

Projected climate changes threaten ancient refugia of kelp forests in the North Atlantic

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Abstract

Intraspecific genetic variability is critical for species adaptation and evolution and yet it is generally overlooked in projections of the biological consequences of climate change. We ask whether ongoing climate changes can cause the loss of important gene pools from North Atlantic relict kelp forests that persisted over glacial–interglacial cycles. We use ecological niche modelling to predict genetic diversity hotspots for eight species of large brown algae with different thermal tolerances (Arctic to warm temperate), estimated as regions of persistence throughout the Last Glacial Maximum (20,000 YBP), the warmer Mid-Holocene (6,000 YBP), and the present. Changes in the genetic diversity within ancient refugia were projected for the future (year 2100) under two contrasting climate change scenarios (RCP2.6 and RCP8.5). Models predicted distributions that matched empirical distributions in cross-validation, and identified distinct refugia at the low latitude ranges, which largely coincide among species with similar ecological niches. Transferred models into the future projected polewards expansions and substantial range losses in lower latitudes, where richer gene pools are expected (in Nova Scotia and Iberia for cold affinity species and Gibraltar, Alboran, and Morocco for warm-temperate species). These effects were projected for both scenarios but were intensified under the extreme RCP8.5 scenario, with the complete borealization (circum-Arctic colonization) of kelp forests, the redistribution of the biogeographical transitional zones of the North Atlantic, and the erosion of global gene pools across all species. As the geographic distribution of genetic variability is unknown for most marine species, our results represent a baseline for identification of locations potentially rich in unique phylogeographic lineages that are also climatic relicts in threat of disappearing.

KEYWORDS

climate change, climatic refugia, ecological niche modelling, genetic diversity, kelp forests, North Atlantic, range shifts

1 | INTRODUCTION

Genetic diversity within species varies geographically as a result of past demographic processes and range shifts. In the Oceans, climate-driven range shifts are ongoing (e.g., Hoegh-Guldberg & Bruno, 2010; Perry, Low, Ellis, & Reynolds, 2005) and can cause the loss of ancient gene pools from populations that have persisted in refugia from past climate extremes (Assis, Serrão, Claro, Perrin, & Pearson, 2014; Neiva

et al., 2015). Despite the importance of these patterns and processes for adaptation and evolution, such intraspecific impacts of climate change have rarely been examined (Pauls, Nowak, Bálint, & Pfenniger, 2013). One reason is that relevant data on the geographical structure of marine diversity are rarely available below the species level. Ecological niche models (e.g., Peterson et al., 2011) can be used to estimate diversity patterns by hindcasting distributions over time and examining potential areas of persistence, extinction, and

colonization (e.g., Assis, Lucas, Bárbara, & Serrão, 2016; Assis et al., 2014; Assis, Coelho, et al., 2016; Neiva, Assis, Fernandes, Pearson, & Serrão, 2014). The inference of stable refugial populations potentially harbouring disproportional levels of genetic diversity can be further extended to anticipate future extinctions under different scenarios of climate change (Neiva et al., 2015; Pfenninger, Bálint, & Pauls, 2012).

The consequences of local population extinction for a species gene pool largely depend on how genetic diversity is distributed throughout the ranges. Geographically skewed distributions of intraspecific diversity are more susceptible to climate change, particularly if bottlenecks take place in populations with higher levels of diversity (e.g., Lourenço et al., 2016; Nicastró et al., 2013). Spatially skewed genetic diversity is expected in species with limited dispersal that were exposed to past climate oscillations across their ranges. While edge populations were subject to founder effects and extinctions under contrasting climate conditions, long-term persistence in refugia allowed the retention of ancient genetic diversity, and regional accumulation of greater proportions of the species diversity (Assis et al., 2014; Maggs et al., 2008; Neiva et al., 2016; Provan & Bennett, 2008), regardless of the relative size of current populations. Small isolated populations of species with limited dispersal are often found persisting in refugial ranges while harbouring high levels of unique genetic diversity not found anywhere else throughout ranges (e.g., Assis, Coelho, et al., 2016; Diekmann & Serrão, 2012). Threats to these refugial areas pose disproportionate risks for species losing adaptive variation for selection (Hampe & Petit, 2005).

Ecological Niche Modeling (ENM), also known as species distributions models, bioclimatic envelope models, or habitat suitability models (for review and definition see, e.g., Peterson et al., 2011; Araújo & Peterson, 2012), has been used to explore the relationships between climate dynamics and several manifestations of species biogeography (Metcalf et al., 2014; Nogués-Bravo, Rodríguez, Hortal, Batra, & Araújo, 2008). One such application is the inference of the distribution of refugial regions free from past extinctions or major bottlenecks. These can be identified by intersecting potential species distributions along present and past climate extremes, such as glacial–interglacial cycles (e.g., Maguire, Nieto-Lugilde, Fitzpatrick, Williams, & Blois, 2015; Terribile et al., 2012), including the Last Glacial Maximum (LGM; 20,000 YBP) and the warmer Mid-Holocene (MH; 6,000 YBP). The modelled distribution of climate refugia often coincides with populations harbouring high and distinct genetic diversity (Assis, Coelho, et al., 2016; Neiva et al., 2014; Waltari & Hickerson, 2013; Waltari et al., 2007).

We develop a modelling framework to project the consequences of future climate change on the 21st century distribution of climatic refugia for North Atlantic kelp forests (large brown algae). Like terrestrial forests, kelp plays a central role in marine ecological systems by providing resources, shelter, and nursery grounds for numerous species (e.g., Steneck et al., 2002). Kelp provides a good model to investigate the broad impacts of climate change on genetic diversity owing to their limited dispersal—which is bound to generate genetically differentiated populations—and high dependence on ocean temperatures—which makes species in these systems highly vulnerable to climate warming (Assis et al., 2014; Assis, Coelho, et al., 2016; Assis

et al., 2017; Filbee-Dexter, Feehan, & Scheibling, 2016; Johansson et al., 2015; Wernberg et al., 2016). Because the effects of climate change differ among species with different climatic niches (e.g., Fosheim et al., 2015), range shifts in our study were inferred for eight species with markedly different thermal tolerances, ranging from species typical of Arctic conditions to warm-temperate regions.

