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Asymmetric competitive effects during species range expansion: an experimental assessment of interaction strength between 'equivalent' grazer species in their range overlap

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Abstract

1. Biotic interactions are central to the development of theory and concepts in community ecology; experimental evidence has shown their strong effects on patterns of population and community organization and dynamics over local spatial scales. The role of competition in determining range limits and preventing invasions at biogeographic scales is more controversial, partly because of the complexity of processes involved in species colonization of novel habitats and the difficulties in performing appropriate manipulations and controls.

2. We examined experimentally whether competition is likely to affect poleward range expansion hindering or facilitating the establishment of the limpet *Scurria viridula* along the southeastern Pacific rocky shore (30°S, Chile) in the region occupied by the congeneric *S. zebrina*. We also assessed whether competition with the "invader" or range expanding species could reduce individual performance of the 'native' *S. zebrina* and depress local populations

3. Geographic field surveys were conducted to characterize the abundance and identity of limpets along the south-eastern Pacific coast from 18°S to 41°S, and the micro-scale (few cm) spatial distribution across the range overlap of the two species. Field-based competition experiments were conducted at the southern leading edge of the range of *S. viridula* (33°S) and at the northern limit of *S. zebrina* (30°S).

4. Field surveys showed poleward range expansion of *S. viridula* of ca. 210 km since year 2000, with an expansion rate of 13.1 km year $^{-1}$. No range shift was detected for *S. zebrina*. The resident *S. zebrina* had significant negative effects on the growth rate of the invading

juvenile *S. viridula*, while no effect of the latter was found on *S. zebrina*. Spatial segregation between species was found at the scale of cms.

5. Our results provide novel evidence of an asymmetric competitive effect of a resident species on an invader, which may hamper further range expansion. No negative effect of the invader on the resident species was detected. This study highlights the complexities of evaluating the role of species interactions in setting range limits of species, but showed how interspecific competition might slow the advance of an invader by reducing individual performance and overall population size at the advancing front.

KEYWORDS

Field experiments, grazers, range overlap, range shift, Pacific Ocean, transitional zone.

1 | INTRODUCTION

The range limits of species are influenced by changes in environmental conditions, suitable habitat scarcity and dispersal limitation (Brown, Stevens, & Kaufman, 1996; Case, Holt, Mcpeek, & Keitt, 2005; Holt & Keitt, 2005; Vermeij, 2005). However, beyond large-scale environmental regulation, increasing theoretical and empirical evidence hints that biotic interactions can determine the distribution boundaries of species (e.g. Cunningham et al., 2009; Firth et al., 2009; Soberón, 2010; Araújo & Rozenfeld, 2014; Godsoe et al., 2017). Theory predicts that in geographic contact zones competitive interactions can leave a strong impact on species distribution at regional scales and can lead to the formation of stable geographic range edges (Araújo & Luoto, 2007; Godsoe, Murray, & Plank, 2015; Phillips, 2012). However, manipulative field studies determining how the strength of competition influences the dynamics of species range limits are still scarce (but see Cunningham et al., 2009).

The performance of species at the limit of their geographic range, where they overlap the distribution of other potentially competing species with similar resource requirements, may be critical in determining the role of competition in establishing the distribution and the probability of range expansion (Godsoe et al., 2015 Phillips, 2012). Range overlap can also drive ecological niche divergence over time (Pigot & Tobias, 2013). Relevant population and individual properties such as density, individual size and fecundity can decrease from central to edge subpopulations due to varying abiotic environmental effects on individual physiology (e.g. Brown, 1984; Sagarin & Gaines, 2002; Gilman, 2006; Rivadeneira et al., 2010). This core-edge adaptive pattern could lead to a concomitant decrease in competitive

ability from central to edge locations, with important implications for competition at the range edges of overlapping populations. For example, competitive exclusion by local species has been proposed to prevent the success of an invading species (Case & Taper, 2000; Godsoe & Harmon, 2012), halting the range expansion of the latter. Therefore, determining the differences in competitive ability between species overlapping at their respective range-edges will improve our understanding of the influence of ecological interactions on species' range variability.

Coastal biogeographic boundaries provide a model system to assess the influence of competition on the geographic distribution of species (Firth et al., 2009). In the Southeastern Pacific (SE) shore, a well-known transition zone (i.e. subtropical-temperate) extending between 30°S and 41°S concentrates the polar or equatorial range edge of at least 7 intertidal species (Camus, 2001; Broitman et al., 2011). Clear signs of range shifts (i.e. contraction or expansion) have been detected here for six intertidal grazer species (e.g. Rivadeneira & Fernández, 2005). Some of these recently shifted populations have increased species co-occurrences, with the potential for pronounced effects on the fitness of previously established ecological and phylogenetically equivalent species.

The scurrinid limpets *Scurria viridula* and *S. zebrina* co-occur across ~300 km of coastline within the transition zone in the SE Pacific shore. These limpets share several characteristics in terms of resource requirements and habitat use. These species are the most recent species of the *Scurria* clade (Espoz, Lindberg, Castilla, & Simison, 2004) and have a similar generalist diet (Camus, Daroch, & Opazo, 2008). They are distributed across similar intertidal habitats (mid to high levels) characterized by flat, inclined and wave-exposed rocky areas, potentially leading to strong competition between populations (e.g. via

interference or exploitation). The population of *S. viridula* has expanded poleward during the last two decades, from 32.3°S to ca. 33°S and hence into the range of *S. zebrina* (Aguilera et al., 2013) (see dotted red line in Fig. 1). This poleward range shift prompts the question as to whether competition with the "native" *S. zebrina* can prevent or limit the establishment of the "invasive" *S. viridula*. Leading edge populations are usually composed of juveniles, which might reduce their competitive abilities against native competitors (e.g. *Collisella*; Gilman, 2006).

Here we take advantage of the current poleward range shift of the subtropical limpet *S. viridula* to examine experimentally two tightly connected questions: Does *S. zebrina* affect negatively the abundance of the leading-edge populations of *S. viridula*? And inversely, does competition with *S. viridula* reduce the ability of populations of the native species *S. zebrina* to persist in time? We hypothesize that, given the high similarity of traits in *S. viridula* and *S. zebrina*, but their reduced local performance (Navarrete, Wieters, Broitman, & Castilla, 2005) (because of their range edge position, Broitman, Aguilera, Lagos, & Lardies, 2018), each species would have reduced competitive ability in its respective range edge. We predict that (1) for the native species, *S. zebrina*, growth and survival should be lower in the presence of adult or juvenile *S. viridula* (blue arrow in Fig.1) and (2) for the leading edge species. *S. viridula*, growth and survival of juveniles should be lower in the presence of either adult or juvenile *S. zebrina* (red arrow in Fig. 1). In addition to examining direct competitive effects, we also assessed small-scale patterns of segregation or aggregation in *S. viridula* and *S. zebrina*. Such spatial patterns can change the effective strength of competitive interactions between species (Bolker & Pacala, 1997; Dixon, 2009). It is expected that small scale segregation (i.e. larger individual-to-individual patterns)

between the *Scurria* species may allow a few individuals of *S. viridula* to grow to adult size in the leading edge, and thus may play some role facilitating local coexistence. Consequently, small scale (cm) interspecific spatial segregation during resting and foraging (i.e. spatial niche segregation; Aguilera et al., 2013) might result in lower heterospecific deleterious effects. Therefore, we examined the distribution of heterospecific nearest neighbor distances and local occurrences at the range overlap of these *Scurria* species. Given that suitable habitat for settlement is one of the main factors determining species distribution and range shift, especially in intertidal species with larval development (Case et al., 2005; Fenberg & Rivadeneira, 2011), we also explore suitable habitat availability for settlement of the expanding *S. viridula* at its leading edge.

2 | MATERIALS AND METHODS

2.1 Study system, range shift and geographic abundance patterns of *Scurria*.

The coastline of the study region is composed mostly of continuous, wave-exposed rocky shores, with only ~20% interspersed sandy beaches. The northern limit of the range overlap (30°S) between *Scurria viridula* and *Scurria zebrina* is characterized by the presence of a large coastal headland, which is recognized as the strongest upwelling area in north-central Chile (Aguirre, Pizarro, Strub, Garreaud, & Barth, 2012).

Previous comparison of abundance and occurrence data over the period 1998-2008 (Aguilera, Valdivia, & Broitman, 2013) and early records suggests that the southern limit of *S. viridula* has shifted from 29°55’S in 1962 to 31°51’S in 2001 (Rivadeneira & Fernández,

2005) to 33°30’S in our study (see below). Recent field surveys (2010-2011) found juvenile *S. viridula* individuals at 33°30’S constituting a new leading edge of this species (Aguilera et al., 2013). Thus a continuous poleward range expansion has been observed over recent decades.

To estimate the rate of recent range expansion of *S. viridula*, we recorded the abundance of both *S. viridula* and *S. zebrina* at 25 sites located along the coast of Chile from 18°S to 41°S (see Fig.S1 in Supporting Information) over the period January 2013 to March 2016. This was done by considering a minimum of 10, 30 × 30 cm quadrats (see Table S1 in Supporting Information) placed in ~5 to 10 m alongshore transects in the mid-high intertidal zone (1.5 to 2.0 m above MLWL) of each site. Transects were conducted along wave-exposed rocky platforms (ranging from 24 to ~500m^2) with 45-80° slope, where most large- and medium-sized *Scurria* individuals can be found. The size of rocky platform ranged from 20 to 120 m^2 (see further details in Table S1 in Supporting Information). A total of 2054 quadrats were sampled, and in addition each platform was inspected in full to detect the presence or corroborate the absence of *S. viridula* or *S. zebrina* at each site.

Surveys encompassed the entire geographic range of *S. zebrina* (from 41°S to 30°S) and about 80% of the geographic range of *S. viridula*, between 18°S and 33°S, representing about 1300 km of coastline. *Scurria viridula* has been found as far north as 12°S in Peru (Espoz et al., 2004). Sampling sites were arbitrarily selected based on accessibility, but were well within the latitudinal range considered by previous authors (Espoz et al., 2004; Rivadeneira & Fernández, 2005). Most sites, except six sites from 37°S to 41°S, were sampled twice per year, and six sites located between 28°S and 33°S were sampled

exceptionally three to four times per year. This sampling gave us information on temporal changes in abundance and the extension of the range overlap of these *Scurria* species. Thus, we estimated the expansion/contraction of *Scurria* species based on information of their previous northern (*S. zebrina*) and southern (*S. viridula*) range edge along the coast (Rivadeneira & Fernández 2005; Aguilera et al., 2013). In addition, we assessed the spatial variation in body size structure of both species using direct measurements of shell length in a subsample of 14 sites, six of them concentrated within the range overlap. We measured with a caliper (0.2 cm precision) the shell length of all individuals encountered in 15-20 m long and 2.0 m wide transects located in the mid-high intertidal level. A total of 6841 individuals were measured. Differences in shell length between species and among the six sites sampled in the range overlap were analyzed by two-way ANOVA. For this analysis, we use shell length of 3748 individuals (i.e. 312 individual per species and per site). In the case of significant effects, post-hoc Tukey's HSD test was used to compare differences in sites, species and sites by species effects. Analyses were made using the library 'vegan' in the R-environment (R Development Core Team, R, 2017)

2.3 Local interspecific distribution patterns

To evaluate the potential micro-scale segregation of the S*curria* species in the field, we quantified the interspecific spatial co-occurrences at small scales (few centimeters) of the *Scurria* species using two complementary techniques; abundance correlation in quadrats and individual nearest neighbor distances (Fortin & Dale, 2005). Quadrat-based sampling was conducted at 4 sites in the range overlap (Guanaqueros, Limarí, Punta Talca and Huentelauquén) and at one site at the leading edge of *S. viridula* (Quintay; see arrows in

Fig. 1). *Scurria* spatial association at the 900-cm2 scale was determined by estimating the lag-0 Pearson correlation (r) between focal limpet species density across quadrats at each locality, which is recommended for data with autocorrelated structure, and is appropriated to describe and test the spatial aggregation or dispersion of species (Fortin & Dale, 2005). Significance was calculated by a t-test corrected for the effective degrees of freedom based on lag-1 autocorrelation estimates of Moran's I (Dutilleul, 1993). At the same localities, finer spatial distribution, i.e. individual-to-individual distances, was characterized by measuring nearest neighbor distances between conspecific and heterospecific individuals (from *S. viridula* to *S. zebrina* individuals and *vice versa*). The shape of the nearest neighbor distance distribution commonly captures processes operating between individuals scale (e.g. behavior) and reflects positive (aggregation) and negative (segregation) associations (Fortin & Dale, 2005). At each locality we selected four 4 × 4 m areas where we estimated all conspecific and heterospecific nearest neighbor distances starting with a selected individual positioned in the middle of the sampling area. To reduce non-independence of measured heterospecific NN distances, the distances from *S. viridula* to *S. zebrina* and from *S. zebrina* to *S. viridula* were measured in different areas. More than 200 individual-to-individual distances were measured at each locality. We analyzed the frequency of heterospecific nearest neighbor distances across sites by constructing contingency tables. Independence was tested with a log-linear model using likelihood Ratio and Pearson's Chi-square statistic ($\alpha = 0.05$) implemented in the 'MASS' library of the R-environment (R Development Core Team, R, 2017)

