

# Climate-driven range shifts explain the distribution of extant gene pools and predict future loss of unique lineages in a marine brown alga

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## Abstract

The climate-driven dynamics of species ranges is a critical research question in evolutionary ecology. We ask whether present intraspecific diversity is determined by the imprint of past climate. This is an ongoing debate requiring interdisciplinary examination of population genetic pools and persistence patterns across global ranges. Previously, contrasting inferences and predictions have resulted from distinct genomic coverage and/or geographical information. We aim to describe and explain the causes of geographical contrasts in genetic diversity and their consequences for the future baseline of the global genetic pool, by comparing present geographical distribution of genetic diversity and differentiation with predictive species distribution modelling (SDM) during past extremes, present time and future climate scenarios for a brown alga, *Fucus vesiculosus*. SDM showed that both atmospheric and oceanic variables shape the global distribution of intertidal species, revealing regions of persistence, extinction and expansion during glacial and postglacial periods. These explained the distribution and structure of present genetic diversity, consisting of differentiated genetic pools with maximal diversity in areas of long-term persistence. Most of the present species range comprises postglacial expansion zones and, in contrast to highly dispersive marine organisms, expansions involved only local fronts, leaving distinct genetic pools at rear edges. Besides unravelling a complex phylogeographical history and showing congruence between genetic diversity and persistent distribution zones, supporting the hypothesis of niche conservatism, range shifts and loss of unique genetic diversity at the rear edge were predicted for future climate scenarios, impoverishing the global gene pool.

**Keywords:** climate change, *Fucus vesiculosus*, genetic diversity, niche modelling, range shifts, rear edge

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## Introduction

Under the niche conservatism hypothesis (Peterson *et al.* 1999), when environmental conditions fall outside physiological tolerances, species either shift their distribution or become extinct (reviewed by Parmesan 2006). The glacial and interglacial cycles of the Quaternary

(~2.6 MYA to present time) were particularly important in shaping the distribution of species, with range expansions and contractions responding to climate oscillations (Provan & Bennett 2008). The Last Glacial Maximum (LGM: ~21 KYA BP) was one of the most extreme periods of the Quaternary, resulting in severe reductions in the northern ranges of cold-temperate species. The restriction of species to small isolated regions of persistence or glacial refugia is frequently hypothesized (reviewed by Maggs *et al.* 2008) although

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broad distributions might be maintained under a scenario of southern expansion. As climate conditions ameliorated throughout the Holocene ( $\sim 12$  KYA to present time), populations persisting within refugia or in extended southern ranges, gradually recolonized northwards (Provan & Bennett 2008). By the mid-Holocene (MH:  $\sim 6$  KYA BP), climate conditions were quite similar to the present, although higher air and sea surface temperatures resulted from greater summer insolation (Mairesse *et al.* 2013) and caused range edge contraction for many species (e.g. Smith & Betancourt 2003). Due to rising concentrations of greenhouse gases, the Holocene has further potential for climate warming and range shifts in the immediate future.

Climate-driven range shifts can leave distinct footprints on the genetic and evolutionary traits of populations along biogeographical ranges. Regions with long-term population persistence often display high genetic diversity and unique gene pools. Differentiation results from the accumulation of mutations in separated populations (Hewitt 2000), and the refugia number, size and their isolation may also play a fundamental role in shaping genetic variation (DeChaine & Martini 2004). In contrast, range reduction or niche peripheralality can leave small and isolated marginal populations, in which drift and bottlenecks may reduce genetic diversity, although this may also increase genetic differentiation. Unnoticed reductions in genetic variation (where prior levels of diversity were unknown), leave impoverished reference baselines. Without predisturbance genetic information lost, diversity will never be known, and the current state is the only detectable baseline (i.e. shifting genetic baselines; Assis *et al.* 2013). Population genetic diversity may also be eroded during expansions due to founder effects at the 'leading edge' of colonization, leaving fewer alleles in newly colonized areas (Neiva *et al.* 2012a). Such signatures retained in the current patterns of species genetic diversity and structure can be tested independently against species distribution models (SDM, see Rushton *et al.* 2004 for a review) based on proxies for past climate to further investigate phylogeographical questions (e.g. Waltari *et al.* 2007). SDM use species distribution records and environmental data to predict the potential distribution of species (Rushton *et al.* 2004; Raybaud *et al.* 2013). Intertidal species are constrained by both atmospheric and oceanic climatic conditions, representing a singular challenge to model and predict biogeographical distributions.

In this study, we ask whether the genetic structure of a species is determined by past climate induced range shifts and infer the implications of future climate change for its global gene pool. To do this, we combined predictive distribution models with microsatellite genetic variation for the intertidal seaweed *Fucus*

*vesiculosus*. We aim to (i) identify the potential habitat for this species during the LGM, MH and in present time (1990s and 2000s), (ii) discriminate among hypotheses for its phylogeographical history and (iii) infer the consequences of future climate change for the global gene pool.

## Methods

### *Study area and focal species*

This study was conducted throughout the distribution of *F. vesiculosus*. This is a structural species on intertidal rocky shores and in saltmarshes. Along the eastern Atlantic, it ranges from northern Norway to western Morocco, or more recently to southern Iberia (Nicastro *et al.* 2013), extending to the White Sea, the Baltic Sea, the Faroe Islands and Greenland. Along the Western Atlantic, it ranges from Canada to North Carolina. This distribution includes regions thought to be ancient refugia and where suitable habitat was extirpated in the past by the advance of ice sheets (Coyer *et al.* 2011a). Furoid algae can migrate across large distances when colonizing novel habitats, but gene flow remains extremely restricted among persistent nearby populations (Neiva *et al.* 2012b).

### *Data on species occurrence and climate*

Distribution maps of *F. vesiculosus* were constructed by developing a transferable model, trained with distribution records in relation to current climate conditions and projected onto different climate scenarios. Presence records, dated from 2000 to 2010, were collected from literature and pseudo-absences were generated by randomly selecting points located at least two degrees away from any presence (the two degrees far method), following the recommendations of Barbet-Massin *et al.* (2012). Distribution records were gridded ( $0.25^\circ$  resolution cells), thus reducing the effects of spatial autocorrelation (e.g. Waltari *et al.* 2007), and divided in two sets. The first, for model training, was generated by randomly selecting 70% of the data. The second, for testing model results by cross-validation, was generated with the remaining 30%.

Environmental predictors were selected based on the biological relevance to *F. vesiculosus* and availability for both past and future climate simulations. These were derived from remote sensing data averaged for the relevant period of 2000 to 2010 (Appendix S1, Supporting information). Intertidal availability was determined by calculating the area above the hydrographical zero (General Bathymetric Chart of the Oceans; BODC 2013) within tidal amplitude (Egbert 2004). All predictors

were gridded using bilinear interpolation to the 0.25° resolution.

