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ORIGINAL PAPER

The role of landscape composition and disturbance type in mediating salt marsh resilience to feral hog invasion

Sean J. Sharp · Christine Angelini

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Abstract Habitat patch composition and configuration mediate the fitness and distribution of many species. However, we know little about how this landscape complementation may influence the distribution of an invasive species' ecological impacts and, in turn, how this affects ecosystem resilience to disturbance. We surveyed > 820 km of coastline to evaluate how landscape complementation mediates patterns in invasive feral hog (*Sus scrofa*) rooting, trampling and wallowing disturbances in southeastern US salt marshes and assessed marsh resilience to these behaviors in an 8-site survey and 13-month field experiment. We discovered that hog rooting and trampling most often occur where hardwood forest comprises > 30% and salt marsh < 22% of habitat surrounding each surveyed site, respectively, while wallowing correlated most strongly with salt marsh invertebrate densities. At the 8 survey sites, vegetation cover, soil organic carbon, and surface elevation were consistently lower, and soil anoxia and porewater ammonium-nitrogen higher, in hog-disturbed relative to undisturbed areas. The experiment revealed that vegetation can recover when rooted or trampled, but remains depressed when wallowed or repeatedly disturbed. Together, these findings provide novel evidence that habitat patch composition at landscape scales can act together with local habitat attributes to dictate invasive species' disturbance patterns and highlight areas most vulnerable to invaders. In salt marshes, insights gleaned from such consideration of landscape complementation can inform conservation and management strategies for curbing the impact of this prolific, global invader.

Keywords Carbon sequestration · Invasive species · Landscape complementation · *Spartina alterniflora* · *Sus scrofa*

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S. J. Sharp (✉) · C. Angelini
Engineering School for Sustainable Infrastructure and Environment, University of Florida, Gainesville, FL 32611, USA
e-mail: seanjsharp@gmail.com

Introduction

Landscape features and habitat patch characteristics can mediate community and population structure (Polis et al. 1997; Wiegand et al. 1999). For example, mapping river networks and measuring river distance between communities can help explain large compositional differences in fish communities that are close in overland distance, but distantly connected via river corridors (Campbell Grant et al. 2007). For many populations, the density (Pope et al. 2009), dispersal

(Roe and Georges 2007) and fitness (Fagan 2002) of individuals can be affected by the size, proximity, and accessibility of critical habitat patches, a concept known as *landscape complementation* (Dunning et al. 1992). Ecosystems with poor landscape complementation in which critical habitat patches containing key resources are small, dispersed, and/or inaccessible typically support smaller (Choquenot and Ruscoe 2003) and more genetically isolated populations (Campbell Grant et al. 2007) than those with high complementation. However, landscape complementation may also influence ecosystem structure and function by mediating the frequency and intensity with which a population exploits a habitat patch (Hobbs 2001). In this context, landscape complementation may be especially useful for understanding and managing outbreaks of invasive species.

The success of invading populations can be influenced by size and spacing of habitat patches that mediate the invader's fitness, such as propagation corridors (Costello et al. 2011), desirable breeding grounds (Soh et al. 2002), and augmented feeding habitat (González-Bernal et al. 2012). Invaders, in turn, can have spatially variable effects on ecosystem structure and function through their exploitation of different patches as they advance across landscapes. The strength and nature of this exploitation likely depend on how patch size and quality mediate the type and intensity of invader activities that occur within a given patch – e.g. the invader may use some patches for foraging and others for nesting. Because these activities vary in the size or severity of disturbance they provoke, habitat patches may, in turn, vary in their resilience (Holling 1973) to species invasions. For instance, invasive nutria (*Myocastor coypus*) excavate creek banks to create nests (Atwood 2007), and also graze vegetation on higher elevation marsh platforms (Ford and Grace 1998)—inducing disturbances that marshes exhibit low and high resilience to, respectively. Despite the potential for landscape complementation to control invasive species success and ecological impacts, no studies have tested how habitat patch composition affects patterns in the behavior of an invasive species, resulting disturbance severity, or habitat patch resilience to different types of behavior.

The feral hog (*Sus scrofa*, hereafter hog) is a prolific invader across Africa, Oceania, and the Americas where it exerts strong ecological effects (Barrios-Garcia and Ballari 2012). Hog use of specific patches can vary spatially and temporally depending on patch quality and seasonal shifts in climate and food availability (Wood and Brenneman 1980). For example, hogs shelter in forests year round, forage for acorns in hardwood hammocks in fall and winter months, use dunes and beaches during summers to depredate sea turtle nests, and invade wetlands during warmer months both to root for invertebrates and plant tubers, and to wallow in the mud to regulate their body temperature (Bracke 2011; Sharp and Angelini 2016). Several studies have examined hog utilization of these habitat patches (Wood and Brenneman 1980; Barrios-Garcia and Ballari 2012; Porter et al. 2014; Persico et al. 2017). However, none have examined whether landscape scale heterogeneity in habitat patch composition drives variation in the extent and nature of hog disturbance within specific patches they utilize.

Hogs are particularly prevalent across the southeast US coastal plain, a region characterized by a mosaic of different habitat patches (Wood and Brenneman 1980; Singer et al. 1984; Kaller and Kelso 2006; Persico et al. 2017). Salt marshes in this region provide several valuable ecosystem services (e.g. maintenance of fisheries, coastal protection, nutrient cycling, and recreation) and are commonly utilized by hogs (Barbier et al. 2011). Recent research suggests that hogs may compromise salt marsh carbon storage capabilities by inhibiting vegetation recovery (Sharp and Angelini 2016; Persico et al. 2017). However, it remains unclear how resilient marshes are to different hog activities, including rooting, wallowing and trampling, and if the extent of these disturbances varies among marshes. Additionally, the relative importance of habitats comprising a hog's home range and of different salt marsh features in controlling hog disturbance is uncertain.

