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Feral hog disturbance alters carbon dynamics in southeastern US salt marshes

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ABSTRACT: Disturbances that remove primary producers and alter substrate chemistry commonly influence ecosystem carbon dynamics. Because coastal wetlands are especially effective in sequestering carbon, quantifying how disturbances may alter their ability to perform this climate-regulating function is important for assessing their carbon storage potential. Here, we quantified soil respiration, litter decomposition, and soil organic carbon (SOC), as a proxy for carbon storage, in areas disturbed by invasive feral hogs *Sus scrofa* and in adjacent, undisturbed areas within 3 southeastern US salt marshes. Contrary to our hypothesis that hog overturning of soils would stimulate soil respiration, this metric was lower and both surface and subsurface litter decomposition rates were similar in disturbed relative to undisturbed areas across all sites. SOC was lower in disturbed versus undisturbed areas at 2 sites as hypothesized, but higher at 1 site. Surveys and analyses reveal that lower and less variable infauna, plant, and benthic algae densities likely suppressed soil respiration in hog-disturbed versus undisturbed areas, while the offsetting effects of lower invertebrate densities and higher soil temperature likely caused decomposition to be consistent within and outside of disturbed areas. Conversely, between-site variation in disturbance intensity, plant canopy structure, and burrowing crab densities mediated the SOC response. These findings suggest that hog removal of plants and disruption of soils can cause tracts of marsh to transition from carbon sinks to sources where these disturbances are intense enough to prohibit rapid plant recovery and promote the gradual respiration of carbon stocks from denuded soils.

KEY WORDS: Carbon cycling · Coastal wetland · Soil respiration · Litter decomposition · *Spartina alterniflora* · Benthic algae

INTRODUCTION

Wetlands mitigate floods, improve water quality, and provide important habitat for wildlife (Mitsch & Gossilink 2000, Tews et al. 2004). Despite occupying only 5 to 8% of the terrestrial land surface, wetlands store 20 to 30% of soil carbon worldwide and therefore play a disproportionately large role in regulating the global carbon cycle and climate (Chmura et al. 2003, Marín-Muñiz et al. 2014). These ecosystems are able to store carbon effectively due to 2 complementary features: their ability to maintain high rates of primary production and their low rates of soil respiration (Bridgham et al. 2006). Another significant mechanism through which wetlands accumulate carbon occurs when wetland plants slow water velocities and facilitate suspended organic matter deposition on the surface (McLeod et al. 2011). Once locally bound in plants or deposited on the surface, organic carbon accumulates in wetlands when waterlogged and anoxic soil conditions stifle microbe-driven carbon respiration belowground, such that rates of carbon input exceed rates of carbon loss (Bernal & Mitsch 2012, Mitsch et al. 2013). Because of these complementary

processes, coastal marshes, mangrove swamps, peatlands, and freshwater mineral soil wetlands accumulate carbon at rates of 2.2, 1.8, 0.71, and 0.17 Mg C ha^{-1} yr^{-1}, respectively (Bridgham et al. 2006); levels comparable to those reported for tropical forests and coral reefs (Whittaker & Likens 1973).

Disturbance can compromise the ability of wetlands to store carbon by smothering or killing plants as in the case of oil spills, drought, livestock grazing, and wrack deposition (Silliman et al. 2005, Alber et al. 2008, Macreadie et al. 2013, Enriquez et al. 2015). Disturbances can also enhance soil respiration through elevated drainage (Moore & Knowles 1989, Gedan et al. 2009) and the export of centuries of stored carbon where outbreaks of burrowing organisms cause creek bank collapse (Coverdale et al. 2014). In fact, the loss of soil carbon, which is particularly sensitive to land-use change, is the leading cause of increased carbon emissions in the last half century (Wantzen et al. 2012). While much research has focused on the mechanisms that enable wetlands to mitigate climate change through carbon sequestration (McLeod et al. 2011), our understanding of how disturbances are altering carbon dynamics through the removal of vegetation and modification of soil chemistry remains limited. This knowledge is essential to determining whether disturbances pose significant threats to wetland carbon storage capacity and if proactive management of disturbed habitats is necessary to maintain this critical wetland ecosystem service.

Coastal wetlands are particularly vulnerable to intensive natural and anthropogenic disturbances including shoreline development, sea-level rise, drought, and storms (Silliman et al. 2005, Lotze et al. 2006, Alber et al. 2008, Angelini et al. 2016). Worldwide, it is estimated that 25% of salt marsh and at least 35% of mangrove habitat has been lost since the 1800s (Valiela et al. 2001, Bridgham et al. 2006). Salt marshes, the focus of this study, are intertidal grasslands that form along temperate, sheltered coastlines where they provide habitat for commercially harvested organisms, improve water quality, stabilize shorelines, and mitigate coastal flooding (Vernberg 1993, Chmura et al. 2003). Like other coastal wetlands, salt marshes also store large quantities of carbon (4.8 to 87.2 Tg C yr^{-1} globally) through their high primary productivity, relatively slow rates of carbon respiration (Davis et al. 2015, Drake et al. 2015), and negligible release of methane (Poffenbarger et al. 2011, Hansen & Nestlerode 2014). While their potential for carbon storage is high, even subtle perturbations are capable of shifting salt marshes from carbon sinks to sources (Macreadie et al. 2013, Pavlov et al. 2014).

Invasive European feral hogs *Sus scrofa* disturb large tracts of land throughout the southeastern USA (Singer et al. 1984, Hayes et al. 2009, Barrios-Garcia & Ballari 2012, Haaverstad et al. 2014), including salt marsh habitats where they forage for plant roots, crabs, and mussels and wallow in the mud (Sharp & Angelini 2016). These activities are particularly apparent during spring and summer when hogs are more reliant on salt marshes because of scarce upland food sources and high temperatures (Wood & Brenneman 1980, Welander 2000, Bracke 2011). Much like the impacts of grazing livestock, hog trampling, rooting, wallowing, and defecation are activities that can intensively disrupt plants and alter soil properties such as soil compaction and nitrogen availability (Krull et al. 2013, Barrios-Garcia et al. 2014, Elschot et al. 2015). How hog disturbances affect salt marsh carbon dynamics and storage has yet to be evaluated (Barrios-Garcia & Ballari 2012).

