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GENERAL WETLAND SCIENCE

Direct and Indirect Effects of Climate Change in Coastal Wetlands: Will Climate Change Influence Wetlands by Affecting Plant Invasion?

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Abstract
Introduced species and climate change can have direct impacts on wetland communities, but they can also produce indirect effects such that climate change (i.e., effects of flooding and salinity) can affect native plants by exacerbating or reducing invasion. We assessed the direct and indirect effects of flooding, salinity, and introduced species on wetland communities across a salinity gradient by analyzing existing monitoring data from over 390 Coastwide Reference and Monitoring Sites (CRMS) using path analysis. As expected, we found that introduced species cover and richness was highest in fresh marshes and decreased across the salinity gradient. In fresh marshes, introduced cover and salinity separately negatively affected native cover and richness, but there were no indirect effects. In intermediate marshes, introduced cover and salinity reduced native cover and richness, and indirect effects were weakly positive because salinity negatively affected introduced cover. In brackish and saline marshes increasing salinity and flooding reduced native cover and richness. Our results suggest that climate change will negatively affect all wetland plant communities, and invasion will negatively affect fresher wetlands; however, climate change will not exacerbate invasions in wetlands and could reduce introduced species effects.

Keywords Coastal wetlands · Plant communities · Sea level rise · Introduced plants · Salinity

Introduction

Coastal wetlands provide important ecosystem services to humans, but they are threatened by numerous anthropogenic stressors. Two notable stressors are climate change and introduced species, both of which can disrupt native wetland plant communities and cause widespread changes in ecosystem structure and function (Zedler and Kercher 2004; Erwin 2009). These stressors separately can have direct impacts on wetland communities, but they can also produce indirect effects such that climate change can affect native plants by exacerbating or reducing invasion. Studies have shown that indirect effects can be equally or more important than direct effects in affecting species responses to climate (Tylianakis et al. 2008; Adler et al. 2009; Ockendon et al. 2014). Determining the strength of direct and indirect factors and how their importance may change across wetland gradients is central to understanding and managing wetlands into the future.

Wetland plant communities are strongly driven by the hydrologic regime, such as tidal amplitude and fresh run-off, that may directly and indirectly determine their structure and composition, for example through facilitating invasion of plant species (Matthews et al. 2009; Keddy 2010). Several authors have suggested that climate-change induced sea-level rise may force shifts in wetland plant communities by modifying flooding and salinity regimes (Hester et al. 2001; Krauss et al. 2009). Shifts in salinity have been predicted to alter marsh habitats by converting communities resulting in a high prevalence of more salt-tolerant species (Sharpe and Baldwin 2012). Similarly, increases in flooding

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and water level have been shown to reduce growth and germination of some species and alter species composition towards more flood tolerant taxa (Fagherazzi et al. 2019). These plant community and ecosystem-level changes are predicted to result in considerably altered ecological function and ecosystem services of these wetlands (Noe et al. 2013; Visser et al. 2013; Stagg et al. 2018). Salinity and water depth could also change because of hydrologic restoration or changes in riverine flow and that these parameters (salinity, water depth) are necessary to assess because they drive marsh vegetation across a landscape gradient, irrespective of climate change (Turner and Lewis 1996; Howard et al. 2017).

Added to the abiotic stressors of saltwater influx and increased flooding is pressure from introduced species that may further indirectly negatively impact coastal wetlands. Introduced species can reduce species diversity and impact the provision of ecosystem services such as habitat for wildlife and birds (Kettenring et al. 2012), especially if introduced species are better equipped to cope with more saline and flooded conditions compared to native plants (Vasquez et al. 2005; Achenbach and Brix 2014). Thus, in addition to the direct stressors of salinity and flooding, climate change may also have indirect negative effects on native wetland communities via promotion of introduced species. Understanding patterns in wetland vegetation response to direct and indirect climate change effects is critical for our ability to better predict future dynamics in coastal systems in the face of rapid climate change.

Coastal marshes comprise a wide array of plant communities as they are arranged along a salinity gradient from fresh to saline habitat; thus it is possible that the effects of climate change and introduced species on these marshes will differ across the landscape (Wang et al. 2006; Glick et al. 2013, Farrer et al. 2021). Marshes differ in species richness and species composition and may have variable tolerances for abiotic and biotic stressors. For example, fresh marshes may be particularly sensitive to increases in salinity due to lack of adaptations for elevated salt, or fresh marshes with higher species richness may be more vulnerable to species loss from invasions (Battaglia et al. 2009). On the other hand, saline marshes may contain particularly flood and salinity tolerant species (Naidoo et al. 1992).

The Gulf of Mexico has experienced the highest wetland loss compared to the other coastal regions in continental USA (Dahl and Stedman 2013). Coastal wetlands in Louisiana experience extensive area loss caused by decreased sediment supply due to Mississippi River leveeing and damming, canal dredging, as well as subsurface fluid extraction (Day et al. 2000; Blum and Roberts 2009; Kolker et al. 2011; Jankowski et al. 2017; Day et al. 2019). It has been estimated that coastal Louisiana has lost approximately 5,000 km^2 of wetlands over the past century and similar trends are predicted to continue as the area experiences the world's highest rates of relative sea-level rise (Couvillion et al. 2011; Couvillion et al. 2016). An increase in relative sea-level not only increases water depth but also saltwater fluxes in these systems. Furthermore, predicted increase in the strength and the number of hurricane events (Estrada et al. 2015; Pant and Cha 2019) that will bring storm surge, flooding and salt water into wetlands can further destabilize wetland plant communities. For example, following Hurricane Sandy in New Jersey, coastal marshes were most affected with severe degradation occurring in almost 50 % of wetlands (Hauser et al. 2015). Here, we test the relative importance of direct (i.e., soil porewater salinity and water depth) and indirect effects (i.e., plant invasions) of climate change on native plant species richness, composition and cover along a landscape-scale salinity gradient in coastal Louisiana using vegetation and soil data from the Coastwide Reference Monitoring System (CRMS).

