Evenness, biodiversity, and ecosystem function of intertidal communities along the Italian coasts: Experimental short-term response to ambient and extreme air temperatures

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HIGHLIGHTS

- Eve intertidal communities are able to mitigate warming temperature effects.
- Short-thermal history was relevant on the response of intertidal community.
- Extreme warming temperatures may cause local physiological responses to fail.
- We confirm the role of biodiversity in buffering stressful temperature conditions.

GRAPHICAL ABSTRACT
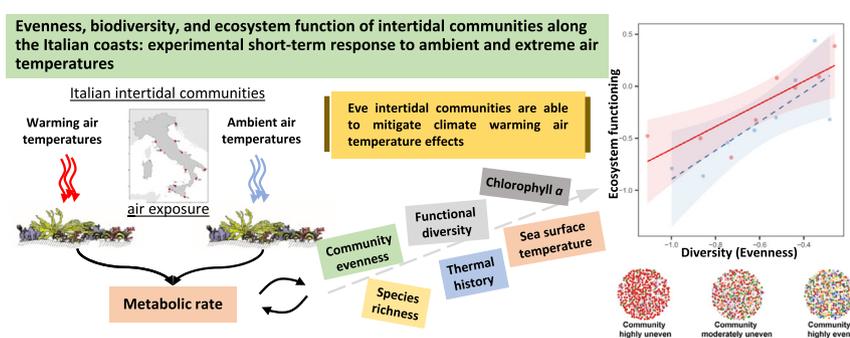
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ABSTRACT

Biodiversity can promote ecosystem functioning in both terrestrial and marine environments, emphasizing the necessity of biodiversity conservation in order to preserve critical ecosystem functions and associated services. However, the role of biodiversity in buffering ecosystem functioning under extreme events caused by climate change remains a major scientific issue, especially for intertidal systems experiencing stressors from both terrestrial and marine drivers. We performed a regional-scale field experiment along the Italian coast to investigate the response of unmanipulated intertidal communities (by using a natural biodiversity gradient) to low tide aerial exposure to both ambient and short-term extreme temperatures. We specifically investigated the relationship between Biodiversity and Ecosystem Functioning (BEF) using different biodiversity indexes (species richness, functional diversity and evenness) and the response of the intertidal communities' ecosystem functioning (community respiration rates). Furthermore, we investigated which other environmental variables could influence the BEF relationship. We show that evenness explained a greater variation in intertidal community ecosystem functioning under both temperature conditions. Species richness (the most often used diversity metric in BEF research) was unrelated to ecosystem functioning, while functional diversity was significantly related to respiration under ambient but not extreme temperatures. We highlight the importance of the short-term thermal history of the communities (measured as body temperature) in the BEF relationship as it was

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consistently identified as the best predictor or response under both temperature conditions. However, Chlorophyll *a* in seawater and variation in sea surface temperature also contributed to the BEF relationship under ambient but not under extreme conditions, showing that short-duration climate-driven events can overcome local physiological adaptations. Our findings support the importance of the BEF relationship in intertidal communities, implying that systems with more diverse and homogeneous communities may be able to mitigate the effects of extreme temperatures.

1. Introduction

Climate change presents a major threat to marine biodiversity and ecosystem functioning, affecting species abundances and distributions at the community level (Sala et al., 2011; Sorte et al., 2010b; Walther et al., 2002; Wernberg et al., 2013). Observed and projected increases in the frequency and intensity of extreme short-term high temperature events are of particular concern (Christidis et al., 2015; Coumou and Rahmstorf, 2012; Hegerl et al., 2011; Oliver et al., 2018; Perkins-Kirkpatrick and Lewis, 2020). Extreme high temperature events such as heat waves intensify the effects of underlying warming trends, because they do not allow time for organisms to acclimate or populations to locally adapt. This places an increasing number of species in danger of extinction (Somero, 2010), and increases the likelihood of biodiversity decline (Smale et al., 2019).

Biodiversity is one of the most important factors regulating ecosystem functioning (Strong et al., 2015; Tilman et al., 2014). Some evidence suggests that it is also able to stabilize ecosystems in the face of climate change, although whether this applies in the face of extreme climate warming events is still not fully understood (Benkwitt et al., 2020; Isbell et al., 2015; Pires et al., 2018). The majority of studies to date have been carried out in terrestrial environments (Gamfeldt et al., 2015), and the few marine studies that have explored these relationships have focused on the responses of individual organisms and populations of one or few seaweed, fish and invertebrate species rather than on the role of biodiversity of intact communities (Román et al., 2020; Smale et al., 2019; van der Plas, 2019; Wernberg et al., 2013). Moreover, our understanding of how extreme climates influence the relationship between Biodiversity and Ecosystem Functioning (BEF) is mostly based on observational studies using long-term datasets (Wernberg et al., 2013), or small experimental studies designed to mimic extreme conditions in the field (Sorte et al., 2010a), whereas data from large spatial scale experiments are lacking (Pires et al., 2018).

Species diversity can be estimated using a variety of different metrics (e.g. richness, Shannon Diversity Index, Hill numbers, evenness and functional diversity). However, dozens of studies on BEF relationships have used only species richness (number of species in a community) as a proxy of biodiversity; far less work has been done on the relationship between species evenness (the relative abundance of the different species in a community) (Smith and Wilson, 1996; Tuomisto, 2012) and ecosystem functioning (Lembrechts et al., 2018). Evenness could strongly influence the stability of ecosystem functioning (Engelhardt and Ritchie, 2001; Hodapp et al., 2015; Maureaud et al., 2019) and it has been observed to more rapidly respond to anthropogenic stressors or environmental constrains than species richness (Hillebrand et al., 2008). Warming, for example, can reduce evenness by increasing species dominance in both terrestrial and aquatic communities (Klanderud and Totland, 2005; Stachowicz et al., 2002). More even communities (with more equal relative abundance of species) are more likely to support functionally redundant species, improving the possibility of absorbing a pulse perturbation. Conversely, when evenness is low (dominance by one or a few species), the resistance of a community to a perturbation is expected to be lower as it is likely determined by the fates of a few dominant species that are tolerant to the perturbation (Allan et al., 2011; Hillebrand et al., 2008; Wittebolle et al., 2009). However, when analyzing the relationship between evenness and ecosystem functioning, factors such as environmental variability and the time scale considered can be important (Norberg et al., 2001). Highly stable habitats can select a few species (lowering community evenness) with optimal traits capable of maintaining high productivity levels. Conversely, unstable environments characterized by high environmental fluctuation, such as those affected by climate instability, can benefit from communities composed of a balanced amount of different species (high evenness) with different traits able of quickly adapting to new environmental constraints and maintaining high productivity levels on a longer time scale (Norberg et al., 2001).

