

Species-specific responses of a marsh-forest ecotone plant community responding to climate change

JUSTUS GRANT DALTON JOBE IV ¹ AND KERYN GEDAN 

The George Washington University, 800 22nd Street, Washington, D.C. 20052 USA

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Abstract. Ecotones are responsive to environmental change and pave a path for succession as they move across the landscape. We investigated the biotic and abiotic filters to species establishment on opposite ends of a tidal marsh-forest ecotone that is moving inland in response to sea level rise. We transplanted four plant species common to the ecotone to the leading or trailing edge of the migrating ecotone, with and without caging to protect them from ungulate herbivores. We found that species exhibited an individualistic response to abiotic and biotic pressures in this ecotone; three species performed better at the leading edge of the ecotone in the coastal forest, whereas one performed better at the trailing edge in the marsh. Specifically, grass species *Phragmites australis* and *Panicum virgatum* grew more in the low light and low salinity conditions of the leading edge of the ecotone (forest), whereas the shrub *Iva frutescens* grew better in the high light, high salinity conditions of the trailing edge of the ecotone (marsh). Furthermore, of the four species, only *P. australis* was affected by the biotic pressure of herbivory by an introduced ungulate, *Cervus nippon*, which greatly reduced its biomass and survival at the leading edge (forest). *P. australis* is an aggressive invasive species and has been observed to dominate in the wake of migrating marsh-forest ecotones. Our findings detail the role of lower salinity stress to promote and herbivory pressure to inhibit the establishment of *P. australis* during shifts of this ecotone, and also highlight an interaction between two non-native species, *P. australis* and *C. nippon*. Understanding migration of the marsh-forest ecotone and the factors controlling *P. australis* establishment are critical for marsh conservation in the face of sea level rise. More generally, our findings support the conclusion that the abiotic and biotic filters of a migrating ecotone shape the resulting community.

Key words: *Cervus nippon*; community assembly; environmental change; global change; marsh migration; range shifts; sika deer.

INTRODUCTION

In response to climate change, many species' ranges are shifting (Rosenzweig et al. 2008, Chen et al. 2011). Investigations of range shifts are often at the scale of a regional flora (e.g., Willis et al. 2008), taxonomic guild (e.g., Flousek et al. 2015), or single species (e.g., Doak and Morris 2010). Studies of range shifts have less commonly been undertaken at the meso-scale, where the ecological mechanisms of community assembly and disassembly can be experimentally tested. In this study, we investigate the potential for range shifts that will affect community disassembly at the scale of an ecotone plant community responding rapidly to climate change (Fig. 1).

Ecotones provide an excellent template on which to investigate abiotic and biotic influences on species responding to climate change, as ecotones often span

steep environmental gradients and are by their nature locations of species' boundaries and high community turnover (Risser 1995). Many ecotones are considered indicators of climate change for their sensitivity to environmental dynamics (Neilson 1993). For example, ecotones responding to climate change include those of boreal forest and tundra (Rupp et al. 2001), alpine tree line (Malanson 2001), grassland and shrubland (Peters 2002, Brandt et al. 2013), and upland and salt marsh habitats (Wasson et al. 2013).

As species colonize a climate-responsive ecotone, they will experience new abiotic and biotic filters impacting their ability to establish and persist. Species will respond idiosyncratically to new filters, which, within a dynamic and transitional community, can drive the development of a novel plant community assemblage within an ecotone (or other transitional habitats, such as one that is highly disturbed) that is unlike plant communities in either adjacent habitat or the ecotone community at present. Differential responses of species to changing environmental factors may pose barriers to species' range shifts, resulting in shifts or disassembly of a

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¹ E-mail: jjjobe@gwmail.gwu.edu

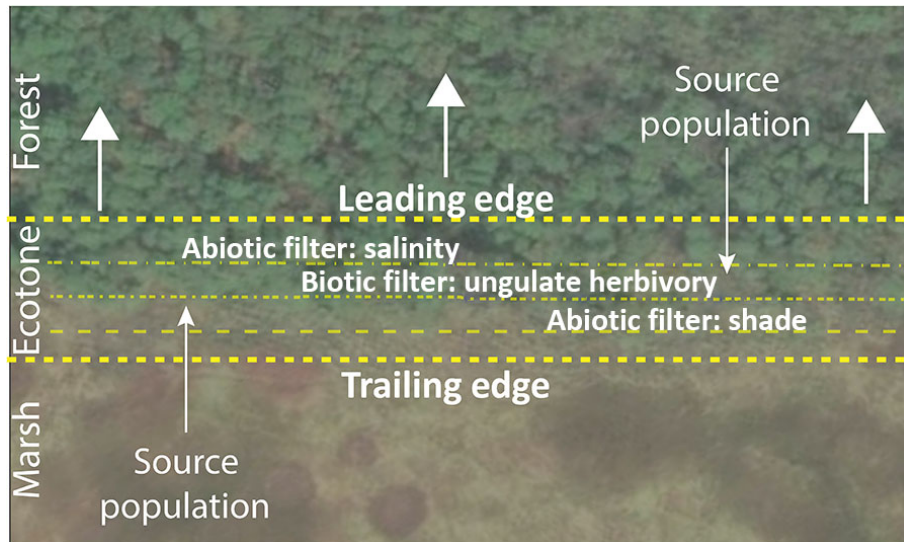


FIG. 1. Conceptual diagram of ecological filters in the formation of the marsh-forest ecotone.

characteristic ecotone “community” in response to climate change (Lutz et al. 2013).

