Kennedy, John Paul, Dangremond, Emily M, Hayes, Matthew A, Preziosi, Richard F, Rowntree, Jennifer K and Feller, Ilka C (2020) Hurricanes overcome migration lag and shape intraspecific genetic variation beyond a poleward mangrove range limit. Molecular Ecology, 29 (14). pp. 2583-2597. ISSN 0962-1083

DOI: https://doi.org/10.1111/mec.15513

Publisher: Wiley

Version: Accepted Version

Hurricanes overcome migration lag and shape intraspecific genetic variation beyond a poleward mangrove range limit

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Funding information: NASA Climate and Biological Response Program grant # NX11AO94G; NSF MacroSystems Biology Program grant # EF1065821; NSF Postdoctoral Fellowship in Biology award #1308565

Running title: Hurricane-driven mangrove dispersal

Abstract

Expansion of many tree species lags behind climate-change projections. Extreme storms can rapidly overcome this lag, especially for coastal species, but how will storm-driven expansion shape intraspecific genetic variation? Do storms provide recruits only from the nearest sources, or from more distant sources? Answers to these questions have ecological and evolutionary implications, but empirical evidence is absent from the literature. In 2017, Hurricane Irma provided an opportunity to address this knowledge gap at the northern range limit of the neotropical black mangrove (*Avicennia germinans*) on the Atlantic coast of Florida, USA. We observed massive post-hurricane increases in beach-stranded *A. germinans* propagules at, and past, this species' present-day range margin when compared to a previously-surveyed, non-hurricane year. Yet, propagule dispersal does not guarantee subsequent establishment and reproductive success (i.e., effective dispersal). We also evaluated prior effective dispersal along this coastline with isolated *A. germinans* trees identified beyond the most northern established population. We used 12 nuclear microsatellite loci to genotype 896 hurricane-driven drift propagules from nine sites and 10 isolated trees from four sites, determined their sources of origin, and estimated dispersal distances. Almost all drift propagules and all isolated trees came from the nearest sources. This research suggests that hurricanes are a prerequisite for poleward range expansion of a coastal tree species and that storms can shape the expanding gene pool by providing almost exclusively range-margin genotypes. These insights and empirical estimates of hurricane-driven dispersal distances should improve our ability to forecast distributional shifts of coastal species.

Keywords: assignment analyses, dispersal kernels, long-distance dispersal, northernmost *Avicennia germinans*, range expansion, tropical cyclones

INTRODUCTION

Species distributional shifts have become commonplace in response to anthropogenic climate change (Pecl et al., 2017; Scheffers et al., 2016). Yet, distributional responses of some species lag behind these changes (Lenoir & Svenning, 2015; Poloczanska et al., 2013). In particular, actual migration of many tree species lags behind projections based on current rates of climatic change and the consequent alterations in habitat suitability (Alexander et al., 2018; Bertrand et al., 2011; Gray & Hamann, 2013; Zhu, Woodall, & Clark, 2012). This phenomenon, known as migration lag, is also forecast to continue or worsen in certain contexts (Gray & Hamann, 2013; Liang, Duveneck, Gustafson, Serra-Diaz, & Thompson, 2018; Prasad, Gardiner, Iverson, Matthews, & Peters, 2013), and can generate changes in forest structure, productivity, and function that have wide-reaching ecosystem-level consequences (Bonan, 2008; Solomon & Kirilenko, 1997).

Modelling efforts to project future distributional shifts are complicated by the fact that numerous factors may constrain plant migration (Corlett & Westcott, 2013; Svenning & Sandel, 2013). Dispersal limitation and niche-related constraints are the two principal factors attributed to migration lag, but temporal variation in these factors is not often considered (Renwick & Rocca, 2015). Episodic events, such as disturbance (Boisvert-Marsh, Périé, & de Blois, 2019; Lembrechts et al., 2016) or extreme climate events (Wernberg et al., 2013), can quickly overcome these migration constraints and lead to periods of rapid range shifts (Renwick &

Rocca, 2015). As a result, migration rates are not constant over time, and instead, colonisation of new areas will often be limited to these transient periods of time (Zeigler & Fagan, 2014).

Extreme storm events (e.g., tropical cyclones, also known as typhoons or hurricanes) are one mechanism that can abruptly overcome migration constraints, in particular for coastal species (Lugo, 2008; Nathan et al., 2008). This is especially true for the Caribbean and Gulf of Mexico, a region frequently impacted by hurricanes (Walker, Lodge, Brokaw, & Waide, 1991) and forecast to experience more intense storms in the future (Murakami, Levin, Delworth, Gudgel, & Hsu, 2018). Numerous examples demonstrate how hurricanes are important vectors for the expansion of diverse taxa within the region, including fish (Johnston & Purkis, 2015), insects (Andraca-Gómez et al., 2015), and plants (Bhattarai & Cronin, 2014; Kendall, Battista, & Hillis-Starr, 2004). However, despite the well-recognised influence of hurricanes on distributions of species, we lack an understanding of how hurricane-driven expansion can impact variation within a species. Do hurricanes provide new recruits simply from the nearest sources? Or, do these high-energy storms provide the conditions necessary for a greater influence of long-distance dispersal? Answers to these questions have important implications for species ecology and evolution with climate change (Nadeau & Urban, 2019 and citations within). Moreover, quantitative analyses of plant dispersal driven by extreme meteorological events are absent from the literature (Nathan et al., 2008; Schurr et al., 2018), yet they would provide empirical estimates of dispersal distances that are needed to improve projections of future distributional shifts (Thuiller et al., 2008).

Hurricane Irma provided an opportunity to address this knowledge gap at the northern range limit of the neotropical black mangrove (*Avicennia germinans*) on the Atlantic coast of Florida, USA. This catastrophic storm, among the strongest and costliest Atlantic hurricanes ever recorded, devastated areas across the northern Caribbean and Florida (Cangialosi, Latto, & Berg, 2018), with massive impacts to coastal forest ecosystems (Branoff, 2019; Radabaugh et al., 2019; Ross et al., 2019). From 10-12 September, 2017, Hurricane Irma progressively weakened from a category 4 storm in the Florida Keys to a tropical storm in north Florida (Cangialosi et al., 2018). Although the storm weakened quickly over Florida, the wind field was extensive, with the strongest tropical-storm-force winds experienced on the northeast coast (Cangialosi et al., 2018) (see Figure S1 for hurricane path and wind speeds).

In this study, we documented numbers of *A. germinans* propagules stranded on beaches along this northeast coast following Hurricane Irma and compared these numbers to those found previously during a non-hurricane year. We then used an extensive population-genetic data set from across the Florida *A. germinans* distribution (Kennedy, Preziosi, Rowntree, & Feller, 2020a) to determine the origin of these drift propagules and to quantify hurricane-driven dispersal distances. It is important to highlight that dispersal to these beaches (where propagules cannot establish) is not analogous to effective dispersal, which would consist of propagule transport plus successful establishment and subsequent reproductive success at the recipient location (Auffret et al., 2017). To assess effective dispersal, we also documented multiple newly-discovered *A. germinans* trees found past the most northern established population of this species. For these trees, we compared measures of their potential reproductive output to those of conspecifics at the present-day range margin and used the same reference data set to determine their source of origin. We refer to these isolated *A. germinans* as ‘vagrant trees’ throughout this publication. Vagrant trees provide evidence of prior effective dispersal along this coastline and insights into the potential filter that establishment may apply to the pool of available drift propagules.

