Time-lagged impacts of extreme, multi-year drought on tidal salt marsh plant invasion

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Abstract. Climate change is projected to increase the frequency of extreme drought events, which can have dramatic consequences for ecosystems. Extreme drought may interact with other stressors such as invasion by non-native species, yet little research has explored these dynamics. Here, we examine the physical mechanisms and temporal scale underlying a dieback of an invasive non-native plant, Lepidium latifolium, in tidal salt marshes of the San Francisco Bay, California, USA, during an extreme, multi-year drought occurring from 2012 to 2015. Using generalized additive mixed models (GAMMs), we explored the relationship between eight years of estuarine salinity data and five years of L. latifolium density data from three marshes spanning a gradient of salinity across the San Francisco Bay. We found a significant time-lagged (3 yr) effect of estuarine salinity on L. latifolium density, with high salinities preceding reductions in L. latifolium densities and low salinities preceding increases. The most dramatic change in stem density, a 54% reduction in 2015, was preceded by a salinity increase of 43% from 2011 to 2012. We found the L. latifolium decline was driven by impacts on mature, rather than young, plants. Additionally, we tested the importance of local precipitation in driving L. latifolium densities in a one-season rain exclusion experiment. We found 100% exclusion of precipitation during one rainy season (January–mid-May) did not have a significant impact on densities of mature stands of L. latifolium. Our finding that estuarine salinity was a key driver of L. latifolium invasion dynamics suggests sea level rise, like extreme drought, may hinder L. latifolium invasion, as it will also raise estuarine salinities. Further, our study highlights the importance of temporal lags in understanding climate change impacts on biological invasions, which has received very little study to date.

Key words: extreme drought; generalized additive mixed models; invasion; Lepidium latifolium; salinity; salt marsh; time-lagged effects.

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INTRODUCTION

Extreme drought events, persisting across multiple years, can have dramatic consequences for ecosystems (IPCC 2014) and are projected to become more frequent in the future due to climate change (Yoon et al. 2015, Swain et al. 2016). Severe droughts have caused large-scale diebacks of native foundation species in forest (Gitlin et al. 2006) and salt marsh (Silliman et al. 2005) ecosystems by creating water stress and salinity stress, respectively. Importantly, extreme
climate events can occur in concert with other stressors, such as biological invasions, yet we know little about how these stressors might interact (Bradley et al. 2010). There are opposing theories predicting extreme drought could help (Davis et al. 2000, Zedler and Kercher 2004, Diez et al. 2012) or hinder (Sorte et al. 2013) invasion. Yet, research has rarely explored the effect of extreme drought on invasive plant populations in any ecosystem (but see Stromberg 1998, Kane et al. 2011, Catford et al. 2014, LaForgia et al. 2018), and none has done so in salt marshes.

In this study, we examine the effect of extreme drought on an invasive plant, *Lepidium latifolium* (Brassicaceae), that has been aggressively invading marshes in the San Francisco Bay, California, USA, and consequences for the native plant community. From 2012 to 2015, California experienced an extreme, multi-year drought completely unprecedented in the paleontological record of 12,000+ years (Griffin and Anchukaitis 2014, Robeson 2015). Individual years between 2012 and 2015 were notably dry, but the event was made truly exceptional by having four dry years in succession (Robeson 2015). In a recent study, we documented a dramatic dieback in *L. latifolium* populations invading tidal salt marshes in the San Francisco Bay in 2015, during California’s severe drought (Kelso et al. 2020). These findings align with the results of a meta-analysis by Sorte et al. (2013) that found invasive species tend to respond more strongly than native species to both favorable and unfavorable climate conditions. Yet, the physical mechanisms and temporal scale underlying this dieback event remain unknown.

