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Research

Warming benefits a native species competing with an invasive congener in the presence of a biocontrol beetle

Xinmin Lu[1,2], Evan Siemann[3], Minyan He[1,2], Hui Wei[1], Xu Shao[1] and Jianqing Ding[1,2]

[1]Key Laboratory of Aquatic Botany and Watershed Ecology, Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan, Hubei 430074, China; [2]Hubei Key Laboratory of Wetland Evolution & Ecological Restoration, Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan, Hubei 430074, China; [3]Department of Biosciences, Rice University, Houston, TX 77005, USA

Authors for correspondence:
Xinmin Lu
Tel: +86 27 87510970
Email: lxm3412@wbgcas.cn

Jianqing Ding
Tel: +86 27 87510970
Email: ding@wbgcas.cn

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Summary

- Climate warming may affect biological invasions by altering competition between native and non-native species, but these effects may depend on biotic interactions.
- In field surveys at 33 sites in China along a latitudinal and temperature gradient from 21°N to 30.5°N and a 2-yr field experiment at 30.5°N, we tested the role of the biocontrol beetle *Agasicles hygrophila* in mediating warming effects on competition between the invasive plant *Alternanthera philoxeroides* and the native plant *Alternanthera sessilis*.
- In surveys, native populations were perennial below 25.8°N but only annual populations were found above 26.5°N where the invader dominated the community. Beetles were present throughout the gradient. Experimental warming (+ 1.8°C) increased native plant performance directly by shifting its lifecycle from annual to perennial, and indirectly by releasing the native from competition via disproportionate increases in herbivory on the invader. Consequently, warming shifted the plant community from invader-dominated to native-dominated but only in the presence of the beetle.
- Our results show that herbivores can play a critical role in determining warming effects on plant communities and species invasions. Understanding how biotic interactions shape responses of communities to climate change is crucial for predicting the risk of plant invasions.

Introduction

Ecological studies that predict responses of non-native species invasions to climate change are critical for invasive species management and native species conservation. Climate change has been shown to facilitate non-native species' spread to higher latitudes or elevations in invaded ranges or to new ranges, and thus is expected to exacerbate their detrimental effects (Hellmann *et al.*, 2008; Walther *et al.*, 2009). In the context of non-native species invasions with climate change, emphasis has been placed on the questions of how distribution and performance of non-native species will respond directly to climate change (Bradley *et al.*, 2010). A great deal of effort has been devoted, therefore, to estimating non-native species' dispersal and performance potential under changing climate with experimental, observational and modeling studies (Smith *et al.*, 2000; Dukes *et al.*, 2011; Chown *et al.*, 2012; Sandel & Dangremond, 2012; Concilio *et al.*, 2013). However, the success and consequent impacts of non-native species in new environments are determined by interactions with native competitors and natural enemies (i.e. pathogens and herbivores) in addition to climate (Kolar & Lodge, 2001; Eskelinen & Harrison, 2013). Moreover, a large body of studies has demonstrated the crucial role of biotic interactions (e.g. facilitation, competition and herbivory) in mediating responses of native plant species and communities to climate change (Peters *et al.*, 2006; Post & Pedersen, 2008; Spasojevic *et al.*, 2014; Alexander *et al.*, 2015). How biotic factors – specifically native competitors and herbivores – affect non-native plant species invasions under changing climate has received comparatively little attention (but see Morriën *et al.*, 2010; Ortega *et al.*, 2012; Lu *et al.*, 2013) and has largely been overlooked in modeling and experimental studies.

Native competitors (e.g. coexisting native plant species) act as an important biotic filter against non-native species invasions (Kolar & Lodge, 2001). The impact of climate change on competition between native and non-native plant species depends on their relative sensitivity to climate change as a function of their physiological and morphological traits (Soudzilovskaia *et al.*, 2013). Compared with co-occurring native species, non-native invasive species as a group generally show higher resource-use efficiency, growth rates and phenotypic plasticity, and earlier emergence (also known as seasonal priority), and these traits have been shown to confer competitive advantages to non-native invasive species (Wolkovich & Cleland, 2011; Drenovsky *et al.*, 2012; Ordonez & Olff, 2013). Climate change is expected to favor plants with these functional traits and thus to further benefit non-native invasive species at the cost of native species (Dukes & Mooney, 1999; Walther *et al.*, 2009). However, in a meta-analysis including 157 non-native species and 204 co-occurring native species, Sorte *et al.* (2013) found that co-occurring non-native and native species respond similarly to climate changes (e.g. increases in temperature or CO_2) in terrestrial habitats, although non-native species show stronger responses in aquatic habitats. The inconsistency between theoretical predictions and empirical findings highlights the importance of studies of functional traits associated with non-native species success that interact with climate change.

Natural enemies (e.g. herbivores and pathogens) are another important biotic factor that regulates native plant community composition (Peters *et al.*, 2006; Post & Pedersen, 2008) and could also be a crucial determinant of non-native species invasions under climate change (Morriën *et al.*, 2010; Lu *et al.*, 2013). Leaving behind their coevolved specialist enemies is recognized as an important reason underlying the success of non-native species in new environments (Enemy release hypothesis; Keane & Crawley, 2002), whereas biotic resistance arising from native herbivores has been proposed to explain their failure (Biotic resistance hypothesis; reviewed by Maron & Vilà, 2001). Climate change, such as warming, can increase herbivore population sizes (Lu *et al.*, 2013) and alter their host preferences (Peters *et al.*, 2006), and thus may increase herbivore impacts on preferred hosts and change their role in non-native species invasions (Fey & Herren, 2014). If insects, such as coevolved specialists introduced for biological control, prefer invasive species (major or target hosts) over native species (minor or nontarget hosts), warming may enhance herbivore impacts on invasive species and indirectly benefit native species by releasing the native species from competition. To date, however, tests of these predictions and evidence from field studies are rare.

Field sampling along latitudinal gradients and *in situ* warming experiments are the main approaches to examining impacts of warming on species and communities in terrestrial ecosystems (De Frenne *et al.*, 2013; Elmendorf *et al.*, 2015). Field surveys along latitudinal gradients with variation in temperature can provide invaluable information about temperature impacts on species and communities at large spatial and temporal scales (De Frenne *et al.*, 2013). If temperature is the major driver affecting latitudinal patterns of plants, insects and their interactions, field surveys across latitudes may help to unravel the current effects of climate warming and predict future trends. However, climate variables besides temperature (e.g. precipitation) may also change along latitudinal gradients and separating temperature effects from those of other factors can be complicated. *In situ* warming experiments, however, can disentangle temperature effects from other environmental factors that co-vary along latitudinal gradients (De Frenne *et al.*, 2013). Thus, combining field surveys along latitudinal gradients with an *in situ* warming experiment can provide powerful information that can improve predictions of climate warming impacts on plant species and communities in terrestrial ecosystems (De Frenne *et al.*, 2013).

