Reports

Mangrove microclimates alter seedling dynamics at the range edge

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Abstract. Recent climate warming has led to asynchronous species migrations, with major consequences for ecosystems worldwide. In woody communities, localized microclimates have the potential to create feedback mechanisms that can alter the rate of species range shifts attributed to macroclimate drivers alone. Mangrove encroachment into saltmarsh in many areas is driven by a reduction in freeze events, and this encroachment can further modify local climate, but the subsequent impacts on mangrove seedling dynamics are unknown. We monitored microclimate conditions beneath mangrove canopies and adjacent open saltmarsh at a freeze-sensitive mangrove-saltmarsh ecotone and assessed survival of experimentally transplanted mangrove seedlings. Mangrove canopies buffered night time cooling during the winter, leading to interspecific differences in freeze damage on mangrove seedlings. However, mangrove canopies also altered biotic interactions. Herbivore damage was higher under canopies, leading to greater mangrove seedling mortality beneath canopies relative to saltmarsh. While warming-induced expansion of mangroves can lead to positive microclimate feedbacks, simultaneous fluctuations in biotic drivers can also alter seedling dynamics. Thus, climate change can drive divergent feedback mechanisms through both abiotic and biotic channels, highlighting the importance of vegetation-microclimate interactions as important moderators of climate driven range shifts.

Key words: Avicennia germinans; coastal wetlands; Laguncularia racemosa; mangrove; range expansion; Rhizophora mangle; saltmarsh; species migration; winter climate change.

Introduction

Understanding processes that control range-edge dynamics have become particularly important given that climate change is altering latitudinal limits of species worldwide (Gallien et al. 2010, Chen et al. 2011). Temperate and tropical plants and animals are moving polewards, altering biodiversity patterns, and impacting ecosystem function (Parmesan and Yohe 2003). Despite these widespread changes, we know relatively little about range-limiting factors for the vast majority of these species (Gaston 2009). Macroclimate modeling approaches have been the predominant mode of studying climate-driven range shifts, providing valuable insights into broad responses to temperature, precipitation, and other conditions. Nevertheless, correlative modeling approaches generally do not address local conditions, particularly microclimates and biotic factors, and are limited in their ability to predict individual species responses (Meynard

and Quinn 2007). In response to these limitations, there have been numerous recent calls for more experimental approaches to studying species' responses to climate change (Kreyling et al. 2014, Cavanaugh et al. 2015). Field experiments in particular can provide a mechanistic understanding of factors controlling species' distributions, reveal cryptic processes not captured in models, and identify non-additive effects among multiple potential drivers.

Climatic gradients are thought to control abrupt transitions across ecosystem types, including transitions from boreal forests to tundra, alpine forests to high-elevation meadows, and from mangrove forests to saltmarshes (D'odorico et al. 2013). However, broad-scale effects of climatic drivers can also be moderated by localized changes in microclimate conditions. For example, the diurnal shade and moisture provided by dense forest canopies can facilitate the survival of cool-season understory species well outside of zones where they would typically persist due to high temperatures and aridity outside of the forest (De Frenne et al. 2013). By trapping radiated heat from the ground, dense forest canopies can also moderate critical freezing nocturnal temperatures at range edges (D'odorico et al. 2013).

Thus, favorable microclimates can facilitate the rate of ecosystem turnover under climate change by promoting localized survival in the face of regionally unfavorable conditions.

