



# Novel co-occurrence of functionally redundant consumers induced by range expansion alters community structure

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**Abstract.** Ongoing climate change is shifting the geographic distributions of some species, potentially imposing rapid changes in local community structure and ecosystem functioning. Besides changes in population-level interspecific interactions, such range shifts may also cause changes in functional structure within the host assemblages, which can result in losses or gains in ecosystem functions. Because consumer-resource dynamics are central to community regulation, functional reorganization driven by introduction of new consumer species can have large consequences on ecosystem functions. Here we experimentally examine the extent to which the recent poleward range expansion of the intertidal grazer limpet *Scurria viridula* along the coast of Chile has altered the role of the resident congeneric limpet *S. zebrina*, and whether the net collective impacts, and functional structure, of the entire herbivore guild have been modified by the introduction of this new member. We examined the functional role of *Scurria* species in controlling ephemeral algal cover, bare rock availability, and species richness and diversity, and compared the effects in the region of range overlap against their respective “native” abutted ranges. Experiments showed depression of per capita effects of the range-expanded species within the region of overlap, suggesting environmental conditions negatively affect individual performance. In contrast, effects of *S. zebrina* were commonly invariant at its range edge. When comparing single species versus polycultures, effects on bare rock cover were altered by the presence of the other *Scurria* species, suggesting competition between *Scurria* species. Importantly, although the magnitude of *S. viridula* effects at the range overlap was reduced, its addition to the herbivore guild seems to complement and intensify the role of the guild in reducing green algal cover, species richness and increasing bare space provision. Our study thus highlights that range expansion of an herbivore can modify the functional guild structure in the recipient community. It also highlights the complexity of predicting how functional structure may change in the face of natural or human-induced range expansions. There is a need for more field-based examination of regional functional compensation, complementarity, or inhibition before we can construct a conceptual framework to anticipate the consequences of species range expansions.

**Key words:** animal–plant interaction strength; biogeographic transition zone; functional diversity; functional role; guild; range overlap; regional compensation.

## INTRODUCTION

Understanding the consequences of human- and climate-induced species range shifts on the functional structure of communities is a central goal of ecology

today (e.g., Harley et al. 2006, Harley 2011, Nyström et al. 2012, Luque et al. 2013). Shifts in the geographic distributions of species change local species composition, leading to novel ecological interactions and, potentially, to fundamentally altered patterns of ecosystem functioning (Worm et al. 2006, Levin and Lubchenco 2008, Wernberg et al. 2012, Sorte 2013, Ling et al. 2015, Usinowicz and Levine 2018). Driven by rapid species introductions and changes in global climate,

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compositional changes are likely to be observed with increased frequency around areas where different biotas overlap, such as biogeographic transition zones (Sexton et al. 2009). In the case of coastal species, these transitional areas can encompass hundreds of kilometers of shoreline (Blanchette et al. 2008), so compositional changes within transition zones can have broad geographic impacts (Russell et al. 2012). Modification of functional structure within consumer guilds driven by species range shifts may result in the incorporation of new functions or the loss of key traits, which can also translate into net gains or losses in resilience of the system (Bellwood et al. 2004, Cardinale et al. 2009, Hughes et al. 2010, Downing et al. 2012). For instance, addition of functionally equivalent or redundant consumer species by range expansions can be considered an insurance against the loss of ecosystem functions following potential future extinctions of species in the recipient guild (Bellwood et al. 2003, 2004, Augustine and McNaughton 2004, Hoey and Bellwood 2009, Pringle et al. 2014, Kaarlejärvi et al. 2017). Theoretical models suggest that trait similarity and complete functional redundancy should be more frequent over regional than local scales (Mouquet and Loreau 2002, Jaksic 2003, Resetarits and Chalcraft 2007). Then, redundancy or equivalence in functional roles could be especially important when species modify their geographic ranges, because expansion of a functionally redundant species would compensate the subsequent range contraction of the recipient or native redundant species (Resetarits and Chalcraft 2007).

Understanding the local functional consequences triggered by the expansion or contraction of species geographic ranges is a threefold challenge. It requires, at a minimum, (1) identifying the functional role of the new species in its original community or assemblage, (2) assessing how the resident members of the functional group respond to the local introduction or extinction (Duffy 2002, Sundstrom et al. 2012), and, finally (3) quantifying the effects of the new set of ecological interactions on community structure and functioning (e.g., competitive exclusion of residents; Stachowicz and Tilman 2005, Simberloff et al. 2013). Incorporation of new consumer species that have similar or redundant roles to those found in the receiving ecological assemblage could strengthen specific functions if their effects are synergistic or additive (Vergés et al. 2014, Ling et al. 2015), as long as the introduction does not cause the extinction of resident members of the guild (e.g., Duffy 2002, Burkepile and Hay 2008, Griffin et al. 2009). The effects of the new species may also be complementary to those of the resident species, leading to more complete (e.g., control of primary producers) or more extensive (over space or time) changes in ecosystem function. Such complementarity may result from the new species having different attributes, or it may result from resource partitioning between residents and the new species, fostering a complementarity in functions, and enhancing ecosystem functions (Duffy 2002, Burkepile and Hay 2008, 2011,

Schmitz 2009). In contrast, the new species could interfere with residents, causing an overall depression of ecosystem function (see, for example, Ling 2008, Ling et al. 2015). Alternatively, the new species can bring a completely novel ecosystem function to the local community, such as habitat provisioning in areas originally devoid of dominant habitat-forming species (e.g., habitat cascade; Thomsen et al. 2010, Altieri et al. 2012, Byers et al. 2012). This situation would be most common when the new species is sessile and does not fit into any resident guild or functional group (Byers et al. 2012). Thus, the individual effects of a new consumer species in the recipient community depend on its species-specific attributes and the effect on local resources relative to the net effect of the total group (Duffy 2002). Exploring how novel co-occurrences between functionally equivalent or distinct species alter the structure of consumer groups can provide important insights into the compensatory potential under species range shifts and hence the stability of ecosystems to environmental change (e.g., Ling 2008, Gonzalez and Loreau 2009, Wernberg et al. 2011, Ghedini et al. 2015, Kordas et al. 2017).

Herbivores have a key function controlling primary production and many aspects of community structure in benthic marine ecosystems (Hawkins and Hartnoll 1983, Paine 2002, Burkepile and Hay 2008, Poore et al. 2012, Kordas et al. 2017). In a context of climate-driven compositional changes, range-expanding herbivores can have important impacts on local (recipient) community structure (see Ling 2008, Ling et al. 2009, 2015, Sorte et al. 2010, Vergés et al. 2014). Such impacts cannot simply be anticipated by the effects in the original community, as the novel environmental conditions encountered by the invader may alter its individual performance. In this study, we take advantage of the recent poleward range expansion of an intertidal rocky shore herbivore, the limpet *Scurria viridula* (Rivadeneira and Fernández 2005, Aguilera et al. 2013b, 2019b). This limpet has recently extended its region of overlap with its closely related congener *S. zebrina* to form a broad transitional zone, where both species co-occur, from 30° to 32° S (Aguilera et al. 2013b, 2019b). Because of the oceanographic conditions around the transition zone, larval arrival of space-dominant mussel and barnacle species is minimal (Navarrete et al. 2005). As a result, the mid-intertidal rocky shore zone of the overlap region is dominated by corticated and green ephemeral algae interspersed with large patches of bare space (Broitman et al. 2001, 2011, Valdivia et al. 2015). This pattern is common in mid- to high-intertidal levels, where both *Scurria* species can show aggregated spatial patterns and reach large shell sizes compared with other members of a diverse group of benthic herbivores. We used this model ecological system to examine the consequences of the introduction of a new species, *S. viridula*, onto the recipient rocky shore communities, studying changes in the functional structure of the herbivore guild to assess three general and informative hypotheses:

