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Climate change may have minor impact on zooplankton functional diversity in the Mediterranean Sea

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Abstract

Aim: To assess the impact of climate change on the functional diversity of marine zooplankton communities.

Location: The Mediterranean Sea.

Methods: We used the functional traits and geographic distributions of 106 copepod species to estimate the zooplankton functional diversity of Mediterranean surface assemblages for the 1965–1994 and 2069–2098 periods. Multiple environmental niche models were trained at the global scale to project the species habitat suitability in the Mediterranean Sea and assess their sensitivity to climate change predicted by several scenarios. Simultaneously, the species traits were used to compute a functional dendrogram from which we identified seven functional groups and estimated functional diversity through Faith's index. We compared the measured functional diversity to the one originated from null models to test if changes in functional diversity were solely driven by changes in species richness.

Results: All but three of the 106 species presented range contractions of varying intensity. A relatively low decrease of species richness (−7.42 on average) is predicted for 97% of the basin, with higher losses in the eastern regions. Relative sensitivity to climate change is not clustered in functional space and does not significantly vary across the seven copepod functional groups defined. Changes in functional diversity follow the same pattern and are not different from those that can be expected from changes in richness alone.

Main conclusions: Climate change is not expected to alter copepod functional traits distribution in the Mediterranean Sea, as the most and the least sensitive species are functionally redundant. Such redundancy should buffer the loss of ecosystem functions in Mediterranean zooplankton assemblages induced by climate change. Because the most negatively impacted species are affiliated to temperate regimes and share Atlantic biogeographic origins, our results are in line with the hypothesis of increasingly more tropical Mediterranean communities.

KEYWORDS
climate change, functional diversity, Mediterranean Sea, niche modelling, null model, zooplankton

1 | INTRODUCTION

Anthropogenic climate change is modifying the physical and chemical properties of the atmosphere and the ocean at an unprecedented rate, altering the biosphere as we know it (Gattuso et al., 2015). Future environmental changes threaten all components of biodiversity from organismic physiology to the biological communities providing ecosystem services (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012). The potential future modifications of biodiversity have thus become a major scientific and societal issue (Cardinale et al., 2012) and prediction of these modifications has required the development of novel approaches embracing key ecological mechanisms (Urban et al., 2016). Among these approaches, trait-based approaches have received increasing interest in the past decade. Functional traits are the characteristics of individuals that imply functional trade-offs and affect their fitness. Therefore, functional traits are assumed to enable the exploration of how community assembly relates to ecosystem functioning and enable the prediction of how these two factors respond to environmental variability (Violle et al., 2007). Functional diversity has emerged as an estimate of the contributions of functional traits to ecosystem functioning that is freed from taxonomic classifications (Mouillot, Graham, Villéger, Mason, & Bellwood, 2013). Indeed, different species may perform analogous functions, generating functional redundancy that prevents the decline of ecosystem performance when species disappear (Rosenfeld, 2002). It is therefore necessary to identify the changes in species richness that imperil ecosystem processes, even in species-rich systems where high rates of functional redundancy are likely (Mouillot et al., 2014). Patterns of functional diversity have been prominently studied in terrestrial (Barbet-Massin & Jetz, 2015; Barnett, Finlay, & Beisner, 2007) and coastal marine systems (Albouy et al., 2015; Henriques et al., 2017; Mouillot et al., 2014). The relationships between trait expression and environmental variability remain poorly understood for oceanic ecosystems, especially for plankton, despite its major importance for ecosystem functioning and global biogeochemical cycles (Barton, Pershing, Litchman, Record, Edwards, Litchman, & Klausmeier, 2013). Planktonic organisms constitute the basis of marine food webs and play an essential role in the biological carbon pump (Steinberg & Landry, 2017). A few recent studies have described community dynamics and composition through trait-based approaches for phytoplankton (Edwards et al., 2013; Litchman & Klausmeier, 2008) and zooplankton (Benedetti, Gasparini, & Ayata, 2016; Brun, Payne, & Kiørboe, 2016; Kenitz, Visser, Mariani, & Andersen, 2017; Pomerleau, Sastri, & Beisner, 2015). The spatio-temporal patterns of zooplankton functional diversity, their underlying drivers and link with ecosystem processes remain poorly understood (Litchman, Ohman, & Kiørboe, 2013). Yet, it is particularly important to develop trait-based approaches to better constrain the role of zooplankton in ecosystem models, as they mediate important energy fluxes through a complex network of functionally different entities (Steinberg & Landry, 2017).

Among species-rich marine systems, the Mediterranean Sea is particularly relevant for studying the links between diversity patterns, environmental gradients and the resilience of ecosystem processes (Lejeusne, Chevaldonné, Pergent-Martini, Boudouresque, & Pérez, 2010). It is a biodiversity hotspot (Coll et al., 2010; Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000) under strong anthropogenic and natural forcings (Coll et al., 2012; The MerMex Group, 2011) and also a climate change hotspot as it ranks among the regions for which the strongest warming rates are predicted (Giorgi, 2006). The ongoing increase in water temperature is modifying the diversity of the basin, with tropical taxa taking over communities, thus triggering a "tropicalization" process (Bianchi, 2007; Raitsos et al., 2010). In this context, previous studies have forecast the impact of future warming on the species richness (Lasram et al., 2010), the community structure (Albouy, Guilhaumon, Araújo, Mouillot, & Leprieur, 2012) and the functional diversity (Albouy et al., 2015) of Mediterranean coastal fish assemblages. To date, the study by Benedetti, Guilhaumon, Adloff, and Ayata (2017) is the only one that modelled climate change impacts on the Mediterranean plankton community composition. The authors predicted a slight decrease in species richness almost all over the basin, with stronger losses in the warmer eastern regions. However, in that study, changes in functional diversity were not addressed despite the fact they might be more relevant than changes in taxonomic diversity for marine ecosystem functioning (Litchman et al., 2013).

