Biol Invasions (2024) 26:169–185
https://doi.org/10.1007/s10530-023-03167-4

ORIGINAL PAPER

Invasive consumers provoke ecosystem-wide disruption of salt marsh functions by dismantling a keystone mutualism

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Received: 23 December 2022 / Accepted: 12 September 2023 / Published online: 26 September 2023
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Abstract Mutualisms enhance ecosystem biodiversity, functioning, and service provisioning through direct and indirect positive interactions. However, invasive species can interrupt mutualisms and disrupt ecosystem functions when they affect foundation species and their keystone mutualist partners. In the southeastern US, mussels aggregate around cordgrass stems, a keystone mutualist-foundation species interaction that controls marsh structure, function, and resilience. Invasive hogs trample cordgrass and consume mussels, yet the multi-scale effects of this mutualism disruption remain uncertain. Here, we quantified the effects of hog-mediated mutualism disruption on four critical ecosystem functions: cordgrass biomass, macroinvertebrate biomass, denitrification, and sediment deposition. We compared a hog-disturbed marsh (27% area disturbed) and a hog-free marsh (0.05% disturbed) and experimentally demonstrated that hog predation causes the observed 93% reduction in mussels on the hog marsh. Plot-scale measurements revealed that hog trampling of cordgrass doubles net denitrification rates but decreases cordgrass biomass, crab biomass, and sediment deposition by 74%, 80% and 55%, respectively, relative to areas without hogs. Mussels stimulate cordgrass biomass, crab biomass, denitrification, and sediment deposition by 19%, 39%, 134% and 140%, effects that are only evident in the mussel-dense hog-free marsh. Using hog damage and mussel cover surveys to extrapolate plot-scale measurements to the 20 m^2 scale, we estimate that hogs stimulate cordgrass biomass and denitrification by 27% and 5% but, by driving mussel loss, depress crab biomass and sediment deposition by 48% and 38%. Disruption of the cordgrass-mussel mutualism by invasive hogs alters ecosystem functioning, modifications which will likely affect marsh ecosystem service provisioning and resilience region-wide.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10530-023-03167-4.

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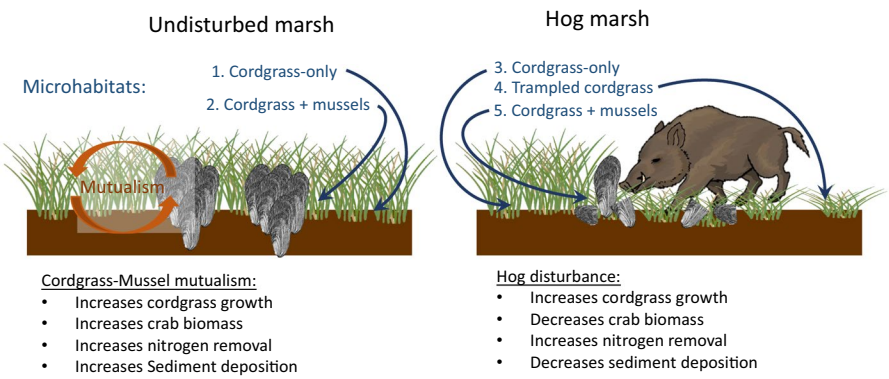
Graphical abstract



Keywords Foundation species · Ecosystem engineer · Ecosystem service · Nitrogen cycling · Salt marsh accretion · Wild hog

Introduction

Mutualisms, interactions between two species that provide mutual benefits, influence ecosystem structure and enhance biodiversity, biogeochemical cycling, and other ecosystem functions (Hay et al. 2004). Studies across marine, terrestrial, intertidal, and rhizosphere ecosystems have demonstrated the critical importance of mutualisms in community organization, energy and nutrient cycling, and resiliency (Hay et al. 2004; Traveset and Richardson 2006; Rodriguez-Cabal et al. 2013). Mutualisms are likely to have particularly important effects on ecosystem structure, functioning, and service provisioning when at least one of the mutualistic partners is a foundation species, i.e. a spatially dominant, habitat-forming species that facilitate other species and regulate resource availability (Dayton 1972; Bruno and Bertness 2001). Mutualistic partners of foundation species are often referred to as keystone mutualists because of the disproportionately large, cascading effects these species have on community structure, biodiversity, and critical ecosystem functions via their positive effects on the foundation species (Power et al. 1996; Rodriguez-Cabal et al. 2013).

These mutualisms, however, are threatened by invasive species. Invasive species are known drivers of mutualism loss, as they consume, compete with, or physically disturb the mutualistic partners (Bond and Slingsby 1984; Traveset and Richardson 2006; Rodriguez-Cabal et al. 2013; Rogers et al. 2017). In plant-pollinator systems, for example, native keystone mutualists have been competitively excluded after the introduction of invasive bumblebees (Ings et al. 2006; Morales et al. 2013). Similarly, consumption of mutualist partners, such as fructivores being consumed by brown treesnakes (Rogers et al. 2017), has been shown to cause declines in foundation species and reduce biodiversity across the ecosystem. Invasives can also destabilize foundation species, as seen with burrowing by invasive mice disturbing foundational cushion plants, with cascading effects for mutualistic epiphytes and resident invertebrate communities (Phiri et al. 2009; Eriksson and Eldridge 2014).

Coastal ecosystems, including salt marshes, mangroves, and coral and oyster reefs, are particularly vulnerable to invasive species due to their long history of human settlement, integral role in commerce, and intermediate salinities (Paavola et al. 2005; Lotze et al. 2006). As these systems are commonly defined and structured by mutualisms between foundation species and keystone mutualist partners (Bruno and Bertness 2001), the disruption of mutualisms by invasives will likely have far reaching consequences on ecosystem functioning and the provisioning of important services such as carbon storage, nursery habitat, nutrient removal, and storm protection—services for which coastal systems are highly valued (Barbier et al. 2011). Although research on the cascading impacts of mutualism disruption in coastal

ecosystems is relatively limited compared to terrestrial systems, there is clear evidence that invasive species affect mutualisms between foundation species and their keystone mutualist partners in various ways. For example, invasive kelps have outcompeted native foundation species in New Zealand rocky shores, leading to a reduction in the number of mutualistic invertebrates (Berthelsen and Taylor 2014; Thomsen and South 2019). Invasive lionfish consume herbivorous fish, with adverse effects on the coral foundation species that benefit from grazing by its keystone mutualist partners (Mumby and Steneck 2008; Albins 2015). Likewise, the trampling of mangroves by invasive cattle has the potential to harm the epiphytic mutualists living amongst the foundation species' pneumatophores (Minchinton et al. 2019). Invasive consumers can directly impact both the foundation species and the keystone mutualist through competition, consumption, or physical disturbance, and can potentially disrupt both players simultaneously. However, the ecosystem-wide implications of an invasive disrupting both partners in a keystone mutualism are unknown.

Across lower-energy North American shorelines from Florida to Nova Scotia, salt marshes are structured by smooth cordgrass *Spartina alterniflora* (hereafter, cordgrass), a foundation species that engages in a keystone mutualism with the ribbed mussel, *Geukensia demissa* (hereafter, mussel). Cordgrass provides attachment substrate and alleviates temperature stress to facilitate mussels, while mussels excrete nutrients and alleviate drought stress to facilitate cordgrass (Bertness 1984; Angelini et al. 2016). Mussels are patchily distributed across the marsh landscape in aggregations of a few to several hundred individuals, and cover between 1 and 10% of the total marsh area (Bertness and Grosholz 1985; Angelini et al. 2015). These aggregations, known as mussel mounds, create hotspots of ecosystem functioning on the landscape with enhanced cordgrass biomass, benthic diatom and invertebrate abundance, net denitrification, and decomposition (Bertness 1984; Angelini et al. 2015; Bilkovic et al. 2017; Crotty et al. 2018).

