Past climate changes and strong oceanographic barriers structured low-latitude genetic relics for the golden kelp Laminaria ochroleuca

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Running title: Climate and ocean currents shaping diversity

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Abstract

Aim: Drivers of intraspecific biodiversity include past climate-driven range shifts and contemporary ecological conditions mediating connectivity, but these are rarely integrated in a common comprehensive approach. This is particularly relevant for marine organisms, as ocean currents strongly influence population isolation or connectivity, keeping or diluting the signatures left by past climates. Here we ask whether the coupling between past range shifts and contemporary connectivity explain the extant gene pools of *Laminaria ochroleuca*, a large brown alga structuring important marine forests from shallow to deep infralittoral grounds.

Location: Northeastern Atlantic Ocean

Taxon: *Laminaria ochroleuca*

Methods: We estimated population genetic diversity and structure of *L. ochroleuca* across its entire distribution range using fifteen (15) polymorphic microsatellite markers. This was compared with the outcomes of a paleoclimatic model predicting latitudinal and depth range shifts from the Last Glacial Maximum (LGM) to the present. Genetic differentiation was further compared with potential connectivity inferred with a biophysical model developed with high-resolution data from HYCOM (Hybrid Coordinate Ocean Model).

Results: The biogeographic distribution of genetic variability showed overall agreement with the predictions from independently inferred past range shifts. Multiple regions of persistence were identified in deep and upwelling settings at the lowest latitudes of the current species distribution, where higher and unique genetic diversity was retained. The biophysical model revealed that despite the possibility of long-distance migration, contemporary oceanographic barriers strongly restrict connectivity of isolated genetic lineages.

Main conclusions: Integrating different processes at biogeographical scales explained the extant gene pools of marine forests of *Laminaria ochroleuca*. Low latitude genetic relics harbor a disproportional evolutionary significance, persisting as ancient populations in isolated deep and upwelling climate refugia. Their inferred rates of dispersal may be insufficient to accommodate anticipated climate warming.

Keywords: climate change; range shifts; connectivity; genetic diversity; marine phylogeography; kelp forests

Introduction

The climate fluctuations of the Quaternary strongly influenced the dynamics of marine populations (Maggs et al., 2008; Assis et al., 2014, 2016; Neiva et al., 2016). During glacial periods (e.g., Last Glacial Maximum, LGM; ~21,000 yr BP), the higher latitudinal range margins of cold- to warm temperate species often retreated, particularly in the northern hemisphere, due to both sea surface temperatures (North Atlantic winter sea temperatures anomalies amount to ~10 °C; Strandberg et al., 2011) and advance of continental ice sheets (Hewitt, 2004). The restriction of populations to small suitable regions beyond ice margins (i.e., refugia) is frequently hypothesized (Provan & Bennett, 2008; Neiva et al., 2016) but large low latitude expansions were also likely (Kettle et al., 2011; Assis et al., 2017a). In contrast, during warmer interglacial periods (e.g., Holocene; ~12,000 yr BP to present time), refugial populations gradually recolonized formerly glaciated regions (Maggs et al., 2008; Provan & Bennett, 2008; Neiva et

63 al., 2016), and range contractions might have occurred at lower latitudes (Assis et al., 2014,
64 2016).

65 The demographic history of populations can be reflected in the present distribution of genetic
66 diversity. Under extreme climate conditions, populations might have lost genetic diversity if
67 effective sizes decreased drastically, increasing genetic drift (Provan, 2013), bottlenecks and
68 local extinctions. Even more pervasive reductions of diversity could take place during range
69 expansions owing to founder effects at leading edges (Excoffier et al., 2009; Neiva et al., 2012a;
70 Assis et al., 2016). Conversely, in regions that kept long-term suitable habitats, persistent
71 populations could accumulate ancient genetic diversity (Hewitt, 2004; Maggs et al., 2008;
72 Provan, 2013; Assis et al., 2016; Neiva et al., 2016). The number and isolation of refugia may
73 have also played an important role in shaping the genetic variation of species (Assis et al., 2014).

74 The paradigm of range-shifting effects of past climate events might not be sufficient to explain
75 the present patterns of diversity, as it may be changed by widespread contemporary dispersal
76 (Silva et al., 2014) or local habitat conditions (Assis et al., 2016; Lourenço et al., 2016). For
77 marine organisms, ocean currents influence relative isolation and connectivity of populations
78 (e.g., Coleman, 2013; Pereyra et al. 2013; Buonomo et al., 2016; Lourenço et al., 2017), keeping
79 or diluting the signatures left by past climate changes (Lourenço et al., 2017). Dispersal
80 predictions are increasingly compared with genetic estimates, but not along species ranges (e.g.,
81 Billot et al., 2003; Alberto et al., 2011; Coleman, 2013; Buonomo et al., 2016). Species with
82 restricted dispersal generally hold fine-scale genetic differentiation (e.g., seaweeds: Neiva et al.,
83 2012b; Assis et al., 2013; Robuchon et al., 2014), while those with larger dispersal probabilities
84 (having larval stages) tend to have variable or little phylogeographic structure (e.g., mussels:
85 Lourenço et al., 2017; pelagic fish: Silva et al., 2014, benthic fish: Klein et al., 2016). In benthic

86 marine organisms, depth range shifts, the equivalent to terrestrial elevation shifts, may further
87 permit long-term persistence of ancient gene pools. Populations colonizing deeper colder waters
88 may safeguard diversity during warming periods, regardless of their inherent dispersal ability
89 (Graham et al., 2007; Santelices, 2007a; Assis et al., 2016). Likewise, coastal upwelling regions
90 may generate pockets of cryptic refugia preserving regional diversity in the face of climate
91 changes (Lourenço et al., 2016).

