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Resistance of benthic intertidal communities to multiple disturbances and stresses

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ABSTRACT: Many ecosystems are facing biodiversity loss and environmental change due to anthropogenic activities, with these impacts occurring within the context of natural disturbance. Understanding ecosystem functioning and the response of communities to these impacts is necessary in order to evaluate the effects of future environmental change. The aim of this study was to determine the consequences of the loss of key species on the structure and function of intertidal communities in a context of nutrient enrichment, so as to ascertain the resistance of these communities when disturbance and stresses are compounded. Subarctic rocky intertidal communities in Quebec were subjected to an orthogonal factorial field experiment with 2 disturbances, macroalgae canopy loss, grazer exclusion, and the stress of nutrient enrichment. Simple and interactive effects of these factors were followed for 4 mo, and responses in structure (% cover and biomass) and productivity were evaluated. The communities that were not subjected to canopy loss showed greater resistance and very limited effects from enrichment and grazer reduction. The loss of canopy altered the community structure (e.g. reduction in richness and biomass) and functioning (reduced productivity), probably due to increased temperatures and desiccation. This lack of resistance was amplified through the addition of a stress. The application of multiple stresses within field experiments allows for a better understanding of the mechanisms affecting community structure and ecosystem functioning under situations of increased natural and anthropogenic stress.

KEY WORDS: Community structure · Functional response · Multiple stressors · Resistance · Canopy disturbance · Grazers · Nutrient addition · Rocky intertidal

INTRODUCTION

In many ecosystems, natural disturbances are coupled with human activities, affecting both abiotic and biotic properties of the system (Vitousek et al. 1997b, Tilman & Lehman 2001). Habitat destruction (Brooks et al. 2002, Tole 2002, Hanski 2005), pollution (McNeely 1992, Oleksyn & Reich 1994) and alterations of biogeochemical cycles (e.g. carbon and nitrogen) by human activities (Vitousek et al. 1997a,b, Rabouille et al. 2001) negatively impact the structure and functioning of many ecosystems (Vitousek et al. 1997b, Hooper et al. 2005). Biodiversity loss is a major threat to ecosystem functioning (Hooper & Vitousek 1997, Tilman 1999, Hooper et al. 2005, Stachowicz et al. 2007) and may be considered equal in importance to other major environmental changes (e.g. climate warming, nutrient loading) in terms of the effects on overall ecosystem health (Hooper et al. 2012). Biodiversity can play an important role in countering stresses on ecosystems; therefore, understanding the consequences of biodiversity loss for ecosystems has prompted numerous ecological studies (Grime 1997, Loreau et al. 2002, Worm et al. 2006).

The link between biodiversity and ecosystem stability has been well studied (MacArthur 1955, Elton 1958, Pimm 1984, Tilman 1996, Lehman & Tilman 2000). Greater diversity generally increases the stability of ecosystems as a greater number of species will encompass a broader range of functional traits and response strategies to disturbance (Tilman & Downing 1994, Tilman 1996, 1999, Yachi & Loreau 1999, Stachowicz et al. 2007). An essential attribute of ecosystem stability is therefore resistance (or ‘inertia’ sensu Underwood 1989), which is defined as the capacity of a system to remain unchanged when faced with disturbance or stress (Pimm 1991, Grimm & Wissel 1997, Lehman & Tilman 2000).

The presence of certain key species may increase the stability (and resistance) of a community (Maggi et al. 2009, Grman et al. 2010, Watson & Estes 2011). In the context of biodiversity loss, the disappearance of key species will likely have a major effect on ecosystem functioning. For instance, habitat-forming species (or ecosystem engineers and bioengineers, sensu Jones et al. 1994) offer refuge and protection for numerous organisms and thus play a crucial role in ecosystem functioning. The loss of habitat-forming species has a negative impact on the surrounding community through a reduction in associated species richness and abundance (Rueda et al. 2009, Pillay et al. 2010, Schein et al. 2012, Do et al. 2013, Watt & Scrosati 2013).

Habitat-forming macroalgae, often dominating the intertidal zone of rocky shore habitats, are considered key species for their ecosystem (Hawkins & Hartnoll 1983, Raffaelli & Hawkins 1996). They play an important role in structuring the community (Hawkins & Harkin 1985, Jenkins et al. 1999a), providing a food supply (Hawkins & Hartnoll 1983), modifying physical conditions and reducing physical stress (e.g. desiccation and wave action) for the understorey community (Bertness & Leonard 1997, Bertness et al. 1999). However, sweeping by canopy algae may also have negative effects on the understorey (Hawkins 1983, Hawkins & Harkin 1985, Jenkins et al. 1999b). Currently, macroalgae (including fucoids) are undergoing a global decline (Eriksson et al. 1998, Walker & Kendrick 1998, Airoldi 2003, Airoldi & Beck 2007, Connell et al. 2008) caused by both climate change and other regional and local-scale human impacts (Hawkins et al. 2009). This loss of fucoids will therefore have major consequences for the understorey community (Jenkins et al. 1999a, Worm & Duffy 2003) by reducing species richness (Schiel & Lilley 2011, Watt & Scrosati 2013) and enhancing ephemeral algae recruitment (Jenkins et al. 1999a, Bulleri et al. 2002, Schiel & Lilley 2007, 2011). Moreover, changes in the abundance of macroalgae could also affect community function by reducing primary production (Tait & Schiel 2011a, Valdivia et al. 2012, Crowe et al. 2013).

Grazers are also an important element structuring intertidal communities, especially during early succession, applying strong top-down control on algal recruitment (Hawkins 1981, Hawkins & Hartnoll 1983, Anderson & Underwood 1997, Jenkins et al. 2005, Coleman et al. 2006, Aguilera & Navarrete 2012), thereby influencing the course of species succession. Grazer exclusion often leads to inhibition of later successional taxa (e.g. *Fucus* spp.) by ungrazed, early settling ephemeral algae such as *Ulva* spp. or *Porphyra* spp. (see Lubchenco 1983, Anderson & Underwood 1997, Jenkins et al. 1999c). On the other hand, human activities that generate nutrient enrichment in coastal environments (e.g. Paerl 1997, Allen et al. 1998) may lead to increases in the abundance of ephemeral algae (Johansson et al. 1998, Korpinen et al. 2007, Kraufvelin et al. 2010), that exacerbate bottom-up controls within communities. Biodiversity can be an important factor buffering against this nutrient loading. For example, canopy and grazer loss lead to a community more sensitive to nutrient addition, and an increased abundance of ephemeral algae (e.g. Worm & Lotze 2006), while the effects on invertebrates are unknown. Such removals simulate anthropogenic removal of canopies (e.g. fucoid harvesting, Ugarte & Sharp 2001) or the collection of grazers (Martins et al. 2010).

Ecological communities are often exposed to multiple interacting disturbances and stresses, both natural and anthropogenic. Studying the potential effects (synergic or antagonistic) of these disturbances and stresses on communities will contribute to our understanding of the cumulative impacts that shape communities. Single, isolated effects of canopy or grazer removal and enrichment have been broadly studied, yet few studies have simultaneously examined the coupled impacts of biodiversity loss and stress. Eriksson et al. (2007) made field manipulations using multiple treatments, but their study focused only on algal community responses (e.g. understorey and recruits). Multiple interactive impacts on both macroalgae and macroinvertebrate assemblage structure and function have not yet been properly studied.

The aim of our study was to determine the *in situ* consequences of the loss of key species (macroalgae canopy and grazers) on ecosystem structure and functioning in the presence of nutrient enrichment and to evaluate the resistance of the benthic community when species loss and stress are coupled. Specifically, we evaluated the response of subarctic benthic communities subjected to both single and interactive effects of canopy removal, grazer exclusion and nutrient enrichment on community structure and functioning (by using community productivity and respiration) and the resistance of intertidal rocky shore communities. This study also provides insight into the respective role of top-down controls, ecosystem engineers and bottom-up forcing in shaping community structure and ecosystem functioning (see also Thompson et al. 2004, Crowe et al. 2011). Such forcing is not yet understood for the subarctic ecosystem of the St. Lawrence Estuary. This site was selected as it is subjected to both natural and anthropogenic stressors including ice-scouring (Archambault & Bourget 1983, Bergeron & Bourget 1984), a predicted increase in water movements (Savard et al. 2008), along with eutrophication (Thibodeau et al. 2006, Gilbert et al. 2007) all which may affect the abundance of macroalgae and grazers in benthic intertidal communities. We hypothesized that in addition to a significant impact from canopy and grazer removal individually, community structure and ecosystem functioning would be even more affected due to synergetic effects when these disturbances are coupled with nutrient enrichment stress.

