

# Intraspecific diversity at two trophic levels influences plant–herbivore interactions

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**Citation:** Noto, A. E., and A. R. Hughes. 2020. Intraspecific diversity at two trophic levels influences plant–herbivore interactions. *Ecosphere* 11(5):e03121. 10.1002/ecs2.3121

**Abstract.** Diversity within species can have community-level effects similar in magnitude to those of species diversity. Intraspecific diversity in producers and consumers has separately been shown to affect trophic interactions, yet we have little understanding of how variation at these two levels could simultaneously affect trophic interactions. Salt marshes dominated by *Spartina alterniflora* are an ideal system in which to ask this question as this plant exhibits substantial genetically based trait variation. Further, herbivores can have sizable impacts on *Spartina*, but the impact of herbivore trait variation is not well understood. We conducted an experiment in a Massachusetts salt marsh to determine how herbivorous crab (*Sesarma reticulatum*) size diversity and *Spartina* genotypic diversity affect the plant community. Herbivore effects on plant traits varied by herbivore size, with large crabs generally having stronger impacts on plants. At times, the effect of small crabs on plant traits depended on plant genotypic diversity. The effects of crab size diversity (i.e., small and large crabs combined) were most often predicted by the independent effects of each size class, though there were synergistic effects on stem density, flowering stems, and mean stem height. Finally, we tested whether herbivore size or size diversity could have reciprocal effects on plant genotypic diversity. Small- and mixed-crab treatments promoted plant genotypic richness, whereas large crabs did not. Our results demonstrate that intraspecific diversity at multiple trophic levels can have simultaneous and sometimes interactive effects on species interactions, highlighting the importance of variation within species for understanding species interactions and community processes.

**Key words:** consumer; eco-evolutionary feedbacks; genetic variation; herbivory; plant–herbivore interactions; salt marsh.

**Received** 9 December 2019; revised 7 February 2020; accepted 11 February 2020; final version received 9 March 2020.  
Corresponding Editor: Jonathan A. Walter.

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## INTRODUCTION

The community-level importance of diversity within species has gained increasing recognition, with compelling examples of intraspecific diversity affecting whole community properties in a range of ecosystems (reviewed in Hughes et al. 2008, Bolnick et al. 2011, Des Roches et al. 2018). Intraspecific diversity can increase resistance and resilience to herbivory or environmental stress (Hughes and Stachowicz 2004, 2011, Reusch et al. 2005), affect ecosystem processes such as

productivity or decomposition (Schweitzer et al. 2004, 2005, Crutsinger et al. 2006, 2009), and determine the number and strength of species interactions (Bolnick et al. 2011). The effects of intraspecific diversity on community processes can even equal those of species diversity or species presence or absence (Cook-Patton et al. 2011, Crawford and Rudgers 2013, Des Roches et al. 2018). These community-wide effects occur at least in part because intraspecific variation alters species interactions, so to better understand the mechanisms by which communities are

impacted, it is necessary to investigate how intraspecific diversity affects particular species interactions. Consumer–resource interactions are a logical starting point, as many previously documented effects of intraspecific diversity within a single trophic level occurred in response to trophic interactions.

Diversity within consumer species can change consumer–resource interactions. For example, intraspecific variation in migratory or feeding behavior of anadromous fish can alter zooplankton prey populations, primary production, and even the strength of trophic cascades (Post et al. 2008, Palkovacs and Post 2009, Harmon et al. 2009). Similarly, size or stage differences within a consumer species can lead to distinct effects on resource species and cascading effects on the community (Rudolf and Rasmussen 2013, Atkins et al. 2015). Size diversity (i.e., the number of size classes) in consumers is less well studied, but it has been shown to lead to higher resource mortality in some cases (Rudolf 2012) though not in others (Toscano and Griffen 2012). One explanation for this discrepancy may be that consumer size diversity only differentially impacts resource populations when it is very strongly related to consumer diet breadth (Ingram et al. 2011). Alternatively, consumer size diversity may decrease resource mortality in cases when there is more interference (e.g., cannibalism) among size classes than within them (Griffin and Silliman 2018). Thus, while intraspecific trait differences among individual consumers often lead to distinct impacts, it remains unclear whether and how intraspecific trait diversity affects resource populations.

Similarly, there is evidence that diversity in or among resource species can determine their responses to and effects on consumers. A meta-analysis of marine experiments found that species diversity in resources generally dampened the effects of consumers (Edwards et al. 2010). Intraspecific diversity in resource (primarily plant) species has similar effects. For instance, more genetically diverse stands of a single species can be more resistant to attack by consumers than lower diversity stands (Hughes and Stachowicz 2004, Abdala-Roberts et al. 2015). Intraspecific plant diversity can even have reciprocal effects on consumers: Diverse plants can decrease consumer performance and survival

(Grettenberger and Tooker 2016, Wetzel et al. 2018) or support insect communities with greater species richness (Johnson and Agrawal 2005, Crutsinger et al. 2006, Johnson et al. 2006). While these studies often measure resource intraspecific diversity in terms of genotypes rather than traits, genotypic diversity has ecologically relevant effects (Bolnick et al. 2011) and genotypes vary in traits, including those related to palatability and defense (Tomas et al. 2011, Zerebecki et al. 2017), such that genotypic diversity is related to (Abbott et al. 2017) and can be a good proxy for overall trait diversity.

Given that various forms of intraspecific diversity at both consumer and resource levels can affect the other, we might expect there to be some kind of feedback or interaction between them. For instance, plant intraspecific diversity only affected plant-detritus consumption in an eelgrass meadow when there was species diversity among consumers (Reynolds et al. 2018), suggesting that intraspecific diversity at multiple trophic levels could also interact. However, most studies focus only on the impact of intraspecific diversity at one trophic level, although some also consider its effect on abundance or species diversity at another (Johnson and Agrawal 2005, Crutsinger et al. 2006, Hughes et al. 2010, Rudolf 2012, Toscano and Griffen 2012). To advance the realism of this field, it is necessary to test the influence of intraspecific diversity at both trophic levels simultaneously to see how they independently and interactively affect resource production, and potentially how they feed back to influence intraspecific diversity at either level.

