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Variance reflects resilience to disturbance along a stress gradient: Experimental evidence from coastal marshes

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Abstract

Quantifying ecosystem resilience to disturbance is important for understanding the effects of disturbances on ecosystems, especially in an era of rapid global change. However, there are few studies that have used standardized experimental disturbances to compare resilience patterns across abiotic gradients in real-world ecosystems. Theoretical studies have suggested that increased return times are associated with increasing variance during recovery from disturbance. However, this notion has rarely been explicitly tested in field, in part due to the challenges involved in obtaining long-term experimental data. In this study, we examined resilience to disturbance of 12 coastal marsh sites (five low-salinity and seven polyhaline [=salt] marshes) along a salinity gradient in Georgia, USA. We found that recovery times after experimental disturbance ranged from 7 to >127 months, and differed among response variables (vegetation height, cover and composition). Recovery rates decreased along the stress gradient of increasing salinity, presumably due to stress reducing plant vigor, but only when low-salinity and polyhaline sites were analyzed separately, indicating a strong role for traits of dominant plant species. The coefficient of variation of vegetation cover and height in control plots did not vary with salinity. In disturbed plots, however, the coefficient of variation (CV) was consistently elevated during the recovery period and increased with salinity. Moreover, higher CV values during recovery were correlated with slower recovery rates. Our results deepen our understanding of resilience to disturbance in natural ecosystems, and point to novel ways that variance can be used either to infer recent disturbance, or, if measured in areas with a known disturbance history, to predict recovery patterns.

KEYWORDS
disturbance, recovery rate, resilience, salinity gradient, tidal marshes, variance

INTRODUCTION

We are experiencing an increasing number of perturbations in an era of rapid global change (Burton et al., 2020; Nguyen & Liou, 2019), and the disturbances resulting from perturbations can affect the structural (Buma, 2015), compositional (Bowd et al., 2018), and functional (Brown & Zinnert, 2020) properties of ecosystems. It has been suggested that recovery time of an ecosystem after a disturbance tends to lengthen as the level of stress to the

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ecosystem increases (Dakos & Bascompte, 2014; Drake & Griffen, 2010). It is therefore instructive to quantify how ecosystem resilience (defined here as the rate of recovery from disturbance [Holling, 1996; Pimm, 1984; Zampieri, 2021]) varies along stress gradients. Several studies have evaluated this idea using observational or modeling approaches. For example, Dodson and Root (2013) found that conifer regeneration following stand-replacing fires was faster at cool, wet sites than at warm, dry ones. Capdevila et al. (2019) showed through projection models that recovery time of a macroalga population after a disturbance significantly increased in warmer scenarios. However, studies that experimentally examine recovery rates of real-world ecosystems along stress gradients remain scarce (Jones et al., 2021; van Belzen et al., 2017). As one example, Schäfer et al. (2019) examined resilience to a severe experimental disturbance of agricultural grasslands across a gradient of land use intensity, and found that resilience decreased with land use intensity. In this study, we present the results of a manipulative experiment in which we tracked long-term recovery from a severe, standardized experiment across an abiotic stress gradient based on multiple response variables.

We created experimental disturbances in 12 tidal marshes that spanned the salinity range from fresh to salt on the coast of Georgia, USA, and measured recovery of vegetation cover, height, and composition in experimentally disturbed plots (compared with control plots) for up to 11 years. We focused on salinity because it is a major structuring agent for intertidal marsh communities (Craft et al., 2009; Wieski et al., 2010) and represents a gradient of increasing abiotic stress (Crain et al., 2004; Guo & Pennings, 2012). Salinity tolerance varies among wetland plant species, with low-salinity areas dominated by strong competitors that are not salt tolerant, and high-salinity areas dominated by salt-tolerant species that are poor competitors (Crain et al., 2004; Guo & Pennings, 2012). We hypothesized that (1) different vegetation types would have differing recovery rates following disturbance, due to intrinsic differences in the growth strategies of different plant species, and (2) recovery rates within a vegetation type would decrease with increasing salinity, because salinity represents a stress that reduces growth.

Our experimental design, using a manipulative experiment rather than observations, allowed us to document patterns in variance that resulted from a known and consistent disturbance, and to rigorously assess the relationship between recovery rate and variance along the salinity gradient. The relationship between recovery and variance is germane to the phenomenon of critical slowing down, which is based on mathematical demonstrations that ecosystems approaching a transition exhibit slowed recovery from pulse disturbances (Patterson et al., 2021; Scheffer et al., 2015; van de Leemput et al., 2018). Differences in return time can be used to indicate increased sensitivity or to explore variation in resilience among systems (Scheffer et al., 2009; van Nes & Scheffer, 2007). For example, Senf and Seidl (2022) used remotely sensed information on canopy disturbance and recovery intervals to map the resilience of Europe's forests. It has also been suggested that increases in variance can indicate that a threshold is approaching (Dakos et al., 2015; Scheffer et al., 2009; Weinans et al., 2021). Implicit in these ideas is the notion that variance increases during recovery from disturbance. In the context of the study presented here, we estimated the within-site variance of the vegetation characteristics in experimental plots during years when they were recovering from disturbance. We hypothesized that (3) disturbed plots would have increased variance during the recovery period as compared to both postrecovery and control plots; and (4) variance in disturbed plots during the recovery period would reflect patterns in recovery rates, making it a more robust indicator of resilience to disturbance along the underlying salinity gradient than the variance of control plots.

