]

1	Title: Soil salinity impacts future community composition of coastal forests						
2 3	Authors: Natasha N. Woods ^{*1,3} , Jenise L. Swall ² , Julie C. Zinnert ¹						
4	Affiliations: ¹ Department of Biology, Virginia Commonwealth University, 1000 W. Cary St.						
5	Richmond, VA 23284						
6	² Department of Statistical Sciences and Operations Research, 1015 Floyd Avenue, Virginia						
7	Commonwealth University, Richmond, VA 23284						
8	³ Biological Sciences Department, Moravian College, 1200 Main Street, Bethlehem, PA 18018						
9							
10 11	Corresponding Author: Natasha N. Woods*, woodsn02@moravian.edu; 610-625-7603						
12 13							

Summary of Comments on Manuscript WELA-D-19-00135-R1 (1).pdf

Page: 1

Number: 1 Author: Anonymous

Subject: Sticky Note

Date: 9/8/2021 2:32:20 PM

Woods, N. N., J. L. Swall, and J. C. Zinnert. 2020. Soil Salinity Impacts Future Community Composition of Coastal Forests. Wetlands 40:1495-1503. https://doi.org/10.1007/s13157-020-01304-6

14 Abstract

With projected increase in storms, sea-level rise and saltwater intrusion in low-lying terrestrial 15 areas, compositional changes that favor more salt tolerant species are likely to occur. Wetland 16 species are expanding into declining forested communities, primarily dominated by trees. Higher 17 salinities for germination may preclude establishment of tree species. We examined the capacity 18 for coastal tree species (Acer rubrum, Liquidambar styraciflua, Pinus taeda, Celtis occidentalis, 19 Persea borbonia) and a wetland shrub (Morella cerifera) to germinate at salinity concentrations 20 of 0, 2, 5, 10, and 20 ppt. A growth chamber experiment was established examining the effect of 21 salinity on germination of common species found in mixed forests throughout the mid-Atlantic 22 coastal plain and Gulf of Mexico, USA. The study revealed that regeneration from seed will be 23 difficult for most of the selected species at salinities >5 ppt with implications for community 24 25 composition with continued saltwater intrusion. Germination of A. rubrum was not impacted at higher salinities, with Pinus taeda not as affected other species. Morella cerifera did not have an 26 advantage at the germination stage over selected tree species. Knowing threshold limits of 27 germination response to salinity is critical for identifying future community trajectories. 28

29 Keywords: Germination, Regeneration, Saltwater Intrusion, Sea-Level Rise, Morella cerifera

30

31

33 Introduction

Factors that facilitate the formation of ghost forests in coastal ecosystems are on the rise 34 and forests are being replaced by more salt-tolerant communities (Kirwan and Gedan, 2019; 35 Fagherazzi et al. 2019). Increases in soil salinity play a major role in forest decline and 36 transitioning at early stages of plant development (Williams et al. 1999). Soil salinity increases in 37 38 plant communities through several factors such as storm surges, drought, salt intrusion through land subsidence, and sea-level rise (Hayden and Hayden 2003; DeSantis et al. 2007; Fernandes et 39 al. 2018; Kirwan et al. 2016; Schieder and Kirwan, 2019). The long-term ecological implications 40 41 for regeneration of forested coastal plant communities is not well understood, particularly in temperate coastal forests (Williams et al. 2013) as plant response to disturbance can shift species 42 distributions (Ash et al. 2017). Disturbances increase heterogeneity within the landscape, resulting 43 in visible (e.g. short-term structural damage) and invisible effects (e.g. long-term community 44 regeneration) on community dynamics (Lugo 2008). Long-lived tree species die over time due to 45 higher salinity; however, the extent to which coastal forests can regenerate is unclear. 46

Coastal communities are highly driven by environmental filtering (i.e. salinity and wind) 47 and plants assemble based on their capacity to withstand environmental stresses (Ehrenfeld, 48 1990). The response to increased salinity can be species-specific and decrease overall total 49 germination (Paudel and Battaglia 2013). Species-specific responses can restructure species 50 dominance in a community when species with lower salt tolerances are impeded from colonizing 51 52 areas with higher salinities (Helm et al. 1991; Lui et al. 2017). The reduction and replacement of coastal forests due to changes in the environment has been reported throughout the Atlantic and 53 Gulf coast regions (Conner et al. 2005; Schieder et al. 2018), particularly, along forest/marsh 54 55 boundaries (DeSantis et al. 2007; Kirwan et al. 2016; Schieder and Kirwan 2019). Sea-level rise,

storm events, and saltwater intrusion result in marsh expansion into upland with differential consequences for long-lived trees that depend on freshwater for survival. A recent study shows that trees may resist tidal marsh expansion (Field et al. 2016); however, little is known about the long-term regeneration ability of trees in areas exposed to higher salinities.