Here we conducted two field surveys along a latitudinal gradient and a warming experiment in China to test the impacts of warming on competition between the global invader *Alternanthera philoxeroides* (Amaranthaceae, alligatorweed) and its native congener *A. sessilis* (Amaranthaceae, sessile joyweed) in the presence or absence of the biocontrol beetle *Agasicles hygrophila* (Coleoptera: Chrysomelidae, alligatorweed flea beetle). *A. hygrophila* infests both *A. philoxeroides* and *A. sessilis*, and uses the invasive species as its major host in China (Wu *et al.*, 1994; Lu *et al.*, 2015). In previous studies, we found that warming has triggered range expansion of *A. hygrophila* (from 28°N to 31.8°N) and *A. philoxeroides* (from 34.7°N to 36.8°N), and could increase the beetle's population size and damage on both the invasive and the native species by enabling the beetle to overwinter at higher latitudes (Lu *et al.*, 2013, 2015). What remains unclear is how the beetle affects competition between the native and non-native species with climate warming.

In this study, our extensive field surveys along a latitudinal gradient from southern to central China (21°N to 30.5°N) aimed to examine the current impact of climate on abundance of *A. hygrophila* and the performance of *A. philoxeroides* and *A. sessilis*. To test the impact of warming on competition between these plant species and investigate the role of the herbivore, we conducted a 2-yr field warming experiment in central China. Specifically, we asked: first, how does warming directly affect the native and invasive plant species and their competition? Second, how does warming indirectly affect the native species via changes in competitive ability of the invasive species in the presence or absence of the beetle?

Materials and Methods

Study species

Alternanthera sessilis (L.) R.Br. ex DC., an annual or perennial herb native to Asia, propagates from seeds or stem buds. It can grow in both terrestrial and aquatic habitats, but rarely occurs in aquatic habitats in China. *Alternanthera philoxeroides* (Mart.) Griseb, native to South America, can grow in both terrestrial and aquatic habitats and has invaded 30 countries (Julien *et al.*, 1995). The plant propagates solely by vegetative means from stem buds in introduced ranges, although it produces seeds in its native ranges (Julien *et al.*, 1995). Relative to its native congener, *A. philoxeroides* has greater phenotypic plasticity to changes in water availability (Geng *et al.*, 2006) and is more tolerant of herbivory (Sun *et al.*, 2010). But, in a 1-yr field experiment, we found *A. sessilis* to be more competitive than *A. philoxeroides* due to a higher number of stems (Lu *et al.*, 2014). In China, *A. sessilis* and *A. philoxeroides* co-occur in regions up to 36.6°N and both can be damaged by the introduced biocontrol beetle *A. hygrophila* Selman and Vogt and native insects including *Cassida piperata* Hope (Coleoptera: Cassididae) and *Hymenia recurvalis* Fabricius (Lepidoptera: Pyralidae) (Lu *et al.*, 2015). In the area below 31.4°N, *A. sessilis* and *A. philoxeroides* are damaged mainly by the introduced beetle (Lu *et al.*, 2015).

Agasicles hygrophila, native to South America, has been released to control *A. philoxeroides* in North America (1964), Australia (1976) and New Zealand (1982) (Julien *et al.*, 1995). The beetle was released in China in 1986. However, so far the beetle has suppressed the weed only in aquatic habitats in warm regions and appears to have limited impacts in terrestrial habitats, partially as a result of high plant tolerance and low beetle population size (Lu & Ding, 2010). In China, lab bioassays and field surveys found that the beetle can only feed and establish populations on *A. sessilis* and *A. philoxeroides* (Wu *et al.*, 1994; Lu *et al.*, 2015). Beetle adults and larvae feed on leaves and stems, causing defoliation and stem damage. Newly developed adults cut emergence holes in stems, causing stem damage and allowing entry of rot-causing organisms (Julien *et al.*, 1995). The third instar larvae pupate in stems of host plants. The beetle overwinters in living invasive host stems as larvae, pupae and adults, or in the underlying soil surface as adults in tropical regions (Liu *et al.*, 2010), whereas it cannot overwinter in terrestrial habitats in temperate regions such as central China (Lu *et al.*, 2013). Our previous field experiments demonstrated that warming could enable the beetle to overwinter in terrestrial habitats in temperate regions and therefore increase both the beetle's control efficacy on *A. philoxeroides* (Lu *et al.*, 2013) and attack on the nontarget plant *A. sessilis* (Lu *et al.*, 2015).

Field surveys

In order to explore warming impacts on competition between the two plant species at large spatial scales, we carried out two field surveys along a latitudinal gradient from 21°N to 33°N in China in 2013 in terrestrial habitats. From 13 to 28 April, we selected sites randomly along the latitudinal gradient so that were multiple locations (larger than 10 × 10 m, at least 10 km apart) within each 1° of latitude that could potentially contain the target species (see Supporting Information Fig. S1). If none of the three species could be found, we selected a different location. In total we conducted the April field survey at 33 sites. In August to September, we surveyed the same sites except for two that were destroyed. During both surveys, *A. hygrophila* was the major defoliator on the two plant species within the whole latitudinal range. In the April survey, we detected *A. hygrophila* only on the two plant species, whereas in the August to September survey we also observed some native insects, including *C. piperata* and *H. recurvalis*, but in low abundances on the two plants.

Our field survey sites ranged from tropical to temperate regions. Given that various climate variables could significantly affect native species life history and plant competition in our study system (Lu *et al.*, 2015), we obtained the following data for the past 50 yr for our survey sites from the National Meteorological Center of China (http://www.nmc.cn/): annual minimum and maximum temperatures, annual average (average of monthly values) minimum and maximum temperatures, and annual precipitation.

Data collection for field surveys

In the April survey, we measured cover and stem length of each plant species (in our survey sites we observed only the native and invasive species), whereas in the August to September survey we measured plant cover only. In each location, we chose 10–15 quadrats (0.5 × 0.5 m) randomly along two or three 10-m transects (spaced at least 3 m apart). We measured plant cover and beetle abundance (number of adults, larvae and eggs of *A. hygrophila*) by placing a 0.5 × 0.5 m frame with 100 cells (each 5 × 5 cm) above the canopy in each quadrat. We visually estimated the percentage cover of each plant species in all cells, and summed across cells to obtain total cover for each plant species in each quadrat. In addition, we counted the beetle in all cells and summed across cells to obtain total numbers for each quadrat. We collected six stems of each plant species in the center of each quadrat if available in the April survey and measured their lengths.