METHODS

Study sites

We studied 12 tidal marshes on the coast of Georgia, USA (Appendix S1: Figure S1). These marshes included 10 permanent study sites (GCE1-GCE10) of the Georgia Coastal Ecosystems Long Term Ecological Research Program (GCE-LTER), and two additional sites (Sites A and B). The sites included two tidal freshwater marshes, dominated by *Zizaniopsis miliacea*, three brackish marshes, dominated by *Juncus roemerianus*, and seven salt marshes, dominated by *Spartina alterniflora* (Table 1; Appendix S1: Table S1), all of which are typical of southeastern US marshes.

We located eight experimental plots parallel to but >10 m away from the creekbank on the marsh platform in each tidal marsh. We measured soil pore water salinity of the plots at the end of each growing season (October) during the course of the study, using the rehydration method (Pennings & Richards, 1998) to characterize the sites with respect to soil pore water salinity. Although these data do not characterize temporal variation in pore water salinity, they do suffice to describe major spatial trends in salinity; values ranged from ~1 at the tidal freshwater sites to >50 at the saltiest salt marsh site (Table 1). Average plant height (across all plant species) decreased as salinity increased, providing evidence of the

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TABLE 1 Attributes of the study sites, including designations of marsh community type and salinity zone.

Site	Soil pore water salinity (PSU)	Marsh community type	Salinity zone	Vegetation cover (%)	Dominant plant species (percentage cover)
Site A	1.1	Freshwater marsh	Low salinity	99.9	*Zizaniopsis miliacea* (82%)
GCE7	1.6	Freshwater marsh	Low salinity	99.1	*Zizaniopsis miliacea* (81%)
GCE8	11.8	Brackish marsh	Low salinity	96.2	*Juncus roemerianus* (83%)
Site B	13.9	Brackish marsh	Low salinity	99.4	*Juncus roemerianus* (56%) and *Spartina cynosuroides* (25%)
GCE1	19.7	Brackish marsh	Low salinity	99.4	*Juncus roemerianus* (85%)
GCE9	25.5	Salt marsh	Polyhaline	96.0	*Spartina alterniflora* (100%)
GCE10	29.3	Salt marsh	Polyhaline	94.7	*Spartina alterniflora* (100%)
GCE4	32.3	Salt marsh	Polyhaline	94.9	*Spartina alterniflora* (100%)
GCE5	36.6	Salt marsh	Polyhaline	93.5	*Spartina alterniflora* (100%)
GCE6	38.9	Salt marsh	Polyhaline	90.0	*Spartina alterniflora* (100%)
GCE2	43.9	Salt marsh	Polyhaline	92.9	*Spartina alterniflora* (100%)
GCE3	50.0	Salt marsh	Polyhaline	98.0	*Spartina alterniflora* (75%) *Sarcocornia* spp. (15%)

Note: Sites are listed in order of soil pore water salinity. Salinity and vegetation cover values are averages observed in control plots at each marsh site over the course of the study. Further information on plant community composition can be found in Appendix S1: Table S1.

underlying stress gradient (Appendix S1: Figure S2). Because replication of freshwater and brackish marshes was limited, we grouped them into "low-salinity" sites for comparison with the seven salt ("polyhaline") marshes. We recognize that some of the patterns we observe within the low-salinity group may be the result of changes in community type (see *Discussion*).

Field experiment

In each tidal marsh, we assigned alternate 3 × 3 m plots to disturbed (four plots) and control (four plots) treatments, with treatments fully interspersed such that each disturbed plot could be assigned a paired control plot. The vegetation in the disturbed and paired control plots was visually similar prior to the disturbance treatment. In the disturbed plots, we removed aboveground vegetation to the soil surface by applying a systemic herbicide (glyphosate) in August 2006, and clipping new shoots that grew into the plots several times a year into October of 2009. Early in March 2010 we clipped new shoots one more time, using a gasoline powered handheld trimmer (similar to disturbance treatments applied in Jones et al., 2021; Slocum & Mendelssohn, 2008; van Belzen et al., 2017). We did not observe any evidence of natural disturbance in the control plots during this study. Our goal was to create a severe disturbance (little or no surviving belowground biomass) that was standardized across the landscape. Disturbances of this size occur in all types of tidal marshes, although most commonly in salt marshes, and are often created by wrack-floating dead vegetation that smothers underlying plants (Li & Pennings, 2016; Pennings & Richards, 1998). For example, Lynn et al. (2023) observed between 15 and 214 wrack patches in an 18-ha Georgia salt marsh over the course of 2 years, with an average size of 6 m^2 (87% were smaller than 10 m^2).

