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1 **Experimental and survey-based evidences for effective biotic**
2 **resistance by predators in ports**

3
4 Jean-Charles Leclerc^{1,*}, Frédérique Viard², Antonio Brante¹

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6 ¹Universidad Católica de la Santísima Concepción, Departamento de Ecología, Facultad de Ciencias,
7 Centro de Investigación en Biodiversidad y Ambientes Sustentables (CIBAS), Casilla 297, Concepción,
8 Chile

9 ²Sorbonne Université, CNRS, UMR 7144 AD2M, Station Biologique de Roscoff, Place Georges Teissier,
10 29680 Roscoff, France

11 *Correspondence: leclercjc@gmail.com

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13
14
15 **Running headline:** Consumptive biotic resistance in ports

16

17

18 **Abstract**

19 Of the suite of species interactions involved in biotic resistance to species invasions, predation can
20 have complex outcomes according to the theoretical and empirical framework of community
21 ecology. In this study, we aimed to determine the likelihood of consumptive biotic resistance within
22 fouling communities in four ports of central Chile. Notably, we examined the influence of micro-
23 (> 1-2 mm, <1-2 cm) and macro- (> 1-2 cm) predators, with a particular focus on their effects on
24 non-indigenous species (NIS). Experimental and observational approaches were combined. An
25 exclusion experiment was carried out over four months to examine predator effect on the early
26 establishment of new assemblages on settlement panels. Later successional stages upon panels
27 were examined over a total of twenty-six months and supported by rapid assessment surveys in the
28 surrounding habitats. Community structure was significantly influenced by the exclusion
29 treatments. Macropredators reduced the fouling biomass and abundance, although conflicting
30 patterns emerged from the exclusion of both categories of predators. Altogether, predators reduced
31 the abundance of most NIS and cryptogenic species, some of them being only observed when the
32 two categories of predators were excluded – a pattern generally sustained over the long-term
33 dynamics in community development. Our results show an effective consumptive biotic resistance,
34 furthermore possibly dependent on predator size. Further work is however needed to determine the
35 influence of the functional diversity of natural enemies on the efficiency of biotic resistance and
36 its interplay with other biotic interactions (competition or mutualism). A comprehensive
37 understanding of these process should in turn help defining management strategies in a context of
38 habitat modification and species loss.

39 **Keywords:** Complementarity, Consumptive resistance, Enemy release, Exclusion experiment
40 Long-term survey, Marine infrastructure, Non-Indigenous Species, Species interactions.

41 **Introduction**

42
43 In ecological studies, the performance of native communities in buffering the establishment of
44 newly introduced species has been experimentally unexplored until the 1990s (Kimbrow et al. 2013;
45 Levine et al. 2004; Papacostas et al. 2017), although this process caught attention much earlier
46 (Elton 1958). The biotic resistance hypothesis predicts that the establishment and spread of
47 introduced species can fail locally in diverse communities owing to interactions with native species
48 (Bulleri et al. 2008; Lockwood et al. 2013). The most commonly explored mechanism underlying
49 biotic resistance has been competition, where a more diverse assemblages of native species is
50 assumed to utilize resources more completely than a less diverse community (Davis et al. 2000).
51 Other mechanisms such as predation *lato sensu* (including herbivory and parasitism, Morin 2011)
52 and mutualism may be particularly important (Lockwood et al. 2013). Beyond regulation of prey
53 populations, predation may mediate competitive interactions and in turn affect species abundance
54 and community structure (Morin 2011). Not surprisingly then, trophic interactions studies and food
55 web theory were required to alleviate the diversity-stability debate and to understand the underlying
56 mechanisms, such as productivity, connectance, interaction strength and opportunism (Connell and
57 Ghedini 2015; Rooney and McCann 2012). Likewise, invasion ecology should benefit from a more
58 comprehensive understanding of the direct and indirect effects of multiple enemies upon introduced
59 species, especially in the framework of the biotic resistance paradigm (Caselle et al. 2018; Smith-
60 Ramesh et al. 2017).

61 In the marine realm, bioinvasions are increasing in response to expanding transportation
62 network, habitat losses and climate change (Chan et al. 2019; Giakoumi and Pey 2017; Seebens et
63 al. 2016). Extra-range dispersal of NIS involve diverse vectors (crafts and ships, marine debris,
64 cultivated and bait species) and pathways, such as mass dispersal shipping routes and physical

65 corridors due to the ‘ocean sprawl’ (i.e., artificial structures built along natural shores) (e.g. Bishop
66 et al. 2017; Seebens et al. 2016). Regarding these conspicuous risks of introduction and
67 establishment of new species, the apparent resistance of particular habitats or regions to species
68 invasions is particularly meaningful to examine in order to determine the underlying ecological
69 processes (Freestone et al. 2013), and thus to build up relevant and effective management strategies
70 (Caselle et al. 2018; Dafforn et al. 2015).

71 Beyond alteration of species connectivity, the ocean sprawl is directly associated with
72 habitat degradation and loss (Bishop et al. 2017). Artificial habitats, such as ports, do not surrogate
73 the diversity and community structure of neighbouring rocky reefs. These habitats constitute a
74 haven for novel species interactions – notably involving non-indigenous species (NIS) – the
75 direction and intensity of which are poorly understood (Chapman and Underwood 2011; Leclerc
76 and Viard 2018; Rogers et al. 2016). Exclusion experiments in such habitats are fortunately
77 flourishing and provide important insights into spatial and temporal variations in consumer effects
78 upon fouling development (e.g. Dumont et al. 2011b; Giachetti et al. 2019; Lavender et al. 2017).
79 Despite invasion theories which predict that a species predisposition to predation may depend on
80 its evolutionary history (e.g. "enemy release" vs. "new association", Colautti et al. 2004; Hokkanen
81 and Pimentel 1989), there has been seldom study that separated consumer effects upon marine
82 native species and NIS (Leclerc and Viard 2018; Rogers et al. 2016). Likewise, there is mounting
83 evidence that all predators do not equally influence fouling community development at local scales
84 (notably depending on their functional/taxonomic group and size) (Lavender et al. 2014; Osman
85 and Whitlatch 1998; Rogers et al. 2016) and yet the implications of such findings for consumptive
86 biotic resistance are so far elusive in marine systems.

