



Genetically based adaptive trait shifts at an expanding mangrove range margin

John Paul Kennedy · Giles N. Johnson ·
Richard F. Preziosi · Jennifer K. Rowntree

Received: 9 January 2022 / Revised: 9 January 2022 / Accepted: 16 February 2022 / Published online: 8 March 2022
© The Author(s) 2022

Abstract Neotropical black mangrove (*Avicennia germinans*) is expanding poleward into temperate salt marsh along Atlantic Florida, USA, with field evidence of trait shifts consistent with greater cold tolerance within range margin populations. However, whether these shifts have a genetic basis remains unanswered. To address this gap, we measured

multiple phenotypic traits of twenty *A. germinans* maternal cohorts from areas in both the Atlantic Florida range core and margin in a 2-year greenhouse common garden with annual temperatures analogous to range margin conditions. Compared to those from the range core, range margin cohorts survived in greater numbers, established (i.e., produced first true leaves) more quickly, and were less stressed under winter temperatures. Range margin cohorts were not taller, but invested more into lateral growth and biomass accumulation that presumably reflects adaptation to their colder and open-canopy environment. Range margin cohorts also exhibited leaf traits consistent with greater resource acquisition that may compensate for a shorter growing season and reduced light quality at higher latitude. Our results suggest that genetically based phenotypic differences better enable these range margin mangroves to thrive within their stressful environment and may facilitate further poleward expansion. An improved understanding of adaptive trait variation within ecologically important mangrove foundation species should also help inform coastal restoration initiatives.

Handling Editor: Emily M. Dangremond

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10750-022-04823-x>.

J. P. Kennedy · R. F. Preziosi · J. K. Rowntree
Ecology and Environment Research Centre, Department
of Natural Sciences, Faculty of Science and Engineering,
Manchester Metropolitan University, Manchester, UK

Present Address:

J. P. Kennedy (✉)
Subtropical Insects and Horticulture Research Unit,
Agricultural Research Service, United States Department
of Agriculture, Fort Pierce, FL, USA
e-mail: kennedy3jp@gmail.com

G. N. Johnson
Department of Earth and Environmental Sciences, Faculty
of Science and Engineering, University of Manchester,
Manchester, UK

Present Address:

R. F. Preziosi · J. K. Rowntree
School of Biological and Marine Sciences, Faculty
of Science and Engineering, University of Plymouth,
Plymouth, UK

Keywords *Avicennia germinans* · Climate change ·
Coastal restoration · Common garden experiment ·
Functional traits · Range expansion

Introduction

Distributional range margins are often defined by a species' inability to tolerate conditions beyond these boundaries (Brown, 1984). However, in response to climate warming, these boundaries are expanding poleward for many species (Pecl et al., 2017; Osland et al., 2021), with individuals that inhabit present-day range margins inherently at the forefront of this change. Due to marginal environmental conditions and novel selection pressures, individuals at range margins may exhibit strong genetic divergence and significant phenotypic differences from conspecifics within more benign portions of their range (Hardie & Hutchings, 2010; Chuang & Peterson, 2016). Understanding whether these unique range margin genotypes are better able to thrive under the extreme climatic conditions at and beyond their current distributional limits can provide important insights into how species may respond to climate change (Rehm et al., 2015; Nadeau & Urban, 2019).

Evaluating genetic and phenotypic changes towards expanding range margins of plant foundation species will be particularly informative because of the direct influence of these species on ecosystem structure and function (Ellison, 2019). Hence, insights into how foundation species will respond to climate change will inevitably inform predictions about responses of entire ecosystems (Bernhardt & Leslie, 2013). A well-documented example of foundation species undergoing climate-driven range expansion is that of mangroves at their poleward range margins (Saintilan et al., 2014; Armitage et al., 2015; Cohen et al., 2020; Fazlioglu et al., 2020; Whitt et al., 2020).

Mangroves are (sub)tropical, intertidal woody plants of significant ecological importance to coastal ecosystems (Lee et al., 2014) and a central component to a growing number of coastal rehabilitation and restoration initiatives (Friess et al., 2019; Waltham et al., 2020). Their distributional limits are defined by region-specific climatic thresholds in minimum temperatures and/or precipitation (Osland et al., 2017). Along Atlantic Florida, USA, the northern extent of mangroves is controlled by a gradient in minimum winter temperatures that drives a transition from the southern range core of dense, closed canopy mangrove forests to the northern range margin of sparsely populated mangrove patches within a landscape of temperate salt marsh (Osland et al., 2017; Cavanaugh

et al., 2018). Milder winters for several decades are linked to ongoing mangrove proliferation at this range margin (Cavanaugh et al., 2014; Rodriguez et al., 2016) and further poleward expansion is forecast as freeze events become less common (Cavanaugh et al., 2015, 2019). This transition from salt marsh to mangrove dominance will have wide-reaching effects on these coastal ecosystems, including increased carbon storage, greater sediment accretion in response to sea level rise, enhanced storm protection, and reduced habitat availability for certain fauna that require open vegetation (Kelleway et al., 2017; Osland et al., 2018).

Neotropical black mangrove, *Avicennia germinans*, is the predominant mangrove species at the Atlantic Florida range margin (Lonard et al., 2017). Range margin populations of *A. germinans* exhibit clear genetic differences from those directly south within the continuous range core (Kennedy et al., 2020b) and are the predominant source of new recruits to northern areas beyond this species' present-day distribution (Kennedy et al., 2020a). Range margin *A. germinans* also demonstrate shifts towards leaf phenotypic traits consistent with greater cold tolerance compared to range core conspecifics (Cook-Patton et al., 2015; Kennedy et al., 2020b), with similar shifts observed at *A. germinans* range margins in the Gulf of Mexico (Méndez-Alonzo et al., 2008; Madrid et al., 2014; Kennedy et al., 2020b). Yet, we lack an understanding of whether these phenotypic differences observed in range margin *A. germinans* in the field have a genetic basis or are plastic responses to their marginal environmental conditions. Extensive trait plasticity in response to environmental variation is well-documented in mangroves (e.g., Lovelock, 2008; Feller et al., 2010; Vovides et al., 2014), while relatively few studies provide evidence for genetically based adaptive trait variation. Evidence of adaptive trait variation within ecologically important mangrove species should provide not only insights into dynamics at expanding range margins, but also help inform source selection for mangrove restoration initiatives.

Common garden experiments are a tool to address this knowledge gap as their uniform environment allows for tests of genetic effects while controlling for trait plasticity (Hoffmann & Sgró, 2011). Furthermore, common gardens with environmental conditions analogous to those that restrict a species' distribution can provide additional insights into how

genetically based trait variation better suited to tolerate these conditions varies geographically within a species (Alberto et al., 2013; Warwell & Shaw, 2017). In this study, we monitored *A. germinans* maternal cohorts from areas in the Atlantic Florida range core and margin in a greenhouse common garden with annual temperatures that resembled those at the Atlantic Florida range margin. We assessed differences in a series of phenotypic traits starting at initial planting of field-collected propagules and continuing until 2 years development.

Our aim was to determine whether there is a genetic basis to previous field observations of trait shifts in *A. germinans* towards its expanding Atlantic Florida range margin. We predicted that, compared to range core cohorts, (1) field-collected propagules from range margin cohorts would survive in greater numbers and establish (i.e., produce first true leaves) more quickly. (2) Range margin cohorts would be less stressed under winter temperatures, which would result in (3) greater growth and biomass accumulation over the 2-year experiment. (4) Range margin cohorts would exhibit more conservative leaf traits (i.e., smaller, increased dry-matter content, reduced specific leaf area) to better tolerate marginal temperature conditions.

Materials and methods

Field sampling

We focused our sampling at the lowest level of genetic inheritance for our studied species (i.e., maternal cohorts). *Avicennia germinans* is a hermaphroditic, insect-pollinated tree or shrub that produces cryptoviviparous propagules (Lonard et al., 2017). Along Atlantic Florida, *A. germinans* exhibit a mixed-mating system with relatively high rates of self-fertilisation (Kennedy et al., 2021b). As such, the maternal cohorts monitored in this research are a mixture of both selfed and outcrossed progeny, with outcrossed progeny being either full- or half-siblings.

On 07 and 08-Oct-2017, we collected mature *A. germinans* propagules systematically from around the entire canopy of maternal trees located in both the Atlantic Florida range core, where mangroves are the dominant coastal foundation species, and the range margin, where salt marsh vegetation is

dominant (Fig. 1a). We collected from three range core and three range margin sites, across similar geographic expanses (inter-site distances: 47.6 – 97.1 km for range core; 33.2 – 71.4 km for range margin), to include a broader representation of genetic variation across these areas (Fig. 1a). Annual minimum temperatures decline with latitude across our sampling area, with temperatures < 10°C, a threshold shown to induce chill stress in *A. germinans* seedlings (Devaney et al., 2021), common only at the range margin sites (Fig. 1b). All propagules collected from each maternal tree were stored together in one labelled plastic bag during field collections and then transported to the greenhouse facility at Manchester Metropolitan University in Manchester, UK (53.4713° N, 2.2412° W). Propagules remained dry and intact during transport and planting began 10 days after collection (see [Common Garden Experiment](#) section).

Maternal tree genotyping

During field sampling, we also collected a leaf from each maternal tree to generate their multi-locus genotypes with 12 nuclear microsatellite loci as outlined in (Kennedy et al., 2020b). We visualised genetic differences among maternal trees with a discriminant analysis of principal components (DAPC) in the adegenet 2.1.1 R-package (Jombart & Ahmed, 2011). For this analysis, we retained nine principal components, which explained ~90% of the total variance, identified two clusters, and retained all five discriminant functions.

