

## LETTER

## Experimental warming causes rapid loss of plant diversity in New England salt marshes

Keryn B. Gedan\* and Mark D. Bertness

Department of Ecology and Evolutionary Biology, Brown University, 80 Waterman St., Providence, RI 02912, USA

\*Correspondence: E-mail: Keryn\_Gedan@Brown.edu

### Abstract

Anthropogenic climate change is predicted to cause widespread biodiversity loss due to shifts in species' distributions, but these predictions rarely incorporate ecological associations such as zonation. Here, we predict the decline of a diverse assemblage of mid-latitude salt marsh plants, based on an ecosystem warming experiment. In New England salt marshes, a guild of halophytic forbs occupies stressful, waterlogged pannes. At three sites, experimental warming of  $< 4$  °C led to diversity declines in pannes and rapid takeover by a competitive dominant, *Spartina patens*. In Rhode Island, near their southern range limit, pannes were more sensitive to warming than farther north, and panne area also declined in control plots over the three-season experiment. These results suggest that warming will rapidly reduce plant diversity in New England salt marshes by eliminating a high diversity zone. Biodiversity in zoned ecosystems may be more affected by climate-driven shifts in zonation than by individual species' distribution shifts.

### Keywords

Climate change, ecosystem warming experiment, forb panne, open-top chamber, *Spartina patens*, water use efficiency.

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### INTRODUCTION

Rapid climate change is predicted to reduce biodiversity (Sala *et al.* 2000). Forecasts of biodiversity reductions stem from models of anticipated species' range shifts following predicted climate changes (Thomas *et al.* 2004; Thuiller *et al.* 2005; Malcolm *et al.* 2006; Fitzpatrick *et al.* 2008). However, species' distributions are shaped by abiotic factors and interspecific interactions in addition to their climate requirements (i.e. 'climate envelope') (Davis *et al.* 1998). Climate change is likely to alter species' distributions by affecting species interactions strengths (Sanford 1999) and non-climate abiotic conditions such as soil moisture/aridity, nutrient availability and substrate temperature (Holtmeier & Broll 2005; Kearney *et al.* 2009), in addition to moving climate envelope spaces. Heterogeneity in abiotic factors at local scales can often override larger scale climate variation in determining species distributions (Helmuth *et al.* 2002; Holtmeier & Broll 2005), complicating predictions of climate-driven range shifts and biodiversity effects.

Zonation, or species sorting across environmental gradients, is a result of local scale biotic and abiotic factors defining species' distributions. Where changes in climate affect zonation, species are likely to shift in aggregate with

their zone. Where climate severely reduces, or 'squeezes', zones, local species extinctions can result (Harley 2003; Harley *et al.* 2006).

Here, we present an experimental test of warming on the diversity of New England salt marsh plant communities. These communities are characterized by elevational plant zonation that results from a competitive hierarchy that limits subordinate competitors to edaphically stressful habitats (Bertness 1991a,b; Ewanchuk & Bertness 2004b). Monocultures of the grass *Spartina patens* (Ait.) Muhl. dominate intermediate elevations (Crain *et al.* 2004), interrupted by waterlogged habitats called forb pannes, where plant diversity is high (Miller & Egler 1950; Theodose & Roths 1999).

The forb panne assemblage consists of over a dozen plant species (Table 1, Miller & Egler 1950; Chmura *et al.* 1997; Theodose & Roths 1999). Miller & Egler (1950) described forb pannes as 'the most variable and colourful of tidal-marsh associations'. Forb pannes are consistently waterlogged, with hypoxic soil and low plant productivity, and a competitive refuge for stress tolerant forbs that are out-competed in graminoid marsh zones (Ewanchuk & Bertness 2004b). Other salt marsh plants cannot tolerate the environmental stress in waterlogged pannes and transplants quickly perish (Ewanchuk & Bertness 2004b). *Spartina patens*

**Table 1** Common plant species in forb pannes, compiled from the literature, and their rarity status in the northeastern states

Species*	(South)		State-wide status†				(North)	
	NJ	NY	CT	RI	MA	NH	ME	
<i>Agalinis maritima</i>						T	SC	
<i>Atriplex patula</i>								
<i>Glaux maritima</i>	E			H				
<i>Juncus gerardii</i>								
<i>Limonium nashii</i>								
<i>Plantago maritima</i>		T						
<i>Puccinellia maritima</i>								
<i>Salicornia bigelovii</i>		T				T	SC	
<i>Salicornia europaea</i>								
<i>Spartina alterniflora</i>								
<i>Spartina patens</i>								
<i>Suaeda maritima</i>								
<i>Triglochin maritima</i>	E							

NJ, New Jersey; NY, New York; CT, Connecticut; RI, Rhode Island; MA, Massachusetts; NH, New Hampshire; ME, Maine.