Differences in co-occurring species’ abilities to pass through new ecological filters can result in the formation of novel assemblages (Huntley 1991, Hobbs et al. 2018). For example, novel assemblages of small mammals were observed after differential species’ range shifts in response to climate change in Yosemite National Park, where closely related species responded idiosyncratically to climate change (Moritz et al. 2008). In Yosemite, some high-elevation species contracted their ranges at the same time as some low-elevation species expanded their ranges in response to climate change, resulting in novel communities at intermediate elevation. The formation of novel assemblages or disassembled communities due to species-specific range shifts can have profound effects on both abiotic and biotic interactions in the community, which can directly impact ecosystem function and services provided by these communities (Zavala et al. 2009, Perring et al. 2012).

In this paper, we investigate the mechanisms of species establishment and persistence within the climate-change-responsive marsh-forest ecotone in the Chesapeake Bay, USA. Historically, the Chesapeake Bay has experienced 3.83 mm/yr of mean sea level rise (Cambridge, Maryland NOAA gauge Station ID:8571892, 1943–2020). Rates have been even higher during short periods (e.g., 8 mm/yr in 2002–2011) (Boesch et al. 2013), and sea level rise is expected to accelerate in Maryland by 0.15–0.18 mm/yr² (Boesch et al. 2018). During periods of sea level rise, coastal ecosystems exhibit a pattern of transgression into adjacent uplands. Sea level rise and saltwater intrusion kills forest trees and results in the

conversion of upland forest into high marsh, at the same time as drowned or eroded areas of marsh convert to open water (Brinson et al. 1995). Within the Chesapeake Bay, approximately 400 km² of uplands have been converted to wetlands since the late nineteenth century, and roughly the same area of marsh has been eroded to open water (Schieder et al. 2018).

Recent research has investigated the ecological dynamics of upland to marsh transition and come up with broad descriptions of the mechanisms and trajectory of change in plant communities (Fagherazzi et al. 2019, Kirwan and Gedan 2019, Taillie and Moorman 2019, Tully et al. 2019). Within these frameworks, the ecotone or “transition zone” is an ephemeral state. Throughout the transition, the ecotone migrates across the landscape. Its location can be tracked as an indicator of change (e.g., Smith 2013). This research seeks to fill a knowledge gap by providing data on the factors regulating survival and growth of plant species within this transitioning ecotone.

For plants, there are two important abiotic filters within the marsh-forest ecotone: (1) salinity, which should exhibit a stronger negative effect on the glycophytic species pool of the forest than the halophytic marsh species, and (2) light availability, which, at low levels, should more strongly inhibit the sun-adapted plant species of the marsh than the understory plants of the forest (Fig. 1). Last, as on many habitat edges (Leopold 1936, Alverson et al. 1988), ungulates traverse the marsh-forest boundary and browse heavily on species within the ecotone, potentially affecting species from both forest and marsh habitats in ways that could limit their establishment and population growth.

We selected four focal species that are common within the marsh-forest ecotone, and comprise a majority of the plant cover in the community (Appendix S1: Table S1). We investigated the relative importance of these three potentially important ecological filters in establishment and persistence within the community: salinity, light availability, and herbivory by ungulates. As this ecotone is primarily transitioning from forest to marsh, we selected three species that have high wetland affinity (*Iva frutescens*, *Baccharis halimifolia*, and *Phragmites australis*) and one species that is upland associated (*Panicum virgatum*; Lichvar 2013). Of these, *P. australis* is an introduced lineage that is widely invasive and a major conservation concern (Saltonstall 2002, Hazelton et al. 2014). The other three plant species are native to the study region. Incidentally, the most common ungulate in the region is also nonnative, the sika deer *Cervus nippon*, which was introduced in the early 1900s (Feldhamer et al. 1978, Kalb and Bowman 2017). Over two years, we observed transplanted individuals on the leading and trailing edge of the marsh-forest ecotone, within and outside of cages, to observe the effects of the three ecological filters (salinity, light, and herbivory) on growth and survival.

METHODS

Site

Blackwater National Wildlife Refuge consists of 11,000 ha of tidal marsh, mixed hardwood and loblolly pine forests, freshwater wetlands, and croplands (U.S. Fish and Wildlife Service 2006). The U.S. Fish and Wildlife Service actively manages *Phragmites australis* expansion, as well as ungulate populations within Blackwater National Wildlife Refuge. Since the 1930s, over 2,000 ha of marsh habitat in Blackwater have converted to open water, including the large Lake Blackwater, due to subsidence and sea level rise (Pendleton and Stevenson 1983, Leatherman et al. 1995).

