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Do positive interactions between marine invaders increase likelihood of invasion into natural and artificial habitats?

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Do positive interactions between marine invaders increase likelihood of invasion into natural and artificial habitats?

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Keywords:	Austrominius modestus, biotic homogenization, epibiosis, Magallana gigas, Patella vulgata, artificial structure
Abstract:	<p>Positive species interactions such as facilitation are important for enabling species to persist, especially in stressful conditions, and the nature and strength of facilitation varies along physical and biological gradients. Expansion of coastal infrastructure is creating hotspots of invasive species which can spillover into natural habitats, but the role of positive species interactions associated with biological invasions remains understudied. Theory suggests that stronger biotic pressure in natural habitats inhibits invasion success. In space-limited marine systems, sessile organisms can overcome this limiting resource by settling as an epibiont on a substrate organism - basibiont. Using a series of spatially extensive surveys, we explored the role of invasive and native basibionts in providing habitat for other invasive and native epibionts, and tested whether environmental context (i.e. if the receiving habitat was natural or artificial), altered ecological outcomes. Overall, provision of space by basibionts was more important for invasive epibionts than for native epibionts but was dependent on the environmental context. Invasive basibionts facilitated invasive epibionts in natural habitats, and appeared to be more important for native epibionts in artificial habitats respectively. Native basibionts facilitated invasive, but not native epibionts in both natural and artificial habitats. These results advance our understanding of facilitation and highlight the idiosyncratic nature of biofouling and epibiosis, and the potentially important influence of environmental context. The degree to which native habitat-forming species vs. invasive habitat-forming species either do or do not facilitate other native or non-native species is a rich area for investigation. Experimental work is required to disentangle the processes underpinning these patterns.</p>

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4 **Abstract**

5

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26 underpinning these patterns.

27

28 **Keywords:** artificial structure, *Austrominius modestus*; biotic homogenisation; epibiosis;
29 *Magallana gigas*; oyster, *Patella vulgata*

30

31 **Introduction**

32 A central goal in ecology is to understand the processes underlying community assembly
33 (Hutchinson 1961; McArthur and McArthur 1961; Kraft et al. 2008). A long history of study
34 demonstrates that negative biological interactions (competition and predation) are important
35 determinants of species' abundances and distributions (Robertson 1947; Connell 1961; Paine
36 1966), the importance of positive interactions such as facilitation has only been more recently
37 considered and incorporated into ecological models (Bruno et al. 2003; Bracken et al. 2014).
38 The strength of positive interactions can vary across physical (Wright and Gribben 2017; Uyá
39 et al. 2020) and biological (Bulleri et al. 2011; Clements and Hay 2015) gradients with
40 facilitation via amelioration of abiotic conditions more important under higher physical
41 stress, whereas under benign conditions facilitation via amelioration of biotic stress (e.g.
42 predation, competition) can be more important (Bertness et al. 1999). Advancing our
43 understanding of how facilitation differs in different environmental contexts will not only aid
44 in targeting conservation efforts but will also advance our understanding of marine
45 community ecology.

46 In space-limited marine ecosystems, such as natural rocky shores, space is often
47 limited and characterised by high biotic pressure. Bare substrate on which to settle is rare,
48 requiring disturbance and mortality events to make space available (Paine and Levin 1981).
49 Sessile organisms, however, can overcome this limiting resource by settling on other

50 organisms - a phenomenon referred to as epibiosis (Wahl 1997). Epibiosis is a spatial
51 association whereby an ‘epibiont’ is attached to the surface of a substrate-organism
52 (‘basibiont’) without trophically depending on it (Wahl 2009). Both positive and negative
53 effects have been identified for both epibiont and basibiont, however, the main advantage for
54 epibionts is that they can colonise an unoccupied space (Wahl 1989; Harder 2009; Gribben et
55 al. 2019). There is evidence to suggest that invasive species are more likely employ epibiosis
56 as a mechanism of recruitment than native species (Hewitt 1993; Reise 1998; Gribben et al.
57 2020). For instance, Leonard et al. (2017) compared bryozoan larval settlement and found
58 that invasive species settled on any surface, whereas natives avoided settling as epibionts.
59 Furthermore, studies have also shown that basibiont species may facilitate the spread of
60 invasive species who settle on them as epibionts (Mendez et al. 2014; Harding et al. 2011),
61 potentially contributing to invasion success (Morgan and Richardson 2009; Mieszkowska et
62 al. 2013). Should these interactive consequences prove pervasive, then ‘invasional
63 meltdowns’ (*sensu* Simberloff and Von Holle 1999) may become increasingly prevalent,
64 especially under future environmental change scenarios.

65 In disturbed marine environments, artificial structures such as harbour walls, pilings and
66 coastal defences are ubiquitous features that replace natural habitats (Thiagarajah et al. 2015;
67 Knights et al. 2016; Chee et al. 2017; Bugnot et al. 2020) with vast swathes of novel habitat
68 potentially suitable for colonisation by rocky reef species (Moschella et al. 2005; Firth et al.
69 2013). Invasive species are often the first colonisers of this novel substrate (Airoldi et al.
70 2015), which can facilitate ‘spillover’ and spread to adjacent natural rocky habitats (Epstein
71 and Smale 2018). Whilst negative biotic interactions may act as a biotic filter to invasive
72 species overspilling into adjacent natural habitats (Elton 1958, Jeschke et al. 2013),
73 basibionts may indeed facilitate invasion success in natural habitats (Ruesink 2007; Altieri et

74 al. 2010; Gribben et al. 2019, 2020) through either physical stress amelioration or
75 associational defence from competitors or consumers.

76 The Pacific oyster, *Magallana gigas* (formerly *Crassostrea gigas*, but see Bayne et al.
77 2017) is a well-known global invader, occurring in >70 countries worldwide (Ruesink et al.
78 2005). It was originally introduced to Europe from Asia for aquaculture and has facilitated
79 the spread of a number of invasive ‘hitch-hikers’ (Blanchard 1997) with widespread negative
80 ecological impacts (Krassoi et al. 2008, see Herbert et al. 2016 for review). In sedimentary
81 environments, *Magallana* is an important ecosystem engineer (*sensu* Jones et al. 1997) that
82 provides a complex three-dimensional habitat for many other species, which can modify the
83 physico-chemical properties of the receiving environment (Markert et al. 2010). Once
84 established, these species may alter environmental conditions in favour of other invaders,
85 such as creating positive feedbacks that accelerate self-recruitment (Simberloff and Van
86 Holle 1999, Diedrich 2005), propagule retention (Lim et al. 2020), and recruitment of other
87 invasive species (e.g. the barnacle *Austrominius modestus*). In Britain, *Magallana* is
88 particularly prevalent in artificial habitats (McKnight and Chudleigh 2015) and is present on
89 many natural bedrock rocky shores albeit at lower abundances (Firth, pers. obs.). Preliminary
90 observations of epibiotic communities associated with *Magallana* in Britain revealed mixed
91 barnacle communities including the non-native *Austrominius modestus* (*Austrominius* herein)
92 and native *Semibalanus balanoides*, *Chthamalus montagui* and *Chthamalus stellatus* (Firth,
93 pers. obs.). Recent studies have shown that in artificial habitats, sheltered and estuarine
94 conditions, not only is *Austrominius* more prevalent than in exposed natural habitats (Gomes-
95 Filho et al. 2010), but it can also completely dominate the barnacle assemblage (Bracewell et
96 al. 2013; Gallagher et al. 2016). Conversely, in natural habitats, *Austrominius* remains
97 relatively sparse where native species richness (Firth et al. 2016a) and biotic pressure (i.e.
98 competition and predation, Gallagher et al. 2015) are greater which may convey biotic

99 resistance (Elton 1958). The novel biogenic substrate provided by rising numbers of
100 *Magallana* could further facilitate *Austrominius* in natural habitats where they are less
101 abundant, but not in artificial habitats where they are typically more abundant.

