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Comparative phylogeography of Antarctic seaweeds: genetic consequences of historical climatic variations

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Abstract: In the Southern Ocean, rapid climatic fluctuations during the Quaternary are thought to have induced range contractions and bottlenecks, which drastically impacted marine communities. For photosynthetic macroalgae that are restricted to very shallow waters, survival in deep-water refugia is not possible. Comparing pattern of distribution of genetic diversity using sequences of mitochondrial and chloroplast markers in distinct species of green, brown and red macroalgae, we sought to detect common responses to

the effect of these glacial cycles. All the Antarctic macroalgae were all characterized by very low genetic diversity, absence of genetic structure and significant signatures of recent population expansion. The eight studied species seem to have barely survived glacial events *in situ*, in a unique refugium from which they recolonized their current distribution area. We propose that polynyas or areas showing long-term geothermal activity along Antarctic continental margins or peri-Antarctic islands could be good candidate as glacial refugium, but more variable genetic markers will be needed to precisely pinpointing its location. Common haplotypes, scattered over hundreds or even thousands of kilometres of coastline, point out to long-distance dispersal of fronds drifting on the strong oceanic currents in the region as main mechanism of postglacial

Key words: Southern Ocean, glacial cycles, Quaternary, bottleneck, reduced genetic diversity, marine macroalgae

3.1 Historical isolation of Antarctic marine macroalgae

Antarctic marine macroalgae diversity, described as less diverse than other areas of the Southern Ocean, is still characterized by high levels of endemism reaching up to 35% (Wiencke and Clayton 2002; Wiencke et al. 2014; [see also Chapter 1 of this book](#)). As recorded for much of the Antarctic flora and fauna (Clarke et al. 2005; Allcock and Strugnell 2012), the presence of various endemic Antarctic macroalgal species has been linked to the major tectonic, oceanographic and climatic changes that have affected the region during the last 50 million years (Ma) (Dell 1972; Crame 1999, 2018; Mackensen 2004; Aronson et al. 2007; Moon et al. 2017; Halanych and Mahon 2018). Indeed, the fragmentation of the continental landmasses and the initiation of the Antarctic Circumpolar Current (ACC) (Figure 3.1) gradually isolated the Antarctic waters from the rest of the Southern Ocean (Crame 1999; Scher and Martin 2006; Aronson et al. 2007; Dalziel et al. 2013; Sijp et al. 2014; Scher et al. 2015). Currently, the Antarctic Polar Front (APF) (Figure 3.1) is considered as an effective barrier for many near-shore marine benthic taxa (but [see Chapter 2 of this book](#)), especially between Antarctic and sub-Antarctic provinces (Clarke et al. 2005; González-Wevar et al. 2012, 2017; Poulin et al. 2014; Billard et al. 2015; Crame 2018; Halanych and Mahon 2018).

Non-endemic Antarctic seaweeds have classically included 1) cosmopolitan species reported on most Antarctic and sub-Antarctic / temperate coasts of the Southern Ocean (e.g. *Plocamium cartilagineum*), 2) cold-water species with disjoint amphiequatorial distribution (e.g. *Acrosiphonia arcta* and *Desmarestia viridis/confervoides*) and 3) more broadly distributed species also occurring in peri- and sub-Antarctic areas of the Southern

Ocean as South Georgia, South Sandwich Islands or even the southern tip of South America (e.g. *Iridaea cordata*, *Gigartina skottsbergii* and *Adenocystis utricularis*) (Wiencke and Clayton 2002; Wiencke et al. 2014). Nevertheless, reconstruction of these Southern Ocean macroalgae species geographic distribution maps relies solely on classical taxonomy. Macroalgae simple anatomy and high degree of phenotypic plasticity could lead to incorrect taxonomic classification of specimens and molecular tools are now recognized as essential for species determination in these organisms (Saunders 2005, 2008). Inaccurate morphological identification and existence of cryptic species have been commonly reported in green, red and brown macroalgae, including in Antarctica (Hommersand et al. 2009; Moniz et al. 2012; Billard et al. 2015; Pellizzari et al. 2017; Dubrasquet et al. 2018; Ocaranza-Barrera et al. 2018).

If few molecular studies have indeed confirmed the existence of macroalgal species characterized by vast disjoint distributions that include Antarctica (i.e., *Acrosiphonia* and *Desmarestia*; van Oppen et al. 1993), most genetic data available support the existence of endemic Antarctic cryptic species. For example, two cryptic species, one Antarctic and one sub-Antarctic, were detected in *G. skottsbergii* and *I. cordata* (Hommersand et al. 2009; Billard et al. 2015; Ocaranza-Barrera et al. 2018). In the same way, even if exhaustive phylogenetic studies have yet to be undertaken for *P. cartilagineum*, Hommersand et al. (2009) noted that ‘unpublished *rbcl* sequence analyses by S. Fredericq show that *P. “cartilagineum”* from Antarctica is distinct from all other species of *Plocamium* investigated so far’. In *G. skottsbergii*, the two cryptic species are clearly separated by the APF (Figure 3.1) with the sub-Antarctic species distributed in

South America along the coasts of Chile and Argentina and the Falkland Islands while the Antarctic species is found in the Antarctic Peninsula, the South Shetland Islands and the South Orkney Islands (Billard et al. 2015). Divergence time estimations between Antarctic and sub-Antarctic cryptic macroalgal species indicate a split between two lineages occurring at the end of the Miocene, some 10 – 5 Ma ago (Hommersand et al. 2009; Billard et al. 2015; Ocaranza-Barrera et al. 2018), long after the physical fragmentation of the Southern Ocean continental landmasses or even to the formation of the ACC (Crame 1999; Mackensen 2004). However, the time of divergence between Antarctic and sub-Antarctic lineages of macroalgae predates the Quaternary glacial cycles (~2 Ma).

The existence of macroalgal species (both nominal species and cryptic species detected only when using molecular tools) entirely restricted to the Antarctic shelf, or at most including some adjacent islands of the maritime Antarctic (i.e., South Shetland Islands, South Orkney Islands and Balleny Islands) and offshore peri-Antarctic islands located south of the APF (i.e., South Georgia and Sandwich Islands), evidenced the long evolutionary history of these organisms within the Antarctic waters. In contrast to the hypothesis that most of the Antarctic biota could be recent colonists, arrived after the deglaciation of the Last Glacial Maximum (LGM) ice sheets (Clarke and Crame 1992), various Antarctic marine species, including macroalgae, have withstood Quaternary glacial cycles *in situ* (Convey et al. 2008, 2009; Allcock and Strugnell 2012).

3.2 Antarctic marine macroalgae: surviving Quaternary glacial cycles *in situ*

The onset of glaciations in Antarctica began during the Eocene-Oligocene boundary and, after a slightly warmer stage (27 – 15 Ma) that seemed to have reduced the extent of Antarctic ice, gradual cooling during the Miocene-Pliocene transition led to the re-establishment of major ice-sheets covering Antarctica (Kennett 1977; Zachos et al. 2001). Later on, the Quaternary (2 Ma – 20 Ka) was characterized by the alternation between glacial and interglacial periods that greatly affected the seasonality and intensity of sea-ice formation in the region (Clarke and Crame 1992; Barker and Thomas 2004; Gersonde et al. 2005; Kemp et al. 2010). During the LGM, ice sheets expansions were accompanied by eustatic drop in sea level (~ 120 m lower than at present), as well as important latitudinal changes in the position of the ACC (Figure 3.1; McCulloch et al. 2000; Simms et al. 2011; Larter et al. 2014; O’Cofaigh et al. 2014; Roberts et al. 2017; White et al. 2018).

The development of large ice sheets generated major landscape and seascape changes in Antarctica (Zachos et al. 2001; Thatje et al. 2005; Davies et al. 2012). For instance, glacial reconstructions of the Antarctic Peninsula during the LGM (20 Ka) showed stable grounding ice sheets advancing up to the continental shelf edge (Larter et al. 2014; O’Cofaigh et al. 2014) (Figure 3.1). Major glacial events in Antarctica are thought to have led to mass extinctions, with ice scouring pushing near-shore marine communities down the steep shelf slopes surrounding the Antarctic continent (Clarke and Crame 1992; Thatje et al. 2005). Antarctic benthic communities, especially sessile organisms with narrow depth distribution range, as macroalgae, would have been remarkably vulnerable to

continental sea-ice advances and retreats (Thatje et al. 2005; Dambach et al. 2012). Nevertheless, it seems that grounded ice did not completely cover the Antarctic continental shelf, not even during the glacial maxima (Klages et al. 2017) and some isolated areas could have acted as *in situ* glacial refugia. A wealth of evidences supports this view, including genetic data obtained for various terrestrial and marine organisms (Convey et al. 2008, 2009; Allcock and Strugnell 2012), fossil evidences (Hiller et al. 1988) and glaciological and oceanographic reconstructions (Paillard and Parrenin 2004; Bentley et al. 2014; Larter et al. 2014; O’Cofaigh et al. 2014; Klages et al. 2017).

