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RESEARCH ARTICLE

Large grazers suppress a foundational plant and reduce soil carbon concentration in eastern US saltmarshes

S. J. Sharp[1] | **K. E. Davidson**[2] | **C. Angelini**[3,4] | **H. S. Fischman**[3] | **S. Pennings**[5] | **M. S. Fowler**[2] | **J. N. Griffin**[2]

[1]Department of Entomology, University of Maryland, College Park, Maryland, USA

[2]Department of Biosciences, Swansea University, Swansea, UK

[3]Department of Environmental Engineering Sciences, Engineering School for Sustainable Infrastructure and the Environment, University of Florida, Gainesville, Florida, USA

[4]Center for Coastal Solutions, University of Florida, Gainesville, Florida, USA

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

Correspondence
S. J. Sharp
Email: sjsharp@umd.edu

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Abstract

1. Large grazers modify vegetated ecosystems and are increasingly viewed as keystone species in trophic rewilding schemes. Yet, as their ecosystem influences are context-dependent, a crucial challenge is identifying where grazers sustain, versus undermine, important ecosystem properties and their resilience.
2. Previous work in diverse European saltmarshes found that, despite changing plant and invertebrate community structure, grazers do not suppress below-ground properties, including soil organic carbon (SOC). We hypothesised that, in contrast, eastern US saltmarshes would be sensitive to large grazers as extensive areas are dominated by a single grass, *Spartina alterniflora*. We predicted that grazers would reduce above- and below-ground *Spartina* biomass, suppress invertebrate densities, shift soil texture and ultimately reduce SOC concentration.
3. We tested our hypotheses using a replicated 51-month large grazer (horse) exclusion experiment in Georgia, coupled with observations of 14 long-term grazed sites, spanning ~1000 km of the eastern US coast.
4. Grazer exclusion quickly led to increased *Spartina* height, cover and flowering, and increased snail density. Changes in vegetation structure were reflected in modified soil texture (reduced sand, increased clay) and elevated root biomass, yet we found no response of SOC. Large grazer exclusion also reduced drought-associated vegetation die-off.
5. We also observed vegetation shifts in sites along the eastern US seaboard where grazing has occurred for hundreds of years. Unlike in the exclusion experiment, long-term grazing was associated with reduced SOC. A structural equation model implicated grazing by revealing reduced stem height as a key driver of reduced soil organic carbon.
6. *Synthesis*: These results illustrate the context dependency of large grazer impacts on ecosystem properties in coastal wetlands. In contrast to well-studied European marshes, eastern US marshes are dominated and structured by a single foundational grass species resulting in vegetation and soil properties being more sensitive to grazing. Coastal systems characterised by a single foundation species

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might be inherently vulnerable to large grazers and lack resilience in the face of other disturbances, underlining that frameworks to explain and predict large grazer impacts must account for geographic variation in ecosystem structure.

KEYWORDS
biodiversity, blue carbon, ecosystem resilience, horses, multifunctionality, *Spartina alterniflora*, *Sporobolus alterniflorus*, trophic cascade

1 | INTRODUCTION

Large herbivores, particularly equids and bovids, exert top-down control on the structure and diversity of vegetated ecosystems (Augustine & Frank, 2001; Waldram et al., 2008). Large grazers were likely more abundant and functionally relevant in the past than in modern ecosystems (Malhi et al., 2016), leading to calls for their inclusion in rewilded systems (Svenning et al., 2016). Large equids form free-roaming, wild or semi-wild populations in many parts of the world, and may already be, at least partially, functionally replacing extinct herbivorous megafauna (Lundgren et al., 2018). Yet, while large grazers are often associated with increased landscape heterogeneity and vegetation diversity (Oldén & Halme, 2016; Waldram et al., 2008), in some contexts they shift communities to non-desirable states (e.g. low vegetation cover; Hempson et al., 2019; McSherry & Ritchie, 2013). Systems with low plant diversity may be especially sensitive to large grazers, particularly when combined with other stressors such as invasive species or climatic extremes because other plant species are not present to replace those targeted by grazers (Biggs et al., 2020). While there is growing understanding of context-dependent effects of large grazers on terrestrial systems (Maestre et al., 2022), progress in coastal wetlands such as saltmarshes has been hampered by a geographic bias in study effort and an emphasis on farmed rather than wild or semi-wild grazers (Davidson et al., 2017).

Saltmarshes are socially and economically important systems, with large biogeographic structural variation that may have implications for their responses to large grazers (Davidson et al., 2017; Yando et al., 2023). These coastal wetlands form extensively around the world's wave-sheltered temperate coastlines (Mcowen et al., 2017), where they provide multiple ecosystem services that mitigate environmental hazards, and provide material goods, recreational opportunities and wildlife habitat (Barbier et al., 2011; Costanza et al., 1997; Pétillon et al., 2023). Saltmarshes are generally characterised by high primary and secondary production, which drives much of their ecosystem service provisioning (Barbier et al., 2011). Although large grazers occur on saltmarshes in all major saltmarsh-containing regions world-wide (Gaskins et al., 2020), their impacts have been most extensively studied in European marshes (Davidson et al., 2017). European marshes host rich floral assemblages, and substantial experimental and observational research has documented that they are resistant to grazing (Elizabeth et al., 2022; Harvey et al., 2019). While grazing reduces above-ground biomass, it tends to increase plant diversity and can even increase soil carbon storage (Elschot et al., 2015; Meirland et al., 2013; Olsen et al., 2011). In comparison, the role of large grazers in structurally varied marshes elsewhere in the world has been largely neglected (Davidson et al., 2017). Saltmarshes in North America, for example, are some of the most extensive in the world, with a long history of grazing by introduced horses and other livestock dating back over 400 years (Mcowen et al., 2017). In the US, although this practice has now declined (Gedan et al., 2009; Gruenberg, 2015; Reimold et al., 1975; Smith et al., 1989), free-ranging horses and cows graze on saltmarshes on multiple barrier islands along the eastern seaboard (Gruenberg, 2015). Most studies of grazing impacts in North American saltmarshes have been purely observational, comparing neighbouring grazed and ungrazed islands (Dolan, 2002; Hay & Wells, 1991; Reimold et al., 1975), or focused strictly on plant dynamics (Furbish & Albano, 1994; Turner, 1987). Yet, previous synthesis tentatively supports a greater sensitivity of these marshes to large grazers than their European counterparts (Davidson et al., 2017).

