

# Complementary influences of co-occurring physical ecosystem engineers on species richness: insights from a Patagonian rocky shore

María Bagur<sup>1</sup> · Jorge L. Gutiérrez<sup>2,3</sup> · Lorena P. Arribas<sup>4</sup> ·  
M. Gabriela Palomo<sup>1,2</sup>

Received: 18 February 2016 / Revised: 17 August 2016 / Accepted: 24 August 2016 /  
Published online: 13 September 2016  
© Springer Science+Business Media Dordrecht 2016

**Abstract** Structural modification of the environment by physical ecosystem engineers often allows for the occurrence of species that are not able to establish in unengineered habitats, thus leading to increased species richness at the landscape-level (i.e., areas encompassing engineered and unengineered habitats). Unlike previous studies that focused on the contribution of a single engineering species to landscape-level species richness, this study evaluates whether co-occurring engineers—i.e., intertidal mussels (primarily *Perumytilus purpuratus*) and rock boring bivalves (*Lithophaga patagonica*)—contribute to landscape-level species richness in a similar or complementary way. Our results show that both mussel and *L. patagonica* patches harbor a substantial number of invertebrate species in addition to those occurring in the unengineered rock substrate. However, the distinctive habitat patches created by each engineer add exclusive subsets of species to the study area, which implies that mussel and *L. patagonica* patches contribute complementarily to overall species richness in our intertidal landscape. Here we postulate that complementary engineering effects on landscape-level species richness will occur when the engineered patches structurally differ from each other and, thus, vary in their relative ability to modulate two

---

Communicated by Robert Cowie.

---

This article belongs to the Topical Collection: Coastal and marine biodiversity.

---

**Electronic supplementary material** The online version of this article (doi:10.1007/s10531-016-1203-x) contains supplementary material, which is available to authorized users.

---

✉ María Bagur  
mbagur@macn.gov.ar

<sup>1</sup> Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN-CONICET), Buenos Aires, Argentina

<sup>2</sup> Grupo de Investigación y Educación en Temas Ambientales (GrIETA), Mar del Plata, Argentina

<sup>3</sup> Facultad de Ciencias Exactas y Naturales and CONICET, Universidad Nacional de Mar del Plata, Mar del Plata, Argentina

<sup>4</sup> Centro Nacional Patagónico (CENPAT-CONICET), Puerto Madryn, Argentina

or more abiotic conditions and/or resources that prevent species establishment in the unengineered state. In spite of its inherently small spatial scale (500 m), our study highlights the potential for complementary engineering impacts at the larger scales that are usually implied in biodiversity conservation and management (tens to hundreds of kilometers) and outlines a simple conceptual basis and approach to address them.

**Keywords** Ecosystem engineers · Species richness · Complementarity · Biodiversity · Mussels

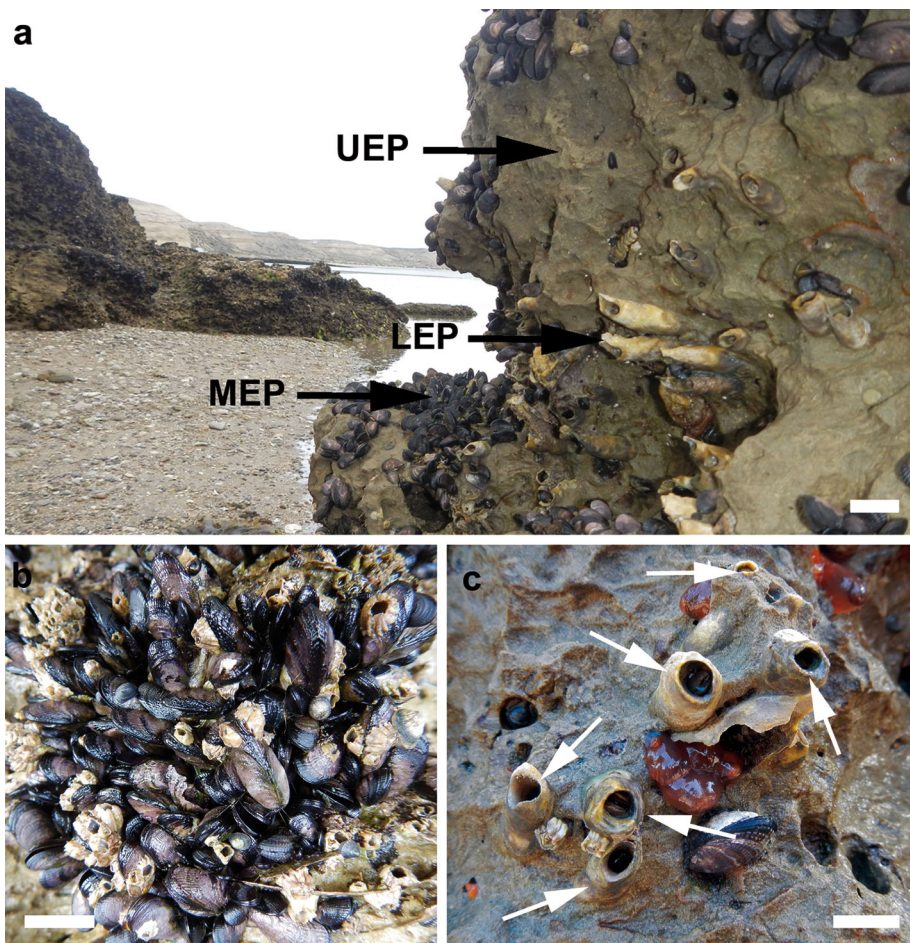
## Introduction

Physical ecosystem engineers are organisms that structurally modify the environment via their presence or their activities (Jones et al. 1997). In so doing, they frequently create more or less distinctive, structurally-modified patches, in turn increasing overall habitat diversity (see Jones et al. 1997; Gutiérrez and Jones 2006). Structural modification of the environment by physical ecosystem engineers often releases other organisms from limited availability of resources such as living space (e.g., Gutiérrez et al. 2003), water (e.g., Wright et al. 2006), or nutrients (e.g., Wesche et al. 2007), and/or protects them from the impact of potentially limiting physical factors such as extreme temperatures (e.g., Badano et al. 2006), desiccation (e.g., Silliman et al. 2011), or strong water currents (e.g., Nakano et al. 2005). As a consequence, engineer-modified patches often allow for the occurrence of species that are not able to establish in unengineered habitats (i.e., patches not modified by the engineer of interest, Badano et al. 2006), thus leading to increased species richness at the landscape-level (i.e., areas encompassing engineered and unengineered patches irrespective of spatial scale, sensu Jones et al. 1997).