Studies have found that other aspects of biodiversity, such as functional diversity, have an impact on ecosystem functioning (Cadotte et al., 2011; McGill et al., 2006; Song et al., 2014; Zhu et al., 2016). The amount of inter-specific variation in functional traits in an ecological community is referred to as functional diversity. In comparison to species-diversity indices, functional diversity recognizes the importance of species traits (a collection of physical, biochemical, behavioral, temporal, or phenological traits) that may affect environmental tolerances and habitat requirements, determining where a species can live and the interaction between species, as well as how species contribute to ecosystem function, such as differences in nutrient use and storage (Cadotte et al., 2011; McGill et al., 2006). One of the most compelling explanations for the strong relationship between functional diversity and ecosystem functioning found in BEF research is that as biodiversity increases, so does the diversity of functional traits (Cadotte et al., 2011). These characteristics regulate how an organism obtains resources from its surroundings. As a result, as functional diversity increases, so does the division of total available resources within a community (McGill et al., 2006).

Here, we explore the response of intertidal communities (the area between the high and low tide mark) to aerial exposure, including during short-term extreme high temperature conditions. To do so, we carried out a large regional scale field experiment to examine if biodiversity can buffer the effects of a pulse disturbance. Intertidal communities are extremely vulnerable to thermal extremes, particularly during low-tide emersion, when sessile organisms may experience rapidly fluctuating and very hot temperatures close to their thermal tolerance limits (Helmuth et al., 2006; Helmuth and Hofmann, 2001; Mislan and Wethey, 2015; Pinsky et al., 2019; Sarà et al., 2014). Subsequently, it's possible that many intertidal species are already living on the edge of their physiological limits, and may have limited room to cope with further temperature increases caused by extreme warming events of climatic origin (Somero, 2010).

Manipulative field experiments are an effective tool for predicting and understanding the impacts of climate change on ecosystems. Field experiments capture all of the otherwise unaccounted-for variables that controlled experiments may miss, including the suite of species at any given location and the idiosyncratic physical conditions at a site. However, the inability to successfully manipulate climate change-related factors in situ has led to a lack of field-based marine climate change experiments, though (Wernberg et al., 2012). Furthermore, some discrepancies have emerged when merging experimental manipulation with climate projections. Many studies have pointed to the problems associated with methods that rely on time-space substitution (Woodin et al., 2013), where current spatial variability is used to understand and model otherwise unobservable temporal processes, most notably past and future events (Blois et al., 2013). However, space-for-time substitution may not always work since warmer sites may not reflect future novel conditions or may have a wholly different suite of species than the site of interest. Thus, in this study, we attempted to overcome this gap by manipulating temperature conditions in the field, experimentally simulating a short-term extreme high temperatures experienced by organisms at each experimental location. Finally, in order to provide an overall "snapshot" of the responses of the Italian intertidal communities to extreme warming conditions, at all eleven sites experiments were completed in only thirty days during the season when extreme high temperature events are expected.

Although reports on the large-scale effects of extreme events have been focused on changes in community structure and composition (Blois et al., 2013; Garrabou et al., 2009; Smale et al., 2019; Wernberg et al., 2013), the impacts on the biological-physical and chemical processes that define community functioning over a series of sites that span a large geographic range have not been studied. To address this gap, we used oxygen consumption as a proxy of community ecosystem functioning. Though oxygen consumption (community respiration) rate obtained through classical respirometry is a widely used metric of aerobic metabolic activity for aquatic species and a valuable surrogate of ecosystem functionality (Rosewarne et al., 2016), it has seldom been used in BEF studies (Roth et al., 2019).

Our aim was to explore the relationships between different diversity indexes (species richness, functional diversity and evenness) and the short-term responses of Italian intertidal communities in terms of respiration rates (ecosystem functioning) under both normal and extreme temperatures. We were especially interested in knowing: (i) which diversity measurement best explains the response of intertidal communities under both ambient and extreme high temperatures conditions? (ii) which other environmental variables contribute to the observed variation?

2. Materials and methods

1.1. Study sites, sampling and experimental design

The experiments were run in summer from June 22nd to July 24th, 2013 at 11 locations along the Italian coast spanning 9 degrees latitude and 8 degrees in longitude with different seawater and aerial temperature conditions (Fig. 1, Supplementary Table 1). The summer season was chosen because the Italian peninsula has previously experienced some of the most severe extreme events during this season (Dong et al., 2017). Data from oceanographic buoys (Istituto Superiore per la Protezione e Ricerca Ambientale; ISPRA, http://www.mareografico.it) placed at each location
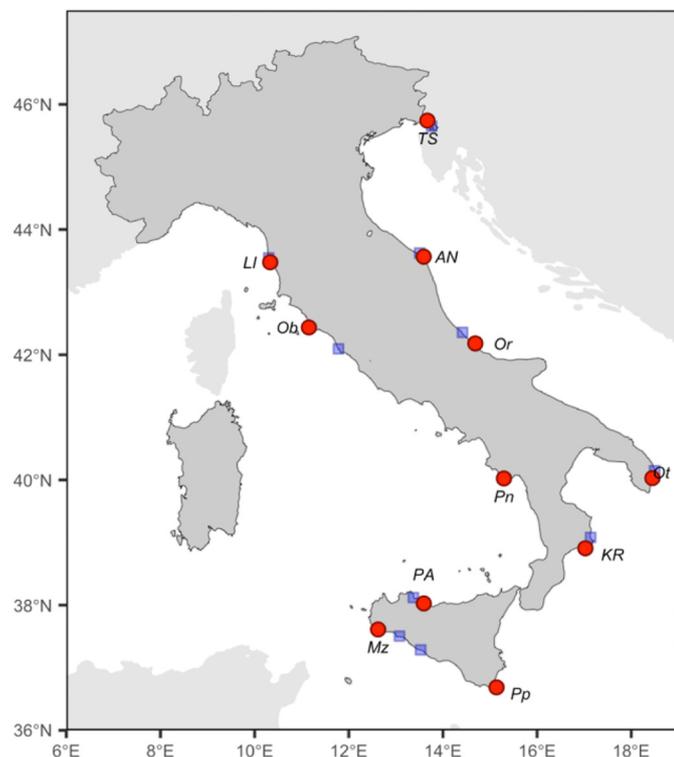
Fig. 1. Map of the study sites. The 11 rocky study sites (red dots) are located along the Italian coast. **Pp**: Siracusa, **Mz**: Trapani, **PA**: Palermo, **KR**: Crotone, **Ot**: Otranto, **Pn**: Palinuro, **Or**: Ortona, **Ob**: Orbetello, **LI**: Livorno, **AN**: Ancona, **TS**: Trieste. ISPRA buoys are represented by blue squares.

