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JQS Journal of Quaternary Science QRA Quaternary Research Association

Comparing the Last Interglacial (MIS 5e) with the present interglacial period (MIS 1) using a multidimensional functional diversity analysis: The marine molluscs from Santa Maria Island (Azores Archipelago, central Atlantic) as a case study

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ABSTRACT: Marine fossil records hold outstanding importance for ecological, evolutionary and biogeographical studies. Santa Maria Island in the Azores Archipelago (central Atlantic) features a remarkable marine fossil record spanning from the Pliocene to recent times. This record includes late Pleistocene outcrops with fossiliferous deposits dated from the last interglacial period (MIS 5e). In this study, we describe a newly discovered MIS 5e outcrop (Ponta do Cedro) and investigate its marine mollusc assemblages. Fifteen taxa (11 gastropods and four bivalves) constitute new records for the MIS 5e highstand deposits of the Azores, increasing the total number of MIS 5e mollusc taxa to 160 (132 gastropods and 28 bivalves). Four genera/species are reported herein for the first time in the global/world fossil record, further emphasising the exceptional palaeobiodiversity of the MIS 5e mollusc assemblages on Santa Maria. Using a functional diversity-based approach, we compared, for the first time, the MIS 5e fossil record with the modern molluscs from the Azores. To achieve this, we compiled two data sets with information covering 35 functional traits from a total of 420 mollusc taxa: 160 from the MIS 5e sedimentary deposits of Santa Maria and 365 modern shallow-water molluscs reported from the Azores. After excluding taxa lacking complete functional trait information, the final data set included 385 mollusc taxa: 132 from the MIS 5e deposits and 320 modern species. All functional alpha-diversity indices were higher for the modern assemblage compared to the MIS 5e, except for Functional Divergence (FDiv), which was greater in the MIS 5e assemblage. This suggests higher productivity, along with the use of a larger number of ecological niches and thus increased niche specialisation for the modern communities compared to the MIS 5e ones. Conversely, the MIS 5e communities appear to have been less resilient to invasions and climate change than their modern counterparts. However, the higher FDiv observed in the MIS 5e communities indicates more efficient use of available resources by these communities, when compared with the modern ones. The results of the multidimensional functional beta-diversity reveal that the nestedness-resultant value is significantly higher than the turnover component. This indicates that the MIS 5e assemblage is a subset of the modern assemblage. Finally, this study provides the first baseline for comparing MIS 5e mollusc assemblages with others, highlighting the unique palaeobiodiversity and functional characteristics of the MIS 5e fossil record on Santa Maria Island. © 2025 The Author(s). *Journal of Quaternary* Science Published by John Wiley & Sons Ltd.

KEYWORDS: Azores archipelago; functional alpha diversity; functional beta diversity; functional traits; marine molluscs; MIS 5e; niche specialisation; palaeobiodiversity; palaeoecology; productivity; Quaternary

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Introduction

For almost 150 years, researchers have explored and published extensively on the geology of Pleistocene shallow marine depositional environments located along both the western and eastern Atlantic continental coasts, studying and describing their fossil marine fauna and flora (e.g., Doderlein, 1872; Gignoux, 1910; Issel, 1914; Lecointre, 1952; Richards, 1962; Martínez et al., 2001; Rojas et al., 2018; Chakroun et al., 2017; Charó, 2021 and references therein), and discussing their palaeoecology, palaeoclimatic and biogeographic relevance (Bauch and Erlenkeuser, 2008). At first glance, the marine fossil record for oceanic islands seems relatively poor compared to that for continents (Soja, 1992). Nevertheless, oceanic islands are of upmost importance for understanding the dispersal of life across oceans and adjacent coastlines. Additionally, their fossil records offer valuable data to disciplines such as evolution, palaeoecology, palaeoceanography, palaeoclimatology and palaeobiogeography (Ávila et al., 2019).

Some oceanic islands located in the Central and Northern Atlantic (Fig. 1) show a rich palaeobiodiversity, holding a substantial number of small, scattered Marine Isotopic Substage 5e (MIS 5e) fossiliferous outcrops that can be studied. The MIS 5e corresponds to the warmest phase of the Last Interglacial (LIG, 130–115 ka; Lisiecki and Raymo, 2005), lasting from approximately 128 to 116 kyr (Oppo et al., 2006). Examples of MIS 5e deposits are known from Bermuda (Muhs et al., 2002), Cabo Verde (García-Talavera, 1999; Cabero del Rio, 2009; Zazo et al., 2007, 2010), Canary Islands (Meco et al., 2008; Cabero del Rio, 2009; Martín-González et al., 2016, 2019); Selvagens (García-Talavera and Sánchez-Pinto, 2001), Madeira (Cotter and Girard, 1892; da Silva, 1956; Gerber et al., 1989) and the Azores (Zbyszewsky et al., 1961; Callapez and Ferreira Soares, 2000; Ávila et al., 2002, 2007, 2009a, 2010, 2015b, 2020a; Madeira et al., 2011; Hyžný et al., 2021; Rebelo et al., 2021; Melo et al., 2022a).

While the Madeira, Canaries and Cabo Verde archipelagos host multiple islands supporting an abundant and diversified fossil marine record as old as the Cretaceous (e.g., Fuerteventura in the Canaries Archipelago; Renz et al., 1992; Castillo et al., 2001), Santa Maria is the only island of the Azores Archipelago where outcropping sedimentary successions of Plio-Quaternary age occur (e.g., Winkelmann et al., 2010; Meireles et al., 2012; Rebelo et al., 2014, 2016; Ávila et al., 2020a, 2022; Hyžný et al., 2021; Sacchetti et al., 2023). Zbyszewsky et al. (1961) were the first to report on the Santa Maria MIS 5e marine fossils from an outcrop at Prainha, located in the southern shores of the island. Subsequently, Callapez and Soares (2000) discovered the MIS 5e deposit at Lagoinhas on the north coast. Vinha Velha, located on the southern coast, was described by Ávila et al. (2015b). Additional MIS 5e outcrops, many still unexplored, were first reported in that paper. Among them was a new locality at Ponta do Cedro, described herein, from the island's eastern coast. The most recent analyses of MIS 5e fossils from Santa Maria were conducted by Melo et al. (2022a, 2022b, 2023) and by Ávila et al. (2025). For a comprehensive review of the most important marine palaeosites on Santa Maria Island, see Madeira et al. (2007) and Ávila et al., (2016, 2018).

Now at the vanguard of biodiversity and ecological research, functional diversity-based approaches (FDB) rely on functional traits to describe variations in species traits and provide a more accurate and complete overview of ecosystems' diversity (Naeem et al., 2012). By adding this functional dimension, FDB metrics add new information and complement traditional alpha- and beta-diversity measures, as well as classic indices such as Shannon's entropy, Simpson's dominance and Pielou's evenness, thereby enriching our understanding of ecological complexity. The link between richness and ecosystem functioning is often weak, whilst compositional effects are commonly much stronger. This suggests that it is the breadth of species functional traits (functional diversity rather than species richness per se) that likely underpins a mechanistic link between diversity and ecosystem functioning. Moreover, the use of functional traits may allow us to identify species that have a greater uniqueness (i.e., species with traits much dissimilar to others, measured by the Functional Originality index, FOri) or that display a high level of specialisation (i.e., species that hold traits with extreme values, best expressed by the functional specialisation index, FSpe), and that may therefore have a disproportionate importance for the functioning of ecosystems or that are of special conservation interest. When such species are locally extirpated or even go extinct, the communities' trait space as well as some specialised ecological roles become empty, thereby reducing the breadth of traits and, consequently, the size of the convex hull multidimensional space (Solan et al., 2004;

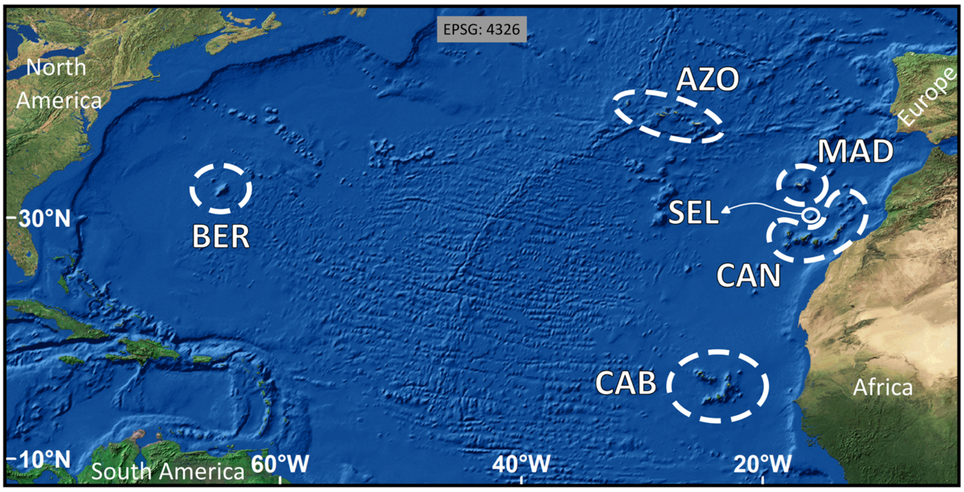

Figure 1. Geographic location of the archipelagos located in the North Atlantic and having fossiliferous outcrops of the MIS 5e. AZO, Azores Archipelago; BER, Bermuda; CAB, Cabo Verde Archipelago; CAN, Canary Archipelago; MAD, Madeira Archipelago; SEL, Selvagens Archipelago. [Color figure can be viewed at wileyonlinelibrary.com]

Mouillot et al., 2013a). As a result, quantifying functional diversity has become a priority in ecological and biogeographical studies.

A literature search performed in April 2025 in the Web of Science Core Collection (Clarivate Analytics) using the following Boolean combination of relevant keywords in the "Topic" field: [(fossil AND marine AND gastrop*) and (function* diversit* OR function* trait*)] yielded 13 articles, only two of which (Rivadeneira and Nielsen, 2017; Grossmann et al., 2023) used FDB. A similar search using [(fossil AND marine AND bivalv*) and (function* diversit* OR function* trait*)] yielded 23 articles, only four of which (Berke et al., 2014; Mcclain et al., 2018; Bryant and McClain, 2022; Grossmann et al., 2023) used FDB. A more exhaustive search identified a few additional studies (e.g., Villéger et al., 2011; Dineen et al., 2014; Foster and Twitchett, 2014; Rivadeneira and Nielsen, 2018). Despite this, FDB are still rarely applied in palaeontology, and they have not yet been applied to the MIS 5e fossil record.

In times of climate change and accelerated global warming as today (Cheng et al., 2019), the MIS 5e—characterised by temperatures 3°C–5°C higher in some Northern Hemisphere locations and sea levels 2–10 m above current levels (Rasmussen et al., 2003; Caputo, 2007; Rohling et al., 2008; Dutton and Lambeck, 2012; O'Leary et al., 2013)—represents a likely analogue for the near-future climatic conditions expected to affect coastal ecosystems worldwide (Gehrels, 2010). Within such a framework, this study aims to (1) describe the Ponta do Cedro fossiliferous outcrop, a new MIS 5e deposit from Santa Maria Island; (2) reconstruct the palaeoenvironment of the sedimentary facies at Ponta do Cedro; (3) update the MIS 5e checklist of the shallow-water marine molluscs from the Azores Archipelago; (4) explore, for the first time in the Last Interglacial fossil record, the functional traits of the MIS 5e Azorean shallow-water marine molluscs using FDB to establish a baseline for the MIS 5e functional diversity; and finally (5), to compare the MIS 5e results with those obtained from a similar analysis on the modern marine molluscs of the Azores (MIS 1), testing in the process how the temporal changes in taxonomic diversity between these two time bins influenced the functional structure of these two interglacial assemblages.

Geographic and geologic setting

The geographic position of the Azores Archipelago in the central North Atlantic, mid-way between Europe and North America, provides an excellent site for evolutionary studies, and serves as a testing ground for theories aiming to understand the evolutionary and biogeographic history of the Atlantic basin during the late Neogene and Quaternary. The Azores archipelago comprises nine volcanic islands aligned on a west–northwest to east–southeast axis (Fig. 2(A)). These islands lie at the intersection of three tectonic plates: the Nubian (Nu), the North American (NA) and the Eurasian (Eu). Santa Maria is part of the Eastern Group of islands, and is the southeastern-most in the Azores, residing on the Nu plate.

Santa Maria is the oldest island in the Azores, and is particularly significant as one of the most favourable oceanic islands for studying the late Neogene and Quaternary marine fossil record in the North Atlantic (Ávila et al., 2018), owing to a combination of factors, among which its vertical motion history is the most important (Quartau et al., 2016; Ramalho et al., 2017). In contrast to all other islands of the Azores, which emerged above sea level during the Pleistocene, Santa Maria emerged at around 6 Ma, showing two main cycles of volcanic growth (5.8–5.3 Ma and 4.1–2.8 Ma; Sibrant et al., 2015; Ramalho et al., 2017), with a dominantly erosive stage in between, during which the island was largely razed by a combination of subsidence and marine erosion. The Pliocene fossils are related to this period, during which deposition of marine sediments took place in a wide, shallow submarine bank (Ramalho et al., 2017; Ávila et al., 2018). Critically, at ca. 3.5 Ma, the island reversed from subsidence to an uplift trend, leading to the exposure of superb submarine volcano-sedimentary sequences (Ávila et al., 2015a, 2018, 2020a; Ramalho et al., 2017; Uchman et al., 2017, 2018, 2020) and the formation of several raised marine terraces, among which the lowest (except for the present day's) was carved during the LIG (Ramalho et al., 2017; Ricchi et al., 2018).

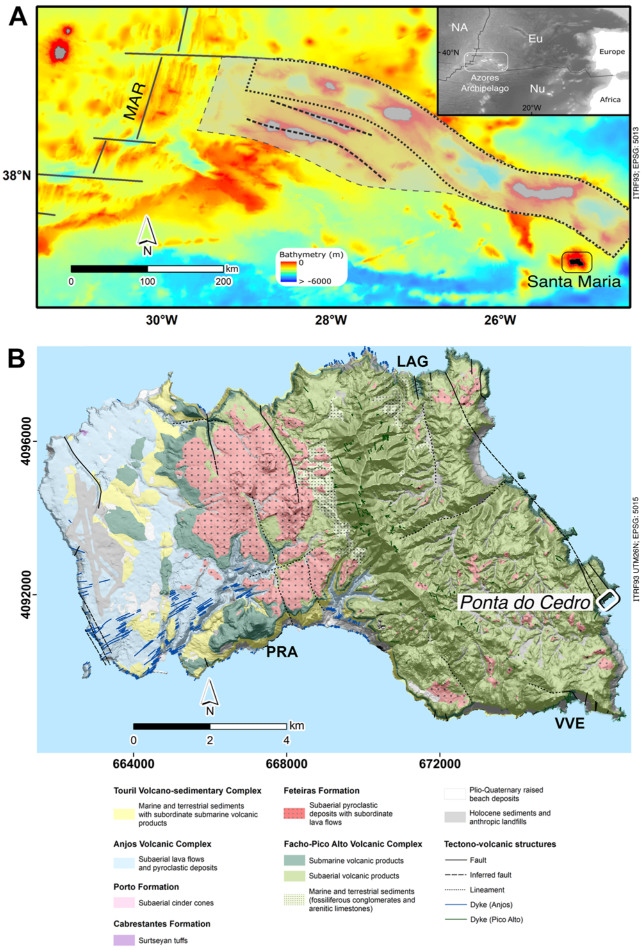

Figure 2. Location maps. (A) Location of the Azores Archipelago within the NE Atlantic (insert) and Santa Maria within the Azores Archipelago. Eu, Eurasian plate; MAR, Mid-Atlantic Ridge; NA, North American plate; Nu, Nubian (African) plate. Bathymetry extracted from GEBCO 2019 (https://www.gebco.net/data_and_products/gridded_bathymetry_data/); coastline delimitation from the Portuguese Hydrographic Institute free data (https://www.hidrografico.pt/op/33). (B) Geological map of Santa Maria Island modified from Serralheiro et al. (1987) and Ramalho et al. (2017), with the location of the Ponta do Cedro outcrop. The other MIS 5e outcrops studied are PRA (Prainha) and VVE (Vinha Velha), both located in the south coast, and LAG (Lagoinhas), located in the north coast of the island. Underlying digital elevation model from the 1:5000 scale digital altimetric database. [Color figure can be viewed at wileyonlinelibrary.com]

One of the most recently discovered MIS 5e deposits from Santa Maria is located on the eastern coast of the island, at Ponta do Cedro. This fossiliferous outcrop consists of two sections situated at an altitude of 6 m (western section) and 7 m

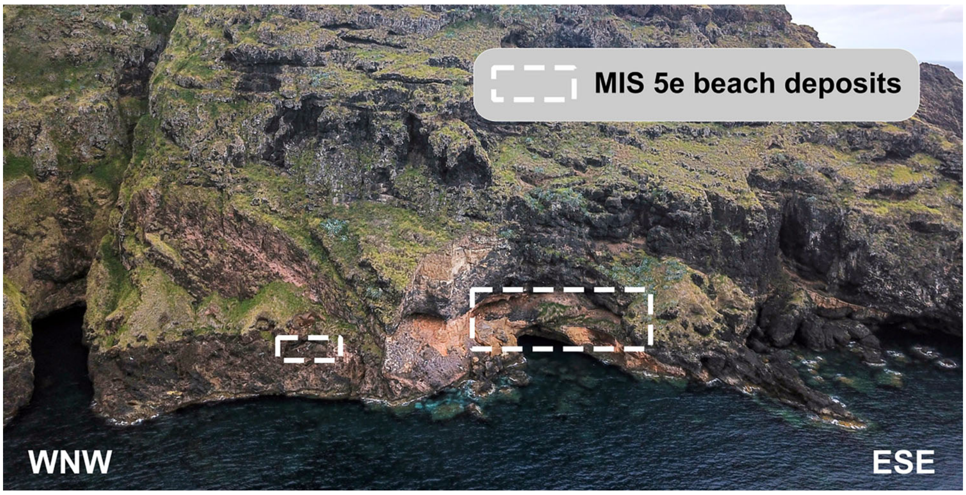

Figure 3. Aerial view of Ponta do Cedro outcrop. The MIS 5e deposits are marked by dashed white lines. The western (smaller dashed white rectangle) and eastern sectors of the MIS 5e at Ponta do Cedro are separated by a Pliocene promontory where the islanders quarried limestone to produce lime. The standardised 1-kg quantitative samples were collected in the western sector. [Color figure can be viewed at wileyonlinelibrary.com]

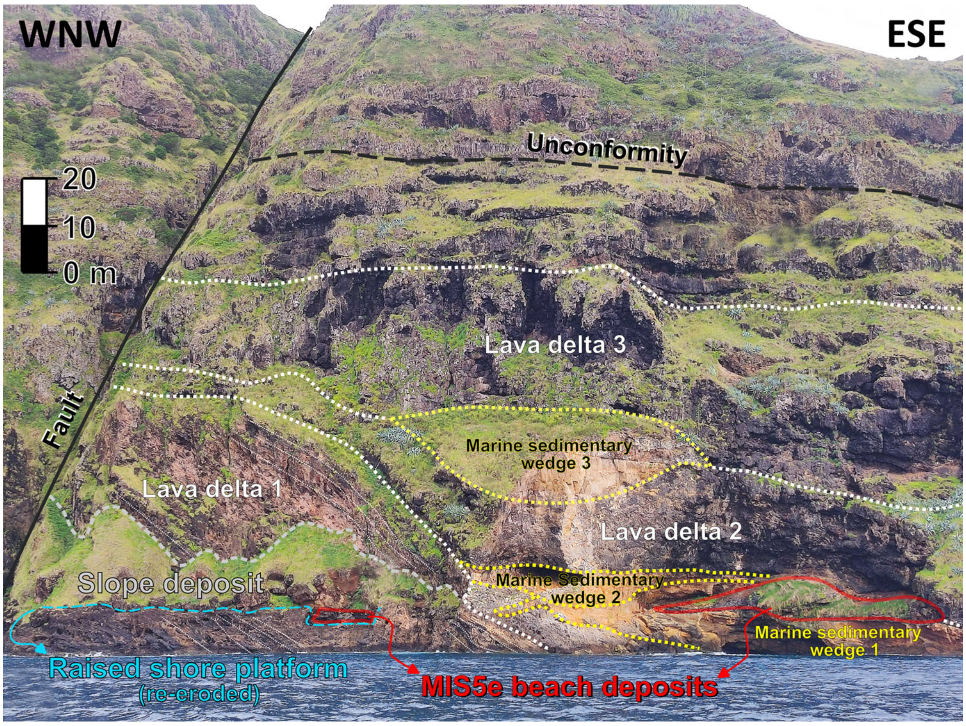

Figure 4. General view of Ponta do Cedro, with the location of the MIS 5e deposits in the context of the Pliocene marine sequence exposed at the sea cliff. [Color figure can be viewed at wileyonlinelibrary.com]

(eastern section) above the present sea level (Ávila et al., 2015b, 2018; Figs. 2 and 3). These sections are separated by a headland where Pliocene fossiliferous deposits arranged in three stacked clinoforms prograding towards the sea and encapsulated between lava flows (Uchman et al., 2020) are present (Fig. 4). Ponta do Cedro is also one of the notable sites on Santa Maria Island where MIS 5e boulder beach deposits are preserved (Ávila et al., 2020b).

