



# Rapid winter warming could disrupt coastal marine fish community structure

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**Marine ecosystems are under increasing threat from warming waters. Winter warming is occurring at a faster rate than summer warming for ecosystems around the world, but most studies focus on the summer. Here, we show that winter warming could affect coastal fish community compositions in the Mediterranean Sea using a model that captures how biotic associations change with sea surface temperature to influence species' distributions for 215 fish species. Species' associations control how communities are formed, but the effect of winter warming on associations will be on average four times greater than that of summer warming. Projections using future climate scenarios show that 60% of coastal Mediterranean grid cells are expected to lose fish species by 2040. Heavily fished areas in the west will experience diversity losses that exacerbate regime shifts linked to overexploitation. Incorporating seasonal differences will therefore be critical for developing effective coastal fishery and marine ecosystem management.**

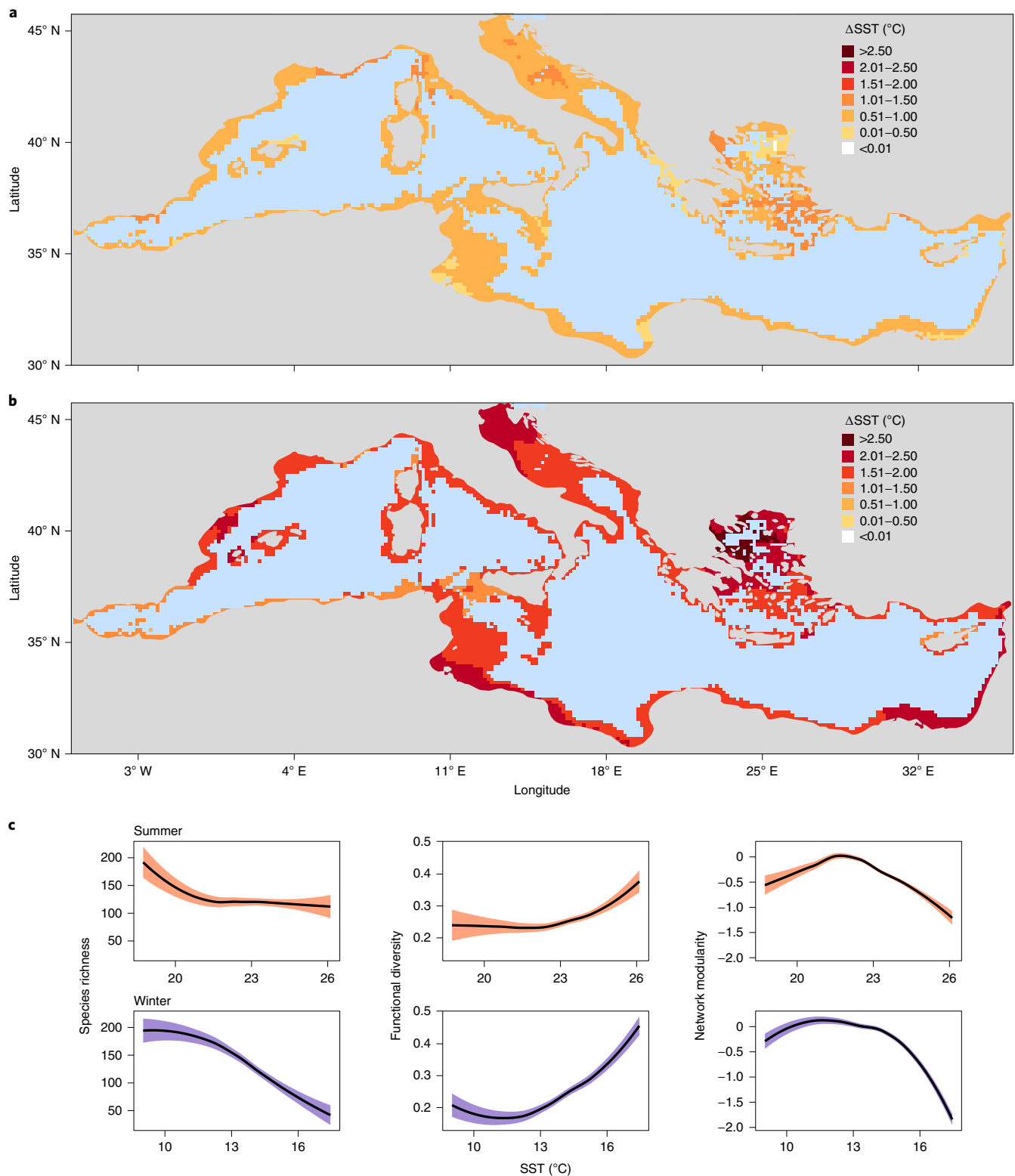
Warming seas affect the structure and function of marine communities by altering distributions of food sources, influencing reproductive behaviours and changing the range of habitats that fall within species' thermal limits<sup>1–5</sup>. These impacts are especially important in coastal areas of the Mediterranean Sea—a biodiversity hotspot that provides food and trade for residents from over 20 countries<sup>6,7</sup> (Extended Data Fig. 3) and already represents one of the world's most heavily impacted ecosystems<sup>8,9</sup>. Shallow continental shelves are highly vulnerable to thermal stress, and these waters account for almost three times the proportional area of the Mediterranean Sea compared with globally (20 versus 7.6%)<sup>10</sup>. Consequently, the average sea surface temperature (SST) in the Mediterranean will be up to 2.8°C warmer by 2100<sup>11,12</sup>. However, disparities in seasonal warming complicate predictions of how fish communities that occupy these waters will respond to climate change<sup>13–15</sup>. IPCC Special Report on Emissions Scenarios (SRES) A2 projections indicate that winter warming of coastal SST will increase at twice the rate of summer warming, with a forecast average winter increase of 1.85°C by 2040 (compared with 0.76°C in summer; Fig. 1a,b). Yet, while environmental constraints on ecosystems are often more apparent during particular seasons<sup>16–19</sup>, few studies disentangle seasonal effects when assessing how SST influences communities (but see refs. <sup>1,20</sup>).

We reveal a robust relationship between SST and the compositions of coastal Mediterranean fish communities. However, we find that winter warming will have a far greater effect on coastal communities than summer warming, highlighting the importance of incorporating seasonal effects in models. We used a conditional random fields (CRF) model that identified associations among the distributions of 215 coastal fish species (approximately one-third of species occurring in the Mediterranean Sea) and quantified how these associations changed in response to summer and winter SST across a grid of 8,154 spatial cells (Extended Data Fig. 1). Spatial generalized additive models (GAMs) were used to assess variation in predicted community compositions. In contrast with the effects of changes in summer SST, which were statistically significant but comparatively

weak, variation in winter SST had a strong influence on the number of fish species in each grid cell (species richness), the diversity of functional traits exhibited by those species (functional diversity) and the degree to which species co-occur with others from the same functional group (network modularity) (Fig. 1 and Supplementary Table 2). Species richness followed a west–east gradient, declining rapidly as winter SST approached and exceeded 12–13°C (Fig. 1c, Extended Data Fig. 2 and Supplementary Table 2). Model simulations using IPCC climate scenarios for two time points (1980 and 2040) revealed that future warming will have profound impacts on coastal communities, with over half (60%) of our 8,154 observations projected to support fewer species in 2040. In contrast, 36% were projected to support more species in 2040. Magnitudes of change will not be spatially uniform. The greatest losses are expected in species-rich regions including areas in the Alboran Sea (one of the most intensively fished coastal regions in the Mediterranean<sup>21</sup>) and the Central Gulfs near Tunis and Tripoli (Fig. 2a and Extended Data Figs. 2–5). As our model did not include indicators of fishing pressure or forecast how fishing tactics may change, we cannot accurately infer how Mediterranean fishing pressures and warming temperatures will interact to exacerbate shifts in coastal fish composition. Insights from this study will help to inform the management of fish stocks moving forward, in particular by raising the need for research to explore how population growth, natural resource harvesting and aquaculture practices will influence the economic effects of climate change<sup>22</sup>.