Within each 3 × 3 m plot, we established two subplots (1 × 1 m, 0.5 m from the edge of the plot in diagonally opposite corners) for vegetation measurements. We averaged the vegetation measurements from these two subplots to yield four replicates for the disturbance treatment and four replicates for the control treatment in each tidal marsh. We monitored the vegetation in each tidal marsh at the end of each growing season (October) from 2010 to 2020. In each subplot, we centered a 0.5 × 0.5 m quadrat with 100 cells and measured vegetation cover by counting the total number of cells occupied by vegetation, and plant community composition by noting the presence or absence of each plant species within each cell and expressing each species as a percentage of cells occupied. We also measured the height of four plants (regardless of species) haphazardly chosen within each subplot. For most of the study sites, the vegetation survey was stopped in October 2014 when the disturbed plots in those study sites had completed recovery (as described below) in all three metrics (vegetation cover, vegetation height and community composition). The vegetation survey at site B was stopped in October 2017, when this site

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completed recovery; the vegetation survey at GCE1 was stopped in October 2020, at which time this site had only partially recovered.

Recovery rates

We evaluated the recovery status of the disturbed plots using three metrics: vegetation cover, vegetation height, and community composition. For each sampling date, we estimated recovery proportion in vegetation cover or height for each tidal marsh by comparing the mean of these metrics in the disturbed plots with the mean of those in the control plots. If the mean in the disturbed plots was within the 95% confidence interval around the mean of that observed in the control plots, we considered the disturbed plots in that tidal marsh to have completed recovery in vegetation cover or height on that date (as in Slocum & Mendelssohn, 2008).

To quantify compositional recovery of the disturbed plots, we calculated Bray–Curtis similarity (1 − Bray–Curtis dissimilarity) between each disturbed plot and its paired control plot based on plant community composition data. Bray–Curtis similarity ranges from 0 to 1, thus we took this index as representing the proportion of compositional recovery of a disturbed plot versus the paired control plot. As the similarity between control plots was rarely exactly 1 (although often close to 1), complete recovery should not be measured by returning to a similarity of 1. For each sampling date, we estimated the recovery proportion in community composition for each tidal marsh using the mean of Bray–Curtis similarities between the disturbed and the paired control plots. If the mean of Bray–Curtis similarities between the disturbed and the paired control plots was within the 95% confidence interval of the average similarity among control plots, we considered that the disturbed plots in that tidal marsh had completed recovery in plant community composition on that date (as in Hillebrand & Kunze, 2020).

We determined recovery time (in months) for each metric (vegetation cover, vegetation height and community composition), and then calculated recovery rates using the formula "relative recovery rate = 1/recovery time in months." For GCE1, which had not completely recovered, the recovery rate was calculated using the formula "relative recovery rate = recovery proportion in 2020/recovery time in months (127 months, from March 2010 to October 2020)". We used these results to examine recovery rates of different vegetation metrics among tidal marsh sites. To test the hypothesis that relative recovery rates would decrease with increasing salinity, we performed linear correlation analyses of recovery rates versus soil pore water salinity.

Variance

We calculated the coefficient of variation (CV) of control plots based on the within-year average and standard deviation of either vegetation cover or height among the four control plots in each tidal marsh from 2010 to 2014, and then averaged across the time period (Appendix S1: Table S3). To test whether variance was elevated during recovery from disturbance, we calculated the within-year CVs as described above using data from disturbed plots. Data on recovery times were used to separate observations in disturbed plots into "during" recovery and "post" recovery (= recovered), and within-year CVs were averaged across the appropriate number of years for both vegetation cover and height for each marsh site. Although this meant that the number of years included in "During" and "Post" observations varied by sites (Appendix S1: Table S3), examination of the data consistently indicated high variability among plots within individual "During" years (Appendix S1: Figures S4 and S5). We used two-way ANOVA without replication, with plot status (Control, During, or Post) and site as the two factors, to compare within-year CVs of plots within each salinity zone.

To test whether variance of plots was related to salinity, within-year CVs of both vegetation cover and height for control plots and during the recovery period in disturbed plots in each tidal marsh, calculated as described above, were plotted against soil pore water salinity, and analyzed by linear correlation within each salinity zone. To further examine the relationship between recovery rates and within-year CVs during recovery period in disturbed plots, recovery rates for both vegetation cover and height of disturbed plots were plotted against the corresponding within-year CVs for each metric during recovery period in each tidal marsh, and analyzed by linear correlation within each salinity zone.

Data of recovery rates and CVs were Log_{10}-transformed to meet the assumption of normality of residuals and homogeneity of variances in the correlation analyses and ANOVAs. All data analyses were performed with SPSS Statistics 21 (IBM, USA). The data that support the findings of this study are publicly available online (Pennings, 2022).

