

Population variation affects interactions between two California salt marsh plant species more than precipitation

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Abstract Species that occur along broad environmental gradients often vary in phenotypic traits that make them better adapted to local conditions. Variation in species interactions across gradients could therefore be due to either phenotypic differences among populations or environmental conditions that shift the balance between competition and facilitation. To understand how the environment (precipitation) and variation among populations affect species interactions, we conducted a common garden experiment using two common salt marsh plant species, *Salicornia pacifica* and *Jaumea carnosa*, from six salt marshes along the California coast encompassing a large precipitation gradient. Plants were grown alone or with an individual of the opposite species from the same site and exposed to one of three precipitation regimes. *J. carnosa* was negatively affected in the presence of *S. pacifica*, while *S. pacifica* was facilitated by *J. carnosa*. The strength of these interactions varied by site of origin but not by precipitation treatment. These results suggest that phenotypic variation among populations can affect interaction strength more than environment, despite a threefold difference in precipitation. Geographic intraspecific variation may therefore play an important role in determining the strength of interactions in communities.

Keywords Competition · Facilitation · Intraspecific variation · Local adaptation · Phenotypic variation

Introduction

Interactions among species can vary geographically in strength and sign. Shifts in the balance between competition and facilitation among species in different locations are often attributed to environmental differences (Bertness and Ewanchuk 2002; Callaway et al. 2002; Tylianakis et al. 2008). The stress-gradient hypothesis predicts that interactions are more competitive under benign environmental conditions and more facilitative under stressful conditions in which the presence of other species moderates the environment (Bertness and Callaway 1994; He et al. 2013). For instance, high salinity, low temperatures or high winds favor facilitative interactions among salt marsh and alpine plants (Bertness and Ewanchuk 2002; Callaway et al. 2002; Tylianakis et al. 2008). Human-driven climate change makes it increasingly urgent to understand the extent to which environment drives variation in interaction strength to better predict if and how interactions may change in the future.

In addition to environmental factors, differences in interaction strength and sign across gradients may be affected by phenotypic variation among populations (Pennings and Silliman 2005; Sanford and Worth 2009). Adaptation to local environmental conditions is common among plant species that occur across large environmental gradients (e.g., Pennings et al. 2003; Woods et al. 2012; Pratt and Mooney 2013; Vergeer and Kunin 2013). Local adaptation can improve plant fitness by affecting traits such as phenology, reproduction and growth, ensuring, for example, that plants flower at a time during which the environment

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is most favorable for successful pollination (Linhart and Grant 1996; Woods et al. 2012).

Because adaptive variation along environmental gradients affects so many aspects of plant fitness, it is also likely to affect interactions among plants. Variation among populations of a plant that occurs on different soil types led to differences in intraspecific interaction strength and sign between populations when grown on the same soil type (Espeland and Rice 2007). Similarly, a grass species grown in arid conditions with local shrubs experienced different interaction strengths depending on its location of origin; Mediterranean grasses experienced stronger facilitation than arid-region grasses (Liancourt and Tielbörger 2011). Thus, interaction strength can be driven by geographic variation among populations as well as the environment. However, few studies have measured the extent to which population variation in multiple species affects their interaction strength along environmental gradients.

We conducted a common garden experiment to determine the effects of population differences and precipitation on interactions between two salt marsh plants. Precipitation is an important environmental variable in California's arid climate that increases dramatically moving from south to north and is related to soil salinity in salt marshes. We collected plants from several marshes along the California coast which span a fourfold precipitation gradient (Arguez et al. 2012). We grew isolates from these populations alone and in combination at three levels of precipitation. We addressed these hypotheses:

1. Plant populations differ based on source, with plants from northern populations less tolerant of low precipitation conditions than southern plants.
2. Consistent with the stress-gradient hypothesis, competition among plants will be stronger under higher precipitation and facilitation stronger in drier conditions.
3. Effects of precipitation treatments on species interactions will depend on the origin of the plant population. Specifically, low precipitation conditions will not be as stressful for plants from southern populations so they

will continue to compete even at low precipitation levels, while plants from northern populations will find these conditions stressful and will facilitate each other under these conditions.

These hypotheses allow us to understand the importance of environment and variation among populations in determining interaction strength.

