



Megatsunami deposits and range expansion of cold-temperate marine species towards the tropics in glacial times

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Abstract

Over geological time, glacial-interglacial cycles affected the geographical range of marine species. Typically, this has been documented by tracking the long-distance dispersal of tropical, shallow-water mollusc species in archipelagos during the last phase of glacial terminations or the early phase of an interglacial episode. Many studies conducted in the Macaronesian archipelagos (i.e., the Azores, Madeira, Selvagens, Canaries and Cabo Verde) support this view. To date, however, such studies exclude data from full glacial periods, owing to difficulties in accessing the geological record of lower sea-level glacial episodes. Here we demonstrate, for the first time, the range expansion into the tropics of cold-water/temperate species during two glacial episodes (MIS 4 and MIS 6), using the Macaronesian region as a case study. For that, we innovate by using megatsunami deposits to unveil biogeographic processes and patterns noticed in the conglomerates of Tarrafal (Santiago Island, Cabo Verde) and of Teno Bajo (Tenerife, Canary Islands), which are interpreted to have been emplaced by megatsunamis triggered by volcanic flank collapses occurred at ~68 ka (MIS 4) and

~170 ka (MIS 6), respectively. Our results detect that not only latitudinal, long-distance dispersal of marine molluscs occurred toward the tropics (mainly between archipelagos, and between European and African shores towards the Macaronesian archipelagos), but also longitudinal range expansion. Moreover, both MIS 4 and MIS 6 megatsunami deposits yielded a high biodiversity (expressed both by species richness and diversity indices) when compared with raised beach sediments. This new finding must be added to the distinctive sedimentological and textural characteristics of tsunami deposits. Finally, we demonstrate that four mollusc species reported from the Teno glacial MIS 6 tsunami deposits, and several temperate and sub-tropical bivalve and gastropod species reported from the Tarrafal glacial MIS 4 tsunami deposits spread to the Canaries and Cabo Verde, respectively, establishing viable populations in those archipelagos. Thus, these species provide evidence of geographical range expansion of marine species from mid-latitudes to low latitudes by means of long-distance, equatorward dispersal of benthic, shallow-, cold-water/temperate marine molluscs between archipelagos and from continental shores to oceanic islands during glacial periods.

Highlights

- Megatsunami deposits are used to unveil biogeographic patterns and processes in the Macaronesian archipelagos.
- Megatsunami deposits record the geographical range expansion of cold-water/temperate species towards the tropics during glacial times.
- Our data demonstrates both latitudinal and longitudinal range shifts of marine molluscs, by means of long-distance dispersal.
- Both MIS 4 and MIS 6 megatsunami deposits analysed yielded a high biodiversity when compared with MIS 5e raised beach sediments.
- A high biodiversity (expressed both by species richness and diversity indices) is a new finding to characterize the distinctive sedimentological and textural characteristics of tsunami deposits.

Keywords

Cabo Verde, Canaries, glacial periods, marine molluscs, Megatsunami deposits, MIS 4, MIS 6, oceanic islands, palaeobiogeography

Introduction

The island biogeography equilibrium theory (MacArthur and Wilson 1963, 1967) and its subsequent advances (Whittaker et al. 2008, 2010; Triantis et al. 2012; Fernández-Palacios et al. 2016) generally has lacked a marine point of view, a situation that changed with topical efforts by Ávila et al. (2009a, 2016a, 2018, 2019), Hachich et al. (2015, 2016, 2020) and Pinheiro et al. (2017). Thus, the understanding of biogeographic patterns and processes of long-distance dispersal in marine species among oceanic archipelagos, and between continental shores and archipelagos, is crucial for extending island-biodiversity evolution to marine ecosystems (Trakhtenbrot et al. 2005; d'Aloia et al. 2015). Ávila et al. (2019) were the first to explore in detail the impact of glacial periods on shallow-water marine species. Their Sea Level Sensitive dynamic model of marine island biogeography put forward several predictions that can be tested on the effects of such glacial episodes. Due to the reduction of the insular shelf area available around islands during glacial periods, and for geotectonically stable or subsiding islands, it was proposed that: (1) extinction rates and extinction debts are higher during glacials in comparison with interglacials; (2) the extirpation rates of thermophilic species and shallow-water species associated with soft sediments will be higher during glacials in comparison with interglacials; (3) the extinction of endemic species will be higher during glacials;

and (4) the rates of speciation will be lower during glacial episodes and higher during interglacials. However, only recently, fossiliferous megatsunami deposits emplaced during glacial periods became available to study.

Global climate changes influence the expansion and contraction of the geographical range distribution of species through different dispersal processes, constituting a common and well-studied biogeographic process, especially in the terrestrial realm (Channell and Lomolino 2000; Gaston 2003; Huang et al. 2023). This scenario is known as the “interglacial expansion hypothesis” (Qian and Ricklefs 2000) or the “expansion-contraction model” (Hofreiter and Stewart 2009), and many examples are known, such as arctic-alpine species like *Dryas integrifolia* Vahl (Tremblay and Schoen 1999) or plant species distributed in low latitudes of eastern Asia, such as *Pinus armandii* Franch. (Liu et al. 2022). For terrestrial taxa, records for both fossil and extant species document poleward shifts stemming from the range expansion of tropical species during interglacial times in addition to the simultaneous range contraction of temperate species (Clark et al. 1999; Jackson and Blois 2015). Similarly, for extant marine species, the geographical range contraction of benthic, shallow-, temperate/cold-water species to higher latitudes (and/or to deeper waters) are also documented as a result of the current global warming (Hiddink et al. 2015), as well as the range expansion of benthic, warm-water species to higher latitudes (Perry et al. 2005; Lima et al. 2007; Ling et al. 2009; Baptista et al. 2021). The fossil record from volcanic oceanic islands also attests to the range expansion of benthic, tropical, shallow-water marine molluscs towards higher latitudes during interglacials through long-distance dispersal (García-Talavera et al. 1978; Meco et al. 2002; Cabero et al. 2013; Ávila et al. 2015; Martín-González et al. 2016; Melo et al. 2022a, b), as well as the range contraction of thermophilic species (with associated local disappearances from some archipelagos) during the Pliocene and Pleistocene climatic cooling (Landau et al. 2007; Ávila et al. 2016b). Planktonic marine species (e.g., foraminifera) are commonly used to reconstruct past sea-surface temperatures (Kucera et al. 2005). These authors have also demonstrated an equatorward (i.e., a latitudinal geographical range expansion of cold-water/temperate planktonic species/morphs towards the tropics) during glacial episodes. These phenomena also relate to range expansions of tropical planktonic species/morphs towards higher latitudes during interglacials (Pailler and Bard 2002; Alessandro et al. 2018, and references therein).

In contrast, few studies have considered the theoretical expected range expansion of benthic-, shallow-, cold-water/temperate marine species towards the tropics during glacial episodes, the most relevant being those by Paulus (1950), Mars (1958), Froget et al. (1972), Malatesta and Zarlenga (1986), Raffi (1986), Di Geronimo et al. (2000), and more recently, Urrea et al. (2023). These authors focused on the Mediterranean area and reported on Atlantic “Northern Guests”, also known as “Boreal Guests” (BG), i.e., cold-water marine molluscs whose geographic

ranges expanded towards lower latitudes, with Atlantic individuals entering and establishing viable populations in the Mediterranean, during glacial episodes; these species have thus important palaeoclimatic significance. Taviani et al. (1991) is among the only studies that deal with the geographic range expansion of BG molluscs along the Atlantic coasts of Europe. However, BG are hard to access either because they are usually deposited under several tens or even hundreds of meters of seawater (e.g., 150–350 m depth; Mars 1958), and/or such deposits are seldom preserved on account of erosion by rising sea levels during the subsequent interglacial episode (Ávila et al. 2022). Exceptions may occur when littoral deposits formed during glacial episodes have been raised by later tectonic or isostatic coastal uplift. However, few places experience uplift rates high enough to exceed the rate of local sea-level rise to preserve such a deposit (Peltier 2004; Seppä et al. 2012). We herein innovate by using glacial-age megatsunami deposits from the Macaronesian islands to infer range shift patterns of littoral marine molluscs during glacial periods, by means of long-distance dispersal.

