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Bioengineer effects on understory species richness, diversity, and composition change along an environmental stress gradient: Experimental and mensurative evidence

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ABSTRACT

Canopy-forming bioengineer species are commonly assumed to increase local species richness and diversity. We tested this notion by investigating the effects of fucoïd seaweed canopies on understory communities along rocky intertidal elevation gradients in Atlantic Canada. Such gradients exhibit increasing thermal extremes and variation from low to high elevations, and are broadly used in stress gradient studies. A manipulative experiment created canopy and no-canopy treatments at the low, middle, and high intertidal zones, eliminating all species (except fucoïd canopies) from replicate quadrats. After recolonization, overall richness and diversity (considering all primary producers and consumers) were higher under canopies than uncovered by canopies at the high and middle zones, but no effects occurred at the low zone. Similarly, species composition was affected by canopies at the high and middle zones, but not at the low zone. A mensurative study that surveyed the full range of canopy cover (0–100%) using nearly five times more quadrats from pristine areas yielded the same results: richness and diversity increased with canopy cover at the high and middle zones (approaching stabilization toward high cover values), but no effects occurred at the low zone. Lack of canopy effects at low elevations is related to mild habitat conditions, which canopies are unable to modify, while positive effects at higher elevations relate to the capacity of canopies to ameliorate harsh conditions. This is the first time that a combined experimental and mensurative approach shows that the same bioengineer species affect overall species richness, diversity, and composition differently along a stress gradient. Overall, protecting canopy-forming bioengineers to preserve local biodiversity should be most effective in stressful environments.

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1. Introduction

An important goal of ecology is to understand the factors that affect the number of species in communities, referred to as species richness (Krebs, 1999). Bioengineer species (also known as ecosystem engineers) are organisms that modify the abiotic conditions of existing habitats or that create new habitats through their complex bodies (Jones et al., 1994). Thus, bioengineers may affect species richness. The bioengineering concept has gained increasing relevance in ecology in recent years, as the existence of common traits in taxonomically different bioengineers lends predictive capacity to the concept (Wright and Jones, 2006; Jones et al., 2010). For example, bioengineers are often considered to increase

local species richness (Wright et al., 2002; Lill and Marquis, 2003; Castilla et al., 2004; Bangert and Slobodchikoff, 2006; Borthagaray and Carranza, 2007; Buse et al., 2008; Bouma et al., 2009; Bravo et al., 2009; Cavieres and Badano, 2009; Altieri et al., 2010; Koivisto and Westerborn, 2010; Pillay et al., 2011; Sueiro et al., 2011). This notion, particularly in relation to the current biodiversity crisis, is frequently used to recommend that bioengineers be considered as primary targets in conservation plans (Fogel et al., 2004; Hastings et al., 2007; Mangialajo et al., 2008).

An evaluation of the environmental context, however, may render the above notion as less general than typically considered. Environmental stress is the negative forcing that the abiotic environment exerts on the ecological performance of organisms. For regional biotas, stress influences local species richness through effects on interspecific interactions (Menge et al., 2002; Crain and Bertness, 2006). For instance, mutualisms limiting the stress experienced by neighboring organisms often structure communities under stressful conditions. Under milder conditions, species do not need facilitative interactions to thrive and neutral or negative

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interactions may prevail (Bruno et al., 2003). For a regional biota, the main facilitators and competitors affecting community structure along stress gradients are often different species (e.g., macroalgae and mussels on marine shores; Menge and Branch, 2001; Bertness, 2007). However, if a species is able to perform well across a wide range of abiotic stress, theoretically it could play different ecological roles depending on the stress level. This suggests that the same bioengineer species may have varying effects on species richness as a function of stress.

Support for this possibility comes from studies that evaluated changes in pairwise species interactions along stress gradients. For some marine and terrestrial systems, those studies have found that the role of some species can indeed change from facilitation at high stress levels to competition under milder conditions (Bertness, 1985; Bertness et al., 1999; Pugnaire and Luque, 2001; Boyden et al., 2005; Choi and Norton, 2005; Kawai and Tokeshi, 2006; Norkko et al., 2006; Sthultz et al., 2007; le Roux and McGeoch, 2008). However, only a small fraction of all possible pairwise interactions in those communities were investigated. Thus, given that indirect interspecific effects often occur in unexpected ways (Menge, 1995; Pearson, 2010; White and O'Donnell, 2010), it is unknown how species richness could have been affected in such studies.

Few studies have directly investigated bioengineer effects on richness at different stress levels. For example, the effects of plant bioengineers on plant species richness were evaluated under high and low salinity levels in an estuarine system (Fogel et al., 2004; Crain and Bertness, 2005) and under different aridity and temperature levels on alpine systems (Cavieres and Badano, 2009). Effects were found to change with stress. However, different bioengineer species were used for tests at different stress levels. Thus, it is unclear whether the same engineer species would affect richness differently depending on stress, as the observed different effects may have resulted from changes in traits that change with bioengineer species. Studies that used the same bioengineer species at different stress levels are very rare. One such example (Arroyo et al., 2003) found that *Azorella monantha* (an alpine cushion plant) enhances plant richness in high-altitude stressful environments but not in lower, milder environments. However, only plant (not overall) species richness was measured in that study. Thus, there is also a need to evaluate bioengineer effects on overall species richness along stress gradients. Here, we investigate whether the effect of the same macroalgal bioengineers on overall richness (including primary producers and consumers) varies predictably with environmental stress. For this purpose, we used intertidal elevation gradients, which are often used as model systems in stress gradient studies.

