Recruitment bottlenecks and reinforcing environmental degradation drive marsh collapse

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Abstract (273 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 found that plant occupancy decreased along the inundation gradient, but the decline did not differ significantly between flood-tolerant and flood-sensitive functional groups. Using transplants of the flood-tolerant rush *Juncus roemerianus*, we show that recruitment limitation arises from multiple, context-dependent mechanisms that vary across sites and performance metrics. In the less saline marsh, competition from established species suppressed clonal growth (shoot production) but had little effect on flowering or survival, whereas in the more saline marsh, competitive effects were weak across all metrics. In dieback patches, transplants performed similarly to source populations in shoot production, flowering and survival, indicating that absence from these patches is driven by dispersal or colonization limitation rather than habitat unsuitability. In contrast, in ponded areas where peat collapse reduced elevation, transplants exhibited reduced shoot production and survival, while reproductive output was less affected, demonstrating strong physical constraints on establishment. Together, these results reveal that marsh collapse arises from compounded recruitment bottlenecks—including dispersal limitation, context-dependent competition, and post-dieback physical degradation—rather than regional species exhaustion. This finding challenges models that infer future species distribution from current occupancy without accounting for recruitment failure. Effective restoration must therefore target multiple stages of recruitment,

including propagule delivery, competitive release, and substrate stabilization, before physical degradation renders habitats unsuitable.

Introduction

Global change exposes many ecosystems to chronic climate stress—from global warming (Hughes et al. 2018), ocean acidification (Nagelkerken and Connell 2022), or sea level rise (Kirwan and Gedan 2019). Some stressed ecosystems undergo gradual shifts in community composition (McCoy et al. 2016, Qi et al. 2021a). For example, ocean acidification can drive community shifts towards non-calcified species or ecosystems (McCoy et al. 2016), while sea level rise can shift salt marsh plant communities toward more flood tolerant species (Qi et al. 2021a). In contrast, other ecosystems experience abrupt, wholesale collapse, such as heatwave-driven transitions of seagrass meadows to barren states or sea-level-rise-induced peat collapse and pond expansion (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 (McCoy et al. 2016, 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 pools or blocked recruitment processes such as dispersal or establishment (Ratajczak et al. 2018, 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 regionally available (Qi

et al. 2016, Waldock et al. 2022). This assumption, grounded in niche theory (Hutchinson 1978), 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 changing environmental conditions (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, theory and models must be refined.

From a conservation perspective, this uncertainty complicates restoration planning. The failure of natural recovery due to impaired recruitment (He et al. 2017, Xie et al. 2019, Liu et al. 2020) can be overcome by actively increasing the propagule supply of an appropriate species (e.g., through transplantation) or the creation of suitable abiotic conditions to recover recruitment, whereas strategies based solely on passive recolonization 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 enhancing 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 (Ratajczak et al. 2018), 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, followed by peat collapse, and finally ponding (Qi et al. 2021a, Qi and Gedan 2025)—providing an ideal setting for exploring colonization constraints (Fig. 1d). 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 in this system—persisting in deteriorating marshes but constrained in its spatial distribution, even as neighboring marsh plant species died back and marsh degraded into ponds (Appendix S1: Table S1, Fig. S1b). In this study, we re-analyzed prior vegetation data (Qi et al. 2021a) to test whether (H1) species dispersal limitation and replacement failure intensifies 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 its tidal marshes have deteriorated in recent decades (Beckett et al. 2016). We selected two deteriorating brackish marshes within the Bay as study areas: Deal Island on the Manokin River (Deal Island Wildlife Management Area, managed by the Maryland Department of Natural Resources) and Farm Creek Marsh on Fishing Bay (owned and managed by the Chesapeake Audubon Society). These marshes are in the early stages of transition from vegetated marsh to open pond (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 (Qi et al. 2021a, Qi and Gedan 2025).

Both Deal Island and Farm Creek Marsh are brackish, with Deal Island exhibiting higher salinity (7-15 parts per thousand) than Farm Creek Marsh (2-5 parts per thousand), 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.* All species reproduce both sexually and clonally. *S. patens* and *D. spicata* are relatively flood-sensitive and typically co-occur in high marsh areas. *S. americanus* has greater flood tolerance than *S. patens* and *D. spicata* and often forms hummock-hollow patches in the high marsh. *Spartina alterniflora* is more flood- and salt-tolerant than *S. americanus* and forms single-species stands in both high and low marsh zones, particularly where soil salinity is higher. *Juncus roemerianus* forms single-species patches in high and mid-marsh areas and is the only species observed to persist for decade following dieback of neighboring vegetation, and it is frequently

observed in isolated patches within marsh ponds (Appendix S1: Table S1, Fig. S1b). At Deal Island, *S. alterniflora* dominated and *S. americanus* is rare, while at Farm Creek Marsh, *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 Deal Island formed sparse meadows on soft, homogenous substrates, while *S. americanus* in Farm Creek Marsh 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 in healthy marsh surrounded by neighboring species and in small islands within ponds.

<Fig. 1>

Vegetation quadrat survey

To test whether species dispersal limitation and replacement failure intensify along inundation stress (H1), 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 and water) 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. As hydrological stress intensifies, the marsh systems undergo plant displacement, and flood-tolerant species replace flood-sensitive ones (Qi et al. 2021a). We used the occupancy of 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 the hydrological gradient within each marsh platform as an indicator of the colonization success of each functional

group. Flood tolerance rankings followed a previous classification (Qi et al. 2021a). Functional-group occupancy was defined as the percentage of the three replicate quadrats located at similar distance to the ponds in which at least one species belonging to a given functional group was present. Species-level occupancy was calculated similarly. Three species with low occurrence (≤1 out of 12 quadrats) and low abundance (<10%) 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. Dieback zones were located between vegetated zones and ponds and had not yet suffered obvious peat collapse or elevation loss. In mid to late April 2019, we excavated 56 blocks of *J. roemerianus* clonal patches from each platform. Each transplant was made up a 20 × 20 × 20 cm block of *J. roemerianus* culms and surrounding soil. Blocks were wrapped with garden cloth and secured with rubber bands.