- Both *Scurria* species drive redundant or equivalent (i.e., functional redundancy; Chalcraft and Reseraris 2003) reduction in the abundance of dominant algal species increasing bare rock availability and reducing species richness and/or diversity. This prediction stems from the strong similarity in *Scurria* foraging and morphological traits that have been previously described (Aguilera et al. 2013b). In this case, additive effects in the range of overlap can be expected (i.e., the sum of individual effects are similar than their combined effects; white square within the dotted zone in Fig. 1A). Alternatively, they may exhibit synergistic effects, in which case their shared function will be enhanced (i.e., “complementary effect”; yellow square in Fig. 1A).
- Individual per capita reduction of algal abundance and bare rock provision exerted by *Scurria* species diminish at the range overlap because of interference competition and/or lower individual performances at species range ends (Broitman et al. 2018, Aguilera et al. 2019b). Thus, the joint effects of *S. viridula* and *S. zebrina* at the range overlap could be nonadditive (i.e., their combined effect on algal production will be lower than expected by the addition of their individual effects; green square in Fig. 1A). Figure 1A also illustrates the possibility of lower per capita effects of the *Scurria* species at their range ends, where they overlap, compared to conspecifics located towards the core of their respective ranges (e.g., Hampe and Petit 2005, Sexton et al. 2009).
- Scurria* novel co-occurrences with other herbivores at the range overlap may either increase or decrease the magnitude of the collective net herbivore guild on controlling algal abundance and bare rock provision. The co-occurrence of both *Scurria* species could reduce (or keep constant) the net effect of the entire herbivore guild across the region of overlap because of interference competition, or, alternatively, intensify it as a consequence of complementarity in foraging or microhabitat use (see Fig. 1B). Similar arguments can be made if per capita effects are not depressed at the range overlap, but the magnitudes will be different, highlighting the need to evaluate experimentally per capita effects at range boundaries and at the core of species distributions.

## MATERIAL AND METHODS

### *Study system and focal species*

*Scurria viridula* and *S. zebrina* inhabit mid- to high-intertidal zones on wave-exposed rocky platforms (Espoz et al. 2004, Aguilera et al. 2013b). They are sister species (Espoz et al. 2004) that share morphological traits (e.g., maximum size) and habitat, but have contrasting behavioral responses to heat stress and predators (Espoz and Castilla 2000, Broitman et al. 2018). Both species have similar feeding habits (Camus et al. 2008), suggesting

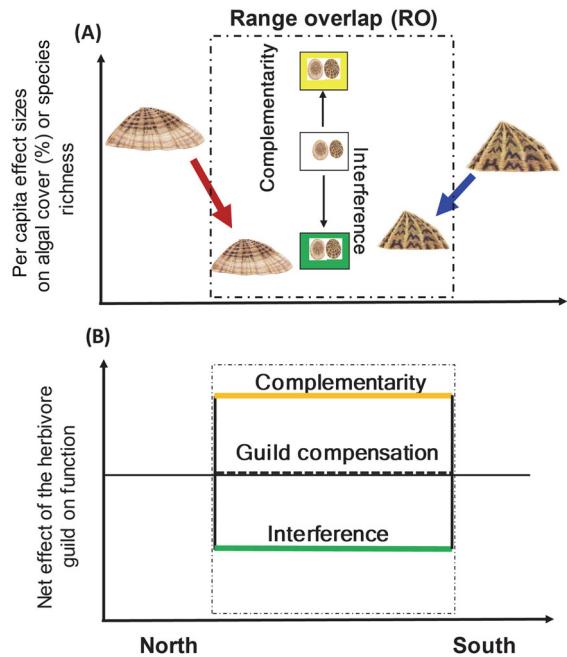


FIG. 1. Scheme of the expected effect sizes on community structure (sessile species cover, richness, and diversity) of the two *Scurria* species and the entire herbivore guild at the region of range overlap (RO), and within their respective equatorward (*Scurria viridula*) and poleward (*Scurria zebrina*) geographic regions. (A) Individual effects of both *Scurria* species are expected to be higher within their respective ranges (north and south) than at the RO, following the reduction of individual performance expected at geographic- range borders. Combined effects of the two species within the RO could be the results of adding their separate impacts (i.e., additivity in effects, white square), but it could also be lower than expected if interference takes place between species (see green square). Alternatively, joint effects could be higher than expected in the case of complementarity of their impacts on the producer assemblage (see yellow square). (B) The net collective effect of the entire herbivore guild may remain relatively constant across the entire region or exhibit a latitudinal gradient. Assuming there is no north-south environmental gradient, the collective effect of the herbivore guild could be unchanged within the RO (despite reductions in performance of the two *Scurria* species) because of compensatory effects by other species in the guild (see dotted black line). It could be reduced because of depression in *Scurria* performances with no compensation. Such a decrease could be further reduced by interference between the two *Scurria* (green line). Alternatively, functional roles could be complementary and therefore enhance the total herbivore effect (top orange line).

that they can have strong joint impacts on benthic primary production through high per capita effects on ephemeral algae and biofilm (Aguilera et al. 2013a).

*Scurria viridula* is found from Peru (12° S) to central-north Chile (32° S), and *S. zebrina* is distributed from central Chile (30° S) to southern Chiloé (~43° S; Espoz et al. 2004), thus overlapping ranges between 30° and 32° S. The largest adult individuals *S. viridula* conspicuously occupy the high intertidal zone on the back sides of vertical rocks directly exposed to waves.

But the bulk of the adult population, juveniles, and recruits occur throughout intertidal platforms, where they can sometimes be mistaken by *S. zebrina* by untrained eyes. These two focal species cooccur across the range overlap with a diverse group of benthic herbivores, including other *Scurria* species (mostly *Scurria araucana*, *Scurria cecilianae*, and *Scurria variabilis*, and, to a lesser extent, *Scurria plana*), chitons (*Chiton granosus*, *Chiton cumingsii*, *Chiton barnesii*), keyhole limpets (*Fisurella crassa*), snails (*Echinolittorina peruviana*, *Austrolittorina araucana*), and a pulmonate limpet (*Siphonaria lessoni*). The benthic herbivore guild has been extensively studied (Santelices 1990, Nielsen and Navarrete 2004, Aguilera and Navarrete 2007, 2011, 2012, Aguilera et al. 2015) and both equivalent and complementary functional impacts have been observed on algal establishment, making this speciose guild functionally diverse (Aguilera and Navarrete 2012). Both *S. viridula* and *S. zebrina* are assumed to be important grazer species; while their densities are never too high compared with other species in the guild, their large maximum adult shell size (from 5.5 to 6.5 cm, Aguilera et al. 2013b) suggests they may have high per capita effects on algal abundance. In the case of *S. viridula*, individual foraging and resting activities concentrate on smooth and inclined rocky surfaces. Here, this species forms clumps of ca. 12–15 individuals (Aguilera et al. 2013b), which increases the potential for intense albeit spatially localized effects on the sessile algal assemblage, leaving visual indications (bare rock) on the substrate. The algal community is highly diverse as the range overlap zone includes several algal species that coexist over a limited part of this region, which corresponds to a transition in oceanographic conditions along the coastline (Broitman et al. 2001, Wieters et al. 2003, Tapia et al. 2009, Aguilera et al. 2019a). Green ephemeral algae like Ulvoids (e.g., *Ulva rigida*, *Ulva compressa*), *Blidingia minima*, *Ulothrix* sp. and the red alga *Pyropia orbicularis* (= *Porphyra columbina*; Guillemain et al. 2016) dominate mid-high and high-intertidal levels across the distributional range. The corticated late-successional alga *Mazzaella laminarioides* is dominant in mid-intertidal levels of central Chile, but it is absent north from 30° S (Broitman et al. 2001, Montecinos et al. 2012; and see Aguilera et al. 2019a for review). Advances in molecular genetics have revealed several cryptic species among dominant habitat-forming algae of the mid- and low-intertidal zones of the rocky shore, including the corticated algae *Mazzaella* and the kelp *Lessonia* (Tellier et al. 2011, Montecinos et al. 2012). Thus, the study took place in a highly diverse biogeographic system characterized by a transitional zone around 30° S in which both top-down and bottom-up processes have been shown to shape intertidal community structure (e.g., Navarrete and Castilla 2003, Nielsen and Navarrete 2004, Aguilera and Navarrete 2012, Aguilera et al. 2015).

### Geographic *Scurria* range overlap

The distribution of the focal *Scurria* species and recent range shifts of *S. viridula* in central-northern Chile have been documented in field studies across the region (see Aguilera et al., 2013b, 2019a, b). Long-term abundance data sets (i.e., 1998–2000, 2003–2005, and 2009–2015) of *Scurria* limpets, estimated through positioning 50 × 50 cm quadrats, from higher to lower intertidal levels, at different sites spanning ~1,600 km from north to central Chile, show a well-defined geographic overlap of both herbivore species between 30° and 32° S (see Fig. 2 and Aguilera et al., 2013b, 2019a, b). We used these data sets to determine the variability in abundance of *Scurria* across the site of range overlap (30° S) and at the new range edge of *S. viridula* species (33° S).