Here, we asked: (a) Were drift-propagule densities higher following Hurricane Irma compared to a non-hurricane year?; (b) Are vagrant trees less reproductive than conspecifics at the present-day range margin?; (c) Where did drift propagules (i.e., hurricane-driven dispersal) and vagrant trees (i.e., prior effective dispersal) come from? Our findings provide novel insights into how hurricanes can overcome migration lag and shape intraspecific genetic variation in a coastal tree species and should improve our ability to forecast future distributional shifts.

MATERIALS AND METHODS

Model species

Mangroves are intertidal forests that provide ecosystem services of ecological and economic importance to coastal ecosystems worldwide (Lee et al., 2014). As coastal species, many mangrove forests are periodically impacted by hurricanes that can result in widespread tree mortality and shifts in forest structure (Krauss & Osland, 2020; Osland et al., 2020). Hurricane-driven dispersal of hydrochorous (water-dispersed) mangrove propagules is an important mechanism for forest regeneration following these episodic events and can continue for extended periods post-storm (Krauss & Osland, 2020), and may facilitate long-distance poleward expansion (Van der Stocken, Wee, et al., 2019).

The widespread neotropical black mangrove (*Avicennia germinans*) is the predominant mangrove species at northern distributional limits in the United States (Lonard, Judd, Summy, DeYoe, & Stalter, 2017). Atlantic Florida *A. germinans* inhabit protected estuaries with access to the ocean via a series of inlets. Propagules generally abscise from maternal trees in great numbers from late August through October, and some eventually exit these estuaries via inlets and become stranded on Atlantic coast beaches (I.C. Feller, *personal observation*). Long-distance dispersal of this species is possible as its propagules remain viable even after extensive flotation periods (Alleman & Hester, 2011b; Rabinowitz, 1978), further supported by genetic evidence for trans-oceanic dispersal (Cerón-Souza et al., 2015; Mori, Zucchi, Sampaio, & Souza, 2015; Nettel & Dodd, 2007). However, *A. germinans* propagules are generally retained within estuaries and most dispersal is restricted to short distances (Sousa, Kennedy, Mitchell, & Ordóñez L, 2007), as evidenced by strong within-estuary spatial genetic structure (Cerón-Souza, Bermingham, McMillan, & Jones, 2012). Establishment success for *A. germinans* propagules is also inversely related to flotation time (Alleman & Hester, 2011b; Simpson, Osborne, & Feller, 2017).

Atlantic Florida mangroves decline in abundance with latitude and are eventually replaced by temperate salt-marsh vegetation at their northern range margin (Kangas & Lugo, 1990), where *A. germinans* exhibits considerable reductions in genetic variation compared to conspecifics farther south (Kennedy, Preziosi, Rowntree, & Feller, 2020b). The frequency and intensity of winter freezes has been linked to the northern extent of mangroves along this coastline (Cavanaugh et al., 2018; Osland et al., 2017), with mangrove proliferation (in particular, *A. germinans*) at this northern range margin for several decades due to a paucity of extreme freeze events (Cavanaugh et al., 2019, 2014; Osland et al., 2018). Further range expansion of *A. germinans* is forecast as winter freezes in the region become even less frequent with climate change (Cavanaugh et al., 2019, 2015).

Beach surveys

We adapted methods used to quantify mangrove dispersal (Clarke, 1993; Sengupta, Middleton, Yan, Zuro, & Hartman, 2005) to survey Atlantic Florida *A. germinans* propagule densities on beaches adjacent to inlets. We surveyed two beaches at the established range margin of this species (29.71 – 29.91°N) (Spalding, Kainuma, & Collins, 2010), three beaches past the range margin (~40-75 km to the north) where no established mangrove populations exist (30.40 – 30.70°N), and one lower-latitude beach within the mangrove-dominated continuous range core as a comparison (27.47°N) (Figure 1). We performed equivalent surveys on 24-28 September, 2014 (a non-hurricane year) and 14-16 October, 2017 (five weeks after Hurricane Irma made landfall in Florida), except for the most northern beach that was only surveyed in 2017. At each survey site, we ran three to eight 100 m transects along the high tide line and counted all putatively-viable drift propagules found within 1 m of the transect line (i.e., decomposed propagules were noted, but not included in these counts). Numbers of transects varied depending on the length of the beach, and each transect line was separated from the next by 100 m. We tested for differences in propagule densities between the two collection years (n = 5 sites per year) with a two-sample Fisher-Pitman permutation test, with 10^4 re-samplings, in the R-package coin (Hothorn, Hornik, van de Wiel, & Zeileis, 2008) in R v3.6.0 (R Core Team, 2013).

We collected all putatively-viable drift propagules during the 2017 post-Hurricane Irma beach surveys. Propagules from each survey site were stored together in plastic bags during field collections. For three of the six surveyed beaches, we subset samples into two collections that corresponded to areas within an inlet and those outside along the Atlantic ocean (i.e., MZ and MB, F2 and F1, each respectively), or to areas separated by an inlet (i.e., H, LT) (Table 1; Figure 1b, c). We haphazardly chose 100 propagules of all sizes from each of these nine collection sites for genetic analysis (n = 900 total propagules) and stored them at -20°C.

We assessed viability of these post-Hurricane Irma drift propagules with another subset of 100 propagules from each of the nine collection sites (n = 900 total propagules). We placed propagules in shallow, plastic trays with a thin layer of wet potting soil/sand until root radicles developed, and then transferred them to individual tree tubes (Ray Leach Cone-tainers, Stuewe and Sons., Inc.; 2.5 cm diameter, 12.1 cm length; 49 ml volume) filled with a 2:1 mixture of commercial potting soil and sand. We placed tubes into racks of 100 and allowed propagules to grow in non-saline, deionized water in flooded plastic tubs with the water depth maintained at 10 cm. All seedlings were grown, with no nutrient additions, in a walk-in environmental growth chamber at the Smithsonian Environmental Research Center (Maryland, USA), with chamber temperature and humidity maintained throughout this period (0:00-6:00: 16°C, 6:00-12:00: 21.5°C, 12:00-18:00: 27°C, 18:00-0:00: 21.5°C; 65% RH). We quantified the number of propagules that established and began growing true leaves (i.e., post-cotyledons).

Vagrant tree surveys

We conducted coastal surveys by vessel over a 12-month period prior to Hurricane Irma (July 2016 to June 2017) along the intercoastal waterway between St Augustine, Florida, and Cumberland Island, Georgia (29.9 – 31.0°N), an area past the most northern established *A. germinans* population. Surveys were conducted by trolling close to shore at low speed and visually searching for trees growing within the salt marsh. A leaf was collected from each discovered tree and dehydrated in silica gel for genetic analysis.

In August 2018, we revisited sites where we had previously found vagrant trees and identified four adult trees producing flowers. For these four trees, we measured height and potential reproductive output as mean inflorescence per terminal stem. We haphazardly selected a large mature branch, counted terminal stems (aiming for at least 60), and then counted how many terminal stems had inflorescence. We divided total inflorescence count by total terminal stem count to calculate inflorescence per terminal stem. We repeated this process three times for each tree and used mean values for analysis. We then selected three trees at the present-day *A. germinans* range margin (29.727°N, 81.239°W) to compare with these four reproductive vagrant trees. We repeated measures of height, terminal stem counts, and inflorescence counts on these three range-margin trees. We selected these particular trees because they were larger than neighbouring trees, and presumably the most mature in the area. We tested for differences in mean inflorescence per terminal stem between the vagrant trees (n = 4) and range-margin trees (n = 3) with a two-sample Fisher-Pitman permutation test, with 10^4 re-samplings, in the R-package coin (Hothorn et al., 2008).

