Litter decomposition in retreating coastal forests

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Abstract: Rising sea levels lead to the migration of salt marshes into coastal forests thereby shifting both ecosystem composition and function. In this study we investigate leaf litter decomposition, a critical component of forest carbon cycling, across the marsh-forest boundary with a focus on the potential influence of environmental gradients (i.e., temperature, light, moisture, salinity, and oxygen) on decomposition rates. To examine litter decomposition across these potentially competing co-occurring environmental gradients, we deployed litterbags within distinct forest health communities along the marsh-forest continuum and monitored decomposition rates over six months. Our results revealed that while the burial depth of litter enhanced decomposition within any individual forest zone by approximately 60% (decay rate= 0.272 ± 0.029 yr^{-1} (surface), 0.450 ± 0.039 yr^{-1} (buried)) we observed limited changes in decomposition rates across the marsh-forest boundary with only slightly enhanced decomposition in mid forest soils that are being newly impacted by saltwater intrusion and shrub encroachment. The absence of linear changes in decomposition rates indicates non-linear interactions between the observed environmental gradients that maintains a consistent net rate of decomposition across the marsh-forest boundary. However, despite similar decomposition rates across the boundary, the accumulated soil litter layer disappears because leaf litter influx decreases from the absence of mature trees. Our finding that environmental gradients counteract expected decomposition trends could inform carbon-climate model projections and may be indicative of decomposition dynamics present in other transitioning ecosystem boundaries.

Key Words: Decomposition, leaf litter, marsh-forest boundary, saltwater intrusion

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Introduction

Accelerating sea-level rise rates (Kemp et al. 2011) promote ecosystem transitions within low-lying coastal landscapes and fundamentally reorganize ecosystem structure (Hein and Kirwan 2023; Langston et al. *in review*). Coastal salt marshes are vital environments that provide ecosystem services such as critical habitat, storm surge protection, and long-term carbon storage (Chmura et al. 2003; Gedan et al. 2009; Möller et al. 2014). Unfortunately, coastal marshes are at the forefront of climate-driven ecosystem loss where projected rates of sea-level rise are expected to overcome internal biophysical feedbacks that maintain ecosystem resilience (Kirwan et al. 2016; Törnqvist et al. 2021; Saintilan et al. 2022). However, across widespread areas, increasing inundation and saltwater intrusion driven by sea-level rise facilitate simultaneous migration of wetlands and retreat of upland forests (Fagherazzi et al. 2019; Kirwan and Gedan 2019). While marsh migration helps to maintain coastal wetland extent, coastal forests that provide unique ecosystem services are lost (Brinson 1991; Smith and Kirwan 2021; Chen and Kirwan 2022). This ecosystem conversion has been shown across the Atlantic Coast of the United States (Chen and Kirwan 2022; Warnell et al. 2022; White et al. 2022), but despite its widespread occurrence, ecological and carbon dynamics during this transition remain understudied.

Although marsh migration results in the eventual ecosystem transition from coastal forest to coastal wetland, subtle changes in ecology and soil biogeochemistry precede widespread forest mortality (Tully et al. 2019). For example, in the early stages of groundwater salinization living trees reduce sap flow and annual growth (Krauss and Duberstein 2010). Likewise, saltwater intrusion increases alkalinity and ionic strength in soils, which leaches critical nutrients and saturates soils (Weston et al. 2006; Tully et al. 2019). As salinization and inundation increase, tree recruitment ceases and immature trees display early signs of mortality such as low needle production (Conner et al. 2007; Kirwan et al. 2007). This creates a forest dominated by mature trees unable to reproduce (Kearney et al. 2019), but as salinity and flooding frequency increase, even these mature salt-tolerant tree species begin to die. The remaining standing dead mature trees form the overstory of the ghost forest transition zone that characterizes the marsh-forest ecotone (Kirwan and Gedan 2019). While past research has emphasized the effect of marsh migration on mature tree communities, ecosystem functions, such as decomposition, remain relatively understudied.

Sea-level driven saltwater intrusion into coastal forests creates an inundation and salinity gradient across the marsh-forest ecotone (Fig. 1). Increased inundation has been shown to have a range of positive to negative effects on litter decomposition in intertidal marsh field and mesocosm experiments (White and Trapani 1982; Hackney 1987; Conner and Day 1991; Halupa and Howes 1995; Kirwan et al. 2013; Janousek et al. 2017). While moisture can facilitate decomposition in dry environments, inundation magnitude, duration, or frequency can modify decomposition responses, such as reducing decomposition when transitioning from aerobic to anaerobic conditions (Happell and Chanton 1993; Langhans and Tockner 2006; Janousek et al. 2017). Parallel with this flooding gradient is the introduction of salts into coastal forests, which can increase labile organic matter decomposition and stimulate soil respiration in short-term exposures (Weston et al. 2006; Chambers et al. 2011; Stagg et al. 2017). However, indirect effects of sea level rise, such as salinity driven shifts in vegetation community, can mitigate increased decomposition at longer time scales, and other studies indicate reduced decomposition under higher salinities (Stagg et al. 2017; Qu et al. 2019). Additionally, shifts in the vegetation community and opening of the forest canopy further alter the abiotic environment by increasing light availability (photodegradation), soil temperatures (microbial respiration and organic matter destabilization), and nutrient enrichment (priming), all of which can potentially increase decomposition rates (Mendelssohn et al. 1999; Austin and Vivanco 2006; Mueller et al. 2018; Jobe IV and Gedan 2021; Kottler and Gedan 2022; Nordio and Fagherazzi 2022; Sward et al. 2023). These co-occurring environmental gradients have variable effects on decomposition independently and interactions between these drivers are often difficult to parse (Stagg et al. 2017; Mueller et al. 2018; Joly et al. 2023), but competition between these drivers may reveal unique decomposition dynamics within this rapidly transitioning boundary. Previous studies have identified these drivers across single ecosystems, but this study presents the first information on litter decomposition across this ecotone.

