



**Manchester
Metropolitan
University**

Kennedy, John Paul and Dangremond, Emily M and Hayes, Matthew A and Preziosi, Richard F and 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

Downloaded from: <https://e-space.mmu.ac.uk/625956/>

Version: Accepted Version

Publisher: Wiley

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

Usage rights: Creative Commons: Attribution 4.0

Please cite the published version

<https://e-space.mmu.ac.uk>

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

3 John Paul Kennedy¹, Emily M. Dangremond², Matthew A. Hayes³, Richard F. Preziosi¹, Jennifer
4 K. Rowntree¹, and Ilka C. Feller⁴

5 ¹Ecology and Environment Research Centre, Department of Natural Sciences, Faculty of Science
6 and Engineering, Manchester Metropolitan University, Manchester M1 5GB, UK

7 ²Department of Biological, Physical, and Health Sciences, Roosevelt University, Chicago, IL
8 60605, USA

9 ³Australian Rivers Institute - Coast & Estuaries, School of Environment & Science, Griffith
10 University, Gold Coast 4222, Queensland, Australia

11 ⁴Smithsonian Environmental Research Center, Smithsonian Institution, Edgewater, MD 21307,
12 USA

13 **Correspondence:** John Paul Kennedy, Email: john.p.kennedy@stu.mmu.ac.uk;
14 kennedy3jp@gmail.com

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

18 Running title: Hurricane-driven mangrove dispersal

19 **Abstract**

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

40

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

43

44 **INTRODUCTION**

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

56 Modelling efforts to project future distributional shifts are complicated by the fact that
57 numerous factors may constrain plant migration (Corlett & Westcott, 2013; Svenning & Sandel,
58 2013). Dispersal limitation and niche-related constraints are the two principal factors attributed
59 to migration lag, but temporal variation in these factors is not often considered (Renwick &
60 Rocca, 2015). Episodic events, such as disturbance (Boisvert-Marsh, Périé, & de Blois, 2019;
61 Lembrechts et al., 2016) or extreme climate events (Wernberg et al., 2013), can quickly
62 overcome these migration constraints and lead to periods of rapid range shifts (Renwick &

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

65 Extreme storm events (e.g., tropical cyclones, also known as typhoons or hurricanes) are one
66 mechanism that can abruptly overcome migration constraints, in particular for coastal species
67 (Lugo, 2008; Nathan et al., 2008). This is especially true for the Caribbean and Gulf of Mexico, a
68 region frequently impacted by hurricanes (Walker, Lodge, Brokaw, & Waide, 1991) and forecast
69 to experience more intense storms in the future (Murakami, Levin, Delworth, Gudgel, & Hsu,
70 2018). Numerous examples demonstrate how hurricanes are important vectors for the expansion
71 of diverse taxa within the region, including fish (Johnston & Purkis, 2015), insects (Andraca-
72 Gómez et al., 2015), and plants (Bhattarai & Cronin, 2014; Kendall, Battista, & Hillis-Starr,
73 2004). However, despite the well-recognised influence of hurricanes on distributions of species,
74 we lack an understanding of how hurricane-driven expansion can impact variation within a
75 species. Do hurricanes provide new recruits simply from the nearest sources? Or, do these high-
76 energy storms provide the conditions necessary for a greater influence of long-distance
77 dispersal? Answers to these questions have important implications for species ecology and
78 evolution with climate change (Nadeau & Urban, 2019 and citations within). Moreover,
79 quantitative analyses of plant dispersal driven by extreme meteorological events are absent from
80 the literature (Nathan et al., 2008; Schurr et al., 2018), yet they would provide empirical
81 estimates of dispersal distances that are needed to improve projections of future distributional
82 shifts (Thuiller et al., 2008).

83 Hurricane Irma provided an opportunity to address this knowledge gap at the northern range
84 limit of the neotropical black mangrove (*Avicennia germinans*) on the Atlantic coast of Florida,
85 USA. This catastrophic storm, among the strongest and costliest Atlantic hurricanes ever

86 recorded, devastated areas across the northern Caribbean and Florida (Cangialosi, Latto, & Berg,
87 2018), with massive impacts to coastal forest ecosystems (Branoff, 2019; Radabaugh et al.,
88 2019; Ross et al., 2019). From 10-12 September, 2017, Hurricane Irma progressively weakened
89 from a category 4 storm in the Florida Keys to a tropical storm in north Florida (Cangialosi et al.,
90 2018). Although the storm weakened quickly over Florida, the wind field was extensive, with the
91 strongest tropical-storm-force winds experienced on the northeast coast (Cangialosi et al., 2018)
92 (see Figure S1 for hurricane path and wind speeds).

93 In this study, we documented numbers of *A. germinans* propagules stranded on beaches
94 along this northeast coast following Hurricane Irma and compared these numbers to those found
95 previously during a non-hurricane year. We then used an extensive population-genetic data set
96 from across the Florida *A. germinans* distribution (Kennedy, Preziosi, Rowntree, & Feller,
97 2020a) to determine the origin of these drift propagules and to quantify hurricane-driven
98 dispersal distances. It is important to highlight that dispersal to these beaches (where propagules
99 cannot establish) is not analogous to effective dispersal, which would consist of propagule
100 transport plus successful establishment and subsequent reproductive success at the recipient
101 location (Auffret et al., 2017). To assess effective dispersal, we also documented multiple newly-
102 discovered *A. germinans* trees found past the most northern established population of this
103 species. For these trees, we compared measures of their potential reproductive output to those of
104 conspecifics at the present-day range margin and used the same reference data set to determine
105 their source of origin. We refer to these isolated *A. germinans* as ‘vagrant trees’ throughout this
106 publication. Vagrant trees provide evidence of prior effective dispersal along this coastline and
107 insights into the potential filter that establishment may apply to the pool of available drift
108 propagules.

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

115

116 **MATERIALS AND METHODS**

117 **Model species**

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

126 The widespread neotropical black mangrove (*Avicennia germinans*) is the predominant
127 mangrove species at northern distributional limits in the United States (Lonard, Judd, Summy,
128 DeYoe, & Stalter, 2017). Atlantic Florida *A. germinans* inhabit protected estuaries with access to
129 the ocean via a series of inlets. Propagules generally abscise from maternal trees in great
130 numbers from late August through October, and some eventually exit these estuaries via inlets
131 and become stranded on Atlantic coast beaches (I.C. Feller, *personal observation*). Long-

132 distance dispersal of this species is possible as its propagules remain viable even after extensive
133 flotation periods (Alleman & Hester, 2011b; Rabinowitz, 1978), further supported by genetic
134 evidence for trans-oceanic dispersal (Cerón-Souza et al., 2015; Mori, Zucchi, Sampaio, & Souza,
135 2015; Nettel & Dodd, 2007). However, *A. germinans* propagules are generally retained within
136 estuaries and most dispersal is restricted to short distances (Sousa, Kennedy, Mitchell, &
137 Ordóñez L, 2007), as evidenced by strong within-estuary spatial genetic structure (Cerón-Souza,
138 Bermingham, McMillan, & Jones, 2012). Establishment success for *A. germinans* propagules is
139 also inversely related to flotation time (Alleman & Hester, 2011b; Simpson, Osborne, & Feller,
140 2017).

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

151

152 **Beach surveys**

153 We adapted methods used to quantify mangrove dispersal (Clarke, 1993; Sengupta, Middleton,
154 Yan, Zuro, & Hartman, 2005) to survey Atlantic Florida *A. germinans* propagule densities on

155 beaches adjacent to inlets. We surveyed two beaches at the established range margin of this
156 species (29.71 – 29.91°N) (Spalding, Kainuma, & Collins, 2010), three beaches past the range
157 margin (~40-75 km to the north) where no established mangrove populations exist (30.40 –
158 30.70°N), and one lower-latitude beach within the mangrove-dominated continuous range core
159 as a comparison (27.47°N) (Figure 1). We performed equivalent surveys on 24-28 September,
160 2014 (a non-hurricane year) and 14-16 October, 2017 (five weeks after Hurricane Irma made
161 landfall in Florida), except for the most northern beach that was only surveyed in 2017. At each
162 survey site, we ran three to eight 100 m transects along the high tide line and counted all
163 putatively-viable drift propagules found within 1 m of the transect line (i.e., decomposed
164 propagules were noted, but not included in these counts). Numbers of transects varied depending
165 on the length of the beach, and each transect line was separated from the next by 100 m. We
166 tested for differences in propagule densities between the two collection years (n = 5 sites per
167 year) with a two-sample Fisher-Pitman permutation test, with 10⁴ re-samplings, in the R-package
168 coin (Hothorn, Hornik, van de Wiel, & Zeileis, 2008) in R v3.6.0 (R Core Team, 2013).

169 We collected all putatively-viable drift propagules during the 2017 post-Hurricane Irma
170 beach surveys. Propagules from each survey site were stored together in plastic bags during field
171 collections. For three of the six surveyed beaches, we subset samples into two collections that
172 corresponded to areas within an inlet and those outside along the Atlantic ocean (i.e., MZ and
173 MB, F2 and F1, each respectively), or to areas separated by an inlet (i.e., H, LT) (Table 1; Figure
174 1b, c). We haphazardly chose 100 propagules of all sizes from each of these nine collection sites
175 for genetic analysis (n = 900 total propagules) and stored them at -20°C.

176 We assessed viability of these post-Hurricane Irma drift propagules with another subset of
177 100 propagules from each of the nine collection sites (n = 900 total propagules). We placed

178 propagules in shallow, plastic trays with a thin layer of wet potting soil/sand until root radicles
179 developed, and then transferred them to individual tree tubes (Ray Leach Cone-tainers, Stuewe
180 and Sons., Inc.; 2.5 cm diameter, 12.1 cm length; 49 ml volume) filled with a 2:1 mixture of
181 commercial potting soil and sand. We placed tubes into racks of 100 and allowed propagules to
182 grow in non-saline, deionized water in flooded plastic tubs with the water depth maintained at 10
183 cm. All seedlings were grown, with no nutrient additions, in a walk-in environmental growth
184 chamber at the Smithsonian Environmental Research Center (Maryland, USA), with
185 chamber temperature and humidity maintained throughout this period (0:00-6:00: 16°C, 6:00-
186 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
187 propagules that established and began growing true leaves (i.e., post-cotyledons).

188

189 **Vagrant tree surveys**

190 We conducted coastal surveys by vessel over a 12-month period prior to Hurricane Irma (July
191 2016 to June 2017) along the intercoastal waterway between St Augustine, Florida, and
192 Cumberland Island, Georgia (29.9 – 31.0°N), an area past the most northern established *A.*
193 *germinans* population. Surveys were conducted by trolling close to shore at low speed and
194 visually searching for trees growing within the salt marsh. A leaf was collected from each
195 discovered tree and dehydrated in silica gel for genetic analysis.

