



The dawn of the tropical Atlantic invasion into the Mediterranean Sea

Paolo G. Albano^{a,1,2} , Lotta Schultz^{a,b,1}, Johannes Wessely^c, Marco Taviani^{d,e} , Stefan Dullinger^c, and Silvia Danise^f

Edited by Geerat Vermeij, University of California, Davis, CA; received December 2, 2023; accepted February 13, 2024

The Mediterranean Sea is a marine biodiversity hotspot already affected by climate-driven biodiversity collapses. Its highly endemic fauna is at further risk if global warming triggers an invasion of tropical Atlantic species. Here, we combine modern species occurrences with a unique paleorecord from the Last Interglacial (135 to 116 ka), a conservative analog of future climate, to model the future distribution of an exemplary subset of tropical West African mollusks, currently separated from the Mediterranean by cold upwelling off north-west Africa. We show that, already under an intermediate climate scenario (RCP 4.5) by 2050, climatic connectivity along north-west Africa may allow tropical species to colonize a by then largely environmentally suitable Mediterranean. The worst-case scenario RCP 8.5 leads to a fully tropicalized Mediterranean by 2100. The tropical Atlantic invasion will add to the ongoing Indo-Pacific invasion through the Suez Canal, irreversibly transforming the entire Mediterranean into a novel ecosystem unprecedented in human history.

biodiversity | biogeography | global warming | Last Interglacial

The Mediterranean Sea is a hot spot of marine biodiversity where almost half of the species are endemic (1). At the same time, this basin is among the fastest warming marine ecoregions worldwide (2) and regional-scale climate-driven biodiversity collapses have already been reported (3). The expected future acceleration and intensification of climate change (4) will likely boost the scale of its ecological and evolutionary consequences, the predictions of which have thus become important contributions to global climate and biodiversity impact assessments (5).

To better forecast the effects of ongoing climate warming, there is considerable interest in the analysis of warm climate intervals in the Earth's history, so-called "past analogs" (6). Despite that such past analogs are always imperfect representations of what awaits us in the coming decades and centuries (7), they represent the only observational source of information for how the climate system operates in a state much warmer than the present (8). Similarly, past biotic assemblages represent windows into how communities responded to warming (9). Despite the responses of species to climate change may be individualistic, making no past community a perfect analog of future scenarios, thermal niches of marine species proved static over the last 3 My suggesting good potential to use the past Earth conditions to predict future climate states (10, 11). Moreover, such past analogs not only account for how species tracked their fundamental niche but also are the result of dispersal processes and biotic interactions, thus being a more realistic representation of climate-change impacts on biotic assemblages than what can be predicted with niche modeling alone.

The Last Interglacial (Pleistocene epoch, sub-stage MIS5e), ca 135 to 116 ka, had a global mean surface temperature overlapping with the low end of the range of temperatures projected under the moderate climate change scenario RCP 2.6 (4), thus making it a conservative analog of future climate. Additionally, this sub-stage had a continental configuration and marine taxonomic diversity almost identical to the present, thus enabling highly meaningful comparisons of both oceanographic and biodiversity patterns. In the Mediterranean, the Last Interglacial fossil record is characterized by the occurrence of West African species that regressed to the tropical belt during the following glaciation (the so-called "warm guests") (12). This tropical pool is now separated from the Mediterranean Sea by a 2,000-km-long barrier of cold water due to the large north-west African coastal upwelling system (Fig. 1). However, as global temperatures approach those of the Last Interglacial, this barrier may weaken enabling the reinvasion of tropical West African species into the Mediterranean. This reinvasion would imply a major reorganization of the shallow shelf marine ecosystem and, in contrast to biological invasions that depend on the availability of a suitable vector, it would not be modulated by any oceanographic or anthropic filter once started.

Significance

Global warming and biological invasions are driving a major reconfiguration of biogeographic provinces. Past warm climate intervals in the Earth's history represent windows into how species responded to warming and can help in predicting future biogeographic configurations. We modeled the suitability of the Mediterranean Sea to West African tropical species that occurred in the basin in the Last Interglacial (135 to 116 ka), and the connectivity along north-west Africa where a large upwelling system is currently delaying the poleward range expansion of tropical species. We show that this barrier may weaken even under intermediate climate scenarios, contributing to the onset of a novel ecosystem in the entire Mediterranean, a process already started with the biological invasion through the Suez Canal.

Author contributions: P.G.A. designed research; P.G.A., L.S., M.T., S. Dullinger, and S. Danise performed research; P.G.A., L.S., J.W., and S. Dullinger analyzed data; and P.G.A., L.S., J.W., M.T., S. Dullinger, and S. Danise wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

Copyright © 2024 the Author(s). Published by PNAS. This article is distributed under [Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 \(CC BY-NC-ND\)](https://creativecommons.org/licenses/by-nc-nd/4.0/).

¹P.G.A. and L.S. contributed equally to this work.

²To whom correspondence may be addressed. Email: pgalbano@gmail.com.

This article contains supporting information online at <https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2320687121/-/DCSupplemental>.

Published April 1, 2024.