Six blocks 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 (H2), 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 (H3), 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 ponds (H4), transplants in ponds were subjected to an elevated substrate treatment (hereafter 'pond

elevated' treatment, see Appendix S1 for details) or ambient elevation treatment (hereafter 'pond control' treatment). Each treatment had 10 replicates.

Plant monitoring

To estimate performance of *Juncus* transplants, we measured shoot number and flowering status, and survival of each transplant. The number of living shoots were recorded in June 2019, 2020 and 2021. Shoot counts included all green stems ≥10 cm tall. Flowering status was recorded in June 2020 and 2021. Since the shoot number and survival presented consistent and gradual changes in response to treatments (Appendix S1: Fig. S3), we use the relative change in shoot number across the experimental period (April 2019 - June 2021) to represent clonal reproduction of transplants. Inflorescence count and survival rate in June 2021 were also analysed to reflect the long-term effect of treatments on sexual reproduction and overall performance of transplants. When calculating survival rate, each transplant was treated as an individual, while the transplants within each treatment were considered a population. Survival rate was therefore calculated as the percentage of individuals that survived within each population.

Physical and chemical conditions

To test the environmental degradation and habitat quality along the deterioration gradient from neighbor patch, to dieback patch and ponds (H4), we measured soil salinity, soil strength, soil redox potential, elevation, hydroperiod and soil saturation index at each marsh zone or transplanting site (see Appendix S1 for detailed methodologies).

Statistical analysis

In the occupancy survey, we expected greater open water and dieback, indicating ecosystem deterioration, along survey transects from upland to ponds. We also expected decreased occupancy

as inundation intensified (H1), and that flood-tolerant species would exhibit higher occupancy than flood-sensitive species in deteriorated areas. A two-way ANOVA was used to test for differences in water depth and dieback area along transects and across marsh platforms.

To study whether occupancy differed between flood-sensitive species and flood-tolerant species along transects, occupancy at functional group level was analysed using a Linear Mixed-Effects Model (LMM) in the "lme4" R package (Bates et al. 2015). In the LLM, flood-tolerance group and sampling point as fixed effects and marsh platform as a random effect.

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 differed significantly between marsh zones and experimental treatments (neighbor removal and substrate elevation, H2-4). To test for differences in soil salinity between marsh platforms over time, we used a LMM, with marsh platform 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 (shoot number, flowering), we used nested ANOVAs with marsh zones nested within platforms, followed by post-hoc tests where significant effects were detected. Finally, LMM 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. All transformation and ultimate statistical tests have been reported in Appendix S1: Table S2.

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 ($F_{4,40} = 10.36, p < 0.001$, Appendix S1: Table S2), indicating increased inundation stress. Dieback area also increased significantly (Fig. 2a, $F_{4,40} = 9.41, p < 0.001$, Appendix S1: Table S2), suggesting a potential lag or incapability of new colonizers to establish in released patches.

Along the marsh deterioration gradient, based on the abundance of each species, 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,* despite the dominant species along the hydrological stress gradient varying between the two marsh platforms (Fig. 2c). Prior work had demonstrated that this same shift also occurs temporally, based on a vegetation interpretation using remote sensing (Qi et al. 2021a). Occupancy varied significantly across sampling points along the marsh deterioration gradient, with lower occupancy observed in the most deteriorated areas near ponds (Fig. 2b, $F_{4,40} = 4.90$, $p = 0.004$,

Appendix S1: Table S2). However, neither the overall effect of flood-tolerance group (Fig. 2b, $F_{1,40} = 0.92$, $p = 0.35$, Appendix S1: Table S2), nor the interaction between flood-tolerance group and sampling point (Fig. 2b, $F_{4,40} = 2.11$, $p = 0.11$, Appendix S1: Table S2) was statistically significant. Consequently, the survey data indicated reduced occurrence and colonization success under increasing inundation stress, but do not by themselves distinguish whether this pattern resulted from replacement failure (H1) or increasing habitat unsuitability.

<Fig. 2>

Environmental differences between Farm Creek Marsh and Deal Island

The two marshes selected for the transplanting experiment differed in several environmental characteristics associated with their location within Chesapeake Bay. Farm Creek Marsh had a significantly lower salinity than Deal Island, by 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. Farm Creek Marsh also had a significantly higher elevation than Deal Island (Fig. 3a, $F_{1,70} = 19.88$, $p < 0.001$, Appendix S1: Table S2). Consistent with these elevation differences, Farm Creek Marsh exhibited higher soil strength at both 20 cm ($F_{1,59} = 71.69$, $p < 0.001$, Fig. 4a) and 50 cm depth ($F_{1,126} = 85.24$, $p < 0.001$, Fig. 4b), as well as higher redox potential ($F_{1,40} = 37.91$, $p < 0.0001$, Fig. 4c) than Deal Island.

Variation in elevation and salinity across marsh deterioration zones

Elevation also differed significantly across marsh zones and elevation treatments (Fig. 3a, $F_{5,79} = 149.27$, $p < 0.001$, Appendix S1: Table S2). Within each marsh platform, pond areas ('pond substrate' in Fig. 3a) were significantly lower than dieback and vegetated areas, and hydroperiods

were significantly longer (Fig. 3b, (Qi and Gedan 2025)), suggesting extra hydrological stress following peat collapse in pond areas.

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

Within Farm Creek Marsh, 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 Deal Island.

<Fig. 4>

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

Transplants in Farm Creek Marsh showed a lower flower production ($F_{1, 95} = 7.49$, $p = 0.007$, Fig. 5b, Appendix S1: Table S2), but relatively higher survival rate of transplants (Fig. 5c) and no significant difference in shoot number (Fig. 5a) compared to Deal Island. Experimental treatments had significant effects on transplant performance: relative shoot number increase ($F_{10,95}= 12.60$, p

286 <0.001, Fig. 5a, Appendix S1: Table S2), inflorescence abundance ($F_{5, 95} = 18.14$, $p < 0.001$ Fig.
287 5b, Appendix S1: Table S2), and survival rate (Fig. 5c) varied by treatment.

