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Deep reefs are climatic refugia for genetic diversity of marine forests

Jorge Assis^{1*}, Nelson Castilho Coelho¹, Thomas Lamy^{2,3}, Myriam Valero³, Filipe Alberto^{1,4} and Ester Álvares Serrão¹

¹CCMAR, University of Algarve, Campus de Gambelas, Faro 8005-139, Portugal,

²Département de Sciences Biologiques, Université de Montréal, Montréal, Québec, Canada, ³UMI 3614 Evolutionary Biology and Ecology of Algae, CNRS, Sorbonne Universités UPMC Univ. Paris 06, Pontificia Universidad Católica de Chile, Universidad Austral de Chile, Station Biologique de Roscoff, 29688 Roscoff Cedex, France,

⁴Department of Biological Sciences, University of Wisconsin-Milwaukee, Milwaukee, WI 53201, USA

ABSTRACT

Aim Past climate-driven range shifts shaped intraspecific diversities of species world-wide. Earlier studies, focused on glacial refugia, might have overlooked genetic erosion at lower latitudes associated with warmer periods. For marine species able to colonize deeper waters, depth shifts might be important for local persistence, preventing some latitudinal shifts, analogous to elevational refugia in terrestrial habitats. In this study, we asked whether past latitudinal or depth range shifts explain extant gene pools in *Saccorhiza polyschides*, a large habitat structuring brown alga distributed from coastal to offshore deep reefs.

Location North-east Atlantic and western Mediterranean basin.

Methods Genetic structure and diversity were inferred using seven microsatellite loci, for 27 sites throughout the entire distributional range. Ecological niche modelling (ENM) was performed with and without information about genetic structure (sub-taxon niche structure) to predict distributions for the Last Glacial Maximum (LGM), the warmer Mid-Holocene (MH) and the present.

Results Both ENM approaches predicted a wider potential distribution in deeper waters than is presently known, a post-glacial expansion to northern shores and the extirpation of southern edges during the warmer MH. Genetic data corroborated range dynamics, revealing three major genetic groups with current boundaries in the Bay of Biscay and the Lisbon coastal region, pinpointing ancient refugial origins. Despite extensive southern range contraction, the southernmost warmer regions are still the richest in genetic diversity, indicating long-term persistence of large populations. ENMs suggested that this could only have been possible due to stable refugia in deeper reefs.

Main conclusions The global distribution of gene pools of temperate marine forests is explained by past range shifts that structured both latitudinal glacial refugia and depth refugia during warmer periods. Deep rear edge populations play a fundamental role during periods of extreme climate, allowing persistence and retaining some of the largest genetic diversity pools of the species' distribution.

Keywords

climate change, depth range shifts, ecological niche modelling, genetic diversity, glacial refugia, kelp forests, marine phylogeography, north-east Atlantic, *Saccorhiza polyschides*, western Mediterranean

*Correspondence: Jorge Assis, CCMAR, University of Algarve, Campus de Gambelas, Faro 8005-139, Portugal.
E-mail: jorgemfa@gmail.com

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INTRODUCTION

As global climate conditions changed over time, so did the distribution and abundance of organisms. The glacial-interglacial cycles of the Quaternary (c. 2.6 Myr to the present)

were particularly important in causing major range shifts (Hewitt, 2000, 2004). Expansion and contraction of ranges structured the genetic and evolutionary traits of many marine species (Maggs *et al.*, 2008). In regions where climate conditions allowed populations to persist (i.e., refugia), high

and unique genetic diversity is expected (Provan & Bennett, 2008). Where ranges contracted or unfavourable niche conditions prevailed, diversity might be presently reduced due to bottlenecks, drift and/or reduced gene flow (Young *et al.*, 1996; Leimu *et al.*, 2006). Erosion of genetic diversity might have also taken place at the 'leading edge' of colonization during range expansions (Hewitt, 1996). These processes created an emerging pattern for several North Atlantic marine species, which now exhibit low genetic diversity and differentiation in regions formerly displaced by glaciations (such as during the Last Glacial Maximum; LGM; *c.* 21 ka) and high and distinct diversity where populations persisted at lower latitudes (Hewitt, 1996, 2004; Provan & Bennett, 2008; Neiva *et al.*, 2014, 2015).

While early studies placed strong emphasis on glacial refugia (e.g., Hewitt, 2004), inferring regions of long-term persistence also requires considering the warmer extremes of climate change (e.g., Assis *et al.*, 2014). The higher insolation during summer in the Northern Hemisphere hindcasted for the Mid-Holocene (MH; *c.* 6 ka) resulted in warmer seasonal temperatures when compared to the present (Wanner *et al.*, 2008). This might have caused genetic erosion at trailing edges (e.g. Assis *et al.*, 2014). Overlooking past warming periods may therefore miss important drivers of the current distribution of genetic diversity.

The size (area) and location of refugia influence the spatial patterns of genetic diversity (DeChaine & Martin, 2004; Assis *et al.*, 2014), although this is further determined by dispersal ecology. Species with limited dispersal might experience local extinctions and bottlenecks whenever unfavourable environmental conditions arise (Parmesan, 2006; Provan & Maggs, 2012). For instance, the contraction of trailing edges predicted for many North Atlantic marine species (e.g. Jueterbock *et al.*, 2013; Raybaud *et al.*, 2013; Neiva *et al.*, 2015) might not be offset by northern expansions because range shifts tend to involve local population fronts (Neiva *et al.*, 2012a), leaving behind distinct diversity at lower latitudes (Provan & Maggs, 2012). Although species respond individually to environmental changes, making refugia species-specific, some patterns are common (Maggs *et al.*, 2008). For example, terrestrial species found refugia in higher elevations regardless of their dispersal ability (e.g. Bush *et al.*, 2004). Likewise, marine species able to colonize deeper colder waters might survive unfavourable sea surface changes. Such deep refugia would allow persistence of distinct gene pools during extreme climate periods, increasing diversity in the long-term. This has much biogeographical and evolutionary relevance, although there is little empirical evidence addressing this hypothesis (but see Perry *et al.*, 2005).