Here, we quantified the effects of hog disturbance on rates and processes linked to salt marsh carbon cycling using data from 3 salt marshes distributed across 220 km of southeastern US Atlantic coastline. We hypothesized that hog disturbances stimulate oxygen- and temperature-dependent soil carbon respiration by overturning and aerating otherwise anoxic soils and by removing vegetation that would otherwise shield organic carbon on the marsh surface from photo-degradation. We predicted that these biogeochemical and physical changes would also result in higher litter decomposition rates and lower soil organic carbon in hog-disturbed than undisturbed salt marsh areas.

MATERIALS AND METHODS

Study sites and disturbance survey

We selected 3 sites within cordgrass *Spartina alterniflora*-dominated salt marshes on the southeastern US Atlantic coast where we confirmed the presence of hog disturbance: Matanzas State Forest, FL (29° 43' N, 81° 15' W); Timucuan Ecological and Historic Preserve, FL (30° 27' N, 81° 28' W); and Ossabaw Island Wildlife Management Area, GA (31° 45' N, 81° 7' W); hereafter, Matanzas, Timucuan and Ossabaw, respectively (Fig. 1). Using Google Earth, we scanned aerial images of each salt marsh for visible hog activity, including wildlife trails and areas with sparse or no vegetation cover. We then queried land managers for
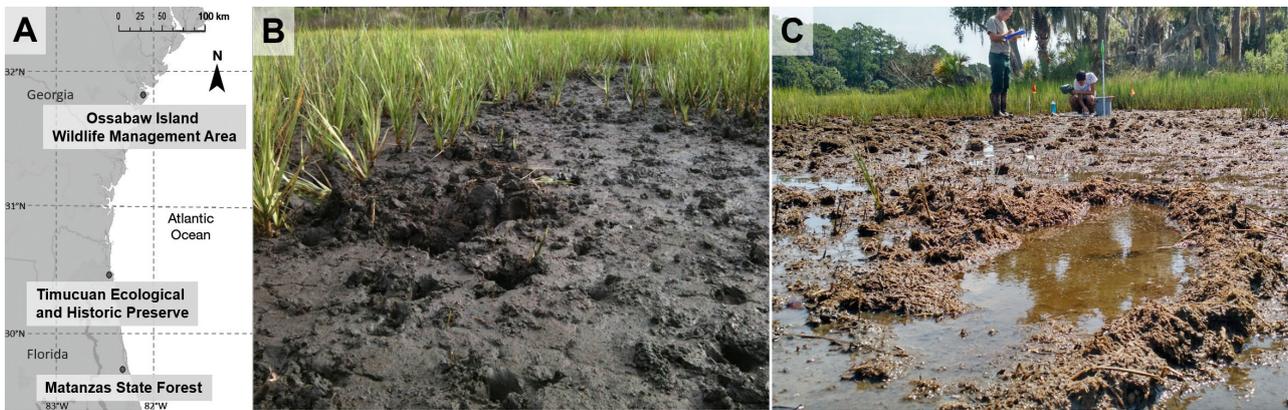
Fig. 1. (A) Location of the 3 salt marsh study sites and examples of feral hog rooting and wallowing (foreground) and healthy (background) *Spartina alterniflora* salt marsh at (B) Matanzas and (C) Ossabaw

knowledge of hog activity in marshes under their jurisdiction and surveyed potential sites on foot for wallows (depressions in the marsh resulting from hogs rolling in the mud), overturned and uprooted plants and soil, scat, and hoof prints. Hog-disturbed areas were delineated by the outward edge of visible hog activity, and measured 182.3 m^2, 115.5 m^2, and 754.7 m^2 in area at Matanzas, Timucuan, and Ossabaw, respectively.

At each site, observations of intact but sparsely distributed scat (<1 scat per 10 × 10 m area), well-defined wallows (i.e. with distinguishable hog head, body, and leg features), and rooting confirmed that hog disturbances were recent. Similar to many other hog-disturbed marsh areas observed across the region, soils in hog-disturbed areas at these 3 sites were softer and looser (i.e. less compact) relative to adjacent undisturbed marsh areas due to hogs breaking up the plant root-mat with their hooves and tusks. At these 3 sites, hog-disturbed areas also had higher porewater nitrogen concentrations relative to undisturbed marsh areas, an effect that arises due to the reduction of nitrogen uptake from fewer or no live plants and, likely to a lesser extent, hog deposition of feces and urine (Krull et al. 2013, Barrios-Garcia et al. 2014, Sharp & Angelini 2016).

Of the 3 sites, Timucuan had relatively less defined wallows and hoof- and tusk-created depressions, suggesting that hogs had less intensively used this site compared to Matanzas and Ossabaw. By tracking disturbance areas in reverse chronological order in Google Earth's historical aerial image database, we confirmed that disturbance areas first appeared in aerial images at both Matanzas and Ossabaw in January 2014. The hog disturbances were not present in historic aerial images at Timucuan, however,

and thus were first noted during our initial ground survey in April 2015.

Undisturbed marsh areas were 40 × 40 m tracts of salt marsh that supported intact cordgrass stands and were positioned approximately 10 m from hog-disturbed areas at the same tidal elevation and distance to both the nearest tidal creek and upland habitat edge as the hog-disturbed areas. In undisturbed areas, the marsh periwinkle snail *Littoraria irrorata*, which is a dominant cordgrass consumer in the region and is capable of expanding marsh die-off areas where they occur in high densities (100 to 600 m^{-2}; Silliman et al. 2005), occurred at densities of 72 ± 10, 12 ± 3, and 71 ± 9 snails m^{-2} at Matanzas, Timucuan, and Ossabaw, respectively. On cordgrass bordering the hog-disturbed areas, snail densities were 0, 0.67 ± 0.67, and 3.2 ± 1.62 snails m^{-2} at Matanzas, Timucuan, and Ossabaw, respectively, indicating snail densities were too low to cause or expand the disturbance at any of these sites. Additionally, there was no evidence of disturbance from other animals known to inhabit the surrounding forests within our study areas, including raccoon or deer.