102 Here, using a combination of surveys, we set out to answer the following three questions:

103 (i) To what extent do native and non-native basibionts facilitate native and non-native
104 barnacle epibionts? and; (ii) Do relationships differ depending on whether the interaction
105 between native/non-native basibionts and native/non-native epibionts occurs in natural or
106 artificial habitats?

107

108 **Materials and Methods**

109 ***Study locations***

110 This study was carried out at six intertidal locations across 1.54° longitude (~114 km) of
111 coast in SW Britain between March and July 2018 (Fig. 1). At each location, both natural and
112 artificial habitats were present in close proximity to one another and thus, characterised by
113 similar environmental conditions. Artificial habitats comprised vertical seawalls (constructed
114 of smooth natural rock and >20 years old) and adjacent (<20 m) natural habitats were
115 characterised by flat smooth vertical/near-vertical bedrock.

116

117 ***Surveys comparing invasive and native taxa between natural and artificial habitats***

118 Preliminary observations indicated that two basibiont species were suitable for this study:
119 the native limpet *Patella vulgata* (*Patella* herein), and the invasive oyster *Magallana gigas*
120 (*Magallana* herein). These two species were selected because they co-occur at the same tidal
121 height in both natural and artificial habitats, have relatively large shells for the attachment of
122 barnacle epibionts, and have been observed to support mixed epibiotic barnacle communities
123 on their shells (Firth, pers. obs.). Whilst, the congeneric limpet *P. depressa* does occur in

124 both natural and artificial habitats, it is much smaller and is often devoid of epibionts (Firth,
125 pers. obs.). Throughout this study, the term 'substrate/substrata' refers to the substrate to
126 which an organism is directly attached (i.e. rock, *Patella*, *Magallana*), and 'habitat' refers to
127 whether the substrate is located in a natural (i.e. rocky shore) or artificial (i.e. seawall)
128 environment.

129 In the first instance, we used surveys at each location to quantify the prevalence of all taxa
130 (i.e. barnacles, *Magallana*, and *Patella*) on natural rocky shore and on artificial seawall
131 habitats. The abundance of *Magallana* and *Patella* on rock substrata was quantified using 15
132 haphazardly-placed quadrats (50 × 50 cm) on flat vertical/near-vertical surfaces within a
133 10m² area at mid-shore elevation. Concurrently, a 3 × 3 cm photo-quadrat was taken within
134 the larger quadrat, then imported into image analysis software (Fiji Cell Counter Tool,
135 Schindelin et al. 2012) and used to quantify the abundance and relative proportion of invasive
136 *Austrominius* and native barnacles living directly on the rock substrata (not as epibionts). In
137 all surveys described below, native barnacles comprised *S. balanoides*, *C. montagui* and *C.*
138 *stellatus* and were identified to species to assign them as native barnacles, but their identity
139 was not considered further as we were interested in the relative differences between native
140 and invasive groups rather than the species themselves. As such, we refer to the native
141 barnacle community as simply 'native barnacles' herein ignoring species identity.

142 Generalized linear mixed models (GLMM; glmer function) with a binomial (logit-link)
143 error distribution was used to assess the probability of presence or absence of all taxa in
144 natural and artificial habitats (fixed) among locations (random factor).

145

146 ***Comparison of facilitation between basibiont species and habitat types***

147 To investigate the relative importance of positive interactions of native and invasive
148 basibionts in natural and artificial habitats, photographs of all *Patella* and *Magallana*

149 individuals encountered within quadrats were taken, alongside a photograph of the adjacent
150 rock substrata. Photo-quadrats (3×3 cm) were placed over the section of the shell with
151 barnacle epibionts. The abundance and relative proportions of invasive and native barnacles
152 within photo-quadrats were counted using the same image analysis process as above.

153 To assess the relative strength of facilitation of invasive barnacle epibionts by invasive
154 and native basibionts in artificial and natural habitats, we compared the percentage difference
155 in invasive epibiont abundance on each basibiont relative to their abundance on rock
156 substrata within both habitat types. To do this, we first calculated the mean abundance of
157 invasive barnacles on rock and then determined the percentage change in invasive barnacle
158 abundance on each basibiont compared to the mean of rock basibionts within each habitat
159 (following Wright and Gribben 2017). For each habitat, we then calculated the mean
160 percentage change and confidence intervals around that mean.

161 Three analyses were performed. (1) A 3-factor linear-effects mixed model (lme) was used
162 to compare the log abundance of invasive and native barnacles on different substrata (i.e.
163 rock, *Patella*, *Magallana*; fixed factor) and habitats (natural, artificial, fixed factor) at each
164 location (random factor). Differences among groups were compared using posthoc Tukey
165 HSD multiple pairwise comparisons. Photo-quadrats with no barnacles were removed from
166 the analysis. (2) A 3-factor negative binomial regression was used to predict the percentage
167 of the barnacle community (relative abundance of invasive and native barnacles in a quadrat
168 where present) on (i) rock substrata or on (ii) a basibiont (*Patella* vs. *Magallana*) in natural
169 and artificial habitats. The maximal model was simplified using the step() function in R with
170 the best model determined using Akaike Information Criterion (AIC). (3) Two-way ANOVA
171 (sqrt transformed) was used to compare differences in facilitation strength between habitat
172 type (natural vs. artificial) and basibiont origin (invasive vs. native). All statistical analyses
173 described above were carried out using the open source software, R (R Core Team 2019).

174

175 **Results**176 ***Comparison of invasive and native taxa between natural and artificial habitats***

177 All taxa were found on rock substrata at all locations in both artificial and natural habitats.
178 For three of the taxa, there was a significant effect of habitat (*Magallana* $-z=-5.72$, $p<0.001$;
179 *Austrominius* $-z=-5.44$, $p<0.001$; native barnacles $-z=8.31$, $p<0.001$), but not location, on the
180 probability of occurrence in a quadrat between artificial and natural habitats (Fig. 2). There
181 was a significantly greater probability of invasive taxa occurring in artificial than natural
182 habitats (*Magallana*; 40% vs. 22%, respectively; *Austrominius*; 75% vs. 57%, respectively).
183 For native taxa, there was either a reduced likelihood of presence in artificial than natural
184 habitats (native barnacles on rock substrata; 69% vs. 90%, respectively) or no significant
185 difference between habitats (*Patella*, $z=0.86$, $p=0.39$).

