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Predators enhance resilience of a saltmarsh foundation species to drought

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Abstract

1. Disturbances are increasing in size and frequency with climate change, facilitating species that opportunistically exploit areas where habitat-forming foundation species have been removed. Although it is well-recognized that consumers, disease and weedy space-holders can affect foundation species' resistance to and recovery from disturbance, how predators influence their resilience is less clear.
2. In salt marshareas de-vegetated by drought and intensive snail *Littoraria irrorata* grazing (hereafter, 'die-offs'), we monitored bird use and experimentally manipulated bird and nekton access to the vegetated borders of die-off mudflats across periods of both vegetation die-off and regrowth to explore how these predators mediate the resilience of cordgrass *Spartina alterniflora*, the foundation species that structures US Atlantic coast salt marshes.
3. Surveys revealed that birds, especially probers that agitate soils, forage year-round for invertebrates in die-off mudflats in our study area but not in adjacent vegetated areas.
4. During periods of die-off, cordgrass borders accessible to bird and nekton predators retreated >3-times slower and snail densities were halved, relative to predator exclusion cages. In predator-accessible plots, slower border retreat corresponded to greater snail infection by a bird host-dependent trematode parasite. During recovery, cordgrass borders revegetated more quickly, and snail densities declined faster over time in unmanipulated controls relative to predator exclusions.
5. *Synthesis*. These findings suggest that birds, through their transmission of parasites to snails, appear to act synergistically with snail-consuming nekton to slow cordgrass loss after drought-snail disturbances. Predator access also corresponds to faster cordgrass recovery as environmental conditions improve, although the mechanisms behind this need further investigation. Thus, predators that opportunistically forage within disturbances have the potential to suppress consumer impacts through multiple mechanisms, including consumption and disease transmission, thereby bolstering foundation species' resilience and modulating whole ecosystem responses to climate change.

KEYWORDS

bird, climate change, food web, nekton, non-consumptive interactions, parasite, *Spartina alterniflora*, trophic cascade

1 | INTRODUCTION

Disturbances that reduce the cover of dominant, habitat-forming foundation species drive variation in nutrient cycling, energy fluxes, species interactions and community structure in many ecosystems (Ellison et al., 2005; Gaylord et al., 2011; Harmon et al., 2009; Polis et al., 1997). Because foundation species play a crucial role in supporting food webs through provisioning of habitat and amelioration of biotic and physical stress, the removal of these species via disturbance often locally simplifies the physical structure of an environment and alters species composition (Bruno et al., 2007; Silliman et al., 2005). These changes in habitat complexity, stress and species assemblages within disturbed areas benefit some species and negatively affect others, thereby altering biodiversity (Kane et al., 2011) and often facilitating invasive species (Mack & D'Antonio, 1998). Such cascading effects on community structure and ecosystem processes can, in turn, influence the post-disturbance responses of the foundation species. Changes in species composition within disturbed areas may cause continued loss of the foundation species after the initial perturbation (Jactel et al., 2012; Silliman et al., 2005) and/or accelerate ecosystem recovery or successional dynamics (Swanson et al., 2011). Although disturbance is a natural feature of every ecosystem, climate change is altering the frequency, duration, size and ecological impacts of these events (Turner, 2010) and causing profound shifts in ecosystem dynamics globally (Anthony et al., 2008). Forecasting ecosystem resilience therefore hinges upon advancing our mechanistic understanding of how shifts in population and community structure within affected areas influence foundation species' resistance to disturbance and their subsequent recovery.

Organisms that opportunistically exploit disturbed areas can alter ecosystems' physical and biotic properties in ways that may harm or benefit the foundation species. Grazers and disease can cause additional die-back on the margins of disturbed habitat patches, for instance, thereby reducing foundation species' resistance to disturbance (Silliman et al., 2013). Likewise, preferential foraging on saplings by browsers can slow the re-establishment of foundational trees in riparian ecosystems (Opperman & Merenlender, 2000). Alternatively, some species that proliferate within disturbed spaces may increase the resilience of the foundation species and accelerate their rate of recolonization, often by ameliorating physical stress, consuming early successional space-holders and/or controlling species that may have negative impacts on the foundation species (Burkepile & Hay, 2008; Connell & Slatyer, 2002). To date, most research on the importance of species interactions in modulating foundation species' resistance to and recovery from disturbance has focused on the importance of grazers and other space-holders. However, predators may be commonly attracted to disturbed areas where prey are either easier to capture due to reduced habitat structure or more abundant due to shifts in community composition. For example, mustelids and felids capitalize on areas disturbed by forest fire where their prey either become more visible as plant cover is reduced or more abundant as prey forage quality increases (Dees et al., 2007; Paragi et al., 1996). Beyond these direct consumptive interactions, predators may also introduce parasites, disease or nutrients through their waste into disturbed ecosystems, thereby exerting indirect control of foundation species and their consumers (Morton & Silliman, 2019). How predators use disturbed patches, and the extent to which they influence foundation species' resistance to and recovery from disturbance, remain outstanding questions in many ecosystems.

Saltmarshes are intertidal grasslands that form along low-energy coastlines around the world, and are often dominated by stands of salt-tolerant macrophytes that support surprisingly complex food webs (Lafferty et al., 2008; McCann et al., 2017). Saltmarshes offer a suitable system for studying how predators may influence ecosystem resilience because they are vulnerable to an array of disturbances that kill foundational marsh plants including drought- and grazer-induced die-offs, and rooting and trampling by hogs, livestock and nutria (Alberti et al., 2010; Angelini & Silliman, 2012; He et al., 2017; Sharp & Angelini, 2019). In saltmarshes that dominate much of the southeastern US Atlantic and Gulf coasts, multiple droughts have been associated with the die-off of thousands of hectares of the foundational grass, *Spartina alterniflora* (hereafter, cordgrass) over the last 20 years (Alber et al., 2008) and with a 30-year decline in cordgrass production (O'Donnell & Schalles, 2016). During drought, cordgrass can die in discrete patches (hereafter, 'die-offs'), leaving behind exposed mud surfaces. These die-offs, which range in size from tens to tens of thousands of square metres, form during drought due to the combination of localized reductions in soil moisture and pH, and increases in soil porewater salinity and metal toxicity, stresses that act together to kill cordgrass (Chalifour et al., 2019; McKee et al., 2004). The marsh periwinkle snail *Littoraria irrorata* (hereafter snail), which feeds on stressed cordgrass tissue, often accumulates in high density fronts on cordgrass bordering die-offs and can drive die-off border retreat by metres per year through their intensive grazing of cordgrass leaves and stems (Silliman et al., 2005). In mudflats where drought stress and snails have killed off cordgrass, resident invertebrate infauna experience elevated temperatures, increased evaporative stress and a loss of structural refugia, factors that can drive the mortality of sessile bivalves, including the ribbed mussel *Geukensia demissa* (hereafter mussels) and the death and/or migration of motile species, like fiddler, mud and marsh crabs (Angelini et al., 2016; McFarlin et al., 2015; Nomann & Pennings, 1998).

