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

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

Ecology

DOI:
[10.1002/ecy.3150](https://doi.org/10.1002/ecy.3150)

Published: 01/11/2020

Peer reviewed version

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

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):
Aguilera, M., Valdivia, N., Broitman, B., Jenkins, S., & Navarette, S. (2020). Novel co-occurrence of functionally redundant consumers induced by range expansion alters community structure. *Ecology*, 101(11), [e03150]. <https://doi.org/10.1002/ecy.3150>

Hawliau Cyffredinol / General rights

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

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

Take down policy

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

Running Head: Functional redundancy and range shift

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

Moisés A. Aguilera^{1,2*}, Nelson Valdivia^{3,4}, Bernardo R. Broitman⁵, Stuart R Jenkins⁶ &, Sergio
A. Navarrete⁷

¹Departamento de Biología Marina, Facultad de Ciencias del Mar, Universidad Católica del Norte, Larrondo, 1281,
Coquimbo, Chile.

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

³Instituto de Ciencias Marinas y Limnológicas, Facultad de Ciencias, Universidad Austral de Chile, Campus Isla
Teja, Valdivia 5110236, Chile

⁴Centro FONDAP de Investigación de Dinámicas de Ecosistemas Marinos de Altas Latitudes (IDEAL)

⁵Departamento de Ciencias Biológicas, Facultad de Artes Liberales, Universidad Adolfo Ibáñez, Viña de Mar, Chile

⁶School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey, LL59 5AB, United Kingdom.

⁷Estación Costera de Investigaciones Marinas, Las Cruces, Center for Applied Ecology and Sustainability (CAPES),
Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile.

*Corresponding Author E-mail address: moises.aguilera@ucn.cl

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 inter-specific 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. Since 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, 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 role; functional diversity; 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, 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, to (i) identify the functional role of the new species in its original community or assemblage, (ii) assess how the resident members of the functional group respond to the local introduction or extinction (Duffy 2002, Sundstrom et al. 2012), and finally (iii) quantify 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 (ysee 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 depends 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). Due to 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 :

(1) both *Scurria* species drive redundant or equivalent (i.e. functional redundancy; Chalcraft & Resetarits 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).

(2) Individual *per capita* reduction of algal abundance and bare rock provision exerted by *Scurria* species diminish at the range overlap due to 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 non-additive (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).

Finally, (3) *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 due to interference competition, or, alternatively, intensify it as a consequence of complementarity in foraging or microhabitat use (see Figure 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 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).

197 *Scurria viridula* is found from Peru (12°S) to central-north Chile (32°S), while *S. zebrina* is
 198 distributed from central Chile (30°S) to southern Chiloé (~43°S) (Espoz et al. 2004), thus
 199 overlapping ranges between 30-32°S. The largest adult individuals *S. viridula* conspicuously
 200 occupy the high intertidal zone on the back sides of vertical rocks directly exposed to waves. But
 201 the bulk of the adult population, juveniles and recruits occur throughout intertidal platforms,
 202 where they can sometimes be mistaken by *S. zebrina* by untrained eyes. These two focal species
 203 cooccur across the range overlap with a diverse group of benthic herbivores, including other
 204 *Scurria* species (mostly *S. araucana*, *S. ceciliana*, and *S. variabilis* and to a lesser extent *S.*
 205 *plana*), chitons (*Chiton granosus*, *C. cumingsii*, *C. barnesii*), keyhole limpets (*Fisurella crassa*),
 206 snails (*Echinolittorina peruviana*, *Austrolittorina araucana*) and a pulmonate limpet (*Siphonaria*
 207 *lessoni*). The benthic herbivore guild has been extensively studied (Santelices 1990, Nielsen and
 208 Navarrete 2004, Aguilera and Navarrete 2007, 2011, 2012, Aguilera et al. 2015) and both
 209 equivalent and complementary functional impacts have been observed on algal establishment,
 210 making this speciose guild functionally diverse (Aguilera and Navarrete 2012). Both *S. viridula*
 211 and *S. zebrina* are assumed to be important grazer species; while their densities are never too
 212 high compared with other species in the guild, their large maximum adult shell size (from 5.5 to
 213 6.5 cm, Aguilera et al. 2013b) suggests they may have high *per capita* effects on algal
 214 abundance. In the case of *S. viridula*, individual foraging and resting activities concentrate on
 215 smooth and inclined rocky surfaces. Here, this species forms clumps of ca. 12-15 individuals
 216 (Aguilera et al. 2013b), which increases the potential for intense albeit spatially localized effects
 217 on the sessile algal assemblage, leaving visual indications (bare rock) on the substrate. The algal
 218 community is highly diverse as the range overlap zone includes several algal species that coexist
 219 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. *U. rigida*, *U. compressa*), *Blidingia minima*, *Ulothrix* sp., and the red alga *Pyropia orbicularis* (= *Porphyra columbina*) (Guillemin 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, 2019). Long-term abundance datasets (i.e. 1998 to 2000, 2003 to 2005 and 2009 to 2015) of *Scurria* limpets, estimated through positioning 50×50 cm quadrats, from higher to lower intertidal levels, at different sites spanning ~1600 km from north to central Chile, show a well-defined geographic overlap of both herbivore species between 30°S to 32°S (see Fig. 2 and Aguilera et al. 2013b, 2019). We used these datasets 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 to 15 months after experimental bare space creation (Aguilera and Navarrete 2012) and it 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 an herbivore enclosure/exclusion experiments in the mid-intertidal shore at three sites located at a) the range overlap of the two *Scurria* species (~31°S), b) equatorward (north) of this zone (26°S), where only *S. viridula* is present, and c) 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 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) 2 *S. zebrina* (SZ) enclosure; 2) 2 *S. viridula* (SV) enclosure; 3) 1 *S. zebrina* plus 1 *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) 2 *S. viridula*; 2) Herbivore Exclusion; 3) Control; 4) Procedural Control. South Poleward of the RO, Las Cruces, 33.5°S (south): 1) 2 *S. zebrina*; 2) Herbivore Exclusion; 3) Control; 4) Procedural Control (see **Table S1** in **Appendix 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 mid- successional species that can colonize within a year 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 02 April 2013 in Punta Talca (RO) and all three experiments ended on 30 April 2014 (spanning about 400 days). 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 level was 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* ind. m^{-2} , roughly 1.6 indiv. 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 individual per plot > 5 mm length) or Chitons, littorinids snails, which were commonly less than 4 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 × 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 (<http://imagej.nih.gov/ij/download.html>). 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, fences were manually cleaned of all algae and growth to reduce fence effects on light and water circulation.