RESULTS

Hypothesis 1, that different vegetation types would have different recovery rates, was supported by our results (Figure 1). Moreover, different vegetation metrics provided different insights into recovery. At the salt marsh sites, the three metrics (vegetation cover, height and composition)

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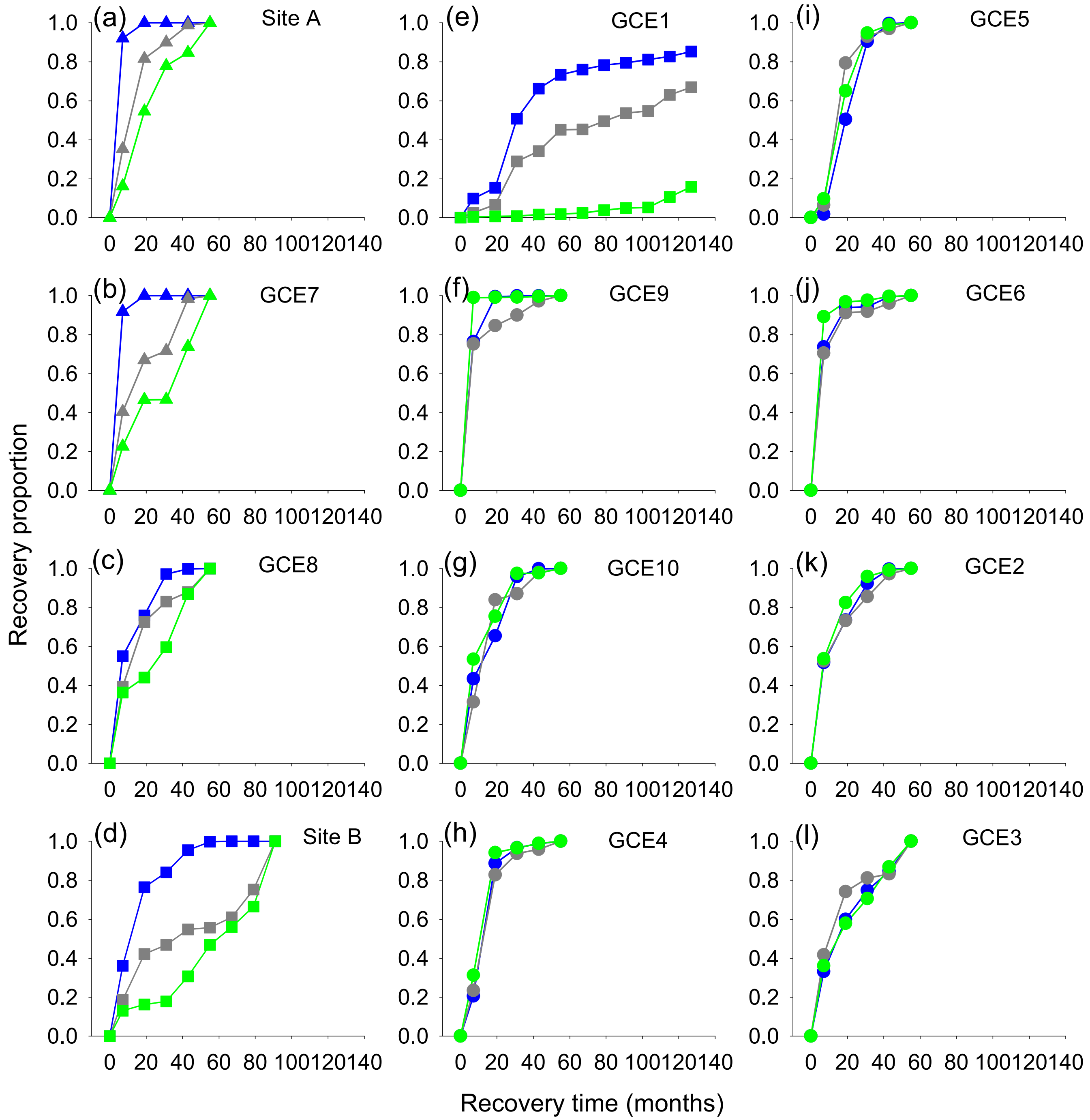

FIGURE 1 Temporal dynamics of recovery proportion for vegetation cover (blue color), vegetation height (gray color) and community composition (green color) for the 12 tidal marshes. Triangle, square and circle symbols represent freshwater, brackish and salt marshes, respectively. Sites are plotted in order of soil pore water salinity (Table 1).

had roughly similar recovery rates (Appendix S1: Table S2). At the freshwater and brackish sites, however, vegetation cover recovered first, followed by vegetation height, and last by community composition (Figure 1). Although there was overlap in recovery rates, the salt marsh sites generally recovered fastest, regardless of metric, with recovery often complete in as few as 7 months, and rarely more than 43 months (Appendix S1: Table S2). The two freshwater sites recovered quickly in terms of vegetation cover (19 months), whereas vegetation height and community composition took between 43 and 55 months. The three brackish marsh sites were the slowest to recover, with one site (GCE1) not recovering for any metric after 127 months.

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Recovery rates decreased with increased salinity in most cases, when low-salinity marshes and salt marshes were analyzed separately, which generally supported Hypothesis 2. In the five low-salinity marshes, the recovery rates for vegetation cover and height decreased as soil pore water salinity increased, with a similar but nonsignificant pattern for community composition (Figure 2). In the seven salt marshes, the recovery rates for vegetation cover and community composition decreased as soil pore water salinity increased (Figure 2a,c), but recovery of vegetation height was not related to salinity (Figure 2b). When all 12 tidal marshes were analyzed together, however, we found no significant correlations between any of the relative recovery rates (vegetation cover, vegetation height or community composition) and soil pore water salinity (Appendix S1: Figure S3).