Data analysis for field surveys

We used the Statistical Analysis System (SAS v.9.4; SAS Institute, Cary, NC, USA) to conduct all data analyses. To examine seasonal priority due to earlier emergence of the non-native invasive species relative to the native species in the April 2013 field survey, we calculated the differences in their stem lengths (native species stem length − invasive species stem length). We treated stem length of the native species as zero in the areas (above 27°N) where it had not yet emerged during our field survey. We regressed native species stem length (April 2013), the difference in native vs invasive stem lengths (April 2013), native and invasive species cover (each survey separately), the ratio of native vs total cover (i.e. native cover + invader cover) (each survey separately), beetle abundance (each survey separately) and climate variables against latitude. We also used multiple regressions to test the effects of annual minimum and maximum temperatures, annual average minimum and maximum temperatures, and annual precipitation on these plant and beetle variables in the April and August to September surveys separately with stepwise, backward and forward methods. We $\log_{10}$-transformed data for native and invasive species cover and the ratio of native vs total cover, and square-root transformed data for beetle abundance.

Field experiment

In order to determine how warming and herbivores affect competition between the native and invasive species, we established a warming experiment in the same field as Lu *et al.* (2013) in Wuhan, China (30°32′44.5″N, 114°24′45.6″E). We conducted the experiment from May 2012 to November 2013. We established twelve 3 × 4 m experimental plots (3 m apart; six warmed, six ambient temperature) in a mowed and hand weeded field (20 × 30 m) and set four 1.0 × 1.0 m subplots (0.5 m apart) in each plot (Fig. S2). We buried plastic edging (0.5 cm thick, 35 cm deep) to delineate subplots and exclude neighboring plants.

The experiment was a split-plot design with warming (warm vs ambient) as a whole-plot factor, plant planting style (native only, invader only and mixture) crossed with herbivore treatments (beetles present or absent) as split-plot factors, with four replicates of each treatment combination (Fig. S2). We heated warming plots with MSR-2420 infrared radiators (Kalglo Electronics, Bethlehem, PA, USA) for 24 h d^{-1} from 27 June 2012 to the end of the experiment. We suspended heaters at a height of 2.25 m and set them at a radiation output of 2000 W. In control plots, we used dummy heaters of the same size and shape to control for shading effects. Warming by infrared heaters has been reported to cause reduction in soil water content (Wan *et al.*, 2002) and may complicate warming impacts; therefore, we watered the plots with a sprinkler irrigation system when necessary throughout the experiment. We monitored soil temperature and moisture at 10 cm depth in the center of one randomly selected subplot in each plot during the trial (for details see Lu *et al.*, 2015). Data indicated that heaters increased soil temperature at 10 cm depth by 2.5°C in winter (December–February), 1.1°C in summer (June to August) and 1.8°C on average throughout the trial, but they did not affect soil moisture (for details, see Lu *et al.*, 2015). The temperature of Wuhan is predicted to increase 1.5–3°C in winter and 1.5–2°C in summer by 2065 (IPCC, 2013).

We assigned each subplot randomly to one of six treatment combinations: undamaged control, *A. philoxeroides*; herbivory, *A. philoxeroides*; undamaged control, *A. sessilis*; herbivory, *A. sessilis*; undamaged control, *A. philoxeroides* + *A. sessilis*; or herbivory, *A. philoxeroides* + *A. sessilis*. Each plot received four of the six split-plot treatment combinations and caused the design to be unbalanced. This type of unbalanced split-plot design is analyzed with the same approach as a balanced split-plot design (including a term for plot as a random factor nested in warming; Milliken & Johnson, 2009). We planted two individuals of the same (monoculture) or different (mixture) plant species in opposite corners of 0.5 × 0.5 m quadrats positioned in the center of each subplot on 27 June 2012. Both the native and invasive species are creeping plants and one individual could occupy a large area in the field. In our previous studies we found that two individuals of each species could fully cover an area of 1.0 × 1.0 m within one growing season (X. Lu & J. Ding, unpublished data). We propagated seedlings of the native species from seeds that we collected from the same plant individual in December 2011, whereas we propagated seedlings of the invader from cut stems. At the experimental site, the native species propagates only from seeds, whereas the invader propagates from overwintering internodes or belowground tissues. We collected all plant materials from the same field in Wuhan. We propagated seedlings of both species in a naturally lit, unheated glasshouse. We caged all subplots immediately after planting with 1 × 1 × 1 m nylon cages. For each warming treatment (ambient and warming), we randomly selected half of the subplots to receive the herbivory treatment and treated the remaining subplots as undamaged controls. Herbivore subplots received two pairs of newly mated *A. hygrophila* on 24 August 2012. These beetles were offspring of field collected individuals from local populations reared on their original host plant *A. philoxeroides* in screen cages.

Data collection for field experiment

In order to test impacts of warming and herbivory on plant competition, we measured plant cover by species on 11 September 2012, and on 4 January; 8, 15, 22 March; 1, 17 April; 13, 28 May; and 4 November 2013 with the same quadrat method as used in the field survey. To test warming impacts on plant phenology, we counted the number of sprouted overwintering buds for each plant species and seedlings germinated from seeds for the native species with the same quadrat methods from 8 March to 17 April 2013.

In order to estimate the impacts of treatments on beetle abundance and to minimize disturbance, we counted beetle emergence holes on each plant species for each herbivore treatment subplot in December 2012 and late November 2013 when the beetles had diapaused. We placed a 0.5 × 0.5 m frame with 100 cells (each 5 × 5 cm) above the canopy in the middle of each subplot, visually counted beetle emergence holes in all cells and summed across cells to obtain the total number in each quadrat. In 2013, the emergence holes formed mostly on new shoots because those formed in 2012 had disappeared when the old shoots decomposed. During the whole trial, neither the native nor invasive species experienced total loss of aboveground tissues (i.e. leaves and stems) due to herbivory, because both plant species could recover rapidly from defoliation (Lu & Ding, 2010; Lu *et al.*, 2014).