Examining coastal forest response to elevated salinity is essential for understanding and 60 predicting community regeneration. The niche in which a seed germinates plays a fundamental 61 role in community regeneration at later life stages (Bochet 2015). The abiotic environment can 62 have a strong influence on when germination occurs in coastal ecosystems, and the timing of 63 germination has consequences for later life stages. If species are plastic in their response, they 64 may be able to withstand perturbations in the environment (Paudel and Battaglia 2013); however, 65 for some species disturbance may delay germination which alters the competitive landscape for 66 interacting species (Walck et al. 2011). If a species cannot recruit, then colonization cannot occur. 67 Relatively little is known about the contribution of early life stages to species distributions 68 in communities (Fraaije et al. 2015). When considering community regeneration an examination 69 of the entire life cycle of species is important because levels of vulnerability to disturbance change 70 with ontogeny. Seed germination and emergence are vital phases of the plant life cycle that are 71 72 highly dependent on environmental filters and can be a bottleneck for community regeneration (Donohue et al. 2010). Since the extent to which plants respond to increases in salinity is unclear, 73 exploring species' tolerances to the post disturbance environment during recruitment and the 74 75 potential for compositional change is necessary.

Morella. cerifera (L.) is a moderately salt-tolerant shrub (Tolliver et al. 1997) that is
encroaching in many coastal areas throughout the Atlantic and Gulf coast regions (Battaglia et al.
2007; Huang et al. 2018). Specifically, *M. cerifera* has expanded over 40% in the last 30 years

79 along the Virginia Coast Reserve barrier islands (Zinnert et al. 2011). The current study is motivated in part by the decrease in coastal forests on Parramore Island, VA, where discontinuous 80 portions of forests are located along a marsh boundary and *M. cerifera* is expanding (Figure 1). It 81 is unknown if there is an advantage for *M. cerifera* at the germination stage of development over 82 coastal species. Through this research we aim to answer the following questions: (1) To what 83 extent does elevated soil salinity impact the percent total germination of selected coastal forest 84 species? (2) What is the effect of elevated soil salinity on the timing of germination for the selected 85 species? and (3) What is the probability of species not germinating due to higher salinities? To 86 87 increase the accuracy of modelling the future trajectory of coastal communities, it is vital to know how species will respond to the altered post-disturbance environment particularly regarding soil 88 salinity during early stage development. 89

90 Methods

91 *Plant Species*

A growth chamber experiment was set up to examine the effect of soil salinity on the 92 germination of common species that can be found in mixed forests throughout the mid-Atlantic 93 coastal plain and Gulf coast regions. Due to high seed availability and germination rates, Acer 94 95 rubrum (L.), Liquidambar styraciflua (L.), Pinus taeda (L.), Celtis occidentalis (L.), Persea borbonia (L.) and M. cerifera were the selected species in this study. Additional species (i.e. 96 Quercus rubra (L.), Ilex opaca (L.), and Juniperus virginiana (L.) were tested but failed to 97 98 germinate due to seed viability or germinated during cold stratification, and thus were not included in the analysis. Acer rubrum, L. styraciflua and C. occidentalis are all deciduous species. Pinus 99 taeda, P. borbonia, and M. cerifera are all evergreen species. 100

101 The species used in this study are broadly distributed in eastern and southeastern US coastal environments. Most of the study species are tolerant to aerosol salt spray in their adult 102 forms including *Morella* spp. (formerly *Myrica* spp.) (Flint 1985; Gilman and Watson 1993; 103 Gilman and Watson 1994; Schultz, 1997). In coastal areas, salt sensitive species are found more 104 inland where salinity is relatively low (Ehrenfeld 1990). Celtis occidentalis, P. borbornia and M. 105 cerifera are bird dispersed. Pinus taeda, L. styraciflua and A. rubrum all are wind dispersed but 106 are capable of dispersing seed away from the parent canopy (Kormanik 1990; Schultz 1997). 107 Capacity for distant dispersal is a vital factor for seedling establishment in favorable habitats 108 109 (Rey and Alcántara 2000). The seedling stage is the most vulnerable stage of development and will succumb more readily to perturbations in the freshwater habitat. Salinity has been shown to 110 adversely impact establishment of woody species (Pezeshi et al. 1992; Middleton 2016). The 111 seed stage of development is more tolerant to perturbation than the seedling stage because seeds 112 can delay germination if conditions are unfavorable (Donohue et al. 2010). The extent to which 113 high salinity precludes the germination of woody species is unclear. 114

115

116 *Growth Chamber Germination Experiment*

All seeds for this study were collected along the Atlantic coastal plain from Virginia and 117 North Carolina and most can also be in Gulf coast regions. Seeds were stratified according to 118 protocols described in Young and Young (1992). In addition to stratification, M. cerifera was 119 scarified to remove the waxy coat. Seed flotation tests were used to determine seed quality for all 120 seeds. To examine the effect of salinity on germination, twenty-five seeds of each of the six species 121 122 were exposed to five salinity treatments (0, 2, 5, 10, and 20 ppt) with four replicates per treatment for each species. Seeds were placed in five rows and five columns on top of the substrate. 123 Germination experiments for each replicate per species were performed in 6 x 6 x 3 clam shell 124

