ECOLOGY LETTERS

Ecology Letters, (2021) **24**: 1038–1051 doi: 10.1111/ele.13718

LETTER

Climate change transforms the functional identity of Mediterranean coralligenous assemblages

Daniel Gómez-Gras,[1]* Cristina Linares,[2] Maria Dornelas,[3] Joshua S. Madin,[4] Viviana Brambilla,[3] Jean-Baptiste Ledoux,[5] Paula López-Sendino,[1] Nathaniel Bensoussan[1] and Joaquim Garrabou[1]

Abstract

Quantifying changes in functional community structure driven by disturbance is critical to anticipate potential shifts in ecosystem functioning. However, how marine heatwaves (MHWs) affect the functional structure of temperate coral-dominated communities is poorly understood. Here, we used five long-term (> 10 years) records of Mediterranean coralligenous assemblages in a multi-taxa, trait-based analysis to investigate MHW-driven changes in functional structure. We show that, despite stability in functional richness (i.e. the range of species functional traits), MHW-impacted assemblages experienced long-term directional changes in functional identity (i.e. their dominant trait values). Declining traits included large sizes, long lifespans, arborescent morphologies, filter-feeding strategies or calcified skeletons. These traits, which were mostly supported by few sensitive and irreplaceable species from a single functional group (habitat-forming octocorals), disproportionally influence certain ecosystem functions (e.g. 3D-habitat provision). Hence, MHWs are leading to assemblages that are deficient in key functional traits, with likely consequences for the ecosystem functioning.

Keywords

Community structure, disturbance, functional change, functional diversity, functional ecology, reefs, stability, temperate, warming.

Ecology Letters (2021) **24**: 1038–1051

INTRODUCTION

Marine life is increasingly threatened by anthropogenic climate change (Smale *et al*. 2019). Global impacts such as ocean warming are altering the biology and ecology of many organisms, populations and species (Scheffers *et al*. 2016). As a consequence, community-level biodiversity changes are emerging in the oceans, with potentially far-reaching consequences for ecosystems' functioning (e.g. Poloczanska *et al*. 2016; Antão *et al*. 2020).

The natural processes (physical, chemical or biological) determining the movement or storage of energy and materials within an ecosystem or its self-maintenance over time are called ecosystem functions (Paterson *et al*. 2012). The joint effects of all individual functions determine the overall ecosystem functioning (Reiss *et al*. 2009). Abiotic (e.g. light, temperature, pH, nutrient) and biotic (e.g. biodiversity or species interactions) factors influence ecosystem functioning in multiple interconnected ways (Reiss *et al*. 2009). Yet, the role of biodiversity has traditionally been considered as highly influential and thus has been the focus of much scientific research (e.g. Hooper *et al*. 2005; Balvanera *et al*. 2006; Reiss *et al*. 2009). In recent decades, the emergence of trait-based approaches is providing new opportunities to understand how changes in community structure translate to changes in its functioning. Specifically, these approaches are shifting from the taxonomic perspective of traditional biodiversity–ecosystem function research to a functional one, and in doing so, proposing that changes in ecosystem function can be better estimated when considering the functional roles among species, as measured by their traits (e.g. McGill *et al*. 2006; Mokany *et al*. 2008; Mouillot *et al*. 2013; Madin *et al*. 2016; Hughes *et al*. 2018).

Two major complementary hypotheses link changes in trait composition to alteration of ecosystem function: the diversity and the mass ratio hypothesis. According to the diversity hypothesis (Tilman *et al*. 1997), both the species and their associated functional traits influence ecosystem processes through mechanisms such as complementary resource use. Therefore, variation in the range of functional traits in a given community (i.e. its functional richness; *Frich*) affect its functioning (Díaz & Cabido, 2001; Tilman, 2001). Alternatively, the mass-ratio hypothesis (Grime, 1998) states that the functional traits of the dominant species are the primary drivers of ecosystem function. Therefore, changes in community composition or species relative abundance may shift the community dominant traits (i.e. its functional identity; *FI*) and subsequently, its functioning (Mouillot *et al*. 2013; Weigel *et al*. 2016). Determining how the richness and mass-ratio of

[1]*Departament de Biologia Marina, Institut de Ciències del Mar (CSIC), Barcelona, Spain*
[2]*Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Institut de Recerca de la Biodiversitat (IRBIO), Universitat de Barcelona, Barcelona, Spain*
[3]*Centre for Biological Diversity and Scottish Oceans Institute, School of Biology, University of St, Andrews, St Andrews, UK*
[4]*Hawai'i Institute of Marine Biology, University of Hawai'i at Mānoa, Kaneohe, HI, USA*
[5]*Centro Interdisciplinar de Investigação Marinha e Ambiental (CIIMAR), Porto, Portugal*
**Correspondence: E-mail: danielgomez@icm.csic.es*

functional traits respond to ecological disturbances is therefore necessary to forecast their functional trajectories (Mouillot *et al.* 2011; Gagic *et al.* 2015). Furthermore, as some functions in the ecosystems are more likely to be influenced by key taxa rather than overall diversity patterns (e.g. bioerosion in oceanic reefs; Bellwood *et al.* 2003), the vulnerability of species or species' groups presenting key trait values needs to be also carefully considered (Bellwood *et al.* 2004; Bellwood *et al.,* 2019a,b).

Increasingly frequent and intense marine heatwaves (MHWs) have recently triggered devastating warming-induced mass mortality events worldwide, affecting a wide range of different species-rich benthic communities such as coral reefs, seagrass meadows or kelp forests (Wernberg *et al.* 2013; Hughes *et al.* 2017; Carlson *et al.* 2018; Smale *et al.* 2019). In the Mediterranean, these extreme warming events have recurrently impacted the coralligenous assemblages, which are endemic reefs home to approximately 10% of Mediterranean species (Cerrano *et al.* 2000; Ballesteros, 2006; Garrabou *et al.* 2009, 2019). Therefore, MHWs are likely causing changes in the structure and functioning of one of the most biodiverse systems in the Mediterranean. However, field surveys (e.g. Garrabou *et al.* 2009; Verdura *et al.* 2019) and aquaria thermotolerance experiments (e.g. Pagès-Escolà *et al.* 2018; Gómez-Gras *et al.* 2019) have suggested contrasting vulnerabilities to warming among co-occurring coralligenous species, in terms of tolerances to or regeneration after MHWs. This phenomenon, called 'response diversity' (Elmqvist *et al.* 2003), can act to stabilise functioning if the more vulnerable species are being replaced by functionally similar (i.e. 'redundant'), but more resistant species (Yachi & Loreau, 1999). On coral reefs, for example a mortality outbreak of the staghorn coral *Acropora cervicornis*, which occurred in Belize during the 1980s due to disease and high temperature, was partially compensated for by the previously uncommon, functionally similar and more thermally resistant lettuce coral, *Agaricia tenuifolia*, that became the main reef builder (Nyström, 2006). Further examples of this stabilising effect can be found in other marine (Steneck *et al.,* 2002; McLean *et al.* 2019) and terrestrial ecosystems (e.g. Walker *et al.* 1999; Stavert *et al.* 2017). However, if vulnerable species are not replaced, or are replaced by species that do not contribute similarly to a given ecosystem process, important functions are likely to be compromised (e.g. provision of 3D habitats, surface stability or benthic-pelagic coupling in the case of coral reefs), with potential detrimental consequences for the associated ecosystem services (Gili & Coma, 1998; Bellwood *et al.* 2003; Nyström, 2006; Cardinale *et al.* 2012).

In this study, we combined long-term (10–15 years) ecological data and *in situ* temperature data to examine MHW-induced functional changes in Mediterranean coralligenous assemblages. By quantifying multidimensional trait spaces, we investigated: (1) whether MHWs have driven fine-scale changes in their functional structure (i.e. *Frich* and *FI*), and (2) whether some functional groups (i.e. clusters of coarsely functionally redundant species sharing similar combinations of traits) are more vulnerable than others to MHWs, which may imply consequences for the maintenance of critical functions in the ecosystem. Our results provide empirical insights into MHW-driven functional changes in one of the most species-rich communities in the Mediterranean. Accordingly, this study takes us a step towards understanding the role of climate change as a driver of functional change in coral-dominated benthic assemblages in temperate regions.

MATERIALS AND METHODS

Monitoring sites

We used coralligenous assemblage data from five sites located within two marine protected areas (MPAs) in the NW Mediterranean Sea: the Port-Cros National Park and Scandola Natural Reserve (Table S1 & Figure S1 in Supporting Information). Three sites, one in Port-Cros (Gabin_par) and two in Scandola (Pzzu_par and Pzzinu_par), are exposed vertical walls dominated by the red gorgonian *Paramuricea clavata* (Risso, 1826). These sites range in depth from the 18 m of Pzzu_par to the 25 m of Gabin_par and Pzzinu_par. The other two sites (Pzzu_cor and Passe_cor) are sheltered in a marine cave at 18 and 29 m depth, respectively, in Scandola and are dominated by the red coral *Corallium rubrum* (Linnaeus, 1758). The sites are part of coralligenous monitoring programs and were selected for this study amongst all because of meeting the three following essential criteria. They were; (1) biologically monitored for at least a decade (i.e. Pzzu_cor; 2003–2018, Passe_cor; 2006–2018, Pzzinu_par; 2006–2016; Pzzu_par; 2006–2018 and Gabin_par; 1999–2009), (2) located within long-term established (> 40 years) and highly enforced MPAs and (3) involved in a long-term seawater temperature monitoring program, therefore allowing the characterisation of thermal regimes and potential exposure to MHWs during the study period.