Several mechanisms could have sustained Antarctic shelf areas uncovered by ice during the Quaternary glacial events. First, areas of open water (polynyas) formed along Antarctic continental margins could have acted as *in situ* marine refugia (Thatje et al. 2008). The possible existence of much more saline waters surrounding Antarctica during glacial periods could have produced more stable and widespread polynyas than previously postulated (Paillard and Parrenin 2004; Thatje et al. 2008). Alternatively, *in situ* refugia could also be associated to volcanoes or areas of geothermal activities (Fraser et al. 2014). Such geothermal refugia could be very important in areas where clusters of long-lived volcanoes are recorded such as the tip of the Antarctic Peninsula, the South Shetland Islands or the Ross Sea (Fraser et al. 2012, 2014). Moreover, geological evidence supports the diachrony of ice-sheet extensions around Antarctica (Anderson et al. 2002) and near-shore marine organisms could ultimately have survived, hopping from one open ice-free continental shelf area to another during glacial periods (Thatje et al. 2008; Allcock et al. 2012; Hughes et al. 2013).

At last, Antarctic near-shore macroalgae could also have endured the Quaternary glacial events south of the APF but beyond the Antarctic continental shelf margins. The coasts of peri-Antarctic islands have been postulated as potential glacial refugia for some species since their distribution generally includes islands of the Scotia Arc such as South Georgia and the South Sandwich Islands and Balleny Islands (Wiencke and Clayton 2002; Wiencke et al. 2014). South Georgia represents the northern limit of distribution for many species of the Antarctic benthos (Barnes et al. 2006), and this area was reported as glacial refugium for some Antarctic marine invertebrates (e.g. the Antarctic limpet *Nacella concinna*: González-Wevar et al. 2013).

3.3 Persistence in multiple isolated glacial refugia vs a single Antarctic refugium

Quaternary climatic oscillations dramatically affected species geographic range and demography, especially at high latitude (Hewitt 2000, 2004; Maggs et al. 2008; Provan and Bennett 2008; Allcock and Strugnell 2012; Fraser et al. 2012). The Expansion-Contraction model (Provan and Bennett 2008) proposed an alternation between the contraction of species distribution ranges during glacial advances and subsequent rapid expansions during interglacial periods. These expansion / contraction cycles had a strong impact on the distribution of genetic variation of high latitude organisms and can be detected nowadays, using molecular tools and phylogeographic analyses (Hewitt 2000, 2004; Provan and Bennett 2008; Allcock and Strugnell 2012). Depending on the number and localization of glacial refugia, different evolutionary scenarios can arise (Figure 3.2).

For species that have survived glacial events in a unique refugium from which they recolonized their current distribution area, a very low level of genetic diversity and a high spatial genetic homogeneity are expected (see scenario 1 in Figure 3.2). In this case, the effect of genetic drift during glacial bottlenecks could be amplified by gene surfing at expanding frontiers leading to extreme erosion of genetic diversity and even complete fixation of pioneer alleles over huge areas (Excoffier and Ray 2008; Excoffier et al. 2009; Hallatschek and Nelson 2010). Supporting this idea, complete genetic fixation has been recorded over distance of hundreds or even thousands of kilometers for some temperate southern hemisphere macroalgae, with the same mitochondrial haplotype covering all regions of the species distribution previously scoured by ice during glacial maxima (e.g. along the Southern coast of Chile: Fraser et al. 2009; Montecinos et al. 2012).

In contrast, population fragmentation in multiple disjoint glacial refugia (see scenario 2 in Figure 3.2) could lead to repeated events of divergence and diversification (Clarke et al. 1992; Allcock and Strugnell 2012). Indeed, small populations could rapidly diverge due to strong genetic drift and, in addition, divergence could be enhanced due to selection if environmental differences exist between refugia. Divergence during isolation could be sufficient to generate reproductive barrier and lead to speciation (Wilson et al. 2009; Allcock and Strugnell 2012; Lecointre et al. 2013). This phenomenon, classically known as the climate “diversity pump” (Haffer 1969), has been proposed to be at the origin of recent evolutionary radiation events in Antarctica (Clarke and Crame 1989; Near et al. 2012; Crame 2018). Such process is expected to be more effective for species having limited dispersal capabilities such as those with non-pelagic development or very short

free-living larval stage (Pearse et al. 2009). Indeed, highly differentiated genetic lineages / sister species have been detected in various Antarctic marine organisms characterized by low dispersal capacity and related to a scenario of isolation in multiple refugia during glacial events (Wilson et al. 2009; Allcock and Strugnell 2012; Hemery et al. 2012). In macroalgae, population fragmentation in multiple refugia has been commonly reported in the North East Atlantic where genetic distinctiveness characterizes patchy populations located at low latitude and inhabiting former refugial areas (Neiva et al. 2016).

3.4 Antarctic macroalgae genetic diversity: COI and *tufA* sequences data sets

Little is known about Antarctic macroalgae genetic diversity and most of the studies have used molecular markers primarily for species identification (Hommersand et al. 2009; Moniz et al. 2012; Mystikou et al. 2014; Pellizzari et al. 2017; Dubrasquet et al. 2018; Ocaranza-Barrera et al. 2018) or phylogenetic inferences among taxa including Antarctic species (van Oppen et al. 1993; Peters et al. 2000). However, information about intraspecific genetic diversity, mostly based on the acquisition of mitochondrial sequences (coding sequences of the Cytochrome c Oxidase I gene, noted COI: Guillemin et al. 2018; Ocaranza-Barrera et al. 2018; non-coding sequences of the intergenic region Cox2-3: Billard et al. 2015) is building up for some red macroalgae in the South Shetland Islands and the Antarctic Peninsula: *Curdiea racovitzae*, *Georgiella confluens*, *Gigartina skottsbergii*, *Iridaea cordata*, *Palmaria decipiens* and *Plocamium cartilagineum*.

Here we used the published COI data set obtained for six species of Rhodophyta (Guillemin et al. 2018) to which we added new COI sequences for one species of Ochrophyta (*Himantothallus grandifolius*) and sequences of the plastid gene *tufA*, encoding for protein synthesis elongation factor Tu (EF-Tu), for one species of Chlorophyta (*Monostroma hariatii*) in order to compare genetic signature among macroalgae phylum. *Monostroma hariatii* and *H. grandifolius* DNA extraction were performed with an E.Z.N.A tissue DNA kit (Omega Bio-tek, Inc. Georgia, USA) following the manufacturer instructions. Primers TufAgf4 and TufAR, and PCR reactions and program described in Fama et al. (2002) were used to amplify *tufA* fragments in *M. hariatii* while a fragment of the COI gene was amplified in *H. grandifolius* using the primers GazF2 and GazR2 and methodology described in Lane et al. (2007). PCR products were purified using the commercial kit UltraClean™ (MO BIO Laboratories, Carlsbad, USA) and sequenced in both directions at the AUSTRAL-omics Core-Facility (Universidad Austral de Chile, Chile).

Sequences of all macroalgae except *H. grandifolius* were obtained from five sampling localities: two located in the South Shetland Islands (in Greenwich and King George Island), two along the Northern part of the West Antarctic Peninsula (WAP) near the Chilean O'Higgins Antarctic base and in Paradise Bay and one along the Central part of the WAP (Marguerite Bay) (Figure 3.1, 3.3 and 3.4). *Himantothallus grandifolius* COI data set includes 17 new sequences obtained from Greenwich Island, King George Island, O'Higgins and Paradise Bay (GENBANK N° MK503231-MK503247) and two sequences available in GENBANK (HE866784, King George Island, Yang et al. 2014; GQ368262, Terre Adelie, Silberfeld et al. 2010). *Monostroma hariatii tufA* sequences correspond to

GENBANK N° MK507414- MK507450. For each species-specific data set, we calculated five diversity indices, Tajima's D (Tajima 1989) and Fu's Fs (Fu 1997) statistics and estimated the observed distributions of pairwise differences between sequences using Arlequin v 3.5 (Excoffier and Lisher 2010). For Tajima's D and Fu's Fs, significant departure from mutation drift equilibrium was tested using 1000 bootstrap replicates in Arlequin (Excoffier and Lisher 2010). Observed distributions of pairwise differences between sequences were compared to estimated values under a model of sudden demographic expansion through a generalized least squares approach and goodness-of-fit was tested using 1000 permutations in Arlequin (Excoffier and Lisher 2010). Haplotype networks were reconstructed using NETWORK v 4.510 (Bandelt et al. 1999).