125 plastic containers with perforations in the bottom and filled with a 3:1 sand: soil mixture. The salinity treatments were made using dilutions of a commercial mixture that approximates ocean 126 salts (Instant Ocean, Aquarium Systems). Hoagland solution was added to each salinity treatment 127 to approximate nutrients in the natural soil environment. Hoagland solution and specific nutrient 128 concentrations were prepared exactly as described by Hoagland and Arnon (1950). There were no 129 differences in nutrients among the five treatments and salinity treatments were verified before 130 application during the experiment. Salinity treatments (containing Hoagland solution) were added 131 to the respective replicates every five days to account for evaporation. Replicates were placed in 132 133 a single growth chamber (model E15, Conviron, Pembina, N. D.) with a 14-hour photoperiod and a 25:20°C temperature regime at a photon flux density of 400 µmol m⁻² s⁻¹. A seed that contained 134 a radicle of 2 mm was counted as germinated. Seeds were treated and observed for 55 days. 135

136 Statistical Analysis

The process of germination was analyzed by determining total germination, mean 137 germination time, mean germination rate and Kaplan-Meier survival curves. To determine the 138 effect of soil salinity on total germination we calculated total percent germination by summing all 139 seeds that germinated per treatment over the course of the experiment. To determine seed vigor, 140 141 we calculated mean germination time (MGT), the time to 50% germination for each species. To determine if there was a delay in germination relative to the control treatment, we calculated mean 142 germination rate (MGR), which measures the speed of germination. MGR was calculated by taking 143 144 the reciprocal of the mean germination time (Ranal et al. 2009). We analyzed these indices using two-way ANOVA and post-hoc Tukey tests to determine significant differences among treatments 145 and species. Kaplan Meier curves were used to determine the probability of not germinating as 146 147 described by McNair et al. (2012). For analysis of the Kaplan Meier survival curves, we performed

multiple log-rank tests to determine significant differences in survival times of species among treatments. Salinity and species were fixed effects in the model and were categorical variables. Each species was modelled separately to examine the effect of salinity. We adjusted the alpha for the multiple comparisons using a Bonferroni correction (α =0.005). JMP Version 13 (SAS Institute, Inc., 2016) software was used for the statistical analyses.

153

154 **Results**

155 *Total Percent Germination*

156 On average total percent germination declined with increasing salinity for all species except A.

157 *rubrum*, Supplementary Figure 1); *A. rubrum* had the highest percent germination and *C.*

158 *occidentalis* the least, regardless of salinity treatment. There was a significant treatment

159 (F=111.4, p<0.0001) and species (F=222.7, p<0.0001) effect for total % germination. There was

also a significant species x treatment interaction (F = 5.2, p < 0.0001, Figure 2). Acer rubrum

and *P. taeda* were the only species to germinate at 20 ppt. *Pinus taeda* germination did not

differ from *A. rubrum* at 0, 2, and 5 ppt; however, at 10 ppt its germination became comparable

to all other species germinating at lower levels of salinity (0 ant 2 ppt). Only *L. styraciflua* at 5

164 ppt had comparable germination to *P. taeda* at 10 ppt. Germination for *M. cerifera* was not

different from *P. borbonia* and *C. occidentalis* with the control or with increases in salinity (2, 5,

166 10 ppt).

167 Mean Germination Time

Increased salinity differentially affected the MGT of the selected species. It took longer
for *P. borbonia* to reach MGT than all other species (p<0.0001) and it took less time for *A. rubrum*to reach MGT (p<0.0001) (Supplementary Figure 2). Mean germination time had a treatment (F

171= 158.5, p < 0.0001), species (F = 116.0, p < 0.0001), and interaction effect (F = 25.0, p < 0.0001;172Figure 3). Salinities of 2, 5 and 10 ppt increased MGT relative to the control (Supplementary173Figure 2). When averaged across all salinities 10 ppt significantly increased mean germination174time. Twenty ppt decreased MGT because *P. borbonia*, *L. styraciflua*, *M. cerifera*, and *C.*175occidentalis did not germinate at this salinity. Acer rubrum was the only species that did not176experience a significant decrease in MGT due to salinity.

177 Mean Germination Rate

As seen in total germination and MGT, there was a treatment (F = 101.4, p < 0.0001) and 178 species (F = 722.4, p < 0.0001) effect for mean germination rate (MGR). There was also a species 179 x treatment interaction (F=8.02, p<0.0001, Figure 4). MGR did not differ at low salinities, 0 and 180 2 ppt but was slowed at all other salinities (Supplementary Figure 3). Across all treatment levels, 181 MGR was fastest in A. rubrum, followed by P. taeda and C. occidentalis (Supplementary Figure 182 3). There were no differences between L. styraciflua and M. cerifera. Persea borbonia had the 183 slowest MGR. MGR was the same for A. rubrum at all salinities and faster than all other treatment 184 and species combinations (Figure 4). *Pinus taeda* germination at higher salinities (5 ppt and 10 185 186 ppt) were significantly different from mean germination rates at lower salinities (0 ppt and 2 ppt). Persea borbonia had the lowest mean germination rate, across all salinity levels, but was not 187 significantly different from *M. cerifera*. 188

