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Climate and geographic adaptation drive latitudinal clines in biomass of a widespread saltmarsh plant in its native and introduced ranges

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Abstract

Introduced plants provide a unique opportunity to examine how plants respond through plasticity and adaptation to changing climates. We compared plants of *Spartina alterniflora* from the native (United States, 27–43°N) and introduced (China, 19–40°N) ranges. In the field and greenhouse, aboveground productivity of Chinese plants was greater than that of North American plants. Aboveground biomass in the field declined with increasing latitude in the native range, a pattern that persisted in the greenhouse, indicating a genetic basis. Aboveground biomass in the field displayed hump-shaped relationships with latitude in China, but this pattern disappeared in field and greenhouse common gardens, indicating phenotypic plasticity. Relationships in both geographic regions were explained by temperature, which is probably the underlying environmental factor affecting aboveground biomass. *S. alterniflora* has evolved greater biomass in China, but in the four decades since it was introduced, it has not yet evolved the genetic cline in biomass seen in its native range. By working at lower latitudes in the introduced range than have been sampled in the native range, we identified an optimum temperature in the introduced range above which aboveground productivity decreases.

Geographic gradients in abiotic conditions such as temperature are important determinants of geographic patterns in species distributions (Walther 2003) and productivity (Berry and Bjorkman 1980; Larjavaara and Muller-Landau 2012). Organisms may respond to climate heterogeneity by phenotypic plasticity or adaptation (Aitken et al. 2008; Pereira et al. 2017). The ability to tolerate climate heterogeneity by matching phenotype to the local environment through one or both of these mechanisms can facilitate or constrain the dispersal and growth of organisms, thereby affecting species ranges (Angert et al. 2011).

Recent increase in global temperature is predicted to have widespread consequences for the distribution and abundance of organisms (Parmesan 2006; Jiang et al. 2017). As temperatures increase, areas of suitable climate will shift poleward and upward in elevation for many species (Burrows et al. 2014). If the rate of global warming exceeds the ability of individuals to respond, local populations will become maladapted to the novel climatic conditions in their current range (Franks et al. 2014; Catullo et al. 2015). Understanding whether geographic clines in the phenotype are based on plasticity or genetic mechanisms is important for predicting the effects of climate change (Woods et al. 2012; Castillo et al. 2014; Li et al. 2016; van Boheemen et al. 2019), because plasticity will in most cases offer a more effective response to rapid abiotic changes.

Climate presents a particular challenge for invasive species, because a single introduction event will consist of individuals adapted only to the particular climatic conditions that occur at the origin site (Rejmánek and Richardson 1996). Some invasive species may have succeeded because they were introduced multiple times from different source populations (Dlugosch and Parker 2008). In the case of invasives sourced from single populations or regions (Bossdorf et al. 2005), however, if an introduction is to spread, the introduced individuals have to either evolve new genetic clines related to climate or acclimate to a wide range of climates via phenotypic plasticity (Maron et al. 2004; Davidson et al. 2011). Thus, "natural experiments" offered by the spread of invasive species offer unparalleled insights into the mechanisms by which plants may respond to changing climate at large spatial scales and at decadal

timescales relevant to understanding global change (Moran and Alexander 2014).

Salt marshes are among the most productive ecosystems in the world and provide numerous ecosystem services and economic benefits (Barbier et al. 2011). Many of these services stem from the productivity and standing biomass of salt marsh systems (Kirwan and Murray 2007). Productive plants promote accretion by trapping sediment and producing belowground biomass, allowing some resilience to relative sea level rise (Kirwan and Megonigal 2013). Previous works indicated that elevated CO_2 level (Langley et al. 2009) and warmer temperatures (Kirwan and Mudd 2012) could increase the ability of marshes to survive accelerated sea level rise by increasing plant productivity and marsh vertical accretion. Other works, however, indicate that, above some critical value, high temperatures will be stressful to marsh plants, leading to lower productivity (Giurgevich and Dunn 1979; Więski and Pennings 2014; Li et al. 2018). Marshes can also persist on the landscape by moving inland as terrestrial habitats submerge, if the shoreward habitat is not blocked by human-made structures (Kirwan and Megonigal 2013; Strong and Ayres 2013).

The dominant plant in North American salt marshes is the grass *Spartina alterniflora*, with a latitudinal range of 27–45°N (Kirwan et al. 2009). *S. alterniflora* was introduced to China in 1979 at Luo Yuan Bay, Fujian Province (26.5°N) from three source populations in the U.S.A.: Morehead City, North Carolina (34.7°N), Sapelo Island, Georgia (31.4°N), and Tampa Bay, Florida (27.7°N) (Xu and Zhuo 1985). *S. alterniflora* now occurs over ~ 20° of latitude in China (An et al. 2007; Liu et al. 2016), from 19°N to 40°N. This has been the largest *Spartina* invasion in the world, and extends to lower latitudes than *S. alterniflora* occupies in North America (Strong and Ayres 2013).

Most previous works indicate that *S. alterniflora* productivity increases with warmer temperatures. There is a strong latitudinal gradient in aboveground biomass across the Atlantic and Gulf Coasts of North America, where biomass in low latitudes is approximately twice as high as biomass in high latitudes (Turner 1976; Kirwan et al. 2009; Crosby et al. 2017). Experimental warming in the northeastern United States, and greenhouse warming experiments, also indicates that productivity increases with temperature (Charles and Dukes 2009). However, studies done at low latitudes suggest that *S. alterniflora* has a relatively low temperature optimum for photosynthesis that could be exceeded with future climate warming. For example, gas exchange measurements suggest that net carbon assimilation (photosynthesis minus respiration) begins to decrease at temperatures typical of summer maximum daily temperatures in Georgia (Giurgevich and Dunn 1979). Consistent with these results, Więski and Pennings (2014) found that annual productivity of *S. alterniflora* in Georgia decreased in warmer years. To date, a decrease in plant biomass at low latitudes has not been observed in geographic studies within the native range of *S. alterniflora*,

perhaps because marshes are replaced by mangroves at low latitudes (below 27°N latitude) in North America. Because invasive *S. alterniflora* grows abundantly from ~ 19°N to ~ 40°N latitude along the coast of China, coexisting with mangroves over the lower latitude part of this range (Zhang et al. 2012), examining latitudinal patterns of plant aboveground biomass in China, where *S. alterniflora* also occupies a wide latitudinal range, should reveal any negative effects of high temperatures.

The phenotype of *S. alterniflora* varies dramatically across latitudinal gradients in its native and introduced ranges (Strong and Ayres 2013; Liu et al. 2016). In its native range in North America, *S. alterniflora* varies across latitude in stem height and diameter (Seliskar et al. 2002; Travis and Grace 2010), flowering time (Crosby et al. 2015), palatability to herbivores (Salgado and Pennings 2005), and other traits (Elsey-Quirk et al. 2011). Much of this latitudinal variation has a genetic basis (Seliskar et al. 2002; Travis and Grace 2010; Salgado and Pennings 2005; Elsey-Quirk et al. 2011). Similarly, the phenotype of *S. alterniflora* varies dramatically across latitudinal gradients in China; however, most of this variation appears to be due to phenotypic plasticity (Liu et al. 2016, 2017), perhaps because plants have not had time to evolve genetic clines in the four decades since their introduction. The only exception to this pattern is sexual reproduction, which appears to be under strong selection for high seed set at high latitudes in China (Liu et al. 2016, 2017). The only study to look at latitudinal variation in *S. alterniflora* biomass in China did not find a latitudinal pattern in biomass (Zheng et al. 2018), but was a literature review of primary studies that used different methodologies at different sites, and covered only a portion (24–34°N) of the geographic range of *S. alterniflora* in China.

