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LIMNOLOGY and OCEANOGRAPHY

ASLO

Limnol. Oceanogr. 9999, 2021, 1–15
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doi: 10.1002/lno.11867

Disturbance is complicated: Headward-eroding saltmarsh creeks produce multiple responses and recovery trajectories

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Abstract

Disturbances are one of the most important processes affecting natural systems, but there is a gap between simple conceptual models of disturbance and complex empirical studies. We studied the perturbation caused by headward-eroding creeks in southeastern USA salt marshes. We measured disturbance responses (magnitude and recovery trajectory) of 19 variables. Some variables (shoot density, root biomass, snail density, soil pH, soil strength, soil temperature, elevation) declined sharply, while other variables (crab burrow density, soil organic matter, soil redox) increased sharply, in response to the burrowed and grazed conditions at the creek head. These variables recovered over subsequent years or decades. Other variables (shoot height, aboveground biomass, rhizome biomass, light interception) declined sharply in the creek head, then overshot control values before recovering. Some variables (benthic algae, soil salinity) did not appear to be disturbed by the creek head. As hypothesized, plants recovered before soils and snails. Disturbance magnitude and time to recovery were often greater directly adjacent to the new creekbank than for the same variables in a parallel transect further away from the creekbank, and in some cases variables never converged with control values, indicating a persistent state change. Reducing the dimensionality of the data set into principal component axes obscured the diverse ways in which different aspects of the system responded to and recovered from the perturbation. Our study illustrates the challenges in moving from simple conceptual models of disturbance to empirical studies in which multiple variables are likely to be affected differently and follow different recovery trajectories.

Disturbance responses are fundamentally important in most ecosystems, because they can affect population densities, nutrient pools and ecological processes, re-set ecosystems to new positions in their successional pathways, and even tip them into new states (Pickett and White 1985; Kominoski et al. 2020). At the same time, the nature of disturbance responses can vary so much within and among ecological systems that a synthetic understanding has been difficult to obtain (Peters et al. 2011; Gaiser et al. 2020). This challenge has been exacerbated by inconsistent use of relevant terminology in different papers (Standish et al. 2014; Angeler and Allen 2016). In this paper, we define a perturbation as a disruption in the environment, and a disturbance response as an ensuing change in an ecosystem property. We characterize the responses of a number of variables in terms of magnitude and recovery time, and define resilience as the ability of the ecosystem to absorb a perturbation without experiencing a state change (Gunderson 2000).

Despite a long history of research, a fundamental disconnect remains between conceptual treatments and empirical studies of disturbance responses. Conceptual models typically focus on the importance of ecosystem conditions and legacies of previous perturbations in mediating disturbance (Peters et al. 2011; Grimm et al. 2017; Gaiser et al. 2020), but usually represent the ecosystem as a single variable, assuming that multiple response variables can somehow be combined into a single index of "ecosystem state" (Pimm 1984; Blonder et al. 2014; Barros et al. 2016), and rarely explicitly quantify disturbance magnitude or recovery (Seidl et al. 2014). In

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contrast, empirical work has long recognized that perturbations affect multiple ecosystem variables differently, and thus that disturbance magnitude and recovery trajectories may differ among ecosystem components (Odum 1969; Turner 2010; Jentsch and White 2019; Schäfer et al. 2019). As a result, there is a pressing need to better understand how to bridge the divide between high-level conceptual treatments of disturbance response and detail-rich empirical studies (Hogan et al. 2020).

Salt marshes have been a productive model system for studying disturbance responses. There are multiple perturbations that affect salt marshes, including wrack (floating dead plant material that is deposited on the marsh surface), ice, soil deposition and erosion, and herbivore outbreaks (Pennings and Bertness 2001; McFarlin et al. 2015). Many of these perturbations can be experimentally manipulated, and disturbance and recovery trajectories of some variables occur within months or years (Bertness and Ellison 1987; Li and Pennings 2017). Most studies of disturbance responses in salt marsh studies, however, have focused on recovery of vegetation, neglecting other aspects of ecosystem recovery.

We studied the ecosystem responses to the perturbation caused by the movement of headward-eroding creeks onto the marsh platform. This phenomenon, which has become increasingly common in salt marshes of the southeastern USA in recent decades (Hughes et al. 2009; Wilson et al. 2012; Crotty et al. 2020), is characterized by fan-shaped depressions up to 50 cm deep and 10–30 m wide found at the heads of creeks (Vu et al. 2017; authors' personal observations). These areas have no living plants but high densities of the herbivorous marsh crab *Sesarma reticulatum* (Fig. 1). As the creek heads move into the marsh platform, which is dominated by the grass *Spartina alterniflora*, densities of crab burrows increase, plant leaves and roots are lost to herbivory, and the soil surface drops due to a combination of erosion, increased decomposition, and intense crab burrowing (Vu et al. 2017). Behind the depressions formed by the creek heads, unconsolidated sediment is re-deposited and robust stands of *S. alterniflora* recolonize the banks of the elongating creeks. The creeks move onto the marsh platform at a rate of 1–2 m yr^{-1}, so that over a decadal scale it is possible to use a space-for-time substitution to estimate the amount of time since a given area was affected by the perturbation.

We used this study system to quantify the disturbance responses of multiple variables, and to evaluate to what extent multiple variables could be combined into a single index of ecosystem state. We measured a variety of edaphic and biological variables, and for each characterized the magnitude of change caused by the perturbation, the time to recovery, and the recovery trajectory. We hypothesized that plant variables would recover faster than soil variables, as plants often establish quickly—within one or 2 yr—during marsh restoration projects, whereas some soil characteristics take decades to converge on those of mature marshes (Craft et al. 1999; Craft and Casey 2000). As the marsh periwinkle snail, *Littoraria irrorata*, is dependent on plants for habitat and food, we hypothesized that this dominant consumer would recover only after plants recovered (Zengel et al. 2015). As marsh crabs require strong soil in which to build burrows (Bertness et al. 2009; Crotty et al. 2020), we hypothesized that they would recover only after soil strength recovered. We hypothesized that all variables would recover faster in perturbed areas distant vs. proximate to the newly-formed creek, because proximity to the newly formed creek implies that some aspects of the perturbation might represent permanent changes rather than pulse events. Finally, we hypothesized that combining variables into a single measure of ecosystem state would be challenging because it would mask the complexity of individual responses.

Methods

We conducted this study at Sapelo Island, Georgia (31°28′N; 81°14′W), located on the Southeastern Atlantic coast of the United States, within the domain of the Georgia Coastal Ecosystems Long-Term Ecological Research program and the Sapelo Island National Estuarine Research Reserve. We selected three headward-eroding creeks at the south end of the island (Table S1) that were relatively straight and unbranched. The head of each creek was located toward the interior of the marsh, and the base of each creek connected to a major channel (either the Duplin River or Doboy Sound).

For each creek, we set up three transects parallel to main axis of the creek (Fig. 1). The first (C, for creek) ran from the marsh platform, through the denuded creek head, and along the newly-formed creekbank, allowing us to sample conditions over a temporal sequence before, during, and at increasing times after the perturbation represented by the creek head. The C transect was located such that the plots behind the creek head would fall along the bank of the newly-formed creek. The second transect, ~4 m away from the creek bank (M, for middle), represented an area that was perturbed by the creek head when it passed through, but where present-day influences of the creek such as tidal flushing and access by nekton were reduced due to distance from the creek. The third transect, ~14 m away from the creek bank (P, for platform), was located outside the area directly affected by the creek head. It served as a control to inform us how areas of the marsh platform that had not experienced the perturbation might vary across the spatial gradient from the marsh interior to the main channel.