Statistical analyses

We examined whether inter-annual 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 non-metric 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-month 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 since 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 mid- successional stages (9-13mo) were not consistent across the study region (**Fig. S1** in **Appendix S2**). At the southern end (Las Cruces) and to a lesser extent the northern end, the sessile community composition observed after 9mo tended to be different than earlier dates, and treatment effects were emphasized, but such successional trends got blurry in the overlap region (**Fig. S1** in **Appendix S2**). Therefore, we preferred to simplify presentation and comparisons across region by calculating treatment effects on the long-term (13mo) average community responses encompassing together early and mid-succession. Statistically significant differences between treatments for each locality (one-way model) were analyzed with PERMANOVA. A Tukey HSD' *post hoc* test for '*betadisper*' (Anderson 2001) were performed with the 'vegan' package in R (R Development Core Team 2018).

353 To quantify *per capita* individual effects of herbivore species on bare rock production and
 354 ephemeral algal cover (i.e. interaction strength) we used the Dynamic Index (DI; see **Appendix**
 355 **S3** for calculation details), as suggested for resources such as early-successional species with
 356 positive exponential growth (Osenberg and Mittelbach 1996, Berlow et al. 1999). Field measures
 357 of *per capita* effects based on exclusion experiments may depend critically on both the
 358 estimations of consumer density, and the assumptions of a linear functional response with respect
 359 to algal density and of no interference or facilitation among consumers (Berlow et al. 1999). As
 360 we considered natural densities of the study species at the different geographic contexts
 361 (**Appendix S3**), it was expected that the index may reflect interference between *Scurria* spp
 362 individuals altering the magnitude but not the direction of effects. This index has been used to
 363 calculate consumer impacts in several consumer-resource systems(e.g. Paine 1992, Berlow et al.
 364 1999, Sala and Graham 2002, Resetarits and Chalcraft 2007), but caution must be exerted when
 365 interpreting the magnitude of the estimates (Berlow et al. 1999). We emphasize here changes
 366 across the region. We also examined if effects of the *Scurria* species can be predicted by an
 367 additive model or sum of their effects estimated when in individual enclosures compared to the
 368 combined total effects estimated from the mixed *Scurria* species enclosure, the polyculture (e.g.
 369 Morin 1995). The net collective effect of the herbivore guild (CE) was also calculated to provide
 370 estimates of the effects of the entire guild. This was calculated as before but contrasting the
 371 controls (open areas), to which all herbivores had access, against the exclusion areas, making
 372 density equal to 1 (following Laska and Wootton 1998, O'Connor et al. 2013). Calculated in this
 373 manner, the collective herbivore effect is more directly comparable to *per capita* individual
 374 *Scurria* effects on algal cover, species richness, and Shannon' diversity index, (see **Appendix**
 375 **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 Emmerson 2005), or among different successional stages of the community (Aguilera and Navarrete 2012). In our field experiments, a mix of early and mid-successional algal species characterized the community inside plots. Thus, our interaction strength estimates are better interpreted as an average herbivore effects over the early- to mid-successional times, including the potential indirect effects within the plots. Since 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' test using the median as center (i.e. 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/m² 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 to 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 inter-annual fluctuations (see **Fig. S1A** in **Appendix S4**). The density of *S. zebrina* at the overlap site also exhibited strong inter-annual 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 **Fig. S1B** in **Appendix S4**), in comparison to *S. zebrina*, which has maintained a persistently moderate abundance (see blue line in **Fig. S1B** in **Appendix S4**). 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, while 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 *Scurria 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, B and C). Specifically, both *Scurria* species increased significantly bare rock cover i.e. 95% 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 **Table S1a** in **Appendix S5**). 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 i.e. 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, **Table S2a** in

Appendix S5). 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 (**Fig. S1A** in **Appendix S6**).

Both species had significantly reduced green ephemeral algae cover (mainly *Ulva rigida*, *U. compressa*, *Blidingia minima* and *Ulothrix* sp.) at their native ranges, as well as the region of overlap (Fig. 3B). However, it must be noted that *S. viridula* had a larger reduction of green algae cover at the native, equatorward location ($-0.006\% \times \text{individual} \times \text{day}^{-1}$), compared to effects observed at the range overlap site (i.e. $-0.0038\% \times \text{individual} \times \text{day}^{-1}$) (compare North_SV vs RO_SV in Fig. 3B, and see **Table S1b** in **Appendix S5**). 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, **Table S1b** in **Appendix S5**). 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, **Table S1b** in **Appendix S5**). 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 non-additive *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 (**Table S2b** in **Appendix S5**). 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* (**Fig. S1B** in **Appendix S6**).