However, recent work has highlighted that this mutualism is threatened by hogs (*Sus scrofa*), an invasive consumer whose rooting, wallowing, and trampling activities are observed in ~ 36% of marshes in the Southeast US (Sharp and Angelini 2019). Hog disturbance in marshes can reduce soil carbon storage and alter plant composition (Persico et al. 2017; Hensel et al. 2021a). In addition to disturbing cordgrass by severing roots, creating depressional wallows, and overturning grass and soil clumps as they forage, hogs consume mussels (Hensel et al. 2021b). Thus, they affect both partners in the foundation species-keystone mutualism and increase heterogeneity in the already patchy landscape. It is known that by targeting mussels for food, hogs can cause the mussel-cordgrass mutualism to collapse and prior work has suggested this disturbance reduces marsh resistance to drought (Hensel et al. 2021b). However, the influence of hog-mediated disruption of the cordgrass-mussel mutualism on key ecosystem functions, such as nitrogen cycling and sediment deposition, remain undocumented. Further, the effects of hog disruption to this marsh-structuring mutualism have yet to be evaluated at the larger, landscape-scales that are most informative to guiding management actions.

Here, we evaluate the impacts of hog-induced mutualism disruption on salt marsh functioning and ecosystem service provisioning. We focus on a marsh system in northeast Florida, USA in which hogs frequently access one salt marsh area located on the western side of a tidal river (hereafter, 'hog marsh') while the adjacent marsh area on the eastern side of the river experiences little-to-no hog activity (hereafter, 'hog-free marsh'; see Figs. 1, 2a). Across the two marshes, we evaluated four complementary metrics of salt marsh ecosystem functioning that represent distinct ecological, biogeochemical, and geological processes: (1) cordgrass biomass, a proxy for primary productivity (Negrin et al. 2012; Crotty et al. 2018); (2) crab biomass, a proxy for secondary production (Angelini et al. 2015); (3) net denitrification (positive N_2 fluxes); and (4) sediment deposition, a process essential to marsh vertical accretion and thus ability to keep pace to rising sea levels (Reed 1989; Crotty et al. 2023). These four metrics contribute to the ecosystem services provided by marshes, including carbon capture, biodiversity, prey availability to nektonic consumers, nutrient removal, and coastal protection (Grimes and Pendleton 1989; Reed 1989; Negrin et al. 2012; Manis et al. 2015; Bilkovic et al. 2017). To account for the patchy nature of both mussel aggregations and hog disturbance across this marsh system, we measured all four functions at the local (1 m^2) scale across five marsh 'microhabitats': (1) undisturbed cordgrass-dominated area on

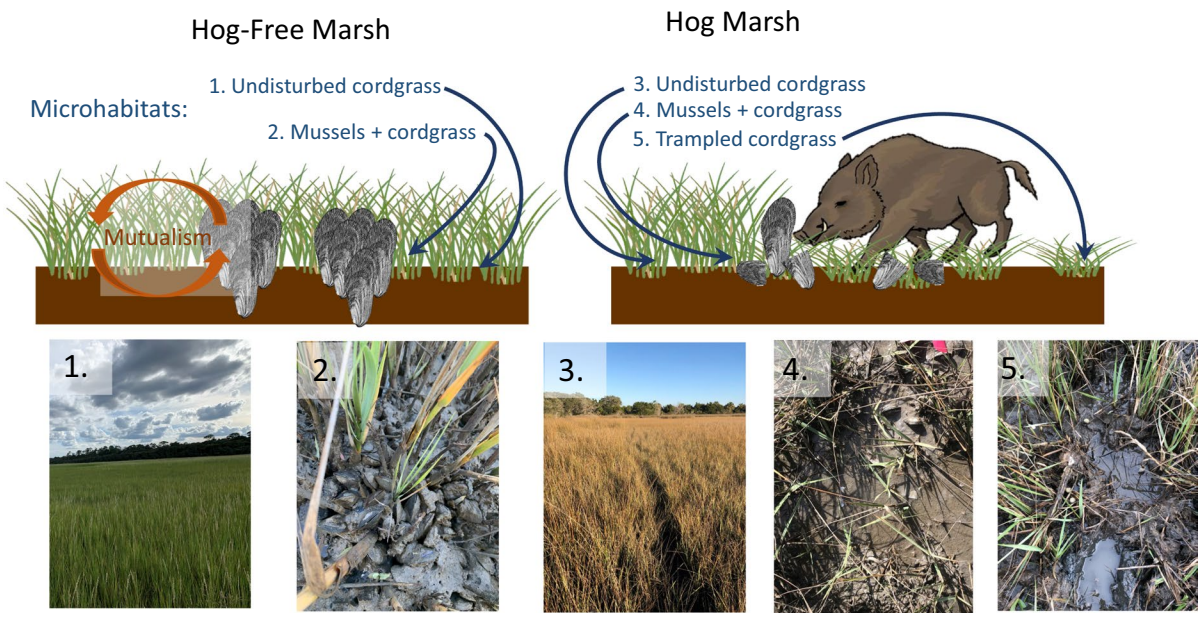


Fig. 1 Microhabitats within the hog-free marsh and the hog marsh. The photos depict undisturbed cordgrass and mussels + cordgrass area in the hog-free marsh (photos 1 and 2, respectively) and undisturbed cordgrass, mussels + cordgrass, and trampled cordgrass areas in the hog marsh (photos 3, 4, and 5, respectively). Note that the undisturbed cordgrass photos (#1 and #3) were taken in different seasons

the hog-free marsh, (2) mussels + cordgrass area on the hog-free marsh, (3) undisturbed cordgrass-dominated area on the hog marsh, (4) mussels + cordgrass area on the hog marsh, and (5) trampled cordgrass-dominated area on the hog marsh (Fig. 1). Of note, the two mussel-containing microhabitats (#2 and #4) differ in their access by hogs and predation impacts. Similarly, the three cordgrass-dominated microhabitats (#1, #3, and #5) are unique. Trampled cordgrass on the hog marsh (microhabitat #5) displays signs of recent hog damage such as hoofprints and uprooted sediment while the undisturbed cordgrass on the hog marsh (microhabitat #3) does not. Given the known, persistent history of hog disturbance within the hog marsh (GTM Reserve Staff, *personal communication*; Sharp and Angelini 2019) and relatively fast recovery time of marsh grasses to hog disturbance (Hensel et al. 2021a), undisturbed cordgrass on the hog marsh (microhabitat #3) has likely been disturbed previously and subsequently recovered, and is additionally impacted by hog presence in a way that undisturbed cordgrass on the hog-free marsh (microhabitat #1) is not. To provide insights about the influence of hogs on mutualism-mediated ecosystem functions at scales relevant to decision making about salt marsh and hog management, we estimated the four ecosystem functions at the larger, 20 m^2 scale (20 m^2 of marsh containing multiple microhabitats) in both the hog and hog-free marshes.

