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Sediment selection: range-expanding fiddler crabs are better burrowers than their historic-range counterparts

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ABSTRACT: Climate change plays a large role in driving species range shifts; however, the physical characteristics of an environment can also influence and alter species distributions. In New England salt marshes, the mud fiddler crab *Minuca pugnax* is expanding its range north of Cape Cod, MA, into the Gulf of Maine (GoM) due to warming waters. The burrowing lifestyle of *M. pugnax* means sediment compaction in salt marshes may influence the ability of crabs to dig, with more compact soils being resistant to burrowing. Previous studies indicate that salt marshes along the GoM have a higher sediment compaction relative to marshes south of Cape Cod. Physical characteristics of this habitat may be influencing the burrowing performance of *M. pugnax* and therefore the continuation of their northward range expansion into the GoM. We conducted a controlled laboratory experiment to determine if compaction affects the burrowing activity of *M. pugnax* in historical and range-expanded populations. We manipulated sediment compaction in standardized lab assays and measured crab burrowing performance with individuals collected from Nantucket (NAN, i.e. historical range) and the Plum Island Estuary (PIE, i.e. expanded range). We determined compaction negatively affected burrowing ability in crabs from both sites; however, crabs from PIE have a higher probability of burrowing in higher sediment compactions than NAN crabs. In addition, PIE crabs were more likely to burrow overall. We conclude that site level differences in compaction are likely altering burrowing behavior in the crab's expanded-range territory by way of local adaptation or phenotypic plasticity.

KEY WORDS: *Minuca* (*Uca*) *pugnax* · Range expansion · Sediment compaction · Abiotic tolerance · Biogeography · Salt marsh · Nantucket · Plum Island Estuary · Massachusetts · Gulf of Maine

1. INTRODUCTION

Global distributions of species are shifting due to warming temperatures (Crozier 2004, Sanford et al. 2006, Ling 2008, Dawson et al. 2010, Johnson 2014). Range expansions are occurring with increasing frequency across a variety of taxa and ecosystems (Krehenwinkel & Tautz 2013, Rochlin at al. 2013, Taulman & Robbins 2014). Of particular concern are range-expanding consumers and ecosystem engineers, as they have the potential to cause significant changes to previously uninhabited areas. For example, the southward range expansion of the sea urchin *Centrostephanus rodgersii* in the Tasman Sea (Ling 2008, Ling et al. 2009, Ling & Johnson 2012) is leading to profound consequences by denuding Tasman kelp forests, driving declines in abalone populations (Strain et al. 2013). It is critically important to understand how range-expanding consumers, such as *C. rogersii*, are shifting their distributions due to climate change. Equally important is understanding the nonthermal factors driving distributions of ecosystem

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engineers globally (Burrows et al. 2014). Many unknowns surround why certain species will successfully alter historic ranges and others will not. Therefore, we must determine all factors, not just temperature, that mediate both the likelihood that a species will shift its distribution and the susceptibility that a given ecosystem will experience a range-expanding ecosystem engineer.

Previous research provides key insight on which non-thermal abiotic factors drive species range limits (Edwards et al. 2013, Alofs & Jackson 2015, Spence & Tingley 2020). For example, water chemistry and stream and lake morphology slowed the expansion of several sport fish species in Canada (Alofs & Jackson 2015). These fish were physically incapable of entering and persisting in some Canadian freshwater bodies where their thermal thresholds were met (Alofs & Jackson 2015). Rusty crayfish *Orconectes rusticus* also began experiencing a northward range expansion facilitated by warmer climates (Phillips et al. 2009). However, *O. rusticus* cannot persist in the Canadian Shield, due to low dissolved calcium (Edwards et al. 2013). Individuals that successfully encroach deplete much of the remaining calcium, further arresting the poleward expansion of this species (Edwards et al. 2013). Physical characteristics in newly expanded habitats beyond temperature could prove to be important mediators of species range expansions in the face of climate change.

