



The buffer effect of canopy-forming algae on vermetid reefs' functioning: A multiple stressor case study

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ABSTRACT

Biodiversity plays a key role for our planet by buffering ongoing and future changes in environmental conditions. We tested if canopy-forming algae enhancing biodiversity (CEB) in a Mediterranean intertidal reef ecological community could alleviate the effect of stressors (heat waves and pollution from sewage) on community metabolic rates (as expressed by oxygen consumption) used as a proxy of community functioning. CEB exerted a buffering effect related to the properties of stressor: physical-pulsing (heat wave) and chronic-trophic (sewage). After a simulated heat wave, CEB was effective in buffering the impacts of detrimental temperatures on the functioning of the community. In reefs exposed to chronic sewage effluents, benefits derived from CEB were less evident, which is likely due to the stressor's contextual action. The results support the hypothesis that ecological responses depend on stressor typology acting at local level and provide insights for improving management measures to mitigate anthropogenic disturbance.

1. Introduction

In the virtual arms race between Man and Nature, ecological communities have one of the most powerful weapons to counteract anthropogenic action: biodiversity. A recent meta-analysis (Pires et al., 2018) shows that biodiversity can buffer the effects of stressors, thus stabilizing ecosystem functioning processes under changing, episodic or fluctuating environmental conditions. Pires et al. (2018) state that the more diverse the communities and the higher the functional redundancy, the greater the likelihood that disturbance effects will be absorbed (Standish et al., 2014). This enables the system to increase local adaptation in a changing environment (Loreau and de Mazancourt, 2013; Zelnik et al., 2018) and prevents the loss of other species from the system (Verhoef and Morin, 2009), ensuring ecological prosperity is preserved. However, local stressful events are increasing in terms of intensity and frequency, challenging the buffering/stabilizing ability of biodiversity (e.g., Gutschick and Bassirirad, 2003; Dal Bello et al., 2017). Despite the detrimental impacts on our planet's environmental conditions, which are exacerbated by climate change and habitat fragmentation (Rahmstorf and Coumou, 2011; Ummenhofer and Meehl, 2017), our collective knowledge on the potential buffering role of biodiversity when faced with multiple stressors remains limited. Many scientific

questions regarding biological and ecological responses to different disturbance typologies remain unanswered (Van de Pol et al., 2017). Stressors have different implications on multi-level hierarchical ecological responses (Sergio et al., 2018). Both the temporal (e.g., timespan and frequency of occurrence, etc.) and spatial components of stressors are useful to predict the potential effects of disturbance on ecological communities (Zelnik et al., 2018). For example, chronic exposure to temperatures that exceed individual temperature optima, may affect individual Darwinian fitness and survival effecting phenotypic plasticity and/or reproduction and growth (Pörtner and Knust, 2007). Pulsing events of thermal stress due to heat waves or hypoxia can impair the survival rate of organisms and affect the internal equilibria of population dynamics (e.g., birth and death of individuals) in local communities (Meehl and Tebaldi, 2004; Hobday et al., 2016; Oliver et al., 2018; Pansch et al., 2018; Sampaio et al., 2021; Sarà et al., 2021). Yet, the magnitude of effects depends on how the pulsing events are temporally clustered and whether the community had been previously exposed to other disturbance events: the so-called legacy effect (Dal Bello et al., 2017; Jackson et al., 2021). Multiple stressors can directly impact biodiversity through alterations to the abiotic components, the structure of populations and the composition of communities, organismal phenology (Edwards and Richardson, 2004; Harley et al., 2006;

