Sediment Selection: Range Expanding Fiddler Crabs are Better Burrowers Than Their Natal Counterparts

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ABSTRACT: Species ranges are shifting in response to climate change. In New England salt marshes, the mud fiddler crab, *Minuca* (*Uca*) *pugnax,* is expanding north of Cape Cod, MA into the Gulf of Maine (GoM) due to warming waters. Physical habitat, in addition to temperature change, may be important in mediating the expansion of several species into novel habitats. *M. pugnax* burrows in the muddy *Spartina alterniflora* dominated low marsh of Eastern U.S. salt marshes. Sediment compaction may influence the ability for *M. pugnax* to burrow, with more compact soils being more resilient to burrowing. Previous studies indicate that salt marshes along the coast of the GoM have higher soil strength (i.e., soil compaction) relative to marshes south of Cape Cod. Taken together, physical characteristics and temperature of this habitat may be influencing the burrowing behavior/performance of *M. pugnax*, and therefore the ability for the mud fiddler crab to continue its northward range expansion into the GoM. To determine if sediment compaction affects burrowing activity of *M. pugnax* in natal and range expanded populations, we conducted a controlled laboratory experiment. We manipulated soil compaction in standardized lab assays and measured the number of burrows and burrow volume created by crabs in trials with one and three crabs over a 4 hour period with crabs collected from Nantucket (i.e., native range) and the Plum Island Estuary (PIE, i.e., expanded range). Soil strength measurements were taken before and after each trial to determine how soil strength influences burrowing behavior, and how burrowing behavior in turn influences soil strength. We determined that crabs from both sites burrowed were less likely to burrow at higher soil strengths; however, crabs from PIE burrowed in 0-25 psi (1.8 kg/cm^2) peat, whereas Nantucket crabs were limited to 0-10 psi (0.7 kg/cm^2) peat. In addition, PIE crabs were more likely to burrow in each soil strength treatment. We also observed no relationship between soil strength and burrow volume between crab source populations and between crab densities. We conclude that site level differences in soil compaction are likely altering fiddler crab burrowing behavior in its expanded range territory by either phenotypic plasticity or rapid evolution. Our study demonstrates that non-temperature physical habitat traits can be as important as temperature in influencing the ability for species to expand their ranges in the face of climate change.

KEYWORDS: *Minuca* (*Uca*) *pugnax*, Range Expansion, Sediment Compaction, Soil Strength, Salt Marsh, Massachusetts, Plum Island Estuary, Nantucket, Gulf of Maine, Biogeography

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Introduction:

Global distributions of species are shifting because of climate change (Crozier, 2004; Dawson, 2010; Ling, 2008; Johnson, 2014; Sanford, 2006). Temperature is a known barrier that creates many species' range borders (Burrows et al., 2014). As temperatures shift, barriers to species' ranges can be breached, leading to range expansions (Parmesan, 2006). Such range expansions are occurring with increasing frequency across a variety of taxa and ecosystems (Krehenwinkel, 2013; Rochlin, 2013;

Taulman, 2014). As they shift their range, species – particularly consumers and ecosystem engineers – can have a large effect in these novel areas. For example, warming waters enabled the southward range expansion of the sea urchin *Centrostephanus rodgersii* in the Tasman Sea (Ling, 2008; Ling et al., 2009; Ling and Johnson, 2012), leading to profound consequences, from the denuding of kelp forests and competition-driven declines in abalone populations (Strain et al., 2013). Temperature, however, is not always the only barrier to species' ranges (Burrows et al, 2014). Unsuitable habitat, lack of prey, and abundance of predators, to name a few, can serve to slow or even stop range expansions. In contrast, plasticity and rapid evolution could counteract this mismatch. How species survive, thrive, and change when expanding their ranges due to opening thermal windows, despite other forms of mismatch, remains relatively unexplored.