186

187 ***Facilitation of barnacle epibionts by native and invasive basibionts in natural and artificial***
188 ***habitats***

189 When considering the observed numbers of barnacles, there was a significant interaction
190 between substrate type (on rock vs. on *Magallana* vs. on *Patella*) and habitat type (artificial
191 vs. natural) on the number of invasive ($F_{2,678} = 8.48$, $p < 0.001$) and native barnacles ($F_{2,770} =$
192 4.34 , $p < 0.05$) recorded. In natural habitats, whilst not significantly different, *Austrominius*
193 tended to be more prevalent on basibionts compared to rock. In artificial habitats,
194 *Austrominius* was most abundant on *Patella*, followed by rock, followed by *Magallana* (Fig.
195 3). Native barnacles were more prevalent on rock than as epibionts in both habitat types, but
196 when occurring as epibionts, they were recorded in greater numbers on *Magallana* than on
197 *Patella* in artificial habitats, and in similar numbers between basibionts in natural habitats
198 (Fig. 3).

199 When considering the percentage of the barnacle community that was invasive, there was
200 a significant 3-way interactive effect of substrate type, habitat type, and overall barnacle
201 density (all species) on the number of invasive *Austrominius* predicted to occur within the
202 community ($\chi^2_{59}=59$, $p<0.001$) with significant differences between habitat depending on
203 basibiont identity (Figure 4a). In natural habitats, epibiosis by invasive barnacles on
204 *Magallana* increased exponentially, comprising 100% of the epibiont community when
205 $>\sim 48\%$ of the surface was occupied. In contrast, in artificial habitats, invasive barnacle
206 epibiosis was relatively low, accounting for $\sim 10\%$ of the barnacle community, and only
207 marginally increasing in prevalence with increasing percentage cover (Fig. 4a). The
208 percentage of invasive barnacles as epibionts on *Patella* increased exponentially with
209 increasing barnacle population size in both natural and artificial habitats; 100% were
210 invasive, even when percentage cover of the shell was relatively low ($\sim 25\text{-}38\%$ cover). On
211 rock substrata, invasive barnacles were typically less common (ordinarily $<10\%$ of the
212 community), and instead dominated by native barnacles in both natural and artificial habitats.

213 Considering the mean strength of facilitation, invasive epibiosis was ~ 2 -fold higher on the
214 invasive basibiont *Magallana* in natural habitats than all other comparisons ($F_{1,1219}=12.63$,
215 $p<0.001$) but strength was also highly variable (Fig. 4b). Further, the role of native and
216 invasive basibionts as facilitators of *Austrominius* reversed between natural and artificial
217 habitats (Fig. 4b); *Magallana* showing positive facilitation strength values in natural habitats
218 and negative facilitation strength values in artificial habitats, and vice versa for *Patella*.

219

220 Discussion

221 The relative importance of biotic and abiotic processes governing interactions within and
222 among native and invasive species can vary in time and space (Byers et al. 2010; Green and
223 Crowe 2014). Both of our invasive species (*Magallana* and *Austrominius*) were more

224 prevalent in artificial than natural habitats. Distribution patterns were less consistent for native
225 species, with *Patella* found in similar numbers in both natural and artificial habitats, and
226 native barnacles were typically more likely to occur in natural habitats over artificial. Whilst
227 basibionts were more important for invasive than native epibionts overall, we also found that
228 invasive basibionts facilitated invasive epibionts in natural habitats, and appeared to be more
229 important for native epibionts in artificial habitats respectively. Native basibionts facilitated
230 invasive, but not native epibionts in both natural and artificial habitats.

231 These findings build on the evidence base that artificial substrata represent poor habitats
232 for native species (Firth et al. 2013, 2016b; Airoidi et al. 2015), but they can represent good
233 habitats for invasive species (Bishop et al. 2015; O'Shaughnessy et al. 2020a; see Mineur et
234 al. 2012 for review). A growing body of research suggests that artificial substrata are too
235 homogeneous and lack the necessary topographic complexity at a range of spatial scales that
236 is required for successful settlement and recruitment of native taxa (Moschella et al. 2005;
237 Firth et al. 2013; Loke and Todd 2016). Many invasive taxa have broader environmental
238 tolerances enabling them to colonise and dominate artificial substrata. In this way,
239 homogenous artificial substrata may function as the 'initial' abiotic environmental filter
240 (Olyarnik et al. 2009) for native taxa but not for invasive taxa.

241 These findings also build on the evidence base that invasive species are more likely to
242 settle as epibionts on the surface of another organism than native species (Hewitt 1993; Reise
243 1998). In both natural and artificial habitats, *Austrominius* was facilitated by the native
244 basibiont, *Patella*. In contrast, comparatively fewer native barnacles occurred as epibionts on
245 *Patella. Magallana*, in particular, strongly facilitated *Austrominius* in natural habitats, but not
246 artificial habitats, where instead they supported native barnacles. Both natural and artificial
247 rock substrata were typically colonised by native barnacles, which were occupied by
248 comparatively fewer invasive *Austrominius*. This highlights the importance of novel substrata

249 (i.e. basibionts) as potential vectors for invasion into natural habitats where space-limitation
250 and enhanced predation may mediate invasion success (Arenas et al. 2006).

251 Previous studies suggest complex decision-making processes undertaken by barnacles and
252 other early-life history stages of marine taxa during settlement in response habitat features
253 including surface roughness (e.g. Berntsson et al. 2004, Herbert & Hawkins 2006),
254 biochemical signals (Dreanno et al. 2007), surface orientation, and other biological cues
255 (Harrington et al. 2004, Hanlon et al. 2018). Selection of 'preferred' habitat at small spatial
256 scales may therefore be less likely (James et al. 2019), with larval retention and recruitment
257 patterns instead, determined by physical processes associated flow characteristics created by
258 surface rugosity (Lim et al. 2020). Our results suggest a degree of selectivity for a specific
259 basibiont is apparent between barnacle species that cannot be explained by this study, but
260 might include surface environment chemistry (McManus et al. 2018), surface rugosity of the
261 basibiont shell and surrounding rock, or the diversity of the surrounding community
262 providing chemical cues (Huggett et al. 2005). Clearly, a suite of complex interactions
263 between incoming organisms and the receiving environment may be at play, but additional
264 work is required to disentangle potential drivers of these differences.

265 Invasive species can augment the receiving environment resulting in positive impacts on
266 organisms in marine (Simberloff and Van Holle 1999), coastal (Demopoulos and Smith
267 2010) and terrestrial environments (Tecco et al. 2006). For instance, Jordan et al. (2008)
268 found that the invasive plants not only self-facilitated but they also had positive effects on
269 other invasives through soil modification. We found that *Magallana* appeared to facilitate
270 *Austrominius* particularly in natural habitats where biotic pressure is greater than artificial
271 ones. The physical structure of the basibiont shell itself may increase attachment points
272 increasing post-settlement stability (Gribben et al. 2011) and/or act as a refuge from
273 predation for new recruits; its complexity restricting foraging efficiency, an effect shown

274 elsewhere for oysters (Grabowski and Powers 2004) and other taxa such as parasitoids (Gols
275 et al. 2005), birds (Adams et al. 2008) and insects (Yanoviak et al. 2017). The surface
276 complexity (rugosity) of shells and the reefs they form can alter boundary layer dynamics
277 over the surface of the shell, creating turbulence that can entrain weakly-swimming (passive)
278 early life-history stages over the shell's surface (Lim et al. 2020) that enhances recruitment
279 success (Koehl and Hadfield 2010).