Considering the estimated LGM extinctions of kelp forest populations at high latitudes due to the expansion of the ice cap and the general cooling of marine waters (e.g., Assis, Coelho, et al., 2016; Fraser, Nikula, Spencer, & Waters, 2009; Johansson et al., 2015; Neiva et al., 2015), present refugia are hypothesized to occur at low latitude ranges. Because climate-driven extinctions for marine forests have been documented and projected globally at such lower latitudes (Araújo et al., 2016; Assis, Lucas, et al., 2016, 2017; Filbee-Dexter et al., 2016; Krumhansl et al., 2016; Raybaud et al., 2013; Wernberg et al., 2016), it is further hypothesized that future climate change will cause major erosion of climatic refugia and, therefore, of the global gene pool of species (e.g., Nicastró et al., 2013). Simultaneously, physiological and community-scale processes are expected to change (Graham, Jennings, MacNeil, Mouillot, & Wilson, 2015; Wernberg et al., 2010), driving the global redistribution of species and biogeographical boundaries (Poloczanska et al., 2013), a process with deep ecological, economic, and social consequences (e.g., Graham et al., 2013; Pecl et al., 2017). Such global changes might depend on the anthropogenic scenarios, with more severe warming likely causing more detrimental effects (e.g., Jueterbock, Smolina, Coyer, & Hoarau, 2016; Neiva et al., 2015; Pereira et al., 2010).

This study provides an overview of how climate-driven range shifts from the recent past to the near future might influence long-term persistence of kelp forests. To achieve this goal, ecological niches of species are modelled using comprehensive species occurrence records examined against physiologically meaningful environmental predictors. The distributions of sites estimated to have high genetic diversity are inferred by projecting areas of long-term persistence over the LGM, MH, and the present (2000–2010). The threat posed on such refugial areas by future climatic change (year 2100) was estimated under two contrasting RCP (Representative Concentration Pathway scenarios; Moss et al., 2010). In addition, the predicted modelled physiological tolerance limits of kelp forest species were compared with expectations from experimental studies.

2 | MATERIALS AND METHODS

All analyses described were performed with R (R Development Core Team, 2016) using the packages *adehabitatHS*, *dismo*, *gbm*, *gstat*, *parallel*, *raster*, *SDMTools*, and *sm*.

2.1 | Focal species and study area

We examined the potential consequences of future climate changes for eight kelp forest species with different climate affinities (as defined by Hoek & Breeman, 1990): Arctic (*Laminaria solidungula*),

Arctic and cold-temperate (*Alaria esculenta* and *Saccorhiza dermatodea*), Arctic and cold- to warm-temperate (*Laminaria digitata*, *Laminaria hyperborea*, and *Saccharina latissima*), cold- to warm-temperate (*Saccorhiza polyschides*), and warm-temperate (*Laminaria ochroleuca*). These species have a complex heteromorphic life cycle, alternating between macroscopic diploid sporophytes and microscopic haploid gametophytes. The two species of *Saccorhiza* spp. (order Tilopteridales) are annual semelparous, with sporophytes recruiting in early spring and reaching largest sizes throughout summer. Both reproduce by releasing spores in late summer and overwinter as microscopic gametophytes or young sporophytes (Keats & South, 1985; Norton, 1977), although local conditions might reduce seasonality (Pereira, Engelen, Pearson, Valero, & Serrão, 2015a). The species *Alaria esculenta*, *Saccharina latissima*, and *Laminaria* spp. (order Laminariales) are perennial, with a lifespan of 2–18 years (Table S1). These also develop new sporophytes mostly in spring but in northern latitudes they are reported to stop growing throughout summer to store photosynthates (Lüning, Yarish, & Kirkman, 1990), which are used during winter to develop new blades and mature sporangia (Kain & Jones, 1975) under lower temperatures, seasonal ice, and shorter days.

The target species are distributed in the North Atlantic and adjacent seas, from the lower intertidal down to ~30 m depth. Yet, *L. ochroleuca* and *S. polyschides* can grow deeper in regions with high water transparency (Table S1) such as in Formigas (Azores Islands), Gorringe seamount, Alboran Sea, and the Strait of Messina.

2.2 | Species distributions and climatic predictors

Detailed georeferenced locations describing the occurrence of species were gathered from several biodiversity information facilities and the available literature (Dataset S1; Fig. S1). These data were resampled to a grid of cells with 0.1° spatial resolution and provide one record per cell alone (overlapped entries discarded to reduce replication). Also, the records falling outside the known vertical distribution of each species (Table S1) were removed. This step was performed by extracting the depth of each record from the General Bathymetric Chart of the Oceans (GEBCO, 2015).

A set of climatic predictors were selected for analysis based on the biological relevance of marine forest species and the availability of data for the past, present and future. Sea surface data on ice thickness and three-dimensional profiles of ocean salinity and temperature were acquired from the Global Observed Ocean Physics Temperature Salinity Reprocessing (Copernicus Marine and Environment Monitoring Service, www.marine.copernicus.eu). Upwelling indices were developed following a standardized implementation (Perez-Brunius, Lopez, Pares-Sierra, & Pineda, 2007) using the eastwards and northwards components of surface wind speed acquired from the European Centre for Medium-Range Weather Forecasts (www.ecmwf.int). To project distributions to the LGM, MH, and the year 2100, data were derived from two Atmosphere-Ocean General Circulation Models (AOGCM): Model for Interdisciplinary Research on Climate 5 (MIROC5) and the Community Climate System Model

4 (CCSM4). These were chosen because they broadly capture the climatic variability found on most AOGCM (Ramstein et al., 2007). Forecasts considered two contrasting scenarios of greenhouse gas emissions: the RCP 2.6 and RCP 8.5 (see Moss et al., 2010 for details).