The effects of the two *Scurria* species on abundance of the ephemeral red alga *Pyropia* sp. at their native ranges were qualitatively similar i.e. a reduction in cover of similar magnitude (Fig. 3C), but the effect was significant only for *S. zebrina* in the southern site i.e. 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, **Table S1c** in **Appendix S5**). Thus, there was an additive effect of both *Scurria* species on this alga i.e. 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, **Table S2c** in **Appendix S5**), but this effects 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 (**Fig. S1C** in **Appendix S6**).

Herbivore effects on community composition

Multivariate patterns. - The effects of both *Scurria* species on intertidal community composition i.e. 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 **Fig. S1A** in **Appendix S7**). 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 and B) were significantly different from herbivore exclusions (green squares in Fig. 4A and 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 Excl: 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 **Figs. S1B** and **C** in **Appendix S7**). Both *S. viridula* (red symbols) and *S. zebrina* (blue symbols) had a

significant i.e. 95% CI bars do not cross zero value, reduction on species richness and diversity
 at the experimental site outside the range overlap (see Fig. 5A and 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, **Table S1d&e** in
Appendix S5). 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. 5 B **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: $W=622$, $P=0.915$) nor diversity ($W=624$,
 $P=0.898$; see Fig. 5C), suggesting an additive reduction of 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, **Table S2d & e** in
Appendix S5). 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 **Fig. S1D & E** in **Appendix S6**).

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 intertidal 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 non-additive joint effects (Fig.1A). In this manner, addition of the novel species would confer 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. i.e. there was no evidence of depression of *per capita* of 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 and 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 non-additive 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 & Navarrete 2004). Since 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, Burkepile 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 effectively contribute to the total herbivore guild effect at the range overlap, 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 due to 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 *Chiton granosus* and *Fissurella crassa* (see **Fig. S1A** in **Appendix S8**). 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 where they don’t coexist (see **Fig. S1A** in **Appendix S8**). 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. *Fissurella crassa*, *Siphonaria lessoni*, *Echinolittorina peruviana*) and other “scraper-grazers” (i.e. those capable of consuming algal spores and plantlets; e.g. *Chiton granosus*, *C. barnesii*, *Scurria ceciliana*, *S. variabilis*) present in the system (see **Fig. S1A** in **Appendix S8**). 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 (Carrizal Bajo), which are either sheltered or under weak, semi-permanent 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 **Fig. S2** in **Appendix S7**) 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 seems 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 **Fig. S2** in **Appendix S7**).

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 over-representation of functionally equivalent species within the guild as the co-occurrence of *Scurria* shown in our study (see also **Fig. S1** in **Appendix S8**) which can reduce functional diversity of consumers and resources. In fact, the functional diversity of consumers modulates resource diversity and composition (e.g. Olff 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.

ACKNOWLEDGEMENTS

This research was funded through FONDECYT #11121360, 1160223, and PAI-CONICYT #79150002 to MAA. BRB was supported by FONDECYT 1181300 and the MUSELS Nucleus, which is funded by Iniciativa Científica Milenio. NV acknowledges the support of FONDAP #15150003 (Centro de Investigación: Dinámica de Ecosistemas Marinos de Altas Latitudes, IDEAL) and FONDECYT #1190529. We thank Tomás Flores, Mauricio Oróstica, Ariel Rojas, Emily Lamb and Rodrigo Uribe for field assistance during the field experimental set-up and surveys. Two anonymous reviewers made very helpful comments to the previous draft of the manuscript. Author contributions: MA conceived the idea, MA and SAN designed the field experiments, MA conducted the field experiments and analyzed the data, MA, NV, BB, SJ, and SAN wrote the paper.

DATA ACCESSIBILITY STATEMENT

Data will be fully available upon author request.

LITERATURE CITED

Aguilera, M. A. 2011. The functional roles of herbivores in the rocky intertidal systems in Chile:

- 723 A review of food preferences and consumptive effects. *Revista Chilena de Historia Natural*
724 84:241–261.
- 725 Aguilera, M. A., B. R. Broitman, J. A. Vásquez, and P. A. Camus. 2019a. Consumer–Resource
726 Interactions on an Environmental Mosaic. Pages 307–332 in S. J. Hawkins, K. Bohn, and L.
727 B. Firth, editors. *Interactions in the Marine Benthos: Global patterns and processes*.
728 Cambridge University Press, Cambridge.
- 729 Aguilera, M. A., and S. A. Navarrete. 2007. Effects of *Chiton granosus* (Frembly, 1827) and
730 other molluscan grazers on algal succession in wave exposed mid-intertidal rocky shores of
731 central Chile. *Journal of Experimental Marine Biology and Ecology* 349.
- 732 Aguilera, M. A., and S. A. Navarrete. 2011. Distribution and activity patterns in an intertidal
733 grazer assemblage: Influence of temporal and spatial organization on interspecific
734 associations. *Marine Ecology Progress Series* 431.
- 735 Aguilera, M. A., and S. A. Navarrete. 2012. Functional identity and functional structure change
736 through succession in a rocky intertidal marine herbivore assemblage. *Ecology* 93:75–89.
- 737 Aguilera, M. A., S. A. Navarrete, and B. R. Broitman. 2013a. Differential effects of grazer
738 species on periphyton of a temperate rocky shore. *Marine Ecology Progress Series* 484:63–
739 78.
- 740 Aguilera, M. A., N. Valdivia, and B. R. Broitman. 2013b. Spatial niche differentiation and
741 coexistence at the edge: Co-occurrence distribution patterns in *Scurria* limpets. *Marine*
742 *Ecology Progress Series* 483:185–198.
- 743 Aguilera, M. A., N. Valdivia, and B. R. Broitman. 2015. Herbivore-alga interaction strength

