

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

Aguilera, Moises A.; Valdivia, Nelson; Jenkins, Stuart; Navarette, Sergio A.; Broitman, Bernardo

**Journal of Animal Ecology**

DOI:  
[10.1111/1365-2656.12917](https://doi.org/10.1111/1365-2656.12917)

Published: 01/02/2019

Peer reviewed version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

*Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):*  
Aguilera, M. A., Valdivia, N., Jenkins, S., Navarette, S. A., & Broitman, B. (2019). Asymmetric competitive effects during species range expansion: an experimental assessment of interaction strength between 'equivalent' grazer species in their range overlap. *Journal of Animal Ecology*, 88(2), 277-289. <https://doi.org/10.1111/1365-2656.12917>

**Hawliau Cyffredinol / General rights**

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal ?

**Take down policy**

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21

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

Moisés A. Aguilera<sup>1,2</sup>, Nelson Valdivia<sup>3,4</sup>, Stuart Jenkins<sup>6</sup> Sergio A. Navarrete<sup>5</sup>, Bernardo  
Broitman<sup>2</sup>

<sup>1</sup>Departamento de Biología Marina, Facultad de Ciencias del Mar, Universidad Católica del Norte, Larrondo  
1281, Coquimbo, Chile

<sup>2</sup>Centro de Estudios Avanzados en Zonas Áridas (CEAZA) Ossandón 877, Coquimbo, Chile.

<sup>3</sup>Instituto de Ciencias Marinas y Limnológicas, Facultad de Ciencias, Universidad Austral de Chile, Campus  
Isla Teja s/n, Valdivia, Chile

<sup>4</sup>Centro FONDAP de Investigación en Dinámica de Ecosistemas Marinos de Altas Latitudes (IDEAL)

<sup>5</sup>Estación Costera de Investigaciones Marinas, Las Cruces, LINCGlobal and Center for Applied Ecology and  
Sustainability, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile.

<sup>6</sup>School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey LL59 5AB, UK

Corresponding author: Moisés A. Aguilera, [moises.aguilera@ucn.cl](mailto:moises.aguilera@ucn.cl)

22 Abstract

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

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

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

41 **4.** Field surveys showed poleward range expansion of *S. viridula* of ca. 210 km since year  
42 2000, with an expansion rate of 13.1 km year<sup>-1</sup>. No range shift was detected for *S. zebrina*.  
43 The resident *S. zebrina* had significant negative effects on the growth rate of the invading

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

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

52

### 53 KEYWORDS

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

55

56

57

58

59

60

61

62

63

64

65

66

67

68

69

70

## 71 1 | INTRODUCTION

72 The range limits of species are influenced by changes in environmental conditions,  
73 suitable habitat scarcity and dispersal limitation (Brown, Stevens, & Kaufman, 1996; Case,  
74 Holt, Mcpeek, & Keitt, 2005; Holt & Keitt, 2005; Vermeij, 2005). However, beyond large-  
75 scale environmental regulation, increasing theoretical and empirical evidence hints that  
76 biotic interactions can determine the distribution boundaries of species (e.g. Cunningham et  
77 al., 2009; Firth et al., 2009; Soberón, 2010; Araújo & Rozenfeld, 2014; Godsoe et al.,  
78 2017). Theory predicts that in geographic contact zones competitive interactions can leave  
79 a strong impact on species distribution at regional scales and can lead to the formation of  
80 stable geographic range edges (Araújo & Luoto, 2007; Godsoe, Murray, & Plank, 2015;  
81 Phillips, 2012). However, manipulative field studies determining how the strength of  
82 competition influences the dynamics of species range limits are still scarce (but see  
83 Cunningham et al., 2009).

84 The performance of species at the limit of their geographic range, where they overlap the  
85 distribution of other potentially competing species with similar resource requirements, may  
86 be critical in determining the role of competition in establishing the distribution and the  
87 probability of range expansion (Godsoe et al., 2015 Phillips, 2012). Range overlap can also  
88 drive ecological niche divergence over time (Pigot & Tobias, 2013). Relevant population  
89 and individual properties such as density, individual size and fecundity can decrease from  
90 central to edge subpopulations due to varying abiotic environmental effects on individual  
91 physiology (e.g. Brown, 1984; Sagarin & Gaines, 2002; Gilman, 2006; Rivadeneira et al.,  
92 2010). This core-edge adaptive pattern could lead to a concomitant decrease in competitive

93 ability from central to edge locations, with important implications for competition at the  
94 range edges of overlapping populations. For example, competitive exclusion by local  
95 species has been proposed to prevent the success of an invading species (Case & Taper,  
96 2000; Godsoe & Harmon, 2012), halting the range expansion of the latter. Therefore,  
97 determining the differences in competitive ability between species overlapping at their  
98 respective range-edges will improve our understanding of the influence of ecological  
99 interactions on species' range variability.

100 Coastal biogeographic boundaries provide a model system to assess the influence of  
101 competition on the geographic distribution of species (Firth et al., 2009). In the  
102 Southeastern Pacific (SE) shore, a well-known transition zone (i.e. subtropical-temperate)  
103 extending between 30°S and 41°S concentrates the polar or equatorial range edge of at least  
104 7 intertidal species (Camus, 2001; Broitman et al., 2011). Clear signs of range shifts (i.e.  
105 contraction or expansion) have been detected here for six intertidal grazer species (e.g.  
106 Rivadeneira & Fernández, 2005). Some of these recently shifted populations have increased  
107 species co-occurrences, with the potential for pronounced effects on the fitness of  
108 previously established ecological and phylogenetically equivalent species.

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

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

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

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

149

## 150 2 | MATERIALS AND METHODS

151

### 152 2.1 Study system, range shift and geographic abundance patterns of *Scurria*.

153 The coastline of the study region is composed mostly of continuous, wave-exposed rocky  
154 shores, with only ~20% interspersed sandy beaches. The northern limit of the range overlap  
155 (30°S) between *Scurria viridula* and *Scurria zebrina* is characterized by the presence of a  
156 large coastal headland, which is recognized as the strongest upwelling area in north-central  
157 Chile (Aguirre, Pizarro, Strub, Garreaud, & Barth, 2012).

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



161 2005) to 33°30'S in our study (see below). Recent field surveys (2010-2011) found  
162 juvenile *S. viridula* individuals at 33°30'S constituting a new leading edge of this species  
163 (Aguilera et al., 2013). Thus a continuous poleward range expansion has been observed  
164 over recent decades.

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

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

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

199

### 200 2.3 Local interspecific distribution patterns

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

207 Fig. 1). *Scurria* spatial association at the 900-cm<sup>2</sup> scale was determined by estimating the  
208 lag-0 Pearson correlation ( $r$ ) between focal limpet species density across quadrats at each  
209 locality, which is recommended for data with autocorrelated structure, and is appropriated  
210 to describe and test the spatial aggregation or dispersion of species (Fortin & Dale, 2005).  
211 Significance was calculated by a t-test corrected for the effective degrees of freedom based  
212 on lag-1 autocorrelation estimates of Moran's I (Dutilleul, 1993). At the same localities,  
213 finer spatial distribution, i.e. individual-to-individual distances, was characterized by  
214 measuring nearest neighbor distances between conspecific and heterospecific individuals  
215 (from *S. viridula* to *S. zebrina* individuals and *vice versa*). The shape of the nearest  
216 neighbor distance distribution commonly captures processes operating between individuals  
217 scale (e.g. behavior) and reflects positive (aggregation) and negative (segregation)  
218 associations (Fortin & Dale, 2005). At each locality we selected four 4 × 4 m areas where  
219 we estimated all conspecific and heterospecific nearest neighbor distances starting with a  
220 selected individual positioned in the middle of the sampling area. To reduce non-  
221 independence of measured heterospecific NN distances, the distances from *S. viridula* to *S.*  
222 *zebrina* and from *S. zebrina* to *S. viridula* were measured in different areas. More than 200  
223 individual-to-individual distances were measured at each locality. We analyzed the  
224 frequency of heterospecific nearest neighbor distances across sites by constructing  
225 contingency tables. Independence was tested with a log-linear model using likelihood Ratio  
226 and Pearson's Chi-square statistic ( $\alpha = 0.05$ ) implemented in the 'MASS' library of the R-  
227 environment (R Development Core Team, R, 2017)

228

229 2.4 Competition experiments at range edges of *S. viridula* and *S. zebrina*

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

254 juveniles; 2) 4 *S. zebrina* juveniles; 3) 2 *S. zebrina* adults; 4) 2 *S. zebrina* juveniles plus 2 *S.*  
255 *zebrina* adults; 5) 2 *S. zebrina* juveniles plus 2 *S. viridula* juveniles; and 6) 2 *S. zebrina*  
256 juveniles plus 2 *S. viridula* adults. Leading edge (LE): 1) 2 *S. viridula* juveniles; 2) 4 *S.*  
257 *viridula* juveniles; 3) 2 *S. viridula* adults; 4) 2 *S. viridula* juveniles plus 2 *S. viridula* adults;  
258 5) 2 *S. viridula* juveniles plus 2 *S. zebrina* juveniles; and 6) 2 *S. viridula* juveniles plus 2 *S.*  
259 *zebrina* adults (see scheme in Fig. 1). *Scurria* individuals were enclosed in experimental  
260 areas (35 × 35 cm) using stainless steel mesh cages (8 cm high, 10 mm mesh size) fastened  
261 to the rock with stainless steel screws (see Appendix 2 for details). Treatments were  
262 randomly allocated to experimental areas and replicated four times. The experiments were  
263 initiated on June 25, 2014 at the Punta Talca and on June 29, 2014 at Las Cruces —both  
264 experiments ended on December 5, 2014.

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

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

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

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

285 To provide accurate estimates of intra- and interspecific interaction (competition)  
 286 strength, and to account for the variation in limpet density and identity between treatments,  
 287 we estimated *per capita* intra- and interspecific effects for each species on limpet growth  
 288 rate (for further details see Appendix S3, and also Aguilera & Navarrete, 2012). For a given  
 289 species *i* (*S. viridula* and *S. zebrina* in their respective range edges) and size class *k* (i.e.

