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Variation in synchrony of production among species, sites, and intertidal zones in coastal marshes

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Abstract

Spatially synchronous population dynamics are important to ecosystem functioning and have several potential causes. By looking at synchrony in plant productivity over 18 years across two elevations in three types of coastal marsh habitat dominated by different clonal plant species in Georgia, USA, we were able to explore the importance of plant species and different habitat conditions to synchrony. Synchrony was highest when comparing within a plant species and within a marsh zone, and decreased across species, with increasing distance, and with increasing elevational differences. Abiotic conditions that were measured at individual sites (water column temperature and salinity) also showed high synchrony among sites, and in one case (salinity) decreased with increasing distance among sites. The Moran Effect (synchronous abiotic conditions among sites) is the most plausible explanation for our findings. Decreased synchrony between creekbank and mid-marsh zones, and among habitat types (tidal fresh, brackish and salt marsh) was likely due in part to different exposure to abiotic conditions and in part to variation in sensitivity of dominant plant species to these abiotic conditions. We found no evidence for asynchrony among species, sites or zones, indicating that one habitat type or zone will not compensate for poor production in another during years with low productivity; however, tidal fresh, brackish and salt marsh sites were also not highly synchronous with each other, which will moderate productivity variation among years at the landscape level due to the portfolio effect. We identified the creekbank zone as more sensitive than the mid-marsh to abiotic variation and therefore as a priority for monitoring and management.

Key words: climate change; salt marsh; *Juncus roemerianus*; *Spartia alterniflora*; synchrony; *Zizaniopsis miliacea*

Introduction

      Synchrony is the tendency of populations to fluctuate together through time (Buonaccorsi et al. 2001, Liebhold et al. 2004). Synchrony is important because it affects regional ecosystem functioning (Bjørnstad et al. 2002, Beaugrand et al. 2003, Defriez et al. 2016): synchronization across space can lead to coordinated temporal fluctuations across large areas, and therefore can promote population outbreaks (Micheli 1999, Keitt 2008) or extinctions (Earn et al. 2000). In contrast, asynchronous population fluctuations, either at a single site or across sites, can stabilize ecosystem function (Tilman 1996) through the portfolio effect (Waddle et al. 2019), in which populations that vary out of phase with each other increase stability in community function. The most common explanation for synchrony at large spatial scales is that multiple populations are forced by the same regional climate factors, such as temperature, precipitation and drought (Liebhold et al. 2004, Koenig and Knops 2013, Defriez and Reuman 2017, Tejedor et al. 2020): this is the "Moran effect" (Moran 1953, Ranta et al. 1997, Hudson and Cattadori 1999). In contrast, asynchrony may occur if different species respond to different aspects of climate variation (Tilman 1996, Bruckerhoff et al. 2020). Synchrony at smaller scales can be caused by dispersal (Blasius et al. 1999, Cavanaugh et al. 2013, Martin et al. 2017). Finally, strong ecological interactions with synchronous species can force synchrony in affected species (Liebhold et al. 2004, Ripa and Ranta 2007).

      We built on a number of studies of synchrony in plant communities in terrestrial (Koenig and Knops 2000, 2013, Shestakova et al. 2016) and algal (Cavanaugh et al. 2013, Defriez et al. 2016, Defriez and Reuman 2017) systems to examine synchrony in production among sites, micro-habitats and species for the emergent plants that dominate coastal wetlands. How coastal wetlands function should be strongly affected by whether or not primary production in these systems is synchronous. Above-ground primary production in coastal wetlands varies two to three-fold from one year to another (Morris et al. 1990, Wieski and Pennings 2014, Liu and Pennings 2019), and because the primary producers are foundation species (Pennings and Bertness 2001), these fluctuations are likely to affect most other species in the community and all aspects of ecosystem function (Lamy et al. 2020). Because coastal wetlands provide numerous ecosystem services to mankind (Barbier et al. 2011, Mitsch et al. 2013), whether primary production and the abundance of the marsh species that contribute to these services (Morris et al. 1990, Rochlin and Morris 2017) is synchronous or

asynchronous at the landscape scale has important management implications. If it is synchronous, managers must allow for boom and bust cycles at the landscape scale; if it is asynchronous, different species or different sites will compensate for each other, and productivity at the landscape scale will be far less variable.

It is not immediately clear whether one should expect primary production in coastal wetlands to be synchronous or asynchronous. On the one hand, coastal wetlands are dominated by a small number of plant species, and these are all affected by a common set of abiotic drivers including temperature (Idaszkin and Bortolus 2011, Kirwan and Mudd 2012, Wieski and Pennings 2014, Li et al. 2018), fluctuations in sea level (Turner 1976, McKee and Patrick 1988, Kirwan and Megonigal 2013, Snedden et al 2015), and freshwater availability (Wieski and Pennings 2014, Li et al. 2018). Thus, one might expect primary production by all species to vary synchronously across large regional areas. On the other hand, the different species vary in their sensitivity to these drivers (Guo et al. 2012), with some more tolerant of flooding (Bertness 1991), and others more tolerant of high salinities (Bertness et al. 1992), and so they might vary asynchronously if climate effects on flooding and salinity were uncorrelated. In addition, coastal wetland plants occupy different intertidal "zones", with creekbank plants in habitats that are flooded daily by high tides and mid-marsh plants in habitats that are less frequently flooded. As a result, we might expect creekbank plants to be more sensitive to conditions in the water column, such as salinity, and the mid-marsh plants to be more sensitive to conditions in the air, such as temperature, and there is some evidence that this is the case (Wieski and Pennings 2014, Li et al. 2018; O'Connell et al. 2020). Thus, one might expect more synchrony within a zone among relatively distant sites than between nearby zones within a single site.