were used to estimate the magnitude of historical extreme air temperatures. This allowed us to simulate site-specific extreme events based on the maximum air temperature observed at each location over the previous 10 years (Supplementary Table 1).

Each site was exposed, gently sloping to sub-vertical rocky platforms, and accessible from the coast without using a boat. The system is typically micro-tidal with mixed semidiurnal tides generally <35 cm in amplitude (Sarà et al., 2014). Communities among sites comprised macroalgae belts mixed to turf-forming algae seaweeds and/or mussels (site abbreviations Pp, Mz, PA, KR, Ot, Pn, Ob, and LI, Fig. 1), or mainly dominated by mussel beds (site abbreviations TS, Or and AN, Fig. 1) (Supplementary Table 2, Supplementary Fig. 1).

At each site, we used hammer and chisel to remove $n = 10$ slabs (12 cm × 12 cm) of rock from intertidal substrata, including associated community of sessile invertebrates and seaweeds. Samples were randomly collected at the infralittoral fringe zone, including a slice of substrate to reduce disturbance of sessile species. Because a large portion of the mobile macrofauna was lost during sampling, we decided to exclude them from the experiment and to focus only on sessile organisms. Slabs of rocks with their associated sessile communities were randomly allocated half to ambient conditions and the other half to warming treatments ($n = 5$ for each factor combination) and acclimated for 1 h in two open-top plastic boxes (30 × 40 × 90 cm) filled with filtered seawater (Fig. 2). The effects of extreme short-term high temperature events were measured under low tide conditions, mimicked by removing the seawater from the plastic boxes for three hours – which represents, in the Mediterranean micro-tidal system, the average duration of aerial exposure experienced by intertidal species on sunny summer days with high atmospheric pressure. The five slabs of rock were assigned to the warming-treatment were exposed below a thermal rack provided with 3 infrared 100-watt lamps (Trixie) adjustable in height to increase surface (body) temperature up to the desired peak. Additionally, GreenPower LED lights were installed on the rack to offer a consistent light intensity (PAR) of 200 mol quanta /m^2 s, preventing the effects of fluctuations in meteorological conditions (light intensity, clouds) between sites. The 5 ambient-treatment slabs of rock were exposed below a rack but without infrared lamps, thereby experiencing low-tide emersion at ambient temperature. Thermometers (± 0.1 °C) placed closer to rock slabs were used to continuously measure the temperature of the near-surface air. Aerial exposure lasted for 3 h. After 1 h, the extreme warming temperature was reached and kept for the remaining 2 h (Fig. 2).

1.1. Respiration rate

After the experimental aerial exposure, each chip was placed in a respirometric glass chamber (2.4 l) filled with air-saturated filtered seawater (Whatman GF/C 0.45 μm) and hermetically closed. To guarantee that the water was constantly mixed, each chamber was agitated using a magnetic stir bar put beneath a petri dish with holes to support each community (Widdows and Staff, 2006). A calibrated optic oxygen meter linked to a data logger monitored the drop in oxygen concentration (μmol /l), i.e. dark respiration (PyroScience Firesting O$_2$). To eliminate oxygen production by algal photosynthesis, chambers were darkened with a black plastic film. Oxygen decline was recorded for 180 s, after omitting a 10-min period during which there was a quicker fall in oxygen due to a disturbance in the sensor's temperature equilibration. Measurements were repeated for 4 times, once after placing rock slabs into the respirometric chamber and once every hour for the subsequent 3 h. Respiration rate (RR, mg/l h^{-1} g^{-1}) was calculated according to Widdows and Staff (2006):

$$RR_{(mg/l\ h-1\ g-1)} = \lfloor (C_{t0m} - C_{t1m}) \times Vol_r \times \frac{60}{(t1m - t0m) \times 60} \times biom^{-1} \rfloor \times 0.039988$$

