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Negative indirect effects of hurricanes on recruitment of range-expanding mangroves

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ABSTRACT: Disturbances often have positive, direct effects on invasions by dispersing propagules or creating environmental conditions that favor invasive species. However, disturbances that alter interactions between resident and invading species could also affect invasion success. In northeast Florida, the black mangrove *Avicennia germinans* is expanding into salt marshes, where it interacts with the dead litter (wrack) of the native marsh cordgrass *Spartina alterniflora*. From 2015–2017, we performed monthly surveys before and after 2 hurricanes in 3 marsh microhabitats (bare sediment, vegetation, wrack) to quantify mangrove propagule and seedling densities. Wrack increased propagule retention up to 10 times relative to other microhabitats. Hurricanes did not directly harm mangrove propagules or seedlings. However, storm surge relocated wrack to upland environments, which indirectly inhibited mangroves by temporarily disrupting the facilitative effects of wrack on propagule recruitment and exposing intertidal bare patches that decreased propagule retention and seedling establishment. Wrack remained absent from intertidal areas for 1–3 mo. Because hurricane season overlaps with propagule recruitment, hurricane timing and wrack return time to intertidal areas influence the degree that hurricanes disrupt wrack–mangrove interactions. We demonstrate that large-scale disturbances can negatively and indirectly affect invader recruitment by altering interactions with resident species.

KEY WORDS: Hurricane · Indirect effects · Dispersal · Range expansion · Disturbance · Mangrove · Wrack · Salt marsh

1. INTRODUCTION

Disturbances are often positively associated with the establishment and spread of invasive species (Lockwood et al. 2013, Jauni et al. 2015). Disturbances that remove or damage resident species can facilitate invasion by creating empty niches and lessening competition with resident species (Sousa 1984, Besaw et al. 2011). For example, wind, lightning, or logging disturbances create canopy gaps in forested landscapes that increase light availability and promote plant invasion (Appleby 1998, Gravel et al. 2010). Similarly, disturbances can also aid invader establishment by removing native predators, parasites, or competitors that provide biotic resistance to invasion (Kotanen 1997, Lafferty & Kuris 2005) or by creating environmental conditions that favor invaders over natives (Byers 2002, Ruhí et al. 2016). Disturbances can also disperse exotic propagules to new locations and facilitate their colonization of previously inaccessible areas; for instance, floods transport invasive plant seeds to new riparian plant communities (Thébaud & Debussche 1991). Although positive associations between disturbance and invasion are well-documented, disturbance can also impede invasion by harming invaders, hindering their dispersal, or perhaps by disrupting facilitative interactions with resident species (Smith & Knapp 1999, Flynn et al. 2010).

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Hurricanes are large-scale disturbances that can facilitate invasive species by increasing dispersal and enhancing establishment (Diez et al. 2012). Hurricanes disperse plants and animals long distances through extreme movements of wind and water (Censky et al. 1998). For example, hurricane disruption of ocean currents transported invasive lionfish larvae across the straits of Florida (USA) to the Bahamas (Johnston & Purkis 2015). Hurricanes can also facilitate species establishment and spread by increasing resource availability or reducing biotic resistance (Bellingham et al. 2005, Bhattarai & Cronin 2014). For example, after Hurricane Andrew, increased light availability in disturbed canopy gaps enabled non-native plant species to invade Florida hardwood forests (Horvitz et al. 1998). Although many studies show that hurricanes facilitate species invasions (Lynch et al. 2009, Steiner et al. 2010, Henkel et al. 2016), a few examples demonstrate that hurricanes can also hinder invasion by increasing invader mortality (Palmer et al. 2007, Flynn et al. 2010). We suggest that hurricanes could further inhibit invasion by limiting dispersal or disrupting facilitative interactions between residents and invaders.

Mangroves are expanding into salt marshes along the northeast Florida coast (Cavanaugh et al. 2014), and this system provides an opportunity to examine effects of hurricane disturbance on an ongoing species invasion. Specifically, hurricanes could alter recruitment of the range-expanding black mangrove *Avicennia germinans*, deposition patterns of the dead litter (wrack) of the resident salt marsh species *Spartina alterniflora*, and the association of these 2 species. Here, recruitment refers to the process by which unrooted, buoyant mangrove propagules establish in high intertidal habitats. At the leading edge of the mangrove expansion, estuarine tides and currents deposit both mangrove propagules and salt marsh wrack in high intertidal salt marsh habitats (Smith et al. 2018); aggregations of propagules and wrack often mark the location of the high tide water line. Wrack alters local light, moisture, and salinity conditions (Brewer et al. 1998, Pennings & Richards 1998, Tolley & Christian 1999), and facilitates mangrove establishment by rafting mangrove propagules into the marsh and retaining them in place until they root (Smith et al. 2018, Smith 2019). Hurricanes can relocate large quantities of wrack to upland environments (Gunter & Eleuterius 1971, Hackney & Bishop 1981), and we hypothesized that hurricane storm surge could directly disrupt mangrove recruitment by moving wrack and associated propagules to upland environments that are outside of propagules' environmental niche. We also expected that wrack removal could indirectly inhibit mangrove propagules by decreasing propagule retention if wrack is no longer present in intertidal areas to facilitate propagules (Smith et al. 2018). Furthermore, because wrack smothers underlying vegetation in the high intertidal, wrack removal could expose bare patches without vegetated structure. This unfavorable bare microhabitat could retain fewer propagules and reduce seedling establishment relative to vegetated areas.