Rocky intertidal habitats exhibit a marked vertical gradient of abiotic stress. As a result of the daily tidal cycles, key factors such as temperature show little variation at low elevations because of long submergence times, but reach extreme values at high elevations because of long exposures to the air. Thus, for an intertidal biota considered as a whole, environmental conditions change from relatively mild at low elevations to very stressful at high elevations (Raffaelli and Hawkins, 1999; Menge and Branch, 2001; Garbary, 2007). For our study, we used elevation gradients from wave-sheltered rocky intertidal habitats from the NW Atlantic coast, focusing on furoid seaweeds as bioengineers. These macroalgae are, by far, the largest organisms in these habitats, covering extensive areas of the substrate with well-developed canopies (Garbary et al., 2006; Scrosati and Heaven, 2007). During low tides, such canopies lay flat on the substrate and reduce thermal variation and water evaporation underneath them, facilitating the performance of understory species when the aerial exposure is long (Bertness et al., 1999).

We addressed our research goals through a manipulative experiment and a mensurative study. Combining both approaches is often productive in ecology, as experiments involve high levels of variable control, while mensurative studies provide the ultimate levels of realism (Krebs, 1999; Gotelli and Ellison, 2004; Sagarin and Pauchard, 2010). Our hypotheses were the same for both approaches. For practical purposes, we divided the intertidal elevation range where furoid canopies occur in three zones with the same vertical extent (low, middle, and high zones) to define three levels of environmental stress: from relatively mild at the low zone, to intermediate at the middle zone, to highest at the high zone (Raffaelli and Hawkins, 1999; Menge and Branch, 2001; Garbary, 2007). At each zone, we tested canopy effects on understory species richness and also on their diversity. Species diversity is a measure of how likely two randomly selected individuals in a community belong to different species. Diversity thus depends on richness, but also on the degree of similarity in abundance among the species (Krebs, 1999). Although richness and diversity are often related across communities, sometimes they may show different trends (Kimbrow and Grosholz, 2006; Scrosati and Heaven, 2007; Wilsey and Stirling, 2007). Both are important community traits because they are related to ecological stability and function (Hooper et al., 2005; Stachowicz et al., 2007; García and Martínez, 2012).

To develop our hypotheses, we considered that habitat amelioration by intertidal canopies is relatively unimportant for understory species at low elevations because habitat conditions are relatively stable as a result of prolonged submergence. However, at high elevations, studies of pairwise species interactions have revealed that furoid canopies facilitate the performance of understory species by protecting them from the harsh conditions that they would otherwise experience because of long exposures to the air (Bertness et al., 1999; Bruno et al., 2003). Therefore, we hypothesized that the effects of furoid canopy cover on understory species richness and diversity would change from small or neutral at low intertidal elevations to significant and positive at higher elevations.

2. Materials and methods

2.1. Study system

We conducted this study in wave-sheltered rocky intertidal habitats on the Atlantic coast of Nova Scotia, Canada, focusing on a 4 km stretch of coastline in the Tor Bay Provincial Park area (45°11'N, 61°21'W). Typical values of maximum water velocity are 3.2–5.6 m s⁻¹ in these habitats (Scrosati and Heaven, 2007), in contrast with values reaching 12 m s⁻¹ in wave-exposed habitats in Nova Scotia (Hunt and Scheibling, 2001). The full intertidal range (vertical extent between the lowest and highest tides) is 1.8 m on this coast. We surveyed the elevation range between 0 m (chart datum, or lowest normal tide in Canada) and 1.5 m (above chart datum) because this is the vertical range where extensive furoid canopies occur. These canopies are largely dominated by *Asco-phylum nodosum* (Fucales, Phaeophyceae), whose fronds can reach 1.6 m in length. Secondarily, furoid canopies also include species of *Fucus* (Fucales, Phaeophyceae), *Fucus vesiculosus* being the most common. Our mensurative study (see below for sampling design) indicated that the relative abundance of these furoid species was similar at the higher, middle, and lower thirds of the surveyed elevation range (Table 1). A previous survey of wave-sheltered habitats along 80 km of coastline including Tor Bay Provincial Park indicated that furoid canopies dominated by *A. nodosum* are the norm in such habitats (Longtin et al., 2009). Broader biogeographic analyses have also shown that such furoid canopies are

Table 1

Composition of furoid canopies (relative abundance of the furoid species, expressed as percentages) at the low, middle, and high intertidal zones on the Atlantic coast of Canada, based on data from 510 quadrats.

Species	Low zone	Middle zone	High zone
<i>Ascophyllum nodosum</i>	63.9%	63.0%	76.6%
<i>Fucus vesiculosus</i>	29.2%	36.3%	23.2%
<i>Fucus distichus evanescens</i>	6.9%	0.7%	0%
<i>Fucus spiralis</i>	0%	0%	0.1%

representative of wave-sheltered habitats on the NW Atlantic coast (Adey and Hayek, 2005).

Rocky intertidal elevation gradients are known to exhibit a pronounced vertical gradient of environmental stress because of tides, from mild conditions at low elevations to stressful ones at high elevations, temperature being a key ecological factor that shows increasing extremes from low to high elevations (Raffaelli and Hawkins, 1999; Menge and Branch, 2001; Garbary, 2007). Furoid canopies are not expected to ameliorate understory conditions much at low elevations because of long submergence times, but canopies should decrease understory thermal variation and extremes at high elevations (Bertness et al., 1999). To confirm this notion for our study system, we did a preliminary study in the summer of 2009. We first divided the surveyed intertidal range (between 0 m and 1.5 m in elevation) in three zones of equal vertical extent, hereafter referred to as the low (0–0.5 m of elevational range), middle (0.5–1 m), and high (1–1.5 m) elevation zones. In late June, we deployed submersible temperature loggers (Stow-Away TidbiTs, Onset Computer, Bourne, MA, USA) under full canopy cover and on substrate with no canopy cover at each of those three zones. Loggers were set to record temperature every half hour for 16 consecutive days. Because of the high cost of these loggers, we could only deploy two of them (canopy and no canopy) at each elevation zone. Thus, we use descriptive statistics to compare both canopy conditions at each elevation. Nonetheless, this preliminary survey confirmed current knowledge on vertical intertidal gradients (Table 2).