189

190 *Kaplan-Meier Probability*

The probability of not germinating increased with salinity for all species except *A*. *rubrum*. Kaplan-Meier curves and log-rank tests revealed significant differences in seed germination based on soil salinity for most of the selected species in this study. All species *L*. *styraciflua*, *P. taeda*, *C. occidentalis*, *P. borbonia* and *M. cerifera* (p<0.0001, p<0.0001, p<0.0001,

p<0.0001, p<0.0001, respectively) showed a response to salinity except A. rubrum. Most of its 195 germination was completed by day 5. However, for L. styraciflua most germination occurring 196 between days 10-30 days (Figure 5). Pinus taeda experienced early germination with most 197 germination occurring between days 5-30. Celtis occidentalis also experienced early germination, 198 but most germination occurred over a shorter period, 5-15 days, after which, most seeds stopped 199 200 germinating. Persea borbonia had the longest germination time with the first germination at day 15 and most of the germination occurring between days 25-50. The shrub, M. cerifera, started 201 germinating on day 15 as well and most of its germination occurred between days 15 and 40. There 202 203 were differences in the patterns of germination for all species affected by higher salinity. Pairwise comparisons show that the threshold for salinities too high for germination to occur appear to be 204 reached between salinities of 2 and 5 ppt for all species responding to the treatments. A salinity of 205 10 ppt is too high for most of the selected species to germinate (Table 1). 206

207

208 Discussion

With projected increases in sea-level rise and saltwater intrusion in low-lying terrestrial 209 and tidal freshwater environments (Sallenger et al. 2012), compositional changes that favor more 210 salt-tolerant species are likely to occur (Conner et al. 2007; Doyle et al. 2010) in coastal forests. 211 In this study we set out to determine the potential for coastal tree species to regenerate at higher 212 salinities and determine if a moderately salt-tolerant shrub that is found in freshwater wetlands, M. 213 cerifera, has advantages during germination that may contribute to its expansion in coastal 214 forests. This study showed that *M. cerifera* does not have an advantage at the germination stage 215 over the tree species in this study. Its total germination was equally affected by salinity as P. 216 borbonia and C. occidentalis and reduced relative to A. rubrum and P. taeda. Salinity increased 217 mean time to germination for M. cerifera, P. borbonia, L. styraciflua, and P. taeda. With increased 218

salinity (> 5ppt) it took longer for these species to reach mean time germination relative to thecontrols.

Soil salinity is an important factor for early stages of development for many 221 species. Paudel and Battaglia (2015) and Middleton (2016) showed that germination decreased 222 for trees and shrubs as salinity increases. However, soil salinity does not always control the 223 distribution of adult vegetation. Martin and Young (1997) documented spatial and temporal 224 differences in soil salinity across Hog Island, VA and noted that J. virginiana patterns were not 225 established in accordance with soil salinity. For some species, zonation patterns are set at earlier 226 227 stages of development. Adult trees and shrubs are still affected by salt in the form of aerosols, which may contribute to their overall persistence (Wells and Shunk 1938; Bellis and Keough 228 1995). Morella cerifera appears limited by soil salinity at earlier life stages (Woods et al. 2019) 229 but can withstand saltwater flooding at the adult stage (Naumann et al. 2008; Liu et al. 2017). The 230 extent to which *M. cerifera* persists at earlier life stages relative to neighboring tree species may 231 determine overall community trajectory. 232

In the current study, A. rubrum and P. taeda, both wind-dispersed species, experienced 233 greater total germination than all other species with increasing levels of salinity. Acer rubrum was 234 235 not affected at all at the germination stage of development by increasing levels of salinity. A recent study showed that after Hurricane Sandy, A. rubrum trees were negatively impacted by saltwater 236 flooding but were able to recover over time (Hallett et al. 2018). Total germination of P. taeda 237 238 decreased at higher salinities; however, even at 10 ppt germination capacity was higher than all other selected species, except A. rubrum and L. styraciflua at low salinities. Records show that P. 239 240 taeda was a dominant species on Virginia barrier islands seven years before Hurricane Isabel in 241 2003 (unpublished data). Both A. rubrum and P. taeda appear to have the capacity to be resilient to soil salinity disturbance at the germination stage but they may be affected by salinity as seedlings
and adults (Johnson and Young, 1993; Donohue et al. 2010; Hallett et al. 2018). As the
environment changes to one with variable soil salinity, these species may be able to persist through
regeneration.