In the case of the mud fiddler crab *Minuca* (*Uca*) *pugnax*, populations are appearing and persisting in previously uncolonized salt marshes of the Gulf of Maine (GoM). Previous research indicates that *M. pugnax* is experiencing a northward expansion due to a warming GoM, which has warmed at a rate faster than 99% of the global average over the last 40 yr (Sanford et al. 2006, Pershing et al. 2015). The mud fiddler crab is a broadcast spawner that has a highly specific thermal threshold driving larval development. Larval time to metamorphose to the next life stage increases exponentially below 18°C, which is higher than the historic (pre-warming) mean summer sea surface temperatures in the GoM (Sanford et al. 2006). However, Sanford et al. (2006) found mature *M. pugnax* north of Cape Cod in Scituate, MA, in 2003. Then in 2014, individuals were discovered further north in the Plum Island Estuary (PIE) (Johnson 2014). Since then, *M. pugnax* has continued to expand northward along the New England coastline, with individuals being found as far north as Hampton, NH (Johnson 2014), and southern Maine (D. S. Johnson unpubl.).

As a burrowing species of crab, *M. pugnax* could be particularly sensitive to the characteristics of salt marsh sediment in both its historic and non-historic ranges. Soil compaction, density, and structure all have been demonstrated to influence the capacity of crabs to burrow (Chen et al. 2017). We see this in the burrowing crab *Helice tientsinensis* in China, which have higher burrow densities in softer and wetter sediments than in harder and drier sediments that are more difficult to burrow into (Li et al. 2018). Fiddler crabs burrow to feed, to avoid predation, and to mate (Bertness & Miller 1984, Luk & Zajac 2013); therefore, an inability to burrow would severely impact the survival and success of *M. pugnax* in its salt marsh habitat. M. S. Roy et al. (unpubl.) demonstrated that average soil strengths in the salt marshes of Nantucket, MA (NAN, i.e. historic-range habitat), were significantly lower (13.8 ± 0.871 psi [95.15 ± 6.00 kPa]) than those in its expanded range in PIE (30.2 ± 1.53 psi [208.22 ± 10.55 kPa], $p < 0.0001$). Vincent et al. (2013) also reported soil strengths of more than 50 psi (344.74 kPa) in marshes north of Cape Cod along the GoM. In addition, fiddler crab densities are low in PIE (~3–6 crabs m^{-2}) relative to salt marshes south of Cape Cod (~150 crabs m^{-2}) (Martínez-Soto & Johnson 2020). One mechanism driving this low density could be partly due to an inhibition in burrowing ability by some physical barrier to survival and growth such as soil strength. Such low densities could also shift burrowing behavior in PIE crabs relative to NAN crabs via reduced pressure for conspecifics to compete for space.

Therefore, to determine the relationship between physical substrate, crab burrowing ability, and crab density in historic versus range-expanded populations, we conducted a controlled laboratory mesocosm experiment of fiddler crab burrowing behavior in varying degrees of sediment compaction. In particular, we asked the following questions: (1) Does soil strength drive the ability of fiddler crabs to burrow (i.e. whether or not a crab burrows) as well as influence the depth of fiddler crab burrows (as measured by burrow volume)? (2) Are there differences in burrowing ability and burrow depth between historic (i.e. NAN) versus expanded (i.e. PIE) fiddler crabs? (3) Are burrowing ability and burrow depth affected by whether other crabs are present or whether crabs are solitary (i.e. intraspecific competition for space)? More compact sediment and higher soil strengths may be difficult for fiddler crabs to penetrate. Therefore, we hypothesized that higher soil strengths negatively affect a crab's burrowing performance (measured by burrow frequency and burrow volume). In other words, compact soil should impede burrowing crabs. We expected to see, for similar-sized crabs, both populations equally impacted by soil strength, indicating a role in higher soil strengths slowing range expansion, as well as no clear effects of spatial competition between crabs. Finally, we expected that burrows will be deeper (thus having larger volumes) at intermediate soil strengths.

