ECOLOGY LETTERS

Ecology Letters, (2017) doi: 10.1111/ele.12721

LETTER

Natural enemies govern ecosystem resilience in the face of extreme droughts

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Abstract

Severe droughts are on the rise in many regions. But thus far, attempts to predict when drought will cause a major regime shift or when ecosystems are resilient, often using plant drought tolerance models, have been frustrated. Here, we show that pressure from natural enemies regulates an ecosystem's resilience to severe droughts. Field experiments revealed that in protected salt marshes experiencing a severe drought, plant-eating grazers eliminated drought-stressed vegetation that could otherwise survive and recover from the climate extreme, transforming once lush marshes into persistent salt barrens. These results provide an explicit experimental demonstration for the obligatory role of natural enemies across the initiation, expansion and recovery stages of a natural ecosystem's collapse. Our study highlights that natural enemies can hasten an ecosystem's resilience to drought to much lower levels than currently predicted, calling for integration into climate change predictions and conservation strategies.

Keywords

Consumer interactions, drought, ecosystem collapse and recovery, protected areas.

Ecology Letters (2017)

INTRODUCTION

Climate warming is projected to perturb the global water cycle, cause major shifts in the distribution of water resources on Earth (Milly *et al.* 2005) and exacerbate the scale and intensity of drought, including mega-drought, in coming decades (Dai 2013). Intensifying drought has been documented to devastate ecosystems in many continents and biomes (Breshears *et al.* 2005; Allen *et al.* 2010; McDowell *et al.* 2011). For instance, drought was found to cause die-offs of > 2 965 000 acres of pine forests (Breshears *et al.* 2005) and > 250 000 acres of salt marshes in the USA (McKee *et al.* 2004). The 2010–2011 drought in temperate China, the worst in 60 years, damaged 19.1 million acres of croplands, with economic damage of billions of USD (FAO 2011).

Although drought impacts are costly and widespread, the resilience of natural ecosystems to drought is not well understood. Current models often assume plant physiological tolerances to decreasing water availability, among other factors (e.g. competition), overwhelmingly determine ecosystem resilience to drought (McDowell *et al.* 2011; Rowland *et al.* 2015). Such models, however, have been found to fail to simulate a large proportion (~ 70% in Steinkamp & Hickler 2015) of the reported drought-associated vegetation mortality events globally. This predictive failure is likely in large part due to the limited understanding of mechanistic processes underlying vegetation die-offs during drought, which is predominantly shaped by the large body of experimental plant drought tolerance studies (e.g. Rowland *et al.* 2015).

Despite the fact that plants in natural ecosystems are often regulated by natural enemies (e.g. grazers and pathogens), to our knowledge, no experimental studies in any natural ecosystem have tested for the relative role of natural enemies in the full process (initiation, expansion and recovery) of ecosystem collapse associated with a real-world drought. Past investigations (e.g. Silliman *et al.* 2005; Hein 2006; Williams *et al.* 2013; Koerner & Collins 2014) were primarily observational, comprised only post-drought experiments, were from agricultural ecosystems (e.g. livestock and rangelands) or focused on effects of simulated drought on plant growth or community composition, rather than ecosystem collapse associated with a real-world drought (sudden losses of vegetation and ecosystem shifts to a contrasting state; Scheffer *et al.* 2001). If natural enemies act additively or synergistically with drought stress, even sublethal drought can lead to ecosystem collapse. This coupling of climate and consumptive stress would then result in an ecosystem's tipping point – at which a sudden ecosystem state shift occurs – to drought being significantly lower than predicted by plant drought tolerance models (McDowell *et al.* 2013; Silliman *et al.* 2013). An experimental demonstration of this hypothesis will provide crucial insight into the mechanisms underlying the resilience of natural ecosystems and can also help improve predictions of ecosystem tipping points to climate stress, a major challenge in ecology and conservation (Scheffer *et al.* 2009).

In this study, to directly test whether natural enemies can lower a natural ecosystem's resilience (i.e. resistance and recovery) to drought, we conducted a series of grazer exclusion experiments in protected salt marshes in temperate China between 2009 and 2015 throughout the extreme 2011 drought. These salt marshes are ideal for experimentally testing this question, as i) they have been experiencing widespread vegetation die-offs (> 16 300 acres; Jia *et al.* 2013) associated with a significant, region-wide drying trend, ii) they are protected areas with lower anthropogenic stress (e.g. coastal development or invasive plants) and iii) plants dominating these salt marshes – *Suaeda salsa* L. – are commonly grazed by the crab *Helice tientsinensis* Rathbun (see photographs of the crab and grazing in Fig. S1), a conspicuous salt marsh grazer (He *et al.* 2015). Furthermore, the annual life cycle of *S. salsa* allows experimentation on vegetation collapse and recovery over multiple life cycles, which, for long-lived grasses, shrubs and trees (Khan *et al.* 1994; Allen *et al.* 2010; Williams *et al.* 2013), would take tens, even hundreds of years and is thus often infeasible.