Large brown algae that can form marine forests (commonly called 'kelp') offer an unique model to investigate the role of climate changes in shaping the global patterns of intraspecific diversity. Kelp have limited dispersal and their distributional ranges are climatically defined (e.g., Raybaud *et al.*, 2013). These are important features to effectively track

distributions as climates change. Furthermore, deep settlements of kelp may occur in specific environments (Graham *et al.*, 2007), although their prevalence is mostly unknown and empirical evidence for their role as refugia has been missing so far.

In this paper, we use microsatellite genetic markers and ecological niche modelling (ENM) to investigate whether past climate changes might have produced major biogeographical shifts and might have shaped the extant gene pools of the large brown alga *Saccorhiza polyschides* (Lightfoot) Batters, 1902, an important ecosystem-building species that forms marine forests. We assessed in particular whether deep-water populations are predicted to persist offshore, beyond the coastal distributional limits, where waters are more transparent and colder, and whether these might function as depth refugia maintaining rich and distinct gene pools.

MATERIALS AND METHODS

Study area and focal species

The study comprised the entire distributional range of *S. polyschides*, from western Norway southward to Morocco. This species inhabits rocky reefs from the intertidal down to 30 m depth (e.g. in Gibraltar) along continental coastlines. Offshore, it extends deeper (maximum *c.* 80 m) in more transparent waters such as the Gorringe seamount, Alboran and the Strait of Messina (Norton, 1977; Assis *et al.*, 2009; Flores-moya, 2012).

S. polyschides is annual semelparous with a complex heteromorphic life cycle typical of most kelp species (but not *Durvillaea* spp., commonly called Southern Hemisphere bull kelp, nor *Ascophyllum nodosum*, commonly called knotted kelp), alternating between a diploid macroscopic sporophyte and a haploid microscopic gametophyte. Sporophytes recruit mainly in spring, reaching highest abundances throughout the summer. Adults mostly release spores in late summer and die during autumn. Settled spores produce gametophytes, and after fertilization sporophytes wait until spring to resume growth (Pereira *et al.*, 2011). This typical seasonal life history fits the seasonality of upwelling processes throughout most of the distribution; however, this relationship can be weaker where nutrient levels are permanently high (Pereira *et al.*, 2015a).

Data on species occurrence and climate

Georeferenced occurrences describing this species' distribution were gathered from field observations and the available literature. Records were only considered from 1990 onwards, and when locations were described in detail down to shore level (132 compiled records, see Appendix S1 in Supporting Information). These were gridded to 0.1° resolution and duplicate entries were only considered once (resulting in 128 gridded records).

Seasonal environmental predictors were produced to reflect the limiting factors and essential resources acting at each stage of this species' complex life cycle (see Norton, 1977; Pereira *et al.*, 2011, 2015a,b). Three-dimensional profiles of ocean temperature (OTemp), ocean salinity (OSal), nutrients (Phosphates and Nitrates) and light availability at the bottom of the ocean (Light) were averaged as summer (months = JAS), winter (months = ONDJF) and spring (months = MAMJ) environmental predictors (Table 1) and gridded to match the resolution of the distributional data (for technical details on environmental data refer to Appendix S2). All environmental surfaces were clipped using the General Bathymetric Chart of the Oceans (GEBCO; BODC 2013) so models would run on coastal regions and offshore banks, where depths are down to 30 m and 80 m respectively. This restriction was performed because there is no information for light attenuation in the data used to model past distributions.

Ecological niche modelling

The ENM in our study followed the methods of Assis *et al.* (2014) and Neiva *et al.* (2014). We chose boosted regression trees for its ability to model complex, non-linear relationships (Elith *et al.*, 2008). The framework used 100 independent cross-validation iterations to increase model generality










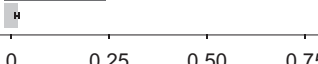

and identify a set of environmental predictors with higher potential for transferability among numerous candidates, using true skill statistics (TSS) as measure of accuracy (for technical details on cross-validation refer to Appendix S2). Models were performed using two approaches: (1) species modelling considering the full range of *S. polyschides* and (2) sub-taxon modelling with phylogeographical structure (i.e. within-taxon niche structure; Pearman *et al.*, 2010), using distinct models for each geographical region identified as genetically differentiated (see genetic analyses below).

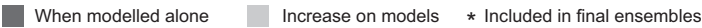
Past and present distribution of *S. polyschides*

In the cross-validation procedure, several models may be identified as equally accurate. Therefore, the final maps were produced by merging (median function) the resulting surfaces of models using the most transferable subset of predictors (i.e. ensemble modelling) along with the full or split set of distribution records, depending on the modelling approach (species or sub-taxon).

The ensembles for the LGM and MH were fed with data from two atmosphere-ocean general circulation models (AOGCMs): the Model for Interdisciplinary Research on Climate (MIROC) and the Community Climate System Model (CCSM). These were chosen as they cover the range of variability found between most AOGCMs (Ramstein *et al.*, 2007).

Table 1 Environmental predictors used in ENM of *Saccorhiza polyschides*, their units, the tipping points for the species model (TP Sp.) and sub-taxon model (TP Sub-T.), and relative importance (TSS – true skill statistics) on the response of species model (for more information refer to Appendix S2).