92 Disentangling how past climate changes and dispersal ecology structured the distribution of
93 intraspecific diversity is of much biogeographical and evolutionary relevance, although only a
94 few studies combined both processes (e.g., Lourenço *et al.*, 2017). Furthermore, while the role of
95 refugia in poleward expansions is well documented (e.g., Neiva et al., 2016), range shifts at low
96 latitudes are insufficiently understood. Most importantly, describing the processes shaping
97 endemic genetic lineages is timely, as their persistence might be threatened by climate changes
98 (Provan & Maggs, 2012; Assis et al., 2017a; Wernberg et al., 2018).

99 A good model to explore the aforementioned topic is the golden kelp *Laminaria ochroleuca*
100 Bachelot de la Pylaie, 1824. These large brown algae structure marine forests providing many
101 ecosystem functions (Araújo et al., 2016). Its niche matches thermal physiological responses (10
102 to 24ºC; Assis *et al.*, 2017b), a crucial feature to track climate-driven range shifts. Long-range
103 dispersal by this species is likely to occur by rafting and not spore dispersal, as kelp spores have
104 short viability (~1 day; Reed et al., 1992; Pereira et al., 2011), settling within tens of kilometers
105 maximum (Gaylord et al., 2002). Whole individuals of *L. ochroleuca* cannot float, but multiple
106 reports of *Laminaria* rafting (Thiel & Gutow, 2005) indicate that fragments may become buoyant
107 and/or entangled in other rafts (Thiel & Gutow, 2005; Clarkin et al., 2012). Since reproductive
108 blades may remain viable for long time (Thiel & Gutow, 2005), dispersal distances may extend

to hundreds of kilometers (e.g., Hernández-Carmona et al., 2006). Additionally, a paleoclimatic niche model for this species estimated low latitude persistent populations, some in deep and upwelling settings (Assis et al., 2017a), likely to retain ancient genetic biodiversity (Assis et al., 2016; Lourenço et al., 2016).

In this paper, we ask whether extant rich gene pools of *L. ochroleuca* can be explained by past climate-driven range shifts, coupled with contemporary dispersal mediated by ocean currents. We matched persistence predictions of a paleoclimatic model (Assis et al., 2017a) against endemic genetic diversity and potential oceanographic connectivity. We hypothesize that (1) climatic refugia display higher and endemic genetic diversity relative to to more recent populations and that (2) effective long-distance dispersal is rare, restricting the homogenization of populations and isolating important biodiversity hotspots.

Methods

Study area and focal species

The study area comprised the entire distributional range of *Laminaria ochroleuca*, from Cornwall (50.0N, 5.5W; England) to Sesimbra (38.4N, 9.2W; Portugal), plus isolated regions where it occurs beyond the more continuous range: Alboran Sea, Morocco upwelling spots, seamounts and Azores islands (Araújo et al., 2016; Assis et al., 2017a). Along continental coastlines, the species is vertically distributed from intertidal pools down to ca. 30 m depth. In the clearer waters of shallow seamounts, islands and the Mediterranean, it can reach 50-80 m depth (e.g., Formigas bank, shallow seamounts off southwestern Iberia, Alboran Sea and Strait of

130 Messina). This is a perennial species with a heteromorphic life cycle alternating between
131 macroscopic sporophytes and microscopic gametophytes.

132

133 **Genetic diversity and structure**

134 Approximately 30 individuals were sampled haphazardly per site (dependent on abundance and
135 accessibility) for genetic analyses (24 sites; Fig. 1a), by removing a piece (~1 cm^2) from the base
136 of the blade. Genomic DNA was extracted using NucleoSpin96 PlantKit II (Macherey-Nagel,
137 Germany). Microsatellite amplification and scoring was performed for 15 polymorphic loci as in
138 Coelho *et al.* (2014).

139 Genetic diversity per site and genetic group (see structure analysis below) was estimated as
140 allelic richness, private alleles and gene diversity (expected heterozygosity). Sample sizes were
141 standardized to the smallest in any population (excluding those ≤10), using 10^4 randomizations.
142 To test the role of refugia, standardized genetic diversity was determined separately for regions
143 of persistence and post-LGM settlements, identified in Assis et al. (2017a; Fig. 1a). The null
144 expectation for refugia was tested as the proportion of 10^4 randomizations retrieving higher
145 diversity and endemism (i.e., private alleles). F_{IS} and departures from Hardy–Weinberg
146 equilibrium were tested per site with Fstat (Goudet, 1995) under 10^4 randomizations of alleles
147 among individuals, and individuals within sites.

