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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 south-eastern 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. 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, Pacific Ocean, range overlap, range shift, 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., Araújo & Rozenfeld, 2014; Cunningham, Rissler, & Apodaca, 2009; Firth, Crowe, Moore, Thompson, & Hawkins, 2009; Godsoe, Jankowski, Holt, & Gravel, 2017; Soberón, 2010). 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; Gilman, 2006; Rivadeneira et al., 2010; Sagarin & Gaines, 2002). 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 south-eastern 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 seven 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, Valdivia, & Broitman, 2013) (see dotted red line in Figure 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 (a) for the native species, *S. zebrina*, growth and survival at its northern limit should be lower in the presence

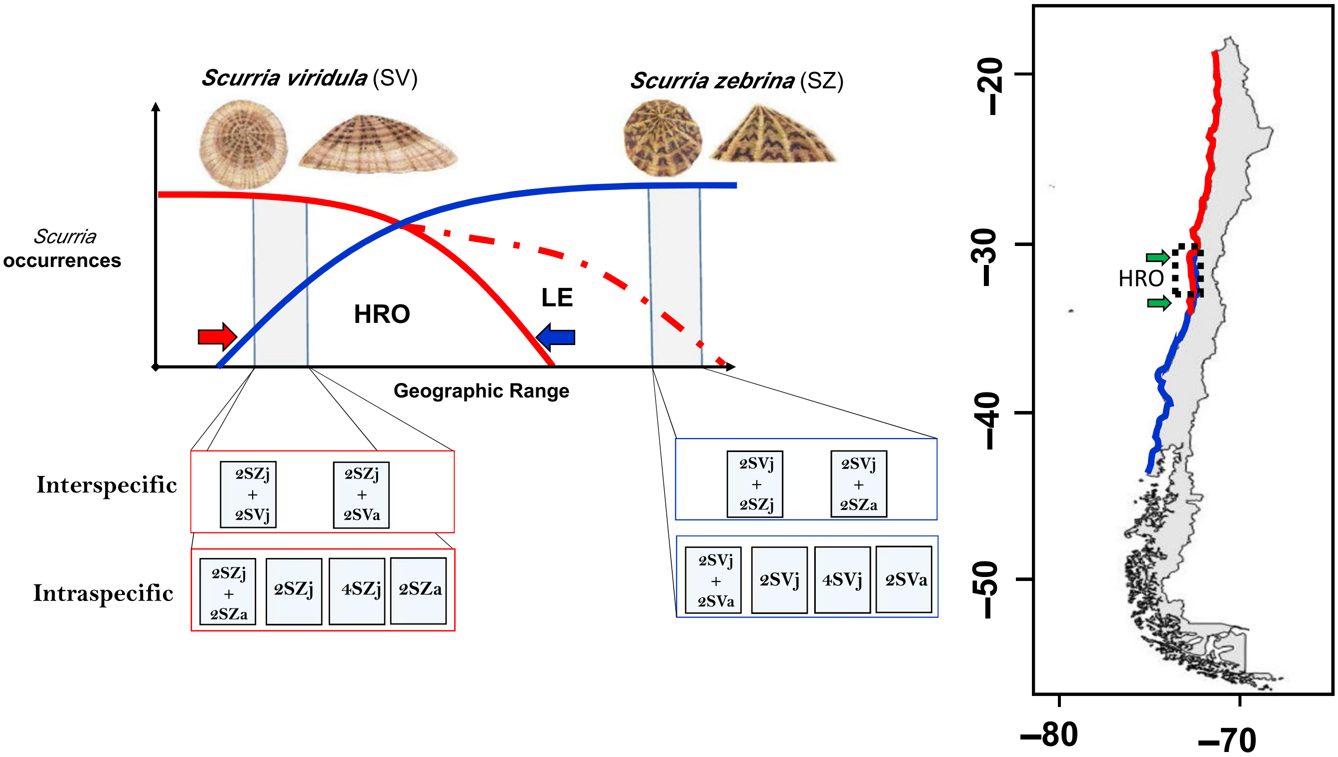

FIGURE 1 Schematic model system and map of the geographic overlap of *Scurria* species and experimental set-up. Previous *Scurria* occurrences generated an historic range overlap, (HRO) at 30°S to 32°S (also indicated as dotted box in the map). Recent (2013) evidence suggests *Scurria viridula* expanded its polar range edge (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 where field experiments were performed. Field experiments (see boxes for intra- and interspecific effects) were conducted at both HRO and LE to 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

