Conditions for collapse: Chronic nutrient enrichment increases native insect density linked to salt marsh dieback

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ABSTRACT

Ecosystems are enduring new intensities and temporal patterns of stressors, yet little is understood about the conditions that result in ecological collapse. We examined how different conditions of nutrient enrichment affect densities of a native insect that feeds upon a salt marsh foundation plant species, with subsequent effects on salt marsh dieback. Dieback is the abrupt death of salt marsh vegetation, leaving barren mudflats. In a natural salt marsh, we set up a full factorial experiment in which we crossed the amount (low, medium, high) with duration (one-year pulse or a two-year press) of nutrient addition. We recorded stem-borer density, plant tissue percent nitrogen, and percent dieback within each plot. We found the most dieback occurred in the high press plots (median of 25 % dieback and maximum of 80 % dieback). When we compared the effects of nutrient amount and duration on dieback, we found an effect of nutrient amount and a marginal effect of nutrient duration. We found that densities of stem-borer larvae were nearly four times greater in high press plots (20 % of stems) than in control plots (5.6 % of stems). By comparing linked and independent Bayesian hierarchical models, we determined both plant percent nitrogen and stem-borer densities contributed to salt marsh dieback. Our findings link nutrient enrichment with an increase in larval herbivory as a cause of salt marsh dieback. Broadly, we provide evidence that chronically high nutrient enrichment has a synergistic effect with a biotic agent and is a condition leading to ecosystem collapse.

1. Introduction

Natural ecosystems are modified and degraded due to human activities, in some cases to the point of collapse (Cumming and Peterson, 2017 Sato and Lindenmayer, 2018). Ecosystem collapse is defined as a degraded ecosystem state that results from the abrupt and substantial loss of biodiversity or ecosystem function, which does not recover without assistance within decadal timescales (sensu Sato and Lindenmayer, 2018). Because many anthropogenic stressors impact ecosystems simultaneously, it is difficult to determine which intensities and temporal patterns of stressors trigger the sudden shift from a functioning state to a collapsed state (Newton et al., 2021 Sato and Lindenmayer, 2018 Scheffer et al., 2015). Studies of the conditions leading to collapse are especially needed in estuarine ecosystems, which have valuable societal benefits such as shoreline protection, fish nurseries, and recreation (Comer et al., 2022 Gedan et al., 2009 Waycott et al., 2009). Numerous concurrent stressors make estuarine ecosystems particularly vulnerable to collapse; these stressors include climate change, human development, and nutrient pollution from upstream sources (Kennish and O'Donnell, 2002 Mahoney and Bishop, 2017).

Notable cases of ecological collapse in estuaries are salt marsh dieback events (also referred to as brown marsh, sudden vegetation dieback, and die-off) (Alber et al., 2008 Bertness and Silliman, 2008 Deegan et al., 2012 Osgood and Silliman, 2009). Dieback events occur when *Spartina alterniflora*, the foundation grass species of these marshes, suddenly and prematurely dies, progressing from standing dead stems to barren mudflats (Alber et al., 2008). Since the late 1990s, dozens of large-scale salt marsh dieback events have happened along the western Atlantic coastline from the Gulf of Mexico to the Canadian subarctic (Alber et al., 2008 Osgood and Silliman, 2009). The area exhibiting dieback has ranged from several hectares (e.g., in the northeastern U.S.) to tens of thousands of hectares (e.g., in Louisiana, U.S.) (Osgood and Silliman, 2009). Dieback areas have been highly patchy across the marsh landscape, located in the mid-marsh, on the creekbank, or both

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(Alber et al., 2008). In many cases, dieback areas repopulate slowly over many years, but in other cases they still have not repopulated at all and remain barren, decades later (Alber et al., 2008 Altieri et al., 2013 Coverdale et al., 2013 Marsh et al., 2016 Rolando et al., 2022). Without a productive *S. alterniflora* population, salt marsh ecosystem functioning is drastically altered and the societal benefits provided by salt marshes are lost (Brisson et al., 2014 Gedan et al., 2009). Many stressors have been linked to salt marsh dieback (e.g., soil chemistry, eutrophication, drought, pathogens, herbivory), but often studies of salt marsh dieback were conducted after the event and thus were unable to identify explanatory factors with certainty (Alber et al., 2008 Edwards et al., 2005 Gaeta and Kornis, 2011 Osgood and Silliman, 2009). Experimental studies have implicated, separately, that nutrient inputs and runaway herbivory are causes of salt marsh dieback (Bertness et al., 2014a Bertness and Silliman, 2008 Deegan et al., 2012 Silliman et al., 2005 Wasson et al., 2017). However, the potential synergistic effects of nutrient enrichment and herbivory on salt marsh dieback have rarely been examined (Canepuccia et al., 2010 Deegan et al., 2007).

Anthropogenic nutrient enrichment has been a driver of ecological degradation globally (Malone and Newton, 2020 Tilman, 1999 Vitousek et al., 1997). In both aquatic and terrestrial environments, nutrient inputs increase primary production and alter biodiversity, which in turn alters trophic interactions and under certain conditions leads to changes in ecosystem functioning (Howarth et al., 2011 Huxel and McCann, 1998 Inouye and Tilman, 1995). Nutrient pollution is one of the most serious stressors in estuarine ecosystems and certain conditions, such as exceeding threshold amounts and/or chronic inputs, can cause ecosystem collapse (Connell et al., 2017 Deegan et al., 2012 Howarth et al., 2011 Kennish, 2002). Nutrient inputs into coastal ecosystems can be sporadic, like sewage overflow pollution during large storm events, or chronic, like routine fertilizer runoff pollution from suburban lawns and agricultural lands (Bertness et al., 2002 Malone and Newton, 2020 Polis et al., 1997b Vitousek et al., 1997). Sporadic (nutrient pulse) and chronic (nutrient press) inputs have different impacts on coastal ecosystems (Malone and Newton, 2020 Murphy et al., 2012 Polis et al., 1997b). Thus, consideration of both amount and duration of nutrient inputs is imperative to better understanding how nutrient enrichment may lead to salt marsh dieback and ecological collapse in other systems.