In November 2013, we counted native species flower number in each subplot by the quadrat method, and we counted seed numbers for 10 randomly selected flowers in each subplot. Then we harvested all the aboveground tissues and sorted them to species. Aboveground tissues of the two plant species can be distinguished easily by their morphology. Then we dried plant aboveground tissues at 80°C for 48 h, and weighed them.

Data analysis for field experiment

We used mixed ANOVAs to test the impact of warming (whole-plot), plant species (split-plot factor), herbivore (split-plot factor), and their interactions (split-plot factor) on inter-annual change in plant cover (cover at the end of the second year – cover at the end of the first year) and plant aboveground biomass in monocultures and mixtures separately. We tested impacts of warming, herbivore, plant planting style (split-plot factor) and their interactions (split-plot factor) on the numbers of sprouted overwintering buds (in April), seedlings germinated from seeds (in April), flowers and seeds of the native with other mixed ANOVAs. We used mixed ANOVAs to test dependence of beetle abundance (emergence holes/average cover) on warming, plant planting type, plant species nested in plant planting type,and their interactions for each year separately. When significant interactive effects occurred, we examined differences among treatment combinations using adjusted means partial difference tests ($P < 0.05$). Data were square-root or log-transformed when necessary to meet assumptions of normality and homogeneity of variances.

In order to evaluate the role of warming and herbivore on competitive ability of the native species relative to the co-occurring invasive species, we calculated competitive ratio (CR) as (native species biomass in mixture/native species biomass in monoculture) ÷ (invasive species biomass in mixture/invasive species biomass in monoculture) (Willey & Rao, 1980). A CR < 1 indicates that the native species is less competitive than the co-occurring invasive species and a CR > 1 indicates that the native species is more competitive than the co-occurring invasive species (Willey & Rao, 1980).

In order to determine the mechanisms underlying the observed impacts of warming on the native and invasive species and their competition, we fitted a structural equation model (SEM) to specifically test for direct effects of warming on the native species and indirect effects mediated through the beetle and invasive species. SEM is a technique used for specifying and estimating models of direct and indirect linear relationships among variables. SEM can divide net effects into direct and indirect effects, and estimating their relative importance and thus is increasingly being chosen by researchers as a framework for understanding causal processes (Alsterberg *et al.*, 2013).

Results

Field surveys

Native plant life history shifted from annual to perennial with decreasing latitude, and the invader dominated plant communities only at high latitudes. In the April survey, there were negative relationships between latitude and native species stem length ($R^2 = 0.5748$, $P < 0.0001$) and stem length difference (R^2 = 0.3252, $P = 0.0015$) (Fig. 1a). Moreover, native species populations were perennial below 25.8°N (individuals from buds and seeds) but only annual populations (individuals only from seeds) were found between 26.5°N and 26.9°N (Fig. 1b). In the area above 26.9°N we observed only the invasive species (Fig. 1c). In the August–September survey, native species cover ($R^2 = 0.2232$, $P = 0.0073$; Fig. 1c) and the ratio of native to total cover ($R^2 = 0.1722$, $P = 0.0203$) decreased and invasive species cover marginally ($R^2 = 0.1196$, $P = 0.0566$; Fig. 1d) increased as latitude increased. Beetle abundance did not depend on latitude as a linear or quadratic function for either year (all $P > 0.05$; Fig. 1d).

Annual minimum (−1.42°C/° latitude; $R^2 = 0.8985$, $P < 0.0001$), annual average minimum (–0.89; $R^2 = 0.8678$, $P < 0.0001$) and annual average maximum temperatures (–0.85; $R^2 = 0.8790$, $P < 0.0001$), and annual precipitation (−57.9 mm/° latitude; $R^2 = 0.4057$, $P < 0.0001$) decreased, whereas annual maximum temperatures increased (+0.10; $R^2 = 0.0800$, $P = 0.0224$, Fig. S1) with increased latitude.

The observed competition patterns between the two species along the latitudinal gradient were driven mainly by temperature change. Multiple regressions with stepwise, backward and forward methods all came up with the same results, which indicated that the observed patterns were driven by temperature and precipitation changes. Multiple regressions indicated that native species cover, the ratio of native vs total cover and beetle abundance in the April survey were positively correlated with annual minimum temperature; however, invasive species cover was negatively correlated with precipitation and stem length difference between the two species was positively correlated with annual average maximum temperature (Table 1). In the August–September field survey, native species cover and the ratio of native to total cover were positively, and invasive species cover was negatively correlated with annual maximum temperature, but beetle abundance was not correlated with temperature or annual precipitation (Table 1).

Field experiment

Warming shifted the life history of the native plant from annual to perennial. Overwintering buds of both species sprouted before 8 March, whereas native seeds started to germinate on 15 March

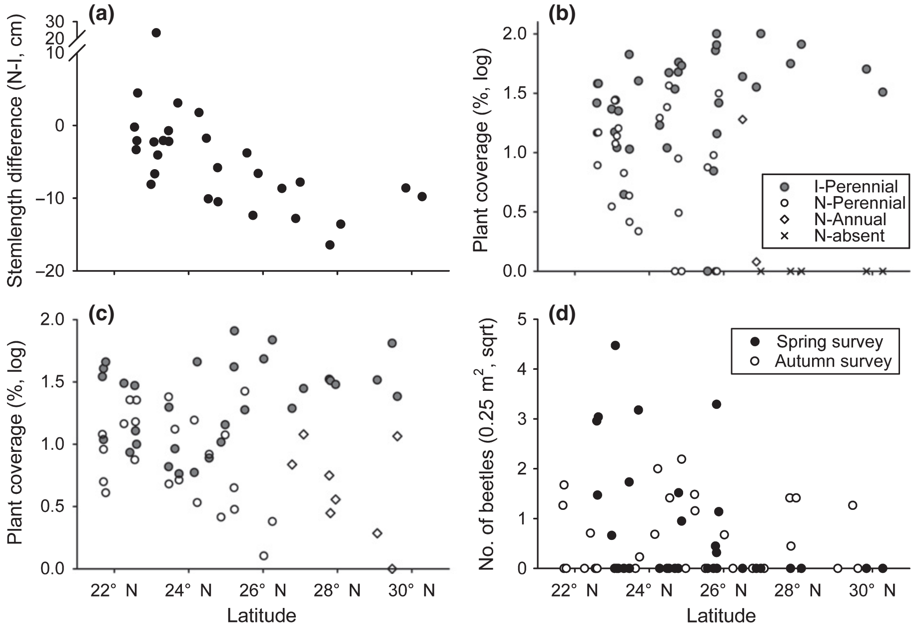

Fig. 1 (a) Stem length difference of the native (N, *Alternanthera sessilis*) vs invasive (I, *Alternanthera philoxeroides*) species (native plant stem length – invasive plant stem length) in April 2013, coverage [$\log_{10}(x + 1)$ transformed] of the two plant species in (b) April and (c) August to September 2013, and (d) beetle (*Agasicles hygrophila)* abundance in both surveys along a latitudinal gradient in our field surveys.