290 juvenile, adult), the *per capita* intraspecific effects (*IS<sub>i</sub>*) were calculated as:  $IS_{i_k} =$

291  $\frac{(RH_{i_k} - RN_{i_k})}{(NH_{i_k} - NN_{i_k})}$ , where  $RN_{i_k}$  is the *per capita* response variable (e.g. growth rate) of species *i* of

292 size class *k* (juvenile or adult) in the average or “natural” density treatment,  $RH_{i_k}$  is the *per*  
 293 *capita* response measured in the high density treatment, and  $NN_{i_k}$  and  $NH_{i_k}$  are the numbers  
 294 of individuals in the natural and high density treatments, respectively. Thus for each

295 location we estimated three intraspecific effects; juvenile on juvenile ( $IS_{ijj}$ ), adult on  
 296 juvenile ( $IS_{i_{aj}}$ ), and juvenile on adult ( $IS_{ija}$ ). For interspecific effects, we considered a total  
 297 *per capita* interspecific effect (Total\_ $IS_{ij}$ ) of species *j* on species *i* calculated as:

298  $Total\_IS_{ijk} = \frac{(RM_{ijk} - RN_{i_k})}{N_{jk}}$ , where  $RM_{ijk}$  is the *per capita* response of species *i* measured in

299 the mixed species enclosures with species  $j$  of size class  $k$ , and  $N_{jk}$  is the number of  
300 individuals of species  $j$  of class  $k$  present in those enclosures. In order to include the effect  
301 of species identity, and to separate the effect of individuals of the same species but of  
302 different size-class, we obtained an estimate of “pure” interspecific *per capita* effect  $IS_{ijk}$   
303 as;  $IS_{ijk} = Total\_IS_{ijk} - IS_{ik}$  (see Appendix S3 for further details).

304

#### 305 2.4.1 *Scurria* microspatial distribution in experimental cages

306 Each two weeks per month, we estimate con- and heterospecific nearest neighbor-distances  
307 in the experimental enclosures in field experiments. We estimated the probability density  
308 function (PDF) for conspecific and heterospecific nearest neighbor distance distribution in  
309 each experimental plot. Thus, considering that nearest neighbor distances are continuous  
310 random variables, the PDF (i.e. kernel density plot) was estimated as the ratio of individual  
311 nearest neighbor distances values *versus* the average total. This analyses provide a useful  
312 way to explore individual (con-and heterospecific) segregation or aggregation (Manly,  
313 1997). Density plots were performed with the package ‘sm’ implemented in R (R  
314 Development Core Team, 2017)

315

#### 316 2.5 Habitat suitability at the leading edge

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

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

325

### 326 3 | RESULTS

327

#### 328 3.1 Range shift and geographic patterns of abundance of *S. viridula* and *S.* 329 *zebrina*

330

331 Field abundance surveys conducted along the coast of Chile from 18°S to 41°S showed  
332 parapatric geographic distributions of the *Scurria* species, with an overlap of about 375 km  
333 in central Chile (Fig. 2 and Fig. S1 in Supporting Information). *Scurria viridula* showed an  
334 poleward range expansion into the range of *S. zebrina* from 32°31' S to 33°33' S in central  
335 Chile (see dotted blue lines in Fig. 2); this corresponds to a range shift of ca. 210 km (linear  
336 length estimates) in 16 years (2000 to 2016), representing a poleward expansion rate of *S.*  
337 *viridula* of about 13.1 km year<sup>-1</sup>. The mean density of *S. viridula* at the historic range  
338 overlap was 0.658 indiv. × 900 cm<sup>-2</sup> (± 0.062), while at the leading edge it was 0.153 indiv. ×  
339 900 cm<sup>-2</sup> (± 0.0234), showing reduced population density. Mean density for *S. zebrina* was  
340 higher at the leading edge of *S. viridula* (2.138 indiv. × 900 cm<sup>-2</sup> ± 0.169) compared to the  
341 historic range overlap (1.035 indiv. × 900 cm<sup>-2</sup> ± 0.116) which correspond to its northern  
342 range limit.

343



344 Shell size of the *Scurria* species was variable across the historic range overlap (HRO),  
345 showing a significant site  $\times$  species interaction effect (two-way ANOVA;  $F_{5, 3735} = 4.581$ ;  $P =$   
346  $0.00036$ ). The recently established population of *S. viridula* at the leading edge (located  
347 from  $33.11^\circ$  to  $33.33^\circ\text{S}$ ) had comparable individual shell size to other range edge  
348 populations (see Fig. S2 in Supporting Information). The more equatorward population of  
349 *S. viridula*, at  $18^\circ\text{S}$  showed a median shell size of 25 mm, slightly less than the  
350 southernmost population at  $33.33^\circ\text{S}$ , which had a median value of 32 mm (Fig. S2). The  
351 shell size of *S. zebrina* was different from that found for *S. viridula* at Punta Talca at the  
352 historic range overlap (Tukey HSD test;  $\text{diff} = -0.556$ ;  $P < 0.0001$ ), but median values for  
353 adult limpets were 29 and 31 mm, respectively (Fig. S2). Significant differences were  
354 found between the species at the leading edge of *S. viridula* at Las Cruces (Tukey HSD test;  
355  $\text{diff} = -0.619$ ;  $P = 0.00002$ ), but not at Pelancura located in the same range (Tukey HSD  
356 test;  $\text{diff} = -0.0596$ ;  $P = 0.998$ ).

357

### 358 3.2 Local interspecific distribution patterns

359

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

367 We determined 813 heterospecific individual nearest neighbor distances (*S. viridula* to *S.*  
368 *zebrina*) in the field across the historic range overlap, and at the leading edge of *S. viridula*.  
369 Overall nearest neighbor median distance between the *Scurria* species was 14.5 cm across  
370 the range considered (see Fig. S3 in Supporting Information); about 300 individuals  
371 (36.9%) showed distances between 0 and 10 cm. A log linear model showed non-  
372 independence of nearest neighbor distances across sites (Likelihood Ratio = 419,  $P =$   
373 0.0125), suggesting individuals of the same species are more likely to cluster than  
374 heterospecifics in the sampling sites. This was reflected in the slightly higher distances  
375 between heterospecifics at the leading edge of *S. viridula* (median distances between 17.2  
376 cm and 19.7 cm), compared to sites located further north (median distances between 14.3  
377 and 15 cm; Fig. S3).

378

### 379 3.3 Competition experiments at range edges of *S. viridula* and *S. zebrina*

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

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

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

401

### 402 3.3.1 *Scurria* microspatial distribution in experimental cages

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

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

414

### 415 3.4 Habitat suitability at the leading edge

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

422

## 423 4 | DISCUSSION

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

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

445

#### 446 4.1 Geographic distribution and *Scurria* occurrence

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

456 0.0029 g × day<sup>-1</sup>). Even an increase in density in experimental enclosures (4 ind./ 900 cm<sup>2</sup>)  
457 at the leading edge had a marginal but non-significant effect on the growth rate of *S.*  
458 *viridula* individuals (0.0157 ± 0.0011 g × day<sup>-1</sup>). These results suggest that even under the  
459 potentially stressful conditions experienced by individuals at a leading edge of distribution  
460 (e.g. Fenberg & Rivadeneira, 2011), *S. viridula* can sustain similar individual growth rates  
461 to those observed at sites towards the center of the range. This raises the question of why  
462 the expanding species is being negatively affected by interspecific competition, even when  
463 individuals do not seem to be compromised physiologically by environmental constraints.

464

## 465 4.2 Competition and species range overlap

466 Experimental and manipulative tests of the role of competition in setting species range  
467 edges remain scarce, largely due to the logistic difficulties associated with scaling up local  
468 processes to large scales (see for example Cunningham et al., 2009; Davis, Jenkinson,  
469 Lawton, Schorrock, & Wood, 2001; Godsoe et al., 2015; Hu & Jiang, 2018). Our study is  
470 therefore a timely experimental demonstration of the importance of considering local  
471 interspecific interactions when interpreting range shifts of species. Grazing limpets  
472 compete for space and food on many rocky shores (e.g. Branch, 1976; Creese &  
473 Underwood, 1982; Boaventura et al., 2002; Firth & Crowe, 2010; Aguilera & Navarrete,  
474 2012). However, food supply (e.g. microalgae and ephemeral algae) is expected to be  
475 relatively high across the range considered in our study due to high nutrient availability  
476 (Wieters, 2005). In our field experimental plots the main algal items consumed by the  
477 *Scurria* species were present even at the end of the experiments (see Table S3 in  
478 Supporting Information). Exploitation competition for food may therefore be less important

479 than other kinds of competition, such as interference, among *Scurria* limpets. The existence  
480 of competition under natural conditions is supported by the observations of small-scale  
481 spatial segregation between adult *Scurria* species at scales of ~150 mm (Aguilera et al.,  
482 2013, this study). Although different processes may affect individual-to-individual  
483 distances in limpets, such as substratum topographic complexity (Chapman & Underwood,  
484 1994) and micro-spatial thermal patterns (Chappon & Seuront, 2011), interspecific  
485 individual encounter reduction by individual dispersion has been described as an effective  
486 way to reduce interspecific competition (Branch, 1975). Micro-scale segregation may allow  
487 a few individuals of *S. viridula* grow to adult size, and if so it may play some role in  
488 facilitating local coexistence. However, the low population densities suggest that the small  
489 segregation is insufficient to overcome the deleterious effects of competition on individual  
490 performance and allow local populations to sustain positive population growth when rare, a  
491 necessary requirement to allow for stable coexistence (Chesson, 2000; Shinen & Navarrete,  
492 2014; Siepielski & Mcpeek, 2010).

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

502 upstream populations, which might halt the advancing front some distance downstream  
503 from the last self-maintained population. Interestingly, population size plays an important  
504 role in the leading range edge of species with longer pelagic larval development (Pringle,  
505 Byers, He, Pappalardo, & Wares, 2017), highlighting the indirect role that competition can  
506 play in species with large dispersal potential. Since other species with pelagic larvae are  
507 expanding their distributions at comparable rates to those of *S. viridula* in the eastern  
508 Pacific (e.g. the limpet *Lottia orbigny*; 13.8 km \*year<sup>-1</sup>, the whelk *Thais haemastoma*;  
509 15.9 km\*year<sup>-1</sup>) (Rivadeneira & Fernández, 2005; Sorte, Williams, & Carlton, 2010), it  
510 would be interesting to evaluate the role of biotic resistance by means of competition of the  
511 native assemblage in influencing species' range shift. Our main results suggest competitive  
512 interactions could have an important role influencing the geographic distribution of  
513 equivalent species in combination with physical and biotic processes operating on larval  
514 dispersal and settlement.