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Suding et al., 2008; Doney et al., 2012; Mills et al., 2013; *sensu* Post, 2019), the distribution range of native species (Hawkins et al., 2009; Mills et al., 2013) and the expansion of invasive species (Simberloff et al., 2013; Rilov, 2016; Sarà et al., 2018). Although marine intertidal species may exhibit high tolerance limits and plasticity, prolonged or recurrent acute exposure to climatic or anthropogenic stressors may have detrimental effects on their metabolism and the ability to cope and adapt to these changing circumstances (Somero, 2002). Consequently, a reduction in energy availability for growth and reproduction may occur over time (Stillman et al., 2003; Pörtner et al., 2005). For example, faced with continually changing circumstances, Mediterranean vermetid reefs, located along the 38–39 parallels from Spain to Israel, are undergoing significant local collapse and extinction in the Levantine Mediterranean basin. This is probably due to the joint action of rising temperatures and increasing anthropogenic stressors that are impairing the ecological performance of native communities and facilitating the spread and establishment of non-native species, which in turn is provoking a shift in local biodiversity (Sarà et al., 2021). This biogenic reef is the result of the complex synergistic building activity of the vermetid mollusc *Dendropoma cristatum* (Biondi 1859) and the encrusting red alga *Neogoniolithon brassica-florida* (Harvey). Since the ecosystem services it provides are multi-faceted (including the protection of coasts from erosion, regulation of sediment transport, carbon sinks, and the provision of habitat for many fish and invertebrates) more efforts to understand its response to changing conditions and to improve conservation management are urgently needed (Gallardo et al., 2016; Rilov, 2016).

In the Mediterranean Sea, vermetid reefs represent a unique and highly diverse biogenic construction structurally comparable to coral reefs in tropical areas (Safriel and Ben-Eliahu, 1991). They are largely colonized by one of the most productive and valuable macroalgal forests, formed by the canopy-forming brown macroalgae belonging to the Order Fucales *Ericaria amentacea* (= *Cystoseira amentacea*) and *Cystoseira compressa*; Mancuso et al., 2018). When present, this canopy-forming brown macroalga increases the local three-dimensional complexity and spatial heterogeneity, providing food, shelter, and nurseries to many associated species, thereby enhancing local biodiversity and productivity (Ballesteros et al., 1998; Cheminée et al., 2013; Gianni et al., 2013; Gorman et al., 2013; Piazzini et al., 2018). Despite the recognized importance, the canopy is threatened by many multi-scale interacting stressors and the detrimental effects and ecological functioning implications of its loss – due to interacting local anthropogenic factors – remain poorly understood. This study attempted to address these knowledge gaps by investigating the role of this canopy-forming macroalga in alleviating the metabolic stress on the underlying community (*i.e.*, the vermetid reef) caused by different stressors (physical and pulsing, *i.e.*, heat wave; trophic and chronic, *i.e.*, organic enrichment), using community metabolic rates (expressed by the standard respiration rate; RR) as a proxy of community functioning. Our findings provide crucial information needed to explain why vermetid reefs are slowly disappearing from the Eastern Mediterranean Sea coasts (Rilov, 2016) and will assist scientists, practitioners and managers when designing and enforcing ecosystem-based management solutions to achieve the resilience of marine ecosystems, promote human well-being and sustainable use of resources (MEA - Millennium Ecosystem Assessment, 2005).

2. Materials and methods

2.1. Selection of stressors

Intertidal organisms are more tolerant to thermal extremes (Somero, 2010) than all other animals thanks to their diurnal exposure at low tides. However extreme events such as heat waves can impair organismal functioning by increasing body temperature and desiccation stress beyond their tolerance range (Dong and Williams, 2011; Tait and Schiel, 2013; Pocklington et al., 2017). The detrimental effects of heat waves

are frequently combined with other chronic stressors such as local organic enrichment from uncontrolled sewage discharge. Sewage can increase the frequency of hypoxia events and chronic contaminations due to several compounds causing stressful exposure over time (Lewis and Santos, 2016). To test the ability of canopy forest to alleviate the detrimental impacts of climatic and anthropogenic stressors on intertidal reef communities, we selected *Ericaria-Cystoseira* canopy algae complex as the CEB and heat waves combined with massive organic enrichment due to sewage discharge as the multiple stressors.