Climate-driven expansion of mangrove forests into saltmarshes has been a topic of much recent interest, with transitions thought to reflect a reduction in extreme freeze events in some regions (Cavanaugh et al. 2014, Osland et al. 2017), but also co-varying gradients of precipitation, air temperature, water temperature, and sea-level rise in others (Saintilan et al. 2014, Armitage et al. 2015, Osland et al. 2016). Recent research has also shown that mangrove expansion into saltmarsh zones can alter microclimatic variables (Guo et al. 2016). Although little investigated, potential vegetation-microclimate feedbacks could have large impacts on the rate of climate-driven range expansions if changes in microclimate are large enough to lead to biologically meaningful differences in plant vital rates. Crucially, it is not yet known if these microclimates generate abiotic and biotic feedback mechanisms that alter survival of mangrove seedlings and thus potentially the overall rate of mangrove expansion. Given that a temperature reduction of only a few °C below zero can lead to species-specific differences in freeze-damage and mortality of co-occurring North American mangrove species (Ross et al. 2009, Osland et al. 2013, Cavanaugh et al. 2015), relatively small changes in temperature due to microclimates could have large impacts on mangrove community dynamics.

We experimentally investigated the potential for mangrove canopies to buffer nocturnal cooling and enhance seedling survival at the mangrove-saltmarsh ecotone. We hypothesized that established individual mangrove canopies would create warmer nocturnal conditions, leading to reduced occurrence of freeze damage and elevated survival, particularly for freeze-sensitive species like white mangrove *Laguncularia racemosa* and red mangrove *Rhizophora mangle*, but less so for freeze-tolerant species like black mangrove *Avicennia germinans* (Cook-Patton et al. 2015). To determine whether established mangrove trees altered other drivers of mangrove seedling dynamics, we also assessed the extent to which established mangroves altered herbivory and fungal infection of seedling transplants under canopy vs. open marsh conditions.

MATERIALS AND METHODS

Study site

The study site is located in the Guana Tolomato Matanzas National Estuarine Research Reserve, northern Florida (29°43′ N, 81°14′ W, Appendix S1: Fig. S1). This region is at the ecotone where the northernmost mangroves of the US Atlantic coast have recently expanded into saltmarsh due to declining numbers of freeze events at the mangrove range edge (Cavanaugh et al. 2014, Rodriguez et al. 2016, Appendix S1:

Fig. S2). Mangroves at the site are dominated by black mangroves (*A. germinans*), established as patches of shrubs within a saltmarsh matrix dominated by cord-grass *Spartina* spp., saltwort *Batis maritima*, and glass-wort *Salicornia* spp., with lesser amounts of red (*R. mangle*) and white mangroves (*L. racemosa*), particularly along the shorelines (Williams et al. 2014).

Characterization of microclimates under mangroves

To determine if mangroves create local microclimates different from the surrounding saltmarsh, we monitored temperatures and light levels beneath black mangrove shrubs (height ranging from 2 to 4 m) and paired adjacent saltmarsh areas at 21 locations across the 80 ha study site (Appendix S1: Fig. S1). Each location consisted of two unshielded temperature/light sensors (Hobo Loggers®, Onset Computer Co. Bourne, MA, USA) mounted on a 50 cm PVC pole, with air temperature (°C) and light (lux ft^{-2}) recorded every 30 min from Jan 9th to May 22nd 2014. We focused on winter temperatures because mangrove abundance and survival at this range edge is related to winter minimum temperatures, with relatively steep threshold responses among different species across temperature gradients (Cavanaugh et al. 2015). At each location, we placed one sensor directly beneath the canopy of a relatively isolated mangrove shrub ("mangrove"), and another in the adjacent open "marsh" 3–4 m from each mangrove station.

Seedling transplant experiment

To determine if seedling dynamics differed under mangrove relative to adjacent saltmarsh, we conducted a 6-month transplant study monitoring the survival of 487 propagules of black, red, and white mangroves planted into the 21 paired mangrove and marsh monitoring stations. We collected undamaged red mangrove propagules on December 2013 (prior to any winter freeze event at this latitude) from multiple parent trees at the nearest established red mangrove population, approximately 80 km to the south of the study site (New Smyrna Beach, 29°03′ N, 80°54′ W). We planted propagules into individual RayLeach Cone-tainers (2.5 cm diameter, 12.1 cm length; 49 ml volume) filled with a 50:50 mixture of potting soil and sand, and then grew them for approximately 1 month in a shaded, outdoor pond filled with 35 ppt seawater (Smithsonian Marine Station, Fort Pierce, FL; 27°26′ N, 80°18′ W), during which time they took root and developed into mangrove seedlings. Red mangroves were planted at the study site on January 9th–14th 2014. On January 21st, we collected young seedlings from black and white mangroves from a site 7 km to the south of the study site, placed them in Cone-tainers with a 50:50 mixture of potting soil and sand, and planted them at the study site on the same day. All Cone-tainers were planted directly into the