A key issue underlying the expected sensitivity of North American marshes to large grazers—and other compounding stressors—is a lack of capacity for functional compensation at both the individual plant and community levels. Many Eastern North American saltmarshes are dominated by a single foundation species, *Spartina alterniflora* (hereafter *Spartina*), which has a powerful influence on ecosystem structure and function (Bortolus et al., 2019). This species forms some of the most productive vegetated systems on Earth, donates substantial root and leaf tissue to soil organic carbon (SOC), provides tall and dense canopies that facilitate deposition of clay particles known to enhance SOC, and supports a diversity of infauna (Altieri et al., 2007; Fagherazzi et al., 2012; Oades, 1988; Reichle, 2023). In turn, soil quality (SOC) and infaunal communities have strong effects on ecosystem functioning and resilience (Angelini et al., 2015, 2016, 2018; Bastida et al., 2021; Bertness, 1985; Carney & Matson, 2005; Daleo et al., 2007; Gittman & Keller, 2013; Griffin & Silliman, 2018; Hensel & Silliman, 2013; Holdredge et al., 2009; Silliman et al., 2005). *Spartina* shows little capacity for compensatory responses to grazing by, for example, shifting to below-ground production (Valdez et al., 2023), and is reduced or eliminated by high densities of invertebrates or vertebrates (Hensel et al., 2021; Silliman et al., 2005). Although succulents may increase in abundance following *Spartina* declines (Bertness et al., 1992), they are unlikely to functionally compensate due to their lower productivity, shorter stature, and lack of mutualistic partnership with resident invertebrates. Despite the dominance and uniqueness of *Spartina* compared with succulent replacements, few studies have investigated how grazing from large herbivores impacts *Spartina*, and how potential vegetation community shifts cascade to saltmarsh soil properties and invertebrate communities, for example crabs, snails, and mussels (Reimold et al., 1975; Turner, 1987). Furthermore, grazing takes place—in the United States and globally—in the context of changing stressors and disturbances, such as invasive species and climate change (Angelini et al., 2018; Gedan et al., 2009; Sharp & Angelini, 2016; Silliman et al., 2005). If large grazers are having strong negative effects on saltmarsh vegetation in US saltmarshes, especially given limits to their functional redundancy, they could undermine ecological stability in the face of other stressors, thereby compromising important ecosystem functions including the accumulation of SOC.

In this study, we combined experimental exclusion and a broad-scale observational survey to investigate how large grazers affect a coastal ecosystem dominated by a single foundation species: US East Coast saltmarshes dominated by *Spartina*. To test causal effects of grazers on community and ecosystem properties when combined with other stressors, we used replicated grazer exclusion plots in *Spartina* saltmarsh on Cumberland Island, Georgia, maintained over 51 months. During this period, the experimental sites underwent marsh die-off, a mass mortality of *S. partina* associated with drought and consumer pressure (Alber et al., 2008; McKee et al., 2004; Silliman et al., 2005), allowing us to explore how large grazers impact marsh 'resilience', as indicated by the capacity of marshes to maintain living *Spartina* cover in the face of die-off. We also experimentally tested how grazing influenced marsh recovery by simulating invasive hog disturbance, a common stressor of eastern US marshes (Sharp & Angelini, 2019). To evaluate the generality of experimental results and assess the effects of long-term (>100 years) grazing across a large spatial scale, we measured similar properties in 14 grazed and 12 ungrazed saltmarshes over ~1100 km of coast between Florida and Maryland, USA. We hypothesised that in contrast to well-studied European marshes, eastern US saltmarshes would be highly sensitive to large grazers due to their dependence on a single foundation grass species. Specifically, we predicted that grazers would reduce *Spartina* above- and below-ground biomass, and since these marshes lack a functional replacement for *Spartina*, grazers would reduce invertebrates, shift soil texture, and ultimately suppress SOC concentration. We further expected grazing to reduce *resilience* to other stressors such as drought and feral hog disturbance as grazing was expected to reduce plant energy reserves, leaving marshes more vulnerable to compounding disturbances. Finally, we predicted that the long-term grazed/ungrazed sites would reflect the dynamics and interactions of both fast processes whose rates change or saturate over time (e.g. plant growth) and slow processes that may require several years to become detectable (e.g. slow change in soil carbon), while the measurable response of short-term exclusion plots would mostly reflect fast processes but depend on the recovery rates of individual variables.

2 | METHODS

2.1 | Data collection

2.1.1 | Experimental study site

Cumberland Island is a 29 km long barrier island located off the coast of Georgia, southeast USA, at 30.85° N, 81.45° W and contains 3490 ha of saltmarsh (Dolan, 2002). Horses have roamed freely on the island since the 18th century, grazing predominantly on sand dune and saltmarsh vegetation (Dolan, 2002; Goodloe et al., 2000). The horses are unmanaged, have no natural predators, and number 150–160 (D. Hoffman, personal communication, 18 July 2019). The island is also grazed by native white-tailed deer (*Odocoileus virginianus*) and is home to invasive feral hogs (*Sus scrofa*), although populations of deer and hogs are hunted. Appropriate fieldwork permits were granted for this study by the relevant governing bodies (see Supplementary Methods: Experimental Study).

2.1.2 | Experimental study design

We studied the effect of horse grazing on saltmarsh properties by excluding large fauna from eight 5 × 5 m experimental plots with barbed wire strung between four corner posts. Each 5 × 5 m experimental plot was paired with a 5 × 5 m grazed plot, consisting of four corner posts but no barbed wire, positioned 8 m away to form a treatment block. Blocks of exclusion and grazed plots were spaced ~120 m (±60) apart. The plots were divided between two marshes lying on either side of a major creek on the southern end of the island (Figure S1a,b). The plots were erected in March 2017 using 2.5 m metal posts driven into the ground to 1 m depth and strung with three strands of high-tensile barbed wire. The plots were positioned 20 m (±5) from the nearest drainage creek, and all were initially similar in elevation, vegetation community, and faunal community. All plots were positioned in the mid-marsh zone of short- and medium-form *Spartina* (canopy height: 30–120 cm), the dominant species in southeastern US marshes (Adam, 1990; Anderson & Treshow, 1980) where the horses mostly graze (Dolan, 2002). We also established six unmarked reference points, plotted mid-way between each block. Grazing indicators were assessed at these points and compared with grazing indicators at the grazed plots, to ensure the corner posts were not acting as an attractant or repellent to the horses or other fauna (e.g. marsh periwinkle snails, *Littoraria irrorata*). We found no differences between reference points and grazed plots, therefore the reference points were not included in any further analyses. Although we did not directly compare grazing intensity between plots at the initiation of the experiment, we did detect a difference in hoofprint density between the two marshes (Figure S1a) and included plot pair and location as a random variable in all models.

