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Special Feature: Pandemic Pivots

A fiddler crab reduces plant growth in its expanded range

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Abstract

Species across the planet are shifting or expanding their ranges because of climate change. These are climate migrants. Although climate migrants are well documented, their impacts on recipient ecosystems are not. Climate migrants that are also ecosystem engineers (species that modify or create habitats) will likely have profound effects on ecosystems. The Atlantic marsh fiddler crab, *Minuca pugnax*, is a burrowing crab that recently expanded its range into the northeastern United States. In its historical range, *M. pugnax* enhances the aboveground growth of the cordgrass *Spartina alterniflora*, a plant critical to marsh persistence. In a control-impact study, however, we found that *Spartina* aboveground biomass was 40% lower when *M. pugnax* was present. Thus, the positive effect of *M. pugnax* on *Spartina* aboveground biomass flipped to a negative one in its expanded range. *Spartina* belowground biomass was also 30% lower on average when crabs were present, a finding consistent with what is seen in the historical range. These impacts on *Spartina* are likely due to burrowing by *M. pugnax*. Benthic microalgae was, on average, 45% lower when crabs were present. Fiddler crabs eat benthic microalgae, and these results suggest that fiddler crabs can control algal biomass via grazing. Because fiddler crabs reduced the biomass of foundational primary producers in its expanded range, our results imply that *M. pugnax* can influence other saltmarsh functions such as carbon storage and accretion as they expand north. Most strikingly, our results suggest that as species expand or shift their range with climate change, not only can they have profound impacts in their new ranges but those impacts can be the inverse of what is seen in their historical ranges.

KEYWORDS
climate change, climate migrant, ecosystem engineer, ecosystem functioning, range expansions, tropicalization

PANDEMIC PIVOT

Originally, we had planned to conduct manipulative caging experiments throughout the expanded and historical ranges to compare the ecological impact of *Minuca pugnax* between ranges. The COVID-19 pandemic, however, prevented us from conducting those experiments. To overcome these challenges, we sampled heavily in the fiddler crab's expanded range in a control-impact study (three marshes, $N = 90$ plots). Because fiddler crab colonies in the

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expanded range are patchy and far from each other (>5 m), it allowed us to sample plots without cages and avoid caging artifacts while maintaining a high sample size ($n = 45$ per treatment, with and without crabs). To compare the ecological impact of *M. pugnax* between ranges, we compared our results with literature values. This allowed us to evaluate two properties of salt marshes that are critical to their functioning: the above- and belowground biomass of the foundational plant *Spartina alterniflora*.

INTRODUCTION

Climate change is driving the largest redistribution of species on Earth since the last ice age (Pecl et al., 2017). As a result, species worldwide are shifting or expanding their ranges poleward, to higher elevations and greater depths (i.e., climate migrants; Chapman et al., 2021; Johnson, Martínez-Soto, et al., 2020; Pecl et al., 2017). These climate migrants may influence community structure (e.g., predator–prey interactions) and ecosystem functioning (e.g., nutrient and carbon cycling, primary production) of recipient ecosystems (Gilson et al., 2021; Pecl et al., 2017; Sorte et al., 2010). Although biologists have documented thousands of climate migrants worldwide (Johnson, 2015; Lenoir et al., 2020; Parmesan & Yohe, 2003; Poloczanska et al., 2013; Sorte et al., 2010), researchers still know little about their ecological effects (Sorte et al., 2010; Wallingford et al., 2020). Given that the number of climate migrants is expected to accelerate in the coming decades (Garciá Molinos et al., 2016) and their potential to influence critical ecosystem processes and services is large (Pecl et al., 2017), there is an urgent need to understand their effects on ecosystems.

Ecological theory predicts, and empirical evidence suggests, that the climate migrants that will have the greatest ecological impacts are those that strongly regulate communities and ecosystem functioning such as foundation species, herbivores, and predators (Gilson et al., 2021; Ling, 2008; Sorte et al., 2010; Urban et al., 2016; Wallingford et al., 2020). For instance, the herbivorous sea urchin *Centrostephanus rodgersii* reduced habitat-forming macroalgal biomass by 99% in its expanded range in Australia and reengineered an algal reef into an urchin barren (Ling, 2008). By modifying the habitat, the sea urchin is also an ecosystem engineer—a species that can modify, maintain, or create habitats (sensu Jones et al., 1994). Other ecosystem engineers such as beavers, trees, termites, burrowing owls, crabs, and earthworms will likely have large ecological impacts as climate migrants because they can control ecosystem functioning, community structure, and physical structure (Guy-Haim et al., 2018).

The ecological impact of an ecosystem engineer may not always be negative (Doughty et al., 2016). For instance, fiddler crabs can facilitate the growth of saltmarsh plants through their burrowing activities and feces (Bertness, 1985; Hughes et al., 2014; Montague, 1982). This crab–plant relationship can be considered a commensalism. As environmental stress increases with global climate change, positive interactions such as mutualisms, facilitation, and commensalisms are predicted to become more important in ecosystems (He et al., 2013). It is unknown, however, whether these positive associations will persist during a climate-driven range expansion.