While conventional blue carbon research may have indicated that a transition from forest to wetland soils would likely increase carbon storage due to inundated, anaerobic conditions, whole-ecosystem carbon stock assessments document an initial, large magnitude loss of carbon during marsh migration (Smart et al. 2020; Smith and Kirwan 2021). This reduction is expected to have decadal scale impacts on regional carbon storage (Smith and Kirwan 2021). However, organic matter preservation and decomposition during marsh migration is largely undefined and could reduce the scale of carbon loss (Valentine et al. 2023; Van Allen et al. 2021). To examine changes to decomposition during marsh migration, we quantified the decay rate of surficial and buried leaf litter at distinct forest health zones along the marsh-forest ecotone.

Methods

Study area and approach

To test how forest leaf litter decomposition differs across the marsh-forest ecotone, we deployed litter bags at the marsh-forest boundary situated near Phillips Creek, a tidal creek within the back-barrier landscape of the Eastern Shore of Virginia, USA (Fig. 2). The study area is located within The Nature Conservancy's Brownsville Preserve, part of the Virginia Coast Reserve and a Long-Term Ecological Research site (Brinson et al. 1995; Kirwan and Blum 2011; Smith et al. 2024). This ecotone is situated within the Mid-Atlantic sea level rise hotspot (Sallenger et al. 2012), which serves as a model region to study the effects of sea-level driven land conversion because rates of relative sea-level rise (between 3 and 6 mm yr^{-1}) in recent decades are twice as fast as eustatic rates (~2 mm yr^{-1}) and the gently sloping, rural coast facilitates marsh migration (Chen and Kirwan 2022). Approximately 400 km^2 of salt marsh have migrated into retreating coastal forests within this region since the mid-nineteenth century (Schieder et al. 2018), and rates of forest retreat are accelerating in parallel with relative sea-level rise (Schieder and Kirwan 2019).

Phillips Creek presents small differences in elevation between the highest and lowest point across the environmental gradient (<0.2 m) which extends the ecotone width and provides an ideal site at which to study sea-level driven changes (Smith and Kirwan 2021). Despite relatively similar elevations, the overstory and understory vegetation communities vary significantly along the ecotone (Supplementary Fig. 1). Specifically, Phillips Creek exemplifies expected forest zonation at the marsh forest boundary including a high forest (HF), mid forest (MF), low forest (LF), and transition zone (TZ), which are characterized and described in Smith and Kirwan (2021; Supplementary Fig. 1). The HF is unaffected by salt intrusion with a mixed-age structure. The mid forest (MF) displays early signs of salt stress through needle browning, increased hardwood tree mortality, and maximized shrub (*Morella cerifera*) encroachment. In the low forest (LF) there are few hardwood trees alive, early signs of salt stress in softwood trees, no forest regeneration in the understory, and shrub encroachment is diminished by increasing soil salinities. Finally, the transition zone (TZ) displays at least 50% of the standing trees are dead and the understory is dominated by *Phragmites australis* and high marsh herbaceous species (Sward et al. 2023).

Litterbag Decomposition Experiment

To measure decomposition of forest litter, we used the litter bag technique, where mesh bags of leaf litter are placed on the forest floor or buried and the amount of mass lost over time is determined (Krishna and Mohan 2017). Bags (20 cm x 20 cm) were constructed using 1 mm polyester mesh (Bioquip Inc.) and nylon thread. An 1 mm mesh size allowed for some macrofauna access to bag contents, but minimized material loss through the mesh (Krishna and Mohan 2017). Fresh litter was collected from the high forest zone at Phillips Creek, VA, dried at 60 °C and sorted into pine needles and mixed-species deciduous leaf litter. Litter bags were filled with 10 g of litter consisting of 6 g of dried pine needles and 4 g of dried deciduous leaves, which is representative of the dry weight fraction present in the leaf litter at the field site. Although litter type affects decomposition rates (Gartner and Cardon 2004), we included both coniferous and deciduous material in the bags to represent the mixed litter present at the site. All bags were labeled, dried, and weighed prior to deployment.

Bags were deployed in March 2022 along a pre-existing gradient within the marsh-forest ecotone (Smith and Kirwan 2021; Fig. 1; Fig. 2). Four sites were selected in each of the dominant vegetation types: high forest, mid forest, low forest, and transition zone. Within the forest zones at Phillips Creek, approximately 600 tree individuals were identified to characterize community composition within the forest zones. At each site, we buried half of the bags at the soil-litter interface (~5 cm) and laid the other half on the surface of the forest floor, on top of the existing litter layer. For each of the vegetation zones and depths (8 combinations), 18 bags were deployed to allow for monthly collection in triplicate over six months.

Litter bags were collected once a month from each location for six months from April to September. Because the system is not in steady state and is rapidly changing in response to sea-level rise, we selected a short time frame compared to other decomposition experiments (Krishna and Mohan 2017). However, our deployment (March - September 2022) covered the summer, when decomposition rates are the highest in a given year and better represent yearly litter decomposition (Morffi-Mestre et al. 2023).