Temperature data

The subsurface thermal environment of the two Mediterranean MPAs has been monitored over the past two decades as part of the T-MEDNet initiative (Bensoussan *et al.* 2019a; www.t-mednet.org). The local seawater temperature conditions were documented based on a standard protocol with temperature samples (accuracy +/- 0.21 °C) collected every hour at 5 m interval between the surface and 40 m depth. To analyse the local climatology of the five monitored assemblages, all corresponding in-situ temperature data (± 1 m with respect to biological surveys in every site except on those sites at 18 m) available until 2018 (Port-Cros: 1999–2018, Scandola: 2003–2018; see Fig. S2a–d), were retrieved from T-MEDNet and averaged at daily time scales. Since significant gradients of temperature (> 1 °C per metre) can be observed during summer between the 15 and 20 m depths in Scandola, and two of the monitored assemblages from this location were located at 18 m (i.e. Pzzu_cor and Pzzu_par), a linear interpolation from the 15 and 20 m data was used for these sites (Fig. S2d and e). Following Hobday *et al.* (2016) MHW detection method, we explored *in situ* exposure to MHW conditions in every assemblage in terms of duration and intensity, and over the entire biological surveying periods (i.e. Pzzu_cor; 2003–2018, Passe_cor; 2006–2018, Pzzinu_par; 2006–2016; Pzzu_par; 2006–2018 and Gabin_par; 1999–2009). Specifically,

MHWs were considered as discrete prolonged periods (at least 5 days) of anomalously warm seawater temperature (>90th percentile of the *in situ* climatology), based on the definition provided by Hobday *et al.* (2016). However, since organisms living in coralligenous assemblages are able to tolerate the normal seasonal temperature range characteristic of Mediterranean waters (i.e. 10–23 °C) (Ballesteros, 2006), and we were interested in exposure to extreme conditions, we only considered MHWs occurring during the warm period of the year (June to November; JJASON). Exposure duration (proxy for chronic thermal stress) was estimated as the cumulative number of consecutive MHW days registered in a given year, whereas exposure intensity (proxy for acute thermal stress) was calculated as the highest temperature reached during MHWs (Bensoussan *et al.* 2019b).

Finally, since we were interested in detecting if the potential occurred changes in functional structure were attributable to MHWs, we classified sites into non-impacted or MHW-impacted prior to conducting the functional analysis. To do so, we plotted years exhibiting MHW conditions in each site along the intensity/duration dimension against a thermotolerance response curve. The thermotolerance response curve was built according to the combined thermotolerance features (i.e. days until the first signs of necrosis at different temperatures) of *P. clavata* and *C. rubrum* (See Appendix S1 for methodology & Fig. S3), which are among the most sensitive species to heat stress in the coralligenous (Torrents *et al.* 2008; Crisci *et al.* 2017). Thus, this procedure allowed us to classify sites into MHW-impacted and non-impacted depending on how likely they had suffered a heat stress strong enough to induce mortality in local coralligenous assemblages (See Results Fig. 1).

Sampling design of ecological data

After discriminating MHW-impacted and non-impacted sites, photographs of the corresponding sites were analysed at three different years or time points (T1, T2, T3) over the entire temperature/biological monitoring periods (i.e. Pzzu_cor; 2003, 2011 and 2018, Passe_cor; 2006, 2011 and 2018, Pzzinu_par; 2006, 2011 and 2016; Pzzu_par; 2006, 2011 and 2018 and Gabin_par; 1999, 2007 and 2009). To minimise any potential effect of seasonality, only surveys occurring during the same period of the year were considered for each site (end of summer vs. autumn for Port-Cros and Scandola respectively). A total of 24 photographic quadrats of 25 × 25 cm (replicates) were analysed for each site and temporal point resulting in 360 pictures in total. The sampling unit (625 cm^2 per replicate) was selected following Kipson *et al.* (2011) and Casas-Güell *et al.* (2015). The percent cover of the different macrobenthic sessile species was calculated in each quadrat by overimposing 100 stratified random points and identifying the underlying species to the lowest possible taxonomic level, using Photoquad photoquadrat (Trygonis & Sini, 2012).

Building the coralligenous trait space

The multidimensional trait space for coralligenous assemblages was quantified using the same functional traits that have been previously used to characterise changes in ecosystem function across CO2 gradients in the same Mediterranean communities (Teixidó *et al.* 2018). Specifically, we used twelve traits that are likely to influence ecosystem functions (*sensu* Paterson *et al.* 2012), namely; morphology, growth rate, physical defence (calcification), maximum longevity, age at

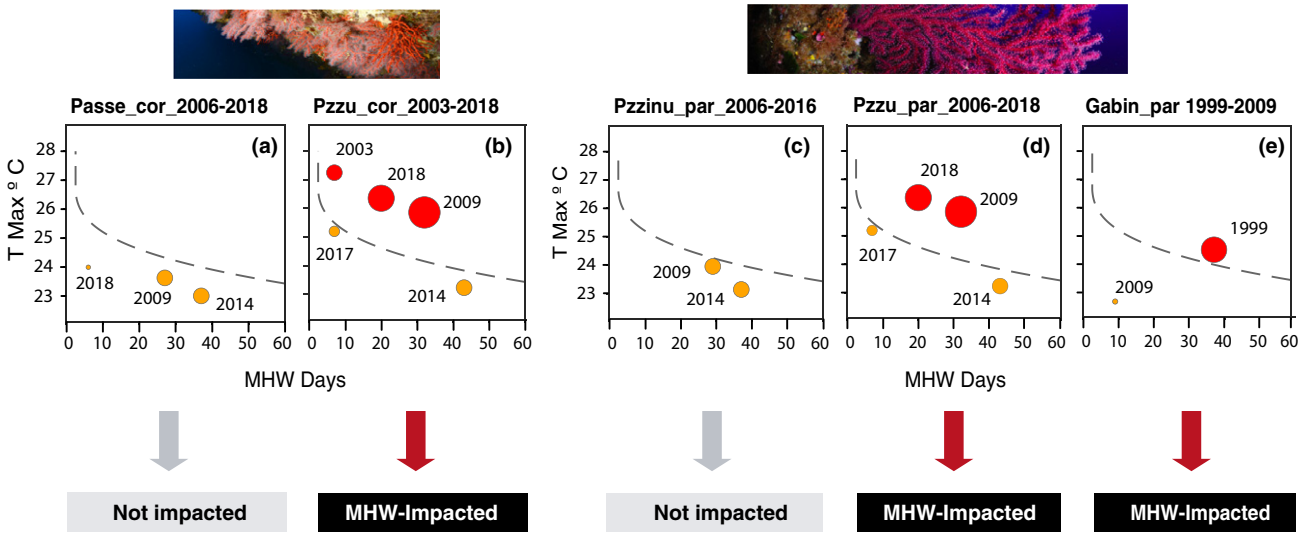

Figure 1 Yearly exposure to MHW conditions in the five study sites and over the monitored periods. Circles represent detected MHWs, and their position represents the intensity and duration of the event. The dashed line is the same for all sites and represents a proxy thermotolerance response curve for coralligenous assemblages. This curve was calculated by fitting the combined thermotolerance (i.e. days until the first signs of necrosis at different temperatures) of *P. clavata* (5 temperature data points) and *C. rubrum* (2 temperature data points) into the single combined curve (see Methods section, Appendix S1 and Fig. S3 for detailed information). Circles over the curve (in red) are years in which severe MHWs occurred, likely inducing mortality on the subjacent coralligenous assemblages. Circles below the curve (in orange), indicate years in which mild MHWs occurred, not likely inducing mortality on coralligenous species. Thus, only sites with circles over the line were classified as MHW-impacted. Circle sizes are merely illustrative and are proportional to their standardised position with respect to x and y axis, thus increasing in size towards the upper right corner of the plot.

reproductive maturity, coloniality, height, width, feeding strategy, major photosynthetic pigment, epibiotic preference and energetic resource (See Table 1 for details on their relation to ecosystem function).

Trait values were selected as the most accurate average description of species-specific traits (see Appendix S2 & Table S5 for details). As some species show plasticity in the expression of certain traits and we were interested in global comparisons across species rather than on intraspecific variation, we applied a fuzzy coding procedure based on coarse ranked and nominal categories (Cheven *et al.* 1994). By using this semiquantitative procedure, we increased the amount of intraspecific variability accounted for in our study, while facilitating the comparison across highly divergent benthic groups (e.g. algae, corals, sponges, etc) and the infilling of data gaps (Weigel *et al.* 2016; Teixidó at al. 2018). Overall, 111 taxonomic units were classified into 52 functional entities (FEs), which are defined as groups of species with an identical combination of categorised/ranked trait values (Teixidó *et al.* 2018). Then, we performed a Principal Coordinate analysis (PCoA) based on a Gower dissimilarity matrix to create multi-dimensional trait spaces in which FEs of each assemblage and temporal point were positioned according to their differences in traits values. The Gower dissimilarity index was chosen because it allows for mixed types of data (Laliberté & Legendre, 2010). Four PCoA dimensions were retained in order to balance the amount of explained variation (75%), the computational times and a low mean squared-deviation index values (mSD = 0.003).

Functional richness (*Frich*) and functional identity (*FI*)

The characterisation of temporal changes in the functional structure of coralligenous assemblages at a fine level of trait-based dissimilarity was conducted by quantifying *Frich* and *FI* (Mouillot *et al.* 2013). Since temporal changes in these metrics were quantified for each assemblage separately (and thus at the same depth over time), our analyses allowed for testing if MHWs significantly altered the functional structure regardless of any potential confounding role of depth.

Frich was calculated as the 4D convex hull volume of the multidimensional trait space previously generated for each assemblage and temporal point (Cornwell *et al.* 2006). A null model was then used to test whether the observed values of *Frich* significantly differed from the null hypothesis that *Frich* of each assemblage remained constant across time. In particular, we simulated 9999 random assemblages for each monitored site and time point, while keeping the number of FEs constant over time within each site's pool (Teixidó *et al.* 2018). The observed values of *Frich* were then compared with the simulated random ones using a bilateral test, with a significant level (α) of 5%.

FI was calculated as the abundance-weighted centroid of the community in the multidimensional trait space (Mouillot *et al.* 2013). Specifically, the position of each FE in the trait space was weighted by its abundance and then averaged in the total assemblage pool. The resulting community mean value of *FI* for each site could be then plotted in function of time to show temporal trajectories across trait space. Finally, to test whether the observed values of *FI* significantly differed in each site from the null hypothesis that the abundance-weighted centroid of the community remained constant across time, we conducted nonparametric analysis of variance PERMANOVA (permutational multivariate analysis of variance) for each site with time as a fixed factor.