Increases in landscape-level species richness due to the creation of structurally modified habitat patches have been documented for a variety of physical ecosystem engineers and ecosystems, e.g., beavers in northeastern US forests (Wright et al. 2002), intertidal sessile invertebrates on South American rocky shores (Castilla et al. 2004; Borthagaray and Carranza 2007; Silliman et al. 2011), leaf-tying caterpillars in eastern US oak forests (Lill and Marquis 2003); shrubs in the Negev desert (Wright et al. 2006), and cushion plants in the high Andes (Badano and Cavieres 2006a, b; Badano et al. 2006). These studies cover engineer-modified patches that range from a few square centimeters (e.g., a pair of tied leaves) to several hundred square meters (e.g., a beaver pond). However, they all compare species richness between engineered and unengineered patches, focusing on the contribution of a single engineering species or the aggregate impacts of species producing similar structures (e.g., oak leaves tied by distinct caterpillar species; Lill and Marquis 2003; multispecific mussel patches; Borthagaray and Carranza 2007) and treating other engineers, when present, as part of the unengineered habitat (see Badano et al. 2006). While this approach has been remarkably useful to estimate the net contribution of focal engineers to landscape-level species richness, it has largely precluded assessing whether distinctive habitat patches made by co-occurring engineers contribute to overall species richness in a similar or complementary way.

In this paper we evaluate how patches of habitat modified by mussels (*Perumytilus purpuratus* plus *Brachidontes rodriguezii*) and rock-boring bivalves (*Lithophaga patagonica*) contribute to invertebrate species richness in intertidal platforms of Argentinean

Patagonia. At the low intertidal zone, these sessile invertebrates each aggregate into small, fairly discrete patches (tens to hundreds of square centimeters) where three-dimensional complexity and the diversity of colonizable surfaces are higher than in the surrounding, unmodified sedimentary rock (Fig. 1a; Table 1). Nonetheless, the structures made by each of these engineers are barely comparable. Mussels aggregate into dense patches (up to 280 individuals  $\text{dm}^{-2}$ ; Table 1) creating interstitial space at the millimeter scale and covering most of the rock surface with their shells (Fig. 1b). *Lithophaga patagonica*, on the other hand, occurs at lower densities (up to 31 individual  $\text{dm}^{-2}$ ; Table 1). It generates boreholes that persist after the death of individuals as well as calcite linings that often protrude from the rock surface, and these structures leave a substantial proportion of exposed bare rock between them (Fig. 1c).



**Fig. 1** a Vertical intertidal rock surface in Puerto Pirámides showing mussel-engineered patches (MEP), *L. patagonica*-engineered patches (LEP), and unengineered habitat (UEP). b Mussel-engineered patch. c *Lithophaga*-engineered patch with six protruding calcite tubes indicated by white arrows. Scale 1 cm (for all three photos)

**Table 1** Structural attributes and abiotic conditions in mussel-engineered patches (MEP), *L. patagonica*-engineered patches (LEP), and unengineered patches (UEP)

	MEP	LEP	UEP	Notes
<b>Structural elements</b>				
Density (individuals $\text{dm}^{-2}$ )	129.72 (58.05)	9.15 (4.75)	–	Mean (SD) number of mussels and <i>L. patagonica</i> boreholes in $10 \times 10$ cm quadrats (n = 60)
Cross-sectional area ( $\text{mm}^2$ )	48.21 (46.60) [200.04]	103.06 (80.85) [706.86]	–	Mean (SD) maximum cross-sectional area of individual mussels and <i>Lithothağa</i> boreholes. They were respectively estimated as the surface of an ellipse after measurement of the maximum width and length of individual mussels (n = 103) and as the surface of a circle after measurement of the maximum diameter of individual boreholes (n = 196). Maximum values are shown in square brackets
Length (mm)	15.59 (17.06) [30.34]	22.69 (9.59) [50]	–	Mean (SD) length of individual mussels (n = 650, measured from the umbo to the shell's distal edge) and <i>L. patagonica</i> protruding calcite linings respectively (n = 250, measured from the opening of the calcite lining to the intersection with the rock surface). Maximum values are shown in square brackets
<b>Whole-patch attributes</b>				
Fractal dimension	1.92 (0.04)	1.89 (0.01)	1.82 (0.01)	Mean (SD) fractal dimension of patch roughness profiles obtained with a contour gauge (n = 3). Profiles copied by the gauge were pictured and their fractal dimension computed by means of the box-counting method using ImageJ (imagej.net)
Sediments ( $\text{g dm}^{-2}$ )	60.1 (15.69)	0.27 (0.26)	None	Mean (SD) dry weight of sediments per unit area. Square, $10 \times 10$ cm portions of mussel patches were removed with a spatula and taken to the lab to separate sediments from mussels (n = 20). The sediment trapped inside 20 <i>L. patagonica</i> burrows was collected using a laboratory spatula, the individual mean calculated and multiplied by the average density of burrows in 60, $10 \times 10$ cm quadrats. All sediments were oven-dried (70 °C, 24 h). Unengineered rock surfaces were not sampled because they do not retain sediments
Desiccation (% water loss)	6.97 (4.86)	4.01 (4.63)	17.61 (7.76)	Mean (SD) percent water loss from seawater-embedded and preweighed sponges (rectangles ca. 3 $\text{cm}^2$ ). Sponges were placed either within the mussel matrix, inside <i>L. patagonica</i> boreholes, or over the rock surface one hour before the minimum low tide and collected two hours later

Increased habitat complexity and substrate diversity in patches modified by mussels and *L. patagonica* suggest that these engineers might create conditions for colonization by species that do not occur in the unengineered state (defined here as exposed rock surfaces lacking these engineers or having only a few isolated mussels), thus increasing landscape-level species richness. Nonetheless, structural differences between mussel and *L. patagonica* patches translate into variation in the abiotic conditions and resources (e.g., sediment accumulation, desiccation rates, see Table 1), which might lead to differences in the identity of species that each patch type adds to the landscape. Here we first quantify the number of invertebrate species occurring in each patch type in addition to those in the unengineered habitat. To do so, we use the same general comparative approach of previous studies that quantify the contribution of a single engineered patch type to landscape-level species richness; see Badano et al. (2006) for a review, and the examples above. Then, we extend this analysis to test for overlap between the species that each patch type adds to those in the unengineered state, using a simple measure of overlap designed for nested subset analysis (see Almeida-Neto et al. 2008). Given larger sediment accumulation, smaller interstitial space (i.e., larger fractal dimension; Table 1) and likely increased protection from flows in mussel than *L. patagonica* patches, we predict that mussel patches will favor relatively small, deposit-feeding species, lacking structures to attach to the substrate, while *L. patagonica* patches will favor larger species showing adhesive structures and other trophic modes. Finally, we outline the general circumstances when co-occurring engineers can have complementary impacts on the overall species richness of habitat mosaics.