MATERIALS AND METHODS

Study site

The experiment was conducted between May and September 2012 near the village of Sainte-Flavie on the south shore of the St. Lawrence Estuary, Quebec, Canada (48° 37' 42.5" N, 68° 11' 55.7" W). The study area is representative of a subarctic flat rocky shore habitat as it is subjected to ice-scouring during winter and early spring (Archambault & Bourget 1983, Bergeron & Bourget 1984). Temperature and salinity range from 4 to 16°C and 24 to 29‰, respectively (Fradette & Bourget 1980, Archambault & Bourget 1983). The intertidal fauna and flora are characteristic of a moderately wave-disturbed environment (Archambault & Bourget 1983). In the mid-intertidal zone, the macroalgal canopy is composed of *Fucus* spp. (*F. distichus edentatus* and *F. vesiculosus*) and the invertebrate assemblage is dominated by gastropod grazers (*Littorina obtusata* and *L. saxatilis*; see Table S1 in the Supplement at www.int-res.com/articles/suppl/XXXpYYY_supp.pdf for a complete list) and by filter feeder blue mussels (composed of *Mytilus edulis, M. trossulus* and hybrids, hereafter referred to as *Mytilus* spp.). The shores of the estuary are often covered with ice during the winter (mid-December until the end of March); the ice sheet provides protection for the biological assemblages against extreme cold. The ice, however, may also act as an indiscriminate disturbance factor on the flat rock surfaces and exposed crevices through heavy ice-scouring (Bergeron & Bourget 1984, Åberg 1992, McKindsey & Bourget 2001).

Experimental design

We used an orthogonal factorial experimental design in order to evaluate the effects of biodiversity loss (canopy [Ca], 2 levels; grazer [Gr], 2 levels) and nutrient enrichment (Nu, 2 levels) on the structure and functioning of the intertidal benthic communities (Fig. 1). All 8 treatments from this design, and a procedural control (for the grazer exclusion; see below) were replicated 4 times (n = 4) and randomly assigned to 36 experimental plots (50 × 50 cm) on emergent rocky substrates within our study area. All plots were placed at a similar height in the mid-intertidal zone (average of 1.34 ± 0.20 m), in a 400 m wide area. The experimental plots, marked using anchor screws, were haphazardly selected with the criteria of homogenous flat substrate, lacking pools or large crevices, with a minimum of 80% cover of *Fucus* spp. A minimum distance of 3 m between plots was respected so as to avoid treatment interaction.

For the canopy treatment, we had 2 treatment levels: canopy present (C+) where the canopy was untouched, and canopy absent (C–) where all canopy taxa (i.e. *Fucus* spp.) holdfasts were removed within the 50 × 50 cm area.

The grazer treatment also had 2 treatment levels: grazers present (G+) and grazers absent (G–). In the latter, the grazers *L. obtusata*, *L. saxatilis* and *L. littorea*, *Tectura testudinalis*, *Margarites* spp. and *Jaera marina* were removed by handpicking. The exclusion treatment was designed using a physical barrier composed of a thin layer of natural sticky barrier (Tree Tanglefoot Insect Barrier; Contech) and a small twisted wire brush (2 cm diameter) placed on cleared (~5 cm width) surfaces along the contour of the experimental plot. When needed, these surfaces were smoothed using a small quantity of concrete (Poly-Plug Bomix; Daubois) and epoxy (West Systems). Procedural controls (n = 4) with incomplete exclusions were also implemented in natural communities. No difference was observed between the control plots (C+, G+ and no enrichment) and the procedural controls for any response variables, with the exception of richness on Date 4. At the study site, the abundance of small grazers (<2 mm) is great and the use of cages with small screens would certainly have had an effect on the natural communities. Moreover, the cageless grazers treatment used in this study did not have the undesired effects of light and flow reduction and detritus retention commonly observed with cage use (Range et al. 2008).

For the nutrient enrichment, 2 levels were used: natural conditions (N–) and enriched conditions (N+) where a controlled addition of slow-release fertilizer pellets of 14% nitrogen (NO_3-N and NH_3-N), 14% P (P_2O_5) and 14% K (K_2O) (Smartcote®; Plant Prod) was used within the experimental plots. Enrichment through slow-release fertilizer pellets has been tested (Worm et al. 2000) and used in many habitats (Worm et al. 2000, Eriksson et al. 2006a, 2007, Korpinen et al. 2007, Jochum et al. 2012). This method produces independent nutrient treatments within a

2 m distance from the source (Worm et al. 2000). Two mesh bags containing 100 g of fertilizer pellets were screwed at the opposite corners of the 50 × 50 cm plots and replaced every month. For all other experimental plots, inert control bags with washed pebbles were used to take into account any bag effects (e.g. as additional substrate). When replaced, the collected nutrient bags were weighed (dry weight loss) to estimate the amount of nutrient diffused into plots. An average of 31 ± 0.15% of weight loss was observed, with a total estimated diffusion of 8.64 ± 0.57 g of total nitrogen per month into each plot. This level of nutrient enrichment is comparable to moderate eutrophication, which is anticipated for the St. Lawrence Estuary (Thibodeau et al. 2006, Gilbert et al. 2007). Pilot tests in the field showed a 3- to 6-fold increase in total nitrogen concentrations in water samples from an enriched quadrat compared to the natural concentration of the St. Lawrence Estuary. *F. distichus edentatus* tissues from control and nutrient-enriched plots were collected at the end of the experiment and their total nitrogen content was compared (analyzed at the INRS Laboratory, Quebec City). The total nitrogen content values in the *Fucus* tissues from nutrient-enriched plots were slightly higher than those in the controls (average of 1.06 ± 0.05% and 0.95 ± 0.04% nitrogen, respectively; $F_{1,20} = 7.07$, $p = 0.015$), providing evidence that the additional nutrients had been incorporated into the algae.

Canopy and grazer treatments were 'press' type perturbation (sensu Bender et al. 1984) experiments, as experimental conditions of the densities of these species into plots were altered and controlled every 9 to 11 d. During each inventory (see following sub-section) and during maintenance (between inventory periods), new *Fucus* spp. juveniles and grazers were estimated/counted and thereafter removed from the plots. Even when grazer abundance was reduced for several days (up to 4 d; L. Joseph, M. Cusson and S. Cimon unpubl. data), the grazer treatment (G–) failed to significantly reduce their abundance during the period between 2 maintenance sessions. However, although grazer removal efficiency failed (about 40% of the time) on a bi-monthly time-scale, some statistically significant differences were observed for the grazer treatments and the treatment was not removed from data analyses. Thus the treatment is referred to as 'grazers reduced' rather than 'grazers absent', and was interpreted accordingly.

Sampling

Structure of the community

The community in each plot was sampled using a 30 × 30 cm quadrat placed in the centre of the experimental plots. Non-destructive visual estimates of abundance as % cover of all identified taxa >1 mm (usually to species level) for each plot were made at 4 distinct times: Date 1 (June 2 to 9, before establishment of the treatments), Date 2 (July 1 to 8), Date 3 (July 31 to August 6) and Date 4 (August 29 to September 4). Inventories were performed before any maintenance of the plot. The % cover of macroalgae and mussels were estimated with the division of the 30 × 30 cm frame into 25 equal squares, each representing 4% of the total quadrat cover. This latter procedure is common (e.g. Scrosati et al. 2011, Crowe et al. 2013), and use of the same unit among abundances is necessary in order to assess the community dominance profiles in our treatments. Mobile invertebrates were counted and later transformed into % cover (e.g. regression to convert density in % cover with n = 129, $R^2 = 0.66$ for *Littorina* sp.; arbitrary value of 0.25% for each individual of *L. littorea*, *T. testudinali*s, and *Nereis* sp.; 0.1% for each individual of *Lacuna vincta* and *Margarites* sp.; 0.01% for each *J. marina*). The cover was estimated per species, so the total summed % in a plot often exceeded 100%. Following the last visual inventory, we destructively sampled in order to collect all biomass (except crustose species) in the sampled 30 × 30 cm plot. The biomass samples were sieved (∅ 1 mm) and all individuals were identified under a microscope and weighed (±0.00005 g). Biomass was converted into energy (kJ) by applying conversion factors from Brey (2004).

