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RESEARCH ARTICLE

The climate crisis affects Mediterranean marine molluscs of conservation concern

Lotta Schultz[1,2] | **Johannes Wessely**[3] | **Stefan Dullinger**[3] | **Paolo G. Albano**[1,2]

[1]Department of Palaeontology, University of Vienna, Vienna, Austria
[2]Department of Marine Animal Conservation and Public Engagement, Stazione Zoologica Anton Dohrn, Naples, Italy
[3]Department of Botany and Biodiversity Research, University of Vienna, Vienna, Austria

Correspondence
Paolo G. Albano, Department of Palaeontology, University of Vienna, Josef-Holaubek-Platz 2, UZA II, Vienna A-1090, Austria.
Email: pgalbano@gmail.com

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Abstract

Aim: The Mediterranean Sea is a hotspot of endemism and it is warming at two to three times the rate of the global ocean. The continental masses that surround it constrain species range shifts. Therefore, as seawater temperature increases, distributions of marine species may contract into few small cooler refugia, with consequent risk of extinction from range contraction and fragmentation, particularly for endemics. We assess this risk for 15 molluscs of conservation concern occurring in the Mediterranean Sea. Invertebrates have been rarely assessed so far, despite their diversity and their importance for ecosystem functioning.

Location: The Mediterranean Sea and Eastern Atlantic Ocean.

Methods: We used ensemble species distribution models to project the future range of our target species and assess their IUCN Red List status.

Results: As hypothesized, our models predicted major range shifts, contractions and fragmentation in the Mediterranean Sea for all species. Under moderate emission scenarios such as RCP4.5, up to 12 of the 15 target species will be eradicated from the eastern and southern warmer sectors. Under severe emission scenarios such as RCP8.5 and by the end of the century, we predict the global extinction of the endemic *Patella ferruginea* and *Pinna nobilis*. Non-endemic species may buffer range loss in the Mediterranean with range gains in the Atlantic Ocean. Still, we predict that only a single species, *Zonaria pyrum*, will have marginal total range gains in future climate warming scenarios.

Main conclusions: Eight species will become threatened and the fate of *Patella ferruginea* and *Pinna nobilis* contrasts the belief that marine species are less prone to extinction than continental species under a warming climate.

KEYWORDS
fragmentation, global warming, IUCN Red List, Mediterranean Sea, Mollusca, range shift, species distribution models

1 | INTRODUCTION

Climate change is occurring at an unprecedented pace and with velocities up to seven times higher in the ocean than on land (Burrows et al., 2011). Model projections and direct observations suggest profound changes in the physical and chemical properties of the ocean, representing major pressures on marine life (IPCC, 2013; Poloczanska et al., 2016). Changes in the geographical distribution of marine species are among the most pervasive responses to warming (Parravicini et al., 2015), because marine ectotherms more fully occupy the latitudinal extent within their thermal tolerance limits (Sunday et al., 2012). Rising temperatures cause range expansions at species leading (poleward) and contractions at their trailing (equatorward) edges (Bates et al., 2014).

The effects of warming-induced range shifts are expected to be particularly critical in semi-enclosed basins such as the Mediterranean Sea where species dispersal potential is physically constrained by land mass barriers (Ben Rais Lasram et al., 2010). Here, species cannot further track their environmental niches towards higher latitudes and thus may restrict their ranges to northern refugia and eventually undergo basin-scale extinction (Cheung et al., 2009; Parravicini et al., 2015). Additionally, the Mediterranean Sea ranks among the most vulnerable ocean regions to climate change and has been warming at two to three times the rate of the global ocean so far (Vargas-Yáñez et al., 2008). This is due to the basin's bioclimatic peculiarities, resulting from its geographic position in the transition between the arid climate of North Africa and the temperate and rainy climate of central Europe (Giorgi & Lionello, 2008) and its semi-enclosed nature that implies limited hydrological exchange with adjacent oceans and thus an increased capacity to store heat (Bethoux & Gentili, 1999; Diffenbaugh et al., 2007).

The already observed consequences of warming-induced range shifts in the Mediterranean Sea are twofold. First, thermophilic species that used to occur in southern waters have extended their ranges northwards and thus caused substantial community reorganizations (Bianchi & Morri, 2000). Second, species sensitive to warming have gotten locally rarer or totally eradicated in the warmer sectors leaving behind a taxonomic and functional void (Albano et al., 2021; Rilov, 2016; Steger et al., 2021). For these species, accelerating warming will first make the coldest northern parts of the Mediterranean Sea the last refugia, but then these sectors will become *cul-de-sacs* leading eventually to high extinction risk for Mediterranean endemic species (Ben Rais Lasram et al., 2010; Gallagher & Albano, 2023). Due to the indented outline of the northern Mediterranean, where peninsulas delimit major sub-basins, such *cul-de-sacs* will host heavily fragmented populations with limited or ultimately no connectivity (Ben Rais Lasram et al., 2010). Range loss and fragmentation may thus lead to increased genetic drift and eventually to high losses of genetic diversity (Frankham et al., 2002). This conservation issue has largely been neglected in studies on responses of marine ecosystems to climate change, as the marine realm is generally characterized by a comparatively high connectivity (Carr et al., 2003).

Range reduction is an important criterion for the assessment of conservation status according to the IUCN (IUCN, 2022). Invertebrates are lagging behind in such assessments which are heavily biased in favour of the more charismatic and well-studied terrestrial vertebrates (Cardoso et al., 2011; Cowie et al., 2022; Régnier et al., 2015). Among marine invertebrates, molluscs are the most represented group in international agreements on the conservation of the Mediterranean Sea (e.g. CITES, Bern and Barcelona conventions, 'Habitats' Directive of the European Union), but their possible fate under future climate warming has not been assessed so far.

We here modelled the distribution of Mediterranean marine molluscs of conservation concern under moderate to severe climate scenarios to quantify range changes and estimate their future conservation status. We expect that (i) species will persist only in northern climatic refugia; (ii) due to the peculiar outline of Mediterranean northern shores, ranges will fragment; and (iii) conservation status will worsen with high risk of global extinction for endemic species in particular.

2 | METHODS

2.1 | Target species and data collection

We focused on 15 of the 17 marine mollusc species of conservation concern in the Mediterranean Sea according to international agreements (Table 1 and Figure S1) (Katsanevakis et al., 2020). *Steromphala nivosa* and *Dendropoma cristatum* were excluded from the study because the former is endemic to the Maltese Archipelago (Evans et al., 2011) and has thus a too restricted range for meaningful modelling at large biogeographic scales, and the second because it is a cryptic species-complex (Calvo et al., 2009; Templado et al., 2016) and occurrences in public databases may not be taxonomically accurate.

Species occurrences were gathered from the Global Biodiversity Information Facility (GBIF), the Ocean Biogeographic Information System (OBIS), from private collections and the Natural History Museum of Vienna (NHMW). Data were quality checked by plotting occurrences and visually excluding those outside the known range or on land. Occurrence records which did not match a cell of the environmental raster layer (see below) due to its coarseness were moved to the closest cell using the *points2nearestcell* function of the 'Pakillo/rSDM' package (Rodriguez-Sanchez, 2020) in the R statistical environment version 4.0.3 (R Core Team, 2021). The maximum moving distance was determined as 9000 m, corresponding to the size of one grid cell. Ultimately, we aggregated multiple occurrence points in the same grid cell to one record per cell (Hu et al., 2021; Qu et al., 2023).