2.2. Manipulative experiment

We tested the effects of presence and absence of a furoid canopy on understory species richness and diversity at each intertidal zone. On 3–4 May 2008, we randomly determined at each elevation zone the position of 10 plots, each one extending for nearly 20 m along the shoreline at each zone and being 50 cm in vertical extent. In each plot, we marked with concrete nails the position of four random quadrats (20 cm × 20 cm) that were fully covered by furoid canopy. For consistency, quadrats were established on rocky surfaces excluding tide pools. In five random plots at each elevation

Table 2

Descriptive statistics for temperature (°C) recorded at three intertidal elevation zones (high, middle, and low) under two canopy conditions (full canopy cover and no canopy) every half hour for 16 consecutive days ($n = 768$) in June–July 2009 on the Atlantic coast of Canada.

	High zone		Middle zone		Low zone	
	Canopy	No canopy	Canopy	No canopy	Canopy	No canopy
Mean	13.20	14.11	12.73	13.14	12.61	12.64
Variance	2.57	14.19	2.25	3.47	1.03	1.35
Coefficient of variation	0.12	0.27	0.12	0.14	0.08	0.09
Minimum	9.8	7.9	8.5	7.6	10.3	9.1
Maximum	20.1	32.0	20.5	23.8	17.3	18.5
Range	10.3	24.1	12.0	16.2	7.0	9.3

zone, we completely removed the furoid canopy covering the quadrats by detaching the holdfasts from where the canopies arose. We left the quadrats from the other five plots at each elevation zone bearing the full canopy cover. Then, we cleared the substrate of all quadrats by scraping all organisms from the substrate (except furoid holdfasts and canopies for canopy-treatment quadrats) using chisels and wire brushes and burning the substrate with a torch afterward. Thus, the experiment included 20 quadrats in each elevation × canopy cover treatment (120 quadrats in total). Natural recolonization was allowed to occur in the quadrats.

On 23–24 April 2009, we measured during low tides the percent cover of each algal and invertebrate species (>1 mm) found in the quadrats, using a 20 cm × 20 cm metallic frame divided in 100 squares with monofilament line. For each quadrat, we determined the percent cover of each species by counting the number of squares in which the species' cover was 50% or more. If a species was present in a quadrat, but covered less than 1% in total, we recorded its cover as 0.5%. We used field guides (Gibson, 2003; Martínez, 2003; Sept, 2008) and taxonomic keys (Pollock, 1998; Sears, 1998) for identifications. For small species and for very similar species, identification was difficult. Thus, for such organisms, we measured cover for the lowest possible taxonomic level, as normally done in studies that document the diversity of all producers and consumers (Kimbrow and Grosholz, 2006; Russell et al., 2006; Thompson et al., 2007; Bishop, 2008; Valdivia and Molis, 2009). We used percent cover to quantify the abundance of species because alternative measures of abundance (e.g., density of individuals) cannot always be determined reliably for clonal species (Scrosati, 2005) or (e.g. biomass) would have required destructive sampling, which was avoided to minimize impact. Additionally, abundance was measured using the same metric for all species because that is a requirement to produce diversity indices (Magurran, 2004).

For each quadrat, we determined richness (S) as the number of species found therein and diversity by calculating Shannon–Wiener's diversity index (H'):

$$H' = - \sum p_i \log(p_i)$$

where p_i was the proportional abundance of species i in the quadrat, i.e., that species' percent cover divided by the sum of percent cover values for all species in the quadrat (Krebs, 1999).

We tested the interactive effects of canopy cover and elevation zone on species richness and diversity by running analyses of variance (ANOVA) separately for richness and diversity. We considered “canopy cover” as a fixed factor with 2 levels (canopy and no canopy), “elevation” as a fixed factor with 3 levels (high, middle, and low), and “plot” as a random factor nested within the elevation × canopy cover interaction. The nested nature of our design accounted for the spatial segregation of the three elevation zones (Underwood, 1997; Wikström and Kautsky, 2007). When the interaction term (elevation × canopy cover) was significant, we ran tests of simple effects to evaluate the effects of canopy cover separately at each elevation zone, using the error mean squares from the main ANOVA for each test (Quinn and Keough, 2002). For each elevation for which canopy effects were found, we determined the effect size by calculating the squared point–biserial correlation coefficient and its significance (Howell, 2002). When expressed as a percentage, the squared point–biserial correlation coefficient measures the percentage of the total variability found in the dependent variable that is attributable to treatment effects (canopy effects in this experiment). Before running the ANOVAs, we tested the normality and homoscedasticity assumptions with normal-probability plots and Levene's tests, respectively. Since both

assumptions were met, no data transformations were necessary. We did these analyses with JMP 5.1 for Macintosh.

We also compared the species composition between the canopy and no-canopy treatments at each elevation zone through a permutational multivariate analysis of variance (PERMANOVA) followed by a multivariate test of simple effects for each elevation zone. The PERMANOVA considered “canopy cover” and “elevation” as fixed factors and “plot” as a random factor nested within the elevation \times canopy cover interaction. Species composition is a measure of the identity of species in addition to their relative abundance. Thus, the comparison of species composition between two treatments may reveal community changes that would otherwise remain undetected if only species diversity were compared and found not to vary significantly between both treatments. We did these analyses with PERMANOVA+ for PRIMER 6.1.11 for Windows.

