the “O₃ climate” of their site of origin (Lyons et al., 1997; Pearson et al., 1996; Reiling & Davison, 1992). Therefore, more studies are needed to test the evolution of O₃ sensitivity/tolerance of invasive species using different populations originating from varied O₃ climates.

In some weed–crop studies, there was a significant interactive effect between O₃ and competition on plant performance. In general, invasive weeds are more tolerant to O₃, which results in greater competitive ability against crops (Grantz et al., 2008, 2019; Grantz & Shrestha, 2006; Paudel et al., 2016; Shrestha & Grantz, 2005). However, there was no significant interactive effect between O₃ and competition on species biomass production and the degree of foliar injury in this study. The situation in which no substantial competition occurs between species due to the use of a single competitor or the relatively short duration of the experiment can also lead to failure in detecting the interaction between competition and O₃. Nevertheless, this could not be the case in this study. Although the overall competition effect was not significant, a separate analysis of the data subset excluding elevated O₃ treatment revealed that competition had a significant effect on aboveground biomass ($p = .003$; Figure S6). Thus, competition could decrease plant biomass production under ambient O₃ conditions. However, there was a marginally significant effect of the interaction between species status and O₃ on the competition outcome ($p = .077$; Figure S7), thereby inferring a mild interaction between O₃ and competition. As this was a relatively short experiment (43 days), the plants might not have responded very strongly to the short period of competition. Therefore, long-term experiments are needed to understand the effect of the interaction between O₃ and competition on native and invasive species.

Our finding that elevated O₃ suppressed the growth of invasive species more than native species has several implications. First, it suggests that the studied invasive species that have already spread in the Northern China might be inhabitable in future, because the
ground-level O₃ concentration is often higher for Northern China than for Southern China (Figure S1). In other words, invasive species might be more competitive relative to their co-occurring native species when they invade to the area with lower O₃ pollution. Second, it indicates that species distribution models might also consider the role of ground-level O₃ concentrations to improve its accuracy when predicting future distributions of invasive species.

In conclusion, we found that the biomass reduction and leaf damage induced by elevated O₃ concentration were greater for invasive species than for native plants. Therefore, our findings highlight that contrary to the positive effects of many global change factors, increasing O₃ pollution might reduce the establishment of alien plant in the future. More studies testing the interactive effects of O₃ pollution and other global change factors are welcome in future.

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CONFLICT OF INTEREST
The authors declare that there is no conflict of interest.

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DATA AVAILABILITY STATEMENT
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**BIOSKETCH**

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Author contributions: YJL conceived the idea. YJL andYL designed the experiment and did the statistical analyses. LCW performed the experiment and collected data. LCW andYL jointly wrote the first draft of the manuscript, with further input from YJL. All authors revised and approved the final version of this manuscript.

**SUPPORTING INFORMATION**

Additional supporting information may be found in the online version of the article at the publisher’s website.

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