where C_{t0m} and C_{t1m} are the average oxygen concentrations at time zero and after 1 h of incubation; Vol_r (l) is the community volume less the respirometric chamber volume; $t0m$ and $t1m$ are the average start and finish times (s) of the measurement period; $biom$ is the biomass (g) of the community obtained by subtracting the Ash Free Dry Weight to the Dry weight of
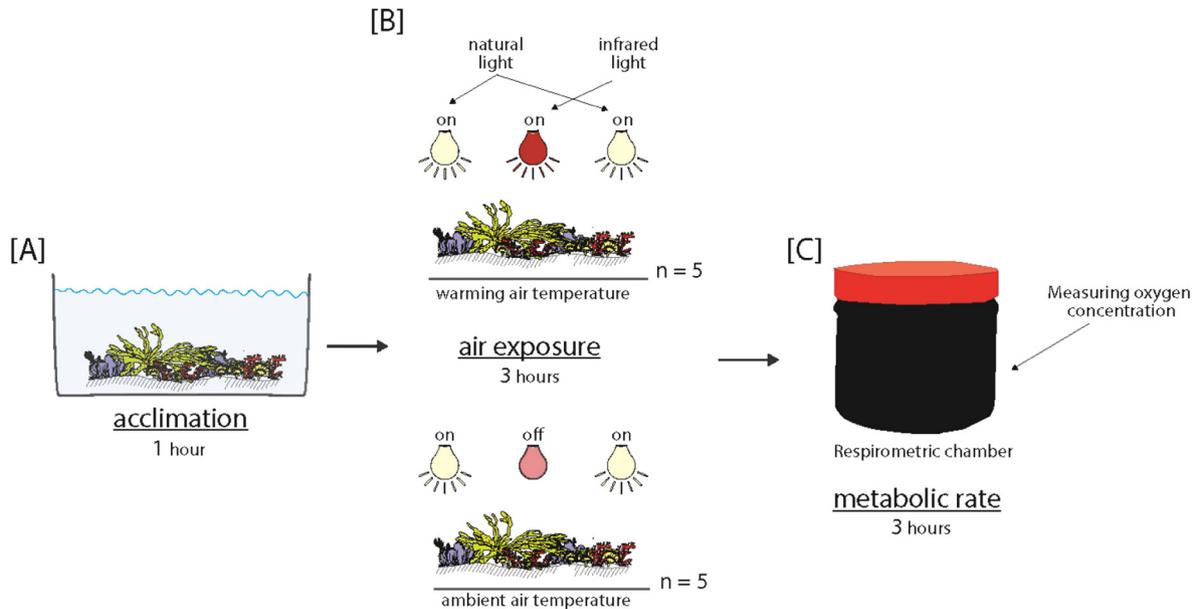
Fig. 2. Design of the field experiment. The experiment was designed to measure the effects of ambient and extreme air temperatures on intertidal communities during low tide conditions. Ten intertidal communities' cores were collected, acclimated for 1 h into plastic boxes filled with natural seawater (**A**) and exposed for 3 h under both ambient and elevated temperatures (**B**). After aerial exposure, the respirometric rate of each community was assessed measuring the oxygen evolution within respirometric chambers (**C**).

the community, while 0.039988 is the multiplication factor for converting the oxygen concentration from μmol/l to mg/l.

The percentage cover of each species represented on rock slabs was calculated by photographing each chip and utilizing the image segmentation tool supplied by PhotoQuad, a free benthic image processing software (Trygonis and Sini, 2012). Later, in order to calculate the community biomass used to standardize the respiration rates, samples were first dried at 60 °C for 48 h (DW, gr) weighed and then ashed at 450 °C for 4 h to obtain the dry mass of organic material combusted (AW, gr) (Stein-Taylor et al., 1985). Biomass was expressed as Ash Free Dry Weight (AFDW, gr) and obtained as DW - AFDW. We used *biom* rather than AFDW as is, because AFDW represents dried materials that have been oxidized (ashed) by removing all biological components, so it primarily reflects all inorganic materials of an organism. Then, AFDW can differ significantly between mussels and algae, as well as between calcified and noncalcified algae. The biomass values used here, on the other hand, only represent the organic part of an organism that is primarily involved in respiration activity (i.e. mussel shells not included).

2.1. Measurements of relevant environmental and biological variables

To explain the variation of ecosystem functioning, we explored the relationship with different environmental and biological variables. Each community chip was characterized based on the overall number of species (S), functional diversity and Pielou's Evenness (J). Functional diversity was estimated on 5 categorical functional traits of the species collected [type of organism: seaweed or mussel; class: green, brown or red algae, animal or mixed seaweeds; morpho-functional group according to the classification suggested by (Balata et al. (2011); type of producer; and habitat former type, such as the species of *Cystoseria* and *Ericaria* and the mussel species, Supplementary Table 3]. Functional richness (FRic), functional dispersion (FDis), Rao's quadratic entropy (RaoQ) and functional evenness (Feve) (Laliberte and Legendre, 2010) were calculated from the trait data. Because preliminary analysis revealed that FDis was more closely related to respiration rates (Supplementary Fig. 3), FDis was used as a metric of functional diversity and referred to as FDiv.

It is widely known that the body temperature of intertidal species exposed to solar radiation during low tide can differ significantly from ambient air temperature (Helmuth et al., 2010). During experimental trials we

eliminated this complication, including dampening any differences in body temperature among each species due to factors such as colour and surface wetness, by using infrared heat lamps in the heat wave trials which provided even heating across the entire community on each rock chip. However, in order to estimate the average body temperature (BT) of each community for the week prior to the start of the low-tide simulation (i.e. short-term thermal history that takes unto account temperature fluctuations experienced by communities in a specific location) we estimated these temperatures using a biophysical heat budget model (Helmuth et al., 2011; Kearney et al., 2010; Sarà et al., 2013b, Sarà et al., 2011). Body temperature is an excellent indicator of an organism's physiological condition because it accounts for the highly nonlinear interactions of the physical environment with an organism to drive its thermal and hydric exchanges (Kearney et al., 2010). This is especially important in the intertidal zone, where organisms are exposed to multiple environmental drivers including air temperature, solar radiation, and wind speed. In this study, BT was used as a generic proxy of the physiological state of each community for the week prior to the experiment. Data for the heat budget model (hourly air temperature, tide amplitude, and wind speed) were gathered from the ISPRA buoy network (2012, http://www.mareografico.it) for the seven days preceding the start of each experiment, whereas daily irradiance data were obtained from the Joint Research Centre (http://re.jrc.ec.europa.eu/pvgis/apps4/pvest.php). Although the model was designed for invertebrates, the fundamental variables influencing the heat budget of algae (the other primary component of intertidal communities) are similar to those influencing the BT of intertidal ectotherms (see Bell, 1992, 1995). We therefore used the BT of a "generic" intertidal ectotherm as proxy of the entire community at each site. We acknowledge that this method ignores the likely variances in body temperature experienced by individuals within a community, but we rationalize that especially when communities are algal dominated, the body temperatures of most species will be driven by overall canopy (surface) temperature and thus be somewhat uniform.