Once drought conditions subside and snail grazing fronts break up, cordgrass begins to recolonize die-off mudflats almost exclusively through vegetative growth from cordgrass surviving along die-off borders and in isolated patches remaining within die-offs (Angelini et al., 2016). The rate at which cordgrass recolonizes mudflats is known to be mediated by spatial factors including the size and distribution of cordgrass patches, the stress-ameliorating effects of mussels that act to reduce porewater salinity and increase nutrient availability, and abiotic factors, including soil anoxia and sulfide stress (Angelini & Silliman, 2012; Derksen-Hooijberg et al., 2017; Sharp & Angelini, 2016). Across this region, blue crabs *Callinectes sapidus*, red drum *Sciaenops ocellatus* and diamondback terrapins

Malaclemys terrapin are nektonic predators that access marsh platforms where they forage on invertebrate prey, including snails and mussels, during higher spring tides. These predators demonstrate seasonal variability in marsh-feeding habits and are typically most abundant during warmer months when water is above 15°C (Fitz & Wiegert, 1991; Gibbons et al., 2001; Parks & Division, 2000). Our observations of wading birds and shorebirds probing the marsh surface for polychaetes, crabs and other infauna, and defecating within die-off areas, at mid to low tides indicate that these motile predators may also be influencing salt marsh invertebrate densities, soil biogeochemistry and cordgrass health (Bosworth & Thibodeaux, 1990; Ligeza & Smal, 2003; Vince et al., 1976). However, the frequency with which bird predators use die-off areas as well as how the various activities of birds and nekton within die-off mudflats interact to affect cordgrass resilience to drought disturbance remain outstanding questions.

Here we investigate the effects of these predators (birds and nekton) in mediating saltmarsh foundation species' resistance to disturbance and recovery dynamics. We hypothesized that nekton and bird predators slow cordgrass border retreat during drought and facilitate cordgrass recovery after drought conditions subside through their consumption of snail grazers. We also hypothesize that avian predators play a secondary role in mediating saltmarsh resilience via indirect effects through parasite transmission to snails. Simultaneously, we surveyed bird use of die-off areas seasonally and across multiple sites to evaluate the guilds of avian predators that may be capitalizing on drought-induced die-off areas as little is known about their response to these increasingly prevalent disturbances. In the face of increasing frequency and severity of drought, a major manifestation of climate change in the region (O'Donnell & Schalles, 2016), there is a critical need to better understand how ecosystems are responding to such large-scale drivers. This study both informs the management of coastal wetlands increasingly stressed by drought by demonstrating that predator-modulated resilience to drought is contingent upon whether marshes are actively dying-off or recovering, and more generally, advances our mechanistic understanding of predator effects on ecosystem resilience.

2 | MATERIALS AND METHODS

2.1 | Cordgrass die-off sites

We conducted the field experiments and surveys within six marsh platform die-offs at the Guana Tolomato Matanzas National Estuarine Research Reserve in Ponte Vedra Beach, Florida, USA (30.02°N, −81.33°W). For this study we define die-off borders as the transition from bare mudflat to cordgrass-vegetated marsh. Although we do not know precisely when the six die-offs first formed, Google Earth historical imagery indicates all six die-offs were vegetated in November 2015. Our observations of standing dead stems in the die-offs in April 2016 suggest they formed in about February/March 2016 as dead stems decompose quickly in the warm, sub-tropical climate of this region (Hensel & Silliman, 2013), leaving behind a bare mudflat. At each site, we used a Trimble Geo7x GPS (2 cm horizontal, 3 cm vertical accuracy) to delineate the border of each die-off, at three time points: (a) the start of the cordgrass retreat experiment in May 2016, (b) the start of the cordgrass recovery experiment, when cordgrass stopped retreating and began recolonizing the die-off mudflats via vegetative growth in January 2017 and (c) at the end of the cordgrass recovery experiment in August 2017. We also delineated the area of any cordgrass patches remaining within each die-off. Using Pathfinder Office (Trimble Geospatial), we subtracted the cordgrass patch areas from the total die-off area to calculate the die-off mudflat area. The initially distinct die-off areas at sites 1 and 2 grew so large during the cordgrass retreat phase that they merged into a single, contiguous die-off; the same phenomena occurred at sites 5 and 6. For the cordgrass retreat experiment and survey, we considered the six sites to be distinct during both the unmerged and merged phases because: (a) the sites and their corresponding experimental treatment blocks were far enough away from each other (>100 m) to be considered independent and (b) bird use of each site could be easily defined given the small size of bird flocks observed (i.e. the largest flocks occupied <100 m^2) relative to the merged die-off areas (>1,000 m^2).

The study region has a 30-year average precipitation of *c*. 10 cm/month, average summer temperature of 27.3°C, and average winter temperature of 14.5°C. Our study started during a relatively dry period (September 2015–August 2016: average monthly rainfall of 5.1 cm) followed by a wetter period (September 2016–August 2017: average monthly rainfall of 13.0 cm; see http://www.ncdc.noaa.gov for data and Figure S1 for climatic data summary). As high salinity and low pH in soil porewater can contribute to cordgrass die-off during hot, dry periods (Angelini et al., 2016; Mendelssohn & Morris, 2002), we used porewater samplers (Rhizons, Rhizosphere Research Products) to collect porewater from the top 5 cm of soil along die-off borders both during cordgrass retreat (18 samples from each of the six die-off sites in September 2016; *N* = 108) and recovery (eight samples from die-off sites 5 and 6 in March 2017; *N* = 16) phases for salinity and pH measurements.