2.2. Study sites and a priori measurements of chronic disturbance

The study was carried out on vermetid reef sites covered by canopy-forming brown algae along the coastline of the “Capo Gallo - Isola delle Femmine” Marine Protected Area (Northern Sicily, Southern Mediterranean Sea) (Fig. 1). The first step was to select sites subjected to the chronic stressor, *i.e.*, organic enrichment. Thus prior to the experiment, we tested whether pre-selected sites for the experiments differed in terms of organic matter discharge due to anthropogenic activities. Two sites were selected: one chronically exposed to discharge from a bivalve nursery based on the coast where bivalves are usually kept for depuration before being sold (hereafter called SEWAGE - 38°11'10.32"N; 13°21'43.64"E) and the second at about 1 km south of the first site (hereafter called NO-SEWAGE or control - 38°10'45.59"N; 13°21'59.52"E). Both sites had the same fetch (Burrows et al., 2008), the same coastal geometry and the same water column depth. Water samples were collected from three NO-SEWAGE sites ($n = 10$ per site) and compared against 10 samples collected from the SEWAGE sites according to the simplest control vs. impact design (Underwood, 1997). Water was collected from the vermetid reefs using Niskin bottles, transported in under 2 h to the Ecology laboratory at the University of Palermo, filtered through pre-washed, pre-combusted (450 °C, 4 h) and pre-weighed Whatman GF/F filters (0.45 mm nominal pore size). To determine total suspended matter (TSM) concentrations, the filters were weighed after desiccation (105 °C, 24 h) using a Mettler balance (accuracy ± 1 mg). The suspended inorganic fraction (ISM) was calculated as the weight of the material remaining after combustion at ~ 500 °C for 4 h and reported as mg l^{-1} . The suspended organic fraction (OSM), used as a proxy of organic enrichment due to the sewage flow, was estimated from the difference between TSM and ISM (Modica et al., 2006). This first preliminary dataset allowed prior estimations of the amount of organic enrichment as a proxy of chronic disturbance. After assessing assumptions of normality and homogeneity of variance a two-sample *t*-test analysis was performed, showing significant difference between the two sites ($t = 5.9711$, $df = 38$, $p\text{-value} = 6.236 \cdot 10^{-07}$), with the SEWAGE sites ($OSM = 2.64 \pm 0.33 \text{ mg l}^{-1}$; $n = 10$) being about 40% more trophically enriched than NO-SEWAGE sites ($OSM = 1.73 \pm 0.44 \text{ mg l}^{-1}$; $n = 30$).

2.3. Vermetid sample collection and measuring stressors' effects

Steps were taken to simulate the effect of a heat wave (48 °C) experienced during summer exposure at low tides (semidiurnal; 6 h) on metabolic rates (Giomi et al., 2016; Sarà et al., 2021; Fig. 1). The oxygen consumption rates (RR) were calculated from the decrease in oxygen content in the respirometric chambers over time, expressed as $\mu\text{mol h}^{-1} \text{g}^{-1}$. Thus, 96 experimental reef patches collected from SEWAGE ($n = 48$) and NO-SEWAGE ($n = 48$) locations, half of them with canopy algae cover and the other half without (CEB vs NO-CEB) were transported to the laboratory and acclimated for 24 h in filtered sea water at the same environmental temperature (26 °C). Following this, patches were firstly immersed independently in water at 26 °C (2.4 l volume of closed respirometers supplied with filtered sea water; Millipore GF/C 0.45 μm), then the water level was gently lowered in all 96 chambers, and the air temperature of 48 of the chambers was increased using heat lamps (UVA; Repti Zoo, Italy; 75 W and 100 W) mounted on a lab-made rack to

