6-13-2019

Field Experiments and Meta-analysis Reveal Wetland Vegetation as a Crucial Element in the Coastal Protection Paradigm

Brian R. Silliman

Qiang He

Christine Angelini

Carter S. Smith

Matthew L. Kirwan
Virginia Institute of Marine Science

See next page for additional authors

Recommended Citation

Silliman, Brian R.; He, Qiang; Angelini, Christine; Smith, Carter S.; Kirwan, Matthew L.; and et al, Field Experiments and Meta-analysis Reveal Wetland Vegetation as a Crucial Element in the Coastal Protection Paradigm (2019). *Current Biology*, 29, 1800-1806.
doi: 10.1016/j.cub.2019.05.017

Article

Current Biology

Field Experiments and Meta-analysis Reveal Wetland Vegetation as a Crucial Element in the Coastal Protection Paradigm

Highlights

- Experimental removal of salt marsh vegetation enhances lateral erosion
- Belowground biomass was the plant trait responsible for resisting erosion
- Meta-analysis shows that plant die-off generally hastens erosion of salt marshes
- Findings support a coastal protection paradigm that incorporates coastal wetlands

Authors

Brian R. Silliman, Qiang He, Christine Angelini, ..., Todd Z. Osborne, James C. Nifong, Johan van de Koppel

Correspondence

brian.silliman@duke.edu

In Brief

Silliman et al. employ field experiments and meta-analysis to show that, contrary to recent lab work, salt marsh plants protect shorelines from erosion. This work substantiates a coastal protection paradigm that incorporates coastal wetlands and highlights disturbances that kill marsh plants as major forces that can indirectly drive coastal erosion.

Silliman et al., 2019, Current Biology *29*, 1800–1806
June 3, 2019
https://doi.org/10.1016/j.cub.2019.05.017

CellPress

Current Biology
Article

Field Experiments and Meta-analysis Reveal Wetland Vegetation as a Crucial Element in the Coastal Protection Paradigm

Brian R. Silliman,[1,10,*] Qiang He,[1] Christine Angelini,[2] Carter S. Smith,[1] Matthew L. Kirwan,[3] Pedro Daleo,[4] Julianna J. Renzi,[1] Jack Butler,[5] Todd Z. Osborne,[6] James C. Nifong,[7] and Johan van de Koppel[8,9]

[1]Division of Marine Science and Conservation, Nicholas School of the Environment, Duke University, 135 Duke Marine Lab Road, Beaufort, NC 28516, USA

[2]Department of Environmental Engineering Sciences, University of Florida, PO Box 116580, Gainesville, FL 32611, USA

[3]Virginia Institute of Marine Science, College of William and Mary, PO Box 1346, 1375 Greate Road, Gloucester Point, VA 23062, USA

[4]Intsituto de Investigaciones Marinas y Costeras (IIMyC), UNMdP, CONICET, CC1260, Mar del Plata 7600, Argentina

[5]Department of Biological Sciences, Old Dominion University, Norfolk, VA 23529, USA

[6]Whitney Laboratory for Marine Science, University of Florida, St. Augustine, FL 32080, USA

[7]Wetlands and Coastal Ecology Branch, US Army Engineer Research and Development Center, Vicksburg, MS 39180, USA

[8]Department of Estuarine and Delta Systems, Royal Netherlands Institute for Sea Research and Utrecht University, PO Box 140, 4400 AC Yerseke, the Netherlands

[9]Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, PO Box 11103, 9700 CC Groningen, the Netherlands

[10]Lead Contact

*Correspondence: brian.silliman@duke.edu

https://doi.org/10.1016/j.cub.2019.05.017

SUMMARY

Increasing rates of sea-level rise and wave action threaten coastal populations. Defense of shorelines by protection and restoration of wetlands has been invoked as a win-win strategy for humans and nature, yet evidence from field experiments supporting the wetland protection function is uncommon, as is the understanding of its context dependency. Here we provide evidence from field manipulations showing that the loss of wetland vegetation, regardless of disturbance size, increases the rate of erosion on wave-stressed shorelines. Vegetation removal (simulated disturbance) along the edge of salt marshes reveals that loss of wetland plants elevates the rate of lateral erosion and that extensive root systems, rather than aboveground biomass, are primarily responsible for protection against edge erosion in marshes. Meta-analysis further shows that disturbances that generate plant die-off on salt marsh edges generally hasten edge erosion in coastal marshes and that the erosion protection function of wetlands relates more to lateral than vertical edge-erosional processes and is positively correlated with the amount of belowground plant biomass lost. Collectively, our findings substantiate a coastal protection paradigm that incorporates preservation of shoreline vegetation, illuminate key context dependencies in this theory, and highlight local disturbances (e.g., oil spills) that kill wetland plants as agents that can accelerate coastal erosion.

INTRODUCTION

Coastal areas will most likely experience a relative rise in sea level that may exceed 1 m over the next century, potentially displacing tens of millions of people [1, 2]. This looming reality, along with increases in the frequency and intensity of coastal disturbance and disasters in recent decades [3, 4], has spurred a global discussion on how best to protect human populations and infrastructure along our coastlines [3, 5]. Many coastal management strategies now aim to maximize shoreline protection, minimize costs, and increase other benefits to humans (e.g., water quality enhancement and fish habitat provisioning) by strategically integrating both natural and man-made structures [3, 6–8]. Fundamental to these hybrid designs is the expectation that natural barriers, specifically coastal wetland plants, are effective in mitigating damage from disturbance and suppressing shoreline loss from wave-induced erosion [4, 9]. Experimental evidence from field studies supporting the wetland protection paradigm is uncommon, however, and those studies that have been conducted have sometimes generated conflicting results [10]. Furthermore, an in-depth, empirical understanding of the mechanisms that underlie this function is also limited (e.g., the relative importance of roots versus aboveground plant material in suppressing erosion).