2.2 | Bird surveys

To gauge if the composition and seasonality of birds foraging within die-off mudflats would influence cordgrass resilience to drought-snail disturbances, we surveyed bird use at our six experimental die-off sites on 20 dates spanning all seasons from June 2016 to July 2017. We initiated each survey by identifying to species and counting all birds within the die-off at each site. We limited our survey to die-off mudflats due to the birds' infrequent use of vegetated areas (i.e. in our >80 hr of observations we only observed one instance of birds foraging in vegetated areas as a flock of 25 white ibis migrated from one die-off area to another) and to time periods when tidewater had receded (i.e. not during high tide) as birds rarely foraged in flooded die-offs. Throughout the survey period, which ranged from

1 to 5 hr, we recorded the departure and arrival of all birds within the die-off area using a Celestron Regal M2 80ED spotting scope, and recorded the identity of any new species that landed. If we did not observe any changes to flock size in a 20 min period (i.e. no arrivals or departures), we would re-count all birds to confirm flock size hadn't changed and no birds had arrived or departed undetected. We tracked changes in 'flock' size (i.e. all birds of the same species present in the die-off) as opposed to individual birds because of the difficulty in keeping track of identical-looking individuals of the same species. When the surveys were complete, we categorized each observed bird species into one of three foraging guilds: probers (continuous tactile), ground foragers (continuous visual + pause-travel) or stalkers (i.e. stand erect and motionless scanning the surface for prey which they quickly strike, Barbosa, 1995; Kushlan, 1976; Smith, 1995). We focus our analyses on foraging guilds given our interest in the potential effects of different forms of bird foraging activity on die-off biogeochemistry, invertebrate composition, invertebrate vulnerability to parasite infection, cordgrass performance, and because some species were observed too infrequently for rigorous analysis of their use patterns.

For each survey period at each of the six experimental sites, we calculated the time-weighted, mean flock density of each foraging guild, similar to time-interval flock size counts (see Petersen & Exo, 1999) using the following equation:

$$\bar{x} = \frac{\sum_{i=1}^{n} t_i x_i}{\sum_{i=1}^{n} t_i},$$

where (t) is the amount of time (in min) between birds of a given foraging guild either joining or leaving the die-off, (x_i) is the number of birds of a given functional group observed at the start of period (t_i) and (n) is the number of total observations made at a given site during a single low-tide survey. We then divided the mean flock size in each foraging guild ($\bar{x}$) by the initial area of the die-off to standardize flock detection by the surveyed area and multiplied this value by 100 to calculate a standardized flock density (i.e. the mean flock size per 100 m^2 area). To examine seasonality of bird use, mean flock density observations were then binned by season (winter: December–February, spring: March–May, summer: June–August; fall: September–November).

To then assess whether birds were actively foraging (activity likely to affect cordgrass via probing and invertebrate composition effects on soil biogeochemistry) or simply resting within the die-offs (activity likely to influence cordgrass via defecation and, hence, transmission of parasites and nutrients), we monitored foraging frequency via two metrics. First, we counted the total number of individual birds of each functional guild observed actively foraging once every 20 min in the die-off to evaluate which functional guilds are foraging most at the flock level in die-offs ($N = 55$ replicate observations conducted over the entire study period). Second, we observed a focal bird of each functional guild for 3 min and recorded its strike rate (strikes/minute). Foraging surveys were conducted at all six die-off sites on 10 dates occurring during the summer and fall when invertebrate prey are most active.

2.3 | Cordgrass retreat experiment

Simultaneous with performing the bird surveys, we tested our hypothesis that marsh bird and nekton predators slow cordgrass retreat and suppress saltmarsh invertebrate densities along die-off borders by establishing a pair of 4 m × 6 m plots in each of six marsh die-off sites in May 2016 and randomly assigning each one of two treatments: predator exclusion or no-cage control. Each plot was oriented with its short, 4m side running parallel to the die-off border and its long, 6 m side intersecting the die-off border such that approximately one-third of each plot was cordgrass-vegetated marsh, one-third was dying cordgrass at the border and one-third was unvegetated mudflat (see Figure S2). Plots were spaced 4–6 m apart. We built predator exclusions by inserting 2.5 cm × 5 cm × 100 cm wooden stakes in the corners and along the edges of each plot and stapling multifilament netting (5 cm × 5 cm mesh; Best Choice Products) over this stake frame to cover the top and sides of the plot. The mesh netting hung approximately 3 cm above the marsh surface to allow small, benthic fauna to move freely in and out of the plot (Figure S2). We selected this mesh size because it is large enough to induce negligible effects on water flow, light availability and the movement of small nekton such as mummichogs, but small enough to exclude all birds, terrapin, larger fish and adult blue crab predators capable of consuming most benthic marsh invertebrates. Control plots were unmanipulated except for the insertion of wooden stakes to mark the plot corners and edges. Our observations of no birds foraging within our exclusion plots and an occasional red drum *S. ocellatus* or blue crab caught in the netting indicate this cage design was effective in excluding these predators. Although it is possible some blue crabs could enter our exclusions through the 3 cm gap, blue crab densities are orders of magnitude lower in northeastern Florida than in more northern latitudes where this species is known to exert top-down control of salt marsh invertebrates (Colton et al., 2014). This prior work as well as our observations from many hours in the field that blue crabs rarely forage in higher elevation marshes indicate they are unlikely to be important drivers of plant resilience in our study region.

Within each plot we established nine, 50 cm × 50 cm permanent subplots (three in the vegetated marsh, three in the dying border and three in the mudflat) that were positioned at least 15 cm from the plot edge and 60 cm apart. To capture infauna and vegetation responses over time throughout the active growing season of our experiment, in May, July and October 2016, we measured cordgrass canopy height (the average of the tallest eight stems) and counted cordgrass stems, small (<1 cm diameter, typical of juvenile fiddler crabs) and large (>1 cm diameter, typical of adult fiddler crabs) crab burrows, all mussels and live and dead (as indicated by empty or crushed snail shells) snails in each subplot. We also scored cordgrass leaf damage caused by snails, which use their radula to incise easy-to-identify wounds, or 'radulations' that run parallel to the leaf venation (Chalifour et al., 2019), by counting presence/absence of snail grazing damage on 20 random leaves per subplot. As snails are very rarely observed off of cordgrass stems (Davidson et al., 2015), we only collected snail density and snail grazing data in vegetated plots farthest from die-off centres. Initial background snail densities in these areas were 688 ± 188 m^{-2} prior to any cage being erected.

