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

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

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1   **Running Head**: Functional redundancy and range shift

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11   Moisés A. Aguilera[1,2*], Nelson Valdivia[3, 4], Bernardo R. Broitman[5], Stuart R Jenkins[6] &, Sergio
12   A. Navarrete[7]

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15   [1]Departamento de Biología Marina, Facultad de Ciencias del Mar, Universidad Católica del Norte, Larrondo, 1281,
16   Coquimbo, Chile.

17   [2]Centro de Estudios Avanzados en Zonas Áridas (CEAZA), Ossandón 877, Coquimbo, Chile.

18   [3]Instituto de Ciencias Marinas y Limnológicas, Facultad de Ciencias, Universidad Austral de Chile, Campus Isla
19   Teja, Valdivia 5110236, Chile

20   [4]Centro FONDAP de Investigación de Dinámicas de Ecosistemas Marinos de Altas Latitudes (IDEAL)

21   [5]Departamento de Ciencias Biológicas, Facultad de Artes Liberales, Universidad Adolfo Ibáñez, Viña de Mar, Chile

22   [6]School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey, LL59 5AB, United Kingdom.

23   [7]Estación Costera de Investigaciones Marinas, Las Cruces, Center for Applied Ecology and Sustainability (CAPES),
24   Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile.

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

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30 **ABSTRACT**

31 Ongoing climate change is shifting the geographic distributions of some species, potentially

32 imposing rapid changes in local community structure and ecosystem functioning. Besides

33 changes in population level inter-specific interactions, such range shifts may also cause changes

34 in functional structure within the host assemblages, which can result in losses or gains in

35 ecosystem functions. Since consumer-resource dynamics are central to community regulation,

36 functional reorganization driven by introduction of new consumer species can have large

37 consequences on ecosystem functions. Here we experimentally examine the extent to which the

38 recent poleward range expansion of the intertidal grazer limpet *Scurria viridula* along the coast

39 of Chile has altered the role of the resident congeneric limpet *S. zebrina,* and whether the net

40 collective impacts, and functional structure, of the entire herbivore guild have been modified by

41 the introduction of this new member. We examined the functional role of *Scurria* species in

42 controlling ephemeral algal cover, bare rock availability, species richness and diversity, and

43 compared the effects in the region of range overlap against their respective 'native' abutted

44 ranges. Experiments showed depression of *per capita* effects of the range-expanded species

45 within the region of overlap, suggesting environmental conditions negatively affect individual

46 performance. In contrast, effects of *S. zebrina* were commonly invariant at its range edge. When

47 comparing single species versus polycultures, effects on bare rock cover were altered by the

48 presence of the other *Scurria* species, suggesting competition between *Scurria* species.

49 Importantly, although the magnitude of *S. viridula* effects at the range overlap was reduced, its

50 addition to the herbivore guild seems to complement and intensify the role of the guild in

51 reducing green algal cover, species richness and increasing bare space provision. Our study thus

52 highlights that range expansion of an herbivore can modify the functional guild structure in the

53 recipient community. It also highlights the complexity of predicting how functional structure

54   may change in the face of natural or human-induced range expansions. There is a need for more

55   field-based examination of regional functional compensation, complementarity or inhibition

56   before we can construct a conceptual framework to anticipate the consequences of species range

57   expansions.

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

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83   INTRODUCTION

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85   Understanding the consequences of human- and climate-induced species range shifts on the

86   functional structure of communities is a central goal of ecology today (e.g. Harley et al. 2006,

87   Harley 2011, Nyström et al. 2012, Luque et al. 2013). Shifts in the geographic distributions of

88   species change local species composition, leading to novel ecological interactions and,

89   potentially, to fundamentally altered patterns of ecosystem functioning (Worm et al. 2006, Levin

90   and Lubchenco 2008, Wernberg et al. 2012, Sorte 2013, Ling et al. 2015, Usinowicz and Levine

91   2018). Driven by rapid species introductions and changes in global climate, compositional

92   changes are likely to be observed with increased frequency around areas where different biotas

93   overlap, such as biogeographic transition zones (Sexton et al. 2009). In the case of coastal

94   species, these transitional areas can encompass hundreds of kilometers of shoreline (Blanchette

95   et al. 2008), so compositional changes within transition zones can have broad geographic

96   impacts (Russell et al. 2012). Modification of functional structure within consumer guilds driven

97   by species range shifts may result in the incorporation of new functions or the loss of key traits,

98   which can also translate into net gains or losses in resilience of the system (Bellwood et al. 2004,

99   Cardinale et al. 2009, Hughes et al. 2010, Downing et al. 2012). For instance, addition of

100   functionally equivalent or redundant consumer species by range expansions can be considered an

101   insurance against the loss of ecosystem functions following potential future extinctions of

102   species in the recipient guild (Bellwood et al. 2003, 2004, Augustine and McNaughton 2004,

103   Hoey and Bellwood 2009, Pringle et al. 2014, Kaarlejärvi et al. 2017). Theoretical models

104   suggest that trait similarity and complete functional redundancy should be more frequent over

105   regional than local scales (Mouquet and Loreau 2002, Jaksic 2003, Resetarits and Chalcraft

106   2007). Then, redundancy or equivalence in functional roles could be especially important when

107   species modify their geographic ranges, because expansion of a functionally redundant species

108   would compensate the subsequent range contraction of the recipient or native redundant species

109   (Resetarits and Chalcraft 2007).

110   Understanding the local functional consequences triggered by the expansion or contraction of

111   species geographic ranges is a threefold challenge. It requires, at a minimum, to (i) identify the

112   functional role of the new species in its original community or assemblage, (ii) assess how the

113   resident members of the functional group respond to the local introduction or extinction (Duffy

114   2002, Sundstrom et al. 2012), and finally (iii) quantify the effects of the new set of ecological

115   interactions on community structure and functioning (e.g. competitive exclusion of residents,

116   Stachowicz and Tilman 2005, Simberloff et al. 2013). Incorporation of new consumer species

117   that have similar or redundant roles to those found in the receiving ecological assemblage could

118   strengthen specific functions if their effects are synergistic or additive (Vergés et al. 2014, Ling

119   et al. 2015), as long as the introduction does not cause the extinction of resident members of the

120   guild (e.g. Duffy 2002, Burkepile and Hay 2008, Griffin et al. 2009). The effects of the new

121   species may also be complementary to those of the resident species, leading to more complete

122   (e.g. control of primary producers) or more extensive (over space or time) changes in ecosystem

123   function. Such complementarity may result from the new species having different attributes, or it

124   may result from resource partitioning between residents and the new species, fostering a

125   complementarity in functions, and enhancing ecosystem functions (Duffy 2002, Burkepile and

126   Hay 2008, 2011, Schmitz 2009). In contrast, the new species could interfere with residents,

127   causing an overall depression of ecosystem function (ysee for example Ling 2008, Ling et al.

128   2015). Alternatively, the new species can bring a completely novel ecosystem function to the

129   local community, such as habitat provisioning in areas originally devoid of dominant habitat-

130   forming species (e.g. "habitat cascade"; Thomsen et al. 2010, Altieri et al. 2012, Byers et al.

131   2012). This situation would be most common when the new species is sessile and does not fit

132   into any resident guild or functional group (Byers et al. 2012). Thus, the individual effects of a

133   new consumer species in the recipient community depends on its species-specific attributes and

134   the effect on local resources relative to the net effect of the total group (Duffy 2002). Exploring

135   how novel co-occurrences between functionally equivalent or distinct species alter the structure

136   of consumer groups can provide important insights into the compensatory potential under species

137   range shifts and hence the stability of ecosystems to environmental change (e.g. Ling 2008,

138   Gonzalez and Loreau 2009, Wernberg et al. 2011, Ghedini et al. 2015, Kordas et al. 2017)

139   Herbivores have a key function controlling primary production and many aspects of

140   community structure in benthic marine ecosystems (Hawkins and Hartnoll 1983, Paine 2002,

141   Burkepile and Hay 2008, Poore et al. 2012, Kordas et al. 2017). In a context of climate-driven

142   compositional changes, range-expanding herbivores can have important impacts on local

143   (recipient) community structure (see Ling 2008, Ling et al. 2009, 2015, Sorte et al. 2010, Vergés

144   et al. 2014). Such impacts cannot simply be anticipated by the effects in the original community,

145   as the novel environmental conditions encountered by the invader may alter its individual

146   performance. In this study we take advantage of the recent poleward range expansion of an

147   intertidal rocky shore herbivore, the limpet *Scurria viridula* (Rivadeneira and Fernández 2005,

148   Aguilera et al. 2013b, 2019b). This limpet has recently extended its region of overlap with its

149   closely related congener *S. zebrina* to form a broad transitional zone, where both species co-

150   occur, from 30 to 32°S (Aguilera et al. 2013b, 2019b). Due to the oceanographic conditions

151   around the transition zone, larval arrival of space-dominant mussel and barnacle species is

152   minimal (Navarrete et al. 2005). As a result, the mid intertidal rocky shore zone of the overlap

153   region is dominated by corticated and green ephemeral algae interspersed with large patches of

154   bare space (Broitman et al. 2001, 2011, Valdivia et al. 2015). This pattern is common in mid to

155   high intertidal levels, where both *Scurria* species can show aggregated spatial patterns and reach

156   large shell sizes compared with other members of a diverse group of benthic herbivores. We used

157   this model ecological system to examine the consequences of the introduction of a new species,

158   *S. viridula*, onto the recipient rocky shore communities, studying changes in the functional

159   structure of the herbivore guild to assess three general and informative hypotheses :

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

161   Chalcraft & Resetarits 2003) reduction in the abundance of dominant algal species increasing

162   bare rock availability and reducing species richness and/or diversity. This prediction stems from

163   the strong similarity in *Scurria* foraging and morphological traits that have been previously

164   described (Aguilera et al. 2013b). In this case, additive effects in the range of overlap can be

165   expected (i.e. the sum of individual effects are similar than their combined effects; white square

166   within the dotted zone in Fig. 1A). Alternatively, they may exhibit synergistic effects, in which

167   case their shared function will be enhanced (i.e. "complementary effect"; yellow square in Fig.

