Palaeobiogeography of NE Atlantic archipelagos during the Last Interglacial (MIS 5e): a molluscan approach to the conundrum of Macaronesia as a marine biogeographic unit

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ABSTRACT

In order to understand the complex evolutionary processes and patterns that explain current island biodiversity, large datasets and long-term analysis are required. The Last Interglacial (LIG) was one of the warmest interglacials during the last million years. How species mobility changed during this period in the Macaronesia geographical region has long intrigued scientists. It is well established that the northward range expansion of tropical species occurred in the Macaronesian geographical region, but as a marine biogeographic unit, the term “Macaronesia” has not gained a consensus among the scientific community. For the first time, a thoroughly revised and updated checklist is presented for shallow-water marine molluscs from the Atlantic and Mediterranean during the LIG. Based on these wide ranging data, the status of Macaronesia as a marine biogeographic unit during the LIG was examined and our scientific understanding of how this unit evolved is improved. The analysis shows that during the LIG, the molluscan faunas of the Canary and Cabo Verde archipelagos were part of the same tropical Late Pleistocene Mediterranean West-African Province, whereas those in the Azores, Madeira and Selvagens archipelagos would be included in the subtropical Late Pleistocene French-Iberian Province. This contrasts with the present-day scenario, where the subtropical/warm temperate Azores and “Webbnesia” marine ecoregions (Lusitanian province) are biogeographically distinct from the Cabo Verde biogeographic subprovince, which in turn belongs to the West African Tropical biogeographic province. A further analysis of the coherence of “Macaronesia” as a marine biogeographical unit was accomplished by coupling Pliocene, LIG, and present-day data, showing that the term “Macaronesia”, and for the marine realm, should only be used in a geographical connotation.

Keywords: Marine Biogeography, Mollusca, Last Interglacial, Macaronesia, Atlantic, Mediterranean Sea

1. INTRODUCTION

1.1. Pliocene to Present-day biogeographic zonation of the NE Atlantic: climatic zones and provincial indicators

The evolution of the Mediterranean and Atlantic marine biogeographic units subsequent to the Neogene has attracted the attention of marine biogeographers since the last century (Raffi et al., 1985; Raffi & Monegatti, 1993; Monegatti & Raffi, 2001, 2007; Hall, 2002; Berning, 2006; Landau et al., 2007, 2011; Silva & Landau, 2007; Ávila et al., 2009a, 2015a, 2016, 2018; Silva et al., 2010, 2011; Lozouet, 2014; Freitas et al., 2019; Landau et al., 2020; Rebelo et al., 2021a; Melo et al., 2022). Ávila et al. (2016) extended the Mio-Pliocene biogeographic zonation of the NE Atlantic façade to include Azorean longitudes but, since the work was based on Pliocene benthic assemblages, a gap in the knowledge regarding insular Atlantic biogeographic evolution during the Last Interglacial (LIG) still remained to be considered. The LIG (0.129 – 0.116 Ma; Shackleton et al., 2020) is considered one of the warmest Quaternary interglacials, with pre-industrial global mean sea surface temperatures (SSTs) ~1 to 2 ºC higher than present-day values (Hoffman et al., 2017; Shackleton et al., 2020). This increase in mean SSTs makes the LIG an excellent analogue (as concerns the biogeography of shallow-water, benthic marine molluscs) to what the present interglacial may become as a result of global warming (e.g., Scarponi et al., 2022).

Temperature is known to be one of the primary determinants of geographical distribution for marine species (Raffi et al., 1985; Hoegh-Guldberg & Bruno, 2010; Doney et al., 2012). Hall (1964) and Petuch (2004) showed that water temperature plays a key role in defining marine biogeographical boundaries, and the latter author went on to propose a classification of the Cenozoic tropical American biogeographical provinces based on this parameter. The Eastern-Atlantic geographical area in which the Macaronesian archipelagos are presently located encompasses two types of climatic zones (sensu Petuch, 2004): tropical regions, defined as "eutropical"; and subtropical or warm-temperate regions, defined as "paratropical". Today, the Azores, Madeira, Selvagens, and Canaries archipelagos are located within a paratropical region, whereas the Cabo Verde Archipelago lies in a eutropical setting (Freitas et al., 2019). The marine molluscan taxa exclusive of each province are characterized as "provincial indicators" sensu Petuch (2013). These taxa are paramount in biogeographic studies, as they are markers of geographic change in the range expansion (or contraction) of genera and species and, consequently, of the evolution of biogeographical provinces.

1.2. The Macaronesia region

Based on terrestrial floras belonging to the north-eastern Atlantic archipelagos and the nearby European and African continental areas, a distinct phytobiogeographic unit was erected for this insular realm. This observation has been attributed to the British botanist Phillip Barker Webb (ca. 1845). Webb's insular biogeographic unit included the volcanic oceanic archipelagos of Madeira, Selvagens, and Canary Islands alone (Stearn, 1973; Sjögren, 2000). Later, the term "Macaronesia" (sensu Engler, 1879) was used to define it, and the Azores and Cabo Verde archipelagos (Engler, 1879; Dansereau, 1961), the southern Iberian Peninsula and some nearby north-western Africa coastal areas were added (Sunding, 1973; Fernández-Palacios, 2011). This led to a broader biogeographic unit far from Webb's initial concept.
The term "Macaronesia" was also used in a marine context but, as a marine biogeographic unit, it never gained consensus within the scientific community (Ávila, 2000). When they defined the present-day marine ecoregions of the world, Spalding et al. (2007) excluded the Cabo Verde Archipelago from Macaronesia. However, their interpretations lacked supporting data. Freitas et al. (2019) re-evaluated the present-day so-called Macaronesia marine biogeographic unit based on a multitaxon analysis and concluded that the Cabo Verde archipelago's faunas should be set apart as an independent biogeographic subprovince within the West African Transition province (sensu Spalding et al., 2007), whereas the Azores should be assigned to a separate ecoregion within the Lusitanian biogeographical province. Moreover, having demonstrated the lack of coherence of the present-day Macaronesian marine biogeographic unit, they coined the term "Webbnesia" ecoregion, which includes the archipelagos of Madeira, Selvagens and the Canaries. Therefore, and from a strictly marine point of view, Freitas et al. (2019) show that there exists no support for the concept of Macaronesia as a coherent present-day marine biogeographic unit.

1.3. Aims

The aims of this contribution are to: i) evaluate the biogeographic coherence of Macaronesia during the LIG from the point of view of the benthic, shallow-water marine malacological faunas; and ii) narrow the gap of knowledge on how the biogeographic units in this region evolved since the LIG. Palaeoecological and palaeoclimatic inferences based on fossil molluscs also are included within this framework. The discussion and conclusions are based on a thoroughly revised and updated checklist that is presented for the first time for the LIG Atlantic and Mediterranean shallow-water marine molluscs. This checklist allows for the possibility to draw correlations between climatic zones and "ecostratigraphic indicators" (i.e., tropical marine species recorded in LIG fossil assemblages from present-day "paratropical" Macaronesian archipelagos, but later extirpated due to the onset of the Last Glacial episode; sensu Melo et al., 2022).

2. METHODS

2.1. Data acquisition

The Atlantic and Mediterranean LIG fossil assemblages used in the biogeographic analyses were distributed and pooled in line with the ecoregions of Spalding et al. (2007; Fig. 1). In the Azores Archipelago, field campaigns for the study of marine fossiliferous outcrops and sampling of fossil mollusc specimens have been conducted at Santa Maria Island since the early 2000s. In total, 18 international workshops on "Palaeontology in Atlantic Islands" and many shorter field trips were organized, resulting in the discovery and study of several Pliocene and LIG outcrops, as well as the sampling of numerous fossil specimens from different marine groups (mostly bivalve and gastropod molluscs) and of their trace fossil representatives (Ávila et al., 2002, 2007, 2009b, 2012, 2015a, 2015b, 2015c, 2016, 2020; Estevens & Ávila, 2007; Madeira et al., 2007, 2011; Janssen et al., 2008; Kroh et al., 2008; Winkelmann et al., 2010; Meireles et al., 2012, 2013; Rebelo et al., 2014, 2016, 2021b; Santos et al., 2015; Uchman et al., 2016, 2017, 2018, 2020; Johnson et al., 2017; Dávid et al., 2021; Hyzny et al., 2021). For the Cabo Verde Archipelago, field campaigns were carried out from 2017 to 2022 on the following islands: Santiago, Maio, Boavista, Sal, São Vicente, and Santo Antão. The catalogued fossil specimens collected in the Azores and Cabo Verde archipelagos are deposited at the DBUA-F – the fossil collection of the Department of Biology of the University of the Azores (Ponta Delgada, São Miguel Island). In the Canaries, fieldwork was carried out from 1995 to 2022, and the catalogued fossil remains of the marine molluscs collected are housed at the MUNA – Museo de Naturaleza y Arqueología (Tenerife Island). For Southern Italy (Taranto area), LIG mollusc specimens were collected and identified by D. Scarponi, and the catalogued fossil remains are housed at the Department of Biological, Geological, and Environmental Sciences of the University of Bologna (Italy).