2.4 Competition experiments at range edges of *S. viridula* and *S. zebrina*

We conducted field experiments at two sites to test the effects of competition on growth and survival of *S. viridula* and *S. zebrina* at their respective range edges. One site, Punta Talca (30°S), corresponded to the historic range overlap of both species and to the trailing edge of *S. zebrina*. The other site, Las Cruces (33°30'S), is at the leading edge of *S. viridula*. The experiments were conducted at each site on 24, 35 × 35 cm natural rock plots with a slope ranging from 50° to 65° in the mid-high intertidal zone. Experimental studies in Europe (Boaventura, Cancela, Fonseca, & Hawkins, 2003), South Africa (Lasiak & White, 1993) and Australia (Marshall & Keough, 1994) have shown that competition in intertidal limpets is more intense between size classes. Since small size classes dominated the size distribution of both *Scurria* species at their range edges (Aguilera et al., 2013); we focused on interactions among these smaller size classes, and between these and larger, adult individuals. Thus, we examined the effect of *S. viridula* on *S. zebrina* juvenile individuals at the historic range overlap (30°S), separating between intraspecific, intra- and inter-size class effects within *S. zebrina* and the interspecific effect of *S. viridula* juveniles and adults on *S. zebrina* (Fig.1 and see Appendix 2 for details). In a separate experiment with the same general design (Fig. 1), we examined the effect of *S. zebrina* on the invading *S. viridula* at the leading edge of the latter species (33°30'S). This experiment also separated between intraspecific, intra- and inter-size class effects within *S. viridula* from interspecific effects of juveniles and adults *S. zebrina* on juveniles of *S. viridula* (Fig.1, see Appendix 2 for details of the experimental design and field deployment). Intraspecific effects were investigated in both sites at natural and high densities (two or four individuals per plot, respectively; see Table 1 and Fig. 1), and interspecific effects were examined using natural densities of each species (two individuals of each species). The design yielded therefore six treatments in each site; Historic range overlap (HRO): 1) 2 *S. zebrina*

juveniles; 2) 4 *S. zebrina* juveniles; 3) 2 *S. zebrina* adults; 4) 2 *S. zebrina* juveniles plus 2 *S. zebrina* adults; 5) 2 *S. zebrina* juveniles plus 2 *S. viridula* juveniles; and 6) 2 *S. zebrina* juveniles plus 2 *S. virdula* adults. Leading edge (LE): 1) 2 *S. viridula* juveniles; 2) 4 *S. viridula* juveniles; 3) 2 *S. viridula* adults; 4) 2 *S. viridula* juveniles plus 2 *S. viridula* adults; 5) 2 *S. viridula* juveniles plus 2 *S. zebrina* juveniles; and 6) 2 *S. viridula* juveniles plus 2 *S. zebrina* adults (see scheme in Fig. 1). *Scurria* individuals were enclosed in experimental areas (35 × 35 cm) using stainless steel mesh cages (8 cm high, 10 mm mesh size) fastened to the rock with stainless steel screws (see Appendix 2 for details). Treatments were randomly allocated to experimental areas and replicated four times. The experiments were initiated on June 25, 2014 at the Punta Talca and on June 29, 2014 at Las Cruces —both experiments ended on December 5, 2014.

At the beginning and at the end of the experiment we measured shell length and weighed all animals. We calculated growth rates of each limpet as $GR = \frac{(Wt - Wo)}{t}$, where Wo = wet weight at the start, Wt = the wet weight at the end, and t = elapsed time in days. All observations and manipulations were conducted during diurnal low-tide hours.

The predictions that growth of *S. zebrina* at the edge corresponding to the historic range overlap, will be negatively affected by *S. viridula* (Prediction 1), and that growth of *S. viridula* at its leading edge will be negatively affected by the *S. zebrina* (Prediction 2) were tested by analyzing separately the results from two experimental sites. For each site, we used nested ANOVAs for each species and dependent variables. Data were log-transformed to improve variance homogeneity and normality after inspection of residuals. Treatment was considered a fixed factor with six treatments from the two experimental sites: three intraspecific treatments (intra-class interactions: juvenile-juvenile, adult-adult; inter-class:

juvenile-adult interaction) with two densities for juvenile-juvenile intra-class treatment (two and four individuals), and two interspecific treatments (juveniles of each species and adult-juvenile). Plots (experimental areas) were considered independent replicates.— Observations on the individuals within plots represented the sub-replication of each plot.

When significant effects where found, the post-hoc Tukey HSD test was used to compare the conspecific treatments against each other (intraspecific effects), and to mixed-species treatment (interspecific effects). All analyses were made using the 'MASS' library and 'vegan' of the R-environment (R Development Core Team, R, 2017).

To provide accurate estimates of intra- and interspecific interaction (competition) strength, and to account for the variation in limpet density and identity between treatments, we estimated *per capita* intra- and interspecific effects for each species on limpet growth rate (for further details see Appendix S3, and also Aguilera & Navarrete, 2012). For a given species *i* (*S. viridula* and *S. zebrina* in their respective range edges) and size class *k* (i.e. juvenile, adult), the *per capita* intraspecific effects (*ISi*) were calculated as: $IS_{i_k} = \frac{(RHi_k - RNi_k)}{(NHi_k - NNi_k)}$, where RNi_k is the *per capita* response variable (e.g. growth rate) of species *i* of size class *k* (juvenile or adult) in the average or ''natural'' density treatment, RHi_k is the *per capita* response measured in the high density treatment, and NNi_k and NHi_k are the numbers of individuals in the natural and high density treatments, respectively. Thus for each location we estimated three intraspecific effects; juvenile on juvenile (ISi_{jj}), adult on juvenile (ISi_{aj}), and juvenile on adult (ISi_{ja}). For interspecific effects, we considered a total *per capita* interspecific effect (Total_*ISij*) of species j on species *i* calculated as: $Total\_IS_{ij_k} = \frac{(RMij_k - RNi_k)}{Nj_k}$, where $RMij_k$ is the *per capita* response of species *i* measured in

the mixed species enclosures with species *j* of size class *k*, and Nj_k is the number of individuals of species *j* of class *k* present in those enclosures. In order to include the effect of species identity, and to separate the effect of individuals of the same species but of different size-class, we obtained an estimate of "pure" interspecific *per capita* effect $ISij_k$ as; $ISij_k = Total\_ISij_k - ISi_k$ (see Appendix S3 for further details).

2.4.1 Scurria microspatial distribution in experimental cages

Each two weeks per month, we estimate con- and heterospecific nearest neighbor-distances in the experimental enclosures in field experiments. We estimated the probability density function (PDF) for conspecific and heterospecific nearest neighbor distance distribution in each experimental plot. Thus, considering that nearest neighbor distances are continuous random variables, the PDF (i.e. kernel density plot) was estimated as the ratio of individual nearest neighbor distances values *versus* the average total. This analyses provide a useful way to explore individual (con-and heterospecific) segregation or aggregation (Manly, 1997). Density plots were performed with the package 'sm' implemented in R (R Development Core Team, 2017)

2.5 Habitat suitability at the leading edge

To provide information on habitat availability, which can limit geographic distribution and range shifts of limpet species (Fenberg & Rivadeneira, 2011), we examined the proportion of habitats available/unavailable for *S. viridula* settlement across its leading

edge. Analyses were conducted by tracing contours of the coast (from 32º S to 33.3º S) in Google Earth Pro ® at a constant elevation (500 m), determining the length of unsuitable (sandy beach) and suitable (rocky shore) habitats present across the range following previous studies (e.g. Fenberg & Rivadeneira, 2011). Coastal artificial structure length present on either rocky or sandy beaches were also considered in the analyses.

3 | RESULTS

3.1 Range shift and geographic patterns of abundance of *S. viridula* and *S. zebrina*

Field abundance surveys conducted along the coast of Chile from 18°S to 41°S showed parapatric geographic distributions of the *Scurria* species, with an overlap of about 375 km in central Chile (Fig. 2 and Fig. S1 in Supporting Information). *Scurria viridula* showed an poleward range expansion into the range of *S. zebrina* from 32°31' S to 33°33'S in central Chile (see dotted blue lines in Fig. 2); this corresponds to a range shift of ca. 210 km (linear length estimates) in 16 years (2000 to 2016), representing a poleward expansion rate of *S. viridula* of about 13.1 km year $^{-1}$. The mean density of *S. viridula* at the historic range overlap was 0.658 indiv.× 900 cm^{-2} (± 0.062), while at the leading edge it was 0.153 indiv.× 900 cm^{-2} (± 0.0234), showing reduced population density. Mean density for *S. zebrina* was higher at the leading edge of *S. viridula* (2.138 indiv.× 900 cm^{-2} ± 0.169) compared to the historic range overlap (1.035 indiv.× 900 cm^{-2} ± 0.116) which correspond to its northern range limit.

Shell size of the *Scurria* species was variable across the historic range overlap (HRO), showing a significant site × species interaction effect (two-way ANOVA; $F_{5, 3735}$= 4.581; P = 0.00036). The recently established population of *S. viridula* at the leading edge (located from 33.11° to 33.33°S) had comparable individual shell size to other range edge populations (see Fig. S2 in Supporting Information). The more equatorward population of *S. viridula*, at 18°S showed a median shell size of 25 mm, slightly less than the southernmost population at 33.33°S, which had a median value of 32 mm (Fig. S2). The shell size of *S. zebrina* was different from that found for *S. viridula* at Punta Talca at the historic range overlap (Tukey HSD test; diff = -0.556; P <0.0001), but median values for adult limpets were 29 and 31 mm, respectively (Fig. S2). Significant differences were found between the species at the leading edge of *S. viridula* at Las Cruces (Tukey HSD test; diff = -0.619; P = 0.00002), but not at Pelancura located in the same range (Tukey HSD test; diff = -0.0596; P = 0.998).

3.2 Local interspecific distribution patterns

Interspecific abundance distribution patterns estimated for quadrats (900cm^2) at the historic range overlap showed a positive, but low, significant correlation (r = +0.0223) at only one site (Huentelauquén, 31.38° S; see Table S2 in Supporting Information). A negative, but not statistically significant, value (r = -0.0741) was observed at the leading edge of *S. viridula* (Quintay, 33.11°S; see Table S2, Supporting Information) suggesting that the pattern of individual heterospecific segregation was not strong enough to be detectable among quadrats.

We determined 813 heterospecific individual nearest neighbor distances (*S. viridula* to *S. zebrina*) in the field across the historic range overlap, and at the leading edge of *S. viridula*. Overall nearest neighbor median distance between the *Scurria* species was 14.5 cm across the range considered (see Fig. S3 in Supporting Information); about 300 individuals (36.9%) showed distances between 0 and 10 cm. A log linear model showed non-independence of nearest neighbor distances across sites (Likelihood Ratio = 419, P = 0.0125), suggesting individuals of the same species are more likely to cluster than heterospecifics in the sampling sites. This was reflected in the slightly higher distances between heterospecifics at the leading edge of *S. viridula* (median distances between 17.2 cm and 19.7 cm), compared to sites located further north (median distances between 14.3 and 15 cm; Fig. S3).

3.3 Competition experiments at range edges of *S. viridula* and *S. zebrina*

At the end of the field experiments (200 days) in the historic range overlap, no differences were observed in *S. zebrina* individual growth rate (i.e. wet weight) in the intraspecific treatments (Fig. 3a and b, Table 2). No significant change was found in the growth rate of juvenile *S. zebrina* enclosed with juvenile or adult *S. viridula* at the historic range overlap or the leading edge (Fig. 3a, Table 2). Juvenile *S. viridula* growth rate was significantly lower in the presence of adult *S. zebrina* at the leading edge (SVj+SZa; Fig. 3b, Table 2) in contrast to the high growth achieved when combined with adults of the same species (SVj+SVa) which was ~2 times higher (Fig. 3b). We also found a significant reduction of adult *S. viridula* enclosed with juvenile *S. zebrina* at the historic range overlap (SVa+SZj, Fig. 3b, Table 2). In that site, there was high mortality of juvenile *S. zebrina* individuals in

the high-density treatment (i.e. independent of *S. viridula*; 4SZj; see Fig. S4 in Supporting Information). No mortality of juvenile *S. viridula* enclosed with adult or juvenile *S. zebrina* (or *vice versa*) was observed (Fig. S4).