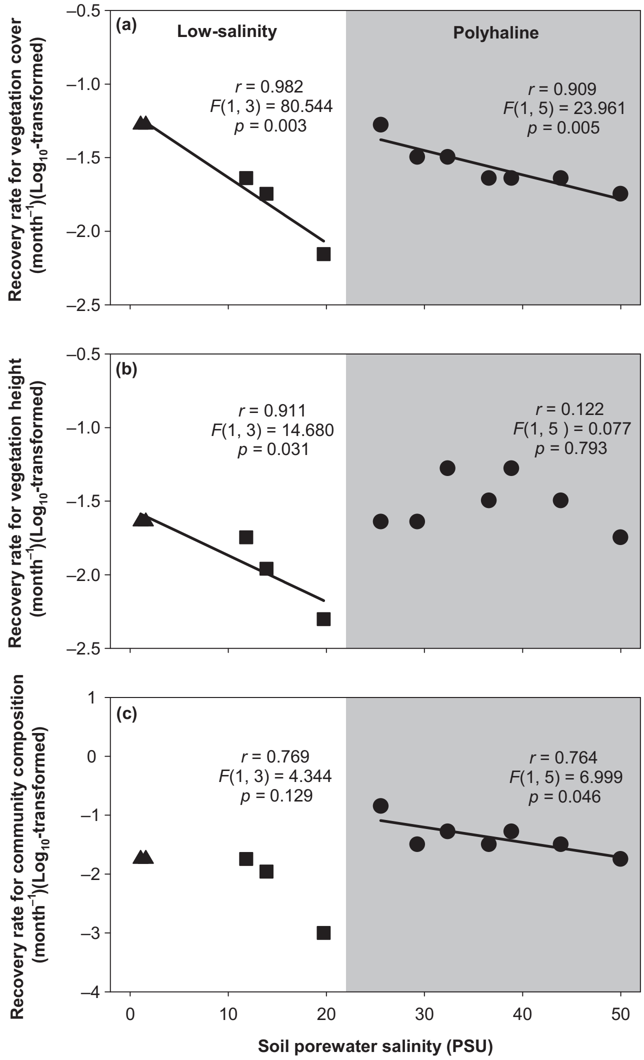

FIGURE 2 Relationships of recovery rates (Log_{10}-transformed) for (a) vegetation cover, (b) vegetation height and (c) community composition versus soil pore water salinity for the tidal marshes. Linear correlations were performed for low-salinity sites (unshaded) and polyhaline sites (shaded) separately. Triangle, square and circle symbols indicate freshwater, brackish and salt marshes, respectively. For each correlation, the *r*, F ($df_{correlation}$, $df_{residual}$) and *p*-value are shown. Solid lines indicate significant correlations ($p < 0.05$).

Disturbed plots had increased variance during the recovery period, which supported Hypothesis 3. At almost every site, the CV of both vegetation cover and height observed in disturbed plots during the years they were recovering from disturbance was substantially elevated above the comparable CV for plots during the years after the plots had recovered, or in control plots (Appendix S1: Table S3). When grouped into low-salinity and salt marsh sites, the average CVs of both vegetation cover and height were significantly higher during recovery than the average CVs observed in either control or recovered plots (Figure 3; Appendix S1: Figures S4 and S5).

Variance during recovery reflected patterns in recovery rates in most cases, which generally supported Hypothesis 4. Not only were CVs elevated during recovery (as described above), they were also related to soil pore water salinity. In both low-salinity and salt marshes, the CVs of vegetation cover averaged over the years during which each site was recovering increased significantly as soil pore water salinity increased, but not in control plots (Figure 4a,c). The CVs of vegetation height during recovery also increased significantly as soil pore water salinity increased in the low-salinity sites, with a similar but nonsignificant pattern at the salt marsh sites, and again there were no relationships in control plots (Figure 4b,d). Finally, recovery rates for vegetation cover and height in disturbed plots were related to the CVs during recovery in a similar manner to that described for soil pore water salinity. For vegetation cover, there were significant correlations within both salinity zones (Figure 5a,c), with decreased recovery rates at sites with higher CVs. For vegetation height, there was a significant negative correlation between recovery rate and CV at the low-salinity sites, but not at the salt marsh sites (Figure 5b,d).

