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Feral hogs control brackish marsh plant communities over time

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Abstract. Feral hogs modify ecosystems by consuming native species and altering habitat structure. These invasions can generate fundamentally different post-invasion habitats when disturbance changes community structure, ecosystem function, or recovery dynamics. Here, we use multiple three-year exclusion experiments to describe how feral hogs affect hyper-productive brackish marshes over time. We find that infrequent yet consistent hog foraging and trampling suppresses dominant plants by generating a perpetually disturbed habitat that favors competitively inferior species and disallows full vegetative recovery over time. Along borders between plant monocultures, trampling destroys dominant graminoids responsible for most aboveground marsh biomass while competitively inferior plants increase fivefold. Hog activities shift the brackish marsh disturbance regime from pulse to press, which changes the plant community: competitively inferior plants increase coverage, species diversity is doubled, and live cover is lowered by 30% as large plants are unable to take hold in hog-disturbed areas. Release from disturbance does not result in complete recovery (i.e., dominant plant monocultures) because hog consumer control is a combination of both top-down control and broader engineering effects. These results highlight how habitats are susceptible to invasive effects outside of structural destruction alone, especially if large consumers are pervasive over time and change the dynamics that sustain recovery.

Key words: competition; feral swine; Juncus romerianus; *marsh grass; pigs;* Schoenoplectus americanus; Spartina cynosuroides; Sus scrofa.

INTRODUCTION

Invasive consumers threaten global biodiversity and are responsible for almost 60% of the total species extinctions worldwide (Doherty et al. 2016). In addition to predation on native species, large invasive consumers cause changes to habitat structure via disturbance that modify ecosystem-level processes like biogeochemical cycling, productivity, and energy flow (Crooks 2002). Invasive changes to biotic interactions or ecosystem processes can cause cascading effects on the long-term functioning, recovery, and stability of natural habitats (Simberloff 2011, Walsh et al. 2016) because invasions destabilize food webs and restructure communities (Grosholz 2002, Strayer et al. 2006, Byrnes et al. 2007). Thus, the effect of large consumers on habitats depends on the coupling of non-trophic (i.e., disturbance) and trophic (i.e., predation) effects over time, while invasive species management needs to understand changes to the distribution and composition of native communities, outcomes of species interactions, and ecosystem function (Pringle 2008, Guy-Haim et al. 2018).

To identify potentially wide-reaching effects of invasive consumers on ecosystems over time, we focus on an invasion by the large consumer feral hog, *Sus scrofa*, in wetlands of the southeastern United States. Feral hogs are one of the strongest vertebrate modifiers of plant communities, as hog foraging and rooting behavior is responsible for destruction of native wetland vegetation and intense damage to forests that change invertebrate, plant, and microbial community structure (Hanson and Karstad 1959, Barrios-Garcia and Ballari 2012). The hog invasion is of particular concern to vulnerable coastal ecosystems where hog populations are rapidly increasing, with intense hog activity reported in marshes, dunes, and coastal plains (Kotanen 1995, Kaller and Kelso 2006, Oldfield and Evans 2016). The coastal southeastern United States contains some of the highest estimated hog densities (6–8 animals/km^2, Appendix S1: Fig. S1) and managers predict that by 2025, every coastal county from Texas to Virginia will contain hogs (Lewis et al. 2019). Because range-expansion, reintroduction, or invasion by large consumers causes broad changes to ecosystem structure and disturbance dynamics, the effects of feral hogs on marsh plant communities could be a major agent of change in these productive habitats. In salt marshes, hogs have direct effects on plant productivity and

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recovery via trampling, and indirect effects on resilience and recovery to climate disturbances via predation of secondary foundation species (Sharp and Angelini 2016; Hensel et al., 2021), but the generality of hog effects in other tidal systems is still unknown.

Observations suggest that feral hog activity (i.e., wallowing, rooting, trampling) is common within tall, productive plant stands in southeastern U.S. brackish marshes. These habitats have the highest aboveground plant biomass, species diversity, and total carbon of all coastal ecosystems in the region (Loomis and Craft 2010, Więski et al. 2010) and lie in a transition zone that experiences an ever-changing dynamic between saltwater intrusion and freshwater discharge (Odum 1988, Craft 2007). Importantly, deterministic factors like recovery from salinity disturbance and direct competition for space and light are responsible for the spatial distribution of hyper-productive monospecific plant zones that form the vast mosaics that characterize this ecosystem (Brewer and Grace 1990, Guo et al. 2014).

Here, we use two, multi-site, multi-year experiments to examine how feral hog consumer control affects brackish marsh ecosystems by disturbing dominant native plants and altering community structure, primary productivity, and recovery from disturbance. We conducted two separate hog exclusion experiments at three sites in coastal Georgia (Fig. 1). First, our border experiment exclusion cages at the border of dominant plant monocultures (*Juncus romerianus* or *Spartina cynosuroides*) and a competitive inferior (*Schoenoplectus americanus*) describe how hog activity alters the plot-level spatial dominance of marsh plants after three years of hog exclusions (border exclusions). We observed that hog trampling and foraging cause the retreat of dominant plant monoculture borders across the marsh and measure this retreat via the distance between dominant plants that remain inside of our exclusion cages and their nearest conspecific border (vegetative stand retreat). Second, our disturbance recovery experiment established hog exclusion cages within recent heavily hog-disturbed areas of marsh at two sites to quantify how repeated hog disturbance affects recovery of marsh plant community structure and diversity, and recovery of live plant cover over three years.