of adult or juvenile *S. viridula* (blue arrow in Figure 1) and (b) for the invader species, *S. viridula*, growth and survival of juveniles at its leading edge should be lower in the presence of either adult or juvenile *S. zebrina* (red arrow in Figure 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 distances) 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 neighbour 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 et al., 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 Supporting Information Figure S1) over the period January 2013 to March 2016. This was done by considering a minimum of 10, 30 × 30 cm quadrats (see Supporting Information Table S1) 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 ~500 m^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 Supporting Information Table S1). 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 (Aguilera et al., 2013; Rivadeneira & Fernández, 2005). 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- to 20-m-long and 2.0-m-wide transects located in the mid-high intertidal level. A total of 6,841 individuals were measured. Differences in shell length between species and among the six sites sampled in the range overlap were analysed by two-way ANOVA. For this analysis, we use shell length of 3,748 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)

2.2 | Local interspecific distribution patterns

To evaluate the potential micro-scale segregation of the *Scurria* species in the field, we quantified the interspecific spatial co-occurrences at small scales (few centimetres) of the *Scurria* species using two complementary techniques: abundance correlation in quadrats and individual nearest neighbour distances (Fortin & Dale, 2005). Quadrat-based sampling was conducted at four 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 Figure 1). *Scurria* spatial association at the 900-cm^2 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, that is individual-to-individual distances, was characterized by measuring nearest neighbour distances between conspecific and heterospecific individuals (from *S. viridula* to *S. zebrina* individuals and vice versa). The shape of the nearest neighbour distance distribution commonly captures processes operating between individuals scale (e.g., behaviour) 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 neighbour distances starting with a selected individual positioned in the middle of the sampling area (see Supporting Information Appendix S1 for further details). 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 analysed the frequency of heterospecific nearest neighbour distances across sites by constructing contingency tables (see Supporting Information Appendix S1). Independence was tested with a loglinear 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).

2.3 | Competition experiments at range edges of *Scurria viridula* and *Scurria 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 northern 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* (Figure 1 and see Supporting Information Appendix S2 for details). In a separate experiment with the same general design (Figure 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* (Figure 1, see Supporting Information Appendix S2 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 Figure 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): (a) two *S. zebrina* juveniles; (b) four *S. zebrina* juveniles; (c) two *S. zebrina* adults; (d) two *S. zebrina* juveniles plus two *S. zebrina* adults; (e) two *S. zebrina* juveniles plus two *S. viridula* juveniles; and (f) two *S. zebrina* juveniles plus two *S. virdula* adults. Leading edge (LE): (a) two *S. viridula* juveniles; (b) four *S. viridula* juveniles; (c) two *S. viridula* adults; (d) two *S. viridula* juveniles plus two *S. viridula* adults; (e) two *S. viridula* juveniles plus two *S. zebrina* juveniles; and (f) two *S. viridula* juveniles plus two *S. zebrina* adults (see scheme in Figure 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 Supporting Information Appendix S2 for details). Treatments were randomly allocated to experimental areas and replicated four times. The experiments were initiated on 25 June 2014 at the Punta Talca and on 29 June 2014 at Las Cruces—both experiments ended on 5 December 2014.

TABLE 1 Treatments used in field experiments conducted at the historic range overlap (HRO; 30°S) of the two *Scurria* species, and the new leading of *S. viridula* (LE; 33°S). Number of individuals per enclosures and average body size (wet weight in g) are presented

Treatment	Limpets in enclosure	Individual biomass ± *SE* (g)
Historic range overlap (HRO)		
Intraspecific interactions		
SZj	2	1.31 ± 0.188
SZa	2	6.96 ± 1.441
SZj × 2 (increased × 2)	4	1.74 ± 1.006
SZj + SZa	2 + 2	6.25 ± 1.426
Interspecific interactions		
SZj + SVj	2 + 2	3.01 ± 0.318
SZj + SVa	2 + 2	9.66 ± 2.257
Leading edge of *S. viridula* (LE)		
Intraspecific interactions		
SVj	2	1.76 ± 0.291
SVa	2	11.02 ± 2.017
SVj × 2 (increased × 2)	4	3.98 ± 0.343
SVj + SVa	2 + 2	7.037 ± 1.929
Interspecific interactions		
SVj + SZj	2 + 2	1.08 ± 0.149
SVj + SZa	2 + 2	7.67 ± 2.006

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 *S. zebrina* (Prediction 2) were tested by analysing separately the results from the 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 levels: 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 were 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 Supporting Information 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 Supporting Information Appendix S3 for further details).