Functioning of the community

To assess the effects of nutrient enrichment on community functioning with or without canopy, measures of primary production were estimated at the end of July, near midday over 3 consecutive sunny days. Estimates were derived from variations in CO_2 concentration (ppm) using benthic chambers following the method described by Migné et al. (2002). Subsampled plots in each treatment (n = 3 for control and N; n = 2 for C and CN) were randomly chosen for primary production measurements and randomly ordered during the sampling days. The chamber consisted of a transparent dome and a base of Plexiglas© placed over the 30 × 30 cm sampled community plot, then sealed airtight to the ground using neutral silicon. CO_2 variations in the chamber were measured using an infrared CO_2 gas analyzer (Li-800; LI-COR) and recorded on a data logger (Li-400; LI-COR) every 15 s for 15 to 20 min. Measurements of CO_2 concentrations were conducted at ambient light (>1000 µmol photon m^{-2} measured at PAR, 600 to 700 nm) for net primary production (NPP) and with an opaque polyethylene sheet placed over the chamber in order to measure respiration (*R*). The CO_2 fluxes for NPP and *R* were calculated using the following formula:

$$\text{Flux (mmol C m}^{-2}\text{ h}^{-1}) = b\,(18.2 \times 60) / (22.4 \times 1000 \times 0.09)$$

where the slope, *b*, is obtained through a linear regression of the CO_2 variations recorded from the chambers, 18.2 = volume (l) of air in the chamber, 60 = min in an hour, 22.4 = molar air by litre in molar volume. The gross primary production (GPP) of the community was then calculated by adding NPP and *R*. Note that this method is not used for calculating a global CO_2 budget but serves to estimate the metabolic state of the community under the same conditions and for comparison among treatments.

Data analysis

All analyses were performed on the associated community only (unless otherwise stated); the manipulated taxa (*Fucus* spp. and grazer species) were excluded from the data prior to analyses.

To test for the effects of the treatments and the interactions between and among them, repeated measures of analysis of variance (RM-ANOVA) with 4 fixed factors (date: 3 levels; Ca, Gr and Nu: 2 levels each) were performed on total abundance (sum of all species in % cover within the 30 × 30 cm sampled plots), richness (*S*) and the Simpson's index of diversity ($1 - \lambda$). Date 1 was not included in the latter analysis. Following this test, we also applied separate 3-way ANOVAs (with factors of C, G and N) performed at each date in order to appreciate the evolution of any effects over time (see Table S2 in the Supplement). A 3-way ANOVA was performed for total biomass abundance, as this variable was only available for the last date. Separate analyses of total abundance and richness of understorey algae and invertebrates (without grazers) were also performed. ANOVA assumptions were checked by graphical examination of the residuals (Montgomery & Mastrangelo 1991, Quinn & Keough 2002); no transformations were necessary. When a factor was significant, a multiple comparison test (Tukey's HSD or if stated, Student's *t*) was performed to look at the differences between treatment levels. Comparisons of taxa abundance for some species were investigated using a *t*-

test or Wilcoxon rank sum test when the assumptions of normality and equality of variances were not met.

The effects of the treatments on the structure of the community (in % cover and biomass data, based on Bray-Curtis similarities) were investigated for each date using a permutational multivariate analysis of variance (PERMANOVA; Anderson et al. 2008) with 999 permutations and with the same factors (C, G and N) as described above. Abundance data for % cover and biomass were square-root transformed and fourth-root transformed, respectively, while data were transformed into presence–absence for effects on compositional community structure. The effects of the treatments were visualized using principal coordinate analysis (PCO). A similarity percentage analysis (SIMPER) was used to assess the percentage contribution of each taxon to the observed dissimilarities among treatments.

The effect of enrichment and canopy loss on GPP, NPP and *R* were analyzed using a Kruskal-Wallis test (treatment fixed 4 levels) among control and N (n = 3) and C and CN (n = 2) treatments (see Fig. 1 for treatment details).

Univariate analyses were made using JMP v.10.0; multivariate analyses and ordinations were conducted using PRIMER+PERMANOVA v.6.1.6 (Clark & Gorley 2006, Anderson et al. 2008). A significance level of $\alpha = 0.05$ was used for all statistical tests, however, observed p-levels close to significance were carefully considered.

RESULTS

A total of 35 different taxa were observed at our site with an average (±SE) of 9.0 ± 0.3 species (min. = 5, max. = 19) per sampled quadrat (30 × 30 cm). Eleven algal taxa were reported, the most abundant being *Fucus distichus edentatus* and *Ralfsia clavata*, along with 24 taxa of invertebrates with grazers (e.g. *Littorina saxatilis, L. obtusata, Tectura testudinalis*) and filter feeders (e.g. *Mytilus* spp.) being the most common. A list of all observed taxa is presented in Table S1 in the Supplement.

Effects of single and multiple stresses

Community abundances and diversity indices

The canopy, grazer and nutrient enrichment treatments had different effects on the associated community, and some of them varied among sampling dates. Total abundance in terms of % cover was not affected by any of the treatments nor by date (Table 1, Table S2a in the Supplement), whereas in all treatments, the average values of richness and diversity were affected by date (Tables 1 & S2b,c). Average richness values were significantly higher (more than 2-fold) at the end of the experiment (Date 4) compared to the other dates ($F_{3,96} = 147$, $p < 0.0001$). This was due to the addition of cryptic taxa (originating, for example, from sediments or in between the mussel aggregations) that had been collected during the destructive sampling method after the last inventory.

Some significant effects were detected before the start of the experiments (Date 1; annexed Table 1). This cannot be easily explained as the treatments had not been yet implemented. Variation between the 2 categories of plots was, however, small in comparison to the differences observed later over the course of the experiment. Plots where the canopy cover was to remain had 3.75 ± 0.32 species and a Simpson's index of diversity of 0.51 ± 0.03, while plots where the canopy was to be removed had a lower richness (2.88 ± 0.10 species) and a diversity of 0.39 ± 0.03. Treatments were randomly assigned to plots along a 400 m wide transect along the shore where some variability among natural communities can occur. However, no effects on community abundance structure were observed (see next section) and the significant effects observed at Date 1 had dissipated by Date 2 (see Table 1).

Species richness was significantly affected by the Date × Ca treatment (Table 1) and differences were seen at both Dates 3 and 4 (Table S2b). Average richness values were lower when the canopy was absent than when present, with differences between C+ and C– of 1.28 and 3.24 at Dates 3 and 4, respectively (cf. Fig. 2a for Date 4). Among dates, the grazer treatment affected richness differently between the enrichment treatments as shown by the significant Date × Gr × Nu interaction (Table S2b, Fig. 2b). Diversity was significantly affected by the grazer treatment in presence of a canopy at Dates 3 and 4, with higher values in grazer-reduced plots (illustrated in Fig. 2c for Date 4, see also Table 1).

In contrast to total abundance as % cover, total abundance as biomass was significantly affected by the canopy treatment (Table 1). When the canopy was removed, more than half of the total biomass of associated taxa disappeared (Fig. 2d), with an average of 95% attributed to a loss of mussel biomass.

When the associated community was separated into 2 groups (understorey algae and invertebrates) and compared with respect to total abundance (% cover) and richness at Date 4, understorey algae had a higher cover when the canopy was absent (Fig. 3a; Student's *t*-test, $t = -3.0$, $p = 0.016$) but had similar species richness ($t = 0.71$, $p = 0.482$, with only *R. clavata* present). Invertebrates were more abundant ($t = 2.0$ $p = 0.05$) and had higher richness ($t = 6.73$, $p < 0.0001$) when a canopy was present (Fig. 3a,b).

Community structure

All communities in the experimental plot categories were similar prior to the start of the experiment (Date 1). The canopy treatment significantly affected the associated community structure (Pseudo-$F_{1,24} = 5.008$, $p = 0.004$; Table 2) only 50 d after the start of the experiment (Date 3), with differences remaining significant until the end of the experiment (Date 4; Fig. 4a). This effect was also detected in the biomass structure (Table 2, Fig. 4b). The associated community abundance structure (either as % cover or biomass) was not affected by the grazer or by the nutrient enrichment treatments. We observed similar results in compositional structure (all abundances transformed into presence–absence, results not shown). The composition changed between dates, and a significant effect of canopy treatment was observed on Dates 3 and 4, but no effect from either the grazer or nutrient enrichment treatments was observed.

Of all treatments (individual or in combination), those that included the canopy treatment had greater average dissimilarities over time when compared to the natural assemblages (i.e. control plots) (Fig. 5). Four weeks after the start of the experiments (Date 2), dissimilarities between the control plots and all other treatments had generally increased. Only after 2 mo (Date 3) did the treatments with the canopy treatment (i.e. CG, CGN, C and CN) become significantly more dissimilar from the natural communities, while the other treatments (i.e. N, G and GN) became more similar to the control plots over time (smaller dissimilarity). At the end of the experiment, larger dissimilarities (compared to controls) were observed with the C, CG and CGN treatments (Fig. 5). At Date 3, the main species causing 90% of the dissimilarity were the mussels *Mytilus* spp., the encrusting algae *R. clavata* and the sea anemone *Aulactinaria stella*. At

Date 4, those same species still accounted for the dissimilarities with an addition of Polychaeta and Oligochaeta.