#### *Transferable distribution model*

Models were performed with the training data and all possible combinations of noncorrelated predictors (Spearman's correlation  $R < 0.7$ ) by means of three methods known for their higher predictive performance: boosted regression trees (BRT; De'ath 2007), maximum entropy (Maxent; Phillips *et al.* 2006) and multivariate adaptive regression splines (MARS; Leathwick *et al.* 2005). This iterative approach was performed 100 times, and in each, pseudo-absences were regenerated along with randomization of training and testing data. For each model, a predictive map was developed and reclassified into a binary presence-absence surface based on a threshold that maximized the sum of sensitivity and specificity. The discriminatory power of these maps and therefore of each subset of predictors was measured by cross-validation, using the area under the receiver-operated characteristic curve (AUC). The importance of each single predictor was evaluated by the number of times it was selected for the best model (with the highest AUC).

#### *Past, present and future distribution of *F. vesiculosus**

Distribution maps were generated by merging with a median function the resulting surfaces of the most discriminatory subset of predictors per modelling method (i.e. ensemble modelling; Araújo & New 2007). The weighting of different sources of data in the ensemble allows partial assessment of uncertainty (Araújo & New 2007). For the LGM and MH, ensemble maps were performed with data from two Atmospheric General Circulation Models (AGCM): the Community Climate System Model (CCSM4) and the Model for Interdisciplinary Research on Climate (MIROC5). Tidal amplitude simulations were also considered (see Egbert 2004; Uehara *et al.* 2006). More recent hindcasting was performed for 1990–2000 (before genetic sampling; see below) and 2000–2010, with remote sensing data (S1). CCSM4 and MIROC5 were also used to forecast the distribution to 2040–2050 and to 2090–2100, under two different scenarios: (i) RCP 2.6, a scenario where greenhouse gas emissions are reduced substantially over time; and (ii) RCP 8.5, characterized by increasing greenhouse gas emissions over time (Moss *et al.* 2010). Because ensemble modelling is also useful for uncertain data sets (Araújo & New 2007), for those maps using AGCMs, in addition to multiple methods, predictions were performed by merging the resulting surfaces of both CCSM4 and MIROC5. The accuracy of the final predictions was

evaluated by determining the sum of sensitivity and specificity (i.e. True Skill Statistic, TSS; Allouche *et al.* 2006) of the ensembles made for the 2000s with data from remote sensing and from the two AGCMs for this particular period.

Distribution maps were reclassified into probability of occurrence (range 0–1), and for illustrative purpose, glacial ice for the LGM was introduced following the reconstructions of Peltier (1994). LGM coastline contour lines were simulated as the isobath of –120 m below current sea level (Peltier 2002).

Regions of long-term persistence were inferred as those where suitable habitat occurred (hindcasts) during the LGM, MH and the 1990s (presampling predictive maps; see below). A visual approach was chosen in preference to others (e.g. Rebelo *et al.* 2012) because in the present study predicted cells differed in position through time due to changes in the coastline. The area of potential habitat was determined for the global distribution and for every region of persistence. All distribution models and related analysis were performed using the packages *gbm*, *dismo*, *mda*, *gam* and *Biomod* for R (R Development Core Team 2013).

#### *Population genetic structure and diversity*

Eighteen sites throughout the distribution of *F. vesiculosus* were sampled (24 individuals per site) from 2001 to 2004 (Table 1). DNA was extracted and genotyped using nine polymorphic microsatellite loci as described in Perrin *et al.* (2007). PCRs were performed on a GeneAmp 9700 thermocycler (PE Applied Biosystems, Foster City, California, USA), and fragment length was analysed on an ABI 377 DNA analyzer (Applied Biosystems).  $F_{IS}$  values were computed using *ESTAT* (Goudet 1995), and deviations from Hardy–Weinberg equilibrium were tested by determining the proportion of randomization (10,000 steps) that gave a larger  $F_{IS}$ -value than the observed.

The number of distinct genetic clusters (K) was estimated using the software *Structure* (Pritchard *et al.* 2000). The program ran with a burn-in time of  $2 \times 10^5$  repetitions and  $1 \times 10^6$  iterations exploring K from 1 to 10, with admixture allowed and without any a priori population assignments. The estimation of the likely number of clusters used the log probability of data  $\Pr(X/K)$  (Pritchard *et al.* 2000) and the DK criteria of Evanno *et al.* (2005). Genetic structure was also analysed by factorial correspondence analysis (FCA) of population multiscores using *GENETIX* 4.05 (Belkhir *et al.* 2004).

Genetic diversity was estimated using allelic richness (A) and Nei's expected heterozygosity ( $H_E$ ) for each locus and site using *StandArich* and *Adegenet* for R. Allelic richness and number of unique alleles were also

**Table 1** List of samples of *Fucus vesiculosus* from the North Atlantic. Region name, site name, sampling year, latitude (LAT), longitude (LON), number of sampled individuals, standardized allelic richness (A), expected heterozygosity ( $H_E$ ) and  $F_{IS}$  multilocus estimates (asterisk meaning significant deviation from Hardy–Weinberg expectations with Bonferroni correction;  $\alpha = 0.05$ ;  $P = 0.003$ )

Region	Site	Year	LAT	LON	<i>n</i>	A	$H_E$	$F_{IS}$
USA Maine S	Quoddy Maine	2005	43.684	−69.857	24	3.579 ± 0.196	0.515	0.074
USA Maine N	Christmascove Maine	2005	43.828	−69.487	23	2.992 ± 0.441	0.372	−0.244
Iceland Reykjavik	Reykjavik	2004	64.159	−22.053	24	5.5 ± 0.234	0.645	0.423*
Faroe Streymoy	Streymoy	2003	62.085	−7.047	24	5.81 ± 0.211	0.681	0.451*
Norway Langesund	Langesund	2004	58.991	9.772	24	6.444 ± 0.269	0.701	0.235*
Ireland Porta Ferry	Porta Ferry	2004	53.858	−6.233	24	6.77 ± 0.319	0.743	0.28*
England Bude	Bude	2002	50.828	−4.563	23	7.016 ± 0.204	0.739	0.376*
France La Crèche	Pointe De La Crèche	2001	50.751	1.592	24	6.556 ± 0.276	0.764	0.161*
France Brignogan	Brignogan	2001	48.672	−4.377	24	6.698 ± 0.35	0.73	0.174*
Spain Ria Del Eo	Ria Del Eo	2004	43.539	−7.035	14	5.333 ± 0	0.617	0.502*
Spain La Guardia	La Guardia	2001	41.902	−8.887	24	4.444 ± 0.235	0.481	0.173
Portugal Viana	Viana Do Castelo	2001	41.693	−8.851	24	4.786 ± 0.141	0.629	0.243*
Portugal Mindelo	Mindelo	2001	41.309	−8.742	24	3.738 ± 0.161	0.457	0.117
Portugal Modego	Figueira Da Foz	2001	40.148	−8.855	24	4.413 ± 0.236	0.526	0.088
Portugal Tejo	Alcochete	2001	38.762	−8.967	24	3.365 ± 0.154	0.42	0.062
Portugal Mira	Rio Mira	2001	37.721	−8.782	24	3.881 ± 0.244	0.563	0.172
Portugal Tavira	Tavira	2001	37.124	−7.643	24	2.762 ± 0.199	0.454	0.205
Morocco Lixus	Lixus	2004	35.198	−6.162	22	3.611 ± 0.113	0.465	0.314*

computed for each genetic cluster and standardized to the smallest group size.