The head of a headward-eroding creek can be divided into zones (Vu et al. 2017). The platform is unperturbed, the "live zone" is a zone of increased crab burrowing but with live plants, the "dead zone" is a zone of intense crab burrowing and sparse dead plant stems, and the "mud zone" is an area of soft, unconsolidated sediments without plants (Fig. 1). We located 20 plots along transect C, starting in front of the creek

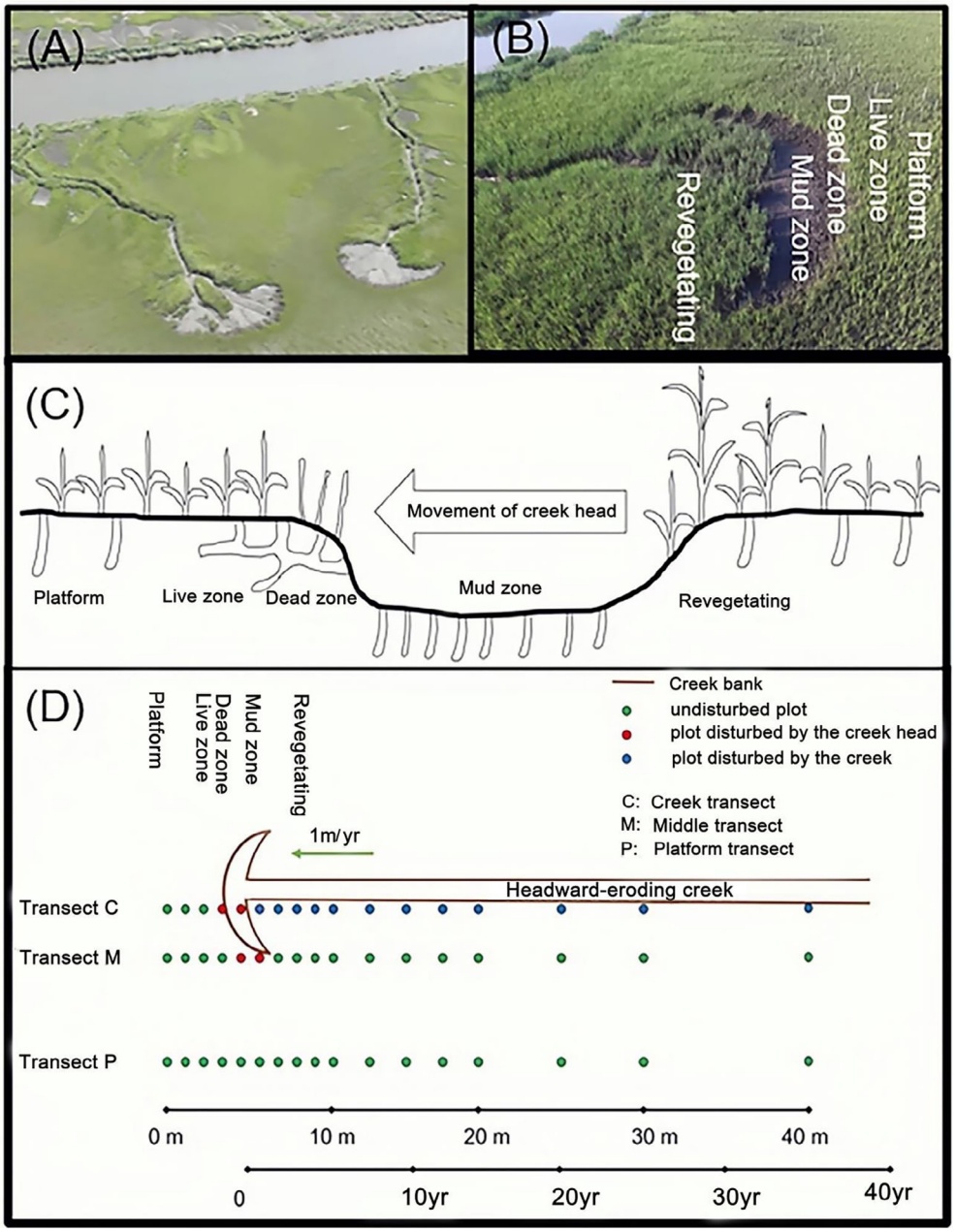

Fig. 1. Schematic diagram of the sampling design. (**A**) Aerial photograph of two typical headward-eroding creeks, (**B**) different "zones" of the creek head, (**C**) cross section of the creek head, showing the creek head zones, and changes in soil elevation, crab burrowing and plant height across the zones, (**D**) layout of the plots along each transect (C: Creek; M: Middle, P: Platform), showing closer spacing of plots near the creek head and wider spacing of plots away from the creek head. Plot colors indicate when plots are disturbed and when they are affected by proximity to the new creek channel. Actual transect length varied from ~40 to ~65 m. An example time axis below the distance axis is shown for a creek growth rate of 1 m^{-y}.

head, with two plots in the platform, one in the live zone, one in the dead zone, one or two in the mud zone, and the remainder placed along the revegetated axis of the creek. We assumed that recovery dynamics would be faster immediately after the perturbation and gradually slow down as the years passed. We therefore spaced the plots closely together near the creek head and farther apart toward the main channel (10 plots in the first ~10 m, 5 plots in the second ~10 m, 3 plots in the third ~10 m, 2 plots in the fourth ~10 m, Fig. 1). We located 20 plots each in transects M and P approximately parallel to each plot of transect C (Fig. 1).

At each plot, we measured elevation, soil and porewater properties, and several measures of the biological community between May 15 and August 10. Each individual variable was

measured on a particular creek within a single day or on two consecutive days at low tide to minimize changes over time. We measured elevation using a Real-Time Kinematic GPS (Trimble R6). We measured soil surface temperature at midday (12.00–13.00 h) using an infra-red temperature gun, with two readings averaged to give a single value per plot. We measured the soil redox potential (uncorrected) using a portable soil redox meter (Thermo Fisher Scientific) inserted to 2 cm and allowed to equilibrate for 30 s. We measured the strength of the surface 4 cm soil using a field shear vane (GEONOR H-60). We collected three soil cores (2 cm diameter, 10 cm deep) in each plot. We dried one core to measure the water content of the soil, expressed as (mass of water)/(mass of wet soil). We rehydrated the dried soil in a known volume of deionized water, measured the salinity of the supernatant with a refractometer, and calculated the salinity of the original porewater. Refractometers are calibrated assuming that all the salt present is NaCl, which is only an approximation for seawater; as a result, the typical units reported for salinity measured with a refractometer (such as practical salinity units, PSU) are not SI units. We therefore report salinity without formal units. We ashed the second core at 450°C to estimate soil organic content. We mixed the third core with three parts deionized water by mass, filtered the mixture, and measured the pH of the water using a portable soil pH meter (Thermo Fisher Scientific). To compare surface conditions with conditions deeper in the soil, we measured temperature and porewater salinity at 10 cm (in the rooting zone) and 50 cm (below the rooting zone) at 6 (temperature) to 8 (porewater) stations along each transect on one of the headward-eroding creeks (Airport South creek) (Appendix methods S1).

We measured the abundance of benthic microalgae with a Benthotorch (bbe moldaenke model 08-067), which uses in vivo fluorescence of algal cells to estimate the biomass of benthic green algae, cyanobacteria, and diatoms. To estimate biomass of the only macrophyte in the plots, *S. alterniflora*, we counted the density of stems. We used a 0.25 × 0.25 m quadrat in most cases where stem density was high, but a 0.5 × 0.5 m quadrat to better estimate stem density in some creek bank plots that had low stem densities, and measured the heights of 10 haphazardly chosen shoots (Airport South creek) or all the shoots in the quadrat (other two creeks). If shoots were completely absent in a quadrat, we recorded shoot height as zero for illustrative purposes. To convert density and height measurements to aboveground biomass, we clipped 40 stems of various heights at each of the three transects at each creek, dried and weighed them in the laboratory, and estimated biomass in each plot by fitting the relationship between height and mass (Table S2). To estimate belowground biomass, we collected a core at each plot (10 cm diameter, 30 cm depth, centered on a culm of *S. alterniflora*), washed the roots and rhizomes free of soil, separated roots and rhizomes, dried them and weighed them. We measured light interception by the vegetation canopy (this variable is related to leaf area index and is an indication of competition between emergent plants and benthic microalgae for light) at midday (12.00–13.00 h) by taking a light reading using a 1 m light wand above and below the canopy at each plot and calculating the proportion of light intercepted.