Much of the Mediterranean's coastal shelf will be at least 1.5°C warmer in winter by 2040, with few grid cells remaining below the 12–13°C threshold (Fig. 1b and Extended Data Fig. 2). Such warming is expected to have negative consequences for ecosystem functioning and marine productivity<sup>12,23,24</sup>. However, our findings indicate that locations remaining below the threshold (primarily in the Adriatic and Aegean seas) could be partially buffered against losses of richness and might even gain species by 2040 (Fig. 2a and Extended Data Figs. 2 and 4). Projections indicate that warming winter SST will not affect the distributions of species equally (Fig. 3a

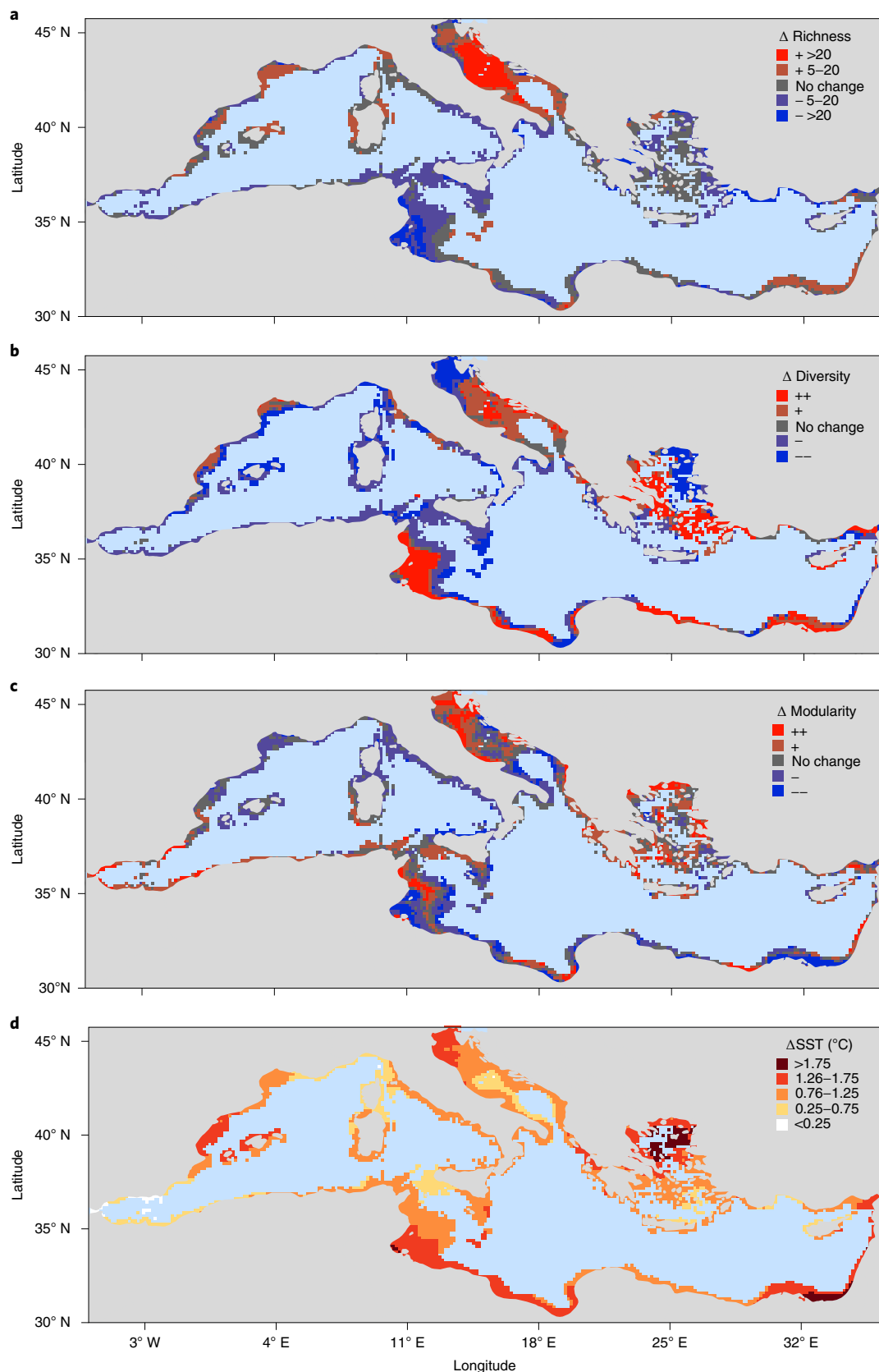
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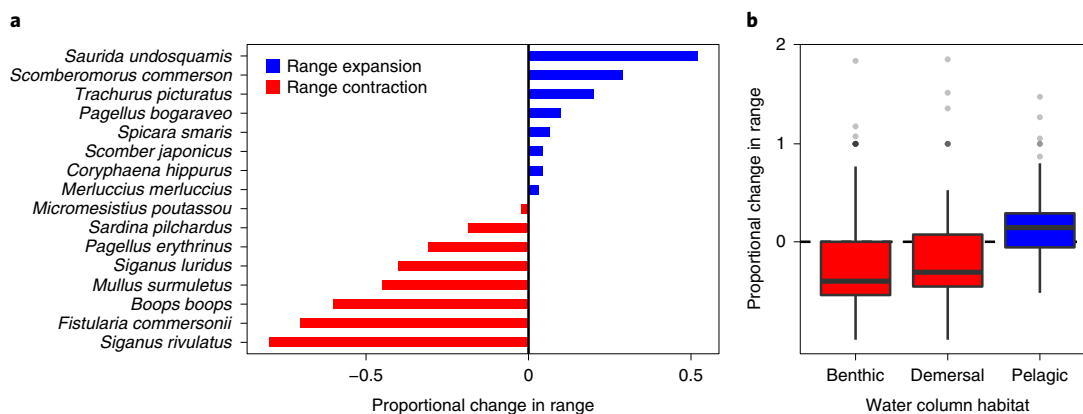
**Fig. 1 | Winter SST gradients have larger effects on Mediterranean fish communities. a, b**, Predicted changes in summer (July to August) SST (**a**) and winter (January to March) SST (**b**) between 1980 and 2040 across the coastal shelf. **c**, Partial effects of summer (top) and winter SST (bottom) on the species richness (left), functional diversity (middle) and network modularity (right) of observed fish communities in 1980. SST covariates were included in spatial GAMs. Black lines show mean effects. Shaded areas show effect 95% confidence intervals.

and Extended Data Figs. 6 and 7). Benthic and demersal dwellers will be more likely to show a range contraction than pelagic species (Fig. 3b and Supplementary Appendix 3), consistent with

evidence that marine species capable of shifting their ranges in response to warming tend to have faster growth rates, earlier ages at maturity and shorter life spans<sup>1,25</sup>. As many benthic and demersal



**Fig. 2 | Warming SSTs will lead to pronounced changes for fish communities across the Mediterranean Sea. a–c,** Predicted changes in fish community species richness (**a**), functional diversity (**b**) and network modularity (**c**) between 1980 and 2040 based on SST projections using IPCC A2 climate observations. **d,** Predicted difference in SST warming rates between winter and summer seasons. See Supplementary Fig. 3 for maps of historical and future projections for each community metric. Predictions were made with a spatial CRF model that included presence versus absence for 215 fish species and covariates describing summer and winter SST.



**Fig. 3 | Range responses will differ across fish species, with bottom dwellers expected to show substantially reduced ranges in response to warming temperatures.** **a, b**, Predicted changes in fish species' geographical ranges between 1980 and 2040 for species of economic and conservation importance, including non-indigenous species with the greatest potential impacts (according to the General Fisheries Commission for the Mediterranean) (**a**); and all 215 species, arranged by water column habitat use (**b**). Range sizes were calculated by summing presence/absence vectors across all 8,154 grid cells. Changes were calculated by dividing the 2040 range size by the 1980 range size. The boxplots in **b** show median values (lines within boxes), 25 and 75% quantiles (hinges), and 5 and 95% quantiles (whiskers).