Methods

Study site

This study was conducted in the salt marshes surrounding the Guana River, a brackish estuary located in the Guana Tolomato Matanzas National Estuarine Research Reserve in Ponte Vedra, Florida USA (30.0109°, − 81.3253°). The marshes in this estuary are similar to other salt marshes in the southeastern United States with regards to their invertebrate community, *Spartina alternifora* cordgrass dominance, and semi-diurnal tidal cycles (average 1.25 m amplitude). As with other marshes in the region, these sites contain high densities of ribbed mussels and, on the western margin of the estuary, are frequently visited by hogs (Sharp and

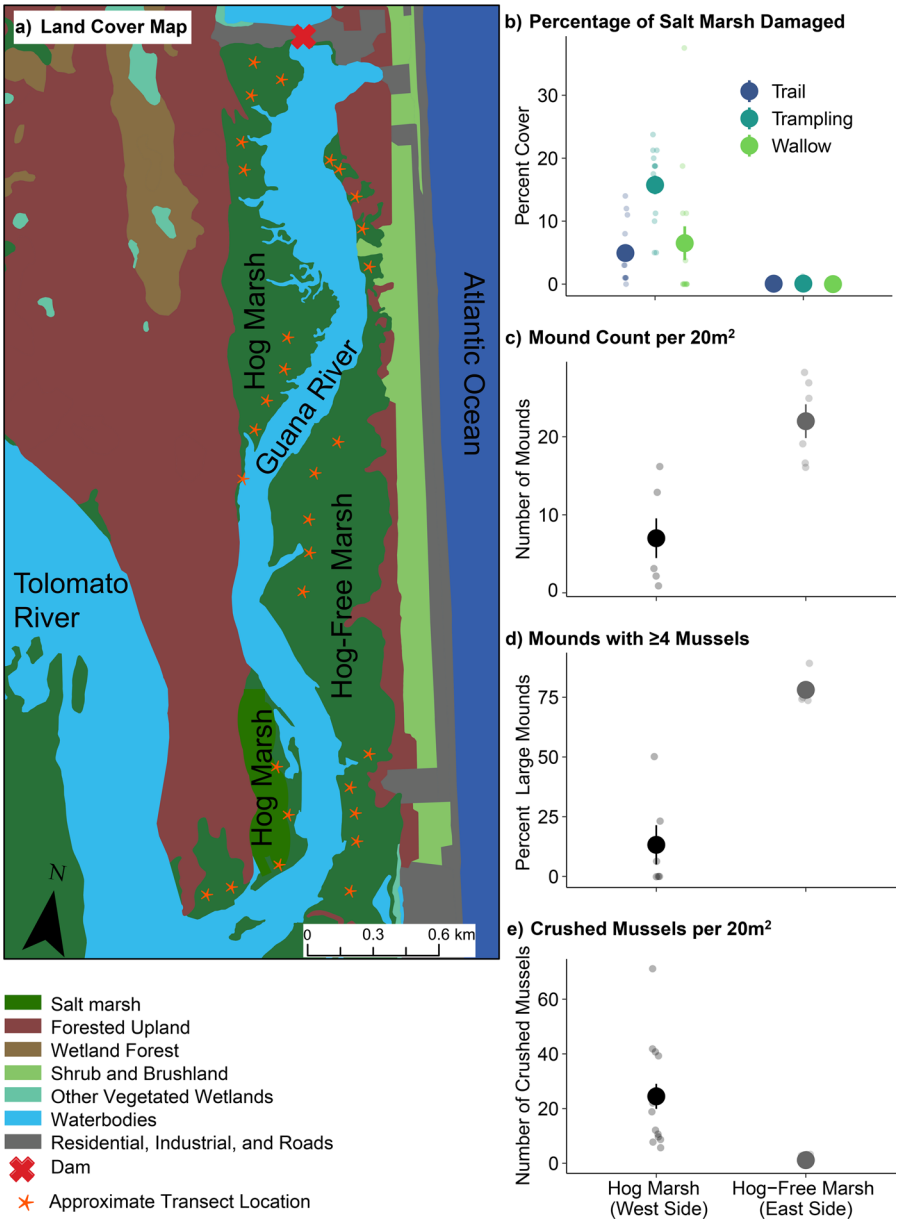


Fig. 2 Map of land cover surrounding the Guana River with hog marsh and hog-free marshes with approximate transect locations shown (**a**). Land Cover Layer from St Johns River Water Management District (2009). Results from the transect surveys: the percent of damaged area within the hog and hog-free salt marshes (**b**), Number of mussel mounds encountered per 20 m^2(**c**), the percentage of mussel mounds with ≥ 4 individuals (**d**), and the number of crushed mussel shells per 20 m^2 visible on the marsh surface (**e**). Graphs show mean ± standard error with raw data behind

Angelini 2019). The Guana River runs approximately 5 km and is bounded to the north by a dam separating the Guana River from Guana Lake and to the south by the Tolomato River. Salt marshes occur on both banks of the Guana River, but the upland habitat differs between the two sides. The western upland is undeveloped and designated as a wildlife management area while the eastern marsh is bordered by dense shrubs, residential neighborhoods, and a major roadway (Fig. 2a). Likely driven by the differences in upland land cover (Sharp and Angelini 2019), the salt marsh on the western bank of the Guana River (hereafter, hog marsh) is commonly accessed by hogs while the marsh on the eastern bank (hereafter, hog-free marsh) is not (Fig. 2a).

Quantifying hog damage and mussel distribution surveys

To characterize the distribution of foundational cordgrass, keystone mutualist mussels, and hog disturbance in this system, we conducted surveys in both the hog and hog-free marshes. We ran 20 m × 1 m transects perpendicular to the Guana River (n = 15 transects per marsh). At each meter along the transects, the percent cover of hog damaged cordgrass was visually estimated within a 1 m^2 frame; damaged cordgrass was classified as either animal trails, hog rooting and trampling, or hog wallowing to identify the drivers of this disturbance (Sharp and Angelini 2019). While various animals may create trails, including deer and raccoons, rooting, trampling, and wallowing are unique to hogs. Within a subset of transects (n = 6 per marsh), all mussel mounds within the transect areas were counted and tallied either as 'small mounds' containing 1–3 mussels or 'larger mounds' containing ≥ 4 individuals. We differentiate between the mound sizes as hogs commonly predate and scatter some of the mussels within larger mounds, leaving smaller mounds in their wake. The number of crushed mussel shells visible on the marsh surface, an indication of predation rather than desiccation, was also counted within all transects. Hogs differ from other mussel predators like crabs and racoons in that they destroy mounds and leave a scattering of crushed shells in their wake. Therefore, large numbers of crushed shells combined with hoof prints and wallows provide confirmation of hog activity. Given the potential for hogs to modify geomorphic properties of salt marshes, we also measured the elevation of each marsh by collecting 240 surface elevation points across the two marshes with an RTK GPS (Trimble Geo7x; vertical accuracy of ± 2 cm). To assess whether the percent cover of disturbed cordgrass, mussel density, the proportion of large mounds, the number of crushed shells, and elevation differed between the hog and hog-free marshes, we first assessed normality using a Shapiro–Wilk Test and then used two-sample t-test (mussel density and marsh elevation) or Wilcoxon Rank Sum tests (disturbance cover, large mounds, and crushed shells).

Hog exclusion experiment

To assess the potential role of hogs in driving differences in mussel cover between the hog and hog-free marshes, a caging experiment was implemented in January 2021. This experiment was deployed and monitored over winter and early spring, when hogs experience a scarcity of food in the uplands and their foraging ranges increase (Baron 1982). Mussels were collected from the hog-free marsh and deployed in 30 replicate aggregations of 20 mussels throughout each marsh, spaced at least 1 m apart. Aggregations were then randomly assigned to either a hog exclusion (caged) or control (uncaged) treatment (N = 15 aggregations per treatment per marsh). We installed two, 10-inch diameter, stacked tomato cages around each hog exclusion aggregation, creating heavy-duty wire frames that allowed access by nektonic predators, small mammalian predators, and invertebrate predators. While these cages could not have withheld a hog actively trying to access the mussels, the lack of predation in cages compared to nearby controls suggested that they acted as a sufficient deterrent to hogs. After six weeks, the mussel aggregations were destructively sampled, and all live and dead mussels were counted. We assessed the importance of hog presence (i.e., hog or hog-free marsh) and predator access (i.e., caged or uncaged) on if the mound was predated using a binomial general linear model.

