



Limited Mangrove Propagule Retention at a Latitudinal Range Limit: Spatiotemporal Patterns at the Patch Scale

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Abstract

Dispersal and establishment dynamics are critical in understanding shifts in species' ranges. We seek to illuminate patch-level dispersal dynamics by examining the shifting salt marsh-mangrove ecotone. Specifically, we ask the following: (1) How are mangrove propagules dispersed, retained, and exported within a discrete patch? (2) How do differences across a flooding gradient influence propagule dispersal dynamics? (3) How does the distribution of established seedlings compare to propagule movements? *Avicennia germinans* is the most temperate mangrove species in the northern Gulf of Mexico forming an ecotone with *Spartina alterniflora* marshes in coastal Louisiana. Sets of 500 distinctively marked mangrove propagules were placed at five different elevations. After their release, we observed dispersal dynamics for 1 month. Retention was limited in the study area (< 10%) with ~70–80% of propagules exporting out of the system and ~20% propagule predation. Retained propagules largely remained at their original elevations and were generally found at the highest elevation. Seedling establishment was also studied and unlike propagule dispersal distributions, peak seedling density occurred at elevations flooded 20–40% of the time. Our study highlights the mass export of mangrove propagules, the disparity between dispersal and establishment dynamics, and the need to explore dispersal at biologically relevant temporal and patch-level spatial scales. By understanding dispersal and establishment dynamics within the ecotonal boundary, we provide one of the first studies on dispersal at a temperature-controlled latitudinal limit for mangroves and highlight some of the drivers needed to better connect plot-, patch-, and landscape-level dynamics at this and other range limits.

Keywords Dispersal · Range limit · Ecotone · Propagule · Mangrove · Salt marsh

Introduction

Dispersal plays a critical role in plant survival and expansion, particularly at range limits and ecotonal boundaries (Howe and Smallwood 1982; Gaston 2009; Sexton et al. 2009).

Patterns of dispersal can be examined at different scales to understand survival and expansion dynamics, as well as population connectivity (Nathan and Muller-Landau 2000). With changing climatic conditions, shifts in key environmental parameters will result in the movement of species distributions, ecotones, and range limits (Walther et al. 2002; Parmesan and Yohe 2003; Walther 2010; Corlett and Westcott 2013). Additionally, new biotic interactions may arise, potentially influencing dispersal and survival (Van der Putten et al. 2010). Modeling efforts often solely rely on abiotic parameters at current rates to predict future distributions in climate envelope analyses (Corlett and Westcott 2013). In reality, a complex of abiotic and biotic conditions need to be accounted for to better predict shifting ecotones and ranges (Sexton et al. 2009; Van der Putten et al. 2010). One portion of this complex is a sound understanding of dispersal strategies and how incumbent ecosystems will impact dispersal dynamics of expanding species.

In coastal saline wetlands, dispersal by water, or hydrochory (Dammer 1892), is an important dispersal vector

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(Nilsson et al. 2010). Mangroves, salt-tolerant, woody plants found on low-energy tropical and subtropical coasts, utilize hydrochorous dispersal (Tomlinson 1994). Mangrove propagules are often viviparous or cryptoviviparous in nature, as they germinate on the tree prior to dispersal (Bhosale and Mulik 1991; Tomlinson 1994). Tides, currents, wind, and wave action are all important factors in determining dispersal distance and direction (Howe and Smallwood 1982; Huiskes et al. 1995; Thiel and Haye 2006). Mangrove dispersal has been documented at large temporal and spatial scales (reviewed by Van der Stocken et al. 2019, for specific examples — Duke 1993; Duke et al. 1998), but only a limited number of studies have examined dispersal at smaller scales (Yamashiro 1961; Clarke 1993; Sousa et al. 2007; Peterson and Bell 2015; Van der Stocken et al. 2015a). The focus in the literature on long-distance dispersal does not provide adequate information to properly inform local- and intermediate-distance dispersal mechanisms and processes (Clarke 1993; Van der Putten et al. 2010).

Interaction dynamics of propagules along environmental gradients (e.g., hydrologic setting), with surrounding vegetation (e.g., mangrove, marsh, upland), and their combined effect are likely to play a critical role in dispersal and establishment dynamics regardless of location. Hydrologic setting has been studied in lab- and mesocosm-based studies (Alleman and Hester 2011b) and on discrete plots in the field (Patterson et al. 1997; Peterson and Bell 2012), but field-based studies utilizing natural or semi-natural hydrological gradients to explicitly explore propagule dispersal and establishment are imperative (Clarke 1993; Peterson and Bell 2015). Nearby vegetation is capable of trapping propagules, and in stressful, early successional or ecotonal habitats, vegetation may also ameliorate soil conditions that can result in improved establishment (McKee 1995b; McKee et al. 2007). Alternatively, surrounding vegetation may also inhibit dispersal (Peterson and Bell 2012; Peterson and Bell 2015) and compete for space and resources (Pickens and Hester 2011, Simpson et al. 2013, Howard et al. 2015, Pickens et al. 2018; reviewed by Saintilan et al. 2009). This set of interactions at the salt marsh-mangrove ecotone has been argued to change across environmental gradients, life-history stage, and local edaphic conditions (Guo et al. 2013; Rogers and Krauss 2019). To better understand these interactions at the landscape-level, there is an increasing need to adequately account for environmental gradients and patch- to meso-scale spatial processes (10–100 meters) (Holling 1992; Niemelä 1999) at dispersal relevant time scales (month).