515

#### 516 4.3 Habitat suitability and *Scurria* range limits

517 The combination of scarcity of suitable habitat and dispersal limitation is one of the main  
518 mechanisms determining species' range borders (Brown et al., 1996; Case et al., 2005; Holt  
519 & Keitt, 2005). In the absence of dispersal information, our examination of the role of  
520 habitat suitability in limiting *S. viridula* expansion by exploring the availability of suitable  
521 (rocky shore) versus unsuitable (sandy beach) habitat across the leading edge seems useful  
522 in this context (e.g. Fenberg & Rivadeneira, 2011; see Fig. S6 in Supporting Information).  
523 We found that the coastline present at the leading edge of *S. viridula* is predominantly  
524 (>51%) made up of wave-exposed rocky platforms that are similar to those occupied by the



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

540

## 541 5 | Concluding remarks

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

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

553

#### 554 **Acknowledgements**

555 This research was funded by FONDECYT #11121360 and #1160223, and PAI-CONICYT  
556 #79150002 to M.A.A. B.R.B. acknowledges support from MINECON ICM Nucleus  
557 MUSELS and FONDECYT grant # 1181300. Additional support for field trips was  
558 provided by FONDECYT #1160289 to S.A.N. N.V. was supported by FONDECYT grants  
559 #1141037 and #1161699 and FONDAP grant #15150003. Alexandra Gangas supported the  
560 sampling of limpets in the southern range financed by FONDECYT #11121360. We thank  
561 Tomás Flores, Mauricio Oróstica, Ariel Rojas and Tatiana Manzur for field assistance. We  
562 thanks to three anonymous reviewers and the Associate Editor, who made very helpful  
563 comments and suggestions to improve the final version of the manuscript.

564

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

568

#### 569 **Data Accessibility.**

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

#### 571 **Supporting Information.**

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

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

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

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

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

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

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

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

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

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

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

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

588

589

590

591

592

593 **REFERENCES**

594

- 595 Aguilera, M. A., & Navarrete, S. A. (2012). Interspecific competition for shelters in  
596 territorial and gregarious intertidal grazers: consequences for individual behaviour.  
597 *PLoS ONE*, 7(9), e46205. doi:10.1371/journal.pone.0046205
- 598 Aguilera, M. A., Valdivia, N., & Broitman, B. R. (2013). Spatial niche differentiation and  
599 coexistence at the edge: co-occurrence distribution patterns in *Scurria* limpets. *Marine*  
600 *Ecology Progress Series*, 483, 185–198. doi:10.3354/meps10293
- 601 Aguirre, C., Pizarro, Ó., Strub, P. T., Garreaud, R., & Barth, J. A. (2012). Seasonal  
602 dynamics of the near-surface alongshore flow off central Chile. *Journal of*  
603 *Geophysical Research: Oceans*, 117(November 2011), 1–17.  
604 doi:10.1029/2011JC007379
- 605 Aiken, C. M., & Navarrete, S. A. (2014). Coexistence of competitors in marine  
606 metacommunities: Environmental variability, edge effects, and the dispersal niche.  
607 *Ecology*, 95(8), 2289–2302. doi:10.1890/13-0472.1
- 608 Araújo, M. B., & Luoto, M. (2007). The importance of biotic interactions for modelling  
609 species distributions under climate change. *Global Ecology and Biogeography*, 16,  
610 743–753. doi:10.1111/j.1466-8238.2007.00359.x
- 611 Araújo, M. B., & Rozenfeld, A. (2013). The geographic scaling of biotic interactions.  
612 *Ecography*, 37, 406–415. doi:10.1111/j.1600-0587.2013.00643.x
- 613 Boaventura, D., Cancela Da Fonseca, L., & Hawkins, S. J. (2002). Analysis of competitive  
614 interactions between the limpets *Patella depressa* Pennant and *Patella vulgata* L. on  
615 the northern coast of Portugal. *Journal of Experimental Marine Biology and Ecology*,  
616 271, 171–188. doi:10.1016/S0022-0981(02)00044-8
- 617 Boaventura, D., Cancela, L., Fonseca, D., & Hawkins, S. J. (2003). Size Matters :  
618 competition within populations of the limpet *Patella depressa*. *Journal of Animal*  
619 *Ecology*, 72(3), 435–446.
- 620 Bolker, B., & Pacala, S. W. (1997). Using moment equations to understand stochastically  
621 driven spatial pattern formation in ecological systems. *Theoretical Population*  
622 *Biology*, 52, 179–197. doi:10.1006/tpbi.1997.1331
- 623 Branch, G. (1975). Mechanisms reducing intraspecific competition in *Patella* spp .:  
624 migration, differentiation and territorial behaviour. *Journal of Animal Ecology*, 44(2),  
625 575–600.

- 626 Branch, G. (1976). Interspecific competition experienced by South African *Patella* species  
627 Journal. *Journal of Animal Ecology*, 45, 507–529.
- 628 Broitman, B. R., Aguilera, M. A., Lagos, N. A., & Lardies, M. A. (2018). Phenotypic  
629 plasticity at the edge: contrasting population level responses at the overlap of the  
630 leading and rear edges of the geographical distribution of two *Scurria* limpets. *Journal*  
631 *of Biogeography*, in press.
- 632 Broitman, B. R., Véliz, F., Manzur, T., Wieters, E. A., Finke, R., Fornes, P., ... Navarrete,  
633 S. A. (2011). Geographic variation in diversity of wave exposed rocky intertidal  
634 communities along central Chile. *Revista Chilena de Historia Natural*, 143, 143–154.
- 635 Brown, J. H. (1984). On the relationship between abundance and distribution of species.  
636 *The American Naturalist*, 124, 255–279.
- 637 Brown, J. H., Stevens, G. C., & Kaufman, D. M. (1996). The geographic range: size, shape,  
638 and internal structure. *Annual Review of Ecology and Systematics*, 27, 597–623.  
639 doi:10.1146/annurev.ecolsys.27.1.597
- 640 Camus, P., Daroch, K., & Opazo, L. (2008). Potential for omnivory and apparent intraguild  
641 predation in rocky intertidal herbivore assemblages from northern Chile. *Marine*  
642 *Ecology Progress Series*, 361, 35–45. doi:10.3354/meps07421
- 643 Case, T. J., Holt, R. D., Mcpeek, M. A., & Keitt, T. H. (2005). The community context of  
644 species' borders : ecological and evolutionary perspectives. *Oikos*, 108, 28–46.
- 645 Case, T. J., & Taper, M. (2000). Interspecific competition, environmental gradients, gene  
646 flow, and the coevolution of species' borders. *The American Naturalist*, 155, 583–605.
- 647 Chapman, M. G., & Underwood, A. J. (1994). Dispersal of the intertidal snail, *Nodilittorina*  
648 *pyramidalis*, in response to the topographic complexity of the substratum. *Journal of*  
649 *Experimental Marine Biology and Ecology*, 179(94), 145–169. doi:10.1016/0022-  
650 0981(94)90111-2
- 651 Chapperon, C., & Seuront, L. (2011). Space-time variability in environmental thermal  
652 properties and snail thermoregulatory behaviour. *Functional Ecology*, 25(5), 1040–  
653 1050. doi:10.1111/j.1365-2435.2011.01859.x
- 654 Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of*  
655 *Ecology and Systematics*, 31, 343–358. Retrieved from  
656 <http://www.jstor.org/stable/10.2307/221736>
- 657 Cunningham, H. R., Rissler, L. J., & Apodaca, J. J. (2009). Competition at the range  
658 boundary in the slimy salamander : using reciprocal transplants for studies on the role  
659 of biotic interactions in spatial distributions. *Journal of Animal Ecology*, 52–62.  
660 doi:10.1111/j.1365-2656.2007.0

- 661 Davis, A. J., Jenkinson, L. S., Lawton, J. H., Schorrocks, B., & Wood, S. N. (2001).  
662 Making mistakes when predicting shifts in species range in response to global  
663 warming. *Nature*, *409*, 363–366. doi:10.1038/35055575
- 664 Dixon, P. (2009). Testing spatial segregation using a nearest-neighbor contingency table.  
665 *Ecology*, *75*(7), 1940–1948.
- 666 Dong, Y. W., Huang, X. W., Wang, W., Li, Y., & Wang, J. (2016). The marine “great wall”  
667 of China: Local- and broad-scale ecological impacts of coastal infrastructure on  
668 intertidal macrobenthic communities. *Diversity and Distributions*, *22*, 731–744.  
669 doi:10.1111/ddi.12443
- 670 Dutilleul, P. (1993). Spatial heterogeneity and the design of ecological field experiments.  
671 *Ecology*, *74*(6), 1646–1658.
- 672 Espoz, C., Lindberg, D. R., Castilla, J. C., & Simison, W. B. (2004). Los patelogastrópodos  
673 intermareales de Chile y Perú. *Revista Chilena de Historia Natural*, *77*(1), 257–283.
- 674 Fenberg, P. B., & Rivadeneira, M. M. (2011). Range limits and geographic patterns of  
675 abundance of the rocky intertidal owl limpet, *Lottia gigantea*. *Journal of*  
676 *Biogeography*, *38*, 2286–2298. doi:10.1111/j.1365-2699.2011.02572.x
- 677 Firth, L. B., Crowe, T. P., Moore, P., Thompson, R. C., & Hawkins, S. J. (2009). Predicting  
678 impacts of climate-induced range expansion: An experimental framework and a test  
679 involving key grazers on temperate rocky shores. *Global Change Biology*, *15*, 1413–  
680 1422. doi:10.1111/j.1365-2486.2009.01863.x
- 681 Firth, L. B., Knights, A. M., Bridger, D., Evans, A. J., Mieszkowska, N., Moore, P. J., ...  
682 Hawkins, S. J. (2016). Ocean Sprawl: Challenges and Opportunities for Biodiversity  
683 Management in a Changing World. *Oceanography and Marine Biology Annual*  
684 *Review*, *54*, 193–269.
- 685 Fortin, M.-J., & Dale, M. R. T. (2005). *Spatial Analysis: a guide to ecologists* (Fourth, p.  
686 360). Cambridge: Cambridge University Press.
- 687 Gilman, S. E. (2006). The northern geographic range limit of the intertidal limpet *Collisella*  
688 *scabra*: A test of performance, recruitment, and temperature hypotheses. *Ecography*,  
689 *29*(June), 709–720. doi:10.1111/j.0906-7590.2006.04572.x
- 690 Godsoe, W., & Harmon, L. J. (2012). How do species interactions affect species  
691 distribution models? *Ecography*, *35*(9), 811–820. doi:10.1111/j.1600-  
692 0587.2011.07103.x
- 693 Godsoe, W., Jankowski, J., Holt, R. D., & Gravel, D. (2017). Integrating biogeography  
694 with contemporary niche theory. *Trends in Ecology and Evolution*, *32*(7), 488–499.  
695 doi:10.1016/j.tree.2017.03.008