280 Natural intertidal rocky habitats are generally characterised by high taxonomic and
281 functional richness (Darwin 1839; Firth et al. 2013) and space is often a limiting resource in
282 these typically highly competitive environments (Worm and Karez 2002). On investigating
283 the differential effects of native competitors and predators on *Magallana* across a range of
284 environmental contexts, Ruesink (2007) found that environmental stress can increase
285 competitive interaction strength reducing individual growth rates of the invasive oyster while
286 facilitating its survival. We found that the additional substrate offered by *Magallana* shells,
287 especially in natural habitats, may offer a refuge from competition pressure, thus facilitating
288 invasive epibionts in this environment.

289 Here, we show how the invasion of natural habitats by the oyster *Magallana* can facilitate
290 the invasive barnacle, *Austrominius modestus*, into a community as an epibiont. When
291 *Magallana* is not present, recruitment of *Austrominius* is limited. This study was carried out
292 in Britain where both invasive taxa are still relatively infrequent in natural rocky intertidal
293 habitats (Gallagher et al. 2016) such that facilitation of invasion into natural shores perhaps
294 remains limited. Coupled with the continued proliferation of artificial structures in the marine
295 environment, and the increased likelihood of spillover of invasive species into surrounding
296 natural habitats (Epstein and Smale 2018), an increase in 'novel habitat' for 'novel taxa' may
297 be expected (Glasby and Connell 1999).

298 Given that once established, invasive species are notoriously difficult to eradicate (Mack
299 and Lonsdale 2002) and the cost of invasion can be extremely high (Pimentel et al. 2005),
300 understanding to what extent the occupation of space by native and non-native species, and
301 subsequent potential to further accelerate invasion are needed. Our results further reinforce
302 the body of evidence that reports artificial habitats as enablers of invasion. But importantly,
303 they also reveal the importance of 'pioneer colonisers' in first occupying newly available free
304 space, as well as their potential to increase invasion by providing habitat for species that
305 ordinarily appears unsuitable. Worldwide, efforts to enhance biodiversity of artificial
306 structures are on-going (see Morris et al. 2018 and O'Shaughnessy et al. 2020b for reviews),
307 including the use of transplantation of ecosystem-engineer species to enhance biodiversity of
308 ordinarily depauperate surfaces (e.g. Ferrario et al. 2015, Ng et al. 2015). To date, these
309 efforts have received relatively little attention, but trials have indicated promising (e.g.
310 Perkol-Finkel et al. 2012), but variable results (Strain et al. 2020). Whilst the use of habit-
311 forming species for restoration efforts has been advocated and may well lead to positive
312 biodiversity outcomes (e.g. Byers et al. 2006), care must also be taken advocating the use of
313 invasive and non-native species, without full consideration of the wider environmental
314 implications (see Sotka & Byers' (2019) criticism of Ramus et al. (2017)) which may yield
315 unexpected results.

316

317 ***Conclusions***

318 The degree to which native habitat-forming species vs. invasive habitat-forming
319 species either do or do not facilitate other native or non-native species is a rich area for
320 investigation. There is growing evidence that positive interactions between native and
321 invasive species are important determinants of their local distribution and abundance
322 (Rodriguez, 2006; Bulleri et al. 2008; Northfield et al. 2018; Gribben et al 2020). Here we

323 show that these interactions may vary strongly with environmental context. It is possible that
324 abiotic environmental filters may be more important for inhibiting the establishment of native
325 taxa in disturbed environments, but that biological filters may be more important for
326 inhibiting the establishment of invasive taxa in natural and undisturbed environments. The
327 type (abiotic stress reduction or associational defence) and strength of facilitation may differ
328 depending on the response variables considered and environmental context. Future research
329 should consider responses of both native and invasive epibionts to native and invasive
330 habitat-forming species across a range of physical and biological contexts. We suggest that
331 particular attention should be given to the role of habitat-forming species in underpinning
332 both facilitation and habitat cascades, with wider ecosystem effects. Experimental work is
333 required to disentangle the processes underpinning these patterns.

334

335

336 **Data Storage**

337 Data will be made available through the Temperate Reef Base Portal.

338 <https://temperatereefbase.imas.utas.edu.au/static/landing.html>

339

340 **Declarations**

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346 Statistics were performed by AMK. All authors contributed to the writing of the paper that
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348

349 **Literature Cited**

- 350 Adams, E. M. and Frederick, P. C. 2008. Effects of methylmercury and spatial complexity on
351 foraging behavior and foraging efficiency in juvenile white ibises (*Eudocimus albus*). -
352 Environmental Toxicology and Chemistry: An International Journal 27: 1708-1712.
- 353 Airoidi, L. et al. 2015. Corridors for aliens but not for natives: effects of marine urban sprawl
354 at a regional scale. - Diversity and Distributions 21: 755-768.
- 355 Arenas, F. et al. 2006. The invasibility of marine algal assemblages: role of functional
356 diversity and identity. - Ecology 87: 2851-2861.
- 357 Bayne, B. L. et al. 2017. The proposed dropping of the genus *Crassostrea* for all Pacific
358 cupped oysters and its replacement by a new genus *Magallana*: a dissenting view. -
359 Journal of Shellfish Research 36: 545-547.
- 360 Berntsson, K. M. et al. 2004. Rejection of unsuitable substrata as a potential driver of
361 aggregated settlement in the barnacle *Balanus improvisus*. - Marine Ecology Progress
362 Series 275: 199-210.
- 363 Bertness, M. D. and Leonard, G. H. 1997. The role of positive interactions in communities:
364 lessons from intertidal habitats. - Ecology 78: 1976-1989.
- 365 Bertness, M. D. et al. 1999. Testing the relative contribution of positive and negative
366 interactions in rocky intertidal communities. - Ecology, 80: 2711-2726.
- 367 Bishop, J. D. et al. 2015. Unheralded arrivals: non-native sessile invertebrates in marinas on
368 the English coast. - Aquatic Invasions 10: 249-264.
- 369 Blanchard M. 1997. Spread of the slipper limpet *Crepidula fornicata* (L. 1758) in Europe.
370 Current state and consequences. - Scientia Marina 61: 109-118
- 371 Bracewell, S. A. et al. 2013. Predicting free-space occupancy on novel artificial structures by
372 an invasive intertidal barnacle using a removal experiment. - PLoS ONE 8: e74457.