\*Common forb panne species named by at least two of the following data sources: Miller & Egler (1950), Chmura *et al.* (1997); Theodose & Roths (1999).

†State-wide status (USDA 2009): H, historical; SC, special concern; T, threatened; E, endangered.

invades pannes when waterlogging stress is relieved, such as by artificial draining (Ewanchuk & Bertness 2004a).

Latitudinal patterns in the abundance and distribution of forb pannes suggest that they are sensitive to climatic variation (Chapman 1974; Chmura *et al.* 1997). Forb pannes are rare in southern New England, common in northern New England, and entirely dominant in Canadian salt marshes (Chapman 1974). Consequently, many forb panne plants have threatened, endangered or historical status in southern New England (Table 1, USDA 2009). *Spartina patens* has the opposite distribution. In the Bay of Fundy, where forb pannes dominate salt marsh plant communities, *S. patens* approaches its northern limit (Ganong 1903; Chapman 1974; Barkworth *et al.* 2007).

We examined the biodiversity effects of warming in salt marsh plant communities with an ecosystem warming experiment at sites spanning the southern end of the forb panne distribution. We hypothesized that warming would affect the zonal boundaries of *S. patens* and forb panne zones, favouring *S. patens* expansion into the forb panne zone and causing a decline in plant diversity, and that this response would be strongest near the southern range limit of the forb pannes.

## METHODS

### Field sites

Field work was performed at three marshes, Nag Creek (41°37'33" N, 71°19'31" W) in Narragansett Bay National

Estuarine Research Reserve (NERR) in Rhode Island (RI), Little River (43°20'10" N, 70°32'36" W) in Wells NERR in Maine (ME), and Drake's Island in Wells, ME, part of the Rachel Carson National Wildlife Refuge (43°19'41" N, 70°33'35" W). Little River is one of the most southern marshes with extensive forb pannes (Chmura *et al.* 1997). Nag Creek is near the southern limit of forb pannes on the east coast of the US.

Plant zonation at all sites is typical of the region (Bertness & Ellison 1987; Ewanchuk & Bertness 2004b), with a high marsh dominated by *Juncus gerardii* Loiseleur, *Spartina patens*, forb pannes and stunted *S. alterniflora* Loiseleur zones. Drainage ditches were present at all sites, but pannes selected for investigation were > 20 m from ditches. See Bromberg Gedan *et al.* (2009), Bertness *et al.* (2008) and Ewanchuk & Bertness (2004a,b) for site details.

### Warming effects on biodiversity

To test warming effects on pannes we placed warming chambers on discrete forb panne/*S. patens* boundaries. Plots (0.5 × 0.5 m), 50% *S. patens* and 50% forb panne, were established at Nag Creek and Little River in May 2004 ( $N_{\text{Nag Creek}} = 42$ ,  $N_{\text{Little River}} = 36$ ) and randomly assigned to one of three warming treatments: unmanipulated control, structural control, or warmed. To confirm the generality of warming effects at Nag Creek and Little River, the experiment was replicated in May 2007 at Drake's Island Salt Marsh ( $N_{\text{Drake's Island}} = 24$ ), where forb panne biodiversity is particularly high.

Warming was achieved with a five-sided open-top chamber (OTC) made of corrugated LEXAN polycarbonate (1 m diameter  $\times$  0.5 m height). OTCs have been used in ecosystem warming studies in a variety of short-statured plant communities to achieve warming of 1.0–1.8 °C in air temperatures and 0.6–3.0 °C in soil temperatures (Marion 1996; Marion *et al.* 1997). OTCs were placed on the marsh in May and removed in September to avoid winter ice and storm damage. Salt marsh plants are senesced from October to April in the study region. Structural controls (mimics) were an open top cylinder of 2.5 cm Vexar mesh (Atlantic Aquaculture Supply, LLC, Warren, RI) with the same dimensions as the OTC.

We quantified treatment effects on plant diversity by measuring species composition through time. Composition was assessed with species cover data taken at the beginning (June) and end (August) of each growing season. Data were collected from 2004 to 2006 at Nag Creek and Little River and in 2007 at Drake's Island. Cover data were collected with the point-intercept method using a 100-point string grid. Due to the threatened status of several of the forb panne species at our field sites, plant biomass was not sampled.