To identify the potential impacts of an engineering climate migrant, we focus on the Atlantic marsh fiddler crab, *Minuca pugnax*, which recently expanded its range. Its historical northern limit was Cape Cod, Massachusetts, USA (Williams, 1984). By 2003, it had expanded north to North Scituate, Massachusetts, USA (Sanford et al., 2006) and to Hampton, New Hampshire, USA, by 2014 (Johnson, 2014). Currently, *M. pugnax* are found as far north as central Maine, USA (Figure 1A, Appendix S1: Table S1). This range expansion is likely due to ocean warming in the Gulf of Maine (Pershing et al., 2015) because the northern limit of *M. pugnax* is limited, in part, by summer water temperatures, which control the development of pelagic larvae (Sanford et al., 2006). Because *M. pugnax* expanded recently, and there are no other fiddler crab species or burrowing crabs in the expanded-range marshes, the crab–plant interaction will likely be novel for the plant.

Cape Cod is a well-defined biogeographic boundary that clearly delineates *M. pugnax* historical and expanded ranges. In its historical range, *M. pugnax* strongly influences several saltmarsh functions, most of which are tied to its relationship with the foundational plant, *Spartina alterniflora* (hereafter *Spartina*). At low to moderate densities, it can enhance *Spartina* aboveground biomass (Bertness, 1985; Gittman & Keller, 2013; Holdredge et al., 2010; Williams & Johnson, 2021) via several mechanisms. First, it can enhance *Spartina* aboveground growth as a result of its burrows, which allow for greater soil drainage and oxygen penetration to the roots (Bertness, 1985). Oxygen is important for root respiration and reduction of soil sulfides, a plant toxin (Mendelssohn & Morris, 2005). Second, fiddler crabs may promote *Spartina* aboveground growth by boosting soil nutrients via nutrient-rich fecal pellets or as their burrows allow oxygen to stimulate the decomposition of soil organic matter and, in turn, release nutrients (i.e., remineralization; Holdredge et al., 2010; Thomas & Blum, 2010). Fiddler crabs can enhance *Spartina* aboveground growth enough to counter the effects of low-level herbivory (Gittman & Keller, 2013; Williams & Johnson, 2021). Because *M. pugnax* can reduce environmental stress and offset herbivory of