Geomorphological theory predicts that wetland vegetation should reduce rates of erosion on edges of salt marshes by dissipating wave energy [11, 12], increasing the shear strength of soils [13], and influencing the elevation and morphology of the marsh edge [14, 15]. Aboveground plant stems exert drag on incoming waves, leading to reduced wave heights, slower flow velocities, and lower shear stress on the marsh soil surface [11], all of which contribute to the protective value of salt marshes for upland infrastructure [16]. In contrast, belowground roots, by promoting cohesion of the soil and increasing its shear

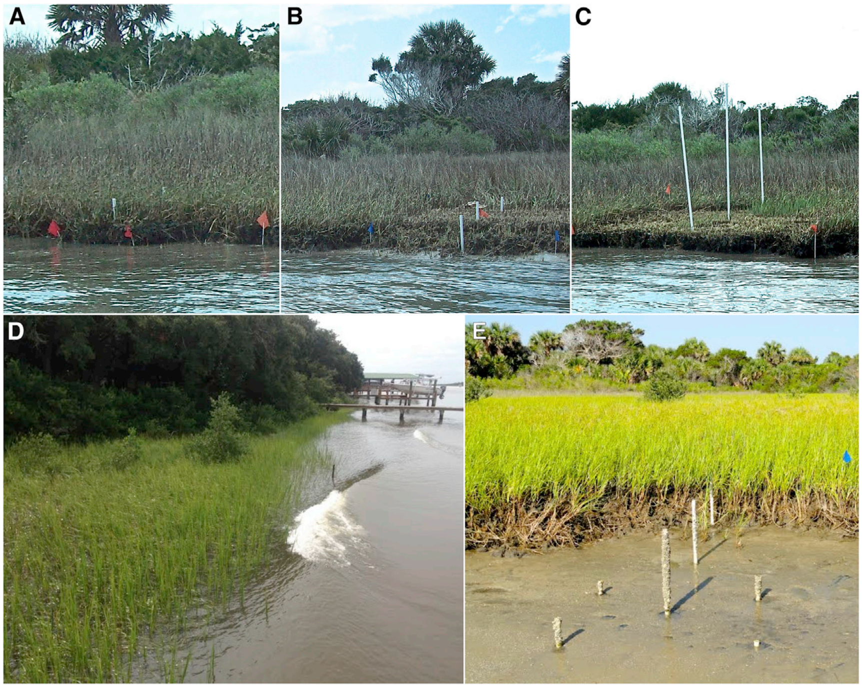

Figure 1. Photographs Showing the Experiment

(A–C) Representative experimental plots. Control (A), aboveground removal and belowground removal (B), and aboveground removal only (C) are shown. Note that the marsh in front of and behind the first white marker pole in aboveground and belowground removal plots has already collapsed, whereas in aboveground removal and control plots the marsh is still intact. Photos were taken 1 year after the beginning of the experiment.

(D and E) Representative photographs showing wave exposure on marsh borders (D) and substantial erosion in aboveground and belowground removal treatments 3 years after the experiment began (E).

strength, are predicted to reduce the vulnerability of wetland shorelines themselves to edge erosion [13, 17, 18]. Over longer time periods, marsh plants may additionally decrease erosion stress by facilitating vertical elevation growth through trapping sediment and contributing organic material.

The theory that marsh vegetation protects shoreline edges from erosion has a rich intellectual history and was established mostly based on early flume and numerical modeling studies. Recently, a direct field-based study has shown contrasting results, however. Specifically, experimental work along the edge of Texas salt marshes found that "salt marsh plants do not significantly mitigate the total amount of erosion along a wetland edge" [10]. These results have been well cited and have received attention in critical investigations and reviews on coastal defense [16, 19, 20]. Furthermore, they have been used to formulate an alternative intellectual framework for coastal defense that holds that wetland vegetation should be considered as a secondary, rather than a central, component in coastal defense systems and that coastal managers should think more critically about current plans to invest in protecting and enhancing coastal wetlands to help defend our shorelines [5].

In contrast to this view, our recent studies investigating impacts of the BP-Deepwater Horizon oil spill indicated that oil-induced death of plants along the edge of Louisiana salt marshes accelerated marsh lateral erosion by ∼100% [4, 21]. Recent syntheses of observational investigations in the field, in addition, contend that coastal vegetation can be effective in buffering against shoreline edge erosion [11, 16, 19]. Combined, the results from these studies highlight the need for further investigation into when and where the loss of coastal wetland plants can increase land erosion at its edge and, if so, the mechanisms involved. The answer to this question has theoretical and practical importance as it is not only at the crux of the emerging academic field of ecogeomorphology but is also at the center of the current consideration about whether significant coastal defense funds should be allocated toward salt marsh protection and augmentation.

To experimentally test whether the presence of wetland vegetation reduces edge erosion along shorelines, we conducted a 3-year salt marsh plant removal study at field sites with similar shoreline morphology and wave exposure and examined treatment effects on both lateral and vertical erosion at the salt marsh edge. To differentiate between aboveground versus belowground plant effects on erosion rate, and to test whether the effects of wetland plants vary with experimental scale, we manipulated vegetation at three levels of plant presence (control, aboveground removal, and aboveground and belowground removal) (see Figure 1) and at three plot widths (2, 4, and 8 m). We tested the generality of our findings with a meta-analysis by synthesizing results from past studies comparing marsh-edge erosion rates under vegetated and vegetation-reduced conditions.

RESULTS

In the field experiment, we observed a significant effect of the presence of vegetation on lateral erosion at the marsh edge ($F_{2,34}$ = 4.80, p = 0.0146; Figure 2A). Although lateral erosion rates in aboveground removal treatments did not differ from those in vegetated control treatments ($p > 0.05$), lateral erosion rates in aboveground and belowground removal treatments (114.19 ± 9.42 cm; mean ± SE, same below) were significantly higher than those in vegetated control treatments (76.76 ± 8.91 cm; $p < 0.05$). Furthermore, lateral erosion was not affected by plot width ($F_{2,34}$ = 0.81, p = 0.45), and no significant interactions between vegetation presence and plot width treatments were found ($F_{4,34}$ = 0.70, p = 0.60). Hence, independent of the scale of the disturbance, the presence of live belowground plant structures significantly slowed the lateral erosion of the marsh edge. We also evaluated the effect of vegetation presence on vertical erosion and found that there were no effects of vegetation presence ($F_{2,34}$ = 0.52, $p > 0.05$), plot width ($F_{2,34}$ = 0.24, $p > 0.05$), or their interaction ($F_{2,34}$ = 0.30, $p > 0.05$; Figure S4).

