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8 LONG-TERM MODIFICATIONS OF COASTAL DEFENCES ENHANCE
MARINE BIODIVERSITY

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SUMMARY

34 Realisation that hard coastal infrastructures support lower biodiversity than
natural habitats has prompted a wealth of research seeking to identify design
36 enhancements offering ecological benefits. Some studies showed that
artificial structures could be modified to increase levels of diversity. Most
38 studies, however, only considered the short-term ecological effects of such
modifications even though reliance on results from short-term studies may
40 lead to serious misjudgements in conservation. In this study, we conducted a
7-year experiment to examine how the addition of small pits to otherwise
42 featureless seawalls could enhance the stocks of a highly exploited limpet.
Modified areas of the seawall supported enhanced stocks of limpets 7 years
44 after the addition of pits. Modified areas of the seawall also supported a
community that differed in the abundance of littorinids, barnacles and
46 macroalgae compared to the controls. Responses to different treatments
(numbers and size of pits) were species-specific and while some species
48 responded directly to differences among treatments, others might have
responded indirectly via changes in the distribution of competing species. This
50 type of habitat enhancement can have positive long-lasting effects on the
ecology of urban seascapes. Understanding of species interactions could be
52 used to develop a rule-based approach to enhance biodiversity.

54 Keywords: Azores, coastal urbanisation, community structure, conservation,
habitat enhancement, long-term, *Patella*

56

INTRODUCTION

58 The replacement of natural shores by hard coastal defence structures (e.g.
seawalls, breakwaters, revetments, groynes) is increasing as a response to
60 the growing need to defend the coast from sea level rise and stormier seas
(e.g. Airoldi *et al.* 2005; Moschella *et al.* 2005; Chapman 2006). Realisation
62 that these structures generally support lower biodiversity than natural habitats
(e.g. Chapman 2003; Chapman 2006; Chapman & Bulleri 2003; Moschella *et*
64 *al.* 2005; Vaselli, Bulleri & Benedetti-Cecchi 2008; Firth *et al.* 2013a; Browne
& Chapman 2014) has focused attention on designing structures that help
66 facilitate specific ecological outcomes (Firth *et al.* 2014).

68 In cases where natural shores are completely replaced by artificial habitats
there will be an obvious loss of habitat and the species therein. However,
70 even when species colonise such artificial structures, they can hardly be
considered as surrogates for the natural shores they replace (see review by
72 Chapman & Underwood 2011). For instance, there is now documented
evidence that on such hard coastal defence structures (e.g. seawalls) there
74 can be changes in the composition of species assemblages (Bulleri *et al.*
2005; Moschella *et al.* 2005), abundances (Chapman 2003), size-structure
76 and reproductive output of populations (Moreira *et al.* 2006) and competitive
interactions (Jackson *et al.* 2008; Iveša *et al.* 2010). Moreover, less obvious

78 changes in community structure can also be found on natural shores
surrounded (Goodsell *et al.* 2007) or in the vicinity (e.g. Martins *et al.* 2009) of
80 such artificial habitats.

82 Lack of habitat heterogeneity has been put forward as the main cause of the
lower level of biodiversity generally observed on sea defence structures
84 (Chapman & Underwood 2011). There is now mounting evidence that
experimentally increasing the complexity and heterogeneity of otherwise
86 topographically simple surfaces, for example by including water-retaining
features, pits and crevices, can substantially increase the biodiversity of the
88 structure (Chapman & Blockley 2009; Firth *et al.* 2013b; Browne & Chapman
2014; Firth *et al.* 2014). Modifications can also be tailored to increase the
90 abundances of species of economic interest (Martins *et al.* 2010). These
studies generally support the idea that hard coastal defence structures can be
92 modified to support an increasing level of diversity and thus contribute toward
the conservation and management of urbanised coastlines whilst providing
94 effective protection from sea-level rise and stormier seas.

96 A common feature of these studies, however, is that their duration is typically
< 1 year (e.g. Martins *et al.* 2010; Browne & Chapman 2014) and little is
98 known about how modifications made to coastal defence structures continue
to influence community structure in the longer term, yet results from short-
100 term experiments may not mirror those in the longer-term (e.g. O'Connor &
Crowe 2005) and this may influence feasible management actions (Callahan
102 1984; Magnuson 1990).

