- 1 Sea Level-Driven Marsh Migration Results in Rapid Net Loss of Carbon
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5 Key Points

- 6 1. Sea level-driven marsh migration leads to a 50% reduction in carbon stocks, driven primarily
- 7 by the loss of carbon stored in woody biomass
- 8 3. We propose a replacement-time metric that indicates marsh soils must survive centuries before
 9 they can offset forest carbon loss
- 3. Large timescales of carbon replacement indicate that marsh migration results in a net loss ofcarbon that is overlooked in coastal budgets

12 Abstract

Sea level rise alters coastal carbon cycling by driving the rapid migration of coastal ecosystems, 13 14 salinization of freshwater systems, and replacement of terrestrial forests with tidal wetlands. Wetland soils accumulate carbon (C) at faster rates than terrestrial soils, implying that sea level 15 rise may lead to enhanced carbon accumulation. Here, we show that carbon stored in tree 16 17 biomass greatly exceeds carbon stored in adjacent marsh soils so that marsh migration reduces total carbon stocks by approximately 50% in less than 100 years. Continued marsh soil carbon 18 accumulation may eventually offset forest carbon loss, but we estimate that the time for 19 20 replacement is similar to estimates of marsh survival (i.e. centuries), which suggests that forest C 21 may never be replaced. These findings reveal a critical C source not included in coastal C

budgets driven by migrating ecosystems and rapidly shifting allocations between carbon storedin soils and biomass.

24 Plain Language Summary

Forests along the upland edge of salt marshes are being killed by rising sea levels and replaced 25 with salt marsh in a process called marsh migration. Marsh soils, unlike soils in forest, quickly 26 accumulate carbon in their soils. This indicates that marsh migration could possibly increase 27 carbon storage across the landscape. Here, we show the opposite, that sea level rise reduces 28 coastal carbon stocks through the loss of woody aboveground biomass. This loss is partially 29 offset with expanding organic soil in the newly formed marsh, but the amount of carbon lost 30 from forest mortality is far greater than that gained by the growing marsh soils. Continued 31 carbon accumulation in wetland soils may eventually compensate for forest carbon loss, but the 32 time it would take for marshes to replace that lost carbon is at the scale of centuries, which is 33 approximately the same amount of time predicted for marshes to drown from rising sea levels. 34 This suggests that forest carbon may never be replaced and reveals a critical source of carbon 35 under climate driven landscape changes. 36

37 Index Terms

Wetlands (0497), Sea level change (1641), Land cover change (1632), Impacts of global change
(1630), Coastal Processes (4217),

40 Keywords

41 Wetland, ecotone, costal forest, blue carbon, sea level rise, carbon-climate feedback

42 1 Introduction

Coastal wetlands are thought to disproportionally influence the global carbon (C) budget 43 44 because of C accumulation rates 1 to 2 orders of magnitude greater than terrestrial systems (Mcleod et al., 2011; Chmura et al., 2003). Salt marshes, mangroves, and seagrasses account for 45 approximately 50% of C buried in the ocean despite covering <2% of the ocean's surface 46 47 (Duarte et al., 2005). However, sea level rise, reduced sediment supply, and other anthropogenic stressors threaten the persistence and strength of the coastal carbon sink (Kirwan and Megonigal, 48 49 2013; Saintilan et al., 2020). Extensive historical loss of coastal ecosystems (Kirwan and Gedan, 2019) suggests that coastal wetlands are simultaneously valuable yet vulnerable C sinks 50 (Theuerkauf and Rodriguez, 2017; Nahlik and Fennessy, 2016; Hopkinson et al., 2012), making 51 it imperative to understand how the coastal C sink will respond to global change (Ward et al., 52 2020). 53

For more than a decade, blue carbon research has focused on quantifying C stored in the 54 soils of single ecosystems, often at single points within an ecosystem (Mcleod et al., 2011; 55 Chmura et al., 2003; Duarte et al., 2005; Ward et al., 2020). However, climate change limits the 56 applicability of this traditional blue carbon approach by altering the position of ecotones, the 57 spatial extents of ecosystems within the coastal landscape, and the partitioning of C between 58 soils and vegetation (Kirwan and Megonigal, 2013; Kirwan et al., 2016a; Kruass et al., 2018; 59 60 Smith, 2013; Osland et al., 2017). For example, sea level rise is leading to the widespread migration of wetlands into retreating upland forests across the Atlantic coast of North America 61 (Kirwan and Gedan, 2019; Schieder et al., 2018), where coastal ecosystems and their carbon 62 63 pools are expected to change rapidly (i.e. at decadal time scales) (Krauss et al., 2018; Schieder and Kirwan, 2019; Wang et al., 2019; Enwright et al., 2016). Following conventional blue 64