DNA isolation and Microsatellite genotyping

For drift propagules, we removed the cotyledons and isolated genomic DNA from 50 mg of frozen hypocotyl/radicle tissue with the DNeasy 96 Plant Kit (Qiagen, Hilden, Germany) following the standard protocol. For vagrant trees, we isolated genomic DNA from 20 mg of dried leaf tissue with the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) following the standard protocol, with an extended incubation of 45 minutes. We genotyped all samples at 12 previously-developed nuclear microsatellite loci (Cerón-Souza et al., 2012; Cerón-Souza, Rivera-Ocasio, Funk, & McMillan, 2006; Mori, Zucchi, Sampaio, & Souza, 2010; Nettel, Rafii, & Dodd, 2005) according to the protocol outlined in Kennedy, Sammy, Rowntree, & Preziosi (2020) for drift propagules and the protocol outlined in Kennedy, Preziosi, et al. (2020b) for vagrant trees. We performed PCR on a Prime thermal cycler (Techne, Straffordshire, UK), analysed fragments on an Applied Biosystems 3730 DNA Analyzer (Applied Biosystems, Foster City, California, USA) with LIZ 500 size standard, and scored alleles in the R-package Fragman

(Covarrubias-Pazaran, Diaz-Garcia, Schlautman, Salazar, & Zalapa, 2016). We re-amplified and re-genotyped 5% of the drift propagule DNA samples to estimate a study error rate (Bonin et al., 2004), and did the same for all of the vagrant tree DNA samples to ensure we had the correct multi-locus genotypes. Microsatellite genotype data are available at the Dryad digital repository (Kennedy, Dangremond, et al., 2020).

Genetic assignments

For all genetic assignments, we used GENECLASS2 (Piry et al., 2004) to calculate (1) the probability that each individual (i.e., multi-locus genotype) could belong to each potential source (based on the allele frequencies within each source) with the Paetkau et al. (2004) Monte Carlo re-sampling method and 10^3 resampled individuals, and (2) source log-likelihood with the Rannala and Mountain (1997) Bayesian assignment method. For potential sources, we used a subset of an *A. germinans* reference data set with trees from 32 Florida collection sites that were genotyped at the same 12 microsatellite loci ($n = 860$ individuals; Kennedy, Preziosi, et al., 2020a) (Figure S2). Simulations demonstrate that the Rannala & Mountain (1997) Bayesian assignment method can achieve 100% correct assignments with ≥10 microsatellite loci, 30-50 sampled individuals from each of 10 populations, and inter-population $F_{ST} = 0.1$, with reduced success at lower F_{ST} (Cornuet, Piry, Luikart, Estoup, & Solignac, 1999; Waples & Gaggiotti, 2006). Hence, we used inter-site $F_{ST} \geq 0.1$ as a threshold to reduce the entire reference data set into 12 potential sources that encompass the entire Florida *A. germinans* distribution (Figure 1a; see Appendix S1, Table S1-S2 for detailed description).

Prior to our assignments of drift propagules and vagrant trees, we used known-origin propagules to test the power of the assignment analyses and to define *a priori* confidence thresholds (similar to methods outlined in Sinclair et al., 2018). Known-origin propagules were collected at three of the 12 potential sources (n = 50 propagules from a single tree for each site) and were genotyped at the same 12 microsatellite loci for a mating system study (Kennedy, Sammy, et al., 2020) (Figure S2). As we knew the origin of these propagules, we used these assignment results to define the (1) p-value for source exclusion and (2) acceptance threshold for unambiguous assignments based on the assignment score of the most-likely source (i.e., the relative likelihood of this source compared to all other sources; Piry et al. 2004) for subsequent genetic assignments of drift propagules and vagrant trees.

For each unambiguous assignment of a drift propagule or vagrant tree, we measured the approximate over-water dispersal distance from the assigned source in Google Earth Pro 7.3.2.5776. We measured dispersal as over-water distances because *A. germinans* propagules are hydrochorous (i.e., water is the predominant dispersal vector), but we cannot be certain how hurricane-force winds may have influenced propagule dispersal pathways. As such, we also measured Euclidean distances from assigned sources in the R-package geosphere (Hijmans, Williams, & Vennes, 2019) as the most conservative estimate possible of dispersal distances.

RESULTS

Beach surveys

In 2014, under non-storm conditions, we found a range from 0 to 317 *A. germinans* propagules at five survey sites. We observed highest densities at the lower-latitude, within-range-core comparison site (27.47°N, 0.26 propagules/m^2), minimal propagule numbers at the two range-margin sites (29.71°N, 0.001 propagules/m^2; 29.91°N, 0.07 propagules/m^2), and no propagules at the two sites past the range margin (30.40°N, 30.49°N) (Table S3; Figure 2). In 2017, five weeks after Hurricane Irma, we found a massive increase in propagule numbers, with a range from 329 to 3,048 *A. germinans* propagules at six survey sites from 27.47 to 30.70°N (Table S3). Propagules were present at higher densities post-hurricane (range: 0.34-10.16 propagules/m^2) than under non-storm conditions (two-sample Fisher-Pitman permutation test, $Z = -1.78$, $p = 0.009$; Figure 2). We observed highest post-hurricane densities at the two range-margin sites (29.71°N, 4.10 propagules/m^2; 29.91°N, 10.16 propagules/m^2) where propagule numbers were orders of magnitude higher than under non-storm conditions (29.71°N, 2014: 2 propagules, 2017: 2,462 propagules; 29.91°N, 2014: 97 propagules, 2017: 3,048 propagules) (Table S3; Figure 2). Almost all post-hurricane drift propagules were viable as 99% (894 of 900) of those planted established and produced true leaves (i.e., post-cotyledons) in the environmental growth chamber.

Vagrant tree surveys

We identified a total of 11 *A. germinans* (10 trees, one seedling) at four locations beyond the most northern established population of this species (Table 2; Figure 1b, c). From south to north, we first identified two trees on the Tolomato River (30.11ºN) that are the documented northernmost *A. germinans* (Williams et al., 2014). Second, we found five trees at Fort George Inlet (30.43ºN). Two larger trees were each isolated from the others by approximately 320 m and 1 km, while a third larger tree was located 40-55 m from two smaller trees. Third, we found two trees and one seedling, which was not sampled to avoid potential damage to its photosynthetic ability, on the north of Big Talbot Island (30.48ºN). The larger of the two trees was located 25 m from the smaller tree. Fourth, we found one tree towards the south of Amelia Island (30.52ºN).

The four vagrant trees that were reproductive (identified at three of the four locations) ranged in height from 183 to 280 cm, and the three trees sampled farther south at the range margin ranged in height from 340 to 400 cm (Figure 3a). Mean inflorescence per terminal stem was not statistically different between these vagrant trees and range-margin trees (Z = 0.80, p = 0.57), with a range of 0.44-1.05 inflorescence/stem and 0.41-0.67 inflorescence/stem, respectively (Figure 3b). One vagrant tree (FG3) was notably more fecund than the other measured trees (Figure 3b).

Genotyping and Genetic assignments

Drift propagules

We genotyped a total of 896 drift propagules (n = 99-100 per survey site; Table 1). We observed a low estimated error rate of 0.97% (6 errors out of 621 allele comparisons). The six individuals, that each exhibited a single locus-specific error, were re-amplified a third time and we used the consensus genotype for assignment analyses.