Methods

MIS 5e depositional benchmarks

The coastal areas of Santa Maria Island were extensively surveyed for fossiliferous deposits during field campaigns within the scope of 19 editions of the "Palaeontology in Atlantic Islands" workshops (2002, 2005–2023). Fieldwork included numerous boat trips around the island's shoreline (Fig. 5(A),(B)) and the most plausible palaeosites were checked onshore. These efforts facilitated the identification of fossils and geological evidence of sea-level highstands, such as beach conglomerates (Fig. 5(C)), raised shore platforms (Fig. 5(D)), shore angles (Fig. 5(E)) and wave-cut notches (Fig. 5(F)). Coastal wave-cut notches are geologic features that are usually present in steep, plunging sea cliffs, and result mostly from mechanical erosion derived from waves and tidal erosion. Such wave-cut notches constitute prime localities for the reconstruction or analysis of marine and coastal palaeoenvironments during the Quaternary, as they provide a benchmark for sea level at the time (Trenhaile, 2015). In addition, notches, like those at the Ponta do Cedro outcrop, often contain rocks

Figure 5. Exploration of the coast of Santa Maria by boat (A, B) allowed direct search onshore of geological evidence of sea-level highstands and the possible existence of fossil deposits. (C) Beach conglomerates (MIS 5e deposit) at Ponta do Castelo. (D) Raised shore platforms with a MIS 5e deposit at Lagoinhas, north coast of Santa Maria Island. (E) Shore angle at the MIS 5e deposit of Vinha Velha. (F) Wave-cut notch located between Malbusca and Vinha Velha; no fossils were found at this geosite (person for scale). [Color figure can be viewed at wileyonlinelibrary.com]

and fossil-bearing deposits, trapped within their crevices. The deposit studied herein at Ponta do Cedro is assigned a last interglacial age (MIS 5e) for two reasons: the height of the deposit in relation to the present sea level, which is consistent with that of dated outcrops (e.g., Prainha), and more importantly, the presence of MIS 5e ecostratigraphic indicator molluscs for the Azores (cf. Ávila, 2025), such as *Conus* spp. and *Claremontiella nodulosa* (C.B. Adams, 1845).

Stratigraphical, sedimentological and palaeontological characterisation

The eastern section of the Ponta do Cedro Pleistocene outcrop (Fig. 6(A)) was first explored during the seventh Palaeontology in Atlantic Islands (PAI) workshop on July 18, 2010. Subsequent sampling campaigns were conducted on July 15, 2012 (ninth PAI) and June 22, 2014 (11th PAI). The western section was discovered and sampled on July 23, 2015, during the 12th PAI; Figs. 3, 4, 6(A),(B), and 7). This outcrop was last visited on July 11, 2023, during the 19th PAI, when a general cross-section of this sequence was recorded. Fig. 4 provides an overview of the western section, while Fig. 8 schematises the stratigraphic interpretation of the cross-section and the locations of two strip logs (Fig. 8(A)). These logs were used to construct stratigraphic sections along a representative vertical profile of this MIS 5e outcrop (Fig. 9). Detailed aspects of the internal structures and contacts of the subunits individualised in the sedimentary deposit are also presented (Fig. 8(B)). Special attention was paid to register changes in facies and fossil content.

An aerial view provides a wider perspective of the MIS 5e deposit, which is placed on a platform shaped like a small amphitheatre (Figs. 6(B) and 10). To further support the description of the outcrop, a 3D model of the western section, focusing on the most sedimentary variability, was also constructed (Figs. 8(B),(C) and S1). This three-dimensional photogrammetric model was obtained using Alice Vision Meshroom (version 2023.1.0) to generate the mesh and texture from photographs and video still frames of the outcrop. The mesh was subsequently processed using Geomagic Wrap 3D Systems, version 2021.2.2.

Fossil surveys and qualitative collections were conducted at both the western and eastern outcrops at Ponta do Cedro. Eleven quantitative and three qualitative samples of MIS 5e sediments were collected in the western section. The qualitative samples were used to update the MIS 5e checklist of Santa Maria Island. The 11 quantitative bulk samples, each of approximately 1 kg, were collected from a pocket of sand facies located at the base of boulders that infill the wave-cut notch (Figs. 7(A),(B) and 8(B),(C)). Sampling was restricted to fresh material from in situ deposits after removal of weathered residues. Samples were disaggregated in the laboratory using a brief ultrasonic treatment and then oven-dried at 60°C for 24 h. Sediment samples were not sieved, thus allowing for hand-picking of all determinable remains of the macrobenthos (including fragments as small as 0.1 mm). Quantitative analysis was limited to molluscs. All specimens collected were identified to the lowest possible taxonomic level and counted. The best-preserved specimens were photographed, including all new records for the MIS 5e of Santa Maria (Tables 1 and S1; Figs. 11 and 12). The raw data of other MIS 5e quantitative samples (each also weighing 1 kg of fossiliferous sediments) collected from Prainha, Lagoinhas and Vinha Velha outcrops, and previously studied by Ávila et al. (2009a, 2015a), were also incorporated into Table S1.

The invertebrate nomenclature follows that adopted in the WoRMS database (http://www.marinespecies.org/) 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 1137, 1156, 1164, 1182, 1184, 1209, 1222, 1233, 1261 and 1263 (quantitative samples), and DBUA-F 1183, 1198 and 1262 (qualitative samples).

Statistical analysis

Bulk samples (each ~1 kg of fossiliferous sediments) from Ponta do Cedro ($n = 11$) were compared with those of Prainha ($n = 8$; Ávila, 2005), Lagoinhas ($n = 10$; Ávila et al., 2009a) and from Vinha Velha ($n = 6$; Ávila et al., 2015b; Table S1). Numerical ecology techniques were used to describe the palaeocommunities of Ponta do Cedro.

The Chao estimator was used to account for potentially undersampled species richness at Ponta do Cedro. It is recommended to have at least 200 individuals in total (Cameron and Prokyszko, 2005), a situation that is fulfilled by our data (cf. Table S1). Individual-based rarefaction curves were computed for each replicate and for all four outcrops, by using the total sum of individuals per 1 kg-bulk sample (Fig. 13).

The complete quantitative MIS 5e database encompassing data from Ponta do Cedro, Prainha, Lagoinhas and Vinha Velha (Table S1) was used for the remaining numerical ecology analysis. Following the methodology of Borcard et al. (2011), calculations were performed in R using a series of data transformation, standardisation and clustering methods. As for cluster analysis, log-transformed species abundances, Bray–Curtis dissimilarity and

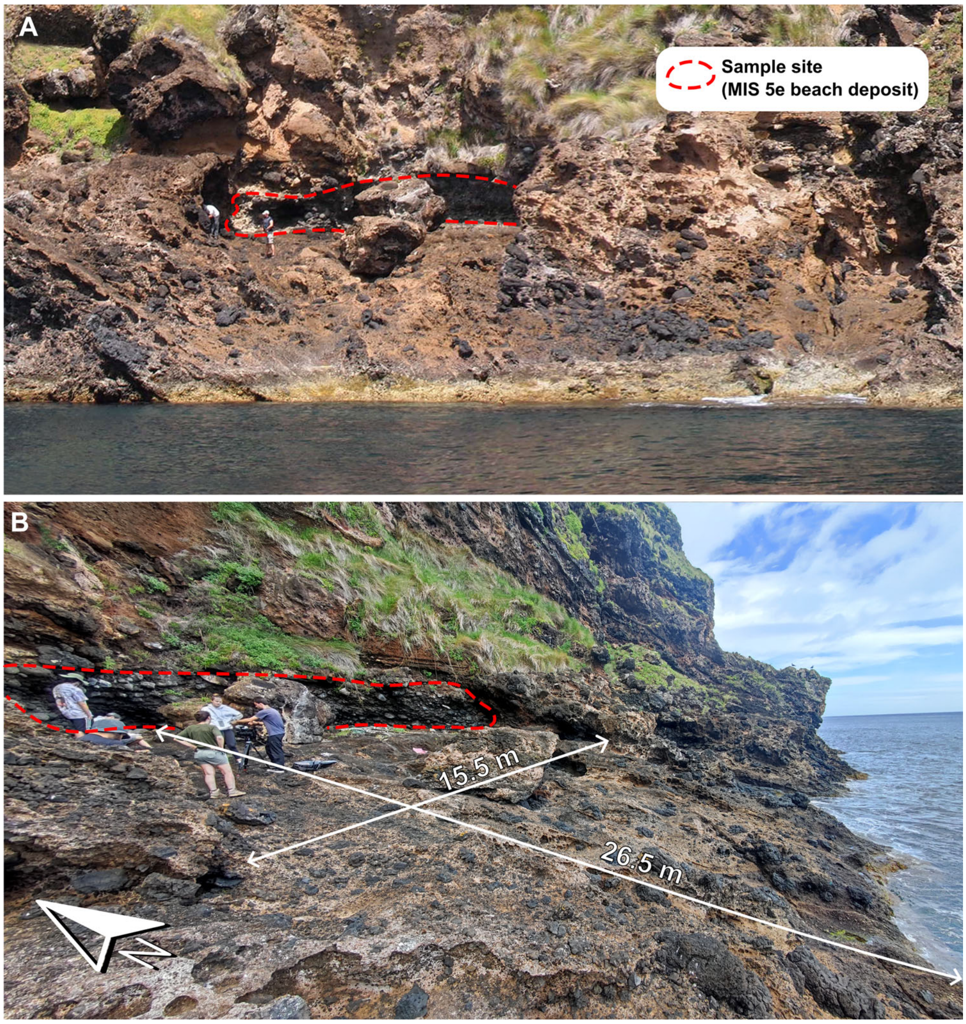

Figure 6. Detailed general views of the western section of Ponta do Cedro outcrop. (A) Frontal view of the outcrop; photo shot from the sea, from south to the north. (B) Lateral view of the outcrop; photo shot from west to the east. The tallest researcher is 1.7 m high. [Color figure can be viewed at wileyonlinelibrary.com]

Ward's minimum variance clustering were selected based on cophenetic correlation values. Optimal cluster numbers were determined using Silhouette graphs and Mantel statistics. Relationships between sites and samples were visualised with a heatmap (based on log-transformed species abundances and Bray–Curtis dissimilarities; cf. Fig. 14) and a dendrogram (Fig. 15).

Indicator species analysis was used to compare the four deposits and to determine the possible association between species and the different sites, based on species abundances. For this analysis, we used the R package "Indicspecies", available through Cran (http://cran.r-project.org/web/packages/indicspecies/). This package is a refinement of the IndVal method originally developed by Dufrêne and Legendre (1997) and enhanced by Cáceres and Legendre (2009). This algorithm calculates two key metrics: fidelity (i.e., the degree to which a species is restricted to a specific site or group of sites) and consistency (the regularity of species occurrence among sites within site groups), providing an indicator statistic value (IndVal) and the respective *p*-value (Table 2). To visualise these relationships, a redundancy analysis based on IndVal was performed, enabling the simultaneous projection of species and samples (Fig. 16). This approach has proven effective in previous studies, including comparisons of ostracod palaeocommunities (Meireles et al., 2014) and mollusc palaeocommunities in the Azores (Ávila et al., 2015b).

The diversity of molluscs for each location was estimated by Hill's series (Hill, 1973), which are defined by a parameter "q", that determines how much weight is given to rare species. For $q = 0$, it represents the number of species in a sample; $q = 1$ is the antilogarithm of the Shannon diversity index; and $q = 2$ is the inverse of the Simpson diversity (cf. Pearson and Rosenberg, 1978; Warwick and Clarke, 1993). Hill's numbers represent a conversion of common indices into true diversity, so that their values are directly comparable (Jost, 2006). The increasing order of Hill's numbers (N0, N1 and N2) indicates an increasing emphasis on the diversity of common and more abundant species. Hill's numbers were calculated using the r package iNEXT (Hsieh et al., 2024). As species richness counts are highly sensitive to the number of individuals sampled (Gotelli and Colwell, 2011), we used extrapolation techniques based on 50 permutations to estimate the numbers of species in a sample of 50 individuals (ES_{50}). Comparison of Hill's numbers among the four locations was achieved using a Generalised Linear Model with a Poisson family and a log link function (var ~ location, family = Poisson(), function "glm", package stats), setting the location Ponta do Cedro (PCE) as the reference level.

Functional diversity analysis

A comprehensive table was compiled to catalogue the functional traits of all 160 fossil mollusc taxa (132 gastropods and 28 bivalves) identified in the MIS 5e outcrops from Santa Maria Island (Table S3). The data set integrates 35 categorical groups and four continuous traits/variables groups,

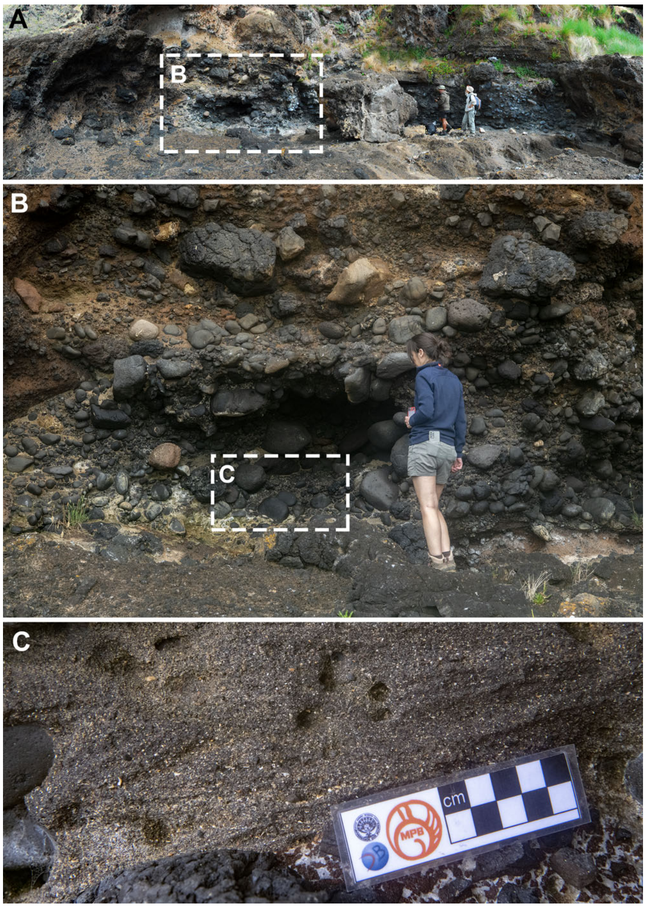

Figure 7. Site of collection of the 11 quantitative bulk samples at the western section of the MIS 5e Ponta do Cedro outcrop. (A) General view of the outcrop. (B) Eleven samples, each of approximately 1 kg, were collected from a pocket of sand facies located at the base of the western sector of the conglomeratic deposit that fill in the wave-cut notch. (C) Detail of the outer surface of the sand pocket. [Color figure can be viewed at wileyonlinelibrary.com]

as functional diversity analysis accommodates the simultaneous use of categorical and continuous variables without bias (Martins et al., 2012). The relevant data cover the following categories:

1. Mode of larval development: three groups (planktotrophic, non-planktotrophic (which included lecithotrophic + direct development) and brooding).
2. Longevity of each species (geological age range): six groups (ranging from the Eocene to the present).
3. Mineralogy of the shell/skeletal structure of the fossils: two groups (aragonite and low-Mg calcite).
4. Type of locomotion: four groups (actively mobile, slow-moving, facultatively mobile and stationary/attached/sedentary).
5. Life habits: six groups (epifaunal, semi-infaunal, boring, infaunal, deep infaunal and nektonic).
6. Diet: five groups (carnivore, herbivore/grazer, deposit feeder, suspension-feeder and chemosymbiotic).
7. Typical substrate: seven groups (hard ground—including rocks, shells, corals, gorgonians, coralline algae and rhodoliths—gravel/pebbles, coarse sand, fine sand, sandy mud to muddy sand, algae and macrophyte meadows).

Information on additional continuous traits was also included: abundance (i.e., number of individuals/species in each replicate), maximum world species size and bathymetric range. Trait information was extracted from two databases curated by the first author (Ávila, 2024a, 2024b). In relation to the typology of traits, we followed the classification proposed by Martini et al. (2020) and used the whole array of typologies: morphological traits (e.g., the maximum world species size), life history traits (e.g., reproduction strategy), physiological traits (e.g., diet) and behavioural traits (e.g., motility/locomotion and substrate relation). These functional species' traits are associated with

1. The overall rate of species survival. For example, in a geological sense, planktotrophic molluscs with wider geographic ranges have greater longevity and face a lower extinction risk in comparison with non-planktotrophic species, which usually have a more restricted geographic range; Scheltema, 1977, 1989; Crampton et al., 2010).
2. The ability to acquire food and the use of resources. Traits such as the type of locomotion, life habit, diet and substrate, all shape the resulting trophic groups; Gravel et al., 2016).
3. Ecosystem processes. For example, the body size defines energetic requirements (Fisher et al., 2010).

Finally, information was further included regarding species exclusively associated with the intertidal zone (Table S2) and species present in the MIS 5e deposits but absent from the modern fauna of Santa Maria Island (Table 3). These extirpated species, mostly warm-water/tropical in origin, likely disappeared locally during the Last Glacial episode (Ávila et al., 2015a; Melo et al., 2022a, 2022b).

A second table was compiled to catalogue the functional traits of the 365 modern (MIS 1) shallow-water (<50 m depth) mollusc shelled species (217 gastropods and 148 bivalves) reported from the Azores (cf. Table S4). The MIS 5e and MIS 1 tables (cf. Tables S3 and S4, respectively) were subsequently merged, the overall database including 420 mollusc species. After thorough review, incomplete records were excluded, resulting in a final data set of 132 MIS 5e and 320 modern species of molluscs. This final data set was analysed using R Studio version 4.4.2 (R Core Team, 2024) and the R package mFD version 1.0.3 (Magneville et al., 2022).

Prior to the analyses, the functional trait matrix was standardised (mean = 0, variance = 1) so that all traits were similarly weighted. As several traits were not continuous, the Gower distance was applied to compute the pairwise functional distance between species, thus allowing the mixing of qualitative/categorical and quantitative/continuous traits (Gower, 1966; Villéger et al., 2008). A principal coordinates analysis (PCoA) was performed on the resulting distance matrix, and the quality of functional spaces was assessed using up to 10 dimensions with the quality fspaces function of the mFD package (Magneville et al., 2022). The mean absolute deviation (*mad*) index was used to determine the minimum number of axes needed to construct a reliable Euclidean space, with the lowest *mad* value indicating the optimal number of axes.

The components of the functional alpha diversity were calculated for the entire fossil malacofauna (MIS 5e) and the modern Azorean molluscs (MIS 1), using the mFD R package (Magneville et al., 2022; cf. Table 4): Species Richness (SpRic), Functional Richness (FRic), Functional Evenness (FEve), Functional Divergence (FDiv), Functional Dispersion (FDis), Functional Originality (FOri), Functional Specialisation (FSpe), Functional Mean Pairwise Distance (FMPD) and Functional Mean Nearest Neighbour Distance (FNND) (Mason et al., 2005; Villéger et al., 2008; Magneville et al., 2022). For a current definition of each functional diversity index used, see Gomes et al. (2023: 7).