Runaway herbivory has also been identified as a cause of ecological collapse (Bertness et al., 2014b Estes et al., 2004 Jefferies et al., 2006). When consumer pressure on a foundation plant population increases drastically, the ecosystem is overgrazed and then may become dominated by a different, less productive plant species or may become barren (Bertness et al., 2014a Estes et al., 2004 Jefferies et al., 2006 Silliman et al., 2005). Rapid herbivore population growth can often be attributed to loss of a predator (top-down control) or increase in resources such as nutrients (bottom-up control) (Bertness and Silliman, 2008 Estes et al., 2004 Polis et al., 1997a). Much work has shown that runaway herbivory results from predator population decline (Bertness et al., 2014b Bertness and Silliman, 2008 Coverdale et al., 2012 Estes et al., 2004). Less is known about how bottom-up effects on herbivores may connect to ecosystem collapse. In coral reef systems, nutrient pollution has been correlated, but not explicitly linked, with runaway herbivory by crown-of-thorns starfish on coral polyps (Ban et al., 2014).

Bottom-up effects are particularly important for amplifying native insect herbivory, which responds readily to changes in primary production (Bertness et al., 2008 Denno et al., 2002 Polis et al., 1997a Price and Hunter, 2005 Sala et al., 2008 Wimp et al., 2010). Nitrogen level of host plants has been linked to insect fecundity, survivorship, and growth rate (Slansky and Feeny, 1977). Nutrient inputs readily increase percent nitrogen content of *S. alterniflora* leaf tissue, which has been shown to increase palatability to insect herbivores (Vince et al., 1981). External insect herbivores, such as grasshoppers and planthoppers, have been shown to suppress *S. alterniflora* productivity but only in eutrophic conditions (Bertness et al., 2008 Sala et al., 2008). These studies did not link insect herbivory to salt marsh dieback specifically, but one guild of

herbivores that has received relatively little attention is stem-boring insects. Stem-borer larvae live inside stems and feed on vital plant tissues, causing meristem death and contributing to whole plant mortality (Canepuccia et al., 2010, 2011 Stiling and Strong, 1983 White et al., 2005). Stem borers are concealed feeders, and thus it is easy to overlook these herbivores because they are not externally visible and are more challenging to sample.

The stem-boring insect guild includes multiple taxonomic families and they are known to be widespread in salt marshes (Gaeta and Kornis, 2011 Li and Pennings, 2017 Stiling and Strong, 1983 White et al., 2005). For instance, a recent survey of fourteen salt marshes along the mid-Atlantic coast (Maine, U.S. to Virginia, U.S.) found stem-boring fly adults at every sampling location (Wimp et al., 2019). Gaeta and Kornis (2011) surveyed a landscape-scale salt marsh dieback event in Georgia, U.S., and found that densities of stem-borer larvae were approximately 40 % in mid-marsh *S. alterniflora* dieback zones. In unaffected mid-marsh areas of the same site, they found 15.4 % of *S. alterniflora* stems had stem-borer larvae (Gaeta and Kornis, 2011). However, a causal link between stem-borer larvae and dieback could not be established via the survey methods (Gaeta and Kornis, 2011). Furthermore, Canepuccia et al. (2010) found evidence that nutrient availability drives stem-boring moth larval herbivory on the related salt marsh plant *Spartina densiflora* in Argentinian salt marshes. In a study of both *S. densiflora* and *S. alterniflora* in Argentina, Canepuccia et al. (2011) showed that stem-boring moth larvae drive detritus production because their feeding behavior produces stems that are more easily broken by tidal impact than stems without larvae. The impact of stem-borer larvae may work in concert with nutrient enrichment, which weakens stems and reduces belowground biomass, promoting stem breakage (Deegan et al., 2012 Johnson et al., 2016). No studies have yet experimentally investigated the interaction between nutrient inputs and stem-borer density on salt marsh dieback. Experiments manipulating the amount and duration of nutrient enrichment and the potential synergy with herbivory are needed to improve understanding of the conditions leading to salt marsh dieback, and the mechanisms leading to ecological collapse more broadly.

Here, we investigate how different conditions of nutrient enrichment interact with native stem-boring insect density, resulting in salt marsh dieback (specifically, mid-marsh). In this study, we added press and pulse nutrient inputs over a range of concentrations to field plots and monitored density of a native stem-borer insect. We then determined the effect of nutrient enrichment and stem-borer density on salt marsh dieback. We ask: (1) how does the amount and duration of nutrient inputs affect salt marsh dieback? (2) does nutrient enrichment impact stem-borer density? and (3) does stem-borer density contribute to salt marsh dieback? We expected the greatest increases in stem-borer densities in the nutrient press plots with high nutrient enrichment conditions, and for both nutrient enrichment and stem-borer density to explain salt marsh dieback.

2. Materials and methods

2.1. Study sites and organisms

We conducted a field experiment in a natural salt marsh in Mullica River – Great Bay estuary in the mid-Atlantic region of the United States, in New Jersey (39° 31.6′N, 74° 19.2′W). Salt marshes in the mid-Atlantic region receive nutrient inputs predominantly from non-point sources (e.g., agricultural run-off, shoreline development), and widely vary from minimally to heavily impacted by nutrient-loading (Bertness et al., 2002 Wimp et al., 2019). The study site and its upstream waterways have been protected for several decades, so it has been considered minimally impacted by human activities (Kennish and O'Donnell, 2002) and an ideal site for experimental investigation of mechanistic responses to nutrient enrichment (Wimp et al., 2010). We situated our experiment in the mid-marsh, where the dominant vegetation is short-form

S. alterniflora (25 cm on average, <50 cm maximum). At this latitude, *S. alterniflora* aboveground biomass has a natural seasonality. Plants produce new shoots in late spring and grow throughout the summer, reaching peak biomass in mid to late August. Flowering occurs annually in late August through early September. In September, aboveground plant material begins to decay and form a thatch layer that covers the salt marsh through the winter. This natural, seasonal cycle starkly contrasts with salt marsh dieback, where patches of *S. alterniflora* abruptly and prematurely die during the growing season. Landscape-level salt marsh dieback has not been observed at our site, but plot-scale dieback was observed in previous nutrient addition experiments conducted at this salt marsh (noted in Wimp et al., 2010 and Murphy et al., 2012). In these previous experiments, researchers noted stem breakage in high nutrient addition plots and observed stem-borer larvae inside broken stems (Wimp, personal observation).