Total germination of L. styraciflua, C. occidentalis, P. borbonia and M. cerifera were all 246 affected by >10 ppt soil salinities, with no germination at 20 ppt. *Liquidambar styraciflua* appears 247 to be more salt-tolerant than C. occidentalis, P. borbonia and M. cerifera at low salinities; however 248 as salinity increased its germination became comparable to species over which it may have had a 249 competitive advantage in a low salinity environment. Total germination of L. styraciflua would 250 be the most impacted by increased salinity because at low salinities it had germination comparable 251 to that of A. rubrum and P. taeda; however, L. styraciflua experienced the greatest loss with 252 253 increased salinity (58% decrease from 2 to 5 ppt). This reduction of regeneration potential in L. styraciflua could cause compositional changes forests where it is dominant if the adult species 254 experience a high mortality event. 255

Altered patterns of regeneration can cause compositional changes in forests (Johnstone et 256 al. 2016). Increased soil salinity delayed germination of L. styraciflua, P. taeda, C. occidentalis 257 258 and *M. cerifera*. As *P. taeda* germination was high, a delay in germination had less impact overall. Conversely, for species with low germination rates C. occidentalis, a delay in germination, due to 259 soil salinity, reduced its regeneration potential. Persea borbonia and M. cerifera, common species 260 261 in wet maritime forests throughout the Atlantic and gulf coasts (Gresham 1985), experienced the lowest MGRs. They were slow to start germinating without increased salinity. They are both 262 broadleaf evergreen species that are often found in association with one another, P. borbonia 263 264 dominant in the canopy layer while, M. cerifera dominant in the shrub layer. While increased

salinity did not delay the germination of *P. borbonia*, it delayed the germination of *M. cerifera* at
10 ppt. A delay in germination could cause nutrients to be usurped by species that can germinate
at higher salinities, which could impact competitive dynamics at the seedling stage of
development. The result of species experiencing delayed germination or being prevented from
germinating due to their level of salinity tolerance is community transitioning or retreating
(Williams et al. 1999; Langston et al. 2017).

Kaplan-Meier curves showed that P. borbonia took the longest to germinate, but 271 germination was steady and consistent once it occurred. Slow germination was not due to higher 272 soil salinities, except at 20 ppt. This indicates that P. borbonia can regenerate up to 10 ppt. 273 However, a delay in germination may affect future forest composition, especially in competition 274 with an expanding shrub population. Conner and Askew (1993) showed that *P. borbonia* and *A.* 275 276 *rubrum* seedlings were not able to persist after up to five days of flooding with a high salinity treatment (20-27 ppt). Even though A. rubrum germinates at salinities as high as 20 ppt, the 277 seedling stage of development may limit its relative abundance in coastal forests under saline 278 flooded conditions. Tolerance to an altered environment at early developmental stages is essential 279 for persistence in a community. 280

With the timing of nor'easters coinciding with the germination of many coastal forest tree species, salinity will be a major factor affecting future tree regeneration. Trees at the forest/marsh boundary are particularly susceptible to loss of habitat as sea-level rises and upland migration of marshes advances. Forests understory tree species are being replaced by halophytic species (Williams et al. 1999). Empirically, the formation of ghost forests and changes in vegetation along many mid-Atlantic and Gulf coast regions suggest that salinities of 5 ppt are regularly exceeded (Williams et al 1999; Thomas et al. 2015; Kirwan and Gedan, 2019). Entire forests in the mid288 Atlantic and southeast are either retreating or transitioning in favor of more salt tolerant species (Williams et al. 1999; DeSantis et al. 2007; Kirwan et al. 2016). It is hard to project changes in 289 salinity for coastal forests with continued sea-level rise and saltwater intrusion because these 290 systems are dynamic. Salt intrusion may increase soil salinity temporarily and prevent 291 germination, but a pulse of freshwater may decrease salinity allowing species to regenerate. The 292 293 current study reveals that if trees succumb to salt intrusion, regeneration from seed will be difficult for most species at higher (i.e. >5 ppt) salinities, potentially altering community composition. 294 Some species (i.e. A. rubrum, P. taeda) can germinate quickly at multiple salinity levels but may 295 296 not grow to adult form with increased salinity. Other species (i.e. C. occidentalis, L. styraciflua, P. borbonia and M. cerifera) are more vulnerable at the seed stage to salinity. Knowing threshold 297 limits of germination response to salinity is critical for future modeling of forest response to sea-298 299 level rise and storm events. Regeneration from seed is slow, but also determines future community 300 trajectory after disturbance events.

301 Acknowledgments

This work was supported by the National Science Foundation Long-Term Ecological Research 302 grants DEB-1237733 and DEB-1832221 to JC Zinnert and Ford Foundation Fellowship to NN 303 304 Woods. The authors thank Amanda Faucette from North Carolina Botanical Garden at the University of North Carolina at Chapel Hill for providing seeds, the Virginia Coast Reserve staff 305 for logistical support, Dot Field with the Virginia Department of Conservation and Recreation for 306 307 permitted access to collect seeds on the eastern shore of Virginia and Caitlin Bishop, Joe Brown, Lauren Wood, Austin Tuley, Michael Sinclair, Audrey Kirschner, Eddie Long and Caroline 308 Baucom for technical support. 309

310 Literature cited

Ash JD, Givnish TJ and Waller DM (2017) Tracking lags in historical plant species' shifts in