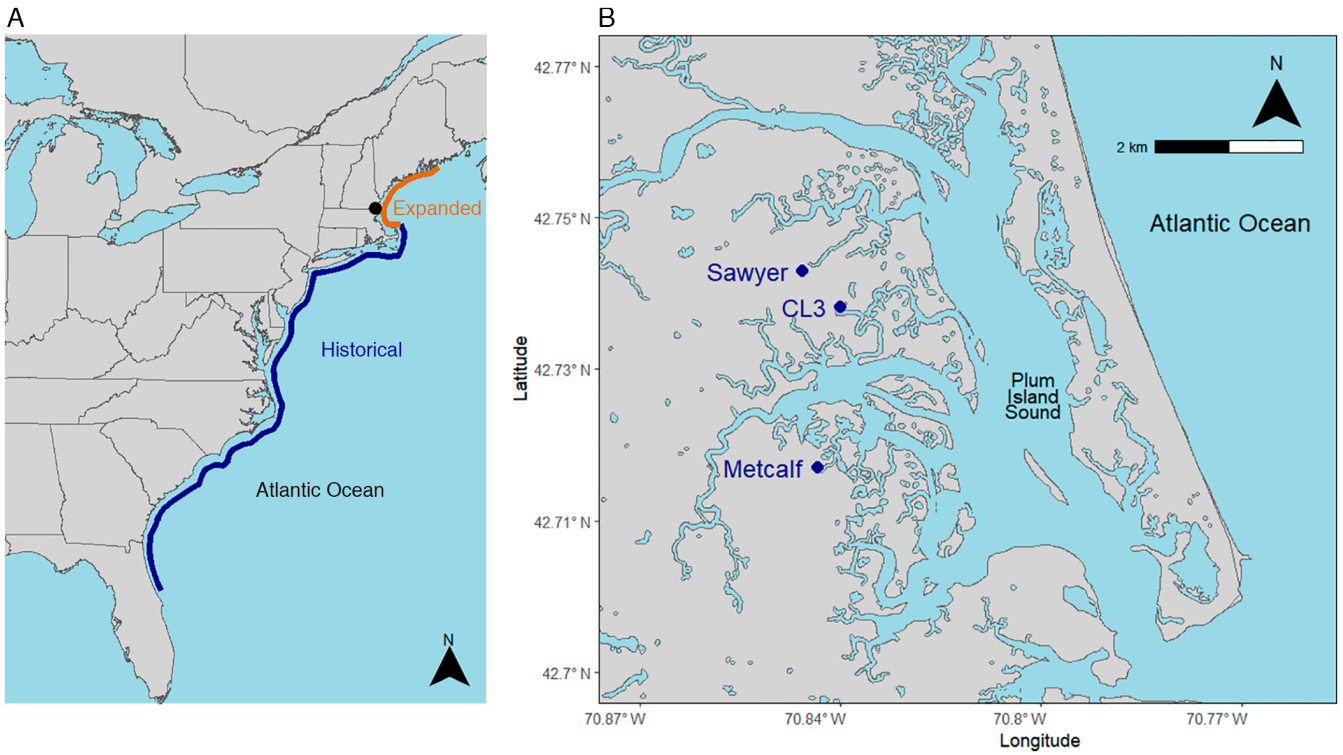


FIGURE 1 (A) Map of *Minuca pugnax* distributions. Historical range based on Williams (1984) and Hopkins and Thurman (2010). Expanded range based on Sanford et al. (2006), Johnson (2014), and Appendix S1: Table S1. Black dot in northeastern Massachusetts indicates area where studies were conducted. (B) Detailed map of study marshes in Plum Island ecosystem.

Spartina and ultimately promote plant production, it may enhance marsh functioning and resilience against global-change drivers such as sea-level rise (Williams & Johnson, 2021). However, *M. pugnax* can reduce *Spartina* belowground biomass (Bertness, 1985; Gittman & Keller, 2013; Thomas & Blum, 2010) and enhance organic-matter decomposition (Bertness, 1985; Thomas & Blum, 2010), which may offset some of its positive effects.

We had two goals in this study: (1) to determine the ecological impact of *M. pugnax* on primary producers and sediment properties in its expanded range and (2) compare its impact on above- and belowground biomass of *Spartina* between ranges. To determine the ecological impact of *M. pugnax* in its expanded range, we used observational experiments in a control-impact design in three salt marshes. We hypothesized that *M. pugnax* would enhance aboveground biomass, percent nitrogen in leaves, but lower belowground biomass, soil organic matter, and benthic microalgae biomass. However, we hypothesized that their effects on *Spartina* would be larger in the expanded range because their interaction with fiddler crabs would be novel for *Spartina* in the expanded range. To evaluate the size of their ecological impact between the expanded and historical ranges, we compared our results to literature values found in the historical range.

MATERIALS AND METHODS

Site description

We conducted our experiments in a control-impact design in three salt marshes in the Plum Island Estuary Long Term Ecological Research site (PIE-LTER) in northeast Massachusetts, USA, which is in the expanded range of *M. pugnax*. *Minuca pugnax* was first seen in these marshes in 2014 (Johnson, 2014); however, it is likely that they arrived in these marshes during or just after the 2012 marine heatwave that occurred in the Gulf of Maine. We sampled the salt marshes lining Sawyer Creek from September 5 to 10, 2020, and Metcalf and Clubhead Third (hereafter CL3) from August 16 to 20, 2021 (Figure 1B). Each marsh was 2–6 km from each other by water. These salt marshes exhibit common plant zonation found in northeastern US marshes. Tall-form *Spartina alterniflora* occupies 1- to 3-m wide bands along creek banks in the low-marsh zone, which is flooded twice a day. The high marsh (above mean highwater) is dominated by *S. patens* and *Distichlis spicata*, with patches of short-form *S. alterniflora* (Johnson et al., 2016). The mean tidal range of the Plum Island Sound Estuary is 2.9 m. In salt marshes to the south, *M. pugnax* can be found in both high- and low-marsh zones (Zajac et al., 2022);

however, it is only found in the low marsh in the Plum Island marshes.

Other invertebrates can strongly influence saltmarsh functioning (e.g., plant biomass) on the US east coast, such as the periwinkle, *Littoraria irrorata* (Silliman et al., 2005), the purple marsh crab, *Sesarma reticulatum* (Bertness et al., 2014; Williams & Johnson, 2021), and other species of fiddler crabs (e.g., *M. minax*, *Leptuca pugilator*). However, these species are absent from our study marshes. The ribbed mussel, *Geukensia demissa*, which can also enhance *Spartina* biomass (Crotty et al., 2018), is present in these marshes; however, their densities are extraordinarily low in these marshes (<1 m^2 vs. 40 m^2 in southern marshes [Crotty et al., 2018]).

Minuca pugnax control-impact study

Although the densities of fiddler crabs can be as high as 176 burrows m^{-2} within their colonies (a group of burrows) in their expanded range (Johnson, 2021), the mean density of fiddler crabs in the expanded range is low (6–15 burrows m^{-2}) at the scale of the ecosystem (Johnson, 2021; Martínez-Soto & Johnson, 2020). This is because their colonies are typically not wider than a meter and are patchily distributed with many colonies separated by 10 m or more. Thus, most of the *Spartina* low marsh has not been colonized by fiddler crabs. This allowed for a natural experiment perfect for a control-impact design without the need for cages.

