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

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## OIKOS

# 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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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

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

## Introduction

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

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

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

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

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

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

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

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

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

## Materials and Methods

### *Study locations*

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

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

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

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

In the first instance, we used surveys at each location to quantify the prevalence of all taxa (i.e. barnacles, *Magallana*, and *Patella*) on natural rocky shore and on artificial seawall habitats. The abundance of *Magallana* and *Patella* on rock substrata was quantified using 15 haphazardly-placed quadrats (50 × 50 cm) on flat vertical/near-vertical surfaces within a 10m<sup>2</sup> area at mid-shore elevation. Concurrently, a 3 × 3 cm photo-quadrat was taken within the larger quadrat, then imported into image analysis software (Fiji Cell Counter Tool, Schindelin et al. 2012) and used to quantify the abundance and relative proportion of invasive *Austrominius* and native barnacles living directly on the rock substrata (not as epibionts). In all surveys described below, native barnacles comprised *S. balanoides*, *C. montagui* and *C. stellatus* and were identified to species to assign them as native barnacles, but their identity was not considered further as we were interested in the relative differences between native and invasive groups rather than the species themselves. As such, we refer to the native barnacle community as simply 'native barnacles' herein ignoring species identity.

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

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

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



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

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

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

## Results

### *Comparison of invasive and native taxa between natural and artificial habitats*

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

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

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

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

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

## Discussion

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

prevalent in artificial than natural habitats. Distribution patterns were less consistent for native species, with *Patella* found in similar numbers in both natural and artificial habitats, and native barnacles were typically more likely to occur in natural habitats over artificial. Whilst basibionts were more important for invasive than native epibionts overall, we also found that 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 findings build on the evidence base that artificial substrata represent poor habitats for native species (Firth et al. 2013, 2016b; Airoidi et al. 2015), but they can represent good habitats for invasive species (Bishop et al. 2015; O'Shaughnessy et al. 2020a; see Mineur et al. 2012 for review). A growing body of research suggests that artificial substrata are too homogeneous and lack the necessary topographic complexity at a range of spatial scales that is required for successful settlement and recruitment of native taxa (Moschella et al. 2005; Firth et al. 2013; Loke and Todd 2016). Many invasive taxa have broader environmental tolerances enabling them to colonise and dominate artificial substrata. In this way, homogenous artificial substrata may function as the 'initial' abiotic environmental filter (Olyarnik et al. 2009) for native taxa but not for invasive taxa.

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

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

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

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

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

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

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

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

## **Conclusions**

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. There is growing evidence that positive interactions between native and invasive species are important determinants of their local distribution and abundance (Rodriguez, 2006; Bulleri et al. 2008; Northfield et al. 2018; Gribben et al 2020). Here we

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

#### **Data Storage**

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

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

#### **Declarations**

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## 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.