288 In Farm Creek Marsh, transplants in neighbor removal treatments showed greater shoot
289 number increases than those in neighbor intact treatments, and no significant difference in
290 flowering and survival rate (Fig. 5). A similar pattern was observed at Deal Island but was not
291 statistically significant for shoot number increases. This indicates that competition from
292 established *S. americanus* in the less saline Farm Creek Marsh significantly suppressed clonal
293 reproduction of *J. roemerianus*, but not sexual reproduction and survival (partially in support of
294 H2). In the more saline Deal Island, competition from *S. alterniflora* was not strong enough to
295 cause significant changes in reproduction and survival of *J. roemerianus* transplants (in opposition
296 to H2).

297 Transplants in the dieback patches showed no significant differences from transplants moved
298 back to the original *Juncus* patches in shoot number increases or inflorescence number, except for
299 a slight drop in survival rate (~ 10%) at Deal Island (Fig. 5). The nearly identical performance
300 between barren dieback zones and *Juncus* patches across both marsh sites indicates that the
301 absence of *J. roemerianus* from dieback zones can be attributed to low efficiency in dispersal or
302 colonization failure of *J. roemerianus* (in support of H3).

303 Elevated substrate treatments in ponds led to increased shoot numbers, more inflorescences
304 and higher survival compared to pond control treatments (Fig. 5). Transplants with elevated
305 substrate performed similarly to those in dieback zones and neighbor patches, achieving equivalent
306 changes in shoot number, inflorescence production and survival rate (Fig. 5). These responses
307 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 (in support of H4).

<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, or runaway environmental degradation) constrain the establishment of stress tolerant species as habitat conditions become 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 found occupancy pattern along could not distinguish whether vegetation loss in highly deteriorating areas resulted from replacement failure (H1) or increasing habitat unsuitability. The transplanting experiment was therefore critical for disentangling these alternative explanations. The transplant experiment with *Juncus* demonstrated that dispersal inefficiency / colonization failure (H3) and reinforced physical habitat degradation (H4) are each key contributors to replacement failure. Competition from established plants was generally weak and had no effect on sexual reproduction or survival, but competition significantly reduced clonal reproduction of *Juncus* at the less saline marsh (context dependent support for H2). Taken 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, Qi and Gedan 2025). At the Deal Island site, we observed greater inundation nearer to pond areas (Fig. 2a).

Consistent with earlier work (Qi et al. 2021a), vegetation shifted from flood-sensitive 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 indicated progressive habitat deterioration. Overall occupancy also declined toward the most deteriorated areas, suggesting reduced colonization success or persistence under increasingly stressful conditions. However, occupancy patterns did not differ significantly between flood-sensitive and flood-tolerant functional groups, making it difficult to determine from survey data alone whether vegetation loss in highly deteriorated areas resulted from replacement failure (H1) or increasing habitat unsuitability. Distinguishing between recruitment limitation and habitat unsuitability therefore required the transplant experiment, which directly tested the establishment success of the dominant flood-tolerant species, *Juncus roemerianus*.

Biotic resistance

Our experiment showed that competition intensity from established species was context-dependent (partial support for H2). Significant suppression of *Juncus* performance occurred only in the less saline Farm Creek Marsh dominated by *Schoenoplectus americanus*, and only clonal reproduction was reduced (Fig. 5); sexual reproduction and survival were unaffected. Although slight suppression of clonal reproduction of *Juncus* by *Spartina alterniflora* was observed at Deal Island, the effect was not significant (Fig. 5a). Previous neighbor-removal experiments between

Juncus roemerianus and *Spartina alterniflora* similarly found mutual release effects on shoot number, whereas biomass was unaffected, suggesting weak competition between the two species (Stanton 1998), especially under flooding or salinity stress (Pennings et al. 2005).

The weaker competition observed at the more saline Deal Island is consistent with theoretical expectations that competitive intensity declines as abiotic stress increases (Bertness and Callaway 1994). A recent study in brackish marshes affected by sea level rise similarly found that competition between sedges and grasses tended to weaken in more flooded, lower elevation zones (Gabriel et al. 2022). Previous studies show that stress-tolerant species may still experience competition from less stress-tolerant species, although competition weakens with increasing stress (Qi et al. 2018). Thus, the generally weak competition experienced by flood-tolerant *Juncus* transplants and the context-dependent suppression of clonal reproduction, can be explained by shifts in competitive strength along the stress gradient.

Dispersal and establishment constraints

Juncus transplants in dieback zones performed similarly to those replanted within source patches, indicating that the absence of *Juncus* from dieback zones resulted from dispersal or colonization limitation rather than habitat unsuitability (H3).

J. roemerianus shows high seed viability (>90%) and can germinate when floating or submerged, although germination is light-dependent and inhibited by burial (Eleuterius 1975, Looney and Gibson 1995). Therefore, seed germination may be low when seeds are covered by sediment or shaded by a dense canopy. Established *J. roemerianus* populations have also been reported to buffer variation in production and senescence across flooding and salinity gradients, resulting in relatively stable patches once established (Christian et al. 1990). However, horizontal expansion can be suppressed by prolonged flooding and elevated salinity (Etheridge 2015).

Together, these charateristics may promote persistence of established patches while limiting the capacity of *J. roemerianus* to colonize newly available habitat.

During the field experiment, we rarely observed *Juncus* seedlings in dieback zones or mature stands of other species (consistent with Eleuterius (1975)), and the absence of seedlings suggests that seed-based regeneration is limited in natural marshes. However, because we did not assess the seed bank or measure seedling survival across habitats, we can make limited inferences about the importance of seed recruitment and seed banks or which recruitment stages (e.g., dispersal, germination, or establishment) are most constrained along the hydrological gradient. These questions warrant further investigation, especially if reseeding is considered as a restoration strategy.