We established 15 paired plots ($n = 30$ plots/site) in the low-marsh zone of each site. Each plot pair consisted of "crabs" and "no crabs" plots. To accomplish this, we walked along the edge of low marshes and when crab burrows were found, we established a 0.0625 m^2 (25 × 25 cm) "crabs" plot. We then established a corresponding "no crabs" plot within 0.5–1 m. All plot pairs were at least 5 m apart. This paired, control-impact design meant that each plot in a pair had a similar elevation and experienced the same hydroperiod and insolation and that any differences observed between plots were likely due to the presence/absence of fiddler crabs. The plots with crabs had a mean burrow density of 64 burrows m^{-2}, which is within the range of previous studies (Gittman & Keller, 2013; Williams & Johnson, 2021).

In each plot, we quantified the number of fiddler crab burrows, ribbed mussels (*G. demissa*), and other macroinvertebrates (e.g., coffee-bean snails, *Melampus bidentatus*). The densities of other invertebrates were too low to be included in our analyses. We also measured the following variables.

Aboveground biomass

To quantify *Spartina* biomass, all stems were harvested within the plot. Prior to drying plants for biomass, we measured the height of all plants. Plants were oven-dried at 60°C to a constant dry weight. We counted all stems harvested to get stem density.

Plant stoichiometry

To determine the percent carbon and nitrogen of aboveground tissues, three leaves were ground to a fine powder using a mini Wiley 178 Mill fitted with a 40-mesh sieve. Samples were run on a CHN elemental analyzer (Exeter Analytical, Inc.) for carbon and nitrogen analysis.

Belowground biomass

To determine the effect of fiddler crabs on *Spartina* roots and rhizomes, we took one belowground biomass core with an aluminum corer (7.62 cm diameter) to a 20-cm depth, which is where more than 80% of the live biomass occurs in these marshes (Deegan et al., 2012). Each core was divided into 0- to 10-cm and 10- to 20-cm sections in the field. Cores were washed over a sieve (1-mm mesh) and plant material, roots, rhizomes, and detritus were separated from sediments. Lastly, samples were dried at 60°C until they reached a constant dry weight.

Bulk density and percent organic matter

A Russian peat corer was used to obtain a 20-cm-deep core to determine bulk density and percent organic matter. The core was divided into the following depths: 0–5 cm, 5–10 cm, 10–15 cm, and 15–20 cm. To determine bulk density (in grams dry weight per cubic centimeter), samples were dried at 60°C for 2 days. Percent organic matter was determined using the loss-on-ignition method. Samples were then ground, and approximately 5 g of ground sediment was placed in tins for each sample and muffled at 550°C for 6 h. Muffled samples were then weighed.

Benthic microalgal biomass

To quantify benthic microalgal biomass, a key food for *M. pugnax* (Johnson, Shields, et al., 2020), we measured diatom biomass using a handheld fluorometer (Benthotorch, bbe Moldaenke GmbH, Germany) placed near the center of the quadrat but not over a burrow. The

fluorometer also measures green algae and cyanobacteria biomass, but the concentrations were too low or absent to be included in analyses.

Quantitative review of *Minuca pugnax* impacts on above- and belowground biomass

To compare the size of the ecological effect of *M. pugnax* between their expanded and historical ranges, we compared our results with those from the primary literature in a quantitative review. We chose to conduct a quantitative review instead of a true meta-analysis since there were not enough data in both ranges for a rigorous meta-analysis. We focused on aboveground and belowground biomass because they contribute to critical ecosystem functioning and services such as carbon storage, sediment trapping, and habitat provisioning. We used studies that followed these criteria: used *M. pugnax* as a treatment, conducted field and/or mesocosm studies, and reported aboveground or belowground biomass for *Spartina alterniflora*. Means, raw values, and SDs/SEs (if available) were extracted from tables, text, or figures. For graphical presentations, we used the Measure Tool in Adobe PDF Reader (Adobe Systems, Inc.) to estimate means or data points. For studies that manipulated a factor in addition to fiddler crabs (e.g., mussels), we only included treatments that manipulated fiddler crabs. Most studies had only two fiddler crab densities to compare; however, two observational studies had a range of fiddler crab densities (Smith, 2015; Williams & Johnson, 2021). To address this, we compared the response variables from the upper and lower 10% of the densities. Once all values were extracted, we calculated effect sizes for each study including our own and then took the average for each range. We calculated effect size using log-response ratios (LnRR):

$$\mathrm{LnRR} = \ln(\text{mean treatment})/\ln(\text{mean control}),$$

where "treatment" refers to high-density plots and "control" to low-density plots.

STATISTICS

Data were first analyzed for normality and homoscedasticity. Data that did not meet these assumptions were either log or square root transformed. We employed a multivariate analysis of variance (MANOVA) to test the significance of effects our predictors had on our response variables. Our multiple responses were aboveground biomass, belowground biomass (to 20 cm), plant height, stem density, percent nitrogen, benthic microalgae biomass, bulk density (to 20 cm), and percent organic matter in sediments (to 20 cm). Our two predictor variables were site (= marsh location) and treatment. Additionally, we tested for interactions between our predictor variables. We used Pillai's trace as our test statistic in the MANOVA. Because our MANOVA found significant effects, we followed up with two-way ANOVAs on each variable to identify those variables driving that significance. Significance for all statistical analyses was determined at $\alpha = 0.05$. All statistical analyses were conducted using R (R Core Team, 2022).

