Ecological and environmental context shape the differential effects of a facilitator in its native and invaded ranges

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Abstract

Non-indigenous species often exhibit disproportionately strong negative effects in their introduced range compared to their native range, and much research has been devoted to understanding the role of shared evolutionary history, or lack thereof, in driving these differences. Less studied is whether non-indigenous species, particularly those that are important as facilitators in their native range, have persistent positive effects in their invaded range despite a lack of a shared evolutionary history with the invaded community. Here, we manipulated the density of a habitat-forming facilitator, the high intertidal acorn barnacle *Balanus glandula*, factorially with herbivore density in its native range (Bluestone Point, British Columbia, Canada) and invaded range (Punta Ameghino, Chubut Province, Argentina) to determine how this facilitator differentially affects associated species at these two locations. Given that high intertidal species at Punta Ameghino (PA) are evolutionarily naïve to barnacles, we predicted that the positive effects of *B. glandula* at PA would absent or weak compared to those at Bluestone Point (BP). However, we found that *B. glandula* had an equally positive effect on herbivore biomass at PA compared to BP, possibly because the moisture-retaining properties of barnacle bed habitats are particularly important in seasonally dry Patagonia. Barnacle presence indirectly decreased ephemeral algal cover at BP by increasing grazer pressure, but barnacles instead facilitated ephemeral algae at PA. In contrast, *B. glandula* increased perennial algal cover at BP, but generally decreased perennial algal cover at PA, likely due to differences in dominant algal morphology. These results suggest that shared evolutionary history is not a prerequisite for strong facilitation to occur, but rather that the nature and strength of novel species interactions are determined by the traits of associated species and the environment in which they occur.

Key words

Invasive species, positive interactions, facilitation, intertidal zone, *Balanus glandula*, British Columbia, Patagonia, environmental stress, biogenic habitat, foundation species

Introduction

Species introductions are changing the composition and dynamics of ecological communities throughout the world (Ricciardi et al. 2013). Many newly arrived species rapidly become ecological dominants that can have an array of positive and negative impacts on native species. As a result, there has been much interest in how the ecology and traits of a species in its native range predict its impacts in newly invaded areas (Fournier et al. 2019).

Ecologists have long supposed that invaders often have stronger negative impacts in their invaded range than in their native range (Darwin 1859; Elton 1958). For example, invasive predators may be able to exploit naïve prey in their invaded range (Sih et al. 2010), as happens with snakes or rodents introduced to islands with no similar predators (Wiles et al. 2003; Harper & Bunbury 2015). Novel weapons such as allelopathic chemicals may increase the negative effects of invading species on the recipient community (Callaway et al. 2012). Invaders, released from their natural parasites and consumers, may become competitive dominants in their invaded range (Keogh et al. 2017; Lucero et al. 2019). Despite the growing list of invasion impact case studies conducted in invaded ranges, explicit comparisons of the effects of non-native species between their native and introduced ranges are rare (Hierro et al. 2005; Gribben & Byers 2020). Available data suggest that many organisms do have stronger negative effects in their introduced ranges, although the mechanisms behind this are not always clear (Callaway et al. 2012; Maurel et al. 2013; Puritty et al. 2018).

Although there are many spectacular examples of their negative impacts, introduced species may also have positive impacts in their recipient community. For example, non-native prey that can be exploited as a dietary resource may bolster native predator abundance (Pintor & Byers 2015), and some introduced generalist pollinators can increase reproductive success in native plants (Agüero et al. 2020). Introduced species may act as ecosystem engineers and provide biogenic habitat for native species, of which there are many examples including: bivalves (Gestoso et al. 2013); bryozoans (Sellheim et al. 2010); mangroves (Demopoulos & Smith 2010); mudsnails (Thyrring et al. 2013); seagrasses (Posey 1988); seaweeds (Wright et al. 2014); and terrestrial woody plants (Procheş et al. 2008).

While few studies have examined how the positive effects of a facilitator change upon its introduction to a new system, we can still make basic predictions about what might occur. Because invaders generally have no recent shared evolutionary history with species in the invaded community, and thus no selection strengthening their association, an introduced facilitator should provide comparatively little benefit to native species (Bronstein 2009). This prediction appears to hold for ectomycorrhizal fungi, which may associate with numerous plant taxa in their native range but often cannot associate with evolutionarily naïve plants elsewhere (Vellinga et al. 2009). Many novel facilitations involve generalist facilitators, where the identity of the associated species is of little importance to the interaction, but these usually form only if a native functional equivalent exists (Aslan et al. 2015). Absent such functional equivalents, we would expect non-native facilitators to have weaker positive effects in their introduced range.

In addition to shared evolutionary history, local environmental context may be a strong driver of facilitators' effects, particularly for those facilitators that benefit the survival and growth of associated species by mitigating environmental stress. The benefit facilitators provide, and thus the strength of facilitation, is often more pronounced in stressful environments (Bertness & Callaway 1994; Bertness & Leonard 1997; He et al. 2013). Thus, if conditions in an invaded range are more stressful than in the native range, then a novel facilitation could be stronger than analogous facilitations in the native range.

Acorn barnacles are important facilitators in high intertidal rocky shore communities around the world. Though these barnacles are often dominant competitors for space (Connell 1961; Dayton 1971), they also provide a prey base for diverse taxa (Connell 1961; Paine 1980) and serve as ecosystem engineers for many species, providing refugia from hydrodynamic and desiccation stress (Harley 2006). Indeed, barnacles have many known facilitative effects: enhanced recruitment of macroalgae by limiting herbivore access (Dungan 1986; Geller 1991); increased recruitment of sessile invertebrates by providing favorable microhabitats (Menge 1976; Navarrete & Castilla 1990; Bertness et al. 2006); and enhanced density and diversity of mobile species by providing refugia, feeding areas, or both (Harley 2006; Harley & O'Riley 2011).