Environmental predictor	Units	TP Sp.	TP Sub-T.	Relative importance (TSS)
LT Ocean Temp. of the coldest winter month	°C	5.7	5.9	
LT Ocean Temp. of the coldest spring month	°C	5.2	5.3	
LT Ocean Temp. of the hottest winter month	°C	21.6	21.4	
LT Ocean Temp. of the hottest summer month	°C	23.6	23.3	
LT Ocean Temp. of the hottest spring month	°C	18.4	18.3	
LT lowest Salinity of the winter months	PSS	32.7	33.0	
LT lowest Phosphates of the summer months	µmol.L ⁻¹	-	-	
LT lowest Phosphates of the spring months	µmol.L ⁻¹	-	-	
LT lowest Nitrates of the summer months	µmol.L ⁻¹	-	-	
LT lowest Nitrates of the spring months	µmol.L ⁻¹	-	-	
LT lowest Light availability of the spring months	-	-	-	



Because only OTemp and OSal were available on AOGCMs, past predictions did not consider Nutrients nor Light. This was adequate for prediction because the distribution of this species was largely explained by OTemp and OSal (see Results). Additionally, an ensemble performed with OTemp and OSal data only from AOGCMs averaged for 1990–2010 showed a good description of this species' distribution and an accuracy of 0.95 (TSS; see Fig. S2 in Appendix S2).

Coastal regions and deep banks for the LGM were simulated by placing bathymetry at -120 m, below current sea level. The individual ensembles per genetic group were merged into a unique composite using a multiplicative probability function (Pearman *et al.*, 2010). Finally, all maps were reclassified using a threshold maximizing sensitivity and specificity (the ability to detect presences and absences respectively), for the outputs (probability of occurrence) to stand for predicted presences and absences (e.g. Assis *et al.*, 2015). Long-term refugia were inferred as those regions where the habitat was suitable during the LGM, MH and present-time (e.g. Assis *et al.*, 2014).

Population genetic structure and diversity

Twenty-seven sites were sampled covering the whole distribution of *S. polyschides* by collecting a piece of the blade above the meristem from *c.* 25 haphazard individuals (Fig. 1a; Table 2). Samples were preserved in silica drying crystals. DNA extraction, polymerase chain reaction and allele scoring were performed as in Assis *et al.* (2013) for seven microsatellite loci developed for this species (Engel *et al.*, 2008). Loci were tested for stuttering and null alleles using the software MICRO-CHECKER 2.2.3 (Van Oosterhout *et al.*, 2004). F_{IS} calculations and tests of Hardy–Weinberg equilibrium used FSTAT 2.9.3 (Goudet, 1995), randomizing alleles (10^4 runs) among individuals within sites.

Genetic structure was inferred using STRUCTURE 2.3.4 (Pritchard *et al.*, 2000) with admixture and without *a priori* population assignment. This ran the correlated allele frequency model with a burn-in time of 2×10^5 repetitions, 1×10^6 iterations and considering a range of clusters (K) from 1 to 10. The number of clusters was estimated using