Mangrove expansion at the expense of salt marshes is expected to occur on temperature-controlled mangrove range limits as the frequency, duration, and severity of freeze events decrease with climate change (Osland et al. 2013; Cavanaugh et al. 2014; Osland et al. 2017). In the southeastern USA, models predict mangrove expansion, but do not take into

account dispersal dynamics, including potential deviations in propagule production, dispersal, and establishment from current conditions (Clarke 1995; Van der Stocken et al. 2019) and changes that might occur once in incumbent salt marsh habitats (Van der Putten et al. 2010; Guo et al. 2013). Each component must be considered to better predict future expansion, particularly linking local and patch scale dynamics to landscape level processes. Although dispersal dynamics have been previously studied within mangrove habitats (e.g., Rabinowitz 1978; Sousa et al. 2003; Sousa et al. 2007; Van Der Stocken et al. 2015b) and at the upslope salt marsh-mangrove ecotone (Clarke and Myerscough 1993; Peterson and Bell 2012; Jiang et al. 2013; Peterson and Bell 2015), no dispersal-focused studies have been conducted at the latitudinal salt marsh-mangrove ecotone in the northern Gulf of Mexico or at other temperature-controlled mangrove range limits to our knowledge. The occurrence of a singular mangrove species (*Avicennia germinans*), due to its freeze tolerance compared to other mangrove species found in the wider region, makes this system an ideal area to examine dispersal dynamics. The northern Gulf of Mexico has been the focus of many studies examining salt marsh-mangrove interactions, mangrove seedling establishment/survival, and propagule production/predation (e.g., Patterson et al. 1993; Patterson et al. 1997; McKee & Rooth 2008; Alleman & Hester 2011a & b; Pickens and Hester 2011; Osland et al. 2013; Krauss et al. 2014, Osland et al. 2019; Yando et al. 2018), but studies explicitly examining dispersal dynamics within and beyond the salt marsh-mangrove ecotone are needed to appropriately predict future shifts in range limits with climate change.

We address this gap by investigating dispersal in-situ along an elevation gradient within the latitudinal salt marsh-mangrove ecotone. Specifically, we explore the following questions: (1) How are mangrove propagules dispersed, retained, and exported within a discrete patch? (2) How do differences across a flooding gradient influence propagule dispersal dynamics? (3) How does the distribution of established seedlings compare to propagule movements? To address these questions, we completed a mark-recapture experiment with marked mangrove propagules along an intertidal elevation gradient in coastal Louisiana, USA, where salt marsh and mangrove species are intermixed to form a vegetation mosaic. The findings of this study provide additional information on how dispersal dynamics impact species range expansion at this temperate-subtropical interface.

Material and Methods

Study Area and Experimental Design

During the winters of 2015 (December–January) and 2016 (November–December), we conducted dispersal studies using

a mark-recapture method with mangrove propagules in a restored coastal saline wetland adjacent to Bayou Lafourche in Port Fourchon, Louisiana (29.127° N, 90.222° W) (Fig. 1a). The typical mangrove production period for this area is from early October to late December (Alleman and Hester 2011b). In early 2012, the study area (~0.5 ha) received sediment slurry from a nearby canal when the dredged slurry spilled over a retention levee, forming an elevation gradient within the study site. The site had previously contained both *Avicennia germinans* and *Spartina alterniflora* and was also planted with both *A. germinans* and *S. alterniflora* shortly after receiving the slurry amendment. With surviving individuals, recently planted cohorts, and natural recruits of both species prior to this experiment, the study site provided a characteristic example of a coastal saline wetland for coastal Louisiana, an area that is heavily impacted by wetland degradation, modification, restoration, and other anthropogenic disturbances. The site was selected for its abutment to the former canal that resulted in the formation of an elevation gradient allowing us to test our questions both within and beyond the normal elevation range for the surrounding wetlands. Areas that exist high in the tidal frame, including the highest elevations of this site, also commonly contain succulent halophytes (e.g. *Salicornia* spp. & *Batis maritima*) and drought-tolerant graminoids (e.g., *Distichlis spicata*) (Lloyd and Tracy 1901).

On the elevation gradient, we established five distinct contours using a laser level (Spectra Precision Laser, LL300, Trimble Navigation Ltd., Sunnyvale, CA, USA) spanning an area of ~1800 m² (30 m × 60 m) and related contour elevations to a previously measured nearby benchmark. Contours were reestablished and referenced to the benchmark each year using real-time kinematic surveying in NAVD88 Geoid 12A (Trimble R8 Receiver & Trimble TSC3 Controller, Trimble Navigation, Ltd., Sunnydale, California) and the real-time Continuous Operating Reference Station (CORS) network (Louisiana State University, GULFNet). Elevation contours corresponded to ~75%, 50%, 25%, 10%, and 1% of the time flooded (5-year average; NOAA 2015) (Fig. 1b). Five sectors (A–E) of ~4 m were established along each elevation contour to further divide the site for analyses (Fig. 1b). The greater Fourchon area is microtidal with a mean tide range of 0.37 m (NOAA 2015), and is heavily influenced by meteorological forces (Reed and Cahoon 1992). Overall, site hydrology remained the same for the two sampling campaigns (A1 & 2). The site included a mosaic of bare sand flat, mangrove, salt marsh, and succulent vegetation which differed over the elevation gradient (Fig. 1). We were not able to separate the combined effects of vegetation and hydrology as they were generally correlated along the elevation gradient (Fig. 2), thus, only hydrology was included in our regression models (see “Data Analyses”).