For the community structure expressed in biomass, C– treatments were significantly more dissimilar from the natural communities; CG and CGN treatments had the highest dissimilarities (Fig. 6).

The grazer treatment using cageless techniques failed to significantly reduce the abundance (in % cover and biomass) of grazer species except for the first month of the experiment (results not shown). Yet the abundances were reduced for several days (up to 4 out of 9 or 10 d; L. Joseph, M. Cusson and S. Cimon unpubl. data). The non-accessibility of the plots at high tides constrained constant removal and hence considerably lower abundance.

A closer examination of the canopy removal effect on grazers (i.e. those that were not considered as part of the associated species in all other analyses) illustrated that the absence of canopy (only in G+ treatment plots) had a significantly negative effect on the abundance of *L. obtusata* and *Jaera marina* (reduction of 94 and 95%, respectively), but was not significant for *Mytilus* spp. (31%). In contrast, it had a positive effect on the average abundance of the gastropods *L. saxatilis* and *L. littorea* (increase of 87 and 100%, respectively) as well as for the encrusting algae *R. clavata*, which increased its percentage cover by 6-fold when the canopy was absent. Using the biomass structure data, the absence of canopy had a significantly negative effect on the biomass of those species (reduction of 98% for both *L. obtusata* and *J. marina*, and 49% for *Mytilus* spp.) except for *L. saxatilis* and *L. littorea* having a higher biomass when the canopy was removed (increase of 53 and 100%, respectively).

Community function

Nutrient enrichment and canopy treatments had no effect on NPP ($\chi^2 = 6.67$, p = 0.083) or *R* ($\chi^2 = 4.36$, p = 0.225) (Fig. 7), while for GPP there was a difference observed for the canopy treatment but no effect from nutrient enrichment ($\chi^2 = 8.13$, p = 0.044) (Fig. 7). However, when the canopy was removed, we observed only very small values of NPP and GPP for the communities. Only positive CO_2 fluxes were observed (Fig. 7) for C– treatments, meaning that the productivity of the understorey algae species was negligible compared to the respiration of heterotrophic organisms.

DISCUSSION

Our study showed that, taken in isolation, canopy loss was the strongest single effect affecting community structure and functioning, while community resistance was observed when grazers were reduced and nutrients were added. When these 3 factors were added together, various trends emerged, suggesting a lower resistance of the community when facing multiple stressors.

Resistance of the community

High resistance of the benthic community to nutrient enrichment and periodic grazer reduction was observed in this study. The absence of canopy, on the contrary, strongly affected the resistance of the associated species. Undoubtedly, the canopy macroalgae played a key role in the stability of the structure and function of the benthic community. Interestingly, the effects of the absence of canopy appeared only after 2 mo of treatment, indicating temporary resistance most likely due to the large number of *Fucus* spp. juveniles that appeared and grew fast as part of an initial resilience (with an average cover of 41 ± 24%), perhaps still providing some protection for the understorey species. This 'pulse' perturbation (after a single event; Bender et al. 1984) was not enough to induce change; maintaining the removal longer, or applying a 'press' perturbation, provoked change. One month after impact, communities in all treatments increased their dissimilarity from the controls. However, C+ treatments thereafter decreased in dissimilarity, while most C– treatments continued to increase their dissimilarities. This suggests less resistance to canopy removal (i.e. Fig. 5).

Effects on community structure

The absence of canopy reduced species richness and affected the entire structure of the associated (unmanipulated) species abundance, both in terms of % cover and biomass. The loss of *Fucus* spp. as a habitat-forming species resulted in less facilitation and an increased stress level (e.g. temperature, wave action, etc.) for the understorey species (Bertness et al. 1999, see also stress as 'lateral modifiers' in Thompson et al. 2004). We often observed temperatures that were >10°C higher on substrates when the canopy was removed (measured by an infra-red camera; data not shown). The presence of the canopy cover may increase richness and diversity by improving conditions, as shown by Schiel & Lilley (2007, 2011) and Watt & Scrosati (2013).

Settling species need to overcome the physical impacts of wave action, higher temperatures and whiplash (Lewis 1964, Hawkins 1983, Jenkins & Hawkins 2003). For example, whiplash by surrounding algae and higher temperatures (i.e. desiccation) can lead to a decrease in recruitment and growth of algal propagules (Kiirikki 1996, Kim & DeWreede 1996, Irving & Connell 2006) and to a higher mortality rate of settling species (Hawkins 1983, Kim & DeWreede 1996, Ingolfsson 2008). Canopy loss may lead to bleaching of algae and the reduction of invertebrates due to their exposition to light, elevated temperatures and wave action (Jenkins et al. 1999a,b, Cervin et al. 2004). When the canopy was removed, more understorey algae (especially encrusting algae *Ralfsia clavata*) and fewer invertebrates were observed (cf. Fig. 3), confirming the findings of the above-cited literature. In our study, canopy absence reduced species richness and negatively affected diversity, but only in the absence of grazers. In addition, the reduced abundance of invertebrates (cf. Fig. 3) with canopy loss might also be caused by lower food supply. *Littorina obtusata*, the dominant grazer in the presence of a canopy, was replaced by *L. saxatilis* when the canopy was removed. This change could be explained by their feeding habits, since although both *L. obtusata* and *L. saxatilis* feed on *Fucus* spp. (Watson & Norton 1987, Barker & Chapman 1990, Laurand & Riera 2006), *L. saxatilis* also feeds on rocky surface biofilms (Sacchi et al. 1977, Hawkins et al. 1989).

The open space created by the removal of the canopy may be colonized by other species such as turf-forming or ephemeral algae (Sousa 1979, Reed & Foster 1984, McCook & Chapman 1993, Lilley & Schiel 2006). In our study, however, only *R. clavata* benefitted from the absence of the canopy by extending its cover (cf. Fig. 3). Propagule availability (Reed & Foster 1984, Sousa 1984) and the timing of treatment initiation in the season (Archambault & Bourget 1983) are critical for recolonization. Even though *Fucus* spp. recruitment occurs primarily during the summer (Archambault & Bourget 1983, Lamote & Johnson 2008), the delayed start of our experiments (late spring) combined with a lack of efficient grazer exclusion probably explain the lack of ephemeral algae. However, Archambault & Bourget (1983) observed rapid colonization of substrate by ephemeral algae after removing the canopy over the same period of the year and in the same region as our study. In the St. Lawrence Estuary, the abundance of ephemeral algae may vary among years, as very few species were observed in our study whereas 1 yr later (i.e. summer 2013), *Porphyra* spp. were very abundant with fewer fucoid juveniles (authors' pers. obs.).

No proliferation of ephemeral algae was observed in our study, although ephemeral species (e.g. *Porphyra* spp., *Ulva* spp. and *Chordaria* spp.) may be abundant in the lower part of the intertidal zone. The reduced grazer treatment in our study led to increased diversity. This seemed to be mainly caused by a small evenness (*J′*) in the G+ treatments due to the dominance of the mussels *Mytilus* spp. (results not shown). Other species accounted for the difference in diversity as the encrusted algae *R. clavata*, the polychaetes *Nereis* spp. and the sea anemone *Aulactinia stella* were more abundant in the treatments when grazers were reduced. This observation is, however, difficult to explain, as grazer treatment effects are mainly expected on algae and not on invertebrates. The fact that our grazer treatment was not as efficient as we expected between maintenance sessions may explain the limited effects that were observed in our study. Sticky barriers have proven their efficiency reducing gastropods grazers in warmer environments (e.g. Australia: 10 × 10 cm plots, Range et al. 2008; California: 10 × 10 cm plots, Aquilino & Stachowicz 2012). In our study, however, the large size of the exclusion (50 × 50 cm) as well as the cold waters of the St. Lawrence Estuary may have reduced their efficiency.