METHODS

Study species

Introduced in Florida by Spanish conquistadors in the 1400s, feral hogs *Sus scrofa* have spread throughout the whole United States and are well established as an ecosystem engineering invasive (Hanson and Karstad 1959, Barrios-Garcia and Ballari 2012). When hogs forage for underground plant materials, they use their snouts to upturn the soil surface, often disturbing the top 15 cm of soil in distinct patches that vary in size (up to 1 ha). Hog foraging and rooting behavior is responsible for decimation of native wetland vegetation and intense damage to forests with varying effects on invertebrate, plant, and microbial community structure (Arrington et al. 1999, Campbell and Long 2009, Barrios-Garcia and Simberloff 2013).

Study sites

To determine how feral hogs affect community dynamics of marsh plants, we set up multiple experiments in three brackish marsh sites in coastal Georgia: Cathead Creek, Broughton Island, and Little St Simons Island (Appendix S1: Fig. S1). At these sites, we observed large (up to ~1 km) interaction zones between two monocultures of tall Graminoids: *Spartina cynosuroides* bordering *Schoenoplectus americanus* (two sites, Cathead Creek and Little St Simons Island) and *Juncus romerianus* bordering *S. americanus* (one site, Broughton Island). Sites were broadly similar in abiotic and biotic factors. Salinity at all sites varied from ~5 to 15 practical salinity units (PSU) throughout the year (Guo et al. 2014). As described by Więski et al. (2010), these sites are made up of different fresh, brackish, or salt marsh plant species but typically characterized by large monoculture zones of the dominant sedges. Each site also contained smaller, colonizing plant species as well as these sedges mentioned above; these were commonly observed within areas disturbed by hogs and are competitively inferior to each of the three tall plants.

We used hog-wire fencing, a galvanized steel material with 10 × 10 cm mesh size, to exclude hogs from 4-m^2 plots, and observed no caging artifacts in our study as mesh size in hog wire fencing is wide enough so shading is minimized and wrack deposition does not occur. Tracks or droppings of other large organisms (e.g., white-tailed deer, Canada geese) that would also be excluded from these plots were not observed at any of our sites at any time. Both experiments began in winter 2012, with data collection occurring at 4–6-month intervals. We chose this frequency of data collection to minimize both human disturbances to plants and human smells, which can disrupt hog activities. We were unable to access our sites in early 2015 and thus report final data from December 2015.

Border experiment: Effect of feral hogs on marsh plant spatial dominance at plot scale (border exclusions) and marsh scale (vegetative stand retreat)

We performed our border experiment at the border between the competitively inferior *Sc. americanus* (present at all sites) and the dominant space-holding marsh plants *Sp. cynosuroides* (Cathead Creek and Little St Simons Island) and *J. romerianus* (Broughton Island). At each site, we marked 16 4-m^2 plots spaced at least 10 m apart along the edge of the dominant plant monoculture, with each plot starting at 100% cover of the competitive dominant (*Sp. cynosuroides* or *J. romerianus*; Fig. 1).