168   1A).

169   (2) Individual *per capita* reduction of algal abundance and bare rock provision exerted

170   by *Scurria* species diminish at the range overlap due to interference competition and/or lower

171   individual performances at species range ends (Broitman et al. 2018, Aguilera et al. 2019b).

172   Thus, the joint effects of *S. viridula* and *S. zebrina* at the range overlap could be non-additive

173   (i.e. their combined effect on algal production will be lower than expected by the addition of

174   their individual effects; green square in Fig. 1A). Figure 1A also illustrates the possibility of

175 lower *per capita* effects of the *Scurria* species at their range ends, where they overlap, compared

176 to conspecifics located towards the core of their respective ranges (e.g. Hampe and Petit 2005,

177 Sexton et al. 2009).

178   Finally, (3) *Scurria* novel co-occurrences with other herbivores at the range overlap may

179 either increase or decrease the magnitude of the collective net herbivore guild on controlling

180 algal abundance and bare rock provision. The co-occurrence of both *Scurria* species could

181 reduce (or keep constant) the net effect of the entire herbivore guild across the region of overlap

182 due to interference competition, or, alternatively, intensify it as a consequence of

183 complementarity in foraging or microhabitat use (see Figure 1B). Similar arguments can be made

184 if *per capita* effects are not depressed at the range overlap, but the magnitudes will be different,

185 highlighting the need to evaluate experimentally *per capita* effects at range boundaries and at the

186 core of species distributions.

187

188 MATERIAL AND METHODS

189 **Study system and focal species**

190   *Scurria viridula* and *S. zebrina* inhabit mid to high intertidal zones on wave-exposed rocky

191 platforms (Espoz et al. 2004, Aguilera et al. 2013b). They are sister species (Espoz et al. 2004)

192 that share morphological traits (e.g. maximum size) and habitat, but have contrasting behavioral

193 responses to heat stress and predators (Espoz and Castilla 2000, Broitman et al. 2018). Both

194 species have similar feeding habits (Camus et al. 2008), suggesting that they can have strong

195 joint impacts on benthic primary production through high *per capita* effects on ephemeral algae

196 and biofilm (Aguilera et al. 2013a).

197 *Scurria viridula* is found from Peru (12ºS) to central-north Chile (32ºS), while *S. zebrina* is

198 distributed from central Chile (30ºS) to southern Chiloé (~43ºS) (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

220 along the coastline (Broitman et al. 2001, Wieters et al. 2003, Tapia et al. 2009, Aguilera et al.

221 2019a). Green ephemeral algae like Ulvoids (e.g. *U. rigida*, *U. compressa*), *Blidingia minima.*

222 *Ulothrix sp.,* and the red alga *Pyropia orbicularis* (= *Porphyra columbina*) (Guillemin et al.

223 2016) dominate mid-high and high intertidal levels across the distributional range. The corticated

224 late-successional alga *Mazzaella laminarioides* is dominant in mid intertidal levels of central

225 Chile, but it is absent north from 30°S (Broitman et al. 2001, Montecinos et al. 2012, and see

226 Aguilera et al. 2019a for review). Advances in molecular genetics have revealed several cryptic

227 species among dominant habitat-forming algae of the mid- and low intertidal zones of the rocky

228 shore, including the corticated algae *Mazzaella* and the kelp *Lessonia* (Tellier et al. 2011,

229 Montecinos et al. 2012)*.* Thus, the study took place in a highly diverse biogeographic system

230 characterized by a transitional zone around 30°S in which both top-down and bottom-up

231 processes have been shown to shape intertidal community structure (e.g. Navarrete and Castilla

232 2003, Nielsen and Navarrete 2004, Aguilera and Navarrete 2012, Aguilera et al. 2015).

233

234 **Geographic *Scurria* range overlap**

235   The distribution of the focal *Scurria* species and recent range shifts of *S. viridula* in central-

236 northern Chile have been documented in field studies across the region (see Aguilera et al.

237 2013b, 2019). Long-term abundance datasets (i.e. 1998 to 2000, 2003 to 2005 and 2009 to 2015)

238 of *Scurria* limpets, estimated through positioning 50×50 cm quadrats, from higher to lower

239 intertidal levels, at different sites spanning ~1600 km from north to central Chile, show a well-

240 defined geographic overlap of both herbivore species between 30°S to 32°S (see Fig. 2 and

241 Aguilera et al. 2013b, 2019). We used these datasets to determine the variability in abundance of

242   *Scurria* across the site of range overlap, (30°S) and at the new range edge of *S. viridula* species

243   (33°S).

244

Functional herbivore effects: enclosure/exclusion experiments

246   Both *Scurria* species can be considered "scraper/grazer" herbivores, capable of abrading the

247   substrate with their radula (i.e. docoglossan type), thus removing periphyton (spores and

248   plantlets of macroalgae), together with microorganisms and early stages of sessile invertebrates

249   (Camus et al. 2008, Aguilera 2011). To determine if their effects on the early colonization of

250   sessile species were qualitatively and quantitatively similar, we estimated the effects of each

251   species on the early colonization of periphyton and on the established stages of early- and mid-

252   successional algal species (i.e. from 1 to 13 months from experimental removal of the

253   community) under the different contexts of geographic co-occurrence. It should be noted that in

254   this system, late successional algae species like the corticated alga *Mazzaella laminarioides*

255   typically colonize 13 to 15 months after experimental bare space creation (Aguilera and

256   Navarrete 2012) and it therefore this species and other late successional sessile species (e.g. the

257   red alga *Gelidium chilense*, the mussel *Perumytilus purpuratus*) were nearly absent from our

258   experimental plots.

259   The prediction that the two *Scurria* species are functionally redundant, and would interfere

260   with each other generating combined effects that are indistinguishable from their isolated effects

261   (Hypotheses 1), or, in contrast that their effects are additive or synergistic increasing the net

262   collective herbivore guild effect (Hypothesis 3), requires assessing potential intraspecific

263   changes in *per capita* effects between geographic regions or origin versus overlap (Hypothesis

264   2). To this end, we conducted an herbivore enclosure/exclusion experiments in the mid-intertidal

265   shore at three sites located at a) the range overlap of the two *Scurria* species (~31°S), b)

266   equatorward (north) of this zone (26°S), where only *S. viridula* is present, and c) poleward

267   (south) of it (33°S), where populations of *S. zebrina* are common and *S. viridula* is present at

268   very low densities as young individuals, having recently expanded its range into this region. For

269   operational purposes, we considered the 33°S sites as 'exclusively' *S. zebrina*, at least at the time

270   of our study. The experimental design consisted of six treatments at the range overlap (RO), and

271   four at the sites within the exclusive range of each *Scurria* species; The sites and experimental

272   design were as follows; <u>Range overlap, Punta Talca, 30.5°S (RO):</u> 1) 2 *S. zebrina* (SZ) enclosure;

273   2) 2 *S. viridula* (SV) enclosure; 3) 1 *S. zebrina* plus 1 *S. viridula* enclosure (Polyculture); 4)

274   Herbivore Exclusion; 5) Control (Open areas); and 6) Procedural Control (Partial fences).

275   <u>Equatorward of the RO, Carrizal Bajo, 28ºS, (north)</u>: 1) 2 *S. viridula;* 2) Herbivore Exclusion; 3)

276   Control; 4) Procedural Control. <u>South Poleward of the RO, Las Cruces, 33.5ºS (south)</u>: 1) 2 *S.*

277   *zebrina*; 2) Herbivore Exclusion; 3) Control; 4) Procedural Control (see **Table S1** in **Appendix**

278   **S1** for summary of the treatment design). All treatments, at each locality, were replicated six

279   times. Each experimental unit consisted of a 35×35 cm rock area that was scraped clean with