Located within the refuge along its northwestern border is Moneystump Swamp, a tidal marsh along the banks of Beaverdam Creek. The marsh consists of two zones, low marsh dominated by *Spartina alterniflora* and high marsh dominated by *Spartina patens*, *Schoenoplectus americanus*, and *Juncus roemerianus*. Upland of the high marsh, there is a high marsh ecotone with *Iva frutescens*, *Panicum virgatum*, and *Baccharis halimifolia*. This ecotone is sometimes referred to as the transition zone in other studies (Brinson et al. 1995). Across much of the high marsh and the ecotone are standing dead loblolly pines referred to as “ghost forest.” Upland of the ecotone is a mixed hardwood and loblolly pine forest with established stands of *Phragmites australis*. Other descriptions of the plant community at the site and region can be found in Rice et al. (2000) and Flores et al. (2011).

Twenty sites were selected at random along the coastal forest and another 20 in the marsh. The coastal forest represents the “leading edge” of the ecotone, areas that will transition into the marsh-forest ecotone. The marsh represents the “trailing edge” of the ecotone, areas that will transition from ecotone to high marsh. The trailing edge was defined as an area where 50% of the loblolly pines were standing dead. Leading edge was defined based on two criteria: first, that the greater majority of trees were alive, and second, that sites were within 50 m of the ecotone boundary in order to have a realistic assumption of marsh migration.

Plant species

Four species that occur in the marsh-forest ecotone were selected to be transplanted into experimental plots: marsh elder (*Iva frutescens*), switchgrass (*Panicum virgatum*), eastern baccharis (*Baccharis halimifolia*), and common reed (*Phragmites australis*). *I. frutescens* and *B. halimifolia* are shrubs in the Asteraceae family, usually found in a narrow band in the upper limits of tidal marsh. *P. virgatum* and *P. australis* are perennial grasses. *Panicum virgatum* primarily occurs in upland and transitional regions directly adjacent to the tidal marshes. *Phragmites australis* is moderately salt tolerant; it thrives along the upper boundary of brackish and salt marsh where freshwater runoff from land keeps salinities slightly lower than within the marsh. Seeds of all four species were collected from plants in Moneystump Swamp during the fall season prior to the experiment. For each species, seeds were collected from over 50 individuals throughout the ecotone in order to capture representative genetic diversity. Seed heads were clipped from plants and seeds were separated from plant material using sieves. Seeds were cold stored over the winter to break dormancy and planted in the spring. All seeds were planted at the same time into trays containing potting mix and grown into seedlings (more than three true leaves) in the greenhouse.

Experimental setup

The 20 replicate sites were spread along 0.6 km of marsh and coastal forest (Fig. 2). Each site was composed of three 1-m² plots: a control plot where there were no structures other than marker flags; a cage control plot, composed of caging on two sides in order to mimic the light conditions of the caged plot while still allowing for herbivory to occur; and a caged plot composed of caging on all four sides preventing access to the plots from ungulates. Both caged plots and cage control plots were constructed with chicken wire (2.54 cm mesh) and 1.22 m tall wooden posts. The dimensions of each cage were 1 × 1 × 1.22 m (width × length × height). The cages were designed to specifically prevent ungulate herbivory; mesh was large enough for small rodents to