Nitrogen is known to be a limiting nutrient for algae in marine habitats. High levels of nitrogen in water are used by algae for growth (Wheeler & North 1980) or storage (Chapman & Craigie 1977). Ephemeral algae are fast-growing species and will therefore use nutrients more rapidly than perennial algae like fucoids (Duarte 1995). Even if we did observe higher nitrogen content in macroalgae, the enrichment treatment did not affect the associated benthic community either in richness or in structure, contrary to other studies. Indeed, higher nutrient availability may enhance algal richness and diversity (Worm et al. 2002, Korpinen et al. 2007) and increase the abundance of ephemeral algae (Johansson et al. 1998, Eriksson et al. 2007, Kraufvelin et al. 2010) and propagules or periphyton (Eriksson et al. 2006b, Korpinen et al. 2007), leading to a higher food supply for the associated community. An additional input of nutrients can modify the food preference of herbivores and change their competitive interactions with grazing shifts (Worm et al. 1999, Russell & Connell 2005), thereby influencing the composition within the assemblage. Enrichment combined with canopy loss can lead to an increase in the abundance of macroalgae (Eriksson et al. 2007), or a shift in dominance towards opportunistic species and a decrease in the invertebrates that had a refuge in the canopy (Benedetti-Cecchi et al. 2001). Some studies have observed an increase in the abundance of either recruits or mature macroalgae with nutrient enrichment when grazers were reduced (Guerry 2008, Masterson et al. 2008, Atalah

& Crowe 2012). Others have shown that under nutrient-enriched conditions and in the absence of grazers, *Fucus* spp. failed to colonize the substrate and were outcompeted by fast-growing ephemeral algae; with grazers present, the opportunistic algae were less abundant (Korpinen et al. 2007, Korpinen & Jormamailen 2008). Neither of these observations was found in our study. A delayed community response to nutrient input is possible. Kraufvelin et al. (2006) and Bokn et al. (2002) observed a delayed response (16 mo to 3 yr) of fucoid species to enrichment even though rapid (within a few months), relatively minor effects on the community structure were detected (increase of *Ulva* spp. and some grazers).

Although the grazer reduction treatment had almost no effect on our community abundance structure, when combined with the canopy treatment we observed, at the end of the experiment, a trend of larger differences with the controls than that observed using only single treatments (cf. Fig. 5). This suggests that multiple disturbances and stresses may act in synergy leading to stronger effects than when applied alone. This highlights the need to analyze interactions among treatments, as they might be important in field situations, and likewise, to allow enough time to pass for these treatments to take effect.

Effects on ecosystem functioning

It is known that macroalgae primary production can be positively affected by nutrient additions (Ylla et al. 2007, Bucolo et al. 2008, Krause-Jensen et al. 2012, but not in Kraufvelin et al. 2010). Still, we did not find an enrichment effect on primary production. If a higher storage of nutrients was observed, primary production measures were not significantly higher with enrichment. On the other hand, we did observe a strong negative effect of canopy loss on GPP. With a community affected by canopy loss, changes in functioning were expected through lower abundance and low productivity of the understorey community (Gollety et al. 2008, Tait & Schiel 2011b, Valdivia et al. 2012, Crowe et al. 2013). In our study, only *R. clavata* was present as crustose algae and its production was probably not sufficient to compensate for the respiration of other heterotrophic organisms present. The lack of increasing ephemeral algae led to a non-significant increase in total abundance and richness of understorey algae for enriched plots (data not shown), resulting in no increase in productivity. Higher diversity may lead to higher productivity in many systems (Naeem et al. 1994); however, some studies in shallow marine habitat systems have shown no increase in primary production with enrichment due to changes in the macrophyte community (Sandjensen & Borum 1991, Nixon et al. 2001).

CONCLUSIONS

In response to different disturbance or stress sources, a community may resist, or fail and change. The benthic communities in our study were not resistant to canopy loss, leading to significant changes in community structure and composition. Our study reconfirms the important role of the dominant habitat-forming species *Fucus* spp. in influencing the structure and function of their associated communities. Following enrichment and grazer reduction, the marine benthic communities of the mid-intertidal zone of the St. Lawrence Estuary remained largely unaffected. Grazer reduction combined with other treatments provoked various responses with effects on the structure in terms of abundance (both % cover and biomass) but with little or no effect on richness, diversity and total abundances. Therefore, in this assemblage, habitat-forming species have a stronger effect than bottom-up forcing and top-down controls. Moreover, our study also provided new insight into possible interactions among treatments, highlighting the importance of testing for potential synergetic or antagonistic effects of multiple stresses. Natural coastal communities often face multiple threats. Therefore, understanding the antagonistic and additive effects of stresses may help identify the ecological mechanisms that solicit shifts in community structure and function. Studying these interactions will also help policy managers establish mitigation and conservation priorities.

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Table 1. Summary of ANOVAs showing the effects of canopy (Ca), grazer (Gr) and nutrient enrichment (Nu) treatments and the crossed factors on % cover, richness, Simpson's index of diversity, and biomass of the associated species of the community for all dates (only Date 4 for biomass). Significant values are shown in **bold**. For an explanation of dates see 'Materials and methods: Sampling'

		Date 1		Date 2		Date 3		Date 4	
	df	*F*-ratio	p	*F*-ratio	p	*F*-ratio	p	*F*-ratio	p
% Cover									
Ca	1	0.167	0.686	0.006	0.937	1.06	0.314	0.257	0.617
Gr	1	0.216	0.647	4.63	**0.042**	0.948	0.340	0.261	0.614
Nu	1	1.658	0.210	0.006	0.940	0.080	0.779	0.620	0.439
Ca × Gr	1	0.654	0.427	0.221	0.643	0.132	0.720	0.457	0.505
Ca × Nu	1	0.324	0.575	1.686	0.207	0.262	0.614	1.633	0.214
Gr × Nu	1	0.000	0.988	0.701	0.411	0.366	0.551	1.481	0.236
Ca × Gr × Nu	1	0.009	0.927	2.892	0.102	2.2607	0.146	0.293	0.593
Residual	24								
C. Total	31								
Richness									
Ca	1	5.765	**0.025**	1.852	0.186	12.741	**0.002**	47.61	**<0.0001**
Gr	1	0.471	0.499	0.000	1.000	0.318	0.578	0.831	0.371
Nu	1	0.118	0.735	0.074	0.788	0.035	0.853	0.017	0.898
Ca × Gr	1	4.235	0.051	1.852	0.186	0.882	0.357	0.831	0.371
Ca × Nu	1	0.118	0.735	0.000	1.000	0.882	0.357	2.051	0.165

Gr × Nu	1	0.000	1.000	3.63	0.069	0.318	0.578	8.966	**0.006**
Ca × Gr × Nu	1	1.882	0.183	0.296	0.591	0.318	0.578	0.017	0.898
Residual	24								
C. Total	31								
Diversity									
Ca	1	6.626	**0.017**	0.012	0.914	3.296	0.082	0.540	0.470
Gr	1	0.058	0.812	0.269	0.608	0.571	0.457	5.875	**0.023**
Nu	1	0.032	0.859	0.303	0.587	0.099	0.756	0.278	0.603
Ca × Gr	1	0.176	0.679	2.850	0.104	5.183	**0.032**	6.566	**0.017**
Ca × Nu	1	1.698	0.205	1.523	0.229	0.210	0.651	0.123	0.729
Gr × Nu	1	0.078	0.782	0.207	0.653	0.414	0.526	0.229	0.637
Ca × Gr × Nu	1	0.264	0.612	0.345	0.562	0.081	0.778	0.300	0.589
Residual	24								
C. Total	31								
Biomass									
Ca	1							14.697	**0.001**
Gr	1							1.217	0.281
Nu	1							0.698	0.412
Ca × Gr	1							2.067	0.163
Ca × Nu	1							0.292	0.594
Gr × Nu	1							0.002	0.965
Ca × Gr × Nu	1							1.017	0.323
Error	24								

C. Total	31

Table 2. Summary of PERMANOVAs showing the effects of canopy (Ca), grazer (Gr) and enrichment (Nu) treatments along with the crossed factors on the structure in abundance in % cover and biomass of the associated species of the communities for all dates (only Date 4 for biomass). Data were square-root transformed for % cover measures and fourth-root transformed for biomass prior to estimating the Bray-Curtis similarities. Significant values are shown in **bold**. For an explanation of dates see ‘Materials and methods: Sampling’

		Date1		Date 2		Date 3		Date 4	
	df	Pseudo-*F*	p	Pseudo-*F*	p	Pseudo-*F*	p	Pseudo-*F*	p
%Cover									
Ca	1	1.971	0.117	0.774	0.525	5.008	**0.004**	9.536	**0.001**
Gr	1	1.814	0.152	2.085	0.118	0.869	0.452	1.279	0.312
Nu	1	0.591	0.608	0.983	0.401	0.440	0.735	0.224	0.894
Ca × Gr	1	0.285	0.848	0.710	0.584	1.604	0.196	1.216	0.297
Ca × Nu	1	0.431	0.717	1.089	0.376	0.254	0.859	1.373	0.260
Gr × Nu	1	0.760	0.499	0.767	0.515	0.435	0.717	1.254	0.305
Ca × Gr × Nu	1	0.899	0.435	0.707	0.581	0.279	0.834	0.469	0.735
Residual	24								
Total	31								
Biomass									
Ca	1							21.614	**0.001**