Quantifying hog and mussel effects on soil properties and porewater nutrients

To evaluate belowground soil and biogeochemical properties that may influence the four ecosystem functions evaluated in this study, we collected soil cores and porewater from randomly selected patches of the five microhabitat types. We quantified soil bulk density, organic content, and porewater inorganic nutrients, variables that are known to influence cordgrass aboveground biomass, crab biomass, net denitrification rates, and sediment deposition (Bertness 1984; Breland and Hansen 1996; Bertness et al. 2009; Bilkovic et al. 2017). Soil cores (5 cm depth × 2.5 cm diameter) were collected (n = 8 per microhabitat), dried at 60 °C for one week until a constant weight was reached, and weighed for bulk density. A subsample of dried cores (n = 4 per microhabitat) were then ground using a mortar and pestle,

and combusted in a muffle furnace at 550 °C for 3 h to calculate soil organic matter as the percentage loss on ignition (Hoogsteen et al. 2015). Porewater was collected using a 10 cm Rhizon sampler (Rhizosphere Research Products; Wageningen, the Netherlands) and a 60 mL syringe in each microhabitat (n = 5 samples per microhabitat). Porewater was analyzed for ammonium using a AA3 AutoAnalyzer (SEAL Analytics; Norderstedt, Germany; detection limit: 0.04 μM) and for nitrate + nitrite using the vanadate reduction method (Doane and Horwáth 2003) with a UV 1900i UV VIS Spectrophotometer (Shimadzu Corporation; Kyoto, Japan; detection limit: 0.11 μM).

We statistically analyzed these data using two separate models. First, we applied a Mussel Presence (mussels vs no mussels) * Marsh (hog vs hog-free) two-way ANOVA to evaluate the significance of mussels and hog activity on the soil properties and porewater nutrient metrics (hereafter "Marsh*Mussels ANOVA"; comparing Microhabitats #1, #2, #3, and #4 in Fig. 1). This test allowed us to examine the influence of hog activity, mussel mutualists, and their interactions on soil characteristics and porewater chemistry and whether the mussel effects are modified by hog activity. Second, to compare the effect of hog activity on microhabitats dominated by the foundation species (i.e., undisturbed cordgrass on the hog-free marsh, undisturbed cordgrass on the hog marsh, and trampled cordgrass on the hog marsh) we applied a one-way ANOVA (hereafter "Cordgrass-only ANOVA"; comparing Microhabitats #1, #3, and #5 in Fig. 1). Conducting two separate tests was necessary due to the non-orthogonal nature of our surveys (i.e., hog trampling does not occur on the hog-free marsh). Data was box-cox transformed as needed to meet model assumptions and Tukey post-hoc tests with Bonferroni corrected p-values were used to determine pairwise differences.

Quantifying local-scale hog and mussel effects on salt marsh ecosystem functions

We evaluated the impacts of hog-induced disruption to the cordgrass-mussel mutualism on ecosystem functions at the plot, or local, scale. Within each microhabitat type, we quantified cordgrass biomass and macroinvertebrate biomass using 25 × 25 cm quadrats, a size chosen to capture community composition entirely within hog damaged areas and within mussel mounds. Quadrats were placed in randomly selected areas of each microhabitat type (n = 12 quadrats per microhabitat). Aboveground cordgrass biomass was quantified within each quadrat by clipping vegetation to the marsh surface, washing, drying at 60 °C, and weighing. Periwinkle snails (*Littoraria irrorata*) and crab burrows (juvenile and adult fiddler crab *Uca pugnax*, purple marsh crab *Sesarma reticulatum*, and mud crabs *Eurytium limosum* and *Panopeus obesus*) were counted and converted to biomass per Angelini et al. 2015 and Crotty et al. 2018. Because snail densities were low but highly variable across the landscape (average density 2.9 ± 1.2 per quadrat vs. > 40 in Angelini et al. 2015), only crab biomass was included in the analysis. We assessed juvenile and adult crab biomass independently, but both metrics produced identical results, so we present total crab biomass for simplicity. Both aboveground cordgrass biomass and crab biomass were scaled to 1 m^2 of marsh for consistency with other ecosystem function metrics.

We then assessed sediment N_2 flux in each microhabitat using continuous flow core incubations. A positive N_2 flux indicates denitrification in excess of fixation (Smyth et al. 2013). Sediment cores (6.35 cm diameter, 10 cm height) were manually collected in acrylic columns (28cm in height) from the five microhabitats (n = 4 per microhabitat). The columns were then filled with site water and transported on ice to the University of Florida's Tropical Research and Education Center in Homestead, Florida. Cores from mussel-containing microhabitats included mussels (3.875 ± 0.2 per core) in addition to sediment as mussels are known to enhance net denitrification (Bilkovic et al. 2017). Cores were left uncapped in a tank containing aerated site water overnight. The next day, cores were capped with a gas-tight lid, kept in the dark to minimize oxygen production, and the incubation began. Aerated site water was pumped over the cores at a rate of 2 mL/min using a peristaltic pump. After a 24-h equilibration period (> 3 turnovers; Miller-Way and Twilley 1996), water samples were collected from the outflow of each core and bypass lines containing only site water in 12 mL exetainer vials (Labco Limited, Lampeter, United Kingdom). Vials were overfilled by three times to avoid air contamination. Samples were collected at 8, 16, and 24 h and analyzed immediately using membrane inlet mass spectrometry to measure dissolved N_2 concentrations

(Kana et al. 1994). N_2 flux was calculated by multiplying the difference between the outflow sample and the bypass sample by the flow rate per unit area. NO_x–N and NH_4^+–N concentrations were measured from filtered water samples collected at the same sampling frequency and analyzed using a SEAL AutoAnalyzer (detection limits: NO_x–N = 0.007 µM, NH_4^+–N = 0.04 µM). All nitrogen fluxes were calculated as µmol N m^{-2} h^{-1}. Fluxes at each sampling point were averaged to determine microcosm-specific fluxes. We define a positive N–N_2 flux, indicating N removal from the system, as net denitrification.

Finally, sediment deposition on the marsh platform, the fourth ecosystem function, was quantified by deploying 9cm Ashless Whatman filter papers within the five microhabitats. At low tide when the marsh was dry, preweighed filters were placed on the marsh surface (n = 20 per microhabitat type) and staked with two small pieces of galvanized wire (Reed 1989). Filters were deployed for 24 h during a summer spring tide (two inundations, tidal amplitude 1.43 m), collected during low tide, and placed into a preweighed aluminum foil packet. Filters were dried at 60 °C until a constant weight was maintained and then weighed to calculate sediment deposition. The mass of sediment deposited on each filter was scaled to 1 m^2 of marsh area for consistency between ecosystem function measurements.

As with the soil and biogeochemical properties discussed above, we analyzed the effect of mussel and hog presence on the four ecosystem function variables using a two-way Marsh*Mussels ANOVA comparing mussels + cordgrass and undisturbed cordgrass microhabitats across both marshes. We evaluated the direct impacts of hogs on the cordgrass-only microhabitats using a one-way Cordgrass-only ANOVA.

Scaling the effects of hog disruption of the mutualism on ecosystem functions to the landscape

To assess how hog disruption of the cordgrass-mussel mutualism may influence ecosystem functions when considered at the 20 m^2 scale, we used the transect survey results to upscale the local scale ecosystem service measurements. We focus on the 20 m^2 scale for our assessment because represents the area of the transects we surveyed. We calculated transect scale values of all four functions within each marsh by multiplying the values of the ecosystem function variables within the five focal microhabitats by the percentage cover of each habitat type recorded across the transects and averaging values per marsh. Transect scale standard error was calculated based on propagation of microhabitat error. Transect scale responses on the hog and hog-free marshes were compared using two sample t-tests. All analyses were conducted in R (version 4.0.3) with the package *FSA* (Ogle et al. 2021). Data manipulations and visualizations were created using the *tidyverse* package (Wickham et al. 2019). All values presented in the text represent the mean ± standard error.