148 Genetic structure was inferred with Structure (Pritchard et al., 2000) without *a priori* population
149 assignment and allowing admixture. This analysis was performed for a range of genetic groups,
150 by running the model of correlated allele frequencies with a burn-in time of $2x10^5$ repetitions and
151 10^6 iterations. The number of groups was inferred with the DeltaK criterion (Evanno et al.,

2005). An additional level of genetic structure was inferred by running a second analysis within genetic groups. Two sites showing admixture in the first hierarchal run (see results below) were included in the pool of each genetic group to better disentangle genetic structure.

Genetic differentiation was estimated between sites and genetic groups with Jost's D. This was used in detriment of F_{ST} because it is more appropriate to compare populations with contrasting levels of genetic diversity (Jost, 2008; Whitlock, 2011; Assis et al., 2016), as in our case (see results).

Connectivity potential

Simulations of potential connectivity used a biophysical model following Buonomo *et al.* (2016), Klein *et al.* (2016) and Cunha *et al.* (2017), with daily data from the Hybrid Coordinate Ocean Model (HYCOM; Chassignet *et al.*, 2007). This high-resolution hindcast accurately reproduces key oceanographic processes like fronts, meandering currents, filaments and eddies (Chassignet et al., 2007; Lett et al., 2008), and its main limitation lies on the inability to simulate processes at scales below its raw resolution (~7 km at mid-latitudes; Fossette et al., 2012). While this can constrain seascape genetic studies focusing on nearshore processes, it may be neglected at the scales of our genetic sampling.

The simulation comprised the ~5000 km of the study area, gridded to 0.01° spatial resolution (~1 km). Virtual particles were released from each cell, daily from April to September. This period covers the reproductive stages that can potentially fragment and drift, releasing spores after dispersal (Thiel & Gutow, 2005; Clarkin et al., 2012) even when rafting for long time (Macaya et al., 2005). Particles were allowed to drift until reaching shore, and their position was determined

hourly with bilinear interpolation on the velocity fields of currents (Klein et al., 2016; Cunha et al., 2017). Since real dispersal times of *L. ochroleuca* are unknown, different simulations were performed with contrasting thresholds of: 1 day, for dispersal by spores, as sporulation lasts 15-18 h (Pereira et al., 2011) and spores stop swimming after ~24 h (inferred for *Macrocystis pyrifera* and *Pterygophora californica*; Reed *et al.*, 1992); 30 days, considering long-lived rafts, in line with the period estimated for other brown algae (Thiel & Gutow, 2005; Monteiro et al., 2016); 60 days, for longer-lived rafts.

The probability of connectivity was computed by dividing the number of particles released from a given cell *i* that ended on cell *j*, by the total number of particles released from cell *i*. Oceanographic variability was taken into account by running independent simulations for the most recent 10-year period available in HYCOM (i.e., from 2003 to 2012). A final asymmetrical connectivity matrix was produced by averaging the products of the annual simulations. To consider the hypothesis of year-to-year stepping-stone migration, a network analysis was implemented, in which vertices were the cells and edges the probabilities of transport between them (e.g., Buonomo *et al.*, 2016). Connectivity was estimated as the shortest path between cells, i.e., the one that minimizes the sum of negative log-transformed probabilities across all possible paths (Floyd–Warshall's algorithm).

The role of ocean currents was tested with linear regression models fitting genetic differentiation (Jost's D) against probability of stepping-stone connectivity between the sites sampled for genetics. The models considered the dispersal periods of 1, 30 and 60 days. A null model of isolation by distance was built by fitting genetic differentiation against alongshore marine distances. The models were compared using adjusted R-square, Pearson's correlation coefficient and Akaike Information Criteria (AIC).

Network community detection was used to identify the major oceanographic regions of the study area, i.e., those with higher within-region connectivity (e.g., Cunha *et al.*, 2017; Lourenço *et al.*, 2017). Excessive connections with unimportant information in the stepping-stone connectivity matrix were removed until a threshold maximizing the goodness of fit index of Modularity (Newman, 2006). The leading eigenvector algorithm (Newman, 2006) used the percolated network to assign a unique membership (oceanographic region) to each vertex. The significance of regions was tested by computing the proportion of 10^4 random assignments of memberships retrieving higher Modularity than observed.

Dispersal simulations and network analyses were implemented in R (R Development Core Team, 2016) with packages: data.table, dismo, doparallel, gstat, igraph, raster and vegan.

Results

Genetic diversity and structure

A total of 262 alleles were found across 649 genotyped specimens. Southern diversity was generally higher, decreasing northwards. Allelic richness (Table 1) was higher in Tarifa (Â > 6) than in all other sites (Â <5). Endemism (i.e., private alleles; Table 1) ranged from very high in southern isolated sites of Formigas and Tarifa to nearly no private diversity in several more northern sites (e.g., Plymouth, Port Blanc, Barrañán). Gene diversity (Table 1), like allelic richness, was highest in Tarifa. Lower diversity and endemism were found in northern sites, and where no standardization was implemented due to low sample size. Significant heterozygote deficit was found in only 1 out of 25 sites (Table 1).

When considering the paleoclimatic model for *L. ochroleuca*, genetic diversity was higher within

refugia (i.e., western Iberia, the Iberian Seamounts, Gibraltar Strait, western Morocco and the Azores; Fig. 1a), accounting for approximately 2-fold higher diversity and 7-fold more private alleles than in regions of post-LGM settlements (i.e., Galicia in northwestern Iberia and western English Channel; Fig. 1a).