Because physiological tolerances may differ between life stages (e.g., Assis, Coelho, et al., 2016; Norton, 1978), the climate predictors were developed separately for “spring-summer” (months = AMJJAS) and “winter” (months = ONDJF). These predictors were interpolated to match the spatial resolution of the grid produced with the occurrence data: ice thickness and upwelling used bilinear interpolation, while ocean temperature and salinity used trilinear interpolation considering the position and depth of bottom cells (inferred from the bathymetry of GEBCO). The predictors for the LGM were developed by placing cells in the current –120 m isopleth, the assumed sea level for that period (Peltier, 2004). Owing to the unavailability of light properties in the AOGCM, the gridded climate predictors were masked with GEBCO to restrict their range to the vertical distribution of each species (e.g., Assis, Coelho, et al., 2016).

2.3 | Ecological niche models

The ENM implemented in this study combined a cross-validation method using independent test data sets with Boosted Regression Trees (BRT), a technique that fits non-linear relationships and interactions between a response variable (species occurrence) and predictor variables (climate data), while seeking to avoid overfitting (i.e., excessively complex fit describing random noise) through a series of optimized parameterization procedures (Elith, Leathwick, & Hastie, 2008). Because BRT requires species presence and absence data, and only presence records were available, pseudo-absences were generated using the a priori calculation of a habitat suitability surface with Mahalanobis distances. This approach used the records of occurrence of each species with the normalized climatic predictors to generate suitability surfaces from which pseudo-absences were extracted. A threshold of 0.2 of the suitability index was used to avoid the overprediction of suitable habitats that would arise if lower scores had been used (Chefaoui & Lobo, 2008). To reduce the possibility of using redundant information, the pseudo-absences were climatically structured, using a unique membership attributed by K-means clustering on the climatic predictors and the number of occurrence records as the k clustering parameter (Senay, Worner, & Ikeda, 2013). To account for unpredictable sources of bias arising from an unbalanced distribution of distribution data, the pseudo-absences were randomly chosen from a probability surface (kernel density) developed with the occurrence records (e.g., Phillips et al., 2009). This further allowed restricting the spatial extent of models to the range of species, a crucial step when modelling ecological niches (Barve et al., 2011; Peterson et al., 2011).

Cross-validation was performed by partitioning the occurrence records (i.e., presences and pseudo-absences) into 10 longitudinal bands; this approach aimed to evaluate the performance of models

with statistically independent datasets (Madon, Warton, & Araújo, 2013; Wenger & Olden, 2012). Models were trained with all combinations of predictors not strongly correlated (Spearman's $R < |0.9|$) and one latitudinal band withheld at a time for evaluating predictive performances. True skill statistics (TSS) were used to compare withheld data with each predicted distribution reclassified into a binomial surface of presences and absences, with a threshold maximizing sensitivity (true positive rate) and specificity (true negative rate). Overfitting was controlled by finding the optimal parameters for each model (i.e., number of trees, tree complexity, and learning rate; see Elith et al., 2008, Assis, Coelho, et al., 2016 and Assis, Lucas, et al., 2016 for details) and by forcing a positive (for minimum temperatures, salinity, and upwelling) or negative (for ice thickness and maximum temperatures) fit to the response of models. To develop simpler models (as desired for prediction), ice thickness and spring-summer salinity, which can drop significantly due to ice melting (Nielsen, Erbs-Hansen, & Knudsen, 2010), were only considered for species with Arctic to cold-temperate distributions; upwelling was only considered for species with warm-temperate distributions because warmer nutrient deprived waters might be locally enriched by this process. The models with higher performance on test data were identified with Kruskal–Wallis rank tests on the TSS values retrieved in each interaction of cross-validation. To this end, the models were ranked by decreasing TSS averaged values and added to independent rank tests until a significance level was found ($p < .05$).

2.4 | Predicting refugia and future range shifts

Distribution maps were produced by combining the models with higher predictive performance (identified in cross-validation), with a median function (Araújo & New, 2007). The projections produced for the past and future merged two datasets of MIROC5 and CCSM4 to reduce uncertainty. All maps were reclassified to reflect presence and absences using the previously described threshold allowing the maximization of specificity and sensitivity (Assis, Lucas, et al., 2016; Jiménez-Valverde & Lobo, 2007). Ancient climatic refugia were considered to be those where suitable habitat was inferred for both past extremes (LGM, MH) and the present (e.g., Assis et al., 2014; Assis, Coelho, et al., 2016; Neiva et al., 2014). Future range shifts were inferred by comparing present ranges with the forecasts performed with the two emission scenarios considered. The loss and gain of suitable habitats (regarding area) were determined for the entire distribution of species and each refugial region.

2.5 | Accuracy and significance of predictive models

The final accuracy of predictions was assessed with sensitivity and TSS (TSS > 0.8 indicating excellent accuracy; Allouche, Tsoar, & Kadmon, 2006). To estimate the potential of using the data provided by MIROC5 and CCSM4, alternative distribution maps for the present were built with data from such simulations.