We tested the effect of one such facilitator – the acorn barnacle *Balanus glandula* (Darwin, 1854) – in its native and its invaded range through concurrent field manipulations in British Columbia, Canada (native range) and Chubut Province, Argentina (invaded range). Historically, there were no mid or high intertidal acorn barnacles along the Atlantic coast of Patagonia (with the exception of Tierra del Fuego, where some chthamalid barnacles are found). However, in the late 1960s, *B. glandula* arrived in Argentina from the west coast of North America. As of 2004, *B. glandula* had spread from its initial foothold in Mar del Plata (-38.0500) to Cabo Peña in Tierra del Fuego (-53.3008) (Schwindt 2007). This stretch of the Patagonian coast is known for its desiccation stress (Bertness et al. 2006; Silliman et al. 2011) and presents a unique opportunity to study the effects of an ecosystem engineer that has been introduced into a habitat with no functionally equivalent native species – which may weaken facilitation – but a considerable level of environmental stress – which may strengthen facilitation.

Because Argentinian high intertidal species are evolutionarily naïve to acorn barnacles, we hypothesized that, even in Patagonia's desiccating environment, the facilitative effects of *B. glandula* would be weaker in their invaded range compared to their native range. To test this hypothesis, we conducted barnacle density manipulations at both Bluestone Point in Barkley Sound, Canada (BP) and Punta Ameghino in the Nuevo Gulf, Argentina (PA) and documented the effects of *B. glandula* on both high intertidal communities. To better assess the mechanisms that may underpin the ecological role of barnacles, we factorially manipulated densities of locally dominant herbivores (the true limpets *Lottia* spp. at BP and the pulmonate limpet *Siphonaria lessonii* at PA). First, we predicted that barnacles would facilitate mobile grazers at BP by providing refugia from abiotic stress, but that this facilitation would be absent at PA, where *S. lessonii* has no shared evolutionary history with barnacle beds. Second, we predicted that *B. glandula* would facilitate macroalgae at BP by providing a refuge from herbivory, but would have a reduced positive, perhaps even negative, effect on naïve macroalgae at PA.

Materials and Methods

Field sites

This research was conducted within the native range of *B. glandula* in British Columbia, Canada from June 2006 to July 2007, and within its invaded range in Chubut Province, Argentina from December 2005 to February 2007 (Appendix S1: Fig. S1).

Research in Canada was conducted on the traditional territories of the Huu-ay-aht First Nations at Bluestone Point (48.8195, -125.1463) near Bamfield in Barkley Sound. Bluestone

Point (BP) is a semi-exposed granitic shore. Conditions are frequently overcast, temperatures are consistently mild, and relative humidity is generally high year-round. Dominant high intertidal grazers include limpets (mostly *Lottia digitalis*) and littorine snails (*Littorina* spp.). Ephemeral algae – *Ulva* sp., *Urospora* sp., *Pyropia* spp., and occasionally filamentous diatom mats – can also be found, particularly in the winter and/or where grazers are rare. Several species of perennial algae co-occur with *B. glandula* with *Fucus distichus* being the most common, and *Mastocarpus* sp., *Pelvetiopsis limitata*, and *Endocladia muricata* occurring in lower abundance.

Experimental manipulations in Argentina were conducted at Punta Ameghino (-42.6185, -64.8643) in the Nuevo Gulf, a large bay in Northern Patagonia. Punta Ameghino (PA) is a semi-protected mudstone shore. Temperatures in this region are generally mild year-round, but desiccation stress occurs seasonally due to exceptionally strong, dry southern trade winds, low precipitation, and low humidity (Bertness et al. 2006; Silliman et al. 2011; Livore et al. 2018). Prior to the arrival of *B. glandula*, there was no native high intertidal barnacle on Argentinian shores beyond the far southern coast (Schwindt 2007). Space occupancy in the high intertidal zone was historically relatively low during the summer, with pulmonate limpets (*Siphonaria lessonii*) being the most common invertebrate above mid intertidal mussel beds. Additional grazers are largely absent in the high intertidal zone (Schwindt, personal observation). A suite of ephemeral algae including *Blidingia minima*, *Bangia fuscopurpurea*, *Pyropia columbina*, *Polysiphonia* spp., and *Dictyota dichotoma* appear during the winter (Raffo et al. 2014). *Ralfsia* sp., a red algal crust, is the sole perennial macroalga found in the high intertidal zone.

Characterization of abiotic stress

High intertidal substratum temperature was measured at hourly intervals using iButton temperature loggers for one summer at each location (DS1921G-F5# Thermochron, Dallas Semiconductor) following similar methods to those of Harley and Lopez (2003). Briefly, iButtons were wrapped in Parafilm and epoxied (Sea Goin' Poxy Putty, Permalite Plastics) into pre-chiseled depressions in the rock such that the epoxy surface was flush with the surrounding rock surface. Fine sand from a beach adjacent to each site was pressed onto the surface of the epoxy before it set to better approximate the characteristics of the natural rock. Substratum temperatures recorded in this way are highly correlated with *B. glandula* body temperature, more so than air temperature (Harley & Lopez 2003).

Monthly relative humidity data were collected for a representative five-year period (2015-2020) from weather stations near each study location to approximate local conditions: Tofino, Canada in the native range (Climate Canada) and Puerto Madryn, Argentina in the invaded range (Centro Nacional Patagónico Laboratorio de Climatología). This period was used because comparable data for both sites were not available during the experimental period.