Fig. 1 a Map of study site location in Louisiana (USA) and b diagram of painted propagules located along an elevation gradient with corresponding percent time flooded and elevations (NAVD88-Geoid12A) in a salt marsh-mangrove vegetation mosaic. Letters on grid (A–E) indicate sub-divisions (hereafter study sector) of study site used to further divide the area and are used in subsequent figures. Images of vegetation courtesy of Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/)

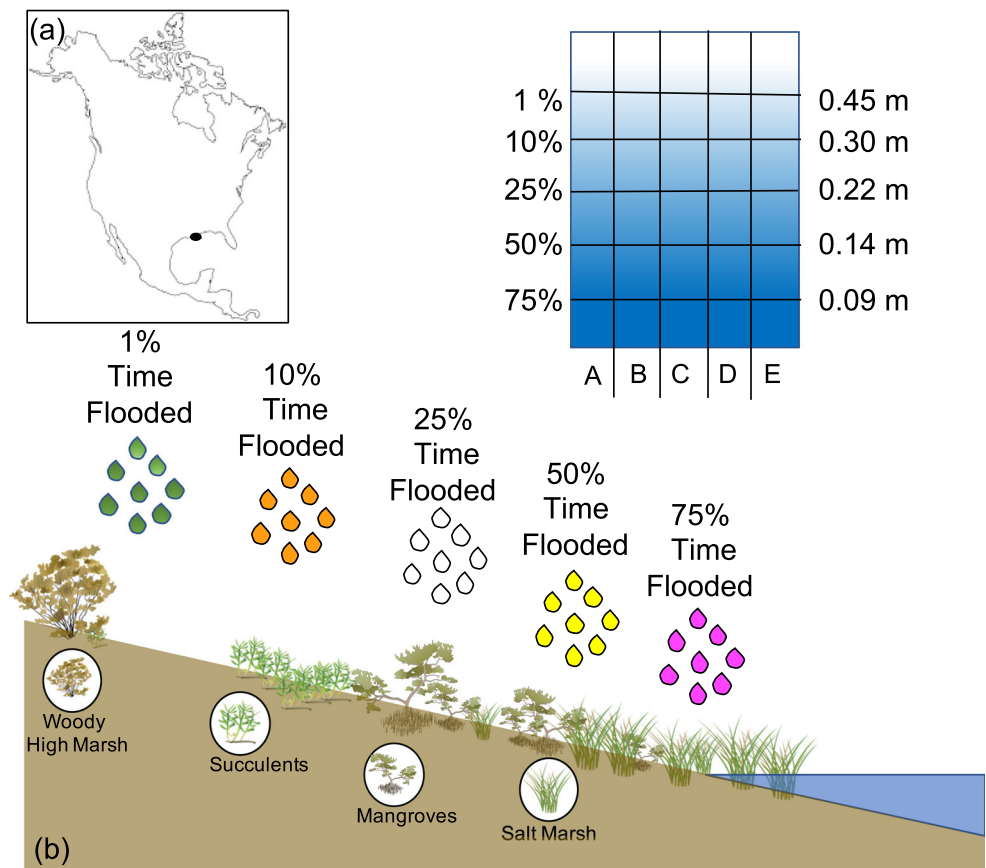
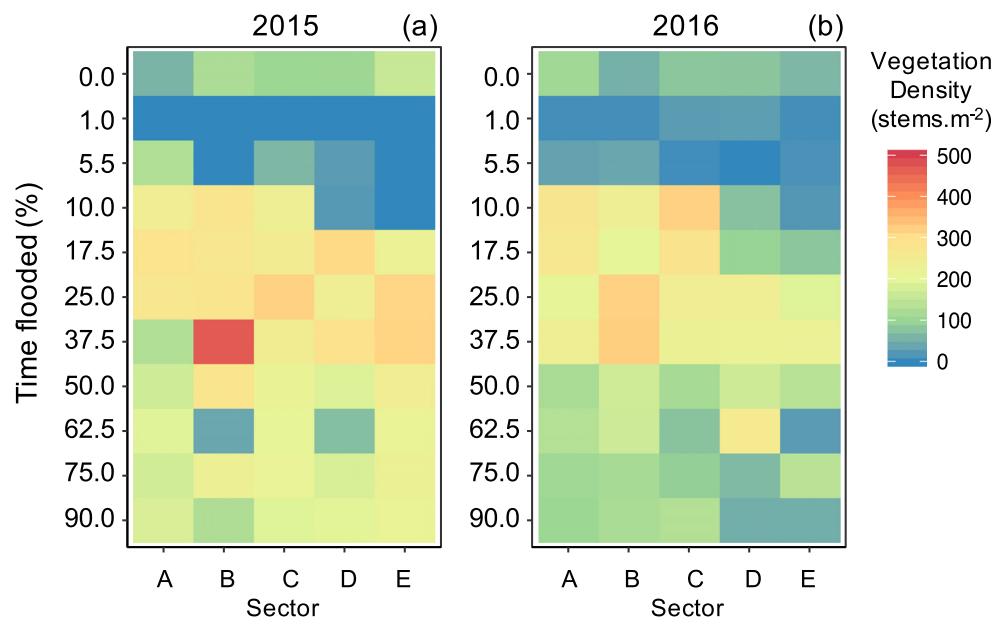


Fig. 2 Map of vegetation density (stems·m⁻²) with respect to the amount of time-flooded contours in 2015 (a) and 2016 (b) by sampling sector



Propagule Dispersal

During each field campaign, mangrove propagules were collected directly off of nearby trees, selecting mature, fully enlarged propagules. Pericarps were removed after a brief soaking period. Propagule exteriors were allowed to air dry and subsequently painted in sets of 500 with five different colors of spray paint (total = 2500 propagules), similar to Sousa et al. (2007-Appendix A) (methods and color specifics in A3 & A4). Propagules that did not shed their pericarps after the brief soaking period were discarded to ensure that all propagules were in their natural dispersal stage. Each set of 500 propagules were placed along their respective elevation contours during spring tides in both years and allowed to freely disperse (Fig. 2) (100 propagules per sector; ~4 cm spacing). Sampling of contours was completed at 1, 5, and 36 days (2015) and 1, 3, 18, and 31 days (2016) after initial placement throughout the study site. We also sampled a 50-m buffer surrounding the area to ensure all propagules remaining locally were located. Sampling utilized a methodical multi-person visual line search. Elevation, minimum distance traveled, and vegetation density and type were measured for each propagule located during each sampling. We determined propagule elevation using the previously described laser leveling techniques and related elevations to nearby benchmarks. Minimum distance traveled was measured using a range finder to determine distance from the propagule to the closest possible release point (TruPulse 200, Laser Technology Inc., Centennial, Colorado, USA). Vegetation type and density in 0.11-m² quadrats (0.33 × 0.33 m) centered on each propagule were also measured by counting individual salt marsh grass or succulent stems, mangrove pneumatophores, or mangrove stems. While salt marsh and mangroves have different

morphological features and succulent species (*Salicornia* spp. & *Batis maritima*) can have intricate branching and multiple stems, this site's succulents, grasses, and mangroves were generally small and often single-stemmed with limited branching. Propagules that dispersed out of the system were defined as exported and propagules preserved within our study system were defined as retained. Exported propagules did not include those that we estimated to have been lost due to predation (methods described below).