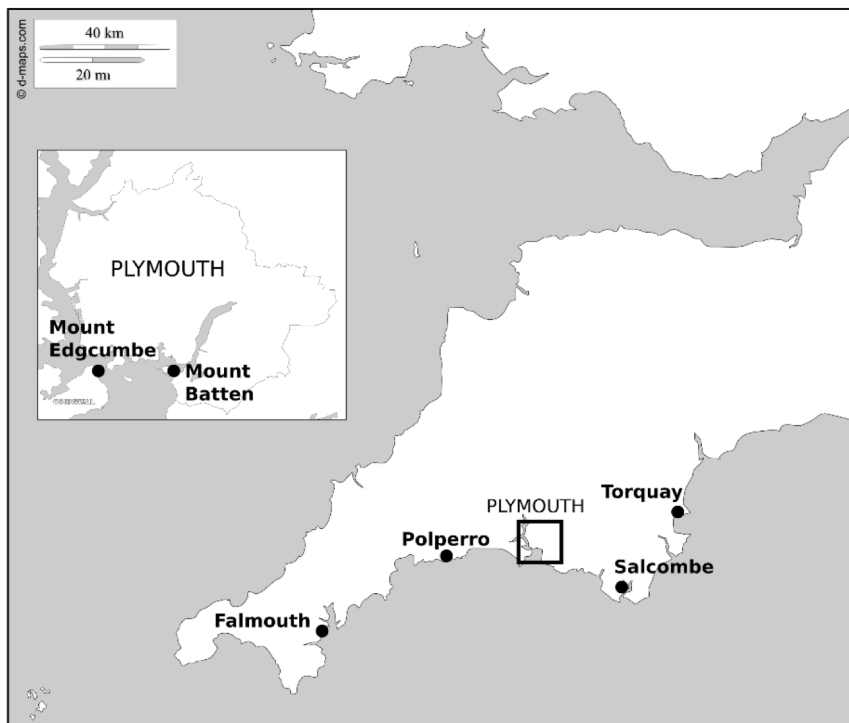


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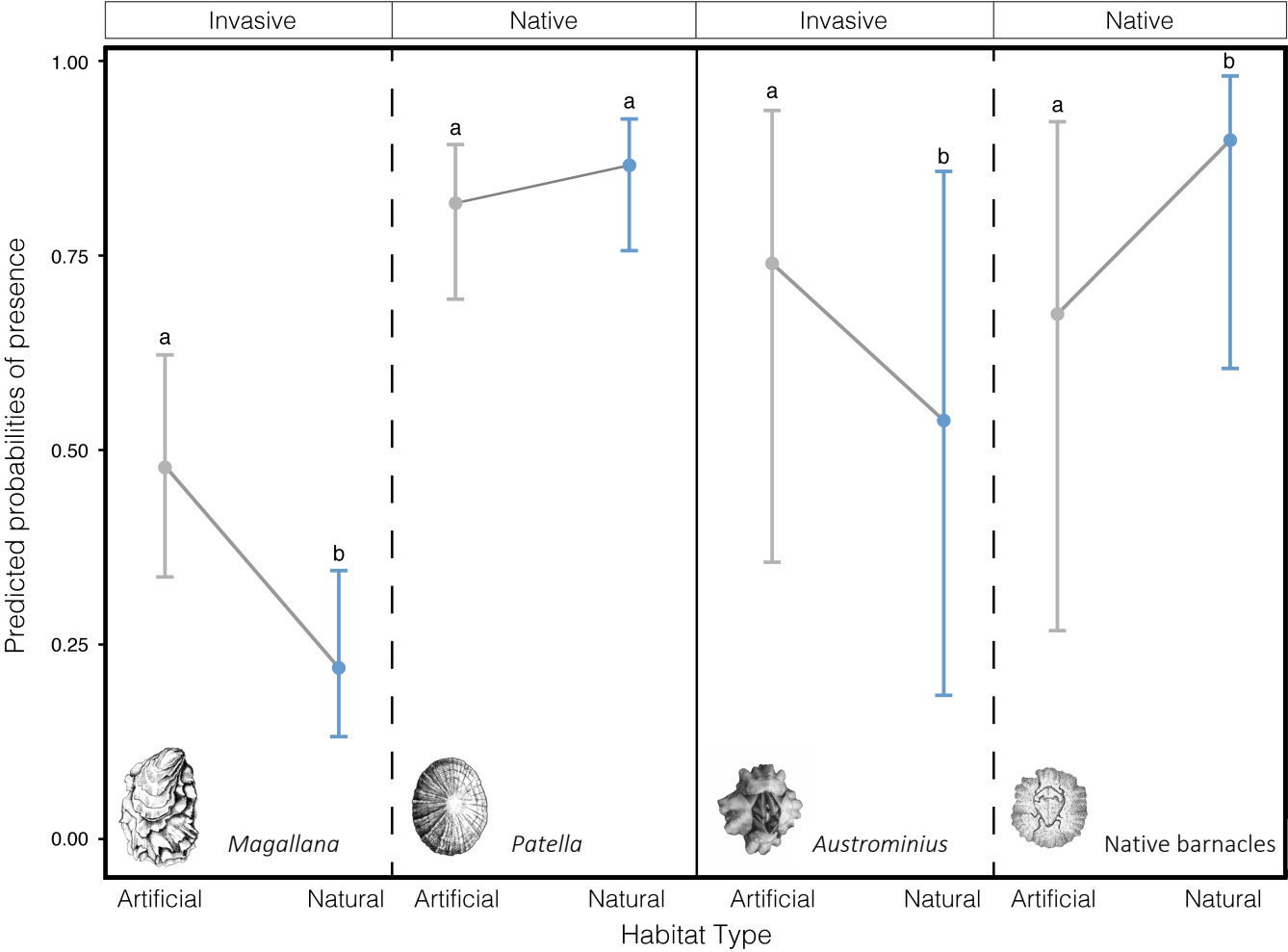