For this experiment, we drew from a long history of study of this salt marsh's food web dynamics and responses to bottom-up forces (Denno et al., 2002 Murphy et al., 2012 Wimp et al., 2010). In decades of studies at this salt marsh, researchers have noticed absence of the consumers that have been linked to salt marsh dieback at New England U.S. salt marshes (purple marsh crab, *Sesarma reticulatum*) and southeastern U.S. salt marshes (periwinkle snail, *Littoraria irrorata*) (Bertness et al., 2004 Coverdale et al., 2013); we did not observe these species during this experiment. At our site, the most abundant crab, marsh fiddler crab (*Uca pugnax*), and the most abundant snail (*Melampus bidentatus*) are detritivores and not suspected to have a role in salt marsh dieback. The most abundant insect herbivores at this site are planthoppers *Prokelisia dolus* and *P. marginata*, and extensive previous research has documented how they respond to nutrient additions (Denno et al., 2002, 2003 Murphy et al., 2012 Wimp et al., 2010). *Prokelisia* are sap feeders that cannot cause chewing damage to the plant. Notably, chewing herbivores that feed externally (e.g., grasshoppers) are rare at the Great Bay marsh (Wimp et al., 2010 Wimp and Murphy, 2021), but internal herbivores (e. g., stem-borer larvae) have been understudied due to their cryptic nature and labor-intensive methods required to document them.

Several stem-borer insects feed on *S. alterniflora*; at our study site the most common are *Incertella* sp. (Diptera: Chloropidae) and *Chaetopsis aenea* (Diptera: Otitidae) (Wimp et al., 2010). Of the stem-borer insects at our site, *Incertella* sp. are most numerically dominant as adults and their density has been shown to increase with nutrient additions (Wimp et al., 2010). Adult females of all stem-borer species oviposit eggs into *S. alterniflora* culms (hereafter referred to as stems). Larvae hatch inside the stems and feed by chewing the internal *S. alterniflora* tissue. There is no evidence that larvae move to new stems. We observed *Incertella* sp. pupae within decaying and dead stems, which indicates they overwinter as pupae inside dead stems and in thatch. Stem-borer larval feeding behavior causes stem death and can contribute to the mortality of the entire *S. alterniflora* plant (Canepuccia et al., 2011 Gaeta and Kornis, 2011 Stiling and Strong, 1983 White et al., 2005).

2.2. Experimental plot establishment

We haphazardly established 10 m^2 experimental plots in short-form *S. alterniflora* across 9 blocks, minimizing microhabitat and elevation variation within each block. The blocks ranged from 10 m apart to 250 m apart. None of our plots included tidal creekbank habitat or tall-form *S. alterniflora*. We ensured the entire area within each plot had full, healthy *S. alterniflora* coverage and no barren mud indicative of dieback. Within each of the 9 blocks, we established 7 plots and randomly assigned these plots to be the control or one of 6 nutrient manipulations. Thus, we had a total of 63 experimental plots (n = 7 plots/block × 9 blocks).

2.3. Nutrient manipulations

Our nutrient manipulations were part of a full factorial design in which we crossed the amount of nutrient addition (low, medium, high) with duration of nutrient addition (short-term pulse or a long-term press) for a total of 6 different nutrient treatments (1. low press, 2. medium press, 3. high press, 4. low pulse, 5. medium pulse, and 6. high pulse). For press treatments, we applied fertilizer in two growing seasons (both 2016 and 2017). For pulse treatments, we applied fertilizer in only one growing season (2017). Importantly, at the end of the experiment the total amount of fertilizer applied at each level (low, medium, or high) was equal for the corresponding press and pulse treatment. For the pulse treatments, the low level was 13.6 g N/m^2, medium level was 27.2 g N/m^2, and high level was 54.4 g N/m^2 (Table 1; refer to Appendix A for detailed description of the fertilization methods). For the press treatments, in each year we added half of the total amount of fertilizer applied in the pulse treatment so their total fertilization amount would be equal (Table 1). We used slow-release fertilizer and applied it over the course of several weeks to promote nutrient uptake by plants and avoid fertilizer burn. We monitored the plots closely and observed no leaf scorching due to fertilizer burn. We set our fertilization levels to reflect the regional variation of nutrient loading in U.S. Atlantic coastal ecosystems and specifically, nitrogen inputs since salt marsh habitats are understood to be nitrogen-limited (Bertness et al., 2002 Deegan et al., 2012 Howarth, 1988 Malone and Newton, 2020 Wimp et al., 2019).

2.4. Stem-borer density and salt marsh dieback

To identify the presence of stem-borer insect larvae and determine their density in *S. alterniflora* stems, we sampled *S. alterniflora* stems from experimental plots and dissected them in the lab. Twice during the second season (July and August 2017, the final season of the two-year experiment), we collected aboveground plant material from one 0.047-m^2 quadrat in each plot (Denno et al., 2002). We sorted the samples into live and dead plant material and counted the number of live *S. alterniflora* stems. For each quadrat, we dissected all of the live *S. alterniflora* stems (n = ~20–40) to document presence or absence of stem-borer insect larvae. We measured the density of stem-borer larvae in each plot by calculating the number of stems with presence of larvae or evidence of their damage divided by the total number of stems in the sample. To represent the holistic impact of stem-borer insects on the plot, we pooled measures of stem-borer density for July and August samples in our analyses. At the end of the two-year experiment (August 2017), we determined the percent dieback within each plot by visually estimating the percentage of barren mud within the plot (Fig. 1).

2.5. Percent nitrogen

After inspection for stem-borer presence or damage, we combined all dissected stems with non-dissected *S. alterniflora* live plant material and dried the samples in a drying oven at 60 °C for three days. We measured the dry live biomass (g). We haphazardly subsampled the dried stems, ground them in a Retsch MM 400 Model mixer mill (Retsch GmbH, Haan, Germany), weighed them using a Mettler-Toledo XP6

Table 1
Amount and duration of nutrient treatments. Pulse treatments only received fertilizer in the second growing season in the equivalent total amount as the corresponding press treatment. Control plots received no fertilizer additions.