196 In August 2018, we revisited sites where we had previously found vagrant trees and
197 identified four adult trees producing flowers. For these four trees, we measured height and
198 potential reproductive output as mean inflorescence per terminal stem. We haphazardly selected
199 a large mature branch, counted terminal stems (aiming for at least 60), and then counted how
200 many terminal stems had inflorescence. We divided total inflorescence count by total terminal

201 stem count to calculate inflorescence per terminal stem. We repeated this process three times for
202 each tree and used mean values for analysis. We then selected three trees at the present-day *A.*
203 *germinans* range margin (29.727°N, 81.239°W) to compare with these four reproductive vagrant
204 trees. We repeated measures of height, terminal stem counts, and inflorescence counts on these
205 three range-margin trees. We selected these particular trees because they were larger than
206 neighbouring trees, and presumably the most mature in the area. We tested for differences in
207 mean inflorescence per terminal stem between the vagrant trees (n = 4) and range-margin trees (n
208 = 3) with a two-sample Fisher-Pitman permutation test, with 10⁴ re-samplings, in the R-package
209 coin (Hothorn et al., 2008).

210

211 **DNA isolation and Microsatellite genotyping**

212 For drift propagules, we removed the cotyledons and isolated genomic DNA from 50 mg of
213 frozen hypocotyl/radicle tissue with the DNeasy 96 Plant Kit (Qiagen, Hilden, Germany)
214 following the standard protocol. For vagrant trees, we isolated genomic DNA from 20 mg of
215 dried leaf tissue with the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) following the
216 standard protocol, with an extended incubation of 45 minutes. We genotyped all samples at 12
217 previously-developed nuclear microsatellite loci (Cerón-Souza et al., 2012; Cerón-Souza,
218 Rivera-Ocasio, Funk, & McMillan, 2006; Mori, Zucchi, Sampaio, & Souza, 2010; Nettel, Rafii,
219 & Dodd, 2005) according to the protocol outlined in Kennedy, Sammy, Rowntree, & Preziosi
220 (2020) for drift propagules and the protocol outlined in Kennedy, Preziosi, et al. (2020b) for
221 vagrant trees. We performed PCR on a Prime thermal cycler (Techne, Staffordshire, UK),
222 analysed fragments on an Applied Biosystems 3730 DNA Analyzer (Applied Biosystems, Foster
223 City, California, USA) with LIZ 500 size standard, and scored alleles in the R-package Fragman

224 (Covarrubias-Pazaran, Diaz-Garcia, Schlautman, Salazar, & Zalapa, 2016). We re-amplified and
225 re-genotyped 5% of the drift propagule DNA samples to estimate a study error rate (Bonin et al.,
226 2004), and did the same for all of the vagrant tree DNA samples to ensure we had the correct
227 multi-locus genotypes. Microsatellite genotype data are available at the Dryad digital repository
228 (Kennedy, Dangremond, et al., 2020).

229

230 **Genetic assignments**

231 For all genetic assignments, we used GENECLASS2 (Piry et al., 2004) to calculate (1) the
232 probability that each individual (i.e., multi-locus genotype) could belong to each potential source
233 (based on the allele frequencies within each source) with the Paetkau et al. (2004) Monte Carlo
234 re-sampling method and 10^3 resampled individuals, and (2) source log-likelihood with the
235 Rannala and Mountain (1997) Bayesian assignment method. For potential sources, we used a
236 subset of an *A. germinans* reference data set with trees from 32 Florida collection sites that were
237 genotyped at the same 12 microsatellite loci ($n = 860$ individuals; Kennedy, Preziosi, et al.,
238 2020a) (Figure S2). Simulations demonstrate that the Rannala & Mountain (1997) Bayesian
239 assignment method can achieve 100% correct assignments with ≥ 10 microsatellite loci, 30-50
240 sampled individuals from each of 10 populations, and inter-population $F_{ST} = 0.1$, with reduced
241 success at lower F_{ST} (Cornuet, Piry, Luikart, Estoup, & Solignac, 1999; Waples & Gaggiotti,
242 2006). Hence, we used inter-site $F_{ST} \geq 0.1$ as a threshold to reduce the entire reference data set
243 into 12 potential sources that encompass the entire Florida *A. germinans* distribution (Figure 1a;
244 see Appendix S1, Table S1-S2 for detailed description).

245 Prior to our assignments of drift propagules and vagrant trees, we used known-origin
246 propagules to test the power of the assignment analyses and to define *a priori* confidence

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

255 For each unambiguous assignment of a drift propagule or vagrant tree, we measured the
256 approximate over-water dispersal distance from the assigned source in Google Earth Pro
257 7.3.2.5776. We measured dispersal as over-water distances because *A. germinans* propagules are
258 hydrochorous (i.e., water is the predominant dispersal vector), but we cannot be certain how
259 hurricane-force winds may have influenced propagule dispersal pathways. As such, we also
260 measured Euclidean distances from assigned sources in the R-package geosphere (Hijmans,
261 Williams, & Vennes, 2019) as the most conservative estimate possible of dispersal distances.

262

263 **RESULTS**

264 **Beach surveys**

265 In 2014, under non-storm conditions, we found a range from 0 to 317 *A. germinans* propagules at
266 five survey sites. We observed highest densities at the lower-latitude, within-range-core
267 comparison site (27.47°N, 0.26 propagules/m²), minimal propagule numbers at the two range-
268 margin sites (29.71°N, 0.001 propagules/m²; 29.91°N, 0.07 propagules/m²), and no propagules at
269 the two sites past the range margin (30.40°N, 30.49°N) (Table S3; Figure 2). In 2017, five weeks

270 after Hurricane Irma, we found a massive increase in propagule numbers, with a range from 329
271 to 3,048 *A. germinans* propagules at six survey sites from 27.47 to 30.70°N (Table S3).
272 Propagules were present at higher densities post-hurricane (range: 0.34-10.16 propagules/m²)
273 than under non-storm conditions (two-sample Fisher-Pitman permutation test, $Z = -1.78$, $p =$
274 0.009; Figure 2). We observed highest post-hurricane densities at the two range-margin sites
275 (29.71°N, 4.10 propagules/m²; 29.91°N, 10.16 propagules/m²) where propagule numbers were
276 orders of magnitude higher than under non-storm conditions (29.71°N, 2014: 2 propagules,
277 2017: 2,462 propagules; 29.91°N, 2014: 97 propagules, 2017: 3,048 propagules) (Table S3;
278 Figure 2). Almost all post-hurricane drift propagules were viable as 99% (894 of 900) of those
279 planted established and produced true leaves (i.e., post-cotyledons) in the environmental growth
280 chamber.

281

282 **Vagrant tree surveys**

283 We identified a total of 11 *A. germinans* (10 trees, one seedling) at four locations beyond the
284 most northern established population of this species (Table 2; Figure 1b, c). From south to north,
285 we first identified two trees on the Tolomato River (30.11°N) that are the documented
286 northernmost *A. germinans* (Williams et al., 2014). Second, we found five trees at Fort George
287 Inlet (30.43°N). Two larger trees were each isolated from the others by approximately 320 m and
288 1 km, while a third larger tree was located 40-55 m from two smaller trees. Third, we found two
289 trees and one seedling, which was not sampled to avoid potential damage to its photosynthetic
290 ability, on the north of Big Talbot Island (30.48°N). The larger of the two trees was located 25 m
291 from the smaller tree. Fourth, we found one tree towards the south of Amelia Island (30.52°N).

292 The four vagrant trees that were reproductive (identified at three of the four locations)
293 ranged in height from 183 to 280 cm, and the three trees sampled farther south at the range
294 margin ranged in height from 340 to 400 cm (Figure 3a). Mean inflorescence per terminal stem
295 was not statistically different between these vagrant trees and range-margin trees ($Z = 0.80$, $p =$
296 0.57), with a range of 0.44-1.05 inflorescence/stem and 0.41-0.67 inflorescence/stem,
297 respectively (Figure 3b). One vagrant tree (FG3) was notably more fecund than the other
298 measured trees (Figure 3b).

299

300 **Genotyping and Genetic assignments**

301 *Drift propagules*

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

306 The probability that each of the 150 known-origin propagules belonged to their respective
307 source ranged from 0.001 to 0.99 (mean = 0.44; Appendix S1). A total of 97% (146 of 150) of
308 these propagules were correctly assigned to their source, with the highest assignment score for a
309 mis-assigned propagule of 0.88 (Appendix S1, Table S4). Based on these results, we assigned the
310 following confidence thresholds to subsequent assignment analyses of drift propagules and
311 vagrant trees. We defined $p < 0.001$, the lowest probability observed, as the threshold to exclude
312 a potential source. We also defined an assignment score ≥ 0.91 as the acceptance threshold for an
313 unambiguous assignment, based on the highest score for a mis-assigned, known-origin

314 propagule. This conservative acceptance threshold indicates that a multi-locus genotype must be
315 at least 10x more likely to belong to the assigned source than to any other potential source.

316 None of the 896 drift propagules were excluded from all 12 potential sources (i.e., $p > 0.001$
317 for at least one source; Table S5), which suggests that all the genotyped drift propagules were
318 sourced from Florida populations. We unambiguously assigned 56% of drift propagules from the
319 eight survey sites at or past the range margin (448 of 796), with a range within-site from 49%
320 (site code: H) to 68% (site code: MB) (Table 1, Table S6). A total of 89% (400 of 448) of these
321 unambiguous assignments were sourced from the range margin (source code: N/GS, GN), 9%
322 (40 of 448) were sourced from the nearest within-range-core source (source code: C/Sp; over-
323 water distance: 75-185 km) and <2% (8 of 448) were transported over longer distances from the
324 Atlantic (East) and Gulf (West) coasts of Florida (over-water distance: 124-1,135 km) (Table 1;
325 Figure 4). Each of these eight survey sites exhibited similar assignment patterns (i.e., 86-100%
326 assigned to range-margin sources), except for the most southern range-margin site (site code:
327 MZ; Figure 4). Almost half of the unambiguous assignments at MZ (46%; 25 of 54) were
328 sourced to the nearest within-range-core source (39%) or via longer distances (7%; over-water
329 distance: 225-1,135 km) (Figure 4). We unambiguously assigned fewer drift propagules at the
330 lower-latitude, within-range-core comparison site (31 of 100; Table 1, Table S6), but observed a
331 similar pattern to the more northern survey sites. Most propagules (68%; 21 of 31) were assigned
332 to the nearest source (source code: A/Sb), with 16% (5 of 31) from adjacent sources (source
333 code: NK/MA, PI), and 16% (5 of 31) via longer distances from sources on the Gulf (West) coast
334 of Florida (over-water distance: 440-870 km) (Table 1; Figure 4). Euclidean distances across all
335 unambiguous assignments ($n = 479$; median: 74 km, range: 1-457 km) were nearly identical to
336 over-water dispersal distances ($n = 479$; median: 74 km, range: 1-1,135 km), except for the

337 limited number (8 of 479) of dispersal events at the longest distance intervals (Table S6; Figure
338 S3). These eight dispersal events were considerably shorter based on Euclidean distance (range:
339 184-457 km) compared to over-water distance (range: 434-1,135 km) (Figure S3).

