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Salt marsh migration into salinized agricultural fields: a novel assembly of plant communities

Running title: Novel plant assembly in saline fields

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Abstract

Questions: Sea level rise and saltwater intrusion are changing low-lying coastal landscapes, converting agricultural land and other upland habitats to tidal marsh. Abandoned, saline agricultural fields are affected by a unique combination of environmental filters, those traditionally found in tidal marsh – salinity and flooding – alongside those of cultivated lands – high nutrient availability and a history of disturbance. We asked how species composition and functional trait composition in saline fields compares to traditional old fields and natural ecotones, and whether trends in succession can be detected in saline fields during the first years post-abandonment.

Location: Chesapeake Bay (Mid-Atlantic, USA)

Methods: We surveyed plant communities assembling in saline fields and compared taxonomic and functional trait diversity to those in old field and marsh-forest ecotone communities. We also assessed changes in the saline fields after two and three years of abandonment to detect the direction of succession.

Results: Saline fields occupied an intermediate taxonomic and trait space between old fields and marsh ecotones. From old fields to saline fields to marsh, communities were less weedy, and more wetland, native, and perennial. Specific leaf area decreased across this transition, in concordance with expected changes in response to salinity. Over time, saline fields became less graminoid and less weedy, and more native, wetland, and woody.

Conclusions: We conclude that marsh migration into abandoned farmland is producing a novel assembly of plant communities. Intermediate functional traits in the saline fields reflect the novel environmental filters imposed by saltwater intrusion and the cultivation legacy. These patterns suggest that abandoned, saline agricultural fields may develop somewhat differently than natural marsh boundaries, with more shrub-dominance and greater resilience to *Phragmites australis* invasion. Importantly, these results suggest that saline fields will provide a facilitating route for marsh migration.

Keywords: *Baccharis*, Ecotone, Functional traits, Invasive species, Old field, *Phragmites*, Saltwater intrusion, Sea level rise

1. Introduction

Tidal marshes are migrating inland in response to rising sea levels (Raabe & Stumpf, 2016; Schieder, Walters, & Kirwan, 2017; Smith, 2013). In the Chesapeake Bay, for example, marsh migration is converting uplands to wetlands at a pace of 0.5 to upwards of 5 linear meters per year (Schieder et al., 2017). The habitats upslope of migrating marshes vary from agricultural land (Smith, Hafner, & Niles, 2017) to coastal forest (Field, Gjerdrum, & Elphick, 2016; Smith, 2013) to residential lawns (Anisfeld, Cooper, & Kemp, 2017) to urban lands (Enwright, Griffith, & Osland, 2016). Often, upslope anthropogenic land uses have been characterized as impermeable to marsh migration (Enwright et al., 2016), and there has been very little accounting for affected upslope habitats other than forest. However, substantial areas of farmland are present in coastal zones that are presently affected by

saltwater intrusion and marsh migration (Moorhead & Brinson, 1995) or predicted to be affected in the near future (DaLio, Carol, Kruse, Teatini, & Tosi, 2015). Moreover, abandoned farms are potentially more amenable to marsh migration than other human landscapes, where hard barriers such as seawalls, levees, and pavement prevent plant establishment (Enwright et al., 2016; Kirwan & Megonigal, 2013).

Old fields undergo different succession trajectories depending on their cultivation legacies and how far agricultural activities have altered conditions from pre-agricultural abiotic and biotic baselines (Cramer, Hobbs, & Standish, 2008). Agricultural lands are characterized by nutrient enrichment and regular disturbances, favoring ruderal traits that prioritize fast growth and completion of the life cycle (Grime, 1977; Lososová et al., 2006). In contrast, the determinant environmental filters in tidal marshes are flooding and salinity, giving preference to traits that confer resistance to osmotic stress, root anoxia and salt toxicity (Eallonardo, Leopold, Fridley, & Stella, 2013; Moor et al., 2017). In abandoned fields affected by sea level rise and saltwater intrusion, the combination of a cultivation legacy with salinity and flooding stress impose a novel combination of environmental filters to the regional species pool: high nutrient availability, a history of frequent disturbance, and saline and flooded conditions. Unravelling which ruderal and wetland species assemble in these fields can be highly informative for a better understanding of trait-based assembly rules (Cramer et al., 2008; Radeloff et al., 2015), and will also provide a foundation for predictions about the trajectory of upslope plant communities facing marsh migration.