Common garden experiment

Our planting trays permitted the inclusion of 20 maternal cohorts in the common garden experiment, with range core (n=10) and range margin (n=10) cohorts equally represented (n=2–4 cohorts per collection site) (Fig. 1a). The experiment consisted of two components: (1) an establishment and initial growth phase that monitored propagule development into seedlings until eight months post-planting (20 maternal cohorts × 30 biological replicates = 600 total propagules), and (2) a subsequent growth phase that monitored a random subset of these seedlings until 2 years post-planting (20 maternal cohorts × 12 biological replicates = 240 total seedlings). We used a randomised complete block design for each

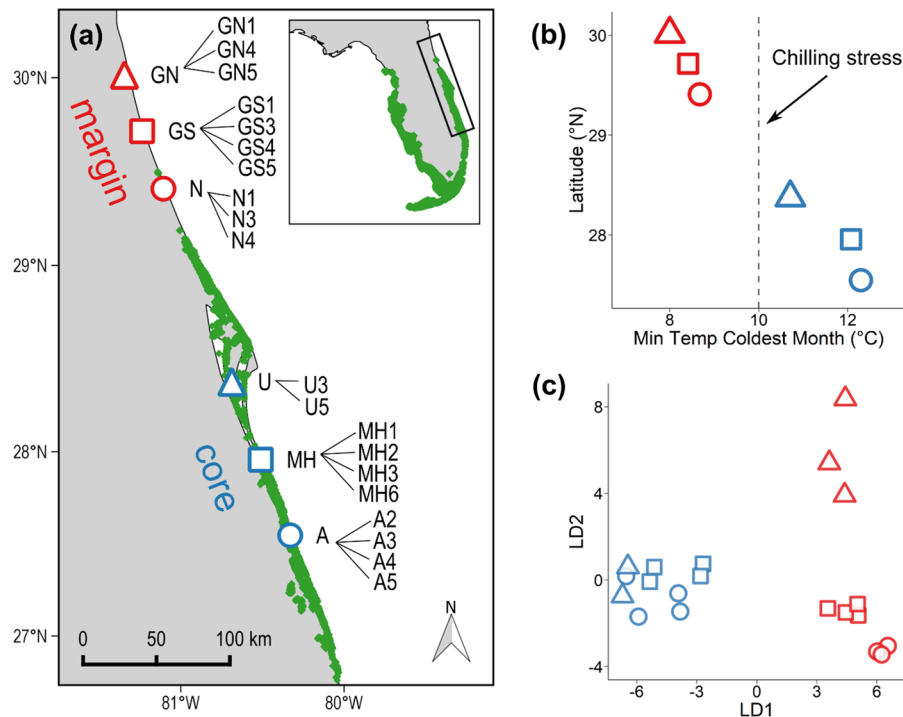


Fig. 1 Field collections of *Avicennia germinans* propagules from Atlantic Florida, USA, for a greenhouse common garden experiment at Manchester Metropolitan University, Manchester, UK. **a** Twenty maternal cohorts from six collection sites were included in the experiment ($n=10$ from range core, $n=10$ from range margin). Mangrove distribution shown in green (Giri et al., 2011) **b** Latitudinal decline in annual minimum temperatures (1970–2000) across the sampled sites, with

chilling stress ($<10^{\circ}\text{C}$) common only at range margin sites. Temperature data from WorldClim2 (Fick & Hijmans, 2017). **c** Discriminant analysis of principal components (DAPC) of the 20 maternal tree genotypes demonstrates a clear separation between range core and margin. Throughout the figure, blue shapes depict range core sites and cohorts, and red shapes depict range margin sites and cohorts

component, with one offspring from each of the 20 maternal cohorts present within each block (i.e., replicate planting tray) (see Online Resource Fig. S1 for photos of the experimental design). Greenhouse temperature and humidity were continuously monitored at 30-min intervals with iButton data loggers (Measurement Systems Ltd, Newbury, UK). We set greenhouse temperatures to resemble those at the Atlantic Florida range margin based on mean monthly values (1981–2010) from St Augustine Lighthouse, Florida (29.8°N), obtained from the National Centers for Environmental Information (<https://www.ncdc.noaa.gov/cdo-web/datatools>). In addition, we superimposed supplemental grow lights (54,800 lm, PLAN-TASTAR 400 W E40; OSRAM, Munich, Germany) onto natural light throughout the day. The duration of this supplemental light was set each month to match mean monthly day length, also at St Augustine

Lighthouse, based on data from the Earth System Research Laboratories (<https://www.esrl.noaa.gov/gmd/grad/solcalc/>).

On 18-Oct-2017, 10 days after collection, we began floating field-collected propagules in a saline water solution ($\sim 15\text{‰}$ Instant Ocean® Sea Salt) for one week, an optimal duration for seedling productivity (Simpson et al., 2017). We selected this salinity level, here and throughout the experiment, because it would provide relatively benign conditions for the plants and is representative of estuarine waters (Col-dren & Proffitt, 2017). On 25-Oct-2017, we towel dried propagules and measured three size metrics to account for variation in maternal investment, specifically weight (g), length (mm), and width (mm). All three metrics exhibited strong positive correlations (Pearson's correlation, $r=0.76\text{--}0.88$, $p<0.001$), so we decided to use propagule weight as our measure of

maternal investment. Propagules were then planted in 7×7×6.5 cm square pots (LBS Horticulture, Colne, UK) filled with a 3:1 mixture of low nutrient commercial potting soil (Levington F1 Seed and Modular Compost; LBS Horticulture, Colne, UK) and sharp horticultural sand (RHS Sharp Sand; LBS Horticulture, Colne, UK), with no subsequent nutrient additions, and placed into 30 replicate trays (Gratnells shallow trays, 42.7×31.2×7.5 cm; YPO, Wakefield, UK). We added a saline water solution (~15 ‰ Instant Ocean® Sea Salt) to 3 cm depth within the trays to maintain soil saturation, and additional fresh water was added each week to return to this volume. Pots were also misted periodically with fresh water to ensure propagules remained hydrated. Every two weeks, trays were systematically rotated around the greenhouse and salinity was measured from six haphazardly chosen trays from across the entire greenhouse with a handheld refractometer (VWR International, Lutterworth, UK). Complete water changes were performed at the end of each month. We determined that propagules had established as seedlings upon appearance of their first true leaves (Finney, 2011). Once the first seedling established, we began monitoring time to establishment for each propagule on a weekly basis until 35 weeks post-planting when 98.5% of surviving propagules had established. We also documented propagule mortality throughout this period.

On 10-Jul-2017, 8 months post-planting, we measured stem height (cm) and total growth as height plus length of any lateral shoots (cm) for all surviving seedlings. Then, on 18-Jul-2017, a random subset of 12 surviving seedlings from each of the 20 maternal cohorts was transferred to larger 11×11×12 cm square pots (LBS Horticulture, Colne, UK) filled with a fresh mix of 3:1 potting soil and sand (as detailed above), with no subsequent nutrient additions, and placed into 12 replicate trays (Garland square garden tray, 60×60×7 cm; LBS Horticulture, Colne, UK). A saline water solution (~15 ‰ Instant Ocean® Sea Salt) was added to 4 cm depth within the trays to ensure soils remained moist, additional fresh water was added each week to return to this volume, and plants were misted periodically. Every month, trays were systematically rotated around the greenhouse and salinity was measured from all trays. Complete water changes were performed every two months. We measured stem height (cm) and total growth (cm) for

all plants at 10, 12, 14, 20, and 24 months post-planting, and documented plant mortality throughout this period.

To evaluate plant stress, we measured maximum quantum yield of photosystem II (F_v/F_m) with a FluorPen FP 100 (Photon Systems Instruments, Drásov, Czech Republic). F_v/F_m is an indicator of plant photosynthetic performance and a widely used diagnostic to measure plant tolerance to environmental stress, with optimal values generally between 0.8 and 0.85 (Maxwell & Johnson, 2000). Measurements were taken on a single, undamaged leaf from the youngest, fully mature leaf pair for all surviving plants at three time points during the experiment: (1) at the start of the second winter (Dec 2018; 13 months post-planting), (2) during a series of nights with sub-zero temperatures (Feb 2019; 15 months post-planting), and (3) at the end of the second summer (Sept 2019; 22 months post-planting). Measurements were taken on three separate dates at time point 1 (04, 11, and 18-Dec-2018) to establish baseline F_v/F_m values before the onset of colder winter temperatures, and a similar approach was taken at time point 2 (measurements on 01, 02, and 03-Feb-2019) to assess plant responses over the course of a cold event. Values were highly correlated among measurement dates in December ($r=0.83$ – 0.88 , $p<0.001$) and February ($r=0.89$ – 0.92 , $p<0.001$), so we used mean values across these dates for statistical analyses. Measures for time point 3 were taken only on 5-Sept-2019 to assess plant performance under more benign temperature conditions. All measurements were taken in the evening on plants that had been dark-adapted for at least two hours.

From 30-Oct to 07-Nov-2019, 24 months post-planting, plants were harvested and dried to obtain biomass measurements. Plants were cut at soil level, divided into roots, shoots, and leaves (roots were gently washed with fresh water to remove sediment), and then dried at 60°C for three days until constant weight (g). Prior to harvest, we collected one leaf from each surviving plant to measure functional traits. Leaves were undamaged and from the youngest, fully mature leaf pair. We measured water-saturated fresh weight (g) by collecting leaves in the morning, immediately sealing them in plastic bags, and taking measurements within thirty minutes (Vaieretti et al., 2007). We used the Petiole smartphone application with calibration pad N° 7 (Petiole LTD; <https://petioleapp>).

com/) to measure leaf area (cm^2). We then oven dried leaves (as outlined above) and measured dry weight (g). Leaf dry-matter content (LDMC; g g^{-1}) was measured as dry weight divided by water-saturated fresh weight, and specific leaf area (SLA; $\text{cm}^2 \text{g}^{-1}$) was measured as leaf area divided by dry weight (Pérez-Harguindeguy et al., 2013). Leaves were then ground into a fine powder with a Retsch mixer mill MM 400 (Retsch, Haan, Germany) and analysed for percent carbon (%C), percent nitrogen (%N), and C:N with an Elementar vario EL cube CHNOS Elemental Analyzer (Elementar, Langensfeld, Germany), with a certified birch leaf reference standard (Elementar Microanalysis, Devon, UK). We did not obtain results from plants in the last experimental block (replicate 12) due to a technical issue during analysis. As such, we analysed nutrient data from 214 of the 234 surviving plants (replicates 1–11).

Statistical analyses

All analyses were conducted in R v4.0.3 (R Core Team, 2020) with RStudio v1.4.1103 (RStudio Team, 2021). We tested for differences between range core and range margin cohorts with a series of mixed effects models using the *lmer* function in the lmerTest R-package (Kuznetsova et al., 2017), with source region as a fixed effect and maternal cohort nested within region as a random effect. Although maternal cohorts were clustered by collection site nested within region, we did not include this random effect as variation attributed to environmental differences among collection sites should be accounted for with our inclusion of propagule weight as a covariate to account for maternal investment (see detailed model descriptions below). For linear models, we assessed fixed effects with the *anova* function with default Type III SS, and we assessed random effects with the *ranova* function with likelihood ratio tests. For the generalised linear model, all effects were assessed with likelihood ratio tests. Refer to Online Resource Table S1 for detailed summaries of each model described below.