DISCUSSION

This study presents experimental evidence that resilience to disturbance varies predictably along a salinity (stress) gradient in tidal marshes within both the low-salinity and polyhaline salinity zones (Figure 2), although the same relationship did not hold across all vegetation types if both salinity zones were pooled. Moreover, we found that variance not only increased during recovery from a

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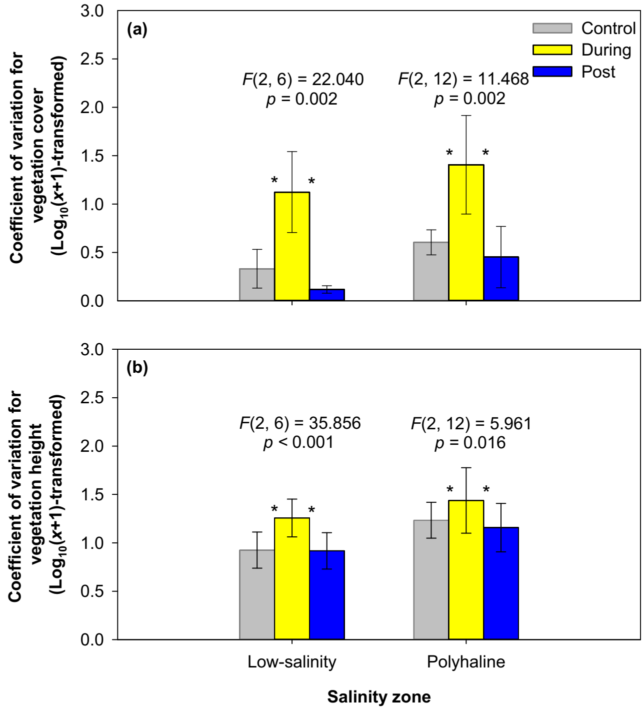

FIGURE 3 Coefficient of variation ($Log_{10}(x + 1)$-transformed) for (a) vegetation cover and (b) vegetation height in the control plots (gray color) and in the periods of during recovery (yellow color) and postrecovery (blue color) in the disturbed plots of the tidal marsh sites in the low-salinity and polyhaline salinity zones. Data are means ± SD. The F ($df_{plot\ status}$, $df_{residual}$) and p-values of two-way ANOVAs without replication are shown above bars, the asterisks indicate significant differences (paired t-tests, $p < 0.05$) between during recovery and control plots ($p_{cover,\ low\text{-}salinity} = 0.019$, $p_{cover,\ polyhaline} = 0.004$, $p_{height,\ low\text{-}salinity} = 0.010$, $p_{height,\ polyhaline} = 0.038$), or between during and postrecovery plots ($p_{cover,\ low\text{-}salinity} = 0.014$, $p_{cover,\ polyhaline} = 0.018$, $p_{height,\ low\text{-}salinity} = 0.008$, $p_{height,\ polyhaline} = 0.046$). GCE1 was not included in the ANOVAs and paired t-tests, as this site had no coefficient of variation data for the poststatus.

known disturbance (Figure 3), but that variance during recovery was also better related to salinity than the variance of control plots (Figure 4). Finally, variance during recovery was correlated with recovery rate (Figure 4). These results confirm our initial hypotheses about the factors affecting the resilience of these communities, and more generally suggest that variance can provide insight into past disturbance and recovery.

We found that vegetation cover, height and composition had differing recovery rates after a disturbance, with several-fold variation in magnitude. In low-salinity marshes vegetation cover recovered relatively rapidly, followed by height and eventually composition. This pattern might be due to the presence of many pioneer plants (Wieski et al., 2010), which were short in stature and eventually excluded by the dominant, taller species. In salt marshes, which were dominated by *S. alterniflora*, there usually was no compositional change during secondary succession: *S. alterniflora* simply re-invaded the plots and all three metrics recovered in parallel.

Recovery rates for most parameters decreased with increasing salinity within each salinity zone. The mechanism for this is straightforward, as coastal marsh plants are stressed by high salinities (Guo & Pennings, 2012; Howard & Mendelssohn, 1999; Li & Pennings, 2019) and do not grow as quickly when stressed. The fact that these relationships did not hold across salinity zones, however, is likely to have been due to the underlying shift in the autecology of the dominant plants, with *Spartina* recovering quickly and *Juncus* slowly. In the salt marshes, the recovery rates of both vegetation cover and community composition decreased with increased salinity, as expected. It is not clear why recovery of vegetation height was not related to salinity, which underscores the importance of measuring multiple variables when documenting ecosystem recovery (Hillebrand & Kunze, 2020; Quinlan et al., 2016; Roberts et al., 2019). Although recovery rates for vegetation cover and height were related to salinity in the low-salinity sites, we note that these patterns might be potentially affected by changes in community composition within the low-salinity group, and could have been confounded by inherent variation in recovery rates among plant species (Mirabel et al., 2020; Thorn et al., 2020; Xu et al., 2017). We did not have enough replicates within the low-salinity group to divide these sites into further groups, but this is an important caveat to the results from the low-salinity sites. These patterns would benefit from further study with increased replication within freshwater and brackish marshes.