sediment under each mangrove or in the paired salt-marsh location within 0.5 m of each data logger, with approximately 5 cm of each Cone-tainer extending above the sediment surface. Holes at the bottom of each Cone-tainer ensured water availability. At each station, we planted 4–7 seedlings of each species per treatment. At the time of planting, black and white seedlings had emerging radicles (allowing for proper planting), had begun to initiate leaf-out, and were free of external signs of damage, similar to the status of the red mangrove seedlings.

On February 9th and again on February 25th (following the final freeze event for the year), we scored seedlings for the presence of principal damage categories, including freeze damage, herbivory by the omnivorous mangrove tree crab *Aratus pisonii*, and fungal attack. Freeze damage was evident as black scorching on the leaves and/or the tip of the seedling and was readily distinguished from herbivore damage, which was typically evident as large gouging wounds (Appendix S1: Fig. S3). Fungal colonization was exhibited as black lesions, similar to that attributed to a *Colletotrichum* sp. reported by (Pickens and Hester 2011). Final survival and damage was scored again in late May 2014 after which the experiment was terminated. At this point, all surviving seedlings had at least one leaf pair.

Analyses

For microclimate monitoring data, we excluded daytime temperatures as direct solar insolation may lead to erroneous readings on unshielded HOBO loggers (Bahr et al. 2016). Hence, we calculated nightly (5 p.m.–7 a.m.) mean, minimum, and maximum temperatures for each treatment at each station. We analyzed the effect of treatment (i.e., mangrove and marsh) on mean, minimum, and maximum temperatures, as well as nightly temperature variation, using linear mixed effects models (lmer in R package *lme4*, R Core Team) with treatment, night, and treatment*night as fixed effects, and station as a random effect. We also tested the effect of treatment on mean daily light availability (11 a.m.–1 p.m.) using linear mixed effects models. For analysis of light measurements, we converted daytime lux to photosynthetically active radiation (PAR; µmol m^{-2} s^{-1}) using the conversion factor for daylight conditions (Thimijan and Heins 1983).

For seedling data, we first tested the relationship between the absolute minimum temperature recorded at each of our 42 monitoring stations and the proportion of seedlings exhibiting freeze damage, using simple linear regressions for each species. Next, we analyzed seedling damage data using logistic regressions (glmer in *lme4*, R Core Team), assessing interspecific differences in the occurrence of freeze, herbivore, and fungal damage. For each damage type, we assessed the binary outcome of damage occurrence using species identity, treatment, and their interaction as predictors. Next, we used logistic

regression to assess differences in seedling survival between transplant treatments (i.e., mangrove and marsh) and species. Finally, we asked whether our measured damage variables could successfully predict seedling survival. We did not statistically assess predictors of white mangrove survival as overall survival at the end of the experiment was negligible (only five seedlings from an initial $n = 126$). Using a binary outcome for survival as a response variable, we used the occurrence of freeze and herbivory damage as fixed predictor variables. For all mixed effect models, Chi-square and P-values were calculated using Likelihood Ratio Tests on models with and without each effect. All statistical analyses were conducted using R software (v3.2.2, R Foundation for Statistical Computing).