Here, we present results from a survey and land cover analyses of 53 salt marshes, a more detailed 8-site survey, and a 13-month experiment that investigate: (1) how landscape composition (i.e. the proportional cover of different habitat patches comprising a hog's home range) and salt marsh features mediate hog rooting, trampling, wallowing, and total hog disturbance extent in salt marshes and, (2) how these unique disturbances affect marsh resistance and recovery. We hypothesized there would be little, intermediate and high levels of hog disturbance within home ranges dominated by urban development, pine stands that provide shelter but produce little hog food, and oak-dominated, mast-producing, upland hardwood forests, respectively. We also predicted that the cover of succulent plants (which hogs easily uproot) would correlate positively with hog rooting disturbance extent. Finally, we hypothesized that salt marsh vegetation and soil carbon stores would exhibit the highest resilience to trampling, intermediate resilience to rooting, and low resilience to wallowing due to the relative impacts of each disturbance to soil structure and infauna (Bertness 1985; Sharp and Angelini 2016). We demonstrate how landscape and local habitat features can predict invasive species' disturbance distribution while assessing salt marsh resilience to hogs based on the nature of their activities.

Materials and methods

Regional hog disturbance survey

From May 2015 to September 2016 we surveyed salt marshes from Florida (29.50°N) to the northern coast of South Carolina (33.86°N) to evaluate hog disturbance distribution across 820 km of the southeastern US coastal plain (Fig. 1a). To establish unbiased survey locations and sample a range of landscape compositions, we used a random number generator to identify 50 latitudes within these survey boundaries. At each latitude, we identified where the salt marsh intersected upland habitat in Google Earth, which, for three latitudes, included sites on both a barrier island and mainland, resulting in a total of 53 survey sites (Table S1). Seasonal hog hunting is permitted at most sites.

We accessed each site once during the growing season (April–October) by foot or motorboat and established a transect that was 20 m wide and ran 500 m parallel to the upland-marsh border. Along each transect we counted all hog wallows and delineated the perimeter of all other hog disturbed areas, defined as the boundary between healthy vegetation and clearly trampled, or rooted marsh, that intersected the transect, and assigned each area a primary cause of disturbance (Fig. 1b; trampled, wallowed, or rooted). High hoofprint densities denoted trampled areas, though we did not assess the degree of trampling, only if it was present or not. Since these areas are not used by any other large animals (e.g. livestock or horses) and hoof prints were observed in trampled areas, we assume trampling damage was primarily caused by hogs. Depressions 0.1–0.2 m deep by approximately 1 m long denoted

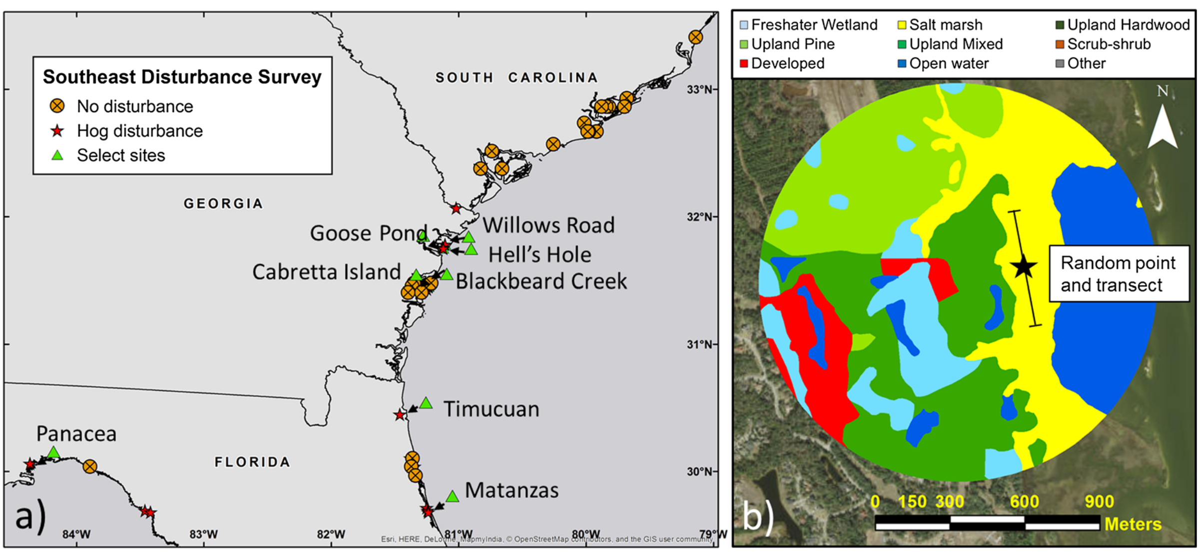

Fig. 1 Hog survey of southeastern US coastal plain showing **a** the distribution of salt marsh sites and **b** land cover classification within a typical 2 km^2 hog home range. "Hog disturbance" sites had some form of hog disturbance observed within 20 m of the 500 m survey transects; "No disturbance" sites had no visible signs of hog disturbance recorded; and "Select sites" were sites surveyed in more detail

areas wallowed by piglets and hogs, and areas in which vegetation and soil had been overturned resulting in snout-sized depressions and adjacent mounds denoted areas rooted by hogs. We also traced the length of trails trampled by hogs, indicated by hog hoofprints and scat within the trial. All disturbed area perimeters and trail lengths were measured using a Trimble Geo 7× GPS receiver accurate to within 1 cm (Trimble, Sunnyvale, California, USA). To standardize disturbance measurements, we converted wallow counts to area by multiplying the average area of a single wallow (0.72 m^2, based on 50 wallow measurements) by the total number of wallows and converted linear trails into trampled area by multiplying trail length by 0.5 m, their average width.