- 744 influences spatial heterogeneity in a kelp-dominated intertidal community. PLoS ONE 10.
- 745 Aguilera, M. A., N. Valdivia, S. Jenkins, S. A. Navarrete, and B. Broitman. 2019b. Asymmetric
- 746 competitive effects during species range expansion: An experimental assessment of
- 747 interaction strength between “equivalent” grazer species in their range overlap. Journal of
- 748 Animal Ecology 88:277–289.
- 749 Altieri, A. H., M. D. Bertness, T. C. Coverdale, N. C. Herrmann, and C. Angelini. 2012. A
- 750 trophic cascade triggers collapse of a salt-marsh ecosystem with intensive recreational
- 751 fishing. Ecology 93:1402–1410.
- 752 Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance.
- 753 Austral Ecology 62:245–253.
- 754 Augustine, D. J., and S. J. McNaughton. 2004. Regulation of shrub dynamics by native browsing
- 755 ungulates on East African rangeland. Journal of Applied Ecology 41:45–58.
- 756 Bellwood, D. R., A. S. Hoey, and J. H. Choat. 2003. Limited functional redundancy in high
- 757 diversity systems: Resilience and ecosystem function on coral reefs. Ecology Letters 6:281–
- 758 285.
- 759 Bellwood, D. R., T. P. Hughes, C. Folke, and M. Nyström. 2004. Confronting the coral reef
- 760 crisis. Nature 429:827–833.
- 761 Bellwood, D. R., T. P. Hughes, and A. S. Hoey. 2006. Sleeping Functional Group Drives Coral-
- 762 Reef Recovery. Current Biology 16:2434–2439.
- 763 Bender, E. A., T. J. Case, and M. E. Gilpin. 1984. Perturbation Experiments in Community
- 764 Ecology : Theory and Practice. Ecology 65:1–13.

- 765 Bennett, S., T. Wernberg, E. S. Harvey, J. Santana-Garcon, and B. J. Saunders. 2015. Tropical
 766 herbivores provide resilience to a climate-mediated phase shift on temperate reefs. *Ecology*
 767 *Letters* 18:714–723.
- 768 Berlow, E. L., S. A. Navarrete, S. Briggs, M. Power, and B. A. Menge. 1999. Quantifying
 769 variation in the strengths of species interactions. *Ecology* 80:2206–2224.
- 770 Blanchette, C. A., C. Melissa Miner, P. T. Raimondi, D. Lohse, K. E. K. Heady, and B. R.
 771 Broitman. 2008. Biogeographical patterns of rocky intertidal communities along the Pacific
 772 coast of North America. *Journal of Biogeography* 35:1593–1607.
- 773 Bradley, B. A., R. Early, and C. J. B. Sorte. 2015. Space to invade? Comparative range infilling
 774 and potential range of invasive and native plants. *Global Ecology and Biogeography*
 775 24:348–359.
- 776 Broitman, B. R., M. A. Aguilera, N. A. Lagos, and M. A. Lardies. 2018. Phenotypic plasticity at
 777 the edge: Contrasting population-level responses at the overlap of the leading and rear edges
 778 of the geographical distribution of two *Scurria* limpets. *Journal of Biogeography* 45.
- 779 Broitman, B. R., S. A. Navarrete, F. Smith, and S. D. Gaines. 2001. Geographic variation of
 780 southeastern Pacific intertidal communities. *Marine Ecology Progress Series* 224:21–34.
- 781 Broitman, B. R., F. Véliz, T. Manzur, E. A. Wieters, G. R. Finke, P. A. Fornes, N. Valdivia, and
 782 S. A. Navarrete. 2011. Geographic variation in diversity of wave exposed rocky intertidal
 783 communities along central Chile. *Revista Chilena de Historia Natural* 84:143–154.
- 784 Burkepile, D. E., and M. E. Hay. 2008. Herbivore species richness and feeding complementarity
 785 affect community structure and function on a coral reef. *Proceedings of the National*

- 786 Academy of Sciences of the United States of America 105:16201–16206.
- 787 Burkepile, D. E., and M. E. Hay. 2011. Feeding complementarity versus redundancy among
788 herbivorous fishes on a Caribbean reef. *Coral Reefs* 30:351–362.
- 789 Byers, J. E., P. E. Gribben, C. Yeager, and E. E. Sotka. 2012. Impacts of an abundant introduced
790 ecosystem engineer within mudflats of the southeastern US coast. *Biological Invasions*
791 14:2587–2600.
- 792 Camus, P. A., K. Daroch, and L. F. Opazo. 2008. Potential for omnivory and apparent intraguild
793 predation in rocky intertidal herbivore assemblages from northern Chile. *Marine Ecology*
794 *Progress Series* 361:35–45.
- 795 Cardinale, B. J., A. L. Downing, D. S. Srivastava, J. J. Weis, M. Sankaran, M. W. Cadotte, M.
796 Loreau, J. P. Wright, J. E. Duffy, A. Hector, C. Jouseau, and I. T. Carroll. 2009. Effects of
797 biodiversity on the functioning of ecosystems: a summary of 164 experimental
798 manipulations of species richness. *Ecology* 90:854–854.
- 799 Chapman, M. G. 2000. Poor design of behavioural experiments gets poor results: Examples from
800 intertidal habitats. *Journal of Experimental Marine Biology and Ecology* 250:77–95.
- 801 Divíšek, J., M. Chytrý, B. Beckage, N. J. Gotelli, Z. Lososová, P. Pyšek, D. M. Richardson, and
802 J. Molofsky. 2018. Similarity of introduced plant species to native ones facilitates
803 naturalization, but differences enhance invasion success. *Nature Communications* 9:1–10.
- 804 Downing, A. S., E. H. van Nes, W. M. Mooij, and M. Scheffer. 2012. The Resilience and
805 Resistance of an Ecosystem to a Collapse of Diversity. *PLoS ONE* 7:1–7.
- 806 Duffy, J. E. 2002. Biodiversity and ecosystem function: the consumer connection. *Oikos* 99:201–