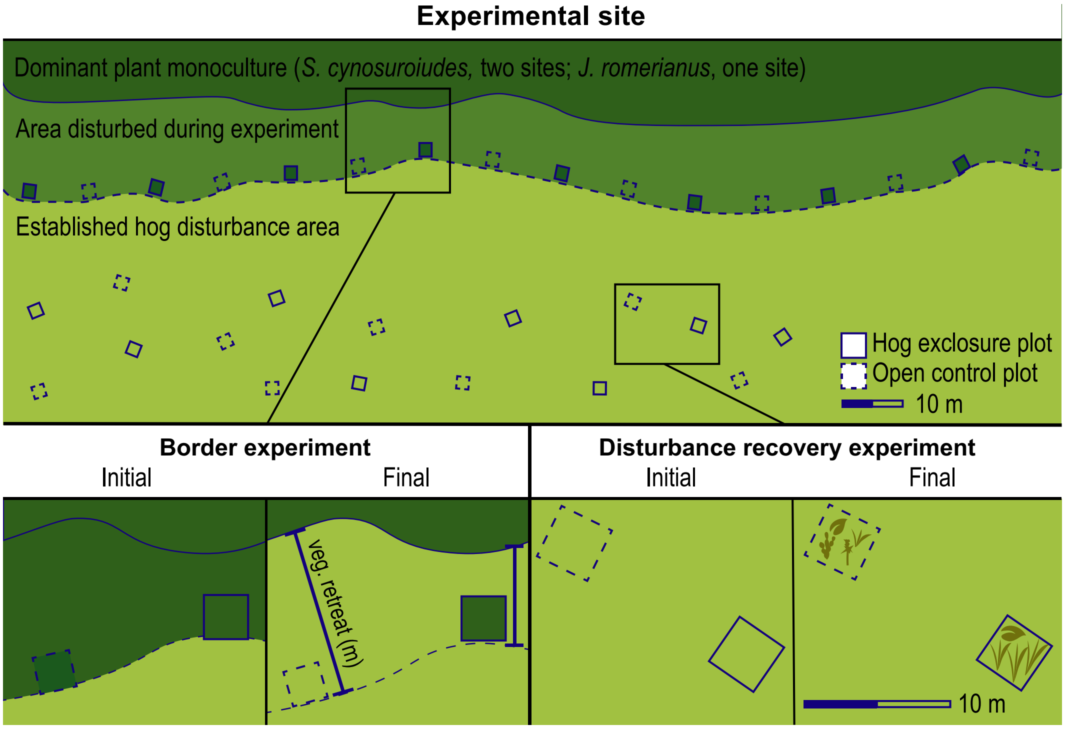

FIG. 1. Experimental site map describing layout of both border experiment (border exclusions and vegetative stand retreat) at three coastal Georgia, USA sites and disturbance recovery experiment at two coastal Georgia sites. At each site, we observed hog activity along the borders of a large dominant plant monoculture zone (*Spartina cynosuroides* at Cathead Creek and Little St. Simons Island, *Juncus romerianus* at Broughton Island) and the competitively inferior *Schoenoplectus americanus.* Here we placed 16 plots for our border exclusions, excluded hogs from half, and quantified differences in plot-level plant and bare ground cover from the beginning of the experiment (100% cover of dominant plant) and end of experiment. Over time, we observed a retreat of the dominant plant monoculture due to hog trampling and rooting and quantified this vegetative (veg.) retreat by measuring the distance between caged plots that still contained dominant plants and the edge of the dominant plant monoculture (i.e., distance to nearest conspecific). We estimated mean vegetative retreat for each stand from these eight measurements (eight cages per site, three sites). For our disturbance recovery experiment, we selected marsh areas adjacent to but at least 50 m from these borders that were previously disturbed by hogs (i.e., many hoofprints, wallows, and upturned soil). We placed 16 plots, excluded hogs from half, and quantified changes in percent cover and live plant cover of all species over time.

Then we excluded hogs from one half, creating 48 total plots (8 plots × 2 treatments × 3 sites). We recorded species and bare ground percent cover and presence in each plot using a gridded quadrat and report final percent cover data from December 2015.

Our plot location selection from border exclusions enabled us to determine if monoculture borders moving over time could be attributed to hog activity or other disturbances like salinity pulses. At the end of the experiment, if the caged plots still contained the dominant plant species but the uncaged plots were occupied by other plant species, we would conclude that the caging treatment (i.e., excluding hog activity) caused differences in response variables. If both caged and uncaged plots contained non-dominant plants, we would conclude that abiotic stressors (i.e., salinity pulses) came through and disturbed all plots equally. To quantify vegetative stand retreat, we measured the distance from each caged plot to the new border "edge" (i.e., distance to nearest conspecific) if it had moved, at each sampling date (see Figs. 1, 3). At each site, we measured the retreat of one large vegetative stand at four different points (4 randomly selected caged plots × 3 sites, $n = 3$ vegetative stands) and report mean vegetative retreat distance of the dominant monoculture stand. To determine if hog activity was correlated with vegetative stand retreat, we counted any hog hoofprints in 1-m^2 haphazardly thrown quadrats and recorded the number of plants that were trampled in the area between caged plots and retreated vegetative stand at each sampling date.

Disturbance recovery experiment: Effects of feral hogs on marsh recovery from disturbance via changes in community structure and live vegetative cover

We marked 16 4-m^2 plots at each of two hog impacted sites (Cathead Creek and Broughton Island) in winter 2012 when marsh plant production slows and the sediment at our sites was mostly bare, with sparse brown vegetation. We selected plots 5–10 m apart, randomly distributed within a previously hog-disturbed muddy patch of marsh (0.05–0.1 km^2), as indicated by extensive hog hoof prints and distinctive hog wallows found at each site. To ensure similar starting conditions in all plots, we removed any remnant brown aboveground vegetation and the first few centimeters of soil, thus starting at 0% vegetation cover and enabling us to track plant community recovery from disturbance over time, and excluded hogs from one-half of these plots (8 plots × 2 treatments × 2 sites). To describe community structure and calculate species richness, we measured percent cover of each species in each plot (sum of cover by species plus bare ground = 100%) using a gridded quadrat at each sampling date and recording live and dead plant cover and bare ground. Because dominant brackish marsh plants (*J. romerianus*, *Sp. cynosuroides*, *Sc. americanus*) can be up to 2.5 m tall and are difficult to harvest for biomass calculations, we used percent cover of all live plants and mean plant height of each species to help estimate aboveground production. Additionally, recorded plants other than these two competitive dominants and the secondary dominants were all short (maximum 0.5 m tall) grasses, succulents, or successional species that make up a small proportion of total brackish marsh aboveground carbon (Więski et al. 2010).

Analyses

To determine the effect of hog exclusions on the percent cover of dominant plants, bare ground, and *S. americanus* at the end of our *Border Exclusion* experiment, we logit transformed our data to meet assumptions of normality and used a linear model. We allowed treatment, site, and their interaction to predict change in percent cover in a factorial ANOVA framework, used Tukey's tests for post-hoc comparisons with the *emmeans* package (Length 2019), and evaluated assumptions of normality of residuals using QQ plots and Shapiro-Wilks tests for normality and found no violations. To describe the effect of hog activity on vegetative stand retreat over time, we fit a linear mixed-effects model using maximum likelihood with months since exclusions began (i.e., time) as a fixed effect and site as a random effect to account for resampling in each site over time. We fit two more identical mixed effects models as above to analyze the effect of time on hog hoofprint density and the number of trampled stems counted at each sampling date. To evaluate change in species richness over time in our disturbance recovery experiment, we fit a linear mixed effect model with sampling date and site as interacting fixed effects and plot as a random effect, as before, to evaluate how hog exclusions affected species richness per plot over time. We also analyzed effects of hog exclusions on the recovery of live plants throughout the experiment with logit transformed percentage data (Warton and Hui 2011) and using a linear mixed effects model with sampling date and site as interacting fixed effects and plot as a random effect. We fit all mixed effects model using the *lme4* package (Bates et al. 2015), and reported results from conditional *F* tests with Satterthwaite degrees of freedom using *lmerTest* package for fixed effects (Kuznetsova et al. 2017). We corrected *P* values of post hoc comparisons using a Tukey's correction method above. To assess model assumptions, we evaluated randomized quantile residuals using the *DHARMa* library and found no violations (Hartig 2021).