The two major groups of invertebrates in the plots were crabs (mostly the fiddler crab *Uca pugilator*, but also *Sesarma reticulatum* and the mud crab *Panopeus* sp. at the creek heads) and snails (*Littoraria irrorata*). We recorded the density of crab burrows (>0.5 cm diameter, all species pooled) and snails (>0.3 cm spire height) in 0.5 × 0.5 m quadrats at each plot.

To reduce the dimensionality of the dataset, we combined variables from all creeks into a single principal components analysis and extracted the first two principal components as potential indices of ecosystem state. We repeated this process four times, looking at (1) only plant variables, (2) only soil variables, (3) only animal variables, and (4) all variables combined.

We expected three types of disturbance response trajectories. In the simplest case (Fig. 2A), a variable measured in the C and M transects might decline (or increase) at the creek head, and then recover to conditions similar to the platform transect at some point after the creek head had passed. In more complicated cases (Fig. 2B), a variable might initially overshoot the platform transect before final recovery. In either of these cases, if a variable did not recover within the period of observation, this could be interpreted as a "state change." By using this terminology, we do not imply that the new state is stable, just that it is persistent throughout the period over which the system was observed. In addition, a state change in a single variable does not necessarily imply a change in ecosystem function sufficient that an informed observer would consider that the entire ecosystem had undergone a state change. In a third case (Fig. 2C), high variability or a weak disturbance response might indicate that the response could not be confidently measured, or that there was no disturbance response. For each variable in the C and M transects, we calculated the magnitude of the disturbance response as the difference between the most extreme value in the creek head vs. the average of the first two plots in the transect. Because each variable was measured in different units, we also calculated a standardized measure of magnitude by calculating a *z*-score distribution for each variable using data from the first 10 plots in the P transect, and then transforming the most extreme creek head value into this *z*-score distribution (Appendix, methods S2).

We calculated the initial recovery time for each variable by determining when the plot values in the C and M transects converged on the values in the P transect. We calculated the range of values observed for each variable over all three transects at the creek (T), and defined convergence as when the values of two consecutive plots in the C and M transects were within 0.1*T of the P transect. We defined an overshoot as when the values in the C or M transect exceeded those from the P transect by at least 0.3*T for at least 3 consecutive plots.

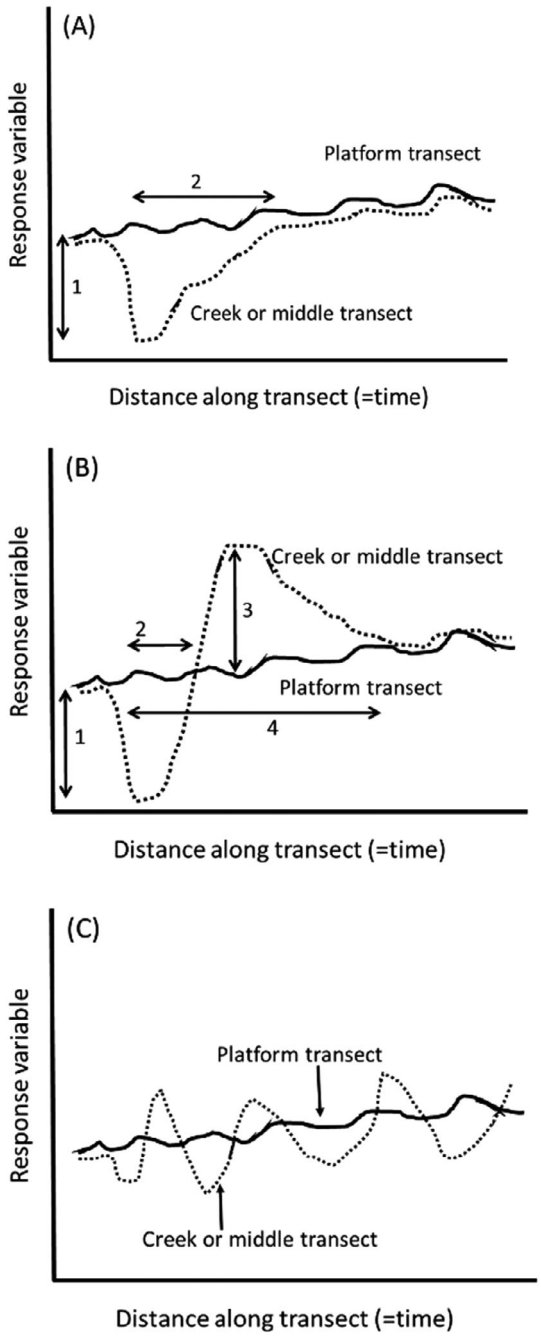

Fig. 2. Expected patterns of perturbation and disturbance response. (**A**) Simple recovery. Arrow 1 indicates disturbance magnitude (which could be a decrease as shown or an increase); arrow 2 indicates recovery. (**B**) Recovery with values first over-shooting the control (P) transect (initial recovery) and then converging again (final recovery). Arrow 1 indicates disturbance magnitude; arrow 2 indicates initial recovery; arrow 3 indicates the magnitude of the over-shoot; arrow 4 indicates final recovery. In either A or B, if a variable did not recover within the period of observation, this could be interpreted as a "state change." (**C**) Data that are too variable to confidently assign disturbance magnitude and recovery values; these cases could also be interpreted as indicating that variables were not disturbed.

We calculated the magnitude of the overshoot using a calculation analogous to our measurement of the magnitude of the initial disturbance response: the difference between the most extreme value in the C or M transects after initial recovery vs. the average of the closest three plots in the P transect (Fig. 2B). If there was an overshoot, we defined the final recovery as when the values of two consecutive plots in the C and M transects returned to within 0.1*T of the P transect. Some variables did not meet the criteria for recovery within the scope of our transects, and their recovery value was set at > the distance to the final plot. If the data were variable enough that we were not confident in assigning these values (scenario Fig. 2C), we left them uncalculated. Interested readers can evaluate our decisions by inspecting the graphs of raw data for each variable (Figs. S1–S3).

We averaged estimates of disturbance response magnitude, initial recovery distance, overshoot magnitude, and final recovery distance across the three replicate creeks. If some creeks met the definition of an overshoot and others did not, we set the magnitude of the overshoot as zero and the final recovery as equal to the initial recovery for those creeks that did not have an overshoot. For variables that did not recover within the length of the transects, we only calculated the median recovery time rather than the average.

Using a catalog of high resolution orthoimages (Table S3), we estimated the year and month at which each GPS point taken along the creekbank transect was located centrally within the creek head. This was deemed the time that the point was perturbed (Appendix methods S3). Each of these points was assigned a qualitative confidence level of "Low," "Medium," or "High" based on our ability to determine the creekhead location. We then estimated the rate of creek elongation by calculating the distance between successive GPS points and dividing by decimal years, using only the High confidence data. To estimate the year when each plot was perturbed by the creek head, we interpolated the creekhead position based on an average migration rate calculated from identifiable time periods. Crotty et al. (2020) found that headward-eroding creeks on Sapelo Island elongated at on average 1.81 m^{-yr} (SEM 0.13 m^{-yr}). In our study, we found that Creeks Airport South, Shell Hammock, and Airport North elongated at 1.45 m^{-yr} (SEM 0.3 m^{-yr}), 1.64 m^{-yr} (SEM 0.18 m^{-yr}), and 1.57 m^{-yr} (SEM 0.36 m^{-yr}), respectively, and so were typical for the region.