- 807   219.
- 808   Duffy, J. E. 2003. Biodiversity loss, trophic skew and ecosystem functioning. *Ecology Letters*
809   6:680–687.
- 810   Duffy, J. E., K. S. Macdonald, J. M. Rhode, and J. D. Parker. 2001. Grazer diversity, functional
811   redundancy, and productivity in seagrass beds: An experimental test. *Ecology* 82:2417–
812   2434.
- 813   Early, R., B. A. Bradley, J. S. Dukes, J. J. Lawler, J. D. Olden, D. M. Blumenthal, P. Gonzalez,
814   E. D. Grosholz, I. Ibañez, L. P. Miller, C. J. B. Sorte, and A. J. Tatem. 2016. Global threats
815   from invasive alien species in the twenty-first century and national response capacities.
816   *Nature Communications* 7.
- 817   Espoz, C., and J. C. Castilla. 2000. Escape responses of four Chilean intertidal limpets to
818   seastars. *Marine Biology* 137:887–892.
- 819   Espoz, C., D. R. Lindberg, J. C. Castilla, and W. B. Simison. 2004. Los patelogastrópodos
820   intermareales de Chile y Perú Intertidal limpets of Chile and Perú. *Revista Chilena de*
821   *Historia Natural* 77:257–283.
- 822   Ferreira, J. A., and A. H. Zwinderman. 2006. On the Benjamini-Hochberg method. *Annals of*
823   *Statistics* 34:1827–1849.
- 824   Ghedini, G., B. D. Russell, and S. D. Connell. 2015. Trophic compensation reinforces resistance:
825   Herbivory absorbs the increasing effects of multiple disturbances. *Ecology Letters* 18:182–
826   187.
- 827   Gonzalez, A., and M. Loreau. 2009. The Causes and Consequences of Compensatory Dynamics

- 828 in Ecological Communities. *Annual Review of Ecology, Evolution, and Systematics*
829 40:393–414.
- 830 Griffin, J. N., V. Méndez, A. F. Johnson, S. R. Jenkins, and A. Foggo. 2009. Functional diversity
831 predicts overyielding effect of species combination on primary productivity. *Oikos* 118:37–
832 44.
- 833 Guillemin, M. L., L. Contreras-Porcia, M. E. Ramírez, E. C. Macaya, C. B. Contador, H. Woods,
834 C. Wyatt, and J. Brodie. 2016. The bladed Bangiales (Rhodophyta) of the South Eastern
835 Pacific: Molecular species delimitation reveals extensive diversity. *Molecular Phylogenetics*
836 and Evolution 94:814–826.
- 837 Hampe, A., and R. J. Petit. 2005. Conserving biodiversity under climate change: The rear edge
838 matters. *Ecology Letters* 8:461–467.
- 839 Harley, C. D. G. 2011. Climate Change, Keystone Predation, and Biodiversity Loss. *Science*
840 334:1124–1127.
- 841 Harley, C. D. G., A. R. Hughes, K. M. Hultgren, B. G. Miner, C. J. B. Sorte, C. S. Thornber, L.
842 F. Rodriguez, L. Tomanek, and S. L. Williams. 2006. The impacts of climate change in
843 coastal marine systems. *Ecology Letters* 9:228–241.
- 844 Hawkins, S. J., and R. G. Hartnoll. 1983. Grazing of intertidal algae by marine invertebrates.
845 *Oceanography and Marine Biology an Annual Review* 21:195–282.
- 846 Hoey, A. S., and D. R. Bellwood. 2009. Limited functional redundancy in a high diversity
847 system: Single species dominates key ecological process on coral reefs. *Ecosystems*
848 12:1316–1328.

- 849 Hughes, T. P., N. A. J. Graham, J. B. C. Jackson, P. J. Mumby, and R. S. Steneck. 2010. Rising
850 to the challenge of sustaining coral reef resilience. *Trends in Ecology and Evolution*
851 25:633–642.
- 852 Jaksic, F. M. 2003. How Much Functional Redundancy Is Out There, or, Are We Willing to Do
853 Away with Potential Backup Species? 162:255–262.
- 854 Kaarlejärvi, E., A. Eskelinen, and J. Olofsson. 2017. Herbivores rescue diversity in warming
855 tundra by modulating trait-dependent species losses and gains. *Nature Communications* 8.
- 856 Kéfi, S., V. Miele, E. A. Wieters, S. A. Navarrete, and E. L. Berlow. 2016. How Structured Is the
857 Entangled Bank? The Surprisingly Simple Organization of Multiplex Ecological Networks
858 Leads to Increased Persistence and Resilience. *PLoS Biology* 14:1–21.
- 859 Kordas, R. L., I. Donohue, and C. D. G. Harley. 2017. Herbivory enables marine communities to
860 resist warming. *Science Advances* 3:e1701349.
- 861 Laska, M., and T. Wootton. 1998. Theoretical Concepts and Empirical Approaches to Measuring
862 Interaction Strength. *Ecology* 79:461–476.
- 863 Levin, S. A., and J. Lubchenco. 2008. Resilience , Robustness , and Marine Ecosystem-based
864 Management. *Bioscience* 58:27–32.
- 865 Ling, S. D. 2008. Range expansion of a habitat-modifying species leads to loss of taxonomic
866 diversity: A new and impoverished reef state. *Oecologia* 156:883–894.
- 867 Ling, S. D., C. R. Johnson, K. Ridgway, A. J. Hobday, and M. Haddon. 2009. Climate-driven
868 range extension of a sea urchin: Inferring future trends by analysis of recent population
869 dynamics. *Global Change Biology* 15:719–731.

