

REPORT

Long-term data reveal that grazer density mediates climatic stress in salt marshes

Carter S. Smith¹  | Y. Stacy Zhang²  | Marc J. S. Hensel^{3,4}  |
Steven C. Pennings⁵  | Brian R. Silliman¹

¹Nicholas School of the Environment,
Duke University Marine Lab, Beaufort,
North Carolina, USA

²Department of Marine, Earth and
Atmospheric Sciences, North Carolina
State University, Raleigh,
North Carolina, USA

³Department of Biological Sciences,
Virginia Institute of Marine Sciences,
College of William and Mary, Gloucester,
Virginia, USA

⁴Nature Coast Biological Station,
University of Florida, Cedar Key,
Florida, USA

⁵Department of Biology and Biochemistry,
University of Houston, Houston,
Texas, USA

Correspondence

Carter S. Smith
Email: carter.smith@duke.edu

Funding information

NSF Division of Ocean Sciences,
Grant/Award Numbers: 0620959,
1237140, 1832178, 9982133

Handling Editor: John G. Lambrinos

Abstract

Understanding how climate and local stressors interact is paramount for predicting future ecosystem structure. The effects of multiple stressors are often examined in small-scale and short-term field experiments, limiting understanding of the spatial and temporal generality of the findings. Using a 22-year observational dataset of plant and grazer abundance in a southeastern US salt marsh, we analyzed how changes in drought and grazer density combined to affect plant biomass. We found: (1) increased drought severity and higher snail density both correlated with lower plant biomass; (2) drought and snail effects interacted additively; and, (3) snail effects had a threshold, with additive top-down effects only occurring when snails were present at high densities. These results suggest that the emergence of multiple stressor effects can be density dependent, and they validate short-term experimental evidence that consumers can augment environmental stress. These findings have important implications for predicting future ecosystem structure and managing natural ecosystems.

KEYWORDS

climate change, drought, grazers, multiple stressor effects, plant–grazer interactions, salt marsh, top-down control

INTRODUCTION

Globally, stressors related to habitat loss, eutrophication, and climate change are increasing in intensity and spatial extent (Halpern et al., 2008). Moreover, the combination of global and local stressors can create unique environmental conditions, and there is a pressing need to better understand, forecast, and mitigate the effects of multiple stressors on ecosystems (Silliman & He, 2018; Vinebrooke et al., 2004). Stressors can act additively (i.e., the combined effect is equal to the sum of individual effects),

antagonistically (i.e., the combined effect is less than the sum of individual effects), or synergistically (i.e., the combined effect is greater than the sum of individual effects) (Côté et al., 2016). Managing for the synergistic effects of stressors can be particularly challenging as they can lead to unpredictable ecosystem decline (Sih et al., 2004; Silliman et al., 2013). These “ecological surprises” can add uncertainty to management plans and future projections of ecosystem resilience (Paine et al., 1998).

Experimental ecology is a crucial tool for revealing and understanding multiple stressor effects and preparing for

different global change scenarios. Yet, because of logistical constraints, most ecological laboratory and field experiments are conducted on small temporal and spatial scales, and simplify real-world situations. Thus, they may not be realistic predictors of long-term trends across larger spatial scales (Englund & Cooper, 2003). Therefore, long-term monitoring and large-scale surveys should be employed as complementary methods to help to capture natural variability in stress levels (Côté et al., 2016) and provide large-scale temporal and spatial tests of the generality of experimental results (Lindenmayer et al., 2012).

Understanding the functional relationship of multiple stressor effects is critically important for predicting ecosystem thresholds and tipping points. Moreover, understanding the relative importance of global versus local stressors can help to inform targeted management strategies that enhance resilience to climatic stressors (Shaver et al., 2018). Salt marshes are an ideal study system to investigate multiple stressor effects as they are controlled by both local forces (e.g., grazing, nutrient run-off; Crotty et al., 2020; Deegan et al., 2012) and a variety of increasing global stressors (e.g., sea level rise, drought; FitzGerald et al., 2008; Silliman et al., 2005). In the southeastern US, the productivity of the dominant salt marsh grass, *Spartina alterniflora*, is suppressed in years with less rainfall (Więski & Pennings, 2014). In particular, episodes of extreme drought in the southeastern US have had strong and negative effects on plant biomass, with 10 m² to 5 km² areas of vegetation dying off in months (Alber et al., 2008; McKee et al., 2004). Experiments and large-scale surveys show that common marsh grazers, like the salt marsh periwinkle snail, *Littoraria irrorata*, can interact with drought to suppress marsh production and lead to large-scale marsh die-off (Silliman et al., 2005). However, the temporal and spatial generality of these results is limited as past experimental studies with snails were done over the short term (1–2 years), in small cages (1 m²), and at a limited number of sites with high snail densities (Silliman et al., 2005). Moreover, periwinkle snails are thought to only apply measurable grazing pressure on grasses above a threshold of ~80 snails m⁻² (Renzi & Silliman, 2021). Critical to testing if experimental studies scale up to explain natural variability over space, time, and consumer densities, is testing their relevance with long-term data from many sites.