3.5 Brown, red and green macroalgae: sharing a common pattern of glacial impact and post-glacial populations recovery?

All the analysed macroalgae are non-buoyant and commonly found in the Antarctic waters. Nevertheless, they present some noticeable ecological differences. While *I. cordata*, *G. skottsbergii*, *C. racovitzae* and *P. decipiens* are mostly found in the intertidal down to the shallow subtidal, *G. confluens* and *P. cartilagineum* are generally found deeper in the subtidal, as understory of large brown macroalgae. *Monostroma hariotii* presents very thin, delicate thalli, is very common in both the intertidal and subtidal zones and is considered a pioneer species able to colonize areas with freshwater influence from glacier run-off, presenting heavy ice scour or recently available for colonization after

glacier retreat (Quartino et al. 2013; Wiencke et al. 2014). With thalli more than ten meters long, *H. grandifolius* is the largest seaweed reported in Antarctica. The species, in combination with other brown macroalgae of the genus *Desmarestia*, form dense beds of canopy-forming algae, dominating the subtidal rocky shores.

3.5.1 Signature of a drastic impact of the Last Glacial Maximum

Regardless of their ecological differences or classification into distinct taxonomic divisions, molecular data show that all eight macroalgae have been strongly impacted by glacial events (Table 3.1, Figures 3.3 and 3.4). Extremely low genetic diversity was observed at the intraspecific level with a number of haplotypes varying between one in *H. grandifolius* up to only seven in the case of *I. cordata* and *P. decipiens* (Table 3.1). These results could be related to historical changes in macroalgae population size in the study area. The complete lack of diversity observed for *H. grandifolius* does not allow to further test this hypothesis, however, the seven other species presented additional results that support this idea: a star-like topology was observed in haplotype networks (Figures 3.3 and 3.4), mismatch distributions were unimodal (hypothesis of sudden expansion could not be rejected when calculated for the sum of squared deviation, SSD, or the Harpending's raggedness index, R_{ag} , except for *M. hariatii* R_{ag} for which a $p < 0.05$ was obtained; Table 3.1; see also Guillemin et al. 2008 for more details on red algae species) and all but the green alga *M. hariatii* presented negative values of Tajima's D and Fu's F_s statistics (Table 3.1). Taken together, these results point out to a possible catastrophic event of near

extinction in Antarctica for macroalgae, followed up by a rapid recolonization of (at least) the coasts of the South Shetland Islands and the Antarctic Peninsula from one unique glacial refugium (scenario 1 in Figure 3.2). None to very few mutations have been accumulated in the populations since expansion from their glacial refugium, strengthening the idea that the demographic expansion occurred recently. We proposed (as in Billard et al. 2015 and Guillemin et al. 2018; estimations based on the calculation of the parameter Tau from models of sudden expansion and previously published mutation rate per sequence per generation for mitochondrial genes in macroalgae) that the demographic bottleneck corresponds to population contraction of macroalgae in refugium during the LGM and that recolonization of the coast begun some 18.000 years ago, at most, a date congruent with time of deglaciation in the area (Simms et al. 2011; O’Cofaigh et al. 2014). Similarly, other studies have related the recent expansion detected in the Southern most populations of sub-Antarctic macroalgae to population recolonizing areas previously covered by ice after the LGM (Fraser et al. 2009, 2012, 2013; Montecinos et al. 2012; Billard et al. 2015).

The level of genetic diversity estimated for Antarctic macroalgae are within the lowest reported for Antarctic marine species with broad distribution, with values of haplotype diversity (H) ranging between 0.000 and 0.398 and nucleotide diversity ($\pi \times 10^2$) ranging between 0.000 and 0.102 (lowest values in *H. grandifolius* and highest values in *I. cordata*; Table 3.1). Rather low level of diversity and complete lack of genetic structure has also been reported in some widespread Antarctic marine invertebrates as *Sterechinus neumayeri* (H = 0.257; $\pi \times 10^2 \times 10^{-2} = 0.036$; Díaz et al. 2018); *Chorismus antarcticus* (H =

0.639; $\pi \times 10^2 = 0.209$; Raupach et al. 2010); *Parborlasia corrugatus* ($H = 0.762$; $\pi \times 10^2 = 0.118$; Thornhill et al. 2008), *Euphausia superba* ($H = 0.856$; $\pi \times 10^2 = 1.394$; Bortolotto et al. 2011); *Nematocarcinus lanceopes* ($H = 0.902$; $\pi \times 10^2 = 0.568$; Raupach et al. 2010) and *Nymphon australe* ($H = 0.918$; $\pi \times 10^2 = 0.657$; Soler-Membrives et al. 2017). The lowest levels of genetic diversity have been observed in benthic marine invertebrates with distribution restricted to shallow waters of the Antarctic shelf and have been related to the extreme effect of ice scouring in these organisms, not able to migrate to deeper waters during glacial maxima (Raupach et al. 2010; Díaz et al. 2018). It is then not surprising to observe genetic diversity congruent with extreme events of mortality due to LGM ice impact in photosynthetic macroalgae, these organisms being characterized by one of the most restricted bathymetry in the marine realm.

Indeed, Antarctic macroalgae are anchored to the sea bottom and cannot survive under ice, without direct sunlight, for long amount of times. Glacial refugia for these organisms should then be limited in depth (generally dense beds of Antarctic macroalgae are reported growing down to 40 – 50 m) and to areas where the sea ice melt during summer. However, periods of ice-free summer as short as two months allow macroalgal beds growth (Norkko et al. 2004) and living specimens of various macroalgae species were retrieved in Terre Adelie under ice sheets in an area that did not melt during summer for two years in a row (S. Hourdez pers. com., specimens kept in the Museum of Natural History, Paris, France). This time period could, however, be considered as a maximum before severe population decline. Indeed, none of the fleshy macroalgae were considered as healthy (but half the encrusting coralline algae were still pigmented) after three years

of permanent sea-ice coverage in the Commonwealth Bay, a polynya affected by the grounding of a huge drifting iceberg in 2010 (Clark et al. 2015). Moreover, Antarctic macroalgae are extremely shade adapted and have been observed to grow at depth of 90 m (Wiencke and Clayton 2002; Wiencke et al. 2007). In other regions of the world, the existence of kelp beds reaching depth of 200 m was even predicted using oceanographic and ecophysiological models (Graham et al. 2007; see also Spalding et al. 2019 for reports of macroalgae growing down to 140 m). Additionally, long-term survival of Antarctic macroalgae in areas highly impacted by ice could be facilitated by the synthesis and accumulation of protective compounds (Wiencke et al. 2007). Some species, as the green algae *Acrosiphonia arcta* and *Prasiola* spp., have developed remarkable adaptations to cope with ice disturbance characteristic of Antarctic habitats. Indeed, both synthesize cryoprotectants that prevent damage by ice to membranes or enzymes and *Prasiola* has been reported to photosynthesize at temperatures as low as -15°C (Jacob et al. 1991; Raymond and Fritsen 2001; Wiencke et al. 2007). Antarctic macroalgae could then be tougher than expected and may have survived in small areas highly impacted by ice during the LGM.

3.5.2 *One refugium to rule them all*

Classically, locations of glacial refugia have been inferred by comparing genetic diversity between populations located within areas potentially free of ice during the LGM and the ones located in recently colonized areas, previously covered by ice (Hewitt 2000, 2004;

Maggs et al. 2008; Provan and Bennett 2008). Since population effective size is more stable in glacial refugia than in recently colonized areas, a much higher genetic diversity is expected to characterize the former than the later (Hewitt 2000, 2004; Maggs et al. 2008; Provan and Bennett 2008). If the particularly low genetic variability observed in our species lead to the idea of one unique refugium in Antarctica, it frustratingly does not allow pinpointing its location. Indeed, whatever the species under study, none of our sampled populations shows a specifically high genetic diversity (Figures 3.3 and 3.4; see also Guillemin et al. 2018 for more details on distribution of genetic diversity of *I. cordata*, *G. confluens*, *G. skottsbergii* and *P. cartilagineum*).