- 696 Godsoe, W., Murray, R., & Plank, M. J. (2015). The effect of competition on species'  
697 distributions depends on coexistence, rather than scale alone. *Ecography*,  
698 38(December 2014), 1071–1079. doi:10.1111/ecog.01134
- 699 Holt, R. D., & Keitt, T. H. (2005). Species' borders: a unifying theme in ecology.  
700 *Ecography*, 1, 3–6.
- 701 Hu, J., & Jiang, J. (2018). Inferring ecological explanations for biogeographic boundaries  
702 of parapatric Asian mountain frogs. *BMC Ecology*, 18, 1–11. doi:10.1186/s12898-018-  
703 0160-5
- 704 Lasiak, T. A., & White, D. R. (1993). Microalgal food resources and competitive  
705 interactions among the intertidal limpets *Cellana capensis* (Gmelin, 1791) and  
706 *Siphonaria concinna* Sowerby, 1824. *South African Journal of Marine Science*, 13,  
707 97–108. doi:10.2989/025776193784287419
- 708 Lester, S., Ruttenberg, B. I., Gaines, S. D., & Kinlan, B. P. (2007). The relationship  
709 between dispersal ability and geographic range size. *Ecology*, 10, 745–758.  
710 doi:10.1111/j.1461-0248.2007.01070.x
- 711 Lett, C., Nguyen-Huu, T., Cuif, M., Saenz-Agudelo, P., & Kaplan, D. M. (2015). Linking  
712 local retention, self-recruitment, and persistence in marine metapopulations. *Ecology*,  
713 96(8), 2236–2244. doi:10.1890/14-1305.1
- 714 Marshall, P. A., & Keough, M. J. (1994). Asymmetry in intraspecific competition in the  
715 limpet *Cellana tramoserica* (sowerby). *Journal of Experimental Marine Biology and*  
716 *Ecology*, 177, 121–138. doi:10.1016/0022-0981(94)90147-3
- 717 Navarrete, S. A., Wieters, E. A., Broitman, B. R., & Castilla, J. C. (2005). Scales of  
718 benthic-pelagic coupling and the intensity of species interactions: from recruitment  
719 limitation to top-down control. *Proceedings of the National Academy of Sciences of*  
720 *the United States of America*, 102, 18046–18051. doi:10.1073/pnas.0509119102
- 721 Phillips, B. L. (2012). Range shift promotes the formation of stable range edges. *Journal of*  
722 *Biogeography*, 39(January 2012), 153–161. doi:10.1111/j.1365-2699.2011.02597.x
- 723 Pigot, A. L., & Tobias, J. A. (2013). Species interactions constrain geographic range  
724 expansion over evolutionary time. *Ecology Letters*, 16, 330–338.  
725 doi:10.1111/ele.12043
- 726 Pringle, J., Byers, J. E., He, R., Pappalardo, P., & Wares, J. (2017). Ocean currents and  
727 competitive strength interact to cluster benthic species range boundaries in the coastal  
728 ocean. *Marine Ecology-Progress Series*, 567, 29–40.

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

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

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

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

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

744 Soberón, J. M. (2010). Niche and area of distribution modeling: A population ecology  
745 perspective. *Ecography*, 33(November), 159–167. doi:10.1111/j.1600-  
746 0587.2009.06074.x

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

750 Tilman, D. (1994). Competition and biodiversity in spatially structured habitats. *Ecology*,  
751 75, 2–16.

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

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

758

759

760



761 **Figure Captions**

762

763

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

771 Field experiments (see boxes for intra- and interspecific effects) were conducted at both  
772 HRO and LE, which test the role of competition in contributing to reduce range expansion  
773 and promote range contraction. It was expected that at their historic range overlap *S.*

774 *viridula* would reduce the growth rate of *S. zebrina* promoting its contraction (red arrow),  
775 while at the leading edge, it was expected *S. zebrina* might contribute to reduction of *S.*

776 *viridula* expansion (blue arrow). Given both *Scurria* species populations present at their  
777 range edge are composed of juvenile individuals, and have lower densities, field

778 experiments considered competitive effects of different size classes; adult (*S. zebrina*; SZa,  
779 *S. viridula*; SVa) and juvenile (SZj, SVj) individuals, and natural (×2 individuals; intra-and  
780 interspecific) and increased (×4 individuals; intraspecific) densities for both *Scurria*

781 species.

782

783

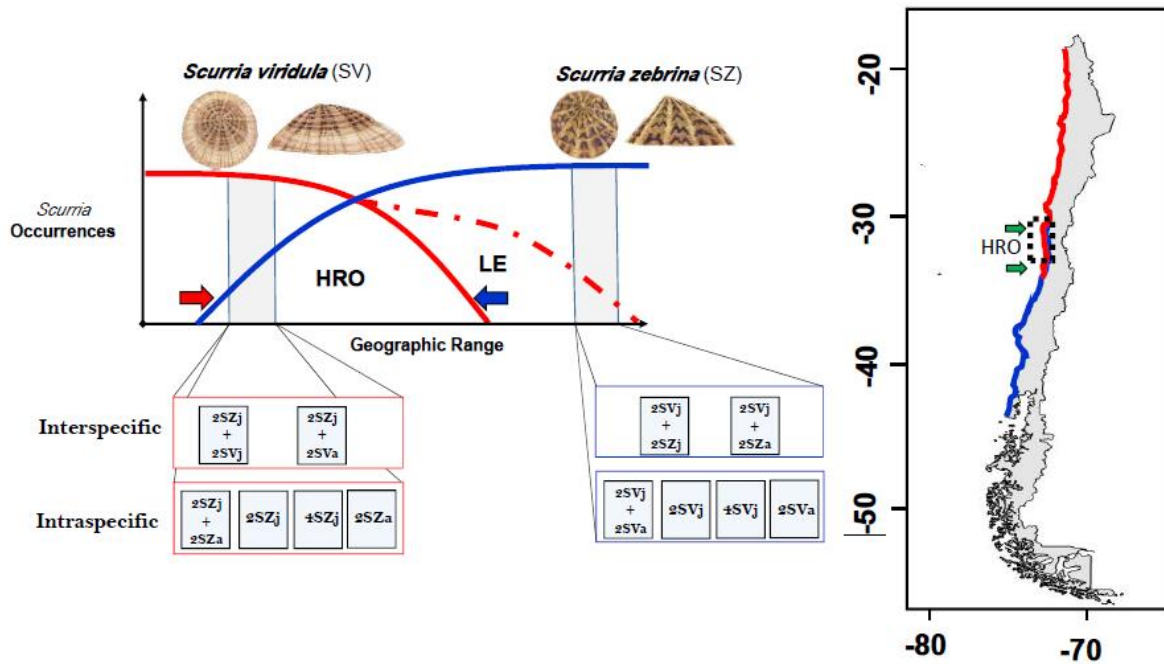
784 **Figure 2.** Latitudinal occurrence (i.e. the proportion of quadrats where a species was found)  
785 of *Scurria viridula* and *S. zebrina* observed from 18°S to 41°S along the coast of Chile.  
786 The red box show the geographic range where the species co-occur in north-central Chile,  
787 their historic range overlap (HRO), while the dotted-blue box depicts the leading edge of *S.*  
788 *viridula* (LE). A map of Chile is shown below, indicating (with blue arrows) the northern  
789 (18°S) and southern (41°S) sites considered in the geographic surveys and the *Scurria*  
790 species range overlap (dotted red lines).

791  
792 **Figure 3.** Average ( $\pm$  SE) change in wet weight of *Scurria zebrina* (a) and *S. viridula* (b)  
793 recorded in experimental arenas at the historic range overlap and the leading edge of *S.*  
794 *viridula*. SZ: *S. zebrina*, SV: *S. viridula*. Subscripts “j” and “a” denote “juvenile” and  
795 “adult” individuals for each species. Means with the same letters were not statistically  
796 significant by Tukey’s multiple comparison test ( $\alpha=0.05$ ).

797  
798 **Figure 4.** *Per capita* intraspecific effects (white symbols), and ‘pure’ interspecific effects  
799 (black symbols) on growth rate (wet weight), estimated for juvenile on juvenile, juvenile on  
800 adult and adult on juvenile individuals of the corresponding focal species considered in  
801 field experiments conducted at the historic range overlap (a) and at the leading edge of *S.*  
802 *viridula* (b). Bars correspond to confidence intervals (95%) estimated by a bootstrapping  
803 procedure. Subscripts “j” and “a” denote “juvenile” and “adult” individuals, respectively.