Here, we compare aboveground biomass of *S. alterniflora* in two geographic regions (North America [native] and China [introduced]). First, we tested whether the latitudinal pattern in aboveground biomass of *S. alterniflora* was the same or different in its native and introduced ranges. Second, we tested whether the relationship between aboveground biomass and temperature was the same in the native and introduced ranges. Third, we used common garden experiments in the field and greenhouse to determine the relative importance of phenotypic plasticity and genetic adaptation in producing these geographic clines.

Materials and methods

Study sites and field sampling

S. alterniflora is continuously distributed along the East and Gulf coasts of the U.S.A., so we sampled 13 geographical locations at intervals of 1–2° of latitude along the East Coast, and additional 3 locations within the Gulf Coast (Fig. 1a; Table S1). The locations ranged over 16° of latitude from 27.7°N (Florida) to 43.3°N (Maine). *S. alterniflora* is discontinuously distributed in the introduced range, limiting our ability
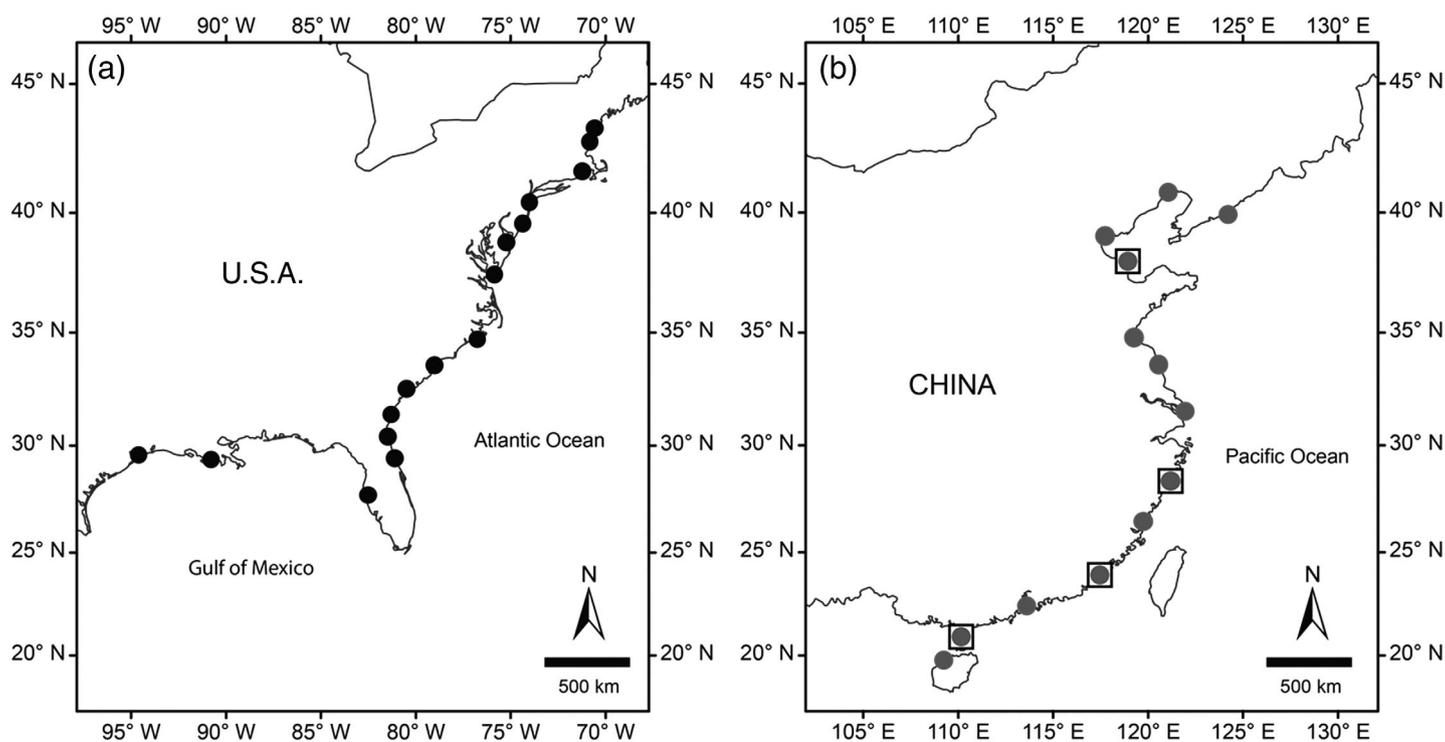
Fig. 1. Map of field sites in the native (U.S.A., black circle: **a)** and introduced (China, gray circle: **b)** ranges. Survey sites are indicated with circles; four field common garden sites are indicated with squares in the introduced range.

to find study sites, so we sampled 13 geographical locations at intervals of 1–2° of latitude in China (Fig. 1b; Table S1). These locations ranged over 20° of latitude from 19.5°N (Hainan province) to 39.9°N (Liaoning province). All sampling was conducted from September to November 2014, except for three sites (Danzhou, Dandong, and Hulu Island) in China that were sampled from September to October 2015, which represented the end of the growing season at all locations. At this time, the peak of flowering had passed and plants were beginning to senesce. Year to year variation can affect plant biomass in *S. alterniflora* (Więski and Pennings 2014), but this variation is weaker than the latitudinal patterns (Liu et al. 2016).

At each location, we worked at two sites, 2–3 km apart. At each site, we sampled five 0.5 × 0.5 m quadrats, with at least 30 m spacing between quadrats. *S. alterniflora* plants vary in height across elevation within a marsh, with "tall-form" plants achieving the greatest heights and standing biomass (Richards et al. 2005). All quadrats were deployed in tall-form *S. alterniflora* where *S. alterniflora* grows along the creekbank or low in the marsh in order to standardize sampling among sites and countries.

We harvested the aboveground biomass from each quadrat and weighed it in the field. A single representative shoot from each quadrat was taken to the laboratory, dried at 60°C to constant mass, and weighed. The dry mass : fresh mass ratio of these shoots was used to calculate dry mass for each

quadrat. Data from the 10 quadrats at each location were pooled to give a single value per location.

Field common gardens in the introduced range

To evaluate the relative importance of abiotic conditions and plant genetic variation in driving latitudinal patterns in aboveground biomass within the introduced range, we established four common gardens along the East Coast of China spanning ~ 20° of latitude (Fig. 1b). The low-latitude sites were located at Leizhou in Guangdong province (20.9°N), mid-latitude sites at Yunxiao in Fujian province (23.9°N), and Yueqing in Zhejiang province (28.3°N), and the high-latitude sites at Dongying in Shandong province (38.0°N). The common garden sites were established in intertidal mudflats in the field in the vicinity of existing *S. alterniflora* populations. Each garden was established from March to April 2013 (Yunxiao garden) or 2014 (Leizhou, Yueqing, and Dongying garden). Each common garden consisted of 10 plots spaced at least 5 m apart. Each plot consisted of 10 PVC tubes (16 cm in diameter and 33 cm deep). Plant germinated from a single-seed family (defined as a single quadrat) from each location was haphazardly assigned to one of the 10 pipes in each garden and allowed to grow until one or two shoots in most PVC tubes flowered, which took one (Yunxiao garden) or two (Leizhou, Yueqing, and Dongying gardens) growing seasons. As plants in each garden senesced, we harvested all aboveground biomass within each PVC tube, dried it, and weighed it from

September to November 2013 (Yunxiao garden) and 2015 (Leizhou, Yueqing, and Dongying gardens). More detailed methods and experimental results for plant height, shoot density, flowering, and seed set are presented in Liu et al. (2016, 2017).