Propagule Predation and Buoyancy

To understand the potential implications of predation on propagule dispersal, retention, and export, we set out five paired sets of tethered propagules along each elevation contour, using dental floss attached to steel landscaping stakes during each sampling effort (one painted to match the elevation contour color, one unpainted) for a total of 50 propagules. Propagule presence/absence and predation damage were quantified at 35 days (2015) and 29 days (2016) (A5). Additionally, in a laboratory experiment, buoyancy of each paint color on propagules was also tested and compared to unpainted propagules (A4).

Propagule Establishment

We calculated local seedling establishment rates of naturally dispersed propagules by sampling 15 0.11-m² (0.33 × 0.33 m) quadrats per elevation contour 3 and 6 months after the 2016 sampling campaign. Seedlings, individuals 30 cm or less in height were counted as these plants are generally 2 years old or less in this system. Presence or absence of cotyledons was also noted.

Data Analyses

Data analyses included regression in a mixed-model framework using package “nlme” (Pinheiro et al. 2017) in R-Studio (Team RStudio 2017) to appropriately analyze our repeated measures design (Zuur et al. 2009) (Table 1). Dependent variables included propagules retained, estimated propagules lost to predation, propagules exported, and seedling density. The fixed portion of all models included either (1) sampling day, sampling campaign, and % time flooded and (2) month and % time flooded (seedling density model). The random portion of all models included sampling day nested within sampling campaign or plot identification nested within sampling month (seedling density). All random portions were utilized to appropriately account for the lack of independence between repeatedly measured experimental units (Zuur et al. 2009). Model selection was based on AICc values and eliminating non-significant model terms to form the simplest model.

For elevation, predation, and buoyancy experiments, analysis of variance and Tukey’s post-hoc tests were utilized. Independent variables included: % time flooded and sampling campaign for elevation analyses, sampling campaign and paint color for the buoyancy analyses, and sampling campaign, % time flooded, and paint color for predation analyses. Dependent variables included: elevation and observed % time flooded for the elevation experiment, number of days propagules remained buoyant for the buoyancy experiment, and confirmed propagule predation, propagule removal, and estimated total propagule predation for the predation experiment.

Results

Propagule Dispersal

The number of propagules retained within the site declined exponentially in both sampling campaigns regardless of elevation (Fig. 3a; Table 1). Propagules that were placed at elevation contours of 10–75% of the time flooded displayed < 10% propagule retention at the end of their respective

campaign. Those at the highest elevation (1% time flooded elevation contour) also displayed an exponential decrease, but with a slower rate of decline compared to other elevations, with ~20% propagule retention after 36 days (Fig. 3a; Table 1). For those propagules not found in the system during each sampling date, a conservative 20% predation rate was estimated (data in present study) and the remainder were considered to have been exported from the immediate area to the broader landscape (Fig. 3b,c; Table 1). Both propagules lost to predation and exported propagules followed an increasing square root function regression over time and were positively influenced by the number of dispersal days, increased flooding, and their interaction (Fig. 3b,c; Table 1).

Those few propagules that were retained within the system generally stayed at their original elevation (Fig. 4), resulting in the majority of propagules to be found at or near the highest elevation at the end of both sampling campaigns (Fig. 5; Table 1). Propagule density was also highly variable over the course of both sampling campaigns (Fig. 5).

Propagule Predation and Buoyancy

Confirmed predation ranged from 0 to 40% (A5). Additionally, some tethered propagules were removed due to unknown causes (e.g., predation, tidal action, rotting). Using predation rates from several other studies to corroborate our findings (Patterson et al. 1997; Sousa and Mitchell 1999; Sousa et al. 2007), we conservatively estimated an average overall predation rate of 20% (overall predation rate = known predation rate + estimated rate of predation on propagules removed for unknown reasons from literature). The overall predation estimate did not differ by sampling campaign, paint treatment (painted or unpainted; paint color), or elevation contour (A5). Finally, buoyancy was not impacted by paint presence or color (A4).

Propagule Establishment

For propagule establishment, we fit a quadratic regression to estimate that seedling density was greatest at ~37% of the

Table 1 Mixed model regression types, model factors, F-statistics, and *p* values for all regression analyses

Metric	Regression type	Dispersal days	Elevation contour	Dispersal days × Elevation contour
Found	Exponential	$F_{1,6} = 26.3^{**}$	$F_{4,28} = 5.6^{**}$	$F_{4,28} = 3.3^*$
Herbivory	Square root	$F_{1,6} = 18.9^{**}$	$F_{4,28} = 9.7^{***}$	$F_{4,28} = 2.9^*$
Export	Square root	$F_{1,6} = 18.9^{**}$	$F_{4,28} = 9.7^{***}$	$F_{4,28} = 2.9^*$
Establishment	Quadratic	Month $F_{1,16} = 25.3^{***}$	Elevation contour ² $F_{2,16} = 7.0^{**}$	Month × Elevation contour ² $F_{2,16} = 5.23^*$

p* < 0.05, *p* < 0.01, ****p* < 0.001

Fig. 3 Number of propagules retained within site (a; circles, solid lines) on each observed sampling day for both sampling campaigns with exponential regression fit shown. Estimated predation (b; triangles, dotted lines) and export (c; squares, dashed lines) utilizing square root power function regression fit for sampling days for both sampling campaigns. See Table 1 for statistical information