2. MATERIALS AND METHODS

To evaluate the impact of sediment compaction on fiddler crab burrowing ability (i.e. whether or not a crab burrows; we will use ability, behavior, and capacity interchangeably throughout), we developed a controlled laboratory mesocosm experiment testing the burrowing behavior of crabs from historic versus range-expanded populations in standardized organic peat moss (i.e. store-bought peat moss with no added pesticides or herbicides) in different levels of compression. Each mesocosm consisted of peat moss saturated with saltwater and compressed using different weights of sand. To create our peat–salt mixture, we combined 10 gallons (gal; 37.85 l) of dry organic peat moss with 4 gal (15.14 l) of saltwater with a salinity of 20 psu in a ~17 gal (66 l) bin. After thoroughly mixing the peat, we left the mixture to sit overnight to fully saturate and settle before using it for the experiment. To acclimate the crabs to the saturated peat moss environment, crabs were housed in clear ~17 gal (66 l) bins with a separately made peat moss–saltwater mixture for the duration of the experimental process.

We then poured a standardized volume of our peat–salt mixture into each of 4 containers (representing each of our 4 soil compaction–strength treatments per trial). We then placed containers full of sand on top of each container (except for the control) to compress and compact the peat mixture (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m674p163_supp.pdf). We reached the desired sediment compactions for each treatment using a formula we developed to find the approximate amount of sand used. Our soil compaction–strength treatments were as follows: 0 psi (0 kPa), 10 psi (68.95 kPa), 20 psi (137.90 kPa), and 25 psi (172.37 kPa). These values represent the average measurements in NAN and PIE in both 2017 and 2018 (M. S. Roy et al. unpubl.). Measurements of soil strength per mesocosm were made with a Humboldt proctor penetrometer with a 6.45 cm^2 needle. For more information on the formula and the design of our experimental setup, see Text S1.

We tested 2 different crab densities to determine the effect of intraspecific competition for space on burrowing behavior: 1 and 3 crabs per experimental chamber. The ~7 gal (28 l) bins, used as chambers, had a surface area of 0.143 m^2. One crab per chamber was equivalent to ~7 crabs m^{-2}. Three-crab trials had a density equivalent to ~21 crabs m^{-2}. We could not test greater than 3 crabs per tank due to limitations in gathering the required numbers of crabs in PIE needed for larger crab density treatments. Crabs were collected from Carolton Creek in Rowley, MA (42.7455° N, 70.8370° W), for the PIE trials and from Folger's Marsh in Nantucket, MA (41.2947° N, 70.0420° W), for the NAN trials (Fig. S3), both at daytime low tides. NAN trials were conducted in the lab of the University of Massachusetts Boston Nantucket Field Station in Nantucket, MA. PIE trials were conducted at the PIE Long Term Ecological Research site in Newbury, MA. There is 1 exception: PIE trial 4 was conducted at the University of Massachusetts Boston (~40 miles [~64 km] south of PIE). Crabs were transported from PIE to the University of Massachusetts Boston the day after trial 3 was completed, and trial 4 was conducted 1 wk after trial 3 to allow for acclimation post transport. Crabs were kept in the same tank before experimentation in a 21.2° C room without food in all 3 locations (NAN, PIE, and University of Massachusetts Boston). All crabs behaved normally at the time of testing. We conducted 4 replications for each crab density and sediment compaction treatment. A total of n = 128 crabs were used for the experiment, i.e. 4 crabs (1- and 3-crab treatments) × 4 soil treatments × 4 trials = 64 crabs from each location (PIE and NAN).

After testing the sediment compaction of the chambers with a Humboldt proctor penetrometer and smoothing over the sediment, crabs were randomly selected, weighed, and sexed and then put into each experimental vessel for 4 h. It is worth noting that male and female fiddler crabs differ in burrowing behavior (Colby & Fonseca 1984). Crabs were randomly collected in the field and randomly selected by size and sex for each trial, excluding egg-bearing females. In NAN, we used 6 females and 58 males; in PIE we used 21 females and 43 males. After we controlled for sex for each site in the analysis, we found that sex had no effect on burrowing probability. We chose 4 h due to logistical constraints. After the burrowing time, we carefully removed the crab(s) and counted burrows in each mesocosm, measured the sediment compaction, and took plaster casts of each burrow we observed for burrow volume. We used burrow volume as a proxy for burrow depth, which we determined by using water displacement by placing the cast in a graduated cylinder. After each trial, each crab used in the experiment was placed in a clear ~17 gal (66 l) bin separate from the bin housing crabs yet to be tested. All crabs were returned back to the creek where they were collected (i.e. NAN crabs in Nantucket marsh, PIE crabs in PIE marsh), once the experiment was completed.