RESULTS

Mangrove microclimates

Mangroves significantly altered abiotic conditions relative to adjacent saltmarsh habitats. Averaged across sampling stations, minimum nightly temperatures in marsh treatments dropped below freezing on five nights during the experiment (ranging from −0.7 to −4.2°C), whereas average minimum nightly temperatures underneath mangroves never went below 0°C (ranging from 0.01 to 1.65°C during open marsh freeze nights, Fig. 1). Differences in nightly minimum temperatures were greatest during coldest nights, with mangrove treatments being 3.24°C warmer on nights when open marsh average minimum temperatures were below 0°C ($\chi^2 = 168.93$, $P < 0.001$). Nightly minimum temperatures in mangrove treatments were, on average, 1.47°C warmer than open marsh temperatures ($\chi^2 = 126.23$, $P < 0.001$). Mean nightly temperatures were also warmer under mangroves, which were on average 0.95°C warmer relative to the open marsh ($\chi^2 = 78.58$,
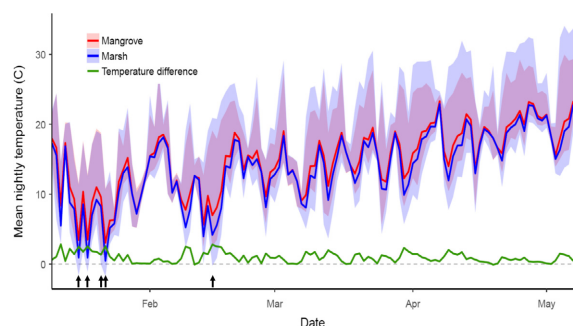

Fig. 1. Mean (continuous line), maximum, and minimum (shaded) nightly temperatures in mangrove (red) and marsh (blue) treatments at GTM National Estuarine Research Reserve, Florida, Jan–May 2014. Green line is the difference in nightly average temperatures under mangroves vs. open marsh. Positive values indicate warmer temperatures under mangroves. Black arrows indicate nights when open marsh minimum temperatures dropped below 0°C.

Reports

$P < 0.001$). Nightly temperature variability was reduced beneath mangrove canopies ($\chi^2 = 508.27$, $P < 0.001$), and open marsh had higher nightly maximum temperatures (1.9°C warmer on average, $\chi^2 = 236.28$, $P < 0.001$). Differences in mangrove and marsh maximum nightly temperatures were greater later in the year when temperatures were higher ($\chi^2 = 93.71$, $P < 0.001$, Fig. 1). The warming effect of mangroves on nightly minimum temperatures was mediated by local weather conditions; nights with maximum wind speeds >15 mph reduced temperature differences by 0.91°C (53% reduction) compared to relatively windless nights (maximum wind speeds <5 mph) ($F = 15.95$, $P < 0.001$, Appendix S1: Fig. S4).

Daily average (11 a.m.–1 p.m.) PAR values were lower beneath mangroves (448 μmol m^{-2} s^{-1}) compared to open marsh (1871 μmol m^{-2} s^{-1}) ($\chi^2 = 12019$, $P < 0.001$, Appendix S1: Fig. S5). Treatment differences in light availability increased with time; mangrove canopies reduced light availability by 74% in January compared to 80% in May ($\chi^2 = 583.89$, $P < 0.001$).

Mangrove survival in microhabitats

Forty-five percent of all seedlings in the open marsh exhibited freeze damage, compared to just 15% beneath mangrove canopies (deviance$_{321.5} = 47.2$, $P < 0.001$, Appendix S1: Table S1). Freeze damage was most prevalent in white mangrove and largely absent in black mangrove, particularly in mangrove treatments (deviance$_{274.3} = 64.4$, $P < 0.001$, Fig. 2). Across stations, proportion of seedlings with freeze damage was negatively related to absolute minimum temperature for both red ($r^2 = 0.12$, $P = 0.037$) and white mangroves ($r^2 = 0.12$, $P = 0.026$), but not for black mangroves ($r^2 = 0.04$, $P = 0.197$, Appendix S1: Fig. S6). Red mangrove suffered more herbivore damage than other species; 51% of the red mangrove seedlings were damaged compared to 15% of the white mangroves (deviance$_{316.39} = 120.39$, $P < 0.001$, Appendix S1: Table S1). Herbivore damage was negligible for black mangroves (2%). Herbivore damage was more common under mangroves than in the open marsh (deviance$_{333.29} = 16.9$, $P < 0.001$). Fungal damage was only found on black mangrove seedlings and did not differ between mangrove and the open marsh (deviance$_{122.29} = 1.86$, $P < 0.17$, Fig. 2).

