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Climate warming affects biological invasions by shifting interactions of plants and herbivores

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Abstract

Plants and herbivorous insects can each be dramatically affected by temperature. Climate warming may impact plant invasion success directly but also indirectly through changes in their natural enemies. To date, however, there are no tests of how climate warming shifts the interactions among invasive plants and their natural enemies to affect invasion success. Field surveys covering the full latitudinal range of invasive *Alternanthera philoxeroides* in China showed that a beetle introduced for biocontrol was rare or absent at higher latitudes. In contrast, plant cover and mass increased with latitude. In a 2-year field experiment near the northern limit of beetle distribution, we found the beetle sustained populations across years under elevated temperature, dramatically decreasing *A. philoxeroides* growth, but it failed to overwinter in ambient temperature. Together, these results suggest that warming will allow the natural enemy to expand its range, potentially benefiting biocontrol in regions that are currently too cold for the natural enemy. However, the invader may also expand its range further north in response to warming. In such cases where plants tolerate cold better than their natural enemies, the geographical gap between plant and herbivorous insect ranges may not disappear but will shift to higher latitudes, leading to a new zone of enemy release. Therefore, warming will not only affect plant invasions directly but also drive either enemy release or increase that will result in contrasting effects on invasive plants. The findings are also critical for future management of invasive species under climate change.

Keywords: biological control, biological invasions, Climate change, indirect impact, plant-insect interaction

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Introduction

Climate change and biological invasions, two major components of global change, significantly affect the environment and quality of life for human (Mack *et al.*, 2000; Thomas *et al.*, 2004). Climate warming and atmospheric nitrogen (N) deposition can affect a species' phenology, distribution, and abundance (Walther *et al.*, 2002; Cleland *et al.*, 2007; Maclean & Wilson, 2011; Concilio *et al.*, 2013), and invasive plants can alter biodiversity and threaten ecosystem services (Mack *et al.*, 2000; Benning *et al.*, 2002). The effects of climate change on the temporal distribution, spatial distribution, and performance of invasive plants have recently received a lot of attention (Walther *et al.*, 2002, 2009; Hellmann *et al.*, 2008; Chown *et al.*, 2012; Concilio *et al.*, 2013; Sorte *et al.*, 2013); however, shifts in interactions between invasive plants and herbivorous insects that may be equally critical for the future management of invasive species are largely unstudied (but see Engelkes *et al.*, 2008). To date, there are no tests of how climate change shifts the interactions among invasive plants and their natural enemies which may in turn influence invasion success and biocontrol efficacy.

Interactions between invasive plants and herbivorous insects may change with environmental conditions. Plant–insect interactions are sensitive to temperature and consequently can be altered by climate warming (Hegland *et al.*, 2009; Yang & Rudolf, 2009). For instance, Liu *et al.* (2011) found that artificial warming of 1.5 °C advanced *Gentiana formosa* flower phenology by a week, causing a dramatic reproductive decline due to significantly increased herbivory by *Melanchra pisi*. Increased N can enhance herbivore performance by improving plant nutrients and food supply (Throop & Lerdau, 2004). For instance, Zehnder & Hunter (2008) reported that simulated N deposition increased the population growth of the aphid, *Aphis nerii* by increasing foliar N concentrations, and plant biomass. Since insect natural enemies play a key role in regulating invasive plant performance (McFadyen, 1998; Keane &

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Crawley, 2002), the direct and indirect (via plants) effects of climate warming and N deposition on insects may determine invasion success under global change (Morriën *et al*., 2010).

Potential shifts in interactions of invasive plants and specialist insects under global change may be particularly important for future efforts at classical biological control (using host-specific natural enemies to suppress invasive plants), which is one of the major approaches to fighting biological invasions (McFadyen, 1998; Thomas & Reid, 2007). From the perspective of biological control efficacy, the consequences of such shifts may be positive, neutral or negative. For example, if climate warming benefits natural enemies more than it does invasive plants, then biological control efficacy may be improved as a result of 'enemy increase'. In contrast, if invasive plants respond to climate change by expanding their ranges more than natural enemies do, then the effectiveness of biological control may be decreased because the natural enemies are left behind ('enemy release') (Morriën *et al*., 2010). However, these predictions have not yet been tested.