Results

General patterns of disturbance response

As hypothesized, we observed several types of patterns of disturbance response after the marsh platform was perturbed by headward-eroding creeks. Some variables declined sharply in the creek head, and then recovered gradually once the creek head had passed (Fig. 3A). The variables shoot density, root

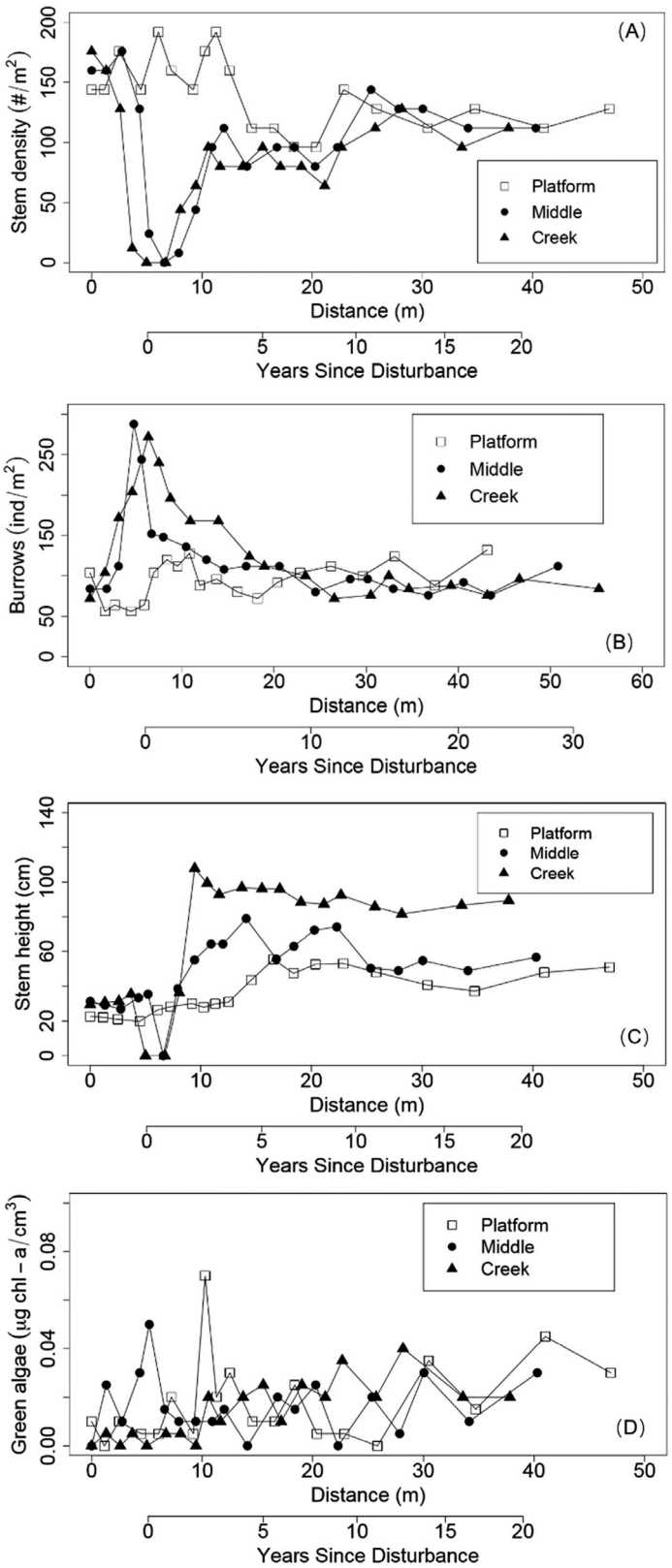

Fig. 3. Examples of different types of disturbance responses. (**A**) Shoot density at Shell Hammock creek. Shoot density was ~168 stems m^{-2} before the perturbation, declined to 0 in the creek head and recovered at ~26.7 m for the creek transect and ~16 m for the middle transect (21.7 and 10 m after the perturbation). (**B**) Burrow density at Airport North creek. Burrow density was ~80 m^{-2} before the perturbation, increased to ~280 m^{-2} in the creek head and recovered at ~16 m for the creek transect and 18 m for the middle transect (11 and 14 m after the perturbation). (**C**) Shoot height at Shell Hammock creek. Shoot height was ~30 cm before the perturbation, declined to zero in the creek head, initially recovered at ~7 m (creek transect) and ~7 m (middle transect) (2 m and 1 m after the perturbation), overshot the platform transect by ~20 cm (middle transect) to ~80 cm (creek transect), and finally recovered at ~35 m for the middle transect and >40 m for the creek transect (~29 m and >35 m after the perturbation). (**D**) Green algal density at Shell Hammock creek. Data were too noisy to estimate disturbance magnitude or recovery values; this may indicate that this variable was not disturbed.

biomass, abundance of snails, soil pH, soil strength, soil temperature, and elevation followed this pattern. Other variables increased sharply in the creek head, and then recovered gradually once the creek head had passed (Fig. 3B). The variables burrow density, soil organic matter, and soil redox followed this pattern. Other variables declined sharply in the creek head, then overshot the platform values before eventually recovering (Fig. 3C). The variables shoot height, aboveground biomass (in some creeks), rhizome biomass, and light interception followed this pattern. Finally, some variables such as algal density and porewater salinity did not show a clear pattern, either because they were too noisy for us to confidently calculate statistics, or because they were not disturbed by the creek head (Fig. 3D).

Magnitude of disturbance response

In general, the magnitude of the disturbance response created by the creek head, expressed in *z*-score units, was greater for the C transect than for the same variable in the M transect (Tables 1–3). Soil elevation and crab burrow number were the variables that were affected most strongly, with values in creek-head plots 13–15 standard deviations away from the control (P transect) mean (Tables 2 and 3). Plant variables were also strongly affected, with values in creek-head plots 3–8 standard deviations away from the control mean (Table 1). Soil variables other than elevation were less (but still strongly) affected, with values in creek-head plots 2–6 standard deviations away from the control mean (Table 3).

Effect on primary producers

We hypothesized that primary producers would recover quickly, because it is usually fairly easy to establish plants in salt marsh restoration projects (Craft et al. 1999; Craft and Casey 2000). We observed that plant variables did recover quickly, but often over-shot control conditions for extended periods of time, with recovery slower at the creekbank vs. the mid-marsh transect. Perturbation by the creek head strongly affected plant variables (Table 1, Figs. S1–S3), although the magnitudes and recovery rates varied. Stem density decreased in the creek head from ~140–220 shoots m^{-2} to 0, and

Table 1. Primary producers. Magnitude of disturbance (in original units and as a *Z*-score) and recovery (measured as distance (m along the transect) and as time (years)). Where variables overshot the original values during recovery, we show both initial recovery and final recovery. Recovery data in brackets are medians; otherwise data are averages ± 1 SE.

	Disturbance		Initial recovery			Final recovery		
Variable	**Transect**	**Magnitude**	**Magnitude (*Z*)**	**Distance (m)**	**Time (yr)**	**Magnitude**	**Distance (m)**	**Time (yr)**
Stem density (shoots m^{-2})	Creek	−216 ± 81.6	−7.14 ± 1.3	31.8 ± 9.4	(27.3 ± 8.3)	—	—	—
	Middle	−148.8 ± 24	−6.89 ± 1.5	29.7 ± 7.6	20.8 ± 6.8	—	—	—
Root biomass (g m^{-3})	Creek	−127.4 ± 42.5	−7.4 ± 1.4	5.9 ± 0.2	2.2 ± 0.2	—	—	—
	Middle	−212.3 ± 42.5	−7.5 ± 1.2	2.1 ± 0.4	1.1 ± 0.4	—	—	
Shoot height (cm)	Creek	−46.0 ± 9.6	−7.2 ± 0.9	2.3 ± 0.5	1.5 ± 0.1	80.1 ± 5.6	(>35.9)	(>22.5)
	Middle	−32.5 ± 11.7	−5.88 ± 2.0	1.6 ± 0.5	0.8 ± 0.2	50.5 ± 5.2	(>36.1)	(>22.3)
Above ground biomass (g m^{-2})	Creek	−358 ± 108.8	−3.58 ± 1.5	4.7 ± 1.2	2.4 ± 0.8	1296 ± 1224	(>35.9)	(>22.5)
	Middle	−286.4 ± 49.6	−3.58 ± 1.5	4.6 ± 1.8	2.1 ± 0.7	—	—	
Light interception (%)	Creek	−45.2 ± 0.9	−4.22 ± 0.5	4.1 ± 0.6	2.3 ± 0.1	22.5 ± 11.2	(>35.9)	(>22.5)
	Middle	−42.0 ± 5.9	−4.22 ± 0.5	3.5 ± 0.5	1.8 ± 0.1	24.2 ± 12.2	(>36.1)	(>22.3)
Rhizome biomass (g m^{-3})	Creek	−1358 ± 254.7	−7.78 ± 0.86	3.1 ± 0.5	1.6 ± 0.1	2120 ± 2120	(>34.3)	(>20.1)
	Middle	−1146 ± 254.7	−7.64 ± 0.99	2.1 ± 0.5	1.0 ± 0.1	—	—	
PC1 of primary productivity	Creek	−2.4 ± 0.3	−3.6 ± 0.3	2.7 ± 0.6	5.8 ± 1.7	3.1 ± 1.8	(>35.9)	(>22.5)
	Middle	−2.3 ± 0.1	−3.7 ± 1.3	2.4 ± 0.7	5.8 ± 1.7	2.4 ± 1.6	17.1 ± 8.8	20.5 ± 5.8

Table 2. Soil properties. Magnitude of disturbance (in original units and as a Z-score) and recovery (in distance (m along the transect) and in time (years)). Recovery data in brackets are medians; otherwise data are averages ± 1 SE.