Species that are stymied or prevented from experiencing range shifts, despite favorable temperature shifts, are often the stopped by non-climate related physical barriers (Alof et al., 2015; Edwards et al., 2013; Spence and Tingley, 2020). Water chemistry and stream and lake morphology, for example, slowed the expansion of several sport fish species in Canada (Alof et al., 2015). These fish were physically incapable of entering and persisting in some Canadian freshwater bodies where their thermal thresholds were met (Alof et al., 2015). Rusty crayfish, *Orconectes rusticus*, are also experiencing northward range expansion facilitated by warmer climates (Phillips et al., 2009). *O. rusticus* cannot persist in the Canadian Shield, however, due to lower dissolved calcium (Edwards et al., 2013). Any small populations that do encroach deplete much of the remaining calcium, further arresting their poleward expansion (Edwards et al., 2013). These examples underscore the necessity of comprehending the full suite of conditions that facilitate shifts in species distributions.

We see a potentially similar story in the mud fiddler crab, *Minuca (Uca) pugnax*, in the Gulf of Maine. Mud fiddlers are expanding their range north due to warming waters but could be slowed by sediment characteristics. In 2002, for the first time in its life history, Sanford et al. (2006) found *M. pugnax* north of Cape Cod, MA, its historic northward range barrier. The proposed mechanism is a warming Gulf of Maine (GoM), which warmed at twice the global mean in the last 40 years (Pershing et al., 2015). Sanford et al. (2006) demonstrated that *M. pugnax* larvae are highly sensitive to temperature; mud fiddler crab larval survival decreases exponentially as temperature falls below an 18°C threshold. As pelagic

planktonic larvae, *M. pugnax* regularly experienced temperatures below this threshold in the GoM for most of its life history.

Although individuals were found north of the Cape by 2002, no individuals made it north of Boston, MA, until discovery of a population in the Plum Island Estuary (PIE) in 2014 (Johnson, 2014). The likely mechanism was an exceptionally warm summer 2012, where sea surface temperatures regularly exceeded 18°C well into the season of mud fiddler crab dispersal. Since 2014, *M. pugnax* has continued to expand northward along the New England coastline. Individuals have been found as far north as Hampton, NH (Johnson, 2014) and southern Maine (D. S. Johnson, *unpublished*). In addition, Sanford et al. (2006) found good gene mixing and adult winter temperature tolerances by crabs found north of the Cape but south of Boston, suggesting limited genetic or thermal barriers to expansion now that they have established populations. Crab larvae from the range edge also grow faster than crabs from south of Cape Cod (Sanford, 2006). This tolerance along with the genetic variability of northern populations suggests that the crabs are adapting to overcome physical barriers.

As a burrowing species of crab, *M. pugnax* could be particularly sensitive to the characteristics of salt marsh sediment in its expanded versus native ranges. In particular, soil compaction or soil density of novel marshes would likely influence the capacity of crabs to burrow; i.e., more compact sediments are more difficult to burrow into. We see this in other burrowing crabs, such as *Helice tientsinensis* in China, which have higher burrow densities in softer and wetter sediments than harder and drier sediments that are more difficult to burrow into (Li et al., 2018). Fiddler crabs burrow to feed, avoid predation, and to mate (Bertness and Miller, 1984; Luk and Zajac, 2013); therefore an inability to burrow would severely impact the basic life history characteristics of *M. pugnax*. Roy et al. (*unpublished, in prep*) demonstrated that compaction in marshes in Nantucket (i.e., native range) were significantly lower (native range, 13.8+/-0.871psi) than PIE (expanded range, 30.2+/-1.53psi, $p<0.0001$). Vincent (2013) also reported soil strengths of more than 50 psi (3.51 kg/cm^2) in marshes along the GoM. In addition, fiddler crab densities are low in PIE (~1-6 burrows/m^2) relative to native marshes south of Cape Cod (~100-250 burrows/m^2) (Luk and Zajac, 2013; Johnson et al., 2019). The mechanism driving this low density could be due to reduced propagule pressure in expanded ranges, or some other physical barrier to survival and growth (e.g., difficult sediment to burrow into), or both.