To examine how hurricane disturbances affect mangrove recruitment, salt marsh wrack deposition, and the association of mangroves and wrack, we performed monthly field surveys before and after 2 hurricane landfalls. We counted mangrove propagules and seedlings in different salt marsh microhabitats in invaded (adult mangroves present) and uninvaded (no adult mangroves) salt marshes in northeast Florida from 2015 to 2017. Overall, these surveys quantified how 2 hurricane disturbances affect invader recruitment and establishment via direct and indirect effects on interacting resident and invading species.

2. MATERIALS AND METHODS

2.1. Site selection

We identified 4 sites located within a 20 km stretch of the Matanzas River estuary, St. Augustine, Florida, that had distinct wrack lines in high intertidal salt marshes (Table S1 & Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m644p065_supp.pdf). The Matanzas Estuary encompasses the present northern edge of the range-expanding black mangrove's distribution (Williams et al. 2014). Black mangroves were the only mangrove species present at our field sites, and within the estuary there is local scale variation in black mangrove invasion of salt marshes. We divided 3 of the sites into 5000 m^2 paired blocks of mangrove invaded (adult mangroves present) and uninvaded salt marsh areas (no adult mangroves present) that were separated by 50–1000 m (Fig. S2 in the Supplement). The predominant plant species in both areas was the marsh cordgrass *Spartina alterniflora*; invaded areas also contained at least 100 m^2 of adult mangrove vegetation. The fourth site included only an invaded area because no comparable uninvaded area was located within 1000 m.

2.2. Baseline surveys

In 2015, we established perpendicular transects from the upland forest to the lower marsh edge at all sites. To spread sampling effort across the entire study area, we spaced 5 transects at 10 m intervals in the invaded and uninvaded areas of each site. We marked transect starting points where the high marsh met the upland forest edge for future resampling (Fig. S2). We then collected all wrack present in one 0.25 m^2 quadrat from where the dominant wrack line intersected each perpendicular transect in invaded and uninvaded areas at 1 site each in August and December 2015 (Sites 1 and 2; Table S1). We dried the wrack at 70°C until the samples reached a constant mass (7–14 d) and weighed the dry mass. We also measured the wrack line distance to the upland (WDU) at each point where the dominant wrack line intersected with the perpendicular transects. In November 2015, we also placed a transect parallel to the water's edge along the dominant wrack line and sampled mangrove propagules in 0.25 m^2 quadrats from wrack and adjacent vegetated microhabitats along each horizontal transect line at the same 2 sites (n = 10 per area at Site 1; n = 5 per area at Site 2; Fig. S2). For the wrack quadrats, we collected, dried, and weighed salt marsh wrack biomass as described above.

2.3. Hurricanes Matthew and Irma

Florida has had the most direct hurricane hits of any US state, and hurricanes disturb the Florida coast on a time scale of years to decades (Blake & Gibney 2011). In October 2016, Hurricane Matthew moved from the tropical Atlantic up the east coast of Florida and brought winds of 135–170 km h^{-1} to the northern Florida region. The Matanzas River measured a record-high storm surge of 2.13 m above mean higher high water (MHHW) (Stewart 2017). Eleven months later in September 2017, Hurricane Irma made landfall in southwestern Florida and passed through central Florida into southeast Georgia. On the northeast Florida coast, winds of up to 80 km h^{-1} created storm surge that measured 1.46 m above MHHW at the Matanzas River (Cangialosi et al. 2018).

2.4. Post-hurricane surveys

Storm surge from Hurricane Matthew arrived at our field sites on 7 October 2016. Starting on 22 October 2016, we conducted monthly field surveys of salt marsh wrack and mangrove propagule abundance until December 2017. Storm surge from Hurricane Matthew removed salt marsh wrack from the intertidal zone and left behind bare areas at each site that demarcated where the wrack line had smothered and killed the underlying vegetation (Fig. 1a,b). For all sites, we measured the pre-Matthew WDU (m) at each point where a bare patch intersected with the permanent perpendicular transect lines from the 2015 baseline surveys to establish a WDU that was specific to each site and transect line (Table S1, Fig. S2). We then examined (1) mangrove propagule retention and seedling establishment in intertidal microhabitats where wrack had been removed by the hurricane and (2) mangrove propagule retention in new wrack lines deposited after Hurricane Matthew.