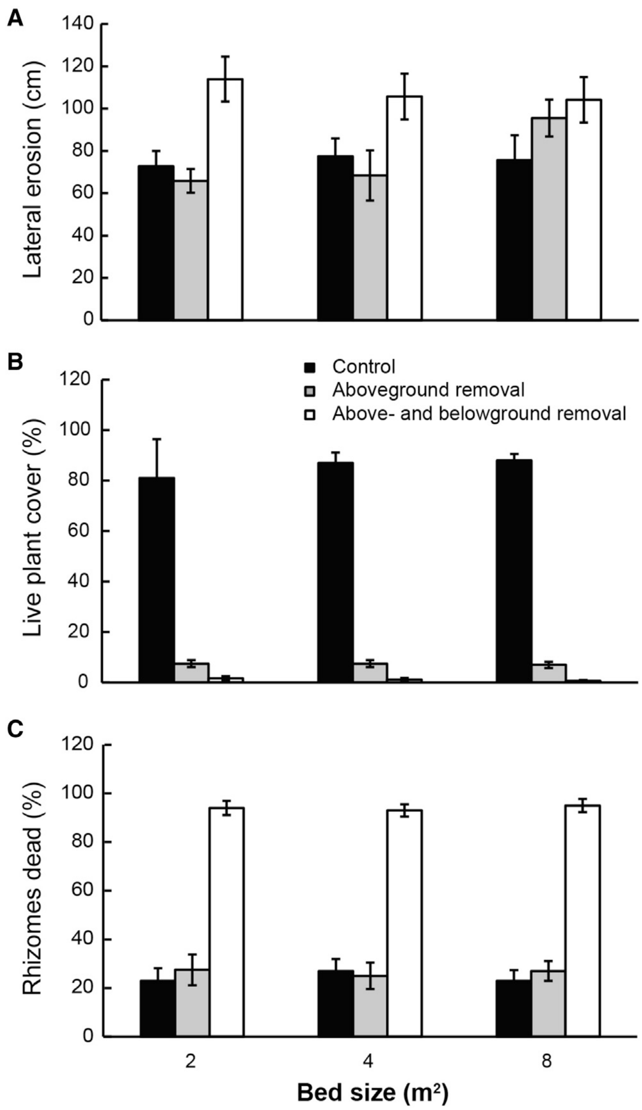

Figure 2. Summary of the Results of the Field Experiment

Erosion rates on the marsh edge (A), plant cover (B), and proportional rhizomes dead (C) in each plant presence by plot width treatment. Shown are means and SEs (n = 4–5). Plant presence treatments significantly affected edge erosion rates (p = 0.0146), plant cover (p < 0.001), and the proportion of dead rhizomes (p < 0.001), but neither bed size alone nor its interaction with vegetation removal affected those vegetation variables or marsh-edge erosion (p > 0.45 in all cases). See also Figure S4.

As expected, aboveground removal significantly eliminated live plant cover in both aboveground and aboveground and belowground removal treatments (df = 2, χ^2 = 368.2, p < 0.001; Figure 2B). Average live plant cover in control treatments was 85.33% ± 5.03%, whereas in aboveground as well as in aboveground and belowground removal treatments live plant cover was <10%. Neither plot width (df = 2, χ^2 = 0.20, p = 0.82) nor the interaction between plant presence and plot width (df = 4, χ^2 = 0.27, p = 0.90) affected live aboveground plant cover. The proportion of dead rhizomes, in addition, was significantly greater in aboveground and belowground removal treatments that received regular herbicide application (df = 2, χ^2 = 260.2, p < 0.001; Figure 2C), indicating that this method for killing belowground plant structures was effective. No effect was found of plot width (df = 2, χ^2 = 0.01, p = 1.00). Whereas the proportion of dead rhizomes in cores was typically 10%–30% in control and aboveground removal treatments, it was >90% in all aboveground and belowground removal treatments. No interaction between plant presence and plot width treatments on rhizome mortality was found (df = 4, χ^2 = 0.90, p = 0.92).

Meta-analysis revealed that the effect of aboveground and belowground removal on marsh-edge lateral erosion measured in the above experiment was comparable to the effect found in 15 previous comparisons of marsh-edge erosion between vegetated and vegetation-reduced conditions (Figure 3). Averaged across comparisons, there was a clear and significantly positive mean effect size of 1.22 (95% confidence interval, 0.65–1.80; p < 0.0001), revealing a generally positive effect of vegetation on the reduction of marsh-edge erosion. Consistent with our field experiment, the effect sizes of vegetation on erosion were significantly related to changes in belowground biomass (R^2 = 0.48, p = 0.05). Greater losses in belowground biomass led to higher increases in erosion (Figure S5).

DISCUSSION

Our field experiment provides clear evidence that the loss of vegetation can increase wave-induced erosion of shoreline edges in coastal wetlands. The finding that vegetation mortality increased lateral erosion rates only when belowground biomass was killed suggests that the impact of plant roots on soil strength is more important than the impact of aboveground plant stems on reducing lateral erosion on shoreline edges. This conclusion is not meant to understate the importance of aboveground vegetation in buffering wave energy and protecting upland infrastructure [11, 16, 19], but rather to highlight the fact that live belowground plant structure is a primary factor controlling edge maintenance in coastal salt marshes and thus indirectly the shoreline protection services that salt marshes provide. Moreover, it emphasizes the relevance of understanding factors that influence resource allocation between above- and belowground portions of wetland plants, such as eutrophication and grazing, for salt marsh resilience [13, 17, 32].

Our synthesis of previous studies testing for impacts of vegetation on marsh-edge erosion rate highlights both the generality of our experimental findings and new understanding in the context dependency of the coastal wetland protection paradigm. Averaged across all studies, the presence of live plants was associated with lower rates of marsh-edge erosion in both lab flume [30] and field [4, 31] studies (Figure 3). This erosion-reduction effect was regularly observed in studies of different causes of vegetation loss (Figure 3): studies using experimental removal of re-growing vegetation [30] and those on vegetation losses due to grazing [22], oiling [4], and eutrophication [17] all observed such an effect. Consistent with our experimental findings, the presence of live belowground plant structures was the primary and general mechanism by which marsh plants suppressed edge erosion (Figure 3). However, although our meta-analysis showed consistency in the impact of belowground biomass loss on edge erosion, it also revealed two critical variables that determine the extent to which wetland plants protect

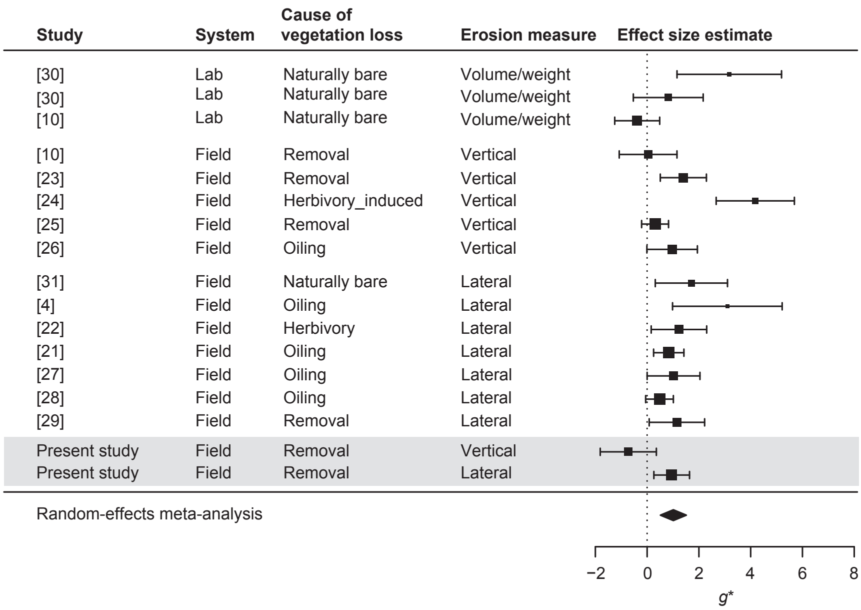

Figure 3. Synthesis of Field and Laboratory Studies on Salt Marsh Vegetation Loss and Marsh-Edge Erosion