We examined intraspecific and interspecific synchrony of three dominant species of tidal marsh plants over 18 years at 10 tidal marshes in coastal Georgia, USA. The Georgia Coastal Ecosystems Long Term Ecological Research program monitors productivity (estimated by end of season above-ground biomass) in two marsh zones (creekbank and mid-marsh) in 10 tidal freshwater, brackish and salt marsh sites distributed over a complex intertidal landscape of ~600 km^2. These sites experience different salinity conditions, and the plants that dominate tidal fresh, brackish and salt marshes differ in their sensitivity to these conditions (Guo et al. 2012). We tested two hypotheses. First, primary production is synchronous across years among sites, marsh zones and species. This

implies that different species of tidal marsh plants respond to abiotic drivers in the same way. Alternatively, there may be lack of synchrony among species if different species respond to different abiotic drivers, or if sensitivity to climate drivers varies as a function of marsh elevation. Second, if sensitivity to climate drivers varies as a function of marsh elevation, or if abiotic conditions become less correlated with increasing distance among sites, synchrony will decline with increasing distance (vertical or horizontal) between sampling zones or sites.

Materials and method

We worked at the monitoring sites of the Georgia Coastal Ecosystems Long-Term Ecological Research (GCE-LTER) program (http://gce-lter.marsci.uga.edu/). The GCE-LTER program monitors 10 permanent sites (GCE1–10) that are dominated by wild rice (*Zizaniopsis miliacea*), needlerush (*Juncus roemerianus*), giant cordgrass (*Spartina cynosuroides*) and smooth cordgrass (*S. alterniflora*) across a gradient from tidal fresh to tidal salt marsh habitat (Figure 1). Tides are semidiurnal and mesotidal, with a range of 2–3m.

At each site, GCE researchers located eight permanent plots (0.5 × 0.5 m) along the creekbank and eight permanent plots in the middle of the marsh platform (henceforth "mid-marsh", 0.25 × 0.25 m) in 2000. A second set of mid-marsh plots were added at site ten in 2005, with the original (2000) set dominated by *S. alterniflora* and the second set dominated by *J. roemerianus*. Plots at site seven were 0.5 x 1 m in size regardless of zone to accommodate the taller but sparser plants at this site. GCE researchers measured the height and flowering status (yes or no) of every shoot in the plots in October of each year. Plots were replaced if lost to disturbance. Using allometric equations specific to each site, marsh zone (creekbank or mid-marsh) and plant species, height and flowering status were converted to estimates of end-of-season aboveground biomass (Wieski and Pennings 2014, Li et al. 2018). The elevation of each plot was measured with a real-time kinematic GPS, and data were averaged across the eight plots to give a single value for each zone at each site. All plant data are publically available (Appendix S1: Table S1; Data S1: [Plot_ data 2000-2017]). For this study, we analyzed only data for sites and zones that were almost completely dominated by a single plant species in order to examine how each species responded to abiotic drivers in the absence of interspecific interactions; therefore, we omitted the creekbank zone at site eight, where the vegetation

consisted of a mixture of *S. cynosuroides* and several other plant species. We included two mid-marsh species at site ten because these occurred in separate stands, each dominated by a single plant species.

We examined several abiotic factors as potential drivers of annual variation in end of season plant biomass: average daily air temperature, cumulative river discharge, cumulative precipitation, average monthly tide range, and average monthly sea level. These predictor variables were not highly correlated with each other (Pearson correlation coefficient r-values ranging from 0.06 to 0.40) and none of the correlations were significant (Appendix S1: Table S4). All datasets are publically available (Appendix S1: Table S2). In each case, long-term abiotic data were filtered to consider only the growing season (here defined as April 1 to September 30). We used air temperature and precipitation data from the Malcolm McKinnon Airport in Brunswick, Georgia, Altamaha River discharge data from the Doctortown gauging station operated by the United States Geographical Survey (USGS), and tide range and sea level data from the National Oceanographic and Atmospheric Administration (station 8670870, Fort Pulaski, Georgia).

To explore temporal variability at different sites and zones, we calculated the average biomass for each zone at each site in each year (Data S1: [Site_data 2000-2017]). To compute synchrony in end of season biomass among sampling locations, we used the meancorr function in the synchrony package in R to calculate the mean Pearson correlation coefficient and its significance using 999 randomizations of the data (Gouhier and Guichard 2014). By default, the *P*-value is based on a two-tailed test and generated by a naive randomization procedure that mitigates both the temporal autocorrelation within and among species at different sites and zones (Legendre 2005). To compare the mean correlations within different species, species pairs, and zones, we calculated the average Pearson correlation coefficient for each comparison. To evaluate the effect of the various abiotic variables on annual biomass, we used a mixed model (Bates et al. 2015) with temperature, temperature^2, elevation, precipitation, river discharge, tide range and sea level as fixed factors, and site or zone as random effects (Data S1: [Model_data 2000-2017]). We used the lmerTest package in R to assess the fixed effect and direction of abiotic factors, we used the t values for each factor from the mixed models to visually assess how they differed among marsh zones and plant species (Kuznetsova et al. 2017). To assess how production and sensitivity of production to environment varied across elevation, we plotted bivariate biomass-elevation and biomass coefficient of variation-

elevation relationships. We assessed the importance of species in these relationships using the aov function in the car package in R to do ANCOVA analysis (Fox and Weisberg 2019). We performed all analyses using R statistical software (R Development Core Team, 2019); see Data S1: [Meancorr and mixed model_R code].