Invasive species are a major threat to ecosystems worldwide (Vitousek et al. 1997, Pejchar and Mooney 2009), causing biotic homogenization (Olden et al. 2004) and loss of species diversity (Davis 2003). Urbanized estuaries are hotspots of invasion because they are exposed to high propagule pressure and nutrient inputs, which facilitate invasion (Carlton and Geller 1993, Zedler and Kercher 2004). In wetland systems, plant invaders can alter community diversity (Silliman and Bertness 2004, Minchinton et al. 2006), physical structure (Reynolds et al. 2017), nutrient cycling (Farrer and Goldberg 2009, Nie et al. 2017), and trophic structure (Levin et al. 2006, Wigginton et al. 2014). One of the most vigorously expanding plant invaders throughout the western United States is *Lepidium latifolium* (henceforth *Lepidium*; DiTomaso and Healy 2007). *Lepidium* invasion in salt marshes has been shown to alter physical structure (Reynolds and Boyer 2010, Kelso 2018), nutrient cycling (Blank 2002), carbon storage (Reynolds and Boyer 2010, Kelso 2018), and invertebrate community structure (Reynolds and Boyer 2010, Wigginton et al. 2014).

Unlike in terrestrial ecosystems where extreme drought creates water stress, in estuarine wetlands drought creates salinity stress by reducing freshwater input from rain and runoff (Silliman et al. 2005, Parker et al. 2011). Salinity is a major structuring force in salt marsh plant communities, altering germination (Noe and Zedler 2001, Noe 2002), productivity (Callaway and Sabraw 1994), competitive dynamics, and survival (Crain et al. 2004). Changes in salinity can also alter invasion dynamics in tidal wetlands. In a series of germination, mesocosm, and greenhouse experiments in southern California, Callaway and Zedler (1998) found reduced salinity increased invasion by the grass *Polypogon monspeliensis* into salt marshes dominated by *Salicornia pacifica*. Silliman and Bertness (2004) found decreased salinity and elevated nutrients associated with shoreline development were the main drivers of invasion by *Phragmites australis* in Narragansett Bay, Rhode Island, USA. A series of laboratory and mesocosm experiments have demonstrated *Lepidium* is sensitive to salinity stress during early life stages and seed production, especially in combination with inundation stress (Spenst 2006, Leininger and Foin 2009, Ahmed and Khan 2010, Gul et al. 2012). In a remote sensing study, Andrew and Ustin (2009) found *Lepidium* tends to invade areas at the marsh–upland boundary and at channel edges, indicating it prefers less stressful inundation and salinity conditions. The impacts of altered salinity on mature stands of *Lepidium* have not been experimentally explored.

The impact of salinity on salt marsh plant communities can depend heavily on the duration of the salinity-change event. In a study of southern California salt marshes, Zedler (1983) found short-term freshening events altered biomass but not species identities, while a long-term
freshening event led to replacement of halophytes with freshwater wetland plants. In a mesocosm experiment of oligohaline marsh plant communities in Louisiana, Howard and Mendelssohn (2000) found both salinity and duration of exposure to salinity significantly impacted plant community structure and composition.

In this study, we explored whether the dramatic dieback of *Lepidium* in 2015 in tidal salt marshes of the San Francisco Bay was driven by drought-induced salinity stress. We asked the following questions: (1) What was the role of reduced site-level precipitation in the *Lepidium* dieback? (2) Was there a relationship between *Lepidium* density and bay salinity? (3) What was the temporal scale of drought-related salinity stress on this invader?

To address these questions, we conducted two studies at salt marsh sites in the San Francisco Bay. First, we tested the effect of reduced site-level precipitation on *Lepidium* densities in a single-season rain exclusion experiment at one site in the winter of 2015–2016. We hypothesized that reduced site-level precipitation would eliminate short-term freshening events and decrease *Lepidium* stem densities. Second, we tested the effect of drought over a longer temporal scale by conducting a multi-year observational study examining the impact of bay water salinity on *Lepidium* stem densities at three salt marsh sites along the estuarine salinity gradient. We hypothesized that longer periods of salinity stress played a key role in causing the observed *Lepidium* dieback.