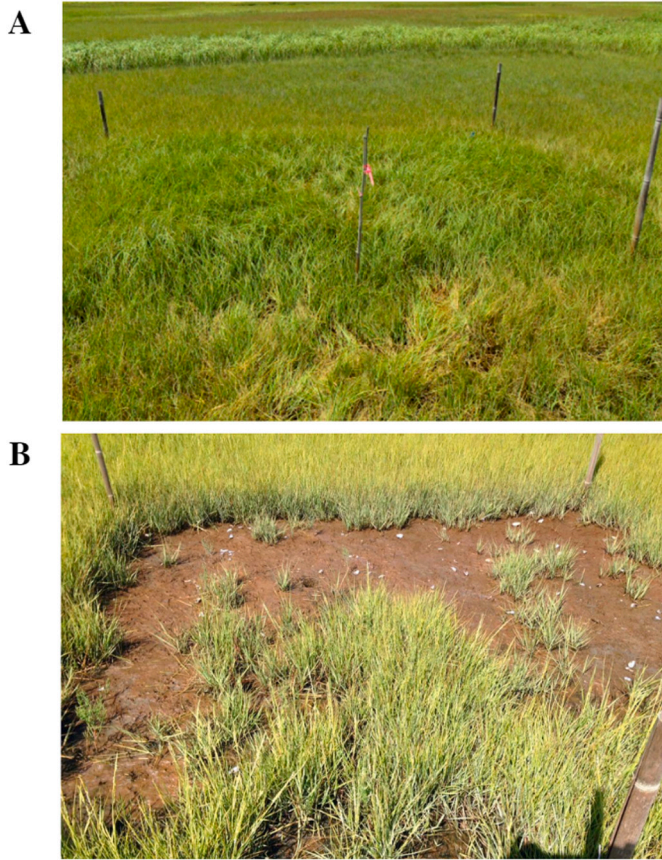| Duration:	Press			Pulse		
Amount:	Low	Medium	High	Low	Medium	High
1st season (2016)	6.8 g N/m^2 2.2 g P/m^2	13.6 g N/ m^2 5.4 g P/ m^2	27.2 g N/m^2 10.8 g P/m^2	None	None	None
2nd season (2017)	6.8 g N/m^2 2.2 g P/m^2	13.6 g N/ m^2 5.4 g P/ m^2	27.2 g N/m^2 10.8 g P/m^2	13.6 g N/m^2 5.4 g P/m^2	27.2 g N/ m^2 10.8 g P/ m^2	54.4 g N/m^2 21.6 g P/m^2

Fig. 1. Two examples of the plot visual appearance at the end of the two-year experiment. Bamboo poles mark the plot corners. (A) High pulse plot with minimal (<10 %) percent dieback. Short-form *S. alterniflora* within the plot appears taller and thicker than short-form *S. alterniflora* outside the plot boundaries. In the top section of the photo, outside the plot boundary, tall-form *S. alterniflora* along a small tidal creek is visible. (B) High press plot with maximal (>50 %) percent dieback. *S. alterniflora* has fully died within the plot boundaries but is unaffected outside the plot boundaries.

microbalance (Mettler-Toledo, Columbus, OH), and rolled them into tin capsules (Elementar Americas). We sent these prepared samples to the Cornell Stable Isotope Laboratory to be analyzed for %N analysis using an elemental analyzer-stable isotope ratio mass spectrometer system (Thermo Delta V Advantage IRMS and Carlo Erba NC2500 EA systems). We averaged the July and August samples from each plot to determine the mean percent nitrogen content of *S. alterniflora* tissue per plot for the season. So we could compare our results with survey data reported in Wimp et al. (2019), we also calculated nitrogen density of *S. alterniflora* per plot by multiplying live biomass per square meter by percent nitrogen.

2.6. Adult stem-borer insects

To collect adult stem-borer insects, we used a D-vac suction sampler with a 21 cm aperture. The aperture was placed in 5 different locations within the plot for 3 s periods (following methods described in Wimp et al., 2010 and Murphy et al., 2012). Immediately after suction sampling, we placed collected arthropods into closed containers with ethyl acetate, then transferred the samples into 75 % ethanol solution. In the laboratory, we identified and counted arthropods under the microscope. For this paper, we analyzed only *Incertella* sp., a stem-borer fly, because their larval feeding behavior causes stem death and their abundance increased in response to nutrient addition in previous experiments conducted at our study site (Wimp et al., 2010).

2.7. Statistical analyses

We calculated descriptive statistics for percent area of salt marsh dieback and stem-borer density. We calculated log response ratios $(LRR = ln\left(\overline{xt}/\overline{xc}\right))$, where $\overline{xt}$ is the nutrient treatment and $\overline{xc}$ is the control within a block, to account for heterogeneity in dieback among our blocks. We used a one-sample, one-tailed *t*-test on log response ratios to determine difference from zero (control). To compare the effects of amount versus duration, we used a two-way ANOVA with amount (low, medium, or high) and duration (press or pulse) as predictors.

We used a blocked ANOVA to test for differences in stem-borer density across the six nutrient treatments and control, followed by a pairwise comparison test with a Bonferroni correction to examine significant differences among nutrient manipulations. Stem-borer density was arcsine transformed to meet homogeneity of variance assumptions. We also used a blocked ANOVA test to determine differences in adult *Incertella* sp. density among treatments, which were log transformed to meet assumptions. We determined differences in *S. alterniflora* percent nitrogen content among treatments using blocked ANOVA tests. We examined the relationship between percent nitrogen content in *S. alterniflora* and stem-borer larval density using a linear regression.