65 carbon approaches focusing on soil C, this transgression should increase coastal C by replacing a low C burial system (upland forest) with a high C burial system (salt marsh) (Mcleod et al., 66 2011; Wang et al., 2019; Elsey-Quirk et al., 2011; Morris et al., 2016). Yet, this traditional 67 approach largely ignores the contribution of C stored in biomass, which is known to be important 68 in other systems. For example, living biomass accounts for approximately 30% of C stored in 69 mangroves and nearly half of C stored in the world's forests (Pan et al., 2011; Hamilton and 70 Friess, 2018). In contrast to terrestrial systems that exhibit positive carbon-climate feedbacks 71 (Melillo et al., 2017), work in coastal wetlands points to a potentially negative carbon-climate 72 73 feedback, where marsh soil carbon accumulation rates increase with warming-driven sea level rise (Kirwan and Mudd, 2012; Doughty et al., 2016). However, we show here that tree biomass 74 rather than soil organic matter dominates C stocks in rapidly migrating marsh-forest ecotones, so 75 that sea level-driven marsh migration leads to a century scale loss of C that is unaccounted for in 76 our conceptual understanding of coastal C cycling. 77

78 **2 Methods**

79 2.1 Approach and Study Area

We measured biomass and soil C stocks across the forest-marsh ecotone at four rapidly 80 transgressing sites in the Chesapeake Bay region of Maryland and Virginia in the United States 81 of America (Figure 1). The Chesapeake Bay serves as a model region for studying the C 82 implications of sea level-driven land conversion because rates of relative sea level rise (between 83 3 and 6 mm yr⁻¹) are twice as fast as eustatic rates (\sim 2 mm yr⁻¹) and the gently sloping, rural 84 coast allows for many opportunities for marsh migration. Approximately 100,000 acres of salt 85 marsh have migrated into retreating coastal forests since the mid-19th century, and rates of forest 86 retreat are accelerating in parallel with relative sea level rise (Schieder et al., 2018; Schieder and 87

Kirwan, 2019). Regional conditions in the Chesapeake Bay create rapid, widespread landscape
changes that exemplify the slower, yet eventual, ecosystem shifts that salinization drives across
the coastal landscape.

91 Within the Chesapeake Bay, we studied sites at Goodwin Island (GI), Phillips Creek (PC), Monie Bay (MB), and Moneystump Swamp (MS). At each site, four transects starting in 92 93 salt-unaffected forest and ending in young salt marsh that was once upland forest were 94 established perpendicular to the marsh-forest ecotone. We identified and delineated five unique vegetation zones along the transects according to vegetation and forest health: high forest, mid 95 96 forest, low forest, transition zone, and high marsh (Figure 1). The high forest is defined as a forest unaffected by salt intrusion displaying a mixed aged structure of both coniferous and 97 hardwood trees. The mid forest displays early signs of salt stress and exhibits 100% hardwood 98 tree mortality, but conifer seedling regeneration is present in the understory and the canopy has a 99 predominantly healthy, mixed age structure. The low forest is defined by relatively higher salt 100 101 stress, indicated by limited conifer regeneration, increased standing conifer tree mortality, and shrub species dominance in the understory. The transition zone has approximately 50% mortality 102 in all standing trees with an understory dominated by *Phragmites australis* and typical high 103 104 marsh herbaceous species. The high marsh is dominated by herbaceous marsh grasses Distichlis spicata, Spartina alterniflora, and Spartina patens, and has no living canopy. This general 105 vegetation pattern is observed in retreating coastal forests throughout the Atlantic Coast (Kirwan 106 107 and Gedan, 2019; Smart et al., 2020; Langston et al., 2017; Brinson et al., 1995; Smith, 2013; Williams et al., 2003), suggesting that our sites are broadly representative of the sea level-driven 108 109 conversion of upland forest to marsh throughout the Atlantic Coast. As discussed below, simple projections of topography and sea level rise suggest that these spatial gradients in vegetation type 110

forest to marsh occurs in less than 100 years on average at our sites (t_{mig} , SI Table 1).