The multidimensional functional alpha diversity was calculated for each of the four studied MIS 5e outcrops (Ponta do Cedro, Prainha, Lagoinhas and Vinha Velha; Table S5), and a multiple comparison test after the Kruskal–Wallis test was implemented to detect significant differences among the outcrops. Comparison of the functional alpha diversity (and its components) between the revised MIS 5e data set (132 mollusc species) and MIS1 species lists (320 molluscs) was also performed. To minimise species

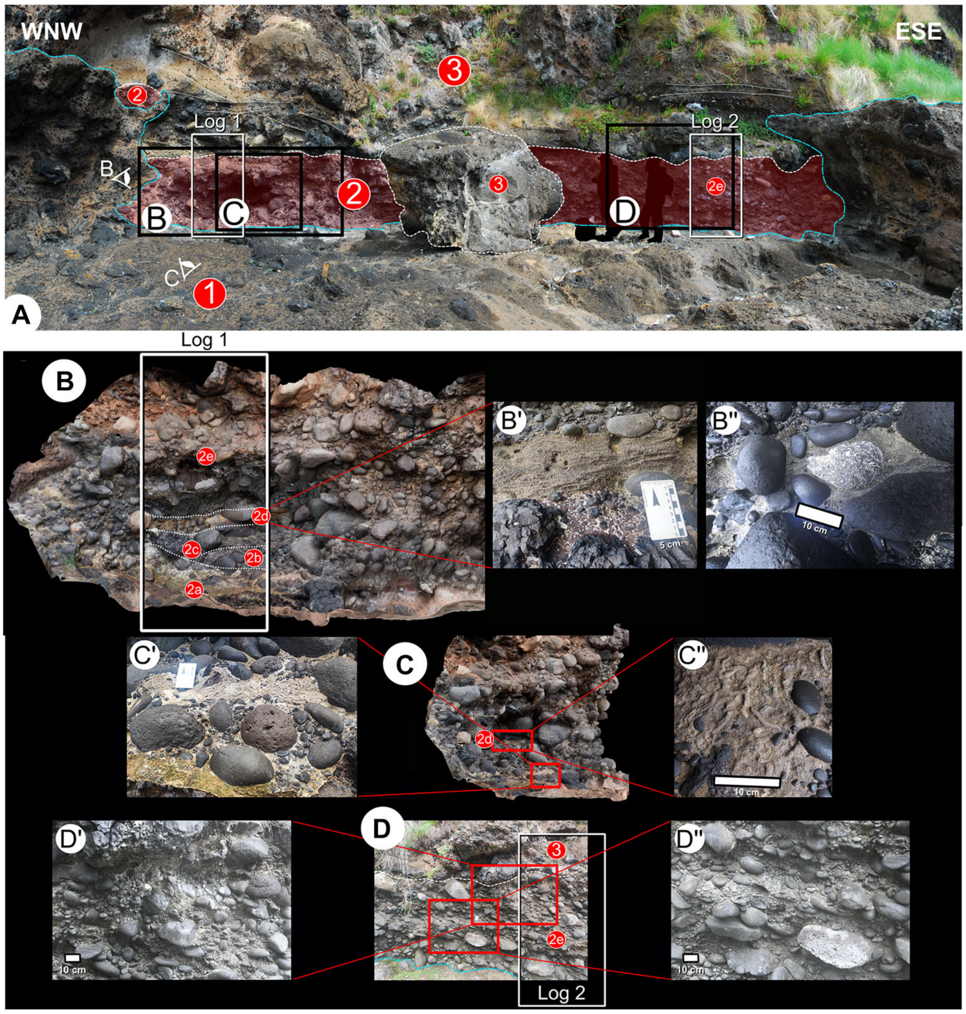

Figure 8. Stratigraphic interpretation of the western section of the MIS 5e deposit at Ponta do Cedro outcrop (shaded in light red). (A) General view. (B) 3D representation of the western sector of the beach conglomerate (viewed from south). (B′) and (B″) Sandy laminar and cross-stratification. (C) Detailed 3D representation of the western sector of the beach conglomerate (viewed from west–northwest). (C′) and (C″) Bioturbation structures (*Macaronichnus segregatis* Clifton and Thompson, 1978). (D) Detailed view of the eastern sector of the beach conglomerate. (D′) and (D″) Appearance of the coarse-grained matrix and of the clast's arrangement (mainly in a stable position, with the minor axis perpendicular to the surface). Numbers correspond to the units displayed in Fig. 9. The light blue dashed line depicts the surface erosion; the white dashed line marks the top/base of the units; the white dotted line marks the sub-units; and eyes represent the viewing perspectives of each 3D model. [Color figure can be viewed at wileyonlinelibrary.com]

richness bias, observed values were compared against expected random values (50 iterations) using 75 species for both data sets, with statistical significance assessed using the Wilcoxon rank-sum test with continuity correction.

Finally, the mFD R package (Magneville et al., 2022) was used to estimate the nestedness and turnover components of beta diversity between MIS5 e and the MIS1 species lists, based on Jaccard dissimilarities (Baselga, 2012; Villéger et al., 2013). The turnover component is the highest when there is no shared traits combination between the two assemblages, whereas the nestedness component is the highest if one assemblage hosts a small subset of the functional strategies present in the other. For computational efficiency, only four axes were used in this analysis.

Results

Geomorphology of pre-existing topography

The two MIS 5e deposits at Ponta do Cedro rest on marine shore platforms carved from hyaloclastites, pillow breccias and marine sedimentary deposits, and are intercalated between a sequence of submarine lavas from the Pico Alto Volcanic Complex (Figs. 2 and 4). In the western outcrop (Fig. 3; main sampling site), the interglacial sequence includes a clast- to matrix-supported cobble-to-boulder conglomerate (beach deposit) and part of a talus deposit, resulting from the dismantling of the cliff, which is still active at present. These deposits were emplaced in a small, amphitheatre-shaped depression within the hyaloclastites and pillow breccias (Figs. 6 and 10). This morphology likely favoured the formation of a boulder beach by providing space for sediment accommodation and enabling the subsequent preservation of the deposit. The beach deposit, partially sealed by the talus deposit, was later eroded almost to the cliff's base and preserved in a small concavity forming the head of the amphitheatre morphology (Figs. 6(A) and 10). A subsequent erosive phase further accentuated the depression and the overall seaward slope of the shore platform (Fig. 6(B)), introducing surface irregularities that have been exacerbated by ongoing erosion. The base of the beach deposit is located about 5.8 m above sea level, relative to the Azores Chart-Datum (Hydrographic Zero).

Facies description, stratigraphy and sedimentological structures at Ponta do Cedro MIS 5e west section

The west section of the Ponta do Cedro MIS 5e deposit (Fig. 6(A)) is composed of a basal marine erosional platform

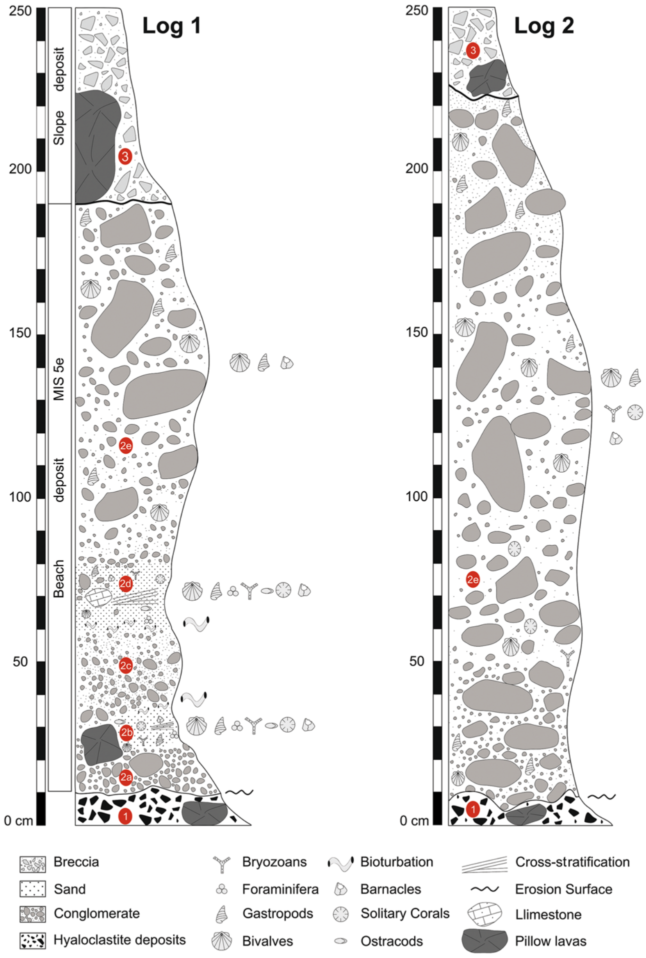

Figure 9. Simplified strip logs of the Ponta do Cedro outcrop, representing main lithologies, sedimentary structures, contacts and fossiliferous content. Numbers correspond to the described depositional units. For the location of the logs, please refer to Fig. 8. [Color figure can be viewed at wileyonlinelibrary.com]

with a 2° to 3° slope that extends for 26.5 m in length from sea level to the cliff wall, where a wave-cut notch with a beach deposit is present (for a complete 3D model of the westernmost sector of the outcrop, see Figs. S1 and 8(B),(C)). This platform shaped like a small amphitheatre is 15.5 m wide (Fig. 6(B), and bordered by two rocky spurs, flanking and protecting the beach deposit (Fig. 10). The beach deposit left inside the wave-cut notch has a maximum thickness of ~2 m and corresponds to a very coarse sedimentary deposit, a clast- to matrix-supported cobble to boulder conglomerate (Fig. 7(B)) with a coarse-grained matrix (sandy-gravelly; Figs. 7(C) and 8(B),(D)). The matrix is more abundant at the top, where it is well graded with small pebbles and some layers of very fossiliferous

Table 1. Species newly reported for the MIS 5e fossil record of Santa Maria (SMA) Island (Azores Archipelago).

	New record for the	
Species	MIS 5e of SMA	World fossil record
Arca noae	1	
Gregariella semigranata (*)	1	1
Limaria loscombi	1	
Thracia phaseolina	1	
Aplysia sp. (ǂ)	1	1
Caecum clarkii	1	
Creseis virgula (*)	1	1
Limacina lesueurii (*)	1	1
Limacina helicina (*)	1	1
Episcomitra zonata	1	1
Parviturbo azoricus (*)	1	
Pseudomelampus exiguus (ǂ, *)	1	1
Raphitoma sp.	1	
Rissoella ermelindoi (*)	1	1
Talassia tenuisculpta (ǂ, *)	1	1

Genus (ǂ) or Species (*) reported for the first time to the world fossil record.

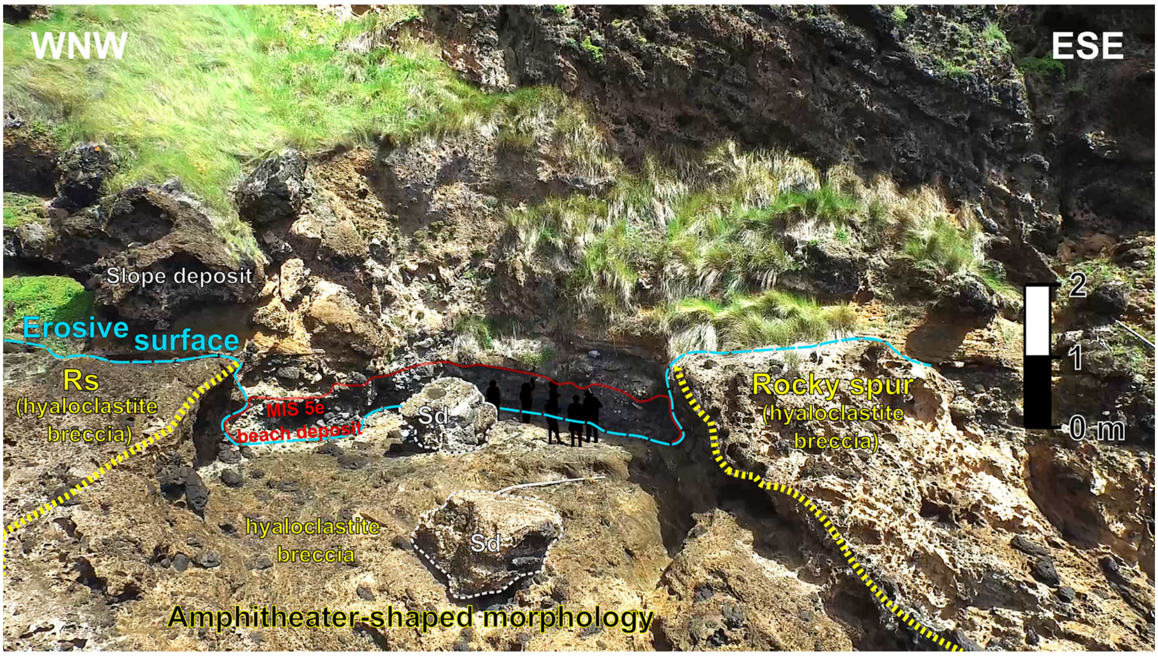

Figure 10. Aerial view showing the most relevant geomorphological features of the western sector of the MIS 5e deposit at Ponta do Cedro, namely, the amphitheatre-shaped morphology and the two rocky spurs (Rs). Sd, slope deposit. [Color figure can be viewed at wileyonlinelibrary.com]

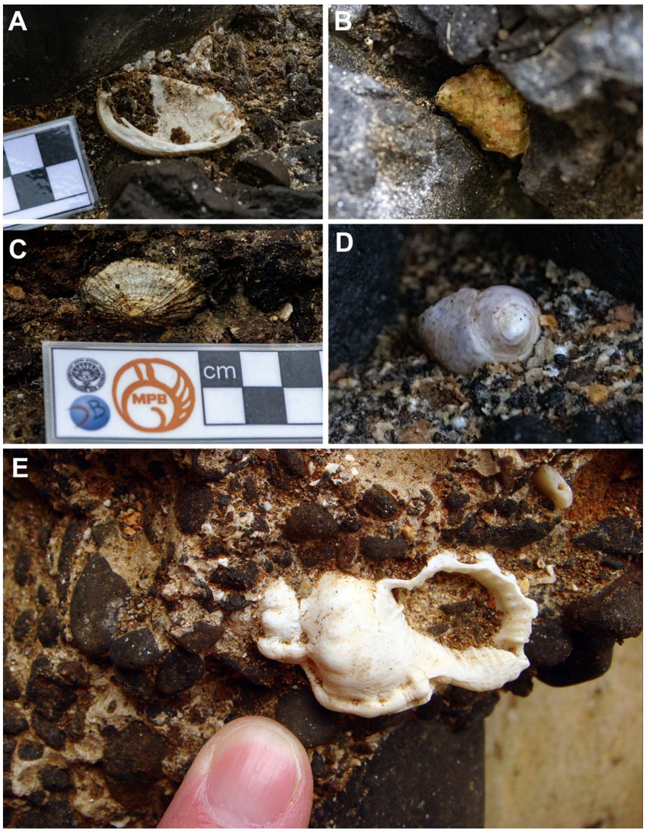

Figure 11. Some common mollusc species reported to the MIS 5e deposits of Ponta do Cedro from Santa Maria Island (Azores) photographed in the field. (A) *Haliotis tuberculata* Linnaeus, 1758. (B) *Stramonita haemastoma* (Linnaeus, 1767). (C) *Patella aspera* Röding, 1798. (D) *Gibbula delgadensis* F. Nordsieck, 1982. (E) *Talisman scrobilator* (Linnaeus, 1758) (31.0 mm). [Color figure can be viewed at wileyonlinelibrary.com]

bioclastic sand. We selected and measured 40 of the largest boulders present in the deposit. The largest of these boulders was 56 × 33 cm and the smallest was 21 × 12 cm (average boulder dimensions: 38 × 18 cm). The bioclastic component is more prevalent at the base of the deposit, where the matrix is less abundant. The pebbles, cobbles and blocks are essentially basaltic, but there are also calcarenites and fragments of the hyaloclastitic unit. The source of the sediment is the adjacent Pliocene cliff, made up of basaltic pillow lavas, hyaloclastites, pillow breccias and terrigenous sediments (Figs. 3 and 4).

Lateral facies variations in the deposit suggest a decrease in hydrodynamic conditions towards the deposit's periphery. The western end features a basal layer in which smaller pebbles predominate (almost no blocks occur), and beds of fine sand, rich in heavy minerals, with some laminar and cross-stratification (Figs. 8(B) and 9). Bioturbation structures by randomly oriented *Macaronichnus segregatis* Clifton and Thompson, 1978 (Fig. 8(C′),(C″)) are visible at the top of this basal layer, suggesting phases of low hydrodynamic conditions [Fig. 8(A) (see the location of log 1), 8(B),(C) and 9]. Conversely, the eastern end displays blocks, pebbles and cobbles mainly arranged in a stable position, with the minor axis perpendicular to the surface (Fig. 8(D)) and with no sand in the matrix, indicating lower transport energy (see the location of log 2; Figs. 8(D) and 9).

Above the beach deposit, and abutting the cliff, lies a slope deposit (Figs. 8(A) and 10). Stratification at the base suggests episodic run-off events, while the upper sections are more massive and incorporate large hyaloclastite blocks.

Palaeobiodiversity and palaeoecology

Molluscs (gastropods and bivalves) were the most abundant marine group found in the samples analysed from Ponta do Cedro. Additionally, remains of foraminifers [including *Miniacina miniacea* (Pallas, 1766)], crustaceans (ostracods, decapods

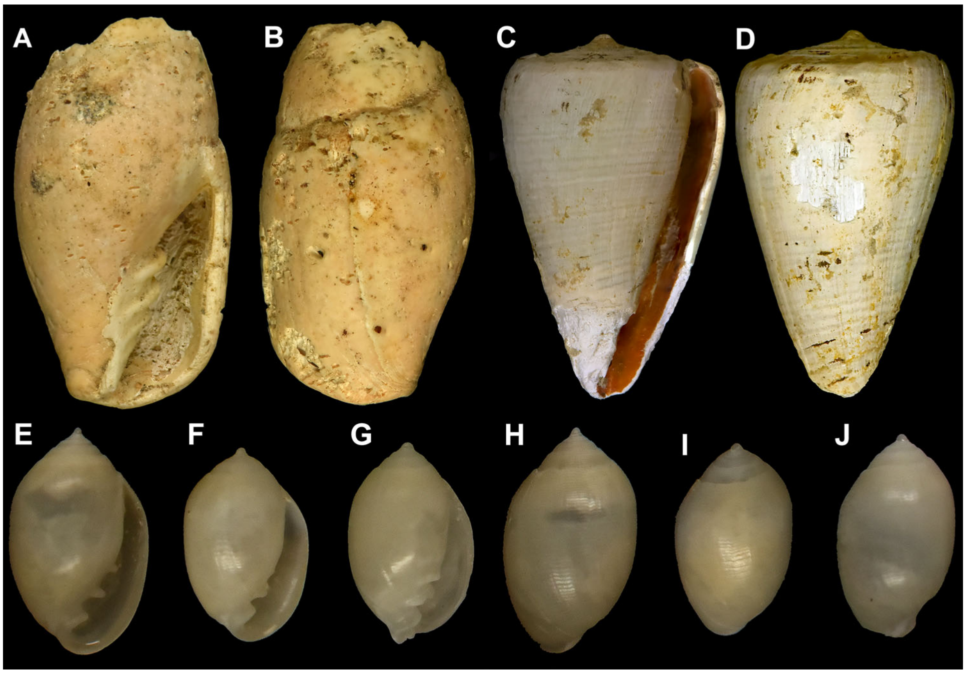

Figure 12. New mollusc species reported to the MIS 5e deposits of Ponta do Cedro (Santa Maria Island, Azores). (A, B) *Episcomitra zonata* (Marryat, 1819), DBUA-F 1184, broken specimen, 17.5 mm. (C, D) *Conus venulatus* Hwass in Bruguière, 1789–1792, DBUA-F 1184, 29.0 mm. (E–J) *Pseudomelampus exiguus* (R. T. Lowe, 1832), DBUA-F 1156. (E–G) Ventral view. (H–J) Dorsal view. (E, H) 35.0 mm. (F, I) 28.0 mm. (G, J) 30.0 mm. [Color figure can be viewed at wileyonlinelibrary.com]

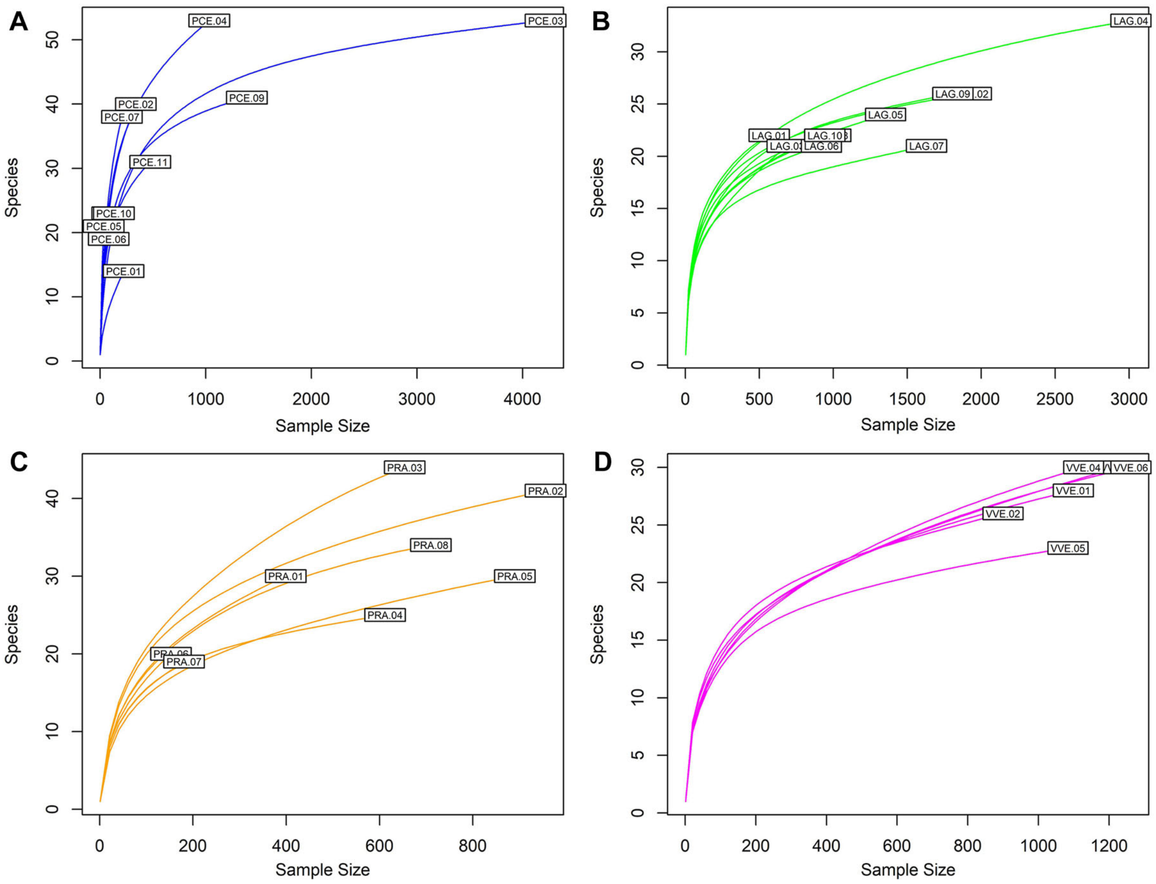

Figure 13. (A–D) Species count estimates with the Chao estimator for the quantitative samples of the four MIS 5e outcrops in Santa Maria Island. (A) Ponta do Cedro. (B) Lagoinhas. (C) Prainha. (D) Vinha Velha. Several new species may be expected to be found at Ponta do Cedro if the collecting effort is increased, because the curves do not reach the horizontal asymptote for most of the samples used, with the single exception of PCE-03. Rarefaction curves were computed using the total sum of individuals per 1 kg-bulk sample (individual rarefaction), with no extrapolation. [Color figure can be viewed at wileyonlinelibrary.com]

(primarily chelae of unidentified crabs) and barnacles), corals and bryozoans were also recovered. A total of 8252 mollusc individuals distributed among 94 specific taxa (15 bivalve species and 79 gastropod taxa; cf. Fig. 11) were counted from the 11 MIS 5e quantitative sediment samples from Ponta do Cedro (Table S1). Notably, 15 new species' records (11 gastropods and 4 bivalves; Table 1 and Fig. 12) increase the total number of fossil molluscs reported from the Santa Maria MIS 5e highstand deposits to 160 specific taxa (132 Gastropoda and 28 Bivalvia; Tables S2 and S3). Two gastropod species were found only in the qualitative samples: *Rissoella alexandrae* (S. P. Ávila & Cordeiro, 2015) and *Episcomitra zonata* (Marryat, 1819) (cf. Fig. 12(A),(B)). It is worth emphasising that nine taxa/species and three genera are reported herein for the first time in the global/world fossil record (cf. Table 1), for example, *Aplysia* sp., *Creseis virgula* (Rang, 1828), *Pseudomelampus exiguus* (R. T. Lowe, 1832) (Fig. 12(E)–(J)) and *Talassia tenuisculpta* (R. B. Watson, 1873). Of these, all except *T. tenuisculpta* are still present in the Azores today. *Talassia tenuisculpta* is reported today from Biscay Gulf to Galicia, the Mediterranean Sea and the Madeira and Canaries archipelagos. Its presence in the MIS 5e deposits of Santa Maria is another adding to the list of 26 taxa (21 gastropods and five bivalves) that expanded their geographic ranges during the Last Interglacial, reaching and colonising the Azorean shores, before being extirpated during the Last Glacial episode (Table 3).