First, we compared native and introduced species richness and cover across wetland types to assess the scale of differences between fresh, intermediate, brackish and saline wetlands. We hypothesize that fresh wetlands have greater diversity of native plants as found in previous studies (Visser et al. 1998; Meyerson et al. 2000). Furthermore, we also hypothesize that fresh wetlands have a greater diversity and cover of introduced plants; however there are few systematic studies of invasion across salinity gradients (Hurst and Boon 2016). Second, using path analysis we teased apart direct and indirect effects of climate change. We hypothesised that (1) direct effects through increases in salinity and water depth regimes will negatively affect native species and will shift competitive dynamics favouring introduced species that are better adapted to environmental fluctuations and disturbance, (2) indirect effects through an increase in introduced species abundance will negatively affect native species communities. Much is unknown about how climate change may impact invasion with cascading effects on native systems, particularly in wetlands (Bradley et al. 2010; Bellard et al. 2013), and both management and policy have generally viewed climate change and plant invasions as important but separate issues (Hellmann et al. 2008; Pyke et al. 2008; Beaury et al. 2020). To our knowledge, this study represents one of the few attempts to comprehensively analyse the role of direct effects of climate change as well as its indirect effects via plant invasion on native plant species richness and composition in coastal wetlands of Louisiana. Our results will contribute to better understanding of the global change effects on coastal wetlands and elucidate which wetlands may be more vulnerable to future global change.

Materials and Methods

CRMS Data

CRMS was established in response to widespread land loss along the northern Gulf of Mexico coast in Louisiana (Couvillion et al. 2011). Since its establishment in 2003, CRMS in Louisiana has provided the collection and developed methods for vegetation assessment that has been used to assess land management activities, including restoration project effectiveness on a coastwide scale at over 390 sites (Cretini et al. 2011).

Using the CRMS data (CPRA 2017) we analysed plant species composition, soil pore water salinity (ppt) and water depth (cm) data that were consistently monitored by CRMS over the period of 11 years (2007–2017) (4234 plots, Online resource 1). Flooding regime term (% of year flooded) was strongly correlated with water depth ($R^2 = 0.81$), indicating strong collinearity, and was removed from the analysis. Each CRMS site contains ten vegetation plots ($4m^2$) (Stagg et al. 2013). Every year, each plot was assigned to one of five community types (i.e., fresh, intermediate, brackish, saline or swamp) based on its vegetation composition (Visser et al. 1998; Visser and Sasser 1998; CPRA 2017), and we assigned each plot a single community type based on the type that was most frequent. Briefly, dominant plant species in fresh marsh are *Panicum hemitomon*, *Hydrocotyle sp.*, *Pontederia cordata*, *Sagittaria sp.*, and *Althernantera philoxeroides* and salinity range is 0–3 ‰ (Visser et al. 1998). In intermediate marsh, the dominant vegetation consists of *Spartina patens*, *Vigna luteola*, *Scirpus califomicus*, *Echinochloa walteri*, *Sagittaria sp.*, *Cladium jamaicense*, and *Phragmites australis* and salinity ranges 2–8 ‰ (Visser et al. 1998). In brackish marsh, dominant species are *Spartina patens*, *Scirpus americanus*, *Scirpus robustus*, and *Eleocharis parvula* and salinity ranges 4–18 ‰ (Visser et al. 1998). In saline marsh, the dominant species are a combination of *Spartina alterniflora*, *Juncus roemerianus*, *Batis maritima*, *Avicennia germinans*, and *Distichlis spicata* and salinity ranges 8–29 ‰ (Visser et al. 1998). For the purpose of this study, we excluded “swamp” vegetation classification data from our analyses. Total vegetation cover of each species in each plot was estimated annually during peak biomass (August-September) (Folse et al. 2008). The sum of vegetation cover may exceed 100 % because of overlapping canopies (Cretini et al. 2011).

We used CRMS soil pore water salinity and water depth data to assess the direct global change effects on vegetation dynamics. Soil pore water was extracted on a monthly basis using 10 cm (3.94 in) and 30 cm (11.81 in) syringe sippers (Sprecher 2000; Bohn 2001). Three salinity measurements per depth per site were taken in at least five (up to ten) vegetation plots during emergent vegetation sampling (Folse et al. 2012). These water quality readings were taken with a portable, hand-held instrument (e.g., YSI 30 or equivalent) (Folse et al. 2012). We used in our analysis soil pore water salinity measurements from top 10 cm only. The water level was measured with submersible data logger (e.g., YSI 600LS, Hydrolab MS5 or equivalent) (Folse et al. 2012) in available water within 200 m of CRMS site or in a well continuously (i.e., hourly) (Steyer et al. 1995).