Intraspecific effects (IS_{ik}) of juvenile on juvenile and adult on juvenile *S. zebrina* growth rate at the historic range overlap (i.e. white symbols in Fig. 4a: SZj-SZj, and SZa-SZj, respectively) were not significant (95% CI cross zero; Fig. 4a). Similarly, no significant interspecific effect of *S. viridula* on *S. zebrina* (i.e. SVj-SZj, SVa-SZj) was observed (black symbols in Fig. 4a). At the leading edge of *S. viridula* at Las Cruces (33°S), no significant intraspecific effect of juvenile or adult *S. viridula* was detected (white symbols in Fig. 4b). Instead, we found that adult *S. zebrina* had negative and significant (95% CI do not cross zero) *per capita* effects on the growth rate of juvenile *S. viridula* (SZa-SVj, Fig. 4b).

3.3.1 *Scurria* microspatial distribution in experimental cages

Nearest neighbor distances of enclosed *S. zebrina* juvenile individuals at the historic range overlap showed a peak between zero and 40 mm, suggesting a more aggregated pattern (see purple band in Fig. S5a, in Supporting Information) than for juvenile to adult *S. zebrina* conspecifics which appeared more segregated, peaking at about 200 mm (turquoise band in Fig. S5a). Distances of juvenile *S. zebrina* to both adult and juvenile *S. viridula* were on average between 50-80 mm (see orange and green bands, respectively, in Fig. S5a, respectively). At the leading edge of *S. viridula*, juvenile *S. viridula* individuals showed both aggregated (0-50 mm) and segregated (~250 mm) intraspecific patterns through the study, (see purple band in Fig. S5b). Juvenile individuals of *S. viridula* tended to be at

distances of 50-100 mm from both adult and juvenile *S. zebrina* individuals (see orange and green bands in Fig. S5b, respectively).

3.4 Habitat suitability at the leading edge

About 54% of the coastline at the leading edge of *S. viridula* is made up of wave-exposed rocky platforms, a suitable habitat for settlement, that are similar to those occupied by the species in the northern part of the range. About 30% of the coastline is made up of sandy beaches that are unsuitable habitat for settlement (see Fig. S6), and ~9% correspond to hard artificial structures (e.g. granite breakwaters, concrete seawalls, pontoons) which are interspersed among sandy and rocky habitats (see Fig. S6).

4 | DISCUSSION

Our study is among the first to examine the ecological dynamics at the range overlap of equivalent established and range-expanding species and that test experimentally the role of biotic interactions on species range shift, linking interaction strength and spatial surveys. Our field surveys, encompassing a large fraction of the geographic distribution of the two *Scurria* species from northern to central Chile, showed that *S. viridula* populations have recently expanded poleward to 33.33°S, about 210 km south of the previously reported distribution. Both juvenile and adult *S. viridula* individuals were present at this new leading edge, suggesting successful colonization although at much reduced population density. Field experiments showed that adult *S. zebrina* significantly reduced growth of juvenile *S.*

viridula at its leading edge, but that *S. viridula* had no effect on *S. zebrina* at its northern range limit corresponding to the historic range overlap of both species. Small scale interspecific spatial segregation of individuals, which likely resulted from interference competition, may reduce to some extent the deleterious effects of competition and help explain the occurrence of adult *S. viridula* at the leading edge. Thus while there are important missing pieces of information that are necessary for a full understanding of the processes leading to the poleward range expansion of *S. viridula* and stasis in *S. zebrina*, which are discussed below, our results demonstrate differential effects of interspecific competition on the distribution of the two limpet species, with a potentially significant role in reducing range expansion of *S. viridula*. Finally, they show that competition can be asymmetric between two equivalent grazers at their range limits, with the range-expanding species counterintuitively not provoking a contraction of the resident grazer species.

4.1 Geographic distribution and *Scurria* occurrence

A decline in abundance towards a species' range boundary is often interpreted as evidence of a reduction in individual success (i.e. growth rate, survival probability), and is usually assumed to reflect a decline in suitable environmental conditions (e.g. Brown et al., 1996; Case & Taper, 2000). In our study, however, comparatively high growth rates and the occurrence of both juvenile and adult *S. viridula* at its leading edge suggests that environmental conditions are not limiting the performance of this species toward its range edge. *S. viridula* juvenile individuals had a positive mean growth rate (0.0172 ± 0.0026 g × day^{-1}) at natural densities in the enclosure experiment at the leading edge (2 ind./ 900 cm^2), which was similar to the growth rate observed at Punta Talca, further north (0.0174 ±

0.0029 g × day^{-1}). Even an increase in density in experimental enclosures (4 ind./ 900 cm^2) at the leading edge had a marginal but non-significant effect on the growth rate of *S. viridula* individuals (0.0157 ± 0.0011 g × day^{-1}). These results suggest that even under the potentially stressful conditions experienced by individuals at a leading edge of distribution (e.g. Fenberg & Rivadeneira, 2011), *S. viridula* can sustain similar individual growth rates to those observed at sites towards the center of the range. This raises the question of why the expanding species is being negatively affected by interspecific competition, even when individuals do not seem to be compromised physiologically by environmental constraints.

4.2 Competition and species range overlap

Experimental and manipulative tests of the role of competition in setting species range edges remain scarce, largely due to the logistic difficulties associated with scaling up local processes to large scales (see for example Cunningham et al., 2009; Davis, Jenkinson, Lawton, Schorrocks, & Wood, 2001; Godsoe et al., 2015; Hu & Jiang, 2018). Our study is therefore a timely experimental demonstration of the importance of considering local interspecific interactions when interpreting range shifts of species. Grazing limpets compete for space and food on many rocky shores (e.g. Branch, 1976; Creese & Underwood, 1982; Boaventura et al., 2002; Firth & Crowe, 2010; Aguilera & Navarrete, 2012). However, food supply (e.g. microalgae and ephemeral algae) is expected to be relatively high across the range considered in our study due to high nutrient availability (Wieters, 2005). In our field experimental plots the main algal items consumed by the *Scurria* species were present even at the end of the experiments (see Table S3 in Supporting Information). Exploitation competition for food may therefore be less important

than other kinds of competition, such as interference, among *Scurria* limpets. The existence of competition under natural conditions is supported by the observations of small-scale spatial segregation between adult *Scurria* species at scales of ~150 mm (Aguilera et al., 2013, this study). Although different processes may affect individual-to-individual distances in limpets, such as substratum topographic complexity (Chapman & Underwood, 1994) and micro-spatial thermal patterns (Chapperon & Seuront, 2011), interspecific individual encounter reduction by individual dispersion has been described as an effective way to reduce interspecific competition (Branch, 1975). Micro-scale segregation may allow a few individuals of *S. viridula* grow to adult size, and if so it may play some role in facilitating local coexistence. However, the low population densities suggest that the small segregation is insufficient to overcome the deleterious effects of competition on individual performance and allow local populations to sustain positive population growth when rare, a necessary requirement to allow for stable coexistence (Chesson, 2000; Shinen & Navarrete, 2014; Siepielski & Mcpeek, 2010).

Our experimental manipulations support the hypothesis of asymmetric interspecific competition: we found lower growth rates of juvenile *S. viridula* at its leading edge when enclosed with adult *S. zebrina*. While this competitive effect could lead to the eventual local extinction of the expanding *S. viridula* by the local *S. zebrina*, competitive exclusion is not necessary for competition to play a major role in stopping the advancement of an invader or range-expanding species. For example, interspecific competition could reduce larval output below the level that guarantees a minimum level of self-replenishment (Aiken & Navarrete, 2014; Lett, Nguyen-Huu, Cuif, Saenz-Agudelo, & Kaplan, 2015) of the invading species. This can make leading populations the sink of larvae produced from

upstream populations, which might halt the advancing front some distance downstream from the last self-maintained population. Interestingly, population size plays an important role in the leading range edge of species with longer pelagic larval development (Pringle, Byers, He, Pappalardo, & Wares, 2017), highlighting the indirect role that competition can play in species with large dispersal potential. Since other species with pelagic larvae are expanding their distributions at comparable rates to those of *S. viridula* in the eastern Pacific (e.g. the limpet *Lottia orbignyi;* 13.8 km *year $^{-1}$, the whelk *Thais haemastoma*; 15.9 km*year^{-1}) (Rivadeneira & Fernández, 2005; Sorte, Williams, & Carlton, 2010), it would be interesting to evaluate the role of biotic resistance by means of competition of the native assemblage in influencing species' range shift. Our main results suggest competitive interactions could have an important role influencing the geographic distribution of equivalent species in combination with physical and biotic processes operating on larval dispersal and settlement.

4.3 Habitat suitability and *Scurria* range limits

The combination of scarcity of suitable habitat and dispersal limitation is one of the main mechanisms determining species' range borders (Brown et al., 1996; Case et al., 2005; Holt & Keitt, 2005). In the absence of dispersal information, our examination of the role of habitat suitability in limiting *S. viridula* expansion by exploring the availability of suitable (rocky shore) *versus* unsuitable (sandy beach) habitat across the leading edge seems useful in this context (e.g. Fenberg & Rivadeneira, 2011; see Fig. S6 in Supporting Information). We found that the coastline present at the leading edge of *S. viridula* is predominantly (>51%) made up of wave-exposed rocky platforms that are similar to those occupied by the

species in the northern part of the range. However, 30% is made up of sandy beaches (unsuitable habitat; see Fig. S6). Extensive sandy beaches present in this area (~8-12 km long) could represent a barrier for the dispersal of species with short pelagic larval duration (PLD) (Lester, Ruttenberg, Gaines, & Kinlan, 2007), although most numerical models of realistic coastal oceans suggest that even species with PLD of 5-10 days can disperse from tens to hundreds of kilometers (Aiken & Navarrete, 2014; Lett et al. 2015). Therefore, it is unlikely that the observed sandy beaches within the region represent an important dispersal barrier. We found that about ~9% of the coastline is made up of hard artificial structures, which are interspersed among sandy and rocky habitats (see Fig. S6). Previous studies have shown that artificial infrastructures like breakwaters can reduce distances between populations and serve as "stepping-stones" for the dispersal of rocky intertidal species with limited dispersal capacity (Dong, Huang, Wang, Li, & Wang, 2016; Firth et al., 2016). *Scurria viridula* commonly uses artificial breakwaters and seawalls as habitat, especially in highly urbanized coasts such as in central Chile (MA Aguilera unpublished), further assisting effective dispersal across sandy beaches.

5 | Concluding remarks

Our results suggest that an ecological interaction such as asymmetric competition could contribute to maintain stability in the location of a species range overlap (i.e. populations are prevented from advancing for a period of time; Phillips, 2012). Our results show that juveniles of an advancing species can be sensitive to interference by the native or established species potentially leading to the inhibition of expansion. Our observations also suggest that fine-scale spatial segregation between grazer species could facilitate further

poleward expansion. If the range-expanding grazer is successful at settling in artificial substrata, it may suggest a trade-off in competitive *versus* colonization abilities between the species (Tilman, 1994). Therefore asymmetrical competition, finer-scale niche segregation and opportunistic exploitation of novel habitats may be critical to understand the mechanisms contributing to maintain the stability of species ranges.

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Author contributions: M.A. conceived the idea; M.A., N.V. conduct the surveys; M.A., S.A.N. design the field experiments; M.A. conduct the field experiments and analyzed the data; M.A., N.V., B.B., S.A.N. and S.J. wrote the paper.

Data Accessibility.

Data associated with this manuscript will be available in the Dryad Digital Repository.

Supporting Information.

Fig. S1. Scatterplot of the density of *Scurria* species recorded along the coast of Chile.

Fig. S2. Shell size of *Scurria* species measured at different latitudes.

Fig. S3. Heterospecific individual nearest neighbor distances measured for both *Scurria* species at HRO and LE.

Fig. S4. Total number of dead individuals found in enclosures in field experiments.

Fig. S5. Density plot of the intra and heterospecific nearest neighbor distances estimated inside experimental enclosures.

Fig. S6. Proportion of suitable and unsuitable habitat from 32°S to 33°S for *S. viridula* expansion.

Table S1. Summary of localities sampled during the study and details of field surveys.

Table S2. Pearson's spatial correlation between *Scurria* species.

Table S3. Average percent cover (%) of algal groups present inside experimental enclosures at the end of field experiments.

Appendix S1. Nearest neighbor distance distribution analyses.

Appendix S2. Field experimental procedures, design and set up.

Appendix S3. Details of interaction strength estimations for field experiments.

