Recruitment bottlenecks and reinforcing environmental degradation drive marsh collapse

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Open Research Statement: We uploaded the data and code used for generating figures and tables in this paper for the editors and reviewers. These data and code will be publicly accessible at Github (currently private at https://github.com/ManQiEcology/Dataset-and-code-for-recruitment-bottleneck-and-marsh-collapse) and Zenodo if the paper is accepted for publication.

Abstract (216 words)

Ecosystem collapse is often attributed to the absence of stress-tolerant species, yet many climate-stressed systems fail even when these species remain regionally present. This raises a critical, unresolved question: does collapse result from species pool depletion, or from failed recruitment? We addressed this by combining vegetation surveys and a three-year transplant experiment in sea level rise–threatened brackish marshes of Chesapeake Bay, USA. We first showed that replacement failure (i.e. suitable species exist in the regional species pool but failed to colonize) intensified along a gradient of increasing inundation, where flood-tolerant species exhibited lower occupancy and colonization of dieback patches compared to flood-sensitive species. By transplanting a dominant flood-tolerant species, *Juncus roemerianus*, into marsh zones of different stages of degradation, we found three main constraints on colonization: (1) competition from established species such as the sedge *Schoenoplectus americanus*, (2) dispersal inefficiency or establishment failure in dieback areas, and (3) post-dieback peat collapse, which rapidly renders unoccupied habitats physically uninhabitable. Our findings reveal that marsh collapse arises from compounded recruitment bottlenecks—not regional species exhaustion. This finding challenges species distribution assumptions that infer future presence from current occupancy without accounting for failed recruitment. Restoration must intervene early to reopen recruitment pathways—by managing competitors, stabilizing substrate, and enhancing propagule delivery—before physical degradation locks ecosystems into collapse.

Keywords:

Plant dieback; peat collapse; marsh stability; sea level rise; plant assembly; recruitment; marsh ponding; regime shift; species replacement; dispersal bottleneck

Introduction

Global change exposes global ecosystems to chronic climate stress—from global warming (Hughes et al. 2018b, Serrano et al. 2021), drought (Batllori et al. 2020), ocean acidification (Nagelkerken and Connell 2022), or sea level rise (Kirwan and Gedan 2019). Stressed ecosystems are observed to either undergo gradual shifts in community composition (McCoy et al. 2016, Agostini et al. 2018, Batllori et al. 2020, Qi et al. 2021a, Zhu et al. 2024) or wholesale collapse (Filbee-Dexter and Scheibling 2014, Ortiz et al. 2017, Serrano et al. 2021). Collapse entails losing structure, function, and the capacity to recover. Theoretically, species replacement is expected in these contexts, as changing environmental conditions alter the competitive balance, allowing stress-tolerant species to replace those less adapted to the new regime (McCormick et al. 2013, McCoy et al. 2016, Batllori et al. 2020, Nagelkerken and Connell 2022). However, for ecosystems that have collapsed, we still have a limited understanding of whether collapse results from depletion of their species pool or blocked recruitment processes such as dispersal or establishment (Ratajczak et al. 2018, Turner et al. 2020, Newton 2021, Serrano et al. 2021).

Distinguishing whether ecosystem collapse results from the exhaustion of regional species pools or from constraints on colonization has far-reaching implications for both theory and practice. From a theoretical standpoint, many ecological models assume that species turnover under environmental stress proceeds as long as suitable replacement species are available regionally (Qi et al. 2016, Waldock et al. 2022). This assumption, grounded in niche theory (Hutchinson 1957, Hutchinson 1978, Holt 2009), simplifies plant assembly mechanisms such as dispersal, establishment and plant–soil feedbacks (Qi et al. 2021b). But in reality, community change is constrained not only by species availability but also by the capacity of those species to colonize new habitats under stress (van Katwijk et al. 2016, He et al. 2017, Xie et al. 2019, Liu et al. 2020). If ecosystems under chronic climate stress collapse due to replacement failure (i.e. suitable species exists in the regional species pool but fail to colonize) rather than species availability, our theory and models must be refined.

From a conservation perspective, this uncertainty complicates restoration planning. The failure of natural recovery due to impaired recruitment (van Katwijk et al. 2016, He et al. 2017, Xie et al. 2019, Liu et al. 2020) is overcome by increasing propagule supply of appropriate species, and strategies based solely on passive recolonization or species reintroduction may prove ineffective (Liu et al. 2024). Understanding when and why colonization fails is essential for developing targeted, process-based restoration approaches to combat climate-driven collapse and enhance ecosystem recovery.

Despite the importance of this question, ecosystem collapse occurring before the exhaustion of regional species pools is rarely documented. This gap likely stems from two challenges: (i) abrupt regime shifts offer a narrow time window in which to diagnose colonization constraints (Hughes et al. 2018a, Ratajczak et al. 2018, Turner et al. 2020), and ii) stress-tolerance hierarchies and replacement sequences are not always known in natural systems, especially where multiple interacting stressors may filter species (Côté et al. (2016), but see Crain et al. (2004), Qi et al. (2018)). Consequently, the mechanisms behind replacement failure remain poorly understood and seldomly tested directly, limiting our capability to anticipate or prevent collapse.