Plots were sampled 0, 7, 13, 18 and 51 months after the experiment was initiated (March 2017 to June 2021). At 0 and 7 months, we sampled from three 0.3 × 0.3 m quadrats distributed haphazardly within each plot and used the mean value of every variable for each plot. After 1 year, each plot was instead divided into four quarters (a–d), and each plot quarter was sampled independently to better account for within-plot variability (Figure S1c). We extracted one soil core (7 cm diameter × 15 cm depth) from each quadrat that was stored on ice for subsequent analysis. Within each plot, the outer 0.5 m edge was used as a buffer zone and was never sampled. We collected data on sediment properties (elevation, redox potential, porewater salinity and pH, soil organic carbon, soil texture and soil moisture), plant properties (living cover, dead cover, proportional cover of *Spartina*, *Salicornia* sp., hereafter *Salicornia* (see Supplementary Methods: Experimental study regarding taxonomy), and *Distichlis spicata*, average stem height, stem density, flowering stem density, root biomass, benthic algae density), the invertebrate community (mussel, snail, and crab density), and grazing intensity (hoofprints, dung piles, and stem damage) as detailed in Table S1. In the absence of direct measurements of SOC, we used the equation from Craft et al. (1991) to convert loss on ignition to SOC, as it was originally parameterised in marshes in the study region (North Carolina) and parameterised global equations do not perform as well. Note that we measure the concentration of soil organic carbon (%), not accumulation rate or per unit area store of carbon which require additional consideration of bulk density and accretion rate (Neubauer et al., 2002). We assess the effects of grazers by comparing the grazed and ungrazed plots at the final time point. We focus on the 51-month data as it integrates effects of grazing over a longer time, thus potentially allowing treatment effects on slower-responding variables (e.g. SOC) to be detected. Although there was considerable time between 18- and 51-month sampling campaigns, including expected background variability in environmental conditions, there was little evidence of unusual extreme events (Figure S2). Furthermore, our random assignment of treatments to experimental plots means that any interaction with background environmental variability through time represents part of the natural and long-term context of the study. We saw no evidence of other large grazers (e.g. deer or hogs) in grazed or reference plots, suggesting horses were the only grazers accessing these marshes. Full details of field and laboratory methods are provided in the Supporting Information.

2.1.3 | Ecosystem resilience

After the start of the experiment, some areas of the study marshes were affected by saltmarsh die-off, a loss of vegetation associated with drought (Alber et al., 2008). Therefore, on every visit, we visually assessed the plot for devegetation of all plant species and gave a score of 0–3 for die-off severity (0: 0%–25% bare ground, 1: 26%–50% bare, 2: 51%–75% bare, 3: 76%–100% bare), which we distinguished from grazing, which left plants alive, by whole plant browning and death. This allowed an indication of saltmarsh resilience to die-off under different grazing treatments. This metric of resilience assesses the general state of vegetation following die-off but does not distinguish die-off impact (resistance) and recovery. Although we do not know the cause of the die-off or when it began, there was a period of severe drought (May–June 2017) that likely influenced die-off severity (Figure S3).

To investigate saltmarsh capacity for recovery under different grazing treatments, we simulated hog damage within a 1 × 1 m area in one-quarter of each plot in October 2017. Although invasive hogs are kept at low densities on Cumberland Island by hunting and did not appear to forage at the study sites, they commonly forage and wallow in marshes elsewhere on barrier islands along the eastern seaboard (Barrios-Garcia & Ballari, 2012; Sharp & Angelini, 2019). Invasive feral hogs damage standing biomass and soil structure through their trampling, rooting, and wallowing activities (Sharp & Angelini, 2016, 2019). In the simulated disturbance, we uprooted and discarded 20 clumps of *Spartina* to simulate root herbivory and two researchers vigorously trampled on a 1 × 1 m square of 1.25 cm plastic mesh for 60 s to simulate wallowing. Data were collected from these 'damaged' quadrats (located in quarter 'b' of each plot) six and 12 months after simulated disturbance and were analysed separately from data collected in undisturbed quadrats (Figure S1b). We measured 'recovery' as the natural log-transformed response ratio (*log*(*RR*), Equation 1) of vegetation metrics (plant cover, stem height, and biomass) in hog-disturbed plots relative to undisturbed reference plots in each grazed or ungrazed treatment block at 6 and 12 months after hog disturbance treatment; recovery was calculated for each plot.

$$\log(\mathrm{RR}) = \ln\left(\frac{\text{Vegetation metric from plots with pig damage}}{\text{Vegetation metric from plots without pig damage}}\right) \quad (1)$$

2.1.4 | Observational study

To assess the variability of grazing effects across the region, we sampled 26 marshes at nine sites (islands or nature reserves) along ~1100 km of coast between 30.52° N (Florida) and 38.30° N (Maryland) during both March and October 2017 (Figure 1, Table S2, see Supplementary Methods: Observational Study for permit information). We identified 14 marshes across five sites that were grazed by large ungulates, then selected 12 ungrazed marshes (seven sites) that could act as ungrazed controls (see Table S2 for site details). When possible, grazed and ungrazed marshes were located at the same site, otherwise, we selected marshes at a nearby site (<25 km) with similar geophysical and hydrologic features (e.g. tidal characteristics, elevation, tidal creek density and protection from open ocean). We assessed the grazing intensity on each marsh as light, moderate or heavy based on visual assessment (Table S3) and information provided by site managers. All grazed marshes were grazed by horses except for one marsh grazed by cattle (Creighton Island, Georgia). We include this cattle-grazed marsh to increase sample size, and because horses and cattle are likely to have similar effects