First, we tested whether the weight of field-collected propagules, a measure of maternal investment, varied between source regions and among maternal cohorts nested within region with a linear mixed effects model. Next, for the establishment and initial growth phase of the experiment (0–8 months),

we tested for effects of source region and maternal cohort nested within region on seedling survival (binary response) with a binomial generalised linear mixed effects model, and on time to establishment, stem height at 8 months, and total growth at 8 months with linear mixed effects models. We included propagule weight as a covariate (fixed) in these models to account for variation in maternal investment and replicate planting tray as a (random) blocking factor to account for environmental variation within the greenhouse. We included time to establishment as an additional covariate (fixed) in the height and total growth models because it proved influential for both response variables, independent of propagule weight (Online Resource Table S1).

For the subsequent growth phase of the experiment (8–24 months), we tested for effects of source region and maternal cohort nested within region on stem height, total growth, biomass, ratios of biomass to height/growth, plant stress (F_v/F_m), and leaf traits (leaf area, LDMC, SLA, %C, %N, and C:N) with linear mixed effects models. We log-transformed C:N for statistical analyses (Isles, 2020). We included plant size at the start of this phase of the experiment (i.e., total growth at 8 months) as a covariate (fixed) to account for variation in both propagule weight (measure of maternal investment) and time to establishment. In addition, we included replicate planting tray as a (random) blocking factor to account for environmental variation within the greenhouse. As stem height and total growth were measured at five time points, we first used repeated-measures models that included the effect of time (fixed) and the time $\times$ source region interaction (fixed) before analysing individual time points. We used the same approach for plant stress (F_v/F_m), which was measured at three time points.

Visual inspection of diagnostic plots for each model confirmed that linear models with a normal error distribution were suitable for all variables, except for survival that was assessed with a binomial error distribution. We did identify two large outliers for both SLA and log-transformed C:N, which were removed for analyses (Online Resource Table S1), although their inclusion did not qualitatively change the results described here. From each model, we calculated estimated marginal means for each source region in the emmeans R-package (Lenth, 2021). We also calculated marginal R^2 (variability explained by

fixed effects) and conditional R^2 (variability explained by both fixed and random effects) for each model with the *r.squaredGLMM* function in the MuMIn R-package (Bartoń, 2020). Values for each model are presented in Online Resource Table S1.

Results

Maternal genotypes

All 20 maternal trees were genetically distinct, with a clear separation between range core and range margin genotypes (Fig. 1c). Range margin maternal trees exhibited greater genetic differences and greater clustering by collection site compared to those from the range core (Fig. 1c).

Greenhouse conditions

Greenhouse temperatures were relatively consistent with long-term averages at the Atlantic Florida range margin (Online Resource Fig. S2). Chilling temperatures ($\leq 10^\circ\text{C}$) were experienced on 29 and 82 days during the first and second year of the experiment, respectively. The number of days $\leq 10^\circ\text{C}$ during the second year was higher than what is generally experienced at the Atlantic Florida range margin (73 ± 1.5 days; Devaney et al., 2021). Sub-zero temperatures were experienced on only two days (02 and 03-Feb-2019), both during the second year of the experiment (min: -1 and -3°C , respectively). Greenhouse mean relative humidity (%) was 55.0 ± 6.3 (SD) across the experimental period, drier than annual values at the Atlantic Florida range margin (76.6 ± 7.9 ; data from St Augustine Airport, obtained from <https://www.ncdc.noaa.gov/data-access/land-based-station-data/land-based-datasets>), but within the range of conditions from mangrove greenhouse studies (Ellison & Farnsworth, 1997; Cruz et al., 2019). Salinity (‰) within replicate trays was 14.0 ± 2.7 (SD) for the establishment and initial growth phase of the experiment and was 18.6 ± 4.3 for the subsequent growth phase.

Establishment and initial growth phase (0–8 months)

Weight of field-collected propagules, a measure of maternal investment, varied among maternal cohorts

($\chi^2(1)=235.7$, $p<0.001$), with a mean increase of 98% from the cohort with the lightest to heaviest propagules (1.85–3.64 g) (Online Resource Fig. S3). Propagules from range margin cohorts were heavier than those from range core cohorts ($F_{1, 18}=7.7$, $p=0.013$), with a 23% increase in the estimated marginal mean (2.77 and 2.26 g, respectively), although there was considerable variation among range margin cohorts (Online Resource Fig. S3).

A total of 529 of 600 planted propagules (88.2%) survived to establishment (i.e., produced first true leaves). Survival ($\chi^2(1)=31.2$, $p<0.001$), time to establishment ($\chi^2(1)=98.4$, $p<0.001$), stem height at 8 months ($\chi^2(1)=94.0$, $p<0.001$), and total growth at 8 months ($\chi^2(1)=122.7$, $p<0.001$) all varied among maternal cohorts (Fig. 2). Survival ranged from only 40% within one range core cohort to 100% within six range margin cohorts (Fig. 2a). Mean increases from the cohort with the lowest to highest values were 14% for establishment time (26.0–30.2 weeks) and 90% for both stem height and total growth (13.6–25.9 cm each) (Fig. 2b, c). Range margin cohorts survived in greater numbers (96%; 289 of 300 planted propagules) compared to range core cohorts (80%; 240 of 300 planted propagules) ($\chi^2(1)=12.1$, $p=0.005$) (Fig. 2a), and established more quickly ($F_{1, 18.9}=7.4$, $p=0.014$) with a 4% decrease in the estimated marginal mean (27.1 and 28.3 weeks) (Fig. 2b). Several range margin cohorts grew more than their range core conspecifics over the first eight months, but there were two notable exceptions that were among the smallest plants in the experiment (cohort: GN4, GN5; Fig. 2c). As a result, estimated marginal means were nearly identical between regions for both stem height ($F_{1, 20.5}=0.9$, $p=0.356$) and total growth ($F_{1, 20.1}=0.3$, $p=0.586$) (Fig. 2c). Propagule weight did not affect survival ($\chi^2(1)=1.2$, $p=0.265$) or establishment time ($F_{1, 466.3}=0.4$, $p=0.525$), but affected stem height ($F_{1, 416.3}=52.5$, $p=0.001$) and total growth ($F_{1, 407.2}=66.7$, $p=0.001$). Time to establishment also affected stem height ($F_{1, 512.7}=305.5$, $p<0.001$) and total growth ($F_{1, 494.8}=268.5$, $p<0.001$).

Subsequent growth phase (8–24 months)

A total of 234 of 240 transferred seedlings (97.5%) survived the subsequent 16 months of the experiment.

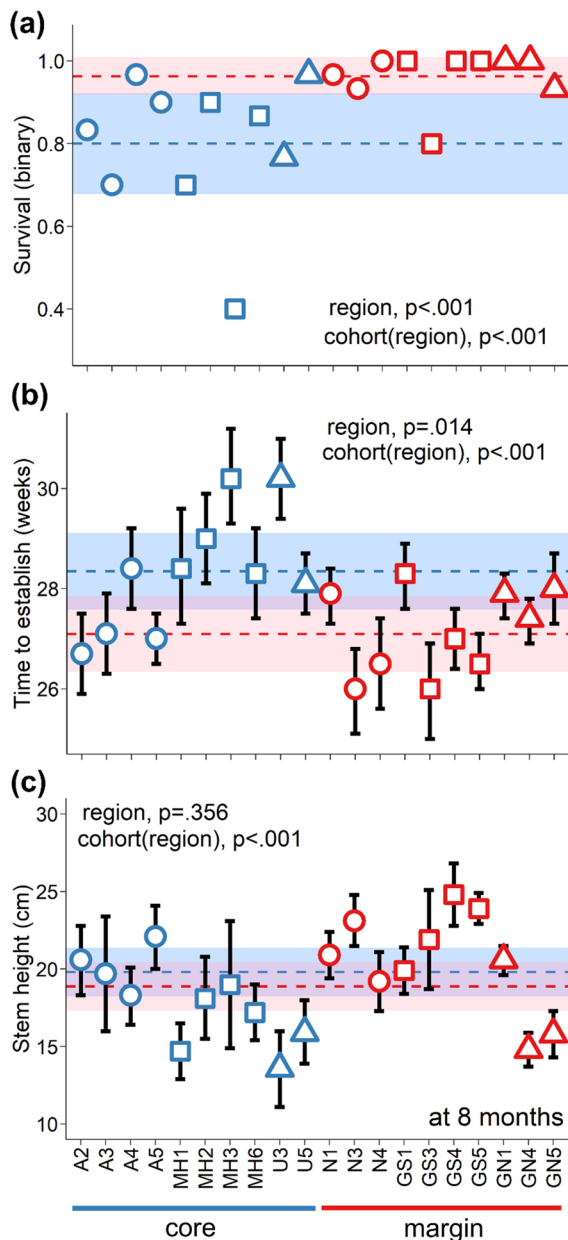


Fig. 2 Range margin cohorts (shown in red) **a** survived in greater numbers and **b** established more quickly, but **c** exhibited similar stem height, and total growth (not shown), at eight months compared to range core cohorts (shown in blue). In the figure, different colour/shape combinations depict the six collection sites (refer to Fig. 1 for geographical locations). Region-level estimated marginal means and 95% confidence intervals are shown with dashed lines and shaded areas in blue for the range core and in red for the range margin. Cohort-level means and 95% confidence intervals are calculated from the raw data

The six mortalities consisted of three range core and three range margin plants.

We assessed plant stress with measurements of the maximum quantum yield of photosystem II (F_v/F_m) in Dec 2018, Feb 2019, and Sept 2019. Mean temperatures were 14.3°C (min/max: 9.8/18.7°C), 6.6°C (-0.7/16.8°C), and 20.4°C (13.3/34.8°C) during these measurement periods, respectively. We found that the effect of source region on plant stress varied temporally (time $\times$ source region: $F_{2, 666.1} = 54.7$, $p < 0.001$; Online Resource Table S1), with the strongest effect of source region observed during the most stressful temperature conditions (Feb 2019). Maternal cohorts exhibited variation in F_v/F_m at each time point (Dec 2018: $\chi^2(1) = 6.8$, $p = 0.009$; Feb 2019: $\chi^2(1) = 18.5$, $p < 0.001$; Sept 2019: $\chi^2(1) = 13.3$, $p < 0.001$), with mean increases from the cohort with lowest to highest F_v/F_m of 15% (0.57 to 0.66), 78% (0.26 to 0.47), and 5% (0.73 to 0.76), respectively (Fig. 3). Range margin cohorts consistently had higher F_v/F_m than range core cohorts (Dec 2018: $F_{1, 18.6} = 39.4$, $p < 0.001$; Feb 2019: $F_{1, 18.7} = 60.7$, $p < 0.001$; Sept 2019: $F_{1, 18.9} = 15.9$, $p = 0.001$), with increases in estimated marginal means of 9% (0.64 and 0.59), 37% (0.41 and 0.30), and 1% (0.75 and 0.74) across the three time points, respectively (Fig. 3). Total growth at 8 months affected F_v/F_m in Dec 2018 ($F_{1, 184.5} = 8.4$, $p = 0.004$) and Feb 2019 ($F_{1, 211.4} = 12.9$, $p < 0.001$), but not in Sept 2019 ($F_{1, 202.6} = 1.4$, $p = 0.246$).