Mediterranean and global zooplankton communities are dominated by copepods, in terms of both taxonomic diversity and abundance of individuals (Kiørboe, 2011; Siokou-Frangou et al., 2010). Copepods frequently contribute to more than 80% of the total mesozooplankton abundance in the different regions of the Mediterranean Sea (Mazzocchi et al., 2014). Copepoda constitute a diverse and relatively well-studied group (Razouls, de Bovée, Kouwenberg, & Desreumaux, 2005–2017) for which relevant functional traits have been described (Brun, Payne, & Kiørboe, 2017). Moreover, functional trait expression in planktonic copepods is strongly regulated by environmental changes from local to global scales (Brun et al., 2016; Kenitz et al., 2017), making it an ideal group to study functional trait biogeography (Barton et al., 2013). Consequently, investigating the future patterns of zooplankton functional diversity in the Mediterranean Sea is crucial and that it can be achieved by focusing on copepod species and their traits.

The goals of the present study are to (a) identify which copepod species would be most affected by the predicted future warming and increasing salinity of the Mediterranean Sea; (b) assess whether those species are functionally redundant with the less sensitive ones; and (c) investigate whether changes in functional diversity between the future and the present conditions are proportional to changes in species richness, or if some functional groups are disproportionately affected. To achieve these goals, we trained multiple environmental niche models (ENMs) at the global scale to project the distribution of 106 copepod species in the present and future conditions of the Mediterranean Sea, under several climate change scenarios. Simultaneously, we ordered the species according to their functional traits in a multidimensional functional space and generated a functional dendrogram. Using this functional dendrogram and

the projected species composition of the assemblages, we calculated copepod functional diversity at each time and location. Then, we estimated the intensity of species range shifts and projected onto the functional space and the dendrogram. Observed estimates of functional diversity changes were compared to estimates generated by null models.

2 | METHODS

2.1 | Species list and distribution data

We merged multiple sources of data on the geographical distribution of copepod species in the Mediterranean Sea to compile an exhaustive species list (Benedetti et al., 2016, 2017). To focus on the most common species, only those with at least 50 different records in the Mediterranean basin were retained, resulting in 193 species. As none of the species retained are endemic to the Mediterranean Sea (Razouls et al., 2005–2017), we calibrated the species niches at the global scale to avoid truncating the response curves and therefore biasing the resulting projections (Thuiller, Brotons, Araùjo, & Lavorel, 2004). To do so, we retrieved the worldwide occurrences recorded between 1965 and 1994 from the Ocean Biogeographic Information System (http://www.iobis.org/; accessed on 2014-11-12) and further excluded the species that exhibited <15 occurrences outside the Mediterranean Sea. The remaining 106 species are representative of the taxonomic diversity of the zooplankton assemblages of the surface Mediterranean Sea (Siokou-Frangou et al., 2010). We gridded the species presences into the 0.25 × 0.25° cells of the World Ocean Atlas 2013 (WOA13; Levitus et al., 2013), which was later used to calibrate the ENMs (see below).

2.2 | Functional traits, groups and dendrogram

For each copepod species, we retrieved four functional traits from Benedetti et al. (2016): maximum body length (mm), trophic group (carnivore, omnivore-carnivore, omnivore, omnivore-herbivore and omnivore-detritivore), feeding strategy (ambush feeding, cruise feeding, current feeding and mixed feeding), and egg-spawning strategy (broadcast-spawner vs. sac-spawner). We selected these traits because of their availability in the literature and because they cover multiple ecological functions that influence ecosystem processes (Brun et al., 2017; Hébert, Beisner, & Maranger, 2016). Body size is a "master trait" that transcends a variety of traits related to ecosystem processes, such as carbon cycling, secondary productivity or nutrient transfer (Hébert et al., 2016), and has been shown to be controlled by seawater temperature (Brun et al., 2016). Trophic group describes the primary food source of a species and therefore its role in food-web dynamics (Pomerleau et al., 2015). Feeding mode has strong implications for prey selection, energy allocation or nutrient cycling (Hébert et al., 2016; Litchman et al., 2013). For instance, ambush feeders targeting motile prey are characterized by lower energy expenditure than active feeders resulting in lower

mortality rates and lower feeding efficiency. Therefore, they are likely to exhibit better fitness in food-depleted environments where competition and predation are higher than in productive environments (Kenitz et al., 2017). Similarly, herbivorous species are likely to relatively more present in areas where phytoplankton bloom. Spawning strategy shapes energy allocation as species developing resting sacs can invest less energy in growth and survival (Litchman et al., 2013).

We performed a multiple correspondence analysis (MCA; Husson & Josse, 2014) based on these four functional traits to ordinate the species in a reduced functional space (Benedetti et al., 2016). In order to make the body length trait categorical, we classified the species maximum body length into four size classes (SC1: 0.5–1.2 mm; SC2: 1.3–1.8 mm; SC3: 1.9–3.0 mm; SC4: 3.4–8.2 mm) using hierarchical agglomerative clustering based on both the Euclidean distance and a synoptic aggregation link (Legendre & Legendre, 2012). Trophic groups were also binarily transformed because it optimizes the computation of the inter-species distance in the functional space. For example, we considered an omnivore–herbivore species as both an "omnivore" (1) and a "herbivore" (1; value equal to 0 for the carnivore and the detritivore categories) and not just "omnivore–herbivore" as an independent trophic group. We kept the principal components with an eigenvalue greater than the mean of eigenvalues (Kaiser-Guttman's criterion; Guttman, 1954). We used the Euclidean distance computed from the species coordinates in this functional space as a measure of functional distance (Faith, 1992). Finally, we performed hierarchical agglomerative clustering using Ward's aggregation method (Legendre & Legendre, 2012) on this functional distance matrix to generate the functional dendrogram. We examined several cutting levels along this dendrogram and the final level was chosen so as to yield ecologically relevant groups that were composed of functionally homogeneous species.