To describe how hog exclusions changed plant community structure, we fit generalized linear latent variable models for multivariate abundance data (Niku et al. 2019) on logit-transformed percent cover per species data. We performed likelihood-ratio tests and used the trace of the residual covariance matrix from models with and without experimental factors (i.e., site and hog exclusion treatment) to estimate the amount of variation explained by each of these factors. We examined QQ plots and Dunn-Smyth residuals to diagnose model fit and found no violations. All analyses were conducted in R (R Core Team 2020).

RESULTS

Border experiment: Effect of feral hogs on marsh plant spatial dominance at both plot scale (border exclusions) and marsh scale (vegetative stand retreat)

From our border exclusion experiment, 3-yr hog exclusions along borders between two monocultures gave us strong evidence that hog disturbance favors *Sc. americanus* over *J. romerianus* and *Sp. cynosuroides* (Fig. 2). Our preliminary neighbor-transplant experiment (Appendix S1: Fig. S2) and previous studies (Więski et al. 2010) confirm that, under no hog disturbance, both *J. romerianus* and *Sp. cynosuroides* are competitively dominant over *Sc. americanus* on the plot and marsh scales. Inside of uncaged control plots at all sites,

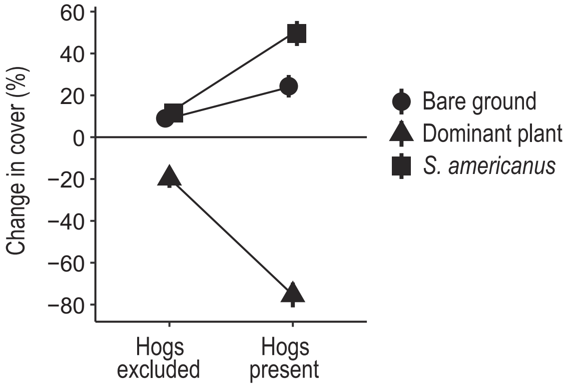

FIG. 2. Border exclusions. In plots on the edge of a plant interaction zone that began with 100% cover of competitive dominants *J. romerianus* or *Sp. cynosuroides* ($n = 10$/site), hog activity converted percent cover of competitive dominants (triangles) to *Sc. americanus* (squares) or bare space (circles) after 3 yr at three sites in coastal Georgia. Error bars represent standard error.

hogs reduced mean cover of the dominant plant to just 24.6% ± 5.94% (mean ± standard error) compared to caged exclusion plots (80.35% ± 4.57% mean cover of dominant) at the end of the 3-yr experiment (exclusion, $F_{1,34} = 51.5$, $P < 0.001$), with the 20% decline in dominant cover inside of cages likely attributable to small-scale salinity pulse disturbances and not physical disturbance. Site was a significant predictor of change in dominant percent plant cover (Appendix S1: Table S2a; site, $F_{2,34} = 0.48$, $P < 0.001$), while post-hoc Tukey's test found significant decreases in either *J. romerianus* or *Sp. cynosuroides* in uncaged control plots at every site ($P < 0.002$ in all comparisons).

Sc. americanus replaced trampled dominant plants inside of uncaged control plots as indicated by a significant interaction between site and exclusion treatment on *Sc. americanus* percent cover change (Fig. 2, Appendix S1: Table S2b; site × exclusion, $F_{2,34} = 5.60$, $P = 0.008$). Hog activity increased mean *Sc. americanus* percent cover fivefold with higher cover in uncaged controls (control: 49.55% ± 5.98% cover) compared to exclusions (11.67% ± 2.84% cover; Appendix S1: Table S2b; exclusion, $F_{1,34} = 17.8$, $P = 0.0002$). Post-hoc Tukey's tests revealed statistically significant increases in *Sc. americanus* cover in control plots vs exclusions in two of three sites, while all three sites had at least double the percent cover of *Sc. americanus* in uncaged plots compared to exclusions. Additionally, the total cover of bare, unvegetated mud was nearly tripled in control plots (24.35% ± 5.37% mean bare ground cover) compared to exclusions (9.00% ± 4.06% mean bare ground cover) at the end of the experiment (exclusion, $F_{1,34} = 51.51$, $P = 0.006$). Site was also a significant predictor in bare ground cover (site, $F_{1,34} = 0.48$, $P = 0.002$), where post-hoc tests revealed higher percent cover of bare ground in uncaged plots than caged plots at every site ($P > 0.001$ in all comparisons). While other plants besides *Sp. americanus* may have entered plots after dominant plants retreated, we did not record any other plants along these borders between monocultures.