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

346

347 *Vagrant trees*

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

353 None of the seven vagrant trees included in assignment analyses were excluded from all 12
354 sources, with highest probabilities from the two range-margin sources and the nearest within-
355 range-core source (Table S5). We unambiguously assigned three of the seven vagrant trees (from
356 two of the four sampled locations), and all three trees were sourced to the most southern range-
357 margin source (source code: N/GS; Table 2, Table S6). The first and second most-likely sources
358 for the remaining four vagrant trees were a combination of the two range-margin and nearest

359 within-range-core sources (Table S6). Hence, although we could not unambiguously assign a
360 source, these four trees also came from the nearest potential sources.

361

362 **DISCUSSION**

363 Migration lag in trees may be the product of multiple constraints, but episodic events can quickly
364 overcome these constraints and lead to transient periods of rapid range shifts (Renwick & Rocca,
365 2015). This study highlights how hurricanes create the conditions needed to drive range
366 expansion at a northern distributional limit of the neotropical black mangrove (*Avicennia*
367 *germinans*) and can shape patterns of genetic variation in expanding populations of this species.
368 These insights, along with empirical estimates of hurricane-driven dispersal distances, should
369 improve our ability to forecast future distributional shifts of this species, and other coastal
370 species often impacted by extreme storm events.

371

372 **Hurricanes are a vector of range expansion**

373 Climate models predict that, at a global scale, storm numbers may decline in the future, but that
374 the strongest storms will become more intense and that sea level rise will exacerbate storm surge
375 effects (Walsh et al., 2016 and citations within). In particular, a greater prevalence of major
376 hurricanes (\geq category 3) is forecast in the Caribbean and Gulf of Mexico as the tropical North
377 Atlantic continues to warm (Murakami et al., 2018). These trends may enhance long-distance
378 dispersal of mangrove propagules and facilitate poleward range expansion (Van der Stocken,
379 Carroll, Menemenlis, Simard, & Koedam, 2019; Van der Stocken, Wee, et al., 2019). After
380 Hurricane Irma, we documented large numbers of *A. germinans* drift propagules along Atlantic
381 Florida beaches at, and past, the present-day range margin of this species. Provision of

382 propagules to these areas, where we found limited or no propagules in 2014 (a non-hurricane
383 year), suggests that hurricanes function as episodic events that are necessary for these estuarine
384 mangroves to expand poleward. Consistent with this conclusion, expansion patterns of invasive
385 species within this region have been linked to hurricane frequency (Bhattarai & Cronin, 2014;
386 Johnston & Purkis, 2015). However, we only document one non-hurricane (2014) and one
387 hurricane (2017) year and, due to the timing of Hurricane Irma, our beach surveys were
388 approximately 2.5 weeks later in 2017. Annual and seasonal differences in propagule production
389 and release could account for some of the variation in drift-propagule densities between our two
390 sampling periods, although only a relatively slight increase in drift-propagule density at the
391 lower-latitude comparison site in 2017 compared to 2014 suggests that these differences may not
392 have had a substantial impact. Instead, *A. germinans* propagules are generally retained within
393 estuaries (Sousa et al., 2007), as are those of a congener (*A. marina*) (Clarke, 1993; Van der
394 Stocken, Vanschoenwinkel, De Ryck, & Koedam, 2018), which would explain why we observed
395 comparatively limited numbers of beach-stranded propagules (and no propagules past the
396 present-day range margin) under non-storm conditions. Extreme high-water events, associated
397 with storm surge, are also needed to disperse mangrove propagules over dense salt-marsh
398 vegetation to enable expansion inland (Peterson & Bell, 2012; Rodriguez, Feller, & Cavanaugh,
399 2016). Therefore, for mangrove range expansion to occur, the pulse of energy and unusually
400 high-water levels provided by hurricanes seem to be the prerequisite needed to flush propagules
401 out of estuaries in large numbers and into more poleward, salt-marsh-dominated areas.

402 We observed highest drift-propagule densities at the lower-latitude comparison site during a
403 non-hurricane year. As Florida mangroves decline in abundance with latitude (Osland et al.,
404 2017), the number of propagules dispersed out of estuaries may generally be dictated by

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

419

420 **Expanding genotypes are from the nearest sources**

421 Where do hurricane-dispersed propagules come from? Extreme storm events have the potential
422 to drive trans-oceanic dispersal (Carlton et al., 2017; Waters, King, Fraser, & Craw, 2018);
423 however, we found that the vast majority of drift propagules collected after Hurricane Irma came
424 from the nearest sources. Hence, hurricanes may provide an expanding gene pool that consists of
425 a much-reduced representation of genetic variation within a species, although even limited long-
426 distance dispersal (as observed here) can lead to substantial increases in genetic variation
427 (Bialozyt, Ziegenhagen, & Petit, 2006). Migration models for terrestrial tree species find a

428 similar pattern, with colonisation past present-day distributions mostly influenced by the species'
429 abundance at the range limit (Iverson et al., 2004). Yet, while forecast migration of these
430 terrestrial trees for the next 100 years is mostly restricted to 10-20 km (Iverson et al., 2004;
431 Prasad et al., 2013), we found dispersal to beaches >100 km from range-margin sources after a
432 single storm event and vagrant trees 80 km from their assigned source. This contrast is consistent
433 with longer transport potential for coastal species (Nathan et al., 2008) and highlights that coastal
434 range expansions have the potential to occur rapidly over large spatial scales.

435 A leptokurtic dispersal kernel, where most dispersal occurs over short distances, is
436 consistent with genetic analyses across mangrove species (Van der Stocken, Wee, et al., 2019
437 and citations within). Local sources are also thought to provide propagules for mangrove forest
438 regeneration after storms (Krauss & Osland, 2020). This pattern is consistent with restricted gene
439 flow in taxa from spatially-discrete estuarine habitats (Bilton, Paula, & Bishop, 2002).
440 Remarkably, the proportions of unambiguous assignments from our eight survey sites at or past
441 the *A. germinans* range margin (89% from range margin, 9% from nearest range core, 2% longer
442 distances) were similar to the proportions of propagules from a congener (*A. marina*) collected
443 within different zones of an East African estuary (83% adjacent to forest, 16% near estuary exit,
444 <1% outside estuary; Van der Stocken et al., 2018). Dispersal patterns of propagules from
445 *Avicennia* species may not change substantially whether within tidal estuaries or following
446 extreme storm events (i.e., most propagules remain closest to their source, very few travel longer
447 distances); however, we found that storms create a transient shift in the dispersal kernel towards
448 massively greater spatial scales (from metres to kilometres). Further genetic research that
449 determines the origins of drift propagules found during non-storm periods will be needed to
450 better quantify the effect of these storms on dispersal distances.

451 Although most dispersal was sourced to the nearest populations, we did find a greater
452 proportion of dispersal from more distant sources at the most southern range-margin survey site
453 and at the lower-latitude comparison site (maximum over-water distance: 1,135 km, 870 km,
454 respectively). Euclidean distances were considerably shorter (maximum distance: 457 km, 327
455 km, respectively), but may be overly conservative as propagules would need to be dispersed
456 overland by wind from the Gulf (West) coast to the Atlantic (East) coast of Florida. Of the nine
457 survey sites in this study, these two sites with greater proportions of long-distance dispersal are
458 the most geographically proximate to larger mangrove forests south of the range margin. Greater
459 geographical isolation from these lower-latitude forests may explain the lack of dispersal over
460 longer distances to the more northern survey sites. In addition, our observations may reflect a
461 density-dependent process, where an overwhelming number of local propagules further dilutes
462 the already small proportion of propagules from more-distant sources (Waters, Fraser, & Hewitt,
463 2013). This possibility may explain why we observed numerous unambiguous assignments to the
464 adjacent range-margin source, but almost no evidence of longer-distance dispersal, at the survey
465 site (code: MB) that borders the most southern range-margin survey site.

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

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

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

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

504

505 **Insights for modelling range shifts**

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

513 Mangrove distributional limits are controlled by climatic thresholds in minimum temperature
514 and/or precipitation (Cavanaugh et al., 2018; Osland et al., 2017). Forecast warming trends
515 indicate that Atlantic Florida mangroves at their present-day range margin will rarely be
516 constrained by periodic freeze events into the future, and as a result will permanently replace
517 neighbouring salt-marsh vegetation (Cavanaugh et al., 2019, 2015). Based on these climate
518 projections, the distribution of *A. germinans* is forecast to expand northward ~160 km over the
519 next 50 years (3.2 km per year; Cavanaugh et al., 2015). However, as highlighted by Cavanaugh

520 et al. (2015), release from this climatic constraint alone does not guarantee range expansion if
521 not accompanied by propagule dispersal and an availability of suitable habitat. Here, we found
522 that *A. germinans* poleward expansion is likely dispersal limited under ‘normal’ conditions, and
523 that episodic extreme storm events are needed to move propagules past the contemporary range
524 limit. In line with this conclusion, the present-day Atlantic Florida mangrove range margin is
525 experiencing rapid range infilling (Simpson, Stein, Osborne, & Feller, 2019), but our coastal
526 surveys indicate very little in terms of poleward expansion. Therefore, Atlantic Florida mangrove
527 expansion will presumably not be a progressive march poleward, and instead, this process will
528 likely occur via a series of starts and stops driven by propagule dispersal out of estuaries and
529 over longer distances following extreme storm events.

530 Incorporating biological mechanisms into predictive models should improve our ability to
531 forecast changes in biodiversity with climate change (Urban et al., 2016). Mechanistic models
532 can provide more realistic predictions and possibly greater transferability across geographic
533 regions, although many uncertainties and shortcomings still remain (Yates et al., 2018).
534 Cavanaugh et al. (2015) took the first step in this direction with their incorporation of a
535 mechanistic predictor (i.e., freeze degree days) to forecast mangrove range expansion along
536 Atlantic Florida, with a fully-mechanistic model of mangrove distributions as a possible next
537 step. Our research suggests that, in addition to physiological thresholds, including hurricane
538 projections (e.g., storm frequencies, trajectories, intensities) is essential for more realistic
539 forecasts of Atlantic Florida mangrove expansion, as poleward dispersal will likely be restricted
540 to these transient windows. We also provide empirical estimates of hurricane-driven dispersal
541 distances (measured as both over-water distance and Euclidean distance, the most conservative
542 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.

556

557 **ACKNOWLEDGEMENTS**

558 This research was funded by a NASA Climate and Biological Response grant # NX11AO94G
559 and an NSF MacroSystems Biology Program grant # EF1065821 to ICF, an NSF Postdoctoral
560 Fellowship in Biology award #1308565 to EMD, and a Manchester Metropolitan University
561 studentship to JPK. Many thanks to R Bardou, G Canas, K Cavanaugh, R Feller, E Geoghegan,
562 C Hyde, S Reed, and L Simpson for field assistance, and to the University of Manchester
563 Genomic Technologies Core Facility and F Combe for fragment analysis. Additional thanks to
564 two anonymous reviewers and the editor for insightful comments on an earlier version of the

565 manuscript. As always, thank you to A Jara Cavieres, C Kennedy, and M Kennedy for
566 unconditional support and big smiles.