To assess synchrony in abiotic conditions across sites, we examined data on water temperature and salinity from moored instruments deployed near marsh sites one, two, three, six, seven, eight, nine and ten. As above, we filtered data to consider only the growing season (April 1 to September 30), and calculated mean temperature and salinity values from daily means for each year (2004-2017 for site ten and 2002-2017 for all other sites).

Results

Fall aboveground biomass of all three tidal plants varied among years (Figure 2). Visual inspection suggests that the pattern of variation was not identical among all species, sites and marsh zones (e.g., contrast panels e and h), although variation did appear similar among some sites (e.g., compare creekbank variation in panels d and f). Within a site, biomass tended to be greater in the creekbank than the mid-marsh zone except at sites where *Juncus roemerianus* occupied the mid-marsh zone (e.g., panels a, j).

Cross-correlation analysis (Figure 3) indicated that variation in fall aboveground biomass of *S. alterniflora* was highly synchronous across sites in the creekbank zone (24 out of 28 individual correlations significant, average r= 0.62±0.03 across all 28 correlations, Figure 4c), moderately synchronous in the mid-marsh zone (ten out of 21 individual correlations significant, average r= 0.38±0.04, Figure 4d), and least synchronous when comparing the creekbank with the mid-marsh (23 out of 56 individual correlations significant, average r= 0.35±0.02, Figure 4b). The three *J. romerianus* comparisons (all mid-marsh) indicated moderate synchrony (one out of three individual correlations significant, average r= 0.46±0.13, Figure 4d), and the one *Z. miliacea* comparison (creekbank versus mid-marsh) also showed moderate synchrony (r=0.41, P>0.05, Figure 4b).

Comparing across species, there was low synchrony between *S. alterniflora* and *J. roemerianus* (13 out of 45 individual correlations significant, average r= 0.33±0.03, Figure 4b, d), low synchrony between *Z. miliacea* and mid-marsh *S. alterniflora* and (eight out of 14 individual

correlations significant, average r= 0.37±0.07, Figure 4b, d), and creekbank *S. alterniflora* (one out of 16 individual correlations significant, average r= 0.21±0.03, Figure 4c), and very little synchrony between *Z. miliacea* and *J. roemerianus* (zero out of six individual correlations significant, average r= 0.16±0.04, Figure 4b, d).

Abiotic conditions were highly correlated among all instrumented sites (Appendix S1: Fig. S1). Twenty-six out of 28 individual correlations for water column temperature were significant (average r=0.65), and 28 out of 28 individual correlations for water column salinity were significant (average r=0.87). The cross-correlations for water column salinity, but not water column temperature, decreased with distance among sites (Appendix S1: Fig. S2).

The three plant species responded similarly to some abiotic drivers and differently to others (Figure 5c-f). In the mixed models for each species, the most common predictor variables that were individually significant were temperature (positive), temperature^2 (negative), elevation (negative), precipitation (mixed), river discharge (positive), and tide range (negative) (Appendix S1: Table S3, Figure 5c-f).

Across all species, sites and marsh zones, average plot elevation predicted plant biomass and sensitivity to climate drivers (Figure 5). Aboveground biomass decreased with increasing elevation (Figure 5a), but the coefficient of variation (CV) of biomass was usually (seven out of nine comparisons) higher in the creekbank habitat than in the mid-marsh habitat at the same site (Figure 5b), indicating less variation among years in the mid-marsh versus the creekbank habitat.

Across all sites, zones and plant species, cross-correlations decreased with increasing elevational differences between sites (Figure 6a). Similarly, cross-correlations decreased with increasing geographic distance between sites, and differed among species (Figure 6b). In both cases, there was also an effect of species, as shown in Figure 2. The interactions between species and geographic distance and between species and elevational distance were not significant (Figure 6).

Discussion

We found evidence for strong synchrony when looking at a single plant species growing in a single intertidal zone (e.g., creekbank or mid-marsh). Synchrony was weaker when comparing the same species across zones or comparing among species, and decreased with elevational and

geographic distance among populations. Synchrony was likely driven by common responses to abiotic drivers (the Moran effect), but was reduced when different species of plants differed in sensitivity to particular drivers.

Synchrony was highest when comparing a single species in a single marsh zone. In particular, synchrony was highest among creekbank populations of *S. alterniflora*, among mid-marsh populations of *J. roemerianus*, and among mid-marsh populations of *S. alterniflora*. Synchrony decreased when comparing between creekbank and mid-marsh populations of *S. alterniflora*, suggesting that responses to abiotic drivers differed between the creekbank and mid-marsh habitats. Synchrony also decreased when comparing across species, suggesting that responses to abiotic drivers differed among species across the coastal landscape. We found no evidence for asynchrony: none of the statistically significant cross-correlations were negative.

One common cause of synchrony among populations is the Moran effect, which postulates that variation in important abiotic conditions is likely to be synchronous among nearby locations, thereby synchronizing population dynamics or productivity among sites (Moran 1953, Kendall et al. 2000, Liebhold et al. 2004). With increasing distance among sites, abiotic conditions are likely to be less correlated, and synchrony will decrease (Estay et al. 2009). The sites that we studied were relatively close to each other (no more than 30 km apart), suggesting that key abiotic drivers such as temperature and water column salinity would likely vary synchronously across the sites. We tested this for water column temperature and salinity, and found strong cross-site correlations in these two variables (Appendix S1: Figure S1), with synchrony in salinity decreasing with increasing distance among sites (Appendix S1: Figure S2). As expected from studies of other plant species (Liebhold et al. 2004, Koenig and Knops 2013), we found that synchrony in production also decreased with increasing geographical distance among sites. This result, however, was partially confounded with turnover in plant species across space, which we discuss later.