804

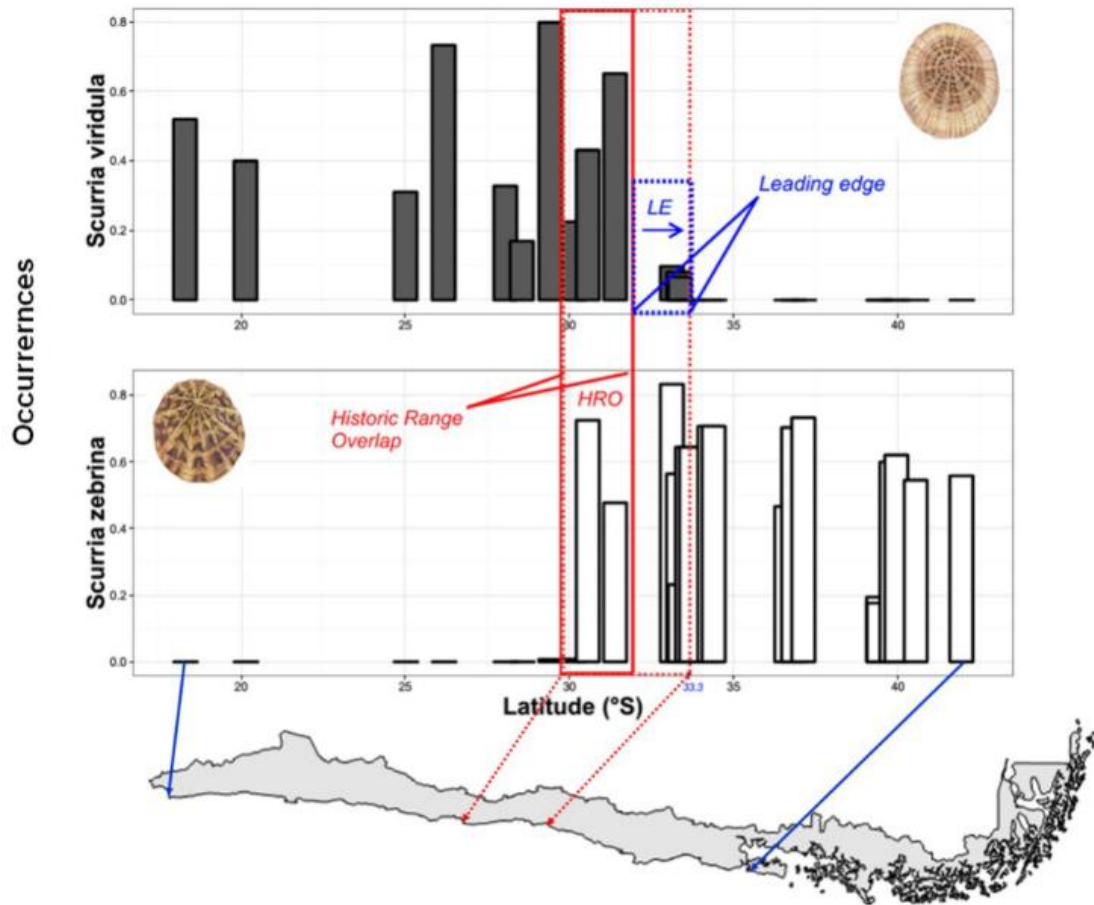
805



806

807 Figure 1

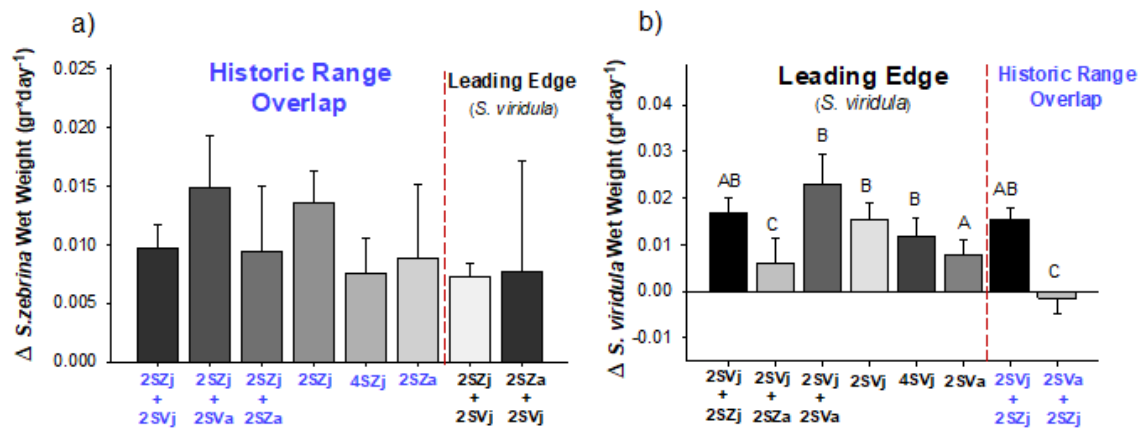
808



809

810 Figure 2

811



812

813 Figure 3

814

815

816

817

818 **Supporting Information. Figures, tables & Appendices**

819

820 **Asymmetric competitive effects during species range expansion: an**  
821 **experimental assessment of interaction strength between ‘equivalent’**  
822 **grazer species at their range overlap**

823

824 Moisés A. Aguilera<sup>1</sup>, Nelson Valdivia<sup>2</sup>, Sergio A. Navarrete<sup>4</sup> and Stuart Jenkins<sup>5</sup> Bernardo  
825 Broitman<sup>3</sup>

826 <sup>1</sup>Departamento de Biología Marina, Facultad de Ciencias del Mar, Universidad Católica del Norte, Larrondo 1281,

827 Coquimbo, Chile

828 <sup>2</sup>Centro de Estudios Avanzados en Zonas Áridas (CEAZA) Ossandón 877, Coquimbo, Chile.

829 <sup>3</sup>Instituto de Ciencias Marinas y Limnológicas, Facultad de Ciencias, Universidad Austral de Chile, Campus Isla Teja

830 s/n, Valdivia, Chile

831 <sup>4</sup>Centro FONDAF de Investigación en Dinámica de Ecosistemas Marinos de Altas Latitudes (IDEAL)

832 <sup>5</sup>Estación Costera de Investigaciones Marinas, Las Cruces, LINCGlobal and Center for Applied Ecology and

833 Sustainability, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile.

834 <sup>6</sup>School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey LL59 5AB, UK