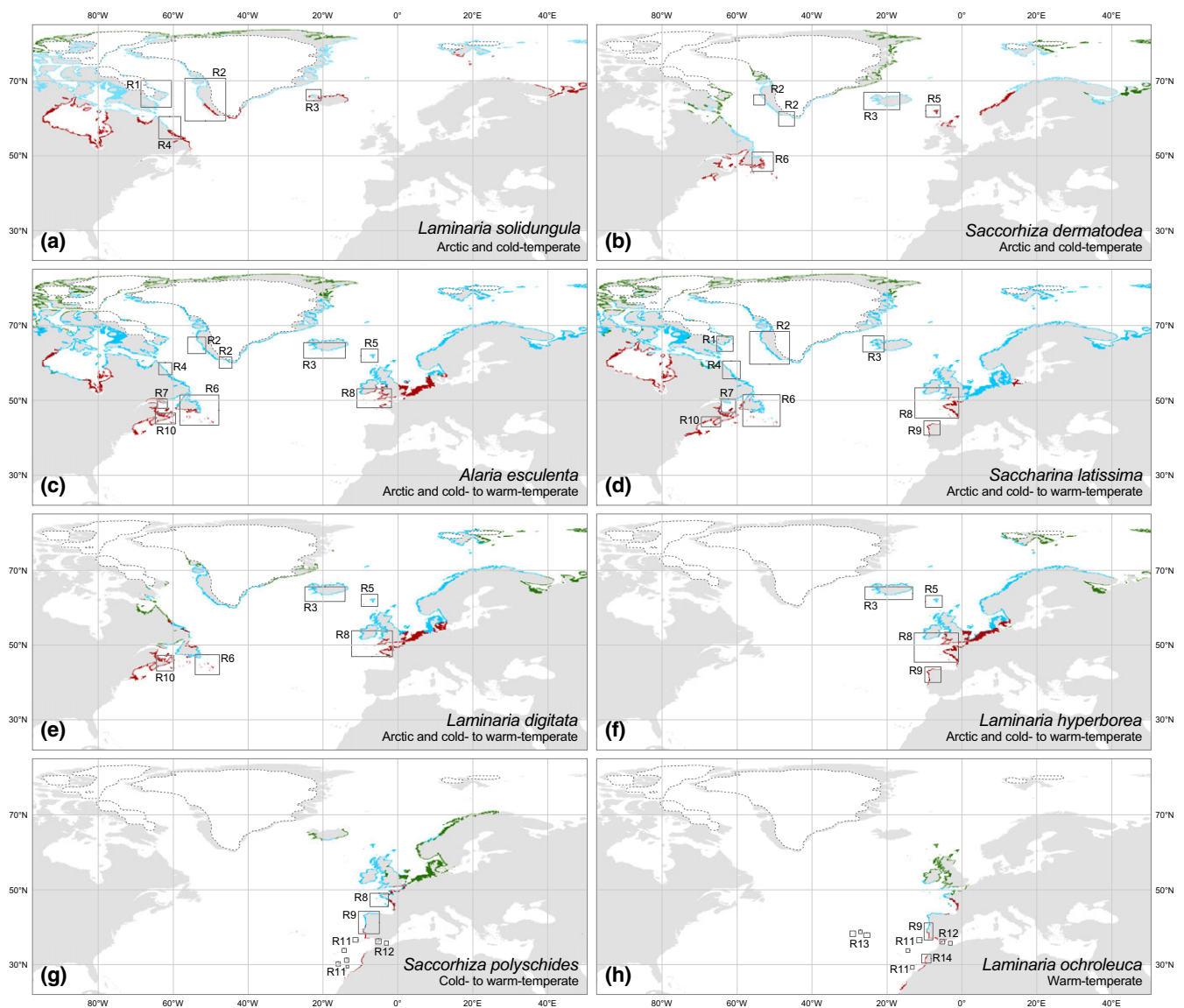
The significance of the models was investigated by determining the relative contribution of each predictor to the overall performance of the models. To this end, the increase on TSS was calculated when the predictors were added to all alternative models. Contributions below the 5% threshold were considered irrelevant. Physiological tolerance limits were further determined and compared with the available literature. These limiting thresholds (maximum and minimum, depending on the predictor) were extracted from the individual functions of each predictor on the response of models, while accounting with the average effect of all alternative predictors (Elith et al., 2008).

Because the methods used in this study differ from the previously published approach for *L. hyperborea* (Assis, Lucas, et al., 2016), all models for this species were rebuilt for proper comparisons.

3 | RESULTS

When projected to the conditions of the LGM, MH, and present (Figs. S2–S9), the models pinpointed 14 regions of ancient persistent climatic refugia, many of which were coincident among species (Figure 1). The Arctic and cold-temperate species shared refugia in Greenland, Iceland, and along the shorelines of Labrador and Newfoundland. The models further predicted long-term persistence in Baffin Island for *L. solidungula* and *S. latissima*, and in Faroe Islands for *A. esculenta* and *S. dermatodea*. *Alaria esculenta* and *S. latissima* might also have found refugia in eastern Québec, Nova Scotia, and Western English Channel. In addition, *S. latissima*, which has a more southern distribution in the Eastern Atlantic, was also predicted to have persisted in western Iberia. The species *L. digitata* and *L. hyperborea* shared refugia in Iceland, Faroe Islands, and Western English Channel. *Laminaria hyperborea* might have also persisted in Western Iberia, while *L. digitata*, occurring on both sides of the Atlantic, might have persisted in Newfoundland and Nova Scotia. Refugia for cold- to warm-temperate species overlapped in western Iberia, the Atlantic seamounts adjacent to the Gulf of Cadiz, Gibraltar, and Alboran. *Saccorhiza polyschides* might have further persisted in the western English Channel, and *L. ochroleuca* in western Morocco and the Azores Islands.

The forecasts produced for 2100 predicted the generalized contraction of low latitude ranges coupled with northwards expansions. With RCP2.6, arctic and cold affinity species undergo moderate shifts when compared to the present (Table 1). The broader range expansions were inferred for cold- to warm-temperate, specifically into Iceland, the North Sea, and northern Norway by *S. polyschides* and the northern British Isles by *L. ochroleuca* (Table 1; Fig. S8–S9). In RCP8.5, larger polewards range shifts are expected for all species. The southern margins will all undergo local extinctions. The species *L. solidungula* might completely disappear from Hudson Bay, Labrador, and the Barents Sea, while the other arctic and cold affinity species might shift their southern ranges from Nova Scotia, NW Iberia, and Brittany towards Newfoundland and SW Ireland. The two species with warm-temperate ranges might shift their southern edge from western Morocco towards western Iberia (Lisbon region). In



¹ Laughinghouse et al., 2015; ² Coyer et al., 2011; ³ Li et al., 2015; ⁴ Govindarajan et al., 2005; ⁵ Reviewed by Maggs et al., 2008; ⁶ Reviewed by Provan, 2013;