Here, we report the impacts of climate warming and nitrogen deposition on the interactions of invasive plants and natural enemies, using alligator weed, *Alternanthera philoxeroides* (Mart.) Griseb. (Amaranthaceae), and the specialist herbivorous insect, *Agasicles hygrophila* Selman and Vogt (Coleoptera: Chrysomelidae) as a model system. Native to South America, *A. philoxeroides* is a worldwide noxious weed. It was introduced into China in the 1930's and had invaded an area up to 34.7°N in China by the end of the last century (Ma, 2001), dramatically affecting biodiversity and causing yield losses in agriculture and aquaculture (Pan *et al*., 2007; Liu *et al*., 2012). In China, *A. philoxeroides* occurs in both aquatic and terrestrial habitats where it forms dense monocultures, though it mainly invades aquatic habitats in Australia, the USA, and New Zealand (Julien *et al*., 1995; Ma, 2001). The specialist beetle *A. hygrophila* was introduced to combat this weed in China in 1986 (Ma, 2001) following introduction from South America into the USA, Australia, and New Zealand from 1960 to 1980 (Coulson, 1977; Julien & Chan, 1992; Stewart *et al*., 1999). In a large-scale survey covering 233 sites in China in 1999, Ma (2001) found that *A. hygrophila* occurred in areas ranging from 20°N to 32°N and caused the heaviest damage to host plants in areas below 30°N. This survey found that the plant range was from 20°N to 34.7°N and its population size was greatest in regions between 30°N and 32.5°N. Previous studies in China found that the beetle has only successfully suppressed *A. philoxeroides* in aquatic habitats but has limited impact in terrestrial habitats, partly due to lower pupal survival (Ma & Wang, 2004) and high plant tolerance of herbivory (Lu & Ding, 2010). Consequently, the terrestrial form of *A. philoxeroides* is still very invasive in China.

China has experienced an increase in temperature of 0.352 and 0.548 °C per decade for maximum and minimum temperatures, respectively, since the 1980's, as a result of rapid urbanization and a rise in atmospheric CO_2 concentration (Zhou *et al*., 2004). Mean temperature is projected to rise by an additional 2–6 °C by the end of this century (IPCC 2007). Atmospheric N deposition in China has also increased (maximum value: 63.53 kg N ha^{-1} yr^{-1}; average value: 12.89 kg N ha^{-1} yr^{-1}) in the last decade (Lü & Tian, 2007). However, the impacts of these global environmental changes on the interactions between *A. philoxeroides* and *A. hygrophila*, and thereby biocontrol efficacy in terrestrial habitats, remain unclear.

In this study, we conducted an extensive field survey of *A. philoxeroides* and *A. hygrophila*, across a latitudinal gradient from south to north China, to investigate their interactions under natural conditions and their potential responses to climate change. To predict the responses of *A. philoxeroides, A. hygrophila* and their interactions to elevated temperature and N deposition, we also conducted a 2-year field experiment near the northern limit of the beetle's distribution. Specifically, we addressed the following questions: (1) How do the performances of the plant and the specialist herbivorous insect vary with climate along latitudes? (2) Do they have similar patterns of geographic variation? (3) How do elevated temperature and N deposition affect the plant, herbivorous insect, and their interactions?

Materials and methods

Study species

Alternanthera philoxeroides is an herbaceous perennial with horizontal and vertical stems. Plants grow rooted in soil on land, or as floating mats attached to banks. Each stem consists of nodes that are capable of producing roots and new shoots and can become new plants if they are disconnected. *A. philoxeroides* has little reproduction from seed in its introduced ranges. Adults and larvae of *Agasicles hygrophila* feed on leaves and stems of *A. philoxeroides*, producing feeding holes and trenches on leaves. Eggs are laid on leaves. Larvae pupate in hollow stems. Adults, pupae, and larvae overwinter (starting in November) in hollow stems or underneath above-ground tissues of *A. philoxeroides* until spring (April). The beetle has up to eight generations per year in south China.

Field survey

To examine the effects of climate on the distribution and occurrence of *A. philoxeroides* and *A. hygrophila*, we conducted a large-scale field survey in terrestrial habitats along a latitudinal transect from 21.5°N to 38.0°N in China during August and September 2012. Along the latitudinal transect, 62 locations were clustered along seven latitudes about 2° apart (see Figure S1). In each latitude cluster, we selected six to nine locations (larger than 10 × 10 m, at least 10 km apart) invaded by *A. philoxeroides*. In each location, 10 to 15 quadrats (0.5 × 0.5 m) were set along two or three 10 m transects (spaced at least 3 m apart), depending on the plant population size. Within each transect, quadrats were spaced 2 m apart. For each quadrat, the number of adults, larvae, and eggs of *A. hygrophila* was counted, and *A. philoxeroides* coverage was measured. To measure plant cover, a 0.5 × 0.5 m frame with 100 cells (each 5 × 5 cm) was placed above the canopy in each quadrat. The percent cover of *A. philoxeroides* was visually estimated in all cells, and summed across cells to obtain average cover in each quadrat. In addition, *A. philoxeroides* above-ground biomass in five quadrats at each site was clipped and weighed directly in the field.