Greenhouse common garden

Although we could plant field common gardens with the introduced populations of *S. alterniflora* in the introduced range, we could not include genotypes from the U.S.A. because we did not want to cause the introduction of additional genotypes to China. Therefore, to compare the importance of genetic differences and phenotypic plasticity in creating the latitudinal patterns of biomass between the native and the introduced ranges, we conducted a common garden experiment in a greenhouse at the Xiang'an campus of Xiamen University (24°37′N, 118°18′E). The common garden consisted of 10 rectangular plastic pools (length: 1.2 m, width: 0.9 m, depth: 0.3 m). Each plastic pool contained 26 plastic buckets (18 cm in diameter and 24 cm deep), which were grouped into five rows and six columns. Each bucket was filled with a mixture of 50% Jiffy's peat substrate (Jiffy Products International BV, Moerdijk, the Netherlands) and 50% vermiculite by volume. Each bucket had four 1 cm diameter holes in the sides and one hole in the bottom to allow exchange of water with the water in the pool.

In March 2015, seeds from each seed family that had been collected during the 2014 field sampling expeditions were germinated and grown in a growth chamber until seedlings were approximately 5 cm tall. One haphazardly chosen seedling per seed family (160 from the U.S.A.; 100 from China) was transplanted into a single, haphazardly selected plastic bucket, with each location (16 from the U.S.A.; 10 from China) replicated once in each pool, and a separate seed family from each location in each pool. Pools were filled with artificial sea water (10 PSU) that had been amended with fertilizer (C:N:P 15-15-15; 0.5 g per bucket) to ~ 2 cm above the soil level in the pots. Water in the pools was completely replaced once a month but without additional fertilizer. Salinity was checked every other day and freshwater was added as needed to maintain salinity.

We harvested all the aboveground biomass from each bucket on 15 October 2015, after most plants had senesced. Biomass was dried at 60°C to constant mass and weighed. In March 2016, we separated a 15–20-cm-long rhizome bearing one or two shoots from each clone, transplanted the rhizome into a new bucket in a new soil mixture, and fertilized the pool as above. Plants were cultivated and biomass measured in October 2016 to give 2 years of data.

Abiotic data

To relate the aboveground biomass of *S. alterniflora* to abiotic conditions, we collected six soil samples near the quadrats at each location during field sampling. Replication was reduced to three at a few locations for logistic reasons. We measured porewater salinity (PSU) using the soil rehydration method (Pennings and Richards 1998). We measured the carbon and nitrogen contents of a subsample of each soil sample with a Vario ELIII elemental analyzer after the soil subsample was air dried in the laboratory and pulverized using an oscillating mill.
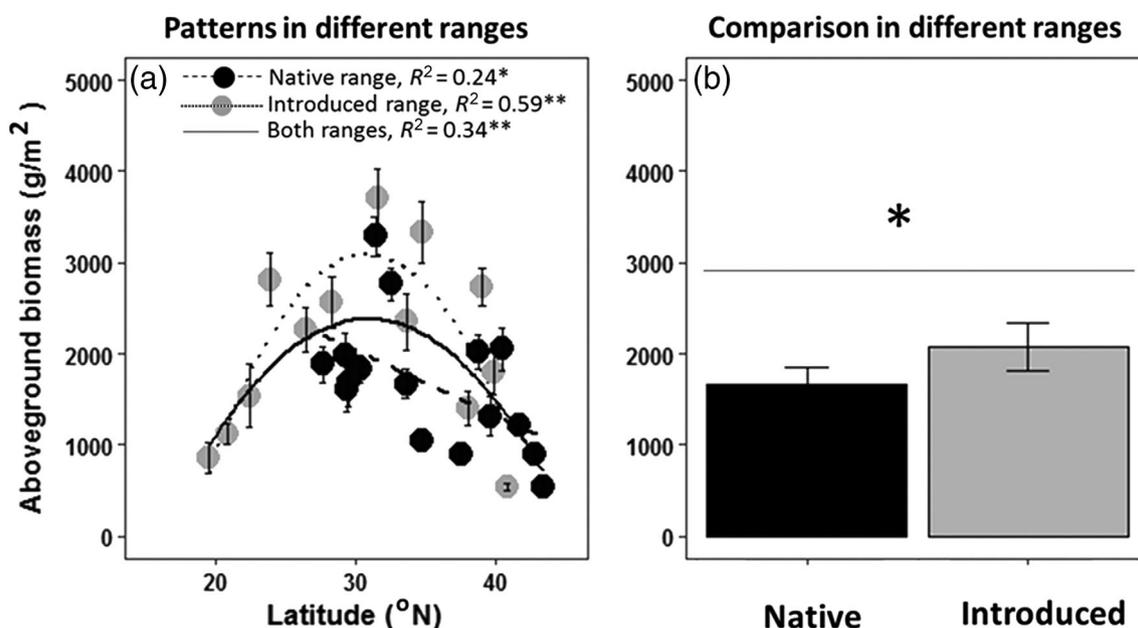

Fig. 2. Aboveground biomass of *Spartina alterniflora*: **(a)** field survey in relation to latitude in the native and introduced ranges. **(b)** Average over all sites for the native and introduced ranges. Significance levels: *$p < 0.05$; **$p < 0.01$.

To relate the aboveground biomass of *S. alterniflora* to climate, we calculated annual mean temperature, the annual number of growing degree days (> 10°C), annual mean precipitation and annual mean tidal range for each location using climate data (1981–2010) and tide range (2013–2015) from NOAA (NCDC, http://www.ncdc.noaa.gov) for sites in the U.S.A. China climate data (1981–2010) and tide data (2004–2013) were obtained from the stations closest to each site in the Climate Information for the China meteorological data sharing service system (http://cdc.nmic.cn/), and in the tide tables published by the National Marine Data & Information Service (http://www.nmdis.gov.cn). Moreover, we also collected climate data during experiment (2013–2015) from the above website to compare the climate differences between years. Growing degree days is a measure of how much daily temperatures exceed a threshold temperature necessary for significant plant growth and therefore reflects both the temperature and the duration of the growing season (Miller et al. 2001).