113 2.2 Field Methods

Within each vegetation zone along each transect, we established a 100 m² plot within 114 which we surveyed vegetation and quantified C stocks. To estimate the total amount of C present 115 within a plot, we estimated C within three distinct C stocks (woody C, herbaceous C, and soil C). 116 Woody C includes the above- (stem wood, bark, and branches) and belowground biomass of the 117 trees and shrubs, and was estimated from allometric estimations of biomass. For trees, we used 118 species-specific allometric equations to predict above and belowground biomass from diameter 119 at breast height (1.37 m) measurements of all trees within the plot (McElligot et al., 2013; Clark 120 and Schroeder, 1985; Jenkins et al., 2003; Ter-Mikaelian and Korzuhkin, 1997; Chojnacky et al., 121 2014; Martin et al., 1998; Norris et al., 2001). Aboveground shrub biomass within the 100 m² 122 plot was approximated from allometric equations as a function of basal diameter and, 123 belowground shrub biomass was approximated using a 1.098 root-to-shoot ratio for marsh shrubs 124 (Conti et al., 2019; Mokany et al., 2006). Herbaceous C includes aboveground macrophyte 125 biomass was destructively harvested from six randomly distributed 0.25 m² plots nested within 126 each 100 m² plot during peak biomass (July-August 2019), separated into live and dead fractions, 127 and dried to a constant weight. 128

Soil C was quantified by collecting three soil samples within each plot using a hand turn,
4-inch soil mud auger in the forest zones and a Russian peat corer in the transition zone and high
marsh. The soil C stock includes all organic C beneath unincorporated detritus and forest litter.
To compare sediment samples from different vegetation zones with variable depths, soil samples
were portioned into two depth intervals: 0 to 10 cm (hereafter referred to as "shallow soils"),

134 which was consistent across vegetation zones, and 10 cm to parent material ("deep soils"), as defined by the point of resistance into inorganic clay or sand (SI Table 1). All soil samples were 135 analyzed for dry bulk density (DBD) and percent organic matter using loss-on-ignition methods. 136 To measure soil C accumulation rates, larger diameter (15cm) cores were taken at two high 137 marsh plots at each site for ²¹⁰Pb gamma emission dating. Elevation relative to a benchmark at 138 each site was measured at the center, highest, and lowest point of the plot using a laser level. The 139 average value of each plot was then referenced to NAVD88, using an RTK GPS at the 140 benchmark location, and mean higher high water (MHHW) using interpolated tide gauge data 141 142 summarized in Holmquist et al. (2006). Statistical differences of similar stocks across the vegetation zones were calculated using a one-way ANOVA with a 95% confidence interval 143 applied to average stock values from the four sites. 144

145 *2.3 Lab and Analytical Methods*

Biomass was converted to C using species-specific conversion ratios (McElligott et al., 146 2013; Norris et al., 2001) or using a general 50% conversion for mixed herbaceous macrophytes, 147 shrub, and deciduous tree biomass. Following the general approach of Craft et al. (1991), we 148 converted the organic content of soils to total organic C (TOC) by constructing an empirical 149 relationship for our sites and vegetation zones. Eight dried soil samples within each vegetation 150 zone were selected to represent the range of organic matter from the vegetation zones. We then 151 measured TOC by packaging approximately 3 mg of homogenized sediment in tin capsules, 152 treating it with aerosolized 6 mol HCl for 12 hours, drying the sample for an additional 12 hours, 153 and processing the sample in a CHN analyzer (Thermo Electron Corporation FlashEA 1112, NC 154 155 Soil Analyzer), which was calibrated using acetanilide standards (71.09% C, 10.36% N). The relationship between organic matter and C was consistent across vegetation zones, so one 156

157 collective relationship was used to estimate soil C content across all zones

158 $(TOC=0.0033(\%OM)^2+0.2967(\%OM)+8.4341, R^2=0.73)$ (SI Figure 1).