In this study, we sought to determine how intraspecific diversity at two trophic levels affects consumptive interactions and whether feedbacks exist between them. This question is particularly relevant in communities dominated by a single plant species, as intraspecific diversity is likely to be particularly important in that species (Whitham et al. 2003, Reusch and Hughes 2006). Further, any changes in intraspecific diversity due to consumption are likely to persist through time in plant species with primarily vegetative reproduction, including many seagrasses, grasses in terrestrial grasslands or salt marshes, and even some shrubs and trees such as aspens. We established an experiment in a U.S. Atlantic coast salt marsh dominated by *Spartina alterniflora*, a grass

species that can reproduce both vegetatively and sexually and is consumed by herbivorous crabs, *Sesarma reticulatum* (Seiple 1979, Seiple and Salmon 1982). Specifically, we addressed the following questions: (1) Does herbivore size or size diversity determine herbivore effects on the plant community? (2) Does plant genotypic diversity influence herbivore effects on plants? (3) Does diversity at these two levels feed back to affect plant intraspecific diversity? We used a series of herbivore enclosures across a gradient of plant genotypic diversity to address these questions.

## METHODS

### Study system

We conducted a field enclosure experiment in a salt marsh in Cape Cod National Seashore, Massachusetts, USA. The site faced onto Wellfleet Harbor, a protected bay off of Cape Cod Bay, and was dominated by *S. alterniflora* (hereafter *Spartina*) with a narrower high marsh zone dominated by *Spartina patens*. *Spartina* genotypes have been shown to differ in their traits (Zerbe et al. 2017), suggesting that genotypic diversity is indicative of trait diversity in *Spartina*. In marshes ranging from southern New England to Florida (Abele 1973), *Spartina* is eaten by *S. reticulatum*, an herbivorous crab known to consume *Spartina* leaves and rhizomes. *Sesarma* has been identified as a potential driver of salt marsh diebacks in several New England marshes, including on Cape Cod (Holdredge et al. 2008, Altieri et al. 2012). While *Sesarma* are common in our study site, we did not observe any signs of dieback over the course of this experiment in or around our enclosures.

### Crab diversity treatments

We tested four crab size treatments: large *Sesarma* only (2 crabs per plot), small *Sesarma* only (4 crabs per plot), large and small *Sesarma* (1 large and 2 small), and no *Sesarma*. We used a substitutive design as we were mainly interested in the interactive effects of *Sesarma* size classes at similar densities, rather than in the effects of changing *Sesarma* densities (Byrnes and Stachowicz 2009). Based on *Sesarma* length–weight relationships (Appendix S1: Fig. S1) and crab sizes in each treatment, we found that these densities resulted in a similar level of total crab biomass

across all plots ( $P = 0.48$ ). We chose experimental densities based on past experiments that indicated moderate crab effects at this level (Angelini et al. 2018).

In May 2018, we haphazardly selected 40  $1 \times 1$  m plots separated by at least 3 m in the *Spartina* zone. Each plot was then enclosed by a cage made of coated hardware cloth with 1.25-cm mesh, small enough that *Sesarma* larger than 15 mm in carapace width could not fit through the holes (see similar methods in Holdredge et al. 2008, Bertness et al. 2014). The cages were buried to at least 30 cm depth to ensure that crabs could not enter or exit enclosures by burrowing beneath them. Horizontal passageways in *S. reticulatum* burrows are typically at a depth of 10–15 cm (Seiple and Salmon 1982), so this cage depth was sufficient to contain the majority of crabs. Cages extended 70 cm above the soil surface and were topped with 15 cm of aluminum flashing to ensure that crabs also could not climb out. Plots were split into statistical blocks based on genotypic richness (see *Genotypic diversity* below), and each plot within a block was randomly assigned to one of the four crab size treatments such that crab treatments were distributed across similar gradients of genotypic richness.

We collected *Sesarma* for our treatments using a combination of pitfall traps and hand collection. We measured the carapace width of all *Sesarma* we collected and used that size distribution to identify size classes: Large *Sesarma* were classified as those greater than 24 mm in width (mean 25.4 mm, SD 1.00 mm) whereas small *Sesarma* were between 17 and 24 mm (mean 20.7 mm, SD 1.77 mm). These mean sizes correspond to mean weights of 12.3 g (SD 2.15 g) and 6.02 g (SD 1.59 g), respectively, predicted from a length–weight regression curve calculated from field data (Appendix S1: Fig. S1). This division was representative of the distribution of sizes in the field, as we found few crabs between 22.5 and 24 mm during initial sampling, although we later found some crabs that fell in that gap. A *Sesarma* study in North Carolina found a maximum size of 26.6 mm and mean of roughly 19 mm (Seiple 1979), suggesting that our size classes are good approximations of large and medium *Sesarma*. In addition, we often found large crabs near the edges of vegetated areas

while small crabs tended to be further from the edges, suggesting that our single crab size treatments are representative of ecologically relevant spatial distributions. *Sesarma* smaller than 17 mm were omitted from the experiment because they were small enough to pass through cages. Because they were not manipulated, their presence was likely consistent across plots, but this could be a source of error depending how realistic that assumption is. Thus, the two size classes used in this study were representative of the variation we observed in the field that we could effectively manipulate (i.e., that were not too small to be enclosed). Additional work using more size classes would be required to examine the shape of the relationship between diversity and plant responses.

After cages were installed, we deployed one pitfall trap in each plot for at least two consecutive days or until no *Sesarma* large enough to be included in the experiment were caught. Two weeks later, crabs for the corresponding treatment were added to each plot. We did not directly observe any evidence of crab death, predation, or escape, but there were few signs of crab effects after the initial four weeks of the experiment. As a result, and because initial experimental densities were low relative to previously reported natural densities (as high as 25 per m<sup>2</sup>; Seiple 1979), we supplemented crabs in each plot every four weeks: one big crab was added to all big-crab plots, two small crabs added to all small-crab plots, and one big and one small crab were added to all mixed-crab plots. Our crab additions in mixed plots were skewed slightly toward big crabs compared to initial treatments because we had few sightings of big crabs in mixed-crab plots early in the experiment, and we were concerned that they were more capable of escaping than small crabs. We then remained consistent in our crab additions throughout the experiment. Our treatments were well within natural densities even if there were 100% survival over the course of the experiment. In addition, we did not see die-off-like effects in our plots, suggesting that our densities were not artificially high.

#### Genotypic diversity

To determine the genotypic diversity of *Spartina* in each plot, we collected leaves from each

plot at both the beginning and end of the experiment. At the beginning, we collected the second-youngest leaf from 30 plants in half of the plots and 10 plants from the other half to determine initial genotypic richness and to evaluate whether 10 samples were sufficient to accurately assess it. Samples were wiped clean, preserved on silica gel, and brought back to the laboratory to be genotyped. We then created a rarefaction curve using samples of 5–20 individuals. By 20 samples, rarefaction curves were generally beginning to saturate, so 20 samples were collected from each plot at the end of the experiment and genotyped, leading to a larger sample size at the end of the experiment than at the beginning. Because not all slopes had fully saturated, final numbers may be a slight underestimate of diversity in high genotypic richness plots.