Because plant–water relations are known to be critical to the maintenance of forb panne zones (Ewanchuk & Bertness 2004a), we assessed the effect of warming treatment on forb water use efficiency (WUE) at Drake's Island Marsh in August 2007 using the relative carbon isotope composition ( $\delta^{13}\text{C}$ ).  $\delta^{13}\text{C}$  is an indicator of the ratio of internal to ambient partial pressures of  $\text{CO}_2$  over the life of the plant.  $\delta^{13}\text{C}$  is higher, or less negative, in halophytes grown in water stressed environments (dry or high salinity), indicating prolonged low stomatal conductance and high WUE (Farquhar *et al.* 1982, 1989). To measure  $\delta^{13}\text{C}$ , three stems of the two most common species in the forb panne, *Plantago maritima* L. and *Triglochin maritima* L., were clipped at the marsh surface, dried, finely ground, and sent for  $\delta^{13}\text{C}$  analysis (relative to Pee Dee belemnite, PBD) at MBL Stable Isotopes Laboratory (Woods Hole, MA, USA).

To examine the effectiveness of the warming treatments, we measured plot temperature with iButton temperature dataloggers (Maxim Integrated Products, Inc., Sunnyvale, CA, USA). Dataloggers were fixed 10 cm above the marsh surface on PVC piping staked in the centre of plots. Dataloggers ( $n = 4$  per treatment per site) recorded temperatures ( $\pm 0.1$  °C) every hour.

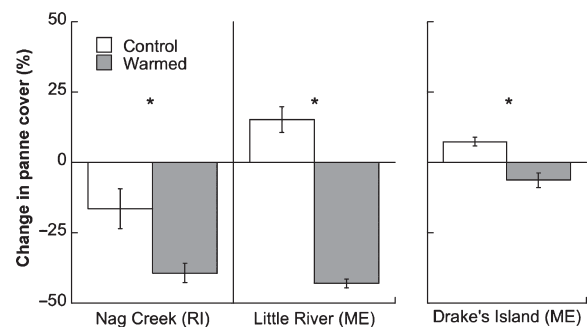
The effects of warming treatments on soil salinity and evaporation were measured on several occasions at each site. Salinity was measured with a refractometer (Sper Scientific, Scottsdale, AZ, USA) and evaporation with water loss of wetted sponges (see Bertness *et al.* 1992 for method).

## Data analysis

We tested for warming treatment and site effects on final species composition with a factorial MANOVA. Species cover was arcsine square root transformed to increase homogeneity of variance. Compositional changes over time were summarized as a deviation of aggregated forb panne cover classes from the initial plot composition of 50%, and warming and site treatment effects were tested with an ANOVA. The same test was used to examine treatment effects on final plant diversity, as measured by the Shannon-Wiener Index ( $H'$ ), species richness ( $S$ ) and evenness ( $E$ ) (Magurran 1988). Drake's Island data were analysed separately, due to the different time periods of the experiments. The effects of warming on  $\delta^{13}\text{C}$  were tested with a one-way ANOVA on each species. *Post hoc* comparisons were made with Tukey's HSD ( $\alpha = 0.05$ ). All tests were performed with JMP statistical software (version 5.0.1.2; SAS Institute, Cary, NC, USA).

## RESULTS

Warming treatments raised air temperatures in all growing seasons. Average seasonal temperature increases due to OTCs ranged from 0.33 to 3.28 °C, depending on site and year (Appendix S1). Warming treatments were milder in the second and third growing seasons of the experiment as OTCs weathered and became less effective (Appendix S1). Salinity was unaffected by warming treatments. Evaporation potential was lower in warming chambers at Little River and Nag Creek ( $F_{2, 78} = 7.24$ ,  $P < 0.0001$ ). Evaporation was also affected by site, greater at Nag Creek than at Little River ( $F_{1, 78} = 23.46$ ,  $P < 0.0001$ ). For all response variables, structural controls were not signifi-



**Figure 1** Deviation ( $\pm 1$  SE) of forb panne cover in warming treatments installed at three salt marsh sites. Initial starting conditions were fixed at 50% forb panne cover and 50% *Spartina patens* cover. Asterisks denote a significant effect of warming over the 2004–2006 experimental period at Nag Creek and Little River sites and in 2007 at the Drake's Island site (Tukey HSD,  $\alpha = 0.05$ ).