280   drill-mounted brushes and manual chisels, removing all organisms including encrusting algal

281   fragments. This procedure reset the community to an early community stage and allowed us to

282   identify the effects of herbivore species on initial successional stages and the establishment of

283   mid- successional species that can colonize within a year time on succession (Aguilera and

284   Navarrete 2012). The field experiments were initiated on 12 March 2013 in Carrizal Bajo

285   (north), 25 March 2013 in Las Cruces (south) and on 02 April 2013 in Punta Talca (RO) and all

286   three experiments ended on 30 April 2014 (spanning about 400 days). To enclose *Scurria*

287   individuals inside the experimental plots (35 $\times$ 35 cm), we used stainless steel mesh fences (8

288   cm high, 10 mm mesh size) fastened to the rock with stainless steel screws. Gaps between the

289   substratum and the base of the fences were sealed with plastic mesh to prevent predators and

290   other benthic grazers to access the experimental plots. We evaluated the effect of fences on

291   sessile organisms by including a partial fence (procedural control) in our treatment design, which

292   consisted in attaching sections of the fence with sufficient separation to allow access to all

293   common grazers. These experimental level was contrasted against control areas (open plots) (see

294   Results section). Limpet enclosures consisted of one adult individual *Scurria* (3.4 ± 0.16 cm

295   shell length) inside the experimental plots, which was carefully collected during nocturnal low

296   tide from the same rocky platform and intertidal zone level where fences were deployed. The

297   resultant *Scurria* densities inside enclosures, at all sites correspond well to natural densities

298   recorded for both species in the range overlap (i.e. 11.9 ± 1.34 *Scurria* ind. m^{-2}, roughly 1.6

299   indiv. per plot area) (Aguilera et al. 2013b). It should be noted that at Las Cruces, densities of *S.*

300   *viridula* are lower than other sites (see Results). but we kept the same experimental densities

301   across all locations for the sake of comparisons. Over the course of the experiment, only two

302   enclosed *S. viridula* individuals had to be replaced from two enclosures in the overlap region site

303   (Punta Talca), and one individual in the northern site (Carrizal Bajo). To control for the potential

304   impact of fences (e.g. confinement) and transplantation on limpet individual behavior (Chapman

305   2000), 10 *S. viridula* and 10 *S. zebrina* individuals were tagged, measured and left in the same

306   experimental place with no fences. Survival and activity patterns (e.g. displacements from

307   original position) and attachment to the substrate of these individuals were checked twice per

308   month at each site. Every month we removed other benthic herbivores found inside

309   enclosure/exclusion plots in the experiment such as *Scurria* spp. and *Siphonaria lessoni* recruits

310   (2-3 individual per plot > 5 mm length) or Chitons, littorinids snails, which were commonly less

311   than 4 individuals per plot. Community composition was assessed monthly from 15 March 2013

312   to 30 April 2014 by recording all species present and quantifying percentage cover of all sessile

313   organisms within experimental areas with 35×35 cm quadrats with 81 uniformly spaced

314   intersection points. Each plot was also photographed with a high-resolution digital camera, and

315   percentage cover re-estimated in the laboratory to compare with field estimates. Each photograph

316   was cropped to include only the quadrat and analyzed using the program image J (http://imagej.-

317   nih.gov/ij/download.html). Organisms were identified to the lowest taxonomic resolution

318   possible. When identification was difficult in the field we collected samples of algae and took

319   them to the laboratory to identify under a stereomicroscope. During each monitoring, fences

320   were manually cleaned of all algae and growth to reduce fence effects on light and water

321   circulation.

322

323   **Statistical analyses**

324   We examined whether inter-annual fluctuations of *Scurria* densities at the geographic

325   overlap, since *S. viridula* expansion, followed similar patterns between the two species. To this

326   end, we used all sampling dates for the range overlap (Punta Talca, 1998-2014) and the poleward

327   site (Las Cruces, 2003-2015), and examined between species association with Kendall's tau

328   correlation, which examines whether positive and negative fluctuations appear correlated over

329   time (synchronous). Additionally, Pearson linear correlation was also used to examine whether

330   abundances of the two species were linearly correlated over time.

331   Herbivore effects on intertidal community composition were tested through the differences in

332   mobile (i.e. small recruits found inside plots) and sessile species composition between treatments

333   for each region over the 13-month experimental period. We used non-metric Multidimensional

334   Scaling (nMDS) on untransformed Bray–Curtis distances, calculated for each replicate plot of

335   each treatment, through the averaged (for each replicate plot over the 13-month of the study) and

336   normalized density and cover for mobile and sessile species, respectively. Thus, we obtained

337   long-term estimates for each replicate plot (n=6), corresponding to each treatment, for each site

338   during the study. We note that since our study did not consider the late successional stages that

339   typically give rise to strong differences among herbivore identities (Aguilera and Navarrete

340   2012), differences in community responses between initial colonization (1-4 months),

341   intermediate establishment (5-8 months) and mid- successional stages (9-13mo) were not

342   consistent across the study region (**Fig. S1** in **Appendix S2**). At the southern end (Las Cruces)

343   and to a lesser extent the northern end, the sessile community composition observed after 9mo

344   tended to be different than earlier dates, and treatment effects were emphasized, but such

345   successional trends got blurry in the overlap region (**Fig. S1** in **Appendix S2**). Therefore, we

346   preferred to simplify presentation and comparisons across region by calculating treatment effects

347   on the long-term (13mo) average community responses encompassing together early and mid-

348   succession. Statistically significant differences between treatments for each locality (one-way

349   model) were analyzed with PERMANOVA. A Tukey HSD' *post hoc* test for '*betadisper*'

350   (Anderson 2001) were performed with the 'vegan' package in R (R Development Core Team

351   2018).

352

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

376   direct and the propagation of indirect effects, including density-dependent feedbacks , making

377   local estimates of interaction strength difficult to compare among studies (Bender et al. 1984,

378   Laska and Wootton 1998, Berlow et al. 1999, Wootton and Emmerson 2005), or among

379   different successional stages of the community (Aguilera and Navarrete 2012). In our field

380   experiments, a mix of early and mid-successional algal species characterized the community

381   inside plots. Thus, our interaction strength estimates are better interpreted as an average

382   herbivore effects over the early- to mid-successional times, including the potential indirect

383   effects within the plots. Since experiments had the same duration across sites we expect our

384   estimates to be affected in roughly similar ways by the propagation of indirect effects. Thus we

385   pooled DI-estimates, calculated for each replicate treatment plot for each sampling times, and

386   averaged over the 13-month period for both *per capita* and collective effects. Confidence

387   intervals (95%) for average effect estimates were obtained through a bootstrapping procedure (

388   following Manly 2007). Previous visual inspection of our data (Q-Q plots) and Levene' test

389   using the median as center (i.e. Brown-Forsythe method), showed they were not normally

390   distributed but have homogeneous variance. Thus, the differences between geographic zones and

391   treatments, for each effect size estimated, were tested by means of Kruskal-Wallis multiple

392   comparisons suggested by Dunn (1964), where P-values were adjusted with False Discovery

393   Rate for familywise comparisons (Ferreira and Zwinderman 2006). Differences between

394   individual *Scurria* effects versus total effects estimated in the polyculture (to test for additivity of

395   effects), were analyzed with a Wilcoxon-Mann-Whitney test independently for all response

396   variables. All analyses were conducted in the R-software environment (R Development Core

397   Team 2018).

398

399   RESULTS

400   *Geographic co-occurrences of the Scurria species*

401   The abundance of *S. viridula*, sampled across a large part of its geographic range, was fairly

402   constant in the equatorward (northern) section, with densities of ca. 1 individual/m^2 yet highly

403   variable around the range edge (red line in Fig. 2). Over the large geographic scale, the

404   abundance of *S. zebrina* mirrored the spatial patterns of abundance of *S. viridula* across its

405   geographic range (blue line in Fig. 2), with high among-site variability within the range overlap.

406   In fact, within the range overlap region, the 30-32°S section, both species reached the highest

407   densities observed across our regional surveys, albeit at different sites. Long-term, seasonal,

408   sampling (1998 to 2014) conducted in the range overlap at Punta Talca (30.92°S) showed an

409   increase in *S. viridula* density from 2009 (previous sampling was in 2005) to 2014 (last seasonal

410   sampling), but with large inter-annual fluctuations (see **Fig. S1A** in **Appendix S4**). The density

411   of *S. zebrina* at the overlap site also exhibited strong inter-annual fluctuations that were

412   positively correlated with *S. viridula* between 2004 and 2014 (Kendall's tau= 0.1145, P

413   <0.0001), suggesting both species are affected in similar direction by environmental fluctuations

414   at this site. No linear relationship between species densities was detected (Pearson's *r*=-0.012,

415   P=0.835). At Las Cruces (33.5°S), our experimental locality poleward of the range overlap, *S.*

416   *viridula* has maintained low densities, since we first observed it in 2013 (see red line in **Fig. S1B**

417   in **Appendix S4**), in comparison to *S. zebrina,* which has maintained a persistently moderate

418   abundance (see blue line in **Fig. S1B** in **Appendix S4**). There was no correlation in species

419   temporal fluctuations across years at this site (Kendall's tau= 0.0972, P = 0.1216), nor between

420   the magnitude of density fluctuations (Pearson´s *r*=0.1062, P=0.240). Based on these results, co-

421   occurrence of the *Scurria* species at their range overlap at about ~30°S seems to date from at

422   least 1999 when we made the first observations, while at about 33°S, the new leading edge of *S.*

423   *viridula*, co-occurrence appears to have started more recently (around 2013).