835

836

837

838 **Supporting Information.**

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

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

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

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

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

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

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

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

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

852

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

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

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

856

857

858

859

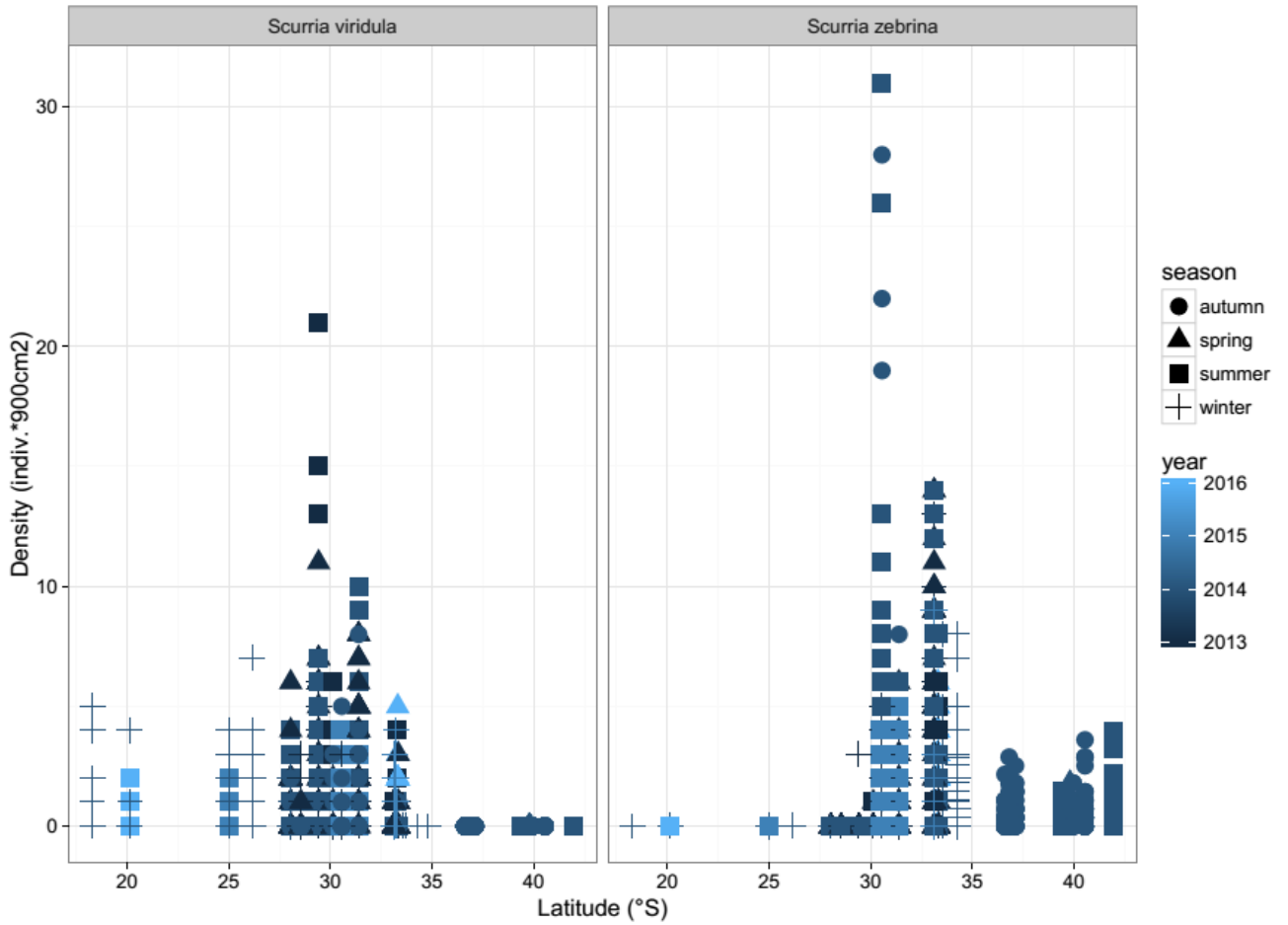
860

861

862

863

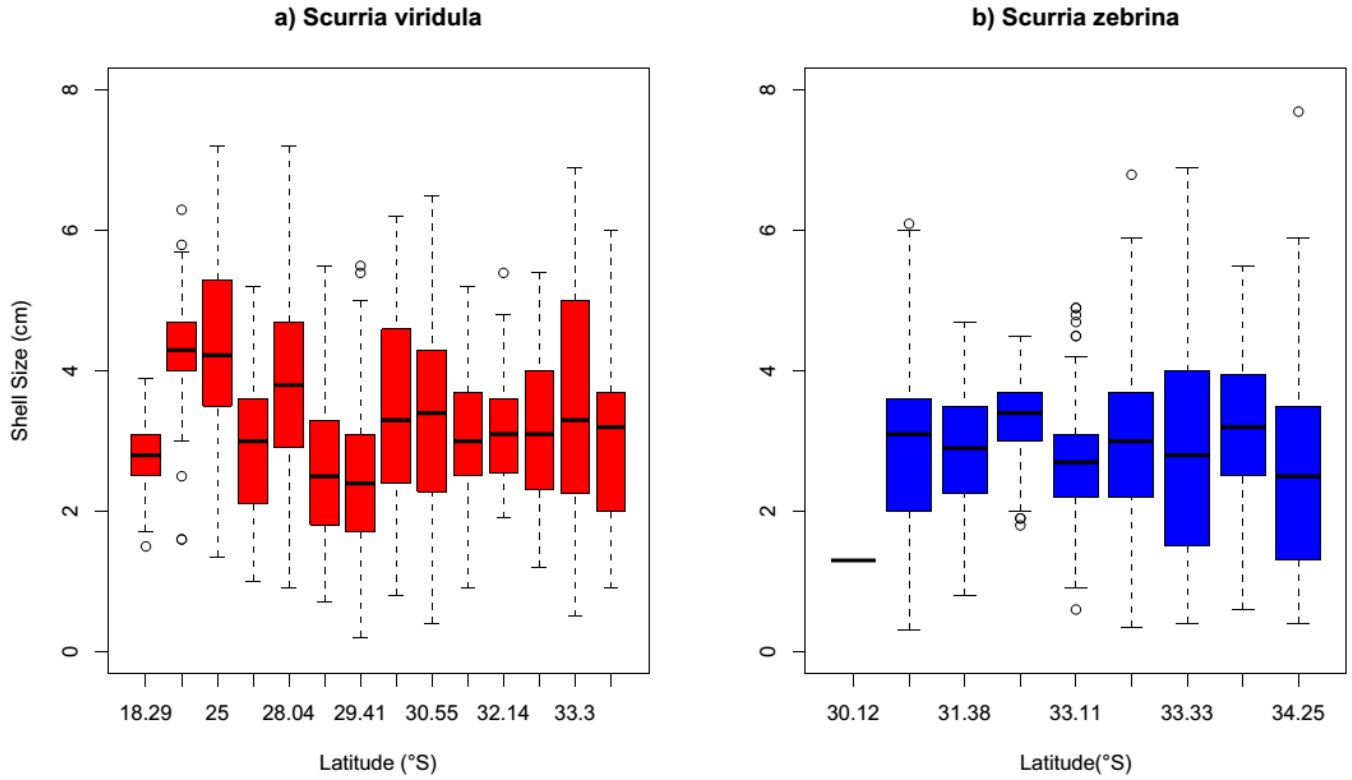
864  
865  
866



867  
868  
869  
870  
871  
872  
873  
874  
875  
876  
877

**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.





878

879

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

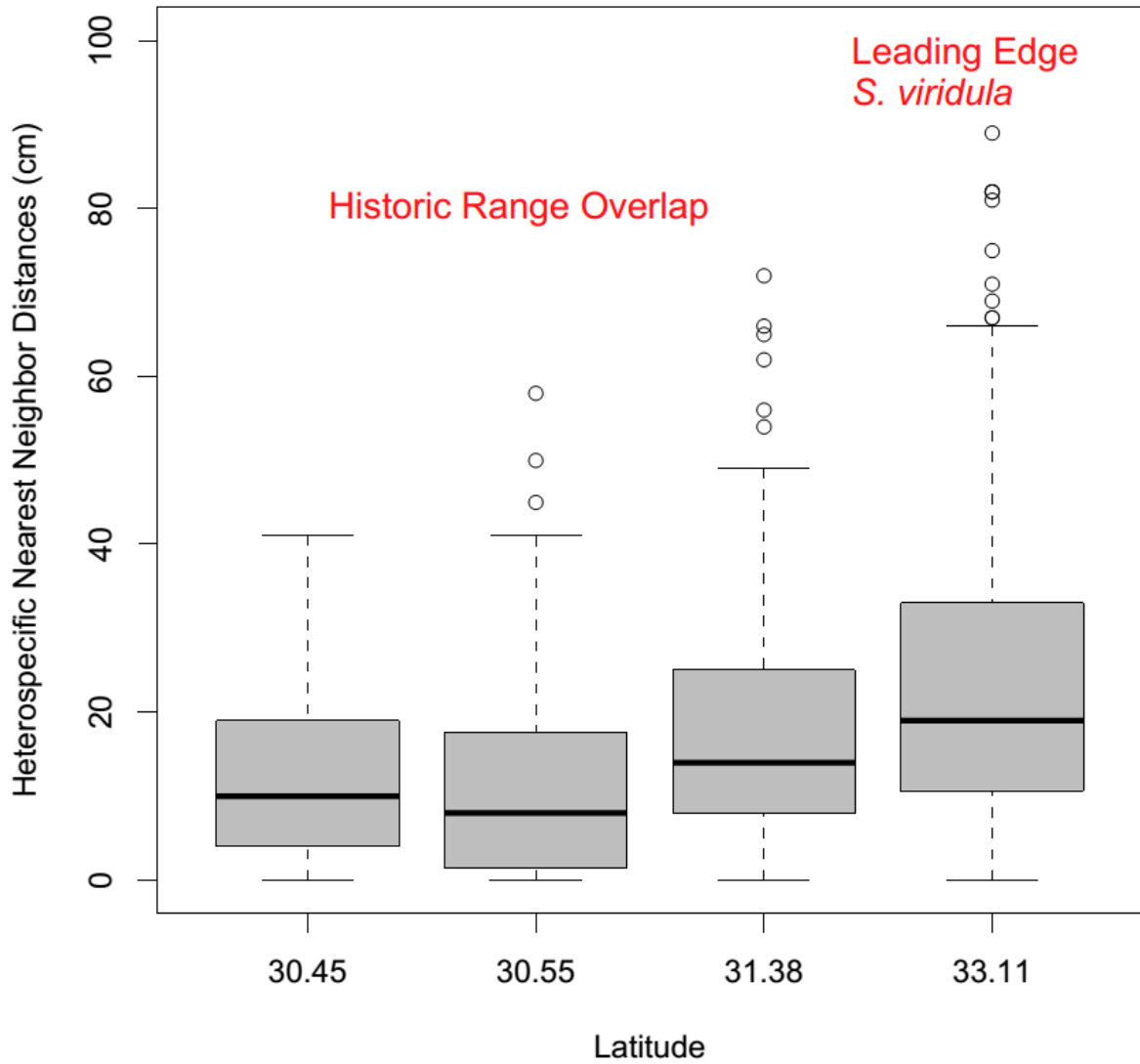
884

885

886

887

888



889

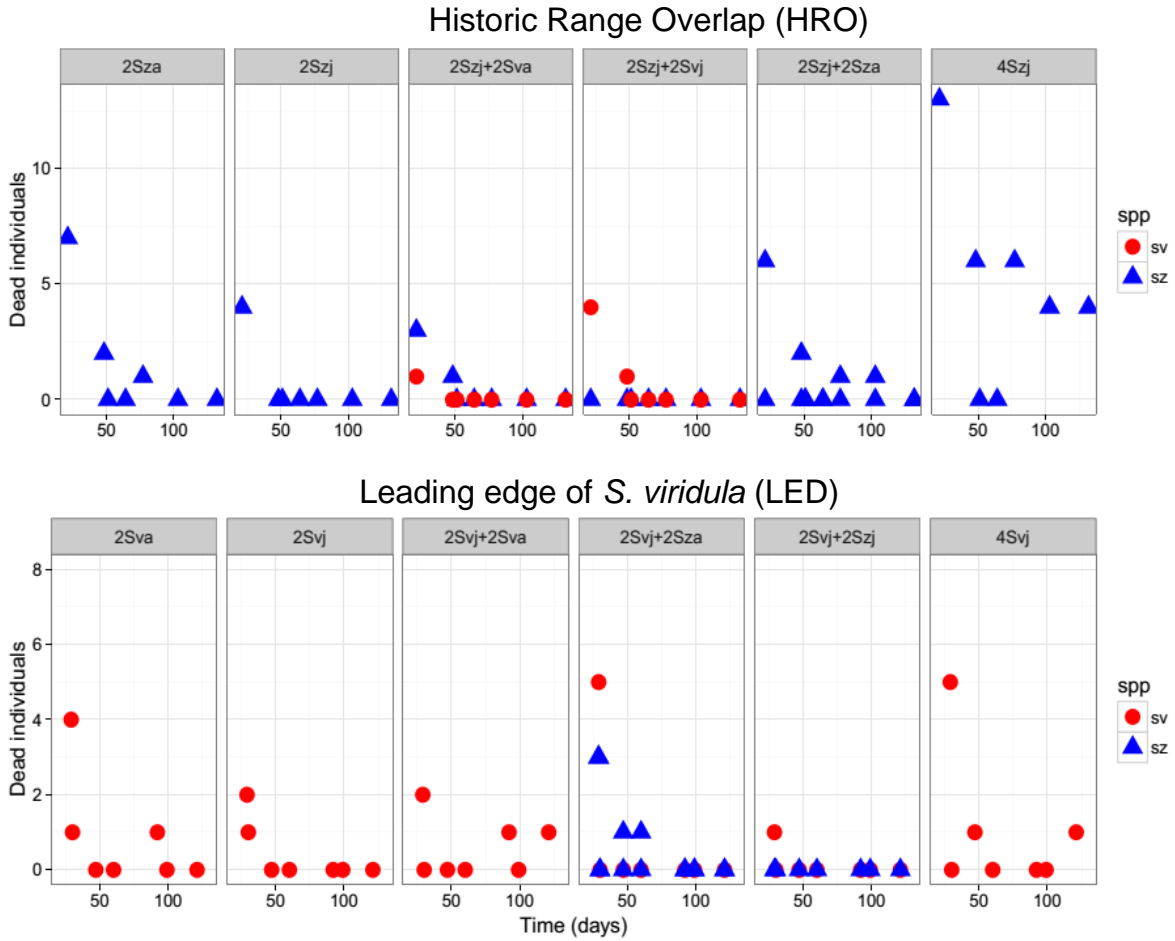
890

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

894

895

896



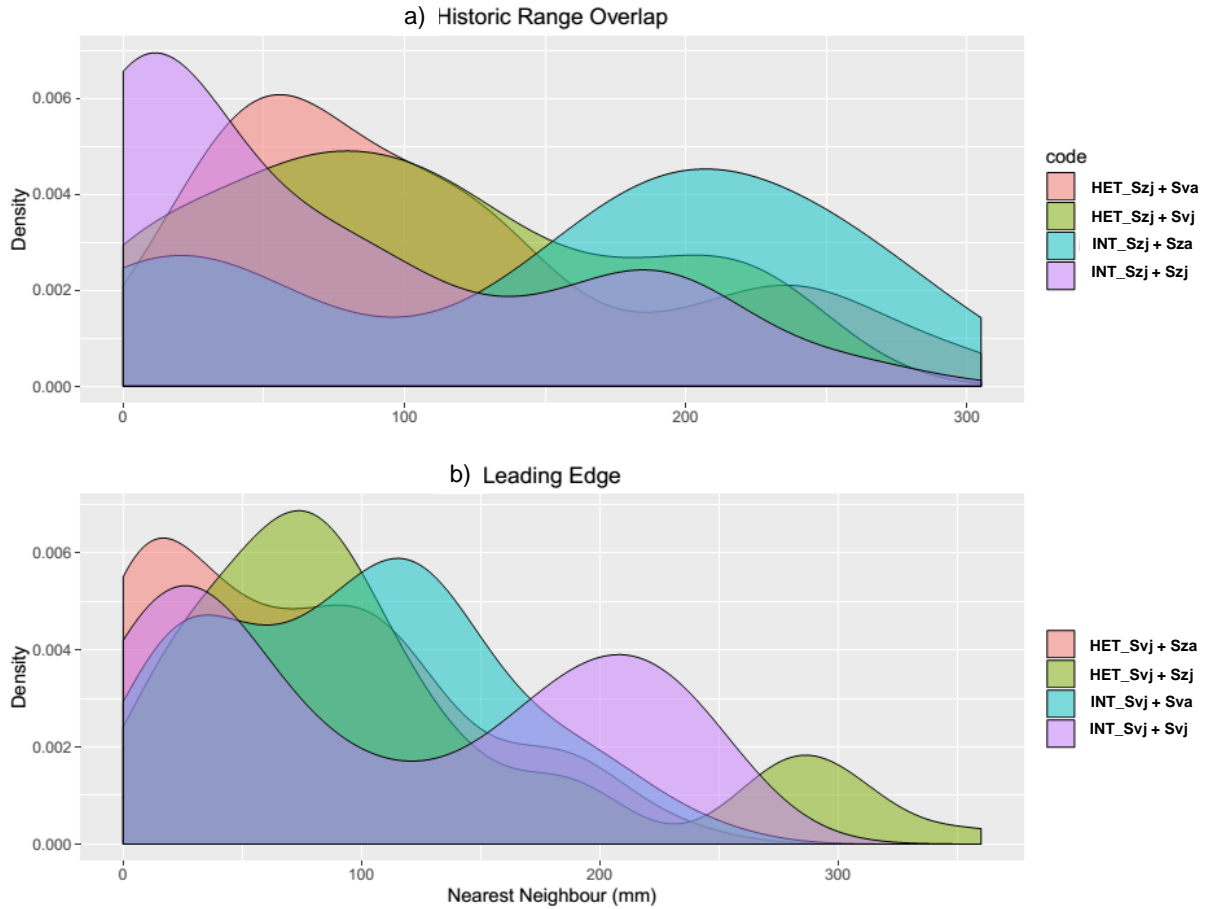
897

898

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

903

904



905

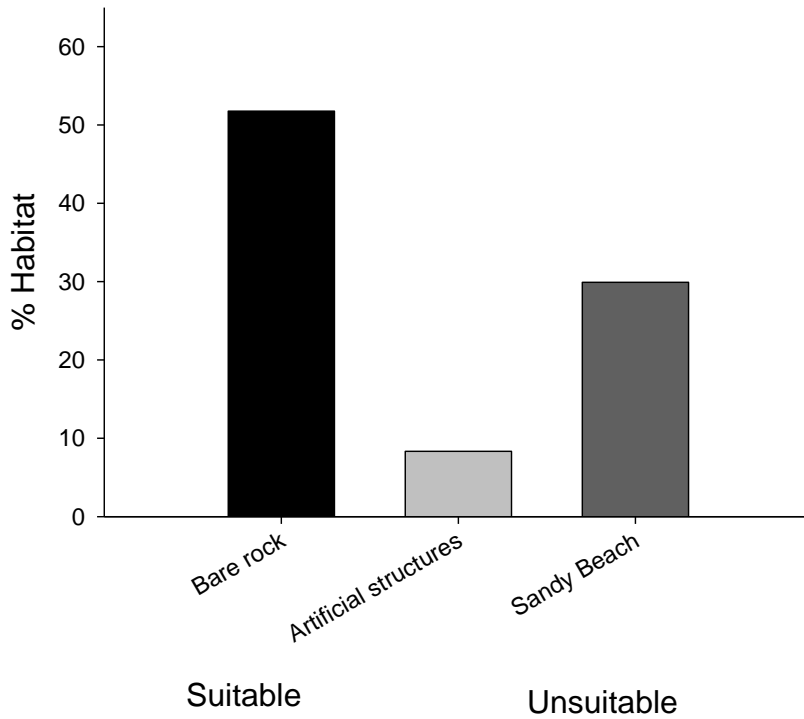
906 **Fig. S5.** Density plot of the intra (INT) and heterospecific (HET) individual nearest  
 907 neighbor distances (NN) estimated inside experimental plots, in experiments conducted in  
 908 the historic range overlap (30°S) a), and at the leading edge of *S. viridula* at Las Cruces  
 909 (33°S) b). SZ: *S. zebrina*; SV: *S. viridula*. Subscripts “j” and “a” denote “juvenile” and  
 910 “adult” individuals, respectively.

911

912

913

Habitat suitability in the expanded range  
of *Scurria viridula* (32°S-33.3°S)



914

915

916

917 **Fig. S6.** Proportion of suitable (bare rock, artificial structures) and unsuitable (sandy beach)  
918 habitat from 32°S to 33°S corresponding to the leading edge of *S. viridula* (LE). Analyses  
919 were conducted through tracing contours of the coast in Google Earth at constant elevation  
920 (500m) (Fenberg & Rivadeneira 2011).

921

922

923

924

925

926

927

928

929

930

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

935

936

Locality	Latitude (°S)	Number of quadrats (30*30 cm)	Rocky platform extent (m <sup>2</sup> )*	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
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
Los Burros	28.5	15	1(24)	Summer	2015
		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
Guanaqueros	30.1	15	1(48)	Winter	2014
		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		
Limarí	30.4	15	1(90)	Autumn	2014
		15	1(90)	Spring	2014
Punta de Talca	30.5	12	1(84)	Summer	2015
		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
Huentelauquén	31.38	15	1(120)	Winter	2014
		15	1(120)	Summer	2015
		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		
Quintay	33.11	19	2(48)	Autumn	2014
		25	1(80)	Summer	2015
		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		
Las Cruces	33.3	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
Cochohgüe	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

937

938

939

940

941

942

943



944

945