- 870 Ling, S. D., R. E. Scheibling, A. Rassweiler, C. R. Johnson, N. Shears, S. D. Connell, A. K.
871 Salomon, K. M. Norderhaug, A. Pérez-Matus, J. C. Hernández, S. Clemente, L. K. Blamey,
872 B. Hereu, E. Ballesteros, E. Sala, J. Garrabou, E. Cebrian, M. Zabala, D. Fujita, and L. E.
873 Johnson. 2015. Global regime shift dynamics of catastrophic sea urchin overgrazing.
874 Philosophical Transactions of the Royal Society B: Biological Sciences 370:1–10.
- 875 Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of
876 herbivore food preference and algal competitive abilities. *The American naturalist* 112:23–
877 39.
- 878 Luque, G. M., M. E. Hochberg, M. Holyoak, M. Hossaert, F. Gaill, and F. Courchamp. 2013.
879 Ecological effects of environmental change. *Ecology Letters* 16:1–3.
- 880 Manly, B. 2007. *Randomization, Bootstrap and Monte Carlo Methods in Biology*. third. Taylor
881 & Francis Group, New York.
- 882 Meneghesso, C., R. Seabra, B. R. Broitman, D. S. Wethey, M. T. Burrows, B. K. K. Chan, T.
883 Guy-Haim, P. A. Ribeiro, G. Rilov, A. M. Santos, L. L. Sousa, and F. P. Lima. 2020.
884 Remotely-sensed L4 SST underestimates the thermal fingerprint of coastal upwelling.
885 *Remote Sensing of Environment* 237:111588.
- 886 Menge, B. A., B. A. Daley, J. Lubchenco, E. Sanford, P. M. Halpin, G. Hudson, and J. L.
887 Burnaford. 1999. Top-Down and Bottom-Up Regulation of New Zealand Rocky Intertidal
888 Communities. *Ecology* 69:297–330.
- 889 Menge, B. A., B. Daley, and P. Wheeler. 1996. Control of Interaction Strength in Marine Benthic
890 Communities. Page 258 *in* G. Polis and K. Winemiller, editors. *Food webs: integration of*
891 *patterns and dynamics*. Springer.

- 892 Montecinos, A., B. R. Broitman, S. Faugeron, P. A. Haye, F. Tellier, and M. L. Guillemin. 2012.
893 Species replacement along a linear coastal habitat: Phylogeography and speciation in the red
894 alga *Mazzaella laminarioides* along the south east pacific. *BMC Evolutionary Biology*
895 12:1–17.
- 896 Morin, P. J. 1995. Functional Redundancy , Non-Additive Interactions , and Supply-Side
897 Dynamics in Experimental Pond Communities. *Ecology* 76:133–149.
- 898 Mouquet, N., and M. Loreau. 2002. Coexistence in metacommunities: The regional similarity
899 hypothesis. *The American Naturalist* 159:420–426.
- 900 Navarrete, S. A., and J. C. Castilla. 2003. Experimental determination of predation intensity in an
901 intertidal predator guild: Dominant versus subordinate prey. *Oikos* 100:251–262.
- 902 Navarrete, S. A., E. A. Wieters, B. R. Broitman, and J. C. Castilla. 2005. Scales of benthic-
903 pelagic coupling and the intensity of species interactions: From recruitment limitation to
904 top-down control. *Proceedings of the National Academy of Sciences of the United States of*
905 *America* 102:18046–18051.
- 906 Nielsen, K. J., and S. A. Navarrete. 2004. Mesoscale regulation comes from the bottom-up:
907 Intertidal interactions between consumers and upwelling. *Ecology Letters* 7:31–41.
- 908 Nyström, M., A. V. Norström, T. Blenckner, M. de la Torre-Castro, J. S. Eklöf, C. Folke, H.
909 Österblom, R. S. Steneck, M. Thyresson, and M. Troell. 2012. Confronting Feedbacks of
910 Degraded Marine Ecosystems. *Ecosystems* 15:695–710.
- 911 O'Connor, N. E., M. C. Emmerson, T. P. Crowe, and I. Donohue. 2013. Distinguishing between
912 direct and indirect effects of predators in complex ecosystems. *Journal of Animal Ecology*

- 913   82:438–448.
- 914   Olden, J. D., and N. L. R. Poff. 2003. Toward a Mechanistic Understanding and Prediction of
915   Biotic Homogenization. *The American Naturalist* 162:442–460.
- 916   Olden, J. D., and T. P. Rooney. 2006. On defining and quantifying biotic homogenization.
917   *Global Ecology and Biogeography* 15:113–120.
- 918   Olf, H., and M. E. Ritchie. 1998. Effects of herbivores on grassland plant diversity. *Trends in*
919   *Ecology and Evolution* 13:261–265.
- 920   Osenberg, C. W., and G. G. Mittelbach. 1996. Food Webs. Pages 497–510 *in* G. Polis and K.
921   Winemiller, editors. *Food webs: integration of patterns and dynamics*. Chapman and Hall,
922   New York.
- 923   Paine, R. T. 1992. Food web analysis through field measurement of per capita interaction
924   strength. *Nature* 359:710–713.
- 925   Paine, R. T. 2002. Trophic control of production in a rocky intertidal community. *Science*
926   296:736–739.
- 927   Poloczanska, E. S., M. T. Burrows, C. J. Brown, J. G. Molinos, B. S. Halpern, O. Hoegh-
928   Guldberg, C. V. Kappel, P. J. Moore, A. J. Richardson, D. S. Schoeman, and W. J.
929   Sydeman. 2016. Responses of marine organisms to climate change across oceans. *Frontiers*
930   *in Marine Science* 3:1–21.
- 931   Poore, A. G. B., A. H. Campbell, R. A. Coleman, G. J. Edgar, V. Jormalainen, P. L. Reynolds, E.
932   E. Sotka, J. J. Stachowicz, R. B. Taylor, M. A. Vanderklift, and J. Emmett Duffy. 2012.
933   Global patterns in the impact of marine herbivores on benthic primary producers. *Ecology*