As the border experiment progressed, we observed that the only dominant plants remaining along the initial border edge were plants inside of our hog exclusion cages (Fig. 3). Distance between exclusion cages that still contained dominant plants and the retreating vegetative stand increased over time at all sites as competitive dominant plant zones were consistently moved by hog activity in the vegetative stand retreat (Fig. 3). Vegetative stand retreat of dominant plant monocultures away from caged plots was strongly affected by time (date, $F_{4,59} = 66.7$, $P < 0.0001$) while *Sc. americanus* or bare ground occupied the vacated space (mean vegetative stand retreat = 4.2 ± 0.4 m; Fig. 3b). We found evidence of consistent hog activity (total stems trampled and hoofprints density) in the area between cages and dominant vegetative stands over time (Fig. 3d; hoofprints, date, $F_{4,73} = 1.96$, $P = 0.11$; trampled stems, date, $F_{4,73} = 8.43$, $P = 0.001$), with a similar number of hoofprints (~2–6 prints$\cdot$m$^{-2}\cdot$sampling date^{-1}) per site and an increasing number of trampled stems per site at each sampling date (7 trampled stems/m^2 at final sampling date). Although we treated each site as a replication unit for these analyses, we also tested differences between sites and found that neither border movement ($P = 0.08$) nor hog activity (hoofprints, $P = 0.8$; trampled stems, $P = 0.07$) differed between sites. Vegetative stand retreat rate does appear to slow over the course of our experiment despite constant, yet limited hog activity, which suggests that monoculture borders may have become more stable or may be a function of increased variation in stand retreat over time.

Disturbance recovery experiment: Effects of feral hogs on marsh recovery from disturbance via changes in community structure and live vegetative cover

In our disturbance recovery experiment, 3-yr hog exclusions at all sites suggested that hogs consistently reset successional processes by trampling and rooting marsh plants. Hog activity thus generated a significantly more diverse plant community, with 3.65 ± 0.2 species/plot in control plots compared to 2.32 ± 0.2 species/plot in exclusions after the first sampling date when all plots were identical (Fig. 4a). This effect increased over time as diversity differences between controls and exclusions became wider with more hog activity (Fig. 4a, Appendix S1: Table S5c; exclusion × date, $F_{1,113} = 7.65$, $P = 0.001$). The highest mean species richness found across the experiment was 4.75 ± 0.25 species/plot (July 2014, Broughton Island), suggesting that the 1.3 species increase per plot represents a significant diversity increase. Hog exclusion treatments were almost all occupied by one (*Sp. cynosuroides* in Cathead Creek) or two species, taller plants like *Sc. americanus* and *Bolboschoenus robustus*, a sedge closely related to *Sc. americanus* (Fig. 4c). Uncaged control plots, however, were occupied in low percent cover by other, smaller plants like *Distichilis spicata*, *Trifolium* sp., *Batis maritma*, *Sarcocornia* sp. that were almost never found in exclusion cages. Multivariate abundance analyses revealed that hog exclusions generated significantly different plant communities at the end of the experiment, as site and exclusion treatment explained 53.41% of the variation in community abundance (treatment × site, difference in log-likelihood (χ^2) = 59.19, $\mathrm{df}_{\mathrm{residual}} = 131$, $P < 0.001$, Appendix S1: Table S4a). Community structure did differ between our two sites, as some plants were not present in the disturbance recovery area of both marshes (i.e., *Schoenoplectus tabernaemontai*, *Trifolium* sp., and *Limonium carolinianum* were not present in Broughton, *Trifolium* sp. and *Iva frutescens* were not present in Cathead Creek), resulting in the site-only model explaining 33.9% of variation in community structure (site, $\chi^2 = 34.7$, $\mathrm{df}_{\mathrm{residual}} = 147$, $P < 0.001$).

This difference in plant community structure, where hogs generate a more diverse but less productive plant