We measured stem height and total growth at 10, 12, 14, 20, and 24 months post-planting. We found that the effect of source region on stem height varied temporally (time $\times$ source region: $F_{4, 1130.0} = 6.6$, $p < 0.001$); whereas we found no temporal variation in the effect of source region on total growth (time $\times$ source region: $F_{4, 1130.0} = 0.7$, $p = 0.625$) (Online Resource Table S1). Stem height varied among maternal cohorts at every time point ($p < 0.001$; Online Resource Table S1). At 24 months, stem height ($\chi^2(1) = 39.0$, $p < 0.001$) and total growth ($\chi^2(1) = 28.0$, $p < 0.001$), varied among maternal cohorts, with mean increases from the cohort with lowest to highest values of 55% (36.7 to 56.9 cm) and 63% (47.2 to 77.1 cm), respectively (Fig. 4a, b). As found at 8 months, the stem height of range margin cohorts did not vary from those of range core cohorts at 10 months ($F_{1, 18.7} = 0.3$, $p = 0.582$) or at 12 months ($F_{1, 18.5} = 2.5$, $p = 0.134$). However, starting at 14 months, range margin cohorts

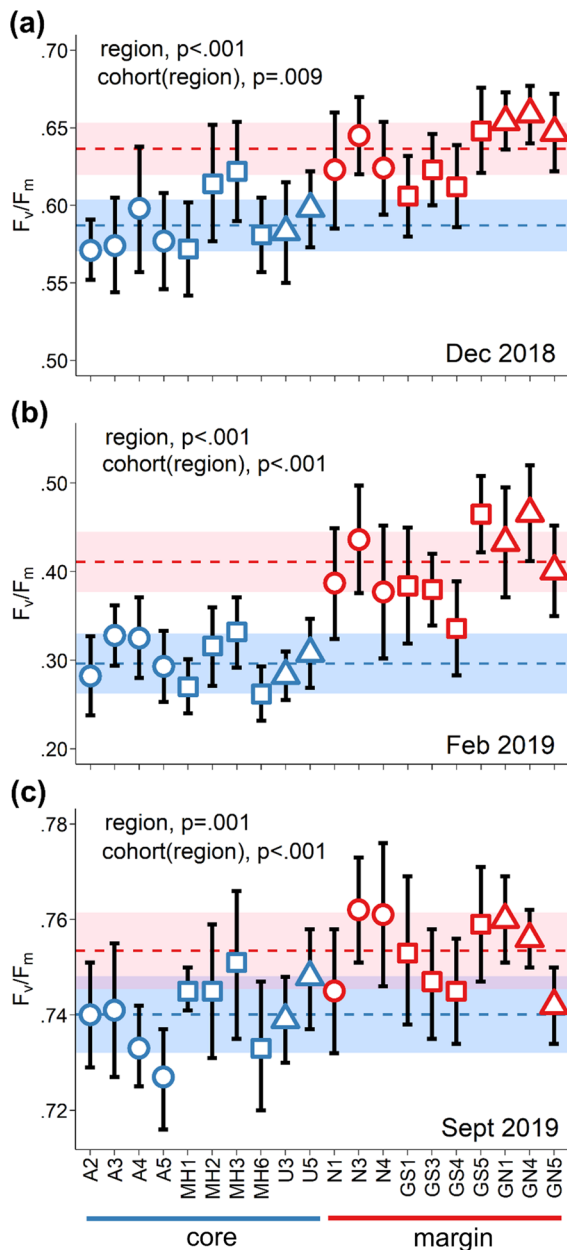


Fig. 3 Range margin cohorts (shown in red) were less stressed than range core cohorts (shown in blue) in **a** December 2018, **b** February 2019 after consecutive nights of sub-zero temperatures, and **c** September 2019. F_v/F_m ; maximum quantum yield of photosystem II. Note that y-axes vary among panels. In the figure, different colour/shape combinations depict the six collection sites (refer to Fig. 1 for geographical locations). Region-level estimated marginal means and 95% confidence intervals are shown with dashed lines and shaded areas in blue for the range core and in red for the range margin. Cohort-level means and 95% confidence intervals are calculated from the raw data

were marginally shorter than range core cohorts ($F_{1, 18.6}=4.5$, $p=0.047$) and this difference progressively became larger at 20 months ($F_{1, 18.4}=5.6$, $p=0.029$) and then at 24 months ($F_{1, 18.6}=7.5$, $p=0.013$), when we found a decrease in the estimated marginal mean of 8% (48.3 and 52.2 cm) (Fig. 4a). In contrast, estimated marginal means for total growth at 24 months were nearly identical between regions ($F_{1, 18.6}=0.0$, $p=0.844$) (Fig. 4b). As detailed for height/growth at 8 months, these patterns were partly shaped by two range margin cohorts that were notable exceptions and among the smallest plants in the experiment (cohort: GN4, GN5; Fig. 4a, b). Total growth at 8 months affected stem height at 24 months ($F_{1, 222.6}=237.5$, $p<0.001$) and total growth at 24 months ($F_{1, 226.5}=452.3$, $p<0.001$).

Total biomass ($\chi^2(1)=35.9$, $p<0.001$) and the ratios of biomass to height ($\chi^2(1)=19.3$, $p<0.001$) and to growth ($\chi^2(1)=20.5$, $p<0.001$) all varied among maternal cohorts, with mean increases from the cohort with lowest to highest values of 87% (8.9 to 16.6 g), 63% (0.19 to 0.31), and 44% (0.16 to 0.23), respectively (Fig. 4c, d; Online Resource Fig. S4). Range margin cohorts accumulated more biomass ($F_{1, 18.5}=7.1$, $p=0.015$) and exhibited greater biomass to height ($F_{1, 18.3}=21.5$, $p<0.001$) and to growth ($F_{1, 18.1}=9.6$, $p=0.006$) compared to range core cohorts, with increases in estimated marginal means of 11% (13.1 and 11.8 g), 17% (0.27 and 0.23), and 11% (0.21 and 0.19), respectively (Fig. 4c, d; Online Resource Fig. S4). Range margin cohorts tended to accumulate more biomass across each measured fraction (i.e., leaves, shoots, and roots), but region-level differences were only statistically significant for leaves ($F_{1, 18.3}=10.8$, $p=0.004$) and roots ($F_{1, 18.7}=9.8$, $p=0.006$), not shoots ($F_{1, 18.6}=0.2$, $p=0.704$) (Online Resource Fig. S4). Again, these patterns were partly shaped by two smaller range margin cohorts (cohort: GN4, GN5; Online Resource Fig. S4). Total growth at 8 months affected total biomass ($F_{1, 227.3}=422.8$, $p<0.001$) and affected the ratios of biomass to height ($F_{1, 219.3}=97.0$, $p<0.001$) and to growth ($F_{1, 220.9}=25.9$, $p<0.001$).

Leaf area ($\chi^2(1)=39.8$, $p<0.001$), leaf dry-matter content (LDMC; $\chi^2(1)=25.8$, $p<0.001$), specific leaf area (SLA; $\chi^2(1)=14.6$, $p<0.001$), and log-transformed C:N ($\chi^2(1)=8.0$, $p=0.005$) all varied among maternal cohorts, with mean increases from the cohort with lowest to highest values of 62% (6.9

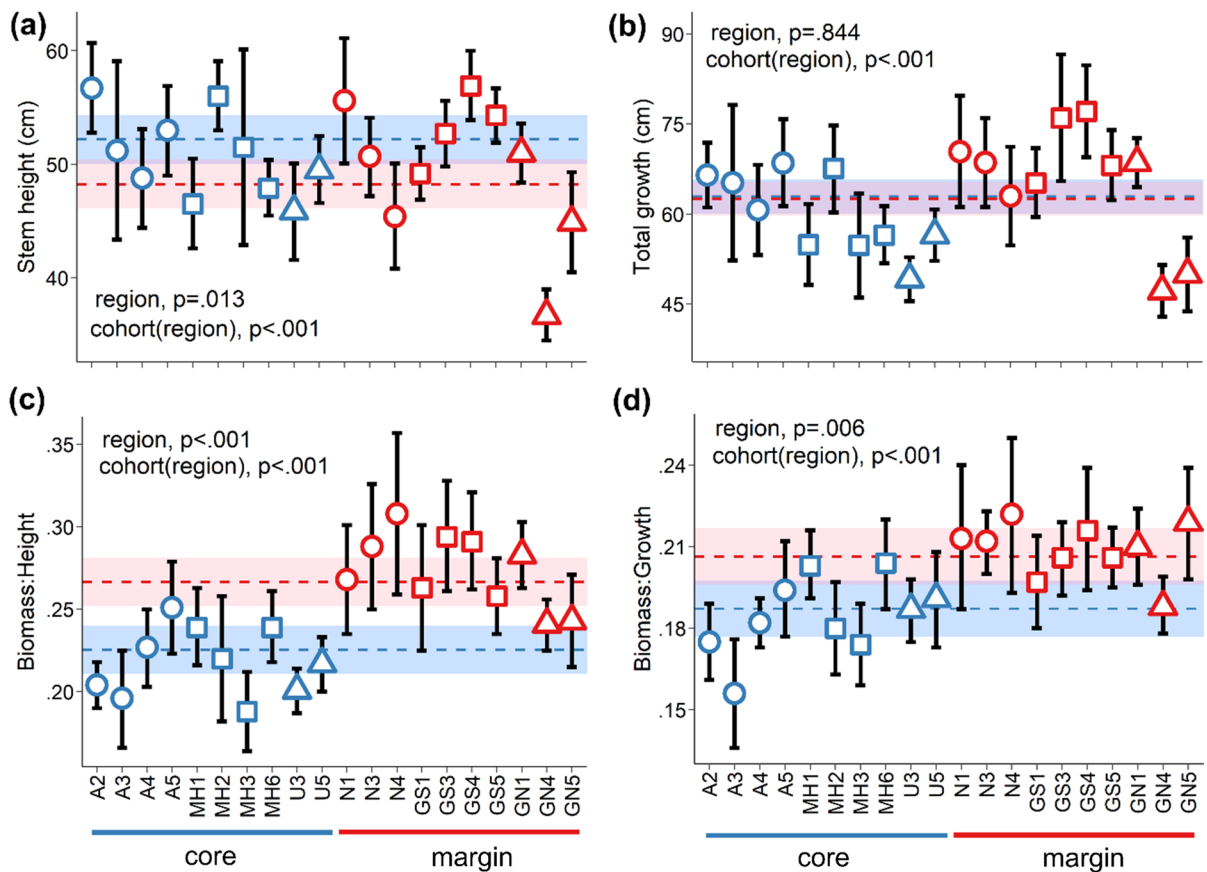


Fig. 4 At 2 years development, range margin cohorts (shown in red) were **a** shorter, but **b** exhibited similar total growth (stem height plus lateral growth), and accumulated a greater proportion of biomass **c** to height and **d** to growth compared to range core cohorts (shown in blue). In the figure, different colour/shape combinations depict the six collection sites (refer