We calculated four metrics for each field survey location by averaging across all of the survey quadrats in a location: beetle occurrence (proportion of quadrats within a location that had *A. hygrophila* of any life stage present), beetle abundance (all life stages combined), *A. philoxeroides* cover (average percent of each quadrat covered), and *A. philoxeroides* biomass (average fresh above-ground biomass). To visualize the relationships of each of these variables with latitude, we calculated the average within two degree intervals starting at 20° and connected these points with a spline curve.

Field experiment

To test the impact of warming and nitrogen deposition on the interactions between *A. philoxeroides* and *A. hygrophila* and thereby efficacy of biocontrol, we set up a 2-year field experiment in Wuhan Botanical Garden (30°32′44.5″N, 114°24′45.6″ E). Located in central China, Wuhan experiences a subtropical monsoon climate with hot, wet summers and cold winters. Mean annual precipitation is 1222 mm, with the majority (ca. 86%) occurring from March to October. Mean temperatures were −0.5 °C in January and 37 °C in July in the past 60 years (http://www.nmc.gov.cn/). The experimental field soils had pH of 7.79 ± 0.046, total N of 1.72 ± 0.16 g kg^{-1}, total P (phosphorus) of 30.54 ± 3.04 mg kg^{-1}, and total K (potassium) of 136.65 ± 7.41 mg kg^{-1}. Prior to the experiment, dominant plant species in the field included *Capsella bursa-pastoris*, *Veronica persica, Sonchus oleraceus, Stellaria media, Euphorbia helioscopia*, and *Plantago virginica*. The field (20 × 30 m) was mowed and weeded, and twelve 3 × 4 m experimental plots, spaced at least 3 m apart, were established in May 2010.

The experiment was a split-plot design with warming as the whole-plot factor, and nitrogen deposition crossed with herbivore treatments as split-plot factors. Warming plots were heated by MSR-2420 infrared radiators (Kalglo electronics, Bethlehem, PA, USA), suspended 2.05 m above the ground and set at a radiation output of 2000 W. In each control plot, one dummy heater of the same shape and size as the infrared heater was used to control shading effects. Warming by infrared heaters has been reported to cause reduction in soil water content (Wan *et al*., 2002) and thus may complicate the impacts of warming; therefore we watered the plots throughout the experiment when necessary, with a sprinkler irrigation system. The experimental field was irrigated 30 min each time (about 3 mm) and 20 times in total during the experiment. Soil temperature at 10 cm depth was recorded automatically with a datalogger (YM-04; Handan Yimeng Electricity Company, Handan, China). The relative humidity 50 cm above the soil surface was recorded automatically with another datalogger (YM-17; Handan Yimeng Electricity Company). These measurements were taken every 10 min and the averages of the six measurements within 1 h were calculated as the hourly means. Soil moisture (10 cm deep) was measured weekly, using a wet sensor (moisture meter type HH2, Delta-T Devices Ltd, Cambridge, UK).

Four 0.8 × 0.9 m subplots (1 m apart) were set in each plot. Buried plastic plates (0.5 cm thick, 35 cm deep) delineated subplots and excluded neighboring plants. *A. philoxeroides* does not root more than 30 cm deep. Each of the subplots was randomly assigned to one of four treatment combinations: (1) undamaged control + unfertilized, (2) herbivory + unfertilized, (3) undamaged control + nitrogen, and (4) herbivory + nitrogen. Twelve cut stems of *A. philoxeroides* from local populations were planted in each subplot on 27 June 2010, and then caged immediately with screen to exclude herbivores. Twenty days later, we thinned each subplot to four similar-sized plants to minimize plant size variation among subplots. On 25 August 2010, two newly mating pairs of *A. hygrophila* were released into each subplot assigned to an herbivory treatment. These beetles were the offspring of field collected individuals from local populations that were reared in screen cages. One week later, we found live beetles in each subplot indicating beetle populations were successfully established.