Gr	1	0.767	0.556
Nu	1	1.357	0.230
Ca × Gr	1	1.313	0.270
Ca × Nu	1	0.272	0.899
Gr × Nu	1	0.585	0.719
Ca × Gr × Nu	1	0.376	0.842
Residual	24		
Total	31		

Fig. 1. Experimental design with the 3 stress factors (canopy, grazer and nutrient enrichment) having 2 levels each (see ‘Materials and methods’ for details). A total of 4 replicates for each treatment were used. The legend shows the letter codes used in the text and figures; 1 letter =1 stress (or treatment) applied, 2 letters = 2 stresses, 3 letters = 3 stresses (i.e. CGN: all 3 applied stresses)

Fig. 2. Mean (±SE) values of (a,b) species richness, (c) Simpson’s diversity index and (d) biomass among the various treatments. Values in (c) are pooled data from Dates 2 to 4, while values in (a), (b) and (d) are only from the end of the experiment (i.e. Date 4). Black and gray bars are the respective treatments with C+: canopy present; C–: canopy removed; G+: grazers present; G–: number of grazers reducedN+: nutrients added; N–: no nutrients added. See Fig. 1 for details. . Replicate number of averages are: n = 16 in (a) and (d); n = 8 in (b); and n = 24 in (c). Lowercase letters indicate significant differences ($p < 0.05$)

Fig. 3. Average (±SE) (a) % cover and (b) richness (n = 16) of understorey algae and invertebrates (without grazers) among the canopy treatment at Date 4 (black bars: canopy present; gray bars: canopy absent). (*) indicates significant differences; see legend of Fig. 1 for further details of treatments

Fig. 4. Principal coordinate analysis (PCO) ordinations illustrating the effect of canopy treatment (diamonds = canopy present; asterisk = canopy absent) at Date 4 on the community structure of the associated species in (a) % cover, square-root transformed, and in (b) biomass, fourth-root transformed. See Fig. 1 for treatment legend and definition of C, G, N; number of letters in the treatment labels represents the quantity of stress applied

Fig. 5. Average dissimilarities (n = 16) between pairs of control and treatments plots at each date for abundance in % cover of the associated species. In the matrix below the graph, treatments underlined with the same line are not significantly different ($p < 0.05$). See Fig. 1 for treatment

legend and definition of C, G, N; number of letters in the treatment labels represents the quantity of stress applied

Fig. 6. Mean (±SE) dissimilarities (n = 16) between pairs of control and other treatment plots in terms of biomass structure of the associated species at Date 4. See Fig. 1 for treatment legend and definition of C, G, N; number of letters in the treatment labels reflects the number of stressors applied. Lowercase letters indicate significant differences (ANOVA test of dissimilarities, $p < 0.05$)

Fig. 7. Average (± SE) community net primary production (Net PP; black bars), respiration (*R*; white bars) and gross primary production (Gross PP; gray bars) when canopy is present (left; n = 3) and when canopy is removed (right; n = 2). See Fig. 1 for treatment legend (abbreviations) ; number of letters in the treatment labels reflects the number of stressors applied. Lowercase letters indicate significant differences ($p < 0.05$)

Figure 1

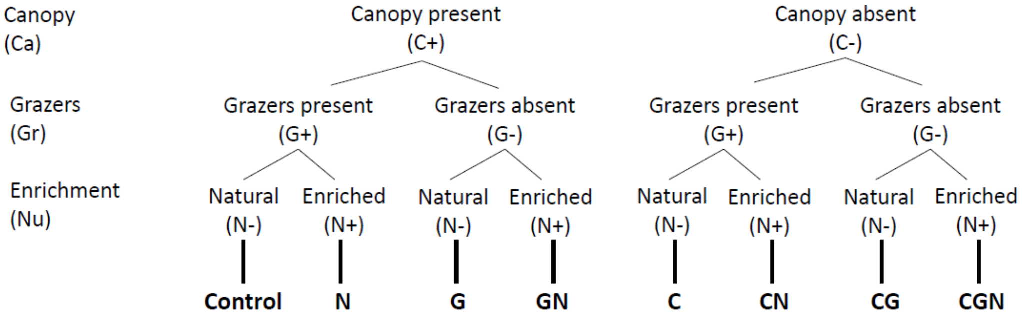

Canopy
(Ca)
Grazers
(Gr)
Enrichment
(Nu)
Canopy present
(C+)
Canopy absent
(C-)
Grazers present
(G+)
Grazers absent
(G-)
Grazers present
(G+)
Grazers absent
(G-)
Natural
(N-)
Enriched
(N+)
Natural
(N-)
Enriched
(N+)
Natural
(N-)
Enriched
(N+)
Natural
(N-)
Enriched
(N+)
Control
N
G
GN
C
CN
CG
CGN