	Disturbance			Recovery	
Variable	**Transect**	**Magnitude**	**Magnitude (*Z*)**	**Distance (m)**	**Time (yr)**
Elevation (m)	Creek	−0.39 ± 0.01	−14.98 ± 4.48	(>35.9)	(>22.5)
	Middle	−0.21 ± 0.03	−5.7 ± 0.3	8.0 ± 1.8	4.5 ± 0.9
Organic content (%)	Creek	12.0 ± 2.2	1.77 ± 0.3	4.6 ± 1.7	2.6 ± 1.0
	Middle	10.7 ± 3.4	2.19 ± 0.92	6.2 ± 0.3	3.0 ± 1.0
Strength (kpa)	Creek	−20.5 ± 1.4	−5.1 ± 1.71	(>35.9)	(>22.5)
	Middle	−19.8 ± 3.4	−4.64 ± 1.51	(>36.1)	(>22.3)
Temperature (°C)	Creek	−4.2 ± 1.2	−3.18 ± 0.82	(>35.9)	(>22.5)
	Middle	−2.9 ± 0.4	−2.45 ± 2.03	5.2 ± 0.6	2.4 ± 0.6
pH	Creek	−0.18 ± 0.02	−5.47 ± 1.18	(>35.9)	(>22.5)
	Middle	−0.14 ± 0.01	−3.6 ± 0.79	11.5 ± 0.5	7.2 ± 1.0
Redox (mv)	Creek	116.8 ± 55.9	5.93 ± 2.02	12.7 ± 1.6	10.0 ± 2.5
	Middle	125 ± 63.7	4.54 ± 1.39	(6.2)	(5.4)
PC2 of soil variables	Creek	−2.7 ± 0.1	−11.1 ± 2.1	(>35.9)	(>22.5)
	Middle	−1.9 ± 0.1	−8.7 ± 2.5	8.1 ± 1.9	4.3 ± 1.0

recovered slowly in both the middle transect (~29.7 m; 20.8 yr) and the creek transect (~31.8 m; 27.3 yr). Shoot height decreased from~32–46 cm to 0 in the creek head and initially recovered quickly (1–3 m) in both transects, but then overshot the platform values, with shoots ~50 cm (middle transect) to ~80 cm (creek transect) taller than in the platform transect. Shoot height never converged with control values within the scope of the creek and middle transects, with plants remaining 10–40 cm higher than the platform transect. Similarly, aboveground biomass decreased from ~280–360 g m^{-2} to 0 in the creek head, and quickly recovered (~5 m; ~2 yr) in both transects. Values in the creek transect then overshot the platform transect by ~1290 g m^{-2} and never converged with control values, remaining ~160–640 g m^{-2} higher than the platform transect. Light interception by the vegetation decreased from ~45% to almost 0 in the creek head. It initially recovered quickly (~4 m; 2 yr) and overshot the platform transect by ~24% in both transects,

Table 3. Invertebrate variables. Magnitude of disturbance (in original units and as a Z-score) and recovery (in distance (m along the transect) and in time (years)). Recovery data in brackets are medians; otherwise data are averages ± 1 SE.

	Disturbance			Recovery	
Variable	**Transect**	**Magnitude**	**Magnitude (*Z*)**	**Distance (m)**	**Time (yr)**
Snails (ind m^{-2})	Creek	−81.2 ± 27.6	−6.5 ± 1.1	(>36.1)	(>22.3)
	Middle	−94.8 ± 22.7	−6.4 ± 1.1	(>34.3)	(>20.1)
Burrows (ind m^{-2})	Creek	172.8 ± 57.6	13.4 ± 7.7	(16.3)	(7.1)
	Middle	206.0 ± 43.2	13.4 ± 6.8	(14.7)	(6.5)
PC 1 of invertebrates	Creek	3.6 ± 0.5	9.9 ± 4.2	21.9 ± 2.5	13.7 ± 3.4
	Middle	2.7 ± 0.5	7.2 ± 4.2	19.1 ± 2.7	12.7 ± 3.5
PC 1 of all variables	Creek	6.6 ± 0.8	15.3 ± 5.2	3.1 ± 1.0	1.7 ± 0.2
	Middle	5.9 ± 0.5	13.5 ± 5.0	2.8 ± 1.1	1.6 ± 0.5

reaching values of ~80% light intercepted, and never converged with control values in either transect. Values for the abundance of benthic algae were highly variable and did not show any clear trends across either transect—indicating either "noisy data" or "no disturbance" (Figs. S1–S3).

Belowground variables associated with primary producers recovered faster than aboveground variables. Rhizome biomass decreased from ~1270 g m^{-3} to 0 in the creek head, and recovered quickly (~2 m; 1.0 yr) in the middle transect. It also recovered quickly (~3 m; 1.6 yr) in the creek transect, but then overshot the platform transect to ~2120 g m^{-3} and never converged with control values. Root biomass decreased in the creek head from ~130–210 g m^{-3} to 0 at the creek head, recovering quickly in the middle (~2.1 m; 1.1 yr) and creek transects (~5.9 m; 2.2 yr).

The first principal component from the PCA analysis using only plant variables (33.7% of the variance) captured the sense that plants declined at the creek head and then overshot the platform values, with the middle transect eventually converging on platform conditions and the creekbank transect never converging (Table 1, Fig. 4A). As a single index of resilience, however, it obscured the fact that different plant variables had different recovery trajectories. The second principal component from the plant variables (17.3% of the variance) was not informative (Fig. S4).

Effect on soil

We hypothesized that soil variables would be slow to recover from the creek-head perturbation, based on slow development of some soil characteristics in salt marsh restoration projects (Craft et al. 1999; Craft and Casey 2000). Our findings indicated that recovery rates varied considerably among soil variables, with recovery faster in general in the mid-marsh than the creekbank transect where many variables never converged with control values. The creek head strongly affected most soil variables (Table 2, Appendix Figs. S1–S3). The elevation of the marsh platform decreased by 20–40 cm in the creek head. It recovered quickly (~8 m; 4.5 yr) in the middle transect, but never converged with control values in the creek transect, remaining 10–40 cm lower than the platform transect. The organic content of the surface soil increased in the creek head from ~20 to ~30%, and recovered quickly (~5.4 m) in both the middle and creek transects. Soil strength decreased by ~20 kPa at the creek head and never converged with control values in either transect. Temperature decreased by 3–4° at the creek head. It recovered quickly (~5.2 m; 2.4 yr) in the middle transect, but remained 2–3° cooler than the platform along the entire creek transect. Surface soil became more acidic in the creek head, recovered slowly (~11.5 m; 7.5 yr) in the middle transect, and never converged with control values in the creek transect. Redox values were variable both within and among creeks, but redox generally increased in the creek head and recovered within 6–12 m (5–10 yr) on both transects. Salinity values were highly variable and did not show any clear trends across either transect, indicating either high variability or no disturbance.

The first principal component from the PCA analysis using only soil variables (26.8% of the variance) was not particularly informative. At one creek, it reflected an along-creek gradient, while at another it appeared to capture some of the disturbance response (Fig. S4). The second principal component (23.1% of the variance) was more informative (Table 3 and Fig. 4B). At all three creeks, it captured the sense that soil variables were strongly disturbed at the creek head and then slowly recovered, with the middle transect recovering faster than the creekbank transect, which did not converge with platform conditions within the period of observation. As a single index of resilience, however, it obscured the fact that different soil variables had different recovery trajectories.