To determine whether sediment compaction strength influenced the probability of crab burrowing (i.e. burrowing ability, whether or not a crab burrowed), we used binomial logistic regression (generalized linear model with logit link) with sediment compaction, crab collection location, their interaction, and crab mass as predictors and burrowing (yes or no) as a response. We fit separate models for the 1- and 3-crab treatments. To assess if sediment compaction affected burrow volume for those crabs that did burrow, we fit using a generalized linear model with a Gamma error and log link to accommodate for overdispersion and the lack of a 0 ml volume possibility. We used the same predictors and total burrow volume as a response. Using a Gaussian error with an identity or log link produced the same results but often led to impossible fitted values.

To determine whether burrowing behavior was due to differences in crab mass, we compared mean mass between crabs from PIE versus crabs from NAN for each of our crab density treatments. There was no significant difference in crab mass between sites for crabs used in our 1-crab treatment trials ($p = 0.363$). However, crabs used for our 3-crab trials were significantly different; PIE crabs were significantly larger than NAN crabs ($p = 0.000494$). Therefore, we modeled crab mass as a covariate for each of our crab density treatments. We found that crab mass did not play a significant role in the likelihood of burrowing or burrow volume in either 1-crab trials ($p = 0.250$ and $p = 0.672$, respectively) or 3-crab trials ($p = 0.923$ and $p = 0.668$, respectively). Nevertheless, to ensure that size had no role in burrowing behavior for our 3-crab treatments, we culled crabs larger than 7.5 g from PIE, which eliminated 9 crabs from the data. To ensure equal sample size, we randomly culled 9 crabs from our NAN trials. We compared mean crab size between sites from these culled samples (PIE and NAN), and there were no significant differences in size ($p = 0.0815$). We then reran our binomial logistic regression with this culled dataset and found that site was still the strongest predictor of burrowing ability ($p = 0.0228$, i.e. PIE crabs were more likely to burrow than NAN crabs).

All analyses were conducted in R version 3.6.1 (R Core Team 2019). All models were assessed for violations of assumptions using randomized quantile residuals using the DHARMa library (Hartig 2020). Code for all analyses can be found at https://github.com/richw1w/Pugnax_SS_Analysis.git.

3. RESULTS

In our 1-crab trials, NAN crabs did not dig at sediment compaction levels past 10 psi (68.95 kPa); however, PIE crabs were able to burrow in all sediment compaction treatments (0–25 psi [0–172.37 kPa]) (Fig. 1A, Table 1). Soil strength, site, and crab mass did not predict the probability of whether a crab would form a burrow. However, the interaction between initial soil strength and site significantly predicted whether or not a fiddler crab would form a burrow ($p = 0.0107$). In other words, how dense the sediment and where the crab came from synergistically determined burrowing probability. Finally, PIE and NAN crabs dug similar numbers of burrows throughout the experiment (5 and 4, respectively).

