Salinity Thresholds for Understory Plants in Coastal Wetlands.

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Research Article

Abstract

The effects of sea level rise and coastal saltwater intrusion on wetland plants can extend well above the high-tide line due to drought, hurricanes, and groundwater intrusion. Research has examined how coastal salt marsh plant communities respond to increased flooding and salinity, but more inland coastal systems have received less attention. The aim of this study was to identify whether ground layer plants exhibit threshold responses to salinity exposure. We used two vegetation surveys throughout the Albemarle-Pamlico Peninsula (APP) of North Carolina, USA to assess vegetation in a low elevation landscape ($\leq$ 3.8 m) experiencing high rates of sea level rise (3-4 mm/year). We examined the primary drivers of community composition change using Non-metric Multidimensional Scaling (NMDS), and used Threshold Indicator Taxa Analysis (TITAN) to detect thresholds of compositional change based on indicator taxa, in response to potential indicators of exposure to saltwater (elevation, Na, and the S Ca + Mg). Salinity and elevation explained 64% of the variation in community composition, and we found two salinity thresholds for both soil Na^+ (265 and 3843 g Na^+/g), and $Ca^+ + Mg^+$ (42 and 126 µeq/g) where major changes in community composition occur on the APP. Similar sets of species showed sensitivity to these different metrics of salt exposure. Overall, our results showed that ground layer plants can be used as reliable indicators of salinity thresholds in coastal wetlands. These results can be used for monitoring salt exposure of ecosystems and for identifying areas at risk for undergoing future community shifts.

Introduction

Coastal wetlands are some of the most vulnerable ecosystems on the frontlines of global change (Craft et al. 2009; Schuerch et al. 2018). As hurricanes and drought become more common, and human infrastructure expands (i.e. canal creation, groundwater extraction for irrigation), the influx of seawater further inland into freshwater dominated systems (i.e. saltwater intrusion) has become a more severe environmental stressor (Hoeppner et al. 2008; Manda et al 2014; Zhou et al. 2017; Bhattachan et al. 2018; Herbert et al. 2018). Soil salinization is an increasing threat throughout the world to biologically diverse wetlands that are home to a high number of endemic species which are vulnerable, threatened, or endangered (Herbert et al. 2018; Noss et al. 2015). One of the most dramatic manifestations of salinization is the rapid mortality of trees in freshwater wetlands, leading to the expansion of "ghost forests" (Kirwan and Gedan 2019; Tully et al. 2019; Ury et al. 2021; White et al. 2021). The potential for biodiversity, carbon storage, and plant community change has prompted recent research on the main drivers of changes in freshwater wetlands and brackish marshes (Pezeshki et al. 1990; Pennings et al. 2005; Desantis et al. 2007; Schile et al. 2017; Greene et al. 2019; Taillie et al. 2019; Smart et al. 2020).

Plant species in these coastal landscapes exhibit wide variation in their sensitivity to the magnitude and frequency of salinization (Poulter et al. 2009). Elevated salt exposure causes osmotic and ionic toxicity stress in plants (Kozlowski, 1997), and alters their ability to use available nutrients in the soil (Eallonardo et al. 2013). Increased salt exposure lowers hydraulic conductance, which leads to reducing whole-plant performance (e.g. growth rates), impeding photosynthetic function, causing leaf loss (Chaves et al. 2009; Parida and Das 2005ab), and limiting regeneration by inhibiting seed germination (Krauss 1998,

Koslowski 1997). Physiological traits govern plants' ability to tolerate, or adapt to, increased stress (Munns and Tester 2008), and adaptations for tolerating salinity are typically associated with trade-offs against growth or reproduction, so the relative abundance of salt-adapted plants should be associated with the historical regime of salt exposure in an area.

Mechanisms responsible for the sensitivity of individual plant taxa to salinity are well studied (Parida and Das, 2005; Parihar et al. 2015); however, comprehensive assessments from field studies that use a quantitative approach for understanding the consequences of species-level sensitivity to salinity on community patterns are sparse in the literature. Often, studies are limited to a small number of species, and the metric of sensitivity is largely based on syntheses, or controlled greenhouse experiments that can be limited in scope (Parida and Das, 2005; Negrão et al. 2017). In addition, the majority of prior research has focused on forest overstory trees, or agricultural crop responses to salinity. Although trees and agricultural crops are ecologically and commercially important, the herbaceous dominated communities that make up the ground layer of coastal forested wetlands, and the majority of biomass in fresh and saltwater marshes, support a high proportion of coastal plain plant diversity (Bratton 1976). In addition to being more diverse, ground layer communities are likely to be more responsive to environmental change than overstory trees because of their shorter life span. Changes in the presence, absence, and relative abundance of ground layer plant taxa may thus serve as an indicator of the abiotic conditions that a community is experiencing, and has experienced in the recent past (Osland et al. 2019).

We know plant species respond to salt exposure quite differently; however, one key unknown is whether variability in sensitivity to salt exposure is distributed somewhat continuously across species in an assemblage, or if a substantial fraction of species in a regional pool exhibit shifts in abundance at similar points along a gradient. The latter response would suggest that the system can be described as having a critical threshold, or tipping point (Biesner et al., 2003; Scheffer et al., 2012). Identifying these thresholds can be useful for multiple reasons. First, if we can identify critical thresholds, we can detect areas on the landscape that are particularly likely to undergo transitions, and where management interventions might be necessary. Secondly, if monitoring of environmental conditions is difficult or costly, identifying sets of species that are most likely to shift in abundance as thresholds are crossed, and focusing monitoring on their presence, absence, or abundance can serve as an alternate tool (i.e., biosensor) for monitoring environmental quality and ecosystem health.

An additional challenge of assessing exposure to marine salts is that while topography and elevation determine vulnerability to flooding and salinity, the vulnerability of ecosystems to salinization is more complex. In addition to rising sea levels along the shoreline (Horton et al. 2009; Kemp et al., 2011), marine salts can penetrate inland well above the high tide line via storm surge, mixing during drought events, and groundwater intrusion. (Manda et al. 2014; Herbert et al. 2015). Shoreline ecosystems are continuously exposed to marine salts, while in inland wetlands, ecosystem salinization depends upon the retention of salts which can vary due to soil exchange, evaporative concentration, or incorporation into organic matter (Herbert et al. 2015). Furthermore, marine salts are chemically complex and the various constituent ions are likely to be differentially retained, and have different effects on vegetation (Tully et al. 2019). Plant

responses are integrated responses to salt exposure over time, and previous work on plant responses to saline stress in mature trees found that while changes in tree basal area showed similar declines in response to concentrations of chloride, sulfate, sodium, and elevation, changes in composition were more weakly associated with these drivers (Ury et al. 2020). Given the greater diversity of the plant community in the ground layer and its more rapid turnover time, it seems likely that composition will be affected by the components of salinity, but to what degree, and whether responses are consistent across different components needs further investigation.