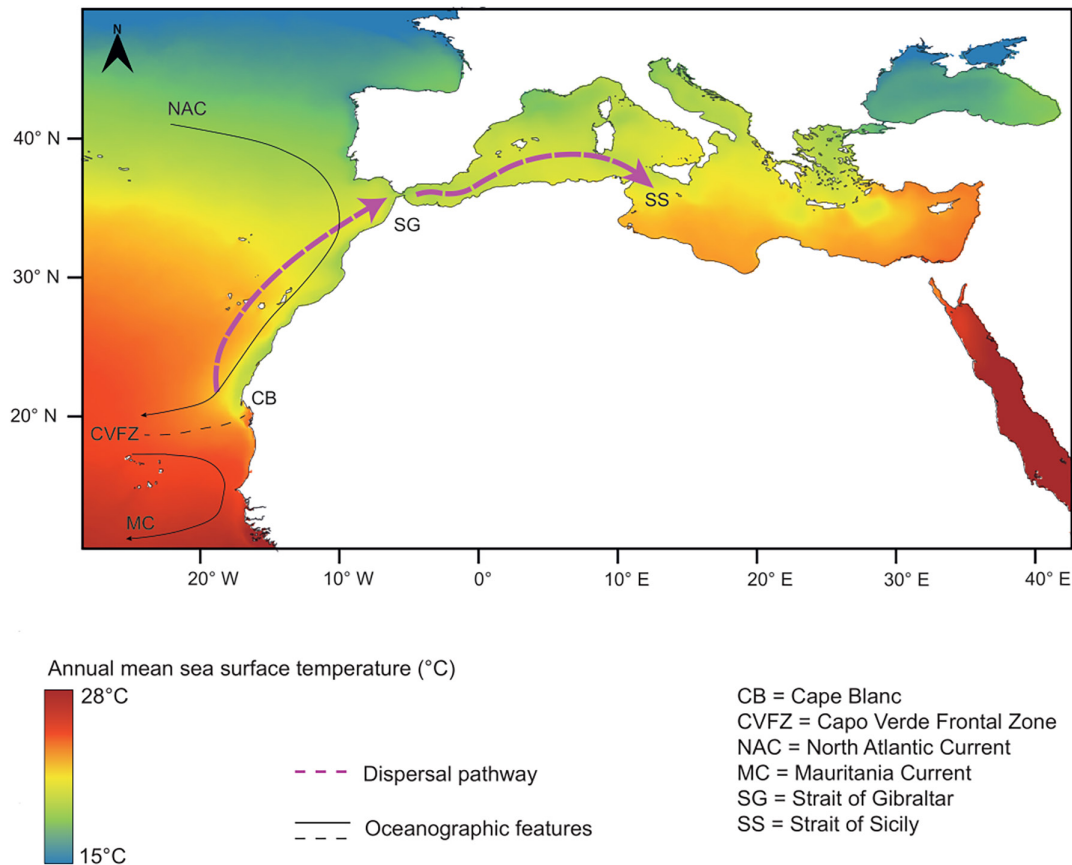


Fig. 1. Oceanographic features and dispersal pathways for West African species in the north-east Atlantic and Mediterranean basins. Despite the warmest south-eastern sectors of the Mediterranean Sea are already thermally suitable for tropical West African species, their entrance is currently blocked by the cold upwelling system off north-west Africa. Once this barrier is overcome, tropical species may pass through the Strait of Gibraltar first and of Sicily later to reach the eastern Mediterranean.

Here, we explore this scenario by building a species distribution model (SDM) with a multitemporal envelope of both Last Interglacial and present climate conditions and species occurrences. Indeed, a major shortcoming of traditional SDMs is that they are usually parametrized on modern occurrences. At a given time, however, species may not be occupying all environmentally suitable areas due to limitations to dispersal, biotic interactions, and source-sink dynamics (13). Consequently, such occurrence datasets may not be representative of the full range of conditions the species can tolerate and SDMs may thus underestimate habitat suitability. By including species distribution data that span a wider temporal extent, it is possible to deliver a more complete representation of the species climatic or environmental niche (14, 15). By exploiting the very good fossil and modern record of marine mollusks, we predict the likelihood, extent, and timing of the invasion of tropical Atlantic biota into the Mediterranean Sea in future climate scenarios, focusing on the suitability of the Mediterranean for tropical West African species and the necessary connectivity between the source pool and the recipient basin. Taken together, our results suggest that unabated global warming will quickly lead to increased connectivity along the north-west African coasts and a full tropicalization of the Mediterranean Sea in worst-case scenarios.

Results

Niche Description. We observed low similarity between the realized fossil and current environmental niches for all tested species, with the Jaccard similarity index in the multidimensional environmental

space (maximum sea surface temperature (SST), average SST, salinity, and chlorophyll) being less than 1%, highlighting the importance of combining modern and fossil data for niche description. Along individual environmental gradients, we found the most pronounced similarity between the fossil and current niche for maximum SST with an overlap of 45% for *Thetystrombus latus*, 32% for *Conus ermineus*, and 17% for *Gemophos viverratus*; in contrast, similarity along the salinity gradient was lowest, <1% for both *T. latus* and *C. ermineus* and 0% for *G. viverratus* (SI Appendix, Figs. S4–S6).

Future Range Suitability in the Mediterranean Sea. Our model projections suggested that already under current environmental conditions the south-eastern sectors of the Mediterranean Sea are suitable for most of the modeled species, in particular the shallow north African shelf above 50 m depth from the Gulf of Gabes in Tunisia to the Middle East (Fig. 2A and SI Appendix, Table S4). Gastropods like *T. latus*, a large mollusk belonging to the tropical family Strombidae and characteristic of the Last Interglacial Mediterranean (reported under the name *Strombus bubonius* in the older literature), would find 30% of the basin already environmentally suitable.

For most target species, environmental suitability increased progressively in these sectors and expanded throughout the Mediterranean under future climate scenarios (Fig. 2B and C). Despite suitability increasing across the entire bathymetric range modeled, the shallow shelf above 50 m depth remained the most suitable, consistent with the current and past environmental