After approximately two growing seasons, we harvested aboveground cordgrass biomass from each subplot in August 2017, dried it at 65°C for 48 hr, and weighed it. The delay in harvest allowed us to continue monitoring border movement in these plots beyond the end of the retreat phase. We recorded elevation, a key factor determining tidal inundation and porewater flushing rates in tidal systems, using the Trimble Geo7x GPS within the centre of each subplot at the start of the experiment to account for any variability between plots. Finally, to assess the rate of cordgrass border movement, we measured the orthogonal distance from the plot border closest to the die-off centre to the first live cordgrass stem encountered—i.e. the border of living vegetation—at five locations (x_1, x_2, ... x_5), spaced 0.7 m apart (y) on each monitoring date. We then used these variables (x and y) to estimate the area of die-off in each treatment plot using a Riemann sum, $\sum_{i=1}^{n}(x_i)y$, and used the difference in the area of die-off between monitoring dates to assess the rate of marsh area loss or gain (m^2/day).

Finally, as marsh birds are known hosts for a prevalent trematode parasite, *Parorchis acanthus*, which infects marsh periwinkle snails and reduces their cordgrass grazing rates (Morton & Silliman, 2019; Pung et al., 2008), we collected live snails from control and predator exclusion plots in March 2017. We sent the snails to Duke Marine Lab in Beaufort, NC, USA to be examined under microscope for *P. acanthus* infection. Due to a freezer malfunctioning, we were only able to collect parasite data from snails collected at sites 5 and 6 (50 snails from each plot at two sites totaling 200 snails) and all snails collected for parasite analyses from the cordgrass recovery experiment were lost.

2.4 | Cordgrass recovery experiment

Seven months after starting the cordgrass retreat experiment, cordgrass ceased dying back and new cordgrass tillers began emerging within the previously denuded die-off mudflat. To test the hypothesis that large predators also affect cordgrass recolonization dynamics and invertebrate densities throughout this recovery phase, we marked pairs of 4 m × 2 m plots, spaced 4–6 m apart, at sites 5 and 6 (which were merged at this point) in a randomized block design and assigned each one of two treatments: predator exclusion or control ($N = 8$ replicate blocks, 16 plots overall). In this experiment which ran from May 2017 to August 2017, plots were oriented such that their long side (4 m) ran parallel to the die-off border and their short side intersected the die-off border such that half of the plot was in dense vegetation behind the border and the other half overlapped the sparsely vegetated border edge (Figure S2). In each plot, we established six, 50 × 50 cm permanent subplots, three of which were located along the border edge where we expected new tillers to emerge, and three of which were in the cordgrass-vegetated area. Each subplot was at least 25 cm from the plot edge and 50 cm apart. Within each subplot, we monitored cordgrass canopy height (eight tallest stems), and counted live and dead stems, mussels and live and dead snails. Measurements at the start of the recovery experiment revealed that snail densities were slightly higher in control compared to treatment plots (166 ± 25 vs. 113 ± 23 snails, mean ± *SE*, a difference in density with no significant effect on snail top-down control, Atkins et al., 2015), but that all other measured variables were equivalent in the two treatments. To better capture the response of cordgrass at the larger plot-scale, we divided each plot into 8-1 m × 1 m quadrats, estimated percent cover of live and dead vegetation in each quadrat and averaged the percent cover of all eight quadrats.

To test the potential for predation to mediate snail populations along die-off borders, we collected 320 snails from an adjacent marsh and tethered 10 snails in each plot (five in the border and five in the cordgrass-vegetated marsh). We used marine epoxy (Splash Zone 2-part epoxy compound, West Marine) to attach a 65 cm long 4 kg test, monofilament line to the back of the snail shell and tied the other end to a 7 cm long landscape staple that we anchored in the marsh. Tethers were long enough to enable snails to freely climb cordgrass stems and forage on the marsh surface. We deployed tethered snails during a neap tide in mid-July 2017, returned the next day to ensure snails were not entangled around cordgrass stems and then recorded snail predation in late July and early August. We recorded if snails were either alive, plucked (only shell remaining) or removed (no remnant of shell or snail) after spring high tides when nekton predators have access to the higher elevation marsh platforms where our plots were situated. Plucked snails were assumed to be consumed by mud crabs, which remove the soft tissue of snails, leaving behind empty shells (Silliman & Bertness, 2002). Empty shells that result from desiccation rather than predations are unlikely as snails are well-adapted to the hot, and sometimes dry conditions that are common in these marshes.

2.5 | Statistical analysis

For bird surveys, we used a GLMM (Table 1) to evaluate the effect size and significance of functional group and season, both treated as fixed variables, and of site, a random effect, on cumulative (sum of all observations) and seasonal mean flock density. We then used one-way ANOVA to evaluate the effect of foraging guild identity on the number of foraging individuals observed and on strike rate. We did not include site as a random effect in this model because several sites had no foraging birds during these survey periods and the majority of observations were made at sites 5 and 6 (82%).