Materials and methods

Study system

Plants were collected from six California salt marshes spanning approximately 1250 km and 8° latitude (Table 1; Fig. 1). Many species are present across the entire range although it includes a fourfold gradient in precipitation and a 6 °C difference in mean temperatures (Table 1; Arguez et al. 2012). We included two sites in San Diego, one on a bay [Kendall-Frost Mission Bay Marsh (KF); Fig. 1] and the other on an estuary [Tijuana Estuary (TJ); Fig. 1], to ensure that marshes located on bays and estuaries were distributed across the latitudinal gradient.

This experiment focused on two common salt marsh plant species: *Salicornia pacifica* and *Jaumea carnosa*. *S. pacifica* is a dominant species in marshes on the eastern coast of the Pacific from Baja California to Canada (Macdonald and Barbour 1974). It is a perennial forb that grows upright, reproduces both vegetatively and from seed, and has a relatively broad elevation range (Sullivan and Noe 2001). Several subordinate species occur in this range, but we chose *J. carnosa* as our focal species as it was the only one present in all sites along the gradient. *J. carnosa* is also a perennial forb, but it typically grows along the ground and reproduces vegetatively, though it can reproduce from seed, particularly when salinities are reduced. It has a smaller elevation range than *S. pacifica* (Sullivan and Noe 2001) suggesting that it may be less tolerant of environmental stress.

Table 1 Location and climate information for marshes where plants were collected in California, USA

	Location (latitude, longitude)	Mean annual precipitation (cm)	Mean temperature (°C)
Humboldt Bay (HUM)	40.7°N, 124.2°W	102.4	11.57
Tomales Bay (TOM)	38.2°N, 122.9°W	108.0	12.01
Elkhorn Slough (ELK)	36.8°N, 121.8°W	51.49	14.00
Carpinteria Salt Marsh (CAR)	34.4°N, 119.5°W	49.35	16.47
Kendall-Frost Mission Bay Marsh (KF)	32.8°N, 117.2°W	31.34	16.44
Tijuana Estuary (TJ)	32.5°N, 117.1°W	26.69	16.94



Fig. 1 Location of sampled marshes where plants were collected in California, USA: Humboldt Bay (*HUM*), Tomales Bay (*TOM*), Elkhorn Slough (*ELK*), Carpinteria Salt Marsh (*CAR*), Kendall-Frost Mission Bay Marsh (*KF*) and Tijuana Estuary (*TJ*)

Experimental design

In summer 2013, we collected 100 cuttings of each species in each site. Cuttings were taken from plants at least 1–2 m apart and were collected over several hundred square meters to reduce the risk of collecting twice from the same plant as these plants often spread vegetatively. Cuttings were rooted in commercial potting soil in a greenhouse in San Diego. After 5 months, plants were transplanted into 10-cm-diameter pots containing equal parts commercial potting soil and sand (Pennings et al. 2009). There were three interaction treatments: *S. pacifica* alone, *J. carnosa* alone, or both species together from the same site. This additive design in which pots with both species had twice as many plants as pots with one species allowed us to assess the effects of interspecific interactions (Inouye 2001). This design did not allow us to compare the magnitude of inter- and intraspecific effects, which was beyond the scope of this experiment. Our design addresses questions of how the effects of interspecific interactions differed among populations and precipitation treatments.

Plants were grown in a common garden outdoors in San Diego from January to September 2014. Pots were contained within bins and maintained with salt water 7 cm below the soil surface. We used Instant Ocean (Aquarium System, Mentor, OH) to make salt water of salinity of approximately 33 parts per thousand (p.p.t.), the concentration of sea water. Each bin contained 18 pots: one for each competition treatment from each location (3 competition treatment levels \times 6 locations). Plants were gradually acclimated to elevated salinity. We initially raised salinities to 1/5 sea water, and after one week, we increased salinity by 5 p.p.t., continuing every 4 days until they reached 33 p.p.t. Water salinity in the bins was monitored and adjusted twice each week to ensure that they remained consistent across time and treatments.