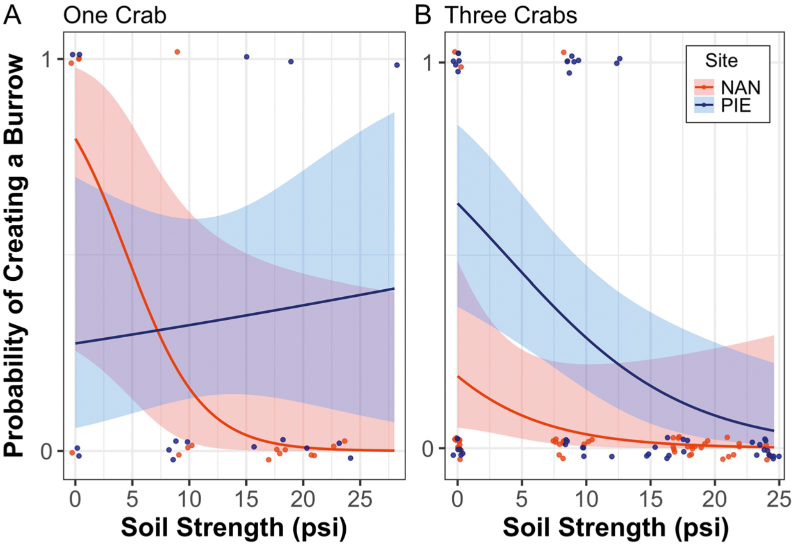

Fig. 1. Burrowing probability in Plum Island Estuary (PIE) and Nantucket (NAN) crabs. PIE crabs are more likely to burrow than those from NAN. The logistic relationship showing how soil strength affects the likelihood of the crab burrowing in trials with both (A) 1 crab ($p = 0.011$) and (B) 3 crabs ($p = 0.002$). Curves are from fit models with 95% CIs. Points represent 1 = burrow or 0 = no burrow. Points are jittered to show overlapping data points and may not align exactly with the true data

Table 1. Analysis of deviance results from probability of crab burrowing model for both the 1-crab trial and 3-crab trial. LR chisq: likelihood ratio chi-square

	Term	LR chisq	df	p
One crab	Soil strength	2.285	1	0.131
	Site	0.240	1	0.624
	Crab mass	1.424	1	0.233
	Soil strength and site interaction	6.535	1	0.011
Three crabs	Soil strength	16.181	1	<0.001
	Site	9.809	1	0.002
	Crab mass	0.009	1	0.923
	Soil strength and site interaction	0.082	1	0.774

In our 3-crab trials, we see a similar relationship as with our 1-crab trials: PIE crabs have a higher probability of burrowing than NAN crabs (Fig. 1B, Table 1). In addition, while PIE crabs dug 4 times as many burrows (PIE = 14 burrows, NAN = 3 burrows) and dug burrows at higher soil compactions than NAN crabs ($p = 0.012$), no crab from either location burrowed in the 20 psi (137.90 kPa) or 25 psi (172.37 kPa) soil strength treatments in the 3-crab treatments. Also, unlike the 1-crab treatment, soil strength ($p < 0.0001$) and site ($p = 0.00173$) independently predict the probability that a crab will burrow, not their interaction ($p = 0.774$). In other words, the probability of whether a fiddler crab will burrow when in the presence of other fiddler crabs differs depending on where the crab comes from or the soil strength it encounters (i.e. independent rather than synergistic effects).

Finally, sediment compaction, site, and our compaction and site interaction did not predict differences in burrow volume in both crab density treatments (Fig. 2, Table 2).

4. DISCUSSION

In contrast to our initial expectations, our experimental results show that *Minuca pugnax* collected from their expanded range (e.g. PIE) are more capable of burrowing in compacted sediment than crabs collected from south of the cape (e.g. NAN) (Fig. 1). Fiddler crabs from Nantucket were unable to dig in sediments with a soil strength greater than 10 psi (68.95 kPa). However, PIE crabs were able to dig up to our most compact sediments, 25 psi (172.37 kPa) when solitary (Fig. 1). We also found that burrow volume did not differ among treatments, regardless of location (i.e. NAN versus PIE), crab size, soil compaction levels, and crab density (Fig. 2). We observed some similarities and differences when fiddler crabs were solitary versus among conspecifics. Overall, PIE crabs were the most likely to burrow and the most likely to burrow at more compact sediments than NAN crabs for both crab density treatments. However, when together, fiddler crabs from both PIE and NAN did not

Table 2. Analysis of deviance results from probability of crab burrow volume model for both the 1-crab trial and 3-crab trial. LR chisq: likelihood ratio chi-square