87 In the SE Pacific and more specifically along the Chilean coastline, the number and extent
88 of artificial structures have dramatically expanded over the last decades in order to promote
89 economic development through shipping trade, mining and aquaculture, but also to protect coastal
90 populations from storms and tsunamis (Aguilera 2018). In this region, shipping pathways have
91 been assumed to be responsible for the introduction of 30-38 % of the NIS currently established
92 (Castilla and Neill 2009). A recent study comparing local and international ports along 100s km in
93 central Chile did not find any evidence that these ports differed in propagule pressure and NIS
94 abundances, suggesting a role for other introduction vectors such as aquaculture or a rapid spread
95 from international to local ports (Leclerc et al. 2018). This latter work also revealed that most NIS,
96 albeit relatively diverse, were scarce, generally restricted to cryptic micro-habitats (out of the reach
97 of large predators) and less effective in colonizing bare substrata than native taxa. In addition,
98 diverse native predators were observed but their influence (indirectly inferred by the abundance of
99 grazing marks) seemingly varied among sites. As such, the authors pointed out that biotic resistance
100 due to consumptive interactions deserved further dedicated investigation.

101 The present study aimed to determine the influence of predators on the diversity and
102 structure of fouling communities in Chilean ports. Combining both experimental and observational
103 approaches, we gathered data from rapid assessment surveys, an exclusion experiment and a
104 community development experiment within three sites (out of four, see methods) of central Chile.
105 Exclusion experiments targeting either macro- (> 1-2 cm) and micro-predators (> 1-2 mm) or
106 macro-predators only (i.e., leaving only micro-predators as putative consumers) were run to (i)
107 quantify their influence on early community development, upon settlement panels and (ii) whether
108 their effects were concentrated upon specific prey categories (i.e., taxonomic and functional
109 groups, native versus non-indigenous taxa). The outcomes (i.e., targeted preys) of this short term

110 experiment were then compared with abundance data from field surveys and from the established
111 panel community, in order to determine whether consumptive biotic resistance upon specific
112 taxa/groups is sustained over time and to give insights into other presumable indirect effects
113 (competition, facilitation) influencing the overall biotic resistance of the study communities.

114

115 **Materials & Methods**

116

117 The study was performed along approximately 100 km of coastline in the Biobío region
118 (Chile) within four ports: Coronel (37.0304°S, 73.1540°W), San Vicente (36.7591°S, 73.1551°W),
119 Lirquén (36.7094°S, 72.9829°W) and Coliumo (36.5377°S, 72.9571°W).

120

121 Predator exclusion design

122 A series of settlement panels (black polypropylene, 15 × 15 cm) were deployed vertically
123 upon two experimental units (110 × 100 cm) made of a plastic fence (mesh 2.5 × 2.5 cm) covered
124 by a mosquito net (ca. 1-2 mm mesh), on two randomly selected pilings (in direct contact with the
125 bottom) separated by 20-50 m within each port, at ca. – 4 m. Each unit was composed of 15 panels,
126 randomly organized as triplicates undergoing five treatments: caged, cage-control, screened,
127 screen-control and open. Cages (20 × 20 × 12 cm) were constructed from galvanized steel fence
128 (diagonal mesh of ca. 2 cm), previously protected by water based-anticorrosive paint. Cage-
129 controls were cages lacking a roof and with two windows (40 x 60 mm) cut out on the sides (Leclerc
130 and Viard 2018). Screened and screen-control treatments were respectively made of the same
131 matrix used for caged and cage-control treatments, but covered by a nylon mosquito net (1-2 mm
132 mesh). Open treatments were panels without cages.

133 The experiment was conducted over four months, between late December 2017 and late
134 March 2018 (austral summer), a season favourable to the settlement of juveniles of many
135 invertebrate species, including NIS, in the study area (Leclerc et al. 2018) and to the maintenance
136 of the experimental units (a first trial was attempted in the previous winter but most cages were
137 damaged by wave action). To prevent flow and recruitment disruption by fouling organisms, cages
138 and meshes were cleaned every 4 weeks using a plastic brush. This cleaning frequency was chosen
139 based on previous knowledge and observations made on pilings with this type of thin material (for
140 instance, lower colonization than on floating pontoons; Leclerc et al., in prep, (Leclerc and Viard
141 2018)). It is noteworthy that at each cleaning occasion, only biofilm and a few vines (e.g.
142 *Bougainvillia muscus*) were observed on the fences and meshes, suggesting that the flow had been
143 properly maintained between consecutive cleaning dates (i.e., limited obstruction, JCL, pers. obs.).
144 By the end of the trial, experimental units were retrieved by divers. On land, panels were quickly
145 collected and cleared from cable tiles. A few screened cages were damaged (2 in Lirquén and 1 in
146 Coliumo). Because mobile predators were recorded on the panels of these screened cages, these
147 replicates were put aside. All the other panels were kept in individual plastic rubble-bags within
148 seawater tanks until being processed in the laboratory.

149

150 Community development upon panels and predators characterization

151 The predator exclusion experiment targeted the early community development. In order to
152 put the results into a longer term perspective, we analysed the community development upon panels
153 deployed in the field over a 26 months-period. In August 2016 (first trial) and March 2017 (second
154 trial), 20 settlement panels (*cf.*, above) were deployed upon two experimental units (90 x 100 cm),
155 at two plots (pilings) per port. After 1, 3, 7, 13 and 19 months, eight panels (four at random per
156 plot) were retrieved using meshed bags, and transported within seawater to the laboratory.

157 In order to complement the settlement panel datasets and to get a more comprehensive list
158 of putative macro-predators of the study communities, we used rapid assessment surveys conducted
159 by the same diver (JCL) in November 2016 and June 2017 in all localities. During 30 minutes, all
160 taxa (including fouling species and mobile taxa > 10 mm) encountered were given a score of semi-
161 abundance according to the SACFOR scale (Superabundant, Abundant, Common, Frequent,
162 Occasional, Rare). These surveys were conducted between ca. – 1.5 m and – 5 m, and usually over
163 the horizontal distance between the experimental plots depending on the site conformation.