567

568 REFERENCES

- 569 Alexander, J. M., Chalmandrier, L., Lenoir, J., Burgess, T. I., Essl, F., Haider, S., ... Pellissier,
570 L. (2018). Lags in the response of mountain plant communities to climate change. *Global*
571 *Change Biology*, 24(2), 563–579. doi: 10.1111/gcb.13976
- 572 Alleman, L. K., & Hester, M. W. (2011a). Refinement of the fundamental niche of black
573 mangrove (*Avicennia germinans*) seedlings in Louisiana: Applications for restoration.
574 *Wetlands Ecology and Management*, 19, 47–60. doi: 10.1007/s11273-010-9199-6
- 575 Alleman, L. K., & Hester, M. W. (2011b). Reproductive Ecology of Black Mangrove (*Avicennia*
576 *germinans*) Along the Louisiana Coast: Propagule Production Cycles, Dispersal
577 Limitations, and Establishment Elevations. *Estuaries and Coasts*, 34(5), 1068–1077. doi:
578 10.1007/s12237-011-9404-8
- 579 Andraca-Gómez, G., Ordano, M., Boege, K., Domínguez, C. A., Piñero, D., Pérez-Ishiwara, R.,
580 ... Fornoni, J. (2015). A potential invasion route of *Cactoblastis cactorum* within the
581 Caribbean region matches historical hurricane trajectories. *Biological Invasions*, 17(5),
582 1397–1406. doi: 10.1007/s10530-014-0802-2
- 583 Auffret, A. G., Rico, Y., Bullock, J. M., Hooftman, D. A. P., Pakeman, R. J., Soons, M. B., ...
584 Cousins, S. A. O. (2017). Plant functional connectivity – integrating landscape structure and
585 effective dispersal. *Journal of Ecology*, 105(6), 1648–1656. doi: 10.1111/1365-2745.12742
- 586 Benoiel Carvalho, S., Torres, J., Tarroso, P., & Velo-Antón, G. (2019). Genes on the edge: A
587 framework to detect genetic diversity imperiled by climate change. *Global Change Biology*,
588 25(12), 4034–4047. doi: 10.1111/gcb.14740
- 589 Bertrand, R., Lenoir, J., Piedallu, C., Dillon, G. R., De Ruffray, P., Vidal, C., ... Gégout, J. C.
590 (2011). Changes in plant community composition lag behind climate warming in lowland
591 forests. *Nature*, 479(7374), 517–520. doi: 10.1038/nature10548
- 592 Bhattarai, G. P., & Cronin, J. T. (2014). Hurricane activity and the large-scale pattern of spread
593 of an invasive plant species. *PLoS ONE*, 9(5), e98478. doi: 10.1371/journal.pone.0098478
- 594 Bialozyt, R., Ziegenhagen, B., & Petit, R. J. (2006). Contrasting effects of long distance seed
595 dispersal on genetic diversity during range expansion. *Journal of Evolutionary Biology*, 19,
596 12–20. doi: 10.1111/j.1420-9101.2005.00995.x
- 597 Bilton, D. T., Paula, J., & Bishop, J. D. D. (2002). Dispersal, genetic differentiation and
598 speciation in estuarine organisms. *Estuarine, Coastal and Shelf Science*, 55(6), 937–952.
599 doi: 10.1006/ecss.2002.1037
- 600 Boisvert-Marsh, L., Périé, C., & de Blois, S. (2019). Divergent responses to climate change and
601 disturbance drive recruitment patterns underlying latitudinal shifts of tree species. *Journal*
602 *of Ecology*, 107(4), 1956–1969. doi: 10.1111/1365-2745.13149
- 603 Bonan, G. B. (2008). Forests and climate change: Forcings, feedbacks, and the climate benefits
604 of forests. *Science*, 320(5882), 1444–1449. doi: 10.1126/science.1155121
- 605 Bonin, A., Bellemain, E., Eidesen, P. B., Pompanon, F., Brochmann, C., & Taberlet, P. (2004).
606 How to track and assess genotyping errors in population genetics studies. *Molecular*

607 *Ecology*, 13(11), 3261–3273. doi: 10.1111/j.1365-294X.2004.02346.x

608 Branoff, B. L. (2019). Mangrove Disturbance and Response Following the 2017 Hurricane
609 Season in Puerto Rico. *Estuaries and Coasts*. doi: 10.1007/s12237-019-00585-3

610 Bush, A., Mokany, K., Catullo, R., Hoffmann, A., Kellermann, V., Sgrò, C., ... Ferrier, S.
611 (2016). Incorporating evolutionary adaptation in species distribution modelling reduces
612 projected vulnerability to climate change. *Ecology Letters*, 19(12), 1468–1478. doi:
613 10.1111/ele.12696

614 Cangialosi, J. P., Latta, A. S., & Berg, R. (2018). National Hurricane Center Tropical Cyclone
615 Report. Hurricane Irma (AL112017) 30 August - 12 September 2017. Retrieved June 4,
616 2018, from National Hurricane Center website:
617 https://www.nhc.noaa.gov/data/tcr/AL112017_Irma.pdf

618 Carlton, J. T., Chapman, J. W., Geller, J. B., Miller, J. A., Carlton, D. A., McCuller, M. I., ...
619 Ruiz, G. M. (2017). Tsunami-driven rafting: Transoceanic species dispersal and
620 implications for marine biogeography. *Science*, 357(6358), 1402–1406. doi:
621 10.1126/science.aao1498

622 Cavanaugh, K. C., Dangremond, E. M., Doughty, C. L., Williams, A. P., Parker, J. D., Hayes, M.
623 A., ... Feller, I. C. (2019). Climate-driven regime shifts in a mangrove–salt marsh ecotone
624 over the past 250 years. *Proceedings of the National Academy of Sciences*, 116(43), 21602–
625 21608. doi: 10.1073/pnas.1902181116

626 Cavanaugh, K. C., Kellner, J. R., Forde, A. J., Gruner, D. S., Parker, J. D., Rodriguez, W., &
627 Feller, I. C. (2014). Poleward expansion of mangroves is a threshold response to decreased
628 frequency of extreme cold events. *Proceedings of the National Academy of Sciences*,
629 111(2), 723–727. doi: 10.1073/pnas.1315800111

630 Cavanaugh, K. C., Osland, M. J., Bardou, R., Hinojosa-Arango, G., López-Vivas, J. M., Parker,
631 J. D., & Rovai, A. S. (2018). Sensitivity of mangrove range limits to climate variability.
632 *Global Ecology and Biogeography*, 27(8), 925–935. doi: 10.1111/geb.12751

633 Cavanaugh, K. C., Parker, J. D., Cook-Patton, S. C., Feller, I. C., Williams, A. P., & Kellner, J.
634 R. (2015). Integrating physiological threshold experiments with climate modeling to project
635 mangrove species' range expansion. *Global Change Biology*, 21(5), 1928–1938. doi:
636 10.1111/gcb.12843

637 Cerón-Souza, I., Bermingham, E., McMillan, W. O., & Jones, F. A. (2012). Comparative genetic
638 structure of two mangrove species in Caribbean and Pacific estuaries of Panama. *BMC*
639 *Evolutionary Biology*, 12, 205. doi: 10.1186/1471-2148-12-205

640 Cerón-Souza, I., Gonzalez, E. G., Schwarzbach, A. E., Salas-Leiva, D. E., Rivera-Ocasio, E.,
641 Toro-Perea, N., ... McMillan, W. O. (2015). Contrasting demographic history and gene
642 flow patterns of two mangrove species on either side of the Central American Isthmus.
643 *Ecology and Evolution*, 5(16), 3486–3499. doi: 10.1002/ece3.1569

644 Cerón-Souza, I., Rivera-Ocasio, E., Funk, S. M., & McMillan, W. O. (2006). Development of six
645 microsatellite loci for black mangrove (*Avicennia germinans*). *Molecular Ecology Notes*,
646 6(3), 692–694. doi: 10.1111/j.1471-8286.2006.01312.x

647 Chakraborty, D., Schueler, S., Lexer, M. J., & Wang, T. (2019). Genetic trials improve the
648 transfer of Douglas-fir distribution models across continents. *Ecography*, 42, 88–101. doi:
649 10.1111/ecog.03888

650 Chen, E., Blaze, J. A., Smith, R. S., Peng, S., & Byers, J. E. (2020). Freeze-tolerance of
651 poleward-spreading mangrove species weakened by soil properties of resident salt marsh
652 competitor. *Journal of Ecology*. doi: 10.1111/1365-2745.13350