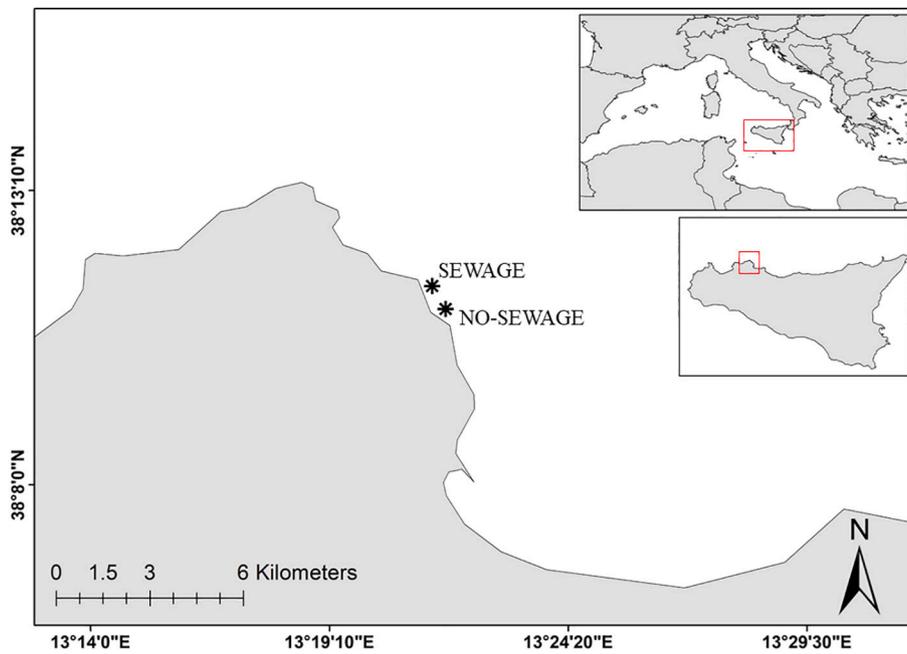


Fig. 1. Map of the study area (Palermo, Sicily) and sampling sites where experimental patches were collected (SEWAGE corresponds with a bivalve nursery location, and NO-SEWAGE refers to a control site).

reach 48 °C. These patches were hereafter referred to as HEATWAVE (See Fig. 2), while the remaining patches (NO-HEATWAVE) were maintained immersed at 26 °C. Both temperatures were maintained for 3 h following a Mediterranean cycle of the semi-diurnal tide (Sarà et al., 2014). The whole emersion phase at HEATWAVE condition lasted 3 h and temperature was continually recorded by thermos-loggers (Alpha-Mac, Canada) set at 1 min. The peak temperature of 48 °C was chosen as in the last decade intertidal biota at these latitudes have experienced this temperature for at least 3 h (ISPRA, <http://www.mareografico.it/>).

After the emersion phase, filtered sea water (Millipore GF/C 0.45 µm) was again gently added to reef patches and after 1 h chambers (1.4 l volume) were hermetically closed, and RR was measured using fibre-

optic oxygen sensors connected to a Pyro Science Firing O2 oxygen meter (PyroScience Inc., Germany). Oxygen concentration within the chambers was recorded with a 1.5 s frequency for each experimental replicate during the whole experiment. An agitator and small magnets were used to maintain homogeneous water mixing inside the experimental chambers (Bosch-Belmar et al., 2016), which were covered with an opaque plastic material to avoid possible interference due to the respiration of encrusting algae. This set of measures allowed the effect of the heat wave (against absence of heat wave) to be estimated, with and without the presence of chronic sewage stress on the reef and with and without algae coverage. Oxygen consumption was standardized by surface area by photographing each patch and estimating the size using