⁷ Reviewed by Neiva et al., 2016; ⁸ Shaw, 2005; ⁹ Assis et al., 2014; ¹⁰ Provan et al., 2005; ¹¹ Hu et al., 2008; ¹² Olsen et al., 2010; ¹³ Blouin & Brawley, 2012;

¹⁴ Provan & Maggs, 2012; ¹⁵ Neiva et al., 2014; ¹⁶ Neiva et al., 2012; ¹⁷ Neiva et al., 2012; ¹⁸ Young et al., 2002; ¹⁹ Assis et al., 2016; ²⁰ Lourenço et al., 2016

FIGURE 1 Potential range shifts for (a) *L. solidungula*, (b) *S. dermatodea*, (c) *A. esculenta*, (d) *S. latissima*, (e) *L. digitata*, (f) *L. hyperborea*, (g) *S. polyschides* and (h) *L. ochroleuca* inferred by comparing the predictions performed for the present with those for future times (2090-2100) using RCP8.5 emission scenario (red, blue and green depicting range loss, stable range and range gain, respectively). Black polygons show refugia regions (R) where the species were predicted to persist during the LGM, the MH and the present. References in the lower panel support the location of refugia with empirical genetic data for marine forest species and additional marine taxa. Dashed lines show the boundaries of permanent ice caps for the present (reconstruction by Peltier, 2004)

contrast, the northern edges of all species will expand into newly available suitable habitat. At higher latitudes, *L. solidungula*, *A. esculenta*, and *S. latissima* were predicted to find complete availability of circum-arctic habitats. Similarly, *S. dermatodea*, *L. digitata*, and

L. hyperborea might expand Arctic ranges throughout Svalbard, the Barents, and White Seas. Cold- to warm-temperate species are also predicted to increase northern expansions, with *L. ochroleuca* forecasted as far north as the Faroe Islands (Figure 1).

TABLE 1 Projected change in suitable habitats (percentage area) from present to future times (2090–2100) under two emission scenarios (RCP2.6 and RCP 8.5), inferred for the entire distribution (ED) and refugial regions (R)

RCP 2.6/8.5	<i>L. solidungula</i>	<i>S. dermatodea</i>	<i>A. esculenta</i>	<i>S. latissima</i>	<i>L. digitata</i>	<i>L. hyperborea</i>	<i>S. polyschides</i>	<i>L. ochroleuca</i>
ED	−4/−26	−1/+6	−1/−17	+1/−11	−2/−16	−7/−27	+65/+81	+22/+57
R1	0/0			+4/+7				
R2	0/−40	0/0	0/0	0/0				
R3	0/−50	0/0	0/0	0/0	0/0	0/0		
R4	0/−69		0/0	0/0				
R5		0/−100	0/0		0/0	0/0		
R6		−22/−66	−7/−39	0/−19	−4/−47			
R7			0/−76	+1/−32				
R8			−10/−81	+1/−53	−9/−55	−13/−79	0/−13	
R9				−1/−100		−96/−100	0/−24	−7/−53
R10			−21/−100	−89/−100	−32/−100			
R11							−30/−44	+49/+16
R12							−100/−100	−89/−100
R13								−23/−85
R14								−41/−100

R1: Baffin Island; R2: Greenland; R3: Iceland; R4: Labrador; R5: Faroe Islands; R6: Newfoundland; R7: E Québec; R8: W Eng. Channel; R9: Iberia Peninsula; R10: Nova Scotia; R11: Atlantic seamounts; R12: Gibraltar and Alboran; R13: Azores Islands; R14: W Morocco.

Bold values indicate losses of suitable habitats above a threshold of 75%.

The long-term persistence refugia, expected to represent putative genetic diversity hotspots, are predicted to undergo losses in both emission scenarios (Table 1). With RCP2.6, such losses were moderate for *A. esculenta*, *L. digitata*, and *S. dermatodea* (−32% to −21%; Table 1); however, *L. hyperborea*, *L. ochroleuca*, *S. latissima*, and *S. polyschides* might almost or completely disappear from their southernmost refugia (Table 1). With RCP8.5, all species but *L. solidungula* were predicted to completely lose at least one refugial region (Figure 1; Table 1). This was particularly striking in the Faroes, Nova Scotia, and Iberia for cold affinity species and in Gibraltar, Alboran and Morocco for those with warm-temperate distributions. Despite this generalized southern loss, deep refugia

might persist, as *S. polyschides* was predicted to remain on the seamounts adjacent to the Gulf of Cadiz and *L. ochroleuca* might even expand its future distribution throughout these deep refugial sites (Table 1).

The predictive maps achieved excellent accuracy and largely matched the known distributions of species (Sensitivities > 0.95, TSS > 0.9; Table 2; Fig. S1). In particular, the inferred refugial regions and range edges where future loss of habitats was predicted, contain key empirical records supporting their present occurrence (Fig. S1). The alternative predictions for the present using data from AOGCM were also highly accurate, indicating good transferability of the models to such simulations of climate (Table S1).

TABLE 2 Accuracy of predictive models developed for kelp forest species (S, Sensitivity; TSS, True Skill Statistics), physiological tolerance limits, and relative contribution of each climatic predictor (Max T, maximum temperature, Min T, minimum temperature, Min Sal, minimum salinity, Max Ice, maximum ice thickness, and Upw, coastal upwelling index; only nonresidual contributions >5% are shown). Seasons defined as spring–summer (SS; months: AMJJAS) and winter (W; months: ONDJF)