To assess salt marsh features, we positioned 0.25 m^2 quadrats every 50 m along each 500 m transect in undisturbed salt marsh areas and in each: visually estimated vegetation percent cover, measured the height of the 5 tallest non-flowering *Spartina alterniflora* and/or *Juncus roemarianus* stems, counted the number of periwinkle snails (*Littoraria irrorata*), ribbed mussels (*Geukensia demissa*), and burrows of mud crabs (*Eurytium limosum*, *Panopeus obesus*), marsh crabs (*Sesarma reticulatu*m), and juvenile (< 1 cm diameter) and adult (≥ 1 cm diameter) fiddler crabs (*Uca pugnax*, *Uca pugilator*). Crab burrow counts correspond very closely with crab densities (Angelini et al. 2018). We also recorded elevation at each quadrat using the GPS receiver, which we converted to average daily inundation period using tidal datum from the nearest NOAA tidal station.

To define and quantify habitat patches surrounding each site, we used ArcGIS v10.2.2 software (ESRI, Redlands, California, USA) to delineate a 2 km^2 geospatially-referenced circle, the average size of a hog's home range in the region (Wood and Brenneman 1980). We positioned each circle's seaward boundary 500 m from the upland-salt marsh border (average width of salt marsh measured from the upland marsh boundary to open water) assessed in the survey (Fig. 1b). We then used available land cover data (Table S2) to classify the habitat patch composition in each circle as salt marsh, open water, scrub-shrub, freshwater wetland, swamp, developed, upland hardwood, pine, mixed forest or other (typically undeveloped cleared land or beach). Finally, we calculated the area (ha) of each habitat type in each home range.

We then built separate regression trees for output wallowed, trampled, rooted, and total disturbed area response variables. In each tree, we included the area of each habitat patch type observed in the home range, inundation period, and salt marsh features as predictors of hog disturbance area. We did not include island or mainland as a covariate for this analysis because hogs are known to frequently swim across tidal channels and are widely distributed across both area types (Georgia DNR, *pers. comm*). Regression trees were built using the analysis of variance (ANOVA) method of recursive partitioning, choosing 0.01 as the complexity parameter and a 10-fold cross-validation. We ran all regression tree analyses using the rpart package in R version 3.2.2 (R Core Team 2014; Therneau and Atkinson 2017).

Disturbance effects on salt marsh communities and soil biogeochemistry

To examine regional variability in hog disturbance effects on marsh vegetation, fauna, soil structure and porewater chemistry, we selected 8 of the 53 survey sites (henceforth 'select sites'), which had verified hog populations, and a range of total hog disturbed area (218–6175 m^2) for detailed data collection. At each site, we haphazardly placed 0.25 m^2 quadrats in disturbed and paired undisturbed marsh areas (approximately 10 m away from disturbed areas) and surveyed vegetation and fauna using the methods described for the regional survey (N = 8–15 quadrats per area type per site). To assess the potential effects of hog disturbance on marsh surface elevation we used the GPS receiver to measure elevation at 3–5 points in each disturbed and adjacent undisturbed area at each site (except Matanzas where these data were corrupted). We also collected 3–15 elevation measurements in the center of hog trails (more measurements taken on longer trails) paired with adjacent measurements in the vegetation 1 m away from the trail at all sites except Matanzas, Timucuan (data corrupted) and Cabretta Island (no trails present).

To assess soil and porewater biogeochemistry, we extracted 10 cm deep soil cores using a 7 cm diameter beveled edge corer from each survey quadrat (N = 8–15 cores per site), and interstitial porewater from the top 10 cm of soil using 10 cm microrhizons (Rhizosphere Research Products, Wageningen, The Netherlands, N = 3 samples per area type per site).

Cores were subdivided into 5 cm sections to represent surface and subsurface horizons. Soil samples were oven-dried at 65 °C, ground with mortar and pestle and sieved through a 2 mm-mesh screen. We then measured soil organic carbon (SOC) on 5 g subsamples using loss on ignition (Craft et al. 1991). Salinity (ppt), pH and ammonium concentrations (mg/L) were measured in each porewater sample (RF20 portable refractometer; Extech Instruments, Nashua, New Hampshire; LaMotte SMART 2 Colorimeter, LaMotte Company, Maryland). We also measured soil reduction–oxidation potential as a measure of available energy for belowground biomass metabolism (hereafter redox) and temperature by placing probes (Thermo Fisher Scientific OrionStar probe and Accumet Portable ORP Meter) 5 cm into the soil (N = 3–5 samples per area type per site). Due to probe malfunction, we were not able to measure redox at Blackbeard Creek.

We used linear mixed effects models (lme4 package) to assess the effect of hog-disturbance on all community and ecosystem function metrics, including site as a random variable, and performed post hoc comparisons using general linearized hypotheses and multiple comparisons (multcomp package) in R version 3.2.2 (Hothorn et al. 2008; R Core Team 2014; Bates et al. 2015).