2.3 | Niche modelling procedure

We used average sea surface temperature (SST), its seasonal variation (σSST) and average sea surface salinity as predictors of the presence of each copepod species. These variables are frequently used when modelling copepod distributions because copepods are poikilothermic, passively dispersed and not exploited by human activities (Richardson, 2008). Thirty-year (1965–1994) climatologies from World Ocean Atlas (WOA13 v2; Levitus et al., 2013) were used to predict the present distributions and assemblage compositions. We averaged the monthly outputs of the NEMOMED8 regional ocean climate model over the 2069–2098 time period to obtain the future conditions of the Mediterranean Sea (Adloff et al., 2015). The updated A2 greenhouse gas scenario forcing of Adloff et al. (2015) was chosen. Then, we used these 30-years climatologies to predict future distributions and assemblage composition (scenarios B1 and A1B were also tested and yielded similar results). We used five different types of ENMs (Artificial Neural Networks, Generalized Linear Models, Multi-Adaptive Regression Splines, Maximum Entropy and Random Forests) to

cover the variety of commonly used niche models. We averaged their outputs to provide an ensemble projection of species assemblage composition for the 1965–1994 (present) and 2069–2098 (future) time periods. To train the selected ENMs, we randomly generated pseudo-absences after applying both environmental and spatial weightings to place those pseudo-absences in the regions of lowest environmental suitability and away from the actual presences (Hengl, Sierdsema, Radović, & Dilo, 2009). We chose this method over a purely random or a spatially weighted random generation of pseudo-absences (Barbet-Massin, Jiguet, Albert, & Thuiller, 2012) because zooplankton are ectotherms with population dynamics closely following environmental changes (Hays, Richardson, & Robinson, 2005) and are passively dispersed over very large spatial scales (Jönsson & Watson, 2016). Therefore, they are likely to be more absent in areas that are remote and unfavourable according to the actual presence records. For every species and every ENM, we split the presences/pseudo-absences datasets into a calibration (80%) and a testing (20%) set. We evaluated the ENMs skill according to the True Skill Statistics (TSS) criterion (Allouche, Tsoar, & Kadmon, 2006) which corresponds to the relative correct identification of presence (sensitivity) and absence (specificity), with a 5-fold cross-validation for replicates. The species average TSS scores are provided in Supporting Information Table S1, average TSS scores range from 0.64 (± 0.10) to 0.96 (± 0.03). The full description of the niche modelling procedure is detailed in Benedetti et al. (2017) and is provided in the Supporting Information Appendix S1.

2.4 | Quantifying species relative sensitivity to climate change

For each species, we transformed the current and future presence probabilities given by the ENMs into presence/absence (1/0) maps through a probability threshold (i.e., all the cells characterized by a presence probability above the threshold are those where the species is considered as present). For each species, we chose a probability threshold that maximized the agreement with current presence records according to the TSS criterion. We then used the spatial distributions of the presences and absences to compute 12 metrics that describe the impact of climate change on the species distribution ranges: (a) *range restriction*: number of cells that are predicted to be lost between the future and the present time periods (n_{lost}); (b) *range expansion*: number of cells gained (n_{gained}); (c) *range retention*: number of cells that are common to both periods ($n_{retained}$); (d) *range exclusion*: number of cells where a species is never projected as present, no matter the time period ($n_{excluded}$). We complemented those absolute values with the (e) *ratio of range restriction to range expansion*:

$$ratio = \frac{range\ restriction}{range\ expansion}$$

which allowed the distinction of "winners" (ratio < 1) from "losers" (ratio > 1). We used the estimates above to compute the (f) *mean*

change in range occupancy (i.e., the percentage of cells lost, or gained, between the two time periods) by subtracting the mean current range occupancy to the mean future range occupancy, as follows:

$$mean\ current\ range\ occupancy = \frac{mean\ (range\ retention) + mean\ (range\ restriction)}{n\text{cells}}$$

$$mean\ future\ range\ occupancy = \frac{mean\ (range\ retention) + mean\ (range\ expansion)}{n\text{cells}}$$

$$mean\ change\ in\ range\ occupancy = mean\ future\ range\ occupancy - mean\ current\ range\ occupancy$$

With $n$cells being the number of total Mediterranean grid cells ($n = 26,490$).

The average longitude and latitude of a species regional distribution were computed to derive its present and future range centroids (longitudinal, latitudinal and mean). The positions of the present and future range centroids were then used to compute the spatial shifts (in km) of a species (again according to (g) longitude only, (h) latitude only, and the (i) average of the two), as well as the corresponding shift speeds (j, k and l) per decade (km/dec).

To summarize these metrics, we performed a scaled principal component analysis (PCA; Legendre & Legendre, 2012) on the ratio and the six shift metrics (distances and speeds) for the 106 species. Due to the greater explanatory power of PC1 with respect to the rest (79.7% of total variance), which reflects high correlation among the six metrics, we used the coordinates of species along PC1 as a synthetic index summarizing the species sensitivity to climate change.

2.5 | Distribution of the relative sensitivity to climate change in functional space

We performed variance analysis (Kruskal & Wallis, 1952) to test if the defined functional groups differed in their relative sensitivity to climate change. We repeated the test on the relative sensitivity index, applying different cutting levels in the functional dendrogram and successively discarding the most sensitive species to account for their greater weight in the analysis. We also tested whether sensitivity to climate change was correlated with species maximal body length to assess if smaller species are favoured compared to larger species in future climate conditions (Winder, Reuter, & Schladow, 2009). Additionally, the species relative sensitivity was plotted along the four MCA axes to assess whether a particular portion of the functional space is threatened under the future Mediterranean salinity and temperature conditions.

To evaluate the robustness of our results, we tested several alternative methods to estimate functional diversity (FD; Buisson, Grenouillet, Villéger, Canal, & Laffaille, 2013; Maire, Grenouillet, Brosse, & Villéger, 2015). We also applied the method of Petchey and Gaston (2006) to estimate FD by drawing a functional dendrogram

TABLE 1 Summary of the range shift metrics for the top 15 and bottom 15 copepod species affected by climate change in the Mediterranean Sea