164

165 Data collection

166 In the laboratory, panels were weighted (corrected wet mass) and then left in seawater tanks
167 until sessile fauna returned to their natural untense state. Sessile taxa (mostly fauna, see Results)
168 were identified, under a dissecting microscope, at the lowest taxonomic level possible by the same
169 observer (JCL). The same observer made at the same time a rough identification of the mobile
170 fauna, incl. micro-predators: amphipods, annelids, shrimps, crabs, likely including macro-predator
171 juveniles, were observed. To avoid edge effects, a 15 mm perimeter was excluded from the
172 analysis. The abundances of the sessile taxa were assessed using cover. Species cover was
173 estimated under 100 random intersection points out of 169 created between evenly spaced lengths
174 of string of quadrat within the working area (120 × 120 mm). Any species identified out of these
175 intersection points was given a cover of 0.5%. Species layering was taken into account, therefore
176 the total cover frequently exceeded 100%. Voucher specimens were collected and preserved in
177 95% EtOH in order to fill in a local reference collection (*cf.*, Leclerc et al., 2018). Taxa were
178 assigned to functional groups based upon their morphology and space occupancy as these traits
179 efficiently classify epibenthic assemblages (Woodin and Jackson 1979). Specimens were also
180 categorized according to their status as ‘native’, ‘non-indigenous’ (NIS), ‘cryptogenic’ or

181 ‘unassigned’ according to the literature and public databases (cf. Leclerc et al. 2018 and references
182 therein). The cryptogenic species, from unknown/uncertain origin, found in this study displayed a
183 cosmopolitan distribution and were potentially non-indigenous to the study area.

184

185 Statistical analyses

186 For the exclusion experiment, patterns in species richness, abundance and community structure
187 as well as species-specific abundances (cover, number) of relevant response variables (selected on
188 the basis of their contribution to community structure, see details below) were examined with a
189 three-way design using PERMANOVAs with 4999 permutations. Factors were ‘treatment’ (fixed,
190 5 levels: open, cage-control, screen-control, caged and screened), ‘site’ (random) and ‘piling’
191 (random, nested with site). Panels, cages and controls were designed to allow sessile fauna
192 colonization through settlement. However, in one site (Coronel), panel colonization was largely
193 due to migration of adult mussels (*Semimytilus algosus*) from the edges of the experimental units
194 – a behaviour strongly limited by cages. Settlement and migration of sessile fauna were thus
195 confounded in this site, which we thus excluded from the analyses. By including the blocking term
196 ‘piling’, part of the total variance was attributed to differences between blocks, thereby reducing
197 the residual unexplained variation (Quinn and Keough 2002). The lowest interaction term
198 ‘treatment × piling (site)’ was however excluded from the main model for two reasons. Firstly, a
199 few screened replicates were damaged and thus excluded from the analyses. The number of
200 replicates was then too small to robustly test for a possible interaction between treatments and
201 pilings. Secondly, and more importantly, with two pilings per site, pairwise comparisons for the
202 most important two-way interaction ‘site × treatment’ (see Results) were limited to a single degree
203 of freedom for each denominator (vs. nine *den. d.f.*, when excluded) and thus could not be made
204 (Anderson et al. 2008). The results of the analyses based on the full model are provided in Table

205 S4, with discussions about their implications on spatial variability in biotic resistance. Univariate
206 analyses were based on Euclidean distance matrices (analogous to the traditional ANOVA)
207 whereas multivariate analyses were based on Bray-Curtis similarity matrices generated from either
208 raw or transformed data. In the case of univariate analyses of the cover and number of individuals,
209 response variables were selected upon their within-site contribution to multivariate structure
210 (SIMPER) at a cut-off level of 90% within at least one treatment. For these response variables, a
211 minimal occurrence of three within at least one Treatment \times Site was considered. Otherwise, the
212 corresponding site was dropped off from the analysis. The homogeneity in univariate or
213 multivariate dispersion was checked among the levels of the interaction term Site \times Treatment
214 using PERMDISP (Anderson et al. 2008). In most cases, no transformation allowed
215 homoscedasticity to be achieved in univariate data, therefore analyses were run on untransformed
216 data (Underwood 1997).

217 As for the long-term survey, patterns in community assembly were examined, within each site,
218 with a three-way design including the factors ‘trial’ (random, 2 levels: 1st vs 2nd), ‘piling’ (random,
219 nested within trial) and ‘age’ (fixed, 5 levels: 1, 3, 7, 13, 19 months). When appropriate,
220 PERMANOVAs were followed by pairwise comparisons and *P*-values were estimated using a
221 Monte Carlo procedure. To make these pairwise tests possible for the most relevant interaction
222 (age \times trial, see Results), the lowest interaction term (age \times piling (trial)) had to be excluded from
223 the model (increasing the degrees of freedom of each denominator from 1 to 13).

224 Univariate analyses were performed either on all variables combined (including unassigned
225 taxa), natives, cryptogenics or NIS. For all multivariate data, PERMANOVA results were
226 supported by ordination using principal coordinate (PCO) analyses and the main taxa or abiotic
227 variables (e.g., bare surface, grazing marks, dead biota) explaining differences among treatments
228 were identified according to their contribution to PCO axes (Anderson et al. 2008). The respective

229 contributions of specific variables to community structure (SIMPER analyses) in each level of the
230 exclusion experiment and of the field survey were determined and considered throughout. All
231 analyses were performed using PRIMER 7 (Anderson et al. 2008).

232

233 **Results**

234 *Diversity of native and non-indigenous sessile taxa across the study ports*

235 Across sites, a total of 56 sessile taxa were identified upon settlement panels used in the
236 exclusion experiment (4 months), largely dominated by fauna (48 taxa). These records included 11
237 non-indigenous and 11 cryptogenic species, of which 4 NIS and 2 cryptogenic taxa were
238 exclusively found under predator exclusion (Table S1). Over the panel community assembly survey
239 (26 months), a similar number of sessile taxa was observed (60 taxa), including 8 NIS and 13
240 cryptogenic species, of which only 1 NIS and 2 cryptogenic species were not observed during the
241 4 months of the exclusion experiment (Table S1). Complete lists and species authorities are
242 provided for sessile taxa in Table S1.

243

244 *Macro-predators reported in the study localities are mostly native*

245 Diverse macro-predators were identified across sites (35 taxa), third of which locally
246 classified as frequent to abundant (Table S2, Figure S5). Of these predators, a total of 18 taxa were
247 observed upon experimental structures by the end of the experiment (Table S2). The vast majority
248 of them (31 taxa; 89%) were native taxa while the four others were unassigned. Locally dominant
249 predators were the native sea urchins *Arbacia dufresnii* and *Tetrapygus niger* in Lirquén, the sea
250 snail *Tegula euryomphala* and the sea star *Patiria chilensis* in Coliumo as well as the barnacle
251 shell-dwelling fish *Hypsoblennius sordidus* in San Vicente, whereas species commonly found

252 across all locations were highly mobile crabs such as *Romaleon setosum*, *Cancer plebejus* and
253 *Taliepus dentatus*.