159 We measured soil salinity by preparing 1:5 soil to water suspensions from the top 10 cm 160 of soil collected from three points in each plot (Hardie and Doyle, 2012). The suspensions were homogenized according to Rhoades (1992), allowed to settle for 18 hours, and then filtered 161 162 through a 20 micron filter to obtain extracts (He et al., 2012), which were measured using a FieldScout EC 450 Meter conductivity probe. To determine soil C accumulation rates in the high 163 marsh sediment cores, we measured Pb²¹⁰ activities down core using gamma spectrometry. We 164 then applied the constant initial concentration (CIC) model, which approximates an average 165 sediment accumulation rate, on dated sediment cores from the high marsh, with Cs¹³⁷ as an 166 independent chronometer (Appleby and Oldfield, 1978; Sanchez-Cabeza and Ruiz-Fernandez, 167 2012) (SI Figure 2). C accumulation rates were obtained by measuring DBD and the 168 concentration of C in dated sediments and multiplying them by the accumulation rates derived 169 from the CIC model (Arias-Ortiz et al., 2018). 170

171 **3 Results and Discussion**

172 *3.1 Shifting C allocations in marsh-forest ecotones*

The total C stock averaged across sites decreased by approximately 50% from the high forest (17.44 +/- 2.9 kg C m⁻²) to the high marsh (9.73 +/- 1.59 kg C m⁻²). Total C was maximized in the mid forest (22.1 +/- 0.63 kg C m⁻²), though total C in the mid forest and high forest were not statistically different (Figure 2a, SI Figure 3-6, p=0.33). Total C stocks increased with increasing elevation (R²=0.21, p=0.05) and decreasing salinity (R²=0.57, p<<0.05) (Figure 2e, Figure 2f); both trends were consistent across all sites (Figure 2e). Based on a regionally

averaged rate of sea level rise (SLR, 4.46 mm y⁻¹) and the difference in elevation between high 179 forest and high marsh, we estimate that our chronosequence represents less than a century 180 $(t_m = \Delta E \text{ levation/SLR})$, though this simple approach ignores pulse events and any dynamic 181 feedbacks that could accelerate or mediate the transgression process (Figure 2e; SI Table 1). 182 The average C stock of living woody vegetation decreased from $13.2 + 4.0 \text{ kg C m}^{-2}$ in 183 the high forest to $0.18 \pm 0.02 \text{ kg C m}^{-2}$ in the high marsh. Specifically, tree carbon decreased 184 from 12.7 kg C m⁻² to 0.09 kg C m⁻² and shrubs decreased from 0.62 kg C m⁻² to 0.09 kg C m⁻². 185 Shrub density was maximized in the mid forest (6.22 kg C m^{-2} , p<<0.05) where it accounted for 186 38% of C stored in woody biomass, but across every forest zone, C stored in trees was found to 187 be greater than C stored in shrubs (Figure 2b, p<<0.05). Forest zones were consistently 188 dominated by above ground, woody C in living biomass rather than herbaceous or soil C 189 (p=0.06). Herbaceous C increased from the high forest $(0.03 + 0.01 \text{ kg C m}^2)$ to the high 190 marsh $(0.34 \pm 0.03 \text{ kg C m}^2)$ (Figure 2c). Herbaceous C was maximized in the transition zone 191 at each site (p=0.08) where *Phragmites australis* presence increased the herbaceous C stock by 192 an average of 57% (Figure 2c, p<<.05), compared to Moneystump Swamp where *P. australis* has 193 historically been removed (Figure 2c, SI Figure 4). The transition zone and high marsh had far 194 195 smaller biomass C stocks, but had substantial contributions from soil C stocks. Deep soil C increased by an order of magnitude along the forest (0.11 kg C m⁻²) to marsh (6.4 kg C m⁻²) 196 gradient while shallow soil C decreased slightly. Overall, soil C approximately doubled across 197 the forest to marsh gradient and deep soil C contributed 70.3% of the total C stock in the high 198 marsh (Figure 2d, Figure 2a, SI Figure 5). Using the CIC model, the average vertical accretion 199 rate across the high marsh zones of four sites was 2.35 ± 0.84 mm y⁻¹ and ranged from 1.44 to 200 3.11 mm y⁻¹ (SI Figure 2, SI Table 1). Carbon accumulation rates calculated from dry bulk 201

density, total organic carbon, and the CIC derived sedimentation rates varied between 0.036 and 0.065 kg C m⁻²y⁻¹ (SI Table 1). Nevertheless, forest zones were consistently dominated by above ground biomass C rather than herbaceous or soil C.

