

**Sustained mangrove reproduction despite major turnover in pollinator
community composition at expanding range edge**

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- **Background and Aims** How well plants reproduce near their geographic range edge can determine whether distributions will shift in response to changing climate. Reproduction at the range edge can be limiting if pollinator scarcity leads to pollen limitation, or if abiotic stressors affect allocation to reproduction. For many animal-pollinated plants with expanding ranges, the mechanisms by which they have overcome these barriers are poorly understood.
- **Methods** In this study, we examined plant-pollinator interactions hypothesized to impact reproduction of the black mangrove, *Avicennia germinans*, which is expanding northward in coastal Florida, USA. We monitored insects visiting *A. germinans* populations varying in proximity to the geographic range edge, measured the pollen loads of the most common insect taxa and pollen receipt by *A. germinans* stigmas, and quantified flower and propagule production.
- **Key Results** We found that despite an 84% decline in median floral visits by insects at northernmost vs. southernmost sites, range-edge pollen receipt remained high. Notably, local floral visitor assemblages exhibited substantial turnover along the study's latitudinal gradient, with large-bodied bees and hover flies increasingly common at northern sites. We also observed elevated flower production in northern populations and higher per capita reproductive output at the range edge. Furthermore, mean propagule mass in northern populations was 18% larger than propagules from the southernmost populations.

- **Conclusions** These findings reveal no erosion of fecundity in *A. germinans* populations at range limits, allowing rapid expansion of mangrove cover in the region. These results also illustrate that substantial turnover in the assemblage of flower-visiting insects can occur at an expanding range edge without altering pollen receipt.

Key words: *Avicennia germinans*, climate change, fruit set, geographic range shift, insect pollination, mangroves, pollen limitation, species distributions, visitation rate.

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INTRODUCTION

The geographic distributions of many taxa are shifting in response to climate change drivers (Chen *et al.*, 2011; Lenoir *et al.*, 2020). For plants and other sessile organisms, range shifts often depend on reproductive performance near the leading range edge. Reproductive failure can be as important as mortality in setting plant range limits (Pigott, 1992; Gaston, 2009). For plants subject to changing climatic conditions, reproductive failure at the range edge can result in a delayed range shift, or in no shift at all (Clark *et al.*, 2001; Brown *et al.*, 2019).

Multiple abiotic and biotic ecological mechanisms can decrease plant fecundity, or the number of viable seeds produced per individual, near geographic range edges. For species with range limits set by environmental tolerances, stressful conditions at the range edge can reduce plant vigor and allocation to reproduction (Reinartz, 1984; Chiariello and Gulmon, 1991; Gaston, 2009). While some plants compensate for early losses to reproductive components or for reduced adult survival, allocation to reproduction generally declines as resources become limiting – particularly for perennial plants (Chiariello and Gulmon, 1991; Wenk and Falster, 2015). Plants that survive, grow, and persist under adverse abiotic conditions may face physiological constraints on reproduction. For instance, Pigott and Huntley (1981) observed prohibitively slow pollen-tube growth in otherwise apparently healthy populations of *Tilia cordata* near its northern range edge, which they attributed to cold spring temperatures. Additional studies have found reproductive failure at range edges where phenology is incompatible with earlier winters or later springs (Tremblay *et al.*, 2002; Griffith and Watson, 2006; Morin *et al.*, 2007; Chuine, 2010).

Biotic factors at a plant's range edge also constitute barriers to reproduction. While negative biotic interactions, particularly competition, have received growing research attention as the causes of species' range limits (Sexton *et al.*, 2009; HilleRisLambers *et al.*, 2013; Svenning *et al.*, 2014), there is increasing recognition of the role that positive species interactions can play in setting species' range limits (HilleRisLambers *et al.*, 2013; Stephan *et al.*, 2021; Fowler *et al.*, 2023). For example, the absence of mutualists beyond a plant's range edge can prevent local establishment (IM Parker, 1997; MA Parker, 2001; Nuñez *et al.*, 2009; Moeller *et al.*, 2012; Afkhami *et al.*, 2014). Plants that rely on

pollinators for full fruit set—i.e. most flowering plants (Ollerton *et al.*, 2011)—face this biotic barrier to range-edge reproduction. Pollinator communities often vary in composition throughout the distribution of a given plant species, potentially creating spatial gradients of pollen limitation (Horvitz and Schemske, 1990; Herrera, 1998; Gómez *et al.*, 2010). If a plant and its pollinators are similarly limited by environmental conditions—e.g. aridity, soil conditions, or temperature—then pollinator availability can decline (and pollen limitation can rise) toward the plant’s range edge (Stone and Jenkins, 2008; Moeller *et al.*, 2012). Alternatively, pollinator visitation can decline at a plant’s range edge if the habitat there contains few floral resources, and therefore supports few pollinators (Chalcoff *et al.*, 2012). Finally, pollination can decline if a plant’s density, height, and/or floral display are reduced at the range edge, thereby reducing its attractiveness to pollinators (Kunin, 1993; Brody and Mitchell, 1997; Hegland and Boeke, 2006).

These conditions are not always present at plants’ range edges, however, and evidence is mixed for the hypothesis that reductions in pollinator abundance or changes in species composition limit plant performance through increased pollen limitation at range boundaries or invasion fronts. Some empirical studies provide strong support (e.g., Parker, 1997; Chalcoff *et al.*, 2012; Moeller *et al.*, 2012; Rivist and Vellend, 2018), while others refute or provide equivocal evidence (e.g., Stanton, 1987; Busch, 2005; Traveset and Richardson, 2014; Hargreaves *et al.*, 2015). A recent meta-analysis suggests that pollen limitation rarely constrains plant species distributions, even for species that depend on animal vectors (Dawson-Glass and Hargreaves, 2022). A second meta-analysis argues that specialized mutualistic relationships constrain range shifts to a greater degree than facultative relationships (Stephan *et al.*, 2021). In addition, plants can respond to poor pollination environments (at range edges and elsewhere) at both short and long time scales by reallocating resources (Haig and Westoby, 1988b), altering their phenology (Bingham and Orthner, 1998), or increasing selfing in order to avoid pollen limitation (Eckert *et al.*, 2006; Hargreaves and Eckert, 2014). In this study, we address the question of reduced pollen receipt and sexual reproduction at plants’ range limits, and the ways in which plants avoid it, using a pollinator-dependent species that has succeeded in rapidly shifting its northern range boundary.

