

**Wetland Vegetation is a Crucial Element in Suppressing Coastal Erosion**

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**(Abstract < 150 words)**

Increasing rates of sea-level rise and wave action threaten coastal human 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 are uncommon, as is the understanding of its context-dependency. Here we provide evidence from field manipulations showing the loss of wetland vegetation, regardless of disturbance size, increases the rate of land loss 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 erosion. Meta-analysis further shows that disturbances that generate plant die-off on salt marsh edges generally hasten erosion in coastal marshes and that this coastal protection function is positively correlated with the amount of belowground plant biomass. Collectively, our findings substantiate a coastal protection paradigm that incorporates preservation of shoreline vegetation and highlight local disturbances (e.g. oil spills) that kill wetland plants as agents that can accelerate coastal erosion.

**(Introduction < 500 words)**

Coastal areas will likely experience a relative rise in sea level that may exceed 1m over the next century, potentially displacing tens of millions of people<sup>1,2</sup>. This looming reality along with increases in the frequency and intensity of coastal disturbance and disasters in recent decades<sup>3,4</sup> has spurred a global discussion on how best to protect human populations and

infrastructure along our coastlines<sup>3,5</sup>. Many coastal management strategies now aim to maximize shoreline protection, minimize costs, and increase other benefits to humans (e.g. water quality enhancement, fish habitat provisioning) by strategically integrating both natural and man-made structures<sup>3,6,7</sup>. Fundamental to these hybrid designs is the expectation that natural barriers, specifically coastal wetlands, are effective in mitigating damage from disturbance and suppressing land loss from wave-induced erosion<sup>4,8</sup>. Experimental evidence from field studies supporting the wetland protection paradigm is uncommon, however, and those that have been conducted have sometimes generated conflicting results<sup>9</sup>. Furthermore, an in-depth, empirical understanding of the mechanisms that underlie this function is also limited (e.g. the relative importance of roots vs. aboveground plant material in suppressing erosion).

Geomorphological theory predicts wetland vegetation should reduce rates of shoreline erosion by dissipating wave energy<sup>10</sup>, increasing the shear strength of soils<sup>11</sup>, and influencing the elevation and morphology of the marsh edge<sup>12</sup>. 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<sup>10</sup>. Belowground roots, by promoting cohesion of the soil and increasing its shear strength, are also predicted to reduce the vulnerability of shorelines to erosion<sup>11,13</sup>. 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”<sup>9</sup>. These results have received attention in recent investigations and reviews on coastal defense<sup>14-17</sup> and resulted in the formulation of an alternative intellectual framework for coastal defense that holds wetland vegetation should be considered as a secondary, rather than a central, component in coastal defense systems and that coastal managers should think critically about current plans to invest in protecting and enhancing coastal wetlands to help defend our shorelines<sup>5</sup>.

In contrast to this emerging view, our recent study 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% (ref. 4). Recent syntheses of observational investigations in the field, in addition, contend that coastal vegetation can be effective in buffering against shoreline edge erosion<sup>10,16,17</sup>. This discussion highlights the need to resolve whether or not 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 or not significant coastal defense funds should be allocated toward salt marsh protection and augmentation.

To experimentally test if wetland vegetation presence 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 treatments effects on both lateral and vertical erosion at the salt marsh edge. To differentiate between above versus belowground plant

effects on erosion rate, and to test if the effects of wetland plants vary with experimental scale, we manipulated vegetation at three levels of plant presence (control, aboveground removal, and aboveground + belowground removal) (see Fig. 1) and at three plot sizes (2, 4, and 8m<sup>2</sup>). 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 ( $F_{2,34} = 4.80$ ,  $P = 0.0146$ ; Fig. 2A), and our experimental removal of aboveground and belowground plant material was successful for their corresponding treatments (Fig. 2B and 2C, see text S1). Lateral erosion was highest in aboveground + belowground removal treatments ( $114.19 \pm 9.42$  cm; mean  $\pm$  SE, same below), and significantly higher when compared to vegetated control treatments ( $76.76 \pm 8.91$  cm;  $P < 0.05$ ). Lateral erosion rates did not differ between aboveground + belowground removal and aboveground removal treatments, nor between aboveground removal and control treatments ( $P > 0.05$ ).

Furthermore, lateral erosion was not affected by plot size ( $F_{2,34} = 0.81$ ,  $P = 0.45$ ), and no significant interactions between vegetation presence and plot size 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 size ( $F_{2,34} = 0.24$ ,  $P > 0.05$ ), nor their

interaction ( $F_{2,34} = 0.30$ ,  $P > 0.05$ ; fig. S1).

The effect of aboveground + 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 vegetated-reduced conditions (Fig. 3), which had a significantly positive mean effect size of 1.22 (95% confidence intervals, 0.65-1.80) ( $P < 0.0001$ ), revealing a generally positive effect of vegetation on marsh edge erosion reduction. Consistent with our field experiment, the effect sizes of vegetation on erosion were significantly related to changes in belowground biomass ( $R^2 = 0.48$ ,  $P = 0.054$ ). Greater losses in belowground biomass led to stronger increases in erosion (fig. S2).