Novel ecosystems are those whose species composition or ecosystem function fall outside of the historical range (Hobbs et al., 2006; Hobbs, Higgs, & Harris, 2009). Some common examples include cities (Aronson et al., 2016), old fields (Cramer et al., 2008), and wetlands invaded by exotic species (Gandy & Rehage, 2017). Novelty is the subject of a heated debate for conservation and ecological restoration practitioners (Miller & Bestelmeyer, 2016; Murcia et al., 2014). For ecology, however, novelty presents opportunities to study key processes in new settings (Radeloff et al., 2015). A case of special interest is the assembly of novel plant communities. Community assembly theory relies on two concepts: a regional species pool; and a set of dispersal, abiotic, and biotic filters that select which species from the regional pool will occur in a given habitat (Kraft & Ackerly, 2014). Whether a species passes through successive filters will depend on its functional traits, and this environment-trait relationship can be described by certain assembly rules (Keddy, 1992). Trait-based assembly rules are increasingly applied in predictions of the behavior of complex ecosystems in the face of global change (Funk et al., 2017). For example, recent research has characterized which land use histories, environmental changes, and plant traits drive community assembly in green roofs (Catalano, Marcenò, Laudicina, & Guarino, 2016) and vacant urban lots (Johnson, Borowy, & Swan, 2017). In this study, we employ this approach of characterizing community change through shifts in functional traits in response to environmental change, to understand and predict community shifts during tidal marsh migration into agricultural and forested landscapes.

The Chesapeake Bay, located in the North Atlantic Coastal Plain of the United States, is an ideal system in which to study marsh migration into abandoned fields. The region has a high-intensity agricultural landscape combined with especially high rates of sea level rise (Ezer & Corlett, 2012; Sallenger, Doran, & Howd, 2012). Moreover, the slope of marsh-

adjacent uplands is relatively shallow (average of 3%, Schieder et al. 2017). Therefore, large areas have been affected by marsh migration (Schieder et al., 2017). In coastal counties, tidal marsh is the predominant intertidal habitat (Baldwin et al., 2012). Adjacent upslope land use is equal parts forest and farmland (Fisher et al., 2010). A proper understanding of marsh migration into farmland can inform land managers to put in place effective mitigation policies, including planned retreat (Song, Fu, Wang, Peng, & Gu, 2017). Communicating with farmers about the removal of barriers such as tide gates requires knowledge of what happens to land following abandonment.

In the last years, we identified several coastal farms where saltwater intrusion has led to field abandonment. This article provides an assessment of the plant communities assembling in these abandoned fields. To our knowledge, this is the first account of vegetation dynamics during salt marsh migration into agricultural fields. Because these fields are affected by the environmental filters of both marsh and old field habitats, our hypothesis is that the communities that are assembling there will be a mixture of marsh and old field species pools, in terms of both taxonomic and functional diversity. Our specific research questions are: (1) how do species composition and functional trait composition of saline fields compare to marsh and traditional old field communities; and (2) what trends in succession can be detected in the first years after abandonment?