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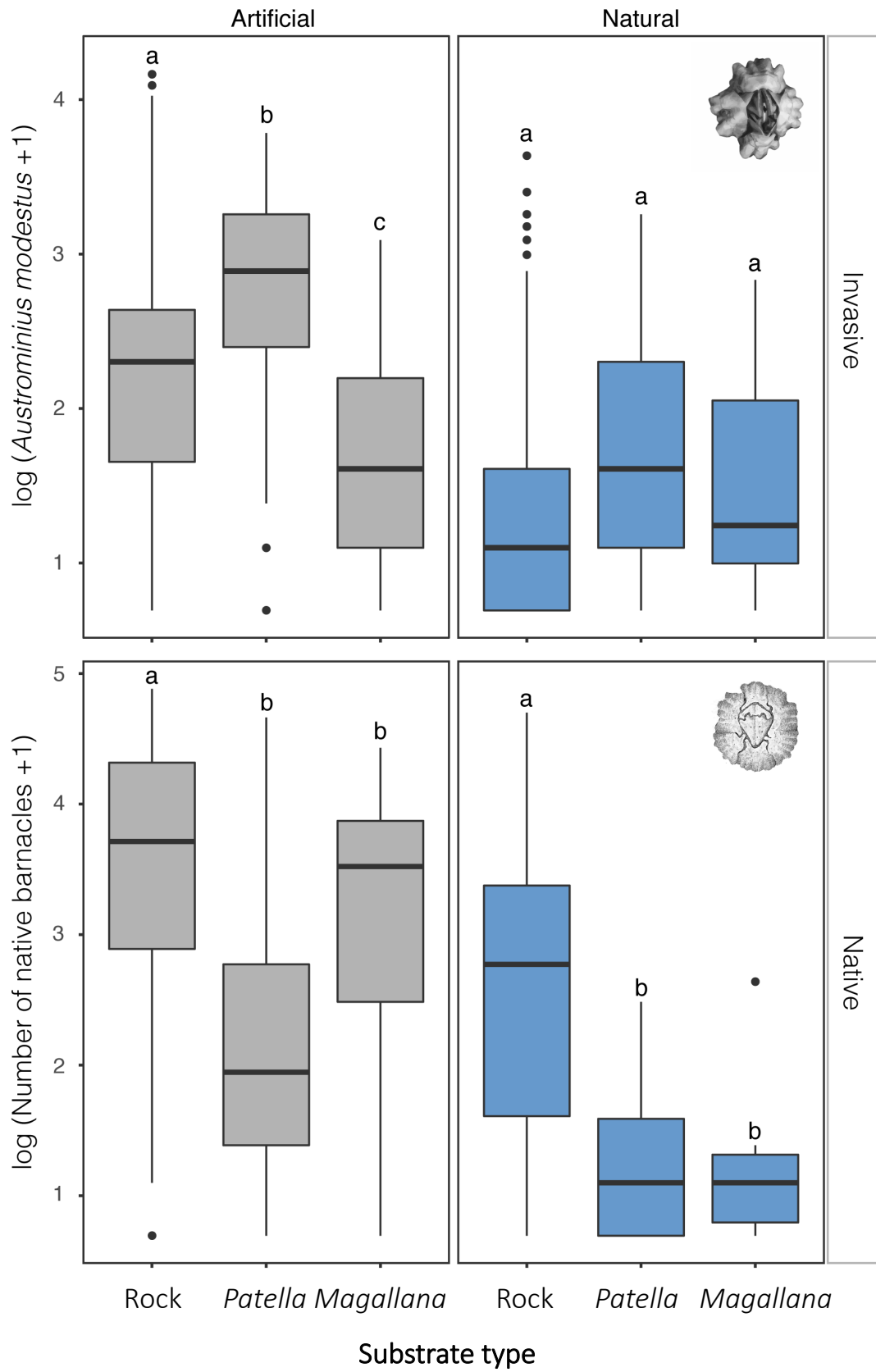