Because data from deeper in the soil were limited in replication, we only conducted a qualitative analysis. Temperature at depth was not disturbed by the creek head, but instead was primarily influenced by date and proximity to the main channel (Fig. S5). Temperature at 10 cm fluctuated up to 4° over time between mid-July and mid-August; temporal fluctuations at 50 cm were limited to ~1°. At both depths, temperatures were warmest at the marsh interior, reflecting a gradient from the marsh interior toward the main channels. Porewater

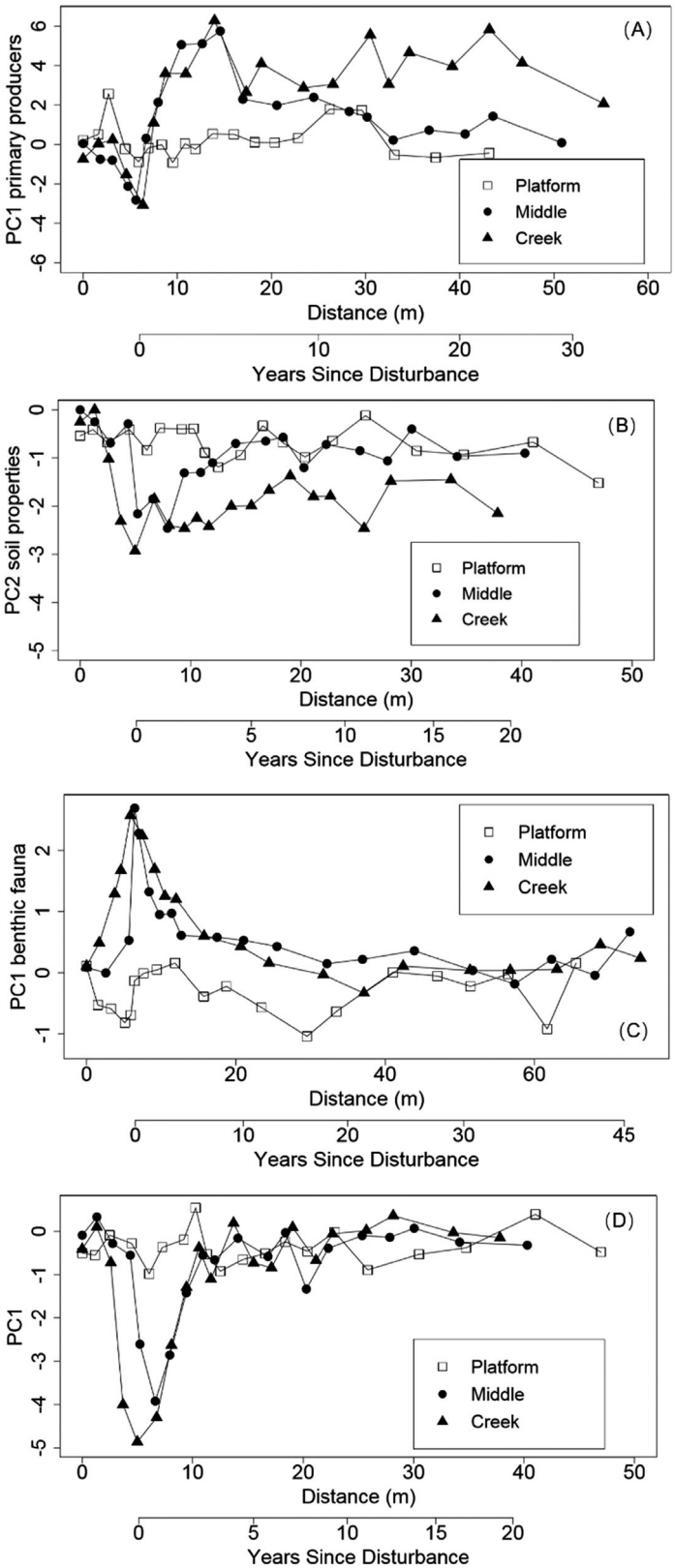

Fig. 4. Examples of responses of principal component analyses of disturbance responses aggregated at different levels. (**A**) PC1 of primary producer variables at Airport North creek. PC1 was ~0.5 before the perturbation, declined to ~3 in the creek head, initially recovered at ~8 m (creek transect) and ~7 m (middle transect), overshot the platform transect by ~5 (middle transect) to ~6 (creek transect), finally recovered at ~28 m for the middle transect, and never recovered in the scope of the creek transect. (**B**) PC2 of the soil variables at Shell Hammock creek. PC2 was ~0 before the perturbation, decreased to ~2–3 in the creek head, recovered at ~12 m for the middle transect, and never recovered the creek transect. (**C**) PC1 of the benthic fauna variables at Airport South creek. PC1 was ~0 before the perturbation, increased to ~2.5 in the creek head, and recovered slowly at ~40 m in both transects. (**D**) PC1 from all the data at Shell hammock creek. PC1 was ~0 before the perturbation, decreased to ~4–5 in the creek head and recovered at ~12 m for the middle and creek transect (~7 m after the perturbation).

salinity at 10 cm depth dropped in all three transects from ~25–30 before the creek head to ~18–26 in or adjacent to the creek head (Fig. S5). The platform transect quickly recovered to ambient values (~25) but values in the middle and creek transect remained low (~22), suggesting improved tidal flushing of soils near the new creek. At 50 cm depth, salinity in the platform and middle transects dropped from ~26–29 down to ~16 in the disturbed area, with values in the platform recovering faster than those in the middle transect. Salinity at 50 cm depth in the creek transect remained constant across the disturbed and recovered plots.

Effect on benthic invertebrates

We hypothesized that recovery of benthic invertebrates would depend on recovery of plants (in the case of snails) and soil strength (in the case of crabs). Benthic invertebrates had strong disturbance responses (Table 3, Figs. S1–S3), but responded in different ways. The abundance of snails decreased from ~80–95 m^{-2} to 0 in the creek head and never converged with control values in either the creek or the middle transects, remaining ~20–80 individuals m^{-2} lower than in the platform transect. In contrast, the density of crab burrows increased strongly, from ~80 to ~280 m^{-2} in the creek head, and recovered at ~14–17 m (7–8 yr) in the middle and creek transects, faster than soil strength recovered.

The first principal component from the PCA analysis using only animal variables (79.0% of the variance) captured the sense that animal densities were strongly disturbed by the creek head, with slow recovery in both creekbank and middle transects (Table 3 and Figs. 4C and S4). As a single index of resilience, however, it obscured the fact that snails and crab burrows had different recovery trajectories. The second principal component (21.0% of the variance) was not informative (Fig. S4).

When plant, soil, and animal variables were combined into a single PCA analysis, the first principal component (20.5% of the variance) captured the general patterns described above. Principal component 1 indicated a large ecosystem response at the creek head, with both transects converging on the platform fairly quickly (Figs. 4D and S4). The second principal component (18.7% of the variance) showed a disturbance response followed by slow or no recovery (Fig. S4). Neither

principal component alone, nor the combination of both of them, was sufficient to describe the range of responses displayed by all the different variables.

Discussion

Where headward-eroding creeks affect the marsh, they represent an intense perturbation of salt marsh ecosystems, dramatically affecting geomorphic evolution, predator–prey interactions, and plant and invertebrate communities (Hughes et al. 2009; Vu et al. 2017; Crotty et al. 2020). The variables that we examined displayed disturbance responses of different magnitudes and a variety of recovery trajectories, with some recovering quickly, some over-shooting control conditions and then recovering, and some never recovering. Although this variety of complex patterns could be mathematically abstracted into one or two principal components axes to evaluate overall ecosystem resilience, this was unsatisfying, as it obscured important aspects of system recovery. At the same time, it also obscured the importance of those variables that did not converge with controls (e.g., elevation, plant productivity), and arguably provide evidence of a persistent state change from mid-marsh to creekbank habitat.