The fossils of LIG marine molluscs collected during fieldwork in the Azores, Canaries, and Cabo Verde archipelagos, and from Taranto (Italy) were identified and a preliminary list was compiled. This initial list was complemented with bibliographic data, retrieved from published works and from "grey literature" (e.g., master and doctoral theses, unpublished scientific reports, etc.). Bibliographic data were obtained from the following areas and authors: Azores (Callapez & Soares, 2000; Ávila et al., 2002, 2007, 2009b, 2015a), Madeira (Cotter & Girard 1892; da Silva, 1956; Gerber et al., 1989), Selvagens (García-Talavera & Sánchez-Pinto, 2001), Canary Islands (Meco et al., 2008; Cabero, 2009; Martín-González et al., 2016, 2019); Cabo Verde (García-Talavera, 1999; Cabero, 2009), NW African coasts (Lecointre, 1952; Weisrock et al., 1999; Plaziat et al., 2008; Chakroun & Zaghbib-Turki, 2017; Chakroun et al., 2017), Mediterranean (Lipparini, 1935; Mirigliano, 1953; Segre, 1954; Bonfiglio, 1962; Bonadonna, 1967; Moshkovitz, 1968; Ruggieri & Bucchieri, 1968; Ruggieri et al., 1968; Issar & Picard, 1969; De Castro, 1971; Fleisch et al., 1971; Cuerda & Sanjaume, 1978; Porta & Martinell, 1981; Cuerda et al., 1986; Ruggieri & Unti, 1988; Cuerda et al., 1989-1990, 1991; Vazzana, 2008; Bracchi et al., 2012), North American Atlantic coasts (Richards, 1962; D'Antonio, 2012), Bermuda (Muhs et al., 2002), and South American Atlantic coasts (Martínez et al., 2001; Aguirre et al., 2011; Rojas & Martínez, 2016; Rojas et al., 2018; Charó, 2021). Works that presented a range of ages for the study of stratigraphic sequences beyond the LIG and works that did not present fossil record lists were not considered for the analysis.

Synonyms were checked using the "Match taxa" tool of the World Register of Marine Species (WoRMS), and species nomenclature and authorities were updated following the WoRMS (WoRMS Editorial Board, 2021). All dubious records were excluded. The final lists are presented in Supplementary Tables 2 and 3, which contains all LIG fossil mollusc bivalve and gastropod species reported in our database from Atlantic and Mediterranean deposits.

Present-day mean Sea Surface Temperatures (SST) were obtained from COBE-SST2 data provided by the NOAA/OAR/ESRL PSL (Hirahara et al., 2014: https://psl.noaa.gov/data/gridded/data.cobe2.html).

2.2. Statistical analyses

The geographic distribution of the LIG shallow-water benthic marine molluscs in each region was noted, resulting in a presence/absence matrix. All statistical analyses were made using R version 4.2.0 (R Core Team, 2022), namely the R packages vegan (Oksanen et al., 2017), ade4 (Dray & Dufour, 2007), cluster (Maechler et al., 2018), gclus (Hurley, 2012), and recluster (Dapporto et al., 2015). A dendrogram depicting the biogeographic relationships among the faunas of the different areas was drawn, using dissimilarity indices and cluster analysis. Numerous classical distance metrics for presence/absence data were used, namely Jaccard (1901), Sørensen (1948), Ochiai (1957) and Simpson (1960) dissimilarities. Also, for each dissimilarity coefficient, various agglomeration methods were tried (Legendre & Legendre, 1998), namely complete linkage, centroid distance, unweighted pair group method with arithmetic mean (UPGMA), and Ward's minimum variance clustering (Sokal & Michener, 1958; Sokal & Sneath, 1963; Ward, 1963). To establish the best combination of dissimilarity measure and agglomeration method, the cophenetic correlation value between the region's distance matrix and the dendrogram representation was calculated (Sokal & Rohlf, 1962). We followed the techniques described in Borcard et al. (2011), and the hierarchical clustering approach described by Pavão et al. (2019). For each dendrogram, the presumed number of groups formed by the target regions was estimated using both the Rousseeuw quality index, which determines the optimal number of clusters according to silhouette widths (Rousseeuw, 1987), and the Mantel statistic (Pearson), which defines the optimal number of clusters (Legendre & Legendre, 1998). This was further sustained by a bootstrap validation, implemented using a recluster package, which provides robust techniques to analyse patterns of similarity in species composition (Kreft & Jetz, 2010; Dapporto et al., 2013, 2014, 2015). Finally, the dendrogram was targeted by a resampling procedure with 100 trees per iteration and a total of 1,000 iterations. All the dissimilarity coefficients were retested using this approach to ensure consistency in the number of groups formed by the target regions. This same method has already been applied by Freitas et al. (2019).

The statistical analysis described above was done using species (Fig. 2) and genera (Fig. 3) of LIG shallow-water benthic marine mollusc gastropods and bivalves. Ecoregions with ≤15 records for gastropod species/genera and ≤10 records for bivalve species/genera were excluded from the statistical analysis. As a result, 16 ecoregions for gastropods and 19 ecoregions for bivalves were used (Figs. 2 and 3).

Finally, we compared the dendrograms depicting the LIG faunal similarities between fossil gastropod and bivalve assemblages of different regions (Fig. 2) with equivalent present-day dendrograms. For the gastropods, this comparison was made using the data presented by Freitas et al. (2019; their Fig. 4), whereas for the bivalves, the comparison was made with unpublished dendrograms from one of the authors (S.P. Ávila).

3. RESULTS

There is a strong bias in published literature about the fossils of the Macaronesian archipelagos, with a high number of studies published for the Canaries (66), an intermediate number for the Azores (24) and Cabo Verde (18), and a low number for Madeira (5) and Selvagens. Indeed, there is a single study published on the LIG fossil record of Selvagens (Table 1) and, therefore, there is a severe lack of data from Selvagens in comparison with the remaining Macaronesian archipelagos (cf. Supplementary Table S2 for LIG gastropods and Supplementary Table S3 for LIG bivalves).

Data compilation resulted in a wide-ranging final list composed of 1,198 specific taxa reported for the LIG [(759 gastropods (Supplementary Table S2) and 439 bivalves (Supplementary Table S3)] distributed along 22 ecoregions/archipelagos for gastropods and 25 ecoregions/archipelagos for bivalves (Table 2).

For gastropods, the ecoregions with the highest number of specific taxa reported for the LIG are WEM (Western Mediterranean) with 219 and IOS (Ionian Sea) with 197, both in the Mediterranean, followed by CAN (Canary Islands) with 190 and AZO (Azores) with 113, both in the NE Atlantic. The ecoregions with the lowest number of specific taxa reported for the LIG are SEL (17), and TUP (Tunisian Plateau/Gulf of Sidra), PGS (Patagonian Shelf), RIG (Rio Grande), BER (Bermuda) and NGB (Northern Grand Banks), all with less than 15 records (Table 2; Fig. 1). Unlike the bivalve record (see below), no data were obtained for gastropods for FLO (Floridian), NGM (Northern Gulf of Mexico) and WGS (West Greenland Shelf) ecoregions.

For bivalves, the ecoregions with the highest number of specific taxa reported for the LIG are VIR (Virginian ecoregion) with 100 and CAR (Carolinian ecoregion) with 96, both eastern North America coastal regions, and the WEM (Western Mediterranean) with 97 and IOS (Ionian Sea) with 96, both in the Mediterranean Sea (Table 2). The ecoregions with the lowest number of specific taxa reported for the LIG are SEL, TUP, PGS, and WGS, all with less than 10 records.

WEM (133), CAN (124), IOS (112), and AZO (80) are the ecoregions showing the highest number of gastropod genera, the least diverse being PGS (2), TUP (6), NGB (7), and RIG (10). As for the number of genera of bivalves, the most diverse ecoregions are CAR (83), VIR (82), IOS (80) and WEM (79), followed by CAN and UBS (53 each), whereas the least diverse ecoregions are WGS (1), SEL (2) and PGS (3) (Table 2).

For the Macaronesian archipelagos, a total of 319 LIG gastropods are reported, corresponding to 42.03% of the total 759 listed LIG gastropods. A total of 105 LIG bivalves are also reported from the Macaronesian archipelagos, corresponding to 23.92% of the total 439 listed LIG bivalves (Table 3). In total, 424 LIG mollusc species/taxa are reported from the Macaronesian islands, which contrasts with 1,224 mollusc species presently reported for the Macaronesian archipelagos (896 gastropods and 328 bivalves; Sérgio Ávila, unpublished data).

Our database detected 16 species of LIG amphi-Atlantic molluscs, i.e., species that at that time occurred simultaneously on the eastern and western coasts of the Atlantic: 12 gastropods (1.58%) and 4 bivalves (0.91%). Expanding this analysis to include other North Sea locations, e.g., the LIG molluscs reported from Denmark (Funder et al., 2002; Petersen, 2004) and the Netherlands (Meijer et al., 2021), two gastropods (*Buccinum undatum* and *Cylichna alba*) and seven bivalves (*Arctica islandica*, *Astarte elliptica*, *Heteranomia squamula*, *Macoma balthica*, *Mya truncata*, *Parvicardium pinnulatum* and *Zirfea crispata*) are added to the list, increasing the total numbers to 25 LIG amphi-Atlantic mollusc species: 14 gastropods (1.84%) and 11 bivalves (2.51%). This is a lower number when compared with the current number of amphi-Atlantic mollusc species: 141 gastropods (3.91%) and 118 bivalves (7.02%) (Sérgio Ávila, unpublished data; cf. Table 3). The number of LIG amphi-Atlantic mollusc species is likely to increase, if other high latitude sites are included, a task that is out of the scope of this study.

The most speciose genera of gastropods are *Alvania* (31 species), *Turbonilla* (21), *Conus* (18) and *Rissoa* and *Tritia* (13 species each), whereas for bivalves, the most speciose genera are

Astarte and *Glycymeris* (9 species each), *Anadara* and *Musculus* (7 species each), and a group of five genera, each with 6 species: *Abra*, *Donax*, *Mactra*, *Nucula* and *Pandora* (Table 4).