The nitrogen addition treatment was conducted by spraying ammonium nitrate NH_4NO_3 dissolved in water (2 g N/L) onto subplots four times in each year with handheld sprayers at the rate of 0.5 ml s^{-1} (1 g N m^{-2} on 12 and 27 August, 13 September and 15 October in 2010, and 1 g N m^{-2} on 15 May, 12 July, 15 August and 20 September in 2011). In total, each subplot received an increase of 8 g N m^{-2} over ambient nitrogen deposition from fall 2010 to fall 2011. Nitrogen control plots received the same volume of water.

In December 2010, a 0.5 × 0.5 m frame with 100 cells (each 5 × 5 cm) was placed at the center of each experimental subplot. The numbers of plant internodes (live, dead, and total) and beetle emergence holes were counted. In the following year, we counted the number of beetles (adults and larvae) on 16 April (the day we firstly observed beetles), 12 May, 13 July, 6 August, 12 October, and 15 November. In late November 2011, we again counted the number of beetle emergence holes in each subplot. These emergence holes were mostly formed on new shoots in 2011, as the emergence holes formed in 2010 had disappeared when the old shoots decomposed. To harvest the plants, we first clipped the above-ground tissues. Then, we dug a soil pit down around the plots to 35 cm and separated roots from soil. Plant above- and below-ground tissues were washed, and dried for 48 h at 80 °C before weighing separately.

We used mixed model ANOVAs to test the impacts of warming (whole-plot factor), nutrient addition (split-plot factor), and herbivore presence (split-plot) and their interactions (split-plot) on the number of internodes (dead, total) at the end of the first year, and plant mass (total, shoot, root) at the end of the experiment. To test the direct impact of warming and nitrogen addition on plant performance, we performed a set of additional ANOVAs using only undamaged control plots for these same plant response variables. We used repeated measures mixed model ANOVAs to test the dependence of adult and larval herbivore abundance (six time periods treated as a categorical variable) or number of emergence holes (two time periods – categorical variable) on warming (whole-plot), nutrient addition (split-plot), and their interaction (split-plot). We performed an additional ANOVA to test how the same independent variables affected the number of emergence holes in 2010. When significant interactive effects occurred, we examined differences among treatment combinations using adjusted means partial difference tests ($P < 0.05$).

Results

Field survey

Along the latitudinal gradient, *A. hygrophila* occurred from 21.5°N to 31.8°N with the highest average population size in areas between 25.5°N and 27.5°N (Fig. 1a and b). However, *A. philoxeroides* occurred from 21.5°N up to 36.8°N, and performed better at higher latitudes up to 34.5°N (Fig. 1c and d). This difference between the two species resulted in a spatial mismatch between their areas of occurrence and peak abundance.

Field experiment

During the experiment, soil temperature at the depth of 10 cm was increased by 1.40°C on average (ambient vs. warming: 19.48 ± 0.75 °C vs. 20.86 ± 0.74 °C,