Because the hog disturbance area at each site existed at the time our study began, we do not have before and after data on ecosystem structure and function in the hog-disturbed and undisturbed areas. Therefore, we cannot exclude the possibility that hogs targeted and created disturbances within areas of each of our 3 marsh sites where plant, invertebrate, and soil characteristics differed from those in adjacent, undisturbed areas. However, because we selected undisturbed and disturbed areas in our natural experiment that were within 10 m of each other and were standardized for elevation, distance to creek, and distance to upland landscape features that

are known to mediate salt marsh structure and function, we assume that the undisturbed areas are indeed representative of the marsh conditions that existed in the hog-disturbed areas before they were impacted by hog activities and thus function as a valid reference in this study.

Hog effects on soil respiration, litter decomposition, and soil organic carbon

To investigate whether hog activities influence soil respiration, we used a Li-COR 8100A flux system equipped with SoilFluxPro software and paired with a 10 cm survey chamber in September 2015 (Model 8100-102; Li-COR). At least 2 h before measurements were taken, 10 cm diameter PVC collars were inserted into the soil to a depth of 5 cm, with approximately 2 cm of the collar protruding from the soil surface (n = 5 collars in hog-disturbed and undisturbed areas per site, 30 collars total). All collars were positioned to exclude cordgrass stems and crab burrows. A single 105 s soil respiration rate measurement, reported in mmol CO_2 m^{-2} h^{-1}, was taken per collar. Nine of the 30 measurements exhibited extremely low values, indicating the collar was not properly sealed or had corrupted files, and thus were omitted from the analyses.

Next, to test whether hog activities influence carbon loss over the course of a season, we deployed litterbags. In early May 2015, we collected belowground cordgrass biomass from the upper 10 cm of soil at our 3 salt marshes sites. We rinsed sediment from roots and rhizomes over a 2 mm sieve and oven-dried the plant material at 65°C for 48 h. We separated the dried rhizomes and cut them into 4 cm segments. Each 5 × 5 cm litterbag was made of 1 mm fiberglass mesh to exclude macrofauna, filled with 15 rhizome segments and fine roots to achieve a final dry weight of 5 g, and heat-sealed. In early June, we deployed bags at 1 of 2 depths (the soil surface or 10 cm below the soil surface) in haphazardly chosen locations in both the hog-disturbed and undisturbed area at each site (n = 5 bags depth^{-1} in hog-disturbed and undisturbed areas per site, 60 total bags deployed). To do so, we carefully cut down to a depth of 10 cm and removed a 5 × 5 cm (length × width) soil core, secured a litterbag beneath, and replaced the core to disturb the soil as little as possible. Approximately 20 wk later, we collected all litterbags, with the exception of 3 bags which could not be found. To separate litter from accrued sediment, we emptied each bag into a bucket of water and poured the water

and contents back and forth between 2 buckets until heavier sediment particles had settled out. We then poured the bucket through a 250 μm sieve and rinsed off the finer sediment particles. Remaining material was oven-dried at 65°C for 48 h and weighed. Decomposition rate was calculated as mg litter lost d^{-1}.

To evaluate if hogs affect carbon storage in salt marshes, we collected 10 cm deep soil cores using a 7 cm diameter corer (n = 5 cores from hog-disturbed and undisturbed areas per site, 30 cores total). Four of the 30 cores were misplaced during transit to the lab and thus were not included in analyses. We divided soil into 0 to 5 and 5 to 10 cm segments to represent upper and lower rooting zones. We burned homogenized, oven-dried sub-samples from each soil core in a muffle furnace at 550°C for 2 h and determined organic matter content by loss on ignition (LOI). We converted organic matter content to soil organic carbon (SOC) using the following equation: SOC = 0.40 (LOI) + 0.0025 (LOI^2) (Craft et al. 1991).

Hog disturbance effects on salt marsh physical conditions and biota

To investigate mechanisms that may mediate hog effects on carbon dynamics within and across our sites, we first collected 20 ml of porewater in randomly chosen locations within hog-disturbed and undisturbed marsh areas (n = 3 measurements in hog-disturbed and undisturbed areas per site, 18 measurements total) using rhizon suction samplers (Rhizosphere Research Products) inserted into the top 10 cm of soil in July 2015. We then measured porewater salinity using a handheld refractometer (Extech Instruments). In July and August, we monitored soil temperature and reduction-oxidation potential—a proxy for oxygen availability (hereafter, redox potential) in locations positioned adjacent to litterbag and soil core extraction sites in hog-disturbed and undisturbed marsh areas. We measured temperature and redox potential 1 and 10 cm beneath the soil surface using an Orion Star A321 probe and Accumet Portable ORP Meter (Thermo Fisher Scientific; n = 5 measurements per depth in hog-disturbed and undisturbed areas per site, 30 measurements total).

To assess the effect of hog disturbance on plant cover and invertebrates, we recorded percent cordgrass cover, percent dead cordgrass cover, and the height of 5 haphazardly chosen, fully emergent stems within 50 × 50 cm plots positioned adjacent to the litterbags in hog-disturbed and undisturbed

marsh in late summer (n = 5 quadrats in hog-disturbed and undisturbed areas per site, 30 quadrats total). We also counted the number of fiddler crab *Uca pugnax*, mud crab (*Panopeus obesus* and *Eurytium limosum*), and marsh crab *Sesarma reticulatum* burrows in each plot as representative density measures for each crab species (Angelini et al. 2015). Finally, we quantified the biomass of diatoms, cyanobacteria, and green algae ($\mu g\ cm^{-2}$) using a handheld BenthoTorch (bbe Moldaenke; n = 5 readings in hog-disturbed and undisturbed areas per site, 30 readings total), as these benthic microbes can mediate soil respiration and contribute to soil organic carbon.