We would expect synchrony in abiotic conditions to be lower among marsh zones than among sites within a single marsh zone. The creekbank habitat is flooded daily by the tide, and as such is strongly influenced by conditions in the water column (Alber and O'Connell 2019). The mid-marsh habitat is flooded less often, is prone to drying out, which causes elevated salinities, and is more influenced by atmospheric conditions (Hughes et al. 2012). We lack abiotic data from individual

zones of individual sites to demonstrate this, but we were able to confirm that synchrony in plant production decreased as elevational differences between sites increased. Notably, the effect on synchrony of micro-habitat (marsh zone) variation of < 1 m in elevation was comparable to the effect of 30 km of geographic distance.

The Moran effect assumes that different populations or species respond to abiotic drivers in the same way. Alternatively, if responses vary among species, or if different abiotic conditions are more important in driving variation in production in different marsh zones, these different responses could partially explain why synchrony decreased with increasing distance. The sites occupied by *Z. miliacea* and *J. roemerianus* were at the edges of the study area (Fig. 1), and so lower synchrony at the greatest geographical distances could be due either to reduced synchrony in abiotic drivers, or to different responses among plant species to abiotic drivers. Similarly, reduced synchrony between marsh zones could be partially explained by differences among species because *J. roemerianus* only occurred in the mid-marsh zone.

To address these possibilities, we examined the responses of each species in each zone to the abiotic drivers (Figure 5). The results suggested that different species in different marsh zones might, in fact, respond somewhat differently to abiotic drivers. The most important driver of *S. alterniflora* production in the creekbank zone was river discharge, but both river discharge and tide range had strong effects on *S. alterniflora* production in the mid-marsh zone. The most important drivers of *J. roemerianus* production in the mid-marsh zone were also river discharge and tide range. Production of *Z. miliacea*, in contrast, was most strongly affected by temperature. These results are broadly consistent with previous studies of these species. Variation in production of *S. alterniflora* among years is known to be driven in large part by factors that affect porewater salinity; these include river discharge, because high discharge reduces estuarine salinities (Odum et al.1984, Di iorio and Castelao 2013), and tidal flooding, because flooding both introduces and flushes salt out of mid-marsh zones prone to hypersalinity (Morris and Haskin 1990, Wieski and Pennings 2014, Hill and Roberts 2017). We are not aware of any long-term studies of productivity of *J. roemerianus* (but see Brinson and Christian 1999), but this species is known to be sensitive to high salinities and variation in tidal flooding (Christian et al. 1990, Woerner and Hackney 1997, Pennings et al. 2005, Touchette 2006, Touchette et al. 2009). A previous study of variation in productivity of *Z. miliacea* at the same study

site that we examined also identified temperature as the primary factor driving variation in biomass (Li et al. 2018). These differences among species in sensitivity to different abiotic drivers, could partially explain why, for example, synchrony was low between *J. roemerianus* and *Z. miliacea*, and between *S. alterniflora* and *Z. miliacea*. Since distance and species identity were confounded, however, unequivocally determining which was the most important in driving the decline in synchrony with geographic distance is difficult with the data that we have.

Alternative explanations to the Moran effect for synchrony among populations include high dispersal (Liebhold et al. 2004, Cavanaugh et al. 2013, Martin et al. 2017), and strong interspecific interactions with a mobile species that creates synchrony among populations by moving between them (Liebhold et al. 2004, Ripa and Ranta 2007). Testing among these possibilities was not the goal of this project; however, neither of these alternatives is likely in this case. The plants that we studied are long-lived clonal species for which dispersal is not thought to affect biomass of established populations (Pennings and Bertness 2001). Some of the plants are affected by herbivory in specific situations (Silliman and Ziemen 2001, Gustafson et al. 2006), but herbivory is greatest in localized areas with conditions favoring high densities of herbivores (Schalles et al. 2013), a pattern that would tend to reduce rather than increase synchrony among sites. Because different herbivores attack different plant species, it is possible, however, that herbivory could help explain our finding of less synchrony among versus within plant species.

The degree of synchrony among sites is important because it determines how climate variation will affect regional ecosystem functioning (Bjørnstad et al. 2002, Beaugrand et al. 2003). At the extremes, high levels of synchrony would lead to an entire region having years with high and low function, whereas asynchrony (negative correlations among sites) would stabilize regional ecosystem functioning, because high-performing sites would compensate for low-performing sites in any given year, just as asynchrony among species within a community can stabilize community function across years (Tilman 1996). Most studies, in a variety of habitat types, have found synchrony among sites within a region (Raimondo et al. 2004, Bearup et al., 2013, Defriez et al., 2016, Defriez and Reuman 2017, Fantinato et al., 2016, Gouveia et al., 2016, Vindstad et al., 2019). Similarly, for coastal wetlands in Georgia, we found a fairly high level of synchrony across sites. As a result, "bad years" are likely to result in poor ecosystem performance across the entire region. However, different

vegetation types may provide a little of a "portfolio effect" to regional function (Waddle et al. 2019), in which low levels of synchrony reduce fluctuations in regional productivity. Overall, however, these results suggest that coastal wetlands will tend towards boom and bust years, and that regional productivity will not be rescued by some sites or species fluctuating asynchronously with the others. We did not investigate how strongly marsh services such as fisheries production are correlated with year to year variation in plant productivity, but this finding suggests the hypothesis that marsh services will also fluctuate synchronously among years across broad regions.