To characterize present-day (averaged for the baseline period 2000–2014) and future climate (projections for 2050 and 2100), we used environmental data provided by Bio-Oracle (https://www.bio-oracle.org/) at a spatial resolution of 5 arcmin (ca 9.2 km at the equator) (Assis et al., 2018). Despite the limited time range of present-day environmental data, we retained species occurrences irrespective of their data of recording, as most pertain to this or an earlier time period and are thus unaffected from the

TABLE 1 Target species, their distribution range and international agreements on their conservation interest (CITES, Convention on International Trade in Endangered Species (1973); 'Habitats' Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora; Bern Convention, Convention on the Conservation of European Wildlife and Natural Habitats (1982); Barcelona Convention, Convention on the protection of the Mediterranean Sea against pollution (1977)).

Class	Family	Species	Distribution range	Bathymetric range	CITES	Habitats Directive	Bern Convention	Barcelona Convention
Gastropoda	Patellidae	*Patella ferruginea* Gmelin, 1791	Endemic to the Mediterranean Sea	Intertidal		Annex IV	Annex II	Annex II
Gastropoda	Patellidae	*Cymbula safiana* (Lamarck, 1819)	Western Mediterranean Sea, East Atlantic along West African Coast and Cape Verde	Intertidal			Annex II	Annex II
Gastropoda	Cypraeidae	*Naria spurca* (Linnaeus, 1758)	Mediterranean Sea, East Atlantic along West African Coast, Canary Islands, Azores and Cape Verde	Shallow subtidal			Annex II	Annex II
Gastropoda	Cypraeidae	*Luria lurida* (Linnaeus, 1758)	Mediterranean Sea, West Africa, Canary Islands, Azores and Cape Verde	Shallow subtidal			Annex II	Annex II
Gastropoda	Cypraeidae	*Schilderia achatidea* (Gray, 1837)	Western Mediterranean Sea, West Africa	Shallow subtidal			Annex II	Annex II
Gastropoda	Cypraeidae	*Zonaria pyrum* (Gmelin, 1791)	Mediterranean Sea, Southern Portugal to West Africa, Canary Islands and Cape Verde	Continental shelf and upper slope			Annex II	Annex II
Gastropoda	Tonnidae	*Tonna galea* (Linnaeus, 1758)	Mediterranean Sea, Atlantic Ocean, Gulf of Mexico and Caribbean Sea	Continental shelf and upper slope			Annex II	Annex II
Gastropoda	Charoniidae	*Charonia lampas* (Linnaeus, 1758)	Western Mediterranean Sea, Southern Portugal to West Africa, Canary Islands and Cape Verde, Southwestern Atlantic	Continental shelf and upper slope			Annex II	Annex II
Gastropoda	Charoniidae	*Charonia variegata* (Lamarck, 1816)	Eastern Mediterranean Sea, Atlantic Ocean, Caribbean Sea, Gulf of Mexico	Shallow subtidal			Annex II	Annex II
Gastropoda	Ranellidae	*Ranella olearium* (Linnaeus, 1758)	Cosmopolitan species mostly found in the Mediterranean Sea, Atlantic Ocean, South Africa and New Zealand. Occasional records in Caribbean Sea, South Indian and southwestern Pacific	Continental shelf and upper slope			Annex II	Annex II
Gastropoda	Mitridae	*Episcomitra zonata* (Marryat, 1819)	Subendemic to the Mediterranean Sea, sparse occurrences in the Azores	Continental shelf and upper slope			Annex II	Annex II
Bivalvia	Mytilidae	*Lithophaga lithophaga* (Linnaeus, 1758)	Subendemic to the Mediterranean Sea with occurrences in the Azores and the Canary Islands	Intertidal	Annex II	Annex IV	Annex II	Annex II
Bivalvia	Pinnidae	*Pinna nobilis* (Linnaeus, 1758)	Endemic to the Mediterranean Sea	Shallow subtidal		Annex IV	Annex II	Annex II
Bivalvia	Pinnidae	*Pinna rudis* (Linnaeus, 1758)	Mediterranean Sea, North East Atlantic, Caribbean Sea, Gulf of Mexico	Shallow subtidal			Annex II	Annex II
Bivalvia	Pholadidae	*Pholas dactylus* (Linnaeus, 1758)	Mediterranean Sea, North East Atlantic along European coast, British Isles	Intertidal			Annex II	Annex II

warming-induced range changes recorded for some marine molluscs (but not for our target species). Future climate was considered under four different IPCC scenarios: Representative Concentration Pathway (RCP) 2.6 (mild scenario), RCP4.5 (intermediate scenario), RCP6.0 (intermediate scenario) and RCP8.5 (severe scenario) (IPCC, 2013). We initially selected six bioclimatic and environmental variables which are known as regulating factors controlling the metabolism of the target species and were thus expected to provide a good approximation of their biophysiological niche: maximum temperature, temperature range, minimum salinity, salinity range, long-term maximum chlorophyll, chlorophyll range (for detailed definition, Table S1). In particular, temperature is an important environmental predictor, as it explains most of a marine ectotherm's distribution (Pinsky et al., 2019), salinity is relevant for mollusc physiological processes (Pourmozaffar et al., 2019), while chlorophyll is a proxy for nutrient availability (Moraitis et al., 2018). Environmental layers were resized for each species to fit their current range plus a buffer area of potentially suitable future range, and according to species bathymetric preferences (Table 1). Predictors were then tested for correlations across occurrence points for each species separately using Pearson correlation test (threshold $|r|>0.7$, cf. Dormann et al., 2013) to avoid collinearity effects on model estimates (Table S2).

2.2 | Modelling and data analysis

We modelled the realized environmental niche of each species and its projection under future climates with an ensemble of four algorithms (generalized linear model (GLM), generalized additive model (GAM), generalized boosted model (GBM) and random forest (RF)) with the 'biomod2' package (Thuiller et al., 2009) in R. The algorithms were parameterized drawing five sets of 10,000 pseudo-absence points each at a minimum distance of 20 km to the closest presence data point. For intertidal environmental layers, the number of pseudo-absences was decreased to 1000 points. Fitted models were evaluated through a repeated data-splitting procedure: 80% of the data were used to calibrate the models and the remaining 20% to test them for their accuracy. This splitting procedure was repeated three times and evaluated with the True Skill Statistic (TSS) and AUC (Area Under the Curve). Using the default settings in biomod, all replicates of all models with a TSS score ≥ 0.6 were then used to compute an ensemble forecast as weighted means of occurrence probabilities projected by the single models (Araujo & New, 2007). Probabilistic ensemble projections were translated into binary (presence/absence) ones using the threshold that maximizes the TSS score (Liu et al., 2005). The model evaluation scores presented in the Results and the Table S4 depict the averaged values over the three repetition runs for each of the modelled species. The importance of individual predictors in the models was assessed by means of a built-in permutation function that scores the impact the respective variable has on the discrimination ability of the model on a scale ranging from 0 to 1 (Thuiller et al., 2009).

Projected range changes for all species were visualized as maps indicating the probability of occurrence (i.e. 0%–100%) of the individual species at a certain cell (File S2). Additionally, we used the binary projections to draw consensus maps for each climate scenario by calculating the percentage of species of the same bathymetric range predicted to be present at a certain cell. Based on binary projections and under the assumption of species unlimited dispersal capability (as most molluscs have a planktonic larval stage), we then calculated proportional range loss and gain over the species full distribution range and at the Mediterranean basin scale. Differences in range loss between climate scenarios and years were tested with a randomization test due to the small sample size and lack of assumptions on variable distributions. We pooled predicted range change values for all species into a single vector and resampled it 10,000 times to build two groups of the same sample size. We then calculated the p-value as the number of resampled values more extreme than the absolute value of the observed difference between the medians ($\alpha = 0.05$). To quantify the fragmentation of suitable range, we followed the approach of Halstead et al. (2019) and clustered contiguous 'presence' cells into patches using the *clump* function in the 'raster' package (Hijmans, 2021) and Figure S2. We then calculated the total number and the mean minimum distance between suitable patches within a species range and in the Mediterranean Sea only.