### Functional herbivore effects: enclosure/exclusion experiments

Both *Scurria* species can be considered scraper/grazer herbivores, capable of abrading the substrate with their radula (i.e., docoglossan type), thus removing periphyton (spores and plantlets of macroalgae), together with microorganisms and early stages of sessile invertebrates (Camus et al. 2008, Aguilera 2011). To determine if their effects on the early colonization of sessile species were qualitatively and quantitatively similar, we estimated the effects of each species on the early colonization of periphyton and on the established stages of early- and mid-successional algal species (i.e., from 1 to 13 months from experimental removal of the community) under the different contexts of geographic co-occurrence. It should be noted that in this system, late-successional algae species like the corticated alga *Mazzaella laminarioides* typically colonize 13–15 months after experimental bare space creation (Aguilera and Navarrete 2012) and therefore this species and other late-successional sessile species (e.g., the red alga *Gelidium chilense*, the mussel *Perumytilus purpuratus*) were nearly absent from our experimental plots.

The prediction that the two *Scurria* species are functionally redundant, and would interfere with each other generating combined effects that are indistinguishable from their isolated effects (Hypotheses 1), or, in contrast that their effects are additive or synergistic increasing the net collective herbivore guild effect (Hypothesis 3), requires assessing potential intraspecific changes in per capita effects between geographic regions or origin versus overlap (Hypothesis 2). To this end, we conducted herbivore enclosure/exclusion experiments in the mid-intertidal shore at three sites located at (1) the range overlap of the two *Scurria* species (~31° S); (2) equatorward (north) of this zone (26° S), where only *S. viridula* is present; and (3) poleward (south) of it (33° S), where populations of *S. zebrina* are common and *S. viridula* is present at very low densities as young individuals, having recently expanded its range into this region. For

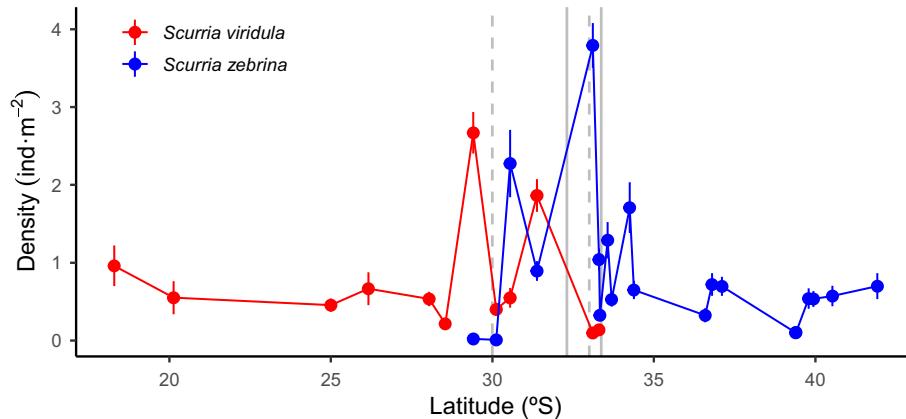


Fig. 2. Density (individuals/m<sup>2</sup>;  $\pm$ EE) of *Scurria viridula* (red) and *Scurria zebrina* (blue) along the coast of Chile from 18° to 42° S. For *S. zebrina*, this corresponds to the complete geographic range of the species. Note the range overlap (RO) of both species is from 30° to 33° S. The range of *S. viridula* expansion is from 32.31° to 33.7° S.

operational purposes, we considered the 33° S sites as “exclusively” *S. zebrina*, at least at the time of our study. The experimental design consisted of six treatments at the range overlap (RO), and four at the sites within the exclusive range of each *Scurria* species. The sites and experimental design were as follows: Range overlap, Punta Talca, 30.5° S (RO): (1) two *S. zebrina* (SZ) enclosures, (2) two *S. viridula* (SV) enclosures, (3) one *S. zebrina* plus one *S. viridula* enclosure (polyculture), (4) herbivore exclusion, (5) control (open areas), and (6) procedural control (partial fences). Equatorward of the RO, Carrizal Bajo, 28° S, (north): (1) two *S. viridula*, (2) herbivore exclusion, (3) control, (4) procedural control. South poleward of the RO, Las Cruces, 33.5° S (south): (1) two *S. zebrina*, (2) herbivore exclusion, (3) control, (4) procedural control (see Appendix S1: Table S1 for summary of the treatment design). All treatments, at each locality, were replicated six times. Each experimental unit consisted of a 35 × 35 cm rock area that was scraped clean with drill-mounted brushes and manual chisels, removing all organisms including encrusting algal fragments. This procedure reset the community to an early community stage and allowed us to identify the effects of herbivore species on initial successional stages and the establishment of midsuccessional species that can colonize within a year’s time on succession (Aguilera and Navarrete 2012). The field experiments were initiated on 12 March 2013 in Carrizal Bajo (north), 25 March 2013 in Las Cruces (south) and on 2 April 2013 in Punta Talca (RO) and all three experiments ended on 30 April 2014 (spanning about 400 d). To enclose *Scurria* individuals inside the experimental plots (35 × 35 cm), we used stainless steel mesh fences (8 cm high, 10-mm mesh size) fastened to the rock with stainless steel screws. Gaps between the substratum and the base of the fences were sealed with plastic mesh to prevent predators and other benthic grazers to access the experimental plots. We evaluated the effect of fences on

sessile organisms by including a partial fence (procedural control) in our treatment design, which consisted in attaching sections of the fence with sufficient separation to allow access to all common grazers. These experimental levels were contrasted against control areas (open plots; see Results section). Limpet enclosures consisted of one adult individual *Scurria* (3.4 ± 0.16 cm shell length) inside the experimental plots, which was carefully collected during nocturnal low tide from the same rocky platform and intertidal zone level where fences were deployed. The resultant *Scurria* densities inside enclosures, at all sites correspond well to natural densities recorded for both species in the range overlap (i.e., 11.9 ± 1.34 *Scurria* individuals/m<sup>2</sup>, roughly 1.6 individuals per plot area; Aguilera et al. 2013b). It should be noted that at Las Cruces, densities of *S. viridula* are lower than other sites (see Results), but we kept the same experimental densities across all locations for the sake of comparisons. Over the course of the experiment, only two enclosed *S. viridula* individuals had to be replaced from two enclosures in the overlap region site (Punta Talca), and one individual in the northern site (Carrizal Bajo). To control for the potential impact of fences (e.g., confinement) and transplantation on limpet individual behavior (Chapman 2000), 10 *S. viridula* and 10 *S. zebrina* individuals were tagged, measured, and left in the same experimental place with no fences. Survival and activity patterns (e.g., displacements from original position) and attachment to the substrate of these individuals were checked twice per month at each site. Every month we removed other benthic herbivores found inside enclosure/exclusion plots in the experiment such as *Scurria* spp. and *Siphonaria lessoni* recruits (2–3 individuals per plot >5 mm length) or Chitons, littorinids snails, which were commonly less than four individuals per plot. Community composition was assessed monthly from 15 March 2013 to 30 April 2014 by recording all species present and quantifying percentage cover of all

sessile organisms within experimental areas with  $35 \times 35$ -cm quadrats with 81 uniformly spaced intersection points. Each plot was also photographed with a high-resolution digital camera, and percentage cover re-estimated in the laboratory to compare with field estimates. Each photograph was cropped to include only the quadrat and analyzed using the program image J.<sup>9</sup> Organisms were identified to the lowest taxonomic resolution possible. When identification was difficult in the field we collected samples of algae and took them to the laboratory to identify under a stereomicroscope. During each monitoring session, fences were manually cleaned of all algae and growth to reduce fence effects on light and water circulation.

### Statistical analyses

We examined whether interannual fluctuations of *Scurria* densities at the geographic overlap, since *S. viridula* expansion, followed similar patterns between the two species. To this end, we used all sampling dates for the range overlap (Punta Talca, 1998–2014) and the poleward site (Las Cruces, 2003–2015), and examined between species association with Kendall's tau correlation, which examines whether positive and negative fluctuations appear correlated over time (synchronous). Additionally, Pearson linear correlation was also used to examine whether abundances of the two species were linearly correlated over time.