## Methods

### Study site and organisms

The study was conducted at Puerto Pirámides, Chubut Province, Argentina (42°34'S, 64°17'W). The site is a ca. 500 m long coastal stretch characterized by an extensive abrasion platform composed of friable sedimentary rock (coquina limestone containing oyster and pectinid shells and cemented by calcium carbonate; Scasso and del Río 1987). It lies at the base of an active cliff and is incised by drainage channels that run nearly perpendicular to the shoreline (Bagur et al. 2013, 2014). Tides are semidiurnal and macrotidal (3.63 m mean amplitude; Servicio de Hidrografía Naval, Argentina, [www.hidro.gov.ar](http://www.hidro.gov.ar)). The climate is temperate (12 °C mean annual temperature) and arid because of low precipitation (<200 mm year<sup>-1</sup>) as well as intense and persistent, dry westerly winds (15–22 km h<sup>-1</sup> mean annual wind speed) (Puelo et al. 1998).

Mussels form dense, extensive beds in the mid intertidal zone at this and nearby sites; these sites are tens to hundreds of meters long with up to 28,000 individuals m<sup>-2</sup> (Olivier et al. 1966, pers. obs.) aggregated into small patches (oval to circular in shape, diameter ranging from centimeters to a few decimeters; pers. obs.) at lower tidal elevations. The dominant mussel species in this region is *Perumytilus purpuratus* (also referred in the literature as *Brachidontes purpuratus*), though scattered individuals of a morphologically similar species, *Brachidontes rodriguezii*, are often found within *P. purpuratus* beds and patches (Rechimont et al. 2013; Trovant et al. 2015). *P. purpuratus* occurs along the Pacific coast of South America from the north of Peru (3°S) to its southernmost tip (Tierra del Fuego archipelago, 55°S) and on the Atlantic coast as far north as El Espigón

(Argentina, 41°07'S; Arribas et al. 2013; Trovant et al. 2015). *Brachidontes rodriguezii* occurs on the Atlantic coast of South America from the state of Rio Grande do Sul (Brazil, 32°S) to Punta Ninfas (Argentina, 42°58'S; Adami et al. 2013; Trovant et al. 2015). Both species show a similar size range (up to 55 mm length, most individuals less than 30 mm; Arribas et al. 2015) and high phenotypic variability, which makes them distinguishable only to experienced taxonomists (Adami et al. 2013; Van der Molen et al. 2013). Therefore, we have conservatively treated mussels as a single species when quantifying species richness. This aggregation of two species into one would have little proportional impact on our species richness estimates since 43 species other than mussels were found at our study site (Table 2).

*Lithophaga patagonica* (or *Leiosolenus patagonicus*; Huber 2010) occurs in the low intertidal zone at this site. This species inhabits intertidal and shallow waters in the southwestern Atlantic from the state of Santa Catarina (Brazil, 28°S) to Puerto Deseado (Argentina, 47°S) and is often very abundant (up to 170 individuals in 2000 cm<sup>3</sup> of rock; Bagur et al. 2014). It bores flask-shaped holes into soft consolidated sediments and oyster shells, and the burrows are usually partially or completely lined with a layer of calcareous material (Bagur et al. 2013; Fig. 1c). Individuals and their boreholes can be as large as 41 mm long and 12 cm<sup>3</sup> in volume, respectively, and the calcareous burrow linings can protrude up to 4 cm from the rock surface (pers. obs.).

Mussels and *L. patagonica* co-occur at this site, as well as at other sites in Chubut (42°S; Sánchez and Zaixso 1995, Cuevas et al. 2006, Rechimont et al. 2013) and Buenos Aires provinces (37°S, Bagur et al. 2014; only *B. rodriguezii* is present at this site). At our site, mussels and *L. patagonica* co-occur in a ca. 1.5 m high fringe at the base of vertical rock surfaces that extend along the low intertidal zone (Fig. 1a). Mussels and *L. patagonica* boreholes and linings form relatively discrete, separate patches on exposed rock surfaces with the intervening space lacking mussels or where mussels occur only as isolated individuals—i.e., the unengineered habitat. Other engineers, such as barnacles, occur both in the unengineered habitat and the two engineered habitat types. However, their structural effects are here considered negligible because of their relatively low densities and small size.

## Invertebrate sampling

The macroinvertebrate species occurring in mussel and *L. patagonica* patches and the unengineered habitat were sampled in March 2012, September 2012, March 2013, and October 2015 using 10 × 10 cm quadrats. Samples were randomly taken from the low intertidal zone, at the level where both mussels and *L. patagonica* co-occur and along the total length of the study area. Samples from mussel patches were taken by removing the mussels and associated sediments with a spatula. These samples were then preserved in alcohol, transported to the laboratory, and sieved (500 µm mesh) to obtain and quantify the macrofauna. Samples from *L. patagonica* patches included the invertebrates inside boreholes, those attached to the surface of protruding calcareous linings, and those occurring on the rock surface around neighboring boreholes and/or linings. A laboratory spatula was used to remove the invertebrates and sediments from inside the boreholes. The invertebrates visible at the external surface of linings or on the rock were either identified and quantified in situ, or collected and preserved in alcohol for subsequent identification in the laboratory. The same approach was adopted for the invertebrates on the rock surface in the unengineered habitat. Samples were taken at least 1 m apart from each other.