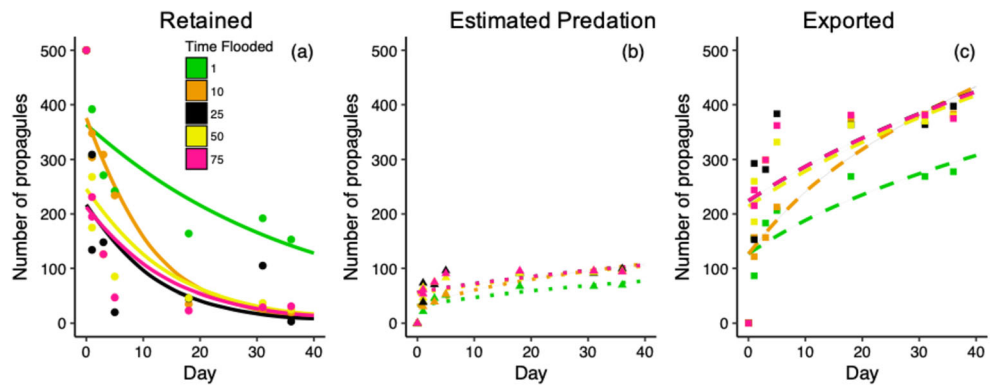


Fig. 4 Relative change in elevation by percentage of propagules across all times flooded for both field sampling campaigns. 2015 — Day 1 (a), Day 5 (c), and Day 36 (f), and 2016 — Day 1 (b), Day 3 (d), Day 18 (e), and Day 31 (g)

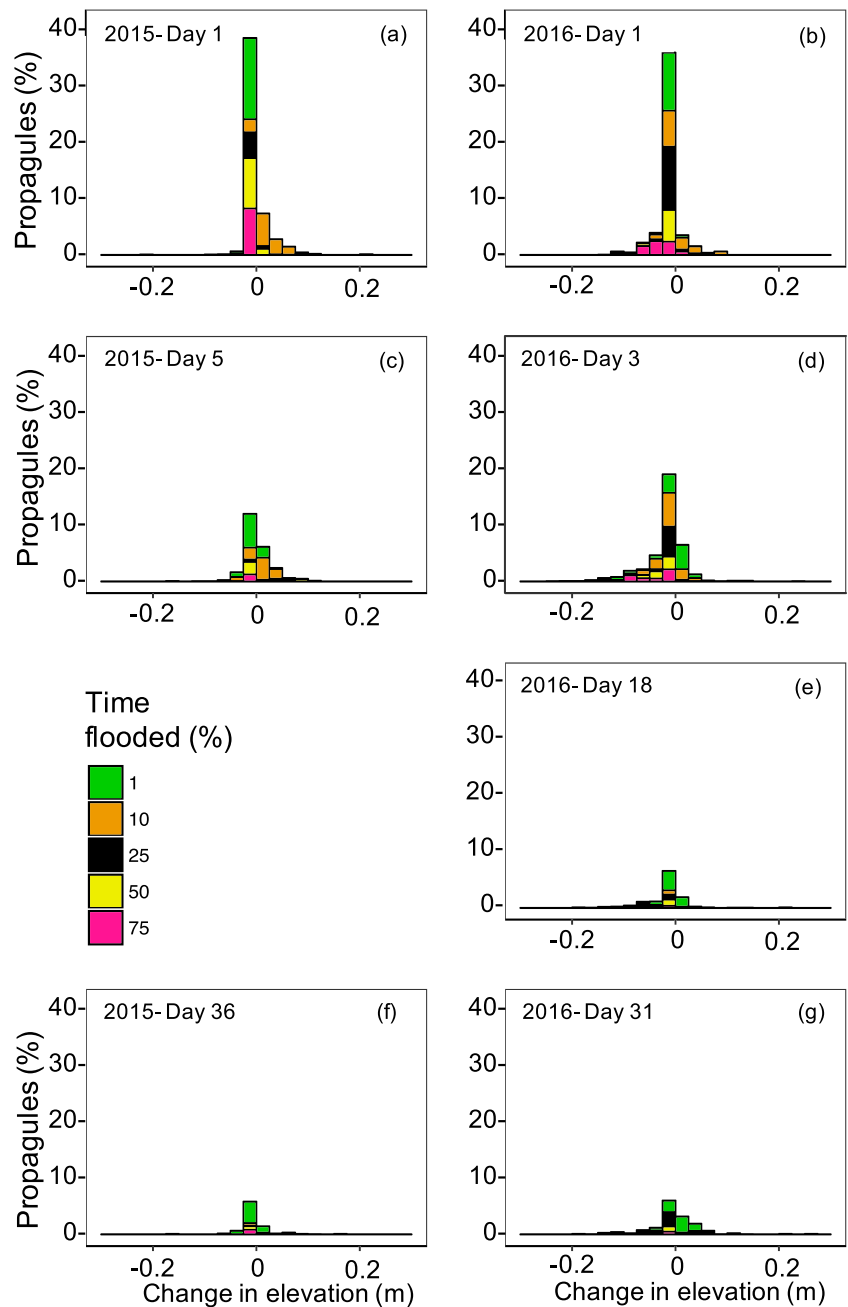
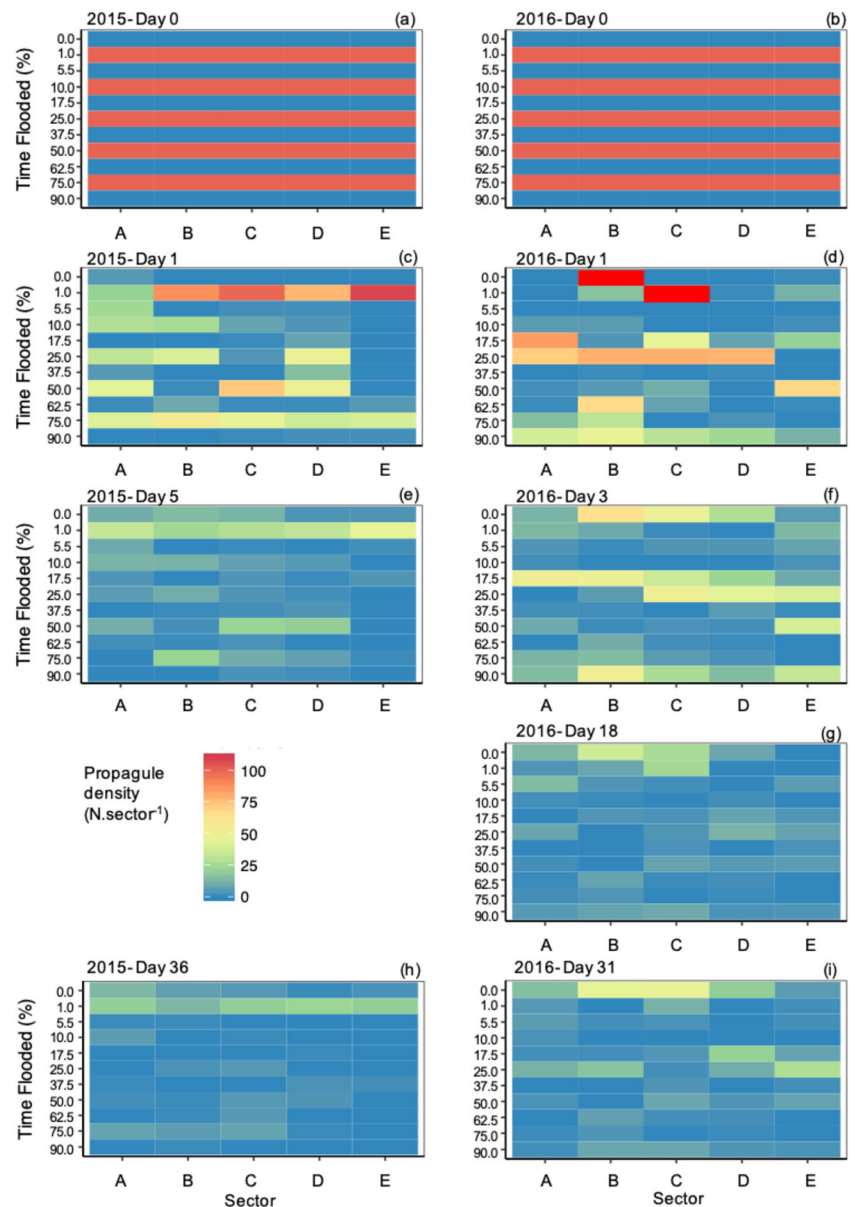