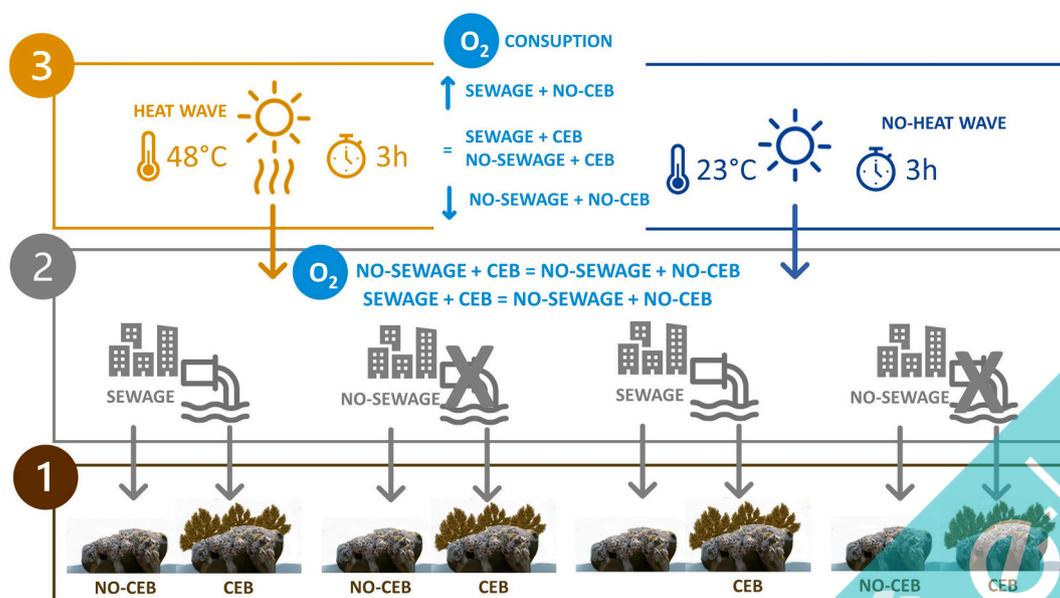


Fig. 2. Experimental design followed in the study and results (in terms of RR) obtained from the comparison of the different treatments applied the presence/absence of sewage as a chronic stressor (2), and exposure/no exposure to the heatwave pulse stressor (3). CEB/NO-CEB acronyms refer to the presence/absence of canopy-forming algae enhancing biodiversity complex (1).

ImageJ® free software to perform picture analysis. The mean area of experimental patches was of $26.3085 \pm 6.57 \text{ cm}^2$.

2.4. Statistical analysis

The assumption of homoscedasticity and normality of the response variable (RR), for each of the treatment levels, were tested using Cochran's C test and box plots, and there were no deviations (Logan, 2010). Thus, differences in RR between the presence/absence of heat wave, organic enrichment, canopy and their interaction, were assessed using the following sampling design: factor "Heat wave" (Presence vs Absence; fixed with 2 levels); factor "Sewage" (SEW, enriched vs non-enriched; fixed with two levels and orthogonal to factor Heat wave); factor "Canopy" (CEB; fixed with two levels and orthogonal to factors Heat wave and Sewage).

Statistical differences were tested through a Generalized Linear Model (GLM) with gamma error family distribution which was the most appropriate as the response variables cannot assume negative values (R Package "mgcv" by Wood, 2017). Ten different models were tested, and the best fitting one was selected based on the lowest Akaike's information criteria (AIC) value and the highest value of explained variance (Supplementary Information Table S1). Once the model was run, we checked the absence of any pattern dealing with the residuals and their normality distribution (SI Figs. S1 and S2). To test the significant difference among the various levels of all factors, we performed a pairwise test using an estimated marginal means (or least-squares means) for factor combinations in the GLM model (R Package "emmeans" by Lenth, 2021). All statistical analyses were performed using R software, version 4.0.3 (R Core Team, 2020, <http://cran.r-project.org>).

3. Results

The metabolic response of the vermetid reef community covered by CEB during heat wave exposure ($48 \text{ }^\circ\text{C} - 3 \text{ h}$) in NO-SEWAGE condition did not show any significant difference (GLM, $p > 0.05$) with respect to no-heat wave/NO-SEWAGE experimental patches (Tables 1 and 2; Fig. 3 - Column 1 vs Column 5). In contrast, under the same undisturbed trophic conditions with NO-CEB, the pulsing effect of increasing temperature due to heat wave generated a significant difference in the community RR (GLM, $p < 0.05$; Table 2, Fig. 3 - Column 2 vs Column 6). Under the sewage condition, when comparing the metabolic response of the vermetid reef community covered by CEB during heat wave exposure, once again, the CEB coverage was able to buffer the effect of the heatwave on the intertidal community's metabolic response, as revealed by the non-significant difference on RR (GLM, $p > 0.05$; Table 2, Fig. 3 - Column 3 vs Column 7). Instead, the absence of canopy (NO-CEB) showed a significant difference on patch metabolic rates after exposure to the pulsing thermal stressor (GLM, $p < 0.05$; Table 2, Fig. 3 - Column 4 vs Column 8). The chronic sewage factor, regardless of the presence of canopy, was reflected by a general lower value of the measured metabolic response of reefs (Fig. 3 - Columns 3, 4 vs Columns 1, 2 and Columns 7, 8 vs Columns 5, 6) both with and without heat wave conditions. Indeed, apart from the non-significant difference between uncovered

Table 1

Statistical results of generalized linear model (GLM) analysis (df = degrees of freedom; SL = significance level; * = $p \leq 0.05$; ** = $p \leq 0.01$; *** = $p \leq 0.001$; ns = no significant difference, $p > 0.05$).