Environmental feedbacks and collapse

Once the ecosystem reaches a threshold where positive feedbacks such as peat collapse occur, natural recovery through *Juncus* expansion is unlikely. The pond elevation experiment confirmed hypothesis (H4), that ponded areas where peat has collapsed are uninhabitable for *Juncus*. Elevation loss in ponded areas significantly supressed survival and reproduction of *Juncus*, whereas restoring elevation to pre-collapse levels recovered these vital rates (Fig. 5).

Elevation loss following dieback (~15 cm in 2 years; (DeLaune et al. 1994)) mirrors elevation differences measured at our sites and highlights the short window available for 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 through erosion, salinization, and anoxia.

At a community level, 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 findings suggest that both sexual and vegetative reproduction at the community level can be progressively suppressed as physical stress increases (i.e. higher salinity in Crain et al 2008 while higher inundation in our study), increasing the risk of species replacement failure through recruitment bottlenecks, even when the species pool remains intact.

Implications for restoration and theory

Our transplanting experiment showed that restoring elevation to pre-peat-collapse levels recovered clonal and sexual reproduction and improved survival of *Juncus* (Fig. 5). This suggests elevating deteriorated marsh surfaces as an effective restoration strategy. While such elevation restoration approaches do not necessarily ensure long-term marsh stability under continued sea level rise, they can increase elevation capital and potentially prolong marsh persistence (Billah et al. 2022, Davis et al. 2022). Some research further suggests that restoring elevation can recover not only plant performance but also plant-soil feedbacks (Davis et al. 2022), thereby partially restoring the capacity of marshes to adapt to sea level rise.

Given the strong recruitment bottleneck we observed, active reintroduction of *Juncus* may accelerate revegetation and recovery of ecosystem functions. A simple back-of-the-envelope calculation illustrates the severity of the recruitment bottleneck (Table S3). Assuming *J. roemerianus* expands laterally at a roughly constant rate each year, we estimated the maximum distance from existing *Juncus* patches to the farthest point in the surrounding water area and divided this distance by 10 years. This yielded required expansion rates of 9 ~ 14 m/yr to occupy the open-water area before widespread peat collapse. By contrast, the realized expansion rate estimated from transplant growth in dieback zones was only approximately 0.064 m yr^{-1}. Thus, *J. roemerianus* would need to spread roughly two orders of magnitude faster than observed to occupy deteriorated marsh surfaces within a 10-year window.

Although revegetation and abiotic restoration strategies, such as elevation enhancement, are both important approaches, their relative contributions to successful restoration have rarely been evaluated (Billah et al. 2022, Liu et al. 2024). Our results suggest that revegetation may become increasingly important when abiotic stress remains high. Future research identifying whether sexual or clonal processes dominate the recruitment bottleneck could inform cost-effective planting or reseeding strategies and identify environmental barriers that must be removed. Before environmental degradation becomes self-reinforcing, actively planting stress-tolerant species could alleviate a recruitment bottleneck, facilitate species displacement, and prevent dieback and runaway degradation. Restoration efforts should therefore directly address recruitment constraints by restoring elevation and enhancing propagule delivery and establishment.

Our findings show that even when stress-tolerant species persist within the local species pool, recruitment bottlenecks can still trigger ecosystem collapse under extreme physical stress. This calls for caution in models relying heavily on space-for-time-substitution (SFTS), including species distribution models (also called ecological niche models) (Kharouba and Williams 2024). When SFTS was applied to project future species presence based on current occupancy, one of the underlying assumptions is that dispersal is sufficiently rapid to track suitable habitat area (several other assumptions can be found at Kharouba and Williams (2024)). Although widely used, the mechanisms determining when and why SFTS succeeds or fails are rarely tested (Kharouba and Williams 2024).

Our study suggests that the reliability of SFTS for plant communities declines as physical stress intensifies. The underlying mechanism is the strengthening of recruitment bottlenecks and the increasing likelihood of self-reinforcing environmental degradation. Therefore, greater caution is warranted when applying SFTS-based models under extreme climatic or physical stress. Our

446 results highlight the need to integrate community assembly theory—particularly dispersal filters,
447 abiotic constraints, and biotic interactions—into predictive models to better capture uncertainty in
448 species distributions along environmental gradients.

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459 **Conflict of Interest Statement**: the authors declare no conflicts of interests.

460

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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 marshes, 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 deteriorating dynamics of coastal marshes that experienced plant diebacks, peat collapse and pond formation as hydrological stress intensifies. The treatment of transplants at each zone of deteriorated marsh (existing plant distributions represented in black and transplants in green). Image created by Man Qi.

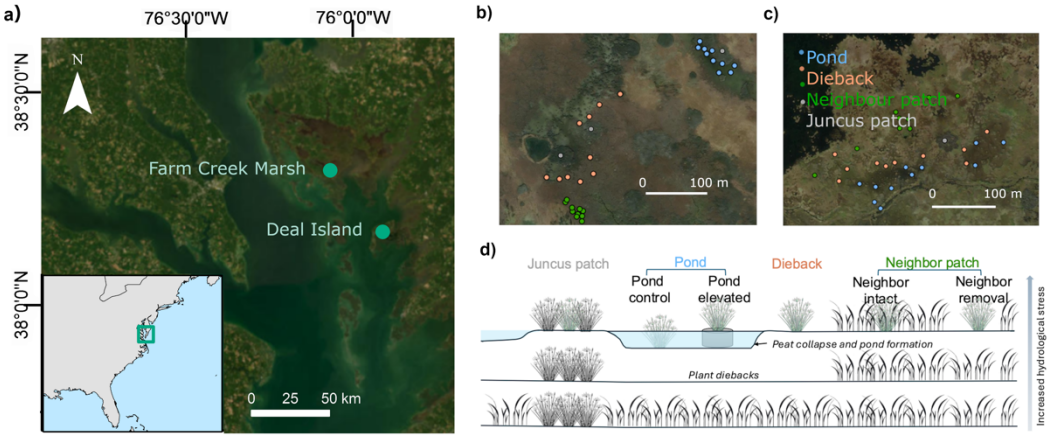
Fig 2. Plant community composition along marsh deterioration gradient across several marshes with different salinity levels. (a) Percentage area of dieback patch and water depth along the transect from upland to ponded area (sampling point A to E). Shaded bands represent 90% confidence intervals across three replicate transects at each of the four marsh sites (n = 12). For water depth, $p = 0.0130$ 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. Values are means ± SE (n = 4 marsh platforms). (c) Mean abundance (circle size) and

584 occupancy (color gradient) of plant species across sampling points (A–E) across four marsh sites
585 (S1-2, S4, S3), ordered by increasing mean soil salinity (site-specific mean soil salinity is shown
586 below each site label in ppt). Species are color-coded by flood tolerance group (flood-sensitive in
587 teal; flood-tolerant in orange). ART transform was applied to water depth and occupancy for
588 statistical test.