The creekbank habitats were more variable among years than the mid-marsh habitat at seven of nine sites, suggesting that they should be a priority for monitoring studies. It is likely that they should also be a priority for management, because sensitivity to abiotic variation combined with anthropogenic impacts may make them more vulnerable. For example, salt marsh loss in New England, whether driven by outbreaks of crabs or eutrophication, has primarily affected creekbank habitats (Holdredge and Bertness 2009, Deegan et al. 2012).

Our results illustrate two general points. First, that drops in synchrony with distance may not be due only to a gradual loss of synchrony in abiotic conditions with distance (the standard explanation for the Moran effect), but may also be due to changes in the taxonomic composition of the community. Second, if a landscape contains multiple micro-habitats, differences in synchrony among micro-habitats may be far greater than differences across large geographic distances. In this case, the drop in synchrony due to less than one meter of elevational change was comparable to that due to 30 km of geographic distance. We suggest that a better and more general understanding of synchrony may come from increased attention to species composition and micro-habitat variation.

Supporting Information

Additional supporting information may be found online at: [link to be added in production]

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Figure Legends

Figure 1 Map of the study site on the coast of Georgia, USA. GCE-LTER permanent monitoring sites that were included in this study are marked with circles. The GCE-LTER program includes ten permanent sites (GCE1–10) that include fresh, brackish, and salt marshes that are dominated by the plant species *Zizaniopsis miliacea*, *Spartina cynosuroides* (not included in this study but present at the creekbank of site 8), *Juncus roemerianus*, and *Spartina alterniflora.* Site one was dominated by *S. alterniflora* at the creekbank and *J. roemerianus* in the mid-marsh. Site ten was dominated by *S. alterniflora* at the creekbank and separate stands of both *S. alterniflora* and *J. roemerianus* in the mid-marsh.

Figure 2 Annual variation in fall aboveground biomass of *Spartina alterniflora*, *Juncus roemerianus* and *Zizaniopsis miliacea* at different sites (numbers above each panel) and marsh zones. Solid symbols indicate the creekbank zone; open symbols indicate the mid-marsh zone. Each point is the average in a given year of the data from the replicate plots in that particular zone at that particular site. The error bars indicate + 1 standard error.

Figure 3 (a) Correlations between annual fall biomass values (Figure 2) for *Spartina alterniflora*, *Juncus roemerianus* and *Zizaniopsis miliacea* between different sites and different marsh zones. Upper right: larger circles and darker shading indicate larger r values. Lower left: r values for the correlations. Significant relationships are indicated by bold numbers and filled circles.

Figure 4 Mean correlations between plant biomass at different sites. Comparisons are (a) within individual species or between species pairs: *Spartina alterniflora* (SA), *Juncus roemerianus* (JR), *Zizaniopsis miliacea* (ZM), *Spartina alterniflora* and *Juncus roemerianus* (SA_JR), *Spartina alterniflora* and *Zizaniopsis miliacea* (SA_ZM), *Juncus roemerianus* and *Zizaniopsis miliacea* (JR_ZM); (b) between the creekbank and mid-marsh habitats for each species or species pair; (c) betweeen creekbank sites for SA and SA_ZM comparisons; and (d) between mid-marsh sites for each species or species pair. The error bars indicate + 1standard error.

Figure 5 Variation across elevation (all species, sites and marsh zones combined) in (a) fall aboveground biomass, (b) CV of fall aboveground biomass, (c) the fixed effect on *Spartina alterniflora* in the creekbank habitat (grey circle), (d) the fixed effect on *Spartina alterniflora* in the mid-marsh habitat (open circle), (e) the fixed effect on *Juncus roemerianus* in the mid-marsh habitat

(open triangle), (f) the fixed effect on *Zizaniopsis miliacea* in the creekbank (grey square) and mid-marsh (open square) habitats. The t values, which we use to assess the fixed effect size on production, are from multiple regressions (Supplementary materials Table S3) with Temperature (T), Tempersture^2 (T^2), Elevation (E), Precipitation (P), River Discharge (RD), Tide Range (TR), and Sea level (SL) as predictor variables, and with GCE sites as random effects for *Spartina alterniflora* and *Juncus roemerianus*, and zone as a random effect for *Zizaniopsis miliacea*, which was studied at only one site. The arrows in panel b indicate that the CV in the creekbank is greater (up) or smaller (down) than the CV in the mid-marsh; an * or # above or below a symbol in panels c-f indicates that the fixed factor was significant (# $0.05 < P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Statistical results are provided in Appendix S1: Table S3.