Broad clustering classification of functional groups (FGs)

The quantification of *Frich* and *FI* based on the computation of FEs allowed us to explore changes in the functional community structure at a fine level of trait-based dissimilarity. Yet, complementing the fine functional characterisation with a broader classification analysis allows to further explore if there are some FGs in which functional redundancy (FR) and response diversity (RD) might be critically lacking (McWilliam *et al.* 2020). That is, if some FGs (i.e. clusters of coarsely functionally redundant species that share similar combinations of traits and therefore are expected to contribute similarly to the ecosystem functioning), could be more vulnerable than others to warming. We conducted a Partition Around Medoids (PAM) clustering analysis to derive broader aggregations of species in trait space, and selected the optimal number of clusters ($k = 8$) using the average silhouette width criterion (Kaufman & Rousseeuw, 1990; see Fig. S5). Then, we explored the way in which FR was distributed among clusters by calculating the number of species packed within each cluster in each site and time point (Laliberté *et al.* 2010). Clusters formed by many species were considered as functionally redundant, as the loss of some species could be functionally compensated by others. By contrast, clusters formed by one species were considered as highly vulnerable, as they are formed by key taxa that are functionally irreplaceable. Eventually, changes in the percent cover of clusters across time were calculated for each monitoring site. Declining clusters following MHWs (functional 'losers'), were considered to have a lack of RD, because their constitutive taxa declined with no alternate responses by functionally similar species.

RESULTS

MHW-impacted vs. non-impacted sites

MHWs were detected in every site along the monitoring periods; a minimum of two times in Pzzinu_par and Gabin_par, and a maximum of five times Pzzu_cor (Fig. 1a–e). However, the event intensity in terms of duration and maximum temperature, which drives the impact on the local biota, varied greatly among sites. In particular, none of the MHWs registered in Passe_cor and Pzzinu_par exceeded the thermotolerance curve used as a proxy for the coralligenous (Fig. 1a and c). These sites should not have suffered major impacts of warming along the monitoring periods and therefore were considered as non-impacted. By contrast, Pzzu_cor, Pzzu_par and Gabin_par suffered at least one intense MHW during which assemblages were potentially affected, and therefore were considered as MHW-impacted.

Table 1 Description of the 12 traits used to generate the multi-dimensional trait space

Trait (Ranked/ Nominal)	Categories	Relation to ecosystem functions*
Morphology (Nominal)	(a) Boring, (b) Encrusting, (c) Filaments, (d) Stolonial, (e) Foliose Erect, (f) Articulated, (g) Corymbose, (h) Cup-like, (i) Mass.-Encr., (j) Mass.-Erect (k) Mass.-Hem. (l), Tree-like	- Determines structural complexity and 3D habitat provision, which influences water flow circulation, food and sediment retention, and the creation of micro-habitats for the settlement and shelter of co-occurring species (Gili & Coma, 1998; Darling et al. 2017). - Influences the ability to withstand disturbance (Loya *et al.* 2001). - Influences the uptake/release of energy or organic matter depending on surface/volume ratios, thus determining the competitive ability for space, light and food, the benthic-pelagic coupling (Zabala & Ballesteros, 1989).
Coloniality (Ranked)	(1) Solitary, (2) Colonial/Gregarious	- Influences mortality risk and competition for space. Growing as a colony reduces whole colony mortality chances by spreading risk among sub-units and by favouring recovery of fragments (Jackson, 1977, 1979).
Maximum longevity (Ranked)	(1) Very low (weeks), (2) Low (months; < 12), (3) Medium (1–3 years), (4) High (3–20 years), (5) Very High (>20 years)	- Proxy for investment in long-term maintenance and survival, and therefore, carbon storage and assemblage stability (Körner, 2017; Craven *et al.* 2018). - Proxy for provision of long-term biological habitats.
Maximum height (Ranked)	(1) Very low (< 1 cm / 1cm), (2) Low (2–5 cm), (3) Medium (5–20 cm), (4) High (20–50 cm), (5) Very High (>50 cm)	- Proxy for habitat three-dimensionality and disruption of water flow, what affects particle deposition and prey capture (Gili & Coma, 1998). - Influences competition for space and resources, predation risk and energy demand. Larger colonies have a more prominent role in benthic − pelagic coupling and in biogeochemical cycles (Zabala & Ballesteros, 1989; Rossi *et al.* 2016)
Maximum width (Ranked)	(1) Very low (< 1 cm / 1cm), (2) Low (2–5 cm), (3) Medium (5–20 cm), (4) High (20–50 cm), (5) Very High (>50 cm)	- Proxy for competition for space and resources, predation risk and energy demand. Larger colonies have a more prominent role in benthic − pelagic coupling and in biogeochemical cycles (Zabala & Ballesteros, 1989; Rossi *et al.* 2016).
Epibiosis preference (Ranked)	(1) Never, (2) Facultative, (3) Obligate	- Epibionts colonise living surfaces, substantially modifying the basibiont-environment interactions (e.g. transference of energy or matter). Thus, they may reduce their fitness, and subsequently, the assemblage stability when structural species are affected (Wahl, 2008).
Energetic resource (Ranked)	(1) Autotroph, (2) Auto-heterotroph, (3) Heterotroph	- Determines primary production, trophic interactions, benthic-pelagic coupling, nutrient cycling and the energy transfer in food webs (Round, 1984; Gili & Coma, 1998).
Feeding strategy (Nominal)	(a) Primary producer, (b) Active filter feeder w. cilia, (c) Active filter feeder by pumping, (d) Passive filter feeder, (e) Mixture, (f) Saprophytic	- Determines trophic interactions, benthic-pelagic coupling, nutrient cycling and the energy transfer in food webs (Round, 1984; Gili & Coma, 1998).
Major photosyn. pigment (Nominal)	(a) None, (b) Chl a/b (e.g. green algae), (c) Chl a/c, Fucoxanthin, (e.g. brown algae), (d) Chl a, Phycocyanin, Phycoerythrin (e.g. red algae), (e) Chl a, Phycocy-anin (Cyanobacteria), (f) Dinoflagellathed, (g) Mix. (e.g. turf)	- Determines light harvesting capability in relation to the light availability, and therefore, the primary production of the ecosystem (Round, 1984).
Age at reproductive maturity (Ranked)	(1) Very low (weeks), (2) Low (months; < 12), (3) Moderate (1–5 years), (4) High (> 5 years)	- Proxy for investment in long-term maintenance and survival during the first stages of the life cycle. By investing in long-term survival, late-reproducers increase mean biomass production relative to the standard deviation of biomass over time, enhancing assemblage stability (Craven *et al.* 2018).
Growth rate (linear extension in cm/ year^{-1}) (Ranked)	(1) Extreme slow (< 1cm* year^{-1}) (2) Slow (~ 1 cm * year $^{-1}$), (3) Moderate (1–5 cm * year $^{-1}$), (4) High (5–10 cm * year $^{-1}$), (5) Very High (> 10 cm * year $^{-1}$)	- Fast-growers have less investment in maintenance (i.e. energy and material storage) and defences. Thus, they typically present lower mean biomass production relative to the standard deviation of biomass over time, which reduces assemblage long-term stability (Craven *et al.* 2018).

(continued)

Table 1 (continued)

Trait (Ranked/ Nominal)	Categories	Relation to ecosystem functions*
Physical defenses (Nominal)	(a) Non-calcifier, (b) Non-calc. spicules, (c) Calc. spicules and sclerites, (d) Carbonate w. discontinuities, (f) Continuous Carbonate, (g) Mixture	- Proxy for carbonate production - Influence ecosystem stability by playing a primary role in defence against predation and in the provision of structural strength, which determines the formation of long-term 3D habitats (Zabala & Ballesteros, 1989; Gili & Coma, 1998).

The categories (ranked/nominal) used for each trait are shown, as well as their ecological relevance for the functioning of coralligenous assemblages. Ecosystem functions are considered here as the natural processes determining the movement or stockage of energy and materials within an ecosystem or its relative stability over time; Paterson *et al*. 2012). Table adapted from Teixidó *et al*. 2018.

Trends of functional richness (*Frich*)

The Principal Coordinate Analysis (PCoA) of the coralligenous trait space based on 12 functional traits and 111 taxonomic units detected across all sites (see Table S2 for detailed information on species presence and cover) revealed up to a 75% of variation condensed in four dimensions, of which 54% (37 and 17%, respectively) were explained in the first two. Considering this maximum possible coralligenous trait-space (*Frich* = 1; grey polygon in Fig. 2a–o), the site-specific relative values of *Frich* differed across sites but remained remarkably stable through time (Fig. 2a–o). For instance up to a 48% difference was observed between Gabin_par_2007 (*Frich* = 0.38) and Pzzu_Par_2018 (*Frich* = 0.86), reflecting a wide range of functional heterogeneity among different coralligenous assemblages. In contrast, the maximum observed temporal difference was a 6% decay in the occupied trait space occurred in Pzzinu_par between 2011 (*Frich* = 0.73) and 2018 (*Frich* = 0.67). Accordingly, no significant differences through time for any of the monitored sites were observed (Fig. 2p–t). Based on *Frich*, MHW-impacted sites remained as stable over time as those not impacted by MHWs.

Trends in functional identity (*FI*)

The *FI* of all assemblages at T1 presented a similar abundance-weighted centroid of the community in the trait-space (represented as red crosses in Fig. 3a–e), indicating that, in stable conditions, dominant species driving ecosystem function in coralligenous assemblages present similar traits; high longevity, big size, coloniality, slow growth, heterotrophic filter-feeding mechanisms or complex morphologies (e.g. arborescent or massive) typical of habitat-forming macro-invertebrates (Fig. 3h–l). When exploring temporal trends, a long-term significant progressive shift in the *FI* across the trait-space (PERMANOVA, $P < 0.05$; see Table S3) occurred in all the MHW-impacted assemblages (Fig. 3b, d–e) but not in the non-impacted ones (Fig. 3a and c), which remained remarkably stable over the entire monitored periods (PERMANOVA, $P > 0.05$; see Table S3). In the case of the impacted *C. rubrum*-dominated assemblage Pzzu_cor (Fig. 3a and b), the *FI* shifted along the PCoA axis 2 from a dominance of long-lived, tall, width or slow-growing taxa such as some habitat-forming sponges and octocorals to short-lived taxa with small size, epibiotic strategies and fast growth such as some hydrozoans, polychaetes or encrusting bryozoans (Fig. 3f). In contrast, in the MHW-impacted *P. clavata*-dominated assemblages (Fig. 3c–e), the *FI* shifted along the PCoA axis 1 from colonial, heterotroph, physically resistant and slow-growing taxa with arborescent, massive or corymbose morphologies typical of sessile habitat-forming macro-invertebrates to faster growing, individual, soft and autotroph taxa with foliose, filamentous or articulated morphologies typical of weedy macroalgae (Fig. 3g).