2.3. Mensurative study

In the summer of 2008, at each of the three elevation zones, we sampled 170 quadrats (20 cm \times 20 cm) that were randomly established following the shoreline in pristine (unmanipulated) areas of the coast, thus totaling 510 quadrats for this study. For each quadrat, we measured the percent cover of species using the sampling frame divided in 100 squares described above. In each quadrat, we first measured the percent cover of furoid canopy by counting the number of squares where canopy cover was 50% or more. Then, we carefully lifted the canopy and measured the percent cover of all understory species (algae and invertebrates) following the method described above. Measurements were done during low tides and excluded tide pools. For each quadrat, we calculated understory species richness and diversity as described above.

We tested the effects of canopy cover (range: 0–100%) on species richness and diversity by analyzing the relationship between canopy cover and each of those two traits separately for the high, middle, and low intertidal zones. Preliminary tests indicated that a quadratic fit was higher than a linear fit for the six data sets. Thus, we calculated the corresponding quadratic equations through standard nonlinear fitting (Quinn and Keough, 2002). To evaluate the significance of each equation, we first calculated the Pearson correlation coefficient (r) between the observed values of richness or diversity (depending on the equation) and the values of richness or diversity predicted by the equation for the corresponding values of canopy cover. Then, we assessed the significance of the resulting six coefficients with the t -test specifically designed to evaluate the significance of correlations (Quinn and Keough, 2002). In general terms, a perfect fit of data to any nonlinear equation would yield a perfect correlation ($r = 1$) between the corresponding equation-predicted values and observed values of the dependent variable. For the relationships that we found to be significant, we calculated the coefficient of determination (r^2), which, when expressed as a percentage, measures the percentage of the variation in the dependent variable than can be explained by the equation (Quinn and Keough, 2002). We did these analyses with SYSTAT 5.2 for Macintosh.

3. Results

3.1. Thermal influences of furoid canopies

Descriptive statistics indicated that furoid canopies influenced temperature differently depending on elevation, following a consistent trend across intertidal zones (Table 2). At the low zone, conditions outside of a canopy remained similar to those under full

canopy cover, as mean temperature was only 0.2% higher, variance 30.9% higher, and maximum temperature 6.8% higher outside of a canopy than under a canopy (Table 2). However, at the high zone, the furoid canopy ameliorated conditions considerably, as mean temperature was 7.0% higher, variance 451.8% higher, and maximum temperature 59.0% higher outside of a canopy than under a canopy (Table 2). At the middle intertidal zone, the increase in these thermal properties from canopy to no-canopy conditions was of intermediate magnitude (Table 2). The vertical trend in thermal traits found outside of canopies (Table 2) supported the known concept that thermal variation and extremes increase from low to high elevations in intertidal habitats.

3.2. Manipulative experiment

We identified a variety of seaweeds and invertebrates (Table 3). The ANOVA revealed that canopy cover ($F_{1,24} = 10.57, p = 0.003$) and elevation ($F_{2,24} = 8.27, p = 0.002$) significantly affected understory species richness. The interaction term (canopy cover \times elevation) was not significant ($F_{2,24} = 0.37, p = 0.698$). Overall differences among plots were significant ($F_{24,90} = 3.46, p < 0.001$), although this result does not bear relevance for our tests of interest (evaluating canopy effects at different elevation zones). Species richness was higher under full canopy cover than outside of canopies (Fig. 1a), but effect size changed markedly across elevation zones: based on squared point–biserial correlation analyses, canopy cover explained 49% of the variation in richness at the high zone ($p < 0.001$) and 57% at the middle zone ($p < 0.001$), but only 3% at the low zone, which was a non-significant result ($p = 0.258$).

Species diversity was also significantly affected by canopy cover ($F_{1,24} = 32.49, p < 0.001$) and elevation ($F_{2,24} = 11.98, p < 0.001$), as indicated by the ANOVA. The interaction term (canopy cover \times elevation) was significant ($F_{2,24} = 4.33, p = 0.025$), while overall differences among plots were not significant ($F_{24,90} = 1.50, p = 0.088$). We ran tests of simple effects to determine how canopy effects differed among the three elevation zones. Diversity was significantly higher under full canopy cover than outside of canopies at the high ($F_{1,8} = 14.80, p = 0.005$) and middle ($F_{1,8} = 34.21, p < 0.001$) intertidal zones, but statistically similar between both canopy treatments at the low zone ($F_{1,8} = 0.73, p = 0.419$; Fig. 1b). Thus, we measured effect size only for the high and middle zones: based on squared point–biserial correlation analyses, canopy cover explained 40% of the variation in diversity at the high zone ($p < 0.001$) and 47% at the middle zone ($p < 0.001$).

Species composition is summarized for each of the six studied treatments in Table 3. The PERMANOVA detected significant main effects of canopy cover ($F_{1,24} = 7.02, p = 0.001$) and elevation zone ($F_{2,24} = 13.79, p < 0.001$). Overall differences among plots were also significant ($F_{24,90} = 1.49, p = 0.003$), although this result is unimportant for our tests of interest (assessing canopy effects at different elevation zones). The interaction term (canopy cover \times elevation) was marginally significant ($F_{2,24} = 1.67, p = 0.059$), so we ran multivariate tests of simple effects to evaluate canopy effects for each elevation zone. Such tests revealed that species composition differed significantly between the canopy and no-canopy treatments at the high ($F_{1,8} = 6.01, p = 0.008$) and middle ($F_{1,8} = 5.53, p = 0.009$) intertidal zones, but remained statistically similar at the low zone ($F_{1,8} = 0.96, p = 0.363$). The difference in composition between both canopy treatments at the high and middle zones resulted primarily from the absence of many species in the no-canopy treatment. For instance, at the high intertidal zone, only 60% of the algae and 43% of the invertebrates occurring in the canopy treatment also occurred in the no-canopy treatment, whereas, at the middle zone, only 25% of the algae and 31% of the invertebrates found in the canopy treatment were also found in the

Table 3
Abundance of species (mean percent cover, with SE in parentheses; $n = 20$ quadrats) found through a manipulative experiment under full canopy cover and under no canopy cover at three intertidal elevation zones on the Atlantic coast of Canada. No data indicates local absence of a species.