Furthermore, we calculated the geographical position of species range centroids under current and future climatic conditions using the *gCentroid* in the 'rgeos' package (Bivand and Rundel, 2021) in order to derive range shifts (differences between future and current centroids).

Finally, we identified the Red List category for each species under criterion A3c 'population reduction projected to be met in the future (up to a maximum of 100 years) based on a decline in area of occupancy (AOO)' under present and future climate scenarios (IUCN, 2022). AOO is specified by the IUCN as the area of all predicted occupied cells for a species at a resolution of 2 × 2 km. We used the 'red' package (Cardoso, 2020) to calculate the current and future AOO for each species based on our binary projections and resizing our cell lattice to the 2 × 2 km one. The different size of cells in the 'biomod2' and 'Red' package outputs accounts for slight differences in the computed range reductions observable in the outputs. For *Pinna nobilis* and *Patella ferruginea*, we considered only the Mediterranean Sea to calculate AOO, as the occurrence of these two endemic species outside the basin is unlikely due to the same barriers to dispersal that made them endemic.

We documented all key steps of our SDM work in an ODMAP protocol as proposed by Zurell et al. (2020) (File S3).

3 | RESULTS

3.1 | SDM performance

A total of 9.081 georeferenced occurrence records were used for modelling the current and future distribution of the 15 target species (Table S3). For all species, the evaluation metric TSS indicated good ensemble model performance (TSS > > 0.8). The most accurate models were RFs with TSS values ranging between 0.76 and 0.91. By contrast, GLMs performed poorest with TSS values between 0.32 and 0.76, and could not be fitted for *Schilderia achatidea* (Table S4). The importance of the different environmental variables varied across species. However, maximum temperature, followed by minimum salinity and temperature range were those exerting the greatest impact on species distributions (Table S5).

3.2 | Projected range losses in the Mediterranean Sea

Thirteen of the 15 target species were projected to lose substantial parts of their currently suitable range in the Mediterranean Sea already by 2050 under all future scenarios (Figure 1). Range contractions span between 9.9% (*Lithophaga lithophaga*) and 96.5% (*Charonia lampas*) under the mildest scenario RCP2.6 and between 12.8% (*Charonia*

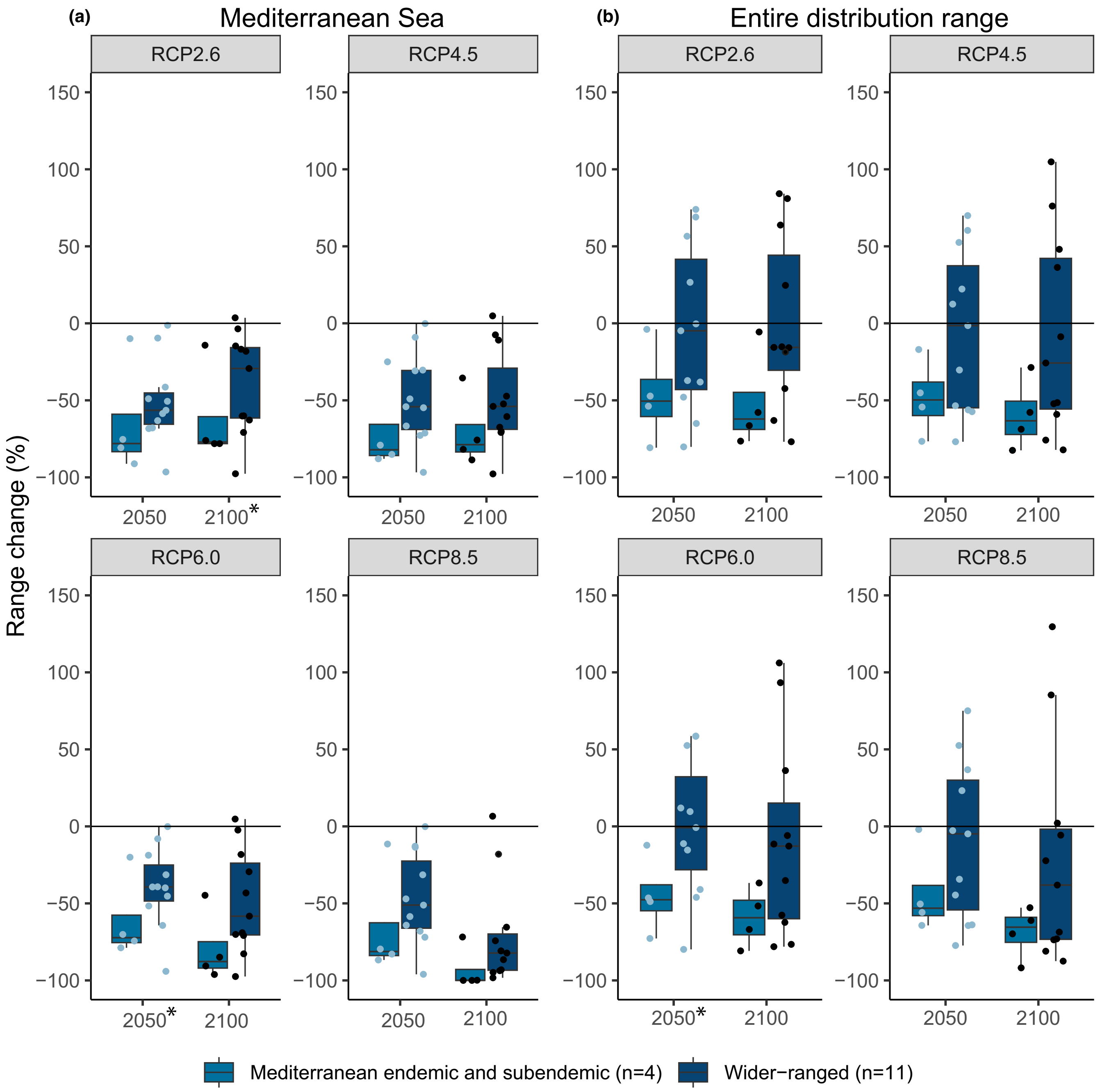

FIGURE 1 Predicted range change of marine molluscs of conservation concern (a) in the Mediterranean Sea and (b) across the entire distribution range. Asterisks indicate statistical significance (randomization test, $p < .05$). All species lose range in the Mediterranean Sea, with extinctions in the most severe scenarios predicted for endemic species in 2100. Considering their entire distribution range, most species with broader distributions also lose range, with few cases of range expansions.

variegata) and 96% (*C. lampas*) under the most severe scenario RCP8.5 (Table S6). Environmental conditions inside the basin were predicted to remain largely suitable only for *Ranella olearium* and *Zonaria pyrum*.

Projected range loss in the Mediterranean Sea was more pronounced for Mediterranean (sub)endemic species than for species occurring also on large areas outside the basin (Figure 1a). Under the most severe scenario RCP8.5 by 2050, ranges of (sub)endemics will contract by 65.2% on average (11.5%–86.7%) as compared to 46.8% (0.6%–96%) for the more widespread species, and by 92.9% (71.8%–100%) compared to 70.1% (6.6%–98.3%) in 2100. For three of the four Mediterranean (sub)endemic species, namely *Patella ferruginea*, *Episcomitra zonata* and *Pinna nobilis*, we predicted extinction in the basin by the end of the century (Table S6).

