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Abstract

Global warming drives large changes in the distribution of species. Marine molluscs are a highly diversified taxon. Most species are benthic and have low mobility and are thus good indicators of environmental change. Anthropogenic activities such as pollution and habitat alteration have driven many species to local eradication or population depletion. In addition, the large potential impacts of human-induced global warming require quantifying the future range of species of conservation concern in order to define appropriate conservation measures. For this study, I built Species Distribution Models (SDMs) of 15 marine mollusc species of conservation concern occurring in the Mediterranean Sea, which is among the world basins with the highest rate and magnitude of temperature increase. I used these SDMs to project the species' future climatically suitable range under four Representative Concentration Pathway (RCP) scenarios for the years 2050 and 2100. I then quantified range changes at the scale of the species' full distribution range and their range in the Mediterranean Sea, respectively. A severe reduction in climatically suitable range was predicted already under the mildest scenario by 2050, and the range contractions were even more pronounced under more severe climate scenarios and over longer timespans. Modelling results indicated significantly higher range losses for species endemic to the Mediterranean Sea than for species with a large part of their ranges outside the basin. This study underpins the potential consequences of global climate change on marine biodiversity and underlines the urgent need for mitigation and conservation measures, in particular for Mediterranean ecosystems.

1. Introduction

1.1. Range shifts in marine ecosystems

Globally, the marine environment is warming and projections for the near future foresee an increasing threat to marine biodiversity. Although marine taxa have adapted to natural climatic variations throughout history, it is suspected that with the currently observed velocity of human-induced climate change many marine species will be unable to adapt to the altered environment by rapid evolution (Hastings et al., 2020; Philippart et al., 2011). Hence, climatic changes in marine ecosystems may result in range reduction (Katsanevakis and Thessalou-Legaki, 2009) or expansion, species extinction (Albano et al., 2021) and species displacement (Ben Rais Lasram et al., 2010).

Distribution patterns correspond closely with species' thermal tolerance limits (Sunday et al., 2012). At the global scale, the cold tolerance limit (i.e. the leading edge) determines the highest latitude where a species can occur, whereas the warm tolerance limit (i.e. the trailing edge) is associated with the most equatorward position of a species range (Hastings et al., 2020). With climate warming, suitable ranges of species will hence move towards the poles, and species are expected to shift their ranges to maintain their thermal niches. Indeed, evidence of such range shifts is accumulating also in the marine realm (Bates et al., 2014; Hastings et al., 2020; Hickling et al., 2006). At the local scale, thermal tolerances also result in strong vertical patterns in the distribution of marine species, reflecting warmer conditions at shallow waters and cooler conditions at deeper water layers. Increasing sea surface temperatures in combination with desiccation and hydrodynamic disturbance events could thus, particularly in coastal habitats such as intertidal and benthic systems, potentially cause not only a poleward movement of marine organisms but also a shift of their distribution towards deeper waters (Harley et al., 2006; Mathieson et al., 1998). Although bathymetric shifts are highly complex phenomena and might to some degree be counteracted by global sea level rise (Mathieson et al., 1998), local changes in zonation patterns in response to warming have already been observed in different marine taxa (Bischof et al., 1998; Graham, 1997; Perry et al., 2005).

Notwithstanding temperature is well known as a pervasive driver of distribution limits of marine organisms (Hutchins, 1947), additional environmental stressors can be associated with species' range edges. For instance, salinity influences the metabolic rate of many marine organisms (Scavia et al., 2002). Salinity patterns are relatively constant in the open ocean but highly variable in coastal biotopes such as estuaries or intertidal zones (Berger and Kharazova, 1997). Climatically forced changes in precipitation patterns are anticipated to alter oceanic salinity, provoking substantial shifts in species distributions at the local scale (Elliott et al., 2015; Harley et al., 2006; Scavia et al., 2002).

Furthermore, biotic factors such as the availability of food and particular substrata are also well known for shaping the realized niche of species and thus influencing range boundaries locally. Although these variables seem less important for species occurrence at the large scale (Cahill et al., 2014), they must still be considered when explaining geographical distribution patterns (Bates et al., 2014; Hastings et al., 2020).

Overall, an ultimate key requirement for species undergoing range shifts is that the areas which have become biotically and abiotically suitable due to climatic changes are geographically accessible. Accordingly, dispersal should not be restricted by any biogeographic or thermal barriers (e.g. land masses or upwelling areas). If this condition is not fulfilled and a species can thus not track its environmental niche towards higher latitudes, it is likely to face local extinction with accelerating global climate change (Ben Rais Lasram et al., 2010). This particular situation occurs when warming-induced contractions of species' trailing edges occur in semi-enclosed systems such as the Mediterranean Sea, where species have a limited potential to geographically shift their distribution (Albano et al., 2021; Marbà et al., 2015).

1.2. The Mediterranean Sea and its vulnerability to climate change

Effects of global climate change are anticipated to appear earlier in the Mediterranean Sea than in open oceans (Coll et al., 2010). This is due to a combination of its semi-enclosed nature and its geographic position (Marbà et al., 2015).

The Mediterranean Sea can be distinguished in two major sub-basins, the eastern and western Mediterranean, that are connected by the Strait of Sicily. The basin as a whole is characterized by a wide range of microclimates resulting from thermohaline circulation and deep-water formation processes in the eastern and western basin (Coll et al., 2010; Skliris, 2014). The Mediterranean thermohaline circulation involves Atlantic Water masses, which enter at the sea surface layer through the Strait of Gibraltar and circulate throughout the basin. The water masses get saltier and warmer towards the east, sink down in the Levantine Sea and spread back to the western basin, where they finally exit at depth in the Atlantic Ocean. As the Mediterranean basin is located in the transition zone of two climatic regimes, the temperate European climate and the arid climate of North Africa, circulation processes are mainly driven by interactions between subtropical and temperate climatic features. Even minor modifications of these elements can cause substantial changes in the Mediterranean climate (Giorgi and Lionello, 2008; Marbà et al., 2015). Moreover, the semi-enclosed nature of the Mediterranean Sea delimits its hydrological exchange with adjacent oceans such as the North Atlantic and simultaneously enables the basin to store heat in high capacity (Marbà et al., 2015). Indeed, these bioclimatic peculiarities exacerbate effects of global climate change in the

Mediterranean Sea, leading to warming of the basin at two to three times the rate for the global ocean (Vargas-Yáñez et al., 2008).

As a consequence, Mediterranean species are forced to seek cooler environments inside the basin, resulting in substantial reorganizations of Mediterranean marine ecosystems (Ben Rais Lasram et al., 2010). For instance in the Ligurian Sea, one of the coldest areas in the Mediterranean basin and thus primarily colonized by cold water species, changes towards thermophilic communities have already been observed in the recent years (Bianchi and Morri, 2000). With accelerating global climate change, however, the physical barriers of the basin will force Mediterranean species to move poleward, resulting in a trapping effect and high extinction risk for Mediterranean endemic species. Indeed, Lasram et al. (2010) predicted that with increasing temperatures the coldest areas of the Mediterranean basin will act as a “cul-de-sac”, driving species adapted to cold water to extinction.

1.3. The target phylum Mollusca and species of conservation concern

Although many marine species respond to climatic alterations, certain taxa react more sensitively to environmental changes than others and thus are good indicators of the environmental state of marine ecosystems (Zettler et al., 2013). For instance, marine molluscs can serve as reliable proxies for studies that quantify anthropogenic impacts on marine ecosystems due to their sensitivity to a wide set of environmental stressors and their restricted occurrence in a specific habitat type (Moraitis et al., 2018; Tyler and Kowalewski, 2017). Marine molluscs are a highly diverse taxon, representing predominantly benthic species occurring from intertidal to deep-sea waters, but also include nektonic (cephalopods) and holoplanktic (gastropods) groups (Sabelli and Taviani, 2014). The distribution ranges of marine molluscs vary between almost cosmopolitan species such as *Ranella olearium* and narrow endemics such as the trochid gastropod *Steromphala nivosus*, which is described as a rare case of marine point endemism on the Maltese Islands (Evans et al., 2011). Biogeographic ranges of marine molluscs are determined by hydrographic factors such as seawater temperature, salinity and chlorophyll parameters, but also by their developmental and predominantly sedentary behaviour. Benthic mollusc species with a direct development are limited in their dispersal capacity to oceanic currents, while species developing from free-living planktotrophic larvae have a wider dispersal variability (Johnson et al., 2001). These characteristics render marine molluscs highly vulnerable to changes in their environmental niche.

Indeed, a large number of marine molluscs are currently of severe conservation concern, suffering from impacts of global climate change as well as from other human activities (Albano et al., 2021; Bianchi and Morri, 2000; Carella et al., 2019; Katsanevakis and Thessalou-Legaki, 2009). For instance, the limpet *Patella ferruginea* is of severe extinction concern as it is commonly collected as seafood

(Rivera et al., 2011) and, moreover, reacts highly sensitively to sewage pollution (Espinosa et al., 2007). Other species are exposed to active exploitation or coastal fisheries such as the Mediterranean endemic *Lithophaga lithophaga* (Bianchi and Morri, 2000). Another important menace to marine molluscs is habitat degradation or complete destruction, which is particularly critical for species associated with, or even restricted to, specific substrata. For example, warming-induced reduction of the habitat-forming Mediterranean seagrass *Posidonia oceanica* has already exacerbated the extinction risk for those molluscan taxa associated with it such as *Pinna nobilis* (Jordà et al., 2012; Katsanevakis and Thessalou-Legaki, 2009; Marbà and Duarte, 2010). Furthermore, the present trend of warming temperatures fosters many exotic mollusc species, potentially causing competitive exclusion of native species. However, the actual risk for autochthonous mollusc species emanating from non-indigenous species is still largely unknown (Albano et al., 2021; Oliverio, 2003).

Although many marine mollusc species are presently facing direct or indirect threats, only a small fraction appears in lists of conservation policies (Oliverio, 2003). Presently, *Lithophaga lithophaga* is the only Mediterranean marine mollusc species included in Annex II of the CITES documents (*Convention on International Trade in Endangered Species of Wild Fauna and Flora*, 1973). Furthermore, 17 Mediterranean mollusc species are protected by Annex II of the European conservation legislation Bern Convention (*Convention on the Conservation of European Wildlife and Natural Habitats*, 1982) and Annex II of the Barcelona Convention (*Convention on the protection of the Mediterranean Sea against pollution*, 1977). The severe menace of habitat decline was considered only for *Patella ferruginea*, *Pinna nobilis* and *Lithophaga lithophaga* by Appendix IV of the Habitats Directive (*Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora*, 1992). Nevertheless, when considering the taxonomic diversity of marine molluscs together with the literature on mollusc population declines and extinction events, specifically for species occurring in the Mediterranean Sea (Albano et al., 2021; Carella et al., 2019; Katsanevakis and Thessalou-Legaki, 2009), these numbers presumably underestimate the real extinction risk for marine mollusc species (Oliverio, 2003). In addition, there is an urgent need to define appropriate conservation measures for marine mollusc diversity and marine ecosystems as a whole, and to quantify potential impacts of global climate change on species of conservation concern.

1.4. Application of Species Distribution Models (SDMs)

Species Distribution Models (SDMs) are a useful tool to predict effects of climate change on species distributions and their risk of extinction. SDM algorithms relate species occurrences (often also absences) to relevant environmental predictor variables to explain the realized niche of the modelled species. These distribution patterns can then be extrapolated in space or time and yield predictions describing the suitability of a certain locality to the species now or in the future (Elith and Graham,

2009; Guisan et al., 2017; Hao et al., 2019). Future projections of SDMs are based on scenarios of climate change such as the Representative Concentration Pathways (RCP), which describe different greenhouse gas concentration trajectories adopted by the IPCC's fifth Assessment Report (AR5) (IPCC, 2013).

While SDMs are still predominantly applied in terrestrial ecosystems, their use for exploring consequences of global climate change in the marine realm has increased with growing availability of marine environmental data. The application of SDMs to marine molluscs has so far focused on a few indicator species (Moraitis et al., 2019), invasive mollusc species (Jones et al., 2013; Raybaud et al., 2015; Sarà et al., 2018), key species for ecosystem functioning (Gormley et al., 2013) or species of economic interest (Russell et al., 2012). Currently, no studies are available regarding the impacts of global climate change on Mediterranean marine molluscs of conservation concern.

1.5. Aim of this study

The present study thus aims at shedding light on potential future range changes of endangered marine mollusc species in the Mediterranean Sea and on wider areas outside the basin. The mollusc target species are particularly relevant in a climate change context because they represent the ecological state of their environment and can thus serve as indicators for the future fate of marine ecosystems. Based on SDMs, I predict range dynamics of endangered molluscs under four Representative Concentration Pathways (RCP) Scenarios by 2050 and 2100. I thereby hypothesize that, first, the modelled species respond to future climatic conditions with a geographical shift towards their leading edge, and second, that projected range changes are particularly profound in the Mediterranean Sea compared to areas along open continental margins. Finally, I investigate whether the target species potentially undergo bathymetric range shifts with future climatic changes. With this work I intend to highlight the major consequences of accelerating global warming for marine and especially Mediterranean biodiversity.

2. Material and Methods

2.1. Dataset

2.1.1. Species data and data collection

For this study we selected 17 marine coastal mollusc species which are listed as threatened or endangered, according to international agreements (Table 1) (*Convention on International Trade in Endangered Species of Wild Fauna and (CITES)*, 1973; *Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention)*, 1982; *Convention on the protection of the Mediterranean Sea against pollution (Barcelona Convention)*, 1977; *Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora*, 1992). All target species occur along the continental shelf with distribution patterns ranging from Mediterranean endemism to wide ranges comprising coastal waters of several oceans (Table 2, and for detailed information Appendix S2: Species Distribution Maps). The preferred bathymetric ranges of the target species were classified into intertidal zone, shallow subtidal zone (-200 m) and deep-water (i.e. continental shelf and upper slope) (-1000 m). In my analyses I distinguished between two biogeographical distribution groups: Mediterranean endemic -and wider distributed species. The bivalve *Lithophaga lithophaga* and the gastropod *Episcomitra zonata* are here considered as Mediterranean endemics because their distribution range is mostly confined to the basin, although they have also been found beyond the Mediterranean Sea (Table 2, and Appendix S2: Species Distribution Maps).

Table 1: Convention and directives listing target species of conservation concern. Convention on International Trade in Endangered Species of Wild Fauna and (CITES), 1973; Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention), 1982; Convention on the protection of the Mediterranean Sea against pollution (Barcelona Convention), 1977; Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora, 1992). Species are listed in systematic order.

Species	CITES Annex I	CITES Annex II	CITES Annex III	Habitats Annex II	Habitats Annex IV	Habitats Annex V	Bern Annex II	Bern Annex III	Barcelona Annex II
<i>Patella ferruginea</i>					X		X		X
<i>Cymbula safiana</i>							X		X
<i>Naria spurca</i>							X		X
<i>Luria lurida</i>							X		X
<i>Schilderia achatidea</i>							X		X
<i>Zonaria pyrum</i>							X		X
<i>Tonna galea</i>							X		X
<i>Charonia lampas</i>							x		X
<i>Charonia variegata</i>							X		X
<i>Ranella olearium</i>							X		X
<i>Episcomitra zonata</i>							X		X
<i>Lithophaga lithophaga</i>		x			X		X		X
<i>Pinna nobilis</i>					x		X		X
<i>Pinna rudis</i>							X		X
<i>Pholas dactylus</i>							x		x

Table 2: Target species and their geographic and bathymetric distribution range (Espinosa et al., 2011; Evans et al., 2011; Harasewych, 2010; Kiliyas, 1962; Lorenz, 2018; MarLIN (Marine Life information Network), 2020; MolluscaBase Eds., 2021; Poppe and Gotō, 1993, 1991). Species are listed in systematic order.

Class	Family	Species	Distribution range	Bathymetric range
Gastropoda	Patellidae	<i>Patella ferruginea</i>	endemic to Mediterranean Sea	Intertidal
Gastropoda	Patellidae	<i>Cymbula safiana</i>	Western Mediterranean Sea, North-East Atlantic	Intertidal
Gastropoda	Cypraeidae	<i>Naria spurca</i>	Mediterranean Sea, North-East Atlantic	Shallow subtidal
Gastropoda	Cypraeidae	<i>Luria lurida</i>	Mediterranean Sea, North-East Atlantic	Shallow subtidal
Gastropoda	Cypraeidae	<i>Schilderia achatidea</i>	Western Mediterranean Sea, North-East Atlantic	Shallow subtidal
Gastropoda	Cypraeidae	<i>Zonaria pyrum</i>	Mediterranean Sea, North-East Atlantic	Continental shelf and upper slope
Gastropoda	Tonnidae	<i>Tonna galea</i>	Mediterranean Sea, Atlantic Ocean	Continental shelf and upper slope
Gastropoda	Charoniidae	<i>Charonia lampas</i>	Mediterranean Sea, Atlantic Ocean	Continental shelf and upper slope
Gastropoda	Charoniidae	<i>Charonia variegata</i>	Mediterranean Sea, Atlantic Ocean, Caribbean Sea, Gulf of Mexico	Shallow subtidal
Gastropoda	Ranellidae	<i>Ranella olearium</i>	Mediterranean Sea, Atlantic Ocean, Indo West Pacific	Continental shelf and upper slope
Gastropoda	Mitridae	<i>Episcomitra zonata</i>	Mediterranean Sea, Azores	Continental shelf and upper slope
Bivalvia	Mytilidae	<i>Lithophaga lithophaga</i>	Mediterranean Sea, Azores, Canary Islands	Intertidal
Bivalvia	Pinnidae	<i>Pinna nobilis</i>	endemic to Mediterranean Sea	Shallow subtidal
Bivalvia	Pinnidae	<i>Pinna rudis</i>	Mediterranean Sea, North East Atlantic, Caribbean Sea, Gulf of Mexico	Shallow subtidal
Bivalvia	Pholadidae	<i>Pholas dactylus</i>	Mediterranean Sea, North Atlantic	Shallow subtidal

Species distribution records 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). Collectors who contributed to the dataset are C. Afonso, P. A. J. Bakker, S.M. Bartolini, C. Bogi, O. Caro, M. Coppini, G. Devauchelle, J. Eikenboom, A. Hoarau, S. van Leeuwen, A. Margelli, P. Micali, G. Mulder, A. Pagli, M. Passamonti, F. Pusateri, A. Raveggi, P. Russo, R. Seitzinger, J. Steger, D. Scuderi, M. Tisselli, A. Villari.

All species' names were verified and checked for synonyms in the World Register of Marine Species. Occurrence records from private collections were received as textual description of the sampling localities with additional information on sampling depth and habitat, size and living vs empty shell state of the individual records. The textual locality information was checked and georeferenced with coordinates in decimal degree format with Google Earth. I further re-examined samples of the target species in the collections of the Natural History Museum. The specimen identities were verified and the geographic locality recorded according to given textual locality descriptions.

Occurrence records from public databases were first visually inspected on maps provided by the respective websites (GBIF and OBIS) and then loaded into RStudio (RStudio Team, 2020) for further data quality analyses. OBIS data was cross referenced with data obtained by GBIF to avoid duplicated records. Species records which were not provided with coordinates by the databases were georeferenced by hand according to their given textual locality description using Google Earth. Doubtful geographic information of public data was flagged using the *cleancoordinates* function of the CoordinateCleaner package (Zizka et al., 2019) and removed from the dataset. Detailed quality check and data cleaning was done manually and is described in 2.1.2.

Two species of conservation concern, namely the gastropods *Steromphala nivosa* and *Dendropoma cristatum*, were excluded from the study. *Steromphala nivosa* is endemic to the Maltese Islands (Evans et al., 2011), a too small range at the spatial resolution of our modelling to provide meaningful results. *Dendropoma cristatum* is likely a species group whose taxonomic status remains to be unclarified (Calvo et al., 2009).

2.1.2. Quality check and data overview

All records were quality checked in terms of taxonomic misidentifications and mismatches between the recorded coordinates and known distribution ranges for each species. For that I visualized the spatial distribution points on geographical maps using QGIS (QGIS.org, 2021). Implausible records that were mapped on land, much beyond the known range, or had insufficient location precision were removed from the dataset. To get an overview of the data availability for each species, I calculated summary statistics and visualized occurrence records geographically, grouped by the availability of information on depth, collecting year and living status of the species record at the time of sampling.

2.1.3. Environmental data and initial predictor selection

All environmental data for modelling was obtained from Bio-Oracle, a widely used marine dataset providing monthly and annual environmental variables for current and future climatic conditions at different depth layers. The environmental layers are available as raster grid layers at a spatial resolution of 5 arcmin (approximately 9.2 km at the equator) (Assis et al., 2018). The raster grid cells provided by Bio-Oracle contain information of in total 13 direct bioclimatic variables divided into six distinct parameters, all measured at the sea surface and at the bottom of the grid cell. The parameters of each variable were computed by using the monthly average values over a period from 2000 to 2014 and are defined as the variables' average, the minimum and maximum records, the long-term average of the minimum and maximum records per year, and the absolute difference (range) between the minimum and maximum records per year (Assis et al., 2018). For detailed description of parameters

see Table 3. Each environmental variable used for modelling is provided by Bio-Oracle for current, as well as for future climatic conditions. The future environmental layers, projected for the years 2050 and 2100, are based on the most recent Representative Concentration Pathways (RCP scenarios), defined in the 5th Assessment Report of the IPCC in 2014 (IPCC, 2013; Moss et al., 2010): The RCP2.6 is a rather moderate scenario describing continuously decreasing greenhouse gas (GHG) concentrations over time and a radiative forcing peak by the mid of the century (van Vuuren et al., 2007). The intermediate RCP4.5 is defined by an GHG concentration peak at the mid-century and a stabilization of radiative forcing levels before 2100 (Clarke et al., 2007). Similar the RCP6.0, assumes a peak around 2080 and a stabilization at higher radiative forcing levels than described by RCP4.5 (Fujino et al., 2006). Both stabilization scenarios require the implementation of new technologies and strategies helping to reduce greenhouse gas emissions. The most severe pathway RCP8.5 is characterized by a continuous increase of GHG concentrations leading to high radiative forcing levels by the end of the century (Riahi et al., 2007).

I loaded all current and future environmental layers in RStudio using functions of the *sdmpredictor* package (Bosch, 2020).

Based on scientific knowledge on the ecology of the target species we initially chose six direct bioclimatic parameters provided by Bio-Oracle to describe the species biophysiological niche as close as possible. All predictor variables are known as regulating factors controlling the metabolism of our target species and were thus expected to provide a good approximation of the real environmental parameters determining the species niche (Guisan et al., 2017). The selected predictor variables are maximum temperature, temperature range, minimum salinity, salinity range, long-term maximum chlorophyll, chlorophyll range (detailed definitions on bioclimatic variables are provided in Table 3).

The depth layers of the predictor variables were chosen for the species preferred bathymetric range. For intertidal species (*Patella ferruginea*, *Cymbula safiana*, *Lithophaga lithophaga*) and shallow subtidal species (*Pinna nobilis*, *Pinna rudis*, *Pholas dactylus*, *Steromphala nivosa*, *Charonia variegata*, *Naria spurca*, *Luria lurida*) I selected the above named parameters at the sea surface only. For species occurring on the continental shelf and upper slope (*Charonia lampas*, *Tonna galea*, *Schilderia achatidea*, *Zonaria pyrum*, *Episcomitra zonata*) I used the selected variables measured at the bottom of the cell at maximum depth for modelling.

Table 3: Definitions of environmental parameters selected a priori to explain the realized niche of the target species. Chlorophyll variables are provided by Bio-Oracle at the sea surface only.

Parameter	Layer Code Current Climate	Definition
Maximum temperature record at the bottom at maximum depth (bdmax) and at the sea surface (ss)	BO2_tempmax_bdmax BO2_tempmax_ss	Average temperature of the warmest month on record. Measured at the bottom at maximum depth and at the sea surface
Range between the maximum and minimum temperature record at the bottom at maximum depth and at the sea surface	BO2_temprange_bdmax BO2_temprange_ss	Absolute difference between minimum and maximum temperature records per year. Measured at the bottom at maximum depth and at the sea surface
Minimum salinity record at the bottom at maximum depth and at the sea surface	BO2_salinitymin_bdmax BO2_salinitymin_ss	Average salinity value of month with lowest salinity record. Measured at the bottom at maximum depth and at the sea surface
Range between the maximum and minimum salinity record at the bottom at maximum depth and at the sea surface	BO2_salinityrange_bdmax BO2_salinityrange_ss	Absolute difference between minimum and maximum salinity records per year. Measured at the bottom at maximum depth and at the sea surface
Long-term chlorophyll maximum at the sea surface	BO2_chloltmax_ss	Average of the highest chlorophyll records per year. Measured at the sea surface.
Range between the maximum and minimum salinity record at the bottom at maximum depth and at the sea surface	BO2_chlorange_ss	Absolute difference between minimum and maximum chlorophyll records per year. Measured at the sea surface

2.2. Species distribution modelling

2.2.1. Reformatting occurrence data

To be useful for SDM parameterization, occurrence records must match a cell of the environmental raster layer. Mismatches for each species were quantified in RStudio by extracting values of the predictor layers at the locations of the occurrence points and via visual inspection using QGIS. Occurrence points without environmental raster cell match were moved to the closest cell containing environmental data using the *points2nearestcell* function of the Pakillo/rSDM package (Rodriguez-Sanchez, 2020). The maximum moving distance of the *points2nearestcell* function was determined at 9000 m, corresponding to the size of one grid cell. Raster mismatching coordinates located more than 9000 m away from the closest cell containing environmental information were checked by hand. Records located close to an environmental raster cell, such as those with coordinates referring to centroids of small islands (e.g. Boa Vista), were assigned to the closest cell. Occurrence records located far away from the closest environmental raster cell (e.g. occurrence records on land or coordinates referring to centroids of big islands; such as Sicily) were removed from the dataset. For further steps in the modelling process, species records were reformatted to cells by aggregating the single

occurrence points located in the same raster grid using the *aggregate* function of the *sp* package (Bivand et al., 2013).

2.2.2.Reformatting environmental predictor layers

In order to project distribution ranges only within accessible geographic areas, i.e. those that could plausibly be reached by the target species within the considered time frame, I computed bathymetric and geographic exclusion layers along the continental shelf according to the individual extent of each species' preferred habitat and geographical range. For intertidal species I set up a buffered exclusion layer corresponding to the size of one grid cell (5 arcmin), for shallow subtidal species and for species occurring at the continental shelf and upper slope I built a <200 m and a <1000 m bathymetry mask layer, respectively. The depth exclusion layers were applied to the current and future environmental layers of interest for the species. To exclude inaccessible geographic areas, I masked the selected environmental layers with shapefiles of the species' individual geographic distribution range.

In order to avoid multicollinearity issues during the modelling procedure, the processed predictor layers were checked for correlations for each species separately using Pearson correlation test (threshold > 0.7, cf. Dormann et al., 2013) in R. The uncorrelated environmental layers (Table 4) were further used to parameterize SDMs.

Table 4: Uncorrelated predictor variables incorporated in the model algorithms for each species. Species are listed in systematic order.

Species	Environmental predictor variable
<i>Cymbula safiana</i>	temperature range, salinity range, chlorophyll range
<i>Patella ferruginea</i>	maximum temperature, minimum salinity, salinity range,
<i>Luria lurida</i>	maximum temperature, temperature range, minimum salinity, chlorophyll range
<i>Naria spurca</i>	maximum temperature, temperature range, minimum salinity, long-term chlorophyll maximum
<i>Schilderia achatidea</i>	maximum temperature, temperature range, minimum salinity, chlorophyll range
<i>Zonaria pyrum</i>	maximum temperature, temperature range, minimum salinity, chlorophyll range
<i>Tonna galea</i>	maximum temperature, temperature range, minimum salinity, chlorophyll range
<i>Charonia variegata</i>	maximum temperature, temperature range, salinity range, chlorophyll range
<i>Charonia lampas</i>	maximum temperature, minimum salinity, salinity range, chlorophyll range
<i>Ranella olearium</i>	maximum temperature, minimum salinity, salinity range, chlorophyll range
<i>Episcomitra zonata</i>	maximum temperature, minimum salinity, chlorophyll range
<i>Lithophaga lithophaga</i>	maximum temperature, temperature range, salinity range, chlorophyll range
<i>Pinna nobilis</i>	maximum temperature, temperature range, minimum salinity, chlorophyll range
<i>Pinna rudis</i>	maximum temperature, temperature range, minimum salinity, chlorophyll range
<i>Pholas dactylus</i>	maximum temperature, temperature range, salinity range, chlorophyll range

2.2.3. Consideration of SDM assumptions

Prior to model parameterization we ensured that the underlying main assumptions of SDMs are met. Following Guisan et al. (2017), the most important assumptions of SDMs are an equilibrium between the modelled species and its environment, unbiased and independent species observations, meaningful and faultless environmental data and suitability of statistical methods (Table 5):

Table 5: Key model assumptions in the application of SDM (Guisan et al., 2017) and their consideration in our analyses.

Assumption	Description
Species-environment equilibrium	Fossil records of the modelled species have been observed throughout the Holocene in their current distribution ranges. We can thus broadly assume that the target species are not actively expanding and that their ranges are stable.
Unbiased species data	During the process of record gathering we attempted to capture the whole currently known distribution range of our target species. All species records were verified in a detailed quality check (2.1.1 and 2.1.2)
Independence of species observations	All species records were checked on duplicates.
Availability of all important predictors to capture the species niche	Proximal predictors were provided by the most widely used data set for the marine environment (i.e. Bio-Oracle) and selected to fit the target species ecology (2.1.3)
Predictors are measured without error	The reliability of predictors used for modelling was verified with in situ quality-controlled data by Assis et al. (2018).
Appropriateness of statistical methods	We chose modelling techniques with respect to our dataset, based on a review on the most recent literature on SDM in general (Guisan et al., 2017) and on the application of SDM to the marine benthos (Moraitis et al., 2019; Reiss et al., 2015).

2.2.4. Model parameterization

Species distribution models were calibrated within the biomod2 modelling framework (Thuiller et al., 2009), run under R4.0.3 (RStudio Team, 2020). Species occurrence data were related to environmental variables (Table 4) by building ensemble models, based on the default set of four single algorithms:

GLM (Generalized linear model): these algorithms are regression-type models which use link functions between predictor and the response variables (Guisan et al., 2017). The link function was in this case a binomial distribution as I work with presence-(pseudo)absence data.

GAM (Generalized additive model): these models are also a regression-based approach and an extension of the strengths of Generalized linear models. With the locally weighted mean the sum of a set of functions (so called smoothers) is built fitting response curves as closely as possible to the data (Reiss et al., 2011).

GBM (Generalized boosting model): it is a machine learning modelling technique, combining the predictions of several individual models. For each model a classification of boosted regression trees is applied (Guisan et al., 2017).

RF (Random Forrest): it is a machine learning modelling technique where predictors (trees) are randomly subsampled and then used to construct classification trees (Prasad et al., 2006).

I trained the algorithms drawing five sets of 10,000 pseudo-absence points each, since my dataset comprises presence only data with no true absences available. Pseudo-absences were selected outside the realized niche, but within geographically reachable areas. The 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 ROC (AUC, area under the curve). The predictive power of each model was examined by their evaluation scores and graphically visualized. The influence of the environmental variables on the models was indicated by variable importance scores and visualized by 2D response plots. Based on the set of calibrated models, I subsequently generated ensemble models, which were defined as the means of projected occurrence probabilities of the single models. To avoid the implementation of poorly calibrated models in the ensemble, I defined a TSS quality threshold of 0.6. Ensemble projections of potential species distribution were generated first under current climatic conditions (period 2000-2014) and then extrapolated under four future climate scenarios (RCP 2.6, RCP 4.5, RCP 6.0 and RCP 8.5) for the years 2050 and 2100. The projected probabilities of occurrence were discretised into binary predictions (presence/absence) using the threshold that maximised the TSS score.

2.3. Further analyses

The resulting probability maps were visualized and processed in QGIS. I used a gradual colour visualization to represent the probability of occurrence (i.e. 0 - 100%) of the individual species at a certain cell. The relative and proportional loss of species' range size was estimated on binary cells, using the *Biomod_RangeSize* function of the biomod package (Thuiller et al., 2009).

All statistical analyses were done in RStudio. To explain the relationship between scenario severity, timespan and the predicted range size changes, I used generalized linear mixed-effects models of the glmmTMB package (Brooks et al., 2017), in which I included the different species as a random-effect term. Calculations of species range loss and gain over the full range of the species were examined, first under the assumption that species do not disperse and second under the assumption of species unlimited dispersal capability.

I then applied a geographic exclusion layer of the Mediterranean Sea on the binaries to analyse whether the degree of predicted range loss differs when the full range or only the range in the Mediterranean basin scale is considered. I did these comparisons both under the no and full dispersal assumptions, respectively.

I further compared differences in predicted cell losses and gains between species endemic in the Mediterranean basin and those with wider ranges using a Wilcoxon-Test (Wilcoxon, 1945).

Finally, I examined whether the magnitude of range shifts differed in shallow waters (i.e. nearshore) and deeper water layers (i.e. offshore). I therefore applied bathymetric exclusion layers for 0-50 m and <50 m depth on the binary prediction layers. Predicted range losses and gains within the two bathymetric ranges were again computed using the *Biomod_RangeSize* function and tested for significant differences with Wilcoxon-Tests.

The described distribution modelling procedure is provided in more detail in Supplementary material Appendix S1: Species distribution models (SDM).

3. Results

3.1. Dataset

The dataset used for modelling comprises 9,081 occurrence records for the 15 marine mollusc target species. I also collected species records for *Dendropoma cristatum* and *Steromphala nivosa*, which were excluded for modelling due to biogeographic and taxonomic issues mentioned in the methods.

Eighty-one percent of the data was collected from GBIF, 15% from private collections, 2% from OBIS (records not present in GBIF) and 1% from the mollusc collection of the Natural history museum in Vienna. Ten percent and 4% of the records correspond to live collected individuals and empty shells, respectively, whereas for 86% of the records no information was available on the state of the samples at the time of sampling. The dataset comprises exact information on the sampling depth for only 27% of the species records. I collected the highest number of occurrence records for *Pinna nobilis* (2337 records) and the smallest number for *Schilderia achatidea* (157 records) (Figure 1). After aggregating the spatial occurrence records to the cells of the environmental predictor layers, I obtained the highest cell number for *Tonna galea* (545 cells) and the lowest number for *Cymbula safiana* (67 cells) (Figure 2). Collected records for *Steromphala nivosa* and *Dendropoma cristatum* included, the total dataset contains 10,229 georeferenced occurrences.

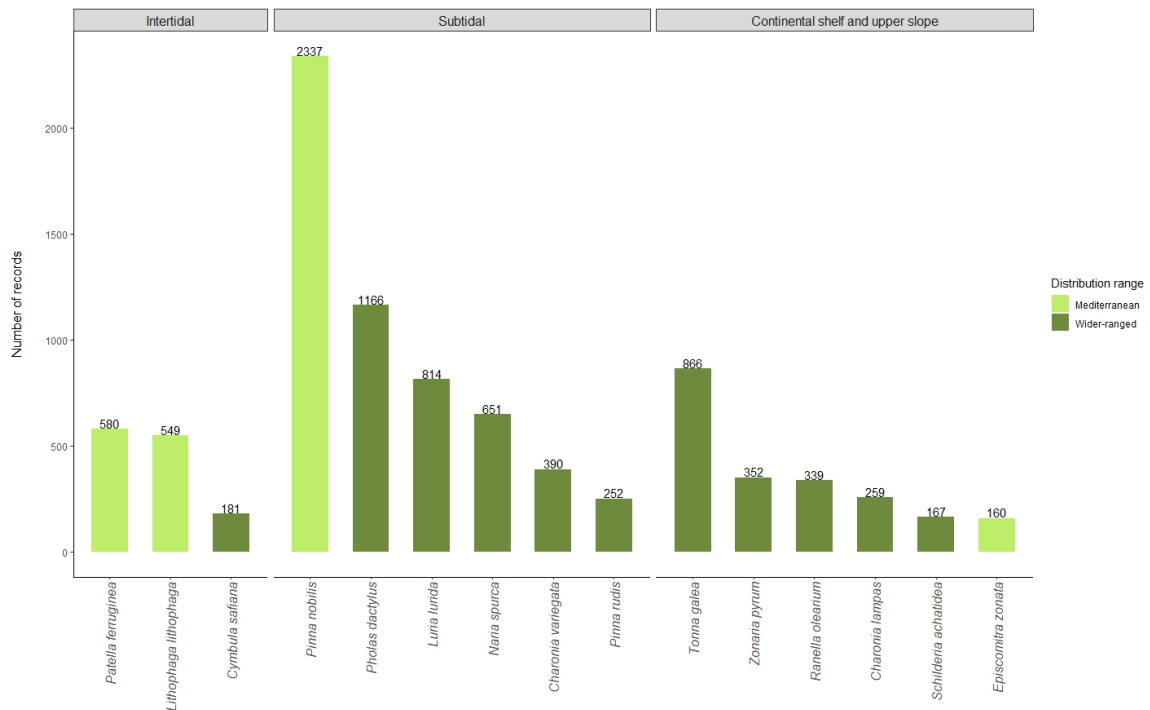


Figure 1: Total number of records, classified by the species' bathymetric range. *Dendropoma cristatum* and *Steromphala nivosa* were excluded from modelling due to taxonomic and biogeographic issues.

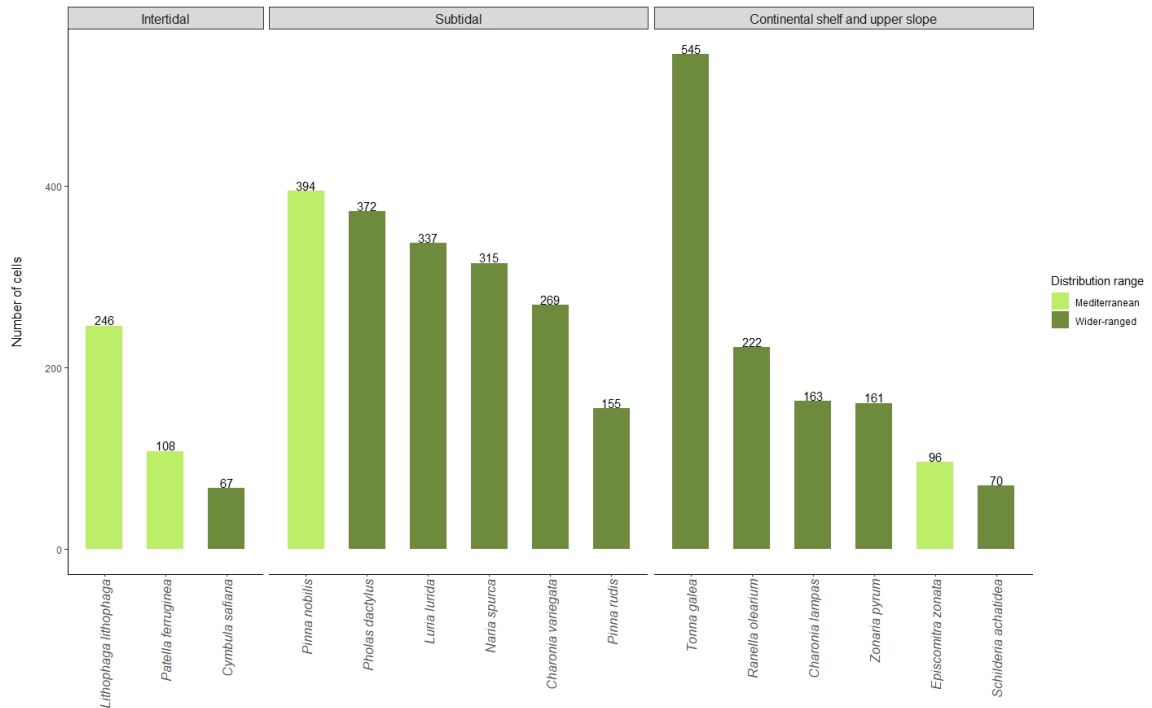


Figure 2: Total number of cells occupied by species occurrences, classified by the species' bathymetric range. *Dendropoma cristatum* and *Steromphala nivosa* were excluded from modelling due to taxonomic and biogeographic issues.

3.2. Model evaluation and variable importance

Overall TSS values, as one evaluation metric, indicated good model performances, with most of the single models exceeding the quality threshold of 0.6 to be implemented in the ensemble model (Table 6). For two species, *Tonna galea* and *Zonaria pyrum*, I could fit only one single model (RF) with a TSS > 0.6. In general, RF performed best with mean TSS scores of 0.75 (± 0.06 SD) over all species and cross-validation runs, followed by GBM (0.69 ± 0.08 SD) and GAM (0.63 ± 0.1 SD). GLM performed poorest with a mean TSS score of 0.58 (± 0.11 SD), and could not be fitted for *Schilderia achatidea*.

Table 6: Mean TSS evaluation scores over all three repetition runs. TSS > 0.6 indicates good model performance and implementation in the ensemble model. Species are listed in systematic order.

Species	GLM (mean TSS)	GBM (mean TSS)	GAM (mean TSS)	RF (mean TSS)
<i>Cymbula safiana</i>	0.7	0.78	0.73	0.79
<i>Patella ferruginea</i>	0.72	0.8	0.78	0.82
<i>Luria lurida</i>	0.61	0.71	0.64	0.78
<i>Naria spurca</i>	0.7	0.78	0.73	0.83
<i>Schilderia achatidea</i>	-	0.71	0.62	0.67
<i>Zonaria pyrum</i>	0.37	0.53	0.38	0.6
<i>Tonna galea</i>	0.49	0.58	0.52	0.7
<i>Charonia lampas</i>	0.73	0.8	0.76	0.82
<i>Charonia variegata</i>	0.68	0.73	0.69	0.81
<i>Ranella olearium</i>	0.59	0.73	0.66	0.76
<i>Episcomitra zonata</i>	0.4	0.64	0.52	0.66
<i>Lithophaga lithophaga</i>	0.49	0.61	0.54	0.72
<i>Pinna rudis</i>	0.64	0.7	0.63	0.75
<i>Pinna nobilis</i>	0.55	0.64	0.57	0.73
<i>Pholas dactylus</i>	0.47	0.65	0.6	0.73
Mean over all species	0.58	0.69	0.63	0.75

Predictor importance differed among the modelled species (Table 7), but also between the modelling techniques (GLM, GBM, GAM, RF). When averaging variable importance across pseudo-absence sets and cross-validation runs, maximum temperature and temperature range were consistently the most important variables in GBM, GLM and GAM with mean importance values ranging between 0.3 and 0.6. Whereas long-term chlorophyll maximum (0.6) and minimum salinity (0.6) were the most important bioclimatic variables in RF, long-term chlorophyll maximum was only used to model one species.

Across all species and independent of the modelling technique, temperature values (maximum temperature and temperature range) were statistically the most important environmental predictors affecting the species distribution. Salinity parameters (minimum salinity and salinity range) were the second most influential variables, whereas chlorophyll parameters (Chlorophyll range and long-term chlorophyll maximum) had, on average, the lowest impact on the algorithms to explain the species distribution (Table 7).

Table 7: Average variable importance calculated as the mean importance across algorithms. The scale ranges from 0 – 1, the higher the score the more important the variable. Species are listed in systematic order.

Species	Variable (most important to least important)
<i>Cymbula safiana</i>	salinity range (0.5), temperature range (0.5), chlorophyll range (0.4)
<i>Patella ferruginea</i>	maximum temperature (0.5), salinity range (0.4), minimum salinity (0.4)
<i>Luria lurida</i>	maximum temperature (0.5), minimum salinity (0.3), temperature range (0.3), chlorophyll range (0.2)
<i>Naria spurca</i>	minimum salinity (0.6), maximum temperature (0.5), maximum chlorophyll (0.4), temperature range (0.3), salinity range (0.3)
<i>Schilderia achatidea</i>	minimum salinity (0.5), maximum temperature (0.4), chlorophyll range (0.4), temperature range (0.4)
<i>Zonaria pyrum</i>	temperature range (0.7), maximum temperature (0.4), chlorophyll range (0.3), minimum salinity (0.2)
<i>Tonna galea</i>	maximum temperature (0.8), temperature range (0.3), chlorophyll range (0.2), minimum salinity (0.1)
<i>Charonia variegata</i>	chlorophyll range (0.6), maximum temperature (0.4), temperature range (0.2), salinity range (0.2)
<i>Charonia lampas</i>	minimum salinity (0.9), maximum temperature (0.4), salinity range (0.2), chlorophyll range (0.2)
<i>Ranella olearium</i>	minimum salinity (0.7), maximum temperature (0.4), salinity range (0.2), chlorophyll range (0.1)
<i>Episcomitra zonata</i>	maximum temperature (0.7), minimum salinity (0.3), chlorophyll range (0.3)
<i>Lithophaga lithophaga</i>	temperature range (0.5), maximum temperature (0.4), salinity range (0.5), chlorophyll range (0.3)
<i>Pinna nobilis</i>	temperature range (0.6), maximum temperature (0.5), minimum salinity (0.3), chlorophyll range (0.2)
<i>Pinna rudis</i>	maximum temperature (0.5), chlorophyll range (0.3), minimum salinity (0.3), temperature range (0.3)
<i>Pholas dactylus</i>	temperature range (0.7), maximum temperature (0.4), salinity range (0.3), chlorophyll range (0.3)

3.3. Model results

3.3.1. Relationship between RCP Scenarios and range loss

Future projections based on the assumption of no dispersal forecasted a decrease of suitable area for all target species, which was predicted to aggravate with time (Figure 3). I identified differences in scenarios already by 2050, but these differences are not ordered linearly along the severity axis: By mid-century I found the lowest mean losses under RCP6.0 (64.9%) and the highest under RCP8.5 (77%) (Figure 3, a). Beyond 2050 future predictions show a linear increase of range loss with scenario severity (GLMM/chi-square, $p < 0.05$) (Figure 3, b). Across all species, mean loss is 71% of the currently suitable range under RCP2.6, 78% under RCP4.5 and 81.9% under RCP6.0, while average range loss accelerated up to 90% under RCP8.5 until 2100.

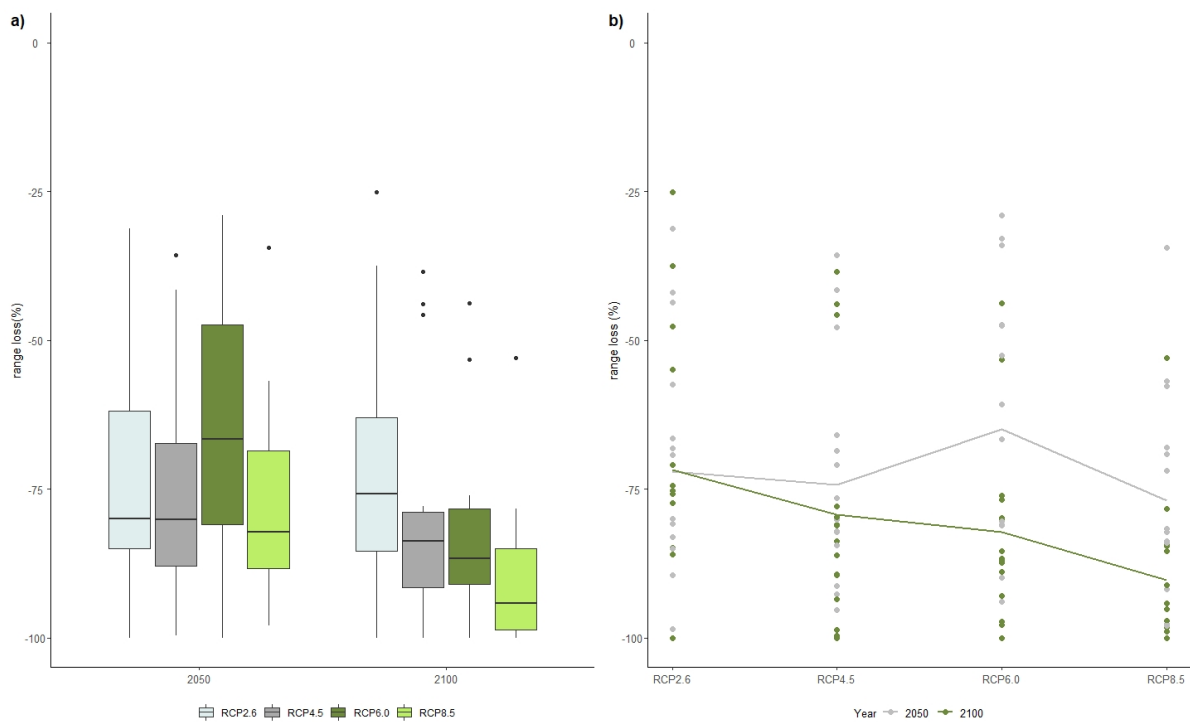


Figure 3: Predicted range loss of marine molluscs of conservation concern based on the assumption that species do not disperse under RCP2.6, RCP4.5, RCP6.0 and RCP8.5 for the years 2050 and 2100. a) shows loss of currently suitable cells across all species. b) shows the relationship between cell loss and scenario severity across all species for 2050 and 2100.