The first hierarchal level of Structure analysis revealed (1) a north group including all continental sites from Plymouth southwards to Ericeira and the Iberian Seamounts, (2) a south group including Tarifa, Morocco and the Azores (Formigas), and (3) an admixture zone in Sesimbra and Espichel (Fig. 2). The second level divided the north group in (1) Western English Channel, (2) Western Iberia and (3) Iberian Seamounts. The south group was divided into four sub-groups corresponding to each site (Fig. 2). The admixture zone grouped with Western Iberia (refer to S1 for DeltaK criterion).

Allelic richness per genetic group (second hierarchical level) was higher in Tarifa, followed by El Jadida, Western Iberia and the Iberian Seamounts (Fig. 2d). Much more private diversity was found in Tarifa (21.2), Formigas and El Jadida. Considering both Moroccan sites, the private diversity of Morocco (16.4) is similar to that in Formigas (16.7). The Western English Channel showed the lowest diversity and endemism (Fig. 2d). Pairwise differentiation (Jost's D) between groups was lower between the three northernmost groups, and also between Tarifa and Essaouira (Fig. 2e). Highest differentiation was between Formigas and all groups (Fig. 2).

Connectivity potential

Genetic differentiation was best explained by stepping-stone connectivity considering dispersal up to 30 days (Fig. 3a; p-value: < 0.001; adjusted R^2: 0.643; Pearson's cor: -0.798; refer to S3 for

241 additional models). The simulations further showed that although dispersal events may occur
242 over dozens to thousands of kilometers, only 5% go beyond 3.93 km (Fig. 3c). The identification
243 of oceanographic regions for *L. ochroleuca* retrieved a significant modularity of 0.827 (p-value:
244 < 0.001; Fig. 3b). This analysis identified fifteen regions, eleven of which within the species'
245 distribution (Fig. 3b).

246

247 **Discussion**

248 This study demonstrates that the distribution of population genetic diversity across species
249 ranges can be highly skewed and structured by processes acting at different scales. By combining
250 theoretical modelling with empirical genetic data, we reveal how range shifts of the recent past
251 (ca. 20,000 yr BP) structured regions of long-term persistence at low latitude (warmer) range
252 margins, where higher and unique genetic diversity was retained. Simulating the potential degree
253 of connectivity further allowed estimating well-defined barriers shaped by physical
254 oceanographic transport, which restrict homogenization of extant populations, leaving genetic
255 biodiversity hotspots demographically and genetically isolated.

256

257 **Past climate changes structuring genetic diversity**

258 The overall genetic diversity distribution of *L. ochroleuca* corroborated expectations underlying
259 estimated past range shifts. The paleoclimatic niche model identified multiple refugia presently
260 located at lower latitudes. These locations displayed significantly higher genetic diversity and
261 disproportional endemism, when compared to populations estimated to be much younger. As in

262 other species (Assis et al., 2016; Neiva et al., 2016), persisting within refugia might have been
263 central to preserve and accumulate genetic diversity. In contrast, founder effects at the leading
264 edge of post-LGM settlements might have produced successive bottlenecks (Excoffier et al.,
265 2009), reducing diversity of higher latitude populations beyond refugia (i.e., Galicia and western
266 English Channel). Such an extremely skewed pattern of genetic diversity contrasts with that of
267 several other brown algae, which currently display higher diversity in the central region of their
268 distributions (Coyer et al., 2003; Hoarau et al., 2007; Assis et al., 2014; Robuchon et al., 2014),
269 despite the uniqueness (i.e., private alleles) of their lower diversity at warmer edges. Lower
270 diversity of endemic genetic lineages at such range margins indicates genetic erosion (if not
271 complete extinction; Nicastro et al., 2013) despite long evolutionary time.

272 Remarkably, although the hotspots of endemic diversity for *L. ochroleuca* occur at the warmer
273 range margins, all are in upwelling coldspots receiving cold nutrient-rich waters (Gibraltar Strait,
274 Morocco, Azores). Offshore seamounts may further retain ancient diversity during warming
275 periods (Assis et al., 2016), as increased light penetration allows deeper (colder) settlements
276 (Graham et al., 2007; Santelices, 2007a; Assis et al., 2017b). The diversity patterns found in the
277 deep populations of the Azores and the Iberian seamounts support the refugial hypothesis,
278 however, the high differentiation of the Azores indicates that this region was colonized much
279 earlier than the separation of all other populations and has remained isolated since then. In
280 Iberian seamounts, fringe environments with steep bathymetric slope (Santelices, 2007b; Assis et
281 al., 2017a) might hypothetically restrict population sizes and promote a large effect of genetic
282 drift, reducing diversity by purging low frequency alleles over time (Young et al., 1996). The
283 isolation of such regions, hundreds of kilometers offshore, may further prevent gene flow from
284 genetically-distinct populations, a process that can further decrease diversity relative to refugium

285 expectations (Hewitt, 2004). Similar population size limitations could have been expected for the
286 small upwelling region of Tarifa and the steep slopes of volcanic islands of the Azores. Yet the
287 high endemic genetic diversity of these two regions indicates that either there have not been
288 major bottlenecks there, or the diversity is still significant but reflects a shifted baseline from an
289 even richer state.