To examine the role of stem-borer density as a contributor to salt marsh dieback, following the approach proposed by Arab and Wimp (2013) we used a linked Bayesian hierarchical model (Model 1) and compared it to an independent Bayesian hierarchical model (Model 2). For Model 1, we modeled the log of mean percent dieback as a function of mean stem-borer density, linked to a model of mean stem-borer density as a function of percent nitrogen content of *S. alterniflora* tissue. Thus, mean stem-borer density served as the predictor variable in the first model (1.1) (with log of mean percent dieback is the response) and it served the response variable in the second model (1.2) with percent nitrogen as the predictor variable, thereby allowing us to examine the indirect effect of nitrogen on dieback via stem-borer larvae. For Model 2, we modeled the log of mean percent dieback as a function of stem-borer density (2.1) and independently modeled mean stem-borer density as a function of percent nitrogen (2.2). To compute the total effect, we included a joint model (3) for both Model 1 and Model 2. The joint model is percent dieback as a function of stem-borer density and percent nitrogen as covariates, where log of mean percent dieback is modeled using stem-borer density and percent nitrogen as the predictor variables.

Model 1

$$\log\left(\mu_{d,i}\right) = \beta_0 + \beta_1\mu_{SB,i} \tag{1.1}$$

$$\mu_{SB,i} = \alpha_0 + \alpha_1 Nitrogen\_Percent_i \tag{1.2}$$

Model 2

$$log\left(\mu_{d,i}\right) = \gamma_0 + \gamma_1 SB\_Percent_i \tag{2.1}$$

$$\mu_{SB,i} = \omega_0 + \omega_1 Nitrogen\_Percent_i \tag{2.2}$$

Joint Model

$$log\left(\mu_{d,i}\right) = \theta_0 + \theta_1 SB\_Percent_i + \theta_2 Nitrogen\_Percent_i \tag{3}$$

To examine the role of stem-borer density as a contributor to salt marsh dieback, following the approach proposed by Arab and Wimp (2013) we used a linked Bayesian hierarchical model (Model 1) and compared it to an independent Bayesian hierarchical model (Model 2). In both models, we assumed percent dieback to follow a negative binomial distribution, $Y_{d,\ i} \sim NegBin(p_i, r)$ where the mean of the negative binomial distribution is defined as $\mu_{d,i} = r\frac{1-p_i}{p_i}$, and stem-borer density was assumed to follow a normal distribution $Y_{SB,\ i} \sim N(\mu_{SB,\ i}, \sigma_{SB})$. For both models, we considered relatively non-informative prior distributions for the unknown parameters (normal prior distributions with mean

0 and variance 10,000 for regression coefficients and gamma prior distributions with mean of zero and variance of 100 for the negative binomial r parameters). Bayesian analyses were conducted based on Markov Chain Monte Carlo (MCMC) methods using the software program JAGS through the R2JAGS package in R. We ran two MCMC chains for 100,000 realizations after 11,000 iterations for burn-in for both Model 1 and Model 2. Code, inclusive of datasets, are reported in Appendix B.

3. Results

3.1. Effects of nutrient enrichment on salt marsh dieback

We found higher percent dieback relative to control in our high press nutrient treatment ($t(8) = 2.0$, $P = 0.04$), and lower percent dieback relative to control in our medium pulse treatment ($t(8) = -2.2$, $P = 0.03$) (Fig. 2). When we examined the effects of fertilization level and duration on percent dieback log response ratio using a two-way ANOVA, we found a significant effect of fertilization level [$F_{(2, 48)} = 4.16$, $P = 0.022$] while the effect of press/pulse is marginal [$F_{(1, 48)} = 3.96$, $P = 0.052$]. We found no interaction between the amount and duration of nutrient manipulations [$F_{(2, 48)} = 0.33$, $P = 0.72$].

3.2. Effects of nutrient enrichment on stem-borer density

Larvae — densities of stem-borer larvae responded to nutrient manipulations [$F_{(6, 55)} = 3.26$, $P = 0.008$; Fig. 3A]. We found higher mean percentages of bored stems for medium press (mean = 20 %; $P = 0.02$) and high press plots (mean = 20 %; $P = 0.02$) compared to control plots (mean = 5.6 %). *Adults* — we detected no relationship between adult *Incertella* sp. density and nutrient manipulations [$F_{(6, 55)} = 0.735$, $P = 0.62$].

Nutrient addition at all fertilization levels and durations significantly increased the percent nitrogen content of *S. alterniflora* tissue [$F_{(6, 55)} = 31.9$, $P < 0.0001$]. We found a positive relationship between stem-borer density and percent nitrogen content of *S. alterniflora* tissue [$F_{(1, 61)} = 24.1$, $R^2 = 0.28$, $P < 0.0001$; Fig. 3B]. Nitrogen density was 3.7 g N/m^2

on average in control plots and ranged from 4.5 g N/m^2 to 15.9 g N/m^2 in treatment plots (Table A4).

3.3. Effects stem-borer density on salt marsh dieback

While nitrogen content of *S. alterniflora* increased percent dieback, the model with the best explanatory power included stem-borer density as the link between *S. alterniflora* nitrogen content and dieback. Specifically, the total effect of Model 1 (which included stem-borer density as an intermediate link between percent nitrogen of *S. alterniflora* tissue and dieback) was 0.91 (Credible Interval: 0.29, 1.5), whereas the total effect of Model 2 (which modeled the impact of percent nitrogen of *S. alterniflora* tissue on stem-borer density, and the impacts of stem-borer density on dieback as independent models) was 0.61 (Credible Interval: 0.14, 1.12). In both Model 1 (Linked Hierarchical Model) and Model 2 (Independent Hierarchical Model) stem-borer density had a significant positive effect on percent dieback (Fig. 4), since the credible interval for the coefficient does not include zero. The posterior mean for the indirect effect of Model 1 (posterior mean = 0.53822) is greater than the indirect effect of Model 2 (posterior mean = 0.23141), indicating stem-borer density increases the indirect effect of *S. alterniflora* nitrogen content on dieback.