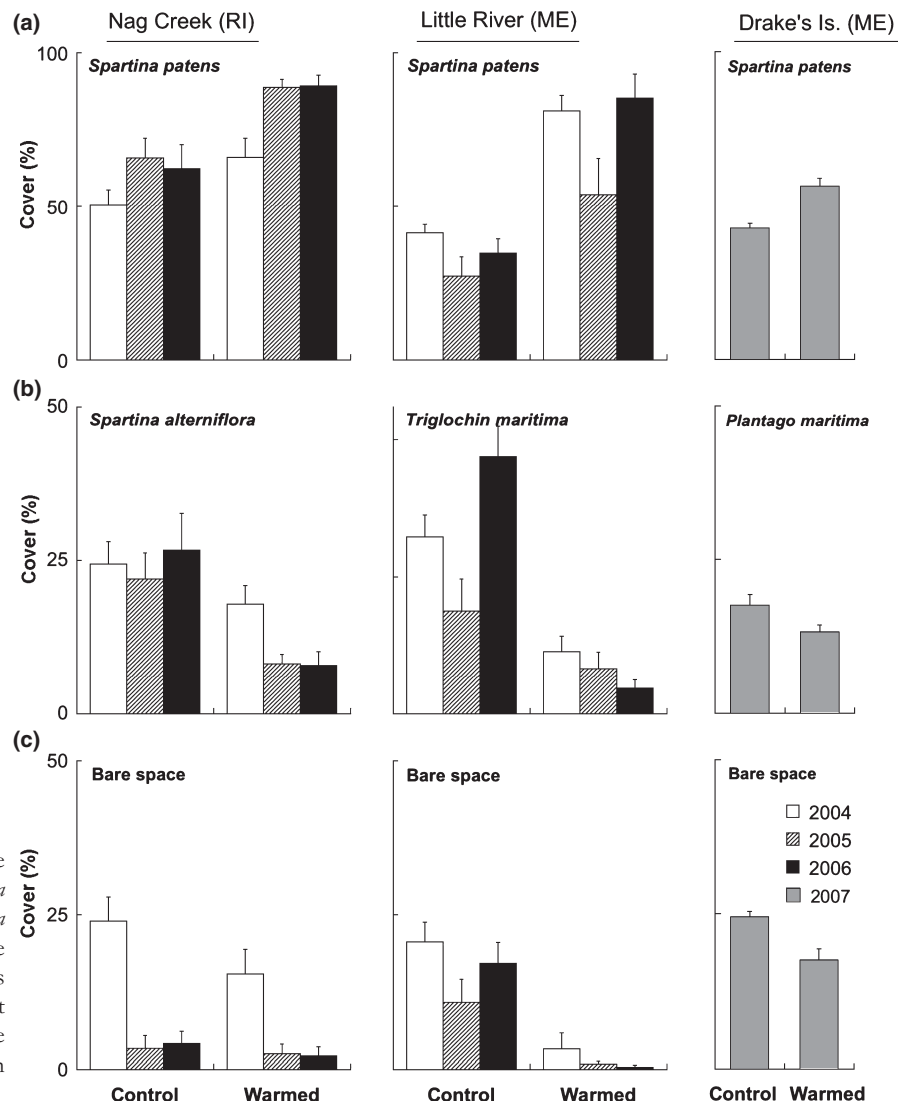
cantly different from controls, and structural control data have been omitted from figures to simplify the display of results.

Warming reduced forb panne cover at all sites (Fig. 1). In the 3-year experiment, warming effects on forb panne cover changes varied by site (ANOVA, warming × site interaction,  $F_{2, 73} = 5.68, P < 0.01$ ). At Little River, ME, panne cover decreased in warmed plots and slightly increased in control plots, whereas at Nag Creek, RI, panne cover declined in both control and warmed plots (Fig. 1). After three growing seasons, panne habitat was < 10% of warmed plots at either site. In one season at Drake's Island, ME, warming reduced panne cover relative to controls (ANOVA,  $F_{2, 21} = 10.77, P < 0.001$ ; Fig. 1).