In general, projected range changes are highly idiosyncratic. For instance, *Zonaria pyrum* was predicted to find suitable range inside the basin throughout the century under all climate scenarios, while *Charonia lampas* will lose up to 96% of its currently suitable range in the Mediterranean Sea already by 2050.

3.3 | Refugia in the Mediterranean Sea

The Gulf of Lion, the Alboran Sea and the south-eastern part of the Aegean Sea will remain the most environmentally suitable areas under future scenarios (Figure 2, Figures S3–S6). In contrast, projection maps pointed to the highest decreases of suitable range in the Tyrrhenian, Ionian and Levantine seas (Figure 2). Some species will respond faster to changes. For example, *Episcomitra zonata* currently finds suitable conditions in the western and central Mediterranean but will restrict its range to the Gulf of Lion and the Alboran Sea already by the mid-21st century and is predicted to go extinct in the Mediterranean by the end of the century. In contrast, species such as *Pinna rudis* will respond more slowly: it will remain broadly distributed in the Mediterranean until 2050, and will persist, despite confined to the Gulf of Lion and the Alboran Sea, until the end of the century. For other species such as *Pinna nobilis*, *Luria lurida* and *Lithophaga lithophaga*, the eastern Adriatic will serve as an additional refugium at least under mild and intermediate climate scenarios. Furthermore, we found that the continental shelf and upper slope might act as a deep-water refugium for some of the target species occurring below the photic zone, such as *Tonna galea*, particularly in the Levantine and Ionian basins (Figure 2).

3.4 | Projected range losses at the global scale

Considering areas outside the Mediterranean and global distributions, some Mediterranean (sub)endemic species are predicted to expand their range outside Gibraltar from Morocco to the Bay of Biscay, still showing significantly higher range losses than more widely distributed species (Figure 1b and Table S6). However, such range expansions may not happen as long as the barriers to dispersal that made these species endemic remain effective.

Species broadly distributed outside the Mediterranean will also lose range. For instance, *Tonna galea* was shown to lose substantial parts of its currently suitable range in the Gulf of Mexico and the Caribbean Sea. In contrast, few species are predicted to experience major range expansions (e.g. *Zonaria pyrum*, *Charonia variegata*, *Charonia lampas* and *Ranella olearium*) (Figure 1 and Table S6). Expansions occur mostly at temperate latitudes such as around the British islands in the northern hemisphere and along Namibia and South Africa in the southern hemisphere. The British Isles account for major range expansions of *Pholas dactylus*, *Charonia lampas*, *Tonna galea* and *Ranella olearium*.

3.5 | Range fragmentation

Suitable range was predicted to fragment severely, with limited connectivity among the remaining range patches. In the Mediterranean Sea, the number of suitable range patches declined for 14 of the 15 target species under all climate scenarios considered (Figure 3 and Table S7). In particular, by the end of this century, the remaining range patches within the basin (see also Section 3.3 and Figure 2) were predicted to be geographically distant from each other, representing major obstacles to the dispersal of the modelled species. Only *Ranella olearium* might experience a more continuous future distribution within the Mediterranean Sea due to range expansions in the cold sectors of the basin. Interestingly, when considering also areas beyond the basin and global distributions, our results still show increased range fragmentation under future climate scenarios (Figure 3). This implies that, although some species are expected to experience range expansions outside the Mediterranean Sea (see par. 3.4), the newly suitable area may still be fragmented and spatially separated from their current ranges. This is for instance the case for *Charonia variegata*, which is predicted to find disconnected suitable range patches along the north-western African coast. By contrast, continuous expansions of suitable ranges at temperate latitudes are likely for *Charonia lampas* and *Ranella olearium* (Figure 3 and Table S7).

3.6 | Range shifts

By the mid-century, the centroid of suitable ranges in the Mediterranean Sea was predicted to shift north-westward for most species (Figure 4). Due to the morphology of the basin that extends mostly from west to east, longitudinal shifts will be in the order of several degrees and up to 11, while latitudinal shifts will be mostly contained to less than two. As an exception to the general trend, *Patella ferruginea* showed a clear south-westward shift, mostly due to the loss of suitable range in the western Mediterranean and its consequent retreat to the climate refugium of the Alboran Sea.

By the end of the century and under the most extreme emission scenario RCP8.5, the centroids of all species will further move north-west, following the temperature gradient of the basin. *Patella ferruginea*, *Pinna nobilis* and *Episcomitra zonata* will be extinct under this