Overall survival was relatively high for red mangroves (30%), but only 4% of white mangrove seedlings were alive at the end of the experiment (deviance$_{203.78} = 37.12$, $P < 0.001$, Fig. 3, Appendix S1: Table S1). Across species, open marsh seedlings had greater survival compared to seedlings transplanted under mangrove canopies (deviance$_{233.2} = 29.42$, $P < 0.001$, Fig. 3). Only the presence of fungal damage predicted mortality of black mangroves, ($\chi^2 = 10.07$, $P < 0.001$, Appendix S1: Table S2). In contrast, the occurrence of herbivore damage was the only significant predictor of mortality of red mangrove seedlings ($\chi^2 = 66.85$, $P < 0.001$, Appendix S1: Table S2).
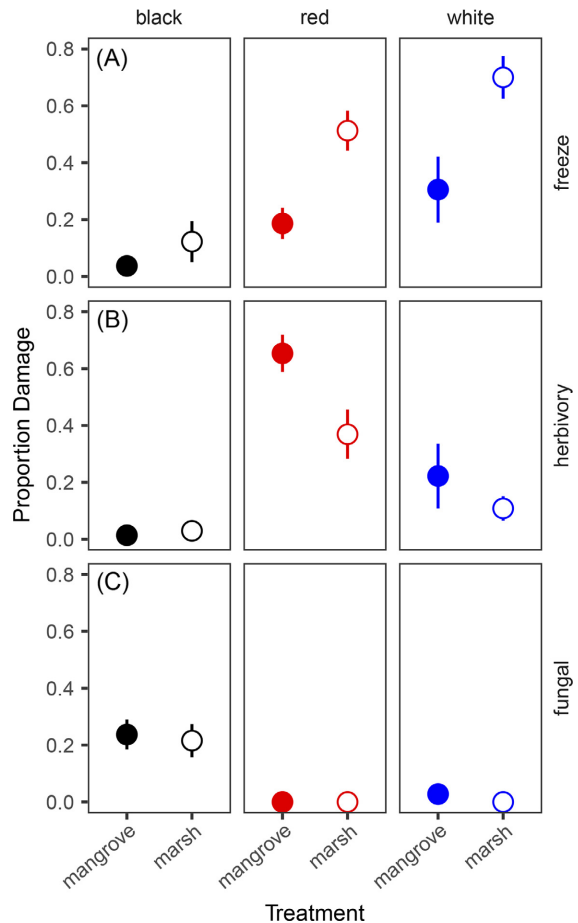

FIG. 2. Proportion (± SE) of transplanted black, red, and white mangrove seedlings exhibiting occurrence of (i) freeze, (ii) herbivory, and (iii) fungal damage after 4 months under mangroves (filled circles) or in the open marsh (open circles).