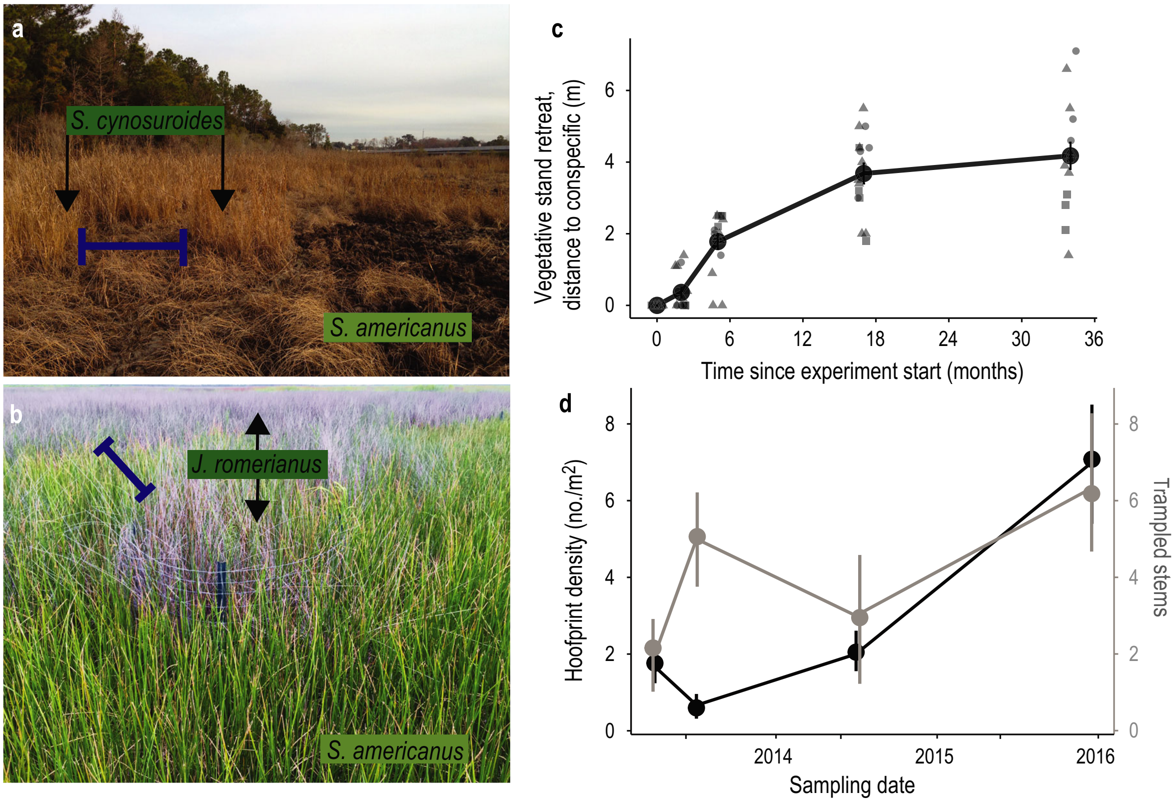

FIG. 3. Vegetative stand retreat. (c) Across all three sites in coastal Georgia brackish marshes, hog activity caused dominant plant vegetative retreat of 4.18 ± 0.37 m (mean and SE at final sampling date) by trampling competitive dominant plants (b, *J. romerianus* and a, *Sp. cynosuroides*). (d) Hog hoofprint density (black circles) and the number of trampled stems (gray circles) counted in this newly disturbed area did not vary over time and between sites but was consistent across our sampling dates. Starting at the beginning of the experiment, hogs forced dominant plants backward, away from exclusion plots and in all sites ($n = 3$ sites), *Sc. americanus* took over cleared space. (a) An example of distance to nearest *Sp. cynosuroides* conspecific (~3 m), during winter in Cathead Creek. (b) An example of distance to nearest *J. romerianus* conspecific at Broughton Island during spring, with *Sc. americanus* fully covering space vacated by *J. romerianus*. Grand mean (black dots) and standard error, with raw data from each site (circles, Broughton Island; triangles, Cathead Creek; squares, Little St. Simons Island) are presented.

community, was also found in our measurements of live plant cover over time as hog activity significantly lowered live percent cover throughout the experiment (Fig. 4b). Hog exclusion plots had almost full coverage of live plants at the end of the experiment (95.00% ± 7.83% live) compared to uncaged plots (67.92% ± 7.83%), an effect that became stronger over time (Appendix S1: Table S5b; exclusion × date, $F_{5,129.8} = 5.16$, $P = 0.025$). In addition to trampled stem and hoofprint data presented in border exclusions, we found consistent but infrequent hog wallows at each disturbance recovery site over time. We counted at least one new wallow at each site in each sampling date, with no variation in number of wallows between sites or over time (mean = 0.65 wallows /date; date $F_{4,73} = 0.19$, $P = 0.94$).

DISCUSSION

Feral hogs exert consumer control on brackish marsh plant communities through infrequent, but pervasive, top-down and engineering effects that change plant biomass, species diversity, and community recovery over time. Hog invasion of brackish marshes immediately changes plant spatial dominance via foraging, trampling, and wallowing disturbances and, as our manipulations suggest, maintain this disturbed habitat over at least 3 yr. When hogs are absent, dominant plants are spatially stable over time under a pulse-disturbance regime from salinity influxes or wrack deposition (Guo and Pennings 2012, Guo et al. 2014). When hogs invade, focused foraging at the edges of plant monocultures suppresses competitive dominants that are trampled, retreat across the marsh, and are replaced by the competitively inferior *Sc. americanus* (border experiment; Figs. 2, 3). Once disturbed by hogs, the marsh remains in an altered state with a more diverse plant community made up of smaller species with less aboveground productivity (disturbance recovery experiment; Fig. 4). Because of a changed disturbance regime, recovery of the competitive dominants appears to be a long process for the hog-invaded brackish marsh communities, as even irregular