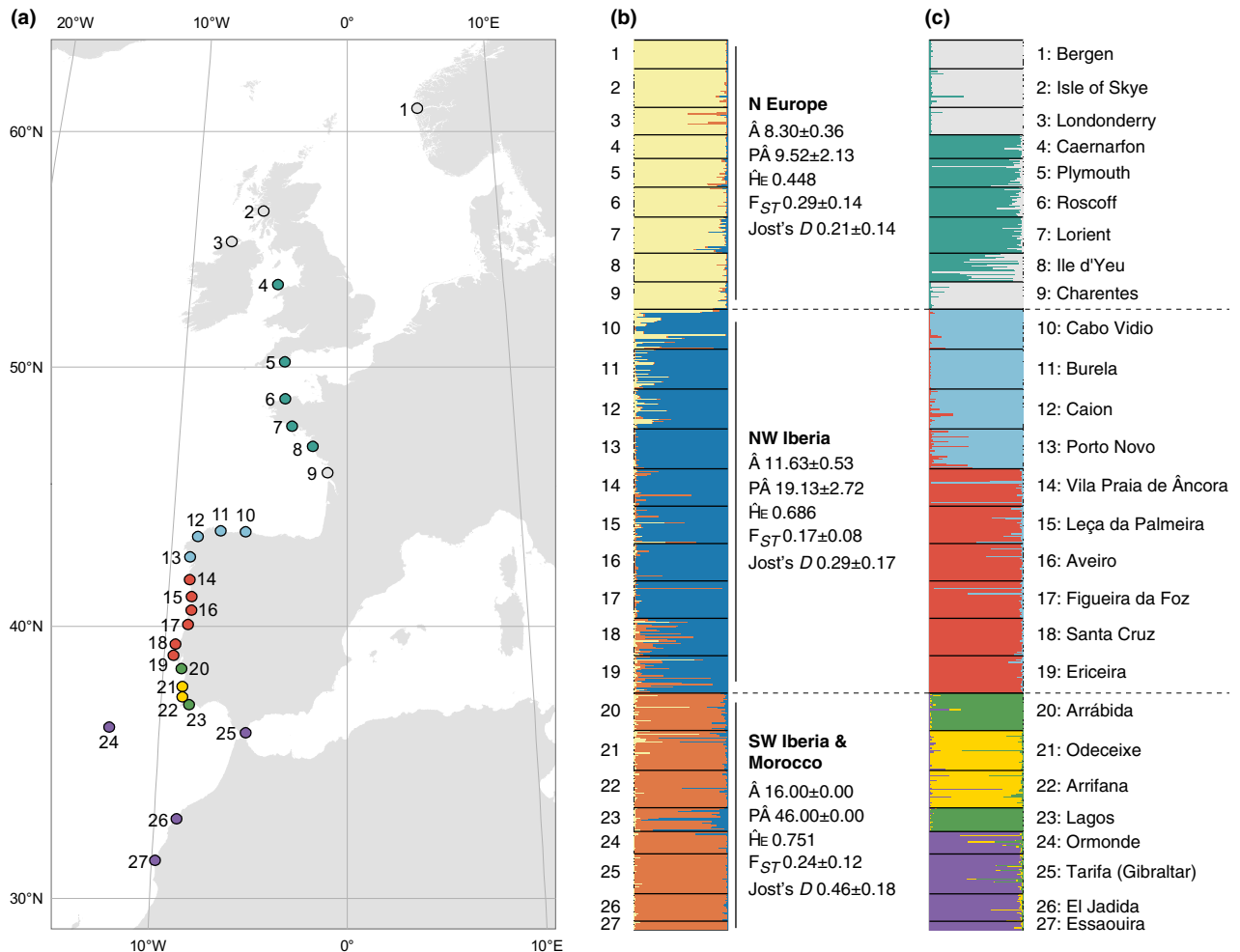


Figure 1 (a) List of samples and genetic subdivision of *Saccorhiza polyschides* based on Structure (individual multilocus genotypes). (b) Uppermost level of genetic structure, standardized allelic richness (\bar{A}), standardized number of private alleles (P \bar{A}) and gene diversity (H_e) per cluster for a common sample of 190 individuals. (c) Second hierarchical level of structure.

Table 2 List of samples of *Saccorhiza polyschides*. Site number (#) and name, country, longitude (Lon) and latitude (Lat) in decimal degrees, depth range (m), sample size (N), standardized allelic richness (\hat{A}) and standardized number of private alleles ($P\hat{A}$) for a common sample size of 18 individuals (\dagger indicates no standardized estimates due to sample size < 18), expected heterozygosity (H_e) and F_{IS} multilocus estimates (* indicates significant deviations from Hardy–Weinberg expectations, with Bonferroni correction for $\alpha = 0.05$).

#	Name	Country	Lon	Lat	Depth	N	\hat{A}	$P\hat{A}$	H_e	F_{IS}
1	Bergen	Norway	4.974	60.444	0–2	23	1.69 ± 0.05	0.00 ± 0.00	0.236	−0.104
2	Isle of Skye	Scotland	−5.844	56.976	0–2	31	2.73 ± 0.2	1.50 ± 0.80	0.244	0.395*
3	Londonderry	Ireland	−7.620	55.254	0–2	22	2.85 ± 0.12	0.13 ± 0.33	0.27	0.095
4	Caernarfon	England	−4.532	53.231	0–2	19	2.14 ± 0	1.38 ± 0.55	0.323	0.116
5	Plymouth	England	−4.081	50.322	0–2	23	4.22 ± 0.19	2.20 ± 1.57	0.44	0.322*
6	Roscoff	France	−3.927	48.729	0–2	24	3.44 ± 0.16	1.79 ± 0.77	0.326	0.121
7	Lorient	France	−3.554	47.761	0–2	29	3.23 ± 0.2	0.65 ± 0.52	0.386	−0.114
8	Ile d'Yeu	France	−2.322	46.688	0–2	23	3.25 ± 0.15	0.74 ± 0.86	0.348	−0.012
9	Charentes	France	−1.415	46.032	0–2	22	3.02 ± 0.11	0.83 ± 0.37	0.336	−0.042
10	Cabo Vidio	Spain	−6.244	43.584	0–2	32	5.66 ± 0.34	5.71 ± 1.42	0.603	0.102
11	Burela	Spain	−7.307	43.618	0–2	32	5.47 ± 0.27	6.03 ± 1.55	0.676	0.210*
12	Caion	Spain	−8.613	43.313	5–10	32	5 ± 0.36	2.59 ± 1.26	0.633	0.133
13	Porto Novo	Spain	−8.849	42.389	5–10	32	3.75 ± 0.23	1.47 ± 0.82	0.603	0.037
14	Vila Praia de Âncora	Portugal	−8.870	41.809	0–2	30	4.49 ± 0.21	0.93 ± 0.68	0.553	0.139
15	Leça da Palmeira	Portugal	−8.713	41.196	0–2	30	4.25 ± 0.26	0.24 ± 0.48	0.546	0.263*
16	Aveiro	Portugal	−8.754	40.644	0–2	30	3.32 ± 0.2	0.15 ± 0.51	0.506	0.234*
17	Figueira da Foz	Portugal	−8.892	40.166	0–2	30	3.37 ± 0.16	0.24 ± 0.46	0.536	−0.023
18	Santa Cruz	Portugal	−9.390	39.134	0–2	30	4.34 ± 0.21	0.90 ± 0.74	0.504	0.165
19	Ericeira	Portugal	−9.422	38.980	0–2	30	3.97 ± 0.2	0.65 ± 0.69	0.522	0.224*
20	Arrábida	Portugal	−9.154	38.416	5–10	30	5.77 ± 0.30	9.42 ± 2.01	0.68	0.383*
21	Odeceixe	Portugal	−8.808	37.444	0–2	32	4.65 ± 0.31	1.77 ± 1.37	0.607	0.393*
22	Arrifana	Portugal	−8.854	37.342	0–2	30	6.52 ± 0.44	5.67 ± 1.86	0.653	0.272*
23	Lagos	Portugal	−8.673	37.087	5–10	19	2.29 ± 0	0.00 ± 0.00	0.243	−0.119
24	Ormonde	Portugal	−10.902	36.905	30–35	18	6.16 ± 0.08	5.90 ± 0.92	0.622	0.298*
25	Tarifa (Gibraltar)	Spain	−5.610	36.004	20–25	32	7.24 ± 0.34	11.8 ± 1.96	0.739	0.212*
26	El Jadida	Morocco	−8.629	33.166	0–2	22	4.52 ± 0.12	1.17 ± 0.72	0.549	0.295*
27	Essaouira	Morocco	−9.771	31.501	0–2	7	4†	2†	0.57	0.117

the DeltaK criterion of Evanno *et al.* (2005). Further structure was inferred by re-running Structure within clusters. Genetic structure was also inferred by factorial correspondence analysis (FCA) of population multiscores using GENETIX 4.05 (Belkhir *et al.*, 2004). Genetic differentiation was estimated between sites and within the main genetic clusters using both F_{ST} and Jost's D , using GENODIVE 2.0 (Meirmans & Van Tienderen, 2004). A hierarchical analysis of molecular variance (AMOVA) was performed in GENODIVE with 10^4 randomizations to test genetic structure (1) between individuals within sites (2), between sites within genetic clusters and (3) between genetic clusters.