589 **Fig. 3** Substantial decrease in elevation (**a**) and increase in hydroperiod (**b**) from vegetated and
590 dieback zones to ponded zones ('pond substrate' in **a** for differentiation from other treatments in
591 pond). Values in panel (**a)** are means ± SE (n=10). Elevated and control pond transplant treatments
592 reflected elevation loss from dieback zones, though a ~10 cm bias was introduced (datum:
593 NAVD88).

594 **Fig. 4** Soil strength (20 cm depth in **a**, 50 cm depth in **b**) and redox potential were higher in Farm
595 Creek Marsh than in Deal Island. In Farm Creek Marsh (upper panels), neighbor patches had
596 stronger and more oxidized soils than dieback zones. No significant zone differences in soil
597 strength were observed in Deal Island (lower panels). ART transform was applied to soil redox
598 potential for statistical test. Values are means ± SE (n=6 for *Juncus* patch, n=10 for other
599 treatments).

600 **Fig. 5.** Elevated substrate and neighbor removal treatment significantly improved transplant
601 performance compared to elevation control and neighbor control treatments. Transplants in the
602 dieback zone performed similarly to those under neighbor removal. The relative increase in shoot
603 number was calculated as the proportional change between 2019 and 2021 for each transplant. In
604 panel (a) and (b), values are means ± SE (n= for *Juncus* patch, n=10 for other treatments).



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606 Fig. 1

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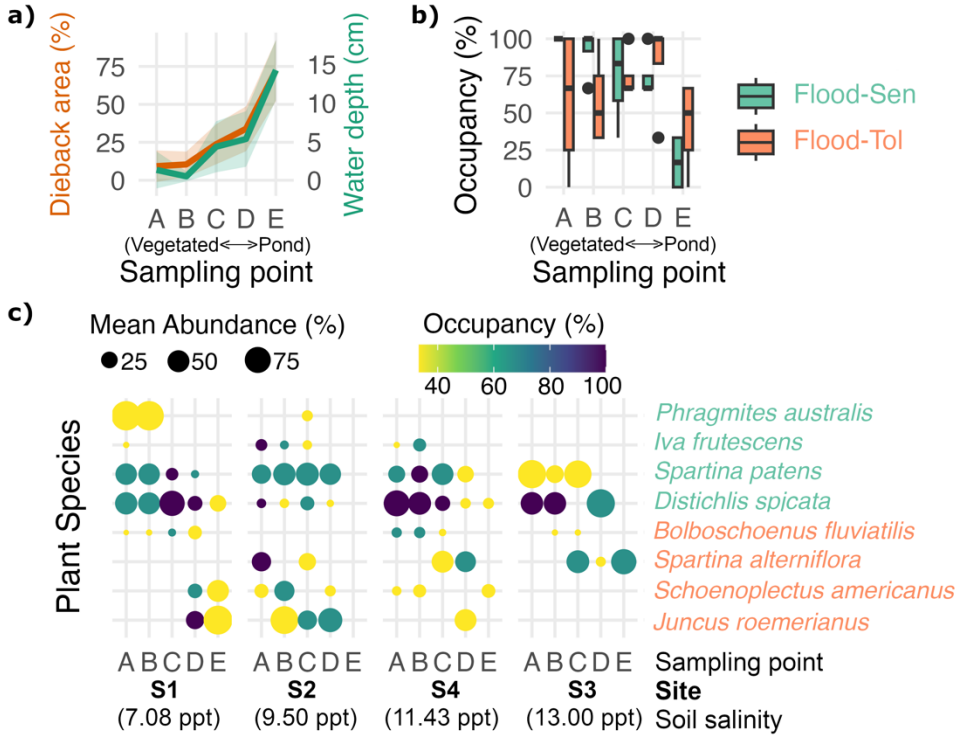

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610 Fig. 2

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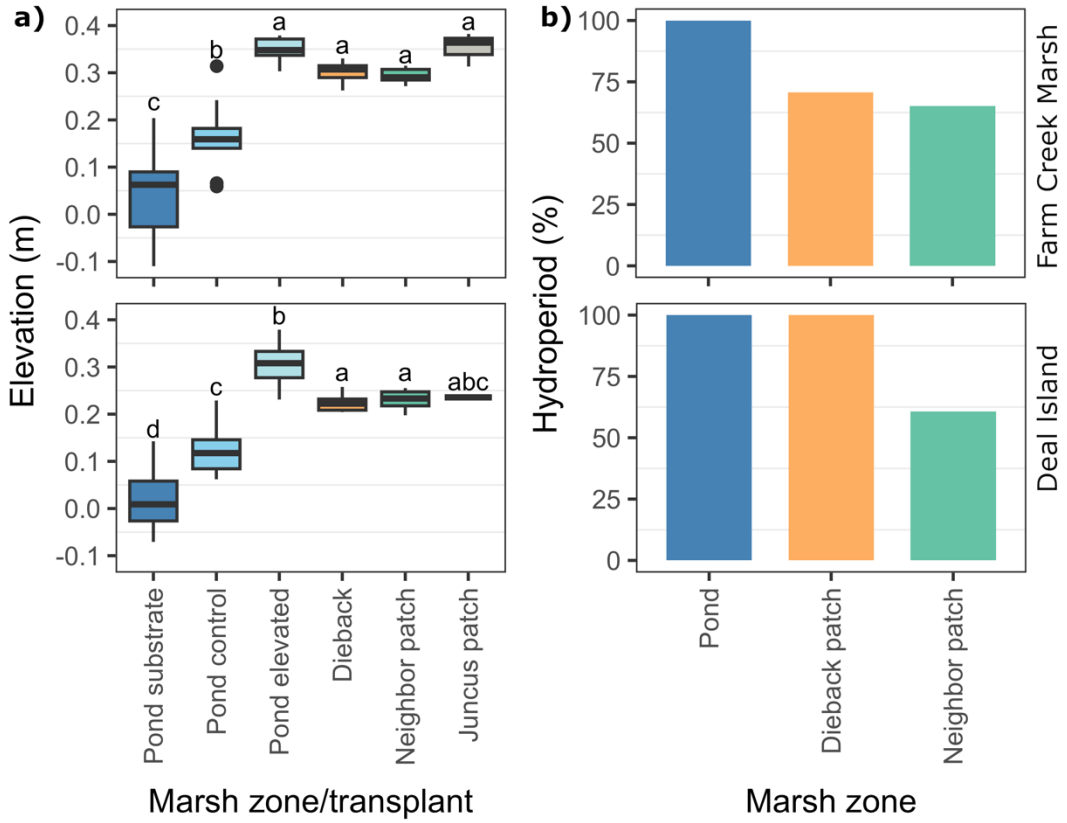