The biological association at Ponta do Cedro reveals a high species diversity, with a predominance of juvenile individuals. By individual sample, the number of mollusc taxa at Ponta do Cedro MIS 5e western section ranges from a minimum of 14 (sample PCE-01) to a maximum of 53 taxa (PCE-03 and PCE-04), while the number of individuals ranges from 35 (PCE-05) to 4218 (PCE-03; cf. Table 5).

Regarding the comparisons of diversity among samples/sites, the Chao estimator applied to the 11 quantitative samples from Ponta do Cedro predicts the presence of additional 18 species likely missed due to undersampling. When applied to the entire data set (Table S1), that is, including all the 35 quantitative samples from four MIS 5e sites—Ponta do Cedro (11 samples), Lagoinhas (10), Prainha (8) and Vinha Velha (6)—the Chao estimator predicts that 20 additional species are expected to be found in Santa Maria, if the sampling effort increases. Rarefaction curves support this, with 10 of the 11 quantitative samples from Ponta do Cedro far from reaching a horizontal asymptote, indicating that species richness at this site is not saturated (Fig. 13). This contrasts with the other MIS 5e outcrops from Santa Maria, where species richness appears to be more saturated. Comparison of Hill's numbers showed that the number of species (Hill's $q = 0$) was significantly lower at Lagoinhas compared to Ponta do Cedro, but otherwise similar among the remaining locations (Fig. 17; Table 7). When considering Hill's numbers $q = 1$ and $q = 2$, the diversity of molluscs at Ponta do Cedro was significantly greater than that in the other three outcrops, in both cases (Fig. 17; Table 7).

Both heatmap (Fig. 14) and cluster analyses (Fig. 15) show a similar pattern: the high within-locality similarity of Lagoinhas and Vinha Velha samples, which is expressed in a low dissimilarity within samples from each of these two outcrops (Fig. 14), produces two well-defined clusters: the first with all 10 samples of Lagoinhas and the second with all six samples from

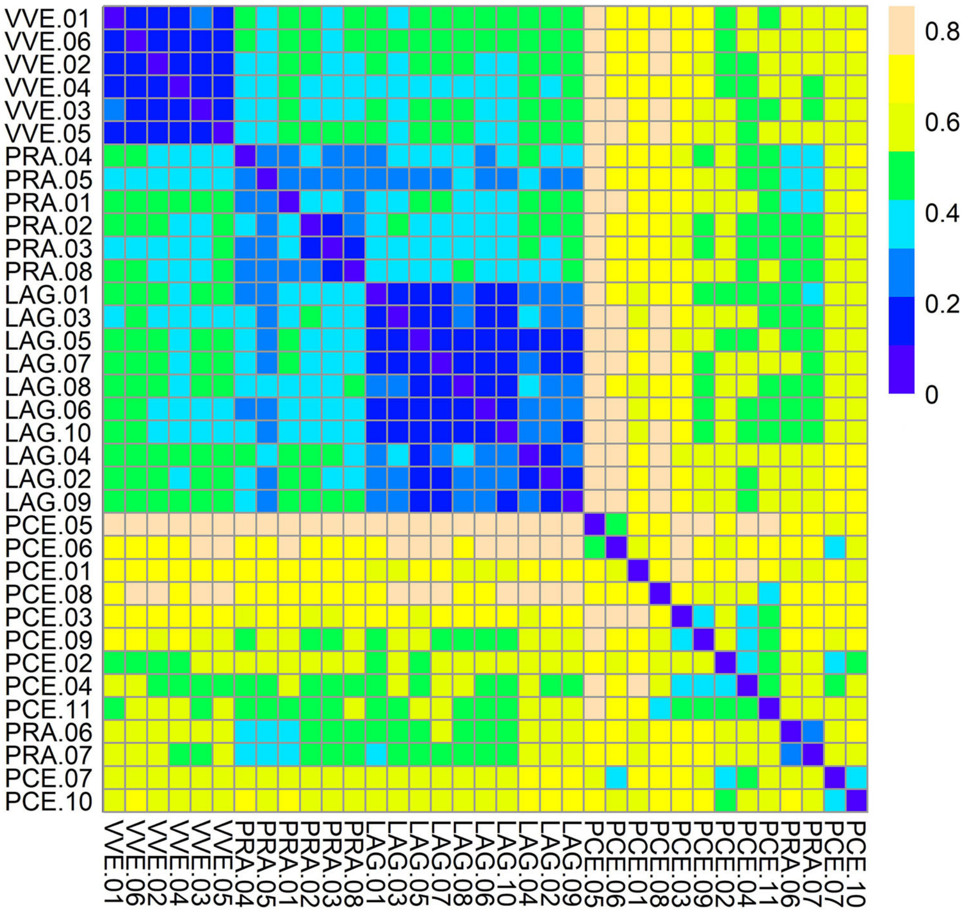

Figure 14. Heatmap based on log-transformed species abundances and Bray–Curtis dissimilarities of the palaeocommunities found at the four outcrops. LAG, Lagoinhas; PCE, Ponta do Cedro; PRA, Prainha; VVE, Vinha Velha. [Color figure can be viewed at wileyonlinelibrary.com]

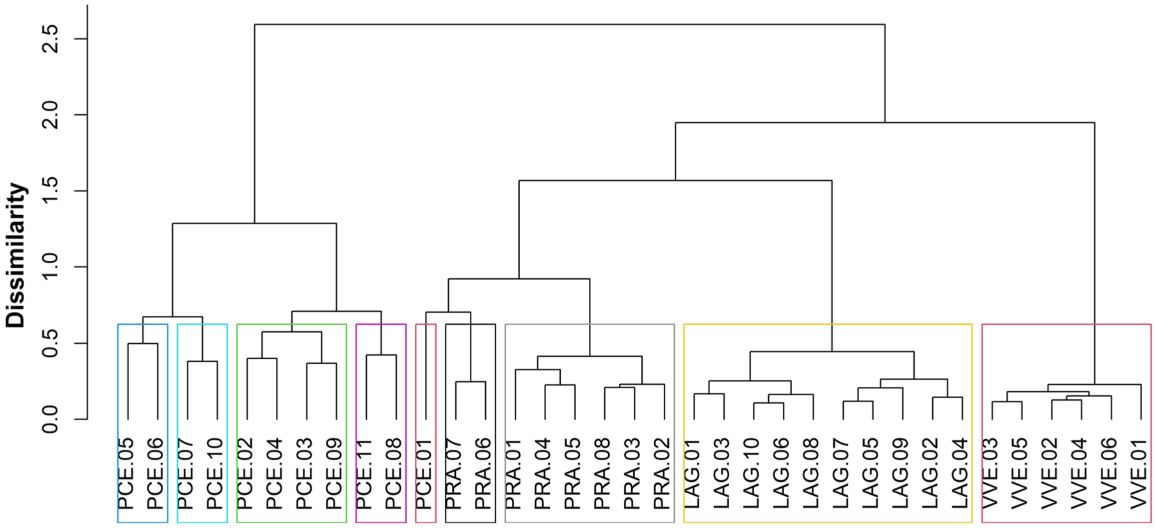

Figure 15. Similarities based on log-transformed species abundances of the palaeocommunities found at the four outcrops. In total, 35 samples of fossiliferous sediments were used, each of 1 kg. Dendrogram based on Ward's clustering of a matrix of Bray–Curtis dissimilarities. Both the analysis of silhouette width and Mantel statistic suggested an optimal number of nine groups. LAG, Lagoinhas; PCE, Ponta do Cedro; PRA, Prainha; VVE, Vinha Velha. [Color figure can be viewed at wileyonlinelibrary.com]

Vinha Velha. In contrast, the higher within-locality dissimilarity of Prainha and Ponta do Cedro samples expressed in the heatmap of Fig. 14 is responsible for the five clusters for Ponta do Cedro samples and two clusters for the Prainha samples (Fig. 15).

Indicator species analysis (IndVal) identified 22 species with significant indicator values among the 90 MIS 5e species. Ponta do Cedro is characterised by the presence (and abundance) of 12 species, the most important being *Ervilia castanea* (Montagu, 1803), *Tectura virginea* (O. F. Müller, 1776), *Sinezona cingulata* (O. G. Costa, 1861), *Botryphallus ovummuscae* (Gofas, 1990), *Mitrella broderipi* (G. B. Sowerby I, 1844) and *Alvania angioyi* van Aartsen, 1982, all with high IndVal ($I > 0.700$) (Table 2; Fig. 16). Vinha Velha is distinguished from the remaining outcrops by the presence/abundance of *Coralliophila meyendorffii*

Table 2. Results of indicator species analysis using IndVal. From a total number of 90 species, 22 were selected as having indicator value: 13 species were associated with one group and nine species were associated with two groups.

PCE	***I***	***p***	**PCE + PRA**	***I***	***p***	**PCE + LAG + PRA**	***I***	***p***
Ervilia castanea	0.905	0.005**	*Tetrarca tetragona*	0.761	0.010**	*Manzonia unifasciata*	0.952	0.005**
Tectura virginea	0.834	0.005**	*Tectarius striatus*	0.759	0.010**	*Claremontiella nodulosa*	0.871	0.020*
Sinezona cingulata	0.798	0.005**	*Skeneopsis planorbis*	0.725	0.015*			
Botryphallus ovummuscae	0.797	0.005**	*Parvicardium vroomi*	0.697	0.030*			
Mitrella broderipii	0.758	0.005**	*Papillicardium papillosum*	0.649	0.035*	**LAG + PRA + VVE**	***I***	***p***
Alvania angioyi	0.720	0.020*				*Melarhaphe neritoides*	0.979	0.005**
Caecum sp.	0.674	0.005**	**LAG + PRA**	***I***	***p***	*Alvania poucheti*	0.930	0.005**
Pedipes pedipes	0.674	0.010**	*Tectonatica prietoi*	0.682	0.020*	*Cingula trifasciata*	0.888	0.015*
Vitreolina philippi	0.674	0.010**	*Calliostoma lividum*	0.666	0.050*	*Mitromorpha azorensis*	0.857	0.005**
Leucophytia bidentata	0.658	0.010**				*Ocinebrina aciculata*	0.751	0.015*
Crisilla postrema	0.644	0.020*	**VVE + PRA**	***I***	***p***	*Pseudopusula grohorum*	0.736	0.010**
Pseudomelampus exiguus	0.603	0.050*	*Lucinella divaricata*	0.979	0.005**			
			Cardita calyculata	0.928	0.005**			
						PCE + PRA + VVE	***I***	***p***
PRA	***I***	***p***	**PCE + VVE**	***I***	***p***	*Patella aspera*	0.880	0.01**
Bosemprella incarnata	0.935	0.005**	*Myosotella myosotis*	0.840	0.005**			
Laevicardium crassum	0.707	0.010**						
			VVE	***I***	***p***			
			Coralliophila meyendorffii	0.969	0.005**			
LAG	***I***	***p***	Vermetidae	0.892	0.005**			
Cerithiopsis sp.	0.876	0.005**	*Patella candei*	0.889	0.005**			
			Lamellaria sp.	0.577	0.020*			

IndVal (I) and probability value (*p*). LAG, Lagoinhas; PCE, Ponta do Cedro; PRA, Prainha; VVE: Vinha Velha. Significance codes for *p*-values: ***(0.001), **(0.01) and *(0.05).

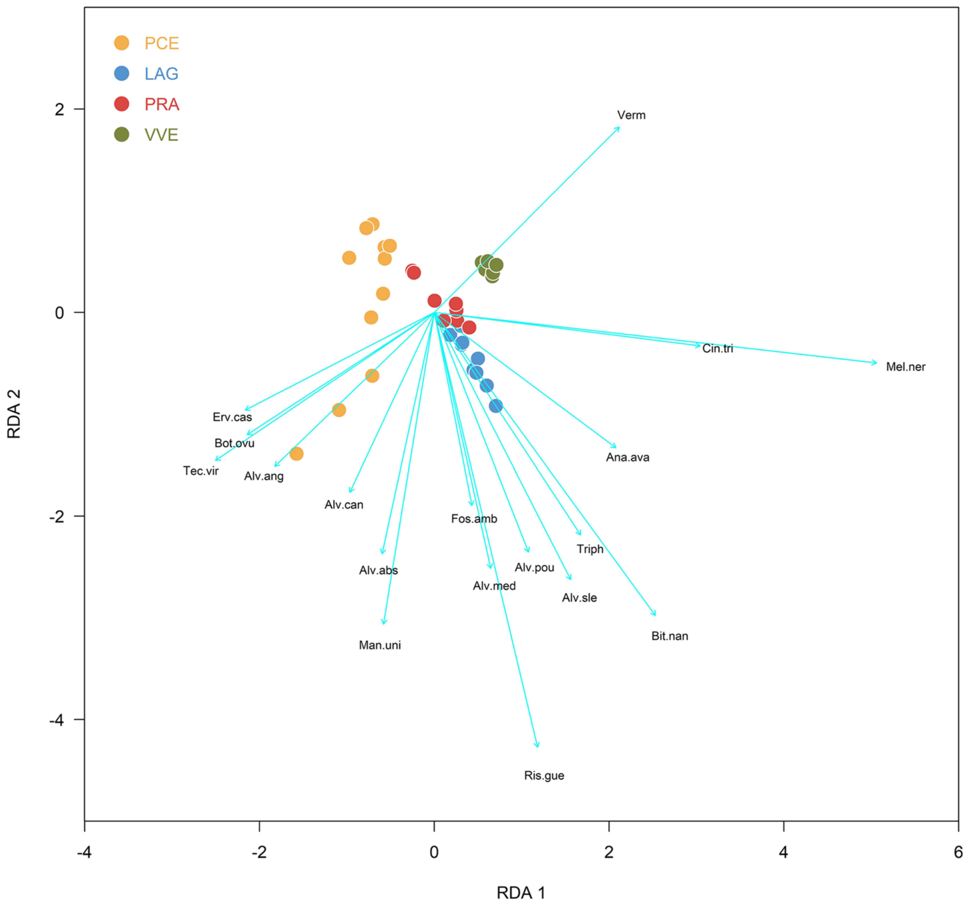

Figure 16. Redundancy analysis based on the IndVal, with species and samples projected in a 2D space. Alv.abs, *Alvania abstersa*; Alv.ang, *Alvania angioyi*; Alv.can, *Alvania cancellata*; Alv.med, *Alvania mediolittoralis*; Alv.pou, *Alvania poucheti*; Alv.sle, *Alvania sleursi*; Ana.ava, *Anachis avaroides*; Bit.nan, *Bittium nanum*; Bot. ovu, *Botryphallus ovummuscae*; Cin.tri, *Cingula trifasciata*; Erv.cas, *Ervilia castanea*; Fos.amb, *Fossarus ambiguous*; Man.uni, *Manzonia unifasciata*; Mel.ner, *Melarhaphe neritoides*; Ris.gue, *Rissoa guernei*; Tec.vir, *Tectura virginea*; Triph, Triphoridae; Verm, Vermetidae. [Color figure can be viewed at wileyonlinelibrary.com]

Table 3. List of species that were found in the MIS 5e outcrops of Santa Maria Island, but that do not occur at the present times in the Azores Archipelago (cf. Cordeiro et al., 2015), and their current geographic distribution. These marine mollusc taxa are inferred to have been extirpated

Species	Class	MAD	SEL	CAN	CAB	BER	NOR	BRI	GAL	POR	MED	MOR	WES	MAU	SEN	GUI	GSL
Ensis minor	Bivalvia						1	1	1	1	1	1					
Glycymeris glycymeris	Bivalvia						1	1	1	1	1	1					
Laevicardium crassum	Bivalvia	1		1			1	1	1	1	1	1					
Leiosolenus aristatus	Bivalvia	1	1	1	1					1	1	1	1	1	1	1	1
Lucinella divaricata	Bivalvia	1		1				1	1	1	1	1					
Alvania aff. *tesselata*	Gastropoda										1						
Alvania sp.	Gastropoda																
Claremontiella nodulosa	Gastropoda				1	1									1		
Conus sp. 1	Gastropoda																
Conus ambiguus	Gastropoda				1									1	1		1
Conus ermineus	Gastropoda				1												
Conus miruchae	Gastropoda				1												
Conus roeckeli	Gastropoda				1												
Conus ventricosus	Gastropoda									1	1						
Conus venulatus	Gastropoda				1												
Gemophos viverratus	Gastropoda		1	1	1										1		1
Linatella caudata	Gastropoda			1	1	1		1									
Mitrella broderipii	Gastropoda	1	1	1						1	1						
Polinices lacteus	Gastropoda	1		1	1	1											
Raphitoma philberti	Gastropoda			1						1	1						
Seila trilineata	Gastropoda			1							1						
Semicassis granulata	Gastropoda	1	1	1	1					1	1						
Talassia tenuisculpta	Gastropoda	1		1					1		1						
Zebina paivensis	Gastropoda	1	1	1							1						
Zonaria picta	Gastropoda				1										1		
Zonaria pyrum	Gastropoda			1						1	1			1	1		1
Total		8	5	13	12	3	3	5	5	10	14	5	1	3	6	1	4

ANG, Angola; BER, Bermuda Island; BRI, British Isles; CAB, Cabo Verde Archipelago; CAM, Cameroon; CAN, Canaries Archipelago; CON, Congo and Democratic Republic of Congo (Zaire); GAB, Gabon and Equatorial Guinea; GAL, Galicia; GHA, Ghana; GSL, Guiné, Sierra Leone and Liberia; GUI, Guinea Bissau; IVO, Ivory Coast; MAD, Madeira Archipelago; MAU, Mauritania; MED, Mediterranean Sea; MOR, Atlantic shores of Morocco; POR, Portugal; NOR, Norway; SEL, Selvagens Archipelago; SEN, Senegal; STP, São Tomé, Príncipe and Annobon; VIR, Virginian Biogeographic

(Calcara, 1845), Vermetidae spp. (Fig. 16) and *Patella candei* A. d'Orbigny, 1840, whereas Prainha is mainly characterised by the bivalve *Bosemprella incarnata* (Linnaeus, 1758) and Lagoinhas by the gastropod *Cerithiopsis* sp. (Table 2). Ponta do Cedro and Vinha Velha share the presence of the ellobiid *Myosotella myosotis* (Draparnaud, 1801); five species [*Tetrarca tetragona* (Poli, 1795), *Tectarius striatus* (P. P. King, 1832), *Skeneopsis planorbis* (O. Fabricius, 1780), *Parvicardium vroomi* van Aartsen, Menkhorst & E. Gittenberger, 1984 and *Papillicardium papillosum* (Poli, 1791)] are typical from the group Ponta do Cedro + Prainha; and finally, two species each characterise the groups Prainha + Lagoinhas (*Tectonatica prietoi* (Hidalgo, 1873) and *Calliostoma lividum* Dautzenberg, 1927) and Prainha + Vinha Velha [*Lucinella divaricata* (Linnaeus, 1758) and *Cardita calyculata* (Linnaeus, 1758)] (Table 2).