To determine the relationship between physical substrate and crab burrowing ability in natal 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 capacity of fiddler crabs to burrow and influence the depth of fiddler crab burrows; 2) Are there differences in burrowing capacity and burrow depth between native (i.e., Nantucket) versus expanded (i.e., PIE) fiddler crabs; and 3) Does fiddler crab population density play a role in burrowing behavior? 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 that, for similar size crabs, both populations would be equally impacted by soil strength, indicating a role in higher soil strengths slowing range expansion, and no clear effect of density.

Methods:

To evaluate the impact of soil strength on fiddler crab burrowing behavior, we developed a controlled laboratory mesocosm experiment testing burrowing behavior of crabs from natal versus range expanded populations in standardized soils varying in levels of compaction. Each mesocosm consisted of saltwater saturated peat moss compressed with varying weights of sand (see Supplementary Methods Figure 1). We combined 10 gallons of dry organic peat moss with 4 gallons of saltwater with a salinity of 20% in a 66 L bin to create our peat/salt mixture. After thoroughly mixing the peat, we left the mixture to sit overnight to fully saturate before using it for the experiment. To acclimate the crabs to the saturated peat moss environment, crabs were housed in clear 66 L bins with separately made peat moss/saltwater mixture.

We tested the following sediment compaction levels: 0 psi (0 kg/cm^2), 10 psi (0.7 kg/cm^2), 20 psi (1.4 kg/cm^2), and 25 psi (1.8 kg/cm^2). These values represent the average range of soil strengths Roy et al. (*unpublished, in prep*) measured in salt marshes along the coast of Massachusetts in 2017 and 2018. We reached the desired soil strength for each treatment using a formula we developed to find the approximate amount of sand used (see Supplementary Methods and Supplementary Figure 1). We then placed the crabs in with the compacted soil for the trial (see Supplementary Methods Figure 2).

We tested two different crab densities to determine the effect of population density on burrowing behavior: one crab and three crabs per experimental chamber. Crabs were collected from Carolton Creek in Rowley, MA (42.745462, -70.836981) for the Plum Island trials and Folger's Marsh in Nantucket, MA (41.294653, -70.041979) for the Nantucket trials (see Supplementary Methods Figure 3), both at daytime low tides. Trials were conducted close to the location where they were collected, except for one Plum Island Estuary trial conducted at the University of Massachusetts-Boston. We conducted four replications for each density and soil strength treatment. Total n = 128, n = 64 from each location (PIE and Nantucket), and n = 16 per replicate with four soil strength treatments and two different crab densities (one and three crabs).

Before each trial, crabs were randomly selected, weighed, and sexed, and then were put separately into their experimental vessel for four hours. After removing the crab(s), we counted burrows in each mesocosm, measured soil strength, and took plaster casts of each burrow found (see Figure 1). We determined burrow volume using water displacement by placing the cast in a graduated cylinder. Crabs were returned where they were collected after the experiment was completed.