Levels of differentiation within genetic clusters were determined by both mean pairwise  $F_{ST}$  and Jost's D. Hierarchical analysis of molecular variance (AMOVA) was computed using GENODIVE (Meirmans & Van Tienderen 2004), based on allele frequency information under 4999 permutations. Variance components were extracted for two hierarchical levels: (i) among sites within groups and (ii) between groups. These groups were partitioned following the outcomes of the Bayesian clustering and the FCA analysis to test whether the clustering assignments own statistical differences in molecular variance.

## Results

### *Past, present and future distribution of Fucus vesiculosus*

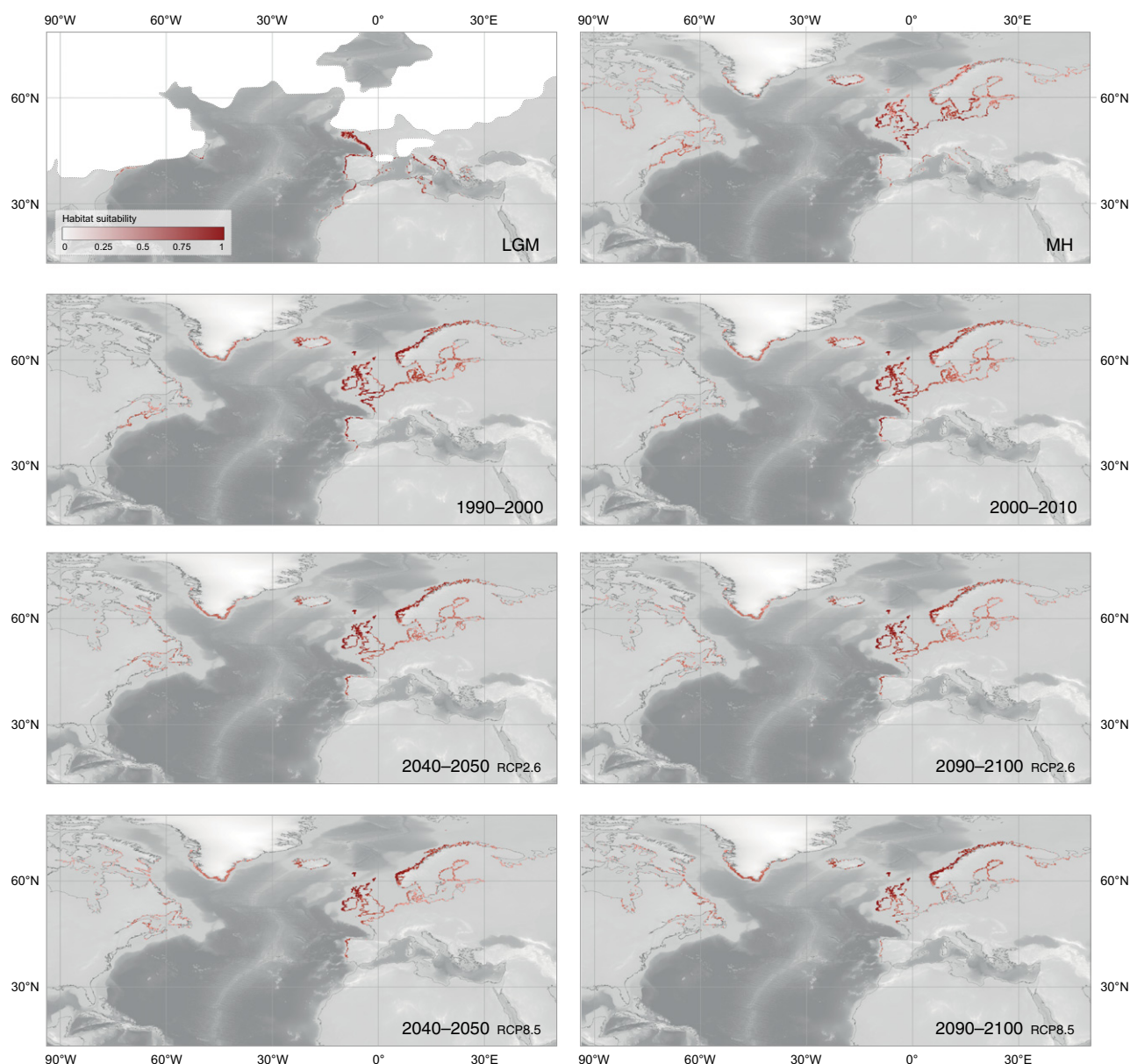
Considering all models performed (16124 × 100 iterations), the most important environmental predictors for the distribution of *F. vesiculosus* (predictors chosen >10% of the times for best models) were the long-term average (LTA) sea surface temperature (SST) of the hottest summer month (MaxSSTS, 99%), followed by the LTA SST of the coldest winter month (MinSSTW, 96%), intertidal availability (IntertidalAv; 65%), LTA air temperature of the hottest summer month (MaxAirTS, 46%), LTA relative humidity of the wettest summer month (MaxAirHumS, 31%) and the LTA air temperature of the coldest

winter month (MinAirTW, 29%). Tidal amplitude and ocean salinity were never chosen for best model.

The ensemble performed with data from the two AGCMs for the 2000s (Appendix S2, Supporting information) had very high discriminatory power (TSS:  $0.946 \pm 0.009$ ). Hindcasting to the LGM revealed a more southern and restricted distribution (Fig. 1). In the western Atlantic, *F. vesiculosus* was predicted to have been confined to a narrow region south of the Laurentide ice sheet from Long Island south to the Connecticut coast, and northeast to the Grand Banks region (Newfoundland). In the eastern Atlantic, models predicted a peri-glacial distribution along the southwest of Ireland and the western English Channel. The north and west coasts of the Iberian Peninsula (including Bay of Biscay) had highly suitable habitat. The Adriatic Sea, northwest Italy, southern France, Tunisia, Malta, eastern Iberia and Atlantic coast of Morocco also had high probability of occurrence (Fig. 1).