DNA was extracted from the silica-preserved plant samples with Omega Bio-Tek E-Z 96 Plant DNA Kit (Omega Bio-Tek, Norcross, Georgia, USA) following the manufacturers' protocol. Extracted DNA was stored at –20°C. We amplified 12 previously characterized microsatellite loci (SPAR.02, SPAR.03, SPAR.05, SPAR.07, SPAR.08, SPAR.09, SPAR.10 from Blum et al. 2004, SPAR.14, SPAR.16, SPAR.17, SPAR.21, SPAR.34 from Sloop et al. 2005). Amplification was performed in a Bio-Rad T100 Thermocycler (Bio-Rad, Hercules, California, USA) using the following program: 5 min at 95°C; 28 cycles of 30 s at 95°C, 90 s at 60°C, 30 s at 72°C; 30 min at 60°C. Samples were submitted to the Yale DNA Sequencing Facility. Peaks at each locus were visualized using the GeneMarker software (v. 2.6; SoftGenetics, State College, Pennsylvania, USA) and manually scored. Using allele frequencies at each locus, individuals were assigned to genotypes and genotypic richness was calculated for each plot.

#### Plant measurements

Plants in all plots were measured two weeks after cage installation, one day before crabs were added. They were then measured once every four weeks for the duration of the experiment. We measured stem density in a 0.25 × 0.25 m subplot 15 cm away from a seaward corner of the plot to avoid potential edge effects from the cages. We assessed average stem height by measuring the height of eight haphazardly chosen stems in the plot (excluding new stems less than

10 cm). There were no significant differences in either metric among treatments at the beginning of the experiment. Beginning in the eighth week of the experiment (August), we also measured the height of the tallest stem in each plot as well as the number of flowering stems in the same  $0.25 \times 0.25$  m subplot in each plot.

At the end of 16 weeks (late October), we harvested above and belowground biomass. Aboveground biomass was collected from a  $10 \times 10$  cm quadrat in the center of the plot by clipping plants at the soil surface. Belowground biomass was harvested in the same location using a 5.5 cm diameter corer, 20–25 cm deep so that all roots were included in the core. When the center of the plot was bare, we shifted quadrats slightly so that they would include biomass that was more representative of vegetated portions of the plot. Aboveground biomass was wiped clean and dried in a drying oven at 60°C for 72 h. Belowground biomass was rinsed and dried at the same temperature to constant weight, at least 72 h.

#### *Environmental measurements*

In the spring following the end of the experiment, we also measured several environmental variables that could be related to genotypic richness (Hughes and Lotterhos 2014) or plant growth (Pearcy and Ustin 1984, Howard 2009). Elevation above mean lower low water was estimated by measuring water levels in each plot at a known time and calculating elevations based on NOAA elevation data and offsets. Porewater salinity was measured in holes made in each plot, and sediment organic matter was measured based on  $1.5 \times 2$  cm soil cores which were dried and combusted in the laboratory.

#### *Data analysis*

We used linear mixed-effects models to determine how both crab diversity treatments and genotypic diversity affected most plant responses to herbivory. All models included initial plot genotypic richness, crab size treatment, time, and their interactions as fixed effects and plot as a random effect to account for resampling over time. Both measures of height initially varied among plots, so we analyzed change in height instead of raw height. We then used likelihood ratio tests to determine which model best fit the

data. Biomass measures were only collected once and therefore were analyzed using fixed-effects models without a time term. Genotypic richness was treated as a continuous variable (i.e., ANCOVA) rather than categorical, as we wanted to understand the overall pattern between genotypic diversity and plant measures, not just whether each level of diversity differed from the others. We omitted one plot that contained six genotypes as it extended the range of one crab size treatment group beyond the others, violating the ANCOVA assumption that the covariate was independent of treatments.

To determine whether plots with a mix of large and small crabs differed from additive expectations based on the performance of large and small crabs alone, we calculated expected values as the average of large- and small-crab treatments (Byrnes and Stachowicz 2009). To account for genotypic diversity, we calculated mean values for large- and small-crab treatments within each level of initial genotypic diversity at each point in time and used those means to calculate expected values at each level of diversity. We then used mixed-effects models to see whether estimates of each plant variable differed among observed and expected values, including plot as a random effect.

We also investigated whether crab size or diversity could feed back to affect genotypic diversity. Analyses of changes in genotypic richness and diversity over time were complicated by differences in sample sizes at the beginning and end of the experiment. Thus, we calculated rarefied genotypic richness for the smallest sample sizes we had ( $n = 10$ ) using the vegan package in R (Oksanen et al. 2018). We used linear models to test whether rarefied richness changed over time or in relation to crab size treatments. To determine whether richness in crab treatments differed from no-crab plots, we calculated effect sizes and their 95% confidence intervals based on differences between no-crab controls and each crab treatment at the end of the experiment.

For other measures of diversity, there is no equivalent to rarefaction so we used permutation and resampling methods to analyze changes in those measures over time and in response to crab treatments. We calculated evenness and Shannon–Wiener diversity in the vegan package in R (Oksanen et al. 2018). We then did permutation

tests randomly reassigning diversity values to crab treatments and dates to see whether the patterns in our data differed from random. We corroborated these results by calculating evenness and Shannon–Wiener diversity using a bootstrapping method in which we sampled 20 times with replacement from the genotypes in each plot at each time point to make sample sizes equal. The results of both methods were consistent. To account for different sample sizes in rank–abundance curves, we used a similar approach and bootstrapped the genotypes in each crab size treatment at the beginning and end of the experiment 100 times, using the average to build rank–abundance curves for each crab size treatment and time point. Because genotypic richness likely affects rank–abundance patterns, we did this only for plots initially containing at least four genotypes.

Finally, we used linear regression to determine relationships between the environment and genotypic richness. All analyses were conducted in R v.3.5.0 (R Core Team 2018).

## RESULTS

Crab size, crab size diversity, and plant genotypic diversity each influenced some aspect of the plant community. Whether crab size or plant genotypic diversity had a stronger impact varied depending on the plant response of interest (Table 1). Genotypic diversity was not correlated with porewater salinity or sediment organic matter, but it was weakly correlated with elevation ( $R^2 = 0.20$ ,  $P = 0.005$ ; Appendix S1: Fig. S2).