During collection, litter on the outside of bags and any vegetation that had grown into the bags was removed. Following collection, bags were dried at 60 °C for at least 48 hours, or until completely dry, and weighed. Control bags containing no leaf litter were collected at the final sampling. Weight change for these control bags was not significantly different than zero and therefore no correction was made for background change in bag weight.

Decomposition data were fit to exponential decay functions (Wider and Lang 1982) in the form:

$$X = e^{-kt} \tag{1}$$

where X is the proportion of initial mass remaining (i.e. $X = X_t/X_o$), -k is the decay coefficient (yr^{-1}), or relative decomposition rate, and t is time. A single exponential decay model is the most common and most intuitive for litter decomposition studies (Wider and Lang 1982 and citations within), and well represents our data. T-tests were used to compare decomposition rates across vegetation communities and depths.

Environmental Gradients

We measured salinity in the forest zones by preparing soil slurries of 1:5 soil to water suspensions from the top 10 cm of soil collected at 12 points within each forest zone. Soil samples were collected once in June 2022 less than 10 m from litterbag deployment sites, and in areas where the overstory community composition and environmental setting were similar. Slurry extracts were measured using a FieldScout EC 450 Meter conductivity probe and converted to soil salinity following equations in Hardie and Doyle (2012; see Smith and Kirwan (2021) for expanded detail). Elevation relative to a benchmark was measured at the center of each deployment site using a laser level. This relative elevation was then referenced to NAVD88 using an RTK GPS deployed at the benchmark location. PAR (photosynthetically available radiation) at the litter surface was measured using a MQ-500 Full Spectrum Quantum Meter (Apogee Instruments) between 2:30 and 3:30 pm at each deployment site in August 2022. Measurements were taken in triplicate and then averaged. While both soil salinity and PAR are expected to be highly variable temporally over the experimental period, our measurements are meant to characterize general trends across the marsh forest boundary. Soil temperature sensors (TER0S12 sensor, METER Group) were deployed 7 and 30 cm below the ground surface along the gradient and collected hourly readings over the study period.

Litterfall was collected approximately monthly from March to December in 2022 from baskets (0.25 x 0.25 m opening) deployed within high, mid, and low forest (n=24 baskets per forest zone) at Phillips Creek. To ensure drainage without the loss of captured litter, baskets were lined with mesh, holes were drilled in the bottom, and baskets were elevated off the ground approximately 25 cm by PVC frames. Litter was dried in drying ovens for a minimum of 48 hours at 60 °C. Litter was sorted by plant species and structure (i.e. fruit, cones, flowers, branches, and leaves or needles). In this paper we report only leaf and needle material to match the contents of the litter bags. After the dry mass of the leaf litter was calculated, this value was divided by the period between collections, which ranged from 14-50 days, to calculate an average daily litter fall rate.

Leaf litter thickness was measured at 16 points within the high, mid, and low forest in May of 2023. Leaf litter thickness was estimated by removing leaf litter from a discrete section of the forest floor and measuring the difference in height between the forest floor and the adjacent, undisturbed litter layer to the nearest 0.5 cm.

Results

Litter Decomposition Rates

The mass of the deployed litter bags decreased over time for all samples and was well-described by a single exponential decay (SI Table 1, Supplementary Fig. 2). Decay coefficients were significantly different ($t(6)=-7.3168$, $p<0.0001$) between the buried and surface bags, where decay coefficients were 1.5 times higher for buried bags compared to surface bags with an average surface leaf litter decomposition of 0.272 ± 0.029 yr^{-1} and an average buried decomposition rate of 0.450 ± 0.039 yr^{-1} (Fig. 3; Supplementary Table 1, Supplementary Fig. 2). However, there was no significant difference in litter decay coefficients (i.e., decomposition rates) across the vegetation zones of the marsh-forest ecotone when comparing similar depth treatments (Fig. 3; Supplementary Table 1). Decomposition rates were higher in the mid forest, both in the surface and buried samples (Supplementary Table 1), but this was not statistically significant due to the limited number of data points. Although we could not demonstrate statistical significance, the mean decomposition rates in the mid forest were 1.5 standard deviations greater than the average decomposition rate for both the surface and buried litter bags and this pattern occurred both in the surface and buried bags.

Decomposition rates increased the most in all zones and treatments between May and June, coincident with an increase in average temperature (Fig. 4). Noticeably, there is no change in decomposition rate during the peak of highest litterfall (Fig. 4). Between the surficial and buried litter bags, decomposition rates were almost always greater in the buried treatment than the surficial treatment across all months and forest zones.

Environmental Parameters

Soil temperatures increased throughout the spring and then plateaued in the summer at all sites (Fig. 4, Supplementary Fig.3). The temperature ranged from 7 to 25 °C, with an overall average temperature of 16.5 °C. Soil temperatures were similar at all sites except in the mid forest where temperatures were the lowest throughout the entire deployment and particularly during the summer high temperatures (Fig.4, Fig. 5).

Soil salinity increased across the marsh-forest boundary with lowest salinity in the high forest (0.4 ± 0.4 ppt) and the highest salinity in the transition zone (7.5 ± 2.6 ppt). Salinity in the mid forest (1.2 ± 0.6 ppt) and low forest (1.8 ± 1.1 ppt) were slightly higher on average than in the high forest, but salinity was not significantly different between these three zones (one-way ANOVA, $p=0.32$; Fig. 5). The lowest amount of light available at the litter layer was within the high forest (4.67 µmol m^{-2} s^{-1}) and increased across the marsh forest boundary to near ambient conditions in the transition zone (78.33 µmol m^{-2} s^{-1}) (Fig. 5).