Statistical analysis

For statistical analyses of field data, results from replicate plots were averaged to yield a single data point for each location. For analysis of greenhouse and field common garden data, results for the surviving seed families (3–10, Table S2) at each location were averaged to yield one single data point for each location. For both field and common garden data, we used linear and quadratic regression to examine potential relationships between aboveground biomass and various predictor variables, including latitude of origin, annual mean temperature, annual growing degree days, annual mean tidal range,

and soil pore-water salinity. We compared aboveground biomass in the field and common garden between the native and introduced ranges using *t*-tests. Range and latitude interaction of aboveground biomass were tested by mixed model with range, latitude, latitude^2, range × latitude, range × latitude^2 as fixed factors, and subsite as random effect due to no replicates for each seed family in the field survey and greenhouse common garden. The quadratic latitude term was dropped from the model if it is not significant. Because the same clones were analyzed in the 2 years of the common garden and aboveground biomass changed in mean scores over years, we used repeated-measures ANOVA (mixed model) to compare aboveground biomass between the introduced and native ranges to develop a time course for the range effect. We used a mixed model with garden location, latitude, garden location × latitude as fixed factors, and seed family as the random effect in the field multiple common gardens in the introduced range. Moreover, we used multivariate correlations to analyze the relationships between latitude and abiotic variables in the introduced and native ranges separately. In an effort to determine the relative influence of the different abiotic factors on aboveground biomass, we examined a full model (Best regression model) consisting of range, temperature (or temperature^2 for nonlinear relationships), precipitation, tide range, range × temperature (or temperature^2 for nonlinear relationships), range × precipitation, and range × tide range to detect the most important factors. Best regressions were selected using stepwise regression based on AIC. We performed all data analyses with the R statistical software (R Development Core Team 2016).
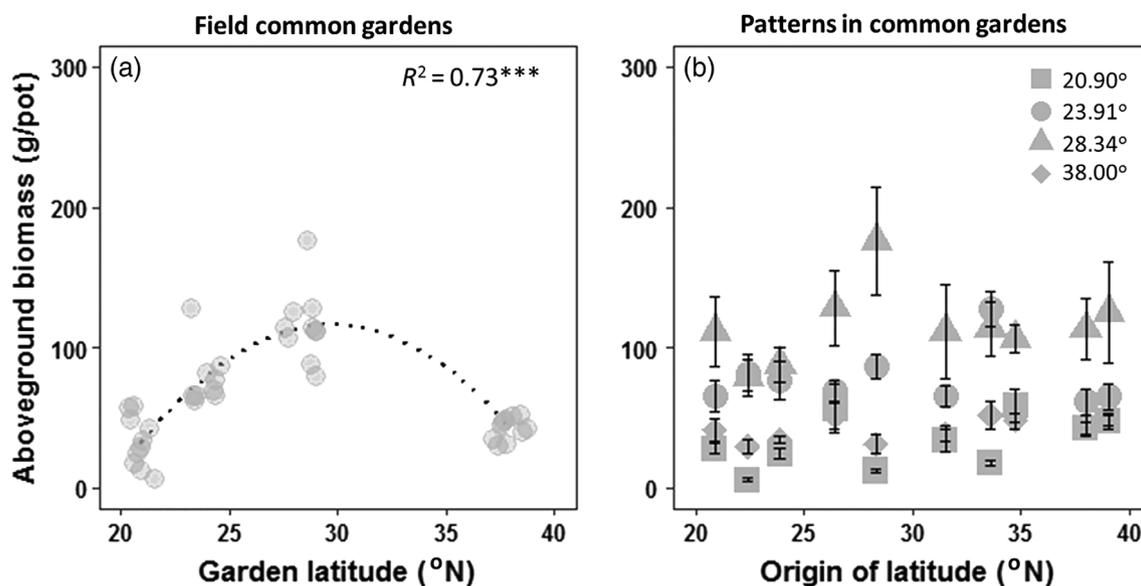

Fig. 3. Aboveground biomass of *Spartina alterniflora*: **(a)** 10 field locations grown in four common gardens relation to latitude in the introduced range. **(b)** Relationships between aboveground biomass and latitude of origin for four common gardens; biomass was not related to latitude of origin. Significance level: ***p < 0.001.

Results

Abiotic conditions across latitude in the introduced and native ranges

The abiotic variables measured were correlated with each other (Fig. S1). In particular, latitude, annual average temperature, annual number of growing degree days, and annual precipitation were strongly correlated with each other. The best multiple regression models for *S. alterniflora* aboveground biomass identified average temperature and salinity as the best predictors of variation in *S. alterniflora* aboveground biomass in the field and field common gardens (Table S3).

Relationship between *S. alterniflora* aboveground biomass and latitude

The aboveground biomass of *S. alterniflora* in the native range decreased with increasing latitude (Fig. 2a). In the introduced range in China, however, which included sites from lower latitudes than were sampled in the native range, biomass showed a hump-shaped relationship with latitude. The relationships differed among ranges (Table S4a). Moreover, the regression relationship peaked at values ~ 1/3 greater than in the native range. Across all the sites, aboveground biomass in the Chinese range was 15% greater than and differed from that in the native range (Fig. 2b; Table S4a). If the data from
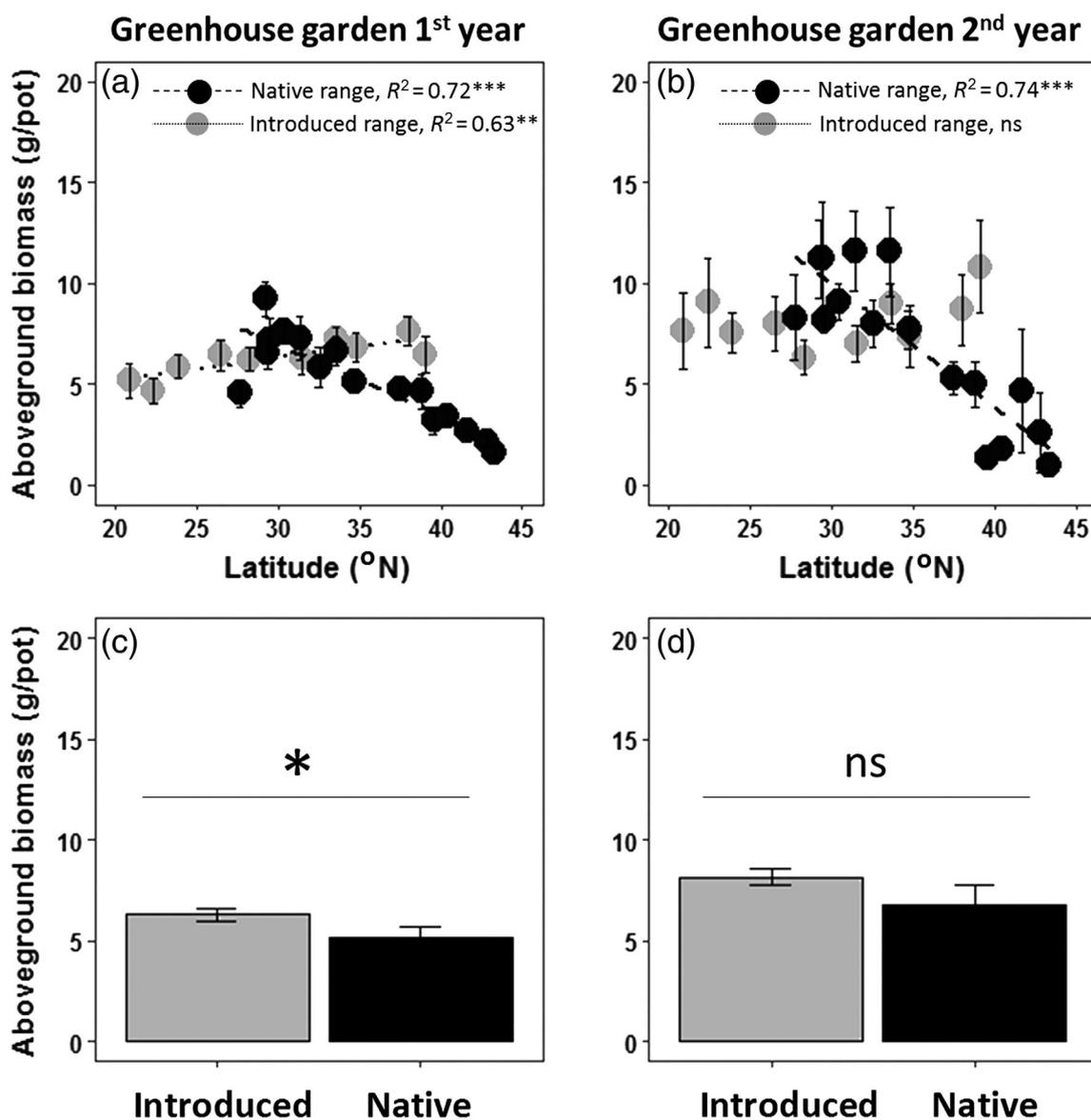