The proximate mechanisms of disturbance response

The perturbation caused by the head of the creek represents a combination of physical and biotic forcing (Fig. 5a). As water moves on and off the marsh through creeks, flows are concentrated at creek heads, increasing erosion (Wilson et al. 2012). The turbulent water flow creates habitats that attract the herbivorous crab, *Sesarma reticulatum* (Vu and Pennings, in review). As a result, the two variables that exhibited the largest magnitude of disturbance were marsh elevation and crab burrow density (Tables 1 and 3). The crab, a voracious herbivore (Holdredge et al. 2009) consumes all the plants in the area, reducing friction to water flow, and excavates extensive burrow networks (Hughes et al. 2009; Vu et al. 2017) that increase erodibility of the soil, oxygen penetration, and decomposition of soil organic matter (Vu et al. 2017). The combination of excavation, erosion, and decomposition leads to a drop in the surface of the marsh sediments by ~30 cm (Fig. 5a). The loss of vegetation leads to higher light penetration to the soil surface, and the increased oxygenation of the soil leads to a drop in pH caused by increased aerobic respiration and oxidation of sulfides and other reduced compounds (Kostka et al. 2002; Koretsky et al. 2008). Surface soil temperature also drops, because the surface sediments are now at a lower elevation and flooded more often by the tides. Soil organic content increases in the creek head, possibly due to deposition of particulate organic matter into the low-lying area, or possibly because erosion uncovers underlying organic-rich peats.

As the creek head moves forward into the marsh platform, eroded sediment is re-deposited at the back of the fan-like basin (Wilson et al. 2012). Although burrow density is high in the perturbed area, most burrows are small in diameter, likely because the soft sediment cannot support larger burrows. In particular, adult *Sesarma reticulatum* crabs do not burrow in the freshly deposited sediments, perhaps because they are at low elevations, highly exposed to nekton predators, or too soft to support burrow structures (Seiple 1979; Bertness et al. 2009; Vu and Pennings, in review). The absence of *S. reticulatum* allows plants to recolonize, and their roots help stabilize the soils (Gedan et al. 2011; Valentine and Mariotti 2019). As the creek head moves forward, the back of the creek head accretes into a creekbank, and supports taller, more productive plants that intercept more light (Fig. 5a). The mechanisms driving the high biomass of plants early in recovery are likely the same as those supporting the gradient from "tall-form" *S. alterniflora* plants at long-established creekbanks to "short-form" plants on the marsh platform: creekbank habitats receive more tidal flushing, have lower levels of toxic sulfides and higher levels of available nitrogen than the marsh platform (Valiela et al. 1978; McKee et al. 2004). Soil temperatures remain low along the creekbank, likely because of heavy shading by the luxuriant vegetation. Snails remain rare, likely because predator access is easy immediately adjacent to the creek (Silliman et al. 2004; Crotty et al. 2020).

We hypothesized, based on studies of salt marsh restoration, that plants would recover faster than soils, that snails would not recover until after plants did, and that crabs would not recover until after soil strength recovered. The first hypothesis was largely supported: plants did recover quickly, and in fact often over-shot control conditions, whereas some soil variables (like soil strength) never recovered. The second hypothesis was also supported: plants grew back, often exceeding control conditions, whereas snails never fully recovered. The third hypothesis was not supported: crab burrow density actually increased in the softest sediments and converged on control values before soil strength did so. It is possible that soils on the marsh platform were so strong as to hinder crab burrowing (Bertness 1985; Crotty et al. 2020), but it is also likely that results would have varied had we distinguished among burrows of different diameters, because the burrows in the softest sediments were all small in diameter (authors personal observations). We think that the third hypothesis would have received stronger support if we had limited our observations to large burrows, but cannot address this possibility with our data set.

For many variables, the magnitude of disturbance was greater in the creek transect than the middle transect: this likely reflects the fact that the depression at the creek head slopes down gradually from its edges to its center, and so the creek transect received a larger perturbation than did the middle transect. In addition, many variables recovered over time along the middle transect, transitioning back toward values typical of the marsh platform (Fig. 5a). In contrast, many variables along the creek transect remained permanently changed over the period of time covered by our space-for-time

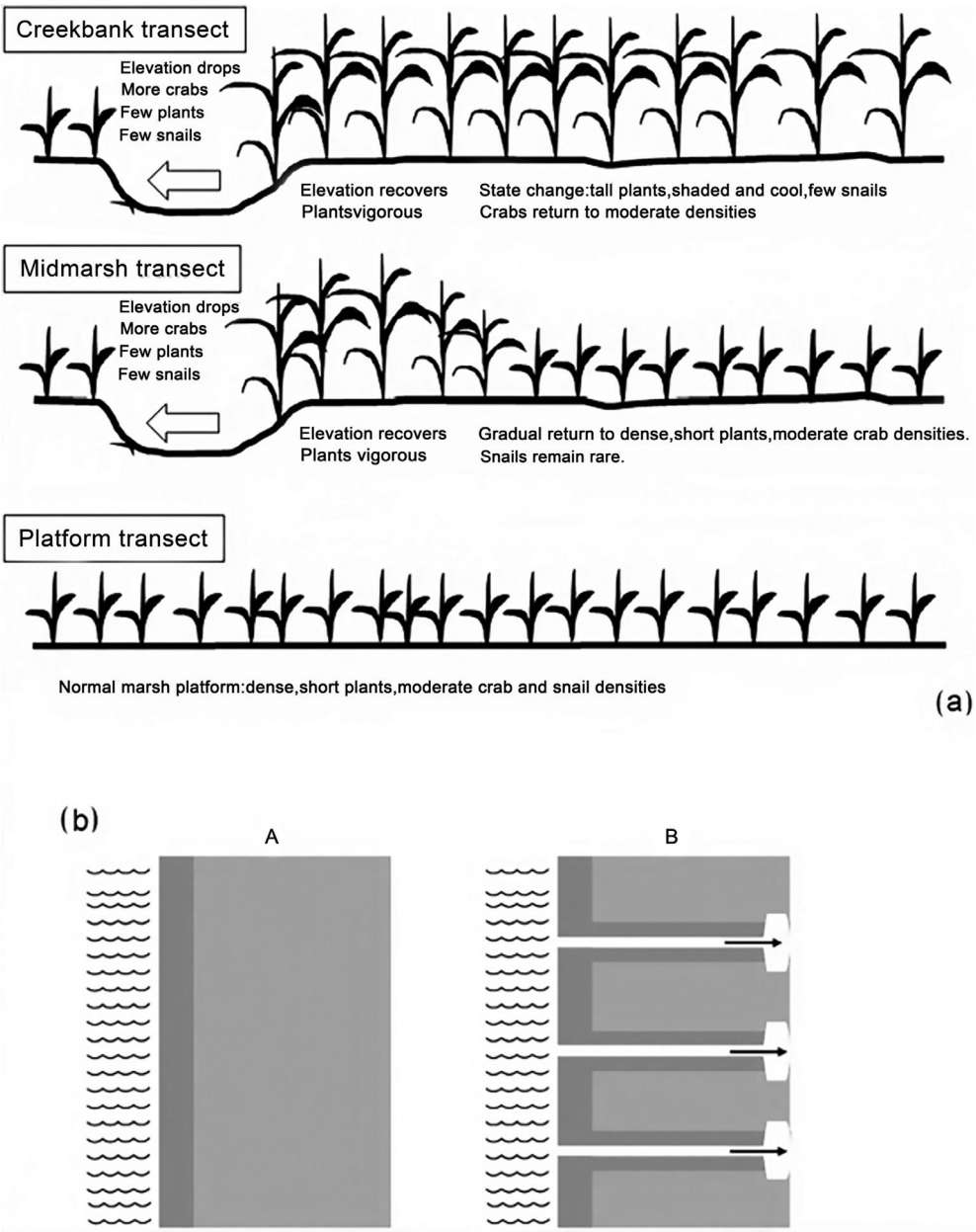

Fig. 5. Conceptual diagrams (not to scale) illustrating (**a**) disturbances caused by the perturbation of the creek head, and recovery in the C and M transects, (**b**) a high marsh platform with (panel **A**) no creek network and a small amount of creekbank habitat (in dark gray), and (panel **B**) the same platform after it has been traversed by a set of headward-eroding creeks. The amount of creekbank habitat is greatly increased in panel B, as is overall habitat heterogeneity.

substitution—a persistent state change—likely reflecting the fact that these locations were now immediately adjacent to a creek, and so were permanently transformed into creekbank habitat.