Crab size was an important independent determinant of several plant community responses to herbivory. Stem density was reduced in plots with crabs in a way that changed over time (Size  $\times$  Time  $P < 0.01$ ,  $\chi^2 = 12.7$ ; Fig. 1a). After the first eight weeks, plots with big crabs or mixed crabs generally had fewer stems than control plots. This difference was significant in the final week of the experiment (none vs. mixed  $P = 0.032$ ; none vs. big  $P = 0.057$ ), while plots with small crabs were not significantly different from control plots, despite a similar trend toward reduction in stem density in those plots (Fig. 1a). Importantly, an end-of-season increase in stem density occurred in control plots in the final sampling period, but it did not occur in any plots

with crabs (Fig. 1a). Flowering stems were also affected by crab size treatment (Size  $\times$  Time  $P = 0.010$ ,  $\chi^2 = 11.6$ ): Plots with big crabs flowered earlier and more than other plots, whereas plots with small crabs flowered less than other plots (Fig. 1b). Over time, the number of flowering stems converged across all size treatments (Fig. 1b). In addition, the ratio of flowering to vegetative stems was higher in plots with big crabs compared to those with small ( $P = 0.013$ ) or no crabs ( $P = 0.0037$ ; Fig. 2), indicating that big crabs led to more flowering stems relative to vegetative stems compared to small- or no-crab treatments (Size  $P = 0.045$ ,  $\chi^2 = 8.1$ ).

The effects of mixed large and small crabs tended to fall between those of either size class alone, consistent with additive expectations. However, there were some instances of synergistic effects in mixed-crab plots. Stem density ( $P < 0.01$ ,  $F_{1,77} = 10.8$ ), flowering stems ( $P = 0.026$ ,  $F_{1,57} = 5.2$ ), and mean height ( $P = 0.040$ ,  $F_{1,77} = 4.3$ ) were less than expected in plots with mixed crabs compared to the additive effect of small and large crabs (Fig. 3). Thus, mixed crabs affected at least some aspects of the plant community more strongly than expected based on small or large crabs alone.

Genotypic diversity alone affected the change in maximum stem height. The change in maximum stem height was marginally greater in plots with high initial genotypic diversity (Size  $\times$  Genotype  $P = 0.063$ ,  $\chi^2 = 3.46$ ; Fig. 4b). Mean height was not affected significantly by genotypic diversity, only by time ( $P < 0.001$ ,  $\chi^2 = 139.3$ ; Appendix S1: Fig. S3).

Crab size and initial plant genotypic diversity interactively affected aboveground biomass ( $P = 0.05$ ,  $F_{3,20} = 3.0$ ) when belowground biomass was a covariate in the model. High-diversity plots allocated more energy to aboveground than belowground biomass in the presence of small crabs, whereas in other crab treatments, there was no clear effect of plant genotypic diversity on allocation to aboveground biomass (Fig. 4a). There were no significant differences due to crab size or genotypic diversity in total biomass or belowground biomass alone (Appendix S1: Fig. S4) and only a marginal interactive effect of genotypic diversity and crab size on aboveground biomass alone ( $P = 0.076$ ,  $F_{3,28} = 2.5$ ), with slightly higher aboveground

Table 1. Coefficient estimates from mixed-effects models.

| Parameter         | Change in<br>max ht    | Change in<br>mean ht | Stem<br>density   | Flowering<br>stems | Flowering<br>vegetative stems | Aboveground<br>biomass     | Belowground<br>biomass | Total<br>biomass |
|-------------------|------------------------|----------------------|-------------------|--------------------|-------------------------------|----------------------------|------------------------|------------------|
| G <sup>‡</sup>    | 1.1 (4.1) <sup>†</sup> | −2.7 (3.8)           | −1.7<br>(2.7)     | −1.3 (1.1)         | 0.032 (0.059)                 | −0.21 (0.15)               | −0.99 (2.3)            | −1.4<br>(2.5)    |
| SMix <sup>§</sup> | −0.94<br>(19.4)        | −8.3 (17.8)          | −16.6<br>(12.4)   | −6.2 (5.1)*        | 0.042 (0.28)*                 | −0.81 (0.70)               | −4.8 (11.0)            | −7.3<br>(11.7)   |
| SNone             | −22.1<br>(21.0)        | −1.7 (19.2)          | −11.1<br>(13.5)   | −3.3 (5.6)*        | 0.084 (0.30)*                 | 0.38 (0.77)                | 11.1 (11.9)            | 12.9<br>(12.7)   |
| SSmall            | −13.6<br>(19.9)        | −9.8 (18.2)          | −11.6<br>(12.8)   | −0.11 (5.3)<br>*   | −0.14 (0.28)*                 | −0.89 (0.70)               | 6.9 (11.3)             | 5.5<br>(12.1)    |
| T <sup>¶</sup>    | 0.20 (0.66)<br>***     | 2.8 (0.78)***        | −1.4<br>(0.59)*** | −0.37<br>(0.24)    | 0.0023 (0.015)                |                            |                        |                  |
| G:SMix            | 0.91 (5.9)             | 0.92 (5.4)           | 2.2 (3.8)         | 0.66 (1.6)         | −0.050 (0.084)                | 0.35 (0.23) <sup>†</sup>   | 1.1 (3.3)              | 2.1 (3.6)        |
| G:SNone           | 9.7 (6.3)              | −0.37 (5.7)          | 1.7 (4.0)         | −0.60 (1.7)        | −0.064 (0.089)                | −0.066 (0.24) <sup>†</sup> | −3.3 (3.5)             | −3.5<br>(3.8)    |
| G:SSmall          | 3.8 (6.2)              | 2.1 (5.7)            | 0.72<br>(4.0)     | 1.5 (1.6)          | −0.016 (0.088)                | 0.48 (0.22) <sup>†</sup>   | −2.0 (3.5)             | −0.20<br>(3.7)   |
| G:T               | −0.25<br>(0.19)        | −0.15 (0.23)         | 0.017<br>(0.17)   | 0.022<br>(0.072)   | −0.0030 (0.0044)              |                            |                        |                  |
| SMix:T            | −1.1 (0.91)            | −0.44 (1.1)          | 0.60<br>(0.82)**  | 0.24<br>(0.072)**  | −0.0057 (0.020)               |                            |                        |                  |
| SNone:T           | 0.19 (0.98)            | −0.86 (1.2)          | 1.8<br>(0.88)**   | 0.13<br>(0.037)**  | −0.017 (0.022)                |                            |                        |                  |
| SSmall:T          | −0.49<br>(0.93)        | −0.89 (1.1)          | 0.48<br>(0.84)**  | 0.037<br>(0.035)** | −0.0030 (0.021)               |                            |                        |                  |
| G:SMix:T          | 0.45 (0.28)            | 0.19 (0.33)          | −0.034<br>(0.25)  | >0.001<br>(0.10)   | 0.0034 (0.0062)               |                            |                        |                  |
| G:SNone:<br>T     | −0.072<br>(0.29)       | 0.21 (0.35)          | −0.23<br>(0.26)   | 0.074<br>(0.11)    | 0.0051 (0.0066)               |                            |                        |                  |
| G:SSmall:<br>T    | 0.25 (0.29)            | 0.31 (0.34)          | 0.16<br>(0.26)    | 0.028<br>(0.11)    | 0.0031 (0.0065)               |                            |                        |                  |

Notes: Biomass was collected at a single time point so biomass models did not include a time effect. Significance is shown for the overall effect of that variable (not the specific comparison).