**Table 2** Species found in mussel patches (MEP), *L. patagonica*-engineered patches (LEP), and unengineered patches (UEP)

Species	Taxa	MEP	LEP	UEP	Degree of attachment	Feeding mode	Size
<i>Siphonaria lessonii</i>	MG	x	B, T, R	x	T	G	M
<i>Mytilus edulis</i>	MB	x	B, T, R	x	P	S	L
<i>Aulacomya atra</i>	MB	x	B, T, R	x	P	S	L
<i>Balanus glandula</i>	CC	x	B, T, R	x	P	S	M
<i>Parabunodactis imperfecta</i>	CA	x	B, T, R	x	P	P	L
<i>Metridium senile lobatum</i>	CA	x	B, T, R	x	P	S	L
<i>Cyrtograpsus altimanus</i>	CD	x	B, R	x	N	P	L
<i>Plaxiphora aurata</i>	MP	x	B, T, R	x	P	G	L
<i>Trophon geversianus</i>	MG	x	B, T, R	x	P	P	L
<i>Eulalia</i> sp.	AP	x	B, R	x	N	P-Sc	L
Serpulidae, undetermined	AP	x	B, T, R	x	P	S	M
<i>Fisurella radiosa tixierae</i>	MG		B, R	x	T	G?	L
<i>Hiatella</i> cf. <i>meridionalis</i>	MB		B, R	x	P	S	M
<i>Anthothoe chilensis</i>	CA		T, R	x	P	P	M
Bryozoa, undetermined	B		B, T, R	x	P	S	S
<i>Halicarcinus planatus</i>	CD	x	B		N	P-G	M
Chironomidae (larvae), undetermined	ID	x	B		N	D	S
<i>Exosphaeroma</i> sp.	CI	x	B, T, R		N	G	M
<i>Lasaea adansoni</i>	MB	x	B		N	S	S
Spionidae, undetermined	AP	x	B		T	D-S	M
<i>Cirriformia</i> sp.	AP	x	B		T	D	M
<i>Thelepus plagiostoma</i>	AP	x	B		T	D	L
<i>Lepidasthenia</i> sp.	AP		B		N	P	L
<i>Austromegabalanus psittacus</i>	CC		T		P	S	L
<i>Epitonium fabrizioi</i>	MG		B		T	P	M
<i>Cliona</i> ? (orange sponge)	P		T, R		P	S	M
<i>Nacella magellanica</i>	MG		R		T	G	L
<i>Lithophaga patagonica</i>	MB		B		P	S	L
<i>Ascidella aspersa</i>	TA		T, R		P	S	L
<i>Arbacia dufresnii</i>	EE		R		T	G-P	L
<i>Perumytilus purpuratus-Brachidontes rodriguezii</i>	MB	x			P	S	L
<i>Neolineus</i> sp.	N	x			N	Sc	L
<i>Ramphogordius sanguineus</i> ?	N	x			N	P-Sc	L
<i>Joeropsis curvicornis</i>	CI	x			N	G	S
<i>Syllis</i> sp.	AP	x			N	P-D	M
<i>Monocorophium</i> aff. <i>insidiosum</i>	CAm	x			N	D-S	S
Maeridae, undetermined.	CAm	x			N	D-G	S
<i>Tanais</i> aff. <i>dulongii</i>	CT	x			N	D-G	S
<i>Eunice argentinensis</i>	AP	x			N	P	L
<i>Lumbrineris</i> sp.	AP	x			N	P	L
<i>Turbonilla madrynensis</i>	MG	x			T	E	S

**Table 2** continued

Species	Taxa	MEP	LEP	UEP	Degree of attachment	Feeding mode	Size
<i>Idotea baltica</i>	CI	x			N	G	M
Nephtyidae, undetermined.	AP	x			N	P	M
<i>Pachycheles chubutensis</i>	CD	x			N	D	M
Total		32	30	15			

In the case of LEP, species were found inside boreholes (B), on the outer surface of calcite tubes (T), or on the rock surface between boreholes and tubes (R). Degree of attachment and size were assigned based on field observations. Feeding modes were obtained from the literature (See references in Online Resource 1 Table A1)

*Taxon*—AP Annelida Polychaeta, B Bryozoa, CnA Cnidaria Anthozoa, CrA Crustacea Amphipoda, CrC Crustacea Cirripedia, CrD Crustacea Decapoda, CrI Crustacea Isopoda, CrT Crustacea Tanaidacea, EE Echinodermata Echinoidea, ID Insecta Diptera, MB Mollusca Bivalvia, MG Mollusca Gastropoda, MP Mollusca Polyplacophora, N Nemertina, P Porifera, TA Tunicata Ascidiacea

*Degree of attachment*—P permanent, T temporary, N none

*Feeding mode*—D deposit-feeder, S suspension-feeder, P predator, G grazer, E ectoparasite, Sc scavenger

*Size* small (S, <5 mm), medium (M, 5–10 mm), large (L, >10 mm)

## Data analysis

Species richness (Sobs) in each habitat type was quantified with sample-based species accumulation curves constructed by means of rarefaction techniques (Gotelli and Colwell 2001). Confidence intervals (95 %) for Sobs were calculated based on the unconditional variance estimate developed by Colwell et al. (2004). Non-overlapping confidence intervals were considered to indicate significant differences between pairs of Sobs values. This approach is regularly used as a simple but conservative criterion of statistical difference between Sobs values in the absence of any computationally practical standard test to compare them (Colwell et al. 2012; Colwell 2013). To evaluate whether our sampling effort sufficed to obtain reliable estimates of species richness in each habitat type, we compared observed Sobs values with the Chao 2 estimate of the total number of species likely to be observed in the community (Chao 1984). The Chao 2 richness estimate uses the ratio of the number of species observed only once in a dataset to the number of species observed twice to approximate the actual number of species present in a habitat type (Colwell and Coddington 1994). The degree to which the Chao 2 estimate matches Sobs provides an indication of how thoroughly the community has been sampled (Badano et al. 2006). EstimateS 9.1.0 (Colwell 2013) was used to construct species accumulation curves and to calculate confidence intervals and the Chao 2 estimate.