To better understand the generality of grazer/stress interactions, we analyzed a 22-year dataset of salt marsh biomass and snail density from the Georgia Coastal Ecosystems Long Term Ecological Research program (GCE LTER). Based on previous experimental research, we hypothesized that long-term data would show: (1) periwinkle snail density and drought conditions negatively correlate with salt marsh biomass; (2) snail density and

drought interact to suppress plant biomass; and, (3) the negative effect of snails emerges only when snails are relatively common, at densities above 80 snails m⁻².

METHODS

Description of long-term data

We compiled data from the GCE LTER program (Alber, 2016; Pennings, 2016), focusing our analyses on seven permanent sites that were *S. alterniflora* dominated and located within approximately 25 km of each other (Appendix S1: Figure S1). Within each site, permanent mid-marsh and creekbank plots have been monitored for a variety of metrics since 2000; we focus on the mid-marsh plots because *L. irrorata* is rare along the creekbank due to higher predation (Silliman & Bertness, 2002). Salt marsh biomass and snail density data were collected separately in October from 2000 to 2021 using established LTER protocols (Appendix S1: Section S1). Additionally, we compiled monthly Palmer Drought Severity Index (PDSI) data for Georgia Region 9 (NOAA, 2023). We calculated an average PDSI value for the 6 months (i.e., May–October) preceding the October GCE LTER sampling in each year, as these 6 months have the highest drought stress values and coincide with the growing season for *S. alterniflora*. We combined the plant biomass data, snail density data, and PDSI data by identifying GCE LTER plots that had measurements for all three metrics in a given year. This resulted in a dataset that covered four plots within each of the seven sites over 22 years with six missing observations ($n = 610$ plots). Additionally, because previous research suggested that there is a threshold of 80 snails m⁻² above which snails have a density-dependent effect on *S. alterniflora* (Renzi & Silliman, 2021), we subset the data into one set of plots with snails at low densities (i.e., ≤ 80 snails m⁻²; $n = 341$ plots) and another set of plots with snails at high densities (i.e., > 80 snails m⁻²; $n = 269$ plots).

Analysis of long-term data

To describe how snail density and drought severity impact *S. alterniflora* biomass, we fit linear mixed-effects models (in the *lme4* package; Bates et al., 2015) using maximum likelihood with snail density and average PDSI as interacting fixed effects. To account for repeat sampling at each site over time, we also included both year and plot nested within site as random effects. The significance of the interaction term was used to evaluate

whether drought and snail density interacted additively or nonadditively (i.e., a p -value >0.05 indicated additivity, whereas a p -value <0.05 indicated nonadditivity). We fit the same model on all three datasets (i.e., full dataset, high-density plots only, and low-density plots only), except that the model for high-density plots only had random effects for year and site because the model would not converge with the full random effects structure. Additionally, because we had reason to believe that the relationship between snail density and salt marsh biomass might be nonlinear (see Atkins et al., 2015; Renzi & Silliman, 2021), we separately fit models with a nonlinear logarithmic function by log-transforming snail densities, and compared model fit to the linear models using Akaike's Information Criterion (AIC_c) from the *MuMIn* package (Bartoń, 2023). To test whether the results of the subset analyses were robust to where we set the threshold (i.e., ± 20 snails m^{-2}), we additionally conducted a post hoc analysis to see if setting different thresholds (i.e., 60 or 100 snails m^{-2}) caused us to change any of our conclusions. Specifically, we re-ran each analysis with the different thresholds to see if it meaningfully changed the interpretation of any of our analyses.

Effect size analysis of extreme drought

To evaluate the independent and combined effects of snail density and drought on *S. alterniflora* biomass during the most severe drought event in our dataset, we conducted an effect size analysis following the methodology and equations used by Darling et al. (2010) (see Appendix S1: Section S2 for detailed equations and methodology). This analysis compared 2 years (i.e., 2009 [before the drought] and 2011 [during the drought]; Appendix S1: Figure S2). We averaged biomass and snail density values across all plots at each site in each year and split the sites into high snail density (Sites 3, 4, and 6, which had average densities of 335, 131, and 294 snails m^{-2} , respectively) and low snail density sites (Sites 2, 5, 9, and 10 which had average snail densities of 59, 64, 28, and 36 m^{-2} , respectively). The sites were split by the 80 snails m^{-2} threshold used above for consistency with the earlier analysis, but also because there was a natural split in the data between 64 and 131 snails m^{-2} . We calculated independent effect sizes for snails and drought, a combined effect size for snails and drought (snails $\times$ drought), and an additive null expectation (snails + drought) that was used to judge whether snails and drought interacted additively (i.e., if the confidence intervals of the observed data overlapped with the null additive expectation, the interaction was classified as additive) (Appendix S1: Section S2). All analyses were conducted in R Statistical Software

(v4.2.1; R Core Team, 2022; see Smith, 2024 for original data and code).