The probability that each of the 150 known-origin propagules belonged to their respective source ranged from 0.001 to 0.99 (mean = 0.44; Appendix S1). A total of 97% (146 of 150) of these propagules were correctly assigned to their source, with the highest assignment score for a mis-assigned propagule of 0.88 (Appendix S1, Table S4). Based on these results, we assigned the following confidence thresholds to subsequent assignment analyses of drift propagules and vagrant trees. We defined $p < 0.001$, the lowest probability observed, as the threshold to exclude a potential source. We also defined an assignment score ≥ 0.91 as the acceptance threshold for an unambiguous assignment, based on the highest score for a mis-assigned, known-origin propagule. This conservative acceptance threshold indicates that a multi-locus genotype must be at least 10x more likely to belong to the assigned source than to any other potential source.

None of the 896 drift propagules were excluded from all 12 potential sources (i.e., p > 0.001 for at least one source; Table S5), which suggests that all the genotyped drift propagules were sourced from Florida populations. We unambiguously assigned 56% of drift propagules from the eight survey sites at or past the range margin (448 of 796), with a range within-site from 49% (site code: H) to 68% (site code: MB) (Table 1, Table S6). A total of 89% (400 of 448) of these unambiguous assignments were sourced from the range margin (source code: N/GS, GN), 9% (40 of 448) were sourced from the nearest within-range-core source (source code: C/Sp; over-water distance: 75-185 km) and <2% (8 of 448) were transported over longer distances from the Atlantic (East) and Gulf (West) coasts of Florida (over-water distance: 124-1,135 km) (Table 1; Figure 4). Each of these eight survey sites exhibited similar assignment patterns (i.e., 86-100% assigned to range-margin sources), except for the most southern range-margin site (site code: MZ; Figure 4). Almost half of the unambiguous assignments at MZ (46%; 25 of 54) were sourced to the nearest within-range-core source (39%) or via longer distances (7%; over-water distance: 225-1,135 km) (Figure 4). We unambiguously assigned fewer drift propagules at the lower-latitude, within-range-core comparison site (31 of 100; Table 1, Table S6), but observed a similar pattern to the more northern survey sites. Most propagules (68%; 21 of 31) were assigned to the nearest source (source code: A/Sb), with 16% (5 of 31) from adjacent sources (source code: NK/MA, PI), and 16% (5 of 31) via longer distances from sources on the Gulf (West) coast of Florida (over-water distance: 440-870 km) (Table 1; Figure 4). Euclidean distances across all unambiguous assignments (n = 479; median: 74 km, range: 1-457 km) were nearly identical to over-water dispersal distances (n = 479; median: 74 km, range: 1-1,135 km), except for the limited number (8 of 479) of dispersal events at the longest distance intervals (Table S6; Figure S3). These eight dispersal events were considerably shorter based on Euclidean distance (range: 184-457 km) compared to over-water distance (range: 434-1,135 km) (Figure S3).

Applying confidence thresholds to assignment analyses reduces the risk of incorrect assignments, but also increases the number of unassigned individuals (Roques, Duchesne, & Bernatchez, 1999). Across all nine survey sites, 417 of 896 drift propagules (47% of all samples) were not unambiguously assigned to a source. Yet, if no acceptance threshold is used and sources are assigned simply based on the lowest log-likelihood, assignment results were equivalent to those presented here (Table S7).

Vagrant trees

Each of the 10 vagrant trees exhibited consistent multi-locus genotypes across two, independent PCR. In addition, multi-locus genotypes were consistent with two smaller trees at Fort George Inlet (30.43ºN) and one smaller tree at Big Talbot Island (30.48ºN) being offspring of adjacent larger trees (Table 2; Appendix S2). As such, these putative offspring were not included in assignment analyses.

None of the seven vagrant trees included in assignment analyses were excluded from all 12 sources, with highest probabilities from the two range-margin sources and the nearest within-range-core source (Table S5). We unambiguously assigned three of the seven vagrant trees (from two of the four sampled locations), and all three trees were sourced to the most southern range-margin source (source code: N/GS; Table 2, Table S6). The first and second most-likely sources for the remaining four vagrant trees were a combination of the two range-margin and nearest within-range-core sources (Table S6). Hence, although we could not unambiguously assign a source, these four trees also came from the nearest potential sources.

DISCUSSION

Migration lag in trees may be the product of multiple constraints, but episodic events can quickly overcome these constraints and lead to transient periods of rapid range shifts (Renwick & Rocca, 2015). This study highlights how hurricanes create the conditions needed to drive range expansion at a northern distributional limit of the neotropical black mangrove (*Avicennia germinans*) and can shape patterns of genetic variation in expanding populations of this species. These insights, along with empirical estimates of hurricane-driven dispersal distances, should improve our ability to forecast future distributional shifts of this species, and other coastal species often impacted by extreme storm events.

Hurricanes are a vector of range expansion

Climate models predict that, at a global scale, storm numbers may decline in the future, but that the strongest storms will become more intense and that sea level rise will exacerbate storm surge effects (Walsh et al., 2016 and citations within). In particular, a greater prevalence of major hurricanes (≥ category 3) is forecast in the Caribbean and Gulf of Mexico as the tropical North Atlantic continues to warm (Murakami et al., 2018). These trends may enhance long-distance dispersal of mangrove propagules and facilitate poleward range expansion (Van der Stocken, Carroll, Menemenlis, Simard, & Koedam, 2019; Van der Stocken, Wee, et al., 2019). After Hurricane Irma, we documented large numbers of *A. germinans* drift propagules along Atlantic Florida beaches at, and past, the present-day range margin of this species. Provision of propagules to these areas, where we found limited or no propagules in 2014 (a non-hurricane year), suggests that hurricanes function as episodic events that are necessary for these estuarine mangroves to expand poleward. Consistent with this conclusion, expansion patterns of invasive species within this region have been linked to hurricane frequency (Bhattarai & Cronin, 2014; Johnston & Purkis, 2015). However, we only document one non-hurricane (2014) and one hurricane (2017) year and, due to the timing of Hurricane Irma, our beach surveys were approximately 2.5 weeks later in 2017. Annual and seasonal differences in propagule production and release could account for some of the variation in drift-propagule densities between our two sampling periods, although only a relatively slight increase in drift-propagule density at the lower-latitude comparison site in 2017 compared to 2014 suggests that these differences may not have had a substantial impact. Instead, *A. germinans* propagules are generally retained within estuaries (Sousa et al., 2007), as are those of a congener (*A. marina*) (Clarke, 1993; Van der Stocken, Vanschoenwinkel, De Ryck, & Koedam, 2018), which would explain why we observed comparatively limited numbers of beach-stranded propagules (and no propagules past the present-day range margin) under non-storm conditions. Extreme high-water events, associated with storm surge, are also needed to disperse mangrove propagules over dense salt-marsh vegetation to enable expansion inland (Peterson & Bell, 2012; Rodriguez, Feller, & Cavanaugh, 2016). Therefore, for mangrove range expansion to occur, the pulse of energy and unusually high-water levels provided by hurricanes seem to be the prerequisite needed to flush propagules out of estuaries in large numbers and into more poleward, salt-marsh-dominated areas.

We observed highest drift-propagule densities at the lower-latitude comparison site during a non-hurricane year. As Florida mangroves decline in abundance with latitude (Osland et al., 2017), the number of propagules dispersed out of estuaries may generally be dictated by neighbouring mangrove abundance (i.e., larger forests produce greater numbers of propagules), consistent with previous mangrove dispersal studies (Sengupta et al., 2005; Van der Stocken et al., 2018). In contrast, following Hurricane Irma, much higher drift-propagule densities were observed at the range margin, where far fewer mangroves exist. This difference suggests that dispersal patterns can vary depending on the unique attributes of each storm. Hurricane Irma produced greater storm surge along northeast Florida compared to areas directly south (Cangialosi et al., 2018), which may explain why greater numbers of drift propagules were deposited on beaches at the range margin compared to the lower-latitude comparison site. Numbers of drift propagules and dispersal direction may be influenced by variation in hurricane trajectory and intensity (Krauss & Osland, 2020), as well as ocean circulation patterns (Kennedy et al., 2017) and latitudinal variation in the timing of propagule release (Van der Stocken, López-Portillo, & Koedam, 2017). Continued monitoring along expected hurricane pathways is needed to better quantify the influence of these factors and to better predict dispersal patterns associated with future storm events.