Because the plots within each site are close to one another in space (i.e., not independent), we averaged species cover, water depth, and soil porewater salinity data over all plots in each site where these data were available (Online resource 1), prior to statistical analysis. Then, we averaged species cover, salinity, and water depth over the available years, resulting in one value for each site. We did this averaging for three reasons: (1) because the data were patchy in time, and few sites had vegetation, salinity, and water depth data for many years, (2) because vegetation dynamics in these plots are relatively slow due to the long-lived, perennial nature of most of the plant species, and (3) because mean annual salinity and water depth measurements were not variable within a site over the 11-year period (compared to their variability among sites and compared to the changes that will likely be seen in the future). Thus, we used a space-for-time substitution to assess how climate change (increase in salinity and water depth) and invasion will affect native marsh communities. The space-for-time-substitution technique assumes that spatial and temporal variation is equivalent, and it uses time as a surrogate for the past environment to model past and future events (Pickett 1989; Blois et al. 2013; Lester et al. 2014). This resulted in a dataset with 49, 62, 42 and 66 sites in fresh, intermediate, brackish, and saline marshes, respectively (Online resource 1). Lastly, to assign each species in the dataset as native/introduced, we obtained a Louisiana introduced species lists from the Louisiana Native Plant Society (https://www.lnps.org/references). To characterize the marshes in terms of their abiotic differences, we plotted mean salinity and mean water depth by marsh type (Online resource 2).

Statistical Analysis

To analyse the differences in native and introduced plant richness and cover across marsh types, we used a one-way Anova ‘aov’ function in R. When the main effect was significant, Tukey’s HSD was used for pairwise comparisons.

The direct and indirect effect of abiotic (water depth and soil porewater salinity) and biotic factors (introduced species cover) on native plant richness, cover, and composition in the four plant communities in the Gulf (fresh, intermediate, brackish and saline) were assessed using path analysis. Composition values were quantified as x-axis coordinates of a Principal Coordinates Analysis (PCoA) computed for each community using R package ‘vegan’ (Oksanen et al. 2017). For all marshes, salinity was highly skewed and contained points with high leverage, so it was log transformed. Collinearity between water depth and salinity was checked and did not occur in any of the community types. All data were then standardized by subtracting the mean and dividing by the standard deviation prior to path analysis so that all effect sizes were directly comparable.

For each community, a pre-defined regression model was fitted using the LAVAAN package (Rosseel 2012). In brief, the full model included the direct effects of salinity and water depth on introduced cover, native cover, native richness, and native composition, the direct effects of introduced cover on native cover, native richness, and native composition, and covariances between all native variables. In brackish and saline marshes, however, we found that introduced species were too infrequent or at too low abundance to include in the model, so only direct effects of climate change factors were tested. Subsequently, the variables with the lowest significance were removed in a backward selection process to find the best suitable model (with the lowest AIC) to balance model fit and parsimony (Grace and Pugesek 1997). The final model fit was assessed with the Chi^2 statistic, the root mean square error of approximation (RMSEA), and the Tucker Lewis Index (because models like ours with low degrees of freedom can yield high RMSEA fits (Kenny et al. 2015)). Chi^2 values associated with a P-value > 0.05 indicate a good model fit. A RMSEA < 0.05, and a TLI > 0.95 indicate a good model fit; while a RMSEA < 0.08 and a TLI > 0.90 indicate an acceptable model fit (Bentler 1990; Hu and Bentler 1999; Kline 2010; Schweizer 2010). Z-statistics were used to determine the significance of each pathway. Only the best fit models are shown. To visualize bivariate patterns among variables in the path analysis, we plotted scatterplots of dependent variables vs. explanatory variables. All analyses were performed in the R 3.4.3 programming language (R Core Team 2018).

Results

Comparison of Native and Introduced Cover and Richness Across Marsh Types

Across marsh types, mean native plant species cover was the highest in fresh marshes and gradually decreased along the salinity gradient (Fig. 1a) ($F_{(3,211)} = 11.56$, $P < 0.001$). Native plant cover in fresh marshes was significantly higher compared to intermediate ($P = 0.03$, Tukey post-hoc test), brackish ($P = 0.004$) and saline marshes ($P < 0.001$), whereas native plant cover in brackish marshes was similar to intermediate ($P = 0.75$) and saline marshes ($P = 0.22$) (Fig. 1a, b, c, d). Similarly, to native species cover, introduced species cover was the highest in fresh marshes but overall, considerably lower than native species cover and more uniform across marsh types ($F_{(3,211)} = 4.34$, $P = 0.005$) (Fig. 1).

Across marsh types, mean native plant species richness was highest in fresh marshes (Fig. 1e) and decreased significantly along a salinity gradient (Fig. 1f, g, h) ($F_{(3,211)} = 108.8$, $P < 0.001$). Introduced species richness followed a similar trend to native species richness ($F_{(3,211)} = 72.85$, $P < 0.001$), however introduced species richness in brackish and saline marshes did not differ significantly and was near zero (Fig. 1). Total number of introduced species in fresh marshes: 22, intermediate: 16, brackish: 4, saline: 2, mean per site values shown in Fig. 1.

The most common native species that were present in the dataset were *Spartina patens* (Poaceae) which had highest cover in all but fresh marshes, and *Leersia hexandra* (Poaceae) and *Panicum hemitomon* (Poaceae) which were most abundant in fresh marshes. *Polygonum punctatum* (Polygonaceae) and *Sagittaria lancifolia* (Alismataceae) were also abundant in fresh and intermediate marshes. *Bolboschoenus robustus* (Cyperaceae), *Distichlis spicata* (Poaceae) and *Spartina alterniflora* (Poaceae) were common across both brackish and saline marshes. *Schoenoplectus americanus* (Cyperaceae) was common in intermediate and brackish marshes. Some native species were abundant only in one particular marsh type, i.e., *Eleocharis sp.* (Cyperaceae) in fresh marshes, *Vigna luteola* (Fabaceae) in intermediate marshes and *Juncus roemarinus* (Juncaceae) in saline marshes.