- 373 Bracken, M. E. et al. 2014. Community context mediates the top-down vs. bottom-up effects
374 of grazers on rocky shores. - *Ecology* 95: 1458-1463.
- 375 Bruno, J. F. et al. 2003. Inclusion of facilitation into ecological theory. - *Trends in Ecology &*
376 *Evolution* 18: 119-125.
- 377 Bugnot, A. B. et al. 2020. Current and projected global extent of marine built structures. -
378 *Nature Sustainability* 1-9.
- 379 Bulleri, F. et al. 2008. Beyond competition: incorporating positive interactions between
380 species to predict ecosystem invasibility. - *PLoS Biology* 6: e162.
- 381 Bulleri, F., Cristaudo, C., Alestra, T. & Benedetti-Cecchi, L. 2011. Crossing gradients of
382 consumer pressure and physical stress on shallow rocky reefs: a test of the stress-gradient
383 hypothesis. - *Journal of Ecology* 99: 335–344.
- 384 Byers, J. E. et al. 2010. Variable direct and indirect effects of a habitat-modifying invasive
385 species on mortality of native fauna. - *Ecology* 91: 1787-1798.
- 386 Byers, J. E. et al. 2006. Using ecosystem engineers to restore ecological systems. - *Trends in*
387 *Ecology & Evolution* 21: 493-500.
- 388 Callaway, R. M. 1995. Positive interactions among plants. - *The Botanical Review* 61: 306-
389 349.
- 390 Chee, S. Y. et al. 2017. Land reclamation and artificial islands: Walking the tightrope
391 between development and conservation. - *Global Ecology and Conservation* 12: 80-95.
- 392 Clements, C.S. & Hay, M.E. 2015. Competitors as accomplices: seaweed competitors hide
393 corals from predatory sea stars. - *Proceedings of the Royal Society B: Biological Sciences*
394 282: 221–229.
- 395 Connell, J. H. 1961. The influence of interspecific competition and other factors on the
396 distribution of the barnacle *Chthamalus stellatus*. - *Ecology* 42: 710-723.
- 397 Darwin C (1839) *Voyage of the beagle*. Collier, New York

- 398 Demopoulos, A.W. and Smith, C.R. 2010. Invasive mangroves alter macrofaunal community
399 structure and facilitate opportunistic exotics. *Marine Ecology Progress Series* 404: 51-67.
- 400 Diederich, S. 2005. Differential recruitment of introduced Pacific oysters and native mussels
401 at the North Sea coast: coexistence possible?. - *Journal of Sea Research* 53: 269-281.
- 402 Dreanno, C. et al. 2007. Involvement of the barnacle settlement-inducing protein complex
403 (SIPC) in species recognition at settlement. - *Journal of Experimental Marine Biology and*
404 *Ecology* 351: 276-282.
- 405 Elton, C. S. 1958. *The Ecology of Invasions by Plants and Animals*. - Methuen, London.
- 406 Epstein, G. and Smale, D. A. 2018. Environmental and ecological factors influencing the
407 spillover of the non-native kelp, *Undaria pinnatifida*, from marinas into natural rocky reef
408 communities. - *Biological Invasions* 20: 1049-1072.
- 409 Ferrario, F. et al. 2016. The overlooked role of biotic factors in controlling the ecological
410 performance of artificial marine habitats. - *Journal of Applied Ecology* 53: 16-24.
- 411 Firth, L. B. et al. 2013. The importance of water-retaining features for biodiversity on
412 artificial intertidal coastal defence structures. - *Diversity and Distributions* 19: 1275-1283.
- 413 Firth, L. B. et al. 2016a. Facing the future: the importance of substratum features for
414 ecological engineering of artificial habitats in the rocky intertidal. - *Marine and*
415 *Freshwater Research* 67: 131-143.
- 416 Firth, L. B. et al. 2016b. Ocean sprawl: challenges and opportunities for biodiversity
417 management in a changing world. - *Oceanography and Marine Biology: an Annual*
418 *Review* 54: 201-278.
- 419 Gallagher, M. C. et al. 2015. The invasive barnacle species, *Austrominius modestus*: Its status
420 and competition with indigenous barnacles on the Isle of Cumbrae, Scotland. - *Estuarine,*
421 *Coastal and Shelf Science* 152: 134-141.

- 422 Gallagher, M. C. et al. 2016. Room for one more? Coexistence of native and non-indigenous
423 barnacle species. - *Biological Invasions* 18: 3033-3046.
- 424 Gaston, K. J. et al. 1997. Interspecific abundance-range size relationships: an appraisal of
425 mechanisms. - *Journal of Animal Ecology* 66: 579-601.
- 426 Gols, R. et al. 2005. Reduced foraging efficiency of a parasitoid under habitat complexity:
427 implications for population stability and species coexistence. - *Journal of Animal*
428 *Ecology* 74: 1059-1068.
- 429 Gomes-Filho, J. G. F. et al. 2010. Distribution of barnacles and dominance of the introduced
430 species *Elminius modestus* along two estuaries in South-West England. - *Marine*
431 *Biodiversity Records* 3: e58.
- 432 Grabowski, J. H., and S. P. Powers. 2004. Habitat complexity mitigates trophic transfer on
433 oyster reefs. - *Marine Ecology Progress Series* 277: 291-295.
- 434 Green, D. S., and T. P. Crowe. 2014. Context- and density-dependent effects of introduced
435 oysters on biodiversity. - *Biological Invasions* 16: 1145-1163.
- 436 Gribben, P. E. et al. 2011. Relative importance of natural cues and substrate morphology for
437 settlement of the New Zealand Green-shelled mussel *Perna canaliculus*. - *Aquaculture*
438 319: 240-246.
- 439 Gribben, P. E. et al. 2019. Facilitation cascades in marine ecosystems: A synthesis and future
440 directions. - *Oceanography and Marine Biology: an Annual Review* 57: 127-168
- 441 Gribben, P. E. et al. 2020. Habitat provided by native species facilitates higher abundances of
442 an invader in its introduced compared to native range. - *Scientific Reports* 10: 1-9.
- 443 Hanlon, N. et al. 2018. Time-dependent effects of orientation, heterogeneity and composition
444 determines benthic biological community recruitment patterns on subtidal artificial
445 structures. - *Ecological Engineering* 122: 219-228.

- 446 Harder, T. 2009. Marine epibiosis: concepts, ecological consequences and host defence,
447 Marine and industrial biofouling. Springer, pp. 219-231.
- 448 Harding, J.M., Walton, W.J., Trapani, C.M., Frick, M.G. and Mann, R., 2011. Sea turtles as
449 potential dispersal vectors for non-indigenous species: the veined rapa whelk as an
450 epibiont of loggerhead sea turtles. - *Southeastern Naturalist* 10: 233-244.
- 451 Harrington, L. et al. 2004. Recognition and selection of settlement substrata determine
452 post-settlement survival in corals. - *Ecology* 85: 3428-3437.
- 453 Herbert, R. J. H. and Hawkins, S. J. 2006. Effect of rock type on the recruitment and early
454 mortality of the barnacle *Chthamalus montagui*. - *Journal of Experimental Marine Biology*
455 *and Ecology* 334: 96-108.
- 456 Herbert, R. J. et al. 2016. Ecological impacts of non-native Pacific oysters (*Crassostrea*
457 *gigas*) and management measures for protected areas in Europe. - *Biodiversity and*
458 *Conservation* 25: 2835-2865.
- 459 Hewitt, CL. 1993. Marine Biological Invasions: The Distributional Ecology and Interactions
460 Between Native and Introduced Encrusting Organisms. PhD dissertation, Department of
461 Biology, University of Oregon, Eugene, USA. (<http://hdl.handle.net/1794/9974>)
- 462 Huggett, M. J., et al. 2005. Settlement of larval blacklip abalone, *Haliotis rubra*, in response
463 to green and red macroalgae. - *Marine Biology* 147: 1155-1163.
- 464 Hutchinson, G. E., 1961. The paradox of the plankton. - *The American Naturalist* 95: 137-
465 145.
- 466 James, M.K. et al. 2019. Reverse engineering field-derived vertical distribution profiles to
467 infer larval swimming behaviors. - *Proceedings of the National Academy of Sciences* 116:
468 11818-11823.
- 469 Jones, C. G. et al. 1997. Positive and negative effects of organisms as physical ecosystem
470 engineers. - *Ecology* 78: 1946-1957.