Litter Inputs

The rate of litterfall was measured monthly from March to December across the high, mid, and low forest by dividing the accumulated litter by the duration of deployment (Fig. 3, Fig. 5). During the litter bag deployment from April to September, the average rate of litterfall was similar across low, mid, and high forest zones (2.70, 2.57, and 2.65 g/d, respectively). However, during the year, the timing of peak litterfall varied by zone. In the low forest, litterfall peaked in July (5.61 g/day). In the mid and high forest, litterfall was highest in November (8.58 g/day and 16.13 g/day for the mid and high, respectively). On average between March and December, litterfall was highest in the high forest (4.37 g/day), intermediate in the mid forest (3.36 g/day) and lowest in the low forest (2.20 g/day). Forest litterfall rate is expected to be negligible in the transition zone due to the low abundance of living trees within this zone (Smith and Kirwan 2021; Langston et al. *in review*) and the absence of forest litter in surficial detritus.

Leaf litter layer thickness varied by habitat. Forest leaf litter was negligible within the transition zone. The detrital layer in this zone was dominated by *Phragmites australis* and there was no visible forest leaf litter on the sediment surface. Within the other zones, leaf litter thickness was not significantly different between the high forest and mid forest (2.0 and 1.9 cm respectively) but was significantly lower in the low forest (0.3 cm) where nearly half of litter thickness measurements were less than 0.5 cm (Fig. 5).

Discussion

Decomposition and Drivers in the Context of the Marsh-Forest Ecotone

Leaf litter decomposition at Phillips Creek followed the same single exponential decay form as in previous forest decomposition experiments. This representation can describe two processes that are occurring at the same time in the forest litter consistent with previous studies.

First, initial rapid decomposition occurs after deployment, representing the leaching and mineralization of labile components of the litter (Weston et al. 2006; Tully et al. 2019). The remaining, more recalcitrant, matter continues to decay, but slower, resulting in decreased decomposition rates later in the deployment. Additionally, temperature increases in the summer (Fig. 4), which typically increases decomposition rates independent of the material composition (Kirwan and Blum 2011). The highest increase in decomposition rates was measured in the summer and coincided with the rapid decrease in mass represented by the single exponential decay function. The litter decay coefficients presented here are consistent with other forest decay studies, which report a median decomposition rate of 0.3 yr^{-1} across 70 studies (Zhang et al. 2008 and citations therein).

In typical forests, decomposition of leaf litter is the process in which organic matter is broken down into CO_2 and nutrients through heterotrophic respiration by soil organisms (bacteria, fungi and macrofauna) (Aerts 1997). On the forest floor, leaf litter decomposition is dominated by aerobic respiration and modified by temperature and moisture, which increase decomposition through increased bacterial and fungal respiration (Meentemeyer 1978). We find that temporally at the marsh-forest boundary, increases in decomposition coincide with a seasonal increase in temperature (Fig. 4). However, contrary to the expectation of a uniform change in decomposition rate across the ecotone, decomposition rates were the highest in the mid forest where temperatures were the lowest (Fig. 5). We observed no significant change in decomposition rates across the marsh-forest ecotone. Our findings suggest that the unique environmental gradients present at the marsh forest boundary potentially disrupt expected forest litter decomposition patterns.

Along the marsh-forest ecotone, competing interactions between environmental drivers may interact and alter expected decomposition patterns. First, the soil can become waterlogged from flooding, leading to a decrease in oxygen availability and suppression of heterotrophic activity. Decomposition in non-coastal forest soils are often dominated by aerobic fungal respiration (Kjøller and Struwe 1992). Therefore, these species may be maladapted for the transition from aerobic to anaerobic environment during marsh migration. Secondly, salt can enter the soils, increasing microbial and fungal stress and decreasing decomposition rates (Elsey-Quirk et al. 2011; Stagg et al. 2017). Litter decomposition is stifled under very high salinities, but otherwise salinity does not have strong direct effects on the rate of litter decomposition (Qu et al. 2019; Stagg et al. 2017; Volik et al. 2021). Furthermore, previous work has indicated that in stressed ecosystems, decomposition rates can decrease (Pascoal and Cássio 2004). Conversely, leaching processes may increase at the introduction of saltwater to leaf litter and organic matter can also destabilize during initial salinization thereby increasing decomposition rates (Weston et al., 2006; Chambers et al. 2011; Tully et al. 2019).

Additionally, salt-stress induced tree mortality and a thinning canopy result in increasing light availability on the forest floor across the marsh-forest boundary (Kottler and Gedan 2022). While higher light availability has been shown to both increase and decrease decomposition rates (King et al. 2012), increasing light availability across the marsh-forest boundary did not affect decomposition rates in a linear way (Fig. 5). However, there is a marked increase in PAR between the high and mid forest (from 4.67 to 32.67 μmol m^{-2} s^{-1}), which may drive some of the changes observed in the mid forest. Ultimately, the combination of standard environmental drivers for decomposition in the forest (e.g., temperature) and the unique environmental drivers introduced at the marsh-forest ecotone (e.g., flooding, saltwater intrusion), negate or balance one another and result in no net trends in litter decomposition along the marsh-forest ecotone.