Differences in the identity of the species added to the unmodified habitat by each engineer were quantified as their paired overlap (PO; Almeida-Neto et al. 2008). Given a species presence-absence matrix in which rows are species and columns  $i$  and  $j$  are the two kinds of engineered habitat with  $j$  adding an equal or lower number of species to the unmodified habitat than  $i$ .,  $PO_{ij}$  is the percentage of presences in column  $j$  that are located at identical row positions to those in column  $i$  (i.e., the percentage of species in habitat  $j$  that are also present in habitat  $i$ ). Thus,  $PO_{ij}$  will be 100 if all species present in habitat  $j$  are also present in habitat  $i$  and will decrease as the proportion of species in habitat  $j$  that are not present in habitat  $i$  increases.  $PO_{ij}$  was calculated here for the original data matrix



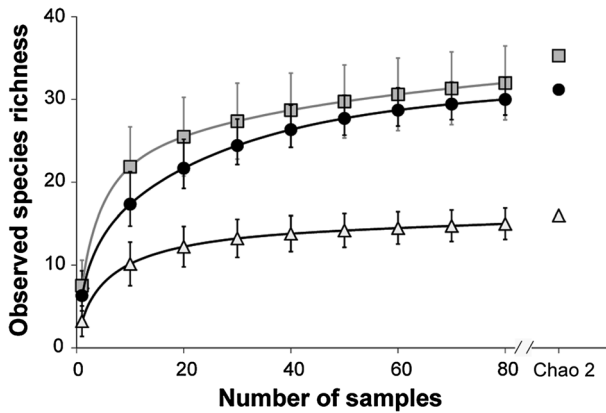
as well as for 1000 matrices of the same size in which the number of species added to the unmodified habitat by each engineered patch type was the same as in the original matrix (i.e., fixed column totals) but the identity of these species was randomized (i.e., presences and absences assigned at random across rows). The species in habitat  $j$  were considered a significant subset of those in habitat  $i$  (i.e., no complementarity) if the observed  $PO_{ij}$  lay within the upper 95 % percentile of the frequency distribution of  $PO_{ij}$  values of the randomized matrices. ANINHADO (Guimarães and Guimarães 2006) was used to obtain  $PO_{ij}$  values from randomized matrices.

Multiple Correspondence Analysis (Greenacre and Blasius 2006) was used to identify associations between species traits (feeding mode, size, and degree of attachment) and the types of patch where they occurred (mussel, *L. patagonica*, unengineered patches, or combinations of any or all of them). Our predictions here are (1) that relatively small species, deposit-feeders, and/or mobile species lacking adhesive structures would be associated with mussel patches because of the larger sediment accumulation, smaller interstitial space, and decreased flow within dense mussel aggregations and, (2) that relatively larger species, non deposit-feeders, and/or species with adhesive structures would be associated with *L. patagonica* patches because of the negligible sediment accumulation, larger interstitial space, and lesser protection from flow in the open space between boreholes and protruding calcite linings (Table 1). To assess these predictions, species were classified in three size groups based on maximum dimension: small (<5 mm), medium (05–10 mm), and large (>10 mm); two feeding groups: deposit feeders (both obligate and facultative) and other; and three degrees of attachment: permanent, temporary, and none (which respectively correspond to sessile species, low motility species such as gastropods or echinoids that remain adhered to the substrate when moving, and mobile species lacking any adhesion mechanism).

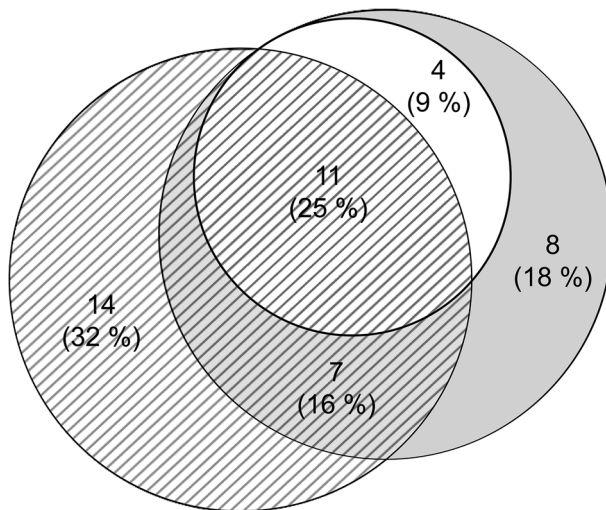
## Results

Thirty-two, 30 and 15 species were found in mussel patches, *L. patagonica* patches, and unengineered patches, respectively (see Table A2 in Online Resource 1 for differences in the species sampled on each date). The species accumulation curves obtained for each habitat approached the asymptote and observed species richness values ( $S_{obs}$ ) were close or equal to the Chao 2 richness estimator (Fig. 2), which suggests that the three habitats were sampled thoroughly enough to characterize their species richness (i.e., few additional species are likely to be found with further sampling).  $S_{obs}$  did not differ between mussel and *L. patagonica* habitats (overlapping confidence intervals in Fig. 2) but was higher at these two engineered habitat types relative to the unengineered habitat (no overlap between confidence intervals; Fig. 2).

Eleven of the 15 species found in the unengineered habitat were shared with the two engineered habitat types, while the remaining four species were shared just with *L. patagonica* habitats (i.e., no species occurred exclusively in the unengineered habitat; Fig. 3; Table 2). Mussel and *L. patagonica* habitats jointly added 29 species to the overall list of species, with 14 species added by the mussel habitat alone, eight species exclusively added by the *L. patagonica* habitat, and 7 species common to both engineered habitat types (Fig. 3; Table 2). Partial overlap ( $PO_{ij}$ ) in the observed data was thus 46.67. This value lay below the upper 5 % percentile of  $PO_{ij}$  values of the randomized matrices (i.e., 86.67),



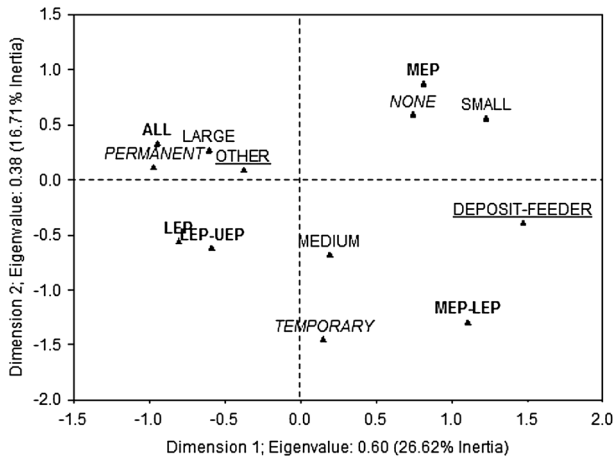
**Fig. 2** Species accumulation curves ( $\pm 95\%$  confidence intervals) in mussel patches (gray squares), *L. patagonica* patches (black circles) and unengineered patches (white triangles). Separate symbols at the right of the curves are the values of the Chao 2 estimate of total species richness at 80 samples



**Fig. 3** Venn diagram illustrating the proportional distribution of species across habitat types. Striped circle mussel patches, gray circle *Lithophaga* patches, white circle unengineered habitat

which indicates that the species added by the *L. patagonica* habitat are not a subset of those added by the mussel habitat ( $P = 0.998$ ).