- 471 Jordan, N. R. et al. 2008. Soil modification by invasive plants: effects on native and invasive
472 species of mixed-grass prairies. - *Biological Invasions* 10: 177-190.
- 473 Knights A. M., et al. 2016. Plymouth – A World Harbour through the ages. - *Regional*
474 *Studies in Marine Science* 8: 297-307.
- 475 Koehl, M. A. R. and Hadfield, M. G. 2010. Hydrodynamics of larval settlement from a
476 larva's point of view. - *Integrative and Comparative Biology* 50: 539-551.
- 477 Kraft, N. J. et al. 2008. Functional traits and niche-based tree community assembly in an
478 Amazonian forest. - *Science* 322: 580-582.
- 479 Krassoi, F. R. et al. 2008. Condition-specific competition allows coexistence of competitively
480 superior exotic oysters with native oysters. - *Journal of Animal Ecology* 77: 5-15.
- 481 Leonard, K. et al. 2017. Epibiotic pressure contributes to biofouling invader success. -
482 *Scientific Reports* 7: 5173.
- 483 Lim, H. S. et al. 2020. Spatial arrangement of biogenic reefs alters boundary layer
484 characteristics to increase risk of microplastic bioaccumulation. - *Environmental Research*
485 *Letters* 15: 064024.
- 486 Loke, L. H. and Todd, P. A. 2016. Structural complexity and component type increase
487 intertidal biodiversity independently of area. - *Ecology*, 97: 383-393.
- 488 MacArthur, R. H. and MacArthur, J. W., 1961. On bird species diversity. *Ecology* 42: 594-
489 598.
- 490 Mack, R.N. and Lonsdale, W. M. 2002. Eradicating invasive plants: hard-won lessons for
491 islands. In Veitch C.R. and M.N. Clout (Eds.) *Turning the tide: the eradication of invasive*
492 *species*, pp.164-172.
- 493 Markert, A. et al. 2010. Recently established *Crassostrea*-reefs versus native *Mytilus*-beds:
494 differences in ecosystem engineering affects the macrofaunal communities (Wadden Sea
495 of Lower Saxony, southern German Bight). - *Biological Invasions* 12: 15.

- 496 McKnight, W. and Chudleigh I. J. 2015. Pacific oyster *Crassostrea gigas* control within the
497 inter-tidal zone of the North East Kent Marine Protected Areas, UK. - Conservation
498 Evidence 12: 28-32.
- 499 McManus, R.S. et al. 2018. Partial replacement of cement for waste aggregates in concrete
500 coastal and marine infrastructure: a foundation for ecological enhancement?. - Ecological
501 Engineering 120: 655-667.
- 502 Mendez, M. M. et al. 2014. Invasive barnacle fouling on an endemic burrowing crab mobile
503 basibionts as vectors to invade a suboptimal habitat. - Thalassas 30: 39–46.
- 504 Mieszkowska, N. et al. 2013. Impacts of climate change on intertidal habitats. MCCIP
505 Science Review 180-192.
- 506 Mineur, F. et al. 2012. Changing coasts: Marine aliens and artificial structures. -
507 Oceanography and Marine Biology: an Annual Review 50: 198-243.
- 508 Morgan, E.H. and Richardson, C.A. 2012. The potential role of an unregulated coastal
509 anthropogenic activity in facilitating the spread of a non-indigenous biofoulant. -
510 Biofouling 28: 743-753.
- 511 Morris, R.L. et al. 2019. Design options, implementation issues and evaluating success of
512 ecologically engineered shorelines. - Oceanography and Marine Biology: an Annual
513 Review 57: 169–228.
- 514 Moschella, P. S. et al. 2005. Low-crested coastal defence structures as artificial habitats for
515 marine life: using ecological criteria in design. - Coastal Engineering 52: 1053-1071.
- 516 Ng, C. S. L. et al. 2015. Enhancing the biodiversity of coastal defence structures:
517 transplantation of nursery-reared reef biota onto intertidal seawalls. - Ecological
518 Engineering 82: 480-486.
- 519 Northfield, T. D. et al. 2018. Native turncoats and indirect facilitation of species invasions. –
520 Proceedings of the Royal Society B 285, 20171936 (2018).

- 521 Olyarnik, S. V. et al. 2009. Ecological factors affecting community invasibility. In Biological
522 invasions in marine ecosystems (pp. 215-238). Springer, Berlin, Heidelberg.
- 523 O'Riordan, R.M. and Murphy O. 2000. Variation in the reproductive cycle of *Elminius*
524 *modestus* in southern Ireland. - Journal of the Marine Biological Association of the United
525 Kingdom 80: 607-616.
- 526 O'Shaughnessy, K.A. et al. 2020a. Occurrence and assemblage composition of intertidal non-
527 native species may be influenced by shipping patterns and artificial structures. - Marine
528 Pollution Bulletin 154: 111082.
- 529 O'Shaughnessy, K.A. et al. 2020b. Design catalogue for eco-engineering of coastal artificial
530 structures: a multifunctional approach for stakeholders and end-users. - Urban Ecosystems
531 23: 431-443.
- 532 Paine, R.T., 1966. Food web complexity and species diversity. - The American Naturalist
533 100: 65-75.
- 534 Paine, R.T., and Levin, S.A., 1981. Intertidal landscapes: disturbance and the dynamics of
535 pattern. - Ecological Monographs 51: 145-178.
- 536 Perkol-Finkel, S. et al. 2012. Conservation challenges in urban seascapes: promoting the
537 growth of threatened species on coastal infrastructures. - Journal of Applied Ecology 49:
538 1457-1466.
- 539 Pimentel, D. et al. 2005. Update on the environmental and economic costs associated with
540 alien-invasive species in the United States. - Ecological Economics 52: 273-288.
- 541 Ramus, A.P. et al. 2017. An invasive foundation species enhances multifunctionality in a
542 coastal ecosystem. - Proceedings of the National Academy of Sciences 114: 8580-8585.
- 543 Reise, K., 1998. Pacific oysters invade mussel beds in the European Wadden Sea.
544 *Senckenbergiana Maritima* 28, 167-175.