The aim of this study was to identify whether there are critical thresholds where large changes in ground layer community composition occur in non-tidal coastal wetlands. Here, we address three questions: 1) Is salinity a primary environmental driver of ground layer plant community composition in coastal wetlands,2) Are there critical thresholds of salinity exposure that are associated with shifts in composition, and 3) If we identify thresholds, are community responses consistent across multiple components of salinity?

To address these questions, we combined understory, ground layer vegetation data from multiple sources across the Albemarle-Pamlico Peninsula (APP) in eastern North Carolina. Both vegetation and soils data were used to calculate taxa-specific indicator values using a well-known indicator species analytical approach (Dufrene et al. 2013) within Threshold Indicator Taxa ANalysis (TITAN, Baker and King 2015), a statistical model for detecting thresholds of community change.

Methods

The APP (Figure 1) is a low-lying region of North Carolina covering ~ 6,000 km^2 with the majority of land area less than 4m in elevation (Moorhead and Brinson 1995; Poulter et al. 2008), and largely comprised of state and federally owned preserves, wildlife refuges, and agricultural lands. Surrounded by the Albemarle, Pamlico, and Croatan Sounds, the APP is the second largest estuarine complex in the United States. The peninsula contains a wide range of woody and herbaceous wetland ecosystems, including upland mesic forests, freshwater forested wetlands, lowland evergreen and hardwood shrublands, pocosins (poorly drained wetlands with acidic soils, rich in organics), cypress and cedar swamps, and brackish marshes (Brinson 1991). Agricultural fields are hydrologically connected through a network of constructed ditches intended to drain water from higher elevation agricultural field. This ditch network makes the APP particularly vulnerable to salt stress especially in recent decades (Bhattachan et al. 2018).

Field surveys

To assess the effects of salinity on herbaceous wetland vegetation in the APP, we used two datasets. One data set (the "transect" data set) had been previously published in papers addressing different questions (Poulter et al. 2005; Taillie et al. 2019), and focused on intensively sampling gradients from marshes to forest at five locations in 2016 and 2017. The transect survey sites were located in public lands throughout the peninsula (Figure 1). Initially sampled by Poulter et al. (2005), this survey included 98 1-

m^2 randomized plots distributed across five forest-marsh transition sites (490 total plots). All five sites were then resampled by Taillie et al. (2019) in 2016. Each site consisted of three adjacent vegetation community zones (intact forest, transition/ghost forest, and brackish marsh) previously characterized by aerial imagery and qualitative visual assessment. Only the data collected during the 2016 survey were used in this study. See Poulter et al (2005) and Taillie et al (2019) for additional information regarding the transect survey protocol.

The second data set (the "peninsula-wide" data set), has not previously been published and focused on sampling a broader gradient of wetland types and environmental conditions in 2016. In total, vegetation surveys were conducted at 34 sites (5 sites from the transect survey, and 29 sites from the peninsula-wide survey) in 669, 1-m^2 plots to assess the range of environmental conditions where species occur throughout the APP (Figure 1). The peninsula-wide data set followed the Carolina Vegetation Survey protocol (CVS, Peet et al. 1998). We delineated 29 sites that were 400 m^2 or 100m^2 depending on the heterogeneity of dominant vegetation. At each site, we systematically located two (in the 100-m^2 sites) or eight (in the 400-m^2 sites) 1-m^2 plots for sampling herbaceous vegetation (woody and non-woody < 2m tall). We estimated percent cover of all species located in these plots. In both data sets, we identified all plants rooted in each plot less than 1m in height and estimated areal cover abundances for each species.

Soils from the transect survey were taken from the top 10 cm, sieved (2-mm mesh), and analyzed major cation using the Mehlich III extraction (Brookside Labs., New Knoxville, Ohio). At each site in the peninsula-wide survey, we sampled soils to 10-cm depths and sieved through 2-mm mesh; extracted fresh soils with deionized water; and analyzed for ion concentrations including base cations (Ca^{2+}, Mg^{2+}, and Na^+) on a CS12A column, and Cl^- using a AS-18 analytical column with Dionex ICS 2000 (Dionex Corporation, Sunnyvale, CA). Because two different soil extraction methods were used in the two different surveys (peninsula-wide and transect surveys), we included methodology as categorical factor within a second set of ordinations to test whether extraction method had a significant contribution to the outcome of the environmental drivers. We used a LiDAR-derived digital surface model (DSM) raster dataset with 6.1-m resolution, and vertical accuracy of +/− 0.13 m for calculating the elevation at each site analyzed in the study. This DSM was part of a statewide dataset collected in the 1990s. (See Bhattachan et al 2018 for additional information.) We calculated the average elevation at each site since microtopography varied across 4-18 points that were at least 10 m apart at each location.

Plant community responses

To determine whether salinity is a major driver of species composition throughout the APP, we used non-metric multidimensional scaling (NMS), a commonly used ordination method for plant community assessment. We used the R version 3.6.3 (R Core Team, 2019) packages *ecodist* (Goslee and Urban 2007) and *vegan* (Oksanen et al. 2019) to run the ordination analyses. We focused on three potential indicators of salinization: Elevation, Na^+ concentrations, and the sum of Ca^+ and Mg^+. Elevation is a variable that is readily available in all contexts and is frequently thought of as a proxy for exposure due to flooding and

sea-level rise, although it may not perfectly predict the risk (Bhattachan et al. 2018) and impacts (Ury et al 2020) of exposure. Sodium and chloride are the most abundant ions in seawater and we focused Na^+ as a metric of salinization because we did not have Cl^- concentrations from the transect survey data set. To confirm that Na^+ would be a good indicator of saltwater intrusion, we tested the correlation of Na^+ and Cl^- (the most abundant ions in seawater) in soils from the peninsula-wide survey of the APP (Figure S1, r^2 = 0.976). Finally, in addition to changes in the ionic strength of soils, one of the major impacts of salinization is through altering the alkalinity of soils (Tully et al. 2019). To assess this impact, we looked at the sum of Ca^+ and Mg^+. All environmental variables included in the ordination analysis were displayed as vectors to further describe the main drivers of species composition throughout the study area (Oksanen et al. 2019; Ury et al. 2019). Prior to analyses, species abundances were relativized and all environmental variables were tested for normality using the Shapiro-Wilk Test.