Additional analyses on *Spartina* biomass

Although our paired control-impact study was designed to minimize environmental variation, it was observational and could not establish cause-and-effect relationships with the same certainty that caging studies can. To address this, we focused on *Spartina* above- and belowground biomass and conducted two additional analyses. First, we correlated the effect size of above- and belowground biomass for each plot pair to its burrow density. Data were combined across marshes. We again used LnRR for the effect size for each plot pair:

$$\mathrm{LnRR} = \ln(\text{crab plot})/\ln(\text{no-crab plot}).$$

Second, we compared our aboveground biomass data from the "crabs" and "no crabs" plots to 9 years of data taken by a long-term project (TIDE Project) within the PIE-LTER in a marsh near the experimental marshes from our study (West Creek marsh, 42°44′16′ N 70°50′55′ W; see Johnson et al., 2016 for methods). We used the 9 years of data prior to the likely arrival of fiddler crabs in the PIE-LTER (2003–2011; Deegan et al., 2022). These data represent a wide range of interannual and spatial variability for *Spartina* aboveground biomass. To statistically compare data, we conducted two *t*-tests: (1) between plots with crabs and the long-term data and (2) between plots with no crabs and the long-term data. Data from the "crabs" and "no crabs" plots was pooled across all marshes prior to analyses. We did not have long-term belowground biomass to make comparisons with.

RESULTS

Minuca pugnax control-impact study

Based on multivariate analysis of variables, there was an effect of site (Pillai = 1.205, $p < 0.0001$) and treatment ("crabs" vs. "no crabs") (Pillai = 0.398, $p < 0.0001$), with no

interaction (Pillai = 0.261, $p = 0.153$, two-way MANOVA). We briefly summarize the results of our univariate analyses of crab effects here (full results available in Appendix S1: Table S4). In the presence of fiddler crabs, *Spartina* aboveground biomass was 40% lower on average compared to plots without fiddler crabs (Figure 2A, Treatment: $F_{1,80} = 22.857$, $p < 0.0001$, ANOVA). Stem density of *Spartina* was 31% lower on average compared to areas without fiddler crabs (Figure 2B, Treatment: $F_{1,80} = 15.312$, $p < 0.0001$, ANOVA). Fiddler crabs did not affect plant height (Appendix S1: Figure S1A, Site: $F_{1,80} = 1.740$, $p = 0.191$, ANOVA) or the percent nitrogen found in leaves (Appendix S1: Figure S1B, Treatment: $F_{1,80} = 0.007$, $p = 0.935$, ANOVA).

Belowground biomass was 30% lower on average in the presence of fiddler crabs, but that reduction depended on site (Figure 2C, Site × Treatment interaction: $F_{2,80} = 5.882$, $p = 0.004$, ANOVA). Fiddler crabs had no effect on sediment bulk density (Appendix S1: Figure S2, Treatment: $F_{1,80} = 0.387$, $p = 0.536$, ANOVA) or percent organic matter in sediments (Appendix S1: Figure S2, Treatment: $F_{1,80} = 2.488$, $p = 0.119$, ANOVA). However, the presence of fiddler crabs appears to have reduced percent organic matter in the top 10 cm of the cores (Appendix S1: Figure S3). The biomass of diatoms was 45% lower on average when fiddler crabs were present (Figure 3, Treatment: $F_{1,80} = 23.786$, $p < 0.0001$, ANOVA).