We hypothesise that: (1) in these protected salt marshes, both drought stress and grazing by plant-killing crabs are needed to initiate intense vegetation die-off; and (2) in post-drought years, grazing expands initial die-off areas by killing otherwise healthy vegetation on die-off borders and continues to suppress plant recovery. We therefore predict that pressure from natural enemies lowers the ecosystem's tipping point to drought, leading to earlier shifts in ecosystem state. To begin to test if natural enemies can potentially be a factor lowering resilience to drought in other natural ecosystems, we conduct a literature review on reports of drought-associated vegetation mortalities and their relevant natural enemies.

MATERIALS AND METHODS

Field sites and the 2011 drought

Experiments were mainly conducted in a high marsh located in the Yellow River Delta (Fuqiaobei, 37°46′ N, 119°09′ E), one of the two nature reserves containing the majority of the remaining native salt marshes in temperate China. This marsh was well vegetated before 2011 (further site information can be found in Text S1). As part of a long-term research project, abiotic and biotic factors (including vegetation, soil salinity and crab abundance) in the marsh have been monitored in spring (late April to May; for the first year 2009, June) and fall (late August to September) every year since 2009 (Cui *et al.* 2011) (changes in soil salinity and crab abundance over the study period can be found in Figs S2 and S3, respectively). We also conducted crab exclusion experiments at other marsh sites: Dawenliu (37°43′ N, 119°07′ E), Mingzhouzha (37°43′ N, 119°03′ E) and Yiqian'er (38°05′ N, 118°43′ E) marshes in the Yellow River Delta, and Dashitou (40°54′ N, 121°47′ E) marsh in the Liao River Delta, where vegetation die-off has been observed for more than a decade (detailed in Text S1). At all sites, marshes are flooded by irregular semidiurnal tides (Jin & Sun 1992) and are often hypersaline due to infrequent flooding and high evaporation: precipitation ratios (Jia *et al.* 2013; He *et al.* 2015). All of these sites were located in protected marshes that were not subject to coastal reclamations or habitat conversions (the main drivers of coastal wetland loss in non-protected areas).

The 2010–2011 China drought hit the Yellow River Delta between November 2010 and February 2011. This winter drought was followed by an extremely dry spring. The total precipitation of 27.3 mm between March and May 2011 (periods of *S. salsa* seedling establishment; He *et al.* 2015), the lowest since 1979 with available records, was only 27% of the long-term average of 100.5 mm (see Fig. S2 for variation in precipitation and standardised precipitation index over the study period). Drought was especially severe in April; soil volumetric water content was ~ 45% lower than in non-drought years (Han *et al.* 2015) and soil salinity more than doubled (Fig. S2a). Drought generally subsided after 2011 (Fig. S2).

Pre-drought experiments on initiation of marsh die-off

We conducted a crab exclusion experiment in 2010 (the pre-drought year), and maintained the experiment in 2011 (the drought year) and 2012 (the post-drought year) (see similar pre–post experimental designs in Schoener *et al.* 2001; Hughes & Stachowicz 2004). To do so, we established 24, 1 m^2 plots (spaced > 5 m apart) in March 2010, eight of which were randomly assigned to each of the three treatments: crab exclusion, exclusion control and unmanipulated control. Crab exclusion cages (1 × 1 × 1 m, $l \times w \times h$; see plot photographs in Fig. S4) were constructed of plastic mesh (7 mm mesh size), held at four corners with wooden stakes and inserted 30 cm into the soil (Hensel & Silliman 2013). Exclusion controls had cages of the same design, except that these cages had two openings (~ 20 × 10 cm) at the soil surface on each side to allow crab access. Treatments were maintained biweekly or monthly as needed. Crabs that entered exclusion plots were removed using pitfall traps (two per plot, ~ 10 cm diameter and 20 cm depth). Crab exclusion controls had similar pitfall traps, but these traps each had a plastic mesh cap. To examine whether the vegetation that survived the 2011 drought in crab exclusions would survive subsequent crab grazing after drought subsidence, three of the crab exclusion cages were removed in April 2012 to re-allow crab access. In late August in each year, vegetation cover in each plot was visually estimated, and aboveground biomass was harvested from a 25 × 25 cm quadrat, oven dried at 60 °C for 48 h and weighed. We used repeated-measures ANOVAS (Hyer & Waller 2014) to examine the effects of crab exclusion vs. control treatments on vegetation cover and biomass in 2010 and 2011, and nonparametric multiple comparisons (Dunn method for joint ranking) to examine differences in cover and biomass among all treatments (including control and exclusion control treatments that had many zero data) in each year, where the ANOVA assumptions cannot be met. All data analyses in this manuscript were conducted using JMP 10 (SAS Institute, Cary, NC, USA).