Multiple Correspondence Analysis (Fig. 4) indicates that the species exclusively found in mussel patches were primarily small and lacked any adhesion mechanism, while those that occurred exclusively in *L. patagonica* patches were essentially medium to large species showing trophic modes other than deposit feeding as well as permanent or temporary adhesion to the substrate. Deposit feeding species were generally exclusive to mussel patches or shared between mussel and *L. patagonica* patches (Fig. 4; see also Table 2).



**Fig. 4** Multiple correspondence analysis showing associations between species traits (feeding mode, size, and degree of attachment) and the type/s of habitat where they occur. Habitat types are shown in **bold uppercase letters**. Sizes, feeding modes, and degrees of attachment are respectively shown as *regular*, *underlined*, and *italicized uppercase letters*. Size categories are defined as small (<5 mm), medium (5–10 mm), and large (>10 mm). Habitat types are mussel-engineered patches (MEP), *L. patagonica*-engineered patches (LEP), unengineered patches (UEP), mussel and *L. patagonica*-engineered patches (MEPLEP), unengineered, mussel and *L. patagonica*-engineered patches (ALL)

Of the species associated with *L. patagonica* patches (29 excluding *L. patagonica*), only two were exclusively found on the rock surface between neighboring boreholes and/or linings (the gastropod *Nacella magellanica* and the echinoid *Arbacia dufresnii*). The remaining species were usually or exclusively found within boreholes, on the external surface of protruding linings, or both (Table 2).

## Discussion

Our results show that both mussel and *L. patagonica* patches harbor twice the number of invertebrate species that occur on the unengineered rock substrate. However, the distinctive habitat patches created by each engineer add substantially different subsets of species to the study area, which implies that mussel and *L. patagonica* patches contribute complementarily to overall species richness in the intertidal landscape. Below we illustrate some of the factors that potentially underlie the positive and complementary impacts of these engineers on overall species richness at our study area and postulate general circumstances under which complementary engineering impacts on landscape-level species richness are expected to occur.

### Why do mussel and *L. patagonica* patches add species to the landscape?

Increased species richness in engineered relative to the unengineered habitats typically occurs when the presence and/or activities of engineers add three-dimensional complexity to the original habitat; see Crooks (2002) for a review. In such cases, three-dimensional structures modify local abiotic conditions and/or resources such that they meet the requirements of species that cannot occur in the unengineered habitat. For instance,

desiccation is extreme in our study region compared to many other rocky shore sites throughout the world, because of the arid climate and persistence of strong, dry winds (Bertness et al. 2006). Desiccation has therefore been proposed as the chief factor limiting the occurrence of several rocky shore invertebrate species to the interstitial space of mussel beds (Silliman et al. 2011). Desiccation is also reduced in *L. patagonica* boreholes (Table 1) and perhaps also in the interstices between adjacent protruding linings. Thus, both mussel and *L. patagonica* patches could be contributing to increased species richness in our study area by facilitating species that would otherwise be excluded by desiccation.

Of course, desiccation is unlikely to be the sole factor limiting species establishment in the unengineered habitat. For example, 13 of the 15 species in the unengineered habitat are sessile (e.g., anthozoans, cirripedians) or low motility organisms that adhere strongly to the substrate (e.g., gastropods, polyplacophorans) (Table 2). Mobile species lacking any adhesion mechanism and therefore prone to being washed out by waves and tidal currents (e.g., small crustaceans, nemerteans) are primarily associated with protected interstitial spaces in the engineered habitats (Fig. 3; Table 2). This suggests that hydrodynamic forces could also be limiting the occurrence of some species in the unengineered habitat. In addition, some mobile and/or deposit-feeding species might also be excluded from the unengineered habitat by high predation pressure or lack of sediments and detrital food sources, both of which can be relieved in the engineered patches (e.g., physical impedance to predator access and sediment trapping in interstitial spaces) (Witman 1985; Tokeshi and Romero 1995).

### Why do species in mussel and *L. patagonica* patches differ?

Mussel and *L. patagonica* patches add largely different subsets of species to the study area, probably because they differ in their relative ability to release species from the impacts of distinct limiting factors. For example, the species that exclusively occur in mussel patches are relatively small mobile organisms, (e.g., tanaidaceans, amphipods; Fig. 3; Table 2). In contrast, those that exclusively occur in *L. patagonica*-engineered patches are mostly larger epibenthic organisms, either sessile or mobile (e.g., gastropods, echinoids; Fig. 3; Table 2). This suggests that differences in the size of interstitial space between patch types (i.e., larger in *L. patagonica* than mussel patches; Table 1) imposes constraints on the size of organisms that colonize them, either as living space (e.g., attachment sites) or shelter (e.g., protection from desiccation, predators or flow impacts; see above).

In the same vein, 5 of the 13 mobile species that occur exclusively in the mussel habitat are deposit-feeders (either obligate or facultative; Table 2), which probably obtain their food from the sediments and detritus retained within the mussel matrix (see also Tokeshi and Romero 1995). In contrast, mobile deposit-feeders are absent among the species that occur exclusively in *L. patagonica* patches (Table 2). Hence, differences in the species associated with mussel and *L. patagonica* patches could also be driven by disparate levels of sediment retention between patch types (Table 1).

These findings are in line with those of Donadi et al. (2015), who showed that co-occurring engineers creating separate, structurally-distinct patches can lead to spatial segregation of functional traits. Our study further illustrates that the structurally different patches created by co-occurring engineers can each add exclusive subsets of species to the landscape. Such complementary engineering contributions to landscape-level species richness are not expected to happen when co-occurring engineers lead to spatial segregation of functional traits. Indeed, functional trait segregation may also happen when all species in the landscape are habitat generalists but some traits are more represented than others across the distinct engineered habitat types.

## When can co-occurring engineers have complementary impacts on landscape-level species richness?

It stems from the above discussion that two engineering species forming separate habitat patches within an unengineered environment will have complementary effects on landscape-level species richness if the two following conditions are met.