## Discussion

Our field experiment provides clear evidence that the loss of vegetation can increase wave-induced erosion of shoreline edges. The finding that vegetation mortality increased lateral erosion rate 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 baffling wave energy on shoreline edges. This result highlights live belowground plant structure as a primary factor generating shoreline protection services on salt marsh edges and emphasizes the relevance of understanding factors that influence resource allocation between above and belowground portions of wetland plants, such as eutrophication and grazing<sup>11,13</sup>.

Our synthesis of previous studies testing for impacts of vegetation on marsh edge erosion rate highlights the generality of our experimental findings. Averaged across all studies, the

presence of live plants was associated with lower rates of marsh edge erosion in both lab flume<sup>19</sup> and field studies<sup>4,21</sup> (Fig. 3). This erosion reduction effect was consistently observed in studies of different causes of vegetation loss (Fig. 3): studies using experimental removal of re-growing vegetation<sup>19</sup> and those on vegetation losses due to grazing<sup>22</sup>, oiling<sup>4</sup> and eutrophication<sup>13</sup> all observed such an effect. Consistent with our experimental findings, the presence of live belowground plant structures appears to be a primary mechanism by which marsh plants suppress lateral erosion, as increases in erosion are positively related with reduction in belowground biomass (fig. S2). The complementary findings of our experiment and meta-analyses validate the long-held perception that wetland plants protect shorelines from lateral erosion and thus act to suppress loss of land on its seaward edge.

These results contrast with the Texas study<sup>9</sup> that suggests that vegetation does not enhance marsh stability. Although our field experimental approaches were similar (vegetation removal), we suggest two differences explain contrasting results. First, we measured erosion as both the lateral retreat of the escarped marsh edge and as vertical erosion of the marsh surface. In our experiment, we found large impacts of plant presence on lateral erosion, but not vertical erosion. By contrast, Feagin et al. assessed impacts of plant presence on erosion in the field only by measuring vertical erosion of the marsh surface<sup>3</sup>, and thus likely missed what we observed as the primary erosional response. Second, our experiment ran for more than twice as long (36 versus 15 months). This ensured that there was near complete mortality of belowground roots in our experiment, and may have allowed ecogeomorphic feedbacks<sup>23,24</sup> to become reinforced, processes that may not have been 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 erosion rate. Enhanced erosion can, in turn, negatively affect the survival and growth of plants ahead of the erosive front<sup>4</sup> and even create or enhance a persistent positive geomorphic feedback<sup>4,14</sup>, 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<sup>25</sup> and North American salt marshes<sup>23</sup>.

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<sup>26,27</sup>. However, processes that cause vegetation loss on the edge of wetlands, such as food-web interactions (e.g. trophic cascades, runaway grazing), increased physical or chemical stress (e.g., pollution, 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. Not



accounting for the potential for 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 underestimating the destructive impacts of grazing that is now common throughout many Western Atlantic salt marshes<sup>26</sup>.

Given these findings, it is imperative that we continue integrating preservation and enhancement of coastal wetlands into our shoreline defense strategies to protect against wave-induced erosion<sup>5</sup>. This should involve both conservation of existing wetlands and active restoration of coastal wetlands on degraded shorelines. Key for effectively integrating wetland vegetation into coastal defense strategies will be unraveling the functional relationship of this now confirmed coastal-wetland-shoreline protection paradigm (i.e. when and where wetlands provide protection 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 ever more energetic seas.

## **Methods (< 3000 words)**

### **Field experiment**

We conducted our experiment from August 2010 to October 2013 in *Spartina alterniflora*-dominated salt marshes fringing the intercoastal waterway (ICW) in Marineland, Florida (29°40'52.56"N, 81°13'26.85"W). 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<sup>20</sup>: an escarped,  $\sim 90^\circ$  edge (40-60cm in height) with exposed rhizomes (Fig 1). This ecosystem edge profile is similar to that of eroding Gulf Coast marshes both in the Feagin et al. experimental study<sup>3</sup> and in the BP-DWH oil impact investigation<sup>4</sup> and the vertical angle of the edges in this study did not vary among treatments (mean =  $82^\circ \pm 4.5^\circ$ ,  $P = 0.43$ ). Second, we found replicate sites with statistically similar slopes over the first 3m 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 (fig. S4). Specifically, the mean slope and fetch were  $0.093 (\pm 0.021, \text{standard deviation})$  and  $174 (\pm 9) \text{ m}$ , 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 2,000m stretch of marsh edge), all replicates were exposed to a very similar frequency and amplitude of both wind- and boat-generated waves (R. Gleeson, *personal communication*). The average tidal range in this area of the ICW is  $\sim 0.76 \text{ m}$ , the marsh surface is  $\sim 10 \text{ cm}$  above the mean water level, and boats are the primary generator of waves in this system.