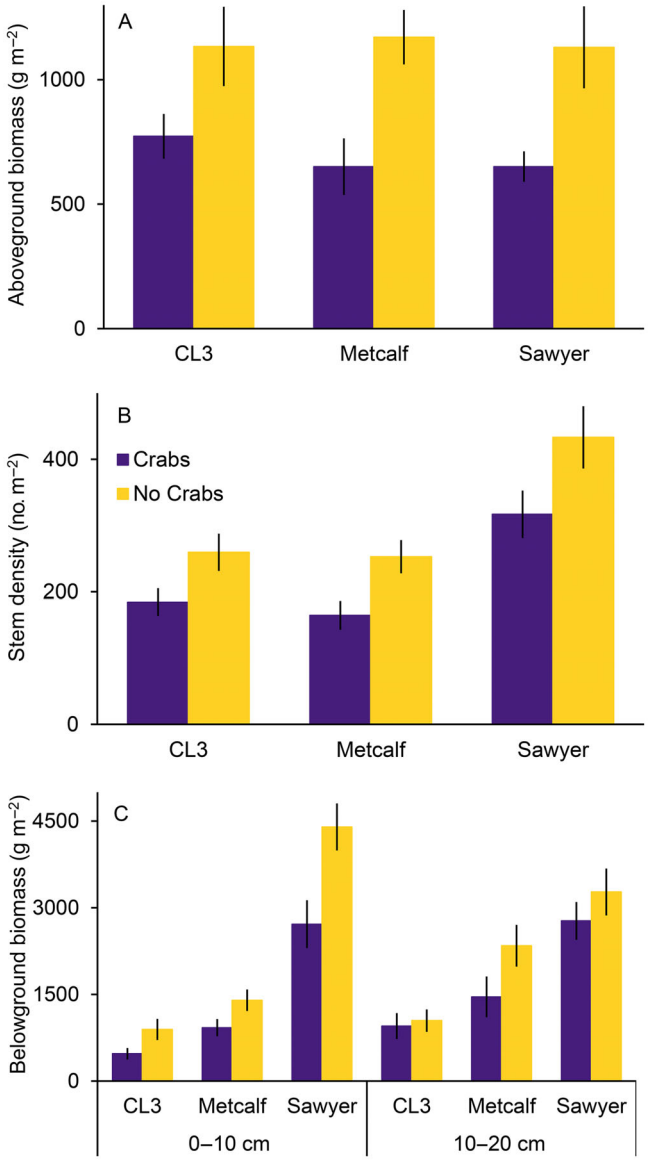


FIGURE 2 (A) Mean (±1 SE) aboveground biomass (dry weight), (B) stem density, and (C) belowground biomass (dry weight) of *Spartina alterniflora* in presence and absence of fiddler crab, *Minuca pugnax*.

Quantitative review of *Minuca pugnax* impacts on above- and belowground biomass

We extracted data from 17 experiments for aboveground biomass and six experiments for belowground biomass to estimate effect sizes in the historical range (Appendix S1: Tables S2 and S3). Fiddler crabs in the expanded range had a large, negative effect on *Spartina* aboveground biomass (LnRR $\bar{X} = -0.503$), which was opposite to the average, positive effect of fiddler crabs on *Spartina* aboveground biomass in the historical range (LnRR $\bar{X} = 0.342$) (Figure 4). Fiddler crabs also had a large, negative effect on *Spartina* belowground biomass in the expanded range (LnRR $\bar{X} = -0.358$), whereas the average effect in the historical range was close to zero (LnRR $\bar{X} = 0.005$) (Figure 4).

Additional analyses on *Spartina* biomass

Spartina above- and belowground biomass declined as burrow density rose (Appendix S1: Figure S4A,B, aboveground Pearson correlation = −0.29, belowground

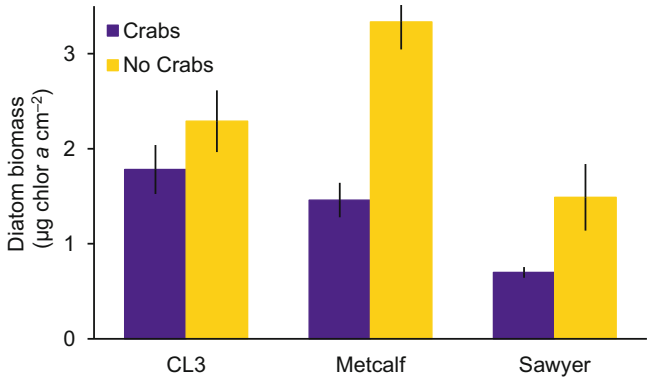


FIGURE 3 Mean (±1 SE) biomass of benthic diatoms in presence and absence of fiddler crab, *Minuca pugnax*.

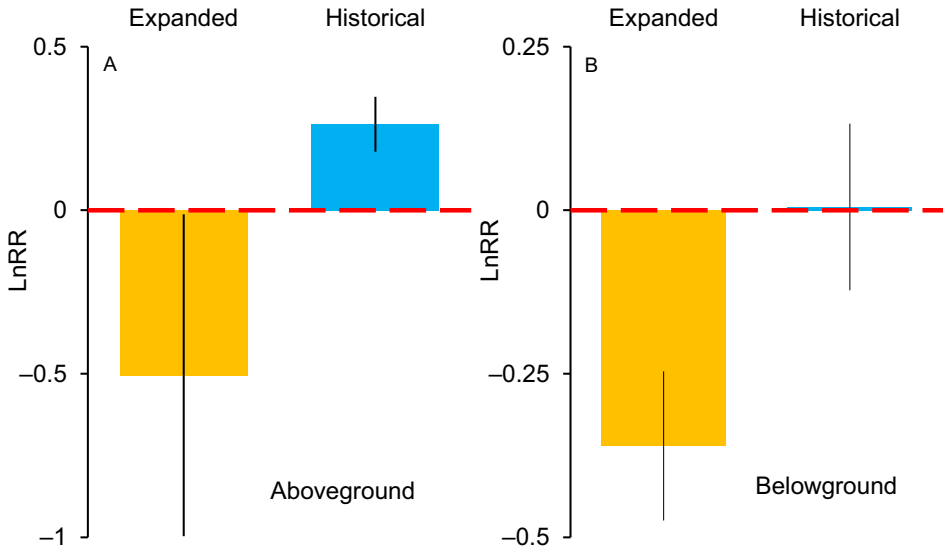


FIGURE 4 (A) Mean (±1 SE) effect size (natural log response ratio) of aboveground biomass in expanded range ($n = 3$) and historical range ($n = 19$). (B) Mean (±1 SE) effect size (natural log response ratio) of belowground biomass in the expanded range ($n = 3$) compared to historical range ($n = 7$).