Cluster analysis using species-level identifications (Fig. 2) from 17 ecoregions for gastropods (Fig. 2A) and 19 ecoregions for bivalves (Fig. 2B) shows 6 clusters for the first (clusters 1 to 6; cf. Fig. 2A) and five clusters for the latter (clusters 7 to 11; Fig. 2B), both validated by Mantel statistics. In the case of gastropods, and for the Macaronesian archipelagos (i.e., AZO – Azores; MAD – Madeira; SEL – Selvagens; CAN – Canaries; and CAB – Cabo Verde), one statistically valid clusters occur: MAD and SEL (cluster 5, Fig. 2A); for the bivalves, there is a stronger similarity between CAN and CAB (cluster 7 validated by Mantel statistics; Fig. 2B).

Cluster analysis using generic level identifications (Fig. 3), based on data from 16 ecoregions for gastropods (Fig. 3A) and 19 ecoregions for bivalves (Fig. 3B), resulted in five clusters for gastropods validated by Mantel statistics (clusters 1 to 5; cf. Fig. 3A) and four clusters for bivalves (clusters 6 to 9; Fig. 3B). Regarding gastropod genera, AZO and MAD cluster together, whereas CAN joins to WEM and IOS (cluster 4; Fig. 3A); CAB joins LES in a different cluster (cluster 5; Fig. 3A). Regarding the dendrogram depicting the relationships among the Macaronesian archipelagos using bivalve generic data, , again, AZO and MAD cluster together, and CAN joins WEM and IOS (cluster 6; Fig 3B).

Nonmetric multidimensional scaling (NMDS; Fig. 4) highlights, both for gastropods (Fig. 4A) and bivalves (Fig. 4B), the high similarity of the Macaronesian archipelagos with the Mediterranean and the NW African coasts. Moreover, as in the cluster analysis (Fig. 2), the NMDS (Fig. 4) highlights dissimilarities between the different provinces, roughly grouping them in three main geographic groups: North America, South America, and NE Atlantic. The biogeographic units cluster in a similar manner for gastropods (Fig. 4A) and bivalves (Fig. 4B). In the former case, the Arctic biogeographic realm joins the Cold Temperate Northwest Atlantic and the Warm Temperate Northwest Atlantic provinces (Table 2); a second group is formed by the Warm Temperate Southwestern Atlantic and Magellanic provinces; and finally, the Lusitanian, Mediterranean Sea and West African Transition provinces cluster together. In the latter case, biogeographic realms and provinces based on LIG bivalves' database cluster as follows: the Mediterranean Sea, Lusitanian and West African Transition provinces make a first group; again, a second group is formed by Warm Temperate Southwestern Atlantic and Magellanic provinces; and, in the last group, Tropical Northwestern Atlantic, Warm Temperate Northwest Atlantic, Cold Temperate Northwest Atlantic, and Arctic provinces cluster together.

4. DISCUSSION

4.1. Palaeoecology and Palaeoclimatology in the Macaronesia during the Last Interglacial: ecostratigraphic indicators

For the Macaronesian archipelagos, and especially for the Azores and Canary Islands, the presence of gastropods of the tropical genus *Thetystrombus* Dekkers, 2008 (Ávila et al., 2016 and references therein) has been used as the main ecostratigraphic indicator sensu Melo et al. (2022) for both Pliocene and Pleistocene LIG deposits. For example, *Thetystrombus coronatus* (=*Strombus coronatus*) (Defrance, 1827), a characteristic species for the lower Plio-Pleistocene Mediterranean molluscan assemblages [Mediterranean Plio-Pleistocene Molluscan Unit 1 (MPMU1) of Raffi & Monegatti (1993); see also Monegatti & Raffi (2001)], is reported from the Lower Pliocene of the NE Atlantic archipelagos of the Azores (Ávila et al., 2016), Canaries (Meco et al., 2015), and Cabo Verde (Serralheiro, 1976), whereas the species *Thetystrombus latus* (Gmelin, 1791) is reported from the Pleistocene of the Canaries (García-Talavera, 1990; Meco et al., 2002; Montesinos et al., 2014; Taviani, 2014) and Cabo Verde (Serralheiro, 1976; García-Talavera, 1999). The extant *T. latus* ranges from Senegal (14º40'N) in the north to Angola (17º15'S) in the south. Favouring mean sea surface temperatures (SSTs) of about 25ºC (Fig. 5), the gastropods of this species inhabit sandy-muddy bottoms and waters with normal salinity (Cornu et al., 1993).

The arrival of thermophilic molluscs to the Azores, Madeira, and Canary archipelagos during the LIG was reported by previous authors (e.g., Meco, 1977; Ávila et al., 2002, 2009a, 2015a; Cabero, 2009; for a review see Melo et al., 2022 and references therein). Nevertheless, like *T. latus*, many other Macaronesian warm-water benthic molluscs used as LIG ecostratigraphic indicators sensu Melo et al. (2022) did not reach the northern archipelagos (Azores and Madeira), showing that SST conditions in these archipelagos were different from those recorded in the Canary Islands and Cabo Verde Archipelago.

The occurrence of *T. latus* in the Canaries (e.g., Meco, 1977) and in the Mediterranean (e.g., Amorosi et al., 2014), but not in the Azores, Madeira, and Selvagens archipelagos, during the LIG, indicates a different placement of the boundaries of the climatic zones in comparison with the boundaries of the Holocene molluscan biogeographical provinces, sensu Raffi et al. (1985) and Monegatti & Raffi (2001). This suggests that during the Last Interglacial, the transition zone between Tropical and Subtropical climatic zones – located today between Cape Blanc and the Canaries (Fig. 6F, sensu Raffi et al., 1985; Monegatti & Raffi, 2007) – was positioned at a higher latitude, in an area along the southern Atlantic coasts of the Iberian Peninsula (Fig. 6E), but away from the Straits of Gibraltar. The interpretation of the location of the transition zone in this area is based on the fact that during the LIG, *T. latus* reached the Mediterranean, which indicates that tropical climatic conditions should have been present at least as far north as the northwestern coasts of Africa, including the Strait of Gibraltar region, and in the

Mediterranean Sea.

Based on the absence of *T. latus* (a large and thick-shelled gastropod easily preserved and recognized in fossil assemblages) in the Pleistocene LIG fossil record of the Madeira and Selvagens archipelagos and considering that *Conus* spp. can withstand a wider thermic amplitude (Melo et al., 2022), it is proposed that the transition zone during the LIG was located at a lower latitude than during the early Pliocene (Fig. 6A and D), positioned between the Selvagens and Madeira archipelagos (Fig. 6B and E), with Madeira Archipelago lying within the paratropical climatic zone. With the LIG latitudinal shift of the transition zone between the eutropical and paratropical zones northwards, both the Canaries and the Cabo Verde archipelagos were located within the same climatic zone, favouring the range expansion of thermophilic species northwards, thus promoting higher similarities between the faunas of the two archipelagos (cf. Fig. 2B). This interpretation is not new (cf. Meco et al., 2002; Meco et al., 2008; Montesinos et al., 2014; Meco et al., 2015), having been hypothesized by Melo et al. (2022) regarding the paths and rates of interchange between the archipelagos and based on a thorough revision and discussion on the timing and conditions leading to the range expansion of tropical species within Macaronesia.

4.2. Palaeobiogeography of the Macaronesia during the Last Interglacial

4.2.1. Dendrogram analysis

The dendrograms resulting from a similarity analysis restricted to the LIG fossil record of the Macaronesian archipelagos (Fig. 7) show a higher similarity of the Canarian (CAN) and Cabo Verdean (CAB) assemblages, for both gastropods (Fig. 7A) and bivalves (Fig. 7B). Madeira (MAD) clusters with Selvagens (SEL) in the case of gastropods (Fig. 7A). Interestingly, while today the CAN, SEL, and MAD gastropod faunas cluster together characterizing the “Webbnesia” ecoregion (cf. Freitas et al., 2019, their Fig. 4), for the LIG, the fossil assemblages of CAN show a higher similarity with CAB (Fig. 7A). These results are consistent with the well-known increase in eastern Atlantic SSTs, especially for the Canary Islands during the LIG (Meco et al., 2002; Zazo et al., 2010; Montesinos et al., 2014; Muhs et al., 2014; Maréchal et al., 2020) and the interpreted ocean current pattern for this time in the area (cf. Melo et al., 2022 and references therein). The combination of these two factors resulted in the range expansion of tropical marine taxa from the lower latitudes of Cabo Verde and the Senegal coast northwards, to the Canary Islands and, eventually, into the Mediterranean. The higher affinity between the faunas of these two archipelagos (CAB and CAN) during LIG was already noted by Melo et al. (2022). Thermophilic taxa were subsequently extirpated from CAN due to the onset of the glacial conditions in the Northern Hemisphere, their range contracting southwards to the present-day situation.

4.2.2. The evolution of the NE Atlantic (Palaeo)Biogeographic Provinces

The changes in (palaeo)biogeographic relationships among the marine molluscan faunas of the Macaronesian archipelagos (Fig. 7), SSTs, and ocean surface currents (cf. Melo et al., 2022 and references therein) resulted in modifications in the position of boundaries and the range of the marine molluscan bioprovinces during the LIG.

Today, following Raffi et al. (1985), the NE Atlantic façade (from Guinea to the UK) is divided into four biogeographic molluscan provinces (Fig. 6C): the tropical Mauritanian-Senegalese Province (MSP); the subtropical Mediterranean-Moroccan Province (MMP); the warm-temperate French-Iberian Province (FIP); and the cool temperate Boreal-Celtic Province (BCP). The Cabo Verde faunas are part of the MSP, while the faunas of the remaining Macaronesian archipelagos are assigned to the MMP. The transition zone between MSP and MMP roughly coincides with the annual mean SST 20°C isotherm, whereas the transition zone between MMP and FIP is defined by the annual mean SST 17°C isotherm (see Figs. 5 and 6C).