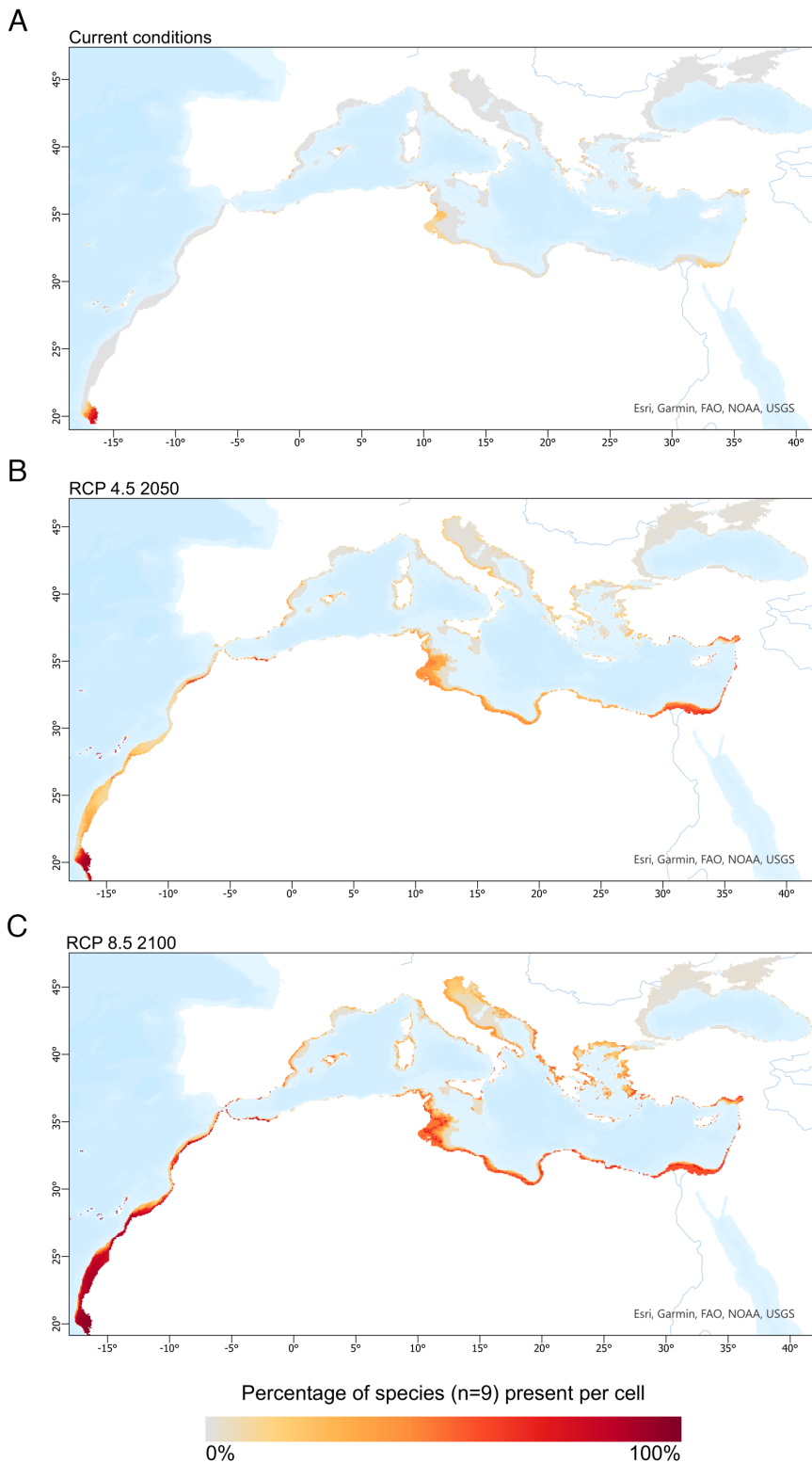


Fig. 2. Environmental suitability of the Mediterranean Sea under current and future scenarios. For each cell, we show the percentage of species ($n = 9$) predicted to be present under (A) the current environmental conditions, (B) RCP4.5 for the year 2050, and (C) RCP8.5 for the year 2100. The southern and easternmost coasts of the Mediterranean Sea are already suitable for the return of some Last Interglacial warm guests. Suitability increases with scenario severity. The north-west African coast also becomes suitable starting in 2050 under RCP 4.5, implying increasing connectivity. (“Ocean Basemap”. Sources: Esri, GEBCO, NOAA, National Geographic, DeLorme, HERE, Geonames.org, and other contributors. October 04.2018).

preferences of the modeled species. A remarkable example was again *T. latus*, which would find 41% of the shallow basin suitable by 2050 under RCP 4.5 and up to 77% under RCP 8.5. This increasing trend with emission scenario severity is consistent among most species. An exception is the bivalve *Acar olivercoseli*, for which suitability remained limited and decreased with scenario severity. The western Mediterranean was less suitable for the modeled species under current conditions, but suitability also increased

with warming. For example, *T. latus* would find a suitable shallow range in between 40% (RCP 4.5 by 2050) and 47% (RCP 8.5 by 2100) of the sector. The Adriatic Sea remained poorly suitable for most species in most scenarios, but its shallow shelf would see a major increase in suitability under the severe scenario RCP 8.5 by 2100 (Fig. 3). The Black Sea would not be affected by the reinvansion of tropical West African mollusks as it is entirely unsuitable in all modeled scenarios, mostly because of its low salinity.

Suitability and Connectivity in North-West Africa. The Atlantic coast of Africa between Cape Blanc (native name Ras Nouadhibou, the southern edge of the north-west African upwelling system) and the Strait of Gibraltar is currently not suitable for the modeled species (the median of the percentage of suitable cells above 50 m depth across species was just 1.2%), consistent with the hypothesis that this large coastal area is a remarkable barrier to the northward spread of tropical West African species. In this very same area, however, suitability increased already under RCP 4.5 by 2050, when the median of the percentage of suitable cells among the modeled species was 6.8%, and became fully suitable under RCP 8.5 by 2100, when four species showed more than 95% of cells above 50 m depth suitable (Fig. 2). There was, however, some variation across species as for two of them, including *T. latus*, only 5% of the cells were suitable in this scenario. However, the shallow shelf of archipelagos off the coastline (i.e. Canaries, Madeira) proved already suitable in current conditions (a median

of 80% cells), in agreement with the actual occurrence of seven out of nine species there today. The suitability of these archipelagos was projected to increase to a median of 100% under RCP 8.5 already by 2050 (Fig. 3).

Connectivity between tropical West Africa and the Strait of Gibraltar will improve considerably in future climate scenarios. Even under intermediate warming (RCP 4.5), suitable range patches will be two orders of magnitude larger than at present already in 2050, suggesting a series of stepping stones of increasing size toward the Mediterranean (Fig. 4A). The average distance among patches initially increases because in the current scenario patches of suitable cells are clustered uniquely in the Canaries and Madeira (thus at relatively short distance from each other) while in future scenarios new patches emerge along the African coast also far away from these archipelagos. Under the most severe scenario RCP 8.5 by 2100, the number of patches is so large and continuously distributed that eventually, the distance between