Massive gravitational flank failures of volcanic island edifices, although infrequent at short geological timescales, may involve considerable volumes of collapsed material, on the order of tens to hundreds of km³ (e.g. Holcomb and Searle 1991; Carracedo 1999; Day et al. 1999; Masson et al. 2002, 2008). As they typically occur catastrophically, they often trigger megatsunamis (sensu Goff et al. 2014) with initial wave magnitudes of hundreds of meters (e.g. Moore and Moore 1984; McMurtry et al. 2004a; Giachetti et al. 2011; Abadie et al. 2012; Ramalho et al. 2015; Paris et al. 2017). These giant waves are capable of inundating near-source coastlines up to several kilometres inland and hundreds of meters in elevation. Megatsunami deposits attesting to such extreme inundations have been documented on several volcanic archipelagos, namely the Hawaiian Islands (Moore and Moore 1984; Moore 2000; McMurtry et al. 2004a, b), the Canary Islands (Hürlimann et al. 2004; Pérez-Torrado et al. 2006; Ferrer et al. 2013; Paris et al. 2017), and the Cabo Verde Archipelago (Paris et al. 2011, 2018; Ramalho et al. 2015; Madeira et al. 2020; Costa et al. 2021). Hence, large tsunami events occurring during glacial periods and able to transport large amounts of marine sediment onshore, away from the erosive action of interglacial high sea levels, represent a geological process providing access to unique glacial fossil assemblages of benthic, shallow-water marine species, otherwise inaccessible.

This study focuses on the very rich fossiliferous sediments deposited during glacial periods by the impact of two megatsunamis: the conglomerates of Tarrafal (Santiago Island, Cabo Verde), and Teno Bajo (Tenerife, Canary Islands). Critically, the Tarrafal conglomerates are here documented in detail for the first time in regard to species composition and palaeobiogeographic relationships. These sediments were deposited by a megatsunami triggered by the flank collapse of the neighbouring Fogo Island (Day et al. 1999), at approximately 68 ka

(Cornu et al. 2021), and with an estimated run-up height of 270 m (Ramalho et al. 2015). A preliminary analysis by Paris et al. (2011) revealed the presence of three species of corals, calcareous algae, molluscs (three species of gastropods and at least four species of bivalves) and skeletons of Bryozoan zooids. None of the specimens were found in original growth positions. According to Paris et al. (2011), the conglomerates represent at least, two main tsunami waves that transported sediments both during inflow and outflow. A minor role is attributed to the impact of the following waves (whose effects were probably limited to a surface reworking of the deposits), as a result of their smaller amplitude and of the decreasing amount of sediment still available offshore. Paris et al. (2011) also noticed that the marine fauna of the Tarrafal conglomerate was different from the present-day and Last Interglacial deposits from Sal and Boavista Islands (Zazo et al. 2007). However, this observation was not further substantiated.

In the Canaries Archipelago, fossiliferous conglomerates in the Teno massif, northwestern Tenerife, were also interpreted as the result of megatsunamis (Ferrer et al. 2013; Paris et al. 2017). Paris et al. (2017) reported 85 gastropod taxa, 31 bivalves, six corals, and one scaphopod species, representing a high biodiversity and a mixing of faunas from different environments (infra-circalittoral fauna being dominant).

The fossiliferous sediments of these two megatsunami events were deposited during glacial periods [the Tarrafal deposits been dated 65–84 ka (Ramalho et al. 2015) and attributed to the flank collapse of nearby Fogo volcano, which probably took place at ca. 68 ka (Cornu et al. 2021), whereas the Teno deposits result from a flank collapse dated of ca. 170 ka (Coello-Bravo et al. 2014)], with similar coeval sea level at about 80 m below present sea level in both cases (Miller et al. 2011). Critically, both events resulted in deposits emplaced several tens of meters above Holocene sea level, ensuring their preservation. Thus, both deposits provide an exceptional opportunity to test the hypothesis of equatorward geographical range expansions of benthic, temperate/subtropical, shallow-water marine species during glacial episodes in an insular environment.

Accordingly, this study aims to: 1) screen the tsunami sediments to identify any cold-water/temperate marine molluscan species/assemblages preserved therein; 2) investigate their palaeoclimatic significance, based on their present geographical range and biogeographical patterns; 3) compare the glacial Marine Isotope Stage 4 (MIS 4, i.e., the period between 57 and 71 ka) molluscan fauna of the Tarrafal megatsunami deposit with the recent and the Last Interglacial fauna of Cabo Verde; 4) compare the glacial Marine Isotope Stage 6 (MIS 6, i.e., the period between 130 and 191 ka ago) molluscan fauna of the Teno megatsunami deposit with the recent and the Last Interglacial fauna of Canary Islands; and 5) test and draw conclusions on the theoretically expected equatorward geographical range expansion of benthic, shallow-, cold-water/temperate marine species during glacial episodes.

Geological setting

Cabo Verde Archipelago

The Cabo Verde Archipelago is located in the tropical Central Atlantic, between 15° and 18°N, and approximately 555–870 km west of mainland Africa. It incorporates 10 main islands arranged in a semi-arc open to the west, the origins of which resulted from long-term mid-plate volcanism associated with the Cabo Verde hotspot (Holm et al. 2008; Ramalho et al. 2010a, b; Ramalho 2011). Although volcanism dates back to 18–26 Ma on the eastern islands of Sal, Boavista and Maio, most of the other islands emerged in the last 2–7 Ma (Plesner et al. 2002; Torres et al. 2002; Duprat et al. 2007; Holm et al. 2008; Ancochea et al. 2010, 2012; Dyhr and Holm 2010; Madeira et al. 2010; Ramalho et al. 2010c). Quaternary volcanism is reported from several islands, but historical volcanism only occurred on Fogo.

Fogo is one of the most active and prominent oceanic volcanoes featuring an eruption every ~20 years, on

average, for the last ~500 years (Mata et al. 2017). Standing over 7 km above the surrounding seafloor, Fogo volcano experienced a massive gravitational flank failure, which displaced a volume in the order of 110–130 km³ into the sea (Masson et al. 2008; Martínez-Moreno et al. 2018; Barrett et al. 2020) and triggered a megatsunami that impacted the neighbouring islands of Santiago, located just 65 km offshore from the collapse site (Paris et al. 2011; Ramalho et al. 2015; Fig. 1), and Maio (Madeira et al. 2020). Tsunami deposits located on northern Santiago, near Tarrafal, document the impact of this tsunami and suggest a minimum run-up of 270 m above coeval sea level. Based on cosmogenic ³He geochronology on stranded megaclasts transported by the Fogo collapse-generated tsunami, Ramalho et al. (2015) suggested a depositional age interval between 65 and 84 ka (mean age ~73 ka), whereas Cornu et al. (2021) suggested an age of ~68 ka based on K-Ar (69±2 ka) and on ⁴⁰Ar/³⁹Ar (66.9±8.3 ka) geochronology of the volcanic sequences at the source, respectively pre- and post-collapse. Therefore, this last age indicates that Fogo's