Post-drought experiments on marsh die-off expansion and recovery

Die-off borders

After the 2011 drought subsided, we investigated impacts of grazers on the potential for the ecosystem to recover. To do so, we first conducted a crab exclusion experiment on marsh die-off/mudflat borders. In late May 2013, we located 24, 0.5 × 0.5 m plots (spaced > 5 m apart), eight of which were randomly assigned to crab exclusion, exclusion control and unmanipulated control treatments. Crab exclusion cages were of similar design as described above. In early September, plants in a 30 × 30 cm area in each plot were counted, and aboveground biomass was quantified. We used nonparametric multiple comparisons (Dunn method for joint ranking) to test for differences in density and biomass between treatments. Second, to quantify the extent of border die-off expansion, we marked eight, 16-m-long die-off borders with PVC poles, and measured the distance these borders moved between May and September 2013. We used a Welch's t test to examine whether the mean width of border die-off expansion differs from zero (data were log transformed for analysis). We additionally examined crab grazing on die-off borders in 2015 during a 2-week revisit in June. To do so, we located on die-off borders 32 plots containing 10–20 similarly sized *S. salsa* seedlings (within the range of natural density), which were assigned to crab exclusion ($n = 16$) and control ($n = 16$) treatments. Plots assigned to crab exclusion treatments were caged with galvanised hardware mesh (7 mm mesh size, 10 cm diameter, 40 and 10 cm high above and belowground, respectively) held by PVC poles. Plants in each plot were thinned to 10 individuals for standardisation (He *et al.* 2015). One of our experiments (described below) has shown that galvanised hardware mesh did not generate experimental artefacts, so exclusion controls were not included here. We conducted the same experiment (but $n = 8$ per treatment) at Dashitou in the Liao River Delta. We counted the number of surviving seedlings in each plot 2 weeks later, and used nonparametric Wilcoxon tests to test for differences between treatments.

Remnant plant patches

To examine the impacts of crab grazing on remnant plant patches within die-off areas, we conducted a crab exclusion experiment in four randomly selected remnant plant patches, where we located 40 plots containing 10–20 similarly sized *S. salsa* seedlings in May 2012 and assigned them to crab exclusion ($n = 16$), exclusion control ($n = 8$) and control ($n = 16$) treatments. Crab exclusion cages (constructed of hardware mesh) were of the same design as described above, and exclusion control plots had the same cages except that these cages had half of their periphery cut to 5 cm above the soil surface to allow crab access. Plants in each plot were thinned to 10 individuals for standardisation. In early September, the number of plants and aboveground biomass in each plot were quantified. We used nonparametric multiple comparisons (Dunn method for joint ranking) to examine differences in density and biomass between treatments. In this analysis, we pooled data from the four patches. The effect of crab exclusion did not vary among the four patches. Additional analyses using generalised linear models (Poisson and normal distribution for density and biomass (after Box–Cox transformation) data, respectively) found no significant effects of patch or patch × crab treatment interactions ($P > 0.20$ in all cases).

Recovery within die-off areas following the 2011 drought

To further strengthen our tests for the impacts of grazers on post-drought ecosystem recovery, we conducted planting and crab exclusion experiments in four marshes spanning across the entire arrange of the protected salt marshes. To do so, we first conducted a planting and crab exclusion experiment in die-off areas following the 2011 drought. In May 2012, we located 30, 0.5 × 0.5 m plots, of which 12, 6 and 12 were assigned to crab exclusion, crab exclusion control and control treatments, respectively (see Fig. S5d for plot photographs). Natural recruitment was extremely limited in die-off areas, so transplants of soil blocks containing emerging *S. salsa* seedlings and seeds were used to supplement natural recruitment (note that planting or seeding is often required in salt marsh restorations due to limited natural soil seed bank or propagule dispersal, as shown in past studies in the USA [Morzaria-Luna & Zedler 2007), Europe (Bakker *et al.* 2002) and China (described below)]. We excavated soil blocks (10 cm diameter, 10 cm depth) containing 20–40 *S. salsa* seedlings from a vegetated area and transplanted nine soil blocks into each of the above plots (arranged in 3 × 3). Vegetation cover in each plot was visually estimated in late August 2012. All treatments were maintained in 2013, and vegetation cover was estimated again in late August 2013, to examine whether the planted vegetation in 2012 (with and without crabs) would persist via natural recruitment in the following year. We tested for differences between treatments in each year using nonparametric multiple comparisons (Dunn method for joint ranking, which addresses the issue of unequal sample size; Zar 1999).