REFERENCES

Aguilera, M. A., & Navarrete, S. A. (2012). Interspecific competition for shelters in territorial and gregarious intertidal grazers: consequences for individual behaviour. *PLoS ONE*, *7*(9), e46205. doi:10.1371/journal.pone.0046205

Aguilera, M. A., Valdivia, N., & Broitman, B. R. (2013). Spatial niche differentiation and coexistence at the edge: co-occurrence distribution patterns in *Scurria* limpets. *Marine Ecology Progress Series*, *483*, 185–198. doi:10.3354/meps10293

Aguirre, C., Pizarro, Ó., Strub, P. T., Garreaud, R., & Barth, J. A. (2012). Seasonal dynamics of the near-surface alongshore flow off central Chile. *Journal of Geophysical Research: Oceans*, *117*(November 2011), 1–17. doi:10.1029/2011JC007379

Aiken, C. M., & Navarrete, S. A. (2014). Coexistence of competitors in marine metacommunities: Environmental variability, edge effects, and the dispersal niche. *Ecology*, *95*(8), 2289–2302. doi:10.1890/13-0472.1

Araújo, M. B., & Luoto, M. (2007). The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography*, *16*, 743–753. doi:10.1111/j.1466-8238.2007.00359.x

Araújo, M. B., & Rozenfeld, A. (2013). The geographic scaling of biotic interactions. *Ecography*, *37*, 406–415. doi:10.1111/j.1600-0587.2013.00643.x

Boaventura, D., Cancela Da Fonseca, L., & Hawkins, S. J. (2002). Analysis of competitive interactions between the limpets *Patella depressa* Pennant and *Patella vulgata* L. on the northern coast of Portugal. *Journal of Experimental Marine Biology and Ecology*, *271*, 171–188. doi:10.1016/S0022-0981(02)00044-8

Boaventura, D., Cancela, L., Fonseca, D., & Hawkins, S. J. (2003). Size Matters : competition within populations of the limpet *Patella depressa*. *Journal of Animal Ecology*, *72*(3), 435–446.

Bolker, B., & Pacala, S. W. (1997). Using moment equations to understand stochastically driven spatial pattern formation in ecological systems. *Theoretical Population Biology*, *52*, 179–197. doi:10.1006/tpbi.1997.1331

Branch, G. (1975). Mechanisms reducing intraspecific competition in *Patella* spp .: migration, differentiation and territorial behaviour. *Journal of Animal Ecology*, *44*(2), 575–600.

Branch, G. (1976). Interspecific competition experienced by South African *Patella* species Journal. *Journal of Animal Ecology*, *45*, 507–529.

Broitman, B. R., Aguilera, M. A., Lagos, N. A., & Lardies, M. A. (2018). Phenotypic plasticity at the edge: contrasting population level responses at the overlap of the leading and rear edges of the geographical distribution of two *Scurria* limpets. *Journal of Biogeography*, *in press*.

Broitman, B. R., Véliz, F., Manzur, T., Wieters, E. A., Finke, R., Fornes, P., … Navarrete, S. A. (2011). Geographic variation in diversity of wave exposed rocky intertidal communities along central Chile. *Revista Chilena de Historia Natural*, *143*, 143–154.

Brown, J. H. (1984). On the relationship between abundance and distribution of species. *The American Naturalist*, *124*, 255–279.

Brown, J. H., Stevens, G. C., & Kaufman, D. M. (1996). The geographic range: size, shape, and internal structure. *Annual Review of Ecology and Systematics*, *27*, 597–623. doi:10.1146/annurev.ecolsys.27.1.597

Camus, P., Daroch, K., & Opazo, L. (2008). Potential for omnivory and apparent intraguild predation in rocky intertidal herbivore assemblages from northern Chile. *Marine Ecology Progress Series*, *361*, 35–45. doi:10.3354/meps07421

Case, T. J., Holt, R. D., Mcpeek, M. A., & Keitt, T. H. (2005). The community context of species ' borders : ecological and evolutionary perspectives. *Oikos*, *108*, 28–46.

Case, T. J., & Taper, M. (2000). Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. *The American Naturalist*, *155*, 583–605.

Chapman, M. G., & Underwood, A. J. (1994). Dispersal of the intertidal snail, *Nodilittorina pyramidalis*, in response to the topographic complexity of the substratum. *Journal of Experimental Marine Biology and Ecology*, *179*(94), 145–169. doi:10.1016/0022-0981(94)90111-2

Chapperon, C., & Seuront, L. (2011). Space-time variability in environmental thermal properties and snail thermoregulatory behaviour. *Functional Ecology*, *25*(5), 1040–1050. doi:10.1111/j.1365-2435.2011.01859.x

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, *31*, 343–358. Retrieved from http://www.jstor.org/stable/10.2307/221736

Cunningham, H. R., Rissler, L. J., & Apodaca, J. J. (2009). Competition at the range boundary in the slimy salamander : using reciprocal transplants for studies on the role of biotic interactions in spatial distributions. *Journal of Animal Ecology*, 52–62. doi:10.1111/j.1365-2656.2007.0

Davis, A. J., Jenkinson, L. S., Lawton, J. H., Schorrocks, B., & Wood, S. N. (2001). Making mistakes when predicting shifts in species range in response to global warming. *Nature*, *409*, 363–366. doi:10.1038/35055575

Dixon, P. (2009). Testing spatial segregation using a nearest-neighbor contingency table. *Ecology*, *75*(7), 1940–1948.

Dong, Y. W., Huang, X. W., Wang, W., Li, Y., & Wang, J. (2016). The marine "great wall" of China: Local- and broad-scale ecological impacts of coastal infrastructure on intertidal macrobenthic communities. *Diversity and Distributions*, *22*, 731–744. doi:10.1111/ddi.12443

Dutilleul, P. (1993). Spatial heterogeneity and the design of ecological field experiments. *Ecology*, *74*(6), 1646–1658.

Espoz, C., Lindberg, D. R., Castilla, J. C., & Simison, W. B. (2004). Los patelogastrópodos intermareales de Chile y Perú. *Revista Chilena de Historia Natural*, *77*(1), 257–283.

Fenberg, P. B., & Rivadeneira, M. M. (2011). Range limits and geographic patterns of abundance of the rocky intertidal owl limpet, *Lottia gigantea*. *Journal of Biogeography*, *38*, 2286–2298. doi:10.1111/j.1365-2699.2011.02572.x

Firth, L. B., Crowe, T. P., Moore, P., Thompson, R. C., & Hawkins, S. J. (2009). Predicting impacts of climate-induced range expansion: An experimental framework and a test involving key grazers on temperate rocky shores. *Global Change Biology*, *15*, 1413–1422. doi:10.1111/j.1365-2486.2009.01863.x

Firth, L. B., Knights, A. M., Bridger, D., Evans, A. J., Mieszkowska, N., Moore, P. J., … Hawkins, S. J. (2016). Ocean Sprawl: Challenges and Opportunities for Biodiversity Management in a Changing World. *Oceanography and Marine Biology Annual Review*, *54*, 193–269.

Fortin, M.-J., & Dale, M. R. T. (2005). *Spatial Analysis: a guide to ecologists* (Fourth, p. 360). Cambridge: Cambridge University Press.

Gilman, S. E. (2006). The northern geographic range limit of the intertidal limpet *Collisella scabra*: A test of performance, recruitment, and temperature hypotheses. *Ecography*, *29*(June), 709–720. doi:10.1111/j.0906-7590.2006.04572.x

Godsoe, W., & Harmon, L. J. (2012). How do species interactions affect species distribution models? *Ecography*, *35*(9), 811–820. doi:10.1111/j.1600-0587.2011.07103.x

Godsoe, W., Jankowski, J., Holt, R. D., & Gravel, D. (2017). Integrating biogeography with contemporary niche theory. *Trends in Ecology and Evolution*, *32*(7), 488–499. doi:10.1016/j.tree.2017.03.008

Godsoe, W., Murray, R., & Plank, M. J. (2015). The effect of competition on species' distributions depends on coexistence, rather than scale alone. *Ecography*, *38*(December 2014), 1071–1079. doi:10.1111/ecog.01134

Holt, R. D., & Keitt, T. H. (2005). Species' borders: a unifying theme in ecology. *Ecography*, *1*, 3–6.

Hu, J., & Jiang, J. (2018). Inferring ecological explanations for biogeographic boundaries of parapatric Asian mountain frogs. *BMC Ecology*, *18*, 1–11. doi:10.1186/s12898-018-0160-5

Lasiak, T. A., & White, D. R. (1993). Microalgal food resources and competitive interactions among the intertidal limpets *Cellana capensis* (Gmelin, 1791) and *Siphonaria concinna* Sowerby, 1824. *South African Journal of Marine Science*, *13*, 97–108. doi:10.2989/025776193784287419

Lester, S., Ruttenberg, B. I., Gaines, S. D., & Kinlan, B. P. (2007). The relationship between dispersal ability and geographic range size. *Ecology*, *10*, 745–758. doi:10.1111/j.1461-0248.2007.01070.x

Lett, C., Nguyen-Huu, T., Cuif, M., Saenz-Agudelo, P., & Kaplan, D. M. (2015). Linking local retention, self-recruitment, and persistence in marine metapopulations. *Ecology*, *96*(8), 2236–2244. doi:10.1890/14-1305.1

Marshall, P. A., & Keough, M. J. (1994). Asymmetry in intraspecific competition in the limpet *Cellana tramoserica* (sowerby). *Journal of Experimental Marine Biology and Ecology*, *177*, 121–138. doi:10.1016/0022-0981(94)90147-3

Navarrete, S. A., Wieters, E. A., Broitman, B. R., & Castilla, J. C. (2005). Scales of benthic-pelagic coupling and the intensity of species interactions: from recruitment limitation to top-down control. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 18046–18051. doi:10.1073/pnas.0509119102

Phillips, B. L. (2012). Range shift promotes the formation of stable range edges. *Journal of Biogeography*, *39*(January 2012), 153–161. doi:10.1111/j.1365-2699.2011.02597.x

Pigot, A. L., & Tobias, J. A. (2013). Species interactions constrain geographic range expansion over evolutionary time. *Ecology Letters*, *16*, 330–338. doi:10.1111/ele.12043

Pringle, J., Byers, J. E., He, R., Pappalardo, P., & Wares, J. (2017). Ocean currents and competitive strength interact to cluster benthic species range boundaries in the coastal ocean. *Marine Ecology-Progress Series*, *567*, 29–40.

Rivadeneira, M. M., & Fernández, M. (2005). Shifts in southern endpoints of distribution in rocky intertidal species along the south-eastern Pacific coast. *Journal of Biogeography*, *32*, 203–209. doi:10.1111/j.1365-2699.2004.01133.x

Rivadeneira, M. M., Hernáez, P., Antonio Baeza, J., Boltaña, S., Cifuentes, M., Correa, C., … Thiel, M. (2010). Testing the abundant-centre hypothesis using intertidal porcelain crabs along the Chilean coast: Linking abundance and life-history variation. *Journal of Biogeography*, *37*, 486–498. doi:10.1111/j.1365-2699.2009.02224.x

Sagarin, R., & Gaines, S. (2002). The "abundant centre"distribution: to what extent is it a biogeographical rule? *Ecology Letters*, *5*, 137–147. Retrieved from http://onlinelibrary.wiley.com/doi/10.1046/j.1461-0248.2002.00297.x/full

Shinen, J. L., & Navarrete, S. A. (2014). Lottery Coexistence on rocky shores: weak niche differentiation or equal competitors engaged in neutral dynamics? *The American Naturalist*, *183*(3), 342–362. doi:10.1086/674898

Siepielski, A., & Mcpeek, M. A. (2010). On the evidence for species coexistence: a critique of the coexistence program. *Ecology*, *91*(11), 3153–3164.

Soberón, J. M. (2010). Niche and area of distribution modeling: A population ecology perspective. *Ecography*, *33*(November), 159–167. doi:10.1111/j.1600-0587.2009.06074.x

Sorte, C. J. B., Williams, S. L., & Carlton, J. T. (2010). Marine range shifts and species introductions: Comparative spread rates and community impacts. *Global Ecology and Biogeography*, *19*, 303–316. doi:10.1111/j.1466-8238.2009.00519.x

Tilman, D. (1994). Competition and biodiversity in spatially structured habitats. *Ecology*, *75*, 2–16.

Vermeij, G. J. (2005). From Europe to America: pliocene to recent trans-Atlantic expansion of cold-water North Atlantic molluscs. *Proceedings of the Royal Society B: Biological Sciences*, *272*(September), 2545–2550. doi:10.1098/rspb.2005.3177

Wieters, E. A. (2005). Upwelling control of positive interactions over mesoscales: a new link between bottom-up and top-down processes on rocky shores. *Marine Ecology Progress Series*, *301*, 43–54.