to Fig. 1 for geographical locations). Region-level estimated marginal means and 95% confidence intervals are shown with dashed lines and shaded areas in blue for the range core and in red for the range margin. Cohort-level means and 95% confidence intervals are calculated from the raw data

to 11.2 cm²), 15% (0.33 to 0.38 g g⁻¹), 26% (57.4 to 72.1 cm² g⁻¹), and 8% (3.39 to 3.67), respectively (Fig. 5). Leaf area ($F_{1, 18.7}=0.0$, $p=0.844$) and LDMC ($F_{1, 18.3}=1.4$, $p=0.251$) did not vary between range margin and range core cohorts (Fig. 5a, b). Instead, range margin cohorts exhibited greater SLA ($F_{1, 19.0}=51.2$, $p<0.001$) and lower log-transformed C:N ($F_{1, 17.0}=12.9$, $p=0.002$) compared to range core cohorts, with an increase in the estimated marginal mean of 12% (66.5 and 59.4 cm² g⁻¹) and a decrease of 3% (3.48 and 3.58), respectively (Fig. 5c, d). Lower C:N in the leaves of range margin cohorts was the product of greater %N ($F_{1, 16.9}=10.8$, $p=0.004$), with an increase in the estimated marginal mean of 8% (1.29 and 1.19%), and not due to changes

in %C ($F_{1, 18.6}=0.8$, $p=0.370$), (Online Resource Fig. S5). Total growth at 8 months affected LDMC ($F_{1, 220.3}=8.4$, $p=0.004$) and SLA ($F_{1, 210.0}=22.0$, $p<0.001$), but did not affect leaf area ($F_{1, 215.7}=0.0$, $p=0.931$) or log-transformed C:N ($F_{1, 179.1}=0.0$, $p=0.923$).

Discussion

Range margin mangroves outperform range core conspecifics

Species at their range margins are often genetically distinct from range core conspecifics and may also

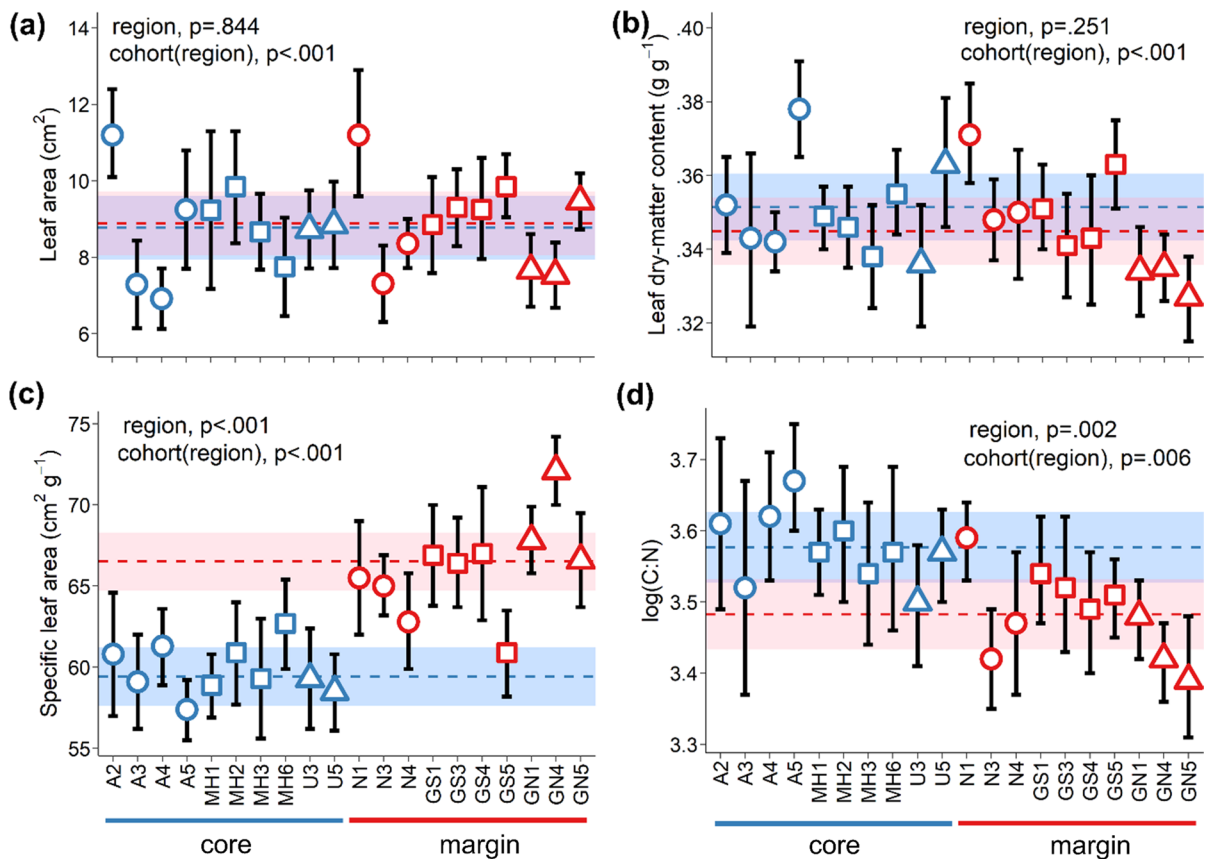


Fig. 5 Range margin cohorts (shown in red) produced leaves of similar **a** size and **b** leaf dry-matter content (LDMC), but with **c** greater specific leaf area (SLA) and **d** lower C:N compared to range core cohorts (shown in blue). In the figure, different colour/shape combinations depict the six collection sites

(refer to Fig. 1 for geographical locations). Region-level estimated marginal means and 95% confidence intervals are shown with dashed lines and shaded areas in blue for the range core and in red for the range margin. Cohort-level means and 95% confidence intervals are calculated from the raw data

exhibit adaptive shifts in morphology, reproductive strategies, and stress tolerance to facilitate establishment and survival in their marginal environment (Chuang & Peterson, 2016). The twenty *Avicennia germinans* maternal trees sampled for this experiment exhibited a clear distinction between range margin and range core genotypes, consistent with population-level genetic differences along Atlantic Florida (Kennedy et al., 2020b). Also, in support of our first prediction, range margin cohorts exhibited clear advantages over range core cohorts during their critical establishment phase by not only surviving in greater numbers, but establishing (i.e., produced first true leaves), on average, more than a week earlier. All plants exhibited signs of stress [i.e., suboptimal values of quantum yield (F_v/F_m)]

under winter chilling and sub-zero temperatures, a ubiquitous plant response to stressful winter conditions (Oliveira & Peñuelas, 2005). Yet, in support of our second prediction, range margin cohorts exhibited higher F_v/F_m under chilling stress and the difference between range margin and range core cohorts was even greater when temperatures dropped below 0°C . These differences suggest that range margin cohorts were better able to maintain photosynthetic efficiency under winter conditions, and that this ability was more pronounced under more extreme conditions often experienced at the Atlantic Florida range margin, but not within the range core. Close to optimal F_v/F_m (cohort means ranged from 0.73 to 0.76), with minimal differences between source regions, under more benign summer

temperatures suggests that all plants subsequently recovered photosynthetic efficiency. Similar values approaching 0.8 are documented in *A. germinans* seedlings under optimal light and salinity conditions (Dangremond et al., 2015).

We found mixed support for our third prediction as greater stress tolerance in range margin cohorts did translate into greater biomass accumulation, but not into greater stem height or total growth (height plus length of lateral shoots). Instead, range core cohorts gradually grew taller as the experiment progressed, while total growth remained nearly identical between source regions throughout the experiment. In other words, over time, range margin cohorts invested more into lateral versus vertical growth. Adult *A. germinans* at the Atlantic Florida range margin demonstrate this same pattern as they grow wider rather than taller (Chapman et al., 2021). Range margin cohorts also accumulated a greater proportion of biomass relative to their size. This shift towards a greater investment into biomass over height may reflect adaptation to novel conditions within the harsh range margin environment, analogous to responses across elevation gradients (Parker et al., 2003). At poleward range margins, shorter *A. germinans* would be less impacted by cold events due to warmer temperatures closer to the soil surface (Osland et al., 2019) and to protection offered by salt marsh vegetation (Pickens et al., 2019). Increased height would also not be as beneficial for developing range margin mangroves in terms of greater access to sunlight as even juvenile trees can outcompete the surrounding low-stature salt marsh for light (Guo et al., 2013). In contrast, increased height would be essential for range core mangroves attempting to reach sunlight within closed canopy forests (Krauss et al., 2008). It is important to note that the patterns outlined here were partly shaped by two range margin cohorts that presented obvious exceptions in terms of growth. These cohorts, both from the most northern collection site, were consistently among the smallest plants in the experiment. However, despite their small stature, these plants were not underperforming as they exhibited clear advantages over range core cohorts at many other measured traits, including greater stress tolerance, greater proportion of biomass to height/growth, and greater resource acquisition (see next paragraph). A reciprocal transplant experiment with planting sites in both the range core and margin could assess whether reduced height

represents local adaptation within range margin *A. germinans*.

Our fourth prediction was not supported as range margin cohorts did not exhibit more conservative leaf traits (i.e., smaller, increased dry-matter content, reduced specific leaf area), which suggests that previous field documentation of systematic shifts in these traits among populations of Atlantic Florida *A. germinans* (Cook-Patton et al., 2015; Kennedy et al., 2020b) may be the product of trait plasticity in response to environmental variation. Instead, in the common garden, we found that range margin cohorts produced leaves of similar size and leaf dry-matter content to those of range core cohorts, but with increased specific leaf area and lower C:N due to greater nitrogen content. These differences within range margin cohorts may reflect leaf development under a less stressed state (Poorter et al., 2009) and metabolic adjustments common in plants adapted to cold temperatures (Woods et al., 2003; Janská et al., 2010). These differences are also consistent with a greater ability among range margin cohorts to capture light and nutrient resources, further supported by their greater accumulation of leaf and root biomass compared to range core cohorts. Plastic shifts towards increased specific leaf area and root growth are found in *A. germinans* seedlings under limited resource availability to maximise resource acquisition (McKee, 1995). Here, we found that similar genetically based shifts also occur along a relatively narrow transition from mangrove range core to margin (27.5 – 30.0°N), presumably to compensate for a shorter growing season and reduced light quality at higher latitude (Spence & Tingley, 2020). An analogous genetically based shift towards greater resource acquisition is found across greater geographic distance (0–28°S) between range core and margin populations of *A. schaueriana*, a closely related congener (Cruz et al., 2019).