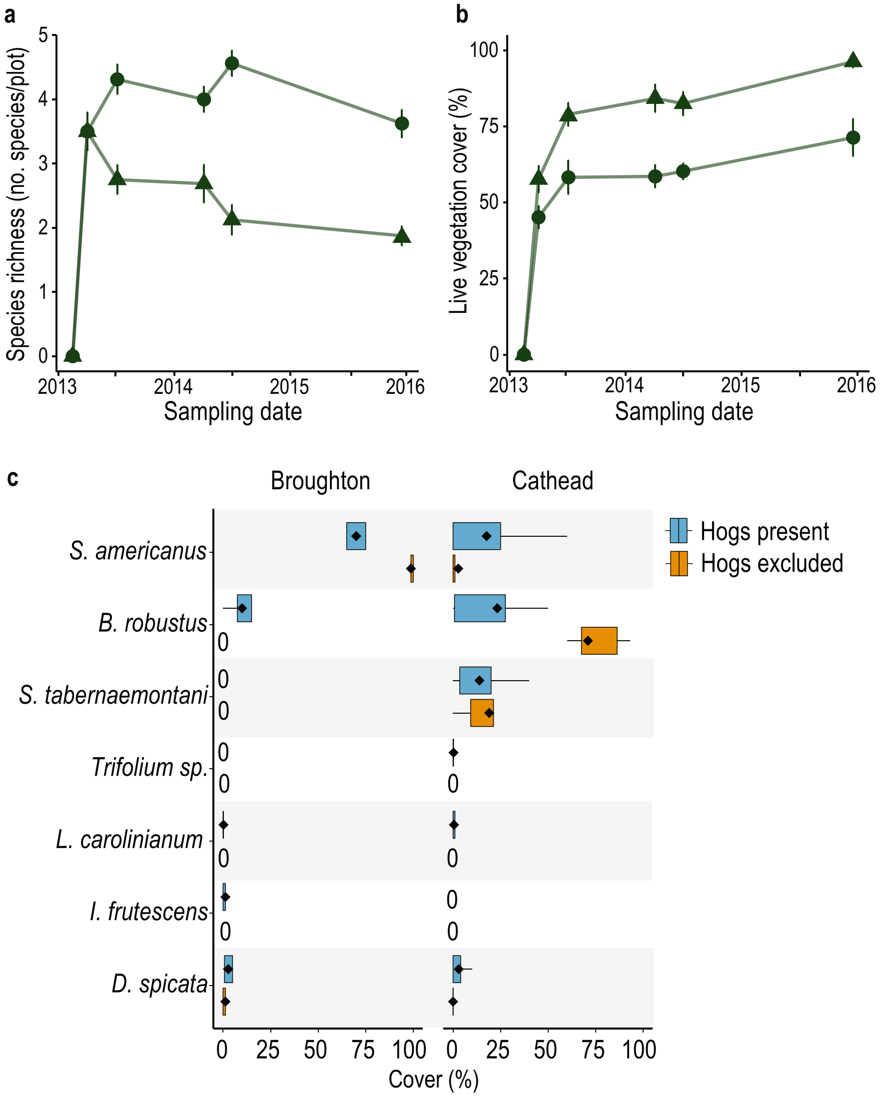

Fig. 4. Disturbance recovery. (a) Species richness (mean and SE) in plots where hogs were excluded (triangles) and uncaged controls (circles) over time in two coastal Georgia marshes. At the beginning of the experiment, we removed all aboveground vegetation in each plot (n = 8 per site). Hog disturbance in uncaged control plots constantly upturned soil, creating (b, right) consistently lower total live vegetative cover over time, and maintaining higher species richness than in hog exclusions. (c) Final plant communities (mean and SE) at both of our two sites (Broughton Island, left, and Cathead Creek, right) were dominated by one or two species inside of hog exclusion cages (orange boxes, interquartile range of hog exclusions; black diamonds, mean) at both sites but hog control plots (blue boxes) contained three or four species on average. *Sc. americanus*, *Bolboschoenus robustus*, and *S. tabernaemontai* are closely related sedges, while the other listed species are smaller, successional plants (*Trifolium sp., Iva frutesens, Distichilis spicata, Limonium carolinianum*). Species with no boxes (i.e., marked with "0") had 0% cover at the final sampling date.

trampling and foraging activity disallows a return to predisturbance structure and productivity.

In our study, feral hogs change the biomass, diversity, and recovery of an ecosystem both through top-down control (i.e., reduction of live plants, Fig. 4b) and through non-trophic engineering of habitat structure (i.e., indirect positive effects on *Sc. americanus* and other competitive inferiors, Figs. 2, 4c). While large consumers have been lost from nearly all habitats (Estes et al. 2011), consumers that remain, invade, or recover can be keystone consumers or ecosystem engineers with important, wide-reaching roles in the regulation of whole communities. Similar to hog effects in brackish marshes, elephants (*Loxodonta africana*) in savannas have both negative and positive effects on understory plant communities through direct consumption and modification of habitat structure that generates associational refuge for other plants (Coverdale et al. 2016).

Large consumers can increase habitat heterogeneity across multiple spatial scales through repeated disturbances that change the competitive hierarchies of communities (Arrington et al. 1999, Pringle 2008, Pringle et al. 2015). While megaconsumers are novel in modern day coastal habitats, isotopic evidence suggests that Pleistocene consumers like mammoths, horses, bison, and mastodons commonly consumed coastal vegetation in the Southeast (Koch et al. 1998). These habitats may have previously been shaped by large consumers and, though currently unique, there may be a historical precedent for large consumer control in brackish marshes (Levin et al. 2002, Gaskins et al. 2020). In fact, ecosystems where rewilding or reintroduction of large consumers has occurred can experience reduction of invasive plant species or orders of magnitude increases in primary productivity (Estes and Palmisano 1974, Cowlishaw 1997, Guyton et al. 2020). Successful large consumer conservation practices can even reestablish food web structure and restore lost ecosystem services (Ripple and Beschta 2012).

Hog trampling and uprooting of dominant plants is a novel disturbance that alters coastal vegetation structure and composition, and is maintained over time. Changes to disturbance regimes by invasive species have profound effects on the structure and function of terrestrial ecosystems (Mack and D'Antonio 1998) and here, hog consumer control shifts the brackish marsh disturbance regime from a salinity-pulse-driven state to a combination of salinity-pulse- and consumer-driven state. Vegetative retreat documented in our border experiment can thus be attributed to either hogs, or an interaction between hog disturbance and abiotic factors. Consistent hog activity changes how the marsh plant community recovers from disturbance, increasing species diversity by limiting regrowth of dominant plants (Fig. 4a). In both our border experiment and disturbance recovery experiment, areas of brackish marsh under the hog disturbance regime were dominated by the more nutrient rich (Appendix S1: Table S7) and less woody *Sc. americanus* or *B. robustus.* Reducing *J. romerianus* and *Sp. cynosuroides* in favor of *Sc. americanus* or *B. robustus* and smaller colonizing species is functionally significant as these are the species responsible for the majority of brackish marsh aboveground biomass with orders of magnitude higher biomass than *Sc. americanus* when hogs are not present (Więski et al. 2010, Guo and Pennings 2012). Although hog effects on productivity are similar to invasive nutria (*Myocaster coypus*) effects in some Louisiana marshes (i.e., 30% reduction; Taylor et al. 1997), the consequences of functional changes in coastal disturbance regimes from invasive ecosystem engineers requires further examination. Differences in community structure found in our experiments were due hog disturbance effects on community assembly and recovery over time, as opposed to complete vegetative destruction as seen by hogs in other systems. Trophic and non-trophic hog effects combine to generate a plant community that is 33% more diverse but less productive, a common result in communities with altered disturbance regimes because changes in top-down control strongly affect primary productivity and, in foundation species like marsh grass or kelps, ecosystem resistance to change (Levin et al. 2002, Ling et al. 2009, Siemann et al. 2009, Johnstone et al. 2016, Sharp and Angelini 2016). Thus, consumer control that changes species dominance through engineering and top-down control has important implications for how coastal habitats recover from disturbance.