Experimental manipulations

To distinguish the direct and indirect effects of barnacles on other species, we factorially manipulated barnacle and dominant grazer densities (Appendix S1: Fig. S2). A total of 36 plots (2 barnacle treatments × 3 grazer treatments x 6 replicates) were established at both PA and BP. In all cases, plots were located on gently sloping surfaces to improve drainage. At PA, the topography of the high intertidal zone was relatively homogenous, allowing us to assign plots to treatments using a stratified random design. At BP, however, local topographic complexity necessitated a blocked design, where all six treatments were replicated once in each of six blocks. Plots within blocks were separated by less than 2 m, and blocks were 10-50 m apart.

Barnacle treatments consisted of either natural *B. glandula* densities (69.9 ± 3.3% cover at BP, 45.7 ± 2.3% at PA, means ± s.e., n = 18) or complete removal of barnacles by careful extraction with scrapers, leaving other sessile taxa undisturbed. There were three grazer treatments: an unfenced control treatment; an inclusion treatment, where *Lottia digitalis* at BP and *S. lessonii* at PA were fenced in at natural densities (5.19 individuals per 100 cm^2 in BC, 6.02 individuals per 100 cm^2 at PA); and an exclusion treatment with the same grazers fenced out. Fences were constructed from metallic copper rings (height = 2.5 cm, diameter = 10.7 cm, internal area = 90 cm^2) and attached to the substratum with epoxy (Sea Goin' Poxy Putty, Permalite Plastics). This design is demonstrably effective for controlling limpet densities on rocky shores (Harley 2002). When plots were inspected every 4-8 weeks, *Lottia digitalis* and *S. lessonii* were removed when found in the exclusion treatment and added to the inclusion treatment when densities dropped to one or fewer, though both events were rare.

Both experiments were initiated at the beginning of the summer in their respective hemispheres – 3 December 2005 at PA, and 15 June 2006 at BP. The experiments were sampled 9-10 times over the following 14-15 months (early summer in year one through mid-late summer in year two). In control plots across all grazer treatments, limpets or pulmonate limpets and littorine snails (BP only) were counted. The percent cover of ephemeral and perennial algal species was visually estimated with the aid of a small quadrat. Finally, barnacle recruits (defined as individuals < 2 mm), both *B. glandula* and *Chthamalus dalli* (BP only), were counted. Because young *B. glandula* typically grow beyond this size faster than the intervening time between our sampling dates (Sanford & Menge 2001), we likely undersampled recruits, but by the same token we were unlikely to double-count individuals as recruits.

Because experimental plots at BP contained littorine snails, but no equivalent existed at PA, we converted herbivore abundances in unfenced control plots to total herbivore biomass to allow comparison between sites (see Appendix S1 for methodological details.

Statistical analyses

All analyses were completed using R version 4.0.2 (R Core Team 2020). We modeled temperature and humidity data using linear models with location as the sole fixed effect and modeled all biological response data using generalized linear mixed models with the *glmmTMB* package (Brooks et al. 2017). To model each biological response variable, we first created full models with the maximum possible level of interaction between fixed effects (grazer treatment, barnacle treatment, time since experiment start, and location if applicable) and a random effect of block nested within location. Removing the random block effect always increased AIC and thus it was always included. Model diagnostics (residuals plots and Durbin-Watson tests) were run using the *DHARMa* package (Hartig 2020). No temporal autocorrelation was detected, and so no random effects for time were included. A dispersion formula was included for models of herbivore biomass, perennial algal cover, and barnacle recruit abundance, which had heteroscedastic residuals. Due to substantive non-linearity in algal cover through time, we chose only three timepoints to analyze using linear modeling – those closest to the spring equinox and both fall equinoxes at each location. Models of herbivore and barnacle recruit abundance were fit using a negative binomial error distribution. Herbivore biomass, ephemeral algal cover, and cover of *F. distichus* were analyzed using a Tweedie error distribution, while perennial algae cover was logit-transformed and fit using a Gaussian error distribution. Full models were reduced according to AIC and term significance with the *drop1* function, and final models were analyzed by Type II ANOVA/ANCOVA using the *car* package (Fox & Weisburg 2019) with a significance threshold of $P < 0.05$. See Appendix S2 for model summaries and statistical outputs.

Results

Abiotic conditions

Stress landscapes differed between the two study locations. High intertidal substratum temperatures at BP were more stressful than at PA (Fig. 1). The average daily maximum temperature was 3.4˚C higher at BP than PA (df = 1, $F = 10.3$, $P = 0.00684$, Fig. 1B). The upper 99th quantile of temperature was 3.9˚C higher at BP than at PA (df = 1, $F = 9.30$, $P = 0.00930$, Fig. 1C). Relative humidity, however, was 35% lower in the Nuevo Gulf than on the west coast of BC near Barkley Sound (df = 1, $F = 1158$, $P < 0.001$, Fig. 1D).

Herbivore response to barnacles

Littorina spp. abundance (Fig. 2A) was high and declined slowly over time in plots containing *B. glandula* but was consistently very low through time where *B. glandula* was absent (barnacles x time, $\chi^2 = 9.379$, df = 1, $P = 0.00219$). The positive effect of *B. glandula* on *Littorina* spp. was especially strong where limpets were excluded (barnacles x grazers, $\chi^2 = 23.45$, df = 2, $P < 0.001$). *Lottia digitalis* abundance at BP (Fig. 2B) was higher where barnacles were present ($\chi^2 = 25.83$, df = 1, $P < 0.001$) and declined with time ($\chi^2 = 9.092$, df = 1, $P = 0.00257$). At PA, *S. lessonii* abundance increased over time where barnacles were present and declined where barnacles were absent (barnacles x time, $\chi^2 = 9.295$, df = 1, $P = 0.00230$). While herbivore biomass generally declined over time, this occurred to a lesser extent at PA compared to BP (location x time, $\chi^2 = 3.857$, df = 1, $P = 0.0495$). Barnacles had a positive, highly significant effect on herbivore biomass at both sites ($\chi^2 = 137.7$, df = 1, $P < 0.001$; Fig. 2C).