Species name	Mean ratio of restriction to expansion	Mean change in range occupancy (%)	Mean distance between range centroids (km)	Mean shift speed between range centroids (km/dec)	Relative sensitivity index
Pseudocalanus elongatus	245.90	40.14	276.41	26.58	14.31
Labidocera wollastoni	14.29	25.02	221.47	21.30	8.32
Temora longicornis	16.41	20.63	216.00	20.77	7.76
Centropages typicus	6.52	19.37	207.04	19.91	7.50
Microsetella norvegica	44.59	23.99	207.78	19.98	7.31
Oithona similis	10.98	27.46	187.23	18.00	6.80
Mecynocera clausi	69.41	21.87	161.69	15.55	5.26
Calanus helgolandicus	8.56	17.88	153.36	14.75	4.81
Pleuromamma borealis	86.10	23.41	127.25	12.24	4.09
Rhincalanus nasutus	3.32	13.16	120.54	11.59	3.46
Acartia (Acartia) danae	3.48	11.18	107.88	10.37	2.67
Pleuromamma abdominalis	5.69	10.60	108.61	10.44	2.29
Clausocalanus jobei	55.00	14.36	95.90	9.22	1.95
Paraeuchaeta hebes	5.57	6.96	102.45	9.85	1.78
Oithona tenuis	3.05	7.74	91.45	8.79	1.61
Scaphocalanus curtus	7.18	3.46	25.18	2.42	-1.90
Corycaeus Agetus typicus	4.89	2.26	25.34	2.44	-1.97
Calocalanus contractus	6.36	2.88	23.04	2.22	-2.03
Candacia ethiopica	2.92	2.38	21.80	2.10	-2.03
Chiridius poppei	14.96	4.52	20.76	2.00	-2.04
Corycaeus furcifer	5.84	2.90	22.49	2.16	-2.05
Paracalanus nanus	5.31	1.97	18.43	1.77	-2.26
Oithona nana	6.88	2.47	17.11	1.65	-2.31
Corycaeus (Agetus) flaccus	6.46	2.71	15.59	1.50	-2.36
Haloptilus acutifrons	3.88	1.93	15.84	1.52	-2.38
Candacia longimana	7.76	4.84	12.74	1.23	-2.42
Phaenna spinifera	34.50	2.46	8.41	0.81	-2.52
Scolecithricella dentata	9.84	2.55	11.92	1.15	-2.54
Acartia (Acartiura) clausi	1.84	0.68	11.38	1.09	-2.61
Candacia bispinosa	7.67	1.40	3.77	0.36	-2.96

Notes. Rankings depend on the relative sensitivity to climate change index obtained from a PCA based on the mean ratio of range restriction/range expansion and the mean shift distances and shift speeds between their current (1965–1994) range centroid and their future (2069–2098) range centroid. The values of the shift metrics and the relative sensitivity to climate change index for the 106 species studied are provided in Table S2. Shift metrics were obtained from each pair of current and future species distributions, and for each climate change scenario and environmental niche model (ENM), after deriving the species current and future range centroids. Mean ratio of restriction to expansion: the ratio of mean range restriction to mean range expansion; mean change in range occupancy: the difference between the mean future range occupancy (retention + expansion/total Mediterranean grid cells) and the mean current range occupancy (retention + restriction/total Mediterranean grid cells). The average longitude and latitude of a species regional distribution was computed to derive its present and future range centroids (longitudinal, latitudinal and mean). The positions of the present and future range centroids were then used to compute the mean distance between the two range centroids (in km) of a species, as well as the corresponding shift speeds (km/dec).

based on a Gower's distance matrix and the UPGMA linkage method (Mérigot, Durbec, & Gaertner, 2010). Then, we performed a principal coordinates analysis (PCoA; Legendre & Legendre, 2012) on the Gower distance matrix to ordinate the species in another functional space (Villéger, Mason, & Mouillot, 2008), in which the species sensitivity to climate change was plotted. In addition, we also computed species functional uniqueness and originality from the species MCA scores (Buisson et al., 2013) and we assessed their covariation with the climate change sensitivity index.

2.6 | Estimating the impact of climate change on functional diversity

To complete our analysis of climate change impacts on Mediterranean copepod functional diversity, we compared the spatial patterns of functional diversity (FD) between the present and the future Mediterranean Sea. We stacked all species distribution maps, according to their emission scenario and ENM, to obtain species assemblages (i.e., the species present and absent in each grid cell) for the present and future periods (Benedetti et al., 2017). We used species assemblages to derive estimates of both species richness (SR; the sum of all the species modelled as present in the assemblage) and FD. The latter was based on the commonly used Faith's index (Faith, 1992) which was computed for each assemblage as the sum of the corresponding branch lengths in the functional dendrogram.

To assess the extent to which climate change impacts FD beyond the expectation from changes in SR only (Albouy et al., 2015; Winter, Devictor, & Schweiger, 2013), we implemented a null modelling framework. We computed null estimates of FD in each assemblage, for the present (FD_{t0}) and the future (FD_{t1}), by randomizing the position of the species affected by climate change (lost or gained in an assemblage) along the functional dendrogram. We left the positions of the species common to both time periods unchanged on the functional dendrogram, as these are not affected by the future changes in conditions. This means that a species affected by climate change can only be randomly reshuffled at the position of another species affected by climate change.

Therefore, the identity of the species to be randomly reshuffled depends on the predicted pattern of ΔSR (if species are lost or gained) and changes in community composition (if lost species are replaced by gained ones). For instance, when species are lost but not replaced, the resulting future assemblage only contains species that were not affected by climate change. Thus, the random reshuffling cannot be performed along the functional dendrogram at t1. Consequently, the null FD estimates can only be obtained by performing the random reshuffling at t0 and between the positions of the species that are lost from the assemblage. Three cases were identified:

1. ΔSR < 0 without species replacement: only the position of the species that are lost from the assemblage were randomly reshuffled when computing the null estimates of FD_{t0} (no reshuffling for FD_{t1}).

2. ΔSR > 0 without species replacement: only the positions of the species that are gained in the assemblage were randomly reshuffled when computing the null estimates of FD_{t1} (no reshuffling for FD_{t0}).

3. ΔSR < 0 or ΔSR > 0 with species replacement: the two cases above were applied. Random reshuffling is therefore performed for both FD_{t0} and FD_{t1}.

We repeated the random reshuffling procedure 500 times to obtain null distributions of net differences in FD (ΔFD) for each assemblage. Then, we compared the observed ΔFD (i.e., the one calculated without reshuffling the tips of the dendrogram) to its corresponding null distribution to obtain a p-value. The latter enabled testing whether the observed ΔFD significantly differs from the ΔFD that can be expected from ΔSR alone. Like Benedetti et al. (2017), we computed consensus projections of ΔSR and ΔFD within every cell by averaging all the obtained values (from each modelling parameter). Each projection generates a p-value thanks to the above-described procedure, but since averaging p-values has no meaning, we computed the frequency of p-values <0.05 within every cell. A frequency equal to zero indicates that ΔFD is never different from the ΔFD that can be expected from ΔSR.