- 934 Letters 15:912–922.
- 935 Pringle, R. M., J. R. Goheen, T. M. Palmer, G. K. Charles, E. DeFranco, R. Hohbein, A. T. Ford,
936 and C. E. Tarnita. 2014. Low functional redundancy among mammalian browsers in
937 regulating an encroaching shrub (*Solanum campylacanthum*) in African savannah.
938 Proceedings of the Royal Society B: Biological Sciences 281.
- 939 R Development Core Team. 2018. R: a language and environment for statistical computing. R
940 Foundation for Statistical Computing, Vienna, Austria.
- 941 Resetarits, W. J., and D. R. Chalcraft. 2007. Functional diversity within a morphologically
942 conservative genus of predators: Implications for functional equivalence and redundancy in
943 ecological communities. Functional Ecology 21:793–804.
- 944 Rivadeneira, M. M., and M. Fernández. 2005. Shifts in southern endpoints of distribution in
945 rocky intertidal species along the south-eastern Pacific coast. Journal of Biogeography
946 32:203–209.
- 947 Rosenfeld, J. 2002. Functional redundancy in ecology and conservation. Oikos 98:156–162.
- 948 Russell, B. D., C. D. G. Harley, T. Wernberg, N. Mieszkowska, S. Widdicombe, J. M. Hall-
949 Spencer, and S. D. Connell. 2012. Predicting ecosystem shifts requires new approaches that
950 integrate the effects of climate change across entire systems. Biology Letters 8:164–166.
- 951 Sala, E., and M. H. Graham. 2002. Community-wide distribution of predator-prey interaction
952 strength in kelp forests. Proceedings of the National Academy of Sciences of the United
953 States of America 99:3678–3683.
- 954 Santelices, B. 1990. Patterns of organizations of intertidal and shallow subtidal vegetation in

- 955 wave exposed habitats of central Chile. *Hydrobiologia* 192:35–57.
- 956 Schmitz, O. J. 2009. Effects of predator functions on grassland ecosystems. *Ecology* 90:2339–
957 2345.
- 958 Schoener, T. W., and D. A. Spiller. 1996. Devastation of prey diversity by experimentally
959 introduced predators in the field. *Nature* 381:691–694.
- 960 Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice. 2009. Evolution and Ecology of
961 Species Range Limits. *Annual Review of Ecology, Evolution, and Systematics* 40:415–436.
- 962 Simberloff, D., J. L. Martin, P. Genovesi, V. Maris, D. A. Wardle, J. Aronson, F. Courchamp, B.
963 Galil, E. García-Berthou, M. Pascal, P. Pyšek, R. Sousa, E. Tabacchi, and M. Vilà. 2013.
964 Impacts of biological invasions: What’s what and the way forward. *Trends in Ecology and*
965 *Evolution* 28:58–66.
- 966 Sorte, C. J. B. 2013. Predicting persistence in a changing climate: Flow direction and limitations
967 to redistribution. *Oikos* 122:161–170.
- 968 Sorte, C. J. B., S. L. Williams, and J. T. Carlton. 2010. Marine range shifts and species
969 introductions: Comparative spread rates and community impacts. *Global Ecology and*
970 *Biogeography* 19:303–316.
- 971 Stachowicz, J. J., and D. Tilman. 2005. Species invasion and the relationships between species
972 diversity, community saturation and ecosystem functioning. Pages 41–64 *Species invasions:*
973 *insights into ecology, evolution, and biogeography.*
- 974 Steneck, R. S., and L. Watling. 1982. Feeding capabilities and limitation of herbivorous
975 molluscs: A functional group approach. *Marine Biology* 68:299–319.

- 976 Sundstrom, S. M., C. R. Allen, and C. Barichievsky. 2012. Species, Functional Groups, and
977 Thresholds in Ecological Resilience. *Conservation Biology* 26:305–314.
- 978 Tapia, F. J., S. A. Navarrete, M. Castillo, B. A. Menge, J. C. Castilla, J. Largier, E. A. Wieters,
979 B. R. Broitman, and J. A. Barth. 2009. Thermal indices of upwelling effects on inner-shelf
980 habitats. *Progress in Oceanography* 83:278–287.
- 981 Tellier, F., J. Tapia, S. Faugeton, C. Destombe, and M. Valero. 2011. The *Lessonia nigrescens*
982 species complex (Laminariales, Phaeophyceae) shows strict parapatry and complete
983 reproductive isolation in a secondary contact zone. *Journal of Phycology* 47:894–903.
- 984 Thomsen, M. S., T. Wernberg, A. Altieri, F. Tuya, D. Gulbrandsen, K. J. McGlathery, M. Holmer,
985 and B. R. Silliman. 2010. Habitat cascades: The conceptual context and global relevance of
986 facilitation cascades via habitat formation and modification. *Integrative and Comparative*
987 *Biology* 50:158–175.
- 988 Usinowicz, J., and J. M. Levine. 2018. Species persistence under climate change: a geographical
989 scale coexistence problem. *Ecology Letters* 21:1589–1603.
- 990 Valdivia, N., M. A. Aguilera, S. A. Navarrete, and B. R. Broitman. 2015. Disentangling the
991 effects of propagule supply and environmental filtering on the spatial structure of a rocky
992 shore metacommunity. *Marine Ecology Progress Series* 538:67–79.
- 993 Vergés, A., P. D. Steinberg, M. E. Hay, A. G. B. Poore, A. H. Campbell, E. Ballesteros, K. L.
994 Heck, D. J. Booth, M. A. Coleman, D. A. Feary, W. Figueira, T. Langlois, E. M. Marzinelli,
995 T. Mizerek, P. J. Mumby, Y. Nakamura, M. Roughan, E. van Sebille, A. Sen Gupta, D. A.
996 Smale, F. Tomas, T. Wernberg, and S. K. Wilson. 2014. The tropicalization of temperate
997 marine ecosystems: Climate-mediated changes in herbivory and community phase shifts.