Table 1 Best-fitted model (multiple regression with stepwise, backward and forward methods) for the dependence of native (*Alternanthera sessilis*) and invasive (*Alternanthera philoxeroides*) species cover, native species proportion (native species cover/(native species cover + invasive species cover)), stem length differences between native and invasive species (native species stem length – invasive species stem length), and beetle (*Agasicles hygrophila*) abundance on annual minimum (January) and maximum (July) temperatures, annual average minimum (monthly averages) and maximum (monthly average) temperatures and annual precipitation along the latitudinal gradient in the spring (April) and autumn (August to September) field surveys

Variables	Predictor	R^2	Coefficient	t	P
Spring field survey					
Invasive species cover	Annual precipitation	0.1864	−0.0013	−2.67	0.0121
Native species cover	Annual minimum temperature	0.3841	0.1145	4.40	0.0001
Native species proportion	Annual minimum temperature	0.1779	0.0125	2.59	0.0145
Stem length difference	Annual average maximum temperature	0.4105	2.4627	4.26	0.0002
Beetle abundance	Annual minimum temperature	0.1542	0.1602	2.38	0.0238
Fall field survey					
Invasive species cover	Annual average maximum temperature	0.1874	−0.0659	−2.59	0.0150
Native species cover	Annual average maximum temperature	0.2461	0.0865	3.08	0.0045
Native species proportion	Annual average maximum temperature	0.2458	0.0190	3.07	0.0046
Beetle abundance	n/a				

n/a, not available.

in 2013 in mixtures (Fig. S3). Native overwintering buds sprouted only under elevated temperature (Figs 2a, S3b), and the number of buds in April was affected by the interaction of warming, herbivore and plant planting style (Table 2a).There were more sprouted buds in mixtures than in monocultures of the native species in the presence of the beetle under elevated temperature (Fig. 2a). Beetles increased the number of native sprouted buds in mixtures, but had no impact in monocultures under elevated temperature (Fig. 2a). Beetles decreased the number of native seedlings under elevated temperature with no impact under ambient temperature in monocultures; warming increased the number of native seedlings in the presence of the beetle, but had no impact in the absence of the beetle in mixtures (Table 2a; Fig. 2b).

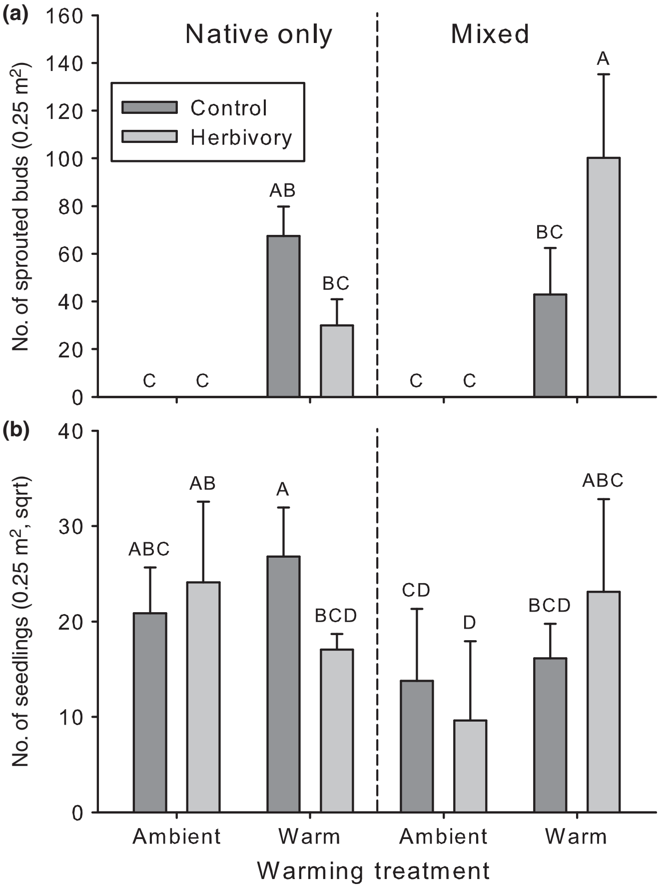

Fig. 2 Number of seedlings that germinated from (a) overwintering buds and (b) seeds of the native plant *Alternanthera sessilis* under ambient and warm temperatures in the presence (Herbivory) or absence (Control) of the introduced *Agasicles hygrophila* beetle when planted in monocultures (native only) or in mixtures with the invasive plant *Alternanthera philoxeroides* (mixed) in April 2013 in the field experiment. Each treatment combination was replicated four times. Means + 1 SE. Means with the same letters were not significantly different in *post hoc* tests, $P < 0.05$.

Interannual change in plant cover was affected only by plant species in monocultures (Table 2b), but was affected by the interaction of warming, herbivore and plant species in mixtures (Table 2b). In monocultures, interannual change of the invasive species cover was higher than that of the native species (Fig. S4a). In mixtures, invasive species cover increased less under elevated temperature in the presence of the beetle than under other conditions, whereas native species cover decreased less under elevated temperature than under ambient temperature at the end of the second year compared with the first year (Fig. S4b).

Warming increased beetles disproportionally on the invader. The number of beetle emergence holes per average area cover was affected only by plant species (Table 3) in the first year, corresponding to higher abundance of beetles on the invasive species than on the native species (Fig. 3a). In the second year, the beetle only emerged in mixtures and invader monocultures under elevated temperature, and in the mixtures there were more beetles on the invasive species than on the native species (Table 3; Fig. 3b).