Genetic diversity was estimated per site as gene diversity (expected heterozygosity, H_e), allelic richness (\hat{A}) and number of private alleles ($P\hat{A}$). These were standardized for the smallest sample sizes in terms of individuals within sites and genetic clusters, using 10^4 randomizations.

RESULTS

Distribution of *Saccorhiza polyschides* through time

The distribution of *S. polyschides* at this scale is mainly explained by ocean temperatures and salinity, particularly

during winter and spring when generally only gametophytes and young sporophytes are present (OTemp ranging from 5.2°C to 21.6°C, and OSal from 32.7 Practical Salinity Scale; Table 1; see Table S2 in Appendix S2). When modelled alone, these predictors obtained good accuracy scores (TSS > 0.60) and when combined with others they produced gains in TSS from 0.11 ± 0.02 to 0.15 ± 0.03 (Table 1). Nitrates and Light produced poor to fair models when used alone ($0.2 < \text{TSS} < 0.6$), while Phosphates had no ability to predict distributions (TSS < 0.2). In general, Nitrates, Phosphates and Light had little contribution to model transferability, adding marginal gains to TSS when combined with other variables (gains in TSS < 0.05).

The species and sub-taxon models produced for present times showed high resemblance to the known species' distribution (Fig. 2c) and retrieved accuracy scores (TSS) of 0.99 and 0.98 respectively. Both agreed that the niche of *S. polyschides* is currently available in depth throughout many north-eastern Atlantic and western Mediterranean seamounts, such as those adjacent to the Gulf of Cadiz, the Alboran Basin and in northern Lanzarote (Conception Bank). Despite similarities, the sub-taxon model predicted less suitable habitat throughout eastern Scottish shores, the seamounts of Celtic Sea, southern Bay of Biscay and southern Morocco. Hindcasting to the LGM

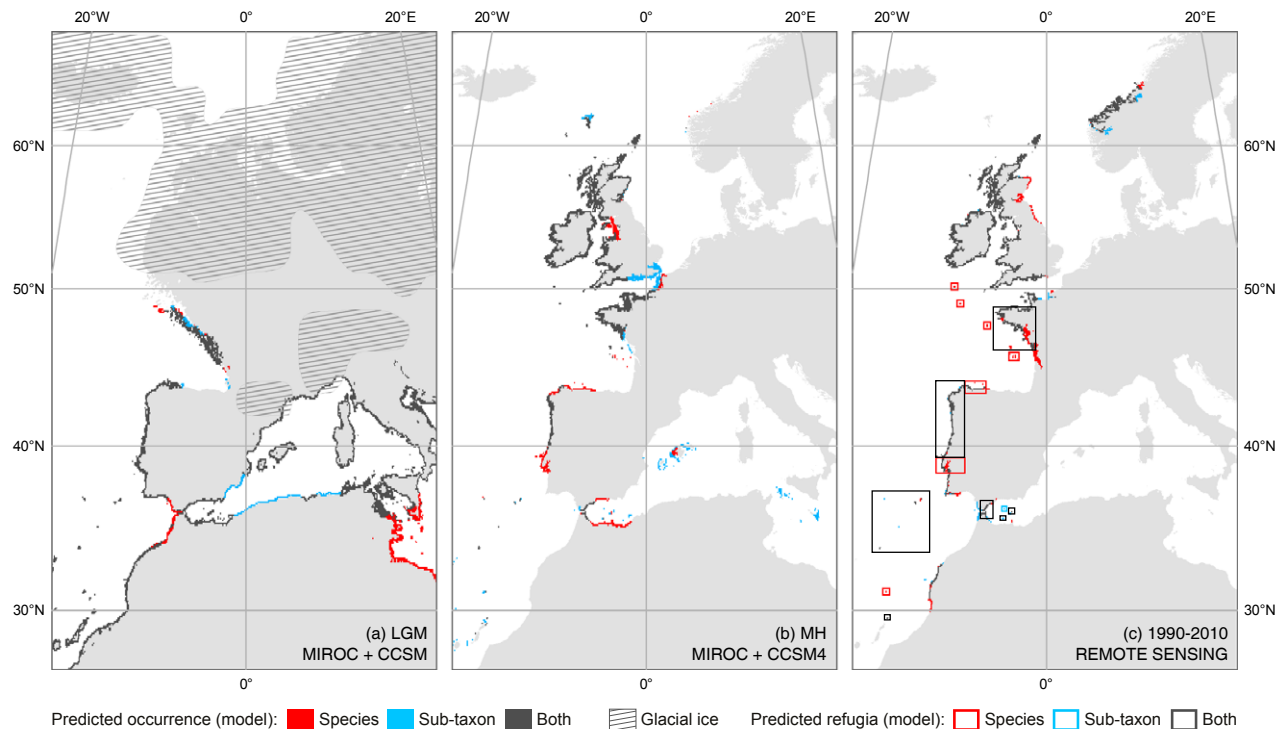


Figure 2 Suitable climatic conditions for *Saccorhiza polyschides* during the Last Glacial Maximum (LGM), the Mid-Holocene (MH) and present (1990–2010). Species (red) and sub-taxon (blue) model outputs reclassified as binary response of occurrence. Coloured boxes illustrate refugia inferred from species (red) and sub-taxon (blue) models. Glacial ice plotted following the reconstruction of Peltier (2004).

indicated that *S. polyschides* might have been distributed from Brittany to the south-west of France (Bay of Biscay), and continuously from north-west Iberia to Cape Bojador in Western Sahara (Fig. 2a). This analysis also supported its past occurrence in Canary and Madeira islands, in the Atlantic seamounts adjacent to the Gulf of Cadiz, and throughout the western Mediterranean Basin. Hindcasting to the MH set ranges similar to present times (Fig. 2b), but with the main difference that no suitable habitat was predicted for south-west Iberian and Norwegian shores (Fig. 2b,c). Additionally, the MH sub-taxon model predicted more suitable habitat in the English Channel and Balearic Islands, and less in NW Iberia and the Alboran Basin.