To investigate the impact of vegetation presence on marsh edge erosion rate, we set up a factorial experiment with plot size and plant presence as factors. There were three levels of plot size (2, 4 and  $8\text{m}^2$ : 1, 2, and 4m parallel to marsh edge  $\times$  2m perpendicular to marsh edge) and three levels of plant presence (control, aboveground removal, and aboveground + belowground

removal). We chose these plot sizes 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 2-4m apart and haphazardly assigned to each plot size 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 50×50cm quadrats) and ratio of dead:live rhizomes in marsh cores in each plot using established methods<sup>4</sup> 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 0.5cm diameter PVC stakes 50cm into the substrate at 0.25m increments along the marsh edge in each plot. To ensure proper orientation of subsequent erosion measurements, we installed 3cm diameter PVC pipes along the medial line of each plot, perpendicular to the shoreline, at three positions: the leading edge of the marsh, 1m from the leading edge, and 2m from the leading edge. After three years, we quantified lateral erosion by measuring the distance between the initial edge and new edge every 25cm 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 + belowground removal plot in fig. S3) (refs. 4,28). 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 pushing 0.5cm diameter PVC stakes 50cm into the substrate 10 cm from the marsh edge, notching the marsh surface soil interface 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.

We used a two-way ANOVA to examine the effects of plot size 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. Differences were considered significant at the level of  $P < 0.05$ . All statistical analysis was performed using R 3.04 (ref. 29).

## **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<sup>16,17,30</sup>, 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 below-ground 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.

We computed Hedges'  $g^*$  effect sizes<sup>31</sup>, a measure of the unbiased, standardized mean

274 difference in erosion rate between vegetation-reduced and vegetated treatments for each study. A  
275 positive effect size indicates the measure of erosion was lower in the presence than absence of  
276 vegetation in the study. Effect sizes are considered significant if their 95% confidence intervals  
277 do not overlap zero. Mean effect sizes across all retained studies were estimated using  
278 random-effects models<sup>31</sup>. Similarly, we computed Hedges'  $g^*$  effect sizes for belowground  
279 biomass where belowground biomass data were available. To examine if variation in the effect  
280 of vegetation on erosion reduction among studies is related to variation in relative changes in  
281 belowground biomass, we examined the relationship between erosion and belowground biomass  
282 effect sizes using a meta-regression.

283         To test for the influence of potential publication bias, we used three analyses. First, we  
284 tested the asymmetry of funnel plots using a regression test with the sampling variance as the  
285 predictor<sup>32</sup>. Second, we estimated mean effect sizes after correcting potential publication bias  
286 using the trim and fill method, which is a nonparametric data augmentation technique to estimate  
287 the number of missing studies due to the suppression of the most extreme results on one side of  
288 the funnel plot. Missing data were estimated and filled in, and mean effect sizes were  
289 re-computed (see details in ref. 32). Third, we computed Rosenthal's fail-safe number to  
290 determine the number of studies with no significant effect that are needed to change the  
291 significance of the meta-analysis<sup>33</sup>. The regression test showed that the funnel plot was  
292 significantly asymmetric ( $z = 3.70$ ,  $P = 0.0002$ ). Adjusting publication bias using the trim and fill  
293 method yielded a smaller but consistently significant mean effect size of 0.95 (0.21-1.69). The  
294 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<sup>32</sup> in R 3.04.

## References

1. United Nations Environment Programme. Marine and Coastal Ecosystems and Human Wellbeing: A Synthesis Report Based on the Findings of the Millennium Ecosystem Assessment. UNEP, Nairobi, Kenya (2006).
2. K. K. Arkema, *et al.*, Coastal habitats shield people and property from sea-level rise and storms. *Nature Clim. Change* **3**, 913–918 (2013).
3. E. B. Barbier, *et al.*, Coastal ecosystem-based management with nonlinear ecological functions and values. *Science* **319**, 321-323 (2008).
4. B. R. Silliman, *et al.*, Degradation and resilience in Louisiana salt marshes after the BP–Deepwater Horizon oil spill. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 11234-11239 (2012).
5. R. A. Feagin, *et al.*, Shelter from the storm? Use and misuse of coastal vegetation bioshields for managing natural disasters. *Conserv. Lett.* **3**, 1-11 (2010).

6. N. Peyronnin, *et al.*, Louisiana's 2012 coastal master plan: overview of a science-based and publicly informed decision-making process. *J. Coast. Res.* **67**, 1-15 (2013).

7. C. M. Duarte, I. J. Losada, I. E. Hendriks, I. Mazarrasa, N. Marbà, The role of coastal plant communities for climate change mitigation and adaptation. *Nature Clim. Change* **3**, 961-968 (2013).

8. A. E. Sutton-Grier, K. Wowk, H. Bamford, 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 (2015).

9. R. Feagin, S. Lozada-Bernard, T. Ravens, I. Möller, K. Yeager, A. Baird, Does vegetation prevent wave erosion of salt marsh edges? *Proc. Natl. Acad. Sci. U.S.A.* **106**, 10109-10113 (2009).