### *The engineered patches differ structurally from each other*

Species colonize engineered habitat patches in response to favorable abiotic conditions and resource levels (e.g., Gutiérrez et al. 2003; Badano et al. 2006; Wright et al. 2006). Abiotic conditions and resources are linked to patch structural attributes (e.g., size, shape, and spatial arrangement of the structural elements; see Gutiérrez et al. 2003) in two general ways. First, structure per se can represent abiotic conditions and/or resources for other organisms (e.g., enemy- or stress-free space, attachment sites, obstacles to movement). Second, structure can interact with different forms of energy (e.g., light, heat, or energized fluids containing dissolved or suspended materials) thereby altering the abiotic conditions and the availability of consumable resources (e.g., reduced desiccation via shading, structural attenuation of water flow with concomitant sediment deposition; Jones et al. 2010). As structural differences between engineered patches are larger, their relative impacts on limiting abiotic conditions and resources, and thus their suitability as habitat for other species, are more likely to vary (see below).

### *Two or more abiotic conditions and resources limit species occurrence in the unengineered habitat*

If two or more abiotic conditions and/or resources limit species occurrence in the unengineered habitat, it is highly possible that structurally different patch types also differ in their relative ability to moderate them. For example, given two structurally different engineered patch types, A and B, and two factors, X and Z, that limit species occurrence in the unengineered state, it may happen that engineered patch A reduces limitation by factor X but has negligible impacts on Z, while engineered patch B moderates factor Z but has little impact on factor X. If distinct subsets of species are limited by X and Z in the unengineered state, then engineered patches A and B will have complementary impacts on landscape level species richness.

In contrast, if a single abiotic condition plays a prominent role in limiting species establishment in the unengineered state (e.g., water for desert plants; see also typical examples of the Stress Gradient Hypothesis, Bertness and Callaway 1994), then each engineered patch can be expected to add species to the landscape in a number that scales with the degree they alleviate the impact of the abiotic factor in question (Wright et al. 2006). In this case, the species added by one engineered habitat type should be the same as or a subset of those added by the other habitat type. Last, if abiotic conditions and resources do not limit species establishment in the unengineered state, then all species in the potential pool of colonizers will succeed therein and the presence of engineered patches will have no impact on the overall species richness of the habitat mosaic.

## Concluding remarks

The fact that the structurally-different patches made by mussels and *L. patagonica* each add exclusive sets of species to our intertidal area highlights the complementary role that co-occurring engineers can have in the maintenance of species richness across landscapes. Although drawn from a small spatial scale, our findings indicate the potential for complementary engineering impacts at the larger scales that are usually implied in biodiversity management and conservation. Appreciating the possibility of complementary impacts in landscapes modified by multiple engineers is particularly important in a context of increased biotic exchange across global ecosystems, which includes widespread establishment of non-native engineers that often produce remarkably novel structural forms in the recipient landscapes (Crooks 2002; Wright et al. 2014). Novel engineered structures can aid the arrival of new colonizers of a landscape with consequences for biodiversity that can well extend across the landscape and even beyond the focal landscape area. We hope that this study provides a provisional conceptual basis and approach to address the contribution of co-occurring engineers to landscape-level biodiversity in these and other circumstances.

**Acknowledgments** We thank Ignacio Chiesa, Brenda Doti, Guido Pastorino, Daniel Lauretta and José Fernández Alfaya for help in species identification; Carlos Sánchez Antelo and Sabrina Soria for field assistance; and the Quiroga family for housing during field trips. We also thank the staff at the municipal camping site in Puerto Pirámides. Two anonymous reviewers improved the manuscript with their comments. The research presented here was partly funded by CONICET grants (Consejo Nacional de Investigaciones Científicas y Técnicas; PIP 11220080100732 and 11220110100024) to MGP and JLG. MB and LPA were supported by CONICET doctoral fellowships. The invertebrates in the protected area of Puerto Pirámides were collected with permission from Chubut Province (Secretaría de Turismo y Áreas Protegidas). This is a contribution to the program of GriETA.

## References

- Adami ML, Pastorino G, Orensanz JM (2013) Phenotypic differentiation of ecologically significant *Brachidontes* species co-occurring in intertidal mussel beds from the Southwestern Atlantic. *Malacologia* 56:59–67
- Almeida-Neto M, Guimaraes P, Guimaraes PR, Loyola RD, Ulrich W (2008) A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* 117:1227–1239
- Arribas LP, Bagur M, Klein E, Penchaszadeh PE, Palomo MG (2013) Geographic distribution of two mussel species and associated assemblages along the northern Argentinean coast. *Aquatic Biol* 18:91–103
- Arribas LP, Bagur M, Gutiérrez JL, Palomo MG (2015) Matching spatial scales of variation in mussel recruitment and adult densities across southwestern Atlantic rocky shores. *J Sea Res* 95:16–21
- Badano EI, Cavieres LA (2006a) Impacts of ecosystem engineers on community attributes: effects of cushion plants at different elevations of the Chilean Andes. *Divers Distrib* 12:388–396
- Badano EI, Cavieres LA (2006b) Ecosystem engineering across ecosystems: do engineer species sharing common features have generalized or idiosyncratic effects on species diversity? *J Biogeogr* 33:304–313
- Badano EI, Jones CG, Cavieres LA, Wright JP (2006) Assessing impacts of ecosystem engineers on community organization: a general approach illustrated by effects of a high-Andean cushion plant. *Oikos* 115:369–385
- Bagur M, Richardson CA, Gutiérrez JL, Arribas LP, Doldan MS, Palomo MG (2013) Age, growth and mortality in four populations of the boring bivalve *Lithophaga patagonica* from Argentina. *J Sea Res* 81:49–56
- Bagur M, Gutiérrez JL, Arribas LP, Palomo MG (2014) Endolithic invertebrate communities and bioerosion rates in Southwestern Atlantic intertidal consolidated sediments. *Mar Biol* 161:2279–2292