Factor	χ -square	df	P	SL
Heat wave (HW)	0.146	1	0.70	ns
Sewage (SEW)	60.043	1	9.28E-15	***
Canopy (CEB)	0.360	1	0.55	ns
HW x SEW	4.203	1	0.04	*
HW x CEB	1.405	1	0.24	ns
SEW x CEB	8.748	1	0.003	**
HW x SEW x CEB	8.849	1	0.002	**

Table 2

Post-hoc Pairwise test comparisons for a) heat wave, b) canopy enhancing biodiversity complex (CEB) and c) sewage factors, by using an estimated marginal means for factors combination in the GLM model.

HEAT WAVE	NO-HW, NO-SEW, CEB	NO-HW, SEW, CEB	NO-HW, SEW, NO-CEB	NO-HW, NO-SEW, NO-CEB
HW, NO-SEW, CEB	0.3235			
HW, SEW, CEB		0.7705		
HW, SEW, NO-CEB			0.015	
HW, NO-SEW, NO-CEB				0.0353
CEB	NO-HW, NO-SEW, CEB	NO-HW, SEW, CEB	HW, NO-SEW, NO-CEB	HW, SEW, NO-CEB
NO-HW, NO-SEW, NO-CEB	0.9968			
NO-HW, SEW, NO-CEB		0.883		
HW, NO-SEW, CEB			0.0025	
HW, SEW, CEB				0.0103
SEWAGE	NO-HW, NO-SEW, CEB	HW, NO-SEW, CEB	NO-HW, NO-SEW, NO-CEB	HW, NO-SEW, NO-CEB
NO-HW, SEW, CEB	<0.0001			
HW, SEW, CEB		<0.0001		
NO-HW, SEW, NO-CEB			<0.0001	
HW, SEW, NO-CEB				0.7551

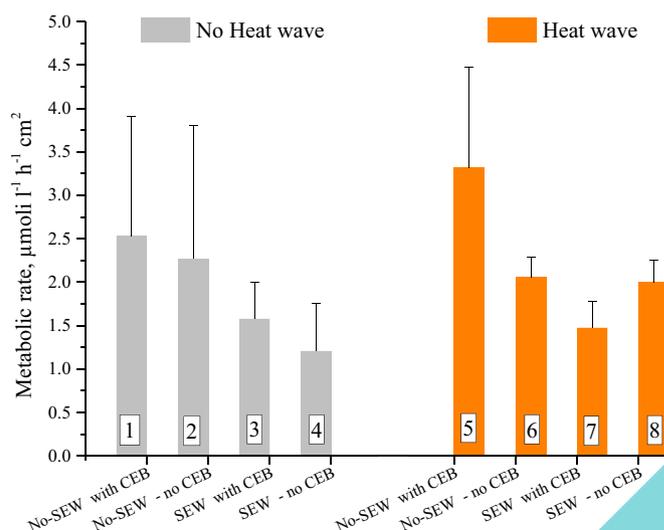


Fig. 3. Metabolic rates of the vermetid reef community (measured through the oxygen consumption as a proxy of community functioning) under *Ericaria-Cystoseira* canopy complex (CEB) cover/uncovered conditions, when exposed to multiple stressors: presence/absence of chronic sewage pollution (SEW/NO-SEW) and a pulsing thermal stressor (heat wave).

reefs (NO-CEB), under heat waves (GLM, $p > 0.05$; Table 2, Fig. 3 - Column 6 vs Column 8), the remaining post-hoc comparisons were significant showing that chronic trophic stress (SEWAGE) significantly affected the reef community metabolic rates (GLM, $p > 0.05$; Table 2, Fig. 3; Columns 1 vs 3; 2 vs 4; 5 vs 7).