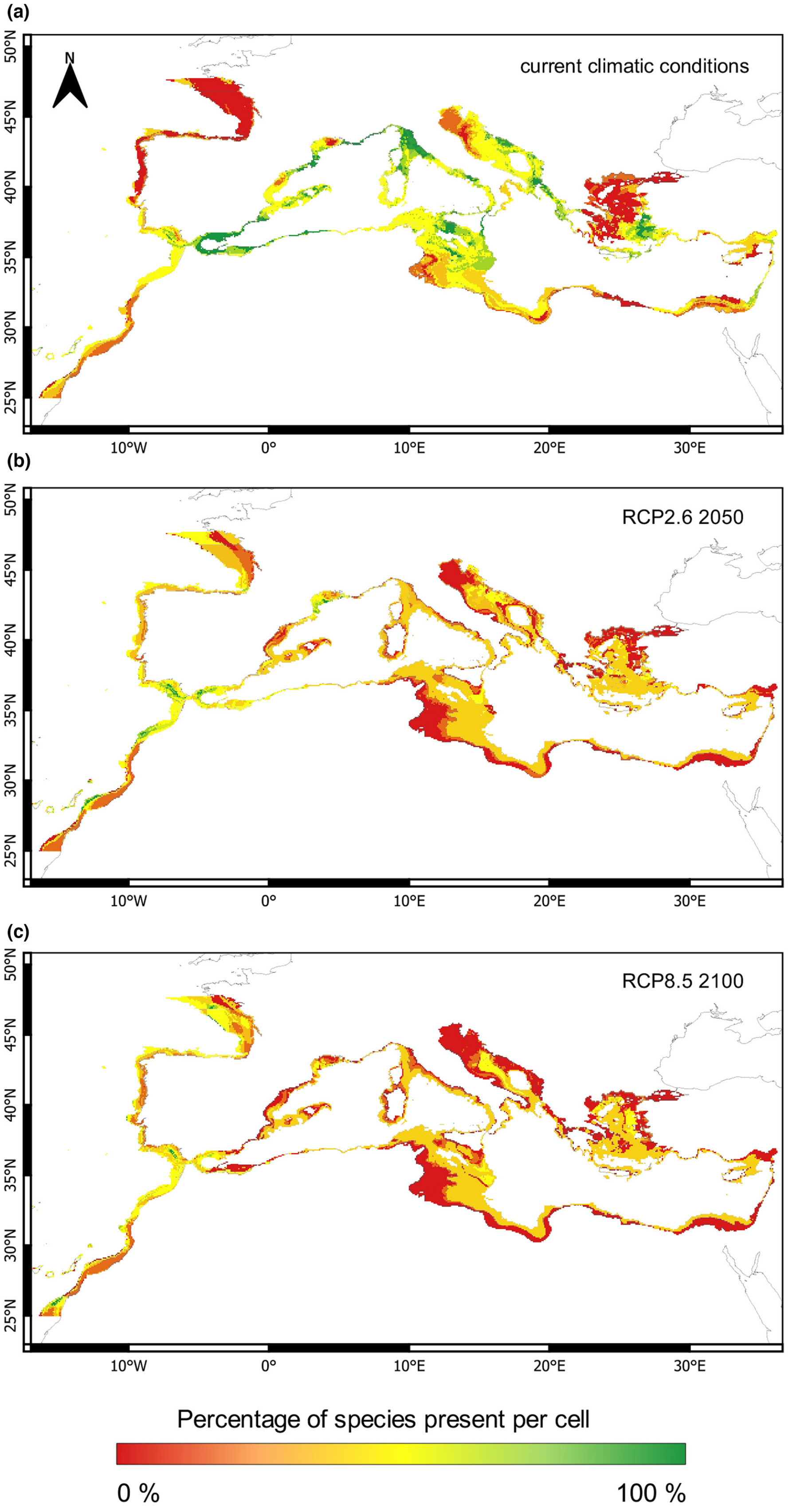

FIGURE 2 Percentage of species ($n = 15$) predicted to be present under (a) current environmental conditions; (b) RCP2.6 for the year 2050; and (c) RCP8.5 for the year 2100. The highest decrease of suitable range is predicted to occur in the Tyrrhenian, Ligurian and Ionian seas; while the last refugia will be the Gulf of Lion in southern France and the Alboran Sea.

scenario. A few species, such as *Lithophaga lithophaga* and *Ranella olearium*, will shift north-eastward due to their exploitation of the refugium in the northern Aegean Sea.

Considering the entire distribution of the target species, we found poleward range shifts in the order of several degrees for 11 of the 15 target species already by mid-century (Figure 5).

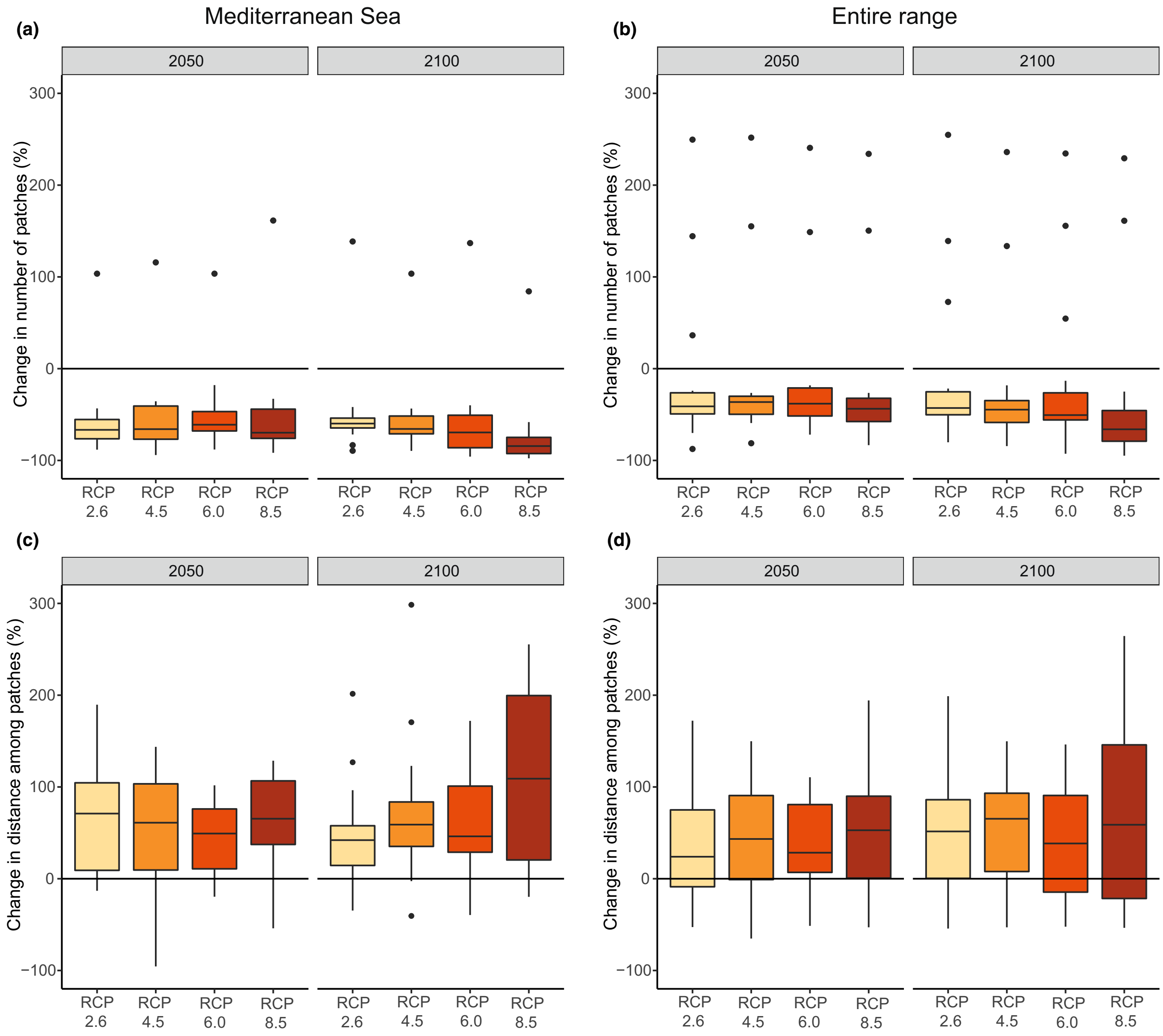

FIGURE 3 Predicted change in range fragmentation expressed as number of suitable patches in the Mediterranean Sea (a) and at the scale of the entire range (b), and as predicted change in the minimum mean distance among suitable patches in the Mediterranean Sea (c) and at the entire range scale (d). The number of suitable patches declines and the distance among them increases in the Mediterranean especially for end-century predictions. At the scale of the entire range, the number of suitable patches declines by the end of the century, with limited changes in distance among patches.

In contrast, *Charonia variegata*, *Zonaria pyrum*, *Patella ferruginea* and *Episcomitra zonata* will move equatorward. For the two latter species in particular, this is the consequence of their retreat in the cold waters of the north-west African coast. The gastropod *Ranella olearium* showed a particularly large shift westward by almost 60°, as a consequence of the loss of range in the Indo-West Pacific Ocean (Figure 5). Eastward shifts for species such as the amphiatlantic *Pinna rudis* mostly derive from the loss of range in the north-west Atlantic, with suitable range mostly occurring in the eastern Atlantic. By the end of the century and with increasing scenario severity, the poleward and westward distribution shifts intensify (Figure 5).

3.7 | Red list assessment

Following the IUCN Red List Assessment criterion A3c, nine of our 15 target species will qualify for global IUCN Red List categories due to projected decrease in AOO (Area of Occupancy) (Table 2 and Table S8). Under RCP2.6 and RCP8.5, *Naria spurca* will qualify as vulnerable by 2050, and under RCP4.5, it will be endangered by the end of the century. *Luria lurida*, *Lithophaga lithophaga*, *Episcomitra zonata* and *Pinna rudis* will be vulnerable under most scenarios by 2050 and endangered by the end of the century. *Cymbula safiana* will be endangered under most scenarios throughout the century and critically