Hog disturbance experiment

To assess marsh resilience to different hog behaviors, we conducted an experiment in a *S. alterniflora*-dominated salt marsh within the Guana Tolomato Matanzas National Estuarine Research Reserve in Ponte Vedra Beach, FL (30.00°N 81.32°W). In July 2015, we established 25, 2 × 2 m plots spaced 2 m apart and assigned each one of five treatments: controls (no disturbance), trampled, rooted, wallowed or mixed disturbance (N = 5 replicates per treatment). Trampled treatments were created by flattening vegetation with our feet and probing the marsh surface 60 times with 3 cm diameter wooden poles to mimic soil penetration by hog hooves. Rooted treatments were created by using hand trowels to overturn soil and roots in 40 points in the plot to mimic hog foraging and rooting behavior. Wallowed treatments were created by depressing a 1.5 × 1 m piece of sheet metal, bent into a half cylinder to resemble a hog body, into the marsh soil using the weight of two researchers, creating 3 wallows per plot. Mixed disturbance treatments received 15 trampling hoof punctures, 15 rooting holes and 1 wallow per plot. To mimic the seasonal return of hogs into the marsh, each treatment was reapplied 1 year after initial treatment in July 2016.

Before the treatments were applied and 1 week, 6 months, and 10 months after the start of the experiment, we estimated vegetation cover and counted ribbed mussels in a 1 m^2 quadrat centered in each plot. We also counted the number of *Spartina* stems, measured the height of the 5 tallest, non-flowering *Spartina* stems and counted and identified all crab burrows in a 0.25 m^2 quadrat centered in each plot. We concluded the experiment at the end of the growing season in August 2016, 1 month after we reapplied the treatments. At this time, we measured the same variables listed above and harvested aboveground stems from 1 m^2 quadrats centered in each plot, which were washed and oven-dried for 48 h at 65 °C. We also extracted one soil core from the center of each plot for SOC assessment. We extracted porewater 6 months after the initial treatment to measure salinity, pH and ammonium concentration (N = 3 samples per plot). Soil and porewater samples were processed using methods identical to those described for the regional survey.

For all response variables measured at multiple times over course of the experiment (vegetation percent cover, height, stem density, mussel density, crab burrow density) we used repeated measures, disturbance treatment ANOVA that included sampling date as a random variable nested in each plot. For all other variables (biomass, SOC, porewater chemistry), we performed a one-way disturbance treatment ANOVA. For all post hoc comparisons, we used Tukey HSD tests.

Results

Regional hog disturbance survey

Across the region, the composition of habitat patches within the 2 km^2 home ranges centered around each of the 53 surveyed sites was often about one-third salt marsh but included many other habitat types (Fig. 1b and Table S3). *Spartina alterniflora* dominated the marsh plant community at 87% of sites, though the vegetation composition, canopy height and invertebrate densities surveyed in undisturbed marsh areas along measured transects varied markedly (Table S3).

Hog disturbance was present at 36% of the sites surveyed, and on average 10% of the approximate 15,000 m^2 survey area at each of those sites was disturbed. Across the region, we often observed hog disturbance mostly in state- and federally-protected areas (80% of disturbed sites) that maintained significant upland hardwood forest and little development. However, large areas of hog-disturbed marsh were found in proximity (~ 2.5 km from city limits) to densely populated urban centers. The total hog-disturbed area recorded at a given site ranged from 60 to 43,148 m^2 and, at half of the sites with observed hog disturbance, we found evidence of all three disturbance types: rooting, wallowing and trampling. Rooting accounted for the most area of disturbed marsh (range across all hog disturbed sites: 0–43,148 m^2) while wallowing accounted for far less (0–13 m^2), and trampling an intermediate amount of disturbed area (0–1288 m^2; Table 1).

Regression tree analyses, used to evaluate the relative importance of habitat patch composition and salt marsh features in mediating hog disturbance extent, revealed that hardwood forest cover was the strongest, and only significant, driver of total hog disturbance area (Fig. 2a). For the 46 survey sites for which hardwood forest cover comprised < 33% of the 2 km^2 home range, the total hog disturbed area measured over the survey transect (mean ± S.E.) averaged only 2.3 ± 0.8%. In contrast, at the seven sites where upland hardwood forest accounted for > 33% of the home range, the total hog disturbance area was 22-times larger and averaged 52.0 ± 39.8% (R^2 = 0.18, full tree).

Regression tree analyses examining the response of rooting, trampling and wallowing disturbance types revealed that hardwood forest cover was also the only significant driver of hog rooted area across the surveyed sites. Specifically, sites where hardwood forests comprised a large proportion of the home range experienced more intensive rooting than sites where this habitat type comprised a smaller proportion of the home range (Fig. 2a; R^2 = 0.17, full tree). This result parallels that found for the total (i.e. rooted + trampled + wallowed) disturbed area, described above, because rooting accounted for a large proportion of the disturbance at most sites.

In contrast, the area of salt marsh within a home range was the strongest driver of hog trampled area (Fig. 2b). Indeed, trampling damage was significantly higher (mean ± S.E.: 472.2 ± 167 m^2) when salt marsh habitat comprised < 43 ha within the home range, while sites > 43 ha of salt marsh had an order of magnitude less trampled area (Fig. 2b; R^2 = 0.40, full tree). Finally, adult fiddler crab burrow density was the strongest correlate of hog wallowed area, followed by mussel density and hardwood forest area (Fig. 2c). In particular, wallowing was observed only at sites where adult fiddler crab burrow densities in undisturbed marsh areas were < 18 burrows m^{-2} or,

Table 1 Composition of hog disturbance types (area in m^2) and elevation differences between disturbed and undisturbed areas (mean cm ± S.E.) across the 8 select survey sites