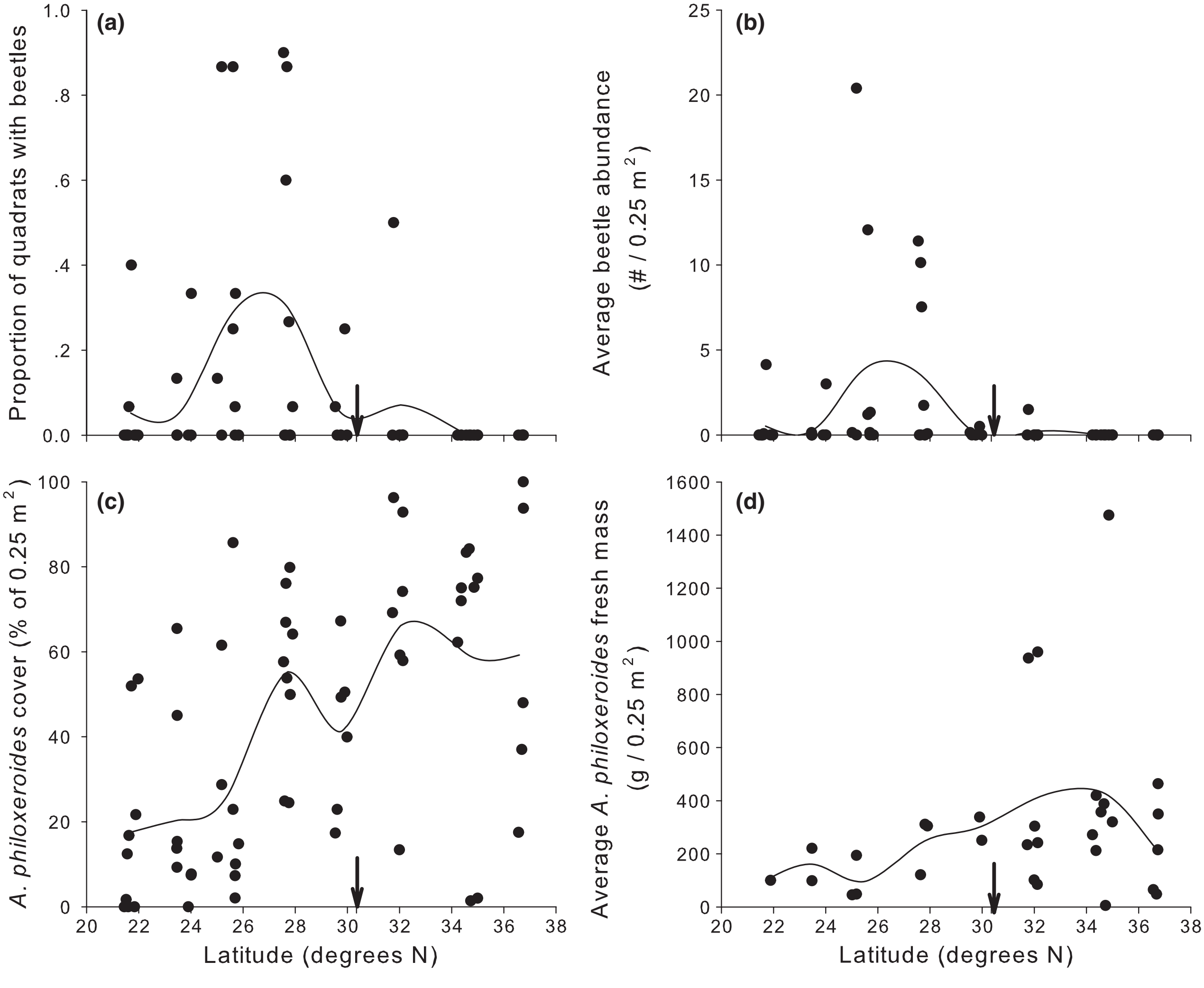

Fig. 1 Field survey showing the dependence of (a) beetle occurrence, (b) beetle abundance, (c) *Alternanthera philoxeroides* cover, and (d) *A. philoxeroides* biomass on latitude. Each point is the average of all quadrats in a location (Figure S1). Arrows indicate the latitude of the experimental location. Lines are spline curves drawn through the average values within 2° intervals.

t_{10341} = 296.7, $P < 0.0001$) by the infrared heaters. Warming decreased air humidity by 2.81% (ambient vs. warming: 86.01 ± 0.11% vs. 83.20 ± 0.13%, $t_{10708} = -30.321$, $P < 0.0001$), but had no impact on soil water content (ambient vs. warming 24.87 ± 0.47% vs. 23.91 ± 0.48%, $t_{59} = 1.892$, $P = 0.063$) at the depth of 10 cm during the trial.

Warming increased beetle population sizes in both years, while N deposition only affected it in the first year (Table 1). At the end of the first year, beetle population sizes were greater in the warming or N deposition plots than in the control plots (Table 1, Fig. 2a, Figure S3). However, in the second year, the beetle only occurred in warming plots (Fig. 2b and c), where the beetle started to emerge in April and reached its highest density in July (Figure S2).

Warming did not affect plant performance in the undamaged control plots (Total mass, $F_{1,10} = 0.55$, $P = 0.4735$; shoot mass, $F_{1,10} = 1.67$, $P = 0.2258$; root mass, $F_{1,10} = 1.88$, $P = 0.2003$; number of internodes, $F_{1,10} = 0.25$, $P = 0.6247$). N deposition increased the total number of internodes by 9.96% ($F_{1,10} = 11.82$, $P = 0.0063$) at the end of the first year.

The varying responses to warming of the beetle and plant resulted in an increased impact of herbivory on plant performance under elevated temperature (Table 2). The number of dead internodes caused by herbivory under elevated temperature was 147% more than that under ambient temperature (Fig. 3a). Moreover, herbivory significantly decreased plant total mass (55.27%; Fig. 3b), shoot mass (49.42%) and root mass (62.29%) under elevated temperature, but herbivory had no significant impacts on these parameters under ambient temperature.