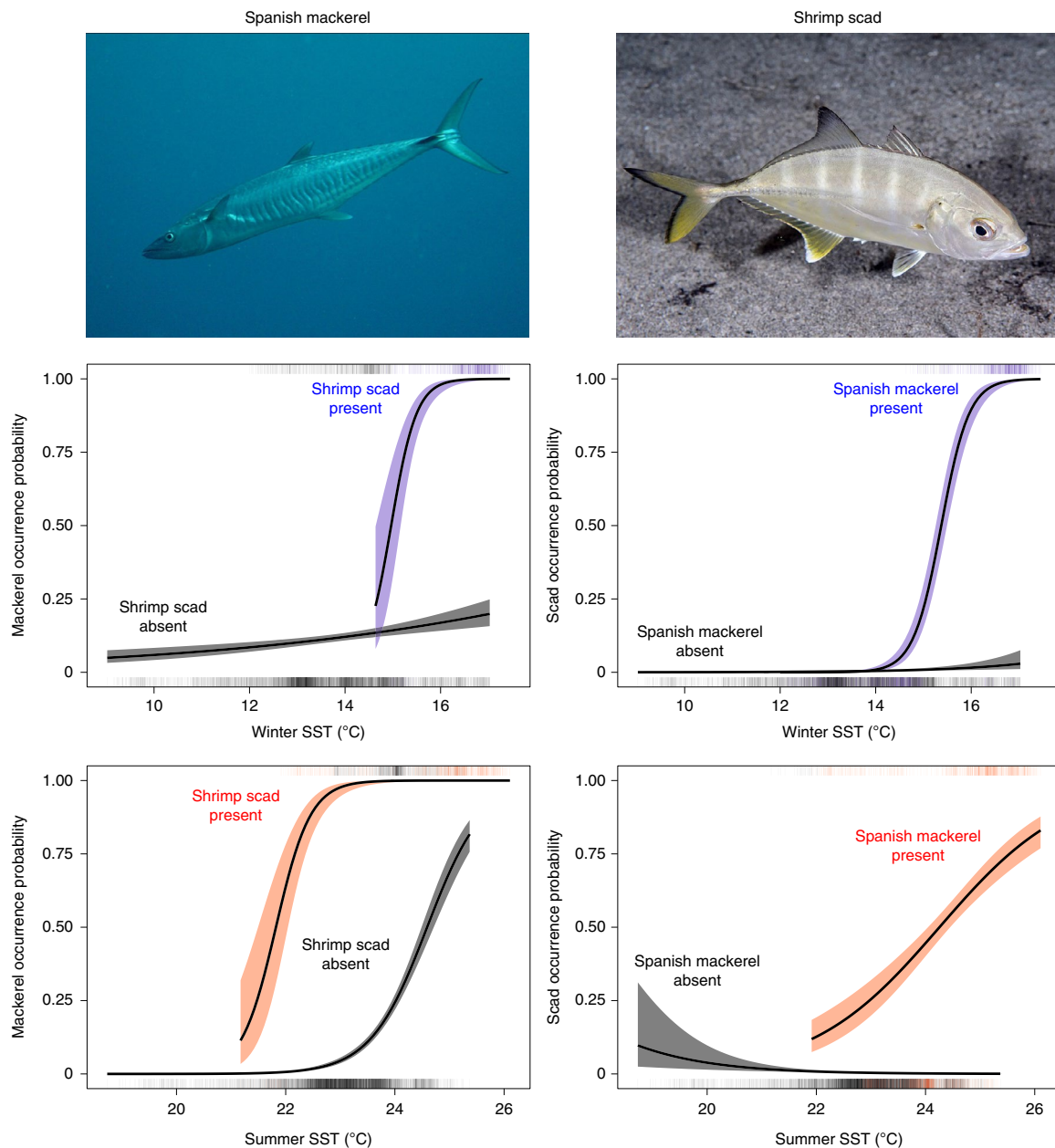
coastal species are specialized endemics, our study contributes to previous evidence that some endemics will experience substantial climate-driven range contractions across the Mediterranean Sea<sup>26</sup>. Areas that remain cool in winter could serve as important refugia for species that prefer colder waters, but this will rely on the ability of at least some species to adapt to temperature changes by shifting their distributions, as has been demonstrated for species in the North Sea<sup>1</sup>. While multiple studies have identified similar potential for cool-water refugia in the Adriatic and Aegean seas<sup>2,26</sup>, we are not aware of empirical evidence showing that meaningful shifts to cooler refugia are taking place.

Many studies exploring how climate change impacts food security recognize that ecosystem services are dependent not only on richness, but also on how functional niche spaces are occupied<sup>2,22,24</sup>. We assessed the relationship of SST with the capacity of grid cells to harbour functionally diverse niches to gain insights into mechanisms that structure fish communities. Unexpectedly, we found that despite being less rich, cells with warmer winter SST were more functionally diverse, supporting species with a broader range of dietary and habitat use traits (Fig. 1c and Supplementary Table 2). Once again, winter SSTs of 12–13 °C represented a threshold for changes in functional diversity, while the effects of summer SST were notably weaker (Figs. 1c and 2b and Supplementary Fig. 4). Examination of 5,266 co-occurrence relationships showed that network modularity, which describes the extent to which species co-occur with species from the same functional group, decreased as winter SST increased (Figs. 1c and 2c). These findings collectively suggest that winter SST acts as an environmental filter that restricts functional equivalence in warmer waters. Steep declines in species richness and reductions in network modularity in locations with winter SSTs above 12–13 °C primarily indicate losses of functionally redundant species, leading to greater diversity metrics when the species that remain are functionally dissimilar. For example, in grid cells off Tunis, where communities are expected to cross the 13 °C winter SST threshold and show declines in richness (Supplementary Figs. 3–5), the peacock wrasse (*Symphodus tinca*) is expected to be lost while its most functionally similar species, the painted comber (*Serranus scriba*), will remain. As both species fill similar functional niches (feeding on invertebrates around rocky reefs in the neritic zone), the loss of one does not reduce functional diversity. Similar relationships between SST and functional redundancy have been found for coral reef fish assemblages across the Pacific<sup>27</sup>, suggesting that an environmental

filtering effect that promotes functional equivalence in cooler waters may be a broad-scale phenomenon. Despite the predicted costs of decreasing richness with future warming, driven primarily by contracting ranges for demersal and benthic dwellers, our analysis indicates that some Mediterranean locations will be buffered against losses of functional diversity (Fig. 2b). To further understand how individual fish populations will respond to warming temperatures, additional information on species' thermal tolerances and other relevant predictors will be necessary to forecast changes in fitness and the carry-on effects on relative abundances<sup>3,22</sup>. Moreover, as we excluded species that did not have associated trait or phylogenetic data, our findings cannot rule out the possibility of future invasions or migrations of unmodelled species that may be able to fill some niche gaps freed by lost species.

By allowing species' distributional associations to vary in response to SST, our model could uniquely identify mechanisms that underlie our finding of increased functional niche filling across winter SST gradients (Supplementary Appendix 3). Winter SST had a strong positive influence on nearly half (41.5%) of the 5,266 identified relationships, while summer SST effects were on average four times weaker (the remaining 58.5% of relationships did not co-vary with SST gradients; Supplementary Table 3). Associations for two invasive species—the shrimp scad (*Alepes djedaba*) and Spanish mackerel (*Scomberomorus commerson*)—illustrate this result. Both species have profound impacts on the abundances of native species and are increasingly captured as bycatch in commercial and residential fisheries<sup>28,29</sup>, yet they occupy different pelagic functional spaces, with the scad feeding on inshore reef invertebrates and the mackerel feeding primarily on small fishes. This lack of functional overlap allowed each species to be 73% more likely to occur when the other was present, but the relationship was modulated by winter SST (Fig. 4). The pair only co-occurred in the warmest 40% of their winter SST ranges (compared with co-occurring throughout their summer SST ranges), with the effect of the mackerel's presence on the scad's occurrence increasing by 76% for every 1.7 °C increase in winter SST (Fig. 4). These estimated association strengths suggest that winter warming will open new areas for these invasive species to co-occur across the Mediterranean in the future.

Our projected changes to Mediterranean fish communities point to new challenges for the stability of fisheries-based economies. Landings for demersal and pelagic fishes in the Mediterranean Sea have been declining since the mid-1990s for a range of important



**Fig. 4 | Winter SSTs impact how species associate and assemble into communities.** Top: the Spanish mackerel (*S. commerson*; left) and shrimp scad (*A. djedaba*; right) are two widespread invasive species that exhibit a strong association: the presence or absence of one predicts whether or not the other will be present in a given location. Analysis of how this association relates to SST showed that increasing winter SST (middle) leads to a more prominent association, while the association does not change across summer SSTs (bottom). Black lines show mean effects. Shaded areas show effect 95% confidence intervals. Rugs show observed presences (tops of graphs) and observed absences (bottoms of graphs). Photograph in the top left panel is adapted from John E. Randall under a Creative Commons licence (<https://creativecommons.org/licenses/by-nc/3.0/au/>). Photograph in the top right panel is reproduced from Rickard Zerpe under a Creative Commons licence (<https://creativecommons.org/licenses/by/2.0/>).

species<sup>30</sup>. In contrast, crustacean and cephalopod landings are increasing, suggesting that regime shifts are already occurring<sup>21</sup>. Our comparison of fishing pressures, calculated as total fishery landings per km<sup>2</sup> of coastal shelf area, overwhelmingly showed that heavily fished areas of the west will exhibit some of the most pronounced losses in diversity and increases in modularity (Extended Data Fig. 5), both of which are signs of ecosystems trending towards collapse. Indeed, western Mediterranean fisheries are verging on being unprofitable due to long histories of overexploitation<sup>21</sup>. In contrast, fisheries stocks in the more artisanally fished eastern zones appear to be declining at a slower rate<sup>21,30</sup>, and our analyses indicate

that these areas could gain diversity and experience more subtle changes in species richness (Extended Data Fig. 5).