In the western section of Ponta do Cedro MIS 5e deposit, the most abundant mollusc species are the endemic Azorean gastropods *Alvania mediolittoralis* Gofas, 1989, which accounts for 37.83% of all individuals, and *Bittium nanum* (Mayer, 1864), with 11.11%. Eight additional gastropod species account for 23.93%, with proportions ranging from 3.83% (*Tectura virginea*) to 2.13% [*Paludinella globularis* (Hanley, 1844)]. The first bivalve species in the ranking is *Ervilia castanea,* which accounts only for 1.81% of the total (Table 6). The most abundant mollusc species at Ponta do Cedro are associated with hard grounds, rocky or gravel bottoms, and the majority of species show bathymetric distributions spanning from strictly intertidal species [e.g., *Fossarus ambiguus* (Linnaeus, 1758) and *Leucophytia bidentata* (Montagu, 1808)] to littoral species (0–50 m) (cf. Table 6).

Functional diversity analysis: alpha diversity

The overall database comprises a total of 420 mollusc specific taxa: 160 from the MIS 5e deposits (Table S3) and 365 modern species (Table S4). After removing species with incomplete information on functional traits, the final data set includes 385 mollusc taxa: 132 from the MIS 5e and 320 from the modern species list.

The lowest mean absolute deviation (*mad* = 0.0499; cf. Fig. S2), calculated using the *quality.fspaces* function of the mFD software package, corresponds to a total of eight axes to be selected as best representing the multidimensional functional space, accounting for 87% of the variation in the assemblages.

Comparison of the box and whisker plots resulting from the alpha-diversity indices calculated for each of the four MIS 5e outcrops studied (Ponta do Cedro, Prainha, Lagoinhas, and Vinha Velha; cf. Table S5) reveals significant statistical differences between the outcrops for all diversity indices, except for SpRic, FRic and FDis, which show no meaningful differences (Fig. 18). In contrast, when using rarefaction to control for differences in sample size ($n = 75$ taxa/species), the comparison of alpha-diversity indices for the entire MIS 5e data set (132 taxa) and the modern Azorean malacofauna (320 species) indicates significant statistical differences for all diversity indices (Fig. 19). Interestingly, the values for all functional alpha-diversity indices are higher in the modern from the Azorean shores during the course of the Last Glaciation.

Geographical distribution												
IVO	GHA	STP	CAM	GAB	CON	ANG	VIR	CRL	GOM	CAR	BRA	ARG
							1	1	1			
		1										
						1						
1	1	1	1	1	1	1		1	1	1		
		1										
	1	1		1		1			1	1	1	
	1			1		1						
		1		1		1			1	1	1	
	1	1	1	1	1	1						
							1	1	1	1	1	
		1		1					1	1	1	1
		1		1				1	1	1	1	1
						1						
1	4	8	2	7	2	7	2	4	7	6	5	2

Province; WES, Western Sahara (sensu Ávila et al., 2012). ARG, Argentina; BRA, Brazil; CAR, Caribbean; CRL, Carolinian Biogeographic Province; GOM, Gulf of Mexico. The regions of most probable origin of the species that reached and colonised the Azores during the final phase of glacial termination 2 or during the initial times of the MIS 5e, as hypothesised by Ávila et al. (2019), are highlighted in dark grey.

assemblage compared to the MIS 5e assemblage, with the exception of FDiv, which shows higher values in the MIS 5e molluscs (Fig. 19). The detailed positioning of each species in the functional space, based on the first three axes of the PCoA, is shown in Figs. 20 and S3.

Functional diversity analysis: beta diversity

The results from the dissimilarity index (diss.) used to calculate the multidimensional functional beta-diversity (Baselga, 2012; Villéger et al., 2013) reveal that the turnover value (turn_diss. = 0.0655) is significantly lower than the nestedness-resultant value (nest_diss = 0.3760).

Discussion

Palaeoenvironmental reconstruction of Ponta do Cedro and comparison with other MIS 5e outcrops

Ricchi et al. (2018) demonstrated that the submarine and subaerial erosional terraces resulting from the uplift of Santa Maria Island, in combination with sea-level variations, have a polygenetic origin. This means that older interglacial highstands, such as those during MIS 9 (337–300 kyr) and MIS 11 (424–374 kyr), might have contributed to the formation of wave-cut notches (Fig. 5(F)) and irregular shore platforms (facies 1, Fig. 9) by marine erosion atop volcanic products during these transgressive episodes, as seen in all studied outcrops (cf. Figs. 6(B) and 10). However, relevant differences are observed when the geological sections of the four MIS 5e outcrops are compared. During the MIS 5e relative sea-level rise, boulder and cobble beaches (facies 2a, 2c, and 2e; Fig. 9) were deposited on top of the shore platform at Ponta do Cedro, Prainha and Lagoinhas, but not at Vinha Velha. At Prainha, Lagoinhas and Vinha Velha (but not at Ponta do Cedro), these shore conglomerates were overlaid and stabilised by a coralline algal biostrome that developed in a shallow-marine, high-energy (shoreface) environment (Ávila et al., 2009a, 2010). Again, at Prainha, Lagoinhas and Vinha Velha (but not at Ponta do Cedro), layers of poorly consolidated sands cover the algal biostrome, with wave–ripple cross-bedding and cross-lamination indicative of a shoreface to foreshore depositional setting (Ávila et al., 2009a, 2010, 2015b, 2018). At Ponta do Cedro, two layers of typically black and poorly consolidated sands with wave–ripple cross-bedding and cross-lamination are also evident (facies 2b and 2 d; Fig. 9). These layers, each less than 20 cm thick, are situated between boulder and cobble beach layers and do not cover an algal biostrome, which is absent at Ponta do Cedro. Finally, the regressive trend following the maximum sea-level rise during MIS 5e is recorded by aeolian dunes at all sites, except Ponta do Cedro. The combination of biogenic sand particles was derived from the skeletal remains of molluscs, echinoderms, bryozoans and coralline algae, with black, basaltic sands. As at Ponta do Cedro (facies 3, Fig. 9), colluvial–alluvial deposits seal all studied deposits.

At a local scale, the two small spurs that border the Ponta do Cedro MIS 5e deposit likely protected it from marine

Table 4. Multidimensional functional alpha-diversity indices computed by the mFD R package for the Last Interglacial (MIS 5e) and the recent molluscs (gastropods + bivalves) of the Azores Archipelago.

Functional alpha-diversity index	Acronym	MIS 5e	Recent
Species richness	SpRic	132	320
Functional richness	FRic	0.1212	0.8060
Functional evenness	FEve	0.7363	0.7967
Functional divergence	FDiv	0.8067	0.8637
Functional dispersion	FDis	0.6662	0.7754
Functional originality	FOri	0.2163	0.2648
Functional specialisation	FSpe	0.5717	0.5816
Functional mean pairwise distance	FMPD	0.6056	0.6957
Functional mean nearest neighbour distance	FNND	0.2694	0.2802

Table 5. Species richness (SpRic) and abundance (*N*, number of individuals) per replicate. The remaining abbreviations are as in Table 2.

Sample	SpRic	*N*
PCE-01	14	223
PCE-02	40	339
PCE-03	53	4218
PCE-04	53	1035
PCE-05	21	35
PCE-06	19	82
PCE-07	38	208
PCE-08	23	115
PCE-09	41	1390
PCE-10	23	131
PCE-11	31	476
LAG-01	22	567
LAG-02	26	1933
LAG-03	21	689
LAG-04	33	3013
LAG-05	24	1354
LAG-06	21	920
LAG-07	21	1631
LAG-08	22	983
LAG-09	26	1809
LAG-10	22	937
PRA-01	30	608
PRA-02	41	3428
PRA-03	44	943
PRA-04	25	799
PRA-05	30	2097
PRA-06	20	279
PRA-07	19	215
PRA-08	35	2519
VVE-01	28	1099
VVE-02	26	900
VVE-03	30	1225
VVE-04	30	1128
VVE-05	23	1084
VVE-06	30	1262

erosion, and are probably responsible for its preservation within the wave-cut notch to this day. A decrease in the prevalent hydrodynamic conditions is evident on the southwestern side of the deposit, where the geological characteristics of the deposit suggest phases of low energy, with no visible blocks, small pebbles predominating and beds of fine sand with cross-stratification and bioturbation structures at the top, including *Macaronichnus segregatis*. Most fossils were collected at this site, from small pockets of sand (facies 2b and 2 d; Fig. 9) at the base of the deposit, where the matrix is less abundant.

Palaeobiodiversity

While molluscs are the most abundant and diversified marine group collected in the MIS 5e samples from Santa Maria Island (Ávila et al., 2002, 2007, 2009a, 2010, 2015b, 2025), other groups have also been sampled on the island, including coralline algae forming rhodoliths (Rebelo et al., 2021), echinoderms (Madeira et al., 2011, 2019), decapod crustacean crabs (Hyžný et al., 2021), fishes (Ávila et al., 2020a) and whales (Ávila et al., 2015c). Crustacean ostracods, barnacles, corals and bryozoans have also been collected but await detailed study.

The present work highlights the remarkable palaeobiodiversity of the MIS 5e molluscs' fossil record of Santa Maria Island, with three genera of gastropods reported herein for the first time to the world fossil record: Aplysia Linnaeus, 1767; *Pseudomelampus* Pallary, 1900, and Talassia Warén and Bouchet, 1988 (Table 1). Moreover, the 15 new records of molluscs (11 gastropods and four bivalves) make Santa Maria Island one of the islands worldwide with a higher MIS 5e palaeobiodiversity (160 taxa), as well as the island with a higher percentage of MIS 5e species in relation to the present number of shallow-water marine molluscs (44.2%; cf. Table 8). By comparison, only 83 taxa are equally reported from the MIS 5e fossil record of both Madeira (17.9%) and Cabo Verde (12.9%) archipelagos, and only 19 taxa from the Selvagens Archipelago (9.8%). Canaries hold a higher number of mollusc taxa reported from the archipelago's MIS 5e outcrops (269 taxa), but in comparison with the total number of modern molluscs, it accounts only to 29.1% (Table 8). The MIS 5e fossil record seems to be better represented in islands than in continents. In fact, the only continental site within the Atlantic or the Mediterranean with a significant number of MIS 5e molluscs is located along the coasts of the Virginian Biogeographic Province, with a total of 173 taxa (62.9% of the total number of recent molluscs reported from this biogeographic province; Table 8). The Mediterranean is a very well-studied region, holding an impressive 316 taxa of MIS 5e marine molluscs (22.5% in relation to the total number of recent molluscs; Table 8). This is in contrast with only 170 MIS 5e taxa reported from the Caribbean region (6.2%) and 95 taxa reported from the MIS 5e outcrops located in the coasts of the Gulf of Mexico (6.1%).

The outstanding palaeobiodiversity of the MIS 5e molluscs' fossil record of Santa Maria Island is further highlighted by the results of the Chao estimator suggesting that 18 species might actually be present at Ponta do Cedro outcrop but were missed due to undersampling. Moreover, when all outcrops are considered, around 20 more species are expected to be found in Santa Maria if the sampling effort increases (cf. Fig. 13).

Palaeoecology

During the sorting process of the quantitative samples collected at the western section of the Ponta do Cedro MIS 5e outcrop, we observed a very high number of juvenile individuals, a pattern that was consistent across most species collected. We interpret this as the result of a natural sieving process, facilitated by the cobbles and pebbles located above the sandy layers. These interspaces between cobbles/pebbles likely allowed the shells and remains of dead marine organisms to concentrate preferentially within the basal sandy layers. Organic material, particularly detached fragments of algae, likely followed the same trend, concentrating at this level, and attracting herbivores and grazers. This sorting process appears to have been driven by gravity and leaching over the lifetime of the beach, leading to the accumulation of

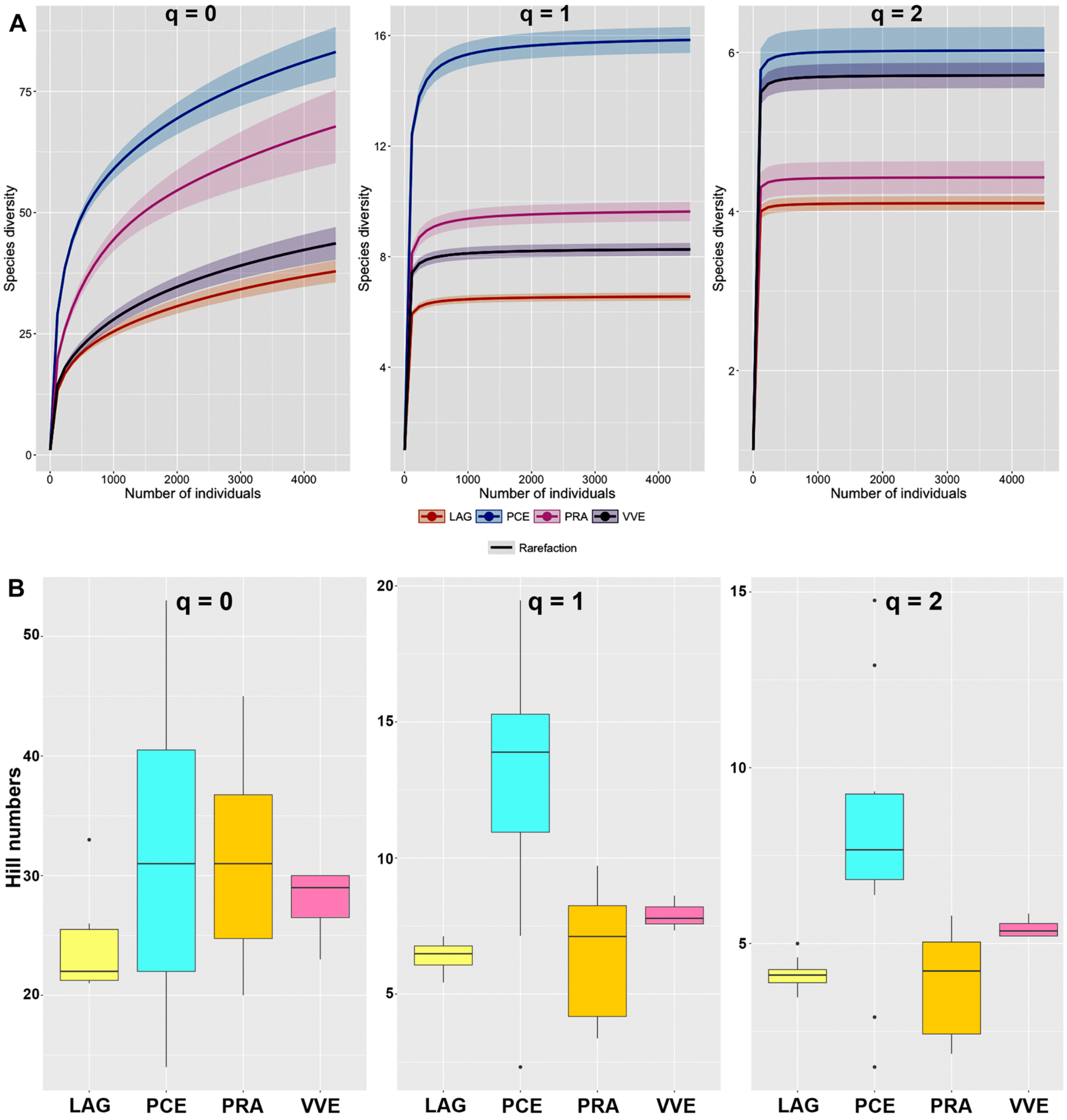

Figure 17. (A) Relation between the number of individuals and the estimated number of species (samples pooled by outcrop). Hill numbers ($q = 0$ for species richness, $q = 1$ for the exponential of Shannon's entropy index and $q = 2$ for the inverse of Simpson's concentration index) were used to estimate the numbers of species in a sample of 50 individuals (ES_{50}). (B) Comparison of the box and whisker plots resulting from the Hill numbers calculated for each of the four studied MIS 5e outcrops. Median values of replicates are represented by the black bar inside the box. Whiskers show the first and third quartiles of data. Outliers are represented by open circles outside of the first and third quartiles. LAG, Lagoinhas; PCE, Ponta do Cedro; PRA, Prainha; VVE, Vinha Velha. [Color figure can be viewed at wileyonlinelibrary.com]

organic material, living individuals and shells at the top and in between the interstices of the sandy layers (facies 2b and 2 d; Fig. 9). The preferential accumulation of microfossils towards the base of the deposit, in association with a sparse sand matrix, corroborates our hypothesis that fine components were primarily transported through the interstices of the coarse deposit by gravity.

The most abundant species found at Ponta do Cedro are associated with hard grounds, rocky shores and gravel environments covered by algae (Table 6). This situation also occurs at Lagoinhas and Vinha Velha, but at Prainha, species associated with sandy environments are also important (e.g., the bivalves *Lucinella divaricata* and *Bosemprella incarnata*; cf. Table 6).

Palaeoecological evidence from the western section of the Ponta do Cedro outcrop, including the analysis of stratigraphic logs, geological characteristics of the deposit, taxonomic composition of the fossil assemblage and shallow bathymetric zonation of the represented species, supports our conclusion that the site originated as a boulder beach. The conglomerates of this beach leaned against the island's coeval palaeocliff. Nowadays, boulder beaches in the Azores that extend up to the supralittoral zone generally appear to be devoid of life, as the scarcity of fixed rocky substrate (rocky reef) prevents the attachment of adult individuals. Exceptions to this are limpets and the intertidal trochid *Phorcus sauciatus* (F. C. L. Koch, 1845). However, when the upper boulders are removed, the lower layers are found to harbour a large amount of loose, decaying algae that provide shelter and food for many juvenile herbivorous and/or detritivorous micro-mollusc species (<5 mm) that require less space to settle and can avoid predation by taking refuge under the boulders or pebbles. These micro-molluscs form the basis of a specialised food chain. Most likely, this was the situation at Ponta do Cedro during the MIS 5e.

Statistical analysis further reveals that the Bray–Curtis ordered distance matrix heat map (Fig. 14) and the dendrogram based on UPGMA clustering of Bray–Curtis dissimilarity matrices (Fig. 15) indicate distinct patterns. While the samples from Vinha Velha and Lagoinhas outcrops make two well-defined groups, each containing all the samples from their respective outcrops (Figs. 14 and 15), the 11 samples from Ponta do Cedro formed five distinct clusters. This is especially evident in Fig. 14, where the Ponta do Cedro samples show high dissimilarity values within samples. The samples from Prainha occupy an intermediate position, showing dissimilarity levels between the two extremes: low dissimilarity within samples at Vinha Velha and Lagoinhas, and high dissimilarity within samples at Ponta do Cedro. The high dissimilarity observed within the Ponta do Cedro samples is explained by the large number of species with s relevant indicator value (12 species) that contrast with just one species at Lagoinhas, four at Vinha Velha and two at Prainha (cf. Table 2 and Fig. 16). The Hill numbers' statistical analysis highlights the higher number of species at both Ponta do Cedro and Prainha, compared to Vinha Velha and Lagoinhas, the latter location being the less diverse of the four MIS 5e outcrops studied (Fig. 17a). Lagoinhas is located in the north coast of Santa Maria Island (Fig. 2) and at present, it endures harsher sea conditions (e.g., stronger winds, higher waves and swell; cf. Ricchi et al., 2020) compared to the remaining MIS 5e locations. It is expected that the current environmental conditions were similar during the MIS 5e period, which probably explains the lower Lagoinhas diversity, clearly visible in Fig. 17.

Table 6. Most frequent species (%) in each of the outcrops investigated and respective type of preferential habitat and range depth (in metres).

Taxa	%	Habitat	Depth range (m)
Ponta do Cedro			
Alvania mediolittoralis	37.83	Algae	0–24
Bittium nanum	11.11	Algae	0–50
Tectura virginea	3.83	Hard ground	0–100
Fossarus ambiguus	3.28	Rocky/Gravel	0–1
Cingula trifasciata	3.17	Gravel	0–20
Odostomia lukisii	3.05	Hard ground	0–150
Manzonia unifasciata	2.97	Algae	0–20
Botryphallus ovummuscae	2.86	n.a.	0–20
Alvania abstersa	2.64	Algae	0–245
Paludinella globularis	2.13	n.a.	0–18
Ervilia castanea	1.81	Sand	3–100
Alvania angioyi	1.68	Algae	0–35
Alvania sleursi	1.68	Algae	0–45
Leucophytia bidentata	1.58	Hard ground	0–2
Gibbula delgadensis	1.30	n.a.	0–40
Jujubinus pseudogravinae	1.18	Algae	0–80
Alvania cancellata	1.13	Algae	2–90
	83.23		
Prainha			
Bittium nanum	44.36	Algae	0–50
Alvania mediolittoralis	10.29	Algae	0–24
Rissoa guernei	8.80	Algae	2–30
Lucinella divaricata	6.19	Sand	0–60
Melarhaphe neritoides	4.94	Rocky	5–0
Anachis avaroides	3.01	Algae	0–60
Jujubinus pseudogravinae	2.55	Algae	0–80
Bosemprella incarnata	2.46	Sand	0–85
Triphoridae	2.24	Rocky	n.a.
	84.84		
Lagoinhas			
Bittium nanum	41.48	Algae	0–50
Alvania mediolittoralis	21.77	Algae	0–24
Rissoa guernei	12.51	Algae	2–30
Alvania sleursi	6.92	Algae	0–45
Melarhaphe neritoides	3.72	Rocky	5–0
	86.40		
Vinha Velha			
Melarhaphe neritoides	30.61	Rocky	5–0
Bittium nanum	17.27	Algae	0–50
Cingula trifasciata	15.27	Gravel	0–20
Vermetidae	14.06	Rocky	n.a.
Alvania mediolittoralis	7.99	Algae	0–24
	85.20		

n.a., no information available.