All statistical analyses were conducted with R version 3.4.0 (R Core Team, 2017). The BIOMOD2 package (Thuiller, Goerges, Engler, & Breiner, 2016) was used for computing the ENMs, the GEOSPHERE package (Hijmans, 2017) was used to compute the distances between the species range centroids, and the multivariate ordination techniques were performed with the FACTOMINER (Le, Josse, & Husson, 2008) and APE (Paradis, Claude, & Strimmer, 2004) packages.

3 | RESULTS

3.1 | Species relative sensitivity to climate change in the Mediterranean

The mean values of the range shift metrics are summarized in Table 1 for the 15 most sensitive species and the 15 least sensitive ones (see Supporting Information Table S2 for the table with the 106 species). Considering the strong correlations between the mean distances (and speeds) in centroid shifts and their latitudinal and longitudinal components (R^2 > 0.98; p-values < 10^{-10}), only the former are shown.

Only three of the 106 modelled species exhibit a higher mean rate of range expansion than a mean rate of range restriction (*Clausocalanus arcuicornis*, *Paracalanus parvus*, *Copilia quadrata*), which translates in low mean range expansions ranging between 1% and 3%. All other 103 taxa show stronger rates of range restriction than rates of range expansions (i.e., mean ratio of lost cells to gained cells >1). Overall, the shift metrics present high variability across species. One species (*Pseudocalanus elongatus*) shows drastic range restriction with a mean ratio of over 245, which corresponds to an average change in range occupancy of nearly −40%. It is followed by *Oithona similis* (mean change in range occupancy ≈ −27%), *Labidocera wollastoni* (−25%) and *Microsetella norvegica*, *Pleuromamma borealis*, *Mecynocera clausi* and *Temora longicornis* (all
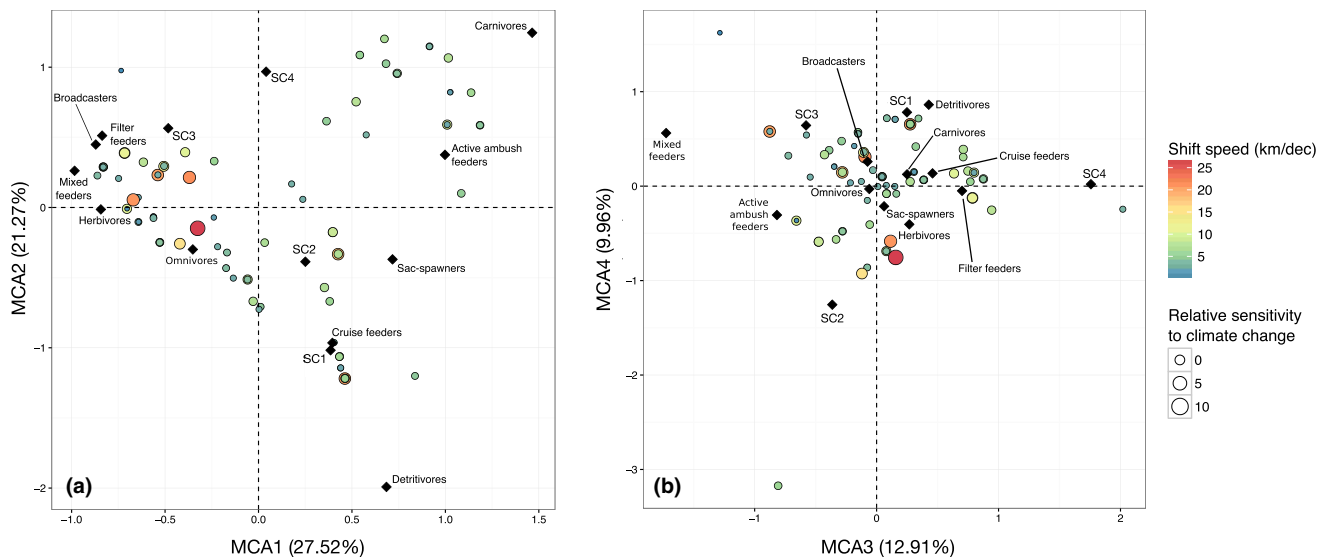
FIGURE 1 Distribution of the species relative sensitivity to climate change index and the species shift speed between their current and future range centroids in the first four dimensions of a functional space obtained with a multiple correspondence analysis (MCA). The MCA was based on four categorical functional traits (size class, trophic group, feeding strategy and spawning strategy) whose contributions to the scoring of the four selected MCA axes are evidenced (a) for MCA1 and MCA2, and (b) for MCA3 and MCA4. The size of the objects (n = 106) illustrates their relative sensitivity to climate change while their colour varies with the intensity of the predicted shift speed between current and future range centroids. Size classes (SC1, SC2, SC3, SC4) are in increasing order, with SC1 gathering the smallest species and SC4 the largest ones

average change in occupancy below −20%). After which all species present mean range restrictions ranging between −19% (*Centropages typicus*) and −0.42% (*Lubbockia squillimana*). The mean ratio is 14.8 (± 26.8), which corresponds to a mean loss in occupancy of −7% (± 6.53). The mean distance between present and future centroids is equal to 61 km (±49 km: maximum = 276 km; minimum = 3 km). The shift speed is 5.8 km/dec (±4.7 km/dec; maximum = 26.6 km/dec; minimum = 0.4 km/dec). All range centroids shift towards the North–West (data not shown).

The first two PCs of the PCA performed on the shift metrics explain 94.9% of total variance. The coordinates of species along PC1 (79.7% of total variance) were used as a synthetic index of relative sensitivity to climate change in the Mediterranean Sea (Table 1). The greater the index value, the higher the rates of range contraction, the larger the distance between the present and future range centroids as well as the quicker the centroid shifts.