Results

Quantifying hog damage and mussel distribution surveys

Surveys of the hog marsh and hog-free marsh revealed differences in the percent cover of damaged cordgrass and mussel cover between the two sites. Damage indicative of hogs, including trails, wallows, and trampled areas, covered 27.2% ± 5.29% of the hog marsh and 0.15% ± 0.15% of the hog-free marsh (Fig. 2b; Wilcoxon Test: $p < 0.0001$). Trampling accounted for the greatest proportion of damage, affecting 15.8% ± 0.2% of the hog marsh, followed by trails and wallows, which accounted for 5.0% ± 0.1% and 6.5% ± 0.5% of hog marsh area, respectively. The hog marsh also supported a third the density of mussel aggregations (Fig. 2c; t-test: $t_{10} = 4.50$, $p = 0.001$) and 83% fewer large mussel mounds (Fig. 2d; Wilcoxon Test: $p = 0.005$) compared to the hog-free marsh. In addition, the number of crushed mussel shells on the marsh surface, a metric indicative of predation, was 22-times higher on the hog than hog-free marsh (Fig. 2e; Wilcoxon Test: $p < 0.0001$). Together, these results suggest that hogs are far more active in the western, hog marsh than eastern, hog-free marsh

Table 1 The precentage of mussel mounds (n = 15 per treatment per marsh) showing predation after six weeks

Percentage of mussel mounds predated	Hog marsh (%)	Hog-free marsh (%)
Hog exclusion cage	0	0
Uncaged control	53.3	0

and this coincides with substantial differences in mussel density, cover, and aggregation size structure. Elevation measurements across the two sites demonstrate that the hog marsh is 6.3 cm lower in elevation than the hog-free marsh (0.359 m ± 0.00993 m mean sea level (MSL) and 0.422 m ± 0.00379 m MSL in the hog and hog-free marsh, respectively; t-test $t_{236} = 5.75$, $p < 0.001$). As these marshes are adjacent with few other differentiating factors, it is likely that hog activity has contributed to, if not caused, a critical loss in marsh elevation.

Hog exclusion experiment

After six weeks of hog exclusion, not a single mussel was predated in caged aggregations on the hog marsh or in either treatment (caged or uncaged) on the hog-free marsh (Table 1). However, 53.3% of uncaged aggregations on the hog marsh experienced predation. Both hog presence (i.e., hog marsh) and hog access (i.e., uncaged mounds) were key drivers of mussel predation (Binomial GLM: Marsh $p < 0.001$, Treatment $p < 0.001$). Within predated mounds, hogs consumed an average of 6.4 ± 1.4 mussels out of the 20 we deployed.

Quantifying hog and mussel effects on soil properties and porewater nutrients

We measured differences in soil and porewater characteristics across microhabitats. The full ANOVA tables and results of pairwise comparisons are presented in Online Resource 1. While mussel-containing microhabitats showed similar soil bulk densities to each other and to undisturbed cordgrass plots on their respective marshes, bulk density within undisturbed cordgrass on the hog-free marsh was double that of undisturbed cordgrass on the hog marsh (Fig. 3a; Marsh*Mussels: $F_{1,28} = 4.53$, $p = 0.042$). The bulk density of undisturbed cordgrass on the hog-free marsh was also 40% greater than in hog trampled cordgrass on the hog-marsh (Cordgrass-only: $F_{2,21} = 4.53$, $p = 0.042$). Soil organic matter was 32% greater on the hog-free marsh than the hog

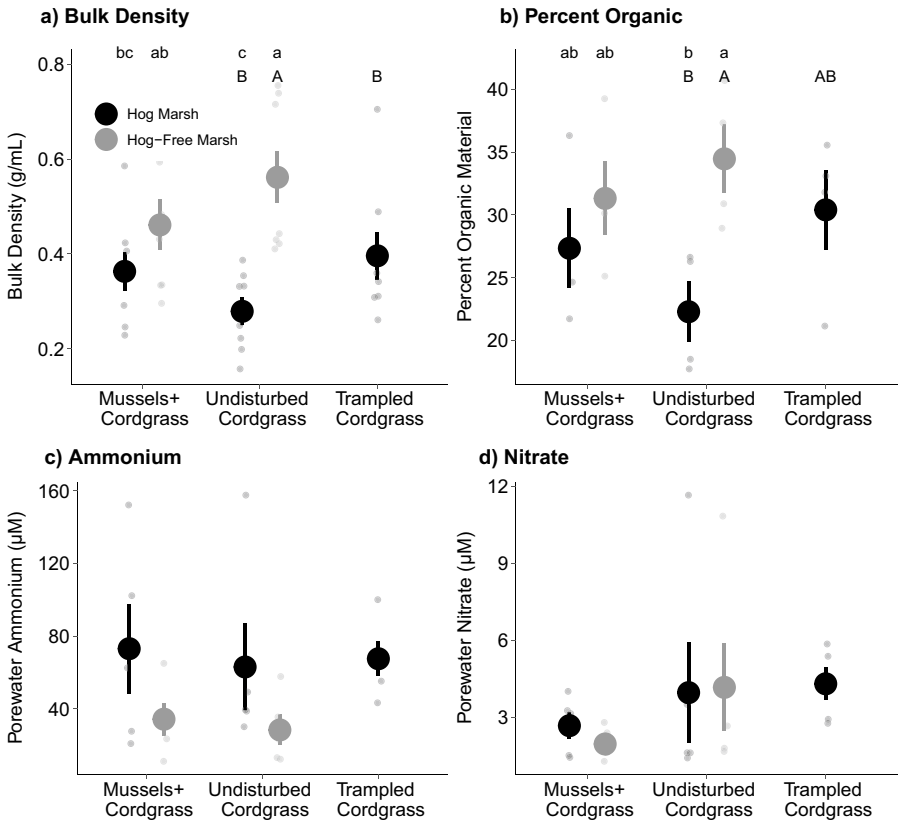


Fig. 3 Soil properties. Soil bulk density (**a**), soil percent organic content (**b**), porewater ammonium ($N–NH_4$) (**c**), and porewater nitrate ($N–NO_x$) (**d**). Lowercase letters indicate significant post-hoc differences in the Marsh*Mussel ANOVA and uppercase letters show significant post-hoc differences in the cordgrass-only ANOVA. There were no significant pairwise comparisons in the ammonium or nitrate data. Graphs show mean ± standard error with raw data behind