Algal cover

The presence of barnacles differentially affected ephemeral algae between sites (Fig. 3). Barnacles at BP reduced ephemeral algal cover, while barnacles at PA increased ephemeral cover (location x barnacles, $\chi^2 = 10.22$, df = 1, $P = 0.00139$). Where grazers were present (in both the herbivore inclusion and unfenced control treatments), ephemeral algal cover was lower than where grazers were excluded, but this difference was significantly more pronounced at BP than PA (location x grazer, $\chi^2 = 20.98$, df = 2, $P < 0.001$). Ephemeral algal cover declined slightly over time for the sampling dates analyzed ($\chi^2 = 7.012$, df = 1, $P = 0.00806$).

Perennial algal cover (Fig. 4; see Appendix S1: Fig. S3 for logit-transformed data and Fig. S4 for BP dominant *Fucus distichus*) at BP increased over time in plots with barnacles but remained consistently low where barnacles were absent. At PA, perennial cover tended to decline slightly over time in plots with barnacles present, though this effect was less clear (time x barnacles x location, $\chi^2 = 8.641$, df = 1, $P = 0.00329$). The presence of grazers had little effect on perennial algal cover at BP, but at PA, cover was significantly greater where grazers were excluded (location x grazers, $\chi^2 = 121.9$, df = 2, $P < 0.001$).

Barnacle recruitment

Herbivores reduced the recruitment of *B. glandula*, but this effect was only evident when recruitment was the greatest: at BP during late spring in the second year (location x grazers x time, $\chi^2 = 26.32$, df = 2, $P < 0.001$; Fig. 5). The presence of barnacles increased *B. glandula* recruitment at BP over time, but no such effect was detected at PA (location x barnacles x time, $\chi^2 = 4.771$, df = 1, $P = 0.0289$). The recruitment of a second barnacle species at BP, *Chthamalus dalli*, varied significantly through time, was highest in unfenced plots and generally lowest in limpet exclusion plots, and the effect of herbivores depended weakly on *B. glandula* presence (Appendix S1: Fig. S5; Appendix S2: Table S12).

Discussion

Through this experiment, we sought to determine how the ecological effects of the acorn barnacle *Balanus glandula* differed between its native range (west coast of Canada) and invaded range (Argentina), and what mechanisms might drive these differences. We hypothesized that the absence of shared evolutionary history between *B. glandula* and co-occurring species at PA would result in weaker facilitative interactions at PA compared to BP. We predicted that at BP, herbivores and algae would be facilitated by barnacles, which can act as refugia from abiotic and grazing stress. At PA, we predicted that *B. glandula* would not facilitate other species and may instead have a neutral or negative effect on herbivores and algae.

Our predictions were only partially supported by our results (see Fig. 6 for a summary of interspecific interactions in both hemispheres). At BP, our results corresponded well with our expectations and with results from other studies conducted in the native range (e.g., Farrell 1991, Harley 2006); *B. glandula* led to increased herbivore biomass, perennial algal cover, and barnacle recruitment. Ephemeral algal cover was reduced by *B. glandula*, particularly when limpets were excluded; similar results have demonstrated elsewhere in the native range (Harley 2006). In the invaded range, we found that while *B. glandula* suppressed perennial algae overall, this effect was relatively weak and inconsistent across grazer treatments and sampling dates.

Surprisingly, *B. glandula* did not substantially affect its own recruitment success at PA. Also unexpectedly, the presence of *B. glandula* at PA increased herbivore biomass to a similar extent as at BP and increased ephemeral algal cover. These observations indicate that *B. glandula* has a range of effects on associated species in both its native and invaded ranges and that facilitation occurred in the invaded range despite a lack of shared evolutionary history with co-occurring species.

One way that *B. glandula* facilitates associated species is by providing refugia from abiotic stress and grazing pressure (Geller 1991; Harley & O'Riley 2011). For example, upright, foliose fucoids have greater recruitment success in barnacle beds, where desiccation stress and grazing accessibility are reduced relative to bare rock (Farrell 1991). Conversely, encrusting perennial algae settle and grow well on bare substratum due to their higher tolerance of abiotic stress and grazing pressure than upright species (Menge et al. 1983; Steneck & Dethier 1994), and thus may compete with barnacles for primary substratum. The extent to which perennial algae benefit from barnacle refugia is thus largely dependent upon algal morphology. The dominant alga at BP, *Fucus distichus*, is a foliose upright and may thus be more susceptible to grazing and abiotic stress, particularly during the germling and juvenile stages; barnacles provide refugia from these stressors, leading to the positive association between *B. glandula* and perennial algal cover at BP. The dominant perennial alga at PA, *Ralfsia* sp. is tolerant to local desiccation stress (Raffo et al. 2014) and although our results show it to be vulnerable to grazing, the presence of barnacles did not mitigate this vulnerability. Since *S. lessonii* at PA was positively associated with barnacles, and given their use of *Ralfsia* as a food source, a negative effect of barnacles on perennial algae may occur indirectly via increased grazing pressure. By the end of the experiment, this trend seemed apparent, but given the complex changes in algal cover over time, a significant interaction of grazer and barnacle treatment could not be resolved.