Site[a]	Disturbed area (m^2)				Elevation difference (cm)[b]	
	Rooted	Trampled	Wallowed	Total	Die-off	Trails
Willows Rd	165.7	53.9	0	219.3	− 14 ± 14	− 22 ± 4
Goose Pond	3807.0	1179.9	12.6	4999.5	− 12 ± 8	− 6 ± 10
Hell's Hole	4885.7	1277.0	12.6	6175.3	− 8 ± 4	− 12 ± 5
Blackbeard Creek	675.2	417.3	0	1092.5	− 14 ± 14	− 9 ± 3
Cabretta Island	1016.8	180.0	3.6	1200.4	+ 2 ± 12	–
Timucuan	40.7	376.2	1.8	418.4	− 6 ± 5	–
Panacea	119.0	99.0	0	218.0	− 4 ± 2	− 3 ± 2
Matanzas	360.0	157.6	6.6	524.2	–	–

[a]Site names are organized from most northern (Willows Rd) to most southern latitude (Matanzas)

[b]Negative elevation difference values indicate lower elevation than adjacent undisturbed marsh areas

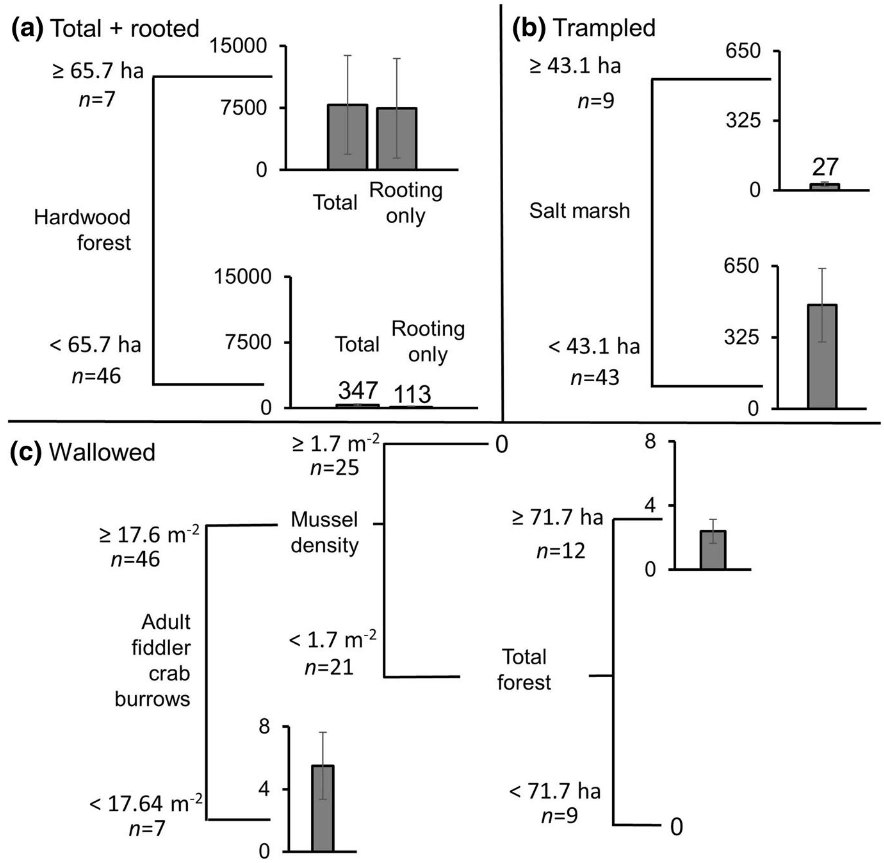

Fig. 2 Regression tree results showing which landscape and local salt marsh features within a hog home range (2 km^2) most strongly correlate with hog disturbance area ($m^2 \pm$ S.E) on **a** the total area disturbed by hogs (a sum of all three disturbance types) and rooted (regression tree outcome identical to total), **b** trampled area and **c** wallowed area

at sites that supported higher adult fiddler burrow densities, where mussel densities were $< 1.7\ m^{-2}$ and hardwood forest comprised > 72 ha of the home range (R^2 = 0.42, full tree).

Disturbance effects on salt marsh community and soil biogeochemistry

The eight select sites differed considerably in their composition of disturbance (Table 1). For instance, while Matanzas had the largest proportion of rooting (98%) and wallowing (1.8%), Timucuan had the largest proportion of trampling disturbance (90%). *Spartina alterniflora* was the dominant vegetation at nearly all sites, with the exception of Panacea, where *J. roemarianus* was dominant. Across the eight sites, vegetation cover (Fig. 3a) and height (range 39–117 cm) were variable in undisturbed marsh areas; however, in disturbed areas, vegetation was consistently more sparse (Fig. 3a; z = 26.0, $P < 0.001$) and shorter (15–29 cm, z = 15.3, $P < 0.0001$). Although invertebrate abundances were generally higher in undisturbed than disturbed areas, these differences were only significant for snails (mean ± S.E, undisturbed: $95.8 \pm 5.1\ m^{-2}$ v. disturbed: $17.0 \pm 5.1\ m^{-2}$; z = 9.4, $P < 0.001$). Finally, marsh surface elevation was typically lower in disturbed than adjacent undisturbed areas but this effect was not statistically significant. However, marsh surface elevation in trails was consistently lower than adjacent undisturbed areas (Table 1, z = 3.5, $P < 0.001$).