During the pre-mid Pliocene (until the onset of the MIS M2 cooling events, ~3.2 Ma; Dolan et al., 2015), the molluscan faunas of the Macaronesian archipelagos pertained to the vast tropical Pliocene Mediterranean-West African Province (PMWAP; Fig. 6A and D) sensu Ávila et al. (2016), the boundary between the tropical and subtropical biogeographic provinces being positioned north of the Azores Archipelago. The onset of later glacial episodes caused the subtropical Pliocene French-Iberian Province (PFIP; Fig. 6A) and later the Late Pleistocene French-Iberian Province (LPFIP; Fig. 6B) to expand southwards, placing today the Mediterranean out of the tropical region and its faunas within the present-day subtropical Mediterranean-Moroccan Province, MMP (Fig. 6C). The reshaping of the early Pliocene biogeographic zonation led to the vanishing of the Pliocene Mediterranean-West African Province (PMWAP), giving rise to the present-day subtropical MMP, and the tropical Mauritanian-Senegalese Province, MSP (Silva & Landau, 2007; Fig. 6C). Thus, our analysis suggests that during the LIG the geographical expression of the biogeographic units of the NE Atlantic façade was different from the present one and closer to what occurred during the Pliocene, showing a partial reinstatement of the PMWAP.

Throughout the LIG, numerous tropical marine taxa with a Cabo Verdean/Senegalese provenance reached the Canary Archipelago (Melo et al., 2022), a well-known fact that is also supported by the LIG similarity analysis (this work), which shows a congruent cluster of CAN with CAB (cf. Figs. 2B and 7). On the other hand, MAD and AZO pertain to a different biogeographic province. Moreover, the few data available from the NW Africa LIG fossiliferous sites (e.g., Lecointre, 1952) show no signs of this range expansion having occurred along the NW African coasts (Melo et al., 2022). Taking this into consideration, it is hypothesized that the Canary upwelling, active during the LIG as today – the more persistent (perennial) and higher productive upwelling region is, in the present times, the one south of Cape Blanc (Abrantes, 1991; Moreno et al., 2002) – generated a "colder" area within the tropical Late Pleistocene Mediterranean-West African Province (LPMWAP; Fig. 6B and E), thus making the area unsuitable for the northward range expansion of the Senegalese warm-water fauna. Notice that, as proposed by Ávila et al. (2019), and later by Melo et al. (2022; section 5.2. and references therein), it is suggested that this northward range expansion occurred during the last phase of glacial Termination 2, during a period when oceanographic barriers such as the Canary Current were weakened and more likely located more offshore (Moreno et al., 2002), and new ephemeral surface ocean currents generated "windows of opportunity" for the long-distance dispersal of marine species along sweepstake routes.

4.3. The Macaronesia marine biogeographic unit paradigm

The discussion on whether "Macaronesia" should be considered as a coherent marine biogeographic unit endures (Ávila, 2000; Freitas et al., 2019). Our opinion is that it was not coherent, either today or in the past. Studies on the biogeographic evolution of the marine faunas in the Macaronesian geographic region (composed of the volcanic oceanic archipelagos of the Azores, Madeira, Selvagens, Canaries, and Cabo Verde) trace this issue back to the late Miocene (Ávila et al., 2016). This epoch is key, as the first island of the Azores Archipelago emerged ~6.03 Ma ago (Ramalho et al., 2017), thus only since then can Macaronesia be considered a separate geographic entity as we know it today.

Until the mid-Pliocene (i.e., until the extremely cold glacial MIS M2 (~3.2 Ma); Naafs et al., 2010, 2020; De Schepper et al., 2014; Dolan et al., 2015), the Macaronesian archipelagos were all located in the same eutropical zone (Fig. 6A and D). This climatic uniformity over wide oceanic regions enhanced the range expansion of tropical marine species towards higher latitudes and gene flow between marine populations of the Macaronesian archipelagos. This is confirmed by the presence of several ecostratigraphic indicators (sensu Melo et al., 2022), namely the gastropod *T. coronatus* in the Azorean lower Pliocene fossil record (Ávila et al., 2016). During this time, the Mediterranean region and the West African coasts were also included in the eutropical climatic zone, their faunas reflecting this situation. Therefore, it is not possible to differentiate an autonomous Macaronesian marine biogeographic unit for that time interval.

The Piacenzian (Pliocene) – Gelasian (Pleistocene) Northern Hemisphere glaciations, from

3.6 Ma to 2.4 Ma (e.g., Mudelsee & Raymo, 2005), potentially related to the Pliocene shoaling of the Central American Seaway (O'Dea et al., 2016), had a noticeable impact in North Atlantic and Mediterranean SSTs (Bolton et al., 2010; Naafs et al., 2020). This is especially true during the mid-early Gelasian, when the lowest SSTs for the complete Piacenzian–Gelasian period occurred in the Western Mediterranean (Serrano, 2020). The coeval decrease of the oceanic water masses temperatures deeply impacted the distribution of thermophilic taxa, a well-documented phenomenon for the Mediterranean (Monegatti & Raffi, 2001) and the NE Atlantic façade (Silva & Landau, 2007; Silva et al., 2011).

As first shown by Ávila et al. (2008) and later expanded by Ávila et al. (2018, 2019), glacial episodes greatly impacted marine species richness, either through the reduction of SSTs and/or through eustatic lowering, which resulted in the reduction of the insular shelf area available around each island during glacial periods. Glaciations are thus periods during which extirpation rates, especially of thermophilic taxa, and even extinctions, are higher. As a result of their more northerly location, the Azores and Madeira archipelagos are expected to be more severely affected by glacial episodes than the southern Macaronesian archipelagos (i.e., Selvagens, Canaries, and Cabo Verde). This means that higher extirpation and extinction rates of species are expected in these insular systems. Furthermore, as proposed by Ávila et al. (2008, 2019), whenever mean sea level (msl) drops below the edge of the insular shelf, mobile sediments are lost to abyssal depths, leaving mobile sediment-dwelling species deprived of adequate habitats for continued survival.

Our data show that during the LIG, the Macaronesian archipelagos were distributed along two different climatic zones (paratropical and eutropical). Moreover, the faunal similarity analysis (Fig. 2) shows no signs of a close relationship among all the archipelagos, therefore being impossible to clearly differentiate an autonomous Macaronesian marine biogeographic unit.

The transition from the late Pleistocene to the Holocene (Greenlandian; sensu Cohen et al., 2020) is again marked by a large-scale glacial event (Clark et al., 2009) with msl falling ~120 m (Miller et al., 2011), thus falling below the edge of the insular shelf (Ávila et al., 2018). The Last Glacial Maximum (LGM) deeply affected the marine faunas of the Macaronesian archipelagos, especially those more to the north (Ávila et al., 2008, 2015a, 2018, 2019), causing high rates of extirpation (cf. Melo et al., 2022) and, probably, also extinction of endemic species (Ávila et al., 2019). Consequently, as also shown by Freitas et al. (2019) for present times, Macaronesia was not a coherent marine biogeographic unit during the LIG. Therefore, from a marine point of view, the term "Macaronesia" should be used with a strict geographic meaning only.

4.4. The Quaternary fossil record in the Macaronesia

Since the middle Pleistocene, only two intervals of time were warmer than the present-day interglacial: the MIS 11c (0.425 to 0.398 Ma; Tzedakis et al., 2012; Past Interglacials Working Group of PAGES, 2016) and the LIG (MIS 5e; Masson-Delmotte et al., 2010). Whereas records of MIS 5e are reported from most of the Macaronesian islands, fossiliferous sedimentary units undoubtedly attributed to the MIS 11c are known only from Gran Canaria and Lanzarote (Canary Islands *fide* Zazo et al., 2002; Montesinos et al., 2014; Muhs et al., 2014; Clauzel et al., 2020), and possibly from Santo Antão (Cabo Verde; Ramalho, 2011).
The lack of MIS 11 records from Santa Maria Island (Azores) has intrigued scientists for years. However, recent bathymetric data has contributed to explain this absence. By combining data from both submerged and raised marine terrace elevations, sea-level oscillations, and the isostatic behaviour of the island, Ricchi et al. (2018; cf. their Fig. 15) showed that under the slow uplift rates that the island experienced during the last ~2 Ma, marine terraces end up being occupied and eroded during several sea-level high-stands, meaning that the features we see today are the result of multi-generation. This leads to a situation in which MIS 5e marine terraces are generally built on top – and at the expense – of older terraces formed during the closest previous interglacials, such as MIS 9e (lower) and especially MIS 11c. As such, MIS 5e marine fossiliferous sediments are usually the only ones preserved above sea level, given that the records of previous interglacials have been largely eroded during subsequent interglacial episodes, especially during MIS 5e.
Despite this, doubts remain about the fossil assemblages, as some archipelagos are still poorly studied (e.g., Madeira, Selvagens and Cabo Verde), and several fossil assemblages need revision. Moreover, regarding some onshore fossiliferous outcrops, questions remain about whether these sites correspond to marine terraces or to high energy events such as tsunami deposits (Paris et al., 2018). The difficulty in accurately dating many of these deposits also adds to uncertainty, given that often it is not possible to confidently assert if a particular marine terrace deposit corresponds to MIS 5e or to MIS 11c, for example.