	Low zone		Middle zone		High zone	
	Canopy	No canopy	Canopy	No canopy	Canopy	No canopy
Seaweeds						
<i>Ascophyllum nodosum</i> (recruits)			0.08 (0.04)		0.08 (0.04)	0.08 (0.04)
<i>Bangia atropurpurea</i>	0.80 (0.80)	0.05 (0.05)	1.55 (1.55)			
<i>Chondrus crispus</i>	0.30 (0.07)	0.45 (0.30)	0.05 (0.03)			
<i>Cladophora rupestris</i>	0.05 (0.03)	0.03 (0.03)				
<i>Cladophora</i> spp.	0.05 (0.03)	0.03 (0.03)				
<i>Cystoclonium</i> spp.	0.05 (0.03)	0.03 (0.03)				
<i>Dumontia contorta</i>	9.23 (3.62)	1.03 (0.85)	0.10 (0.10)			
<i>Fucus</i> spp. (recruits)	0.15 (0.06)	1.28 (0.69)	0.10 (0.05)	0.60 (0.45)	0.10 (0.05)	0.13 (0.05)
<i>Hildenbrandia rubra</i>	0.10 (0.10)	0.05 (0.05)	0.33 (0.12)		0.58 (0.31)	
<i>Laminaria longicuris</i>	0.03 (0.03)	0.03 (0.03)				
<i>Lithothamnion glaciale</i>	0.10 (0.05)		0.03 (0.03)			
<i>Petalonia fascia</i>	0.03 (0.03)					
<i>Rhodochorton purpureum</i>	2.65 (1.26)	5.90 (4.16)			0.15 (0.11)	
<i>Scytosiphon</i> spp.	0.28 (0.25)	2.50 (1.84)				
<i>Ulothrix</i> spp.		1.10 (0.81)	0.03 (0.03)	6.00 (3.18)	8.30 (2.83)	19.43 (6.12)
<i>Ulva lactuca</i>	0.25 (0.11)	0.70 (0.41)				
Lichen						
<i>Verrucaria maura</i>		0.18 (0.06)	0.23 (0.20)	1.30 (1.11)	0.23 (0.06)	1.60 (1.31)
Invertebrates						
<i>Acmaea testudinalis</i>	0.23 (0.06)	0.28 (0.06)				
<i>Anomia simplex</i>	0.03 (0.03)					
<i>Bittium alternatum</i>	0.03 (0.03)	0.03 (0.03)				
Bryozoa		0.03 (0.03)	0.03 (0.03)			
<i>Coryphella</i> spp.	0.03 (0.03)					
<i>Dynamena pumila</i>	0.05 (0.03)		0.05 (0.03)			
<i>Gammarus</i> sp. (biramous uropod)	0.08 (0.04)	0.05 (0.03)	0.23 (0.06)		0.33 (0.06)	
<i>Gammarus</i> sp. (uniramous uropod)	0.03 (0.03)	0.03 (0.03)				
<i>Jaera marina</i>	0.05 (0.03)	0.05 (0.03)	0.23 (0.06)			
<i>Lacuna vincta</i>	0.23 (0.06)	0.13 (0.05)				
<i>Littorina littorea</i>	1.00 (0.21)	2.35 (1.07)	0.78 (0.24)	0.68 (0.19)	0.03 (0.03)	
<i>Littorina obtusata</i>	0.25 (0.06)	0.23 (0.06)	0.50 (0.01)	0.28 (0.06)	0.25 (0.06)	0.05 (0.03)
<i>Littorina saxatilis</i>	0.03 (0.03)	0.03 (0.03)	0.13 (0.05)	0.08 (0.04)	0.38 (0.05)	0.15 (0.05)
<i>Margarites costalis</i>	0.15 (0.05)	0.08 (0.04)				
<i>Mytilus</i> spp.	0.03 (0.03)				0.10 (0.05)	
Nemertea			0.03 (0.03)			
<i>Nucella lapillus</i>	0.13 (0.06)	0.08 (0.06)	0.03 (0.03)			
<i>Obelia</i> spp.			0.03 (0.03)			
Oligochaeta	0.08 (0.04)	0.08 (0.04)	0.18 (0.06)		0.08 (0.04)	
<i>Semibalanus balanoides</i>	0.43 (0.04)	0.43 (0.04)	4.58 (3.97)	4.20 (3.73)	0.70 (0.34)	0.30 (0.06)
<i>Spirorbis spirorbis</i>	0.60 (0.34)	0.20 (0.07)	0.10 (0.05)			
<i>Urosalpinx cinerea</i>	0.03 (0.03)	0.03 (0.03)				

no-canopy treatment. Conversely, no species occurred only in the no-canopy treatment at those two elevation zones. Among the few species that occurred in both canopy treatments at those two zones, green filamentous algae (*Ulothrix*) and a lichen (*Verrucaria*) were slightly more abundant without canopy cover than when covered by a canopy, while the reverse was true for grazing snails (*Littorina*), the other species remaining similar in abundance between both treatments. The organisms that only occurred under canopies at the high and middle zones were red algae and sessile and mobile invertebrates. At the low intertidal zone, species typically occurred in both canopy treatments and showed generally small differences in abundance between both treatments (Table 3).