- 653 Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid Range Shifts
654 of Species Associated with High Levels of Climate Warming. *Science*, 333(6045), 1024–
655 1026. doi: 10.1126/science.1206432
- 656 Clarke, P. J. (1993). Dispersal of grey mangrove (*Avicennia marina*) propagules in southeastern
657 Australia. *Aquatic Botany*, 45, 195–204. doi: 10.1016/0304-3770(93)90021-N
- 658 Coldren, G. A., & Proffitt, C. E. (2017). Mangrove seedling freeze tolerance depends on salt
659 marsh presence, species, salinity, and age. *Hydrobiologia*, 803, 159–171. doi:
660 10.1007/s10750-017-3175-6
- 661 Cook-Patton, S. C., Lehmann, M., & Parker, J. D. (2015). Convergence of three mangrove
662 species towards freeze-tolerant phenotypes at an expanding range edge. *Functional*
663 *Ecology*, 29(10), 1332–1340. doi: 10.1111/1365-2435.12443
- 664 Corlett, R. T., & Westcott, D. A. (2013). Will plant movements keep up with climate change?
665 *Trends in Ecology and Evolution*, 28(8), 482–488. doi: 10.1016/j.tree.2013.04.003
- 666 Cornuet, J. M., Piry, S., Luikart, G., Estoup, A., & Solignac, M. (1999). New methods
667 employing multilocus genotypes to select or exclude populations as origins of individuals.
668 *Genetics*, 153(4), 1989–2000.
- 669 Covarrubias-Pazarán, G., Diaz-Garcia, L., Schlautman, B., Salazar, W., & Zalapa, J. (2016).
670 Fragman: an R package for fragment analysis. *BMC Genetics*, 17(62), 1–8. doi:
671 10.1186/s12863-016-0365-6
- 672 Cruz, M. V., Mori, G. M., Oh, D. H., Dassanayake, M., Zucchi, M. I., Oliveira, R. S., & Souza,
673 A. P. de. (2020). Molecular responses to freshwater limitation in the mangrove tree
674 *Avicennia germinans* (Acanthaceae). *Molecular Ecology*, 29(2), 344–362. doi:
675 10.1111/mec.15330
- 676 Cruz, M. V., Mori, G. M., Signori-Müller, C., da Silva, C. C., Oh, D. H., Dassanayake, M., ... de
677 Souza, A. P. (2019). Local adaptation of a dominant coastal tree to freshwater availability
678 and solar radiation suggested by genomic and ecophysiological approaches. *Scientific*
679 *Reports*, 9, 19936. doi: 10.1038/s41598-019-56469-w
- 680 Dangremond, E. M., & Feller, I. C. (2016). Precocious reproduction increases at the leading edge
681 of a mangrove range expansion. *Ecology and Evolution*, 6(14), 5087–5092. doi:
682 10.1002/ece3.2270
- 683 Dangremond, E. M., Simpson, L. T., Osborne, T. Z., & Feller, I. C. (2019). Nitrogen Enrichment
684 Accelerates Mangrove Range Expansion in the Temperate–Tropical Ecotone. *Ecosystems*.
685 doi: 10.1007/s10021-019-00441-2
- 686 Devaney, J. L., Lehmann, M., Feller, I. C., & Parker, J. D. (2017). Mangrove microclimates alter
687 seedling dynamics at the range edge. *Ecology*, 98(10), 2513–2520. doi: 10.1002/ecy.1979
- 688 Giri, C., Ochieng, E., Tieszen, L. L., Zhu, Z., Singh, A., Loveland, T., ... Duke, N. (2011).
689 Status and distribution of mangrove forests of the world using earth observation satellite
690 data. *Global Ecology and Biogeography*, 20, 154–159. doi: 10.1111/j.1466-
691 8238.2010.00584.x
- 692 Goldberg, N. A., & Heine, J. N. (2017). Life on the leading edge: Phenology and demography of
693 the red mangrove *Rhizophora mangle* L. at the northern limit of its expanding range. *Flora*,
694 235, 76–82. doi: 10.1016/j.flora.2017.09.003
- 695 Gray, L. K., & Hamann, A. (2013). Tracking suitable habitat for tree populations under climate
696 change in western North America. *Climatic Change*, 117, 289–303. doi: 10.1007/s10584-
697 012-0548-8
- 698 Guo, H., Zhang, Y., Lan, Z., & Pennings, S. C. (2013). Biotic interactions mediate the expansion

699 of black mangrove (*Avicennia germinans*) into salt marshes under climate change. *Global*
700 *Change Biology*, 19(9), 2765–2774. doi: 10.1111/gcb.12221

701 Guo, Z., Li, X., He, Z., Yang, Y., Wang, W., Zhong, C., ... Shi, S. (2018). Extremely low
702 genetic diversity across mangrove taxa reflects past sea level changes and hints at poor
703 future responses. *Global Change Biology*, 24(4), 1741–1748. doi: 10.1111/gcb.13968

704 Hayes, M. A., Shor, A. C., Jess, A., Miller, C., Kennedy, J. P., & Feller, I. C. (2020). The role of
705 glycine betaine in range expansions; protecting mangroves against extreme freeze events.
706 *Journal of Ecology*, 108(1), 61–69. doi: 10.1111/1365-2745.13243

707 Hickling, R., Roy, D. B., Hill, J. K., Fox, R., & Thomas, C. D. (2006). The distributions of a
708 wide range of taxonomic groups are expanding polewards. *Global Change Biology*, 12(3),
709 450–455. doi: 10.1111/j.1365-2486.2006.01116.x

710 Hijmans, R. J., Williams, E., & Vennes, C. (2019). *geosphere: Spherical Trigonometry. R*
711 *package version 1.5-10*. Retrieved from <http://cran.r-project.org/package=geosphere>

712 Hothorn, T., Hornik, K., van de Wiel, M., & Zeileis, A. (2008). Implementing a class of
713 permutation tests: The coin package. *Journal of Statistical Software*, 28(8), 1–23. doi:
714 10.18637/jss.v028.i08

715 Iverson, L. R., Schwartz, M. W., & Prasad, A. M. (2004). How fast and far might tree species
716 migrate in the eastern United States due to climate change? *Global Ecology and*
717 *Biogeography*, 13(3), 209–219. doi: 10.1111/j.1466-822X.2004.00093.x

718 Johnston, M. W., & Purkis, S. J. (2015). Hurricanes accelerated the Florida-Bahamas lionfish
719 invasion. *Global Change Biology*, 21(6), 2249–2260. doi: 10.1111/gcb.12874

720 Kangas, P. C., & Lugo, A. E. (1990). The distribution of mangroves and saltmarsh in Florida.
721 *Tropical Ecology*, 31(1), 32–39.

722 Kawecki, T. J. (2008). Adaptation to Marginal Habitats. *Annual Review of Ecology, Evolution,*
723 *and Systematics*, 39, 321–342. doi: 10.1146/annurev.ecolsys.38.091206.095622

724 Kendall, M. S., Battista, T., & Hillis-Starr, Z. (2004). Long term expansion of a deep
725 *Syringodium filiforme* meadow in St. Croix, US Virgin Islands: The potential role of
726 hurricanes in the dispersal of seeds. *Aquatic Botany*, 78, 15–25. doi:
727 10.1016/j.aquabot.2003.09.004

728 Kennedy, J. P., Dangremond, E. M., Hayes, M. A., Preziosi, R. F., Rowntree, J. K., & Feller, I.
729 C. (2020). Data from: Hurricanes overcome migration lag and shape intraspecific genetic
730 variation beyond a poleward mangrove range limit. *Dryad Digital Repository*. doi:
731 10.5061/dryad.2280gb5pd

732 Kennedy, J. P., Garavelli, L., Truelove, N. K., Devlin, D. J., Box, S. J., Chérubin, L. M., &
733 Feller, I. C. (2017). Contrasting genetic effects of red mangrove (*Rhizophora mangle* L.)
734 range expansion along West and East Florida. *Journal of Biogeography*, 44, 335–347. doi:
735 10.1111/jbi.12813

736 Kennedy, J. P., Preziosi, R. F., Rowntree, J. K., & Feller, I. C. (2020a). Data from: Is the central-
737 marginal hypothesis a general rule? Evidence from three distributions of an expanding
738 mangrove species, *Avicennia germinans* (L.) L. *Dryad Digital Repository*. doi:
739 10.5061/dryad.69p8cz8xh

740 Kennedy, J. P., Preziosi, R. F., Rowntree, J. K., & Feller, I. C. (2020b). Is the central-marginal
741 hypothesis a general rule? Evidence from three distributions of an expanding mangrove
742 species, *Avicennia germinans* (L.) L. *Molecular Ecology*, 29(4), 704–719. doi:
743 10.1111/mec.15365

744 Kennedy, J. P., Sammy, J. M., Rowntree, J. K., & Preziosi, R. F. (2020). Mating system variation

745 in neotropical black mangrove, *Avicennia germinans*, at three spatial scales towards an
746 expanding northern distributional limit. *Estuarine, Coastal and Shelf Science*, 106754. doi:
747 10.1016/j.ecss.2020.106754

748 Krauss, K. W., Lovelock, C. E., McKee, K. L., López-Hoffman, L., Ewe, S. M. L., & Sousa, W.
749 P. (2008). Environmental drivers in mangrove establishment and early development: A
750 review. *Aquatic Botany*, 89(2), 105–127. doi: 10.1016/j.aquabot.2007.12.014

751 Krauss, K. W., & Osland, M. J. (2020). Tropical cyclones and the organization of mangrove
752 forests: a review. *Annals of Botany*, 125(2), 213–234. doi: 10.1093/aob/mcz161

753 Langston, A. K., Kaplan, D. A., & Angelini, C. (2017). Predation restricts black mangrove
754 (*Avicennia germinans*) colonization at its northern range limit along Florida’s Gulf Coast.
755 *Hydrobiologia*, 803, 317–331. doi: 10.1007/s10750-017-3197-0

756 Lee, S. Y., Primavera, J. H., Dahdouh-Guebas, F., McKee, K., Bosire, J. O., Cannicci, S., ...
757 Record, S. (2014). Ecological role and services of tropical mangrove ecosystems: A
758 reassessment. *Global Ecology and Biogeography*, 23(7), 726–743. doi: 10.1111/geb.12155

759 Lembrechts, J. J., Pauchard, A., Lenoir, J., Nuñez, M. A., Geron, C., Ven, A., ... Milbau, A.
760 (2016). Disturbance is the key to plant invasions in cold environments. *Proceedings of the
761 National Academy of Sciences of the United States of America*, 113(49), 14061–14066. doi:
762 10.1073/pnas.1608980113

763 Lenoir, J., & Svenning, J. C. (2015). Climate-related range shifts - a global multidimensional
764 synthesis and new research directions. *Ecography*, 38, 15–28. doi: 10.1111/ecog.00967

765 Liang, Y., Duvencek, M. J., Gustafson, E. J., Serra-Diaz, J. M., & Thompson, J. R. (2018). How
766 disturbance, competition, and dispersal interact to prevent tree range boundaries from
767 keeping pace with climate change. *Global Change Biology*, 24, e335–e351. doi:
768 10.1111/gcb.13847

769 Lonard, R. I., Judd, F. W., Summy, K., DeYoe, H., & Stalter, R. (2017). The Biological Flora of
770 Coastal Dunes and Wetlands: *Avicennia germinans* (L.) L. *Journal of Coastal Research*,
771 33(1), 191–207. doi: 10.2112/07-0933.1

772 Lugo, A. E. (2008). Visible and invisible effects of hurricanes on forest ecosystems: An
773 international review. *Austral Ecology*, 33(4), 368–398. doi: 10.1111/j.1442-
774 9993.2008.01894.x

775 Mori, G. M., Zucchi, M. I., Sampaio, I., & Souza, A. P. (2010). Microsatellites for the mangrove
776 tree *Avicennia germinans* (Acanthaceae): Tools for hybridization and mating system
777 studies. *American Journal of Botany*, 97(9), 79–81. doi: 10.3732/ajb.1000219

778 Mori, G. M., Zucchi, M. I., Sampaio, I., & Souza, A. P. (2015). Species distribution and
779 introgressive hybridization of two *Avicennia* species from the Western Hemisphere
780 unveiled by phylogeographic patterns Phylogenetics and phylogeography. *BMC
781 Evolutionary Biology*, 15, 61. doi: 10.1186/s12862-015-0343-z

782 Murakami, H., Levin, E., Delworth, T. L., Gudgel, R., & Hsu, P. C. (2018). Dominant effect of
783 relative tropical Atlantic warming on major hurricane occurrence. *Science*, 362(6416), 794–
784 799. doi: 10.1126/science.aat6711

785 Nadeau, C. P., & Urban, M. C. (2019). Eco-evolution on the edge during climate change.
786 *Ecography*, 42(7), 1280–1297. doi: 10.1111/ecog.04404

787 Nathan, R., Schurr, F. M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., & Tsoar, A. (2008).
788 Mechanisms of long-distance seed dispersal. *Trends in Ecology and Evolution*, 23(11), 638–
789 647. doi: 10.1016/j.tree.2008.08.003