Worldwide, winter warming is expected to proceed at a faster rate than summer warming for many marine and terrestrial ecosystems. Marked increases in winter SSTs predicted for shallow coastal waters will have a disproportionately large influence on the composition of fish communities in the Mediterranean, most notably causing considerable loss of fish species and exacerbating regime shifts in fishery-dependent regions. Winter warming is likely to be a major driver of long-term trends in fish diversity and community composition in the Mediterranean. Our research

highlights the critical importance of incorporating seasonal differences in assessing the ecological impacts of climate change. This information, enabling greater insight into how communities will respond to global warming, will be crucial for policymakers and managers in the development of future ecosystem and resource management strategies.

### Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41558-020-0838-5>.

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## Methods

**The FishMed database.** FishMed is an open-source database that captures historical and projected distributions for fish species across 8,154 spatial grid cell locations in the Mediterranean Sea's continental shelf<sup>31</sup> (Fig. 1; note that blue areas in the maps represent areas with no data). The database includes evolutionary (a phylogenetic tree) and functional trait data (a matrix of habitat, diet and morphological variables) for select fish species, as well as back-projected (to the period 1961–1980) and forward-projected (to 2040–2059 and 2080–2099) SST according to the IPCC SRES A2 scenario<sup>32</sup>. SRES A2 was chosen as it predicts intermediate climate forcing compared with other SRES scenarios<sup>33</sup> and because the availability of undersea three-dimensional projections has led to this scenario being the model of choice for studying climate change in the Mediterranean<sup>34</sup>. Historical distributions were compiled using the *Fishes of the North-Eastern Atlantic and the Mediterranean* atlas<sup>35</sup>. This atlas combines regional datasets with expert knowledge and provides basin-wide information on the extent of occurrence of all Mediterranean fish species. Distributions were projected onto a spatial grid covering the Mediterranean's shallow coastal shelf and filtered by clipping areas with depths known to be outside the vertical distributions occupied by each species using data on their bathymetric ranges and a bathymetry map of the Mediterranean Sea<sup>2</sup>, resulting in 8,154 locations for which the geographical distributions of 635 fish species are represented. The database also includes predicted species distributions for the two future climate scenarios, which were generated using single-species distribution models trained on SST values<sup>2,31</sup>. However, our model only relied on the historical observations of fish distributions that were originally compiled from trusted sources and expert opinion. We did not use future projections as data to avoid relying on observations that were the outcomes of earlier modelling and interpretation efforts. We removed species that did not have associated trait or phylogenetic data, as the absence of such data meant we could not accurately assess correlates of diversity or modularity. This resulted in 336 species including 140 benthic, 93 demersal and 103 pelagic species. We omitted species recorded in <10% or >90% of total observations, as estimating occurrence probabilities for binary outcomes that are too rare or too common leads to imprecise estimates of network topology<sup>36</sup>. Cut-off values were chosen as initial models revealed that the strong class imbalances for species outside these thresholds hampered the ability of cross-validation routines to estimate coefficients (that is, a cross-validation fold containing nearly all zeros or all ones is not informative for estimating effects of predictors<sup>37</sup>). The dataset covered 215 fish species including 105 benthic, 57 demersal and 53 pelagic species (see Supplementary Appendix 1 for details of data filtering). We calculated mean summer SST (averaged across the three warmest months; that is, July to September) and winter SST (averaged across the three coldest months; that is, January to March) for each grid cell in the 1980 and 2040 periods. Effects of temperature on reproductive success or metabolism were not available for all of our studied species, so we did not include parameters to capture how thermal tolerances will impact range shifts.

**Modelling co-occurrence with CRFs.** A key step in predicting biodiversity responses to changing climates is determining how community structures change along environmental gradients. Co-occurrence patterns between species are useful in this domain as they can help build a picture of how communities form. Whether two species are more or less likely to co-occur in certain habitats can influence biotic interactions such as competition or facilitation<sup>38–40</sup>. Studying co-occurrences across changing environments can uncover mechanisms influencing community assembly, such as abiotic filters that prevent the establishment of species with particular traits or systematic drivers of local abundances<sup>41,42</sup>. Accounting for co-occurrences should therefore improve model-based predictions of species' distributions across heterogeneous environments<sup>43,44</sup>.

Undirected graphical models such as CRFs are gaining traction for their ability to outperform null models when uncovering co-occurrences and projecting multispecies distributions<sup>45,46</sup>. CRFs represent conditional dependencies (termed herein as associations to align with network notation) among variables as an undirected network, and can incorporate covariates to quantify how associations vary along environmental gradients<sup>47,48</sup>. The ability to determine effects of other species, environmental variables and species × environment interactions on distributions can help disentangle mechanisms that influence community composition in changing landscapes.

We applied CRFs using the framework described by Clark et al.<sup>49</sup> and references therein. Briefly, the log-odds of observing species  $j$  was modelled as:

$$\log \left[ \frac{P(y_j = 1 | y_{\setminus j}, x)}{1 - P(y_j = 1 | y_{\setminus j}, x)} \right] = \alpha_{j0} + \beta_j^T x + \sum_{k:k \neq j} (\alpha_{jk0} + \beta_{jk}^T x) y_k \quad (1)$$

where  $y_j$  is a vector of binary observations for  $j$ ,  $y_{\setminus j}$  represents vectors of binary observations for all other species,  $\alpha_{j0}$  is the intercept and  $\beta_j^T$  is a coefficient for the effect of covariate  $x$  on  $j$ 's probability of occurrence. Association parameters are represented by  $\alpha_{jk0}$  and  $\beta_{jk}^T x$  (defined below). Parameterization of the likelihood was estimated using LASSO regularized logistic regression, which forces coefficients to zero if they have minimal effects. This ensured that the model only included well-supported biotic effects. Tenfold cross-validation was implemented to

choose penalties that minimize error. Because CRFs are undirected, coefficients representing species interactions and coefficients representing effects of covariates on these interactions must be symmetrical (that is,  $\alpha_{jk0} = \alpha_{kj0}$  and  $\beta_{jk}^T x = \beta_{kj}^T x$ ). Symmetry was guaranteed by averaging the corresponding parameter estimates, ensuring that parameters were unified into a network only after maximizing each species' conditional log-likelihood<sup>50</sup>. If  $\alpha_{jk0} = 0$ , distributions of  $j$  and  $k$  were conditionally independent after accounting for covariates and all other species. If  $\alpha_{jk0} \neq 0$  but  $\beta_{jk}^T x = 0$ , species' occurrences were conditionally dependent, but the strength of this association did not co-vary with  $x$ .

The above CRF accounted for all combinations of other species and environmental covariates (winter and summer SST) on a species' occurrence probability but did not account for possible spatial autocorrelation. However, a key feature of spatial occurrence datasets such as FishMed is the non-independence of the source data that arises due to possible spatial autocorrelation, which can result in biased and inflated parameter estimates when using statistical models that ignore spatial structure. We therefore built a second CRF that included smoothed spatial regression splines in the linear predictor to assess whether incorporation of spatial terms improved the model fit. Central coordinates for each grid cell were used to construct penalized Gaussian process regression splines that capture non-independence among spatially adjacent cells<sup>51,52</sup>. Isotropic Gaussian processes are appropriate in this context as we have no previous evidence that autocorrelation in fish distributions are non-stationary, although we recognize that other methods to capture spatial effects are available in competing models. For both models, continuous predictors were scaled to unit variance. We calculated model fit metrics (the proportion of true predictions, positive predictive value, sensitivity and specificity) to assess performance and to validate our models (see Supplementary Appendix 2 for details of CRF fitting and metric calculations). Across all metrics, the spatial CRF was the better-performing model (Supplementary Table 1), correctly predicting >92% of the 1,753,110 total binary observations (215 species × 8,154 observations), compared with 88% for the non-spatial model. We therefore present the results from the spatial model herein.