Figure 2

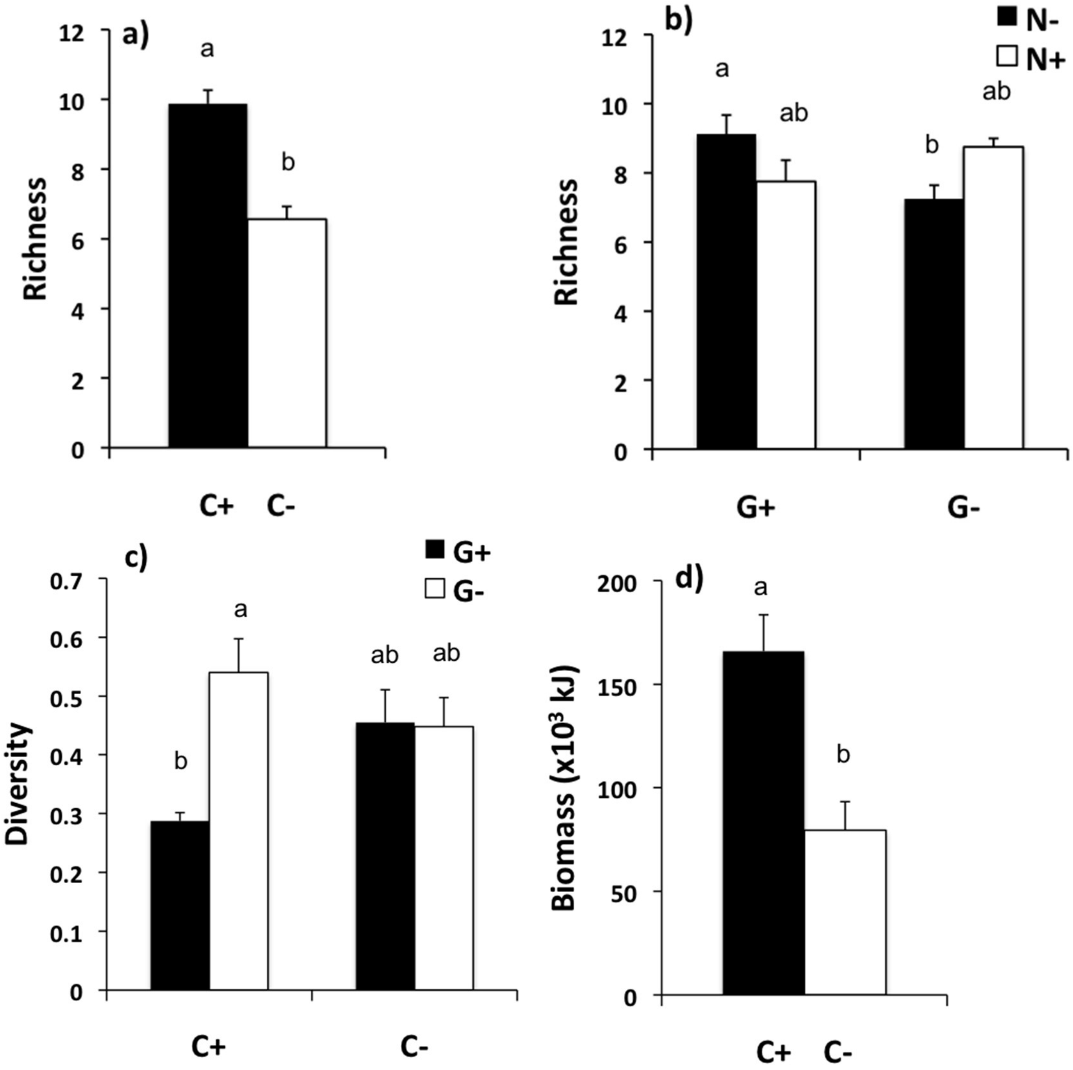
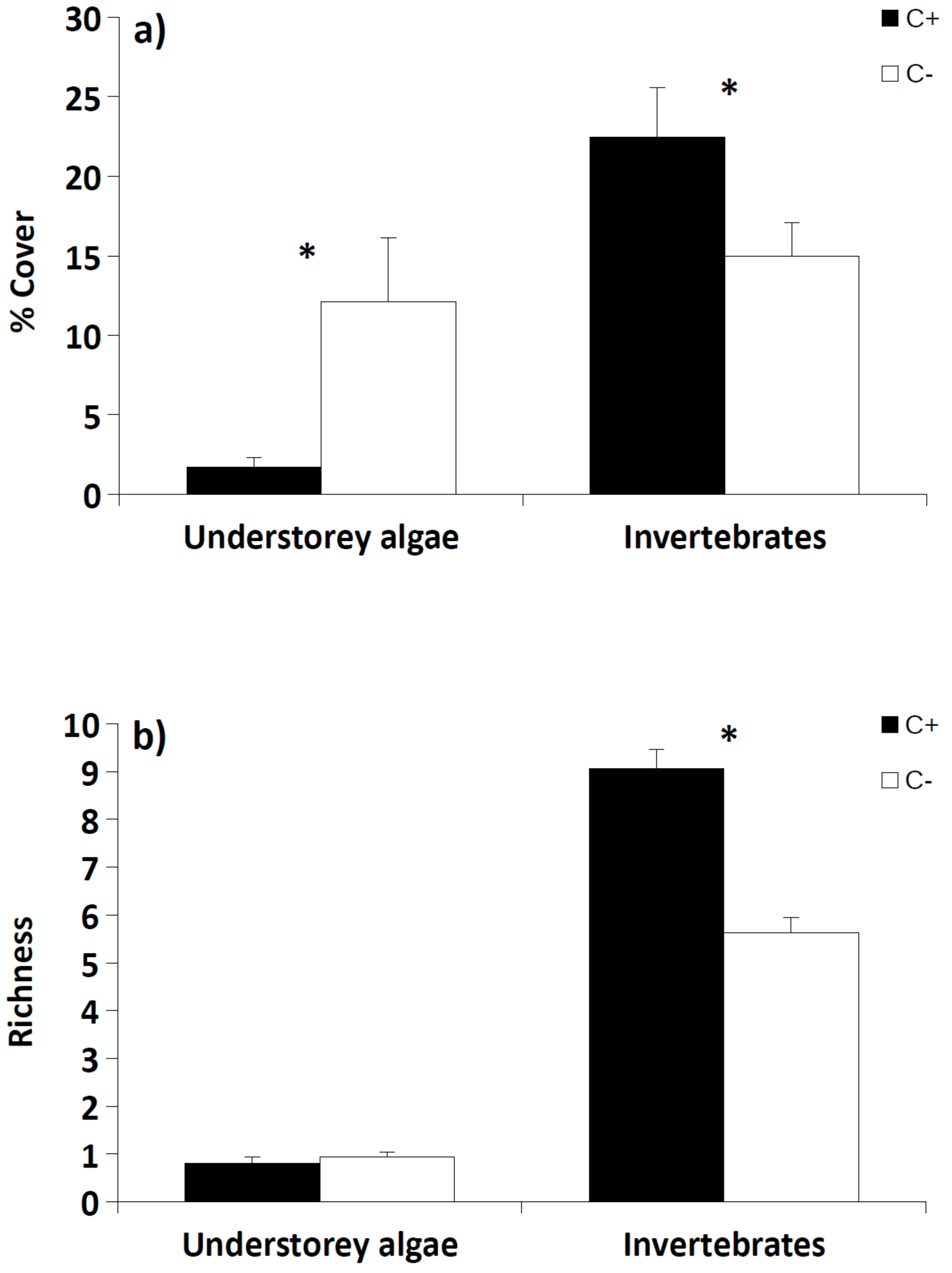
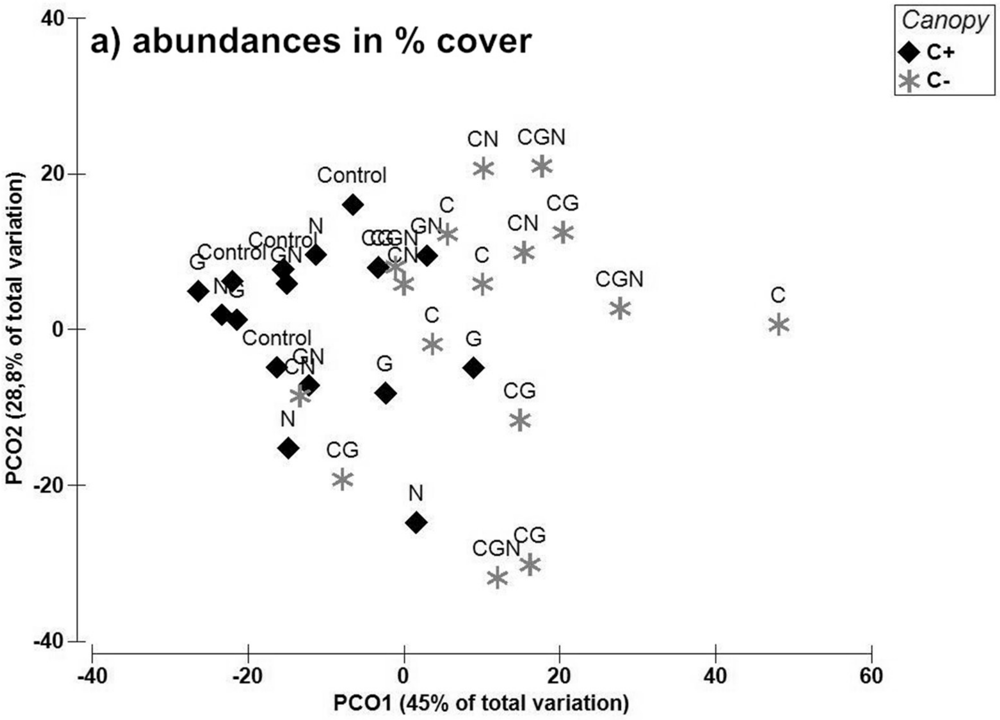

a)
Richness
12
10
8
6
4
2
0
a
b
C+
C-
b)
■ N-
□ N+
Richness
12
10
8
6
4
2
0
a
ab
b
ab
G+
G-
c)
■ G+
□ G-
Diversity
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
b
a
ab
ab
C+
C-
d)
Biomass (x10³ kJ)
200
150
100
50
0
a
b
C+
C-

Figure 3

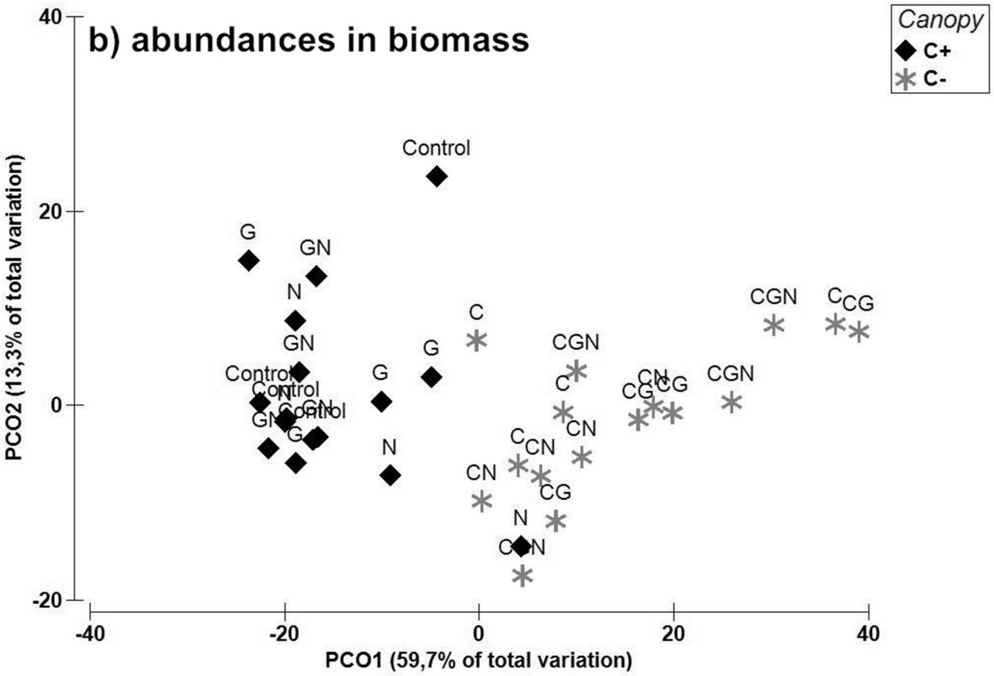

a)
% Cover
30
25
20
15
10
5
0
■ C+
□ C-
*
*
Understorey algae
Invertebrates
b)
Richness
10
9
8
7
6
5
4
3
2
1
0
■ C+
□ C-
*
Understorey algae
Invertebrates