To investigate colonization constraints and replacement failure, we studied coastal marshes in Chesapeake Bay experiencing sea level rise–induced degradation (Beckett et al. 2016). Interior marsh zones with high inundation and low accretion provide a natural gradient of hydrological stress and degradation—from vegetated marsh to dieback, peat collapse, and ponding—providing an ideal setting for exploring colonization constraints (Qi et al. 2021a, Qi and Gedan 2025). These zones also differ in elevation, a key physical driver of vegetation loss and feedback that can lock marshes into collapse trajectories (Mariotti 2016, Qi and Gedan 2025). Previous spatiotemporal analyses showed flood-intolerant species displaced by flood-tolerant ones along this gradient (Qi et al. 2021a), with *Juncus roemerianus*—the most flood-tolerant species—persisting in intact marsh but absent from nearby dieback zones and ponds (Appendix S1: Fig. S1). In this study, we re-analyzed prior vegetation data (Qi et al. 2021a) to test whether (H1) species dispersal limitation and replacement failure intensify with inundation stress. We also conducted a three-year transplant experiment to assess whether *J. roemerianus* establishment is hindered by (H2) competition from established vegetation, (H3) dispersal inefficiency or colonization failure, or (H4) reinforcing environmental degradation such as peat collapse and prolonged flooding.

By explicitly testing when and why colonization fails despite the presence of suitable species, we aim to uncover the processes that undermine species replacement and accelerate ecosystem collapse. While rooted in a coastal wetland context, this research will contribute to resilience theory and restoration planning in many systems facing climate change-driven collapse.

Materials and Methods

Study area

The Chesapeake Bay is one of the largest microtidal estuaries in the world, and has experienced increasing deterioration in recent decades (Kearney et al. 1988, Beckett et al. 2016). We selected two deteriorating brackish marshes within the Bay as study areas: Deal Island on the Manokin River (DI, Deal Island Wildlife Management Area, managed by the Maryland Department of Natural Resources) and Farm Creek Marsh on Fishing Bay (FCM, owned and managed by the Chesapeake Audubon Society). These marshes are in the early stages of transition from vegetated marsh to open pond (Walker et al. 2019, Qi et al. 2021a). Areas in various stages of deterioration, from vegetated marsh to dieback and open pond, can be found in the marsh interiors of each platform. Tidal attenuation and poor drainage have led to open water formation in many interior marsh areas of the region (Walker et al. 2019, Qi et al. 2021a, Qi and Gedan 2025).

Both DI and FCM are brackish, with DI exhibiting higher salinity (7-15 ppt) than FCM (2-5 ppt), based on measurements in summer 2019. Emergent vegetation in both marshes is typical of brackish marshes along East Coast of United States, and includes grasses *Spartina patens*, *Distichlis spicata,* and *Spartina alterniflora*, the sedge *Schoenoplectus americanus*, and the rush *Juncus roemerianus.* At DI, *S. alterniflora* dominated and *S. americanus* is rare, while at FCM, *S. americanus* dominates and *S. alterniflora* is rare, reflecting difference in the salinity tolerances of these two species. Where inundated or poorly drained, *S. alterniflora* in DI formed sparse meadows on soft, homogenous substrates, while *S. americanus* in FCM formed heterogeneous hummocks and hollows. *S. patens* and *D. spicata* at both marsh platforms presented either as healthy firm marsh in higher elevation areas or small patches with hummocks and hollows in deteriorated marsh. At both platforms, *Juncus roemerianus* appeared either in healthy marsh surrounded by neighboring species or in small islands within ponds.

<Fig. 1>

Vegetation quadrat survey

We conducted a vegetation quadrat survey in August 2018 across four ponded marsh platforms at Deal Island. At each marsh platform, we surveyed three 150 m long transects that each ran from an upland direction to a ponded area. Along each transect, we recorded percent cover of each plant species (and bare soil or water if observed) and water depth in five evenly spaced 1 × 1 m quadrats. Full methods and survey details are available in Qi et al. (2021a). Depth of water was used to represent hydrological stress, and the percentage of bare soil and water was used to represent the extent of ecosystem collapse. Because some species were present in one marsh platform but not in other, we calculated the within-marsh-platform occupancy of each plant species across the three replicate quadrats that are at similar distance to the ponded area, to represent the colonization success of marsh plants within each marsh platform. Species with low occurrence (≤1 out of 12 quadrats) and low abundance (<10%) across all quadrats (*i.e. Saliconia depressa*, *Setaria geniculata*, and *Pluchea odorata*) were removed from the analysis.

Transplanting experiment

In early April 2019, we selected 10 points within each of three zones (pond, dieback, and vegetated) per platform for *J. roemerianus* transplanting. In mid to late April 2019, we excavated 55 ~ 56 blocks of *J. roemerianus* clonal patches from each platform. Each transplant was made up of all culms of *J. roemerianus* within a 20 × 20 × 20 cm block of soil. Soil blocks were wrapped with garden cloth and secured with rubber bands.

Of the *J. roemerianus* transplants, 5 ~ 6 were transplanted back to their original patches as controls (Fig. 1d), and 50 were transplanted into pond (n=20), dieback (n=10) and vegetated (n=20) zones, at each platform. To study whether competition from neighboring marsh plants can suppress *J. roemerianus* colonization before dieback of the former, transplants in the vegetated zone were assigned to a neighbor intact or neighbor removal treatment. In the neighbor removal treatment, neighboring plants within a 0.5 m radius were clipped monthly. To study whether colonization of *J. roemerianus* in dieback patches is inhibited by dispersal limitation or habitat unsuitability, we transplanted *J. roemerianus* to dieback patches where substrate elevation had not yet collapsed. To study whether peat collapse following dieback prohibited colonization of *J. roemerianus* in ponded areas, transplants in ponds were subjected to a substrate elevation treatment or ambient elevation treatment. Each treatment had 10 replicates.

To determine the substrate elevation level that was appropriate for each transplanting location, we measured the elevation drop from the nearest pond bank to the pond bottom with a hand sight level (Sight Level No. 801 Supreme Japan Vintage). The resulting substrate elevation treatment was 22.7 ± 9.2 cm at DI and 30.25 ± 10.23 cm at FCM. To elevate the substrate, transplants were placed in flowerpots filled with in-situ marsh peat substrate and elevated using additional pots also filled with in-situ marsh peat substrate beneath them. PVC pipes (2 cm diameter) were driven into the substrate to stabilize the structure.