We found that, of 46,010 possible pairwise species associations, 5,266 (11.5%) acted as important predictors of variation in community composition. Nearly half (41.5%) of these associations were environmentally dependent, becoming more positive as SSTs warmed (Supplementary Table 3 and Supplementary Appendix 3). This broadly demonstrated the utility of our approach by showing that the presence of one species acts as an increasingly useful signal of another's likelihood of being present as temperatures increase. The effects of changing winter SST on these pairwise associations were over two times larger than summer SST effects (mean change in association strength = 0.045 versus 0.019, respectively; Supplementary Table 3 and Supplementary Appendix 3). When considering those pairs that were less likely to co-occur in warmer areas, mean effects on association strengths were −0.016 versus −0.006 for winter and summer SST, respectively (Supplementary Table 3 and Supplementary Appendix 3).

Estimated associations may change if other predictors are added to the model, as many of the inferred co-occurrence associations could be the result of joint responses to missing covariates. However, while these missing predictors may limit network inference, a major benefit of our framework is that they should not heavily impact prediction. Considering that much of the variance captured by our model was attributed to associations, and that the model achieved robust prediction accuracy, inclusion of multispecies data should at least partially account for missing predictors, such as nutrient densities or salinity, that may play important roles in determining species' range limits<sup>50</sup>. Ecological forecasting studies have generally not recognized this rich information, instead relying on remote-sensing data for which concerns have been raised over temporal mismatch, incomplete coverage or areal unit problems. The CRF approach also has the added benefit of helping avoid the potential problem of regression dilution bias that occurs when inclusion of predictors that are difficult to measure (for example, habitat availability or complexity) leads to measurement errors that sometimes have profound effects on coefficient estimates<sup>53</sup>.

### Estimating community diversity and network composition across SST gradients.

We used the spatial CRF to predict species' distributions for the 1980 scenario and to calculate model-based estimates of species richness, functional diversity and phylogenetic diversity for each grid cell. Using these predictions (rather than observed data) allowed us to account for uncertainty when assessing influences of SST on community structure, and facilitated direct comparisons with future projections (see below). To calculate functional diversity, we applied hierarchical clustering to a distance matrix representing traits previously highlighted for their ability to uncover assembly patterns of coastal fish communities<sup>54,55</sup>. These included ten binary variables representing species' use of habitat categories, six dietary binary variables and a continuous body length variable. The functional dendrogram and phylogenetic tree (stored in the FishMed database) were used to calculate standardized diversity metrics based on the net relatedness index<sup>56,57</sup>, which were then included as response variables in GAMs to assess how diversity changed along SST gradients. For each GAM, we included smooth spline functions for winter and summer SST (both as thin plate regression smooths) to account for nonlinear relationships. To control for spatial autocorrelation, we included Gaussian process spatial smooths using geographical

coordinates of grid cells (the Gaussian process smooth function was found to yield a better fit compared with a thin plate smooth; see Supplementary Appendix 3 for details on GAMs). However, comparisons of functional and phylogenetic diversity were highly correlated (Pearson's  $R^2 = 0.79$ ), so we focused our analyses on functional diversity only.

Next, we tested whether co-occurrence networks were predicted to become more or less modular with increasing SST. Modularity assesses the degree to which a network is composed of densely connected groups of nodes that exhibit sparse associations with other groups<sup>58</sup>. By assigning species to groups based on habitat use in the water column (see details below) and estimating modularity, we could uncover useful insights into the mechanisms underlying variation in community composition. For example, high modularity would indicate that a species' occurrence was more strongly associated with occurrences of species from the same group. This could reflect environmental conditions that influence one group more strongly than others (for example, the presence or absence of an upwelling site may have stronger influences on distributions of pelagic than bottom-dwelling species). Low modularity may indicate a dynamic ecosystem composed of species that associate with a diverse array of partners. We integrated occurrence probabilities with estimated pairwise associations to generate adjacency matrices for each observation, allowing us to ask how network topology and community structure were expected to change. Specifically, association edges were predicted for each observation and then converted into a weighted, undirected adjacency matrix. If a linear prediction for a given species in a given grid cell fell below our threshold of 0.5, the species was considered absent from the cell and could not participate in the network, and any edges that would otherwise have connected to that species (from its associated partners) would be removed. The resulting networks (one for each grid cell in the data) were based on co-occurrence associations, rather than direct (or indirect) species interactions such as predator–prey relationships or facilitation. This provided information on community assembly, as whether species from different functional groups were more or less likely to co-occur in certain habitats could reflect underlying drivers of community composition. However, these networks did not reflect biotic interactions such as competition or facilitation, so they could not be validated against empirical interaction estimates from the literature. We calculated a standardized modularity metric for each observation by grouping species based on their vertical distributions in the water column (assigned to one of three categories: benthic, demersal or pelagic) and extracting the residuals from a linear regression between modularity (calculated using functions in the *igraph* R package<sup>59</sup>) and richness. Residuals were used for assessment of patterns because of the known bias that increasing richness can have on estimates of network modularity<sup>60</sup>. As above, we accounted for possible nonlinear relationships by fitting GAMs with thin plate regression smooths for SST predictors and a Gaussian process smooth for geographical coordinates. For all GAMs, comparisons of variograms for raw data and model residuals suggested that spatial smooth effects efficiently captured most of the spatial autocorrelation in the data (Supplementary Appendix 3).

**Projecting changes in communities using the IPCC SRES A2 scenario.** SST values across our coastal grid are predicted to warm by an average of 0.76°C in summer and 1.85°C in winter between 1980 and 2040. A final step in our analysis was to draw inferences about how communities may change under warming conditions. Combining our CRF results with SST values for 1980 and 2040 scenarios, we predicted species' future distributions by simulating from our model's posterior using a multivariate boosted regression tree<sup>61</sup>. We repeated the steps above to calculate expected richness, diversity and network modularity for each grid cell. While we did not include indicators of fishing zones or fishing pressure as predictors in the model, mapping our estimates for both time periods allowed us to assess how communities are expected to change under the future scenario and to draw inferences about how changes may vary across different Mediterranean fishing zones. For distribution projections, species were expected to occur in a cell if their predicted probability of occurrence was  $\geq 0.5$ .

Analyses were conducted in R version 3.3.3 (ref. <sup>62</sup>). CRF models were fit using functions in the MRFcov R package<sup>63</sup>. GAM models were fit using functions in the mgcv R package<sup>64</sup>. Data manipulation and figure generation primarily relied on the packages *dplyr*<sup>65</sup>, *ggplot2* (ref. <sup>66</sup>) and *ape*<sup>67</sup>. A schematic (Extended Data Fig. 1) and explanation of the model framework are included in the Supplementary Information.

### Data availability

The Mediterranean fish binary occurrence data and IPCC SRES A2 SST projections that support the findings of this study are described in ref. <sup>31</sup> and are available in the *Ecological Archives* (accession E096-203-D1).

### Code availability

All R code needed to extract data from public repositories, replicate all of the analyses and generate the figures is presented in the Supplementary Information file and stored in a licensed GitHub repository (<https://github.com/nicholasjclark/Mediterranean-Fishes-MRF>).

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### Author contributions

N.J.C. conceived of the idea, conducted the analyses and wrote most of the first draft of the paper. J.T.K. and C.I.F. contributed conceptual advice and helped with writing the paper and with refining later drafts.

### Competing interests

The authors declare no competing interests.