From the LGM to the MH, a profound reshaping of the distribution was predicted, with a global northward expansion adding ~13.44% more potential habitat (Fig. 2), which left the distribution very similar to the present-day's. However, the distribution may have been more widespread in the western Atlantic, specifically in Newfoundland, Quebec, and throughout southern Hudson Bay, although with low probability of occurrence. The Greenland distribution was predicted to have been more restricted than currently. In the eastern Atlantic, the distribution in Norway was less continuous, while





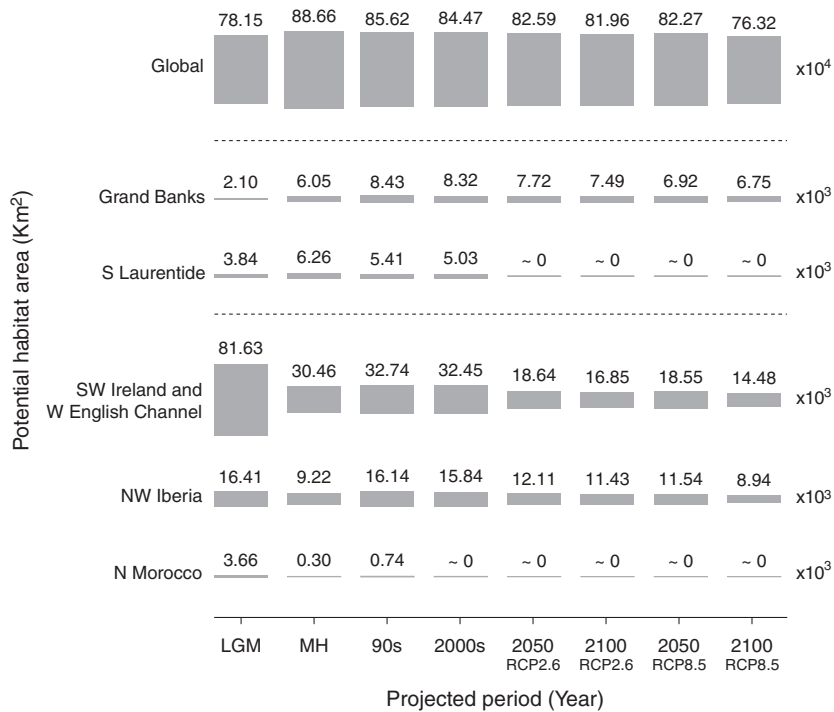
**Fig. 1** Ensemble maps of distribution of *Fucus vesiculosus* for the Last Glacial Maximum (LGM), Mid-Holocene (MH), present time (1990s and 2000s) and future (2050s and 2100s) using remote sensing, direct observations and two Atmospheric general circulation models (CCSM4 and MIROC5) with different climate scenarios (RCP26 and RCP85).

northern Spain and southwest Portugal were generally unsuitable for *F. vesiculosus*, leaving the southern range reduced to few sites in southern Spain and northwest Morocco (Fig. 1). The northern Adriatic Sea, northwest Italy, southern France and eastern Iberia were also regions of occurrence but with lower probability than during the LGM (Fig. 1).

The predictions for the present day retrieved an accurate description of distribution (TSS:  $0.954 \pm 0.011$ ). These estimated a global contraction of distribution from the MH to the 1990s (~3.55% less available habitat;

Fig. 2), mainly in northern territories such as Newfoundland and southern Hudson Bay in the western Atlantic, and the Barents Sea in the eastern Atlantic. This northern contraction was coupled with an expansion towards northern Iberia, southwest Portugal and northwest Morocco.

Taken together, past projections allowed us to pinpoint regions of long-term persistence (refugia) prior to our genetic sampling. These are southeastern (i) Grand Banks of Newfoundland (43.00°N to 44.00°N) and (ii) south of the Laurentide ice sheet, from Long



**Fig. 2** Area of potential habitat of *Fucus vesiculosus* for each region of persistence and globally.

Island to Connecticut (37.50°N to 42.50°N), in the Western Atlantic, and (iii) southwest Ireland and Western English Channel, including the western coast of France from Brittany southwards to Poitou-Charentes (50.00°N to 46.00°N), (iv) northwest Iberia, from Galicia (Spain) to central Portugal (43.75°N to 38.50°N), and a few sites in (v) northwest Morocco (35.50°N to 34.75°N) in the eastern Atlantic. From the LGM to the 1990s, these refugia responded differently to climate. The Grand Banks area was estimated to have expanded through time, while south of the Laurentide ice sheet expanded from the LGM to the MH and then contracted into the 1990s (Fig. 2). In the eastern Atlantic, all refugia achieved a maximum predicted area during the LGM, followed by contraction during MH and subsequent expansion up to the 1990s (Fig. 2).

A global decrease in distributional area was further predicted from the 1990s to the 2000s (~1.36%), particularly at the southern range edge of the Eastern Atlantic distribution and at the northern Iberian Peninsula (especially in the Bay of Biscay). All refugia were predicted to decrease, particularly in the southern ranges (losses: Grand Banks ~1.43%, S Laurentide ice sheet ~7.54%, SW Ireland and W English Channel ~0.89%, NW Iberia ~1.86% and N Morocco ~99.98%). Future projections follow this recent trend, with range shifts and decreasing area (Fig. 2). Specifically, a northward shift is predicted in the western Atlantic, expanding along Newfoundland and Hudson Bay, and contracting the southern limit to Nova Scotia. In the eastern Atlantic, predictions

include an expansion towards the Barents Sea and contraction of both southwest and northern populations of the Iberian Peninsula. The retreat of southern populations is intensified with RCP 8.5, which is predicted to impact populations from northwest Iberia and western English Channel (Fig. 1). In both scenarios, historical refugia are expected to suffer a strong habitat reduction, of ~9.98–18.88% by 2100 in the Grand Banks, while the S Laurentide ice sheet refugium is predicted to be extinct in 2050, in any emissions scenario. Similarly, SW Ireland and W English Channel are expected to lose ~49.13–57.22% and NW Iberia ~18.4–46.5% of the potential habitat (Figs 1 and 2).

#### Population genetic structure and diversity

A total of 163 alleles were observed in 418 unique multilocus genotypes of *F. vesiculosus*. The nine microsatellites had 8–30 alleles per locus (mean = 18.11, SD = 8.02). Significant  $F_{IS}$  values were obtained in 10 of the 18 sites (Table 1).