3.3.2. Range loss assuming no dispersal

Under the assumption of no dispersal, the effects of future climatic conditions were significantly more pronounced for Mediterranean endemic species than for species that also occur outside the Mediterranean basin (Wilcoxon-Test, $p < 0.05$) (Figure 4).

Until 2050 suitable range for Mediterranean endemic species was predicted to diminish on average by 89.3% (± 14.1) under RCP2.6, by 92.4% (± 7.3) under RCP4.5, by 90.2% (± 9.8) under RCP6.0 and by 92.9% (± 6.6) under RCP8.5 assuming that target species do not disperse. 2050 projections for more widely distributed species showed the lowest range losses under RCP6.0 (55.8% ± 19.7) and the highest under RCP8.5 (71.1% ± 16.6), while models under RCP2.6 forecasted 65.7% (± 19.4) and under RCP4.5 67.7% (± 18.4) loss of currently suitable range (Figure 4).

Until the end of the century the predictions indicated that Mediterranean endemic species are likely to face a reduction of range size by 91.2% (± 11.7) under the mildest climate scenario and up to 99.6% (± 0.8) under the most severe scenario (Figure 4 and *Episcomitra zonata* as example in Figure 5). Based on the assumption that target species do not disperse, the range contractions became more pronounced with time for wider distributed species, too, indicated by a mean cell loss of 64.3% (± 19) under RCP 2.6 up to 86.5% (± 13.1) under RCP 8.5 by 2100 (Figure 4 and *Charonia lampas* as an example in Figure 6).

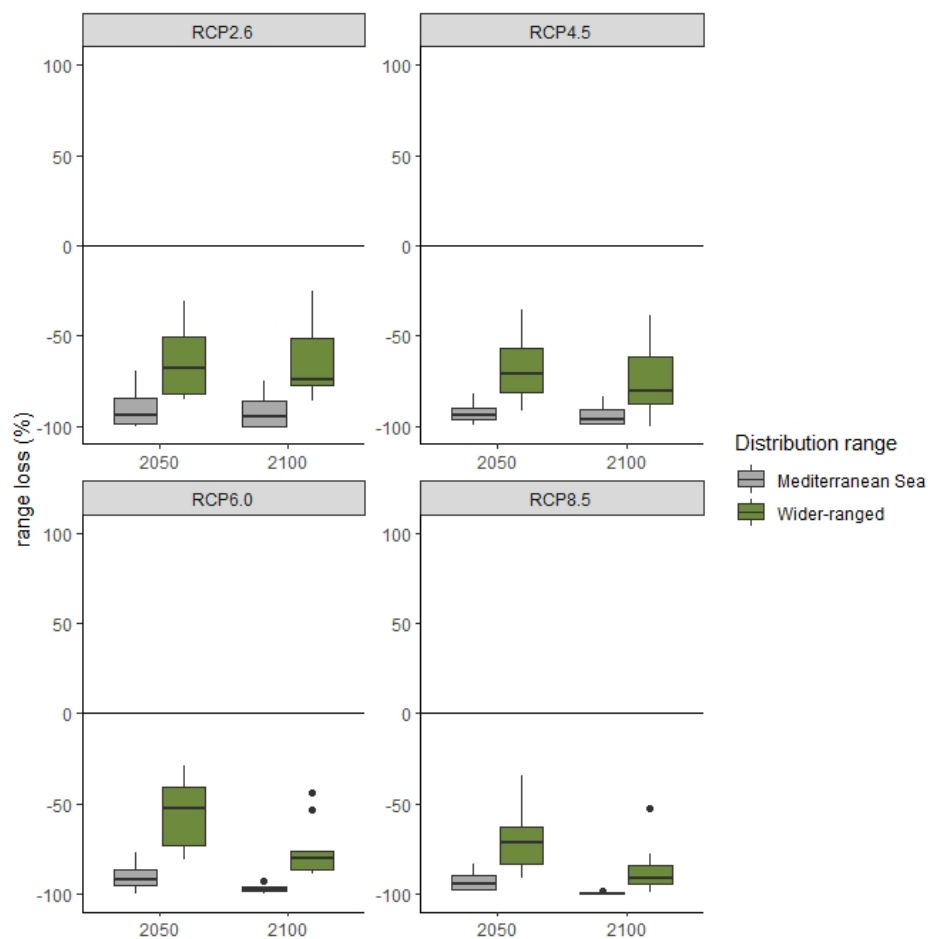
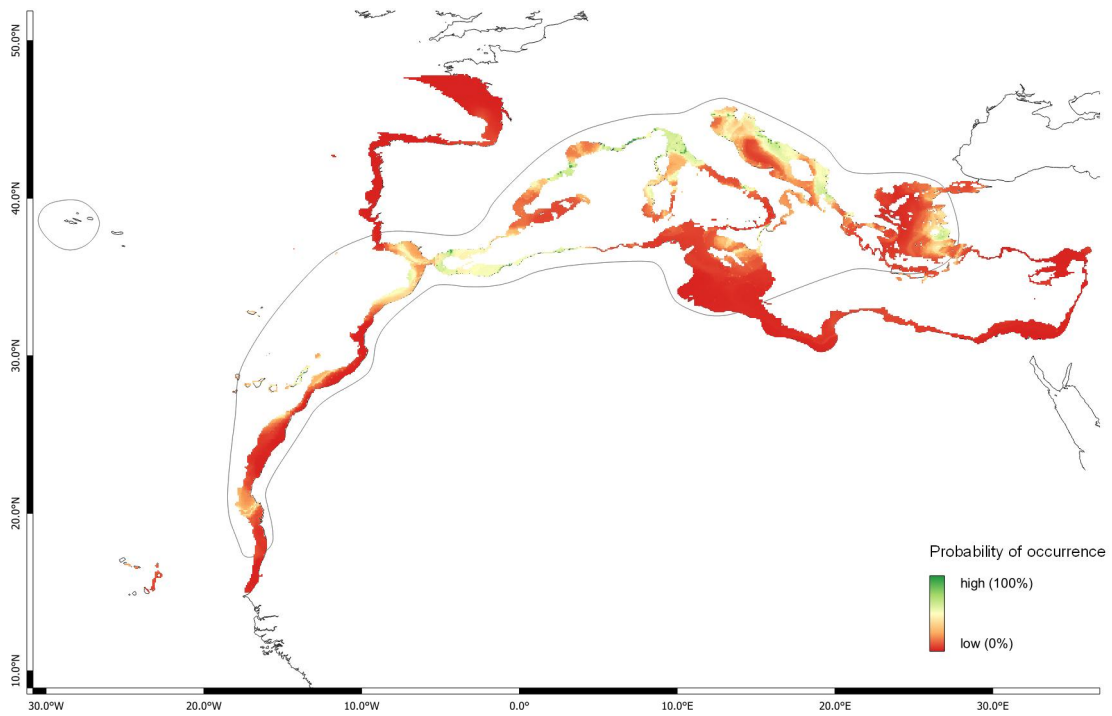
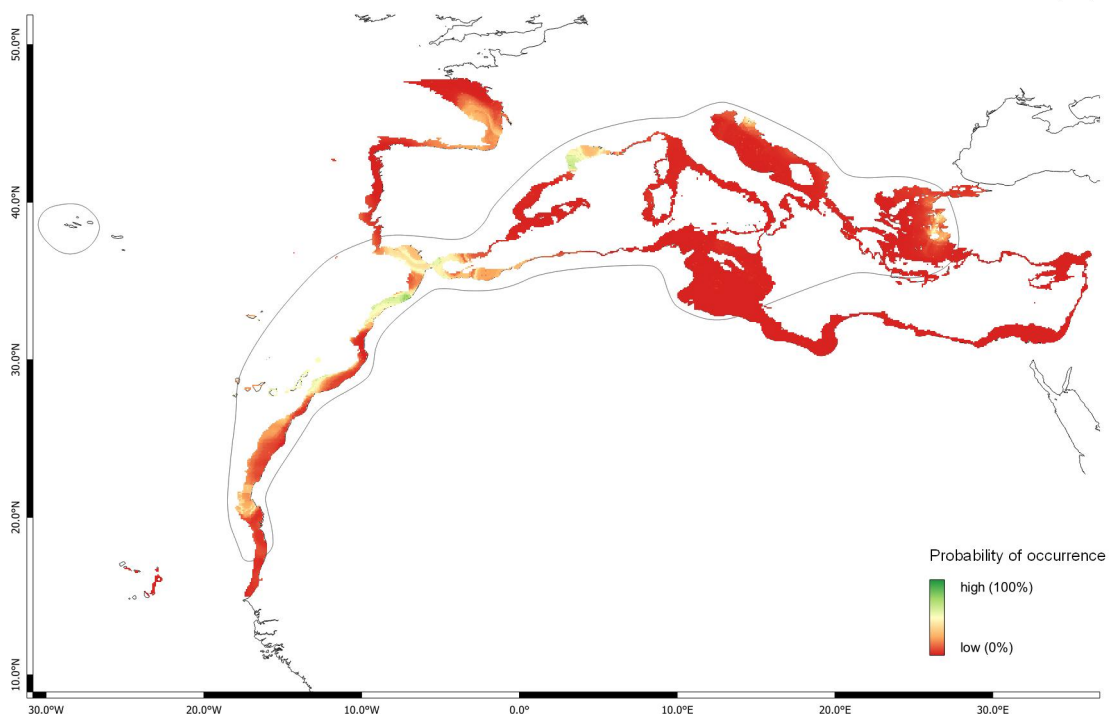


Figure 4: Predicted range loss of marine molluscs of conservation concern based on the assumption that species do not disperse. Range loss is shown for Mediterranean endemic ($n = 4$) and more widely distributed species ($n = 11$), under the climate scenarios RCP 2.6, RCP 4.5, RCP 6.0, RCP 8.5 by the years 2050 and 2100.

a) *Episcomitra zonata*
Current climatic conditions



b) *Episcomitra zonata*
RCP4.5 Year 2050



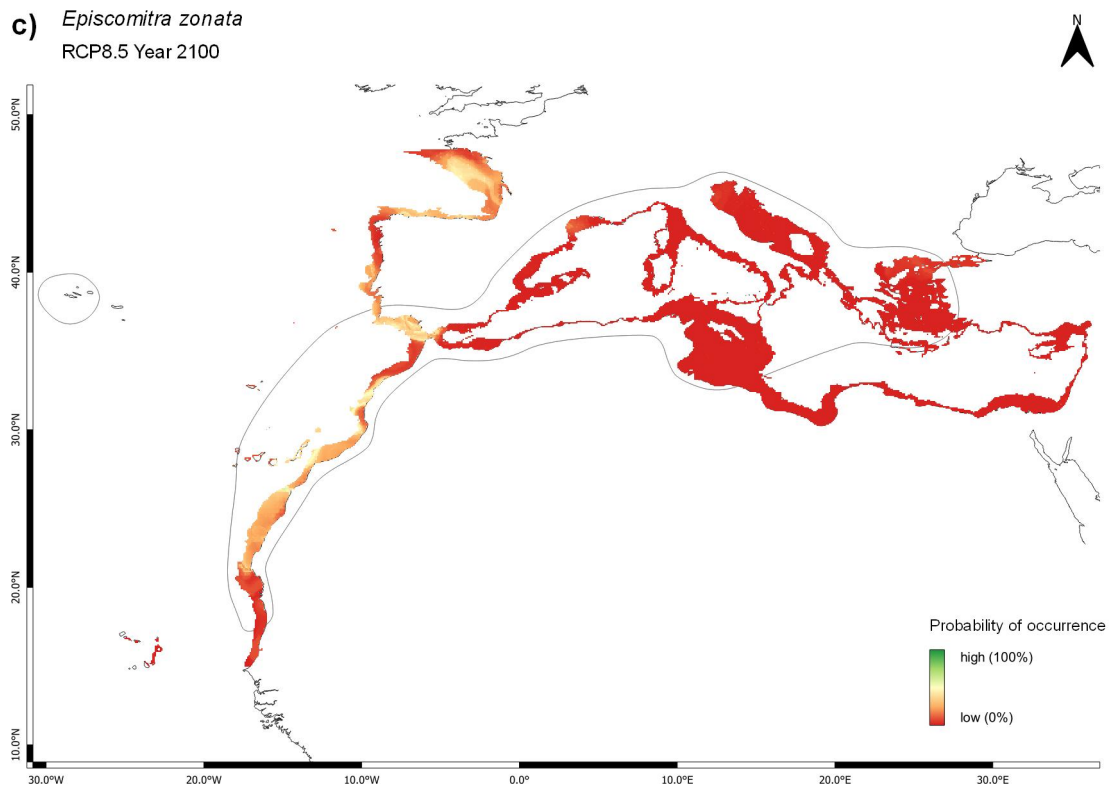
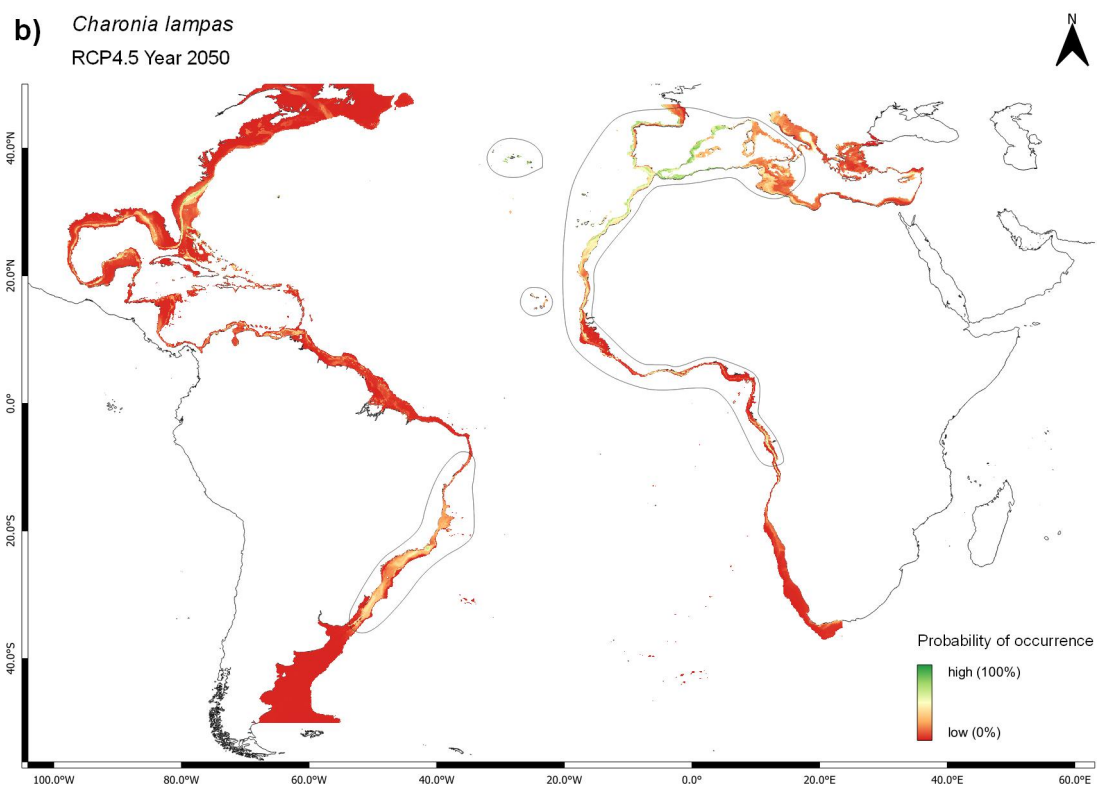
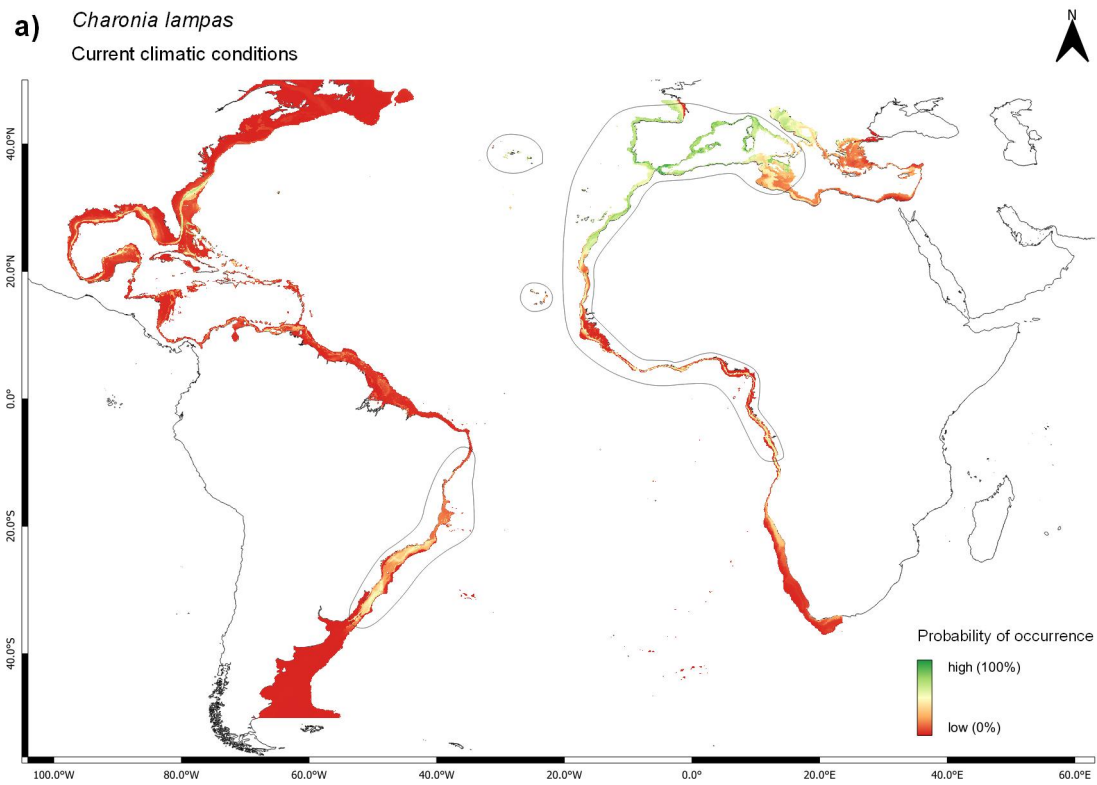


Figure 5: Modelled distribution of *Episcomitra zonata* on deep-water environmental layers under current climatic conditions (a), future climatic conditions under RCP 4.5 for the year 2050 (b) and future climatic conditions under RCP 8.5 for the year 2100 (c). Prediction maps are based on the assumption of unlimited dispersal within the projected area. Red areas: range which is likely to be unsuitable for the species, in yellow areas *E. zonata* has an intermediate probability to occur, while green areas are expected to be highly suitable for the species. Black outline: current range of *E. zonata*.



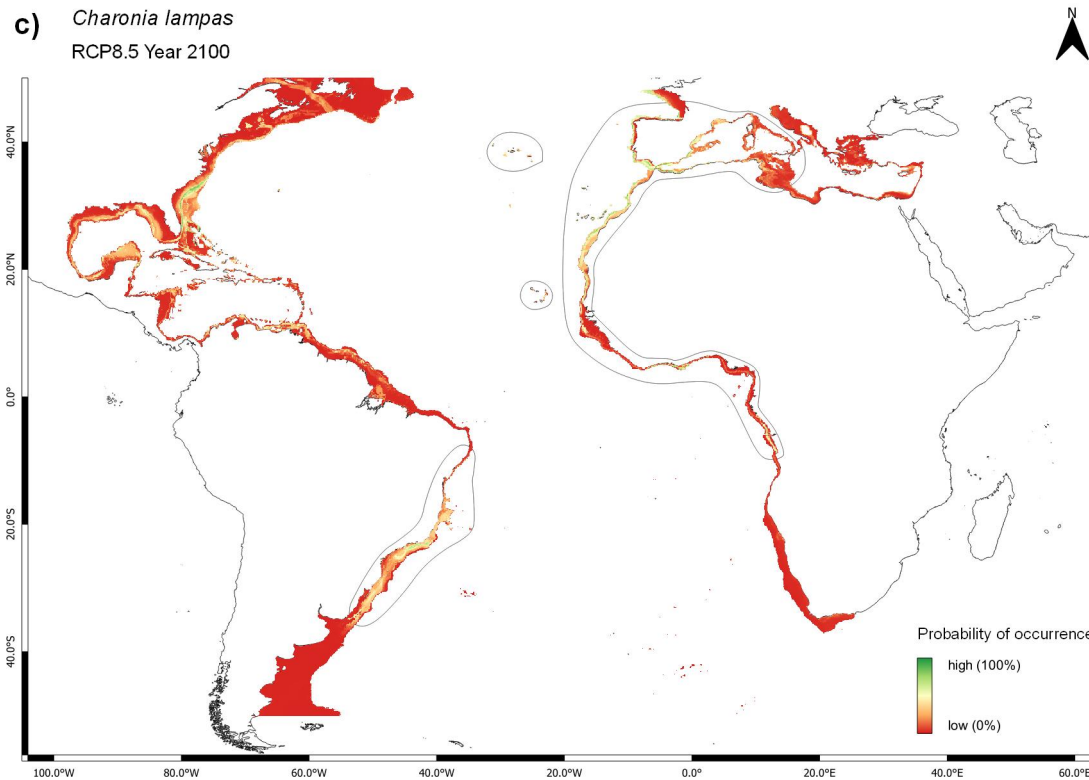


Figure 6: Modelled distribution of *Charonia lampas* on deep-water environmental layers under current climatic conditions (a), future climatic conditions under RCP 4.5 for the year 2050 (b) and future climatic conditions under RCP 8.5 for the year 2100 (c). Prediction maps are based on the assumption of unlimited dispersal within the projected area. Black outline: current distribution range of *C. lampas*.

3.3.3. Range shifts assuming unlimited dispersal capability

Projections based on the assumption of unlimited dispersal capability indicated that, despite some outliers, more widely distributed species will on average experience a net loss of climatically suitable range, whereas Mediterranean species were predicted to theoretically expand their current range under all RCP scenarios (Figure 7). Only for one Mediterranean species, namely *Episcomitra zonata*, predictions under RCP8.5 indicated a range loss by 2100 even when dispersal capacity would be unlimited (Outlier, Figure 7). However, the maps illustrated that the range which was forecasted to become climatically suitable for Mediterranean endemic species is located predominately outside the Mediterranean basin (*Episcomitra zonata* in Figure 5, *Pholas dactylus* in Figure 8 and explained in detail in 3.3.5).

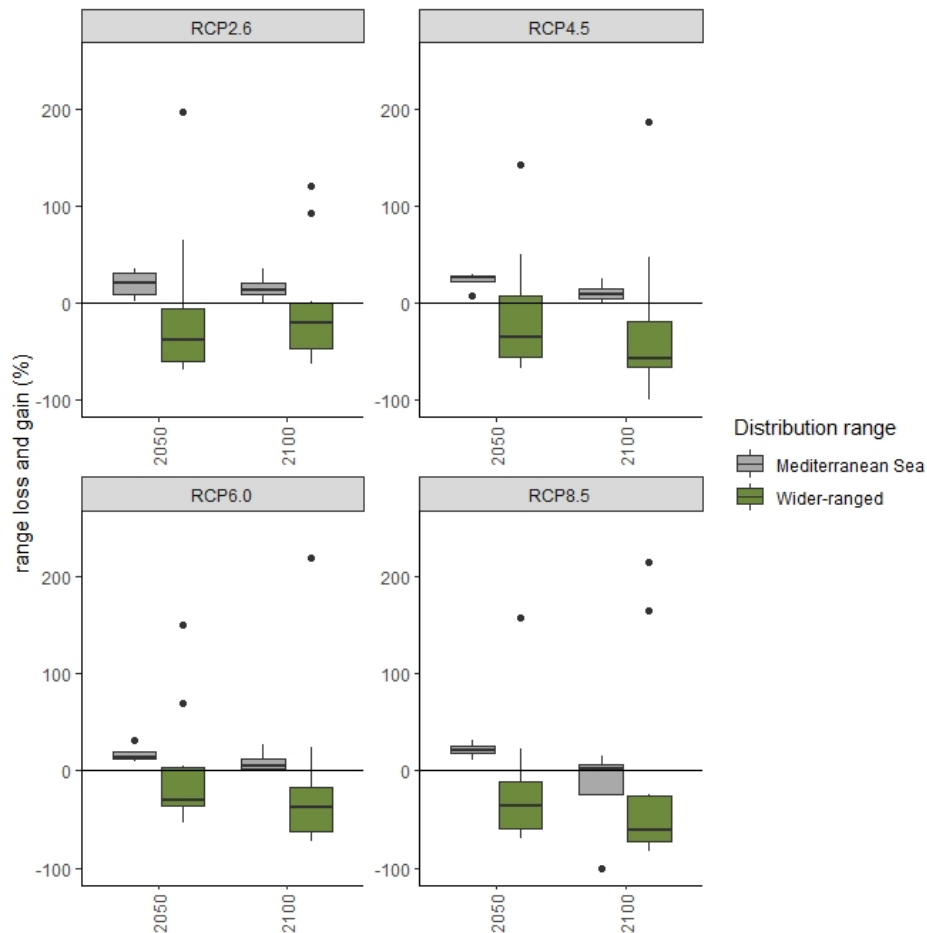


Figure 7: Predicted range size change of marine molluscs of conservation concern based on the assumption that species have unlimited dispersal ability. Cell loss and gain(%) is shown for Mediterranean endemic (n=4) and more widely distributed target species (n=11), under the climate scenarios RCP 2.6, RCP 4.5, RCP 6.0, RCP 8.5 by the years 2050 and 2100.

Contradicting the general trend of forecasted net loss for wider ranged species, some species were shown to potentially profit from future climatic conditions, assuming that they are able to disperse to the entire range becoming suitable for them without delay. Model results for *Pholas dactylus* indicated a large increase in climatically suitable area under all scenarios by 2050 and 2100 (Outlier Figure 7, Figure 8). Furthermore, for *Charonia variegata* a net range expansion by 2050 is likely and under mild climate scenarios also until the end of the century. The projections for 2100 for *Zonaria pyrum* indicated that the species might benefit from severe climatic changes and potentially gains range under pronounced RCP scenarios, whereas 2050 predictions for *Tonna galea* and *Ranella olearium* indicated range expansion under moderate climate scenarios.

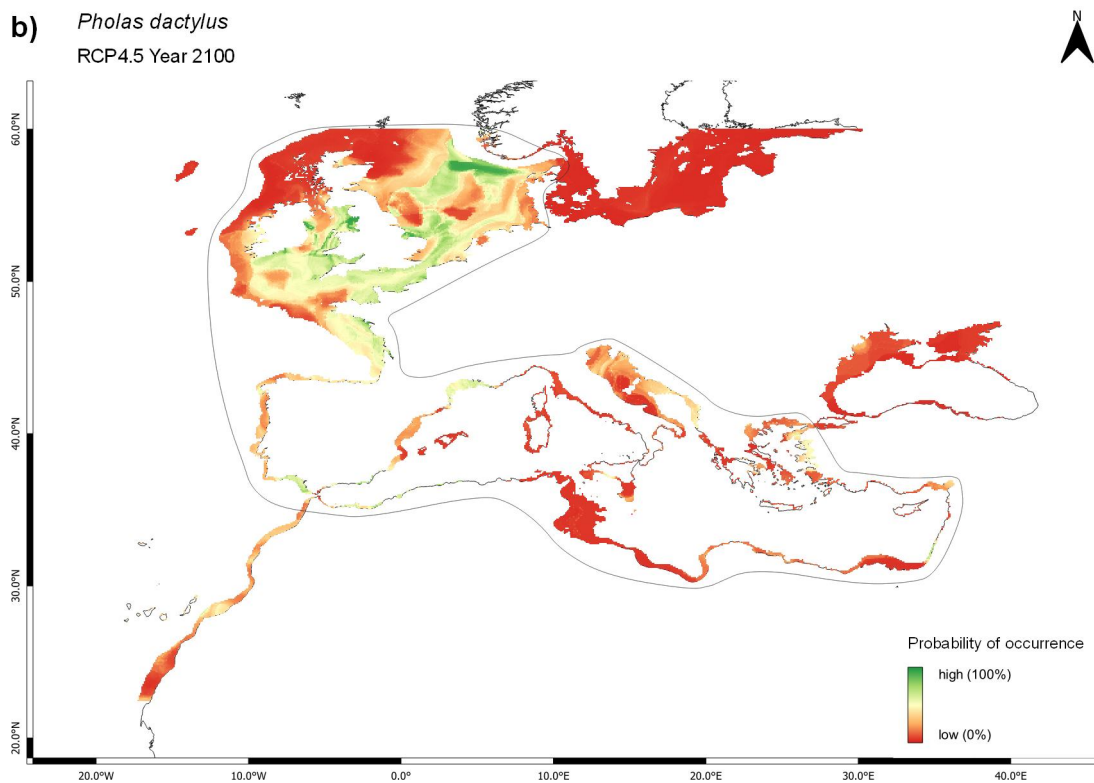
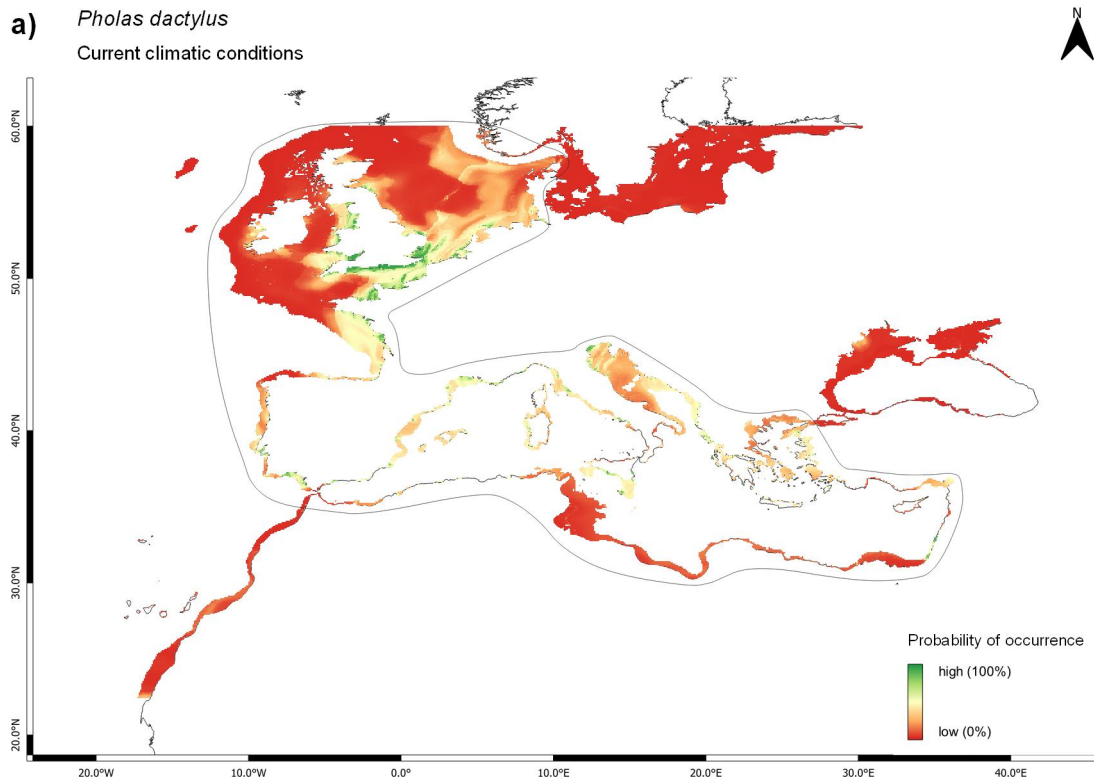


Figure 8: Modelled distribution of *Pholas dactylus* on shallow-subtidal environmental layers under current climatic conditions (a) and future climatic conditions under RCP 4.5 for the year 2100 (b). Prediction maps are based on the assumption of unlimited dispersal within the projected area. Black outline: current distribution range of *P. dactylus*.

3.3.4. Range loss in the Mediterranean Sea assuming dispersal capability

Focussing on the effects of future climate change on species distribution in the Mediterranean basin, I found that the Mediterranean Sea is likely to become largely unsuitable for non-endemic target species and almost completely unsuitable for Mediterranean endemic target species (Figure 9 and explained in detail in 3.3.5). Even though these projections assume unlimited dispersal inside the basin, model results showed that only two species potentially enlarge their current range size inside the Mediterranean Sea (Outlier Figure 9): *Tonna galea* was predicted to gain range in the Mediterranean basin under all scenarios by 2050 and under RCP2.6, RCP4.5 and RCP6.0 until the end of the century, whereas results for *Zonaria pyrum* indicated large range expansion inside the basin in 2100 projections under RCP4.5, RCP6.0 and RCP8.5. Overall, the mean potential range loss in the Mediterranean Sea was significantly more profound for Mediterranean endemic than for wider-distributed species (Wilcoxon-Test, $p < 0.05$) (Figure 9).

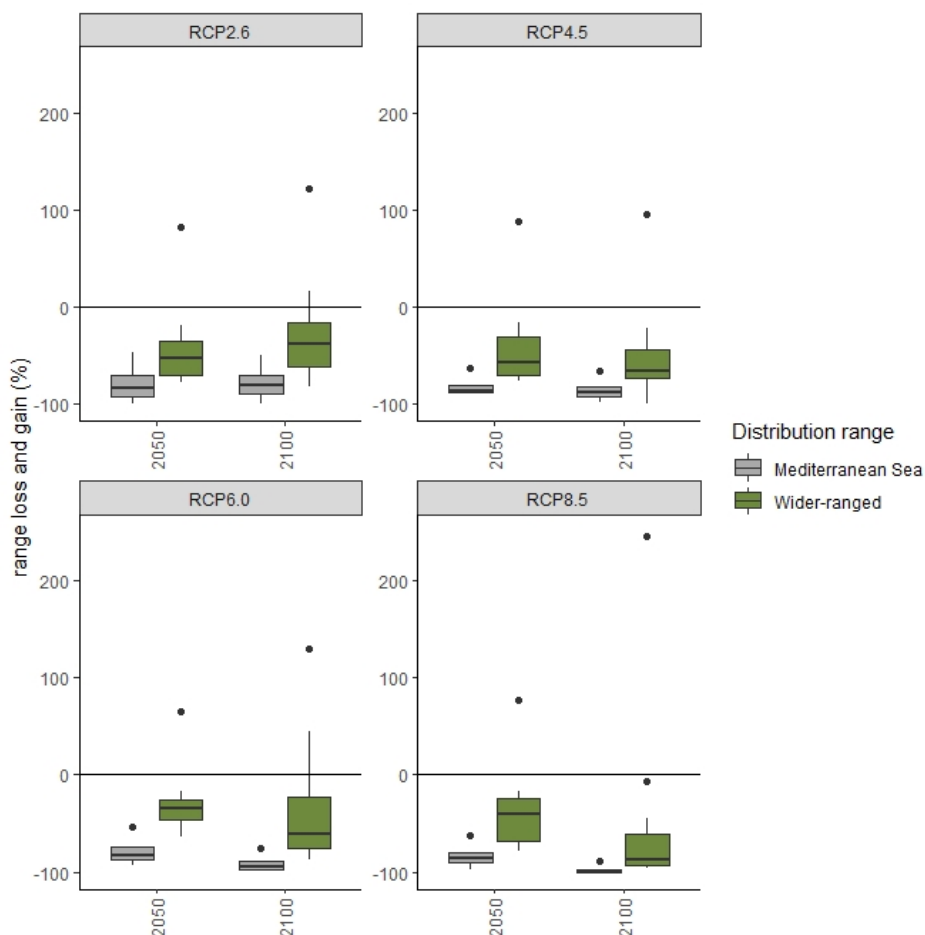
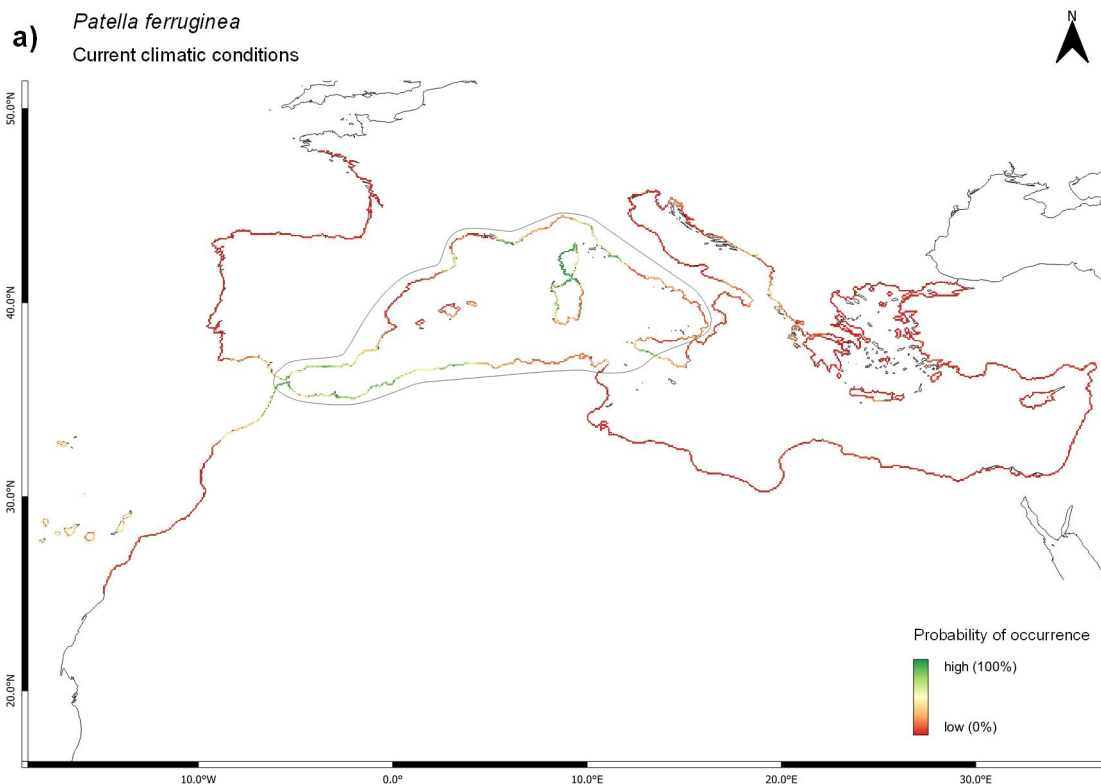


Figure 9: Predicted range size change of marine molluscs of conservation concern in the Mediterranean Sea based on the assumption that species have unlimited dispersal ability. Cell loss and gain(%) is shown for Mediterranean endemic (n=4) and more widely distributed target species (n=11), under the climate scenarios RCP 2.6, RCP 4.5, RCP 6.0, RCP 8.5 by the years 2050 and 2100.

Mediterranean endemic species were projected to experience range reduction inside the basin by 78.4% (± 23.3) under RCP 2.6, by 81.5% (± 12.2) under RCP 4.5, by 77.9% (± 16.8) under RCP 6.0 and by 83% (± 15) under RCP 8.5 already by 2050. Excluding the two outliers *T. galea* and *Z. pyrum*, the predictions for 2050 for wider distributed species showed the lowest mean range reduction under RCP6.0 ($38.2\% \pm 14$) and the highest under RCP8.5 ($52\% \pm 22.1$).

By the end of the century models for Mediterranean endemic species projected range loss inside the basin from 77.8% (± 21.4) under RCP2.6 up to 97.3% (± 5.2) under RCP8.5. Under intermediate and strong climate scenarios, three of the Mediterranean endemic species, namely *Patella ferruginea*, *Episcomitra zonata* and *Pinna nobilis*, are likely to face extinction by losing 100% of their currently suitable range inside the Mediterranean basin at the latest by the end of the century (Figure 9, as an example *P. ferruginea* is shown in Figure 10).

As predicted for Mediterranean endemic species, projections for 2100 for more widely distributed species also showed more profound reduction in range size compared to the first period of simulations; this is indicated by average range losses from 47.3% (± 25) under RCP 2.6, up to 83.9% (± 16.7) under RCP 8.5 (outliers excluded) (Figure 9, as an example *P. rudis* is shown in Figure 11).



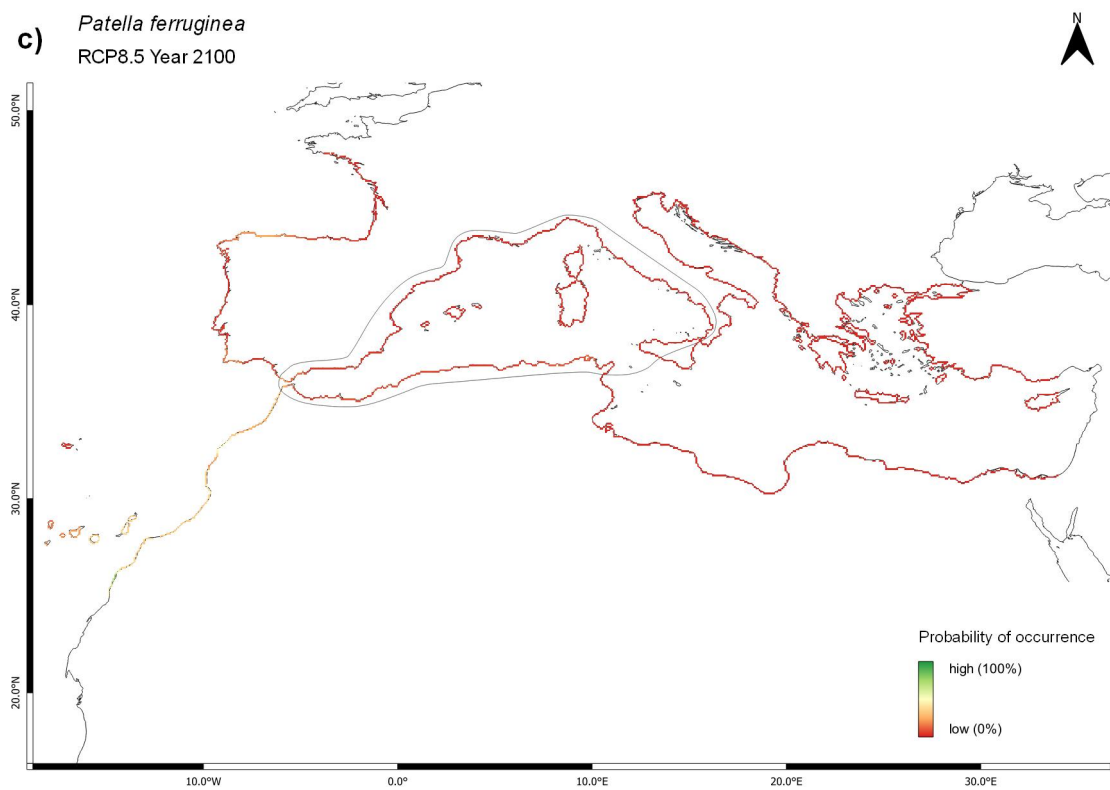
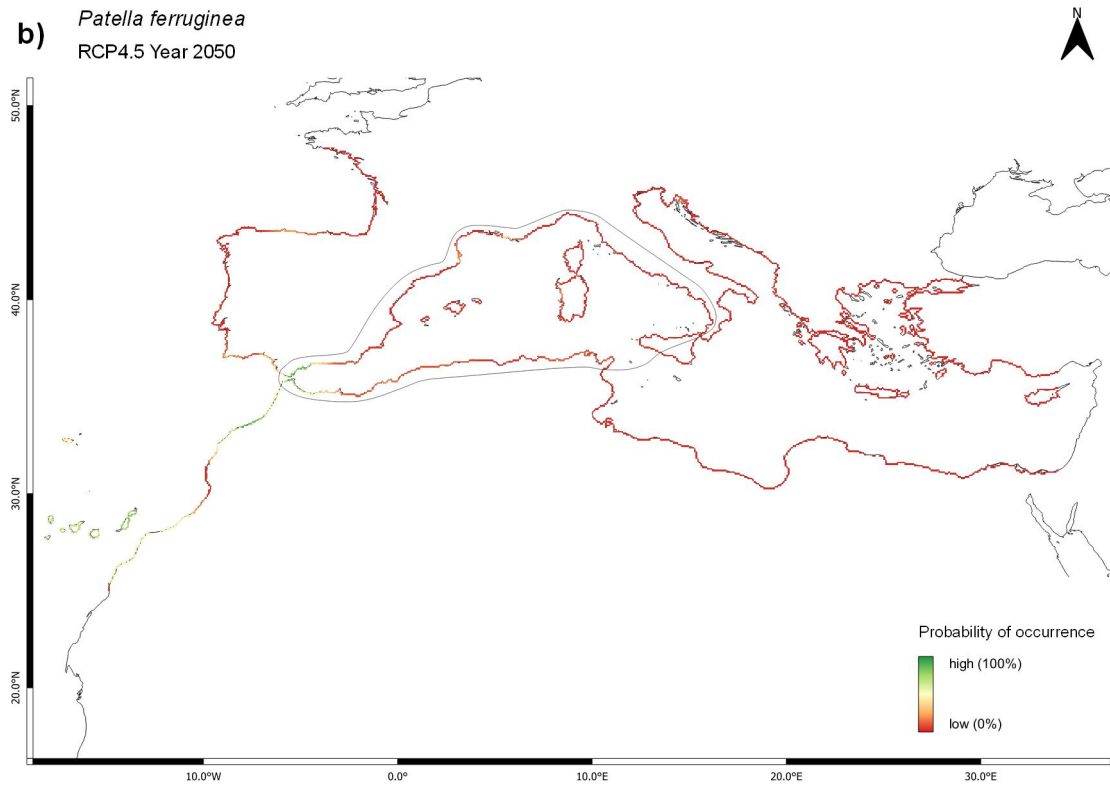
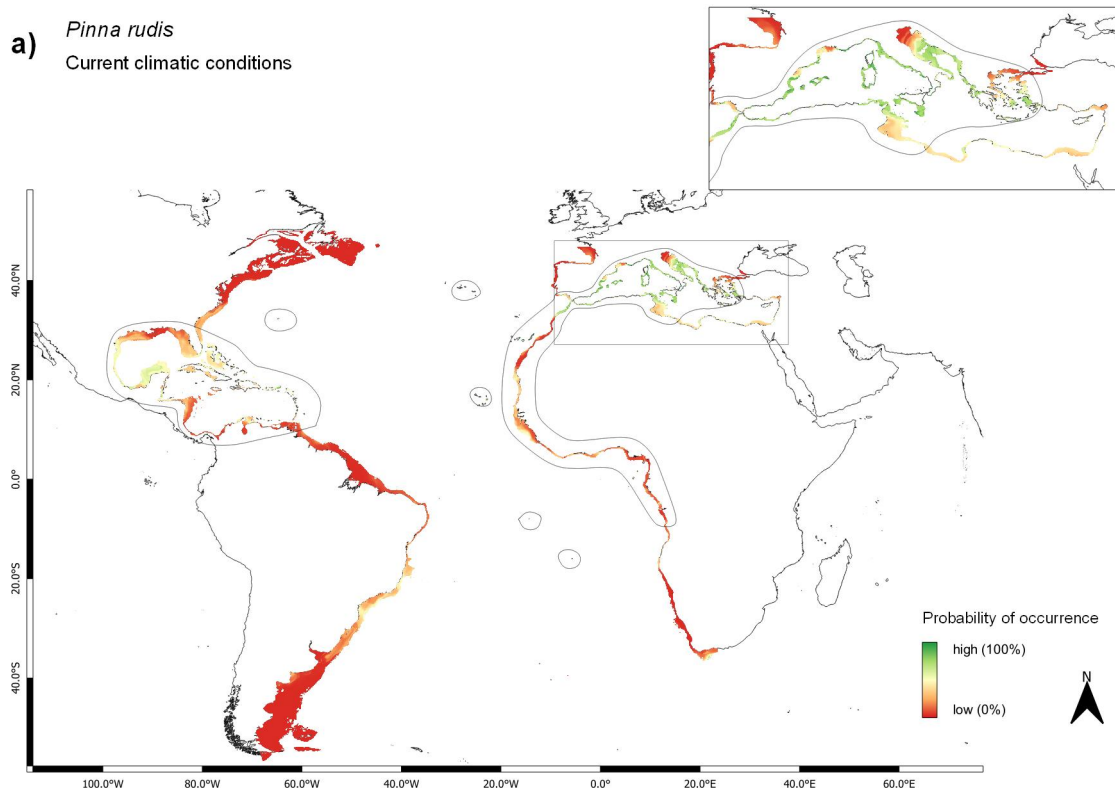
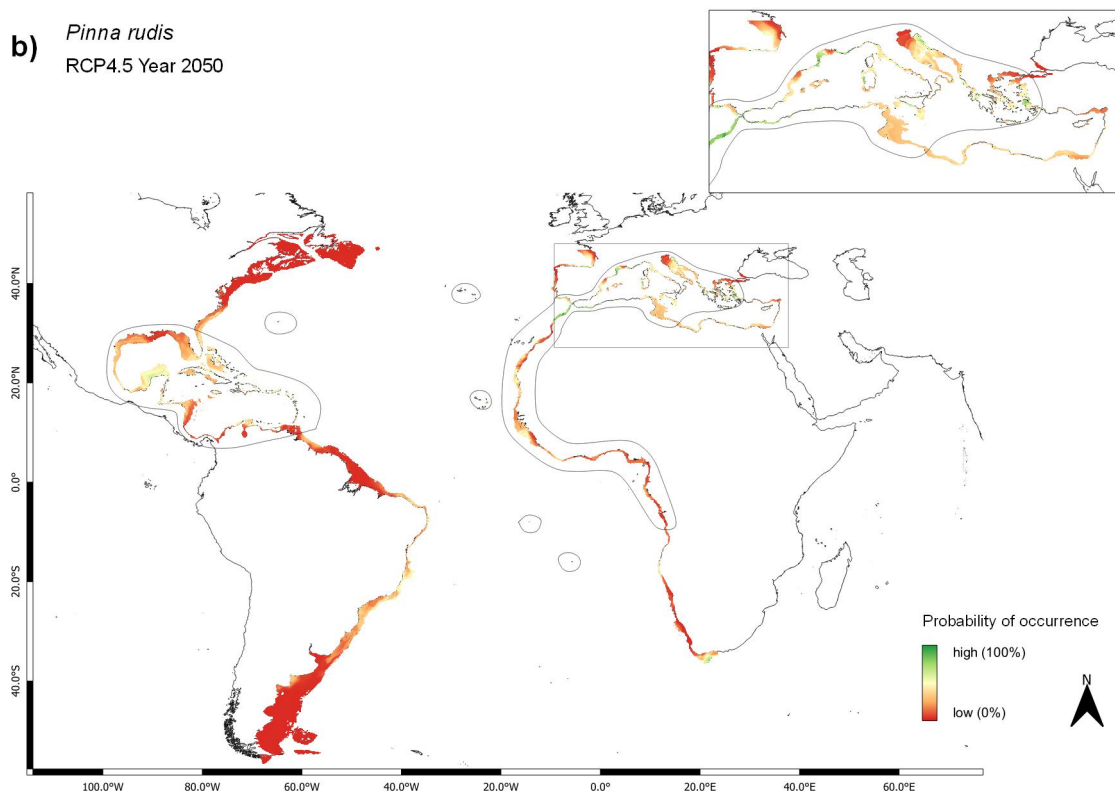


Figure 10: Modelled distribution of *Patella ferruginea* on intertidal environmental layers under current climatic conditions (a), future climatic conditions under RCP 4.5 for the year 2050 (b) and future climatic conditions under RCP 8.5 for the year 2100 (c). Prediction maps are based on the assumption of unlimited dispersal within the projected area. Black outline: current distribution range of *P. ferruginea*.

a) *Pinna rudis*
Current climatic conditions



b) *Pinna rudis*
RCP4.5 Year 2050



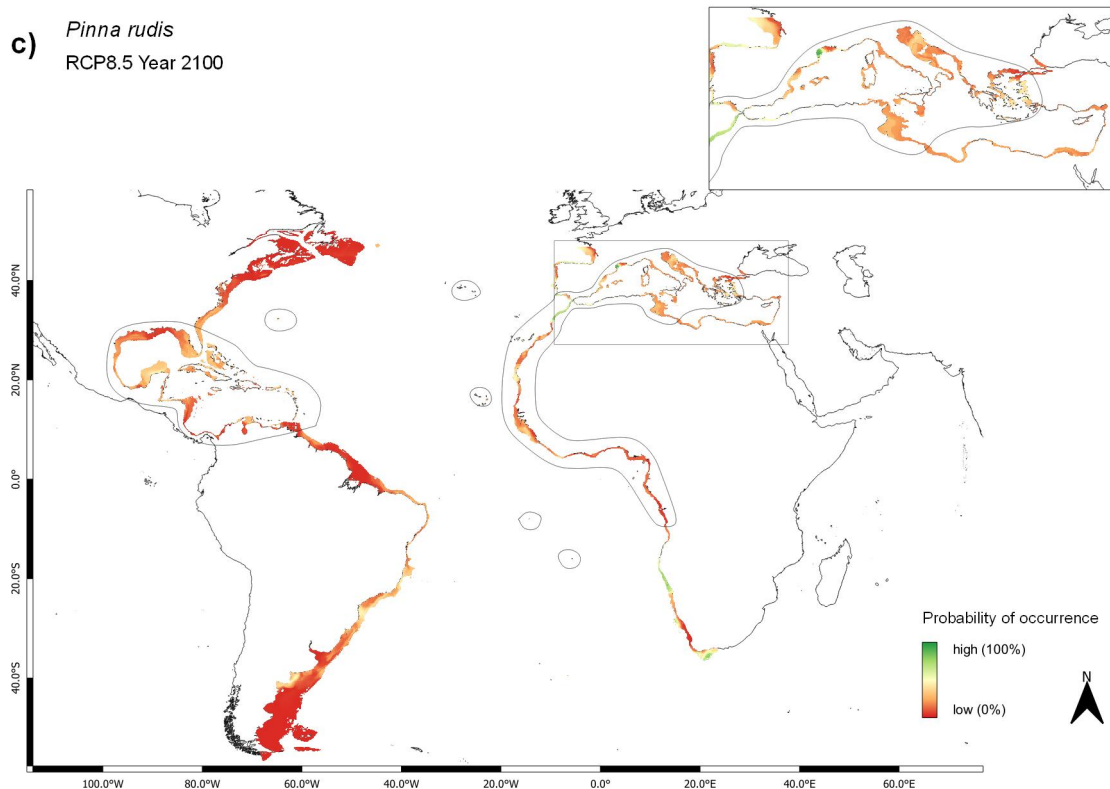


Figure 11: Modelled distribution of *Pinna rudis* on shallow-subtidal environmental layers at full distribution range and in the Mediterranean Sea (detail) under current climatic conditions (a), future climatic conditions under RCP 4.5 for the year 2050 (b) and future climatic conditions under RCP 8.5 for the year 2100 (c). Prediction maps are based on the assumption of unlimited dispersal within the projected area. Black outline: current distribution range of *P. rudis*.