All study species were *Spartina alterniflora* [4, 10, 21–29], except for Coops et al. [30], which studied *Scirpus lacustris* (the lower one) and *Phragmites australis* (the upper one), and Benner et al. [31], which examined a mixed group of grasses and sedges. Data points and error bars are effect sizes (Hedges' *g**) and 95% confidence intervals. Positive effect sizes indicate vegetation reduces erosion. Effect sizes are significant if their 95% confidence intervals do not overlap zero. Although five of the 15 comparisons had an insignificant effect size, three were actually reported as being significantly positive in the original studies (only our more conservative test found them to be insignificant). See also Figure S5.

shorelines edges: the erosion type measured and the amount of belowground biomass removed. Specifically, our synthesis revealed that the loss of wetland plants on salt marsh edges is much more likely to exacerbate lateral erosion processes as compared to vertical ones. In addition, we found that the magnitude of this effect on lateral erosion is dependent on the amount of belowground plant material that is lost after disturbance, as increases in erosion are positively related with reduction in belowground biomass (Figure S5). Combined, these findings validate the theory that wetland plants protect shorelines from edge erosion and provide important context dependency and mechanistic understanding of when and where plants protect shorelines—quantitative knowledge critical for improving geomorphological and shoreline protection models.

At first, these results seem to contrast with the Texas study [10] that suggests that vegetation does not enhance marsh stability; however, Feagin et al. [10] assessed impacts of plant presence on erosion only by measuring vertical erosion of the marsh surface (and inferring lateral erosion) and thus most likely missed what we observed as the primary erosional response—a conclusion supported by our meta-analysis showing that lateral, but not vertical, edge erosion is generally impacted by plant loss. Second, our experiment ran for more than twice as long (36 months versus 15 months). This ensured that there was near-complete mortality of belowground roots in our experiment and may have allowed ecogeomorphic feedbacks [33, 34] to become reinforced, processes that may not have be captured in the Texas study.

Our results, combined with past studies, reveal important processes underlying vegetation-geomorphology interactions: loss of plant root structures on the edge of coastal wetlands can trigger a powerful ecogeomorphic response of elevated lateral erosion rate. Enhanced erosion can, in turn, negatively affect the survival and growth of plants ahead of the erosive front [4] and even create or enhance a persistent positive geomorphic feedback [4, 35], where erosion leads to permanent wetland habitat loss. When erosive fronts form, the remaining protective effect of the vegetation on top of the escarpment can be overwhelmed as continued wave action leads to undercutting and eventual collapse of the escarped wetland edge. Such runaway erosion of wetland edges can persist for decades and lead to extensive marsh loss, as is observed along many European [36] and North American [34] salt marshes, and thus to loss of the coastal protection services for upland infrastructure.

This new theoretical synthesis highlights the need for wetland science and management to more fully incorporate lateral erosion, fueled by vegetation die-off on the wetland edge, as a primary agent of wetland loss. This is a crucial element to coastal wetland conservation, as wetland vegetation itself is typically highly resilient to disturbances that impose mortality without the potential for elevated erosion, even when these occur at dramatic, ecosystem-wide scales [37, 38]. However, processes that cause vegetation loss on the edge of wetlands, such as food-web interactions (e.g., trophic cascades and runaway grazing), increased physical or chemical stress (e.g., pollution and eutrophication), or human activities (e.g., haying), can accelerate erosion and subsequent land loss, reducing the potential for wetland recovery. Hence, wetland vegetation on the ecosystem edge acts as a nexus for strong, indirect interactions between species interaction networks, biogeochemistry, anthropogenic impacts, and geomorphology (Figure 4). Not accounting for the potential of this powerful ecogeomorphic feedback can lead to incorrect predictions of the impact of large-scale vegetation loss on wetland coverage (e.g., from massive oiling events) and underestimation of the destructive impacts of, for instance, runaway snail and crab grazing, that is now common throughout many western Atlantic and Asian salt marshes [37, 39, 40]. Moreover, as natural and human-induced disturbances trigger marsh erosion, there will be a reduction in the delivery of ecosystem services (e.g., carbon sequestration, pollutant filtration, and coastal protection), which may exacerbate future disturbances to the marsh and create a negative feedback loop (Figure 5).

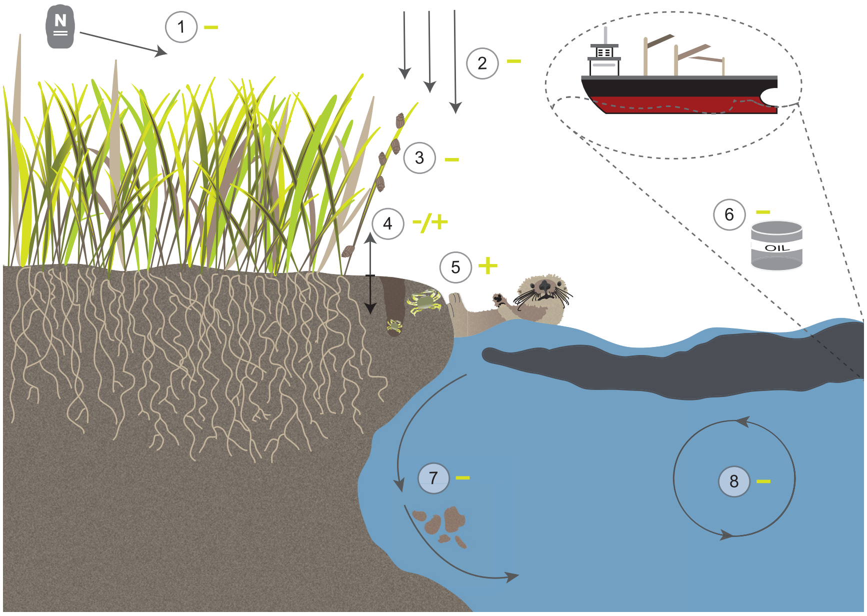

Figure 4. Conceptual Rendition of Biotic and Abiotic Factors that Interact to Influence Edge Erosion in Coastal Wetlands via Control of Belowground Plant Biomass

Marsh edges are a nexus for biological and geochemical interactions, which can increase or decrease marsh-edge erosion (via control of belowground biomass) as follows: (1) eutrophication can decrease belowground biomass; (2) intense drought can lead to marsh dieback and loss of below- and aboveground biomass; (3) overfishing and/or hunting of top predators can lead to runaway grazing and burrowing and decreased below- and aboveground biomass; (4) interactions between these factors, along with other physical factors like salinity and elevation, can influence the allocation of above- and belowground biomass and thus sediment stability; (5) reintroduction of predators (e.g., otters) or management of mesopredators (e.g., blue crabs) that consume marsh grazers (e.g., snails) can maintain below- and aboveground biomass; (6) oiling can lead to marsh die-off along edges and loss of belowground biomass; (7) ambient wave energy, storms, and boat wakes can all cause undercutting of the marsh platform leading to loss of belowground biomass and marsh slumping; and (8) factors 1–7 can lead to feedback loops, making marshes even more susceptible to runaway edge erosion.