Herbivore effects on intertidal community composition were tested through the differences in mobile (i.e., small recruits found inside plots) and sessile species composition between treatments for each region over the 13-month experimental period. We used nonmetric multidimensional scaling (nMDS) on untransformed Bray–Curtis distances, calculated for each replicate plot of each treatment, through the averaged (for each replicate plot over the 13 months of the study) and normalized density and cover for mobile and sessile species, respectively. Thus, we obtained long-term estimates for each replicate plot ( $n = 6$ ), corresponding to each treatment, for each site during the study. We note that because our study did not consider the late-successional stages that typically give rise to strong differences among herbivore identities (Aguilera and Navarrete 2012), differences in community responses between initial colonization (1–4 months), intermediate establishment (5–8 months) and midsuccessional stages (9–13 months) were not consistent across the study region (Appendix S2: Fig. S1). At the southern end (Las Cruces) and to a lesser extent the northern end, the sessile community composition observed after 9 months tended to be different than earlier dates, and treatment effects were emphasized, but such successional trends got blurry in the overlap region (Appendix S2: Fig. S1). Therefore, we preferred to simplify presentation and comparisons across regions by

calculating treatment effects on the long-term (13 months) average community responses encompassing both early and midsuccession. Statistically significant differences between treatments for each locality (one-way model) were analyzed with PERMANOVA. Tukey honestly significant difference (HSD) post hoc tests for “*betadisper*” (Anderson 2001) were performed with the “vegan” package in R (R Development Core Team 2018).

To quantify per capita individual effects of herbivore species on bare rock production and ephemeral algal cover (i.e., interaction strength) we used the Dynamic Index (DI; see Appendix S3 for calculation details), as suggested for resources such as early-successional species with positive exponential growth (Osenberg and Mittelbach 1996, Berlow et al. 1999). Field measures of per capita effects based on exclusion experiments may depend critically on both the estimations of consumer density, the assumptions of a linear functional response with respect to algal density, and of no interference or facilitation among consumers (Berlow et al. 1999). As we considered natural densities of the study species at the different geographic contexts (Appendix S3), it was expected that the index may reflect interference between *Scurria* spp. individuals altering the magnitude but not the direction of effects. This index has been used to calculate consumer impacts in several consumer-resource systems (e.g., Paine 1992, Berlow et al. 1999, Sala and Graham 2002, Resetarits and Chalcraft 2007), but caution must be exerted when interpreting the magnitude of the estimates (Berlow et al. 1999). We emphasize here changes across the region. We also examined if effects of the *Scurria* species can be predicted by an additive model or sum of their effects estimated when in individual enclosures compared to the combined total effects estimated from the mixed *Scurria* species enclosure, the polyculture (e.g., Morin 1995). The net collective effect of the herbivore guild (CE) was also calculated to provide estimates of the effects of the entire guild. This was calculated as before but contrasting the controls (open areas), to which all herbivores had access, against the exclusion areas, making density equal to 1 (following Laska and Wootton 1998, O'Connor et al. 2013). Calculated in this manner, the collective herbivore effect is more directly comparable to per capita individual *Scurria* effects on algal cover, species richness, and Shannon diversity index (see Appendix S3). It should be noted that empirical measurements over large periods of time may include both direct and the propagation of indirect effects, including density-dependent feedbacks, making local estimates of interaction strength difficult to compare among studies (Bender et al. 1984, Laska and Wootton 1998, Berlow et al. 1999, Wootton and Emmerston 2005), or among different successional stages of the community (Aguilera and Navarrete 2012). In our field experiments, a mix of early- and midsuccessional algal species characterized the community inside plots. Thus, our interaction strength estimates are better interpreted

<sup>9</sup><http://imagej.nih.gov/ij/download.html>.

as average herbivore effects over the early- to midsuccessional times, including the potential indirect effects within the plots. Because experiments had the same duration across sites we expect our estimates to be affected in roughly similar ways by the propagation of indirect effects. Thus we pooled DI estimates, calculated for each replicate treatment plot for each sampling times, and averaged over the 13-month period for both per capita and collective effects. Confidence intervals (95%) for average effect estimates were obtained through a bootstrapping procedure (following Manly 2007). Previous visual inspection of our data (Q-Q plots) and Levene's test using the median as center (i.e., the Brown-Forsythe method), showed they were not normally distributed but have homogeneous variance. Thus, the differences between geographic zones and treatments, for each effect size estimated, were tested by means of Kruskal-Wallis multiple comparisons suggested by Dunn (1964), where  $P$  values were adjusted with false discovery rate for familywise comparisons (Ferreira and Zwinderman 2006). Differences between individual *Scurria* effects versus total effects estimated in the polyculture (to test for additivity of effects), were analyzed with a Wilcoxon–Mann–Whitney test independently for all response variables. All analyses were conducted in the R-software environment (R Development Core Team 2018).

## RESULTS

### *Geographic co-occurrences of the Scurria species*

The abundance of *S. viridula*, sampled across a large part of its geographic range, was fairly constant in the equatorward (northern) section, with densities of ca. 1 individual/m<sup>2</sup> yet highly variable around the range edge (red line in Fig. 2). Over the large geographic scale, the abundance of *S. zebrina* mirrored the spatial patterns of abundance of *S. viridula* across its geographic range (blue line in Fig. 2), with high among-site variability within the range overlap. In fact, within the range overlap region, the 30–32° S section, both species reached the highest densities observed across our regional surveys, albeit at different sites. Long-term seasonal sampling (1998–2014) conducted in the range overlap at Punta Talca (30.92° S) showed an increase in *S. viridula* density from 2009 (previous sampling was in 2005) to 2014 (last seasonal sampling), but with large interannual fluctuations (see Appendix S4: Fig. S1A). The density of *S. zebrina* at the overlap site also exhibited strong interannual fluctuations that were positively correlated with *S. viridula* between 2004 and 2014 (Kendall's tau = 0.1145,  $P < 0.0001$ ), suggesting both species are affected in similar direction by environmental fluctuations at this site. No linear relationship between species densities was detected (Pearson's  $r = -0.012$ ,  $P = 0.835$ ). At Las Cruces (33.5° S), our experimental locality poleward of the range overlap, *S. viridula* has maintained low densities since we first observed it in

2013 (see red line in Appendix S4: Fig. S1B), in comparison to *S. zebrina*, which has maintained a persistently moderate abundance (see blue line in Appendix S4: Fig. S1B). There was no correlation in species temporal fluctuations across years at this site (Kendall's tau = 0.0972,  $P = 0.1216$ ), nor between the magnitude of density fluctuations (Pearson's  $r = 0.1062$ ,  $P = 0.240$ ). Based on these results, co-occurrence of the *Scurria* species at their range overlap at about ~30° S seems to date from at least 1999 when we made the first observations, whereas at about 33° S, the new leading edge of *S. viridula*, co-occurrence appears to have started more recently (around 2013).

### *Herbivores' functional roles (impacts) on algal abundances and bare space provision*

The magnitude and direction of the individual per capita effects (DI) that *S. viridula* and *S. zebrina* had on the abundance of dominant sessile species and availability of bare rock were, generally, equivalent across the region (red and blue symbols, respectively, in Fig. 3A–C). In particular, both *Scurria* species increased bare rock cover significantly; that is, 95% confidence interval (CI) bars do not cross zero; production (Fig. 3A), with comparable magnitude between “native” (=within their historical distributional range), and range overlap (North\_SV vs. RO\_SV and South\_SZ vs. RO\_SZ, for *S. viridula* and *S. zebrina*, respectively). Thus, no indication of *Scurria* per capita depression on bare rock availability was observed at their range edges. In the polyculture, where both species were included together (brown diamond, Fig. 3A), the average per capita increase in bare rock (averaging across species) was similar to individual *Scurria* effects at that latitude (RO\_Polyculture vs. RO\_SV and RO\_SZ in Fig. 3A). Thus, no significant differences were observed between treatments in the per capita increase of bare rock cover at the geographic ranges considered (see Appendix S5: Table S1a). However, the total increase in bare rock availability estimated in the polyculture was lower than that expected by an additive (sum) model of the per capita effect of two individual *Scurria* limpets; that is, the interaction does lead to alteration of feeding effects on the provision of bare rock (Fig. 3D, Wilcoxon test:  $W = 0.001$ ;  $P = 0.00018$ ). At all sites, the herbivore guild, considering all species foraging in control areas, significantly increased availability of bare rock (black symbols in Fig 3A), but the effect was 3–4 times larger at the range overlap than at the sites north or south (Fig. 3A; Appendix S5: Table S2a). This pattern corresponds well with the absolute increase in bare rock recorded in open plots (control areas), where all herbivores had access, observed at the range overlap (Appendix S6: Fig. S1A).