10. I. Möller, *et al.*, Wave attenuation over coastal salt marshes under storm surge conditions. *Nat. Geosci.* **7**, 727-731 (2014).

11. N. C. Howes, *et al.*, Hurricane-induced failure of low salinity wetlands. *Proc. Natl. Acad. Sci. U.S.A.* **107**, 14014-14019 (2010).



12. G. Mariotti, S. Fagherazzi, A numerical model for the coupled long-term evolution of salt marshes and tidal flats. *J. Geophys. Res. Earth* **115**, F01004 (2010).
13. L. A. Deegan, *et al.*, Coastal eutrophication as a driver of salt marsh loss. *Nature* **490**, 388-392 (2012).
14. J. van de Koppel, D. van der Wal, J. P. Bakker, P. M. Herman. Self-organization and vegetation collapse in salt marsh ecosystems. *Am. Nat.* **165**, E1-E12 (2005).
15. M. Marani, A. d'Alpaos, S. Lanzoni, M. Santalucia, Understanding and predicting wave erosion of marsh edges. *Geophys. Res. Lett.* **38**, L21401 (2011).
16. C. C. Shepard, C. M. Crain, M. W. Beck, The protective role of coastal marshes: a systematic review and meta-analysis. *PLoS ONE* **6**, e27374 (2011).
17. K. B. Gedan, M. L. Kirwan, E. Wolanski, E. B. Barbier, B. R. Silliman, The present and future role of coastal wetland vegetation in protecting shorelines: answering recent challenges to the paradigm. *Clim. Change* **106**, 7-29 (2011).
18. A. H. Altieri, M. D. Bertness, T. C. Coverdale, E. E. Axelman, N. C. Herrmann, P. L. Szathmary, Feedbacks underlie the resilience of salt marshes and rapid reversal of

consumer-driven die-off. *Ecology* **94**, 1647-1657 (2013).

19. H. Coops, N. Geilen, H. J. Verheij, R. Boeters, G. van der Velde, Interactions between waves, bank erosion and emergent vegetation: an experimental study in a wave tank. *Aquat. Bot.* **53**, 187-198 (1996).

20. S. Francalanci, M. Bondoni, M. Rinaldi, L. Solari, Ecomorphodynamic evolution of salt marshes: Experimental observations of bank retreat processes. *Geomorphology* **195**, 53-65 (2013).

21. C. Benner, P. Knutson, R. Brochu, A. Hurme, Vegetative erosion control in an oligohaline environment Currituck Sound, North Carolina. *Wetlands* **2**, 105-117 (1982).

22. T. C. Coverdale, C. P. Brisson, E. W. Young, S. F. Yin, J. P. Donnelly, M. D. Bertness, Indirect human impacts reverse centuries of carbon sequestration and salt marsh accretion. *PLoS ONE* **9**, e93296 (2014).

23. G. Mariotti, S. Fagherazzi, Critical width of tidal flats triggers marsh collapse in the absence of sea-level rise. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 5353-5356 (2013).

24. M. L. Kirwan, A. B. Murray, W. S. Boyd, Temporary vegetation disturbance as an

379 explanation for permanent loss of tidal wetlands. *Geophys. Res. Lett.* **35**, L05403 (2008).

381 25. D. Van der Wal, A. Wielemaker-Van den Dool, P. M. Herman, Spatial patterns, rates and  
382 mechanisms of saltmarsh cycles (Westerschelde, The Netherlands). *Estuar. Coast. Shelf Sci.* **76**,  
383 357-368 (2008).

385 26. B. R. Silliman, J. Van de Koppel, M. D. Bertness, L. E. Stanton, I. A. Mendelssohn, Drought,  
386 snails, and large-scale die-off of southern US salt marshes. *Science* **310**, 1803-1806 (2005).

388 27. C. Angelini, B. R. Silliman, Patch size-dependent community recovery after massive  
389 disturbance. *Ecology* **93**, 101-110 (2012).

391 28. G. McClenachan, R. E. Turner, A. W. Tweel, Effects of oil on the rate and trajectory of  
392 Louisiana marsh shoreline erosion. *Environ. Res. Lett.* **8**, 044030 (2013).

394 29. R Core Team, R: A Language and Environment for Statistical Computing. R Foundation for  
395 Statistical Computing, Vienna, Austria (2013).

397 30. M. L. Pinsky, G. Guannel, K. K. Arkema, Quantifying wave attenuation to inform coastal  
398 habitat conservation. *Ecosphere* **4**, art95 (2013).

31. M. Borenstein, L. V. Hedges, J. P. Higgins, H. R. Rothstein. Introduction to Meta-Analysis.  
John Wiley & Sons (2009).

32. W. Viechtbauer. Conducting meta-analyses in R with the metafor package. *J. Stat. Softw.* **36**,  
1-48 (2010).

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## **Author contributions**

BS, QH, CA, MK, PD, JB, JN, JvdK wrote the paper; BS, CA and JN designed study, QH and  
BS analyzed data.