Fig. 4. Aboveground biomass of *Spartina alterniflora* in relation to latitude in the native and introduced ranges in the greenhouse common garden **(a)** in the first year and **(b)** second year; overall average for field populations grown in greenhouse common garden **(c)** in the first year and **(d)** second year; native range (U.S.A.) n = 16 locations; introduced range (China) n = 10 locations. Significance levels: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.
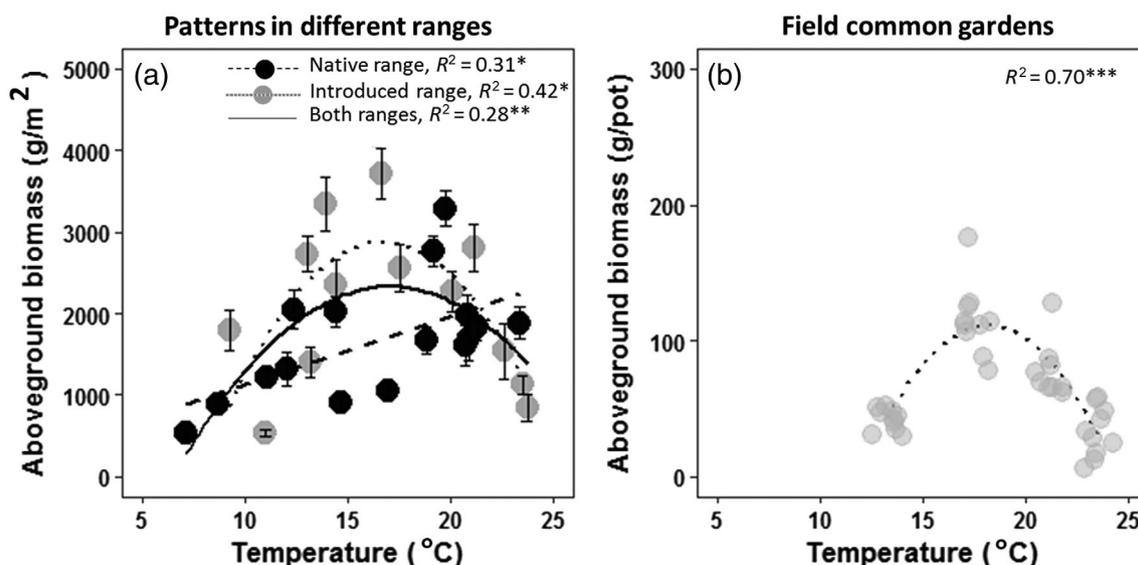
Fig. 5. Field aboveground biomass of *Spartina alterniflora* in relation to annual mean temperature **(a)** in the native and introduced ranges and **(b)** in the field common gardens. Significant levels: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

both ranges were pooled, they showed a hump-shaped relationship with latitude (Fig. 2a).

Aboveground biomass variation in field and greenhouse common gardens

In the four field common gardens in China, aboveground biomass of *S. alterniflora* showed a hump-shaped relationship with garden latitude (Fig. 3a). However, aboveground biomass did not vary with latitude of origin (Fig. 3b; Table S4b).

In the greenhouse common garden, aboveground biomass of *S. alterniflora* plants from the native range decreased with latitude of origin in both years (Fig. 4a,b). However, aboveground biomass of plants from China showed a weak positive relationship with latitude in the first year and no relationship in the second year (Fig. 4a,b). Averaged across all locations of origin, aboveground biomass of plants from the introduced range tended to be higher than biomass of plants from the native range, but this difference was only statistically significant in the first year (Fig. 4c,d; Table S4c,d). Otherwise, for the two-year greenhouse common garden, with years considered in the aggregate using repeated measure ANOVA, there is no significant difference between range, but differ among years (Table S4e).

Relationship between *S. alterniflora* aboveground biomass and temperature

Whether in the field or in the common gardens, end-of-season aboveground biomass of *S. alterniflora* was correlated with annual mean temperature. In the native range, biomass increased linearly with temperature (Fig. 5a). In China, biomass showed a hump-shaped relationship with temperature, peaking at ~ 17°C (Fig. 5a). If the data from both ranges were pooled to

identify an overall pattern, they showed a hump-shaped relationship with temperature. Similar results were obtained using annual growing degree days instead of annual mean temperature (Fig. S2a). In the field common gardens, biomass again showed a hump-shaped relationship with the annual mean temperature of the common gardens, again peaking at ~ 17°C (Fig. 5b). Similar results were obtained using annual growing degree days instead of annual mean temperature (Fig. S2b).

We found aboveground biomass increased with tide range (Fig. S3a), and decreased with soil pore-water salinity (Fig. S3b). However, we did not find other correlations with annual mean precipitation, soil C, N, and C : N ratios (data not shown).

Discussion

We found strong evidence for hump-shaped relationships between *S. alterniflora* aboveground biomass and latitude in introduced plants (Fig. 2a), which contrasts with our findings (Fig. 2a), and previous work (Turner 1976; Kirwan et al. 2009) showing a continuous increase in biomass with decreasing latitude in native plants in North America. The most likely abiotic driver of these patterns is temperature, which also showed a hump-shaped relationship with aboveground biomass in the introduced range. This, together with other data from the native range, indicates that there is an optimum temperature for *S. alterniflora* productivity, beyond which warmer temperatures lead to reduced *S. alterniflora* productivity.

Niche theory predicts that a species should perform optimally in the middle of its latitudinal range, with decreased performance toward higher or lower latitudes (Cody 1991). Many geographically widespread species show this pattern (Moles et al. 2009). Given this, it is surprising that past studies

of geographic variation in *S. alterniflora* in its native range (considering sites at 27°N and higher latitudes) found that biomass increased linearly from high to low latitudes (Turner 1976; Kirwan et al. 2009; Crosby et al. 2017). In contrast, studies of *S. alterniflora* shoot height in China that considered sites at latitudes as low as 20°N found a hump-shaped pattern, but they did not report on plant biomass (Liu et al. 2016, 2017). Here, we show that *S. alterniflora* biomass exhibits a hump-shaped pattern vs. latitude in China. Moreover, because the humps peak around the latitudes that represent the lowest-latitude sites sampled in North America, it is likely that previous studies from North America did not find a hump-shaped pattern simply because they did not sample at sufficiently low latitudes.

In the native range, *S. alterniflora* is replaced by mangroves at low latitudes in the Mississippi River deltaic plain (McKee et al. 2004), Florida (Osland et al. 2013), and Texas (Guo et al. 2013). In contrast, intertidal areas in southern China have large areas suitable for *S. alterniflora* but below the elevations at which local mangroves occur (Zhang et al. 2012), allowing *S. alterniflora* to spread to lower latitudes than those it occupies in its native range.