104 *Patella candei* d'Orbigny is endemic to Macaronesia where it is extensively
exploited for human consumption. In the Canary Islands, for instance, *P.*
106 *candei* is virtually extinct, presumably due to over-exploitation (Côrte-Real *et*
al. 1996; Navarro *et al.* 2005). In the Azores, *P. candei* stocks collapsed in the
108 mid-1980s (Hawkins *et al.* 2000) and may constitute the largest anthropogenic
impact on Azorean coastal ecosystems, being correlated with archipelago-
110 wide changes in the balance between consumers and producers (Martins *et*
al. 2008). In 1993, legislation established fishing protected zones (where the
112 collection of limpets is fully prohibited), seasonal fishing closures and
minimum catch sizes but these have proved largely unsuccessful due to lack
114 of enforcement and the limpets still show signs of over-exploitation (Martins *et*
al. 2011).

116

In 2006, experimental habitat enhancements, consisting of the addition of pits
118 differing in size drilled into seawalls at different densities, showed that over
the short-term (4 months) the abundance of limpets increased in enhanced
120 areas of the seawall (in comparison to unmanipulated controls) as a result of
both animal immigration and new recruitment (Martins *et al.* 2010). Overall
122 effects of pit density and size varied with limpet size class, with the numbers
of large limpets being limited by the availability of pits of the larger size,
124 whereas small limpets were limited by the density of pits of whatever size.
Here we re-surveyed the experiment to evaluate effects of experimental
126 habitat enhancement on the abundances of the limpet *P. candei* after seven
years. We also examined the wider community level impacts of changes in

128 patellid limpet populations, because patellid limpets play a key community
structuring role on European shores (e.g. Hawkins & Hartnoll 1983; Jenkins *et*
130 *al.* 2005; Coleman *et al.* 2006), suggesting that variation in the distribution of
limpets as a response to different habitat enhancements may have led to
132 community-wide effects. Moreover, different species of grazing gastropods
have distinct influences on the community (e.g. Hawkins *et al.* 1989;
134 O'Connor & Crowe 2005; Griffin *et al.* 2010).

136 **METHODS**

Study sites and community

138 The study area was São Roque (São Miguel Island, Azores), which has a
gentle sloping basaltic rocky shore with many rock pools, that has been
140 largely replaced by the construction of a 4-5 km long seawall for shoreline
protection . Our experimental habitat enhancement was applied to a seawall
142 made of 2 m wide natural basaltic blocks; these had smooth surfaces and
lacked the micro-topographic rugosity characteristic of adjacent natural shores
144 (Martins *et al.* 2010). The experimental treatments were applied at mid-shore
level just above the algal-dominated lower shore in areas where the barnacle
146 *Chthamalus stellatus* is the dominant space occupier and the limpet *Patella*
candei reaches its largest abundance. Other patellid limpets (*P. aspera*)
148 present on Azorean shores are not common at this tidal height. At this height,
macroalgae are generally restricted to ephemeral species (e.g. *Ulva* spp.,
150 *Chaetomorpha* spp.) and a few perennial turf-forming algae (e.g.
Caulacanthus ustulatus). Other grazing gastropods, including the littorinids
152 *Tectarius striatus* and *Melarhappe neritoides*, can also be locally abundant.

154 At each of two sites 200 m apart, 25 areas of 25 × 25 cm were marked and
randomly assigned to 5 treatments. Five replicate areas were assigned to
156 unmanipulated controls. The remaining 20 areas were randomly assigned to a
2-way orthogonal design including the factors pit size (small and large) and pit
158 density (high and low) with five replicates per treatment. Small and large pits
were 12 and 24 mm in diameter (both with a depth of 10 mm). Lesser and
160 greater density treatments corresponded to 8 and 16 pits drilled within each
area. Pits were drilled using an electrical power drill and were evenly spaced
162 within the experimental areas. The sizes and densities of pits used are within
the range of sizes and densities of pits observed on natural shores (for further
164 details see Martins *et al.* 2010). The experimental habitat enhancement was
established between November and December 2006.

166

Sampling design

168 Experimental areas were resurveyed in November 2013 (84 months after
establishment) and March 2014 (87 months after establishment). During the
170 period of time between the start of the experiment and the initial sampling to
determine short-term effects of habitat enhancements (see Martins *et al.*
172 2010) and the resurveys in 2013 and 2014, the experimental areas were left
untouched and no sampling occurred. In November 2013, experimentally
174 enhanced plots were re-located and assessed to ensure that pits within
experimental treatments were still evident and not masked by natural erosion.
176 At this time, the abundance of mobile gastropods (*Patella candei*, *Tectarius*
striatus and *Melarhappe neritoides*) within each area (25 x 25 cm) was