- 998   Proceedings of the Royal Society B: Biological Sciences 281.
- 999   Wardle, D. A., R. D. Bardgett, R. M. Callaway, and W. H. Van Der Putten. 2011. Terrestrial
1000   ecosystem responses to species gains and losses. *Science* 332:1273–1277.
- 1001   Wernberg, T., B. D. Russell, M. S. Thomsen, C. F. D. Gurgel, C. J. A. Bradshaw, E. S.
1002   Poloczanska, and S. D. Connell. 2011. Seaweed communities in retreat from ocean
1003   warming. *Current Biology* 21:1828–1832.
- 1004   Wernberg, T., D. A. Smale, and M. S. Thomsen. 2012. A decade of climate change experiments
1005   on marine organisms: Procedures, patterns and problems. *Global Change Biology* 18:1491–
1006   1498.
- 1007   Wieters, E. A., D. M. Kaplan, S. A. Navarrete, A. Sotomayor, J. Largier, K. J. Nielsen, and F.
1008   Véliz. 2003. Alongshore and temporal variability in chlorophyll a concentration in Chilean
1009   nearshore waters. *Marine Ecology Progress Series* 249:93–105.
- 1010   Wootton, J. T., and M. Emmerson. 2005. Measurement of interaction strength in nature. *Annual*
1011   *Review of Ecology, Evolution, and Systematics* 36:419–444.
- 1012   Worm, B., E. B. Barbier, N. Beaumont, J. E. Duffy, C. Folke, B. S. Halpern, J. B. C. Jackson, H.
1013   K. Lotze, F. Micheli, S. R. Palumbi, E. Sala, K. A. Selkoe, J. J. Stachowicz, and R. Watson.
1014   2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314:787–790.
- 1015
- 1016
- 1017
- 1018

1019

1020 **Figure Legends**

1021 **Figure 1.** Scheme of the expected effect sizes on community structure (sessile species cover,
 1022 richness and diversity) of the two *Scurria* species and the entire herbivore guild at the region of
 1023 range overlap (RO), and within their respective equatorward (*S. viridula*) and poleward (*S.*
 1024 *zebrina*) geographic regions. **A.** Individual effects of both *Scurria* species are expected to be
 1025 higher within their respective ranges (north and south) than at the RO, following the reduction of
 1026 individual performance expected at geographic range borders. Combined effects of the two
 1027 species within the RO could be the results of adding their separate impacts (i.e. additivity in
 1028 effects, white square), but it could also be lower than expected if interference takes place
 1029 between species (see green square). Alternatively, joint effects could be higher than expected in
 1030 the case of complementarity of their impacts on the producer assemblage (see yellow square). **B.**
 1031 The net collective effect of the entire herbivore guild may remain relatively constant across the
 1032 entire region or exhibit a latitudinal gradient. Assuming there is no north-south environmental
 1033 gradient, the collective effect of the herbivore guild could be unchanged within the RO (despite
 1034 reductions in performance of the two *Scurria* species) due to compensatory effects by other
 1035 species in the guild (see dotted black line). It could be reduced due to depression in *Scurria*
 1036 performances with no compensation. Such a decrease could be further reduced by interference
 1037 between the two *Scurria* (green line). Alternatively, functional roles could be complementary
 1038 and therefore enhance the total herbivore effect (top orange line).

1039

Figure 2. Density (ind./m²) ($\pm$ EE) of *Scurria viridula* (red) and *S. zebrina* (blue) along the coast of Chile from 18°S 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°S to 33°S. The range of *S. viridula* expansion is from 32.31°S to 33.7°S.

Figure 3. *Per capita* individual effect of *Scurria viridula*, *S. 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*, *U. 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% CIs, 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.

Figure 4. Non-metric 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 the equatorward site (Carrizal Bajo) (A), at the range overlap (Punta Talca) (RO) (B), and at the poleward site (Las Cruces) (C) of the *Scurria* species. EXC: herbivore exclusion, POLY: Polyculture; Enclo_SV: Enclosures of *S. viridula*; Enclo_SZ: Enclosures of *S. zebrina*.

1062

1063

1064

1065

1066

1067

1068
1069
1070
1071
1072
1073
1074
1075
1076
1077
1078
1079
1080
1081
1082
1083
1084
1085
1086
1087
1088

Figure 5. *Per capita* individual effect of *Scurria viridula* and *S. 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% CIs, which were estimated through bootstrapping.

Figures

Figure 1.

Figure 2.

Figure 3.

Figure 4.

Figure 5.