205 *3.2 Upland transgression decreases C stocks*

For the last two decades, the paradigm in blue carbon research has maintained that 206 vegetated intertidal systems disproportionately affect the global C cycle because rates of soil C 207 burial far exceed those of terrestrial systems (Mcleod et al., 2011; Chmura et al., 2003; Duarte et 208 al., 2005). By inference, sea level-driven conversion of terrestrial forests to tidal marshes would 209 be expected to increase rates of C burial and consequently increase soil C stocks over time 210 (Wang et al., 2019; Elsey-Quirk et al., 2011; Morris et al., 2012). Our finding that the magnitude 211 of C stored in marsh soils is greater than coastal forest soils is consistent with this paradigm 212 (Figure 2d). However, we also show that C stored within the living biomass of terrestrial, coastal 213 forests far exceeds the total amount of C stored in adjacent marshes (Figure 2a). This observation 214 suggests that sea level-driven land conversion could lead to substantial losses of C that are not 215 considered in current conceptual models of coastal C cycling. 216

217 The total C stock in forested zones was dominated by C stored in living trees, and tree mortality drove the decrease in total C across the forest-marsh ecotone (Figure 2a). We observed 218 a strong, significant relationship between increasing soil salinity and decreasing total C (Figure 219 2f), which is consistent with previous work that identifies salinity as a primary driver of tree 220 mortality and forest retreat (Brinson et al., 1995; Williams et al., 2003). Our measures do not 221 account for dead yet present vegetation, such as logs or standing dead trees, suggesting that we 222 223 potentially overestimate the gradient in C stocks across the forest zones, and underestimate the gradient between stressed forest and high marsh. However, previous work suggests that living 224

225 trees dominated the aboveground C stock while dead woody vegetation comprised < 9% of aboveground C (Krauss et al., 2018). Additionally, far greater C stocks in live tree biomass than 226 in marsh soils (Figure 2a, Smart et al., 2020) suggests that most carbon stored in live trees does 227 not persist in marsh soils and is instead lost through decomposition, as indicated by rapid 228 decomposition rates (Kozlowski, 1997) and elevated tree methane fluxes near the marsh-forest 229 boundary (Norwood et al., 2020; Martinez and Ardon, 2021). This indicates that forest carbon 230 preservation is relatively small, but the exact quantification of preserved forest carbon is still 231 unknown. The expansion of shrubs and *P. australis* and increasing soil organic matter thickness 232 233 may increase C accumulation in migrating forest-marsh ecotones (Smith, 2013; Elsey-Quirk et al., 2011; Craft, 2000; McTigue et al., 2019) (Figure 2a). However, we find that these processes 234 only partially offset tree mortality and that the net total C stock decreases by approximately 50% 235 with the conversion of forest to marsh (Figure 2a). 236

Previous work in other transgressing coastal ecosystems suggests that sea level rise and 237 238 saltwater intrusion may decrease total C stocks more generally. Ecosystem transgression in many regions of the U.S. is characterized by encroachment into wetland forests rather than the upland 239 forests considered here (Doyle et al., 2010.; Brinson et al., 1995). Wetland forests, despite 240 241 having organic rich soils, experience decreased aboveground biomass associated with tree mortality where marshes replace forested wetlands (Krauss et al., 2018; Brinson et al., 1995; 242 Krauss et al., 2007). In other systems, salinization and salt water intrusion into tidal freshwater 243 244 systems has been shown to reduce C fixation (Herbert et al., 2018), increase soil respiration (Chambers et al., 2011), and lead to peat collapse (Chambers et al., 2014), resulting in decreased 245 soil C stocks. Additionally, salt water intrusion reduces belowground biomass while also 246 enhancing greenhouse gas efflux after prolonged exposure (Wilson et al., 2018; Ardon et al., 247

2018). These observations from mostly freshwater systems offer mechanistic insight into the
processes that lead to decreases in specific carbon stocks and suggest that the patterns of loss we
observe may apply more generally to other types of transgressing coastal systems (Smith and
Goetz, 2021).