	Term	LR chisq	df	p
One crab	Soil strength	0.900	1	0.343
	Site	1.073	1	0.300
	Crab mass	0.152	1	0.697
	Soil strength and Site interaction	0.306	1	0.580
Three crabs	Soil strength	0.065	1	0.799
	Site	0.089	1	0.766
	Crab mass	0.187	1	0.665
	Soil strength and Site interaction	2.963	1	0.085

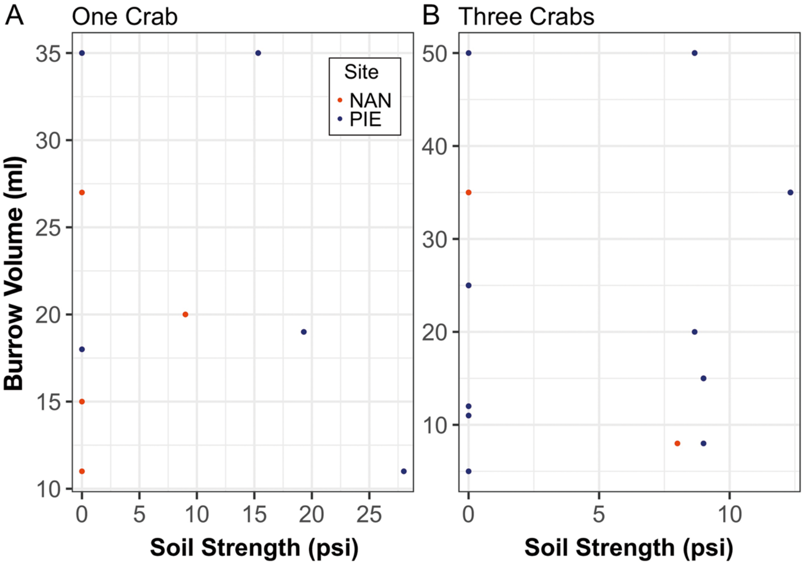

Fig. 2. Burrowing volume in Plum Island Estuary (PIE) and Nantucket (NAN) crabs. Site, soil strength, and crab mass do not predict differences in burrow volume in our experiment once a crab chooses to burrow. Data representing crab burrow volumes in trials with (A) 1 crab or (B) 3 crabs. No curves are shown, as no explanatory variables explained variability in the data

burrow in the strongest soil strengths (20 psi [137.90 kPa] and 25 psi [172.37 kPa]). Nevertheless, when taken together, our study demonstrates that crab population (i.e. NAN and PIE crabs) and soil strength are the strongest predictors of whether or not a fiddler crab will build a burrow.

Such differences in burrowing abilities between these populations suggest that PIE crabs are better burrowers in higher sediment compactions than NAN counterparts. This could be due to northern crabs being inherently stronger or possessing different burrowing strategies (such as investing more energy or spending more time to burrow). We know this difference is not due to size, as we found no significant influence of crab mass on either the likelihood of burrowing or burrow volume in our analyses or additional analyses to address questions about crab size (Fig. S4). This does not mean size might not play a role in the wild, as PIE crabs tend to be larger than their southern counterparts (Johnson et al. 2019). However, some other trait (either physical or behavioral) is generating the observed difference in burrowing ability of these 2 populations. Therefore, the specific mechanism behind the variation in propensity to burrow between the 2 populations remains unclear. Nevertheless, our work shows that individuals of *M. pugnax* in PIE can penetrate sediment compaction levels that NAN individuals cannot.

Selective pressure, phenotypic plasticity, behavioral variation, or some combination of these factors could be drivers of the kind of differential burrowing ability between northern and southern *M. pugnax* populations. Selection on newly settled crabs coming from southern populations could mediate the ability of crabs to burrow in more compact northern sediment. Populations of *M. pugnax* in the GoM are likely experiencing strong selective pressure due to increased soil compactions north of the cape, potentially driving local adaptation in PIE for burrowing ability (Sakai et al. 2001, Sanford & Kelly 2011). Expanded-range populations that have undergone selection may become future sources for larval dispersal in the GoM, enforcing local adaptations. Counteracting local adaptation, *M. pugnax* is a broadcast spawner and experiences high gene flow north and south of Cape Cod (Sanford et al. 2006). This helps to both establish a persisting population and dull the effects of local adaptation (Cornwell 2020). Alternatively, more compact sediment could lead to changes in crab phenotypes if these traits are plastic, leading to stronger crabs. Rapid local adaptation and phenotypic plasticity have aided in colonization for many invasive species before (Smith 2009, Stapley et al. 2015) and could lead to interesting effects on expanded-range habitat for an ecosystem engineer like *M. pugnax*.