Structure revealed three main clusters ( $K = 3$ ) using the Evanno criteria (Appendix S3, Supporting information): western Atlantic, northern Europe (from Norway and Iceland to northwest Iberia) and southern Iberia (from Figueira da Foz southwards) to Morocco. Using a secondary level of subdivision ( $K = 4$  using Pritchard criterion; S3), northwest Iberia became separated from the northern Europe cluster (Fig. 3). The FCA supported the same four clusters identified by the secondary level

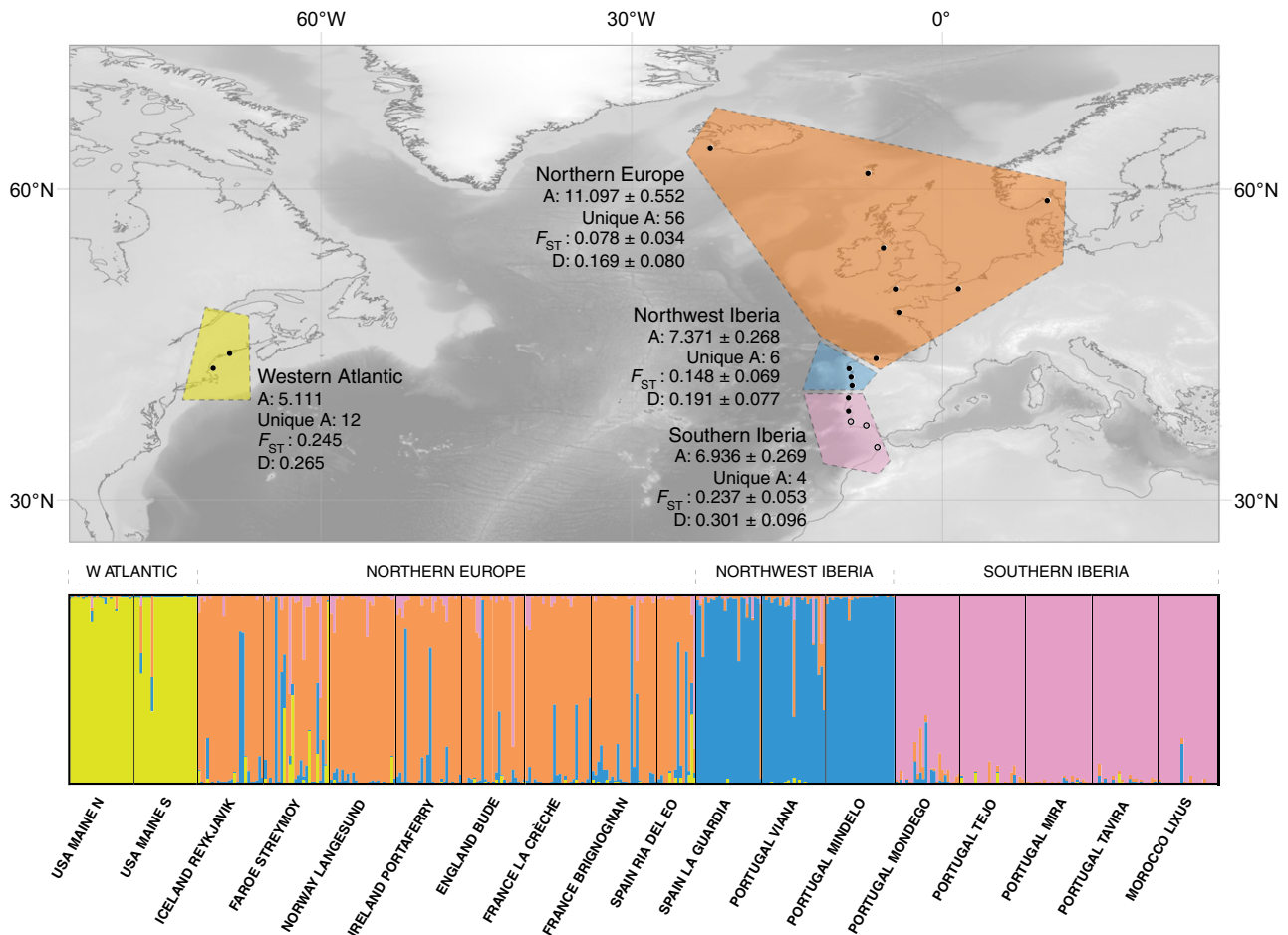
of subdivision of Structure (Fig. 4). Based on these results, some of the analyses below are conducted separately for these four clusters, hereafter designated as Western Atlantic, Northern Europe, northwest Iberia and southern Iberia, composed of 2, 8, 3 and 5 sites, respectively (Fig. 3).

The allelic richness (A) per site varied from  $2.762 \pm 0.199$  to  $7.016 \pm 0.204$ . Sites belonging to the Northern Europe genetic cluster had the highest values, on average *c.* 1.5 fold higher than in northwest Iberia, and *c.* twofold higher than the sites in the Western Atlantic and southern Iberia clusters (Table 1). Gene diversity ( $H_E$ ) revealed a similar pattern, with higher levels predominantly in Northern Europe and northwest Iberia sites and lower values in Western Atlantic and southern Iberian sites (Table 1).

Within clusters, pairwise  $F_{ST}$  and Jost's D intersite differentiation were higher in the Western Atlantic ( $F_{ST}$

0.245, D 0.265) and southern Iberia ( $F_{ST}$   $0.237 \pm 0.053$ , D  $0.301 \pm 0.096$ ). In contrast, Northern Europe had the lowest differentiation between sites ( $F_{ST}$   $0.078 \pm 0.034$ , D  $0.199 \pm 0.080$ ), followed by northwest Iberia ( $F_{ST}$   $0.148 \pm 0.069$ , D  $0.191 \pm 0.077$ ) (Fig. 3; Appendix S4, Supporting information). All differentiation levels were significant between sites within genetic clusters and among genetic clusters (AMOVA; S4). The sites belonging to Northern Europe were less genetically distant than those within the three other clusters (FCA analysis).

The allelic richness per cluster, standardized for a minimum common sample size of 47 individuals, was higher for Northern Europe ( $11.097 \pm 0.552$ ), followed by northwest Iberia ( $7.371 \pm 0.268$ ), southern Iberia ( $6.936 \pm 0.269$ ) and lowest in the Western Atlantic sites (5.111, Fig. 3). The number of unique alleles was also higher in Northern Europe (56 unique alleles), but this was followed by the Western Atlantic (12, very high



**Fig. 3** Genetic subdivision of *Fucus vesiculosus* based on Structure (each bar represents an individual multilocus genotype). Standardized allelic richness (mean A ± standard deviation), number of unique alleles (Unique A), mean  $F_{ST}$  (±standard deviation) and mean Jost's D (±standard deviation) levels of differentiation per genetic group. Circles indicate sampling sites (open circles currently extinct).