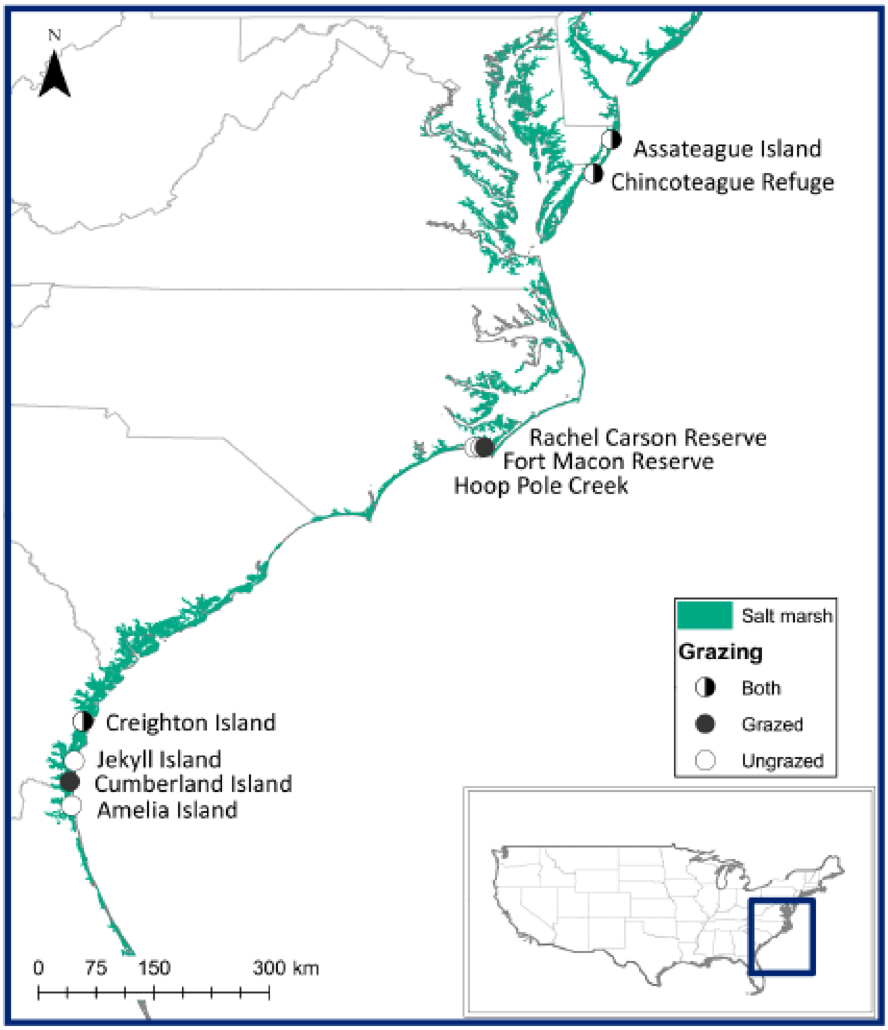

FIGURE 1 Location of observational sites along the southeast US coast. Each site contained between 2 and 5 survey marshes. See Table S2 for further details of location, grazing history, and grazing levels at the 26 surveyed marshes.

due to their similar body size, energy requirements, and grazing habits (Cymbaluk, 1990; Halls, 1970; He & Silliman, 2016; Hubbard & Hansen, 1976).

At each marsh, we surveyed two parallel transects, starting 10–20 m from the creek edge and running inland up to 100 m. At the start, midpoint and end of each transect, we surveyed a 1 × 1 m quadrat for sediment characteristics (redox potential, porewater salinity and pH, soil organic carbon, soil texture), vegetation properties, and invertebrate abundance using the same methods as the experimental study (Supplementary Methods: Observational study).

During the March 2017 surveys, we also measured vegetation and invertebrate variables in quadrats placed every 10 m along the transect to increase sample resolution of these features. In total we collected data from 308 quadrats (113 ungrazed, 57 lightly grazed, 81 moderately grazed, 57 heavily grazed) and 150 soil cores (65 ungrazed, 22 lightly grazed, 42 moderately grazed, 21 heavily grazed).

2.2 | Data analysis

To test the effect of horse grazing on ecosystem properties in both the experimental and observational study we used generalised linear mixed models (LMM) and Akaike Information Criterion (AIC) with grazing presence or grazing intensity (observational study) as predictors (see Supplementary Methods: Data Analysis for details about each analysis). Models were used for eight sediment, 13 vegetation, and five invertebrate fixed response variables. In the experimental study, blocks were treated as a random effect. In the observational study, season, creek distance, and latitude were treated as covariates and site as a random effect while grazing intensity was binned as ungrazed, light, moderate or heavy. We used binomial error families for proportional data (species presence, live and dead vegetation cover) and Gaussian families for all other data. We performed all analyses on *z*-transformed predictor variable data to allow comparison of each response on the same scale. Model assumptions were verified by inspecting residual plots for deviations from normality (graphically and using the Shapiro–Wilk test) and testing goodness-of-fit (Kolmogorov–Smirnov) of observed versus expected values. Response variables were transformed as necessary using Box–Cox transformation. We used likelihood ratio tests using maximum likelihood (ML) estimation to test the significance of each fixed effect (correcting *p*-values to control the false discovery rate within sets of soil, vegetation, plant, and invertebrate response variables within each study; Benjamini & Hochberg, 1995) and used post hoc Tukey tests for pairwise comparison of intensity levels (ungrazed, light, moderate and heavy) when grazing intensity was found to be a significant predictor.

Generally, SOC is negatively correlated with higher sand content in soils (Oades, 1988) and grazers could potentially prefer sandier, firmer substrate, driving a spurious association between grazing and SOC. To test their influence on SOC in the observational survey, we developed a global LMM and models with only soil sand content or grazing, then compared AIC to assess the best predictors of SOC. We also developed a Structural Equation Model to elucidate indirect relationships between grazing intensity, plant, invertebrate, and soil metrics (Table S4, Figure S4). We then tested the significance of added or removed pathways using tests of directed separation and evaluated global goodness-of-fit.

All statistical analyses were conducted in R Studio running R3.5.2 (R Core Team, 2019). Generalised LMMs were fitted using *lme4* (Bates et al., 2015) and R^2 values were calculated using *piecewiseSEM* (Lefcheck, 2016). We used the *emmeans* package (Lenth et al., 2019) to perform post hoc pairwise contrasts of factor levels and calculate predicted means for graphing. Non-parametric tests were conducted using the *vegan* package (Oksanen et al., 2019).

3 | RESULTS

3.1 | Experimental study

3.1.1 | Effect of grazing on community and ecosystem properties

There was no difference between grazed plots and unmarked reference points or ungrazed experimental plots at the start of the experiment for any recorded variable (Tables S5 and S6). After 51 months of grazer exclusion, there were significant changes to multiple plant properties: the exclusion of horses led to increased stem height, flowering, stem density, above- and below-ground biomass, and *Spartina* cover, but reduced *Salicornia* cover and die-off intensity of all vegetation (see Figure 2, noting that it is orientated to show the effect of grazing rather than exclusion, also see Table S7 for model outputs). We also observed an increase in clay and decrease in sand content, and higher densities of periwinkle snails, but SOC was not significantly affected by grazer exclusion.