424

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

426   The magnitude and direction of the individual *per capita* effects (DI) that *Scurria viridula* and

427   *S. zebrina* had on the abundance of dominant sessile species and availability of bare rock were,

428   generally, equivalent across the region (red and blue symbols, respectively, in Fig. 3A, B and C).

429   Specifically, both *Scurria* species increased significantly bare rock cover i.e. 95% CI bars do not

430   cross zero, production (Fig. 3A)*,* with   comparable magnitude between 'native' (= within their

431   historical distributional range) and range overlap (North_SV *vs* RO_SV and South_SZ *vs*

432   RO_SZ, for *S. viridula* and *S. zebrina*, respectively). Thus, no indication of *Scurria per capita*

433   depression on bare rock availability was observed at their range edges. In the polyculture, where

434   both species were included together (brown diamond, Fig. 3A), the average *per capita* increase

435   in bare rock (averaging across species) was similar to individual *Scurria* effects at that latitude

436   (RO_Polyculture *vs* RO_SV and RO_SZ in Fig.3A). Thus, no significant differences were

437   observed between treatments in the *per capita* increase of bare rock cover at the geographic

438   ranges considered (see **Table S1a** in **Appendix S5**). However, the total increase in bare rock

439   availability estimated in the polyculture was lower than that expected by an additive (sum) model

440   of the *per capita* effect of two individual *Scurria* limpets i.e. the interaction does lead to

441   alteration of feeding effects on the provision of bare rock (Fig. 3D, Wilcoxon test: W=0.001;

442   P=0.00018). At all sites, the herbivore guild, considering all species foraging in control areas,

443   significantly increased availability of bare rock (black symbols in Fig 3A), but the effect was 3-4

444   times larger at the range overlap than at the sites north or south (Fig. 3A, **Table S2a** in

445   **Appendix S5**). This pattern corresponds well with the absolute increase in bare rock recorded in

446   open plots (control areas), where all herbivores had access, observed at the range overlap (**Fig.**

447   **S1A** in **Appendix S6**).

448   Both species had significantly reduced green ephemeral algae cover (mainly *Ulva rigida, U.*

449   *compressa, Blidingia minima* and *Ulothrix* sp.) at their native ranges, as well as the region of

450   overlap (Fig. 3B). However, it must be noted that *S. viridula* had a larger reduction of green

451   algae cover at the native, equatorward location (-0.006 % $\times$ individual $\times$ day^{-1}), compared to

452   effects observed at the range overlap site (i.e. -0.0038% $\times$ individual $\times$ day^{-1}) (compare

453   North_SV vs RO_SV in Fig. 3B, and see **Table S1b** in **Appendix S5**). The *S. viridula* effects

454   were also higher than the effect of *S. zebrina* at its native, poleward site (North_SV vs South_SZ;

455   Fig. 3B, **Table S1b** in **Appendix S5**). In contrast, the limpet *S. zebrina* had asignificantly higher

456   *per capita* reduction effect of green algae abundance at the range overlap compared with the

457   poleward site (RO_SZ vs South_SZ; Fig. 3B, **Table S1b**). Thus, there was a depression of

458   individual effects of   green algae at the range overlap of *S. viridula* but not *S. zebrina*. The

459   average *per capita* reduction of green algae cover in the polyculture with both species was larger

460   only compared with *S. viridula* enclosures at the range overlap, (Fig. 3B, **Table S1b** in

461   **Appendix S5**). The sum of both individual *Scurria* on the reduction of green algal cover was

462   higher than the total effect estimated for the polyculture (Fig. 3D, Wilcoxon test: W=100;

463   P<0.001) indicating a non-additive *Scurria* effect. The herbivore guild drove an important

464   reduction of green algal cover at all sites, which appeared larger at the region of overlap (black

465   symbols, RO_Control in Fig. 3B,). However, differences were not significant when compared to

466   the total reduction of algal cover at the sites north and south of the range overlap (**Table S2b** in

467   **Appendix S5**). Corresponding with the general pattern of herbivore reduction of green algae, we

468   observed an absolute reduction in total algal cover in the control areas at the range overlap and

469   specifically when compared with the southern site exclusive of *S. zebrina* (**Fig. S1B** in

470   **Appendix S6**).

471   The effects of the two *Scurria* species on abundance of the ephemeral red alga *Pyropia* sp. at

472   their native ranges were qualitatively similar i.e. a reduction in cover of similar magnitude (Fig.

473   3C), but the effect was significant only for *S. zebrina* in the southern site i.e. 95% CI do not cross

474   zero value. At the range overlap, the *per capita* reduction in *Pyropia* sp. abundance by both

475   Scurria species was diminished and neither had significant effects on this algal cover. Average

476   *per capita* reduction in *Pyropia* sp. cover in the polyculture was similar to the effects of both

477   *Scurria* species when isolated (Fig. 3C, **Table S1c** in **Appendix S5**). Thus, there was an additive

478   effect of both *Scurria* species on this alga i.e. there were no differences between the sum of

479   individual species effect and total effect estimated in the polyculture (Fig. 3D Wilcoxon test:

480   W=72, P=0.104). Reductions in *Pyropia* sp. cover in control areas by the entire herbivore guild,

481   were significant and similar at the poleward site and the region of overlap (black symbols,

482   RO_Control vs South_Control in Fig. 3C, **Table S2c** in **Appendix S5**), but this effects was

483   nearly zero at the equatorward site (North_Control; Fig. 3C). In concordance with this result, we

484   found that absolute abundance of *Pyropia* sp. inside control plots, open to all herbivores, was

485   higher in the northern site than the others (**Fig. S1C** in **Appendix S6**).

486

487   *Herbivore effects on community composition*

488   *Multivariate patterns.* - The effects of both *Scurria* species on intertidal community

489   composition i.e. cover of algae and sessile invertebrates, were relatively similar across sites over

490   the 13-month period of the field experiments (Fig. 4). Fences used in herbivore

491   enclosure/exclusion areas had no effect on community composition in our field experiments,

492   because control and procedural control had similar community structure (see **Fig. S1A** in

493   **Appendix S7**). To the north of and in the overlap region, species composition inside *S. viridula*

494   (SV) and *S. zebrina* (SZ) enclosures (red and blue triangles in Fig. 4A and B) were significantly

495   different from herbivore exclusions (green squares in Fig. 4A and B, respectively,

496   PERMANOVA: <u>North</u> ($F_{3,76}$=6.65,P=**0.001**); Tukey's *post hoc*: SV *vs* Exclusion: diff=-0.115;

497   P=**0.040**; <u>Range Overlap</u> ($F_{5,85}$=8.47,P=**0.001**); SV *vs* Exclusion: diff=-0.1654, P=**0.014**; SZ *vs*

498   Exclusion: diff=-0.206, P= **0.017**; Polyculture *vs* Exclusion: diff=0.1956, P=**0.028**). Poleward of

499   the range overlap, control and exclusion plots differed widely and significantly as well (Tukey's

500   *post hoc*: diff= -0235; P=**0.004**), but the post-hoc comparison showed that composition of the

501   sessile community within *S. zebrina* enclosures was significantly different to controls but not

502   exclusions (PERMANOVA: <u>South</u> ($F_{3,76}$=4.775, P=**0.02**); Tukey's *post hoc*: SZ *vs* Control:

503   diff=0.715, P=**0.016;** SZ *vs* Excl: diff=0.25; P=0.218). In the polyculture treatment, we observed

504   a similar pattern in community composition compared to individual *Scurria* enclosures and

505   controls (Brown diamonds in Fig. 4B, PERMANOVA Tukey's *post hoc*: Polyculture *vs* SV:

506   diff=0.040, P=0.806; Polyculture *vs* SZ: diff=-0.051, P=0.976; Polyculture *vs* Control:

507   diff=0.048, P=0.980*)*.