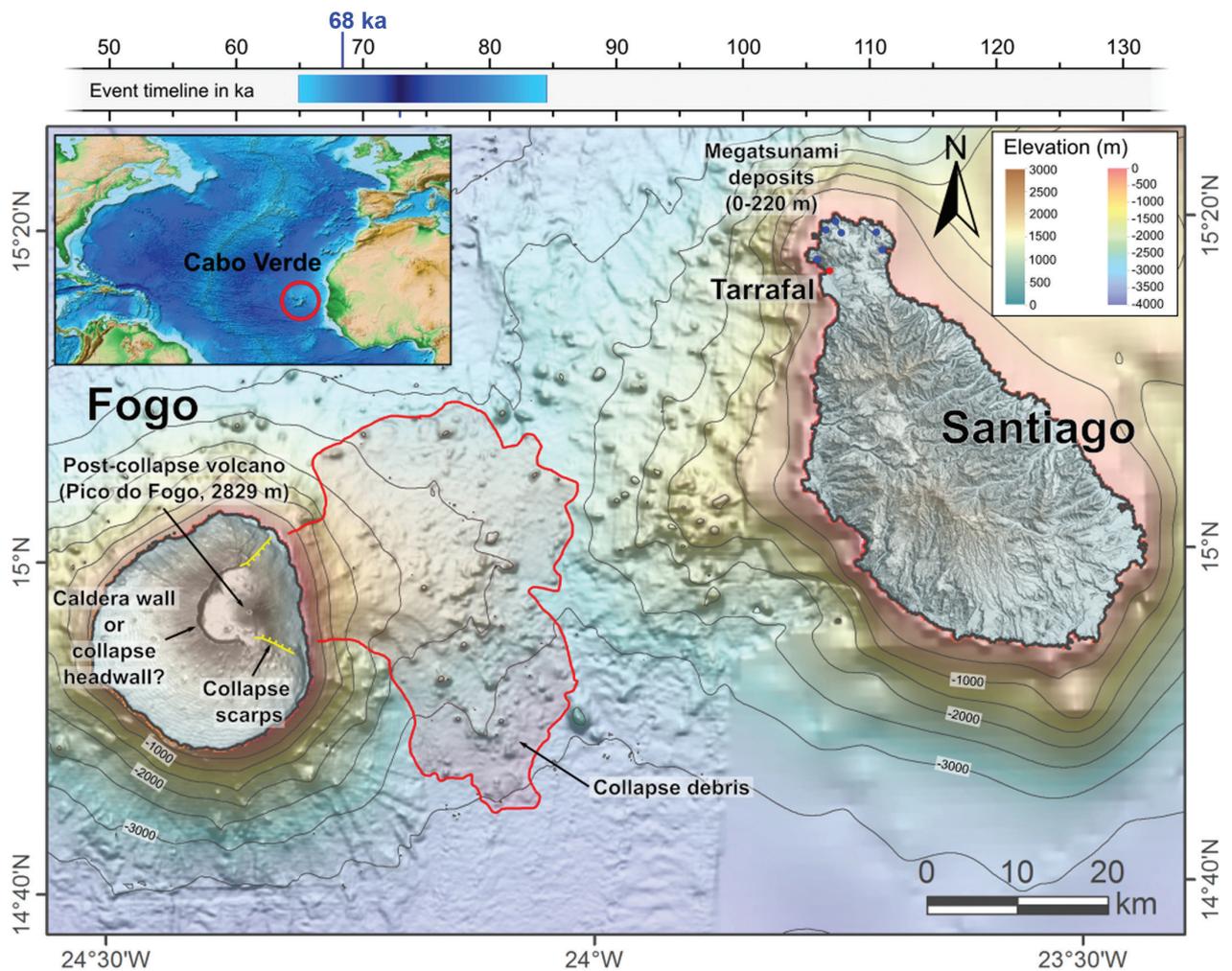


Figure 1. Location of Cabo Verde Archipelago in the Atlantic Ocean (insert). Map of Fogo and Santiago Islands and the surrounding seafloor (modified from Ramalho et al. 2015). The area in red corresponds to the avalanche debris field that attests to Fogo's tsunamigenic flank collapse (Masson et al. 2008). Tarrafal (red dot) is located NW of Santiago Island. The blue dots represent the location of contemporaneous tsunami deposits reported by Ramalho et al. (2015). The event timeline at the top shows the depositional age interval for Santiago's tsunami deposits, based on surface exposure dating of tsunami megaclasts by Ramalho et al. (2015) and on K-Ar and ⁴⁰Ar/³⁹Ar of volcanic sequences at Fogo by Cornu et al. (2021), indicating the most probable age of ca. 68 ka.

megatsunami occurred during MIS 4, a glacial seastand, when, according to Miller et al. (2011), the coeval sea level was about 80 m lower than present-day sea level.

Megatsunami deposits from northern Santiago Island (Cabo Verde Archipelago) are characterized by fields of stranded boulders and chaotic conglomerates left on the slopes of the island up to 220 m in elevation (Ramalho et al. 2015; Madeira et al. 2017; Ramalho et al. 2017). One of the best exposures is found north of Tarrafal beach, at elevations between 6.5 and 20 m above present sea level (a.p.s.l.), consisting of a slightly calcretised fossiliferous conglomerate with a maximum lateral extension of about 50 m (for a detailed description see Paris et al. 2011). At Tarrafal, these tsunami deposits correspond to 3 to 5 layers, up to 4 m thick, of poorly-stratified to non-stratified chaotic conglomerates having variable amounts of coarse biogenic sand matrix (Fig. 2). The conglomerates are generally poorly sorted and composed of a mixture of rounded beach boulders and angular clasts of basalt and phonolite up to meter-sized boulders. They rest on a paleosol, indicating deposition on land and blanket the coastal slope up to 20 m a.p.s.l. Their base is erosive, and the deposits include fragile clasts ripped-up from friable subaerial substrates. Directional fabrics such as imbricated or oriented flat clasts show that the sediments were deposited both during inflow and outflow by two major waves (Paris et al. 2011).

Canaries Archipelago

The Canaries Archipelago is located in the Atlantic, between 27° and 29°N, and approximately 97 km west of mainland Africa. The archipelago corresponds to 8 main islands that extend for almost 490 km in an east-west direction. Alongside a group of prominent seamounts to the northeast (Concepcion Bank, Lars, Anika, Dacia, Nico) and Selvagens Archipelago to the north, they form the Canary volcanic province that sits on oceanic crust with ages ranging from 180 to 150 Ma (Troll and Carracedo 2016). Fuerteventura (23 Ma), Gran Canaria and Lanzarote (15 Ma) are the oldest islands (Bogaard 2013), La Palma (1.7 Ma) and El Hierro (1.1 Ma) being the youngest (Carracedo et al. 2001). The general decrease in age of the islands from east to the west derives from the movement of the African plate over a mantle plume (Carracedo et al. 1998; Geldmacher et al. 2005). Like Cabo Verde, Quaternary volcanism in the Canaries Archipelago is also reported from several islands. Sixteen historical eruptions are reported in the archipelago, the latest being the 2011–2012 submarine eruption on El Hierro (Martí et al. 2013a, b) and the 2021 subaerial La Palma event (Carracedo et al. 2021; Day et al. 2022).

Massive flank collapses are reported from all the Canary Islands (Masson 1996; Carracedo 1999; Masson et al. 2002; Acosta et al. 2003; León et al. 2017). On Tenerife Island, megatsunami deposits are preserved in the northwest, at several locations around Teno peninsula and Isla Baja, at altitudes up to 132 m a.p.s.l. (Paris et al. 2017). These deposits were first described by García-Talavera et

al. (1989), Zazo et al. (2003) and Criado and Yanes (2005). Ferrer et al. (2013) attributed the deposits to a tsunami generated by the mega-collapse of the north flank of Las Cañadas volcanic edifice, at about 180–150 ka. The deposits were later fully explored by Coello-Bravo et al. (2014), Martín-González et al. (2016), and Paris et al. (2017), who reported on their fossil content and provided a checklist of the marine taxa. Based on the structure, composition, and spatial distribution of the tsunami deposits, Paris et al. (2017) distinguished two successive tsunamis. The first event left gravel composed of local basaltic rocks and abundant marine bioclasts at altitudes up to 20 m a.p.s.l. It may have been generated by a submarine failure of the northern flank of Las Cañadas stratovolcano preceding the paroxysm of the Abrigo eruption ca. 170 ka ago (González-García et al. 2022). Thereafter, resulting from the debris avalanche of the upper part of the volcano, a second tsunami reached higher altitudes (up to 132 m a.p.s.l.) and incorporated freshly-deposited pumice from the eruption. The age of the deposits indicates that the megatsunami that inundated Teno Bajo and Isla Baja occurred during the MIS 6 glacial seastand, when coeval sea level was about 80 m lower than present-day sea level (Miller et al. 2011).

Methods

Tarrafal (Cabo Verde Archipelago)

Seven bulk samples, each consisting of about 1 kg of the sand matrix, were collected at the Tarrafal outcrop (15°16'58.44"N, 23°45'8.78"W; refer to Fig. 3 of Paris et al. 2011), at an elevation of 9 to 11 m a.p.s.l. Sampling was performed on fresh material, obtained after the removal of weathered residues and the larger volcanic clasts. When necessary, samples were disaggregated in the laboratory by a brief ultrasonic treatment followed by oven-drying at 60 °C for 24 h. A vibratory sieve shaker AS 200 was used, with a minimum mesh width of 0.250 mm (2 φ), allowing for the retrieval of almost all determinable remains of the macrobenthos (including fragments). A quantitative analysis was restricted to the molluscs, the only abundant and diversified group to allow a statistical analysis. All mollusc specimens collected were identified and counted. The best-preserved specimens were photographed. A table was compiled for all fossil taxa present in the tsunami deposit of Tarrafal, incorporating information on depth range, life habits (epifaunal, infaunal), trophic group (chemosymbiotic, suspension-feeder, omnivore, grazer, carnivore), typical substrate (hard ground, gravel, coarse sand, fine sand, sandy-mud, muddy-sand, algae) and present geographic distribution (Suppl. material 1: tables S1–S4). Additionally, quantitative data from Last Interglacial (MIS 5e) highstand deposits from Santa Maria Island (Azores, North Atlantic; Madeira et al. 2007; Ávila et al. 2009a, b, 2015) were also included for the purpose of comparing diversity indices. Commonly used indices of diversity (e.g. Shannon-Wiener, Gini-Simpson) are prone mathematical artefacts (Jost 2006),