Soil composition and porewater chemistry also varied between hog disturbed and undisturbed areas and among the eight sites. Although SOC varied four-fold between sites, it was up to twice as high in undisturbed versus disturbed plots at surface (Fig. 3c, $F_{1,123} = 4.10$, $P < 0.05$) and sub-surface (Fig. 3d, $F_{1,120} = 10.0$, $P < 0.01$) depths. Soils were consistently more anoxic, as indicated by lower redox potential values, and less variable in hog disturbed relative to undisturbed areas across sites (Fig. 3e; $F_{1,104} = 4.05$, $P < 0.05$). Finally, porewater

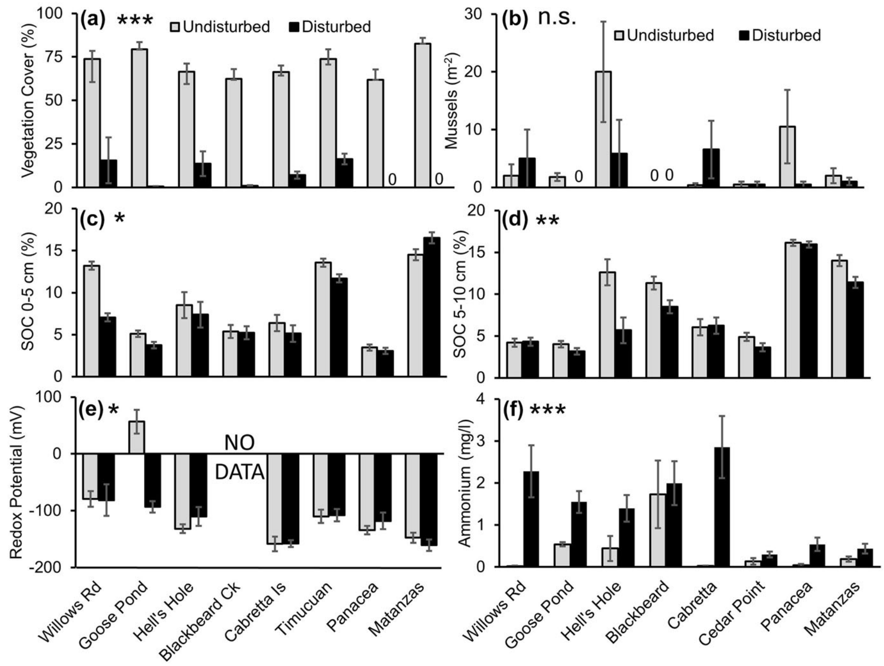

Fig. 3 Effects of hog disturbance on salt marsh biotic and abiotic variables. Sites are arranged across the x-axis from northern to southern latitudes (left to right). Data are shown as mean ± S.E. of 8–15 replicates from each area type at each site. *$P < 0.05$ **$P < 0.01$ ***$P < 0.001$ *n.s.* not significant

ammonium concentrations were up to two orders of magnitude greater in hog disturbed than undisturbed areas (Fig. 3f; $F_{1,84} = 14.2$, $P < 0.001$). However, porewater pH (7.12 ± 0.5 v. 7.05 ± 0.5 in disturbed and undisturbed, respectively) and salinity (34.4 ± 7.1 ppt v. 33.4 ± 7.0 ppt in disturbed and undisturbed, respectively) were similar regardless of the presence of hog disturbance.

Hog disturbance experiment

Over the course of the field experiment, wallowed and mixed disturbance treatments had much stronger, negative effects on vegetation cover (Fig. 4; $F_{4,95} = 22.1$, $P < 0.001$) and stem density (Table S4; $F_{4,70} = 20.3$, $P < 0.001$) than trampled and rooted treatments, which slightly depressed these metrics relative to controls. Stem height was only significantly lower in mixed treatments while all other treatments were similar to controls (Table S4, $F_{4,95} = 6.12$, $P < 0.001$).

At the experiment's conclusion, vegetation biomass was lower in wallowed and mixed disturbance compared to control treatments, and was intermediate in trampled and rooted treatments, which did not vary from other treatments (Fig. 5a; $F_{4,20} = 4.85$, $P < 0.01$). Surface SOC did not differ between treatments ($F_{4,20} = 0.80$, P = 0.54). However, subsurface SOC was significantly higher in rooted than mixed treatments ($F_{4,20} = 2.99$, $P < 0.01$) but was similar across all other treatments (Table S4). Finally, porewater ammonium concentrations were nearly twice as high in rooted, trampled and mixed treatments compared to controls, and intermediate in wallowed treatments (Fig. 5b; $F_{4,73} = 6.77$, $P < 0.001$).

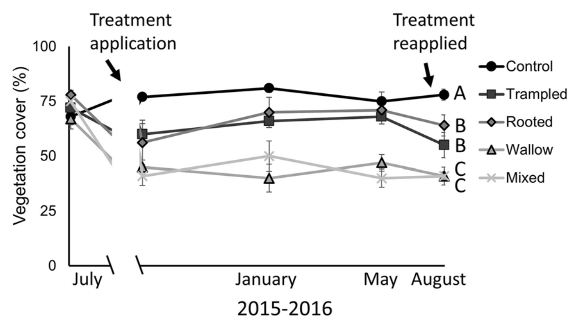

Fig. 4 *Spartina alterniflora* vegetation percent cover over time in experimental treatment plots where hog disturbance was mimicked. "Mixed" treatments were a combination of the other three treatment types. Arrows indicate when hog disturbance treatments were applied in each year; data are shown as the mean ± S.E of 5 replicate plots. Different letters next to bars indicate significant differences between treatments

Juvenile fiddler crab burrow density was up to seven-times higher in wallowed compared to all other