4. Discussion

Our findings show that both the amount and duration of nutrient inputs contribute to salt marsh dieback by increasing stem-borer densities. At the end of our two-year experiment, we observed significantly greater dieback response only in our high nutrient press plots. In high press plots, we discovered stem-borer larvae in 20 % of stems, which was nearly four times greater than stem-borer density in control plots. We did not detect a change in either dieback nor stem-borer density in high pulse plots, even though high pulse plots received twice the amount of fertilizer during a single growing season and an equivalent total amount of fertilizer over the course of the experiment relative to high press plots. Further, although we applied the same single-season amount of fertilizer in medium pulse plots as we applied in high press plots, we found that
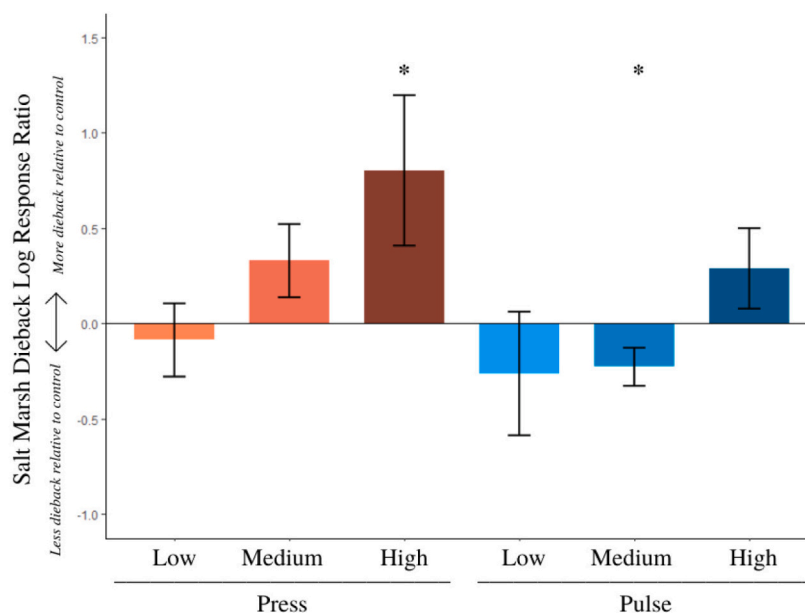

Fig. 2. Salt marsh dieback response to nutrient manipulations. Effects of two-year press and one-year pulse nutrient additions at low, medium, and high amounts on percent dieback (means ± 1 SE). Responses with asterisks were significantly different from zero by *t*-test ($p < 0.05$), meaning that the treatment and control plots differ. Responses below zero indicate less dieback relative to control and responses above zero indicate more dieback relative to control.
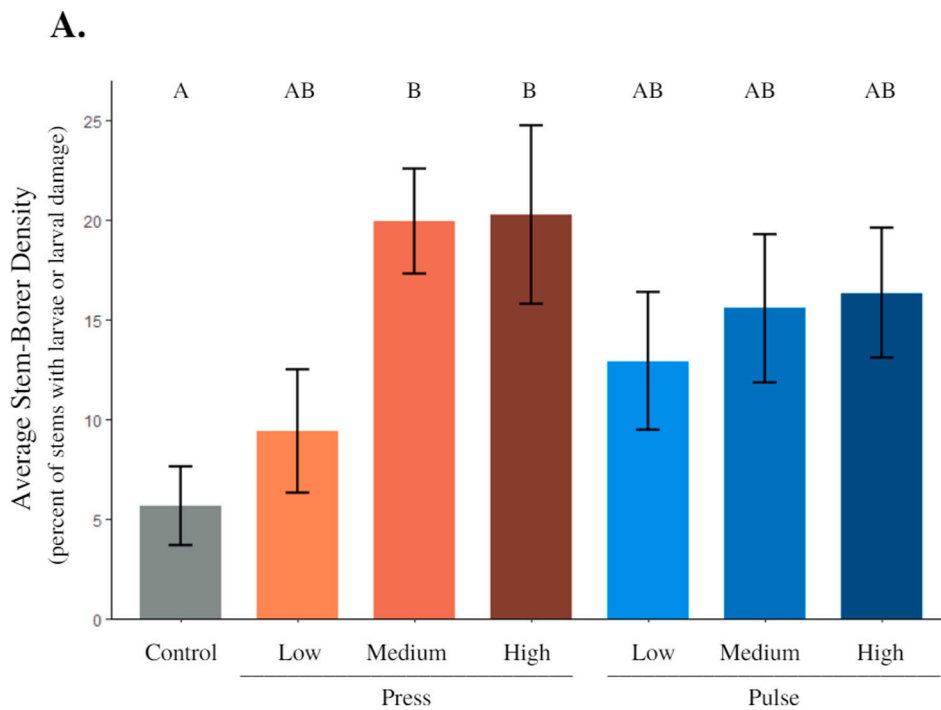
A.

B.

Fig. 3. Effects of nutrient enrichment on stem-borer density. (A) Nutrient treatments increased average stem-borer density with the most pronounced increase in medium and high press treatments. Bars are raw means ± 1 SE. (B) Percent nitrogen content of *S. alterniflora* tissue strongly correlates with stem-borer density: y = −0.53 + 0.22x, $F_{(1, 61)}$ = 24.1, R^2 = 0.28, P < 0.0001. Points represent raw stem-borer density for the plot (n = 63). Data are arcsine transformed for statistical analysis, but we present the raw data for clarity of interpretation.
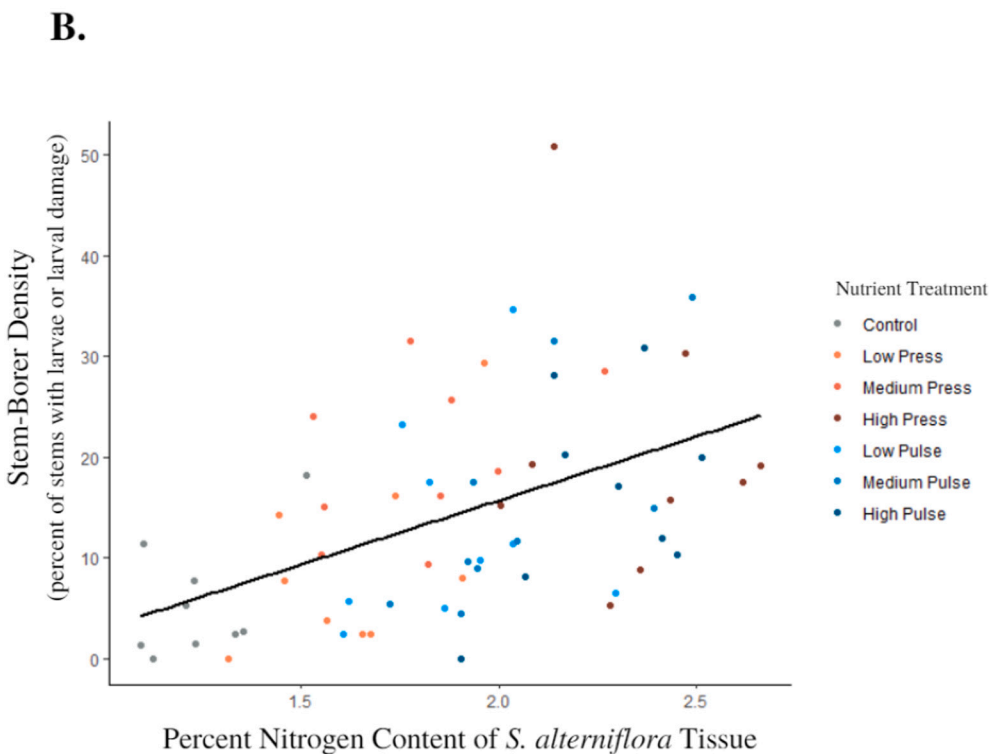
the medium pulse treatment did not significantly increase stem-borer density and had significantly less dieback response, instead promoting *S. alterniflora* cover. That we documented more vegetation coverage in medium pulse plots but more vegetation death in our high press plots emphasizes the importance of considering both duration and amount of stress leading to ecological collapse.