Nonlinear Change Across the Ecotone

Interestingly, there is no statistical difference in decomposition between high forest, low forest, and the transition zone within a given treatment (surface or buried), despite different flooding and light regimes. We hypothesize that while a range of environmental conditions drive decomposition across the ecotone, the competing environmental drivers offset, resulting in a minimal net change in decomposition. For example, fungus growth decreases with increasing salinity (Yunasfi et al. 2021), and is therefore expected to be minimized in the transition zone where salinities are highest. Meanwhile, photodegradation from light is shown to increase decomposition, and light availability is greatest in the transition zone. Therefore, one might expect decomposition to decrease when considering only the fungal community while another might expect decomposition to increase when only considering light availability. This exemplifies that the combination of these competing factors may offset, leading to leaf litter that decomposes at approximately equal rates across the forest-marsh transition.

Importantly, however, there is a change in decomposition rate at the mid forest compared to the other zones, where decomposition rates are higher (+ 1.5 standard deviations) relative to the other zones (Fig. 5). Although this result is not statistically significant, partially due to low sample size, the change in decomposition rate occurs in the mid-forest at both the surface and buried bags, hinting at a potentially important process occurring in this area. The resulting nonlinear response with a peak in decomposition mid-way through the gradient points to an emergent property of the marsh-forest transition. The mid-forest is at the front of saltwater intrusion and therefore may be expressing elevated changes (Tully et al. 2019). We posit there is a nonlinear combination of environmental parameters (temperature, salinity, light availability) that arise at the first vestiges of saltwater intrusion, which is within the mid forest. The overlap of environmental parameters representative of a marsh and a forest that occur in the mid forest create an ecotone where invertebrates and other macrofauna from both the salt marsh and the forest can thrive. Invertebrates acclimatize litter by physical breakup and enhancing microbial activity (Anderson 1995; Krishna and Mohan 2017). In the mid forest, invertebrate communities in leaf litter at Phillips Creek exhibit the highest rarified Shannon diversity and species richness, indicative of an overlap of salt marsh and forest species (Goetz 2023), which could facilitate increased decomposition through physical breakup of leaf litter. Additionally, the rapid expansion of shrubs into the forest understory seen in the mid forest could be facilitating the creation of a nutrient-enriched microclimate that potentially enhances decomposition (Thompson et al. 2017; Sward et al. 2023). More data are needed to corroborate the apparent increased decomposition rate in the mid forest.

Role of Litter Burial Depth in Decomposition

Across the forest, independent of location, buried litter bags had higher decomposition rates compared to the surface litter bags (Fig. 5, Supplementary Table 1). Our findings support previous work (McClellan et al. 1990; Silver and Miya 2001; Zhang et al. 2008) that found similar trends across multiple ecosystems. Within the leaf litter, environmental conditions vary with depth. For example, moisture content increases with depth (Taylor and Parkinson 1988). The increase in moisture content can increase fungal productivity and microbial productivity (Osono et al. 2006), leading to increased decomposition rates. Furthermore, repeated wetting and drying can increase the decomposition rates (Taylor and Parkinson 1988), and flooding tends to increase mass loss compared to non-flooded sites (Brinson 1977; Yates and Day 1983). Ultimately, buried litter tends to have conditions that are more favorable for decomposition.

Role of Litter on the Forest Floor

Litter on the forest floor is important for forest ecosystem dynamics and is vital to carbon and nutrient cycling in forests and provides a protective layer to the forest floor (Olson 1963; Sayer 2006). In this study, although decomposition rates were highest in the mid forest, measured litter thickness remained constant within the high forest and mid forest, but was almost entirely absent in the low forest and transition zone (Fig. 5). This pattern appears to be driven by litterfall inputs, which followed the same pattern. While diminishing litter layers within soils can destabilize microclimate conditions and alter nutrient and carbon cycling (Sayer 2006), it also indicates relatively limited connectivity and preservation of organic matter during this ecosystem transition.

Leaf litter decomposition is a critical factor for understanding the carbon cycle under global climate change (Liski et al. 2003; Brennan et al. 2009). While a plethora of studies have examined leaf litter decomposition and climate change in marshes (e.g., Wu et al. 2016; Ouyang et al. 2023) and in forested landscapes (e.g., Yang et al. 2007; Prieto et al. 2019), there is a paucity of studies in a transitional forest along the coast. Global climate models do not resolve coastal processes (Ward et al. 2020), and even models of the marsh-forest boundary poorly parameterize coastal forest litter decomposition (Kirwan et al. 2016; Reeves et al. 2022; Valentine et al. 2023). This transition zone, or ecotone, will become increasingly relevant with future marsh landward migration and associated shifts in land management through retreat and upland migration (Kirwan and Gedan 2019; Van Dolah et al. 2020; Molino et al. 2022; Osland et al. 2022). Our results highlight an area for forward progress in understanding the marsh-forest ecotone and improvement of both coastal and global modeling frameworks.