Plant monitoring

Shoot height and the number of living shoots were recorded monthly from June to September 2019 and again in June 2020 and 2021. Shoot height was measured for the five tallest living shoots per transplant. Shoot counts included all green stems ≥10 cm tall. Flowering status was recorded in June 2020 and 2021. We assessed transplant performance using three metrics: 1) relative shoot height increase between April 2019 and June 2021, 2) relative shoot number increase for the same period, and 3) inflorescence count in June 2021.

Physical and chemical conditions

Soil salinity, strength, and redox

Soil porewater salinity was measured at transplanting locations monthly (June-Sep 2019) and seasonally (June 2020, June 2021). A push point sampler (M.H.E. Products, East Tawas, MI) connected to a syringe was inserted to 20 cm depth to collect porewater, and salinity was measured in the field with a refractometer (Vee Gee Scientific, Vernon Hills, IL). In June 2019, transplanting waypoints spanning across all marsh zones of FCM and DI were randomly selected for porewater salinity measurement. Since very limited variation in soil salinity was observed among zones within each marsh platform, thereafter five to seven salinity measurements spanning all zones of each marsh were sampled on each subsequent occasion.

In August 2019, soil shear strength was measured at 20 cm and 50 cm depths at all transplanting waypoints using a field vane shear set (Humboldt H-4227).

Redox potential was measured in August 2019 using a Hach HQd Portable Meter with Lange MTC301 probe pushed 5 cm into the soil. Measurements were taken in vegetated and dieback zones only; these data were not collected in ponds where the substrate was unconsolidated.

Elevation

Substrate elevation within 0.5 m of each transplant was measured in May 2019 using a Trimble R8 Real Time Kinematic Global Positioning System (RTK-GPS). A plastic frisbee (2 mm thin, 20 cm wide) was used to hold the RTK-GPS at the soil surface, since the soil substrate in some marsh zones and ponds was soft or even fluid. Within each 0.5 m radius circle, readings of elevation were taken from five randomly selected points. For transplants in the ponds, one additional reading of substrate elevation within a flowerpot was taken to test the effectiveness of manipulated elevation.

Groundwater depth

Wells were installed in each marsh zone, and water levels were recorded at 15 min intervals from May 2019 to March 2020 using HOBO U20L-04 water level loggers. Surface elevation of each well was measured within a 0.5 m radius of the well location in May 2019 with RTK-GPS system to reference the water table data to NAVD88. Hydroperiod and a soil saturation index were calculated for the measurement period to investigate the differences in hydrological regime across different marsh zones (Qi and Gedan 2025).

Statistical analysis

In the occupancy survey, we expected to observe greater open water and dieback, indicating ecosystem deterioration, along survey transects from upland to ponds. We also expected flood-tolerant species would exhibit higher occupancy than flood-sensitive species in deteriorated areas. Two-way ANOVA was used to test for differences in water depth and dieback area along transects and across marsh platforms. A two-way linear model was used to assess whether occupancy differed between flood-sensitive species (e.g. *I. frutescens, S. patens* and *D. spicata*) and flood-tolerant species (e.g. *S. alterniflora*, *S. americanus*, *J. roemerianus*) along transects. Flood tolerance rankings followed previous classification (Qi et al. 2021a).

In the transplanting experiment, we tested for differences in soil salinity between marsh sites and over time, and whether the elevation, soil strength, redox potential of transplanting location, and performance of transplants differ significantly between marsh zones and experimental treatments (neighbor removal and substrate elevation). To test for differences in soil salinity between marsh platforms over time, we used a General Linear Mixed-Effects Model (GLMM) in the “lme4” R package (Bates et al. 2015). Marsh platform was treated as a fixed effect and sampling month as a random effect. To assess differences between marsh zones in soil strength, redox potential, and plant performance metrics (height, shoot number, flowering), we used nested ANOVAs with marsh zones nested within platforms, followed by post-hoc tests where significant effects were detected. Finally, GLMM was used to test for elevation differences across platforms, zones, and elevation treatments. Marsh platform, zone, and their interaction, as well as elevation treatments, were considered as fixed effects, while transplanting points were random effects. Post-hoc tests were used to compare means among groups. All analyses were performed in R (Team 2024).

Assumptions of nested ANOVA were evaluated by testing residual normality using the Shapiro–Wilk test and homogeneity of variances using Levene’s test. Where assumptions were violated, data were log-transformed. If assumptions remained violated after transformation, we applied an aligned rank transform (ART) two-way ANOVA, which provides valid tests of main and interaction effects under non-normal conditions. For linear mixed models (LMMs), assumptions were assessed using simulation-based diagnostics implemented in the DHARMa package (Hartig 2024). Normality (Kolmogorov–Smirnov test), variance homogeneity (dispersion test), and influential observations (outlier test) were evaluated. Given that LMMs are generally robust to moderate deviations from normality and to a small number of outliers, we proceeded with the fitted models when only mild violations were detected and variance homogeneity was satisfied. In cases of severe violations, we attempted log transformation, and if assumptions were still not met, an ART approach was used. All transformation and ultimate statistical tests have been reported in Appendix S1: Table S1.

Results

Plant community composition shifts along hydrological stress gradients

Along the deterioration gradient, from vegetated to pond areas (left to right in Fig. 2a), water depth increased significantly ($F_{4,40} = 13.36, p < 0.001$), indicating increased inundation stress. Dieback area also increased significantly ($F_{4,40} = 9.14, p < 0.001$), suggesting a potential lag or incapability of new colonizers to establish in released patches.