Headward-eroding creeks and salt marsh function

Scientists only recently became aware of headward-eroding creeks in southeastern salt marshes (Hughes et al. 2009). To the best of our knowledge, the formation of these creeks is a consequence of relative sea level rise (Hughes et al. 2009). As the tidal prism (the amount of water moving on and off the marsh with each high tide) increases, a greater network of creeks is needed to support water transport (Hughes et al. 2009; Alpaos et al. 2010). As a result, new creeks form in marsh platforms that historically were perched relatively high in the tidal frame and therefore lacked a dense creek network (Wilson et al. 2012). By improving water transport on and off the marsh, these new creeks may reduce ponding of water on

the marsh surface after high tide, thereby ameliorating some of the effects of sea level rise on marsh biota (Hughes et al. 2009; Wilson et al. 2012; Crotty et al. 2020). At the same time, however, the new creeks represent a loss of marsh area, albeit a small one, and thus could be seen as an early indicator of marsh loss due to relative sea level rise. Any such losses could be offset by marsh transgression into adjacent upland habitats (Enwright et al. 2016; Kirwan and Gedan 2019); the extent to which this occurs depends on the availability and slope of adjacent upland habitats (Kirwan et al. 2016), topics that are beyond the scope of this paper. We limit our discussion, therefore, to processes in the existing marsh habitat, while recognizing that transgression into uplands is happening simultaneously.

An immediate consequence of the growth of headward-eroding creeks into a marsh platform that previously lacked a dense creek network is that the heterogeneity of the marsh habitat increases. This is most obvious in the transformation of extensive stands of short-form *S. alterniflora* into a mixture of tall, medium, and short-form plants. Because tall- and medium-form *S. alterniflora* is more productive than short-form plants, it is likely that overall productivity of the marsh increases despite the loss of some vegetated habitat. This effect remains to be quantified; however, we can use conservative parameter values to show that it must be important. If we assume that headward-eroding creeks are spaced 100 m apart with channels that are 2 m wide (Hughes et al. 2009), that the marsh platform is 200 m wide from the main channel to the upland, and that the 4 m closest to any creek or main channel represents creekbank habitat, then a high intertidal marsh platform lacking a creek network would contain 2% creekbank habitat (all along the main channel), whereas the same marsh platform traversed by headward-eroding creeks would lose 2% of high marsh habitat to creek and convert 8% of high marsh habitat to creekbank, a five-fold increase in creekbank habitat (Fig. 5b). Because plants in the creekbank habitat are 2–3 times as productive as in the high marsh (Więski and Pennings 2014), this would represent a net gain in plant productivity.

In addition, because creekbank habitat differs from the marsh platform in soil chemistry and access to predators, the heterogeneity of almost every other aspect of marsh structure and function, from soil nutrient availability to predation rates, must increase with a denser creek network (Schalles et al. 2013). As one example, because nekton predators such as shrimp, blue crabs and redfish access the marsh platform from creeks (Meyer and Posey 2009; Jin et al. 2010), spatial variability in predation rates across the marsh will increase if the marsh platform has a dense creek network. Thus, although headward-eroding creeks represent a small proportion of marsh area, they likely have important consequences at the landscape level. Although we do not formally measure these consequences in this manuscript, the likely connections between what happens at the plot level and what happens at the landscape level point out the importance of spatial scale in assessing disturbance responses. Because disturbances are often patchy, the degree to which the entire landscape is affected depends both on the proportion of the habitat that is disturbed, and on how localized disturbances affect adjacent undisturbed habitat.

Bridging the gap between empirical studies and disturbance theory

Ecologists have a longstanding interest in disturbance responses (Pickett and White 1985; Jentsch and White 2019), although research on this topic has been disproportionately conducted in terrestrial and freshwater ecosystems (Donohue et al. 2016). Most conceptual models assume a fairly simple whole system response to a perturbation: a system is perturbed, and is unaffected (meaning no disturbance response), or it responds and then either recovers or transitions to a new state (Spencer et al. 2011; Donahue et al. 2013; Blonder et al. 2014; Barros et al. 2016). Our results, however, illustrate that a single system may respond to a single perturbation in a myriad of ways depending on the variables measured. Some variables recovered; others overshot initial values and then recovered; others never converged with controls, indicating a persistent state change over the period of observation, and others were not affected in the first place. It seems likely that if we had measured additional variables, we might have observed additional types of recovery trajectories. This suggests that how our understanding of how an ecosystem responds to a perturbation may depend on which variables are measured, and that we need to examine recovery trajectories for different variables individually in order to understand how different aspects of ecosystem function change. Although conceptual models assume that we can aggregate multiple variables into a single index describing "ecosystem state," our attempts to do this obscured important response by the system. For example, PC1 of the plant variables suggested that the system over-shot control values in the middle transect but then recovered; in fact, some plant variables did not overshoot control values, and others never converged with controls. PC2 of the soil variables indicated recovery in the middle transect but not in the creek transect; in fact, some soil variables in the middle transect never recovered, and some variables in the creek transect did. PC1 of the animal data indicated recovery in both transects; in fact, snails never recovered in either transect. PC1 for all variables combined suggested rapid recovery in both transects and PC2 suggested no recovery in both transects; in fact, few individual variables showed either exact pattern. Although not surprising, this illustrates that condensing multiple variables into one or two principal components obscures rather than clarifies what is actually happening in the system. It may be useful in some contexts as a high-level abstraction, but is not likely to provide insight into the actual magnitude of the disturbance effects or the mechanisms of recovery. An alternative approach may be to identify groups

of variables that behave in similar ways. For example, studies of hurricanes suggest that water-column variables are likely to recover faster from the perturbation than organismal variables (Patrick et al. 2020). We made loose generalities about recovery of plants, soils, and animals, but these were weak given the variety of different responses within each category. Another alternative, for systems that are well understood, would be to identify "master" variables that control other aspects of ecosystem function. For example, in salt marshes, elevation is a master variable affecting many other aspects of ecosystem functioning, and the persistent change to a lower elevation along the creekbank transect likely explains many of the other changes observed along this transect, such as greater plant height and biomass. Although elevation alone cannot explain the recovery trajectories of many variables that we measured, a process-based model incorporating time since disturbance and changes in elevation might go a long way toward integrating our results, and might offer additional insights into which variables are informative of "state changes" and which are not.

Understanding the complex effects of perturbations on natural systems is necessary to properly understand and manage ecosystems and is a pressing problem given that the number of perturbations is increasing due to global change (Donahue et al. 2016). Our study illustrates the challenge in moving from theoretical abstractions of ecosystem state to a mechanistic understanding of a given system. Conceptual models, as currently formulated, are useful for thinking about general disturbance responses, but the insights gained here would not have been possible without detailed information on the disturbance magnitude and recovery trajectories of specific variables. Bridging the gap will require new approaches that incorporate more detail about the abiotic and biotic components of ecosystems, how they respond to perturbations, and how they affect each other during secondary succession.

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Acknowledgments

This material is based upon work supported by the National Science Foundation through the Georgia Coastal Ecosystems Long-Term Ecological Research program under Grant No. OCE-1832178. Fengrun Wu and Chunfu Tong thank the funds from the Shanghai Science and Technology Committee (19DZ1203801) and the National Natural Science Foundation of China (42030411, U2040202). We thank Clark Alexander for assembling the high-resolution aerial imagery, and Dontrece Smith for collecting RTK data. We appreciate helpful comments from the Associate Editor and reviewers that greatly improved the manuscript. This is contribution number 1096 from the University of Georgia Marine Institute.

Conflict of interest

None declared.

Submitted 15 October 2020
Revised 27 March 2021
Accepted 23 May 2021

Associate editor: James Heffernan