Whether *B. glandula* facilitates ephemeral algae seems contingent upon the extent to which grazing is hindered by barnacles. Ephemeral algae readily colonize bare shores (Viejo et al. 2008) and may be expected to compete with *B. glandula* for substratum. However, ephemeral algae are more palatable than perennial algae and may thus experience greater grazing pressure (Alestra & Schiel 2014). While barnacles can reduce the efficiency of limpet-like herbivores that prefer grazing on smooth surfaces (Creese 1982; Geller 1991), intact barnacle beds and empty barnacle tests can facilitate other mobile grazers (Harley 2006; Sueiro et al 2011). For example, limpet and littorinid snail abundances are usually greater when barnacles are present (Creese 1982; Qian & Liu 1990), a finding consistent with our results at both study sites. However, grazing pressure was greater in the native versus the invaded range. While limpets significantly suppressed ephemeral algal cover at both locations, their effect was greater at BP. When barnacles were present at BP, grazing pressure on ephemeral algae was substantial even where limpets were excluded due to the presence of barnacle-associated littorine snails. Herbivores in the native range of *B. glandula* have a long history of association with barnacles – littorine snails and other mesograzers are adapted to use barnacle beds as habitat, while native limpets may be better adapted to graze over barnacles. Because barnacles facilitate herbivores at BP, they also increase grazing pressure and indirectly reduce the cover of ephemeral algae. At PA, *B. glandula* may instead provide a grazing refuge for palatable ephemeral algae from evolutionarily naïve grazers, producing the observed positive effect of barnacles on ephemeral algal cover.

In addition to differences in species traits, differences in environmental stress may have influenced the strength of facilitative interactions between sites. The strength of facilitation may increase with ambient environmental stress (Bertness & Callaway 1994). In this study, ephemeral algae at PA were facilitated by barnacles. While this trend can be explained by differences in the ecology and traits of species between locations, the local environment may also be important. While temperature stress was slightly higher at BP, PA has substantially lower humidity due to seasonal desiccation stress (Bertness et al. 2006). Desiccation stress negatively affects the germination rate, development, and survival of algal spores and recruits of various species (reviewed in Vadas et al. 1992). Barnacles retain moisture and, in a desiccating environment like PA, facilitation by *B. glandula* may more substantially enhance the survival and performance of algal recruits than in a humid environment such as BP (Mendez et al. 2015).

Patterns of barnacle recruitment also differed between sites. Barnacles, including *B. glandula*, are notoriously gregarious, preferentially settling near other barnacles to allow for sexual reproduction (Wu 1981). This behavior was evident at BP but not PA. Barnacle recruits can be inadvertently removed by limpet grazers as they feed (Dayton 1971), which was observed at BP during peak recruitment in treatments where *L. digitalis* was present, but was not seen at PA. Recruitment patterns seen at BP may have been undetectable at PA due to insufficient propagule pressure at this particular site (Savoya & Schwindt 2010).

Facilitation occurred at PA despite the lack of shared evolutionary history between high intertidal native species and *B. glandula*, which may be due to the generalist nature of this facilitation. Most documented novel facilitations are generalist in nature, particularly when the interaction has only recently been established (Aslan et al. 2015). For example, tube-dwelling polychaetes on mudflats can form mutualisms with an invasive alga just as they do with rare, native macroalgae, providing favorable substratum to the alga, which in turn attracts amphipod prey for the polychaetes (Kollars et al. 2016). A novel mutualism with the invasive alga may form only because there are functionally similar native species in the system. Similarly, even though Argentinian species are evolutionarily naïve to *B. glandula*, they could already have the behavioral adaptations needed to utilize barnacle bed habitats if there are functionally equivalent precedents in the system. At PA, these precedents could include native cordgrass (Sueiro et al. 2011) or crevices and holes naturally present in bedrock (Bazterrica et al. 2007; Bagur et al. 2019), all of which increase physical complexity, retain moisture, and/or increase food supply where they are present. *S. lessonii* commonly associates with these features, and thus may have pre-evolved behaviors that drive its association with invasive barnacles. *Balanus glandula* may assuage desiccation stress to directly reduce *S. lessonii* mortality or indirectly increase the presence of algal food for grazers. The latter possibility is supported by the increase in ephemeral algae at PA in the presence of barnacles. We also note that limpet removal at BP resulted in a disproportionately strong competitive release of *Littorina* sp. in plots containing barnacles, which could reflect barnacle enhancement of microalgae as a result of greater available surface area and/or suitable microhabitats within plots. Regardless, either food enhancement or desiccation reduction could produce the observed positive effect of *B. glandula* on grazers at PA.

Overall, we found that while shared evolutionary history may play a role in determining the strength of facilitation, other factors were more important in driving interactions at the two locations studied. *Balanus glandula* facilitated herbivores at PA and BP; this positive interaction likely occurred because barnacles ameliorate local desiccation stress to enhance survival of associated species, including the algal resource base. *Siphonaria lessonii*, while it has no prior evolutionary experience with barnacles, has encountered topographically similar structures, which could favor an association with *B. glandula*. The morphology of the dominant perennial alga at each site determined whether perennial algae as a whole were facilitated by *B. glandula*.

While *B. glandula* provides a refuge from limpet-like herbivores, littorine snails at BP use barnacle beds as habitat, thereby increasing grazing pressure for ephemeral algae attached to barnacles at BP. No analogous species exist in the high intertidal zone of Patagonia, so barnacles instead facilitated ephemeral algae by providing a moist microhabitat that enhanced settlement, survival, or growth regardless of grazer presence. Finally, the type and degree of environmental stress can also shape facilitative interactions – seasonal desiccation stress present at PA may have strengthened facilitation. Our results demonstrate the complex nature of predicting the effects of invasive species. More studies are needed that explicitly compare the effects of non-native species between their native and introduced ranges and explore the relative importance of ecological, environmental, and evolutionary context in shaping novel facilitations.

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Author contributions

C.H. and E.S. collected data. C.H. initially drafted the introduction and methods. A.H. analyzed data and completed writing the manuscript. All authors guided data interpretation and revision.