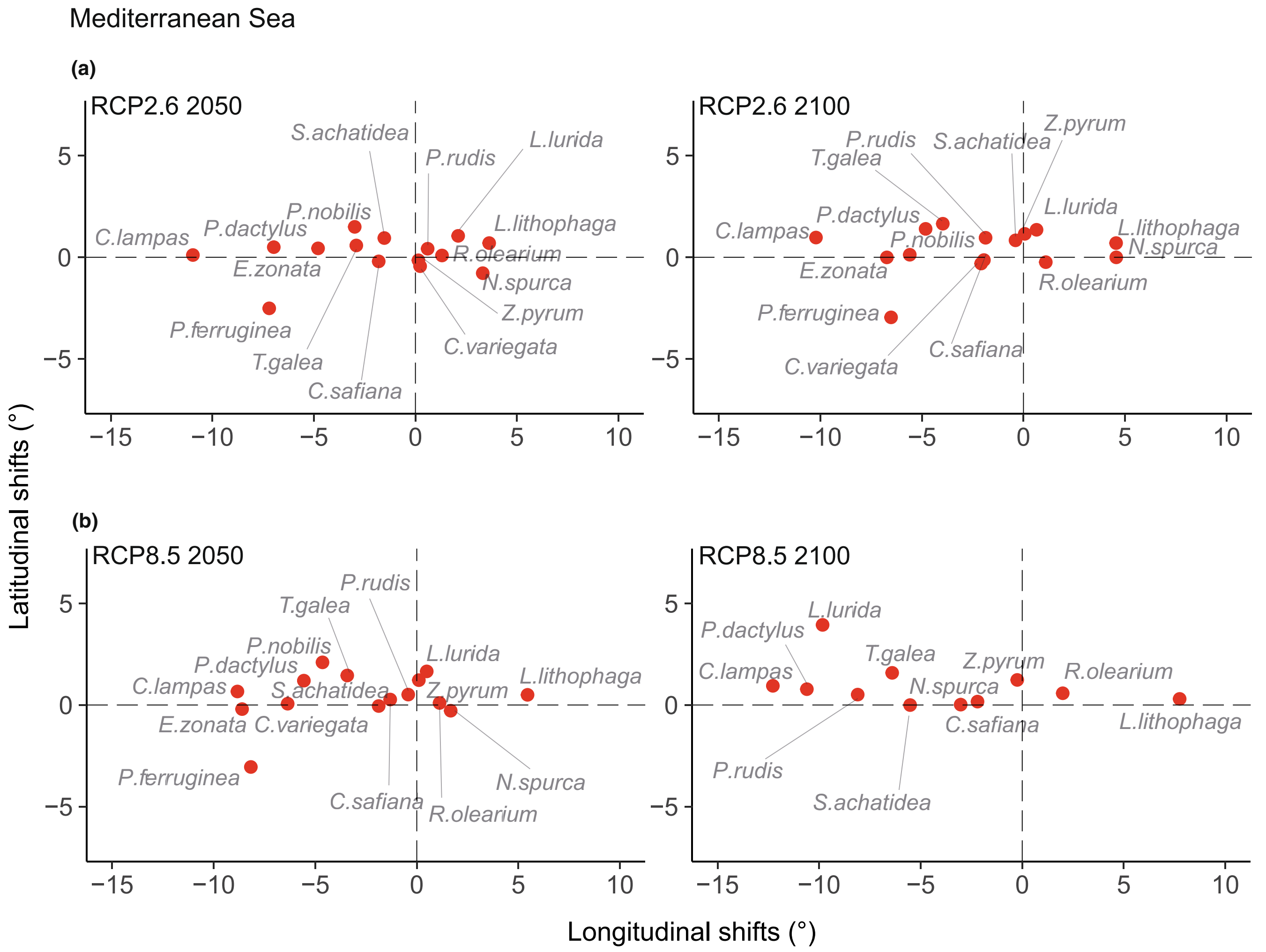

FIGURE 4 Projected geographical range shifts of the 15 marine mollusc species in the Mediterranean Sea under (a) RCP 2.6 and (b) under RCP 8.5 for the years 2050 and 2100. Latitudinal shifts >0° and < 0° indicate poleward and equatorward shift, respectively, compared to their current distribution. Under RCP8.5 2100, *Charonia variegata* shows an extreme westward shift (−27°), an outlier not illustrated here. Most species show a north-westward shift that intensifies by the end of the century. *Episcomitra zonata*, *Patella ferruginea* and *Pinna nobilis* were projected to become extinct under RCP8.5 in 2100 and are thus absent from the plot.

endangered under the most severe scenario by 2100. *Tonna galea* will classify either as critically endangered or as endangered under all scenarios throughout the century. The Mediterranean endemic *P. ferruginea* and *Pinna nobilis* will be critically endangered under most scenarios and even reach the extinct status under RCP8.5 by 2100. The latter species has already been assessed by IUCN Red List and is today listed as critically endangered.

4 | DISCUSSION

4.1 | Range shifts, contractions and fragmentation in the Mediterranean Sea

Our models predicted major range shifts, contractions and fragmentation for the 15 mollusc species in the Mediterranean Sea. All the target species (with the single exception of *Pholas dactylus*) are of warm water affinity, with those not endemic to the Mediterranean Sea distributed in warm temperate to tropical oceans (Table 1). Their projected range shifts towards the northern and western cooler sectors of the basin (Figure 3) fit the ongoing process of the establishment of species of warm-water affinity at northern latitudes observed since the 1990s (Albano, 2014; Bianchi, 2007; Bianchi & Morri, 1994), the so-called 'tropicalization' of the Mediterranean Sea (Bianchi and Morri, 1993).

Notwithstanding this warm water affinity, the northward retreat of the trailing edge of ranges will cause the eradication of most species from the eastern and southern warmer sectors of the Mediterranean even under moderate emission scenarios (Figure 2), exacerbating the recently documented loss of native diversity (Albano et al., 2021; Rilov, 2016). Additionally, the species of cold-water affinity like *Pholas dactylus* will be likely increasingly restricted to the colder parts of the Mediterranean such as the Gulf of Lyon or the Alboran Sea, as predicted for fishes and molluscs of commercial importance (Ben Rais