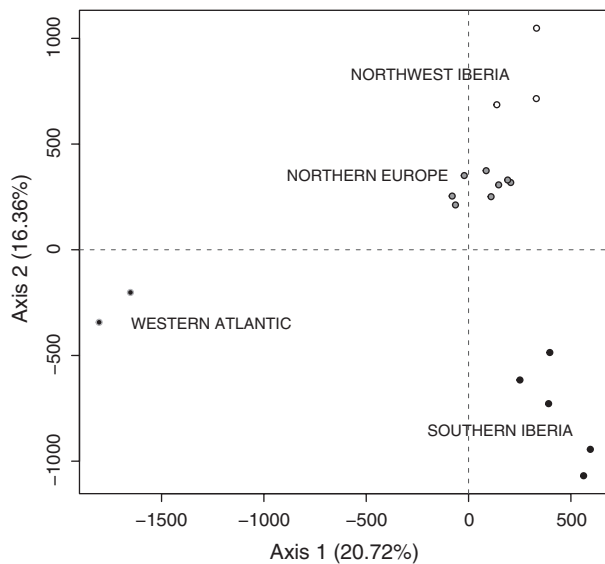


Fig. 4 Genetic differentiation of *Fucus vesiculosus* illustrated by factorial correspondence analysis of population multiscores. Inferred groups are divided by different circle patterns.

given that this is the smallest sample size), and lowest in northwest Iberia and southern Iberia (six and four unique alleles, respectively; Fig. 3).

## Discussion

This study reports an agreement between locations of long-term persistence and of past range shifts, inferred by distribution models, and the current genetic variability across a species distributional range. Distribution models provided evidence for multiple climatic refugia for *F. vesiculosus* and supported persistence of western Atlantic populations during the LGM, contradicting previous mitochondrial evidence. A novel approach to understand the role of habitat persistence in genetic diversity was applied here by estimating the areas of suitable habitat over long-term climatic extremes. This explained the genetic clusters and their total and private diversity currently found by genetic methods. Future distributional range shifts were also predicted, involving significant range contraction and further extinctions where unique genetic lineages occur.

### Transferable distribution model

In contrast to strictly marine or terrestrial organisms, both air and sea temperatures together with intertidal habitat area explained the global distribution of this intertidal species. The most relevant predictors of the geographical range of *F. vesiculosus* were extreme SST (minimum winter and maximum summer) and intertidal availability, but maximum summer air temperatures and

humidity were also identified as relevant predictors. These findings concur with experimental demonstration of the adverse effects of extreme values of those factors on the physiology of fucoids (reviewed by Davison & Pearson 1996; Wahl *et al.* 2011) and demonstrate the feasibility of combining both marine and terrestrial data to model intertidal species. The relevance of intertidal area for this species distribution provides first evidence that niche predictions may include dependences related to the mating systems and reproductive success, rather than the environmental conditions alone. This can be particularly critical for dioecious species like *F. vesiculosus*, which cannot persist if the suitable habitat area is insufficient for a minimal threshold in population size of males and females allowing for successful reproduction (i.e. an Allee effect). The use of this predictor allowed the species distribution to be more accurately modelled by excluding regions that lacked sufficient intertidal area to maintain breeding populations (despite a favourable climate niche). The distribution of *F. vesiculosus* has been previously inferred by SDM, with contrasting results compared with our study (see Jueterbock *et al.* 2013). Such differences may be due to the inclusion of misidentified records outside the ranges of *F. vesiculosus* (Jueterbock *et al.* 2013), particularly some southern regions where *F. guiryi* exists, but not *F. vesiculosus*.

The performance of our models was generally high, and their integration in an ensemble proved to be a robust approach (as found also by Araújo & New 2007), with the predicted distribution consistent with observed records. The model's transferability to AGCM data for present time also produced accurate predictions, pointing to a good estimation of climate despite the uncertainties of such simulations to hindcast/forecast distributions (Ramstein *et al.* 2007).

### Persistence and extinction of *F. vesiculosus* through time

Hindcasting revealed contrasting distribution patterns compared with the present day, particularly for the LGM. The extreme environmental conditions of this period caused a substantial reduction in suitable habitat for *F. vesiculosus*, shifting its distribution southwards and allowing a wide colonization of northern Africa and of the northern and eastern basins of the Mediterranean. However, as the AGCM data used tend to underestimate the drying and cooling throughout southern Europe (Ramstein *et al.* 2007), our models might overestimate the Mediterranean distribution of *F. vesiculosus* during the LGM. Nevertheless, such an expansion towards the Mediterranean has been proposed for other northern Atlantic marine species using different proxies of climate change (e.g. Kettle *et al.* 2011). Changes in



coastal morphodynamics and intertidal habitat depletion for the LGM (Peltier 1994) were also evident in our predictions, namely in areas where ice sheets advanced over continental shelves and where sea level drop reduced the available intertidal area. In southwest Iberia for instance, *F. vesiculosus* would have been absent due to habitat size limitation despite other favourable conditions, while at the southern Laurentide ice sheet, persistence would have been possible, but highly restricted to a narrow stripe of intertidal coast.

The widest predicted distribution of *F. vesiculosus* took place during the MH when a northern shift was particularly evident in the Barents Sea and southern Hudson Bay, regions that were already ice free and some ~2 °C warmer at this time (Diffenbaugh & Sloan 2002). Our models coupled this expansion with southern extinctions throughout the Mediterranean, northern Africa, southern and northern Iberia. Such a northern expansion-southern contraction is not unique for marine taxa (e.g. Maggs *et al.* 2008).

Predictive models revealed five refugia where this species was extant during the 1990s and where it could have persisted during the cold LGM and the warm MH climatic extremes. Similar refugia have been reported for distinct intertidal species, however never altogether for a single taxon. In the western Atlantic, our two predicted refugia (Grand Banks and S Laurentide ice sheet) sustained many intertidal animal species (e.g. Bigg *et al.* 2008; Ilves *et al.* 2010). In the eastern Atlantic, the region of SW Ireland and W English Channel was partly ice free during the LGM and provided refuge for several marine species (reviewed in Maggs *et al.* 2008). This area may have contracted due to the advance of the British-Irish Ice Sheet at about 24 KYBP, although it must not have severely affected species living there, because it was a short-lived event on the scale of tens of kilometres (Scourse *et al.* 2009; Ó Cofaigh *et al.* 2012a, b). The following retreat placed the ice sheet at latitudes known as the most plausible trends during the LGM (as those shown in Fig. 1; Bowen *et al.* 2002; Ó Cofaigh *et al.* 2012a). NW Iberia has also been proposed as a refugium for marine species, including fucoids (e.g. Coyer *et al.* 2003; Hoarau *et al.* 2007; Neiva *et al.* 2012a). In contrast, NW Africa (Morocco) has not previously been reported as a refugium for cold-temperate species, but putatively represents the rear edge (or in cases like *F. vesiculosus*, the historical rear edge) for many Atlantic cold-temperate species.