508   *Effects on species richness and diversity. -* The *per capita* effects of individual *Scurria* species

509   on sessile and mobile community richness and diversity (Shannon's H) were heterogeneous

510   across the region. As before, control and procedural control had similar species richness and

511   diversity, thus we assume there were no artifacts from fences in our field experiments (see **Figs.**

512   **S1B** and **C** in **Appendix S7**). Both *S. viridula* (red symbols) and *S. zebrina* (blue symbols) had a

513   significant i.e. 95% CI bars do not cross zero value, reduction on species richness and diversity

514   at the experimental site outside the range overlap (see Fig. 5A and B). At the range overlap, *S.*

515   *viridula* drove a reduction in the magnitude of effects on species richness and diversity compared

516   with its effect at the equatorward site (RO_SV *vs* North_SV in Fig. 5A & B, **Table S1d&e** in

517   **Appendix S5**). In contrast, *S. zebrina* reduced diversity at the range overlap to a similar extent as

518   in the poleward site (RO_SZ vs South_SZ Fig. 5 B **Table S1d&e**), but reduction in species

519   richness was not significant at this site (Fig. 5A). In the polyculture, where both species were

520   enclosed together, there was a significant reduction only on diversity, resembling the pattern

521   found for *S. viridula* at the range overlap, but we found significant differences in the magnitude

522   of the reduction in diversity between these treatments (Fig. 5B, **Table S1d & e**). There were no

523   differences between the sum of individual species effect and total effect estimated in the

524   polyculture for species richness (Wilcoxon test: W=622, P=0.915) nor diversity (W=624,

525   P=0.898; see Fig. 5C), suggesting an additive reduction of diversity between both *Scurria*

526   species. There was also a net collective reduction of species richness and diversity driven by the

527   entire herbivore guild at the three locations (black circles in Fig. 5A & B). Despite this invariant

528   pattern, especially for effects on species richness, a larger reduction of diversity by the herbivore

529   guild was observed at the range overlap compared to the northern site (Fig. 5B, **Table S2d &e** in

530   **Appendix S5**). This corresponds well with the absolute reduction in diversity in control (open to

531   all herbivores) areas, compared with the invariant pattern for richness, observed at the range

532   overlap (see **Fig. S1D & E** in **Appendix S6**).

533

534   DISCUSSION

535   As species shift their geographic ranges, community regulation pathways may change to a

536   greater or lesser extent and ecosystem functioning may be altered. To guide research in our study

537   system along the mid intertidal rocky shores of central-northern Chile, we hypothesized that the

538   range extension of *Scurria viridula* could become redundant in the recipient community because

539   of its similarity with the local *S. zebrina.* Indeed, such similarity could lead to interference

540   competition and lower individual performances when together than isolated, resulting in non-

541   additive joint effects (Fig.1A). In this manner, addition of the novel species would confer

542   insurance-type of resilience (Mouquet and Loreau 2002) to the local guild. Our results

543   demonstrate that the functional effects of these introductions are complex, that they must be

544   evaluated in comparison with sites beyond the novel range overlap, and that they depend on the

545   community variable that is examined. First, the two focal *Scurria* species had equivalent roles on

546   community composition, and these effects resemble the effects they have at their respective

547   individual ranges. i.e. there was no evidence of depression of *per capita* of effects at range ends.

548   The two species had similar effects on community composition and bare rock provision when

549   species were together than when they were separate (isolated), suggesting the addition of the

550   novel species is redundant within the guild. Second, the strength of the consumptive effects of *S.*

551   *viridula* on green algal cover, and on species richness and diversity declined in a consistent way

552   at the range overlap in line in this case with our hypothesis of depression of *per capita* effects. In

553   contrast, *S. zebrina* varied less in its per capita effect at the range overlap, and even showed a

554   slight increase in the magnitude of its *per capita* negative effects on green ephemeral algae,

555   contrary to our hypothesis expectation. The effects when both species were enclosed together

556   (polycultures), were lower for bare rock provision and green algal cover than those expected by

557   an additive effects model, suggesting that both *Scurria* species interfere with each other at small-

558   scales at the range overlap confirming our predictions. Third, when examining effects on

559   *Pyropia* sp., species richness and diversity, effects in polycultures were similar to those expected

560   by and additive effects model suggesting no interaction of the *Scurria* species. Our results also

561   confirm the hypothesis that *Scurria* co-occurrences, likely by complementarity in foraging, does

562   enhance herbivore guild effects on provision of primary substrate and species diversity (see

563   Fig.1B).

564   Overall, our results provide a strong basis for the presence of local and regional functional

565   redundancy in effects between similar herbivore species. In general, there is a degree of

566   functional compensation (see predictions depicted in Fig. 1B) on bare rock provision and in the

567   control of ephemeral algae within the herbivore guild, and the potential for complementarity in

568   reduction of species diversity at the range overlap. Thus, the novel species co-occurrence may

569   cause a reduction in local community diversity potentially owing to a homogenization of the

570   intertidal community and the herbivore guild structure.

571

572   *Functional equivalence and compensation at local and regional scales*

573   Our results showed that the two focal herbivores had equivalent roles within their respective

574   local geographic ranges, providing evidence that they could compensate each other in their roles

575   at regional scales. However, as *S. zebrina* has not contracted its geographic range, which is

576   documented by previous studies (Aguilera et al. 2013b, 2019b), the formal test of this hypothesis

577   at the regional-level still requires further confirmation. Nonetheless, our study showed that both

578   species have equivalent effects on community composition, abundance of green algae and in bare

579   rock provision across the study region spanning their range overlap and geographic edges. In our

580   study, although we did not consider the late successional stages (i.e. 13-15 months, with presence

581   of corticated algae like *Mazzaella*, *Gelidium* and *Perumytilus*) that typically give rise to strong

582   differences among herbivore functional identities (Aguilera and Navarrete 2012), we were able

583   to detect strong and redundant effects of *Scurria* on early to mid-successional community

584   composition. Despite this equivalence in roles, we found that *S. viridula* control on ephemeral

585   algae, species richness and diversity was much reduced at the range overlap where they co-occur,

586   compared with *S. zebrina* which enhanced control on ephemeral algae at this range. As predicted

587   by theoretical studies (and see Fig.1A), environmental conditions at the range overlap, the former

588   range edge of the poleward expanding species (*S. viridula*), are likely stressful for the focal

589   species (Hampe and Petit 2005, Sexton et al. 2009). In this context, a concurrent study reported

590   that both *Scurria* species experience stressful conditions at sites located in the range overlap, at

591   about 30.5, to 33.4ºS (Broitman et al. 2018). In addition, in our field experiments we found that

592   *Scurria* species have non-additive effects in bare rock provision and green algal control, which

593   may be result of direct interference between species. Thus, it seems probable that the magnitude

594   of effects of *S. viridula* at its range edge can be effectively reduced by stressful conditions, and

595   also by interference with *S. zebrina* thus reducing growth rates (Aguilera et al. 2019b). In this

596   context, previous experimental studies showed that herbivore control on ephemeral algae could

597   be higher in low- than high-upwelling sites (Nielsen & Navarrete 2004). Since Punta Talca,

598   located at the range overlap (RO), is a site with high-upwelling intensity a reduction of *S. zebrina*

599   effects could be expected compared with the poleward site which is less exposed to strong

600   upwelling (Wieters et al. 2003; Tapia et al. 2009). The invariant, or even enhancement (on green

601   algae), in the magnitude of effects of *S. zebrina* at the range overlap compared with the southern

602   site, is surprising in this context and deserves further research.

603

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

605   Functional herbivore guild structure characterized by either functional complementarity or

606 equivalence (i.e. redundancy), can greatly influence resource abundance and community

607 composition at local scales (Duffy et al. 2001, Bellwood et al. 2003, Resetarits and Chalcraft

608 2007, Griffin et al. 2009, Burkepile and Hay 2011, Bennett et al. 2015). Species introduction or

609 range expansion/contraction could impose an alteration in the functional structure of local or

610 resident guilds if novel roles are incorporated into the system (e.g. Duffy et al. 2001, Duffy 2002,

611 Rosenfeld 2002, Bellwood et al. 2006). Our results show that, despite that *S. viridula* diminishes

612 the magnitude of their *per capita* effect at the range overlap, co-occurrence of both *Scurria*

613 species greatly contributed to the net collective effect of the herbivore guild on bare rock

614 production, green algae control and reduction in diversity. In this context, we observed in our

615 experiments that when together in polyculture, total effects of *Scurria* were much reduced on

616 bare rock provision and green algae control compared with an additive model of the individual

617 *Scurria* effects. This implies that to effectively contribute to the total herbivore guild effect at the

618 range overlap, both species may segregate spatially at scales larger than those used in our

619 enclosures. This space partitioning could account for the reduction in deleterious effects of

620 interspecific competition as previously documented in this system (Aguilera et al. 2019b). In

621 general, the contribution to the entire herbivore guild at the range overlap could happen due to

622 both compensatory and complementarity effects (see predictions in Fig 1B), where, as our

623 results show, both *Scurria* species largely contribute to increase bare rock provision and to

624 control the colonization of dominant green algae, a function also shared with other herbivores in

625 the system (Nielsen and Navarrete 2004, Aguilera and Navarrete 2012). For example, *S. viridula*

626   has strong similarity in consumptive effects with herbivores of the mid- and high intertidal zone

627   assemblage such as *Chiton granosus* and *Fissurella crassa* (see **Fig. S1A** in **Appendix S8**).