790 Nettel, A., & Dodd, R. S. (2007). Drifting propagules and receding swamps: Genetic footprints

791 of mangrove recolonization and dispersal along tropical coasts. *Evolution*, 61(4), 958–971.
792 doi: 10.1111/j.1558-5646.2007.00070.x

793 Nettel, A., Rafii, F., & Dodd, R. S. (2005). Characterization of microsatellite markers for the
794 mangrove tree *Avicennia germinans* L. (Avicenniaceae). *Molecular Ecology Notes*, 5, 103–
795 105. doi: 10.1111/j.1471-8286.2004.00851.x

796 NOAA. (2017). National Hurricane Center GIS Archive - Tropical Cyclone Best Track for
797 AL112017. Retrieved February 7, 2020, from National Oceanic and Atmospheric
798 Administration website:
799 https://www.nhc.noaa.gov/gis/archive_besttrack_%0Aresults.php?id=all1&year=2017&name=Hurricane
800

801 Osland, M. J., Feher, L. C., Anderson, G. H., Vervaeke, W. C., Krauss, K. W., Whelan, K. R. T.,
802 ... Cahoon, D. R. (2020). A Tropical Cyclone-Induced Ecological Regime Shift: Mangrove
803 Forest Conversion to Mudflat in Everglades National Park (Florida, USA). *Wetlands*. doi:
804 10.1007/s13157-020-01291-8 WETLANDS

805 Osland, M. J., Feher, L. C., Griffith, K. T., Cavanaugh, K. C., Enwright, N. M., Day, R. H., ...
806 Rogers, K. (2017). Climatic controls on the global distribution, abundance, and species
807 richness of mangrove forests. *Ecological Monographs*, 87(2), 341–359. doi:
808 10.1002/ecm.1248

809 Osland, M. J., Feher, L. C., López-Portillo, J., Day, R. H., Suman, D. O., Guzmán Menéndez, J.
810 M., & Rivera-Monroy, V. H. (2018). Mangrove forests in a rapidly changing world: Global
811 change impacts and conservation opportunities along the Gulf of Mexico coast. *Estuarine,
812 Coastal and Shelf Science*, 214, 120–140. doi: 10.1016/j.ecss.2018.09.006

813 Paetkau, D., Slade, R., Burden, M., & Estoup, A. (2004). Genetic assignment methods for the
814 direct, real-time estimation of migration rate: a simulation-based exploration of accuracy
815 and power. *Molecular Ecology*, 13, 55–65. doi: 10.1046/j.1365-294X.2004.02008.x

816 Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I. C., ... Williams,
817 S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and
818 human well-being. *Science*, 355, eaai9214. doi: 10.1126/science.aai9214

819 Peterson, J. M., & Bell, S. S. (2012). Tidal events and salt-marsh structure influence black
820 mangrove (*Avicennia germinans*) recruitment across an ecotone. *Ecology*, 93(7), 1648–
821 1658. doi: 10.1890/11-1430.1

822 Pickens, C. N., Sloey, T. M., & Hester, M. W. (2019). Influence of salt marsh canopy on black
823 mangrove (*Avicennia germinans*) survival and establishment at its northern latitudinal limit.
824 *Hydrobiologia*, 826, 195–208. doi: 10.1007/s10750-018-3730-9

825 Pironon, S., Papuga, G., Villellas, J., Angert, A. L., García, M. B., & Thompson, J. D. (2017).
826 Geographic variation in genetic and demographic performance: new insights from an old
827 biogeographical paradigm. *Biological Reviews*, 92(4), 1877–1909. doi: 10.1111/brv.12313

828 Piry, S., Alapetite, A., Cornuet, J. M., Paetkau, D., Baudouin, L., & Estoup, A. (2004).
829 GENECLASS2: A software for genetic assignment and first-generation migrant detection.
830 *Journal of Heredity*, 95(6), 536–539. doi: 10.1093/jhered/esh074

831 Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J.,
832 ... Richardson, A. J. (2013). Global imprint of climate change on marine life. *Nature
833 Climate Change*, 3(10), 919–925. doi: 10.1038/nclimate1958

834 Prasad, A. M., Gardiner, J. D., Iverson, L. R., Matthews, S. N., & Peters, M. (2013). Exploring
835 tree species colonization potentials using a spatially explicit simulation model: Implications
836 for four oaks under climate change. *Global Change Biology*, 19(7), 2196–2208. doi:

837 10.1111/gcb.12204

838 R Core Team. (2013). *R: A language and environment for statistical computing*. Vienna, Austria.

839 Website: R-project.org: R Foundation for Statistical Computing.

840 Rabinowitz, D. (1978). Dispersal properties of mangrove propagules. *Biotropica*, 10(1), 47–57.

841 doi: 10.2307/2388105

842 Radabaugh, K. R., Moyer, R. P., Chappel, A. R., Dontis, E. E., Russo, C. E., Joyse, K. M., ...

843 Khan, N. S. (2019). Mangrove Damage, Delayed Mortality, and Early Recovery Following

844 Hurricane Irma at Two Landfall Sites in Southwest Florida, USA. *Estuaries and Coasts*.

845 doi: 10.1007/s12237-019-00564-8

846 Rannala, B., & Mountain, J. L. (1997). Detecting immigration by using multilocus genotypes.

847 *Proceedings of the National Academy of Sciences*, 94(17), 9197–9201. doi:

848 10.1073/pnas.94.17.9197

849 Rehm, E. M., Olivas, P., Stroud, J., & Feeley, K. J. (2015). Losing your edge: Climate change

850 and the conservation value of range-edge populations. *Ecology and Evolution*, 5(19), 4315–

851 4326. doi: 10.1002/ece3.1645

852 Renwick, K. M., & Rocca, M. E. (2015). Temporal context affects the observed rate of climate-

853 driven range shifts in tree species. *Global Ecology and Biogeography*, 24, 44–51. doi:

854 10.1111/geb.12240

855 Rodriguez, W., Feller, I. C., & Cavanaugh, K. C. (2016). Spatio-temporal changes of a

856 mangrove–saltmarsh ecotone in the northeastern coast of Florida, USA. *Global Ecology and*

857 *Conservation*, 7, 245–261. doi: 10.1016/j.gecco.2016.07.005

858 Rogers, K., & Krauss, K. W. (2018). Moving from Generalisations to Specificity about

859 Mangrove –Saltmarsh Dynamics. *Wetlands*. doi: 10.1007/s13157-018-1067-9

860 Roques, S., Duchesne, P., & Bernatchez, L. (1999). Potential of microsatellites for individual

861 assignment: The North Atlantic redfish (genus *Sebastes*) species complex as a case study.

862 *Molecular Ecology*, 8(10), 1703–1717. doi: 10.1046/j.1365-294X.1999.00759.x

863 Ross, M. S., Ogurcak, D. E., Stoffella, S., Sah, J. P., Hernandez, J., & Willoughby, H. E. (2019).

864 Hurricanes, Storm Surge, and Pine Forest Decline on a Low Limestone Island. *Estuaries*

865 *and Coasts*. doi: 10.1007/s12237-019-00624-z

866 Scheffers, B. R., De Meester, L., Bridge, T. C. L., Hoffmann, A. A., Pandolfi, J. M., Corlett, R.

867 T., ... Watson, J. E. M. (2016). The broad footprint of climate change from genes to biomes

868 to people. *Science*, 354(6313), aaf7671. doi: 10.1126/science.aaf7671

869 Schurr, F. M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., Tsoar, A., & Nathan, R. (2018). Long-

870 distance seed dispersal. *Annual Plant Reviews Online*, 204–237. doi:

871 10.1002/9781119312994.apr0413

872 Sengupta, R., Middleton, B., Yan, C., Zuro, M., & Hartman, H. (2005). Landscape

873 characteristics of *Rhizophora* mangle forests and propagule deposition in coastal

874 environments of Florida (USA). *Landscape Ecology*, 20, 63–72. doi: 10.1007/s10980-004-

875 0468-8

876 Simpson, L. T., Feller, I. C., & Chapman, S. K. (2013). Effects of competition and nutrient

877 enrichment on *Avicennia germinans* in the salt marsh-mangrove ecotone. *Aquatic Botany*,

878 104, 55–59. doi: 10.1016/j.aquabot.2012.09.006

879 Simpson, L. T., Osborne, T. Z., & Feller, I. C. (2017). Establishment and Biomass Allocation of

880 Black and Red Mangroves: Response to Propagule Flotation Duration and Seedling Light

881 Availability. *Journal of Coastal Research*, 335, 1126–1134. doi: 10.2112/JCOASTRES-D-

882 16-00108.1

883 Simpson, L. T., Stein, C. M., Osborne, T. Z., & Feller, I. C. (2019). Mangroves dramatically
884 increase carbon storage after 3 years of encroachment. *Hydrobiologia*, *834*, 13–26. doi:
885 10.1007/s10750-019-3905-z

886 Sinclair, E. A., Ruiz-Montoya, L., Krauss, S. L., Anthony, J. M., Hovey, R. K., Lowe, R. J., &
887 Kendrick, G. A. (2018). Seeds in motion: Genetic assignment and hydrodynamic models
888 demonstrate concordant patterns of seagrass dispersal. *Molecular Ecology*, *27*(24), 5019–
889 5034. doi: 10.1111/mec.14939

890 Solomon, A. M., & Kirilenko, A. P. (1997). Climate change and terrestrial biomass: what if trees
891 do not migrate? *Global Ecology and Biogeography Letters*, *6*(2), 139–148. doi:
892 10.2307/2997570

893 Sousa, W. P., Kennedy, P. G., Mitchell, B. J., & Ordóñez L, B. M. (2007). Supply-side ecology
894 in mangroves: Do propagule dispersal and seedling establishment explain forest structure?
895 *Ecological Monographs*, *77*(1), 53–76. doi: 10.1890/05-1935

896 Spalding, M., Kainuma, M., & Collins, L. (2010). *World atlas of mangroves*. London, UK:
897 Earthscan.

898 Svenning, J. C., & Sandel, B. (2013). Disequilibrium vegetation dynamics under future climate
899 change. *American Journal of Botany*, *100*(7), 1266–1286. doi: 10.3732/ajb.1200469

900 Thuiller, W., Albert, C., Araújo, M. B., Berry, P. M., Cabeza, M., Guisan, A., ... Zimmermann,
901 N. E. (2008). Predicting global change impacts on plant species' distributions: Future
902 challenges. *Perspectives in Plant Ecology, Evolution and Systematics*, *9*, 137–152. doi:
903 10.1016/j.ppees.2007.09.004

904 Urban, M. C., Bocedi, G., Hendry, A. P., Mihoub, J. B., Pe'er, G., Singer, A., ... Travis, J. M. J.
905 (2016). Improving the forecast for biodiversity under climate change. *Science*, *353*(6304),
906 aad8466. doi: 10.1126/science.aad8466

907 Van der Stocken, T., Carroll, D., Menemenlis, D., Simard, M., & Koedam, N. (2019). Global-
908 scale dispersal and connectivity in mangroves. *Proceedings of the National Academy of
909 Sciences of the United States of America*, *116*(3), 915–922. doi: 10.1073/pnas.1812470116

910 Van der Stocken, T., López-Portillo, J., & Koedam, N. (2017). Seasonal release of propagules in
911 mangroves – Assessment of current data. *Aquatic Botany*, *138*, 92–99. doi:
912 10.1016/j.aquabot.2017.02.001

913 Van der Stocken, T., Vanschoenwinkel, B., De Ryck, D., & Koedam, N. (2018). Caught in
914 transit: offshore interception of seafaring propagules from seven mangrove species.
915 *Ecosphere*, *9*(4), e02208. doi: 10.1002/ecs2.2208

916 Van der Stocken, T., Wee, A. K. S., De Ryck, D. J. R., Vanschoenwinkel, B., Friess, D. A.,
917 Dahdouh-Guebas, F., ... Webb, E. L. (2019). A general framework for propagule dispersal
918 in mangroves. *Biological Reviews*, *94*(4), 1547–1575. doi: 10.1111/brv.12514

919 Walker, L. R., Lodge, D. J., Brokaw, N. V. L., & Waide, R. B. (1991). An Introduction to
920 Hurricanes in the Caribbean. *Biotropica*, *23*(4a), 313–316.