Discussion

Human-induced changes to the climate are having profound effects on species' distributions on local, regional, and global scales (Chen et al. 2011). However, at many ecosystem transition zones, rate of species' range shifts is affected not only by changing abiotic conditions, but by complex, interacting macroclimate, microclimate, and biotic factors. Here, we show that at an expanding mangrove range edge, mangrove canopies modify microclimate conditions relative to open saltmarsh, with warmer conditions under mangroves reducing freeze damage, a critical predictor of survival for these freeze-insensitive species. However, seedling survival was also significantly impacted by herbivory, which in general was higher beneath mangroves. Hence, while low temperature stress is a key driver of poleward expansion of mangroves, the role of concomitantly changing biotic effects may be more important than previously considered. We argue that the rate of species' range shifts under climate change is likely influenced by interacting
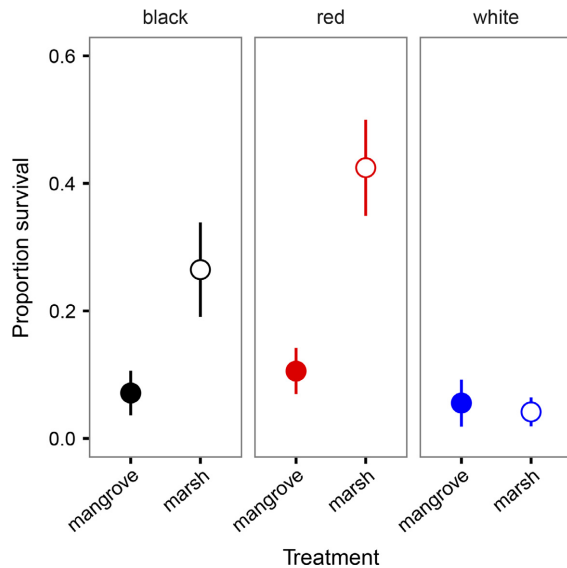
Fig. 3. Proportion survival (± SE) of transplanted black, red, and white mangrove seedlings after 4 months under mangroves (filled circles) or in the open marsh (open circles).

abiotic and biotic microhabitat feedbacks, which are best examined through a combination of field observations, experiments, and modeling approaches.

Microclimate effects

The occurrence of low temperature damage on our study species followed expected patterns (Olmsted et al. 1993, Cook-Patton et al. 2015). Although freeze damage was low on black mangroves, the most northerly occurring and freeze tolerant mangrove species of the eastern Atlantic coastline, canopy microclimate buffering effects may play an important role for conspecifics during more severe winters. The effect of mangrove canopies was markedly stronger for red mangroves. Although the average magnitude of temperature difference between mangrove and marsh treatments was low, small changes in abiotic conditions at range edges may have significant impacts on the likelihood of establishment of freeze-sensitive species. Mangroves in southeastern United States appear to respond strongly to distinct winter temperature thresholds, with tipping points leading to landscape-scale changes in ecosystem structure, i.e., the presence of either mangrove vs. saltmarsh (Osland et al. 2013, Cavanaugh et al. 2014). Our results suggest that small increases in temperature afforded by the presence of mangrove canopies during winter months may be sufficient to allow the establishment of seedlings in suitable microhabitats, a positive feedback loop proposed by D'odorico et al. (2013) and Osland et al. (2015). Multiple authors have reported ontogenetic differences in freeze induced damage and/or mortality of mangroves (Lugo and Patterson-Zucca 1977, Sherrod and McMillan 1985, Olmsted et al. 1993), with lower levels of seedling damage compared to established mangroves, speculatively attributed to beneath canopy temperature buffering effects (Ross et al. 2009, Osland et al. 2015). Thus, if microclimate temperature effects are considered in isolation, our evidence supports the assertion of Osland et al. (2015); positive feedbacks could lead to faster rates of mangrove expansion into saltmarshes than is currently predicted based on macroclimate factors alone (Fig. 4).
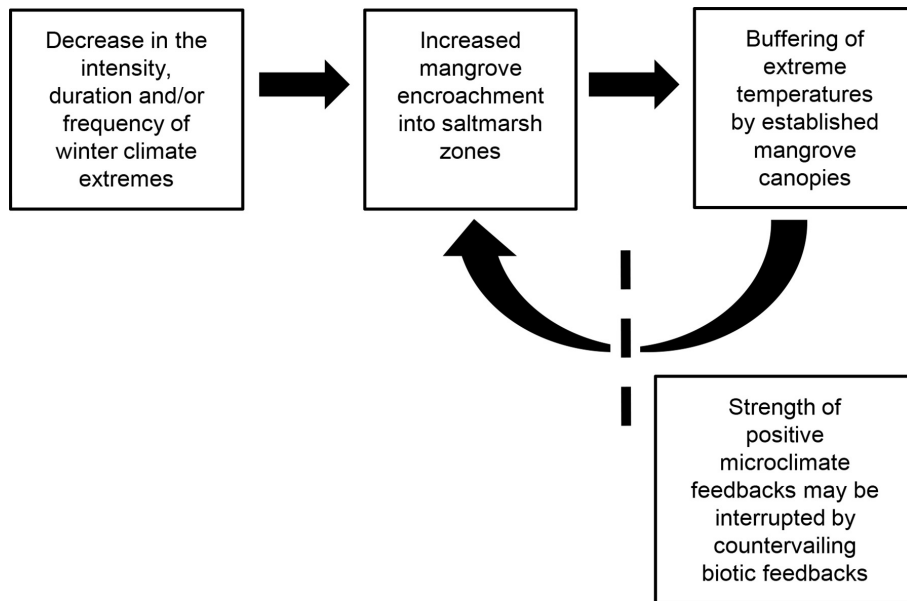