For properties that were significantly different at final observation, we investigated their responses to grazer exclusion at each time point (0, 7, 13, 18, 51 months; contingent on data availability,

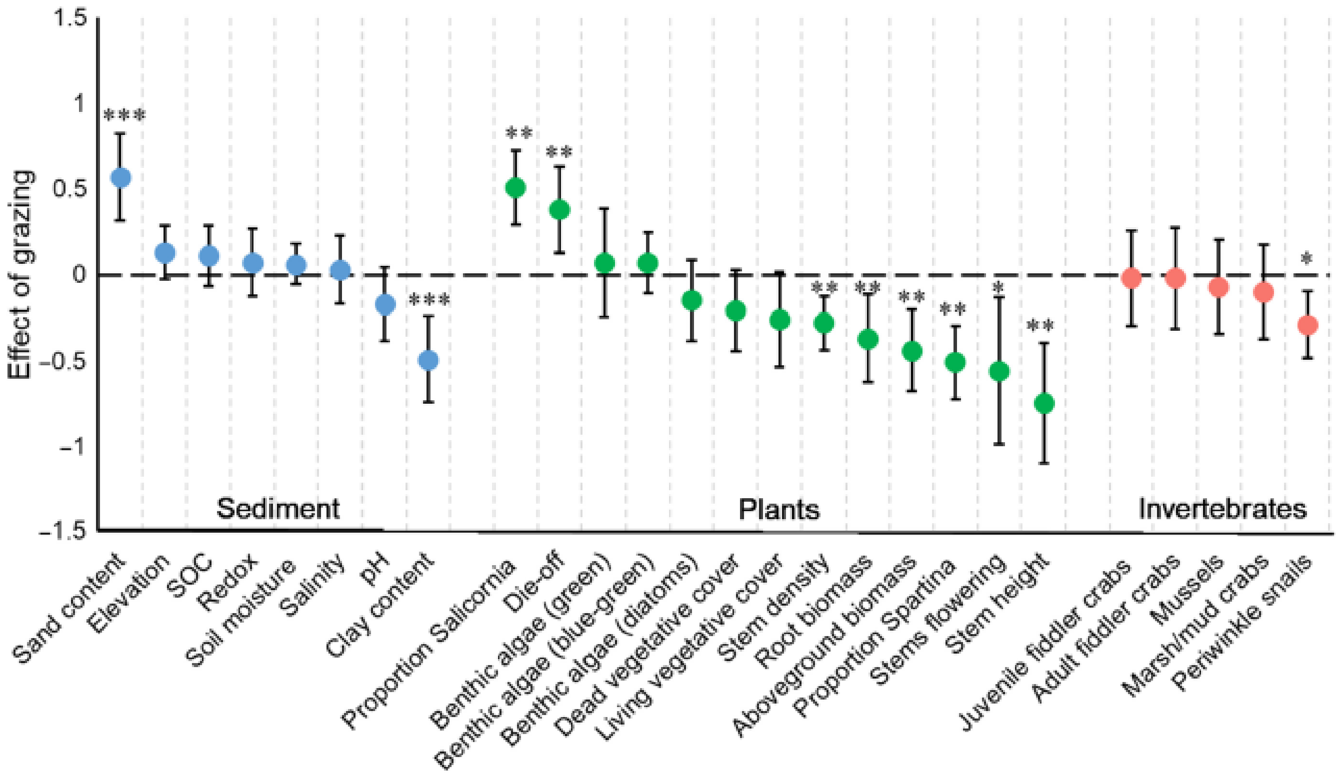

FIGURE 2 The effect of grazing horses on ecosystem properties based on data from the final sampling period (18 months after grazer exclusion for Elevation, Redox, and Flowering or 51 months after exclusion for all other data) in the grazer exclusion experiment. Points show the standardised coefficients ±95% confidence intervals (calculated on z-transformed response variable data) for the effect of grazing (in control plots) using linear mixed models. The figure is orientated to show the effect of grazing (rather than exclusion) to facilitate comparisons with observational data in Figure 4. FDR corrected-p values indicated as $^{*}<0.05$; $^{**}<0.01$; $^{***}<0.001$. SOC, soil organic carbon, accompanying statistics are reported in Table S7.

Table S8). The increase in stem height and above-ground biomass was significant after just 7 months, but stem density and the increase in relative *Spartina* cover and decrease in relative *Salicornia* cover were not apparent until 13 months, and stem flowering until 18 months (although flowering could have occurred in the first year but did not align with our monitoring). The decrease in periwinkle snail density was significant at 7 and 51 months (October and June, respectively) and may represent underlying seasonal differences in snail grazing and movement. Root biomass (aggregated and upper horizon), die-off resistance, sand content, and clay content took 51 months to diverge from grazed plots.

While simulated hog damage had enduring impacts on several key vegetation variables, large grazers do not appear to further compound these effects and hamper recovery (Figure 3, Table S9). After 12 months, hog-damaged areas in grazed and ungrazed plots did not differ, statistically, though in grazed plots stem height in hog-damaged areas had converged with undamaged areas (Figure 3, Table S9).

3.2 | Observational study

Grazing was associated with significant differences in three sediment and two plant properties, but not with any invertebrate properties (Figure 4, Table S10). Grazing was associated with higher stem density, but lower plant cover and stem height. The effects of grazing on stem density and stem height strengthened with increased grazing intensity (Figure S5, Table S11). Raw plant species composition data (Figure S6) indicate that grazing is associated with reduced *Spartina* cover and increased cover of other species (*Salicornia*, *Distichlis spicata*, *Juncus roemarianus* and *Batis maritima*), although the increased species richness and reduced probability of a grazed quadrat being 100% *Spartina* were not statistically significant (Table S11). Grazing did, however, significantly affect plant community composition, irrespective of whether a presence/absence or abundance-related community dissimilarity measure was used (PERMANOVA $F_{1,305} = 3.66$, $p = 0.039$ and $F_{1,305} = 4.89$, $p = 0.014$ for Sørensen and Bray–Curtis dissimilarity matrices, respectively). Multivariate tests of group

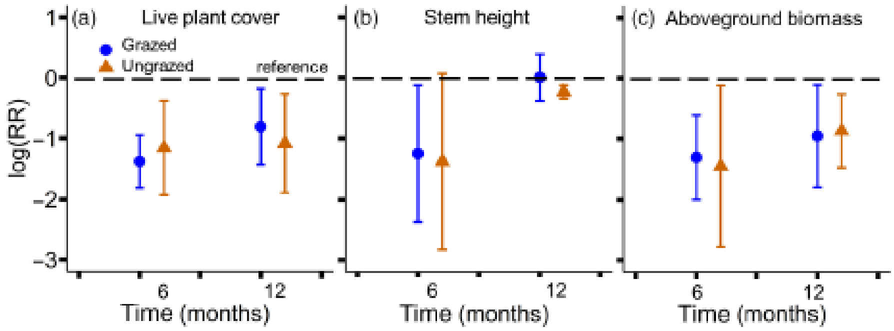

FIGURE 3 Natural log-transformed response ratio—*log*(*RR*)—of (a) live plant cover, (b) stem height of *Spartina alterniflora*, and (c) aboveground biomass recovering from simulated hog damage with reference to undamaged plots (damaged/undamaged equivalent) in grazed (blue) and ungrazed (orange) plots after 6 months and after 12 months. There are no significant differences between grazing treatments for any given time point or response variable. Points show response ratio means ±95% confidence intervals. See Table S9 for pairwise effects of hog damage in each grazing treatment. Dashed line indicated the reference level of undamaged marsh in equivalent treatments (i.e. grazed or ungrazed).