Species	Accuracy		Max T SS (°C)	Max T W (°C)	Min T W (°C)	Min Sal SS (PSS)	Min Sal W (PSS)	Max Ice SS (m)	Upw SS (m ³ s ^{−1} km ^{−1})
	S	TSS							
<i>L. solidungula</i>	0.95	0.94	15.8***	10.5***	−1.8*	—	—	6.4**	—
<i>S. dermatodea</i>	0.95	0.91	18.1***	13.8***	−1.8**	—	—	1.5**	—
<i>A. esculenta</i>	0.99	0.99	19.0***	16.4***	−1.4**	10.2*	12.2*	4.4**	—
<i>S. latissima</i>	0.99	0.99	20.9***	19.0***	−1.7**	6.8*	6.8*	2.7**	—
<i>L. digitata</i>	0.98	0.96	20.2***	17.0***	−1.6**	7.3*	7.5*	1.3**	—
<i>L. hyperborea</i>	1.00	1.00	21.2***	18.0***	−1.4**	6.6*	6.7*	0.6**	—
<i>S. polyschides</i>	1.00	0.95	23.3***	21.7***	5.2***	—	—	—	32.6*
<i>L. ochroleuca</i>	0.98	0.93	24.7***	22.8***	7.7***	—	—	—	19.7*

Relative contribution of climatic predictors: *low 5%–10%, **moderate 10%–25%, ***high >25%.

The models used to infer range shifts through time included multiple climatic predictors from which maximum winter temperatures had a prominent role in improving predictions (relative contributions >25%). This was clear for all species but *A. esculenta*, which responded similarly to both winter and spring-summer maxima (Table 2; Table S2). Minimum temperatures were also important in the models developed for cold- to warm-temperate species. In contrast, for species with arctic ranges, minimum temperatures only caused low-to-moderate improvements (gains in accuracy from 8.9% to 13.3%) and further depended on ice thickness to boost accuracy scores (up to 17.2%). The contribution of salinity did not vary considerably between seasons and was only relevant for *A. esculenta*, *L. digitata*, *L. hyperborea*, and *S. latissima*, producing marginal gains from 5.7% to 8.9% (Table 2; Table S2). Upwelling index, implemented for cold- to warm-temperate species, added gains of 5.1% (*S. polyschides*) and 7.2% (*L. ochroleuca*).

The maximum critical temperatures inferred were mostly species specific, with a large variation between species upper limits from 15.8°C to 24.7°C in spring-summer, and 10.5°C to 22.8°C in winter (Table 2; Figs. S10–S17). The minimum critical temperatures also changed among species except for species with arctic ranges, which had similar thresholds close to the freezing point of seawater (−1.8°C and −1.4°C). Ice thickness limits were above 0.6 m for all cold affinity species, with *L. solidungula* finding suitable habitats where ice can be up to 6.4 m thick in spring-summer (Table 2). The species *S. latissima*, *L. digitata*, and *L. hyperborea* reach similar minimum salinities (6.6 and 7.5 PSS), yet higher seasonal thresholds were inferred for *A. esculenta* (10.2 PSS and 12.2 PSS; Table 2). Upwelling produced a positive effect on the models (Figs. S10–S17) above the levels (even doubling those) known to provide favourable conditions for the enrichment of coastal waters (when indices >16 m³ s^{−1} km^{−1}; (Perez-Brunius et al., 2007).

4 | DISCUSSION

Our implementation of ecological niche models for North Atlantic kelp forest species reveal that future climate change is expected to produce local potential losses at low latitude ranges where the most ancient climatic refugia are projected to occur. Such loss is expected to erode the global gene pool of species and, consequently, reduce their evolutionary potential as a whole. The species modelled are not expected to be endangered as a consequence of climate change as large polewards expansions are also projected, but the most ancient and diverse gene pools occurring within southern refugia are likely to be threatened. Remarkably, the use of three-dimensional oceanographic profiles of climatic data allowed identifying discrete climatic anomalies and cryptic deep refugial sites with the potential to locally reduce polewards range shifts and buffer the southern loss of marine biodiversity.

The models projected a set of well-defined regions where kelp could have persisted in the long term. The populations presently inhabiting such areas tend to harbour higher genetic diversity than

where past range shifts or bottlenecks occurred (Assis et al., 2014; Maggs et al., 2008; Neiva et al., 2014; Provan, 2013). This hypothesis can only be corroborated for *S. polyschides*, the modelled species for which genetic data are available for the entire distributional range (Assis, Lucas, et al., 2016). Nevertheless, several empirical studies focusing on arctic, cold, and warm-temperate marine species observed higher genetic diversity in the same regions where our models predicted refugia (reviews by Maggs et al., 2008; Provan & Bennett, 2008; Neiva et al., 2016; Figure 1 for additional references), with a unique exception for the Labrador region. Yet, the reconstructions showing the Laurentide ice sheet not completely covering the coastlines of Labrador (Peltier, 2004) support this as putative refugial region. Some studies explain the current distribution of cold affinity species in the NW Atlantic as strictly resulting from European (re)colonizations after the last glaciation, discarding the hypothesis of persistence in NW Atlantic refugia (reviewed by Provan, 2013; discussed by Assis et al., 2014). By predicting past range shifts for different climate niches, this study suggests that pan-Atlantic distributions for North Atlantic kelp forests were indeed determined by the capacity of species to cope with the Laurentide periglacial conditions. This is exemplified by *L. hyperborea*, *L. ochroleuca*, and *S. polyschides*, the species less tolerant to colder environments, for which the current distribution and predicted refugia are restricted to the NE Atlantic.

The models predicting past range shifts also allow verifying that populations presently inhabiting formerly glaciated regions might have originated recently from the nearest (i.e., the northernmost) refugia, leaving genetically distinct populations in lower latitudes that were not involved in postglacial expansions (Assis, Lucas, et al., 2016; Hoarau, Coyer, Veldsink, Stam, & Olsen, 2007; Neiva, Pearson, Valero, & Serrão, 2012a). This is because species with limited dispersal tend to expand ranges by means of the highly increased fitness of few individuals just due to their position at the expansion front (Excoffier & Ray, 2008), creating founder effects that leave homogeneous low diversity expansion zones, even after the contact of distinct lineages or species (Neiva, Pearson, Valero, & Serrão, 2010, 2012b). The sorting of alleles at the edge of expansion zones may further promote unique evolutionary opportunities through the selection of rare but advantageous alleles fitted for colder northern environments (Excoffier & Ray, 2008). Furthermore, if such expansion fronts encounter differentiated but still reproductively compatible populations, then the recombination of genomes can create diversity in the form of new allelic combinations (e.g., Neiva et al., 2010, 2017), which is not to be confounded with the creation of new alleles by mutations at longer time scales.