Data analysis

We analyzed the significance of site and hog disturbance on soil respiration, invertebrate community, and biogeochemistry response metrics using 2-way ANOVA. With 2-way nested ANOVA, we analyzed the effect size and significance of hog disturbance and the interaction of hog disturbance and site on litter decomposition, SOC, temperature, and redox potential with soil depth nested within each soil core or plot. For response metrics in which a significant interaction between hog disturbance and site was found, we conducted *a priori* tests to assess the significance of hog disturbance in each site using Bonferroni-adjusted p-values of 0.017 (0.5 divided by 3) to account for multiple tests and family-wise Type I error (Quinn & Keough 2002).

To evaluate the significance and relative importance of measured physical conditions and biota in mediating soil respiration, litter decomposition, and SOC response variables, we first tested for covariance among the environmental predictor variables (infauna densities, vegetation cover and canopy height, redox potential, and soil temperature) using a correlation matrix. We then ranked each predictor variable by total number of significant covariates: the highest-ranking variable had the largest number of covariates with p < 0.05. To remove redundant predictor variables, we removed all that co-varied with the highest-ranking predictor variable and repeated this process on the second highest-ranking predictor variable and so on until no predictor variable covariates remained. In cases where more than one predictor variable had equal numbers of covariates, we ranked higher the predictor variable that, according to our knowledge of the literature, should best explain the variation in the response variable. As a result of this covariate removal process, 6 out of

the 14 measured environmental predictor variables remained for inclusion in multivariate analyses in undisturbed marsh areas (surface soil temperature, total vegetation cover, marsh crab, mud crab and fiddler crab burrow density, and mussel density) and hog-disturbed marsh areas (surface soil temperature, subsurface redox potential, standing dead vegetation cover, marsh crab and fiddler crab burrow density, and mussel density).

For soil respiration, litter decomposition, and SOC response variables, we built generalized linear mixed-effects models (GLMMs) that included the remaining predictor variables with site as a random effect. We first centered and scaled all model predictor variables to interpret relative importance of each predictor variable indicated by regression coefficients in multivariate GLMM models (Schielzeth 2010). We then used backward stepwise regression to remove one variable at a time and selected the most parsimonious model by comparing the corrected Akaike's information criterion (AIC_c) values (Sugiura 1978). To summarize variance explained with and without the random effect of site in each model, we calculated conditional (R^2_C, including random effect of site) and marginal (R^2_M, not including random effect of site) R^2 values for GLMMs where the difference between R^2_C and R^2_M equals the variance explained by site alone (Nakagawa & Schielzeth 2013). We conducted separate analyses for hog-disturbed and undisturbed marsh areas for each response variable to discern whether different predictor variables governed each response in each area type.

All analyses were conducted using the statistical computing software R v.3.2.2 (R Core Team 2014).

RESULTS

Contrary to our hypothesis, flux chamber measurements indicated that soil respiration rates were 1.6-, 2.0-, and 7.3-times higher, on average, in the undisturbed than hog-disturbed areas at Matanzas, Timucuan, and Ossabaw, respectively (Table 1, Fig. 2). Litterbag analyses revealed that surface decomposition rates varied significantly between sites. Within sites, surface decomposition rates were relatively consistent in disturbed areas but highly variable in undisturbed areas (range in hog-disturbed vs. undisturbed areas across all sites: 10.0 to 10.3 vs. 6.33 to 17.0 mg d^{-1}, respectively; Table 1). Although differences between hog-disturbed and undisturbed salt marsh areas were not significant at any site, *a priori* tests

Table 1. Results from a 2-way nested ANOVA for response variables measured in 3 salt marsh sites on the Atlantic coast of Florida and Georgia in feral hog-disturbed and adjacent undisturbed marsh area types. SOC: soil organic content. Significant effects (p < 0.05) are highlighted in **bold**