- 545 Robertson, J. H. 1947. Responses of range grasses to different intensities of competition with
546 sage-brush (*Artemisia tridentata* Nutt.). - Ecology 28: 1-16.
- 547 Rodriguez, L. F. 2006. Can invasive species facilitate native species? Evidence of how,
548 when, and why these impacts occur. – Biological Invasions 8: 927-939.
- 549 Ruesink, J. L. et al. 2005. Introduction of non-native oysters: ecosystem effects and
550 restoration implications. - Annual Review of Ecology, Evolution & Systematics 36: 643-
551 689.
- 552 Ruesink, J. L. 2007. Biotic resistance and facilitation of a non-native oyster on rocky shores.
553 - Marine Ecology Progress Series 331: 1-9.
- 554 Schindelin, J. et al. 2012. Fiji: an open-source platform for biological-image analysis. -
555 Nature Methods 9: 676-682.
- 556 Simberloff, D. and Von Holle B. 1999. Positive interactions of nonindigenous species:
557 invasional meltdown?. - Biological Invasions 1: 21-32.
- 558 Sotka, E. E. and Byers, J. E. 2019. Not so fast: promoting invasive species to enhance
559 multifunctionality in a native ecosystem requires strong(er) scrutiny. - Biological
560 Invasions 21: 19-25.
- 561 Strain E. M. et al. 2020. A global analysis of complexity-biodiversity relationships on marine
562 artificial structures. - Global Ecology and Biogeography. DOI: 10.1111/geb.13202
- 563 Tecco, P.A. et al. 2006. Positive interaction between invasive plants: the influence of
564 *Pyracantha angustifolia* on the recruitment of native and exotic woody species. - Austral
565 Ecology 31: 293-300.
- 566 Thiagarajah, J. et al. 2015. Historical and contemporary cultural ecosystem service values in
567 the rapidly urbanizing city state of Singapore. - Ambio 44: 666-677.
- 568 Uyà, M. et al. 2020. Facilitation of an invader by a native habitat-former increases along
569 interacting gradients of environmental stress. - Ecology 101: p.e02961.

- 570 Wahl, M., 1997. Living attached: Aufwuchs, fouling, epibiosis. Fouling Organisms of the
571 Indian Ocean: Biology and Control Technology.
- 572 Wahl, M. 1989. Marine epibiosis. I. Fouling and antifouling: some basic aspects. - Marine
573 Ecology Progress Series 58: 175-189.
- 574 Wahl, M., 2009. Epibiosis. In Marine hard bottom communities (pp. 61-72). Springer, Berlin,
575 Heidelberg.
- 576 Worm, B. and Karez, R., 2002. Competition, coexistence and diversity on rocky shores. In
577 Competition and coexistence (pp. 133-163). Springer, Berlin, Heidelberg.
- 578 Wright, J. T. and Gribben P. E. 2017. Disturbance-mediated facilitation by an intertidal
579 ecosystem engineer. - Ecology 98: 2425-2436.
- 580 Yanoviak, S.P. et al. 2017. Surface roughness affects the running speed of tropical canopy
581 ants. - Biotropica 49: 92-100.

582 **Figure Titles**

583 Figure 1. (a) Location of the six survey locations in southwest UK where pairs of natural and
584 artificial sites were exposed to similar environmental conditions.

585

586 Figure 2. Predicted probability of presence in quadrats by the invasive oyster, *M. gigas*, the
587 native limpet, *P. vulgata*, and invasive, *A. modestus* and native barnacles (on rock only, not
588 as epibionts) in artificial and natural habitats. Letters over bars indicate same or different
589 groupings between habitat type. Bars around the means represent 95% confidence intervals.

590

591 Figure 3. The effect of habitat type (natural, artificial) and substrate type (rock, invasive
592 habitat-former (*Magallana*), native basibiont (*Patella*)) on invasive (*Austrominius*) and native
593 barnacles (median, x,y,z).

594

595 Figure 4. (a) Predicted percentage of overall barnacle community that are invasive
596 (*Austrominius*) on native (*Patella*, left) and invasive (*Magallana*, middle) basibionts and rock
597 substrata (right) in artificial (grey shading) and natural (blue shading) habitats based on
598 negative binomial fits. Shading indicates 95% Confidence Intervals. (b) Relative strength of
599 facilitation of the total abundance of invasive barnacles (*Austrominius*) by native
600 (*Patella*) and invasive (*Magallana*) basibionts between artificial (grey bars) and natural (blue
601 bars) habitats. Letters over bars indicate same or different groupings between habitat type.