Along the marsh deteriorating gradient, community composition shifted from flood sensitive species, *e.g. I. frutescens, S. patens* and *D. spicata*, to flood tolerant species, *e.g. Bolboschoenus fluviatilis*, *S. alterniflora*, *S. americanus*, and *J. roemerianus,* though the dominant species along the hydrological stress gradient varied between the two marsh platforms (Fig. 2c). Prior work had demonstrated that such shift also happened temporally, based on remote sensing vegetation interpretation (Qi et al. 2021a). On average, flood-sensitive species exhibited significantly higher (58% versus 48%) occupancy than flood-tolerant species across sampling points along marsh deteriorating gradient ($F_{1,61} = 5.13$, $p = 0.027$). Occupancy of flood-sensitive species did not vary significantly along the gradient itself ($F_{4,61} = 0.79$, $p = 0.535$), and no interaction was found between flood tolerance group and sampling point ($F_{4,61} = 0.53$, $p = 0.714$) (Fig. 2b).

<Fig. 2>

Variation in elevation and salinity across marsh deterioration zones

FCM had a significantly lower salinity than DI by approximately 4.26 ppt ($F_{1,106}$ = 90.61, $p < 0.001$, Appendix S1: Fig. S2). Random variability due to sampling month ($\sigma^2 = 14.26$) exceeded residual variance ($\sigma^2 = 5.17$), reflecting substantial temporal variation. FCM has a significantly higher elevation than DI ($F_{1,70}$ = 19.88, $p < 0.001$). Elevation also differed significantly across marsh zones and elevation treatments ($F_{5,79}$ = 149.27, $p < 0.001$). Within each marsh platform, pond zones ('pond substrate' in Fig. 3a) were significantly lower than dieback or vegetated zones, and hydroperiods were significantly longer (Fig. 3b).

Elevation variability was low among replicates ($\sigma^2 = 0.00096$, SD = 0.031) relative to residual variance ($\sigma^2 = 0.00132$, SD = 0.036), indicating consistent elevation within each site-treatment combination. Manipulated elevations in pond treatments ("pond elevated" and "pond control") effectively captured elevation loss from dieback to pond zones. However, the manipulated elevations were on average ~10 cm higher than the target reference zones, introducing an unintended bias in elevation that should be considered when interpretating transplant performance. These higher elevations, however, did not significantly exceed the elevation range of the natural *Juncus* patch at either platform.

<Fig. 3>

Variation in soil physical and chemical properties across marsh deterioration zones

FCM exhibited significantly higher soil strength at 20 cm ($F_{1,59} = 71.69$, $p < 0.001$, Fig. 4a) and 50 cm ($F_{1,126} = 85.24$, $p < 0.001$, Fig. 4b), and higher redox potential ($F_{1,40} = 37.91$, $p < 0.0001$, Fig. 4c) than DI. Within FCM, neighbor patches exhibited a higher soil strength than dieback zones and *Juncus* patches, and a higher soil redox potential than dieback zones. No significant differences in soil strength were observed among zones in DI.

<Fig. 4>

Effects of marsh deterioration zones and neighbor and elevation manipulations on plant performance

Transplants in FCM showed a greater decrease in shoot height ($F_{1, 95} = 10.10$, $p = 0.002$) and lower flower production ($F_{1, 95} = 7.49$, $p = 0.007$), but no significant difference in shoot number compared to DI. Experimental treatments had significant effects on transplant performance: relative shoot height increase ($F_{5, 95} = 5.83$, $p < 0.001$), relative shoot number increase ($F_{10,95} = 12.60$, $p < 0.001$), and inflorescence abundance ($F_{5, 95} = 18.14$, $p < 0.001$) varied by treatment, but relative shoot number was most responsive to different treatments.

In FCM, transplants in neighbor removal treatments showed greater shoot number increases than those in neighbor intact treatments, and no significant difference in shoot height and flowering (Fig. 5b). A similar pattern was observed at DI but was not statistically significant. This indicates that competition from established marsh plants suppressed *J. roemerianus* colonization, and the intensity of suppression varied across sites: competition from *S. americanus* in the less saline marsh was greater than competition from *S. alterniflora* in the more saline marsh.

Transplants in the dieback patches showed no significant differences from transplants moved back to the original *Juncus* patches, in any metric of transplant performance, indicating barren dieback zones are suitable habitat for *J. roemerianus.* Apparently, low efficiency in spread of *J. roemerianus* constrained its colonization or spread into dieback patches at these sites, where it would have been released from competition with established plants. Elevated substrate treatments in ponds led to reduced shoot height declines (though not significant), increased shoot numbers, and more inflorescences compared to pond control treatments.

Transplants with elevated substrate performed similarly to those in dieback zones and neighbor patches, achieving equivalent changes in shoot height, shoot number and inflorescence production. These responses suggest that peat collapse following plant dieback makes the conditions less habitable for *J. roemerianus* and constrains its distribution to patches successfully colonized by *J. roemerianus* prior to peat collapse.

<Fig. 5>

Discussion

Our study combined vegetation surveys with a multi-year transplant experiment to test whether one or more processes (i.e. interspecific competition, dispersal inefficiency, runaway environmental degradation) constrain the establishment of stress tolerant species as habitat conditions get more stressful. Prior work demonstrated that in deteriorating tidal marshes, flood-sensitive species are being replaced by flood-tolerant ones (Qi et al. 2021a). Here, we further demonstrate that even where habitat degradation was apparent in environmental conditions, flood tolerant species still remained low in occupancy, while flood-sensitive species were found to have higher occupancy at the other end of the gradient. Low occupancy capability of flood tolerant species aligns with increased dieback areas as community composition shifts toward flood-tolerant species. This supports our hypothesis (H1) that replacement failure intensifies with inundation stress. The transplant experiment demonstrated that competition from established plants (H2), dispersal inefficiency or colonization failure (H3), and reinforced physical habitat degradation (H4) are each key contributors to this failure. Taking together, our findings show that ecosystem collapse arises from recruitment barriers and rapid environmental degradation, not regional species pool exhaustion.