Fig. 5 Density map of number of propagules per partitioned sampling sector ($N \cdot \text{sector}^{-1}$) along time-flooded elevation contours for both field sampling campaigns. 2015 — Day 0 (a), Day 1 (c), Day 5 (e), and Day 36 (h), and 2016 — Day 0 (b), Day 1 (d), Day 3 (f), Day 18 (g), and Day 31 (i)



time flooded after 3 months (Table 1). After 6 months, total seedling density decreased and the peak density shifted to areas flooded $\sim 25\%$ of the time (Fig. 6).

Discussion

Dispersal is a key aspect of survival and range expansion of any species. In this study, we highlight the importance of understanding patch-level dispersal dynamics in mangroves along a flooding gradient. This system's singular mangrove species and distinctive propagules intermixed with the surrounding salt marsh species allow for dispersal to be studied within an ecotone at a species' range limit, something that would likely not be possible in systems with greater numbers

of species. Our results emphasize the dominance of propagule export out of the system and the disparity between propagule stranding and seedling establishment across a flooding gradient. This study highlights the importance of considering patch-level dynamics to predict future shifts by focusing on the existing ecotone.

Export and Predation

In the present study, $< 10\%$ of marked propagules were retained within the system after 1 month with the exception of propagules placed at the highest elevation, which were retained at a rate of $\sim 20\text{--}25\%$. The number of propagules retained within our site is much lower than most other mangrove dispersal studies, 60% in Belize after 4 weeks for

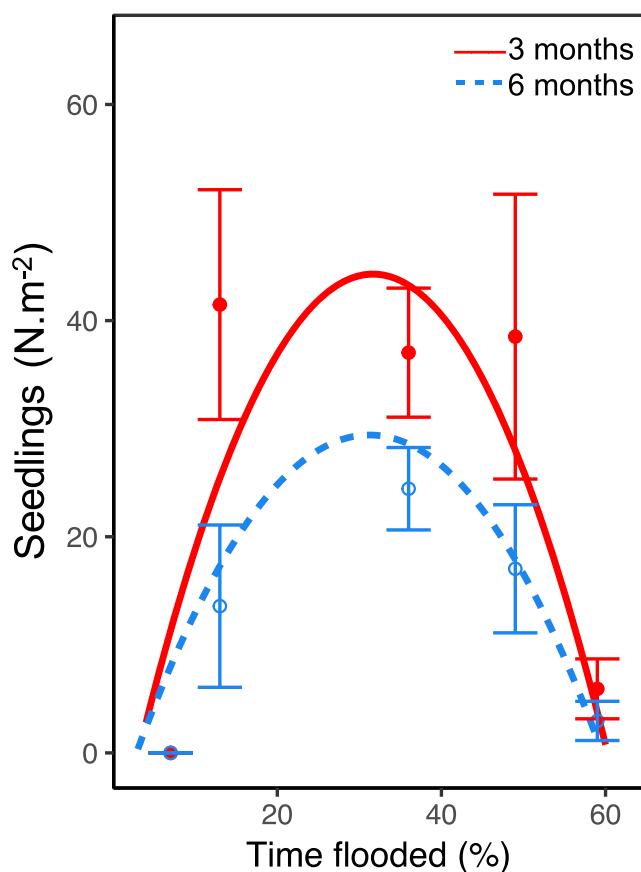


Fig. 6 Number of established seedlings per square meter ($\text{N}\cdot\text{m}^{-2}$) (mean \pm SE) with respect to time flooded (%) at 3 (red, solid line; quadratic model) and 6 (blue, dashed line; quadratic model) months after the second field campaign