**METHODS**

**Invader and site descriptions**

*Lepidium* is a perennial herbaceous plant that flowers from April to August, senesces its aboveground biomass in late fall, and re-sprouts from root reserves shortly after the first winter rains (*personal observations*). Its broad tolerance of salinity and moisture conditions has allowed it to invade diverse habitats throughout the western United States, including agricultural fields, riparian corridors, and tidal salt marshes (Young et al. 1995). Once established at a site, *Lepidium* spreads largely through vegetative reproduction and seedlings are rarely observed in the field (Young et al. 1997).

We conducted this research at three salt marshes in the San Francisco Bay, California, USA, which were invaded with *Lepidium*: (1) Palo Alto Baylands Nature Reserve (37.462°, −122.112°), (2) Point Pinole Regional Shoreline (38.003°, −122.341°), and (3) Martinez Regional Shoreline (38.022°, −122.148°; Fig. 1). These sites were arranged along a salinity gradient in the San Francisco Bay (see Fig. 2a for range of annual salinities at each site). Our study area at Palo Alto Baylands, the most saline site, was a high marsh berm transitioning into a fully tidal marsh where the dominant native plants were *Salicornia pacifica* and *Frankenia salina*. Point Pinole, our next most saline site, was a tidal marsh separated from the bay by a sandy barrier beach with inundating tidal flow coming from secondary tidal channels where the dominant native plants were *S. pacifica*, *Jaumea carnosa*, *F. salina*, and *Distichlis spicata*. Martinez, our lowest salinity site, was directly inundated by the bay, and the dominant native plants were *S. pacifica*, *J. carnosa*, *D. spicata*, and *Atriplex prostrata*.

**Precipitation manipulation**

We manipulated precipitation in 1-m² experimental plots at our Palo Alto site between 12
January 2016 and 15 May 2016 by applying one of four precipitation treatments ($N = 6$ plots per treatment): rain exclusion (all rain excluded), rain exclusion control (all rain excluded, plots hand-irrigated to ambient precipitation levels after rain events), rain addition (5.3 cm of water added in addition to ambient precipitation), and unmanipulated control (ambient precipitation). Treatments were randomly assigned to plots, which were spaced 2 or more meters apart along a transect at 7.9 ft MLLW. At the time of establishment, each plot contained an average of $19.97 \pm 2.50$ (SE) $Lepidium$ stems.

Rain exclosures were modified from the design of Yahdjian and Sala (2002), using PVC and greenhouse-grade plastic, which let through full spectrum light (see Appendix S1 and Fig. 3 for construction details). Within 48 h of each rain event, we hand-irrigated rain exclusion control plots with the amount of water that had been excluded (see Appendix S1 for detailed methods of re-irrigation). Rain addition plots received ambient rainfall plus an additional 5.3 cm of freshwater, consistent with regional projections for future precipitation due to climate change (Neelin et al. 2013). Supplemental water from the city of Palo Alto was added during four simulated rain events in February and March (see Appendix S2 for details on the quantity and timing of supplemental water application). Unmanipulated control plots received ambient rainfall.

Prior to manipulation in September 2015, we collected baseline data in each plot. The total number of $Lepidium$ stems and bases were counted. Bases were defined as areas of tuberous growth producing a cluster of individual $Lepidium$ stems. Additionally, we collected percent cover data for all plants utilizing a quadrat demarcated at 1% intervals.
Post-manipulation Lepidium stem and base counts were conducted at the time of peak Lepidium biomass in mid-July 2016. At this time, we also measured percent cover of all plant species within our plots. We measured the effect of exclosures on air temperature using HOBO loggers, rainfall using rain gauges, humidity using an AcuRite 00613 Humidity Monitor, and light penetration using a Li-COR LI-1400 datalogger (see Appendix S3 for details on the sampling and Appendix S3: Table S1 for summary data on these metrics). To assess the impact of exclosures on soil salinity, we redeployed three structures during winter 2017–2018 and sampled soil salinity using the paste method (Richards 1954) before and after two rain events (see Appendix S4 for detailed salinity sampling methods).