Table 2 Effects of warming (Warm), herbivory (Herb), plant planting style (Plant) and plant species (species) on (a) the number of sprouted buds and seedlings per quadrat (0.25 m^2) of the native plant *Alternanthera sessilis* in April, the number of flowers and seeds per quadrat (0.25 m^2) of the native plant at the end of the field experiment, and (b) aboveground biomass and interannual change in plant cover in mixtures and monocultures. Warming was a whole-plot factor, other factors were split-plot factors, and there were four replicates of each treatment combination

		No. of sprouted buds		No. of seedlings			No. of flowers		No. of seeds	
(a) Effect	df	*F*	*P*	*F*	*P*	df	*F*	*P*	*F*	*P*
Warm	1, 10	**31.05**	**0.0002**	1.82	0.2072	1, 10	**44.7**	**< 0.0001**	4.07	0.0714
Herb	1, 14	0.21	0.6546	0.15	0.6999	1, 14	**32.29**	**< 0.0001**	0.65	0.4351
Warm × Herb	1, 14	0.21	0.6546	**0.08**	**0.0442**	1, 14	**10.02**	**0.0069**	0.13	0.7234
Plant	1, 14	1.12	0.3075	9.92	0.7828	1, 14	**90.02**	**< 0.0001**	**10.26**	**0.0064**
Warm × Plant	1, 14	1.12	0.3075	**3.41**	**0.0071**	1, 14	**41.36**	**< 0.0001**	**5.17**	**0.0393**
Herb × Plant	1, 14	**4.81**	**0.0457**	1.87	0.0859	1, 14	**46.91**	**< 0.0001**	0.11	0.7467
Warm × Herb × Plant	1, 14	**4.81**	**0.0457**	**6.77**	**0.0209**	1, 14	**9.84**	**0.0073**	**4.73**	**0.0472**

		Biomass in monoculture		Cover change in monoculture			Biomass in mixture		Cover change in mixture	
(b) Effect	df	*F*	*P*	*F*	*P*	df	*F*	*P*	*F*	*P*
Warm	1, 10	0.03	0.8609	0.05	0.8305	1, 8	**9.39**	**0.0155**	1.23	0.2994
Species	1, 14	**39.5**	**< 0.0001**	**35.08**	**< 0.0001**	1, 16	**218.95**	**< 0.0001**	**100.8**	**< 0.0001**
Warm × Species	1, 14	**12.03**	**0.0038**	3.45	0.0844	1, 16	**105.02**	**< 0.0001**	**20.25**	**0.0004**
Herb	1, 14	**14.21**	**0.0021**	2.45	0.1402	1, 16	2.33	0.1467	0.57	0.4598
Warm × Herb	1, 14	1.78	0.2036	0.04	0.8429	1, 16	0.35	0.5619	1.46	0.2451
Herb × Species	1, 14	4.46	0.0531	2.71	0.1221	1, 16	**43.97**	**< 0.0001**	1.25	0.2799
Warm × Herb × Species	1, 14	**9.33**	**0.0086**	1.31	0.2711	1, 16	**21.21**	**0.0003**	**5.82**	**0.0282**

Significant results are shown in bold.

Table 3 The effects of warming (Warm), plant planting style (Plant) and plant species (Species) nested in planting style on the introduced *Agasicles hygrophila* beetle abundance (number of emergence holes per average cover) in the first and second year of the field experiment. Warming was a whole-plot factor, other factors were split-plot factors, and there were four replicates of each treatment combination

		Beetle abundance in the first year		Beetle abundance in the second year	
Effect	df	*F*	*P*	*F*	*P*
Warm	1, 10	0.6	0.456	**66.3**	**< 0.0001**
Plant	1, 14	0.58	0.4583	**19.76**	**0.0006**
Warm × Plant	1, 14	0.70	0.4168	**19.76**	**0.0006**
Species (Plant)	2, 14	**9.51**	**0.0025**	**31.33**	**< 0.0001**
Warm × Species(Plant)	2, 14	3.05	0.0797	**31.33**	**< 0.0001**

Significant results are shown in bold.

Warming shifted plant communities from invader-dominated to native-dominated only in the presence of the beetle. Herbivores decreased invader biomass with no impact on native biomass under elevated temperature, and herbivores had no impacts on biomass of either species under ambient temperatures in monocultures (Table 2b; Fig. 4a). In mixtures, herbivores increased native biomass but decreased invader biomass under elevated temperature, and had no impact on either species under ambient temperature (Table 2b; Fig. 4b). In mixtures, the native species accumulated more aboveground biomass than the invasive species under elevated temperature and in the presence of the beetle (Fig. 4b), but the invasive species accumulated more aboveground biomass than the native species under other conditions (Fig. 4b).

Warming increased native plant performance only in the presence of both the beetle and the invader. Both warming and herbivores increased native flower and seed numbers, and the native species produced the most flowers (Fig. 5a; Table 2a) and seeds (Fig. 5b; Table 2a) when heated with the beetles in mixtures. Warming and herbivores had no impact on native species flower and seed numbers in monocultures (Figs 5a,b; Table 2a).

Warming and herbivores increased the competitive ability of the native species relative to the co-occurring invader. The invader was more competitive in the presence (CR = 0.021) and absence (CR = 0.039) of the beetle under ambient temperature. Warming reduced this advantage in the absence of the beetle (CR = 0.167) and the native was more competitive with beetles and warming (CR = 2.056; Fig. S5).

The SEM indicated that warming increased native biomass directly and increased beetle abundance, which, in turn, negatively affected native and invader biomass. Warming also decreased invader biomass which in turn positively affected native biomass (Fig. 6).

Discussion

In our field experiment, we found that warming increased native plant performance directly by shifting its life cycle from annual