178 counted. Control areas were not evaluated and sampled at this time. In March
2014, we resurveyed the experiment and recounted all gastropods including
180 those in control areas. In addition, we estimated the percentage cover of
sessile species (macroalgae and barnacles). For this purpose, we used a 25 ×
182 25 cm sampling quadrat divided in 25 sub-quadrats. Within each sub-quadrat,
a score between 0 (absent) and 4 (full cover) was attributed to all species
184 present. Total percentage cover was obtained by summing the scores of the
25 subquadrats (see Dethier *et al.* 1993 for further details). Mobile animals
186 (limpets and littorinids) were counted as described above, and limpets were
measured (shell maximum length) using a Vernier calliper. We were able to
188 find all areas except 3 control locations (marks were gone). We replaced
these missing controls with 3 randomly selected areas scattered among
190 experimental areas. No attempt was made to sample communities
surrounding the experimental areas (25 x 25 cm) since the strongest
192 interacting species in this system, *P. candei*, exhibits a homing behaviour
(Cacabelos unpublished data) and was thus unlikely to influence assemblage
194 structures a few centimetres away from the experimental areas.

196 **Data analysis**

A mixed model asymmetrical analysis of variance (ANOVA) was used to test
198 for differences in the abundance of taxa among experimental treatments using
the factors 'site' (random) and 'among all' (fixed and orthogonal to site). The
200 latter was partitioned into 'control vs treatments', to compare the abundance
of taxa in control areas to the average of the enhanced areas, and 'among
202 treatments'. In addition, the factor 'among treatments' was further

decomposed and restructured to allow testing the effects of pit 'size' (fixed)
204 and 'density' (fixed and orthogonal to 'size'). These are effectively two
separate analyses, which can subsequently be built together into a single
206 ANOVA table. Residuals were also decomposed to match changes in the
numbers of replicates for both analyses.

208

Prior to analysis, data were checked for heterogeneity of variances and
210 transformations were applied where necessary (Underwood 1997). Student-
Newman-Keuls (SNK) tests were used a posteriori to examine for differences
212 within significant terms.

214 The variables analysed were the abundance of the gastropods (*Patella*
candei, *Tectarius striatus* and *Melarhappe neritoides*) and the percentage
216 cover of the barnacle *Chthamalus stellatus* and macroalgae. Prior to analysis,
macroalgae were grouped into two morpho-functional groups (Steneck &
218 Dethier 1994) uncorticated ephemeral algae including both filamentous
(*Chladophora* spp.) and foliose (*Ulva* spp.) species (hereafter referred to as
220 ephemerals alone) and corticated perennial turfs such as *Caulacanthus*
ustulatus (hereafter referred to as corticated turfs alone). Encrusting algae
222 were also present in some areas, but their overall abundance was very low (<
1%) and was not analysed. This analysis was applied to data sampled on
224 March 2014 as no controls were sampled during November 2013. A simple 3-
way ANOVA with 'site' 'pit density' and 'pit size' was used to analyse
226 November 2013. Results were similar between these two dates and we only

present data from March 2014 for simplicity (analysis of November 2013 in
228 Appendix S2).

230 The chi-squared test of independence (or association) was used to test the
null hypothesis of no association between the frequency of the three species
232 of grazing gastropods and the experimental treatments. The mean number of
each species in each of the four treatments was used as observed
234 frequencies, respectively.

236 We used Pearson's product-moment correlation to highlight potential
relationships emerging from changes in the abundance of grazers as a
238 consequence of treatments on the abundance of sessile taxa.

240 RESULTS

Enhanced vs control areas

242 Analysis of the gastropod assemblages showed that all the three species
(*Patella candei*, *Tectarius striatus* and *Melarhappe neritoides*) were on
244 average, more abundant in enhanced areas of the seawall compared to
unmanipulated controls (Fig. 1 A-C). This result was significant in the cases of
246 *P. candei* and *T. striatus* (Table S1 - Appendix S1), which were around 5 and
11 times more abundant in enhanced areas of the seawall, respectively.

248 Although the abundance of *M. neritoides* was over 2 times greater in
enhanced areas of the seawall (Fig. 1C), no significant effect of seawall
250 modification was found (Table S1). The mean limpet biomass per plot (dry
body weight estimated for each individual from an established length-mass

252 relationship, see Martins et al., 2008) of *P. candei* was also approximately 5
times greater (mean limpet biomass in mg \pm SE, control: 38.2 ± 17.2 ,
254 enhanced areas: 182.9 ± 30.4) in enhanced areas of the seawall. When
considering the entire grazing assemblage (all species together), there was
256 on average a significantly greater number of grazers in enhanced areas of the
seawall than in unmanipulated controls (Fig. 1D, Table S1).