Various areas could be proposed as *in situ* refugia along the coast of Antarctica for our seaweeds and these include localities close by to active volcanoes (as Deception Island, Penguin Island and Bridgeman Island in the South Shetland Islands or the coast of the Western Ross Sea; Fraser et al. 2014) or localities where the shelf seafloor was free of grounded ice during glacial maxima (i.e. Alexander Island, Eastern Amundsen Sea Embayment, Western Ross Sea, George V Land and Prydz Bay; Klages et al. 2017).

Moreover, all eight macroalgal distributions include offshore peri-Antarctic Islands located south of the APF, as the South Orkney Islands, South Sandwich Islands and South Georgia (Wiencke and Clayton 2002; Wiencke et al. 2014; Griffiths and Waller 2016). We then cannot rule out a recolonization of the Antarctic coasts from these more northern areas. Supporting this idea, a study based on molecular markers allowed the recent discovery of one cryptic species of the brown alga *Adenocystis utricularis* endemic to South Georgia (Fraser et al. 2013). The authors related this result to a persistence of *Adenocystis* in local

refugium along the island coasts during the LGM (Fraser et al. 2013). Antarctic samples were not included in the study of Fraser et al. (2013) and level of genetic divergence between peri-Antarctic and Antarctic *Adenocystis* remain to be estimated in order to test for a possible recolonization of the Antarctic shelf from a South Georgia glacial refugium. However, ice coverage during the LGM strongly impacted South Georgia (White et al. 2018) and coastal glacial refugia could have been as scarce in the offshore peri-Antarctic Islands as at the margins of the Antarctic shelf itself (Figure 3.1). Indeed, the complete eradication of populations of another brown alga, the intertidal / shallow subtidal *Durvillaea antarctica*, from the coasts of most peri-Antarctic Islands (in particular in Macquarie Island, Falkland Islands, South Georgia, Marion Island and Kerguelen Islands) during the LGM have been established (Fraser et al. 2009, 2012).

Unfortunately, in order to locate glacial refugia in the region, we will need more variable genetic markers and a much better sampling of the coasts of the Antarctic shelf (i.e. Alexander Island, Western Ross Sea, George V Land and Prydz Bay, see Griffiths and Waller 2016), adjacent islands of the maritime Antarctic and offshore peri-Antarctic Islands south of the APF where populations of macroalgae have been reported (in particular, South Orkney Islands, South Sandwich Islands and South Georgia, Bouvet Island, Heard Island and Balleny Islands). Sampling localities that could have been less affected by ice scour during the Last Glacial Maximum should be a priority.

The proposed scenario of one unique *in situ* refugium in Antarctica contrasts with history of glacial perturbations in Arctic macroalgae. Indeed, based on patterns of genetic diversity and distribution of private haplotypes, the existence of various marine glacial

refugia has been proposed in the Northern Hemisphere for these organisms (Maggs et al. 2008; Provan and Bennett 2008; Neiva et al. 2016). Less severe cooling in the Arctic than the Antarctic could explain, in part, these differences between hemispheres (Pointing et al. 2015). Moreover, Arctic macroalgae distribution during glacial cycles could have shifted along continuous coastlines spanning a huge latitudinal gradient (Fraser et al. 2012; Neiva et al. 2016), while no such opportunity was available for Antarctic species, bounded by the deep water of the Southern Ocean, leading to a more thorough extinction along the Antarctic coastline during the LGM.

3.5.3 Postglacial recolonization: widespread haplotypes drifting around Antarctica?

Apart from their very low genetic diversity, all eight algae under study present a common striking characteristic: one or a few haplotypes were encountered in all localities even when situated hundreds or even thousands of kilometers apart (Figures 3.3 and 3.4). For all six red algae and for the green alga *M. hariatii*, the most common haplotype was observed from King George Island in the South Shetland Islands down to Marguerite Bay, a sampling point located along the Central part of the WAP (Figures 3.3 and 3.4). These common haplotypes are spread over more than 450 km of coast and within two distinct biogeographic sub-regions (the South Shetland Islands and the WAP; Linse et al. 2006; Spalding et al. 2007; Terauds et al. 2012). Shared haplotypes have been observed even between the WAP and South Orkney Island, reaching distances greater than 1600 km, in the red alga *G. skottsbergii* (same Cox2-3 haplotype from Marguerite Bay to the South

Orkney Islands; Billard et al. 2015). The same pattern is observed in *I. cordata* for which the same COI haplotype has also been sequenced along the WAP and South Orkney Island (Guillemin M-L. unpublished data, no genetic differences detected between the most common haplotype encountered along the WAP and three individuals from South Orkney Island sequenced for 632 pb). For *H. grandifolius*, the distribution of the unique COI haplotype encountered in our study zone could be extended to Terre Adelie, in a sampling site located almost on the other side of the Antarctic continent (Figure 3.4, sequence from Silberfeld et al. 2010). *Himantothallus grandifolius* is then the first register of a non-buoyant seaweed displaying a true Antarctic circumpolar distribution supported by genetic data. Complete circum-Antarctic distribution has been described for other seaweeds, including common species of brown (*Desmarestia menziesii*), green (*M. hariotii* and *Urospora penicilliformis*) and red (*I. cordata*, *P. cartilagineum*, *P. decipiens*, *Phyllophora Antarctica* and *Phycodrys Antarctica*) macroalgae (Wiencke et al. 2014). However, for these species, all sequences available to the date have been obtained for specimens located in the South Shetland Islands and/or the WAP (van Oppen et al. 1993; Peters et al. 2000; Hommersand et al. 2009; Dubrasquet et al. 2018; Ocaranza-Barrera et al. 2018). One could thus wonder if other common Antarctic macroalgae species will present the same pattern as *H. grandifolius* and samples should be gathered from the Western Ross Sea, Terre Adelie and Prydz Bay and sequenced in order to test this hypothesis.

In contrast to what was reported for pelagic species or benthic species exhibiting extensive dispersal by planktonic stage (Lange et al. 2002; Raupach et al. 2010; Sromek et

al. 2015; Soler-Membrives et al. 2017; Caccavo et al. 2018), we believe that the presence of widespread haplotypes in our data sets clearly reflects Antarctic macroalgae past glacial demographic histories but not necessarily contemporary high gene flow. Benthic macroalgae free-living stages (i.e. for all species except buoyant ones, Macaya et al. 2016, [see Chapter 5 of this book](#)) are generally extremely restricted to short-lived gametes and spores that quickly sink a few meters or dozens of meters, at most, from thalli of origin (Valero et al. 2011). However, in these organisms, large-scale spread of haplotypes was commonly related to strong genetic drift and allelic surfing at species' leading edges during postglacial range expansions or after transoceanic colonisation (Maggs et al. 2008; Provan and Bennett 2008; Montecinos et al. 2012; Fraser et al. 2013; Guillemin et al. 2014; Neiva et al. 2016). Non-buoyant macroalgal species, for which both population genetic and phylogeographic data sets are available, show well this discrepancy with, on one hand the presence of haplotypes distributed over thousands of kilometers in area of recent colonization and, on the other hand, current reproduction and recruitment occurring at a very local scale (in *Gracilaria*: Guillemin et al. 2008; Guillemin et al. 2014, in *Fucus*: Neiva et al. 2016; Jueterbock et al. 2018). Exceptional events of thalli rafting on strong oceanic currents and colonising new areas when depleted of abundant algal coverage (Waters et al. 2013) have been advanced to explain these patterns (Montecinos et al. 2012; Fraser et al. 2013; Guillemin et al. 2014; Neiva et al. 2016). In order to test for actual gene flow between studied populations of macroalgae, more variable genetic markers, as microsatellites or SNPs (i.e. Single Nucleotide Polymorphism), will be needed. Indeed, highly variable microsatellite loci revealed a clear regional substructure of

populations in *Phaeocystis antarctica*, a brown micro algal planktonic species for which no clear phylogeographic patterns were described before around Antarctica using nuclear and plastid sequences (Lange et al. 2002; Gäbler-Schwarz et al. 2015).