Each bin was exposed to one of three precipitation treatments: high (average rainfall in Eureka 45.4 cm over the course of the experiment), medium (average of Eureka and San Diego rainfall 29.3 cm), or low (average rainfall in San Diego 13.3 cm); the treatments were replicated seven times. We supplemented ambient rainfall weekly by hand-watering pots based on average monthly precipitation to simulate seasonality. When ambient rainfall in San Diego exceeded the target weekly volume, we reduced water additions for the following weeks. Because this experiment occurred during a drought (2014), we supplemented rainfall for all treatments.

Plant measurements

Biomass and flowering were used to measure plant performance. At the end of the season, plants were harvested and above- and belowground biomass were measured. Plants, including roots, were rinsed clean of soil and salt and aboveground biomass was separated from belowground. Belowground biomass of plants grown with a neighbor could not be separated by species as the roots were indistinguishable and too tangled to be separated. All biomass was dried at 40 °C until plant weight was constant. We also measured the number of *S. pacifica* branches and *J. carnosa* shoots weekly throughout the experiment as these can vary in response to competition and the environment (Seliskar 1985; Ellison 1987).

We conducted weekly flowering surveys to note the date of first flowering and determine the maximum number of flowers at any time. *J. carnosa* has large individual flowers, so we counted all flowers weekly. *S. pacifica* has tiny flowers that cannot be accurately counted non-destructively, so we counted the number of branches with flowers each week.

Statistical analyses

The effects of neighbor presence, precipitation and plant source on plant biomass were analyzed with ANOVA after square-root transformation to meet assumptions. Visual assessments of residuals and normality were used to determine when transformations were necessary. Shoot and branch data were collected weekly, so we used a mixed-effects model to account for the autocorrelation of measurements from one week to the next (Crawley 2007). These data were also square-root transformed to meet assumptions. Because belowground biomass could not be separated by species, we compared total belowground biomass from plants grown together with the sum of belowground biomass of *S. pacifica* and *J. carnosa* grown alone from the same site in the same bin. Higher belowground biomass when plants were grown together suggests that

plants increased root biomass in response to competition. We natural log transformed these data to analyze the effect of treatments on the ratio of aboveground to belowground biomass. Maximum number of flowers could not be transformed to meet ANOVA assumptions. Instead, we used randomizations to generate a null distribution to test hypotheses for each species separately. Effect sizes for all variables were calculated as η^2 : sum of squares $SS_{\text{between}}/SS_{\text{total}}$ from ANOVA. All analyses were done in R version 3.2.0 (R Development Core Team 2015).

Results

Biomass and plant structure

J. carnosa aboveground biomass was significantly reduced in the presence of *S. pacifica* and by low precipitation (Table 2; Fig. 2a–c). There was also a significant population by neighbor presence effect (Table 2) indicating that plants from different populations responded differently to neighbors, although there was no clear latitudinal trend in

Table 2 η^2 -values (sum of squares $SS_{\text{between}}/SS_{\text{total}}$) from ANOVA results measuring effect sizes on plant biomass and number of flowers

	df	<i>Jaumea carnosa</i> biomass	<i>Salicornia pacifica</i> biomass	<i>J. carnosa</i> flowers	<i>S. pacifica</i> flowers	Aboveground:belowground biomass
Source (S)	5	0.015	0.36***	0.29	0.12***	0.016*
Competition (C)	1	0.52***	0.060***	0.079	0.015*	0.70***
Precipitation (P)	2	0.038***	0.011 ⁺	0.0064	0.0018	0.021***
<i>S</i> × <i>C</i>	5	0.020*	0.026 ⁺	0.091***	0.024	0.011
<i>S</i> × <i>P</i>	10	0.022	0.022	0.046*	0.045	0.014
<i>C</i> × <i>P</i>	2	0.004	0.0029	0.00024***	0.0034	0.0026
<i>S</i> × <i>C</i> × <i>P</i>	10	0.017	1.23	0.019	0.030	0.0080