The forecasts produced for kelp forests agree with the general expectation of polewards range shifts for North Atlantic species, dependent on the emission scenario considered (Assis et al., 2014, 2017; Neiva et al., 2015; Raybaud et al., 2013). The optimistic scenario RCP2.6 boosted northwards expansions for cold- to warm-temperate species only (as in Muller et al., 2009), likely due to less ice thinning (Moss et al., 2010) potentially halting the northern expansion of cold affinity species. Such patterns of range shifts seem

to have started already, with studies reporting range contractions at low latitude ranges throughout the globe although no evidence has yet been brought forward of new arrivals on Arctic shores (Araújo et al., 2016; Assis et al., 2013; Bates et al., 2014; Filbee-Dexter et al., 2016; Krumhansl et al., 2016; Mineur et al., 2015; Muller et al., 2009; Wernberg et al., 2016). Much more drastic consequences were inferred with RCP8.5. The warmer climate at higher latitudes, together with the lack of light-attenuating ice, led to projections of complete borealization of kelp forests (as for other taxa Fossheim et al., 2015), as all circum-Arctic habitats become colonized by kelp (*A. esculenta*, *L. solidungula*, and *S. latissima*). Concomitantly, lower latitude edges of Atlantic kelp forests might be completely redefined: to Newfoundland and SW Ireland for cold affinity species and western Iberia for warm affinity species. Considering the current overlap between the southern ranges of kelp forests and those of numerous species (e.g., cold-temperate fucoids, Neiva et al., 2016), the forecasts produced with this scenario likely depict the new future locations of North Atlantic biogeographical transition zones between cold- and warm-temperate regions.

The projected range shifts seem plausible as empirical evidence already documented their beginning. The main consequences for genetic diversity should be considered. If range reductions eliminate refugia as projected, the expected and observed (Assis, Lucas, et al., 2016) higher genetic diversity there might be reduced or even lost (Provan & Maggs, 2012; Young, Boyle, & Brown, 1996). Such reduction in genetic diversity was mostly projected for Nova Scotia and Iberia for cold- to warm-temperate species, and Gibraltar, Alboran, and western Morocco for warm-temperate species, regardless of the emission scenario. The low latitude refugia of the arctic species *L. solidungula* and *S. dermatodea*, located in Labrador and Newfoundland, were projected to undergo less drastic consequences even under the most extreme RCP8.5 scenario. The reduced warming there results from a reduction in heat transport from tropical latitudes forecasted for the thermohaline circulation (Buchholz, Krause, & Buck, 2012). Nevertheless, the projected exposure to limiting niche conditions, and consequently to reduced population sizes, limited gene flow, and random drift (Sagarin, Gaines, & Gaylord, 2006), might also carry significant genetic erosion (Eckert, Samis, & Loughheed, 2008). This was stressed for *S. polyschides* in Morocco (Assis, Lucas, et al., 2016) and for *L. digitata* and *S. latissima* in southern Brittany (Guzinski, Mauger, Cock, & Valero, 2016; Robuchon, Le Gall, Mauger, & Valero, 2014), and may become a major force reducing the extant diversity of range edge populations in the years to come.

The loss of refugia projected under the two emission scenarios might cause loss of genetic diversity that is not counteracted by migration due to the limited dispersal of kelp (Assis et al., 2017). Even if northern habitats allow settlements in the future, gene pools at lower latitudes might not be rescued because, as mentioned before, range expansions for such species are mediated by founder events from local sources. The prevalence of priority colonization effects in pre-established populations (Neiva et al., 2012b), together with important oceanographic barriers, may further prevent polewards expansion of alleles. Such is the case of permanent oceanic

currents southwards (e.g., Labrador current) directing dispersal pathways towards unsuitable habitats (Wilson et al., 2016). The development of new ecotypes at lower latitudes is also unlikely, given the larger temporal scales on which these evolutionary mechanisms operate (Quintero & Wiens, 2013), compared to the time span of the present forecasts. In addition, there is still no clear evidence supporting higher thermal phenotypic plasticity in the southern range of marine forest species (Pearson, Lago-Leston, & Mota, 2009; Pereira, Engelen, Pearson, Valero, & Serrão, 2015b). Even if particular genotypes suited for new climate conditions exist, the typical small size of range edge populations (Assis et al., 2013; Sagarin & Gaines, 2002) likely promotes demographic stochasticity long before populations can effectively adapt (Bell & Gonzalez, 2009). Such a loss of unique range edge diversity reduces species gene pools globally, further restricting the variability needed for potential adaptation by selection under future conditions (Hampe & Petit, 2005; Provan, 2013). As most population genetic variability is not generally visible in the phenotypes, its loss tends to occur unnoticed.

Alongside with global genetic reduction, the loss of canopy-building species in low latitude ranges might cause important cascading effects with high potential to reduce the overall biomass and diversity of associated species (Graham, 2004; Ling, 2008; Perry et al., 2005). The release of important resources (e.g., light and space; Gorman & Connell, 2009) is expected to facilitate the establishment of warm adapted crustose and foliose turf seaweeds, which are known to structure less diverse habitats and support less biodiversity (Filbee-Dexter et al., 2016; Smale, Burrows, Moore, O'Connor, & Hawkins, 2013; Wernberg et al., 2016). Even when kelp forests thrive, the predicted changes in species composition may also impact regional biodiversity. For instance, in the Western English Channel, *L. ochroleuca* is expected to replace *L. hyperborea*. While both species are almost morphologically identical, the latter supports little epiphytes and therefore less associated species (Smale, Wernberg, Yunnice, & Vance, 2015). In fact, species that are somehow dependent on marine forests (e.g., epiphytes) may share similar thermal tolerances, resulting from long-term evolutionary forces. This hypothesis is of much relevance as such species would have the same predicted refugia as their supporting seaweeds and might therefore also be at risk of losing genetic diversity.