3.3.5. Probability maps: Where might suitable conditions prevail in the future?

Across the entire study area, the Mediterranean Sea was shown to currently provide the most suitable conditions for all of the modelled species. With future climatic changes, probability maps indicated that over the species' full potential, i.e. climatically suitable range, the degree of loss is expected to be most profound in the Mediterranean basin.

Range changes in the Mediterranean Sea

Projections showed congruent patterns among the modelled species, pointing to a general decrease of potential suitable conditions in the currently warmest Mediterranean marine regions (Tyrrhenian Sea, Ionian Sea and Levantine Sea, Figure 12). In contrast, the coldest areas in the basin (Gulf of Lion, Adriatic sub-basin, Aegean Sea and Alboran Sea, Figure 12) were predicted to offer more suitable range to a high proportion of the target species (as an example *P. nobilis* is shown in Figure 13) under a future climate at least until the mid-century. However, the probability of occurrence throughout the basin decreased with scenario severity and in particular with timespan. According to projections to the year 2100, the Mediterranean Sea will become completely unsuitable for the Mediterranean endemics

Episcomitra zonata (Figure 5), *Patella ferruginea* (Figure 10) and *Pinna nobilis* (Figure 13), representing full extinction inside the basin. Nonetheless, for these three species environmental suitability is expected to increase in some areas outside the basin, such as in northern parts of the west African coast (*Episcomitra zonata*, *Patella ferruginea*, shown in Figure 5 and Figure 10 respectively) and along the southern Portuguese coast, as well as at the Gulf of Biscay (*Lithophaga lithophaga* and *Pinna nobilis*, shown in Figure 13).

A potential range expansion inside the Mediterranean Sea was predicted only for *Tonna galea* and *Zonaria pyrum*. Probability maps for these two species showed a range gain for *Z. pyrum* and *T. galea* in the northern Adriatic Sea, the northern Aegean Sea, the Levantine Sea and in small areas in the Balearic Sea.

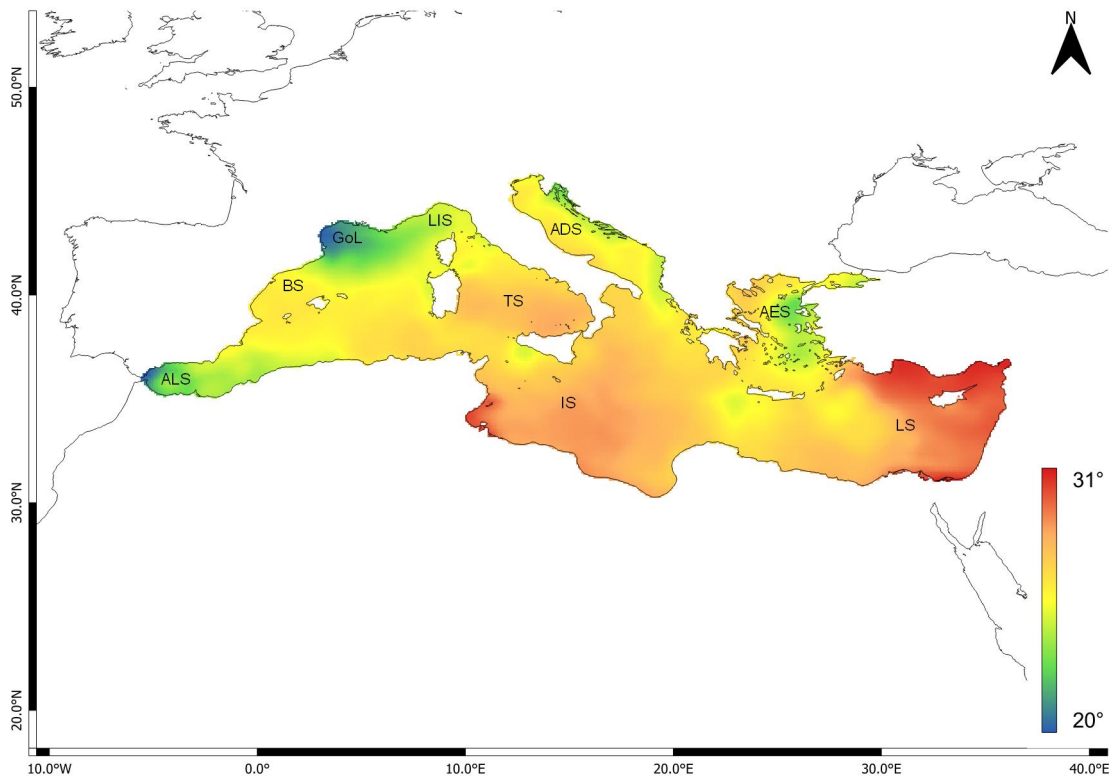
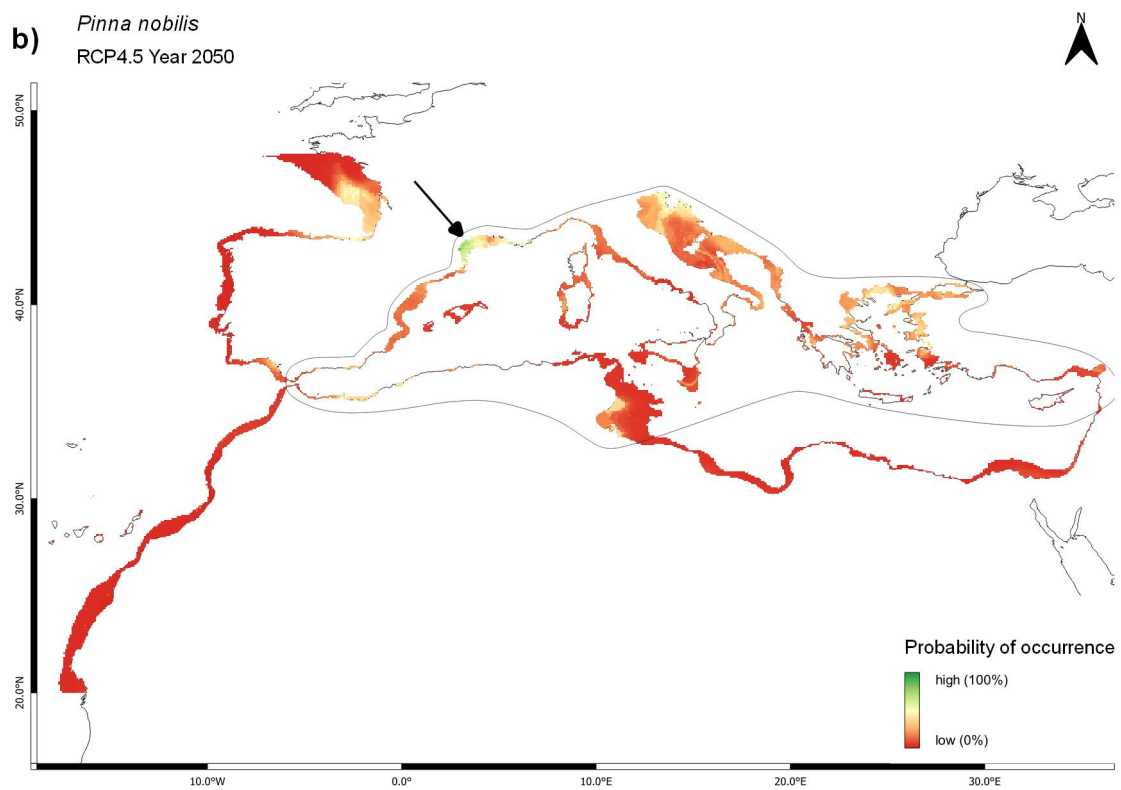
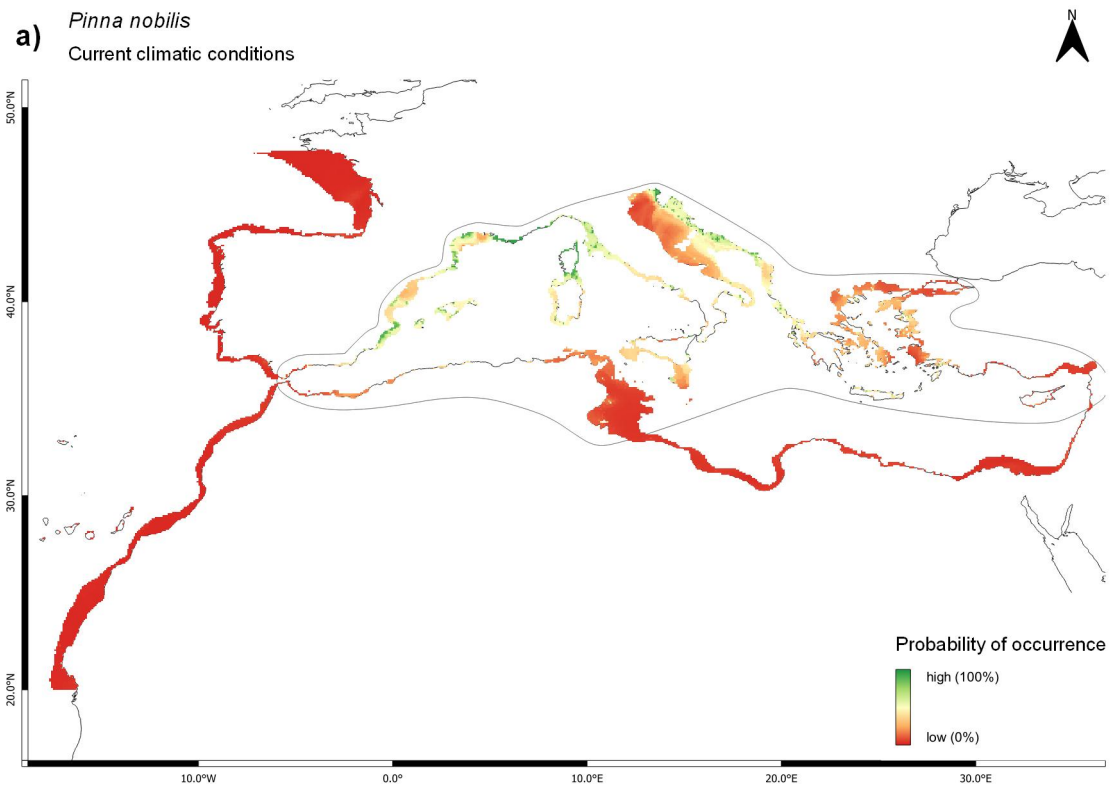


Figure 12: Mean sea surface temperature of the warmest month in Mediterranean marine regions: Alboran Sea (ALS), Balearic Sea (BS), Gulf of Lion (GoL), Ligurian Sea (LIS), Tyrrhenian Sea (TS), Adriatic Sea (ADS), Ionian Sea (IS), Aegean Sea (AES), Levantine Sea (LS)



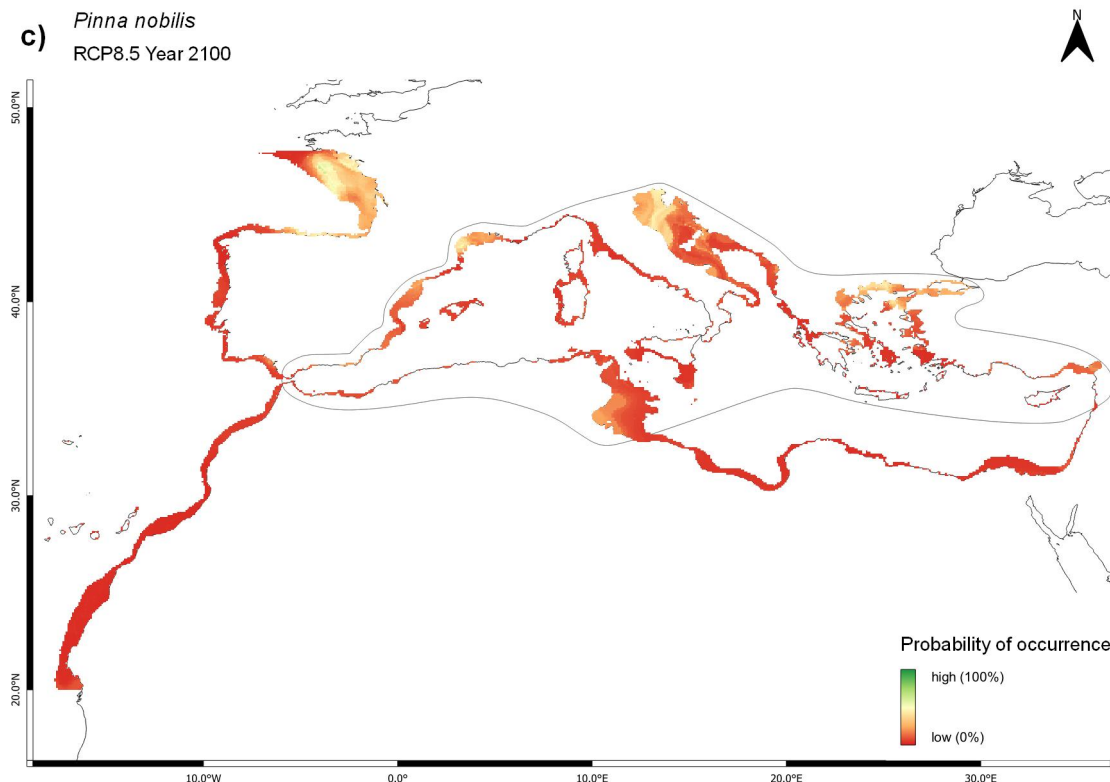


Figure 13: Modelled distribution of *Pinna nobilis* on shallow-subtidal environmental layers under current climatic conditions (a), future climatic conditions under RCP 4.5 for the year 2050 (b) and future climatic conditions under RCP8.5 for the year 2100 (c). Prediction maps are based on the assumption of unlimited dispersal within the projected area. Black arrow in (b): suitable future conditions at the Gulf of Lion; black outline: current distribution range of *P. nobilis*.

Range changes outside the Mediterranean Sea

With warming temperatures, the projections pointed to an overall shift of climatically suitable conditions from the Mediterranean basin towards the North Atlantic, particularly along northern parts of the west African coast and in some areas at the Portuguese and French coast. Along open continental margins we observed increased range suitability at higher latitudes for most of the modelled species.

Probability maps demonstrated poleward range gains under a future climate for *Luria lurida*, *Charonia variegata*, *Naria spurca*, *Pinna rudis* (Figure 11) and *Cymbula safiana*, with increased range suitability at the South-West African coast and a high probability of occurrence at the southern-most coast of South Africa. Conversely, a northward range expansion at least in the East-Atlantic was predicted for *Pinna rudis* (Figure 11), *Ranella olearium* (Figure 14), *Schilderia achatidea*, *Cymbula safiana*, and *Pholas dactylus* (Figure 8). For the latter species, the modelling results showed an increase of suitable range, driven by a gradual expansion towards northern shallow water areas including the Gulf of Biscay and most of the British Isles. Reduced range suitability at equatorial zones was predicted only for *Cymbula safiana* and *Charonia lampas* (Figure 6) at the West-African coast. These species, however, are likely

to lose range also across their entire distribution range. For the amphi-atlantically distributed *Charonia variegata*, equatorial regions at the South American and West African coast were predicted to largely prevail under a future climate.

Range losses on North Atlantic islands were most pronounced around the Azores and the Cape Verdes, while the Canary Islands were forecasted to remain largely suitable. For species occurring also in the West Atlantic and the Caribbean, probability maps indicated losses of their current range under severe scenarios in the Gulf of Mexico (*Pinna rudis*, shown in Figure 11 and *Charonia variegata*), while the South American coastline was predicted to remain predominantly suitable under future climatic conditions (*Charonia lampas*, shown in Figure 6 and *Charonia variegata*). For the only species with an almost worldwide distribution range, *Ranella olearium*, the probability maps indicated suitable conditions under a future climate towards northern waters (Northern Europe and North America), whereas the Mediterranean Sea and areas in the Indian Ocean (Southern Australia, East-African Coast) were predicted to become largely unsuitable (Figure 14).

3.4. Vertical range shifts

The analyses on range size-changes in nearshore areas (0-50 m depth) and offshore (> 50 m depth) did not reveal a general pattern of vertical shifts towards deeper water layers under a future climate (Wilcoxon-Test, $p < 0.05$).

Nevertheless, for some species (mainly those occurring along the continental shelf and upper slope) I detected higher losses in areas close to the shore compared to offshore, whereas gain of suitable range was conspicuously higher seawards versus nearshore. For instance *Charonia lampas* (Figure 6) and *Ranella olearium* (Figure 14), two of the species occurring at the continental shelf and upper slope showed a clear shift towards offshore waters in large areas in Northern Europe and North America (*R. olearium*,) and in the Mediterranean Sea, the Gulf of Biscay and the Portuguese coast (*C. lampas*). Likewise, two shallow-water species, *Luria lurida* and *Naria spurca*, were predicted to find locally suitable conditions in offshore waters along the eastern coast of Sicily. Moreover, *P. dactylus* (Figure 8) showed huge range expansion in offshore waters around the British Isles, whereas the nearshore gain of suitable range in this area was comparably low.

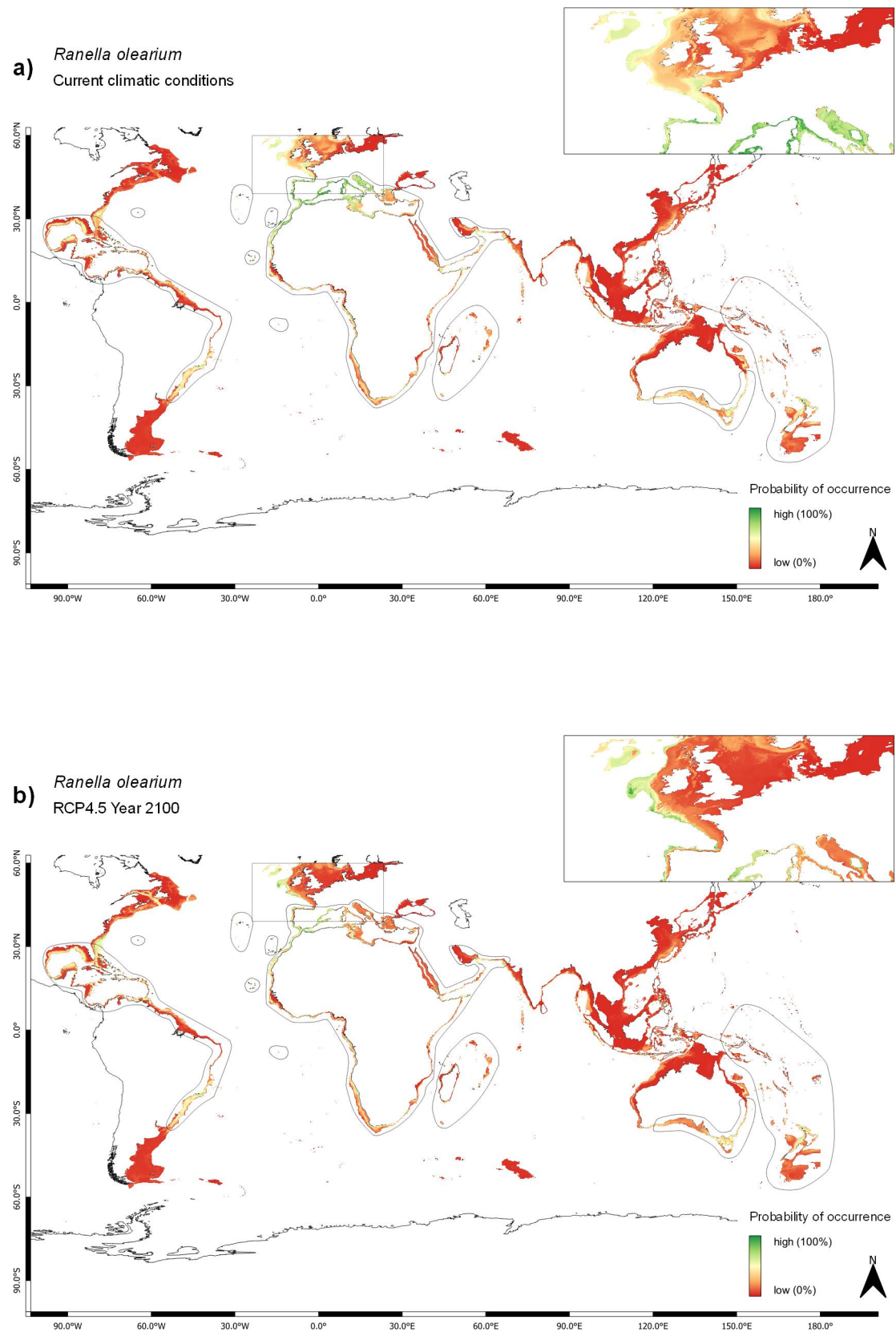


Figure 14: Modelled distribution of *Ranella olearium* on deep-water environmental layers under current climatic conditions (a) and future climatic conditions under RCP 4.5 for the year 2100 (b). Detail shows the projected offshore shift in the North Atlantic. Black outline: current distribution range of *R. olearium*.

4. Discussion

Taken together, the results showed that with warming climate the modelled marine mollusc species of conservation concern will be under increasing threat during the 21st century. The key findings of my study are that, first, overall the target species will experience a severe reduction in accessible range size under a future climate; this is predicted to intensify with scenario severity in the second half of the century. Second, loss of suitable range will be significantly more profound for Mediterranean endemics than for more widely distributed species, at least under the plausible assumption that these species will not manage to colonize newly suitable areas outside the basin over the next century. Indeed, three of the four Mediterranean endemic study species face complete loss of suitable habitat and hence high risk of extinction by the end of the century. And third, the Mediterranean basin can be considered a 'hotspot of range decline' for all of the modelled species under the climatic scenarios explored.

4.1. RCP Scenarios

This study is based on four climate scenarios. Although they do not provide precise forecasts of climate change, together they span the range of climate futures currently considered possible (Porfirio et al., 2014). Hence, our results should be discussed in the context of the scenario's definition.

I found differences in scenarios already in 2050, but they were not ordered linearly along the severity axis: By 2050 RCP6.0 resulted, on average, in the least drastic range reduction for our target species. The degree of range loss in this first period of simulation was most pronounced under RCP8.5 followed by RCP4.5. and RCP2.6. Beyond 2050 our projections became more profound with scenario severity. This predicted pattern of range loss is coherent with the trajectories on greenhouse gas concentrations and the consequent global warming increase described by the RCP scenarios for the 21st century. By the mid-century, the envelopes of global mean surface temperature in the moderate (RCP2.6) and intermediate (RCP4.5 and RCP6.0) scenarios are largely overlapping. Nonetheless, the peaks of greenhouse gas concentrations and hence also the projected temperature increase of the individual scenarios are described at different times. RCP2.6 and RCP4.5 are characterized by a peak around 2050, whereas RCP6.0 describe the highest radiative forcing levels only by 2060-2080. This time lag explains the comparably low effect of RCP6.0 on range suitability in the first time period of our simulations. After mid-century continuously reducing greenhouse gas emissions under RCP2.6 lead to the smallest changes in global mean temperature relative to pre-industrial levels, whereas RCP4.5 and RCP6.0 stabilize at high radiative forcing, and hence, also at high temperature levels before 2100. RCP8.5 describes continuously increasing greenhouse gas concentrations throughout the century, leading to the highest warming rates by 2100 (IPCC, 2013). In conclusion, our results perfectly reflect the

described trajectories of the RCP scenarios throughout the century, with projected range loss substantially increasing with the severity of climate scenario in the second half of the century.

4.2. Future fate of Mediterranean endemic species

A particularly striking result is the severe vulnerability of Mediterranean endemic species. Under the assumption that target species are able to disperse without any limitations, Mediterranean endemic species are likely to experience a net expansion of their currently suitable range. Importantly, however, the probability maps and calculations of range loss at the basin scale demonstrated that those areas projected to become suitable for Mediterranean endemic target species are located predominantly outside the basin. In other words, Mediterranean endemic mollusc species may survive future climate warming only if they are able to access newly suitable areas outside of the Mediterranean basin.

Regarding Mediterranean endemics, at least for *Pinna nobilis* and *Patella ferruginea*, the palaeontological documentation is limited to the Mediterranean Sea with fossil records dating back to the Pleistocene at least (Bracchi et al., 2020; Forli et al., 2004). They will most likely not manage any kind of long-distance migration and will continue to be confined to the Mediterranean basin. Moreover, *Pinna nobilis* is often associated with seagrass meadows of the Mediterranean endemic *Posidonia oceanica* (Vázquez-Luis et al., 2014). Because this plant does not live outside the basin, the colonization by *Pinna nobilis* of areas outside the basin seems unlikely. Combining these arguments and the model predictions, warming temperatures in the Mediterranean Sea put these two species under a high risk of extinction. Conversely, the Mediterranean species *Episcomitra zonata*, which was also projected to face complete extinction in the Mediterranean Sea, currently also occurs in the adjacent Atlantic Ocean around the Azores and the northern-most West African coast. Hence, survival outside the basin could be possible, at least under moderate climatic changes.

Suitability maps further highlighted an interesting case for the fourth Mediterranean endemic *Lithophaga lithophaga*, which currently also occurs in small areas outside the basin. This species was predicted to experience a large range reduction inside the basin, with only the coldest Mediterranean regions left as suitable habitat. Outside the Mediterranean Sea, *L. lithophaga* is likely to find suitable climate niches solely in the Gulf of Biscay but not on the western Portuguese coast. For most of our target species this would represent an insuperable dispersal distance. Nonetheless, planktonic larvae of many *Lithophaga* species have been shown to remain in the plankton for extended times (i.e. up to several weeks) (Mokady et al., 1993). This expands the potential period of dispersal and would thus increase the chances of reaching a suitable range even over longer migration distances.

4.3. Range changes within the Mediterranean basin

Focussing on range changes inside the Mediterranean basin, future projections demonstrated large reductions in suitable range, not only for Mediterranean endemics but also for target species occurring in large areas outside the basin. The Mediterranean marine regions forecasted to become unsuitable under a future climate were largely the same across the modelled species.

Range loss was particularly profound in the Tyrrhenian Sea, the Ionian Sea and the Levantine Sea, whereas the reduction of suitability was less dramatic in the Adriatic sub-basin, the Alboran Sea and the northern Aegean Sea. The Gulf of Lion was predicted to remain or even become more suitable for most of the modelled species. With temperature variables being the most important parameters in the niche models of our target species, this spatial pattern of suitability decline perfectly reflects the known sea surface temperature gradient over the Mediterranean basin. Deep-water formation processes within the cyclonic gyre of the Gulf of Lions result in high sea surface temperature in the Tyrrhenian Sea and particularly cold temperatures in the Gulf of Lion, whereas eastern Mediterranean deep water formed in the southern Adriatic leads to high water temperatures in the Ionian basin and cold temperatures in the northern Adriatic (Skirris, 2014). The Aegean basin as well as the Alboran basin are affected by water exchange with the adjacent Black Sea and North Atlantic, respectively, and thus are relatively cold (Shaltout and Omstedt, 2014), whereas the Levantine basin is characterized by warm and very saline water masses (Skirris, 2014). With global climate change, the previously described warmest areas of the basin (Tyrrhenian Sea, Ionian Sea, Levantine Sea) are expected to become even warmer and will hence provide the least climatically suitable regions for our modelled species. By contrast, the coldest areas of the Mediterranean Sea (Gulf of Lion, Adriatic Sea, Alboran Sea, Aegean Sea) are likely to serve as the last cold refugium in the Mediterranean basin for the vast majority of our target species.

I highlight here as an example *Lithophaga lithophaga*. This species is currently abundant in the whole basin but it is predicted to find the last suitable climatic niches inside the Mediterranean Sea in the Gulf of Lion, the northern Adriatic and the northern Aegean basins by the end of the century. This finding supports results from previous studies modelling the future climatic niches of Mediterranean endemic species. Ben Rais Lasram et al. (2010) projected Mediterranean endemic fish to find the last climatically suitable areas in the Gulf of Lion and the Adriatic Sea. Those authors described them as a possible “cul-de-sac”, driving cold-water species with further climate warming to the brink of extinction.

Tonna galea and *Zonaria pyrum* were the only species forecasted to profit from a future climate in the Mediterranean Sea expanding their current distribution range in the northern Adriatic, the northern Aegean and in the Levantine Sea. Note, however, that the models for these two species were the least

accurate, with TSS-values mostly <0.6, and predictions for them should thus be interpreted with caution.

4.4. Range changes beyond the Strait of Gibraltar

The magnitude of range loss was overall less profound outside the Mediterranean basin. Although more widely distributed species were on average predicted to experience a net range loss at their full distribution range, probability maps indicated range changes along open continental margins for some of our target species.

Under a future climate, a poleward gain of suitable range was detectable for *Luria luida*, *Charonia variegata*, *Naria spurca*, *Pinna rudis* and *Cymbula safiana* towards southern coastal regions indicated by a high probability of occurrence at the southernmost coast of South Africa, whereas distribution maps indicated a northward trend for *Pinna rudis*, *Ranella olearium*, *Schilderia achatidea*, *Cymbula safiana*, and *Pholas dactylus*. The latter species, *P. dactylus*, is of rather cold-water affinity and currently already abundant in northern European waters. Under a future climate this species showed a clear gradual expansion to the north, almost tripling its current range around the British Isles and the Gulf of Biscay and concurrently losing climatically suitable area inside the Mediterranean basin. Although some species were predicted to gain suitable range towards the poles, we could not identify a general simultaneous reduction in range size at the trailing edge (i.e. the equatorward limit). The models predicted losses of climatically suitable area near the equator for *Cymbula safiana* and *Charonia lampas*, but these species are also expected to lose suitable range across the entire study area and most profoundly in the Mediterranean basin. Although our results are not broadly consistent with the confirmed evidence of gradual poleward range shifts in the marine environment (Hastings et al., 2020), they support findings of idiosyncratic responses of marine molluscs to future warming along open continental margins. Under future climate Saupe et al. (2014) found a similar incoherent pattern of marine molluscs in the North Atlantic shifting their distribution poleward, without concurrent reduction in range size at the species low-latitude limits.

Apparent inconsistencies of predictions may reflect the fact that, although temperature was overall the pervasive proximate variable defining the target species niche, other variables also significantly affected species distribution. For instance, for *Charonia variegata*, SDMs determined annually constant chlorophyll values as the most important limiting factor. In general, chlorophyll is a good proxy for productivity and can thus serve as valuable variable describing a species' biophysiological niche. *C. variegata*, however, is a selective feeder with a diet mainly based on echinoderms (Doxa et al., 2013); hence, for this specific species, chlorophyll is more likely to serve as an indicator than as a causal factor.

Although the biology of single species did not explain the correlations between environmental gradients and species distributions in the SDMs, the predicted multispecies pattern is consistently interpretable in terms of altering environmental gradients associated with climate change. Finally, the idiosyncratic range shifts projected along open continental margins, compared to the unambiguous pattern of range loss in the Mediterranean basin, highlight once again the specific vulnerability of the biota of the Mediterranean Sea to a future warming climate.

4.5. Vertical range shifts

Vertical zonation patterns are anticipated to shift with climatic changes (Mooney et al., 1993) and marine species have already been documented to move to deeper water layers as a response to climatic alterations (Bischof et al., 1998; Perry et al., 2005). Although my results did not broadly support this pattern, I predicted a shift towards offshore waters for *Charonia lampas* and *Ranella olearium*, two species occurring at the continental shelf and upper slope, in some areas in the North Atlantic. Likewise, for the two shallow-water species *Luria lurida* and *Naria spurca*, suitability maps indicated local offshore shifts along the eastern coast of Sicily at least under moderate scenarios by 2050. Interestingly, for all these species, salinity was a relevant predictor in the niche models. Coastal salinity is expected to be affected by changes in precipitation patterns induced by global climate change (Harley et al., 2006). Alterations in coastal salinity are particularly conspicuous at the local scale, where the variability of this parameter is the highest and thus clearly visible in particular regions such as around the British Isles or at the Gulf of Biscay in prediction maps for *C. lampas* and *R. olearium*.

4.6. Other possible threats for marine molluscs

SDMs are known to often overestimate (Sax et al., 2013) or underestimate (Lawler et al., 2009) extinction risk for modelled species. Nevertheless, range loss induced by climate change is likely to be even greater than predicted due to factors not considered in our models.

For instance, SDMs do not take into account indirect warming effects such as potential competitive pressure from exotic species that invade the native ranges of the modelled species or direct anthropogenic pressure. Indeed, human activities such as habitat degradation and overexploitation of natural habitats are well-known threats for marine molluscs. One example is the endangered Mediterranean date-mussel *Lithophaga lithophaga*, which has been exploited as seafood for centuries. Furthermore, its collection through rock-hammering implies the destruction of its surrounding habitat (Bianchi and Morri, 2000). For *Patella ferruginea*, which we predicted to become extinct with climate warming, some additional concern exists regarding its very sensitive reaction to sewage pollution (Espinosa et al., 2007). Beyond climatic changes, another aggravating threat was recently recorded for

Pinna nobilis, with huge populations suffering from a mycobacterial disease that has already led to basin-scale mass mortality events (Carella et al., 2019; Katsanevakis, 2019).

Unfortunately, assessing the interactive effects of these proven threats with climate change is difficult and cannot be achieved by Species Distribution Models alone. We therefore suggest that the range size reduction we demonstrate here may still represent a conservative prediction of the real risk these species will face in the 21st century.

4.7. Limitations

The use of Species Distribution Models to predict range shifts under a future climate has important limitations that need to be considered when interpreting modelling results. First of all, like every predictive study, our results do not represent an accurate forecast, but rather an estimate of how climatic changes potentially affect the future distribution of our target species. The inherent uncertainty of our modelling results stems from a cascade of RCP scenario uncertainty and limitations of model algorithms.

Crucially, trajectories of future greenhouse gas emissions described in the RCP scenarios are no exact description for the coming decades because there are intrinsic uncertainties in how technological advances or international policies will alter radiative forcing levels. Accordingly, the trajectories must be interpreted as an envelope of possible climatic futures (Freer et al., 2017). To account for these limitations, we incorporated multiple RCP scenarios in our analyses and communicate our results with awareness of climate uncertainty.

Another important caveat in this study is the selection of environmental predictors. They provide only an approximation and not a faultless definition of the realised niche of the modelled species. For instance, our environmental dataset does not account for substratum or bottom type, although these are relevant factors explaining distribution patterns of benthic molluscs at the small scale (Reiss et al., 2015). Indeed, many of our target species are associated with specific substrata, for example *Pinna nobilis* with the Mediterranean endemic seagrass *Posidonia oceanica*, or *Lithophaga lithophaga*, which is restricted to calcareous rocks. The absence or eradication of such habitat types would no doubt further accelerate predicted range size declines and extinctions. These relevant benthic predictor variables are presently available only at the local scale. Nevertheless, initiatives such as Bio-Oracle (Assis et al., 2018), MARSPEC (Sbrocco and Barber, 2013) and the Nippon Foundation (Seabed 2030 Project, 2021) are currently taking the first steps towards providing large-scale environmental seafloor predictors what will undoubtedly improve future SDM applications in the marine environment. The missing contribution of a proximal or distal environmental variable to describe a species' realised niche can lead to unsatisfactory model evaluations and hence to inaccurate predictive performance (Fabri-

Ruiz et al., 2019). With regard to our study, this might explain the low evaluation scores for *T. galea* and *Z. pyrum* as unreliable modelling inferences due to spatial bias in sampling records can largely be rejected.

Another major drawback of SDMs that lead to predictive uncertainties is the missing incorporation of biotic aspects such as dispersal range or migratory behaviour. This hampers the algorithms to capture the full ecological niche of the modelled species. For instance, in this study we only distinguished between the assumptions of a) lack of dispersal ability and b) unlimited dispersal ability either at full projection range or at the Mediterranean basin scale. The approach of modelling the future fate of species that assumes no dispersal at all clearly overestimates extinction risk. In contrast, expecting that species are able to migrate towards any suitable environmental conditions and with sufficient velocity to track their changing environmental niche is certainly over-optimistic for our target species. Adequate dispersion is very difficult to model and requires other modelling approaches. Nevertheless, by bracketing the extremes of dispersal abilities, our results do depict the range of the target species' potential vulnerability to climate change.

5. Conclusion

Global temperature will continue to rise for several centuries even if greenhouse gas emissions stabilize at present levels (IPCC, 2013). The so far observed responses of the Earth's biota are thus only a fraction of the imminent changes in global ecosystems. With accelerating climate change, we risk a substantial long-term loss of marine biodiversity (Harley et al., 2006). Because it seems unlikely that climate warming will be stopped or reversed within this century, it is important to predict the potential effects on marine species in order to adopt mitigation strategies. The species-specific distribution forecasts provided by our analysis show the severe vulnerability of endangered marine molluscs and highlight the Mediterranean Sea as a hotspot for the climate change threat to its biota. The timeliness of this study cannot be outlined enough, considering the recent evidence of major changes in marine and particularly Mediterranean ecosystems (Albano et al., 2021; Coll et al., 2010; Marbà et al., 2015). Here we projected solely the potential effects of future climatic changes on the target species, but many other stressors also exert enormous pressure on marine biota. This calls for multidisciplinary approaches and modelling strategies to unravel the linkages between the impacts of climate change and other threats and their ultimate ecological outcome. We focussed on predicting the probability of species-specific occurrence under future climatic conditions, but additional forecasts on biomass and abundance are crucial to fully grasp climate change effects on large-scale ecosystem processes. This understanding, together with additional research explicitly relevant to policy decisions, can help to design conservation strategies that will mitigate biodiversity decline in the Mediterranean Sea and at the scale of the world's oceans.

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Supplementary material

Appendix S1: Species distribution models (SDM)

In the following I provide R Codes (RStudio Team, 2020) that were used to obtain GBIF records, reformat occurrence and environmental data, build SDMs and compute further analyses on projected range size.

S1.1: Quality check

With the following codes I obtained and inspected species occurrence data from GBIF. OBIS records were added manually after checking them for duplicates with GBIF records. I used the *clean_coordinate* function only to get an overview on the quality of GBIF data. Detailed record cleaning was done manually. I further georeferenced records provided without coordinates using Google Earth and combined all occurrence records obtained from the different sources in a final dataset. The spatial distribution points were visualized and quality checked in QGIS.

R input

```
#####  
#Load GBIF records#  
#####  
#load libraries  
library(dplyr)  
library(ggplot2)  
library(rgbif)  
library(maps)  
library(CoordinateCleaner)  
  
#First, I downloaded and inspected data WITH Coordinates  
# add scientific species name in function  
coorddata <- occ_search(scientificName = "", limit = 5000, hasCoordinate = T)  
coorddata <- coorddata $data  
  
#select columns of interest  
coorddata <- coorddata %>%  
  dplyr::select(species, countryCode, country, stateProvince, locality, decimalLatitude,  
    decimalLongitude, year, month, day, habitat, depth, individualCount, organismQuantity, gbifID,  
    coordinateUncertaintyInMeters, samplingProtocol, basisOfRecord, institutionCode,  
    datasetName, specificEpithet, taxonomicStatus)  
  
# I then downloaded and inspected data WITHOUT Coordinates  
data <- occ_search(scientificName = "", limit = 5000, hasCoordinate = F)  
data <- data $data  
  
#select columns of interest  
data <- data %>%  
  dplyr::select(species, countryCode, country, stateProvince, locality, year,  
    month, day, habitat, depth, individualCount, organismQuantity, gbifID,  
    coordinateUncertaintyInMeters, samplingProtocol, basisOfRecord, institutionCode,  
    datasetName, specificEpithet, taxonomicStatus)
```



```

#I plotted data to get a rough overview. I additionally visualized the occurrence data in QGIS
wm <- borders("world", colour="gray50", fill="gray50")
ggplot()+ coord_fixed()+ wm +
geom_point(data = datpn, aes(x = decimalLongitude, y = decimalLatitude),
colour = "darkred", size = 0.5)+
theme_bw()
# I used the Coordinate cleaner to flag problematic records
flags <- clean_coordinates(x = data,
                           lon = "decimalLongitude",
                           lat = "decimalLatitude",
                           countries = "countryCode",
                           species = "species",
                           seas_scale = 50,
                           seas_ref = buffland,
                           tests = c())
#check problematic records
summary(flags)
dat_flag <- data[flags$.summary,]
plot(flags, lon = "decimalLongitude", lat = "decimalLatitude")

```

S1.2: Reformatting Species data

With the following codes I counted mismatches between the “raw” spatial occurrence points and an exemplary, unprocessed environmental layer. I then moved the coordinates to the closest cell containing environmental information using a maximum moving distance of 9000 m (corresponding to the size of one grid cell). Species data points located >9000 m from the closest environmental raster cell were visually checked in QGIS and either moved by hand or discarded from the dataset. I retraced the moving process for the single occurrence points by calculating Euclidean distances between the original and new (i.e. moved) coordinates. Finally, I aggregated multiple occurrence records in the same grid cell.

R input

```

#####
#Mismatches between occurrences and raster layer#
#####
#load libraries
library(readxl)
library(raster)
library(sdmprdictors)
library(rSDM)
library(stats)

#load occurrence data (spatial species record points)
occurrences <- read_excel("", na="NA", sheet=1)

#load exemplary raster layer
summer_SST <-load_layers("BO_sstmax")

#extract the value of the predictor from the raster file
summer_SST_v <- raster::extract(summer_SST, occurrences[,c("Longitude", "Latitude")])

#count how many occurrences have no environmental raster match

```

```

sum(is.na(summer_SST_v))

#extract coordinates and tell R that they are in WGS84
coord <- occurrences[,c("Longitude","Latitude")]
coordinates(coord) = ~Longitude + Latitude
crs(coord) <- CRS("+init=epsg:4326")

#move coordinates to the closest cell with valid value
#species data points located > 9000 m from the closest cell containing env. value have to be visually checked in QGIS #and
moved by hand
fixed <- points2nearestcell(locs=coord, ras=summer_SST,distance=9000, showmap=FALSE); beep(sound = 3, expr = NULL)
fixed_coord <- as.data.frame(fixed)

#add the fixed coordinates to the occurrence df
occurrences$Longitude_fixed <- fixed_coord$Longitude
occurrences$Latitude_fixed <- fixed_coord$Latitude

#####
#Euclidean distance between old and new coordinates#
#####
#subset old coordinates
old <- occurrences[,c("Longitude","Latitude")]
coordinates(old) = ~Longitude + Latitude
crs(old) <- CRS("+init=epsg:4326")

#subset new coordinates
new <- occurrences[,c("Longitude_fixed","Latitude_fixed")]
coordinates(new) = ~Longitude_fixed + Latitude_fixed
crs(new) <- CRS("+init=epsg:4326")

#calculate euclidean distance in meters
eucdist<-pointDistance(old, new, type='Euclidean')
euc_dist<-as.data.frame(eucdist)
occurrences <- cbind(occurrences, euc_dist)

#subset for moved values
sub<-occurrences[occurrences$eucdist>0,c(1:29)]
sub<-as.data.frame(sub)

```

R input

```

#####
#From occurrences to cells#
#####
#load libraries
library(readxl)
library(sp)

#load occurrence data (spatial species records with fixed coordinates)
occ_cells <- read_excel("", na="NA", sheet=1)

#define resolution 5 arcminutes
resolution <- 1/12
occ_cells$X_round <- round(occ_cells$Longitude/resolution)*resolution + resolution/2 #X is longitude (W-E)
occ_cells$Y_round <- round(occ_cells$Latitude/resolution)*resolution + resolution/2 #Y is latitude (S-N)
occ_cells$occ <- 1

```

```
#aggregate multiple occurrences in the same grid cell
cells <- aggregate(occ_cells$occ, by=list(X_round = occ_cells$X_round, Y_round = occ_cells$Y_round, Species =
occ_cells$Species), FUN=sum)
cells$ID <- seq.int(nrow(cells))

#aggregate per species to obtain a table with the number of occupied cells in the dataset
cells$occ <- 1
spp_occurrences <- aggregate(cells$occ, by=list(cells$Species), FUN="sum")
```

S1.3: Reformatting environmental data

With the following codes I created mask layers according to the species' individual bathymetric and geographic distribution range. For intertidal species I computed a buffer layer. For subtidal species and species occurring at the continental shelf and upper slope I built exclusion layers for cells <200 m and <1000 m, respectively. The bathymetric mask layers were applied on the selected environmental predictor layers. To obtain a biogeographic mask I drew polygons of the species' individual distribution range in QGIS and applied them as shapefile on the environmental layers.