A. germinans (Sousa et al. 2007), 85% for *Avicennia marina* after one high tide in Moreton Bay, Australia (Breitfuss et al. 2003), 48% and 85% for *Ceriops tagal* and *Rhizophora mucronata*, respectively, after 3 days in Kenya (Van der Stocken et al. 2015a), and in Florida, 60–70% after 6 weeks for *A. germinans* (Peterson and Bell 2015). However, some studies saw similar numbers, < 10% after 4 months for *Ceriops tagal* in northern Australia (McGuinness 1997b), 1–30% for *C. tagal*, and 15–65% for *R. mucronata* after 2 weeks in Kenya depending on release location (De Ryck et al. 2012), and ranging between 36 and 75% after 31 days for *R. mucronata* in Thailand (Komiyama et al. 1992). Alternative fates for mangrove propagules include export out of the system and predation (Van der Stocken et al. 2019). The effect of the natural vegetation was not explicitly tested as it could not be separated from the effect of flooding in our study, but would be of interest for future studies through both manipulative experiments and modeling efforts.

The majority of propagule loss (~70%) was estimated to be from those exported out of the system. Export in coastal wetlands and coastal waters is driven primarily by tides (Huiskes et al. 1995), dynamic nearshore currents (Siegel et al. 2008),

and wind (Feller and Sitnik 1996; Van Der Stocken et al. 2015b) at the landscape level. The importance of wind with significant winter storms is likely a key driver of propagule export in this system, as cold-front passages can drastically lower water levels in Louisiana's otherwise microtidal system (Hester and Mendelssohn 1989) and pull propagules away from the parent plant. Despite two sampling campaigns having different frequency and amplitude of high-water events and local weather conditions, rates of propagule retention and export did not differ. Thus, the mass export out of this system is likely due to both local- and landscape-level factors such as the generally low elevations and high inundation frequency that these wetlands exist at (De Ryck et al. 2012), the small size of *A. germinans* propagules (in comparison to large propagules such as many *Rhizophora* spp. or *Bruguiera* spp., thus possibly reducing entrapment) (Rabinowitz 1978; De Ryck et al. 2012), the large impact of a few high water or storm events (Van der Stocken et al. 2019), and the close proximity of this patch to a tidally connected body of water (Breitfuss et al. 2003).

The observed export of propagules provides a possible mechanism for moderate and long-distance dispersal (Huiskes et al. 1995) that may be important at larger temporal and spatial scales (Duke et al. 1998; De Ryck et al. 2012), although their ultimate fate is difficult to truly understand (Van der Stocken et al. 2019). This strategy of mass export, however, is stochastic and successful dispersal and establishment are likely sporadic (Alleman and Hester 2011a; reviewed by Van der Stocken et al. 2019). We observed large numbers of propagules floating in the water column in the greater study area, particularly at the mouth of tidal creeks on outgoing tides (per. obs.). Other studies have found exported propagules at ranges from 10 m to 10 km from study sites (e.g. Clarke 1993). While the current study could only account for patch-level export, as we were unable to expand our search to the broader landscape, the large number of propagules exporting out of this system empirically supports the mass export dispersal strategy of mangroves at their range limits. Furthermore, increased propagule production at the latitudinal limit has been found in other mangrove species (Dangremond and Feller 2016), but has yet to be examined in *A. germinans*. Mass export is likely to play a key role in the expansion of species at range limits and ecotones as species realize their new climatic envelope (sensu Box 1981; Pearson and Dawson 2003; Corlett and Westcott 2013) with global climate change. There is a need to better understand limitations to mangrove dispersal and establishment within and beyond their current range limit. Recent research has highlighted the role hurricanes play in a significant poleward mangrove expansion (Rodriguez et al. 2016), and has provided a greater mechanistic understanding of temperature thresholds at range limits (Krauss et al. 2008; Osland et al. 2019).

Predation of propagules is another potential mechanism of propagule loss in our study. We conservatively estimated that 20% of propagules were lost due to predation, regardless of propagule elevation. These rates are similar to other *A. germinans* predation studies which reported 11% predation in Louisiana (Patterson et al. 1997), ~20% in Belize (Sousa et al. 2007), 25% in Panama (Sousa and Mitchell 1999), and 10–40% for *A. marina* in southeastern Australia (Clarke 1993). Higher rates of predation (60–100%) have been reported for *Avicennia* spp. elsewhere in the literature (Smith et al. 1989, McKee 1995b, McGuinness 1997a, Van Nederveelde et al. 2015, reviewed by Van der Stocken et al. 2019). While we only observed propagule damage and relocation of propagules to nearby crab burrows (pers. obs.), predators of *A. germinans* propagules in Louisiana have previously been identified as the square back marsh crab (*Armases cinerum*) and the marsh periwinkle (*Littorina irrorata*) (Patterson et al. 1997). The small size, proportionally large, nutritious cotyledons, and low levels of defense compounds make *Avicennia* spp. propagules highly palatable (McKee 1995a) and suitable in size for consumption by common predators (Smith 1987).