Multi-year analysis of Lepidium density and estuarine salinity

We monitored Lepidium populations at Palo Alto from 2013 to 2017 in 35 unmanipulated plots along the same transect and with the same methods described in the precipitation manipulation methods, with Lepidium stem and base counts and percent cover of all plant species estimated within our plots. We also monitored Lepidium populations at Point Pinole (3.5 ft MLLW) and Martinez (3.7 ft MLLW) from 2014 to 2017. At these latter two sites, we established three 20-m transects in patches of Lepidium in spring 2014. Within each transect, ten 1-m² plots were sampled. Transects were chosen randomly within sites, and plots were spaced evenly along the length of the transect on alternating sides of the transect centerline to fully capture Lepidium density variation within each patch. Within each plot, Lepidium stems were counted and percent cover of all plants was measured via visual estimation in 5% bins.

To determine the relationship between estuarine salinity and marsh plant community dynamics, we used monthly salinity data gathered during USGS water quality cruises (Schraga and Cloern 2017, Schraga et al. 2020) from 2010 to 2017 at sampling stations adjacent to each of our three study sites (see Appendix S5 for details of salinity data aggregation). We used data from the surface 5 m of water to calculate average annual salinities for each site. Annual salinities were calculated by water year (October of previous calendar year through September; see Fig. 2 for salinity ranges among sites and years).

Statistical analyses

Precipitation manipulation.—We used generalized linear models (GLMs) to determine the impacts of our precipitation treatments on Lepidium stem and base counts in 2016. The full models included precipitation treatment and the 2015 stem or base counts as fixed factors. To determine if our precipitation manipulation had a one-year lagged effect, we constructed GLMs with stem and base counts in 2017 as the response variable and precipitation treatment, stem/base counts in 2015, and stem/base counts in 2016 as explanatory variables. Because in some cases densities of Lepidium at the beginning of the experiment (2015) significantly impacted densities at the end of the experiment, we standardized across different starting conditions by constructing models using the ratio of densities at the end of the experiment to densities at the beginning of the experiment as the response variable. We report the results of the models using the density ratios as the response variable. We also constructed GLMs with percent native plant...
cover in 2016 as the response variable and precipitation treatment and the 2015 native cover as fixed factors. We used Gaussian error distributions for both stem ratio and native cover models. We used t-tests to understand the effect of our rain exclusion treatments on soil salinity.

Multi-year analysis of bay salinity on plant community.—To understand patterns in bay water salinity through space and time, we constructed a generalized linear model (GLM) using site, year, and the interaction of the two variables. In this model, both site and year were treated as fixed effects in order to understand variation among sites and years. We constructed two GLMs, one for Lepidium stem density data and one for native plant cover, to understand how the plant community changed through space and time. These models contained the same independent variables as those in our bay water model. Our Lepidium and native plant models used data from Palo Alto (2013–2017), Martinez (2014–2017), and Point Pinole (2014–2017). Our bay water salinity model used USGS data from the 2010–2017 water years.

To explore whether the observed changes in Lepidium density were driven by impacts on Lepidium plants of particular life stages, we constructed GLMs with our Lepidium stem and base data from Palo Alto Baylands (2013–2017). We used multi-stem bases as our proxy for mature plants and single-stem bases as our proxy for young plants and new recruits, though it is possible that some single-stem bases were mature plants producing only one stem. We constructed separate GLMs for multi-stem base density, single-stem base density, and number of stems per base, with year as an independent, fixed variable.

We used Gaussian error distributions for salinities and native plant cover, negative binomial error distributions for Lepidium stem densities, and Poisson error distributions for the base and stem/base analyses at Palo Alto Baylands. For all GLMs, the full models included all explanatory variables, as described above, and stepwise model simplification was performed using likelihood-ratio tests when necessary (Crawley 2013). Post hoc tests for GLMs were performed using Tukey’s HSD test.