258

Using SNK tests to examine for differences within the factor 'among all' (and
260 not only the control to the average of enhanced areas) showed that, in
comparison to controls, the numbers of limpets were effectively and
262 significantly greater in all of the enhanced treatments but one (small and low
pit density)(Table S2 – Appendix S1). In the case of *T. striatus*, and despite
264 the significant effect detected between controls and the average of enhanced
areas, SNK tests failed to find significant differences between control and all
266 the four enhanced treatments but one (small and low pit density)(Table S2).

268 Among the remainder of the assemblage, a significant difference was also
found between controls and the average of enhanced areas in the abundance
270 of barnacles and corticated turfs (Table S1). These were nearly twice and 11
times more abundant in enhanced areas than in controls respectively (Fig.
272 2A,B). In contrast, the abundance of ephemerals was highly variable and did
not respond consistently to treatments (Fig. 2C, Table S1)

274

Using SNK tests to examine for differences within the factor 'among all' (and
276 not only the control to the average of enhanced areas) showed that, in

comparison to controls, the abundance of barnacles was significantly greater
278 in treatments with large pits, independently of their density (Table S2). For
corticated turfs, results were spatially variable; at one site no difference was
280 found, whilst on the other site there were significant differences only between
controls and areas with large and high density of pits (Table S2).

282

Effects of pit size and density

284 Species making up the gastropod assemblage had variable responses to the
different treatments. The limpet *P. candei* responded positively to both the
286 density and size of pits (Fig. 1A), being significantly more abundant in
enhanced areas with a higher density of pits and in areas with larger pits
288 (Table S1). In contrast, the littorinids *T. striatus* and *M. neritoides* did not
respond to pit density, but were significantly more abundant in areas of the
290 seawall enhanced with small pits (Fig. 1B-C, Table S1). For *M. neritoides* this
result was only detected at one of the sites examined.

292

Overall, the null hypothesis of no association between the gastropod
294 assemblage and the experimental treatments was rejected (Table 1). This
result suggests that each enhancement treatment supports a structurally
296 divergent assemblage of grazers (Fig. 1D). This was especially evident in
those treatments that differed the most (small pit size and low density vs large
298 pit size and high density) - as indicated by the relative chi-squared
contribution of each treatment (Table 1). All the above patterns were also
300 present and similar 4 months earlier in November 2013 (Appendix S2)
suggesting that this pattern was temporally consistent.

302

When considering the remainder of the assemblage, the abundance of
304 barnacles was significantly greater in areas with large pits (Fig. 2A, Table S1).
A significant interaction between site, pit density and pit size was detected in
306 the case of corticated turfs (Table S1). Inspection of Figure 2B suggests that
these tended to increase in abundance with increasing pit area although
308 results were spatially variable (see SNK tests in Table S2).

The abundance of ephemerals also varied among enhancement treatments
310 (Fig. 2C). A significant interaction was found between site and pit density, and
to lesser extent ($\alpha = 0.10$) between site and pit size (Table S1). SNK tests
312 showed that the abundance of ephemerals was greater in areas with lower pit
density (Fig. 2C), although this was only significant at site 1 (Table S2).

314

Strong correlations were found between the abundance of barnacles, turfs
316 and ephemerals and *P. candei* (Table 2). The correlation was positive for
barnacles and turfs, but negative between ephemerals and limpets. The
318 abundance of barnacles and ephemerals was also weakly positively
correlated with *T. striatus* but there was a strong and negative correlation
320 between the later and the abundance of turfs (Table 2). All the sessile taxa
(barnacles, turfs and ephemerals) showed a negative correlation with the
322 abundance of *M. neritoides* (Table 2).

324 DISCUSSION

Long-term effects on the target species

326 Our results suggest that those areas of the seawall that were experimentally
modified to enhance the abundance of the highly exploited limpet *Patella*
328 *candei*, have had a long-term impact. Although no sampling was done in
between the two periods, our resurvey has shown that the short-term
330 enhancement of *P. candei*, observed by Martins et al (2010) has been
maintained over a 7-year period. Thus the simple approach of drilling pits in
332 the rock is highly effective in promoting the abundance and biomass of this
exploited species over many years; the abundance and biomass of *P. candei*
334 7 years on was at least 5 times greater in enhanced compared to control
areas of the seawall.