Behavioral variability among individuals of *M. pugnax* could also explain the different burrowing behavior between populations. Higher soil strengths in PIE marshes could be selecting (or influencing plastic responses) not only for crabs that are stronger but also for crabs that possess better burrowing abilities. Fiddler crab burrowing behavior is not consistent among individuals of different species (Qureshi & Saher 2012) or of the same species (Neylan et al. 2019). Therefore, the more compact sediment in PIE could be selecting crabs with enhanced burrowing capabilities. We want to emphasize, however, that this study does not attempt to mechanistically determine why there are differences in burrowing performance. Importantly, our study does not directly link variation to genetic differences, potentially from selection during initial colonization, or phenotypically plastic responses to crabs growing up in marshes with stronger sediments. Rather, we hope this work will help other researchers working in this system asking and answering key questions about the role of local adaptation in *M. pugnax* specifically and range-expanding species broadly. Future studies regarding changes in population genetics should attempt to elucidate the specific mechanism driving this better burrowing capacity in expanding-range versus historic-range fiddler crabs.

Our lab experiments also provide a starting point for further investigations into differences in the burrowing behavior of fiddler crabs out of their historic range. While our sediment compactions were limited to a maximum of 25 psi (172.37 kPa), crabs further north in the GoM are likely to experience twice that (Vincent et al. 2013). Therefore, future experimental studies involving *M. pugnax* burrowing should involve soil compactions over 50 psi (344.74 kPa) to display the effects of the more compact northern marshes. Sediment grain size in addition to pure compaction influences fiddler crab burrowing (Crane 1975, Aspey 1978, Neylan et al. 2019). We addressed this by using standardized peat moss in our experiment. Future experiments might cross grain sizes found in natal and expanded habitats with compaction to elegantly tease out differences in burrowing behavior due to changes in environmental conditions.

Interestingly, PIE crabs were capable of burrowing in more compact sediment, and yet none of the treatments in our experiment affected fiddler crab burrow volume (Fig. 2, Table 2). We expected that crabs would burrow deeper, thus having larger burrow volumes, into intermediately strong sediment (10 psi [68.95 kPa]) in comparison to strong compactions (20 psi [137.90 kPa]). We hypothesized that the weakest sediment would not be firm enough for crabs to maintain deep burrows, while the strongest sediment would be too firm for crabs to burrow too deeply. However, there were no significant differences in burrow volume across the entire range of soil strengths from 0 psi (0 kPa and 172.37 kPa respectively) to 25 psi (344.74 kPa). Chen et al. (2017) found that burrow depth is directly proportional to soil strength, such that fiddler crab burrows are deepest with soil types that have the highest soil strengths (e.g. clay-rich mudflats). Our soil compaction levels reflect those observed in the field for both locations; however, it does not reflect the full maximum values observed at PIE as noted above (>50 psi [344.74 kPa], Vincent et al. 2013). This was due to constraints in compacting sediment at such high levels, the weight of which would have damaged our experimental chambers. Had we tested higher soil compaction levels, we may have observed higher burrow volumes for PIE crabs. We feel confident that our study captured burrowing depth dynamics for NAN crabs given their inability to burrow at the strongest soils we tested as well as the range of sediment strengths they experience in the field.