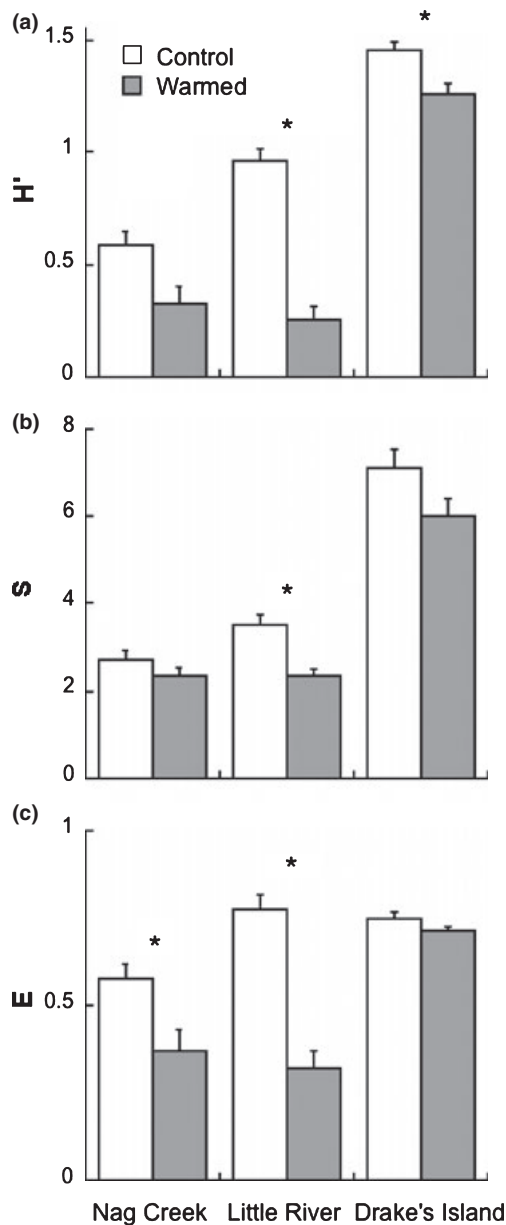
Plant species composition also shifted in response to warming (MANOVA Nag Creek, Little River, site × warming interaction,  $F_{12, 136} = 11.45, \text{Wilks } \lambda < 0.0001$ ; MANOVA Drake's,

warming effect,  $F_{20, 24} = 2.77, \text{Wilks } \lambda < 0.01$ ; Fig. 2). In warmed plots, *S. patens* was favoured, and panne species and bare space cover were reduced (Fig. 2). As a result of these shifts, plant diversity was reduced in warmed plots relative to controls (ANOVA<sub>Nag Creek, Little River</sub>, site × warming interaction,  $F_{2, 73} = 6.02, P < 0.01$ ; ANOVA<sub>Drake's</sub>, warming effect  $F_{2, 21} = 9.15, P < 0.01$ ; Fig. 3a). Warming-induced reductions in Shannon-Wiener diversity were caused by a joint decrease in species richness and evenness (richness: ANOVA<sub>Nag Creek, Little River</sub>, warming effect,  $F_{2, 73} = 14.05, P < 0.0001$ , site effect,  $F_{2, 73} = 7.08, P < 0.01$ ; ANOVA<sub>Drake's</sub>,  $F_{2, 21} = 1.99$ , not significant; Fig. 3b; Evenness: ANOVA<sub>Nag Creek, Little River</sub>, warming effect,  $F_{2, 73} = 20.26, P < 0.0001$ , site effect,  $F_{2, 73} = 6.15, P < 0.05$ ; ANOVA<sub>Drake's</sub>,  $F_{2, 21} = 3.59, P < 0.05$ ; Fig. 3c).

After three growing seasons, warming reduced Shannon diversity by 74% at Little River and 44% at Nag Creek. A



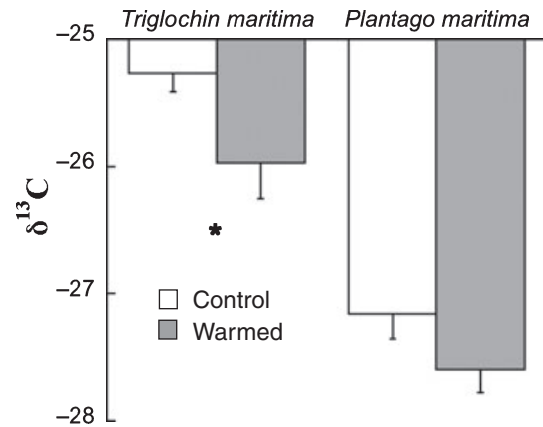
**Figure 2** Abundance ( $\pm 1$  SE) of the three most common cover classes, (a) *Spartina patens*, (b) forb panne species *S. alterniflora* (Nag Creek, RI), *Triglochin maritima* (Little River, ME), and *Plantago maritima* (Drake's Island, ME) and (c) bare space, throughout the four experimental growing seasons. The experiment began with species composition fixed at 50% *S. patens* cover in all plots.



**Figure 3** Experimental warming caused reductions in (a) Shannon-Wiener species diversity ( $H'$ ), (b) species richness ( $S$ ) and (c) evenness ( $E$ ) of plant communities at Nag Creek Marsh, RI, Little River Marsh, ME and Drake's Island Marsh, ME. \*Significant difference between warmed and control treatments (Tukey HSD,  $\alpha = 0.05$ ).

single season of warming reduced Shannon diversity by 14% at Drake's Island.