Although we have plotted data as a function of latitude, plants are not responding to latitude per se but to some abiotic factor(s) that correlate with latitude (Fig. S1; Hijmans et al. 2005). The most likely candidate is temperature (Table S3). Our results demonstrating climate-related geographic adaptation in productivity of *S. alterniflora* are consistent with other research that has shown strong localized temperature adaptation in both experimental and natural settings (Kirwan et al. 2009; Liu et al. 2016). At high latitudes, cold temperature limits the survival of *S. alterniflora* (Idaszkin and Bortolus 2011), and rising temperatures are likely to increase annual net primary production (ANPP) (Charles and Dukes 2009). In contrast, unusually high temperatures at low latitudes are likely to decrease ANPP (Dunn et al. 1987; Więski and Pennings 2014; Liu and Pennings 2019). Thus, our finding of a hump-shaped relationship between aboveground biomass and average temperature across large areas in the introduced range is consistent with previous site-specific work, and indicates an optimum annual average temperature of ~ 17°C for *S. alterniflora* productivity.

Previous studies at particular sites suggested additional controls on biomass, including river discharge and rainfall (Więski and Pennings 2014), both of which affect salinity (Snedden et al. 2015) and tide range (Turner 1976; Snedden et al. 2015). Thus, temperature is not the only relevant causal factor of plant productivity. For example, biomass increases with tidal range and decreases with salinity in all Northern Hemisphere data pooled together, but neither explains much of the variation in biomass ($R^2 = 0.06$, $p = 0.09$ and $R^2 = 0.15$, $p = 0.04$, respectively, Fig. S3a,b). We also acknowledge that population variation in biomass may have been affected by other abiotic factors, such as inundation time (Snedden et al. 2015; Peng

et al. 2018) and eutrophication (Deegan et al. 2012). Nevertheless, we consider temperature to be a more likely cause of between-population variation in biomass than these other factors. Given increasing global temperatures, we focus here on population adaptation to temperature.

In the common gardens in China, aboveground biomass did not vary with latitude of origin. Although common gardens were conducted in different years, the temperature annual variation had little impact on the results. We therefore conclude that geographic patterns are due to plasticity rather than genetic differences. Genetic studies of *S. alterniflora* in China show relatively little differentiation across latitudes (Deng et al. 2007), which is expected given that *S. alterniflora* was introduced less than four decades ago (Xu and Zhuo 1985; An et al. 2007). In contrast, native range plants still show biomass differences in the common garden, indicating genetic variation across latitude from the native range. Genetic studies of *Spartina* in North America show clear geographic differentiation (Strong and Ayres 2013). However, this genetic differentiation has not been correlated with phenotypic differences. We are currently unable to confirm whether genotypes respond to climate in distinct ways, and how these interactions affect the patterns in the native range, but multiple common garden experiments are a powerful method to test it in the future (Liu et al. 2017).

Biomass was higher in China than in North America in both the field and the greenhouse common garden. Possible explanations are genetic mixing during introduction (Strong and Ayres 2013; Qiao et al. 2019), or eutrophication (Zhao et al. 2015). Another possibility is that plants make the marsh less suitable over time (Edwards and Mills 2005), either by using up resources or accumulating pathogens. All plants were sampled in low marsh or creekbank habitats, so differences in biomass were not likely due to differences in elevation.

Plant growth modulates above- and belowground processes that build soil (Kirwan and Megonigal 2013), suggesting that our findings are applicable to understanding marsh resilience in the face of sea level rise and other environmental drivers. Aboveground biomass enhances the deposition of mineral sediment on the soil surface, whereas belowground biomass contributes directly to increases in soil volume (Morris et al. 2002; Nyman et al. 2006; Langley et al. 2009; Mudd et al. 2010). Therefore, marsh accretion may be enhanced or diminished by the nonlinear temperature responses we observed, where temperatures higher or lower than optimum may reduce salt marsh resilience. Nevertheless, we did not quantify belowground biomass, and so do not know whether it follows the same latitudinal patterns that we observed for aboveground biomass. For example, Crosby et al. (2017) found that *S. alterniflora* allocated relatively more biomass belowground in high- than low-latitude marshes. Therefore, it remains uncertain to what extent our observations of aboveground biomass will actually influence vertical accretion and salt marsh resilience.

Together, our results uniquely illustrate a hump-shaped relationship between productivity and latitude that can only be observed with studies that extend beyond *S. alterniflora*'s native range. Given this, and given that *S. alterniflora* already performs poorly at low latitudes in its native range in warm years (Więski and Pennings 2014), our results suggest that climate warming may have negative consequences for *S. alterniflora* across much of the southern portion of its native range.

Finally, we found that phenotypic plasticity plays an important role in mediating variation in productivity across latitude in the introduced range in China. This variation is mainly induced by latitudinal variation in annual mean temperature, which gave us a model to test whether warming will decrease the productivity of *S. alterniflora* elsewhere in the world. However, genetic adaptation plays a major role in mediating geographic variation in productivity in the native range. This suggests the possibility that the plastic responses observed in China four decades after the introduction of *S. alterniflora* may become fixed genetic responses over longer time scales through genetic assimilation (Lande 2009).

References

Aitken, S. N., S. Yeaman, J. A. Holliday, T. Wang, and S. Curtis-McLane. 2008. Adaptation, migration or extirpation: Climate change outcomes for tree populations. Evol. Appl. **1**: 95–111. doi:10.1111/j.1752-4571.2007.00013.x

An, S., and others. 2007. *Spartina* invasion in China: Implications for invasive species management and future research. Weed Res. **47**: 183–191. doi:10.1111/j.1365-3180.2007.00559.x

Angert, A. L., L. G. Crozier, L. J. Rissler, S. E. Gilman, J. J. Tewksbury, and A. J. Chunco. 2011. Do species' traits predict recent shifts at expanding range edges? Ecol. Lett. **14**: 677–689. doi:10.1111/j.1461-0248.2011.01620.x

Barbier, E. B., S. D. Hacker, C. Kennedy, E. W. Koch, A. C. Stier, and B. R. Silliman. 2011. The value of estuarine and coastal ecosystem services. Ecol. Monogr. **81**: 169–193. doi:10.1890/10-1510.1

Berry, J., and O. Bjorkman. 1980. Photosynthetic response and adaptation to temperature in higher plants. Annu. Rev. Plant Physiol. **31**: 491–543. doi:10.1146/annurev.pp.31.060180.002423

Bossdorf, O., H. Auge, L. Lafuma, W. E. Rogers, E. Siemann, and D. Prati. 2005. Phenotypic and genetic differentiation between native and introduced plant populations. Oecologia **144**: 1–11. doi:10.1007/s00442-005-0070-z

Burrows, M. T., and others. 2014. Geographical limits to species-range shifts are suggested by climate velocity. Nature **507**: 492–495. doi:10.1038/nature12976

Castillo, J. M., B. J. Grewell, A. Pickart, A. Bortolus, C. Peña, E. Figueroa, and M. Sytsma. 2014. Phenotypic plasticity of invasive *Spartina densiflora* (Poaceae) along a broad latitudinal

gradient on the Pacific Coast of North America. Am. J. Bot. **101**: 448–458. doi:10.3732/ajb.1400014