R input

```
#####
## buffer layer for intertidal species##
#####
#load libraries
library(raster)
library(terra)
library(sdmprpredictors)

#loading one env layer
summer_SST_layer <- load_layers("BO_sstmax")

# setting extent limits
#Mediterranean limits
lon_min <- -20; lon_max <- 40; lat_min <- 24; lat_max <- 48; limits <- extent(lon_min, lon_max, lat_min, lat_max)
#West African limits
lon_min <- -26; lon_max <- 22; lat_min <- -36; lat_max <- 24; limits <- extent(lon_min, lon_max, lat_min, lat_max)
#Whole extent
lon_min <- -26; lon_max <- 38; lat_min <- -36; lat_max <- 48; limits <- extent(lon_min, lon_max, lat_min, lat_max)

#running the buffer loop
#step in lat-long degrees (size of the minimum cell in the loop); MUST BE >=1
step = 4

#ATTENTION! Choose the right ext0
#rund Atl-Med and W Africa separately
ext0 <- extent(lon_max - step, lon_max, lat_min, lat_min + step)
#entire study area
ext0 <- extent(lon_max - step, lon_max, lat_max - step, lat_max)

# crop the env layer on the extent
resized_shape <- crop(summer_SST_layer, ext0)
r1 <- is.na(resized_shape)
r1[r1==0] <- NA
```

```

#create a first cell to start the loop
buffered_layer_final <- terra::buffer(r1, width = 10000); beep(sound = 1, expr = NULL)
for (i in seq(lon_min, lon_max-(step*2), step)) {
  for (j in seq(lat_min+step, lat_max-step, step)) {
    resized_shape <- crop(summer_SST_layer, extent(i, i+step, j, j+step))
    if (length(resized_shape@data@values[is.na(resized_shape@data@values)])>0 &
        length(resized_shape@data@values[is.na(resized_shape@data@values)])<144*step^2)
    {r1 <- is.na(resized_shape)
     r1[r1==0] <- NA
     print(paste("i=", i, "j=", j))
     buffered_layer <- terra::buffer(r1, width = 10000);
     print(paste("portion lon_min =", i, " lon_max =", i+step, "; lat_min =", j, "lat_max =", j+step));
     buffered_layer_final <- raster::merge(buffered_layer_final, buffered_layer)
   } } }; beep(sound = 1, expr = NULL)

# saving the output of the buffer loop
#ATTENTION: choose the right save line!
save(buffered_layer_final, limits, file = "/buffered_layer_final_Med_Atl.Rdata")
save(buffered_layer_final, limits, file="/buffered_layer_final_W_Africa.Rdata")
save(buffered_layer_final, limits, file="/buffered_layer_final_Med_Atl_W_Africa.Rdata")

# final steps to deliver the buffer
buffered_layer_final[!is.na(buffered_layer_final)] <- 1

#apply the final buffer layer on selected environmental layers
r <- raster(nrow=2160, ncol=4320) #chlorophyll layers need to be resampled
tmax <- load_layers("BO21_tempmax_ss");tmax<-tmax* buffered_layer_final
trange<-load_layers("BO21_temprange_ss");trange<-trange* buffered_layer_final
salmin<-load_layers("BO21_salinitymin_ss");salmin<-salmin* buffered_layer_final
salrange<-load_layers("BO21_salinityrange_ss");salrange<-salrange* buffered_layer_final
chlorange<-load_layers("BO21_chlorange_ss");chlorange <- resample(chlorange, r, method='bilinear');chlorange<-
chlorange* buffered_layer_final
chloltmax<-load_layers("BO21_chloltmax_ss");chloltmax <- resample(chloltmax, r, method='bilinear');chloltmax<-
chloltmax* buffered_layer_final

#read in shapefile to build a geographic mask layer
#shapefiles were computed in QGIS for each species separately according to the species specific distribution ranges
ext<-readOGR("")

#mask env layer with biogeographic exclusion layer
tmax<-mask(tmax, ext)
trange<-mask(trange, ext)
salmin<-mask(salmin, ext)
salrange<-mask(salrange, ext)
chloltmax<-mask(chloltmax, ext)
chlorange<-mask(chlorange, ext)

#save environmental layers as tif file on hard disk
writeRaster(tmax,file="")

```

R input

```

#####
##Depth exclusion layers for subtidal and continental shelf and upper slope species##
#####
#load libraries
library(sdmprredictors)
library(rgdal)
library(raster)

```

```

#load bathymetry layer containing information about depth for each cell
bathymin<- load_layers("BO_bathymin")

#exclude depth (subtidal species -200 m, continental shelf and upper slope species -1000 m)
depth<- bathymin>-1000 # or -200

#set cells =0 to NA and all other cells to 1
depth[depth == 0] <- NA
depth[!is.na(depth)] <- 1

#read in shapefile to build a geographic mask layer
#shapefiles were build in QGIS for each species seperately according to the species specific distribution ranges
ext<-readOGR("")

#mask depth layer with biogeographic exclusion layer
mask<-mask(depth, ext)

#load environmental layers of interest and assign them with exclusion layer
r <- raster(nrow=2160, ncol=4320) #chlorophyll layers need to be resampled
tmax <- load_layers("BO21_tempmax_ss");tmax<-tmax*mask
trange<-load_layers("BO21_temprange_ss");trange<-trange*mask
salmin<-load_layers("BO21_salinitymin_ss");salmin<-salmin*mask
salrange<-load_layers("BO21_salinityrange_ss");salrange<-salrange*mask
chlorange<-load_layers("BO21_chlorange_ss");chlorange <- resample(chlorange, r, method='bilinear');chlorange<-
chlorange*mask
chloltmax<-load_layers("BO21_chloltmax_ss");chloltmax <- resample(chloltmax, r, method='bilinear');chloltmax<-
chloltmax*mask

#save environmental layers as tif file on hard disk
writeRaster(tmax,file="")

```

S1.4: Final modelling input data

In this section I checked for raster mismatches between the aggregated occurrence cells and the processed environmental layers. Occurrence cells without environmental raster match were moved again by the *points2nearestcell* function (max. 9000 m). Distances greater than 9000 m were visually checked in QGIS. The processed predictor layers were checked for correlations for each species separately using Pearson correlation test (threshold >0.7, cf. Dormann et al., 2013).

R input

```

#####
## Cell mismatches##
#####
#load libraries
library(readxl)
library(dplyr)
library(rSDM)

#load aggregated species cell data
cells <- read_excel("", na="NA", sheet=1)

#load reformatted environmental layer from hard drive
tmax<- stack("/tmax.tiff")

```

```

#extract values
ext <- raster::extract(tmax, cells[,c("Longitude", "Latitude")])
cells <- cbind(cells,ext)

#check for NAs
sum(is.na(ext))

#extract coordinates and tell R that they are in WGS84
coord <- cells[,c("Longitude", "Latitude")]
coordinates(coord) = ~Longitude + Latitude
crs(coord) <- CRS("+init=epsg:4326")

#move coordinates to nearest cell containing valid values
#species cells located >9000 m from the closest cell with valid env. value have to be visually checked in QGIS and moved by hand
fixed <- points2nearestcell(locs=coord,ras=tmax,distance=9000, howmap=FALSE); beep(sound = 3, expr = NULL)
fixed_coord <- as.data.frame(fixed)

#add the fixed coordinates to the occurrence df
cells$Longitude_fixed <- fixed_coord$X_round
cells$Latitude_fixed <- fixed_coord$Y_round

```

R input

```

#####
##Predictor Correlation##
#####
#load libraries
library(readxl)
library(raster)
library(rSDM)
library(corrplot)

#stack processed environmental layers for species
myExpl<- stack("")

#crop it to extent for species of interest
e <- as(extent(), "SpatialPolygons")
crs(e) <- crs(myExpl)
myExplcrop <- crop(myExpl, e)
myExplcrop<-stack(myExplcrop)

#load the species data (cells file)
cells <- read_excel("", na="NA", sheet=1)

#subset species (here as an example P. ferruginea)
ss<-c("Patella ferruginea")

species<-dplyr::filter(cells, Species%in%ss)

#get coordinates
myRespCoord_ss <- species[,c("Longitude", "Latitude")]

#extract climate data from raster stack
pred <- raster::extract(myExplcrop,myRespCoord_ss)

#check length of input and outcome
nrow(pred)

```

```

nrow(species)

#combine species and climate data
finaldata <- cbind(species,pred)

#check for cells without value in raster stack
sum(is.na(finaldata$tmax))

#compute a correlation matrix and write it on hard disk
cor = round(cor(finaldata[7:12],use="complete.obs"),2)

write.table(cor,"",dec = ".", row.names = TRUE,col.names = TRUE,quote = FALSE,sep=";")

#visualize correlations using corrplot()
col <- colorRampPalette(c("black", "grey", "red"))
corrplot(cor, method="number",col=col(50),tl.col = "black")

```

S1.5: Species Distribution Modelling using Biomod2

The following codes show the final modelling process. To project current and future distribution of the 15 target species, I generated ensemble species distribution models (SDMs) using the biomod2 modelling framework (Thuiller et al., 2009). For calibration and settings I mainly referred to Guisan et al. (2017) and to the expertise of my supervisors S. Dullinger, J. Wessely and P.G. Albano.

Biomod2 relates presence-absence data of the modelled species to associated environmental information at the same spatial points using statistical species distribution models. The single models are further combined to an ensemble forecast. Data are split in two sub-datasets. One to calibrate the selected models and one to evaluate them using different evaluation measures like the True Skill Statistics and the area under the curve (AUC). The data splitting procedure can be repeated several times. Model projections exceeding a determined quality threshold are combined in an ensemble model. The calibrated and evaluated models are further extrapolated in space and time.

I ran the algorithms for each of the 15 target species separately. In the first section, environmental and occurrence data are imported and defined as input data. In *Biomod_FormattingData* I added 10,000 pseudo-absence points with random sampling in five repetition runs. In the *Biomod_Modeling* function I chose GLM,GAM,GBM and RF as algorithms and evaluated the runs with 3-fold cross-validation in a 80/20 Data splitting performance. In *Biomod_EnsembleModelling* I excluded all models having a TSS score lower than 0.6. Once the models were calibrated and evaluated, I projected the current and future distribution under RCP2.6, RCP4.5,RCP6.0 and RCP8.5 for the years 2050 and 2100 of the 15 target species. Binary predictions were computed based on the threshold that maximises TSS evaluation scores. As modelling output I received the probability of occurrence of a species in a certain cell and the corresponding binary prediction.

```
#####  
##Species distribution modelling##  
#####  
#load libraries  
library(readxl)  
library(dplyr)  
library(raster)  
library(biomod2)  
library(beepr)  
  
#####  
##Load data##  
#####  
#Stack uncorrelated environmental layers (tiff files)  
myExpl<- stack("")  
  
#rename the layers  
names(myExpl) <- paste("predictor",1:3,sep="")  
#load the species data (aggregated cells)  
cells <- read_excel("", na="NA", sheet=1)  
  
#subset the species of interest (here P.ferruginea)  
Patella.ferruginea<-dplyr::filter(cells, Species == "Patella ferruginea")  
  
#get the coordinates  
myRespCoord <- Patella.ferruginea[,c("Longitude", "Latitude")]  
#extract climate data from stack  
pred <- raster::extract(myExpl,myRespCoord)  
head(pred)  
  
#combine species data and climate data and check for cells without valid value  
finaldata <- cbind(Patella.ferruginea,pred)  
sum(is.na(finaldata$predictor1))  
  
#reduce data  
dataUse <- finaldata[,c(1,5:9)]  
head(dataUse)  
  
#####  
##Define Modelling input##  
#####  
#extract all data to use from dataUse:  
#the presence/absences data for the species (must be a numeric 0/1 vector)  
dataUse$P.ferruginea <- 1  
  
#Response name for models (name of species)  
myRespName<-"P.ferruginea"  
myResp<-as.numeric(dataUse[, "P.ferruginea"])  
  
#the XY coordinates of species data (must be a 2 columns dataframe or matrix)  
myRespCoord <- dataUse[,c("Longitude", "Latitude")]  
str(myRespCoord)
```



```
#####
##Format input data##
#####

myBiomodData <- biomod2::BIOMOD_FormatingData(resp.var= myResp,
                                              expl.var=myExpl,
                                              resp.xy= myRespCoord,
                                              resp.name=myRespName,
                                              PA.nb.rep=5,
                                              PA.nb.absences =10000,
                                              PA.strategy ="random")

#print properties of formatted data, and plot formatted data
myBiomodData
x11()
plot(myBiomodData)

#####
##Define modelling options##
#####

#define models
modelset= c("GLM","GAM","GBM","RF")

#define options: here I used default settings
myBiomodOption <- biomod2::BIOMOD_ModelingOptions()

#####
##Model Calibration##
#####

myBiomodModelOut <- biomod2::BIOMOD_Modeling(myBiomodData,
                                              models=modelset ,
                                              models.options=myBiomodOption,
                                              NbRunEval= 3,
                                              DataSplit= 80,
                                              Prevalence= 0.5,
                                              VarImport = 3,
                                              models.eval.meth = c("TSS", "ROC", "KAPPA"),
                                              SaveObj= F,
                                              rescal.all.models= T,
                                              do.full.models= T)

#####
##Model evaluation and variable importance##
#####

#model evaluation
evaluation <- biomod2::get_evaluations(myBiomodModelOut)

write.table(evaluation,"",dec = ".", row.names = TRUE,col.names = TRUE,quote = FALSE,sep=";")

#visualizing model evaluations
models_scores_graph(myBiomodModelOut, by = "models" ,
                    metrics = c("ROC","TSS","KAPPA"), xlim = c(-1,1), ylim = c(-1,1))

models_scores_graph(myBiomodModelOut, by = "data_set" ,
                    metrics = c("ROC","TSS","KAPPA"), xlim = c(-1,1), ylim = c(-1,1))

models_scores_graph(myBiomodModelOut, by = "cv_run" ,
```

```

metrics = c("ROC", "TSS", "KAPPA"), xlim = c(-1,1), ylim = c(-1,1))

# variable importance
variable_imp <- get_variables_importance(myBiomodModelOut)

write.table(variable_imp, "", dec = ".", row.names = TRUE, col.names = TRUE, quote = FALSE, sep = ";")

# Plot response curves for visualizing species modelled response to a given variable
for(model in modelset)
{myModels <- biomod2::BIOMOD_LoadModels(myBiomodModelOut, models=model)
  x11()
  myRespPlot2D <- response.plot2(models = myModels,
    Data= get_formal_data(myBiomodModelOut,'expl.var'),
    show.variables= get_formal_data(myBiomodModelOut,'expl.var.names'),
    do.bivariate= FALSE, fixed.var.metric ='median',
    legend = TRUE, col = c('blue','red','green','black','pink'),
    data_species= get_formal_data(myBiomodModelOut,'resp.var'))}

#####
##Ensemble Models##
#####

myBiomodEM <- biomod2::BIOMOD_EnsembleModeling(modeling.output = myBiomodModelOut,
  chosen.models = "all",
  em.by = "all",
  eval.metric= c("TSS"),
  eval.metric.quality.threshold = c(0.6),
  prob.mean= F,
  prob.cv = F,
  prob.ci= F,
  prob.ci.alpha= 0.05,
  prob.median= F,
  committee.averaging= F,
  prob.mean.weight = T,
  prob.mean.weight.decay= "proportional")

## get ensemble models evaluation
evaluation_em <- get_evaluations(myBiomodEM)
write.table(evaluation_em, "", dec = ".", row.names = TRUE, col.names = TRUE, quote = FALSE, sep = ";")

#####
##Projections on current climatic conditions##
#####

#single models
projection <- biomod2::BIOMOD_Projection(modeling.output = myBiomodModelOut,
  new.env= myExpl,
  proj.name = "current",
  selected.models= "all",
  binary.meth= "TSS",
  compress= "xz",
  keep.in.memory= FALSE,
  on_0_1000 = TRUE,
  build.clamping.mask= F)

# Ensemble Projections
ensemble <- BIOMOD_EnsembleForecasting(projection.output = projection,
  EM.output = myBiomodEM,
  output.format= ".grd",
  binary.meth= "TSS")

```

```
#####
##Projections on future climatic conditions##
#####
##RCP 26 Year 2050

#stack future data RCP26 year 2050 (tiff files)
myExplFuture26<-stack("")

#rename the layers names need to be the same as for current projections
names(myExplFuture26) <- paste("predictor",1:3,sep="")

#first project the single models
proj_future26 <- BIOMOD_Projection(modeling.output = myBiomodModelOut,
                                   new.env= myExplFuture26,
                                   proj.name= "RCP262050",
                                   selected.models = "all",
                                   binary.meth= "TSS",
                                   clamping.mask= F)

#now project the ensemble models
ensemble_future26 <- BIOMOD_EnsembleForecasting(projection.output = proj_future26,
                                                EM.output= myBiomodEM,
                                                output.format= ".grd",
                                                binary.meth= "TSS",
                                                clamping.mask= F)

#first project the single models
proj_future26_100 <- BIOMOD_Projection(modeling.output = myBiomodModelOut,
                                       new.env = myExplFuture26_100,
                                       proj.name= "RCP262100",
                                       selected.models = "all",
                                       binary.meth= "TSS",
                                       clamping.mask= F)

#now project/forecast the ensemble models
ensemble_future26_100 <- BIOMOD_EnsembleForecasting(projection.output = proj_future26_100,
                                                    EM.output= myBiomodEM,
                                                    output.format= ".grd",
                                                    binary.meth= "TSS",
                                                    clamping.mask= F)

##RCP 45 Year 2050:
# stack future data RCP45 year 2050 (tiff files)
myExplFuture<-stack("")

# rename the layers names need to be the same as for current projections
names(myExplFuture) <- paste("predictor",1:3,sep="")

# first project the single models
proj_future <- BIOMOD_Projection(modeling.output = myBiomodModelOut,
                                 new.env = myExplFuture, #climatic conditions under RCP45 for the year 2050
                                 proj.name= "RCP452050",
                                 selected.models = "all",
                                 binary.meth= "TSS",
                                 clamping.mask= F)
```

```

# now project the ensemble models
ensemble_future <- BIOMOD_EnsembleForecasting(projection.output = proj_future,
      EM.output= myBiomodEM,
      output.format= ".grd",
      binary.meth= "TSS",
      clamping.mask = F)

###RCP 45 Year 2100:
#stack future data RCP45 year 2100 (tiff files)
myExplFuture_100<-stack("")

#rename the layers
names(myExplFuture_100) <- paste("predictor",1:3,sep="")

#first project the single models
proj_future_100 <- BIOMOD_Projection(modeling.output = myBiomodModelOut,
      new.env= myExplFuture_100,
      proj.name= "RCP452100",
      selected.models = "all",
      binary.meth= "TSS",
      clamping.mask= F)

#now project the ensemble models
ensemble_future_100 <- BIOMOD_EnsembleForecasting(projection.output = proj_future_100,
      EM.output = myBiomodEM,
      output.format= ".grd",
      binary.meth= "TSS",
      clamping.mask= F)

###RCP 60 Year 2050:
#stack future data RCP60 year 2050 (tiff files)
myExplFuture60<-stack("")

#rename the layers names need to be the same as for current projections!!
names(myExplFuture60) <- paste("predictor",1:3,sep="")

#first project the single models
proj_future60 <- BIOMOD_Projection(modeling.output = myBiomodModelOut,
      new.env= myExplFuture60,
      proj.name= "RCP602050",
      selected.models = "all",
      binary.meth = "TSS",
      clamping.mask= F)

#now project the ensemble models
ensemble_future60 <- BIOMOD_EnsembleForecasting(projection.output = proj_future60,
      EM.output= myBiomodEM,
      output.format = ".grd",
      binary.meth = "TSS",
      clamping.mask= F)

###RCP 60 Year 2100:
# stacking future data RCP60 year 2100 (tiff files)
myExplFuture60_100<-stack("")

```

```

# rename the layers
names(myExplFuture60_100) <- paste("predictor",1:3,sep="")
# first project the single models
proj_future60_100 <- BIOMOD_Projection(modeling.output = myBiomodModelOut,
                                     new.env= myExplFuture60_100,
                                     proj.name= "RCP602100",
                                     selected.models = "all",
                                     binary.meth = "TSS",
                                     clamping.mask= F)

# now project the ensemble model
ensemble_future60_100 <- BIOMOD_EnsembleForecasting(projection.output = proj_future60_100,
                                                    EM.output= myBiomodEM,
                                                    output.format= ".grd",
                                                    binary.meth= "TSS",
                                                    clamping.mask= F)

##RCP 85 Year 2050:
#stack future data RCP85 year 2050 (tiff files)
myExplFuture85<-stack("")

#rename the layers names need to be the same as for current projections!!
names(myExplFuture85) <- paste("predictor",1:3,sep="")

#first project the single models
proj_future85 <- BIOMOD_Projection(modeling.output = myBiomodModelOut,
                                   new.env= myExplFuture85,
                                   proj.name= "RCP852050",
                                   selected.models = "all",
                                   binary.meth= "TSS",
                                   clamping.mask= F)

#now project the ensemble models
ensemble_future85 <- BIOMOD_EnsembleForecasting(projection.output = proj_future85,
                                                EM.output= myBiomodEM,
                                                output.format= ".grd",
                                                binary.meth= "TSS",
                                                clamping.mask= F)

##RCP 85 Year 2100:
#stacking future data RCP85 year 2100 (tiff files)
myExplFuture85_100<-stack("")

#rename the layers
names(myExplFuture85_100) <- paste("predictor",1:3,sep="")

#first project the single models
proj_future85_100 <- BIOMOD_Projection(modeling.output = myBiomodModelOut,
                                       new.env= myExplFuture85_100,
                                       proj.name = "RCP852100",
                                       selected.models = "all",
                                       binary.meth= "TSS",
                                       clamping.mask= F)

```

```
#now project the ensemble models
ensemble_future85_100 <- BIOMOD_EnsembleForecasting(projection.output = proj_future85_100,
                                                    EM.output= myBiomodEM,
                                                    output.format= ".grd",
                                                    binary.meth= "TSS",
                                                    clamping.mask= F)
```

S1.6: Further analyses

I then calculated relative and proportional projected range size. All range size calculations are based on binary predictions (presence/absence). First, I computed range size analyses at full distribution range. I further applied a biogeographic mask of the Mediterranean Sea on the binary projections and computed again range size analyses at the basin scale. To compare range changes in areas nearshore to offshore, I built bathymetric exclusion layers.

R input

```
#load libraries
library(raster)
library(biomod2)

#####
##Calculations on relative and proportional projected Range size##
#####
#load current and future binary projections
currentPred<- raster::stack("")
future2650 <- raster::stack("")
future26100 <- raster::stack("")
future45100 <- raster::stack("")
future4550 <- raster::stack("")
future60100 <- raster::stack("")
future6050 <- raster::stack("")
future8550 <- raster::stack("")
future85100 <- raster::stack("")

# call the Range size function for each scenario
# the function calculates the proportion and relative number of pixels lost, gained and stable under current and future
climatic conditions
###RCP26 2050
rs2650 <- biomod2::BIOMOD_RangeSize(CurrentPred=currentPred,FutureProj=future2650);
rs2650<-rs2650$Compt.By.Models

###RCP26 2100
rs26100 <- biomod2::BIOMOD_RangeSize(CurrentPred=currentPred,FutureProj=future26100);
rs26100<-rs26100$Compt.By.Models

###RCP45 2050
rs4550 <- biomod2::BIOMOD_RangeSize(CurrentPred=currentPred,FutureProj=future4550);
rs4550<-rs4550$Compt.By.Models

###RCP45 2100
rs45100 <- biomod2::BIOMOD_RangeSize(CurrentPred=currentPred,FutureProj=future45100);
rs45100<-rs45100$Compt.By.Models
```

```
##RCP60 2050
rs6050 <- biomod2::BIOMOD_RangeSize(CurrentPred=currentPred,FutureProj=future6050);
rs6050<-rs6050$Compt.By.Models

##RCP60 2100
rs60100 <- biomod2::BIOMOD_RangeSize(CurrentPred=currentPred,FutureProj=future60100);
rs60100<-rs60100$Compt.By.Models

##RCP85 2050
rs8550 <- biomod2::BIOMOD_RangeSize(CurrentPred=currentPred,FutureProj=future8550);
rs8550<-rs8550$Compt.By.Models

##RCP85 2100
rs85100 <- biomod2::BIOMOD_RangeSize(CurrentPred=currentPred,FutureProj=future85100);
rs85100<-rs85100$Compt.By.Models

# bind calculations together and save them on hard disk
RangeSize<-rbind(rs2650,rs26100,rs4550,rs45100,rs6050,rs60100,rs8550,rs85100)

write.table(Rangesize,"",dec = ".", row.names = TRUE,col.names = TRUE,quote = FALSE,sep=";")
```

R input

```
#####
##Exclusion layer for the Mediterranean Sea and range changes at the basin scale##
#####
#load libraries
library(raster)
library(rgdal)
library(biomod2)

#load binaries
cur<-stack("")
fut26_50<-stack("")
fut26_100<-stack("")
fut45_50<-stack("")
fut45_100<-stack("")
fut60_50<-stack("")
fut60_100<-stack("")
fut85_50<-stack("")
fut85_100<-stack("")

#load shapefile of the Mediterranean Sea, created in QGIS
mask<-readOGR("")

#mask the binary maps with shapefile and apply BiomodRangeSize function
maskcur<-mask(cur,mask,inverse=FALSE)

mask2650<-mask(fut26_50,mask,inverse=FALSE);
rs2650<-biomod2::BIOMOD_RangeSize(maskcur,mask2650);rs2650<-rs2650$Compt.By.Models

mask26100<-mask(fut26_100,mask,inverse=FALSE);
rs26100<-biomod2::BIOMOD_RangeSize(maskcur,mask26;rs26100<-rs26100$Compt.By.Models

mask4550<-mask(fut45_50,mask,inverse=FALSE);
rs4550<-biomod2::BIOMOD_RangeSize(maskcur,mask4550;rs4550<-rs4550$Compt.By.Models

mask45100<-mask(fut45_100,mask,inverse=FALSE);
```

```

rs45100<-biomod2::BIOMOD_RangeSize(maskcur,mask45100;rs45100<-rs45100$Compt.By.Models

mask6050<-mask(fut60_50,mask,inverse=FALSE);
rs6050<-biomod2::BIOMOD_RangeSize(maskcur,mask6050;rs6050<-rs6050$Compt.By.Models

mask60100<-mask(fut60_100,mask,inverse=FALSE);
rs60100<-biomod2::BIOMOD_RangeSize(maskcur,mask60100;rs60100<-rs60100$Compt.By.Models

mask8550<-mask(fut85_50,mask,inverse=FALSE);
rs8550<-biomod2::BIOMOD_RangeSize(maskcur,mask8550;rs8550<-rs8550$Compt.By.Models

mask85100<-mask(fut85_100,mask,inverse=FALSE);
rs85100<-biomod2::BIOMOD_RangeSize(maskcur,mask85100;rs85100<-rs85100$Compt.By.Models

## bind calculations together and save them on hard disk
MedCount<-rbind(rs2650,rs26100,rs4550, rs45100,rs6050,rs60100,rs8550,rs85100)

write.table(MedCount,"",dec = ".", row.names = TRUE,col.names = TRUE,quote = FALSE,sep=";")

```

R input

```

#####
##Bathymetric exclusion layer and vertical range changes##
#####
#load libraries
library(raster)
library(rgdal)
library(biomod2)
library(sdmpredictors)

# load binary predictions
cur<-stack("")
fut26_50<-stack("")
fut26_100<-stack("")
fut45_50<-stack("")
fut45_100<-stack("")
fut60_50<-stack("")
fut60_100<-stack("")
fut85_50<-stack("")
fut85_100<-stack("")

#load bathymetry layer (Bio-Oracle)
bathymin<- load_layers("BO_bathymin")

#build bathymetry mask: excluding cells deeper than -50 m
mask<- bathymin>-50
mask[mask == 0] <- NA
mask[!is.na(mask)] <- 1

#crop bathymetry mask to extend of probability layers
mask<-crop(mask,extent(cur))

#mask the binary maps with depth 0 to -50m and calculate Rangesize
maskcur<-mask(cur,mask,inverse=FALSE);maskcur<-stack(maskcur)

mask2650<-mask(fut26_50,mask,inverse=FALSE);mask2650<-stack(mask2650);
rs <- biomod2::BIOMOD_RangeSize(maskcur,mask2650);rs<-rs$Compt.By.Models

mask26100<-mask(fut26_100,mask,inverse=FALSE);mask26100<-stack(mask26100);
rs1 <- biomod2::BIOMOD_RangeSize(maskcur,mask26100);rs1<-rs1$Compt.By.Models

```



```

mask4550<-mask(fut45_50,mask,inverse=FALSE);mask4550<-stack(mask4550);
rs2 <- biomod2::BIOMOD_RangeSize(maskcur,mask4550);rs2<-rs2$Compt.By.Models

mask45100<-mask(fut45_100,mask,inverse=FALSE);mask45100<-stack(mask45100);
rs3 <- biomod2::BIOMOD_RangeSize(maskcur,mask45100);rs3<-rs3$Compt.By.Models

mask6050<-mask(fut60_50,mask,inverse=FALSE);mask6050<-stack(mask6050);
rs4 <- biomod2::BIOMOD_RangeSize(maskcur,mask6050);rs4<-rs4$Compt.By.Models

mask60100<-mask(fut60_100,mask,inverse=FALSE);mask60100<-stack(mask60100);
rs5 <- biomod2::BIOMOD_RangeSize(maskcur,mask60100);rs5<-rs5$Compt.By.Models

mask8550<-mask(fut85_50,mask,inverse=FALSE);mask8550<-stack(mask8550);
rs6 <- biomod2::BIOMOD_RangeSize(maskcur,mask8550);rs6<-rs6$Compt.By.Models

mask85100<-mask(fut85_100,mask,inverse=FALSE);mask85100<-stack(mask85100);
rs7 <- biomod2::BIOMOD_RangeSize(maskcur,mask85100);rs7<-rs7$Compt.By.Models

# bind calculations together and save them on hard disk
bathyshore<-rbind(rs,rs1,rs2,rs3,rs4,rs5,rs6,rs7)

write.table(bathyshore,"",dec = ".", row.names = TRUE,col.names = TRUE,quote = FALSE,sep=";")

#now the same again for cells deeper than 50 m --> clear environment before!
# load binary predictions
cur<-stack("")
fut26_50<-stack("")
fut26_100<-stack("")
fut45_50<-stack("")
fut45_100<-stack("")
fut60_50<-stack("")
fut60_100<-stack("")
fut85_50<-stack("")
fut85_100<-stack("")

#load bathymetry layer
bathymin<- load_layers("BO_bathymin")

# exclude cells shallower than 50 m
mask<- bathymin<(-50)
mask[mask == 0] <- NA
mask[!is.na(mask)] <- 1

#crop bathy mask to extend of probability layers
mask<-crop(mask,extent(cur))

## mask the binary maps with depth exclusion layer < (-50 m)
maskcur<-mask(cur,mask,inverse=FALSE);maskcur<-stack(maskcur)
writeRaster(maskcur,file="C:/Users/lotta/OneDrive/Desktop/maskbathy.tiff")

mask2650<-mask(fut26_50,mask,inverse=FALSE);mask2650<-stack(mask2650);
rs <- biomod2::BIOMOD_RangeSize(maskcur,mask2650);rs<-rs$Compt.By.Models

mask26100<-mask(fut26_100,mask,inverse=FALSE);mask26100<-stack(mask26100);
rs1 <- biomod2::BIOMOD_RangeSize(maskcur,mask26100);rs1<-rs1$Compt.By.Models

mask4550<-mask(fut45_50,mask,inverse=FALSE);mask4550<-stack(mask4550);
rs2 <- biomod2::BIOMOD_RangeSize(maskcur,mask4550);rs2<-rs2$Compt.By.Models

```

```

mask45100<-mask(fut45_100,mask,inverse=FALSE);mask45100<-stack(mask45100);
rs3 <- biomod2::BIOMOD_RangeSize(maskcur,mask45100);rs3<-rs3$Compt.By.Models

mask6050<-mask(fut60_50,mask,inverse=FALSE);mask6050<-stack(mask6050);
rs4 <- biomod2::BIOMOD_RangeSize(maskcur,mask6050);rs4<-rs4$Compt.By.Models

mask60100<-mask(fut60_100,mask,inverse=FALSE);mask60100<-stack(mask60100);
rs5 <- biomod2::BIOMOD_RangeSize(maskcur,mask60100);rs5<-rs5$Compt.By.Models

mask8550<-mask(fut85_50,mask,inverse=FALSE);mask8550<-stack(mask8550);
rs6 <- biomod2::BIOMOD_RangeSize(maskcur,mask8550);rs6<-rs6$Compt.By.Models

mask85100<-mask(fut85_100,mask,inverse=FALSE);mask85100<-stack(mask85100);
rs7 <- biomod2::BIOMOD_RangeSize(maskcur,mask85100);rs7<-rs7$Compt.By.Models

## bind calculations together and save them on hard disk
bathyoffshore<-rbind(rs,rs1,rs2,rs3,rs4,rs5,rs6,rs7)

write.table(bathyoffshore,"",dec = ".", row.names = TRUE,col.names = TRUE,quote = FALSE,sep=";")

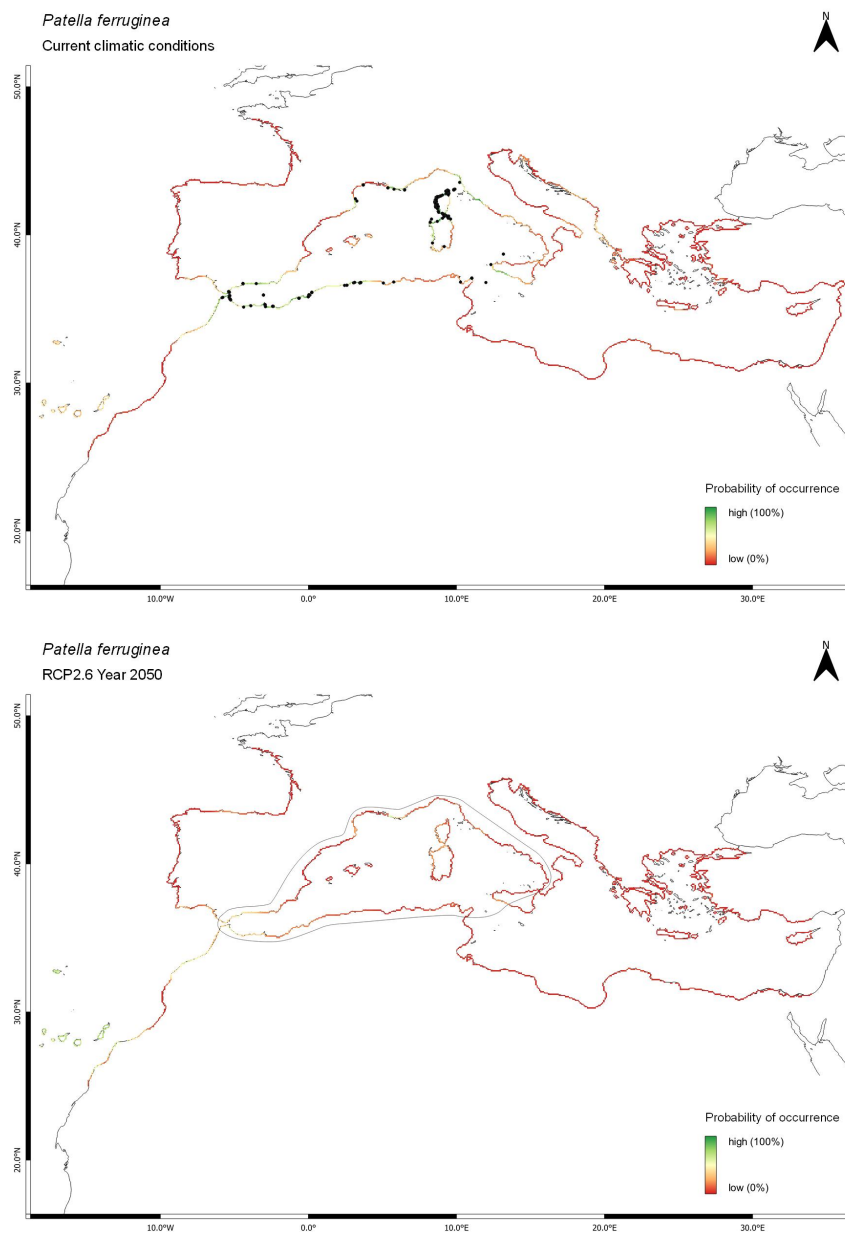
```

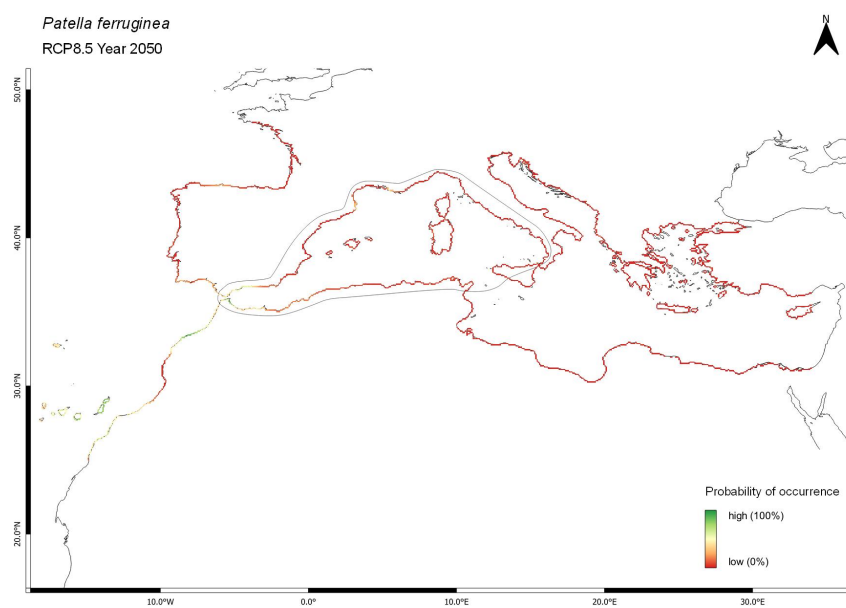
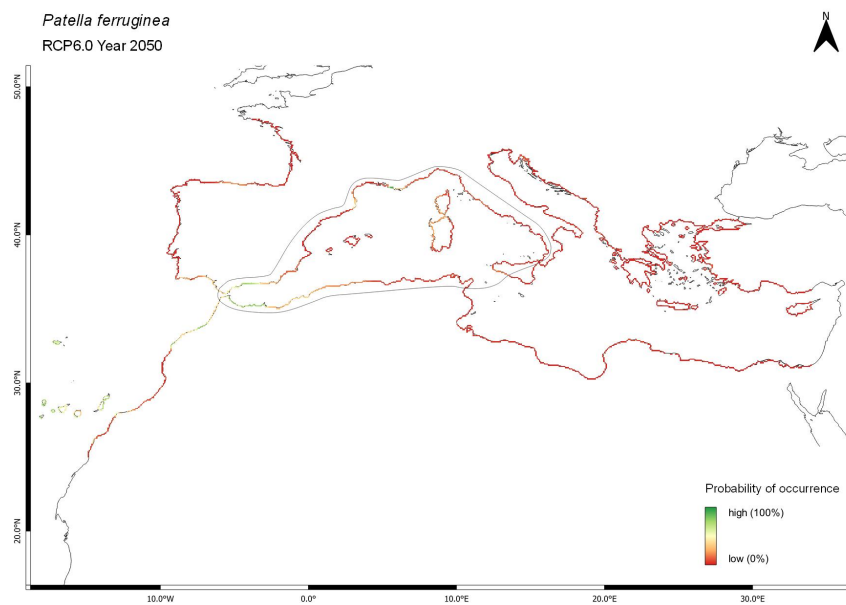
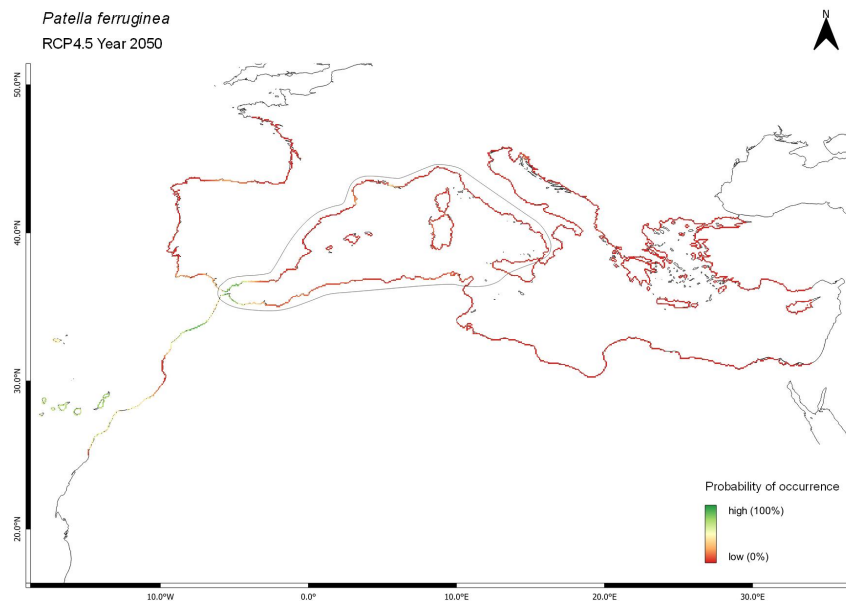
Appendix S2: Species Distribution Maps

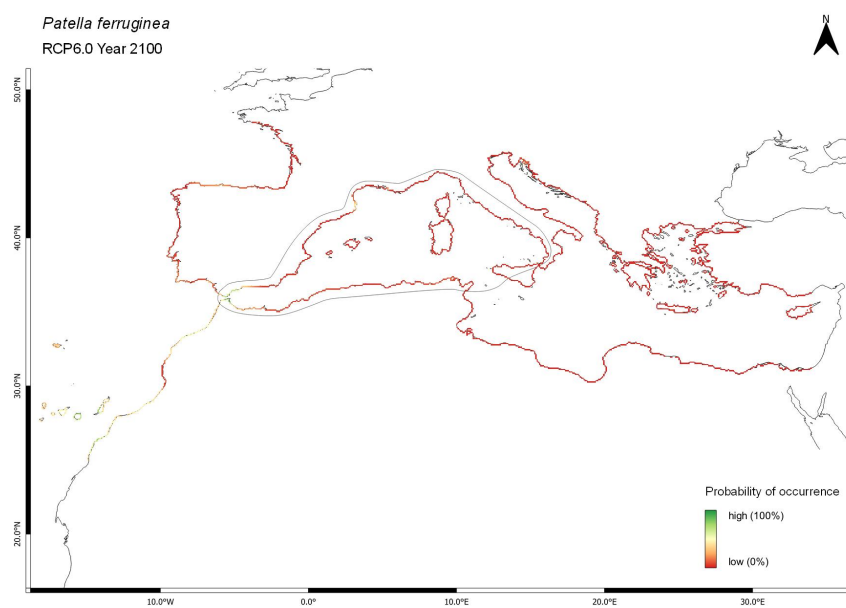
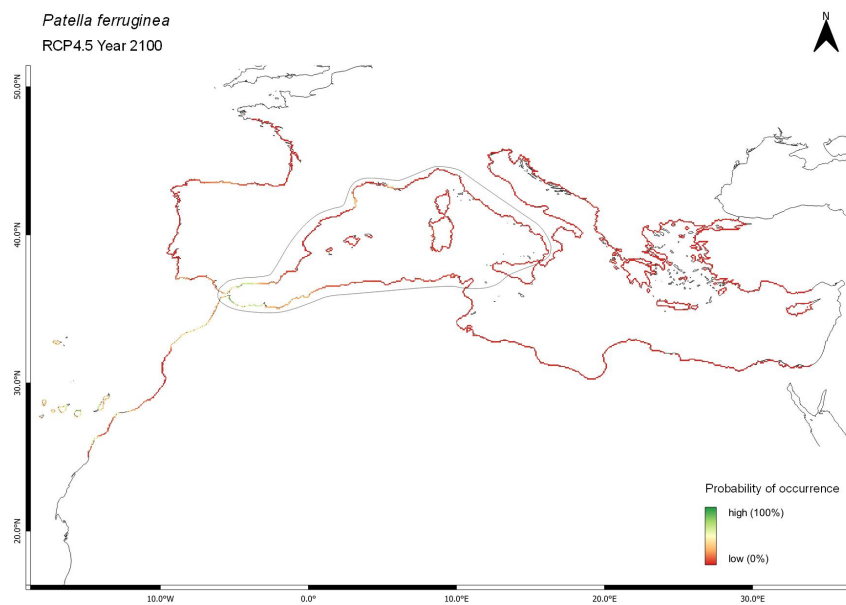
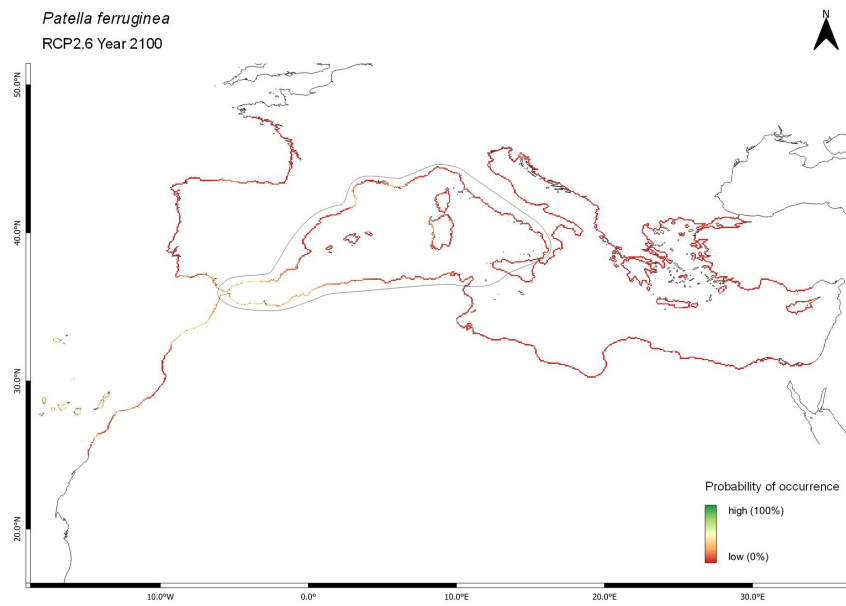
In this part I provide probability maps for all species under the four RCP scenarios explored for the years 2050 and 2100. For each species the first map (modelled distribution under current climatic conditions) shows the observed distribution points.