## **Competing interests**

The authors declare that they have no competing interests.

## **Additional information**

Supplementary information is available for this paper:

Text S1. Treatment effects on plant cover and rhizomes in the field experiment.

421 Fig. S1. Vertical erosion rates in each plant presence x plot size treatment.

422 Fig. S2. Meta-regression of the effect sizes of vegetation on erosion against relative changes in

423 belowground biomass.

424 Fig. S3. Experimental field site and photographs showing different experimental treatments

425 Fig. S4. Map of the site where the experiment took place.

426

## FIGURE LEGENDS

**Fig. 1. Photographs showing the experiment.** (A-C) Representative experimental plots. (A) Control, (B) aboveground removal belowground removal, and (C) aboveground removal only. Note that the marsh in front of and behind the first white marker pole in aboveground+belowground removal plots has already collapsed while in aboveground removal and control plots the marsh is still intact. Photos were taken one year after the beginning of the experiment. (D-E) Representative photographs showing wave exposure on marsh borders (D) and substantial erosion in aboveground+belowground removal treatments three years after the experiment began (E).

**Fig. 2. Summary of the results of the field experiment.** (A) Erosion rates on the marsh edge, (B) plant cover, and (C) proportional rhizomes dead in each plant presence  $\times$  plot size 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 proportion of dead rhizomes ( $P < 0.001$ ) and while neither bed size alone nor its interaction with vegetation removal affected those vegetation variables or marsh edge erosion ( $P > 0.45$  in all cases).

**Fig. 3. Synthesis of field and laboratory studies on salt marsh vegetation loss and marsh edge erosion.** All study species were *Spartina alterniflora*, except that Coops et al. (1996) examined *Scirpus lacustris* (the lower one) and *Phragmites australis* (the upper one) and that Benner et al. (1982) examined a mixed group of grasses and sedges. Data points and error bars

448 are effect sizes (Hedges'  $g^*$ ) and 95% confidence intervals. Positive effect sizes indicate  
449 vegetation reduces erosion. Effect sizes are significant if their 95% confidence intervals do not  
450 overlap zero. Although five of the 15 comparisons had an insignificant effect size, three were  
451 actually reported as being significantly positive in the original studies (only our more  
452 conservative test found them to be insignificant).

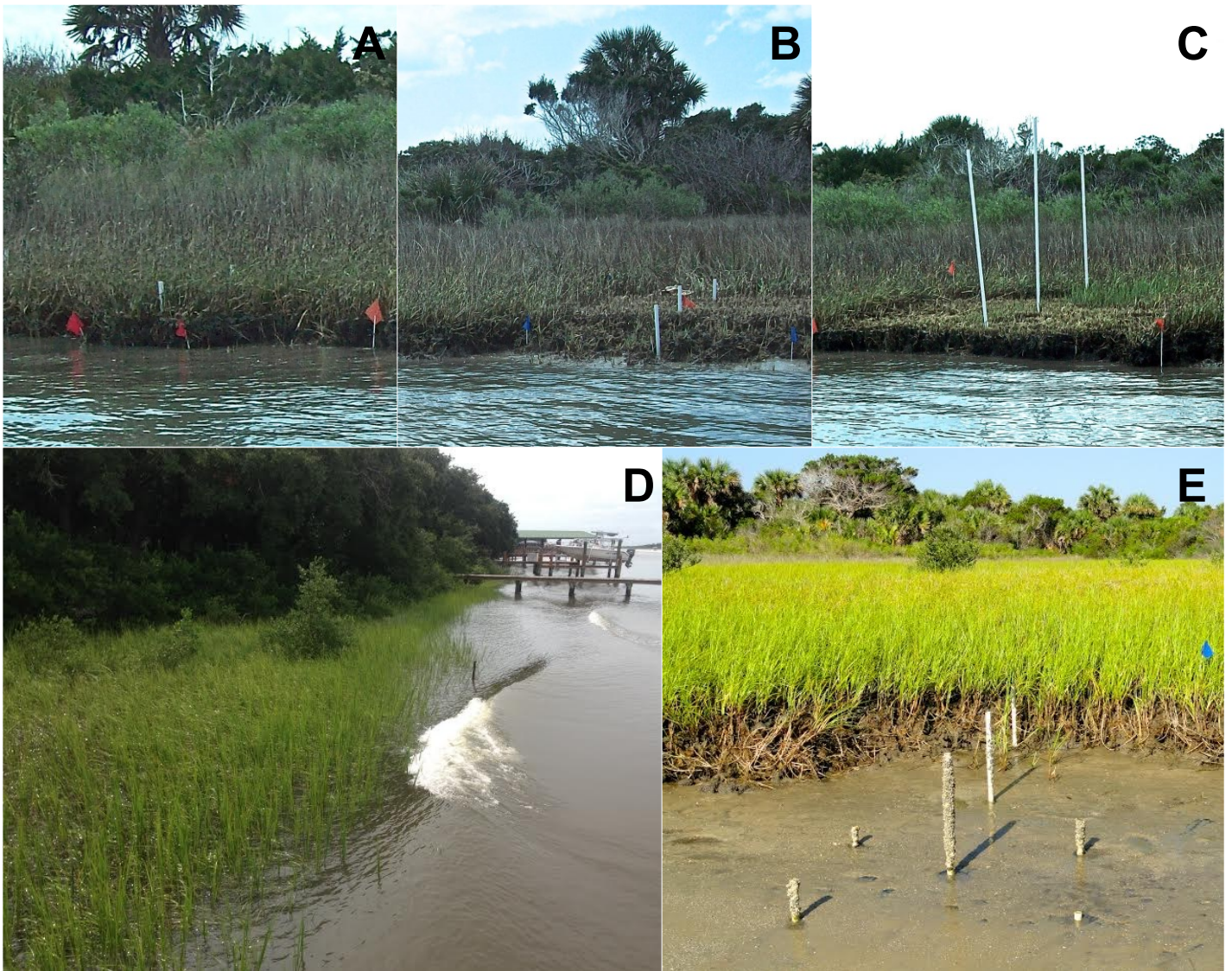
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454 **Figures**