2.3.1 | *Scurria* microspatial distribution in experimental cages

Each two weeks per month, we estimate con- and heterospecific nearest neighbour distances in the experimental enclosures in field experiments. We estimated the probability density function (PDF) for conspecific and heterospecific nearest neighbour distance distribution in each experimental plot. Thus, considering that nearest neighbour distances are continuous random variables, the PDF (i.e., kernel density plot) was estimated as the ratio of individual nearest neighbour distances values vs. the average total (see Supporting Information Appendix S1 for further details). These analyses provide a useful way to explore individual (con- and heterospecific) segregation or aggregation (Manly, 2007). Density plots were performed with the package "sm" implemented in R (R Development Core Team, 2017).

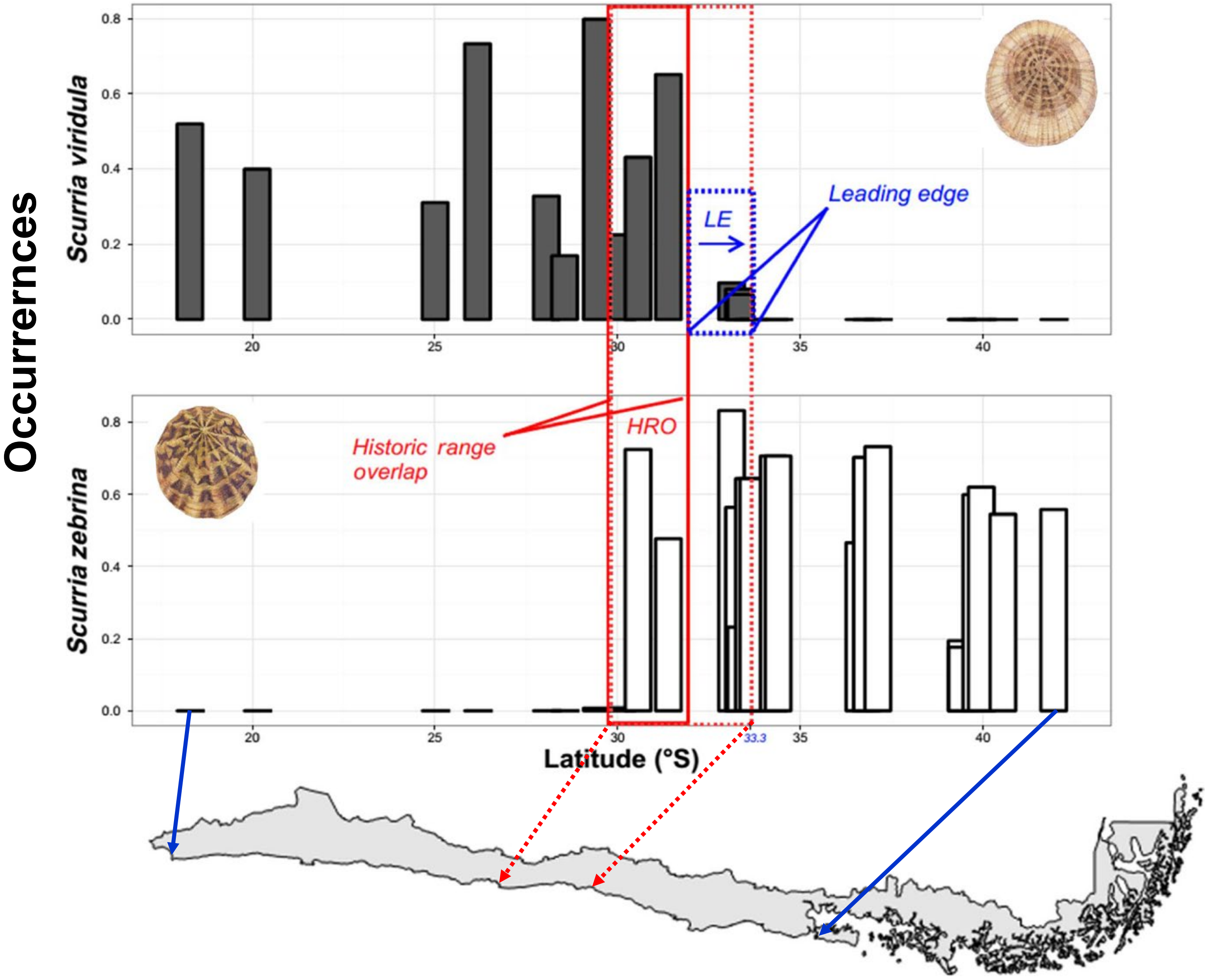

FIGURE 2 Latitudinal occurrence (i.e., the proportion of quadrats where a species was found) of *Scurria viridula* and *S. zebrina* observed from 18°S to 41°S along the coast of Chile. The red box shows the geographic range where the species co-occur in north-central Chile, their historic range overlap (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)

2.4 | 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 32° S to 33.3° 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 was also considered in the analyses.

3 | RESULTS

3.1 | Range shift and geographic patterns of abundance of *Scurria viridula* and *Scurria 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 (Figure 2 and Supporting Information Figure S1). *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 Figure 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 Supporting Information Figure S2). 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 (Supporting Information Figure 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 (Supporting Information Figure 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 at the same latitudinal range (Tukey HSD test; diff = −0.0596; $p = 0.998$).

3.2 | Local interspecific distribution patterns