Figure 6 Relationship between cross-correlations of end-of-season biomass for all plant species at all stations and (a) differences in elevation between stations, and (b) differences in geographic distance between stations. Open (panel a) and filled (panel b) circles indicate cross correlation r values between GCE sites.
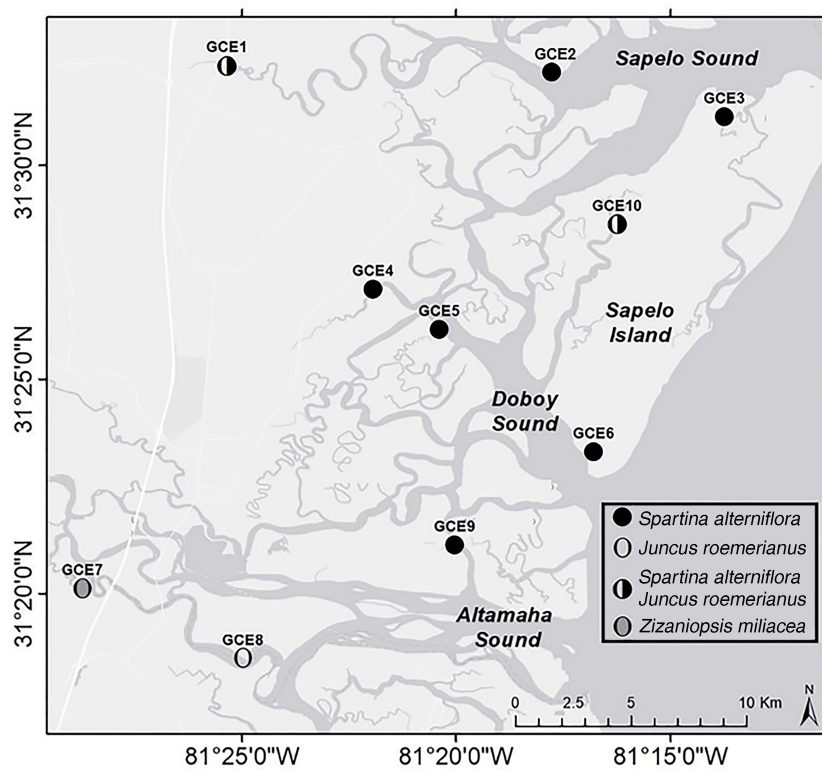
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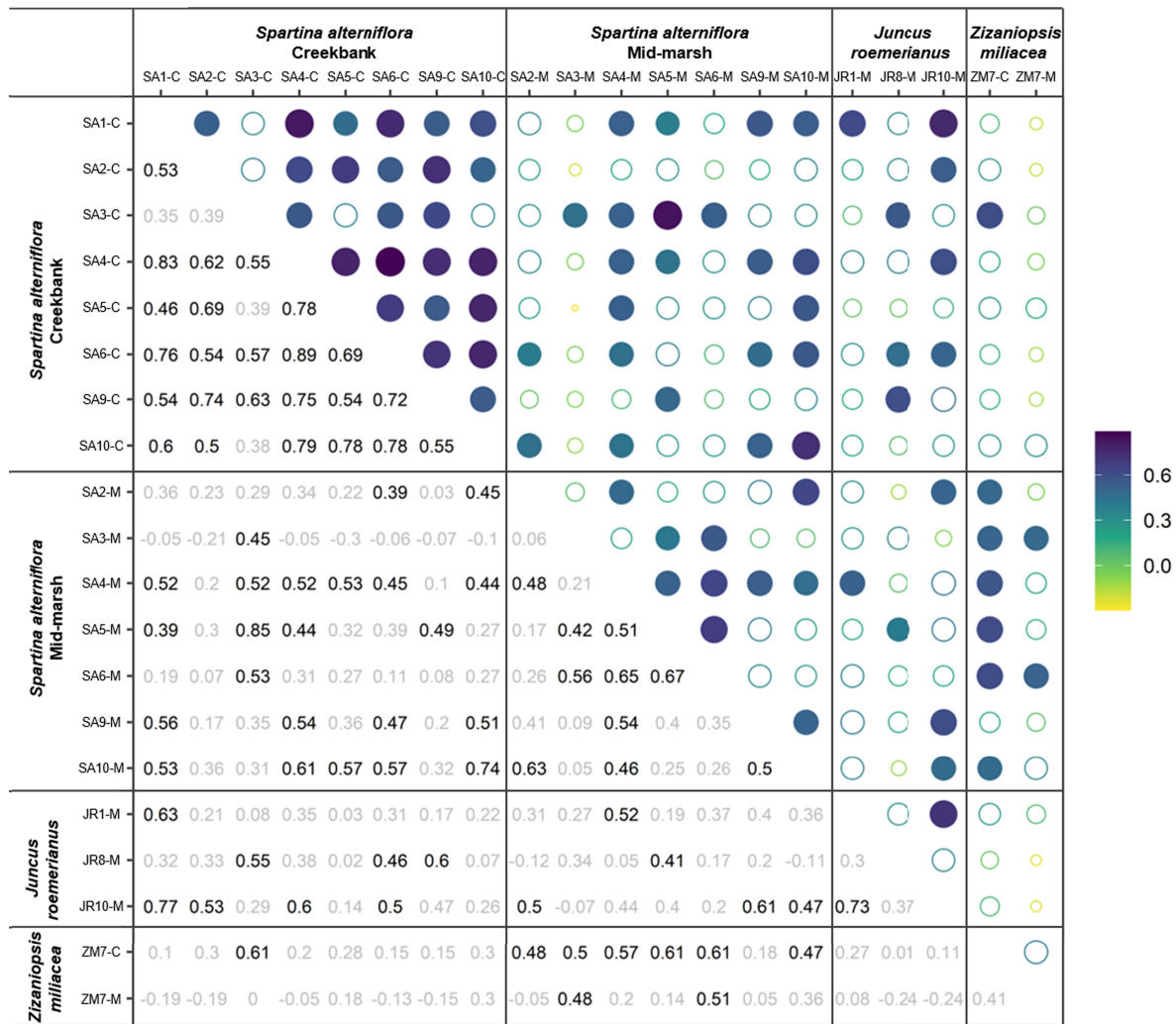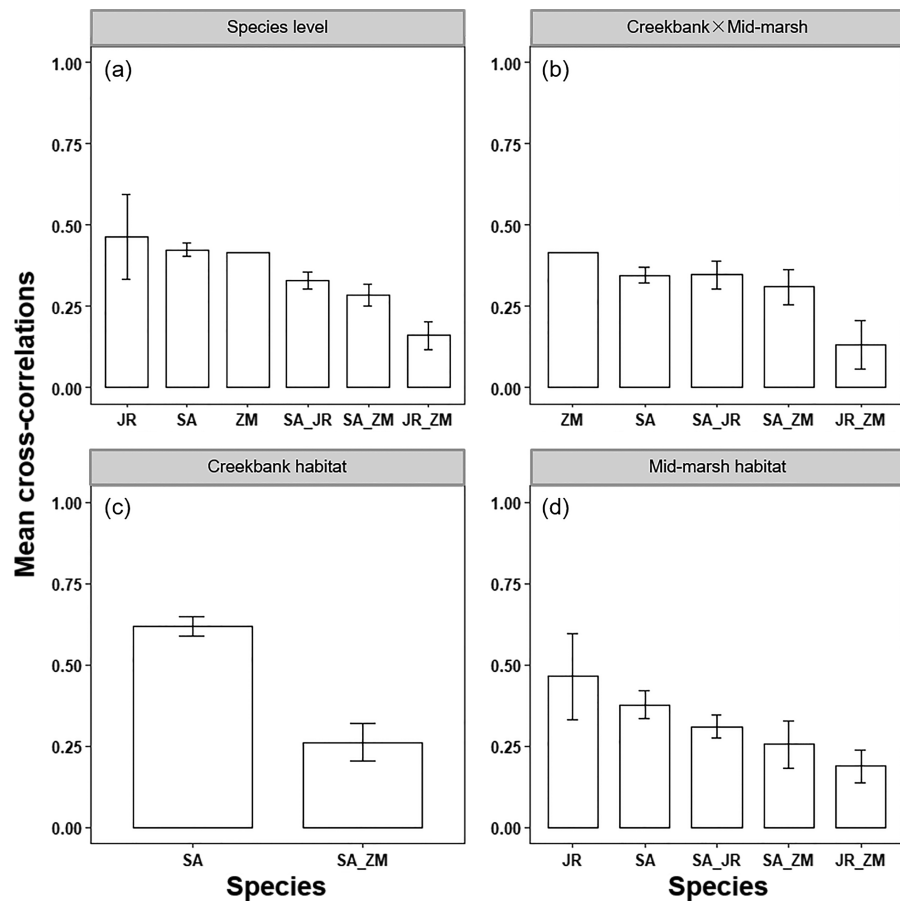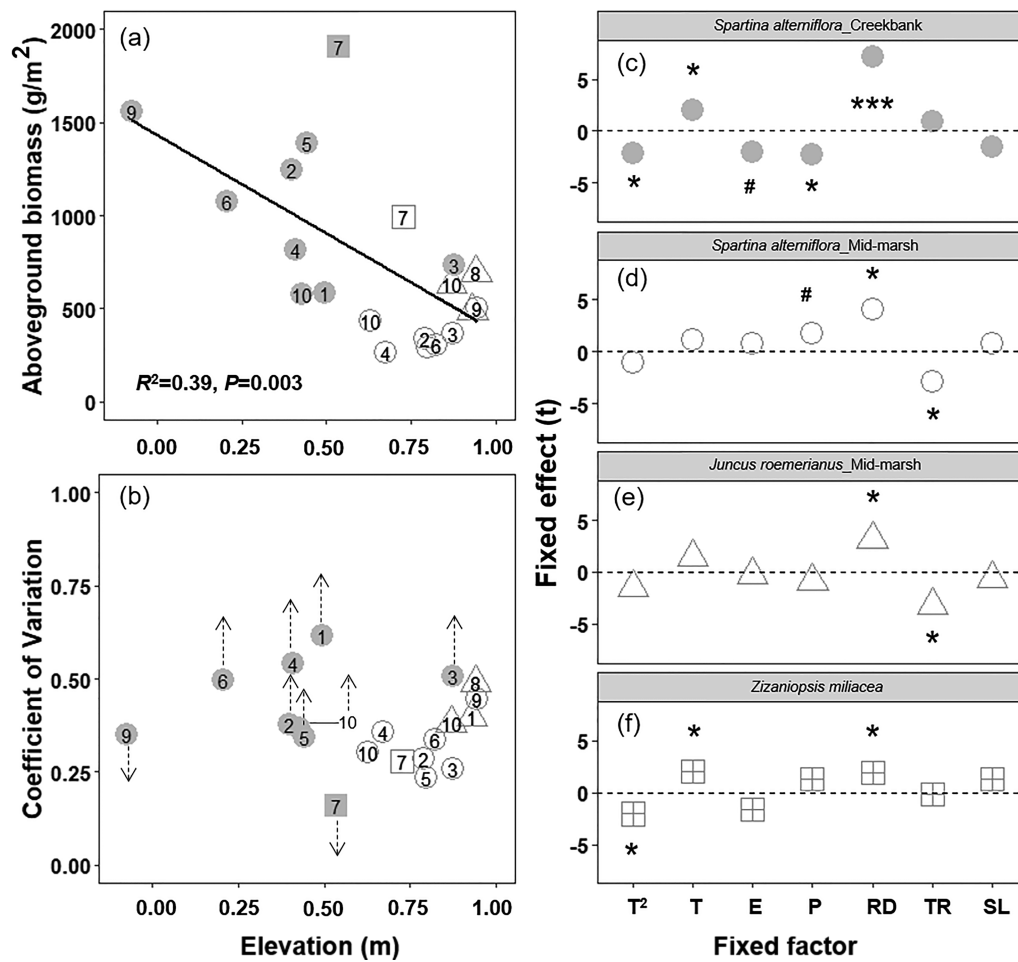|	SA1-C	SA2-C	SA3-C	SA4-C	SA5-C	SA6-C	SA9-C	SA10-C	SA2-M	SA3-M	SA4-M	SA5-M	SA6-M	SA9-M	SA10-M	JR1-M	JR8-M	JR10-M	ZM7-C	ZM7-M
SA1-C																				
SA2-C	0.53																			
SA3-C	0.35	0.39																		
SA4-C	0.83	0.62	0.55																	
SA5-C	0.46	0.69	0.39	0.78																
SA6-C	0.76	0.54	0.57	0.89	0.69															
SA9-C	0.54	0.74	0.63	0.75	0.54	0.72														
SA10-C	0.6	0.5	0.38	0.79	0.78	0.78	0.55													