254

255 *Exclusion treatments influence the fouling community development*

256 Exclusion treatments significantly affected community structure over the four months of
257 the exclusion experiment, across all study sites (Table 1, Table 2, and Table S4). Caged and
258 screened treatments differed from each other, and from all other treatments (Table 1). As compared
259 to cage-control, the caged treatment (i.e., macro-predators exclusion) resulted in fouling
260 assemblages reaching significantly greater biomass (Fig. 1A), and occupying more space in two of
261 three sites (, Fig 1B-C). In contrast, the full exclusion of both macro- and micro-predators (screened
262 treatment versus screen-control) led to variable results among sites (Fig. 1). In particular, the
263 biomass increased significantly in Coliumo only (Fig. 1A). In addition, surprisingly, the screening
264 negatively affected both the biomass (Fig. 1A) and the occupied space (Fig. 1C), concomitantly to
265 an increase in bare space (Fig. 1B), in San Vicente. This later result suggested that the recruitment
266 may have been limited locally by the complete envelopment of panels with the thin mesh used.

267

268 *Taxa-specific responses to predator exclusion*

269 The exclusion performed had an effect upon species richness, but the outcomes were
270 ambiguous considering all taxa (Table 2, Table S4, Fig. 1D). Interestingly, only the non-indigenous
271 species richness was influenced by the exclusion experiment (i.e., native and cryptogenic richness
272 were not affected Table 2, Table S4 Fig. 2A-C). As mentioned above, it is noteworthy that 27% of
273 the NIS and cryptogenic species were recorded only when predators were excluded (Table S1). As
274 compared to open treatment, NIS richness was greater under macro-predators exclusion (i.e., caged
275 treatment) in Lirquén and Coliumo (Fig. 2A-B, Fig. S6). Micro- and macro-predators exclusion

276 (i.e., screen treatment) reduced NIS richness in all sites (Fig. 2A-C), though there may have been
277 a screening effect in San Vicente (Fig. S6).

278 Irrespective of the group of taxa considered, total species abundances (covers) were affected
279 by the exclusion experiment, though patterns differed among sites ('site × treatment' interactions,
280 Table 2, Fig. 2A-C, see also Table S4 and Fig. S6). Overall, predator exclusion increased the cover
281 of either NIS, cryptogenic taxa or both in the three sites (Fig. 2, Fig. S6). Altogether, the more
282 drastic biotic resistance due to predation was observed in Lirquén, where macro- and micro-
283 predator exclusions respectively led to 73% and 21% increases in NIS cover (Fig. 2A, Fig. S6).
284 According to the principal component analysis (PCO, Fig. 2A), the respective effects of macro-
285 and micro-predators could be responsible of ca. 56% (*cf.*, ordination along axis 1) and 16% (axis
286 2) of variation in community structure in Lirquén. Examining the variables correlated to the
287 different treatments suggests species-specific responses to predation across sites (Fig. 2A-C),
288 which were further scrutinized by univariate analyses (Table S5, summarized in Fig. 3). Site-
289 specific effects of treatments were detected on 3 natives (18%), 2 cryptogenics (18%) and 5 NIS
290 (45%). The strongest biotic resistance played by macro-predators was observed in Lirquén, where
291 6 to 10 fold-reduction in the cover of colonial NIS, such as *Bougainvillia muscus* and *Bugulina*
292 *flabelatta*, were observed. In contrast, the effect of macro-predators was mainly concentrated upon
293 native barnacles (up to 4 fold-reduction) in San Vicente. Along with total cover and biomass
294 reduction mentioned above (Fig. 1), exclusion of micro- and macro-predators led to an unexpected
295 decrease in the cover of *Balanus laevis* in two sites and *Amathia cf. gracilis* in one of them (Fig.
296 3), suggesting that the full screened caged locally limited their recruitments, especially in San
297 Vicente where the bare surface was greater in this treatment compared to the others. Nonetheless,
298 the full predator exclusion had clearer effects (according to pairwise tests) on the abundance of
299 diverse non-indigenous and cryptogenic species, such as the bryozoans *Bugula neritina*, *Exochella*

300 sp. nov., and three ascidians: *Corella eumyota*, *Ciona robusta*, and *Diplosoma listerianum* – the
301 latter two species being virtually absent from treatments exposed to predators in Lirquén and
302 Coliumo, respectively (cf. infinite fold-change values, Fig. 3).

303

304 *Panel community changes over time and under predation*

305 Regarding the long-term settlement panel survey, the deployment date resulted in
306 contrasting community development (significant two way-interaction “Trial × Age”) in Lirquén
307 (Pseudo- $F_{4,68} = 14.04$, $P < 0.001$, Fig. 4A), Coliumo (Pseudo- $F_{4,68} = 9.69$, $P < 0.001$, Fig. 4B) and
308 San Vicente (Pseudo- $F_{4,68} = 17.56$, $P < 0.001$, Fig. 4C). Irrespective of the trial, important
309 differences in community structure were however observed in all sites according to the time elapsed
310 since the deployment (pairwise tests: 1 ≠ 3 ≠ 7 ≠ 13 ≠ 19 months with P_{MC} values ranging from <
311 0.001 to 0.01). In all study sites, the first axis of the principal coordinate analyses – respectively
312 responsible of 34.0, 39.3 and 30.0% of the total variation in Lirquén (Fig. 4A), Coliumo (Fig. 4B)
313 and San Vicente (Fig. 4C) – illustrated the overall pattern of development of the panel communities
314 from 1 month (dominated by bare surface, on the left in Fig. 4) to 19 months (dominated by native
315 and a few cryptogenic species, on the right in Fig. 4).