Plant community dynamics and replacement failure along physical stress gradients

Interior microtidal marshes experience attenuated tidal flow, diminished drainage, and low accretion, making them especially vulnerable to sea level rise (Kirwan et al. 2016, Zapp and Mariotti 2024, Qi and Gedan 2025). At the Deal Island site, we observed greater inundation nearer to ponded areas (Fig. 2a). Consistent with earlier work (Qi et al. 2021a), vegetation shifted from flood-sensitive species to flood-tolerant species, though the specific composition varied with salinity level at each marsh site (Fig. 2c). Some differences between sites, such as the exclusion of comparatively salt-sensitive species like *Phragmites australis* and *Iva frutescens* from high salinity sites (Bertness et al. 1992, Crain et al. 2004, Qi et al. 2018), were explained by differences in salinity between sites (7 vs. 13 ppt). *Schoenoplectus americanus*, less salt tolerant than *S. alterniflora* or *J. roemerianus*, was also not detected in saltier sites (Baeza et al. 2013, Qi et al. 2017, Stalter and Lonard 2023).

Increasing water depth and dieback near ponds supported hypothesis (H1) that replacement failure is exacerbated by physical stress. Elevated dieback in high-stress zones indicated either recruitment failure or narrow colonization windows. In the surveyed transects, occupancy of flood-tolerant species was lower than that of flood-sensitive ones across the hydrological (or deteriorating) gradient (Fig. 2b), suggesting poor dispersal or establishment as physical stress intensifies - a phenomenon that has been observed in experimentally disturbed marshes along physical stress gradients (Crain et al. 2008, van Belzen et al. 2017).

Biotic resistance

Our experiment confirmed (H2), that established species, especially *Schoenoplectus americanus,* can supress *Juncus* growth via competition. This effect diminished at the saltier Deal Island site, where *S. alterniflora* dominates. This aligns with the Stress Gradient Hypothesis (Bertness and Callaway 1994); the SGH predicts that stress-sensitive species will experience positive interactions under physical or consumer stress, while stress-tolerant colonizers will face competition, though competition intensity will diminish as competitive ability of stress sensitive species decrease along the stress gradient (Qi et al. 2018).

Dispersal and establishment constraints

Our transplant experiment in dieback patches supported hypothesis (H3), that dispersal or colonization constrains *J. roemerianus* establishment on dieback patches rather than unsuitability of the unoccupied habitat. *J. roemerianus* shows high seed viability (>90%) and can germinate when floating or submerged (Eleuterius 1975, Looney and Gibson 1995). Our field transplant experiment also found elevation loss in ponded areas suppressed flowering of *Juncus* transplants (Fig. 5c), indicating reduced sexual reproduction under inundation stress. Vegetative expansion of *J. roemerianus* can also be suppressed by inundation, as indicated by the finding that shoot number of *Juncus* transplants in ponded areas was significantly lower than at higher elevations (Fig. 5b). Reduced horizonal expansion of *J. roemerianus* in more stressful conditions of higher salinities and inundation periods was also observed by Etheridge (2015). In a landscape scale monitoring of secondary succession dynamics, (Crain et al. 2008) found reduced diversity and abundance in the seed bank along the salinity gradient of a coastal marsh, as well as fewer viable seeds for species with broad stress tolerance. These results suggest sexual and vegetative reproduction can both be suppressed by high physical stress.

Environmental feedback and collapse

Once the ecosystem reaches a point of deterioration where positive feedbacks take hold in the form of peat collapse, recovery by *Juncus* is unlikely. The pond elevation experiment confirmed hypothesis (H4), that *J. roemerianus* performs poorly once peat collapses. When elevation is experimentally restored, growth resumes. Elevation loss following dieback (~15 cm in 2 years; (DeLaune et al. 1994)) mirrors elevation differences measured at these sites and underscores the short window available for successful colonization. Similar feedbacks have been documented in other marshes and seagrass beds (Kirwan et al. 2016, Qi et al. 2018, Serrano et al. 2021), where vegetation loss accelerates ecosystem collapse via erosion, salinization, and anoxia.

Implications for theory and restoration

Our findings show that even when stress-tolerant species persist within the local species pool, recruitment bottlenecks can still trigger ecosystem collapse. This challenges models that infer future species distributions solely from the presence or absence of established populations, without accounting for constraints on recruitment, or perhaps other sensitive life history stages. Our results highlight the need to better integrate recruitment dynamics into community assembly theory—particularly under conditions of extreme environmental stress. From a restoration perspective, this means interventions should directly address the recruitment bottleneck by suppressing competitors, restoring elevation, and enhancing propagule delivery and establishment to repair disrupted colonization pathways.

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Figure captions

Fig. 1 Study area and design of transplanting experiment. A *J. roemerianus* transplanting experiment was conducted in two deteriorating brackish marsh, i.e. Farm Creek Marsh and Deal Island (**a**). Transplants in Farm Creek Marsh (**b**) and Deal Island (**c**) in marshes zones that were undergoing different extents of deterioration (from most to least): pond, dieback zone, vegetated zone (neighbor patch & *Juncus* patch- source locations of *Juncus* transplants). **d** illustrated the treatment of transplants at each zone of marsh (existing plant distributions represented in black and transplants in green).