3.3. Mensurative study

We identified a variety of seaweeds and invertebrates through this study (Table 4). The quadratic relationship between fucoid canopy cover and understory species richness was highly significant for the high ($r = 0.67$, $p < 0.001$) and middle ($r = 0.71$, $p < 0.001$) intertidal zones, but not significant for the low zone ($r = 0.14$, $p = 0.078$; no significant linear relationship occurred for the low zone either). The equations for the high and middle zones

(Fig. 2) indicate that understory species richness generally increased with canopy cover, approaching stabilization toward the highest values of cover. Canopy cover explained 45% of the variation in species richness at the high intertidal zone and 50% at the middle zone.

The quadratic relationship between canopy cover and understory species diversity was also highly significant for the high ($r = 0.44$, $p < 0.001$) and middle ($r = 0.55$, $p < 0.001$) intertidal zones, but not significant for the low zone ($r = 0.10$, $p = 0.215$; no significant linear relationship was found for the low zone either). The equations for the high and middle zones (Fig. 3) indicate that understory species diversity generally increased with canopy cover, approaching stabilization toward the highest cover values. Canopy cover explained 19% of the variation in species diversity at the high intertidal zone and 31% at the middle zone.

4. Discussion

This study has found that, for the same baseline species pool, the effects of macroalgal canopies on understory species richness and diversity changed markedly depending on intertidal elevation. While at the low intertidal zone such effects were neutral, at the

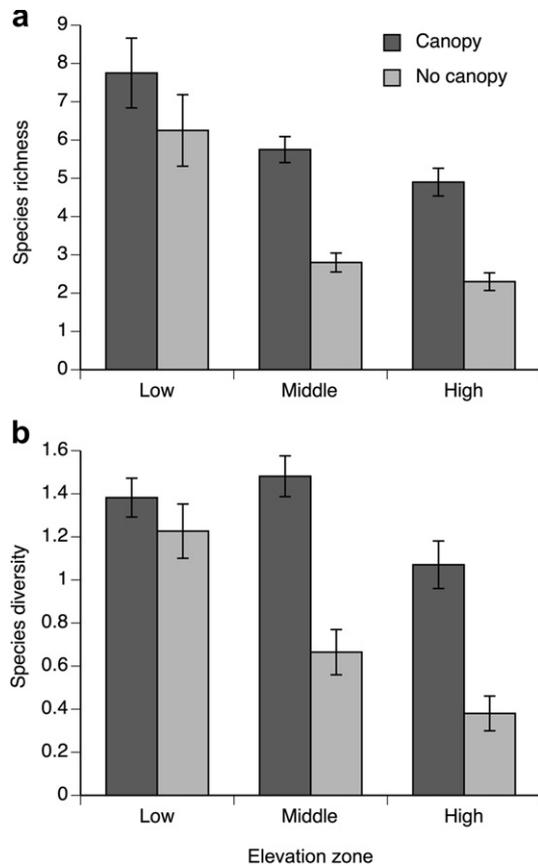


Fig. 1. (a) Species richness and (b) diversity (mean \pm SE; $n = 20$) found through a manipulative experiment in canopy-present and canopy-absent quadrats at the low, middle, and high intertidal zones on the Atlantic coast of Canada.

middle and high zones they were significant and positive. Species composition, which considers the identity of species in addition to their relative abundance, also remained unaffected by canopies at low elevations, while also depended on canopy cover at middle and high elevations. Our temperature data confirmed the notion that, in intertidal habitats, thermal conditions are relatively benign at the low zone but increasingly stressful (with higher extremes and variability) as elevation increases (Raffaelli and Hawkins, 1999; Menge and Branch, 2001; Garbary, 2007). The observed trend across elevations in thermal differences between canopy and no-canopy conditions also confirmed the notion that fucoid canopies ameliorate understory conditions at middle and high elevations but have almost no effects at low elevations (Bertness et al., 1999). Therefore, our study suggests that the capacity of fucoid canopies to enhance understory richness and diversity relates to their ability to improve conditions in stressful environments. Thus, the findings of this study challenge the extended concept that bioengineer species normally enhance local richness and diversity (Wright et al., 2002; Lill and Marquis, 2003; Castilla et al., 2004; Bangert and Slobodchikoff, 2006; Borthagaray and Carranza, 2007; Buse et al., 2008; Bouma et al., 2009; Bravo et al., 2009; Cavieres and Badano, 2009; Altieri et al., 2010; Koivisto and Westerbom, 2010; Pillay et al., 2011; Sueiro et al., 2011). Clearly, effects depend on local environmental conditions.

Explaining why individual species differed in abundance between the two canopy treatments at high and middle elevations was beyond the intent of this study. The abundance of species in communities is determined by a complexity of direct and indirect interspecific interactions (Menge, 1995), but that information is

Table 4

List of understory species found through a mensurative study in intertidal fucoid macroalgal beds on the Atlantic coast of Canada, based on 510 quadrats.