#### *Phylogeographical traits of F. vesiculosus*

Genetic structure was congruent with expectations from the distribution models, as expected in such approaches. Four genetic clusters were found, showing

high differentiation between groups and private alleles, suggesting strong effects of genetic drift that are not offset by gene flow. Temporary barriers to connectivity created by climate conditions were validated by our models. In the LGM, suitable habitat was predicted from southwest Ireland to southwest Iberia. Despite this, MH warming shaped three isolated populations corresponding to the eastern Atlantic genetic clusters found here: Northern Europe, northwest Iberia and southern Iberia. The agreement between molecular and modelling data highlights the effect of climate in shaping intraspecific genetic diversity and is particularly remarkable in revealing a role for the MH, which has received much less attention than the LGM in this context.

If formerly panmictic populations became isolated by changes in niche distribution (e.g. Maggs *et al.* 2008), admixture might be expected during subsequent expansion periods. Furthermore, despite the limited dispersive capacity of fucoid propagules, large-scale spread driven by floating rafts certainly occurred during recolonization of distant newly available empty habitats (e.g. Neiva *et al.* 2010). However, the spread of new colonizers might be limited by density barrier effects when encountering well-established populations, maintaining genetic mosaics at scales of tens of kilometres (e.g. Neiva *et al.* 2012b). Thus, sharply distinct genetic compositions can be maintained despite proximity and absence of (physical) barriers to gene flow along a continuous distribution. Additionally, species dependent on rare dispersal opportunities may remain absent from suitable habitats after historical range reduction, thus maintaining functional barriers to gene flow.

Our results show the Western Atlantic as a genetically distinct group, despite the few samples available from this region. The origin of *F. vesiculosus* on this coast had been hypothesized to be a recolonization from Europe following two possible events (Muhlin & Brawley 2009): an ancient colonization, long before the LGM, supported by a mitochondrial clock, or a more recent (post-LGM) colonization, supported by its low and nonprivate haplotype variability (Muhlin & Brawley 2009). Our results support the first hypothesis raised by Muhlin and Brawley (2009), as distribution models predicted persistence during the LGM in the western Atlantic, and nuclear loci showed many private alleles and high genetic differentiation relative to any of the eastern Atlantic groups. Such a genetic pattern does not agree with the scenario of recent expansions, as reported for other *Fucus* species (Coyer *et al.* 2003; Neiva *et al.* 2012a). However, it remains unclear why the western Atlantic has such low organellar genetic diversity in contrast with its nuclear genetic diversity. Although organellar genomes have been useful in phylogeographies in distinct species in the genus *Fucus*

(Coyer *et al.* 2003, 2011b; Hoarau *et al.* 2007; but see Neiva *et al.* 2010), they have been shown by the results of Coyer *et al.* (2011a) to be inaccurate to estimate the evolutionary history of *F. vesiculosus*. Mitochondrial DNA (mtDNA) places this species within the *F. spiralis* species complex, with shared haplotypes and low variability globally (Coyer *et al.* 2011a). This is in contrast to tens of independent nuclear loci that support these entities as distinct species (Serrão *et al.* 1999; Cánovas *et al.* 2011). The causes for such different phylogeographical histories and diversities of nuclear and organellar genomes in *F. vesiculosus* may result from 'genetic surfing' – organellar sweeps caused by past introgression and their spread at expansion fronts (Neiva *et al.* 2010) – or selection on any organelle gene (e.g. by temperature, Doi *et al.* 1999) that may easily cause a selective sweep. These processes can facilitate the spread of introgressed mtDNA and reduce haplotype variability (Ballard & Whitlock 2004). Therefore, the fixation of unique haplotypes throughout the western Atlantic populations does not rule out the long-term persistence of populations that occur there. However, notwithstanding the origin of *F. vesiculosus* on the western Atlantic coast, present-day genetic structure demonstrates effective barriers to gene flow with the eastern Atlantic.

The distribution models were consistent with the genetic diversity observed within clusters. In the Northern Europe cluster, the high genetic diversity found in Ireland, England and France is supported by the distribution models that predicted these as a region of persistence (SW Ireland and W English Channel refugium).

The favourable climatic niche found in this region during the LGM was absent at more northern glaciated areas. During the postglacial period, *F. vesiculosus* may have followed the melting ice, losing diversity in the course of colonization due to founder events (as in other such expansions, e.g. Neiva *et al.* 2012a). This could explain the lower levels of diversity of the northern sites Iceland, Faroe and Norway, as well as the lack of differentiation found between these sites and those persisting in SW Ireland and W English Channel, the closest refugium and most likely recolonization source (S4). The Northern Europe cluster includes northern Iberia (Ria del Eo), possibly a more recent colonization from northern populations, because this was predicted as unsuitable for *F. vesiculosus* during the MH. Likewise, other species were extinct from northern Spain during the MH (e.g. *L. littorea*) and recently recolonized these shorelines (Clark 1971).

Despite the higher genetic diversity found throughout Northern Europe, most sites within this cluster showed evidence for heterozygote deficiency. The first hypothesis that could explain such a deficit is the occurrence of

null alleles, although this is poorly supported because almost all loci amplified in individual DNAs, and the nine microsatellites used here already showed no evidence of null alleles in other studies (e.g. Perrin *et al.* 2007). A second and most likely explanation could be related to the Wahlund effect, with populations exhibiting a reduction in heterozygosity due to subpopulation structure. Given the high persistence and diversity found throughout Northern Europe, such structuring could arise via phenological differences within coexisting subpopulations at local scales (temporal Wahlund effect; Morand *et al.* 2002). A third nonexclusive explanation could be biparental inbreeding. As a dioecious species with very low dispersal capacity, in regions where populations are dense due to favourable niche conditions (as throughout northern Europe), there may be a high probability of mating between closely related individuals causing departures from random mating.

Northwest Iberia was also characterized by relatively high genetic diversity. As a cluster located within a predicted refugium, it was expected to retain higher diversity compared with the more recently colonized northern areas. However, the size (area) of habitat within NW Iberia was c. 2- to 3-fold lower than SW Ireland or W English Channel. This may have limited the size of populations that could persist there, facilitating genetic drift. This hypothesis highlights the advantage of using SDM in phylogeography, by allowing the determination of the size of past potential habitats, which are correlated with population sizes and genetic diversity. The lower diversity found in northwest Iberia might also be a function of the present geographical location of this region, which is less central along the current species range than SW Ireland and W English Channel. Genetic diversity tends to decrease towards the edges of species distributions (see Eckert *et al.* 2008 and references within), in line with the higher abundance and success of individuals in climatic optima near the centre of the range. The higher differentiation between the northwest Iberian sites may also reflect smaller population sizes (and greater drift) and greater geographical isolation limiting gene flow (see Young *et al.* 1996).