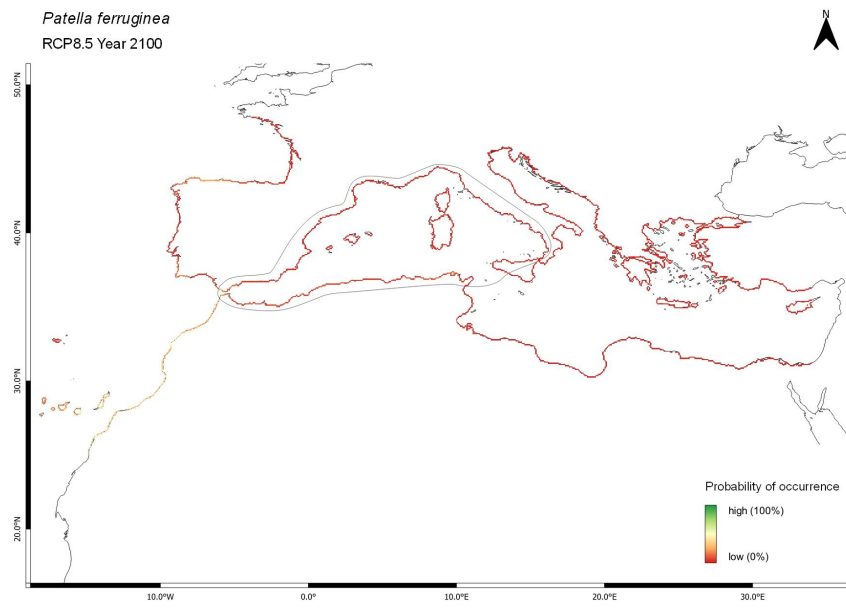
S2.1 Mediterranean endemic species

Patella ferruginea:

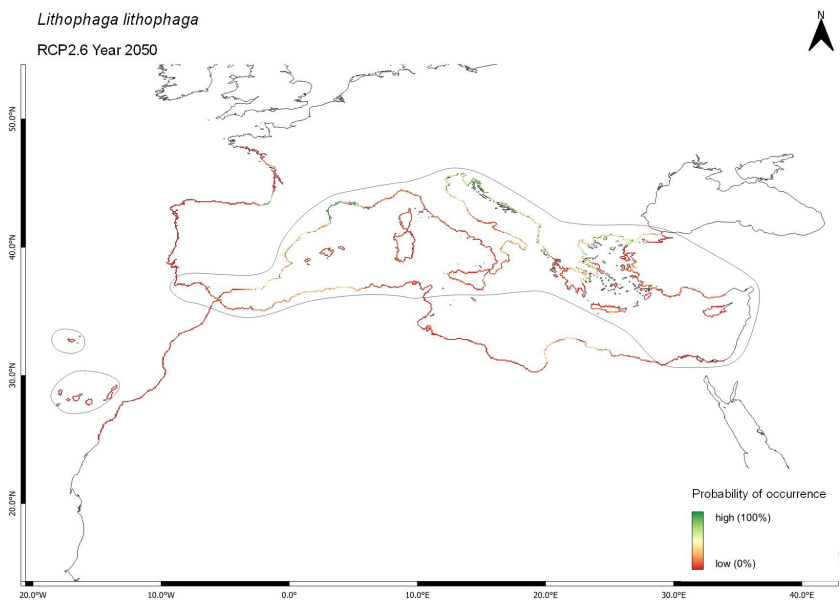
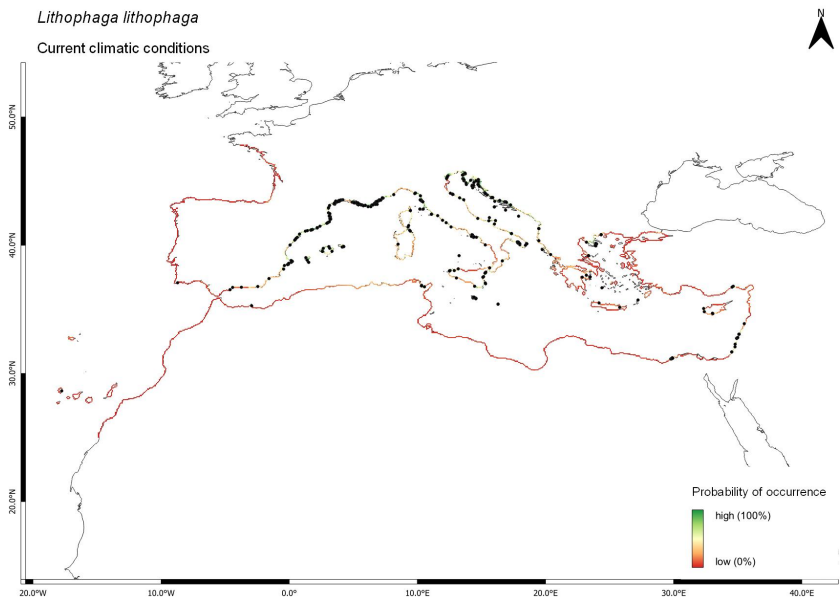






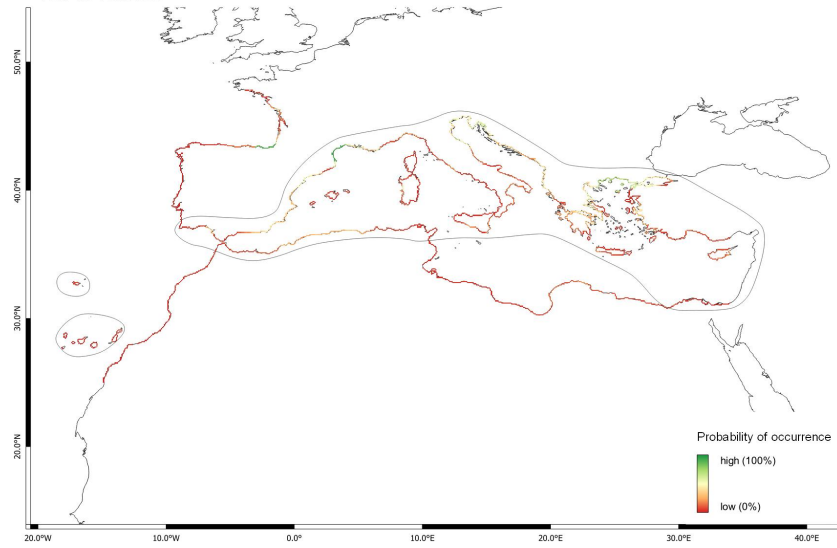


Lithophaga lithophaga:



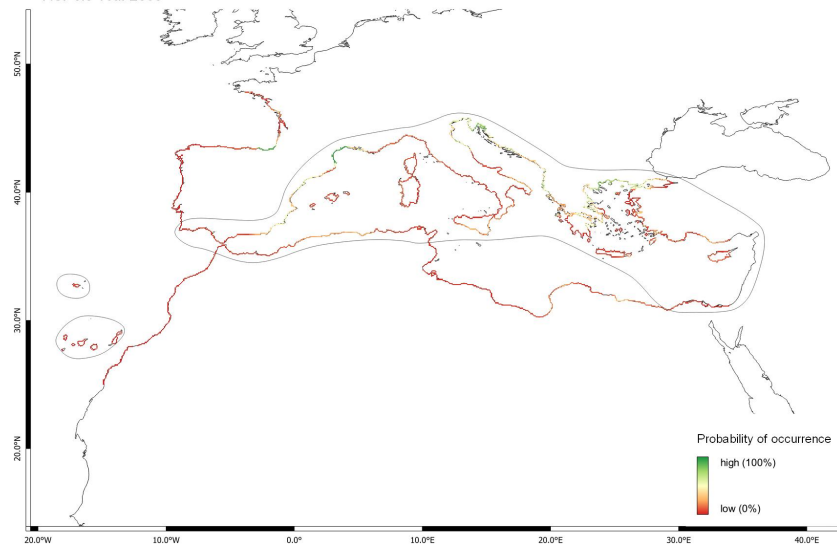
Lithophaga lithophaga

RCP4.5 Year 2050



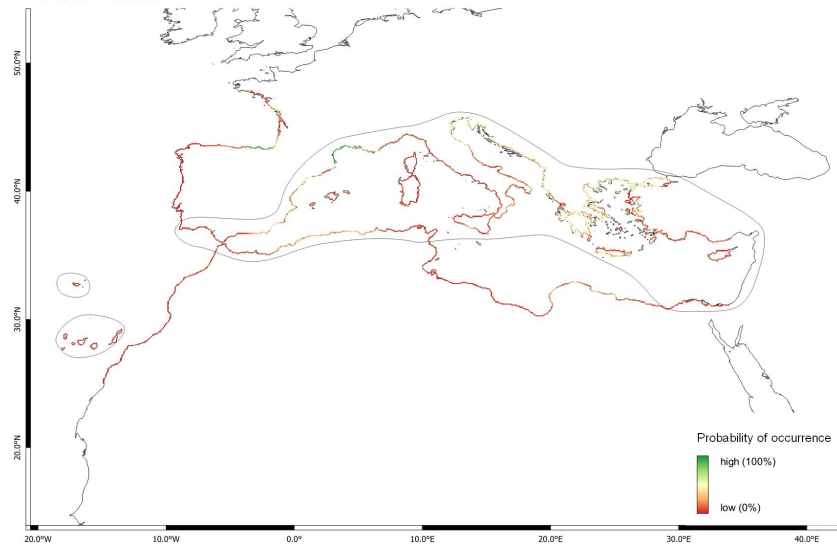
Lithophaga lithophaga

RCP6.0 Year 2050



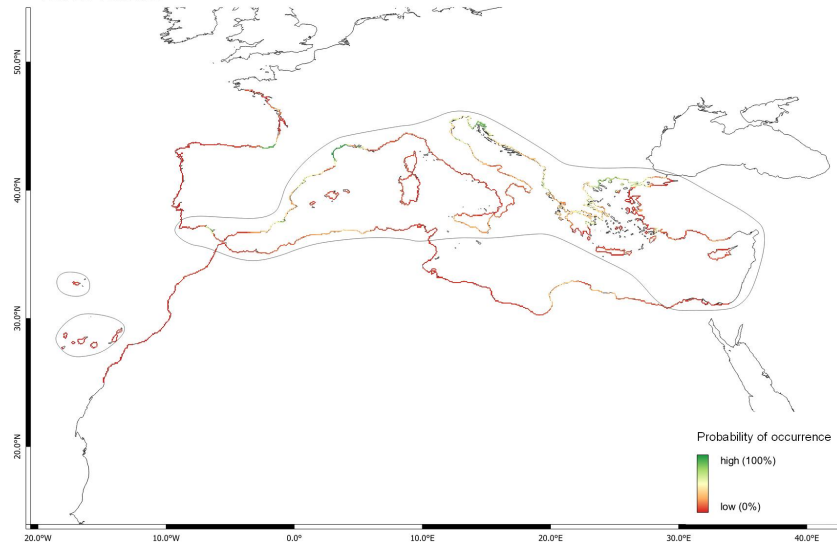
Lithophaga lithophaga

RCP8.5 Year 2050



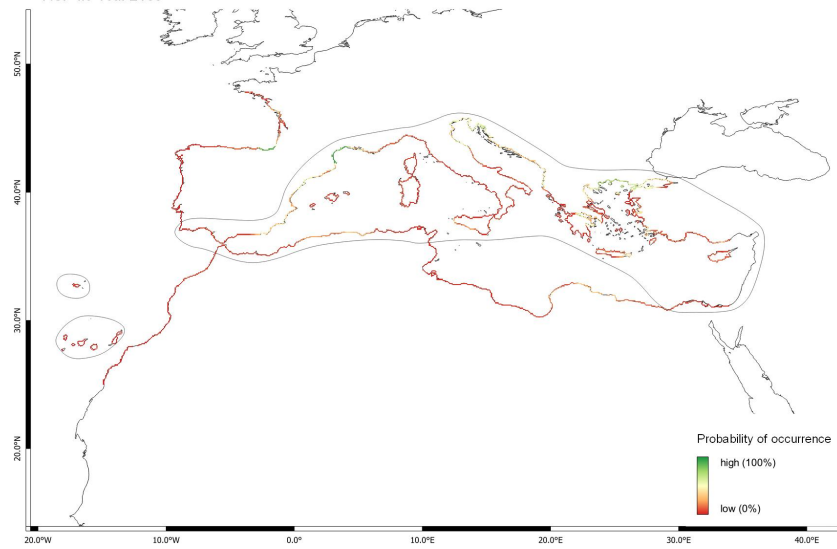
Lithophaga lithophaga

RCP2.6 Year 2100



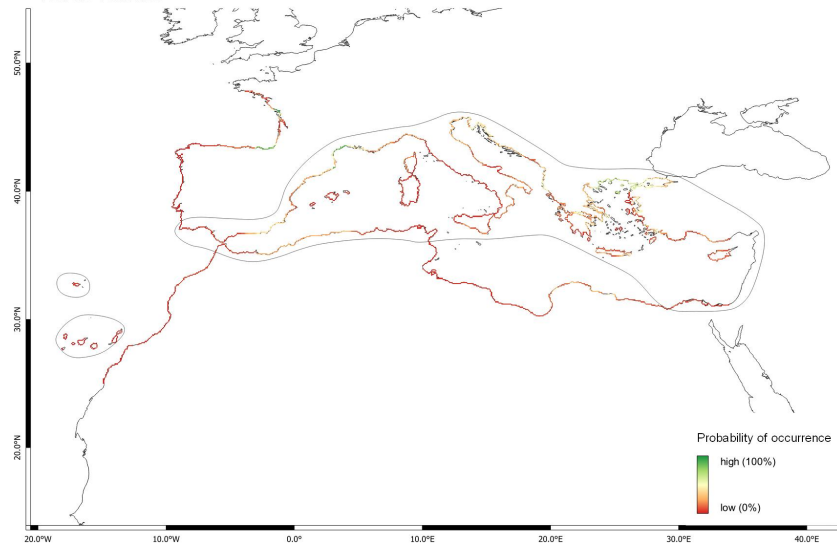
Lithophaga lithophaga

RCP4.5 Year 2100



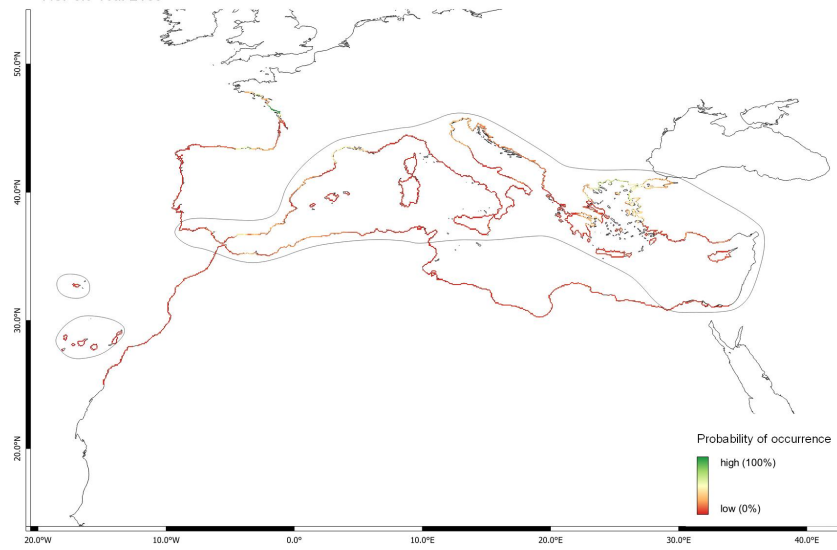
Lithophaga lithophaga

RCP6.0 Year 2100

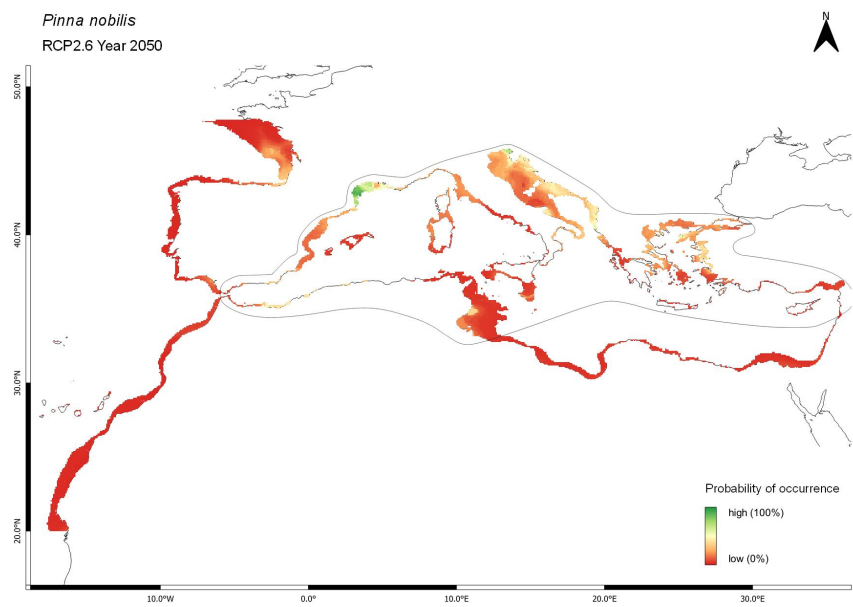
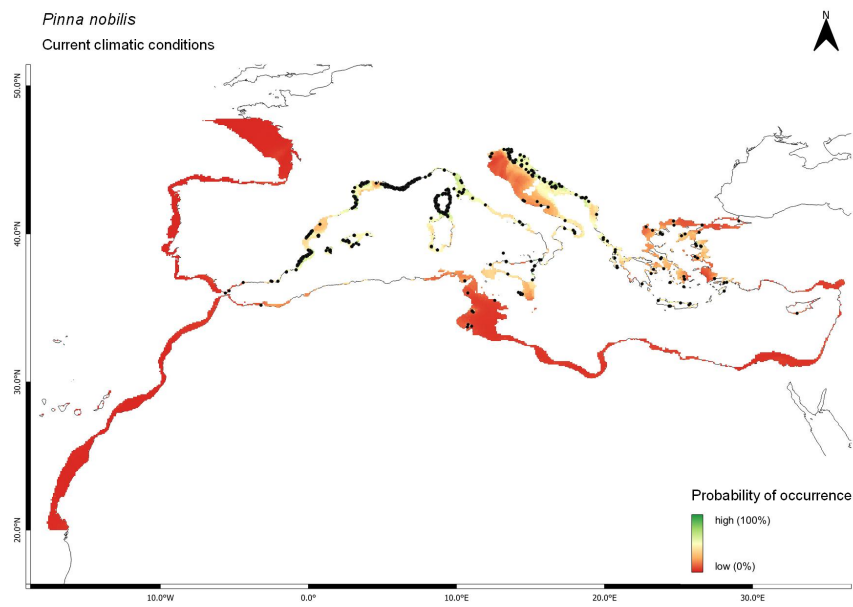


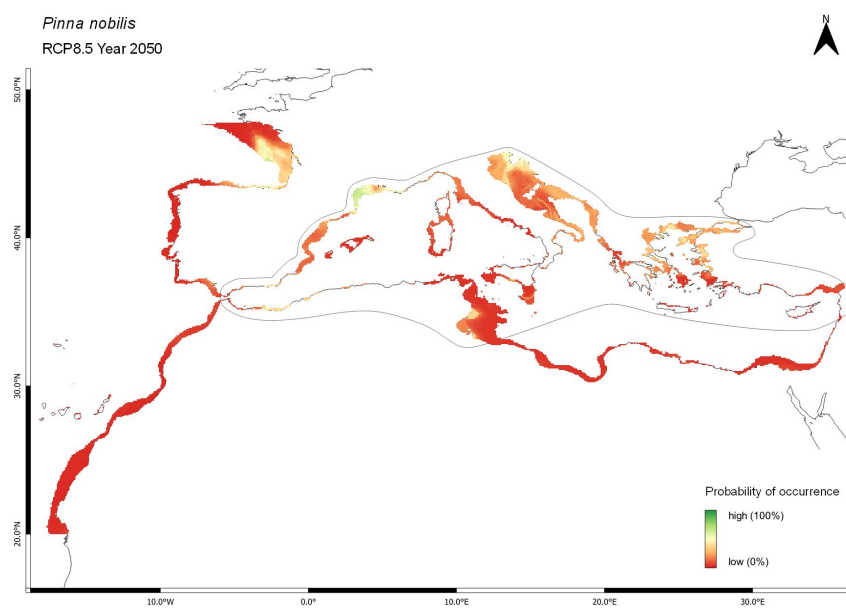
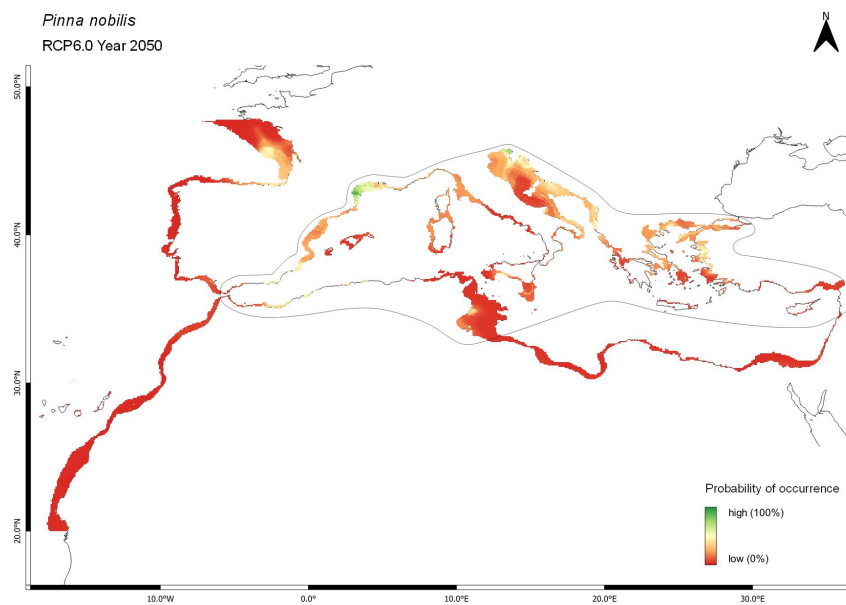
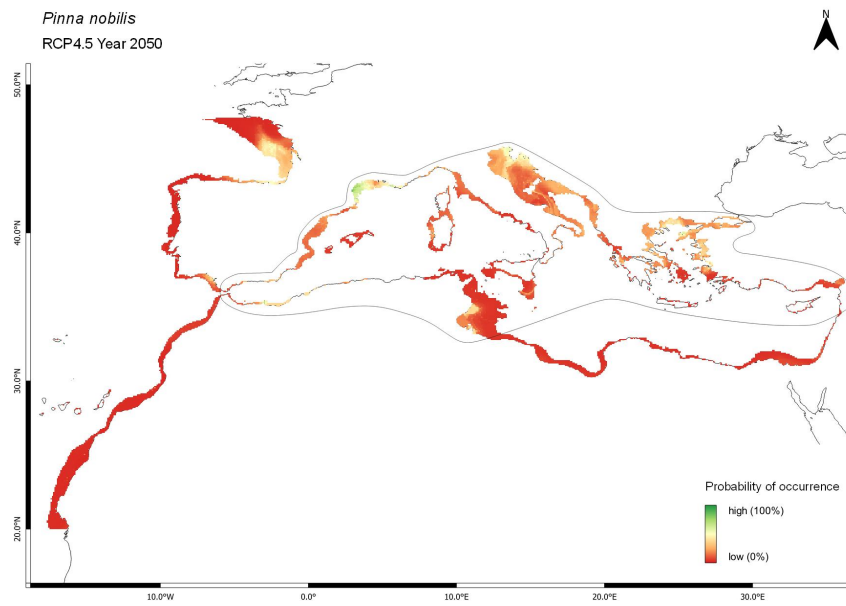
Lithophaga lithophaga

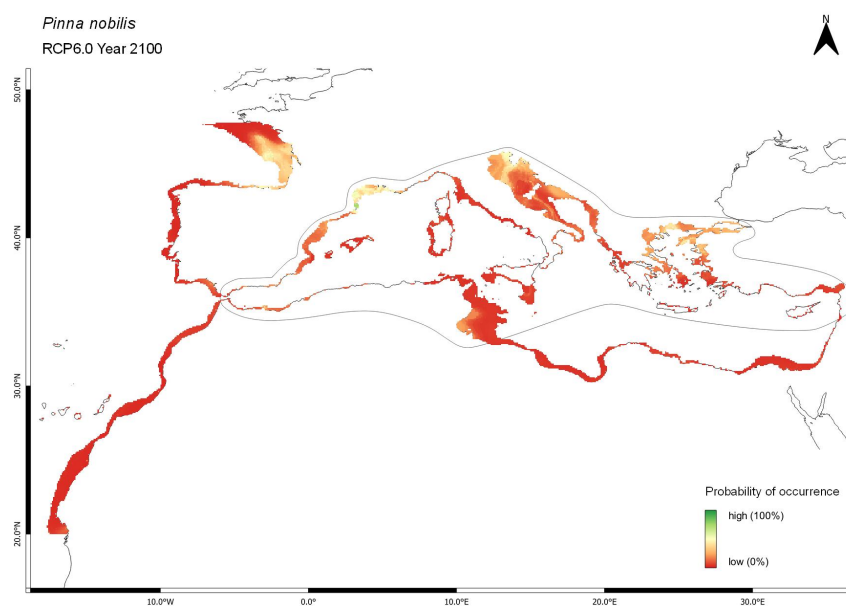
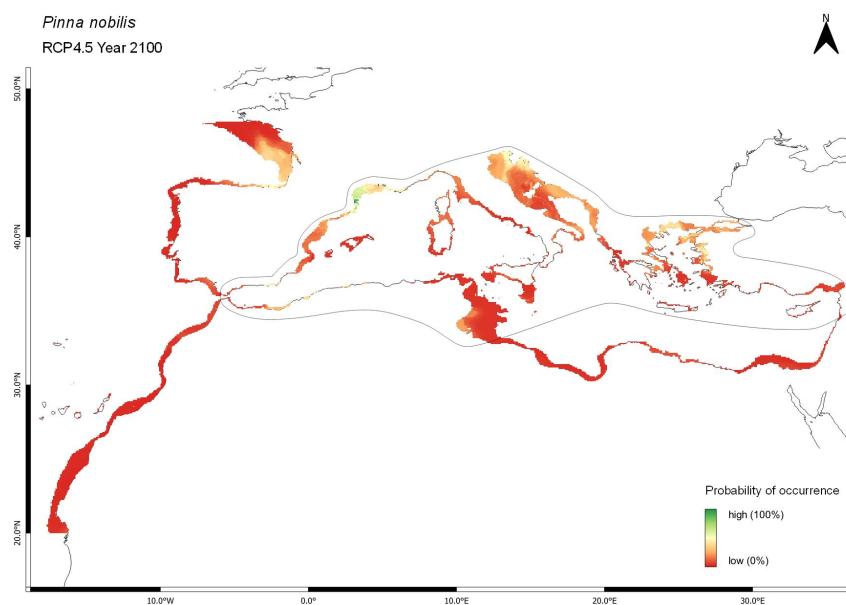
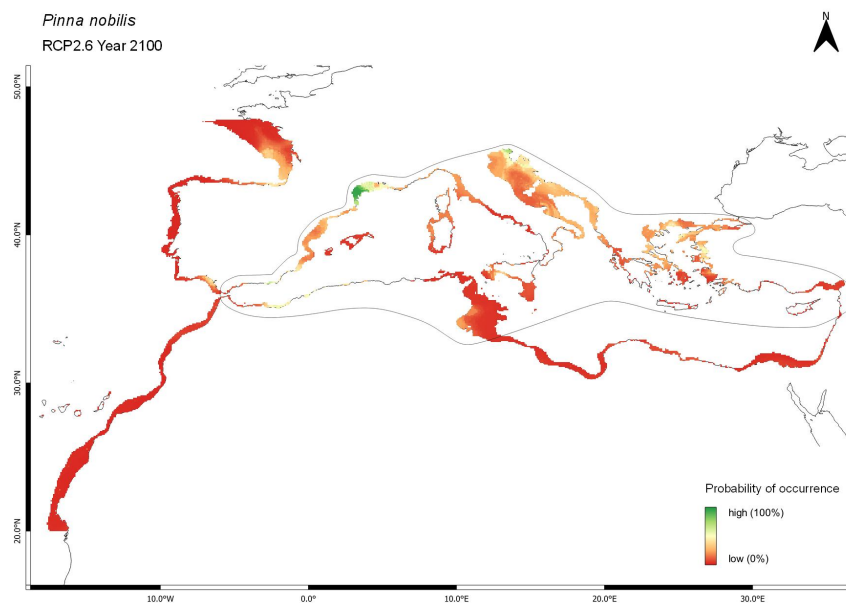
RCP8.5 Year 2100

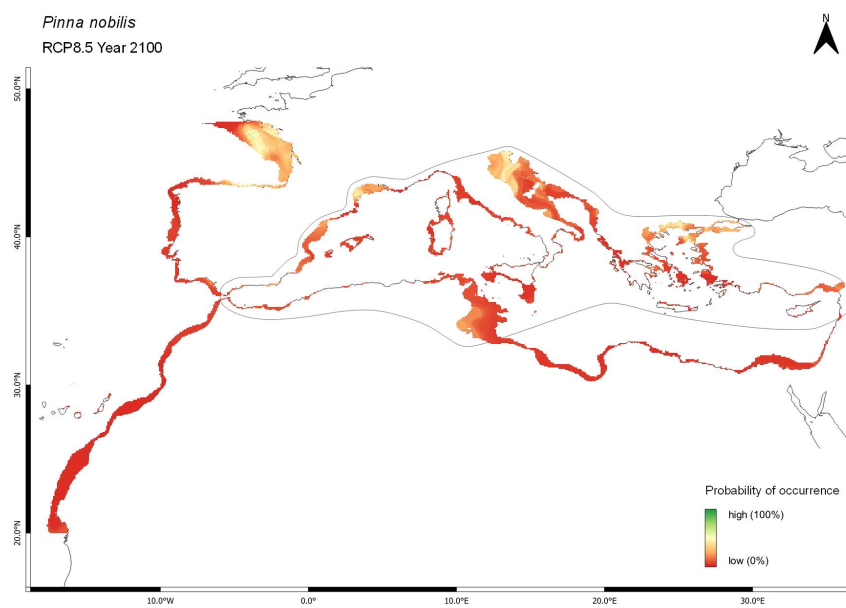


Pinna nobilis:

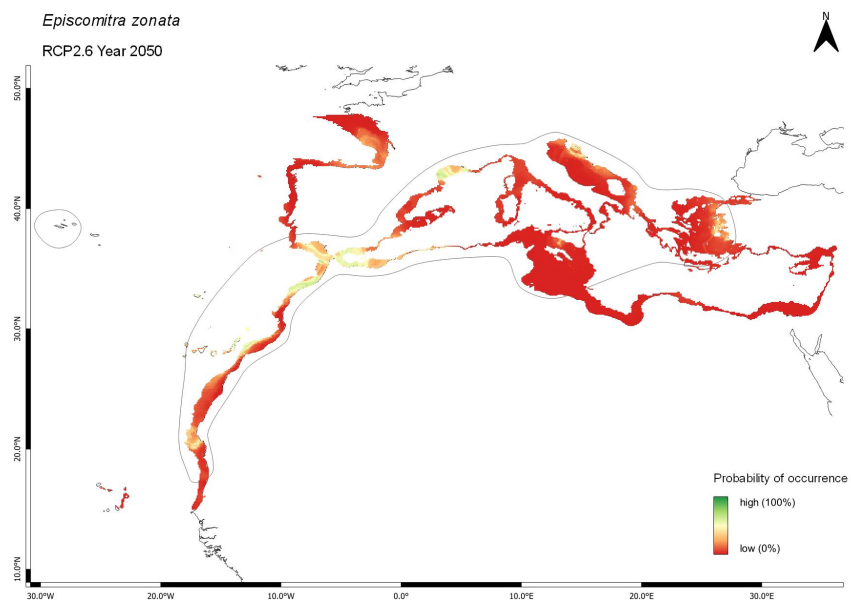
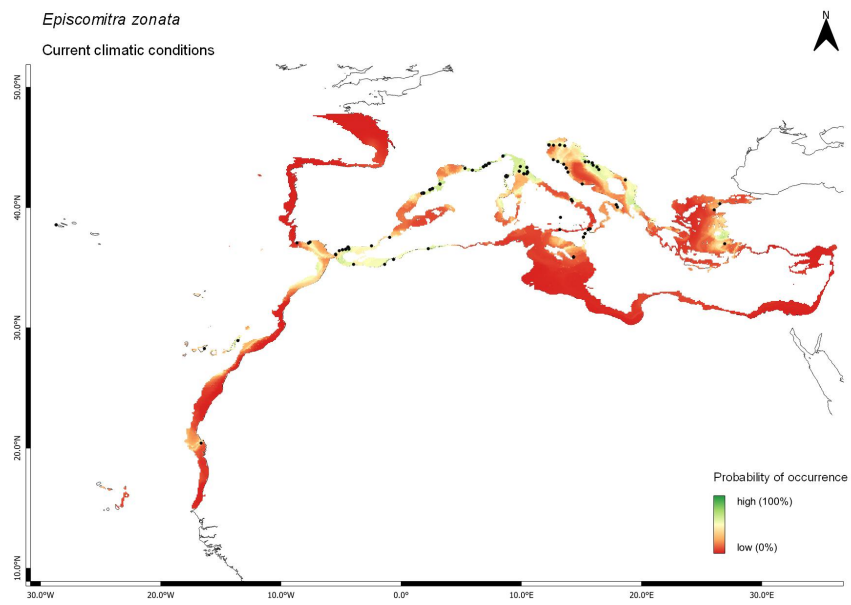


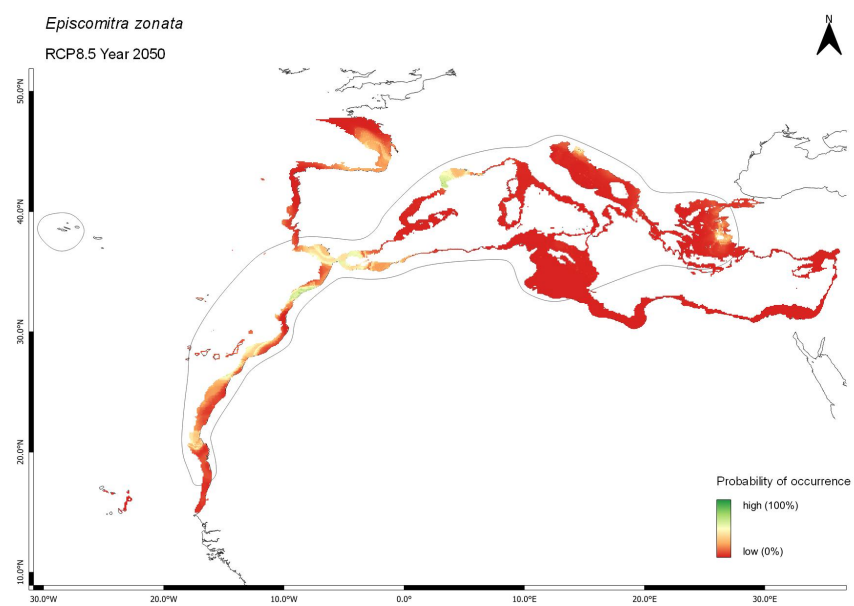
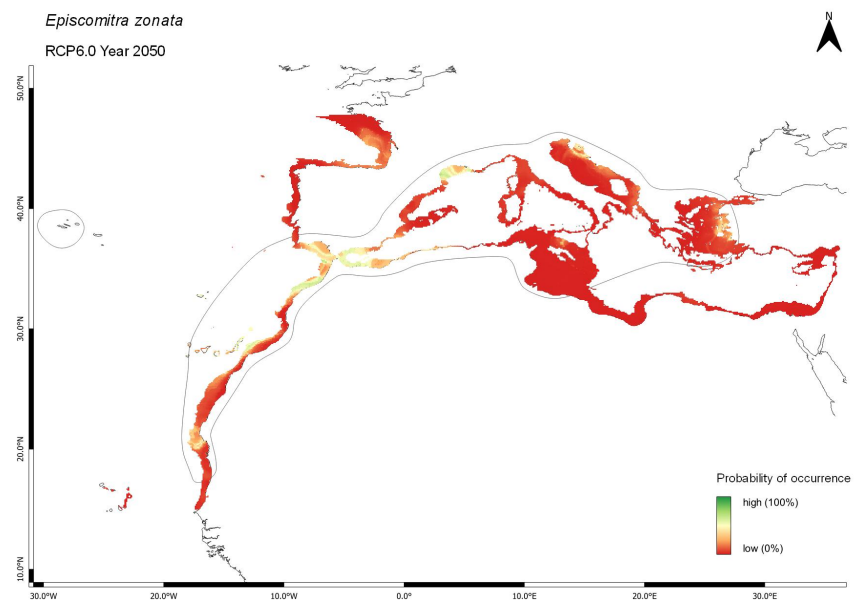
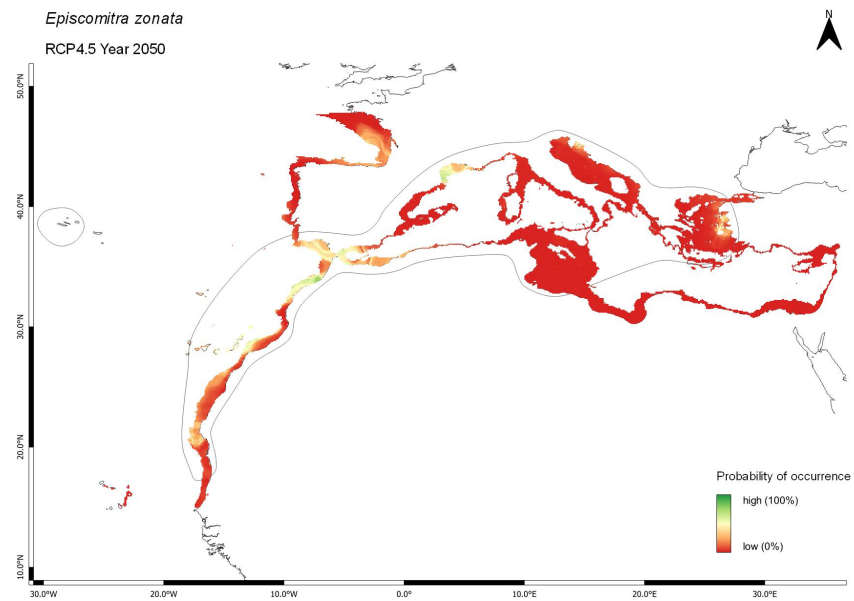


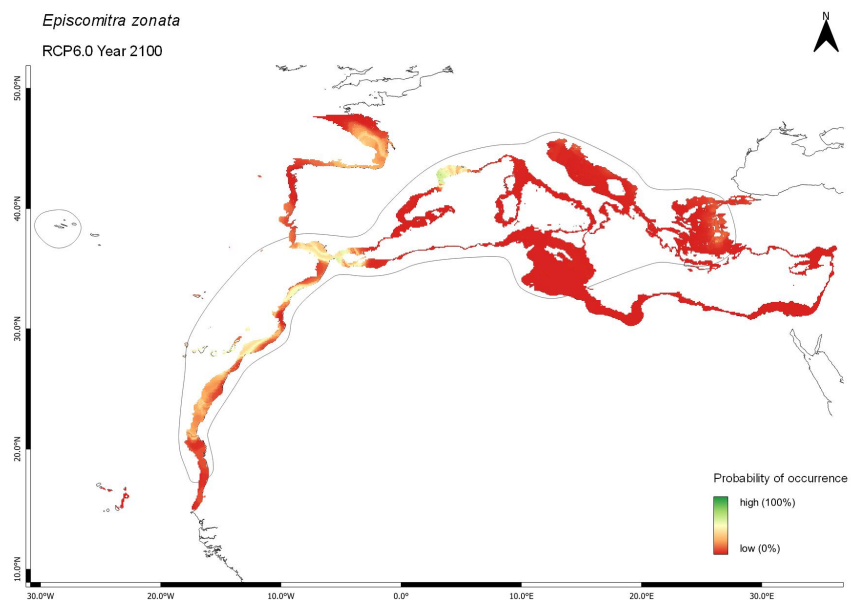
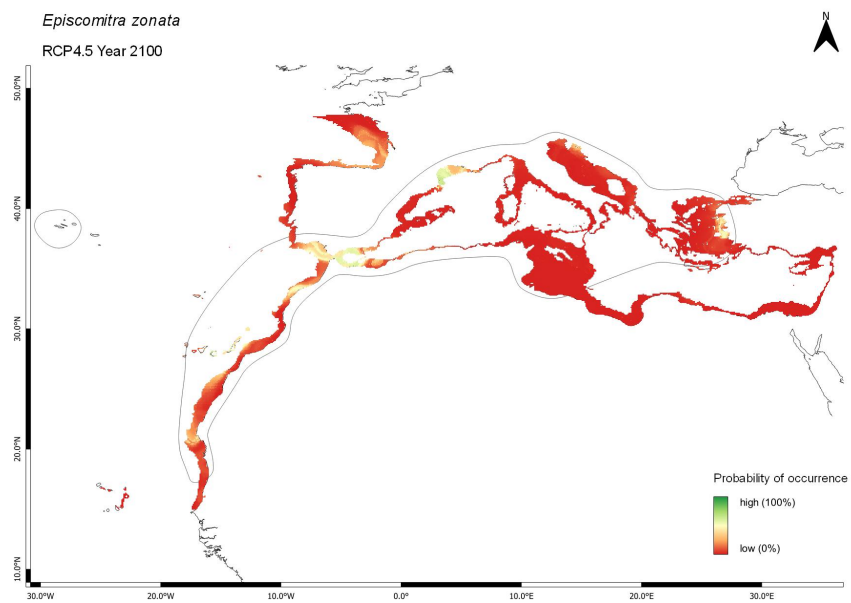
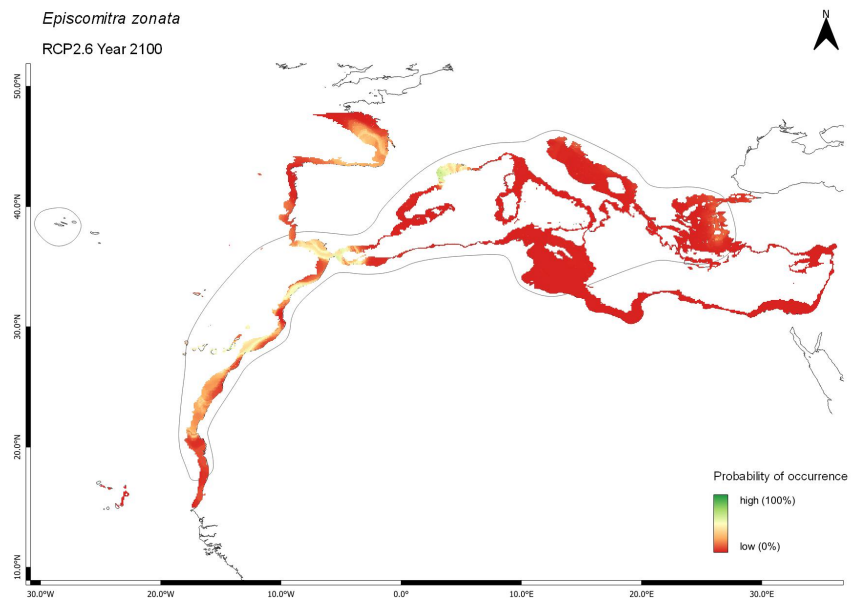


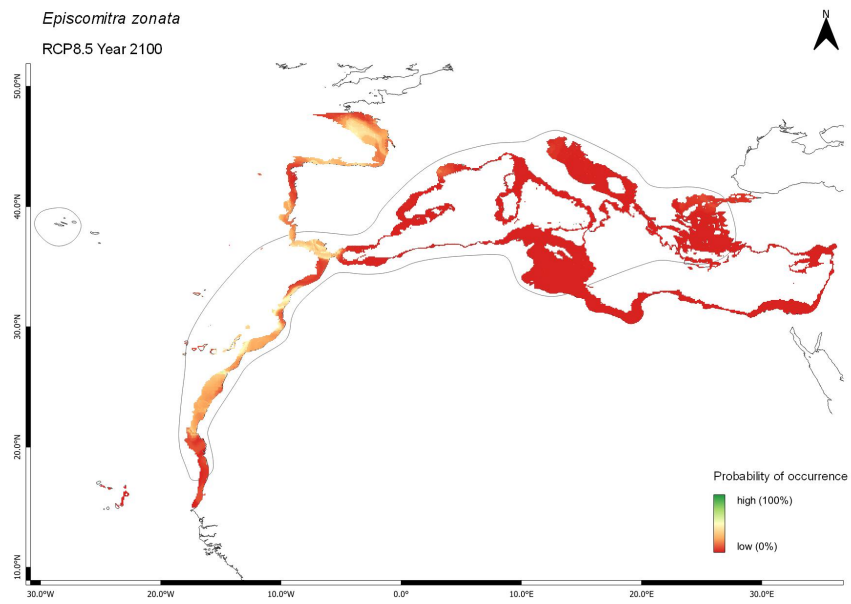


Episcomitra zonata:



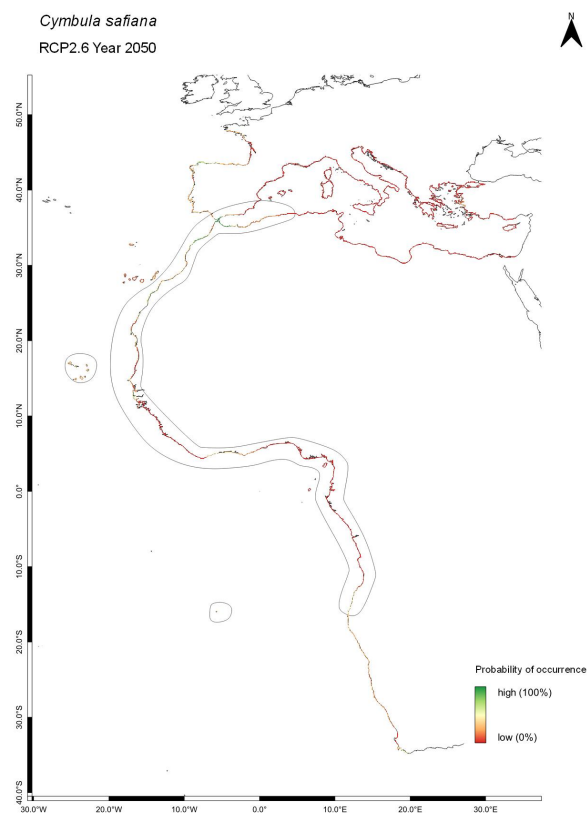
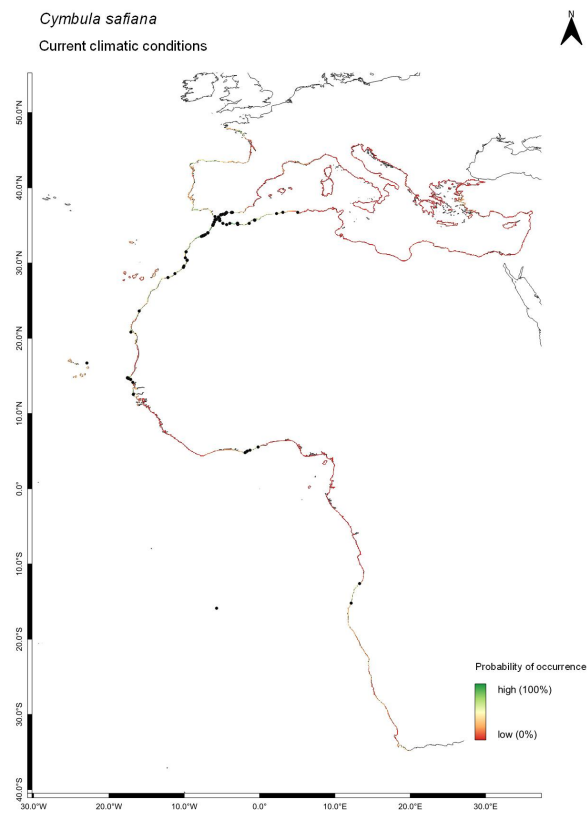