316 Of the seven NIS that contributed to the multivariate structure in the exclusion experiment
317 and were affected by predators (Fig. 2 and above), only two contributed to the long term community
318 dynamics using the same criteria ($r > 0.5$): *Bougainvillia muscus* in Lirquén and *Exochella* sp. nov.
319 in Coliumo. It is noteworthy that in the very same sites, these two species were also the main NIS
320 contributors to the community structure under predator influence after 4 months of the exclusion
321 experiment (9.8 and 28.4% of total similarity, respectively, Fig. 3). In Lirquén, the maximal
322 contributions of *B. muscus* to the community structure were observed on 3 months-old panels from
323 the first trial (29.7%, SIMPER analyses) and 7 months-old panels from the second one (40.9%,

324 axis 2 on Fig. 4A), respectively sampled at the same period (spring) of two consecutive years
325 (November 2016 and October 2017). In this site, the cumulated contribution of other NIS ranged
326 from 0% (12 months– trial 1) to 11.3% (12 months – trial 2) due to occasional emergence of
327 *Bugulina flabelatta* and *Hydractinia* sp. In Coliumo, maximal contributions of *Exochella* sp. nov.
328 were observed after 13 (26.0%) and 7 months (15.7%) of the first and second trials, respectively
329 (Fig. 4B). In this site, the cumulated contribution of other NIS remained < 3% all over the survey.
330 Likewise, it is noteworthy that *Exochella* sp. nov. contributed up to 15.5% of the community
331 structure in San Vicente on one occasion (7 months – second trial) while the cumulated contribution
332 of all other NIS never exceeded 2% in this site. In parallel, the cumulated contribution of native
333 species generally increased over community development: 60-70% at the end of the first trial and
334 28-31% at the end of the second one – when the contribution of either cryptogenic species (e.g.
335 *Clytia linearis* in Lirquén, *Amphisbetia operculata* in San Vicente) or the bare space (in Coliumo)
336 was locally important.

337

338 **Discussion**

339

340 While similar numbers of sessile taxa were observed during the short-term exclusion and
341 the long-term panel experiments, a greater number of non-indigenous species (NIS) was observed
342 upon settlement panels after the four months-duration of the exclusion experiment than over the
343 twenty-six months of the colonization survey, during which the panels were left exposed to
344 predators. Overall, the predation affected the early stage of community development. Micro- and
345 macro-predators together reduced the abundance of most NIS and cryptogenic species, of which
346 six taxa were only recorded under predator exclusion. This result, associated with the poor

347 contribution of NIS to the community structure observed over more than two years of colonization
348 experiment, strongly suggests consumptive biotic resistance in the study systems.

349

350 *Towards novel natural enemies*

351 Besides the enemy release hypothesis which is the foundation of invasive species
352 management by biological control, the new association principle emerged as a framework where
353 biocontrol capitalizes on consumptive and “native” biotic resistance (Colautti et al. 2004;
354 Hokkanen and Pimentel 1989). Such approach does not involve the introduction of a new species,
355 albeit a natural enemy, and could thus avoid dramatic drawbacks (Elton 1958; Pearson and
356 Callaway 2003). The new association principle stands on the hypothesis that a NIS is a naive
357 prey/host, thus likely less efficient to defend itself against a novel predator/enemy.

358 In our exclusion experiment, all non-indigenous (and cryptogenic) ascidians were affected
359 by predators in terms of cover and number of individuals whereas the native ascidians did not
360 virtually suffer from any type of predators, except *Pyura chilensis* in Coliumo (Fig. 2, 3). This
361 pattern was sustained over the long term survey where the native ascidian *P. chilensis* progressively
362 became one of the dominant space occupiers in the other sites, i.e. Lirquén (cover: $20.6 \pm 39.2\%$
363 after 18 months, pooled for trials \pm SD) and San Vicente ($54.1 \pm 46.8\%$), whereas non-indigenous
364 ascidians remained virtually absent upon panels (Fig. 4) – other than rare records of *Ciona robusta*
365 juveniles in Lirquén.

366 While predators can efficiently regulate post-settlement survival of ascidians, they can also
367 be quite selective (Nydam and Stachowicz 2007; Osman and Whitlatch 1995; Rius et al. 2014). In
368 New England, both micro-gastropods *Cotonopsis lafresnayi* and *Astyris lunata* limited the survival
369 of various non-indigenous or native ascidian recruits, such as *Botryllus schlosseri* and *Diplosoma*
370 *sp.*, although *Botrylloides diegensis* was generally avoided (Osman and Whitlatch 1995). In

371 addition, traits that facilitates rapid colonization are often accompanied by costs to competitive
372 advantage, such as defense against predators (Papacostas et al. 2017). As it grows, *P. chilensis*
373 develops a thick cellulosic tunic and resist attacks from most local predators in northern Chile
374 (Dumont et al. 2011a). Although other possible defense mechanisms may be involved (e.g.
375 Stoecker 1980), non-indigenous and fleshy ascidians (e.g., *Ciona robusta*) were herein apparently
376 more naive to predation than their native counterpart, and thus not released from their new enemies.
377

378 *Consumptive biotic resistance might vary according to predator diversity*

379 Although outcomes vary among habitats, the body of knowledge accumulated in terrestrial
380 systems generally supports the hypothesis that the more diverse are natural enemies, the more likely
381 they are to control pests (Letourneau et al. 2009). In the framework of the complementarity model,
382 these previous results also suggest that additive (e.g., synchrony) and synergistic (e.g., facilitation)
383 effects among enemies can be stronger than antagonistic effects (e.g., due to intraguild predation)
384 at high richness. Notwithstanding all emergent implications of such finding for biotic resistance,
385 the influence of predator diversity upon marine invaders has so far seemingly been generally
386 overlooked (Byrnes and Stachowicz 2009; Dumont et al. 2011b for multiple-predator experiments
387 in fouling communities; but see Nydam and Stachowicz 2007). Our caging experiment showed that
388 macro-predators were responsible for a sharp reduction in abundance of the introduced vine
389 hydrozoans (e.g., *Bougainvillia*) and tree-like bryozoans (e.g., *Bugulina*), in two of the three study
390 sites. While this pattern is consistent with results from previous studies (Dumont et al. 2011b;
391 Osman and Whitlatch 1998), further work would be needed to separate the effects of predator
392 categories and to determine their interactions upon these focal invaders. Indeed, micro-predators
393 could not be excluded without excluding also macro-predators. In addition, screening may have
394 locally limited the recruitment of some taxa (as suggested by the variations of bare surface in San

395 Vicente). Even so, we clearly observed a collapse of non-indigenous ascidians in the presence of
396 micro-predators (i.e., in all treatments except screened) in every study sites. Because they
397 presumably forage on different preys (and possibly on different life stages, Dumont et al. 2011a;
398 Rius et al. 2014), it may be worth scrutinizing whether micro- and macro-predator effects are
399 complementary at the assemblage level. This aspect may be critical for the biotic resistance in the
400 study area, with regards to the non-indigenous status of most of these preys and their poor
401 contribution to community structure over long-term community development and in established
402 communities. A thorough examination of the associated food web would be needed to examine
403 further this hypothesis which could have implications for impact mitigation and NIS establishment
404 management strategies (Smith-Ramesh et al. 2017).