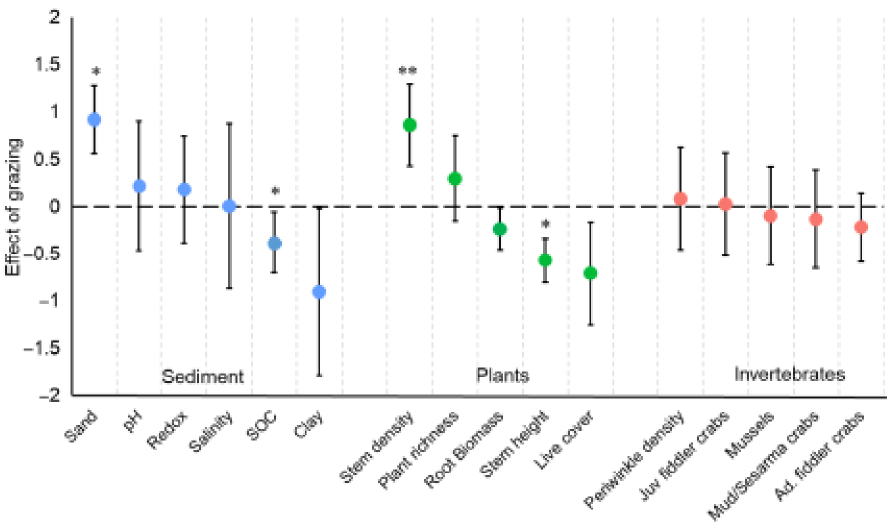

FIGURE 4 The relationship between large mammal grazing and ecosystem properties at a landscape scale. Points show the standardised coefficients ±95% confidence intervals (calculated on *z*-transformed response variable data) for the effect of grazer presence relative to ungrazed control marshes using linear mixed models. Models also controlled for season, distance from creek, and latitude as fixed effects, and marsh nested within site as a random effect. *<0.05; **<0.01-FDR corrected *p* values. SOC, soil organic carbon; Ad., adult; Juv., juvenile.

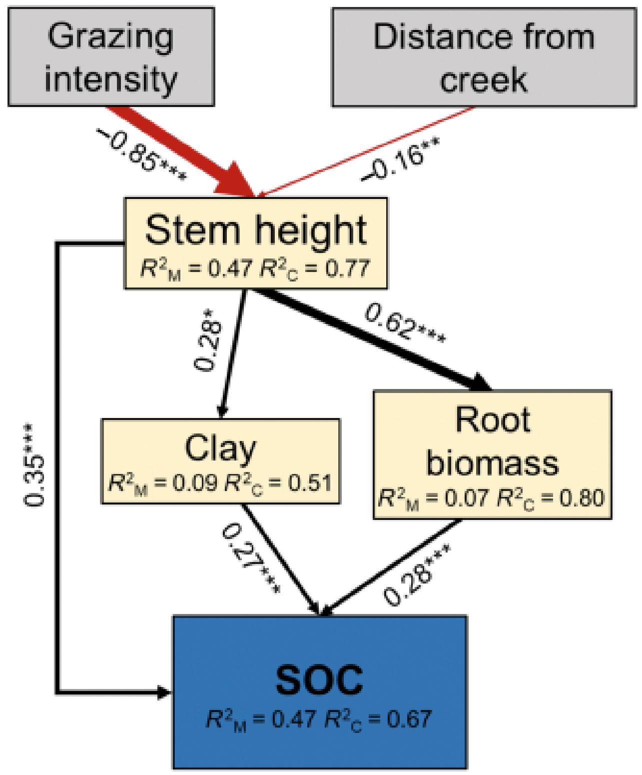

FIGURE 5 Structural equation model (SEM) showing direct and indirect effects of grazing and marsh properties on soil organic carbon (SOC). Grey boxes indicate exogenous variables, yellow boxes endogenous variables, and blue box the response variable. Arrow size directly corresponds to *z*-transformed effect size. Site was treated as a random effect. $^*p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

dispersions indicate that these differences were due to increased dispersion within grazed marshes, that is, the plant communities within grazed marshes were more dissimilar than the plant communities within ungrazed marshes (PERMDISP $F_{1,305} = 4.28$, $p = 0.044$ and $F_{1,305} = 6.79$, $p = 0.008$ for Sørensen and Bray–Curtis dissimilarity matrices, respectively).

Grazing was associated with lower SOC, but also with higher sand content. However, our experimental results provide causal evidence that grazers substantially increase sand content and decrease clay content, demonstrating they can drive—rather than simply respond to—soil texture and SOC. We also compared soil texture (sand or clay) and grazing as alternative predictors of SOC and found that grazing was consistently the best predictor (Table S12). Furthermore, our Structural Equation Model (Figure 5), which is consistent with the data (Fisher's $C = 11.038$, $p = 0.53$, $\mathrm{df} = 12$), suggests that grazing has a strong, negative indirect effect on SOC primarily by regulating *Spartina* canopy height, which in turn drives SOC loss directly and indirectly through loss of soil clay and root biomass (Figure 5).

4 | DISCUSSION

Context dependency is presumed to be common in ecological systems but identifying the underlying causes is necessary for broad understanding (Catford et al., 2022). In saltmarshes, previous research on the effects of large grazers has been dominated by studies on floristically diverse European marshes, with comparatively little known about the structural and functional consequences of large grazers in other global regions, including the extensive yet low diversity—and potentially less resistant—North American marshes. Our combined results from a grazing exclusion experiment and a large-scale observational survey build on these findings by demonstrating that large grazers affect multiple structural and functional ecosystem attributes in eastern US saltmarshes. Grazers cause reductions in above- and below-ground biomass of the foundational plant (*Spartina*), shift and disrupt vegetation towards a less productive succulent (*Salicornia*), and make soil sandier, all of which leads to soils holding lower concentrations of soil organic carbon (SOC). Although the observational study alone could not conclusively determine that horses increased sand content, our field experiment demonstrates that grazers increase sand content and reduce clay content in marsh soils. Invertebrates, on the other hand, were relatively resistant to grazing. Moreover, our experiment indicated that grazing was associated with marsh die-off intensity but did not affect recovery from simulated hog damage. Collectively, and when compared with previous work on European marshes, these results illustrate large-scale variation in the impacts of grazers on coastal wetlands and show how multiple functionally relevant plant and soil properties lack resistance to large grazers in a system structured by a single foundational plant species.