The black mangrove *Avicennia germinans* (L.) L. (Acanthaceae) is an insect-pollinated

species that has expanded its geographical range with contemporary climate change in the southeastern United States. A freeze-intolerant tree that depends on pollinators for full fruit set and does not reproduce asexually (Tomlinson, 2016), *A. germinans* has spread rapidly northward in the Gulf of Mexico and northern Florida over the past three decades, in tandem with a decline in the frequency of hard freezes over that period (Osland *et al.*, 2013; Cavanaugh *et al.*, 2014). Recent work has reconstructed a longer history of mangrove extent in the region, revealing a highly dynamic range edge that has oscillated between mangrove dominance and salt marsh dominance for more than 150 years, mirroring decadal-scale fluctuations in the region's climate (Rodriguez *et al.*, 2016; Cavanaugh *et al.*, 2019). These repeated and rapid contractions and expansions of the *A. germinans* range demonstrate its sensitivity to changing climatic conditions. However, the role of range-edge pollination and reproduction in the current geographic range expansion of *A. germinans* beyond its historical limits remains unexplored (Kennedy *et al.*, 2021).

In this study, we ask how *A. germinans* pollinators, pollen receipt, flowering, and fecundity vary along a geographical gradient from the range interior to the leading range edge. Specifically, we examined whether or not floral visitor abundance and pollen receipt decline from the core of the distribution toward the northern range edge, where patchy mangrove stands are embedded within a matrix of wind-pollinated salt marsh species. We investigated variation in local pollinator assemblages by quantifying (a) the relationship between proximity to the range edge and the abundance and identity of floral visitors, and (b) the variation among floral visitors in their pollen loads. Additionally, considering that northern populations of *A. germinans* are subject to colder temperatures and a shorter growing season (conditions that affect their leaf and vascular morphology, Cook-Patton *et al.*, 2015), we predicted reduced flowering in range-edge populations. Finally, we asked whether or not *A. germinans* fruit set rates and fecundity decline from the range center to the range edge, and how spatial variation in floral visitor abundance and identity, pollen receipt, and flowering contribute to observed trends.

MATERIAL AND METHODS

Study system

Avicennia germinans is an intertidal tree or shrub with a global distribution that bears bisexual flowers on terminal panicles of spikes (Tomlinson, 2016). Floral corollas are white, ~1cm in diameter, and open in pairs within each spike (Fig. 1). Flowers contain four stamens and a gynoeceum with four ovules and a single style and bilobed stigma. The flowers are protandrous, with anthers that release pollen prior to the opening of the stigmatic lobes (Borg and Schönenberger, 2011; Daniel, 2016). *A. germinans* is self-compatible (Nettel-Hernanz *et al.*, 2013), but exhibits significant outcrossing in all studied populations (Kennedy *et al.*, 2021). A closely related sister species, *Avicennia schaueriana* Moldenke, which is also self-compatible and exhibits protandry, appears incapable of spontaneous self-pollination, relying on pollinators for fruit formation (de Lima Nadia *et al.* 2012). As with many mangrove taxa, flowers produce a single seed that germinates while still attached to the parent plant, giving rise to a dispersive seedling known as a ‘propagule’ (Tomlinson, 2016). Although reproduction occurs year-round in the tropics (Daniel, 2016), in northern subtropical regions *A. germinans* flower synchronously May-August and later release their propagules in September through November (*unpublished data*).

Data were collected over the course of three years (2013-2015) at eleven sites containing *A. germinans* populations in eastern Florida (Fig. 1, Supplementary data Table S1). These sites span the full extent of Florida’s eastern mangrove-marsh ecotone – an approximately 200-km coastal zone where salt marsh in the north transitions to mangroves in the south – and extend southward into a region that has been continuously mangrove-dominated for several thousand years (Scholl 1964).

The southernmost sites (latitudes 27.1-27.9°N) are dominated by stands of three Caribbean mangrove species (with *Rhizophora mangle* L. [Rhizophoraceae] and *Laguncularia racemosa* [L.] C.F. Gaertn. [Combretaceae]), in varying stages of regeneration following impoundment for mosquito control in the first half of the 20th century. Within the mixed mangrove-marsh ecotone (latitudes 28.5-29.1°N), sites are characterized by mangrove stands edging waterways, with salt marsh vegetation landward (primarily *Distichlis spicata* [L.] Greene [Poaceae], *Spartina alterniflora* Loisel. [Poaceae],

Batis maritima L. [Bataceae], and *Salicornia* spp. L. [Amaranthaceae]). At the northern end of the study region (latitudes 29.6-29.9°N), sites contain some of Florida's northernmost mangroves, primarily within the Guana-Tolomato-Matanzas National Estuarine Research Reserve (GTM) (Cavanaugh *et al.*, 2019). Here, clusters of short (generally <3m tall) mangroves – almost exclusively *A. germinans* – are embedded in a salt marsh matrix consisting primarily of *S. alterniflora*, *B. maritima*, and *Salicornia* spp.

Floral visitors

The identity and frequency of *A. germinans* insect floral visitors were assessed over the course of three flowering seasons (May–July, 2013–2015). Because we did not unambiguously establish which taxa were true pollinators versus nectar/pollen thieves, we use the term “floral visitors” when referring to the insects observed in this study. Each of eleven sites were monitored repeatedly within at least one year, although no more than seven were monitored in any given year (Supplementary data Table S1). In total, floral visitors were observed for 105.5hrs, 67hrs, and 33.5hrs in 2013, 2014, and 2015, respectively.