2. Methods

2.1 Study sites

The study took place in Dorchester and Somerset Counties, MD, USA, on the lower Eastern Shore of the Chesapeake Bay (Figure 1). Agricultural fields affected by saltwater intrusion (hereafter, saline fields) were selected with the assistance of professionals in the Maryland Department of Agriculture and University of Maryland Extension Service familiar with the problem of salinization. At saline field sites, landowners confirmed the land had been abandoned due to poor corn and soybean crop performance as a result of salinization. In the summer of 2016, we surveyed the vegetation of two saline fields that were in their second year of abandonment. During summer 2017 we revisited these sites twice, and extended the study to six additional sites: two more saline fields (in their first and fourth year of abandonment), two old fields not affected by salinity in their first year of abandonment (hereafter, old fields), and two marsh-forest ecotones located within protected areas (Blackwater National Wildlife Refuge and Deal Island Wildlife Management Area; hereafter, marsh ecotones). Old fields, located far inland from tidal creeks, were fallow because they were leased to a solar energy company, rather than due to salinization, and groundwater salinities were 0 psu. Marsh-forest ecotone sites were located within well characterized brackish marsh complexes where salinities varied from 2 to 14 psu. Groundwater salinities in saline fields were intermediate to old fields and marsh-forest ecotones and varied from 0.5 to 6 psu.

In each site, we haphazardly placed eight to twelve 1 m² permanent vegetation quadrats. The number of quadrats per site varied depending on the site area. At the saline fields, we noted visual differences in the plant community composition at the field edge and interior and therefore stratified our design to sample separately in both areas, while at the other more homogeneous sites we sampled the area as a whole. We surveyed the 2016 sites once in that

year and twice in 2017, the rest of the sites only once. The total number of quadrats was 170, including the repeated sampling of the 2016 sites. Appendix 1 includes information on the number of plots per site and the dates of the surveys.

2.2. Vegetation and functional trait data

At each quadrat, we recorded all live vascular plant species and their abundance on a 1 to 100 percent cover scale. We provide the full vegetation dataset in Appendix 1. We standardized species names according to The Plant List (2013) and obtained the following species traits (Table 1): From the USDA Plants Database (2017), duration of the life cycle, graminoid or not, woody or not, native or introduced, and wetland status for the Atlantic coastal plain; From Uva *et al.* (1997), weed designation; From the TRY database (Kattge *et al.*, 2011), plant height, seed mass and specific leaf area. We excluded duplicate TRY records and those with an error risk above four. The last three traits had several gaps and we used alternate sources to fill them: Gleason & Cronquist (1991) for plant height; the Seed Information Database for seed mass (Royal Botanic Gardens Kew, 2017); and the LEDA Traitbase for specific leaf area (Kleyer *et al.*, 2008). For specific leaf area, we had to use the genus average due to data availability. We accessed all databases in October 2017. Appendix 2 has the final trait data per species.

2.3 Statistical analyses

Unless noted otherwise, analyses were done in R (R Core Team, 2017), and a script of R analyses is provided in Appendix 3. For each quadrat, we calculated diversity measures using the packages ‘vegan’ (Oksanen *et al.*, 2017), ‘SYNCSA’ (Debastiani & Pillar, 2012), and ‘FD’ (Laliberté, Legendre, & Shipley, 2014): (1) species richness; (2) Shannon’s diversity index H; (3) Pielou’s evenness index J; (4) Rao’s functional diversity Q based on the species traits (calculated using the square root of the one-complement of Gower’s similarity index); and (5) the community-weighted means (CWMs) of the species traits for each quadrat.

To examine the multivariate species composition data, we used non-metric multidimensional scaling (NMDS) with the Bray–Curtis dissimilarity in the ‘vegan’ package to produce an ordination of the vegetation composition. We estimated the indicator species of each community with the Dufrene–Legendre method implemented in the package ‘labdsv’ (Roberts, 2016).

To analyze the relationship between plant traits and the environment, we used the double constrained correspondence analysis (dc-CA) approach as proposed by ter Braak *et al.* (ter Braak, Šmilauer, & Dray, 2018) and implemented in Canoco 5.11 (ter Braak & Šmilauer, 2018). This approach allows to test for links between species composition and species traits, and species composition and the environment (Zelený, 2018); avoiding the inflated type I error that has been reported for approaches based only on CWMs (Peres-Neto, Dray, & Braak, 2017). The Canoco projects calculating dc-CAs are provided as Appendix 4.