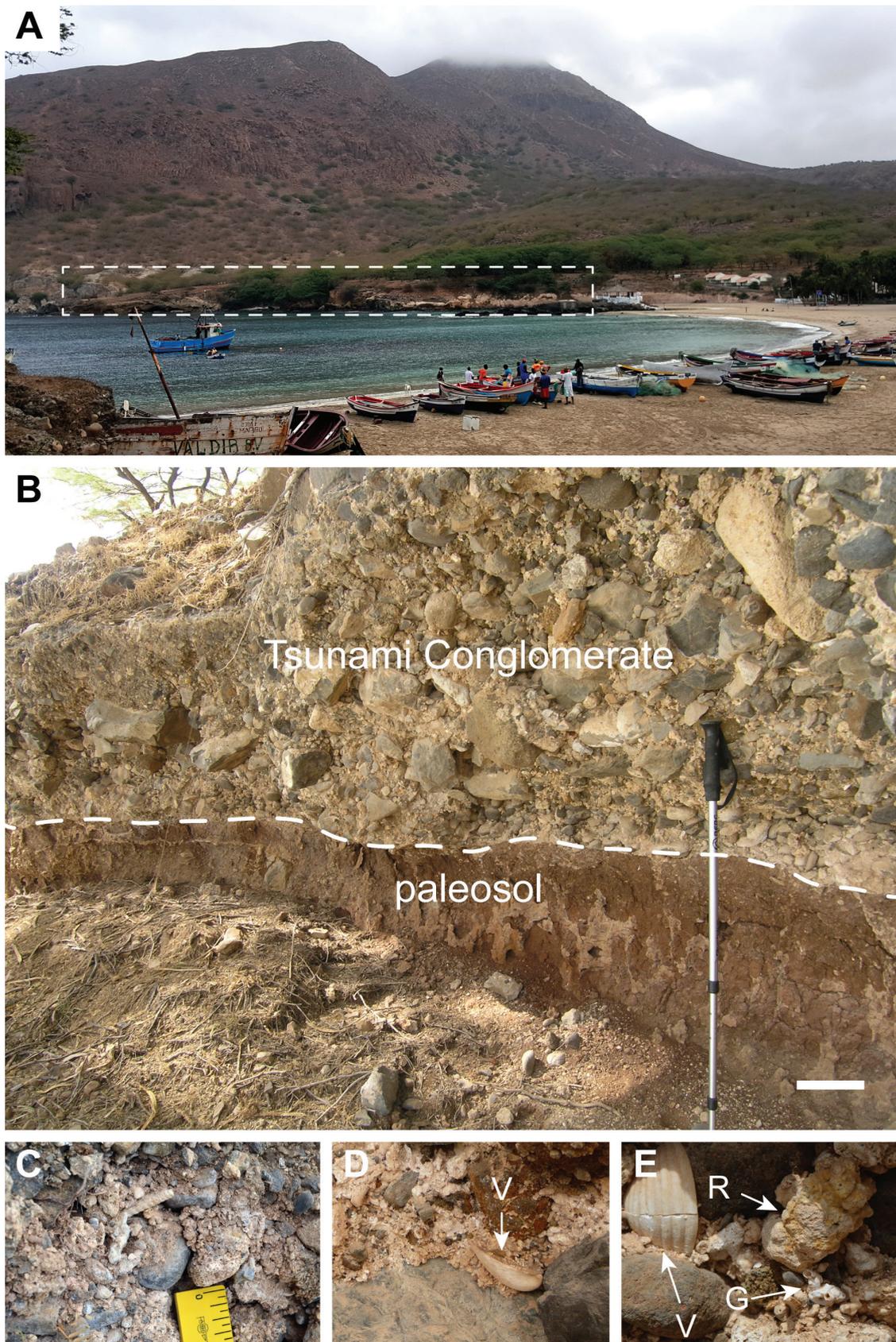


Figure 2. **A.** Panoramic view of the Tarrafal beach, looking to the NNE. The tsunami deposit drapes the surface of the area enclosed by the white dashed line. Monte Graciosa is in the foreground. **B.** General aspect of the tsunami conglomerates overlying a paleosol at Tarrafal; note the chaotic texture of the sediments and the predominance of angular clasts. The walking stick (as scale) is 1.2 m long. **C.** Detail of the matrix of the conglomerate. **D, E.** Aspects of fossil content of the middle section of the tsunami conglomerate; disarticulated valves of bivalve molluscs (V), Rhodoliths (R) and vermetid shells (Mollusca: Gastropoda) (G). Scale bar: 10 cm (**B**).

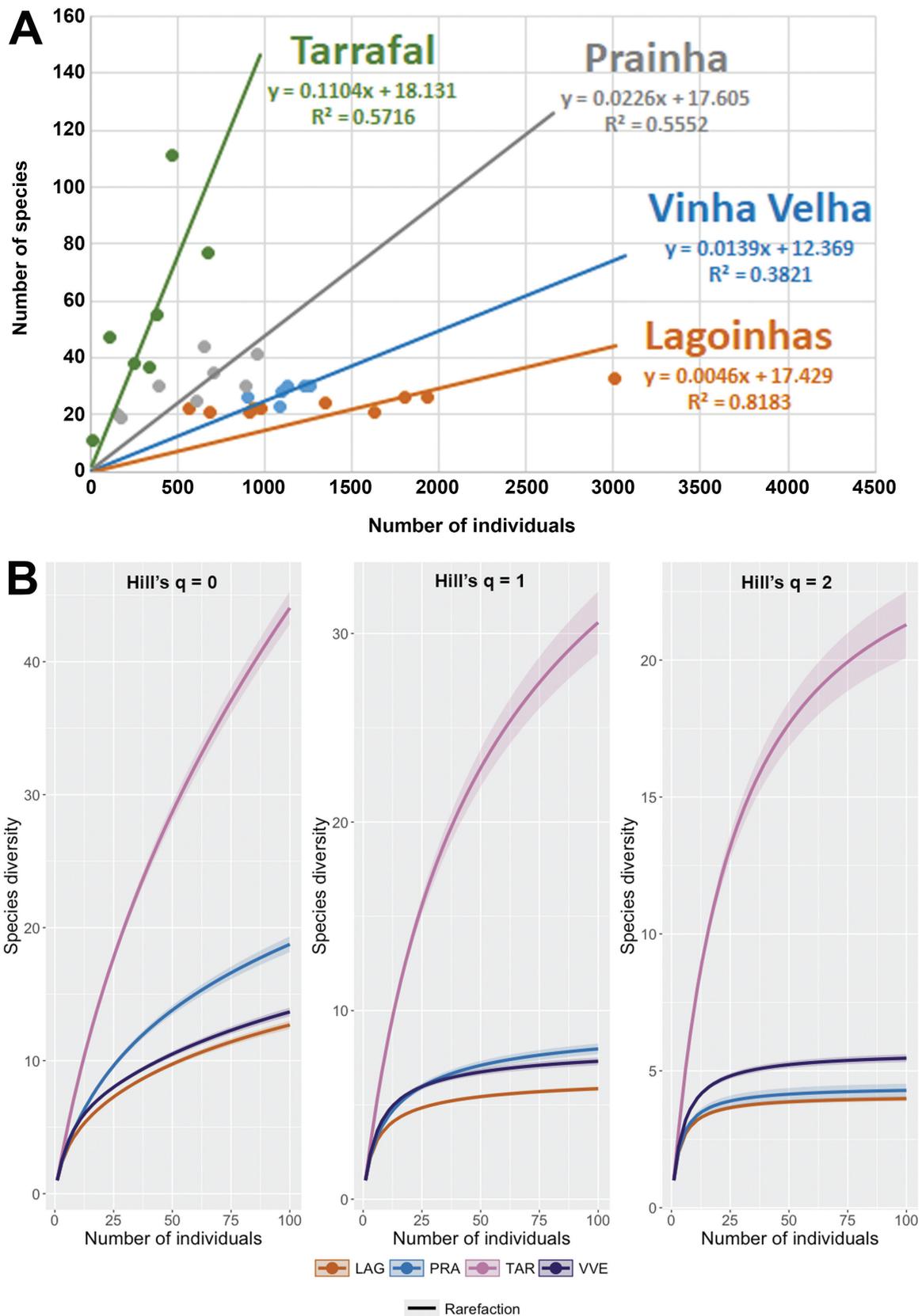


Figure 3. A. Relation between the number of individuals and the number of species for the 31 samples of fossiliferous sediments analysed (each weighing 1 kg): 7 samples from the glacial MIS 4 megatsunami deposit of Tarrafal (Santiago Island, Cabo Verde), and 24 samples from the Last Interglacial (MIS 5e) deposits of Lagoinhas, Prainha and Vinha Velha, all located in Santa Maria Island (Azores Archipelago). **B.** Relation between the number of individuals and the estimated number of species (samples pooled by outcrop). Hill numbers ($q = 0$ for species richness, $q = 1$ for the exponential of Shannon's entropy index, and $q = 2$ for the inverse of Simpson's concentration index) were used to estimate the numbers of species in a sample of 50 individuals (ES50). LAG: Lagoinhas. PRA: Prainha. VVE: Vinha Velha. TAR: Tarrafal.

which makes them unsuitable for comparing assemblages in many situations. Hill numbers, or the effective number of species, are increasingly used to characterize the taxonomic, phylogenetic or functional diversity of an assemblage. Here, we used Hill numbers ($q = 0$ for species richness, $q = 1$ for the exponential of Shannon's entropy index, and $q = 2$ for the inverse of Simpson's concentration index) to estimate diversity of samples using the `hillR` package in R. Moreover, the numbers of individuals among our samples ranged between 14 and 3,013. Since species richness counts are highly sensitive to the number of individuals sampled (Gotelli and Colwell 2011), we used extrapolation (1 sample) and rarefaction (all other samples) techniques based on 50 permutations to estimate the numbers of species in a sample of 50 individuals (ES50) using the `iNEXT` package in R, and thus making comparisons among samples more realistic. All the above was done at the scale of the individual samples and at the scale of the location, the latter obtained by pooling data from all samples together within each location.