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Figure 1. Abiotic characteristics of study sites at BP (native range) and PA (invaded range) **a)** Average maximum daily temperatures recorded by intertidal iButtons during the first summer at each site, a proxy for invertebrate body temperature. Ribbon width represents standard error. Time is relative to summer solstice in each hemisphere (time = 0). **b)** Mean daily maximum temperature recorded during the same period. **c)** upper 99th percentile of temperature recorded during the same period. **d)** mean relative humidity recorded in Tofino, BC (60 km north of Barkley Sound, BS) and near PA (Nuevo Gulf, NG) from January 2015 to January 2020.

Figure 2. Change in herbivore abundance over time across treatments and sites. **a)** *Littorina* spp. abundance at BP, separated into the control, exclusion, and inclusion grazer treatments. **b)** Abundance of true limpets (*Lottia digitalis* at BP in blue) and pulmonate limpets (*Siphonaria lessonii* at PA in red) in unfenced grazer control treatments only. **c)** Estimated biomass (dry tissue weight) of herbivores in experimental plots. Error bars represent standard error.

Figure 3. Percent cover of ephemeral algae within experimental plots over time, separated by grazer treatment. Note that the y-axis limits vary between panels. Only data for the timepoints nearest fall and spring equinoxes were used for analyses; all points excluded from analysis are light grey. Error bars represent standard error. Data for the initial PA survey are not shown due to spurious inflation of algal cover in the -B treatment; an ephemeral microalga was exposed when *B. glandula* was removed, but this alga was only observed at the initial timepoint.

Figure 4. Percent cover of perennial algae within experimental plots over time, separated by grazer treatment. Only data for the timepoints nearest fall and spring equinoxes were used for analyses; all points excluded from analysis are light grey. Error bars represent standard error.

Figure 5. Density of *B. glandula* recruits over time, separated by grazer treatment. Note the difference in y-axis limits vary between panels. Error bars represent standard error.

Figure 6. Species interaction diagrams for the native range of *B. glandula* in Barkley Sound, Canada (top) and the invaded range in the Nuevo Gulf, Argentina (bottom). Green and blue represent positive and negative interactions, respectively. Solid and dashed lines represent direct and indirect effects, respectively. Arrow weight represents the relative strength of interactions.

Figure 1.

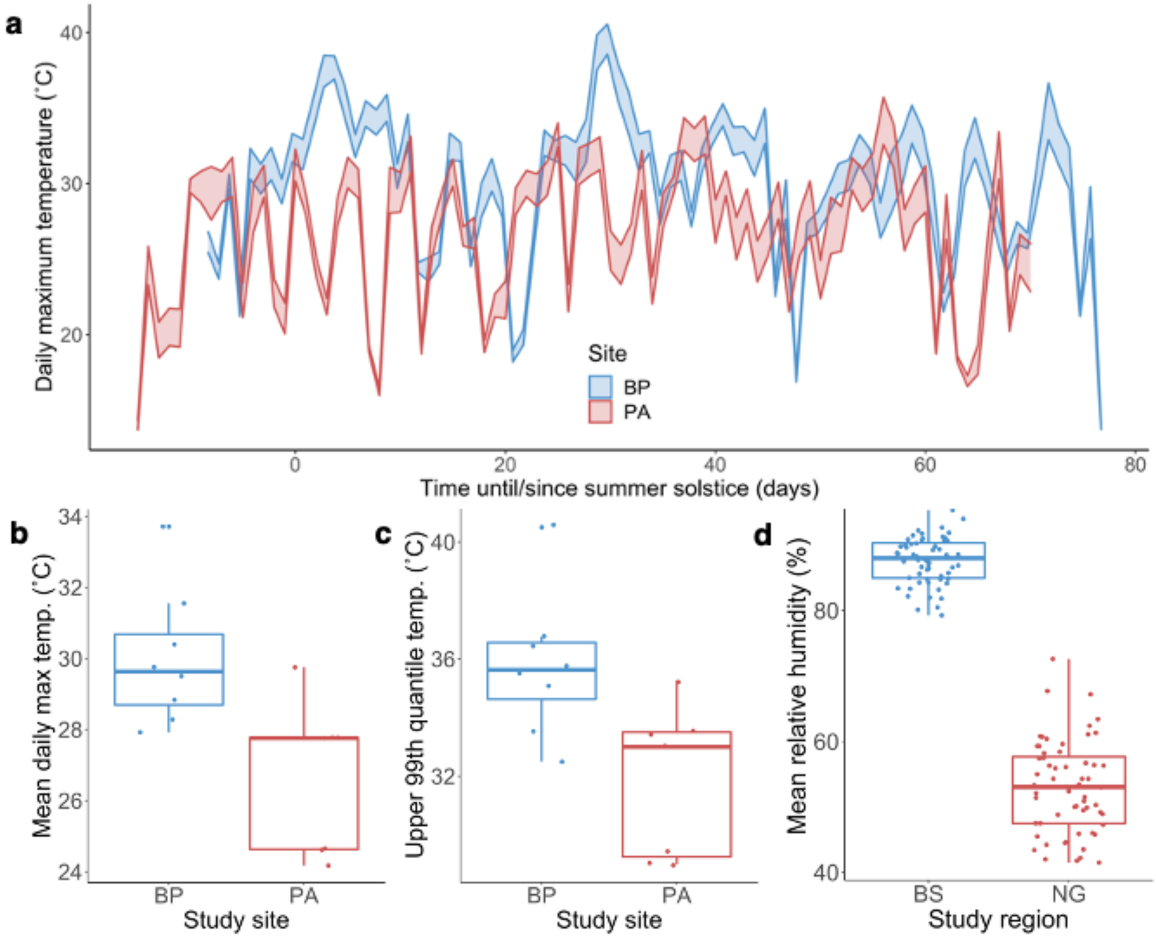

a
Daily maximum temperature (°C)
40
30
20
0
20
40
60
80
Time until/since summer solstice (days)
Site
BP
PA
b
Mean daily max temp. (°C)
34
32
30
28
26
24
BP
PA
Study site
c
Upper 99th quantile temp. (°C)
40
36
32
BP
PA
Study site
d
Mean relative humidity (%)
80
60
40
BS
NG
Study region

Figure 2.