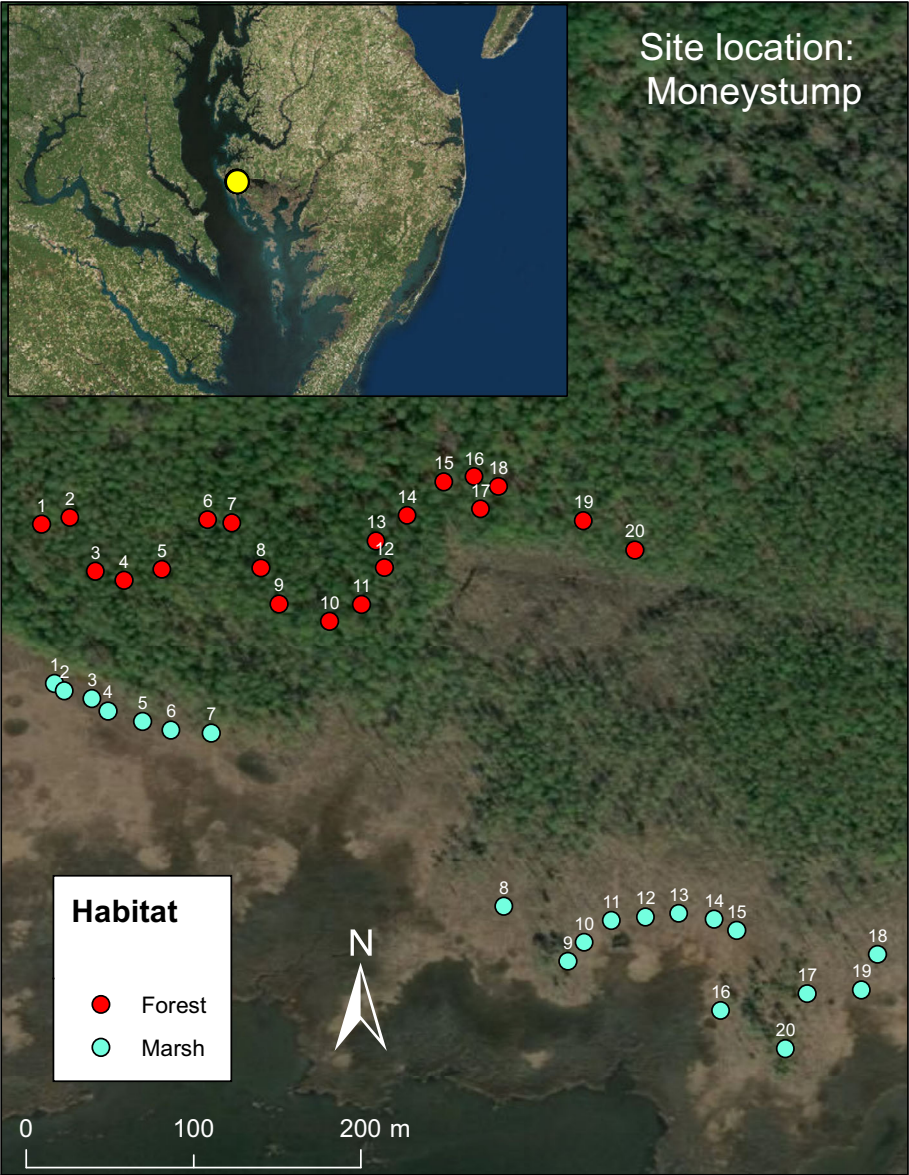


FIG. 2. Map of Moneystump Swamp in Blackwater National Wildlife Refuge, Maryland, USA, highlighting locations of plots within the coastal forest and marsh on the leading and trailing edges of the ecotone. Inset shows the Chesapeake Bay Region.

enter caged plots. After marking and caging the plots, preexisting vegetation was clipped in the plots using lawn clippers. Then, one individual of each of the four plant species was transplanted into each of the three plots. Four holes were dug using a trowel, and seedlings were randomly planted into one of the four holes. Plants that did not survive transplanting past the first week were replaced the following week.

During the two growing seasons, plots were monitored weekly for signs of ungulate herbivory. When signs of herbivory were observed, we recorded the extent of

herbivory by noting the number of remaining stems and leaves that could be subtracted from the most recent growth data as a conservative estimate of biomass removed.

We collected growth data (plant height, number of stems, and number of leaves) on all transplanted plants, at four time points over two growing seasons: just after transplant (April 2017), at the end of the first growing season (September 2017), at the beginning of the second growing season (April 2018), and just prior to biomass harvest (August 2018) at the end of the second growing



FIG. 3. Photograph captured by a trail camera in the coastal forest of a hind Sika deer (*Cervus nippon*) consuming plants within a control plot.

season. At the conclusion of the second growing season, when species were at peak biomass, all aboveground biomass was collected for each individual that survived the 16-month experiment. Each individual was cleaned of any debris, dried in a drying oven at 60°C for 72 h, and weighed.

Camera traps

To identify herbivore consumers, trail cameras (Ape-man International Company, Shenzhen, China) were installed within both the marsh and forest areas. Camera traps were established 2 m away from a control plot at one randomly selected site in the marsh and forest habitats. Cameras were installed two weeks after the initial establishment of the plots and moved throughout the growing season to various plots in the marsh and forest. They were set to capture both an image and a 10-s video of any motion occurring in front of the camera trap. After the motion sensor was triggered and images captured, they could not be retriggered again by motion for 5 minutes, in order to reduce the probability of multiple captures of the same herbivory event. Images were reviewed on a biweekly basis for evidence of herbivory and identification of wildlife. Cameras remained active until the conclusion of data collection.

Salinity and light

In order to understand the gradients in potential environmental filters that could impact the establishment of seedlings in the ecotone, light availability and salinity were monitored in the marsh and forest sites. Two groundwater wells were dug in the soil to a depth of 1 m.

One well was located within the forest and another well was located on the marsh. Both were in close proximity to established plots. Wells were made of PVC pipes with multiple one-quarter inch (0.635 cm) holes drilled into the bottom 30 cm. Holes were covered with pantyhose mesh to prevent sediment from entering the well. A HOB0 Saltwater Conductivity and Salinity data logger (Part #:U24-002-C; Onset, Bourne, Massachusetts, USA) was placed in each well. Salinity in wells were recorded every 4 h for the duration of the growing season each year.

To measure light availability in each habitat, photosynthetically active radiation (PAR) was measured at each plot with a MQ-200 Quantum Separate Sensor (Apogee Instruments, Logan, Utah, USA). We collected light measurements in the four corners of every plot at the height of the plants (from 10 to 60 cm). All light data were normalized as a proportion of the total photosynthetically active radiation (TPAR) measured during that 20-minute interval by a HOB0 Temperature and Light Pendant data logger (Part #:UA-002-08; Onset) placed in open sun, far from any light obstructions such as trees. This allowed for calculation of the proportion of PAR reaching each plot during point measurements, a better representation of the light regime at the plot than point measurements of PAR. Light availability and salinity were recorded for both growing seasons.