4.1 | Plant above- and below-ground responses

Grazing reduced multiple indicators of plant productivity, with implications for ecosystem services. In both our experimental and observational studies, grazers reduced above-ground biomass, stem height and cover of *Spartina*, as expected from previous work (Turner, 1987). Grazers correspondingly reduced root biomass in our experiment. Although most plant responses aligned across the two approaches, stem density without grazing was lower in the observational, but higher in the experimental study. In the observational study, marshes without grazing likely undergo self-thinning as taller stems shade their neighbours while marshes where grazing was recently excluded have yet to exhaust soil nutrients and reach this density-dependent feedback (Liu & Pennings, 2019). Notwithstanding, reduced above-ground plant biomass and structure in grazed marshes are likely to impair multiple ecosystem services, such as shoreline stabilisation due to reduced accretion (Turner et al., 2002), storm protection due to reduced wave attenuation (Fairchild et al., 2021; Möller et al., 2014; Shepard et al., 2011), fisheries support due to less detrital biomass entering the marine food chain (Baker et al., 2016; Levin et al., 2002), and provision of habitat for wildlife that rely on tall vegetation for nesting (Sherr, 2015). Reduced biomass can also decrease soil organic carbon accumulation, a large component of 'blue' carbon stores, due to reduced plant inputs and lower clay accretion (Kelly et al., 1996; Oades, 1988), an outcome of grazing also consistent with the results in our study.

4.2 | Soil texture and organic carbon responses

Grazers consistently affected soil texture and, in the long-term grazed sites, reduced soil organic carbon concentration. Grazer-driven shifts in sediment texture away from fine-grained clay towards sand were evident in our experiment, concordant with reduced vegetation biomass having a lowered capacity to capture fine clay particles (Mudd et al., 2010). Higher sand alone is associated with lower SOC (Oades, 1988), and grazers could prefer sandier substrate, thus sand content could potentially drive a spurious association between grazing and SOC. However, the experiment provides causal evidence to corroborate the novel conclusion that grazers are *driving* long-term and large-scale changes in sediment composition in eastern US marshes, rather than *responding to* firmer underfoot conditions that likely result from coarser sediment. In these long-term grazed marshes, we observed lower SOC, which again we attribute to grazers causing rather than responding to soil texture. We draw this conclusion both because grazing emerged as a parsimonious predictor of SOC over and above soil texture, and our SEM supported a plausible mechanism whereby grazing reduces canopy height, which also indirectly reduces root biomass and clay content, thus reducing biotic *Spartina* inputs to the SOC pool. Indeed, these biotic inputs are likely to be especially crucial in those North American marshes without significant sediment inputs (e.g. marshes of eastern North America removed from the influence of large rivers) which mostly accrete by accumulation of organic matter (biogenic) rather than by deposition of silt and sand (minerogenic)—the dominant mechanism of accumulation in European marshes (Bai et al., 2016; Hu et al., 2014; Kelleway et al., 2016; Mudd et al., 2010). At smaller scales, the influence of nearby tidal creeks can also be an important predictor of soil properties (Table S10) and may modulate the influence of grazing on SOC.

The lack of a SOC response in the experiment compared to the long-term observational sites was not unexpected, as changes in marsh SOC are slow and can take several decades to manifest (Craft, 2001). Yet, importantly, key mechanisms linking grazing to reduced SOC appeared to be in motion in both the experimental and observational studies, such as reduced soil clay content, reduced above- and below-ground biomass, and shifts in vegetation composition away from *Spartina*. One caveat to our results is that we only measured SOC in the top 15 cm of the soil. Past work suggested that surficial ungulate grazing likely only affects SOC in the top 5 cm of the soil (Augustine & McNaughton, 2006; Schulz et al., 2016). Nevertheless, there could be impacts on deeper SOC that we did not account for. In the absence of multi-decadal experimental tests of large grazers in North American marshes, we suggest that the combination of experimental and observational results provided here, together with previous meta-analysis results (Davidson et al., 2017), offer strong evidence that large grazers are drivers of reduced SOC concentration in eastern US marshes and may thus have significant influences on ecosystem function, including carbon storage, microbial diversity, and nutrient cycling (Bastida et al., 2021; Carney & Matson, 2005).

4.3 | Ecological responses

Within the time frame of our experiment, removal of grazers had mixed impacts on ecological resilience. Large grazers decreased resistance to marsh die-off, an important issue facing eastern US saltmarshes (Alber et al., 2008), and may act similarly to marsh periwinkles (Silliman et al., 2005) in worsening and promoting the expansion of die-offs. Coastal managers must account for large grazers in plans to predict or enhance die-off resilience, especially as multiple stressors associated with die-offs appear to be ramping up under climate change (Adams, 2020; Crotty et al., 2017). We suggest that without positive interactions of tall neighbouring vegetation, including self-shading, desiccation increased (Angelini et al., 2016). Grazing may also initiate a positive feedback in which leaf tissue C:N is reduced, increasing palatability to grazers and decomposers, which further reduces below-ground resources—including non-structural carbohydrates in rhizomes necessary for shoot regrowth and lateral recolonization (Roth et al., 2023). Regardless of the mechanisms, our result suggests that interactions between climate-driven stressors and large herbivores may play an important role in coastal wetlands.

However, despite simulated hog damage exerting lasting impacts on saltmarsh vegetation, grazer removal had little effect on marsh recovery from hog damage. This could be due to the different timing of these disturbances. The simulated disturbance took place relatively early in the experiment, before root biomass had diverged between grazing treatments, thus both grazed and ungrazed plots likely had similar below-ground resource pools to fuel recovery. Alternatively, the more intense disturbance caused by our simulation, which damaged both above- and below-ground biomass of plants, may have overwhelmed prior effects of grazing damage. Together, these differential effects of grazing on die-off resistance and simulated hog disturbance underline that stability responses vary with properties of disturbances and facets of stability (Donohue et al., 2013; Radchuk et al., 2019).