The most common introduced species in the data set across all marsh types was *Phragmites australis* (Poaceae); we classified *Phragmites australis* as introduced because the CRMS did not distinguish among haplotypes and because all *Phragmites australis* in the Gulf region are highly likely to be either recent or ancient introductions (Lambertini et al. 2012; Farrer et al. 2021). We have recently reported the presence of both Gulf haplotype (haplotype I) and Delta haplotype (haplotype M1) in Louisiana (Farrer et al. 2021). All *P. australis* haplotypes in Louisiana are expanding their range and behaving like invasive species (Meyerson et al. 2010; Bhattarai and Cronin 2014; Meyerson et al. 2016; Farrer et al. 2021). Though we include *Phragmites australis* as an introduced species, excluding it from our analysis does not change the results. *Alternanthera philoxeroides* (Amaranthaceae) was the second most common overall and was present in all but saline marshes. *Colocasia esculenta* (Araceae) and *Ludwiga grandiflora* (Myrtaceae) were common only in fresh and intermediate marshes. *Panicum repens* (Poaceae) was common only in intermediate and saline marshes. Some introduced plants were abundant in only fresh marshes, i.e., *Luziola peruviana* (Poaceae), while others, i.e., *Echinochloa crus-galli* (Poaceae) and *Amaranthus sp.* (Amaranthaceae) were more abundant in brackish marshes. For full list of native and introduced plant species see Online resource 3.

Path Analysis

We analysed both direct (i.e., soil porewater salinity and water depth) and indirect effects (i.e., via plant invasions) of climate change on native plant species cover, richness, and composition. The results from path analysis were largely marsh type

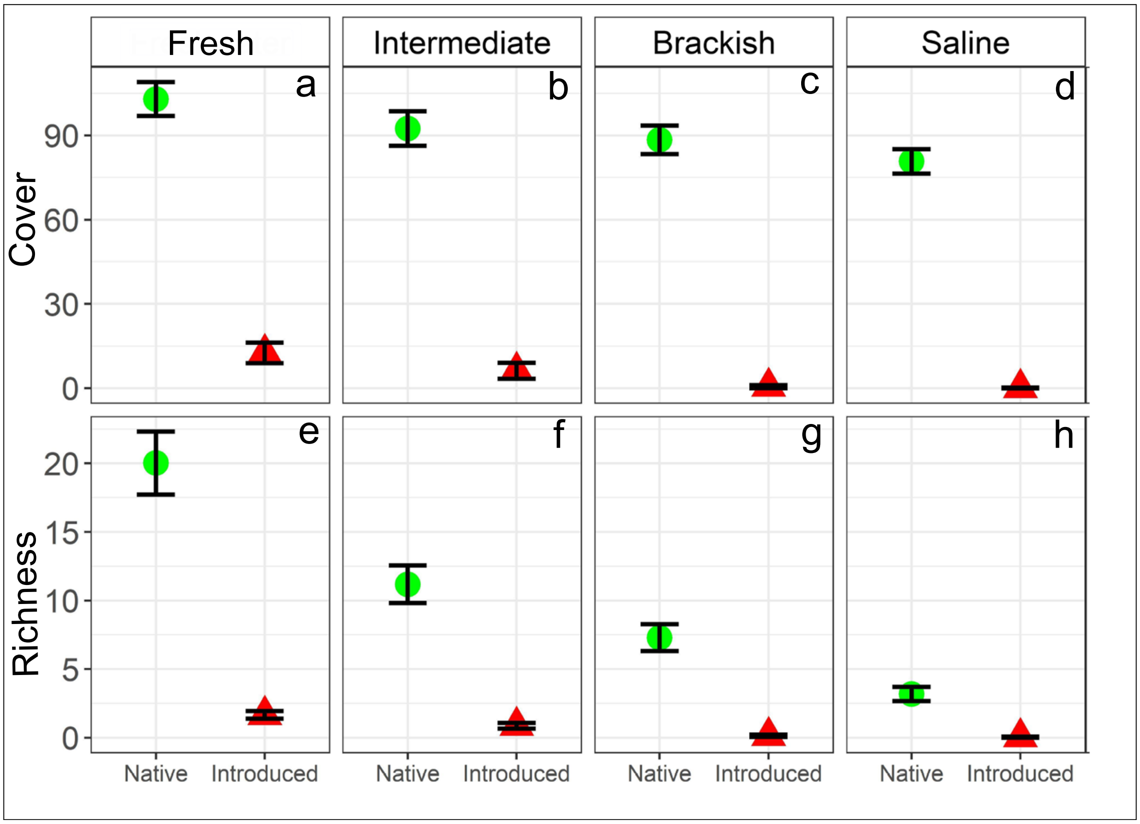

Fig. 1 Mean native and introduced plant species cover (%, ±SE) (a, b, c, d) and richness (n, ±SE) (e, f, g, h) in fresh, intermediate, brackish and saline marshes, respectively, from 2007 to 2017 based on Coastwide Reference Monitoring System (CRMS) data for Louisiana, USA

specific (see Fig. 2 for path analyses, and Figs. 3 and 4 and Online resource 4, 5 for bivariate relationships among variables).

In fresh marsh communities, we found that salinity and introduced plant cover both separately affected aspects of native plant community structure (Figs. 2a and 3a and b; Online resource 4 and 5); however, no indirect effects were found because climate variables did not affect introduced cover (Figs. 2a and 4a and b). Specifically, soil porewater salinity and introduced cover had strong negative effects on native species cover and also strongly altered native species composition (Fig. 3a, b, Online resource 4e). Soil porewater salinity reduced native species richness as well (Online resource 5a).