Natural herbivory transects

To determine the probability of herbivory on naturally occurring plants of our four focal species, we monitored herbivory events on the four species along 10 transects in the marsh and 10 transects in the forest. Each transect

ran 50 m, oriented parallel to the ecotone–forest boundary. The total number of individuals of each focal species within 1 m of the transect tape was recorded, and each individual encountered was evaluated for signs of herbivory. Herbivory was identified as substantial removals of biomass (larger bite marks) that could be attributed to ungulate browsing. Insect herbivory (smaller bite marks or interior leaf damage) was not recorded.

Statistical analysis

We tested for an effect of habitat (marsh and forest) on the environmental variable of light availability with a *t* test between habitats, to determine if light availability differed between the forest and marsh. These variables were checked and met assumptions of normality and homogeneity of variance. To test for differences in harvested biomass between caging treatments and habitats, we used a linear mixed effects model for each transplanted species. Since this was a split-plot design with site replicate as a block, we treated site as a random effect in the model, while habitat and caging treatment were treated as fixed effects. To investigate survival of our four focal species in the two habitats and three caging treatments, we used a Kaplan-Meier estimator to produce survivorship curves with 95% confidence intervals. We used a log-rank test, which produced expected values of survival, to test for differences in survival between caging treatments. Differential survival among habitats was also tested using a log-rank test between caged plots in the ecotone and forest. To test for the effect of species and habitat on the likelihood of herbivory on each of the four plant species on natural herbivory transects, we used a two-way ANOVA with the main effect of species, habitat, and species-habitat interaction. Tukey's post hoc tests were used to explore significant effects in the split-plot and two-way ANOVA models.

RESULTS

Camera traps

Sika deer (*Cervus nippon*) were the only herbivore captured on the camera traps in both the marsh and the coastal forest in both years of the experiment (Fig. 3; Appendix S1: Table S2). There was approximately six times the number of sightings of sika deer in close proximity to plots in the coastal forest compared to the marsh (Appendix S1: Table S2).

Salinity and light

Light availability was significantly lower in the forest than in the marsh ($t = -9.2251$; $df = 264$; $P < 0.001$). On average, $40.5\% \pm 3.7\%$ (mean \pm SE) of available light reached transplants in the forest compared to $76.9\% \pm 1.3\%$ of available light in the marsh

(Appendix S1: Table S3). Groundwater salinity was also lower in the forest than in the marsh, with an average salinity of 3.94 ± 0.03 ppt and range of 2.49–5.11 ppt in the forest compared to an average of 13.02 ± 0.04 ppt and range of 9.97–14.27 ppt in the marsh (Appendix S1: Table S3; Appendix S1: Fig. S1).

Transplant survivorship

Herbivory affected the survivorship of only one of the four focal species (Fig. 4). Survival of *P. australis* varied between caging treatments in the forest only, with greater survival in caged compared to cage control ($P = 0.0003$) and control plots ($P = 0.0129$) (Appendix S1: Table S4). The other three species' survivorships were not affected by ungulate herbivory in either the forest or the marsh. However, all species experienced differential survival between habitats within caged plots (Appendix S1: Table S5). *P. virgatum* and *P. australis* experienced greater survivorship in the coastal forest compared to the marsh in caged plots (*P. australis*, $\chi^2 = 6.9$, $P = 0.009$; *P. virgatum*, $\chi^2 = 8.3$, $P = 0.004$), whereas *I. frutescens* experienced higher survivorship in the marsh compared to the coastal forest ($\chi^2 = 3.1$, $P = 0.05$). *Baccharis halimifolia* experienced low survivorship across both habitats; however, it was slightly higher in the forest compared to the marsh ($\chi^2 = 9.6$, $P = 0.002$).

Aboveground biomass

Phragmites australis biomass was affected by a significant interaction between caging treatment and habitat in a linear mixed effects model (Appendix S1: Table S6). Specifically, *P. australis* in caged treatments in the forest were distinctly different from all other possible combinations with a biomass of 39.72 ± 8.15 g, an order of magnitude greater than any other treatment across both habitats (Fig. 5). *P. virgatum* exhibited significantly different productivity between habitats (Appendix S1: Table S6) with greater biomass production in the forest (10.24 ± 1.40 g) compared to the marsh (3.30 ± 0.73 g) whereas *I. frutescens* exhibited significantly greater biomass production in the marsh (27.65 ± 3.44 g) compared to the forest (2.55 ± 0.63 g, Appendix S1: Table S6). There was no significant effect of habitat or caging treatment on *B. halimifolia* biomass.