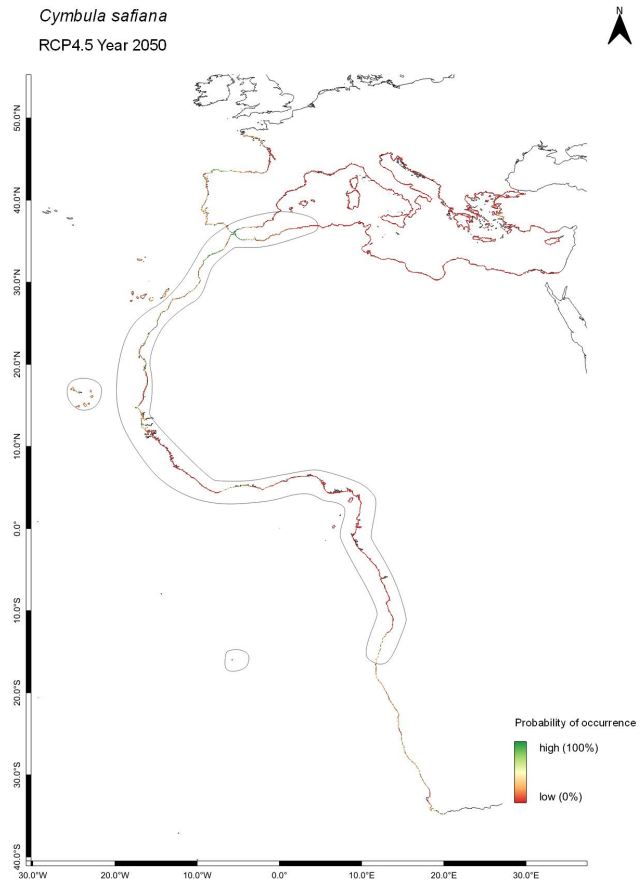


S2.2. Wider distributed species

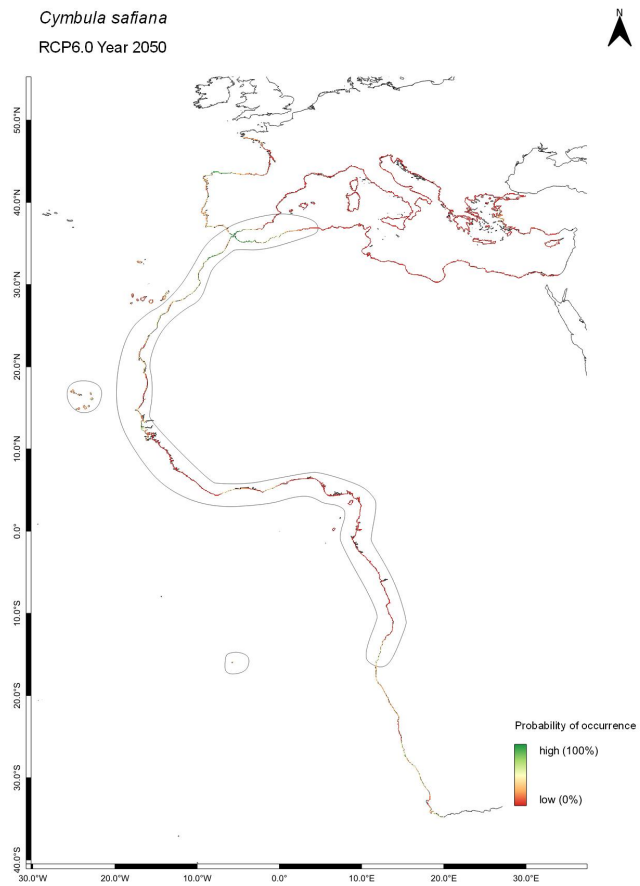
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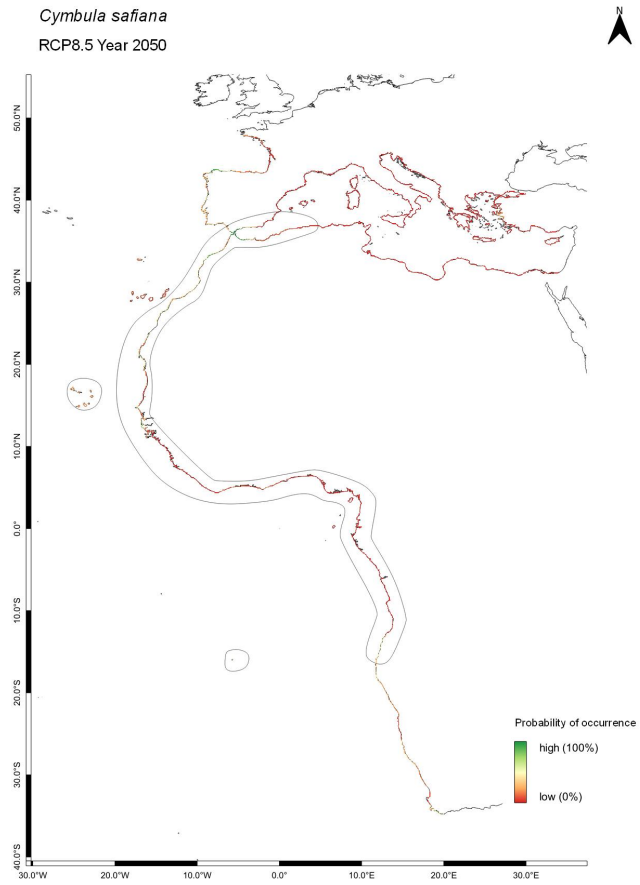
Cymbula safiana
RCP4.5 Year 2050



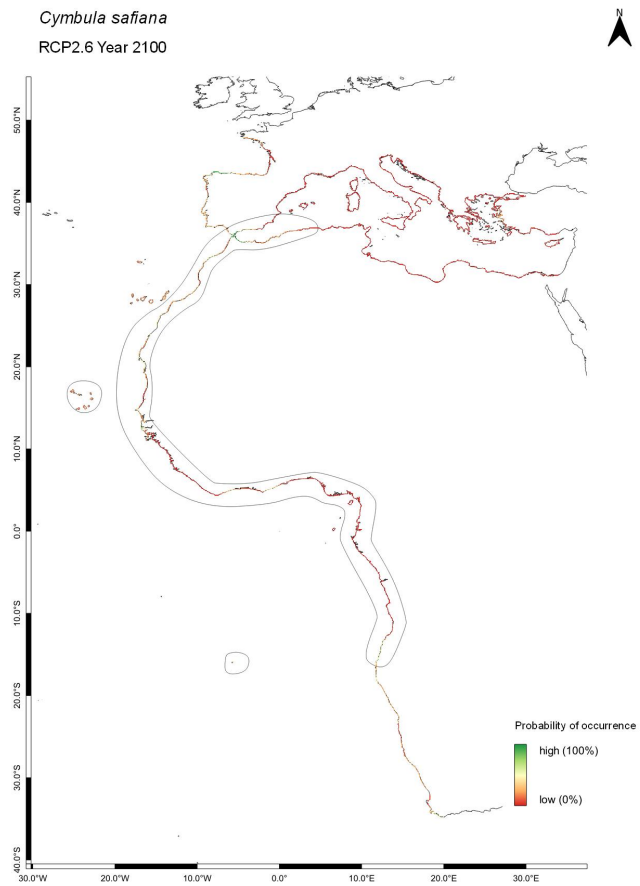
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RCP6.0 Year 2050



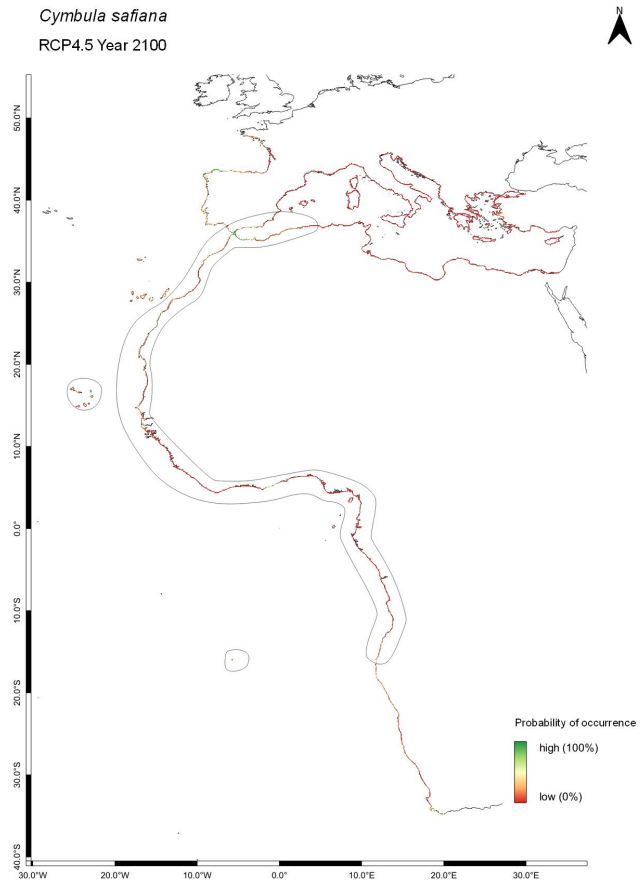
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RCP8.5 Year 2050



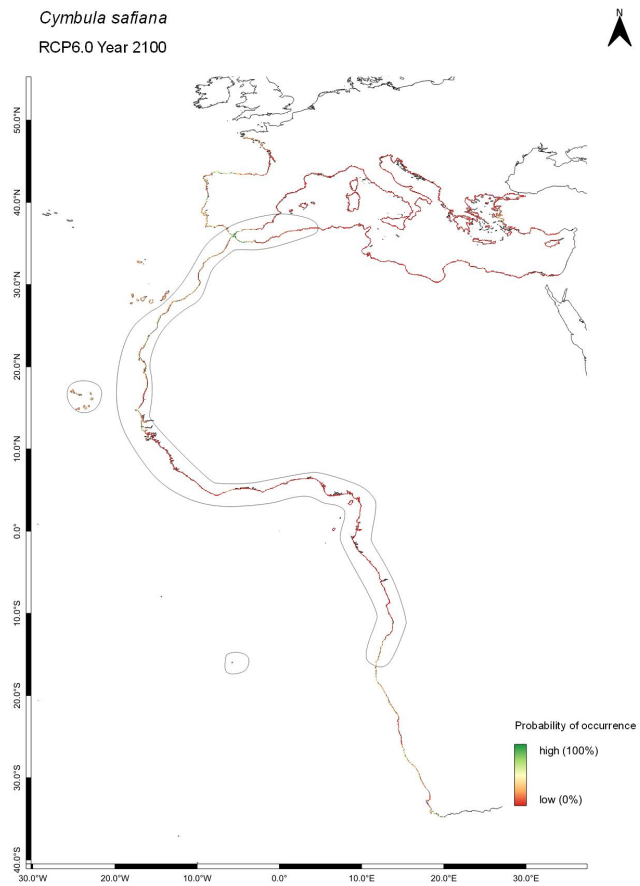
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RCP2.6 Year 2100



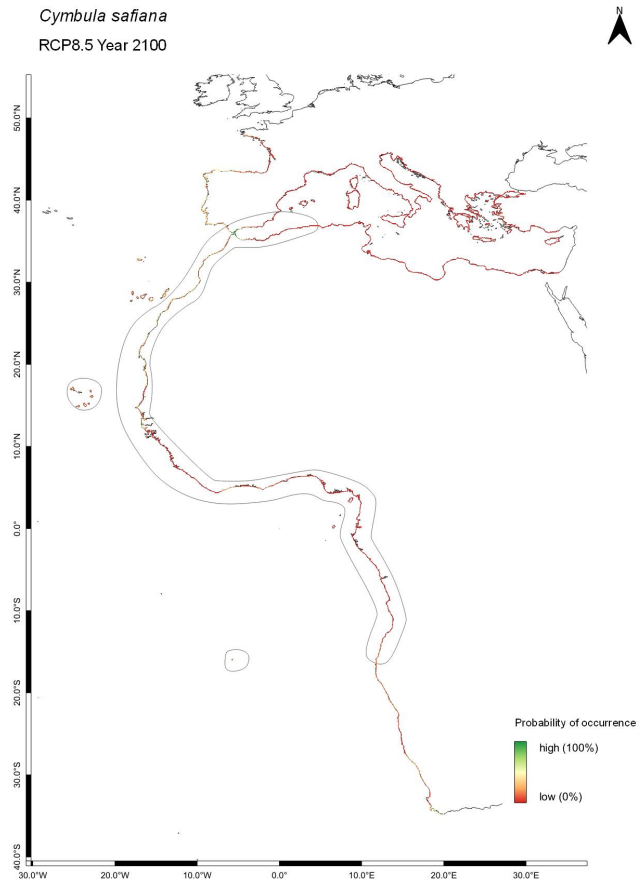
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RCP4.5 Year 2100



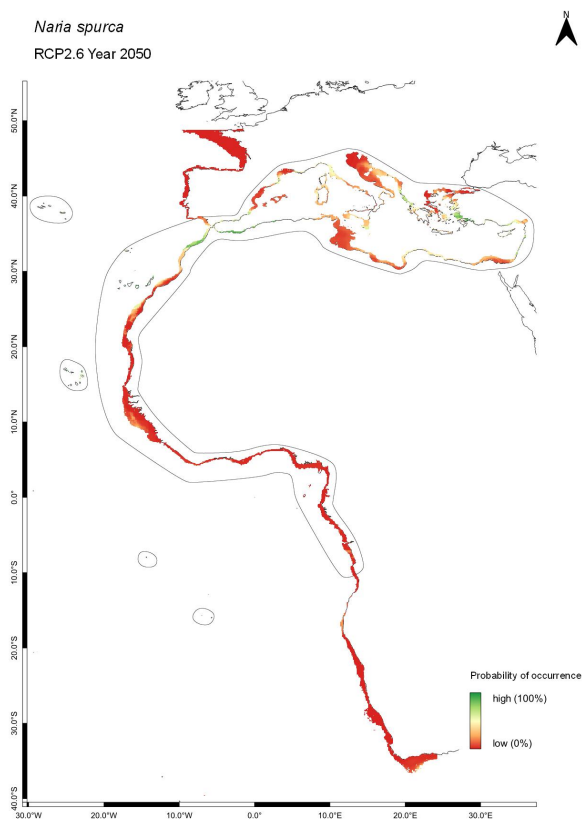
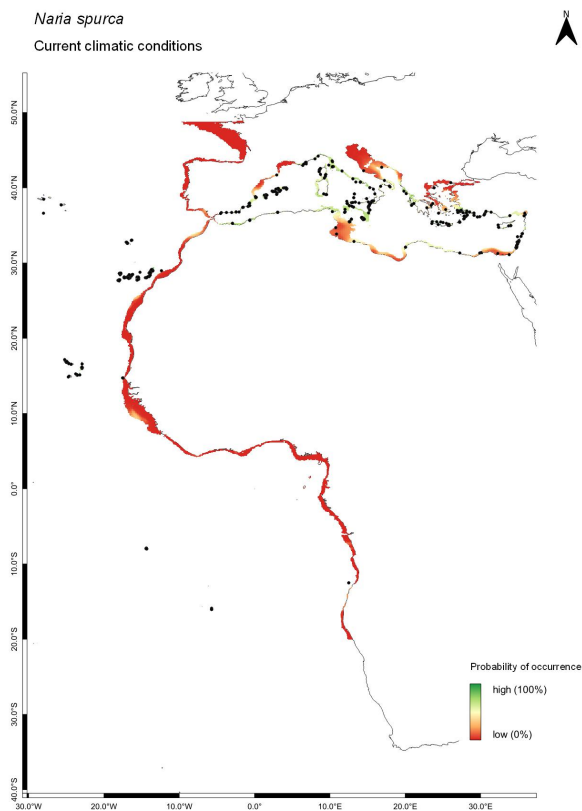
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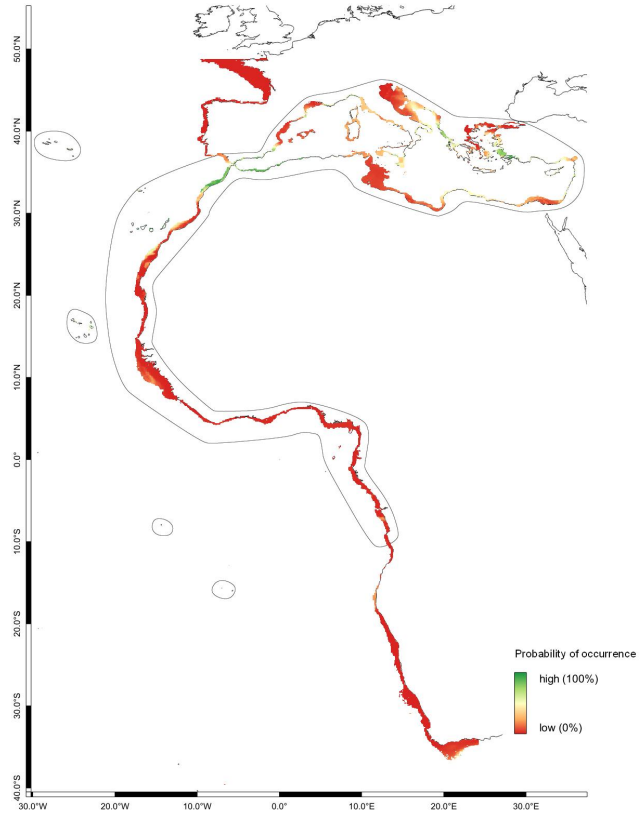
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RCP8.5 Year 2100



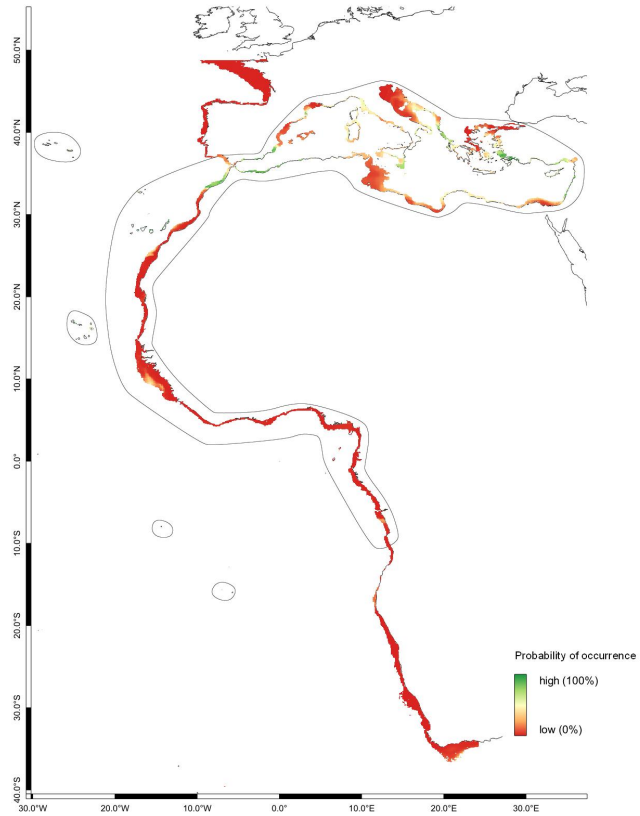
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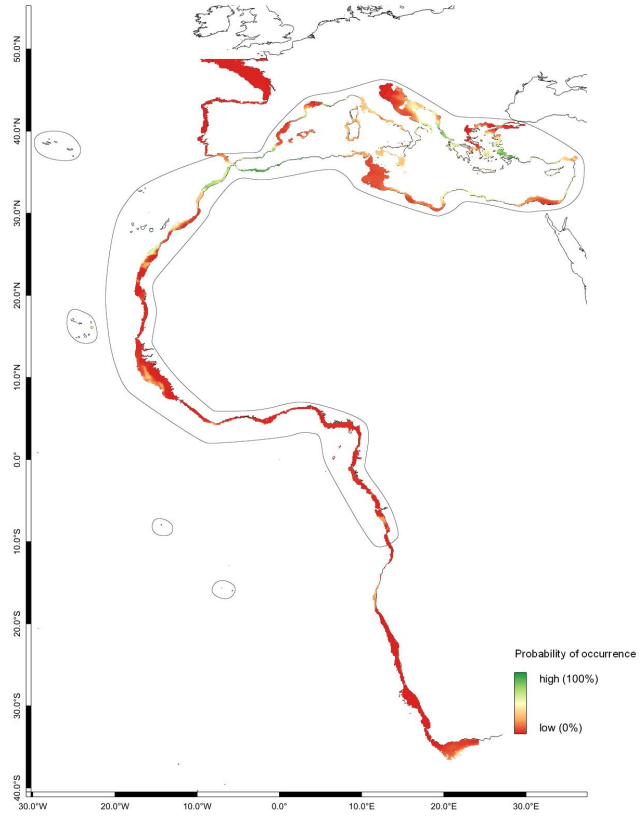
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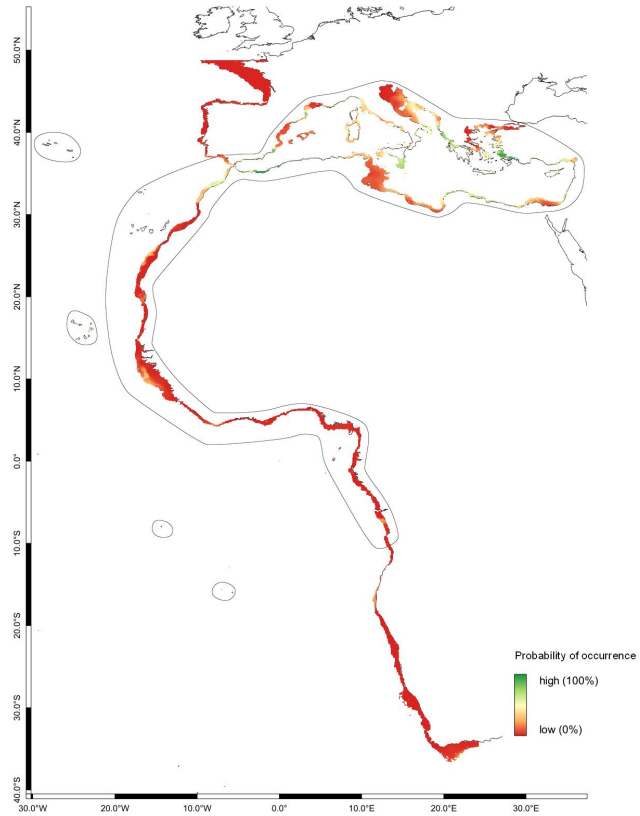
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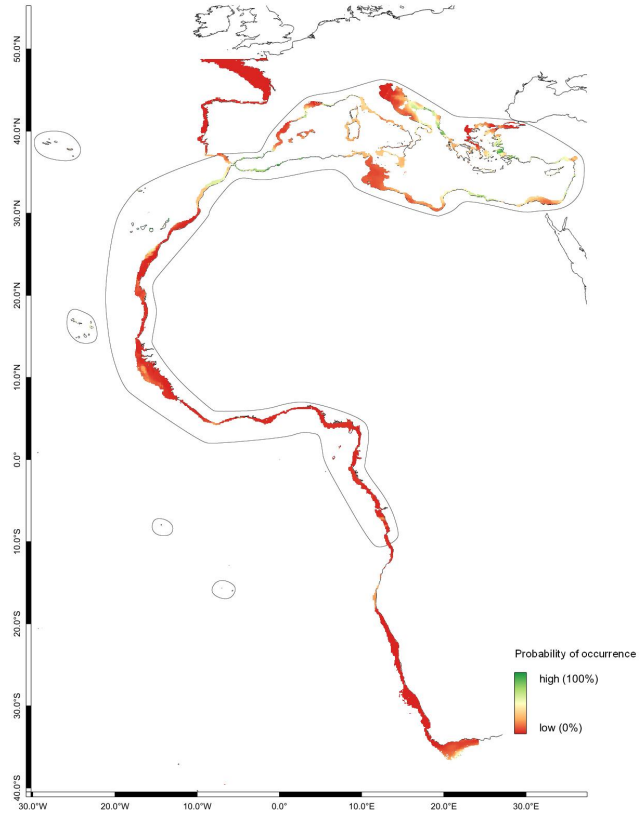
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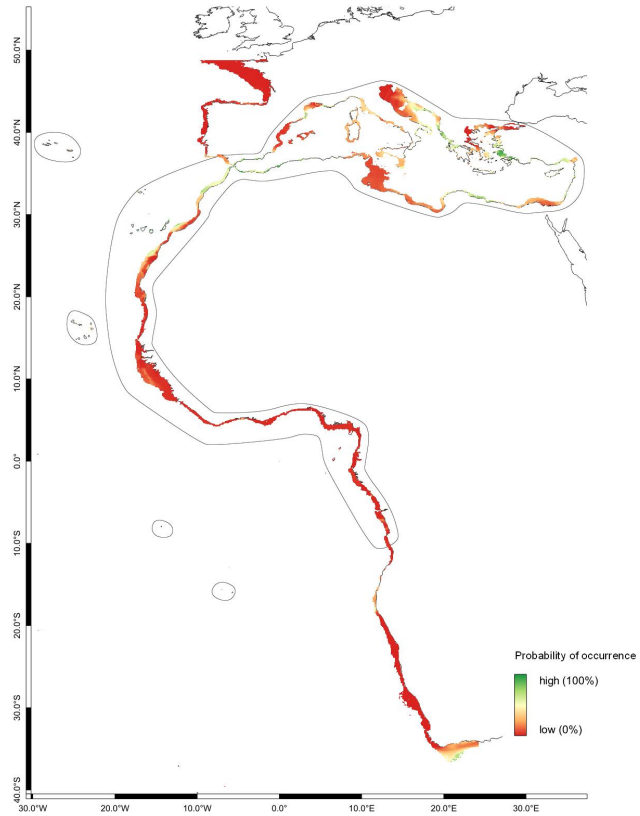
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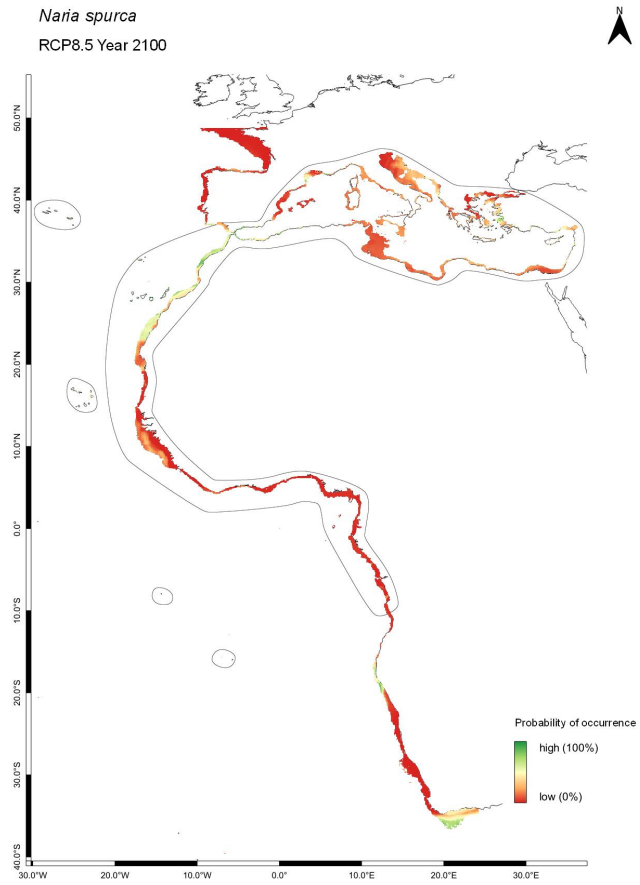
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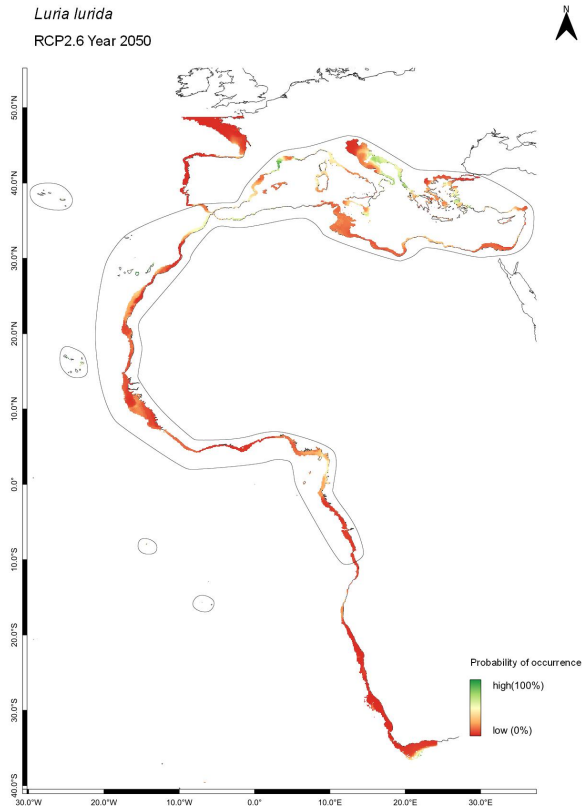
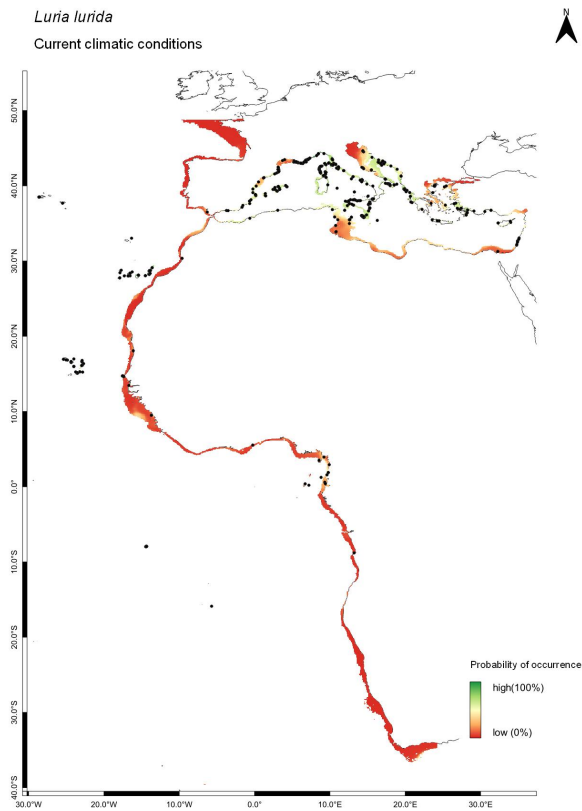
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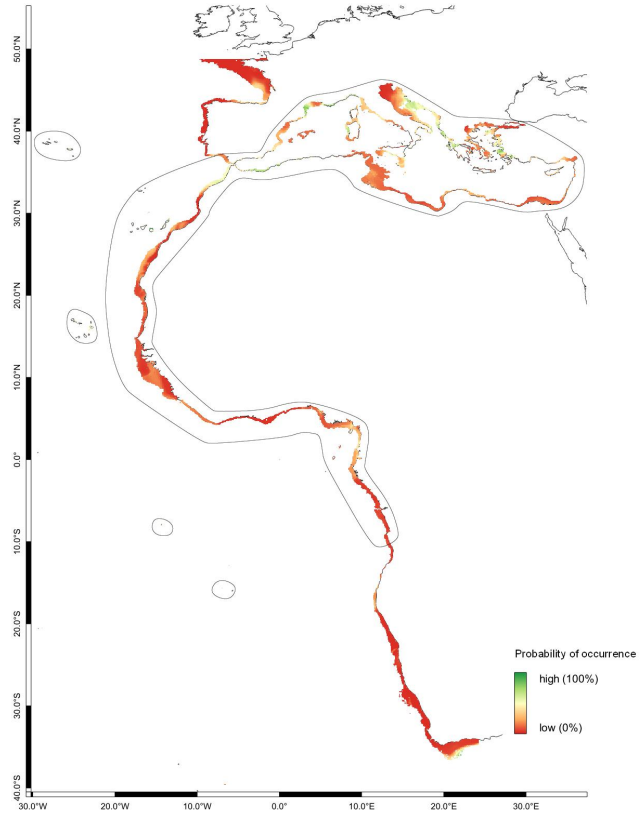
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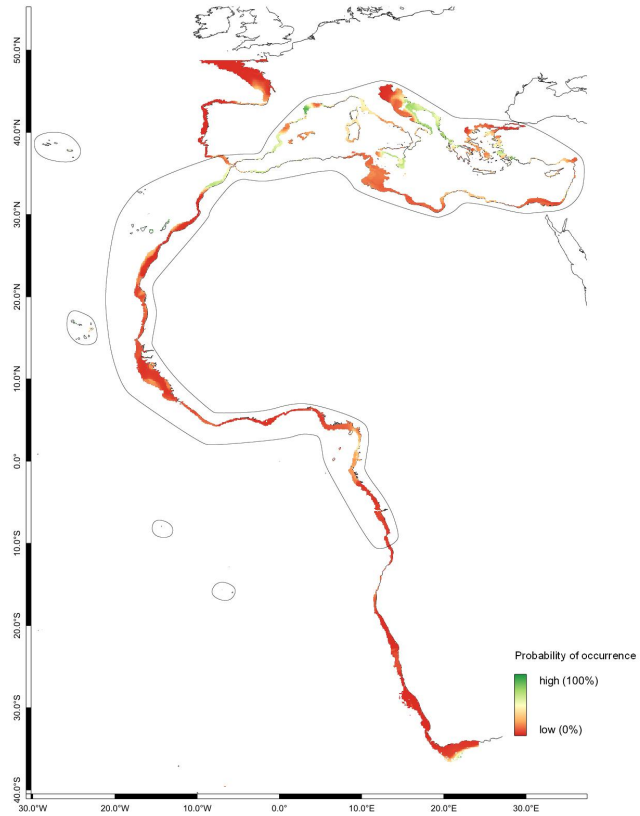
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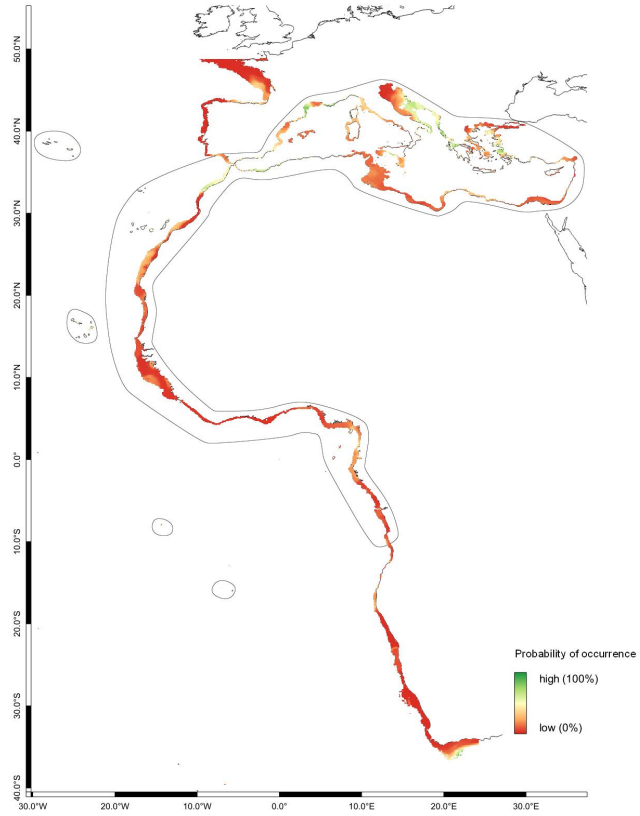
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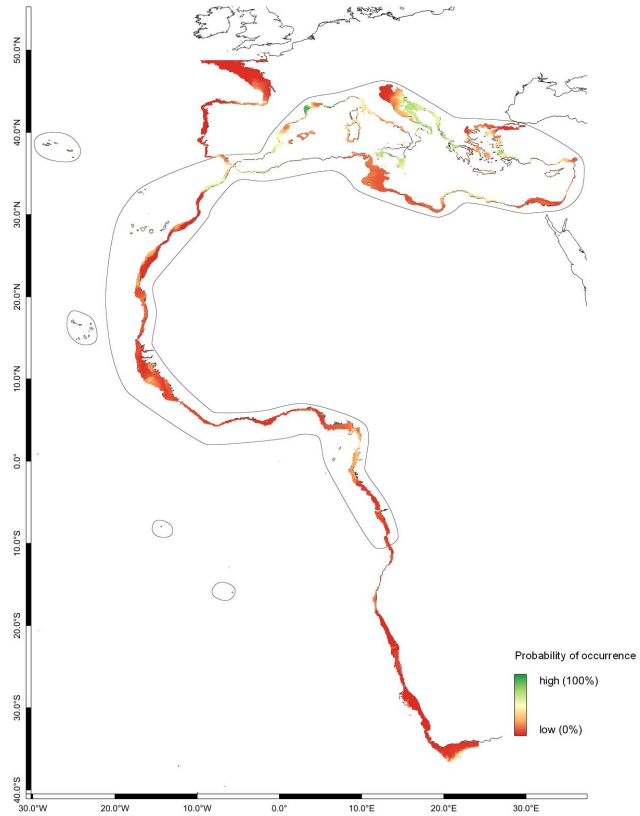
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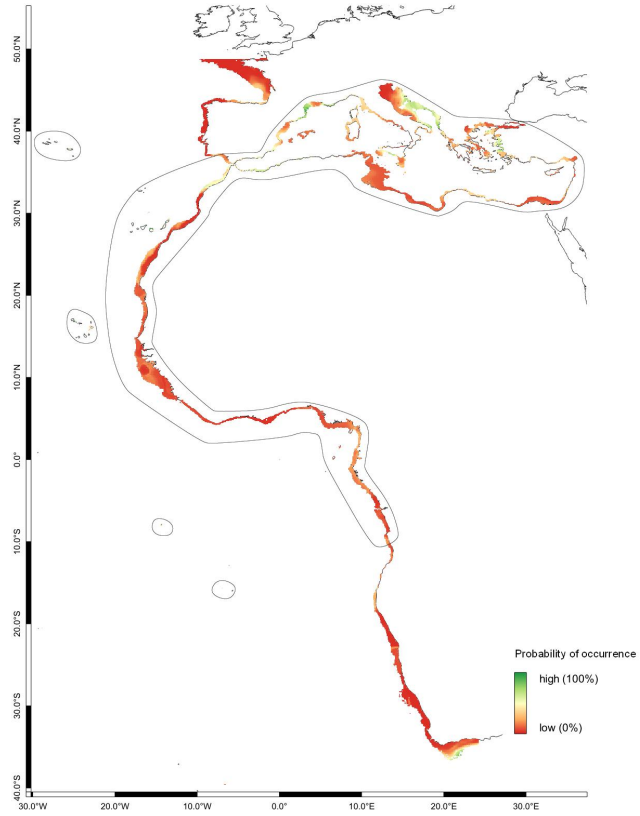
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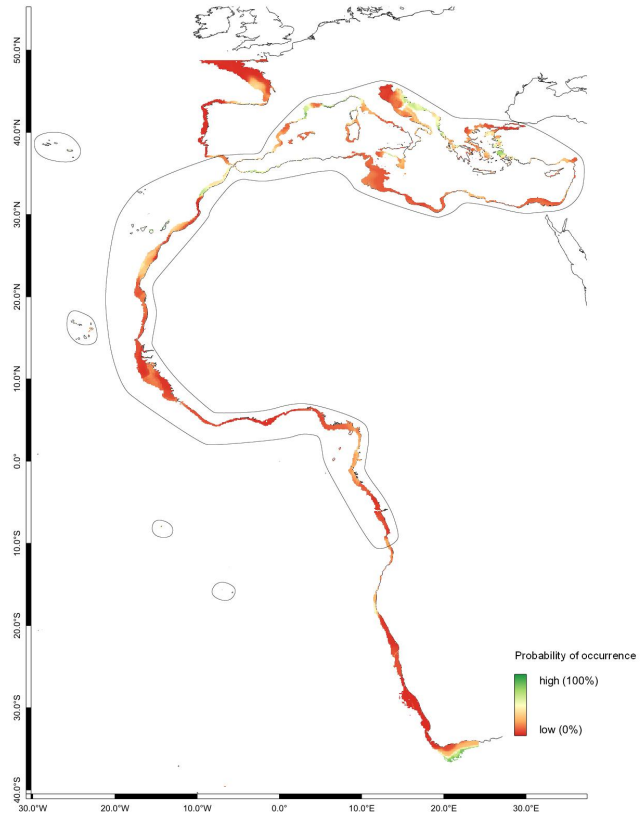
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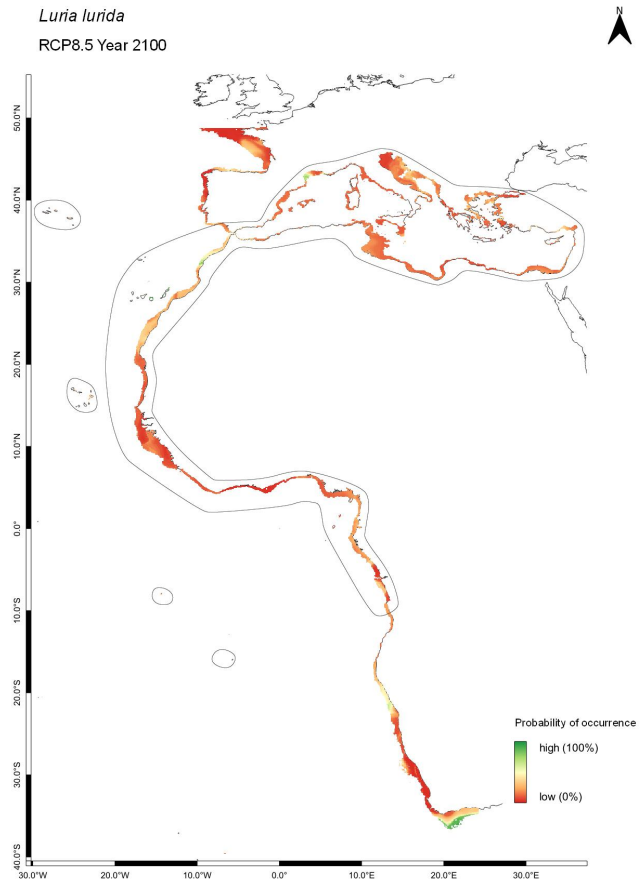
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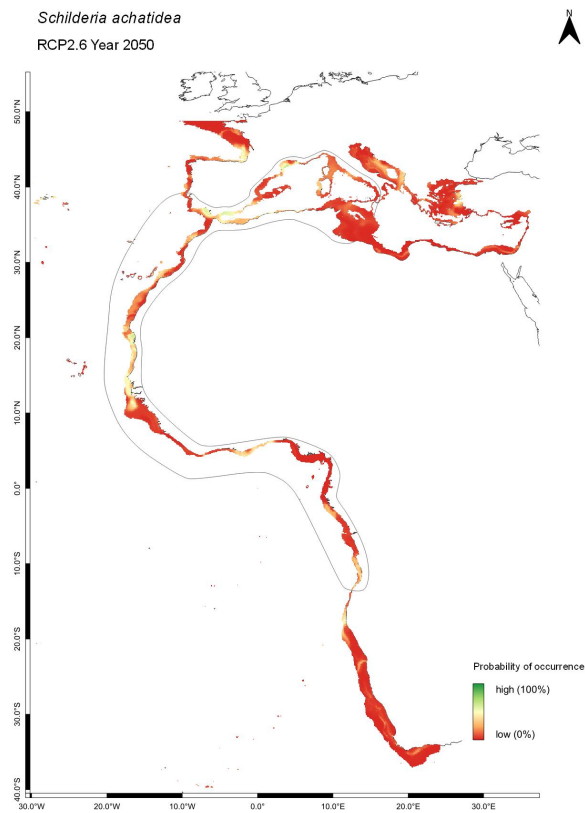
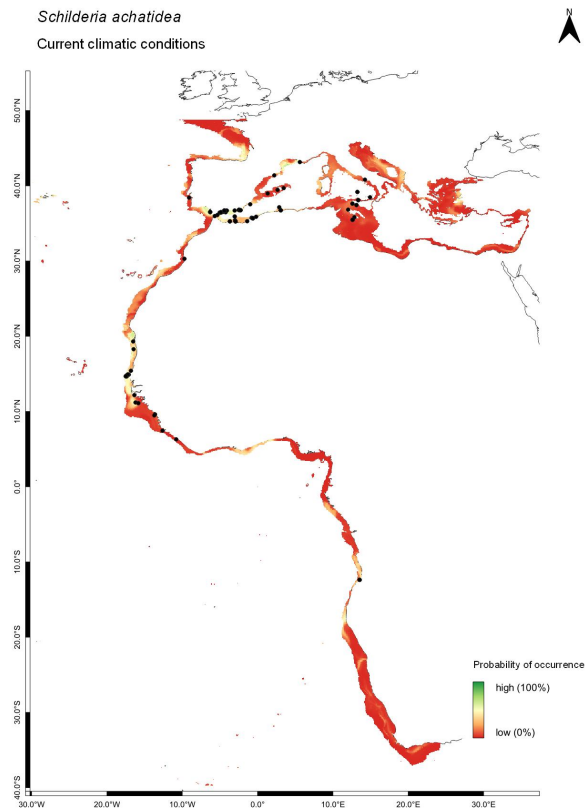
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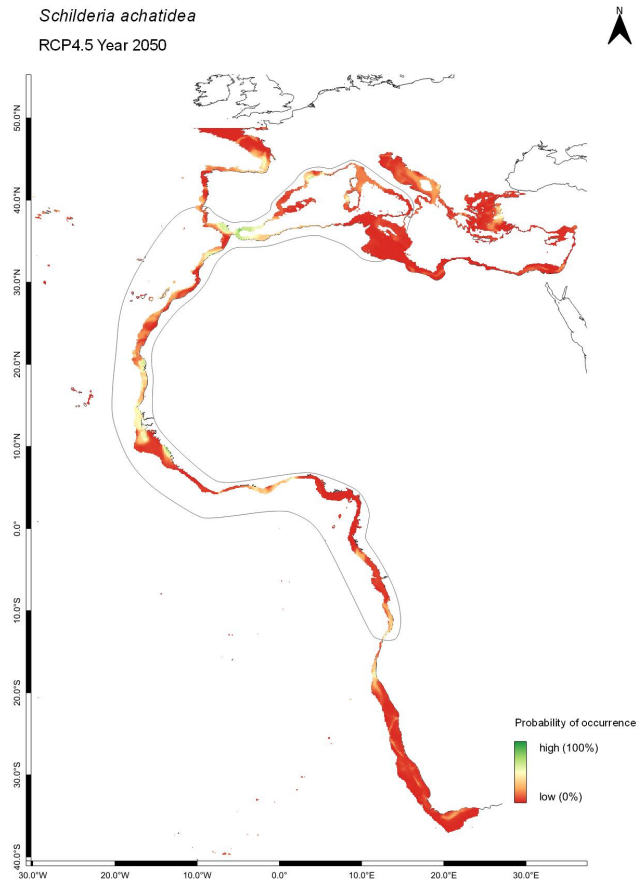
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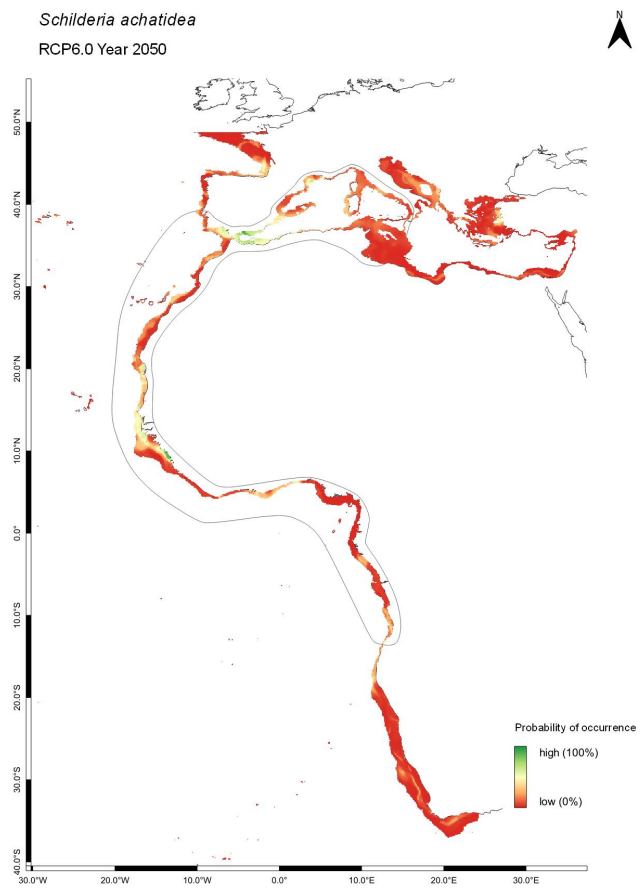
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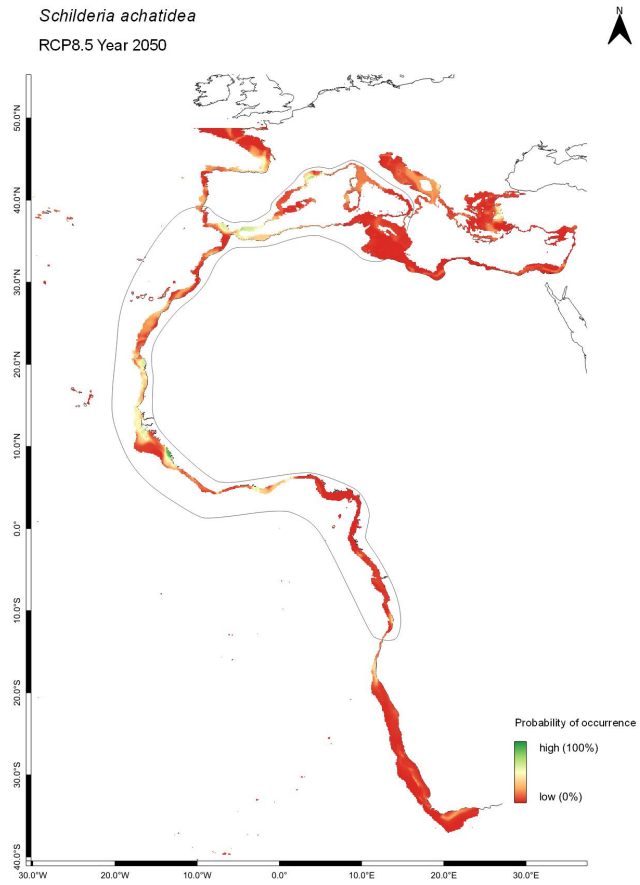
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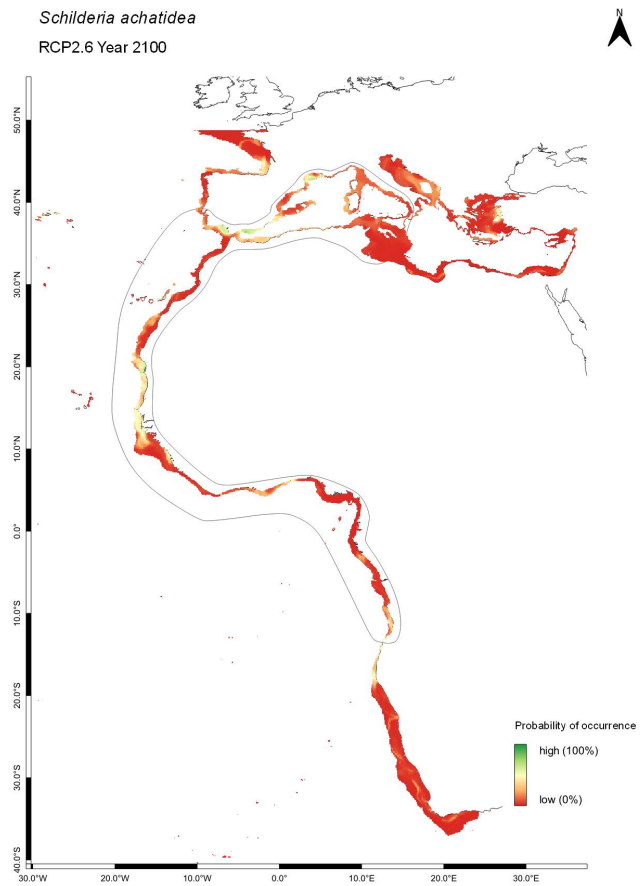
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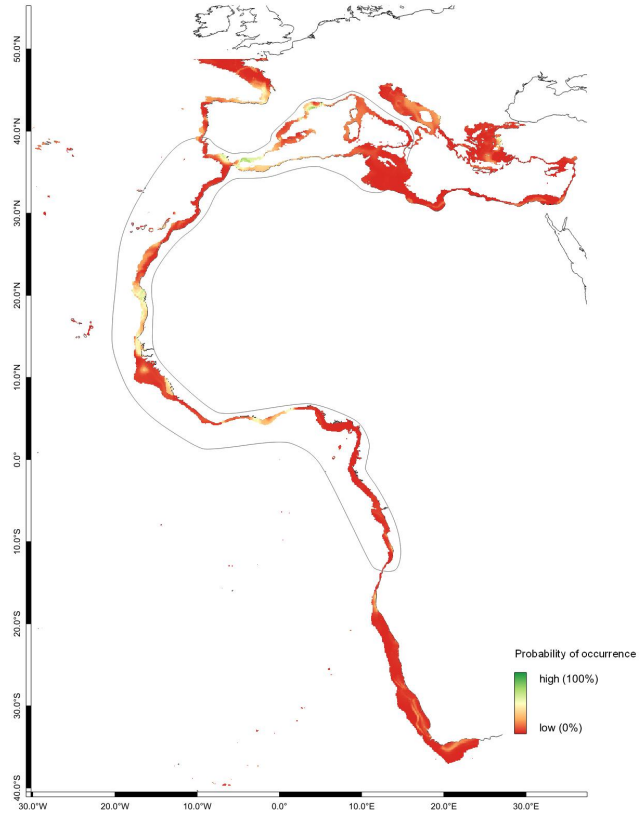
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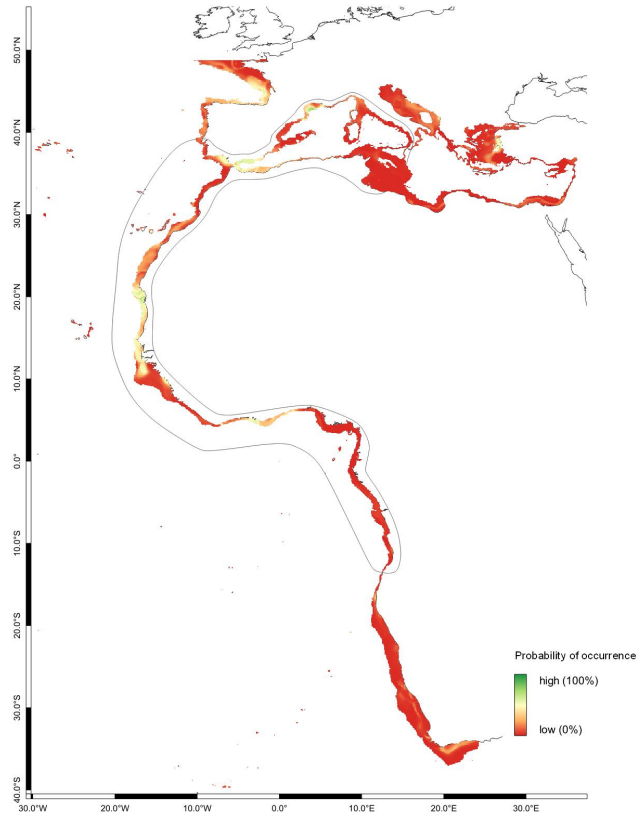
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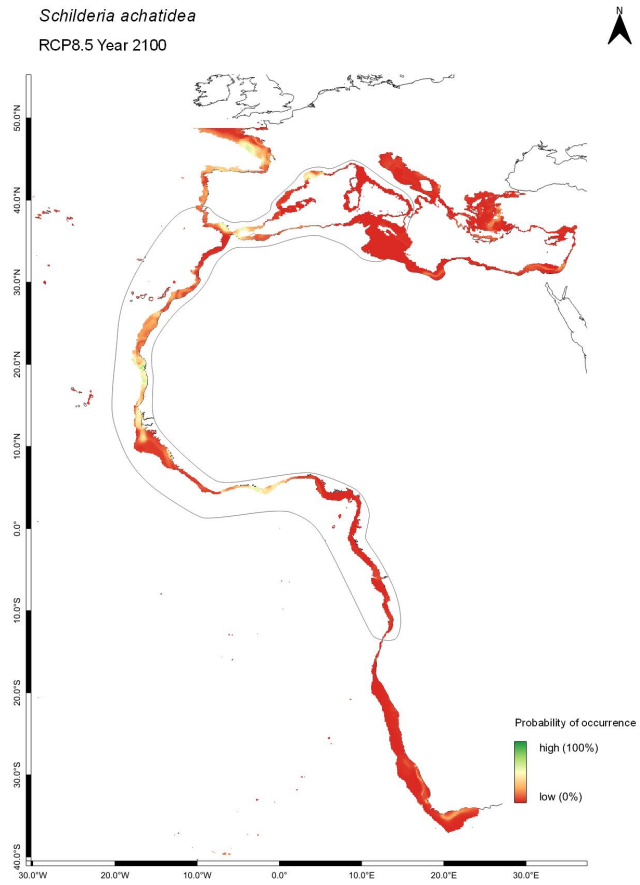
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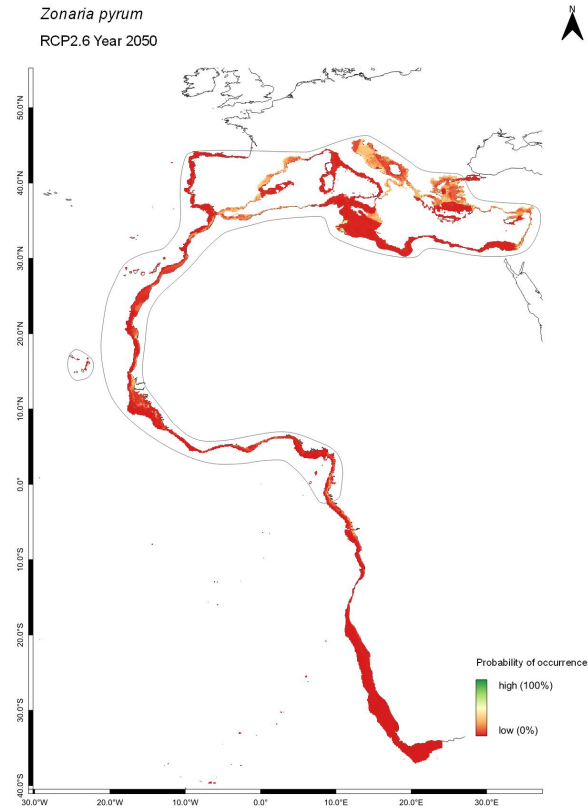
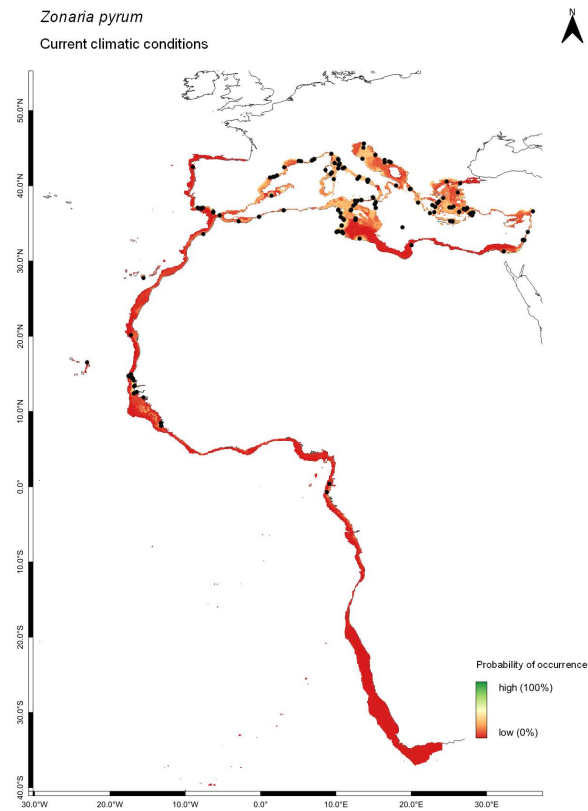
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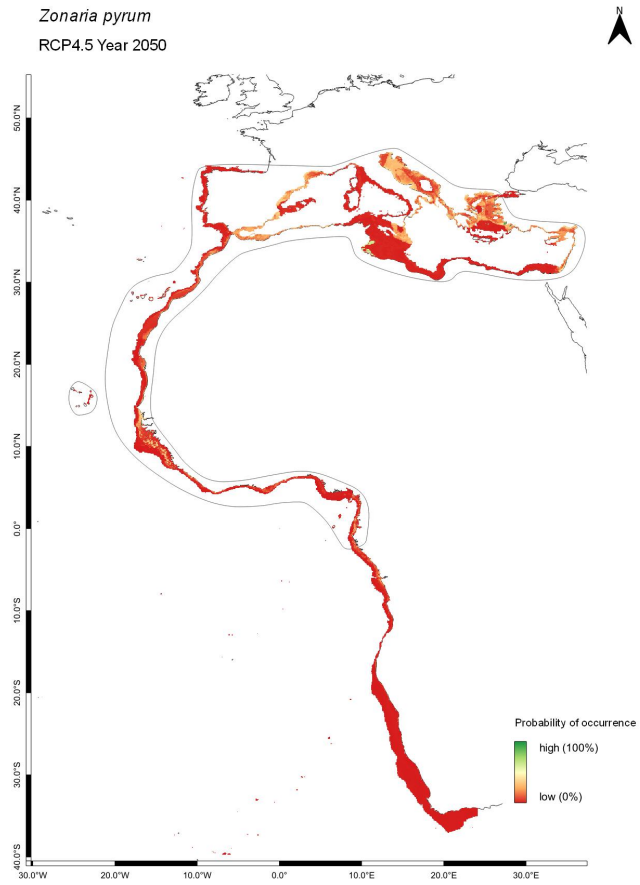
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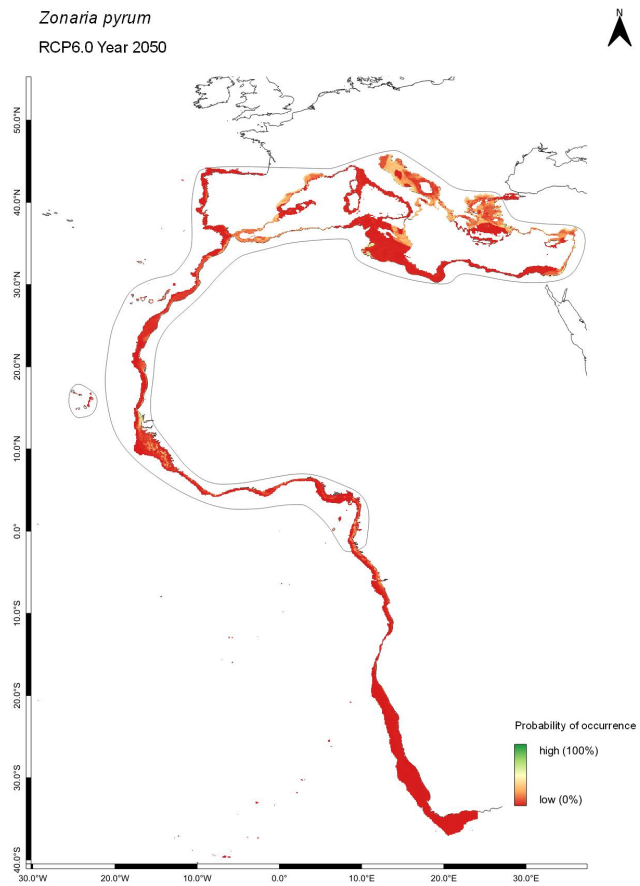
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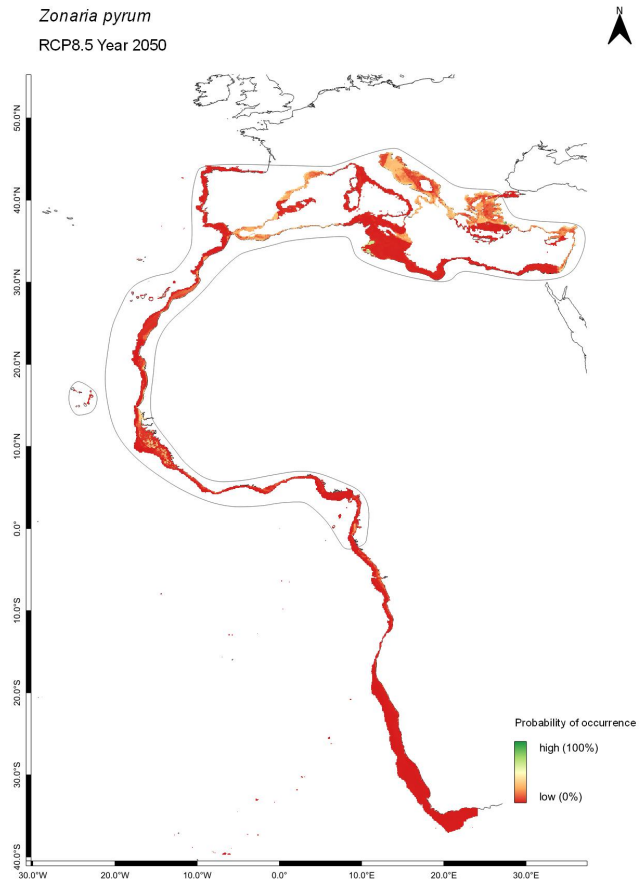
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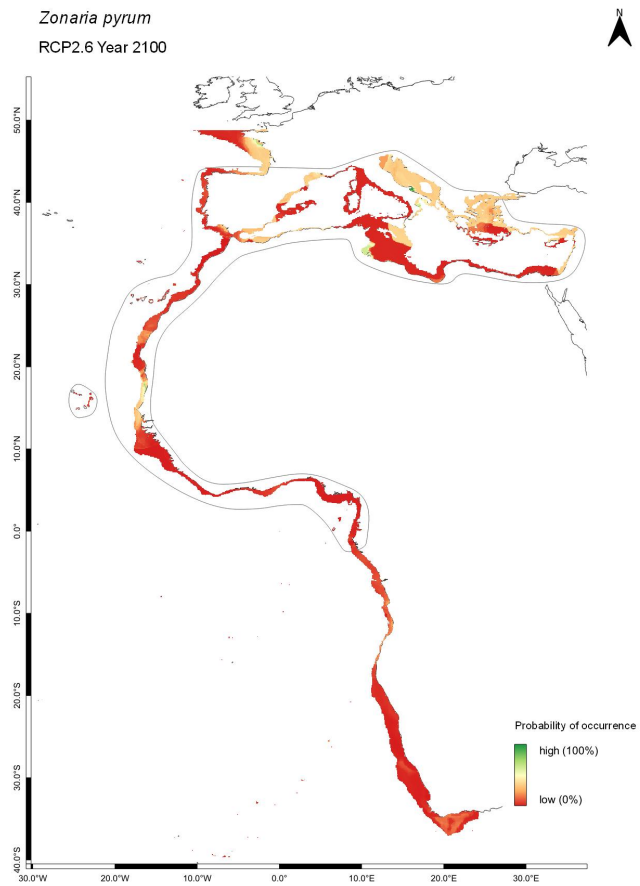
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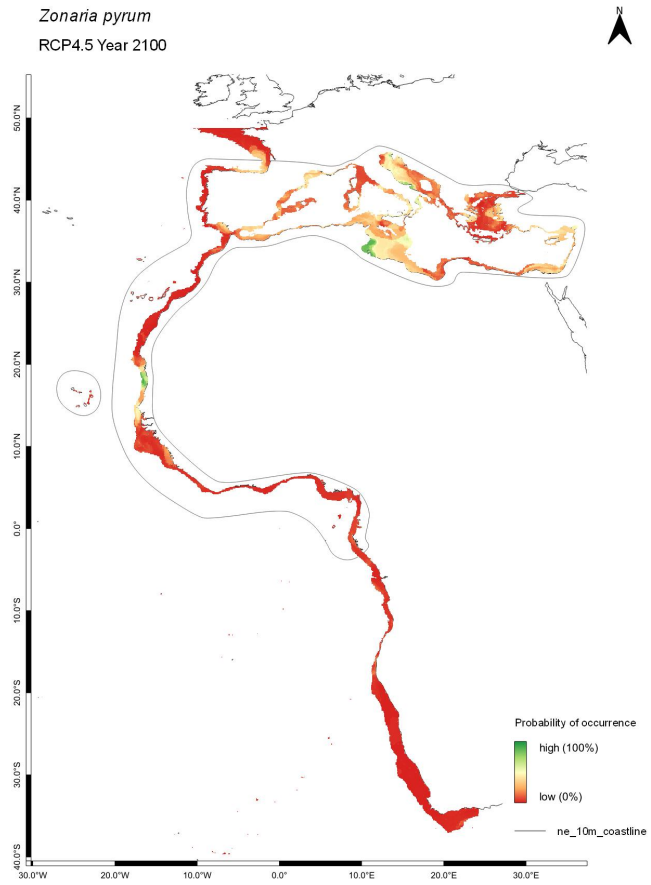
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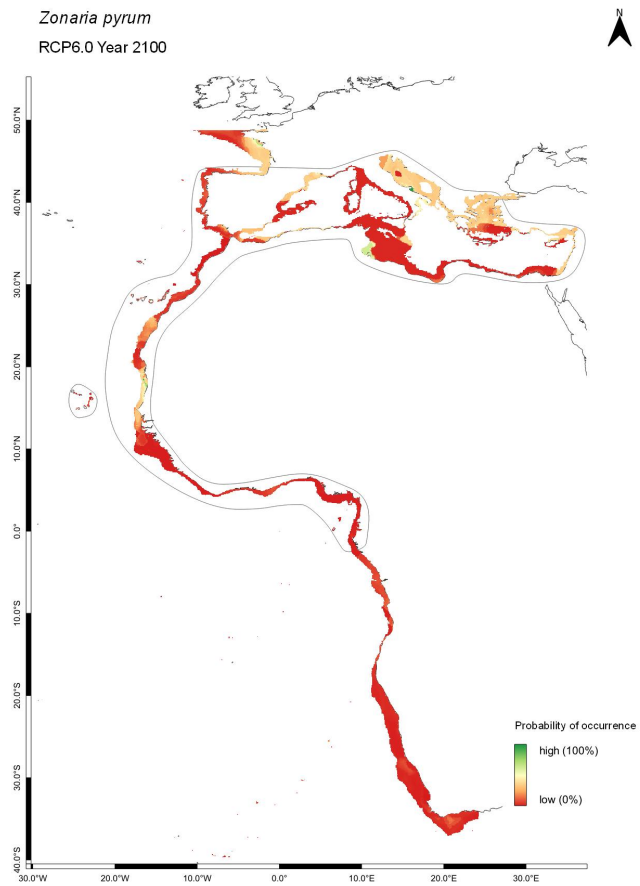
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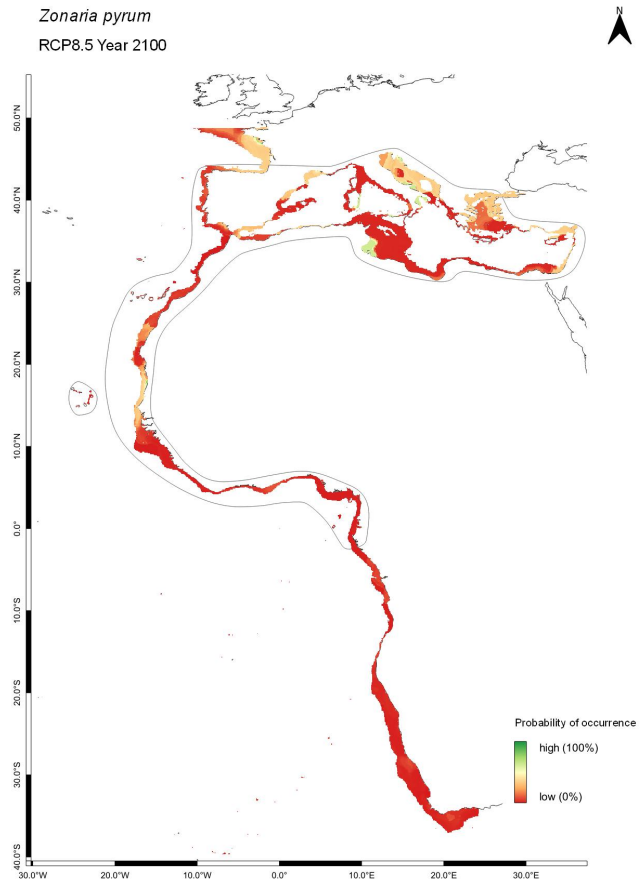
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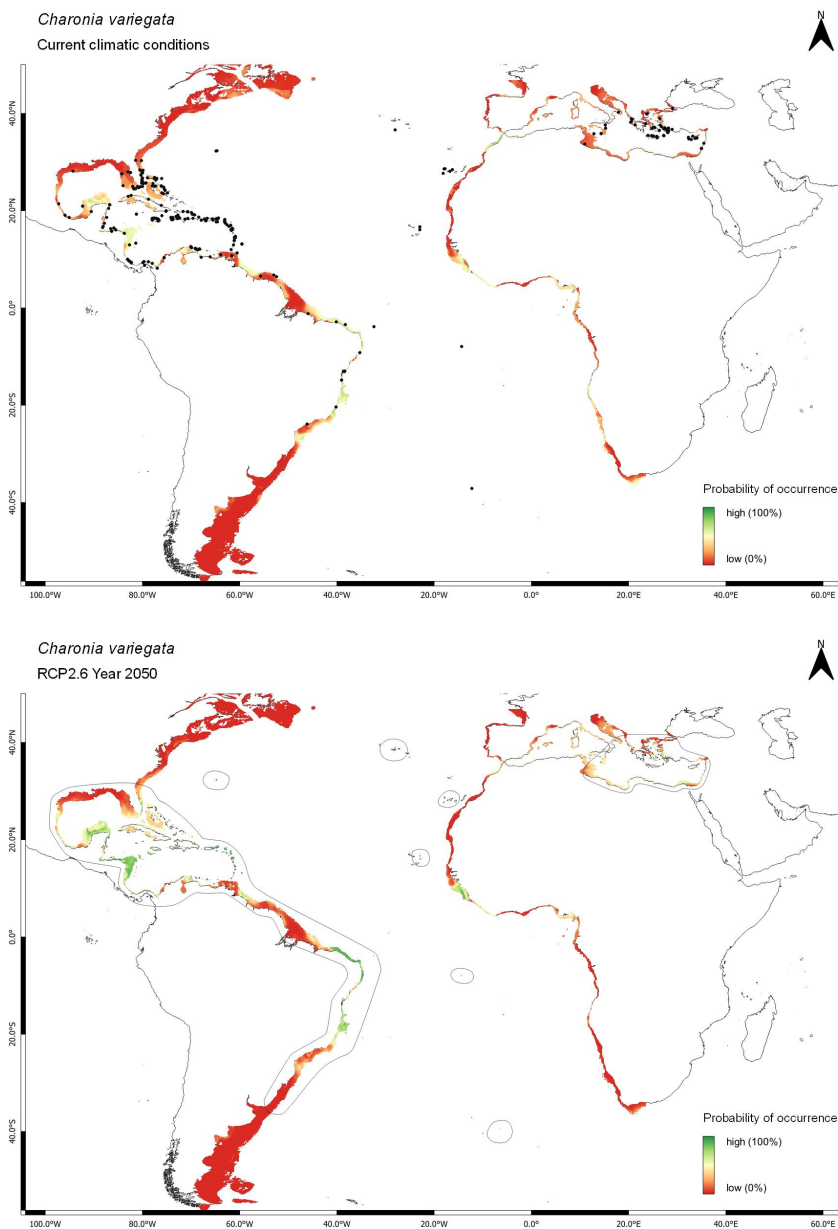
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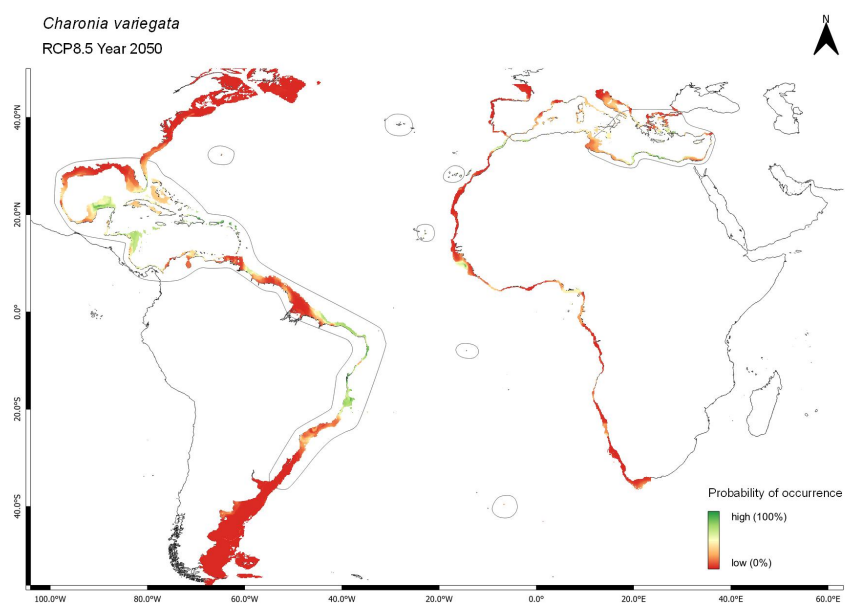
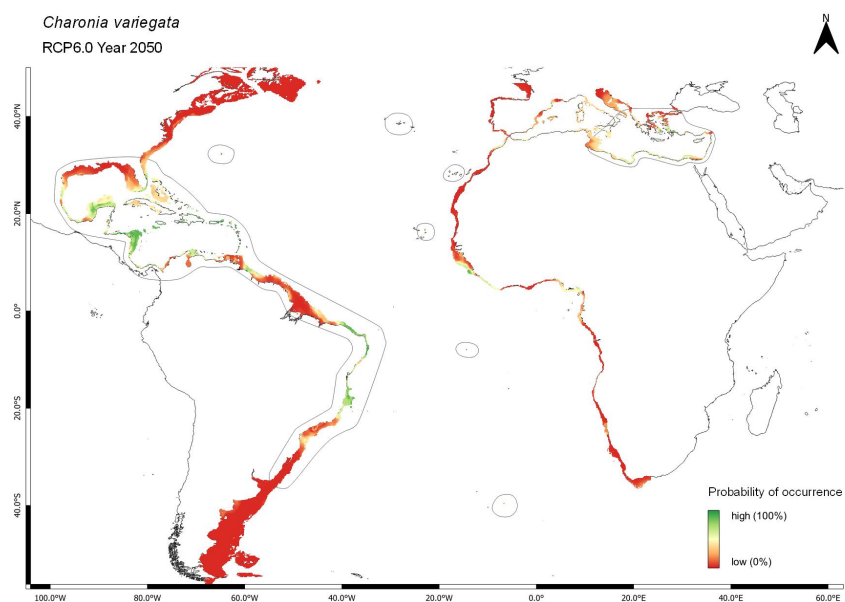
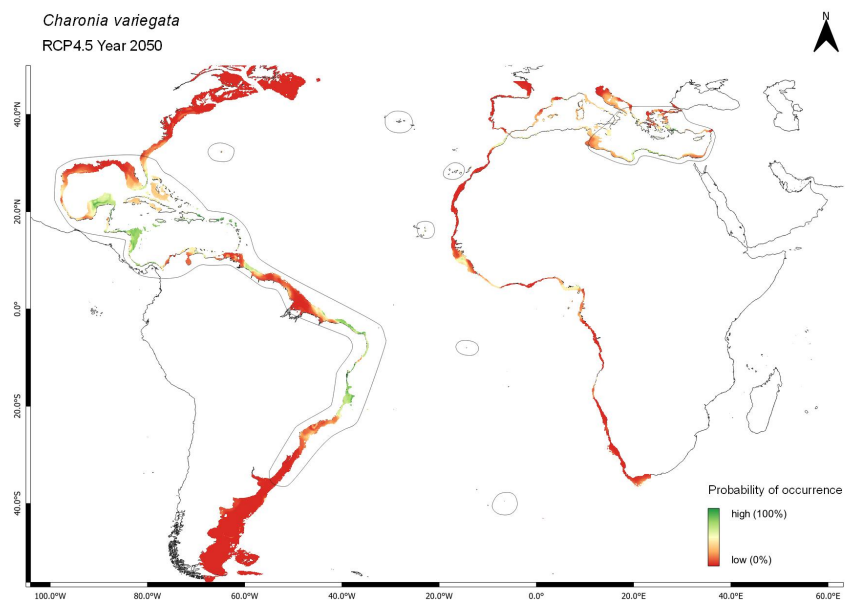