4.5. Ecological factors aside SSTs

Since most research has focused on SST oscillations (Meco et al., 2002; Zazo et al., 2010; Montesinos et al., 2014; Muhs et al., 2014; Maréchal et al., 2020), changes in ecological conditions occurring during the LIG and not directly related to temperature remain poorly understood. For example, the oyster *Saccostrea cuccullata* (Born, 1778) has a similar geographic distribution as *T. latus* for the Eastern Atlantic, thriving in brackish water environments – river mouths and estuaries – along the eastern Atlantic coasts of Africa, from Ghana to Angola (Dye, 1989). *Saccostrea cuccullata* is reported from MIS 11c of the Canary Islands (Montesinos et al., 2014) and from the Quaternary marine sediments from Cabo Verde

(Serralheiro, 1976), but no longer occurs in either of those archipelagos. Whereas the SST oscillations may explain the extirpation of this species from the Canary Islands, a similar explanation cannot be used for the Cabo Verde Archipelago.

5. CONCLUSIONS

Whereas today, from a phytobiogeographic point of view, Macaronesia might be a coherent terrestrial biogeographic unit that includes the Azores, Madeira, Selvagens, Canary Islands, and Cabo Verde archipelagos, a different situation occurs in the marine realm (Freitas et al., 2019), with the faunas of Cabo Verde clearly standing apart in a different biogeographic context. Ávila et al. (2016) dealt with this subject, and inferences were made for the biogeographic zonation of the Macaronesian geographic region during the Pliocene. The large time gap previously left unaccounted for is now partially filled, employing novel insights for the Late Pleistocene (LIG: 0.129 – 0.116 Ma). Based on the data presented and discussed herein, it may be concluded that:

- The Azores and Canary marine communities were the most susceptible to climatic changes, probably due to their proximity to climate zone boundaries (Fig. 6A, C);
- Until the mid-Pliocene, the Azores Archipelago, as well as its shallow marine faunas, were included within the same tropical climatic zone and in the same broad biogeographic unit of the remaining Macaronesian archipelagos (Fig. 6A), i.e., the Pliocene Mediterranean West-African Province. However, the coherence and uniformity of this very broad biogeographic unit was never tested, and this is a task that remains to be accomplished;
- During the LIG, the Canarian and Cabo Verdean marine faunas were part of the same tropical late Pleistocene Mediterranean West-African Province, as shown both by cluster analysis (Fig. 2B) and taxa provenance (cf. Melo et al., 2022); in contrast, the Azores, Madeira and Selvagens marine faunas were part of the subtropical late Pleistocene French-Iberian Province (Fig. 6B);
- A higher similarity existed between the marine molluscan faunas of the Canary Islands and Cabo Verde during the LIG, as shown by the cluster analysis restricted to the Macaronesian archipelagos (Fig. 7). This layout contrasts with the present-day situation;
- During the LIG, the northern limit of the tropical climatic zone was located closer to the Azores, Madeira, and Selvagens archipelagos than today, thus making possible a northwards range expansion among southern warm-water marine taxa;
- Based on data analysis from the pre-mid Pliocene, LIG, and present-day, we conclude

that, from a marine perspective, “Macaronesia” is not a coherent biogeographic concept and should not be treated as a biogeographic unit.

Finally, it is clear from this study that further research of past Quaternary interglacials is still needed, particularly in what concerns the MIS 11c interglacial, as necessary to reveal ecological conditions under which marine communities evolved in the Macaronesian archipelagos. The identification of onshore fossiliferous sediments deposited above present-day sea level during a glacial low stand as a result of coeval megatsunamis (e.g. Ramalho et al., 2015; Ávila, 2017; Paris et al., 2018; Costa et al., 2021, Madeira et al., 2020) may also help unlock some of the most enigmatic aspects of this puzzle.

To conclude, the type of long-term analysis utilized herein and tested for the Macaronesia geographical region is applicable to other geographical areas to better understand biogeographical relationships.

Author contribution:

CSM, CMS, SPA: Conceptualization, Methodology, Data curation, Writing - Original draft preparation; **DS, EMG, ER, AR, SM, LS, MEJ, ACR, LB, AV, RSR:** Methodology, Data curation, Writing- Reviewing and Editing. **SPA, RSR**: Funding. Authorship has been limited to those who contributed substantially to the work. All authors have read and agreed to the published version of the manuscript.

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M3.3.G/EXPEDIÇÕES CIENTÍFICAS/005/2022 and M3.3.G/EXPEDIÇÕES CIENTÍFICAS/004/2022 and M3.3.G/EXPEDIÇÕES CIENTÍFICAS/005/2022).

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TABLES AND FIGURES

Table 1. Publication effort of palaeontological studies related to the Macaronesian archipelagos.

Table 2. Number of specific taxa reported for the LIG (# spec. taxa) and genera (# genera) reported from each ecoregion. n.a. – not applicable. (*) Freitas et al. (2019) was followed in classifying the Madeira (MAD), Selvagens (SEL), and the Canaries (CAN) archipelagos as a single ecoregion, the “Webbnesia”; the remaining biogeographical classifications are in accordance with Spalding et al. (2007).

Table 3. Total number of gastropods and bivalves from the LIG and the present times in the assembled databases, total number of species/taxa present in the Macaronesian islands and number and percentage of amphi-Atlantic gastropods and bivalves. (*) Unpublished data taken from a large database on the shallow-water (<50 m depth) mollusc gastropods from the Atlantic Ocean and the Mediterranean Sea, curated by Sérgio Ávila. (‡) Unpublished data taken from a large database on the shallow-water (<100 m depth) mollusc bivalves from the Atlantic Ocean and the Mediterranean Sea, curated by Sérgio Ávila.

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Figure 2. Cluster analysis of the LIG gastropod and bivalve species, validated by Mantel statistics (Pearson). A – Gastropoda (Jaccard/UPGMA, cophenetic correlation = 0.961; B – Bivalvia (Jaccard/UPGMA, cophenetic correlation = 0.971). Realms and ecoregions according to Spalding et al. (2007). Bold numbers represent the statistically significant groups. Dotted cluster denotes a group not validated by Mantel statistics (Pearson). Underlined

acronyms refer to the Macaronesian archipelagos. Arctic biogeographic realm: HDC – Hudson Complex ecoregion; NGB – Northern Grand Banks – Southern Labrador ecoregion. Temperate Northern Atlantic biogeographic realm: AZO – Azores ecoregion; CAN – Canary Islands; CAR – Carolinian ecoregion; GOM – Gulf of Maine/Bay of Fundy ecoregion; GSL – Gulf of St. Lawrence – Eastern Scotian Shelf ecoregion; IOS – Ionian Sea ecoregion; LES – Levantine Sea ecoregion; MAD – Madeira archipelago; SAU – Saharan Upwelling ecoregion; VIR – Virginian ecoregion; WEM – Western Mediterranean ecoregion. Tropical Atlantic biogeographic realm: CAB – Cabo Verde archipelago; FLO – Floridian ecoregion. Temperate South America biogeographic realm: NPG – North Patagonian Gulfs ecoregion; RIG – Rio Grande ecoregion; RIP – Rio de la Plata ecoregion; UBS – Uruguay-Buenos Aires Shelf ecoregion. Macaronesian archipelagos are underlined. For further information, please refer to Table 2.

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Figure 5. Present-day annual mean sea surface temperatures (SSTs in ºC) recorded from the North Atlantic Ocean. White numbers represent the SSTs for the specific isotherm. Highlighted are the Macaronesian archipelagos. Background digital elevation model generated from GEBCO 2020 (https://www.gebco.net/data_and_products/gridded_bathymetry_data/). Delimitation of the landmasses from the Portuguese Hydrographic Institute free data (https://www.hidrografico.pt/op/33). Mean Sea Surface Temperatures from COBE-SST2 data provided by the NOAA/OAR/ESRL PSL, (Hirahara et al., 2014: https://psl.noaa.gov/data/gridded/data.cobe2.html).

Figure 6. A–C: General view and E–F: detailed view of the NE Atlantic Biogeographic Molluscan Provinces from the Early Pliocene (A and D, 5.333–3.3 Ma), Late Pleistocene/LIG (B and E, 0.129–0.116 Ma) and the present (C and F), modified from Raffi et al. (1985), Monegatti & Raffi (2007), Silva & Landau (2007), Silva et al. (2011), and Ávila et al. (2016).

The names attributed to the biogeographical units follow the International Code of Area Nomenclature, as defined by Ebach et al. (2008). Climatic and (palaeo)biogeographical units after Hall (1964), Raffi et al. (1985), Landau et al. (2007), Monegatti & Raffi (2007), Silva & Landau (2007), Silva et al. (2011) and Ávila et al. (2016). Note the shift in the transition zones between the biogeographic molluscan provinces from the Pliocene to the present times. During the Late Pleistocene LIG (B and E) the transition zone between the tropical (LPMWAP) and subtropical (LPFIP) biogeographical provinces is remarkably different from its present location (C and F).

Figure 7. Dendrograms depicting the results of the cluster analysis for gastropod (A; Ochiai/UPGMA, cophenetic correlation = 0.928) and bivalve (B; Jaccard/UPGMA, cophenetic correlation = 0.915) species from the LIG of the Macaronesian archipelagos, validated by Mantel statistics (Pearson). Small size numbers correspond to the bootstrap values providing support for each tree node (100 repetitions of 100 trees). Bold numbers represent the statistically significant groups. Selvagens Archipelago (SEL) was not included in the case of the bivalves due to the low number of reports – just two specific taxa (cf. Table 2).

Table 1. Publication effort of palaeontological studies related to the Macaronesian archipelagos.