In intermediate marshes, soil porewater salinity directly reduced native species richness and native species cover and altered native composition (Figs. 2b and 3e; Online resource 4f, 5b). Soil porewater salinity also had a negative effect on introduced species cover which in turn reduced native richness and cover; thus, creating a weak positive indirect effect (Figs. 2b and 4c). However, water depth (cm) did not affect introduced cover (Fig. 4d).

In brackish and saline marshes, introduced cover was too low to include in the analysis (Fig. 1c, d), but path diagrams were analysed to investigate direct effects and compare to the other marsh types. In brackish marshes, water depth had strong negative effects on both native species richness and native species cover (Figs. 2c and 3h, Online resource 5 g), whereas soil porewater salinity had a negative effect on native species richness (Online resource 5c). In saline marshes, soil porewater salinity had the strongest negative effect on native species cover (Figs. 2d and 3i) followed by negative effects also on native species richness (Online resource 5d). Water depth also reduced native species cover (Fig. 3j).

Discussion

Coastal marshes play a key role globally by supporting biodiversity and providing important ecosystem functions such as coastal flood defence and bio sequestration of greenhouse gases (Burkett and Kusler 2000; Barbier et al. 2011; Cronk and Fennessy 2016; Carnell et al. 2018). Teasing apart how direct and indirect effects of anthropogenic factors on wetland plant communities may change across the landscape is essential for effective management. In general, we found strong negative direct effects of salinity and flooding on native plant communities across the gradient. Introduced species were more prevalent and negatively affected native communities at the fresh end of the gradient (in fresh and intermediate marshes). However, we only detected indirect effects of