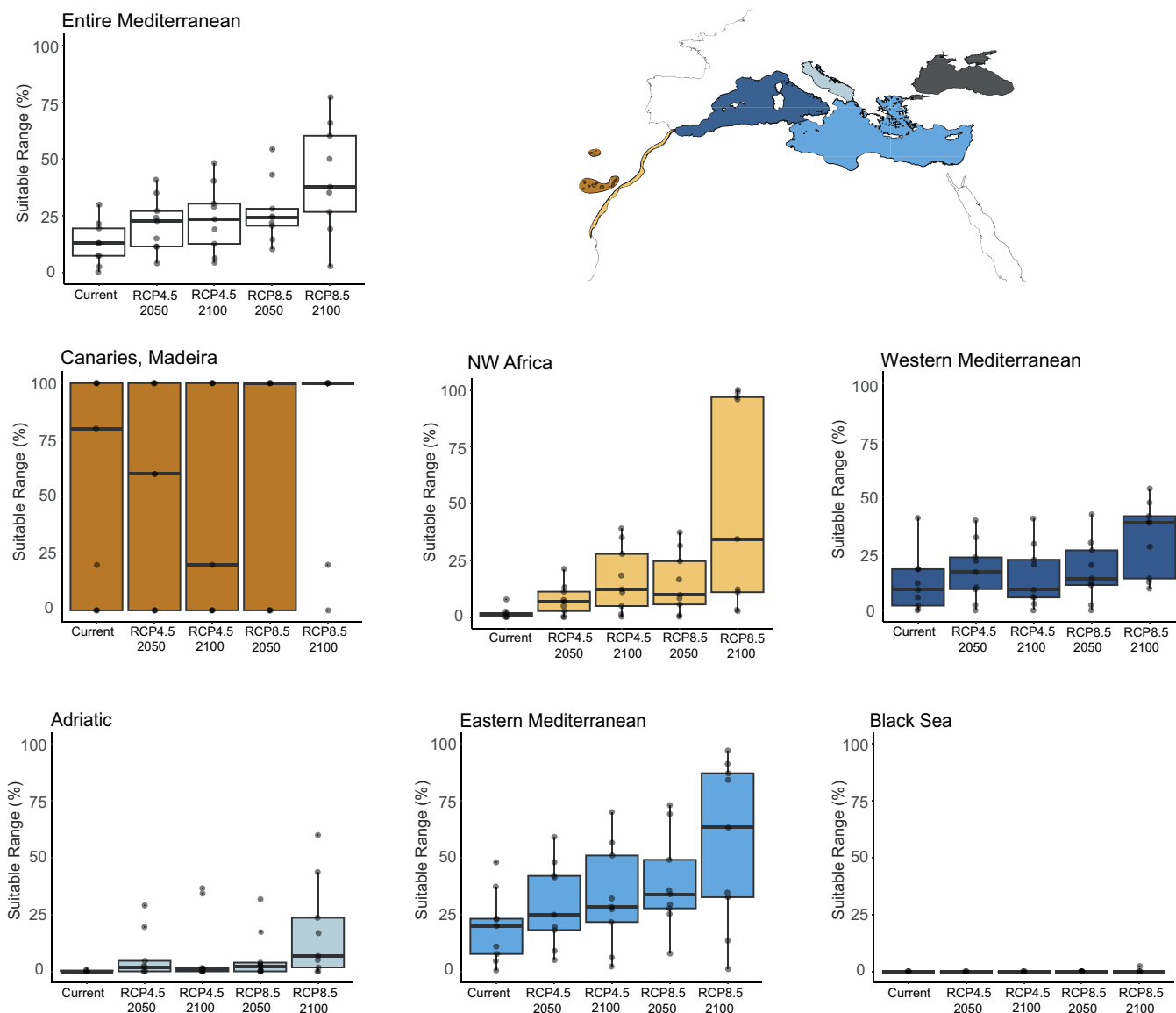


Fig. 3. Environmental suitability of the shallow shelf (above 50 m depth) in north-west Africa and the Mediterranean Sea under future climate scenarios. The extent of suitable area increases with increasing scenario severity. Ample areas of the eastern Mediterranean are already and will increasingly become suitable for tropical West African species, but the western Mediterranean and the Adriatic Sea will also become increasingly suitable. Importantly, an increasing number of suitable areas will emerge also on the shallow shelf of north-west Africa; such areas and the archipelagos of the Canaries and Madeira will be stepping stones for the spread of species into the Mediterranean Sea.

patches decreases in relation to the current situation (Fig. 4C). Further dispersal throughout the Mediterranean will be possible due to the increase in patch size and decrease in distance amongst patches in the western Mediterranean under all future climate scenarios (Fig. 4 B and D) with the consequent arrival of species in the eastern Mediterranean.

Discussion

The warmest south-eastern sectors of the Mediterranean Sea are already environmentally suitable for the establishment of tropical West African species that occurred in the basin in the Last Interglacial 135 to 116 ka and regressed to the tropical belt during the following glaciation. The suitability of this region for tropical species is also

demonstrated by the thriving populations of hundreds of Indo-Pacific species that entered the basin after the opening of the Suez Canal and of Caribbean non-indigenous species likely introduced by shipping (16), confirming its long-thought potential to host a tropical fauna given the establishment of natural or anthropogenic connectivity (17, 18). Suitability will increase even under the intermediate RCP 4.5 scenario, both in terms of areal extent per species and of number of species per cell. The north-west African coastline, now completely unsuitable for these species, will also become much more suitable to most species with warming. Under the intermediate climate scenario, the Canary Islands and Madeira archipelagos will likely play a key role as stepping stones in facilitating spread to northern latitudes and then into the Mediterranean consistent with what may have happened in the Last Interglacial (19), also considering that