Species responses

To assess whether there were community level thresholds in ground level species responses to the salinization gradients, we used the TITAN (version 2.1, King and Baker 2015) package in R (R Core Team, 2019). TITAN identifies change points in abundance (i.e. thresholds) for each individual taxa along each environmental gradient tested. We categorized taxa as negative/decreasing (z^-) or positive/increasing (z^+) responders to the three environmental gradients associated with salinization. We used a plot by species matrix for all taxa that occurred at ≥3 plots throughout the study area to ensure that species change points could be estimated.

Based on species abundance and frequency in the data, each species was given a taxa-specific indicator value (IndVal) for the indicator species analysis (Dufrêne & Legendre 1997). By relativizing the species abundance data, TITAN assigned z scores to each species z^- or z^+ responders, which were summed for community-level analyses. At the community-level, TITAN can identify two thresholds along the gradient each corresponding to negative or positively responding taxa. Bootstrap replication (n = 500) was used to estimate uncertainty in the change points. We only reported results from pure (change in abundance and frequency of a given species was in the same positive or negative direction along the gradient for >95% of the bootstrap replicate runs) and reliable (>95% of bootstrap replicate runs needed to be significantly different from a random distribution of ($p < 0.05$)) taxa. We used filtered z-score values which only includes pure and reliable taxa in the model.

Results

Environmental variables associated with soil salinity

Mean elevation of plots was 0.51 m (SD = 0.65) with 91.6% of plots below 1 m (Figure 2), but the two data sets had different means ("transect" = 0.32 ± 0.20 m; "peninsula wide" = 0.96 ± 1.02 m). The distribution of soil Na^+ concentrations was right skewed with a mean concentration of 1718 µg Na^+/g soil (SD = 1891.3, Figure 2). The sum of water extractable $Ca^+ + Mg^+$ was bimodal with a peak in plots below

25 μeq Ca$^+$Mg$^+$/g soil, and a mean concentration of 106.7 μeq Ca$^+$Mg$^+$/g soil (SD = 82.6, Figure 2). Mean Ca$^+$ + Mg$^+$ concentrations differed across the two surveys (transect survey = 145.1 ± 65.44 m; peninsula wide survey = 13.86 ± 27.56 m). Sodium and Ca$^+$ + Mg$^+$ were significantly correlated (p = <0.005, r^2 = 0.497, Figure 2). We observed higher ionic strength values (mean = 1927.4 g Na$^+$/g) in plots less than 1m in elevation, and lower salinity (mean = 106.7 g Na$^+$/g) in plots greater than 1m in elevation (Figure 2). Low elevation plots also exhibited large variance in salinity values.

Effects of salinization on community composition

We identified 112 plant species in the study area, and 84 species occurred in more than three plots across the study. Of those species identified in both surveys, 25 species occurred in at least 5% of the plots and were included in the NMS ordinations. Sodium, Ca$^+$ + Mg$^+$ and elevation collectively explained 64% of the variability in community composition in the ordination combining both surveys (Figure 3). NMS1 explained 32.3% of the variability, and all three salinity variables (Na$^+$, Ca$^+$ + Mg$^+$, and elevation) were significant drivers of this axis (p =   0.01) (Table 1). NMS2 explained 31.7% of the variation and was driven by Na$^+$ and elevation (r = 0.178 and 0.176) (Table 1). Because the distributions of these variables differed between the two surveys, we also ran ordinations for each survey separately. For the transect survey, Na$^+$ and Ca$^+$ + Mg$^+$ were significant drivers on both NMS1 and NMS2 (r = -0.15-0.50, p = 0.01), but not elevation. For the peninsula wide survey, elevation was a significant predictor of community composition (p = 0.01) as was Cl$^-$, Ca$^+$, and Mg$^+$ (p = 0.01-0.03) (Table 1). Together, these analyses show that soil Na$^+$ was the strongest driver of community composition across all plots in both surveys. Ca$^+$ + Mg$^+$ was also a significant driver across all plots, but only marginally significant in the peninsula-wide survey, although Mg$^+$ was also significant (Table 1, Figure S3). On the other hand, elevation was a significant driver of composition in the peninsula-wide survey, but was not significant when only considering the lower elevations (< 1m above sea level) as seen in the transect survey (Table 1, Figure S2).

Threshold Indicator Taxa ANalysis (TITAN)

TITAN retained 54 reliable taxa (66% of all taxa) along the Na$^+$ gradient. Forty-three of those taxa were categorized as decreasing (z$^-$) species, and 11 as increasing (z$^+$) species accounting for 81.1% and 18.9% of the taxa along the Na$^+$ gradient, respectively (Table 2, Figure 4). Thresholds for individual decreasing species were between 75-3017 μg Na$^+$/g, and the summed z$^-$ community threshold (the point along the gradient at which the largest number of sensitive taxa were declining in abundance) was 265 μg Na$^+$/g. Thresholds for individual increasing taxa (z$^+$) were between 353-4388 μg Na$^+$/g, and the summed community threshold was 3843 μg Na$^+$/g (Table 2, Figure 4).

Results using marine base cations (Ca$^+$ and Mg$^+$) were similar to the Na$^+$ gradient analysis. TITAN retained 51 reliable taxa (or 62% of all taxa) along this gradient. Forty decreasing (z$^-$) and 11 increasing (z$^+$) species accounted for 78.4% and 21.6% of taxa along the Ca$^+$ + Mg$^+$ gradient, respectively (Table 3,

Figure S4). Thresholds for individual decreasing taxa (z^-) along the $Ca^+ + Mg^+$ gradient occurred between 0.98-110.6 µeq/g with a community threshold at 42.01 µeq/g. Increasing taxa (z^+) thresholds occurred between 62.9-264.8 µeq/g with a summed community threshold at 126.31 µeg/g (Table 2, Figure S5)..