Expanding genotypes are from the nearest sources

Where do hurricane-dispersed propagules come from? Extreme storm events have the potential to drive trans-oceanic dispersal (Carlton et al., 2017; Waters, King, Fraser, & Craw, 2018); however, we found that the vast majority of drift propagules collected after Hurricane Irma came from the nearest sources. Hence, hurricanes may provide an expanding gene pool that consists of a much-reduced representation of genetic variation within a species, although even limited long-distance dispersal (as observed here) can lead to substantial increases in genetic variation (Bialozyt, Ziegenhagen, & Petit, 2006). Migration models for terrestrial tree species find a similar pattern, with colonisation past present-day distributions mostly influenced by the species' abundance at the range limit (Iverson et al., 2004). Yet, while forecast migration of these terrestrial trees for the next 100 years is mostly restricted to 10-20 km (Iverson et al., 2004; Prasad et al., 2013), we found dispersal to beaches >100 km from range-margin sources after a single storm event and vagrant trees 80 km from their assigned source. This contrast is consistent with longer transport potential for coastal species (Nathan et al., 2008) and highlights that coastal range expansions have the potential to occur rapidly over large spatial scales.

A leptokurtic dispersal kernel, where most dispersal occurs over short distances, is consistent with genetic analyses across mangrove species (Van der Stocken, Wee, et al., 2019 and citations within). Local sources are also thought to provide propagules for mangrove forest regeneration after storms (Krauss & Osland, 2020). This pattern is consistent with restricted gene flow in taxa from spatially-discrete estuarine habitats (Bilton, Paula, & Bishop, 2002). Remarkably, the proportions of unambiguous assignments from our eight survey sites at or past the *A. germinans* range margin (89% from range margin, 9% from nearest range core, 2% longer distances) were similar to the proportions of propagules from a congener (*A. marina*) collected within different zones of an East African estuary (83% adjacent to forest, 16% near estuary exit, <1% outside estuary; Van der Stocken et al., 2018). Dispersal patterns of propagules from *Avicennia* species may not change substantially whether within tidal estuaries or following extreme storm events (i.e., most propagules remain closest to their source, very few travel longer distances); however, we found that storms create a transient shift in the dispersal kernel towards massively greater spatial scales (from metres to kilometres). Further genetic research that determines the origins of drift propagules found during non-storm periods will be needed to better quantify the effect of these storms on dispersal distances.

Although most dispersal was sourced to the nearest populations, we did find a greater proportion of dispersal from more distant sources at the most southern range-margin survey site and at the lower-latitude comparison site (maximum over-water distance: 1,135 km, 870 km, respectively). Euclidean distances were considerably shorter (maximum distance: 457 km, 327 km, respectively), but may be overly conservative as propagules would need to be dispersed overland by wind from the Gulf (West) coast to the Atlantic (East) coast of Florida. Of the nine survey sites in this study, these two sites with greater proportions of long-distance dispersal are the most geographically proximate to larger mangrove forests south of the range margin. Greater geographical isolation from these lower-latitude forests may explain the lack of dispersal over longer distances to the more northern survey sites. In addition, our observations may reflect a density-dependent process, where an overwhelming number of local propagules further dilutes the already small proportion of propagules from more-distant sources (Waters, Fraser, & Hewitt, 2013). This possibility may explain why we observed numerous unambiguous assignments to the adjacent range-margin source, but almost no evidence of longer-distance dispersal, at the survey site (code: MB) that borders the most southern range-margin survey site.

Almost all of the collected drift propagules were viable, but beach-stranded propagules are not analogous to effective dispersal (Auffret et al., 2017). Our documentation of vagrant *A. germinans* trees provides evidence of previous successful establishment beyond the most northern established population, and these trees were exclusively sourced to range-margin (or possibly the nearest range core) populations. Effective dispersal only from the nearest potential sources may simply be the result of the much greater local supply of propagules from these sources, or could indicate that post-dispersal establishment applies a filter to the pool of available drift propagules based on shorter flotation times for range-margin propagules (Alleman &

Hester, 2011b; Simpson et al., 2017) or on local adaptation to environmental conditions (Cruz et al., 2019).

Intraspecific variation is an important consideration when formulating conservation strategies and adaptation planning with climate change (Benoliel Carvalho, Torres, Tarroso, & Velo-Antón, 2019; Chakraborty, Schueler, Lexer, & Wang, 2019). Our findings suggest that hurricanes may be a prerequisite for poleward range expansion of a coastal tree species and that these storm events can shape the expanding gene pool by providing new recruits almost exclusively from range-margin sources. Expansion of range-margin genotypes, that are presumably better adapted to climatic extremes experienced beyond the current distribution, may facilitate species range expansion with climate change (Rehm, Olivas, Stroud, & Feeley, 2015). Limited immigration from range-core sources may also expedite adaptation to these marginal environments (Kawecki, 2008). However, range margins may already exhibit reduced genetic variation compared to more central portions of a distributional range (Pironon et al., 2017). Considerable reductions in genetic variation are documented in these Atlantic Florida range-margin *A. germinans* compared to conspecifics farther south (Kennedy, Preziosi, et al., 2020b). Further reductions in genetic variation due to founder effects and minimal gene flow from more diverse sources could constrain evolutionary responses and reduce fitness in these expanding populations (Nadeau & Urban, 2019 and citations within). For instance, less genetically-diverse mangrove species were less resilient to extended flooding, analogous to forecast impacts of sea level rise (Z. Guo et al., 2018). Yet, we found that vagrant *A. germinans* trees were not simply surviving past this species' range limit, but instead, appear to be thriving. Vagrant trees were as potentially reproductive as range-margin conspecifics and we found genetic evidence that two individuals had successfully reproduced, consistent with evidence of precocious reproduction

(Dangremond & Feller, 2016) and greater reproductive success (Goldberg & Heine, 2017) in a co-occurring range-margin mangrove, *Rhizophora mangle*. Range-margin *A. germinans* also exhibit shifts towards more cold-tolerant leaf traits (Cook-Patton, Lehmann, & Parker, 2015; Kennedy, Preziosi, et al., 2020b) and their seedlings can survive climatic conditions well past their present-day range limit (Hayes et al., 2020). Further work is needed to understand how intraspecific variation at, and past, this expanding range margin may shape population-level responses to future climate change (e.g., Cruz et al., 2020, 2019).

Insights for modelling range shifts

Plant dispersal and migration patterns are one of the most significant uncertainties for forecasting future distributional shifts with climate change (Thuiller et al., 2008 and citations within). Modelling efforts are further complicated as migration rates are not constant over time because of the transient nature of dispersal and colonisation (Zeigler & Fagan, 2014). Research that identifies mechanisms that overcome migration constraints and lead to episodic range shifts will enhance our understanding of why many species lag behind climate-change projections and will advance efforts to forecast future range shifts (Renwick & Rocca, 2015).