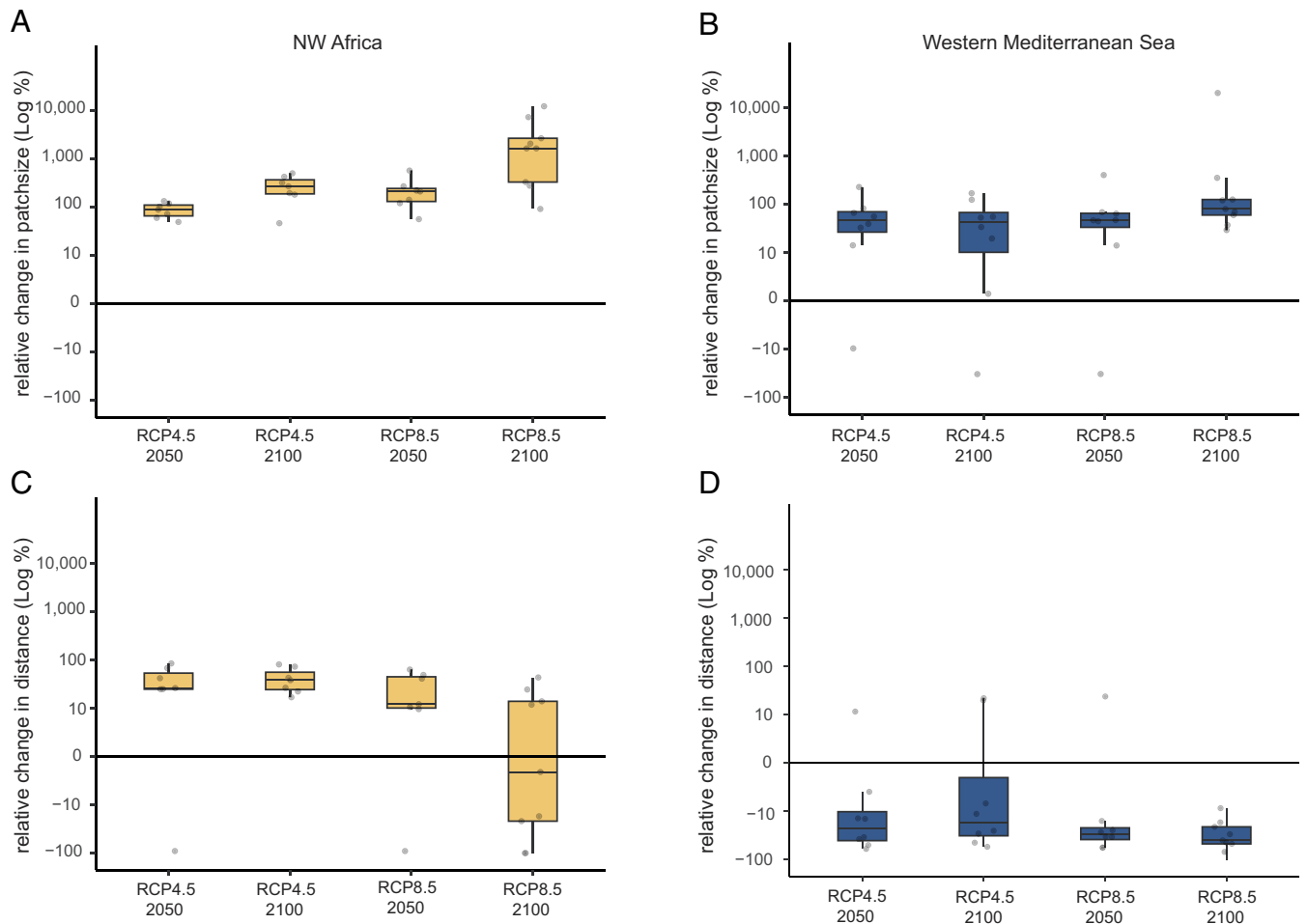


Fig. 4. Connectivity across the north-west African coast and in the western Mediterranean in future climate scenarios. Connectivity is expressed as (A and B) changes in the size of suitable area (patch size) and as (C and D) the distance among suitable areas relative to current conditions. Patch size increases in both north-west Africa and the western Mediterranean with scenario severity. Distance among suitable areas initially declines in north-west Africa because new suitable patches emerge far from the few already present which are clustered mainly in the Canary Islands but under RCP 8.5 in 2100, the number of suitable patches become packed enough to reduce their distance compared to the current scenario.

most of the western Sahara coastline is sandy and thus poorly suitable for some hard-substrate species. Under RCP 8.5—that is, if the human action to abate warming will be largely insufficient—the entire African coastline will become a major route to a fully tropicalized Mediterranean Sea.

The current average global warming estimate is 1.09 °C compared to the preindustrial period, that is, already within the estimated 0.5 to 1.5 °C global mean surface temperature increase of the warmest millennia of the Last Interglacial (around 129 to 125 ka) (4). Due also to its geomorphological and biological similarity to the present, this sub-stage is an apt analog of the short-term climate scenarios ahead of us (4). During the Last Interglacial, the CO₂ concentration in the atmosphere was similar to the preindustrial period and warming was mostly due to orbital forcing (20). Consequently, global temperature anomalies were characterized by temporal and spatial heterogeneity: Warming during the boreal summer but also cooling in winter occurred, and the northern hemisphere warmed more than the southern hemisphere (20). Current anthropogenic climate warming is globally more uniform in space and time. Irrespective of these differences, the fossil record shows that tropical West African species occurred in the Mediterranean in several of the warmest interglacials of the Quaternary (21), highlighting the plausibility of our predictions. Additionally, the intermediate scenario RCP 4.5—where progress toward sustainability is slow—implies an increase in global temperatures corresponding to the mid-Pliocene Warm Period about 3 Ma, when not only continental configuration and marine species diversity but also the CO₂ concentration was similar to the present (22). In this period, West Africa and the Mediterranean were part of the same tropical biogeographic province and had a broader array of species in common compared to the Last Interglacial (23), suggesting that our results may eventually prove to be conservative.

A key uncertainty, however, is the response of the north-west African upwelling system to global warming, because the complex dynamics of such systems makes them difficult to predict (24). This area belongs to the large Canary Current upwelling system stretching from 12° N (Senegal) to 43° N (Galicia, Spain). The general prediction in a warmer planet is that winds that drive upwelling will intensify in poleward regions and weaken or remain stable in equatorward regions due to the poleward migration of atmospheric high-pressure systems (25). Under RCP 8.5, upwelling is predicted to weaken off north-west Africa and to increase off the Iberian Peninsula, consistent with the general prediction (26–28). However, there is empirical evidence of a weaker upwelling already now and, accordingly, surficial water has warmed over the entire Canary Current system in the last decades (29). Importantly, paleoclimatological evidence from a sediment core collected off north-west Africa showed a curtailment of coastal upwelling for over 6,000 y from 126 to 120 ka corresponding to an increase in average annual sea surface temperature of 3 °C after the warmest millennia from 129 to 125 ka (30). These results suggest that a magnitude of global warming comparable to the one of the Last Interglacial was indeed enough to weaken significantly this oceanographic feature. The main uncertainty may lie in the inertia of the system and thus the time required to realize this scenario. However, the collapse of the Atlantic meridional overturning circulation may happen by mid-century under the current scenario (31), suggesting that major changes in oceanographic features can happen on short time scales.

Due to the evidence already accumulated about the warming off the north-west African coast, is tropical Atlantic biodiversity already responding by establishing populations in the Mediterranean Sea via natural connectivity? In the last decades, two conspicuous tropical Atlantic mollusks have been recorded in the Mediterranean [the

sea hares *Aplysia dactylomela* Rang, 1828 since 2001, and *Bursatella leachii* Blainville, 1817 since the 1950s (32, 33)]. Both species were initially observed in its easternmost sectors followed by a more recent westward spread, consistent with the current greater suitability of the eastern Mediterranean to tropical species here projected. Similarly, the tropical Atlantic large and colorful crab *Percnon gibbesi* (H. Milne Edwards, 1853) was first recorded in the Mediterranean in 1999, spreading quickly afterward (34). The population genetic structure, the pattern of records, and the larval stages with long planktonic life suggest that all three species may have entered the Mediterranean unaided by anthropic vectors. Multiple less conspicuous invertebrates of tropical Atlantic origin have been recorded in the Mediterranean Sea recently and more studies become urgent to ascertain their biogeographic status and mode of entry in the basin to build a better picture of the ongoing biotic reorganization. Among fishes, 25 new Atlantic species have been recorded in the Mediterranean in recent decades, most with range cores in tropical West Africa and the Caribbean (35). Although their status still requires deeper investigation, all are supposed to have entered the basin without active or passive human help.

Warming periods in Earth's history are powerful engines of biotic interchange (36). Notwithstanding past analogs can help in predicting future states of biodiversity (37), the dramatic scale of human modification of the Mediterranean Sea implies that the future will not simply be a re-edition of the Last Interglacial or earlier warm episodes (38). The opening of the Suez Canal has broken a long-standing biogeographic barrier with the Indo-Pacific realm and the flow of species is unlikely to be halted anytime soon. This invasion, coupled with the climate-driven collapse of native species, is about to reorganize the functioning of the entire ecosystem (39, 40). Additionally, Indo-Pacific species are extending their ranges westward because biogeographic barriers within the Mediterranean weaken as a consequence of global warming (41). As the westward spread of Indo-Pacific species continues and the establishment of tropical Atlantic species starts, biota of two contrasting biogeographic origins will meet realizing predictions that just a decade ago looked futuristic (42). This new Mediterranean—vaguely reminiscent of the Tethyan Seaway that connected the Atlantic and the Pacific until 13.8 Ma—in fact is already about to become realized in its easternmost sector (3) and will further become a novel ecosystem with abiotic and biotic conditions much different from its historical Holocene state. This irreversible shift will require a profound rethinking of the aims and methods of mitigation, adaptation, and restoration.