The southern Iberia and Western Atlantic clusters had depauperate genetic diversity as reported by previous studies (Perrin *et al.* 2007; Muhlin & Brawley 2009). This likely resulted from exposure to extreme climatic events in peripheral niches, increasing differentiation through time. This hypothesis is consistent with the predictive models that placed both populations at the range edges of distribution during the MH and in the present day. This emphasizes the importance of assessing the consequences of the interglacial warming periods on the contraction of cold-temperate ranges, a process that may

impoverish the genetic diversity at the rear edges and strongly shift the genetic baselines of extant populations.

The unique genetic diversity found within the N Europe, NW Iberia, S Iberia and W Atlantic clusters, alongside with the high genetic differentiation between them, matching our predictive models, suggests the existence of at least four putative refugia throughout the global range of *F. vesiculosus* (SW Ireland and W English Channel, NW Iberia, N Morocco and S Laurentide). A previous study based on mtDNA only supported the existence of a unique refugium (Coyer *et al.* 2011a) located in SW Ireland/Hurd Deep (i.e. English channel). This divergence in results may arise from the effects that can alter the history of mitochondria discussed above that do not reflect the species history. Unfortunately, our sampling in the western Atlantic does not allow us to confirm whether the Grand banks region (not sampled) acted as refugium in the past, as predicted by our models.

The relationship found between the levels of genetic diversity within clusters and the location/size of refugia cannot be explained by hybridization processes. These were analysed biogeographically by Moalic *et al.* (2011) for *F. vesiculosus*, and shown to be significant only in NW Iberia, an area of transition between sympatric and allopatric species ranges, probably due to lower reinforcement against hybridization in allopatry (Moalic *et al.* 2011). However, hybridization and introgression affected mainly the low diversity gene pool of the hermaphroditic species rather than the dioecious and much more diverse *F. vesiculosus* (Moalic *et al.* 2011).

Finally, we verified that most of the contemporary range of *F. vesiculosus* comprises the postglacial expansion from the SW Ireland and W English Channel refugium. In contrast to species with high dispersal abilities (e.g. Silva *et al.* 2014), expansions to new suitable habitats in *F. vesiculosus* and related taxa (Coyer *et al.* 2003; Hoarau *et al.* 2007; Neiva *et al.* 2010, 2012b) do not involve the whole refugial gene pool, but rather rely on unique local fronts, leaving distinct pools of genetic diversity in other refugial zones.

#### *Niche conservatism and future climate change*

The congruence between the predictive models and the patterns of genetic structure and diversity we found supports the hypothesis of niche conservatism in *F. vesiculosus*, at least from the late Pleistocene to the Holocene (Peterson *et al.* 1999; Waltari *et al.* 2007). Absence of niche evolution is not unusual, as it has been demonstrated in a wide range of species (e.g. Peterson *et al.* 1999). This is particularly important because species that conserved their niche and experienced range shifts during the past are most likely to shift their distribution under future warming scenarios (Lavergne *et al.* 2013).

Along the southern range edge in the eastern Atlantic, particularly severe recent extinctions of *F. vesiculosus* have been documented (Nicastro *et al.* 2013). Our models corroborate these findings in predicting a loss of suitable habitat from the 1990s to the 2000s, in Iberia and northern Africa. *F. vesiculosus* is not a unique case of an intertidal species with distributional shifts associated with recent climate change; other species have recently shifted ranges along both sides of the North Atlantic (Helmuth *et al.* 2006). Our predictions for future climate change scenarios suggest increasingly stronger range shifts for *F. vesiculosus*, particularly for the long-term projection with increasing greenhouse gas emissions over time (RCP 8.5). Such shifts in range can cause genetic erosion of the remaining populations and compromise the evolutionary potential of *F. vesiculosus* as a whole (Pujol & Pannell 2008; Provan & Maggs 2012). This is predicted to be more severe at the southern range edge on both sides of the Atlantic, where populations may vanish within the next 40 years, independent of the emission scenario. Such extinctions would result in the loss of entire genetic lineages, which cannot be preserved anywhere else over the entire species range. Because distinct genetic lineages are not evident morphologically, such major losses of entire genetic pools might occur at range edges while remaining undetected (the process of shifting genetic baselines; Assis *et al.* 2013).

Model projections also predicted a future expansion to newer northern territories (as in Raybaud *et al.* 2013). Intertidal shores that will remain ice-free year round are particularly good candidates to receive new populations of *F. vesiculosus* (Adey & Hayek 2005). Such shifts may become an additional concern during future climate change. New settlements of this habitat-structuring species may have unpredictable effects on the recruitment, growth and survival of native organisms in cold northern Atlantic waters (Bertness *et al.* 1999).

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J.A., E.A.S. and G.P. conceived and designed the experiments. J.A., B.C. and C.P. performed the experiments. J.A., B.C. and C.P. analysed the data. E.A.S. and G.P. contributed reagents/materials/analysis tools. J.A., E.A.S., C.P. and G.P. wrote the manuscript.

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## Data accessibility

R code used for the SDM analyses, along with the input files (raster files for environmental/tidal data), microsatellite data and presence records collected from

literature are available in the Dryad repository at <http://datadryad.org>, doi:10.5061/dryad.62797.

### Supporting information

Additional supporting information may be found in the online version of this article.

**Appendix S1** Environmental predictors used for modeling proposes (LT: Long term average). Derived metric by predictor (summer: AMJJAS; winter: ONDJFM), source of data, predictors' type (RS: Remote sensing, OM: Ocean model), predictors' units and spatial and temporal resolution. NCEP, OI SST, CPC and NCEP/NCAR data provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from [www.esrl.noaa.gov/psd/](http://www.esrl.noaa.gov/psd/)

**Appendix S2** Ensemble map of *Fucus vesiculosus* distribution for the 2000s, using two Atmospheric General Circulation Models (CCSM4 and MIROC5).

**Appendix S3** Estimation of the most probable number of groups (K) based on Bayesian clustering for K = 1–12 and 25 runs each (STRUCTURE: Pritchard *et al.* 2000). (A) Mean log-likelihood of the data per K, i.e. standard output from Structure. (B) Mean absolute difference of the second order rate of change with respect to K (Evanno *et al.* 2005).

**Appendix S4** Pairwise levels of differentiation between sites ( $F_{ST}$  and Jost's D) and Analysis of Molecular Variance, among sites within genetic clusters, and between genetic clusters.