### Additional information

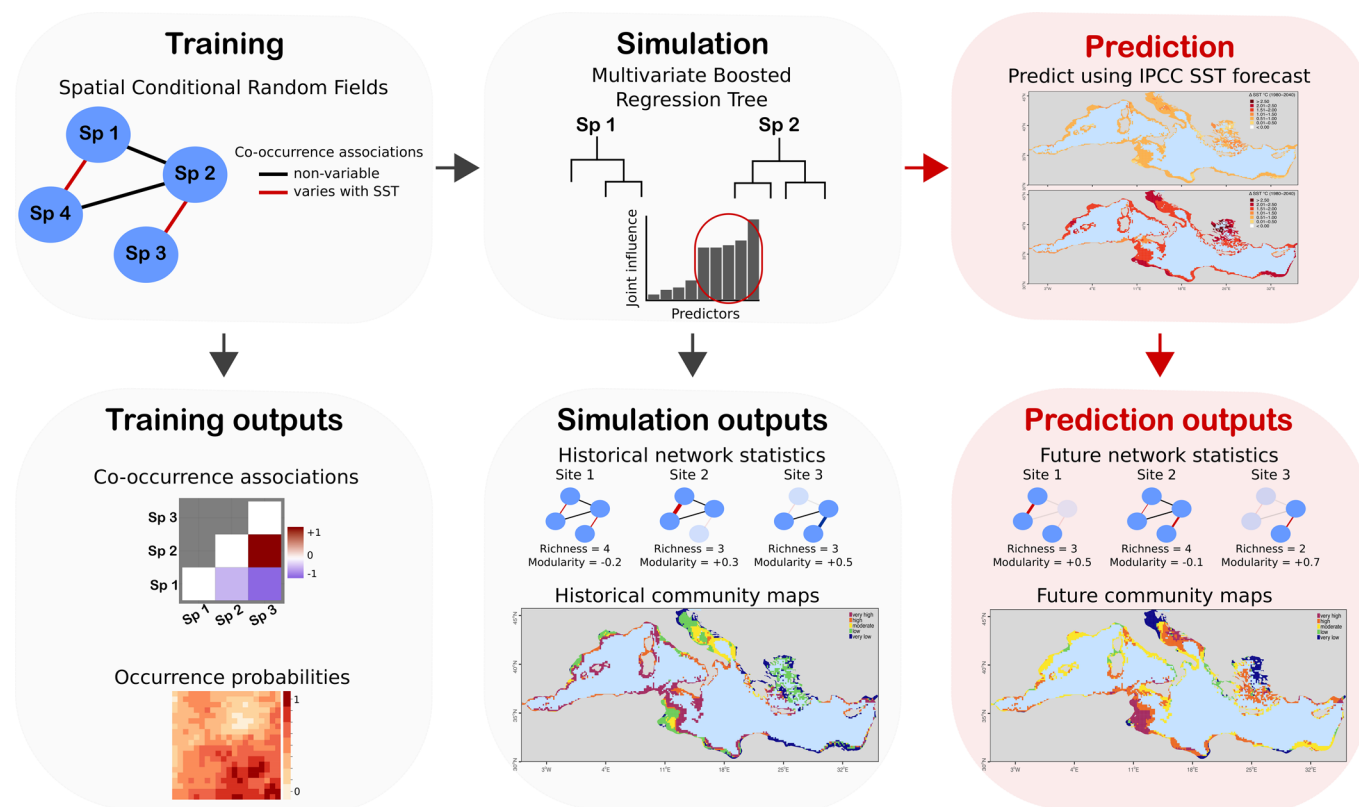
**Extended data** is available for this paper at <https://doi.org/10.1038/s41558-020-0838-5>.

**Supplementary information** is available for this paper at <https://doi.org/10.1038/s41558-020-0838-5>.

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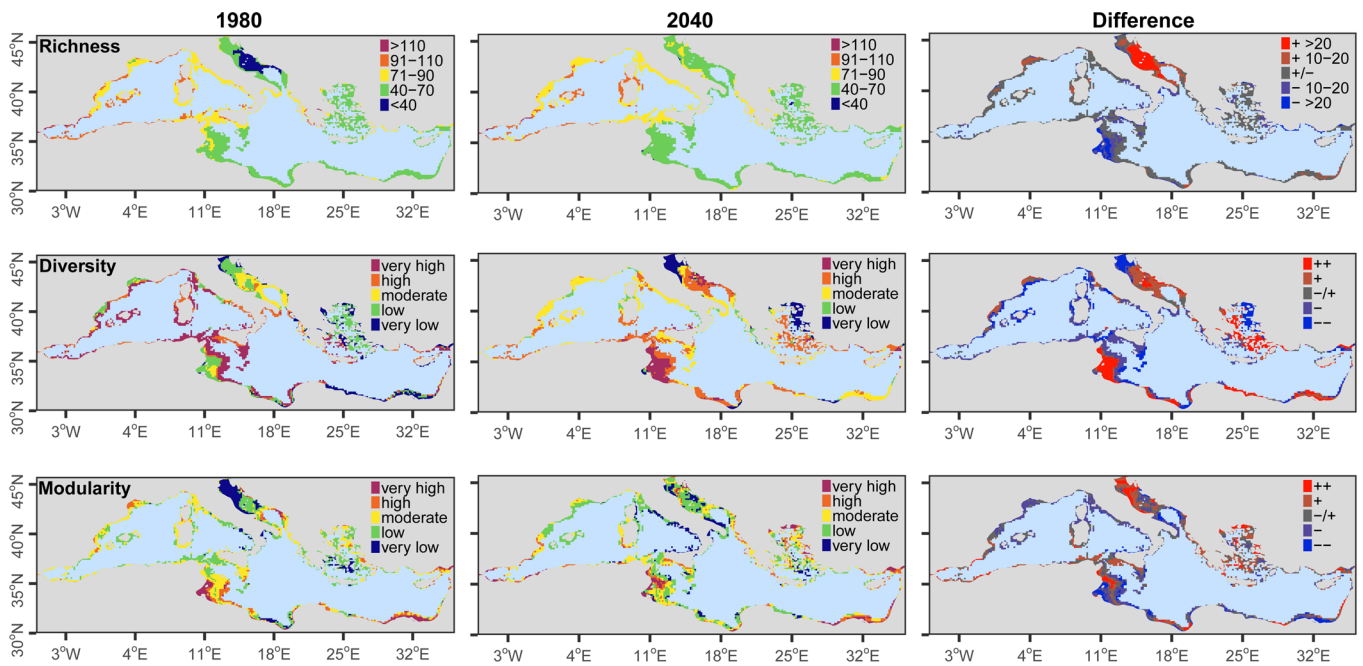
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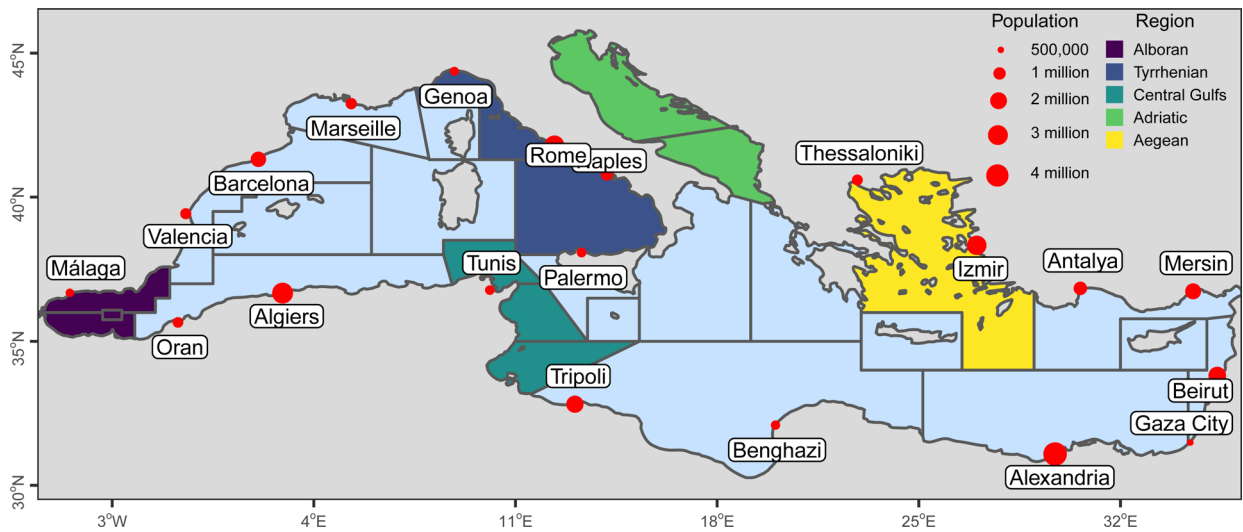


**Extended Data Fig. 1 | Schematic overview of the ensemble modelling approach and examples of key outputs produced at each step of analysis.**