Data from both cordgrass retreat and recovery field experiments were analysed using GLMMs (Table 1) in which treatment was a fixed variable and either replicate die-off site (cordgrass retreat) or block (cordgrass recovery experiment) were random effects (ε). We also included elevation as a fixed variable, but only for analysis of retreat experiments where sites were dispersed across >5 km of coastline and exhibited more pronounced variation in elevation (i.e. the range

TABLE 1 Model variables for generalized linear mixed models, including main and nested (in parentheses) random effects (ε). Treatment indicates experimental treatment (control or predator exclusion)

Model response variable	Predictor variable	Covariate	Random effect (ε)
Bird survey analysis			
Mean flock density	Foraging guild	—	Site
Mean flock density	Season	—	Site
Retreat phase analysis			
Monthly border retreat	Treatment	Elevation	Site
Invertebrate densities	Treatment	Elevation	Site
Plant metrics	Treatment	Elevation	Site
Recovery phase analysis			
Monthly border recovery	Treatment	—	Block
Invertebrate densities	Treatment	—	Block
Plant metrics	Treatment	—	Block

of elevation of plots in the retreat experiment, 1.70–1.99 m a.s.l.) relative to the recovery experiment (plot elevation range: 1.73–1.89 m a.s.l.). As we only tested porewater, pH and salinity differences between retreat and recovery phases and not between treatments, we only use die-off phase (retreat/recovery) as a fixed effect and site as a random effect for the analysis of these variables. For proportional data (i.e. percent vegetation cover, snail radulation damage and tethered snail predation), we tested the effect of treatment with generalized linear mixed models with a binomial error distribution. We evaluated the effect of predator exclusion on the proportion of snails with and without trematode infection using a Chi-square test. Residuals were plotted for all analyses to test for appropriateness of fitted models. All data in this study were analysed using the LME4 software package (Bates et al., 2015) in the statistical computing environment R Version 3.2.2 (R Core Team, 2014).

3 | RESULTS

3.1 | Cordgrass die-off sites

By monitoring soil porewater and changes in the location of die-off borders over time, we found that porewater salinity was higher (54.0 ± 0.7 vs. 49.8 ± 0.8 ppt [mean ± *SE* here and below], $F_{1,10} = 5.2$, $\varepsilon_{\text{Standard Deviation}} = 4.12$, $p < 0.05$) and pH lower (5.7 ± 0.1 vs. 6.9 ± 0.03, $F_{1,10} = 8.5$, $\varepsilon_{\text{SD}} = 0.56$, $p < 0.01$; Figure S3) in the period spanning May 2016 to January 2017 compared to the subsequent period of February 2017–August 2017. Correspondingly, cordgrass retreated steadily, expanding each die-off area, from May 2016 to January 2017 (−1.63 ± 0.2 cm^2 of vegetation loss per metre of lateral border per day) and die-off area nearly tripled at some sites (see Figure S4 for further details). As soil porewater conditions became more tolerable for plant growth between January and August 2017, recovery varied considerably across sites, with sites 3, 5 and 6 recovering from 0.5 to 3.1 m^2/day and die-off area in sites 1, 2 and 4, changing little in size or slightly expanding (Figure S4).

3.2 | Bird survey

Our survey of bird use of die-off areas revealed that these denuded mudflats sometimes support >200 foraging birds at a given time. Despite pulses of large numbers of birds foraging during some survey periods, no birds would visit die-offs for hours during other periods, resulting in an average bird density of 0.23 ± 0.05 bird 100 m^{-2} with bird density varying little across all survey sites ($F_{9,66} = 1.0$, $p = 0.5$, $\varepsilon_{SD} = 0.11$). Probers were 10 times more common than stalkers, and ground foragers occurred at moderate densities in die-offs ($F_{2,17} = 3.4$, $p < 0.05$, Figure 1). Flock density was highest in the fall, intermediate in the winter and summer and lowest in the spring surveys ($F_{3,17} = 3.1$, $p < 0.05$, $\varepsilon_{SD} = 0.16$, Figure 1). The largest single species flock of probers was of white ibis *Eudocimus albus* and contained 137 birds, while semipalmated plovers *Charadrius semipalmatus* represented the largest ground forager flock (91 birds) and snowy egrets *Egretta thula* the largest stalker flock (seven birds) respectively (Table 2). In total, we observed 17 different bird species in die-off areas during our survey (Table 2).

Our surveys of bird behaviour revealed that 79 ± 6% (mean ± *SE*) of all birds were foraging at any given time. Ground foragers and stalkers were observed foraging more frequently than probers ($F_{2,105} = 9.93$, $p < 0.001$, Figure 2). However, probers averaged 3- and 4-times more strikes per minute, than ground foragers and stalkers respectively ($F_{2,105} = 4.15$, $p < 0.05$, Figure 2). Prey items we

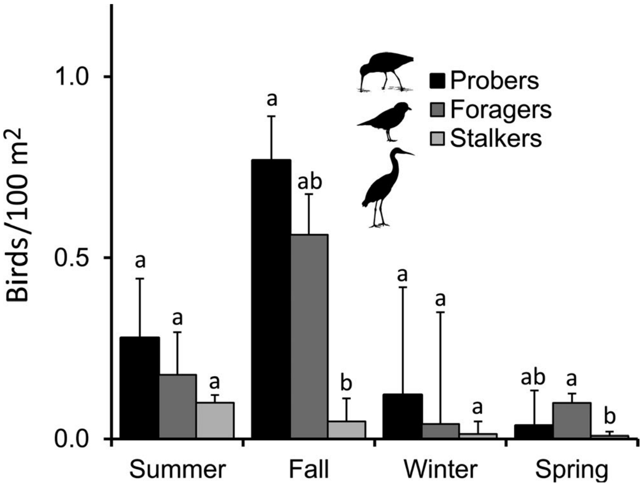

FIGURE 1 Seasonal variation of mean flock density (mean birds observed per 100 m^2 ± *SE*) observed across all die-off mudflats surveyed in summer (Jun–Aug), fall (Sep–Nov), winter (Dec–Feb) and spring (Mar–May) of 2016–2017. Birds were categorized by foraging strategy: Probers, ground foragers and sit-and-wait stalkers

TABLE 2 Bird species observed during surveys of marsh die-off from summer 2016 to spring 2017. Max flock size indicates the larger flock observed in a single die-off area during low-tide surveys while frequency of occurrence refers to the presence of a species at any point during a single low-tide survey ($N = 55$ surveys). Species in each group are listed in the order of their abundance

Functional group	Species observed	Max. flock size	Frequency of occurrence (%)
Probers	White ibis *Eudocimus albus*	137	18
	Spotted sandpiper *Actitis macularius*	136	16
	Willet *Tringa semipalmata*	36	27
	Least sandpiper *Calidris minutilla*	11	5
	American oystercatcher *Haematopus palliates*	2	4
	Dunlin *Calidris alpina*	1	2
	Lesser yellowlegs *Tringa flavipes*	1	4
Ground foragers	Semipalmated plover *Charadrius semipalmatus*	91	16
	Black-bellied plover *Pluvialis squatarola*	48	25
	Ruddy turnstone *Arenaria interpres*	15	7
	Herring gull *Larus argentatus*	6	9
	Whimbrel *Numenius phaeopus*	1	4
Stalkers	Snowy egret *Egretta thula*	7	33
	Little blue heron *Egretta caerulea*	7	15
	Tricolored heron *Egretta tricolor*	4	7
	Great egret *Adrea alba*	1	7
	Great blue heron *Adrea herodias*	1	2