Interspecific abundance distribution patterns estimated for quadrats (900 cm^2) at the historic range overlap showed a positive, but low, significant correlation ($r = +0.0223$; $p = 0.0145$) at only one site (Huentelauquén, 31.38°S; see Supporting Information Table S2). A negative, but not statistically significant, value ($r = -0.0741$; $p = 0.0803$) was observed at the leading edge of *S. viridula* (Quintay, 33.11°S; see Supporting Information Table S2) suggesting that the pattern of individual heterospecific segregation was not strong enough to be detectable among quadrats.

We determined 813 heterospecific individual nearest neighbour distances (*S. viridula* to *S. zebrina*) in the field across the historic range overlap, and at the leading edge of *S. viridula*. Overall nearest neighbour median distance between the *Scurria* species was 14.5 cm across the range considered (see Supporting Information Figure S3); about 300 individuals (36.9%) showed distances between 0 and 10 cm. A loglinear model showed non-independence of nearest neighbour 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; Supporting Information Figure S3).

3.3 | Competition experiments at range edges of *Scurria viridula* and *Scurria 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 (Figure 3a,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 (Figure 3a, Table 2). Juvenile *S. viridula* growth rate was significantly lower in the presence of adult *S. zebrina* at the leading edge (SVj+SZa; Figure 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 (Figure 3b). We also found a significant reduction of adult *S. viridula* enclosed with juvenile *S. zebrina* at the historic range overlap (SVa+SZj, Figure 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 Supporting Information Figure S4). No mortality of juvenile *S. viridula* enclosed with adult or juvenile *S. zebrina* (or vice versa) was observed (Supporting Information Figure 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 Figure 4a: SZj-SZj, and SZa-SZj, respectively) were not significant (95% CI cross zero; Figure 4a). Similarly, no significant interspecific effect of *S. viridula* on *S. zebrina* (i.e., SVj-SZj, SVa-SZj) was observed (black symbols in Figure 4a). At the leading edge of *S. viridula* at Las Cruces (33°S), no significant intraspecific effect of