290 Western Iberia was also predicted as persistent climate refugium, as suggested also by the high
291 private diversity (see Sesimbra, Amorosa, Peniche). However, compared to refugia further south,
292 it has lower diversity. This refugium was the northern range margin during colder periods (like
293 the LGM, Fig. 1b) and is presently the southern range margin of the continuous continental
294 distribution. Thus, it might have experienced genetic drift and bottlenecks owing to reduced
295 population sizes while occurring near niche thresholds (Eckert et al., 2008; Oppliger et al.,
296 2014). Even when climate conditions in this region approximated niche optimum, priority
297 colonization effects (Tellier et al., 2011; Neiva et al., 2012b) and/or strong oceanographic
298 barriers (see discussion below) could have limited gene flow from richer populations. Also, one
299 cannot discard the uncertainty of paleoclimatic models (Pearson et al., 2006), which could
300 overrate the refugial potential of some regions. The climate data used for the LGM predictions
301 might underestimate winter cooling of western Iberia (Ramstein et al., 2007), rendering local
302 extinctions if temperatures dropped below the 10°C limit (Assis et al., 2017a). However, the
303 genetic data do not support this possibility, given the considerable private diversity of this
304 region, even when each population is considered separately (e.g., Sesimbra, Amorosa and
305 Peniche).

306

Oceanographic barriers isolating ancient genetic diversity

We discovered that *L. ochroleuca* has two main genetic groups, which coincide with the regions of persistence over the cold and warm climate maxima (Assis et al., 2017a). Within lineages, further structure was revealed, comprising seven groups. Their significant differentiation indicates low gene flow, not counterbalancing genetic drift and/or mutation.

The simulations of connectivity suggest the possibility of long distance dispersal, up to 30 days. Despite the expected 1-day kelp spore viability (Reed et al., 1992), *Laminaria* are recurrently recorded rafting offshore (Thiel & Gutow, 2005) and *L. ochroleuca* crossed the English Channel and reached the Azores in the mid-Atlantic. Paradoxically, despite the possibility of such events, *L. ochroleuca* and other kelp maintain strong genetic structure (Fraser et al., 2010; Johansson et al., 2015; Assis et al., 2016), suggesting that long effective dispersal (i.e., resulting in settlement and recruitment) is possible but very rare, in agreement with our simulations, as rafts unable to accomplish connectivity in the first days are typically lost in the open ocean (also demonstrated for other large brown algae; Buonomo et al. 2017). This further agrees with its low expansion potential along the English Channel (5 km/year; Straub et al., 2016). Moreover, priority colonization in well-established populations (Tellier et al., 2011; Neiva et al., 2012b) may block effective dispersal by later migrants. Our data show that dispersal over long distances is not common in *L. ochroleuca*, preventing the homogenization of phylogroups, but must have been crucial for colonization of distant habitats across large water masses (e.g., Iberian seamounts and the Azores) and during post-glacial expansions.

Connectivity simulations identified 11 oceanographic regions within the species range, that largely match the distribution of genetic groups, particularly in lower latitudes (i.e., Iberian

Seamounts, Alboran, Morocco and Azores). However, colonization pathways can be hypothesized from our genetic data for the more recent populations in the English Channel and Galicia, both appearing derived from the Iberian refugium. The former could have resulted from a (rare) long-distance dispersal from a population similar to that currently present in Viana do Castelo (less differentiated) towards Brittany, followed by Channel crossing. Founder effects during these events would have shaped the distinct genetic group found in this northern range (Neiva et al., 2012b; Assis et al., 2016). Galicia could have been colonized by near shore range expansion, hypothetically starting from a population similar to that observed in Amorosa. There is no evidence of any involvement of the remaining lower latitude populations in northern colonizations. Indeed, expansions by low dispersal species tend to be mediated by few individuals that happen to be located at the leading edge of the expanding front (Hoarau et al., 2007; Excoffier et al., 2009; Neiva et al., 2012a; Assis et al., 2016).

The temporal scale of range expansions may surpass the contemporary oceanographic processes simulated in the present study, preventing connectivity with distant regions, across large water masses. In particular, our results of ocean transport could not explain migration to the Azores, even for 2 months of potential dispersal (Refer to S4). However, there are several records of cold temperate algae found drifting in the Azores, even though they do not occur there (e.g., *Ascophyllum nodosum*; Neto, 1994), which could originate from both sides of the Atlantic with increased dispersal periods (Putman & He, 2013). Also, long-distance events might have occurred more frequently in a past with different oceanographic patterns and glacial coastlines, such as when the LGM sea level dropped -120m (e.g., Peltier, 2004), potentially increasing stepping stone connectivity (Fig. 1b) through habitats that are submerged today (Assis et al., 2016). Human-mediated transport cannot explain the establishment of such remote populations

of *L. ochroleuca* because these are so genetically distinct that their existence is expected to be much more ancient than the colonization of the Azores by humans. In contrast, colonization by *Fucus serratus* of Atlantic North America is correlated with historical shipping pathways, but population divergence is still very low (Brawley et al., 2009).