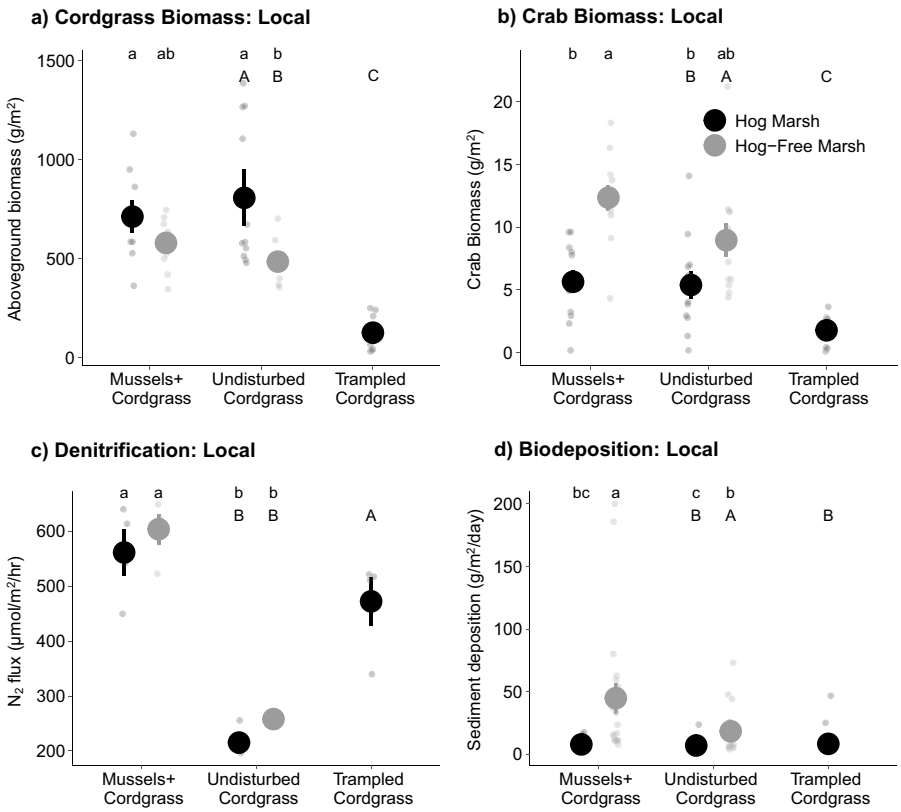


Fig. 4 Local (1 m^2) values for **a** cordgrass aboveground biomass, **b** crab biomass, **c** denitrification ($N–N_2$ flux), and **d** sediment deposition. Lowercase letters indicate significant post-hoc differences in the Marsh*Mussel ANOVA and uppercase letters show significant post-hoc differences in the cordgrass-only ANOVA. Graphs show mean ± standard error with raw data behind

marsh (Fig. 3b; Marsh: $F_{1,12}=8.16$, $p=0.014$) and 54% greater within undisturbed cordgrass on the hog-free marsh than undisturbed cordgrass on the hog marsh (Cordgrass-only: $F_{2,9}=4.91$, $p=0.036$). Porewater ammonium levels were 216% greater on the hog marsh than the hog-free marsh (Fig. 3c; Marsh: $F_{1,16}=4.83$, $p=0.043$), though no significant pairwise comparisons or differences between cordgrass-only microhabitats were observed. There were no significant differences observed in porewater $N–NO_x$ for either comparison (Fig. 3d; $p>0.05$).

Quantifying local-scale hog and mussel effects on salt marsh ecosystem functions

At the local, 1 m^2 scale, cordgrass aboveground biomass, crab biomass, net denitrification, and sediment deposition differed across microhabitats. The full ANOVA tables and results of pairwise comparisons are presented in Online Resource 2. While mussels had no effect on cordgrass biomass ($p=0.70$), this ecosystem function metric was 43% greater on the hog marsh than the hog-free marsh (Fig. 4a; Marsh: $F_{1,44}=14.3$, $p<0.001$). Undisturbed cordgrass on the hog marsh showed a 66% greater biomass than undisturbed cordgrass on the hog-free marsh and 5-times greater biomass than trampled cordgrass (Cordgrass-only: $F_{2,33}=58.0$, $p<0.0001$). Crab biomass was drastically suppressed on the hog marsh and unaffected by mussel presence (Fig. 4b; Marsh: $F_{1,44}=21.8$, $p<0.0001$). Within cordgrass-only areas, crab biomass was 66–400% greater within undisturbed cordgrass on the hog-free marsh than either microhabitat on the hog marsh. In the hog marsh, this metric was 67% lower in trampled areas than undisturbed cordgrass areas (Cordgrass-only: $F_{2,33}=16.33$, $p<0.0001$). Together, the cordgrass and crab biomass results suggest that hog disturbance significantly impacts salt marsh functioning through alterations to the foundation species.

All N_2 fluxes were positive, indicating denitrification rates exceeded nitrogen fixation rates. Net denitrification was 266% greater in areas containing mussels than areas without mussels (Fig. 4c; Mussels: $F_{1,12}=255$, $p<0.0001$) and 11% greater on the hog-free marsh than the hog marsh (Marsh:

$F_{1,12} = 5.50$, $p = 0.037$). Trampled cordgrass areas also showed enhanced net denitrification compared to either undisturbed cordgrass area (Cordgrass-only: $F_{2,9} = 32.4$, $p < 0.0001$). Thus, both the presence of the keystone mutualist and trampling by invasive hogs enhanced net denitrification, though the undisturbed cordgrass and mussels + cordgrass microhabitats were elevated on the hog-free marsh versus the hog marsh. Finally, sediment deposition was 4-times higher in the hog-free marsh than the hog marsh and 230% higher in the presence of mussels than mussel-free areas (Fig. 4d; Marsh: $F_{1,97} = 50.1$, $p < 0.0001$; Mussels: $F_{1,97} = 7.33$, $p = 0.008$). Deposition rates were two times higher in undisturbed cordgrass on the hog-free marsh than either cordgrass-only treatment on the hog marsh (Cordgrass-only: $F_{2,68} = 7.79$, $p = 0.001$). These results suggest variation in sediment deposition within this system. Mussels enhance sediment deposition locally within mussel mounds and the higher elevation hog-free marsh supports increased sediment deposition rates compared to the lower elevation hog marsh.

Scaling the effects of hog disruption of the mutualism on ecosystem functions to the landscape

By scaling up the local, microhabitat-scale results to account for the relative cover of each microhabitat within the system, we estimate that the hog marsh supports a 27% higher cordgrass biomass than the hog-free marsh at the 20 m^2 scale (t-test: $t_{28} = 17.6$, $p < 0.0001$; Fig. 5a), a result primarily driven by the high biomass of the undisturbed cordgrass on the hog marsh. In contrast, crab biomass is 107% greater within the hog-free than the hog marsh ($t_{28} = 46.1$, $p < 0.0001$; Fig. 5b). We estimate net denitrification is 5% greater in the hog marsh than