628   These two species also have wide differences in body size with our focal species (Aguilera and

629   Navarrete 2011, 2012), use different microhabitats (i.e. they use crevices for shelter; Aguilera

630   and Navarrete 2011), and differ in their feeding modes (i.e. "scraping" and "browsing",

631   respectively; Aguilera and Navarrete 2012). Both *Scurria* species have chiefly a

632   "scraping/grazing" mode of feeding (following their radular capabilities; Steneck and Watling

633   1982). The presence or addition of a novel species to a local herbivore guild, such as the site at

634   the range overlap of our focal species, may thus be the main factor bolstering the net collective

635   effect of the intertidal herbivore guild on green algae colonization and bare rock provision. It

636   should be noted that despite diminished effects of *S. viridula* at the range overlap, both *Scurria*

637   species can be considered strong interactors in this system (Paine 1992) given their control of

638   green algae, large bare rock provision and reduction in diversity compared with the other

639   intertidal herbivores even within the sites were they don't coexist (see **Fig. S1A** in **Appendix**

640   **S8**). However, in our experiments we found the focal *Scurria* species were less efficient

641   controlling the red alga *Pyropia* sp. at the range overlap site, which has high growth rates and a

642   life cycle with an encrusting stage (Santelices 1990). This alga seems mostly controlled by the

643   complementary effect of herbivores with a "browser" mode of feeding (i.e. species consuming

644   alga fronds, e.g. *Fissurella crassa*, *Siphonaria lessoni*, *Echinolittorina peruviana*) and other

645   "scraper-grazers" (i.e. those capable of consuming algal spores and plantlets; e.g. *Chiton*

646   *granosus, C. barnesii Scurria ceciliana*, *S. variabilis*) present in the system (see **Fig. S1A** in

647   **Appendix S8**). The herbivore guild seems less efficient in controlling this alga at the northern

648   site. As discussed before, previous studies in this system showed that under persistent upwelling

649   conditions the role of the herbivore guild could be reduced by either high algal growth rate or an

650   increase in consumer-resistant algal cover, and thus convergence in algal abundance between

651   herbivore 'present' versus 'absent' condition may be expected (Nielsen and Navarrete 2004). At

652   the range overlap site (Punta Talca) coastal upwelling is intense (Tapia et al. 2009) compared

653   with the southern (Las Cruces) and northern site (Carrizal Bajo), which are either sheltered or

654   under weak, semi-permanent upwelling, respectively, (Tapia et al. 2009, Meneghesso et al.

655   2020). Differences in community composition recorded inside exclusion, herbivore-free, areas at

656   our experimental sites (see **Fig. S2** in **Appendix S7**) may well reflect these oceanographic

657   differences (see also Broitman et al. 2001). In our study, the intertidal herbivore guild exerted a

658   strong control of ephemeral algae colonization at the range overlap likely aided by co-occurrence

659   of the *Scurria* species. Therefore, both top-down and bottom-up processes in this system seems

660   especially relevant to explain differences in community composition (Menge et al. 1996, 1999)

661   as those presented in our study (and see comparison between control and exclusion areas in **Fig.**

662   **S2** in **Appendix S7**).

663

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

665   Complementarity in feeding habits has been invoked as the main mechanism behind the

666   detrimental impacts of tropical marine herbivores expanding their ranges and reducing algal

667   production in temperate systems (Ling 2008, Vergés et al. 2014, Ling et al. 2015). As we

668   observed in our system, co-occurrence of previously parapatric herbivore species can translate

669   into a net reduction in community diversity, hence a potential harbinger of functional

670   homogenization (Olden and Poff 2003, Olden and Rooney 2006). Our main results suggest that

671   an expansion of the area where *Scurria* species coexist could progressively reinforce the

672   production of bare space, triggering a reduction in community spatial heterogeneity and

673   productivity. As evidence of this process, range expansion and consumption intensification have

674   led to rapid phase shifts in temperate subtidal ecosystems through the loss of habitat-forming

675   species like kelps (Vergés et al. 2014, Ling et al. 2015), potentially slowing down successional

676   trajectories (Lubchenco 1978).

677   The impact of novel or introduced species on local ecosystem structure and functioning is an

678   important concern in both terrestrial and aquatic ecosystems (e.g. Schoener and Spiller 1996,

679   Stachowicz and Tilman 2005, Wardle et al. 2011, Simberloff et al. 2013, Early et al. 2016).

680   Similarity or differences in functional traits between introduced species versus residents, seems

681   one of the main determinants of successful establishment of alien species in novel ranges

682   (Divíšek et al. 2018). Our results provide important insights about the functional consequences

683   of the arrival of novel species to local communities, in terms of impacts on resources and

684   diversity inputs on consumer guild structure, following the wholesale species range shifts taking

685   place in the oceans worldwide (Sorte et al. 2010, Sorte 2013, Bradley et al. 2015, Poloczanska et

686   al. 2016). In particular, we highlight the potential for regional functional compensation when the

687   new species have similar roles to the resident consumer, and the intensification of collective

688   consumer impacts when newcomers are complementary to the local guild which could produce

689   significant alteration of the community structure. The recent range expansion of *S. viridula* and

690   the apparent lack of range contraction by *S. zebrina* signals that effective functional

691   compensation between these herbivores may take place. Such functional compensation over

692   regional scales could be a source of stability of ecosystem functioning in the next decades, a

693   process which deserves further consideration. Indeed, herbivores can promote community

694   stability after disturbances through trophic compensation (e.g. Ghedini et al. 2015, Kordas et al.

Aguilera et al.

695 2017), but a different effect could result from an over-representation of functionally equivalent

696 species within the guild as the co-occurrence of *Scurria* shown in our study (see also **Fig. S1** in

697 **Appendix S8**) which can reduce functional diversity of consumers and resources. In fact, the

698 functional diversity of consumers modulates resource diversity and composition (e.g. Olff and

699 Ritchie 1998, Duffy 2002, Schmitz 2009, Bennett et al. 2015), and also has a key role in the

700 stability of ecosystem functioning (Duffy 2003, Ghedini et al. 2015). As the functional structure

701 and the potential resilience of ecosystems can also be eroded by human exploitation (Kéfi et al.

702 2016), it is urgent to understand the responses of equivalent species to different anthropogenic

703 drivers at regional scales in order to manage and predict the alteration of critical ecosystem

704 functions in the face of Global Change scenarios.

705

717

718 DATA ACCESSIBILITY STATEMENT
719 Data will be fully available upon author request.
720

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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).

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1040 **Figure 2.** Density (ind./m^2) (± EE) of *Scurria viridula* (red) and *S. zebrina* (blue) along the coast

1041 of Chile from 18°S to 42°S. For *S. zebrina*, this corresponds to the complete geographic range of

1042 the species. Note the range overlap (RO) of both species is from 30°S to 33°S. The range of *S.*

1043 *viridula* expansion is from 32.31°S to 33.7°S.

1044

1045 **Figure 3.** *Per capita* individual effect of *Scurria viridula, S. zebrina* and net collective effect of

1046 the herbivore guild (A-C), and additive versus joint effect of *Scurria* species (D) on bare rock,

1047 green ephemeral algae species (*Ulva rigida, U. compressa, Ulothrix sp, Blidingia minina*) and

1048 *Pyropia* sp., estimated at the range overlap (RO) of the *Scurria* species, and north and south of

1049 this range. All data are means and 95% CIs, which were estimated through bootstrapping. Red

1050 triangles: *S viridula* enclosures; Blue triangles: *S. zebrina* enclosures; Brown diamond:

1051 'Polyculture' (*S viridula + S. zebrina*). In D), additive effects correspond to the sum of *per capita*

1052 individual *Scurria* effects (magenta triangle) estimated in field experiments conducted at RO,

1053 whereas joint *Scurria per capita* effects correspond to those estimated in the 'polyculture'

1054 treatment (brown diamond) in the same experimental site.