<sup>†</sup>  $P < 0.08$ , \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

<sup>‡</sup> Initial plot genotypic richness.

<sup>§</sup> Crab size treatments, for example, SMix indicates mixed-crab treatment.

<sup>¶</sup> Time of sampling.

biomass in plots with small crabs (Appendix S1: Fig. S4).

Finally, we tested whether crab size treatments changed the genotypic diversity and composition of the plant community over the course of the single growing season of our experiment. We documented an overall decrease in genotypic richness during the experiment (Time  $P = 0.012$ ,  $F_{1,71} = 6.7$ , Fig. 5a), and the magnitude of this decrease varied among crab size treatments. In particular, mixed and small-crab plots had greater richness than control plots at the final time point, whereas big-crab plots were not different from no-crab controls (Fig. 5b). Other diversity metrics—evenness and Shannon–Wiener diversity—also decreased over time but were not differentially affected by crab size

treatments. Similarly, a PERMANOVA showed no significant differences in overall genotypic composition based on crab size treatment. However, rank–abundance curves showed qualitative differences among crab size treatments in the way that rare and common species changed over time. Considering only those plots with four or more genotypes, the number of genotypes increased over the course of the experiment in small-crab plots, in contrast with a decrease in all other crab size treatments (Fig. 6). Big-crab and no-crab plots had increased abundances of the most common genotypes, while small- and mixed-crab plots had little change in maximum abundances and instead had increases in rare genotypes (i.e., the number of genotypes in the tail). If anything, small-crab plots had a decrease

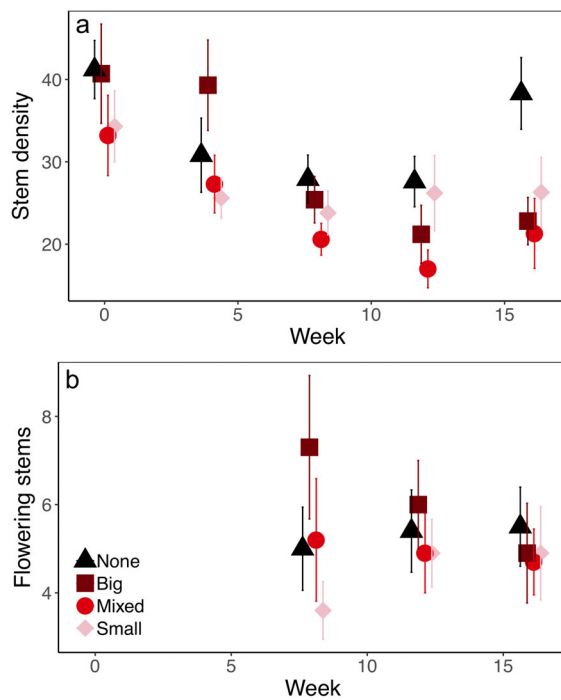


Fig. 1. Change in (a) stem density (number of stems/0.0625 m<sup>2</sup>) and (b) flowering stems (number/0.0625 m<sup>2</sup>) over the course of the experiment in plots with big crabs (maroon squares), a mix of big and small crabs (red circles), small crabs (pink diamonds), or no crabs (black triangles). Flowering stems were only counted starting in week 8 (mean  $\pm$  SE).

in the abundance of the most common genotypes (Fig. 6a, b). When rare genotypes are defined as those with abundances of one or less (excluding zeros), big crabs and no crabs also had increases in rare genotypes over time.

## DISCUSSION

Crab size and plant genotypic diversity each independently affected plant morphology and biomass. Although their effects were of similar magnitude, they rarely influenced the same response variable (i.e., crab size affected stem density, whereas plant genotypic diversity influenced growth), with the exception that crab size and plant genotypic diversity interactively affected biomass allocation. The effects of combined small and large crabs (mixed-crab treatments) were generally additive. Important

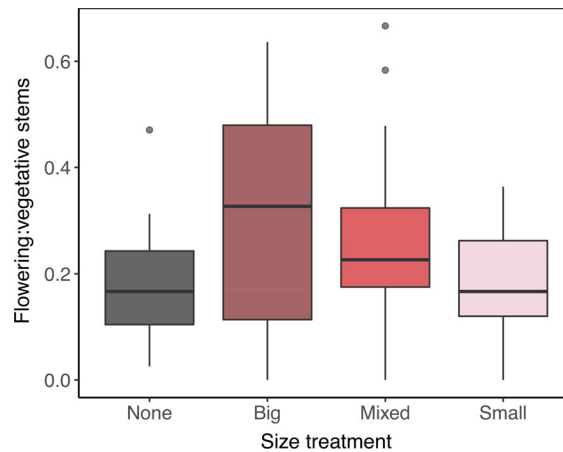


Fig. 2. Ratio of flowering to vegetative stems in 0.0625-m<sup>2</sup> subplots differed among crab size treatments ( $n = 30$  per treatment; median). All sampling points are combined as there was no significant effect of time.

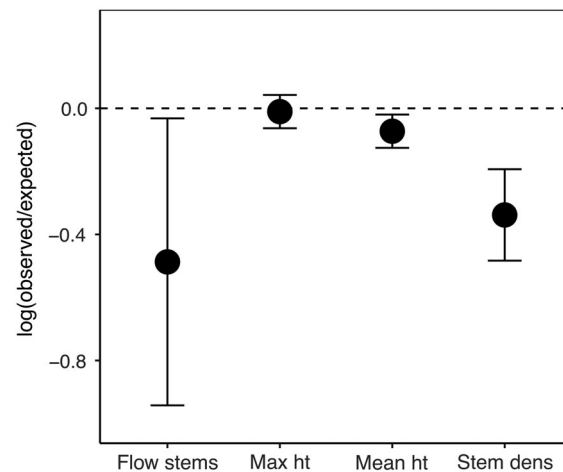


Fig. 3. Observed effects of mixed crabs compared to the expectation of additive effects of small and large crabs. Values below the dotted line indicate synergistic effects of mixed crabs. Data are combined across all time points (means  $\pm$  95% CI).

exceptions to that pattern were for mean stem height, stem density, and flowering, which were more negatively affected by mixed crabs than expected based on the effects of small and large crabs alone. Despite the relatively short time frame of our experiment, crab size had detectable (though small) effects on plant genotypic