Natural herbivory transects

On natural herbivory transects, species across each habitat experienced significantly different levels of ungulate herbivory (two-way ANOVA; species \times habitat interaction, $F_{3,72} = 5.992$; $P = 0.0011$). This was primarily driven by *P. australis* experiencing a significantly higher rate of herbivory in the coastal forest relative to the marsh with 77% of individuals experiencing herbivory in the forest compared to 38% in the marsh

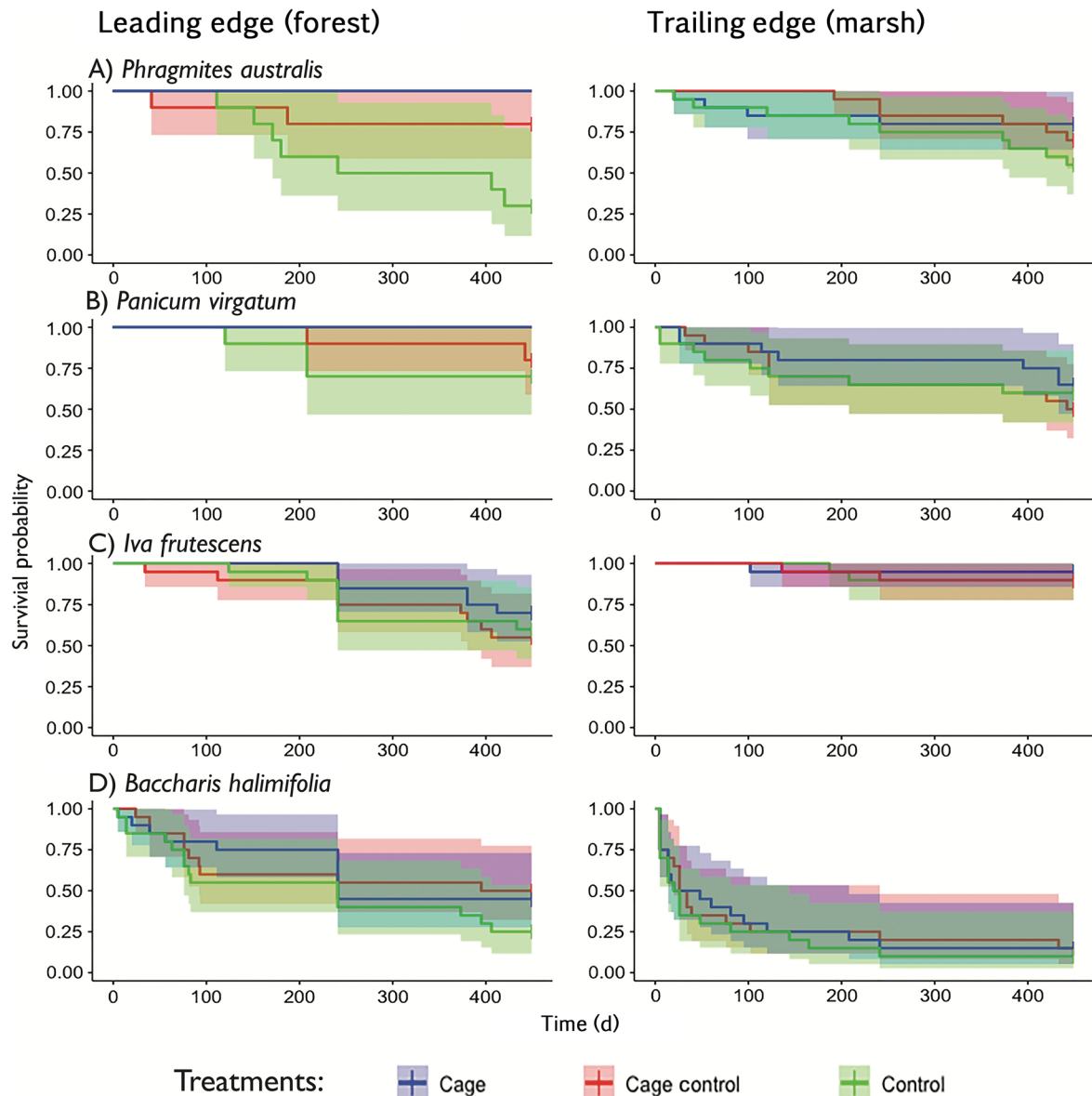


FIG. 4. Kaplan-Meier survivorship curves over two full growing seasons for transplanted individuals of the four focal species. Confidence intervals (95%) are shown as shaded regions around survival curves.

(Fig. 6, Tukey's post hoc test, $P = 0.0015$). The level of herbivory on *P. virgatum* did not vary between habitats, but were comparable to *P. australis* across both habitats. Both *P. virgatum* and *P. australis* experienced significantly higher levels of herbivory than *I. frutescens* and *B. halimifolia* across both habitats (Fig. 6; Table S7).

DISCUSSION

The marsh-forest ecotone spans a steep environmental gradient. We found drastically different abiotic conditions over a span of <50 m between these two habitats.

At the trailing edge of the ecotone (marsh), there were high levels of light availability and higher salinity in the groundwater, whereas, in the leading edge of the ecotone (forest), there were low levels of light availability but also lower groundwater salinity. These constitute inverse stress gradients for plants in light availability and salinity that we hypothesized would have differential effects on species as they expand their distribution upslope in response to climate change.