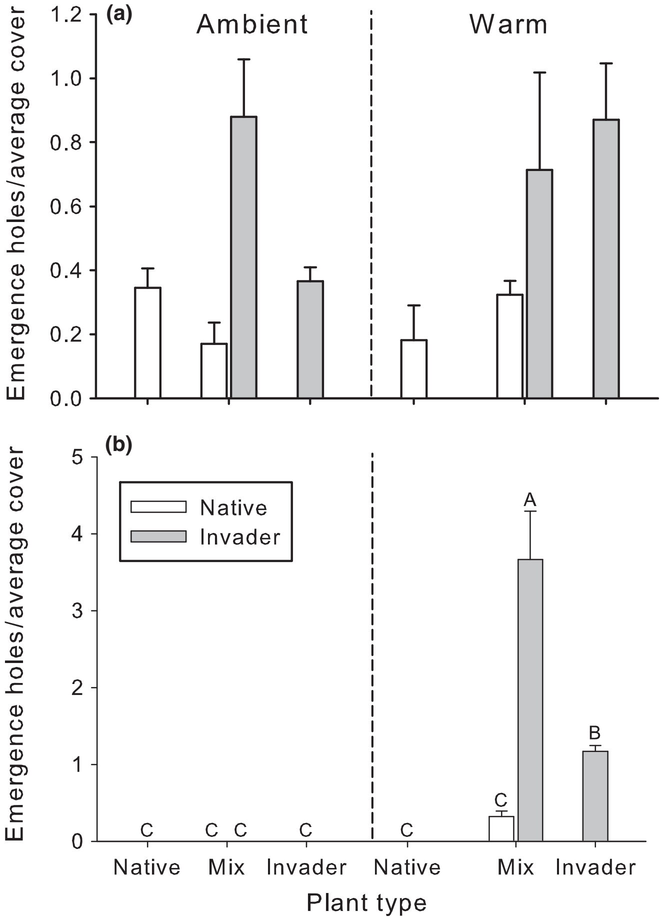

Fig. 3 *Agasicles hygrophila* beetle abundance on the native (*Alternanthera sessilis*) and invasive (*Alternanthera philoxeroides*) plant in monocultures and mixtures under ambient and warm temperatures in the field experiment. Each treatment combination was replicated four times. (a) Number of emergence holes per average cover (where 1 denotes 1 hole per 0.25 m^2 at 100% coverage) at the first year. (b) Number of emergence holes per average cover at the second year. Means + 1 SE. Means with the same letters were not significantly different in *post hoc* tests, $P < 0.05$.

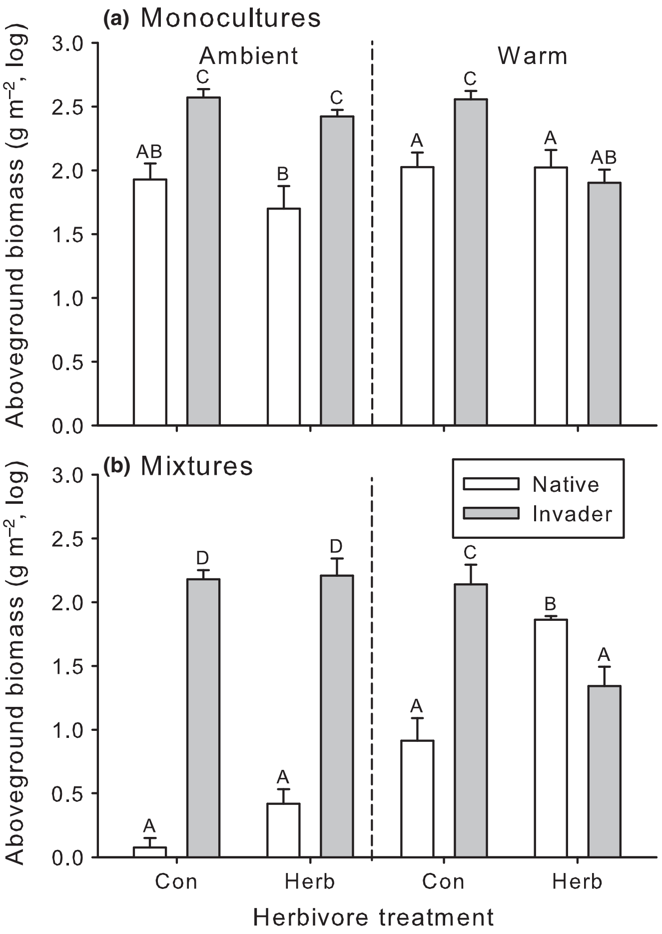

Fig. 4 Aboveground biomass of the native (*Alternanthera sessilis*) and invasive (*Alternanthera philoxeroides*) plants in (a) monocultures and (b) mixtures under ambient and warm temperatures in the presence (Herb) or absence (Con) of the introduced *Agasicles hygrophila* beetle at the end of the field experiment. Each treatment combination was replicated four times. Means + 1 SE. Means with the same letters were not significantly different in post-hoc tests, $P < 0.05$.

to perennial, and indirectly by releasing the native from competition via disproportionate increases in herbivory on the invasive plant that reduced invader performance. In field surveys we found the native species was more abundant at low latitudes than at high latitudes and the invader dominated only at higher latitudes (above 25.8°N). Together, these results may suggest that, under climate warming, herbivores contribute to the change from a plant community dominated by invasive species to one with abundant native species by releasing nonpreferred host species from competition. The results highlight the importance of biotic interactions, such as herbivory, in prediction of biological invasions and conservation of native species under climate change scenarios.

The competitive superiority of non-native species relative to their native competitors due to earlier emergence, higher phenotypic plasticity and herbivory tolerance is acknowledged as an important reason leading to their success in new environments (Kolar & Lodge, 2001; Wolkovich & Cleland, 2011; Drenovsky *et al.*, 2012). Results of our field surveys and field experiment suggest that earlier emergence, and not plasticity or herbivory tolerance, underlies the success of this invasive species in competing with its native congener. In the early spring (April) only the invasive species emerged above 26.5°N, although the native species was present at higher latitudes as evidenced in the autumn (August–September) survey, indicating earlier emergence of the invasive species in a large area. In addition, our field experiment demonstrated earlier emergence of the invasive species than the native species in the spring under ambient temperature due to its perennial life cycle and higher cold-tolerance (Lu *et al.*, 2015). Thus, earlier emergence was likely the main reason underlying dominance of the invasive species in areas where the native species was annual along the latitude gradient.

However, warming decreased the invasive species' seasonal priority by changing the life history of the native species in our study. Increasing temperature shifted the native species' life history from annual to perennial, but did not impact the life history