252 3.3 Timescales of C replacement

Although we find that marsh migration consistently leads to a net loss of total carbon (Fig 253 2a, SI Figure 6), our finding that soil C stocks increase across the marsh-forest ecotone (Figure 254 2d) suggest that C stored in marshes may increase through time and perhaps eventually offset C 255 lost from forest mortality. C stored in marsh soils increases through time as belowground organic 256 matter accumulates in newly flooded, anaerobic soils (Craft et al., 1999; Stagg et al., 2016). 257 Sediment cores taken from our study sites in much older sections of the marsh display deeper, 258 organic rich soils reflecting larger carbon stocks typical of mature salt marshes (Schieder and 259 Kirwan, 2019; Thomas, 2004; Dontis et al., 2020). Carbon accumulation rates are also expected 260 to increase with increasing tidal inundation associated with accelerated sea level rise (Kirwan 261 and Mudd, 2012; McTigue et al., 2019; Rogers et al., 2019; Gonneea et al., 2019). Thus, the size 262 of the C stock in marshes and its ability to offset C loss due to forest mortality depends on marsh 263 264 age.

Given the high carbon accumulation rate in marsh soils and the high soil C content of older marshes (Krauss et al., 2018; Elsey-Quirk et al., 2011; Holmquist et al., 2018), salt marshes may eventually offset C that is lost during marsh migration. We estimate the "time to replacement" of forest C at each site as:

$$t_r = \frac{\Delta C_f}{CAR_m} \tag{1}$$

270	where ΔC_f is the total amount of C lost from the forest during transgression (kg m ⁻²), CAR _m is the
271	C accumulation rate in the adjacent high marsh (kg m ⁻² y ⁻¹), and t_r is the time (y) needed to
272	replace the forest C lost with marsh soil C. The inheritance of carbon from terrestrial systems
273	into the migrating marsh soils is unknown and beyond the scope of this paper. To account for the
274	unknown amount of inherited C, we calculate C_f in two ways. First, we assume that all C in the
275	forest is lost during the transgression process so that $\Delta C_f = C_f$, where C_f is the total forest C stock
276	observed in the mid or high forest. This calculation represents the maximum time to replacement
277	$(t_{r,\max})$ as it assumes no preservation of forest C in soils. Alternatively, we assume that a
278	substantial fraction of C measured in the high marsh soils is C that has been preserved from
279	forests, so that $\Delta C_f = C_f - C_m$ where C_m is the measured marsh C stock, representing the minimum
280	total C stock during marsh migration. This calculation represents a minimum time to replacement
281	$(t_{r,\min})$ as it includes refractory C in forest soils that has been preserved in soils during
282	transgression, and assumes that any forest C in the high marsh soil will continue to be preserved
283	in the future. Based on measured values of C_f , C_m , and CAR_m at each of our sites, eqn. 1 predicts
284	that it will take approximately 130 to 760 years for marsh soil C to replace forest C lost during
285	transgression (SI Table 1). This approach intentionally compares rates of C accumulation in one
286	system with C stocks in another system, allowing us to calculate replacement timescales
287	associated with migrating ecosystem boundaries in a manner that is easily applicable across
288	ecosystems and spatial scales.

Our proposed replacement time metric leads to a conceptual model of changing carbon stocks that may be relevant to a variety of migrating ecosystems (Figure 3). In our system, the initial total C stock in the upland forests (C_f) decreases with the onset of salt water intrusion (**a**). Progressive forest mortality leads to C loss until the total C stock is minimized (C_m) when forests 293 are first replaced by marshes (b), but developing marsh soils increase the total C stock through time and the system begins to partially offset lost C. As the marsh ages, soil C stocks increase 294 with sea level rise as developing marsh soils accumulate carbon until submergence (c), 295 potentially compensating for or even exceeding the lost forest carbon (d). However, in the 296 studied Chesapeake Bay region, marshes submerge or erode on timescales (c_1 , c_2 ; Hussein, 2009; 297 Kirwan et al., 2016b; Schieder et al., 2018) that overlap with estimated times of carbon 298 replacement (d, 130-760 years) (SI Table 1), suggesting that complete replacement of forest 299 carbon is tenuous. Moreover, salt intrusion can lead to forest die-off without marsh migration 300 301 (Taylor et al., 2020), leading to a large loss of aboveground C with little to no replacement in accumulating soil C stocks. 302

While the conceptual model is potentially generalizable across systems, the magnitude 303 and rate of change would be expected to vary. For example, rapidly decreasing aboveground 304 biomass and increasing belowground carbon stock is likely a common response to inundation 305 306 and salinization, though rates would be determined by particular species tolerance and biogeochemical settings (Flester and Blum, 2020; Field et al., 2016). In contrast to our reported 307 long timescales of replacement, we expect t_r to be relatively short in sequences beginning as 308 309 freshwater wetlands or agricultural fields due to low values of ΔC_f from initial high soil C stocks or limited aboveground biomass, respectively (Krauss et al., 2018; Van de broek et al., 2016). 310 Additionally, this framework can be applied to other transgressing systems, such as mangrove 311 forest encroachment into hypersaline salt flats, to show that some transgressing ecosystems lead 312 to rapidly increased carbon storage without having to replace lost C (Yando et al., 2016). The 313 314 general framework we present is intentionally simplistic, thereby allowing for its application to

larger scale landscape models parameterized with spatially variable terms or to othertransgressing ecosystems with site specific information.