336

As with results from the short-term experiment (Martins *et al.* 2010), limpets
338 responded differently to the different habitat enhancement treatments.
Observations after 7 years indicate that limpet abundance as a whole (not
340 differentiating among different size classes; see Martins *et al.* 2010) was
positively influenced by the abundance and size of pits, suggesting that
342 particularly the availability of large pits is potentially a limiting factor. This
information can thus be used when designing new infrastructure; in order to
344 enhance limpet stocks, emphasis should be placed on designing structures
that offer a high density of pits of the larger size. It should be noted that the
346 larger individuals in this study were all able to fit within the larger pits. It is
unclear what happens to animals larger than those that fit into pits. Such
348 larger animals may eventually seek other areas of the seawall as reliance on
pits decreases with increasing animal size (Martins *et al.* 2010). Such larger

350 individuals are, however, uncommon on Azorean shores due to over-
exploitation (Martins *et al.* 2008).

352

Community-wide effects

354 Even though the modifications made to the seawall were initially designed
considering one specific species (*P. candei*), a longer-time perspective allows
356 examination of the influence on the structure of the entire assemblage,
including littorinids, barnacles and macroalgae (see Fig. 2). When considering
358 littorinids, it is interesting to note that their response to the distinct treatments
differed from that observed for limpets. While limpets appeared to be limited
360 by the availability of large pits, littorinids were more abundant in the smaller
pits. Their abundance also did not appear to be limited by the density of pits in
362 contrast to that found for limpets. This might reflect the gregarious nature of
littorinids as several individuals of both *T. striatus* and *M. neritoides* were
364 often found sharing a single pit, as was also noted by Skov *et al.* (2011). This
was uncommon among limpets that were generally found inhabiting pits
366 alone. This different behaviour between limpets and littornids likely reflects
differences in the relative strength of intraspecific competition among these
368 gastropods (Underwood 1978).

370 Substantial variation in abundance of the other taxa (barnacles and
macroalgae) was also observed among experimental treatments, especially in
372 relation to pit size. This suggests that the modifications made to the seawall
may have also influenced species other than prosobranch gastropods. This is
374 not surprising as surface topography is known to affect the settlement by

many organisms (e.g. Crisp 1955; Harlin & Lindbergh 1977; Raimondi 1988).

376 There is, however, an alternative explanation: that changes in the abundance
of barnacles and macroalgae are an indirect effect of treatments through
378 changes in the structure of the grazer assemblage (e.g. Hartnoll & Hawkins
1985; Lubchenco 1983; Farrell 1988; Johnson *et al.* 1998; Jenkins *et al.*
380 2005). For instance, the abundance of ephemeral algae, in contrast with that
of limpets, tended to decrease with increasing pit area. Although in such
382 areas there were also increased densities of littorinids, there was little
difference in the community structure between these areas and the smooth
384 unmanipulated control areas of the seawall. This result suggests that
littorinids have little influence on the overall structure of the community - as
386 noted also by O'Connor & Crowe (2005) and Griffin *et al.* (2010) - even
though their abundance was enhanced by the addition of small pits. In
388 contrast, areas of the seawall enhanced by the addition of large pits
supported the most distinct community structure with a comparatively higher
390 abundance of limpets, corticated turfs and barnacles, and a lower abundance
of ephemeral algae (Fig. 3). Unlike ephemeral algae, a positive correlation
392 was found between barnacles and corticated turfs and the abundance of
limpets suggesting that the latter may facilitate their establishment. As is
394 widely known, intertidal limpets generally have a large negative effect on the
abundance of ephemeral algae (Hawkins 1983; Van Tamelen 1987).

396 Ephemeral algae, in turn, can have an inhibitory effect of the establishment of
perennial algae (e.g. Sousa 1979; Hawkins 1981; Viejo *et al.* 2008, Jenkins &
398 Martins 2010). Selective removal of ephemerals by high density of limpets in
areas of the seawall enhanced with large pits may have thus indirectly

400 facilitated the establishment of barnacles and corticated perennial turfs
(Hawkins & Hartnoll 1983; Van Tamelen 1987; Benedetti-Cecchi 2000) (Fig.
402 4). Overall, these results appear to suggest that the changes seen in the
community structure in areas of the seawall enhanced with the addition of
404 large pits may be a result of modifications to the network of interactions
among intertidal species (as schematically represented in Figure 3).