We used generalized additive mixed models (GAMMs) to determine if there were non-linear, additive effects of bay water salinity on Lepidium stem densities and native plant percent cover. Our full GAMM included a smoothing term for bay water salinity in the same year as the growing season of interest, bay water salinity in the previous year, bay water salinity two years prior, and bay water salinity three years prior. Additionally, the model had a smoothing term for prior season Lepidium stem density. Smoothing terms modify the linear model, which allows for non-linear relationships. Site was included in all models as a fixed effect. We assigned year as a random effect to help account for sources of interannual variation aside from bay water salinity. The same process was used to model native plant percent cover. We used negative binomial error distributions to allow for overdispersion in the Lepidium stem density data and Gaussian distributions for native plant cover. To identify our best GAMM, we used the restricted maximum likelihood (REML) estimation, which is a shrinkage approach to variable selection that removes colinear terms (Marra and Wood 2011). We found equivalent results using a forward model selection process (in the manner of Zuur et al. 2009). We report results based on visual interpretation of the partial effects of the smoothing terms.

Nonsignificant interactions for both GAMMs and GLMs are not presented in the results. Statistical analyses were performed using R software version 3.3.2. GLM analyses were conducted with the LME4, EMMEANS, and MASS packages for R. GAMM analyses were conducted with the MGCV package.

Results

Precipitation manipulation

Testing the efficacy of our rain exclosures, we found soil salinities inside the exclosures were elevated compared to salinities outside the exclosures after each of the two rain events ($t = -3.17$, $df = 4$, $P = 0.03$ for 0.91-cm rain event; Fig. 4). After the subsequent inundating high tide, soil salinities inside precipitation exclosures were still higher, but trending toward becoming equivalent with control salinities ($t = -2.79$, $df = 4$, $P = 0.05$; Fig. 4).

Despite our exclosures significantly influencing soil salinity, we did not find a significant
effect of the precipitation treatments on the ratio of 2016 to 2015 *Lepidium* stems (Fig. 5). Similarly, we did not detect a significant effect on the ratio of 2016 to 2015 *Lepidium* bases. One year later, we found a significant effect of the treatments on the ratio of 2017 to 2015 *Lepidium* stem counts (GLM, Gaussian, $\chi^2 = 8.93$, df = 3, $P = 0.03$; data not shown). Post hoc analysis revealed only the water addition and the rain exclusion control treatments differed from one another, with the water addition plots having a greater proportional increase in stems from 2015 to 2017 than the rain exclusion control plots. Similarly, we found a significant effect of treatment on the ratio of 2017 to 2015 *Lepidium* bases (GLM, Gaussian, $\chi^2 = 9.74$, df = 3, $P = 0.02$; data not shown), with the same pattern of treatment impacts shown in the stem ratios. Native plant percent cover showed no response to the precipitation manipulation.

**Multi-year analysis of Lepidium density and estuarine salinity**

In our analysis of how bay water salinities differed among sites and years, we found both site and year were significant (GLM, Gaussian, $\chi^2 = 13077$, df = 8, $P < 0.001$) and there was no significant interaction between the two factors (Fig. 2). Post hoc tests revealed all three sites had significantly different salinity profiles. Bay water salinity increased through the duration of the drought, with drought years (2012–2015) more similar to one another than non-drought years. In 2016, the year the drought ended, salinities were statistically equivalent to those observed in...
the first year of the drought (2012). The water year 2017 had salinities statistically indistinguishable from the last pre-drought year (2011; Fig. 2). Similarly, in our analysis of how Lepidium densities differed across sites and years, we found both factors were significant (GLM, negative binomial, \( \chi^2 = 19.33, \text{df} = 2, P < 0.0001 \)) and we did not detect a significant interaction between the two (Fig. 6). Post hoc analysis showed years 2015–2017 had significantly lower stem densities than 2014, with 2017 showing the lowest total densities.