Retention and Local Dispersal

Despite mass export, those propagules that were retained within the local patch did not move significantly up or down slope (Fig. 4). This lack of movement has been reported in other halophytic coastal plants (Huiskes et al. 1995; Rand 2000; Sousa et al. 2007). Other studies have shown the importance of propagule trapping and facilitation by surrounding vegetation in both mangrove and nearby marsh species (McKee et al. 2007; Peterson and Bell 2012; Guo et al. 2013; Peterson and Bell 2015). While our study did not explicitly examine the impact of vegetation, no patterns of clustering were observed at the highest vegetation densities (250–350 stems m^{-2} at ~25% time flooded) (Fig. 5) within the natural vegetation. As described above, this limitation elicits the need for explicit experimental work to disentangle vegetation and hydrology impacts. Regardless, the differences between our study and others' highlight the possible shift from vegetation trapping at short time scales (i.e., days) on mangrove propagules to hydrological influences at intermediate time scales (i.e., months). Additionally, it is also important to account for the impact of small stature vegetation, small propagule size, the relative position in the tidal frame, and proximity to tidal channel, as previously mentioned (Breitfuss et al. 2003; Van der Stocken et al. 2019).

A comprehensive understanding of hydrology at intermediate time scales and a patch's position in the broader landscape is needed to understand dispersal dynamics. The ability to track exported propagules is an imperative next step, but often challenging at patch- to landscape-levels and often relies

on modeling efforts (Van der Stocken et al. 2019). Understanding establishment barriers and mechanisms at eventual stranding locations is another key component that also remains to be examined at and beyond the current latitudinal limit (although see Pickens et al. 2018). The opportunity for successful establishment is not without long-term risk as genetic isolation, population bottlenecks (Kennedy et al. 2017; Binks et al. 2019), and potentially stressful conditions (abiotic and/or biotic) (Clarke et al. 2001; Louthan et al. 2015) may hinder colonization efforts. The needed understanding of dispersal and establishment dynamics at patch- and landscape-scales is also imperative to inform restoration in coastal wetlands especially if practitioners aim to release propagules, as it may be far more effective to allow for natural dispersal if nearby source populations exist (Lewis 2005).

The few propagules that were retained within the system were primarily those retained at or dispersed to the highest elevations, and followed a similar pattern of stranding on ebb tides as seen by Clarke (1993). This highest elevation was too high in the tidal frame for successful establishment, and propagules were often observed to be desiccated after the first few sampling days as environmental conditions were not suitable (Balke et al. 2011). The seedling establishment experiment confirms our initial observation that the highest elevations were too high for survival (Fig. 6), with no seedlings present at these elevations likely due to a lack of tidal inundation, hypersalinity, water stress, and possibly seedling predation (Clarke and Allaway 1993; Clarke and Myerscough 1993; Patterson et al. 1997; Clarke and Kerrigan 2002).

Observed seedlings and peak seedling densities were generally midway through the intertidal zone, with peak locations receiving daily inundation on most tidal cycles, and hydroperiods similar to values reported for both seedlings and adults by Alleman and Hester (2011a) and Guo et al. (2013). The contraction of the area under the curve and shift in the peak for seedling density (Fig. 6) between the 3- and 6-month sampling periods paired with the location of dispersed propagules highlights the survival dynamics for *A. germinans* from dispersal, to establishment, to survival in the propagule and seedling stages. This also elucidates the huge reproductive effort of *A. germinans* in this location, its low rate of successful establishment (potentially less than 1 in 500 propagules), and suggests that future studies consider utilizing more propagules to adequately understand dispersal and establishment. The disconnection between dispersal location and establishment of propagules in this study also highlights the need to better understand suitable conditions in the field for propagule establishment, particularly in areas at and beyond current range limits to better inform future projections. While work highlighting differences between the elevation of seedlings and adults has occurred at the ecotone (Alleman and Hester 2011b), the processes controlling propagule arrival and establishment at moderate scales beyond the current range

limit will provide an understanding of possible feedbacks, limitations, and bottlenecks beyond temperature, particularly in areas that are undergoing erosion, subsidence, and other processes resulting in lower elevations.

Summary

Our study addresses the importance of understanding dispersal dynamics at the patch scale and following them for at least a month. In this system and at this scale, propagule export is high, with those propagules that are retained generally persisting at their original elevations. Furthermore, our findings demonstrate the dominant role of hydrology and landscape position in structuring dispersal dynamics in this system at a month-long time scale. This difference, compared to other studies, highlights the importance of scale on factors influencing propagule dispersal and how the relative importance of hydrology differs through time and across environmental gradients. With shorter time scales and smaller areas, different drivers are likely to control dispersal [microtopography, vegetation structure/height, storm events, wave height, time flooded (%), predation rates] compared to intermediate time- and patch-level scales [time flooded (%), predation rates] (similar to Gosz 1993). Vegetation, hydrology, and storm/wind events influencing dispersal dynamics are likely to be temporally and spatially dependent (Morton et al. 2018), so an adequate understanding of processes must be scale-dependent. As retained propagules were primarily found at elevations not suitable for establishment, mangroves in this system likely produce a vast number of propagules in order to disperse into suitable habitat and establish in appropriate windows of time (Alleman and Hester 2011b; Balke et al. 2011). Thus, the mechanisms and potential rates of mangrove expansion into incumbent marsh habitat are likely different depending on the scale being examined. We believe that the information within our study can improve mangrove expansion models by allowing them to move beyond reliance on temperature limits alone. Further, we elucidate the need to adequately parameterize both patch and local dynamics, while also accounting for scale-dependent interactions with mangrove propagule expansion at and within the salt marsh-mangrove ecotone. There is additionally a need to incorporate stochastic events into modeling efforts, such as hurricanes and freezes (Rodriguez et al. 2016), to explore how those events influence dispersal dynamics at local, patch, and landscape scales. By achieving greater insights into dispersal and establishment factors at patch-level scales, a more mechanistic understanding of expansion dynamics is possible at this latitudinal range limit when appropriately paired with propagule ecophysiological tolerances, mangrove population genetics studies, and modeling efforts.

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