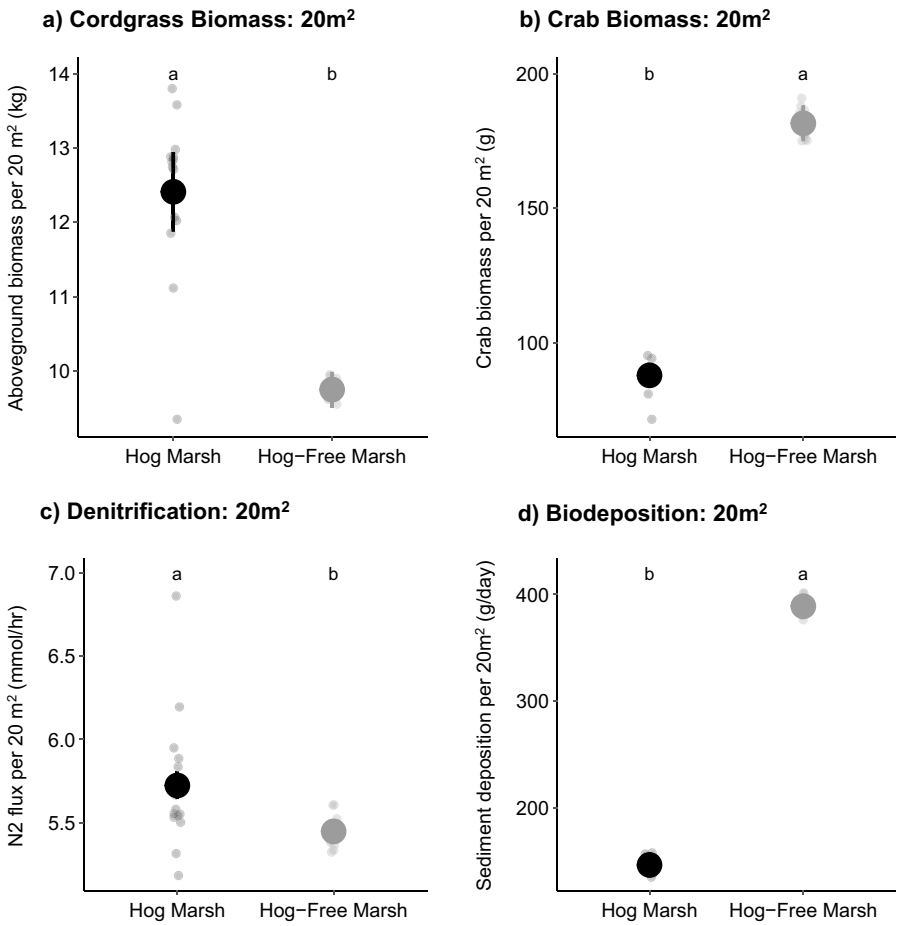


Fig. 5 Transect-scale (20 m^2) values for **a** cordgrass aboveground biomass, **b** crab biomass, **c** denitrification, and **d** sediment deposition accounting for the relative proportion of trampled cordgrass, undamaged cordgrass, and mussel areas on within each marsh. Letters indicate significant differences. Graphs show mean ± standard error with raw data behind

the hog-free marsh ($t_{28} = 12.1$, $p < 0.0001$; Fig. 5c) due to the trampled cordgrass microhabitat occupying a larger percent cover of marsh than mussel-containing microhabitats. Sediment deposition was 160% higher in the hog-free marsh than the hog marsh ($t_{28} = 45.3$, $p < 0.0001$; Fig. 5d).

Discussion

Our field surveys, caging experiments, ecosystem function measures, and transect scale extrapolation highlight that invasive hog disturbance to both players in the cordgrass-mussel mutualism can drive significant local- and landscape-scale variability across four key ecosystem functions. Hogs and mussels both contribute to a heterogenous marsh landscape, causing ecosystem functioning and service provisioning to vary across this patchy mosaic. Our surveys and caging experiment indicate that, within the hog-accessed marsh, hogs have trampled up to 27% of the marsh and eliminated, via foraging and consumption, over 65% of mussels. In their wake, hogs leave relatively few and almost-universally small mussel aggregations that provide reduced ecosystem function benefits compared to the larger, undisturbed aggregations (Angelini et al. 2015). Moreover, in evaluating soil properties, porewater nutrients, and surface elevations, our work sheds light on the widespread and far-reaching influence of hogs. By assessing four complementary ecosystem functions at multiple scales, this work highlights that invasive hogs are substantially constraining several functions (i.e., cordgrass biomass, crab biomass, and sediment deposition) fundamental to the health and sustainability of our coastlines through their influence on cordgrass, mussels, and their interaction. Our transect scale extrapolation of ecosystem functions indicates that the strong influence of hogs persists at a larger scale. This work provides evidence supporting our broader hypothesis that, where invasive species disrupt foundation species and their mutualist partners, they can powerfully modify community structure and ecosystem functions at the whole system level.

Hog disturbance is modifying the habitat structure provided by the dominant foundation species, decreasing cordgrass biomass locally while increasing it at the transect scale. This nuance is explained by undisturbed cordgrass on the hog marsh having the highest cordgrass biomass of all microhabitats. When upscaled to 20 m^2 where undisturbed cordgrass occupied 76% of the hog marsh in our transect surveys, the high cordgrass biomass of this microhabitat leads to the hog marsh having a higher cordgrass biomass than the hog-free marsh. Had a greater percentage of the cordgrass in the hog marsh been trampled (and therefore a reduction in undisturbed cordgrass cover), we likely would have observed the opposite trend due to the decreased biomass in trampled areas. Recent hog disturbance decreases primary production directly within damaged areas (Sharp and Angelini 2019), while prior disturbance and subsequent recovery can stimulate primary productivity (Oldfield and Evans 2016; Wu et al. 2021). Additionally, the hog marsh exhibited reduced bulk densities, which can increase nitrogen mineralization and contribute to higher levels of ammonium compared to the hog-free marsh (Fig. 3; Breland and Hansen 1996). Further, spillover of ammonium from hog wallows (Sharp and Angelini 2016), combined with additional input from hog feces, may further explain the increased cordgrass biomass on the hog marsh, as nitrogen is the limiting nutrient in the system (Jordan and Valiela 1982). Lastly, it is well-established that cordgrass biomass decreases with increasing marsh elevation (e.g. from 'tall-form' to 'short-form' cordgrass; McKee and Patrick 1988), so the 6.3cm reduction in the surface elevation of the hog marsh may have contributed to the pronounced differences in cordgrass biomass we observed. Though mussels are known to enhance cordgrass biomass (Bertness 1984; Angelini et al. 2015; Derksen-Hooijberg et al. 2018), this trend was not observed in either mussels + cordgrass microhabitat in this study. We speculate that the influence of mussels on cordgrass biomass was muted at our study site because this site contains higher porewater ammonium levels and smaller mussel mounds than locations farther north where the mutualism has been previously described (Angelini et al. 2015; Derksen-Hooijberg et al. 2018), minimizing the nitrogen-fertilization effect of the mutualism and suggesting that, at this site, hogs exert more influence on cordgrass biomass than mussels.

Hogs reduced crab biomass primarily by impacting both the cordgrass foundation species, and, to a lesser extent, its keystone mutualist. Crab biomass was reduced on the hog marsh compared to the hog-free marsh and, within cordgrass-only microhabitats,

was highest in undisturbed cordgrass on the hog-free marsh and lowest within trampled cordgrass. A similar reduction in macroinvertebrate biomass in the presence of hogs has been seen in comparable studies (Persico et al. 2017) and is likely caused by changes in soil integrity from hog trampling, a reduction in mussel cover, and direct predation of crabs by hogs. Soil bulk densities are known to mediate marsh crab distributions, as softer substrates cannot support burrows (Bertness et al. 2009) and soil bulk densities were lower in cordgrass-only areas on the hog marsh (Fig. 3a). Although we did not observe a statistically significant effect of mussels, mussels + cordgrass plots on the hog-free marsh were elevated compared to undisturbed cordgrass areas on the same marsh. Mussels also facilitate marsh crab populations across the larger marsh landscape (Angelini et al. 2015; Derksen-Hooijberg et al. 2019), and the reduction in mussel cover on the hog marsh likely contributed to a reduced crab population. Finally, hogs are known predators of fiddler crabs (Wood and Roark 1980) and may have reduced the marsh crab population through direct consumption. Hogs drove a > 50% reduction in crab biomass at the 20 m^2 scale in the hog marsh compared to the hog-free marsh. Given that diverse nekton utilize marshes as foraging habitat and feed on benthic marsh crabs (Rogers et al. 1984), the substantial reduction of crab biomass within hog damaged areas has the potential to cascade to higher-level predators, many of which sustain valuable recreational and commercial fisheries in the region.