We did not set out to formally identify thresholds or evaluate potential alternative states along the salinity gradient, as our interest was in examining patterns of resilience to disturbance at sites that were typical of the various marsh types, and none of our sites were in transitional areas. This is in contrast with previous studies in salt marshes that have examined transitions between vegetated marsh and mud flats along elevation gradients (Jones et al., 2021; Slocum & Mendelssohn, 2008; van Belzen et al., 2017). However, the marsh types that we studied naturally occur as near monocultures with abrupt transitions between them, maintained by competition and salt stress (Guo & Pennings, 2012), and it is predicted that they will shift upstream in response to salt water intrusion as the result of sea level rise, with freshwater marsh converting to brackish and brackish marsh converting to salt marsh (Craft et al., 2009; Li & Pennings, 2019; Solohin et al., 2020). The most saline of the low-salinity sites (GCE1), which is a brackish

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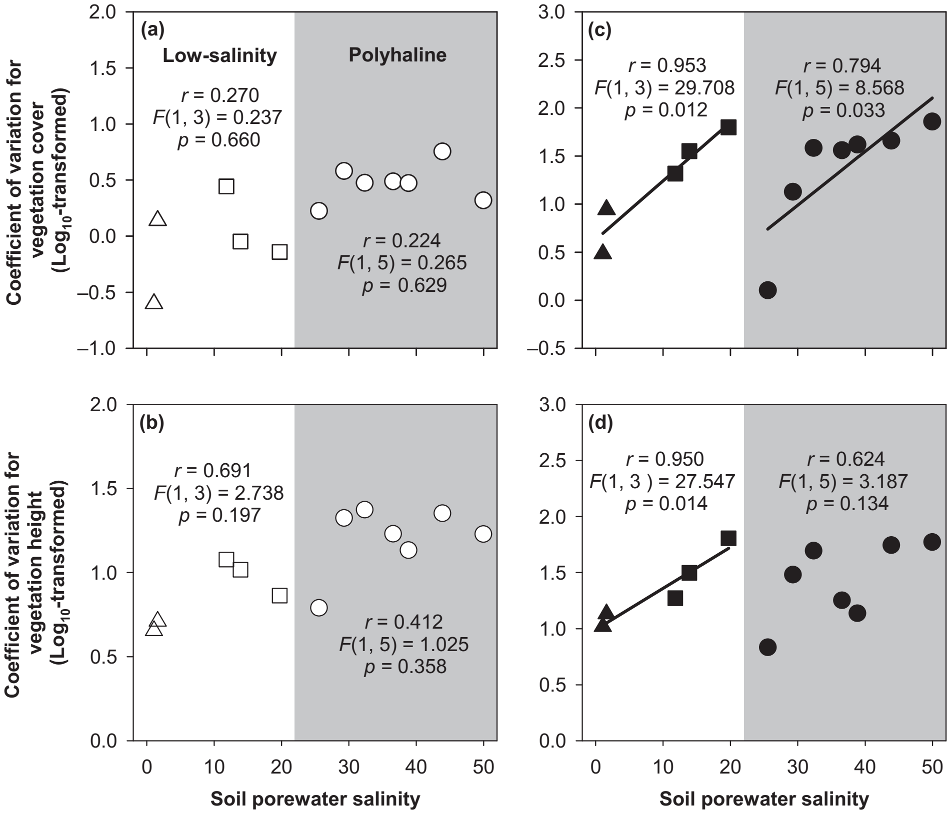

FIGURE 4 Relationships of the average coefficient of variation (Log_{10}-transformed) for (a) vegetation cover and (b) vegetation height in the control plots, and for (c) vegetation cover and (d) vegetation height during the recovery period in the disturbed plots versus soil pore water salinity for the tidal marshes in low-salinity (unshaded) and polyhaline salinity (shaded) zones. Linear correlations were performed for low-salinity sites and polyhaline sites separately. Triangle, square and circle symbols represent freshwater, brackish and salt marshes, respectively. For each correlation, the r, F ($df_{correlation}$, $df_{residual}$) and p-value are shown. Solid lines indicate significant correlations ($p < 0.05$).

marsh dominated by *J. roemerianus*, provides some insight into this transition. The disturbed plots at this site were largely dominated, after 11 years, by the relatively salt-tolerant *S. alterniflora*, with little recovery of the site dominant plant *J. roemerianus*. This again illustrates the value of using multiple metrics for recovery, because this site was close to recovery for vegetation cover, but not at all close for community composition. Although we expect that *J. roemerianus* will eventually recover if the area remains undisturbed, this site appears very close to the conditions that would cause a transition to dominance by *S. alterniflora*. It is therefore likely that another pulse disturbance overlaid on the press of ongoing sea level rise would cause a permanent transition in the vegetation of this site. If one did not know the disturbance history of this site, it would present as having a bimodal distribution of community states (i.e., patches of *J. roemerianus* and patches of *S. alterniflora*, with very few mixed stands), which is one of the lines of evidence commonly presented to argue for a threshold between alternative states (Henderson et al., 2016; Ratajczak et al., 2014). This underscores the point that it is important to understand the disturbance history and the rate of recovery following disturbance of a site when evaluating possible transitions.

The CVs of both vegetation cover and height during recovery from disturbance increased significantly compared with both control and recovered plots across all site types. This increase reflects plot-to-plot differences during the recovery process, as compared to control and recovered plots that were tightly constrained around high cover by the dominant plant species and thus showed little variation. The concept that disturbance increases variability is not new (Odum, 1985), but our results provide experimental evidence for the notion that variability in field data can be used to detect disturbance, even if the disturbance is difficult to directly observe, and thus that variability is an important indicator of system behavior (Fraterrigo & Rusak, 2008).