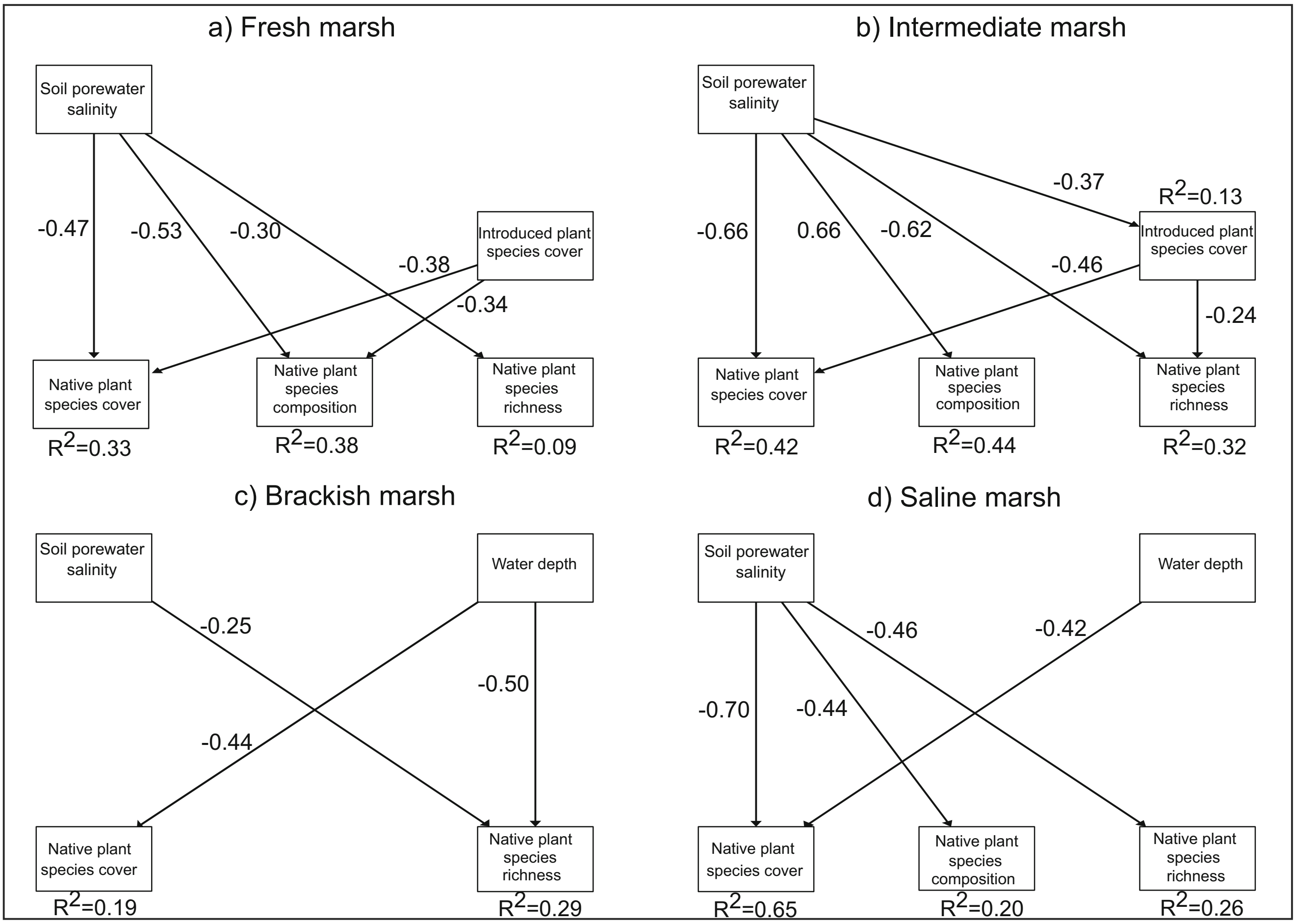

Fig. 2 Path analysis showing significant ($P < 0.05$) relationships among direct and indirect environmental drivers (i.e., log transformed soil porewater salinity (ppt), water depth (cm) and introduced plant species cover (%)) on native plant species richness (n), cover (%) and composition from 2007–2017 in fresh (a), intermediate (b), brackish (c), and salt (d) marshes in Louisiana, USA. Models had a good overall fit: fresh ($Chi^2 = 2.9$, P = 0.41, RMSEA < 0.001, TLI = 1.0), intermediate ($Chi^2 = 0.20$, P = 0.66, RMSEA < 0.001, TLI = 1.1), brackish ($Chi^2 = 2.5$, P = 0.28, RMSEA = 0.082, TLI = 0.93), saline ($Chi^2 = 4.8$, P = 0.09, RMSA = 0.15, TLI = 0.90)

climate change via introduced species in intermediate marshes, and indirect effects were surprisingly positive because invaders there were negatively affected by climate change.

Our results support previous research (Visser et al. 1998; Meyerson et al. 2000) showing that fresh, intermediate, brackish and saline marshes differed significantly in their native plant species richness, with fresh marshes being the most diverse (i.e. on average twenty plant species) with richness gradually decreasing and saline marshes being the most species poor (i.e. on average four plant species). Introduced species richness and cover followed the same pattern, but generally there were few introduced species in these marshes. These results are consistent with the general assumption that more saline marshes are immune to invasion (Hurst and Boon 2016). Much research has shown that saline conditions are an important stressor of wetland plants that limit the diversity and distribution of coastal marsh species (Burdick and Konisky 2003; Crain et al. 2004; Engels and Jensen 2010; Cui et al. 2011; Batriu et al. 2015). Another considerable stressor in saline wetlands is hydrogen sulfide which acts as a phytotoxin and may accumulate as a result of microbial reduction of sulfate during anaerobiosis, particularly in saline marshes (Sharpe and Baldwin 2012; Lamers et al. 2013). Sulfide can negatively affect plant nutrient uptake disturbing cell metabolism and energy transfer, increase root loss and impair plant growth rate (Lamers et al. 2013). Overall, these comparisons of richness across community types suggest that increases in salinity exposure in the future may reduce both native and introduced plant richness and may further suggest that fresher marshes are more susceptible to impacts by introduced species; however, analyses we performed on each community type are necessary to understand shorter-term or transitional dynamics that may occur at a particular point along the landscape gradient.

We found support for our hypothesis that climate change had strong direct negative impacts on native species richness and cover and altered community composition across all

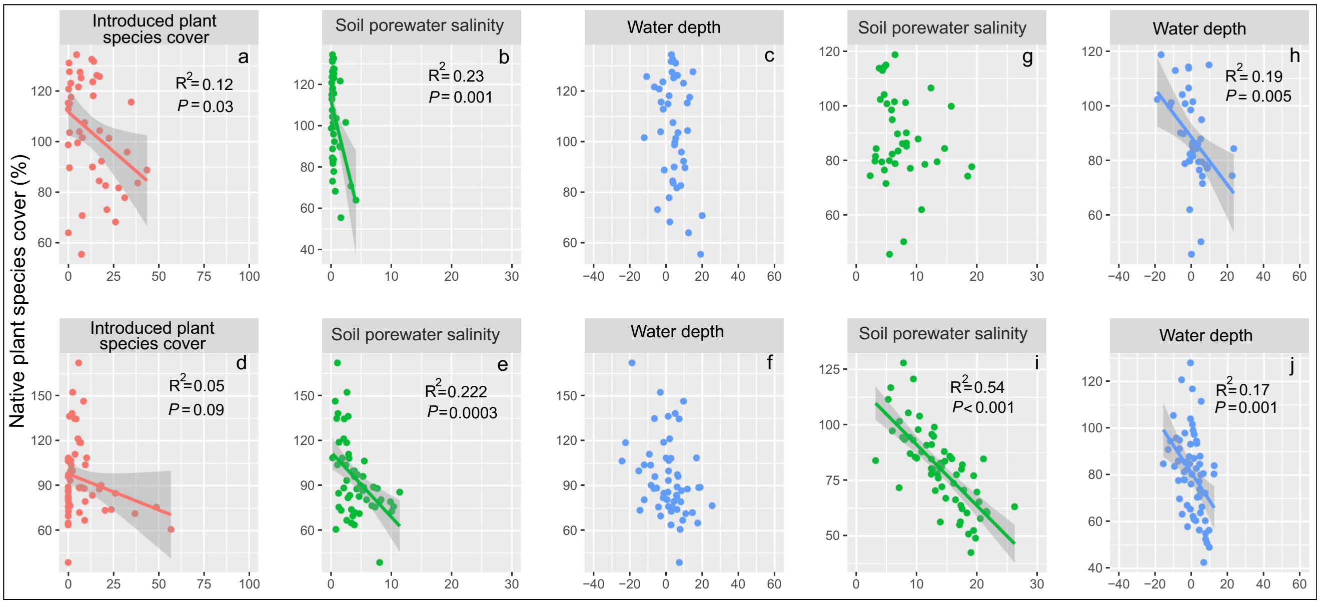

Fig. 3 Relationships between fresh marsh native plant species cover (%) and introduced plant species cover (%) (a), soil porewater salinity (ppt) (b) and water depth (cm) (c); intermediate marsh native plant species cover % and introduced plant species cover (d), soil porewater salinity (e) and water depth (f); brackish marsh native plant species cover and soil porewater salinity (g) and water depth (h); and saline marsh native plant species cover and soil porewater salinity (i) and water depth (j) from 2007 to 2017 based on Coastwide Reference Monitoring System (CRMS) data for Louisiana, USA. Data used in the path analysis are shown (with the exception of salinity which is not log-transformed here for ease of visualization); lines and bivariate R^2 values and P values are only shown for significant relationships in the path analysis ($P < 0.001$). Note that the bivariate R^2 and P values here may be different from the path analysis (Fig. 2), because the path analysis is a multivariate analysis