A. germinans flowers were monitored for floral visitors during 15-minute observation periods, which we conducted in fair weather from mid-morning to mid-day. Focal *A. germinans* were selected haphazardly; trees were at least 10m apart and contained at least 10 open flowers. We conducted a single observation period per day at each focal tree (i.e. no tree was monitored twice on the same date). During each observation period, the observer selected 4-10 open flowers in close proximity to one another, and recorded the identity of each floral visitor and the number of focal flowers visited by each individual insect. Insects were typically identified to family, with the exception of the Apidae (Hymenoptera) which were identified to genus or species. A complete list of the 29 taxonomic labels used in floral monitoring, as well as the study-wide visit totals for each taxon, are available in Table 1. Observers recorded the focal tree's height (to the nearest 0.5m) and estimated the total number of open flowers on the tree.

We applied generalized linear models (GLM) and generalized linear mixed models (GLMM)

for all analyses in R version 3.5.0 (R Development Core Team, 2018). We evaluated response data modeled as counts for overdispersion and used the negative binomial error distribution in such cases. For GLMMs, we used a bootstrapping method in the pbrtest package (Halekoh and Højsgaard, 2014) to test the significance of each fixed effect in the model. Marginal and conditional R^2 – measures of variance explained by fixed effects (R^2_m) and variance explained by both fixed and random effects (R^2_c), respectively – were calculated following Nakagawa and colleagues (2017) and implemented in the MuMIn package (Barton, 2015). For GLMs, McFadden’s pseudo- R^2 was calculated using the rsq package (Zhang, 2020).

Floral visits were modeled three separate ways: as total visits across all taxa (to explain overall trends in insect abundance), as a binary presence/absence variable across all taxa (to specifically examine patterns of pollinator absence; see explanation below), and as visits by specific taxa (to explore changes in the floral visitor assemblage; see explanation below). In all cases, the number of flowers watched during an observation period was included as an offset, for ease of modeling and to account for variable sampling effort. To model total visits across all taxa, we used a GLMM with a negative binomial error distribution. Latitude (mean-centered in all analyses), year, the number of flowers open on the focal tree, and tree height were included as fixed effects; date was included as a random effect (multiple observation periods were conducted on the same date). Floral visitor presence/absence was modeled similarly in a GLMM, except with a binomial error distribution (lme4 package, Bates *et al.*, 2015). For the response variable, all non-zero visit totals were converted to 1. For these two models, we used bootstrapping to test latitude’s importance as a predictor.

To assess changes in the floral visitor assemblage across the latitudinal gradient of the study sites, we constructed a third GLMM with a random slope term that allowed the effect of latitude to vary among taxa. For this analysis, we chose to include taxa irrespective of their likely effectiveness as pollinators, because variation in the abundance of nectar thieves can alter the behavior of legitimate pollinators, thereby influencing plant reproduction (Zhang *et al.*, 2014). We subset the raw visits data to contain just the 12 most abundant taxa (representing 97% of all flower visits; see Table 1), and used a negative binomial error distribution in the glmmADMB package (Fournier *et al.*, 2012). In addition to the by-taxon random slope and intercept terms, the model included random terms for date and

observation period (as individuals observed during the same observation period might behave similarly), and a single fixed effect for latitude. A likelihood ratio test was used to determine the importance of the by-taxon random slope term. We then plotted the model-estimated random slopes to assess differences among taxa in their variation with latitude. Finally, we performed a non-metric multidimensional scaling (NMDS) on visitation rates (vegan package, Oksanen *et al.*, 2015), using the 12 most abundant taxa and summing across observation periods made at the same site and on the same date (to avoid problems associated with low abundance per sample). The NMDS used Bray-Curtis dissimilarities.

To assess the relative importance of individual taxa as potential pollinators of *A. germinans*, in June and July of 2013 we captured floral visitors and measured the size of their pollen loads. Using hand nets, we collected individual insects representing 11 of the 12 most frequently observed floral visitor taxa, directly from *A. germinans* flowers (one frequent taxon – Pompilidae – was not encountered during this time). We collected as close to 10 individuals per taxon as possible (see sample sizes in Supplementary data Table S2). We quickly immobilized the insects in coolers with ice packs, later transferring specimens to a -20°C freezer and pinning them for examination under a dissecting microscope.

In the lab, each insect was pinned and swabbed with a ~2mm³ cube of fuchsin jelly for up to 10 minutes to sample its pollen load. In the case of *Apis mellifera* L. (Hymenoptera: Apidae) and *Bombus* spp. (Hymenoptera: Apidae), hydrated corbicular pollen was avoided, as it is thought to be unlikely to contribute to pollination (Thorp, 2000). The fuchsin jelly was then transferred to a microscope slide, where the number of *Avicennia* and non-*Avicennia* pollen grains could be counted using a compound microscope at 100X and 400X magnification. To test for variation among taxa in the size of their pollen loads, we used the *MASS* package (Venables and Ripley, 2002) to construct a negative-binomial GLM with a single fixed effect of taxon, and used a post hoc Tukey test to compare individual taxa.

Pollen receipt

To assess pollen receipt by *A. germinans* flowers, we collected stigmas from six sites in 2015 (Supplementary data Table S1). Each site was visited twice – once in the early flowering season and once in the mid-flowering season. During each site visit 12 trees were haphazardly selected (for two site visits, poor weather limited data collection to just three and eight trees, respectively), and we collected up to eight flowers with mature stigmas from throughout the tree canopy. Mature stigmas could be identified by their spread lobes, which open on approximately day 3 of anthesis (*personal observation*, M.N.); flowers are syncarpous, with a single stigma per flower. In total, we collected 768 stigmas across the six sites. In the lab, each stigma was removed from its flower and mounted in fuchsin jelly on a microscope slide, which we inspected at 100X and 400X magnification on a compound microscope. Given the sometimes-large number of pollen grains present, we counted the number of *A. germinans* pollen grains three times on each stigma, and used the average of these three counts for analysis. We modeled pollen receipt with a negative-binomial GLMM, with latitude as the single fixed effect and tree ID as a random effect. We used bootstrapping to test for the importance of latitude.

Flowering

Flower production, or the number of open flowers per tree, was measured during each observation period for floral visitors, as described above. Flower production was modeled with a negative binomial GLM (due to overdispersion in the response) with latitude and tree size as predictors. We used a likelihood ratio test to compare this model to one without latitude.