Our study is the first to experimentally link nutrient enrichment to increased stem-borer larval herbivory and show the combined impact of these factors on salt marsh dieback. Stem-borer density at our site was strongly associated with percent nitrogen content of *S. alterniflora* tissue, which is consistent with studies showing that insect herbivory and egg laying corresponds with nutritional quality of host plants (Price and Hunter, 2005 Slansky and Feeny, 1977). We did not detect a response of adult *Incertella* sp. to nutrient enrichment; this is likely explained by high mobility via flight of adult stem-borer insects while stem-borer larvae are fully restricted to the stem where they are laid as an egg. Additionally, percent nitrogen content of *S. alterniflora* tissue better reflects nutrient enrichment than our categorical fertilization levels, especially
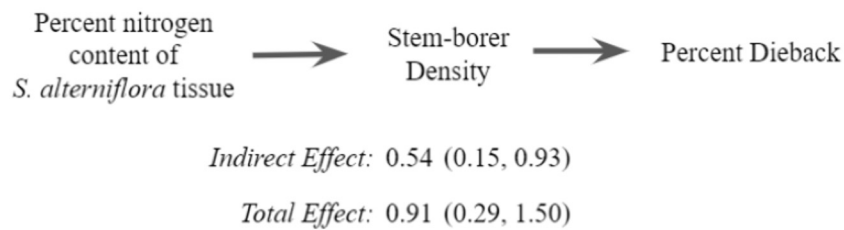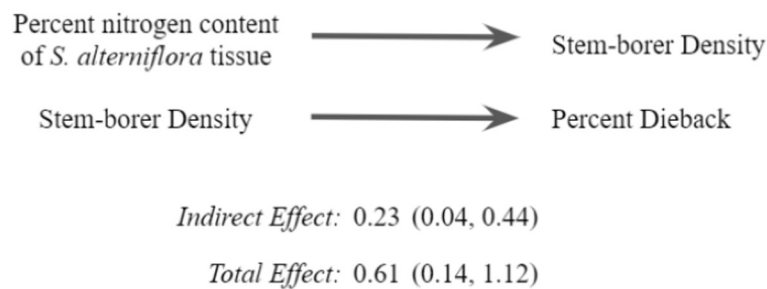
Model 1: Linked Hierarchical Model

Percent nitrogen content of *S. alterniflora* tissue → Stem-borer Density → Percent Dieback

Indirect Effect: 0.54 (0.15, 0.93)

Total Effect: 0.91 (0.29, 1.50)

Model 2: Independent Hierarchical Model

Percent nitrogen content of *S. alterniflora* tissue → Stem-borer Density

Stem-borer Density → Percent Dieback

Indirect Effect: 0.23 (0.04, 0.44)

Total Effect: 0.61 (0.14, 1.12)

Fig. 4. Bayesian hierarchical models summarizing the effects of percent nitrogen content of *S. alterniflora* tissue on stem-borer density and stem-borer density on salt marsh dieback, showing posterior means and credible intervals for indirect effect and total effect. The intervals shown in parentheses present the 95 % credible intervals for the effects.

given the limitation of the plot-scale experiment with dry fertilizer application methods compared to whole ecosystem experiments (Deegan et al., 2012 Johnson et al., 2016). In our Bayesian hierarchical modeling, we found that Model 1 linking stem-borer density to percent nitrogen content of *S. alterniflora* more strongly explained percent dieback in our plots than Model 2 (Fig. 4). In other words, although both models explained percent dieback, including stem-borers as an intermediate link between nutrient enrichment and dieback had the greatest explanatory power. While previous studies have found that nutrient enrichment drives dieback (Deegan et al., 2012) and, separately, that stem-borer larval density correlates with dieback (Gaeta and Kornis, 2011), here we show that nutrients increase the densities of stem-borer insects, which in turn increase dieback.

We intended our nutrient press treatments to reflect nitrogen inputs transported into ecosystems at relatively lower levels over longer time periods by waterways (i.e., fertilizer runoff) and atmospheric deposition (i.e., fossil fuel emissions). Globally and in the US, these ongoing, diffuse sources make up the majority of all nitrogen inputs to coastal ecosystems, with the mid-Atlantic Chesapeake Bay estuaries among the most impacted (Malone and Newton, 2020). In contrast, we intended our pulse treatments to reflect relatively higher but discrete nitrogen inputs, like those from sewer overflow pollution events in Jamaica Bay, New York (Benotti et al., 2007). From our fertilizer applications, our treatment plots reached nitrogen densities (g plant N/m^2) ranging from 4.5 g N/m^2 to 15.9 g N/m^2 (Table A4). This range of nitrogen density is within the range reported in the recent survey of fourteen Atlantic coastal salt marshes by Wimp et al. (2019); they recorded a minimum of 1 g N/m^2 (Awcomin Marsh, New Hampshire), median of 4 g N/m^2, and a maximum of 25 g N/m^2 (Jamaica Bay, New York). Wimp et al. (2019) found *Incertella* sp. adults at every sampling location in all fourteen salt marshes, but our findings suggest that adult stem borer abundance will not indicate larval densities or susceptibility to dieback. Future surveys could specifically examine stems for larvae in salt marshes with high

nitrogen density.