Predicting distributions through time pinpointed 4 main regions of long-term persistence (Fig. 2c), although with few differences depending on the modelling approach: (1) Brittany to Charentes (49.0°N to 45.5°N) and adjacent seamounts, (2) Northwest Iberia (44.0°N to 39.0°N or to 38.5°N in species model), (3) Gibraltar and Alboran Basin (36.5°N to 35.5°N), the (4) Atlantic seamounts adjacent to the Gulf of Cadiz (37.0°N to 33.3°N) plus Conception bank in Lanzarote (29.5°N) and Dagia seamount (31.0°N; species model only).

Population genetic structure and diversity

A total of 162 alleles resulted from 714 unique multilocus genotypes (23.14 ± 9.71 alleles per locus, ranging from 10 to

38) sampled throughout 27 sites (Fig. 1a; Table 2). MICROCHECKER showed no signs of stuttering error while null alleles were rare to uncommon (proportion per locus < 0.2) and with no consistency among regions or sites. Significant F_{IS} values were obtained in 12 out of 27 sites (Table 2).

The STRUCTURE analysis performed with the Evanno criterion revealed three main clusters: (1) northern Europe, (2) north-west Iberia and (3) south-west Iberia & Morocco (Fig. 1b; see Appendix S3). The subsequent hierarchical level of genetic structure divided N Europe and NW Iberia in two sub-clusters, whereas SW Iberia & Morocco was divided into three sub-clusters (Fig. 1c; see Appendix S3). The FCA retrieved similar results (Fig. 3), supporting the aforementioned clusters of N Europe, NW Iberia (including Arrábida and Lagos; sites 20 and 23) and SW Iberia & Morocco.

The FCA analysis also showed that genetic differentiation within each of the three main clusters increases from north-south. Sites are less differentiated within the N European cluster, followed by NW Iberia and SW Iberia & Morocco. This trend was supported by pairwise Jost's D but not by pairwise F_{ST} (Fig. 1b; see Appendix S3).

Allelic richness per site was highest in the southern sites Tarifa, Arrifana and Ormonde, followed by the northern Iberian sites from Cabo Vidio to Caion and by Arrábida and Odeceixe in SW Iberia (Table 2). These sites had approximately 1.5–2-fold higher diversity than most of the others.

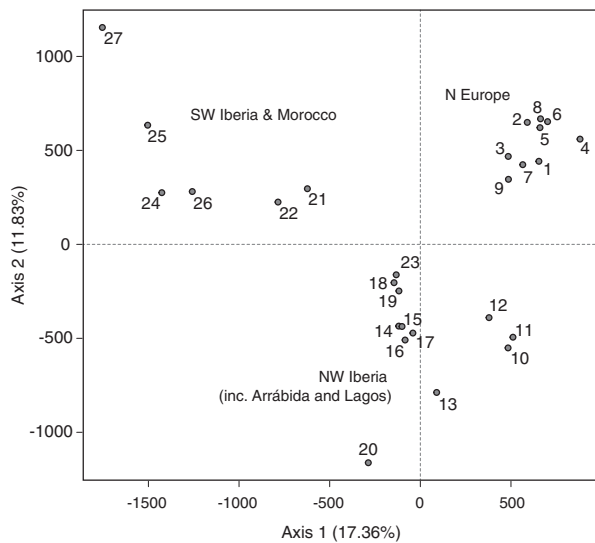


Figure 3 Genetic differentiation of *Saccorhiza polyschides* inferred by factorial correspondence analysis of population multiscores. Numbers refer to sites as listed in Fig. 1 and Table 2.

The number of private alleles was also highest in Tarifa, Arrábida, Arrifana and Ormonde. Gene diversity (H_e) showed a pattern similar to allelic richness, higher in N and SW Iberia, Ormonde and Tarifa, followed by W Iberia (from Vila Praia de Âncora to Ericeira), and Morocco (El Jadida and Essaouira). The lower values were found in northern Europe (sites 1–9) and Lagos (Table 2). Allelic richness per cluster, standardized for 190 individuals, and gene diversity per cluster, were higher in the south decreasing northwards (Fig. 1b). Private alleles per cluster showed the same pattern (Fig. 1b). The values of genetic diversity and differentiation were consistent across all loci (see Appendix S3).

DISCUSSION

Coupling ENM with genetic analyses for a marine forest species, *Saccorhiza polyschides*, revealed how past climate changes produced major range shifts that shaped its global genetic variability, structuring distinct putative latitudinal and depth refugia. Results indicate that *S. polyschides* might display a wider potential distribution in deep offshore waters than previously assumed, and highlight the role of deep reefs as safeguards for persistent genetic diversity.