Both species had significantly reduced green ephemeral algae cover (mainly *U. rigida*, *U. compressa*, *Blidin-gia minima*, and *Ulothrix* sp.) at their native ranges, as well as the region of overlap (Fig. 3B). However, it must

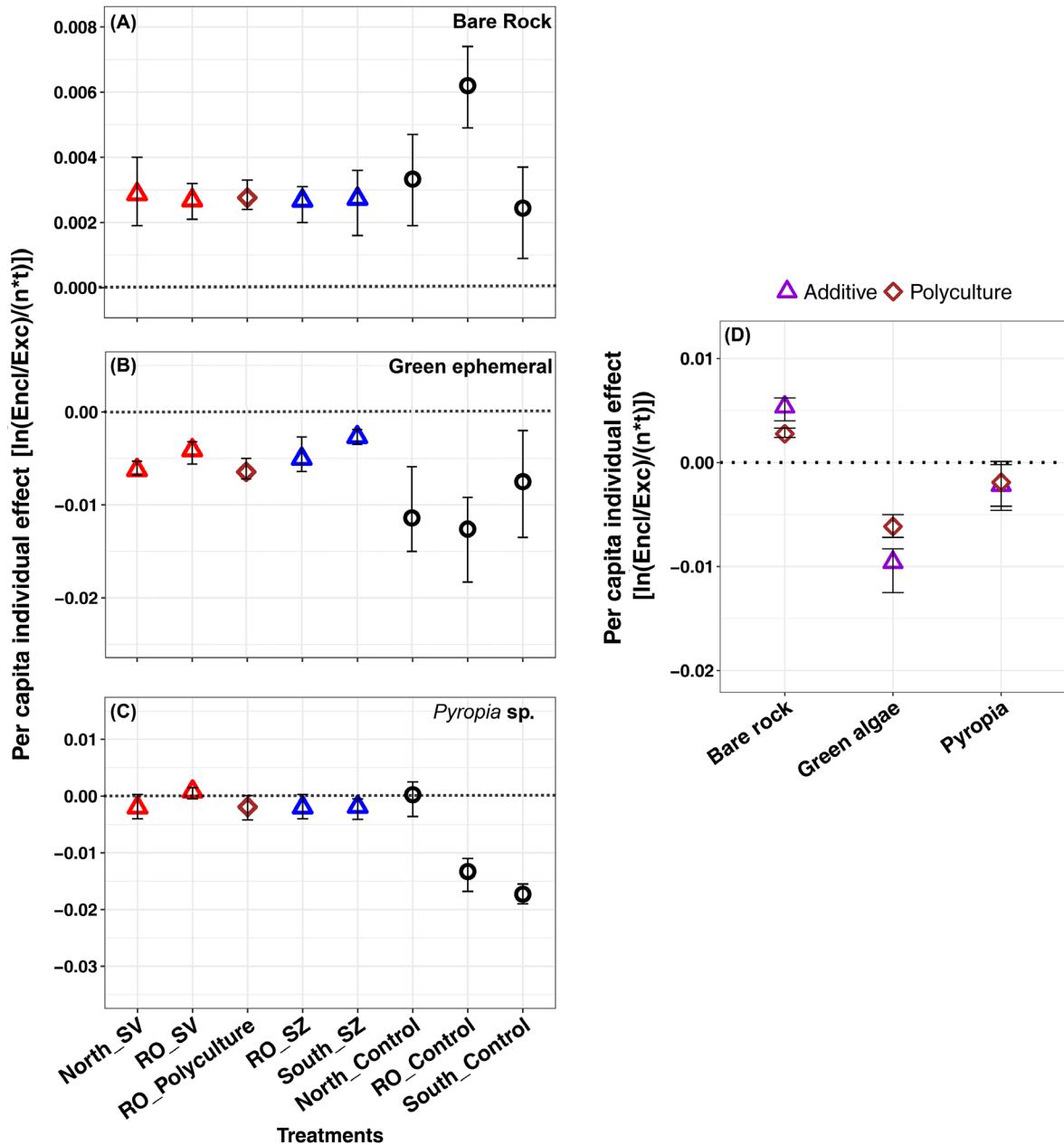


FIG. 3. Per capita individual effect of *Scurria viridula*, *Scurria zebrina*, and net collective effect of the herbivore guild (A)–(C), and additive versus joint effect of *Scurria* species (D) on bare rock, green ephemeral algae species (*Ulva rigida*, *Ulva compressa*, *Ulothrix* sp., *Blidingia minina*) and *Pyropia* sp., estimated at the range overlap (RO) of the *Scurria* species, and north and south of this range. All data are means and 95% confidence intervals, which were estimated through bootstrapping. Red triangles: *S. viridula* enclosures; blue triangles: *S. zebrina* enclosures; brown diamond: polyculture (*S. viridula* + *S. zebrina*). In (D), additive effects correspond to the sum of per capita individual *Scurria* effects (magenta triangle) estimated in field experiments conducted at RO, whereas joint *Scurria* per capita effects correspond to those estimated in the polyculture treatment (brown diamond) in the same experimental site.

be noted that *S. viridula* had a larger reduction of green algae cover at the native, equatorward location ( $-0.006\%$ -individual-day $^{-1}$ ), compared to effects observed at the range overlap site (i.e.,  $-0.0038\%$ -individual-day $^{-1}$ ; compare North\_SV vs. RO\_SV in Fig. 3B, and see Appendix S5: Table S1b). The *S. viridula* effects were

also higher than the effect of *S. zebrina* at its native, poleward site (North\_SV vs. South\_SZ; Fig. 3B; Appendix S5: Table S1b). In contrast, the limpet *S. zebrina* had a significantly higher per capita reduction effect of green algae abundance at the range overlap compared with the poleward site (RO\_SZ vs. South\_SZ; Fig. 3B,

Table S1b). Thus, there was a depression of individual effects of green algae at the range overlap of *S. viridula* but not *S. zebrina*. The average per capita reduction of green algae cover in the polyculture with both species was larger only compared with *S. viridula* enclosures at the range overlap, (Fig. 3B; Appendix S5: Table S1b). The sum of both individual *Scurria* on the reduction of green algal cover was higher than the total effect estimated for the polyculture (Fig. 3D, Wilcoxon test:  $W = 100$ ;  $P < 0.001$ ) indicating a nonadditive *Scurria* effect. The herbivore guild drove an important reduction of green algal cover at all sites, which appeared larger at the region of overlap (black symbols, RO\_Control in Fig. 3B). However, differences were not significant when compared to the total reduction of algal cover at the sites north and south of the range overlap (Appendix S5: Table S2b). Corresponding with the general pattern of herbivore reduction of green algae, we observed an absolute reduction in total algal cover in the control areas at the range overlap and specifically when compared with the southern site exclusive of *S. zebrina* (Appendix S6: Fig. S1B).

The effects of the two *Scurria* species on abundance of the ephemeral red alga *Pyropia* sp. at their native ranges were qualitatively similar, that is, a reduction in cover of similar magnitude (Fig. 3C), but the effect was significant only for *S. zebrina* in the southern site; that is 95% CI do not cross zero value. At the range overlap, the per capita reduction in *Pyropia* sp. abundance by both *Scurria* species was diminished and neither had significant effects on this algal cover. Average per capita reduction in *Pyropia* sp. cover in the polyculture was similar to the effects of both *Scurria* species when isolated (Fig. 3C; Appendix S5: Table S1c). Thus, there was an additive effect of both *Scurria* species on this alga; there were no differences between the sum of individual species effect and total effect estimated in the polyculture (Fig. 3D; Wilcoxon test:  $W = 72$ ,  $P = 0.104$ ). Reductions in *Pyropia* sp. cover in control areas by the entire herbivore guild were significant and similar at the poleward site and the region of overlap (black symbols, RO\_Control vs. South\_Control in Fig. 3C; Appendix S5: Table S2c), but this effect was nearly zero at the equatorward site (North\_Control; Fig. 3C). In concordance with this result, we found that absolute abundance of *Pyropia* sp. inside control plots, open to all herbivores, was higher in the northern site than the others (Appendix S6: Fig. S1C).