Mangrove distributional limits are controlled by climatic thresholds in minimum temperature and/or precipitation (Cavanaugh et al., 2018; Osland et al., 2017). Forecast warming trends indicate that Atlantic Florida mangroves at their present-day range margin will rarely be constrained by periodic freeze events into the future, and as a result will permanently replace neighbouring salt-marsh vegetation (Cavanaugh et al., 2019, 2015). Based on these climate projections, the distribution of *A. germinans* is forecast to expand northward ~160 km over the next 50 years (3.2 km per year; Cavanaugh et al., 2015). However, as highlighted by Cavanaugh et al. (2015), release from this climatic constraint alone does not guarantee range expansion if not accompanied by propagule dispersal and an availability of suitable habitat. Here, we found that *A. germinans* poleward expansion is likely dispersal limited under 'normal' conditions, and that episodic extreme storm events are needed to move propagules past the contemporary range limit. In line with this conclusion, the present-day Atlantic Florida mangrove range margin is experiencing rapid range infilling (Simpson, Stein, Osborne, & Feller, 2019), but our coastal surveys indicate very little in terms of poleward expansion. Therefore, Atlantic Florida mangrove expansion will presumably not be a progressive march poleward, and instead, this process will likely occur via a series of starts and stops driven by propagule dispersal out of estuaries and over longer distances following extreme storm events.

Incorporating biological mechanisms into predictive models should improve our ability to forecast changes in biodiversity with climate change (Urban et al., 2016). Mechanistic models can provide more realistic predictions and possibly greater transferability across geographic regions, although many uncertainties and shortcomings still remain (Yates et al., 2018). Cavanaugh et al. (2015) took the first step in this direction with their incorporation of a mechanistic predictor (i.e., freeze degree days) to forecast mangrove range expansion along Atlantic Florida, with a fully-mechanistic model of mangrove distributions as a possible next step. Our research suggests that, in addition to physiological thresholds, including hurricane projections (e.g., storm frequencies, trajectories, intensities) is essential for more realistic forecasts of Atlantic Florida mangrove expansion, as poleward dispersal will likely be restricted to these transient windows. We also provide empirical estimates of hurricane-driven dispersal distances (measured as both over-water distance and Euclidean distance, the most conservative estimate possible) that are needed to parameterise these models (Van der Stocken, Carroll, et al., 2019). Further work is necessary to understand how expansion from a restricted set of sources may shape adaptive capacity in newly-colonised populations, which can also be incorporated into future models (Bush et al., 2016). However, physiological thresholds and dispersal are not the only constraints to mangrove expansion. Smaller-scale, niche-related constraints also influence mangrove establishment, survival, and growth (Krauss et al., 2008), including hydroperiod and salinity (Alleman & Hester, 2011a; Coldren & Proffitt, 2017), salt-marsh interactions (E. Chen, Blaze, Smith, Peng, & Byers, 2020; H. Guo, Zhang, Lan, & Pennings, 2013; Pickens, Sloey, & Hester, 2019; Simpson, Feller, & Chapman, 2013), predation or herbivory (Devaney, Lehmann, Feller, & Parker, 2017; Langston, Kaplan, & Angelini, 2017), and nutrient availability (Dangremond, Simpson, Osborne, & Feller, 2019). In closing, multiple interacting factors, at both large and small spatial scales, will influence mangrove range expansion (Rogers & Krauss, 2018) and need to be considered to better anticipate future changes in these coastal ecosystems with climate change.

ACKNOWLEDGEMENTS

This research was funded by a NASA Climate and Biological Response grant # NX11AO94G and an NSF MacroSystems Biology Program grant # EF1065821 to ICF, an NSF Postdoctoral Fellowship in Biology award #1308565 to EMD, and a Manchester Metropolitan University studentship to JPK. Many thanks to R Bardou, G Canas, K Cavanaugh, R Feller, E Geoghegan, C Hyde, S Reed, and L Simpson for field assistance, and to the University of Manchester Genomic Technologies Core Facility and F Combe for fragment analysis. Additional thanks to two anonymous reviewers and the editor for insightful comments on an earlier version of the manuscript. As always, thank you to A Jara Cavieres, C Kennedy, and M Kennedy for unconditional support and big smiles.

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DATA ACCESSIBILITY

Microsatellite genotype data are publicly available on Dryad: https://doi.org/10.5061/dryad.2280gb5pd

AUTHOR CONTRIBUTION

JPK, EMD, MAH and ICF designed and performed the research. JPK analysed the data. RFP, JKR and ICF supervised the research. EMD, MAH and ICF drafted sections of the manuscript. JPK wrote the final manuscript with input from all co-authors.

Table 1 Hurricane-driven *Avicennia germinans* drift propagule survey sites and approximate over-water dispersal distances of unambiguously assigned propagules. Drift propagules were collected after Hurricane Irma at survey sites at or past the present-day *A. germinans* range margin and from one lower-latitude comparison site. n_G, number of drift propagules genotyped; assign, number of drift propagules unambiguously assigned to a source. [a] Maximum Euclidean distance (the most conservative estimate of dispersal possible) differed considerably from maximum over-water distance. Maximum Euclidean distances were: MZ, 457 km; FP, 327 km.

							dispersal distance (km)	
Site	Code	Location	Latitude	Longitude	n_G	assign	median	range
Fort Clinch (inlet)	F2	past margin	30.703	-81.445	99	53	109	74–109
Fort Clinch (beach)	F1	past margin	30.701	-81.434	100	60	109	74–230
Amelia Island	AI	past margin	30.506	-81.453	100	61	91	56–165
Little Talbot	LT	past margin	30.437	-81.407	100	54	81	46–307
Hanna Beach	H	past margin	30.381	-81.397	99	49	75	40–149
Vilano Inlet	V	margin	29.914	-81.289	99	50	24	12–146
Matanzas Beach	MB	margin	29.710	-81.227	99	67	2	2–124
Matanzas Inlet	MZ	margin	29.708	-81.231	100	54	36	1–1,135[a]
Fort Pierce Inlet	FP	comparison	27.475	-80.291	100	31	10	10–870[a]

Table 2 Ten vagrant *Avicennia germinans* trees found at four locations beyond the most northern established population of this species. Three of the 10 trees were unambiguously assigned to the most southern range-margin source (source code: N/GS) and three of the 10 trees were identified as putative offspring of adjacent larger trees. assign, whether trees were unambiguously assigned to a source (or classified as putative offspring of adjacent trees); source, assigned source (or putative parent); dispersal distance, approximate over-water distance from the assigned source (Euclidean distance was identical). [a] Documented northernmost *A. germinans* (Williams et al., 2014).