RESULTS

Long-term data

The average mid-marsh snail density across the entire LTER dataset was 134 ± 7 snails m^{-2} (mean $\pm$ SE), with a median density of 60 snails m^{-2} . Long-term average snail densities at different sites ranged from a low of 31 snails m^{-2} at Site 9 to 400 snails m^{-2} at Site 3 (Appendix S1: Figure S3). Plots with snail densities above 400 snails m^{-2} were relatively rare, and only one plot with more than 1000 snails m^{-2} was observed (Appendix S1: Figure S4). Within the 22-year dataset, there were 6 years that qualified as moderate drought (average PDSI <-2 , but >-3), 3 years that qualified as severe drought (average PDSI <-3 , but >-4), and 1 year that qualified as extreme drought (average PDSI <-4 ; Svoboda et al., 2002; Appendix S1: Figure S2).

For the entire long-term dataset, the relationship between snail density and average PDSI on salt marsh biomass was best explained by a logarithmic function ($\Delta AIC_c > 2$; Appendix S1: Table S1). Wetter years (i.e., years with higher average PDSI) had significantly higher biomass ($\beta = 37.0$, $t(602) = 3.7$, $p < 0.001$). Snail density did not significantly affect plant biomass ($\beta = 15.4$, $t(602) = 1.5$, $p = 0.13$), and the interaction between snail density and average PDSI was also nonsignificant ($\beta = 4.9$, $t(602) = 0.7$, $p = 0.50$; Figure 1a; Appendix S1: Table S2). Visual analysis of the overall model suggested that it did a poor job of describing the full range of snail densities and that the equation failed to capture the hump-shaped nature of the relationship (i.e., snails appeared to have a positive effect at low densities and a negative effect at high densities). Moreover, there was a visually evident break in the data around approximately 75 snails m^{-2} (Appendix S1: Figure S5).

For plots with ≤ 80 snails m^{-2} , a linear function best described the relationship between snail density and marsh biomass, but the fit of the model was very similar to the logarithmic model ($\Delta AIC_c = 0.04$; Appendix S1: Table S1). Less severe drought conditions correlated with higher plant biomass ($\beta = 32.3$, $t(333) = 2.1$, $p = 0.04$), but snail density had no effect on aboveground plant biomass ($\beta = 10.3$, $t(333) = 0.8$, $p = 0.43$), and the interaction between snail density and average PDSI was also nonsignificant ($\beta = 6.4$, $t(333) = 0.5$, $p = 0.59$; Figure 1b; Appendix S1: Table S3). For plots with > 80 snails per m^2 , a logarithmic function best described the relationship between snail density and

marsh biomass ($\Delta AIC_c > 2$; Appendix S1: Table S1). Less severe drought conditions led to higher plant biomass ($\beta = 41.3$, $t(262) = 4.1$, $p < 0.001$) and higher snail densities led to lower plant biomass ($\beta = -30.2$, $t(262) = -2.8$, $p = 0.006$). The interaction between snail

density and average PDSI was nonsignificant ($\beta = 3.7$, $t(262) = 0.4$, $p = 0.68$), suggesting that snails and drought interacted additively (Figure 1c; Appendix S1: Table S3). Increasing or decreasing the snail density threshold for our subset analyses (to 60 or 100 snails m^{-2}) did not change any of the conclusions drawn from the analysis.