Given these findings, it is imperative that we continue integrating preservation and enhancement of coastal wetlands into our coastal defense strategies to protect against shoreline erosion [5, 8]. This should involve both conservation of existing wetlands and active restoration [41] of coastal wetlands on degraded shorelines. Key for effectively integrating wetland vegetation into coastal defense strategies will be continued unraveling of the functional relationship of this now-confirmed coastal-wetland-shoreline protection paradigm (i.e., when and in which contexts wetlands provide protection against shoreline erosion and when they do not). This will require integration of observations, large-scale experimental studies, and mathematical approaches that can scale up non-linearities in wave protection functions and geomorphological dynamics to provide a thorough understanding of the stability and persistent effectiveness of coastal wetlands as an integrated line of defense against the rising and more energetic seas.

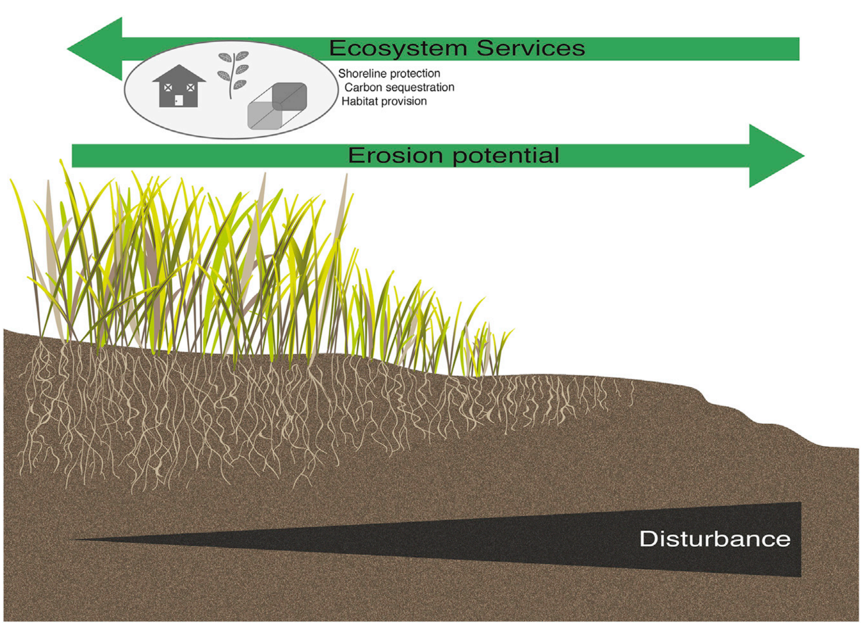

Figure 5. The Potential for Disturbance to Affect Salt Marsh Biomass, Lateral Erosion, and Ecosystem Service Delivery

As disturbance intensity on plants on the marsh edge increases, belowground biomass decreases and lateral erosion potential increases. The erosive loss of salt marsh on its edges leads to a decrease in the delivery of ecosystem services (e.g., carbon sequestration, pollutant filtration, etc.), which can in turn make the salt marsh more vulnerable to future disturbances. Arrows indicate the direction of the effects. Investigating whether this relationship is linear or non-linear should be the focus of future research.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- CONTACT FOR REAGENT AND RESOURCE SHARING
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
  - Spartina alterniflora
- METHOD DETAILS
  - Field experiment
  - Meta-analysis
- QUANTIFICATION AND STATISTICAL ANALYSIS
  - Field experiment
  - Meta-analysis
- DATA AND SOFTWARE AVAILIBILITY

SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at https://doi.org/10.1016/j.cub.2019.05.017.

ACKNOWLEDGMENTS

Funding for this work was provided in part by an NSF CAREER grant to B.R.S. (BIO-OCE; no. 1439504), the NSF Long-Term Ecological Research program (GCE; no. 1445834), and a Netherlands Royal Society Visiting Professorship to B.R.S. The Florida Park Service granted a permit (no. 03251013) for this work.

AUTHOR CONTRIBUTIONS

B.R.S. devised of project and wrote the manuscript with the help of Q.H., C.A., C.S.S., M.L.K., P.D., J.J.R., and J.v.d.K. B.R.S., Q.H., C.A., J.B., T.Z.O., and J.C.N. assisted with fieldwork, and Q.H. and P.D. collected data for the meta-analysis. Data were analyzed by Q.H. and B.R.S.

DECLARATION OF INTERESTS

The authors declare no competing interests.

Received: February 12, 2019
Revised: April 6, 2019
Accepted: May 3, 2019
Published: May 23, 2019