To target microhabitats where Hurricane Matthew removed wrack from intertidal areas, 2 wk after the hurricane we established 30 × 1 m fixed horizontal transects along the pre-Matthew wrack line in both invaded and uninvaded areas. We counted mangrove propagules in 0.25 m^2 quadrats haphazardly placed in patches of bare sediment and adjacent vegetation (n = 10 each) along each fixed transect (Fig. S2). Beginning in January 2017, we also counted mangrove seedlings from the 2016 propagule cohort that established after Hurricane Matthew in the quadrats. We identified seedlings as members of the 2016 cohort based on the number of stem nodes and the presence of cotyledons in the months after establishment.

We also sampled within new intertidal wrack deposits to assess wrack characteristics and to examine the association between salt marsh wrack and mangrove propagules. In contrast to the measurements taken from bare and vegetated patches along the fixed horizontal transect line, the location of this wrack sampling shifted between sampling events based on the location of the dominant wrack line. If more than 1.5 m^2 of new wrack was present, we counted mangrove propagules in 0.25 m^2 quadrats (n = 5) placed haphazardly along a transect set up along the newly deposited wrack line (Fig. 1c,d; Fig. S2). Transect length varied based on the length of the wrack line, but did not exceed 30 m.

To quantify properties of the newly deposited salt marsh wrack, we collected, dried, and weighed the wrack biomass for each quadrat as described above. We also recorded the maximum wrack depth (cm) of each wrack line in each invaded and uninvaded area and the new WDU of each wrack line where it intersected with permanent perpendicular transect lines

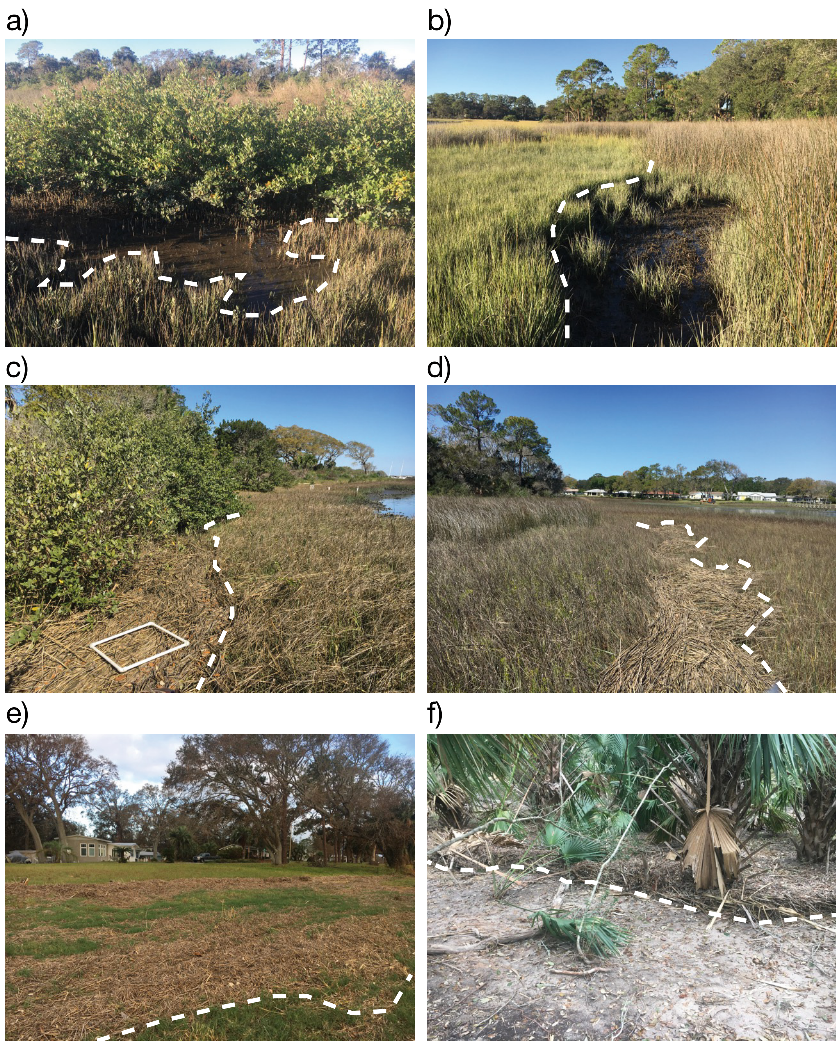

Fig. 1. Bare patches left behind after wrack removal by Hurricane Matthew in (a) mangrove-invaded and (b) uninvaded salt marsh areas. Wrack lines that returned in March 2017 after Hurricane Matthew for (c) invaded and (d) uninvaded salt marsh areas. Wrack lines deposited in upland (e) residential and (f) terrestrial forest habitats after Hurricane Irma. Dashed lines mark the lower edge of the wrack lines. Photos by R.S. Smith