Fig 2. Plant community composition along marsh deterioration gradient across several marshes with different salinity levels. (a) Percentage area of dieback patch and water depth along the transect from upland to ponded area (sampling point A to E). Shaded bands represent 90% confidence intervals across three replicate transects at each of the four marsh sites (n = 12). For water depth, $p = .0130$ and 7.44×10^{-6} for two-way ANOVA test of site and transect locations respectively (n = 3). For dieback area, p=.2383 and 1.86×10^{-5} for site and point. (b) Comparison of occupancy (%) between flood-sensitive (Flood-Sen) and flood-tolerant (Flood-Tol) species groups. (c) Mean abundance (circle size) and occupancy (color gradient) of plant species across sampling points (A–E) across four marsh sites (S1-2, S4, S3), ordered by increasing mean soil salinity (site-specific mean soil salinity is shown below each site label in ppt). Species are color-coded by flood tolerance group (flood-sensitive in teal; flood-tolerant in orange). ART transform was applied to water depth and occupancy for statistical test.

Fig. 3 Substantial decrease in elevation (**a**) and increase in hydroperiod (**b**) from vegetated and dieback zones to ponded zones ('pond substrate' in **a** for differentiation from other treatments in pond). Elevated and control pond transplant treatments reflected elevation loss from dieback zones, though a ~10 cm bias was introduced (datum: NAVD88).

Fig. 4 Soil strength (20 cm depth in **a**, 50 cm depth in **b**) and redox potential were higher in Farm Creek Marsh than in Deal Island. In Farm Creek Marsh (upper panels), neighbor patches had stronger and more oxidized soils than dieback zones. No significant zone differences in soil strength were observed in Deal Island (lower panels). ART transform was applied to soil redox potential for statistical test.

Fig. 5. Elevated substrate and neighbor removal treatment significantly improved transplant performance compared to elevation control and neighbor control treatments. Transplants in the dieback zone performed similarly to those under neighbor removal. The relative increase in shoot height or shoot number was calculated as the proportional change between 2019 and 2021 for each transplant. Specifically, it was: (s_{2021}-s_{2019})/s_{2019}, where s represents either shoot height or shoot number. ART transform was applied to height growth rate and inflorescence number for statistical test.

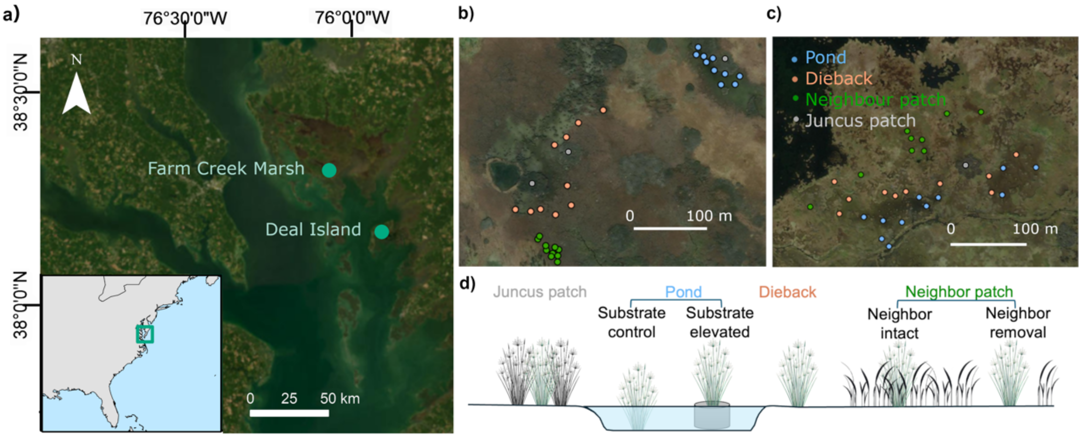
a)
76°30'0"W
76°0'0"W
38°30'0"N
38°0'0"N
N
Farm Creek Marsh
Deal Island
0 25 50 km
b)
0 100 m
c)
Pond
Dieback
Neighbour patch
Juncus patch
0 100 m
d)
Juncus patch
Pond
Substrate control
Substrate elevated
Dieback
Neighbor patch
Neighbor intact
Neighbor removal

Fig. 1

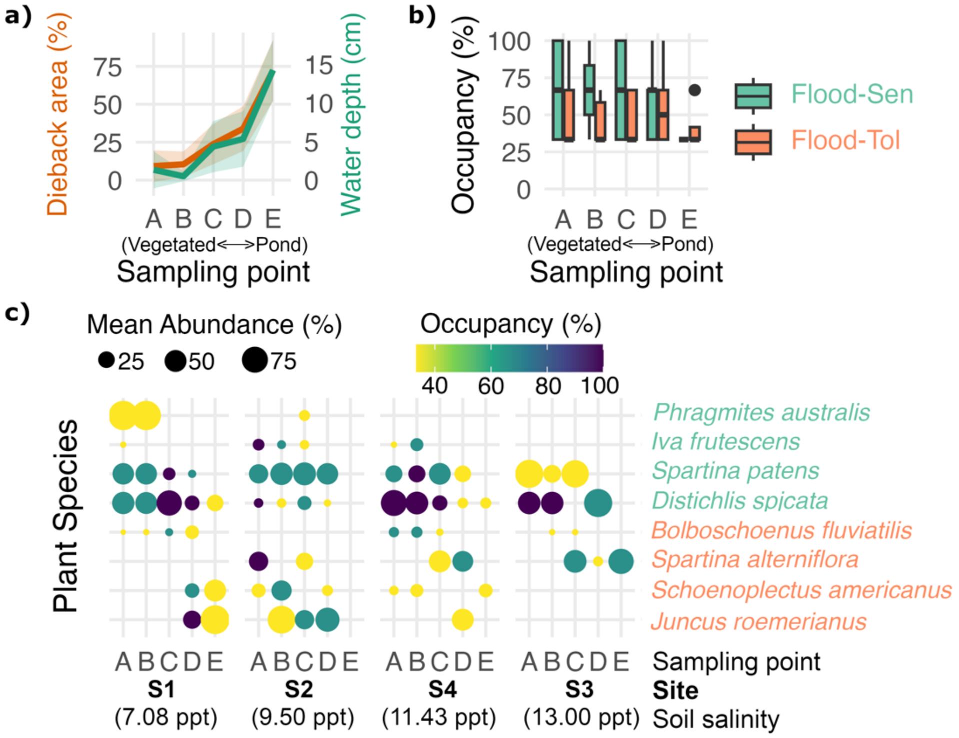
a)
Dieback area (%)
Water depth (cm)
0
25
50
75
0
5
10
15
A B C D E
(Vegetated<—>Pond)
Sampling point
b)
Occupancy (%)
0
25
50
75
100
A B C D E
(Vegetated<—>Pond)
Sampling point
Flood-Sen
Flood-Tol
c)
Mean Abundance (%)
25
50
75
Occupancy (%)
40
60
80
100
Plant Species
Phragmites australis
Iva frutescens
Spartina patens
Distichlis spicata
Bolboschoenus fluviatilis
Spartina alterniflora
Schoenoplectus americanus
Juncus roemerianus
A B C D E
S1
(7.08 ppt)
S2
(9.50 ppt)
S4
(11.43 ppt)
S3
(13.00 ppt)
Sampling point
Site
Soil salinity