The agreement between the inferred physiological tolerance limits and those from empirical evidence (Table 2, Table S3) strengthened the significance of the models and provided evidence on how niche limits alone define the ranges of marine forest species (as verified for other taxa, Lee-Yaw et al., 2016). Specifically, maximum winter temperatures had a prominent role, as shown by physiological studies, emphasizing their potential to limit the development of sporangia (Muller et al., 2009; Norton, 1978), the establishment and survival of the gametophytes (Rinde & Sjøtun, 2005; Sjøtun & Schoschina, 2002), and the viability of young sporophytes (Norton, 1978). However, because of the relatively high correlation between maximum temperatures across seasons (Table S4), one cannot rule out an additional effect of spring-summer temperatures (Bartsch, Vogt, Pehlke, & Hanelt, 2013; Lüning et al., 1990). Because warm

ocean waters are usually nutrient depleted (Kamykowski & Zentara, 1986), high temperatures might be a proxy for limitation of nutrients for sporophytes, particularly at the southern warmer ranges of *S. polyschides* and *L. ochroleuca*. The use of the upwelling index in this context assisted on predicting true presences for both species in the western Iberian Peninsula and Morocco (see also Assis et al., 2017), specific low latitude regions where nutrient-rich waters are upwelled throughout summer (Lourenço et al., 2016; and references therein; Fig. S18).

The models further highlighted the role of minimum temperatures on setting the northern range of marine forests, although in the Arctic this resulted mostly from responses to ice thickness. The common baseline of 0.6 m likely represents the regions that are ice free during most of the summer and provide sufficient light for sporophyte growth and photosynthate storage (Lüning et al., 1990). Above this threshold, the species *A. esculenta*, *L. solidungula*, and *S. latissima* might cope with increasing ice thickness by improving the efficiency of photosynthesis (Wiencke, Gómez, & Dunton, 2009). Accordingly, these are the species occurring deeper in the Arctic (Lee, 1980; Wiencke et al., 2009), which have the ability to complete a full life cycle under perennial ice, such as in northern Baffin Bay (Lee, 1980), where the models predicted true presences. Phenology also explains how species persist under limiting light conditions. For instance, *L. solidungula*, for which the models inferred higher tolerance to ice thickness, stores photosynthates during the short summer, and strictly grows under the ice (Muller et al., 2009; and references therein), whereas *S. latissima* and others rely on active photosynthesis to grow (Henley & Dunton, 1995).

Salinity was important to explain the distribution of *A. esculenta*, *L. digitata*, *L. hyperborea*, and *S. latissima* in the two main hyposaline regions (<10 PSS) of the study area, i.e., the Baltic Sea and southern James Bay (Hudson Bay). Still, steep gradients in salinity prevailing in the vicinities of both regions (e.g., Gustafsson & Stigebrandt, 1996) might be smoother in the climate data used and lead to the overprediction of less tolerant species (e.g., *A. esculenta* along the west coast of Sweden). Biotic interactions are generally less relevant to explain the latitudinal variation in marine forest species (Cavanaugh et al., 2013; Rinde & Sjøtun, 2005), however, these may become important drivers of range shifts as climate changes. For instance, the increase in abundance of warm adapted grazers (e.g., fish and urchins) may overcome the direct physiological effect of abiotic factors (e.g., temperature and nutrients) by strongly controlling recruitment of kelp (Vergés et al., 2016; Wernberg et al., 2016). Such process may lead to novel unknown ecosystem states, where species with contrasting climate affinities interact.

Taken together, the results of this study provide a comprehensive insight on the ecological niche of North Atlantic kelp forests, the putative location of ancient climatic refugia, and the bio- and phylogeographic consequences arising from anthropogenic climate change. While past range shifts might have structured regions with higher and distinct genetic diversity, future climate causes predictions of substantial loss of such refugia. Despite this general trend, the use of three-dimensional oceanographic profiles of climatic data

for the sea allowed predicting persistence of cold- to warm-temperate species in deep offshore seamounts (adjacent to the Bay of Cádiz and the Azores Islands). Like elevational range shifts for terrestrial taxa (Epps, Palsbøll, Wehausen, Roderick, & McCullough, 2006), persisting in deep colder waters may become an important mechanism to preserve regional genetic diversity in future periods of warmer climate (Assis, Lucas, et al., 2016). Similarly, the upwelled regions of Morocco, Tarifa, and Alboran were also expected to continue as persistent refugia (Assis et al., 2017; Lourenço et al., 2016) but models predicted range loss on such regions despite intensification of coastal upwelling (particularly in western Morocco; Fig. S18). This was caused by overpassing tolerance limits for more important climatic predictors (e.g., maximum temperatures) by 2100.

Empirical evidence suggests that polewards range shifts are ongoing for kelp forest species and, despite uncertainties in climatic forecasts, the future seems now strongly dependent on policy actions, with the extreme RCP8.5 emissions scenario (Moss et al., 2010) yielding more detrimental effects to ancient populations of kelp (e.g., Neiva et al., 2015). Considering the lack of broad-scale genetic data for these species (exception for *S. polyschides*, Assis, Lucas, et al., 2016), the current projections provide a valuable baseline for Climate Change Integrated Conservation Strategies for endangered phylogeographic lineages (Hannah, Midgley, & Millar, 2002). They further assist on guiding specific surveys aiming at the relics of marine biodiversity, which might be elusively distributed given the typical small size and isolation of range edge populations (Assis et al., 2013; Hampe & Petit, 2005), or limited to cryptic deep locations, as predicted for warmer species. The focus on species with different climatic affinities further allowed extrapolating results beyond modelled taxa and anticipating an emerging pattern for the North Atlantic, reshaping the current climatic transitional zones from cold- to warm-temperate regions.

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