	Residual df	Area type (df = 1)		Site (df = 2)		Area type × site (df = 2)	
		F-value	p-value	F-value	p-value	F-value	p-value
Carbon cycling							
Respiration	15	15.1	**<0.01**	3.41	0.06	1.20	0.33
Surface decomposition	23	0.09	0.77	5.29	**<0.05**	5.70	**<0.01**
Subsurface decomposition	22	0.06	0.81	1.25	0.81	1.77	0.39
SOC 0–5 cm	21	2.66	0.12	4.94	**<0.05**	11.4	**<0.001**
SOC 5–10 cm	23	8.29	**<0.01**	4.43	**<0.05**	3.74	**<0.05**
Soil and porewater							
Salinity	10	16.5	**<0.01**	95.9	**<0.001**	0.05	0.95
Temperature at 0 cm	24	20.9	**<0.001**	16.7	**<0.001**	13.7	**<0.001**
Temperature at 10 cm	24	42.0	**<0.001**	16.9	**<0.001**	22.3	**<0.001**
Redox potential (10 cm; mV)	24	10.2	**<0.01**	2.61	0.09	1.72	0.20
Vegetation and benthic fauna							
Cordgrass cover	24	509	**<0.001**	5.57	**<0.05**	5.47	**<0.05**
Average stem heights	24	239	**<0.001**	6.46	**<0.01**	13.1	**<0.001**
Mussel density	24	1.57	0.22	0.10	0.91	0.22	0.80
Fiddler crab burrow density	24	8.55	**<0.01**	0.27	0.77	2.36	0.12
Mud crab burrow density	24	2.70	0.20	0.83	0.59	0.45	0.64
Marsh crab burrow density	24	2.70	0.11	6.43	**<0.01**	13.9	**<0.001**
Diatom density	24	12.84	**<0.01**	16.2	**<0.001**	6.16	**<0.01**
Cyanobacteria density	24	1.44	0.24	9.50	**<0.001**	0.42	0.66
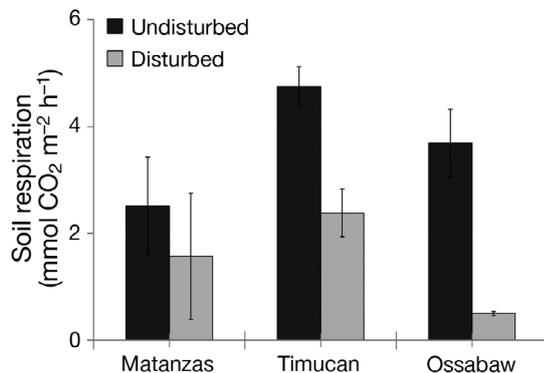
Fig. 2. Soil respiration in feral hog-disturbed and undisturbed marsh areas. Data are shown as the mean ± SE of 30 replicate readings per area type per site
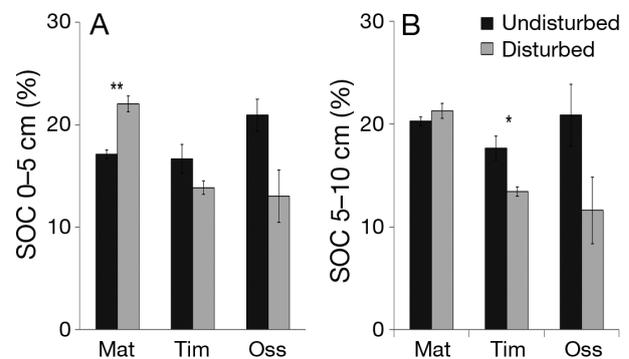
Fig. 3. Soil organic carbon (SOC) (mean ± SE) at (A) 0–5 cm (n = 5) and (B) 5–10 cm (n = 5) depths in feral hog-disturbed and adjacent undisturbed marsh areas along Atlantic coasts of Florida and Georgia, USA. Asterisks indicate significant pairwise differences (*p < 0.05; **p < 0.01) between area types

revealed that surface decomposition rates differed most between hog-disturbed and undisturbed areas at Matanzas, where decomposition was higher in undisturbed than hog-disturbed marsh area, and least at Timucuan. At 10 cm depth, decomposition rates varied little across sites or with hog disturbance (range of all measurements: 9.3 to 10.0 mg d^{-1}). At Timucuan and Ossabaw, SOC at both 0 to 5 and 5 to 10 cm depths was lower in hog-disturbed relative to undisturbed marsh areas, although this effect was only significant at subsurface depths in Timucuan

($a priori$ test for the effect of hog disturbance on subsurface SOC at Timucuan: $F_{1,8}$ = 10.8, p < 0.02; Fig. 3, Table 1). However, the reverse pattern was observed at Matanzas, where SOC was significantly higher in surface soils in hog-disturbed than undisturbed areas ($a priori$ test for the effect of hog disturbance on surface SOC at Matanzas: $F_{1,7}$ = 36.1, p < 0.001; Table 1, Fig. 3A). SOC was also higher in the hog-disturbed area at the subsurface at this site, but this effect was not significant.
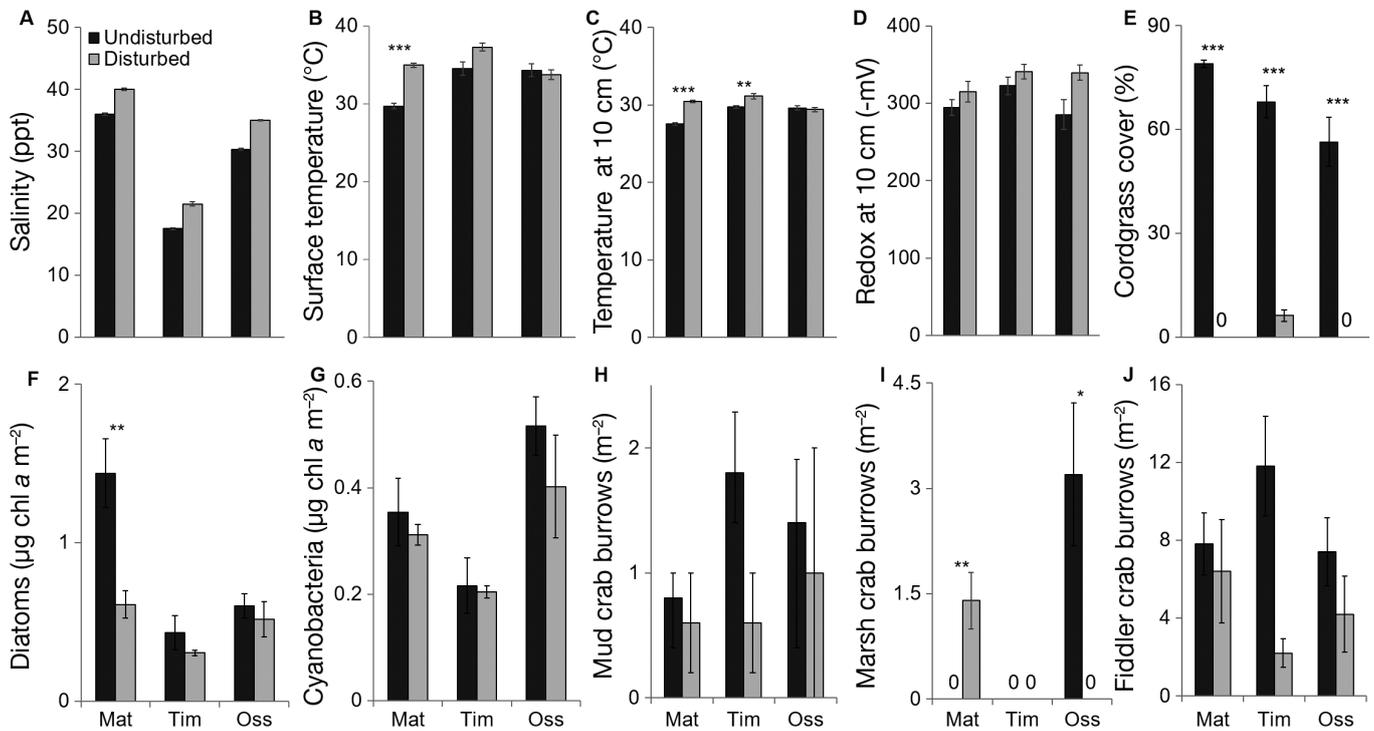
Fig. 4. Physical and biotic conditions (mean ± SE) in undisturbed (black) and hog-disturbed (grey) marsh areas at the same 3 salt marsh study sites as in Figs. 2 & 3. Redox: reduction-oxidation potential. Asterisks indicate significant pairwise differences (*p < 0.05; **p < 0.01; ***p < 0.001) between hog-disturbed and undisturbed areas for factors that had a significant interaction between site and hog disturbance