At the local scale, net denitrification was elevated within the hog-free marsh, in mussel-containing microhabitats, and, across the cordgrass-only microhabitats, in hog trampled areas. The increased denitrification within these microhabitats suggests that hogs and mussels serve similar functions in stimulating nitrogen removal from the system. Mussels enhance sediment denitrification through their excretion of ammonium (Jordan and Valiela 1982; Derksen-Hooijberg et al. 2018) and oxygenation of the sediment (Bilkovic et al. 2017), resulting in coupled nitrification–denitrification. Similarly, hogs increase ammonium and aerate the sediment (Fig. 3c; Sharp and Angelini 2016; Hensel et al. 2021b), contributing to coupled nitrification–denitrification and net denitrification. The role of hog disturbance in stimulating denitrification is a novel finding and highlights the importance of measurements at multiple scales. Locally, the hog-free marsh supported elevated net denitrification within mussels + cordgrass and undisturbed cordgrass areas (Fig. 4c). But, at the transect scale, which accounts for areas with and without hog trampling, net denitrification is increased in the hog marsh (Fig. 5c). By aerating the sediment and increasing ammonium production, hogs have the potential to enhance the nitrogen removal services of the estuary. Further, an increase in hog disturbance or disturbance frequency would likely increase net denitrification across the marsh landscape because of the high N_2 fluxes in the trampled cordgrass. This pattern contrasts our cordgrass biomass metric where increasing the prevalence disturbance would decrease whole-marsh biomass. Of note, the N_2 fluxes recorded in mussel microhabitats are on par with other bivalve studies, but the non-mussel measurements, particularly within the trampled cordgrass microhabitat, are on the higher than other coastal marsh studies (Smyth et al. 2013; Bilkovic et al. 2017).

The 160% increase in sediment deposition on the hog-free marsh compared to the hog marsh is likely explained both by hogs consuming mussels, which enhance sediment deposition, and by hogs directly decreasing sediment accumulation via trampling and wallowing. The decreased deposition rates within cordgrass-only areas on the hog marsh compared to the hog-free marsh parallel our findings that the hog marsh is on average 6.3 cm lower in elevation than the hog-free marsh. Biodeposition by mussels is a known source of sediment deposition to salt marshes (Smith and Frey 1985), and biodeposits can enhance deposition rates in areas beyond the mussel mound (Crotty et al. 2023). We found that the highest deposition rates occurred in the mussels + cordgrass areas on the hog-free marsh and that deposition rates are reduced on the mussel-poor hog marsh, suggesting that mussels may be a key source of sedimentation. Additionally, as aboveground vegetation is an important driver of marsh sedimentation through its water baffling effects (Baustian et al. 2012), hog trampling of cordgrass has the potential to locally reduce deposition. In prior studies, reductions in marsh sedimentation in response to megafauna disturbance have been recorded, although results are inconsistent (Andresen et al. 1990; Elschot et al. 2013). Additionally, megafauna have been shown to decrease marsh elevation (Bakker et al. 2020), aligning with our elevation surveys. Our deposition measurements were

collected over a 24-h period (two high tides). Over a longer timeframe, these differences in deposition have the potential to be further amplified and to exacerbate the elevation reduction in the hog marsh versus the hog-free marsh (Crotty et al. 2023).

Effects of invasive-driven mutualism loss on ecosystem functioning and marsh persistence

Hogs are unique from other marsh grazers and consumers in that they affect both the dominant foundation species and its keystone mutualist partner. We expect greater disruptions to marsh functioning from hogs compared to other fauna because of the two-pronged disruption to a keystone mutualism. Specifically, hogs differ from nutria, another invasive species in the Southeastern US that reduces cordgrass biomass, because nutria impacts are limited to vegetation and cordgrass recovery is rapid following its removal (Shaffer et al. 2015). Invasive-driven mutualism loss has been identified in other systems and can have cascading impacts throughout food webs (e.g., Rogers et al. 2017). Yet even across a wide range of ecosystems and mutualistic interactions, hogs are unique among invasives for their impacts to both mutualistic partners (see Bond and Slingsby 1984; Traveset and Richardson 2006; Rodriguez-Cabal et al. 2013 for other examples of invasive-driven mutualism loss). Further, we show that the loss of a keystone mutualism alters ecosystem function and service provisioning, and that these effects can span spatial scales, spilling-over to locations outside of where the mutualism directly occurs (i.e., outside of mussel mounds).

The complex interactions between hog disturbance, mutualism loss, and other human-driven stressors are nuanced. Hogs pose a significant threat to marshes by reducing marsh sedimentation, disturbing sediment through trampling and wallowing, consuming sediment-accreting mussels, and lowering marsh elevation, factors that amplify marsh vulnerability to drowning. Sea level rise in the region has occurred at a rate of 3.18 ± 0.51 mm/yr for the past 50 years (Station 8720218 Mayport, FL, NOAA Tides & Currents) and the hog marsh, with an elevation 6.3 cm lower than the hog-free marsh and reduced sediment deposition, is considerably more susceptible to drowning due to sea level rise than the hog-free marsh. At the same time, hogs stimulated cordgrass biomass and net denitrification at the transect scale (Fig. 5), services also enhanced by mussels (Bertness 1984). Thus, while hogs are generally seen as a harmful, nuisance species in Southeast US (Giuliano 2010), their overall effects on marsh ecosystem service provisioning are somewhat ambiguous (Barrios-Garcia and Ballari 2012), and, for cordgrass biomass and nitrogen removal, their activities somewhat replace those of the mutualist mussel they are consuming. However, the ecosystem functions that hogs decrease (i.e., crab biomass and sediment deposition) show a greater proportional reduction than the increase in functioning from the metrics that are enhanced by hogs (i.e., cordgrass biomass and net denitrification).

While the mussel-cordgrass mutualism increases marsh resilience and resistance (Angelini et al. 2016; Derksen-Hooijberg et al. 2018) and hogs benefit marshes by enhancing nitrogen removal services, hog-driven mutualism disruption likely decreases marsh resistance to climate change by reducing marsh recovery from drought (Hensel et al. 2021b) and increasing marsh susceptibility to drowning (this study). Interestingly, human development, which is typically seen as a threat to marshes (Crain et al. 2009), appears to be providing these marshes a refuge from hogs. In our study, hogs are present in the marsh bordered by a wildlife management area and absent from a neighboring marsh bordered by human development, a trend that is common to salt marshes across the southeastern United States (Sharp and Angelini 2019). Human development along the marsh upland border is constraining access by hogs and, in doing so, not only preventing their direct impacts to cordgrass and marsh soil structure but also supporting the persistence of mussels, a vital mutualist in the system.

Taken together, our results lend support for concerted efforts to suppress hog populations, especially in areas where hogs intensively forage and wallow within salt marshes. Controlling hog populations is crucial to mitigate their adverse impacts on the cordgrass-mussel mutualism that is essential to the structure, function, and resilience of this high valued coastal ecosystem. Salt marshes are vulnerable to a host of human-induced stressors including development, rising sea levels, droughts, overgrazing, and nutrient pollution (Bromberg Gedan et al. 2009; Crain et al. 2009). Given that hogs compound some of these stressors both directly and by disrupting a critical mutualism, localized management to alleviate

the destructive effects of this prolific invasive consumer may be essential to sustaining these systems.

Acknowledgements Field work assistance from Sydney Williams, Julie Grissett, Kristie Perez, Emory Wellman, Donovan Mitchell, Chloe Schwab, and Jonathan Crabill. Lab assistance from Katie Heiden, Gabriela Reyes, and Heather Donnelly. We thank Andrew Altieri for his comments on the manuscript and an anonymous reviewer for their detailed comments.

Author contributions All authors contributed to the study conception and design. Data collection was performed by HF and AS. Data analysis was performed by HF. The first draft of the manuscript was written by HF and CA, AS provided edits on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding Funded by Florida Sea Grant (PD-21-03) and NSF Career Award (#1652628) to C. Angelini, UF/IFAS Early Career Seed Grant, USDA National Institute of Food and Agriculture (Hatch project FLA-TRC-005764), and NOAA NERR Science Collaborative to A. Smyth, and a Ruth D. Turner Fellowship to H. Fischman.

Data availability Datasets generated during this study are included as Online Resource 3. At the conclusion of the project, data will be publicly archived with the NOAA Centralized Data Management Office.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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