established during the 2015 baseline surveys. When storm surge from Hurricane Irma arrived at our field sites on 11 September 2017, it deposited large wrack lines landward from the marsh (Fig. 1e,f). Thus, during our post-Irma sampling event on 21 September 2017, we sampled both the hurricane-deposited wrack line in the upland and wrack lines that had been deposited in intertidal areas in the 10 d since Irma.

2.5. Analysis

We used the 'lme4' package in R (version 3.5.2) to create separate generalized linear mixed models to examine propagule abundance as a function of microhabitat (bare sediment, vegetated, wrack) for the invaded and uninvaded areas during the peak propagule recruitment season (October to December) for each year (2016, 2017) (Bates et al. 2015, R Core Team 2017). We defined the peak recruitment season as months where propagules were present at all sites. Wrack was absent from all sites during the 2016 propagule recruitment season, so we only assessed bare sediment and vegetated quadrats for 2016. For seedlings, we analyzed differences in abundance for January 2017 (i.e. after the 2016 propagule recruitment season) as a function of microhabitat (bare sediment, vegetated) using 2 separate generalized linear mixed models for the invaded and uninvaded areas. We fit all propagule and seedling abundance models with Poisson distributions, tested for overdispersion, and re-fit the models with negative binomial distributions if the data were overdispersed. All models included site as a random intercept.

To assess variation in wrack deposition location based on marsh invasion status, we used a linear mixed model fit with a Gaussian distribution to examine pre-Matthew WDU as a function of marsh invasion status (invaded, uninvaded), including site as a random intercept. We also used linear mixed models to examine whether the wrack lines deposited in the terrestrial upland during Hurricane Irma differed from wrack lines deposited in intertidal areas at the prior sampling date (August 2017) in terms of wrack biomass density, change in wrack line distance from the upland (ΔWDU), and wrack depth. To examine whether wrack was deposited in similar locations before and after hurricanes, we calculated ΔWDU from the pre-Matthew WDU measured along the same perpendicular transect line to relativize each new wrack line to the location of the pre-Matthew wrack line. Measuring ΔWDU from its original position on each transect line accounted for locally influential factors related to transect location and site characteristics. We fit a separate model for invaded and uninvaded areas for each wrack response variable (biomass density, ΔWDU, depth) as a function of wrack line location (intertidal marsh, terrestrial upland). We fit each model with a Gaussian distribution and included site as a random intercept. We checked residual plots and where necessary, square root transformed wrack response variables to meet assumptions of normality and homogeneity.

3. RESULTS

Propagule abundance exhibited a distinct seasonality that began in September, peaked from October to December, and then ended in January (Fig. 2a). Mangrove propagules and seedlings were more abundant in invaded areas compared to uninvaded areas (Fig. 2). Propagule abundance also varied by microhabitat. In fall 2016, wrack was not present in