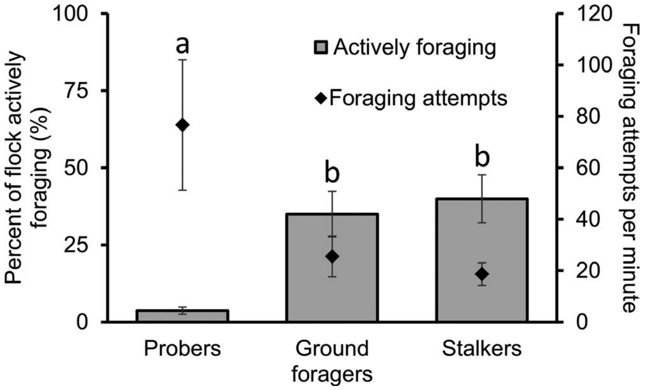

FIGURE 2 The per cent of birds in flocks observed to be actively foraging (a) and the foraging rate of individual birds in each foraging guild of each foraging guild in salt marsh die-off sites surveyed in summer and fall 2016. Different letters above bars indicate significant differences between groups in both per cent of flock and foraging attempts. Data are shown as the mean ± *SE* of all observations made for each functional guild in each season

could discern among all guilds included bloodworms (*Glycera* spp.), burrowing crabs (*Uca* spp., *Panopeus* spp., and *Sesarma reticulatum*, and ribbed mussels *G. demissa*. However, we never observed birds preying upon marsh periwinkle snails *L. irrorata* in our more than 80 hr of survey observations. Due to difficulty in consistently identifying prey organisms and prey capture by bird predators, we could not compare differences in prey types or prey capture rates among foraging guilds.

3.3 | Cordgrass retreat experiment

To relate predator presence to rates of border retreat and snail grazing pressure over the growing season, we present snail densities at the end of the growing season as an absolute measure, and snail decline relative to pre-experiment densities (standardized to 100 days) as a relative measure. After one growing season (May–October 2017) of the cordgrass retreat experiment, snail densities were lower ($F_{1,5} = 9.4$, $p < 0.01$, $\varepsilon_{SD} = 7.5$, Figure 3a) and declined twice as fast ($F_{1,5} = 8.1$, $p < 0.01$, $\varepsilon_{SD} = 0.07$; Figure 3b) in control plots than in predator exclusions. We observed a lower proportion of cordgrass stems with snail grazing (48.0 ± 7.2 vs. 63.6 ± 6.1%; $F_{1,5} = 3.1$, $p < 0.01$, $\varepsilon_{SD} = 0.2$) and cordgrass retreat was three times slower ($F_{1,5} = 5.8$, $p < 0.05$, $\varepsilon_{SD} = 0.34$, Figure 3c) in control relative to predator exclusion plots. We observed similar differences in other metrics of plant health between control and predator exclusion plots such as higher stem density (210 ± 27 vs. 127 ± 24 stems/m^2; $F_{1,5} = 13.8$, $p < 0.001$, $\varepsilon_{SD} = 27.1$), cordgrass biomass (126.1 ± 17.2 vs. 89.0 ± 15.3 g dry-weight·m^{-2}; $F_{1,5} = 3.3$, $\varepsilon_{SD} = 14.4$, $p < 0.05$) and percent vegetation cover (55 ± 4 vs. 42 ± 6%; $F_{1,5} = 5.2$, $p < 0.05$, $\varepsilon_{SD} = 0.22$), suggesting an overall thinning of biomass in plots inaccessible to nekton and bird predators. The few stems remaining in predator exclusions were taller than in controls (40.3 ± 1.6 vs. 35.8 ± 1.8 cm; $F_{1,5} = 10.3$, $\varepsilon_{SD} = 0$, $p < 0.001$), mussel densities were 3 times higher in predator exclusions than controls ($F_{1,5} = 4.7$, $\varepsilon_{SD} = 0.36$, $p < 0.05$, Figure 4a), while small ($F_{1,5} = 0.6$, $p = 0.43$, $\varepsilon_{SD} = 0$) and large ($F_{1,5} = 0.7$, $p = 0.39$,

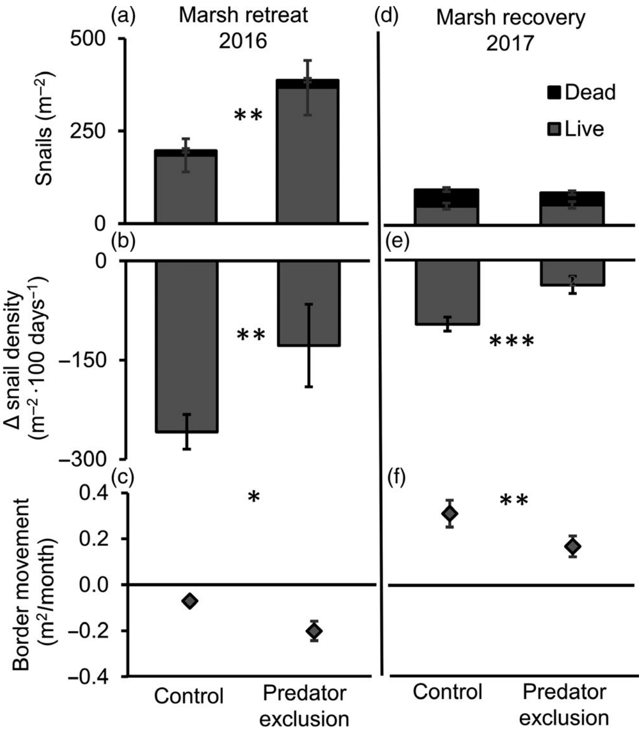

FIGURE 3 Response of snail *Littoraria irrorata* densities and border movement (mean ± *SE*) to predator-accessible (control) and predator-exclusion treatments during phases of marsh vegetation retreat from 6 die-off sites (left column) and recovery from two die-off sites (right columns). Snail densities (a, d) were recorded after experiments were in place for one growing season. Change in snail densities (b, e) were interpolated from snail densities measured throughout the growing season, standardized to 100 days intervals. Initial background snail densities (mean ± *SE*) were 688 ± 188 (retreat) and 139 ± 17 m^{-2} (recovery). Border movement during (c) retreat and (f) recovery phases indicates area per metre of border (negative when marsh vegetation is being lost and replaced by die-off area and positive when vegetation is recolonizing and expanding into die-off areas). $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