⁺ $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

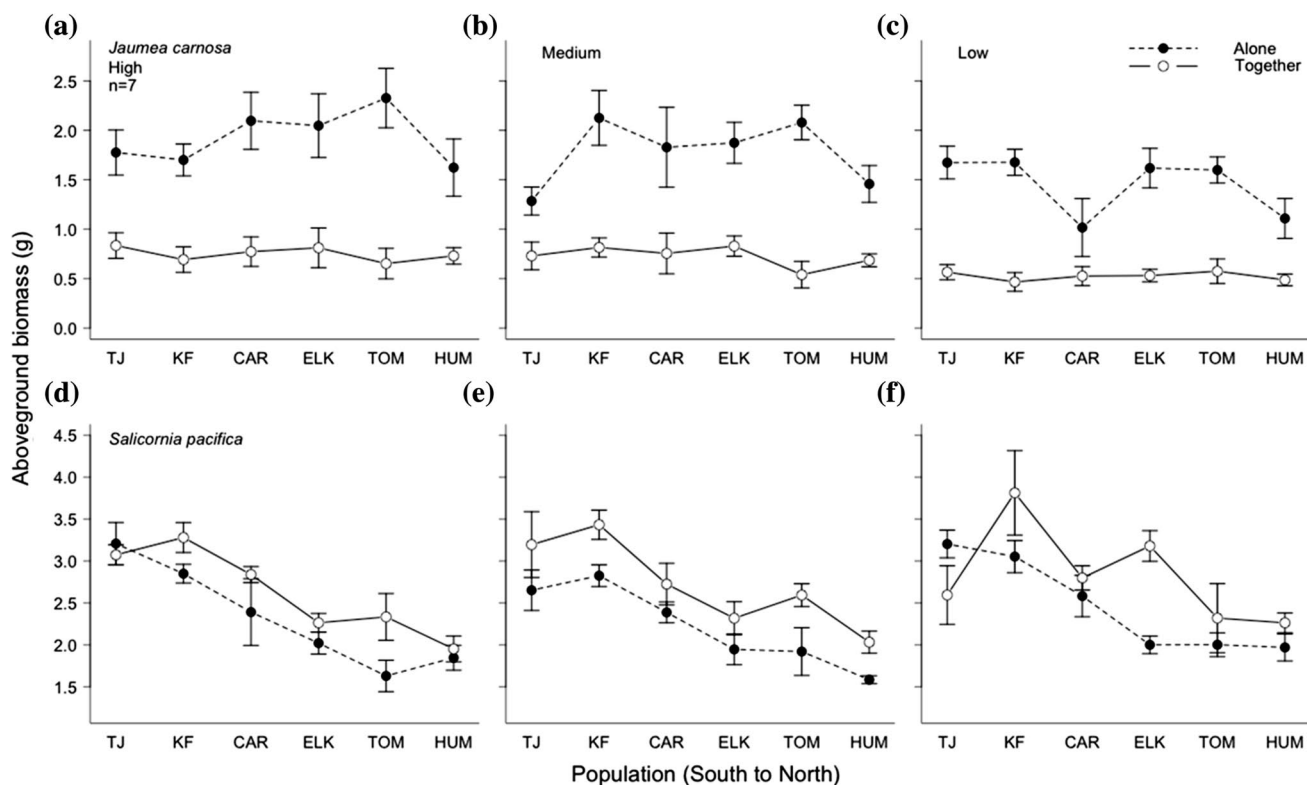


Fig. 2 Population differences in aboveground biomass of *Jaumea carnosa* (a–c) and *Salicornia pacifica* (d–f) grown alone and with a neighbor of the other species in treatments with a, d high, b, e

medium and c, f low precipitation. Populations are listed in order of latitude, south to north. Values are mean \pm SE ($n = 7$). For abbreviations, see Fig. 1