Repeated hog usage generates a more diverse, less productive brackish marsh as hogs return to these areas and continually disturb plant communities through several foraging behaviors. First, hogs appear to prefer to travel along edges of tall plants with extensive root systems to avoid sinking in mud or being exposed (i.e., along the borders of *J. romerianus*), as seen in important edge-recovery effects in salt marshes (Sharp and Angelini 2016; Hensel et al., 2021). Similar to marsh grazing from the Canada goose (Jefferies and Rockwell 2002), concentrated consumer activity on the edge can be more powerful than effects in the middle of habitats. Here, expansion of disturbed areas requires hogs to locally overwhelm and cause ecosystem decline. Also, hogs may return to marsh areas to forage for clams (*Polymesoda carolinia*) and other soil invertebrates that live in *J. romerianus* and *Sp. cynosuroides* zones and have been found in hog stomachs in coastal South Carolina (Wood and Roark 1980, Graves 1984). Last, hogs may prefer to consume new vegetation that grows in disturbed marshes (e.g., *Sc. americanus*, *S. tabernaemontani*, *B. robustus*) that is easier to consume with higher nutrient levels (Appendix S1: Table S7). Hogs can consume roots of *Sp. cynosuroides* (Wood and Roark 1980) but we found no published nor observational evidence that hogs consume the woody *J. romerianus* (i.e., no grazing marks observed). Thus, like elephants in Kenya (Coverdale et al. 2016) and hogs in Georgia dunes (Oldfield and Evans 2016) and Texas pine forests (Siemann et al. 2009), the plants most commonly consumed by feral hogs appear to be the same plants that benefit the most from hog disturbances. All these behaviors contribute to the role of feral hogs as engineers in brackish marshes and add to recent findings that ecosystem engineering is strong in marine ecosystems (Romero et al. 2015). Our study on hog behavior in brackish marshes adds to a relative dearth of observations of hog impacts in aquatic ecosystems compared to terrestrial ecosystems (Barrios-Garcia and Ballari 2012) and, along with manipulations of invasive nutria (Taylor and Grace 1995, Taylor et al. 1997, Ford and Grace 1998), form a groundwork for describing the broad effects of destructive invasive ecosystem engineers in wetlands.

Describing the effects of large consumers like feral hogs on ecosystem dynamics is an emerging frontier in wetlands ecology. Feral hogs are now included with sea otters and American alligators as large organisms that can have strong, pervasive effects on marshes that expand over time based on animal behavior (Gaskins et al. 2020). Recent research indicates that feral hog effects are also relevant in many coastal ecosystems. Effects of hog invasion on outcomes of interaction networks in the coastal southeastern United States, for example, vary in mechanism: in salt marshes, hog activity is concentrated in areas with nearby hardwood forest during summers (Sharp and Angelini 2019), where hogs trample recovering grass and prey on ribbed mussels, breaking down facilitation networks and lowering resilience (Hensel et al., 2021). Repeated but infrequent hog visits to coastal Georgia dunes facilitate long term success of an invasive plant while lowering overall productivity of the rest of the community (Oldfield and Evans 2016). In all cases, hog activity is pervasive, as disturbed habitats are maintained over time, but hogs do not fully destroy vegetation, unlike in other systems (Campbell and Long 2009, Bevins et al. 2014). The ability for hogs to engineer habitats has strong implications for the future of these ecosystems as management beyond intense hunting pressure is unreliable and/or unsuccessful (Geisser and Reyer 2004, Barrios-Garcia and Ballari 2012). Our experiments suggest that southeastern U.S. marshes, like other ecosystems that have experienced an invasion or range expansion of large consumers, will be structured differently and less productive without intense feral hog hunting or the reintroduction of natural predators.

The spread of invasives is one of many anthropogenic effects that combines with climate change to ultimately create new communities with different structure and ecosystem functioning, forcing novel management and adaptation of conservation plans (Morse et al. 2014, He and Silliman 2019). Large consumers like hogs, with generalist predatory behavior and lower trophic feeding, can simultaneously alter habitat structure, food web structure and energy flow, and shift biomass pyramids (Crooks 2002, Woodson et al. 2018). Thus, to increase resilience to climate change in coastal wetlands, managing for both local species interactions and effectively managing large consumers is essential. Large invasive consumer changes to disturbance regimes, species interactions, and ecosystem processes must all be explicitly considered as these effects are particularly long lasting, even in resilient habitats (Mack and D'Antonio 1998, Johnstone et al. 2016, Guy-Haim et al. 2018). Understanding how large consumers change habitat structure and the strength of top-down control is needed to forecast how communities and food webs will function, resist, and recover from increasingly variable human impacts on natural ecosystems.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3572/suppinfo

Open Research

Data and code (Hensel 2021) used to generate figures and perform analyses are available in Zenodo: https://doi.org/10.5281/zenodo.5160268.