Archipelago	Number of studies
Azores	24
Madeira	5
Selvagens	1
Canary Islands	66
Cabo Verde	18

Table 2. Number of specific taxa reported for the LIG (# spec. taxa) and genera (# genera) reported from each ecoregion. n.a. – not applicable. (*) Freitas et al. (2019) was followed in classifying the Madeira (MAD), Selvagens (SEL), and the Canaries (CAN) archipelagos as a single ecoregion, the "Webbnesia"; the remaining biogeographical classifications are in accordance with Spalding et al. (2007).

				Gastropoda		Bivalvia	
Biogeographic Realms	**Province**	**Ecoregion**	**Acronym**	**# spec. taxa**	**# genera**	**# spec. taxa**	**# genera**
Arctic	n.a.	Hudson Complex	HDC	24	18	24	17
		Northern Grand Banks - Southern Labrador	NGB	8	7	17	15
		West Greenland Shelf	WGS	n.a.	n.a.	1	1
Temperate Northern Atlantic	Cold Temperate Northwest Atlantic	Gulf of St. Lawrence - Eastern Scotian Shelf	GSL	40	28	28	22
		Gulf of Maine-Bay of Fundy	GOM	34	22	61	43
		Virginian	VIR	73	55	100	82
	Warm Temperate Northwest Atlantic	Carolinian	CAR	74	54	96	83
		Northern Gulf of Mexico	NGM	n.a.	n.a.	10	10
	Lusitanian	Azores	AZO	113	80	24	23
		Webbnesia	MAD (*)	54	45	29	22
			SEL (*)	17	14	2	2
			CAN (*)	190	124	79	53
		Saharan Upwelling	SAU	44	39	42	32
	Mediterranean Sea	Tunisian Plateau-Gulf of Sidra	TUP	6	6	9	9
		Ionian Sea	IOS	197	112	96	80
		Levantine Sea	LES	21	20	17	15
		Western Mediterranean	WEM	219	133	97	79
Tropical Atlantic	West African Transition	Cabo Verde	CAB	53	45	30	26
	Tropical Northwestern Atlantic	Bermuda	BER	12	12	10	10
		Floridian	FLO	n.a.	n.a.	14	14
Temperate South America	Warm Temperate	Rio Grande	RIG	12	10	25	21

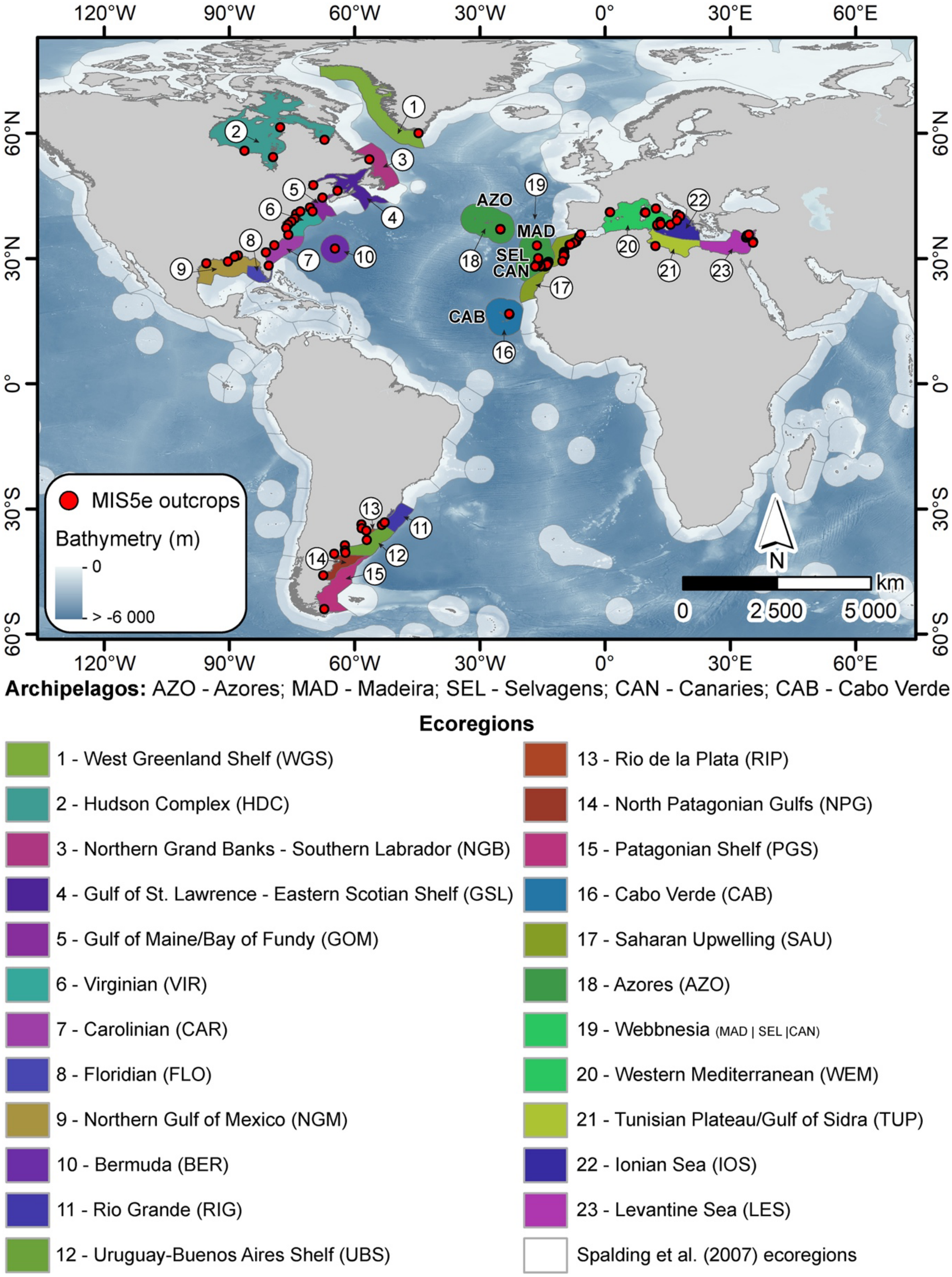
	Southwestern Atlantic	Rio de la Plata	RIP	23	23	39	35
		Uruguay-Buenos Aires Shelf	UBS	29	25	60	53
	Magellanic	North Patagonian Gulfs	NPG	26	20	11	11
		Patagonian Shelf	PGS	2	2	3	3
			TOTAL	**759**	**308**	**439**	**249**

Table 3. Total number of gastropods and bivalves from the LIG and the present times in the assembled databases, total number of species/taxa present in the Macaronesian islands and number and percentage of amphi-Atlantic gastropods and bivalves. (*) Unpublished data taken from a large database on the shallow-water (<50 m depth) mollusc gastropods from the Atlantic Ocean and the Mediterranean Sea, curated by Sérgio Ávila. (‡) Unpublished data taken from a large database on the shallow-water (<100 m depth) mollusc bivalves from the Atlantic Ocean and the Mediterranean Sea, curated by Sérgio Ávila.

		TOTAL database	**Total Macaronesian archipelagos**	**Amphi-Atlantic**	**% Amphi-Atlantic**
LIG	Gastropoda	759	319	12	1.58
	Bivalvia	439	105	4	0.91
Present	Gastropoda	3,609 (*)	896 (*)	141 (*)	3.91 (*)
	Bivalvia	1,680 (‡)	328 (‡)	118 (‡)	7.02 (‡)

Table 4. List of the most speciose LIG genera of gastropods and bivalves reported from the Atlantic Ocean and the Mediterranean Sea.

Class	**Genus**	**Number of species**
Gastropoda	*Alvania*	31
Gastropoda	*Turbonilla*	21
Gastropoda	*Conus*	18
Gastropoda	*Rissoa*, *Tritia*	13
Gastropoda	*Patella*	12
Gastropoda	*Odostomia*	11
Gastropoda	*Gibbula*, *Mitrella*	9
Gastropoda	*Crepidula, Cerithiopsis, Epitonium, Euspira, Mangelia, Phorcus*	8
Gastropoda	*Buccinum, Cerithium, Chauvetia, Monoplex, Retusa, Steromphala*	7
Gastropoda	*Bittium, Diodora, Caecum, Calliostoma, Fissurella, Jujubinus*	6
Bivalvia	*Astarte, Glycymeris*	9
Bivalvia	*Anadara, Musculus*	7
Bivalvia	*Abra, Donax, Mactra, Nucula, Pandora*	6