Porewater salinity was 4 to 5 ppt higher, on average, in hog-disturbed than undisturbed marsh areas across all sites (Table 1, Fig. 4A). Hog-disturbed areas generally had higher average soil temperatures at the surface and at 10 cm depth than undisturbed areas, but the magnitude of this response varied between sites: Matanzas exhibited the largest difference in temperature at both depths, followed by Timucuan and Ossabaw (Table 1, Fig. 4B,C). Soil redox potential was significantly more positive, indicating higher oxygen availability, in undisturbed areas than hog-disturbed when all sites were pooled (Table 1, Fig. 4D).

Hog disturbance also mediated marsh biota, such that lower plant cover and lower densities of most fauna were observed in hog-disturbed than undisturbed areas. At both Matanzas and Ossabaw, we observed no cordgrass in the disturbed areas and just 6.2% cordgrass cover at Timucuan. In undisturbed marsh areas, cordgrass percent cover averaged at least 55% at all 3 sites, which was significantly higher than hog-disturbed areas (Table 1, Fig. 4e). Stems remaining in the Timucuan hog-disturbed area (the one site that maintained some cordgrass cover) were also significantly shorter than in the adjacent, undisturbed marsh area (*a priori* test for the effect of hog disturbance on stem height at Timucuan: $F_{1,8}$ = 15.0, p < 0.01). While we observed 33, 50, and 100% fewer mussels, on average, in hog-disturbed than undisturbed marsh areas at Matanzas, Timucuan, and Ossabaw, respectively, these differences were not statistically significant due to the clustered distribution of this species in the marsh and, hence, the high variability in the number of mussels m^{-2} (Table 1). Benthic diatom biomass was 2.4-, 1.4-, and 1.2- times higher in hog-disturbed than undisturbed areas at Matanzas, Timucuan, and Ossabaw sites, respectively (Table 1, Fig. 4F). In contrast, cyanobacteria biomass was generally lower in hog-disturbed than in undisturbed areas, although these differences were not significant. Cyanobacteria biomass differed across sites, however, with Ossabaw having approximately 40 and 200% higher cyanobacteria biomass than Matanzas and Timucuan, respectively (Table 1, Fig. 4G). Green algae biomass was very low (<0.04 µg cm^{-2}) and did not differ across sites or with hog disturbance.

Mud crab burrow densities did not differ across sites or with hog disturbance and were generally low (<1 burrow m^{-2} on average; Fig. 4H). Marsh crab burrows were only present at Matanzas in hog-disturbed

Table 2. Results of generalized linear mixed-effects model analyses testing the effects of environmental predictor variables on carbon-related response variables in salt marsh areas with disturbance from feral hogs (e.g. overturned soil, wallow pits, and trampled vegetation) versus undisturbed salt marsh areas on the Atlantic coast of the southeastern USA. Conditional (includes random effect of site) R^2_C and marginal (without random effect of site) R^2_M values and ΔAIC_c score representing goodness of model fit compared to a null model indicate the strength of each model. Mussels: ribbed mussel density; marsh: marsh crab burrow density; mud: mud crab burrow density; veg cover: standing vegetation. Models with no significant improvement (<2.0 ΔAIC_c) from their respective null model were omitted. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$

Response variable	Model variables	Coefficient	R^2_C	R^2_M	n	ΔAIC_c
Surface decomposition						
Disturbed	Mussels*	2.2	0.49	0.48	15	4.13
Subsurface decomposition						
Undisturbed	Marsh**	1.01	0.72	0.38	14	16.0
SOC 5–10 cm						
Undisturbed	Marsh*** + Mud*** + Veg cover*	4.2–2.0–1.5	0.96	0.59	15	11.9

areas and at Ossabaw in undisturbed areas (*a priori* tests for the effect of hog disturbance at Matanzas: $F_{1,8} = 12.25$, p < 0.01; and Ossabaw: $F_{1,8} = 9.85$, p < 0.05; Table 1, Fig. 4I). There were fewer fiddler crab burrows in hog-disturbed than undisturbed areas at Timucuan and Ossabaw, but similar densities at Matanzas in hog-disturbed and undisturbed areas (Table 1, Fig. 4J).

GLMMs revealed that surface decomposition in hog-disturbed areas was positively correlated with ribbed mussel density, with only 1% of the variation in this response variable being explained by random site effects (Table 2). At subsurface depths in undisturbed areas, however, decomposition rate was most positively correlated with marsh crab burrow density with 34% of the variance explained by random site effects (Table 2). Similarly, subsurface SOC (5 to 10 cm depth) was positively correlated with marsh crab burrow density, which extend through the deeper soil depths from which these cores were taken, and was secondarily negatively correlated with mud crab burrow density and cordgrass cover, with 37% of variation in this response variable explained by random site effects (Table 2). No environmental predictor variables explained significant variation in soil respiration in hog-disturbed or undisturbed marsh areas, surface decomposition or SOC in undisturbed marsh areas, or surface decomposition, surface SOC, or subsurface SOC in disturbed marsh areas.