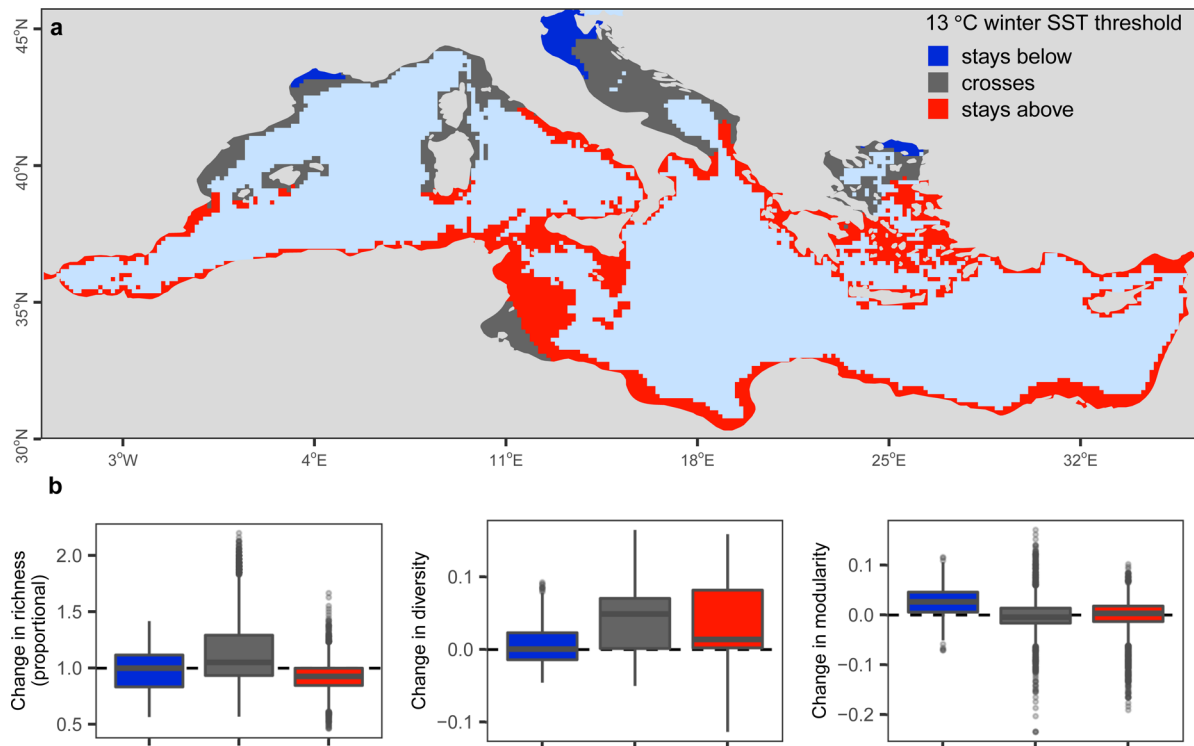
Schematic overview of the ensemble modelling approach and examples of key outputs produced at each step of analysis. A spatial Conditional Random Fields (CRF) model was trained on 1980 binary occurrence vectors for 215 fish species across 8,154 coastal sample sites in the Mediterranean Sea, using mean summer and mean winter Sea Surface Temperatures as external predictors. To generate predictions for a range of climate scenarios, simulation from the CRFs posterior predictive distribution was accomplished using a multivariate boosted regression tree that learned complex, nonlinear relationships and prioritised those predictors that had large influences on covariance in species' occurrence probabilities. These simulations allowed for more direct comparisons among historical and future predictions, avoiding the biases that can occur when comparing observed and predicted community measurements.



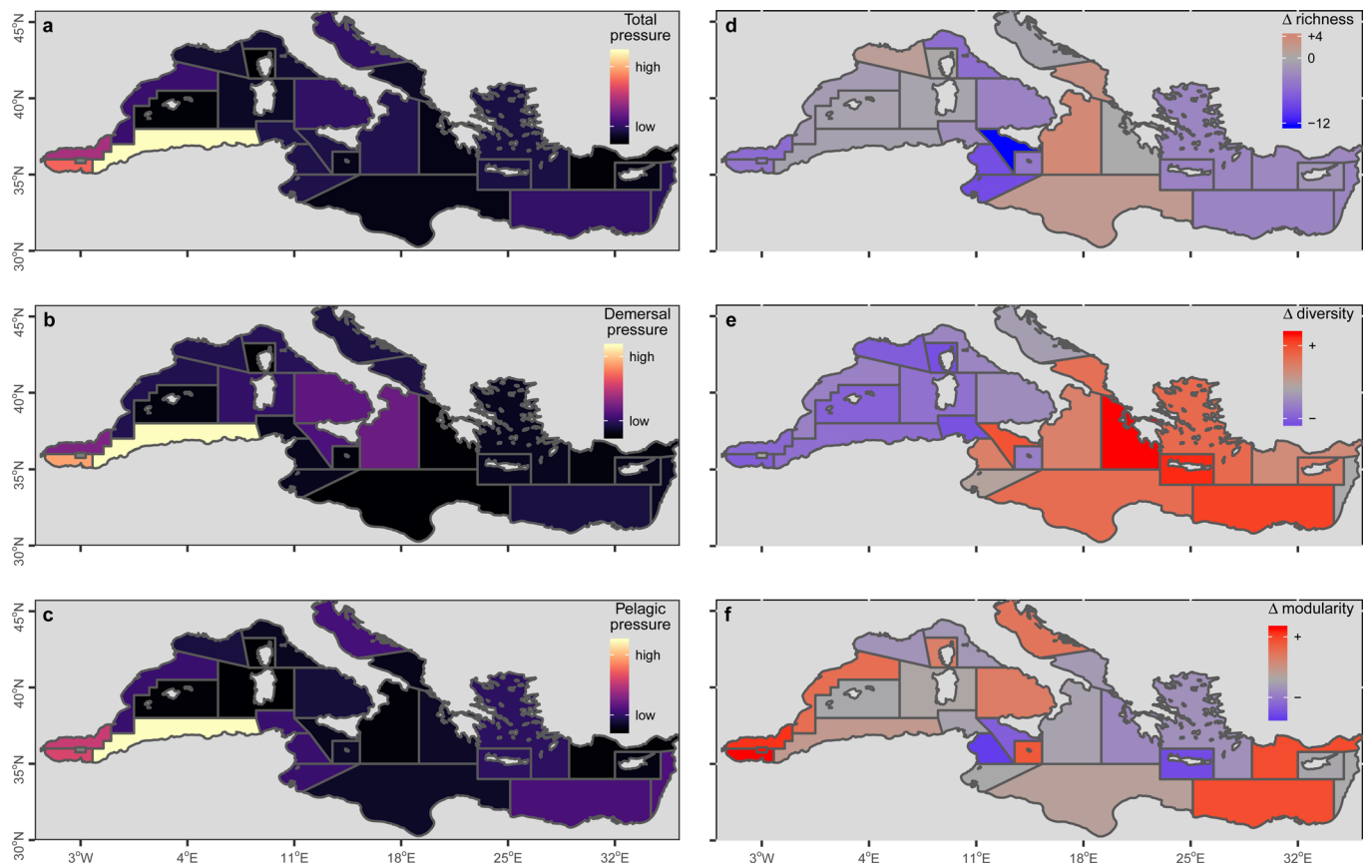
**Extended Data Fig. 2 | Predicted historical and future metrics of fish community species richness, functional diversity and network modularity across coastal grid cells in the Mediterranean Sea.** Predicted historical (1980) and future (2040) metrics of fish community species richness, functional diversity and network modularity across coastal grid cells in the Mediterranean Sea. Predictions were based on sea surface temperature (SST) estimates using IPCC SRES A2 climate scenarios. Note that functional diversity and network modularity metrics are unitless and are therefore presented as standardised estimates where very low:  $\leq 7.5$  percentile; low: 7.5 - 37.5 percentile; moderate: 37.5 - 62.5 percentile; high: 62.5 - 92.5 percentile; very high:  $\geq 92.5$  percentile.