Figures and Tables

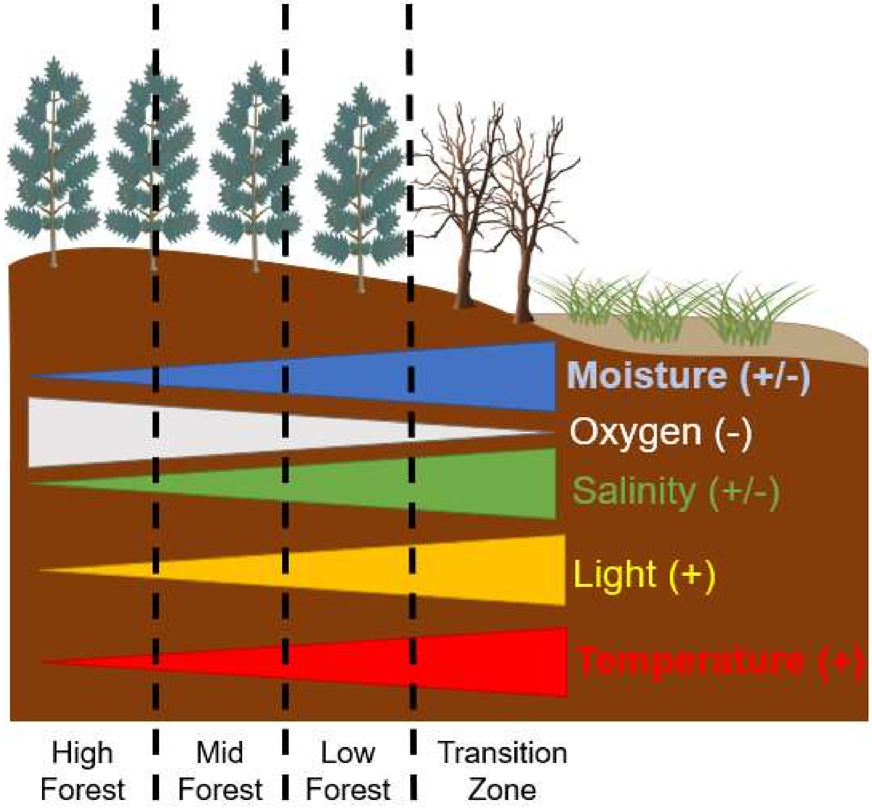
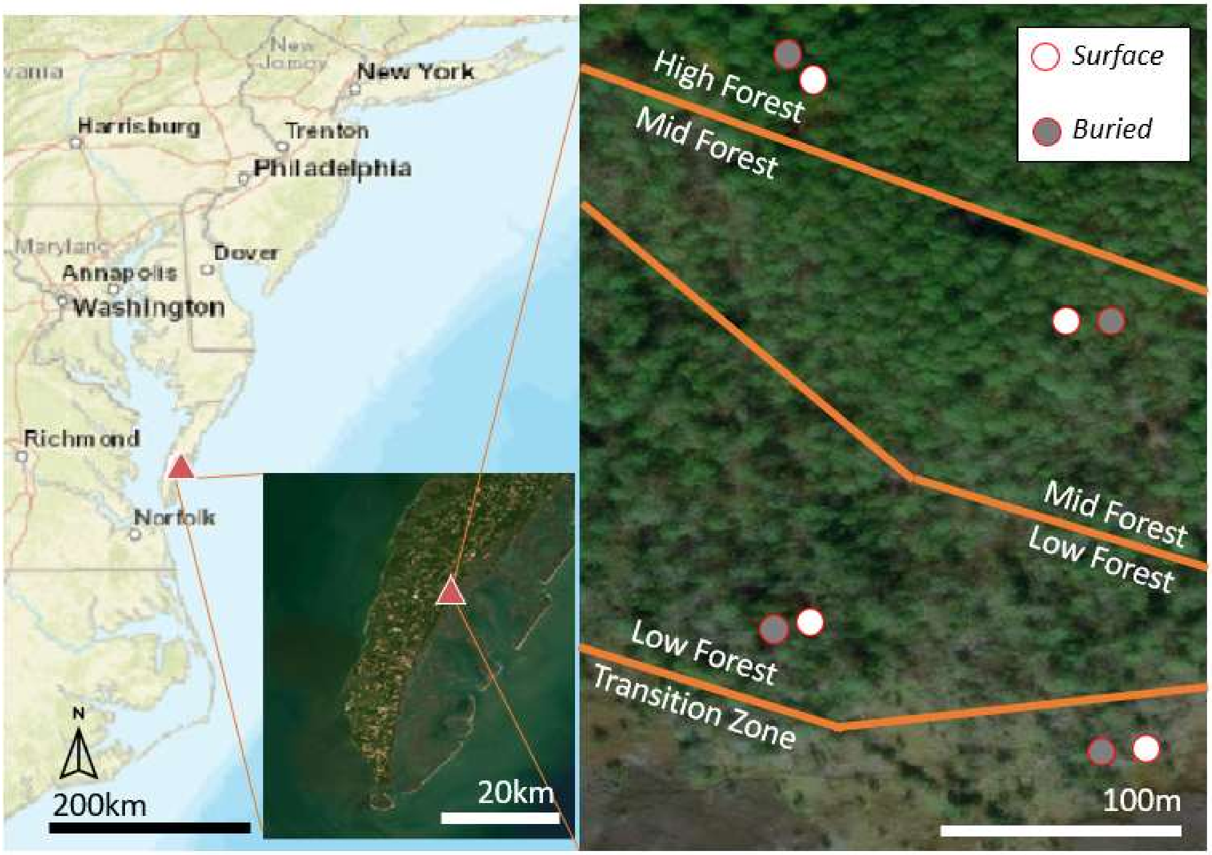


Fig. 1


vania
New Jersey
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Dover
Annapolis
Washington
Richmond
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N
200km
20km
○ Surface
● Buried
High Forest
Mid Forest
Mid Forest
Low Forest
Low Forest
Transition Zone
100m