Functional groups (FGs) in coralligenous assemblages

The broad clustering characterisation of the coralligenous assemblages resulted in 8 optimum functional clusters distributed along the trait-space (Fig. 4a and Table S4). Each of them represents a FG constituted by different organisms that present similar combinations of functional traits and therefore are assumed to influence ecosystem functioning similarly. Cluster 1 is mainly formed by colonial, massive, long-lived and heterotroph species that grow at a moderate rate and pump water as the main feeding strategy. Cluster 2 present traits that are ubiquitous in many Mediterranean bryozoans but also in some polychaetes, such as relatively small sizes, heterotrophy, active ciliated feeding or the presence of continuous carbonated skeleton. Cluster 3 is mainly constituted by encrusting red calcareous algae that form the basal layer that cements the coralligenous assemblages. Cluster 4 includes a mixture of taxa that are mostly colonial, heterotroph, with low or very low height, such as some encrusting bryozoan, ascidians and hydrozoans. Clusters 5 and 6 refer to autotrophs primary producers that grow and reproduce moderately fast and present foliose, stolonifera or filamentous morphologies typical of macroalgae. Cluster 7 groups mostly solitary corals with hard continuous carbonated skeletons, small sizes, slow growths and passive filter feeding strategies. Cluster 8 includes taxa with high longevity and height, arborescent morphologies, late reproduction, heterotrophy or high mechanical resistance based on semi-rigid skeletons formed by calcareous sclerites.

The clustering characterisation of the coralligenous assemblages also revealed a disequilibrium in the way functional redundancy (FR) is packed within the eight functional clusters. While some are highly redundant and involved many different organisms (up to 24) in all sites (e.g. Clusters 1 or 2), others such as the Cluster 8 are only represented by one or

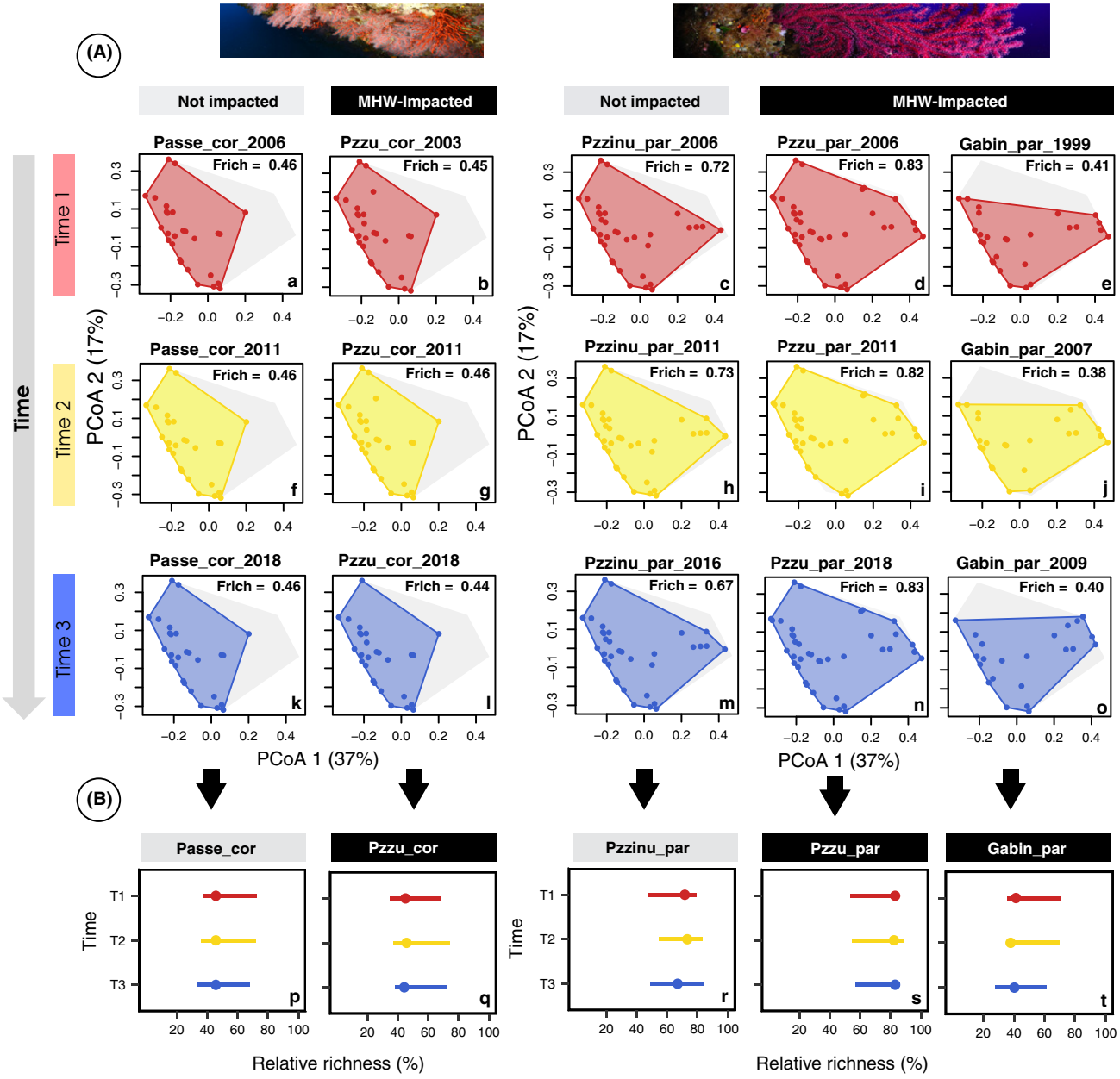

Figure 2 (A) Temporal changes in the % of trait space occupied (*Frich*; represented as coloured polygons) in non-impacted (a, f, k; c, h, m) versus MHW-impacted sites (b, g, l; d, i, n; e, j, o) for both *C. rubrum* and *P. clavata* dominated assemblages. The global trait space for all species found in this study is represented as a grey polygon in each panel (100% of space occupied / *Frich* = 1). Null models of *Frich* across time in each specific site are shown in (B), from (p) to (t) panels. The points indicate the observed values of *Frich* whereas bars represent the 95% confidence interval of expected values under a null model simulating a random sorting of species from a given site pool but in which the number of functional entities over time has been maintained.

two species, which make them especially vulnerable (Fig. 4b–f). Regarding the temporal trends, the number of species within each cluster remained relatively constant over time in all assemblages, with an overall variation of 1 ± 2 and 2 ± 2 (mean $\pm$ SD) species per cluster in non-impacted and MHW-impacted assemblages respectively (Fig. 4g–k). Finally, when looking at temporal changes in % cover of each functional clusters in each site, cluster 8 was the only one which was systematically reduced in all MHW-impacted assemblages, with a minimum reduction of 65% and a maximum of 93% (Fig. 4l–p and Fig. S7).

DISCUSSION

MHWs linked to climate change have recurrently impacted Mediterranean temperate reefs in recent decades, leading to mass mortality events and changes in patterns of biodiversity (Cerrano *et al.* 2000; Garrabou *et al.* 2009, 2019; Verdura *et al.* 2019). Here, we show that MHWs have also induced marked changes in functional trait composition that are likely to impact ecosystem functioning.

We examined abundance distributions of functional entities (species sharing identical combinations of traits) across the