Tree	Latitude	Longitude	assign	source	dispersal distance (km)
AI1	30.523646	-81.446147	no		
BT1	30.483861	-81.428389	no		
BT2	30.483641	-81.428397	*offspring*	*[BT1]*	
FG1	30.421436	-81.422169	no		
FG2	30.430226	-81.421208	YES	N/GS	80
FG3	30.432978	-81.419474	YES	N/GS	80
FG4	30.432814	-81.419853	*offspring*	*[FG3]*	
FG5	30.433205	-81.420011	*offspring*	*[FG3]*	
NA1[a]	30.110310	-81.371722	no		
NA2[a]	30.109874	-81.371555	YES	N/GS	45

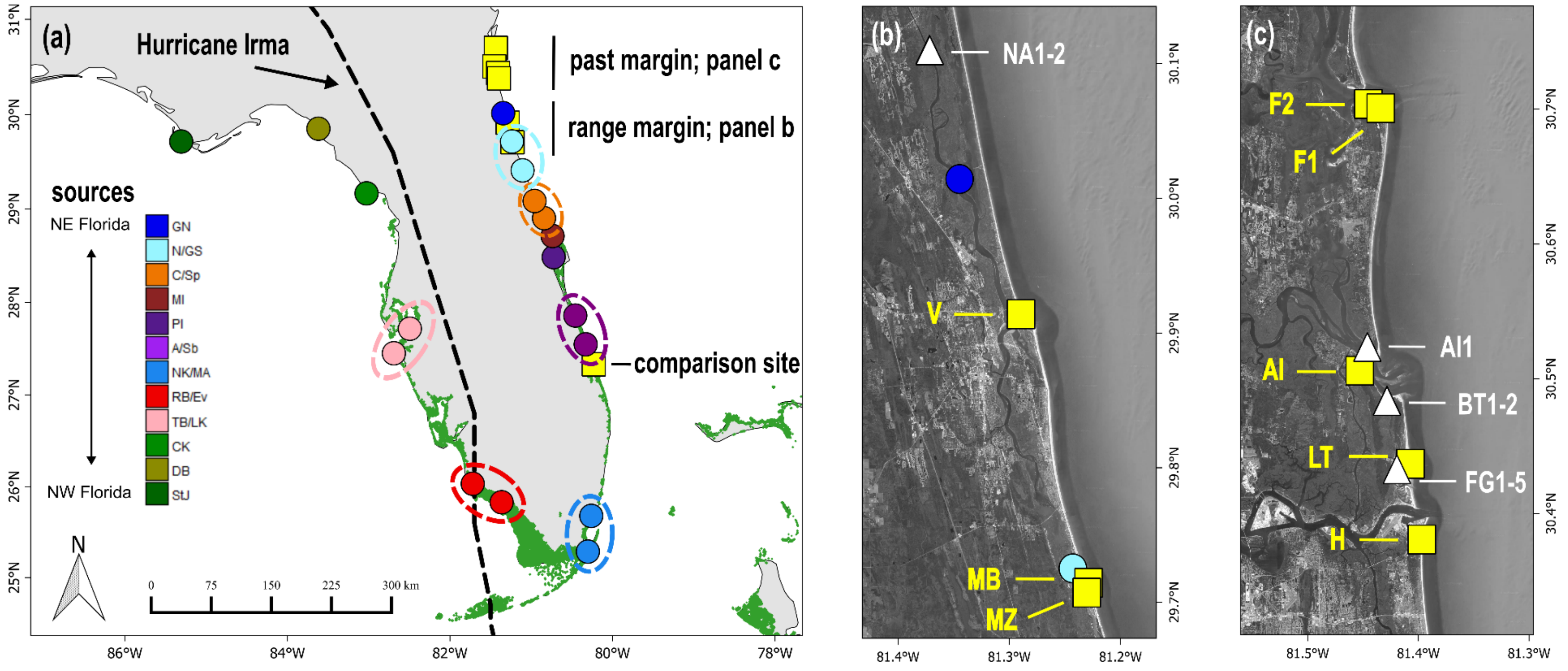

Figure 1 Survey sites for *Avicennia germinans* drift propagules (shown as yellow squares), vagrant *A. germinans* trees past the most northern established population of this species (shown as white triangles), and 12 potential source populations (shown as circles). (a) Path of Hurricane Irma shown with a dashed line (NOAA, 2017) and mangrove distribution shown in green (Giri et al., 2011). (b) Close-up of the location of three drift propagule survey sites, two vagrant trees, and the two northernmost Atlantic Florida source populations at the established *A. germinans* range margin (29.7 – 30.1°N). (c) Close-up of the location of five drift propagule survey sites and eight vagrant trees ~40-75 km past the present-day *A. germinans* range margin where no established populations exist (30.4 – 30.7°N). Source population genetic data from Kennedy, Preziosi, et al. (2020a).

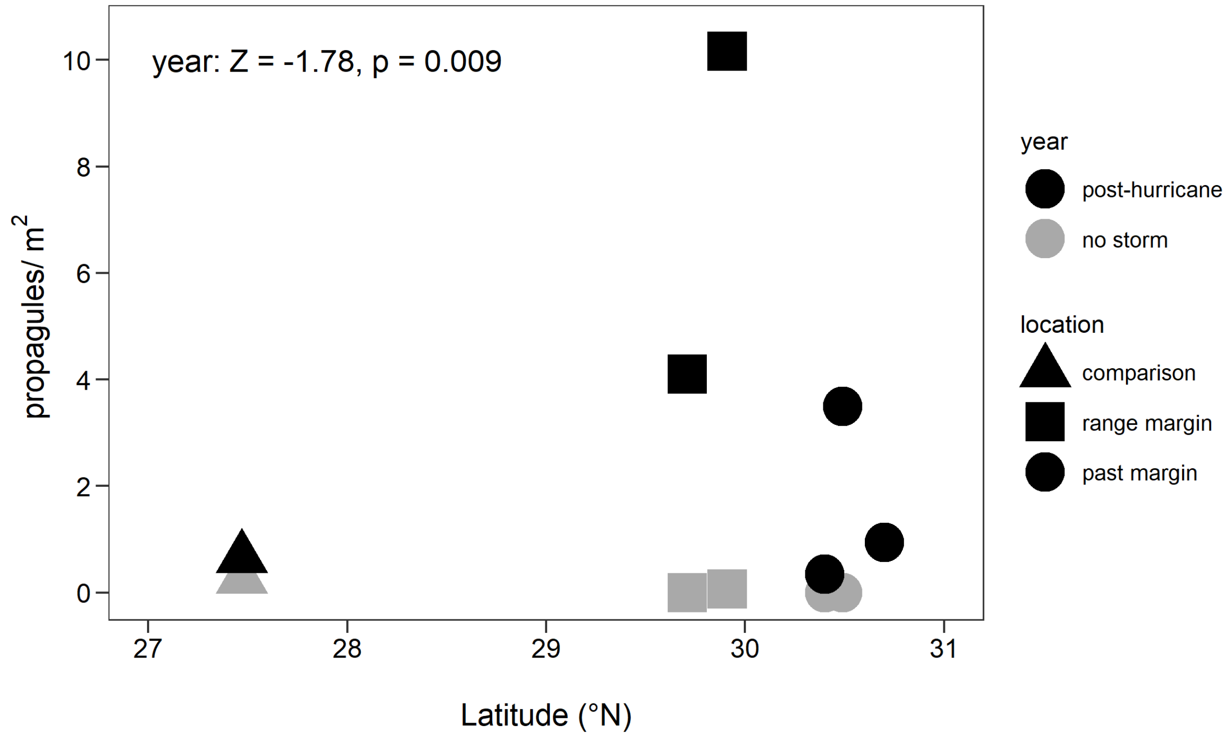

Figure 2 Massive increases in *Avicennia germinans* propagule dispersal to Atlantic Florida beaches following Hurricane Irma (2017) compared to a non-hurricane year (2014). Two beaches were surveyed at the established range margin (29.71 – 29.91°N), three beaches past the range margin (30.40 – 30.70°N), and one lower-latitude beach within the mangrove-dominated continuous range core as a comparison (27.47°N).