3.2 | Species relative sensitivity in functional space

The MCA based on the species functional traits generated 11 dimensions but only the first four are kept according to the Kaiser-Guttman criterion. Each of the four significant MCA axes represents 27.52%, 21.27%, 12.91% and 9.96% of functional trait variance, respectively (71.66% in total). Trophic groups, spawning strategy and feeding strategy contribute the most to MCA1 (Figure 1a). The first axis separates sac-spawning carnivores and detritivores, with active ambush feeding or cruise feeding strategies, from broadcasting omnivores and herbivores presenting filter or mixed feeding behaviours. Size class (SC 2 and SC 3 vs. SC 4) and trophic groups (carnivores vs.

omnivores) mainly contribute to MCA2. MCA 3 opposes small (SC 1 and SC 2) ambush and mixed feeders to larger (SC 3 and SC 4) cruise and filter feeders (Figure 1b). Finally, the fourth MCA axis separates small herbivores from larger detritivores (Figure 1b).

The species coordinates along the selected MCA axes are used to identify groups of species sharing similar trait combinations from a functional dendrogram. Seven functional groups are defined: large sac-spawning carnivores, small ambush-feeding carnivores, large filter-feeding herbivores, small broadcasting filter-feeding herbivores together with mixed feeders, small sac-spawning herbivores, small sac-spawning detritivores and small ambush-feeding omnivores (but see Benedetti, Vogt, Righetti, Guilhaumon, & Ayata, 2018 for a thorough description).

The most sensitive taxa are located on the negative side of MCA1 (Figure 1a): small filter-feeding herbivores and omnivores seem less affected by climate change than large carnivores and detritivores. However, the least sensitive species are also found in this part of functional space, so no correlation is found between the species' relative sensitivity and their coordinates along the first two MCA axes (p-value > 0.1). The species shift speed or sensitivity to climate change could not be correlated with their position along MCA 3 and 4 (Figure 1b). Additionally, the sensitivity index (or any of the change metrics described above) does not show significant variations between the seven functional groups we defined (Kruskal-Wallis tests, p-value > 0.05; Supporting Information Figure S1). No significant variations are found when choosing a higher cutting-level on the functional dendrogram (i.e., fewer but larger functional groups). This is also true when exploring sensitivity to climate change across functional traits instead of

groups. Consequently, even though the most sensitive species are located among the large and small filter-feeding herbivores, these functional groups also comprise less sensitive species, preventing a whole functional group from being especially sensitive to climate change in the Mediterranean Sea.

We tested the robustness of our results to the choice of methods to estimate FD. The species sensitivity index was clearly not clustered in a functional space defined through a PCoA based on Gower's distance (Supporting Information Figure S2). The functional dendrogram drawn from the Euclidean distance matrix based on the MCA scores is similar to the Gower distance matrix based on the same trait values apart from the body length which was kept continuous as their cophenetic correlation equals 0.72 (Mérigot et al., 2010). In addition, estimates of species functional uniqueness and originality were not significantly correlated with

the species climate change sensitivity index, or with any of the shift metrics (p-values > 0.05).

3.3 | Projected changes in species richness and functional diversity

The patterns of ΔSR between the 2068–2098 and the 1965–1994 time periods (Figure 2a) show losses in diversity over almost the entire Mediterranean Sea (97% of the grid cells, Figure 2a). The average ΔSR is equal to −7.42. The highest decreases in diversity (ΔSR < −10) are found in the eastern basin, whereas the western basin presents very low decreases in richness. The only gains in SR are located in the northernmost regions of the Adriatic and Aegean Seas.

Our projections of ΔFD follow the same patterns as ΔSR (Figure 2b): declines in FD are found over most of the basin but they
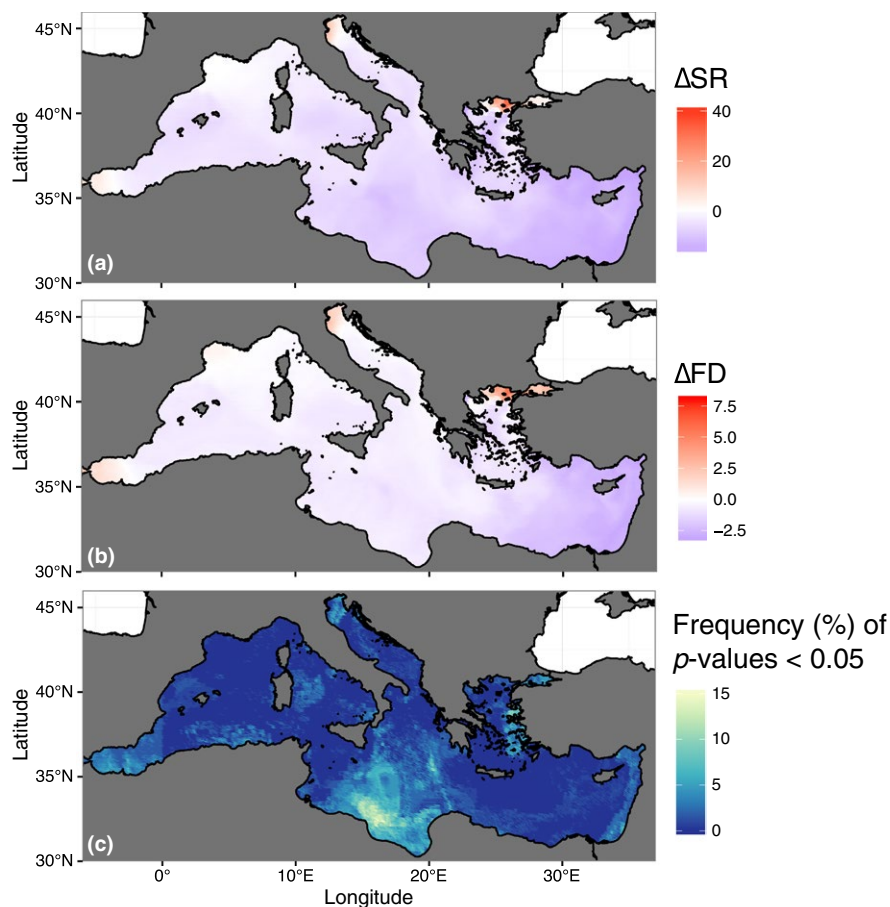