405 Biotic resistance is amongst the main targeted ecological services of eco-engineering in the
406 context of ocean sprawl. Promoting the local abundance of invader-enemies seems a promising
407 avenue (Bishop et al. 2017; Dafforn et al. 2015), as our results also mirror. The outcomes of
408 consumptive biotic resistance may however be particularly conflicting in realistic food webs,
409 especially interacting with species exploitation (Caselle et al. 2018). Both macro-predators (all
410 crabs identified) and native sessile taxa (incl. ascidians, barnacles and mussels) are fished in the
411 study region, including within ports. One can thus wonder whether the concomitant regional
412 changes in habitats (ocean sprawl, e.g. Aguilera 2018) and fisheries (Andreu-Cazenave et al. 2017)
413 may interact and to which extent it might decrease the biotic resistance herein reported – hypothesis
414 that could be addressed through further experimental and modelling approaches.

415

416 *Predator escapes and maintenance of discrete invader populations*

417 Ecological interactions have the potential to limit the abundance of NIS, but rarely enable
418 communities to fully resist biological invasions (Levine et al. 2004). While predators partially

419 constrained the cover of the introduced hydrozoan *Bougainvillia muscus* in Lirquén, they also
420 liberated 10-fold as much bare surface (Fig. 3) available to colonization, notably by colonial species
421 in place. Over the long term survey, *Bougainvillia muscus* consistently bloomed over two
422 subsequent springs (Fig. 4). Whether it was due to specific invader traits (e.g. phenology in
423 reproduction and/or vegetative growth) or temporal variability in predator effects – here likely
424 mainly due to the native sea urchin *Arbacia dufresnii* (Leclerc et al. 2018), our results suggest that
425 biotic resistance may have complex dynamics in fluctuating environments (Stachowicz and Byrnes
426 2006). In the recently constructed jetty of Coliumo, where the bryozoan *Exochella* sp. nov. has
427 been recorded for the first time within the study region (in March 2017, Leclerc et al. 2018), none
428 of the exclusion treatments affected its abundance. This species became one of the dominant space-
429 occupiers on well-developed panel assemblages (7-13 months) and established communities in
430 surrounding habitats (Table S3). After a first record in September 2017, *Exochella* sp. nov. also
431 contributed substantially to community structure in San Vicente, where the species apparently met
432 at least one efficient enemy – likely absent from Coliumo – among micro-predators (Fig. 3).
433 Although both our experiments suggest that the proliferation of this species may be limited locally
434 by consumptive and/or competitive biotic resistance, they also suggest that none of these processes
435 could have prevented its establishment. Besides, *Exochella* sp. nov. was also found as epibiont of
436 *Crepidatella fecunda* and *Balanus laevis*, the dominant space occupiers at Coliumo in older
437 assemblages (19 months, Fig. 4), suggesting that, even facultative, mutualistic interactions could
438 impede biotic resistance processes over community assembly (Bulleri et al. 2008).

439 It is finally worth emphasizing that even non-indigenous ascidians, which experienced
440 severe predation pressure on pilings at the depth investigated, were occasionally observed as few
441 individuals or colonies (Table S3, Fig. S5) in diverse micro-habitats (ropes, buoys, cavities, jetty
442 stairwells), likely out of the reach of most predators (Dumont et al. 2011a; Rogers et al. 2016). As

443 our full model also suggested, exclusion treatments could have contrasting effects across pilings
444 on community structure and on a few response variables (Table S4). Further work would be
445 necessary to disentangle between within site-variability in predation and propagule pressures,
446 among other confounding factors. While drastic abundance reduction can mitigate both the
447 negative effects an invader may have on a focal habitat and its probability of spread (Levine et al.
448 2004), our results altogether suggest that, across multiple scales, both spatial and temporal
449 variability in biotic resistance may provide invaders with escape opportunities to establish discrete
450 and viable populations.

451
452 In conclusion, our experimental study showed that the abundance of most NIS was reduced
453 under predation within the study region. Moreover, some NIS were only recorded when predators
454 were excluded. In light of a two-year survey of panel colonization and field censuses, our results
455 suggest that this consumptive biotic resistance is sustainable. Further work is however needed to
456 determine whether this predation effect also influences biotic interactions (competition, mutualism)
457 among fouling species. Our study also suggests some complementarity among predator categories
458 (here according to their size). Unraveling local food webs and predator functions in urban areas
459 might be helpful to develop NIS management strategies.

460

461 **Authors' contributions**

462 JCL, FV and AB conceived the idea and designed the study. JCL designed the methodology,
463 collected the data and led the writing of the manuscript. FV and AB significantly contributed to
464 manuscript writing and critical review.

465

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475

476 **Data accessibility**

477 Most of the data are provided in the supplementary material associated with the manuscript.
478 Detailed data are available from the corresponding author upon reasonable request.

479

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590

591

592 **Tables**

593 **Table 1.** Results of PERMANOVA test for differences in fouling community structure among
 594 levels of the main factors (site and exclusion) and their interaction (PERMDISP T × S: $F_{14,72} =$
 595 6.587, $P < 0.001$). Post-hoc pairwise tests are summarized.

Factor	df	SS	MS	Pseudo- F	P
Site = S	2	123510	61756.0	25.890	< 0.001
Plot (Site) = P	3	7161	2387.0	4.4730	< 0.001
Treatment = T	4	23011	5752.8	1.571	0.114
T x S	8	30522	3815.2	6.628	< 0.001
Res	69	36824	533.7		

Pairwise tests:
 Lirquén: Op = CC = SC ≠ Cag ≠ Scr
 Coliumo: Op = CC = SC ≠ Cag ≠ Scr
 San Vicente: Op = CC = SC ≠ Cag ≠ Scr

596

597

598

599 **Table 2.** Results of PERMANOVA tests for differences in response variables among levels of the
 600 main factors and their interaction. Transformations (Transf.) and PERMDISP tests (T × S) are
 601 summarized. ^{ns}: non-significant at $\alpha = 0.05$, *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$.