The glacial MIS 4 mollusc assemblage from Tarrafal was then compared to the present and Last Interglacial (MIS 5e) species' geographical distribution, to detect possible latitudinal and/or longitudinal shifts. An asymmetrical ANOVA was also used to compare the seven MIS 4 quantitative 1 kg-samples from Tarrafal (Cabo Verde Archipelago) with the 24 MIS 5e quantitative 1 kg-samples from Santa Maria Island (Azores Archipelago).

The invertebrate nomenclature follows that adopted in the WoRMS for the extant species, and the "MolluscaBase" database (<https://www.molluscabase.org/>) for the fossil taxa. All material is stored in the fossil collection of the Department of Biology of the University of the Azores (Ponta Delgada, São Miguel Island), under references DBUA-F 1247, 1249, 1251, 1251-A, 1253, 1254, 1257.

Teno (Canaries Archipelago)

A database with all mollusc species reported from the glacial MIS 6 mollusc assemblage of Teno megatsunami deposits was compiled from the literature [e.g., Coello-Bravo

et al. (2014), Martín-González et al. (2016)]. This list was reviewed, its taxonomy updated based on the WoRMS database (<http://www.marinespecies.org/>) and complemented with data from the collection housed at MUNA-Museo de la Naturaleza y Arqueología (Tenerife). This table also includes information on depth range, life habits, trophic group, typical substrate, and present geographic distribution (Suppl. material 1: tables S5, S6). Finally, following the same methodology used by Melo et al. (2022a, b), a comparison was performed between the glacial MIS 6 mollusc assemblage from the Teno megatsunami deposit (Suppl. material 1: tables S5, S6) and the present and Last Interglacial (MIS 5e) species geographical distribution, to detect possible latitudinal and/or longitudinal shifts.

Results

Tarrafal megatsunami deposit

A total of 209 specific taxa of molluscs (39 Bivalvia, 169 Gastropoda and one Polyplacophora) from the fossiliferous tsunami sediments of Tarrafal (cf. Table 1) was obtained from a total of 2,260 specimens (566 disarticulated valves of bivalves, 1,691 gastropod shells and three plates of an unidentified polyplacophoran). Among these, 150 taxa (71.8%) could be identified down to the species level (37 Bivalvia and 113 Gastropoda; Suppl. material 1: tables S1, S2). Of these 150 species, 134 are shallow-water species (sensu Ávila et al. 2018), i.e., species restricted to water depths shallower than 50 m (34 Bivalvia and 100 Gastropoda) and 14 are deeper-water species inhabiting water depths greater than 50 m: three Bivalvia (Suppl. material 1: table S3) and 11 Gastropoda (Suppl. material 1: table S4). Two gastropods correspond to pelagic species – *Cavolinia inflexa* (Lesueur, 1813) and *Creseis virgula* (Rang, 1828) (Suppl. material 1: table S4). The marine bioclasts also included subordinate specimens of fish otoliths, plates of unidentified barnacle crustaceans, one lobster antenna, echinoderm spines, bryozoans, foraminifers, fragments of corals (mostly branching forms) and rhodoliths.

Table 1. Number of taxa of shallow-, deep-water and pelagic species of Mollusca (Bivalvia and Gastropoda) identified from the glacial MIS 4 tsunami sediments from Tarrafal (Santiago Island, Cabo Verde) and from Teno (Tenerife Island, Canaries Archipelago) megatsunami deposits.

		Number of species			
		Bivalvia	Gastropoda	Polyplacophora	Total
Tarrafal deposit	All taxa	39	169	1	209
	Shallow-water species (< 50 m depth)	34	100	0	134
	Deep-water species (\geq 50 m depth)	3	11	0	14
	Pelagic species	0	2	0	2
		37	113	0	150
Teno deposit	All taxa	28	73	0	101
	Shallow-water species (< 50 m depth)	27	65	0	92
	Deep-water species (\geq 50 m depth)	1	3	0	4
	Pelagic species	0	0	0	0
		28	68	0	96

The 37 bivalve species found in the Tarrafal sequence indicate a wide range of habitats, with 17 associated with more than one type of substrate. There is a prevalence of species associated with hard grounds (19 species), coarse sand (17) and gravel (16), and a few species associated with fine sand (9), muddy bottoms (8) and algae (1). In relation to the life habits of the bivalves, 20 are epifaunal species, 18 are infaunal and one is semi-infaunal. Relative to the trophic group, 37 are suspension feeders, one chemosymbiotic and one deposit feeder (Suppl. material 1: table S3).

The majority of the 169 gastropod taxa from Tarrafal's tsunami deposits show an epifaunal life habit (157 taxa) in contrast with only 10 semi-infaunal species and two planktonic species. In relation to the trophic group/feeding mode, most of the 169 gastropod taxa found in these deposits are carnivores (98 taxa), followed by grazers (56) and six suspension-feeders (Suppl. material 1: table S4). Three endemic bivalves and 34 endemic gastropod species from Cabo Verde are here reported for the fossil record of this archipelago, most of them for the first time (Suppl. material 1: tables S3, S4).

A total of 32 taxa from the glacial MIS 4 tsunami sediments of Tarrafal (14 bivalve and 18 gastropod species) do not presently inhabit the warm waters of Cabo Verde (Suppl. material 1: tables S3, S4). Moreover, for 14 of these 32 taxa, the Canary Islands constitute their present-day southernmost geographical location. In total, we detected the equatorward successful latitudinal range expansion to Cabo Verde Archipelago of 12 bivalves and 14 gastropods. Additionally, we record the longitudinal range expansion from West-African shores towards the Cabo Verde Archipelago of seven bivalves and nine gastropods.

Teno megatsunami deposit

Out of the 101 specific taxa of molluscs (28 Bivalvia, 73 Gastropoda; Table 1) found in the fossiliferous megatsunami sediments of Teno, 96 taxa (95.0%) could be identified down to the species level (28 Bivalvia and 68 Gastropoda; Suppl. material 1: tables S5, S6). Of these 96 species, 92 are shallow-water species (27 Bivalvia and 65 Gastropoda) and four are deeper-water species inhabiting water depths below 50 m: one Bivalvia (Suppl. material 1: table S5) and three Gastropoda (Suppl. material 1: table S6).

The 28 bivalve species from the Teno megatsunami deposits also show a wide range of habitats, with 19 species being associated with more than one type of substrate. Again, and as for Tarrafal, there is a prevalence of species associated with gravel (15), hard grounds (13 species) and coarse sand (11). Fewer species are associated with fine sand (9) and muddy bottoms (9). In relation to the life habit of the bivalves, 14 are epifaunal species, 13 are infaunal and one is semi-infaunal. Relative to the trophic group, all are suspension feeder bivalve species (Suppl. material 1: table S5).

Most of the 73 gastropod taxa found within Teno's megatsunami deposits show an epifaunal life habit (67 taxa) in contrast with just six semi-infaunal species. In re-

lation to the trophic group/feeding mode, most of the 73 gastropod taxa found in these deposits are carnivores (47 taxa), followed by grazers (20) and four suspension-feeders (Suppl. material 1: table S6).

A total of eight species from the glacial MIS 6 tsunami sediments of Teno (four bivalves and four gastropods) do not presently inhabit the waters of the Canary Archipelago (Suppl. material 1: table S5). In total, we detected the equatorward successful latitudinal range expansion to the Canary Archipelago of three bivalves (*Glycymeris glycymeris* (Linnaeus, 1758), *Pecten maximus* (Linnaeus, 1758) and *Ostrea edulis* Linnaeus, 1758) and of three gastropods [*Littorina littorea* (Linnaeus, 1758), *Pseudopusula grohorum* (Fehse & Grego, 2008) and *Petalococonchus glomeratus* (Linnaeus, 1758)]. Additionally, we record the longitudinal range expansion from Moroccan shores towards the Canary Archipelago of four bivalves.