At Palo Alto Baylands, we found density of single-stem Lepidium bases (our proxy for young plants) did not differ among years (GLM, Poisson, \( \chi^2 = 7.52, \text{df} = 4, P = 0.11 \)). In contrast, the density of multi-stem Lepidium bases (our proxy for mature plants) did differ significantly among years (GLM, Poisson, \( \chi^2 = 31.35, \text{df} = 4, P < 0.001 \)). Post hoc analysis revealed the density of multi-stem Lepidium bases was significantly lower in 2015 and 2017 than in 2013 and 2014 (2015, 1.89 ± 0.41; 2017, 1.71 ± 0.51; 2013, 3.00 ± 0.39; 2014, 3.85 ± 0.76), while 2016 had intermediate densities (2016, 2.57 ± 0.56). The number of stems per base also differed among years (GLM, Poisson, \( \chi^2 = 142.07, \text{df} = 4, P < 0.001 \)), with post hoc tests revealing that 2013 and 2014 (2013, 10.49 ± 1.25; 2014, 13.25 ± 2.52) had more stems per base than all other years (2015, 6.19 ± 1.38; 2016, 7.24 ± 1.56; 2017, 5.11 ± 1.38).

In our analysis of the relationship between bay water salinity and Lepidium stem density, our best-fit GAMM included the smoothing term of bay water salinities two years and three years prior to the growing season of interest, the smoothing term of Lepidium stem densities in the prior growing season, year as a random effect, and the fixed effect of site. All terms aside from the fixed effect of site were significant (GAMM, negative binomial; Year, \( \chi^2 = 8.01, \text{df} = 3, P < 0.001 \), Prior Year Lepidium stems, \( \chi^2 = 108.91, \text{df} = 9, P < 0.001 \), Two Year Prior Bay Water Salinity, \( \chi^2 = 42.76, \text{df} = 7, P < 0.001 \), Three Year Prior Bay Water Salinity, \( \chi^2 = 94.13, \text{df} = 7, P < 0.001 \); Fig. 7). This model explained 32% of the deviance in the data. There was a shallow, positive relationship between prior year’s Lepidium densities and the current year’s stem densities. We found a strong relationship between salinity three years prior and Lepidium stem density, with high salinities preceding lower Lepidium stem densities and low salinities preceding higher Lepidium densities. The confidence interval for the effect of bay water salinity three years prior to the growing season of interest was tight at both high (drought year) and low (fresh year) salinities and did not include zero. Alternatively, the confidence interval for the effect of bay water salinity two years prior to the growing season of interest was large and included zero for high and low salinities.

In our analysis of how native plant percent cover differed across years and sites, we found a
significant interaction between year and site ($\chi^2 = 54.33$, df = 6, $P < 0.001$; Fig. 8). Post hoc analysis revealed all years showed an increase in native cover when compared to 2014, with Martinez showing the largest increase from 2014 to 2017.

In our analysis of the relationship between native plant cover and bay water salinity, our best-fit GAMM included the smoothing term of...
bay water salinities one year prior to the growing season of interest and during the growing season of interest, the smoothing term of \( Lepidium \) stem densities during the growing season of interest, the smoothing term of year as a random effect, and the fixed effect of site. All terms aside from site and year were significant (GAMM, negative binomial; \( Lepidium \) stem density, \( \chi^2 = 20.49, df = 9, P < 0.001 \); Current Year Bay Water Salinity, \( \chi^2 = 9.66, df = 9, P < 0.001 \); Year Prior Bay Water Salinity, \( \chi^2 = 3.43, df = 9, P < 0.001 \); Fig. 9). This model explained 71% of the deviance in the data. Native plant cover had a strong, negative linear relationship with \( Lepidium \) stem densities. During the current growing season, bay water salinities below 18 psu were associated with higher native cover, whereas salinities above this threshold did not seem to impact native cover positively or negatively (Fig. 9b). In contrast, lower bay water salinities during the prior growing season resulted in a decrease in native plant cover and higher salinity during the prior growing season resulted in an increase in native plant cover (Fig. 9c).