DISCUSSION

In this study, we showed that feral hog disturbances can stifle soil respiration, have little net effect on litter decomposition, and drive loss of SOC, and that the

magnitude of these effects varies across marshes. In trampling cordgrass, this system's dominant foundation species, and homogenizing soil gradients critical for regulating hydrology, biochemical processes, and biota as they forage for crabs, mussels, and roots (Lane et al. 1998, Moffett et al. 2012), hogs change the physical and biological conditions that govern carbon uptake, storage, and release. In particular, hogs destroy patches of cordgrass, whose stems take up and store carbon aboveground, facilitate dissolved organic matter deposition, and shade the soil surface to modulate photo-degradation of deposited organic material, and whose roots store carbon and mediate microbial and autotrophic respiration. Hogs also depress the density of some benthic invertebrate ecosystem engineers (e.g. mussels and crabs) by directly consuming some species as well as by removing the cordgrass habitat upon which many species depend. Together, the results from our natural experiment indicate that hog-provoked shifts in environmental conditions can cause soil respiration rates to slow, litter decomposition rates to change little due to offsetting mechanisms, and SOC to decline at sites where hogs do not leave behind persistent pools that facilitate suspended organic carbon deposition and depress respiration. Over the long term, we anticipate that hog activities will transform patches of salt marsh from carbon sinks to sources by reducing their soil carbon accumulation capacity via the loss of cordgrass and enabling carbon previously stored in marsh soils to be gradually lost via respiration.

Contrary to our hypothesis, soil respiration rates were significantly lower in hog-disturbed than undisturbed areas when all 3 sites were pooled. Other studies have shown that soil respiration increases up to 33 times that of undisturbed soil immediately fol-

lowing disturbances caused by tilling, hog rooting, or geese grubbing (La Scala et al. 2005, Gesch et al. 2007, van der Wal et al. 2007). However, after approximately 10 d, much less than the time from initial disturbance to time of the soil respiration measurements that we report on herein, respiration returns to pre-disturbance or even lower levels (La Scala et al. 2005). The relatively high respiration rates that we observed in undisturbed marsh areas may be explained by at least 3 complementary characteristics of these areas: enhanced benthic diatom biomass and microbial turnover (Gribsholt et al. 2003), higher densities of burrowing crabs and mussels, and higher live cordgrass cover relative to disturbed areas. The burrowing crabs and mussels that we observed in higher densities in undisturbed areas can play a key role in aerating the soil and stimulating microbial respiration (Bertness 1985, Angelini et al. 2015). Concurrently, the higher live cordgrass cover in undisturbed areas also enhances respiration both through the presence of oxygen-leaking aerenchyma that boost soil aeration and through autotrophic respiration (Houghton & Woodwell 1980). The high cordgrass cover in undisturbed areas, which was as much as 7 times greater than in hog-disturbed areas, also permits litter to be supplied more continuously to the marsh surface, thereby fueling microbial respiration (Currin et al. 1995). Although the GLMMs did not reveal significant relationships between these biotic predictor variables and soil respiration to provide clear support for these proposed mechanisms, we suspect this was due to the relatively small number of respiration measurements taken (n ≤ 5 in hog-disturbed or undisturbed areas) at each site and the limited variability in many of these biotic predictor variables measured (Table 2, Fig. 4). Despite respiration being greater in undisturbed areas, a prior study revealed that rates of carbon uptake via photosynthesis from lush cordgrass canopies observed in these areas may be 2.6 times greater than rates of carbon loss (Mendelssohn & Morris 2002), indicating that undisturbed marsh areas experience a net gain in carbon over time. In hog-disturbed areas, conversely, little carbon uptake from scraps of remaining cordgrass with stunted growth (Sharp & Angelini 2016) and low benthic algae biomass coupled with sustained soil respiration is likely resulting in the observed reduction of stored soil organic carbon.

Also in contrast to our predictions, litter decomposition was not consistently higher at the soil surface or subsurface in hog-disturbed compared to undisturbed areas. However, these results are consistent with other studies that have compared litter decomposition

in hog-disturbed versus undisturbed areas in different forest types (Krull et al. 2013, Barrios-Garcia et al. 2014). We suspect that we did not detect a substantial difference in litter decomposition at the soil surface because of the high variability in this measure, particularly in undisturbed areas, and because of the presence of different and offsetting mechanisms mediating this process within hog-disturbed and undisturbed areas. Specifically, our analyses revealed that the slightly lower surface litter decomposition rates measured in the disturbed areas may have arisen due to fewer mussels in these areas. The pseudofeces of mussels enrich the soil, potentially enhancing decomposition rates in undisturbed areas (Gribsholt et al. 2003, Derksen-Hooijberg et al. 2017), which generally have more mussels compared to hog-disturbed areas. At the subsurface in undisturbed areas, our analyses found that litter decomposition was positively correlated with the burrow density of marsh crabs, a species that maintains burrows that penetrate far deeper than mud or fiddler crab burrows. This indicates that spatial variation in bioturbating animals may be a key driver of decomposition across soil depths within tracts of undisturbed marsh.