Diversity indices

Data in Table 2 compare the diversity indices obtained from the marine mollusc taxa quantitative data (each consisting of 1 kg standardised samples). These highlight the higher values of the Hill numbers of the samples from the megatsunami deposit of Tarrafal in comparison to the quantitative samples published by Ávila et al. (2015) from the Last Interglacial (MIS 5e) of Santa Maria Island (Azores). The detected differences are statistically significant when MIS 4 samples from Tarrafal are compared with the average values from MIS 5e samples from Santa Maria Island ($p = 0.0000$ for all Hill numbers used, i.e., for $q = 0$, $q = 1$, and $q = 2$; cf. Table 3). There is also a clear trend for a higher number of species and a comparatively lower number of individuals in the glacial MIS 4 samples from Tarrafal when compared with those from Santa Maria (Fig. 3). No other quantitative 1-kg standardized samples are available from any Atlantic oceanic island fossiliferous outcrops of similar ages to compare with our samples.

Discussion

In common with other fossiliferous deposits left by megatsunamis (e.g., McMurtry et al. 2004b; Pérez Torrado et al. 2006; Paris et al. 2017), a mixture of deep- and shallow-water species (including pelagic species), as well as an assortment of species with very different preferential habitats and ecological conditions is detected in the Tarrafal sediments. This allochthonous, highly biodiverse assemblage, with well-preserved micromollusc species, is attributed to the peculiar genesis of the fossiliferous deposit resulting from a megatsunami, with a rapid deposition and minor reworking of the bioclasts. Such an outcome is reported for similar deposits existing elsewhere, such as the Teno deposits in Tenerife, emplaced during the glacial MIS 6 (Coello-Bravo et al. 2014; Martín-González et al. 2016; Paris et al. 2017). The extremely high biodiversity of these

Table 2. Comparison of the diversity indices obtained from 1 kg standardised bulk samples containing fossil marine molluscs collected in the Last Interglacial (MIS 5e) deposits of Santa Maria Island (Azores) and in the Last Glacial (MIS 4) megatsunami deposits of Tarrafal (Santiago Island, Cabo Verde). VVE – Vinha Velha; LAG – Lagoinhas; PRA – Prainha; TAR – Tarrafal. For the MIS 5e deposits of Santa Maria Island, please refer to Ávila et al. (2009b, 2015). Est. Div. – Estimated Diversity.

Island	Outcrop	Sample	Hill q = 0	Estimated richness (ES50) and 95% confidence interval			Hill q = 1	Estimated richness (ES50) and 95% interval			Hill q = 2	Estimated richness (ES50) and 95% interval		
				Est. Div.	Lower 95%	Upper 95%		Est. Div.	Lower 95%	Upper 95%		Est. Div.	Lower 95%	Upper 95%
Santa Maria Island (MIS 5e) - Azores	Vinha Velha	VVE-01	28	10.339	9.676	11.002	7.8978	6.560	6.182	6.938	5.4935	5.059	4.776	5.342
		VVE-02	26	11.215	10.521	11.909	8.6179	7.125	6.631	7.619	5.8497	5.358	4.949	5.768
		VVE-03	30	9.987	9.363	10.610	7.5500	6.276	5.945	6.608	5.2223	4.831	4.584	5.077
		VVE-04	30	10.227	9.628	10.826	7.6726	6.393	5.997	6.790	5.2125	4.824	4.501	5.147
		VVE-05	23	9.749	9.072	10.426	7.3409	6.220	5.844	6.596	5.2128	4.825	4.542	5.107
		VVE-06	30	10.882	10.291	11.473	8.3044	6.868	6.453	7.283	5.5917	5.138	4.807	5.470
	Lagoinhas	LAG-01	22	10.555	9.870	11.241	6.9516	5.862	5.365	6.358	4.2536	4.015	3.601	4.428
		LAG-02	26	10.235	9.794	10.676	6.8370	5.716	5.395	6.037	4.2565	4.002	3.768	4.237
		LAG-03	21	9.091	8.469	9.713	6.4849	5.629	5.194	6.064	4.6093	4.320	3.980	4.659
		LAG-04	33	9.954	9.612	10.296	6.5519	5.429	5.239	5.618	3.9727	3.753	3.610	3.896
		LAG-05	24	9.849	9.316	10.382	7.1233	6.022	5.719	6.325	4.9993	4.642	4.437	4.846
		LAG-06	21	9.334	8.818	9.849	6.0714	5.201	4.856	5.545	3.8661	3.667	3.372	3.963
		LAG-07	21	8.911	8.524	9.297	5.4282	4.678	4.447	4.909	3.4693	3.311	3.150	3.471
		LAG-08	22	9.535	8.828	10.241	6.4800	5.538	5.099	5.977	4.2323	3.987	3.672	4.302
		LAG-09	26	9.272	8.731	9.813	5.9764	5.053	4.733	5.373	3.7576	3.566	3.343	3.790
		LAG-10	22	9.378	8.783	9.972	6.0745	5.186	4.855	5.518	3.9428	3.734	3.494	3.975
	Prainha	PRA-01	30	13.211	12.025	14.397	8.7001	6.944	6.188	7.700	4.4731	4.216	3.700	4.733
		PRA-02	41	14.674	13.908	15.439	10.2306	7.708	7.084	8.331	4.7895	4.468	4.049	4.888
		PRA-03	44	15.201	14.299	16.103	10.9043	8.104	7.343	8.865	5.0171	4.670	4.119	5.221
		PRA-04	25	11.882	11.053	12.711	7.5293	6.188	5.580	6.797	4.0001	3.791	3.319	4.263
		PRA-05	30	11.117	10.435	11.800	6.6587	5.449	4.974	5.923	3.4826	3.327	2.994	3.659
		PRA-06	20	12.510	10.821	14.199	8.3155	7.182	5.956	8.408	4.9334	4.684	3.551	5.816
		PRA-07	19	11.827	10.279	13.375	7.7881	6.741	5.715	7.767	4.8016	4.550	3.707	5.392
		PRA-08	34	13.203	12.234	14.172	9.0697	7.113	6.437	7.790	4.6036	4.314	3.822	4.806
Santiago Island (MIS 4) - Cabo Verde	Tarrafal	TAR-01	111	27.726	26.151	29.300	40.2059	19.554	17.532	21.575	16.0898	12.665	10.638	14.691
		TAR-02	37	17.994	16.573	19.416	16.7944	12.551	11.320	13.783	10.8602	9.291	8.282	10.300
		TAR-03	38	19.990	18.224	21.756	19.9706	14.687	12.864	16.510	13.5049	11.248	9.525	12.970
		TAR-04	77	25.514	24.211	26.817	34.3322	20.011	18.500	21.522	21.2991	15.475	13.896	17.054
		TAR-05	55	21.731	20.059	23.403	25.1816	16.816	15.314	18.318	17.1469	13.373	12.072	14.675
		TAR-06	47	28.570	25.480	31.660	33.3212	23.872	20.810	26.934	25.5018	19.849	17.116	22.581
		TAR-07	11	28.177	14.751	41.603	10.0204	23.388	9.021	37.755	8.9091	15.854	1.975	29.732

megatsunami deposits is emphasized when compared with raised beach sediments sampled similarly (Fig. 3). In a series of studies, Ávila and co-workers sorted, identified and counted molluscs from 24 samples of 1 kg each, from fossiliferous sands of the MIS 5e (Last Interglacial) deposits of Santa Maria Island (Ávila 2005; Ávila et al. 2009b, 2015). In total, they found 136 marine molluscan-specific taxa and counted 25,090 specimens (Ávila et al. 2009a, b, 2015), which contrasts with the present study, where the 7 samples of 1 kg each, of fossiliferous sediments from the glacial MIS 4 deposit of Tarrafal, yielded 209 marine molluscan taxa (Table 1), but only 2,257 specimens (Table 2). A similar pattern was found by Coello-Bravo et al. (2014), who identified 117 marine molluscan taxa and counted 1,941 specimens collected from the glacial MIS 6 Teno tsunami deposits. The distinctive sedimentological and textural characteristics that confirm marine fossiliferous

conglomerates as tsunami deposits include distribution of the conglomerates at variable elevations, many of them out of the range of marine highstand deposits; chaotic textures and the extremely poorly-sorted distribution of clast size; mixing of sediment and bioclast assemblages (planktonic, benthonic, littoral and terrestrial) from different provenances; and fossils never found in life position – for recent reviews on the subject see Goff et al. (2014) and Paris et al. (2018). In addition to these characteristics, this work highlights another trait of megatsunami deposits: the extremely high palaeobiodiversity and evenness of their fossil content.