Pearson correlation = −0.48). Based on medians, aboveground biomass was greater from the 9-year data set than both plots with (Appendix S1: Figure S5, $t_{79} = 2.51$, $p = 0.014$) and without fiddler crabs (Appendix S1: Figure S5, $t_{91} = 9.11$, $p < 0.001$). The data from the plots without crabs had a range similar to that of the data from the 9-year data set. However, 97% of the plots with crabs had aboveground biomass values that were lower than the median of the 9-year data set (Appendix S1: Figure S5).

DISCUSSION

The Earth is experiencing the largest redistribution of species due to climate change since the last glacial maximum 20,000 years ago (Pecl et al., 2017). While scientists have identified thousands of climate migrants, researchers still know little about their ecological influence. Our results demonstrate that *M. pugnax* can strongly reduce the biomass of primary producers. For instance, diatom biomass was lower when fiddler crabs were present. Because fiddler crabs eat diatoms, this result suggests that crabs can control diatom biomass through grazing and potentially sediment disturbance from grazing (Johnson, Shields, et al., 2020). *Spartina* aboveground biomass, stem density, and belowground biomass were lower when *M. pugnax* was present. *Minuca pugnax* impact on *Spartina* aboveground biomass was, on average, large in our study and in the opposite direction to its impact in the historical range (Figure 4). This result demonstrates that the effect of *M. pugnax* on *Spartina* aboveground biomass flipped from positive in the historical range to negative in the expanded range. Our results suggest that not only can climate migrants have profound ecological impacts but their impacts may be the inverse of those found in their historical range for key functions.

The prevailing paradigm for the past 40 years was that *M. pugnax* and other fiddler crabs promote *Spartina* aboveground biomass in their historical range (Bertness, 1985; Gittman & Keller, 2013; Montague, 1982; Williams & Johnson, 2021, Figure 4). However, we found the opposite pattern in the expanded range. Why? We suggest two mechanisms.

First, fiddler crabs may reduce the type of N favored by *Spartina* for growth, ammonium, available in the sediment porewater. As burrows allow oxygen to penetrate the sediment, nitrification (the microbial conversion of ammonium into nitrate) is stimulation, and as a result, ammonium may be depleted. *Spartina* is nitrogen limited (Mendelssohn, 1979), and its growth is influenced by N availability (Bowen et al., 2020; Johnson et al., 2016; Wigand et al., 2004). Ammonium is energetically favored over nitrate for *Spartina* uptake (Mendelssohn & Morris, 2005) and enhances aboveground growth more than nitrate does (Bowen et al., 2020). However, we found no difference in percent N in the leaves, which suggests that fiddler crabs do not affect nitrogen availability or uptake.

A second and more likely explanation is that fiddler crabs damage *Spartina* roots while digging and maintaining their burrows. Fiddler crabs in the expanded

range are larger and more active burrowers than those in the historical range (Johnson et al., 2019; Wong et al., 2021). Most burrows are within 20 cm of the surface (Bertness & Miller, 1984; Katz, 1980), which corresponds to where 80% of *Spartina* root biomass is found (Deegan et al., 2012). It is unclear, however, how root damage done by digging animals translates into reduced aboveground biomass. If root damage is analogous to root herbivory, then digging may result in lower aboveground biomass by cutting nutrient uptake (Agrawal, 2004; Barber et al., 2011). Burrowing may disrupt the *Spartina*–fungi mutualisms in the soil, which is critical for nutrient uptake (Bulseco et al., 2019). Again, however, we found no effect of fiddler crabs on percent N in *Spartina* leaves. Alternatively, plants may divert energy from aboveground growth to repair or replace roots damaged by fiddler crabs. Regardless of the proximate mechanism, if fiddler crabs reduce aboveground biomass in their expanded range through the physical act of burrowing, then their effects resemble those of other burrowers that inhibit plant growth such as lugworms, *Arenicola marina*, in seagrass beds (Govers et al., 2014) and pikas, *Ochotona curzoniae*, in alpine meadows (Zhao et al., 2021).

Why would fiddler crabs reduce *Spartina* aboveground biomass in its expanded but not historical range? One possibility is *Spartina*'s lack of ecological and evolutionary experience with burrowing crabs in the expanded range (Johnson, 2011; Johnson et al., 2007). As a result, the genotypes of *Spartina* populations in this range may not be adapted to the presence of fiddler crabs and so may be unable to compensate for even moderate amounts of root damage. Thus, what is a commensalism (+/0) between *Spartina* and *M. pugnax* in the crab's historical range is an amensalism (−/0) in its expanded range. This amensalism may, however, switch to a commensalism as the plants adapt to the presence of fiddler crabs, and this may happen quickly. For example, blue mussels, *Mytilus edulis*, adapted within 15 years to the presence of an invasive crab predator by thickening its shells (Freeman & Byers, 2006).