REFERENCES

1. United Nations Environment Programme (2006). Marine and Coastal Ecosystems and Human Wellbeing: A Synthesis Report Based on the Findings of the Millennium Ecosystem Assessment (UNEP).
2. Arkema, K.K., Guannel, G., Verutes, G., Wood, S.A., Guerry, A., Ruckelshaus, M., Kareiva, P., Lacayo, M., and Silver, J.M. (2013). Coastal habitats shield people and property from sea-level rise and storms. Nat. Clim. Chang. *3*, 913–918.
3. Barbier, E.B., Koch, E.W., Silliman, B.R., Hacker, S.D., Wolanski, E., Primavera, J., Granek, E.F., Polasky, S., Aswani, S., Cramer, L.A., et al. (2008). Coastal ecosystem-based management with nonlinear ecological functions and values. Science *319*, 321–323.
4. Silliman, B.R., van de Koppel, J., McCoy, M.W., Diller, J., Kasozi, G.N., Earl, K., Adams, P.N., and Zimmerman, A.R. (2012). Degradation and resilience in Louisiana salt marshes after the BP-Deepwater Horizon oil spill. Proc. Natl. Acad. Sci. USA *109*, 11234–11239.
5. Feagin, R.A., Mukherjee, N., Shanker, K., Baird, A.H., Cinner, J., Kerr, A.M., Koedam, N., Sridhar, A., Arthur, R., Jayatissa, L.P., and Lo Seen, D. (2010). Shelter from the storm? Use and misuse of coastal vegetation bioshields for managing natural disasters. Conserv. Lett. *3*, 1–11.
6. Duarte, C.M., Losada, I.J., Hendriks, I.E., Mazarrasa, I., and Marba, N. (2013). The role of coastal plant communities for climate change mitigation and adaptation. Nat. Clim. Chang. *3*, 961–968.
7. Peyronnin, N., Green, M., Richards, C.P., Owens, A., Reed, D., Chamberlain, J., Groves, D.G., Rhinehart, W.K., and Belhadjali, K. (2013). Louisiana's 2012 coastal master plan: overview of a science-based and publicly informed decision-making process. J. Coast. Res. *67*, 1–15.
8. Vuik, V., Borsje, B.W., Willemsen, P.W.J.M., and Jonkman, S.N. (2019). Salt marshes for flood risk reduction: quantifying long-term effectiveness and life-cycle costs. Ocean Coast. Manage. *171*, 96–110.
9. Sutton-Grier, A.E., Wowk, K., and Bamford, H. (2015). Future of our coasts: the potential for natural and hybrid infrastructure to enhance the resilience of our coastal communities, economies and ecosystems. Environ. Sci. Policy *51*, 137–148.
10. Feagin, R.A., Lozada-Bernard, S.M., Ravens, T.M., Möller, I., Yeager, K.M., and Baird, A.H. (2009). Does vegetation prevent wave erosion of salt marsh edges? Proc. Natl. Acad. Sci. USA *106*, 10109–10113.
11. Möller, I., Kudella, M., Rupprecht, F., Spencer, T., Paul, M., Van Wesenbeeck, B.K., Wolters, G., Jensen, K., Bouma, T.J., Miranda-Lange, M., and Schimmels, S. (2014). Wave attenuation over coastal salt marshes under storm surge conditions. Nat. Geosci. *7*, 727–731.
12. Leonardi, N., Ganju, N.K., and Fagherazzi, S. (2016). A linear relationship between wave power and erosion determines salt-marsh resilience to violent storms and hurricanes. Proc. Natl. Acad. Sci. USA *113*, 64–68.
13. Howes, N.C., FitzGerald, D.M., Hughes, Z.J., Georgiou, I.Y., Kulp, M.A., Miner, M.D., Smith, J.M., and Barras, J.A. (2010). Hurricane-induced failure of low salinity wetlands. Proc. Natl. Acad. Sci. USA *107*, 14014–14019.
14. Cahoon, D.R. (2006). A review of major storm impacts on coastal wetland elevations. Estuaries Coast. *29*, 889–898.
15. Mariotti, G., and Fagherazzi, S. (2010). A numerical model for the coupled long-term evolution of salt marshes and tidal flats. J. Geophys. Res. Earth Surf. *115*, F01004.
16. Shepard, C.C., Crain, C.M., and Beck, M.W. (2011). The protective role of coastal marshes: a systematic review and meta-analysis. PLoS ONE *6*, e27374.
17. Deegan, L.A., Johnson, D.S., Warren, R.S., Peterson, B.J., Fleeger, J.W., Fagherazzi, S., and Wollheim, W.M. (2012). Coastal eutrophication as a driver of salt marsh loss. Nature *490*, 388–392.
18. Leonardi, N., and Fagherazzi, S. (2015). Effect of local variability in erosional resistance on large-scale morphodynamic response of salt marshes to wind waves and extreme events. Geophys. Res. Lett. *42*, 5872–5879.
19. Gedan, K.B., Kirwan, M.L., Wolanski, E., Barbier, E.B., and Silliman, B.R. (2011). The present and future role of coastal wetland vegetation in protecting shorelines: answering recent challenges to the paradigm. Clim. Change *106*, 7–29.
20. Marani, M., d'Alpaos, A., Lanzoni, S., and Santalucia, M. (2011). Understanding and predicting wave erosion of marsh edges. Geophys. Res. Lett. *38*, L21401.
21. Silliman, B.R., Dixon, P.M., Wobus, C., He, Q., Daleo, P., Hughes, B.B., Rissing, M., Willis, J.M., and Hester, M.W. (2016). Thresholds in marsh resilience to the Deepwater Horizon oil spill. Sci. Rep. *6*, 32520.
22. Coverdale, T.C., Brisson, C.P., Young, E.W., Yin, S.F., Donnelly, J.P., and Bertness, M.D. (2014). Indirect human impacts reverse centuries of carbon sequestration and salt marsh accretion. PLoS ONE *9*, e93296.
23. Altieri, A.H., Bertness, M.D., Coverdale, T.C., Axelman, E.E., Herrmann, N.C., and Szathmary, P.L. (2013). Feedbacks underlie the resilience of salt marshes and rapid reversal of consumer-driven die-off. Ecology *94*, 1647–1657.
24. Brisson, C.P., Coverdale, T.C., and Bertness, M.D. (2014). Salt marsh die-off and recovery reveal disparity between the recovery of ecosystem structure and service provision. Biol. Conserv. *179*, 1–5.