921 Walsh, K. J. E., McBride, J. L., Klotzbach, P. J., Balachandran, S., Camargo, S. J., Holland, G.,
922 ... Sugi, M. (2016). Tropical cyclones and climate change. *Wiley Interdisciplinary Reviews:
923 Climate Change*, *7*(1), 65–89. doi: 10.1002/wcc.371

924 Waples, R. S., & Gaggiotti, O. (2006). What is a population? An empirical evaluation of some
925 genetic methods for identifying the number of gene pools and their degree of connectivity.
926 *Molecular Ecology*, *15*(6), 1419–1439. doi: 10.1111/j.1365-294X.2006.02890.x

927 Waters, J. M., Fraser, C. I., & Hewitt, G. M. (2013). Founder takes all: Density-dependent
928 processes structure biodiversity. *Trends in Ecology and Evolution*, *28*(2), 78–85. doi:

- 929 10.1016/j.tree.2012.08.024
930 Waters, J. M., King, T. M., Fraser, C. I., & Craw, D. (2018). An integrated ecological, genetic
931 and geological assessment of long-distance dispersal by invertebrates on kelp rafts.
932 *Frontiers of Biogeography*, 10(3–4), e40888. doi: 10.21425/F5FBG40888
933 Wernberg, T., Smale, D. A., Tuya, F., Thomsen, M. S., Langlois, T. J., De Bettignies, T., ...
934 Rousseaux, C. S. (2013). An extreme climatic event alters marine ecosystem structure in a
935 global biodiversity hotspot. *Nature Climate Change*, 3, 78–82. doi: 10.1038/nclimate1627
936 Williams, A. A., Eastman, S. F., Eash-Loucks, W. E., Kimball, M. E., Lehmann, M. L., &
937 Parker, J. D. (2014). Record Northernmost Endemic Mangroves on the United States
938 Atlantic Coast with a Note on Latitudinal Migration. *Southeastern Naturalist*, 13(1), 56–63.
939 doi: 10.1656/058.013.0104
940 Yates, K. L., Bouchet, P. J., Caley, M. J., Mengersen, K., Randin, C. F., Parnell, S., ... Sequeira,
941 A. M. M. (2018). Outstanding Challenges in the Transferability of Ecological Models.
942 *Trends in Ecology and Evolution*, 33(10), 790–802. doi: 10.1016/j.tree.2018.08.001
943 Zeigler, S. L., & Fagan, W. F. (2014). Transient windows for connectivity in a changing world.
944 *Movement Ecology*, 2, 1. doi: 10.1186/2051-3933-2-1
945 Zhu, K., Woodall, C. W., & Clark, J. S. (2012). Failure to migrate: Lack of tree range expansion
946 in response to climate change. *Global Change Biology*, 18(3), 1042–1052. doi:
947 10.1111/j.1365-2486.2011.02571.x
948
949

950 **DATA ACCESSIBILITY**

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

953
954

955 **AUTHOR CONTRIBUTION**

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

959 **Table 1** Hurricane-driven *Avicennia germinans* drift propagule survey sites and approximate over-water dispersal distances of
 960 unambiguously assigned propagules. Drift propagules were collected after Hurricane Irma at survey sites at or past the present-day *A.*
 961 *germinans* range margin and from one lower-latitude comparison site. n_G, number of drift propagules genotyped; assign, number of
 962 drift propagules unambiguously assigned to a source. ^a Maximum Euclidean distance (the most conservative estimate of dispersal
 963 possible) differed considerably from maximum over-water distance. Maximum Euclidean distances were: MZ, 457 km; FP, 327 km.
 964

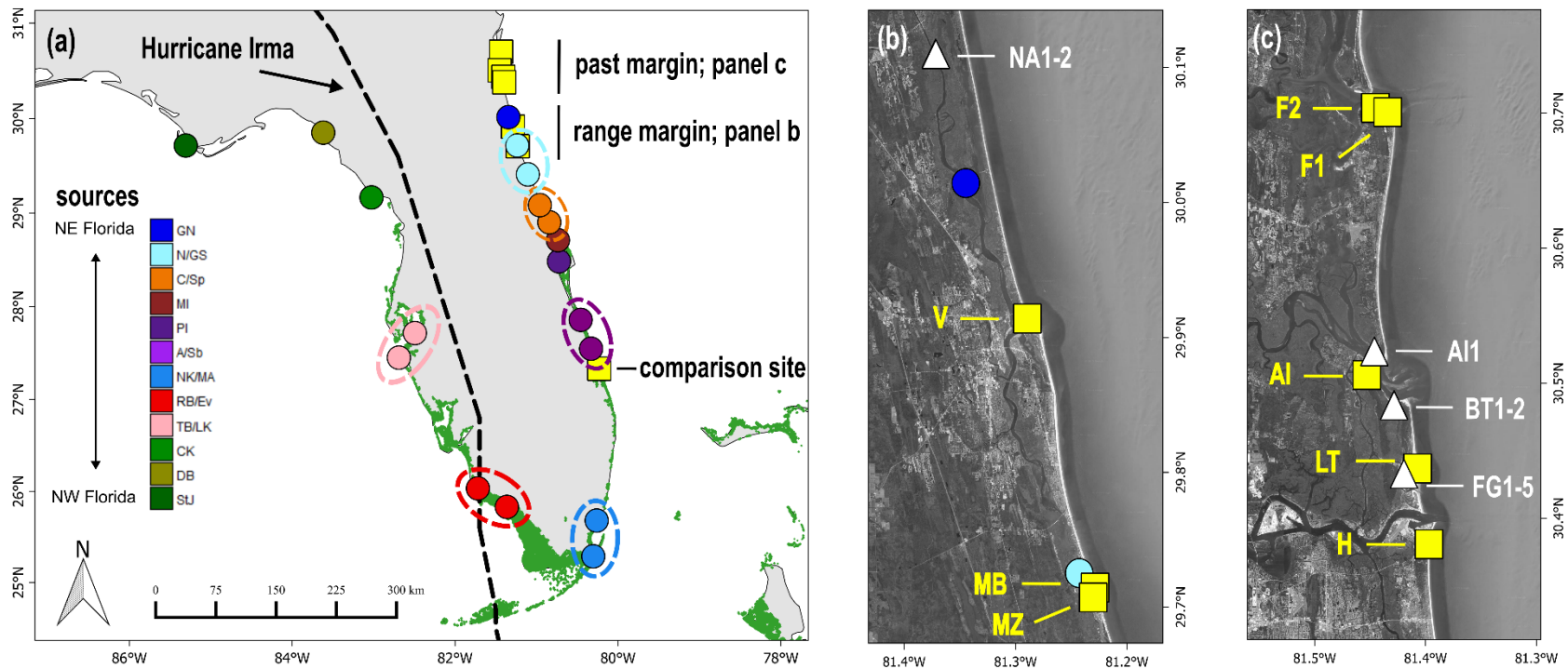
Site	Code	Location	Latitude	Longitude	n _G	assign	dispersal distance (km)	
							median	range
Fort Clinch (inlet)	F2	past margin	30.703	-81.445	99	53	109	74–109
Fort Clinch (beach)	F1	past margin	30.701	-81.434	100	60	109	74–230
Amelia Island	AI	past margin	30.506	-81.453	100	61	91	56–165
Little Talbot	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

965

966 **Table 2** Ten vagrant *Avicennia germinans* trees found at four locations beyond the most northern
 967 established population of this species. Three of the 10 trees were unambiguously assigned to the
 968 most southern range-margin source (source code: N/GS) and three of the 10 trees were identified
 969 as putative offspring of adjacent larger trees. assign, whether trees were unambiguously assigned
 970 to a source (or classified as putative offspring of adjacent trees); source, assigned source (or
 971 putative parent); dispersal distance, approximate over-water distance from the assigned source
 972 (Euclidean distance was identical). ^a Documented northernmost *A. germinans* (Williams et al.,
 973 2014).