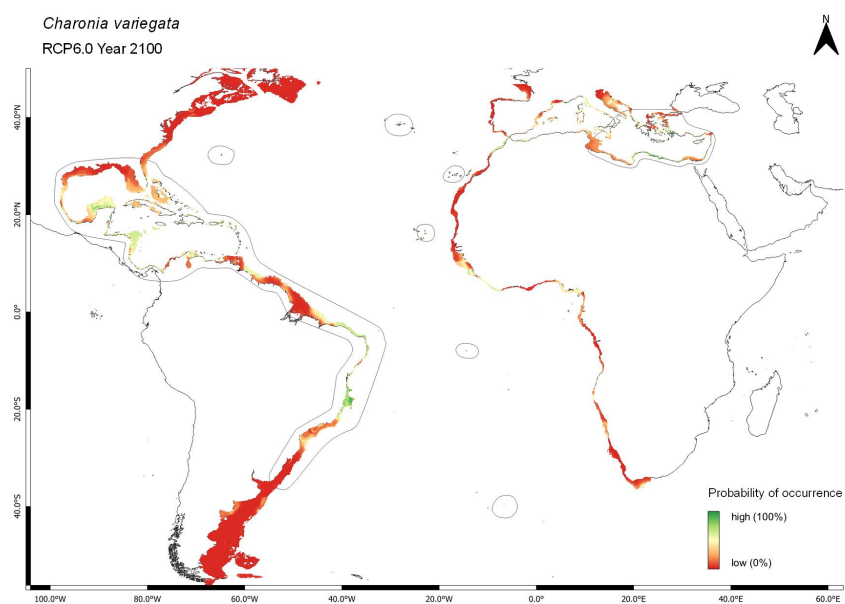
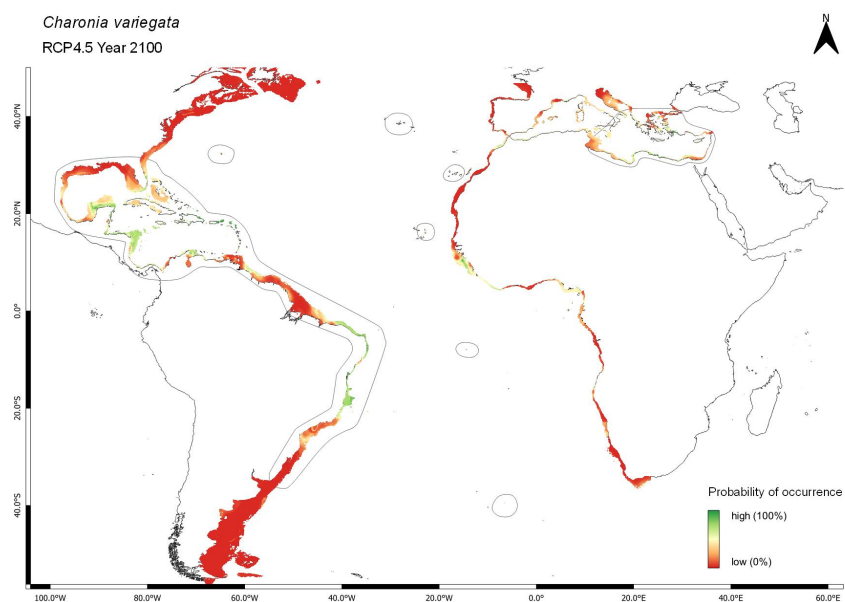
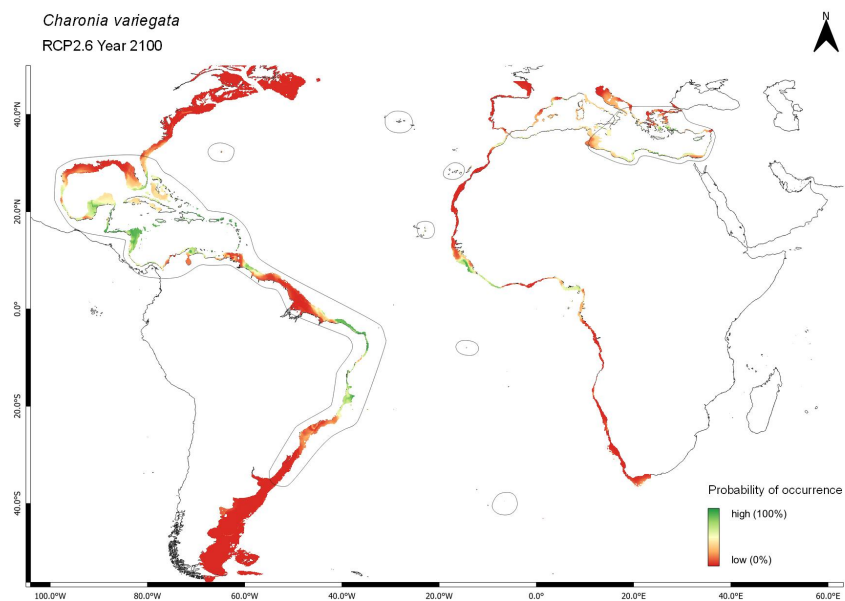
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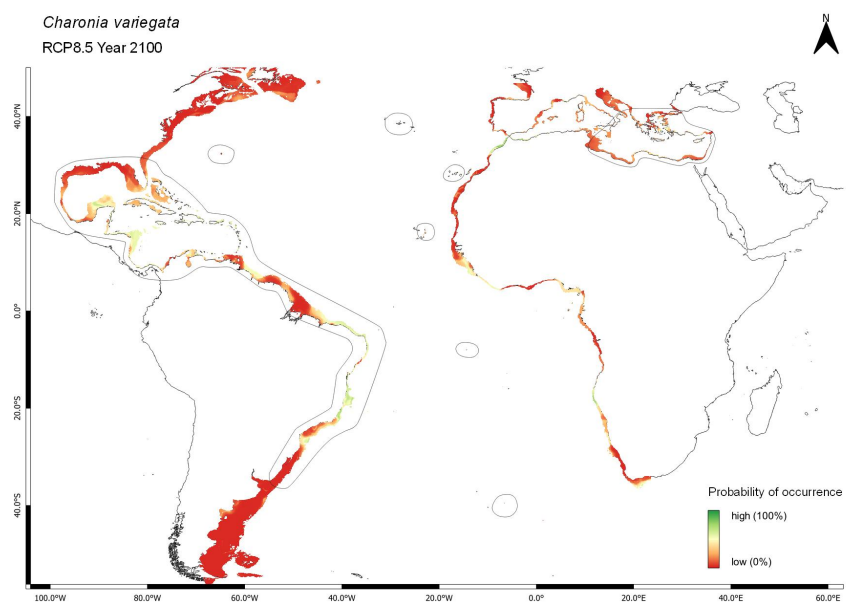


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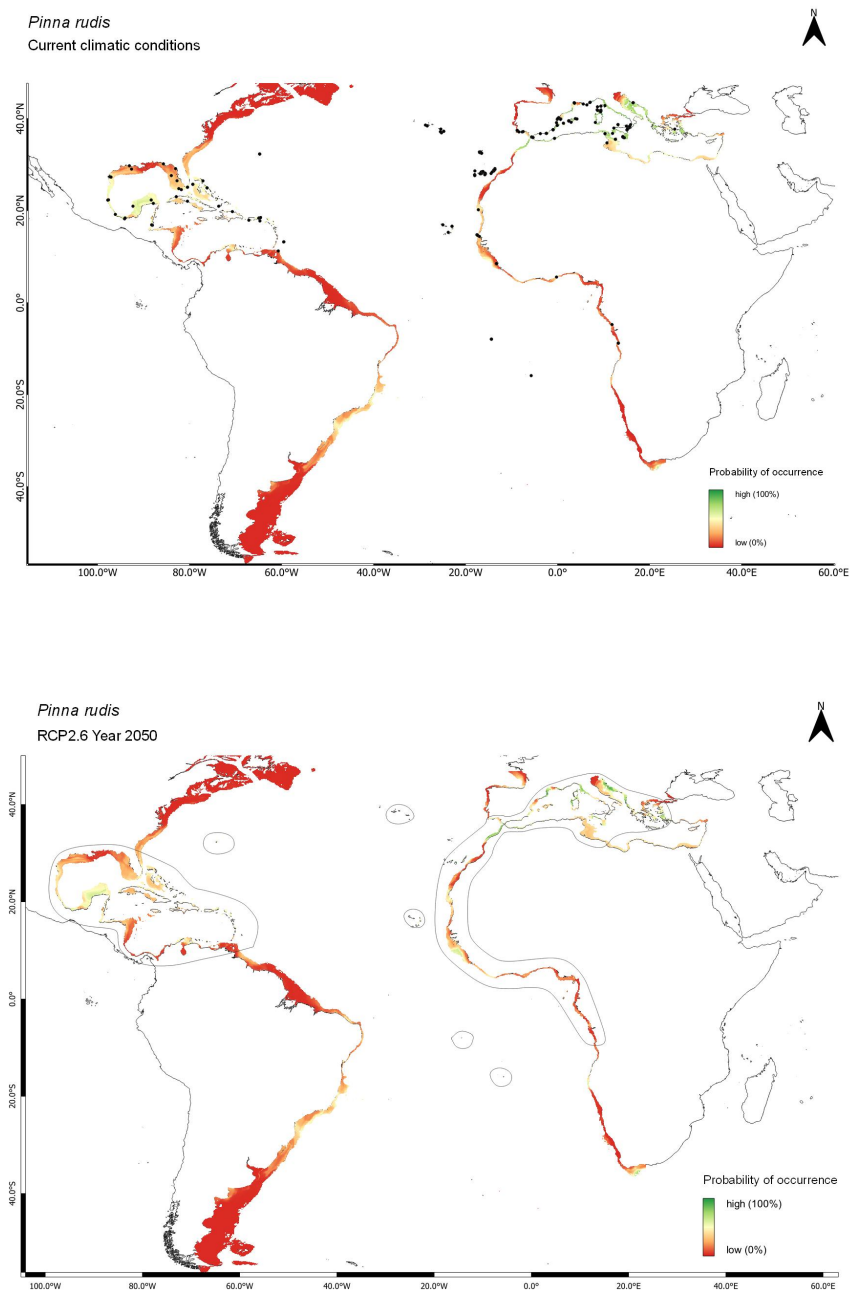


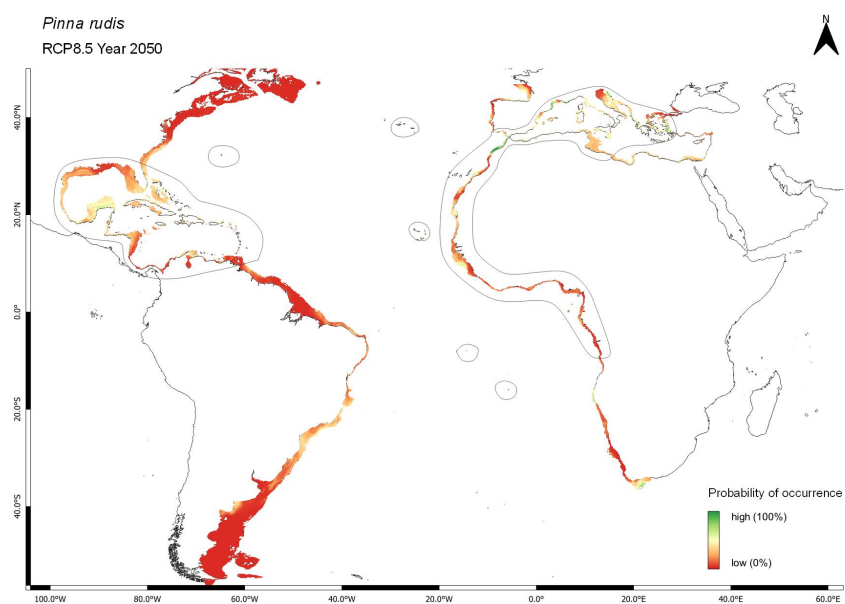
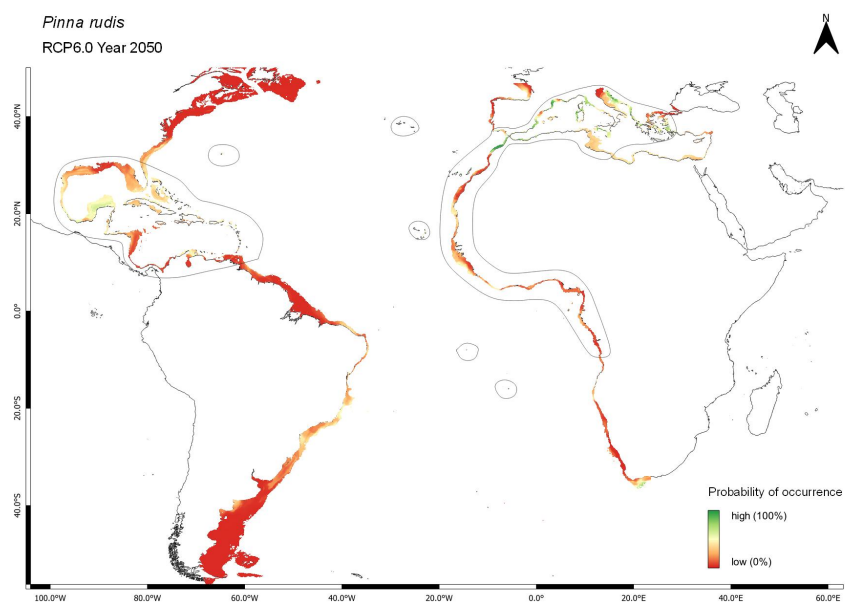
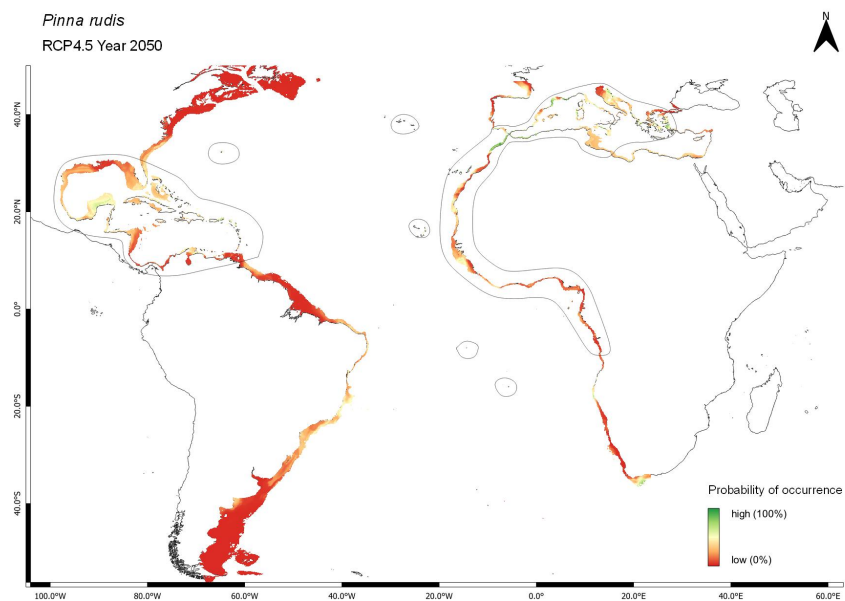


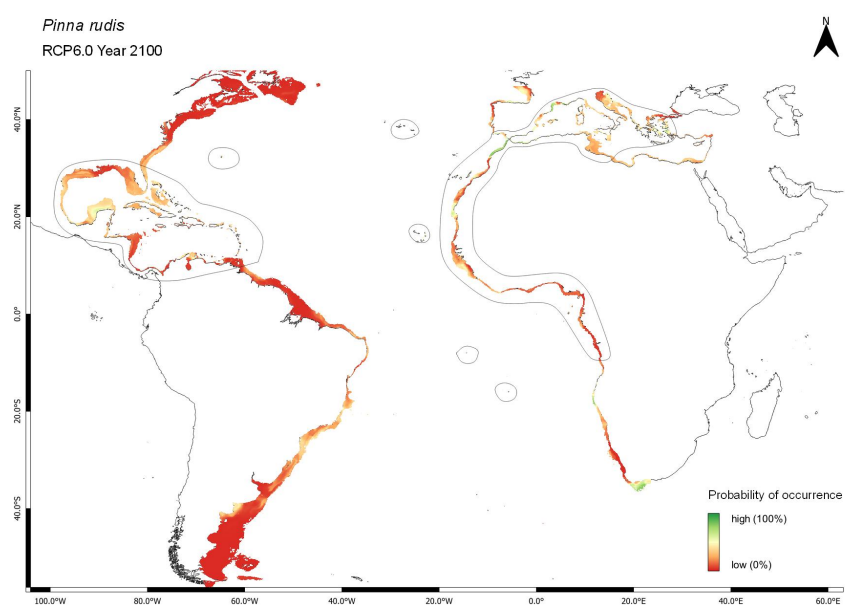
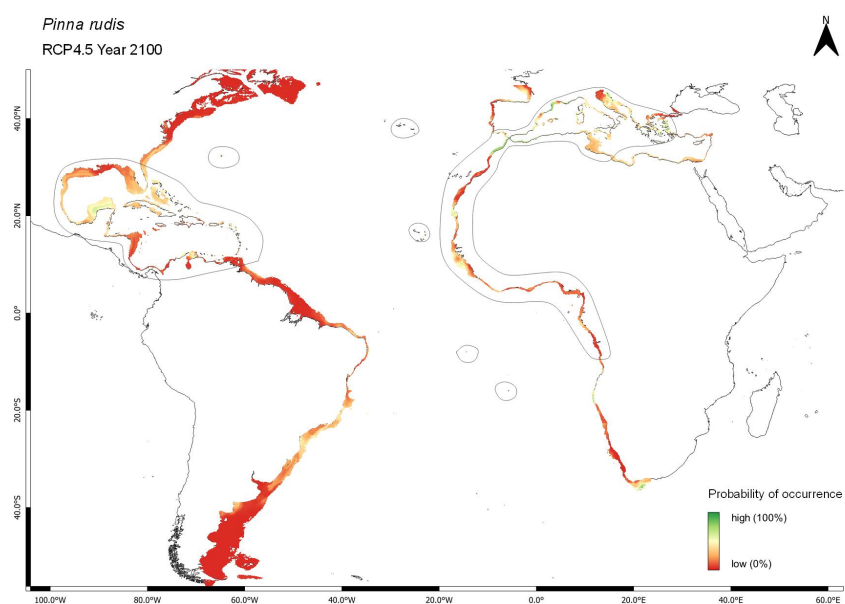
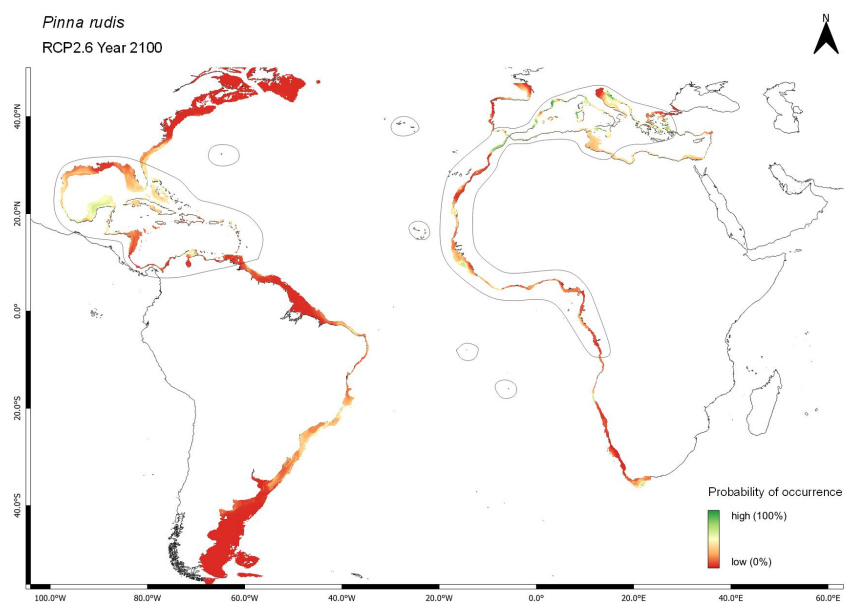