#### Herbivore effects on community composition

**Multivariate patterns.**—The effects of both *Scurria* species on intertidal community composition, that is, cover of algae and sessile invertebrates, were relatively similar across sites over the 13-month period of the field experiments (Fig. 4). Fences used in herbivore enclosure/exclusion areas had no effect on community composition in our field experiments, because control and procedural

control had similar community structure (see Appendix S7: Fig. S1A). To the north of and in the overlap region, species composition inside *S. viridula* (SV) and *S. zebrina* (SZ) enclosures (red and blue triangles in Fig. 4A, B) were significantly different from herbivore exclusions (green squares in Fig. 4A, B, respectively, PERMANOVA: North ( $F_{3,76} = 6.65$ ,  $P = 0.001$ ); Tukey's post hoc: SV vs. exclusion: diff =  $-0.115$ ;  $P = 0.040$ ; range overlap ( $F_{5,85} = 8.47$ ,  $P = 0.001$ ); SV vs. exclusion: diff =  $-0.1654$ ,  $P = 0.014$ ; SZ vs. exclusion: diff =  $-0.206$ ,  $P = 0.017$ ; polyculture vs. exclusion: diff =  $0.1956$ ,  $P = 0.028$ ). Poleward of the range overlap, control and exclusion plots differed widely and significantly as well (Tukey's post hoc: diff =  $-0.235$ ;  $P = 0.004$ ), but the post hoc comparison showed that composition of the sessile community within *S. zebrina* enclosures was significantly different to controls but not exclusions (PERMANOVA: South [ $F_{3,76} = 4.775$ ,  $P = 0.02$ ]; Tukey's post hoc: SZ vs. Control: diff =  $0.715$ ,  $P = 0.016$ ; SZ vs. exclusion: diff =  $0.25$ ;  $P = 0.218$ ). In the polyculture treatment, we observed a similar pattern in community composition compared to individual *Scurria* enclosures and controls (brown diamonds in Fig. 4B, PERMANOVA Tukey's post hoc: polyculture vs. SV: diff =  $0.040$ ,  $P = 0.806$ ; polyculture vs. SZ: diff =  $-0.051$ ,  $P = 0.976$ ; polyculture vs. control: diff =  $0.048$ ,  $P = 0.980$ ).

**Effects on species richness and diversity.**—The per capita effects of individual *Scurria* species on sessile and mobile community richness and diversity (Shannon's  $H$ ) were heterogeneous across the region. As before, control and procedural control had similar species richness and diversity; thus we assume there were no artifacts from fences in our field experiments (see Appendix S7: Figs. S1B, C). Both *S. viridula* (red symbols) and *S. zebrina* (blue symbols) had a significant effect, that is 95% CI bars do not cross zero value, on reduction of species richness and diversity at the experimental site outside the range overlap (see Fig. 5A, B). At the range overlap, *S. viridula* drove a reduction in the magnitude of effects on species richness and diversity compared with its effect at the equatorward site (RO\_SV vs. North\_SV in Fig. 5A, B; Appendix S5: Table S1d, e). In contrast, *S. zebrina* reduced diversity at the range overlap to a similar extent as in the poleward site (RO\_SZ vs. South\_SZ Fig. 5B; Table S1d, e), but reduction in species richness was not significant at this site (Fig. 5A). In the polyculture, where both species were enclosed together, there was a significant reduction only on diversity, resembling the pattern found for *S. viridula* at the range overlap, but we found significant differences in the magnitude of the reduction in diversity between these treatments (Fig. 5B; Table S1d, e). There were no differences between the sum of individual species effect and total effect estimated in the polyculture for species richness (Wilcoxon test:  $W = 622$ ,  $P = 0.915$ ) or diversity ( $W = 624$ ,  $P = 0.898$ ; see Fig. 5C), suggesting an additive reduction of

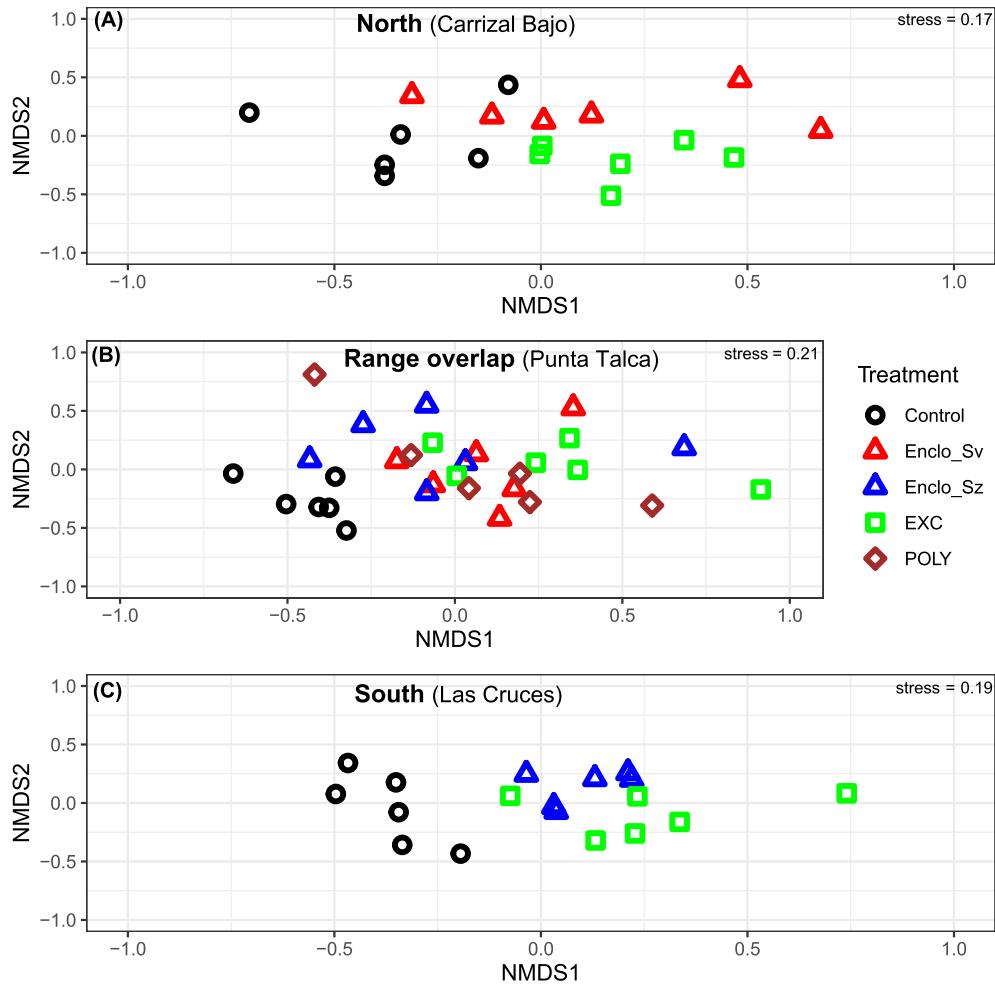


FIG. 4. Nonmetric multidimensional scaling (nMDS) of species composition (sessile and mobile species diversity) recorded within experimental replicate areas ( $n = 6$ ) from field experiments (averaged for over the 13 months of study) conducted at (A) the equatorward site (Carrizal Bajo), (B) at the range overlap (Punta Talca) (RO), and (C) at the poleward site (Las Cruces) of the *Scurria* species. EXC: herbivore exclusion, POLY: polyculture; Enclo\_SV: enclosures of *S. viridula*; Enclo\_SZ: enclosures of *S. zebrina*.

diversity between both *Scurria* species. There was also a net collective reduction of species richness and diversity driven by the entire herbivore guild at the three locations (black circles in Fig. 5A, B). Despite this invariant pattern, especially for effects on species richness, a larger reduction of diversity by the herbivore guild was observed at the range overlap compared to the northern site (Fig. 5B; Appendix S5: Table S2d, e). This corresponds well with the absolute reduction in diversity in control (open to all herbivores) areas, compared with the invariant pattern for richness observed at the range overlap (see Appendix S6: Fig. S1D, E).