Even if none of the study models possess floating structures, large amounts of all eight species can easily be found cast ashore after storm events, including huge adult specimens of *H. grandifolius* (authors pers. obs.). Passive transport of detached fronds could therefore play a major role in Antarctic non-buoyant macroalgae long-distance dispersal, a mechanism most probably facilitated by the strong oceanic currents in the region (Loeb 2007). Classically, the circumpolar current (ACC, see Figure 3.1) was reported as a structuring force in the Southern Ocean and has been proposed to be the main connecting current between populations of marine organisms located around Antarctica (e.g. Fraser et al. 2009; Soler-Membrives et al. 2017). For the red algae *G. skottsbergii* and *I. cordata*, fronds rafting on the ACC could easily explain the spread of the most common haplotypes between localities of the South Shetland Islands, the Antarctic Peninsula and even South Orkney Island (Billard et al. 2015; Guillemin et al. 2018; Ocaranza-Barrera et al. 2018). Indeed, the ACC flows northeastward from the Bellingshausen Sea through the South Shetland Islands and the South Orkney Islands, before entering the Scotia Sea (Loeb 2007). However, since it deflects from the Antarctic coasts during most of its journey around the continent (from the Weddell Sea, to Prydz Bay and the Western Ross Sea, see Loeb 2007), rafting on the ACC does not easily explain the presence of the same COI haplotype in Terre Adelie and the Antarctic Peninsula for *H. grandifolius*. It is highly probable that fronds transport between these two distant regions was promoted by the Antarctic Coastal

Current (ACoC), a current that flows in a counter-clockwise motion and located near the coast of the Antarctic shelf (Loeb 2007). The importance of transport by the ACoC was also proposed to be at the origin of the widespread haplotypes observed in marine species with distribution restricted to the shallow waters of the shelf, as in the sea urchin *S. neumayeri* (Díaz et al. 2018). Remarkably, a study following the track of icebergs around Antarctica shows that a large majority do travel counter-clockwise around the continental shelf and that the ACoC can very easily connect Terre Adelie with the tip of the Antarctic Peninsula (Stuart and Long 2011).

3.6 Concluding remarks

Macroalgae are very important primary producers and ecosystem engineers in Antarctic coastal ecosystems, serving as food for herbivores and detritivores and providing habitat for many associated organisms (see [chapters 15 and 16 of this book](#)). Even if these species have developed remarkable adaptations to cope with the high level of disturbances characteristic of Antarctic shallow depth (Wiencke et al. 2007; Wiencke et al. 2014) they could be highly vulnerable to actual threats intensifying in the region as global warming, pollution and introduction of invasive species. As seawater temperature rise around Antarctica, a trend particularly noticeable along the Antarctic Peninsula, extent and duration of sea ice coverage decline and glaciers are in retreat (Cook et al. 2016). At first sight, this scenario seems highly favourable for Antarctic macroalgae that can rapidly colonise these newly deglaciated areas (Quartino et al. 2013). Indeed, in the Arctic, the

long-term study of Kortsch et al. (2012) shows that decrease in sea ice cover can produce rapid shift in marine communities from benthic habitats dominated by calcareous algae and sea anemones to dense beds of fleshy, habitat-forming macroalgae. However, climatic changes are also associated with higher probability of ice-sheet collapse and icebergs calving. Scouring by these drifting icebergs, that can even get stuck and ground in polynyas, may have highly detrimental effect on macroalgae beds (Clark et al. 2015).

Climate changes have also been related to possible alteration in large-scale ocean circulation and gyre and eddy kinetic in the Southern Ocean, leading to breaches in the dispersal barriers (APF and ACC) established since the Eocene / Oligocene in the region (Barker and Thomas 2004; Fraser et al. 2018). When coupled with the intensification of maritime transport (linked to both touristic and scientific activities) between Antarctic and sub-Antarctic provinces, these oceanic changes could lead to an increase in propagule pressure and introduction of sub-Antarctic macroalgae species in the Antarctic waters. To the date, only one green alga (i.e., *Enteromorpha intestinalis*) has been reported as an established introduced alien species in the South Shetland Islands, probably arriving as fouling on the hull of a visiting vessel (Clayton et al. 1997). However, macroalgae highly successful in recolonising sub-Antarctic coasts after glacial retreat have recently been reported to recurrently reach the Antarctic coasts as cast ashore living thalli (i.e., *Durvillaea antarctica*, Fraser et al. 2018). The capacity of Antarctic macroalgae to withstand competition from sub-Antarctic invaders has not been studied yet.

Nonetheless, Antarctic macroalgae are organisms highly adapted to the local stenothermal environment. Studies report temperature optima between -2°C and 10°C for

most Antarctic species with limitation or even failure in growth or gametogenesis at temperature higher than 5°C in *G. confluens*, *G. skottsbergii*, *P. cartilagineum* and *D. antarctica* (Wiencke et al. 2007; Wiencke et al. 2014). In the actual context of rapid temperature increase, populations of sub-Antarctic or even more temperate colonisers may then more easily settle along the Antarctic coasts.

Antarctic macroalgae were clearly able to cope with changes related to the cooling and then freezing of the Southern Ocean waters and have survived Quaternary glacial perturbations *in situ*. However, our study shows that maximal glacial events have led to mass extinction in all eight model species, whatever their taxonomic divisions. Will these species be able to keep pace with the current rapid environmental fluctuations? Genetic adaptation could be key in enhancing resistance and resilience to climatic changes and high level of genetic diversity has classically been related to high population fitness, resilience and future adaptability (Reed and Frankham 2003; Jump and Peñuelas 2005). Due to strong bottleneck during the LGM, standing genetic diversity in Antarctic macroalgae populations seems to be extremely depleted and adaptive response of Antarctic algae populations to future changes could be limited. Nevertheless, recent studies on the brown seaweed *Sargassum muticum* show a complete absence of genetic diversity in all populations of the invaded range when tested using mitochondrial sequences or even nuclear microsatellites and only a very low level of diversity when using more than 8000 SNPs (Cheang et al. 2010; Le Cam et al. 2019). Rapid and successful invasion of Europe and the USA was clearly not impaired by the extremely low genetic diversity in *S. muticum*. In order to predict possible outcome of future climatic changes on

macroalgae populations it is now essential to use more variable genetic markers in order to detect subtle genetic structure along the Antarctic coasts and point out restricted regional or local genotypes that could be of interest (see results using SNPs in Le Cam et al. 2019) and to experimentally test for existence and extent of phenotypic plasticity / acclimatization potential (a mechanism that can potentially buffer negative effects of climate change long enough to allow for populations adaptation; Jump and Peñuelas 2005) and potential for an *in situ* adaptive response to climate change of these organisms.

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Figure legends:

Figure 3.1: Reconstruction of the Antarctic and sub-Antarctic ice coverage during the Last Glacial Maximum (LGM; ~20,000 ka) and in the present day. Putative LGM ice extension is based on various recent glaciological studies published for the tip of South America (McCulloch et al. 2000), the Antarctic Peninsula and the South Shetland Islands (Simms et al. 2011; Larter et al. 2014; Cofaigh et al. 2014) and South Georgia (White et al. 2018). Current ice extension is drawn based on [®]GoogleEarth satelital images. Arrow: Antarctic Circumpolar Current (ACC); thickness represent the strength of the ACC (Roberts et al. 2017). Dotted blue lines: Antarctic Polar Front (APF; mean position of the Polar Front is represented) and sub-Antarctic Front (SAF) (Roberts et al. 2017). The five sampling areas where Antarctic seaweeds were sampled are noted with back points (more details are given in the text and in Figures 3.3 and 3.4).

Figure 3.2: Putative effects of genetic bottleneck due to intense ice scouring during glacial periods (i.e. the LGM) and post-glacial range expansion following ice retreat yielding to the species current distribution. Two distinct scenarios have been considered: 1) the existence of only one in situ glacial refugium and 2) the existence of multiple (here three) in situ glacial refugia. Species distribution area is drawn in grey; each circle represents one individual; distinct colours represent genetic variants (e.g. distinct haplotypes). Effects of bottleneck and postglacial expansion on the current genetic diversity and phylogeographic

structure potentially observed nowadays in species affected by the glacial cycles are given on the right.

Figure 3.3: Haplotype networks and pie charts showing the geographical distribution of haplotypes for the mitochondrial genetic marker COI (632 bp) in *Curdiea racovitzae* and *Palmaria decipiens*. In the networks, each circle represents a haplotype and its size is proportional to the frequency in which the haplotype was encountered, black lines correspond to one mutational step. The five localities correspond, from north to south, to King George Island (GEO), Greenwich Island (PRA), O'Higgins (OHI), Paradise Bay (PAR), and Marguerite Bay (MAR). The number of sequenced individuals is given between brackets. From the six species of red algae studied (Guillemin et al. 2018) only results obtained for *C. racovitzae* and *P. decipiens* are illustrated since these two species represent the less and the most diverse Rhodophyta sampled along the coasts of the Antarctic Peninsula and the South Shetland Islands, respectively. Underwater photographs of specimen's characteristic of both species were taken by I. Garrido, please note the impact of ice scour on sea bed nearby *P. decipiens* populations (King George Island).