Functional diversity analysis: Alpha diversity

Among all MIS 5e outcrops studied at Santa Maria Island, Ponta do Cedro stands out as the site with the highest values for each of the functional diversity indices used in this study, when compared to Lagoinhas, Vinha Velha or Prainha (Fig. 18). The only exception is Vinha Velha, which shows higher values for the functional originality index (FOri). According to Mouillot et al. (2013a), FOri measures the "isolation of a species in the functional space occupied by a given community", whereas Magneville et al. (2022) defined it as "the weighted mean distance to the nearest species from the global species pool". Communities with high values of FOri may be interpreted as holding increased niche specialisation, allowing more species to coexist. In contrast, Lagoinhas is the site with the least functional diversity, as it shows the lowest values for the following functional diversity indices: species richness (SpRic), functional mean pairwise distance (FMPD), functional mean nearest neighbour distance (FNND), functional evenness (FEve), functional richness (FRic) and FOri (Fig. 18). Our data (cf. Table S5) also indicate a strong positive correlation between SpRic and FRic (Fig. S3). Although SpRic and FRic are not expected to have a direct relationship (Mason et al., 2005) and recent studies have shown that FRic plateaus after a certain threshold of SpRic (McLean et al., 2019; Mouton et al., 2020), other studies highlighted a positive relationship between them (e.g., Villéger et al., 2008). The explanation for this relationship is straightforward: communities with a higher

Table 7. Results of Generalised Linear Models comparing Hill's series (diversity indices) among outcrops. 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.

	Hill $q=0$			Hill $q=1$			Hill $q=2$		
Source	Estimate	z	v	Estimate	z	p	Estimate	z	p
Intercept	3.48	65.61	<0.001	2.54	29.95	<0.001	2.07	19.31	<0.001
LAG	−0.31	−3.67	<0.001	−0.68	−4.52	<0.001	−0.65	−3.44	<0.001
PRA	−0.03	−0.38	0.707	−0.67	−4.10	<0.001	−0.72	−3.44	<0.001
VVE	−0.15	−1.61	0.108	−0.47	−2.81	<0.01	−0.38	−1.84	0.066
Null deviance		98.02			59.45			43.89	
Residual deviance		82.16			30.07			25.49	

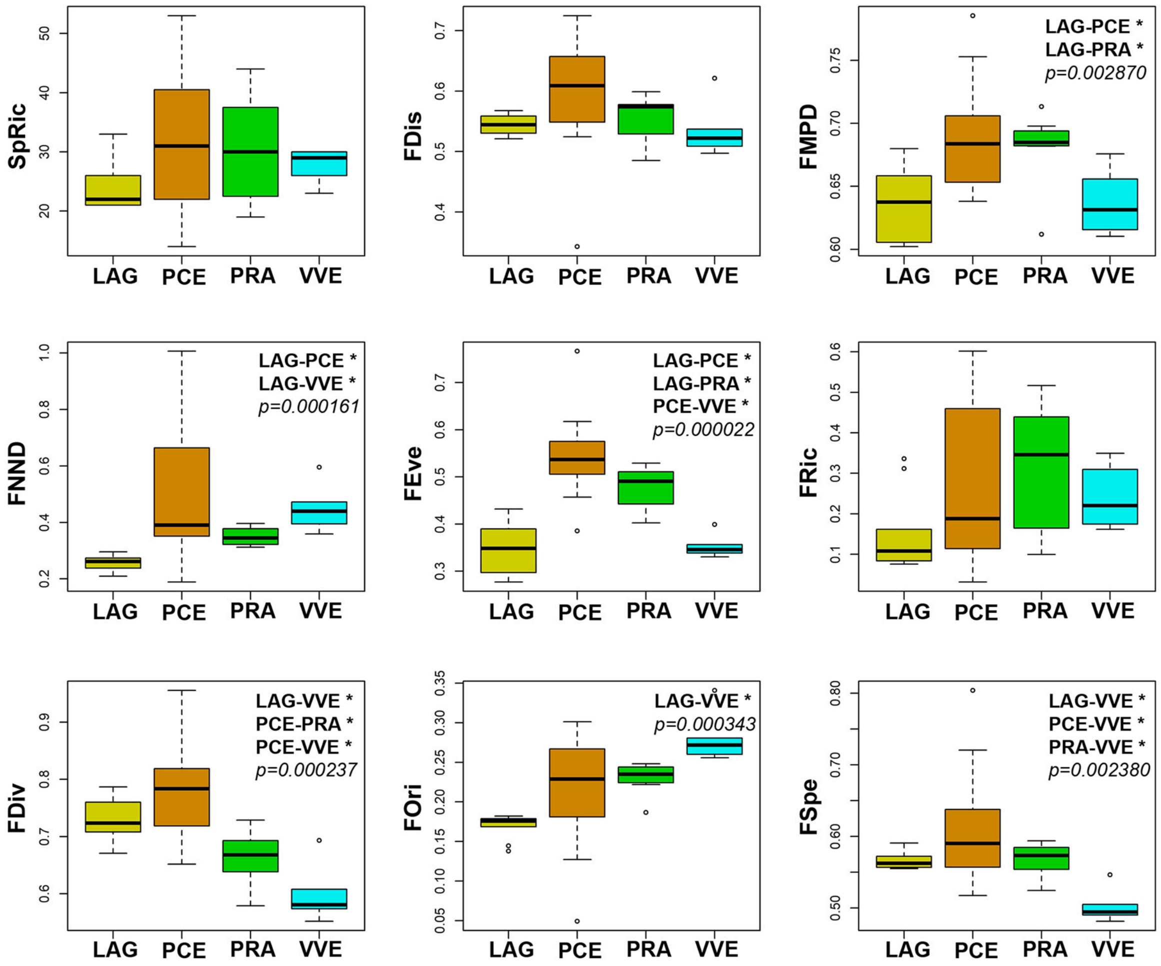

Figure 18. Comparison of the multidimensional functional alpha diversity calculated for each of the four studied MIS 5e outcrops, using box and whisker plots: LAG, Lagoinhas; PCE, Ponta do Cedro; PRA, Prainha; VVE, Vinha Velha. FDis, functional dispersion; FDiv, functional divergence; FEve, functional evenness; FMPD, functional mean pairwise distance; FNND, functional mean nearest neighbour distance; FOri, functional originality; FRic, functional richness; FSpe, functional specialisation; SpRic, species richness. *p*-values represent the result of a multiple comparison test after the Kruskal–Wallis test and are statistically significant at 95%. [Color figure can be viewed at wileyonlinelibrary.com]

number of species will likely have a higher diversity of traits and, consequently, will probably perform a broader range of functions (Halpern and Floeter, 2008). Other statistically relevant positive relationships also were found among some of the functional diversity indices used to characterise the four MIS 5e assemblages, notably between FMPD and FSpe, and between FDiv and FSpe (Fig. S3).

When the whole MIS 5e assemblage is compared with the modern community (cf. Table 4), it is evident that taxonomic richness increases from the MIS 5e period to the present. This pattern is consistent with other studies that also report an increase in alpha diversity between past and modern communities (Powell and Kowaleski, 2002; Bush and Bambach, 2004; Alroy et al., 2008). Although the processes and time scales are admittedly very different—global increases in taxonomic and functional diversity in deep time are driven by evolution of new species and higher taxa, whereas changes since the last interglacial are primarily driven by the balance of extirpation of local populations and immigration—functional diversity approach methods are also able to detect extant community responses to disturbances (Mouillot et al., 2013a), therefore are also sensitive to small time scales. Additionally, the number of functional entities also increases from the MIS 5e (80 functional entities) to the modern times (215 functional entities) a pattern that is also consistent with the results of Bambach et al. (2007) and Villéger et al. (2011) for longer timescales. These patterns are not a result of the larger number of modern mollusc species in the database compared to the MIS 5e data set, because when randomised samples of 75 taxa from both the MIS 5e and modern assemblages are compared, all functional diversity indices (except FDiv) show higher values in the modern samples than in the MIS 5e samples (Fig. 19). Thus, these results suggest that modern Azorean mollusc communities have a higher contribution to the filling of overall functional space than the MIS 5e communities, which occupied a less extensive functional space (Fig. 20).

By definition, FRic represents the amount of functional space/volume filled by a given community relative to the global convex hull (Villéger et al., 2008). The lower FRic values observed in the MIS 5e (Fig. 19) imply that some of the resources (alpha niches) that are currently utilised by modern Azorean mollusc communities were not accessible or used by the MIS 5e molluscs. According to Petchey (2003), we can also hypothesise that the MIS 5e community had reduced productivity when compared with that of the modern community.

Masson et al. (2005) described FEve as the evenness of abundance distribution in a functional trait space. In a more recent definition by Mouillot et al. (2013a), FEve corresponds to the “regularity of the distribution and relative abundance of species in functional space for a given community”. Our results show that FEve in the MIS 5e community is lower than in the modern community (Fig. 19), indicating that some parts of the MIS 5e niche space were underutilised, even if

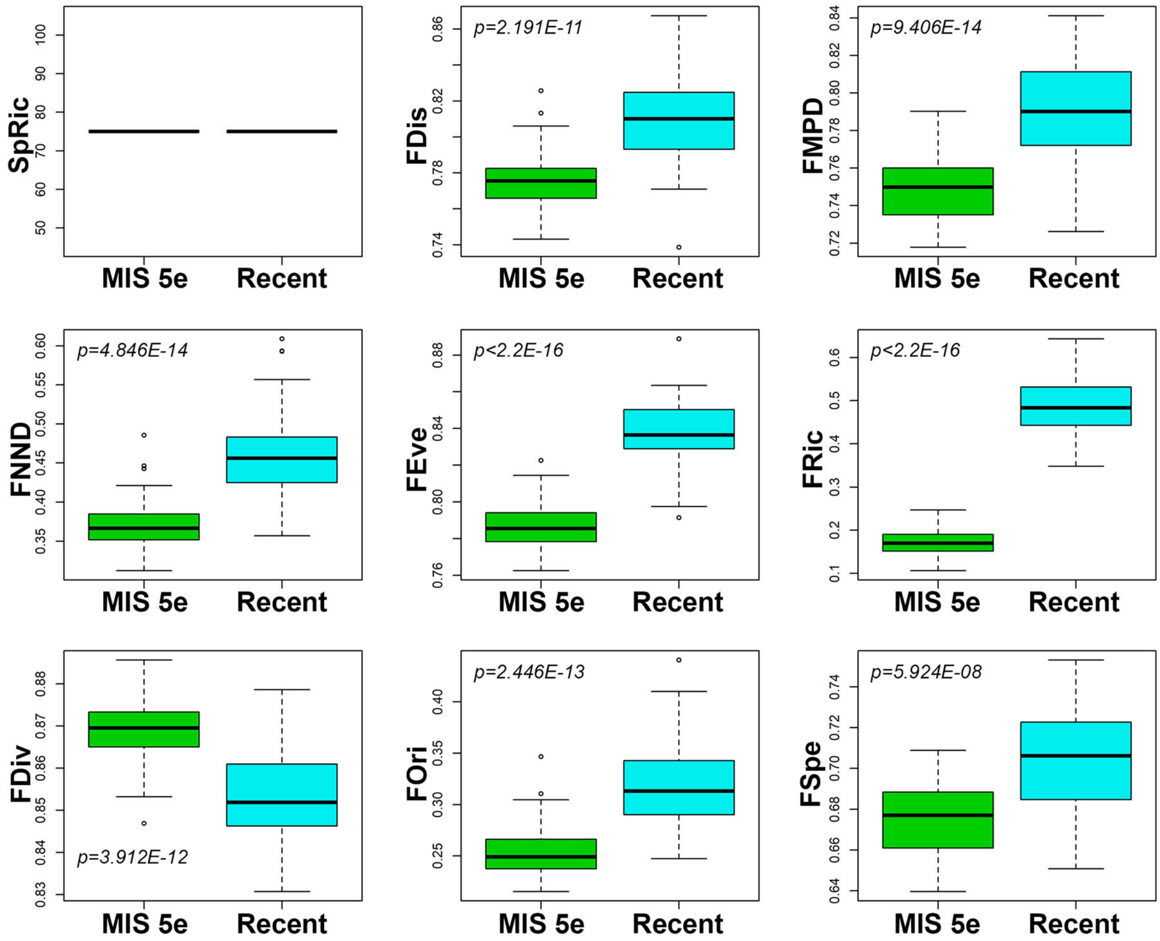

Figure 19. Comparison of the multidimensional functional alpha diversity calculated for the whole MIS 5e data set with the recent shallow-water molluscs' checklist from the Azores, using box and whisker plots. For the remaining abbreviations, please see the legend of Fig. 18. *p*-values represent the Wilcoxon rank sum test with continuity correction and are statistically significant at 95%. [Color figure can be viewed at wileyonlinelibrary.com]

occupied. This is a condition also associated by authors with a decreased productivity and less resilience to invaders and/or climate change (Petchey et al., 2004).

Based on Bellwood et al. (2006), Villéger et al. (2010) proposed an index for functional specialisation (FSpe) that computes the relative position of a given species in relation to the gravity centre calculated for the whole species pool. Gomes et al. (2023) recently defined FSpe as the "mean Euclidean distance between each species and the average position of all species in the functional space". Mason and Mouillot (2013) suggested that in species-rich assemblages, increased energy inputs (which boost primary productivity) enable more species to coexist and maintain viable populations, because such species explore specialised niches. However, our data do not support a positive relationship between FSpe and primary productivity. Despite higher mean annual sea surface temperatures (SSTs) during the MIS 5e compared to modern times (Hillaire-Marcel et al., 1996; Muhs et al., 2002), MIS 5e FSpe values are lower than modern ones (Fig. 19). Mason and Mouillot (2013) also acknowledged that this "niche specialisation" hypothesis, where "increasing temperatures causes an increase in the availability of resources used by specialists" has yet to be proven. Therefore, we interpret our results of higher FSpe (indicating a higher proportion of specialised niche mollusc species) in the modern assemblages as unrelated to SSTs. Hence, other factors likely influence the FSpe of mollusc assemblages and this is an interesting result that warrants further investigation.

Magneville et al. (2022) defined FDis as "the weighted deviation to center of gravity of species in the assemblage". According to Cooke et al. (2019), FDis measures the breadth of functional roles performed by species. These authors found that species-rich regions had high functional redundancy but low FDis and suggested that FDis should be used as an indicator of response diversity for conservation purposes. As a rule, communities with high FDis are expected to have higher functional, indicating a broader range of responses to environmental stressors (Elmqvist et al., 2003; Ordonez and Svenning, 2016). Our data suggest that modern Azorean marine communities are better prepared to face global climate changes than their MIS 5e counterparts were (Fig. 19). Finally, and although not directly comparable with our study, Floyd et al. (2020) showed that FDis decreases with latitude along the western Australian coasts, and hypothesised that environmental filtering contributes to this decrease in functional dispersion of mollusc assemblages at higher latitudes.

In terms of the FOri, our data indicate that this index is higher in the modern communities (up to 31%) in relation to the MIS 5e communities (Fig. 19). As mentioned before, communities with high FOri may be interpreted as holding increased niche specialisation, permitting more species to coexist. This, along with the low chances of very rare species to fossilise/be recovered from the fossil record, partially explain the higher number of modern species. We also conclude that the resilience of the MIS 5e assemblage to disturbances was reduced because of its relatively low FOri value (~25%; cf. Fig. 19).

Functional mean pairwise distance (FMPD) is used to measure the breadth of trait diversity in a given community (Murley et al., 2024) and it is the functional equivalent to Δ+,

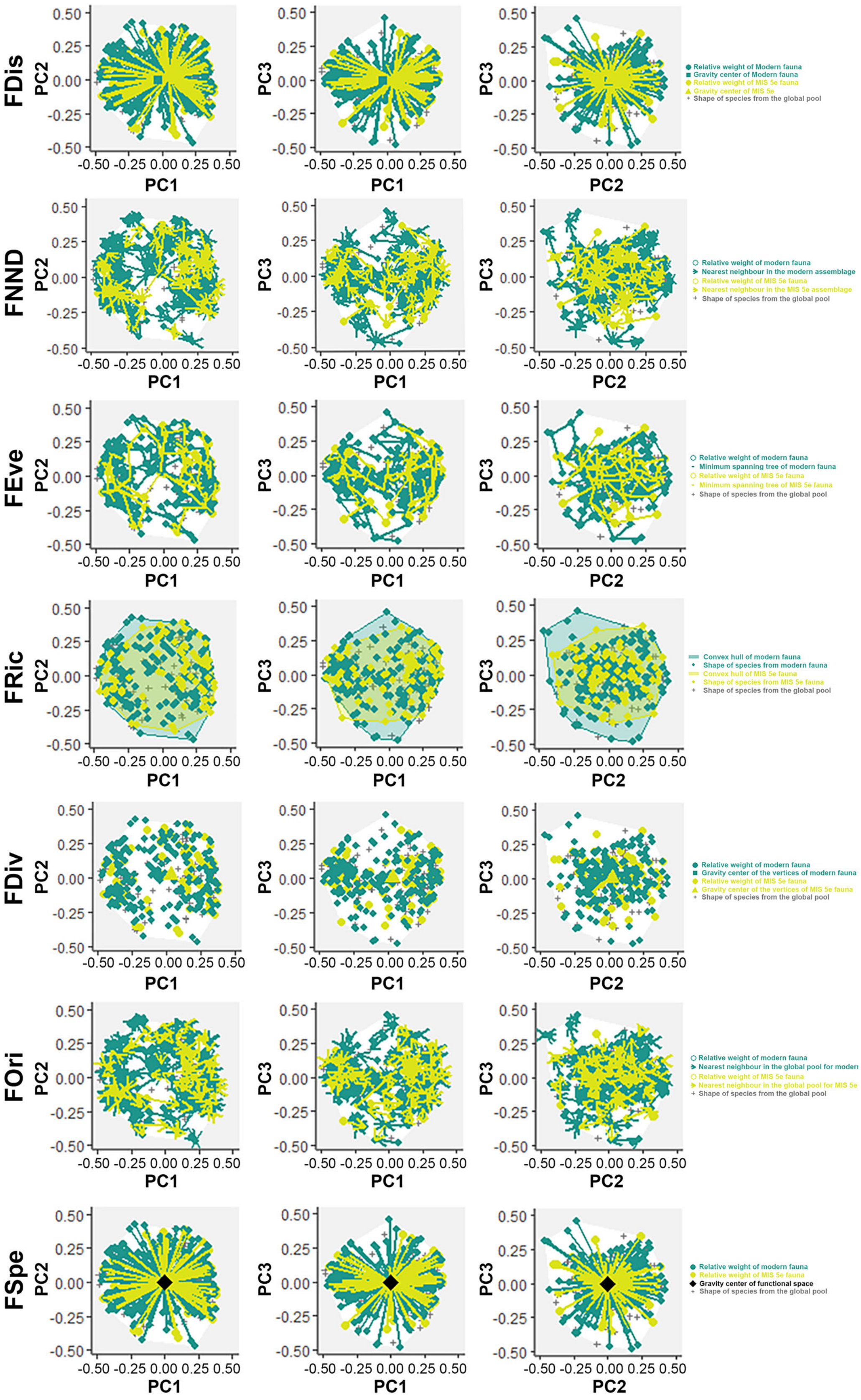

Figure 20. Functional space (first three axes out of eight) occupied by the modern and MIS 5e mollusc assemblages at Santa Maria Island. PC1, PC2 and PC3 represent the first three axes of the principal coordinates analysis. Dots represent individual MIS 5e (yellow) and modern species (green). The remaining abbreviations are as in Fig. 18. [Color figure can be viewed at wileyonlinelibrary.com]

the average taxonomic distinctness (Laliberté and Legendre, 2010). We interpret our results, with higher FMPD values in the modern assemblages compared to the MIS 5e ones (Fig. 19), as meaning that the breadth of functional trait diversity is greater in modern assemblages.

FNND, defined by Weiher et al. (1998) as "the weighted distance to the nearest neighbour within the assemblage", quantifies the filling of the functional trait space and the extent to which species occupy distinct niches (Magneville et al., 2022). Our results show higher FNND values in modern

Table 8. Number of recent gastropod (Gast) and bivalve (Biv) species compared with those reported from the MIS 5e.