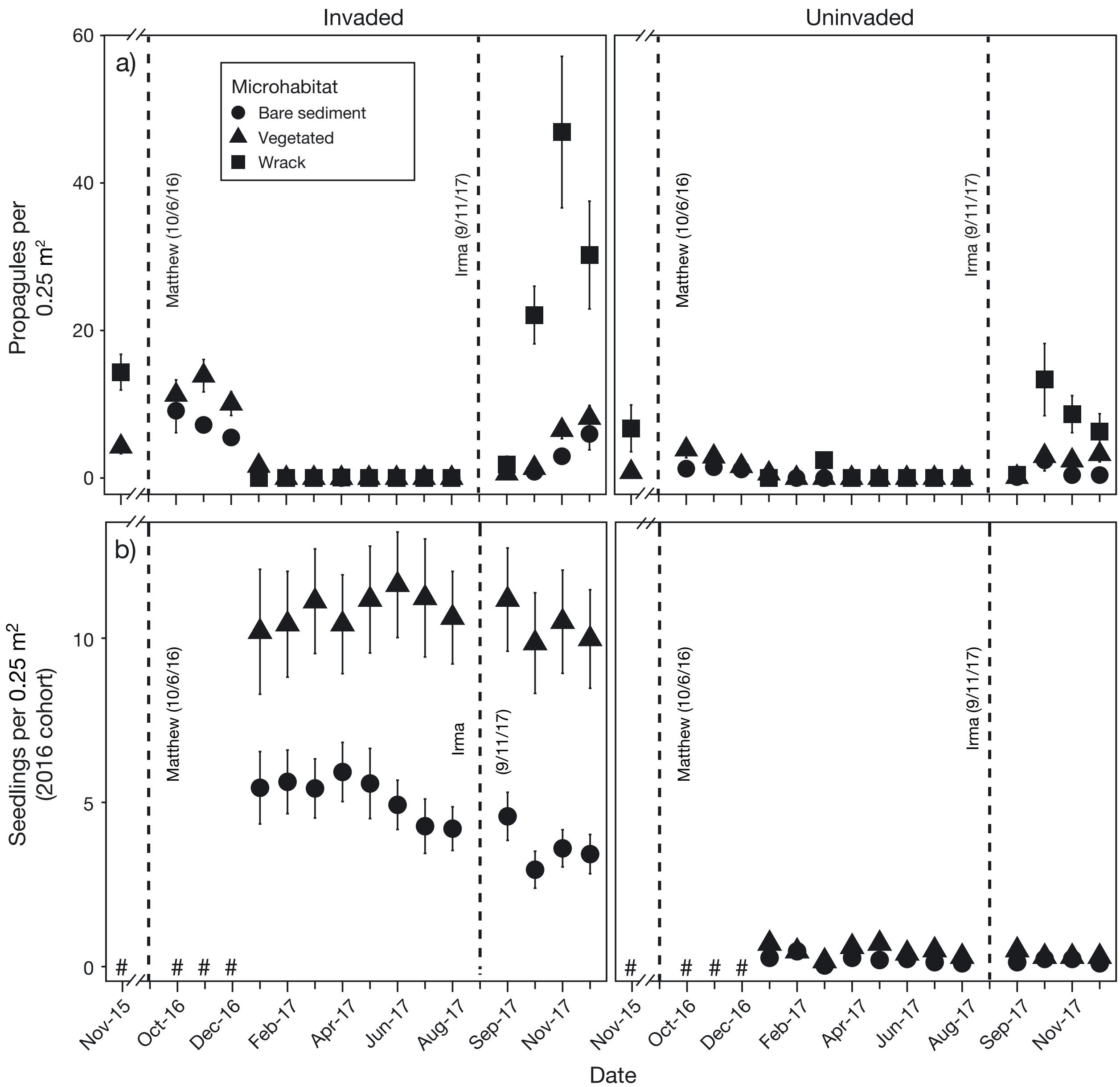

Fig. 2. Means ± SE of mangrove (a) propagules and (b) seedlings in 0.25 m^2 quadrats in intertidal microhabitats from monthly surveys in 4 mangrove-invaded and 3 uninvaded areas for 15 mo following Hurricane Matthew (vegetated, n = 10; bare sediment, n = 10; wrack deposits, n = 5 per area per month). All seedlings are from the 2016 propagule cohort, and we did not collect seedling data from October to December 2016 (pound signs, #). We did not collect seedling data from wrack microhabitats. Dashed lines represent the timing of Hurricanes Matthew (6 October 2016) and Irma (11 September 2017)

intertidal locations, and about twice as many propagules were present in vegetated patches compared to bare patches in both invaded (χ^2 = 12.59, df = 1, p = 0.00039) and uninvaded areas (χ^2 = 8.50, df = 1, p = 0.0036; Table S2). Wrack was present during the propagule recruitment season in fall of 2017; propagules were 6 to 10 times as abundant in wrack compared to bare or vegetated patches in invaded areas (χ^2 = 205.28, df = 2, p < 0.0001; Table S2) and 3 to 9 times more abundant in wrack in uninvaded areas (χ^2 = 72.85, df = 2, p < 0.0001; Table S2). In January 2017, twice as many seedlings were present in vegetated patches compared to bare patches in invaded (χ^2 = 7.38, df = 1, p = 0.0066) and uninvaded areas (χ^2 = 5.61, df = 1, p = 0.018); however, overall seedling abundance was low in uninvaded areas (<1 seedling per 0.25 m^2; Table S2). Seedling abundance of the 2016 cohort was maintained throughout the year (Fig. 2b; Table S2).