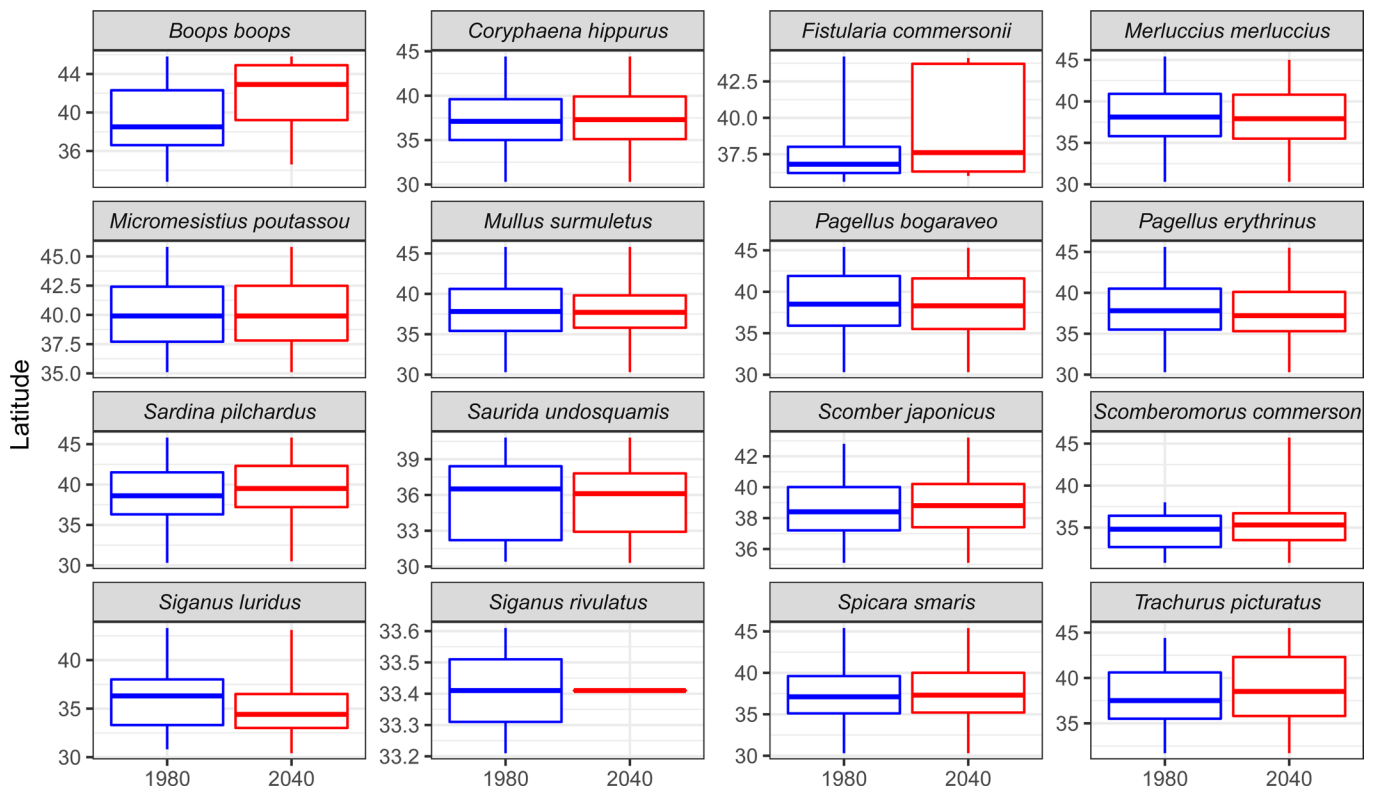
**Extended Data Fig. 3 | Geographical distributions of coastal fishing zones and populous coastal cities in the Mediterranean Sea.** Geographical distributions of coastal fishing zones (Geographical Subareas; GSAs) and populous coastal cities in the Mediterranean Sea. Regions highlighted in colour correspond to key geographical areas that are expected to experience marked changes in their coastal fish communities in response to warming sea surface temperatures.



**Extended Data Fig. 4 | Relationships between winter warming classification and predicted changes in coastal fish community richness, functional diversity and network modularity between 1980 and 2040 IPCC SRES A2 climate scenarios. (a)** Coastal sample sites in the Mediterranean Sea classified according to whether a grid cell is predicted to surpass a 13 °C winter sea surface temperature (SST) threshold by the year 2040. **(b)** Relationships between winter warming classification and predicted changes in coastal fish community richness, functional diversity and network modularity between 1980 and 2040 IPCC SRES A2 climate scenarios. Boxplots show: medians (lines within boxes), 25% and 75% quantiles (hinges) and 5% and 95% quantiles (whiskers).

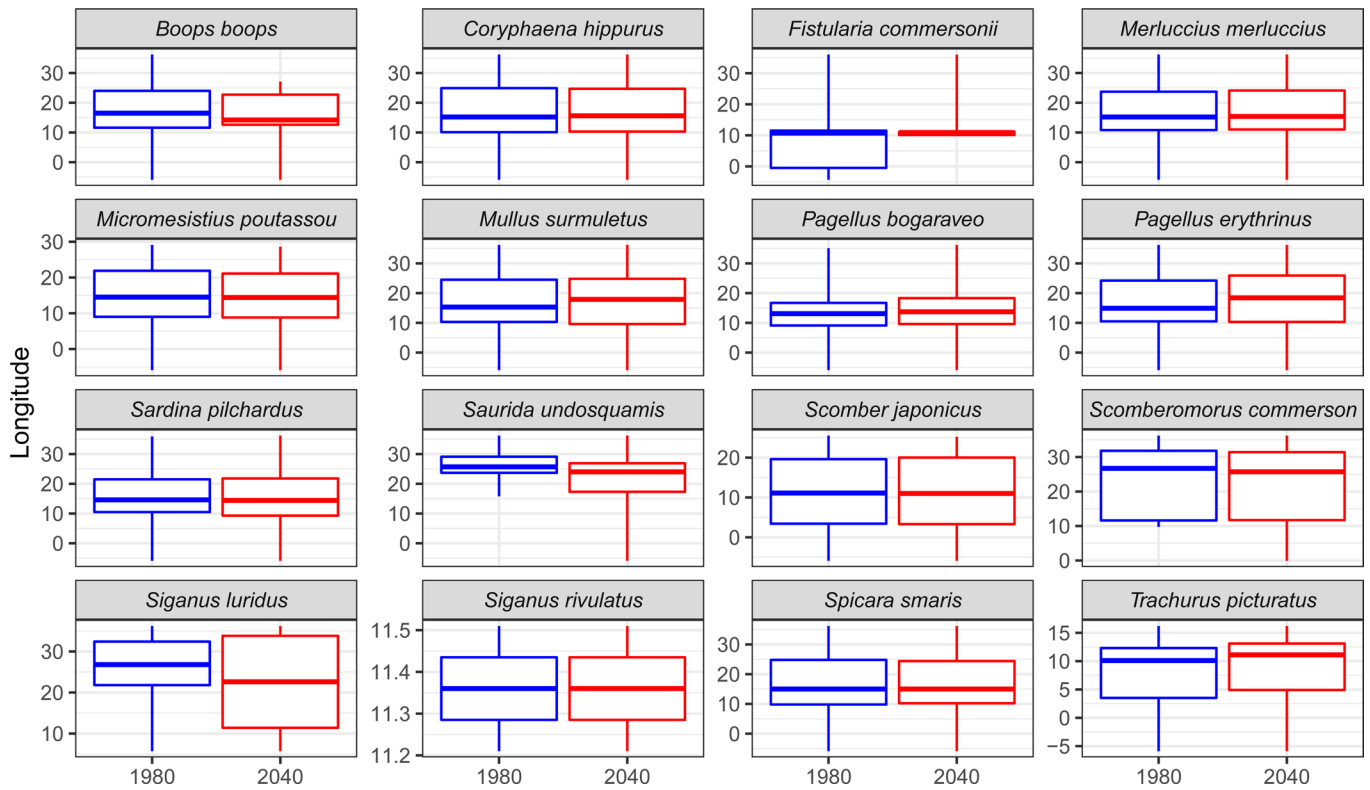


**Extended Data Fig. 5 | Average predicted changes in coastal fish species community richness, functional diversity and network modularity across GSAs between 1980 and 2040 IPCC SRES A2 climate scenarios. (a, b, c)** Geographical variation in fishing pressures across Mediterranean Sea GSAs, calculated as total landings per km<sup>2</sup> of coastal shelf area, for total fishes, demersal species and pelagic species. **(d, e, f)** Average predicted changes in coastal fish species community richness, functional diversity and network modularity across GSAs between 1980 and 2040 IPCC SRES A2 climate scenarios.



**Extended Data Fig. 6 | Predicted latitudinal distributions in the 1980 and 2040 time periods for species of economic and conservation importance.**

Predicted latitudinal distributions in the 1980 and 2040 time periods for species of economic and conservation importance, including non-indigenous species with the greatest potential impacts (according to the General Fisheries Commission for the Mediterranean). Range sizes were calculated by summing the predicted presence / absence vectors in each time period across all 8,154 grid cells.



**Extended Data Fig. 7 | Predicted longitudinal distributions in the 1980 and 2040 time periods for species of economic and conservation importance.** Predicted longitudinal distributions in the 1980 and 2040 time periods for species of economic and conservation importance, including non-indigenous species with the greatest potential impacts (according to the General Fisheries Commission for the Mediterranean). Range sizes were calculated by summing the predicted presence / absence vectors in each time period across all 8,154 grid cells.



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