Climate change transforms the functional identity of Mediterranean coralligenous assemblages

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), disproportionately 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.

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) affects 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
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 currently 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 in press), 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, 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, Pzzu_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 cm² 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 imposing 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...
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 semi-quantitative 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 non-parametric 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 FEs (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) Stolional, (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). - 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). |
| **Coloniality (Ranked)** | (1) Solitary, (2) Colonial/Gregarious | - 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 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) - 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). - Epibionts colonise living surfaces, substantially modifying the benthos environment interactions (e.g. transferance of energy or matter). Thus, they may reduce their fitness, and subsequently, the assemblage stability when structural species are affected (Wahl, 2008). |
| **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) | - Determines primary production, trophic interactions, benthic-pelagic coupling, nutrient cycling and the energy transfer in food webs (Round, 1984; Gili & Coma, 1998). - Determines trophic interactions, benthic-pelagic coupling, nutrient cycling and the energy transfer in food webs (Round, 1984; Gili & Coma, 1998). - Determines light harvesting capability in relation to the light availability, and therefore, the primary production of the ecosystem (Round, 1984). |
| **Epibiosis preference (Ranked)** | (1) Never, (2) Facultative, (3) Obligate | - Determines primary production, trophic interactions, benthic-pelagic coupling, nutrient cycling and the energy transfer in food webs (Round, 1984; Gili & Coma, 1998). - Determines light harvesting capability in relation to the light availability, and therefore, the primary production of the ecosystem (Round, 1984). |
| **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). - Determines light harvesting capability in relation to the light availability, and therefore, the primary production of the ecosystem (Round, 1984). |
| **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 primary production, trophic interactions, benthic-pelagic coupling, nutrient cycling and the energy transfer in food webs (Round, 1984; Gili & Coma, 1998). - Determines light harvesting capability in relation to the light availability, and therefore, the primary production of the ecosystem (Round, 1984). |
| **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, Phycocyanin (Cyanobacteria), (f) Dinoflagellated, (g) Mix. (e.g. turf) | - Determines primary production, trophic interactions, benthic-pelagic coupling, nutrient cycling and the energy transfer in food webs (Round, 1984; Gili & Coma, 1998). - 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) | - Determines primary production, trophic interactions, benthic-pelagic coupling, nutrient cycling and the energy transfer in food webs (Round, 1984; Gili & Coma, 1998). - Determines light harvesting capability in relation to the light availability, and therefore, the primary production of the ecosystem (Round, 1984). |
| **Growth rate (linear extension in cm/ year^{−1}) (Ranked)** | (1) Extreme slow (< 1 cm * 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}) | - Determines primary production, trophic interactions, benthic-pelagic coupling, nutrient cycling and the energy transfer in food webs (Round, 1984; Gili & Coma, 1998). - Determines light harvesting capability in relation to the light availability, and therefore, the primary production of the ecosystem (Round, 1984). |

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Table 1 (continued)

| Trait (Ranked/Nominal) | Categories                                                                 | Relation to ecosystem functions* |
|------------------------|-----------------------------------------------------------------------------|----------------------------------|
| Physical defenses      | (a) Non-calculator, (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 Pzzuin_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 heterotrophic filtering 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, wide 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 autotrophic 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, later 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 more.
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 ± 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
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 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.

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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,
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 disproportionately 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. 4i-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., 2004, 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).

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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.

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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.69p8ec91g

REFERENCES

Angellini, C., Altieri, A.H., Stillman, 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. Ann., 44, 123–195.

Bulvanera, 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., Perring, 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., Poniatiowski, M., McGeek-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-Giulli, 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.

Cheyne, F., Doleade, 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/s41598-019-4979-4.

Cornwell, W.K., Schwill, 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-Jamai, 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., Pirolli, N., 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. & Persson, L. (2003). Response diversity, ecosystem change, and resilience. Front. Ecol. Environ., 1, 488–494. https://doi.org/10.1890/1540-9295.

Gagarin, V., Bartomeus, I., Jonsson, T., Taylor, A., Winquist, 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.

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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, 14aaf7671. 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.

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., Villegé, S. et al. (2018). Functional biodiversity loss along natural CO2 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.

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.

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.

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