Moreover, we included environmental variables over much longer time periods (whenever available, at least 10 years) that can used as proxy for long-term community adaptation. In particular we included, the annual variation in sea surface temperature "SST-variation" (determined by subtracting the mean temperatures of the hottest and coldest months of the year), tidal range, annual Chlorophyll *a* seawater concentration as proxy of eutrophication. The SST-variation and tidal range were computed

using the nearest ISPRA buoy to the point of interest (temporal range 2000–2012). Annual average Chlorophyll *a* concentrations at each site were acquired from the Environmental Marine Information System (EMIS, mcc.jrc.ec.europa.eu/emis/, spatial resolution 4 km, temporal range 2003–2012,) using the "EMISR" R package (Dubroca, 2014).

2.2. Statistical analysis

We compared the response of intertidal communities under ambient and high air temperature conditions using RR as proxy of ecosystem functioning. Our main assumption was that the lower the RR, the lower the impact of temperatures would have on the community. However, to simplify data interpretation with other BEF studies, we used the opposite of RR (−RR). Increasing in -RR can then be translated as better ecosystem functioning. Since community chips were different from each other (for example, in terms of the number of species and biomass), we avoided direct comparison between air ambient and warming conditions, but rather treated the two conditions with a distinctive analysis.

To investigate the link between biodiversity and ecological function (species richness, functional diversity and evenness), multiple linear regression models (MLRs) were built with the function "lm" of the R package "base." Because of the presence of site-specific fixed effects factors, such as latitude and some environmental variables, site-level variation was built into the fixed effects. Three distinct models were created, one for each index of biodiversity (species richness, functional diversity and evenness). To assess the impact of biodiversity while taking into account other factors that may influence ecosystem function (respiration rates), all models included a series of additional predictors: mean body temperature 7 days before the experiments, air and water temperatures, latitude, SST-variation, tidal range, and mean marine Chlorophyll *a* concentration in seawater. Model assumptions were checked using the function "check_model" of the R package "performance" (Lüdecke et al., 2021). Multicollinearity between independent variables were checked using Variable Inflation Factors (VIF). Predictors with VIF major than 5 were dropped to bring down the multicollinearity between variables. If heteroskedasticity warning was detected, robust standard errors were calculated using the function "vcovHC" from the R package "sandwich" (Zeileis et al., 2020). The function "scale" in the R-package "base," which centers and scales our data to enable comparison, was used to scale all variables.

A natural log transformation was applied to species richness, evenness, FDiv and respiration rates. This was used to model the relationship between diversity and ecosystem structure on a log–log scale, since it has the most

scientific evidence across a wide range of aquatic environments. In addition, in log–log models, $\beta1$ is equal to the power coefficient, allowing us to define the form of the relationship between diversity and ecosystem functioning ($\beta > 1$ represents concave-up/non-saturating, while $\beta < 1$ denotes concave-down/saturating).

After checking for multicollinearity, the function "buildmer" (Voeten, 2021) was used to apply backward stepwise elimination procedure in order to find the most parsimonious model. Biodiversity indexes (species richness, evenness and FDiv) were kept in the model at all times passing them in the "include" argument (Voeten, 2021).

Preliminary analysis of the data on the relationship between latitude and RR showed that sites seem to cluster into two groups according to their geographical position (Supplementary Fig. 4). We thus decided to include a categorical factor called geographical position with two levels (south, which grouped the sites Pp, Mz, PA, KR, Pn and Ot, and north that contained the sites LI, TS, AN, Or and Ob) to determine if geographical position affected BEF relationships.

To summarize the BEF relationship we aggregated respiration rates values of all the communities according to 8 evenness ranks. The number of ranks was chosen to maintain as much variability as possible. The effects of biodiversity (evenness) on ecosystem function were assessed using Linear Models (LMs) with Gaussian distribution.

R software 3.5.1 was used to conduct statistical analysis (R Core Team, 2018). See the "*Data availability and reproducible research*" section for further details. Some replicates were excluded due to data unreliability Supplementary Table 4.

3. Results

3.1. BEF relationship on intertidal communities

BEF relationship differed depending on whether species richness, functional diversity or evenness was used as a measure of biodiversity (Figs. 3–4, Supplementary Table 9). In particular, species richness and respiration rates had a non-significant relationship under both ambient (MLR, estimate 0.05, 95 % CI −0.05 to 0.15, $p = 0.299$) and warming (estimate = 0.00, 95 % CI −0.07 to 0.07, $p = 0.976$) conditions and will not be further described (Figs. 3a and 4a, Supplementary Table 9).