Fecundity

In 2014 and 2015, after flowering was completed but well before propagules matured, we installed mesh bags over infructescences to measure fruit set rates, defined here as the number of mature propagules produced per floral bud. Each year, we haphazardly selected up to 30 *A. germinans* at each site (six sites in 2014 and seven in 2015; see Supplementary data Table S1), and installed up to three bags per tree. We then collected the bags in late October-early November, and counted the number of propagules (both abscised and still attached to the pedicel) as well as the total number of floral bud scars. Fruit set rate was calculated as the total number of propagules produced by a given

inflorescence/infructescence, divided by the number of floral bud scars. We modeled fruit set rate using a binomial GLMM, with the total number of original floral buds set as a weight, or number of trials. Latitude was the sole fixed effect; tree ID was included as a random predictor, as was an observation-level random effect, to handle overdispersion. We used bootstrapping to test latitude's importance as a predictor.

At these same sites, in late October-early November of 2014 and 2015 when propagules were maturing on parent trees, we established transects to measure propagule production and the density of reproductive *A. germinans*. At each site, we identified three areas of high *A. germinans* density and laid out one 20m transect in each area (oriented to maximize the number of trees intersected), resulting in three transects per site. To measure propagule production per tree, we then randomly selected five reproductive trees along each transect and estimated the number of propagules present by counting the number on a representative portion of the tree and extrapolating to the entire canopy. Because different sites were in different stages of propagule drop, we corrected these estimates to account for propagules that had already fallen. We did this using the mesh bags described above (which we had also used to calculate fruit set rates); by collecting falling propagules these bags allowed us to calculate the fraction of total propagules that remained attached to the pedicel. Multiplying our original propagule counts by the inverse of this fraction let us estimate the total number of propagules originally produced by the trees. Note that we were unable to correct for any effect the bags themselves had on the rate of propagule drop. Propagule production was analyzed with a negative-binomial error distribution, and was modeled in two ways, in order to 1) test latitude as a predictor of *A. germinans* fecundity (latitude included as a fixed effect); and 2) to explore inter-site differences in fecundity (site included as a fixed effect). Both models were GLMMs, with canopy volume as an additional fixed effect and transect as a random effect. Bootstrapping was used to test the importance of latitude and site.

While measuring propagule production, we also recorded reproductive tree densities using the same transects described above. To do this, we counted the number of reproductive *A. germinans* over 0.5m tall that occurred within 1m of the transect tape. Reproductive tree density was modeled with a negative binomial GLM to handle overdispersion, with latitude as a predictor. We used likelihood

ratio tests to compare the model to one without latitude.

In 2015, using the same sites and mesh bags described above (see Supplementary data Table S1 for sites), we collected and measured the fresh weight of mature propagules to the nearest 0.001 g. To avoid bias resulting from earlier phenology at the northern sites, we collected only mature propagules that had dropped from their pedicels into the bags ($N = 326$). Propagule mass was modeled with a single fixed effect of latitude and a random effect of tree ID, using a linear mixed-effects model with Gaussian errors. We used bootstrapping to test for the importance of latitude.

RESULTS

Floral visitors

Altogether, we observed 6,844 insect visits to *A. germinans* flowers. Visit totals were strongly skewed, particularly at northern sites; across the three northernmost sites closest to the *A. germinans* range edge, the median visitation rate was 1.0 visits hr^{-1} flower $^{-1}$ (interquartile range: 0–4.2 visits hr^{-1} flower $^{-1}$), while the median of the three southernmost sites was 6.1 visits hr^{-1} flower $^{-1}$ (interquartile range: 3.0–9.7 visits hr^{-1} flower $^{-1}$). Note that we modeled the number of visits recorded during a 15-minute period, with an offset for the number of flowers observed; we have converted these values into visitation rates per-hour per-flower here for interpretability. Summed across all taxa, total visits declined significantly as latitude increased (bootstrap statistic = 7.07, $P = 0.03$) (Fig. 2A). The number of flowers on the focal tree, tree height, and year each were not significant predictors of total visits (respectively, bootstrap statistics = 2.13, 3.25, and 0.23; $P = 0.16, 0.07, \text{ and } 0.68$); the complete model had low explanatory power ($R^2_m = 0.04, R^2_c = 0.15$). However, a model in which floral visits were treated as presence/absence (binomial) explained more variation ($R^2_m = 0.08, R^2_c = 0.26$), and revealed a marked northward decline in the proportion of observations that recorded at least one floral visitor (bootstrap statistic = 6.53, $P = 0.01$) (Fig. 2B).

The composition of the *A. germinans* floral visitor assemblage shifted along the north-south geographical ecotone. Estimates of the taxon-specific random slopes revealed that some taxa—like pierid butterflies, ants, and honey bees (*A. mellifera*, the most abundant floral visitor observed; Table 1)—visited *A. germinans* flowers less often at northern sites. However, visits by other taxa—primarily

Xylocopa bees (Hymenoptera: Apidae), *Bombus*, and hover flies (Diptera: Syrphidae)—were positively associated with latitude (Fig. 3A). Positions of taxa in the NMDS (stress = 0.19) mirrored the results of the random slopes model, with southern sites clustering near honey bees and northern sites falling closer to *Xylocopa*, *Bombus*, and hover flies (Fig. 3B). Total visits by each insect taxon recorded at each site are available in Supplemental data Table S2.

Pollen load size varied significantly among flower-visiting taxa ($\chi^2 = 70.96$, d.f. = 10, $P < 0.001$), with large-bodied bees and wasps – e.g. *Xylocopa*, *A. mellifera*, *Bombus*, and crabronid wasps (Hymenoptera: Crabronidae) – carrying the largest amounts of *A. germinans* pollen on their bodies (Supplementary data Fig. S1). Ants and pierid butterflies carried the smallest pollen loads, each with a median of 0 *A. germinans* pollen grains collected from the individuals sampled.

Pollen receipt

Pollen receipt was unrelated to latitude (bootstrap statistic = 2.27, $P = 0.14$, model $R^2_m < 0.01$, $R^2_c = 0.27$). We observed substantial intra-site variation in the amount of *A. germinans* pollen deposited on floral stigmas, with a median of 11 pollen grains and an interquartile range of 3-34 pollen grains per stigma.