406

Conclusion

408 The experimental modifications made to coastal engineering can have long-
lasting effects. This result is important from a conservation perspective and
410 reinforces the concept that simple modifications made to coastal defence
structures, that are unlikely to affect structural integrity of the building blocks,
412 can be used as a lasting and effective tool for the conservation of species,
provided that a solid understanding of the ecology of the focal species is
414 known. While the enhancement of unprotected coastal infrastructures may be
pointless, many infrastructures actually have regulated access. In these
416 cases, coastal infrastructures may positively influence stocks of important
species but also impact nearby areas via spill-over effects. Our results,
418 however, also suggest that the modifications to the seawalls can influence
non-targeted species both directly, by affecting the spatial distribution of the
420 organisms, and indirectly, by affecting the spatial distribution of competitors
and predators. Understanding the interactions between species can lead to a
422 rule-based approach to interventions to enhance biodiversity.

424 **Supplementary material**

For supplementary material accompanying this paper, visit

426 <http://www.journals.cambridge.org/ENC>

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438

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Table 1. Results of χ^2 tests of independence comparing the mean abundance
 600 of grazers among treatments (χ^2 global = 30.26, d.f. = 4, $P < 0.001$)

		Species of grazers		
602	Treatment	<i>P. candei</i>	<i>T. striatus</i>	<i>M. neritoides</i>
Large, High				
604	Observed	19.6	2.3	6.0
	Expected	10.07	5.89	11.94
606	χ^2 contribution	9.03	2.19	2.96
Large, Low				
608	Observed	8.3	1.9	8.5
	Expected	6.74	3.95	8.00
610	χ^2 contribution	0.36	1.06	0.03
Small, High				
612	Observed	8.5	6.9	16.7
	Expected	11.58	6.78	13.74
614	χ^2 contribution	0.82	<0.01	0.64
Small, Low				
616	Observed	1.2	10.9	13.4
	Expected	9.20	5.38	10.91
618	χ^2 contribution	6.96	5.65	0.57

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Table 2. Pearson's product-moment correlation coefficients between the
624 abundance of grazers and the sessile taxa in experimental enhanced areas of
the seawall.

626		Barnacles	Turfs	Ephemerals
	<i>P. candei</i>	+0.36	+0.36	-0.31
628	<i>T. striatus</i>	-0.03	-0.27	+0.08
	<i>M. neritodes</i>	-0.16	-0.32	-0.20

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648 Figure caption

Fig. 1. Mean (+SE) abundance each of the prosobranch gastropod species (a) *P. candei*, (b) *T. striatus*, (c) *M. neritoides* and (d) their combined abundance, in unmanipulated controls and habitat-enhanced areas of the seawall in November 2014. C – control, SL – small and low pit density, LL – large and low pit density, SH – small and high pit density, LH – large and high pit density. In (d) bar length corresponds to the mean abundance of *Patella candei* (black), *Tectarius striatus* (grey) and *Melarhappe neritoides* (white). Data from the two sites was pooled together for clarity as there was no significant variation between sites (Table S1).

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Fig. 2. Mean (+SE) percentage cover of (a) barnacles, (b) corticated turfs and (c) ephemerals in November 2014. See legend on Figure 1.

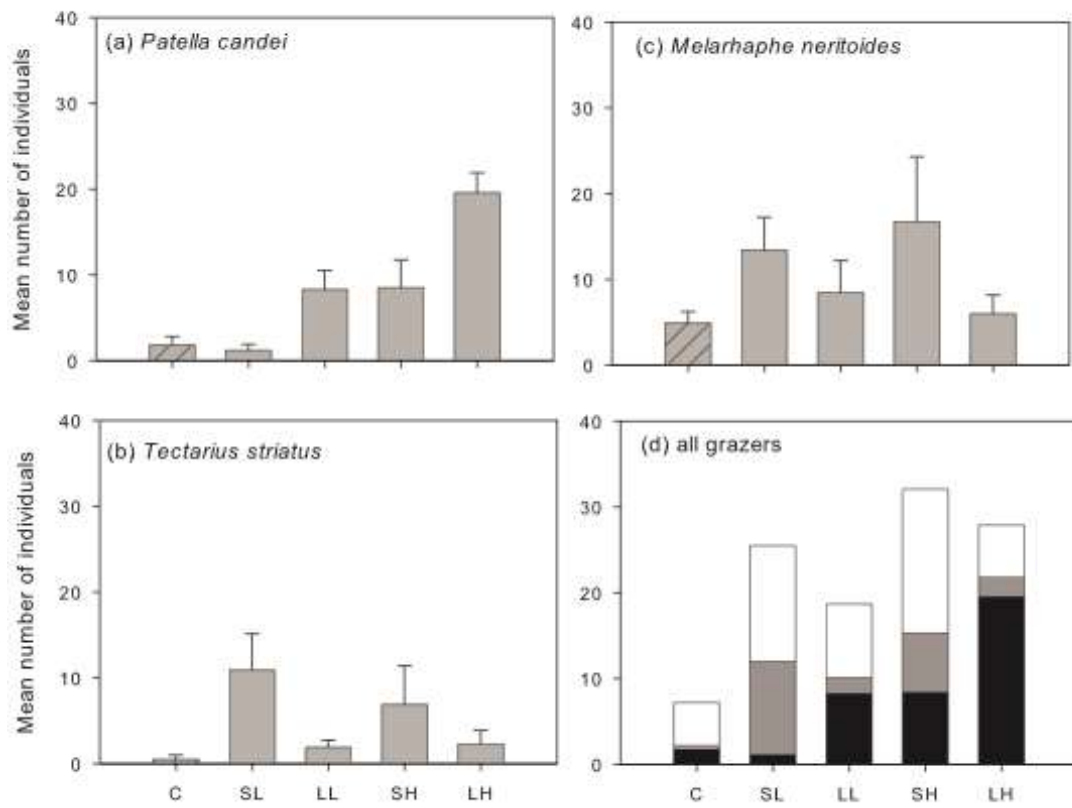
Fig. 3. Conceptual representation of the possible network of interactions as result of habitat enhancement treatments. Continuous arrow – direct effect, dashed arrow – indirect effect. Arrow thickness indicates the relative strength of effect; \pm indicates whether effects are negative or positive.