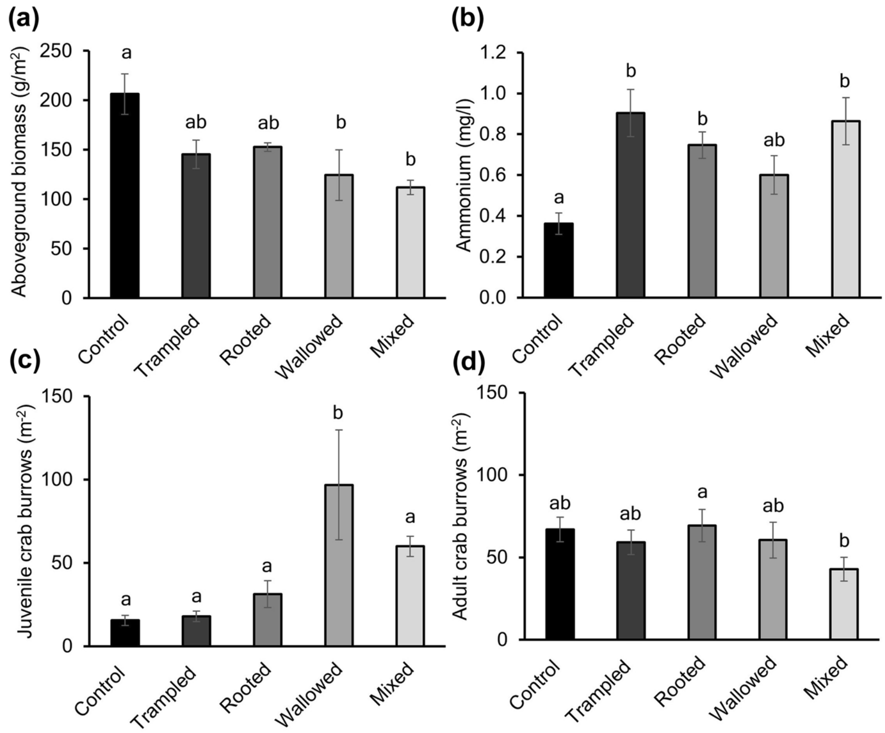

Fig. 5 Effects of experimental trampled, rooted, wallowed and mixed hog disturbances on **a** aboveground vegetation biomass, reported in grams of dry mass per m^2, **b** porewater ammonium concentrations, analyzed from pore water extracted from top 5 cm of soil, **c** juvenile and **d** adult fiddler crab burrow densities. Data are shown as the mean ± S.E of 5 replicate plots. Different letters indicate significant differences between treatments

treatments (Fig. 5c; $F_{4,70} = 4.03$), while adult burrow density was lower in the mixed compared to rooting treatments, and intermediate in both were similar to the other treatments (Fig. 5d; $F_{4,70} = 2.72$). Mussels occurred at relatively low and similar densities across all treatments (range 1.4 ± 0.6–$3.7 \pm 1.0\ m^{-2}$).

Discussion

In this study we discovered that the composition of habitats at landscape scales interact with local habitat features to shape the spatial extent and type of disturbance that invasive hogs impose. Specifically, hog home ranges with expansive hardwood hammock had 20-times more rooting and total disturbed salt marsh area than those where this habitat accounted for less cover, while marshes within home ranges with less marsh area were most heavily trampled, and marshes that supported low invertebrate densities were most heavily wallowed. In assessing the 'select' survey sites and field experiment, we discovered that hog disturbance decreases marsh resilience by reducing cover of foundational plants, often to bare soil, and preventing plant recovery, especially in marshes affected by wallowing, a mixture of disturbances, or repeated disturbance. In addition to reduced plant cover, areas affected by hogs often had reduced soil organic carbon, suggesting this invader is compromising the ability of regional salt marshes to provide habitat, and take up and store carbon. Together, these finding highlight that landscape complementation can be an important driver of this prolific invasive species' impacts and, more broadly, can be a useful tool in identifying where conservation and management of invasive species may be most impactful.

Analyses of landscape complementation effects on hog disturbance indicated that the coverage of a single high-quality habitat, hardwood forest, could explain more variation in total and rooting hog disturbance in salt marshes than any other habitat type or features of the marsh itself (Fig. 1b, Table 1). This relationship likely occurs because hardwood forest, which is numerically dominated by several oak species, is an important habitat for hogs in the US (Singer et al. 1984) and across hog's native and introduced range (Barrios-Garcia and Ballari 2012), as a preferred nesting habitat and where acorns or mast produced by oaks and other trees provide high quality food for this consumer (Wood and Brenneman 1980). Therefore, hog populations are likely to increase with increasing hardwood forest area in our study area, enabling high densities of hogs to focus their foraging activities in salt marshes in spring and summer months when acorns become depleted in nearby forests. Additionally, because hogs are foraging in exposed salt marshes during warmer months, we often find more wallowing, a behavior hogs use to regulate body temperature, in areas that are also heavily rooted (Table 1).

In contrast, we observed particularly large areas trampled by hogs at sites where salt marsh habitat comprised a small percent of the home range (Fig. 2b). This result may suggest that since the amount of rooting and wallowing damage from hogs is similar regardless of available marsh area, hogs use access points more frequently, resulting in more heavily trampled trails when used repeatedly (Rodríguez-Estévez et al. 2010). Indeed, we observed concentrated trampling at several sites with small, tucked-away salt marsh 'coves' surrounded by forest. Importantly, the hog trails that result from this activity are consistently lower in elevation than adjacent marsh areas (Table 1), indicating that hog trampling along upland marsh borders may have cascading effects on marsh hydrology by channeling flood and ebb tidal flows. In addition, marsh sites supporting low densities of fiddler crab burrows were most heavily wallowed, potentially because soft soil conditions that inhibit crab burrowing (Bertness and Miller 1984) are preferable for wallowing. Collectively, the divergence in factors that appear to predict each hog disturbance type suggests that hogs exploit salt marshes in different ways depending on the larger, landscape context in which the marsh is embedded and the marsh's own features. More broadly, these findings highlight the utility of quantifying and understanding both landscape and local factors in controlling invasive species' ecological impacts.