Generality in other die-off sites

To examine whether crab grazing affects vegetation recovery in die-off areas in other marshes, we further conducted planting and crab exclusion experiments at Dawenliu, Mingzhouzha and Yiqian'er (note that in the Liao River Delta, governmental efforts have been taken to convert salt barrens into vegetated marshes for tourist attraction, but restored marshes often did not self-sustain, and replanting was required due to low survival rates of planted vegetation; He *et al.* 2013; Jia *et al.* 2013). In May 2013, we collected soil blocks (10 cm diameter, 10 cm depth) containing *S. salsa* seedlings from a vegetated area in Fuqiaobei, thinned each to 10 similarly sized individuals and transplanted 20 of these blocks into each site (including Fuqiaobei; soil blocks were spaced > 2 m apart), half of which were assigned to crab exclusion (using hardware mesh cages of the same design as described above) and unmanipulated control treatments, respectively. In early September, the number of plants in each plot was counted, and aboveground biomass was quantified. We used nonparametric Wilcoxon tests to examine differences between treatments at each site.

Pre- and post-drought remote-sensing analysis

We further used GIS analyses to estimate the extent of marsh die-offs at Fuqiaobei before, during and after the 2011 drought. Landsat ETM+ and OLI images taken at low tide on clear, cloud-free days in fall (September–October) between 2009 and 2015 (unavailable for 2012) were downloaded from the US Geological Survey website (http://glovis.usgs.gov/). Following standard methods (Teillet *et al.* 2006; Chander *et al.* 2009), satellite images were corrected for atmospheric effects, converted into top-of-atmospheric reflectance and cross-calibrated using common ground targets with low (ocean) and high (urban built-up) reflectance, to allow for temporal comparison. Then we computed the normalised difference vegetation index (NDVI, a most widely used and well-understood remote-sensing vegetation index; Pettorelli *et al.* 2005) to estimate vegetation coverage. Image pixels with NDVI < 0.10–0.20 (the exact NDVI value used to delimit bare soils varies with study and ecosystem) are typically identified as bare, non-vegetated soils (Sobrino & Raissouni 2000; Kustas *et al.* 2003; Fernandez-Buces *et al.* 2006; Jeong *et al.* 2011). In our study, we verified that die-off areas (identified in ground surveys along die-off borders) had NDVIs < 0.10, whereas vegetated areas had NDVIs of ~ 0.15–0.30 (see Fig. S6 for spatial variation in NDVI in different years). We used the number of pixels with NDVI < 0.10 as a conservative estimate of the extent of marsh die-off in each year). These GIS analyses were done using Quantum GIS 2.14 (QGIS Development Team 2016).

RESULTS

Initiation of vegetation die-off in protected salt marshes

Our long-term field surveys, supported by remote-sensing analysis, revealed dramatic vegetation loss following the 2011 drought (Fig. 1a); vegetation cover was ~ 60–80% in the pre-drought years in 2009 and 2010, but dropped to < 10% after 2011. Our grazer exclusion experiment, however, revealed that drought alone affected salt marsh vegetation only moderately and that both drought and attack by natural enemies were needed to cause ecosystem die-off. In the pre-drought year in 2010, vegetation cover did not differ significantly between control and crab exclusion treatments ($P = 0.31$; Fig. 1b). During the drought year in 2011, vegetation cover in crab exclusion plots decreased to ~ 60%. In contrast, in control plots open to crab grazing, vegetation nearly completely disappeared, having a mean cover of < 10% (Fig. 1b; see Fig. S4 for biomass responses and photographs). Comparing between drought and non-drought years, the interaction between drought and grazing appeared synergistic, with disproportionally stronger impacts of grazing occurring in drought years (see test statistics in Table S1).