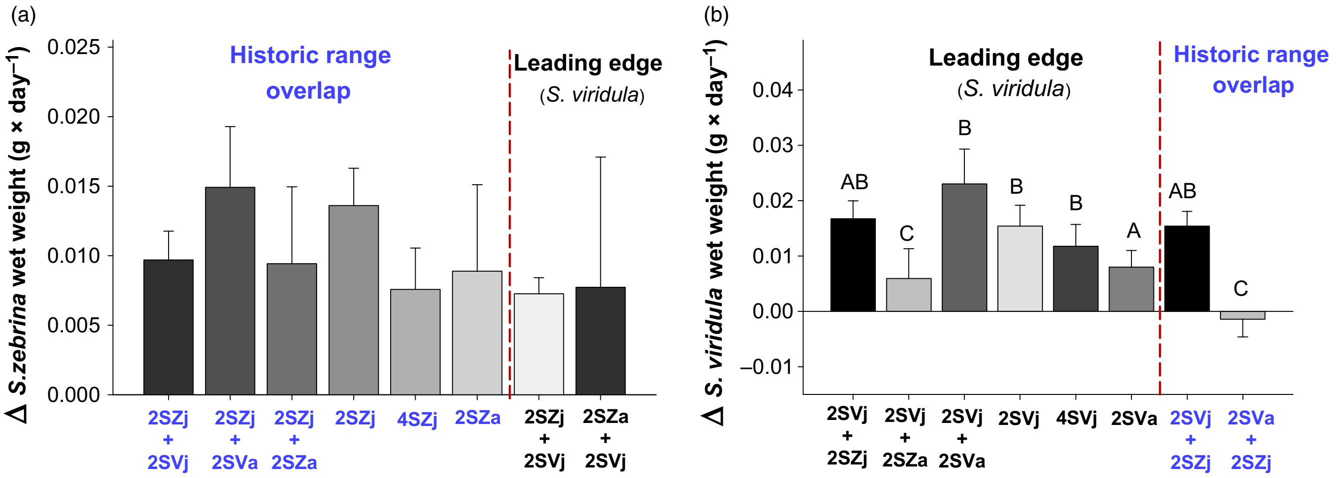

FIGURE 3 Average (± *SE*) change in wet weight of *Scurria zebrina* (a) and *S. viridula* (b) recorded in experimental arenas at the historic range overlap and the leading edge of *S. viridula*. SZ: *S. zebrina*, SV: *S. viridula*. Subscripts "j" and "a" denote "juvenile" and "adult" individuals for each species. No significant differences were observed in (a). Means with the same letters showed in (b) were not statistically significant after Tukey's multiple comparison test (α = 0.05)

juvenile or adult *S. viridula* was detected (white symbols in Figure 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, Figure 4b).

3.3.1 | *Scurria* microspatial distribution in experimental cages

Nearest neighbour 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 Supporting Information Figure S5a) than for juvenile to adult *S. zebrina* conspecifics which appeared more segregated, peaking at about 200 mm (turquoise band in Supporting Information Figure S5a). Distances of juvenile *S. zebrina* to both adult and juvenile *S. viridula* were on average between 50 and 80 mm (see orange and green bands, respectively, in Supporting Information Figure 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 Supporting Information Figure 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 Supporting Information Figure 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 Supporting Information Figure S6), and ~9% correspond to hard artificial structures (e.g., granite breakwaters, concrete seawalls, pontoons) which are interspersed among sandy and rocky habitats (see Supporting Information Figure 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

TABLE 2 Nested ANOVA on average growth rate (i.e., wet weight) of individuals present in experimental areas (plots) in the different treatments considered in field experiments conducted at HRO and LE

Source	DF	MS	*F*	*p*
Scurria zebrina				
Historic range overlap (HRO)				
Treatment (T)	5	0.00035	0.153	0.978
Plot $_{(T)}$	6	0.00086	0.374	0.893
Residual	60	0.00229		
Leading edge (LE)				
Treatment (T)	1	0.0582	1.286	0.279
Plot $_{(T)}$	2	0.00022	0.049	0.953
Residual	12	0.00452		
Scurria viridula				
Leading edge (LE)				
Treatment (T)	4	0.00113	3.802	**0.0114**
Plot $_{(T)}$	16	0.00038	1.28	0.2633
Residual	35	0.000297		
	diff	*p*		
Tukey HSD comparisons[a]				
Intraspecific (2Svj vs. 2Svj+2Sva)	−0.0178	**0.0451**		
Interspecific (2Svj+2Sza vs. 2Svj+2Sva)	0.0264	**0.0095**		
Historic range overlap (HRO)				
Treatment (T)	1	0.00137	11.622	**0.00518**
Plot $_{(T)}$	2	0.000089	0.754	0.49131
Residual	12	0.00012		

Notes. Significant *p*-values (α = 0.05) are presented in bold. Subheadings indicate a: adult individuals; j: juvenile; SV: *S. viridula;* SZ: *Scurria zebrina.*
[a]Only post hoc comparisons related to main hypotheses are presented (see text for details).