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614 Fig. 3

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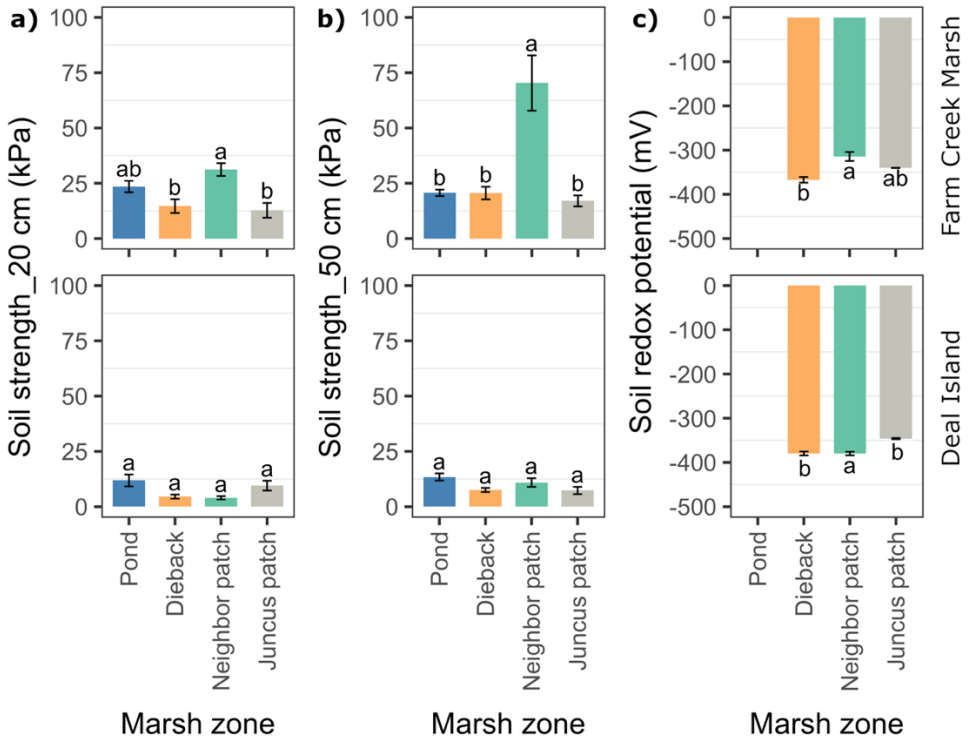

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617 Fig. 4

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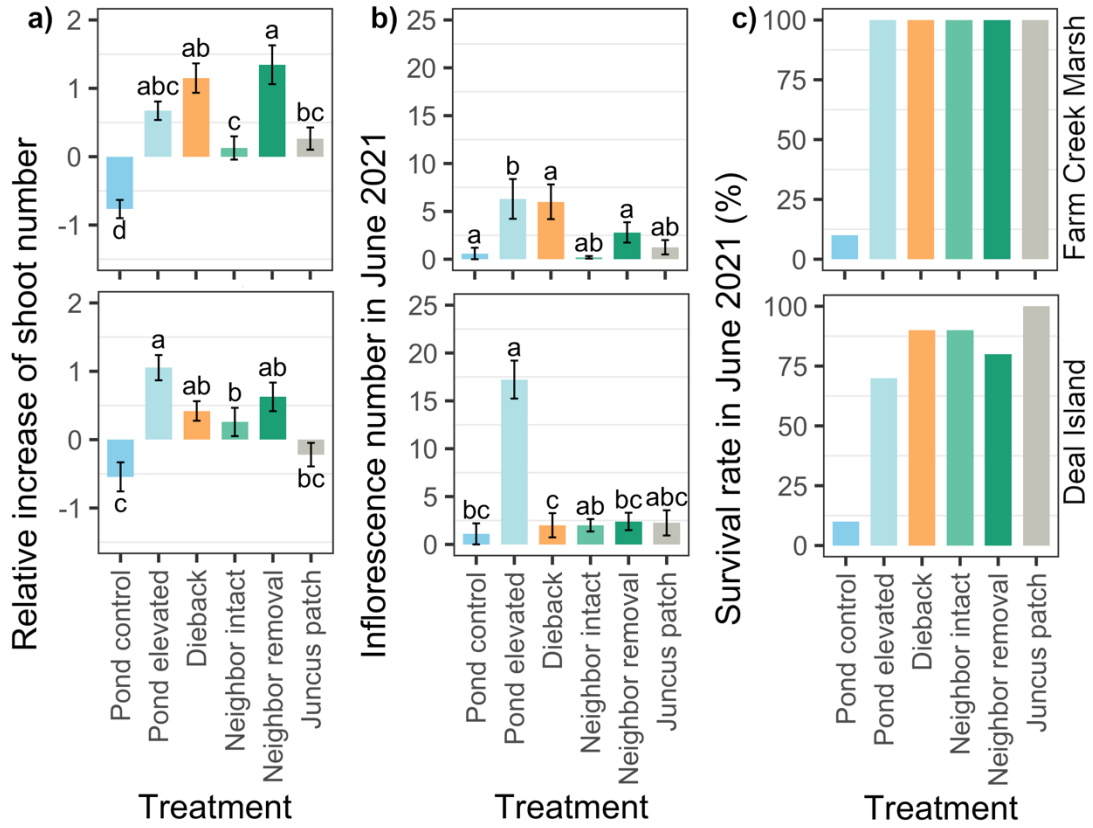