#### DISCUSSION

As species shift their geographic ranges, community regulation pathways may change to a greater or lesser extent and ecosystem functioning may be altered. To

guide research in our study system along the mid-inter-tidal rocky shores of central-northern Chile, we hypothesized that the range extension of *Scurria viridula* could become redundant in the recipient community because of its similarity with the local *S. zebrina*. Indeed, such similarity could lead to interference competition and lower individual performances when together than isolated, resulting in nonadditive joint effects (Fig. 1A). In this manner, addition of the novel species would confer an insurance type of resilience (Mouquet and Loreau 2002) to the local guild. Our results demonstrate that the functional effects of these introductions are complex, that they must be evaluated in comparison with sites beyond the novel range overlap, and that they depend on the community variable that is examined. First, the two focal *Scurria* species had equivalent roles on community composition, and these effects resemble the effects they have at their respective individual ranges;

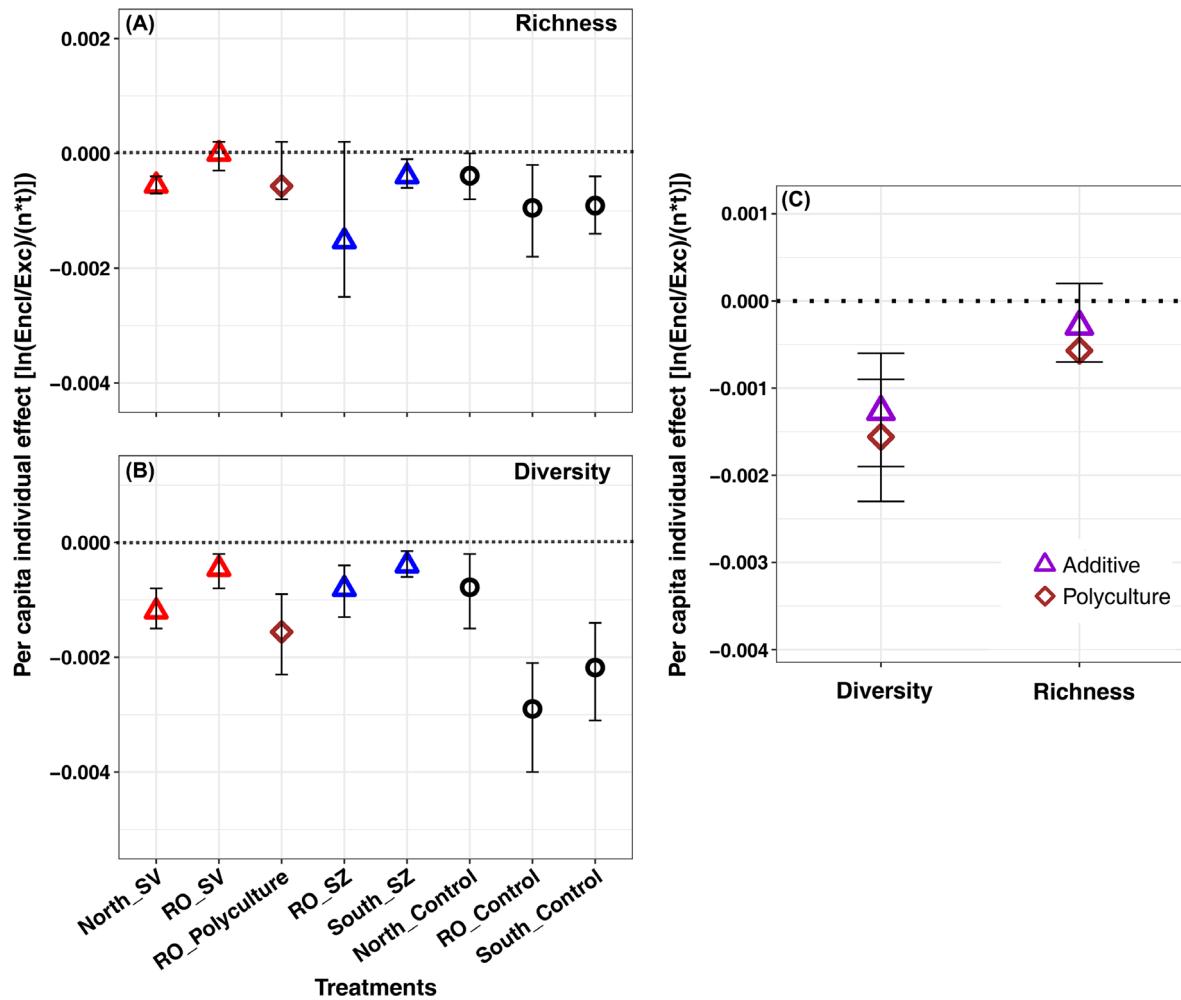


Fig. 5. Per capita individual effect of *Scurria viridula* and *Scurria zebrina*, and net collective effect of the guild (A), (B) and additive versus joint effect of *Scurria* species (C) on richness and diversity (Shannon,  $H'$  index) estimated at the range overlap (RO), and north and south of this range exclusive to each *Scurria* species. All data are means and 95% confidence intervals, which were estimated through bootstrapping.

that is, there was no evidence of depression of per capita effects at range ends. The two species had similar effects on community composition and bare rock provision when species were together than when they were separate (isolated), suggesting the addition of the novel species is redundant within the guild. Second, the strength of the consumptive effects of *S. viridula* on green algal cover, and on species richness and diversity declined in a consistent way at the range overlap in line in this case with our hypothesis of depression of per capita effects. In contrast, *S. zebrina* varied less in its per capita effect at the range overlap, and even showed a slight increase in the magnitude of its per capita negative effects on green ephemeral algae, contrary to our hypothesis expectation. The effects when both species were enclosed together (polycultures), were lower for bare rock provision and green algal cover than those expected by an additive effects model, suggesting that both *Scurria* species interfere with each other at small-

scales at the range overlap confirming our predictions. Third, when examining effects on *Pyropia* sp., species richness and diversity, effects in polycultures were similar to those expected by an additive effects model suggesting no interaction of the *Scurria* species. Our results also confirm the hypothesis that *Scurria* co-occurrences, likely by complementarity in foraging, does enhance herbivore guild effects on provision of primary substrate and species diversity (see Fig. 1B).

Overall, our results provide a strong basis for the presence of local and regional functional redundancy in effects between similar herbivore species. In general, there is a degree of functional compensation (see predictions depicted in Fig. 1B) on bare rock provision and in the control of ephemeral algae within the herbivore guild, and the potential for complementarity in reduction of species diversity at the range overlap. Thus, the novel species co-occurrence may cause a reduction in local community diversity, potentially owing to a

homogenization of the intertidal community and the herbivore guild structure.

*Functional equivalence and compensation at local and regional scales*

Our results showed that the two focal herbivores had equivalent roles within their respective local geographic ranges, providing evidence that they could compensate each other in their roles at regional scales. However, as *S. zebrina* has not contracted its geographic range, which is documented by previous studies (Aguilera et al. 2013b, 2019b), the formal test of this hypothesis at the regional level still requires further confirmation. Nonetheless, our study showed that both species have equivalent effects on community composition, abundance of green algae, and in bare rock provision across the study region spanning their range overlap and geographic edges. In our study, although we did not consider the late-successional stages (i.e., 13–15 months, with presence of corticated algae like *Mazzaella*, *Gelidium*, and *Perumytilus*) that typically give rise to strong differences among herbivore functional identities (Aguilera and Navarrete 2012), we were able to detect strong and redundant effects of *Scurria* on early to mid-successional community composition. Despite this equivalence in roles, we found that *S. viridula* control on ephemeral algae, species richness, and diversity was much reduced at the range overlap where they co-occur, compared with *S. zebrina*, which enhanced control on ephemeral algae at this range. As predicted by theoretical studies (and see Fig. 1A), environmental conditions at the range overlap, the former range edge of the poleward expanding species (*S. viridula*), are likely stressful for the focal species (Hampe and Petit 2005, Sexton et al. 2009). In this context, a concurrent study reported that both *Scurria* species experience stressful conditions at sites located in the range overlap, at about 30.5° to 33.4° S (Broitman et al. 2018). In addition, in our field experiments we found that *Scurria* species have nonadditive effects in bare rock provision and green algal control, which may be result of direct interference between species. Thus, it seems probable that the magnitude of effects of *S. viridula* at its range edge can be effectively reduced by stressful conditions, and also by interference with *S. zebrina*, thus reducing growth rates (Aguilera et al. 2019b). In this context, previous experimental studies showed that herbivore control on ephemeral algae could be higher in low- than high-upwelling sites (Nielsen and Navarrete 2004). Because Punta Talca, located at the range overlap (RO), is a site with high-upwelling intensity, a reduction of *S. zebrina* effects could be expected compared with the poleward site, which is less exposed to strong upwelling (Wieters et al. 2003, Tapia et al. 2009). The invariant, or even enhancement (on green algae), in the magnitude of effects of *S. zebrina* at the range overlap compared with the southern site is surprising in this context and deserves further research.