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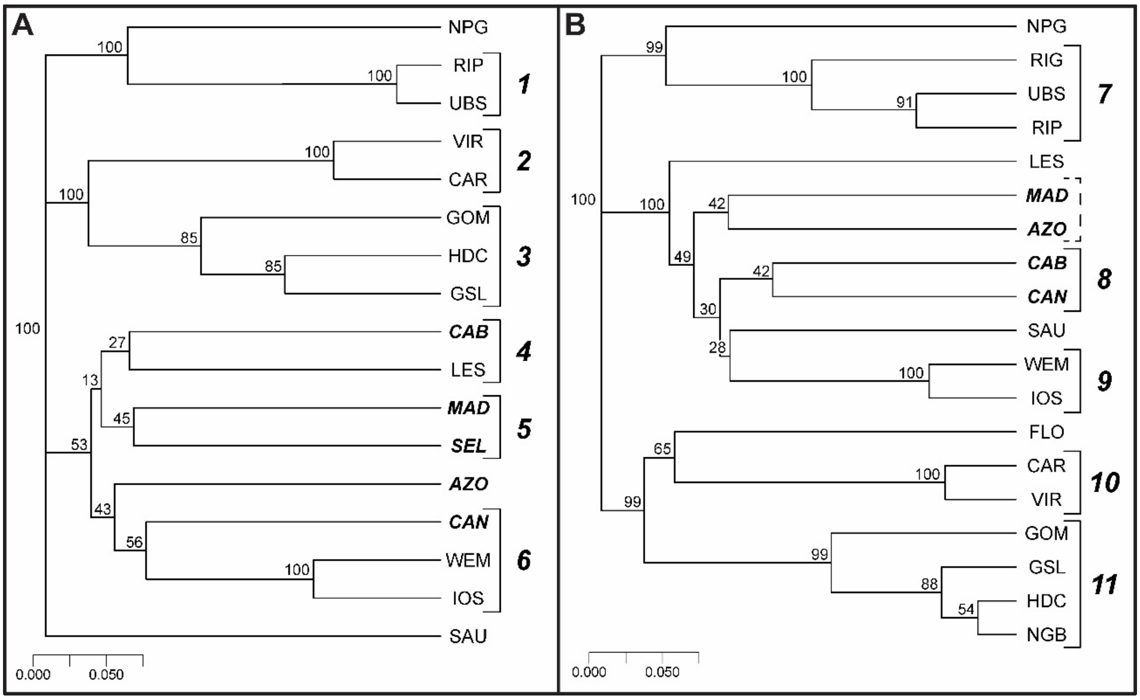

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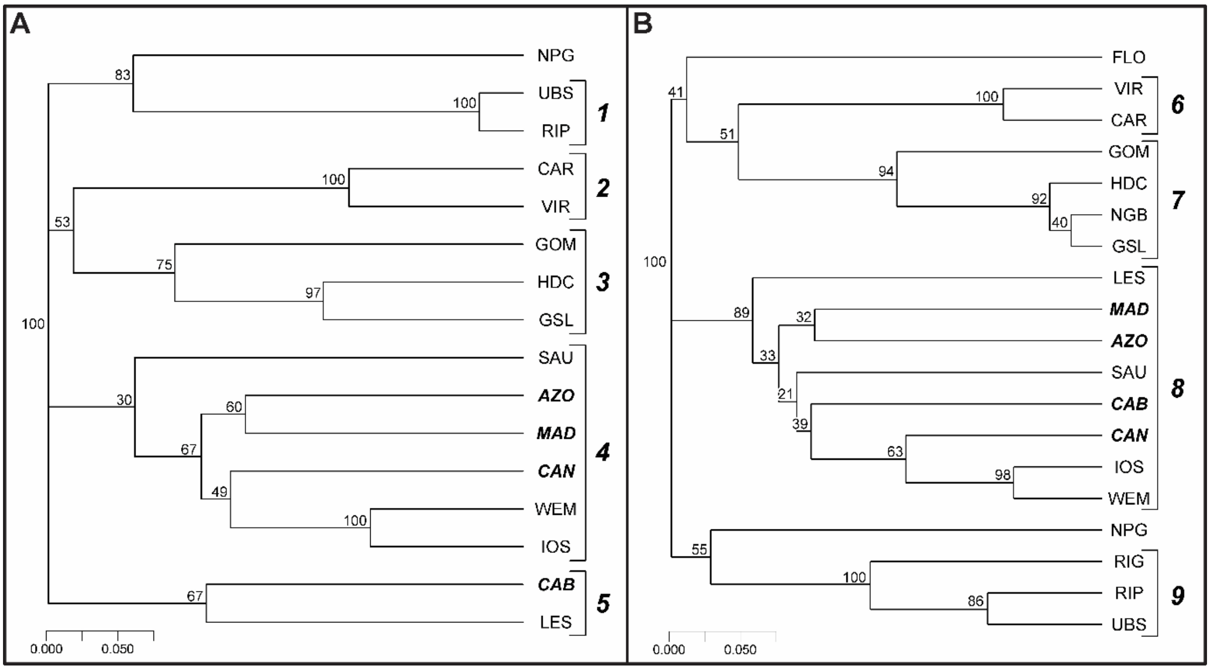

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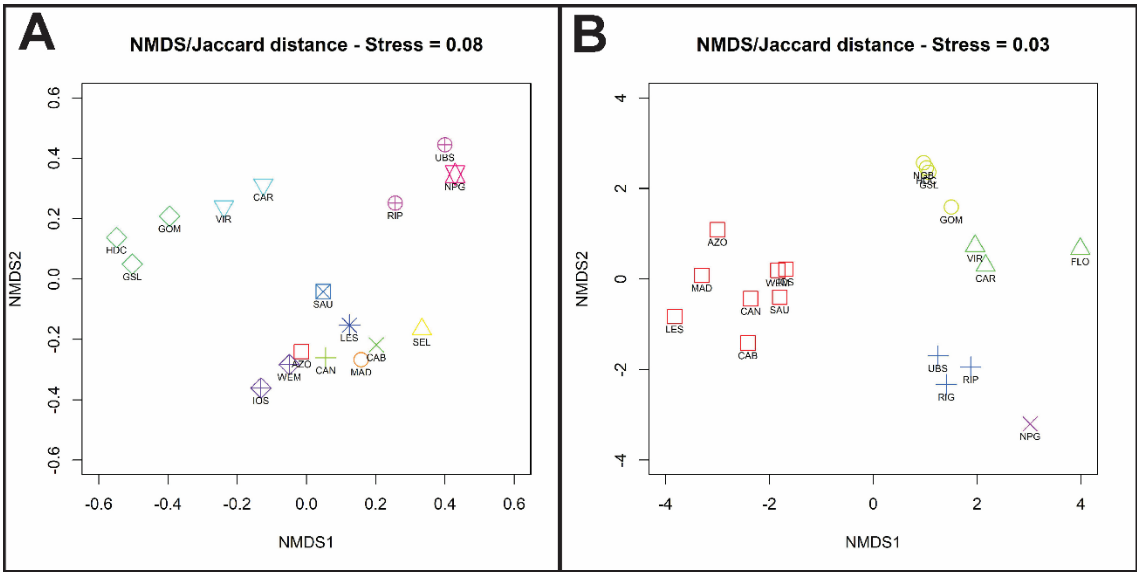


Figure 4. Nonmetric multidimensional scaling (NMDS) groups plots in the NMDS space in accordance with the cluster analyses output (see Fig. 2). A – Gastropoda; B – Bivalvia.