In contrast, a positive correlative BEF relationship was found between the other two diversity indexes (functional diversity and evenness) and ecosystem function. Although the relationship with evenness was significant under both ambient and warming conditions (ambient temp.: estimate
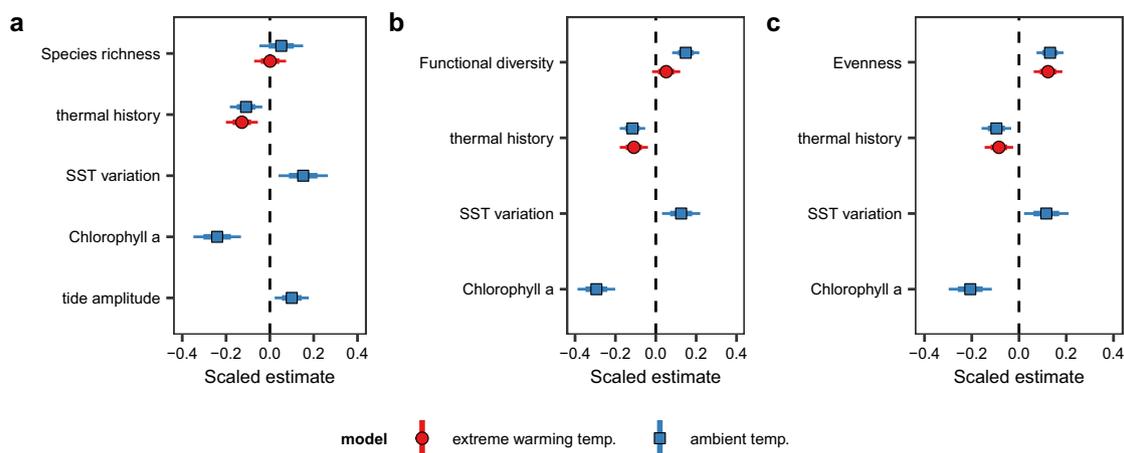
Fig. 3. Relationships between species richness (a), functional diversity (b) evenness (c) and best selected predictors. Points indicate estimates from multiple linear regression models (MLRs) examining each explanatory variable's impact on ecosystem function (respiration rates) of intertidal communities exposed at air ambient (blue squares, $n = 45$) or extreme warming (red dots, $n = 48$) temperatures. Thin lines denote 95 % CIs, whereas thick lines denote 75 % CIs. To make it easier to compare the impact sizes among the explanatory factors, the estimates and confidence intervals (CIs) are scaled (mean-centered and scaled by one standard deviation). Thermal history = the average body temperature of each community for the week prior the experiment; SST variation = annual variation in sea surface temperature; chlorophyll *a* = annual average Chlorophyll *a* seawater concentrations; tide amplitude = tidal range.
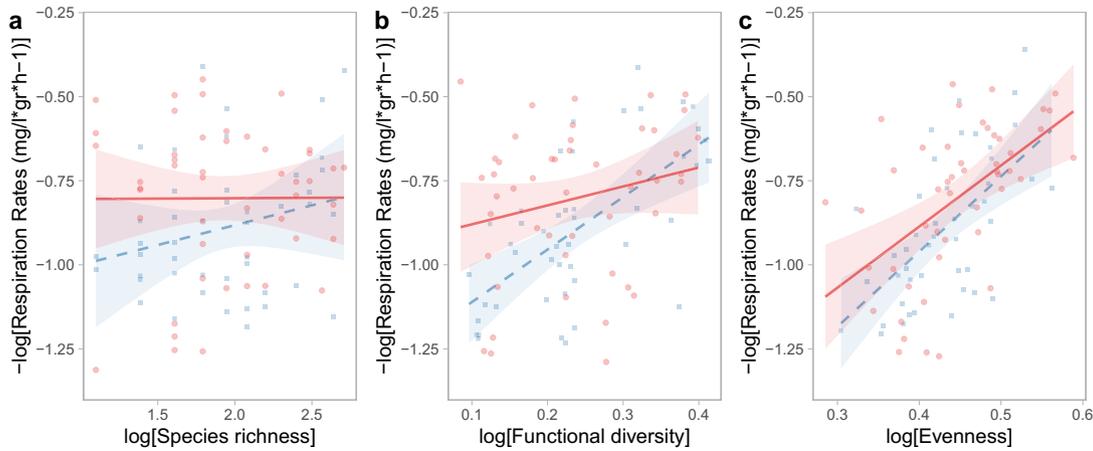
Fig. 4. BEF relationships in intertidal communities at ambient (blue dashed line, n = 45) and extreme warming (red solid line, n = 48) air temperatures. Respiration rates are expressed as a function of species richness (a), functional diversity (b) and evenness (c) of intertidal communities. Each point represents the observed respiration rate of a community controlling the effects of the other predictors under ambient (blue squares) and extreme warming (red dots) conditions. Lines are predicted (fitted) values from MLRs while shaded areas represent 95 % CIs.

0.13, 95 % CI 0.07 to 0.19, $p < 0.001$, warming temp.: estimate 0.12, 95 % CI 0.06 to 0.18, $p < 0.001$, Figs. 3c, 4c, Supplementary Table 9), functional diversity was significantly related only at ambient temperatures (ambient temp.: estimate 0.15, 95 % CI 0.07 to 0.23, $p < 0.001$, warming temp.: estimate 0.05, 95 % CI -0.02 to 0.12, $p = 0.145$, Figs. 3b, 4b, Supplementary Table 9). The BEF relationships were non-saturating for both biodiversity indexes, with evenness more related with ecosystem functioning compared to functional diversity at both ambient (Evenness adj.$R^2 = 0.57$, p < 0.001, Functional diversity adj.$R^2 = 0.56$, p < 0.001) and warming (Evenness adj. $R^2 = 0.43$, p < 0.001, Functional diversity adj.$R^2 = 0.25$, p < 0.001) temperature conditions (Figs. 3b-c, 4a-b, Supplementary Table 9). When the geographical variability was removed and values of ecosystem functioning were aggregated based on diversity ranks, BEF relationships became stronger for evenness (LM ambient temp.: adj.$R^2 = 0.60$, $p = 0.014$; LM warming temp.: adj.$R^2 = 0.65$, $p = 0.009$, Fig. 5, Supplementary Table 10), but nonsignificant for functional diversity (Supplementary Table 10).

### 3.2. Relationship with environmental variables and exposure history

Under ambient temperature conditions, thermal history (body temperature over the previous week), Chlorophyll *a* seawater concentration and variation in sea surface temperature all contributed significantly to the BEF relationship (Fig. 3, Supplementary Table 9). Higher Chlorophyll *a* seawater concentrations had a negative relationship with ecosystem functioning (Fig. 3, Supplementary Table 9). Conversely, Chlorophyll *a* seawater concentration and seawater temperature variation were not relevant (i.e., excluded by model selection) under warming conditions (Fig. 3, Supplementary Table 9).

By grouping sites according to their geographical position (south and north), northern sites had higher RR values compared to southern sites (Fig. 6). However, although under ambient temperature the BEF relationship remained equal (positive for both southern and northern sites), under extreme warming conditions the BEF relationship was lower at southern compared to northern sites (Fig. 6, Supplementary Table 11).