Figure 3.4: Haplotype network and pie charts showing the geographical distribution of haplotypes for the plastid genetic marker *tufA* (772 bp) in *Monostroma hariotii* and distribution of the unique haplotype detected in the 19 COI sequences (mitochondrial marker, 619 bp, include HE866784 from King George Island and GQ368262 from Terre

Adelie already published in GENBANK) in *Himantothallus grandifolius*. In the network, each circle represents a haplotype and its size is proportional to the frequency in which the haplotype was encountered, black line corresponds to one mutational step. The five localities correspond, from north to south, to King George Island (GEO), Greenwich Island (PRA), O'Higgins (OHI), Paradise Bay (PAR), and Marguerite Bay (MAR). The number of sequenced individuals is given between brackets. An underwater photograph of a mixed high subtidal bed of *M. hariatii* (arrow) and *H. grandifolius* (arrow heads) is given on the top (King George Island; photograph by I. Garrido).

Table 1: Genetic diversity indices and neutrality test in six red algae, one brown alga and one green alga sampled along the Antarctic Peninsula and South Shetland Islands. Sequences used for analyses of all six species of Rhodophyta and *Himantothallus grandifolius* correspond to the mitochondrial gene COI while the plastid gene *tufA* was used for analyses of *Monostroma harti*.

Species	N	k	S	H	Π	π ($\times 10^2$)	Tajima's D	Fu's FS	Mismatch distribution
Rhodophyta									
<i>Curdiea racovitzae</i>	42	2	1	0.048	0.048	0.008	-1.120*	-1.491 ^{ns}	Unimodal [†]
<i>Georgiella confluens</i>	20	4	4	0.363	0.489	0.077	-1.638*	-1.613 ^{ns}	Unimodal [†]
<i>Gigartina skottsbergii</i>	28	2	1	0.071	0.071	0.011	-1.151 ^{ns}	-1.155 ^{ns}	Unimodal [†]
<i>Iridaea cordata</i>	90	7	5	0.398	0.623	0.102	-0.797 ^{ns}	-2.882 ^{ns}	Unimodal [†]
<i>Palmaria decipiens</i>	35	7	6	0.318	0.343	0.054	-2.103***	-7.041***	Unimodal [†]
<i>Plocamium cartilagineum</i>	64	4	4	0.122	0.155	0.025	-1.759***	-3.466**	Unimodal [†]
Ochrophyta									
<i>Himantothallus grandifolius</i>	19 [§]	1	0	0.000	0.000	0.000			
Clorophyta									
<i>Monostroma harti</i>	37 [£]	2	1	0.378	0.378	0.049	0.846 ^{ns}	1.223 ^{ns}	Unimodal [%]

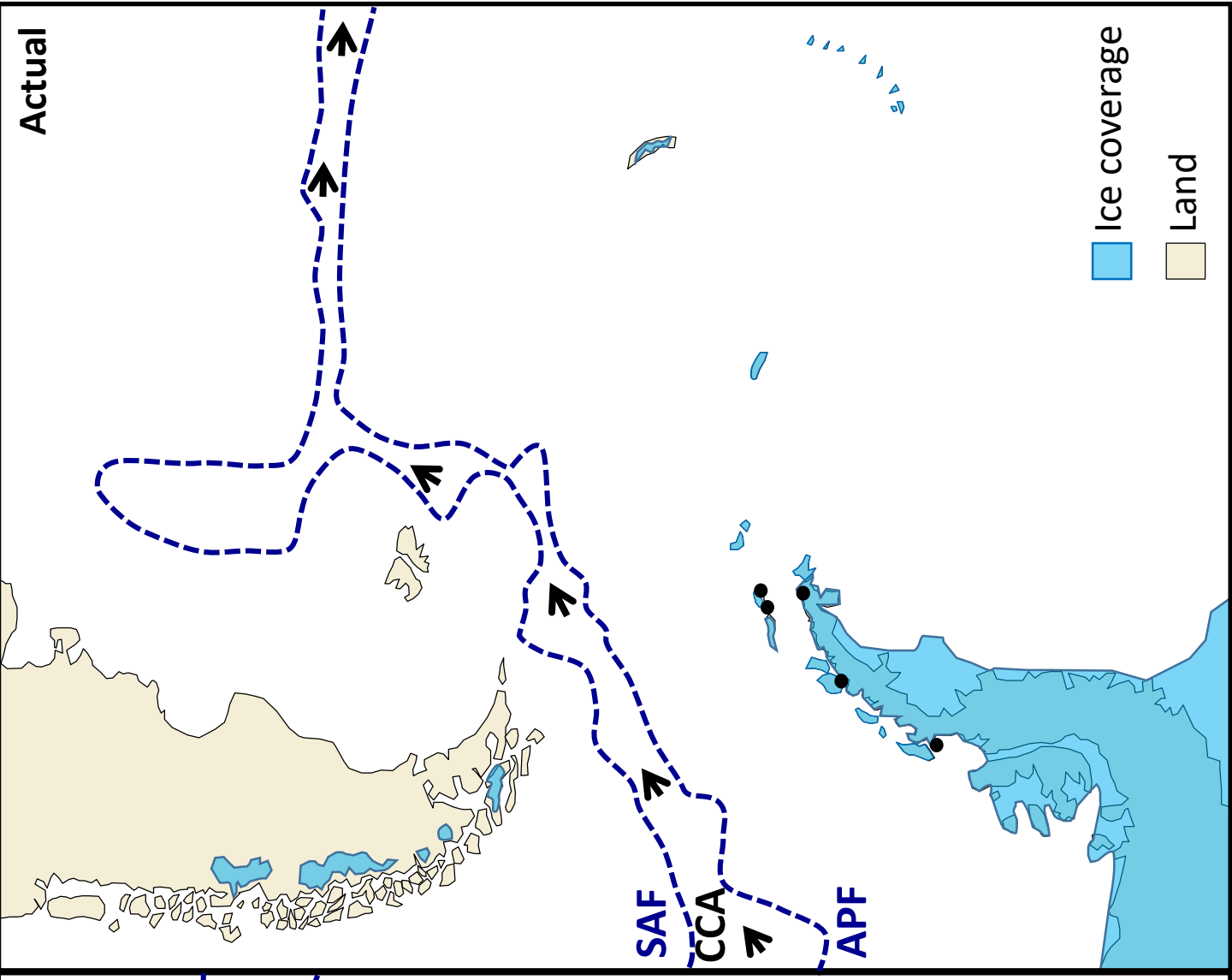
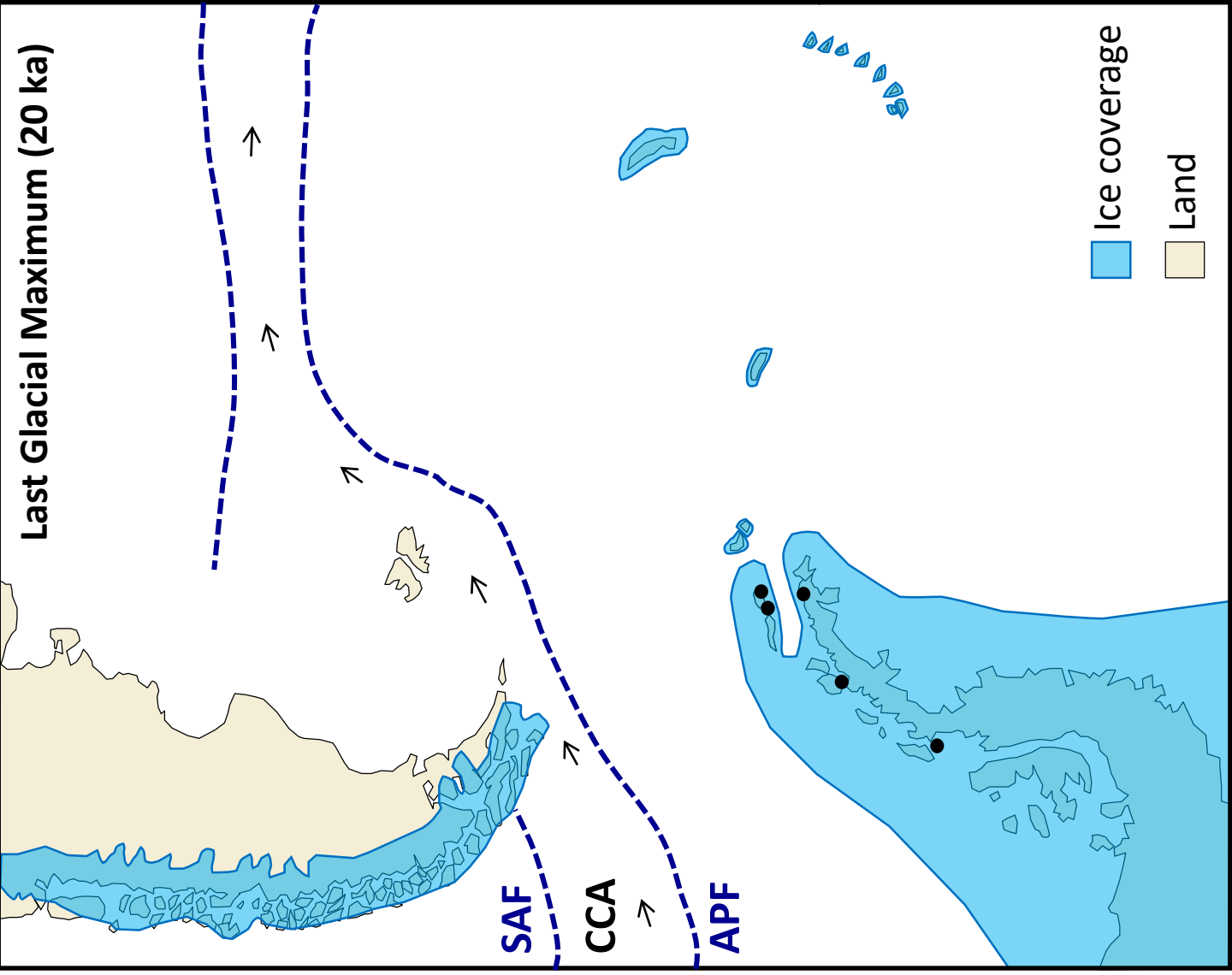
N: number of sampled specimens; k: number of haplotypes; S: polymorphic sites; H: haplotype diversity; Π : average number of nucleotide difference; π : nucleotide diversity. ns: non-significant; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$. All results obtained for Rhodophyta were taken from Guillemin et al. (2018), COI sequences are of 632 base pair (bp).