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674 Fig. 1

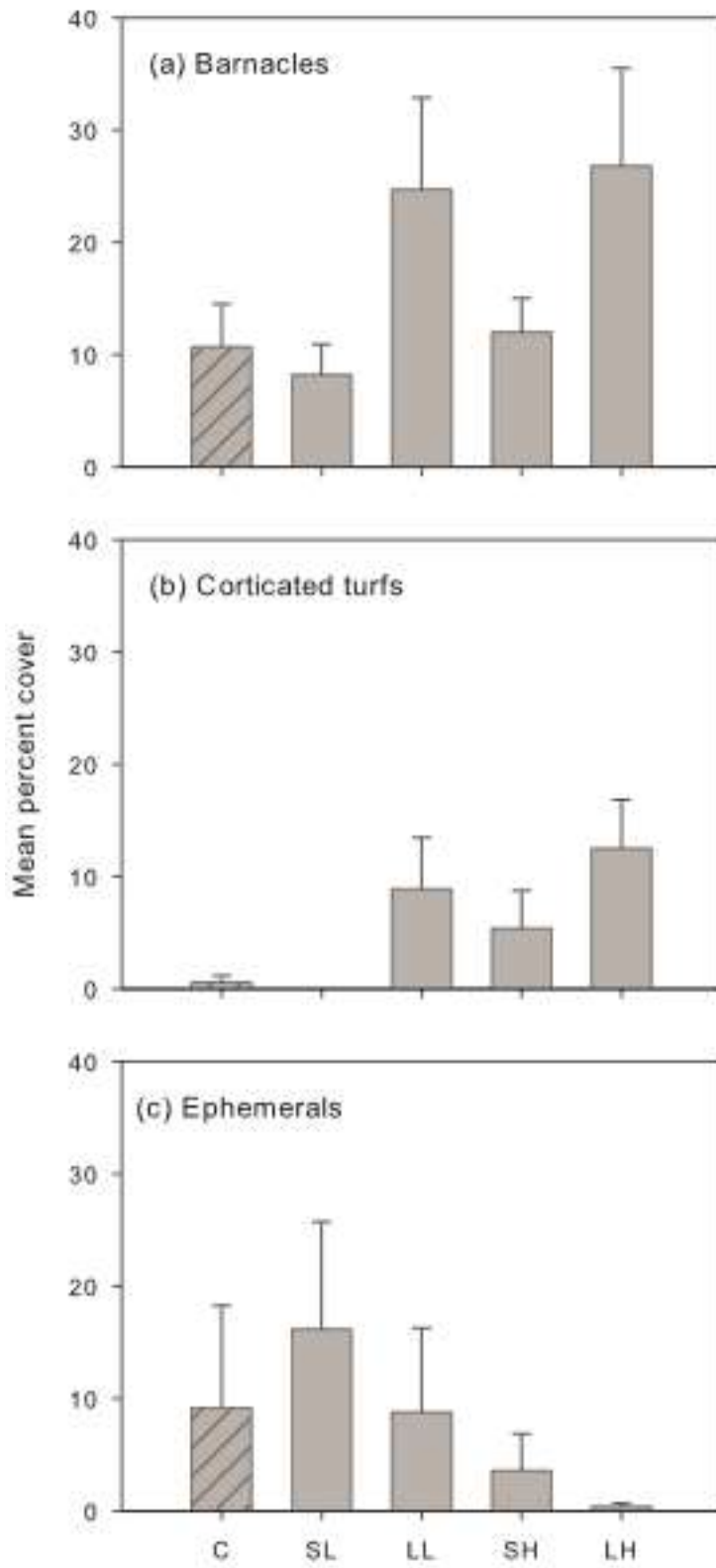
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