Catullo, R. A., S. Ferrier, and A. A. Hoffmann. 2015. Extending spatial modelling of climate change responses beyond the realized niche: Estimating, and accommodating, physiological limits and adaptive evolution. Glob. Ecol. Biogeogr. **24**: 1192–1202. doi:10.1111/geb.12344

Charles, H., and J. S. Dukes. 2009. Effects of warming and altered precipitation on plant and nutrient dynamics of a New England salt marsh. Ecol. Appl. **19**: 1758–1773. doi:10.1890/08-0172.1

Cody, M. L. 1991. Niche theory and plant growth form. Vegetatio **97**: 39–55. doi:10.1007/BF00033900

Crosby, S. C., A. Angermeyer, J. M. Adler, M. D. Bertness, L. A. Deegan, N. Sibinga, and H. M. Leslie. 2017. *Spartina alterniflora* biomass allocation and temperature: Implications for salt marsh persistence with sea-level rise. Estuar. Coast. **40**: 213–223. doi:10.1007/s12237-016-0142-9

Crosby, S. C., M. Ivens-Duran, M. D. Bertness, E. Davey, L. A. Deegan, and H. M. Leslie. 2015. Flowering and biomass allocation in US Atlantic coast *Spartina alterniflora*. Am. J. Bot. **102**: 669–676. doi:10.3732/ajb.1400534

Davidson, A. M., M. Jennions, and A. B. Nicotra. 2011. Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. Ecol. Lett. **14**: 419–431. doi:10.1111/j.1461-0248.2011.01596.x

Deegan, L. A., D. S. Johnson, R. S. Warren, B. J. Peterson, J. W. Fleeger, S. Fagherazzi, and W. M. Wollheim. 2012. Coastal eutrophication as a driver of salt marsh loss. Nature **490**: 388–392. doi:10.1038/nature11533

Deng, Z., and others. 2007. Genetic structure and habitat selection of the tall form *Spartina alterniflora* Loisel in China. Hydrobiologia **583**: 195–204. doi:10.1007/s10750-006-0529-x

Dlugosch, K. M., and I. M. Parker. 2008. Invading populations of an ornamental shrub show rapid life history evolution despite genetic bottlenecks. Ecol. Lett. **11**: 701–709. doi:10.1111/j.1461-0248.2008.01181.x

Dunn, R., S. M. Thomas, A. J. Keyss, and S. P. Long. 1987. A comparison of the growth of the C4 grass *Spartina anglica* with the C3 grass *Lolium perenne* at different temperatures. J. Exp. Bot. **38**: 433–441. doi:10.1093/jxb/38.3.433

Edwards, K. R., and K. P. Mills. 2005. Aboveground and belowground productivity of *Spartina alterniflora* (Smooth Cordgrass) in natural and created Louisiana salt marshes. Estuaries **28**: 252–265. doi:10.1007/bf02732859

Elsey-Quirk, T., D. M. Seliskar, and J. L. Gallagher. 2011. Differential population response of allocation, phenology, and tissue chemistry in *Spartina alterniflora*. Plant Ecol. **212**: 1873–1885. doi:10.1007/s13157-010-0139-2

Franks, S. J., J. J. Weber, and S. N. Aitken. 2014. Evolutionary and plastic responses to climate change in terrestrial plant populations. Evol. Appl. **7**: 123–139. doi:10.1111/eva.12112

Giurgevich, J. R., and E. L. Dunn. 1979. Seasonal patterns of CO_2 and water vapor exchange of the tall and short height forms of *Spartina alterniflora* Loisel in a Georgia salt marsh. Oecologia **43**: 139–156. doi:10.1007/bf00344767

Guo, H., Y. Zhang, Z. Lan, and S. C. Pennings. 2013. Biotic interactions mediate the expansion of black mangrove (*Avicennia germinans*) into salt marshes under climate change. Glob. Chang. Biol. **19**: 2765–2774. doi:10.1111/gcb.12221

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. **25**: 1965–1978. doi:10.1002/joc.1276

Idaszkin, Y. L., and A. Bortolus. 2011. Does low temperature prevent *Spartina alterniflora* from expanding toward the austral-most salt marshes? Plant Ecol. **212**: 553–561. doi:10.1007/s11258-010-9844-4

Jiang, M., B. S. Felzer, U. N. Nielsen, and B. E. Medlyn. 2017. Biome-specific climatic space defined by temperature and precipitation predictability. Glob. Ecol. Biogeogr. **26**: 1270–1282. doi:10.1111/geb.12635

Kirwan, M. L., and A. B. Murray. 2007. A coupled geomorphic and ecological model of tidal marsh evolution. Proc. Natl. Acad. Sci. **104**: 6118–6122. doi:10.1073/pnas.0700958104

Kirwan, M. L., and J. P. Megonigal. 2013. Tidal wetland stability in the face of human impacts and sea-level rise. Nature **504**: 53–60. doi:10.1038/nature12856

Kirwan, M. L., and S. M. Mudd. 2012. Response of salt-marsh carbon accumulation to climate change. Nature **489**: 550–553. doi:10.1038/nature11440

Kirwan, M. L., G. R. Guntenspergen, and J. T. Morris. 2009. Latitudinal trends in *Spartina alterniflora* productivity and the response of coastal marshes toglobal change. Glob. Chang. Biol. **15**: 1982–1989. doi:10.1111/j.1365-2486.2008.01834.x

Lande, R. 2009. Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. J. Evol. Biol. **22**: 1435–1446. doi:10.1111/j.1420-9101.2009.01754.x

Langley, J. A., K. L. McKee, D. R. Cahoon, J. A. Cherry, and J. P. Megonigal. 2009. Elevated CO_2 stimulates marsh elevation gain, counterbalancing sea-level rise. Proc. Natl. Acad. Sci. USA **106**: 6182–6186. doi:10.1073/pnas.0807695106

Larjavaara, M., and H. C. Muller-Landau. 2012. Temperature explains global variation in biomass among humid old-growth forests. Glob. Ecol. Biogeogr. **21**: 998–1006. doi:10.1111/j.1466-8238.2011.00740.x

Li, J., L. Du, W. Guan, F. Yu, and M. van Kleunen. 2016. Latitudinal and longitudinal clines of phenotypic plasticity in the invasive herb *Solidago canadensis* in China. Oecologia **182**: 755–764. doi:10.1007/s00442-016-3699-x

Li, S., C. S. Hopkinson, J. P. Schubauer-Berigan, and S. C. Pennings. 2018. Climate drivers of *Zizaniopsis miliacea* biomass in a Georgia USA tidal fresh marsh. Limnol. Oceanogr. **63**: 2266–2276. doi:10.1002/lno.10937

Liu, W., and S. C. Pennings. 2019. Self-thinning and size-dependent flowering of the grass *Spartina alterniflora* across space and time. Funct. Ecol. **33**: 1830–1841. doi:10.1111/1365-2435.13384

Liu, W., D. R. Strong, S. C. Pennings, and Y. Zhang. 2017. Provenance-by-environment interaction of reproductive traits in the invasion of *Spartina alterniflora* in China. Ecology **98**: 1591–1599. doi:10.1002/ecy.1815

Liu, W., K. Maung-Douglass, D. R. Strong, S. C. Pennings, and Y. Zhang. 2016. Geographical variation in vegetative growth and sexual reproduction of the invasive *Spartina alterniflora* in China. J. Ecol. **104**: 173–181. doi:10.1111/1365-2745.12487

Maron, J. L., M. Vilà, R. Bommarco, S. Elmendorf, and P. Beardsley. 2004. Rapid evolution of an invasive plant. Ecol. Monogr. **74**: 261–280. doi:10.1890/03-4027

McKee, K. L., I. A. Mendelssohn, and D. M. Materne. 2004. Acute salt marsh dieback in the Mississippi River deltaic plain: A drought-induced phenomenon? Glob. Ecol. Biogeogr. **13**: 65–73. doi:10.1111/j.1466-882x.2004.00075.x

Miller, P., W. Lanier, and S. Brandt. 2001. Using growing degree days to predict plant stages. Bozeman, MT: Montana State Univ..