Materials and Methods

Fossil and Modern Species Data. We modeled nine species of shallow-shelf marine mollusks reported from the Last Interglacial in the Mediterranean and now occurring exclusively in the tropical Atlantic. These species are an ideal model because mollusks are well represented in the fossil record and shallow water assemblages are those particularly affected by climate warming.

We selected the species by first reviewing the Last Interglacial molluscan fauna integrating literature data with Global Biodiversity Information Facility (GBIF) fossil occurrences. Then, we filtered for those species now occurring in the tropical Atlantic but not in the Mediterranean anymore, ending up with 19 species. We downloaded GBIF modern occurrence data for them and cleaned occurrences manually in QGIS by removing unlikely records, including those on land or clearly outside a species known range. Occurrence records that did not match a cell of the environmental raster layer (see below) were moved to the closest cell using the "points2nearestcell" function of the "Pakillo/rSDM" package in the R statistical environment version 4.2.2 (43). Ultimately, for the fossil and modern occurrences separately, we aggregated multiple occurrence points to one record per cell. We retained for modeling the nine species that had at least two fossil and 30 modern cell occurrences (*Thystrambus latus*, *Monoplex trigonus*, *Polinices lacteus*, *Gemophos viverratus*,

Conus ermineus, *Ateocina knockeri*, *Acar olivercoseli*, *Brachidontes puniceus*, *Cardita rufescens*; *SI Appendix, Table S1 and Fig. S1 and Dataset S1*).

Environmental Data. Present-day climate (averaged for the period 2000 to 2014) and future climate data (simulations for 2050 and 2100 averaged over 10 y) were retrieved from Bio-Oracle (<https://www.bio-oracle.org/>) at a spatial resolution of 5 arcmin (ca 9.2 km at the equator) (44). Future climate was considered under two different Intergovernmental Panel on Climate Change (IPCC) scenarios: Representative Concentration Pathway (RCP) 4.5 (intermediate scenario) and RCP 8.5 (severe scenario) (4). We derived climate data for the Last Interglacial from simulations of the Community Earth System Model version 2 (CESM2) (45) via the CMIP6-Paleoclimate Modelling Intercomparison Project (PMIP4) (20). The CESM2 is one of the latest large-scale climate models (46) and its Last Interglacial simulations have been shown to be close to the mean of a multimodel ensemble of 17 climate models (20). CESM2 simulation outputs were available in 14 × 50-y-long slices, totaling 700 y of monthly data at a 1° × 1° resolution (ca 110 × 110 km at the equator). Given the minimal variation observed across the 14 time slices (*SI Appendix, Fig. S2*), we used environmental data from the initial 50-y slice out of the 700-y model simulations. We chose three environmental variables that are known to be ecologically limiting for modern marine mollusks and were available for all time periods considered: sea surface temperature (SST), sea surface salinity (SSS), and seawater chlorophyll (SWC). Using bilinear interpolation, we resampled the environmental layers to a resolution of 5 arcmin, corresponding to the spatial resolution of our current and future climate datasets. Eventually, we converted monthly Last Interglacial climate data to maximum, minimum, and average yearly composites. We resized the environmental layers to fit the fossil and current distribution for each species and masked areas deeper than 200 m to account for the species bathymetric preferences. Finally, we tested the environmental parameters for correlation with the Pearson's correlation coefficient using a cut-off value of 0.7. We ultimately retained four environmental parameters: yearly average SST, yearly maximum SST, yearly minimum SSS, and monthly average SWC.

Species Distribution Model. We associated modern and fossil distribution data with the current and Last Interglacial climate data layers, respectively, to describe the species present, past, and combined environmental ("Hutchinsonian") niche (i.e., the hypervolume of environmental conditions within which a species can survive and reproduce) using functions of the "biomod2" package (47). To quantify the improvement in niche description using both modern and fossil data, we compared the environmental niche space occupied by the species during the LIG and the present time period for species with at least 10 fossil-occupied cells (*T. latus*, *G. viverratus*, and *C. ermineus*). We therefore measured Jaccard similarity in multidimensional niche space and along individual environmental gradients (i.e., maximum SST, average SST, salinity, and chlorophyll) using functions of the "hypervolume" package.

For each time period, we generated pseudo-absences equaling the number of observed presences outside a minimum distance of 20 km to the next presence point. This pseudo-absence sampling procedure was repeated 10 times. We then combined modern and fossil datasets to provide a closer approximation of the species' environmental niche. Applying an ensemble model approach (47, 48), we used this multi-temporal envelope of climate and species occurrences to project species distributions in current and future climates, assuming the stability of species environmental niches as shown for mollusks and foraminifera for the last few million years (10, 11). Our ensemble models consisted of five algorithms: generalized linear model (GLM), generalized additive model (GAM), generalized boosted model (GBM), random forest (RF), and artificial neural network (ANN). We calibrated the models using a repeated data-splitting procedure: 80% of the original data was used to train the models and the remaining 20% to evaluate them by measuring the true skills statistics (TSS) and the area under the receiver-operating characteristic (ROC) curve (AUC) scores. The splitting procedure was repeated five times. Using the default settings in biomod, all replicates of all single models with a TSS ≥ 0.6 were used to

build ensemble models defined as weighted means of occurrence probabilities projected by the single models (49). We translated the projected probabilities of occurrence into binary (presence/absence) predictions using the threshold that maximizes the TSS score (50). The importance of each environmental variable was computed as a mean value across all models, with the importance in each model weighted by the model's TSS score.

We successfully fitted ensemble models for all nine marine mollusk target species. The cross-validation evaluation scores of the single SDMs were good to very good and similar across all species (*SI Appendix, Table S1*). The best performance was achieved by RF (TSS > 0.87) followed by GBM (TSS > 0.84), ANN (TSS > 0.77), GAM (TSS > 0.75), and last GLM (TSS > 0.72). The importance of the integrated environmental variables varied across the modeled species. However, overall monthly maximum SST and minimum SSS were the most important variables to explain the species distributions. In contrast, annual mean SST and mean SWC exerted little influence on the species distributions (*SI Appendix, Tables S2 and S3*).

Model Output Analysis. Predicted range changes for all species were visualized as maps indicating the probability of occurrence (i.e., 0 to 100%) of the individual species at each cell (*Dataset S2*). Additionally, we used the binary projections to draw aggregate maps for each climate scenario by calculating the percentage of species predicted to be present in any cell.