Nutrient enrichment conditions that sustain an elevated *S. alterniflora* nitrogen content for multiple growing seasons make salt marshes more vulnerable to dieback. We know from previous work that after nutrient pulses, *S. alterniflora* nitrogen content and arthropod densities return to ambient state, but during nutrient presses, these ecological responses are sustained (Murphy et al., 2012). Similarly, Deegan et al. (2012) showed that multiple consecutive years of nutrient enrichment resulted in decreased *S. alterniflora* root biomass and weakened stems of smooth cordgrass, resulting in plant breakage and collapse on salt marsh tidal creek banks. Multiple studies have observed that *S. alterniflora* root biomass significantly decreases under nutrient enriched conditions (Deegan et al., 2012 Hanley et al., 2021 Johnson et al., 2016). With weakened belowground structure due to nutrient inputs, *S. alterniflora* may be more likely to die when stem-borer larval herbivory damages aboveground stems. Our findings agree with Deegan et al. (2012) that chronic conditions of nutrient enrichment are an explanation for salt marsh dieback, and further we found nutrient enrichment acts in concert with stem-borer larval herbivory to cause dieback.

Increased stem-borer larval herbivory is due to bottom-up effects in the salt marsh where dieback occurs, which differs from the role of herbivory in most other studies of salt marsh dieback (but see Canepuccia et al., 2010). Migratory geese decimated Arctic salt marshes after their populations increased, but this population growth was due to their winter feeding in productive US agricultural lands, not in the salt marshes they subsequently overgrazed (Jefferies et al., 2006). Runaway herbivory by *Sesarma* crabs in the northeast US marshes and by *Littoraria* snails in the southeast US marshes have been attributed to loss of top-down control, due to human overfishing of striped bass in the northeast and blue crabs in the southeast (Bertness and Silliman, 2008 Coverdale et al., 2013 Silliman et al., 2005). Interestingly, He et al. (2017) determined that while drought-stress was the cause of dieback of a salt

marsh in China, crab herbivory prevented plant regrowth in the dieback zones. Although our experiment did not test whether stem-borer larval herbivory prevented *S. alterniflora* recovery, we observed that dieback persisted in the plots for years following the end of the experiment (Wimp personal observation). Future research should examine the role of herbivory in maintaining the collapsed state.

We detected a significant dieback response to high nutrient press treatment, but we found huge variability of percent dieback in high press plots, ranging from 8 to 80 % (Table A2). Notably, of all samples taken, the highest stem-borer density value was 51 % of stems with larvae or larval damage and this was recorded in the high press plot that had 80 % dieback. Variability in dieback response could be explained by intraspecific trait variation in the *S. alterniflora* population. We know from previous work that whether *S. alterniflora* responds to nutrient inputs by increasing percent nitrogen in leaf tissue or by increasing aboveground biomass varies among *S. alterniflora* populations across the mid-Atlantic region (Murphy et al., 2012). Also, *S. alterniflora* is a partially clonal plant species and recent evidence suggests plant genetic diversity influences its productivity and herbivore responses (Edwards et al., 2005 Walker et al., 2021 Zerebecki et al., 2017). Insect herbivory is responsive to nutritional quality and chemical defenses of host plants, traits which are typically determined by both environment and genetics (Price and Hunter, 2005). More work to determine how *S. alterniflora* genetic diversity influences responses to stressors and herbivores may help explain the variability in salt marsh dieback events.

When it occurs, ecosystem collapse is often surprising because work to identify thresholds, indicators, and interactions between multiple stressors is relatively recent and challenging to synthesize across systems (Comer et al., 2022 Cumming and Peterson, 2017 Newton et al., 2021 Sato and Lindenmayer, 2018 Scheffer et al., 2015). However, even without knowing the cause of collapse, efforts to mitigate the impact of stressors at local and regional scales show that degradation can be reversed and collapse is not inevitable (Brisson et al., 2014 Lefcheck et al., 2018 Mahoney and Bishop, 2017 Waycott et al., 2009). In the early 2000s, the U.S., Europe, and China began to implement new policies to reduce nutrient inputs to watersheds, but these most effectively mitigated point sources while non-point sources remain an ongoing problem (Malone and Newton, 2020). Our study demonstrates a mechanism by which chronic nutrient enrichment amplifies herbivory and increases the likelihood of ecological collapse. Our findings underscore the importance of monitoring the ecological effects of nutrient enrichment in estuarine ecosystems consistently over years and examining the synergy between anthropogenic stressors and natural factors. Additionally, percent nitrogen content in tissue of foundation species may be useful for development into an indicator for susceptibility to collapse due to nutrient enrichment. Even where nutrient inputs are below presumed thresholds, impacts of chronic nutrient inputs may accumulate and interact with other biotic agents in estuarine ecosystems (Ban et al., 2014 Connell et al., 2017 Deegan et al., 2012 Wasson et al., 2017). Given the societal and intrinsic importance of estuarine ecosystems, further work to better understand their vulnerability to various interacting stressors and action to better protect them are urgently needed.

CRediT authorship contribution statement

Jewel Tomasula: Conceptualization, Formal analysis, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Billie Maguire:** Conceptualization, Formal analysis, Writing – original draft, Writing – review & editing. **Tyler M. Rippel:** Conceptualization, Writing – review & editing. **Eddie Lopez:** Conceptualization, Methodology, Investigation. **Stephanie Perez:** Conceptualization, Methodology, Investigation. **Ali Arab:** Formal analysis, Data curation, Writing – review & editing. **Shannon M. Murphy:** Investigation, Resources, Writing – review & editing. **Gina M. Wimp:** Conceptualization, Methodology, Formal analysis, Investigation, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Stem Borer Salt Marsh Dieback (Original data) (Mendeley Data).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2022.109882.

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