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621 Fig. 5

Recruitment bottlenecks and reinforcing environmental degradation drive marsh collapse

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Appendix S1

Supplemanrty methodology for 'pond-elevated' treatment

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 Deal Island and 30.25 ± 10.23 cm at Farm Creek Marsh. To elevate the substrate, transplants were placed in flowerpots with holes at the bottom and filled with in-situ marsh peat substrate. Additional pots also filled with in-situ marsh peat substrate were used beneath them to elevate the substrate. PVC pipes (2 cm diameter) were driven into the substrate to stabilize the structure.

Supplemanrty methodology for physical and chemical conditions measurement

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) and reported as parts per thousand (ppt). In June 2019, transplanting waypoints spanning across all marsh zones of Farm Creek Marsh and Deal Island were randomly selected for porewater salinity measurement. Since 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.

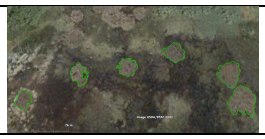
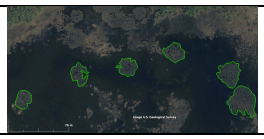
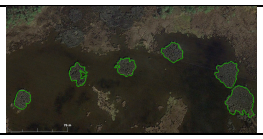
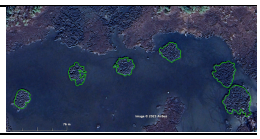
Elevation

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.

Hydrological stress

One well was installed in each marsh zone (vegetated, dieback, and pond) at each marsh platform. 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).

Table S1 *Juncus roemerianus* vegetation patches (outlined in green) are stable in deteriorated interior marshes of Deal Island and persist for over a decade after the dieback of neighboring marsh plant species. The dominant neighboring marsh plant species is *Schoenoplectus americanus* for both sites, accompanied by *Spartina patens* and *Distichlis spicata*.

Location \ Date	06/08/2005	03/01/2007	10/20/2013	11/04/2023
Site 1 (38°11'52.55"~ 38°11'58.22" N, 75° 50'12.47"~ 75°50'03.45" W)				
Site 2 (38°13'11.59"~ 38°13'16.89' N', 75°48'43.32"~ 75°48'27.66" W)				

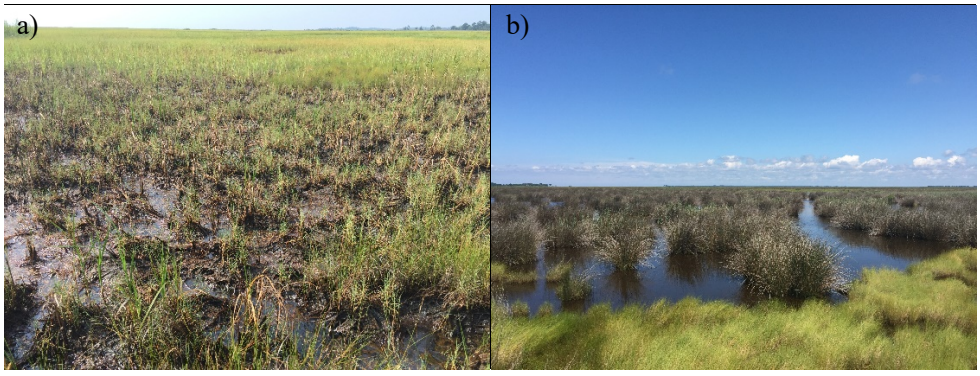


Fig. S1 Dieback of *S. patens* and *D. spicata* before being displaced by more flood tolerant species, such as *S. americanus* (a) or *J. roemerianus* (b) in interior marsh of Deal Island. Photo credit: Man Qi.

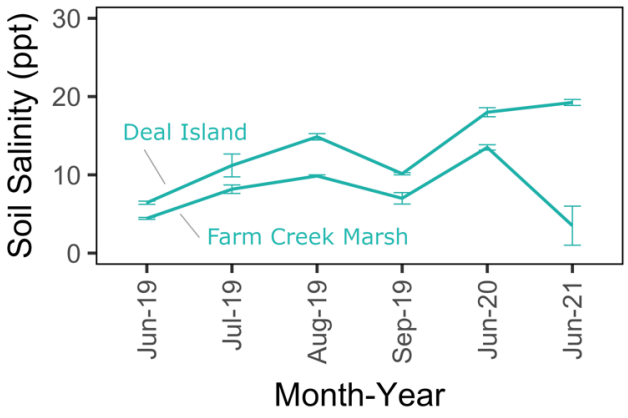


Fig. S2 Deal Island (*Spartina alterniflora* dominant) had higher soil salinity than Farm Creek Marsh (*Schoenoplectus americanus* dominant).