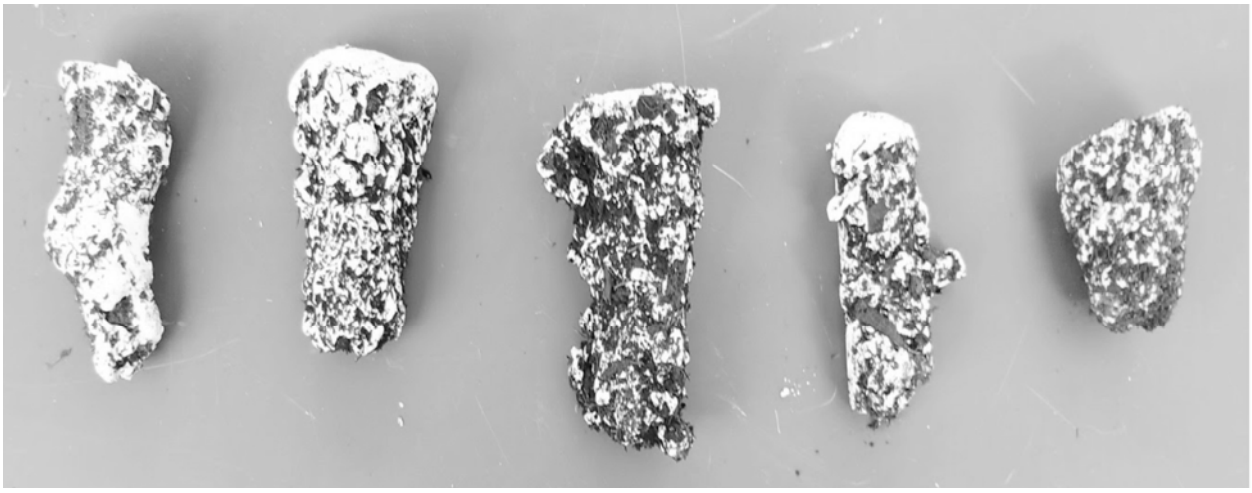

Figure 1: Example fiddler crab burrow casts. These were cleaned with a gentle toothbrush and placed into a graduated cylinder to find burrow volume.

To determine how soil strength influenced the probability of crab burrowing, we used binomial logistic regression (generalized linear model with logit link) with soil strength, crab natal location, their interaction, and crab mass as predictors and burrowing (yes/no) as a response. We fit separate models for the one and three crab experiments. To assess if soil strength 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. Note, using a gaussian error with an identity or log link produced the same results, but often led to impossible fitted values. 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 (Florian Hartig 2020). Code for all analyses can be found at https://github.com/richw1w/Pugnax_SS_Analysis.git

Results:

Broadly, our results show that crabs collected in the Plum Island Estuary (expanded range) display better burrowing performance than Nantucket (native range) crabs. In our one crab trials, Nantucket fiddler crabs were less likely to burrow at high soil strengths, whereas PIE fiddler crabs burrowed at all soil strengths (interaction effect, Figure 2A, Table 1, Supp. Table 1). Nantucket fiddlers did not dig at soil compaction levels past 10 psi, even though PIE crabs were able to burrow in all soil strengths (see Figure 3A). In three crab trials, crabs were less likely to burrow at higher soil strengths; PIE crabs in general have a higher probability of burrowing at all soil strengths (Table 1, Figure 2B) and, again, were the only crabs to burrow at >10 psi. Neither soil strength, site, their interaction, or any other predictor affected burrow volume of those crabs that did burrow (Table 2, Figure 3).

Table 1: Analysis of Deviance results from probability of crab burrowing model for both the one crab trial and three crab trial.

	Term	LR Chisq	DF	P-Value
One Crab	Soil Strength Before	2.2851	1	0.131
	Site	0.2401	1	0.624
	Crab Mass	1.4235	1	0.233
	Soil Strength Before:Site	6.5353	1	0.011
Three Crabs	Soil Strength Before	16.1831	1	< 0.001
	Site	9.8093	1	0.002
	Crab Mass	0.0093	1	0.923
	Soil Strength Before:Site	0.0823	1	0.774