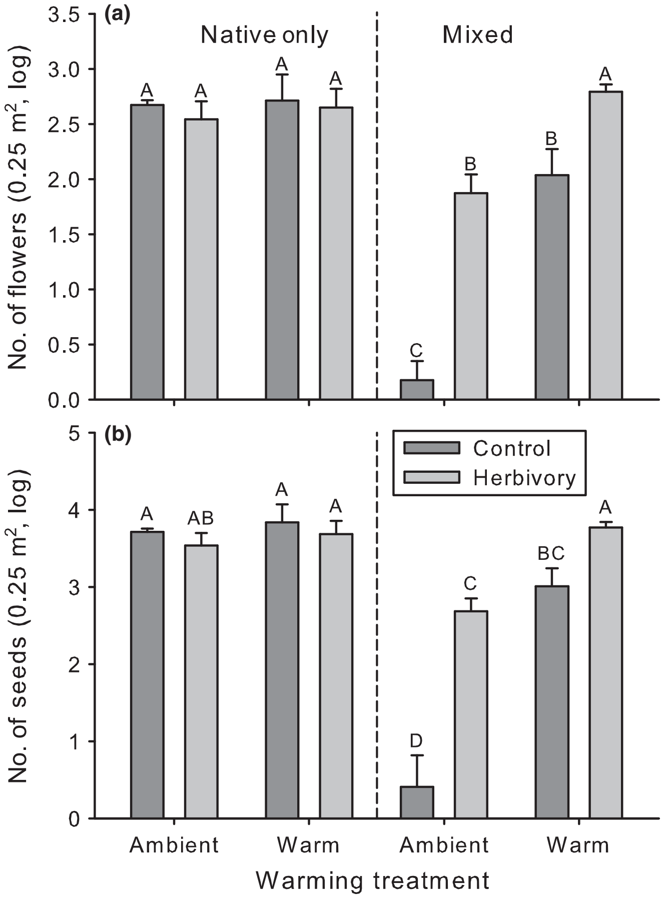

Fig. 5 Number of (a) flowers and (b) seeds of the native plant *Alternanthera sessilis* under ambient and warm temperatures in the presence (Herbivory) or absence (Control) of the introduced *Agasicles hygrophila* beetle when planted in monocultures (native only) or in mixtures with the invasive plant *Alternanthera philoxeroides* (mixed) at the end of the field experiment. Each treatment combination was replicated four times. Means + 1 SE. Means with the same letters were not significantly different in *post hoc* tests, $P < 0.05$.

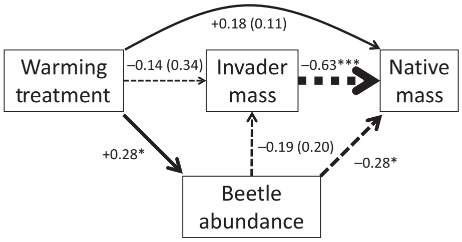

Fig. 6 Structural equation model of experimental warming effects on the native plant (*Alternanthera sessilis*), the invasive plant (*Alternanthera philoxeroides*) and beetle (*Agasicles hygrophila*) abundance directly and indirectly in our field experiment. Solid lines note positive effects, dashed lines note negative effects. Arrow widths are proportional to standardized path coefficients. Numbers adjacent to arrows are path coefficients (*P*-values). *, $P < 0.05$; ***, $P < 0.0001$.

of the perennial invasive species in both field surveys and the field experiment. Although warming increased native cover, aboveground biomass and competitive ability, it did not reduce dominance of the invasive species in the absence of the beetle. The results suggest that decreasing seasonal priority of the invasive species may partially contribute to the higher abundance of the native species at low latitudes. Our results agree with the view that climate change can affect plant phenology substantially (Cleland *et al.*, 2007) and the phenology of short-lived species is more sensitive to climate change than that of long-lived species (Morris *et al.*, 2008; Dalgleish *et al.*, 2010). However, some ecosystems are invaded mainly by annual plants (e.g. California grasslands) and these invasive species benefit from earlier emergence in competition with native species (Wolkovich & Cleland, 2011). In contrast to our system, climate warming may further favor these annual non-native invasive species by increasing their seasonal priority (Willis *et al.*, 2010; Chuine *et al.*, 2012). Together, these studies highlight the importance of plant phenology and its climate sensitivity in predicting non-native species invasions under warming climate conditions.

Herbivores that are expected to reduce the abundance of preferred host plants play an important role in non-native species invasion and responses of plant communities to climate warming (Keane & Crawley, 2002; Peters *et al.*, 2006). In our system, the introduced beetle uses the target invasive species as the major host, although it can also cause damage to the nontarget native species. Warming enabled the beetle to establish and sustain populations only in the presence of the invader that is a suitable overwintering host. Heavier herbivory on the preferred invasive host suppressed its performance and indirectly released the native species from competition in mixtures under elevated temperature. As a result, the beetle enhanced the positive effects of warming on the native species (aboveground biomass, flower number and competitive ability), and shifted plant communities to native species dominance under warming temperature. Consistent with this, the beetle was more abundant and suppressed the invasive species in low latitudes, but had limited impacts in high latitudes (Lu *et al.*, 2013).These results suggest that the biocontrol beetle may play a key role in determining the outcome of competition between the native and invasive species under warming climate conditions.

Similar to the biocontrol beetle, some native herbivores, including insects, mammalian herbivores and molluscs, prefer non-native species over native species and thus reduce invasion success of non-native species (Parker *et al.*, 2006). Given the importance of herbivore host preference in determining plant community responses to climate change, as suggested by the present study, we predict that climate change may increase biotic resistance arising from native herbivores that prefer non-native species. However, it is also the case that a large number of native herbivores prefer native species over non-native species, which results in enemy release for non-native species (Maron & Vilà, 2001). Warming can affect species phenology and abundance, and species of differing trophic levels such as herbivorous insects and plants may differ in their sensitivity to climate changes (Voigt *et al.*, 2003). Therefore, climate warming may also increase the degree of enemy release. The net effects of herbivores on non-native species invasions will be determined by herbivore community composition, species-specific host preferences and warming impacts on herbivore abundance in target regions.

In summary, this study shows that herbivores can affect the impact of climate warming on non-native species invasions and native species recovery. Consistent with other studies, we found that climate warming changed species' phenology/life history, and altered seasonal priority due to earlier emergence of non-native species relative to native competitors. Because we used only one genotype of the native species in our study, it needs to be clarified whether the observed effects of warming and herbivory on native plants were specific to this genotype. Our findings that the native species dominated communities only in the presence of the beetle under warming temperature highlight the importance of herbivores in shaping plant communities and non-native species invasions with climate change. Thus, understanding how biotic interactions shape the responses of plant community to climate change is crucial for predicting non-native species invasions and conserving native plant species.

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Author contributions

X.L. and J.D. planned and designed the research; X.L., M.H., H.W. and X.S. carried out the field surveys and field experiment; X.L., J.D. and E.S. analyzed data, interpreted the results and wrote the manuscript.

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Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

Fig. S1 Sites for the field surveys and temperature and precipitation changes along the latitudinal gradient.

Fig. S2 Diagram of the warming experiment conducted in the field.

Fig. S3 Dynamics of bud sprouting of the native (*Alternanthera sessilis*) and invasive (*Alternanthera philoxeroides*) plants, and seedling germination of the native plant in mixture plots of the field experiment in spring 2013.

Fig. S4 Interannual change in cover of the native (*Alternanthera sessilis*) and the invasive (*Alternanthera philoxeroides*) plants in monocultures and mixtures in the field experiment.

Fig. S5 Competitive ratios of the native plant *Alternanthera sessilis* relative to the invasive plant *Alternanthera philoxeroides* under varying treatments in the field experiment.