Flowering

Flower production per tree was significantly higher at northern sites ($\chi^2 = 26.4$, d.f. = 1, $P < 0.001$), rising from a median of 150 flowers per tree at the southernmost site to 380 flowers per tree at the northernmost (Fig. 4A).

Fecundity

Fruit set rate (the rate at which flowers develop into propagules) declined slightly with latitude (bootstrap statistic = 14.46, $P = 0.01$, $R^2_m < 0.01$, $R^2_c = 0.08$), from 0.31 at the southernmost site to 0.26 for *A. germinans* nearest the range edge (Fig. 4C). However, fecundity – measured as the number of propagules produced per tree – did not vary consistently with latitude (bootstrap statistic = 1.02, $P = 0.38$, $R^2_m = 0.17$, $R^2_c = 0.35$), but did vary significantly among sites (bootstrap statistic = 18.50, $P = 0.021$, $R^2_m = 0.30$, $R^2_c = 0.38$) (Fig. 4B).

The density of reproductive *A. germinans* increased significantly with latitude ($\chi^2 = 14.32$,

d.f. = 1, $P < 0.001$), growing from 2.5 ± 1.0 (mean \pm s.d.) trees per transect at the southernmost site to 21.2 ± 14.3 trees per transect at the northernmost site (Fig. 5A). Substantial variation in reproductive tree density remained unexplained by the model, however (McFadden's pseudo- $R^2 = 0.04$). The mass of individual propagules was also significantly larger at higher latitudes, increasing by 0.210g ($\pm 0.075\text{g}$ s.d.) with every northward degree of latitude (bootstrap statistic = 7.68, $P = 0.010$, $R_m^2 = 0.02$, $R_c^2 = 0.16$) (Fig. 5B).

DISCUSSION

We found that *A. germinans* fecundity remained high in populations near the leading range edge, due to substantial allocation to flower and propagule production and, potentially, to changes in floral visitor assemblages. Overall, floral visits declined substantially toward the range margin, with a median visitation rate at the northernmost sites just 16% of the southernmost sites. However, the amount of pollen received by *A. germinans* stigmas did not decline, suggesting that pollen limitation does not increase toward the range edge or limit reproduction there more than elsewhere. This might be attributed to turnover in the assemblage of flower-visiting insects, with taxa carrying large pollen loads increasing in relative frequency at northern sites. Incidentally, fruit set rates declined in northern populations of *A. germinans*, but this may be due to the effect of greatly increased flowering and to the considerable resource allocation required to scale up propagule production. *A. germinans* propagules are large structures—especially at the range edge, where propagule size was on average 18% larger than at the southernmost site—and may be too resource-intensive to scale proportionally with increased flower production (Haig and Westoby, 1988b). In combination with the high relative density of reproductive trees in northern populations, these findings point to this species' capacity to reproduce along an expanding range edge.

Floral visitors and pollen receipt at the range edge

While floral visits declined toward the *A. germinans* range edge (Fig. 2), we found that range-edge pollen receipt remained high. The reason for this anomaly could lie in the substantial latitudinal turnover in the floral visitor assemblage that we observed: southern and mid-range floral visitor assemblages were dominated numerically by *A. mellifera*, whereas northern sites were notable for its

scarcity and for the higher relative abundance of hover flies and large bees, *Bombus* and *Xylocopa* (Fig. 3). There are likely multiple reasons for this turnover, ranging from local availability of nesting or oviposition sites and larval habitat, to the presence of co-flowering plants, and variation in solar radiation (Keil *et al.*, 2008; Kennedy *et al.*, 2013; Orr *et al.*, 2021). Given their pollen loads and local abundance, these taxa may function as pollinators, with large-bodied *Xylocopa* and *Bombus* bees capable of carrying greater amounts of *A. germinans* pollen and potentially foraging over greater distances (Greenleaf *et al.*, 2007). While we did not conduct pollen supplementation experiments, our findings imply that range-edge *A. germinans* do not experience more pollen limitation than trees located in our other studied populations. However, without explicitly testing for pollen limitation, we cannot rule out the possibility that variation in resource availability among sites is masking inter-site differences in pollen limitation (Haig and Westoby, 1988b).

These results are in line with those of Dawson-Glass and Hargreaves (2022), whose recent meta-analysis showed that just two of 14 cases in which researchers explicitly tested for pollen limitation with respect to a plant's range edge showed significantly higher pollen limitation at the range edge compared to the range interior. Even when exclusively considering plants that rely on vectors (animals or wind) for pollination, their study found little support for the premise that pollination frequently limits plant distributions. Given that pollen limitation is common (Knight *et al.*, 2005), why might it only rarely constrain plant range limits?

This study offers three explanations for how pollen receipt remains high at the *A. germinans* range edge. First, our findings suggest that a variety of insect taxa could serve as effective pollinators, buffering *A. germinans* against the local decline of any one pollinator (Waser *et al.*, 1996; Bennett *et al.*, 2020). Given that “extensive generalization in plant-pollinator interactions is the rule rather than the exception” (p. 2423, Olesen and Jordano, 2002), most zoophilous plants may tolerate some degree of spatial turnover in the pollinator community. Second, although regional mangrove cover decreases toward the northern *A. germinans* range limit (Cavanaugh *et al.*, 2014), at least some range-edge populations have high densities of reproductive trees. These range-edge stands can collectively produce a sizeable floral display, which may contribute to their ability to attract pollinators. Thus, *A. germinans* avoids the prospect of thinly dispersed range-edge individuals that struggle to draw

pollinators from neighboring upland habitat, even within a matrix of saltmarsh wind-pollinated grasses. The fact that many (if not most) species do not adhere to the ‘abundant-center’ distribution (Sagarin and Gaines, 2002; Santini *et al.*, 2019) suggests that local population density may not serve as a barrier to pollinator attraction at the range edge, except in cases where range-edge plant populations are very isolated (Steffan-Dewenter and Tschardt, 1999). The third factor by which range-edge *A. germinans* avoids reduced pollen receipt may be its heavy investment in floral displays, which could aid in pollinator attraction. We discuss this finding in more detail below. Although we cannot rule out the possibility of autogamy in this species, we note its protandry and the absence of autogamy in a closely related sister species (de Lima Nadia *et al.*, 2013).