Oceanographic barriers may maintain contact zones between parapatric populations, with high but not unique local diversity, due to admixture. This may be the case for the admixture region (Arrábida) between the two main lineages of *L. ochroleuca*, over an oceanographic barrier in front of the Tagus estuary. Contact zones may also increase regional homozygosity if differentiated gene pools have some reproductive isolation (Wahlund effect). While this was not verified in Arrábida, it could hypothetically explain homozygote excess in São Bartolomeu do Mar, where an oceanographic barrier was identified separating northwest from western Iberian shorelines.

Concluding, our results show key roles of multiple refugia (from past climate changes) in safeguarding most of the species genetic diversity. Simulating connectivity further showed how such biodiversity hotspots are kept isolated by contemporary ocean currents (oceanographic barriers). While the present range of *L. ochroleuca* shows that long-distance dispersal is possible, our results suggest that these events are rare.

The strong divergence and endemism of low latitude populations, coupled with their strong oceanographic isolation, represent the most remarkable feature of the species phylogeography. These populations, occurring mostly in deep or upwelled pockets within the warmer range margin, have not contributed to post-LGM expansion. These traits are not unique to *L. ochroleuca* (e.g., Neiva et al., 2014; Johansson et al., 2015; Assis et al., 2016) and render a

disproportionate evolutionary significance to marine forest refugia populations. Their hypothetical future loss could dramatically reduce genetic diversity and compromise adaptive potential (Hampe & Petit, 2005; Provan & Maggs, 2012; Wernberg et al., 2018), also causing ecosystem changes in overall richness and biomass of associated species (Hoegh-Guldberg & Bruno, 2010).

The general agreement between paleoclimatic models and observed genetic diversity suggests broad niche conservatism, implying low plasticity and adaptive potential on a wide scale. Low latitude refugial regions are in risk of disappearing, even when associated with upwelling (Gibraltar and Morocco for *L. ochroleuca*; Assis et al., 2017a). This might not be compensated by reported and predicted poleward expansions (Smale et al., 2015; Assis et al., 2017a) because we showed here that low-latitude biodiversity hotspots are not involved in high latitude expansions. In contrast, detrimental climate effects are not expected for the deep refugia of the Iberian seamounts and Azores Islands (Assis et al., 2017a) representing safer sites for ancient diversity than cold upwelling spots. However, currently no empirical evidence distinguishes the different refugial roles provided by both environments.