Figure Captions

Figure 1. Schematic model system and map of the geographic overlap of *Scurria* species and experimental set-up. Previous *Scurria* occurrences generated an historic range overlap, (HRO) at 30°S to 32°S (also indicated as green arrows in the map). Recent (2013) evidence suggests *Scurria viridula* expanded its polar range edge (dotted red line) conforming a new leading edge (LE) (around 33°30'S). Red and blue lines show the model (scheme) and real (map) range distribution of *S. viridula* and *S. zebrina*, respectively, along the coast of Chile. Green arrows in the map show also the locations were field experiments were performed.

Field experiments (see boxes for intra- and interspecific effects) were conducted at both HRO and LE, which test the role of competition in contributing to reduce range expansion and promote range contraction. It was expected that at their historic range overlap *S. viridula* would reduce the growth rate of *S. zebrina* promoting its contraction (red arrow), while at the leading edge, it was expected *S. zebrina* might contribute to reduction of *S. viridula* expansion (blue arrow). Given both *Scurria* species populations present at their range edge are composed of juvenile individuals, and have lower densities, field experiments considered competitive effects of different size classes; adult (*S. zebrina*; SZa, *S. viridula*; SVa) and juvenile (SZj, SVj) individuals, and natural (×2 individuals; intra-and interspecific) and increased (×4 individuals; intraspecific) densities for both *Scurria* species.

Figure 2. Latitudinal occurrence (i.e. the proportion of quadrats were a species was found) of *Scurria viridula* and *S. zebrina* observed from 18°S to 41°S along the coast of Chile. The red box show the geographic range where the species co-occur in north-central Chile, their historic range overlap (HRO), while the dotted-blue box depicts the leading edge of *S. viridula* (LE). A map of Chile is shown below, indicating (with blue arrows) the northern (18°S) and southern (41°S) sites considered in the geographic surveys and the *Scurria* species range overlap (dotted red lines).

Figure 3. Average (± SE) change in wet weight of *Scurria zebrina* (a) and *S. viridula* (b) recorded in experimental arenas at the historic range overlap and the leading edge of *S. viridula*. SZ: *S. zebrina*, SV: *S. viridula*. Subscripts "j" and "a" denote "juvenile" and "adult" individuals for each species. Means with the same letters were not statistically significant by Tukey's multiple comparison test (α=0.05).

Figure 4. *Per capita* intraspecific effects (white symbols), and 'pure' interspecific effects (black symbols) on growth rate (wet weight), estimated for juvenile on juvenile, juvenile on adult and adult on juvenile individuals of the corresponding focal species considered in field experiments conducted at the historic range overlap (a) and at the leading edge of *S. viridula* (b). Bars correspond to confidence intervals (95%) estimated by a bootstrapping procedure. Subscripts "j" and "a" denote "juvenile" and "adult" individuals, respectively.

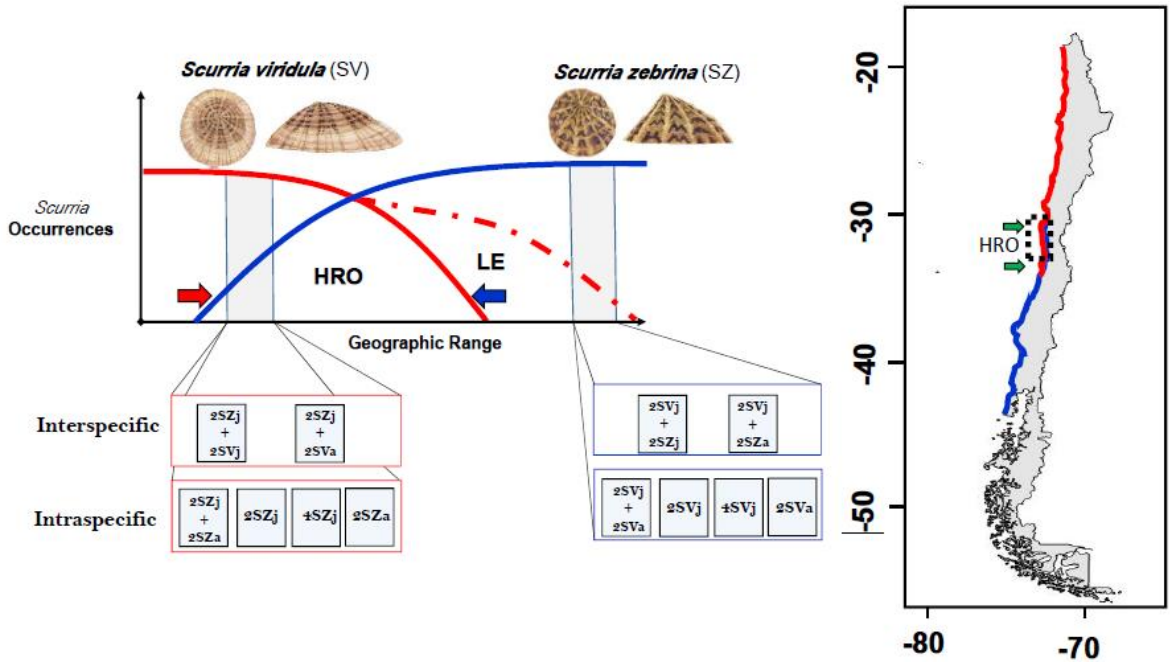
Scurria viridula (SV)
Scurria zebrina (SZ)
Scurria
Occurrences
HRO
LE
Geographic Range
Interspecific
Intraspecific
2SZj + 2SVj
2SZj + 2SVa
2SZj + 2SZa
2SZj
4SZj
2SZa
2SVj + 2SZj
2SVj + 2SZa
2SVj + 2SVa
2SVj
4SVj
2SVa
-20
-30
-40
-50
-80
-70
HRO

Figure 1

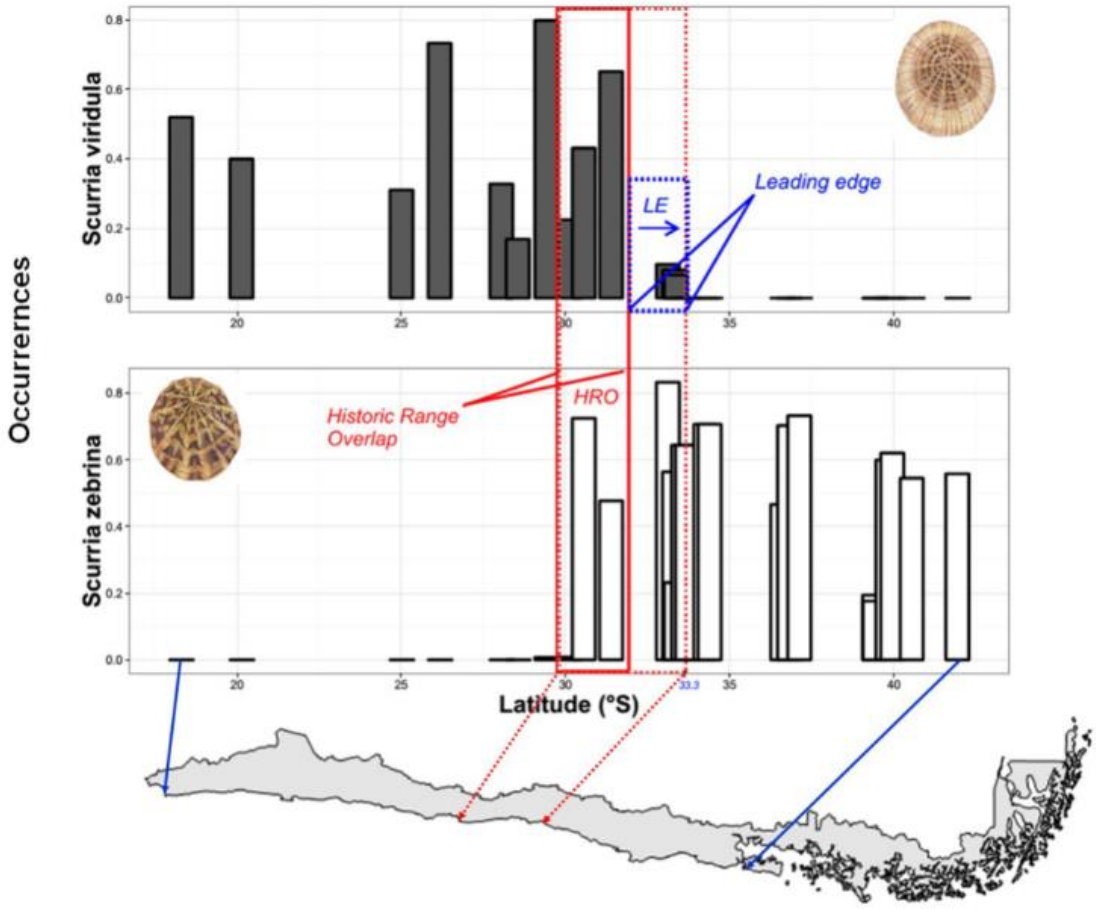
Occurrences
Scurria viridula
Scurria zebrina
Leading edge
LE
Historic Range
Overlap
HRO
Latitude (°S)
0.0
0.2
0.4
0.6
0.8
20
25
30
33.3
35
40

Figure 2

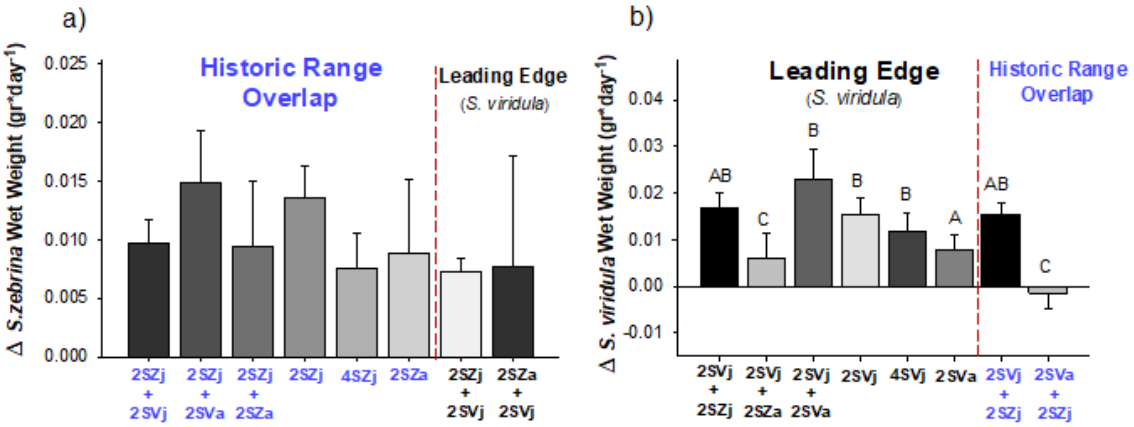
a)
Historic Range Overlap
Leading Edge
(S. viridula)
Δ S.zebrina Wet Weight (gr*day-1)
0.025
0.020
0.015
0.010
0.005
0.000
2SZj + 2SVj
2SZj + 2SVa
2SZj + 2SZa
2SZj
4SZj
2SZa
2SZj + 2SVj
2SZa + 2SVj
b)
Leading Edge
(S. viridula)
Historic Range Overlap
Δ S. viridula Wet Weight (gr*day-1)
0.04
0.03
0.02
0.01
0.00
-0.01
AB
C
B
B
B
A
AB
C
2SVj + 2SZj
2SVj + 2SZa
2SVj + 2SVa
2SVj
4SVj
2SVa
2SVj + 2SZj
2SVa + 2SZj

Figure 3

Supporting Information. Figures, tables & Appendices

Asymmetric competitive effects during species range expansion: an experimental assessment of interaction strength between 'equivalent' grazer species at their range overlap

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Supporting Information.

Fig. S1. Scatterplot of the density of *Scurria* species recorded along the coast of Chile.

Fig. S2. Shell size of *Scurria* species measured at different latitudes.

Fig. S3. Heterospecific individual nearest neighbor distances measured for both *Scurria* species at HRO and LE.

Fig. S4. Total number of dead individuals found in enclosures in field experiments.

Fig. S5. Density plot of the intra and heterospecific nearest neighbor distances estimated inside experimental enclosures.

Fig. S6. Proportion of suitable and unsuitable habitat from 32°S to 33°S for *S. viridula* expansion.

Table S1. Summary of localities sampled during the study and details of field surveys.

Table S2. Pearson's spatial correlation between *Scurria* species.

Table S3. Average percent cover (%) of algal groups present inside experimental enclosures at the end of field experiments.

Appendix S1. Nearest neighbor distance distribution analyses.

Appendix S2. Field experimental procedures, design and set up.

Appendix S3. Details of interaction strength estimations for field experiments.