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 suggest that environmental conditions are not limiting the performance of this species towards 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 centre 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, Cancela Da Fonseca, & Hawkins, 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 Supporting Information Table S3). 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 microspatial 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).

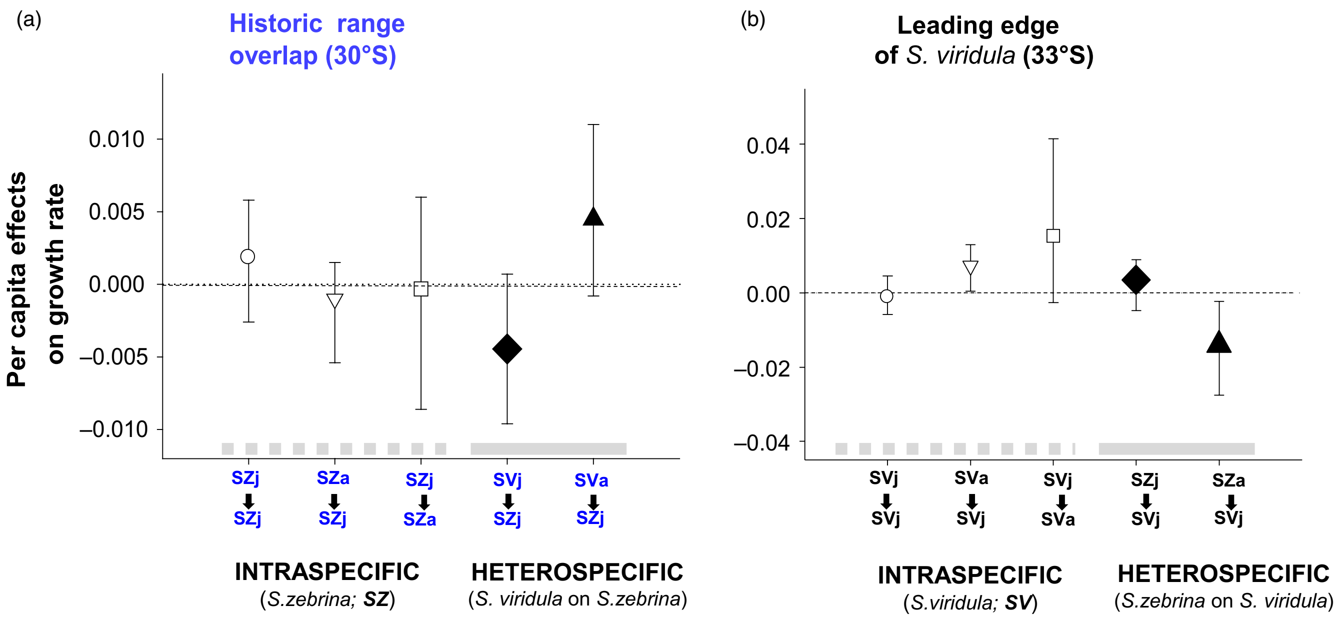

FIGURE 4 *Per capita* intraspecific effects (white symbols), and "pure" interspecific effects (black symbols) on growth rate (wet weight), estimated for juvenile on juvenile, juvenile on adult and adult on juvenile individuals of the corresponding focal species considered in field experiments conducted 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

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) vs. unsuitable (sandy beach) habitat across the leading edge seems useful in this context (e.g., Fenberg & Rivadeneira, 2011; see Supporting Information Figure S6). 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 Supporting Information Figure 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 kilometres (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 Supporting Information Figure 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 (M.A. Aguilera, unpublished), further assisting effective dispersal across sandy beaches.

5 | CONCLUSIONS

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 vs. 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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AUTHORS' CONTRIBUTIONS

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

DATA ACCESSIBILITY

Data associated with this manuscript are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.dr9712v (Aguilera, Valdivia, Jenkins, Navarrete, & Broitman, 2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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