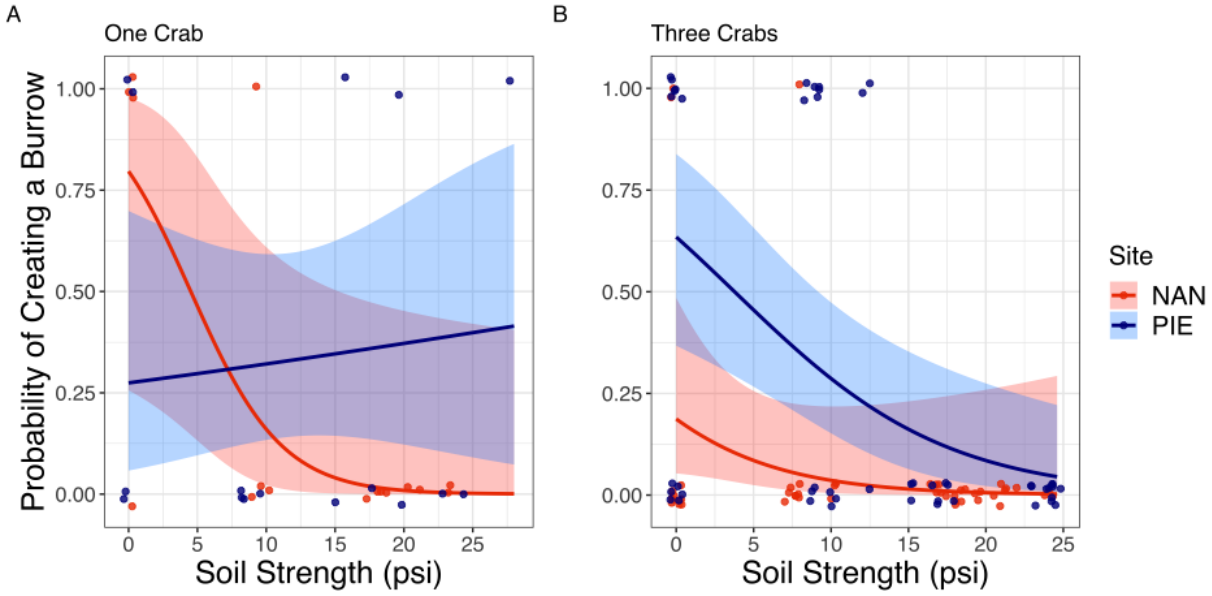

Figure 2: PIE crabs are more likely to burrow than those from Nantucket. The logistic relationship showing how soil strength affects the likelihood of the crab burrowing in trials with (A) one crab or (B) three crabs. Red represents Nantucket crab data, and blue represents PIE crab data. Curves are from fit models with 95% Confidence intervals. Points represent 1 = burrow or 0 = no burrow. Points are jittered in order to see overlapping data points and may not align exactly with the true data.

Table 2: Analysis of Deviance results from probability of crab burrow volume model for both the one crab trial and three crab trial.

	Term	LR Chisq	DF	P-Value
One Crab	Soil Strength Before	0.9003	1	0.343
	Site	1.0727	1	0.3
	Crab Mass	0.1517	1	0.697
	Soil Strength Before:Site	0.3063	1	0.58
Three Crabs	Soil Strength Before	0.0645	1	0.799
	Site	0.089	1	0.766
	Crab Mass	0.187	1	0.665
	Soil Strength Before:Site	2.9625	1	0.085