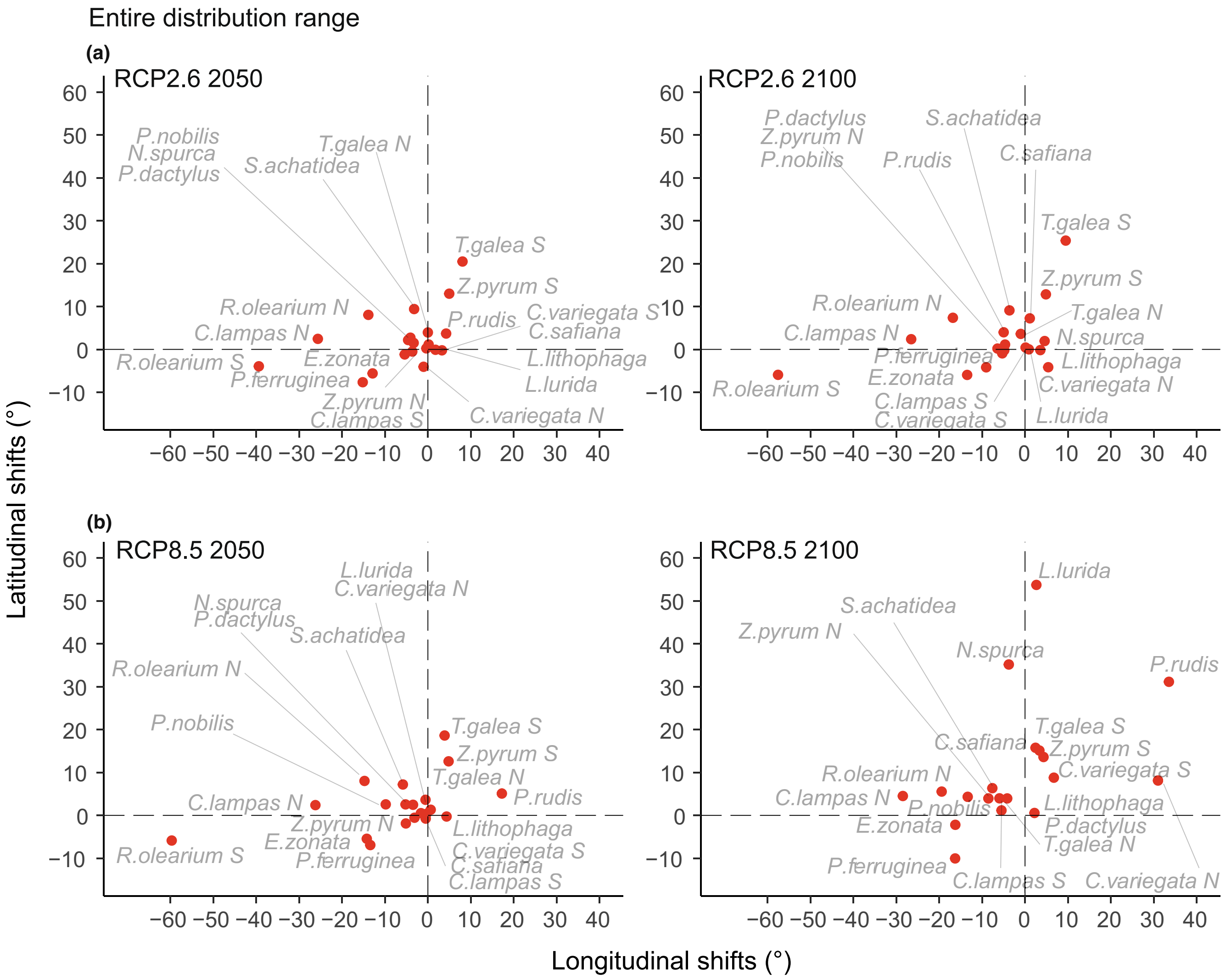

FIGURE 5 Projected geographical range shifts for the 15 marine mollusc species at their entire distribution range under (a) RCP 2.6 and (b) under RCP 8.5 for the years 2050 and 2100. Latitudinal shifts >0° and <0° indicate poleward and equatorward shift, respectively, compared to their current distribution. For species occurring in both the northern and southern hemisphere, centroid shifts were calculated separately for the northern and southern range. The majority of the species show a clear poleward range shift, that intensifies by the end of the century. Under RCP8.5 2100, *Ranella olearium* shows an extreme centroid shift towards the western hemisphere (−72°), an outlier not illustrated here.

Lasram et al., 2010; Gallagher & Albano, 2023). The retreat of such species into cooler refugia started to be observed in the 1990s when the first heat waves caused unusually long periods of high temperatures and a very deep thermocline in southern France (Chevaldonné & Lejeusne, 2003). The frequency of occurrence of marine heatwaves and consequent mass mortalities has increased since, even in long-considered cool refugia like the Gulf of Lyon and the Alboran Sea, and may constitute one of the drivers of native species collapses (Garrabou et al., 2022). Our models built an environmental envelope that is based on long-term data and may thus underestimate the effects of peaks of temperature as it happens during heat waves. That is, increased frequency of extreme events may cause faster range shifts and contractions than here stated.

Range contractions are here predicted to be massive—often above 80%—for most species, especially under the most extreme emission scenarios by the end of the century. We predict global extinction for the endemic *Patella ferruginea* and *Pinna nobilis* by end of the century under the worst emission scenario RCP8.5. Both species are already in decline. *Patella ferruginea* is a western Mediterranean species that is now restricted to few locations after a range contraction ongoing since the early 20th century attributed to human harvesting for food and bait and habitat loss due to coastal infrastructures (Espinosa et al., 2014; Ferranti et al., 2019). The species is a protandrous hermaphrodite and the removal of the larger female specimens has a disproportionate effect on population persistence (Espinosa et al., 2006). *Pinna nobilis* has been affected by a mass mortality induced by the parasite *Haplosporidium pinnae* and other pathogens since 2016. This mass mortality built on previous range contractions due to the extirpation of seagrass meadows, its favourite habitat, recorded in the previous decades (Ramos, 1998), bringing the species to the brink of extinction

TABLE 2 Current IUCN Red List classification and Red List category assigned according to proportional reduction in Area of Occupancy (AOO).

		Year 2050				Year 2100			
	Current IUCN classification	RCP2.6	RCP4.5	RCP6.0	RCP8.5	RCP2.6	RCP4.5	RCP6.0	RCP8.5
Cymbula safiana	NA	−66% EN	−55.9% EN	−46.7% VU	−65.1% EN	−62.7% EN	−76.9% EN	−78.7% EN	−80.8% CR
Patella ferruginea	NA	−90.9% CR	−84.5% CR	−73.6% EN	−82.3% CR	−75.2% EN	−81.1% CR	−90.4% CR	−100% EX
Luria lurida	NA	−48.5% VU	−53.8% EN	−10.8% LC	−45% VU	−15.5% LC	−53.1% EN	−57.5% EN	−72.6% EN
Naria spurca	NA	−34.9% VU	−28.2% LC	−13% LC	−32.6% VU	−16.5% LC	−50.8% EN	−33.6% VU	−34.4% VU
Schilderia achatidea	NA	0.8% LC	17.8% LC	18.4% LC	3% LC	−10.5% LC	−22.6% LC	−7.7% LC	−17.9% LC
Zonaria pyrum	NA	57.1% LC	54.6% LC	54.5% LC	54.6% LC	64% LC	75.3% LC	88.5% LC	116.3% LC
Tonna galea	NA	−82.2% CR	−79.2% EN	−81.8% CR	79.6% EN	−79.2% EN	−83.9% CR	79% EN	88.8% CR
Charonia variegata	NA	73.9% LC	63.8% LC	62.4% LC	39.3% LC	85.8% LC	51.3% LC	−5.1% LC	−69.2% EN
Charonia lampas	NA	67.3% LC	64.5% LC	56.2% LC	68.3% LC	77% LC	91% LC	90.9% LC	72.9% LC
Ranella olearium	NT (1996) Needs updating	12.3% LC	9.5% LC	1.5% LC	9.3% LC	11.7% LC	19% LC	16.2% LC	−6.% LC
Episcomitra zonata	NA	−43.4% VU	−50.7% EN	−45% VU	−52.6% EN	−54.7% EN	−55% EN	−48% VU	−51.7% EN
Lithophaga lithophaga	NA	−48.5% VU	−53.7% EN	−10.8% LC	−45% VU	−15.5% LC	−53.1% EN	−57.5% EN	−72.6% EN
Pinna nobilis	CR (2019)	−81.2% CR	−88.2% CR	−79% CR	−87% CR	−78.2% EN	−88.8% CR	−96.2% CR	−100% EX
Pinna rudis	NA	−36.8% VU	−56.2% EN	−40.9% VU	−63.7% EN	−40.5% VU	−58.2% EN	−62.2% EN	−72.4% EN
Pholas dactylus	NA	−4.4% LC	−6.1% LC	−5.3% LC	−9.4% LC	−17.6% LC	−13% LC	−16.5% LC	−12.7% LC

Note: Expansion or reduction <30%: Least Concern (LC); reduction ≥30%: Vulnerable (VU, green); reduction ≥50%: Endangered (EN, orange); reduction ≥80%: Critically endangered (CR, red); Reduction = 100%: Extinct (EX, black); Not assessed (NA); Near threatened (NT).