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

950

951

Site	Pearson's $r$ <i>P-value</i>
Guaqueros (30.12°S; HRO)	-0.0388 <i>0.3907</i>
Punta Talca (30.55°S; HRO)	0.0323 <i>0.7397</i>
Huentelauquén (31.38 °S; HRO)	0.0223 <b><i>0.0145</i></b>
Quintay (33.11°S; LE)	-0.0741 <i>0.0803</i>

956

957

958

959

960

961

962

963

964

965

966

967

968

969

970

971

972

973

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

978

<b>Leading edge of <i>Scurria viridula</i> (LE)</b>			
Treatment	Ephemeral	Periphyton	Crustose algae
<b>2Svj + 2Szj</b>	<b>76.25 <math>\pm</math> 4.27</b>	<b>10.75 <math>\pm</math> 5.37</b>	<b>3.25 <math>\pm</math> 1.18</b>
<b>2Svj + 2Sza</b>	<b>32.5 <math>\pm</math> 7.5</b>	<b>25.75 <math>\pm</math> 18.27</b>	<b>7.0 <math>\pm</math> 27.1</b>
<b>2Svj + 2Sva</b>	<b>16.25 <math>\pm</math> 14.01</b>	<b>8.25 <math>\pm</math> 0.5</b>	<b>40 <math>\pm</math> 3.14</b>
<b>2Svj</b>	<b>71.75 <math>\pm</math> 14.0</b>	<b>3.5 <math>\pm</math> 0.5</b>	<b>6.25 <math>\pm</math> 3.14</b>
<b>4Svj</b>	<b>25.0 <math>\pm</math> 18.92</b>	<b>7.5 <math>\pm</math> 2.5</b>	<b>13.5 <math>\pm</math> 10.5</b>
<b>2Sva</b>	<b>33.25 <math>\pm</math> 16.42</b>	<b>2.25 <math>\pm</math> 0.75</b>	<b>42.0 <math>\pm</math> 21.94</b>

<b>Historic range overlap (HRO)</b>			
<b>2Szj + 2Svj</b>	<b>16.15 <math>\pm</math> 6.88</b>	<b>1.5 <math>\pm</math> 0.866</b>	<b>0</b>
<b>2Szj + 2Sva</b>	<b>3.75 <math>\pm</math> 3.75</b>	<b>1.25 <math>\pm</math> 1.25</b>	<b>0</b>
<b>2Szj + 2Sza</b>	<b>20 <math>\pm</math> 12.47</b>	<b>0.75 <math>\pm</math> 0.75</b>	<b>1.5 <math>\pm</math> 1.0</b>
<b>2Szj</b>	<b>53.75 <math>\pm</math> 12.5</b>	<b>0.75 <math>\pm</math> 0.74</b>	<b>0</b>
<b>4Szj</b>	<b>28.33 <math>\pm</math> 0.13</b>	<b>0</b>	<b>0</b>
<b>2Sza</b>	<b>10 <math>\pm</math> 5.77</b>	<b>1.2 <math>\pm</math> 1.0</b>	<b>0</b>

979

980

981

982

983

984

985

986

987

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

989

990 The NN distances measured in the field surveys were analyzed by generating contingency  
991 tables of the proportion of individuals that had specific NN distances (e.g. ranging from 0.0  
992 to 89.0 cm). Independence of NN across the different localities was tested with the  
993 likelihood ratio test and Pearson's chi-square. For these analyses, reflexive NN distances  
994 (i.e. when 2 individuals are mutually nearest neighbors; Cox, 1981) were not considered.  
995 Because con- and heterospecific NN-distances estimated in the experimental enclosures in  
996 field experiments include non-independent measures (same individuals sampled through  
997 time) and small sample size, they were analyzed differently; we estimated the probability  
998 density function (PDF) for conspecific and heterospecific NN distance distribution in each  
999 experimental plot. Thus, considering that NN-distances are continuous random variables,  
1000 the PDF (i.e. kernel density plot) was estimated as the ratio of individual NN distances  
1001 values *versus* the average total. This non-parametric estimation utilizes a kernel smoothing  
1002 (in this case Gaussian) to plot values, allowing for comparison of smoother distributions,  
1003 and providing a useful way to explore individual segregation or aggregation (Manly, 1997).  
1004 Density plots were performed with the package 'sm' implemented in R (R Development  
1005 Core Team, 2017).