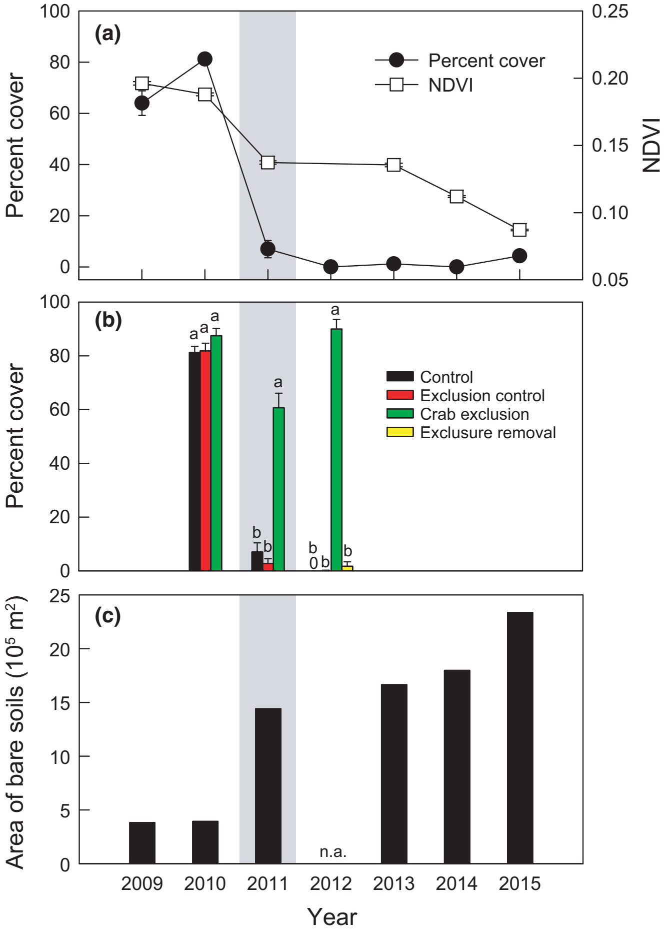

Figure 1 Salt marsh vegetation before, during and after the 2011 drought. Shaded area indicates the 2011 drought. (a) Vegetation cover (averages of 8–25 field plots) and normalised difference vegetation index (NDVI) between 2009 and 2015 (also see NDVI maps in Fig. S6). NDVI was unavailable for 2012. (b) Vegetation cover in different crab exclusion treatments before, during and after the 2011 drought. Data are means (± SE). Within a year, bars sharing a letter are not significantly different from one another ($P > 0.05$). (c) Area of bare soils in each year. n.a. indicates not available.

Vegetation die-off expansion and recovery

After the drought subsided, plants on marsh die-off/mudflat borders thrived in crab exclusion plots, while in control and exclusion control plots with free crab access plants were completely eliminated (Fig. 2a,b). Over just one growing season in 2013, intense grazing on marsh die-off borders linearly extended marsh die-off by 49.6 ± 18.2 m (SE) on average ($t_7 = 10.45$, $P < 0.0001$; see Fig. S5a for active crab grazing on die-off borders). Intense grazing on marsh die-off borders was also observed in 2015 and in other Chinese marshes (see Fig. S7 for detailed results testing for crab grazing in these additional years/sites). In addition to expanding die-offs at their edges, crab grazing diminished remnant plant patches found within die-off areas (Fig. 2c,d). Our GIS survey, combined with our field studies, indicates that grazing expanded die-off areas after the drought subsided by 62.2%, from 1 440 900 in 2011 to 2 336 400 m^2 in 2015 (Figs 1c, S6), a period without recurrent drought.

Our exclusion experiment also revealed that grazers suppressed the high potential for this plant ecosystem to recover from natural recruitment. After the drought subsided in 2012, few plants re-established in open areas, but in crab exclusion plots, plants thrived and reached a cover of ~ 90% on average (Fig. 1b) and thus fully recovered within just a year of drought subsidence. Removing exclusion cages to re-allow crab access revealed that drought-weakened vegetation in crab exclusions, however, did not recover with subsequent access to crabs, but nearly completely vanished (Fig. 1b).

The impacts of grazers on post-drought ecosystem recovery from recruitment were further demonstrated in our planting and crab exclusion experiments in four marshes across the protected salt marshes. In die-off areas established following the 2011 drought, planting succeeded in marsh recovery only in crab exclusion plots (Figs 2e,f, S5). Where crabs were excluded, planted vegetation in 2012 thrived via natural recruitment in the following year (i.e. self-sustainable; Fig. 2e). Crab grazing also suppressed plant recovery in other marshes where die-off (potentially associated with earlier droughts and declines in estuarine freshwater discharge; see Text S1) has persisted with no sign of recovery for at least a decade (see satellite images showing die-offs at these marshes in Fig. S8). At only one site experiencing intense erosion stress (Chu *et al.* 2006) did planted vegetation die even in the absence of crabs (Fig. 2f).