Not only did CVs of vegetation cover and height increase during recovery from disturbance, but also the

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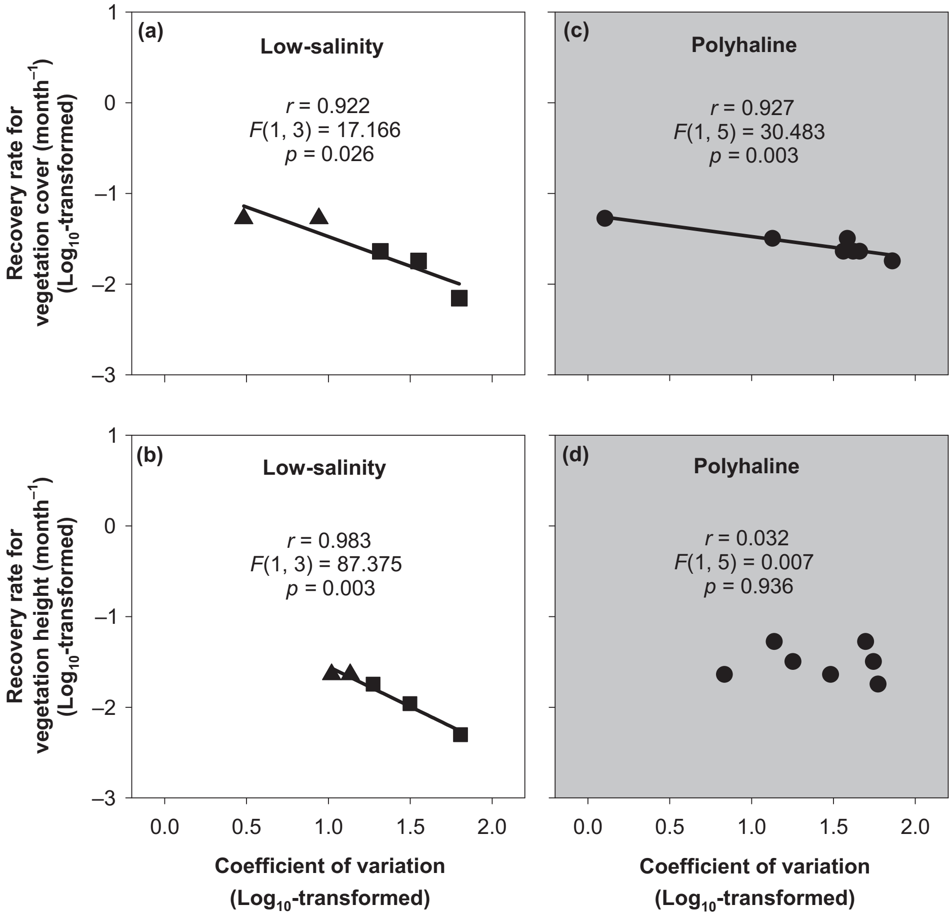

FIGURE 5 Relationships of the recovery rate (Log_{10}-transformed) for (a, c) vegetation cover and (b, d) vegetation height versus the corresponding coefficient of variation (Log_{10}-transformed) during the recovery period in the disturbed plots for the tidal marshes in low-salinity (unshaded) and polyhaline salinity (shaded) zones. Triangle, square and circle symbols represent freshwater, brackish and salt marshes, respectively. For each correlation, the r, F ($df_{correlation}$, $df_{residual}$) and p-value are shown. Solid lines indicate significant correlations ($p < 0.05$).

patterns were well related to salinity in most cases (Figure 4c,d). In sharp contrast, CVs were generally poorly related to salinity when based on unmanipulated (control) plots (Figure 4a,b). The use of variance as an early warning signal of proximity to a transition has had mixed success (e.g., Dakos & Bascompte, 2014; van Belzen et al., 2017; Veldhuis et al., 2022), and our results suggest that trends in variability are more difficult to discern when the sites are not experiencing pulse disturbance (i.e., in the control plots), despite an underlying environmental gradient. Finally, we found that CV during recovery was negatively correlated with recovery rate in three out of four cases, with faster recovery associated with lower variability. Presumably, at sites with low average recovery rates, stochastic factors affecting colonization and growth of plants were relatively important, leading to high variation among plots.

This study represents one of the few field tests of how resilience to disturbance varies along an abiotic gradient. The results show that resilience varies predictably along an abiotic stress gradient within habitats (i.e., marsh salinity zones). Because resistance to disturbance also can vary along abiotic gradients (De Battisti, 2021), consideration of how both resistance and resilience vary with abiotic stress may provide a framework for understanding spatial variation in the importance of disturbance within many ecosystems. Our results also suggest that variance increases during recovery from disturbance. If this finding is confirmed in other systems, it suggests that variance may provide a tool for both inferring recent disturbances and predicting future recovery rates.

AUTHOR CONTRIBUTIONS

YW, HG, MA and SCP conceived the study. YW, HG and SCP collected the data. YW and HG performed statistical analyses and wrote the first draft of the manuscript. YW, HG, MA and SCP edited the successive drafts.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Pennings, 2022) are available in the Environmental Data Initiative's EDI Data Portal at https://doi.org/10.6073/pasta/6df40a30859a7293db9a76fc4fff8cec.

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