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Figures

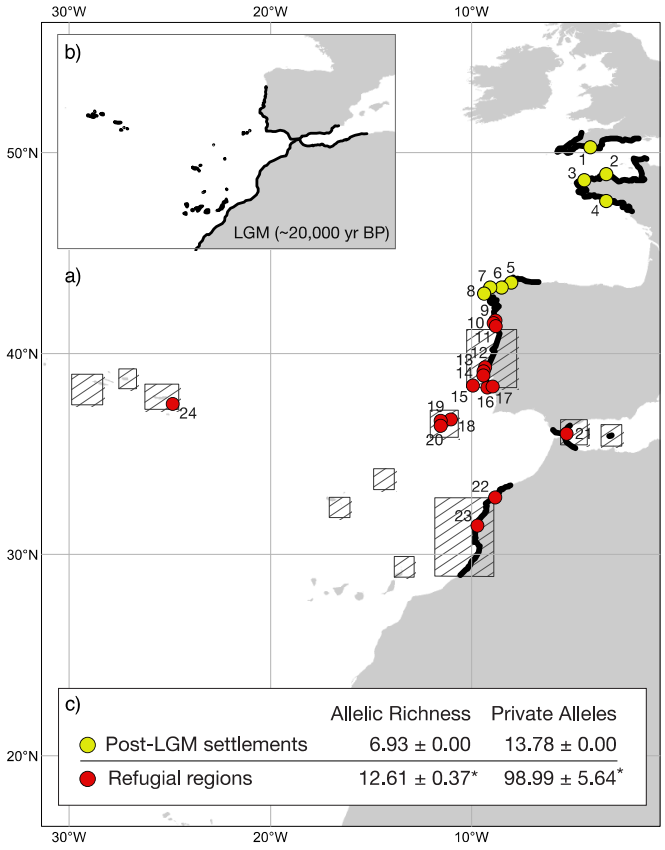
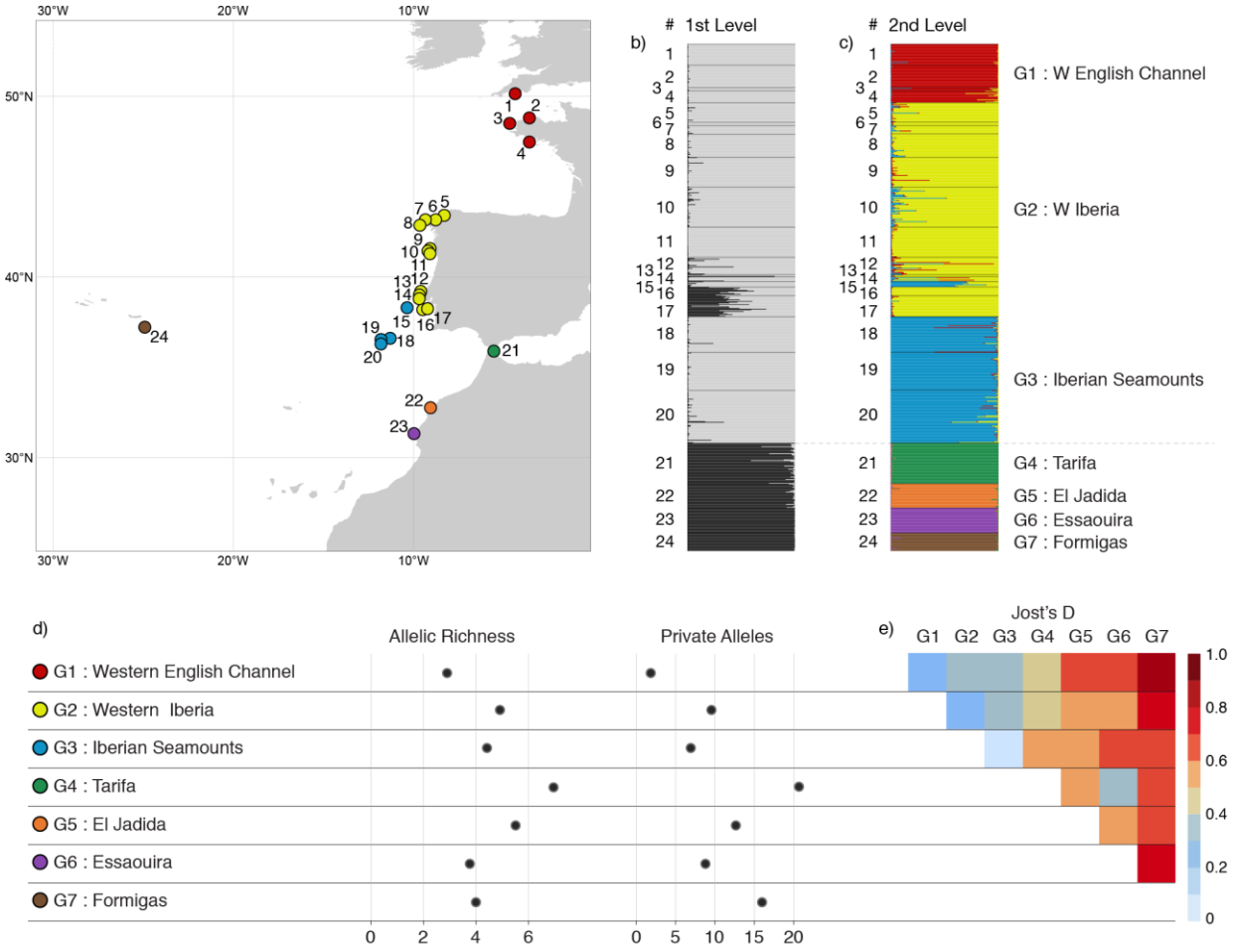


Figure 1. (panel a) Current distribution of *Laminaria ochroleuca* (black line; inferred by Assis *et al.*, 2017a; Araújo *et al.*, 2016), sampled sites and refugial regions (striped polygons; Assis *et al.*, 2017b). (panel b) Distribution during the Last Glacial Maximum (Assis *et al.*, 2017a). (panel c) Standardized diversity for refugia and post-LGM settlements (* indicates significant values).

Table 1. Site number (#) and name, depth (m), sample size (n), standardized allelic richness (Â), private alleles (PÂ) and expected heterozygosity (He) († indicates no standardization due to small sample), and F_{IS} multilocus estimates (* indicates significant deviations from Hardy–Weinberg with Bonferroni correction).