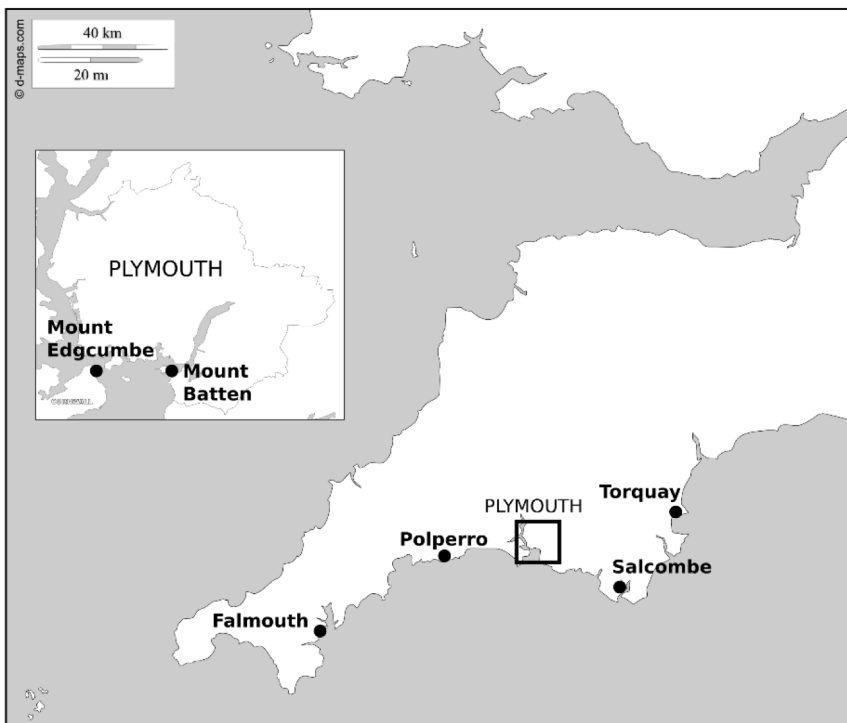


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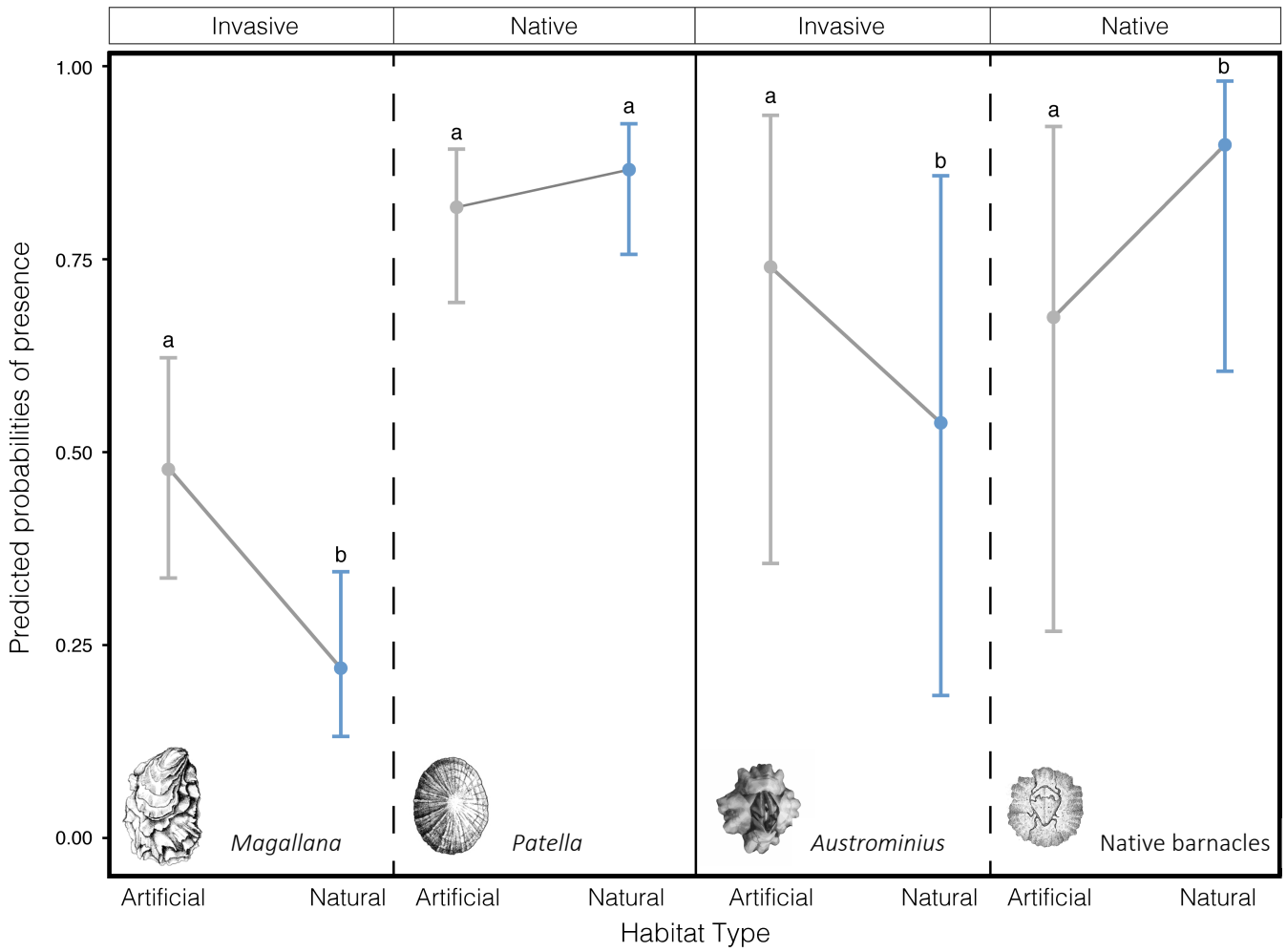


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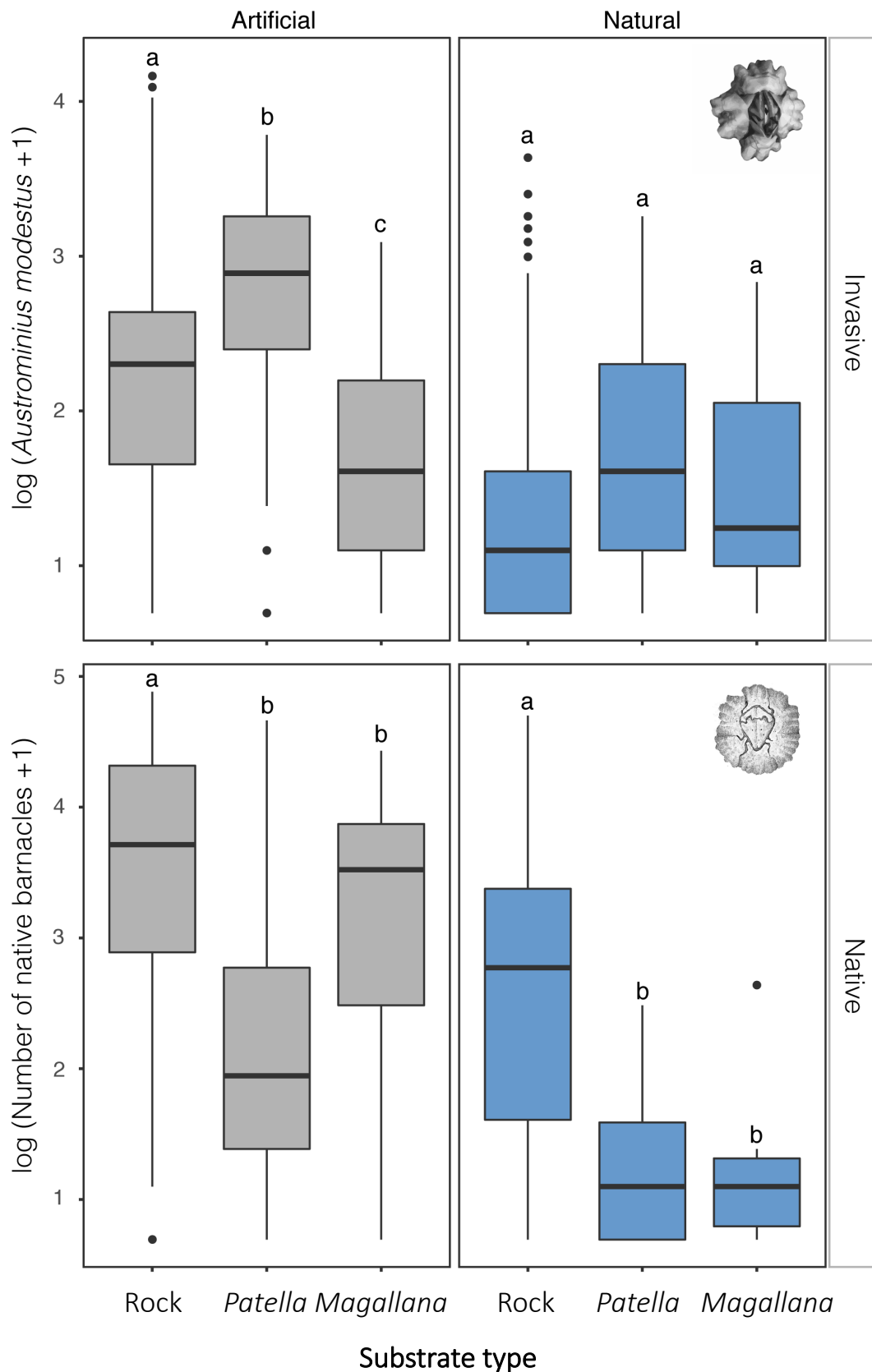


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