455 **Figure 1**

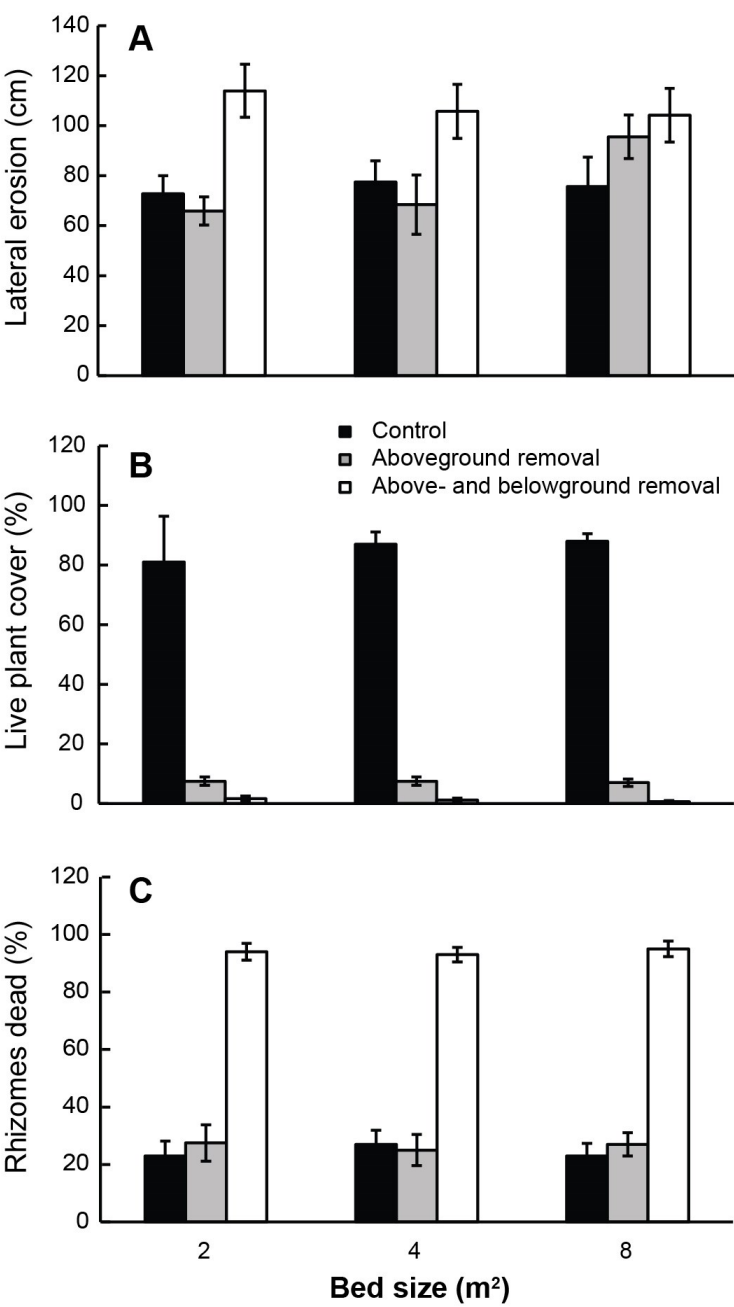
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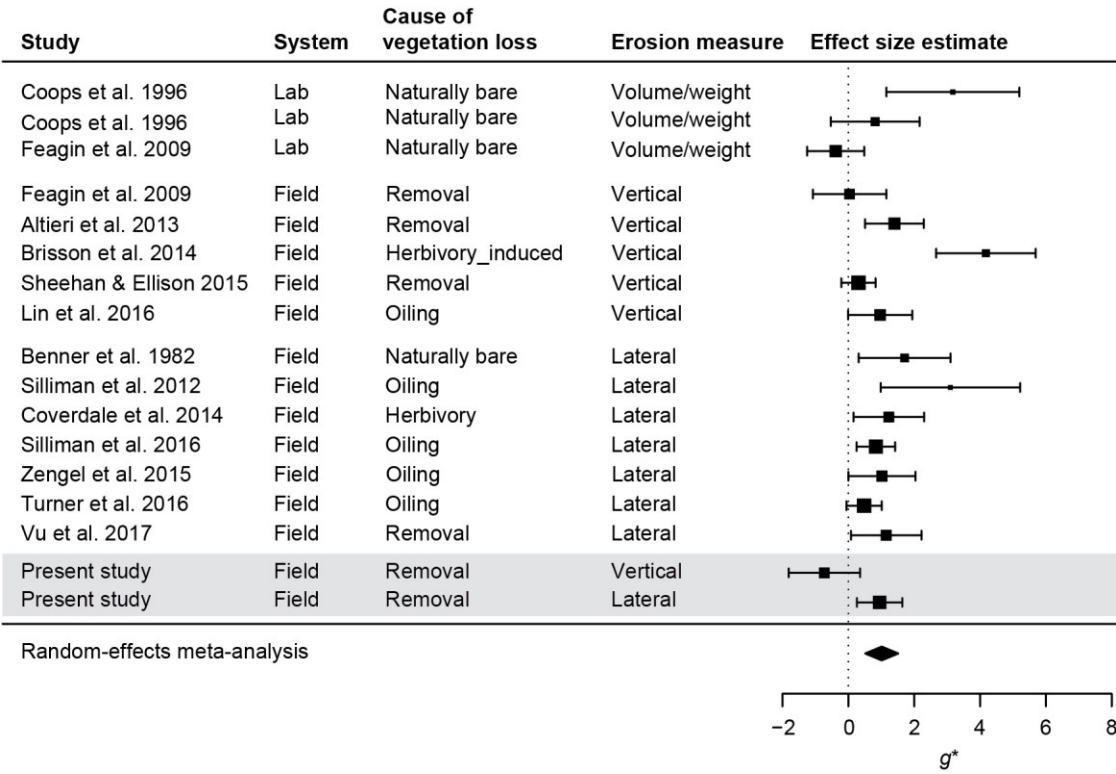