3. Results

3.1 Taxonomic diversity

We observed 80 vascular plant species across all sites during the two years. The three most frequent and abundant species in the dataset were *Aster subulatus* (occurrence in 48% of

quadrats), *Digitaria sanguinalis* (32%) and *Sorghum halepense* (29%). The average species richness was lower in the marsh ecotones (mean and standard deviation = 4.2 ± 0.9 species m^{-2}) and saline interiors (4.6 ± 0.6 species m^{-2}) than in the old fields (5.3 ± 0.9 species m^{-2}) and saline edges (5.5 ± 0.6 species m^{-2}). The four plant communities had similar values for their taxonomic or functional diversity indices (Figure 2). When we compared saline fields after two and three years of abandonment, we found that over time, plots became more species rich (3.9 ± 1.0 species m^{-2} in 2016 vs. 5.2 ± 1.0 species m^{-2} in 2017); but there was no change in any of the diversity indices.

NMDS ordination achieved a convergent solution in two dimensions with a stress value of 0.135 after 1212 iterations. The ordination indicated a clear separation between the marsh ecotone and the old field vegetation, with the saline fields occupying the space between them (Figure 3). The vegetation of the marsh ecotone and the old fields was more distinct and had more species with indicator value. In the case of the marsh ecotone, these included coastal plants, such as salt marsh hay *Spartina patens* and marsh elder *Iva frutescens*, and generalist grasses *Panicum virgatum* and *Festuca rubra*. The indicator species for the old fields were common agricultural weeds, including marehail *Erigeron canadensis*, Japanese bristle grass *Setaria faberi*, and Johnsongrass *Sorghum halepense*, and seedlings of the early successional tree red maple *Acer rubrum*, which was present in 11 out of 20 old-field quadrats.

The invasive common reed *Phragmites australis* occurred in 8 of 22 marsh ecotone quadrats with an average abundance of $6.2 \pm 13.4\%$. It occurred less frequently in the saline edges (3 of 64 quadrats, $0.4 \pm 2.6\%$ abundance) and interiors (3 of 64 quadrats, $0.6 \pm 3.4\%$ abundance). It was absent from the old fields.

3.2 Functional diversity

To test for differences between community types in their functional traits (Figure 2), we performed a dc-CA using only one 2017 sampling date per site to normalize sampling effort across singly and repeatedly sampled sites. The dc-CA indicated a significant relationship between species composition and functional traits (pseudo-F = 1.3, $p = 0.002$, 24.21 % of total variation explained by traits); as well as between species composition and community types (pseudo-F = 4.4, $p = 0.002$, 12.51 % of total variation explained by community type). The triplot produced by dc-CA shows the patterns of variation in traits (Figure 4). Marsh ecotone quadrats and saline edges were mostly native while the saline interiors and old fields had a majority of introduced species. There was a progression in weediness from the weed-free marsh ecotone and saline edges, to the interiors, and finally the weed-dominated old fields. The marsh ecotone and the saline fields had a higher wetland affinity than the old fields. The marsh ecotones were largely perennial and graminoid, the most abundant species being switchgrass *Panicum virgatum* ($26 \pm 24.3\%$) and salt marsh hay *Spartina patens* ($21.6 \pm 24.7\%$). The saline and old fields, on the other hand, had a mix of annual and perennial plants. Of these, the saline edges were more perennial, but differed from the marsh ecotones in the dominance of annual Asteraceae forbs such as eastern annual saltmarsh aster *Aster subulatus* ($14 \pm 19.9\%$) and common ragweed *Ambrosia artemisiifolia* ($10.5 \pm 24.1\%$). The annual grass *Digitaria sanguinalis* dominated the saline interiors ($23.4 \pm 31.9\%$). Woody species were generally rare, with a tendency towards higher woodiness in the marsh ecotone because of the presence of adult individuals of marsh elder *Iva frutescens* ($4.6 \pm 7.3\%$).

Another wetland shrub, *Baccharis halimifolia*, was present in several saline edge and saline interior quadrats (23 and 10 of 64 quadrats, respectively), but its abundance was low (2.2 ± 6.0 and $0.6 \pm 2.3\%$, respectively) and mostly in the form of regenerating seedlings. Old field communities had the tallest plants, and marsh ecotones the smallest specific leaf area.