SA2-M	0.36	0.23	0.29	0.34	0.22	0.39	0.03	0.45												
SA3-M	-0.05	-0.21	0.45	-0.05	-0.3	-0.06	-0.07	-0.1	0.06											
SA4-M	0.52	0.2	0.52	0.52	0.53	0.45	0.1	0.44	0.48	0.21										
SA5-M	0.39	0.3	0.85	0.44	0.32	0.39	0.49	0.27	0.17	0.42	0.51									
SA6-M	0.19	0.07	0.53	0.31	0.27	0.11	0.08	0.27	0.26	0.56	0.65	0.67								
SA9-M	0.56	0.17	0.35	0.54	0.36	0.47	0.2	0.51	0.41	0.09	0.54	0.4	0.35							
SA10-M	0.53	0.36	0.31	0.61	0.57	0.57	0.32	0.74	0.63	0.05	0.46	0.25	0.26	0.5						
JR1-M	0.63	0.21	0.08	0.35	0.03	0.31	0.17	0.22	0.31	0.27	0.52	0.19	0.37	0.4	0.36					
JR8-M	0.32	0.33	0.55	0.38	0.02	0.46	0.6	0.07	-0.12	0.34	0.05	0.41	0.17	0.2	-0.11	0.3				
JR10-M	0.77	0.53	0.29	0.6	0.14	0.5	0.47	0.26	0.5	-0.07	0.44	0.4	0.2	0.61	0.47	0.73	0.37			
ZM7-C	0.1	0.3	0.61	0.2	0.28	0.15	0.15	0.3	0.48	0.5	0.57	0.61	0.61	0.18	0.47	0.27	0.01	0.11		
ZM7-M	-0.19	-0.19	0	-0.05	0.18	-0.13	-0.15	0.3	-0.05	0.48	0.2	0.14	0.51	0.05	0.36	0.08	-0.24	-0.24	0.41	