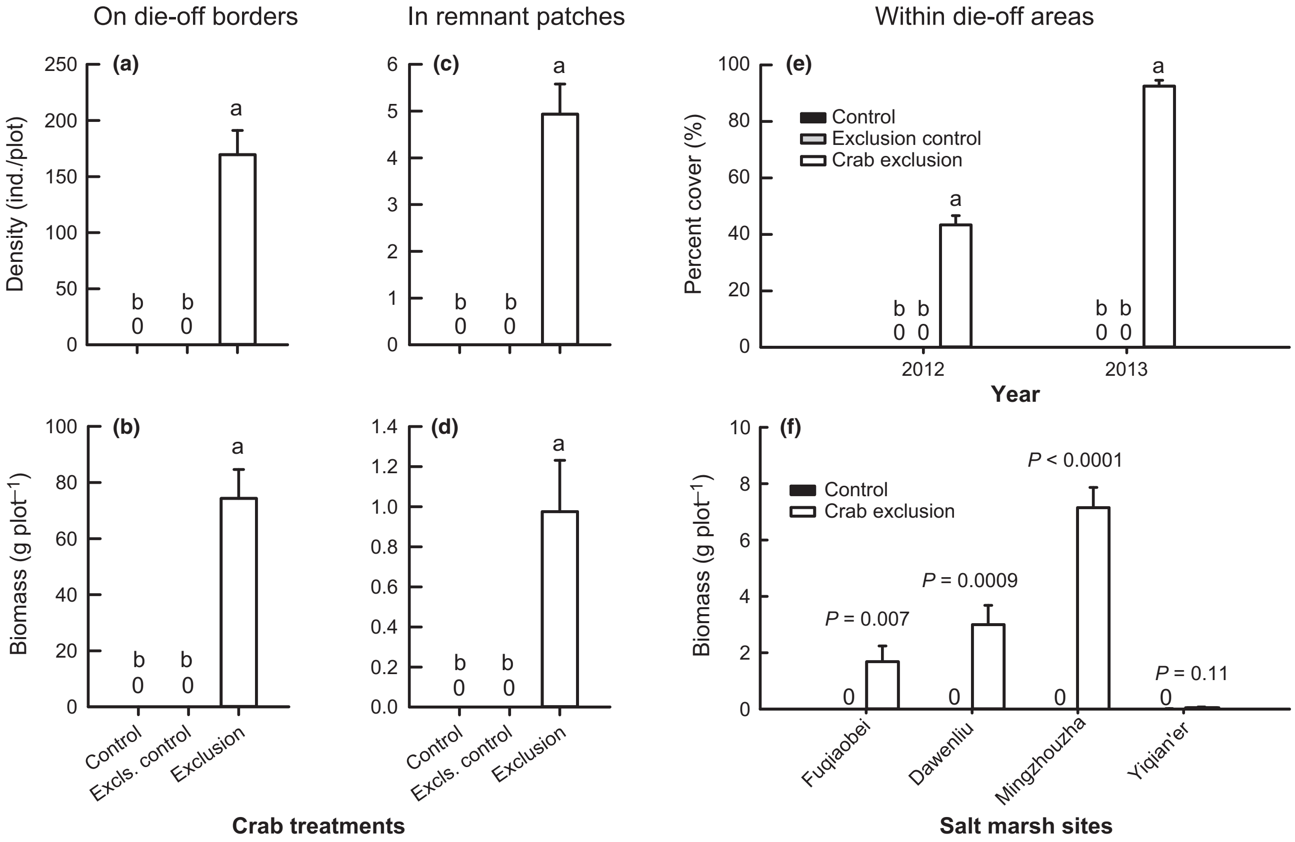

Figure 2 Additional experiments testing post-drought marsh die-off expansion and recovery as affected by grazers. (a–d) Crab grazing and expansion of marsh die-off on die-off borders (a and b) and in remnant plant patches (c and d). (e and f) Crab grazing and marsh recovery from plantings across years and sites. Shown are means (+SE). See Fig. S5 for relevant photographs and data from additional years/sites in Fig. S7. In (a–e), bars sharing a letter are not significantly different ($P > 0.05$). In (f), P values from nonparametric Wilcoxon tests are shown.

DISCUSSION

Our experiments across pre-, during and post-drought periods unambiguously show that pressure from natural enemies can regulate the resilience of an ecosystem to severe droughts. Plants in the protected salt marshes could well survive the climatic extreme, but only when plant-eating grazers were excluded. Outside grazer exclusions, grazing decimated drought-stressed vegetation, resulting in catastrophic vegetation loss. Such drought–natural enemy synergisms can have multiple mechanisms. In our study, the abundance of grazing crabs declined following the drought (Fig. S3), suggesting that the grazer–drought synergism was caused by compromised plant condition rather than by increased grazer abundance. The grazer–drought synergism could have occurred due to increased plant susceptibility to grazing following drought – which has been widely documented (Jactel *et al.* 2012; McDowell *et al.* 2013), or the compounding effects of grazers congregating on remaining plants as plant abundance declines (Silliman *et al.* 2013). The sudden decline in vegetation cover in 2011 could not be attributed to a cumulative herbivory effect (if there was any), as (1) the herbivory effect was insignificant in the pre-drought year of 2010 and (2) vegetation cover was similar between the two pre-drought years 2009 and 2010. If there was a considerable cumulative herbivory effect, then vegetation cover in 2010 would have been much lower than in 2009. This, however, was not the case (Fig. 1a). Synergistic interactions have been also found to be common between other environmental stressors (Crain *et al.* 2008; Darling & Côté 2008). Synergistic grazer–drought interactions are contrary to the environmental stress model predicting that consumer control weakens with increasing physical stress (Menge & Sutherland 1987), but support the recently proposed consumer stress model hypothesising that consumer stress can interact additively or synergistically with physical stress (Silliman *et al.* 2013). Our work provides the first direct experimental evidence that such grazer–drought synergisms can trigger the collapse of a natural ecosystem under a real-world drought event.