Fewer taxa were retained for the TITAN analysis of responses to the elevation gradient (30 species); 17 taxa were categorized as decreasing/tolerant (z^-) and 10 as increasing/sensitive (z^+), accounting for 66.7% and 33.3% of total retained taxa, respectively (Table 3, Figure S5). In this TITAN analysis, increasing taxa (higher elevation, less salt tolerant) occurred between 0.29-3.76 meters with the summed community threshold (z^+) at 1.61 m, and decreasing taxa (lower elevation/more salt tolerant) between 0.01-0.53 m with a summed community threshold (z^-) at 0.24 m (Table 2, Figure S5).

Of the three gradients we analyzed in TITAN, Na^+ and $Ca^+ + Mg^+$ had the most taxa in common (65.4%), and elevation had 51.9% of species in common with Na^+ and 48.1% with $Ca^+ + Mg^+$ (Table 3). However, in some cases TITAN classified decreasing and increasing species differently among all three environmental gradients (Table 3). For example, *Sagittaria latifolia* was classified as a decreasing species as Na^+ or $Ca^+ + Mg^+$ increased, but as a decreasing species as elevation increased. Similarly, *Toxidendron radicans* was classifiedas a decreasing species on the Na^+ gradient, but an increasing species on the $Ca^+ + Mg^+$ gradient (Table 3).

Discussion

This study sought to identify whether there are critical thresholds where changes in ground layer community composition occur in non-tidal coastal wetlands in response to salinity exposure. Here, we combined NMS and TITAN analyses to reveal a strong association between soil salinity and plant community composition, with the majority of ground layer species (herbaceous and woody) responding negatively to higher levels of salinity. Therefore, our analyses confirm that salinity is a primary environmental driver of understory plant community composition in coastal wetlands, and suggests that there is a narrow range of salt concentrations where most sensitive taxa are lost. Specifically, when soil salinity exceeded 265 µg Na^+/g, 44% of species were lost. Our results also indicated that species responses were largely congruent across multiple indicators of salinity exposure (Na^+, $Ca^+ + Mg^+$, and elevation), although responses to elevation were not as consistent. We revealed a number of reliable indicator taxa that may be useful as early warning signals of salinization in freshwater wetlands in the coastal plain of the southeastern U.S.

Associations of community composition and environmental drivers

As predicted, the ground layer plant communities in this landscape were structured by factors associated with salt exposure. We looked at metrics of risk of exposure (elevation), the effects of ionic strength (Na^+) and the effects of changes to base cations ($Ca^+ + Mg^+$), and determined all three vectors were correlated with community composition. However, in this remarkably flat landscape (Figure 1), differences in

elevation proved to be a less important driver of community composition than measured salinity impacts, consistent with Taillie et al (2019, i.e. the transect survey). It was only when including the relatively higher elevation plots present in the peninsula-wide survey that we were able to detect an impact of elevation on composition. Salinity (Na^+, and $Ca^+ + Mg^+$) concentrations were extremely variable in plots that were < 1m elevation and not as variable in higher elevation plots >1m elevation. Nevertheless, salinity associated variables were significant predictors of composition across the entire data set as well as in each of the individual datasets. Local microtopography and slope are strong drivers of plant occurrence when studying low-lying coastal wetland ecosystems (Moleno et al. 2021). Elevation can be an important driver of species presence or absence, but it becomes more important with increasing geographic scale, while hydrology and salinity typically appear to be more influential as local-scale drivers on plant communities in coastal ecosystems (Herbert et al.,2015).

Reliable indicators of salinity thresholds

This study applied formalized indicator taxa analysis (e.g. TITAN) for assessing sensitivity of coastal wetland plants to salinity stress. We were able to identify community thresholds based on where the greatest change in abundance and frequency of understory plant taxa occurred along the soil salinity gradient. As we expected, taxa most sensitive to soil salinity were those typical of higher elevation forest types, dominated by seedlings and saplings of deciduous hardwoods (e.g. *Acer rubrum*, *Carya ovata*, *Clethra alnifolia*, *Asimina triloba*, and *Liriodendron tulipifera*), and evergreens trees and shrubs (*Pinus taeda* and *Ilex opaca*). These species typically have limited exposure to seawater except for large hurricanes which can deliver seawater further inland to higher elevation sites (Middleton 2016). However, adults of species like *P. taeda* and *P. serotina* are dominant in coastal freshwater wetlands, and tolerate periodic pulses of salts at low concentrations (Poulter et al. 2008), and as seedlings have been shown to increase aboveground biomass in response to salt exposure (Anderson 2020). We also identified salt sensitive herbaceous indicator taxa characteristic of upland forests (e.g. *Arundinaria tecta*, *Clethra alternifolia*, *Mitchella repens*), and salt tolerant taxa common to brackish conditions: grasses (e.g. *Distichlis spicata*, *Sporobolus* (formerly *Spartina*) *alterniflora*, *Spartina patens*) and sedges (e.g. *Cladium jamaicense*, *Scirpus americanus*).

We identified a particular range of salinity concentrations between the summed z^- and z^+ community threshold (Na^+ = 265-3843 µg/g, $Ca^+ + Mg^+$ = 42.01-126.31 µeq/g, elevation = 0.24-1.61 m) where taxa are likely to be good indicators, or early warning signs, of projected vegetation change. It is in this range where the abundance of decreasing (z^-) and increasing (z^+) taxa along the salinity gradient overlap, reminiscent of preexisting or currently expanding transitional/"ghost" forests in the transect survey. Sites in this range of salinity values had a mix of salt sensitive and salt tolerant herbaceous layer taxa, some with live mature trees and others with dead trees. For example, we documented transitioning forests dominated by evergreen saplings (e.g. *Persea palustris* and *Ilex glabra*) and rhizomatous shrubs (e.g. *Lyonia lucida*). These species have relatively high salt sensitivities and form dense shrub-scrub thickets where relatively salt tolerant fern species (e.g. *Osmunda regalis*, *Woodwardia virginica*) are common. We

found that other species that occur within highly saline regions along the salinity gradient beyond the z^- threshold include invasive generalists (e.g. *Phragmites australis*), natives often associated with disturbed, or recovering, forests from salt, inundation or fire exposure (e.g. *Morella cerifera, Baccharis halimifolia, Iva frutescens,Rubus spp.,* and *Toxidendron radicans*), as well as salt tolerant freshwater marsh species (e.g. *Juncus roemarianus, Kosteletzkya pentacarpos*). It is important to note that our results reflect a snapshot approach despite the potentially dynamic nature of soil salinization over space and time throughout the coastal plain (Tully et al 2019). The overall landscape dynamics suggest that these associations may be unstable (Smart et al., 2020), and we predict that areas once dominated by forest species intolerant to salty conditions have converted to shrub-scrub and ghost forests documented in Palmetto Peartree Preserve on the APP between 1996 and 2017 (White et al., 2021), and will eventually be colonized by salt tolerant marsh species (Crain et al. 2004; Sutter et al. 2015).