25. Sheehan, M.R., and Ellison, J.C. (2015). Tidal marsh erosion and accretion trends following invasive species removal, Tamar Estuary, Tasmania. Estuar. Coast. Shelf Sci. *164*, 46–55.
26. Lin, Q., Mendelssohn, I.A., Graham, S.A., Hou, A., Fleeger, J.W., and Deis, D.R. (2016). Response of salt marshes to oiling from the Deepwater Horizon spill: Implications for plant growth, soil surface-erosion, and shoreline stability. Sci. Total Environ. *557-558*, 369–377.
27. Zengel, S., Bernik, B.M., Rutherford, N., Nixon, Z., and Michel, J. (2015). Heavily oiled salt marsh following the Deepwater Horizon oil spill, ecological comparisons of shoreline cleanup treatments and recovery. PLoS ONE *10*, e0132324.
28. Turner, R.E., McClenachan, G., and Tweel, A.W. (2016). Islands in the oil: Quantifying salt marsh shoreline erosion after the Deepwater Horizon oiling. Mar. Pollut. Bull. *110*, 316–323.
29. Vu, H.D., Wie Ski, K., and Pennings, S.C. (2017). Ecosystem engineers drive creek formation in salt marshes. Ecology *98*, 162–174.
30. Coops, H., Geilen, N., Verheij, H.J., Boeters, R., and van der Velde, G. (1996). Interactions between waves, bank erosion and emergent vegetation: an experimental study in a wave tank. Aquat. Bot. *53*, 187–198.
31. Benner, C.S., Knutson, P.L., Brochu, R.A., and Hurme, A.K. (1982). Vegetative erosion control in an oligohaline environment Currituck Sound, North Carolina. Wetlands *2*, 105–117.
32. Daleo, P., Alberti, J., Jumpponen, A., Veach, A., Ialonardi, F., Iribarne, O., and Silliman, B. (2018). Nitrogen enrichment suppresses other environmental drivers and homogenizes salt marsh leaf microbiome. Ecology *99*, 1411–1418.
33. Kirwan, M.L., Murray, A.B., and Boyd, W.S. (2008). Temporary vegetation disturbance as an explanation for permanent loss of tidal wetlands. Geophys. Res. Lett. *35*, L05403.
34. Mariotti, G., and Fagherazzi, S. (2013). Critical width of tidal flats triggers marsh collapse in the absence of sea-level rise. Proc. Natl. Acad. Sci. USA *110*, 5353–5356.
35. van de Koppel, J., van der Wal, D., Bakker, J.P., and Herman, P.M. (2005). Self-organization and vegetation collapse in salt marsh ecosystems. Am. Nat. *165*, E1–E12.
36. van der Wal, D., Wielemaker-Van den Dool, A., and Herman, P.M. (2008). Spatial patterns, rates and mechanisms of saltmarsh cycles (Westerschelde, The Netherlands). Estuar. Coast. Shelf Sci. *76*, 357–368.
37. Silliman, B.R., van de Koppel, J., Bertness, M.D., Stanton, L.E., and Mendelssohn, I.A. (2005). Drought, snails, and large-scale die-off of southern U.S. salt marshes. Science *310*, 1803–1806.
38. Angelini, C., and Silliman, B.R. (2012). Patch size-dependent community recovery after massive disturbance. Ecology *93*, 101–110.
39. Silliman, B.R., McCoy, M., Angelini, C., Holt, B., Griffin, J., and von de Koppel, J. (2013). Consumer fronts, global change and runaway collapse in ecosystems. Annu. Rev. Ecol. Evol. Syst. *44*, 503–538.
40. He, Q., Silliman, B.R., Liu, Z., and Cui, B. (2017). Natural enemies govern ecosystem resilience in the face of extreme droughts. Ecol. Lett. *20*, 194–201.
41. Silliman, B.R., Schrack, L., He, Q., Santoni, A., Jacobi, R., Jacobi, M., van der Heide, T., and von de Koppel, J. (2015). Facilitation shifts paradigms and can increase success of coastal restoration. Proc. Natl. Acad. Sci. USA *112*, 14295–14300.
42. Francalanci, S., Bendoni, M., Rinaldi, M., and Solari, L. (2013). Ecomorphodynamic evolution of salt marshes: Experimental observations of bank retreat processes. Geomorphology *195*, 53–65.
43. McClenachan, G., Turner, R.E., and Tweel, A.W. (2013). Effects of oil on the rate and trajectory of Louisiana marsh shoreline erosion. Environ. Res. Lett. *8*, 044030.
44. Pinsky, M.L., Guannel, G., and Arkema, K.K. (2013). Quantifying wave attenuation to inform coastal habitat conservation. Ecosphere *4*, 1–16.
45. Langsrud, Ø. (2003). ANOVA for unbalanced data: use type II instead of type III sums of squares. Stat. Comput. *13*, 163–167.
46. Fox, J., and Weisberg, H.S. (2010). An R Companion to Applied Regression, Second Edition (Sage Publications).
47. R Core Team (2014). R: A Language and Environment for Statistical Computing (R Foundation for Statistical Computing).
48. Borenstein, M., Hedges, L.V., Higgins, J.P., and Rothstein, H.R. (2009). Introduction to Meta-Analysis, First Edition (John Wiley & Sons).
49. Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. J. Stat. Softw. *36*, 1–48.
50. Rosenthal, R. (1991). Meta-analytic Procedures for Social Research, First Edition (SAGE Publications).

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological Samples		
Spartina alterniflora	Wild salt marsh, Marineland, Florida, USA	N/A
Software and Algorithms		
R v 3.04	https://www.r-project.org/	N/A
R package "car"	https://cran.r-project.org/web/packages/car/car.pdf	N/A
R package "metafor"	https://cran.r-project.org/web/packages/metafor/metafor.pdf	N/A

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Brian R. Silliman (brian.silliman@duke.edu).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Spartina alterniflora

Our field experiments were conducted in naturally occurring *Spartina alterniflora*-dominated salt marshes along the intracoastal waterway in Marineland, Florida (Figure S1).

METHOD DETAILS

Field experiment

We conducted our experiment from August 2010 to October 2013 in *Spartina alterniflora*-dominated salt marshes fringing the intracoastal waterway (ICW) in Marineland, Florida (29°40'52.56''N, 81°13'26.85''W, see Figure S2). We selected this location for our study for the following reasons. First, many of the salt marshes along the ICW in this area display the defining characteristic of an eroding coastal wetland [42]: an escarped, ~90° edge (40-60 cm in height) with exposed rhizomes (Figures 1 and S1). This ecosystem edge profile is similar to that of eroding Gulf Coast marshes both in the Feagin et al. [10] experimental study and in the BP-DWH oil impact investigation [4] and the vertical angle of the edges in this study did not vary among treatments (mean = 82° +/− 4.5°, $p = 0.43$). Analysis of 5 sediment cores from the study area reveal that the average sediment composition was 20% sand, 77% silt, and 3% clay. The sediment organic matter content was 10.3%. Second, we found replicate sites with statistically similar slopes over the first 3 m from the edge; fetch also did not vary between treatments, as the width of the ICW is relatively constant and the directionality is nearly straight with no significant bends in this area (Figures S2 and S3). Specifically, the mean slope and fetch were 0.093 (±0.021, standard deviation) and 174 (±9) m, respectively, and did not differ among treatments ($p = 0.54$ and 0.81, respectively). These data (edge angle, slope, and fetch) suggest that the erosion potential for our sites did not vary among treatments. Third, because of the relatively close proximity of all sites (all replicates were located along a 2,000 m stretch of marsh edge), all replicates were exposed to a very similar frequency and amplitude of both wind- and boat-generated waves (Supplemental Information and Figure S2). The average tidal range in this area of the ICW is ~0.76 m, the marsh surface is ~10 cm above the mean water level, and boats are the primary generator of waves in this system. Ninety percent of boat wakes along this shoreline are less than 0.3 m high (indicative of recreational boat traffic), but larger wakes reaching heights of 1.3 m occur multiple times per day (C.A. and A. Sheremet, unpublished data). There were no major (tropical or hurricane) storm events within 25 miles of this site during the study period. The ICW in this area has a relatively uniform depth of approximately 5 m (Figure S2).

To investigate the impact of vegetation presence on marsh edge erosion rate, we set up a factorial experiment with plot width and plant presence as factors. There were three levels of plot width (1, 2, and 4 m parallel to marsh edge × 2 m perpendicular to marsh edge, for total plot sizes of 2, 4 and 8 m^2) and three levels of plant presence (control, aboveground removal, and aboveground and belowground removal). We chose these plot widths as they encompass the sizes of die-off patches that naturally occur along marsh edges due to disturbance by mats of vegetation, algae, or oil. Plots (43 in total) were positioned 2-4 m apart and haphazardly assigned to each plot width and plant presence treatment combination (replicated 4-5 times).