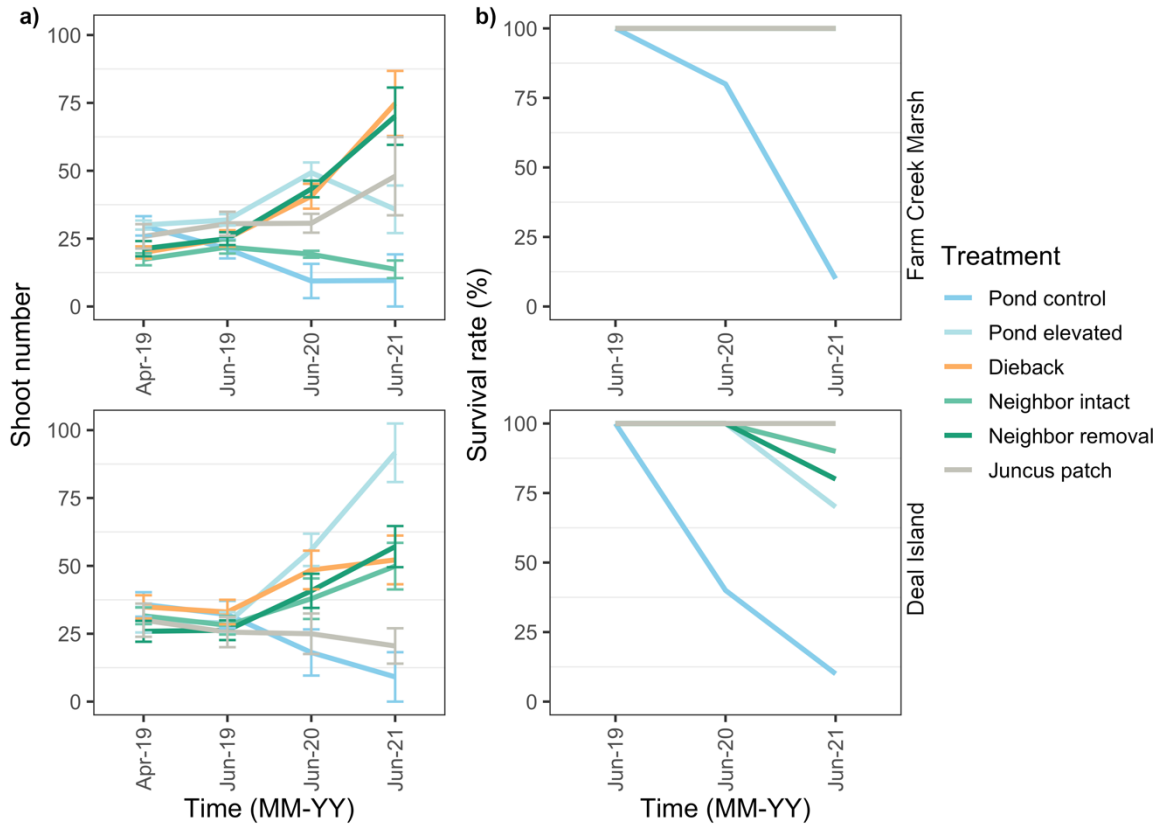


Fig. S3 Temporal change of shoot number and survival rate of Juncus transplants from the beginning (April 2019) to the end of the experiment (June 2021).

Table S2 Summary of statistical test and data transform (log transformation or ART) made for response variables to meet the assumptions. Degrees of freedom (DF), F-values, and associated *p*-values are reported. Significance levels are denoted as follows: $p > 0.05$ (ns), $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***).

Response Variable	Transform	Statistic test	Factor	DF	F-value	p-value	Significance
Water depth	ART	Two-way ANOVA	Site	3, 40	4.07	0.0130	*
			Point	4, 40	10.36	7.44E-06	***
			Site × Point	12, 40	2.48	0.0155	*
Dieback area	Log	Two-way ANOVA	Site	3, 40	1.47	0.2383	ns
			Point	4, 40	9.41	1.86E-05	***
			Site × Point	12, 40	1.27	0.2712	ns
Occupancy	None	LMM	Flood class	1, 40	0.92	0.35	ns
			Point	4, 40	4.90	4.20E-03	*
			Flood class× Point	4, 40	2.11	0.11	ns
Elevation	None	LMM (outlier detected)	Site	1, 70	19.88	2.22E-06	***
			Treatment	5, 79	149.27	2.22E-16	***
			Site × Treatment	5, 79	1.21	0.96	ns
Soil strength at 20 cm	None	Nested ANOVA	Site	1, 59	74.69	8.93E-12	***
			Site: Zone	6, 59	6.51	2.59E-05	***
Soil strength at 50 cm (kPa)	Log	Nested ANOVA	Site	1, 126	85.24	8.06E-16	***
			Site: Zone	6, 126	6.92	2.25E-06	***

Soil salinity	None	LMM (normality failed)	Site	1, 106	90.61	6.59E-16	***
Shoot_GR	None	Nested ANOVA	Site Site: Treatment	1, 95 10, 95	1.92 12.60	0.169 1.13E-13	ns ***
Inflorescence number	ART	Two-way ANOVA	Site Treatment Site × Treatment	1, 95 5, 95 5, 95	7.49 18.14 8.78	0.0074 1.34E-12 7.12E-07	** *** ***

Table S3 Back-of-the-envelope estimates of the lateral expansion rate required for *Juncus roemerianus* to occupy adjacent open-water areas within 10 years. For each site, we estimated the maximum distance from the nearest existing *Juncus* patch to the farthest point in the surrounding water area. Required dispersal speed was calculated as this distance divided by 10 years, assuming that lateral expansion distance was approximately constant from year to year. Realized dispersal speed was estimated from transplant growth in dieback areas. Realized dispersal speed was estimated from the increase in shoot number of transplants established in dieback areas. Assuming patch area scales with shoot number, we observed a threefold increase in shoot number over two years for transplants in dieback zones, which corresponds to an annual lateral expansion of approximately 0.064 m/yr. This calculation is intended as an order-of-magnitude estimate rather than a mechanistic prediction.

Features / Location	Juncus area (m^2)	Water area (m^2)	Total perimeter of Juncus patches (m)	Required dispersal speed (m/yr)	Realized dispersal speed (m/yr)
Site 1	12146	17290	1095	14	0.064
Site 2	3413	42369	673	9	0.064

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Qi, M., and K. Gedan. 2025. Tidal Attenuation and Poor Drainage Make Interior Microtidal Marshes Vulnerable to Sea Level Rise. Geophysical Research Letters **52**:e2025GL118637.