4. Discussion

Our results show that the ecosystem functioning of the intertidal communities investigated here were unrelated to species richness. Species richness is a straightforward and widely used indicator of diversity, with reports of higher number of species increasing ecosystem functioning in fully controlled experimental conditions (Duffy et al., 2017). These relationships, however, can be more difficult to detect under more "natural" experimental conditions, as those of our study, where the composition of the communities was not a priori controlled (Balvanera et al., 2006). Our results are in accordance with weak or even negative BEF correlations that have been observed in a variety of regional studies, including phytoplankton and benthic macrofauna (Heip et al., 1992; Lehtinen et al., 2017; Valdivia and Molis, 2008) and fish (Greenstreet et al., 2012; Maureaud et al., 2019). This indicates that a universal positive BEF relationship may not be detected in natural marine environments when diversity is expressed only as species richness (Balvanera et al., 2006).
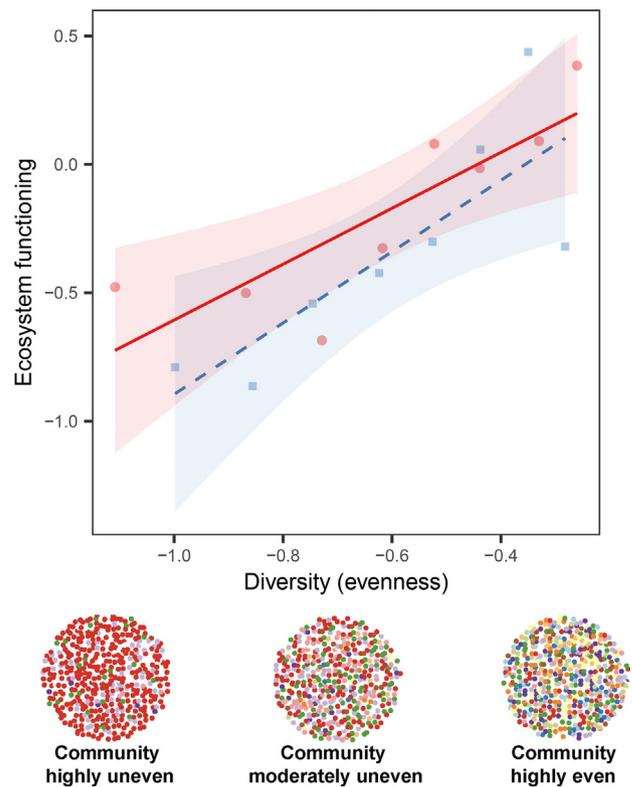
Fig. 5. Summary of the relationships between evenness and ecosystem functioning. Log-log relationship between evenness and respiration rates of intertidal communities. Values of respiration rates were grouped according to 8 evenness ranks of intertidal communities experiencing ambient (blue dashed line and squares, $n = 8$) and extreme high (red solid line and dots, n = 8) air temperatures. Lines are predicted (fitted) values from LMs while shaded areas represent 95 % CIs.
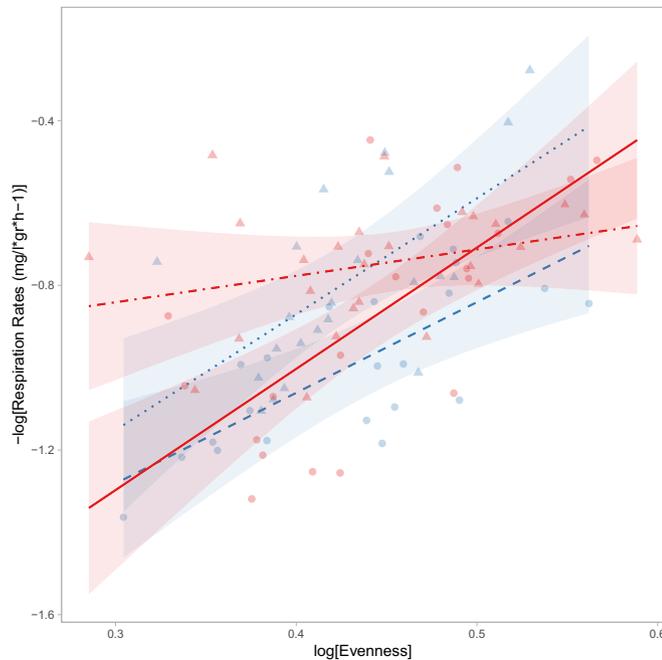
Fig. 6. BEF relationships in intertidal communities at ambient (blue dashed and dotted lines) and extreme warming (red solid and dotdashed lines) air temperatures according to south (dotted and dotdashed lines) and north (solid and dashed lines) sites. Respiration rates are expressed as a function of community evenness of intertidal communities. Each point represents the respiration rate of a community. Lines are predicted (fitted) values from MLRs while shaded areas represent 95 % CIs.

Conversely, our findings show that community evenness and functional diversity were able to explain larger part of the variation of the intertidal ecosystem function, with evenness explaining greater variation at both temperature conditions. Evenness has been proposed to be more strongly related to ecosystem functioning than species richness (Duncan et al., 2015; Hillebrand et al., 2008), and frequently adapts more quickly to environmental constraints (Chapin et al., 2000). This metric, however, is rarely employed in studies examining BEF relationships (Hillebrand and Matthiessen, 2009), despite the evidence of its role in driving ecosystem functioning in marine environments (Engelhardt and Ritchie, 2001; Hodapp et al., 2015; Maureaud et al., 2019). Our results confirm the importance of evenness in the BEF relationship, where communities with high evenness (with more equal relative abundance of species) are likely to provide a distribution and variance of traits able to increase the stability of the system (Hillebrand et al., 2008) at both unstressed and stressed conditions. Moreover, our study's calculated slopes are consistent with theoretical predictions for the shape of BEF connections in natural ecosystems, which consistently have yielded non-saturating patterns (Mora et al., 2014). This shows that BEF interactions in natural systems are consistent across many spatial scales and functions.

Among the environmental variables investigated, Chlorophyll *a* seawater concentration and sea surface temperature had a significant effect on the BEF relationship, suggesting that adaptation to local environmental conditions appears to regulate community responses under ambient air temperature conditions. Chlorophyll *a* is thought to be a direct effect or primary symptom of eutrophication (Ferreira et al., 2011), and it could be connected to nutrient loading brought on by coastal urbanization, which is often linked to deteriorating water quality (Doering et al., 2006). Our findings indicate that water quality may have a significant impact on the physiological functioning of intertidal ecosystems. Moreover, we observed that communities adapted to large variance of seawater temperature responded better (positive relationship) than those exposed to more stable water temperatures, confirming the importance of submerged (water) temperature on the animals' functional and life cycle features, as reported in other rocky intertidal species (Giomi et al., 2016; Mancuso et al., 2018; Sarà et al., 2013a).