(Carella et al., 2019; Catanese et al., 2018; Katsanevakis, 2019). The other two subendemic species, *Episcomitra zonata* and *Lithophaga lithophaga*, broadly distributed in the Mediterranean and with few records in the Canaries and the Azores have distinct fates under future climatic scenarios. *Episcomitra zonata* is predicted to decline rapidly and abruptly and will be extinct by the end of the century under the most severe climate change scenario. *Lithophaga lithophaga* shows only modest declines under most scenarios and would become largely eradicated only in the most extreme ones. However, *L. lithophaga* is subject to illegal harvesting in many Mediterranean countries (Colletti et al., 2020; Katsanevakis et al., 2011) a practice that may contribute to the species demise notwithstanding its high fecundity (Galinou-Mitsoudi & Sinis, 1994).

Non-endemic species will also likely experience large range contractions in the Mediterranean, with a single winner: the gastropod *Zonaria pyrum*, the only species to remain stable or even experience marginal range gains. Only few of the non-endemic species will compensate the range loss in the Mediterranean Sea with significant gains at the global scale. This is mostly the case of Tonnoidean gastropods such as *Charonia lampas* and *Ranella olearium* whose teleplanic larvae have an exceptionally long planktonic life enabling very large ranges in the oceans and thus high capacity to colonize newly suitable areas. The ranges of some species with smaller distributions which include some regions of the eastern Atlantic Ocean may expand at northern latitudes further than they will retract at the equatorward limit (e.g. *Luria lurida*, *Naria spurca*, *Schilderia achatidea*) under most moderate scenarios. Despite some endemic species are here predicted to gain suitable range outside the Mediterranean Sea (e.g. in the Atlantic Ocean between Portugal and Morocco or in the Bay of Biscay), we are sceptical that they will pass the barriers to dispersal that made them endemic and which are related to the oceanographic fronts in the Alboran Sea and the Strait of Gibraltar (e.g. Backeljau et al., 1994; Ríos et al., 2002).

Even before the major range contractions or extinctions will happen, most species will likely experience range fragmentation within and beyond the Mediterranean Sea implying limited connectivity between populations. Small and isolated populations often show increased genetic drift, subsequent losses of genetic diversity and increased inbreeding (Duran et al., 2004; Keyghobadi et al., 2005; Pérez-Losada et al., 2002; Song et al., 2021; Wright, 1931). Such processes would compromise the fitness of populations and their ability to adapt to environmental changes (Frankham et al., 2002), making populations more vulnerable to impacts and thus prone to extirpation (Carr et al., 2003; Gibbs, 2001).

4.2 | Conservation of marine molluscs in the Mediterranean Sea

Despite the fact that all 15 target species are of conservation concern in the framework of regional and international agreements, only two, *Ranella olearium* and *Pinna nobilis*, have been assessed by IUCN Red List criteria to date (IUCN, 2021). The former is listed as 'Near Threatened' based on an assessment published in 1996 with very limited supporting information. The latter is listed as 'Critically Endangered' due to the basin-scale mass mortality described in the previous section. This is a further example of the under-representation of invertebrates in IUCN Red Lists which show a strong bias in favour of vertebrates, despite the evidence that has been contributed on invertebrate demise by scientific, regulatory and conservation practices (Cardoso et al., 2011; Cowie et al., 2017, 2022; Régnier et al., 2009, 2015).

All four (sub)endemic species (*Patella ferruginea*, *Episcomitra zonata*, *Lithophaga lithophaga* and *Pinna nobilis*) will become threatened under most future climate scenarios according to the Red List criterion on the area of occupancy. The two strictly endemic *Patella ferruginea* and *Pinna nobilis* are predicted to be extinct by the end of the century under the worst climate scenario RCP 8.5. Also the intertidal limpet *Cymbula safiana* and the large, iconic, tun shell *Tonna galea*—one of the largest gastropods occurring in the Mediterranean Sea—will be threatened under most future climate scenarios despite their large distributions outside the basin. *Luria lurida*, *Naria spurca* and *Pinna rudis* will be threatened under most future scenarios too. In contrast, most other species with broad distributions in the Atlantic Ocean and beyond (*Schilderia achatidea*, *Zonaria pyrum*, *Charonia variegata*, *Charonia lampas*, *Ranella olearium* and *Pholas dactylus*) will not be significantly threatened and will be classified 'Least concern'. These results, however, only refer to climate change impacts and do not take into consideration other pressures such as habitat loss (e.g. coastal development, trawling), harvesting (either direct, e.g. for consumption of *Patella ferruginea*, *Charonia lampas* and *Lithophaga lithophaga*, or indirect, e.g. *Tonna galea*, *Ranella olearium* and *Episcomitra zonata* as by-catch of trawlers), pollution and diseases, nor the fact that population fragmentation may increase extinction risk (Crooks et al., 2017).

The two extinctions that we predict contrast the belief that marine species are less prone to extinction than continental species due to a combination of factors related to large ranges, high connectivity and high fecundity (e.g. Régnier et al., 2009). Despite only few extinctions in the marine realm have been documented to date (Dulvy et al., 2009), many more are thought to have gone undetected or underreported (Cowie et al., 2022; Roberts & Hawkins, 1999). Indeed, the smaller number of recorded extinctions in marine species is mostly explained by differences in the proportion of species assessed by IUCN Red Lists and in the level of taxonomic knowledge (Webb & Mindel, 2015). Our target species—and those predicted to go extinct in particular—show large sizes, long life cycles, sex change (e.g. protandry in *Patella ferruginea*), low adult mobility, narrow vertical depth range, nearshore distribution and endemism, characteristics that render marine species vulnerable to extirpation and extinction (Roberts & Hawkins, 1999). Additionally, in a study with the same methodology targeting molluscs of commercial interest in the Mediterranean, three out of 13 modelled species are predicted to lose more than 95% of their range in the basin by the end of the century under the worst emission scenario RCP 8.5 (Gallagher

& Albano, 2023). Such range losses may well approximate global extinctions being all three strictly endemic species. Our results apply to large-sized species with unambiguous taxonomy and ample distributions within the Mediterranean. Species with very small ranges (e.g. the top shell *Steromphala nivosa* whose distribution is limited to the Maltese Archipelago (Evans et al., 2011)) or those that are species groups with clades endemic to sub-basins like *Dendropoma* spp. (Calvo et al., 2009) may face a similar fate. That is, unabated global warming will likely cause numerous extinctions in the marine realm further contributing to the current anthropogenic extinction crisis (Ceballos et al., 2015; Harnik et al., 2012; IPBES, 2019).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The file with the raw occurrence data used for our models are accessible in Dryad: https://datadryad.org/stash/share/B2K4JmhFy068PzlaPwnbyx0eDnh5yi-4wF13BmaB0jY

ORCID

Lotta Schultz https://orcid.org/0000-0002-1659-0856
Johannes Wessely https://orcid.org/0000-0001-7753-3532
Stefan Dullinger https://orcid.org/0000-0003-3919-0887
Paolo G. Albano https://orcid.org/0000-0001-9876-1024

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BIOSKETCHES

Lotta Schultz is interested in global change ecology, biogeography and conservation biology. Her current research focuses on the drivers of large-scale biodiversity patterns and the impacts of climate warming on species distributions.

Paolo G. Albano explores marine biodiversity over multiple spatial and temporal scales, with a particular interest in the drivers of its demise.

Author contributions: PGA contributed to conceptualization, methodology, data curation, funding acquisition, writing—original draft and writing—review and editing. LS contributed to methodology, data curation, formal analysis, visualization, writing—original draft and writing—review and editing. JW and SD contributed to in methodology, formal analysis and writing—review and editing.

SUPPORTING INFORMATION

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

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