In a second analysis focusing on the saline fields, we studied how their CWMs changed in the transition from the second to the third year of abandonment (Figure 5). In this case we calculated the dc-CA using the repeated surveys conducted in saline fields only in August 2016 and August 2017 (i.e., this analysis did not reuse any of the surveys included in the first dc-CA). Again, the dc-CA indicated a significant relationship between species composition and functional traits (pseudo-F = 1.3, $p = 0.028$, 39.88 % of total variation explained by traits); as well as between species composition and community types (pseudo-F = 3.4, $p = 0.002$, 9.08 % of total variation explained by year and community type). The resulting triplot (Figure 6) shows how, over time, graminoids and weeds became less prevalent in saline field communities, as native and wetland plants became more prevalent.

4. Discussion

Traditional plant communities from the marsh ecotone and the old fields have few similarities. Their species composition is unequivocally different, with only three common species: seedlings of *Acer rubrum* and *Pinus taeda*, and the annual forb *Aster subulatus*. The marsh ecotone is predominantly native and has more wetland species, whereas old fields have a majority of introduced agricultural weeds. Perennial plants dominate marsh ecotone communities that, as wetlands, favor a persistence strategy based on vegetative reproduction (Moor et al., 2017; Sosnova, van Diggelen, & Klimešova, 2010). Old-field communities on the other hand are primarily annual, a cardinal feature of weeds adapted to the regular disturbances of agriculture (Lososová et al., 2006). Competition for light in the short inter-disturbance period also explains why old-field communities are taller and have a larger specific leaf area (Moles et al., 2009; Westoby, 1998). The smaller specific leaf area of marsh communities is adaptive in the water stress conditions produced by salinity (Eallonardo et al., 2013; Moor et al., 2017), and allows for extended leaf lifespans (Westoby, 1998).

In saline fields, plant communities are assembling which show intermediate characteristics between the marsh ecotone and traditional old field communities. Their species composition is transitional, sharing 14 species with the marsh ecotone (out of 21 species in that community) and 25 with the old fields (out of 27). Saline fields are a mix of native and introduced, perennial and annual, wetland and non-wetland, and weedy and non-weedy species. Saline-field plant communities are not as tall as those in the traditional old fields, which is in agreement with a shift in environmental filters from competition for light to tolerance of salinity and flooding (Eallonardo et al., 2013; Moles et al., 2009). Within saline fields, differences exist between the interior and the edge, with the latter being more similar to marsh ecotone communities. The most likely explanation is the proximity of drainage ditches to field edges that now allow infiltration of saline tidewater into the groundwater (Poulter, Goodall, & Halpin, 2008) and may also favor hydrochoric dispersal of marsh plants (Soomers, Karszenberg, Verhoeven, Verweij, & Wassen, 2013). Saline edges have a high abundance of annual native forbs with wetland affinity like *Aster subulatus* and *Solidago sempervirens*. Short annual graminoids with a large specific leaf area - especially

Digitaria sanguinalis - dominate the saline interiors. The smaller specific leaf area may indicate that edges experience higher osmotic stress, or lower nutrient availability, as low specific leaf area can help to withstand both of these stresses (Eallonardo et al., 2013). It seems that saline field edges are the first areas of saline fields to transition, followed by compositional and functional shifts in field interiors.