Our study also provides a novel experimental demonstration that pressure from natural enemies can lead to a persistent shift in ecosystem state following drought, generating a drought legacy effect (*sensu* Anderegg *et al.* 2013, 2015). First, after the drought subsided, plant-eating grazers expanded initial die-off areas along die-off borders. This process of grazer-driven expansion of vegetation die-off along die-off borders, often driven through the formation and movement of consumer fronts along the edges of remaining plant prey populations, has also been observed in marsh die-off areas in Argentina (Daleo *et al.* 2011), the southeastern USA (Silliman *et al.* 2005) and New England (Altieri *et al.* 2012). Importantly, our results show that grazers further restrict vegetation recovery by suppressing plant recruitment within established die-off areas. This top-down control over ecosystem recovery occurred even when plant recruitment was supplemented and could survive in an unvegetated, physically stressful flat. Indeed, massive marsh plantings in restorations by the Chinese government in 2015 failed to establish, an obvious driver of which was intense grazing by crabs (see Fig. S9 for photographs). Although crab abundance generally declined following the drought, some crabs persisted in areas devoid of marsh plants, likely because crabs can switch/supplement their diet from plants to algae or animals (Kennish 1996) or move into subtidal or terrestrial systems.

Recovery is a fundamental process underlying the fate of ecosystems after disturbance (Suding *et al.* 2004; van Nes & Scheffer 2007). Our finding highlighting grazer suppression of ecosystem recovery from drought concurs with studies from other marine or terrestrial ecosystems showing that vegetation regrowth following other disturbances (e.g. heat wave, storm or fire) can be constrained by grazers, including sea urchins (Konar & Estes 2003; Filbee-Dexter & Scheibling 2014), fishes (Wernberg *et al.* 2016), elephants (Dublin *et al.* 1990) or exotic mammals (Ramirez *et al.* 2012; Perry *et al.* 2015), and lead to the emergence of an alternative state (e.g. kelp forests vs. urchin barrens/seaweed turfs, and forests/woodlands vs. grasslands). Alternatively, when natural enemies are lethal only to drought-stressed plants but do not kill post-drought plant recruitment, ecosystems may recover following drought subsidence (Angelini & Silliman 2012; Williams *et al.* 2013). Recovery can also be affected by other factors, and in our study, by a positive plant–soil feedback loop: initial vegetation loss leads to elevated salinity and moisture stresses (owing to loss of vegetation shading, as shown in our past studies; He *et al.* 2012) that further limit plant establishment. Such processes are known to contribute to alternate stable states in many ecosystems (Rietkerk *et al.* 2004), including long-term salt marsh die-offs in the Arctic (generated by eutrophication-fuelled geese grazing) (Srivastava & Jefferies 1996).

The impacts of natural enemies on ecosystem resilience to drought are potentially common in other ecosystems, although experimental demonstration is often lacking. A past global review of drought-associated tree mortality events (Allen *et al.* 2010) and our own review updating Allen *et al.* (2010) and including herbaceous and shrubby vegetation (see Text S2 for detailed review methods) both suggest that many past vegetation mortality events also had some type of natural enemy, including insects, fungal pathogens, parasitic plants, marine crustaceans and mammals, as a contributing factor (Fig. 3). It should be noted that evidence for the roles of natural enemies in driving vegetation die-off in those ecosystems, however, remains largely observational. The relative strength of natural enemy effects in those vegetation die-off events requires further explicit experimental tests across pre-, during, and post-drought periods.