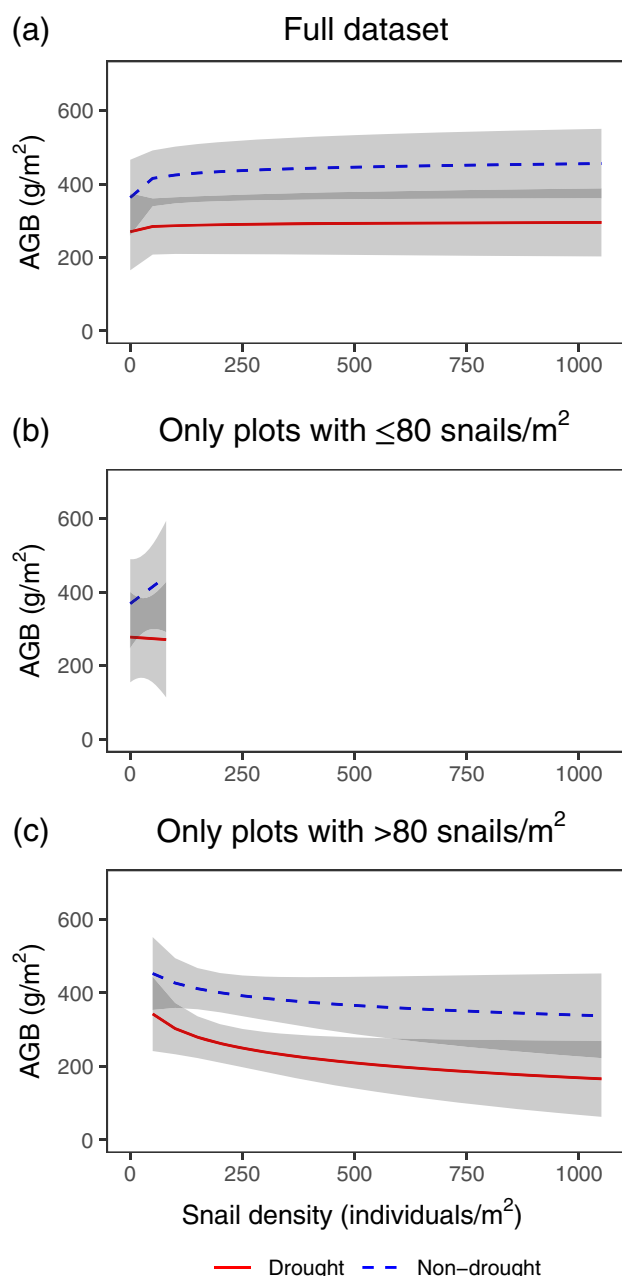


FIGURE 1 Model predictions (mean $\pm$ 95% confidence intervals) for the effects of snail density and average Palmer Drought Severity Index on aboveground *Spartina alterniflora* biomass (AGB) for the complete long-term dataset (a), only plots that had ≤ 80 snails m^{-2} (b), and only plots that had > 80 snails m^{-2} (c). Predictions were back transformed from the model to appear on the original scale. Data were collected over 20 years from seven sites that are part of the Georgia Coastal Ecosystems Long Term Ecological Research program.

Effect size analysis of severe drought

Both drought and snails had negative effects on aboveground plant biomass, reducing plant biomass by an average of 51% and 42%, respectively (drought effect size 95% CI = 18%–84%; snail effect size 95% CI = 9%–75%). Snails and drought combined to reduce plant biomass by an average of 49% (95% CI = 17%–80%) which was lower than the additive null expectation in absolute terms (null model of Drought + Snails = 72%, 95% CI = 52%–92%), but there was high overlap of the confidence intervals and thus we could not reject the additive null hypothesis and the interaction was classified as additive (Figure 2).

DISCUSSION

Using 2 decades of long-term observational data, we find that drought and high grazer densities interacted additively to reduce marsh plant biomass. Specifically, while drought consistently lowered marsh plant productivity, snail density only correlated with lower productivity when the snails were at sufficiently high densities (> 80 snails m^{-2}). Additionally, our effect size analysis confirms that drought and snails interacted additively during the most extreme drought event in the southeastern US over the last 20 years, and their effects had similar magnitudes. Altogether, these results suggest that the emergence of multiple stressor effects is likely to be density dependent, which has profound implications for predicting and managing ecosystem thresholds to multiple stressors. Moreover, these results illustrate the value of long-term spatiotemporal data collection, which in this case largely validates experimental data suggesting that salt marsh consumers can augment the effects of climatic stressors.

Drought conditions significantly reduced salt marsh biomass across our study period. Drought can control salt marsh productivity by inducing hypersalinity in soils (Hughes et al., 2012). *Spartina alterniflora* is tolerant to high soil salinities but rapid increases in salinity or long durations of elevated salinity can suppress osmoregulation (Howard & Mendelsohn, 1999), ultimately reducing growth (Linthurst & Seneca, 1981). Drought events have

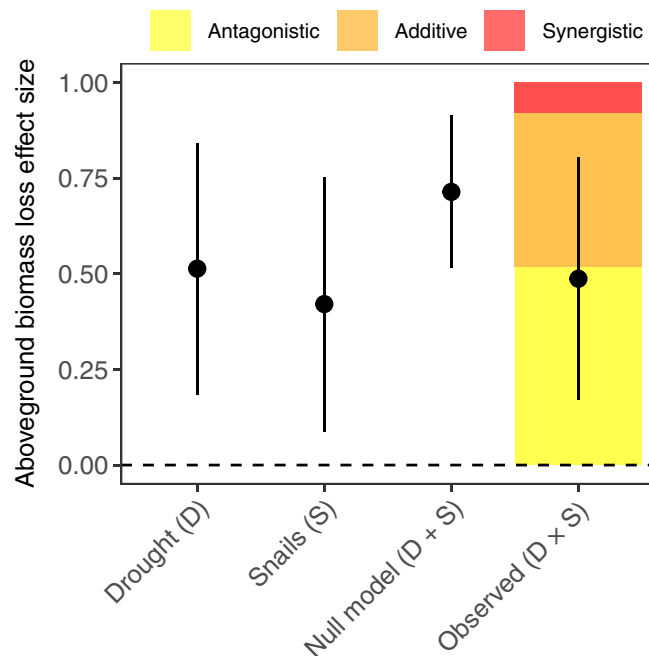


FIGURE 2 Effect sizes of snails (high density vs. low density) and drought on *Spartina alterniflora* aboveground biomass from before to during a severe drought event (2009 vs. 2011). Mean effect sizes are pictured with 95% confidence intervals, and the plot is color coded based on predictions from the null model. The confidence intervals for the null additive model overlapped with the observed interaction, and therefore the interaction was classified as additive. Data were collected from seven sites that are part of the Georgia Coastal Ecosystems Long Term Ecological Research program.

initiated large-scale salt marsh dieback in the southeastern US (Alber et al., 2008; Silliman et al., 2005), and our effect size analysis during an extreme drought event confirms the role that drought plays in lowering salt marsh biomass. Moreover, analysis of the long-term data that covered wet and dry periods is consistent with past analyses indicating that drought-induced higher salinities regulate salt marsh aboveground biomass over larger time scales that include benign periods (Więski & Pennings, 2014). Further research is required to elucidate how thresholds in drought severity and drought duration elicit extreme ecological responses in marshes.