Moles, A. T., and others. 2009. Global patterns in plant height. J. Ecol. **97**: 923–932. doi:10.1111/j.1365-2745.2009.01526.x

Moran, E. V., and J. M. Alexander. 2014. Evolutionary responses to global change: Lessons from invasive species. Ecol. Lett. **17**: 637–649. doi:10.1111/ele.12262

Morris, J. T., P. V. Sundareshwar, C. T. Nietch, B. Kjerfve, and D. R. Cahoon. 2002. Responses of coastal wetlands to rising sea level. Ecology **83**: 2869–2877. doi:10.1890/0012-9658(2002)083[2869:ROCWTR]2.0.CO;2

Mudd, S. M., A. D'Alpaos, and J. T. Morris. 2010. How does vegetation affect sedimentation on tidal marshes? Investigating particle capture and hydrodynamic controls on biologically mediated sedimentation. J. Geophys. Res. Earth **115**: 1–14. doi:10.1029/2009JF001566, F3

Nyman, J. A., R. J. Walters, R. D. Delaune, and W. H. Patrick Jr. 2006. Marsh vertical accretion via vegetative growth. Estuar. Coast. Shelf Sci. **69**: 370–380. doi:10.1016/j.ecss.2006.05.041

Osland, M. J., N. Enwright, R. H. Day, and T. W. Doyle. 2013. Winter climate change and coastal wetland foundation species: Salt marshes vs. mangrove forests in the southeastern United States. Glob. Chang. Biol. **19**: 1482–1494. doi:10.1111/gcb.12126

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. Syst. **37**: 637–669. doi:10.1146/annurev.ecolsys.37.091305.110100

Peng, D., L. Chen, S. C. Pennings, and Y. Zhang. 2018. Using a marsh organ to predict future plant communities in a Chinese estuary invaded by an exotic grass and mangrove. Limnol. Oceanogr. **63**: 2595–2605. doi:10.1002/lno.10962

Pennings, S. C., and C. L. Richards. 1998. Effects of wrack burial in salt-stressed habitats: *Batis maritima* in a southwest

Atlantic salt marsh. Ecography **21**: 630–638. doi:10.1111/j.1600-0587.1998.tb00556.x

Pereira, R. J., M. C. Sasaki, and R. S. Burton. 2017. Adaptation to a latitudinal thermal gradient within a widespread copepod species: The contributions of genetic divergence and phenotypic plasticity. Proc. R. Soc. B **284**: 20170236. doi:10.1098/rspb.2017.0236

Qiao, H., W. Liu, Y. Zhang, Y. Y. Zhang, and Q. Q. Li. 2019. Genetic admixture accelerates invasion via provisioning rapid adaptive evolution. Mol. Ecol. **28**: 4012–4027. doi:10.1111/mec.15192

R Development Core Team. 2016. R: A language and environment for statistical computing. R Fundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. Available from http://www.R-project.org/

Rejmánek, M., and D. M. Richardson. 1996. What attributes make some plant species more invasive? Ecology **77**: 1655–1661. doi:10.2307/2265768

Richards, C. L., S. C. Pennings, and L. A. Donovan. 2005. Habitat range and phenotypic variation in salt-marsh plants. Plant Ecol. **176**: 263–273. doi:10.1007/s11258-004-0841-3

Salgado, C. S., and S. C. Pennings. 2005. Latitudinal variation in palatability of salt-marsh plants: Are differences constitutive? Ecology **86**: 1571–1579. doi:10.1890/04-1257

Seliskar, D. M., J. L. Gallagher, D. M. Burdick, and L. A. Mutz. 2002. The regulation of ecosystem functions by ecotypic variation in the dominant plant: A *Spartina alterniflora* salt-marsh case study. J. Ecol. **90**: 1–11. doi:10.1046/j.0022-0477.2001.00632.x

Snedden, G. A., K. Cretini, and B. Patton. 2015. Inundation and salinity impacts to above-and belowground productivity in *Spartina patens* and *Spartina alterniflora* in the Mississippi River deltaic plain: Implications for using river diversions as restoration tools. Ecol. Eng. **81**: 133–139. doi:10.1016/j.ecoleng.2015.04.035

Strong, D. R., and D. R. Ayres. 2013. Ecological and evolutionary misadventures of *Spartina*. Annu. Rev. Ecol. Evol. Syst. **44**: 389–410. doi:10.1146/annurev-ecolsys-110512-135803

Travis, S. E., and J. B. Grace. 2010. Predicting performance for ecological restoration: A case study using *Spartina alterniflora*. Ecol. Appl. **20**: 192–204. doi:10.1890/08-1443.1

Turner, R. E. 1976. Geographic variations in salt marsh macrophyte production: A review. Contrib. Mar. Sci. **20**: 47–68.

van Boheemen, L. A., D. Z. Atwater, and K. A. Hodgins. 2019. Rapid and repeated local adaptation to climate in an invasive plant. New Phytol. **222**: 614–627. doi:10.1111/nph.15564

Walther, G. R. 2003. Plants in a warmer world. Perspect. Plant Ecol. Evol. Syst. **6**: 169–185. doi:10.1078/1433-8319-00076

Więski, K., and S. C. Pennings. 2014. Climate drivers of *Spartina alterniflora* saltmarsh production in Georgia, USA. Ecosystems **17**: 473–484. doi:10.1007/s10021-013-9732-6

Woods, E. C., A. P. Hastings, N. E. Turley, S. B. Heard, and A. A. Agrawal. 2012. Adaptive geographical clines in the growth and defense of a native plant. Ecol. Monogr. **82**: 149–168. doi:10.2307/41739362

Xu, G., and R. Zhuo. 1985. Preliminary studies of introduced *Spartina alterniflora* Loisel in China (in Chinese). J. Nanjing Univ. **40**: 212–225.

Zhang, Y., G. Huang, W. Wang, L. Chen, and G. Lin. 2012. Interactions between mangroves and exotic *Spartina* in an anthropogenically disturbed estuary in southern China. Ecology **93**: 588–597. doi:10.1890/11-1302.1

Zhao, H., W. Yang, L. Xia, Y. Qiao, Y. Xiao, X. Cheng, and S. An. 2015. Nitrogen-enriched eutrophication promotes the invasion of *Spartina alterniflora* in coastal China. CLEAN–Soil, Air, Water **43**: 244–250. doi:10.1002/clen.201300844

Zheng, S., D. Shao, and T. Sun. 2018. Productivity of invasive saltmarsh plant *Spartina alterniflora* along the coast of China: A meta-analysis. Ecol. Eng. **117**: 104–110. doi:10.1016/j.ecoleng.2018.03.01

Conflict of Interest

The authors have no competing interests.