Based on binary projections, we separately quantified the range size in the Mediterranean Sea, its sub-basins (the western and the eastern Mediterranean, the Adriatic Sea and the Black Sea), the African coast between Cape Blanc and the Strait of Gibraltar, and the islands off north-west Africa (Canary Islands and the Madeira archipelago). Since our target species occur predominantly in shallow water, we did these range size quantifications for the entire continental shelf (i.e., down to 200 m depth) but also for shallower waters (cells down to 50 m depth).

To better quantify connectivity between species ranges in tropical West Africa and the Mediterranean Sea, we considered the two consecutive dispersal pathways: the first along the West African coast and through the Canaries and Madeira archipelagos from Cape Blanc north to the Strait of Gibraltar, the doorstep of the Mediterranean Sea, and the second through the western Mediterranean to the Strait of Sicily, enabling dispersal into the eastern Mediterranean (Fig. 1). Along these two dispersal pathways, we quantified connectivity by calculating the size and the mean minimum distance between the suitable patches, a patch being a cluster of continuously suitable cells identified with the "clump" function in the "raster" package (51) (*SI Appendix, Fig. S3*). The larger the size of the patches and the smaller the minimum distance between suitable ones, the greater the connectivity.

Data, Materials, and Software Availability. All study data are included in the article and/or supporting information.

ACKNOWLEDGMENTS. This study was conducted in the framework of the project "Ecological effects of species range-expansions driven by climate: insights from the Last Interglacial (MIS5e, Pleistocene) of the Mediterranean Sea" funded by the Italian Ministry for University and Research [programme PRIN 2022 supported by National Recovery and Resilience Plan, grant 2022P3425X to P.G.A. and S. Danise. (CUP C53D23003470006 and B53D23012220006, respectively)]. L.S.' stay at Stazione Zoologica Anton Dohrn was co-funded by an ERASMUS traineeship and P.G.A.'s institutional research funds. L.S. acknowledges support during the finalization of this study from Trond Mohn Stiftelse (TMS) and University of Bergen for the startup grant "TMS2022STG03" to Suzette G.A. Flantua (BIO-Uib). This is ISMAR-CNR, Bologna, scientific contribution n. 2080.

Author affiliations: ^aDepartment of Marine Animal Conservation and Public Engagement, Stazione Zoologica Anton Dohrn, Naples 80121, Italy; ^bDepartment of Biological Sciences, University of Bergen, Bergen 5006, Norway; ^cDepartment of Botany and Biodiversity Research, University of Vienna, Vienna 1030, Austria; ^dInstitute of Marine Sciences, National Research Council, Bologna 40129, Italy; ^eDepartment of Integrative Marine Ecology, Stazione Zoologica Anton Dohrn, Naples 80121, Italy; and ^fDepartment of Earth Sciences, University of Florence, Florence 50121, Italy

1. M. J. Costello *et al.*, Marine biogeographic realms and species endemism. *Nat. Commun.* **8**, 1057 (2017).
2. N. S. Diffenbaugh, F. Giorgi, Climate change hotspots in the CMIP5 global climate model ensemble. *Clim. Change* **114**, 813–822 (2012).
3. P. G. Albano *et al.*, Native biodiversity collapse in the eastern Mediterranean. *Proc. R. Soc. B Biol. Sci.* **288**, 20202469 (2021).

4. Intergovernmental Panel on Climate Change (IPCC), Ed., "Changing state of the climate system" in Climate Change 2021 – The Physical Science Basis: Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change (Cambridge University Press, 2023), pp. 287–422.
5. C. Parmesan, Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* **37**, 637–669 (2006).