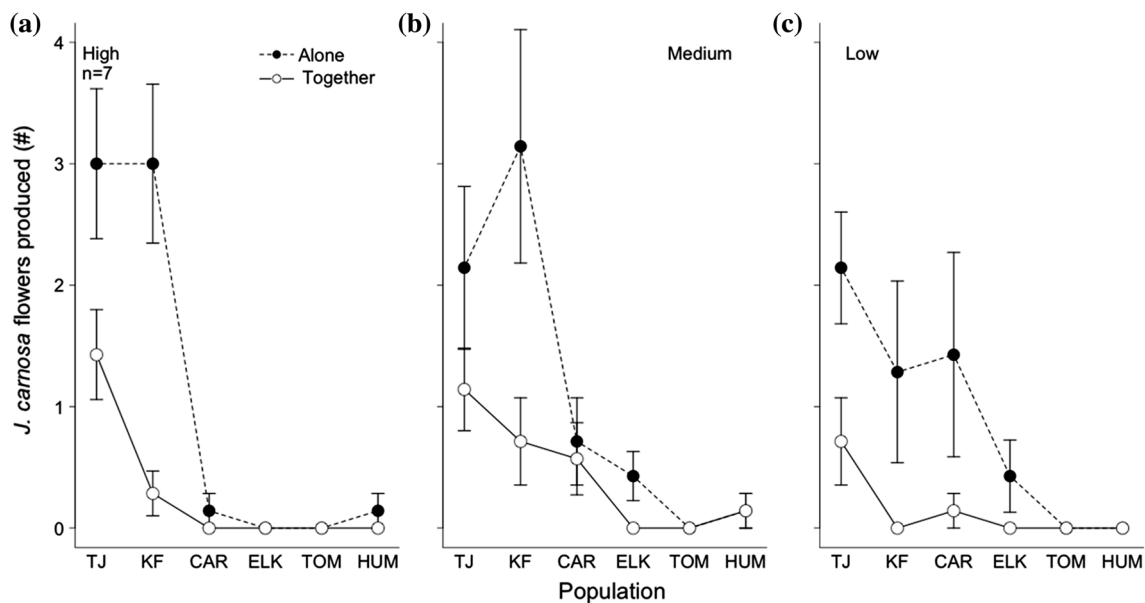


Fig. 3 Population differences in maximum number of flowers produced by *J. carnosa* when grown alone or together in treatments with **a** high, **b** medium and **c** low precipitation. Values are mean ± SE ($n = 7$). For abbreviations, see Fig. 1

these differences (Fig. 2a–c). Neighbors had smaller effects on the biomass of plants from both the southernmost and northernmost populations (TJ and HUM) compared to plants from more central populations such as Elkhorn Slough (ELK) or Tomales Bay (TOM) which experienced strong negative impacts of competitors (Fig. 2a–c).

S. pacifica produced more aboveground biomass in the presence of *J. carnosa*, indicating facilitation (Table 2; Fig. 2d–f). However, greater belowground biomass relative to aboveground biomass when plants were grown together indicates that competition occurred even as *S. pacifica* was facilitated aboveground (Table 2; Online Resource, Fig. A1). Aboveground biomass differed significantly among populations with plants from northern sites being smaller than plants from southern populations (Table 2; Fig. 2d–f). *S. pacifica* biomass showed a marginally significant effect of precipitation and interaction between population and neighbor presence (Table 2) suggesting that population may affect interaction strength, but there was not a latitudinal trend in this effect (Fig. 2d–f). Despite originating from similar latitudes, *S. pacifica* from TJ and KF populations responded differently to the presence of *J. carnosa*, with the KF population being facilitated more than the TJ one (Fig. 2d–f).

Plant morphology was affected by population and interactions between population and neighbor presence but not by precipitation. *J. carnosa* plants generally had more shoots when grown alone, but the effect was variable among populations (Table 3). *S. pacifica* plants from southern populations had more branches than those from

Table 3 *P*-values from mixed-effect models indicate effects of variables on plant morphology

	<i>df</i>	<i>J. carnosa</i> shoots	<i>S. pacifica</i> branches
Source (<i>S</i>)	5	6.30***	42.6***
Competition (<i>C</i>)	1	6.95**	1.61
Precipitation (<i>P</i>)	2	0.587	0.224
<i>S</i> × <i>P</i>	10	1.57	0.504
<i>S</i> × <i>C</i>	5	1.98 ⁺	2.49*
<i>C</i> × <i>P</i>	2	0.343	1.24
<i>S</i> × <i>P</i> × <i>C</i>	10	0.439	0.426

⁺ $P < 0.01$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

northern populations (Fig. 4). Neighbor presence and population affected *S. pacifica* interactively such that southern plants branched more when grown alone than when grown with a neighbor, while northern plants branched most when grown with a neighbor (Fig. 4).