Interestingly, our results show that environmental variables related to long-term exposure of each community, such as Chlorophyll *a* seawater concentration and seawater temperature variation, did not contribute to the BEF relationship under warming conditions, implying that the effect of extreme warming can overcome local adaptation on intertidal systems. We believe this is concerning because it implies that adaptation to local environmental conditions will be insufficient to buffer effects of extreme temperature exposure during low tide on intertidal organisms in these communities. This, however, contradicts recent research that has demonstrated that individual species exposed to warming events might build stress memory through epigenetic alterations, allowing them to survive repeated stressors (Hackerott et al., 2021; Jueterbock et al., 2021; Maher et al., 2019; Nguyen et al., 2020; Pazzaglia et al., 2022; Xu et al., 2022). These conflicting results may highlight one limitation of this study. In fact, the short-term responses examined in our study may not be enough to monitor species' adaptative responses, which would require a long-term recovery assessment following the application of warming stressors. Thus, further studies aimed to analyses the response of intertidal communities should include longer-term responses (i.e. after a second low tide aerial exposure). Furthermore, because climate change is increasing the frequency and intensity of extreme short-term warming events, species may not have the ability or time to fully recover from repeated intense perturbation. Future research focused at exploring the real effects of intense warming events should employ a more complicated experimental design that includes a series of short warming events of varying intensity that are stochastic and unpredictable (e.g. Drake et al., 2017). Our study, on the other hand, analyzes the response of the entire community rather than a single species. Then, even if a single species has developed a form of stress memory, its response may be masked by that of other species in the community that have no physiological adaptation. Exploring long-term variation in community structure after extreme warming events in future studies can help detect or infer species' possible physiological tolerance. If species in the community exhibits stress memory, there will be no significant variation in composition or evenness. On the contrary, if some species are better adapted to stress than others, there will be selection, which can result in a decline in community evenness and the selection of a few dominating tolerant species.

It's worth noting that body temperature was the only variable that was consistently selected on both ambient and warming temperature conditions, implying that the intertidal communities' short-term thermal history (based on one week prior to the extreme warming event) is critical. The inclusion of BT rather than air temperatures in model selection can be explained by the fact that when intertidal organisms are exposed to air, wind speed, solar radiation, humidity and air temperature interact to drive heat flux to and from an organism's body temperature (Denny and Harley, 2006; Helmuth, 1999, Helmuth, 1998). As a result, organism temperature is frequently very different from ambient air temperature (Helmuth, 2002). Thus, air temperature measurements are less likely to provide reliable indications of the physiological response of intertidal organisms than body temperature (it should be noted that because of the design of our experimental heating treatments, which used infrared heat lamps, the difference between air temperature and body temperature was likely minimal). Thermal history can play a primary role in species selection and local adaptation (Teske et al., 2019). Community composition is therefore probably affected by prior extreme warming events, so that sensitivity to extreme events (and thus RR response) may be lower in sites that have historically experienced heat waves. This aspect can in part explain why we observed a similar "overlapping" response of intertidal communities under ambient and warming temperatures. While here we used a generic estimate of body temperature for all species within a community, a further extension of this work would be to independently measure or model thermal history based on the body temperatures of each organisms in the community. Further research into community recovery would also allow for a more accurate interpretation of the role of local community adaptation under thermal stress.

Finally, our results also highlight a relevant role of geographical position in the BEF relationship. In fact, north sites were generally subjected to higher stress during aerial exposure regardless of whether they are exposed to ambient or extreme warming temperatures. These results led us to hypothesize that southern sites would be more vulnerable to extreme warming temperatures compared to northern sites. These results are consistent with previous studies suggesting geographically complex patterns of thermal stress in this region (Sarà et al., 2011).

Extreme warming temperatures may alter the structure of marine ecosystems by removing organisms from different species in food webs, which has a massive effect on evenness. Communities that are more even are more likely to sustain functionally redundant species, increasing the likelihood of absorbing a pulse perturbation. When evenness is low, a community's resistance to a disturbance may be lower since the chances that few dominant species are resistant to the perturbation are likely to be low (Allan et al., 2011; Hillebrand et al., 2008; Wittebolle et al., 2009). The positive BEF relationship found in this study emphasizes the importance of conserving biodiversity to maintain ecosystem functions in the face of climate change (Benkwitt et al., 2020; Isbell et al., 2015; Pires et al., 2018), implying that biodiversity conservation is critical for the long-term management of ecosystems.

5. Conclusions

In summary, our results supported a non-saturating BEF relationship in intertidal communities, providing further evidence that positive BEF relationships on ecosystems may be one of the few general rules in ecology. Our results also confirm the role of biodiversity in buffering stressful conditions generated by extreme high temperature events of climatic origin (Benkwitt et al., 2020; Isbell et al., 2015), with evenness as the better metric than functional diversity and species richness. Moreover, our results highlight a relevant role of short-term thermal history of body temperature on the responses of intertidal organisms under both ambient and extreme warming temperatures.

Despite its limitations, the regional-scale field experiments carried out in the shortest time possible, the use of intertidal communities without manipulating species composition, and the investigation of the effect of an extreme air warming temperature rather than water temperature, are the most innovative aspects of this study. To our knowledge, few BEF studies have been conducted in the central region of the Mediterranean Sea, where the effects of future and ongoing climate change, particularly extreme warming events, are pushing intertidal species beyond their physiological tolerance, and where changes in intertidal species survival and distribution have already been observed (Bevilacqua et al., 2021; Sarà et al., 2021). Knowing the BEF relationship in these situations is then crucial for preserving the biodiversity of intertidal systems. In this regard, our large regional field experiments allowed us to identify the conditions in this intertidal system that will sustain ecosystem functions in the face of both ambient and extreme climate events, which is a top priority for conservationists and practitioners.

CRediT authorship contribution statement

F.P.M., performed the experiment, identified seaweeds, analyzed the data, wrote the paper and lead the writing; C.G., performed the experiment, wrote the paper; M.C.M., wrote the paper; L.A., conceived and funded the experiment, wrote the paper; B.H., conceived the experiment and wrote the paper; G.S. conceived and funded the experiment, wrote the paper and lead the writing.

Declaration of competing interest

The authors state that they have no known competing financial or personal interests that could have seemed to affect the work reported in this study.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.160037.

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