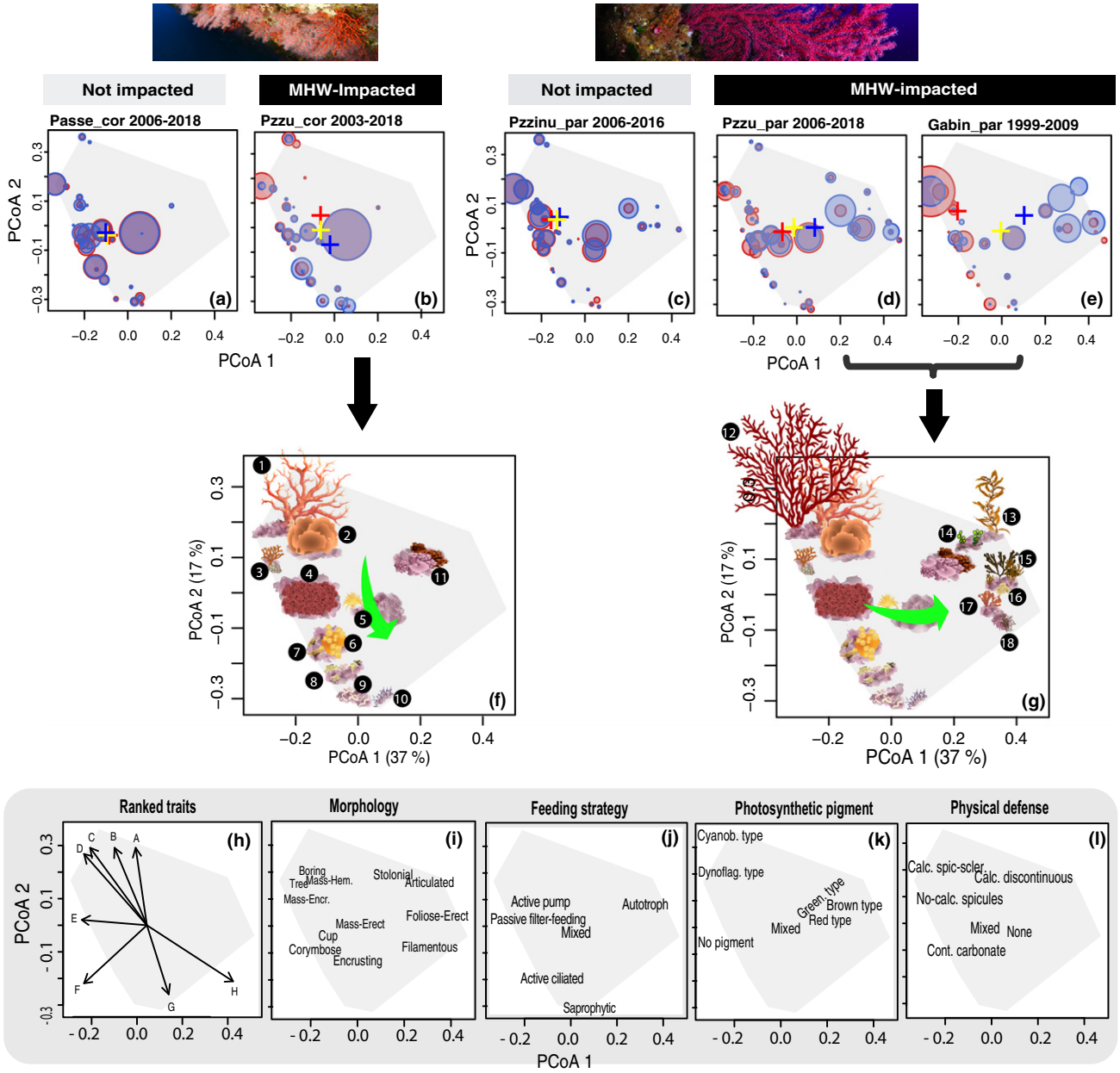

Figure 3 Temporal changes in *FI* across the trait space in non-impacted (a and c) versus MHW-impacted sites (b, d and e) for the *C. rubrum* and *P. clavata* dominated assemblages. For each site, the abundance distribution of FEs at time 1 (size of red circles) has been plotted against the abundance distribution of FEs at time 3 (size of blue circles). Despite circles have only been plotted for Times 1 and 3 (see Fig. S6 for extended version), *FI* values are also shown for Time 2 as follows; red cross (*FI* at Time 1), yellow cross (*FI* at Time 2) and blue cross (*FI* at Time 3). A schematic representation of the functional change that MHW-impacted sites suffered for *C. rubrum* and *P. clavata* dominated habitats is shown in (f) and (g) respectively. Images of coralligenous organisms have been added to help in the visualisation (1; *Corallium rubrum*, 2; *Agelasoroides*, 3; *Myriapora truncata*, 4; *Crambe crambe*, 5; *Leptopsammia pruvoti*, 6; *Parazoanthus axinellae*, 7; *Reteporella grimaldii*, 8; Encrusting bryozoans, 9; Serpulids, 10; Hydrozoans, 11; Corallinales, 12; *Paramuricea clavata*, 13; *Sargassum sp*; 14; *Caulerpa cylindracea*; 15; *Dyctiota sp*, 16; *Padina pavonica*, 17; *Erythroglossum* type; 18; algal turf. Panel (h) shows the direction and longitude (importance) of the vectors representing the eight ranked traits, namely; (A) height, (B) width, (C) maximum longevity, (D) age at reproduction, (E) coloniality, (F) heterotrophy, (G) epibiosis preference and (H) growth rate. (i–l) represent the distribution across the trait space of the 4 categorical traits; (i) morphology, (j) feeding strategy, (k) major photosynthetic pigment and (l) physical defences.

trait space and found that, whereas non-impacted coralligenous assemblages maintained their functional richness (range of traits values) and functional identity (dominant trait values) through time, MHW-impacted assemblages exhibited shifts in their functional identity. In particular, MHWs decreased the abundances of taxa with large sizes, arborescent and massive morphologies, coloniality, high physical defences, slow-growing and long-lived life histories or heterotrophic filter-feeding strategies. For benthic systems such as tropical and temperate reefs, these are traits that confer important ecosystem

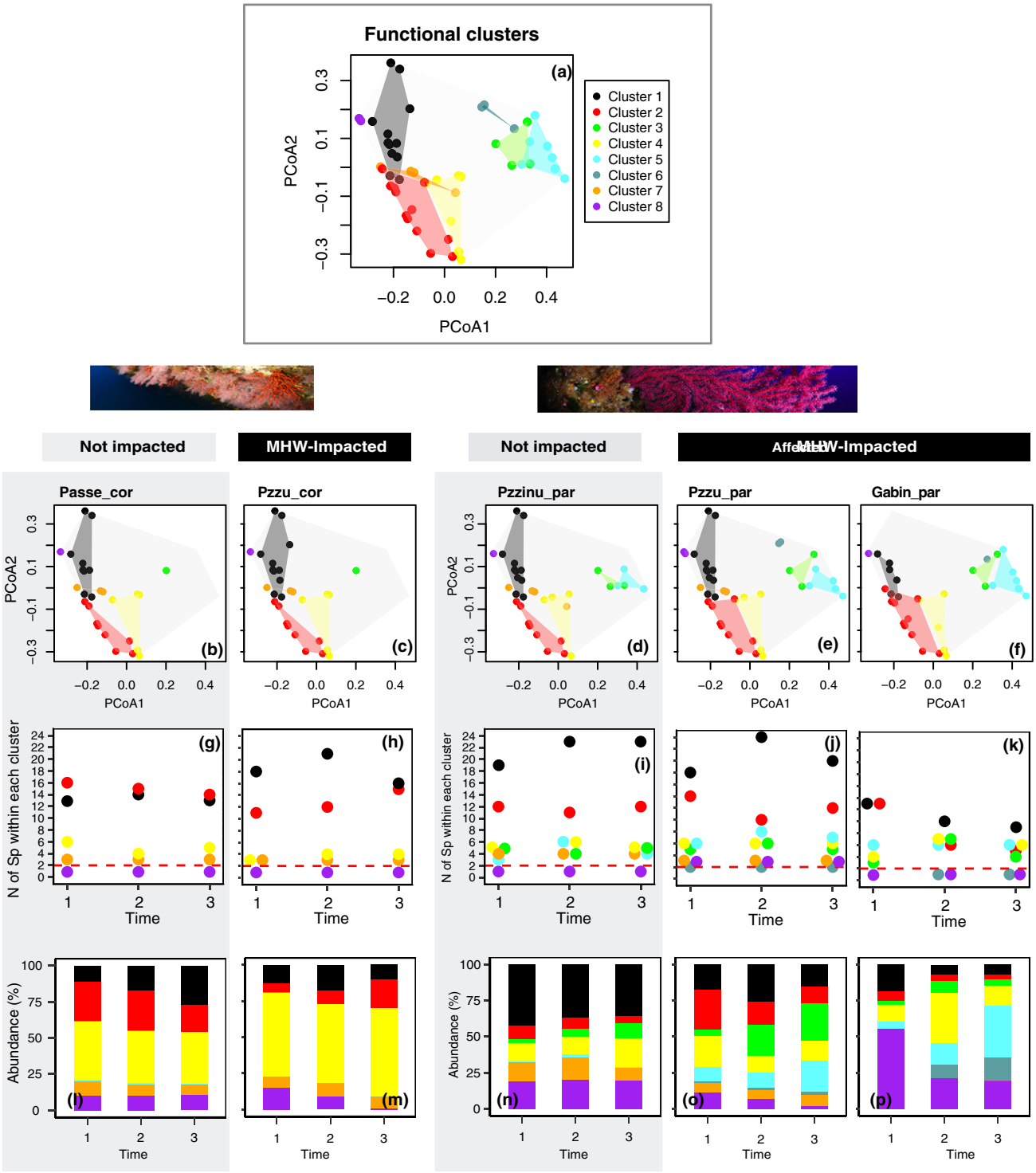

Figure 4 (a) Results from the PAM clustering analysis of the total pool of coralligenous species. The clusters (functional groups) found in each site are shown from (b–f), whereas the number of species per cluster (functional redundancy) in each temporal point are shown from (g–k). Clusters formed by many species are considered functionally redundant, as the loss of some species could be functionally compensated by others. By contrast, clusters formed by one species (under the red dashed line) are considered highly vulnerable, as they are functionally irreplaceable. For clarity reasons, only clusters representing more than 1% cover were shown in (g–k). Panels (l–p) show the temporal changes in abundance for each functional cluster in each site. Patterns of cluster 8 can be seen in more detail in Fig. S7.

functions, including the provision of habitat structure, nutrient cycling, carbon storage or benthic pelagic coupling (Gili & Coma, 1998; Loya *et al.* 2001; Graham & Nash, 2013; Darling *et al.* 2017; Paoli *et al.* 2017; Coppari *et al.* 2019). Thus, their decline in MHW-impacted assemblages in benefit of other traits (e.g. small sizes, fast-growing and reproduction,

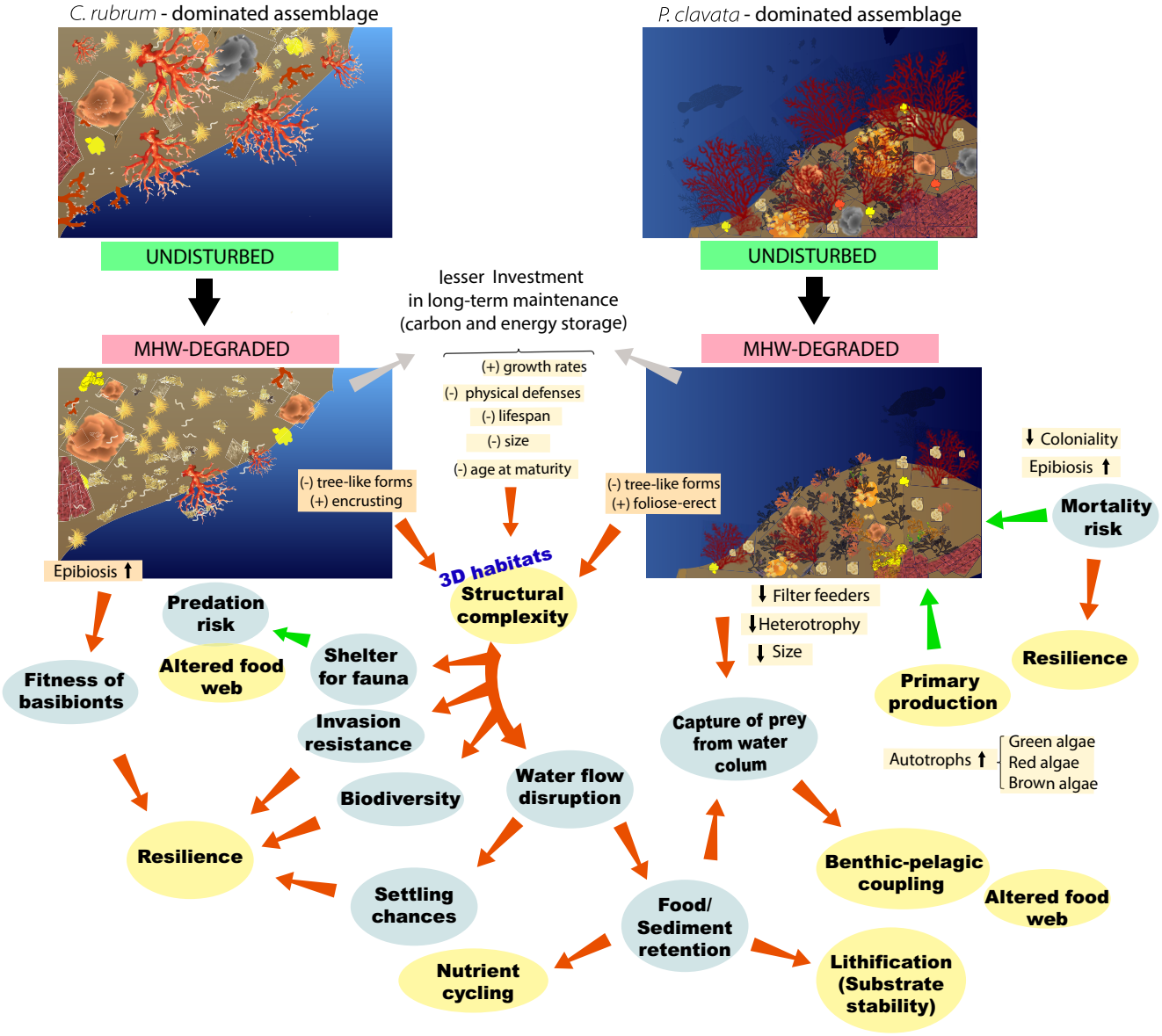

Figure 5 Schematic representation of functional traits shifts (light yellow boxes) observed in MHW-impacted *C. rubrum* and *P. clavata* dominated assemblages and their potential consequences for different ecological processes (in grey bubbles) and their associated ecosystem functions (in yellow bubbles). Red arrows indicate a reduction of a given process or function while green arrows represent an increase.