FIGURE 2 Spatial distribution of the (a) average difference in copepod species richness (ΔSR), (b) average difference in copepod functional diversity (ΔFD) between current (1965–1994) and future (2069–2098) surface assemblages of the Mediterranean Sea, and (c) how ΔFD estimates differ from predictions from the ΔSR projections alone. Estimates of average species richness (SR) for the current and future time periods were derived from the species distributions modelled through an ensemble of five Environmental Niche Models (ENMs) under a A2 emission scenario. Average functional diversity (FD) was estimated through Faith's index based on a functional dendrogram. The functional dendrogram was drawn from the Euclidean distance matrix obtained using the species coordinates along the four components of a multiple correspondence analysis (MCA) based on the species functional traits (size class, trophic group, feeding strategy and spawning strategy). Null estimates of ΔFD were obtained by randomizing the position of the species affected by climate change on the functional dendrogram. The observed ΔFD estimates were compared to the distributions of null ΔFD estimates to estimate their statistical significance (p-values). The frequency (%) of p-values <0.05 per assemblages (i.e., cell grid) indicates how frequently ΔFD differs from the changes in FD that can be expected from ΔSR alone

rarely exceed −2.5. Relatively higher declines of FD occur in the eastern basin while the western basin shows very little to no changes in FD. Gains in FD occur in the same areas as gains in SR. At the chosen significance threshold (α = 5%) and over the entire basin, variations in FD very seldom differ from a null distribution (Figure 2c). Indeed, the frequency of observed ΔFD estimates with a p-value lower than 0.05 (i.e., significantly different than the null estimates) is generally lower than 5%. The maximal frequency of observed non-null ΔFD is of nearly 15% and is only observed in the southern Ionian Sea (off Libya) and in the Eastern Aegean Sea. Overall, our results indicate that climate change-induced variations in FD do not differ from the variations that can be expected from changes in species richness alone. This is in line with the above results: the sensitivity of copepods to climate change is not clustered in functional space.

4 | DISCUSSION

4.1 | Climate change has little impact on zooplankton functional diversity

Our study is the first to explore the potential impacts of future warming and increased salinity on zooplankton functional diversity in the Mediterranean Sea. At the scale of the basin, we predict climate change impacts on FD that do not differ disproportionally from its impacts on SR (Figure 2): decrease in SR spreads across functional groups and does not lead to disproportionate losses in FD. In addition to low rates of species losses, the limited impact of climate change on FD is also explained by functional redundancy within the assemblages (Rosenfeld, 2002). Indeed, the species that are lost from the initial assemblages share similar traits with the species that remain, or that are gained, in the future assemblages (Supporting Information Figures S1 and S2). Such functional redundancy between "losers" and "winners" may provide a buffer against the attenuation or loss of functions within the ecosystem (Mouillot et al., 2013). This is supported by the distribution of the relative sensitivity index in functional space (Figure 1) or across functional groups: the functional space is homogeneously impacted by the future temperature and salinity conditions that have been projected for the Mediterranean Sea. Analogous patterns were also reported for coastal Mediterranean fish assemblages (Albouy et al., 2012, 2015). These results imply that the functional redundancy of Mediterranean assemblages is spread across trophic levels. However, the extent to which the current links between trophic levels will be maintained under the future climate conditions of the Mediterranean Sea remains unknown. Beyond shifts in the spatial distribution of species, shifts in their phenology may also lead to trophic link disruptions between prey and predators and thus alter food-web functioning (Mackas et al., 2012).

4.2 | Implications for conservation and marine policy

The higher rates of future warming and salinity increases predicted in the southeastern Mediterranean Sea (Adloff et al., 2015) trim the southeastern parts of the species ranges. As a consequence, all species range centroids shift towards the North–West, but none of the species is expected to have its realized distribution range entirely reduced. Therefore, no copepod species is predicted to disappear from the region by the end of the century through a "cul-de-sac" effect, contrary to what is expected for some coastal endemic fishes (Lasram et al., 2010). However, local extinctions remain possible since our methodology does not account for drivers of zooplankton distribution that prevail at finer scales (e.g., biotic interactions, community succession, dispersal limitation). The resilience of marine organisms at the sub-regional and local scales can be promoted through the establishment of Marine Protected Areas (MPAs; Micheli et al., 2012). However, it has been shown that the current Mediterranean MPA network performs as good as random when it comes to covering the different facets of diversity in coastal areas (Guilhaumon et al., 2015). This is partly due to the much wider coverage of the MPA network in the northwestern Mediterranean coasts compared to the southern ones (Mouillot et al., 2011). Our results underline that such asymmetrical spatial distribution of MPAs might be critical for the conservation of biological communities as the strongest decrease in copepod richness and FD are predicted to occur in the South-East Mediterranean Sea (Figure 2). This implies that southeastern communities might be particularly at risk because of future diversity losses within lower trophic levels, on top of stronger temperature increase (Adloff et al., 2015), and poor MPA coverage. Our study highlights the urgent need to extend the current MPA network and to include climate-driven changes in the zooplankton in the process for setting realistic and efficient management targets (McQuatters-Gollop et al., 2017). However, the copepod species studied might not be the most suited to set management targets because: (a) none are expected to disappear at the regional scale, (b) they present relatively lower conservation value compared to charismatic taxa (e.g., marine mammals, sea birds or turtles) and (c) they are dispersed over very large scales so their conservation must incorporate complex connectivity patterns that may also be altered in the future (Dubois et al., 2016). However, as the dynamics of these priority taxa do rely on zooplankton through food-web interactions, we encourage the inclusion of zooplankton FD as a surveillance indicator to better understand their current distribution and how these may change in the future (Shephard, Greenstreet, Piet, Rindorf, & Dickey-Collas, 2015). Adopting zooplankton FD as an indicator within the Marine Strategy Framework Directive would fall in line with an ecosystem-based management of diversity and ecosystem services (McQuatters-Gollop et al., 2017). Our study identifies the copepod species that might be the most affected by climate change in the Mediterranean Sea (Table 1). These most sensitive species could be adequate candidates to help track climate change impacts on Mediterranean marine ecosystems. Consequently, we encourage the current environmental and biological monitoring programmes to better understand the role of these species in Mediterranean food webs and how changes in their presence or relative abundance may affect ecosystem functioning.

4.3 | Towards a more tropical Mediterranean zooplankton?