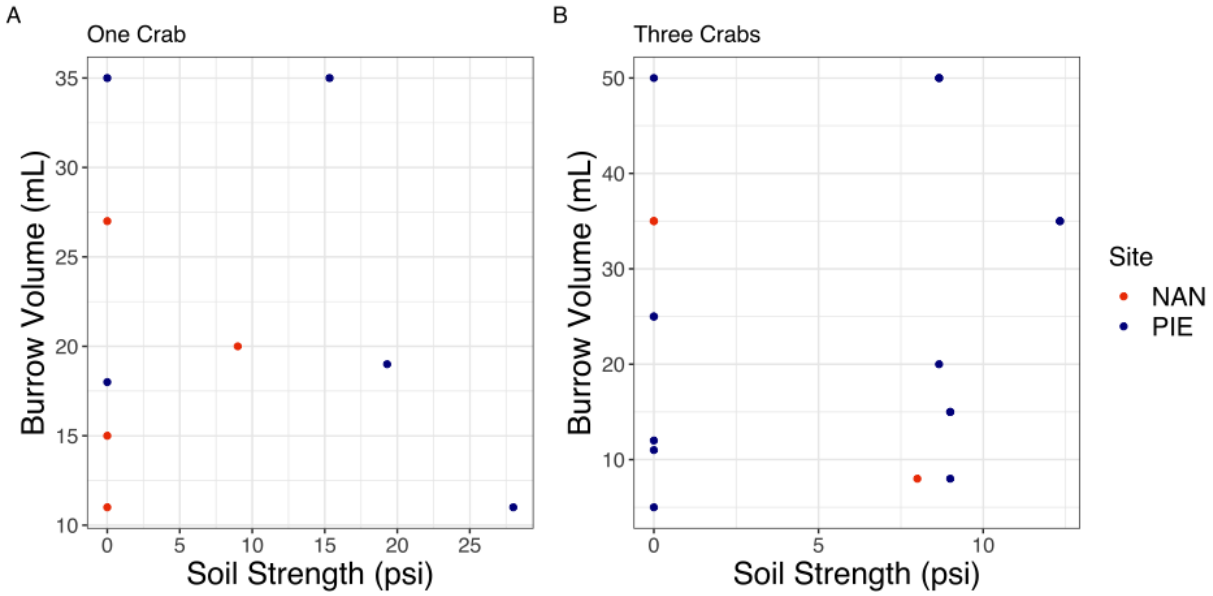

Figure 3: Nothing affects burrow volume in our experiment once a crab chooses to burrow. Data shown of crab burrow volumes in trials with (A) one crab or (B) three crabs. Red represents Nantucket crab data, and blue represents PIE crab data. No curves are shown as no explanatory variables explained variability in the data.

Discussion:

In contrast to our initial expectations, our experiment shows that *M. pugnax* have likely changed their burrowing behaviors as they have expanded their ranges. We show that mud fiddlers living north of the Cape (e.g., PIE) are more capable of burrowing in compact soils than crabs living south of Cape Cod (e.g., Nantucket) (see Figure 2), less than 200 miles away (see Supplementary Methods Figure 3). In our trials with one crab per experimental chamber, PIE crabs were able to burrow in more compact soils than Nantucket (NAN) crabs (see Figure 3A). No Nantucket fiddler crabs were able to dig in soil strengths greater than 10 psi, however Plum Island Estuary crabs were able to dig in our densest soil treatment, 25 psi (see Figure 2A). These are directly comparable to the soil strengths that each population is experiencing in the environment from which they were collected (Roy et al.*, unpublished, in prep*). Even in trials with three crabs per chamber, PIE crabs were more likely to burrow than Nantucket crabs in all soil strength treatments (see Figure 3B). The difference between burrowing abilities in the two populations suggest that PIE crabs are stronger and able to dig in higher soil strengths. Although our results are from crabs originating in only one natal and one range expanded population, given soil strength differences south versus north of Cape Cod, we suggest this represents a more general trend. Our results do not speak to whether this is inherent genetic variation in the two populations driven by selection for stronger crabs or phenotypic plasticity of crabs settling in marshes with harder soils. Regardless, our results show that processes other than temperature have influenced this species as it has expanded its range.

Further, we suggest that although stronger soil compactions north of Cape Cod could be stymieing the northern range expansion of mud fiddler crabs, they are clearly not stopping it. Ranges are determined by many biotic and abiotic factors (Alof et al., 2015; Burrows et al., 2014; Cassini et al., 2013; Geber, 2008; Jackson, 2009). In order to colonize new territory, they must overcome some of those barriers. We know *M. pugnax* is expanding its range (Johnson, 2014) given the populations of *M. pugax* persisting north of Cape Cod, MA. This expansion is likely driven by the warming waters of the Gulf of Maine (GoM) (Sanford, 2006); however, their densities are lower north of Cape Cod (Johnson, 2014). Other factors, such as soil compaction, could be the reason the mud fiddler fails to colonize northern New England marshes in the same densities as in their native habitat. Soil strengths between 0 and 15 psi (1.1 kg/cm^2) (Roy et al.*, unpublished, in prep*) are more representative of salt marshes south of the Cape,

where the mud fiddler is native; whereas, the marshes of along the GoM can reach much greater compactions, more than 50 psi (3.51 kg/cm^2) (Vincent, 2013).