Fig. 2

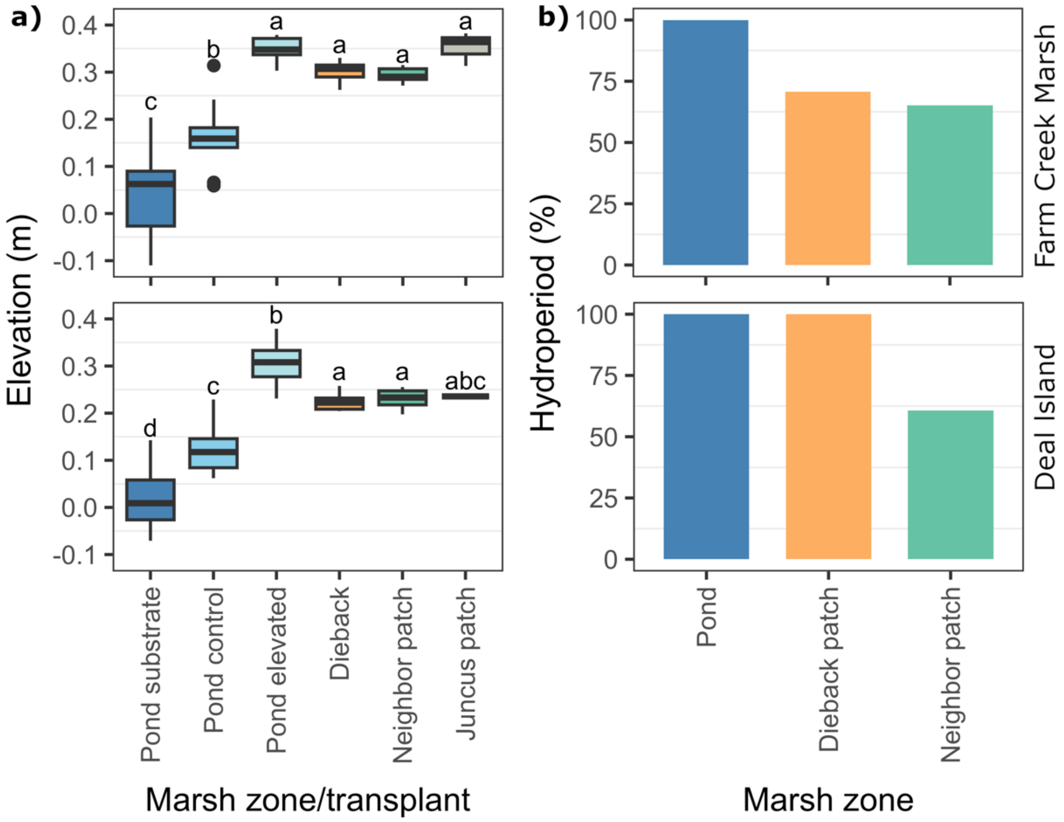
a)
Elevation (m)
0.4
0.3
0.2
0.1
0.0
-0.1
c
b
a
a
a
a
d
c
b
a
a
abc
Pond substrate
Pond control
Pond elevated
Dieback
Neighbor patch
Juncus patch
Marsh zone/transplant
b)
Hydroperiod (%)
100
75
50
25
0
Farm Creek Marsh
Deal Island
Pond
Dieback patch
Neighbor patch
Marsh zone