312	relation to regional climate change. Global Change Biology 23:1305-1315
313	Battaglia LL, Denslow JS, Hargis TG (2007) Does woody species establishment alter herbaceous
314	community composition of freshwater floating marshes? Journal of Coastal Research
315	23:1580-1587
316	Bellis VJ, Keough, J. R. (1995) Ecology of maritime forests of the southern Atlantic Coast: a
317	community profile. U.S. Department of Interior, Washington, DC
318	Bochet E (2015) The fate of seeds in the soil: a review of the influence of overland flow on seed
319	removal and its consequences for the vegetation of arid and semiarid patchy
320	ecosystems. Soil 1:131-146
321	Boose ER, Foster DR, Fluet M (1994) Hurricane Impacts to tropical and temperate forest
322	landscapes. Ecological Monographs 64:369-400
323	Conner WH, Askew GR (1993) Impact of saltwater flooding on red maple, redbay, and Chinese
324	tallow seedlings. Castanea pp 214-219
325	Conner WH, Mixon WD, Wood GW (2005) Maritime forest habitat dynamics on Bulls Island
326	Cape Romain National Wildlife Refuge, S. C., following Hurricane Hugo. Forest
327	Ecology and Management 212:127-134
328	Conner WH (2007) Ecology of tidal freshwater forested wetlands of the southeastern United
329	States Dordrecht: Springer pp 448-450
330	DeSantis LR, Bhotika S, Williams K, Putz FE (2007) Sea-level rise and drought interactions
331	accelerate forest decline on the Gulf Coast of Florida, USA. Global Change Biology
332	13:2349-2360
333	

334 Donohue K, de Cosas RR, Burghardt L, Kovach K, Willis CG (2010) Germination, post

335	germination, adaptation and species ecological ranges. Annual Review of Ecology,
336	Evolution, and Systematics 41:293-319
337	Doyle TW, Krauss KW, Conner WH, From, AS (2010) Predicting the retreat and migration of
338	tidal forests along the northern Gulf of Mexico under sea-level rise. Forest Ecology and
339	Management 259: 770-777
340	Ehrenfeld JG (1990) Dynamics and processes of barrier-island vegetation. Reviews in Aquatic
341	Sciences 2:437-480
342	Fagherazzi S, Anisfeld SC, Blum LK, Long E., Feagin RA, Fernandes A, Kearney,
343	WS, Williams K. (2019) Sea level rise and the dynamics of the marsh-upland
344	boundary. Frontiers in Environmental Science 7 Article 25
345 346	Field CR, Gjerdrum C, Elphick CS, (2016) Forest resistance to sea-level rise prevents landward
347	migration of tidal marsh. Biological Conservation 201:363-369
348	Flint HL. (1985) Plants showing tolerance of urban stress. Journal of Environmental
349	Horticulture 3:85-89.
350	Fraaije RG, ter Braak CJF, Veryuyn B, Breeman LBS, Verhoven JTA, Soons MB (2015) Early
351	plant recruitment stages set the template for the development of vegetation patterns along
352	a hydrological gradient. Functional Ecology 29: 971-980
353	Gilman, E.F. and Watson, D.G., 1993. Celtis occidentalis Common Hackberry. Available: n
354	http://hort. ufl. edu/database/documents/pdf/tree_fact_sheets/celocca. pdf.
355	Gilman, EF; Watson, D.G., 1994. Persea borbonia Redbay. Available: n
356	http://hort.ufl.edu/trees/PERBORA.pdf
357	Gresham, CA, 1985. Analysis of composition, environmental gradients, and structure in the
358	Coastal Plain lowland forests of South Carolina. Castanea pp 207-227
359	Hallett R, Johnson ML, Sonti NF (2018) Assessing the tree health impacts of saltwater flooding

in coastal cities: A case study in New York City. Landscape and Urban Planning

361	177:171-177
362	Hayden BP, Hayden NR. (2003) Decadal and century-long changes in storminess at long-
363	term ecological research sites. Climate Variability and Ecosystem Response at Long-
364	Term Ecological Research Sites. Oxford University Press, New York, NY, USA, pp.262-
365	285
366 367	Hoagland DR, Arnon DI (1950) The water-culture method for growing plants without
368	soil. Circular. California Agricultural Experiment Station 347 2nd ed.
369	Huang H, Zinnert JC, Wood LK, Young DR, D'Odorico P (2018) Non-linear shift from
370	grassland to shrubland in temperate barrier islands. Ecology 99:1671-1681
371	JMP [®] , Version 13Pro. SAS Institute Inc., Cary, NC, 1989-2016-
373	Johnson SR, Young DR (1993) Factors contributing to the decline of <i>Pinus taeda</i> on a Virginia
374	barrier island. Bulletin of the Torrey Botanical Club 120:431-138
375	Johnstone JF, Allen CD, Franklin JF, Frelich LE, Harvey BJ, Higuera PE, Mack MC,
376	Meentemeyer RK, Metz MR, Perry GL, Schoennagel T (2016) Changing disturbance
377	regimes, ecological memory, and forest resilience Frontiers in Ecology and the
378	Environment 14: 369-378
379	Kearney WS, Fernandes A, Fagherazzi S (2019) Sea-level rise and storm surges structure coastal
380	forests into persistence and regeneration niches. PloS One 14:e0215977
381	Kirwan ML, Gedan KB (2019) Sea-level driven land conversion and the formation of ghost
382	forests. Nature Climate Change 9: 450
383	