Moreover, the few studies that analyse palaeobiodiversity in tsunami deposits using diversity indices applied to quantitative fossil data (e.g., Coello-Bravo et al. 2014; Martín-González et al. 2016; this study) point to high evenness index values in the fossil record in these sediments, in stark contrast to highstand fossil deposits. This

Table 3. Asymmetrical ANOVA comparing the 7 MIS 4 samples from Tarrafal (Cabo Verde Archipelago) with the 24 MIS 5e samples from Santa Maria Island (Azores Archipelago). Hill numbers ($q = 0$, $q = 1$, and $q = 2$) refer, respectively, to the species richness estimate, the Shannon's entropy index, and the inverse of Simpson's concentration index.

Source	df	q = 0				q = 1				q = 2			
		SS	MS	F	P	SS	MS	F	P	SS	MS	F	P
Location	3	1013.44	337.81	70.43	0.0000	855.18	285.06	66.57	0.0000	511.48	170.49	61.49	0.0000
MIS 4 vs MIS 5e	1	961.63	961.63	336.22	0.0000	844.19	844.19	153.64	0.0000	506.87	506.87	220.00	0.0000
Among MIS 5e	2	51.82	2.86	3.32	0.0426	10.99	5.49	16.51	0.0000	4.61	2.30	15.45	0.0000
Residual	27	129.50	4.80			115.62	4.28			74.87	2.77		
Res MIS 4	6	111.39	18.56			108.64	18.11			71.74	11.96		
Res MIS 5e	21	18.12	0.86			6.99	0.33			3.13	0.15		

apparent non-occurrence of abundant/dominant species on tsunami deposits was an unexpected result, yet predicted by Behrensmeyer et al. (2000). Fossiliferous marine sediments deposited during highstands (e.g., MIS 5e) are typically the result of several hundred or even a few thousand years of gradual accumulation of biological remains, mainly on supratidal locations, and are usually associated with several storm events (Ávila et al. 2010). Because of this long-duration process, the resulting death assemblage (which mirrors the populations of the local biocoenose and involves the steady accumulation and deposition of their faunal remains; cf. Lyman 2008) is a time-averaged collection of species/specimens. Moreover, and unless taphonomical biases interfere, it is expected that the most abundant species present in the biocoenose to also be the most abundant species present in the death assemblage. In the long term, it is also expected that these species will be the most abundant in the fossil assemblage. This is so, because specimens of dominant species will increase in number faster than rare ones, in the context of long-term sedimentation. Hence, time-averaged samples are biased towards higher taphonomical durability species and to the most abundant species (Behrensmeyer et al. 2000; Kidwell 2013). In contrast, megatsunami deposits are instantaneous events at geological time scales, being responsible for a single-event fossil assemblage. Additionally, tsunami sedimentary deposits mostly result from en-mass transport and deposition by long-wavelength inundation (Paris et al. 2018; Madeira et al. 2020), rather than repetitive energetic mechanisms (such as swell- and wind-driven waves), with much less sorting and destruction, resulting in very-well preserved fossil assemblages more representative of the full range of faunas from the ecological zones they sample. As such, during such catastrophic events, a few mega-waves produce an instantaneous sampling of a varied biological community that includes living and dead remains, the latter also time-averaged, collected from different depths and habitats – thus the usual presence on tsunami deposits of permanent and transient species (e.g., pelagic species) –, and by its transport and deposition high on the slopes of the islands. As a result, the mixed-zonation fossil content found in tsunami deposits is highly biodiverse and might be characterized by the absence of dominant species (as only a few waves are involved). Correspondingly high values of species richness estimates

(Hill's $q = 0$ and ES50), Shannon's entropy index (Hill's $q = 1$), and the inverse of Simpson's concentration index (Hill's $q = 2$) are explained by this relationship (cf. Table 2).

Three species of bivalves presently absent from the Cabo Verdean islands (*Tetarca tetragona*, *Ostrea stentina*, and *Venus verrucosa*) were found in the MIS 5e (Melo et al. 2022a) and in the MIS 4 fossil record of Cabo Verde (this work); the populations of these species therefore must have been extirpated from the archipelago during the last glacial episode, after MIS 4. Our data also show that, during the glacial MIS 4, several temperate and sub-tropical bivalve and gastropod species were able to reach the Cabo Verdean islands through long-distance dispersal (cf. Table 4); these species were subsequently extirpated from the malacofauna of the archipelago, most probably during the present interglacial. Most of the 24 species listed in Table 4 have in the present-day their southernmost range distribution at the Canaries (10 bivalves and 12 gastropods; Fig. 4) or at the Northwest-African coasts (Atlantic Morocco, from the Straits of Gibraltar south to Cape Vert in Senegal, including Western Sahara and Mauritanian shores; 7 bivalves and 7 gastropods). These 24 species were not present in Cabo Verde during the Last Interglacial (Cabero 2009; Cabero et al. 2013; Melo et al. 2022a, b) and so, their presence during the glacial MIS 4 conclusively supports the equatorward long-distance dispersal and successful establishment of viable populations, with the consequential geographical range expansion of benthic, shallow-, cold-water/temperate marine species to volcanic oceanic islands during glacial episodes.

Interestingly, four mollusc species listed in Table 5 and reported from the glacial MIS 6 Teno's tsunami deposits (e.g., Coello-Bravo et al. 2014; Martín-González et al. 2016; Paris et al. 2017), also support an equatorward geographical range expansion of temperate/cold-water species towards lower latitudes. None of these species presently occur in the Canary waters and their southernmost present geographical distribution is in the Mediterranean Sea, Madeira and Selvagens archipelagos.

Fig. 4 shows that, during glacial times, the most probable direction of the detected range expansion of shallow-water marine species was from medium latitudes towards the Cabo Verde Archipelago (MIS 4, Fig. 4A, B), and to the Canary Islands (MIS 6, Fig. 4C). As today, also during the MIS 4 and MIS 6 glacial episodes, the dispersal of these mollusc species most probably occurred during

Table 4. List of mollusc species found in the MIS 4 fossil record of Tarrafal (Santiago Island, Cabo Verde Archipelago); none of these species is reported from the MIS 5e (Last Interglacial) and none is known from the Cabo Verde Archipelago today, thus constituting solid evidence of range expansion of these species to the Cabo Verdean islands. * – Bivalve species present in CAN during MIS 5e, although not present in CAN today. CAB – Cabo Verde Archipelago; CAN – Canaries Archipelago; SEL – Selvagens Archipelago; MAD – Madeira Archipelago; SEN – Senegal; MAU – Mauritania; WES – Western Sahara; MOR – Atlantic Morocco; MED – Mediterranean.

BIVALVIA	Most plausible direction of migration								
	Species	CAN to CAB	SEL to CAB	MAD to CAB	SEN to CAB	MAU to CAB	WES to CAB	MOR to CAB	MED to CAB
<i>Acar clathrata</i>	1								
<i>Asperarca nodulosa</i>	1				1				
<i>Bathyarca philippiana</i>	1								
<i>Cardita rufescens</i>	1*				1				
<i>Glycymeris glycymeris</i>	1*							1	
<i>Lucinoma borealis</i>	1			1		1			
<i>Striarca lactea</i>	1*				1				
<i>Karnekania sulcata</i>	1								
<i>Pododesmus patelliformis</i>	1				1				
<i>Talochlamys pusio</i>			1						
<i>Ervilia castanea</i>	1								
TOTAL	10	1	1	4	1	0	1	0	
GASTROPODA									
Species	CAN to CAB	SEL to CAB	MAD to CAB	SEN to CAB	MAU to CAB	WES to CAB	MOR to CAB	MED to CAB	
<i>Caecum engli</i>	1								
<i>Crepidula porcellana</i>	1			1					
<i>Bittium</i> spp.	1								
<i>Melanella</i> cf. <i>polita</i>	1			1					
<i>Haedropleura septangularis</i>	1				1				
<i>Villiersiella tenuicosta</i>								1	
? <i>Mitromorpha</i> sp.	1								
<i>Babelomurex benoiti</i>	1							1	
<i>Euspira obtusa</i>	1					1			
<i>Cyrellia linearis</i>	1								
<i>Gibbula magus</i>	1			1					
<i>Jujubinus exasperatus</i>	1								
<i>Turritella turbona</i>	1						1		
TOTAL	12	0	3	1	1	1	1	2	

Table 5. List of mollusc species found in the MIS 6 fossil record of Teno (Tenerife Island, Canaries Archipelago); none of these species is known from the Canaries Archipelago today. CAN – Canaries Archipelago; SEL – Selvagens Archipelago; MAD – Madeira Archipelago; POR – Portugal; MED – Mediterranean.