4. Discussion

A wide number of studies have focused on the role of biodiversity in stabilizing community ecological responses along environmental pressure gradients (Loreau and de Mazancourt, 2013; Sarà et al., 2021), yet less attention has been paid to how stressor properties and occurrence (*sensu* Miller et al., 2011) may affect the ability of biodiversity to fulfil this stabilizing function. The active-warming experiment presented here provides insights into these questions. It suggests that canopy enhancing biodiversity, exerts a buffering effect on the metabolic respiration rate of the underlying vermetid reef community, and that this depends on stressor properties, *i.e.*, type (physical vs trophic) and frequency and duration (chronic vs pulse). After an extreme event such as a heat wave, the canopy buffering effect seems able to maintain the plot-scale climate, *i.e.*, the microclimatic conditions (Ettinger et al., 2019) of the underlying vermetid community. This outcome has been documented in previous studies, in both terrestrial and aquatic habitats, which investigated the role of diversity in absorbing and countering detrimental effects deriving from environmental change pulses (Ghedini et al., 2015; Ettinger et al., 2019). What is less well understood is that when we measured metabolic rates after a one time shot (*i.e.*, a pulse due to a heat wave event) or when we measured metabolic rates in patches that usually live under chronic conditions of organic sewage pollution (*i.e.*, eutrophication), the metabolic community response becomes more complex. Indeed, when one pulsing stressor (*e.g.*, a heat wave) exerted its effect in parallel with the one generated by chronic sewage effluents (*sensu* Gunderson et al., 2016), the benefits deriving from canopy enhancing biodiversity complex appeared to be weakened - demonstrated by the tendency for metabolic flattening. While such findings need further testing (*e.g.*, on more marine system models, across more geographic areas), we can infer that the effect of chronic stressors appeared to diminish the metabolic response capacity, reducing the community's ability to maintain metabolic equilibriums.

We know that each stressor, depending on its nature (biotic, abiotic, chemical or physical), can exert different multilevel effects (Harley et al., 2006; Suding et al., 2008; Doney et al., 2012; Mills et al., 2013; Connell et al., 2018; Sarà et al., 2018). However, this is more often conceptualized rather than measured in practice, as not many datasets comparing stressor effects on the same response variable are available (*sensu* Ettinger et al., 2019). Given that community response is the sum of responses of all individuals belonging to the species composing the community (Loreau, 2010; Worm and Tittensor, 2018), if a system lost its metabolic equilibrium, the stressor effect is exerted on all individuals of most species within the community. Unfortunately, this study may have some experimental limitations since we did not measure the stressor effect along a gradient of species richness. Yet it is still possible to derive interesting insights on how canopy forest can successfully alleviate the effect of pulsing climatic stressors on intertidal community's metabolism and raises questions on the potential role played by associated canopy biodiversity in this buffering function. Indeed, a system exposed to non-climatic anthropogenic stressors is potentially more vulnerable when exposed to climatic stressors, as such, understanding detrimental functioning thresholds warrants further investigation (*sensu* Cardinale et al., 2012).

While global climate change is a well-ascertained fact (Prober et al., 2019), this current work corroborates the idea that ecological responses are - in the end - driven mostly by the local context and the stressors properties which are acting at the local level. As such, efforts to manage disturbances should include information not only on the scale of the impact (both temporal and spatial; Post, 2019), but also measures of disturbance typology and properties (Crain et al., 2008). Restoration measures, such as canopy transplanting that facilitates the local persistence or adaptation of biodiversity, are useful but they only represent a small part of the solution. In fact, the role of scientists, practitioners and managers continues to be more challenging as they must explore new or more complex frameworks and options that consider the interactive

effects of global and local anthropogenic stressors. They will need to focus more on designing tailored local actions to alleviate the effects of non-climatic anthropogenic stressors and assist highly valued species or ecosystems to withstand climate stress (*e.g.*, heat waves; Prober et al., 2019). Increasing the resilience and the adaptability of native species (*e.g.*, the *Ericaria-Cystoseira* canopy complex considered in this study) through early warning actions, based on site-focused measures (*e.g.*, nutrient/organic sewage reduction) when extreme events (*e.g.*, heat waves, cold snaps, rainfall, *etc.*) are expected to occur are possible "key, low-regret approaches" (Prober et al., 2019). These approaches could help prevent biodiversity loss, safeguard ecosystem functioning (Baron et al., 2009; Stein et al., 2013) and allow the correct and rigorous attribution of biological and ecological responses to disturbance properties (Van de Pol et al., 2017).

CRediT authorship contribution statement

GS designed the study, drafted the early version of this ms., provided lab facilities and funds for fieldwork to support surveys and experiments. GS and MBB performed mesocosm experiments; GM performed the statistical analyses and all co-authors critically revised the later version of the ms.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marpolbul.2021.112713>.

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