Seaweeds
Bangia atropurpurea
Calothrix sp.
Ceramium sp.
Chaetomorpha sp.
Chondrus crispus
Chordaria flagelliformis
Cladophora rupestris
Cladophora sp.
Corallina officinalis
Cystoclonium sp.
Devaleraea ramentacea
Dumontia contorta
Elachista chondrii
Hildenbrandia rubra
Laminaria digitata
Laminaria longicuris
Lithothamnion glaciale
Mastocarpus stellatus
Palmaria palmata
Petalonia fascia
Polysiphonia sp.
Porphyra sp.
Ralfsia sp.
Rhodochorton purpureum
Rhomela confervoides
Scytosiphon sp.
Spongomorpha aeruginosa
Ulva lactuca

Lichen
Verrucaria maura

Invertebrates
Acmaea testudinalis
Anomia simplex
Asterias vulgaris
Astyris lunata
Bittium alternatum
 Bryozoa (other than *Electra pilosa* or *Membranipora* sp.)
Buccinum undatum
Cancer irroratus
Carcinus maenas
 Chironomidae
Clava multicornis
Coryphella sp.
Crenella glandula
Dynamena pumila
Electra pilosa
Flustrellidra hispida
Gammarus sp. (biramous uropod)
Gammarus sp. (uniramous uropod)
 Halacaridae
Halichondria bowerbanki
Halichondria panicea
Halisarca sp.
Harmothoe imbricata
Hiatella arctica
Idotea balthica
Idotea phosphorea
Jaera marina
Lacuna vineta
Leptasterias tenera
Leucosolenia botryoides
Littorina littorea
Littorina obtusata
Littorina saxatilis
Margarites costalis
Membranipora sp.
Mytilus spp.
 Nematoda
 Nemertea
Nereis sp.
Nucella lapillus

(continued on next page)

Table 4 (continued)

<i>Obelia</i> sp.
<i>Oligochaeta</i>
<i>Ophiopholis aculeate</i>
<i>Semibalanus balanoides</i>
<i>Spirorbis borealis</i>
<i>Spirorbis spirorbis</i>
<i>Strongylocentrotus droebachiensis</i>
<i>Tonicella rubra</i>
<i>Urticina felina</i>
<i>Urosalpinx cinerea</i>

largely unavailable for the species associated to our furoid algal beds. Nonetheless, it is possible to speculate that the greater abundance attained by green filamentous algae and lichens in no-canopy quadrats, relative to canopy quadrats, may have resulted from competitive release through canopy absence. However, the absence of many algal and invertebrate species in no-canopy quadrats may have resulted simply from the increasing levels of thermal stress (and likely desiccation) recorded toward higher elevations when canopy cover was lacking. Then, the lower abundance of littorinid snails in no-canopy quadrats, compared with canopy quadrats, may have resulted from a lower food supply in addition to increased stress. Clearly, unraveling the interspecific interactions that determine the abundance of understory species from furoid algal beds requires experimental investigation.

The notion that bioengineers affect species richness differently along stress gradients has been suggested previously, but through studies that used different engineer species at different levels of stress (Fogel et al., 2004; Crain and Bertness, 2005; Cavieres and Badano, 2009). It is difficult to draw definitive conclusions from such studies because different bioengineer species could differ in traits affecting their propensity to increase species richness regardless of environmental conditions (Badano and Cavieres, 2006; Lamit et al., 2011). One recent study did use the same bioengineer species at different stress levels in a terrestrial system, finding that this plant increases species richness under stressful conditions but not in mild conditions (Arroyo et al., 2003). However, all of those studies only evaluated effects on plant species richness. With a marine system, our study provides experimental evidence using the same bioengineer species and evaluating effects on overall richness, including primary producers and consumers. Although furoid canopies from our coast are composed of more than one species, their relative abundance is similar across the surveyed elevation zones (Table 1), which strengthens the case for environment, not canopy species, modulating the observed canopy effects on understory communities along the intertidal gradient.

It is possible that the species composition of the quadrats from our manipulative experiment may not have reached the stage shown by the most stable (and, therefore, old) quadrats measured in the mensurative study. However, the key finding from our research is that the manipulative experiment and the mensurative study both yielded the same conclusions, namely that bioengineer canopies have different effects on understory communities depending on intertidal elevation. While the experiment identified furoid canopy as an important driver of richness and diversity at high and middle elevations but not at low elevations, the mensurative study revealed the generality of such patterns by surveying a larger sample size from pristine areas that summarized canopy effects after many years. We note that, despite the stabilization in the values of richness and diversity found by our mensurative study toward the highest values of canopy cover at middle and high elevations, the increase in richness and diversity from low-cover to high-cover quadrats in that study matched the results of the manipulative experiment. Mensurative approaches are most useful