Reproductive allocation at the range edge

Instead of declining toward the range edge, *A. germinans* fecundity was maintained even within the northernmost range-margin populations. This could be due in part to turnover in the pollinator community, as described above. It is also partly attributable to an increase in flowering. Contrary to expectations, flowering was greater in populations near the range edge, with the northernmost trees producing over twice as many flowers as the southernmost, despite substantially smaller sizes of northern shrubs. Large floral displays may allow range-edge *A. germinans* to attract pollinators (Kunin, 1993; Ghazoul, 2005), especially for solitary trees or small stands surrounded by salt marsh vegetation, helping northern *A. germinans* avoid pollen limitation. It remains to be seen whether floral rewards (e.g., volume and sugar concentration of nectar) are maintained in range-edge populations.

Increased allocation to reproduction was not restricted to flowers; propagules produced by these northern trees were significantly larger than propagules from populations closer to the range center (Fig. 5). This increase in propagule size from the range center to the range edge has also been reported for a co-occurring mangrove species in this region, *Rhizophora mangle* (Dangremond and Feller, 2016). Seed size is an important life history trait that is plastic intraspecifically and subject to selection (Haig and Westoby, 1988a). In *A. germinans*, large propagules produce seedlings that grow much faster than those from small propagules (Sousa *et al.*, 2003) and survive differentially under

environmental stress (Kennedy *et al.*, 2022). Rapid growth and improved performance of range-edge *A. germinans* seedlings may then contribute to the observed ability of this species to track changing climatic conditions (Kennedy *et al.*, 2021).

A. germinans might increase allocation to flower and propagule production near its range edge for several reasons. Similarly to how some plant species have a “suicidal” strategy of compensating for herbivore damage by increasing reproductive output (Trumble *et al.*, 1993), *A. germinans* might respond to cold stress at northern sites by allocating more resources to reproduction. Alternatively, range-edge *A. germinans* may, somewhat counter-intuitively, experience better growing conditions in northern Florida, despite infrequent die-offs due to hard freezes (Cavanaugh *et al.*, 2019). Competitively superior to some dominant salt marsh plants (Kangas and Lugo, 1990; but see McKee and Rooth, 2008), and released from competition with other mangrove species for space, nutrients, and light, northern populations of *A. germinans* may be under less physical stress and resource limitation, translating into greater reproductive output (Haig and Westoby, 1988b; Chiariello and Gulmon, 1991). Saltmarsh vegetation at the range edge may also promote *A. germinans* vigor by facilitating initial survival and establishment via buffering environmental stress (Guo *et al.*, 2013). Finally, density-dependent selection or the founder effect could be acting on range-edge populations to produce phenotypes that reproduce early, often, and copiously (Phillips *et al.*, 2010; Dangremond and Feller, 2016; Kennedy *et al.*, 2022).

The reproductive assurance provided by these larger, dense *A. germinans* floral displays at northern latitudes may have important implications for this species’ mating system and genotypes at the expanding range edge. Dense floral displays can encourage the movement of pollinators among flowers within the same tree and among neighboring close relatives, increasing selfing (Barrett, 2003; Karron *et al.*, 2004). Indeed, Kennedy *et al.* (2021) found significantly lowered outcrossing rates for *A. germinans* populations in the region studied here, compared to Mexican populations closer to the range core. The smaller floral visitor assemblage we have documented in northern Florida could contribute to this effect. While greater selfing can lead to inbreeding and its associated genetic costs, there is little empirical evidence of inbreeding depression in this species. Taken together, these lines

of evidence suggest that the increased flowering we observed at the *A. germinans* range edge could promote genetic differentiation there, including the generation of novel phenotypes that contribute to this species' rate of northward spread—such as the larger propagules documented herein (Dangremond and Feller, 2016; Kennedy *et al.*, 2022).

CONCLUSIONS

This study demonstrates that the climatic constraints operating at the *A. germinans* range margin do not necessarily limit range-edge allocation to reproduction, and that substantial turnover in floral visitors can occur at an expanding range edge without altering pollen receipt (see also Kennedy *et al.*, 2021). Our findings further suggest that pollinator community composition can be as important as abundance in supporting plant reproductive success at an expanding range edge. These results are consistent with research showing recent, rapid increases in mangrove cover in northern Florida, coinciding with a decrease in the frequency of hard freezes (Cavanaugh *et al.*, 2014; Cavanaugh *et al.*, 2019). Of course, there is more to range expansion than maintaining fecundity; dispersal, establishment, germination, and seedling survival and growth are also critical for range shifts (Angert *et al.*, 2011). Given the capacity of *A. germinans* for long-distance dispersal (Dodd *et al.*, 2002), reproduction close to the leading range edge may not be essential for sustained northward expansion. Still, local reproduction will be important for the growth of frontier populations around new colonizers, which can, in turn, promote further dispersal (Shigesada *et al.*, 1995). The fate of range-edge propagules and the origins of range-edge colonizers—from range-edge populations, or from populations closer to the interior of the distribution—is worthy of further study. So, too, is the underlying cause of spatial variation in pollinator abundance and identity, in order to better predict future *A. germinans* spread and the range shifts of other pollinator-dependent plants.

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https://datadryad.org/stash/share/aykkRWFSCR8OiVvcPhxaBkZ_niO9ba6E0gfzPLLtysk

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TABLE 1. Taxonomic categories assigned to *A. germinans* floral visitors, and total number of visits by each taxon observed, across sites and years, over the course of the study. Taxa in bold are the 12 most frequent *A. germinans* floral visitors.