epibiotic strategies, less complex encrusting and foliose morphologies, less calcification or autotrophic photosynthetic strategies) may likely lead to changes in the ecosystem functioning (Figure 5). For instance a decrease of large, colonial, calcifying, morphologically complex, or slow-growing, long-lived organisms that have a high investment in long-term maintenance (e.g. arborescent corals, massive sponges or erect bryozoans) is likely to lead to reductions in the creation of three-dimensional, long-term, biogenic habitats that could also store carbon for decades (Darling *et al.* 2017; Coppari *et al.* 2019). In benthic ecosystems, the three-dimensionality of organisms plays a fundamental role in the organisation, function and resilience. It has been associated to positive effects on biodiversity (e.g. by ameliorating physical and biological stresses for the associated species), productivity, invasion resistance or stability over time (Angelini *et al.* 2011; Ponti *et al.* 2014, 2018; Darling *et al.* 2017; Verdura *et al.* 2019; De la Torriente *et al.* 2020). Moreover, since structural complexity determines water flow disruption, its reduction in MHW-impacted assemblages may minimise the time that suspended particles remain close to the benthos, depleting prey capture chances, larval settlement probabilities and sedimentation, and thus also the benthic-pelagic coupling and nutrient cycling (Gili & Coma, 1998). Similarly, since heterotrophic filter feeders significantly interact with the water column by depleting food particles and sediments and by transferring energy and nutrients from the water column to the benthos, their decrease in some impacted assemblages may also reduce the benthic-pelagic coupling, the nutrient cycling, the carbon storage, the energy transfer through the food webs or the lithification processes that contribute to the building up of the coralligenous structure (Cloern 1982; Officer *et al.* 1982;

Marshall, 1983; Kimmerer *et al*. 1994; Gili & Coma, 1998). The increased abundance of epibiotic organisms in some impacted assemblages may also hinder the assemblage resilience, since it may lead to the reduction of the resistance and recovery capacity of structural species. In particular, an increase in epibiosis may reduce the fitness of the overgrown organisms by disrupting the energy and material fluxes between their surfaces and the environment (Wahl, 2008). Likewise, the observed increase in ruderal organisms with fast life-history strategies (e.g. algal turfs or weedy macroalgae) may contribute to a rapid colonisation of free spaces after MHWs, thus potentially hindering the recruitment and recovery of the previously dominant macro-invertebrates and the overall assemblage resilience (Kuffner *et al*. 2006; Linares *et al*. 2012).

Overall, the observed MHW-driven changes in functional identity suggest that environmental filtering is taking place with particular functions being gradually reduced (losers), in detriment of others (winners). This indicates a limited capacity for response diversity and functional redundancy for maintaining the functioning in MHW-impacted coralligenous assemblages (McWilliam *et al*. 2020). Interestingly, our clustering analysis suggests that the observed changes in functional identity could be mostly the consequence of the lack of both functional redundancy and response diversity in a single functional group (FG); the Cluster 8 grouping the habitat-forming octocorals. In fact, whereas most FGs were highly redundant and were represented by many species (up to 24 in some cases), Cluster 8 was no redundant and only consisted of one species in most sites. Such lack of redundancy in an abundant cluster indicates that the constitutive species may present unique traits that may contribute disproportionally to the ecosystem functioning and stability (Ellison *et al*. 2005). Therefore, if the species are also highly vulnerable and get their abundance reduced, no functional compensation will occur and serious detrimental consequences for the overall ecosystem functioning may unfold (Bellwood *et al*. 2003; Nyström, 2006). Unfortunately, Cluster 8 was not only low in redundancy, but low resistant as well. This FG exhibited collapsing trajectories in coverage (from 65 to 93% reductions) in all MHW-impacted assemblages (Fig. 4l-p & Fig. S7). Consequently, although all the other FGs and their underlying ecosystem functions count on certain degree of insurance against MHWs, the quality of those functions that are disproportionately influenced by Cluster 8 (e.g., provision of long-term 3D habitats, the benthic-pelagic coupling, the nutrient cycling, the resilience, or the long-term carbon storage) might be highly compromised. For instance, although the increasingly dominant erect macroalgae could provide three-dimensionality in some MHW-impacted assemblages, the function will presumably be of less quality and less durability than when the larger, calcified and longer-lived species from Cluster 8 used to dominate. Similarly, the emergent encrusting sponges or bryozoans may partially replace the filtering role of the collapsing habitat-forming octocorals. Yet, not only the type of captured prey would be different, but the overall associated lesser structural complexity would likely reduce their capturing rates as well, affecting the amount of energy and matter transferred from the water column.

Overall, our analyses at different levels of trait-based dissimilarity show MHW-induced changes in community structure to assemblages that are now deficient in key functional traits. Similarly to what has been observed in tropical coral reefs (e.g. Hughes *et al*. 2018), our results indicate that MHWs are likely inducing severe changes in the ecosystem functioning of Mediterranean temperate reefs. Given the predicted increase in the frequency and intensity of MHWs (Oliver *et al*. 2019), identifying and preserving the mechanisms of reef stability that maintain essential functions and services is critical (Bellwood *et al*. ,b2004, 2019a; Hughes *et al*. 2018). Here, we have shown that the functional stability (considered here as the maintenance of functional structure over time in terms of both functional richness and identity, and thus of what functions are in the system and how they are performed) of Mediterranean coralligenous assemblages can be highly compromised by the decline of just few pivotal species with unique trait values. Thus, if we aim to preserve these temperate reefs in a way in which their essential ecological functions are maintained, further efforts will be needed to; i) globally reduce CO2 emissions and ii) further investigate the effectiveness of ocean-based solutions that could promote the resilience of their key habitat-forming species to MHWs (e.g. the operationalisation of a climate-responsive design and management of a fully protected network of MPAs in the Mediterranean; Gattuso *et al*. 2018; Bates *et al*. 2019).

ACKNOWLEDGEMENTS

We acknowledge the funding of the Spanish government through the 'Severo Ochoa Centre of Excellence' accreditation (CEX2019-000928-S). This research has also been partially funded by the HEATMED project (RTI2018-095346-B-I00, MCIU/AEI/FEDER, UE), Interreg Med Programme (Projects MPA-ENGAGE; 5216 | 5MED18_3.2_M23_007 and MPA-Adapt, 1MED15_3.2_M2_337) 85% cofunded by the European Regional Development Fund, the MIMOSA project funded by the Foundation Prince Albert II Monaco, the Perfect project funded by the TOTAL Foundation, the Medchange project funded by the Agence Nationale pour la Recherche (ANR) and the European Union's Horizon 2020 research and innovation programme under grants agreements 689518 (MERCES) and SEP-210597628 (FutureMARES). D.G.G. is supported by an FPU grant (FPU15/05457) from the Spanish Ministry of Education. CL gratefully acknowledges the financial support by ICREA under the ICREA Academia programme. VB is supported by the Templeton Foundation (grant #60501, 'Putting the Extended Evolutionary Synthesis to the Test'). J-B.L is supported by the strategic Funding UIDB/04423/2020 and UIDP/04423/2020. We thank M. Zabala, J.M Gili and A. Santín for their valuable help in trait definition. D.G.G, C.L, J-B.L, N.B, P.L.S & J.G are part of the Marine Conservation research group (www.medrecover.org) (2017 SGR 1521) from the Generalitat de Catalunya.

AUTHORSHIP

DGG, CL, MD, JSM and JG conceived the ideas and designed the methodology. CL, JG and JBL obtained the data

in the field by performing photographic transects. NB obtained and analysed the temperature data. DGG and PLS analysed the photographic samples. DGG and VB performed the functional analyses on the obtained ecological data. DGG led the writing of the manuscript, and all authors contributed critically to the drafts and gave final approval for publication.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ele.13718.

DATA AVAILABILITY STATEMENT

The data and code related to the manuscript have been placed in the Dryad Digital Repository: https://doi.org/10.5061/dryad.69p8cz91g

REFERENCES

Angelini, C., Altieri, A.H., Silliman, B.R. & Bertness, M.D. (2011). Interactions among foundation species and their consequences for community organization, biodiversity, and conservation. *Bioscience*, 61, 782–789. https://doi.org/10.1525/bio.2011.61.10.8.

Antão, L.H., Bates, A.E., Blowes, S.A., Waldock, C., Supp, S.R., Magurran, A.E. *et al.* (2020). Temperature-related biodiversity change across temperate marine and terrestrial systems. *Nat. Ecol. Evol.*, 4, 927–933. https://doi.org/10.1038/s41559-020-1185-7.

Ballesteros, E. (2006). Mediterranean coralligenous assemblages: a synthesis of present knowledge. *Oceanogr. Mar. Biol.*, 44, 123–195.

Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.S., Nakashizuka, T., Raffaelli, D. *et al.* (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol. Lett.*, 9, 1146–1156. https://doi.org/10.1111/j.1461-0248.2006.00963.x.