Our analyses show a long-term, density-dependent role of periwinkle snails in regulating aboveground salt marsh biomass across our study area, a result that largely confirms past experimental work across the southeastern US. Significant top-down control only emerged in models examining plots with snail densities above 80 snails m^{-2} , which agrees with previous short-term experimental research (Atkins et al., 2015; Renzi & Silliman, 2021). Moreover, we found that the relationship between snail

density and salt marsh biomass was best described by a logarithmic function, which supports the idea that snails have a density-dependent effect (Atkins et al., 2015; Renzi & Silliman, 2021). Because periwinkles are primarily detritivores, preferring to feed on fungus or dead plant material over green grass, snail effects are negligible at low densities. In fact, low densities of snails could even have a positive effect on marsh productivity by clearing out accumulated dead material and increasing light or nutrient availability. Increased intraspecific competition (i.e., higher densities of snails) and a dearth of their preferred detrital food source are required for snails to graze on live grass (Silliman & Newell, 2003). At high snail densities, sufficiently intense snail grazing will diminish available snail habitat by lowering marsh plant densities and compromising the snail's refuge from predation, potentially initiating a negative feedback loop. In fact, this may help explain why the relationship between snail density and plant biomass was logarithmic and we observed a dampening effect of snails at higher densities. Overall, our large-scale and long-term findings are consistent with many past experimental studies showing that snails can exert top-down control on marsh plants across southeastern and gulf states (Virginia: Silliman & Zieman, 2001; North Carolina: Gittman & Keller, 2013; Morton & Silliman, 2020; South Carolina: Gustafson et al., 2006; Georgia: Silliman & Newell, 2003; Louisiana: Silliman et al., 2005) and that consumer control by the salt marsh periwinkle only emerges at high snail densities (Renzi & Silliman, 2021).

In contrast to experimental findings (see Silliman et al., 2005), we found that snails and drought had additive, not synergistic, effects on salt marsh biomass. Although our study does show top-down control on drought-stricken plants, the difference in effect sizes between the long-term data reported here and previous short-term experimental results could be because snail densities at our sites were lower than those used in the experiments. Snail densities at the GCE sites were variable, but averaged 134 ± 7 snails m^{-2} . These averages are well within natural observed snail densities, but quite a bit lower than the extremes that are occasionally observed (i.e., >2000 snails m^{-2} ; Silliman et al., 2005; Silliman & Zieman, 2001). While high snail densities did occur in our dataset, they were relatively rare. Remote sensing data from the Duplin River Watershed in Georgia similarly suggest that snail densities >500 individuals m^{-2} occurred over less than 1% of the landscape (Schalles et al., 2013). Previous research suggests that snails do not fully defoliate an area of marsh unless they are large bodied and at densities of more than ~ 140 snails m^{-2} (Silliman & Zieman, 2001), or are small to medium sized and at densities greater than 300–600

individuals m^{-2} (Silliman & Bertness, 2002). Moreover, synergistic effects of snails and drought have only been observed at sites with snail densities of approximately 400–1000 snails m^{-2} (Silliman et al., 2005; Silliman et al., 2013), so it is possible that the emergence of synergistic effects may not occur until very high snail densities are reached. Snails can reach high densities locally within a site by aggregating into snail “fronts” (Silliman et al., 2013), and further exploration of the frequency of snail fronts and the potential density dependence of synergistic effects is warranted.

Given that snail densities were consistently low (averaging <100 snails m^{-2}) at four of the seven sites we studied, it is likely that top-down control of marsh plants, and interactions between snails and drought, occur in only some parts of the coastal landscape. Periwinkle distribution is thought to be driven largely by predation pressure (Hutchens & Walters, 2006; Rietl et al., 2018), but also potentially by salinity and nitrogen content in marsh plants (Anderson et al., 2022; Rietl et al., 2018). Previous research has shown that periwinkle densities peak in the mid-marsh (Hutchens & Walters, 2006), and conversely that densities nearest tidal creeks and the marsh edge are low due to higher predation (Rietl et al., 2018; Silliman & Bertness, 2002). Nevertheless, further research is needed to fully elucidate the factors affecting snail density across seascapes, and thus the conditions under which top-down control is most likely.

Foundational ecological theories, including the Environmental Stress Model and the Stress-Gradient Hypothesis (Bertness & Callaway, 1994; Menge & Sutherland, 1987), predict that top-down control by predators and herbivores will dampen as physical stressors increase. In our study, we found instead that consumer pressure remained an important controlling factor of salt marsh plant biomass, even during a severe drought. Menge and Olsen (1990) suggest that specific predictions from Environmental Stress Models depend on whether consumers or prey are more strongly impacted by stress (i.e., Consumer Stress Models versus Prey Stress Models). When prey is more strongly impacted, consumer control can be more prevalent in stressful versus benign environments. Our study system is most consistent with a Consumer Stress Model, as plants are more susceptible to drought than snails (Silliman & He, 2018). For example, extreme drought has been shown to cause rapid and widespread marsh die-off (Alber et al., 2008; Silliman et al., 2005), whereas snail grazing can actually intensify when plants are salt stressed, with extreme densities of snails along die-off borders (Silliman et al., 2005).