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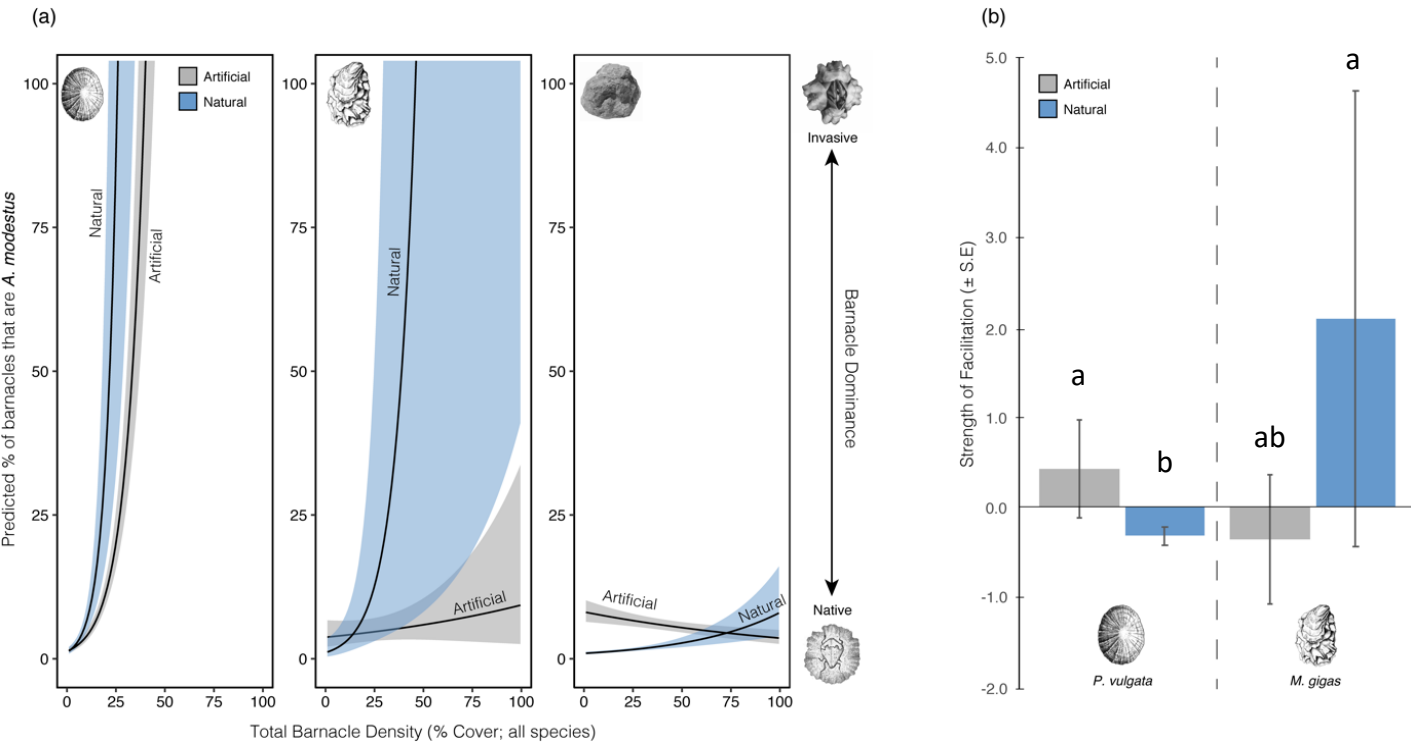


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