Warming significantly increased carbon isotope discrimination in *Triglochin maritima* ( $F_{1, 14} = 4.89$ ,  $P < 0.05$ ; Fig. 4) and there was a trend towards greater discrimination in *Plantago maritima* as well ( $F_{1, 14} = 2.66$ ,  $P = 0.13$ ; Fig. 4).



**Figure 4**  $\delta^{13}C$  values ( $\pm 1$  SE) of *Triglochin maritima* and *Plantago maritima* plants grown in experimental warming treatments at Drake's Island Marsh, ME, during summer 2007. More negative  $\delta^{13}C$  values indicate lesser water stress and water use efficiency due to less  $CO_2$  drawdown associated with high stomatal conductance. \*Significant difference between warmed and control treatments (Tukey HSD,  $\alpha = 0.05$ ).

## DISCUSSION

Warming had dramatic effects on plant composition in New England salt marshes. Warming favoured *Spartina patens* growth over forb panne species, which were subsequently reduced in cover or lost from warmed plots. By affecting the distribution of the *S. patens* zone, warming reduced plant diversity by 74% at Little River Marsh and 44% at Nag Creek in just three growing seasons (Fig. 3a). Diversity loss due to warming occurred after only a single season at Drake's Island (Fig. 3a), demonstrating that the effects of warming on salt marsh plant composition are robust and rapid. The decline in cover of all forb panne species, regardless of species identity, was remarkably uniform (Fig. 2b), indicating that this diverse assemblage responds to temperature change as a zone, rather than according to species-specific climate preferences.

Climate models predict increases in New England summer air temperatures of 3.3–7.8 °C by the end of the century (Frumhoff *et al.* 2007). The experimental warming treatment was more conservative, corresponding to temperature increases expected in the next 30 years (Frumhoff *et al.* 2007). Moreover, our experimental evidence suggests that changes in forb panne distribution due to temperature are already happening. We expected climate-driven forb panne losses to be strongest in warmer regions at the southern range boundary. Over the 3-year experimental period, we saw a significant reduction in forb panne cover in the unwarmed control plots at Nag Creek Marsh, RI (Fig. 1). Rhode Island is close to the current southern limit of the forb panne distribution, and summer temperatures are higher than in northern New England (during the study period:



4.2 °C higher in 2004, 3.8 °C in 2005 and 2.8 °C in 2006). While the experimental manipulation had stronger effects on diversity in Maine than in Rhode Island (Fig. 3), the decline in forb panne cover in control plots in Rhode Island over the experimental period (Figs 1 and 2c) indicates that climate effects are already reducing panne habitat area and species diversity in southern New England marshes.

In other studies, *S. patens* has been capable of invading the forb panne environment only when waterlogging stress is reduced, as by draining (Ewanchuk & Bertness 2004a,b). We found more negative  $\delta^{13}\text{C}$  values in warmed plots (Fig. 4), indicating that under warmer conditions, forb panne species use water less efficiently and transpire more. We also found reduced evaporation in warmed plots, indicating elevated humidity due to high transpiration. Both forb panne species and *S. patens* were more productive in warmed plots (KBG, personal observation), indicating that the invasion of *S. patens* and decline in forb panne species was not a result of simple resource competition. These data thus suggest that the mechanism driving changes in species composition is increased transpiration by forb panne species that ameliorates waterlogging stress and permits *S. patens* incursion. Warming is expected to increase evapotranspiration and lead to soil drying in a wide variety of plant communities (reviewed in Luo 2007), and this may be a common mechanism of plant species replacement in response to warming. Increased productivity of *S. patens* in warmer conditions may also contribute to its ability to colonize anoxic forb panne areas.

### Consequences of climate-driven biodiversity loss in New England salt marshes

These results reveal that predicted climate change may cause rapid loss of forb pannes throughout New England. Zonal squeeze of forb pannes by *S. patens* will reduce regional salt marsh plant diversity and threaten several endangered plant species (Table 1). Beyond the loss in aesthetic value (Ehrlich & Ehrlich 1992), we expect that the loss of forb pannes will also affect ecosystem function. Forb panne zones exhibit comparatively greater nutrient availability and turnover rates (Theodose & Roths 1999; Theodose & Martin 2003) and substantially lower primary productivity than salt marsh graminoid zones (Theodose & Roths 1999; Ewanchuk & Bertness 2004a,b). Therefore, we predict that the takeover of forb pannes by *S. patens* will alter nutrient dynamics and increase primary productivity. Overall, we find that warming will reduce the complexity of New England salt marshes by decreasing plant and zonal diversity.