Understanding how global stressors interact with local species interactions and food webs will be important

for informing appropriate management interventions to protect and restore ecosystems. We suggest that the presence of consumers at a local scale can impact the tolerance of many coastal ecosystems to stressors operating at a regional or global scale (i.e., drought). For example, in coral reefs, removal of corallivorous snails reduced coral tissue loss from an extreme bleaching event (Shaver et al., 2018). Similarly, in marshes, the management of high-density snail populations by hand removal, fence exclusions, or predator supplementation might reduce the impacts of drought stress on salt marsh productivity; however, because high densities of snails only occur in patches and only at some sites within the landscape, these approaches may only be needed in some locations. Across coastal ecosystems, naturally high densities of consumers may increase the risk to foundation species during extreme events, especially if the system is most consistent with a Consumer Stress Model. Our work joins a growing body of literature suggesting that mitigation of local stressors like grazers (e.g., this study, Blake & Olin, 2022; Shaver et al., 2018), nutrient run-off (Hensel et al., 2023; Lefcheck et al., 2018), or invasive species (Hensel et al., 2021) can increase resilience, promote recovery, and enhance biodiversity. Thus, to provide hope for coastal managers who are rarely able to directly alleviate climate change effects, we find that a focus on local mitigation may be able to lessen the effects of global change stressors (Côté et al., 2016; Silliman & He, 2018). However, if global stressors are severe, they may overwhelm any attempts at local mitigation (Bruno & Valdivia, 2016), in which case the only way to maintain natural ecosystems will be to address the root causes of global change.

AUTHOR CONTRIBUTIONS

Carter S. Smith and Brian R. Silliman conceived of the manuscript. Steven C. Pennings collected data. Carter S. Smith completed all analyses with help from Marc J. S. Hensel and Y. Stacy Zhang. Carter S. Smith drafted the manuscript, and all authors contributed substantially to reviewing and editing the manuscript.

ACKNOWLEDGMENTS

We thank the two anonymous reviewers whose comments greatly improved the manuscript. This material is based upon work supported by the National Science Foundation through the Georgia Coastal Ecosystems Long Term Ecological Research program under grant nos. OCE 9982133, 0620959, 1237140, and 1832178. This is contribution number 1118 from the University of Georgia Marine Institute. We thank the various scientists and GCE staff who collected and curated the data used in this manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Smith, 2024) are available in Zenodo at <https://doi.org/10.5281/zenodo.10685008>.