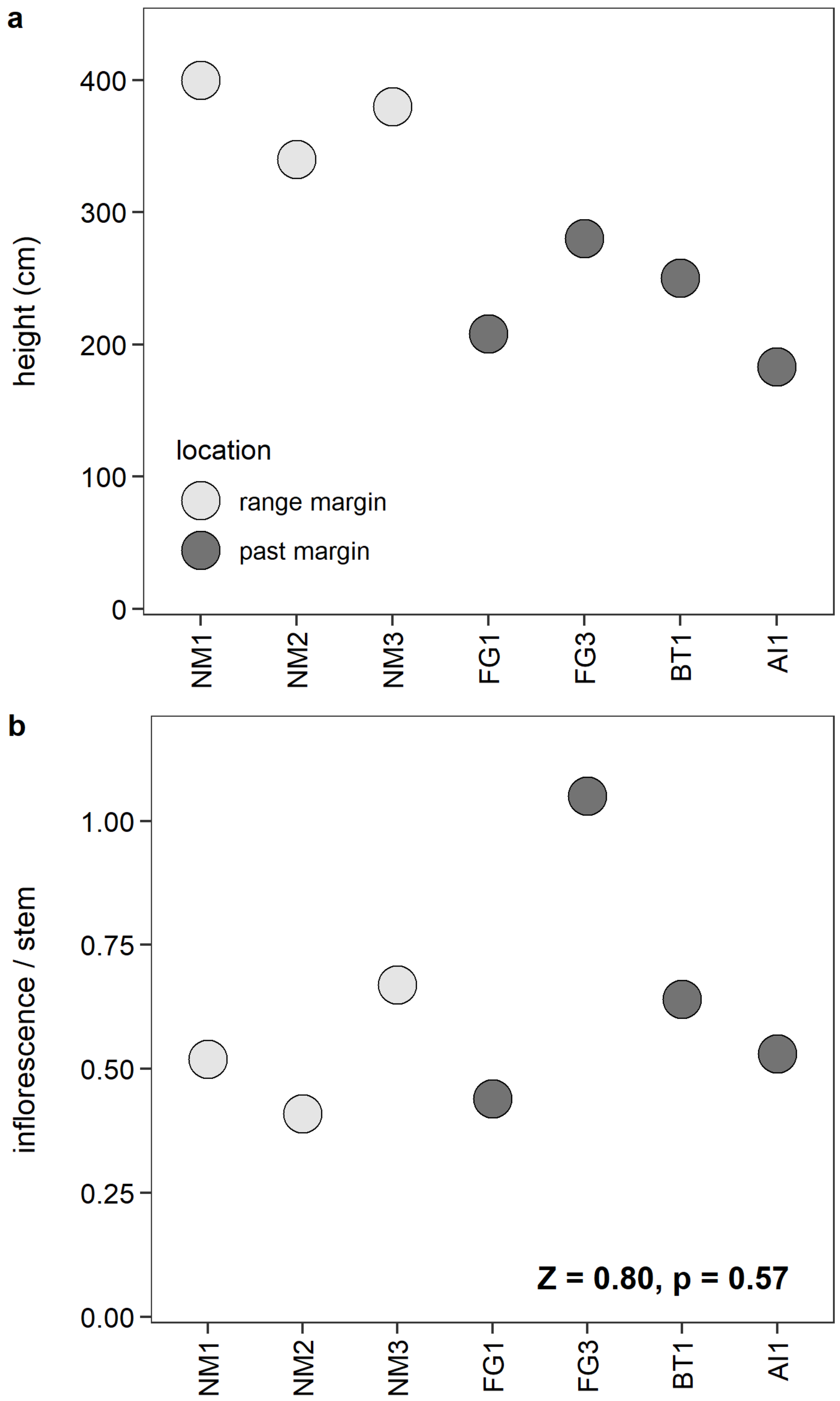

Figure 3 Four vagrant *Avicennia germinans* trees, discovered past the most northern established population of this species, are as potentially reproductive as three mature trees at the present-day range margin of this species. (a) Heights and (b) mean inflorescence per terminal stem (i.e., potential reproductive output) of three range-margin trees (29.72ºN; shown in light grey) and four vagrant trees (30.43 – 30.52ºN; shown in dark grey).

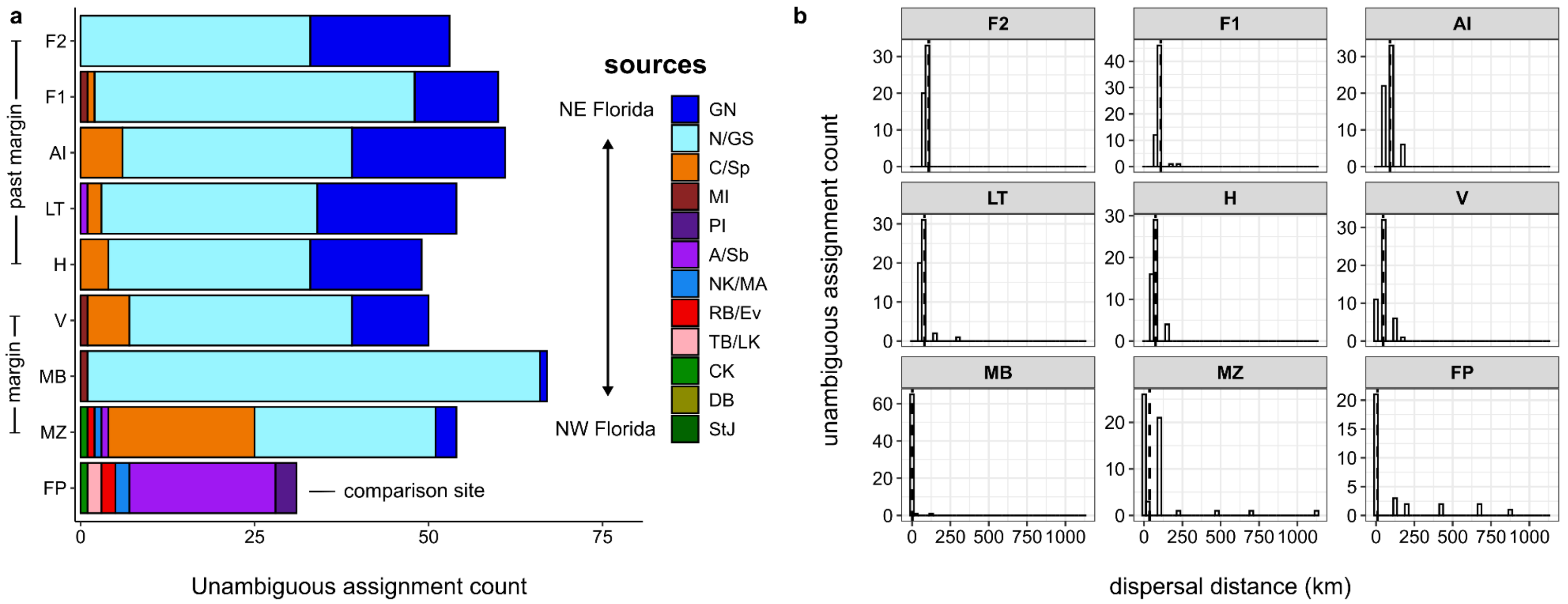

Figure 4 Hurricane-driven *Avicennia germinans* drift propagules were almost exclusively from the nearest sources. (a) Unambiguous assignment results for drift propagules from three survey sites at the present-day *A. germinans* range margin (29.7 – 29.9°N), from five survey sites past the range margin (30.3 – 30.7°N), and from one lower-latitude comparison site within the continuous range core (27.4°N). (b) Histograms of approximate over-water dispersal distances for unambiguously assigned propagules at each of the survey sites. Median distance is shown with a dashed line and bin width is 25 km. Note: y-axes vary among survey sites. Refer to Figure 1 for geographic locations of the 12 potential sources from northeast Florida (Atlantic coast) to northwest Florida (Gulf coast). Refer to Table S6 and Figure S3 for Euclidean dispersal distances.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.