317 3.4 Broader Implications

The traditional focus on wetland soils leads to an important and unique negative carbon-318 climate feedback proposed for the coastal zone, where accelerated sea level rise drives faster soil 319 320 C accumulation (Wang et al., 2019; Kirwan and Mudd, 2012; Rogers et al., 2019). In contrast, our finding that C stored in the biomass of woody vegetation is far greater than the C stored in 321 young, adjacent marshes (Figure 2) implies that sea level rise will lead to a net loss of C that 322 cannot be predicted on the basis of wetland soil C stocks alone. Furthermore, our simple 323 estimates of time to replacement suggest that the loss of C from forests following marsh 324 migration will work against the proposed negative carbon-climate feedback in marsh soils at the 325 scale of centuries (SI Table 1). Together, these findings help broaden the scope of traditional 326 blue carbon research by connecting adjacent ecosystems, identifying a C source not considered 327 in our current conceptual understanding of coastal carbon-climate feedbacks, and demonstrating 328 that sea level rise will lead to fundamental changes in C allocation between soils and biomass at 329 the coastal interface. 330



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Figure 1. A general map of the Chesapeake Bay in Virginia and Maryland (U.S.) showing the

region's location along the mid-Atlantic seaboard, site locations, and four inset maps showing

individual sampling locations across the marsh forest boundary at each site (**a**: Moneystump

336 Swamp, **b**: Monie Bay, **c**: Goodwin Island, **d**: Phillips Creek). The vegetation zones are

differentiated by symbol color. High marsh is blue, transition zone is purple, low forest is

338 yellow, mid forest is orange, and high forest is red. The dashed line delineates the general marsh-

339 forest boundary.



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Figure 2. The C stock of distinct pools across the high forest to high marsh gradient, where the C 341 stock refers to the average stock of four sites in the Chesapeake Bay. (a) Cumulative average C 342 stocks by pool, (b) woody C partitioned into C stored in trees and shrubs, (c) herbaceous C 343 separated into sites with and without *P. australis*, (d) soil C in upper 10 cm ("shallow") and from 344 10 cm to parent material depth ("deep"). Relationships between total C stock and elevation (e) 345 and soil salinity (f) for each site and vegetation zone. The black dashed lines indicate the linear 346 347 regression between total carbon stock and elevation (e, y=12.63x+8.323) and salinity (f, y=-0.563x+16.706). Roman numerals represent statistically significant differences between 348 vegetation zones while asterisks (*) represent statistically significant differences between sites 349

350 with and without *P. australis*.



Figure 3. Conceptual diagram of the changing total C stock associated with the transition from 352 forest to marsh. The total carbon stock in the forest (C_f) decreases through time following salt 353 water intrusion (a) in response to forest mortality. Carbon stocks reach a minimum (C_m) when 354 forests are first replaced by marshes (b), but then increase through time as developing marsh 355 soils accumulate carbon. Carbon stocks increase with sea level rise until marshes submerge (c), 356 potentially compensating for the loss of forest carbon (d). Variable times to submergence (c_1, c_2) 357

358 relative to the time to replacement (d) suggest that complete replacement of forest carbon is 359 tenuous.

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554 Author Contributions

- 555 A.J.S. designed the sampling procedure, performed the methods, and drafted the manuscript.
- 556 M.L.K conceived the study. Both authors interpreted results and edited the manuscript.

557 **Competing Interests**

558 The authors declare no competing interests.

559 Data Availability

- 560 Elevation data was corrected using data available in this in-text data citation reference:
- Holmquist et al. (2006). Carbon datasets generated from this project are publicly available in the
- 562 Virginia Coastal Reserve Long Term Ecological Research Data Catalog.
- 563 Smith, A., M. Kirwan, and T. Messerschmidt. 2021. Carbon stocks in forests transitioning to salt
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566 Materials and Correspondence

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