ε = 0.72) crab burrow densities were similar across treatments. No snails from predator exclusions were infected with *P. acanthus* trematodes, but 13% were infected in the controls ($\chi^2(1) = 13.9$, $p < 0.001$, Figure 4c). Although elevation was included as a covariate in all models related to this experiment, this factor had no significant effect on any of the response variables.

3.4 | Cordgrass recovery experiment

At the end of the cordgrass recovery experiment, snail densities were similar across treatments ($F_{1,7} = 0.11$, $\varepsilon_{SD} = 4.02$, $p = 0.74$; Figure 3d) yet declined faster in control plots than in predator exclusions over the course of the growing season ($F_{1,7} = 17.8$, $p < 0.001$, $\varepsilon_{SD} = 0.17$, Figure 3e), while mussels ($p = 0.2$, Figure 4b), cordgrass live stems ($p = 0.6$) and live biomass ($p = 0.1$) were unaffected. However, cordgrass laterally expanded into bare mudflat twice as fast in control compared to predator exclusion plots ($F_{1,7} = 9.8$, $p < 0.01$, $\varepsilon_{SD} = 0.2$, Figure 3f).

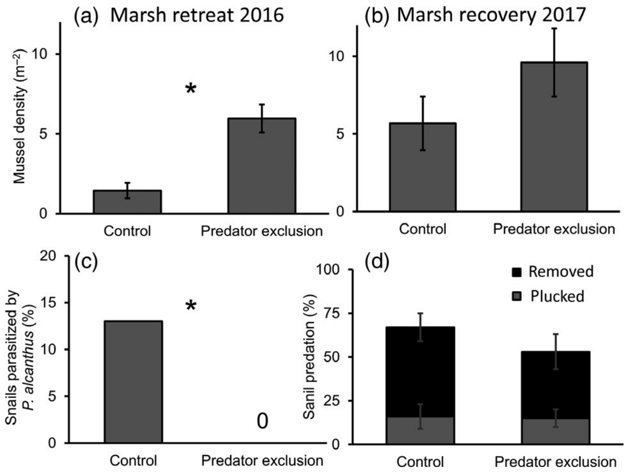

FIGURE 4 Salt marsh fauna characteristics in predator-accessible (control) and predator-exclusion treatments after one growing season of both marsh vegetation retreat (left columns) and recovery (right columns). Mussel density (mean ± *SE*) in (a) retreat and (b) recovery phases extrapolated from 0.5 m^2 quadrats. We measured (c) the proportion of snails *Littoraria irrorata* infected with *Parorchis acanthus*, a trematode parasite at the end of the retreat experiment growing season and (d) estimated snail predation (designated as removed completely or plucked from inside shell) at by monitoring tethered snails over a spring tide (*c*. 2 weeks) during the recovery growing season. $^{*}p < 0.05$

The percent of tethered snails that were plucked, a signature of being predated by juvenile white-clawed mud crabs *Eurytium limosum*, a benthic predator capable of migrating in and out of the predator exclusion plots, was similar across treatments ($p = 0.96$). However, 13% fewer snails were removed on average (though not statistically significant), a signature of blue crab and nekton predation, in predator exclusions than controls (Figure 4d).

4 | DISCUSSION

Experimental and empirical field data presented in this study demonstrate that the presence of marsh predators can slow saltmarsh die-off expansion and accelerate the recovery of foundational cordgrass. Specifically, predator presence was associated with declines in the density of snails, a key grazer known to denude cordgrass when aggregated in high densities (Silliman & Bertness, 2002), corresponding to slower rates of cordgrass border retreat and faster rates of cordgrass lateral expansion in uncaged controls. Using our experimental field data to parameterize simple simulations of die-off areal expansion and contraction/recovery across die-off patches varying in initial size, we estimate that the presence of marsh predators acts to decrease die-off expansion, and coincident cordgrass loss, over a 1-year period of drought- and snail-driven die-off by up to 69%, relative to die-off expansion scenarios where predators have been hypothetically removed from the system (see Supporting Information S5 for additional details and results). Likewise, in simulations of die-off recovery and coincident cordgrass recolonization, we estimate that cordgrass can recolonize up to 38% more die-off area in the presence than absence of predators over 1 year. Collectively, these simulations of whole die-off dynamics and our plot-scale experimental data suggest that predators may be significantly reducing both the size and duration of drought- and snail-driven die-off disturbances that are occurring in southeastern US saltmarshes (Figure S5). Additionally, our many hours of bird foraging observations provide evidence supporting the idea that avian predators slow die-off expansion and stimulate cordgrass recovery not by consuming snails, but rather by reducing snail grazing intensity via their transmission of a trematode parasite, and potentially by ameliorating soil stresses to improve cordgrass growth, although these effects were not explicitly measured in our study but shown in prior work (Anderson & Polis, 1999; Elliott & Vernes, 2019). Together, these findings provide evidence that disturbances shift where predators forage and mediate disease transmission within landscapes, changes that have the potential to provoke powerful, cascading effects on ecosystem resilience.