Discussion

This study is the first, to our knowledge, to document the effects of climate warming and atmospheric N

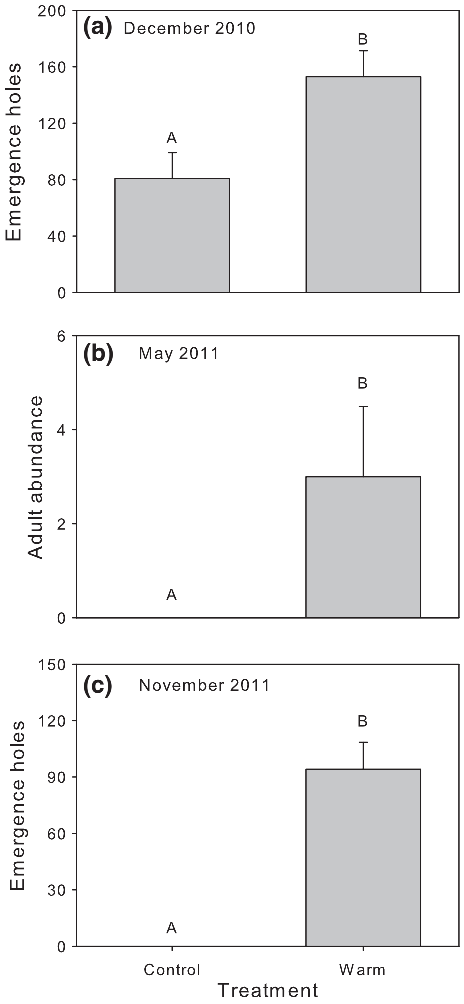

Fig. 2 The effects of warming treatments on beetles in the field experiment. (a) emergence holes in *Alternanthera philoxeroides* stems from new adult beetles at the end of year 2010 [first year]; (b) adult beetle abundance in May 2011 [second year]; (c) emergence holes at the end of year 2011 [second year]. Means + 1 SE. Means with the same letters were not significantly different in *post hoc* multiple comparisons of means at the $P = 0.05$ level.

Table 1 The effects of warming, nitrogen deposition, and time on beetles in the field experiment. For adult and larval abundances, time refers to six surveys over 2 years (2010 and 2011). For emergence, time refers to one survey per year. Warming was a whole-plot factor. Nitrogen was a split-plot factor. Significant results are shown in bold

	Adults			Larvae			Emergence			Emergence 2010		
Effect	d.f.	*F*	*P*	d.f.	*F*	*P*	d.f.	*F*	*P*	d.f.	*F*	*P*
Warming	**1,10**	**46.25**	**<.0001**	**1,10**	**18.85**	**0.0015**	**1,10**	**24.60**	**0.0006**	**1,10**	**7.71**	**0.0195**
Nitrogen	1,10	1.77	0.2135	1,10	1.16	0.3075	1,10	2.94	0.1174	**1,10**	**5.40**	**0.0425**
Warming*Nitrogen	1,10	1.77	0.2135	1,10	1.16	0.3075	1,10	1.34	0.2746	1,10	1.10	0.3194
Time	**5,100**	**22.38**	**<.0001**	**5,100**	**4.65**	**0.0007**	**1,20**	**37.78**	**<.0001**			
Warming*Time	**5,100**	**22.38**	**<.0001**	**5,100**	**4.65**	**0.0007**	1,20	0.93	0.3460			
Nitrogen*Time	5,100	1.12	0.3535	5,100	0.52	0.7587	**1,20**	**5.03**	**0.0364**			
Warming*Nitrogen*Time	5,100	1.12	0.3535	5,100	0.52	0.7587	1,20	0.39	0.5374			

Table 2 The effects of warming, nitrogen deposition, and herbivores on plant performance in the field experiment. Warming was a whole-plot factor. Nitrogen and herbivores were split-plot factors. Significant results are shown in bold

		Total mass		Shoot mass		Root mass		# live internodes		# dead internodes	
Effect	d.f.	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Warming	1,10	**12.73**	**0.0051**	**18.31**	**0.0016**	0.14	0.7195	<0.01	0.9468	4.59	0.0578
Nitrogen	1,30	0.10	0.7522	0.47	0.5000	2.24	0.1445	1.80	0.1894	0.39	0.5381
Warming*Nitrogen	1,30	0.96	0.3360	1.34	0.2563	0.14	0.7112	0.90	0.3513	0.23	0.6381
Herbivore	1,30	**27.13**	**<0.0001**	**26.42**	**<0.0001**	**11.14**	**0.0023**	**21.25**	**<.0001**	**31.90**	**<0.0001**
Warming*Herbivore	1,30	**9.26**	**0.0048**	**7.95**	**0.0084**	**7.40**	**0.0108**	2.05	0.1625	**5.27**	**0.0288**
Nitrogen*Herbivore	1,30	3.11	0.0879	3.55	0.0694	0.06	0.8150	0.06	0.8024	<0.01	0.9488
Warming*Nitrogen*Herbivore	1,30	0.26	0.6150	0.01	0.9243	3.80	0.0608	0.03	0.8663	0.34	0.5665