Genetic basis to trait variation in range margin mangroves

Range margins may foster unique genetic adaptations that enable species to persist under extreme climatic conditions and that can dictate future responses to climate change (Rehm et al., 2015). Evidence, although still limited, supports genetically based adaptive shifts in chilling tolerance (Markley et al.,

1982; Short et al., 2021), freezing tolerance (Hayes et al., 2020), resource acquisition (Cruz et al., 2019), and precocious reproduction (Dangremond & Feller, 2016) towards cold-sensitive mangrove distributional margins, with further work needed to understand these adaptive shifts towards precipitation-limited mangrove range margins (see Adame et al., 2021). Evidence for selection is also found along climatic gradients across mangrove distributions in Brazil (Cruz et al., 2020; Da Silva et al., 2021). Therefore, despite the immense trait plasticity within mangroves that enables their proliferation across highly variable environments (Feller et al., 2010), trait evolution may also be a common phenomenon in these systems, in particular towards range margins where selection pressures are inherently at their highest. Multiple interacting processes could drive this change, including selective mass mortality, genetic drift, and spatial sorting (Nadeau & Urban, 2019), as well as epigenetic changes (Mounger et al., 2021). A broader understanding of the processes driving these adaptive shifts in mangroves could be achieved with further evaluations of trait changes towards multiple range margins defined by distinct climatic thresholds and colonisation histories (e.g., Bardou et al., 2021).

Our findings also provide insight into how an ecologically important mangrove species (*A. germinans*) may respond to climate change at its poleward range margin. Phenotypic differences outlined above present clear advantages for range margin over range core genotypes in terms of proliferation within currently occupied range margin sites and colonisation of more poleward areas. Mangrove proliferation is forecast along Atlantic Florida as freeze events become less common (Cavanaugh et al., 2015, 2019), but poleward expansion of *A. germinans* along this coastline may be restricted to periods following extreme storm events that provide new recruits almost exclusively from range margin sources (Kennedy et al., 2020a). Hence, an expanding gene pool with a greater representation of range margin genotypes, that are better able to thrive under the climatic extremes beyond the current mangrove distribution, will presumably facilitate future *A. germinans* range expansion.

Considerations and next steps

Offspring may exhibit phenotypic differences because of several factors, specifically the genetic makeup of

their parents, their growing environment, and maternal effects that are shaped by both maternal genetics and maternal environment (Wolf & Wade, 2009). Here, we monitored the development of field-collected propagules in a single greenhouse environment. Therefore, differences observed among maternal cohorts are the product of parental genetics and maternal effects. Some of the variation observed within maternal cohorts will be attributed to differences in pollination (i.e., proportions of progeny that are selfed, outcrossed full-siblings, and outcrossed half-siblings). However, geographical variation in mating system should not have systematically impacted our region-level results as there is not a systematic change in outcrossing rates along our range core to margin sampling gradient (Kennedy et al., 2021b). Field-collected propagules from range margin maternal trees were also, on average, heavier than those from range core trees, consistent with other studies towards the Atlantic Florida range margin for *A. germinans* (Nathan, 2020) and for the co-occurring red mangrove, *Rhizophora mangle* (Dangremond & Feller, 2016). Propagule size is often influenced by maternal environment and is a common proxy for maternal effects, although the strength of environmentally induced maternal effects in plants generally declines as offspring age (Maruyama et al., 2016). Propagule weight, and subsequently total growth at 8 months, both proved highly influential in terms of growth and biomass accumulation across our 2-year experiment. Yet, after accounting for this variation, we still observed significant effects of source region on stem height and biomass. In addition, greater propagule weight had no discernible effect on survival or establishment time and total growth at 8 months had a limited effect (compared to source region) on stress tolerance and most leaf traits.

Controlled common garden experiments can determine whether there is a genetic basis to phenotypic differences within a species, but inherently lack the reality and complexity of natural field conditions. Our greenhouse experiment demonstrates that range margin *A. germinans* maternal cohorts may be better suited to thrive under stressful temperature conditions analogous to those at the Atlantic Florida range margin over the first 2 years of their development. However, in addition to temperature, multiple interacting abiotic and biotic factors will influence the establishment, survival, and growth of these range

margin mangroves (Rogers & Krauss, 2019). Longer-term in situ common gardens are, therefore, a logical next step to better predict how these coastal foundation species will respond to climate change. Although challenging because of long generation times, networks of common gardens have provided a wealth of knowledge regarding how forest trees have adapted to different environments and how they may respond to changing environmental conditions (Alberto et al., 2013). A series of common gardens both at and beyond mangrove range margins could further our understanding of the long-term fitness and persistence of these mangroves and of the factors that may limit or facilitate further range expansion.

Implications for mangrove rehabilitation and restoration

Initiatives to rehabilitate and restore degraded coastal ecosystems are growing in number (Waltham et al., 2020). Mangrove foundation species are a central component of many such initiatives because of the ecosystem services they provide, in particular their ability to sequester and store carbon (Friess et al., 2019). Mangrove replanting may often not be necessary (Lewis, 2005), and not a viable alternative at high-stress range margins (Macy et al., 2021); however, our findings of substantial differences in survival, stress tolerance, growth, and biomass accumulation (key success criteria for rehabilitation and restoration projects) at the level that replanting occurs (i.e., propagules collected from maternal trees) highlight how source selection could influence the outcome of initiatives where mangrove replanting is needed. For instance, after 2 years, we harvested 1.3 kg of total biomass from the surviving plants sourced from range core trees and 1.6 kg from the same number of plants sourced from range margin trees. This translates into a 23% increase in biomass return determined by propagule source region that could be even larger with the exclusion of the two exceptionally small range margin cohorts. Survival, growth, biomass allocation patterns, and age to reproduction have also been found to vary among source populations and maternal cohorts of the red mangrove, *R. mangle* (Proffitt & Travis, 2010; Richards et al., 2021), a species commonly planted for restoration.

Clear advantages exhibited by range margin cohorts grown under temperatures analogous to range margin conditions could be viewed as support for using local sources, or sources with similar environmental conditions, in restoration projects (Bucharova et al., 2017). Records of propagule source and basic monitoring data on phenotypic variation within growth nurseries could help inform source selection and potentially improve replanting success. However, much more work is needed to understand how the genetic background of propagules used for replanting may influence the responses of these developing plants to the multiple interacting stressors common in mangrove systems (e.g., salinity, inundation, herbivory, irradiation). In addition, genetic variation within restoration plantings could shape the associated communities of organisms that colonise and inhabit these areas (Breed et al., 2018), with evidence that mangrove maternal genotype can influence soil microbial communities (Craig et al., 2020) and that genetic differences among mangrove hosts can correlate with the composition of endophytic fungal communities (Kennedy et al., 2021a). Embedding in situ common garden experiments (as described in the previous section) into larger adaptive management experiments (Ellison et al., 2020) could begin to uncover how intraspecific genetic variation may impact mangrove restoration and within which contexts these effects are most influential.

Conclusion

In this study, we demonstrated that there is a genetic basis to adaptive trait shifts towards an expanding range margin of a mangrove foundation species. Maternal cohorts from the northern Atlantic Florida range margin consistently outperformed those from the southern range core under annual temperatures analogous to range margin conditions in a 2-year greenhouse common garden experiment, with evidence of greater survival during initial establishment, greater stress tolerance over winter, greater biomass accumulation, and greater resource acquisition among range margin cohorts. Our findings suggest that genetically based phenotypic differences better enable these range margin mangroves to thrive under their stressful conditions and may facilitate further range expansion with climate change. In addition, an improved understanding of adaptive trait variation

among maternal cohorts of ecologically important mangrove species should help inform future coastal restoration initiatives.

Acknowledgements This research was funded by a Manchester Metropolitan University (MMU) studentship to JPK. Many thanks to IC Feller and R Feller, and the Smithsonian Marine Station at Fort Pierce, Florida for logistical support during fieldwork; to C Jameson, CM Kennedy, W Potdevin, and J Sammy for assistance with experiment set-up and growth measurements; to R Solymosi for R-programming help with monitoring data; to M da Silva and G Mori for sharing an R-script for climatic data analysis; to the MMU technical staff, in particular C Dean and D McKendry, for assistance throughout this project; and to the University of Manchester Genomic Technologies Core Facility and F Combe for fragment analysis. Additional thanks to two anonymous reviewers for insightful comments that improved 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.

Author contributions JPK, GNJ, RFP, and JKR conceived and designed the experiment. JPK performed the experiment, collected and analysed the data, and wrote the manuscript. GNJ, RFP, and JKR provided technical advice, contributed critically to the manuscript drafts, and gave final approval for publication.