Bates, A.E., Cooke, R.S.C., Duncan, M.I., Edgar, G.J., Bruno, J.F., Benedetti-Cecchi, L. *et al.* (2019). Climate resilience in marine protected areas and the "Protection Paradox". *Biol. Conserv.*, 236, 305–314. https://doi.org/10.1016/j.biocon.2019.05.005.

Bellwood, D.R., Hoey, A.S. & Choat, J.H. (2003). Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. *Ecol. Lett.*, 6, 281–285. https://doi.org/10.1046/j.1461-0248.2003.00432.x.

Bellwood, D.R., Hughes, T.P., Folke, C. & Nyström, M. (2004). Confronting the coral reef crisis. *Nature*, 429, 827–833. https://doi.org/10.1038/nature02691.

Bellwood, D.R., Pratchett, M.S., Morrison, T.H., Gurney, G.G., Hughes, T.P., Álvarez-Romero, J.G. *et al.* (2019b). Coral reef conservation in the Anthropocene: confronting spatial mismatches and prioritizing functions. *Biol. Conserv.*, 236, 604–615. https://doi.org/10.1016/j.biocon.2019.05.056.

Bellwood, D.R., Streit, R.P., Brandl, S.J. & Tebbett, S.B. (2019a). The meaning of the term 'function' in ecology: a coral reef perspective. *Funct. Ecol.*, 33(6), 948–961. https://doi.org/10.1111/1365-2435.13265.

Bensoussan, N., Cebrian, E., Dominici, J.M., Kersting, D.K., Kipson, S. *et al.*(2019a) Copernicus marine service ocean state report, Issue 3. *Journal of Operational Oceanography*, 12(sup1), S1–S123. https://doi.org/10.1080/1755876X.2019.1633075.

Bensoussan, N., Chiggiato, J., Buongiorno-Nardelli, B., Pisano, A. & Garrabou, J. (2019b) Copernicus marine service ocean state report, issue 3. *Journal of Operational Oceanography*, 12(sup1), S1–S123. https://doi.org/10.1080/1755876X.2019.1633075.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P. *et al.* (2012). Biodiversity loss and its impact on humanity. *Nature*, 486, 59–67.

Carlson, D.F., Yarbro, L.A., Scolaro, S., Poniatowski, M., McGee-Absten, V. & Carlson, P.R. (2018). Sea surface temperatures and seagrass mortality in Florida Bay: spatial and temporal patterns discerned from MODIS and AVHRR data. *Remote Sens. Environ.*, 208, 171–188. https://doi.org/10.1016/j.rse.2018.02.014.

Casas-Güell, E., Teixidó, N., Garrabou, J. & Cebrian, E. (2015). Structure and biodiversity of coralligenous assemblages over broad spatial and temporal scales. *Mar. Biol.*, 162, 901–912. https://doi.org/10.1007/s00227-015-2635-7.

Cerrano, C., Bavestrello, G., Bianchi, C.N., Cattaneo-vietti, R., Bava, S., Morganti, C. *et al.* (2000). A catastrophic mass-mortality episode of gorgonians and other organisms in the Ligurian Sea (northwestern Mediterranean), summer 1999. *Ecol. Lett.*, 3, 284–293. https://doi.org/10.1046/j.1461-0248.2000.00152.x.

Chevene, F., Doléadec, S. & Chessel, D. (1994). A fuzzy coding approach for the analysis of long-term ecological data. *Freshw. Biol.*, 31, 295–309. https://doi.org/10.1111/j.1365-2427.1994.tb01742.x.

Cloern, J.E. (1982). Does the benthos control phytoplankton biomass in South San Francisco Bay? *Mar. Ecol. Prog. Ser.*, 9, 191–202.

Coppari, M., Zanella, C. & Rossi, S. (2019). The importance of coastal gorgonians in the blue carbon budget. *Sci. Rep.*, 9, 13550. https://doi.org/10.1038/s41598-019-49797-4.

Cornwell, W.K., Schwilk, D.W. & Ackerly, D.D. (2006). A trait-based test for habitat filtering: convex hull volume. *Ecology*, 87, 1465–1471. https://doi.org/10.1890/0012-9658.

Craven, D., Eisenhauer, N., Pearse, W.D. *et al.* (2018). Multiple facets of biodiversity drive the diversity–stability relationship. *Nat. Ecol. Evol.*, 2, 1579–1587. https://doi.org/10.1038/s41559-018-0647-7.

Crisci, C., Ledoux, J.B., Mokhtar-Jamaï, K., Bally, M., Bensoussan, N., Aurelle, D. *et al.* (2017). Regional and local environmental conditions do not shape the response to warming of a marine habitat-forming species. *Sci. Rep.*, 7, 50–69. https://doi.org/10.1038/s41598-017-05220-4.

Darling, E.S., Graham, N.A.J., Januchowski-Hartley, F.A., Nash, K.L., Pratchett, M.S. & Wilson, S.K. (2017). Relationships between structural complexity, coral traits, and reef fish assemblages. *Coral Reefs*, 36(2), 561–575.10.1007/s00338-017-1539-z

De la Torriente, A., Aguilar, R., González-Irusta, J.M., Blanco, M. & Serrano, E. (2020). Habitat forming species explain taxonomic and functional diversities in a Mediterranean seamount. *Ecol. Indic.*, 118, 106747. https://doi.org/10.1016/j.ecolind.2020.106747.

Díaz, S. & Cabido, M. (2001). Vive la Difference: Plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.*, 16, 646–655. https://doi.org/10.1016/S0169-5347(01)02283-2.

Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R. *et al.* (2005). Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. *Front Ecol Environ.*, 3, 479–486.

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B. *et al.* (2003). Response diversity, ecosystem change, and resilience. *Front. Ecol. Environ.*, 1, 488–494. https://doi.org/10.1890/1540-9295.

Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C. *et al.* (2015). Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *P. Roy. Soc. B – Biol. Sci.*, 282, 20142620. https://doi.org/10.1098/rspb.2014.2620.

Garrabou, J., Coma, R., Bensoussan, N., Bally, M., Chevaldonne, P., Cigliano, M. *et al.* (2009). Mass mortality in Northwestern Mediterranean rocky benthic communities: effects of the 2003 heat wave. *Global Change Biol.*, 15, 1090–1103. https://doi.org/10.1111/j.1365-2486.2008.01823.x.

Garrabou, J., Gómez-Gras, D., Ledoux, J.B., Linares, C., Bensoussan, N., López-Sendino, P. *et al.* (2019). Collaborative database to track mass mortality events in the Mediterranean Sea. *Front. Mar. Sci.*, 6, 707. https://doi.org/10.3389/fmars.2019.00707.

Gattuso, J.-P., Magnan, A.K., Bopp, L., Cheung, W.W.L., Duarte, C.M., Hinkel, J. *et al.* (2018). Ocean solutions to address climate change and its effects on marine ecosystems. *Front. Mar. Sci.*, 5, 337. https://doi.org/10.3389/fmars.2018.00337.

Gili, J.M. & Coma, R. (1998). Benthic suspension feeders: their paramount role in littoral marine food webs. *Trends Ecol. Evol.*, 13, 316–321.

Gómez-Gras, D., Linares, C., de Caralt, S., Cebrian, E., Frleta-Valić, M., Montero-Serra, I. *et al.* (2019). Response diversity in Mediterranean coralligenous assemblages facing climate change: insights from a multispecific thermotolerance experiment. *Ecol. Evol.*, 9(7), 4168–4180. https://doi.org/10.1002/ece3.5045.

Graham, N.A.J. & Nash, K.L. (2013). The importance of structural complexity in coral reef ecosystems. *Coral Reefs*, 32, 315–326.

Grime, J.P. (1998). Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.*, 86, 902–910. https://doi.org/10.1046/j.1365-2745.1998.00306.x.

Hobday, A.J., Alexander, L.V., Perkins, S.E., Smale, D.A., Oliver, E.C.J. *et al.* (2016). A hierarchical approach to defining marine heatwaves. *Prog. Oceanog.*, 141, 227–238. https://doi.org/10.1016/j.pocean.2015.12.014.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S. *et al.* (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.*, 75, 3–35. https://doi.org/10.1890/04-0922.

Hughes, T.P., Kerry, J.T., Álvarez-Noriega, M., Álvarez-Romero, J.G., Anderson, K.D., Baird, A.H. *et al.* (2017). Global warming and recurrent mass bleaching of corals. *Nature*, 543, 373–377. https://doi.org/10.1038/nature21707.

Hughes, T.P., Kerry, J.T., Baird, A.H., Connolly, S.R., Dietzel, A., Eakin, C.M. *et al.* (2018). Global warming transforms coral reefs assemblages. *Nature*, 556, 492–496. https://doi.org/10.1038/s41586-018-0041-2.

Jackson, J.B.C. (1977). Competition on marine hard substrata: The adaptive significance of solitary and colonial strategies. *Amer Naturalist*, 111(980), 743–767.

Jackson, J.B.C. (1979). Morphological strategies of sessile animals. In *Biology and Systematic of Colonial Organisms*. (eds Larwood, G.P., Rosen, B.R.). Academic Press, London, pp. 499–555.

Kaufman, L., & Rousseeuw, P.J. (1990). Partitioning around medoids (program PAM). In: *Finding Groups in Data: An Introduction to Cluster Analysis*. John Wiley & Sons, Inc., Hoboken, NJ, pp. 87–88. https://doi.org/10.1002/9780470316801.

Kimmerer, W.J., Gartside, E. & Orsi, J.J. (1994). Predation by an introduced clam as the probable cause of substantial declines in zooplankton in San Francisco Bay. *Mar Ecol Prog Ser.*, 113, 81–93.

Kipson, S., Fourt, M., Teixidó, N., Cebrián, E., Casas, E. *et al.* (2011). Rapid biodiversity assessment and monitoring method for highly diverse benthic communities: A case study of Mediterranean coralligenous outcrops. *PLoS One*, 6(11), e27103. https://doi.org/10.1371/journal.pone.0027103.

Körner, C. (2017). A matter of tree longevity. *Science*, 355(6321), 130–131. https://doi.org/10.1126/science.aal2449.

Kuffner, I.B., Walters, L.J., Becerro, M.A., Paul, V.J., Ritson-Williams, R. & Beach, K.S. (2006). Inhibition of coral recruitment by macroalgae and cyanobacteria. *Mar Ecol Prog Ser.*, 323, 107–111. https://doi.org/10.3354/meps323107.

Laliberté, E. & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91, 299–305. https://doi.org/10.1890/08-2244.1.