**DISCUSSION**

This study explored the mechanisms underlying the first known instance of extreme drought driving a landscape-level dieback of an invasive salt marsh plant. In our multi-year analysis, we found a time-lagged effect of bay water salinity three years prior to the growing season of interest, which impacted \( Lepidium \) density both negatively (high salinity induced reduction) and positively (low salinity induced increase). The largest \( Lepidium \) reduction we observed, a 54% stem density decrease from 2014 to 2015, occurred three years after the onset of drought conditions, when bay water salinities increased 43% from the previous water year (from 13.86 psu in 2011 to 19.78 psu in 2012). Our model also detected a relationship between bay water salinity two years prior to the year of interest and \( Lepidium \) density, but the confidence interval
around this effect was large and included zero for both high (drought year) and low (rainy year) salinity extremes, which are the focus of this paper. Therefore, we conclude the three-year effect is the primary driver of drought-induced *Lepidium* density changes. Interestingly, we did not detect a significant effect of salinity on *Lepidium* density during the year of interest or the year prior, which highlights the importance of conducting multi-year experiments to study the effect of extreme climate events on ecosystems.

We found the dieback of *Lepidium* was driven by damage to mature plants, as evidenced by our field observations of many dead mature *Lepidium* plants across all our sites and our analyses of unmanipulated plots at Palo Alto Baylands, which identified a decrease in multi-stem bases and a severe reduction in the number of stems per base. *Lepidium* allocates up to 40% of its biomass to roots (Renz and Blank 2004), and these belowground energy stores allow the plant to withstand stressful conditions. The slow depletion of these reserves is likely the mechanism for the lagged effect of drought on *Lepidium*. This mechanism is similar to that proposed by Reichmann et al. (2013), who manipulated precipitation in the Chihuahuan Desert and found low precipitation two years prior created a lagged decrease in invasive grass aboveground net primary productivity by decreasing tiller density in the intervening year. Unlike mature *Lepidium* plants, *Lepidium* seedlings and young plants do not have the same belowground energy stores, making them more susceptible to harsh conditions (Spence 2006). If the dieback of *Lepidium* had been driven mostly by impacts on seedlings and young plants, instead of impacts on mature plants, the drought may have had a more immediate effect on *Lepidium* populations.

To date, *Lepidium* densities have not recovered to pre-drought levels at any of our three study sites. Much like the time lag described above, we attribute the persistence of the *Lepidium* dieback identified in our multi-year analysis to the depletion of belowground energy stores of mature plants, which could have rendered them unable to rebound quickly once conditions became more favorable. In contrast, a shorter or less severe drought may have affected only young plants, resulting in a more rapid recovery after the drought. In addition to suppressing vegetative growth, damage to mature plants could also have hampered post-drought sexual reproduction because high salinity suppresses *Lepidium* seed production (Leininger and Foin 2009) and viability (Spence 2006). Working in California grasslands, LaForgia et al. (2018) found three years of severe drought dramatically diminished the seed bank of invasive annual grasses, and a similar mechanism may have functioned in our system to compound the legacy effect of drought.

In our rain exclusion experiment, we found no effect of precipitation-mediated, short-term freshening events on *Lepidium* density. Despite our rain exclusion structures diverting 100% of precipitation during the winter of 2015–2016 (28.17 cm of rain) and successfully preventing the associated short windows of marsh freshening, we found no impact on stem density of *Lepidium* stands. This result is consistent with the findings from our multi-year bay water analysis, as we found no evidence in either experiment that short-duration salinity changes, either one year without rain-induced freshening events or a single year of high-salinity bay water, drove shifts in *Lepidium* density. Few studies have explored the importance of temporal duration of high- and low-salinity events in tidal salt marshes, and even fewer have examined this in relation to plant invasion. The studies that exist found longer-duration salinity changes have a greater impact than shorter changes (Zedler 1983, Zedler et al. 1990, Chambers et al. 2003), although short-duration salinity changes can have important impacts on early life stages of both native and invasive plants (Chambers et al. 2003, Shippey 2014).