Despite significant variability in the relative abundance of different marsh species across the eight 'select sites', vegetation cover and biomass, snail density, marsh elevation and SOC were often lower and soils were consistently more anoxic in hog-disturbed compared to adjacent undisturbed areas (Fig. 3). Although these sites were explicitly selected for hog disturbance, other animals, like raccoon and nutria, might also opportunistically forage in disturbed areas created by hogs or if these areas are high quality foraging patches, confounding the effects of disturbance on the marsh. Predictably, as hogs trample vegetation and turn over soils, they also reduce the canopy structure that snails depend on as refuge from nekton predators and for food (Silliman and Zieman 2001), collapse interstitial soil spaces, obstruct porewater flushing and allow floodwater to pool and concentrate salts in hog-created depressions (Schrama et al. 2013). These impacts can inhibit the revegetation of hog created depressions and rutted trails, leading to potentially irreversible shifts to unvegetated mudflats or ponds (Day et al. 2011; Sharp and Angelini 2016). This loss of foundational plants can, in turn, reduce atmospheric carbon uptake and organic carbon deposition and, hence, the ability of salt marshes across this region to function as important carbon repositories and provide habitat for other biota (Fig. 3c,d; Chmura et al. 2003; Persico et al. 2017).

In contrast to the survey results, the field experiment demonstrated that vegetation cover was only briefly suppressed in rooted and trampled treatments (the most common disturbance types we observed in our survey) and recovered to within 5% of control plots cover after 10 months (Fig. 4). Although the treatment application in our field experiment was limited (1 per year), this could be realistic if hogs avoid or infrequently use salt marshes, especially on hot summer days when wallowing may not be sufficient to protect them from exposure to the sun and heat. Additionally, high salt intake from foraging here may cause physiological stress, although some feral hog populations have adapted to this (Zervanos et al. 1983). However, if hogs return to sites more than once per year, more significant damage to the marsh than we found in our experiment may result from hog's repeated rooting and trampling activity. Indeed, some European hog populations exhibit strong site fidelity, returning repeatedly to known sites (Keuling et al. 2008) and this may also be true of southeastern US hog populations with smaller home ranges.

In wallow and mixed treatments, *Spartina* regrowth was stifled likely due to the wallows mechanically breaking down the root mat to soften the soil and creating substantial depressions where tide and rain water could collect (Figs. 4 and 5). These effects can result in reduced redox levels by collapsing interstitial pore spaces, inhibiting gas exchange (Sharp and Angelini 2016), and deterring adult fiddler crabs from burrowing into and aerating soils in wallowed plots given the energetic costs these crabs experience in excavating burrows in soft sediments (Bertness and Miller 1984). Although juvenile fiddler crabs tend to thrive in softer soils as also indicated by our results (Fig. 5c), their smaller, shallower burrows are far less effective in oxygenating the soil (Derksen-Hooijberg et al. *in revision*). In addition to experiencing more anoxic conditions, *Spartina* roots may have reduced access to porewater ammonium in and around the wallows as well, potentially due to these features pooling surface water and thereby diffusing ammonium away from root accessible pore space. Together, these structural and biogeochemical changes induced by wallowed treatments (and more subtly in the mixed treatments where only one wallow was created) appear to make these hog disturbances particularly problematic for *Spartina*'s persistence.

These results indicate that marshes can be slow to recover after hog disturbances or may never fully recover when these disturbances are more intense. Light trampling or one-time rooting events may have little effect on salt marsh resilience as was demonstrated in the field experiment. However repeated and/or more intense rooting and trampling disturbance might closely resemble the effect of wallowing by repeatedly displacing, overturning and compacting soil in salt marshes. These impacts also lower marsh surface elevation and in doing so affect local hydrology and drainage, potentially compromising this system's capacity to keep pace with sea level rise (Day et al. 2011). It should be noted that since our study was conducted during warmer months (April–October) when hogs are more active in marshes (Graves 2016), our finding are only applicable to this season. When hog habitat shifts inland during winter months, marsh soil can recover as disturbance is infilled or washed out from repeated tidal inundation, even though vegetation is dormant. Since we likely underreport total hog disturbance as tides wash it away over time or obscure it from our survey, our findings suggest that the areal extent of hog disturbances in marshes rivals other types of marsh disturbance, like drought- or herbivore-induced die-off (Silliman et al. 2005). Based on the results of this study, managers might better control the negative ecological impacts of hogs through targeted analyses of where robust populations likely exist (i.e. landscapes with high upland hardwood cover) and identification of sites vulnerable to their spatially extensive and/or intensive damage.

More broadly, this study implements a framework whose general concept has been proposed by others (e.g. Milbau et al. 2009; Gurevitch et al. 2011) but never used explicitly on animal invaders, by which analyses of landscape complementation can be used to identify habitat patches particularly vulnerable to invader impacts and thus guide activities to better manage invader outbreaks. Of potentially equal importance, future studies of landscape complementation in this context can be used to help elucidate why populations fail to establish in some areas and increase in density in others, dynamics that may be particularly relevant for understanding species extinctions as well as biological invasions. Overall, this study provides evidence that understanding species' habitat requirements and resource needs across multiple scales can be useful for managing threatened and/or valuable ecosystems by better predicting the behavior of the organisms that use them.

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