1006

1007 **References**

1008 Aguilera, M. A., & Navarrete, S. A. (2012). Interspecific Competition for shelters in  
1009 territorial and gregarious intertidal grazers: consequences for individual behaviour.  
1010 *PLoS ONE*, 7(9), e46205. doi:10.1371/journal.pone.0046205

1011 Aguilera, M. A., Valdivia, N., & Broitman, B. R. (2013). Spatial niche differentiation and  
1012 coexistence at the edge: co-occurrence distribution patterns in *Scurria* limpets. *Marine*  
1013 *Ecology Progress Series*, 483, 185–198. doi:10.3354/meps10293

1014 Cox, T. F. (1981). Reflexive Nearest Neighbours. *International Biometric*, 37(2), 367–369.

1015 Manly, B. (1997). *Randomization, Bootstrap and MonteCarlo Methods in Biology* (p. 388).  
1016 Chapman & Hall.

1017 R Development Core Team. (2017). *R: a language and environment for statistical*  
1018 *computing*. R Foundation for Statistical Computing, Vienna, Austria. (R. F. for S.  
1019 Computing, Ed.). Vienna. Retrieved from URL <http://www.R-project.org/>.

1020

1021

1022

## 1023 **Appendix 2.** Field experiments: main protocols

1024

### 1025 *Field experiments design and set up*

1026

1027 To examine the effect of *S. viridula* on *S. zebrina* juvenile individuals at the historic range  
1028 overlap (30°S), we established treatments examining both intraspecific effects of *S. zebrina*  
1029 (juvenile-juvenile, adult-adult and juvenile-adult interactions) and interspecific effects  
1030 (juveniles of each species and juveniles of *S. zebrina* interacting with adults of *S. viridula*)  
1031 (see Fig. 1 in the main text). To examine the effect of *S. zebrina* on *S. viridula* juvenile  
1032 individuals in the leading edge of the latter species (33.3°S), we deployed the three  
1033 treatments (see information provided in the main text) to examine intraspecific effects, but  
1034 in this case on *S. viridula*, and both treatments designed to examine interspecific effects  
1035 (i.e. juveniles of each species and *S. zebrina* adult-*S. viridula* juvenile). In both sites,

1036 intraspecific effects were investigated at either natural or high densities (two or four  
1037 individuals per plot, respectively; see Table 1 and Fig. 1 in the main text), and interspecific  
1038 effects were examined using natural densities of each species (two individuals of each  
1039 species).

1040 Experimental treatment considered at each site; Historic range overlap (HRO): Intraspecific  
1041 effects: 1) 2 *S. zebrina* juveniles; 2) 4 *S. zebrina* juveniles; 3) 2 *S. zebrina* adults; 4) 2 *S.*  
1042 *zebrina* juveniles plus 2 *S. zebrina* adults (inter-size effect). Interspecific effects: 5) 2 *S.*  
1043 *zebrina* juveniles plus 2 *S. viridula* juveniles, and 6) 2 *S. zebrina* juveniles plus 2 *S. viridula*  
1044 adults; Leading edge (LE): 1) 2 *S. viridula* juveniles; 2) 4 *S. viridula* juveniles; 3) 2 *S.*  
1045 *viridula* adults; 4) 2 *S. viridula* juveniles plus 2 *S. viridula* adults, 5) 2 *S. viridula* juveniles  
1046 plus 2 *S. zebrina* juveniles, and 6) 2 *S. viridula* juveniles plus 2 *S. zebrina* adults.

1047 Treatments were randomly allocated to experimental areas and replicated four times. Mixed  
1048 species treatment at high densities were not considered (see Table 1 in the main text) , due  
1049 to the reduced densities of *S. viridula* at the leading edge, and to avoid artefacts caused by  
1050 large individuals enclosed in small areas. *Scurria* individuals were enclosed in  
1051 experimental areas (35 × 35 cm) using stainless steel mesh cages (8 cm high, 10 mm mesh  
1052 size) fastened to the rock with stainless steel screws. Gaps between the substratum and the  
1053 base of the fences were sealed with plastic mesh. Any losses/mortality after the formal start  
1054 of the experiment in Punta Talca and Las Cruces were attributed to competition (e.g.  
1055 individual contests or food shortage). To control for the potential impact of cages (e.g. light  
1056 reduction, water flow), 12 *S. viridula* and 12 *S. zebrina* juvenile individuals were tagged,  
1057 measured and left in the same place with no cage. Survival and activity patterns of these  
1058 individuals were checked twice per month. This procedural control was conducted at both

1059 sites. All *Scurria* individuals were collected in the same intertidal zone (mid-high intertidal  
1060 level ~2.0 MLWL) where the experiments were performed, and where both species inhabit  
1061 (Aguilera, Valdivia, & Broitman, 2013), the experimental plot and collection sites were  
1062 distanced ~3-4 meters apart. At the start of the experiments each organism was weighted  
1063 (wet), sized and labelled with a bee tag before deployment into the experimental  
1064 enclosures. Previous studies showed the foraging range of *Scurria* species encompass a  
1065 radius of ~12-18 cm around their home scar (Aguilera et al. unpublished). For both species,  
1066 the discrimination between juvenile and adults was based on readily visible morphological  
1067 differences (see Aguilera et al., 2013) corroborated by observations of first sexual maturity  
1068 of both species occurring in individuals of 35 mm in shell length. Average shell length of  
1069 juveniles for each species used in the experiments was  $23.5 \pm 0.1$  mm (wet weight =  $2.1 \pm$   
1070  $0.04$  g); average shell length of adults was  $50.5 \pm 0.7$  mm ( $20.6 \pm 0.7$  g; Table 1).

1071

1072

## 1073 **Appendix S3**

1074

### 1075 **Interaction strength measures for field experiments**

1076 In order to provide estimates of interaction strength between species and between size  
1077 classes for each species in experimental treatments (described above and in the main text),  
1078 we estimated per capita intra- and interspecific effects as follow (see also Aguilera &  
1079 Navarrete, 2012): For a given species  $i$  (*S. viridula* and *S. zebrina* in their respective range  
1080 edges) and size class  $k$  (i.e. juvenile, adult), the *per capita* intraspecific effects ( $IS_i$ ) were  
1081 calculated as:  $IS_{i_k} = \frac{(RH_{i_k} - RN_{i_k})}{(NH_{i_k} - NN_{i_k})}$ , where  $RN_{i_k}$  is the *per capita* response variable (e.g.  
1082 growth rate) of species  $i$  of size class  $k$  (juvenile or adult) in the average or “natural”

1083 density treatment,  $RHi_k$  is the *per capita* response measured in the high density treatment,  
1084 and  $NNi_k$  and  $NHi_k$  are the numbers of individuals in the average and high density  
1085 treatments, respectively. Thus for each location we estimated three intraspecific effects;  
1086 juvenile on juvenile ( $ISi_{jj}$ ), adult on juvenile ( $ISi_{aj}$ ), and juvenile on adult ( $ISi_{ja}$ ). The total  
1087 *per capita* interspecific effect (Total\_ $ISij$ ) of species  $j$  on species  $i$  was then calculated as:  
1088  $Total\_ISij_k = \frac{(RMij_k - RNi_k)}{Nj_k}$ , where  $RMij_k$  is the *per capita* response of species  $i$  measured in  
1089 the mixed species enclosures with species  $j$  of size class  $k$ , and  $Nj_k$  is the number of  
1090 individuals of species  $j$  of class  $k$  present in those enclosures. *Per capita* interspecific  
1091 effects do not separate between “pure” *per capita* effects due to addition of a different  
1092 species (identity effect), from the expected changes observed if individuals of the same  
1093 species, but of different size class, were added to the arena (intraspecific effects) (Aguilera  
1094 & Navarrete, 2012). Therefore, considering that *per capita* intraspecific effects would  
1095 maintain constant (and linear over the density range and size class considered) in the  
1096 presence of heterospecifics, we obtained an estimate of “pure” *per capita*  $ISij_k$  as;  
1097  $ISij_k = Total\_ISij_k - ISi_k$ . Confidence intervals for estimates of *per capita* interaction  
1098 strengths were obtained through bootstrapping our observations 1000 times (Manly, 1997).  
1099 We then evaluated whether the 95% bootstrapped confidence intervals overlapped zero to  
1100 judge if the particular effect was statistically significant. All analyses were conducted in the  
1101 R environment v. 3.1.3 (R Development Core Team, 2017).

1102

## 1103 References

1104 Aguilera, M. A., & Navarrete, S. A. (2012). Interspecific Competition for shelters in  
1105 territorial and gregarious intertidal grazers: consequences for individual behaviour.  
1106 *PLoS ONE*, 7(9), e46205. doi:10.1371/journal.pone.0046205

- 1107 Aguilera, M. A., Valdivia, N., & Broitman, B. R. (2013). Spatial niche differentiation and  
1108 coexistence at the edge: co-occurrence distribution patterns in *Scurria* limpets. *Marine*  
1109 *Ecology Progress Series*, 483, 185–198. doi:10.3354/meps10293
- 1110 Cox, T. F. (1981). Reflexive Nearest Neighbours. *International Biometric*, 37(2), 367–369.
- 1111 Manly, B. (1997). *Randomization, Bootstrap and MonteCarlo Methods in Biology* (p. 388).  
1112 Chapman & Hall.
- 1113 R Development Core Team. (2017). *R: a language and environment for statistical*  
1114 *computing*. R Foundation for Statistical Computing, Vienna, Austria. (R. F. for S.  
1115 Computing, Ed.). Vienna. Retrieved from URL <http://www.R-project.org/>.
- 1116
- 1117
- 1118