Aboveground removal treatments were maintained by trimming all stems within plots down to the substrate and repeating this treatment each month to ensure treatment integrity. The presence of emergent shoots from rhizomes indicated belowground plant structures remained alive through the duration of the experiment. Aboveground + belowground removal treatments were maintained by trimming stems, as above, and dripping Rodeo herbicide into the exposed, cut stems bi-monthly. Herbicide was applied in this fashion to ensure it only contacted plants and thus would not interact directly with the sediment or infauna. As a procedural control,

control plots received a similar amount of walking activity as plant removal treatments. To assess the effect of experimental treatments, we measured live plant cover (in 50 × 50 cm quadrats) and ratio of dead:live rhizomes in marsh cores in each plot using established methods [4] after one year.

To quantify the effect of experimental treatments on shoreline erosion, we demarcated the marsh edge at the beginning of the study by pushing 0.5 cm diameter PVC stakes 50 cm into the substrate at 0.25 m increments along the marsh edge in each plot. To ensure proper orientation of subsequent erosion measurements, we installed 3 cm diameter PVC pipes along the medial line of each plot, perpendicular to the shoreline, at three positions: the leading edge of the marsh, 1 m from the leading edge, and 2 m from the leading edge. After three years, we quantified lateral erosion by measuring the distance between the initial edge and new edge every 25 cm of shoreline within each plot and averaged all measurements collected per plot. We used this spatial interval for measurements and averaging approach because the erosion of escarped edges occurs via the slumping off and washing away of clumps of marsh and is therefore variable over short distances (see photo of aboveground and belowground removal plot in Figure S1) [4, 43]. Consequently, multiple measurements along the edge are needed to avoid place-based sampling biases that can occur from having designated measurement points that occur on areas with either slumping or not. We estimated changes in vertical erosion by hammering 0.5 cm diameter PVC stakes into the substrate until refusal (at least 50 cm depth), which happens within 1 m of the surface at this site because of a prominent sand layer. PVC stakes were located 100 cm from the marsh edge and we notched the marsh surface soil interface when the PVC was placed and then measured vertical change after 1 year. Each plot had 2 vertical PVC pipes for measuring vertical erosion. The amount of vertical erosion did not differ between year 1 and 3, so we reported vertical erosion after 1 year.

Meta-analysis

To examine whether vegetation generally suppresses marsh lateral erosion, we conducted a synthesis of relevant studies. We focused on marsh edge erosion because it provides a direct measure of the capacity of a wetland to withstand the stress of small to intermediate waves that impact the marsh on its edge. Vegetation effects on sedimentation and elevation changes in marsh interiors or on wave attenuation have been well established in previous syntheses [16, 19, 44], so were not considered here.

To compile a list of relevant studies on vegetation's effect on marsh edge erosion, we first searched Web of Science for articles using the search query TS = marsh* AND TS = (erosion OR retreat OR loss). This search resulted in 1243 articles between 2010 and 2017. Then, for studies prior to 2010, we considered those included in a previous meta-analysis [16], which examined the protective role of marsh vegetation but did not specifically investigate the effect of vegetation on marsh edge erosion, the focal question of our study. Studies from these two sources that compared erosion rates in vegetated and vegetation-reduced conditions were retained for data extraction. Studies could be observational or experimental, and vegetation reduction could have been caused by experimental removal or other factors that depressed above- and/or belowground vegetation. For each study, mean erosion rates in vegetated and vegetation-reduced treatments, as well as their standard errors/deviations and sample sizes, were extracted from tables, figures or text, and the study system (either lab flume or field setting), study species, cause of vegetation reduction (e.g., experimental removal, naturally unvegetated, oil-, herbivory-, or eutrophication- induced loss), and the measure of edge erosion (weight/volume loss, elevational loss, or lateral loss) were recorded. When available in the above studies, belowground biomass data (means, standard errors/deviations and sample sizes) in both vegetated and vegetation-reduced treatments were also extracted.

QUANTIFICATION AND STATISTICAL ANALYSIS

Field experiment

We used a two-way ANOVA to examine the effects of plot width and plant presence treatments on lateral and vertical marsh erosion rates. Post hoc Tukey HSD multiple comparisons were conducted to examine if marsh erosion rate differs between each pair of treatments. Generalized linear models (GLM) were used to examine the individual and interactive effects of plot width and plant presence treatments on live plant cover and the proportion of dead rhizomes. Quasi-Poisson distributions were used to account for overdispersion (overdispersion parameters were 2.83 and 3.11 for live plant cover and proportional of dead rhizomes data, respectively). Effects of plot width and plant presence treatments and their interactions were tested by comparing the resulting deviances to Wald χ^2 test statistics using the Type II sum of squares in R *car* package [45, 46]. Differences were considered significant at the level of $p < 0.05$. All statistical analysis was performed using R 3.04 [47].

Meta-analysis

We computed Hedges' *g** effect sizes [48], a measure of the unbiased, standardized mean difference in erosion rate between vegetation-reduced and vegetated treatments for each study. A positive effect size indicates the measure of erosion was lower in the presence than absence of vegetation in the study. Effect sizes are considered significant if their 95% confidence intervals do not overlap zero. Mean effect sizes across all retained studies were estimated using random-effects models [48]. Similarly, we computed Hedges' *g** effect sizes for belowground biomass where belowground biomass data were available. To examine if variation in the effect of vegetation on erosion reduction among studies is related to variation in relative changes in belowground biomass, we examined the relationship between erosion and belowground biomass effect sizes using a meta-regression.

To test for the influence of potential publication bias, we used three analyses. First, we tested the asymmetry of funnel plots using a regression test with the sampling variance as the predictor [49]. Second, we estimated mean effect sizes after correcting potential publication bias using the trim and fill method, which is a nonparametric data augmentation technique to estimate the number of missing studies due to the suppression of the most extreme results on one side of the funnel plot. Missing data were estimated and filled in, and mean effect sizes were re-computed (see details in [49]). Third, we computed Rosenthal's fail-safe number to determine the number of studies with no significant effect that are needed to change the significance of the meta-analysis [50]. The regression test showed that the funnel plot was significantly asymmetric (z = 3.70, p = 0.0002). Adjusting publication bias using the trim and fill method yielded a smaller but consistently significant mean effect size of 0.95 (0.21-1.69). The Rosenthal's fail-safe number was 346, higher than 5n +10, where n is the number of studies (i.e., 15) included in our analysis. Collectively, they indicate that our results were robust to publication bias. All analyses were conducted using the *metafor* package [49] in R 3.04.

DATA AND SOFTWARE AVAILIBILITY

Data from this work will be available on the GCE-LTER data portal website, https://gce-lter.marsci.uga.edu/portal/.