Insect Order	Taxon	# Visits
Hymenoptera	<i>Apis mellifera</i>	3,223
	<i>Melissodes</i>	429
	<i>Bombus</i>	354
	<i>Xylocopa</i>	65
	<i>Triepeolus</i>	2
	Halictidae	26
	Megachilidae	20
	Vespidae	207
	Crabronidae	72
	Pompilidae	51
	Sphecidae	54
	Formicidae	1,246
Lepidoptera	Pieridae	297
	Hesperiidae	19
	Nymphalidae	9
	Lycaenidae	3
	Noctuidae	3
Diptera	Syrphidae	578
	Muscidae	19
	Ulidiidae	20
	Stratiomyidae	14
	Anthomyiidae	6
	Dolichopodidae	4
	Calliphoridae	2

	Unk. Diptera	28
Coleoptera	Oedemeridae	72
	Scarabaeidae	13
	Coccinellidae	6
Orthoptera	Unk. Orthoptera	2

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Figure Legends

FIG. 1. Study location and focal species. (A) Map of study sites in Florida, USA. See Table S1 for site descriptions. (B) Partial map of the *A. germinans* distribution in North and South America; rectangle indicates study extent shown in (A). (C) Photo of an *A. germinans* inflorescence. Scale bar = 1 cm.

FIG. 2. Pollinator visitation to black mangroves by latitude. (A) The frequency of all insect visits to *A. germinans* flowers declined slightly from south to north. Line shows model-estimated relationship between latitude and visitation rate across all taxa. Points are jittered. Note that visit counts were modeled, with an offset for the number of flowers observed; these values have been converted to rates here for interpretability. (B) Likewise, the probability of at least one insect visiting *A. germinans* flowers during an observation period declined significantly at higher latitudes. Line shows model-estimated relationship.

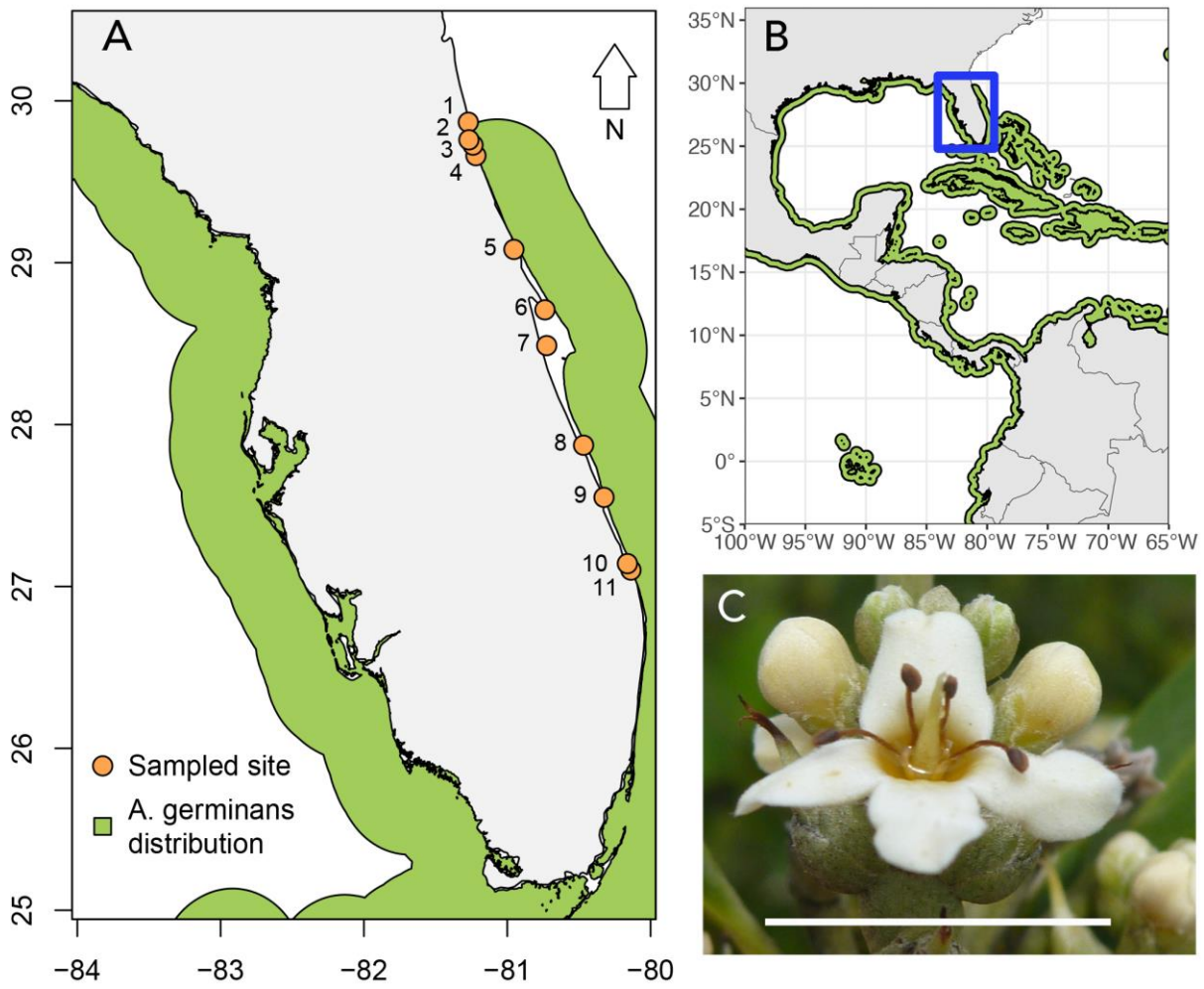
FIG. 3. Shifts in floral visitor community composition with latitude. (A) Random slope estimates, representing taxon-specific relationships between visitation frequency and latitude. Points falling near the dashed line at 0 indicate taxa whose visitation rate varied little with latitude; points above/below the line represent taxa that increased/decreased in visitation frequency with latitude, respectively. Bars show SD. (B) Nonmetric multidimensional scaling (NMDS) of floral visitors observed at each site and date. Points are color-coded to indicate site latitude: red represents southern sites, blue represents northern sites.

FIG. 4. Flowering, fecundity, and fruit set by latitude. (A) *A. germinans* flowering increased with latitude, but (B) fecundity showed no relationship with latitude. (C) Consequently, the fruit set rate declined slightly at northern sites. Note the logarithmic scale of the Y-axes in (a) and (b). Lines show model-estimated relationships.