6. H. Fischer *et al.*, Palaeoclimate constraints on the impact of 2 °C anthropogenic warming and beyond. *Nat. Geosci.* **11**, 474–485 (2018).
7. A. M. Haywood *et al.*, Are there pre-Quaternary geological analogues for a future greenhouse warming? *Philos. Trans. R. Soc. Math. Phys. Eng. Sci.* **369**, 933–956 (2011).
8. J. E. Tierney *et al.*, Past climates inform our future. *Science* **370**, eaay3701 (2020).
9. S. Danise, R. J. Twitchett, C. T. S. Little, Environmental controls on Jurassic marine ecosystems during global warming. *Geology* **43**, 263–266 (2015).
10. E. E. Saupe *et al.*, Macroevolutionary consequences of profound climate change on niche evolution in marine molluscs over the past three million years. *Proc. R. Soc. B* **281**, 20141995 (2014).
11. G. S. Antell, I. S. Fenton, P. J. Valdes, E. Saupe, Thermal niches of planktonic foraminifera are static throughout glacial-interglacial climate change. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e2017105118 (2021).
12. B. Sabelli, M. Taviani, "The making of the Mediterranean molluscan biodiversity" in The Mediterranean Sea: Its History and Present Challenges, S. Goffredo, Z. Dubinsky, Eds. (Springer Netherlands, 2014), pp. 285–306.
13. K. C. Maguire, D. Nieto-Lugilde, M. C. Fitzpatrick, J. W. Williams, J. L. Blois, Modeling species and community responses to past, present, and future episodes of climatic and ecological change. *Annu. Rev. Ecol. Evol. Syst.* **46**, 343–368 (2015).
14. L. A. Jones *et al.*, Coupling of palaeontological and neontological reef coral data improves forecasts of biodiversity responses under global climatic change. *R. Soc. Open Sci.* **6**, 182111 (2019).
15. M. S. Lima-Ribeiro *et al.*, Fossil record improves biodiversity risk assessment under future climate change scenarios. *Divers. Distrib.* **23**, 922–933 (2017).
16. B. S. Galil, A. Marchini, A. Occhipinti-Ambrogi, East is east and West is west? Management of marine bioinvasions in the Mediterranean Sea. *Estuar. Coast. Shelf Sci.* **201**, 7–16 (2018).
17. M. Oliverio, M. Taviani, The Eastern Mediterranean Sea: Tropical invasions and niche opportunities in a "Godot Basin". *Biogeographia* **24**, 313–318 (2003).
18. M. Taviani, The Mediterranean benthos from late Miocene up to present: Ten million years of dramatic climatic and geologic vicissitudes. *Biol. Mar. Mediterr.* **9**, 445–463 (2002).
19. C. S. Melo *et al.*, Range expansion of tropical shallow-water marine molluscs in the NE Atlantic during the last interglacial (MIS 5e): Causes, consequences and utility of ecostratigraphic indicators for the Macaronesian archipelagos. *Quat. Sci. Rev.* **278**, 107377 (2022).
20. B. L. Otto-Bliesner *et al.*, Large-scale features of Last Interglacial climate: Results from evaluating the *lig127k* simulations for the Coupled Model Intercomparison Project (CMIP6)–Paleoclimate Modeling Intercomparison Project (PMIP4). *Clim. Past* **17**, 63–94 (2021).
21. V. Garilli, Mediterranean Quaternary interglacial molluscan assemblages: Palaeobiogeographical and palaeoceanographical responses to climate change. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **312**, 98–114 (2011).
22. E. De La Vega, T. B. Chalk, P. A. Wilson, R. P. Bysani, G. L. Foster, Atmospheric CO₂ during the Mid-Piacenzian Warm Period and the M2 glaciation. *Sci. Rep.* **10**, 11002 (2020).
23. C. M. D. Silva, B. M. Landau, Cenozoic Atlanto-Mediterranean biogeography of *Spiricella* (Gastropoda, Umraculidae) and climate change: Filling the geological gap. *The Veliger* **49**, 19–26 (2007).
24. S. J. Bograd *et al.*, Climate change impacts on eastern boundary upwelling systems. *Annu. Rev. Mar. Sci.* **15**, 303–328 (2023).
25. R. R. Rykaczewski *et al.*, Poleward displacement of coastal upwelling-favorable winds in the ocean's eastern boundary currents through the 21st century. *Geophys. Res. Lett.* **42**, 6424–6431 (2015).
26. M. C. Sousa, I. Alvarez, M. deCastro, M. Gomez-Gesteira, J. M. Dias, Seasonality of coastal upwelling trends under future warming scenarios along the southern limit of the canary upwelling system. *Prog. Oceanogr.* **153**, 16–23 (2017).
27. M. C. Sousa, M. deCastro, I. Alvarez, M. Gomez-Gesteira, J. M. Dias, Why coastal upwelling is expected to increase along the western Iberian Peninsula over the next century? *Sci. Total Environ.* **592**, 243–251 (2017).
28. A. Sylla, J. Mignot, X. Capet, A. T. Gaye, Weakening of the Senegalo-Mauritanian upwelling system under climate change. *Clim. Dyn.* **53**, 4447–4473 (2019).
29. J. Aristegui *et al.*, Sub-regional ecosystem variability in the Canary Current upwelling. *Prog. Oceanogr.* **83**, 33–48 (2009).
30. M. Maslin, M. Sarnthein, J.-J. Knaack, P. Grootes, C. Tzedakis, Intra-interglacial cold events: An Eemian-Holocene comparison. *Geol. Soc. Lond. Spec. Publ.* **131**, 91–99 (1998).
31. P. Ditlevsen, S. Ditlevsen, Warning of a forthcoming collapse of the Atlantic meridional overturning circulation. *Nat. Commun.* **14**, 4254 (2023).
32. E. Bazzicalupo *et al.*, Population genetics of *Bursatella leachii* (De Blainville, 1817) and implications for the origin of the Mediterranean population. *Helgol. Mar. Res.* **72**, 19 (2018).
33. Á. Valdés *et al.*, The origin and dispersal pathway of the spotted sea hare *Aplysia dactylomela* (Mollusca: Opisthobranchia) in the Mediterranean Sea. *Aquat. Invasions* **8**, 427–436 (2013).
34. A. Sparrow, F. Badalamenti, C. Pipitone, Contribution to the knowledge of *Percnon gibbesi* (Decapoda, Grapsidae), an exotic species spreading rapidly in sicilian waters. *Crustaceana* **74**, 1009–1017 (2001).
35. E. Azzurro, S. Smeraldo, M. D'Amen, Spatio-temporal dynamics of exotic fish species in the Mediterranean Sea: Over a century of invasion reconstructed. *Glob. Change Biol.* **28**, 6268–6279 (2022).
36. G. J. Vermeij, P. D. Roopnarine, The coming Arctic invasion. *Science* **321**, 780–781 (2008).
37. D. Nogués-Bravo *et al.*, Cracking the code of biodiversity responses to past climate change. *Trends Ecol. Evol.* **33**, 765–776 (2018).
38. S. Dominić, S. Danise, Mediterranean onshore-offshore gradient in the composition and temporal turnover of benthic molluscs across the middle Piacenzian Warm Period. *Geol. Soc. Lond. Spec. Publ.* **529**, 365–394 (2023).
39. O. Peleg, T. Guy-Haim, E. Yeruham, J. Silverman, G. Rilov, Tropicalisation may invert trophic state and carbon budget of shallow temperate rocky reefs. *J. Ecol.* **108**, 844–854 (2019).
40. J. Steger *et al.*, Non-indigenous molluscs in the Eastern Mediterranean have distinct traits and cannot replace historic ecosystem functioning. *Glob. Ecol. Biogeogr.* **31**, 89–102 (2021).
41. E. Azzurro, M. D'Amen, Climate change paves the way for a new inter-ocean fish interchange. *Front. Ecol. Environ.* **20**, 558–563 (2022).
42. G. J. Vermeij, The tropical history and future of the Mediterranean biota and the West African enigma. *J. Biogeogr.* **39**, 31–41 (2012).
43. R Core Team, R: A language and environment for statistical computing (Version 4.2.2., R Foundation for Statistical Computing, Vienna, Austria, 2022).
44. J. Assis *et al.*, Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. *Glob. Ecol. Biogeogr.* **27**, 277–284 (2018).
45. G. Danabasoglu, NCAR CESM2 model output prepared for CMIP6 PMIP *lig127k* (Version 2022.08.10, Earth System Grid Federation, 2019), <https://doi.org/10.22033/ESGF/CMIP6.7673> (August 10, 2022).
46. B. L. Otto-Bliesner *et al.*, A comparison of the CMIP6 *midHolocene* and *lig127k* simulations in CESM2. *Paleoceanogr. Paleoclimatol.* **35**, e2020PA003957 (2020).
47. W. Thuiller, B. Lafourcade, R. Engler, M. B. Araujo, BIOMOD—a platform for ensemble forecasting of species distributions. *Ecography* **32**, 369–373 (2009).
48. L. Schultz, J. Wessely, S. Dullinger, P. G. Albano, The dawn of the tropical Atlantic invasion into the Mediterranean Sea – code for modeling. Zenodo. <https://doi.org/10.5281/zenodo.10610763>. Deposited 2 February 2024.
49. M. Araujo, M. New, Ensemble forecasting of species distributions. *Trends Ecol. Evol.* **22**, 42–47 (2007).
50. C. Liu, P. M. Berry, T. P. Dawson, R. G. Pearson, Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* **28**, 385–393 (2005).
51. R. J. Hijmans *et al.*, raster: Geographic Data Analysis and Modeling (Version 3.5-29, 2022) (Accessed 26 September 2022).