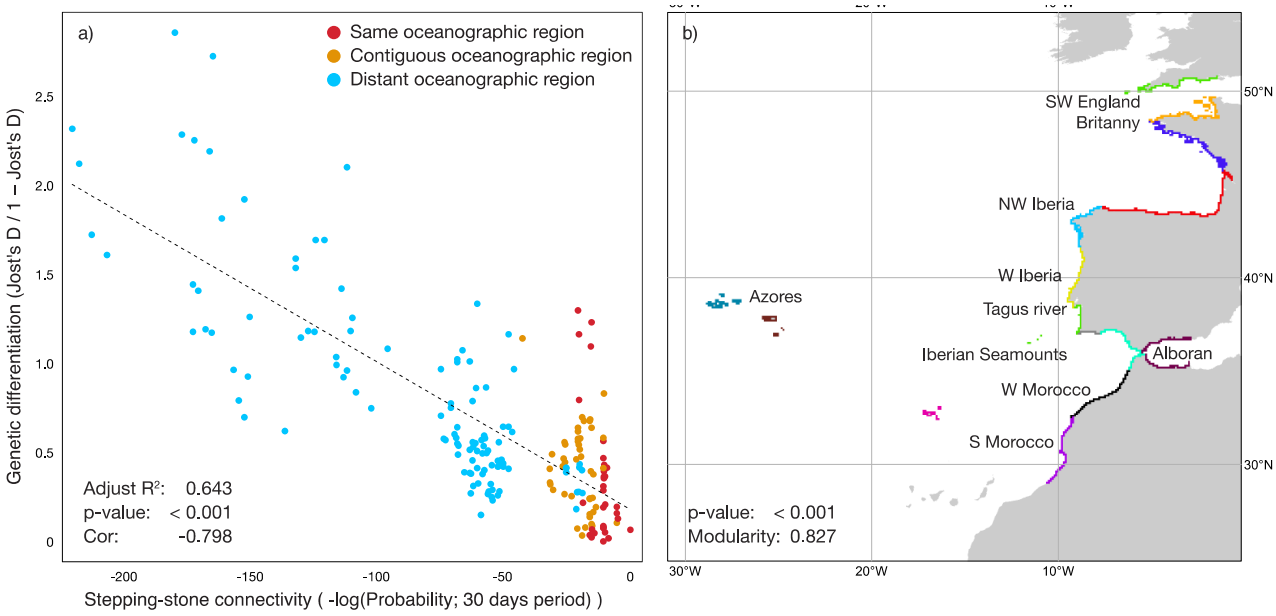
#	Site	Depth	n	Â	PÂ	He	FIS
1	Plymouth	0	27	2.19±0.12	0.17±0.38	0.18	-0.02
2	Port Blanc	0	29	2.03±0.06	0.49±0.50	0.26	-0.12
3	Brignogan-Plages	0	4	2.13†	1.01±0.17	0.29	0.25
4	Lorient	0	15	2.33±0.00	1.97±0.85	0.27	0.07
5	A Coruña	0	25	3.33±0.20	1.80±0.97	0.35	0.02
6	Barrañán	0	4	2.07†	0.27±0.45	0.34	-0.09
7	Laxe	0	11	2.95±0.00	1.87±0.85	0.38	0.03
8	Camariñas	0	30	3.91±0.13	2.83±1.11	0.31	0.02
9	Viana do Castelo	0	38	3.33±0.16	1.49±0.99	0.33	0.06
10	Amorosa	0	51	4.58±0.21	3.18±1.54	0.42	0.01
11	S. Bartolomeu do Mar	0	39	2.10±0.10	0.94±0.64	0.28	0.31*
12	Peniche	0	22	4.52±0.18	3.07±1.15	0.50	0.03
13	Ribeira de Ilhas	0	3	1.93†	1.00±0.00	0.49	0.34
14	Ericeira	10	6	2.00†	0	0.24	0.37
15	Camões seamount	40	7	3.00†	2.11±0.62	0.42	0.04
16	Espichel	10	11	2.16±0.00	1.44±0.58	0.32	0.03
17	Sesimbra	10	27	4.49±0.22	4.60±1.52	0.41	0.12
18	Ormonde seamount	50	46	3.30±0.22	0.73±0.64	0.35	0.04
19	Gorringe seamount	50	48	3.28±0.20	2.96±1.83	0.34	0.11
20	Gettysburg seamount	50	68	3.60±0.28	2.15±1.24	0.34	0.02
21	Tarifa (Gibraltar Strait)	20	52	6.38±0.33	10.19±2.14	0.53	-0.01
22	El Jadida	0	31	4.71±0.21	8.75±1.96	0.48	0.09
23	Essaouira	0	32	3.38±0.13	5.71±1.72	0.32	0.08
24	Formigas (Azores)	50	23	3.63±0.18	11.14±1.87	0.35	0.01



414

415 Figure 2. (panel a) Sampled sites with colors depicting genetic subdivision inferred with
416 Structure. (panel b) First and (panel c) second hierarchical level of genetic subdivision with
417 Structure. (panel d) Standardized genetic diversity and endemism per genetic group (note:
418 Morocco upwelling region, i.e., G5 and G6 together, have endemic diversity similar to the
419 Azores; see results). (panel e) Population pairwise differentiation (Jost's D, average) between
420 genetic groups.

421



c)

	Maximum	Mean ± SD	Median	95th percentile
Distance of connectivity events (km)	1050.21	59.10 ± 89.07	28.46	3.93
Drifting period of connectivity events (day)	30.00	9.20 ± 7.50	6.91	1.39

Figure 3. (panel a) Linear regression of genetic differentiation against probability of connectivity (30 days dispersal period). Colors depicting pairs located in the same oceanographic region (red), in contiguous regions (orange) and non-contiguous regions (blue). (panel b) Oceanographic regions inferred with pairwise connectivity probabilities (depicted as different colors). Names provided for oceanographic regions and barriers of interest. (panel c) Maximum, average, median and 95th percentile distance (km) and drifting period (day) of connectivity events (30 days dispersal period).

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628

629 **Data accessibility**

630 Microsatellite data are permanently available at https://doi.org/10.6084/m9.figshare.6275387.v2.

631

632 **Biosketch**

633 Jorge Assis is a post-doctoral researcher at CCMAR. His research is mainly focused on the
634 evolutionary consequences arising from climate changes and the drivers mediating gene flow in
635 marine populations.

636

637 **Supplementary information**

638 S1. Estimation of the number of genetic groups for the first and second hierarchical levels of
639 Structure analyses.

640 S2. Analysis of Molecular Variance and pairwise differentiation levels between sites.

641 S3. Supplementary results for the simulations of potential dispersal.

642 S4. Stepping stone connectivity matrix (simulation with 60 days dispersal period).