Fig. 2

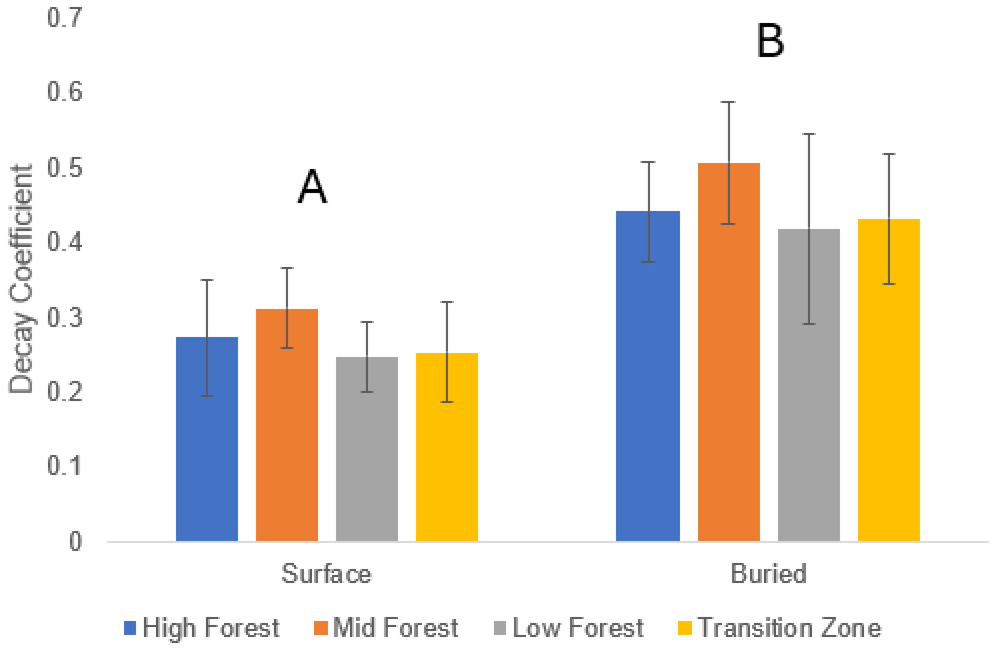
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Decay Coefficient
A
B
Surface
Buried
■ High Forest
■ Mid Forest
■ Low Forest
■ Transition Zone

Fig. 3

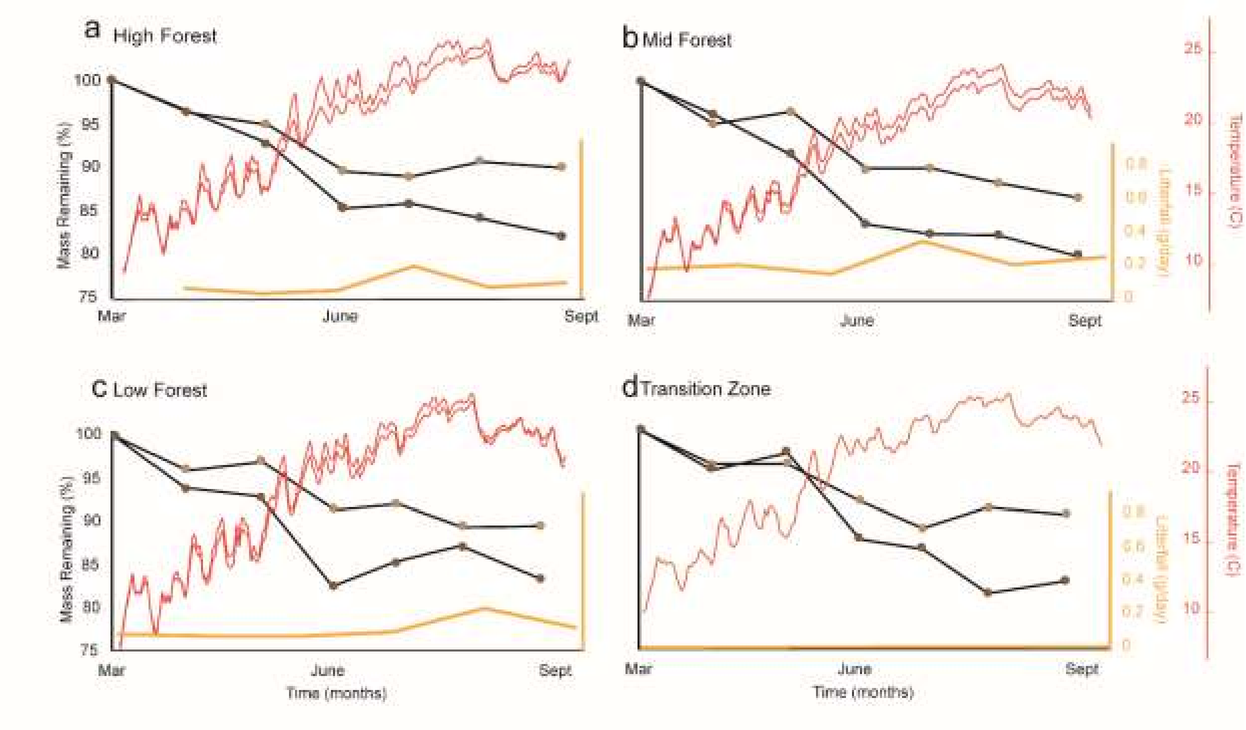
a High Forest
b Mid Forest
c Low Forest
d Transition Zone
Mass Remaining (%)
100
95
90
85
80
75
Mar
June
Sept
Time (months)
Litterfall (g/day)
0.8
0.6
0.4
0.2
0
Temperature (C)
25
20
15
10