Response variable	Transf.	PERMANOVA Factor (df. total = 86)				PERMDISP	
		Site = S (2)	Plot(Site) = P (3)	Treatment = T (4)	T x S (8)		
Community structure	SqRT	25.890***	4.473***	1.571 ^{ns}	6.628***	***	
Biomass (g)	None	38.703***	1.169 ^{ns}	1.324 ^{ns}	10.394***	ns	
Bare surface (%)	None	439.370***	0.191 ^{ns}	1.281 ^{ns}	9.897***	***	
Abundances (%)							
	All	None	50888.0***	0.001 ^{ns}	1.537 ^{ns}	8.649***	ns
	Native	None	2129.9***	0.1934 ^{ns}	1.577 ^{ns}	12.189***	***
	Cryptogenic	FoRT	6.360 ^{ns}	3.914*	0.174 ^{ns}	5.408***	ns
	NIS	None	53.350*	1.523 ^{ns}	3.031 ^{ns}	4.434***	***
Richness S							
	All	None	7.001*	4.732**	1.168 ^{ns}	2.814*	ns
	Native	None	7.966 ^{ns}	1.955 ^{ns}	2.316 ^{ns}	1.557 ^{ns}	ns
	Cryptogenic	SqRT	0.389 ^{ns}	11.300***	0.411 ^{ns}	0.855 ^{ns}	ns
	NIS	None	8.658***	7.220***	4.771*	2.917**	ns

602 SqRT: Square root transformed, FoRT: Fourth root transformed

603

604 **Figure captions**

605

606 **Figure 1.** Biomass (A), bare surface cover (B), occupied cover (C) and species richness (D) on
607 experimental panels across treatments and sites. Upper letters indicate differences among
608 treatments within each study site.
609

610 **Figure 2.** Community structure (principal coordinate analysis, left panels), richness and
611 abundances (right panels) of native (blue), cryptogenic (orange) and non-indigenous taxa (red)
612 across treatments in each site. Detailed graphs, including control treatments (CC, SC), can be found
613 in Figure S6. Vector plots of variables correlated with the PCO axes are indicated, with $r > 0.5$.
614 Only the genus name is given. Note that scales differ among site plots.
615

616 **Figure 3.** Summary of the major species-specific and abiotic variable responses to predation (cf.
617 Table S5). Color code is as in figure 2. Predation effects are presented as fold-changes of the species
618 cover (normal font) and of the numerical abundance (*italic*). Fold-changes were obtained by
619 comparing the average values of open and control panels with caged/screened treatments.
620 Significant changes are in bold, with numbers in bracket indicating a possible caging effect. “-”
621 indicates that the species is present but with an occurrence too small to make statistical inferences.
622 Following the scale presented, backward shade indicates the average within-site contribution of
623 each taxon/response variable to the community upon open and control panels (i.e., exposed to all
624 predators).
625

626 **Figure 4.** Temporal variation in community structure (PCO) upon panels deployed in August 2016
627 (trial 1) and March 2017 (trial 2) in each study site. Color code in vector plots are as in Figure 2.
628

Fig. 1

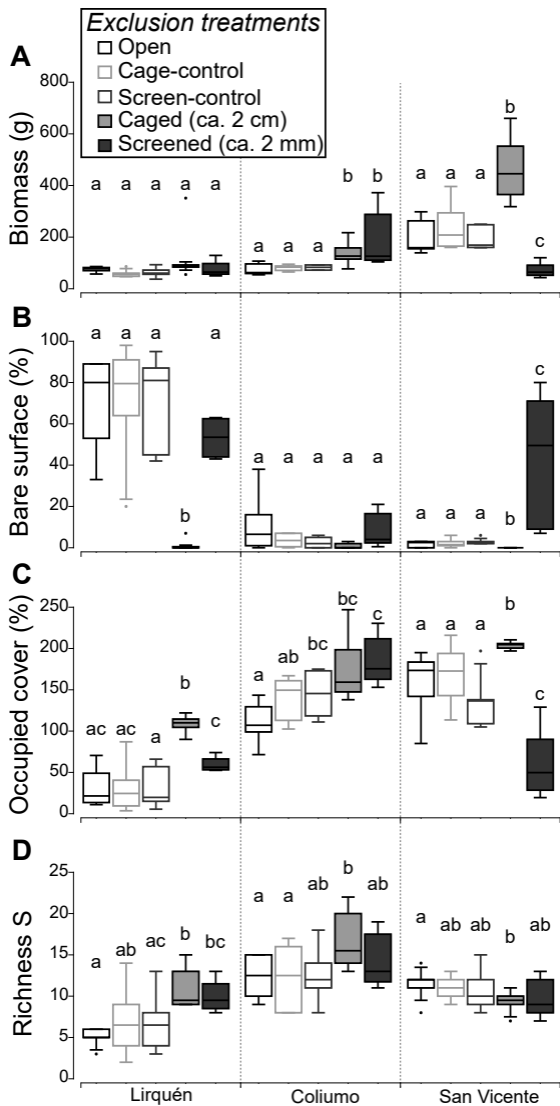
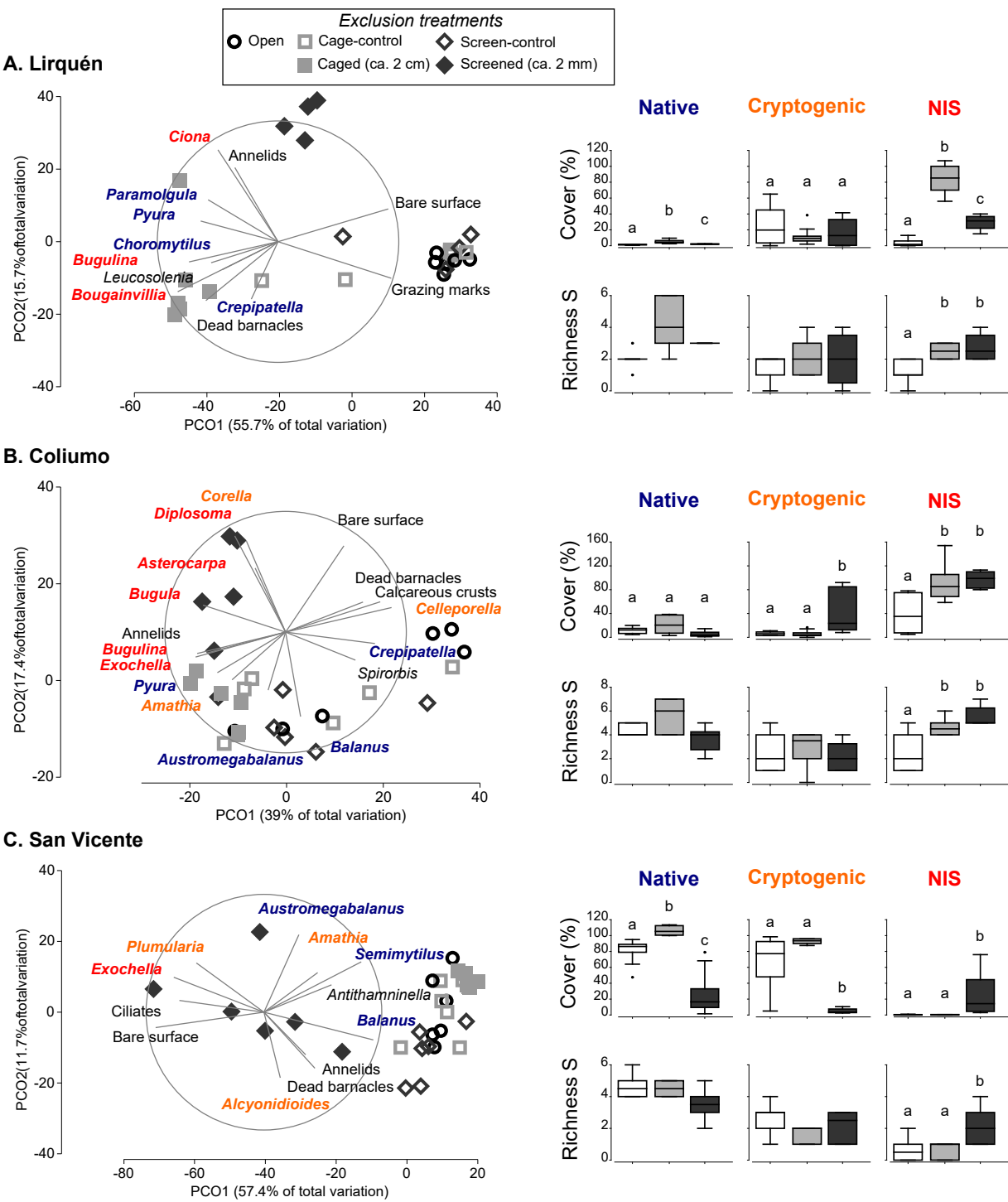