458     Figure 2.



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460      Figure 3.



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## Supplementary Materials

### Text S1. Treatment effects on plant cover and rhizomes in the field experiment

Generalized linear models (GLM) were used to examine the individual and interactive effects of plot size 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 size and plant presence treatments and their interactions were tested by comparing the resulting deviances to Wald  $\chi^2$  test statistics using the Type II sum of squares in R *car* package<sup>30,31</sup>.

As expected, aboveground removal significantly eliminated live plant cover in both aboveground and aboveground + belowground removal treatments ( $df = 2$ ,  $\chi^2 = 368.2$ ,  $P < 0.001$ ; Fig. 2B). Average live plant cover in control treatments was  $85.33 \pm 5.03\%$ , while in aboveground and aboveground + belowground removal treatments live plant cover was  $< 10\%$ . Neither plot size ( $df = 2$ ,  $\chi^2 = 0.20$ ,  $P = 0.82$ ) nor the interaction between plant presence and plot size ( $df = 4$ ,  $\chi^2 = 0.27$ ,  $P = 0.90$ ) affected live aboveground plant cover. The proportion of dead rhizomes, in addition, was significantly greater in aboveground + belowground removal treatments that received regular herbicide application ( $df = 2$ ,  $\chi^2 = 260.2$ ,  $P < 0.001$ ; Fig. 2C), indicating this method for killing belowground plant structures was effective. No effect was found of plot size ( $df = 2$ ,  $\chi^2 = 0.01$ ,  $P = 1.00$ ). While the proportion of dead rhizomes in cores was typically 10-30% in control and aboveground removal treatments, it was  $> 90\%$  in all

484 aboveground + belowground removal treatments. No interaction between plant presence and plot  
485 size treatments on rhizome mortality was found ( $df = 4$ ,  $\chi^2 = 0.90$ ,  $P = 0.92$ ).