Before Hurricane Matthew, wrack in invaded areas was deposited on the waterward edge of adult mangrove vegetation, whereas wrack in uninvaded areas was deposited at the upland border between high marsh and forest vegetation. Thus, wrack in invaded areas was deposited significantly farther from the upland (41.59 ± 6.12 m; mean ± SE) relative to uninvaded areas (13.69 ± 2.36 m; mean ± SE; χ^2 = 37.25 df = 1, p < 0.0001; Table S1). In October 2016, Hurricane Matthew relocated wrack from intertidal areas to upland terrestrial locations at all sites (Fig. 1e,f), although we did not quantify these upland deposits. Wrack did not return to salt marsh areas until January 2017 (Fig. 3a). Wrack accumulated regularly throughout the rest of the year, and its location was nearly identical to the pre-Matthew WDU until September 2017, when storm surge from Hurricane Irma again exported wrack from the intertidal (Fig. 3a). Irma established a new wrack line 42.05 ± 13.12 m (mean ± SE) landward from the pre-Matthew WDU in invaded areas and 33.72 ± 5.80 m landward from the pre-Matthew WDU in uninvaded areas (Fig. 3a). These hurricane-deposited wrack lines were located 12.68 ± 6.65 m landward from the upland-marsh edge in invaded areas and 15.90 ± 4.13 m landward from the upland-marsh edge in uninvaded areas in terrestrial forest, roadside, and residential locations (Fig. 1e,f). This new wrack line was located significantly upland relative to the previous month's wrack line location in invaded (χ^2 = 22.01, df = 1, p < 0.0001) and uninvaded areas (χ^2 = 46.75, df = 1, p < 0.0001). We also collected more than 3 times the wrack biomass density from the hurricane-deposited upland wrack line compared to the previous month's intertidal wrack line in both invaded (χ^2 = 9.55, df = 1, p = 0.002) and uninvaded areas (Fig. 3b; χ^2 = 31.01, df = 1, p < 0.0001). The upland wrack line was also more than 6 times deeper than the prior month's intertidal wrack line in invaded areas (χ^2 = 6.47, df = 1, p = 0.011) and more than 2 times deeper in uninvaded areas (Fig. 3c; χ^2 = 8.42, df = 1, p = 0.0037). New wrack was deposited in intertidal areas within 2 wk of Irma (Fig. 3).

4. DISCUSSION

Although disturbances are well known to directly and positively affect invasions, we found that hurricanes can negatively and indirectly affect an ongoing invasion. Black mangrove propagule recruitment, resident salt marsh wrack deposition, and the Atlantic hurricane season temporally and spatially overlap in northeast Florida. We found that salt marsh wrack retained up to 10 times more mangrove propagules relative to vegetated and bare intertidal microhabitats. However, hurricane storm surge exported salt marsh wrack from intertidal locations and deposited it in the terrestrial upland. Although hurricanes did not appear to directly affect mangrove propagules or uproot seedlings, they indirectly influenced propagule and seedling success by removing wrack from intertidal areas. Wrack was no longer present in the intertidal to retain mangrove propagules in high abundance after hurricanes, and the export of wrack to the upland uncovered intertidal bare patches that retained fewer propagules. Reduced propagule retention likely contributed to lower seedling densities in bare patches in subsequent seasons relative to vegetated habitats. The magnitude of hurricane effects on the mangrove expansion likely depends on the amount of time that wrack is absent from intertidal areas.

The Atlantic hurricane season lasts from 1 June to 30 November, and most hurricanes occur in September and October (Blake & Gibney 2011), which coincides with mangrove recruitment and salt marsh wrack deposition. Mangrove propagule recruitment began in September, peaked from October to December, and ended in January, which matches the timing of the propagule recruitment season in other North American temperate areas (Van der Stocken et al. 2017). We expected that the coincident timing of hurricanes and propagule recruitment would directly inhibit propagule dispersal by transporting mangrove propagules to inhospitable upland environments, especially for the abundant propagules associated with wrack. However, for the 2 storms that we