Fig. 2



Macropredators effect

Micro- and macro-predators effect

Form	Group	Phylum	Taxa	Lirquén	Coliumo	San Vicente	Lirquén	Coliumo	San Vicente
			Bare surface	 × 57.0	× 7.0	(× ∞)	× 1.3	× 1.5	÷ 19.0
Col.	Vines	Cni	<i>Bougainvillia muscus</i>	÷ 5.8	+ 2.0	+ 1.0	× 3.4	× ∞	+ 6.0
Sol.	Sedentary	Ann	Annelid tubes	× 1.2	÷ 3.5	× 1.3	+ 6.1	+ 1.5	× 5.1
Sol.	Sessile	Cru	<i>Austromegabalanus psicattus</i>		÷ 4.0	÷ 3.7		× 1.1	÷ 1.1
Sol.	Sessile	Cru	<i>Balanus laevis</i>	+ 2.7	× 1.2	÷ 1.2	× 1.3	× 10.1	× 3.7
Sol.	Sessile	Cru	Dead barnacles	÷ 13.0	+ 2.2	× 5.2	+ 3.5	+ 1.6	× ∞
Col.	Vines	Bry	<i>Amathia cf. gracilis</i>		+ 1.1	(+ 1.7)		× 21.0	× 15.2
Col.	Trees	Bry	<i>Bugulina flabellata</i>	÷ 9.7 + 8.4	+ 1.1 - 2.0	-	+ 3.2 + 4.5	× 1.4 × 1.5	-
Col.	Trees	Bry	<i>Bugula neritina</i>		÷ 13.6 ÷ 9.0			÷ 7.5 ÷ 5.4	
Col.	Sheets	Bry	<i>Exochella sp. nov.</i>		+ 1.2 - 1.2	-		+ 1.2 ÷ 1.1	+ 138.0 ÷ 86.0
Col.	Sheets	Cho	<i>Diplosoma listerianum</i>		+ 30.0 + 12.0			÷ 349.2 (÷ 111.6)	
Sol.	Sessile	Cho	<i>Ciona robusta</i>	+ 456.0 + 51.0		× 1.1 ÷ 1.2	÷ 855.0 + 67.5	÷ ∞ + ∞	+ 22.5 × 1.5
Sol.	Sessile	Cho	<i>Corella eumyota</i>		+ 2.0 + 1.3	-		+ 67.6 + 25.1	-
Sol.	Sessile	Cho	<i>Pyura chilensis</i>	+ 2.6 + 3.0	+ 2.1 ÷ 6.1	× 1.2 × 1.9	+ 3.2 ÷ 1.2	+ 1.4 ÷ 1.8	× 2.3 × 1.4

Contribution to within-site similarity under predator influence:

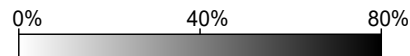
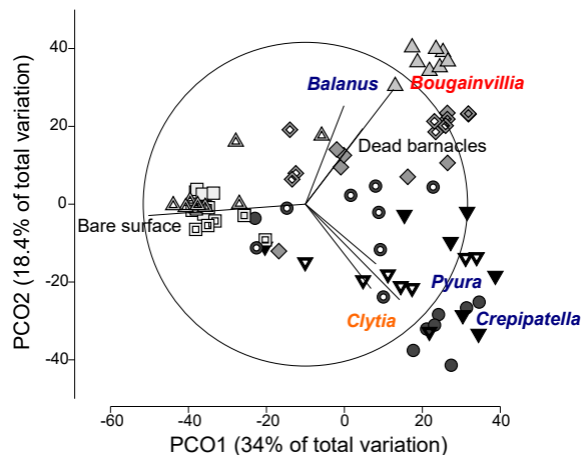
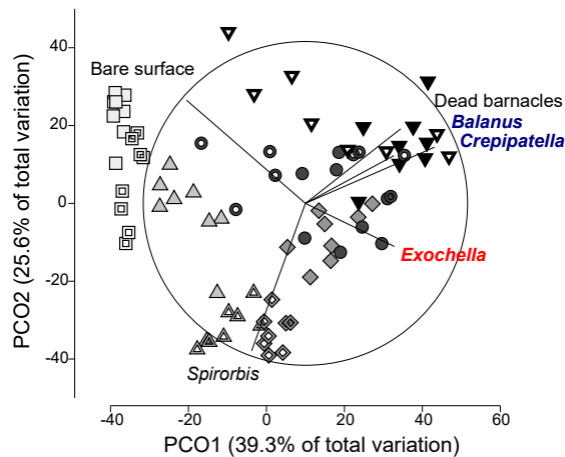


Fig. 4

A. Lirquén



B. Coliumo



C. San Vicente