[†] hypothesis of sudden expansion could not be rejected when calculated for the sum of squared deviation or the Harpending's raggedness index (i.e., $0.000 < SSD < 0.007$; $0.179 < Rag < 0.821$; all $p > 0.05$). See Guillemin et al. (2018) for more detail.

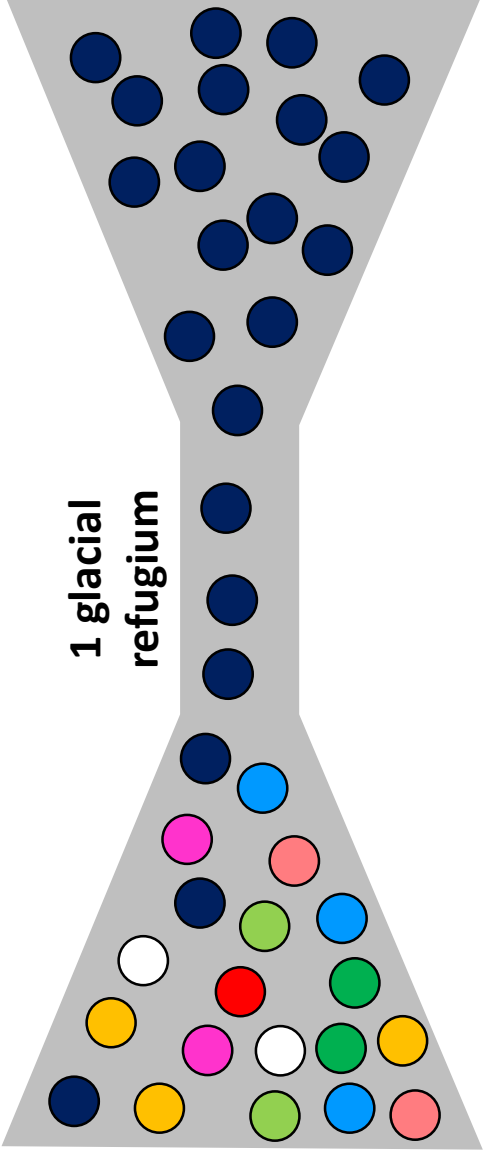
[%] Goodness-of-fit tests for a model of sudden expansion calculated in ARLEQUIN v.3.5 for the sum of squared deviation ($SSD = 0.005$, $p = 0.0001$) and for the Harpending's raggedness index ($Rag = 0.202$, $p = 0.459$)

[§]Include two sequences available in GENBANK: HE866784 from King George Island (Yang et al. 2014) and GQ368262 from Terre Adelie (Silberfeld et al. 2010). All COI sequences are of 619 bp.

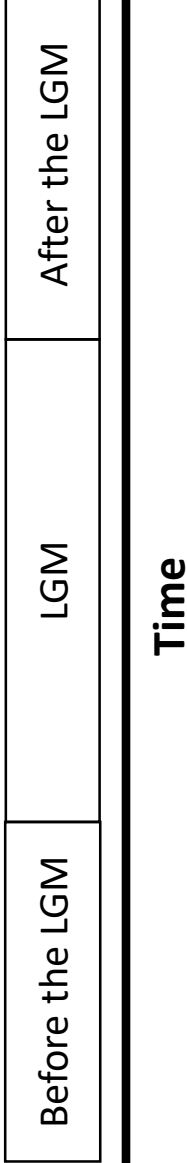
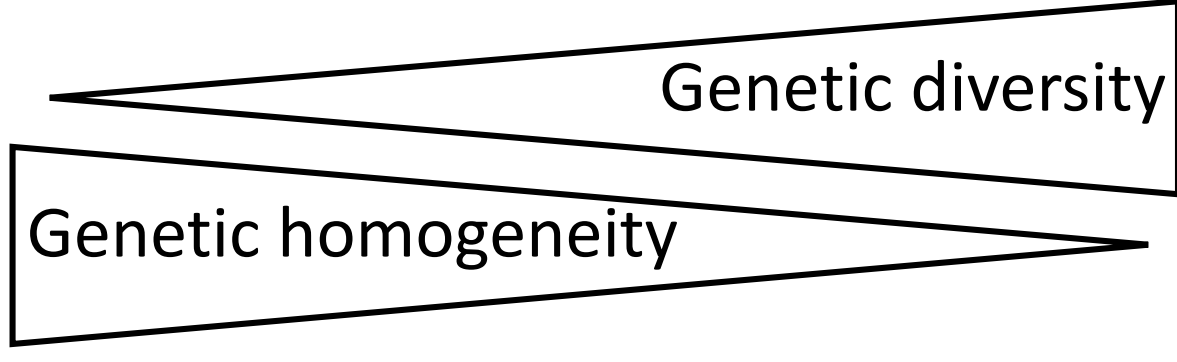
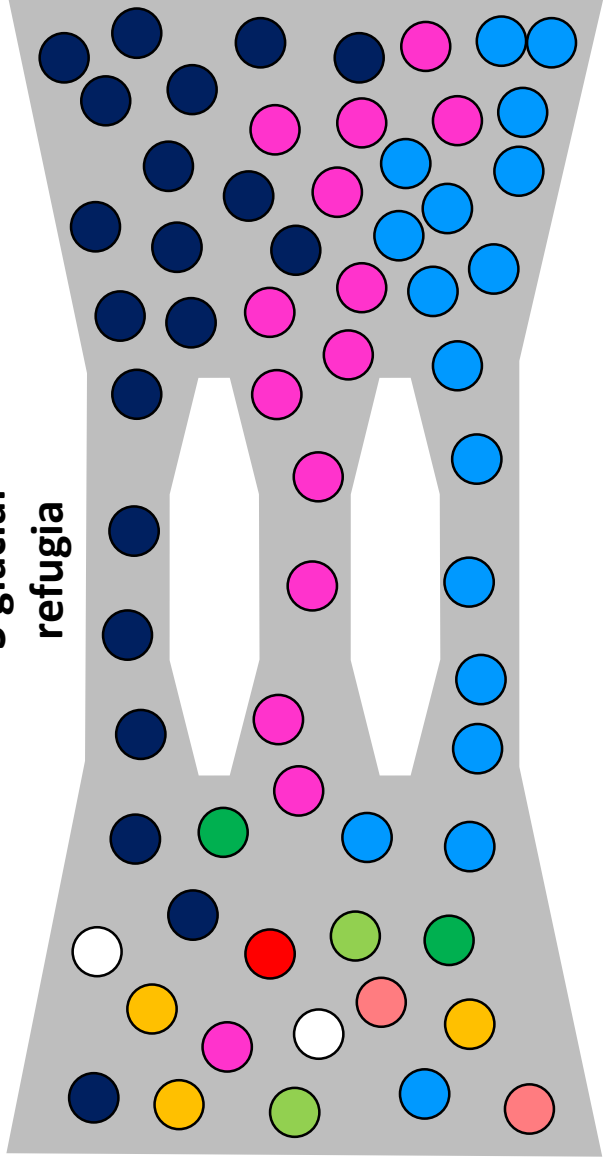
[‡]Sequences for the plastid gene *tufA* were all of 772 bp, except for the individual GGVMG0575, which was 52bp shorter. Since the 3' part of the *tufA* gene was not variable in our whole data set GGVMG0575 was completed to 772bp as in the other individuals before analyse