ORCID

Carter S. Smith  <https://orcid.org/0000-0002-6652-3010>

Y. Stacy Zhang  <https://orcid.org/0000-0001-6611-9846>

Marc J. S. Hensel  <https://orcid.org/0000-0002-9292-9858>

Steven C. Pennings  <https://orcid.org/0000-0003-4757-7125>

REFERENCES

- Alber, M. 2016. "Long-Term Mollusc Population Abundance and Size Data from the Georgia Coastal Ecosystems LTER Fall Marsh Monitoring Program." Georgia Coastal Ecosystems LTER Project, University of Georgia, Long Term Ecological Research Network. <https://doi.org/10.6073/pasta/651d603e2930d7ff608d7325230418e8>.
- Alber, M., E. M. Swenson, S. C. Adamowicz, and I. A. Mendelssohn. 2008. "Salt Marsh Dieback: An Overview of Recent Events in the US." *Estuarine, Coastal and Shelf Science* 80(1): 1–11.
- Anderson, C. J., C. Garcia, and J. S. Cash. 2022. "Distribution and Morphology of *Littoraria irrorata* in Mesohaline Tidal Marshes Dominated by *Juncus Roemerianus*." *Estuaries and Coasts* 45(8): 2650–59.
- Atkins, R. L., J. N. Griffin, C. Angelini, M. I. O'Connor, and B. R. Silliman. 2015. "Consumer–Plant Interaction Strength: Importance of Body Size, Density and Metabolic Biomass." *Oikos* 124(10): 1274–81.
- Bartoń, K. 2023. "MuMIn: Multi-Model Inference." R Package Version 1.47.5. <https://CRAN.R-project.org/package=MuMIn>.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67(1): 1–48.
- Bertness, M. D., and R. Callaway. 1994. "Positive Interactions in Communities." *Trends in Ecology & Evolution* 9(5): 191–93.
- Blake, R. E., and J. A. Olin. 2022. "Responses to Simultaneous Anthropogenic and Biological Stressors Were Mixed in an Experimental Saltmarsh Ecosystem." *Marine Environmental Research* 179: 105644.
- Bruno, J. F., and A. Valdivia. 2016. "Coral Reef Degradation Is Not Correlated with Local Human Population Density." *Scientific Reports* 6(1): 29778.
- Côté, I. M., E. S. Darling, and C. J. Brown. 2016. "Interactions among Ecosystem Stressors and their Importance in Conservation." *Proceedings of the Royal Society B* 283(1824): 20152592.
- Crotty, S. M., C. Ortals, T. M. Pettengill, L. Shi, M. Olabarrieta, M. A. Joyce, A. H. Altieri, et al. 2020. "Sea-Level Rise and the Emergence of a Keystone Grazer Alter the Geomorphic Evolution and Ecology of Southeast US Salt Marshes." *Proceedings of the National Academy of Sciences* 117(30): 17891–902.
- Darling, E. S., T. R. McClanahan, and I. M. Côté. 2010. "Combined Effects of Two Stressors on Kenyan Coral Reefs Are Additive or Antagonistic, Not Synergistic." *Conservation Letters* 3(2): 122–130.
- Deegan, L. A., D. S. Johnson, R. S. Warren, B. J. Peterson, J. W. Fleeger, S. Fagherazzi, and W. M. Wollheim. 2012. "Coastal Eutrophication as a Driver of Salt Marsh Loss." *Nature* 490(7420): 388–392.
- Englund, G., and S. D. Cooper. 2003. "Scale Effects and Extrapolation in Ecological Experiments, Scale Effects and Extrapolation in Ecological Experiments." *Advances in Ecological Research* 33: 161–213.
- FitzGerald, D. M., M. S. Fenster, B. A. Argow, and I. V. Buynevich. 2008. "Coastal Impacts Due to Sea-Level Rise." *Annual Review of Earth and Planetary Sciences* 36: 601–647.
- Gittman, R. K., and D. A. Keller. 2013. "Fiddler Crabs Facilitate *Spartina alterniflora* Growth, Mitigating Periwinkle Overgrazing of Marsh Habitat." *Ecology* 94(12): 2709–18.
- Gustafson, D. J., J. Kilheffer, and B. R. Silliman. 2006. "Relative Effects of *Littoraria irrorata* and *Prokelisia Marginata* on *Spartina alterniflora*." *Estuaries and Coasts* 29: 639–644.
- Halpern, B. S., S. Walbridge, K. A. Selkoe, C. V. Kappel, F. Micheli, C. d'Agrosa, J. F. Bruno, et al. 2008. "A Global Map of Human Impact on Marine Ecosystems." *Science* 319(5865): 948–952.
- Hensel, M. J., C. J. Patrick, R. J. Orth, D. J. Wilcox, W. C. Dennison, C. Gurbisz, M. P. Hannam, et al. 2023. "Rise of *Ruppia* in Chesapeake Bay: Climate Change–Driven Turnover of Foundation Species Creates New Threats and Management Opportunities." *Proceedings of the National Academy of Sciences* 120(23): e2220678120.
- Hensel, M. J., B. R. Silliman, J. van de Koppel, E. Hensel, S. J. Sharp, S. M. Crotty, and J. E. Byrnes. 2021. "A Large Invasive Consumer Reduces Coastal Ecosystem Resilience by Disabling Positive Species Interactions." *Nature Communications* 12(1): 6290.
- Howard, R. J., and I. A. Mendelssohn. 1999. "Salinity as a Constraint on Growth of Oligohaline Marsh Macrophytes. I. Species Variation in Stress Tolerance." *American Journal of Botany* 86(6): 785–794.
- Hughes, A. L., A. M. Wilson, and J. T. Morris. 2012. "Hydrologic Variability in a Salt Marsh: Assessing the Links Between Drought and Acute Marsh Dieback." *Estuarine, Coastal and Shelf Science* 111: 95–106.
- Hutchens, J. J., and K. Walters. 2006. "Gastropod Abundance and Biomass Relationships with Salt Marsh Vegetation within Ocean-Dominated South Carolina, USA Estuaries." *Journal of Shellfish Research* 25(3): 947–953.
- Lefcheck, J. S., R. J. Orth, W. C. Dennison, D. J. Wilcox, R. R. Murphy, J. Keisman, C. Gurbisz, et al. 2018. "Long-Term Nutrient Reductions Lead to the Unprecedented Recovery of a Temperate Coastal Region." *Proceedings of the National Academy of Sciences* 115(14): 3658–62.
- Lindenmayer, D. B., G. E. Likens, A. Andersen, D. Bowman, C. M. Bull, E. Burns, C. R. Dickman, et al. 2012. "Value of Long-Term Ecological Studies." *Austral Ecology* 37(7): 745–757.
- Linhurst, R. A., and E. D. Seneca. 1981. "Aeration, Nitrogen and Salinity as Determinants of *Spartina alterniflora* Loisel. Growth Response." *Estuaries* 4: 53–63.
- McKee, K. L., I. A. Mendelssohn, and M. D. Materne. 2004. "Acute Salt Marsh Dieback in the Mississippi River Deltaic Plain: A