*Herbivore guild functional diversity at the range overlap; equivalence versus complementarity*

Functional herbivore guild structure characterized by either functional complementarity or equivalence (i.e., redundancy), can greatly influence resource abundance and community composition at local scales (Duffy et al. 2001, Bellwood et al. 2003, Resetarits and Chalcraft 2007, Griffin et al. 2009, Burkepille and Hay 2011, Bennett et al. 2015). Species introduction or range expansion/contraction could impose an alteration in the functional structure of local or resident guilds if novel roles are incorporated into the system (e.g., Duffy et al. 2001, Duffy 2002, Rosenfeld 2002, Bellwood et al. 2006). Our results show that, despite that *S. viridula* diminishes the magnitude of their per capita effect at the range overlap, co-occurrence of both *Scurria* species greatly contributed to the net collective effect of the herbivore guild on bare rock production, green algae control, and reduction in diversity. In this context, we observed in our experiments that when together in polyculture, total effects of *Scurria* were much reduced on bare rock provision and green algae control compared with an additive model of the individual *Scurria* effects. This implies that to contribute to the total herbivore guild effect at the range overlap effectively, both species may segregate spatially at scales larger than those used in our enclosures. This space partitioning could account for the reduction in deleterious effects of interspecific competition as previously documented in this system (Aguilera et al. 2019b). In general, the contribution to the entire herbivore guild at the range overlap could happen because of both compensatory and complementarity effects (see predictions in Fig. 1B), where, as our results show, both *Scurria* species largely contribute to increase bare rock provision and to control the colonization of dominant green algae, a function also shared with other herbivores in the system (Nielsen and Navarrete 2004, Aguilera and Navarrete 2012). For example, *S. viridula* has strong similarity in consumptive effects with herbivores of the mid- and high-intertidal zone assemblage such as *C. granosus* and *Fissurella crassa* (see Appendix S8: Fig. S1A). These two species also have wide differences in body size with our focal species (Aguilera and Navarrete 2011, 2012), use different microhabitats (i.e., they use crevices for shelter; Aguilera and Navarrete 2011), and differ in their feeding modes (i.e., scraping and browsing, respectively; Aguilera and Navarrete 2012). Both *Scurria* species have chiefly a scraping/grazing mode of feeding (following their radular capabilities; Steneck and Watling 1982). The presence or addition of a novel species to a local herbivore guild, such as the site at the range overlap of our focal species, may thus be the main factor bolstering the net collective effect of the intertidal herbivore guild on green algae colonization and bare rock provision. It should be noted that despite diminished effects of *S. viridula* at the range overlap, both *Scurria* species can be considered strong interactors in this system (Paine 1992)

given their control of green algae, large bare rock provision and reduction in diversity compared with the other intertidal herbivores even within the sites were they do not coexist (see Appendix S8: Fig. S1A). However, in our experiments we found the focal *Scurria* species were less efficient controlling the red alga *Pyropia* sp. at the range overlap site, which has high growth rates and a life cycle with an encrusting stage (Santelices 1990). This alga seems mostly controlled by the complementary effect of herbivores with a browser mode of feeding (i.e., species consuming alga fronds, e.g., *F. crassa*, *S. lessoni*, *E. peruviana*) and other scraper-grazers (i.e., those capable of consuming algal spores and plantlets; e.g., *C. granosus*, *C. barnesii*, *Scurria cecilianae*, *S. variabilis*) present in the system (see Appendix S8: Fig. S1A). The herbivore guild seems less efficient in controlling this alga at the northern site. As discussed before, previous studies in this system showed that under persistent upwelling conditions the role of the herbivore guild could be reduced by either high algal growth rate or an increase in consumer-resistant algal cover, and thus convergence in algal abundance between herbivore present versus absent condition may be expected (Nielsen and Navarrete 2004). At the range overlap site (Punta Talca) coastal upwelling is intense (Tapia et al. 2009) compared with the southern (Las Cruces) and northern site (Carriçal Bajo), which are either sheltered or under weak, semipermanent upwelling, respectively (Tapia et al. 2009, Meneghesso et al. 2020). Differences in community composition recorded inside exclusion, herbivore-free, areas at our experimental sites (see Appendix S7: Fig. S2) may well reflect these oceanographic differences (see also Broitman et al. 2001). In our study, the intertidal herbivore guild exerted a strong control of ephemeral algae colonization at the range overlap likely aided by co-occurrence of the *Scurria* species. Therefore, both top-down and bottom-up processes in this system seem especially relevant to explain differences in community composition (Menge et al. 1996, 1999) as those presented in our study (and see comparison between control and exclusion areas in Appendix S7: Fig. S2).

#### *Forecasting the impact of species range shift on community structure*

Complementarity in feeding habits has been invoked as the main mechanism behind the detrimental impacts of tropical marine herbivores expanding their ranges and reducing algal production in temperate systems (Ling 2008, Vergés et al. 2014, Ling et al. 2015). As we observed in our system, co-occurrence of previously parapatric herbivore species can translate into a net reduction in community diversity, hence a potential harbinger of functional homogenization (Olden and Poff 2003, Olden and Rooney 2006). Our main results suggest that an expansion of the area where *Scurria* species coexist could progressively reinforce the production of bare space, triggering a reduction in community spatial heterogeneity

and productivity. As evidence of this process, range expansion and consumption intensification have led to rapid phase shifts in temperate subtidal ecosystems through the loss of habitat-forming species like kelps (Vergés et al. 2014, Ling et al. 2015), potentially slowing down successional trajectories (Lubchenco 1978).

The impact of novel or introduced species on local ecosystem structure and functioning is an important concern in both terrestrial and aquatic ecosystems (e.g., Schoener and Spiller 1996, Stachowicz and Tilman 2005, Wardle et al. 2011, Simberloff et al. 2013, Early et al. 2016). Similarity or differences in functional traits between introduced species versus residents, seems one of the main determinants of successful establishment of alien species in novel ranges (Divíšek et al. 2018). Our results provide important insights about the functional consequences of the arrival of novel species to local communities, in terms of impacts on resources and diversity inputs on consumer guild structure, following the wholesale species range shifts taking place in the oceans worldwide (Sorte et al. 2010, Sorte 2013, Bradley et al. 2015, Poloczanska et al. 2016). In particular, we highlight the potential for regional functional compensation when the new species have similar roles to the resident consumer, and the intensification of collective consumer impacts when newcomers are complementary to the local guild which could produce significant alteration of the community structure. The recent range expansion of *S. viridula* and the apparent lack of range contraction by *S. zebrina* signals that effective functional compensation between these herbivores may take place. Such functional compensation over regional scales could be a source of stability of ecosystem functioning in the next decades, a process which deserves further consideration. Indeed, herbivores can promote community stability after disturbances through trophic compensation (e.g., Ghedini et al. 2015, Kordas et al. 2017), but a different effect could result from an overrepresentation of functionally equivalent species within the guild as the co-occurrence of *Scurria* shown in our study (see also Appendix S8: Fig. S1), which can reduce functional diversity of consumers and resources. In fact, the functional diversity of consumers modulates resource diversity and composition (e.g., Olf and Ritchie 1998, Duffy 2002, Schmitz 2009, Bennett et al. 2015), and also has a key role in the stability of ecosystem functioning (Duffy 2003, Ghedini et al. 2015). As the functional structure and the potential resilience of ecosystems can also be eroded by human exploitation (Kéfi et al. 2016), it is urgent to understand the responses of equivalent species to different anthropogenic drivers at regional scales in order to manage and predict the alteration of critical ecosystem functions in the face of global change scenarios.

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