Fig. 4. Hypothetical positive feedback showing that countervailing biotic effects (including increased herbivory) may dampen mangrove encroachment into saltmarsh (adapted from Osland et al. 2015).

Given the high prevalence of freeze damage on white mangrove seedlings in our study, it is likely that cold temperature sensitivity was the principal cause of the almost complete mortality. A high proportion of white mangrove seedlings exhibited freeze damage under mangroves, despite average nightly temperatures in this treatment remaining above 0°C throughout. Surprisingly, however, buffering effects of established mangrove shrubs did not enhance survival of white mangroves in our study, although they may play a role during warmer winters.

In contrast to warming effects during winter, cooling effects of mangrove canopies in summer may confer a competitive advantage to mangrove seedlings over saltmarsh grasses that show increased growth in response to chronic warming (Coldren et al. 2016). Thus, at mangrove-saltmarsh ecotones, cooling of summer temperature extremes beneath mangrove canopies may enhance microclimate induced positive feedback mechanisms. The magnitude of temperature difference between mangrove vs. marsh was reduced on nights with higher wind speeds. Higher ambient wind velocities can lead to increases in turbulent mixing of beneath canopies and the atmosphere, moderating the strength of microclimate feedbacks (D'odorico et al. 2013). Some predictions of future climate in Florida and other mangrove regions indicate increased frequency and intensity of extreme weather events such as windstorms (Mann and Emanuel 2006, Alongi 2008). Thus, non-warming impacts of climate change, such as potential higher frequency of extreme wind speeds, will likely interact with microclimatic feedbacks and potentially influence the rate of mangrove expansion.

The presence of mangroves canopies in our study also reduced light availability relative to open marsh. The importance of shading on establishment of our three study species is equivocal, however. Survival and growth of black mangrove was positively correlated with increasing light availability in one study (Lopez-Hoffman et al. 2007), although this effect may be related to increased herbivory in shaded canopy areas rather than light specifically. Across a similar light gradient to ours, red mangrove exhibit significant morphological and physiological plasticity allowing it to thrive in a broad range of microhabitats (Farnsworth and Ellison 1996). Both McKee (1995) and Ball (1980) suggest that white mangroves are shade intolerant. We propose that mortality of black and red mangrove seedlings in our study are unlikely due to reduced light availability. In contrast, shading beneath mangroves may have partly contributed to high white mangrove mortality, although experimental evidence for shade-induced mortality is lacking.