The mechanism behind the variation between the two populations remains unclear. Our work shows that soils in marshes of the GoM are penetrable by mud fiddlers currently found there, but in many instances might not be so for crabs from south of Cape Cod. This difference could be due to size, as Johnson et al. (2019) determined that PIE crabs are larger than southern counterparts; however, we controlled for size in our analyses and, although the largest crabs in our trials came from PIE, the majority were of comparable size (see Supplementary Results Figure 1). This suggests then that some other trait (either physically or behaviorally) influences the ability for PIE crabs to burrow in their expanded range. Our observed patterns could be due to selection on newly settled crabs coming from southern populations for only those with the ability to burrow in harder northern soils. In contrast, harder soils could lead to changes in crab phenotypes through time if these traits are plastic. Indeed, in some crab species claw morphology is even linked to water temperature (Baldridge and Smith, 2008). Both phenotypic plasticity and adaptation aid in colonization for many invasive species, which provides a compelling baseline to understand species range expansions (Smith, 2009, Stapely et al., 2015). Populations of *Minuca pugnax* in the Gulf of Maine may possess the requirements for adaptation (Sakai et al., 2001), including selective pressure (suggested by this experiment) and genetic variability (Sanford, 2006). However future studies regarding changes in population genetics should attempt to elucidate the specific mechanism driving this better burrowing capacity in PIE versus Nantucket fiddler crabs.

M. pugnax burrows affect the productivity, biogeochemistry, and sediment structure of their native habitat salt marshes, and so could similarly do so in ecosystems that they are expanding into (Bertness et al., 1985; Smith and Tyrrell, 2012; Johnson, 2014). *M. pugnax* can increase soil drainage, soil oxidation reduction potential, and *in situ* decomposition rates (Bertness *et al.*, 1985, Thomas and Blum, 2010) in both the low and intermediate marsh. Degradation or loss of salt marsh area is already exacerbated by climate change and sea level rise (Deegan et al., 2012) in PIE and other marshes north of Cape Cod. Crab burrows negatively affect the belowground growth of the soil stabilizing *S. alterniflora* (Thomas and Blum, 2010), making these low and intermediate sections of marsh the most susceptible to erosion. Bioengineers in novel habitats (such as *M. pugnax*) may cause additional unforeseen changes to the

structure and function of PIE and other northern salt marshes. Fortunately, our results suggest that effects in novel habitat may be predictive.

PIE crabs were capable of burrowing in harder soils, although they did not exhibit any different behavior in burrow volume once they did dig. Given that they were more likely to dig, we expected the burrowing fiddlers from PIE to displace more soil than those from Nantucket, and thus potentially affect their habitat more than Nantucket crabs. This was not the case; the burrow volume from the two populations of crabs were the same (see Figure 3). Absolute changes in soil strength due to crabs are thus likely to be similar to those in more Southern habitats. Whether the softening of harder northern marshes has comparable effects on the ecosystem relative to fiddler-induced softening of marshes south of Cape Cod remains to be seen.

Range expansions in response to global temperature increase are well documented (Davis and Shaw, 2001; Jackson et al., 2009, Loarie et al., 2009). The effect of other (sometimes subtle) physical habitat characteristics on range expanding species is not as widely explored (Brown and Vellend, 2014; Spence and Tingley, 2020). The range expansion of *Minuca pugnax* provides a wide variety of novel opportunities to study range expansions, adaptation and plasticity, and ecosystem engineering in a single species. Further, understanding if *M. pugnax* behaves as an invasive species could further clarify what impacts these range expanding crabs will have on marshes in along the Gulf of Maine through time.

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