marsh types. Increasing soil porewater salinity reduced native species richness and/or cover across all marshes. Water depth reduced native species richness and/or cover in brackish and saline marshes. As mentioned above, salinity represents an acute stress to plants, and water depth too represents a stressor as it causes anoxia in the rooting zone (Jackson and Colmer 2005). Thus, it is not surprising that within each marsh community type, variation in these stressors is associated with a reduction in richness and cover of native plants. Interestingly, native plant composition was affected by salinity in all but brackish marshes and was never affected by water depth; because species within different marsh types likely vary in salinity tolerance, a shift in community composition with salinity stress is not surprising. In addition to salinity and water depth, duration of flooding, although not tested in our study, is an important factor that has been shown to negatively affect the biomass of some grass species in these marsh systems, i.e. *S. patens* (Snedden et al. 2015; Visser and Peterson 2015).This clearly warrants further investigation.

Introduced species were predominantly present in fresh and intermediate marshes and their presence was strongly associated with change in native composition and reduction in native cover and richness. In brackish and saline marshes, introduced species were too rare and infrequent to test their effect statistically. In fresh marshes, the negative impacts of introduced plants did not translate to indirect effects, because introduced cover was unaffected by climate change. In intermediate marshes, salinity actually had a negative effect on introduced cover, resulting in a net positive indirect effect of climate change on native plant cover and richness. However, these net positive indirect effects were small (cover: -0.37*-0.46 = 0.17, richness: -0.37*-0.24 = 0.089), and did not offset the large negative direct effects of salinity on native cover (-0.66) and richness (-0.62). The result that direct effects of climate change are much stronger than indirect effects via species interactions is consistent with some research in semi-arid grassland communities (Chu et al. 2016) and tallgrass prairie (Adler and HilleRisLambers 2008) but not work in other grasslands (Adler et al. 2012; Farrer et al. 2015). Theory posits that the strength of direct effects should increase with the strength of niche differences and with greater variation in direct effect (Adler et al. 2012; Kleinhesselink and Adler 2015). Future research in coastal systems should be aimed at understanding which native species are at risk from (i.e., have the greatest niche overlap with) common invaders and to understand the variation that may exist in the direct effects of climate change on different native species, which we study here in aggregate.

To investigate patterns at a more species-specific level, we showed that the introduced species with the highest cover across all marsh types were *P. australis* and *A. philoxeroides* which are common wetland invaders across North America (Hunt et al. 2017; Tanveer et al. 2018). These two species, especially *P. australis*, are likely to withstand future sea level