In the meantime, fiddler crabs may magnify the effects of climate change. For instance, sea-level rise threatens to drown salt marshes (Crosby et al., 2016). When conditions are right, salt marshes can accrete (build up) to keep up with sea-level rise. Plants are critical to this process as aboveground shoots trap sediment and the belowground biomass adds soil volume (Carey et al., 2017; Morris et al., 2002; Nyman et al., 2006). However, when above- and belowground biomass is diminished, the marsh's ability to accrete also suffers (Kirwan & Megonigal, 2013; Williams & Johnson, 2021). We showed that fiddler crabs reduced aboveground biomass by up to 40% and belowground biomass by up to 30%, on average (Figures 2A and 3). By reducing *Spartina* biomass in the expanded range, fiddler crabs may amplify the effects of climate change by reducing the marsh's ability to keep pace with accelerated sea-level rise. We recommend field experiments and observations that measure geomorphic processes such as sediment trapping, accretion, and erosion in areas with and without fiddler crabs to test this hypothesis (Raposa et al., 2018).

Although we did not see a dramatic loss in organic matter in the sediments, our results still suggest that fiddler crabs may reduce a salt marsh's ability to store carbon over time. Salt marshes excel at storing carbon because they are productive, their sediments are anoxic, which slows decomposition, and they accrete (Kirwan & Megonigal, 2013; Smith et al., 2022). By limiting the belowground biomass of *Spartina*, as found in the expanded range (this study) and historical range (Gittman & Keller, 2013; Thomas & Blum, 2010), fiddler crabs reduce the amount of carbon that can be stored in the marsh. Fiddler crabs may further diminish carbon storage by liberating stored carbon by enhancing decomposition as a result of their burrows. We were unable to measure decomposition in our experiments, but Thomas and Blum (2010) estimated a net loss of carbon of 3 g C m^{-2} $year^{-1}$ in a Virginia salt marsh when fiddler crabs were present. Thus, *M. pugnax* and other burrowing species may limit carbon storage in salt marshes (Grow et al., 2022).

Although our paired control-impact study was designed to minimize environmental variation, it was observational and could not establish cause-and-effect relationships with the same certainty that caging studies can. However, there are several reasons our results are likely due to *M. pugnax*. First, the distance between the paired "crabs"/"no crabs" plots was small (≤1 m), which minimized environmental variation. Second, *Spartina* above- and belowground biomass was negatively correlated with burrow density in our study (Appendix S1: Figure S4). The relationship we found for belowground biomass is consistent with what is seen in *M. pugnax*'s historical range (Bertness, 1985; Thomas & Blum, 2010). However, for aboveground biomass, this relationship is the inverse of what is seen in the historical range, where *Spartina* aboveground biomass and burrow density are strongly and positively correlated (e.g., Smith, 2015; Williams & Johnson, 2021). These results suggest that as *M. pugnax* densities rise in the historical range, so does *Spartina* aboveground biomass, but in the expanded range *Spartina* aboveground biomass falls as crab densities rise. Finally, for *Spartina* aboveground biomass, 97% of the plots with fiddler crabs had values less than the median of local long-term data (Appendix S1: Figure S5), which was taken 9 years prior to the arrival of fiddler crabs. The long-term data capture the full range of spatial

and interannual variability in aboveground biomass for marshes in this region, and the plots without fiddler crabs matched that variation. The fact that the aboveground biomass in the plots without fiddler crabs consistently had a lower distribution than the plots without fiddler crabs and the long-term data suggests that fiddler crabs are driving those patterns.

Engineering species worldwide, such as kelp (Gilson et al., 2021), urchins (Ling, 2008), grasses (Kerner et al., 2022), and mangroves (Chapman et al., 2021), have expanded their ranges due to climate change. Our results show that climate migrants can influence key ecosystem functions such as primary production and trophic interactions in their new ranges in unexpected ways. For instance, we found that fiddler crabs reduced the aboveground biomass of *Spartina*, which is the opposite pattern that many other researchers have found in the historical range (e.g., Bertness, 1985; Montague, 1982; Smith, 2015; Williams & Johnson, 2021). This implies that when a species shifts or expands its range, researchers cannot assume that its ecological impact will be the same in the expanded range as it is in the historical range.

AUTHOR CONTRIBUTIONS

Kayla S. Martínez-Soto: Conceptualization, methodology, validation, formal analysis, investigation, writing original draft, visualization, and review and editing. **David S. Johnson**: Conceptualization, methodology, validation, writing and editing, supervision, and funding acquisition.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Johnson & Martínez-Soto, 2023) are available from the Environmental Data Initiative at https://doi.org/10.6073/pasta/5e0eb4ee4ae58cb5903d50417c6ff736.

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SUPPORTING INFORMATION

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

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