Fig. 3

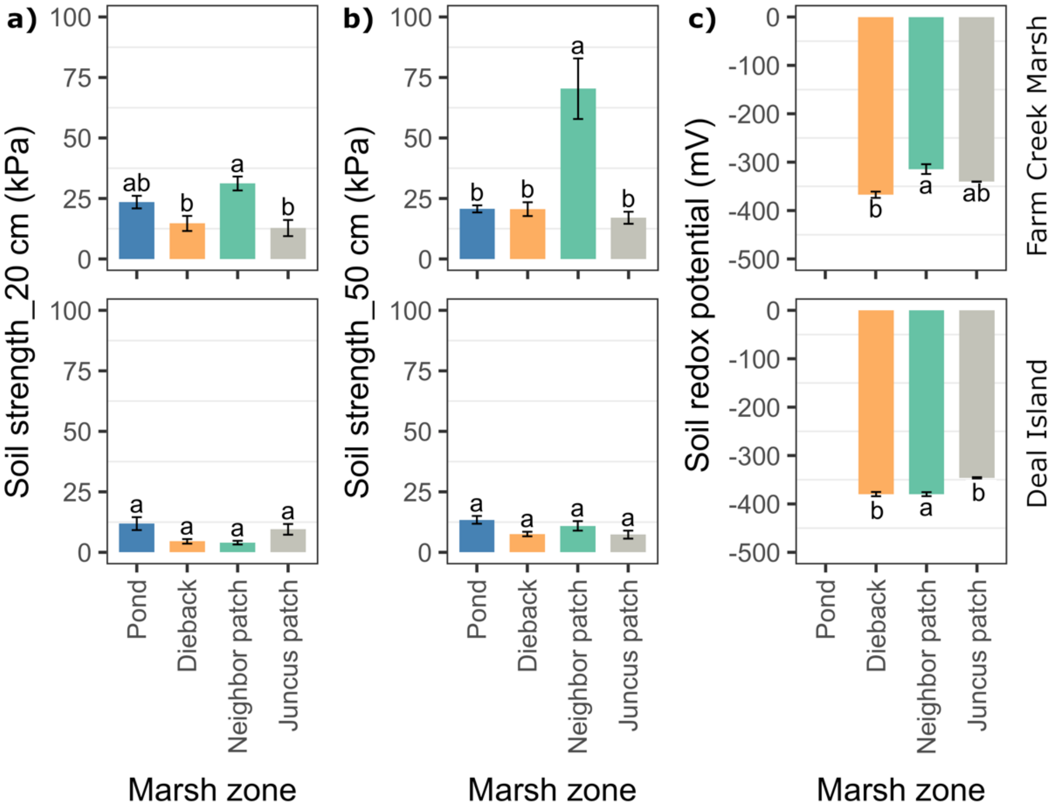
a)
b)
c)
Soil strength_20 cm (kPa)
Soil strength_50 cm (kPa)
Soil redox potential (mV)
100
75
50
25
0
0
-100
-200
-300
-400
-500
ab
b
a
b
a
a
a
a
b
b
a
b
a
a
a
a
b
a
ab
b
a
b
Farm Creek Marsh
Deal Island
Pond
Dieback
Neighbor patch
Juncus patch
Marsh zone

Fig. 4

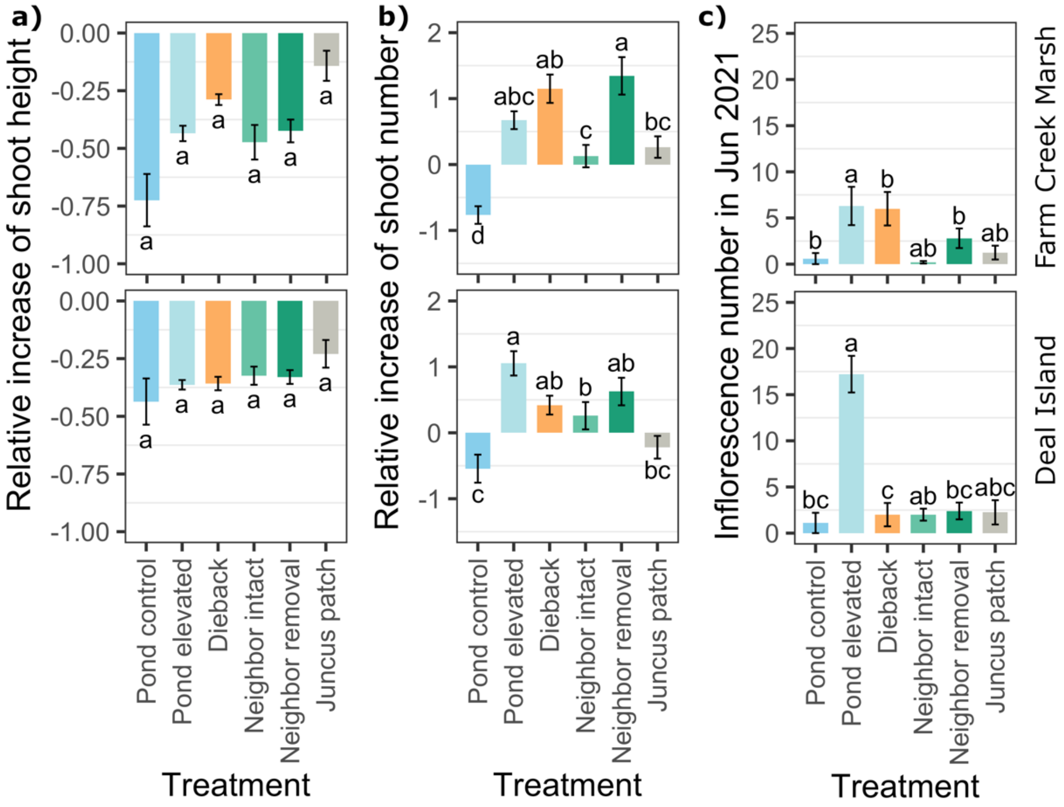
a)
b)
c)
Relative increase of shoot height
Relative increase of shoot number
Inflorescence number in Jun 2021
0.00
-0.25
-0.50
-0.75
-1.00
2
1
0
-1
25
20
15
10
5
0
a
a
a
a
a
a
d
abc
ab
c
a
bc
b
a
b
ab
b
ab
a
a
a
a
a
a
c
a
ab
b
ab
bc
bc
a
c
ab
bc
abc
Farm Creek Marsh
Deal Island
Pond control
Pond elevated
Dieback
Neighbor intact
Neighbor removal
Juncus patch
Treatment

Fig. 5