Biotic interactions

As with freeze damage, interspecific differences in herbivory by *A. pisonii* followed expectations (Erickson et al. 2003), with higher damage on red mangroves and infrequent damage on white and black mangroves. Indeed, despite relatively high amounts of freeze damage on red mangroves, mortality was mostly attributable to herbivory. *A. pisonii* is a dominant folivore of red mangroves in Panama and Belize, but herbivory rates are even higher at the northern range edge in Florida (Feller et al. 2013). Previous studies in Florida have estimated the percentage of red mangrove leaves damaged by *A. pisonii* ranges from 8% to 81% (Beever et al. 1979, Erickson et al. 2003). *A. pisonii* has outpaced the poleward expansion of mangroves along the eastern coastline of the United States, being reported 121 km to the north at Little Satilla Creek, Georgia (Riley et al. 2014). Nonetheless, the higher incidence of damage occurring beneath woody canopies in our study suggests that mangroves remain a preferred habitat, perhaps related to increased structural complexity relative to saltmarsh, or to the thermal refugia provided by isolated mangroves at the ecotone. Assessing crab herbivory on *A. marina* in an Australian mangrove forest, Osborne and Smith (1990) reported a similar pattern, with seedling damage being higher beneath the understory than in adjacent canopy gaps. The authors also attributed this to a canopy microclimate effect, with crabs being more abundant in cooler understory areas. In contrast, at a mangrove-saltmarsh ecotone on the northern Gulf Coast of the USA, Patterson et al. (1997) found that predation rates of black mangrove were higher in marsh relative to mangroves, although predation was dominated by the saltmarsh affiliated snail *Littoraria irrorata* and crab *Sesarma cinereum*. Taken together with data showing that recruitment of black mangroves into saltmarsh areas along Florida's Gulf Coast is restricted by predation by the grapsid crab *Sesarma reticulatum* (Langston et al. 2017), we speculate that the strength of top-down controls on mangrove expansion in saltmarsh may be underestimated.

Survival of black mangrove followed a general Janzen-Connell pattern (Janzen 1970, Connell 1971); recruitment was reduced in proximity to adults of the same species. Black mangrove-specific fungal pathogens may be more abundant beneath established black mangrove adults vs. open marsh, leading to increased seedling mortality under mangroves. However, treatment differences in the proportion of black mangrove seedlings damaged by fungal colonization were not significant. The fungal species observed in our study was not identified, but it is likely a *Colletotrichum* sp. tentatively identified on black mangrove seedlings in Louisiana by Pickens and Hester (2011). Indeed, this species affects the growth of black mangrove seedlings in greenhouses (Pickens and Hester 2011). To date, no studies have quantified whether fungal colonization limits black mangrove recruitment, either at the center of its distribution or at the range edge. The rapid expansion of woody tropical mangroves into temperate zones affords the opportunity for future research to assess the strength of plant enemy-related Janzen-Connell effects in transition zones.

Implications of microclimate and biotic effects on range expansion

In woody communities, canopy microclimates have been considered in terms of providing cool daytime refugia at species warm range edges, but they may also increase the rate of climate-related poleward shifts by affording protection against frosts. Here, climate-driven expansion of black mangroves, a cold-tolerant foundation species, leads to microclimates that reduce freeze damage for mangrove seedlings, potentially increasing the rate of ecosystem change at the range edge. Tree canopies modify surface energy balances, generally leading to nocturnal warming (D'odorico et al. 2013), and reduction of low temperature damage. Similar patterns have been observed in forest-tundra (Chapin et al. 2005) and forest-alpine meadow (Maher et al. 2005) transition zones, where canopy warming amplifies the rate of woody encroachment. However, microclimates may also lead to negative biotic feedbacks by providing refugia for natural enemies, thus dampening the effects of microclimates on climate-driven range shifts (Fig. 4). These antagonistic abiotic and biotic factors will likely further interact with other ecosystem processes affected by climate change, including sea-level rise and elevated atmospheric CO_2.

Shifting patterns of species' geographic distributions is an important consequence of anthropogenic climate change, with pervasive environmental, social, and economic ramifications. Conventional approaches to modeling species' range shifts have focused on macroclimatic responses, yet there is growing appreciation for the need to incorporate local abiotic and biotic factors into niche models (Guisan et al. 2006, González-Salazar et al. 2013). We provide evidence for divergent abiotic and biotic microclimate-related feedbacks at an ecotone already shifting due to macroclimatic drivers. Taken together, these results highlight the need for stronger links between modeling-based approaches and experimental field-based observations which together can improve our understanding of species' responses to global change.

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SUPPORTING INFORMATION

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