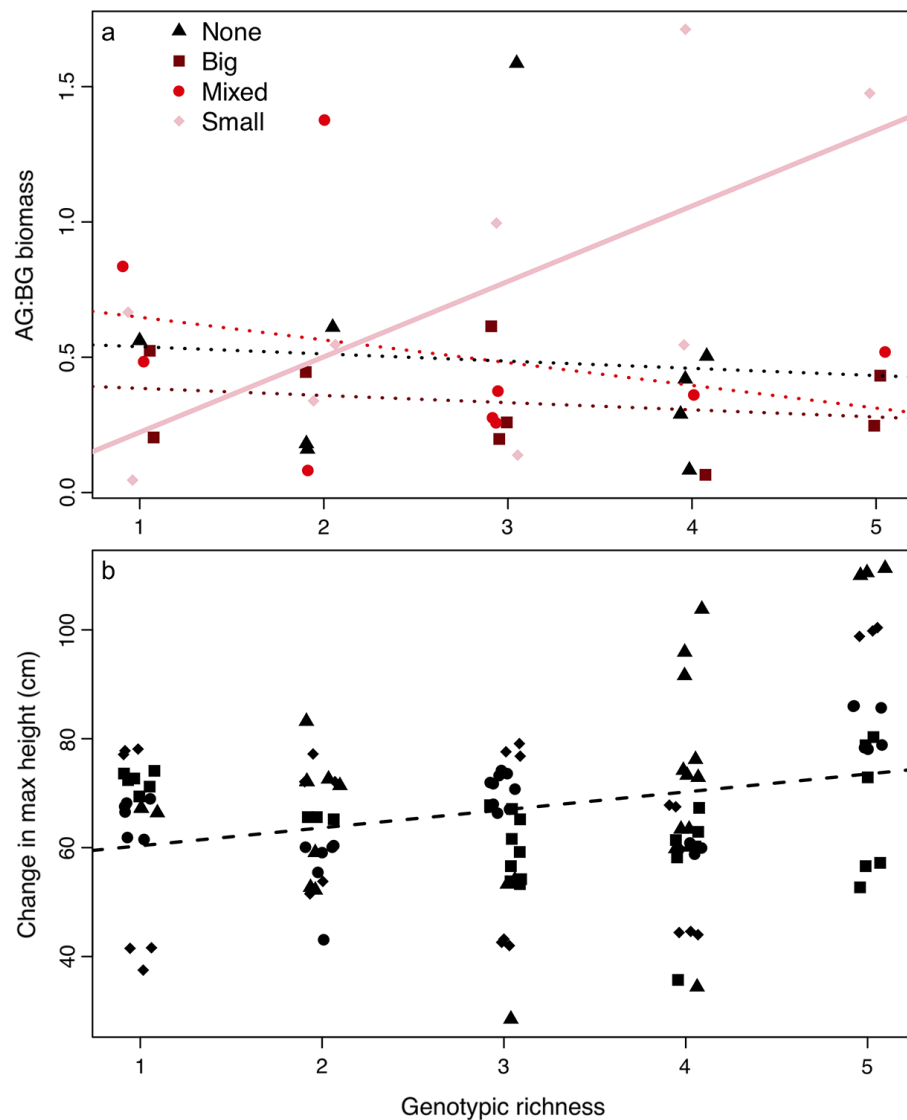


Fig. 4. Relationship between initial genotypic diversity (observed richness in 10 samples) and (a) ratio of above to belowground biomass and (b) change in maximum height from initial measurements in big (squares)-, mixed (circles)-, small (diamonds)- and no-crab (triangles) treatments. Biomass was only collected at the final time point while change in maximum height is shown at all time points. Colors in (a) indicate a significant interaction between size treatment and genotypic diversity with each color corresponding to a size treatment. Solid lines represent significant relationships within a crab size treatment, dashed lines indicate marginally significant relationships, and dotted lines represent relationships that are not significant.

diversity and composition that highlight the potential for feedbacks between intraspecific diversity at adjacent trophic levels.

Herbivorous crabs of different sizes had distinct effects on the plant community, with small crabs often having less dramatic effects than big

crabs, despite similar overall biomass. For instance, small crabs did not significantly affect stem density or the ratio of flowering to vegetative stems relative to no-crab controls (Figs. 1, 2). In contrast, plots with big crabs had fewer stems, more of which were flowering, compared to

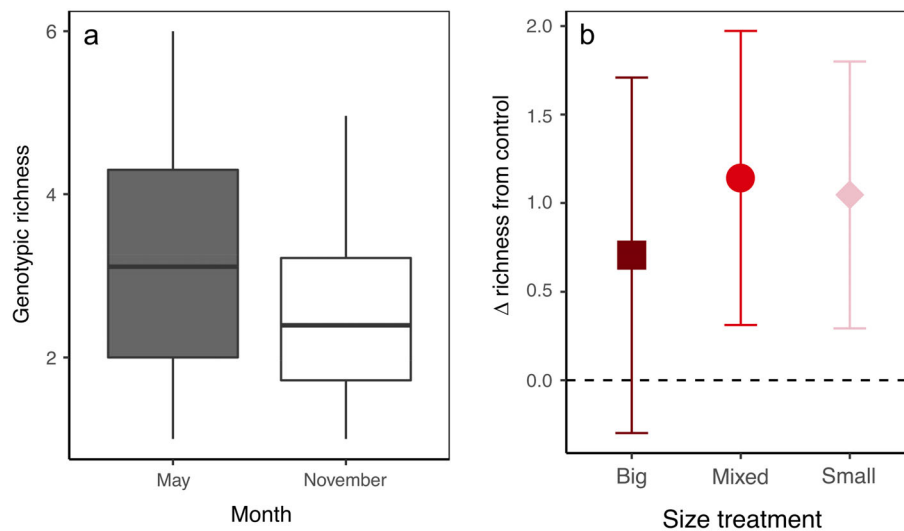


Fig. 5. (a) Change in rarefied genotypic richness from the beginning of the experiment to the end (median). (b) Difference in richness between control plots and big-, mixed-, and small-crab plots at the end of the experiment (mean  $\pm$  95% CI).

control plots. Flowering can be a plant response to stress (van Zandt et al. 2003, Diaz-Almela et al. 2007, Takeno 2016, Ruiz et al. 2018), and *Spartina* has been shown to respond to herbivory and other disturbances by producing more flowering stems (Zerebecki and Hughes 2013, Li and Pennings 2017). Conceptual models and empirical results show that it is advantageous for clonal plants to invest in sexual reproduction instead of vegetative growth when ramet mortality is high and sexual reproduction would allow dispersal from suboptimal habitats (Loehle 1987, Sakai 1995, Gardner and Mangel 1999, van Zandt et al. 2003, Li and Pennings 2017). Thus, the reduced stem density and increased relative proportion of stems that flowered in big-crab plots suggest that big crabs have a sufficiently strong impact to cause *Spartina* to shift its reproductive strategy while small crabs do not.