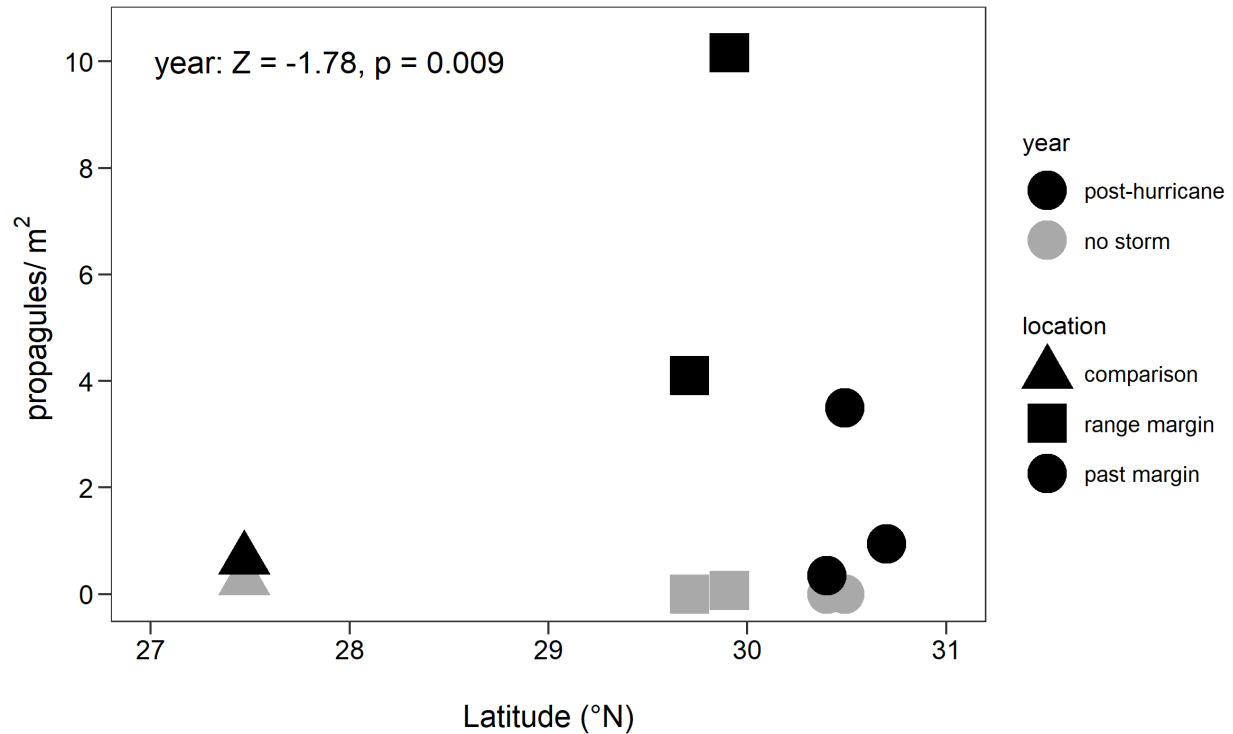
Tree	Latitude	Longitude	assign	source	dispersal distance (km)
AI1	30.523646	-81.446147	no		
BT1	30.483861	-81.428389	no		
BT2	30.483641	-81.428397	<i>offspring</i>	<i>[BT1]</i>	
FG1	30.421436	-81.422169	no		
FG2	30.430226	-81.421208	YES	N/GS	80
FG3	30.432978	-81.419474	YES	N/GS	80
FG4	30.432814	-81.419853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

974



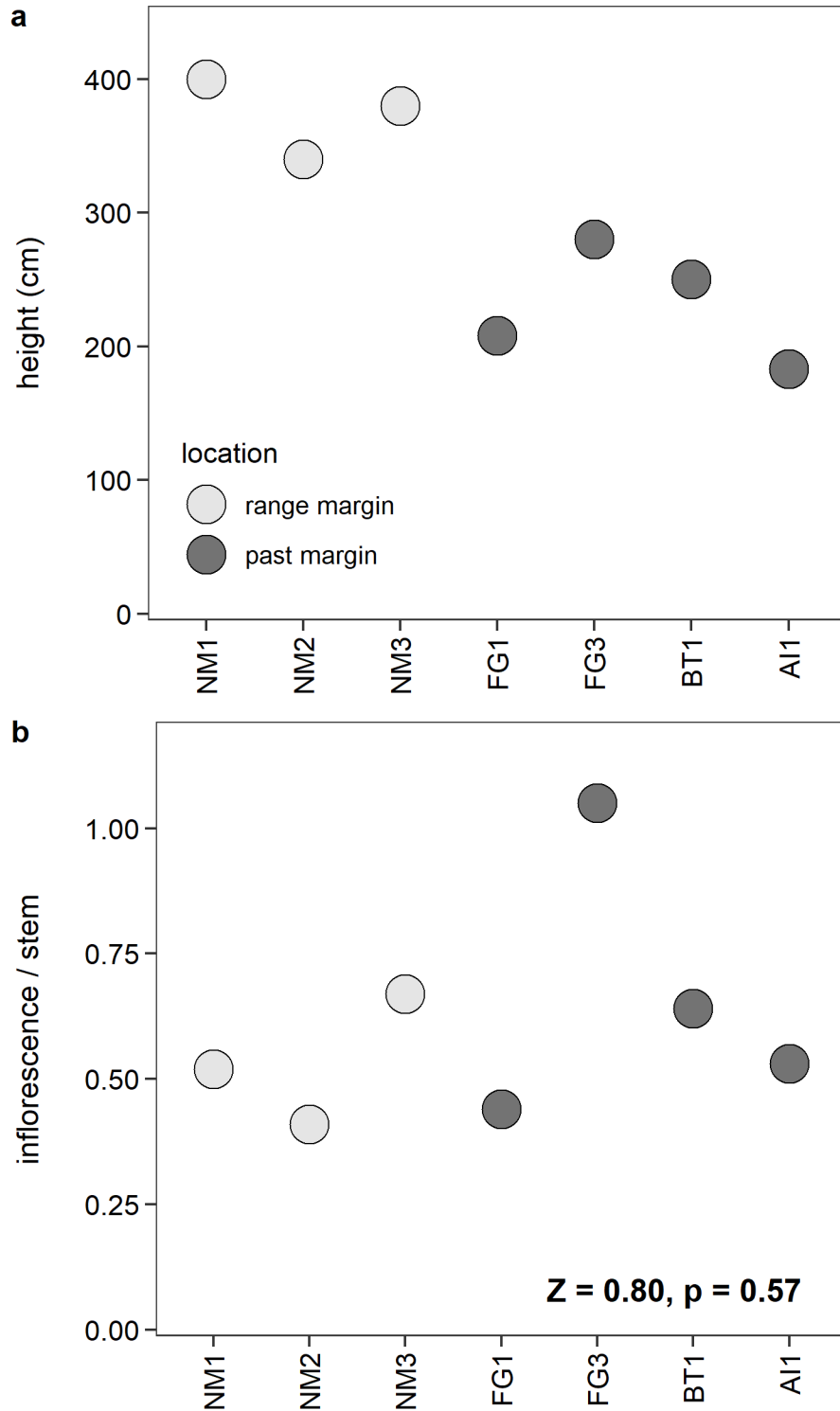
975

976 **Figure 1** Survey sites for *Avicennia germinans* drift propagules (shown as yellow squares), vagrant *A. germinans* trees past the most
 977 northern established population of this species (shown as white triangles), and 12 potential source populations (shown as circles). (a)
 978 Path of Hurricane Irma shown with a dashed line (NOAA, 2017) and mangrove distribution shown in green (Giri et al., 2011). (b)
 979 Close-up of the location of three drift propagule survey sites, two vagrant trees, and the two northernmost Atlantic Florida source
 980 populations at the established *A. germinans* range margin (29.7 – 30.1°N). (c) Close-up of the location of five drift propagule survey
 981 sites and eight vagrant trees ~40-75 km past the present-day *A. germinans* range margin where no established populations exist (30.4 –
 982 30.7°N). Source population genetic data from Kennedy, Preziosi, et al. (2020a).



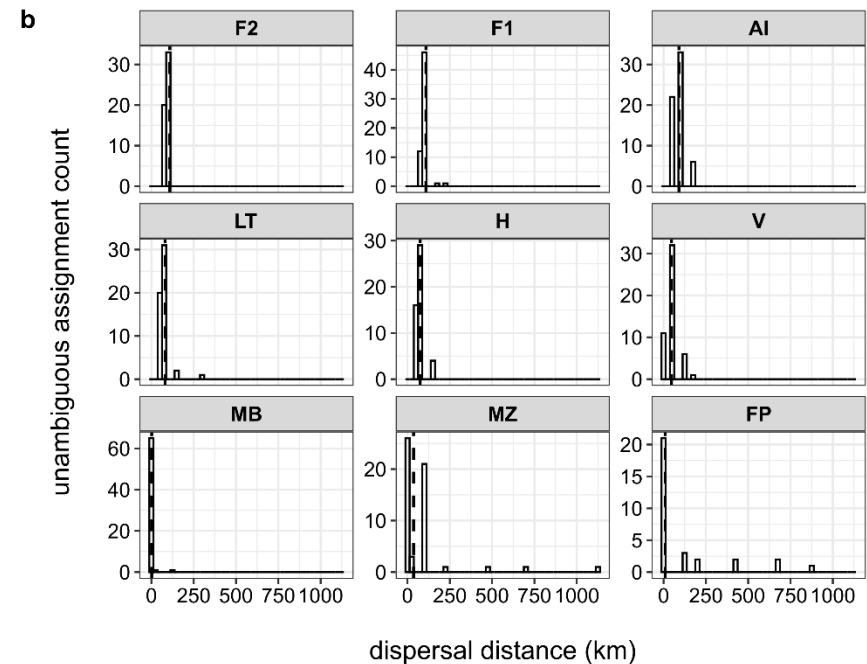
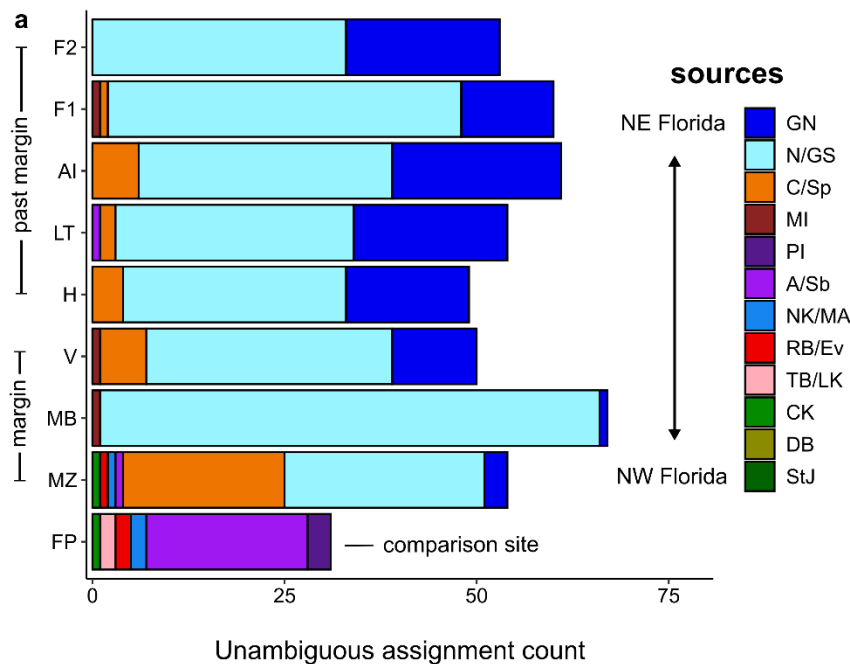
983

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



989

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



995

996 **Figure 4** Hurricane-driven *Avicennia germinans* drift propagules were almost exclusively from the nearest sources. (a) Unambiguous
 997 assignment results for drift propagules from three survey sites at the present-day *A. germinans* range margin (29.7 – 29.9°N), from
 998 five survey sites past the range margin (30.3 – 30.7°N), and from one lower-latitude comparison site within the continuous range core
 999 (27.4°N). (b) Histograms of approximate over-water dispersal distances for unambiguously assigned propagules at each of the survey
 1000 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
 1001 geographic locations of the 12 potential sources from northeast Florida (Atlantic coast) to northwest Florida (Gulf coast). Refer to
 1002 Table S6 and Figure S3 for Euclidean dispersal distances.

1003

1004 **SUPPORTING INFORMATION**

1005 Additional supporting information may be found online in the Supporting Information section at the end of the article.