1055

1056 **Figure 4.** Non-metric Multidimensional scaling (nMDS) of species composition (sessile and

1057 mobile species diversity) recorded within experimental replicate areas (n=6) from field

1058 experiments (averaged for over the 13 months of study) conducted at the equatorward site

1059 (Carrizal Bajo) (A), at the range overlap (Punta Talca) (RO) (B), and at the poleward site (Las

1060 Cruces) (C) of the *Scurria* species. EXC: herbivore exclusion, POLY: Polyculture; Enclo_SV:

1061 Enclosures of *S. viridula*; Enclo_SZ: Enclosures of *S. zebrina*.

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1063 **Figure 5.** *Per capita* individual effect of *Scurria viridula* and *S. zebrina*, and net collective effect

1064 of the guild (A-B), and additive versus joint effect of *Scurria* species (C) on richness and

1065 diversity (Shannon, H' index) estimated at the range overlap (RO), and north and south of this

1066 range exclusive to each *Scurria* species. All data are means and 95% CIs, which were estimated
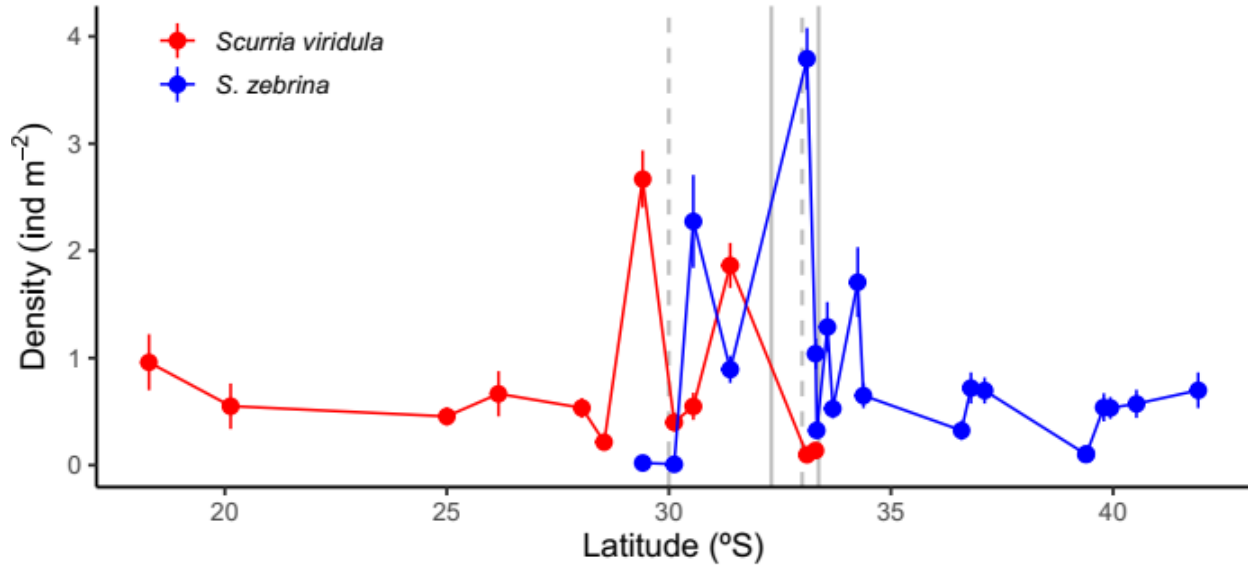
1067 through bootstrapping.

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1090 **Figures**

1091 **Figure 1.**
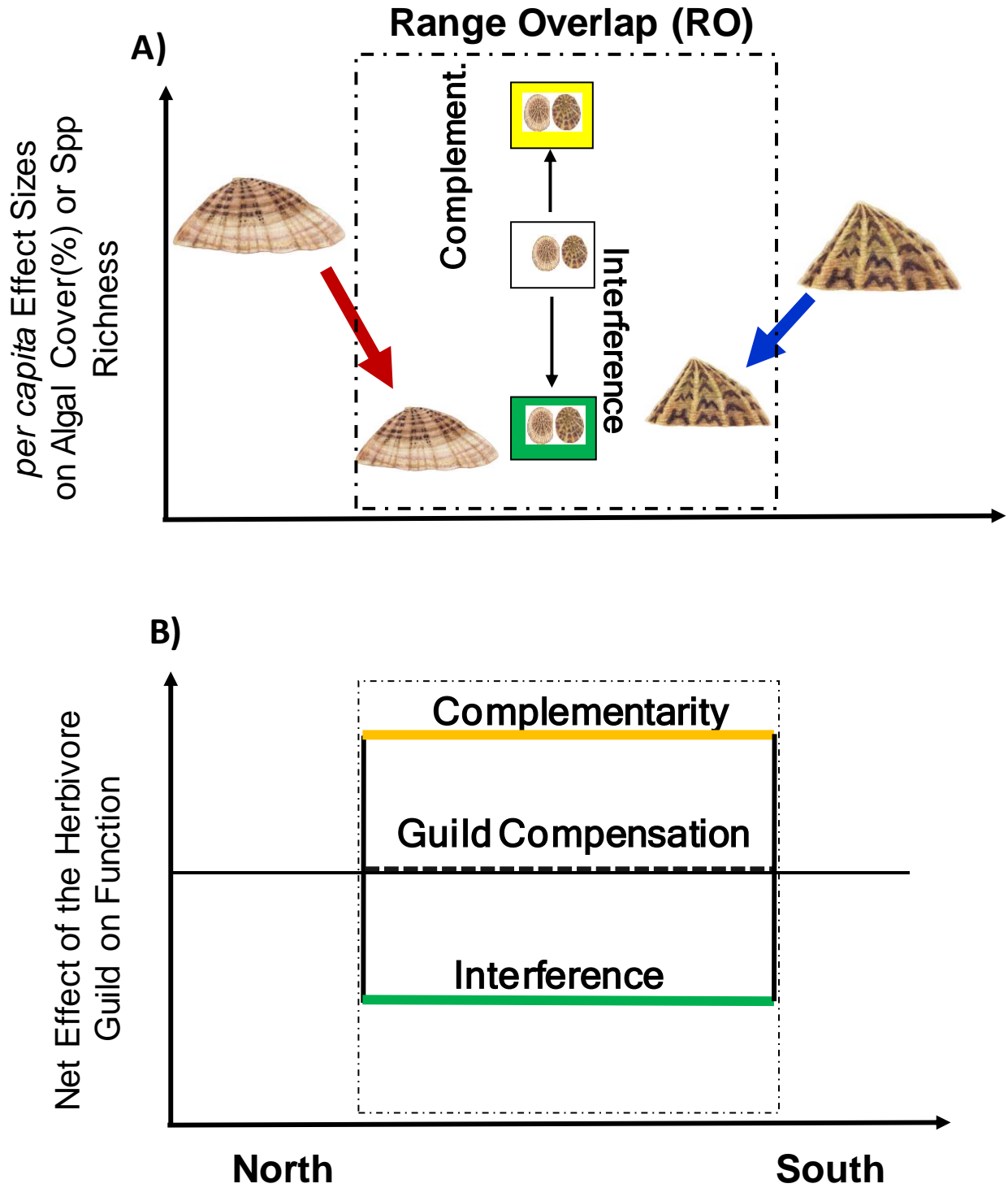
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1094 **Figure 2.**