All three salinity gradients (Na^+, $Ca^+ + Mg^+$, and elevation) were drivers of community composition and they each identified two critical salinity thresholds for each species, however species salinity thresholds were not all consistent across the gradients. We documented consistent responses in 19 species across all three gradients, consistent responses of 22 species between Na^+ and elevation, and consistent responses of 21 species between elevation and $Ca^+ + Mg^+$. Most strikingly, 42 species had consistent responses between Na^+ and $Ca^+ + Mg^+$, which suggests that elevation alone is not as good a predictor of exposure to salinity because marine salts can be delivered, concentrated or leached by hydrologic droughts, hurricanes and storm surges. It is likely that a large proportion of coastal wetland communities experience salinities in this range over short time periods, but long-term exposure is more episodic.

This study presents a compelling case for characterizing salinity thresholds by conducting indicator taxa analyses of understory plant communities. We demonstrated that Na^+, $Ca^+ + Mg^+$, and elevation are main abiotic drivers of community composition. We were able to define salinity thresholds for the majority of taxa identified in the region, and subsequently two community-level thresholds for each salinity gradient. The study demonstrates the reliability of combining ordination and threshold indicator taxa analyses as a quantitative approach to understanding the vulnerability of plant communities to salinity and other stressors. Moreover, TITAN is a promising tool for identifying understory plant communities that are likely to experience shifts as a result of increasing saltwater intrusion events. Our work presents an additional use of TITAN for plant community assessment across a naturally occurring gradient. These techniques should continue to be tested for multiple stressors across other habitat types and be used more widely for management and conservation efforts of vulnerable ecosystems over space and time.

Declarations

Conflicts of interest/Competing interests

Not applicable

Data availability statement

The data from the peninsula-wide survey are archived and openly available for download via Dryad (https://datadryad.org/), and data from the transect survey are available via Taillie and Poulter (2019) via Pangaea (https://doi.pangaea.de/10.1594/PANGAEA.896941).

Code Availability

Code is available on request from the lead author

Authors' contributions

J. Wright, E. Bernhardt, C. Moorman, and M. Ardón procured funding to support this research; S. Anderson, J. Wright, E. Bernhardt, and E. Ury conceived the primary research idea; S. Anderson, P. Taillie, and E. Ungberg collected field data; S. Anderson, B. Poulter and P. Taillie selected research sites; S. Anderson conducted all analysis and wrote the manuscript with J. Wright; E. Ury generated maps; and all authors discussed results and contributed in edits to manuscript.

Ethics Approval

Not applicable

Consent to Participate

Not applicable

Consent for Publication

Not applicable

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Tables

Due to technical limitations, table 1-3 is only available as a download in the Supplemental Files section.
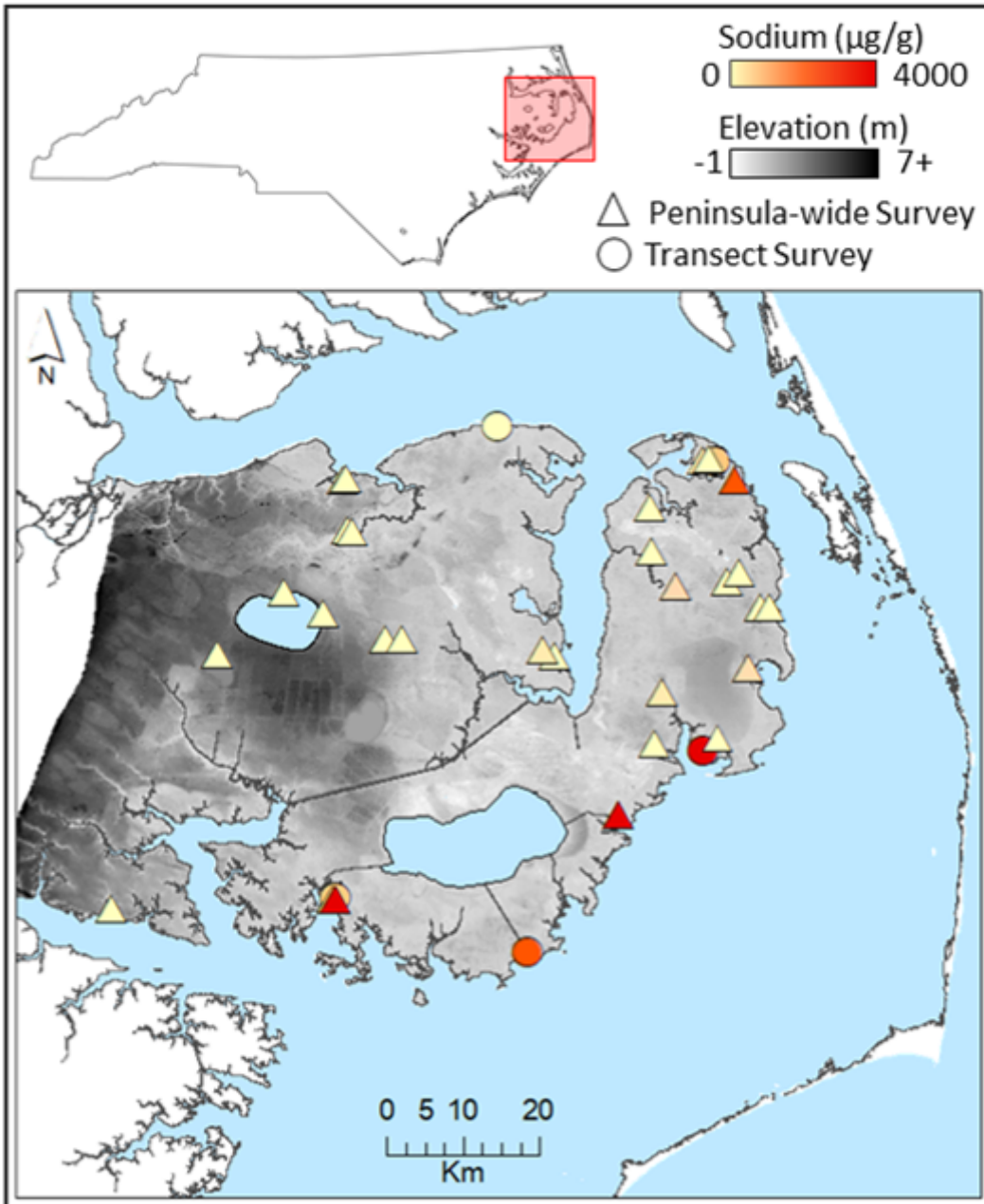
Figures