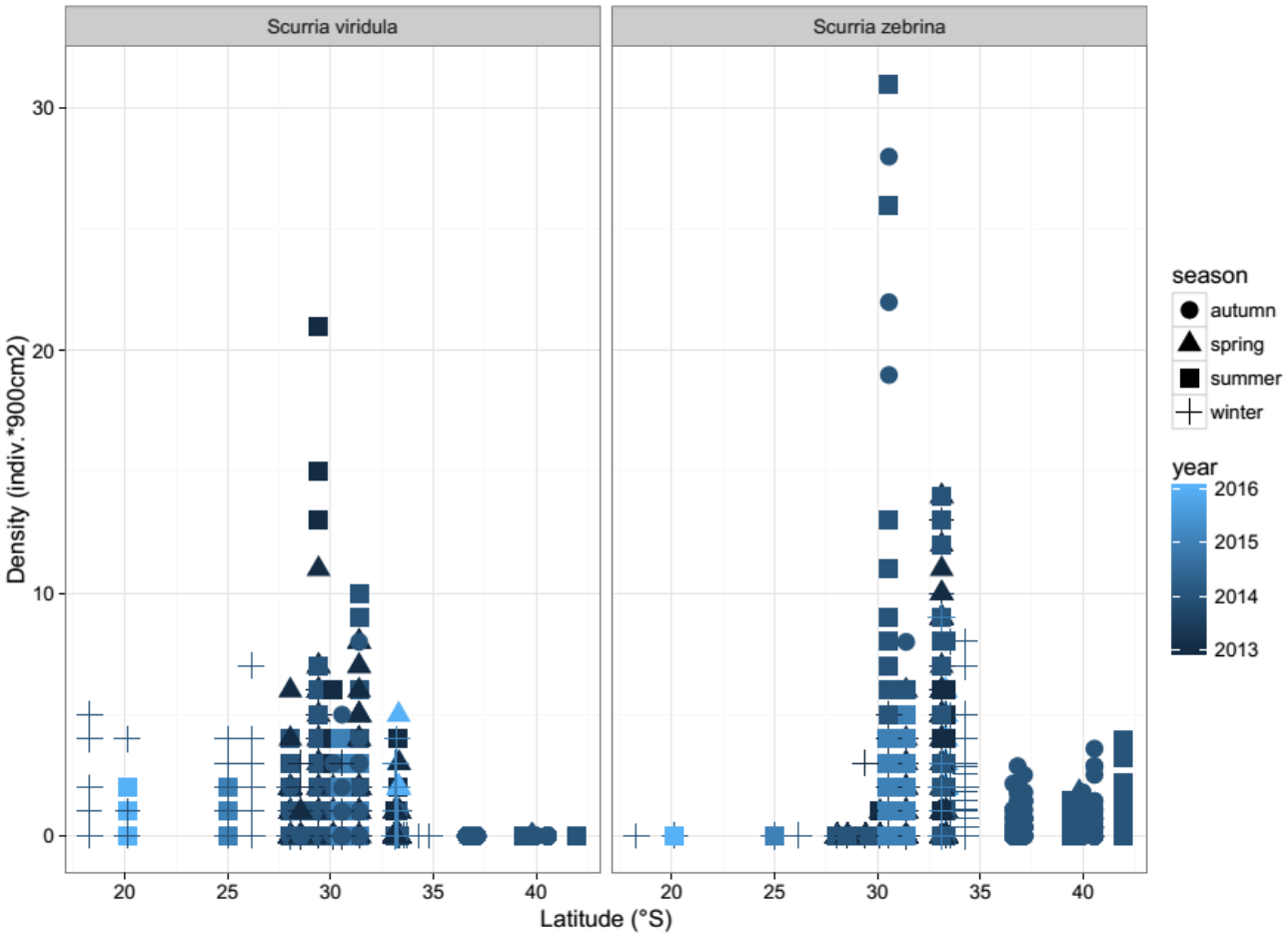

Fig. S1. Scatterplot of the density (indiv. per quadrat) of both *S.viridula* and *S. zebrina*, recorded along the coast of Chile (from 18°S to 41°S) at different platforms, sites, seasons and years.

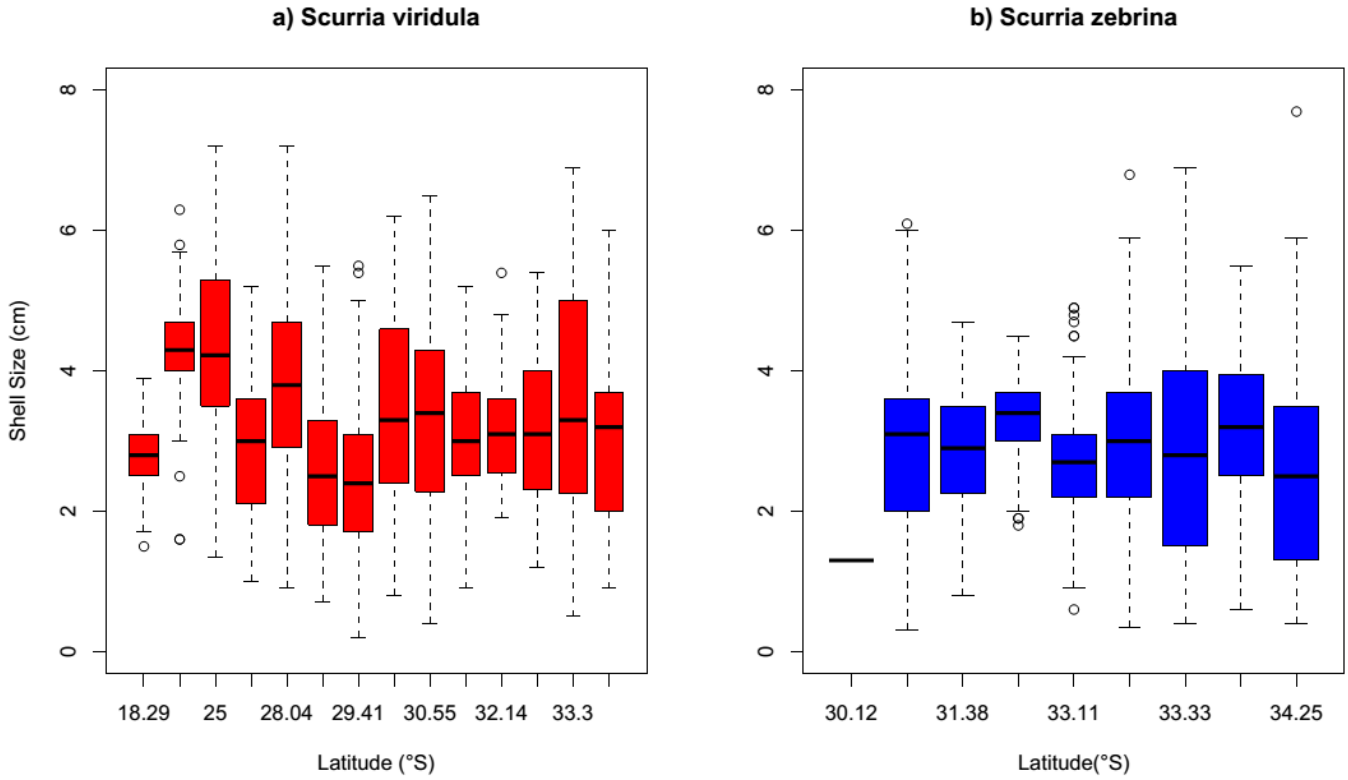

Fig. S2. Box plots of shell size of a) *S. viridula* (red) and b) *S. zebrina* (blue) across different latitudes from north to central Chile. The black line in each box is the median, the boxes define the hinge (25-75% quartile, and the line is 1.5 times the hinge). Points outside the interval (outliers) are represented as dots

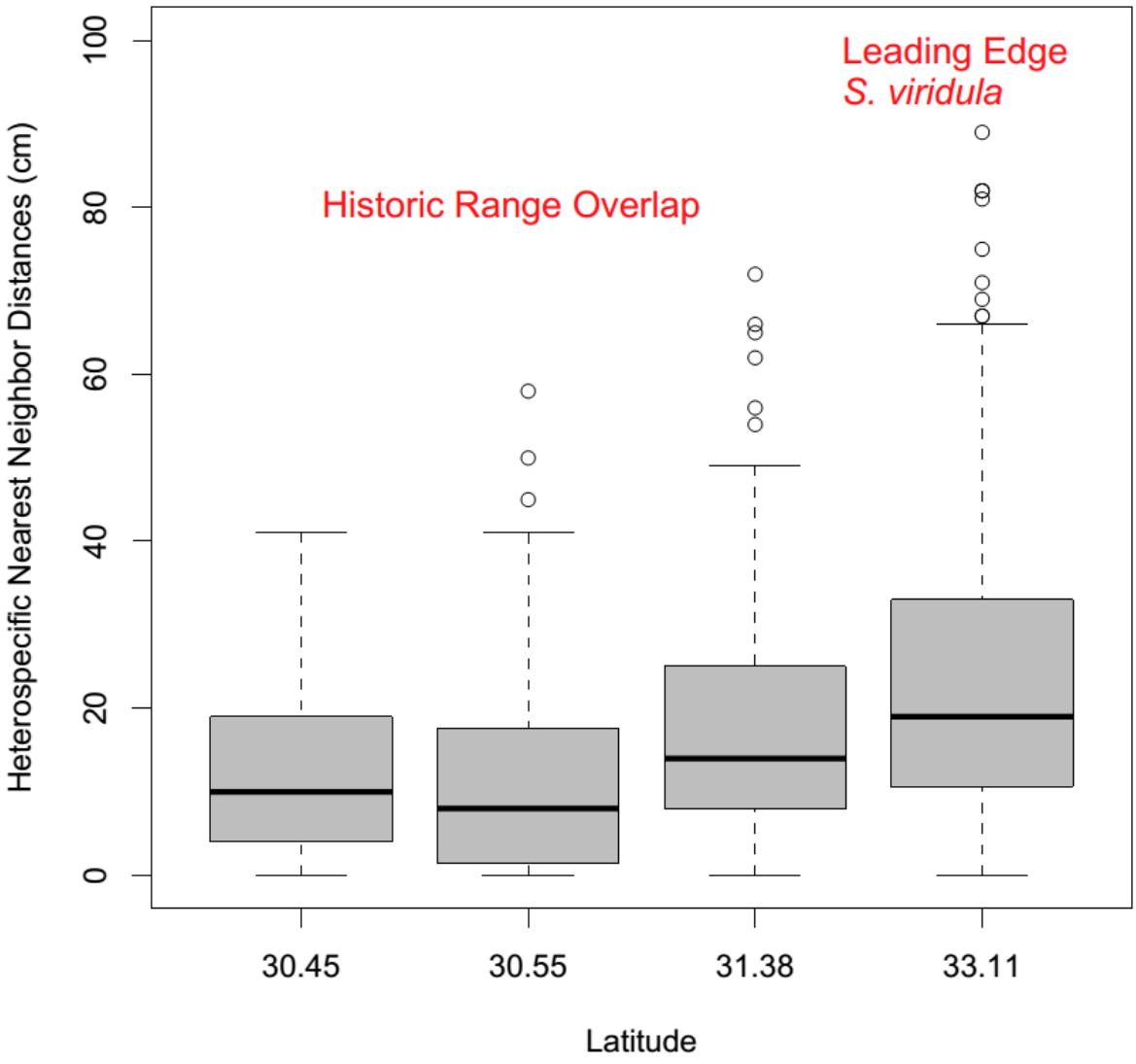

Fig. S3. Box plots of the heterospecific (*S. viridula* to *S. zebrina*) individual nearest neighbor distances, estimated in the field across the *Scurria* historic range overlap and at the leading edge of *S. viridula* (Quintay; 33.11°S).