385	Kirwan ML, Temmerman S, Skeehan EE, Guntenspergen GR, Fagherazzi S. (2016)
386	Overestimation of marsh vulnerability to sea level rise. Nature Climate Change, 6:253.
387	Kormanik P. 1990. Liquadambar styraciflua, sweetgum. In: Silvics of North America: 2.
388	Hardwoods. Burns, R.M., and B.H. Honkala, Tech. Coords. http://www.na.fs.fed.us/
389	Arboriculture & Urban Forestry 33(2): March 2007 95 ©2007 International Society of
390	Arboriculture spfo/pubs/silvics_manual/table_of_contents.htm (accessed 3/8/06)
391	Agriculture Handbook 654 Vol. 2 of the USDA Forest Service, Washington, DC. 877 pp.
392	Kribel JR, Ware S (2014) Hurricane-caused tree loss on permanent plots in a temperate
393	hardwood forest. Castanea. 79:1-7
394	Langston AK, Kaplan DA, Putz F (2017) A casualty of climate change? Loss of freshwater
395	forest islands on Florida's Gulf Coast. Global Change Biology 5383-5397
396	Liu X, Conner WH, Son B, Jayakaran AD (2017) Forest composition and growth in a freshwater
397	forested wetland community across a salinity gradient in South Carolina, USA. Forest
398	Ecology and Management 389: 211-219
399	Lugo AE (2008) Visible and invisible effects of hurricanes on forest ecosystems: an international
400	review. Austral Ecology 33:368-398
401	Martin DW, Young DR (1997) Small-scale distribution and salinity response of Juniperus
402	virginiana on an Atlantic Coast barrier island. Canadian Journal of Botany 75:77-85
403	McNair JN, Sunkara A, Frobish D (2012) How to analyse seed germination data using statistical
404	time-to-event analysis: non-parametric and semi-parametric methods. Seed Science
405	Research 22:77-95
406	Middleton BA (2016) Differences in impacts of Hurricane Sandy on freshwater swamps on the
407	Delmarva Peninsula, Mid-Atlantic Coast, USA. Ecological Engineering 87: 62-70
408	Naumann JC, Young DR, Anderson JE (2008) Leaf chlorophyll fluorescence, reflectance, and

409	physiological response to freshwater and saltwater flooding in the evergreen shrub,
410	Myrica cerifera. Environmental and Experimental Botany 63: 402-409
411	Paudel S, Battagilia LL (2013) Germination responses of the invasive Triadica sebifera and two
412	co-occurring native woody species to elevated salinity across a gulf coast transition
413	ecosystem. Wetlands 33:527-535
414	Paudel S, Battaglia LL (2015) The role of light, soil and human factors on the probability of
415	occurrence of an invasive and three native plant species in coastal transitions of coastal
416	Mississippi, USA. Journal of Plant Ecology 8:491-500
417	Peterson CJ, Cannon JB, Godfery CM (2016) First steps toward defining the wind disturbance
418	regime in central hardwoods forest In: Greenberg, C., Collins B. (eds) Natural
419	Disturbances and Historic Range of Variation. Managing Forest Ecosystems 32. Sringer,
420	Cham
421	Pezeshki SR. (1992) Response of Pinus taeda L to soil flooding and salinity. In Annales des
422	sciences forestières EDP Sciences 49:149-159
423 424	Prengaman KA, Kribel JRG, Ware S (2008) Effects of Hurricane Isabel on a maturing hardwood
425	forest in the Virginia Coastal Plain. Journal of the Torrey Botanical Society 135:360-66
426	Ranal MA, Santana, DGD, Ferreira, WR, Mendes-Rodrigues C (2009) Calculating germination
427	measurements and organizing spreadsheets. Brazilian Journal of Botany 32:849-855
428	Rey PJ, Alcántara JM. (2000) Recruitment dynamics of a fleshy-fruited plant (Olea europaea):
429	connecting patterns of seed dispersal to seedling establishment. Journal of
430	Ecology 88:622-633.
431	Sallenger AH, Doran KS, Howd PA (2012) Hotspot of accelerated sea-level rise on the Atlantic
432	coast of North America. Nature Climate Change 2:884-888
433	Scheele BC, Foster CN, Banks SC, Lindenmayer DB (2017) Niche contractions in declining