- Bertness MD, Callaway R (1994) Positive interactions in communities. *Trends Ecol Evol* 9:191–193
- Bertness MD, Crain CM, Silliman BR, Bazterrica MC, Reyna MV, Hidalgo F, Farina JK (2006) The community structure of Western Atlantic Patagonian rocky shores. *Ecol Monogr* 76:439–460
- Borthagaray AI, Carranza A (2007) Mussels as ecosystem engineers: their contribution to species richness in a rocky littoral community. *Acta Oecol* 31:243–250
- Castilla JC, Lagos NA, Cerda M (2004) Marine ecosystem engineering by the alien ascidian *Pyura praeputialis* on a mid-intertidal rocky shore. *Mar Ecol Progr Ser* 268:119–130
- Chao A (1984) Non-parametric estimation of the number of classes in a population. *Scand J Stat* 11:265–270
- Colwell RK (2013) EstimateS: Statistical estimation of species richness and shared species from samples. Version 9 User's Guide and application. <http://purl.oclc.org/estimates>
- Colwell RK, Coddington JA (1994) Estimating terrestrial biodiversity through extrapolation. *Phil Trans R Soc B* 345:101–118
- Colwell RK, Mao CX, Chang J (2004) Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* 85:2717–2727
- Colwell RK, Chao A, Gotelli NJ, Lin SY, Mao CX, Chazdon RL, Longino JT (2012) Models and estimators linking individual-based and sample-based rarefaction, extrapolation, and comparison of assemblages. *J Plant Ecol* 5:3–21
- Crooks J (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* 97:153–166
- Cuevas JM, Martin JP, Bastida R (2006) Benthic community changes in a Patagonian intertidal: forty years later comparison. *Thalassas* 22:31–39
- Donadi S, van der Heide T, Piersma T, van der Zee EM, Weerman EJ, van de Koppel J, Olf H, Devine C, Hernawan UE, Boers M, Planthof L, Eriksson BK (2015) Multi-scale habitat modification by coexisting ecosystem engineers drives spatial separation of macrobenthic functional groups. *Oikos* 124:1502–1510
- Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol Lett* 4:379–391
- Greenacre M, Blasius J (2006) Multiple correspondence analysis and related methods. CRC Press, Boca Raton, p 581
- Guimarães PR, Guimarães P (2006) Improving the analyses of nestedness for large sets of matrices. *Environ Model Softw* 21:1512–1513
- Gutiérrez JL, Jones CG (2006) Physical ecosystem engineers as agents of biogeochemical heterogeneity. *Bioscience* 56:227–236
- Gutiérrez JL, Jones CG, Strayer DL, Iribarne OO (2003) Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. *Oikos* 101:79–90
- Huber M (2010) Compendium of bivalves. A full-color guide to 3,300 of the world's marine bivalves. A status on Bivalvia after 250 years of research. ConchBooks, Hackenheim, p 901
- Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78:1946–1957
- Jones CG, Gutiérrez JL, Byers JE, Crooks JA, Lambrinos JG, Talley TS (2010) A framework for understanding physical ecosystem engineering by organisms. *Oikos* 119:1862–1869
- Lill JT, Marquis RJ (2003) Ecosystem engineering by caterpillars increases insect herbivore diversity on white oak. *Ecology* 84:682–690
- Nakano D, Yamamoto M, Okino T (2005) Ecosystem engineering by larvae of net-spinning stream caddisflies creates a habitat on the upper surface of stones for mayfly nymphs with a low resistance to flows. *Freshw Biol* 50:1492–1498
- Olivier SR, Kreibohm de Paternoster I, Bastida R (1966) Estudios biocenóticos en las costas de Chubut (Argentina) I. Zonación biocenológica de Puerto Pardelas (Golfo Nuevo). *Bol Inst Biol Mar* 10:5–74
- Paruelo JM, Beltran A, Jobbagy E, Sala OE, Golluscio RA (1998) The climate of Patagonia: general patterns and controls on biotic processes. *Ecol Austral* 8:85–101
- Rechimont ME, Galván DE, Sueiro MC, Casas G, Piriz ML, Diez ME, Primost M, Zabala MS, Marquez F, Brogger M, Alfaya JEF, Bigatti G (2013) Benthic diversity and assemblage structure of a north Patagonian rocky shore: a monitoring legacy of the NaGISA project. *J Mar Biol Assoc UK* 93:2049–2058
- Sánchez V, Zaixso HE (1995) Secuencias de recolonización mesolitoral en una costa rocosa del Golfo San José (Chubut, Argentina). *Nat Patagón Cienc Biol* 3:57–83
- Scasso RA, del Río CJ (1987) Ambientes de sedimentación y proveniencia de la secuencia marina del Terciario Superior de la región de Península Valdés. *Rev Asoc Geol Argent* 42:291–321

- Silliman BR, Bertness MD, Altieri AH, Griffin JN, Bazterrica MC, Hidalgo FJ, Crain CM, Reyna MV (2011) Whole-community facilitation regulates biodiversity on Patagonian rocky shores. *PLoS One* 6(10):e24502. doi:[10.1371/journal.pone.0024502](https://doi.org/10.1371/journal.pone.0024502)
- Tokeshi M, Romero L (1995) Filling a gap: dynamics of space occupancy on a mussel-dominated subtropical rocky shore. *Mar Ecol Prog Ser* 119:167–176
- Trovant B, Orensanz JL, Ruzzante DE, Stotz W, Basso NG (2015) Scorched mussels (Bivalvia: Mytilidae: Brachidontinae) from the temperate coasts of South America: Phylogenetic relationships, trans-Pacific connections and the footprints of Quaternary glaciations. *Mol Phylogenet Evol* 82:60–74
- Van der Molen S, Márquez F, Idaszkin YL, Adami M (2013) Use of shell-shape to discriminate between *Brachidontes rodriguezii* and *Brachidontes purpuratus* species (Mytilidae) in the transition zone of their distributions (south-western Atlantic). *J Mar Biol Assoc UK* 93:803–808
- Wesche K, Nadrowski K, Retzer V (2007) Habitat engineering under dry conditions: the impact of pikas (*Ochotona pallasi*) on vegetation and site conditions in southern Mongolian steppes. *J Veg Sci* 18:665–674
- Witman JD (1985) Refuges, biological disturbance, and rocky subtidal community structure in New England. *Ecol Monogr* 55:421–445
- Wright JP, Jones CG, Flecker AS (2002) An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia* 132:96–101
- Wright JP, Jones CG, Boeken B, Shachak M (2006) Predictability of ecosystem engineering effects on species richness across environmental variability and spatial scales. *J Ecol* 94:815–824
- Wright JT, Byers JE, DeVore JL, Sotka EE (2014) Engineering or food? Mechanisms of facilitation by a habitat-forming invasive seaweed. *Ecology* 95:2699–2706