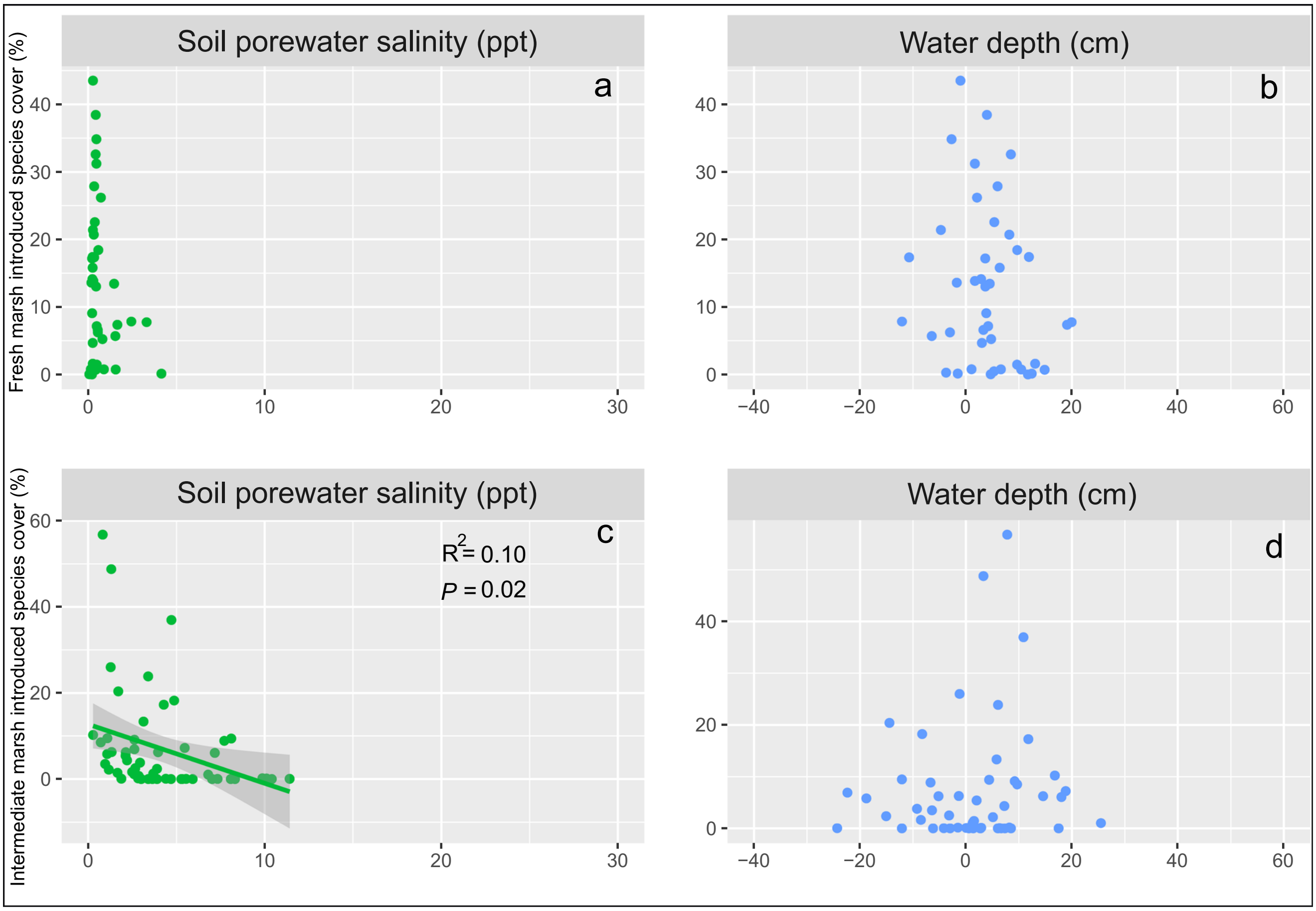

Fig. 4 Introduced plant species cover (%) relationship with soil porewater salinity (ppt) and water depth (cm) in fresh marshes (a, b), respectively, and intermediate marshes (c, d), respectively, from 2007 to 2017 based on Coastwide Reference Monitoring System (CRMS) data for Louisiana, USA. Data used in the path analysis are shown (with the exception of salinity which is not log-transformed here for ease of visualization); lines and bivariate R^2 values and P values are only shown for significant relationships in the path analysis ($P < 0.001$). Note that the bivariate R^2 and P values here may be different from the path analysis (Fig. 2), because the path analysis is a multivariate analysis

rise associated with climate change as they are able to occupy a large salinity gradient and thus do not appear to be confined by specific abiotic conditions (data not shown). On the other hand, some introduced species were more restricted to fresh marshes (i.e., *L. peruviana*) or brackish marshes (i.e., *E. crus-galli* and *Amaranthus sp.*) and were less common in other marsh types, suggesting that these species may be somewhat constrained in their ability to respond to climate change. As sea level rises and salinity increases, these species will exhibit declines in abundances in their current locations and would have to shift their distribution and disperse to new areas with suitable salinity levels. The dominant native species differed across the different marsh types, which suggests that native species were more confined by the abiotic conditions, compared to introduced species, in these marsh systems making them more susceptible to future abiotic and biotic changes. For example, native *Eleocharis sp.*, *V. luteola* and *J. roemarinus* may be most at risk of decreasing in abundance in the future as they almost exclusively occur in a specific marsh type and are thus susceptible to changes in abiotic and biotic conditions compared to other species that are able to grow along a salinity gradient.

The path analyses allow us to predict short-term outcomes of climate change in these marsh communities, for example before significant dispersal among community types initiates permanent conversion from one community to another (Smith et al. 2009). In fresh marshes, the negative direct effects of climate change and the negative impacts of introduced plants on natives, together with the lack of direct climate effects on introduced plants suggest that marshes in the future will see a relative increase in the cover of introduced plants and a relative (and absolute) decline in natives. In intermediate marshes, the introduced species, while still negatively affected by climate change, were more tolerant of salinity compared to native species (the coefficient describing salinity effect on native cover was more negative than the coefficient for introduced cover), thus there too a relative increase in introduced plants is predicted for the near future. For brackish and saline systems, native cover and richness is predicted to decline with future climate change, but invasion dynamics are unclear. In brackish systems, invaders were present in 33 % of the plots, but at very low abundances (mean 1.7 % cover), thus they have the potential to increase with climate change. We therefore encourage future research to examine invasion-climate dynamics in brackish marshes. In saline marshes, however, invaders were only present in 3 % of the plots, so we do not believe these marshes are likely to see a systematic increase in introduced cover over the short-term.

While our study overall suggests strong negative effects of climate change in coastal marshes, it also has implications for any natural or anthropogenic hydrologic modifications that influence marsh salinity or flooding. For example, many large-scale river diversions are slated for Louisiana in the near future (CPRA 2017), and our work suggests that diversions that freshen marshes may increase native species richness and cover relative to invasive plants in the short term but also may increase their susceptibility to invasion in the long term. Our results also suggest that brackish and saline areas will be most vulnerable to reductions in native richness and cover from increases in water depth due to natural subsidence from sediment compaction.

In conclusion, our study suggests that climate change will cause degradation of marsh communities across the entire landscape salinity gradient and invasion will negatively affect fresher wetlands; however, climate change will not exacerbate invasions in coastal wetlands and could actually reduce introduced effects by limiting the invaders as well. The dominance of direct effects in this system and lack of indirect effects suggests that invasion and climate impacts may be managed separately. Understanding how salinity vs. flooding differentially impacts different aspects of community structure (richness, cover, composition) across the landscape gradient is important for managing for desired functions in particular marshes into the future and is also key for predicting the outcomes of our management efforts.

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Data Availability Data are available in the Mendeley Data Digital Repository, https://data.mendeley.com/datasets/tpz77s9c58/1 (Birnbaum et al., 2021)

Code Availability Code is available in the GitHub Digital Repository, https://github.com/PWaryszak/CRMS

Declarations

Conflicts of Interest/Competing Interests Authors declare no conflict of interest.

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