Flowering

Flowering showed similar responses to aboveground biomass. The maximum number of flowers at one time on *J. carnosa* was affected by all two-way interactions among neighbor presence, population and precipitation (Table 2). Plants from southern populations flowered more and earlier than northern populations, and neighbor presence reduced flowering (Fig. 3). The effects of neighbors on the number of flowers became smaller as precipitation decreased,

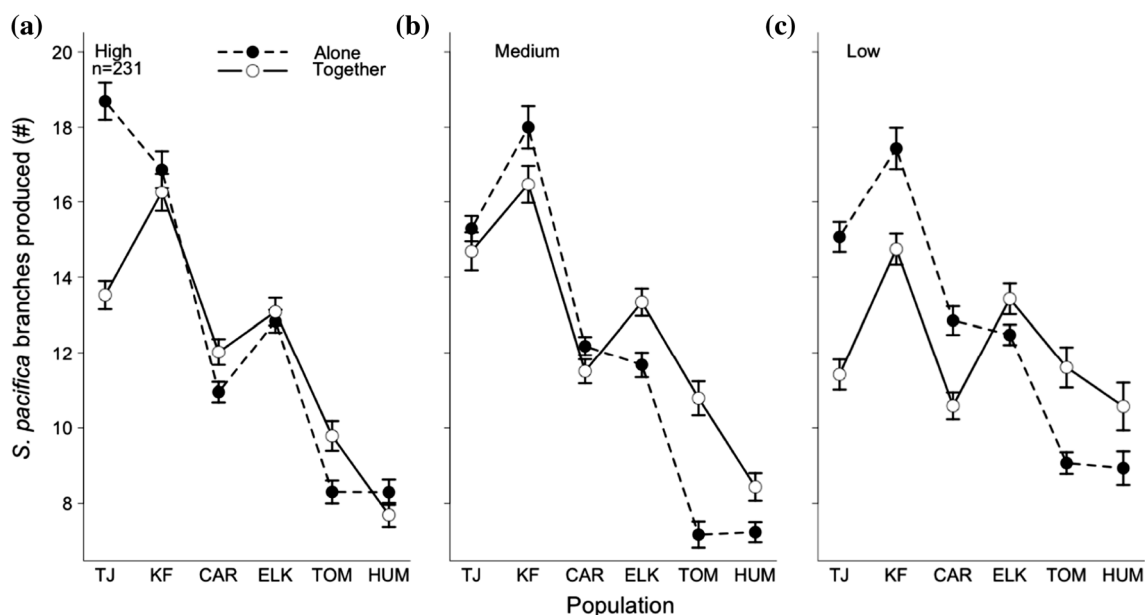


Fig. 4 Population difference in number of branches produced by *S. pacifica* when grown alone or together in treatments with **a** high, **b** medium and **c** low precipitation. Values are mean \pm SE ($n = 231$). For abbreviations, see Fig. 1

indicating that the inhibitory effect of neighbors on flowering decreased at low precipitation (Fig. 3).

S. pacifica flowering was affected by population and the presence of neighbors but not by precipitation (Table 2). Like its biomass, *S. pacifica* flowering increased when it was grown with *J. carnosa* (Online Resource, Fig. A2). Flowering differed among populations of *S. pacifica*, but unlike those of *J. carnosa*, there was no geographical trend in flowering. Flowering was low among plants from TJ, TOM and HUM populations and higher among plants from the southern KF and central ELK populations (Online Resource, Fig. A2).

Discussion

Our experiment shows that species interaction strength can vary among populations independently of the environment. Source population determined the effect of species interactions on plant performance more frequently and strongly than precipitation. Although population variation is rarely considered as a cause of geographic differences in species interactions along environmental gradients, our study shows that such effects on species interactions can be even stronger than those of the environment.

Variation among populations affected the strength of species interactions but did not follow the latitudinal precipitation gradient of the source populations, contrary to expectations. We anticipated that southern plants would be less affected by stress and more competitive under drier

conditions due to local adaptation. This would be consistent with studies that found that individuals adapted to stressful environments compete even under harsh conditions (Espeland and Rice 2007; Liancourt and Tielbörger 2011). However, we did not find consistently stronger or more negative interactions among southern than northern populations (Fig. 2), although we did not explicitly test this relationship. One potential explanation is that the focal species' ranges extend to soil salinities beyond what was achieved by our precipitation treatments, so that conditions in our experiment were not physiologically stressful enough to promote a change in interaction strength (Macdonald and Barbour 1974; He and Bertness 2014). Another possibility is that differences in interaction strength among populations may be related to other environmental conditions that do not vary latitudinally, such as nutrients or inundation.