Figure 1

Map of the Albemarle-Pamlico Peninsula with peninsula-wide survey (triangles) and the transect survey (circles) plots colored by Na+ concentration (µg Na+/g soil). Digital elevation model (DEM) of the Albemarle-Pamlico Region is shown in grey color ramp. Water is denoted by light blue areas and regions with no DEM in white. See Ury et al 2019 and Taillie et al 2019 for additional sampling details.
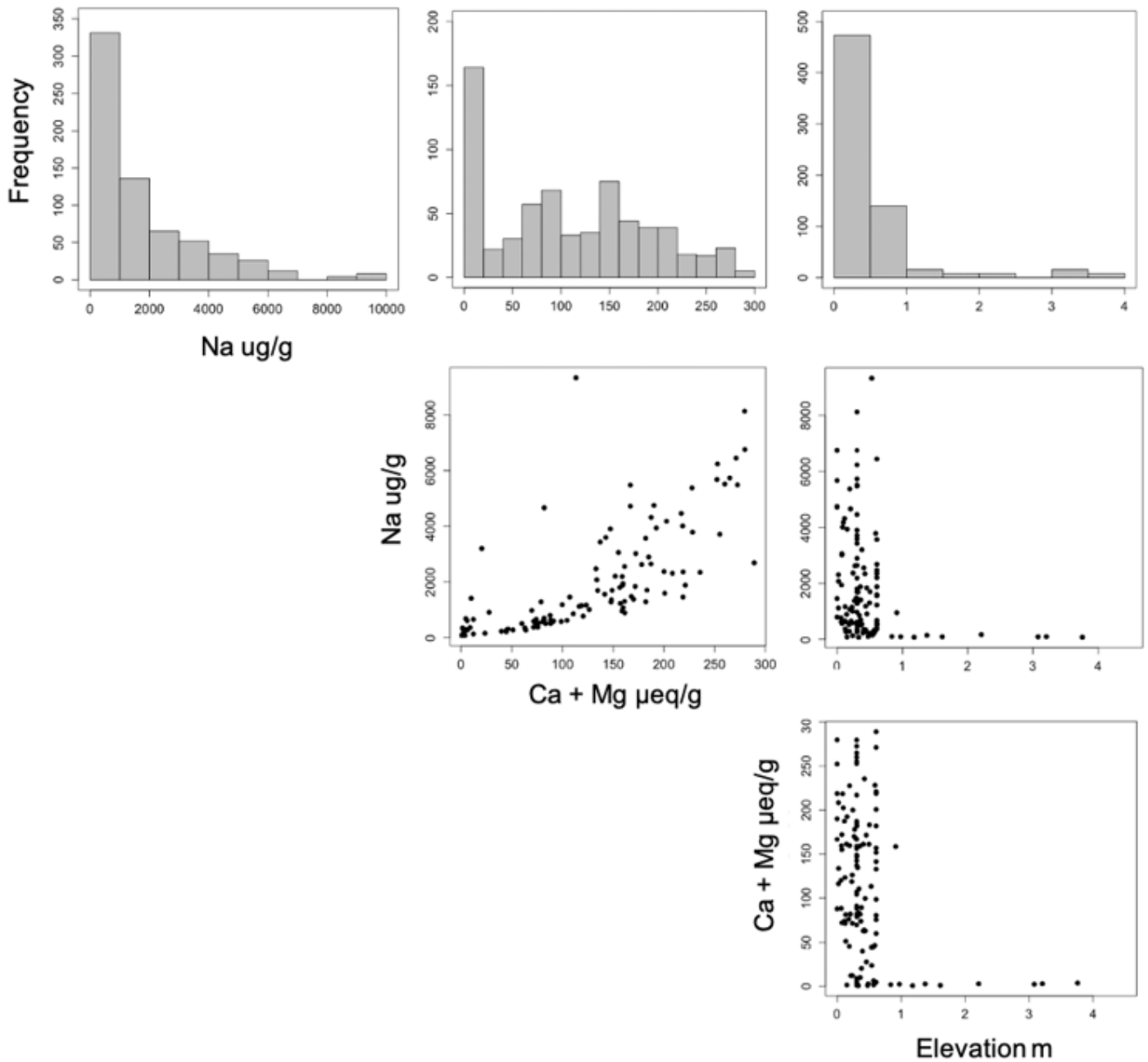
Fig. 2