Fig. 4

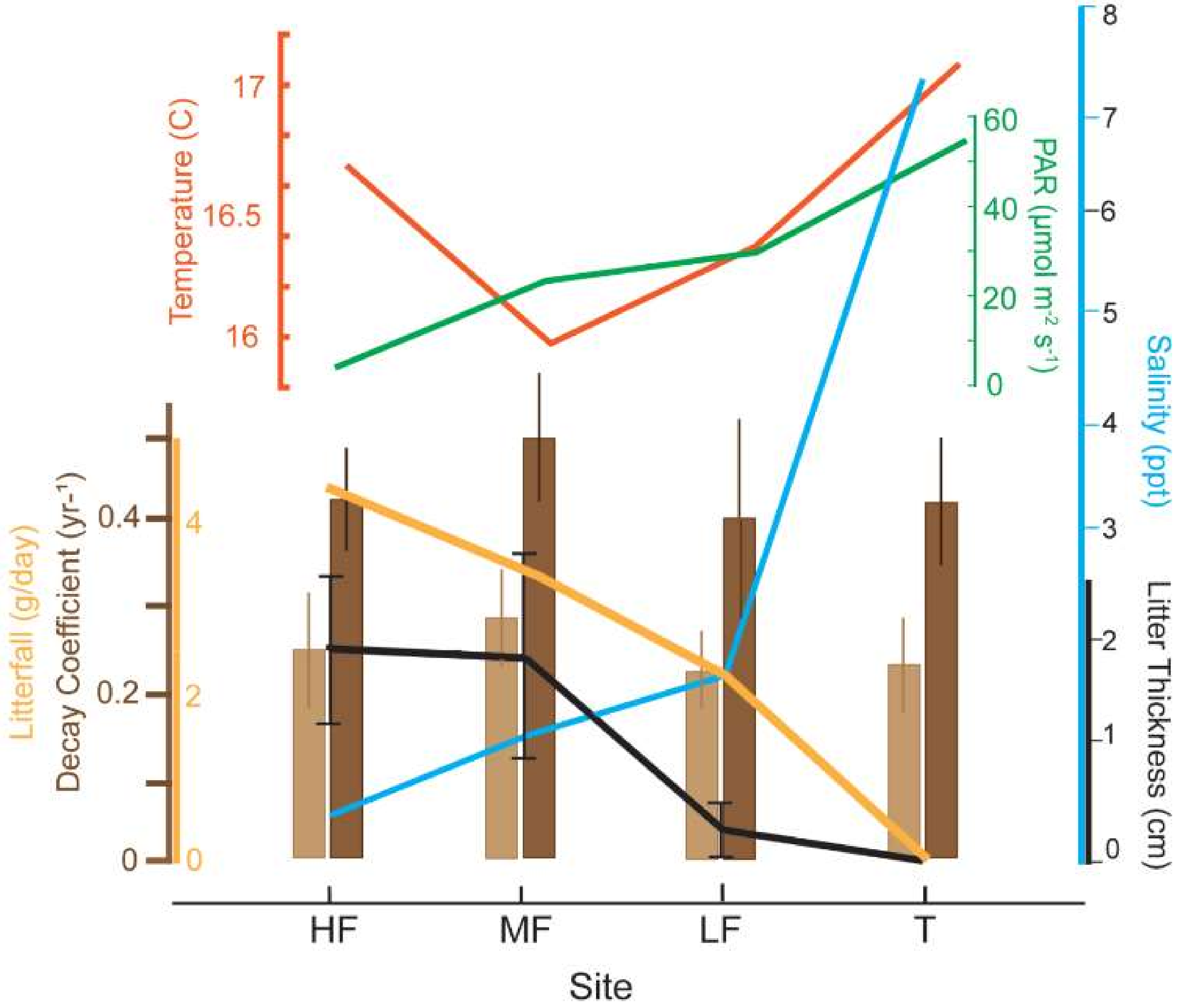

Fig. 5

Figure Captions

Fig. 1 Schematic of a cross section of the coastal landscape at Phillips Creek depicting the marsh-forest ecotone from coastal forest (to the left) to salt marsh and various environmental drivers driving decomposition

Fig. 2 A general map of the North American mid-Atlantic region (A) with inset maps showing satellite imagery of the Eastern Shore of Virginia (B) as well as the study site at Phillips Creek (C; 37°27'48.0"N 75°50'11.9"W). The locations of the leaf litter deployment sites within the forest health zones are indicated within Figure 2c as either white circle (surficial deployments) or gray circles (buried deployments)

Fig. 3 Calculated decay coefficients across all zones and treatments. Error bars represent the 95% confidence interval on the fitting of the exponential relationship. A and B indicate a significant difference between the decomposition rate at the surface and buried

Fig. 4 Temporal changes in decomposition rates, temperature, and litterfall in the high forest (a), mid forest (b), low forest (c), and transition zone (d) throughout the study period. Temperature and litterfall data are not quantified for the transition zone. Both shallow and deep soil temperature sensors are reported and show similar trends at a given site.

Fig. 5 The measured decay coefficients of forest litter decomposition (light brown = surface, dark brown = buried) across the marsh-forest boundary with relevant changing environmental gradients: litter thickness (black), litterfall (tan), soil salinity (blue), PAR (green), and average temperature (red). Litterfall data represents all litterfall March – December.

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