We have focused on one facet of climate change, warming during the growing season that was previously unknown to structure New England salt marsh plant communities. Other facets of climate change, such as increases in CO<sub>2</sub> concentration, winter temperatures and sea

level rise (Frumhoff *et al.* 2007), may have additional independent or interactive effects. Increases in CO<sub>2</sub> are predicted to increase the productivity of marsh C<sub>3</sub> species (like forbs) without affecting C<sub>4</sub> grass species (Erickson *et al.* 2007). Our results suggest that increased forb productivity and evapotranspiration may only speed the loss of forb panne areas to *S. patens*. On the other hand, sea level rise is predicted to increase the area of waterlogged forb pannes (Warren & Niering 1993). However, the rapid loss of forb pannes due to warming is likely to outpace the slow rescue effect of sea level rise, and several forb species that are already at risk of regional extinction may no longer be present in the regional pool if and when recolonization opportunities occur.

We found that New England salt marsh plant zones shifted in response to warming, with critical implications for regional plant diversity. Using ecological knowledge of the underlying structuring mechanisms of zonation may prove useful in predicting climate-mediated biodiversity changes and distributional shifts in other zoned ecosystems such as riparian areas, alpine slopes and rocky shores.

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### REFERENCES

- Barkworth, M.E., Anderton, L.K., Capels, K.M., Long, S. & Piep, M.B. (2007). *Manual of Grasses for North America*. Utah State University Press, Logan, UT.
- Bertness, M.D. (1991a). Interspecific interactions among high marsh perennials in a New England salt marsh. *Ecology*, 72, 125–137.
- Bertness, M.D. (1991b). Zonation of *Spartina patens* and *Spartina alterniflora* in a New England salt marsh. *Ecology*, 72, 138–148.
- Bertness, M.D. & Ellison, A.M. (1987). Determinants of pattern in a New England salt marsh plant community. *Ecol. Monogr.*, 57, 129–147.
- Bertness, M.D., Gough, L. & Shumway, S.W. (1992). Salt tolerances and the distribution of fugitive salt marsh plants. *Ecology*, 73, 1842–1851.
- Bertness, M.D., Crain, C.M., Holdredge, C. & Sala, N. (2008). Eutrophication and consumer control of New England salt marsh primary productivity. *Conserv. Biol.*, 22, 131–139.
- Bromberg Gedan, K., Crain, C.M. & Bertness, M.D. (2009). Small-mammal herbivore control of secondary succession in New England tidal marshes. *Ecology*, 90, 430–440.
- Chapman, V.J. (1974) *Salt Marshes and Salt Deserts of the World*, 2nd edn. Verlag von J. Cramer, Lehre.