- Drought-Induced Phenomenon?" *Global Ecology and Biogeography* 13(1): 65–73.
- Menge, B. A., and A. M. Olson. 1990. "Role of Scale and Environmental Factors in Regulation of Community Structure." *Trends in Ecology & Evolution* 5(2): 52–57.
- Menge, B. A., and J. P. Sutherland. 1987. "Community Regulation: Variation in Disturbance, Competition, and Predation in Relation to Environmental Stress and Recruitment." *The American Naturalist* 130(5): 730–757.
- Morton, J. P., and B. R. Silliman. 2020. "Parasites Enhance Resistance to Drought in a Coastal Ecosystem." *Ecology* 101(1): e02897.
- NOAA. 2023. "National Centers for Environmental Information, Climate at a Glance: Divisional Time Series, Georgia Region 9 from Jan-1895 to Jun-2023." <https://www.ncei.noaa.gov/access/monitoring/climate-at-a-glance/divisional/time-series>.
- Paine, R. T., M. J. Tegner, and E. A. Johnson. 1998. "Compounded Perturbations Yield Ecological Surprises." *Ecosystems* 1: 535–545.
- Pennings, S. C. 2016. "Long-term Plant Biomass Monitoring Data from the Georgia Coastal Ecosystems LTER Project on Sapelo Island, Georgia." Georgia Coastal Ecosystems LTER Project, University of Georgia, Long Term Ecological Research Network. <https://doi.org/10.6073/pasta/dc4bff1f792600ec50f8134618398516>.
- R Core Team. 2022. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing <https://www.R-project.org/>.
- Renzi, J. J., and B. R. Silliman. 2021. "Increasing Grazer Density Leads to Linear Decreases in *Spartina alterniflora* Biomass and Exponential Increases in Grazing Pressure across a Barrier Island." *Marine Ecology Progress Series* 659: 49–58.
- Rietl, A. J., M. G. Sorrentino, and B. J. Roberts. 2018. "Spatial Distribution and Morphological Responses to Predation in the Salt Marsh Periwinkle." *Ecosphere* 9(6): e02316.
- Schalles, J. F., C. M. Hladik, A. A. Lynes, and S. C. Pennings. 2013. "Landscape Estimates of Habitat Types, Plant Biomass, and Invertebrate Densities in a Georgia Salt Marsh." *Oceanography* 26(3): 88–97.
- Shaver, E. C., D. E. Burkepile, and B. R. Silliman. 2018. "Local Management Actions Can Increase Coral Resilience to Thermally-Induced Bleaching." *Nature Ecology & Evolution* 2(7): 1075–79.
- Sih, A., A. M. Bell, and J. L. Kerby. 2004. "Two Stressors Are Far Deadlier than One." *Trends in Ecology & Evolution* 19(6): 274–76.
- Silliman, B. R., and M. D. Bertness. 2002. "A Trophic Cascade Regulates Salt Marsh Primary Production." *Proceedings of the National Academy of Sciences* 99(16): 10500–10505.
- Silliman, B. R., and Q. He. 2018. "Physical Stress, Consumer Control, and New Theory in Ecology." *Trends in Ecology & Evolution* 33(7): 492–503.
- Silliman, B. R., M. W. McCoy, C. Angelini, R. D. Holt, J. N. Griffin, and J. van de Koppel. 2013. "Consumer Fronts, Global Change, and Runaway Collapse in Ecosystems." *Annual Review of Ecology, Evolution, and Systematics* 44: 503–538.
- Silliman, B. R., J. Van De Koppel, M. D. Bertness, L. E. Stanton, and I. A. Mendelssohn. 2005. "Drought, Snails, and Large-Scale Die-off of Southern US Salt Marshes." *Science* 310(5755): 1803–6.
- Silliman, B. R., and J. C. Zieman. 2001. "Top-Down Control of *Spartina alterniflora* Production by Periwinkle Grazing in a Virginia Salt Marsh." *Ecology* 82(10): 2830–45.
- Silliman, B. R., and S. Y. Newell. 2003. "Fungal Farming in a Snail." *Proceedings of the National Academy of Sciences* 100 (26): 15643–48.
- Smith, C. 2024. "Data/Code from: Long-term Data Reveal that Grazer Density Mediates Climatic Stress in Salt Marshes." Zenodo, Data Set. <https://doi.org/10.5281/zenodo.10685008>.
- Svoboda, M., D. LeCompte, M. Hayes, R. Heim, K. Gleason, J. Angel, B. Rippey, et al. 2002. "The Drought Monitor." *Bulletin of the American Meteorological Society* 83: 1181–90.
- Vinebrooke, R., K. L. Cottingham, J. Norberg, M. Scheffer, S. I. Dodson, S. C. Maberly, and U. Sommer. 2004. "Impacts of Multiple Stressors on Biodiversity and Ecosystem Functioning: The Role of Species Co-Tolerance." *Oikos* 104(3): 451–57.
- Więski, K., and S. C. Pennings. 2014. "Climate Drivers of *Spartina alterniflora* Salt Marsh Production in Georgia, USA." *Ecosystems* 17: 473–484.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Smith, Carter S., Y. Stacy Zhang, Marc J. S. Hensel, Steven C. Pennings, and Brian R. Silliman. 2024. "Long-Term Data Reveal that Grazer Density Mediates Climatic Stress in Salt Marshes." *Ecology* 105(7): e4323. <https://doi.org/10.1002/ecy.4323>