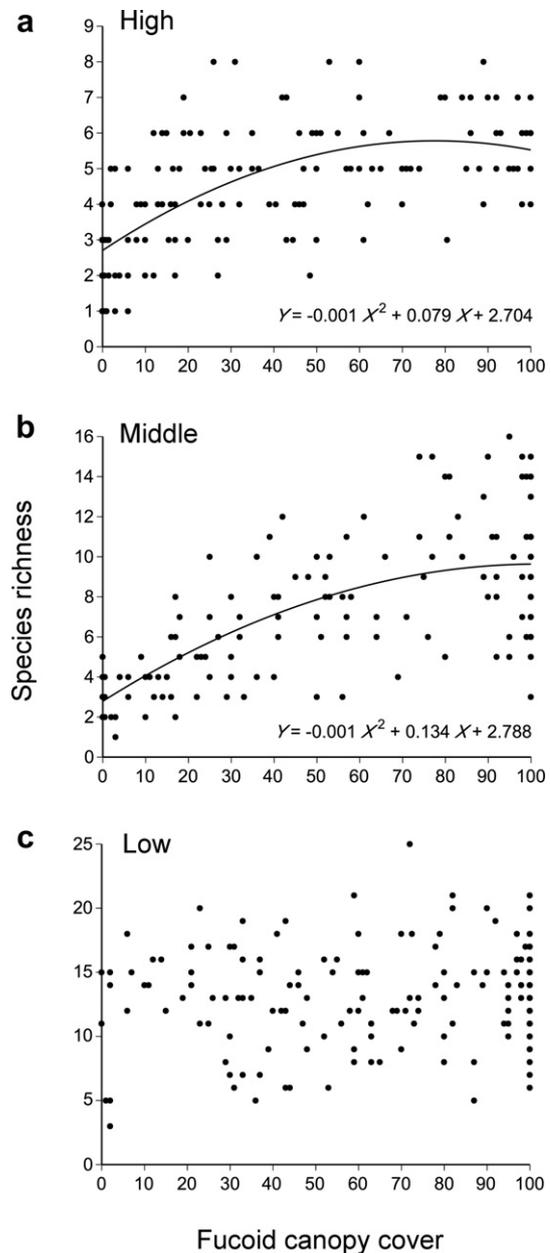


Fig. 2. Relationship between furoid canopy cover (%) and understory species richness found through a mensurative study for the (a) high, (b) middle, and (c) low intertidal zones on the Atlantic coast of Canada ($n = 170$ quadrats per zone). Significant relationships only occurred for the middle and high zones (see Section 3.3 for details), so the corresponding functions are only shown for panels (a) and (b).

when they complement and expand on what can reasonably be studied in a manipulative context (Agrawal et al., 2007), which was the case with our work.

The loss of bioengineers is a concern because these organisms often have wide-ranging and cascading effects (Coleman and Williams, 2002). Therefore, protecting these species is at the forefront of global conservation efforts (Hastings et al., 2007). However, careful consideration needs to be made when designing conservation areas, because bioengineer effects can vary depending on the stress level that sites experience. Jones et al. (1997) argued that being able to predict the types of ecosystems where bioengineers play the most critical roles would be vital for conservation efforts. The present study provides evidence indicating that the effects of the same bioengineers change depending on the stress level,

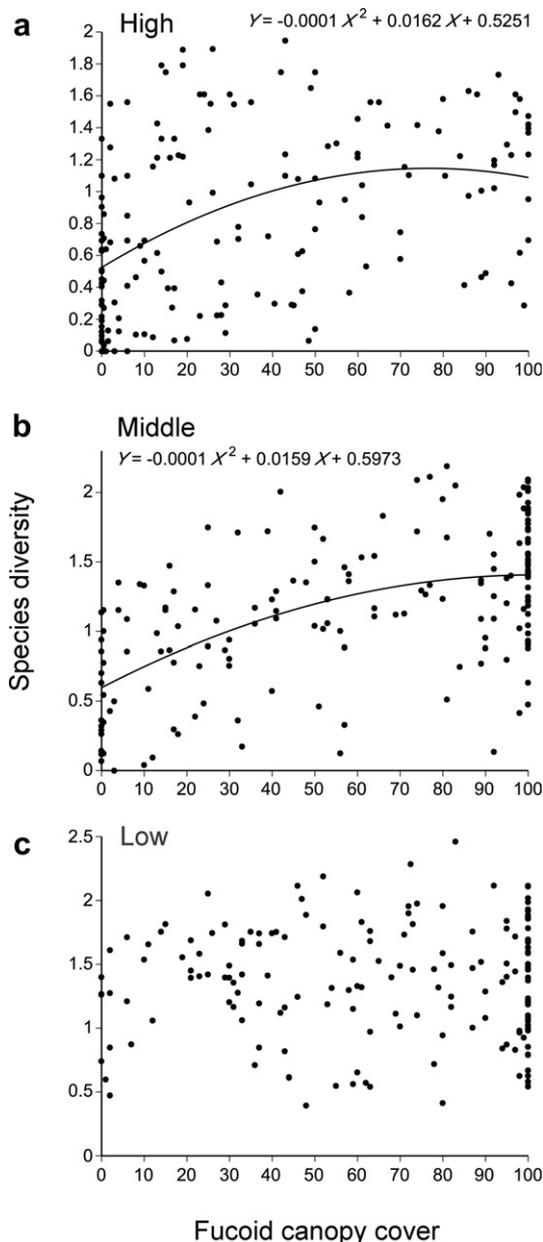


Fig. 3. Relationship between fucoid canopy cover (%) and understory species diversity found through a mensurative study for the (a) high, (b) middle, and (c) low intertidal zones on the Atlantic coast of Canada ($n = 170$ quadrats per zone). Significant relationships only occurred for the middle and high zones (see Section 3.3 for details), so the corresponding functions are only shown for panels (a) and (b).

supporting a community organization model (Bruno et al., 2003) that predicts that facilitation should be important as a structuring agent of communities at high levels of environmental stress for a given biota. Thus, our study suggests that such a model may be a valuable tool to predict the impact of bioengineers.

In addition, our study provides evidence suggesting that the effects of bioengineers also depend on their abundance, as understory species richness increased as bioengineer abundance increased in stressful environments for most of the natural range of canopy cover. Thus, biologists need to consider not only whether bioengineers are present, but also the abundance required to elicit positive changes in communities. Bioengineers may become even more influential as climate change develops, by maintaining refuges for organisms subjected to harsher abiotic stresses than they

are accustomed (Cavieres et al., 2002). The impact of climate change on bioengineers themselves is thus also of particular concern (Menge et al., 2008; Cole and McQuaid, 2010). Bioengineers hold great potential for conservation biology, and they should be targeted for conservation efforts, since their management can influence entire communities (Crain and Bertness, 2005). Our study suggests that the protection of canopy-forming bioengineers to preserve the associated biodiversity should be most effective in stressful environments.

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