Figure 2

Frequency distributions and correlations of all three environmental parameter (elevation, Na+, and the Σ Ca+ and Mg+) hypothesized to be the main drivers of understory community composition and used later in the threshold indicator taxa analyses.
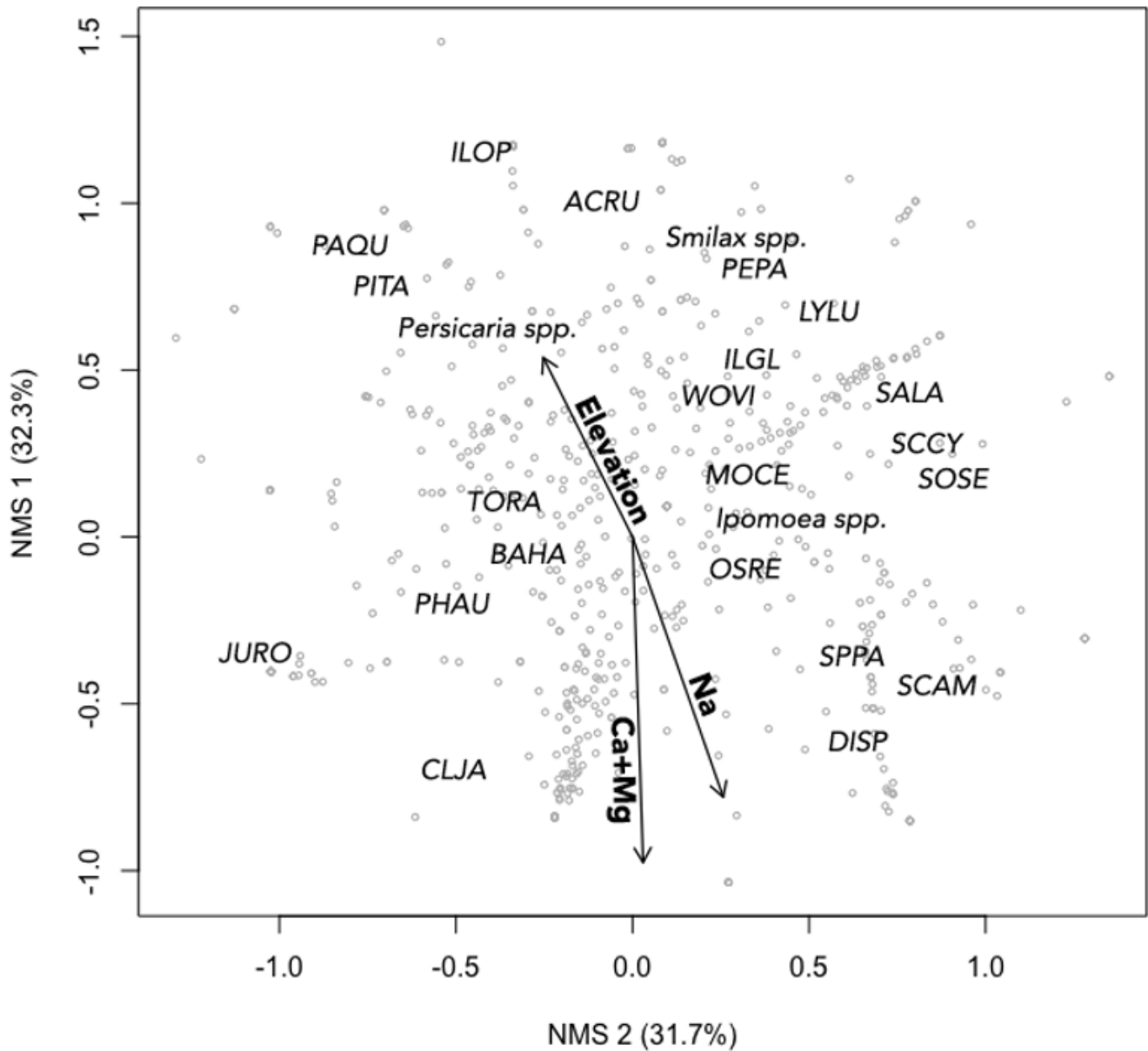
Figure 3

Non-metric multidimensional scaling (NMS) ordination analysis of all sites with three significant environmental variables fit as vectors (p < 0.05). Sodium, elevation, calcium and magnesium explains 64% herbaceous plant community composition in two axes. Each plot is indicated by solid gray circles. Taxa names are weighted average abundance based on species presence. The length of the arrow indicates a large degree of statistical significance. See Table 1 for statistics of NMS1 and NMS2, and see Table 3 for taxa full names.
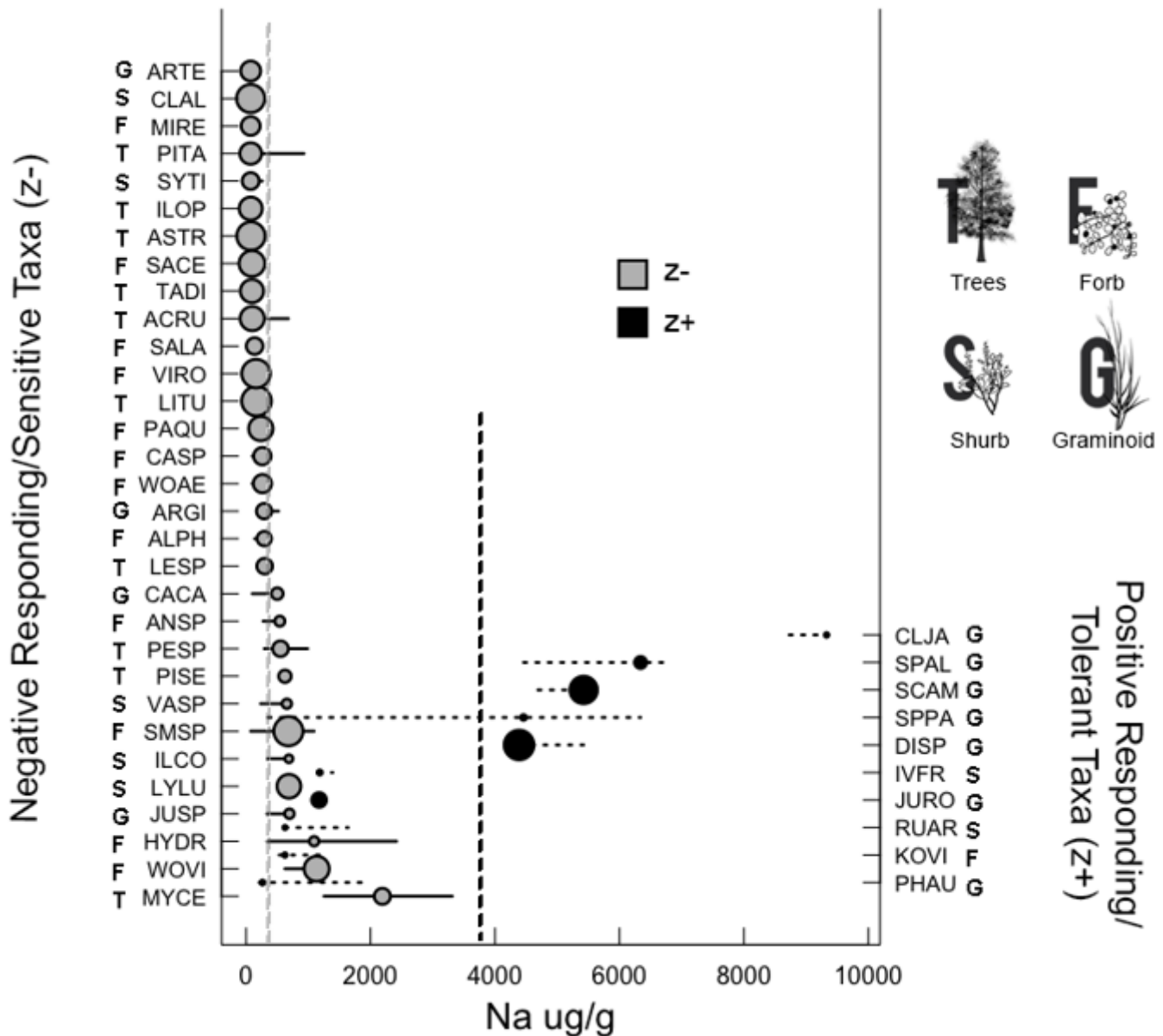
Figure 4