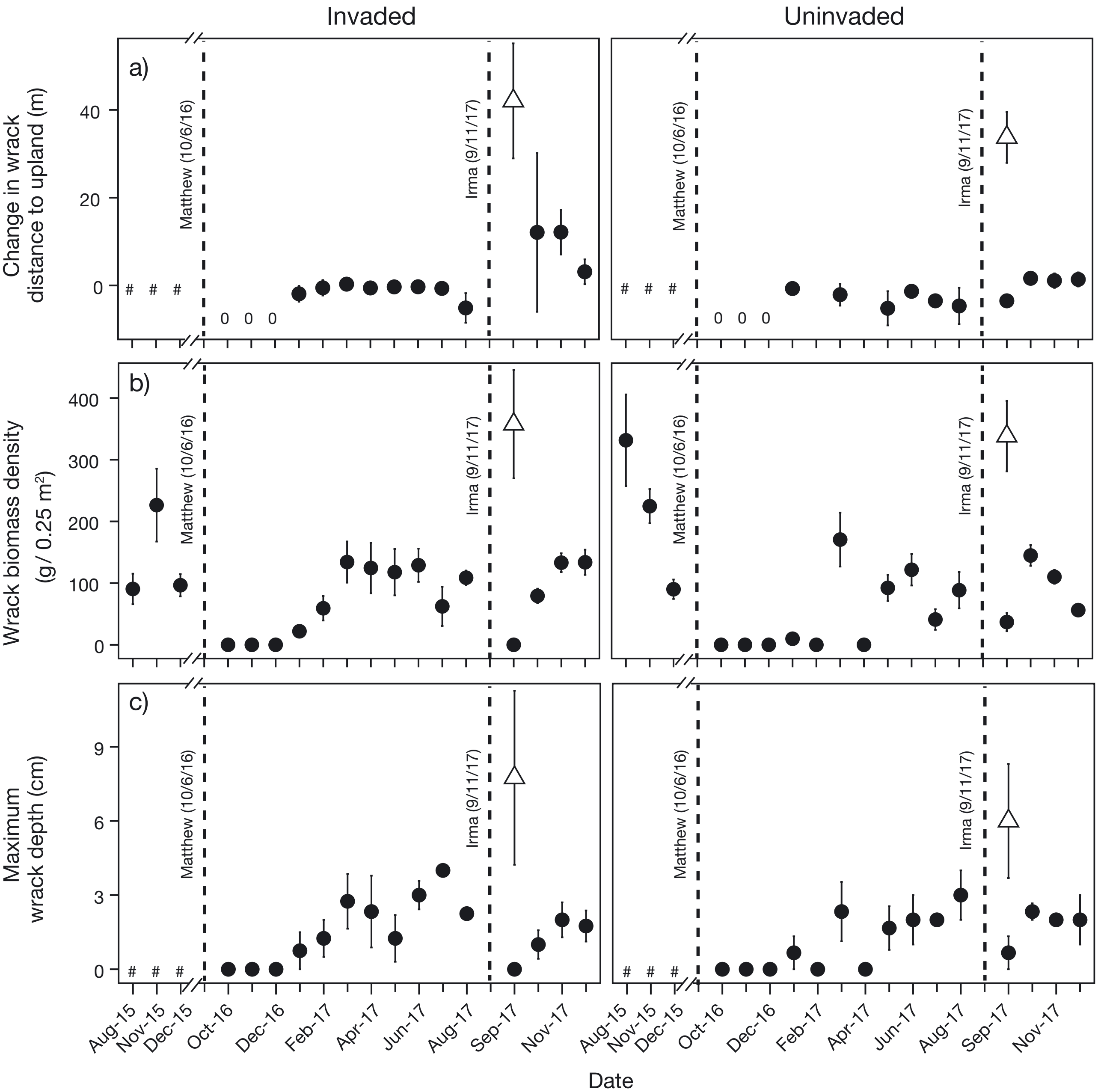

Fig. 3. Means ± SE of (a) change in wrack distance to the upland (ΔWDU, m) relative to the pre-Matthew WDU, (b) wrack dry biomass density (g per 0.25 m^2), and (c) maximum wrack depth (cm) from surveys of 0.25 m^2 quadrats (n = 5) from 4 mangrove-invaded and 3 uninvaded areas for 15 mo following Hurricane Matthew. Positive (negative) values of ΔWDU represent landward (seaward) movement of wrack. Open triangles represent the wrack line deposited in the upland by Hurricane Irma, whereas closed circles represent monthly wrack lines that were deposited in intertidal locations in the marsh. We observed wrack in upland areas after Hurricane Matthew but did not quantify it. Pound signs (#) represent time points where we did not collect data. In (a), zeros above the *x*-axis represent the absence of wrack at all sites. Wrack biomass density (g per 0.25 m^2) from 2015 field surveys for invaded and uninvaded areas at 1 site (n = 5 quadrats per area) are included as a pre-hurricane reference. Dashed lines mark the timing of Hurricane Matthew (6 October 2016) and Hurricane Irma (11 September 2017)

documented, we did not observe strong direct effects of storm surge on mangrove propagules in terms of moving propagules to upland areas. Hurricane Irma occurred prior to peak propagule release, and we did not observe substantial propagule movement to the upland as a result of the storm. In the first post-Irma sampling event, mean propagule abundance in the upland and intertidal wrack lines was less than 1 propagule per 0.25 m^2 quadrat in both locations. We expect that hurricanes could have stronger direct negative effects on mangrove propagule recruitment when storms coincide with peak propagule dispersal. Although Hurricane Matthew occurred closer to peak recruitment than Irma, we did not quantify propagule abundance in upland areas. Propagules remained on adult mangrove trees after Hurricane Matthew, and propagule abundances were similar in vegetated microhabitats for the 3 observed propagule seasons (Fig. 2a), which suggests that Matthew did not substantially deplete the propagule supply. Still, storm timing relative to propagule release likely influences the magnitude of hurricane effects on mangrove recruitment, and other studies have observed reduced recruits and fewer reproductive mangrove trees after hurricanes (Proffitt et al. 2006). In addition to moving propagules to the upland, extreme meteorological events are often associated with long-distance seed dispersal (Reed et al. 1988, Nathan et al. 2008), and the storms could have also moved propagules and wrack offshore or to other remote locations that we did not assess in our field surveys (Roman & Daiber 1989, Li & Pennings 2016).