In contrast to the patchy litter decomposition dynamics in undisturbed areas, it is likely that strong and persistent solar radiation reaching the litterbags, elevated soil surface temperatures caused by the lack of vegetation shading, and potentially higher nitrogen availability offset lower biotic activity levels to modulate litter breakdown in hog-disturbed areas (Krull et al. 2013, Sharp & Angelini 2016). Solar radiation can increase both photochemical degradation of surface organic matter and respiration rates of surface detritivores, thereby accelerating decomposition (Moran et al. 2000). However, no predictor variables related to these mechanisms (e.g. soil temperature, cordgrass cover) emerged as significant drivers of surface or subsurface decomposition in hog-disturbed areas according to our analyses (Table 2), a finding that may be due to the limited variation in decomposition rates measured across soil depths in hog-disturbed areas. Importantly, because our litterbag mesh size was small enough to prevent macrofauna from directly accessing and fractionating the litter to initiate decomposition (Barrios-Garcia et al. 2014) but was large enough to allow very small litter shreds to leak out, the decomposition rate measurements reported herein provide a relative, rather than absolute, measure of the litter decomposition process. Regardless of the variation in and limitation of these surface and subsurface litter decomposition measures, a net loss of organic carbon will arise in hog-disturbed areas over

time. This is because these disturbed areas experience less local input of organic carbon from senescing live plants (Janzen et al. 1998), lower plant-trapping of suspended organic material (McLeod et al. 2011), and continuous soil carbon loss via litter decomposition and soil respiration (Raich & Schlesinger 1992). Collectively, these altered dynamics result in carbon export exceeding import in denuded areas.

Indeed, our SOC measures indicate that belowground carbon stores are likely beginning the process of gradual, sustained loss in hog-disturbed areas within 2 of our 3 study sites, despite the fact that these disturbed salt marsh tracts exhibit suppressed rates of soil respiration and decompose litter at rates indistinguishable from the undisturbed marsh areas. At Timucuan and Ossabaw, SOC, and hence soil carbon pools (Macreadie et al. 2017), was slightly lower in hog-disturbed relative to undisturbed areas, indicating that carbon in disturbed marsh areas was being exported or lost via respiration faster than it was being stored (Jobbágy & Jackson 2000). Our results, which indicate a 20 and 39% loss in surface SOC in hog-disturbed areas on average at Timucuan and Ossabaw, respectively, are similar in magnitude to those reported in Macreadie et al. (2013) which found that wrack-disturbed areas experience a 30% loss in SOC compared to undisturbed areas in the 1 to 5 cm depth zone. At Matanzas, the only site that exhibited higher SOC in hog-disturbed areas, we suspect that hog-generated wallows and pools not only facilitated the accumulation of tidally-imported fine and particulate suspended organic carbon but also created anoxic, high salinity conditions to suppress microbial activity, leading to increased SOC levels relative to the adjacent undisturbed marsh. Specifically, the Matanzas hog-disturbed area was characterized by many depressions filled with stagnant, highly saline water and flocculent debris (Fig. 1B), while the surrounding vegetated areas had no standing surface water. Due to the significantly different dynamics occurring at Matanzas versus the other sites, the GLMM model revealed no significant predictors of surface SOC.

We also found that SOC was positively correlated with marsh crab burrow density at the subsurface and negatively correlated with mud crab burrow densities and vegetation cover in healthy, undisturbed marsh areas. Marsh crabs *Sesarma reticulatum* are known to colonize substrates with high structural integrity (i.e. those with high soil carbon content) that can support their large burrow complexes (Bertness et al. 2009). Therefore, rather than marsh crabs stimulating subsurface SOC, marsh

areas exhibiting relatively high SOC, such as those observed at Matanzas, may simply attract higher marsh crab densities. Similarly, mud crabs tend to burrow in soft, muddy substrates, such as those found on mussel mounds and creek banks (Kneib & Weeks 1990), and were thus negatively correlated with subsurface SOC in undisturbed marshes (areas with low subsurface SOC tend to be soft). Finally, the significant, negative correlation between vegetation cover and subsurface SOC in undisturbed marshes seems counter-intuitive given that vegetation is a primary contributor to SOC. However, this result may arise due to lower vegetation cover in undisturbed marsh areas being associated with short-form cordgrass, which has a higher ratio of belowground to aboveground biomass than intermediate- and tall-form cordgrass, thereby increasing subsurface SOC despite low overall cover (Ellison et al. 1986). The substantial variability in SOC and soil structure that we observed between our 3 sites has been found in other coastal marshes disturbed by livestock grazing. In particular, livestock often cause a significant decrease in carbon storage and loss of soil compaction in naturally softer, sediment-based marsh sites, but initiate the opposite pattern in tougher, peat-based marshes that can better support these heavy-bodied grazers (Hirota et al. 2005, Wantzen et al. 2012, Elschot et al. 2015, Enriquez et al. 2015, Davidson et al. 2017). At all of our sites, however, it is unlikely that there was a large enough supply of organic carbon, whether imported or locally produced by benthic algae, to offset the near complete loss of vegetation in hog-disturbed areas. Thus, we suspect that, while hog-created depressions have the potential to locally increase carbon stocks by accruing carbon from external sources, hogs generally decrease salt marsh carbon storage over time.

CONCLUSIONS

Cumulatively, our findings support prior research in suggesting that highly productive live marsh plants and intact marsh soil structure operate in concert to create conditions conducive to enhancing soil carbon storage. In disrupting both these critical features, hogs and likely many other agents of disturbance in salt marshes (e.g. invasive nutria, Ford & Grace 1998; crab herbivores released from predator-control, Holdredge et al. 2009; drought-induced die-off, Silliman et al. 2005; wave-driven creek back collapse, van de Koppel et al. 2005; direct anthropogenic manipulation, Wasson & Woolfolk 2011; livestock grazing, Elschot et

al. 2015; and wrack, Macreadie et al. 2013) undermine their carbon storage potential. Moving forward, ecologists and managers are challenged to work together to identify which of these disturbance agents have the most detrimental effects on carbon sequestration processes as well as what features make some wetlands more vulnerable to carbon storage loss than others. Information derived from such collaboration will be critical for prioritizing where investments in management (e.g. hog culling, shifting livestock grazing regimes, reducing overharvesting of predators to stabilize food webs) should be made to sustain the carbon storage capacity of coastal landscapes.

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