The larger impact of big crabs may result from differences in grazing patterns among size classes. Crabs consume rhizomes opportunistically when they encounter them while burrowing, and belowground biomass in burrows is almost completely consumed (Coverdale et al. 2012, Vu and Pennings 2018). Because big crabs have more extensive burrows (A. Noto, *personal observation*), they are more likely to encounter and consume rhizomes. In addition, feeding

belowground uses more energy than feeding aboveground as it requires crabs to dig burrows (Vu and Pennings 2018), and big crabs have greater energy reserves than small crabs. Belowground disturbance can also lead to an increase in sexual reproduction in clonal plants (Xiao et al. 2015), consistent with the observed effects of big crabs on *Spartina* in our field study. Grazing patterns may also differ aboveground: In mesocosms, we found that big crabs grazed a larger proportion of leaves overall (Appendix S1: Fig. S5). In addition, big crabs reduced the number of live vegetative stems relative to small crabs ( $P < 0.001$ ), even when accounting for the larger biomass of the big crabs and despite the fact that big and small crabs did not cause differences in the number of dead stems or stems showing signs of herbivory (Appendix S1: Fig. S6). Thus, we conclude that the distinct effects of big and small crabs on *Spartina* are potentially due to behavioral differences among the two size classes.

The synergistic effects of big and small crabs may similarly be a result of different feeding behaviors. Several studies have found that consumer diversity can lead to synergistic effects on prey when that diversity also leads to differences in feeding behavior or preferences (Duffy et al. 2003, Ingram et al. 2011, Rudolf 2012). In

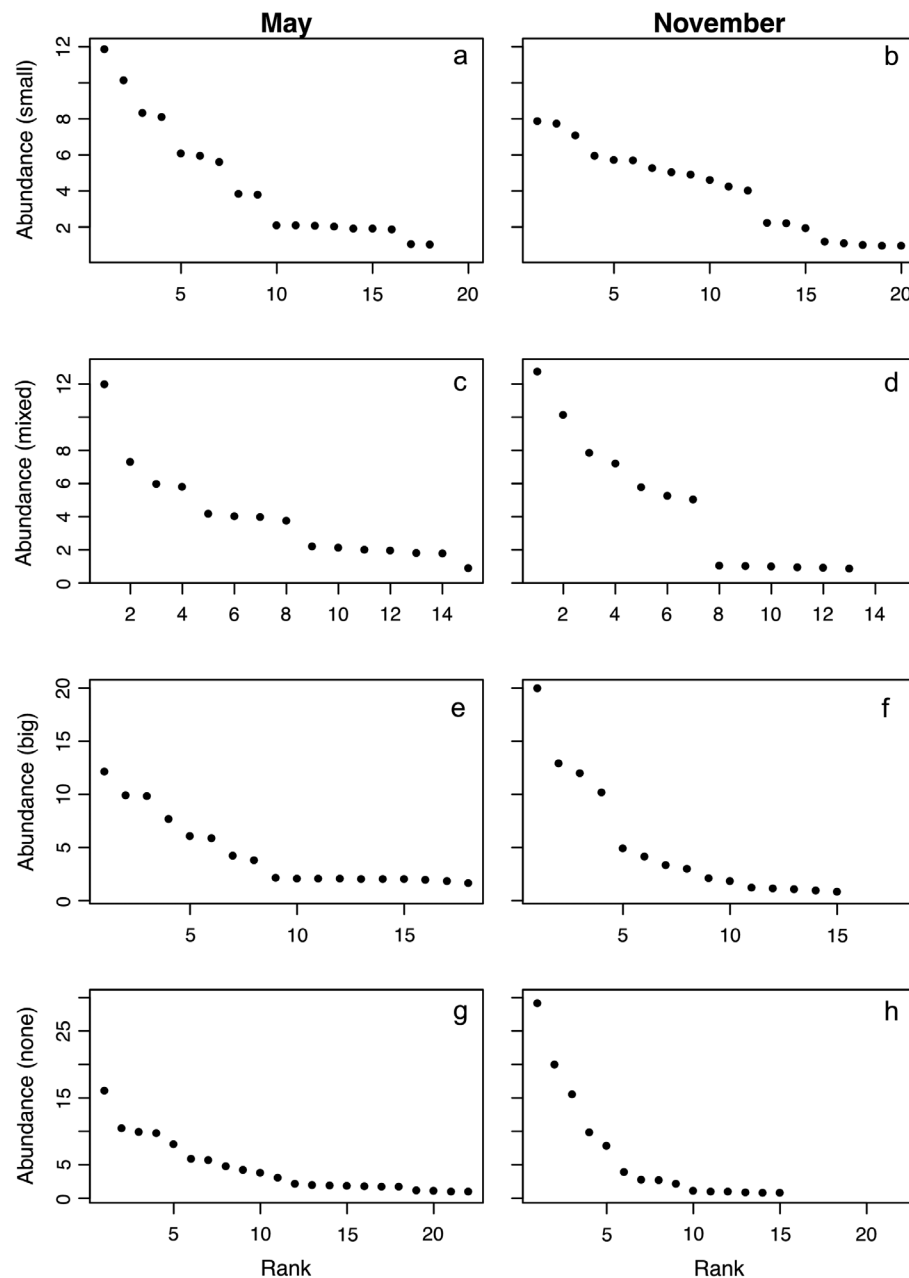


Fig. 6. Rank–abundance curves for plots that initially had four or more genotypes in May (left column) compared to November (right column) in plots exposed to small crabs (a, b), mixed crabs (c, d), big crabs (e, f), and no crabs (g, h).

this case, lower stem density and mean height than expected in mixed-crab plots may result from big crabs feeding more intensely on each stem, or from belowground rhizome consumption by big crabs impeding recovery from

simultaneous aboveground consumption by small crabs (Tolvanen 1994). Consistent with these synergistic effects being due to different feeding behavior among size classes, flowering was stimulated less than expected in mixed

plots, likely because reduced density of big crabs led to a reduction in belowground disturbance to ramets (Xiao et al. 2015). Surprisingly, we saw no synergistic effect of mixed crabs on biomass. This apparent lack of a response may be a result of our method of measuring biomass: By subsampling plots and preferentially sampling in areas with some biomass present to better capture differences in vegetation structure, we likely minimized differences in total biomass across plots and potentially obscured differences among crab treatments.