Monitoring communities through time, over years to decades, is the most effective way to document patterns in succession. Some differences became apparent in the saline fields between the second and third year after abandonment. Third year communities are relatively closer to the marsh ecotone features: they have more native and wetland plants; and less weeds. The trend towards marsh ecotone features, however, does not hold for all traits, as third year fields also have less graminoids and lighter seeds. A relevant aspect of this change is a tendency towards more woodiness, with more frequent seedlings of the shrub *Baccharis halimifolia*. Within its native range in North America, this shrub occupies coastal habitats just above the flooding line, but it has shown weedy and invasive potential in human-disturbed habitats and natural wetlands of Europe and Australia (Caño, Campos, García-Magro, & Herrera, 2013). A similar trend towards shrubs was observed in Big Bend, Florida, where halophytic shrubs were an important but transitional part of the plant community during 20 years of marsh migration (Langston, Kaplan, & Putz, 2017). Another difference between saline fields and marsh ecotones is that saline fields appear to be less favorable than marsh ecotones for the recruitment of coastal forest trees like *Acer rubrum* and *Pinus taeda*, at least during early succession. A final consideration is the apparent lack of colonization by *Phragmites australis*. The invasive genotype of this species is a major component of migrating marsh communities in the eastern US, as it creates monotypic stands in areas of forest die-back (Smith, 2013), and was present at or very nearby to all sampled sites. Our surveys indicate that saline fields are relatively resilient to *Phragmites australis* invasion, potentially increasing their wetland habitat value, at least compared to transitioning coastal forest stands. Over the next years, we will continue to monitor these sites to document whether these differences in saline field succession hold. Taken together, these trends suggest that the saline fields might progress towards something resembling a shrub-dominated marsh-forest ecotone. Future sampling of the study sites is needed to confirm this trajectory of succession. Continued surveys of the saline fields will also shed light on the environmental factors that control the spread of both *Baccharis halimifolia* and *Phragmites australis*. We are also aware of other possible futures for salt-affected agricultural lands, such as the wholesale conversion to open water observed in impounded, subsided agricultural areas in Delaware, USA during marsh migration (Smith et al., 2017), or the development of a unique ecosystem of conservation interest, as in the brackish grazing marshes of southern England and northern France (Cook & Moorby, 1993).

In conclusion, marsh migration into abandoned farmland is producing a novel assembly of plant communities. A trait-based community assembly approach in this system allowed a richer characterization of this community and its trajectory than taxonomic description and diversity indices alone. No-analogue communities in saline fields incorporate species from marsh and old field regional pools, and show intermediate functional traits that relate to the novel environmental filters imposed by saltwater intrusion and the cultivation legacy. This novel ecosystem presents challenges and opportunities for conservation and ecological

research. The future of migrating coastal ecosystems will be largely affected by landowner decisions and priorities (Field, Dayer, & Elphick, 2017). A correct understanding of saline fields and their succession trajectories can inform interventions to preserve native biodiversity, ecosystem services, and socio-economic well-being in landscapes affected by sea level rise and saltwater intrusion.

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Author contributions: KG identified field sites, KG and EFP surveyed plant communities, EFP collected functional trait data, EFP performed the statistical analyses, and both authors wrote the manuscript.

Data Availability Statement

All data used in this study is available in the appendices of this article.

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Appendices

Appendix 1 Plant species composition and abundance data.

Appendix 2 Average species traits.

Appendix 3 R script with the statistical analyses of this article.

Appendix 4 Canoco projects calculating dc-CA.

Table 1 Species traits used in this study, with explanation of the possible values and percentage of species for which data was available.

Species trait	Type	Possible values	Species coverage (%)
Graminoid	Binary	1 = graminoid; 0 = other	100
Native	Binary	1 = native species; 0 = introduced	100
Perennial	Ordinal	1 = perennial; 0.5 = biennial; 0 = annual	100
Plant height	Numeric	m from 0.1 (<i>Anagallis arvensis</i>) to 31 (<i>Pinus taeda</i>)	95
Seed mass	Numeric	mg from 0.2 (<i>Juncus tenuis</i>) to 203 (<i>Xanthium strumarium</i>)	96
SLA (Specific leaf area)	Numeric	mm ² mg ⁻¹ from 1.9 (<i>Juniperus virginiana</i>) to 52 (<i>Phytolacca americana</i>)	71
Weed	Binary	1 = weed; 0 = non-weed	100
Wetland	Ordinal	5 = obligate wetland; 4 = facultative wetland; 3 = facultative; 2 = facultative upland; 1 = obligate upland	91
Woody	Binary	1 = tree, shrub or subshrub; 0 = other	100