We observed interesting intraspecific interactive effects in our 3-crab density treatments. When alone, *M. pugnax* from PIE burrowed in all soil strength treatments. When in the presence of other conspecifics, PIE crabs burrowed as high as 10 psi (68.95 kPa) only (NAN crabs still burrowed predominately in 0 psi add [0 kPa] metric conversion soil strength). One possible explanation for this pattern could be that fiddler crabs take more time to burrow when in the presence of conspecifics, and thus our experiment potentially did not run long enough to fully capture burrowing behavior in the 3-crab treatments. Alternatively, when in the presence of other individuals, *M. pugnax* potentially expends more energy engaging in behavioral displays or defense. This may reduce the energy needed to initiate a burrow at the strongest compactions or, again, may contribute to the time needed to form a burrow in the presence of conspecifics. It is important to note that our 3-crab treatment represented a higher density than what is typical of PIE (~3–6 crabs m^{-2}; Martínez-Soto & Johnson 2020) and a lower density typical of southern ranges (80–120 crabs m^{-2}; Bertness 1985, Martínez-Soto & Johnson 2020). This represents as close to an intermediate range of fiddler crab densities as we could possibly test due to limitations in gathering the required numbers of crabs in PIE needed for larger crab density treatments. Therefore, to determine the specific contribution of fiddler crab density on burrowing behavior, it will be critical to measure fiddler crab burrowing across a greater range of fiddler crab densities, soil compaction levels, and time scales in future studies.

Fiddler crabs are ecosystem engineers. As such, they affect productivity, biogeochemistry, and sediment structure in their historic habitats south of Cape Cod (Bertness 1985, Smith & Tyrrell 2012, Johnson et al. 2020). Given our results and the literature on fiddler crab impacts on ecosystem function, we suggest the possibility that fiddler crabs in PIE could mediate both the aboveground biomass of *Spartina alterniflora* and sediment stability over time. *M. pugnax* at intermediate tidal heights (i.e. the low marsh zone) increases aboveground biomass and reduces root mat density (Bertness 1985). Thomas & Blum (2010) found that crab burrows have also been shown to reduce the belowground biomass of *S. alterniflora* in Virginia, potentially increasing the susceptibility of erosion among *M. pugnax* habitat at low and intermediate sections of marsh. These marsh zones are already at risk of erosion due to climate change and sea level rise (Deegan et al. 2012) in PIE and other marshes north of Cape Cod. Conversely, Gittman & Keller (2013) found the opposite result, showing that *S. alterniflora* produced more growth in the presence of crabs through a reduction in the snail population. *M. pugnax* burrowing may also increase marsh productivity (Wang et al. 2010). Therefore, it will be critical to closely monitor how the mud fiddler crab influences ecosystem functioning such as soil drainage and sediment stability over time, particularly if their densities reach what is typical in habitats south of the cape.

Research tells us that species are shifting their distributions due to changes in global air and sea surface temperatures (Crozier 2004, Sanford et al. 2006, Ling 2008, Dawson et al. 2010, Johnson 2014). However, our study underscores the need to understand non-thermal drivers of species distributions such as physical substrate. Burrows et al. (2014) demonstrated how species distributions track thermal envelopes for some, but not all, species. The fiddler crab *M. pugnax* began shifting its distribution, likely due to a warming GoM, facilitating an increase in larval survival rates in this ecosystem (Sanford et al. 2006). However, this does not account for how adults interact with this environment, especially since adult *M. pugnax* likely survive cold northern New England winters due to the presence of fully grown adults in late spring in PIE (Martínez-Soto & Johnson 2020). Non-climatic factors of species ranges are found in a variety of taxa such as plants (Brown & Vellend 2014), fish (Alofs & Jackson 2015), and crustaceans (Phillips et al. 2009). Our study shows that physical substrate via soil compaction mediates the ability of fiddler crabs to burrow. Despite PIE fiddler crabs being better burrowers, PIE has far lower fiddler crab densities than Nantucket, which could be due to many factors including recruitment, settlement survival, and food web dynamics in PIE, among others (Grimes et al. 1989). Our study demonstrates that structural complexity, including soil strength, is a likely mediator to crab survival and continued success in its expanded range. Our work emphasizes the need for future scholarship to mechanistically link all the drivers that influence species ranges in the face of environmental change.

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