Data availability All data generated and analysed in this article, along with the R-code to reproduce analyses, are publicly available on figshare: <https://doi.org/10.6084/m9.figshare.19310501.v1>

Declarations

Conflict of interest The authors declare that they have no competing interests.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Adame, M. F., R. Reef, N. S. Santini, E. Najera, M. P. Turschwell, M. A. Hayes, P. Masque, & C. E. Lovelock, 2021. Mangroves in arid regions: Ecology, threats, and opportunities. *Estuarine, Coastal and Shelf Science* 248: 106796.
- Alberto, F. J., S. N. Aitken, R. Alía, S. C. González-Martínez, H. Hänninen, A. Kremer, F. Lefèvre, T. Lenormand, S. Yeaman, R. Whetten & O. Savolainen, 2013. Potential for evolutionary responses to climate change – evidence from tree populations. *Global Change Biology* 19: 1645–1661.
- Armitage, A. R., W. E. Highfield, S. D. Brody, & P. Louchouart, 2015. The contribution of mangrove expansion to salt marsh loss on the Texas Gulf Coast. *PLoS ONE* 10: e0125404.
- Bardou, R., J. D. Parker, I. C. Feller & K. C. Cavanaugh, 2021. Variability in the fundamental versus realized niches of North American mangroves. *Journal of Biogeography* 48: 160–175.
- Bartoń, K., 2020. MuMin: Multi-Model Inference. R Package Version 1.43.17. <https://CRAN.R-project.org/package=MuMin>.
- Bernhardt, J. R. & H. M. Leslie, 2013. Resilience to climate change in coastal marine ecosystems. *Annual Review of Marine Science* 5: 371–392.
- Breed, M. F., P. A. Harrison, A. Bischoff, P. Durruty, N. J. C. Gellie, E. K. Gonzales, K. Havens, M. Karmann, F. F. Kilkenny, S. L. Krauss, A. J. Lowe, P. Marques, P. G. Nevill, P. L. Vitt & A. Bucharova, 2018. Priority actions to improve provenance decision-making. *BioScience* 68: 510–516.
- Brown, J. H., 1984. On the relationship between abundance and distribution of species. *The American Naturalist* 124: 255–279.
- Bucharova, A., W. Durka, N. Hölzel, J. Kollmann, S. Michalski & O. Bossdorf, 2017. Are local plants the best for ecosystem restoration? It depends on how you analyze the data. *Ecology and Evolution* 7: 10683–10689.
- Cavanaugh, K. C., J. R. Kellner, A. J. Forde, D. S. Gruner, J. D. Parker, W. Rodriguez & I. C. Feller, 2014. Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. *Proceedings of the National Academy of Sciences* 111: 723–727.
- Cavanaugh, K. C., J. D. Parker, S. C. Cook-Patton, I. C. Feller, A. P. Williams & J. R. Kellner, 2015. Integrating physiological threshold experiments with climate modeling to project mangrove species' range expansion. *Global Change Biology* 21: 1928–1938.
- Cavanaugh, K. C., M. J. Osland, R. Bardou, G. Hinojosa-Arango, J. M. López-Vivas, J. D. Parker & A. S. Rovai, 2018. Sensitivity of mangrove range limits to climate variability. *Global Ecology and Biogeography* 27: 925–935.
- Cavanaugh, K. C., E. M. Dangremond, C. L. Doughty, A. P. Williams, J. D. Parker, M. A. Hayes, W. Rodriguez & I. C. Feller, 2019. Climate-driven regime shifts in a mangrove–salt marsh ecotone over the past 250 years. *Proceedings of the National Academy of Sciences* 116: 21602–21608.
- Chapman, S. K., I. C. Feller, G. Canas, M. A. Hayes, N. Dix, M. Hester, J. Morris, & J. A. Langley, 2021. Mangrove growth response to experimental warming is greatest near the range limit in northeast Florida. *Ecology* 102: e03320.
- Chuang, A. & C. R. Peterson, 2016. Expanding population edges: Theories, traits, and trade-offs. *Global Change Biology* 22: 494–512.

- Cohen, M. C. L., E. Rodrigues, D. O. S. Rocha, J. Freitas, N. A. Fontes, L. C. R. Pessenda, A. V. de Souza, V. L. P. Gomes, M. C. França, D. M. Bonotto, & J. A. Bendassolli, 2020. Southward migration of the austral limit of mangroves in South America. *Catena Elsevier* 195: 104775.
- Coldren, G. A. & C. E. Proffitt, 2017. Mangrove seedling freeze tolerance depends on salt marsh presence, species, salinity, and age. *Hydrobiologia* 803: 159–171.
- Cook-Patton, S. C., M. Lehmann & J. D. Parker, 2015. Convergence of three mangrove species towards freeze-tolerant phenotypes at an expanding range edge. *Functional Ecology* 29: 1332–1340.
- Craig, H., J. P. Kennedy, D. J. Devlin, R. D. Bardgett & J. K. Rowntree, 2020. Effects of maternal genotypic identity and genetic diversity of the red mangrove *Rhizophora mangle* on associated soil bacterial communities: a field-based experiment. *Ecology and Evolution* 10: 13957–13967.
- Cruz, M. V., G. M. Mori, C. Signori-Müller, C. C. da Silva, D. H. Oh, M. Dassanayake, M. I. Zucchi, R. S. Oliveira & A. P. de Souza, 2019. Local adaptation of a dominant coastal tree to freshwater availability and solar radiation suggested by genomic and ecophysiological approaches. *Scientific Reports* 9: 19936.
- Cruz, M. V., G. M. Mori, D. H. Oh, M. Dassanayake, M. I. Zucchi, R. S. Oliveira & A. P. de Souza, 2020. Molecular responses to freshwater limitation in the mangrove tree *Avicennia germinans* (Acanthaceae). *Molecular Ecology* 29: 344–362.
- Da Silva, M. F., M. V. Cruz, J. D. D. Vidal Júnior, M. I. Zucchi, G. M. Mori & A. P. De Souza, 2021. Geographical and environmental contributions to genomic divergence in mangrove forests. *Biological Journal of the Linnean Society* 132: 573–589.
- Dangremond, E. M. & I. C. Feller, 2016. Precocious reproduction increases at the leading edge of a mangrove range expansion. *Ecology and Evolution* 6: 5087–5092.
- Dangremond, E. M., I. C. Feller & W. P. Sousa, 2015. Environmental tolerances of rare and common mangroves along light and salinity gradients. *Oecologia* 179: 1187–1198.
- Devaney, J. L., J. Pullen, I. C. Feller, & J. D. Parker, 2021. Low humidity and hypersalinity reduce cold tolerance in mangroves. *Estuarine, Coastal and Shelf Science* 248: 107015.
- Ellison, A. M., 2019. Foundation Species, Non-trophic Interactions, and the Value of Being Common. *iScience* 13: 254–268.
- Ellison, A. M. & E. J. Farnsworth, 1997. Simulated sea level change alters anatomy, physiology, growth, and reproduction of red mangrove (*Rhizophora mangle* L.). *Oecologia* 112: 435–446.
- Ellison, A. M., A. J. Felson & D. A. Friess, 2020. Mangrove rehabilitation and restoration as experimental adaptive management. *Frontiers in Marine Science* 7: 327.
- Fazlioglu, F., J. S. H. Wan & L. Chen, 2020. Latitudinal shifts in mangrove species worldwide: evidence from historical occurrence records. *Hydrobiologia* 847: 4111–4123.
- Feller, I. C., C. E. Lovelock, U. Berger, K. L. McKee, S. B. Joye & M. C. Ball, 2010. Biocomplexity in mangrove ecosystems. *Annual Review of Marine Science* 2: 395–417.
- Fick, S. E. & R. J. Hijmans, 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37: 4302–4315.
- Finney, W., 2011. Comparative growth and propagule viability of Louisiana-harvested Black Mangrove, *Avicennia germinans*. Master Thesis, Nicholls State University.
- Friess, D. A., K. Rogers, C. E. Lovelock, K. W. Krauss, S. E. Hamilton, S. Y. Lee, R. Lucas, J. Primavera, A. Rajkaran & S. Shi, 2019. The state of the world's mangrove forests: past, present, and future. *Annual Review of Environment and Resources Annual Reviews* 44: 89–115.
- Giri, C., E. Ochieng, L. L. Tieszen, Z. Zhu, A. Singh, T. Loveland, J. Masek & N. Duke, 2011. Status and distribution of mangrove forests of the world using earth observation satellite data. *Global Ecology and Biogeography* 20: 154–159.
- Guo, H., Y. Zhang, Z. Lan & S. C. Pennings, 2013. Biotic interactions mediate the expansion of black mangrove (*Avicennia germinans*) into salt marshes under climate change. *Global Change Biology* 19: 2765–2774.
- Hardie, D. C. & J. A. Hutchings, 2010. Evolutionary ecology at the extremes of species' ranges. *Environmental Reviews* 18: 1–20.
- Hayes, M. A., A. C. Shor, A. Jess, C. Miller, J. P. Kennedy & I. C. Feller, 2020. The role of glycine betaine in range expansions; protecting mangroves against extreme freeze events. *Journal of Ecology* 108: 61–69.
- Hoffmann, A. A. & C. M. Sgró, 2011. Climate change and evolutionary adaptation. *Nature* 470: 479–485.
- Isles, P. D. F., 2020. The misuse of ratios in ecological stoichiometry. *Ecology* 101: 1–7.
- Janská, A., P. Maršík, S. Zelenková & J. Ovesná, 2010. Cold stress and acclimation – what is important for metabolic adjustment? *Plant Biology* 12: 395–405.
- Jombart, T. & I. Ahmed, 2011. adegenet 1.3-1: New tools for the analysis of genome-wide SNP data. *Bioinformatics* 27: 3070–3071.
- Kelleway, J. J., K. Cavanaugh, K. Rogers, I. C. Feller, E. Ens, C. Doughty & N. Saintilan, 2017. Review of the ecosystem service implications of mangrove encroachment into salt marshes. *Global Change Biology* 23: 3967–3983.
- Kennedy, J. P., E. M. Dangremond, M. A. Hayes, R. F. Preziosi, J. K. Rowntree & I. C. Feller, 2020a. Hurricanes overcome migration lag and shape intraspecific genetic variation beyond a poleward mangrove range limit. *Molecular Ecology* 29: 2583–2597.
- Kennedy, J. P., R. F. Preziosi, J. K. Rowntree & I. C. Feller, 2020b. Is the central-marginal hypothesis a general rule? Evidence from three distributions of an expanding mangrove species, *Avicennia germinans* (L.) L. *Molecular Ecology* 29: 704–719.
- Kennedy, J. P., R. E. Antwis, R. F. Preziosi & J. K. Rowntree, 2021a. Evidence for the genetic similarity rule at an expanding mangrove range limit. *American Journal of Botany* 108: 1331–1342.
- Kennedy, J. P., J. M. Sammy, J. K. Rowntree, & R. F. Preziosi, 2021b. Mating system variation in neotropical black mangrove, *Avicennia germinans*, at three spatial scales towards an expanding northern distributional limit. *Estuarine, Coastal and Shelf Science* 248: 106754.