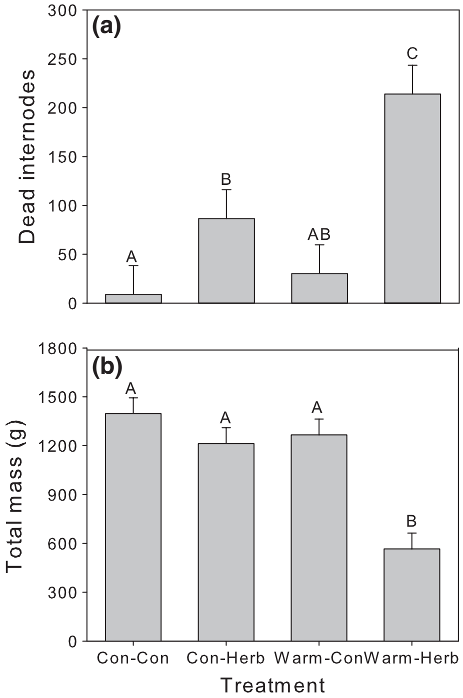

Fig. 3 The dependence of plant performance in warming and herbivore treatments in the field experiment. (a) The number of dead internodes per quadrat at the end of 2010; and (b) total mass per plot for all treatments at the end of the experiment in 2011. Means + 1 SE. Means with the same letters were not significantly different in *post hoc* multiple comparisons of means at the $P = 0.05$ level.

addition on the interactions of invasive plants and their biological control agents. Our experiments clearly showed that warming increased biological control insect populations and enhanced herbivory, resulting in a dramatic decline in invasive plant growth. These results were consistent with our field surveys which showed that the beetle generally maintained higher populations at lower latitudes where the invasive plant also performed poorly relative to higher latitudes. Our results suggest that climate warming may shift the interactions of invasive plants and insects, in some cases increasing efficacy of biocontrol against invasive species in presently temperate ranges.

The responses of invasive plants to elevated temperature and N addition have received a lot of attention recently (Walther *et al.*, 2002, 2009; Hellmann *et al.*, 2008; Dukes *et al.*, 2011; Chown *et al.*, 2012; Sorte *et al.*, 2013). Increased N availability generally increases plant performance because it is frequently a limiting nutrient (Harpole *et al.*, 2011). However, we did not find a significant effect of N addition on plant growth. High levels of N deposition are found throughout China (Liu *et al.*, 2013). For example, in central China where our experiment was conducted, N deposition is about 40 kg ha^{-1} yr^{-1} and apparently is not a limiting nutrient (Lu *et al.*, 2012). Therefore, our treatment of additional N deposition that further increased N deposition had no impact on *A. philoxeroides* in this study. Similarly, it is not surprising that elevated temperature did not affect plant growth as *A. philoxeroides* occurs far north and south of Wuhan where we conducted our experiment.

Global change may significantly affect invasive plants through its impact on the population growth rates of biocontrol agents. Elevated temperature can increase population size of insects (Currano *et al.*, 2008; Mitton & Ferrenberg, 2012) and consequently increase efficacy of biocontrol. In our experiment, elevated temperature increased the total number of beetles that occurred in experimental plots in both 2010 and 2011 (Fig. 1). Although nitrogen deposition has been reported to increase insect population growth by elevating resource availability (Room & Thomas, 1985; Throop & Lerdau, 2004; Center & Dray, 2010), we found N addition only increased insect populations in the first year. It is possible that, in our experiment, the insect populations were more constrained by food quantity rather than food quality in the second year.

Global change and climate warming in particular may allow insects to exploit new habitats already invaded by their host plants. High phenotypic plasticity is an important mechanism behind alien plant invasion as it enables many plants to invade successfully in diverse environments (Richards *et al*., 2006), for example, the invasion of *A. philoxeroides* into both aquatic and terrestrial habitats (Geng *et al*., 2007). *A. hygrophila* was previously reported as an aquatic insect that could not overwinter in terrestrial habitats that lack suitable shelters (plant above-ground tissues) in winter (Julien *et al*., 1995). This may cause a local-scale spatial mismatch of invasive plants and insects that reduces the efficacy of biocontrol. Critically, elevated temperature enabled the beetle to overwinter in terrestrial habitats in our experiments. The plant's above-ground tissues that survived through the winter under elevated temperature may have provided suitable overwintering habitats for the beetle (Liu *et al*., 2010). Thus, ongoing climate warming may enable biocontrol agents to develop viable populations in new areas where they currently have no available overwintering habitats.