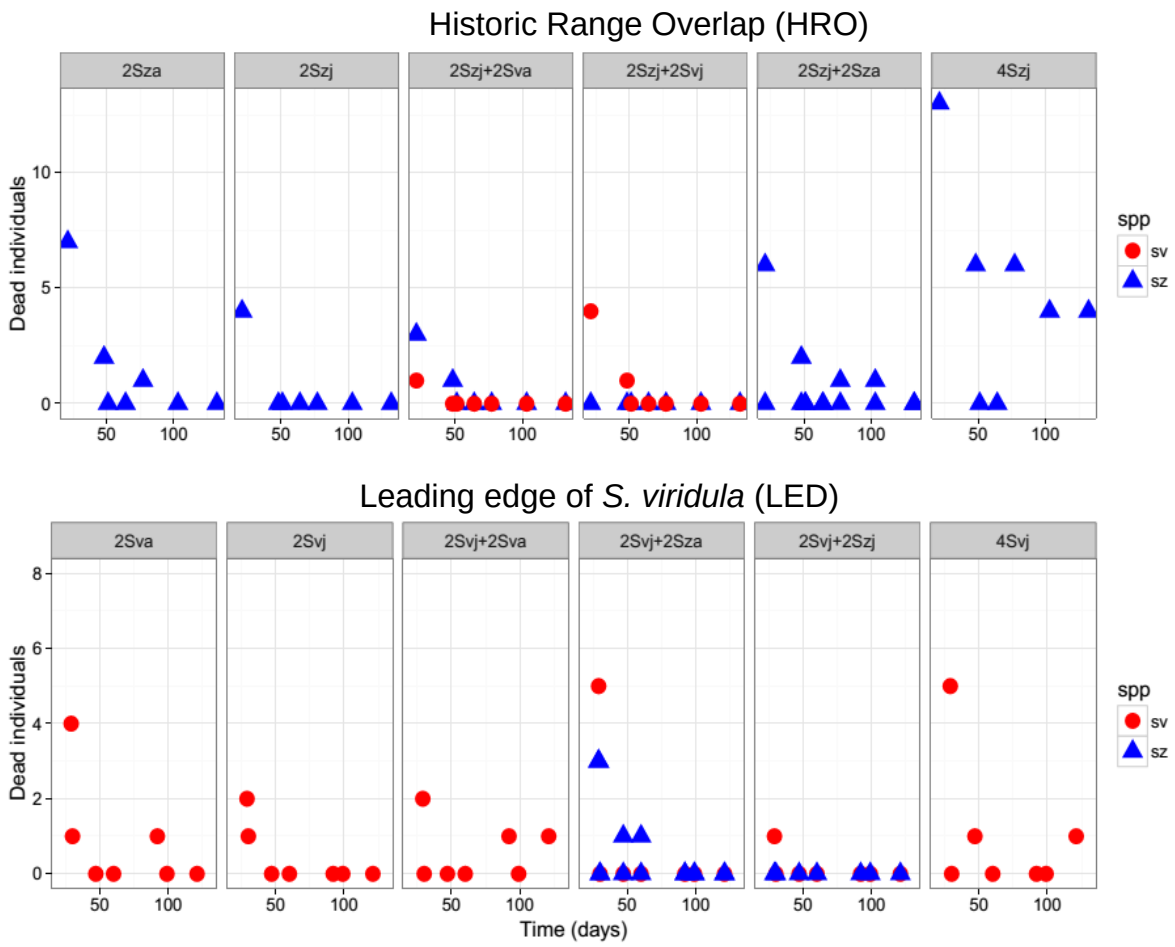

Fig. S4. Total number of dead individuals (3 replicate per treatments) found inside experimental enclosures through time, in field experiments conducted at the Historic Range Overlap (HRO) and at the leading edge (LE) of *S. viridula*. SV: *Scurria viridula*; SZ: *S. zebrina*.

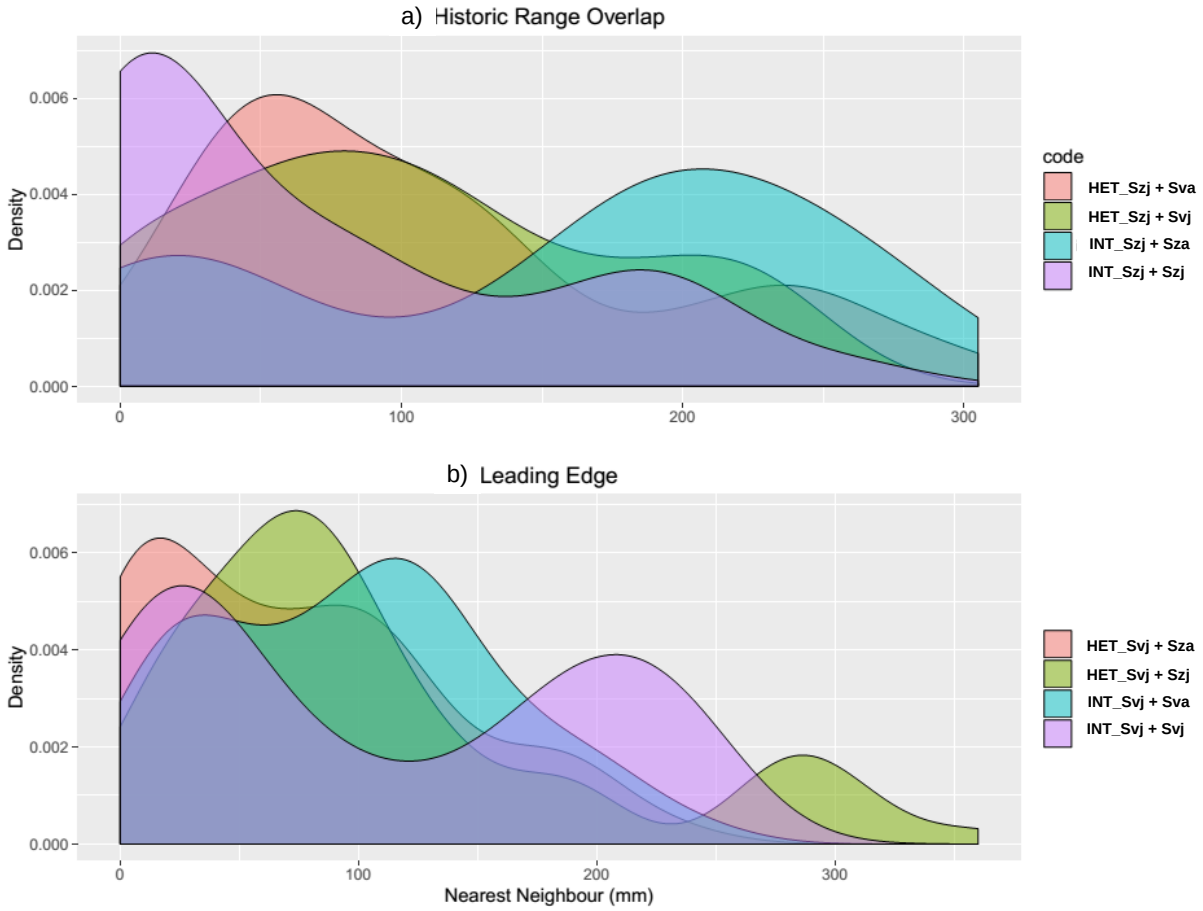

Fig. S5. Density plot of the intra (INT) and heterospecific (HET) individual nearest neighbor distances (NN) estimated inside experimental plots, in experiments conducted in the historic range overlap (30°S) a), and at the leading edge of *S. viridula* at Las Cruces (33°S) b). SZ: *S. zebrina*; SV: *S.viridula*. Subscripts "j" and "a" denote "juvenile" and "adult" individuals, respectively.

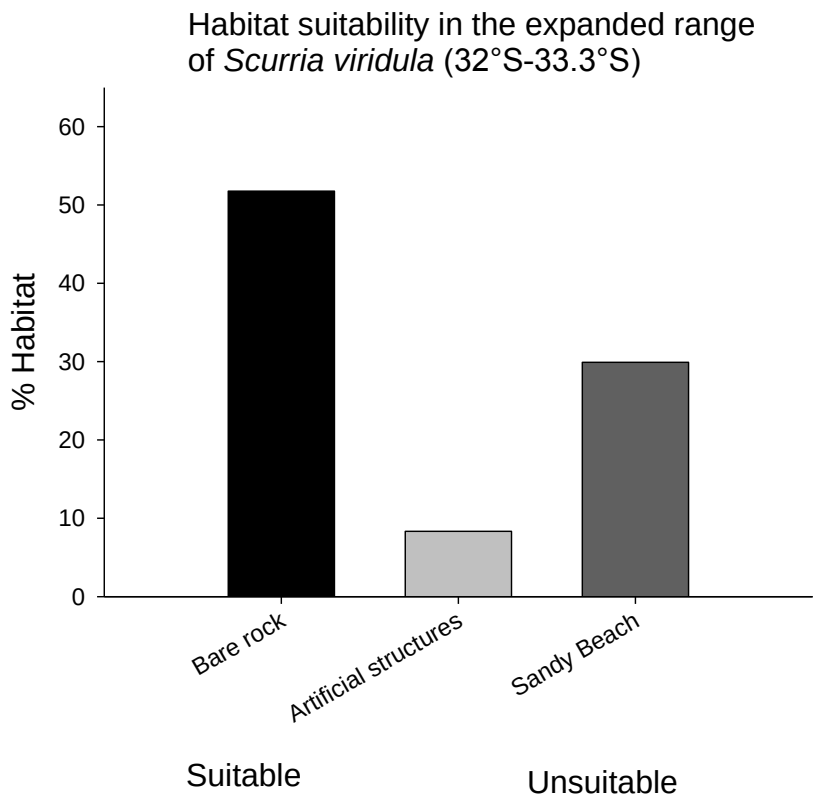

Fig. S6. Proportion of suitable (bare rock, artificial structures) and unsuitable (sandy beach) habitat from 32°S to 33°S corresponding to the leading edge of *S. viridula* (LE). Analyses were conducted through tracing contours of the coast in Google Earth at constant elevation (500m) (Fenberg & Rivadeneira 2011).

Table S1. Summary of the different localities sampled during the study, and the number of quadrat deployed in different transects (rocky platforms) at different year and seasons. *Platform extent correspond to the entire sampled areas included in the quadrat sampling, and which were also completely checked (visually) for presence of *Scurria* species.

Locality	Latitude (°S)	Number of quadrats (30*30 cm)	Rocky platform extent (m^2)*	Season	Year
Arica	18.28	25	1 (60)	Winter	2014
		20	2(87)	Winter	2014
		23	3(60)	Winter	2014
		12	1(60)	Summer	2016
		12	2(60)	Summer	2016
Iquique	20.14	12	1 (75)	Summer	2013
		21	2(60)	Summer	2013
		26	3(60)	Summer	2013
		20	1(75)	Winter	2014
		15	2(60)	Winter	2014
		25	3(60)	Winter	2014
		15	1(75)	Summer	2016
		15	2(60)	Summer	2016
		15	3(60)	Summer	2016
Paposo	25.2	15	1(35)	Summer	2014
		20	2(35)	Summer	2014
		20	1(35)	Winter	2014
		15	2(35)	Winter	2014
		20	3(30)	Winter	2014
		15	1(35)	Summer	2015
		15	2(35)	Summer	2015
Pan de Azúcar	26.17	15	1(20)	Winter	2014
		10	2(20)	Winter	2014
Carrizal Bajo	28	15	1(80)	Spring	2013
		25	2(24)	Spring	2013
		20	1(24)	Summer	2014
		20	2(24)	Summer	2014
		20	1(24)	Autumn	2014
		16	2(24)	Autumn	2014
		15	1(24)	Summer	2015
Los Burros	28.5	12	1(43)	Winter	2013
		17	1(43)	Spring	2013
		15	1(43)	Summer	2014
		16	1(43)	Autumn	2014

Arrayán	29	25	1(48)	Summer	2013
		26	2(80)	Summer	2013
		10	1(48)	Autumn	2013
		15	1(48)	Winter	2013
		15	1(48)	Spring	2013
		18	1(48)	Summer	2014
		15	2(80)	Summer	2014
		15	1(48)	Winter	2014
Guanaqueros	30.1	13	1(90)	Summer	2013
		16	1(90)	Winter	2013
		12	2(55)	Winter	2013
		13	1(90)	Spring	2013
		28	2(55)	Spring	2013
		16	1(90)	Summer	2014
		15	2(55)	Summer	2014
		15	1(90)	Autumn	2014
		15	1(90)	Spring	2014
Limarí	30.4	12	1(84)	Summer	2015
Punta de Talca	30.5	15	1(120)	Winter	2013
		15	2(128)	Winter	2013
		18	1(120)	Spring	2013
		18	1(120)	Summer	2014
		20	1(120)	Autumn	2014
		15	1(120)	Winter	2014
		15	1(120)	Summer	2015
Huentelauquén	31.38	10	1(80)	Summer	2013
		16	1(80)	Winter	2013
		20	1(80)	Spring	2013
		18	1(80)	Summer	2014
		20	2(48)	Summer	2014
		20	1(80)	Autumn	2014
		19	2(48)	Autumn	2014
		25	1(80)	Summer	2015
Quintay	33.11	20	1(35)	Summer	2013
		20	2(60)	Summer	2013
		20	1(35)	Spring	2013
		20	2(60)	Spring	2013
		21	1(35)	Winter	2013
		15	2(60)	Winter	2013
		20	1(35)	Summer	2014
		15	1(35)	Winter	2015
Las Cruces	33.3	21	1(84)	Summer	2013
		12	2(56)	Summer	2013

		13	3(45)	Summer	2013
		12	1(84)	Winter	2013
		12	2(56)	Winter	2013
		15	1(84)	Summer	2014
		12	2(56)	Summer	2014
		15	1(84)	Autumn	2014
		15	1(84)	Winter	2014
		13	2(56)	Winter	2014
		15	1(84)	Winter	2015
		16	1(84)	Summer	2016
		15	2(56)	Summer	2016
Pelancura	33.33	30	1(120)	Summer	2013
		15	2(100)	Summer	2013
		25	1(120)	Winter	2013
		24	2(100)	Winter	2013
		30	1(120)	Summer	2014
		27	1(120)	Autumn	2014
		20	1(120)	Summer	2015
Matanzas	33.57	15	1(78)	Winter	2014
		15	2(65)	Winter	2014
		15	3(42)	Winter	2014
Pichilemu	34.25	25	1(425)	Winter	2014
		25	2(234)	Winter	2014
		25	3(513)	Winter	2014
Cocholgüe	36.35	30	1(125)	Autumn	2014
Desembocadura	36.6	27	1(40)	Autumn	2014
Colcura	37.11	30	1(40)	Autumn	2014
Punta Ronca	39.39	36	1(45)	Autumn	2014
Cheuque	39.4	15	1(78)	Summer	2014
Calfuco	39.79	30	1(80)	Summer	2014
Chaihuin	39.94	30	1(46)	Autumn	2014
Pucatrihue	40.53	44	1(84)	Autumn	2014
Puñihuil	41.92	34	1(34)	Summer	2014

Table S2. Pearson´s spatial correlation (r) between *Scurria* species abundances estimated in the field through a quadrat (30×30cm) sampling protocol. Significance (α=0.05) was calculated through a t-test, corrected for the effective degrees of freedom based on lag-1 autocorrelation estimates of Moran's *I* (Dutilleul 1993).