Geographic variation in interactions among salt marsh plants is frequently attributed to environmental differences, with stronger facilitation in stressful environments and stronger competition in benign ones (Bertness 1991; Bertness and Hacker 1994; Bertness and Callaway 1994). We saw facilitation of *S. pacifica* by *J. carnosa*, but surprisingly, interaction strength was not affected by precipitation (Table 2). Similarly, precipitation did not determine how strongly *J. carnosa* was inhibited in the presence of *S. pacifica* in a plus/minus interaction termed "antagonistic facilitation" (Stachowicz 2001; Jones et al. 2012). Facilitation typically occurs when one species benefits another species by alleviating environmental stress (Niering et al. 1963; Bertness and Callaway 1994; Callaway et al. 2002;

Whitcraft and Levin 2007). Facilitation by *J. carnosus*, which grows low to the ground, is likely caused by shading soil, thereby reducing evaporation and salinity. Precipitation may have had little effect on facilitation because little precipitation occurs during the hottest times of the year when facilitation would be most beneficial. Rainfall did have some effect on interactions as *S. pacifica* presence reduced *J. carnosus* flowering less when precipitation was low, consistent with stronger competition at higher precipitation (Fig. 3). Nevertheless, the magnitudes of facilitation and competition varied more among populations than in relation to precipitation at the site of population origin.

Morphology of *S. pacifica* was the only trait to show the expected latitudinal shift in interactions among populations. We found that branching was reduced by neighbors in southern plants but increased in northern plants, consistent with our prediction that populations from low precipitation areas would show the strongest effects of competition. However, morphology of *S. pacifica* was not affected by precipitation or its interaction with population. Plant morphology is often altered by competition, and reduced branching is a common response in *Salicornia* species to high salinity and neighbors (Seliskar 1985; Ellison 1987; Richards et al. 2005). *Salicornia* species shift resource allocation to height rather than branching under competition (Ellison 1987). The long-term fitness effects of reduced branching by *S. pacifica* under competition are unknown, but our results indicate that in the case of morphology, the effects of species interactions vary latitudinally among source populations.

The expected latitudinal shifts from competition to facilitation may not have been seen in most variables measured in this experiment because plants that co-occur are adapted to the same environmental conditions and therefore have similar tolerances (Pennings et al. 2003). In our experiment, southern populations of both species may be stronger competitors than northern populations resulting in no net shift in interaction strength. Alternatively, latitudinal shifts in interactions may not occur if phenotypes do not vary consistently with latitude. Without testing differences in competitive abilities among plants from different populations it is impossible to distinguish which of these is occurring. Future studies should address variation in competitive abilities among populations as individuals are increasingly moved from place to place and species migrate at different rates in response to climate change.

These results also have implications for salt marsh restoration, suggesting that restoration efforts should use local plants whenever possible as population differences affect community interactions. Informing effective restoration techniques is necessary as restoration efforts are becoming increasingly widespread due to the Clean Water Act mandating salt marsh restoration as remediation for damage to

wetlands (National Research Council 2001; Zedler 2005; UNEP 2006). Consistent with studies largely focused on single plant species that found that plant source affects restoration success (van Andel 1998; Howard 2010; O'Brien and Krauss 2010), our results indicate that species dominance in restored communities may be affected by the geographic origin of the populations.

Our study provides evidence that intraspecific variation contributes to geographic variation in species interactions across broad environmental gradients. Surprisingly, plant source population affected more components of performance in the presence of neighbors than a three-fold difference in precipitation did. Thus, the effects of intraspecific variation on species interactions can be of the same or even greater magnitude than precipitation. Future studies of geographic variation in interactions should explicitly consider the role of intraspecific variation and local adaptation in order to fully understand why species interactions differ along environmental gradients. Intraspecific variation may be more important for determining the outcome of species interactions along environmental gradients than previously recognized.

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Author contribution statement A. E. N. and J. B. S. conceived and designed the experiments. A. E. N. performed the experiments and data analysis. A. E. N. wrote the manuscript and J. B. S. provided editorial advice.

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