Die-offs are a ubiquitous feature of marshes in the southeastern US and are attractive foraging ground for predators (Alber et al., 2008). These predators play a unique role in saltmarshes by increasing their resilience to continued die-off. We suspect that nekton predators, including blue crabs and red drum (Hettler, 1989), that forage extensively in marsh platforms when water is deep enough (e.g. during spring tides) benefit from drought locally removing foundational cordgrass. Die-offs create areas with little obstruction to swimming and also concentrate snail prey along still vegetated die-off borders. Marsh die-off areas also appear to be attractive foraging grounds for shorebirds, an avian guild known to forage in mudflats that exist lower in the tidal frame and may migrate to drought-generated marsh die-offs during daily tidal cycles when low elevation foraging grounds (e.g. mudflats) are tidally submerged (Darnell & Smith, 2006). Here avian predators can easily see prey on the denuded surface, navigate on the ground without obstruction from vegetation, clearly spot threats (e.g. raptors) and flock in numbers that deter predators (Patten & O'Casey, 2007). The attraction of open foraging grounds to predators after disturbances remove foundation species is not unique to saltmarshes but to date has only been documented in forested ecosystems, warranting further study (Dees et al., 2007; Gates & Gysel, 1978; Paragi et al., 1996). Likewise, predators that control primary consumers and ameliorate environmental stress may similarly enhance resilience to disturbance in these ecosystems as well.

During phases of marsh retreat that started in the summer and extended through the fall when birds were most actively using the die-off areas, predator exclusion had a significant effect on snail and mussel populations. As we observed snails to be an uncommon part of birds' diets (i.e. we observed no birds eating snails during our foraging surveys), we suspect their effects on snails are primarily non-consumptive in nature, while nekton predators may be consuming snails more frequently. Indeed, *P. acanthus*, a trematode parasite that uses birds as a definitive host and is transmitted to snails at a larval stage, was only found in snails from plots with bird access, although our evaluation of this pattern was not rigorous as we had intended (i.e. 100 snails randomly sampled from all control and predator exclusion plots at only two sites) due to the majority of our samples being compromised (see Section 2). This trematode parasite is not lethal to intertidal snails, but it does slow snail movement and grazing rates, reducing grazing pressure on cordgrass-mudflat borders and possibly making them more susceptible to predation (Belgrad & Smith, 2014; Morton & Silliman, 2019). As snails at high densities are known to graze down marsh vegetation along these borders (Silliman et al., 2005), we suspect the reduction in snail grazing intensity provoked by bird-induced trematode infection coupled with snail predation by nekton predators—such as red drum and blue crabs—were key factors driving the reduced the rates of cordgrass loss and die-off border retreat we observed in uncaged controls during this phase. However, further research is needed to parse out the consumptive and non-consumptive effects of birds and nekton in mediating grazer behaviour and population sizes as well as cordgrass resistance to further die-off.

During the retreat phase, mussel densities were also significantly higher in predator exclusions compared to control plots (Figure 4a). Unlike snails, we did observe mussels being consumed by birds foraging in die-off areas, indicating that these sessile bivalves may have experienced enhanced predation by avian predators along die-off borders. Mussels are known to enhance cordgrass survival during drought- and snail-driven die-off as these filter-feeders form dense aggregations that locally enhance both soil moisture and nutrient availability and enhance cordgrass' resistance to drought and grazing stress (Angelini et al., 2016). Therefore, we anticipate that bird consumption of mussels may act to indirectly exacerbate drought stress on cordgrass along die-off borders. However, despite their negative impact on mussel densities, the slower retreat of cordgrass borders we observed in predator-accessible plots suggests that predators—both nekton and avian—have a net positive effect on marsh resistance to drought, primarily as a result of their top-down control of grazing snails.

During the marsh recovery phase, lateral recolonization of cordgrass along die-off borders varied considerably across sites, but the borders in predator-accessible control plots consistently recovered much more quickly than in predator exclusion cages. In general, die-off events initiated by drought form due to many interacting stressors, including snail grazing and soil stress (McKee et al., 2004; Silliman et al., 2005). During recovery, snail densities fell by nearly 7-fold across all treatments compared to densities observed during the retreat phase regardless of treatment, indicating a reduction in grazing pressure. Since snail densities were similarly low across treatments, higher rates of recovery in control plots may also be related to the effect avian predators have on soil properties, like soil aeration and nutrient deposition, caused by the soil probing and defecating of foraging birds (Bosworth & Thibodeaux, 1990; Ligeza & Smal, 2003). As cordgrass began to recover and expand into mudflats, their demands for soil resources, like oxygen and nutrients, increases and amendments to these resources by foraging birds may have a more pronounced effect than during phases of cordgrass border retreat. In these instances, the role of predators on cordgrass resilience may shift from controlling grazing snail densities and parasite exposure during retreat phases to enriching anoxic or nutrient poor soils during recovery phases. However, as we did not comprehensively measure soil biogeochemistry metrics, these mechanisms demand more investigation.

5 | CONCLUSIONS

This study is novel in demonstrating that disturbances that remove habitat-forming foundation species can attract multiple guilds of predators that interact to control both ecosystem resistance and recovery. By reducing the number of grazing snails and their grazing intensity, birds and nekton, along with other predators potentially excluded by our cages such as raccoons, slowed border retreat and continued loss of marsh vegetation. As blue crab densities are low in our study region, the reduction of grazing intensity may be amplified in more northern latitudes where densities of this important saltmarsh predator are higher, and needs further investigation. As snails densities were less affected by predation during the recovery phase, we suspect that as disturbances begin to recover the role of predators may shift from reducing grazing pressure to alleviating soil stress, such as through soil aeration and nutrient deposition, accelerating plant growth and expansion along borders of disturbances. Together these findings suggest that different predator guilds promote resilience via distinct and complementary mechanisms and that these mechanisms can shift in nature as disturbed areas transition from being recently formed features to those undergoing successional processes. Further, the linkage of avian predators to ecosystem resilience in this study comes at a time when avian populations, and by association their contribution to ecosystem resilience, are experiencing widespread decline (Rosenberg et al., 2019) and that efforts to conserve birds may also induce positive, cascading effects on coastal wetland resilience. Broadening our understanding of predator effects on ecosystem resilience by exploring dynamics of top-down grazer control and disease transmission across different ecosystems is an important step to understanding how ecosystems will be structurally and functionally altered both by species declines and by disturbances that are becoming more frequent, intense and larger in the future.

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AUTHORS' CONTRIBUTIONS

S.J.S. and C.A. conceived the project ideas and designed the methodology; S.J.S. installed the experiments, collected data and analysed data. All authors contributed equally to the writing of the manuscript and gave final approval for publication.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Archived data available through the Institutional Repository at University of Florida found at the following permanent link: https://ufdc.ufl.edu/IR00011264/00001

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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