Small-crab plots had more pronounced interactions with genotypic diversity than other crab size treatments. Similarly, in a rocky intertidal system, small predatory crabs would be affected by prey diversity as they could not consume all prey species, while big crabs could consume any prey (Toscano and Griffen 2012). Prey diversity's distinct effect on large and small consumers could be due to size classes' differing susceptibility to (1) prey defenses or (2) prey size. Among chewing insect herbivores, small species are more affected by plant defenses than large ones (Čížek 2005), and other consumers may show similar trends. Palatable, poorly defended genotypes may be abundant in low-diversity plots as there is often a genetically based trade-off between growth ability and defense against herbivory (Coley 1986, Donaldson et al. 2006, Hanley et al. 2007, Tomas et al. 2011), and fast-growing genotypes are most likely to dominate an entire plot. In contrast, high-diversity plots contained unique genotypes that may have been slow-growing but better defended. Thus, small crabs may be more affected by plant diversity because they are more susceptible to plant defenses. Alternatively, this trend may occur because *Spartina* reaches a size refuge from *Sesarma* aboveground but not belowground (Coverdale et al. 2012). If small crabs preferentially feed aboveground, their consumption will be limited by plant size; because plants in high-diversity plots tend to grow faster, they may reach the size refuge more quickly. Big crabs will not be affected by the size refuge if they feed belowground, so diversity increasing aboveground growth will not affect them. Thus, size and feeding mode allow big crabs to be unaffected by variable plant traits that affect small crabs.

Previous research shows that genotypic richness often affects production (sensu Hughes et al. 2008), while we saw only marginal effects of genotypic diversity on plant biomass. Genotypic diversity leads to greater stem density in many other systems (Crutsinger et al. 2008, Hughes and Stachowicz 2009, Hughes 2014), but it did not in this case. Thus, any effects of genotypic diversity on production were likely mediated by plant height.

A potential caveat to our interpretation of the effects of genotypic diversity in this system is that we did not directly manipulate genetic diversity, and thus, environmental factors correlated with genotypic diversity could influence our results. Neither porewater salinity nor sediment organic matter was correlated with genotypic richness, but genotypic richness was generally higher at higher elevations, as in a prior study (Hughes and Lotterhos 2014). However, including elevation did not improve the model fit for either plant measure affected by genotype (change in height and aboveground-to-belowground biomass ratio), suggesting that elevation was unlikely to be driving the genotype effects we observed.

Crab size and size diversity had small but detectable effects on plant genotypic richness by the end of the experiment, suggesting the potential for feedbacks over longer time scales. Although plant genotypic richness decreased over the course of the growing season in all treatments, this reduction was tempered in small- and mixed-crab plots relative to plots with big or no crabs. Rank-abundance curves revealed that the number of rare genotypes increased over time in small and mixed-crab plots, consistent with intermediate levels of herbivory promoting diversity (Borer et al. 2014). In contrast, the most common genotypes increased in abundance in control plots and those with big crabs. Despite similar patterns in big-crab plots and controls, the mechanisms underlying changes in genotypic richness likely differ. Removing grazers often decreases plant species diversity in terrestrial systems by increasing competition (e.g., for light; Hillebrand et al. 2007, Borer et al. 2014), so we expect that competitive exclusion contributed to a reduction in genotypes in control plots. In contrast, consumer pressure in big-crab plots may have been so intense that only the most

tolerant genotypes could persist (Olf and Ritchie 1998). Despite differences in rank–abundance plots, we saw little change in evenness or genotypic composition associated with crab treatment over time, suggesting that the full effects of herbivory on genotypic diversity may not be realized over the course of one growing season.

These herbivore legacies on plants are likely to persist into the next growing season via both plant growth and genotypic diversity. For instance, stem density in control plots increased at the end of the growing season, while plots with crabs continued to have low stem densities. Shoots that emerge in the fall are critical for *S. alterniflora* overwintering success, and when those shoots and dead *S. alterniflora* material are removed, few shoots regrow in the spring (Wijte and Gallagher 1991). If crabs affect both types of plant material, plants exposed to crabs may have fewer clonal shoots grow back the following growing season. In big-crab plots, the combination of fewer clonal shoots in subsequent growing seasons and reduced genotypic richness could lead to long-term declines in genotypic diversity. However, a large proportion of stems flowered in big-crab plots, and this shift to sexual reproduction may eventually increase genotypic diversity again, although likely at a scale beyond the original plot given seed dispersal distances. In contrast, small-crab plots gained a substantial proportion of genotypes over the course of the season that more than compensated for genotype loss (Appendix S1: Fig. S7), suggesting that they may have more diverse plots in the following year than in plots without crabs. Mixed-crab plots are intermediate, with a slight decrease in genotypic diversity but less shift to sexual reproduction than big-crab plots. Thus, crab herbivory may cause long-term changes in diversity resulting from differences in plant persistence and shifts in reproductive effort with specific effects and mechanisms depending on herbivore size.

Our results highlight that intraspecific diversity at the consumer and resource levels simultaneously affect consumer–resource interactions and can even do so interactively. Considering the impact of intraspecific diversity at multiple trophic levels may be particularly important in systems dominated by one or a few plant species (Reusch and Hughes 2006) where diversity can influence species interactions and perhaps even

long-term patterns of coexistence among plant genotypes. Although not tested here, intraspecific variation at the resource level may also feed back to impact diversity at the consumer level. Plant genotypes often differ in palatability and nutritional value and that variation may reduce herbivore performance and reproduction (Grettenberger and Tooker 2016, Wetzel et al. 2016, Zerebecki et al. 2017). These feedbacks between intraspecific diversity at adjacent trophic levels mediated by species interactions indicate the potential for eco-evolutionary dynamics in this system. Evidence for such eco-evolutionary feedbacks has accumulated across a range of systems (Post and Palkovacs 2009, Turcotte et al. 2011) and indicates the importance of considering genetic effects in ecological studies.

## ACKNOWLEDGMENTS

Field help was provided by K. Sklar, B. Reardon and A. Noble. T. C. Hanley and T. C. Gouhier provided additional help and guidance in the laboratory and with statistical analyses respectively, and S. M. Smith provided assistance in finding a field site. Funding was provided by NSF BIO-1710782 to AEN and NSF IOS-1556738 to ARH. Resources purchased with funds from the NSF FMSL program (DBI 1722553, to Northeastern University) were also used to generate data for this manuscript. A.E.N. conceived the idea; A.E.N. and A.R.H. designed the experiment; A.E.N. conducted the research and analyzed the data; A.E.N. wrote the first manuscript draft and both authors contributed to subsequent drafts.

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## DATA ACCESSIBILITY

Data are available in the Northeastern University Digital Repository Service: <http://hdl.handle.net/2047/D20338336>

## SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3121/full>