Site	Pearson's r *P-value*
Guanaqueros (30.12°S; HRO)	-0.0388 *0.3907*
Punta Talca (30.55°S; HRO)	0.0323 *0.7397*
Huentelauquén (31.38 °S; HRO)	0.0223 ***0.0145***
Quintay (33.11°S; LE)	-0.0741 *0.0803*

Table S3. Average percent cover (± SE) of the main algal groups observed inside experimental enclosures at the end of the field experiments. Ephemerals: *Ulva compressa*, *U. rigida*, *Scytosiphon lomentaria* and *Bangia* sp., Periphyton: Microalgae (diatoms, cyanophytes), Crustose algae: *Hildenbrandia lecanelleri*, *Ralfsia* sp.

Leading edge of *Scurria viridula* **(LE)**			
Treatment	Ephemeral	Periphyton	Crustose algae
2Svj + 2Szj	**76.25 ± 4.27**	**10.75 ±5.37**	**3.25 ± 1.18**
2Svj + 2Sza	**32.5 ± 7.5**	**25.75 ±18.27**	**7.0 ± 27.1**
2Svj + 2Sva	**16.25 ± 14.01**	**8.25 ± 0.5**	**40 ± 3.14**
2Svj	**71.75 ± 14.0**	**3.5 ± 0.5**	**6.25 ± 3.14**
4Svj	**25.0 ± 18.92**	**7.5 ± 2.5**	**13.5 ± 10.5**
2Sva	**33.25 ±16.42**	**2.25 ± 0.75**	**42.0 ± 21.94**
Historic range overlap (HRO)			
2Szj + 2Svj	**16.15± 6.88**	**1.5 ± 0.866**	**0**
2Szj + 2Sva	**3.75 ± 3.75**	**1.25 ± 1.25**	**0**
2Szj + 2Sza	**20 ± 12.47**	**0.75 ± 0.75**	**1.5 ± 1.0**
2Szj	**53.75 ± 12.5**	**0.75 ± 0.74**	**0**
4Szj	**28.33 ± 0.13**	**0**	**0**
2Sza	**10 ± 5.77**	**1.2 ± 1.0**	**0**

Appendix S1. **Nearest neighbor distance distribution analyses**

The NN distances measured in the field surveys were analyzed by generating contingency tables of the proportion of individuals that had specific NN distances (e.g. ranging from 0.0 to 89.0 cm). Independence of NN across the different localities was tested with the likelihood ratio test and Pearson's chi-square. For these analyses, reflexive NN distances (i.e. when 2 individuals are mutually nearest neighbors; Cox, 1981) were not considered. Because con- and heterospecific NN-distances estimated in the experimental enclosures in field experiments include non-independent measures (same individuals sampled through time) and small sample size, they were analyzed differently; we estimated the probability density function (PDF) for conspecific and heterospecific NN distance distribution in each experimental plot. Thus, considering that NN-distances are continuous random variables, the PDF (i.e. kernel density plot) was estimated as the ratio of individual NN distances values *versus* the average total. This non-parametric estimation utilizes a kernel smoothing (in this case Gaussian) to plot values, allowing for comparison of smoother distributions, and providing a useful way to explore individual segregation or aggregation (Manly, 1997). Density plots were performed with the package 'sm' implemented in R (R Development Core Team, 2017).

References

Aguilera, M. A., & Navarrete, S. A. (2012). Interspecific Competition for shelters in territorial and gregarious intertidal grazers: consequences for individual behaviour. *PLoS ONE*, *7*(9), e46205. doi:10.1371/journal.pone.0046205

Aguilera, M. A., Valdivia, N., & Broitman, B. R. (2013). Spatial niche differentiation and coexistence at the edge: co-occurrence distribution patterns in Scurria limpets. *Marine Ecology Progress Series*, *483*, 185–198. doi:10.3354/meps10293

Cox, T. F. (1981). Reflexive Nearest Neighbours. *International Biometric*, *37*(2), 367–369.

Manly, B. (1997). *Randomization, Bootstrap and MonteCarlo Methods in Biology* (p. 388). Chapman & Hall.

R Development Core Team. (2017). *R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.* (R. F. for S. Computing, Ed.). Vienna. Retrieved from URL http://www.R-project.org/.

Appendix 2. Field experiments: main protocols

Field experiments design and set up

To examine the effect of *S. viridula* on *S. zebrina* juvenile individuals at the historic range overlap (30°S), we established treatments examining both intraspecific effects of *S. zebrina* (juvenile-juvenile, adult-adult and juvenile-adult interactions) and interspecific effects (juveniles of each species and juveniles of *S. zebrina* interacting with adults of *S viridula*) (see Fig. 1 in the main text). To examine the effect of *S. zebrina* on *S. viridula* juvenile individuals in the leading edge of the latter species (33.3°S), we deployed the three treatments (see information provided in the main text) to examine intraspecific effects, but in this case on *S. viridula*, and both treatments designed to examine interspecific effects (i.e. juveniles of each species and *S. zebrina* adult-*S. viridula* juvenile). In both sites,

intraspecific effects were investigated at either natural or high densities (two or four individuals per plot, respectively; see Table 1 and Fig. 1 in the main text), and interspecific effects were examined using natural densities of each species (two individuals of each species).

Experimental treatment considered at each site; Historic range overlap (HRO): Intraspecific effects: 1) 2 *S. zebrina* juveniles; 2) 4 *S. zebrina* juveniles; 3) 2 *S. zebrina* adults; 4) 2 *S. zebrina* juveniles plus 2 *S. zebrina* adults (inter-size effect). Interspecific effects: 5) 2 *S. zebrina* juveniles plus 2 *S. viridula* juveniles, and 6) 2 *S. zebrina* juveniles plus 2 *S. virdula* adults; Leading edge (LE): 1) 2 *S. viridula* juveniles; 2) 4 *S. viridula* juveniles; 3) 2 *S. viridula* adults; 4) 2 *S. viridula* juveniles plus 2 *S. viridula* adults, 5) 2 *S. viridula* juveniles plus 2 *S. zebrina* juveniles, and 6) 2 *S. viridula* juveniles plus 2 *S. zebrina* adults. Treatments were randomly allocated to experimental areas and replicated four times. Mixed species treatment at high densities were not considered (see Table 1 in the main text) , due to the reduced densities of *S. viridula* at the leading edge, and to avoid artefacts caused by large individuals enclosed in small areas. *Scurria* individuals were enclosed in experimental areas (35 × 35 cm) using stainless steel mesh cages (8 cm high, 10 mm mesh size) fastened to the rock with stainless steel screws. Gaps between the substratum and the base of the fences were sealed with plastic mesh. Any losses/mortality after the formal start of the experiment in Punta Talca and Las Cruces were attributed to competition (e.g. individual contests or food shortage). To control for the potential impact of cages (e.g. light reduction, water flow), 12 *S. viridula* and 12 *S. zebrina* juvenile individuals were tagged, measured and left in the same place with no cage. Survival and activity patterns of these individuals were checked twice per month. This procedural control was conducted at both

sites. All *Scurria* individuals were collected in the same intertidal zone (mid-high intertidal level ~2.0 MLWL) where the experiments were performed, and where both species inhabit (Aguilera, Valdivia, & Broitman, 2013), the experimental plot and collection sites were distanced ~3-4 meters apart. At the start of the experiments each organism was weighted (wet), sized and labelled with a bee tag before deployment into the experimental enclosures. Previous studies showed the foraging range of *Scurria* species encompass a radius of ~12-18 cm around their home scar (Aguilera et al. unpublished). For both species, the discrimination between juvenile and adults was based on readily visible morphological differences (see Aguilera et al., 2013) corroborated by observations of first sexual maturity of both species occurring in individuals of 35 mm in shell length. Average shell length of juveniles for each species used in the experiments was 23.5 ± 0.1 mm (wet weight = 2.1 ± 0.04 g); average shell length of adults was 50.5 ± 0.7 mm (20.6 ± 0.7 g; Table 1).

Appendix S3

Interaction strength measures for field experiments

In order to provide estimates of interaction strength between species and between size classes for each species in experimental treatments (described above and in the main text), we estimated per capita intra- and interspecific effects as follow (see also Aguilera & Navarrete, 2012): For a given species *i* (*S. viridula* and *S. zebrina* in their respective range edges) and size class *k* (i.e. juvenile, adult), the *per capita* intraspecific effects (*ISi*) were calculated as: $IS_{i_k} = \frac{(RHi_k - RNi_k)}{(NHi_k - NNi_k)}$, where RNi_k is the *per capita* response variable (e.g. growth rate) of species *i* of size class *k* (juvenile or adult) in the average or ‘‘natural’’

density treatment, RHi_k is the *per capita* response measured in the high density treatment, and NNi_k and NHi_k are the numbers of individuals in the average and high density treatments, respectively. Thus for each location we estimated three intraspecific effects; juvenile on juvenile (ISi_{jj}), adult on juvenile (ISi_{aj}), and juvenile on adult (ISi_{ja}). The total *per capita* interspecific effect (Total_*ISij*) of species j on species *i* was then calculated as: $Total\_IS_{ij_k} = \frac{(RMij_k - RNi_k)}{Nj_k}$, where $RMij_k$ is the *per capita* response of species *i* measured in the mixed species enclosures with species *j* of size class *k*, and Nj_k is the number of individuals of species *j* of class *k* present in those enclosures. *Per capita* interspecific effects do not separate between ‘‘pure’’ *per capita* effects due to addition of a different species (identity effect), from the expected changes observed if individuals of the same species, but of different size class, were added to the arena (intraspecific effects) (Aguilera & Navarrete, 2012). Therefore, considering that *per capita* intraspecific effects would maintain constant (and linear over the density range and size class considered) in the presence of heterospecifics, we obtained an estimate of “pure” *per capita* $ISij_k$ as; $ISij_k = Total\_ISij_k - ISi_k$. Confidence intervals for estimates of *per capita* interaction strengths were obtained through bootstrapping our observations 1000 times (Manly, 1997). We then evaluated whether the 95% bootstrapped confidence intervals overlapped zero to judge if the particular effect was statistically significant. All analyses were conducted in the R environment v. 3.1.3 (R Development Core Team, 2017).

References

Aguilera, M. A., & Navarrete, S. A. (2012). Interspecific Competition for shelters in territorial and gregarious intertidal grazers: consequences for individual behaviour. *PLoS ONE*, *7*(9), e46205. doi:10.1371/journal.pone.0046205

Aguilera, M. A., Valdivia, N., & Broitman, B. R. (2013). Spatial niche differentiation and coexistence at the edge: co-occurrence distribution patterns in Scurria limpets. *Marine Ecology Progress Series*, *483*, 185–198. doi:10.3354/meps10293

Cox, T. F. (1981). Reflexive Nearest Neighbours. *International Biometric*, *37*(2), 367–369.

Manly, B. (1997). *Randomization, Bootstrap and MonteCarlo Methods in Biology* (p. 388). Chapman & Hall.

R Development Core Team. (2017). *R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.* (R. F. for S. Computing, Ed.). Vienna. Retrieved from URL http://www.R-project.org/.