Sharp decline in the majority of taxa below 2,000 µg/g. Negative (gray) and positive (black) responding taxa (on y-axis) from TITAN along the Na+ gradient. Grey vertical line at 265 µg/g denotes the summed z-scores for negative responding (z-) community threshold, and the dark grey vertical line at 3843 µg/g denotes the summed z-scores for positive responding (z+) community threshold. Letters next to each taxa abbreviation relate to whether it is a tree, shrub, forb, or graminoid species as noted in the legend. Points indicate the change point (or threshold) for each species sized by its indicator value (IndVal) which corresponds to individual species contribution to the summed z-score/community-level threshold. Horizontal lines for each species indicate the 5-95% quartile range of that taxa.
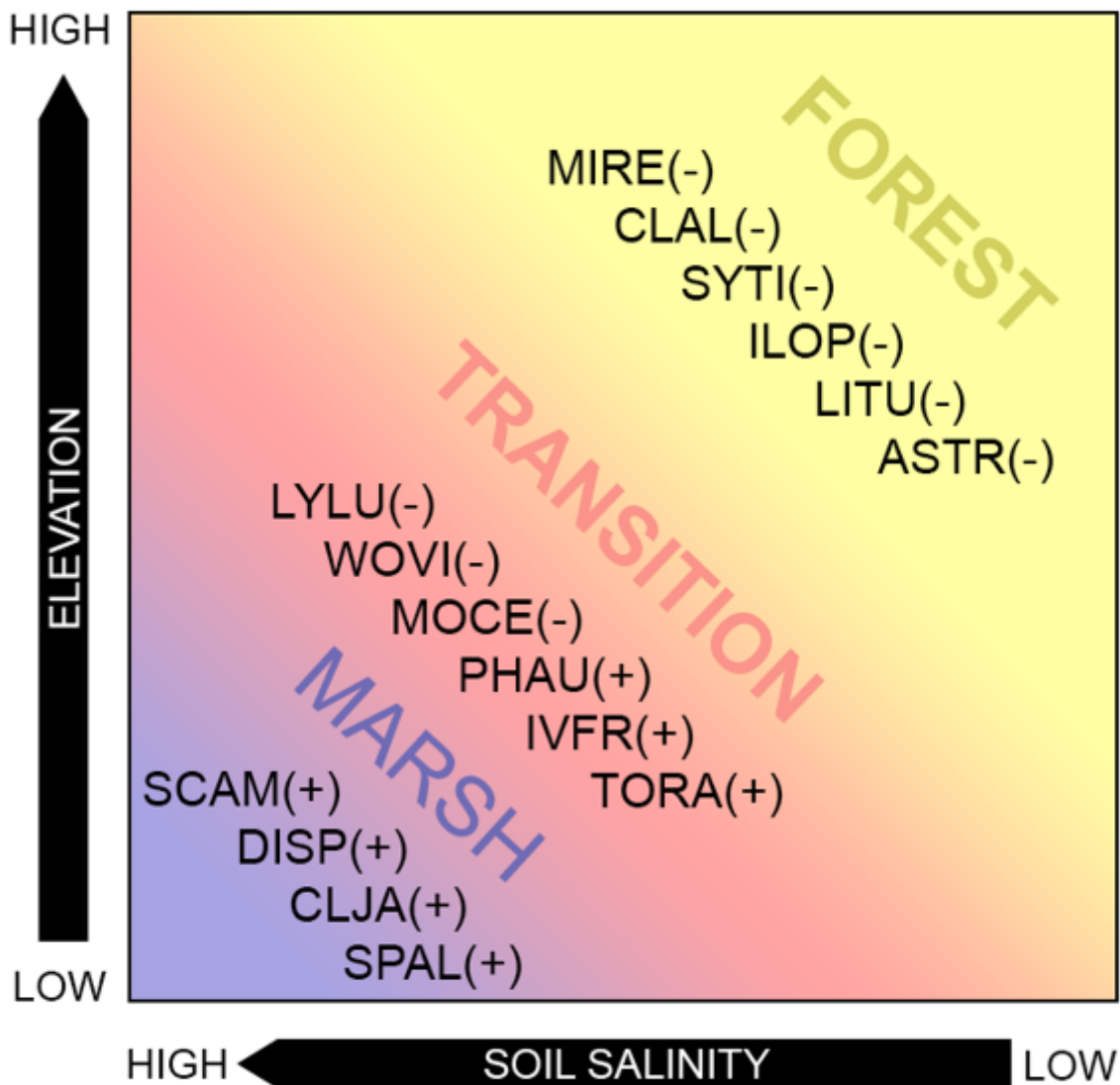
Figure 5

Conceptual model of changes in plant communities controlled by soil salinization and elevation/flooding from sea-level rise and climate change as seen in NMS analyses. Examples of indicator species, decreasing (z-) and increasing (z-) taxa from the TITAN analyses characteristic of forest (yellow), transition (pink) or marsh (purple) communities. This model builds on the model presented by Fagherazzi et al. (2019).

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Tables.pdf
- Supplementaryfile.docx