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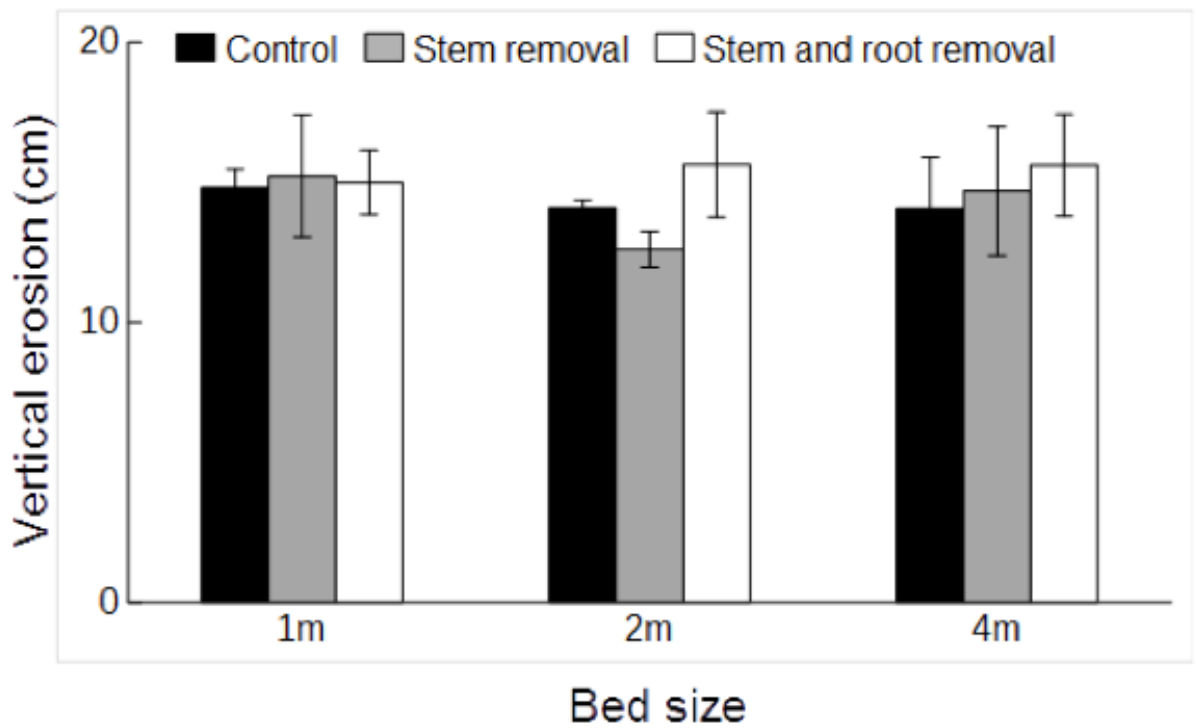
487 30. Ø. Langsrud, ANOVA for unbalanced data: Use Type II instead of Type III sums of squares.  
488 *Stat. Comput.* **13**, 163-167 (2003).

489

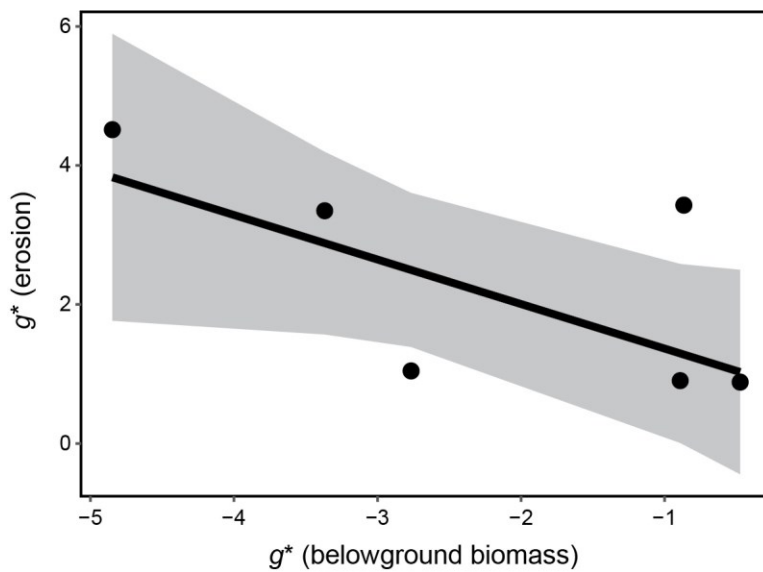
490 31. J. Fox, H. S. Weisberg, An R Companion to Applied Regression, second edition. Sage  
491 Publications (2010).

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**Fig. S1.** Vertical erosion rates in each plant presence x plot size treatment. Shown are means and SEs ( $n = 4-5$ ).



**Fig. S2** Meta-regression of the effect sizes of vegetation on erosion against relative changes in belowground biomass. Negative  $g^*$  (belowground biomass) indicates reduction in belowground biomass, and positive  $g^*$  (erosion) indicates that higher erosion rate in vegetation-reduced treatments than in control treatments. The meta-regression model is nearly significant ( $R^2 = 0.48$ ,  $P = 0.054$ ). Shaded areas are 95% confidence intervals.



**Fig. S3.** Experimental field site and photo showing, from left to right, (1) 1x2m aboveground + belowground removal, (2) 1x2 m control plot, (3) 2x2m aboveground removal, and (4) 2x2m aboveground+belowground removal. Note that the escarped edge indicates that the shoreline is already eroding and that there are clumps of marsh eroding from the aboveground + belowground removal plot.



**Fig. S4.** Map of the ICW ~ 30km south of St. Augustine Florida where the experiment took place. Note consistent width of the ICW in this area. Yellow line indicates the area and the side of the ICW where this study took place.