		Recent			MIS 5e			MIS5e/ extant %
	Site	Gast	Biv	Total	Gast	Biv	Total	
Islands	AZO	222	149	371	132	28	160	43.1
	MAD	332	132	464	54	29	83	17.9
	SEL	155	39	194	17	2	19	9.8
	CAN	697	227	924	190	79	269	29.1
	CAB	520	125	645	53	30	83	12.9
Continent	MED	1034	372	1406	219	97	316	22.5
	BER	380	148	528	12	10	22	4.2
	VIR	112	163	275	73	100	173	62.9
	GME	1118	438	1556	34	61	95	6.1
	CAR	2139	602	2741	74	96	170	6.2
	BRA	748	448	1196	12	25	37	3.1
	ARG	242	131	373	26	13	39	10.5

ARG, Argentina; AZO, Azores Archipelago; BER, Bermuda; BRA, Brasil; CAB, Cabo Verde Archipelago; CAN, Canaries Archipelago; CAR, Caribbean; GME, Gulf of Mexico; MAD, Madeira Archipelago; MED, Mediterranean Sea; SEL, Selvagens Archipelago; VIR, Virginean Biogeographical Province.

assemblages compared to MIS 5e ones (cf. Figs. 19 and 20), suggesting that species in modern assemblages occupy more dissimilar niches than during the MIS 5e.

Finally, FDiv measures how abundance is distributed within the hull volume of functional trait space occupied by species (Villéger et al., 2008). A high functional divergence translates into a high degree of niche differentiation, and thus low resource competition. Hence, as the MIS 5e communities as a whole present higher functional divergence than the modern assemblages (Fig. 19), we conclude that they enjoyed increased ecosystem function, likely as a result of a more efficient use of available resources.

Functional diversity analysis: Beta diversity

Besides alpha diversity, the differences in biodiversity across time and/or space can also be assessed using beta-diversity, a highly useful approach for the investigation of assembly rules and for the establishment of macroecological patterns (De Bello et al., 2009). Beta diversity reflects the variation in species composition between two or more time beans and/or different locations (Baselga, 2010). By definition, the beta diversity is partitioned into two additive components: the turnover component (i.e., the replacement of species between time beans/assemblages, which is not influenced by the difference in species richness between time beans/assemblages) and the nestedness component, in which low species richness communities are subsets of high species richness' assemblages. Additionally, the turnover component is highest when there is no shared traits combination between the two compared communities, whereas the nestedness component is the highest when one assemblage with low species richness/low number of functional traits is a subset of a more diverse assemblage (Baselga, 2010; Villéger et al., 2013).

Our results of the Dissimilarity index used to calculate the multidimensional functional beta diversity show that the nestedness-resultant value outweighs the turnover component. This suggests that the MIS 5e assemblage is essentially a subset of the modern assemblage. This outcome was somewhat unexpected as, despite the higher taxonomic richness of the modern assemblage when compared to that of the MIS 5e, there is a relevant group of 26 marine molluscs that characterise the last interglacial deposits at Santa Maria Island, and whose species are not found in the Azores in the present times (cf. Table 3). This group includes: (i) the lithophagous bivalve *Leiosolenus aristatus* (Dillwyn, 1817) that was able to drill an algal ridge/algal reef framework, that is, a crustose coralline algae buildup, that reached a maximum thickness of 50–60 cm at Prainha, and that was also abundant in other sites along the shores of Santa Maria Island (e.g., at Lagoinhas; Rebelo et al., 2021). This species was extirpated during the course of the last glacial episode, coinciding with the extirpation of some of the four algae species that built these frameworks (Ávila et al., 2002, 2009a, 2010, 2015b; Rebelo et al., 2021); (ii) three shallow-water bivalve species associated with fine sediments—*Ensis minor* (Chenu, 1843), *Laevicardium crassum* (Gmelin, 1791) and *Lucinella divaricata*—that were extirpated from Santa Maria Island when sea level dropped below the edge of the insular platform during the last glacial episode and fine sediments were lost to the abyssal depths that surround the island as a result of the high slopes (Ávila et al., 2008, 2019); and (iii), a large group of thermophilic gastropod species that includes, among others, several species of *Conus*, *Claremontiella nodulosa* (C. B. Adams, 1845), *Gemophos viverratus* (Kiener, 1834) and *Zonaria picta* (J. E. Gray, 1824), whose geographic ranges expanded northwards and that were able to reach, colonise and establish viable populations in the Azores during the final phase of glacial Termination 2 (the short period of time between MIS 6 and MIS 5e), or during the initial times of the MIS 5e (Ávila, 2005; Ávila et al., 2009b, 2015b, 2020a; Hyžný et al., 2021; Melo et al., 2022a, 2022b).

Thus, functional turnover in this context was driven by two main factors: MIS 5e species that were extirpated from the Azorean ecosystem as previously explained and changes in the number of species between the MIS 5e and the modern assemblages. The latter might also reflect an artefact related to the low fossilisation potential of very rare MIS 5e species. Moreover, and with a high probability, high levels of functional trait redundancy are here also involved, in a similar way to the marine fish faunas, where lower turnover components of beta-diversity were observed among assemblages when compared to the nestedness/taxonomic facet of beta-diversity (Mouillot et al., 2013b; McLean et al., 2021).

Conclusions

Functional diversity-based approaches (FDB) have two main advantages over classical taxonomic-based diversity indices. First, FDB provides deeper insights into biodiversity metrics by emphasising the role of functional traits in shaping the ecology patterns and biogeographic processes that characterise a given assemblage across spatial and temporal scales. Additionally, the functional traits (e.g., morphological, physiological, behavioural) are critical determinants of individual characteristics such as growth rates, reproductive success and ultimately the very survival, thus impacting the fitness of individuals (Laureto et al., 2015). These traits are directly reflected in the values of the various functional diversity indices. Second, FDB encompasses a wider spectrum of application that include: (i) understanding the role of species in ecosystem functioning (Chapin et al., 1997); (ii) examining the response of species to natural or anthropogenic disturbance or even to global climate changes (Hooper et al., 2000; Villéger et al., 2010, 2011; Mouillot et al., 2013a, 2013c, 2014; Zhang et al., 2021); (iii) investigating the influence of niche evolution on the variation of species alpha diversity across spatial and environmental gradients (Duarte et al., 2023); (iv) elucidating community assembly rules (Kraft et al., 2008; Mouchet et al., 2010); (v) informing biodiversity conservation strategies (Petchey and Gaston, 2002); (vi) investigating how functional diversity links to the functions and services of the ecosystem (Balvanera et al., 2006; Cardinale et al., 2012), in particular in ecological restoration (Carlucci et al., 2020; Gornish et al., 2023); and finally, (vii) the definition of the biogeographic boundaries between different biogeographic ecoregions and/or provinces (Ficetola et al., 2017; Myers et al., 2021).

The use of different functional diversity indices allowed us to detect some ecological processes and to raise hypothesis to be tested soon. Consistent with prior studies, our results also support an increase of alpha diversity when past and modern communities are paralleled. A reduced productivity is inferred for the MIS 5e communities in comparison with the modern ones, as evidenced by lower values of FRic, FEve and FSpe in the former communities (Petchey, 2003; Petchey et al., 2004). These findings suggest that modern communities occupy and use a greater number of ecological niches, and that modern communities have increased niche specialisation, in comparison with the MIS 5e. The lower MIS 5e values for FEve, FOri and FDis indicate that the MIS 5e communities were less resilient to invaders and/or climate change in comparison with the modern ones. In contrast, higher FDiv in MIS 5e communities translates into a more efficient use of available resources by these communities compared to modern assemblages. Based on our results of higher FSpe (i.e., higher proportion of specialised niche mollusc species) in the modern assemblages when compared with the MIS 5e ones, we raise the hypothesis that factors beyond SSTs may account for this trend.

Finally, this study provides critical baselines not only for the comparison with other MIS 5e assemblages but also for the study of modern assemblages, providing a framework for early detection of variations in the functional diversity caused by ongoing climate change.

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Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Supporting information

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

Figure S1. 3D model of the western section of the Ponta do Cedro outcrop.

Figure S2. Analysis of the quality of functional spaces. Each column represents a functional space and the *X*-axis of all panels represents trait-based distances. The *Y*-axis is different for each row: on the first row, it represents species functional distances in the multidimensional space; on the second row, it shows the raw deviation of species distances in the functional space compared to trait-based distances; and on the third row, it shows the absolute or squared deviation of the ("scaled") distance in the functional space.

Figure S3. Statistically significant relationships between the various functional diversity indices used. For abbreviations, see the legend of Fig. 18.

Table S1. Quantitative data from the marine molluscs (bivalves and gastropods) collected in the four MIS 5e outcrops of Santa Maria Island (Azores). PCE: Ponta do Cedro; LAG: Lagoinhas; PRA: Prainha; and VVE: Vinha Velha.

Table S2. Functional traits of the marine molluscs (bivalves and gastropods) from the quantitative samples collected at the four MIS 5e outcrops of Santa Maria Island (Azores).

Table S3. Functional traits of the 160 marine molluscs (bivalves and gastropods) reported from the MIS 5e outcrops of Santa Maria Island (Azores).

Table S4. Functional traits of the 365 shallow-water (<50 m depth) mollusc shelled taxa (217 gastropods and 148 bivalves) presently reported from the Azores Archipelago.

Table S5. Functional diversity of the MIS 5e samples collected at Santa Maria Island, expressed as Species Richness (Spe Ric), Functional Richness (FRic), Functional Evenness (FEve), Functional Divergence (FDiv), Functional Dispersion (FDis), Functional Originality (FOri), Functional Specialisation (FSpe), Functional Mean Pairwise Distance (FMPD) and Functional mean Nearest Neighbour Distance (FNND). PCE: Ponta do Cedro; LAG: Lagoinhas; PRA: Prainha; and VVE: Vinha Velha.

References

van Aartsen, J.J., Menkhorst, H.P.M.G. & Gittenberger, E. (1984) The marine mollusca of the Bay of Algeciras, Spain, with general notes on Mitrella, Marginellidae and Turridae. *Basteria*. (Suppl 2), 1–135.

Adams, C.B. (1845) Specierum novarum conchyliorum, in Jamaica repertorum, synopsis. Proceedings of the Boston Society of Natural History, 2, 1–17.

Alroy, J., Aberhan, M., Bottjer, D.J., Foote, M., Fürsich, F.T., Harries, P.J. et al. (2008) Phanerozoic trends in the global diversity of marine invertebrates. *Science*, 321(5885), 97–100. Available from: https://doi.org/10.1126/science.1156963

Ávila, S.P. (2005) Processos e Padrões de Dispersão e Colonização nos Rissoidae (Mollusca: Gastropoda) dos Açores, x + 329 pp. Unpublished PhD thesis in Biology, Universidade dos Açores, Ponta Delgada.

Ávila, S.P. (2024a) Atlantic and Mediterranean Gastropoda: geographical distribution and functional traits database. V.1.0. https://www.researchgate.net/publication/385907293_Atlantic_and_Mediterranean_Gastropoda_geographical_distribution_and_functional_traits_database_Version_1_0 [Accessed 24th June 2025].

Ávila, S.P. (2024b) Atlantic and Mediterranean Bivalvia: geographical distribution and functional traits database. v.1.0. Available at: https://www.researchgate.net/publication/387085775_Atlantic_and_Mediterranean_Bivalvia_geographical_distribution_and_functional_traits_database_Version_10 [Accessed 21st June 2025].

Ávila, S.P. (2025) Distributional range shifts caused by glacial–interglacial cycles: a review on timing, main processes, and patterns of late Pleistocene marine dispersal by invertebrates in the NE

Atlantic. *Journal of Marine Science and Engineering*, 13, 2024. Available from: https://doi.org/10.3390/jmse13112024

Ávila, S.P., Amen, R., Azevedo, J.M.N., Cachão, M. & García-Talavera, F. (2002) Checklist of the Pleistocene marine molluscs of Prainha and Lagoinhas (Santa Maria island, Azores). *Açoreana*, 9(4), 343–370.

Ávila, S.P., Azevedo, J.M.N., Madeira, P., Cordeiro, R., Melo, C.S., Baptista, L. et al. (2020a) Pliocene and Late-Pleistocene actinopterygian fishes from Santa Maria Island (Azores: NE Atlantic Ocean): systematics, palaeoecology and palaeobiogeography. *Geological Magazine*, 157(9), 1526–1542.

Ávila, S.P., Cachão, M., Ramalho, R.S., Botelho, A.Z., Madeira, P., Rebelo, A.C. et al. (2016) The palaeontological heritage of Santa Maria Island (Azores: NE Atlantic): a re-evaluation of geosites in GeoPark Azores and their use in geotourism. *Geoheritage*, 8, 155–171.

Ávila, S.P. & Cordeiro, R. (2015) Rissoella alexandrae. In: Cordeiro, R. & Ávila, S.P. (2015) New species of Rissoidae (Mollusca, Gastropoda) from the Archipelago of the Azores (northeast Atlantic) with an updated regional checklist for the family. ZooKeys, 480, p. 1–19.

Ávila, S.P., Cordeiro, R., Rodrigues, A.R., Rebelo, A.C., Melo, C. & Madeira, P. et al. (2015c) Fossil Mysticeti from the Pleistocene of Santa Maria Island, Azores (NE Atlantic Ocean), and the prevalence of fossil cetaceans on oceanic islands. *Palaeontologia Electronica*, 18.2.27A, 1–12.

Ávila, S.P., Goud, J. & de Frias Martins, A.M. (2012) Patterns of diversity of the Rissoidae (Mollusca: Gastropoda) in the Atlantic and the Mediterranean Region. *The Scientific World Journal*, 2012, 1–30. Article ID 164890. Available from: https://doi.org/10.1100/2012/164890

Ávila, S.P., Johnson, M.E., Rebelo, A.C., Baptista, L. & Melo, C.S. (2020b) Comparison of modern and Pleistocene (MIS 5e) coastal boulder deposits from Santa Maria Island (Azores Archipelago, NE Atlantic Ocean). *Journal of Marine Science and Engineering*, 8(6), 386.

Ávila, S.P., Landau, B., Ávila, G.C., Hipólito, A., Uchman, A., Johnson, M.E. et al. (2025) A call to address the taxonomic gap in the Pleistocene of Santa Maria Island (Azores Archipelago). *Acta Geologica Polonica*, 75(1), e40.

Ávila, S.P., Madeira, P., García-Talavera, F., da Silva, C.M., Cachão, M. & Martins, A.M.F. (2007) *Luria lurida* (mollusca: gastropoda), a new record for the Pleistocene of Santa Maria (Azores, Portugal). *Arquipélago*, 24, 53–56.

Ávila, S.P., Madeira, P., da Silva, C.M., Cachão, M., Landau, B., Quartau, R. et al. (2008) Local disappearance of bivalves in the Azores during the last glaciation. *Journal of Quaternary Science*, 23, 777–785.

Ávila, S.P., Madeira, P., Zazo, C., Kroh, A., Kirby, M., Silva, C.M. et al. (2009a) Palaeoecology of the Pleistocene (MIS 5.5) outcrops of Santa Maria island (Azores) in a complex oceanic tectonic setting. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 274, 18–31.

Ávila, S.P., Melo, C., Berning, B., Sá, N., Quartau, R., Rijsdijk, K.F. et al. (2019) Towards a "Sea-Level Sensitive" dynamic model: impact of island ontogeny and glacio-eustasy on global patterns of marine island biogeography. *Biological Reviews*, 94(3), 1116–1142.

Ávila, S.P., Melo, C., Silva, L., Ramalho, R., Quartau, R., Hipólito, A. et al. (2015b) A review of the MIS 5e highstand deposits from Santa Maria Island (Azores, NE Atlantic): palaeobiodiversity, palaeoecology and palaeobiogeography. *Quaternary Science Reviews*, 114, 126–148.

Ávila, S.P., Ramalho, R., Habermann, J., Quartau, R., Kroh, A., Berning, B. et al. (2015a) Palaeoecology, taphonomy, and preservation of a lower Pliocene shell bed (coquina) from a volcanic oceanic island (Santa Maria Island, Azores, NE Atlantic Ocean). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 430, 57–73. Available from: https://doi.org/10.1016/j.palaeo.2015.04.015

Ávila, S.P., Ramalho, R., Habermann, J. & Titschack, J. (2018) The marine fossil record at Santa Maria Island (Azores). In: Kueppers, U. & Beier, C. (Eds.) *Volcanoes of the Azores. Revealing the Geological Secrets of the Central Northern Atlantic Islands. Active Volcanoes of the World*. Berlin, Heidelberg: Springer, pp. 155–196.

Ávila, S.P., Ramalho, R.S., Silva, C.M.da, Johnson, M.E., Uchman, A. & Berning, B. et al. (2022) *Os fósseis de Santa Maria (Açores). 2. Pedra-que-pica: uma história com 5 milhões de anos*. Lagoa: OVGA—Observatório Vulcanológico e Geotérmico dos Açores, 160 pp. ISBN 978-989-8164-25-4.

Ávila, S.P., Rebelo, A.C., Medeiros, A., Melo, C., Gomes, C. & Bagaço, L. et al. (2010) *Os fósseis de Santa Maria (Açores). 1. A jazida da Prainha*. Lagoa: OVGA—Observatório Vulcanológico e Geotérmico dos Açores, 103 pp. ISBN 978-989-8164-09-04.

Ávila, S.P., da Silva, C.M., Schiebel, R., Cecca, F., Backeljau, T. & Martins, A.M.F. (2009b) How did they get here? The biogeography of the marine molluscs of the Azores. *Bulletin of the Geological Society of France*, 180, 295–307.

Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D. et al. (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, 9, 1146–1156.

Bambach, R.K., Bush, A.M. & Erwin, D.H. (2007) Autecology and the filling of ecospace: key Metazoan radiations. *Palaeontology*, 50, 1–22.

Baselga, A. (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19(1), 134–143.

Baselga, A. (2012) The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography*, 21, 1223–1232.

Bauch, H.A. & Erlenkeuser, H. (2008) A "critical" climatic evaluation of last interglacial (MIS 5e) records from the Norwegian Sea. *Polar Research*, 27, 135–151.

De Bello, F., Thuiller, W., Lepš, J., Choler, P., Clément, J.C., Macek, P. et al. (2009) Partitioning of functional diversity reveals the scale and extent of trait convergence and divergence. *Journal of Vegetation Science*, 20(3), 475–486.

Bellwood, D.R., Wainwright, P.C., Fulton, C.J. & Hoey, A.S. (2006) Functional versatility supports coral reef biodiversity. *Proceedings of the Royal Society B: Biological Sciences*, 273, 101–107.

Berke, S.K., Jablonski, D., Krug, A.Z. & Valentine, J.W. (2014) Origination and immigration drive latitudinal gradients in marine functional diversity. *PLoS One*, 9(7), e101494.

Borcard, D., Gillet, F. & Legendre, P. (2011) *Numerical ecology with R*. New York: Springer. p. 306.

Bruguière, J.G. (1789–1792) Encyclopédie méthodique ou par ordre de matières, par une Societe de gens de Lettres, de Savans et D'Artistes. Histoire naturelle des Vers, Paris, Pancoucke. 1: i-xviii, 1–344.

Bryant, S.R.D. & McClain, C.R. (2022) Functional space expansion driven by transitions between energetically advantageous traits in the deep sea. *Proceedings of the Royal Society B: Biological Sciences*, 289, 20221302.

Bush, A.M. & Bambach, R.K. (2004) Did alpha diversity increase during the Phanerozoic? Lifting the veils of taphonomic, latitudinal, and environmental biases. *Journal of Geology*, 112, 625–642.

Cabero del Rio, A. (2009) Registro costero de los cambios eustáticos y climáticos durante los interglaciares recientes cuaternarios: Sur y Sureste peninsular, islas Baleares, Canarias y Cabo Verde. Unpublished PhD thesis in Geology, University of Salamanca, 451 pp.

Cáceres, M.D. & Legendre, P. (2009) Associations between species and groups of sites: indices and statistical inference. *Ecology*, 90, 3566–3574.

Calcara, P. (1845) Cenno sui molluschi viventi e fossili della Sicilia da servire di supplimento ed insieme di critiche osservazioni all'opera di R.A. Philippi. *Stamperia Reale, Palermo*, 65.

Callapez, P. & Ferreira Soares, A. (2000) Late Quaternary warm marine mollusks from Santa Maria (Azores) paleoecologic and paleobiogeographic considerations. *Ciências da Terra*, 14, 313–322.

Cameron, R.A.D. & Pokryszko, B.M. (2005) Estimating the species richness and composition of land mollusc communities: problems, consequences and practical advice. *Journal of Conchology*, 38(5), 529–547.

Caputo, R. (2007) Sea-level curves: perplexities of an end-user in morphotectonic applications. *Global and Planetary Change*, 57, 417–423.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P. et al. (2012) Biodiversity loss and its impact on humanity. *Nature*, 486, 59–67.

Carlucci, M.B., Brancalion, P.H.S., Rodrigues, R.R., Loyola, R. & Cianciaruso, M.V. (2020) Functional traits and ecosystem services in ecological restoration. *Restoration Ecology*, 28(6), 1372–1383. Available from: https://doi.org/10.1111/rec.13279

Castillo, C., Casillas, R., Ahijado, A., Gutiérrez, M. & Martín-González, E. (2001) Síntesis geológica y paleontológica de la isla de Fuerteventura: Itinerarios científicos de las XIV Jornadas de Paleontología. *Revista Española de Paleontología Ext*, 16(3), 59–80.