- Krauss, K. W., C. E. Lovelock, K. L. McKee, L. López-Hoffman, S. M. L. Ewe & W. P. Sousa, 2008. Environmental drivers in mangrove establishment and early development: a review. *Aquatic Botany* 89: 105–127.
- Kuznetsova, A., P. B. Brockhoff & R. H. B. Christensen, 2017. lmerTest package: tests in linear mixed effects models. *Journal of Statistical Software* 82: 1–26.
- Lee, S. Y., J. H. Primavera, F. Dahdouh-Guebas, K. McKee, J. O. Bosire, S. Cannicci, K. Diele, F. Fromard, N. Koedam, C. Marchand, I. Mendelssohn, N. Mukherjee & S. Record, 2014. Ecological role and services of tropical mangrove ecosystems: a reassessment. *Global Ecology and Biogeography* 23: 726–743.
- Lenth, R. V., 2021. emmeans: Estimated Marginal Means, aka Least-Squares Means. R Package Version 1.5.4. URL: <https://CRAN.R-project.org/package=emmeans>.
- Lewis, R. R., 2005. Ecological engineering for successful management and restoration of mangrove forests. *Ecological Engineering* 24: 403–418.
- Lonard, R. I., F. W. Judd, K. Summy, H. DeYoe & R. Stalter, 2017. The biological flora of coastal dunes and wetlands: *Avicennia germinans* (L.) L. *Journal of Coastal Research* 33: 191–207.
- Lovelock, C. E., 2008. Soil respiration and belowground carbon allocation in mangrove forests. *Ecosystems* 11: 342–354.
- Macy, A., M. J. Osland, J. A. Cherry, & J. Cebrian, 2021. Effects of chronic and acute stressors on transplanted black mangrove (*Avicennia germinans*) seedlings along an eroding Louisiana shoreline. *Restoration Ecology* 29: e13373.
- Madrid, E. N., A. R. Armitage & J. López-Portillo, 2014. *Avicennia germinans* (black mangrove) vessel architecture is linked to chilling and salinity tolerance in the Gulf of Mexico. *Frontiers in Plant Science* 5: 503.
- Markley, J., C. McMillan & G. Thompson Jr., 1982. Latitudinal differentiation in response to chilling temperatures among populations of three mangroves, *Avicennia germinans*, *Laguncularia racemosa*, and *Rhizophora mangle*, from the western tropical Atlantic and Pacific Panama. *Canadian Journal of Botany* 60: 2704–2715.
- Maruyama, C., Z. Goepfert, K. Squires, T. Maclay, Q. Teal-Sullivan & M. S. Heschel, 2016. Effects of population site and maternal drought on establishment physiology in *Impatiens capensis* Meerb. (Balsaminaceae). *Rhodora* 118: 32–45.
- Maxwell, K. & G. N. Johnson, 2000. Chlorophyll fluorescence – a practical guide. *Journal of Experimental Botany* 51: 659–668.
- McKee, K. L., 1995. Interspecific variation in growth, biomass partitioning, and defensive characteristics of neotropical mangrove seedlings: response to light and nutrient availability. *American Journal of Botany* 82: 299–307.
- Méndez-Alonzo, R., J. López-Portillo & V. H. Rivera-Monroy, 2008. Latitudinal variation in leaf and tree traits of the mangrove *Avicennia germinans* (Avicenniaceae) in the central region of the Gulf of Mexico. *Biotropica* 40: 449–456.
- Mounger, J., M. T. Boquete, M. W. Schmid, R. Granado, M. H. Robertson, S. A. Voors, K. L. Langanke, M. Alvarez, C. A. M. Wagemaker, A. W. Schrey, G. A. Fox, D. B. Lewis, C. F. Lira & C. L. Richards, 2021. Inheritance of DNA methylation differences in the mangrove *Rhizophora mangle*. *Evolution and Development* 23: 351–374.
- Nadeau, C. P. & M. C. Urban, 2019. Eco-evolution on the edge during climate change. *Ecography* 42: 1280–1297.
- Nathan, M., 2020. Plant-insect interactions in a shifting coastal ecosystem: *Avicennia germinans* and its associated arthropods. PhD Dissertation, University of Maryland.
- Oliveira, G. & J. Peñuelas, 2005. Effects of winter cold stress on photosynthesis and photochemical efficiency of PSII of the Mediterranean *Cistus albidus* L. and *Quercus ilex* L. *Plant Ecology* 175: 179–191.
- Osland, M. J., L. C. Feher, K. T. Griffith, K. C. Cavanaugh, N. M. Enwright, R. H. Day, C. L. Stagg, K. W. Krauss, R. J. Howard, J. B. Grace & K. Rogers, 2017. Climatic controls on the global distribution, abundance, and species richness of mangrove forests. *Ecological Monographs* 87: 341–359.
- Osland, M. J., L. C. Feher, J. López-Portillo, R. H. Day, D. O. Suman, J. M. Guzmán Menéndez & V. H. Rivera-Monroy, 2018. Mangrove forests in a rapidly changing world: global change impacts and conservation opportunities along the Gulf of Mexico coast. *Estuarine, Coastal and Shelf Science* 214: 120–140.
- Osland, M. J., A. M. Hartmann, R. H. Day, M. S. Ross, C. T. Hall, L. C. Feher & W. C. Vervaeke, 2019. Microclimate influences mangrove freeze damage: implications for range expansion in response to changing macroclimate. *Estuaries and Coasts* 42: 1084–1096.
- Osland, M. J., P. W. Stevens, M. M. Lamont, R. C. Brusca, K. M. Hart, J. H. Waddle, C. A. Langtimm, C. M. Williams, B. D. Keim & A. J. Terando, 2021. Tropicalization of temperate ecosystems in North America: the northward range expansion of tropical organisms in response to warming winter temperatures. *Global Change Biology* 27: 3009–3034.
- Parker, I. M., J. Rodriguez & M. E. Loik, 2003. An evolutionary approach to understanding the biology of invasions: local adaptation and general-purpose genotypes in the weed *Verbascum thapsus*. *Conservation Biology* 17: 59–72.
- Pecl, G. T., M. B. Araújo, J. D. Bell, J. Blanchard, T. C. Bonebrake, I. C. Chen, T. D. Clark, R. K. Colwell, F. Danielsen, B. Evengård, L. Falconi, S. Ferrier, S. Frusher, R. A. Garcia, R. B. Griffis, A. J. Hobday, C. Janion-Scheepers, M. A. Jarzyna, S. Jennings, J. Lenoir, H. I. Linnetved, V. Y. Martin, P. C. McCormack, J. McDonald, N. J. Mitchell, T. Mustonen, J. M. Pandolfi, N. Pettorelli, E. Popova, S. A. Robinson, B. R. Scheffers, J. D. Shaw, C. J. B. Sorte, J. M. Strugnell, J. M. Sunday, M. N. Tuanmu, A. Vergés, C. Villanueva, T. Wernberg, E. Wapstra, & S. E. Williams, 2017. Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. *Science* 355: eaai9214.
- Pérez-Harguindeguy, N., S. Díaz, E. Garnier, S. Lavorel, H. Poorter & P. Jaureguiberry, 2013. New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany* 61: 167–234.
- Pickens, C. N., T. M. Sloey & M. W. Hester, 2019. Influence of salt marsh canopy on black mangrove (*Avicennia*

- germinans*) survival and establishment at its northern latitudinal limit. *Hydrobiologia* 826: 195–208.
- Poorter, H., U. Niinemets, L. Poorter, I. J. Wright & R. Villar, 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist* 182: 565–588.
- Proffitt, C. E. & S. E. Travis, 2010. Red mangrove seedling survival, growth, and reproduction: effects of environment and maternal genotype. *Estuaries and Coasts* 33: 890–901.
- R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://R-project.org>.
- Rehm, E. M., P. Olivas, J. Stroud & K. J. Feeley, 2015. Losing your edge: climate change and the conservation value of range-edge populations. *Ecology and Evolution* 5: 4315–4326.
- Richards, C. L., K. L. Langanke, J. Mounger, G. A. Fox, & D. B. Lewis, 2021. Trait response to nitrogen and salinity in rhizophora mangle propagules and variation by maternal family and population of origin. *Frontiers in Marine Science* 8: 756683.
- Rodriguez, W., I. C. Feller & K. C. Cavanaugh, 2016. Spatio-temporal changes of a mangrove–saltmarsh ecotone in the northeastern coast of Florida, USA. *Global Ecology and Conservation* 7: 245–261.
- Rogers, K. & K. W. Krauss, 2019. Moving from generalisations to specificity about Mangrove–Saltmarsh dynamics. *Wetlands* 39: 1155–1178.
- RStudio Team, 2021. RStudio: Integrated Development for R. RStudio, PBC, Boston, MA. <https://rstudio.com>.
- Saintilan, N., N. C. Wilson, K. Rogers, A. Rajkaran & K. W. Krauss, 2014. Mangrove expansion and salt marsh decline at mangrove poleward limits. *Global Change Biology* 20: 147–157.
- Short, A. W., R. Chen, & A. K. S. Wee, 2021. Comparison between parapatric mangrove sister species revealed higher photochemical efficiency in subtropical than tropical coastal vegetation under chilling stress. *Aquatic Botany* 168: 103323.
- Simpson, L. T., T. Z. Osborne & I. C. Feller, 2017. Establishment and biomass allocation of black and red mangroves: response to propagule flotation duration and seedling light availability. *Journal of Coastal Research* 335: 1126–1134.
- Spence, A. R. & M. W. Tingley, 2020. The challenge of novel abiotic conditions for species undergoing climate-induced range shifts. *Ecography* 43: 1571–1590.
- Vaieretti, M. V., S. Díaz, D. Vile & E. Garnier, 2007. Two measurement methods of leaf dry matter content produce similar results in a broad range of species. *Annals of Botany* 99: 955–958.
- Vovides, A. G., J. Vogt, A. Kollert, U. Berger, U. Grueters, R. Peters, A. L. Lara-Domínguez & J. López-Portillo, 2014. Morphological plasticity in mangrove trees: salinity-related changes in the allometry of *Avicennia germinans*. *Trees* 28: 1413–1425.
- Waltham, N. J., M. Elliott, S. Y. Lee, C. Lovelock, C. M. Duarte, C. Buelow, C. Simenstad, I. Nagelkerken, L. Claassens, C. K. C. Wen, M. Barletta, R. M. Connolly, C. Gillies, W. J. Mitsch, M. B. Ogburn, J. Purandare, H. Possingham & M. Sheaves, 2020. UN decade on ecosystem restoration 2021–2030 – what chance for success in restoring coastal ecosystems? *Frontiers in Marine Science* 7: 71.
- Warwell, M. V. & R. G. Shaw, 2017. Climate-related genetic variation in a threatened tree species, *pinus albicaulis*. *American Journal of Botany* 104: 1205–1218.
- Whitt, A. A., R. Coleman, C. E. Lovelock, C. Gillies, D. Ierodiaconou, M. Liyanapathirana, & P. I. Macreadie, 2020. March of the mangroves: Drivers of encroachment into southern temperate saltmarsh. *Estuarine, Coastal and Shelf Science* 240: 106776.
- Wolf, J. B. & M. J. Wade, 2009. What are maternal effects (and what are they not)? *Philosophical Transactions of the Royal Society B: Biological Sciences* 364: 1107–1115.
- Woods, H. A., W. Makino, J. B. Cotner, S. E. Hobbie, J. F. Harrison, K. Acharya & J. J. Elser, 2003. Temperature and the chemical composition of poikilothermic organisms. *Functional Ecology* 17: 237–245.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.