These differences in abiotic conditions between the two habitats did translate into effects on the productivity and survival of common species in the ecotone. Species

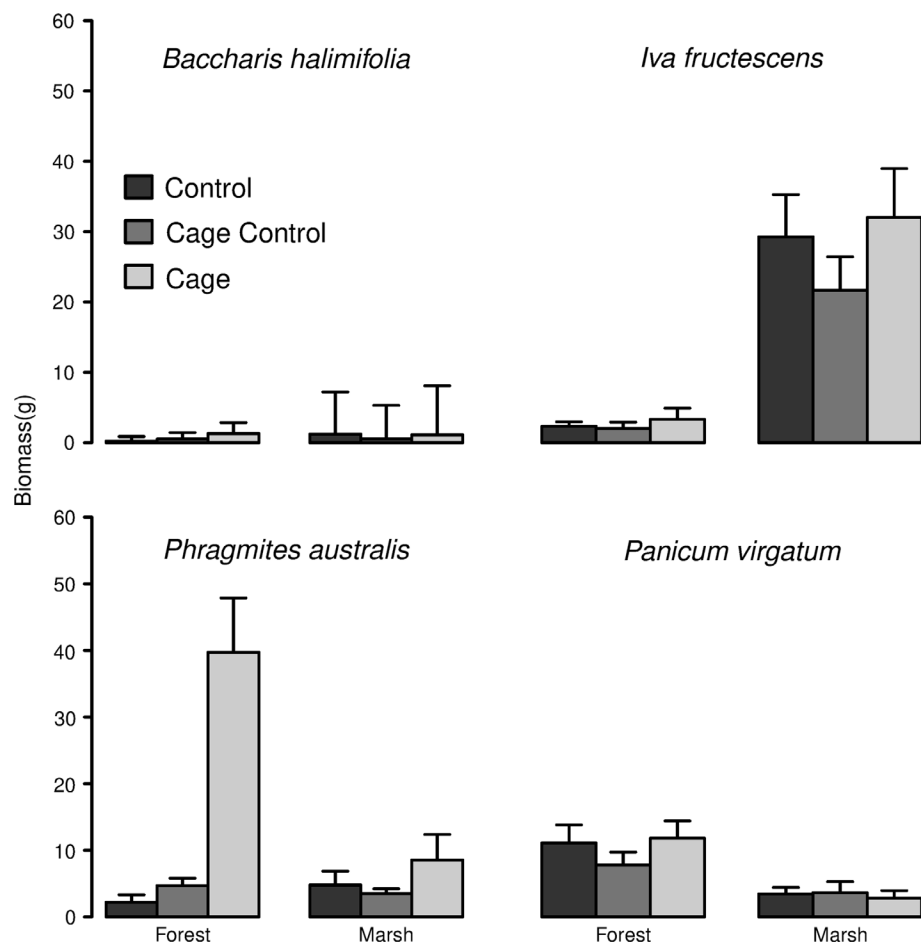


FIG. 5. Dry mass (mean + SE) at the end of the experiment for transplanted individuals of the four focal species.

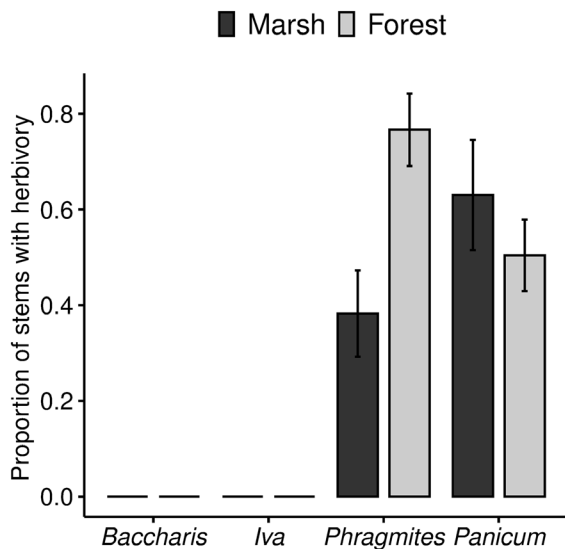


FIG. 6. Proportion of each species experiencing herbivory (mean ± SE) on transects in the marsh and coastal forest.

responded in an individualistic or species-specific manner. Grasses (*Phragmites australis* and *Panicum virgatum*) performed significantly better in the low light and low salinity stress of the coastal forest than in the marsh, as demonstrated by their high growth in caged plots in the forest (Fig. 5). Whereas the shrub *Iva frutescens*, survived and grew significantly better in the high light and high salinity stress of the marsh. *Baccharis halimifolia* showed low growth and survival across both habitats. *B. halimifolia* in the marsh died off rapidly at the beginning of the experiment with 12 of 20 transplants dying in the first 90 d, whereas *B. halimifolia* in the forest died off more gradually over the two years. We expect that successful establishment of *B. halimifolia* must require windows of more benign salinity conditions that did not occur during the study years. Low light availability appears to limit *B. halimifolia* from the leading edge of the ecotone, since it was able to expand landward in U.S. Gulf Coast ecotones that were disturbed by Hurricane Katrina (Pivovarov et al. 2015). Overall, our study demonstrated species-specific responses, more than a common signal to all four species, to the different abiotic

conditions of the leading and trailing edge of the marsh-forest ecotone.

Other investigations of the response of communities or suites of species to environmental change have also found that species respond individually. For example, Kopp and Cleland (2014) found that elevational range expansions of focal plant species due to climate change were species specific in arid mountain ranges in the Western United States. Research in California forests has found that, similar to the small mammals in Yosemite (Moritz et al. 2008), some species have shifted upslope, while others have shifted downslope, resulting in a slow but progressive disassembly of these forest communities (Rapacciuolo et al. 2014, Serra-Diaz et al. 2016).