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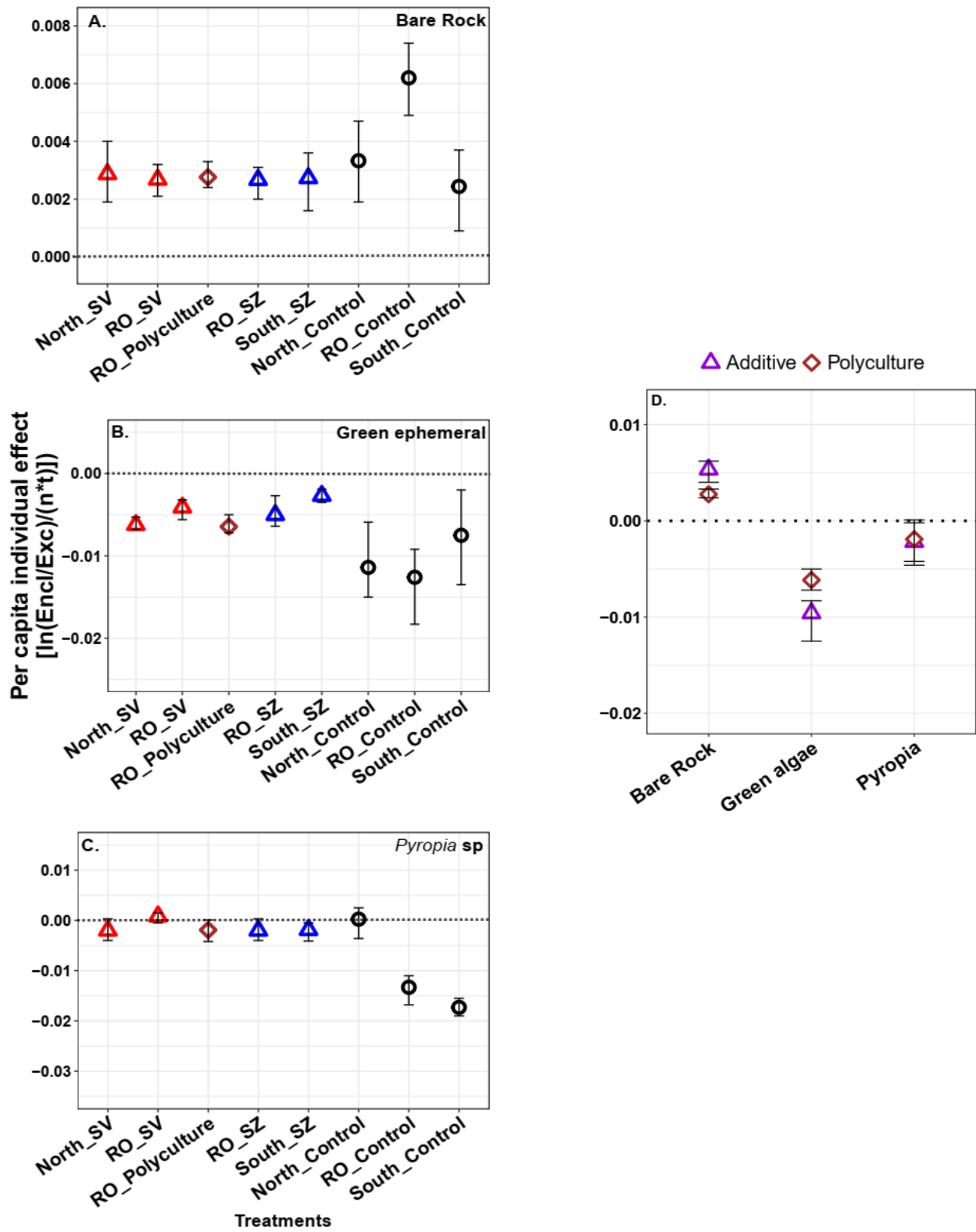1097
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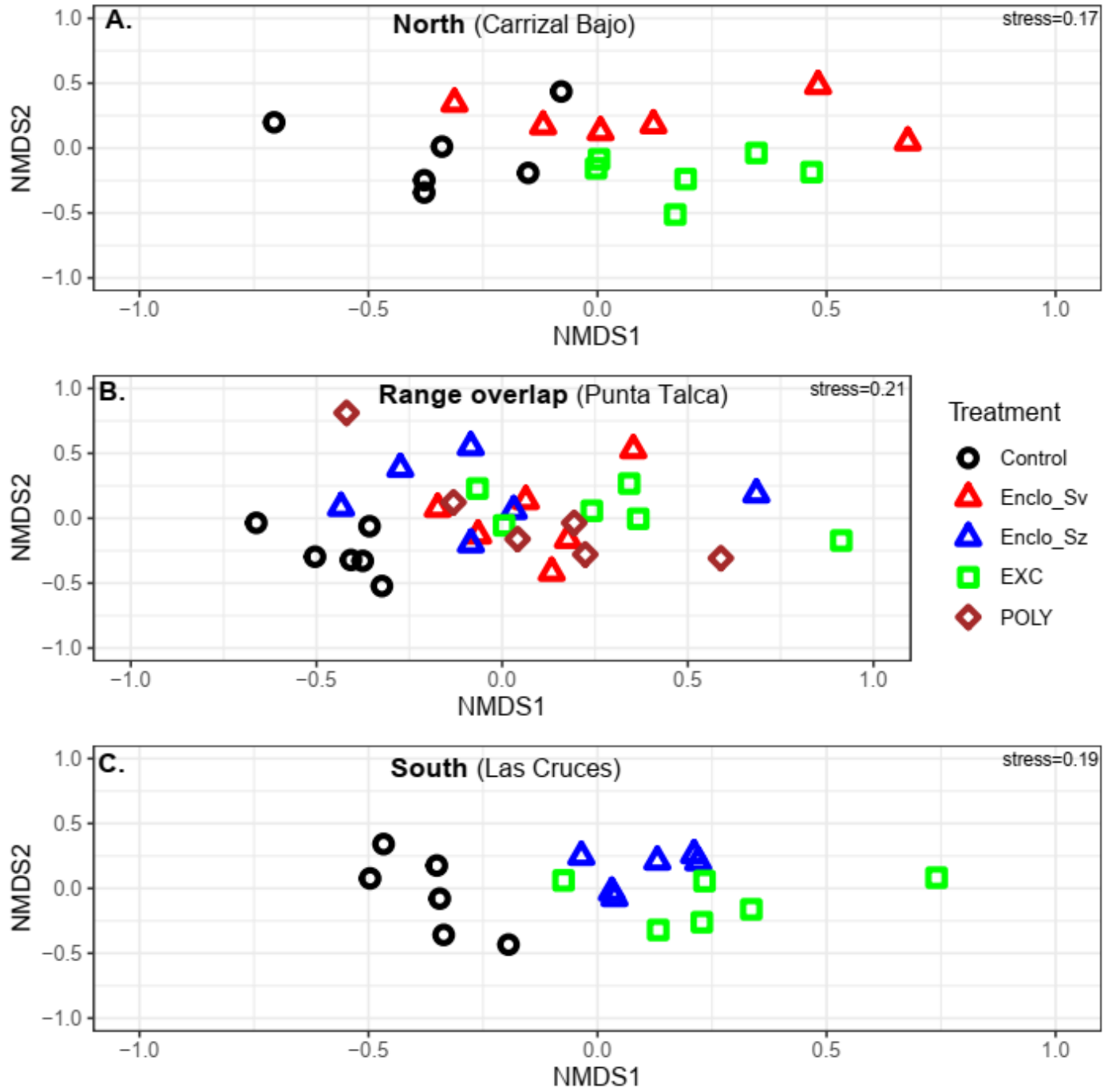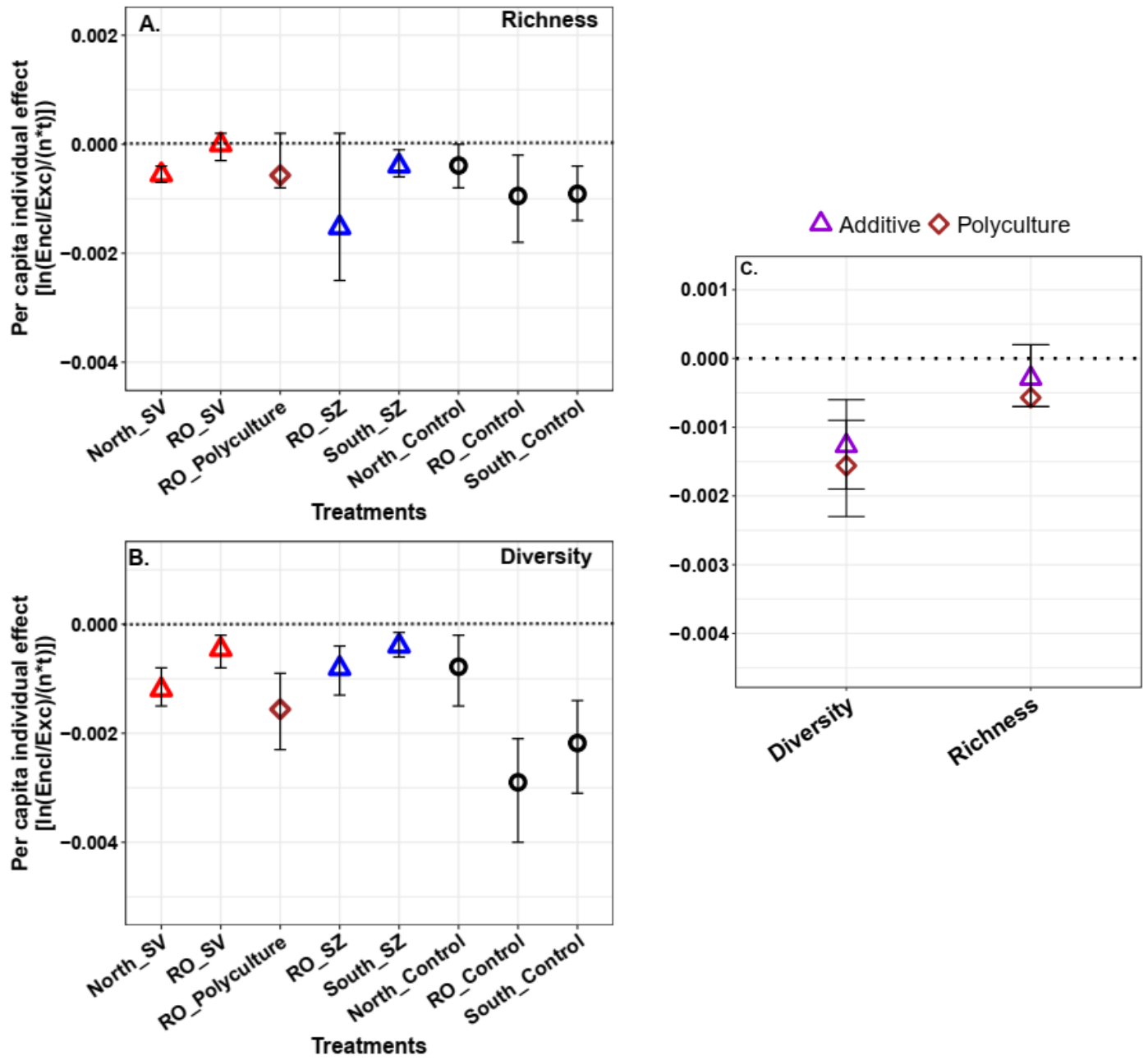1112   **Figure 3.**

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1115 **Figure 4.**

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1121 **Figure 5.**

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