Scenario 1
Distribution
area



Scenario 2
Distribution
area



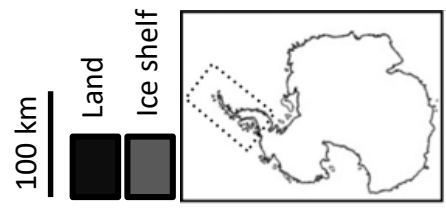
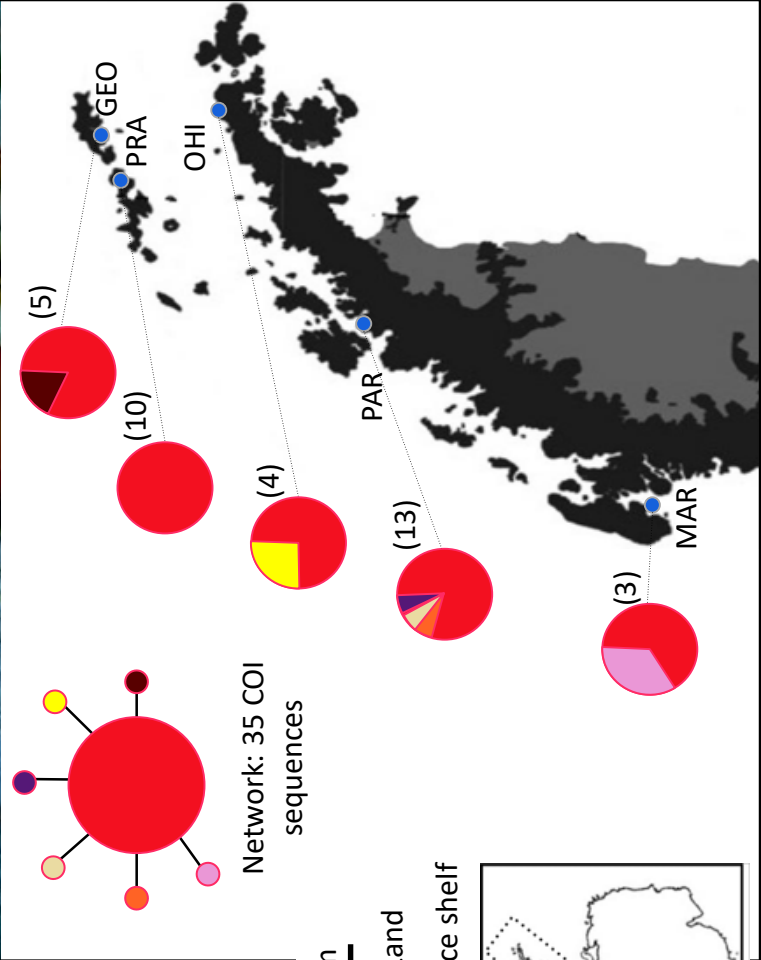
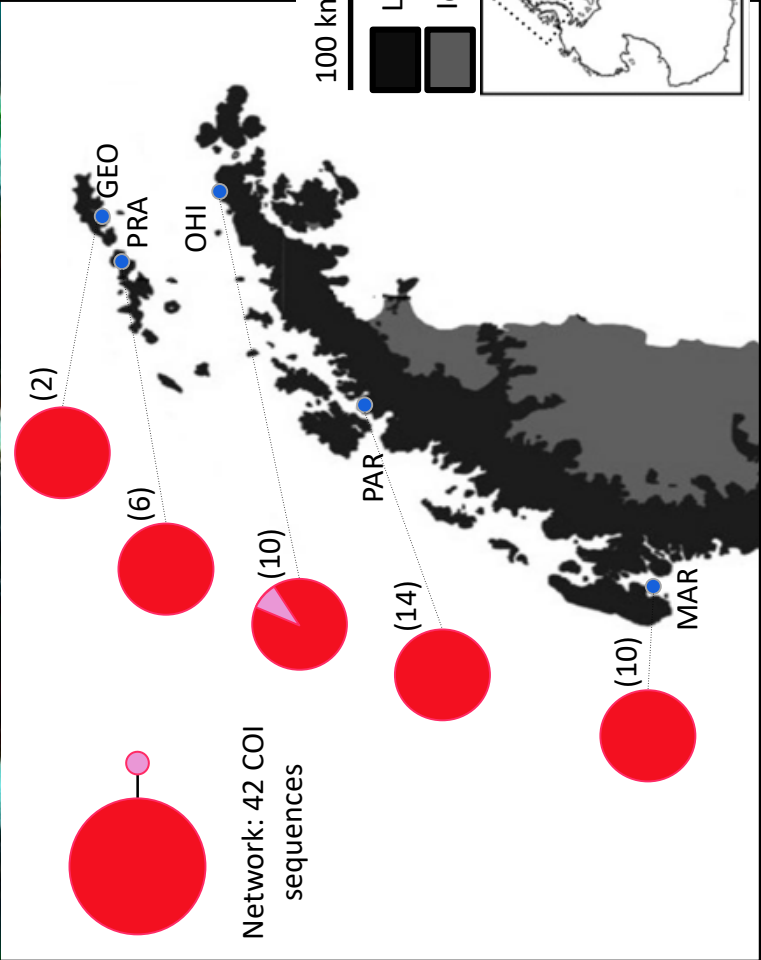
Expected effect on genetic diversity and phylogeographic structure



Curdia racovitzae



Palmaria decipiens





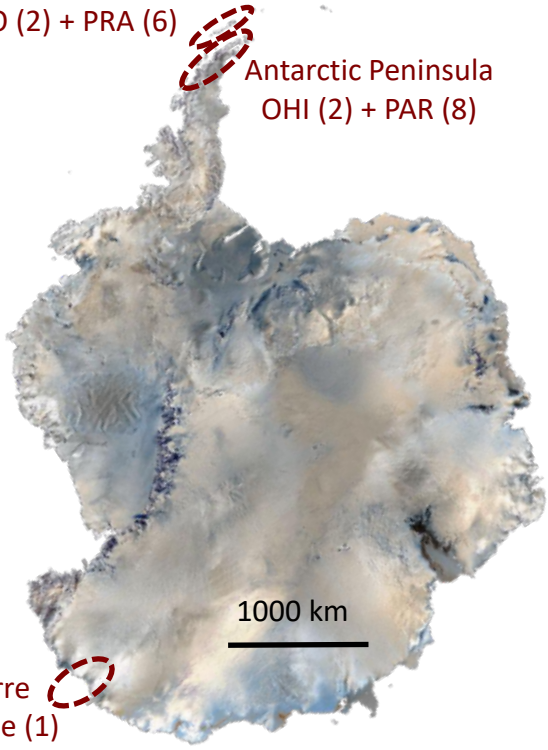
Himantothallus grandifolius

19 COI sequences, only one haplotype detected

South Shetland Islands
GEO (2) + PRA (6)

Antarctic Peninsula
OHI (2) + PAR (8)

Terre Adelie (1)



Monostroma hariotii

Network: 37
tufA sequences