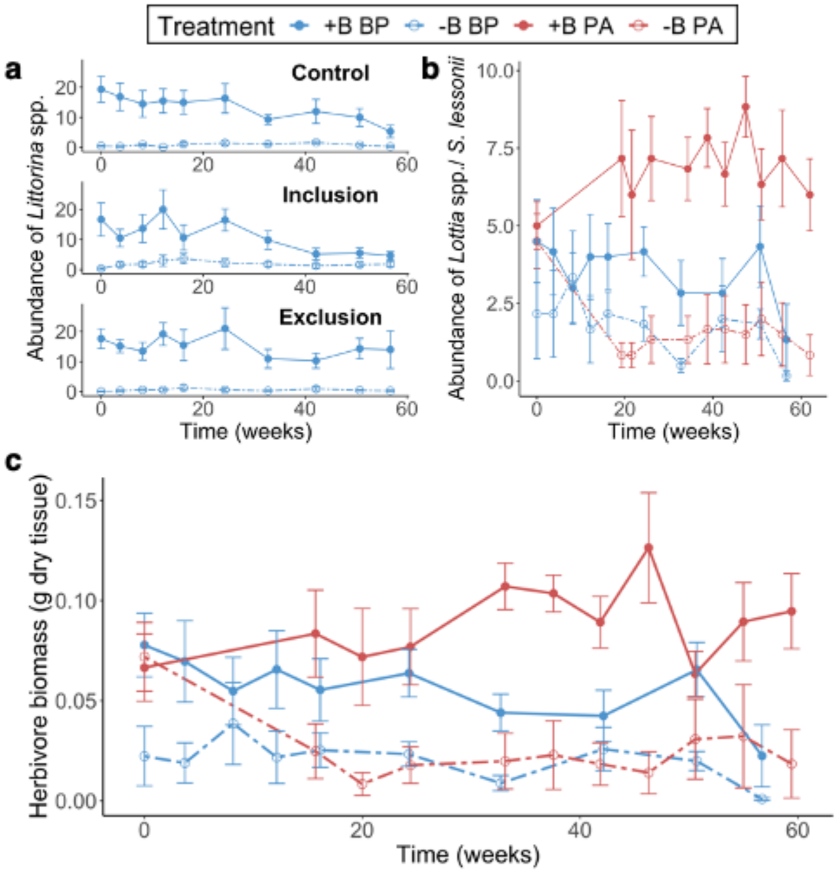

Treatment
+B BP
-B BP
+B PA
-B PA
a
Control
Inclusion
Exclusion
Abundance of *Littorina* spp.
0
10
20
0
20
40
60
Time (weeks)
b
Abundance of *Lottia* spp./ *S. lessonii*
0.0
2.5
5.0
7.5
10.0
0
20
40
60
Time (weeks)
c
Herbivore biomass (g dry tissue)
0.00
0.05
0.10
0.15
0
20
40
60
Time (weeks)

Figure 3

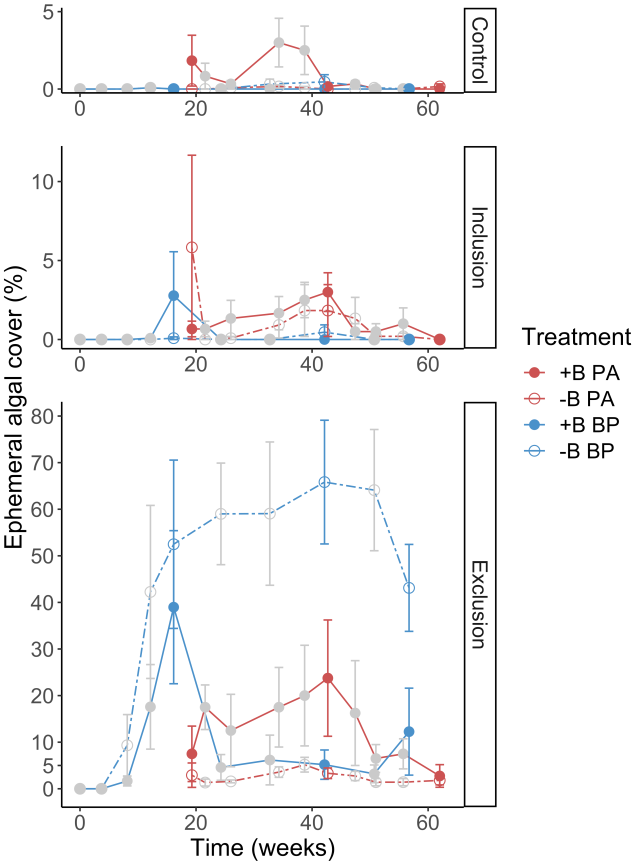
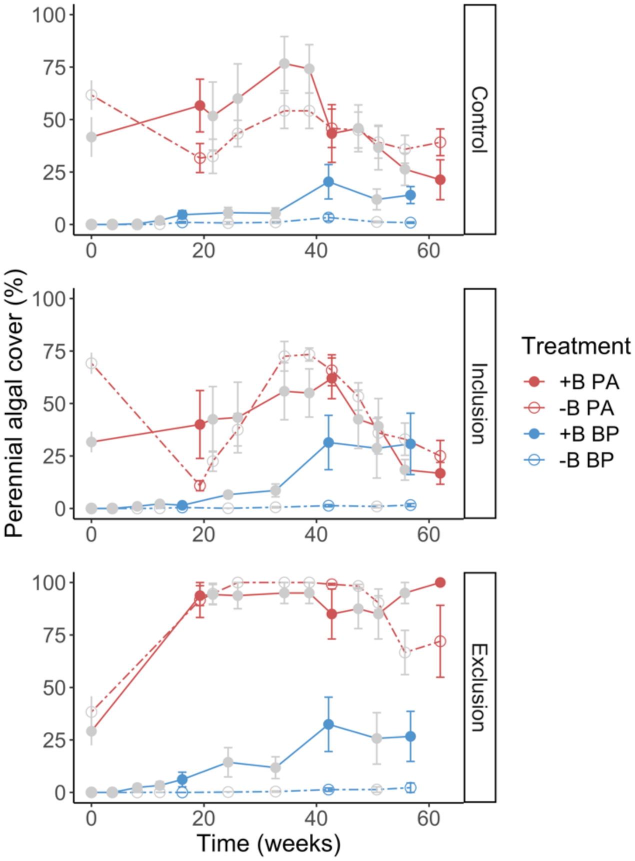