In contrast to the invader, native plant cover remained high both during and after the drought due to the broad salinity tolerance of the native plants and indirect benefits from the dieback of the invader. The results from both our manipulative experiment and our multi-year analysis demonstrate the native plant community’s salinity tolerance. In our manipulative experiment, we found no impact of rain exclusion on native cover. Our multi-year analysis showed that native plants did not decrease their cover during drought and increased their cover within the same growing season when favorable, low-salinity conditions were present. Altered competitive dynamics also contributed to the native plant community’s response.
to drought. Counterintuitively, in our multi-year experiment we found that low bay water salinities in the prior year resulted in decreased native cover, and high bay water salinities in the prior year resulted in increased native cover, an effect we attribute to salinity’s time-lagged impact on *Lepidium* and the resulting changes in competition experienced by native plants. The indirect benefit of drought to native plants through invader dieback was corroborated by Kelso et al. (2020) who compared native plant responses to drought in invaded and uninvaded salt marsh areas. The hardiness of the native plants to drought conditions and their ability to expand into the gaps created by *Lepidium*	extquotesingle s dieback likely reinforced the persistence of the *Lepidium* decline by creating a more challenging post-drought competitive environment for *Lepidium*. Spenst (2006) found the presence of native plants strongly suppressed recruitment of *Lepidium* seedlings. Similarly, Renz et al. (2012) found the presence of broadleaf perennials, be they native or invasive, suppressed vegetative growth of *Lepidium* into uninvaded areas. This was particularly true for *Atriplex* species, which were abundant at our Palo Alto Baylands site. Therefore, competition from native plants may have suppressed both sexual and vegetative reproduction of *Lepidium* after the drought.

A major driver of long-term salinity change in estuaries is sea level rise, which is projected to be 26–82 cm by 2100 (IPCC 2014). Sea level rise, like extreme drought, is projected to increase estuarine salinities (Parker et al. 2011). In a modeling study of Chesapeake Bay, Rice et al. (2012) found sea level rise of 1 m would cause an average increase in salinity of 4 psu, which is similar in scale to the 6 psu change due to extreme drought we explored in this paper. In the San Francisco Bay, the effect of rising sea level on salinity is compounded by projected changes in snowpack and snowmelt runoff also caused by climate change (Knowles and Cayan 2002). Together, these changes are projected to cause increases in bay salinity on the order of 0.33–0.46 psu per decade through the end of the century (Cloern et al. 2011). Sea level rise will concurrently increase inundation regimes, which also stresses *Lepidium* (Spenst 2006, Andrew and Ustin 2009), and may therefore amplify the detrimental impacts of salinity on this invader.

We propose extreme droughts generally favor native plants over invaders in estuarine tidal marshes and result in invader diebacks. This is because extreme drought causes salinity stress in estuaries and many native salt marsh plants are halophytes (Adam 1990), which are adapted to acute salinity conditions (Flowers et al. 1977). Halophytes have a greater ability to both maintain cover and expand during high-salinity events. This broad regeneration niche (sensu Grubb 1977) allowed native plants in our system to expand into gaps created by the invader dieback during the drought. In contrast, many salt marsh invaders are not halophytes (e.g., *Lepidium*, *Typha orientalis*, *Phragmites australis*) and several studies have found these invaders fare poorly under conditions of increased salinity stress, including *Phragmites australis* (Chambers et al. 2003, Vasquez et al. 2006) and *Typha orientalis* (Zedler et al. 1990). Further study is needed to determine if the pattern we propose here holds true for salt marsh invaders that are halophytes (e.g., *Spartina* spp.). Wetland ecosystems are hotspots of plant invasion (Zedler and Kercher 2004); thus, understanding how extreme drought, one of the major consequences of climate change, impacts invasion dynamics in these systems is critical.

In conclusion, we found a significant, time-lagged decrease in invasive plant density driven by high estuarine salinities three years prior. In contrast, we found no impact of single-year salinity changes on invasive plants. These findings highlight the importance of conducting multi-year studies to understand how climate change impacts biological invasions. We found native plants expanded into gaps created by invader dieback, indicating drought helped native plants at the expense of the invader. Land managers could amplify their invasive plant control programs by strategically including the impacts of drought in their adaptive management plans.

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