434	species: mechanisms and consequences. Trends in Ecology and Evolution. 32:346-355
435	Schieder NW, Walters DC, Kirwan ML (2018) Massive upland to wetland conversion
436	compensated for historical marsh loss in Chesapeake Bay, USA. Estuaries and Coasts
437	41:940-951
438	Schultz RP. 1997. Loblolly pine: the ecology and culture of loblolly pine (Pinus taeda
439	L.). Agriculture Handbook 713. Washington, DC: US Department of Agriculture, Forest
440	Service. 493 p.
441	Tolliver K, Martin DW, Young DR (1993) Freshwater and saltwater flooding response for
442	woody species common to barrier island swales. Wetlands 17:10-18
443	Walck JL, Hidayati SN, Dixon KW, Thompson K, Poschlod P (2011) Climate change and plant
444	regeneration from seed. Global Change Biology 17:2145-2161
445	Wells BW, Shunk IV (1938) Salt spray: an important factor in coastal ecology. Bulletin of the
446	Torrey Botanical Club 65:485–493
447 448	Williams SJ (2013) Sea-level rise implications for coastal regions. Journal of Coastal Research 63:184-196
449 450	Woods NN, Dows BL, Goldstein EB, Moore LJ, Young DR, Zinnert JC (2019)
451	Interaction of seed dispersal and environmental filtering affects woody encroachment
452	patterns in coastal grassland. Ecosphere 10(7), p.e02818
453 454 455	Young JA, Young CG (1992) Seeds of Woody Plants in North America. Dioscorides Press. Portland, Oregon
456	Zinnert JC, Shiftlett SA, Vick JK, Young DR (2011) Woody vegetative cover dynamics in
457	response to recent climate change on an Atlantic Coast barrier island: a remote sensing
458	approach Geocarto International 26:595-612



Fig. 1

461 Maritime forest along a tidal marsh boundary on Parramore Island, VA 2018. Showing from

462 foreground to background marsh grasses, invasive *Phragmites* spp., *M. cerifera* and *P. taeda*.

463 Photo credit, Natasha Woods.



469 Fig. 2

- 470 Total Percent Germination graphs show that total percent germination decreased for *L*.
- 471 styraciflua, P. taeda, C. occidentalis, P. borbonia and M. cerifera with increased salinity. Only
- 472 A. rubrum and P. taeda germinated at 20 ppt. Different letters represent significant differences in
- 473 salinities at which species germinated. These results are from two-way ANOVA analysis.





478 Mean germination time (MGT) graphs show that *P. borbonia* took longer to reach mean time germination that any other species at 5
479 and 20 ppt. Of all species *A. rubrum* took the least amount of time to reach MGT. Different letters represent significant differences in
480 salinities at which species germinated. These results are from two-way ANOVA analysis.





483	Mean germination rate	(MGR)	shows that there is a	delay in ge	ermination at higher	salinities for L.	styraciflua, P. taea	la, C
-----	-----------------------	-------	-----------------------	-------------	----------------------	-------------------	----------------------	-------

484 occidentalis, and M. cerifera. Acer rubrum at all salinities had a higher MGR. Different letters represent significant differences in

- salinities at which species germinated. These results are from two-way ANOVA analysis.
- 486
- 487





490 Kaplan-Meier survival curves show the probability of each species not germinating over the 55-day time period. Each time step



⁴⁹¹ represents a germination event.

493 **Table 1**

494 P-values of Kaplan Meier survival curve pairwise comparisons of salinity treatments within each species. Alpha level was adjusted for

495 multiple comparisons using a Bonferroni correction (α=0.005). Acer rubrum was not included because there were no significant

496 differences among treatments. Asterisks represent significant differences in salinities at which species germinated.

Pairwise Comparisons			Species		
	L. styraciflua	P. taeda	C. occidentalis	P. borbonia	M. cerifera
0 ppt: 2 ppt	0.1110	0.8930	0.0960	0.1220	0.1020
0 ppt: 5 ppt	<0.0001*	0.0080	<0.0001*	0.0141*	0.1510
0 ppt: 10 ppt	<0.0001*	<0.0001*	< 0.0001*	<0.0001*	<0.0001*
0 ppt: 20 ppt	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*
2 ppt: 5 ppt	0.0002*	0.0080	0.0030*	0.3690	0.0010*
2 ppt: 10 ppt	<0.0001*	<0.0001*	< 0.0001*	<0.0001*	<0.0001*
2 ppt: 20 ppt	<0.0001*	<0.0001*	< 0.0001*	<0.0001*	<0.0001*
5 ppt: 10 ppt	0.0020*	0.0002*	0.0280	0.0003*	0.0070
5ppt: 20 ppt	<0.0001*	<0.0001*	< 0.0001*	<0.0001*	< 0.0001*
10 ppt: 20 ppt	<0.0001*	<0.0001*	0.0130	<0.0001*	<0.0001*



501 Total Percent Germination graphs show that *A. rubrum* had the highest percent germination when averaged across all treatments

followed by *P. taeda* and *L. styraciflua*. Salinity treatments of 0 ppt and 2 ppt had significantly higher germination when averaged

across all species. Different letters represent significant differences among species (or treatment groups).

504



506 Supplementary Fig. 2

507 Mean germination time (MGT) graphs show that *P. borbonia* took the longest MGT) and *A. rubrum* took the least amount of time to

reach MGT. When averaged across all salinities 10 ppt significantly increase mean germination time. 20 ppt is very low because *P*.

509 borbonia, L. styraciflua, M. cerifera, and C. occidentalis did not germinate at this salinity. Different letters represent significant

510 differences among species (or treatment groups)





512 Supplementary Fig. 3

- 513 Mean Germination Rate (MGR) graphs show that *A. rubrum* had the fastest germination rate followed by *P. taeda*, and *C.*
- 514 *occidentalis*. When averaged across all salinities, 0 ppt and 2 ppt had the fastest rates of germination. Different letters represent
- significant differences among species (or treatment groups)