Combined, our results reveal that although drought generated only sublethal physical stress for salt marsh vegetation, drought stress in combination with pressure from plant-killing grazers generated enough stress to trigger intensive marsh die-off. The presence of this grazing synergism thus lowered the ecosystem's tipping point, along a gradient of escalating drought stress, at which the plant community collapses. Grazers, however, not only suppressed resistance of salt marsh plants to drought, but additionally (1) expanded initial die-off areas by killing otherwise healthy vegetation on die-off borders, and (2) has continued to suppress plant recovery for over 4 years after the drought subsided. These results suggest that vegetation can be remarkably more vulnerable to drought than forecasted by current models that predict vegetation resilience based predominately on plant drought tolerances, and that suppressed resilience can occur when climate intensifies the impacts of natural enemies on habitat-forming species, such as trees, kelps and corals. Our study supports the idea that trophic control can explain the existence of "ecosystems

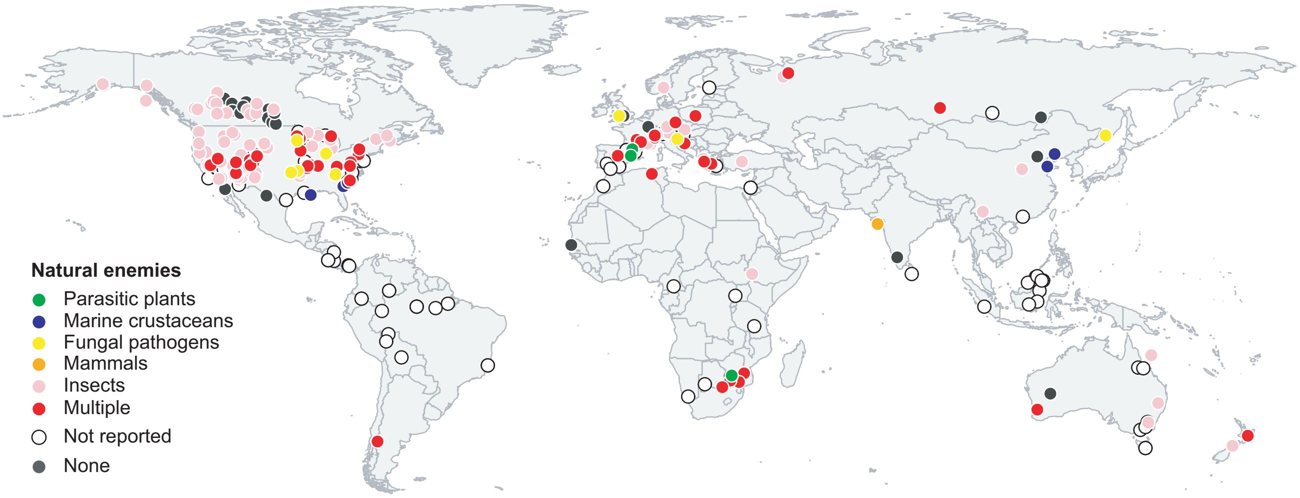

Figure 3 Drought-associated vegetation mortalities and their potentially relevant natural enemies reported in the literature. Six main types of natural enemies are considered. A list of these vegetation mortality events and their associated natural enemies is given in Dataset S1. Note that while natural enemies have been considered a contributing factor in many of these events, the relative strength of natural enemy vs. drought effects in these events requires further experimental tests (see Discussion). The blue points in northeast Asia indicate the protected salt marshes examined in this study.

uncertain" – realised ecosystems that do not conform to their potential as predicted by climate variables (*sensu* Whittaker 1975; see Bond 2010). Our work highlights that natural enemies should no longer be considered ancillary to the primary force of drought but indeed a likely powerful counterpart that cannot only act additively to kill ecosystems but also suppress their recovery after drought subsides.

These findings also have important implications for conservation. Many ecosystems are well protected from local human disturbances, such as deforestation and habitat transformations (Murray *et al.* 2014). Our study, however, shows that the once lush marshes in well-protected nature reserves are being transformed into salt barrens (Figs 2c, S5, S8) by plant-killing grazers acting additively with drought stress. Protected areas are in many instances the dominant conservation strategy for ecosystems (Kareiva & Marvier 2015). Our study calls for full integration of the impacts of natural enemies into understanding of drought-associated ecosystem collapses, as this advance will not only substantially improve understanding and predicting ecosystem resilience to climate change but can also help conservationists pinpoint and manage for earlier tipping points that are likely to occur under intensifying drought.

ACKNOWLEDGEMENTS

We thank A. H. Altieri, M. D. Bertness, Y. Cai, B. B. Hughes, S. C. Pennings and X. Shao for generous support at different stages. Jim Estes, anonymous reviewers and the editor provided constructive comments. Funding was provided by National Key Basic Research Program of China (2013CB430406). Q.H. was partly supported by the Edward Stolarz Foundation.

AUTHORSHIP STATEMENT

QH, BRS and BC designed the research. QH and ZL conducted the experiments, data collection and analysis. QH and BRS wrote the article. All authors commented on and edited the manuscript.

DATA ACCESSIBILITY STATEMENT

Data associated with this manuscript have been permanently archived in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.1sm3f.

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Editor, Mary O'Connor
Manuscript received 12 October 2016
Manuscript accepted 18 November 2016