Column groups: *Spartina alterniflora* Creekbank (SA1-C–SA10-C); *Spartina alterniflora* Mid-marsh (SA2-M–SA10-M); *Juncus roemerianus* (JR1-M, JR8-M, JR10-M); *Zizaniopsis miliacea* (ZM7-C, ZM7-M).
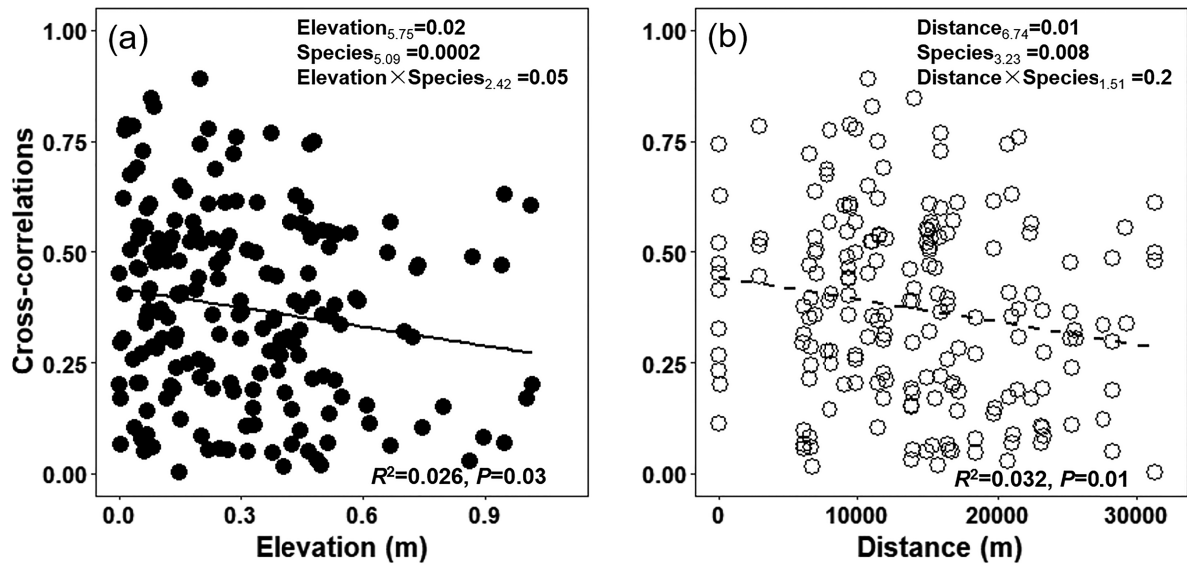
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