4.4 | Invertebrate responses

Despite significant changes to saltmarsh vegetation with grazing, most saltmarsh invertebrates were unaffected by grazing. The experiment did, however, show that ungulate grazing reduces marsh periwinkle densities. Marsh periwinkles are closely associated with *Spartina*, on which they farm fungi (Silliman & Newell, 2003) and climb to escape benthic predators (Griffin & Silliman, 2011). In turn, while reduced periwinkle density might be expected to temper their impacts, the relatively low densities observed during our study would have precluded strong feedback (Atkins et al., 2015). It is likely that snails in the experiment dispersed from grazed areas of stunted grass to taller grass in the exclusion plots. This kind of local dispersal to taller plants was not an option in the observational study in which entire marshes were grazed, explaining the similar snail densities between grazed and ungrazed areas that we recorded in our observational survey. This suggests that invertebrate assemblages in eastern US marshes are either largely robust to grazing and associated competition and disturbance or respond nonlinearly such that our surveys fail to capture their subtle responses.

This result contrasts with a significant negative effect of large ungulates on herbivorous saltmarsh invertebrates seen in a global meta-analysis (Davidson et al., 2017). It is possible that the high productivity of east coast US marshes, restricted distribution of large grazers, frequent tidal flooding and redistribution of organic matter, and a flexible diet of the common invertebrates (Teal, 1962), means that invertebrates are unaffected by competition or disturbance from large herbivores. The lack of invertebrate response in this observational study indicates that functions related to invertebrates such as secondary production, bioturbation, and infiltration (Angelini et al., 2015; Hensel & Silliman, 2013) are likely not affected by horse grazing.

4.5 | Vegetation composition and *Spartina* as the singular foundation species

Large grazers drove reduced plant biomass (both studies), substantial shifts in soil texture (both studies), and reduced soil organic carbon (observational study) largely due to their impacts on *Spartina*. Despite evidence of compensatory responses of less palatable species (Furbish & Albano, 1994), these results illustrate the singular foundational role of *Spartina* in the functioning and service provisioning of these marshes. While grazing-driven compositional shifts across species were straightforward in the experiment, from *Spartina* to the succulent *Salicornia*, over large scales and outside experimental conditions, a more complex picture emerged. The observational study showed an increase in compositional variation among grazed plots, indicative of an increase in ß-diversity. Although greater compositional variation (ß-diversity) may support ecosystem functioning in some systems (Mori et al., 2018), it may also indicate degraded states, such as where patchy disturbances and inconsistent ecological responses generate spatial turnover in vegetation composition.

Vegetation shifts away from *Spartina* dominance, observed in both studies, can be expected to impair multiple ecosystem services. *Spartina* supports higher rates of soil carbon accumulation than other saltmarsh plant genera (Ouyang & Lee, 2014), and indeed our results support a key role of *Spartina* canopy in supporting this process. Further, as one of the tallest saltmarsh plants (Adam, 1990), it is particularly effective for wave attenuation (Narayan et al., 2016; Shepard et al., 2011). Finally, *Spartina* facilitates saltmarsh establishment (Altieri et al., 2007; Yando et al., 2019), so reduced belowground stores in *Spartina* necessary for shoot emergence and lateral spread may lower the capacity to establish new marshes or recolonise following disturbance or die-back. Ecosystem services, including biogenic inputs that drive SOC, may be markedly reduced by grazing in US marshes because of reliance on the single foundation species (*Spartina*) compared to more diverse European marshes (Adam, 1990) that may confer an increased redundancy, and thus resistance and adaptability to grazing (Callaway et al., 2005; Meirland et al., 2013). The effects of grazing on marshes in other parts of the world remain understudied (Davidson et al., 2017), although some studies suggest that South American and Asian marshes similarly lack redundancy and show vulnerability to large grazers (Isacch et al., 2006; Meng et al., 2020).

More generally, while there has been much interest in how functional redundancy can increase resilience to disturbance, particularly exerted by large grazers in grasslands (Biggs et al., 2020; Chillo et al., 2011; Laliberté et al., 2010), our findings point towards the inherent vulnerability of ecosystems supported by single foundation species. When disturbance, including herbivory, parasitism, and disease, selectively target singular species lacking a stabilising functional analogue, declines in ecosystem function should be greater than in systems with compensatory redundancy (Johnson et al., 1996). Therefore, ecosystems with a singular foundation species supporting multiple functions (e.g. monotypic stands of *Rhizophora mangle* in neotropical swamps or *Tsuga canadensis* in temperate forest of the Eastern US; Deyoe et al., 2020; Ellison et al., 2019) may be most vulnerable to perturbation and collapse, especially as stressors increase in number and intensity under global change.

AUTHOR CONTRIBUTIONS

Kate E. Davidson and John N. Griffin conceived the ideas and, with Sean J. Sharp, Christine Angelini, and Steve Pennings, designed methodology; Kate E. Davidson, Sean J. Sharp and Hallie S. Fischman collected the data; Kate E. Davidson and Sean J. Sharp analysed the data; Kate E. Davidson, Sean J. Sharp, and John N. Griffin led the writing of the manuscript. Mike S. Fowler provided guidance for statistical analyses. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

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Data available from Zenodo https://doi.org/10.5281/zenodo.10035682 (Sharp et al., 2023).

ORCID

K. E. Davidson https://orcid.org/0000-0001-7452-5561
C. Angelini https://orcid.org/0000-0002-6669-5269
S. Pennings https://orcid.org/0000-0003-4757-7125
J. N. Griffin https://orcid.org/0000-0003-3295-6480

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SUPPORTING INFORMATION

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

Table S1. Location, grazing history, and grazing levels at the 26 surveyed marshes.

Table S2. Visual indicators used to allocate qualitative grazing levels.

Table S3. Responses measured at Cumberland Island experimental site at 0, 7, 13, 18 and 51 months.

Table S4. Conceptual grazing impacts on soil organic carbon.

Table S5. Grazed control v. ungrazed exclusion baseline comparisons.

Table S6. Grazed control v. reference baseline comparisons.

Table S7. Effect of grazing on ecosystem properties after 51 months.

Table S8. Effect of grazing on ecosystem properties at each time point.

Table S9. Effect of grazing on recovery from hog damage.

Table S10. Effect of grazing on ecosystem properties in observational study.

Table S11. Effect of grazing on ecosystem properties in observational study with grazing intensity.

Table S12. Results of LMMs to predict SOC from grazing, soil, and plant properties.

Figure S1. Experimental plot layout.

Figure S2. Extreme water level data history for the study area.

Figure S3. Palmer Drought Severity Index 2015–2020.

Figure S4. Conceptual diagram for structural equation model.

Figure S5. The relationship between grazing intensity and stem density, stem height.

Figure S6. Raw species data for observational survey marshes.

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