1012

1013 Figure 4



1014



1015

Figure 5

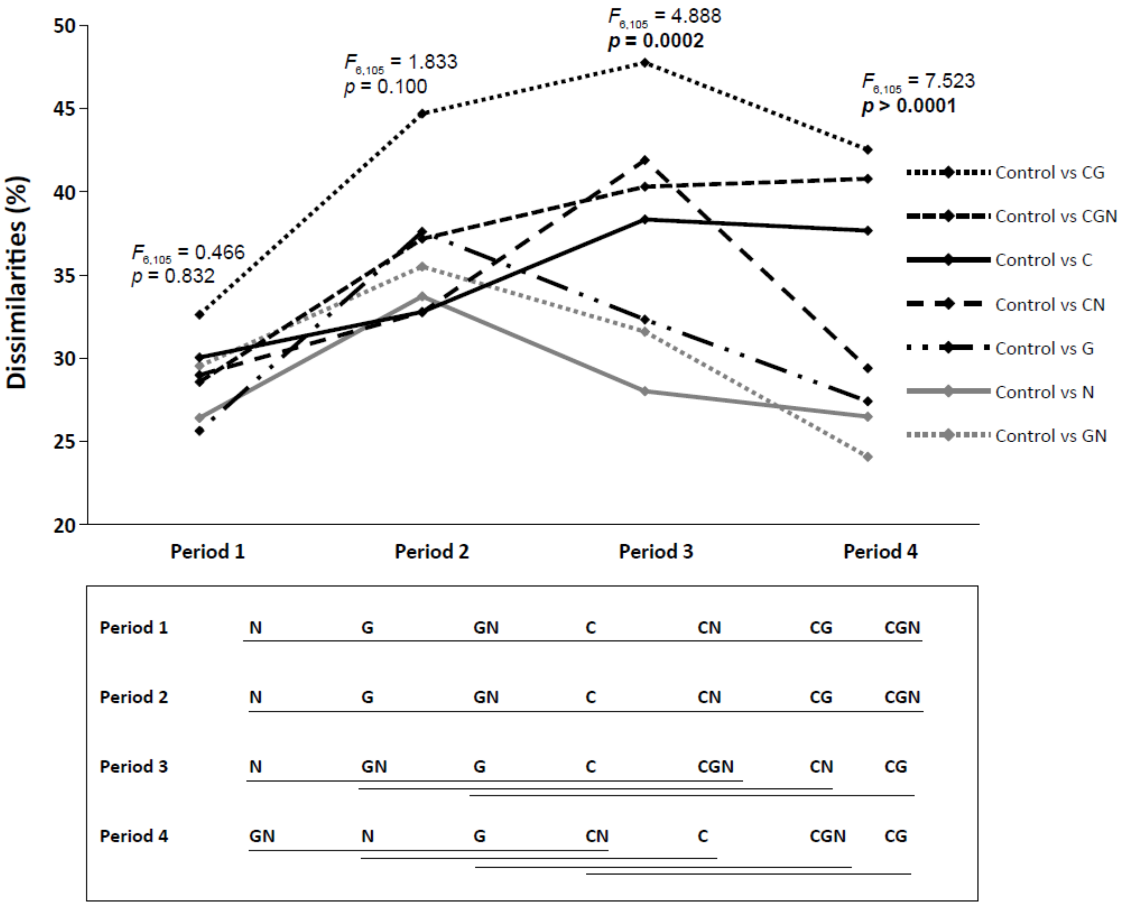

Dissimilarities (%)
50
45
40
35
30
25
20
Period 1
Period 2
Period 3
Period 4
$F_{6,105}$ = 0.466
p = 0.832
$F_{6,105}$ = 1.833
p = 0.100
$F_{6,105}$ = 4.888
p = 0.0002
$F_{6,105}$ = 7.523
p > 0.0001
Control vs CG
Control vs CGN
Control vs C
Control vs CN
Control vs G
Control vs N
Control vs GN
Period 1 N G GN C CN CG CGN
Period 2 N G GN C CN CG CGN
Period 3 N GN G C CGN CN CG
Period 4 GN N G CN C CGN CG

Figure 6

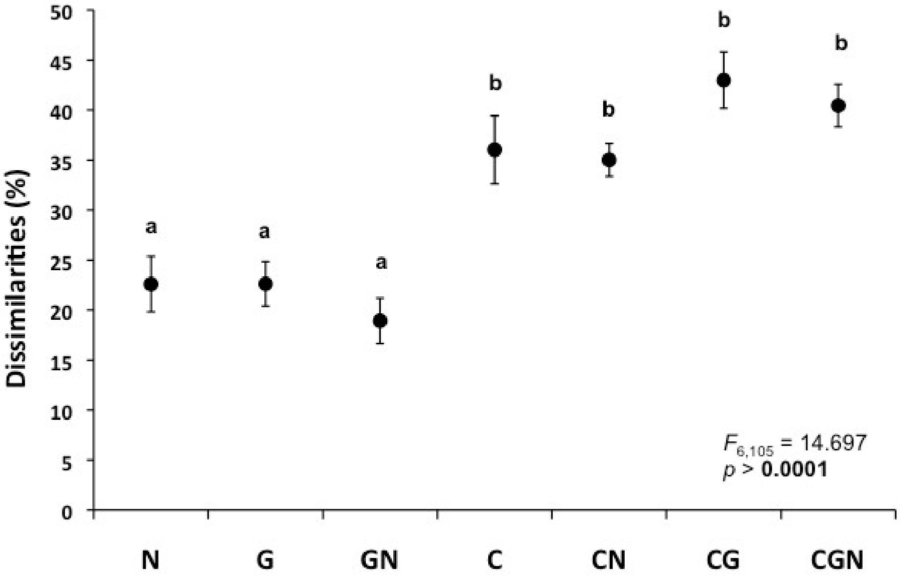
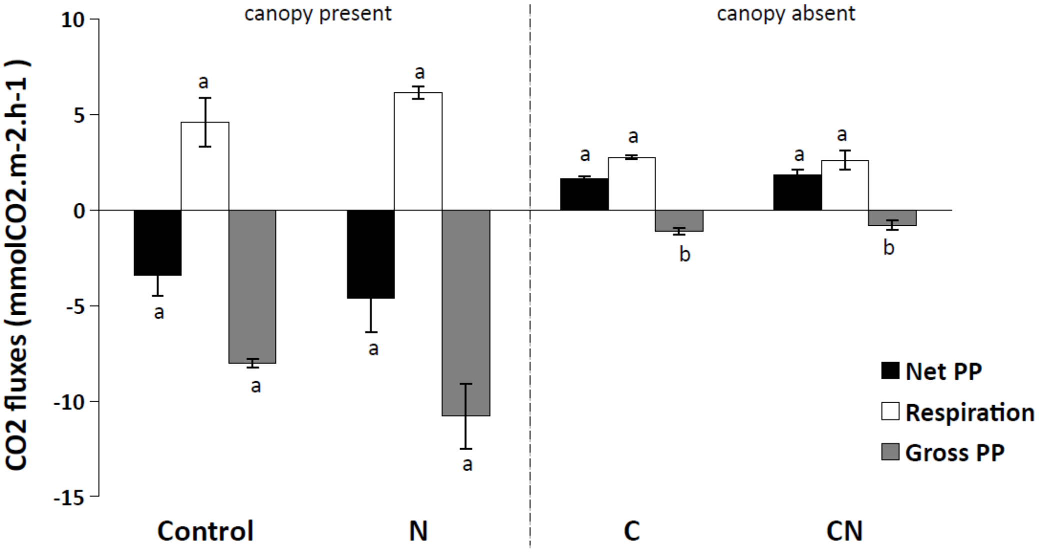

Dissimilarities (%)
50
45
40
35
30
25
20
15
10
5
0
a
a
a
b
b
b
b
$F_{6,105}$ = 14.697
p > **0.0001**
N
G
GN
C
CN
CG
CGN

Figure 7


canopy present
canopy absent
10
5
0
-5
-10
-15
CO2 fluxes (mmolCO2.m-2.h-1)
a
a
a
a
a
a
a
a
b
a
a
b
■ Net PP
□ Respiration
▨ Gross PP
Control
N
C
CN