Although hurricanes did not appear to directly affect mangrove propagules in our study, hurricane removal of wrack from intertidal areas seemingly affected mangrove recruitment and establishment indirectly by temporarily disrupting the association between mangroves and salt marsh wrack. Because wrack strongly facilitates propagule retention and rooting (Smith et al. 2018), extended removal of wrack from the system could minimize propagule establishment in suitable intertidal areas. The duration of wrack absence likely affects the degree to which hurricanes could disrupt the wrack–propagule relationship. Following Hurricane Matthew in October 2016, no new wrack arrived in intertidal areas until January 2017, after the propagule recruitment season had ended. Thus, facilitative effects of wrack were not restored to the system during the propagule recruitment season. In contrast, after Hurricane Irma in September 2017, salt marsh wrack returned to the system within 2 wk, perhaps due to lower storm surge or other differences in hydrodynamic conditions associated with the storm. However, after Hurricane Irma, mangrove propagules were more abundant in wrack compared to other intertidal microhabitats for the remainder of the 2017 propagule recruitment season. Additionally, the export of wrack to upland habitats uncovered bare patches in the intertidal that retained fewer propagules relative to adjacent vegetation. The effect of this reduction persisted as propagules developed into seedlings, and mangrove seedling abundances were also lower in bare sediment compared to vegetation (Fig. 2b). Propagules that retained and rooted in intertidal areas generally survived as seedlings over the 15 mo period; seedlings that established after Hurricane Matthew were robust to the storm surge and hydrodynamic forces associated with Hurricane Irma, which suggests that seedlings had surpassed sediment scouring and hydrodynamic establishment thresholds (Balke et al. 2011, 2013). Hurricanes can kill, defoliate, and uproot adult mangroves (Armentano et al. 1995, Smith et al. 2009, Feller et al. 2015), especially when trees are close to a storm's eye wall (Milbrandt et al. 2006). In our study, hurricanes appeared to minimally affect seedling survival, likely because storm surge covered mangroves and protected them from damaging winds (Smith et al. 1994, 2009, Armitage et al. 2020). Indeed, hurricanes could even benefit seedlings by removing wrack, which can inhibit seedlings by blocking access to light and attracting herbivores (Smith 2019).

Hurricanes likely have larger effects on mangrove recruitment in invaded areas due to differences in propagule supply and wrack deposition patterns. Mangrove propagules and seedlings were more abundant in invaded areas, which suggests that local propagule supply is important to mangrove expansion into salt marshes. Although mangrove propagules can travel substantial distances from their parent tree (Nathan et al. 2008, Van der Stocken et al. 2018), most propagule dispersal likely occurs within meters of adult trees (Clarke 1993, Sousa et al. 2007). Thus, hurricanes likely have larger effects on mangrove recruitment in invaded areas with a proximate propagule supply. In invaded areas, wrack was also located farther from the upland, likely due to interactions among hydrodynamics, geomorphology, and physical structures that deposit wrack in predictable locations (Fischer et al. 2000, Alexander 2008). Propagules associated with wrack may experience different tidal conditions in invaded areas that could affect propagule establishment; for example, propagules may be less prone to desiccation, but more likely to be uprooted by hydrodynamic forces (McKee 1995, Balke et al. 2011). We also observed greater landward movement of intertidal wrack lines after Hurricane Irma at invaded sites relative to uninvaded sites (Fig. 3a); it is possible that fall king tides moved wrack closer to the upland and that adult mangroves then trapped wrack at these higher tidal elevations after the king tides.

In summary, although disturbances are often positively associated with invasion, we found that disturbance can negatively and indirectly affect invasion by altering interactions between resident and invading species. Our work suggests that it is important to consider negative effects of disturbance on invasion; in particular, disturbances that indirectly disrupt invader dispersal or facilitative interactions between resident and invading species are overlooked mechanisms that inhibit invasion. Additionally, in our system, the intensity and frequency of hurricanes is expected to increase over the coming decades (Michener et al. 1997), and black mangroves are predicted to move north at a rate of 2.2–3.2 km yr^{-1} over the next 50 yr (Cavanaugh et al. 2015) into areas with larger salt marsh wrack inputs (Pennings & Richards 1998). As climate change and anthropogenic stressors increasingly alter disturbance regimes, understanding how disturbances affect species invasions can improve predictions of invasibility, rate of spread, and ultimately, invader impact.

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