Transferable distribution model

The contribution of each predictor to the models is corroborated by empirical evidence demonstrating that the microscopic and young life stages of *S. polyschides* are more susceptible to extreme temperatures (5.2 °C and 21.6 °C) than the adults (Norton, 1997; Fernández, 2011). Because high temperature waters are generally nutrient depleted (Kamykowski & Zentara, 1986), temperature responses could be linked to nutrient limitation. The need for cold spring

temperatures may be such a case, given the high dependence on nutrients of recruiting sporophytes (Dayton, 1985) and the stronger response to Nitrates during this season. This relationship may be particularly important in the southern ranges of *S. polyschides*, where the upwelling conditions delivering cold nutrient-rich waters have high seasonal variation (Pastor *et al.*, 2008; Pereira *et al.*, 2015a). The importance of salinity is also supported by evidence showing that this species' development is irreversibly inhibited when exposed to low salinities (Norton & South, 1969). The minor contribution of Light in the models is likely the result of our modelling space structure, which reflected a prior step segregating coastal cells (down to 30 m depth) from offshore banks, and missing enough spatial resolution to distinguish areas above and below depth limits where light effectively restricts coastal distributions (e.g. Graham *et al.*, 2007).

Both the species and the sub-taxon models retrieved very similar predictions, physiological tipping points and accuracy scores. These results do not support a previous study showing that sub-taxon models predict wider suitable habitats and improve accuracies, when compared to entire range models (Pearman *et al.*, 2010). The non-overlapping character of phylogroups, together with the conservative nature of our pseudo-absences (high thresholds), may be the cause for the more truncated niche distributions of sub-taxon models. Either way, because this class of models relies on combining distinct niche responses throughout ranges, the general agreement found between modelling approaches points to niche conservatism across distinct genetic groups in *S. polyschides*; a hypothesis already verified for populations belonging to different genetic groups (N Europe versus NW Iberia), which showed identical physiological responses to extreme environmental stress (Pereira *et al.*, 2015b). The lack of niche differentiation provides better support for our modelling results, which are particularly relevant for some regions like deep offshore reefs, where this kelp may currently find favourable habitat conditions. While we were able to validate this for Ormonde (c. 35 m depth), many other Atlantic and Mediterranean seamounts, unsurveilled to date, seem plausible candidates. For instance, loose fronds of *S. polyschides* were found c. 30 km from Conception Bank (northern Lanzarote; Ballesteros *et al.*, 1992), where our models predicted it at depth (c. 70 m depth, as inferred from GEBCO).

Hindcasting to the LGM showed that the distribution in northern Europe might have been restricted to a single population distributed from Brittany to the Bay of Biscay, whereas a wider distribution was likely throughout northern Africa, the Atlantic islands and the Mediterranean, as predicted for other brown algae (e.g. Neiva *et al.*, 2014). Hindcasting to the MH suggested a contrasting trend, with extensive range expansion to northern regions and southern contraction, as in other marine taxa displaying similar distribution (Assis *et al.*, 2014). By combining the ENM outcomes, we were able to identify four regions where this species may have found refugia. Other studies partially agree with our findings, also suggesting a broad region from

Brittany to Charentes and NW Iberia as putative refugia for cold-temperate species (e.g., Maggs *et al.*, 2008; Neiva *et al.*, 2014). In contrast, neither the deep Gibraltar and Alboran regions, nor Atlantic seamounts had been previously highlighted for their refugial roles. While the former two fall within the NW Africa refugium where intertidal species may have persisted (Assis *et al.*, 2014), their deep refugial role and that of seamounts are novel and bring forward new hypotheses for the role of deep reefs in harbouring persistent populations of subtidal species during warmer periods like the MH or the near future (e.g. Raybaud *et al.*, 2013).

Phylogeography of *S. polyschides*

Our results revealed three main genetic clusters, followed by a second and more complex level of structure comprising seven clusters. All showed significant differentiation and private alleles, suggesting large effects of drift, not offset by regular gene flow. The isolation of phylogroups was in general agreement with our models, which predicted disjunct distributions between N Europe and NW Iberia. Most of SW Iberia & Morocco was further predicted far apart (Atlantic seamounts, Gibraltar and Morocco). However, differentiation between Arrábida and its northern neighbouring sites was higher than expected given their proximity. This region displays identical genetic breaks for other marine species, a pattern previously explained by nearshore discontinuities in ocean currents (Diekmann *et al.*, 2005). Sharp genetic structure at such short distances may also result from the higher densities found north of Arrábida (Assis *et al.*, 2013), which could halt the expansion of immigrant genes by density barrier effects (Neiva *et al.*, 2012b). Likewise, the absence of strong oceanographic barriers between the west and north shores of Iberia (Ruiz-Villarreal *et al.*, 2006), where structure was found at short distances (sites 13–14, Fig. 1c), further suggests that density may influence gene flow in *S. polyschides*.

The current northern European distribution may stem from a single refugium, from which complex colonization routes are suggested by the patterns of genetic structure and differentiation. During expansion, northern territories might have been colonized using both the alongshore current (Charria *et al.*, 2013) across the English Channel and into the Irish Sea, and the deeper offshore current (Pingree & Le Cann, 1989), from Charentes polewards to western Ireland, Scotland and Norway. In any case, founder effects may have contributed markedly to the current genetic structure in northern Europe.

The lower diversity and fewer private alleles in sites colonized after the LGM is expected from founder effects at leading edges (Hewitt, 1996; Excoffier *et al.*, 2009). However, the decreasing gradient in diversity found from Plymouth towards Charentes was unexpected, because our models predicted some degree of persistence in that region. Hence, erosion of genetic diversity might have occurred there, possibly due to low effective population size when currently found at

a distributional edge (near a range gap), off their climatic optima (Eckert *et al.*, 2008; Assis *et al.*, 2014). Indeed, our models predicted marginal, although persistent, populations in Charentes during the MH and the present.