Although the most negatively impacted species are not clustered in functional space (Figure 1), they do share similar biogeographic origins that we will now discuss. The contemporary biodiversity of the Mediterranean results from its complex geological history and large-scale climatic variability that led to cycles of connections and disconnections with the surrounding Atlantic and Indian basins (Bianchi & Morri, 2000). As a consequence, taxa from diverse biogeographic provinces were able to establish populations in the region (Bianchi & Morri, 2000; Meynard, Mouillot, Mouquet, & Douzery, 2012). No planktonic copepod species is clearly endemic to the Mediterranean Sea (Razouls et al., 2005–2017). The zooplankton communities mix ubiquitous species with taxa from the Atlantic Ocean, the Red Sea and the tropical Indian Ocean (Razouls et al., 2005–2017; Zenetos et al., 2010). In this respect, the species for which we estimate the strongest rates of range restriction (Table 1) are known for their Atlantic origins. Species such as *Acartia (Acartia) danae* (Belmonte & Potenza, 2001), *Calanus helgolandicus* (Bonnet et al., 2005), *Oithona atlantica* (Mazzocchi, Licandro, Dubroca, Di Capua, & Saggiomo, 2011; Razouls et al., 2005–2017), *Pseudocalanus elongatus* (Unal, Frost, Armbrust, & Kideys, 2006) or *Temora longicornis* (Champalbert, 1996) are considered as indicators of the entrance of Atlantic waters and temperate conditions, and are usually sampled in the coldest and more productive regions (northwest Mediterranean Sea, Alboran Sea, Northern Adriatic and Aegean seas). At the global scale, they are frequently sampled in the North Atlantic, as opposed to the least sensitive species that are more frequently sampled in the Indian Ocean (http://www.iobis.org/). Our results are in line with expectations from the niche patterns found in another study (Benedetti et al., 2018), where the most sensitive species were found to be affiliated to colder, fresher, more seasonally varying and more productive conditions, contrary to the least sensitive species which were associated with more tropical and oligotrophic conditions. The decline of the distribution of taxa affiliated to temperate conditions to the benefit of species associated with tropical ones is part of the wider "tropicalization" process of Mediterranean biodiversity, with warm-water species (alien or native) being favoured to the detriment of cold-water species (Bianchi, 2007). Consequently, our results support the hypothesis of the "tropicalization" of the Mediterranean zooplankton. The extent to which the increasing prevalence of tropical taxa may translate into a shift towards smaller and less energetic species (i.e., less rich in lipids) remains to be tested (Beaugrand, Edwards, & Legendre, 2010).

It should be noted that the species pool considered here does not comprise species from the Red Sea and the Indian Ocean that are too rare and/or not abundant enough in the Mediterranean yet. As a consequence, it is possible that future warming facilitates the establishment of such species in the Mediterranean Sea, a process that we would have misrepresented in our study (Lasram &

Mouillot, 2009; Parravicini, Azzurro, Kulbicki, & Belmaker, 2015). This bias could lead to an underestimation of turnover rates between present and future copepod species assemblages (Benedetti et al., 2017).

More generally, our projections fall in line with the global and coherent imprint of climate change on marine biodiversity (Poloczanska et al., 2013): the increases in temperature lead to the poleward range shift of species tracking their optimal thermal habitat. The present range shifts and speeds (Table 1) are comparable to the ones predicted in the North Atlantic for copepods (Villarino et al., 2015) and phytoplankton (Barton, Irwin, Finkel, & Stock, 2016). They are also coherent with in situ observations at the global scale (Poloczanska et al., 2013). ENMs-derived projections in range shifts are generally verified by observations for the marine plankton (Poloczanska et al., 2013), since the latter benefit from tremendous dispersal potential (Jönsson & Watson, 2016) and short life cycles, which enable them to efficiently adapt to changing climate conditions (Sunday, Bates, & Dulvy, 2012).

Our approach is limited by the functional traits that are available in the literature for the taxa studied. Among the traits composing the typology of Litchman et al. (2013), only four were used to estimate FD and define functional groups since others were not accessible. Accounting for a large number (over 100) of copepod species is relevant in our case as copepods largely dominate the abundance and diversity of zooplankton in the Mediterranean Sea without a single genus prevailing (Siokou-Frangou et al., 2010), contrary to *Calanus* spp. in the North Atlantic (Helaouët & Beaugrand, 2007). Focusing on so many zooplankton species prevents us from using a more comprehensive set of traits. Quantitative physiological and morphological traits such as biovolume, growth rates or excretion rates are available only for a very limited number of taxa (often belonging to the Calanoïda), for which sampling and culturing is mastered (Brun et al., 2017). This limitation could be removed through the exploitation of plankton imaging techniques that measure several morphometric traits at the individual level simultaneously, and that can simultaneously describe the emerging properties and the community composition of the plankton (Gorsky et al., 2010). The development of imaging techniques will also help integrating the relative fitness of different zooplankton functional groups by providing abundance data which are generally not accessible at the macroecological scale. This is crucial because presence/absence data, such as those used here, fail to describe the variations of functional traits at the scale of individuals, which is the scale that mediates the functioning of ecosystems.

To conclude, this is the first study to estimate the potential impacts of future environmental changes on the FD of the zooplankton in the Mediterranean Sea. We find that future changes in surface temperature and salinity will have little impact on copepod FD as the most negatively impacted species are spread out across functional groups. Our results suggest that climate change may not weaken one of the ecological functions performed by copepods. Yet, the data currently available do not allow to resolve the role of intra-species traits variations or the functional groups'

relative abundance in the functioning of the pelagic ecosystems. It is urgent that current plankton monitoring programmes and future studies incorporate the functional dimension of diversity so we can better understand the possible responses of pelagic ecosystems to climate change.

DATA ACCESSIBILITY

All input data and R functions for estimating the FD of Mediterranean copepod assemblages are publicly available through the references and online sources cited in the text.

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BIOSKETCH

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Author contributions: F.B. gathered the biological data and designed the study with F.G. and S.-D.A.F.A. provided the environmental layers for the future Mediterranean Sea. J.-O.I. optimized the functional diversity analysis. All co-authors contributed to the writing of the manuscript led by F.B.

SUPPORTING INFORMATION

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