FIG. 5. *Avicennia germinans* stand and propagule traits by latitude. **(A)** The density of reproductive *A. germinans* (those with at least one inflorescence/infructescence at the time of survey) increased with latitude, **(B)** as did the mass of individual propagules. Note the logarithmic scale of the Y-axis in (A). Lines show model-estimated relationships.

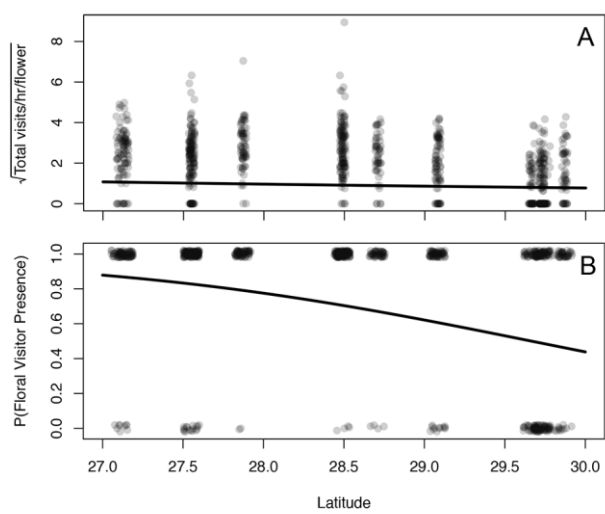
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Figure 1



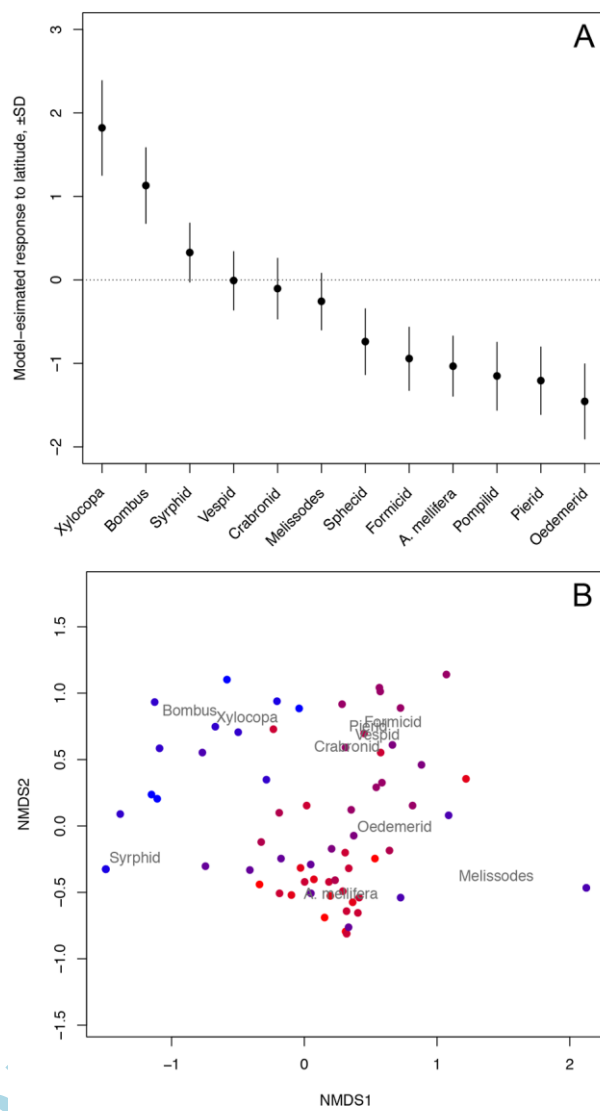
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Figure 2



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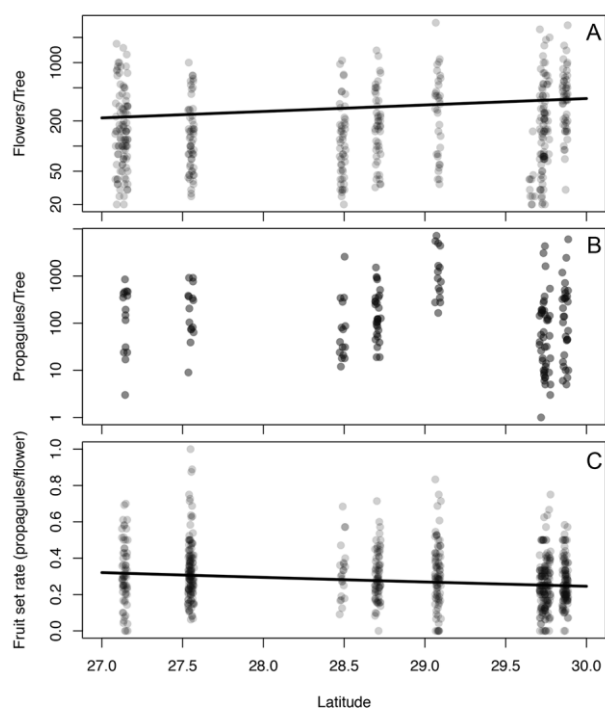
Figure 3



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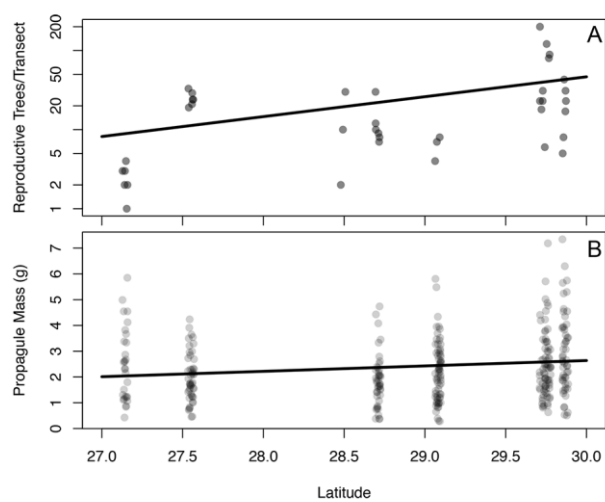
Figure 4



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Figure 5



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