Control
Inclusion
Exclusion
Ephemeral algal cover (%)
Time (weeks)
0
20
40
60
5
10
30
50
70
80
Treatment
+B PA
-B PA
+B BP
-B BP

Figure 4.



Perennial algal cover (%)
100
75
50
25
0
0
20
40
60
Control
Inclusion
Exclusion
Time (weeks)
Treatment
+B PA
-B PA
+B BP
-B BP

Figure 5.

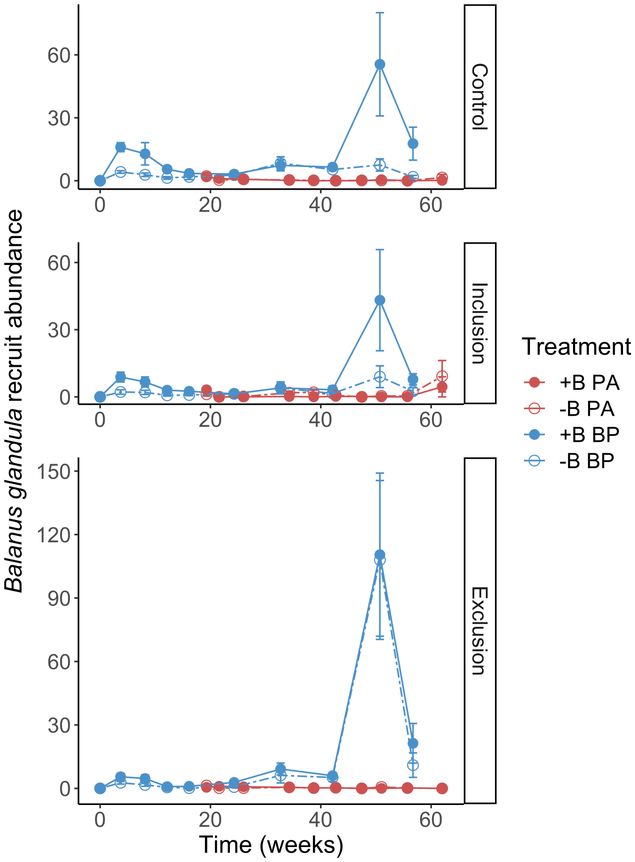
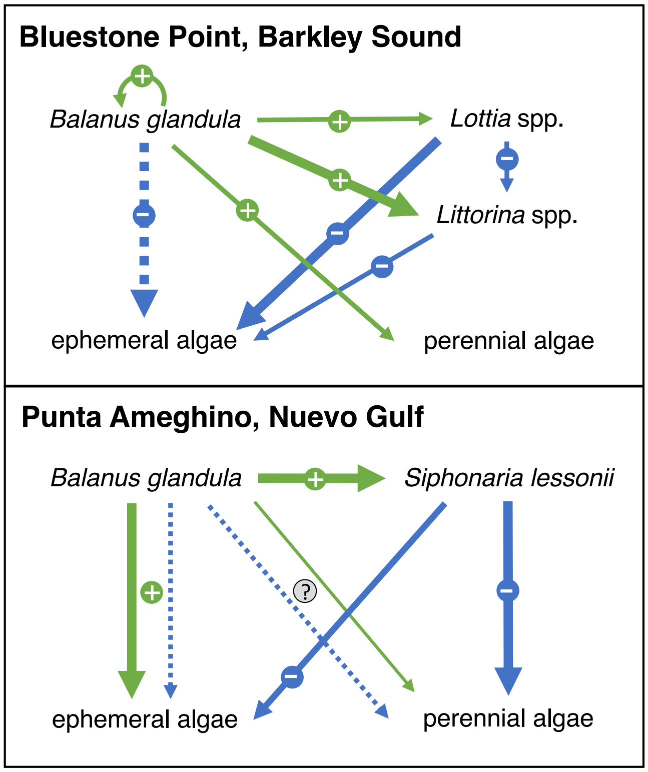

Balanus glandula recruit abundance
Time (weeks)
Control
Inclusion
Exclusion
Treatment
+B PA
-B PA
+B BP
-B BP
0
30
60
90
120
150
0
20
40
60

Figure 6.


Bluestone Point, Barkley Sound
+
Balanus glandula
+
Lottia spp.
−
+
+
−
−
Littorina spp.
−
ephemeral algae
perennial algae
Punta Ameghino, Nuevo Gulf
Balanus glandula
+
Siphonaria lessonii
+
?
−
−
ephemeral algae
perennial algae