The diversity and private alleles found in Tarifa and Ormonde agree with our models, which placed these sites within refugia. Unexpectedly, Tarifa is the hotspot of genetic diversity for this species, despite being very isolated and located at the warm range edge. This might be related to the persistent upwelling system occurring there, which provides nutrients to sub-surface waters (Sarhan *et al.*, 2000). The also remarkable private diversity found in Arrábida likewise supports long-term persistence, as predicted by the species modelling approach. These sites could be the remnants of a much wider southern population that may have (re)colonized SW Iberia (Arrifana and Odeceixe) and Morocco (El Jadida and Essaouira) after the predicted range contraction during the MH; thereby preserving the high regional diversity of these lower latitudes. However, the large number of private alleles in some SW Iberian sites (e.g. Arrifana), suggests population reestablishment from other unknown sources of diversity, or persistence there, in contrast to our predictions. The genetic bottlenecks inferred there could result either from the recent documented local extinctions (Assis *et al.*, 2013) or from the MH contraction *per se*, because populations could have persisted, although with lower effective sizes. The low diversity throughout Morocco, where populations are currently restricted to small (area) and isolated upwelling pockets (Pastor *et al.*, 2008), could have resulted from random drift. However, the few private alleles there do not support persistence but rather a post-MH (re)colonization.

The present diversity in NW Iberia, although lower relative to southern sites, also coincides with an inferred climate refugium. The lower diversities may result from the smaller population sizes, as this region only comprises c. 200 km of coastline (as for Morocco). Additionally, recent bottlenecks due to poorer niche conditions may also have occurred, as populations now have shorter generations and a smaller fraction becomes reproductive (Fernández, 2011). Peripheral niche conditions may further explain the even lower diversity found from that region southwards (from Porto Novo to Ericeira), as it might have been the rear edge of the Iberian distribution during the MH. Because these sites are mostly restricted to shallow waters (Assis *et al.*, 2009), deeper colonizations might not have been possible during warming periods. Later, as climate conditions ameliorated, dispersal barriers acting there (e.g. oceanographic and/or density, as previously discussed) might have blocked admixture with richer populations, maintaining the lower levels of diversity.

Higher genetic differentiation towards southern latitudes was revealed both by FCA and Jost's D, which is more appropriate than F_{ST} to compare populations with contrasting levels of diversity (Whitlock, 2011), as in our case. This differentiation is consistent with the isolated nature of south-

ern sites, mostly found at deeper reefs or particular regions of upwelling. The exceptionally high differentiation between Lagos and its neighbouring sites while being very similar to sites further north, is likely the result of a recent colonization taking place after 1970 (absent before, Ardré, 1970), probably from Arrábida or Ericeira (Fig. 3; see Appendix S3). The low diversity and complete absence of private alleles in Lagos further supports this and points to the effectiveness of rare dispersal events driven by floating rafts.

We also found a southward trend in increasing homozygosity, despite the increasing diversity. One hypothesis for this pattern is related to subpopulation structure. If arrested, development of microscopic stages (Carney *et al.*, 2013) is more common towards the warmer and nutrient-poorer south (one of the hypotheses in Assis *et al.*, 2013), it could generate co-existence of multiple subpopulations thereby promoting departures from random mating (temporal Wahlund effect; Morand *et al.*, 2002). A second and non-exclusive hypothesis is supported by the lower sporophyte densities at most southern sites (Assis *et al.*, 2013). The higher spatial distance between sporophytes in the south implies that spores settle surrounded by siblings, resulting in gametophytes that are less intermingled with those from more genetically distant individuals, thereby increasing selfing and biparental inbreeding. The presence of null alleles could also explain such pattern, although this is poorly supported given their low prevalence in our data and the absence of a particular geographical trend.

Taken together, our results show evidence of how diverse factors shape the genetic traits of species at multiple scales. At larger scales, the trajectory of climate changes defines source and sink ranges, while at finer scales, nearshore currents and density barrier effects result on a mismatch between gene flow and the dispersal capacity of *S. polyschides*. Most of this species' phylogeography was also unravelled, particularly from the LGM to present times. Great part of the present species range comprises the post-glacial expansion zone, which may stem from an unique source from the Brittany to Charentes region, whereas there is no evidence for range expansion derived from the NW Iberian refugium. The deep populations in Gibraltar, Alboran and the Atlantic seamounts are supported as important safekeepers of diversity at southern latitudes.

The implementation of the MH in our models showed that the erosion of genetic diversity driven by climate changes may not be unique to the lower latitude trailing edges. These processes may mask regions of persistence with lower diversity, despite formerly richer states. Furthermore, the predicted consequences of the warmer MH may serve as a reasonable proxy for those happening in the near future. While local extinctions reduce the overall genetic diversity and therefore the evolvability of species as a whole (Hampe & Petit, 2005), our study suggests that species like kelp may find refugia at depth, away from the overall warming trend of surface waters. Depth range shifts have been reported for other kelp species in response to warm-

ing trends (e.g., Ladah & Zertuche-Gonzalez, 2004; Pehlke & Bartsch, 2008). Like terrestrial elevational range shifts in the face of climate change (Epps *et al.*, 2006), going deep may allow unique genetic lineages to persist in small pockets of cryptic refugia that might otherwise become extinct, in contrast with vanishing intertidal populations likely unable to shift in depth (e.g., Assis *et al.*, 2014; Neiva *et al.*, 2015).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Records of occurrence for ENM.

Appendix S2 Supplementary methods and results regarding climate data and ENMs.

Appendix S3 Supplementary results regarding genetic structure, diversity and differentiation.

DATA ACCESSIBILITY

Microsatellite data used for genetic analyses are available in the Figshare repository at <http://dx.doi.org/10.6084/m9.-figshare.1510947>.

BIOSKETCH

Jorge Assis is a post-doctoral researcher at CCMAR, University of Algarve. His research is focused on ecological niche modelling, past and future climate-driven range shifts and landscape genetics at multiple temporal and spatial scales.

Author contributions: J.A., M.V., F.A. and E.A.S. conceived the ideas. J.A., T.L. and F.A. collected samples, N.C.C. and T.L. genotyped samples, J.A. analysed data. J.A., M.V. and E.A.S. led the writing.

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