Laliberté, E., Wells, J.A., DeClerck, F., Metcalfe, D.J., Catterall, C.P., Queiroz, C. *et al.* (2010). Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecol. Lett.*, 13, 76–86. https://doi.org/10.1111/j.1461-0248.2009.01403.x.

Linares, C., Cebrian, E. & Coma, R. (2012). Effects of turf algae on recruitment and juvenile survival of gorgonian corals. *Mar. Ecol. Prog. Ser.*, 452, 81. https://doi.org/10.3354/meps09586.

Loya, Y., Sakai, K., Yamazato, K., Nakano, Y., Sambali, H. & van Woesik, R. (2001). Coral bleaching: the winners and the losers. *Ecol Lett.*, 4, 122–131. https://doi.org/10.1046/j.1461-0248.2001.00203.x.

Madin, J.S., Hoogenboom, M.O., Connolly, S.R., Darling, E.S., Falster, D.S., Huang, D. *et al.* (2016). A trait-based approach to advance coral reef science. *Trends Ecol. Evol.*, 31(6), 419–428. https://doi.org/10.1016/j.tree.2016.02.012.

Marshall, J.P. (1983). The fate of borings: relations between bioerosion, internal sediment infill and submarine cementation In: *Proceedings of the Inaugural GBR Conference* (eds Baker, J.T., Carter, R.M., Sammarco, P.W., & Stark, K.P.)., Australia, pp. 129–234.

McGill, B., Enquist, B., Weiher, E. & Westboy, M. (2006). Rebuilding community ecology from functional traits. *Trends Ecol. Evol.*, 21(4), 178–185. https://doi.org/10.1016/j.tree.2006.02.002.

McLean, M., Auber, A., Graham, N.A.J., Houk, P., Villeger, S., Violle, C. *et al.* (2019). Trait structure and redundancy determines sensitivity to disturbance in marine fish communities. *Global Change Biol.*, 25, 3424–3437. https://doi.org/10.1111/gcb.14662.

McWilliam, M., Pratchett, M.S., Hoogenboom, M.O. & Hughes, T.P. (2020). Deficits in functional trait diversity following recovery on coral reefs. *Proc. R. Soc. B.*, 287, 20192628. https://doi.org/10.1098/rspb.2019.2628.

Mokany, K., Ash, J. & Roxburgh, S. (2008). Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. *J. Ecol.*, 96, 884–893. https://doi.org/10.1111/j.1365-2745.2008.01395.x.

Mouillot, D., Graham, N.A., Villéger, S., Mason, N.W. & Bellwood, D.R. (2013). A functional approach reveals community responses to disturbances. *Trends in Eco. Evol.*, 28, 167–177. https://doi.org/10.1016/j.tree.2012.10.004.

Mouillot, D., Villéger, S., Scherer-Lorenzen, M., & Mason, N.W.H. (2011). Functional structure of biological communities predicts ecosystem multifunctionality. *PLoS ONE*, 6(3), e17476. http://dx.doi.org/10.1371/journal.pone.0017476.

Nyström, M. (2006). Redundancy and response diversity of functional groups: Implications for the resilience of coral reefs. *Ambio*, 35, 30–35. https://doi.org/10.1579/0044-7447-35.1.30.

Officer, C.B., Smayda, T.J. & Mann, R. (1982). Benthic filter feeding: a natural eutrophication control. *Mar Ecol Prog Ser.*, 9, 203–210.

Oliver, E.C.J., Burrows, M.T., Donat, M.G., Sen Gupta, A., Alexander, L.V., Perkins-Kirkpatrick, S.E. *et al.* (2019). Projected marine heatwaves in the 21st century and the potential for ecological impact. *Front. Mar. Sci.*, 6, 734. https://doi.org/10.3389/fmars.2019.00734.

Pagès-Escolà, M., Hereu, B., Garrabou, J., Montero-Serra, I., Gori, A., Gómez-Gras, D. *et al.* (2018). Divergent responses to warming of two common co-occurring Mediterranean bryozoans. *Sci. Rep.*, 8, 174555. https://doi.org/10.1038/s41598-018-36094-9.

Paoli, C., Montefalcone, M., Morri, C., Vassallo, P. & Bianchi, C.N. (2017). Ecosystem functions and services of the marine animal forests. In *Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots* (eds Rossi, S., Bramanti, L., Gori, A., Orejas, C.). Cham, Switzerland, Springer International, pp. 1271–1312.

Paterson, D.M., Defew, E.C. & Jabour, J. (2012). Ecosystem function and co-evolution of terminology in marine science and management. *Marine biodiversity and ecosystem functioning*. M. Solan, R. J. Aspden and D. M. Paterson, Oxford University Press, 1, 1-240.

Poloczanska, E.S., Burrows, M.T., Brown, C.J., Molinos, J.G., Halpern, B.S., Hoegh-Guldberg, O. *et al.* (2016). Responses of marine organisms to climate change across oceans. *Front. Mar. Sci.*, 3, 62. https://doi.org/10.3389/fmars.2016.00062.

Ponti, M., Parlini, R.A., Ventra, V., Greco, D., Abbiati, M. & Cereno, C. (2014). Ecological shifts in Mediterranean coralligenous assemblages related to gorgonian forest loss. *PLoS One*, 9(7), e102782. https://doi.org/10.1371/journal.pone.0102782.

Ponti, M., Turicchia, E., Ferro, F., Cerrano, C. & Abbiati, M. (2018). The understorey of gorgonian forests in mesophotic temperate reefs. *Aquat. Conserv.*, 28(5), 1153–1166. https://doi.org/10.1002/aqc.2928.

Reiss, J., Bridle, J.R., Montoya, J.M. & Woodward, G. (2009). Emerging horizons in biodiversity and ecosystem functioning research. *Trends Ecol Evol.*, 24(9), 505–514. https://doi.org/10.1016/j.tree.2009.03.018.

Rossi, S., Coppari, M. & Viladrich, N. (2016). Benthic-pelagic coupling: New perspectives in the animal forests. In: *Marine Animal Forests* (eds Rossi, S., Bramanti, L., Gori, A., Saco, O., del Valle, C.). Springer, Cham. https://doi.org/10.1007/978-3-319-17001-5_23-1.

Round, F.E. (1984). *The ecology of Algae*. Cambridge University Press, Cambridge, p. 79.

Scheffers, B.R., Meester, L.D., Bridge, T.C.L., Hoffmann, A.A., Pandolfi, J.M., Corlett, R.T. *et al.* (2016). The broad footprint of climate change from genes to biomes to people. *Science*, 354, aaf7671. https://doi.org/10.1126/science.aaf7671.

Smale, D.A., Wernberg, T., Oliver, E.C.J., Thomsen, M., Harvey, B.P., Straub, S.C. *et al.* (2019). Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nat. Clim. Change*, 9, 306–312. https://doi.org/10.1038/s41558-019-0412-1.

Stavert, J.R., Pattemore, D.E., Gaskett, A.C., Beggs, J.R. & Bartomeus, I. (2017). Exotic species enhance response diversity to land use change but modify functional composition. *Proc. R. Soc. B.*, 284, 20170788. https://doi.org/10.1098/rspb.2017.0788.

Steneck, R.S., Graham, M.H., Bourque, B.J. & Corbett, D. (2002). Kelp forest ecosystems: biodiversity, stability and future. *Environ. Conserv.*, 29, 436–459. https://doi.org/10.1017/S0376892902000322.

Teixidó, N., Gambi, M.C., Parravacini, V., Kroeker, K., Micheli, F., Villegér, S. *et al.* (2018). Functional biodiversity loss along natural CO_2 gradients. *Nat. Comm.*, 9, 5149. https://doi.org/10.1038/s41467-018-07592-1.

Tilman, D. (2001). Functional diversity. *Encyclopedia of Biodiversity*, 3, 109–120. https://doi.org/10.1006/rwbd.1999.0154.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. (1997). The influence of functional diversity and composition on ecosystem processes. *Science*, 277, 1300–1302. https://doi.org/10.1126/science.277.5330.1300.

Torrents, O., Tambuté, E., Caminiti, N. & Garrabou, J. (2008). Upper thermal thresholds of shallow vs. deep populations of the precious Mediterranean red coral *Corallium rubrum*: assessing the potential effects of warming in the NW Mediterranean. *J. Exp. Mar. Biol. Ecol.*, 357, 7–19. https://doi.org/10.1016/j.jembe.2007.12.006.

Trygonis, V. & Sini, M. (2012). photoQuad: a dedicated seabed image processing software, and a comparative error analysis of four photoquadrat methods. *J. Exp. Mar. Biol. Ecol.*, 424–425, 99–108. https://doi.org/10.1016/j.jembe.2012.04.018.

Verdura, J., Linares, C., Ballesteros, E., Coma, R., Uriz, M.J., Bensoussan, N. *et al.* (2019). Biodiversity loss in a Mediterranean ecosystem due to an extreme warming event unveils the role of an engineering gorgonian species. *Sci. Rep.*, 9, 5911. https://doi.org/10.1038/s41598-019-41929-0.

Wahl, M. (2008). Ecological lever and interface ecology: epibiosis modulates the interactions between host and environment. *Biofouling*, 24, 427–438. https://doi.org/10.1080/08927010802339772.

Walker, B., Kinzig, A. & Langridge, J. (1999). Plant attribute diversity, resilience, and ecosystem function; the nature and significance of dominant and minor species. *Ecosystems*, 2, 95–103.

Weigel, B., Blenckner, T. & Bonsdorff, E. (2016). Maintained functional diversity in benthic communities in spite of diverging functional identities. *Oikos*, 125(10), 1421–1433. https://doi.org/10.1111/oik.02894.

Wernberg, T., Smale, D.A., Tuya, F., Thomsen, M.S., Langlois, T.J., de Bettignies, T. *et al.* (2013). An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nat. Clim. Change*, 3, 78–82. https://doi.org/10.1038/nclimate1627.

Yachi, S. & Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc. Natl. Acad. Sci. U.S.A.*, 96, 1463–1468. https://doi.org/10.1073/pnas.96.4.1463.

Zabala, M. & Ballesteros, E. (1989). Surface-dependent strategies and energy flux in benthic marine communities or, why corals do not exist in the Mediterranean. *Scientia Marina*, 53(1), 3–17.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Editor, Tim Wootton
Manuscript received 20 August 2020
First decision made 1 February 2021
Manuscript accepted 3 February 2021