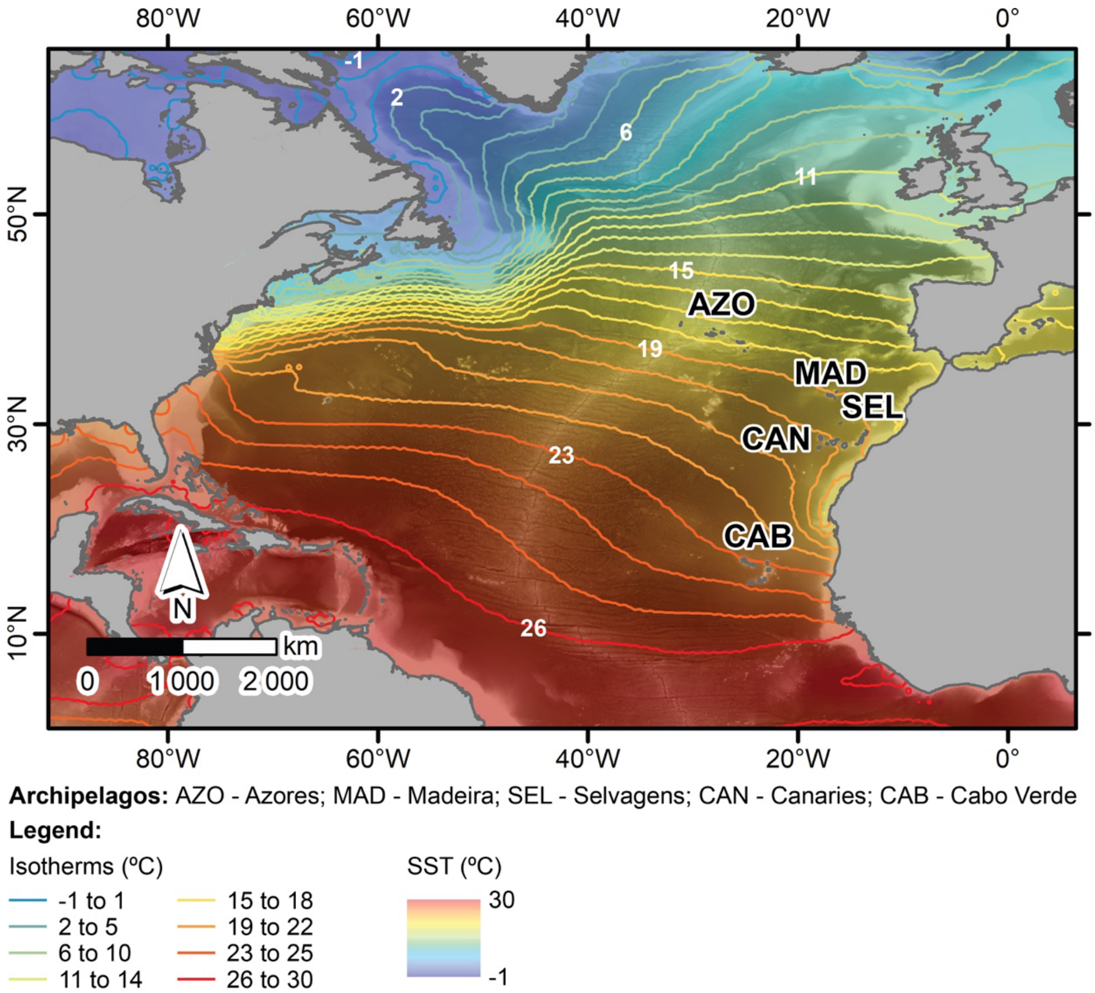
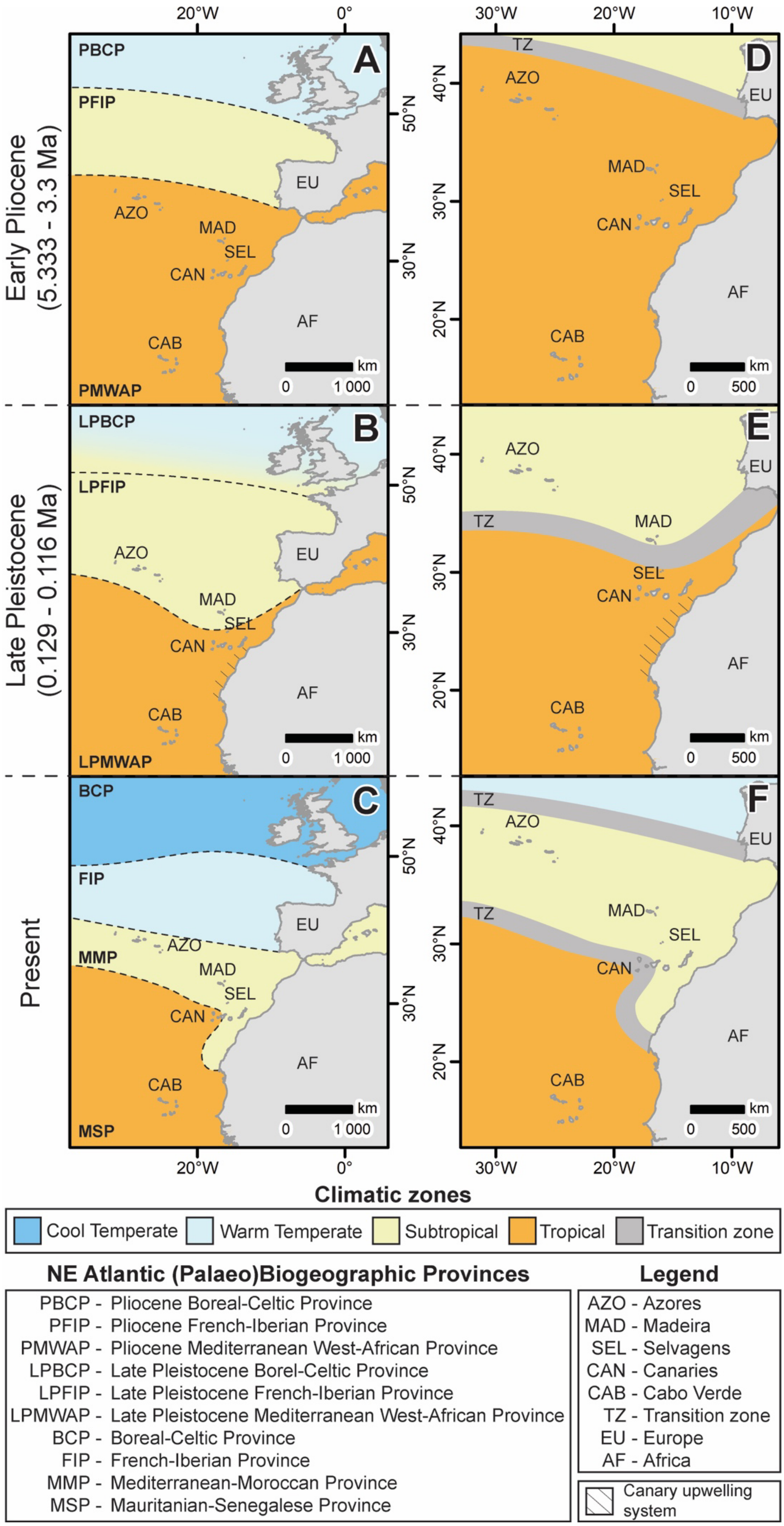


Figure 5. Present-day annual mean sea surface temperatures (SSTs in ºC) recorded from the North Atlantic Ocean. White numbers represent the SSTs for the specific isotherm. Highlighted are the Macaronesian archipelagos. Background digital elevation model generated from GEBCO 2020 (https://www.gebco.net/data_and_products/gridded_bathymetry_data/). Delimitation of the landmasses from the Portuguese Hydrographic Institute free data (https://www.hidrografico.pt/op/33). Mean Sea Surface Temperatures from COBE-SST2 data provided by the NOAA/OAR/ESRL PSL, (Hirahara et al., 2014: https://psl.noaa.gov/data/gridded/data.cobe2.html).



20°W
0°
30°W
20°W
10°W
Early Pliocene (5.333 - 3.3 Ma)
Late Pleistocene (0.129 - 0.116 Ma)
Present
A
PBCP
PFIP
PMWAP
EU
AZO
MAD
SEL
CAN
CAB
AF
50°N
30°N
km
0 1 000
B
LPBCP
LPFIP
LPMWAP
C
BCP
FIP
MMP
MSP
D
TZ
E
F
40°N
30°N
20°N
0 500
Climatic zones
Cool Temperate
Warm Temperate
Subtropical
Tropical
Transition zone
NE Atlantic (Palaeo)Biogeographic Provinces
PBCP - Pliocene Boreal-Celtic Province
PFIP - Pliocene French-Iberian Province
PMWAP - Pliocene Mediterranean West-African Province
LPBCP - Late Pleistocene Borel-Celtic Province
LPFIP - Late Pleistocene French-Iberian Province
LPMWAP - Late Pleistocene Mediterranean West-African Province
BCP - Boreal-Celtic Province
FIP - French-Iberian Province
MMP - Mediterranean-Moroccan Province
MSP - Mauritanian-Senegalese Province
Legend
AZO - Azores
MAD - Madeira
SEL - Selvagens
CAN - Canaries
CAB - Cabo Verde
TZ - Transition zone
EU - Europe
AF - Africa
Canary upwelling system

Figure 6. A–C: General view and E–F: detailed view of the NE Atlantic Biogeographic Molluscan Provinces from the Early Pliocene (A and D, 5.333–3.3 Ma), Late Pleistocene/LIG (B and E, 0.129–0.116 Ma) and the present (C and F), modified from Raffi et al. (1985), Monegatti & Raffi (2007), Silva & Landau (2007), Silva et al. (2011), and Ávila et al. (2016). The names attributed to the biogeographical units follow the International Code of Area Nomenclature, as defined by Ebach et al. (2008). Climatic and (palaeo)biogeographical units after Hall (1964), Raffi et al. (1985), Landau et al. (2007), Monegatti & Raffi (2007), Silva & Landau (2007), Silva et al. (2011) and Ávila et al. (2016). Note the shift in the transition zones between the biogeographic molluscan provinces from the Pliocene to the present times. During the Late Pleistocene LIG (B and E) the transition zone between the tropical (LPMWAP) and subtropical (LPFIP) biogeographical provinces is remarkably different from its present location (C and F).

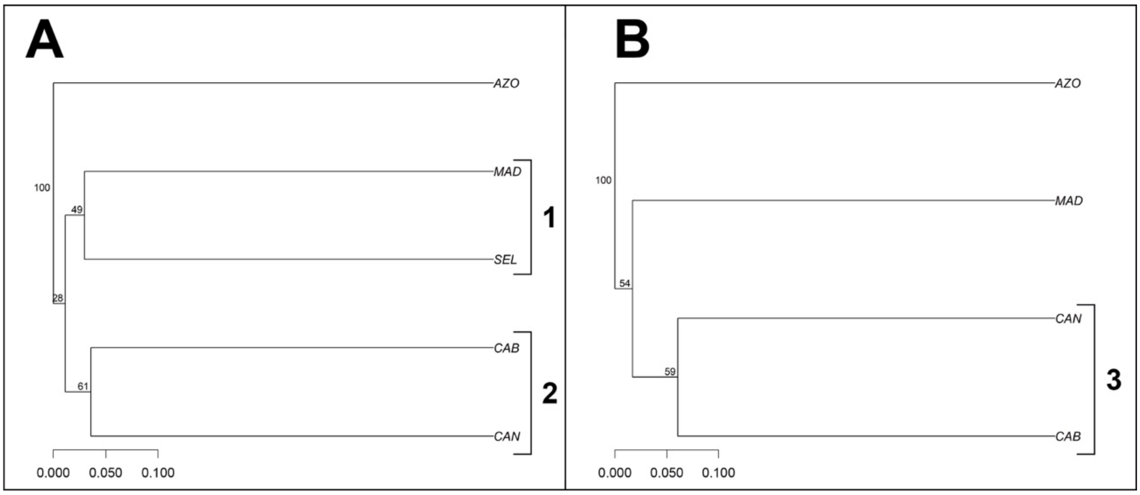


Figure 7. Dendrograms depicting the results of the cluster analysis for gastropod (A; Ochiai/UPGMA, cophenetic correlation = 0.928) and bivalve (B; Jaccard/UPGMA, cophenetic correlation = 0.915) species from the LIG of the Macaronesian archipelagos, validated by Mantel statistics (Pearson). Small size numbers correspond to the bootstrap values providing support for each tree node (100 repetitions of 100 trees). Bold numbers represent the statistically significant groups. Selvagens Archipelago (SEL) was not included in the case of the bivalves due to the low number of reports – just two specific taxa (cf. Table 2).