In our system, the species-specific response was not limited to abiotic conditions but were especially apparent in the effects of herbivory. Caging had a dramatic effect on only one species, *P. australis*, and only in the forest habitat. In the forest, *P. australis* exhibited 100% survival in the caging treatment, compared to 25% when exposed to ungulate herbivory. Herbivory also had a considerable impact on *P. australis*' growth. In the coastal forest, ungulate herbivores consumed 94.4% of aboveground biomass. Herbivory did not have an effect on the other three focal plant species in either habitat. However, on natural herbivory transects, ungulate herbivory occurred on both *P. australis* and *P. virgatum*. Similar to experimental transplants, naturally occurring *P. australis* on transects experienced higher levels of herbivory in the forest relative to the marsh, whereas *P. virgatum* herbivory did not vary by habitat.

We find that it is not just variation in species' tolerances to more extreme environmental conditions that results in a species-specific response, but variation in the identity of the biotic or abiotic factor that defines their range. This type of variation, in the limiting factor for species within the same taxonomic guild, is particularly challenging for species distribution models (SDMs), which are frequently used to predict species' responses to global change. SDMs typically relate species distributions to spatially explicit abiotic conditions (Guisan and Zimmermann 2000), and often neglect biotic interactions that can be important in setting species' range limits. Moreover, biotic interactions can strongly influence how climate change impacts a species at a wide range of scales, reducing our ability to predict a species shift in response to environmental change when biotic interactions are not accounted for (Wisz et al. 2013). Our study has shown that biotic interactions exert an important influence on a species' ability to respond to climate change.

The importance of biotic interactions were apparent in the transplant study and naturally occurring herbivory survey, which both showed that ungulate herbivory on plant species within the marsh-forest ecotone is species specific. The heavy herbivore pressure on *P. australis* is likely a response of herbivores to the high

protein concentration in its tissues (Hendricks et al. 2011, Silliman et al. 2014). *C. nippon* often target protein-rich sources of food (Takatsuki and Ikeda 1993), particularly in an attempt to accumulate body mass for the rutting season (Yokoyama et al. 2001) and winter (Mitchell et al. 1976).

Large herbivores often show a high level of selectivity, and can prevent the establishment of species that are otherwise well adapted to the abiotic conditions of a local community (Augustine and McNaughton 1998, Begley-Miller et al. 2014). At the same time, some species are adapted to high levels of ungulate herbivory and can more readily recover, mitigating herbivore impacts (Lloyd et al. 2003, 2010). Though ungulate herbivory has been well established as an ecological process shaping plant communities in the forest understory (Augustine and Frelich 1998, Rooney and Waller 2003), it has not been considered as a factor that may shape plant communities during marsh migration. Here, we show that it can be critical to preventing the establishment and spread of *P. australis* in the ecotone, where this species often becomes a dominant species (Smith 2013) and is cause for conservation concern (Kirwan and Gedan 2019, Tully et al. 2019). This also brings to light the importance of considering invasive-invasive interactions, as the primary ungulate within the system is Sika deer (*Cervus nippon*) a nonnative species from Japan. Whereas many studies have focused on the negative impacts of invasive ungulates on native plant communities (Wardle et al. 2001, Vázquez 2002), little consideration has been given to positive indirect interactions between invasive ungulates and native plant communities through their consumption of invasive plant species.

Overall, the results of this experiment indicate species-specific migration of the marsh-forest ecotone. Some ecotone species are more able to survive and grow in coastal forests than others due to the investigated ecological filters of light availability, salinity, and ungulate herbivory. *P. virgatum* should be an initial colonist in the leading edge of the ecotone as well as *P. australis*, when and where it can find a refuge from herbivory. Even though ungulate herbivory limited *P. australis*' productivity, we anticipate that the filtering effect of ungulates is overwhelmed if *P. australis* individuals reach a size or density refuge, since we observed *P. australis* establishment in the ecotone despite high rates of ungulate grazing on both transplants and natural herbivory transects. Once it establishes a clonal stand, *P. australis* can reduce the distribution and abundance of native flora (Amsberry et al. 2000). If *P. australis* becomes established in coastal forest at the ecotone leading edge, it can competitively exclude other species from migrating into the ecotone.

Most marsh migration models are based on elevation alone, to answer the question, "Will marsh habitat migrate?" However, we have shown that individual species respond differently to the abiotic and biotic filters of a climate-responsive ecotone, raising the more important

question, "Which marsh species will migrate?" As climate change and other types of anthropogenic disturbances shift species' ranges, we expect species-specific responses like the ones identified in this study to disassemble many familiar ecological communities and reassemble them through the new ecological filters of the changing environment. In the case of the marsh-forest ecotone plant community of the Chesapeake Bay, the filters of low light availability and salinity appear to favor grasses including an aggressive invasive species.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.3296/supinfo>

DATA AVAILABILITY

All data and R code are available in Zenodo (Jobe and Gedan 2020): <http://doi.org/10.5281/zenodo.4282665>.