Biological control insects may expand their ranges under climate warming. Numerous studies have documented that climate change can alter community structure, since plant and insect species may show species-specific responses in terms of their phenology, distribution, and abundance (Visser & Holleman, 2001; Hegland *et al*., 2009; Yang & Rudolf, 2009; Gilman *et al*., 2010; Liu *et al*., 2011). *A. philoxeroides* has invaded in both warm and presently temperate regions (below approximately 37°N, Figure S1), but *A. hygrophila* was only found in warmer regions (below approximately 32°N, Figure S1), showing a spatial mismatch likely due to their difference in sensitivity to low winter temperature. In our study, elevated temperature enabled the beetle to overwinter (Fig. 2) and sustain a population across years, suggesting that, under climate warming, this mismatch will be decreased as the beetle may be able to disperse and establish populations in areas where it cannot presently overwinter.

A large spatial mismatch between invasive plants and biocontrol insects, however, may still exist under global warming due to their different tolerance of low temperature. Our field survey clearly shows *A. philoxeroides* occurs at higher latitudes than *A. hygrophila,* indicating the plant is able to tolerate cold weather better than the insect. This is consistent with results of field surveys (Ma, 2001), insect overwintering experiments (Li *et al*., 1994), and model predictions (Julien *et al*., 1995). Based on the plant's distribution in its native South America, Julien *et al.* (1995) used CLIMEX and predicted that *A. philoxeroides* could only occur in areas below 31.5°N in central and south China. However, given the fact that the isotherm has been moving northward in winter in China during the last decades (Lu *et al*., 2008), the recently continuing invasion by *A. philoxeroides* to north China (now to 36.8°N, Figure S1) may indicate that warmer winters have enabled the plant to shift its range to higher latitudes. Therefore, we predict that the distribution of *A. philoxeroides* will be still broader than that of *A. hygrophila* under climate warming, though the insect will expand its range as well. Therefore, the gap between the plant and the insect may not disappear but will shift from presently temperate regions to higher latitudes in the future.

Our findings have important implications for predicting plant invasions and the impact of natural enemies under climate change. Shifts in the synchrony of plant–insect interactions could result in contrasting effects on plant invasions, as different rates of range expansion between invasive plants and their feeding insects may result in either 'enemy release' by leaving the insects behind, or 'enemy increase' by increasing insect population size and expanding distribution (Engelkes *et al*., 2008; Morriën *et al*., 2010). As climate warming and other global environmental change drivers may benefit invasive plants, invaders may expand to new areas where environments are not suitable for insects even in new conditions, such that biological control efficacy will be decreased. However, warming may also allow insects to expand their range and exploit new habitats where the plants also invade, such that climate warming will enhance biological control efficacy. This also illustrates the importance of examining the effects of global change on trophic interactions (Suttle *et al*., 2007) that play a key role in regulating the occurrence and abundance of plants and insects directly and/or indirectly. Thus, we recommend that future modeling or experimental studies on the effects of climate change on invasive species should also consider trophic interactions.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Locations of the sites for the field survey across China. In total, the field survey covered 61 sites invaded by *Alternanthera philoxeroides* and 715 quadrats (0.5 × 0.5 m). Red dots indicate sites that had both *A. philoxeroides* and *A. hygrophila*. Blue dots only had *A. philoxeroides*. Dashed and solid black lines note the northern limits of *A. hygrophila's* distribution in 1999 and 2012, respectively, where the beetle could overwinter in aquatic habitats and establish sustainable populations. Dashed and solid red lines represent the northern limits of *A. philoxeroides'* distribution in 1999 and 2012, respectively. The triangle indicates the experimental site, and the star indicates the site where the beetle can currently overwinter in terrestrial habitats.

Figure S2. The dynamics of *Alternanthera hygrophila* adult and larval abundance (mean ± 1 SE) in 2011 under elevated temperatures. Beetle emergence began in middle April and they had the highest density in July. The beetle did not occur under ambient temperature in the field in 2011.

Figure S3. The mean number (+1 SE) of *Alternanthera hygrophila* emergence holes per quadrat at the end of 2010 for each nitrogen and warming treatment combination. Means with the same letters were not significantly different in *post hoc* multiple comparisons of means at the $P = 0.05$ level.