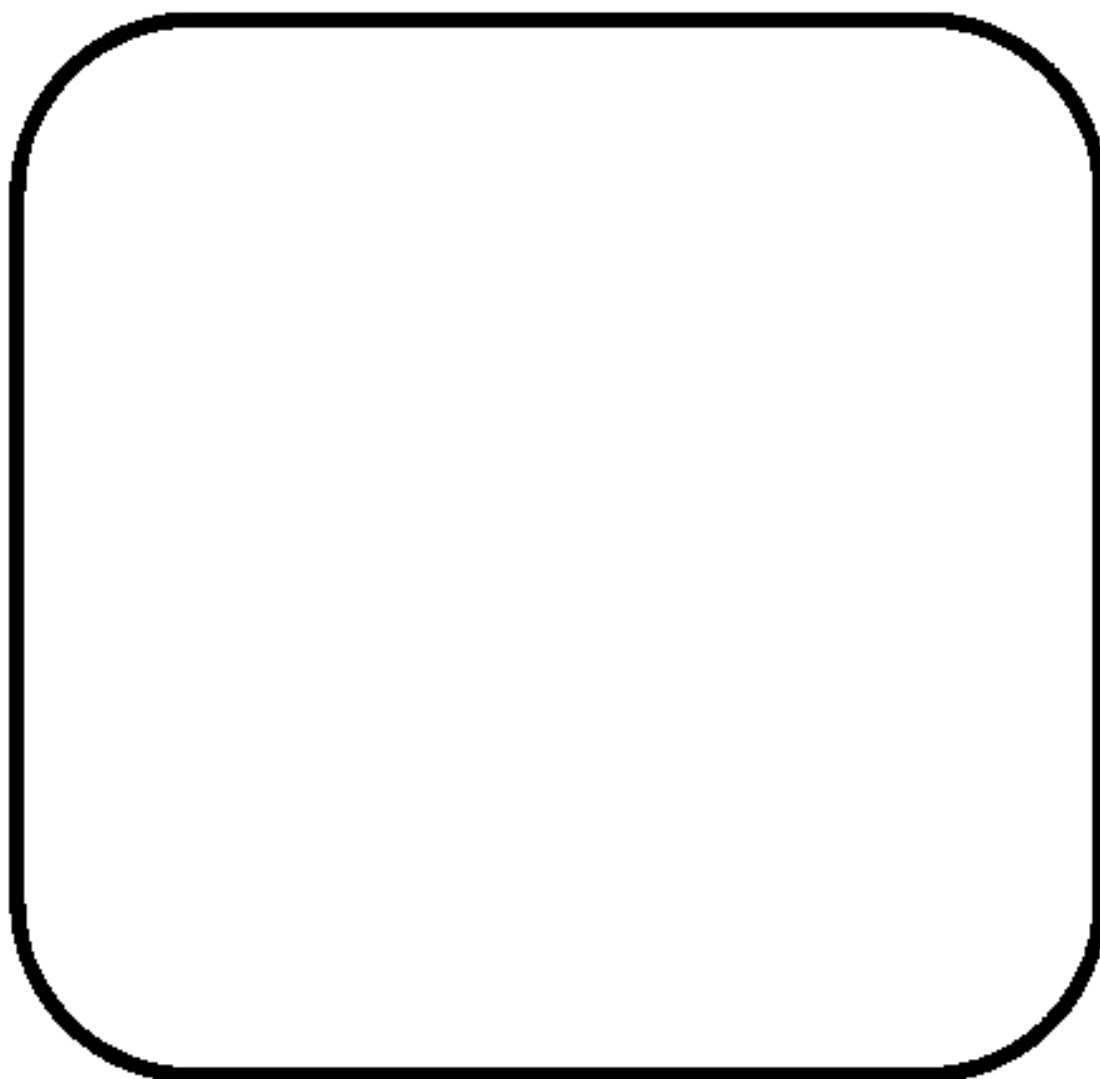
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688 Fig. 2

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692 Fig. 3