- Chmura, G.L., Chase, P. & Bercovitch, J. (1997). Climatic controls of the middle marsh zone in the Bay of Fundy. *Estuaries*, 20, 689–699.
- Crain, C.M., Silliman, B.R., Bertness, S.L. & Bertness, M.D. (2004). Physical and biotic drivers of plant distribution across estuarine salinity gradients. *Ecology*, 85, 2539–2549.
- Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B. & Wood, S. (1998). Making mistakes when predicting shifts in species range in response to global warming. *Nature*, 391, 783–786.
- Ehrlich, P.R. & Ehrlich, A.H. (1992). The value of biodiversity. *Ambio*, 21, 219–226.
- Erickson, J.E., Megonigal, J.P., Peresta, G. & Drake, B.G. (2007). Salinity and sea level mediate elevated CO<sub>2</sub> effects on C<sub>3</sub>-C<sub>4</sub> plant interactions and tissue nitrogen in a Chesapeake Bay tidal wetland. *Glob. Chang. Biol.*, 13, 202–215.
- Ewanchuk, P.J. & Bertness, M.D. (2004a). The role of waterlogging in maintaining forb pannes in northern New England salt marshes. *Ecology*, 85, 1568–1574.
- Ewanchuk, P.J. & Bertness, M.D. (2004b). Structure and organization of a northern New England salt marsh plant community. *J. Ecol.*, 92, 72–85.
- Farquhar, G.D., Ball, M.C., von Caemmerer, S. & Roksandic, Z. (1982). Effect of salinity and humidity on δ<sup>13</sup>C value of halophytes - evidence for diffusional isotope fractionation determined by the ratio of intercellular/atmospheric partial pressure of CO<sub>2</sub> under different environmental conditions. *Oecologia*, 52, 121–124.
- Farquhar, G.D., Ehleringer, J.R. & Hubick, K.T. (1989). Carbon isotope discrimination and photosynthesis. *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, 40, 503–537.
- Fitzpatrick, M.C., Gove, A.D., Sanders, N.J. & Dunn, R.R. (2008). Climate change, plant migration, and range collapse in a global biodiversity hotspot: the *Banksia* (Proteaceae) of Western Australia. *Glob. Chang. Biol.*, 14, 1–16.
- Frumhoff, P.C., McCarthy, J.J., Melillo, J.M., Moser, S.C. & Wuebbles, D.J. (2007). Confronting climate change in the U.S. Northeast: Science, impacts, and solutions. In: Synthesis Report of the Northeast Climate Impacts Assessment (NECIA). Union of Concerned Scientists, Cambridge, MA.
- Ganong, W.F. (1903). The vegetation of the Bay of Fundy salt and diked marshes: an ecological study (continued). *Bot. Gaz.*, 36, 349–367.
- Harley, C.D.G. (2003). Abiotic stress and herbivory interact to set range limits across a two-dimensional stress gradient. *Ecology*, 84, 1477–1488.
- Harley, C.D.G., Hughes, A.R., Hultgren, K.M., Miner, B.G., Sorte, C.J.B., Thornber, C.S. *et al.* (2006). The impacts of climate change in coastal marine systems. *Ecol. Lett.*, 9, 228–241.
- Helmuth, B., Harley, C.D.G., Halpin, P.M., O'Donnell, M., Hofmann, G.E. & Blanchette, C.A. (2002). Climate change and latitudinal patterns of intertidal thermal stress. *Science*, 298, 1015–1017.
- Holtmeier, F.K. & Broll, G. (2005). Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. *Glob. Ecol. Biogeogr.*, 14, 395–410.
- Kearney, M., Shine, R. & Porter, W.P. (2009). The potential for behavioral thermoregulation to buffer “cold-blooded” animals against climate warming. *Proc. Natl Acad. Sci. USA*, 106, 3835–3840.
- Luo, Y. (2007). Terrestrial carbon-cycle feedback to climate warming. *Annu. Rev. Ecol. Evol. Syst.*, 38, 683–712.
- Magurran, A.E. (1988). *Ecological Diversity and Its Measurement*. Princeton University Press, Princeton, NJ.
- Malcolm, J.R., Liu, C., Neilson, R.P., Hansen, L. & Hannah, L. (2006). Global warming and extinctions of endemic species from biodiversity hotspots. *Conserv. Biol.*, 20, 538–548.
- Marion, G.M. (1996). Temperature enhancement experiments. In: *ITEX (International Tundra Experiment) Manual* (eds Molau, U. & Mølgaard, P.). Danish Polar Center, Copenhagen, pp. 17–22.
- Marion, G.M., Henry, G.H.R., Freckman, D.W., Johnstone, J., Jones, G., Jones, M.H. *et al.* (1997). Open-top designs for manipulating field temperature in high-latitude ecosystems. *Glob. Chang. Biol.*, 3(Suppl. 1), 20–32.
- Miller, W.R. & Egler, F.E. (1950). Vegetation of the Wequetequoick-Pawcatuck tidal-marshes, Connecticut. *Ecol. Monogr.*, 20, 143–172.
- Sala, O.E., Chapin, F.S.I., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R. *et al.* (2000). Global biodiversity scenarios for the year 2100. *Science*, 287, 1770–1774.
- Sanford, E. (1999). Regulation of keystone predation by small changes in ocean temperature. *Science*, 283, 2095–2097.
- Theodose, T.A. & Martin, J. (2003). Microclimate and substrate quality controls on nitrogen mineralization in a New England high salt marsh. *Plant Ecol.*, 167, 213–221.
- Theodose, T.A. & Roths, J.B. (1999). Variation in nutrient availability and plant species diversity across forb and graminoid zones of a Northern New England high salt marsh. *Plant Ecol.*, 143, 219–228.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C. *et al.* (2004). Extinction risk from climate change. *Nature*, 427, 145–148.
- Thuiller, W., Lavorel, S., Araujo, M.B., Sykes, M.T. & Prentice, I.C. (2005). Climate change threats to plant diversity in Europe. *Proc. Natl Acad. Sci. USA*, 102, 8245–8250.
- USDA (2009). *The PLANTS Database*. National Plant Data Center, Baton Rouge, LA.
- Warren, R.S. & Niering, W.A. (1993). Vegetation change on a northeast tidal marsh: interaction of sea-level rise and marsh accretion. *Ecology*, 74, 96–103.

## SUPPORTING INFORMATION

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

**Appendix S1** Effects of open top chambers on average daily temperature.

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