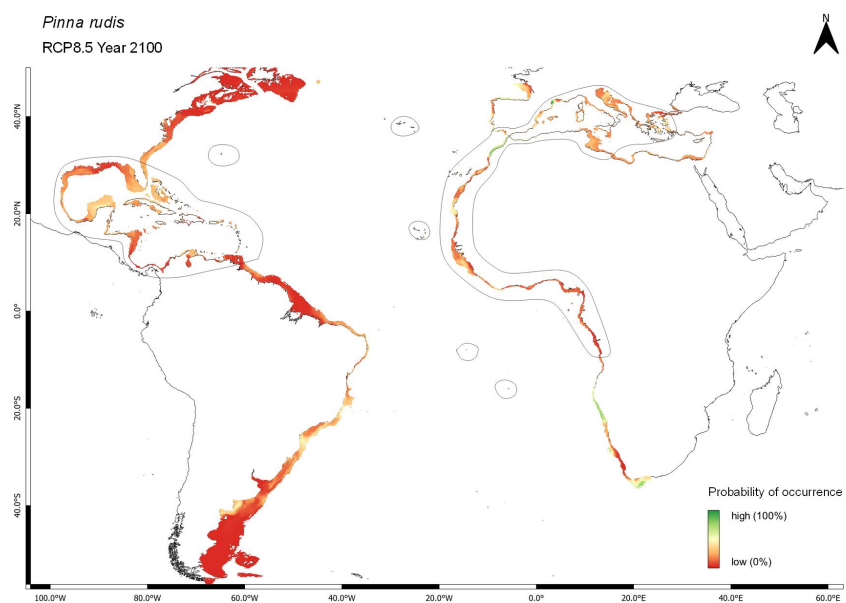


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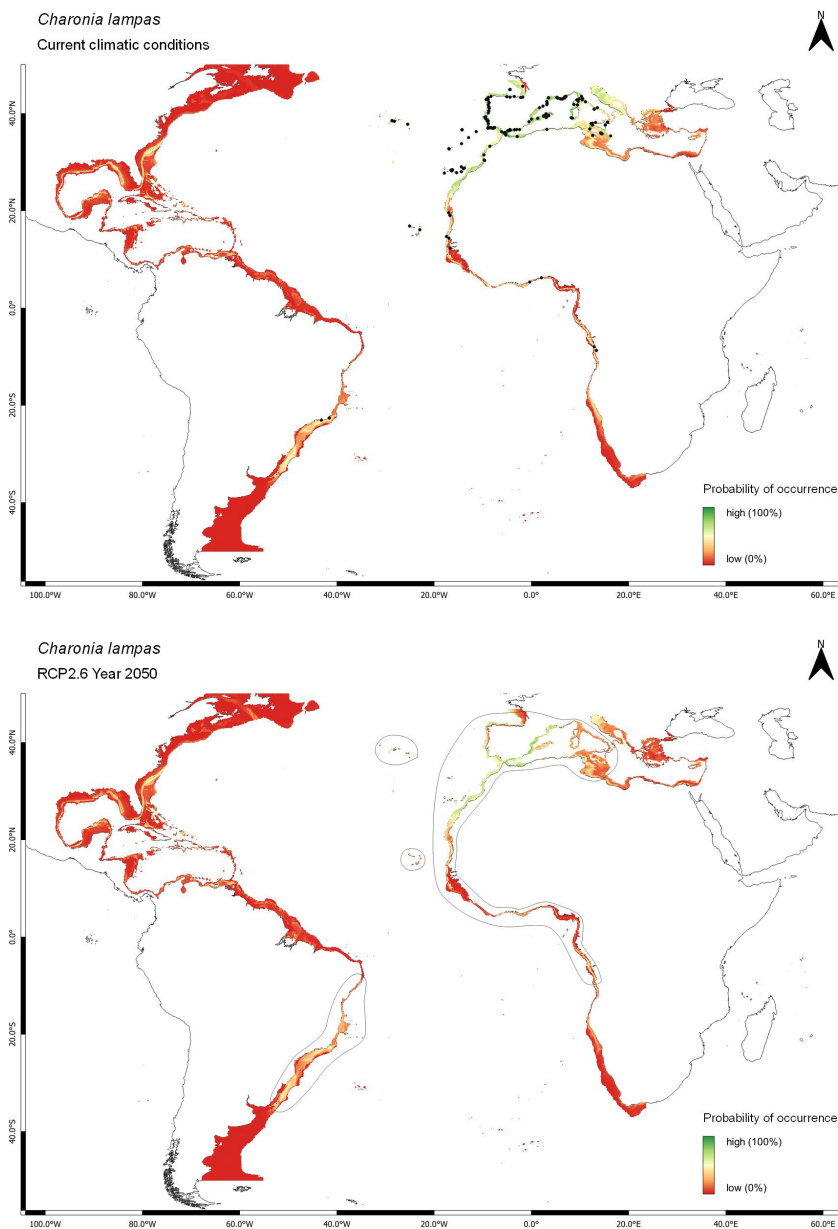


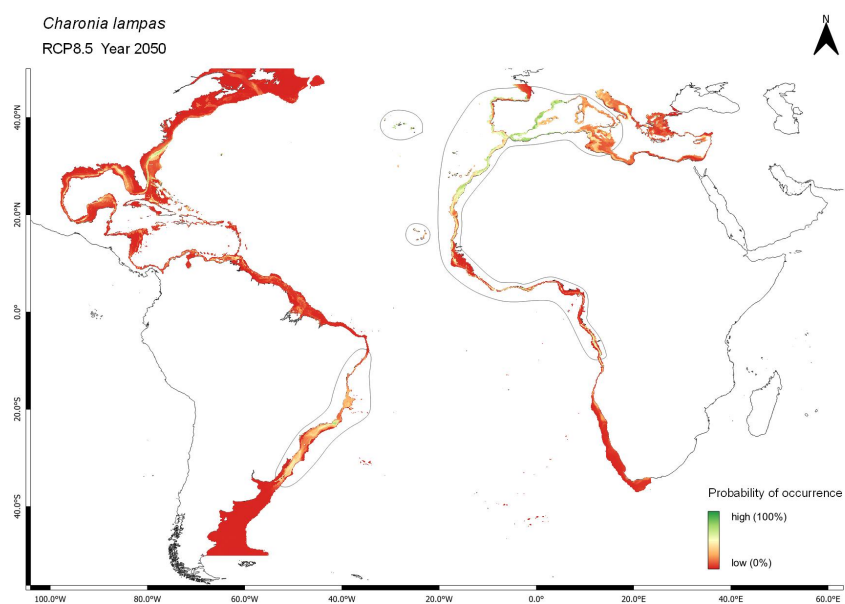
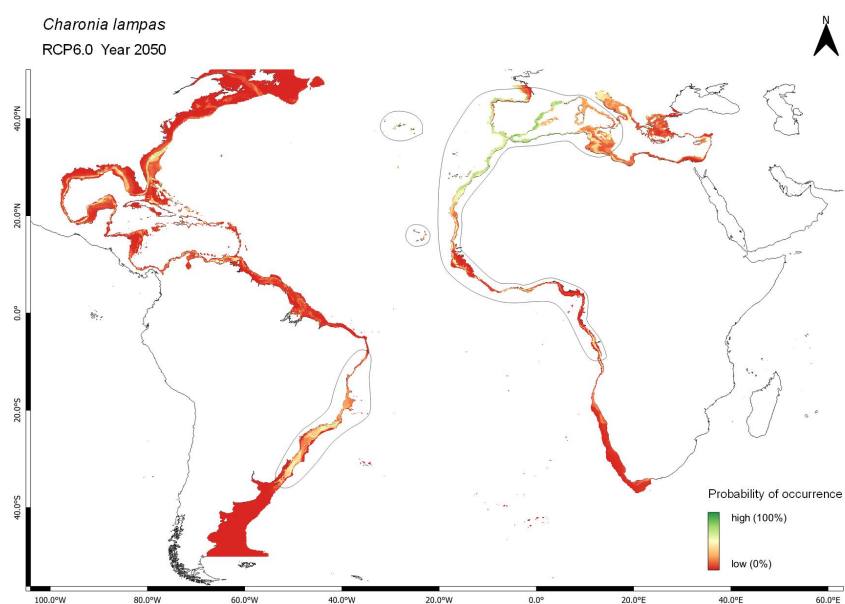
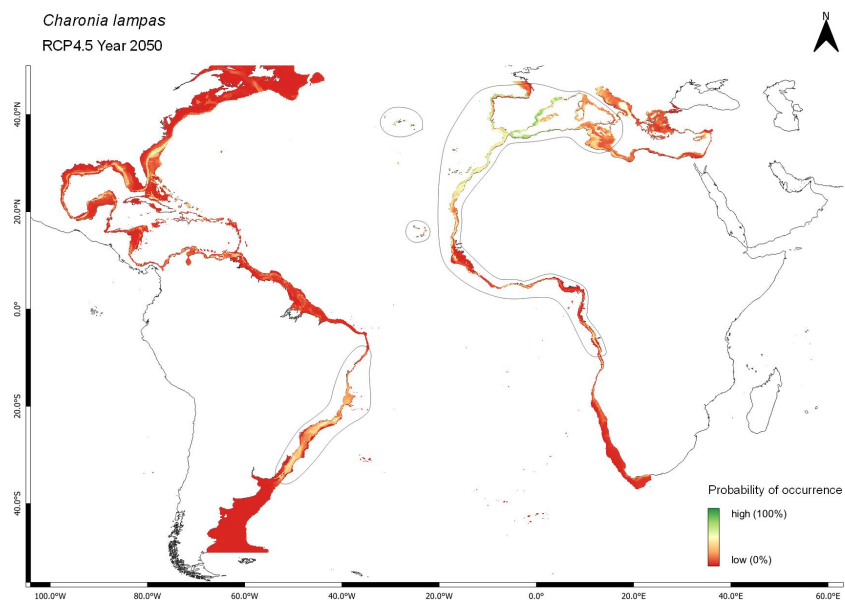


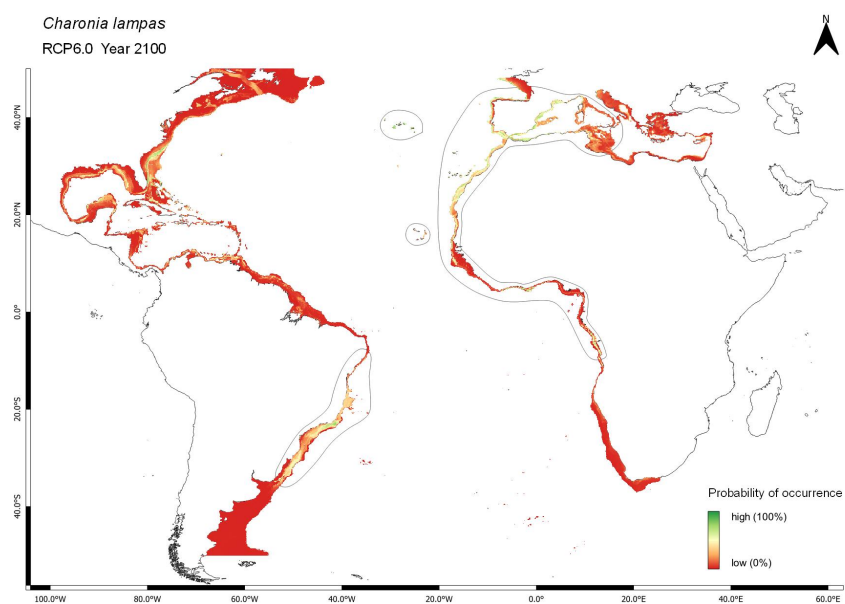
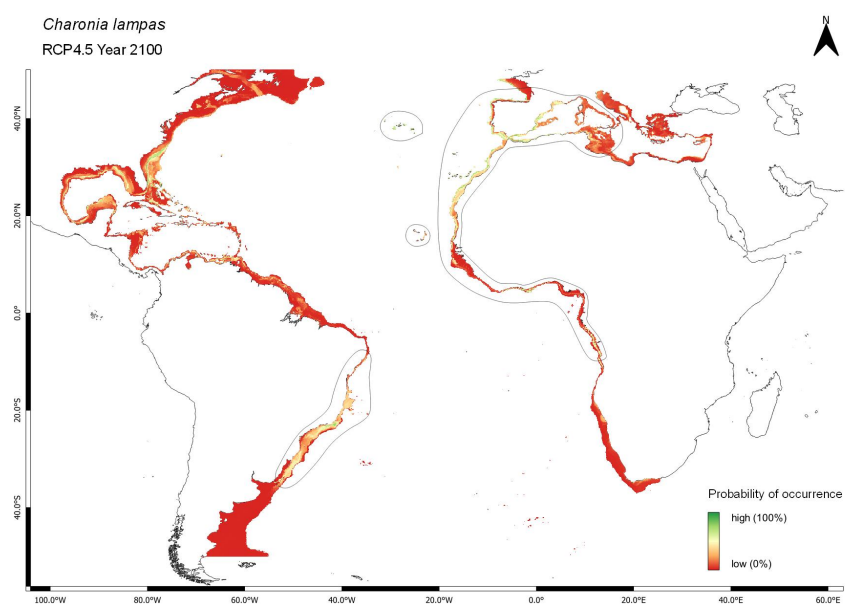
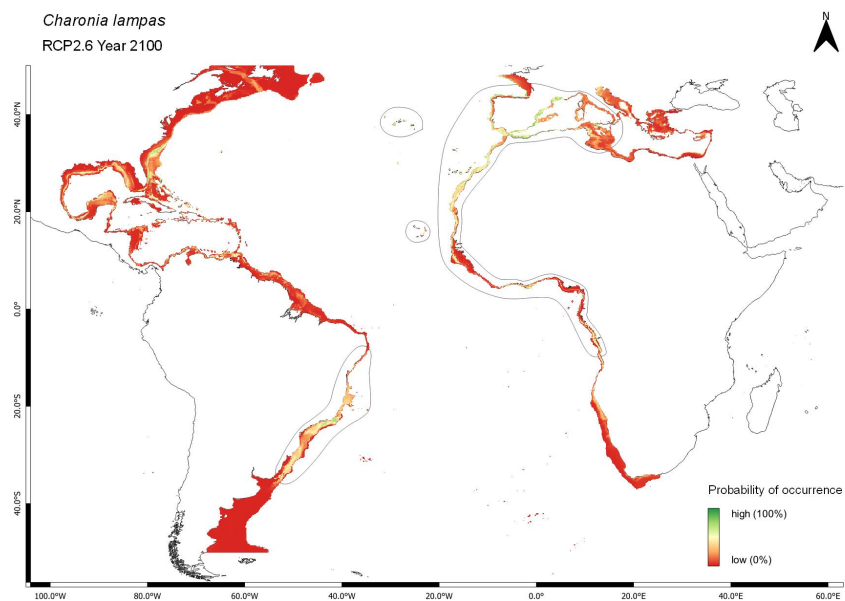


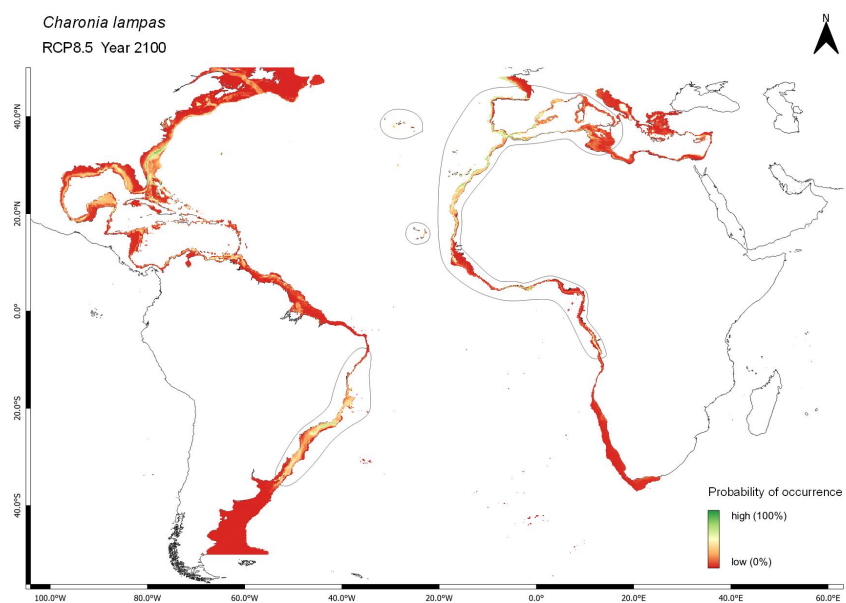


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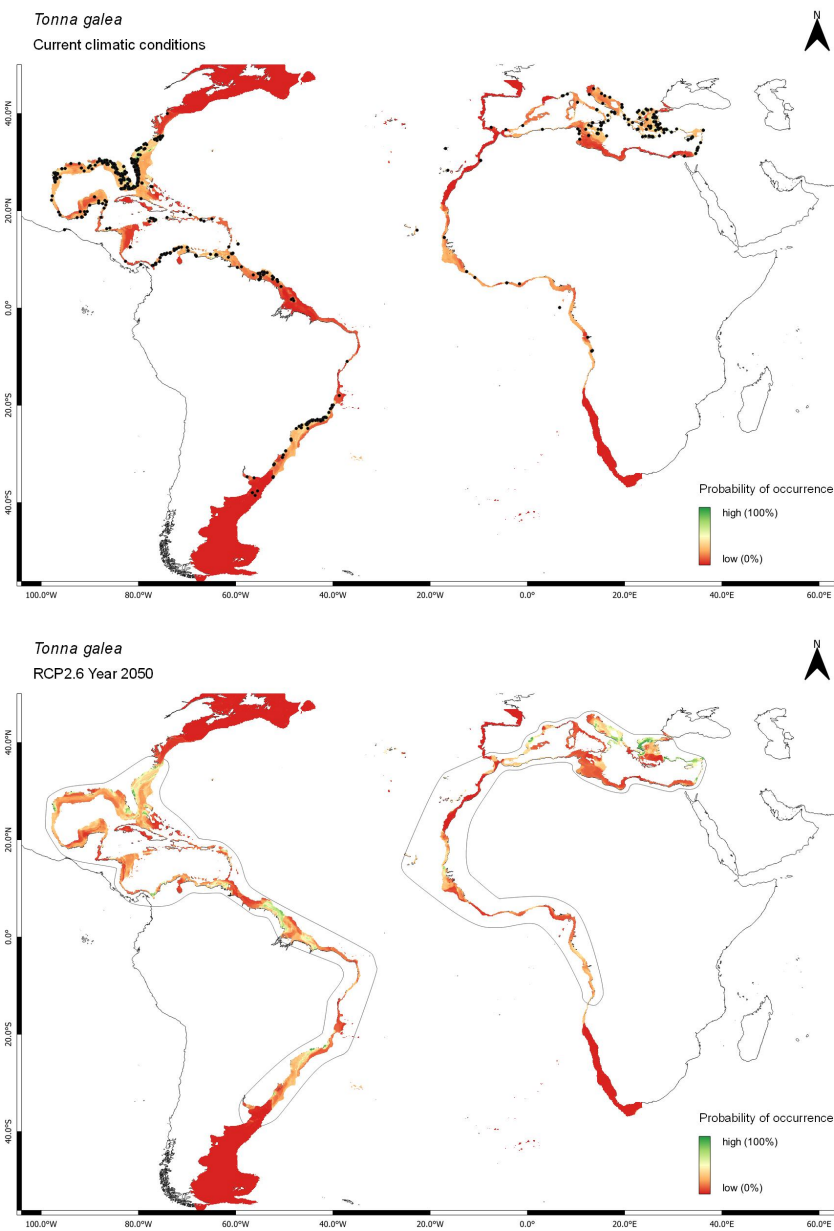


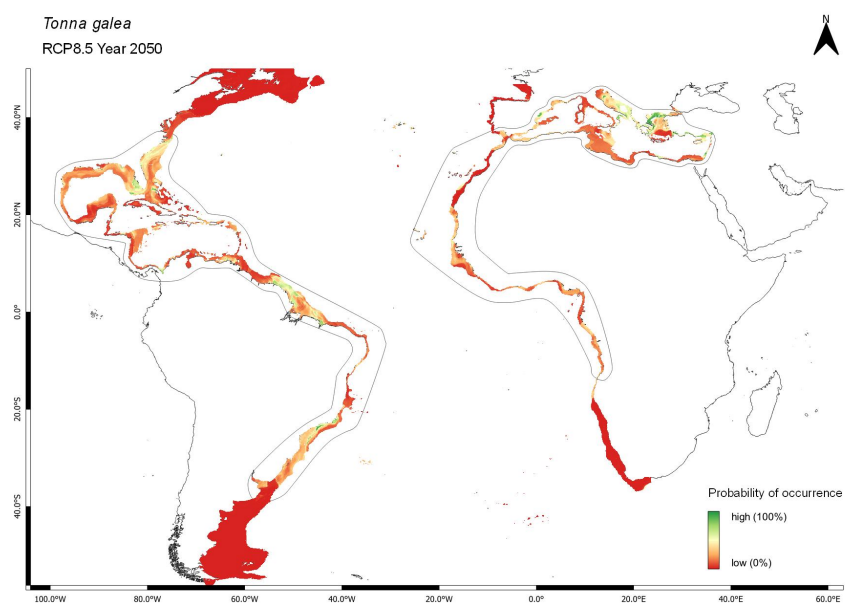
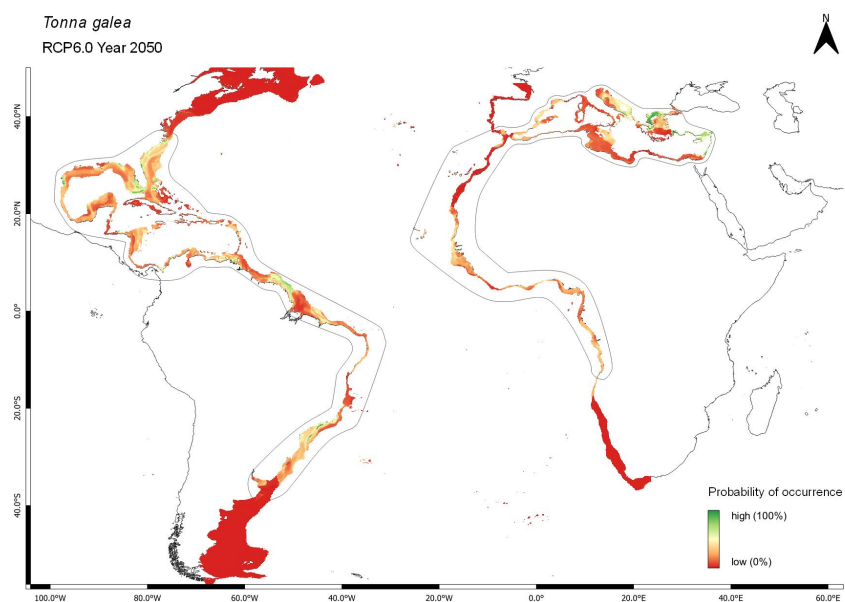
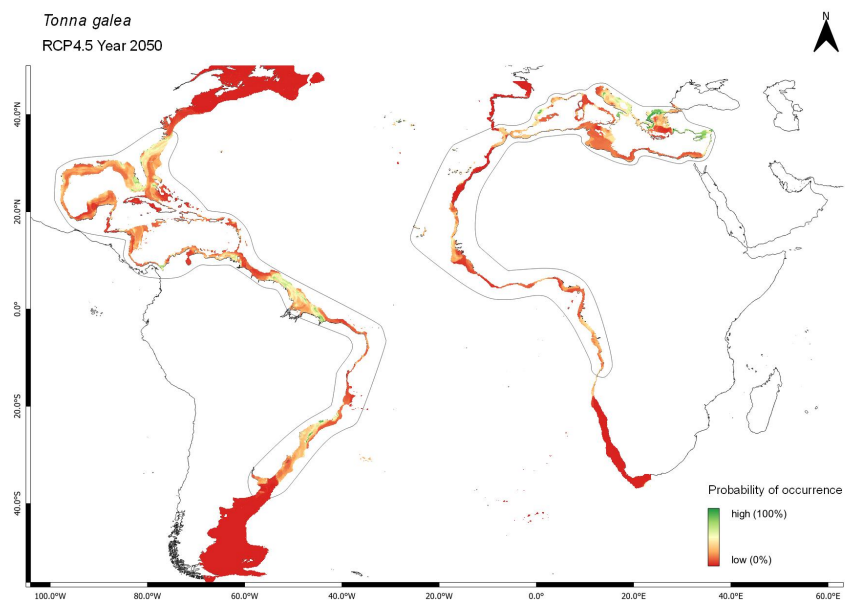


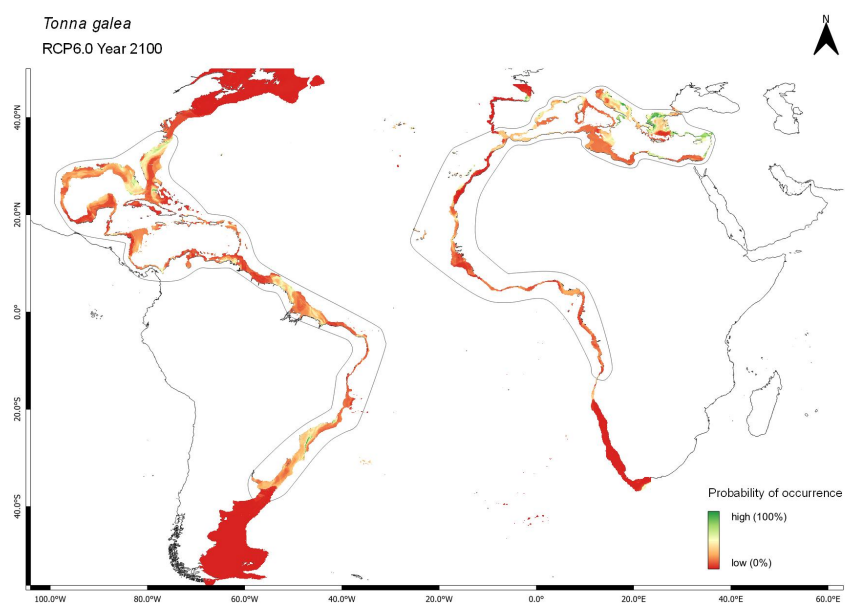
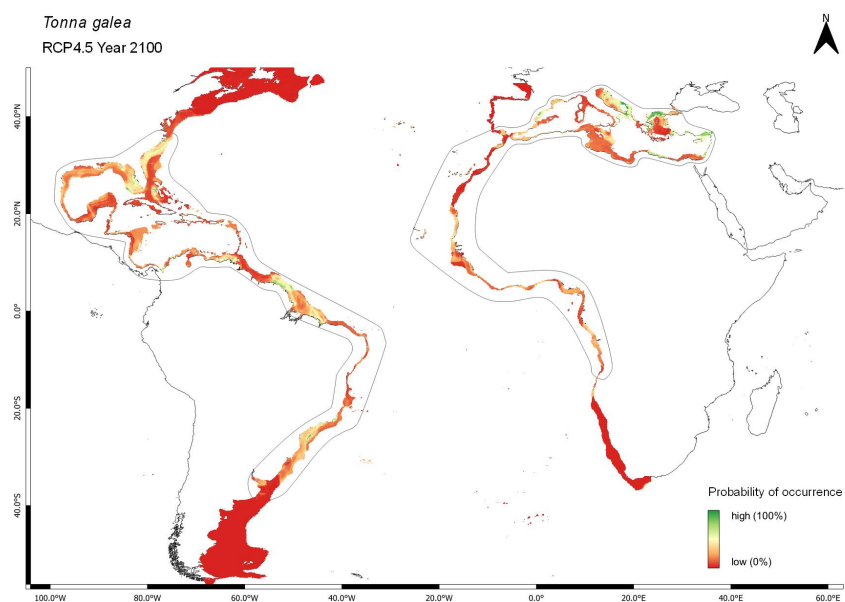
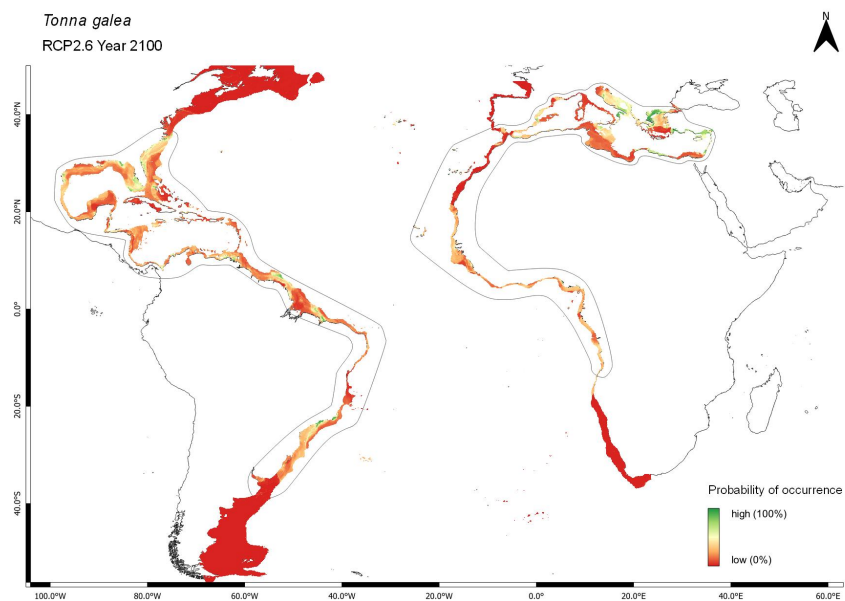


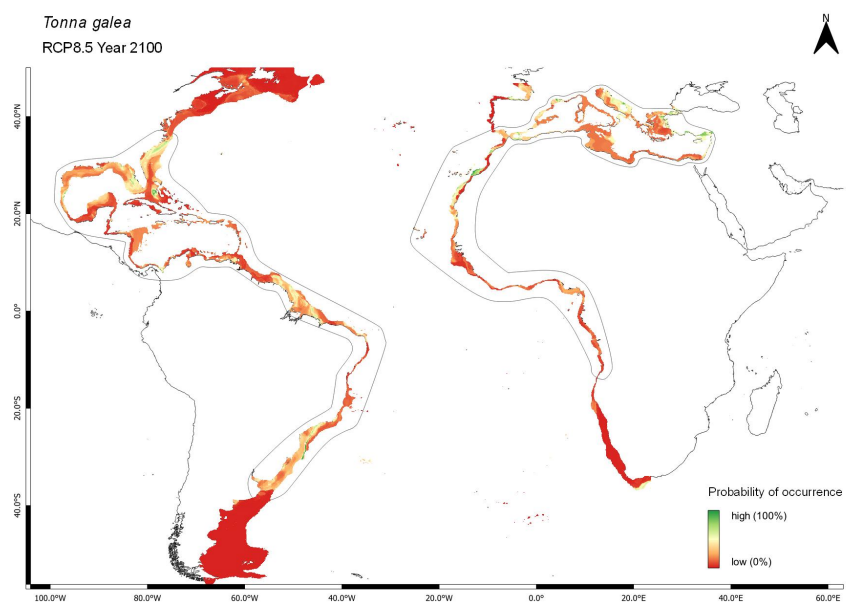


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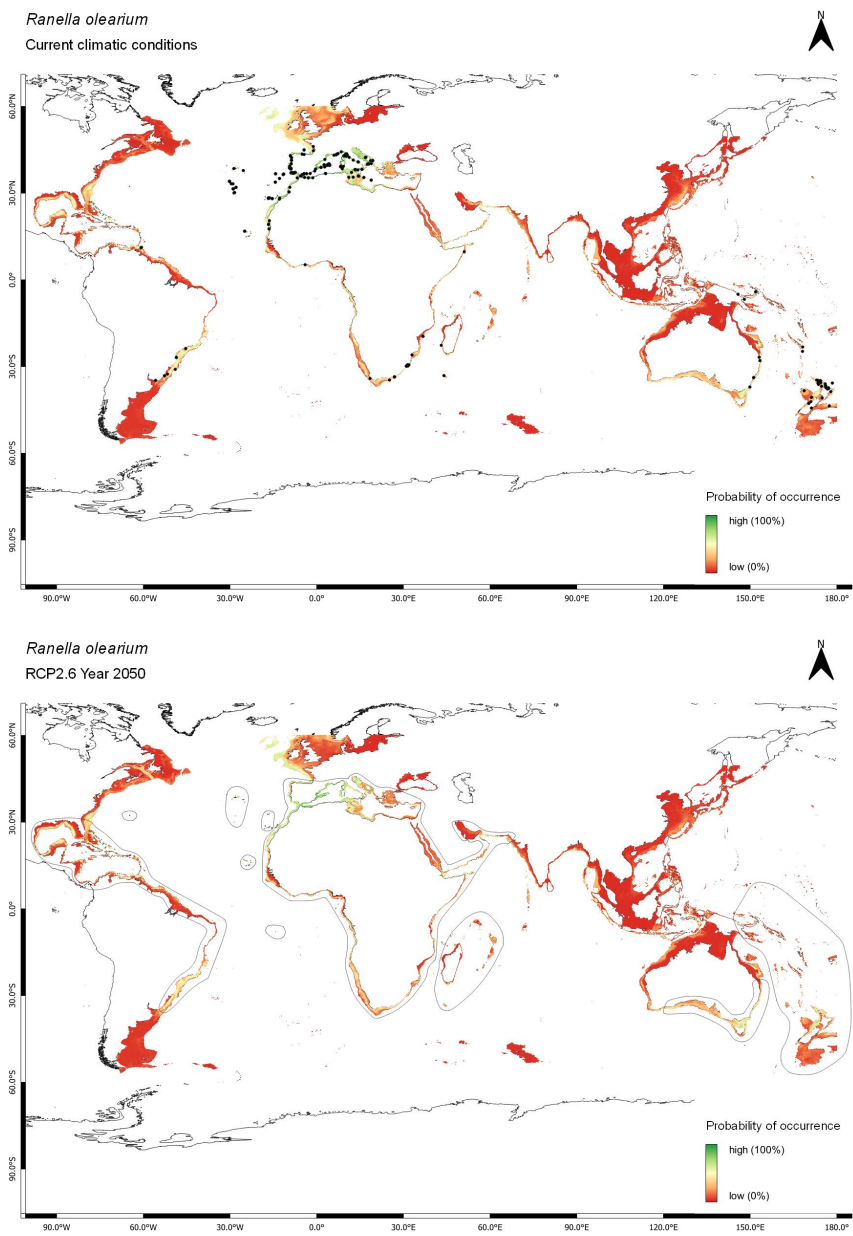




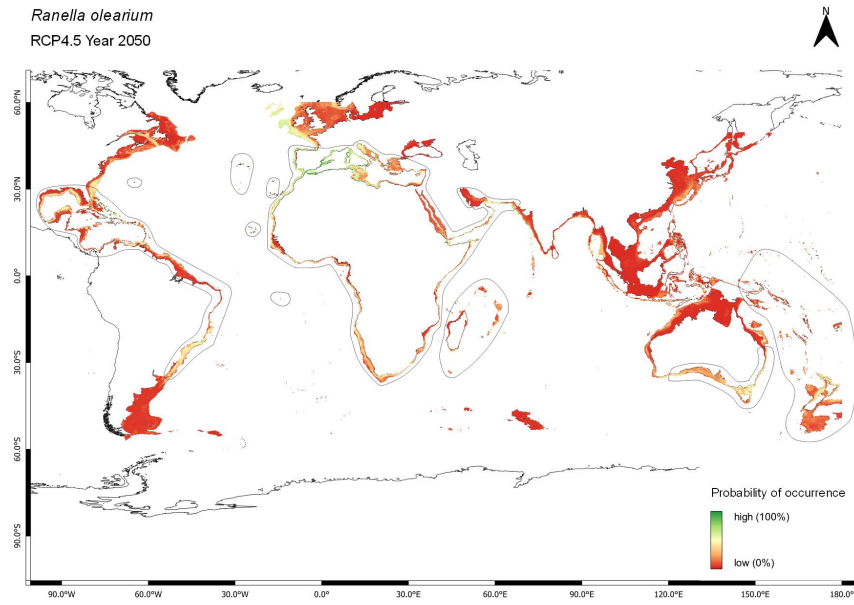




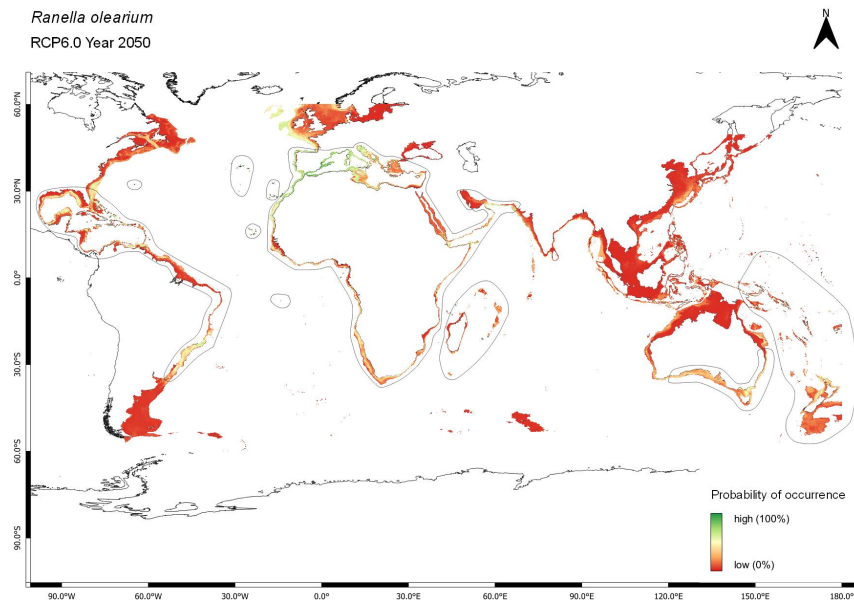
Ranella olearium:



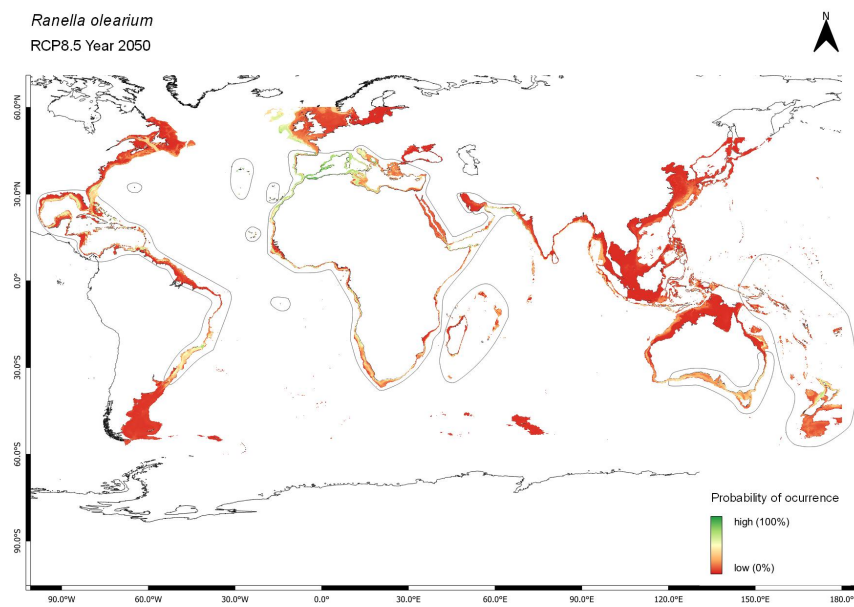
Ranella olearium
RCP4.5 Year 2050



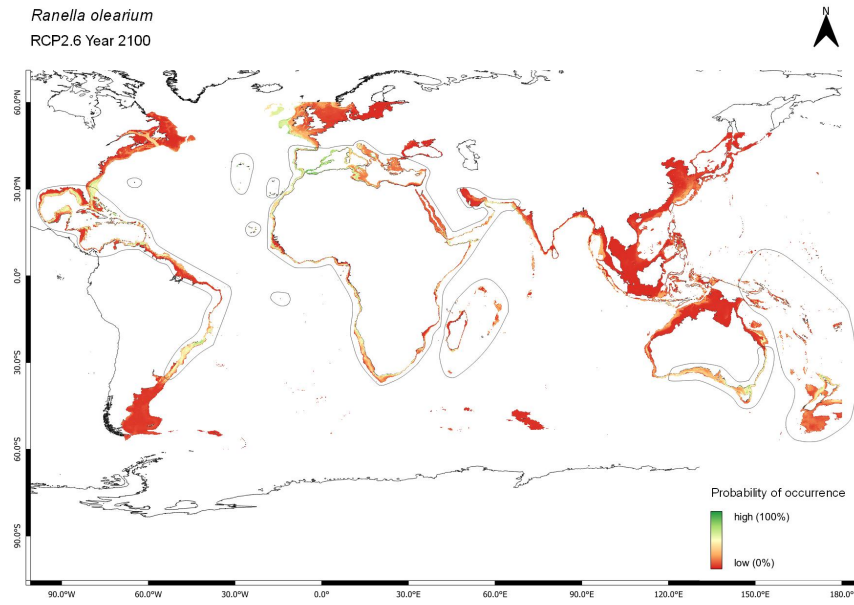
Ranella olearium
RCP6.0 Year 2050



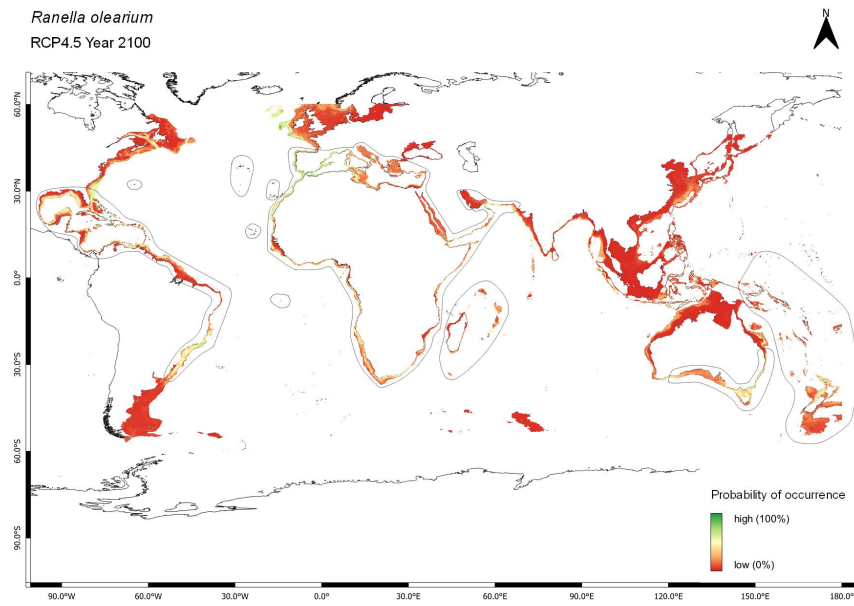
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RCP8.5 Year 2050



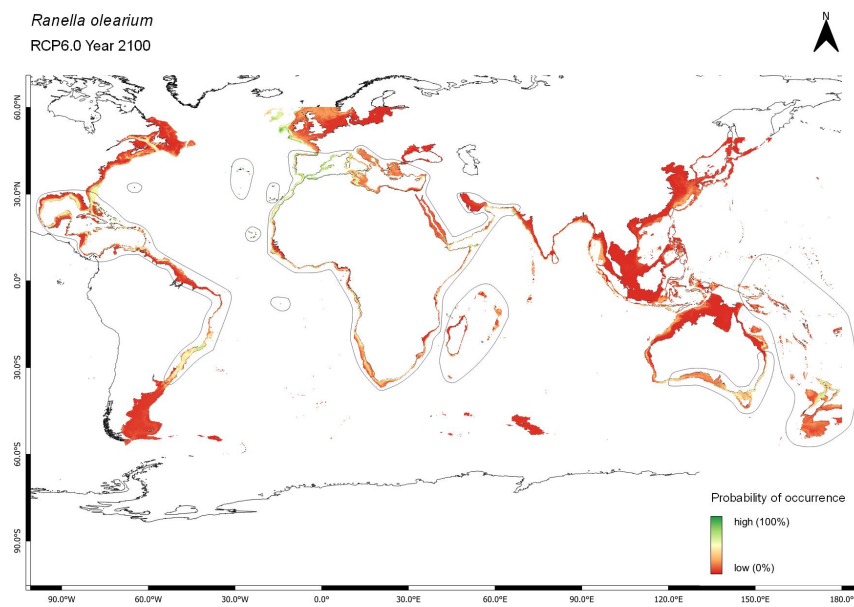
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RCP2.6 Year 2100



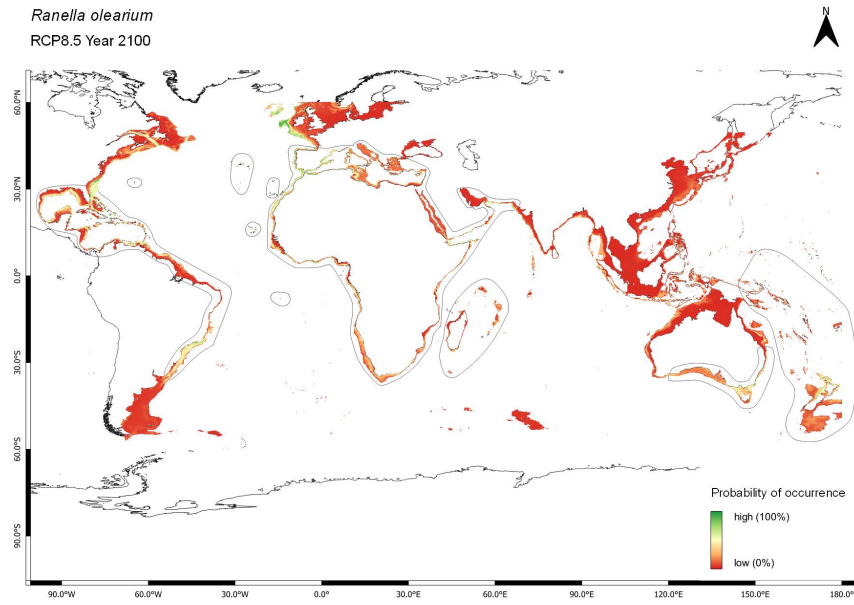
Ranella olearium
RCP4.5 Year 2100



Ranella olearium
RCP6.0 Year 2100



Ranella olearium
RCP8.5 Year 2100



Die globale Erderwärmung führt für viele Arten zu gravierenden Veränderungen ihrer bevorzugten Umweltbedingungen. Marine Mollusken gelten durch ihre nur bedingt mobile Lebensweise als sensible Indikatoren für die ökologischen Konsequenzen der aktuellen Klimaveränderungen in Meeresökosystemen. Anthropogene Einflüsse wie Überfischung, Schadstoffeinträge und Degradation mariner Habitate haben bereits heute zur Gefährdung und einer deutlichen Abnahme von vielen Mollusken-Populationen beigetragen. Um adaptive Schutzstrategien für gefährdete Arten und marine Ökosysteme im Allgemeinen zu entwickeln, ist es maßgeblich, die Auswirkungen von klimatischen Veränderungen auf Arealverbreitungen gefährdeter Arten verstehen und abschätzen zu können.

Für die vorliegende Studie habe ich bioklimatische Artverbreitungsmodelle (Species distribution models, SDM) erstellt, um die potentielle zukünftige Verbreitung von 15 gefährdeten marinen Mollusken Arten unter vier verschiedenen Klimaszenarien (RCP2.6, RCP4.5, RCP6.0, RCP8.5) für die Jahre 2050 und 2100 vorherzusagen. Die untersuchten Arten sind in Küstengewässern des Mittelmeers aber auch zu großen Teilen in anderen Weltmeeren weit verbreitet. In meiner Arbeit habe ich zum einen prognostizierte Arealveränderungen im kompletten Verbreitungsgebiet der modellierten Arten und zum anderen mit speziellem Fokus auf das Mittelmeer quantifiziert. Die Ergebnisse zeigen schon unter dem optimistischsten Klimaszenario (RCP2.6), dass klimatische Veränderungen zu einer drastischen Reduktion von geeigneten Habitaten der untersuchten Arten führen könnten und deuten außerdem auf ein erhöhtes Aussterberisiko für die analysierten Mittelmeer Endemiten hin. Meine Arbeit zeigt die tiefgreifenden Auswirkungen des anthropogenen Klimawandels auf marine Ökosysteme und insbesondere auf das Mittelmeer.