GASTROPODA	SEL to CAN	MAD to CAN	POR to CAN	MED to CAN
Species				
<i>Cumia intertexta</i>			1	1
<i>Littorina littorea</i>			1	1
<i>Pseudopusula grohorum</i>		1		
<i>Petalocochnus glomeratus</i>	1			
TOTAL	1	1	2	2

larval stages (in the case of planktotrophic species), aided by sea-surface currents and trade winds, or by rafting in natural floating devices (in the case of non-planktotrophic species), e.g., wooden logs, algae, as attached eggs/juveniles/adults (Scheltema 1971, 1989, 1995). Our results, which are based in the glacial fossil record (MIS 4

of Cabo Verde and MIS 6 of Canaries), allow us to speculate that the inferred equatorward dispersal of marine species (Fig. 4A–C) will only be possible if and when the prevailing oceanographic barriers that exist today, such as the Canary Current (nowadays located between the Canaries and Cabo Verde archipelagos) shifts its position to a more southern location, thus allowing the arrival of mid-latitude species to Cabo Verde. Alternatively, if the Canaries Current weakens during glacial episodes, the equatorward range expansion of marine species may also occur. In both cases (shifting of the position of the Canary Current or weakened Canary Current), some cooling of the sea-surface temperatures at Cabo Verde latitudes is expected to occur in glacial times, enabling settlement of temperate/cold-water species. In contrast, the detected longitudinal dispersal of species (in this case, from the continental African shores of Senegal and Mauritania towards Cabo Verde – Fig. 4A, B) is expected to occur if the West African upwelling, that today dominates along the Senegal shores, increases in intensity.

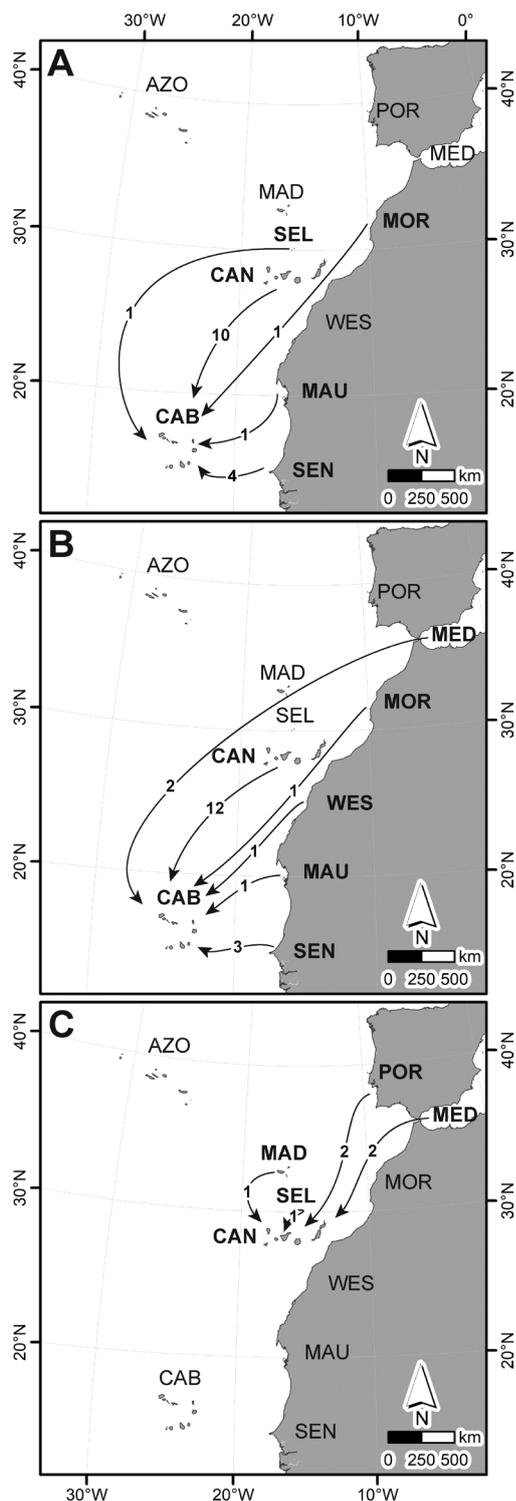


Figure 4. Most probable direction of the detected range expansion processes of mollusc taxa towards the Cabo Verde Archipelago during the glacial MIS 4 (A. Bivalvia; B. Gastropoda), and to the Canary Islands during the glacial MIS 6 (C – Gastropoda). Numbers indicate the number of taxa that underwent such range expansion processes. CAB – Cabo Verde Archipelago; CAN – Canaries Archipelago; SEL – Selvagens Archipelago; MAD – Madeira Archipelago; AZO – Azores Archipelago; SEN – Senegal; MAU – Mauritania; WES – Western Sahara; MOR – Atlantic Morocco; MED – Mediterranean. Delimitation of the landmasses from the Portuguese Hydrographic Institute available data (<https://www.hidrografico.pt/op/33>).

Indeed, mid-latitude North Atlantic records clearly show a decrease in sea surface temperature (SST) during both MIS 4 and MIS 6 (e.g. Iberian margin: Martrat et al. 2007; Azores: Naafs et al. 2013) caused by the weakening of the Atlantic Meridional Overturning Circulation (AMOC) (McManus et al. 2004; Lippold et al. 2009; Böhm et al. 2014). The AMOC reduction has favoured the southward displacement of the Intertropical Convergence Zone (ITCZ) triggering very dry conditions over northwestern Africa and intensified NE trade winds (Castañeda et al. 2009) which contribute for huge amounts of dust supply to the adjacent ocean (Skonieczny et al. 2019). Increased NE trade winds contributed for the intensification of the upwelling in this region and therefore for high marine productivity (Abrantes 1991; Adkins et al. 2006).

Finally, we wish to emphasize that Patiño et al. (2017) conducted a collaborative horizon-scanning approach to identify the 50 most fundamental questions for the continued development of the field of island biogeography. Although the preliminary list of 187 questions contained 27 related to “Palaeoecology and Palaeobiogeography”, only one of these remained in the final list of 50 questions. This reflects not only the low percentage of current biologists that identify “Palaeoecology and Palaeobiogeography” as their field of expertise (Patiño et al. 2017), but also the usual lack of knowledge of biologists in the fields of Geology and Palaeontology. However, island biogeography theory requires the integration of state-of-the-art studies on these three areas of research (Biology, Palaeontology and Geology), and therefore, the formation of multidisciplinary teams is a superior approach for this task. Our study demonstrates, for the first time in the Atlantic Ocean Macaronesian archipelagos, the theoretically expected equatorward geographical range expansion of benthic, shallow-, cold-water/temperate marine species during glacial episodes, a conclusion that was only possible because of the joint efforts of an inter-disciplinary team of biologists, palaeontologists and geologists.

Conclusions

Glacial-age marine fossiliferous deposits are seldom preserved worldwide due to erosion by rising sea levels during the subsequent interglacial episode. Megatsunami events occurring during glacial times are thus one of the best ways to preserve such glacial fossil assemblages, given that they transport and deposit large amounts of sediment onshore, away from the erosive action of subsequent interglacial high sea levels. Moreover, as demonstrated by this study, megatsunami deposits have extremely high palaeobiodiversity and evenness, and these features may constitute additional criteria to distinguish megatsunami deposits from normal sea level highstand deposits.

To conclude, this is the first study in the Atlantic domain that provides conclusive evidence of long-distance dispersal of shallow-water marine mollusc species among

different archipelagos and from continental shores to oceanic islands during glacial periods, with both latitudinal and longitudinal inferred range shifts that resulted in successful geographical range expansion processes of marine species from medium to low latitudes. In times of accelerated global changes, knowing the distributions of species during Pleistocene glacial and interglacial periods is crucial to our understanding of biogeography, ecology, and evolution over the past one million years in fragile marine ecosystems such as those of archipelagic settings.

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Author contributions

SPA, RP and RR conceived the ideas; funding acquisition: RR, SPA, RP, and EMG; SPA, RP, RR, CSM and JM collected the samples during fieldwork at Santiago Island; SPA identified and counted the fossil molluscs, with contributions from CSM, GCA, EMG and ER; GMM and SPA performed the statistical analysis; and SPA, RR, MEJ and JM led the writing. All authors have read and agreed with the final version of the manuscript.

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material 1

Suppl. tables S1–S6 (.docx)

Link: <https://doi.org/10.21425/fob.18.138319.suppl1>