Chakroun, A., Chahid, D., Boudad, L., Campmas, E., Lenoble, A., Nespoulet, R. et al. (2017) The Pleistocene of Rabat (Morocco): mollusks, coastal environments and human behavior. *African Archaeological Review*, 34, 493–510.

Chapin III, F.S., Walker, B.H., Hobbs, R.J., Hooper, D.U., Lawton, J.H., Sala, O.E. et al. (1997) Biotic control over the functioning of ecosystems. *Science*, 277, 500–504.

Charó, M.P. (2021) Quaternary marine mollusk associations of the last interglacials in North Patagonia (Argentina): paleoecology and paleoclimates. In: Ray, S. & Mukherjee, S. (Eds.) *Update on malacology*. London: IntechOpen.

Cheng, L., Abraham, J., Hausfather, Z. & Trenberth, K.E. (2019) How fast are the oceans warming? *Science*, 363, 128–129.

Clifton, H.E. & Thompson, J.K. (1978) Macaronichnus segregatis; a feeding structure of shallow marine polychaetes. *Journal of Sedimentary Research*, 48(4), 1293–1302.

Cooke, R.S.C., Bates, A.E. & Eigenbrod, F. (2019) Global trade-offs of functional redundancy and functional dispersion for birds and mammals. *Global Ecology and Biogeography*, 28(4), 484–495. Available from: https://doi.org/10.1111/geb.12869

Cordeiro, R., Borges, J.P., Martins, A.M.F. & Ávila, S.P. (2015) Checklist of the littoral gastropods (Mollusca: Gastropoda) from the Archipelago of the Azores (NE Atlantic). *Biodiversity Journal*, 6(4), 855–900.

Costa, O.G. (1861) Microdoride mediterranea; o, Descrizione de poco ben conosciuti od affatto ignoti viventi minuti e micoscropici del Mediterraneo, pel professore O. G. Costa. Tomo primo. Con tredici tavole. i-xviii. *Stamperia dell'Iride, Napoli*, 1–80.

Cotter, J.C.B. & Girard, A.A. (1892) Alguns Fósseis Terceários do Archipelago da Madeira e Alguns Moluscos Terrestres Fósseis do Archipelago da Madeira. *Communicações da commissão dos trabalhos geológicos*, 2(2), 1–19.

Crampton, J.S., Cooper, R.A., Beu, A.G., Foote, M. & Marshall, B.A. (2010) Biotic influences on species duration: interactions between traits in marine molluscs. *Paleobiology*, 36(2), 204–223.

Dautzenberg, P. (1927) Mollusques provenant des campagnes scientifiques du Prince Albert Ier de Monaco dans l'Océan Atlantique et dans le Golfe de Gascogne. *Résultats des Campagnes Scientifiques Accomplies sur son Yacht par Albert Ier Prince Souverain de Monaco*, 72, 1–401.

Dineen, A.A., Fraiser, M.L. & Sheehan, P.M. (2014) Quantifying functional diversity in pre- and post-extinction paleocommunities: a test of ecological restructuring after the end-Permian mass extinction. *Earth-Science Reviews*, 136, 339–349.

Doderlein, P. (1872) Note illustrative della Carta Geologica del Modenese e del Reggioano 1870. *Atti della Rivista dell'Accademia delle Scienze, Lett., Arti Moderna*, 9, 1–74.

Draparnaud, J.P.R. (1801) Tableau des mollusques terrestres et fluviatiles de la France. Montpellier/Paris (Renaud/Bossange, Masson & Besson), 1–116.

Duarte, L., Nakamura, G., Debastiani, V., Maestri, R., João Ramos Pereira, M., Cianciaruso, M. et al. (2023) There and back to the present: a model-based framework to estimate phylogenetically constrained alpha diversity gradients. *Ecography*, 2023, e06544. Available from: https://doi.org/10.1111/ecog.06544

Dufrene, M. & Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, 67, 345–366.

Dutton, A. & Lambeck, K. (2012) Ice volume and sea level during the last interglacial. *Science*, 337, 216–219.

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B. et al. (2003) Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment*, 1, 488–494.

Fabricius, O. (1780) Fauna Groenlandica, systematice sistens animalia groenlandiae occidentalis hactenus indagata, quoad nomen specificium, triviale, vernaculumque, synonyma auctorum plurimum, descriptionem, locum, victum, generationem, mores, usum capturamque singuli, pro ut detegendi occasio fuit, maximaque parte secundum proprias observationes. *Hafniae & Lipsiae, Ioannis Gottlob Rothe*, xvi + 452.

Ficetola, G.F., Mazel, F. & Thuiller, W. (2017) Global determinants of zoogeographical boundaries. *Nature Ecology & Evolution*, 1(4), 0089. Available from: https://doi.org/10.1038/s41559-017-0089

Fisher, J., Frank, K. & Leggett, W. (2010) Global variation in marine fish body size and its role in biodiversity-ecosystem functioning. *Marine Ecology Progress Series*, 405, 1–13.

Floyd, M., Mizuyama, M., Obuchi, M., Sommer, B., Miller, M.G., Kawamura, I. et al. (2020) Functional diversity of reef molluscs along a tropical-to-temperate gradient. *Coral Reefs*, 39, 1361–1376.

Foster, W.J. & Twitchett, R.J. (2014) Functional diversity of marine ecosystems after the Late Permian mass extinction event. *Nature Geoscience*, 7(3), 233–238.

García-Talavera, F. (1999) Fauna malacológica del Cuaternario Marino de Cabo Verde. *Revista Académica Canaria de Ciências*, 11(3–4), 9–25.

García-Talavera, F. & Sánchez-Pinto, L. (2001) Moluscos marinos fósiles de Selvagem Pequenha e Ilheu de Fora (Islas Salvajes). Descripción de una nueva especie de neogasterópodo. *Revista da Academia Canaria de Ciencias*, 13(4), 9–21.

Gehrels, W.R. (2010) Late Holocene land- and sea-level changes in the British Isles: implications for future sea-level predictions. *Quaternary Science Reviews*, 29, 1648–1660.

Gerber, J., Hemmen, J. & Gröh, K. (1989) Eine pleistozäne marine Molluskenfauna von Porto Santo (Madeira - Archipel). *Mitteilungen der Deutschen Malakozoologischen Gesellschaft Heft*, 44(45), 10–30.

Gignoux, M. (1910) Sur la classification du Pliocène et du Quaternaire dans l'Italie du Sud. *Comptes Rendus Académie des Sciences*, 150, 841–844.

Gofas, S. (1989) Two new species of Alvania (Rissoidae) from the Azores. *Publicações Ocasionais da Sociedade Portuguesa de Malacologia*, 14, 39–42.

Gofas, S. (1990) The littoral Rissoidae and Anabathridae of Sao Miguel, Azores. *Açoreana, Suplemento*, 1, 97–134.

Gomes, L.C., Dias, R.M., Ruaro, R. & Benedito, E. (2023) Functional diversity: a review on freshwater fish research. *Neotropical Ichthyology*, 21(2), e230022.

Gornish, E.S., Campbell, C., Svejcar, L., Munson, S.M., Vaughn, K., Spaeth, M.K. et al. (2023) Functional traits are used in restoration practice: a response to Merchant et al. (2022). *Restoration Ecology*, 31(7), e13880. Available from: https://doi.org/10.1111/rec.13880

Gotelli, N.J. & Colwell, R.K. (2011) Estimating species richness, In: Magurran, A.E. and McGill, B.J., (Eds.) *Biological diversity: frontiers in measurement and assessment*. Oxford, UK: Oxford University Press. pp. 39–54.

Gower, J.C. (1966) Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika*, 53, 325–338.

Gravel, D., Albouy, C. & Thuiller, W. (2016) The meaning of functional trait composition of food webs for ecosystem functioning. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 371, 20150268. Available from: https://doi.org/10.1098/rstb.2015.0268

Grossmann, M., Nielsen, S.N., Rivadeneira, M.M. & Valdivia, N. (2023) The latitudinal gradient of functional diversity of Miocene marine mollusks from Chile. *Ecography*, 2023, e06344.

Halpern, B. & Floeter, S. (2008) Functional diversity responses to changing species richness in reef fish communities. *Marine Ecology Progress Series*, 364, 147–156.

Hanley, A. (1844) Cingula globularis. In: Thorpe, C. *1844. British marine conchology; Being a descriptive catalogue, arranged according to the Lamarckian system, of the salt water shells of Great Britain*. London: Edward Lumley. p. l + 267.

Hidalgo, J.G. (1873) Description de deux espèces de Natica des mers d'Espagne. *Journal de Conchyliologie*, 21, 332–335.

Hill, M.O. (1973) Diversity and evenness: a unifying notation and its consequences. *Ecology*, 54, 427–432.

Hillaire-Marcel, C., Gariépy, C., Ghaleb, B., Goy, J.-L., Zazo, C. & Cuerda Barcelo, J. (1996) U-series measurements in tyrrhenian deposits from mallorca—further evidence for two last-interglacial high sea levels in the Balearic Islands. *Quaternary Science Reviews*, 15, 53–62.

Hsieh, T., Ma, K. & Chao, A. (2024) *iNEXT: interpolation and extrapolation for species diversity*. R package version 3.0.1. Available from: https://sites.google.com/view/chao-lab-website/software/inext

Hyžný, M., Melo, C.S., Ramalho, R.S., Cordeiro, R., Madeira, P., Baptista, L. et al. (2021) Pliocene and late Pleistocene (MIS 5e) decapod crustaceans from Santa Maria Island (Azores Archipelago: Central Atlantic): systematics, palaeoecology and palaeobiogeography. *Journal of Quaternary Science*, 36, 91–109.

Issel, A. (1914) Lembi fossiliferi quaternary e recenti osservati nella Sardegna meridionale dal prof. D. Lovisato. *Rendiconti della Real Accademia Nazionale dei Lincei*, 23, 759–770.

Jost, L. (2006) Entropy and diversity. *Oikos*, 113, 363–375.

King, P.P. (1832) Description of the Cirrhipeda, Conchifera and Mollusca, in a collection formed by the officers of H.M.S. Adventure and Beagle employed between the years 1826 and 1830 in surveying the southern coasts of South America, including the Straits of Magalhaens and the coast of Tierra del Fuego. *Zoological Journal*, 5(125), 332–349.

Koch, F.C.L. (1845) Trochus sauciatus. In: Philippi, R. A. 1842-1850. Abbildungen und Beschreibungen neuer oder wenig gekannter Conchylien unter Mithülfe mehrerer deutscher Conchyliologen. Cassel, T. Fischer.

Kraft, N.J.B., Valencia, R. & Ackerly, D.D. (2008) Functional traits and niche-based tree community assembly in an Amazonian forest. *Science*, 322, 580–582.

Laureto, L.M.O., Cianciaruso, M.V. & Samia, D.S.M. (2015) Functional diversity: an overview of its history and applicability. *Natureza & Conservação*, 13, 112–116.

Lecointre, G. (1952) *Recherches sur le Néogène et le Quaternaire marins de la côte Atlantique du Maroc*. Protectorat de la République Française au Maroc, Direction de la Production Industrielle des Mines, Division des Mines et de la Géologie, Service Géologique, Tome II Notes et Mémoires 99. Paris: Paléontologie, pp. 1–225.

Linnaeus, C. (1758) Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. *Impensis Direct. Laurentii Salvii. Holmiae [Stockholm]*, 1(10), [iii] 824.

Linnaeus, C. (1767) Systema naturae per regna tria naturae: secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Ed. 12. 1., Regnum Animale. Vols. 1 & 2. Holmiae, Laurentii Salvii. 1–532.

Lisiecki, L.E. & Raymo, M.E. (2005) A Pliocene-Pleistocene stack of 57 globally distributed benthic δ18O records. *Paleoceanography*, 20, PA1003. Available from: https://doi.org/10.1029/2004PA001071

Lowe, R.T. (1832) On the genera Melampus, Pedipes and Truncatella with experiments tending to demonstrate the nature of the respiratory organs of these Mollusca. *Zoological Journal*, 5, 280–305.

Madeira, P., Kroh, A., Cordeiro, R., de Frias Martins, A.M. & Ávila, S.P. (2019) The echinoderm fauna of the Azores (NE Atlantic Ocean). *Zootaxa*, 4639(1), 1–231. Available from: https://doi.org/10.11646/zootaxa.4639.1

Madeira, P., Kroh, A., Cordeiro, R., Meireles, R. & Ávila, S.P. (2011) The fossil echinoids of Santa Maria Island, Azores (Northern Atlantic Ocean). *Acta Geologica Polonica*, 61, 243–264.

Madeira, P., Kroh, A., Martins, A.M.F. & Ávila, S.P. (2007) The marine fossils from Santa Maria Island (Azores, Portugal): an historical overview. *Açoreana Suplemento*, 5, 59–73.

Magneville, C., Loiseau, N., Albouy, C., Casajus, N., Claverie, T., Escalas, A. et al. (2022) mFD: an R package to compute and illustrate the multiple facets of functional diversity. *Ecography*, 2022, e05904 (ver. 1.0). Available from: https://doi.org/10.1111/ecog.05904

Marryat, F. (1819) Descriptions of two new shells. . *Transactions of the Linnean Society of London*, 12(2), 338–339.

Martín-González, E., Galindo, I., Mangas, J., Romero, C., Sánchez, N., González-Rodríguez, A. et al. (2019) Revisión de los depósitos costeros del estadio isotópico marino 5e (MIS5e) de Fuerteventura (islas Canarias). *Vieraea Folia scientiarum biologicarum canariensium*, 46, 667–688.

Martín-González, E., González-Rodríguez, A., Vera-Peláez, J.L., Lozano-Francisco, M., de, C. & Castillo, C. (2016) Asociaciones de moluscos de los depósitos litorales del Pleistoceno Superior de Tenerife (Islas Canarias, España). *Vieraea*, 44, 87–106.

Martini, S., Larras, F., Boyé, A., Faure, E., Aberle, N., Archambault, P. et al. (2020) Functional trait-based approaches as a common framework for aquatic ecologists. *Limnology and Oceanography*, 9999, 1–30. Available from: https://doi.org/10.1002/lno.11655

Martins, G.M., Arenas, F., Neto, A.I. & Jenkins, S.R. (2012) Effects of fishing and regional species pool on the functional diversity of fish communities. *PLoS One*, 7(8), e44207.

Martínez, S., Ubilla, M., Verde, M., Perea, D., Rojas, A., Guérèquiz, R. et al. (2001) Paleoecology and geochronology of Uruguayan coastal marine Pleistocene deposits. *Quaternary Research*, 55(2), 246–254.

Mason, N.W.H., Mouillot, D., Lee, W.G. & Wilson, J.B. (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos*, 111, 112–118.

Mayer [Mayer-Eymar], K. (1864) Die Tertiär-Fauna der Azoren und Madeiren. Systematisches Verzeichniss der fossilen Reste von Madeira, Porto Santo und Santa Maria nebst Beschreibung der neuen Arten. Published by the author, Zürich, vi + 107.

Mcclain, C.R., Heim, N.A., Knope, M.L. & Payne, J.L. (2018) Is biodiversity energy-limited or unbounded? A test in fossil and modern bivalves. *Paleobiology*, 44(3), 385–401.

McLean, M., Mouillot, D., Lindegren, M., Villéger, S., Engelhard, G., Murgier, J. et al. (2019) Fish communities diverge in species but converge in traits over three decades of warming. *Global Change Biology*, 25, 3972–3984.

McLean, M., Stuart-Smith, R.D., Villéger, S., Auber, A., Edgar, G.J., MacNeil, M.A. et al. (2021) Trait similarity in reef fish faunas across the world's oceans. *Proceedings of the National Academy of Sciences of the United States of America*, 118(12), 1–10.

Meco, J., Betancort, J.F., Ballester, J., Fontugne, M., Guillou, H., Scaillet, S. et al. (2008) Historia Geológica del Clima en Canarias. Laboratorio de Paleontología, Departamento de Biología, Universidad de Las Palmas de Gran Canaria (ULPGC), 296.

Meireles, R.P., Faranda, C., Gliozzi, E., Pimentel, A., Zanon, V. & Ávila, S.P. (2012) Late Miocene marine ostracods from Santa Maria Island, Azores (NE Atlantic): systematics, palaeoecology and palaeobiogeography. *Revue de Micropaléontologie*, 55, 133–148.

Meireles, R.P., Keyser, D., Borges, P.A., Silva, L., Martins, A.M.F. & Ávila, S.P. (2014) The shallow marine ostracods communities of the Azores (Mid-North Atlantic): taphonomy and palaeoecology. *Geologica Acta*, 12(1), 53–70.

Melo, C.S., Marques da Silva, C., Scarponi, D., Martín-González, E., Rólán, E., Rojas, A. et al. (2023) Palaeobiogeography of NE Atlantic archipelagos during the Last Interglacial (MIS 5e): a molluscan approach to the conundrum of Macaronesia as a marine biogeographic unit. *Quaternary Science Reviews*, 319, 108313.

Melo, C.S., Martín-González, E., da Silva, C.M., Galindo, I., González-Rodríguez, A., Baptista, L. et al. (2022a) Range expansion of tropical shallow-water marine molluscs in the NE Atlantic during the last interglacial (MIS 5e): causes, consequences and utility of ecostratigraphic indicators for the Macaronesian archipelagos. *Quaternary Science Reviews*, 278, 107377.

Melo, C.S., Martín-González, E., da Silva, C.M., Galindo, I., González-Rodríguez, A., Baptista, L. et al. (2022b) Reply to the comment by Meco et al. on "Range expansion of tropical shallow-water marine molluscs in the NE Atlantic during the last interglacial (MIS 5e): causes, consequences and utility of ecostratigraphic indicators for the Macaronesian archipelagos". *Quaternary Science Reviews*, 288, 107535.

Montagu, G. (1803) Testacea Britannica or natural history of British shells, marine, land, and fresh-water, including the most minute: Systematically arranged and embellished with figures. *J. White, London, Vol. 1, xxxvii + 291*, 2, 293–606.

Montagu, G. (1808) Supplement to Testacea Britannica with Additional Plates. *Woolmer, Exeter*, v + 183.

Mouchet, M.A., Villéger, S., Mason, N.W.H. & Mouillot, D. (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, 24, 867–876.

Mouillot, D., Bellwood, D.R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M. et al. (2013c) Rare species support vulnerable functions in high-diversity ecosystems. *PLoS Biology*, 11, e1001569.

Mouillot, D., de Bortoli, J., Leprieur, F., Parravicini, V., Kulbicki, M. & Bellwood, D.R. (2013b) The challenge of delineating biogeographical regions: nestedness matters for Indo–Pacific coral reef fishes. *Journal of Biogeography*, 40(12), 2228–2237.

Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H. & Bellwood, D.R. (2013a) A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution*, 28, 167–177.

Mouillot, D., Villéger, S., Parravicini, V., Kulbicki, M., Arias-González, J.E., Bender, M. et al. (2014) Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 13757–13762.

Mouton, T.L., Tonkin, J.D., Stephenson, F., Verburg, P. & Floury, M. (2020) Increasing climate-driven taxonomic homogenization but functional differentiation among river macroinvertebrate assemblages. *Global Change Biology*, 26, 6904–6915.

Muhs, D.R., Simmons, K.R. & Steinke, B. (2002) Timing and warmth of the Last Interglacial period: new U-series evidence from Hawaii and Bermuda and a new fossil compilation for North America. *Quaternary Science Reviews*, 21, 1355–1383.

Müller, O.F. (1776) Zoologiae Danicae Prodromus, seu Animalium Daniae et Norvegiae Indigenarum characters, nomina, et synonyma imprimis popularium. *Typis Hallageriis, Havniae*, 32, 1–282.

Murley, M., Hovey, R.K. & Prince, J. (2024) Temperate intertidal ecosystems are functionally richer but more vulnerable to loss than tropical ecosystems. *Ecology and Evolution*, 14, e70657.

Myers, E.M.V., Eme, D., Liggins, L., Harvey, E.S., Roberts, C.D. & Anderson, M.J. (2021) Functional beta diversity of New Zealand fishes: characterising morphological turnover along depth and latitude gradients, with derivation of functional bioregions. *Austral Ecology*, 46, 965–981.

Naeem, S., Duffy, J.E. & Zavaleta, E. (2012) The functions of biological diversity in an age of extinction. *Science*, 336, 1401–1406.

O'Leary, M.J., Hearty, P.J., Thompson, W.G., Raymo, M.E., Mitrovica, J.X. & Webster, J.M. (2013) Ice sheet collapse following a prolonged period of stable sea level during the last interglacial. *Nature Geoscience*, 6, 796–800.

Oppo, D.W., McManus, J.F. & Cullen, J.L. (2006) Evolution and demise of the Last Interglacial warmth in the subpolar North Atlantic. *Quaternary Science Reviews*, 25, 3268–3277.

Orbigny, A.d'. (1836–1842) Mollusques, Echinodermes, Foraminifères et Polypiers recueillis aux Iles Canaries par MM. Webb et Berthelot. In: Barker-Webb, P. & Berthelot, S., (Eds.) *Histoire naturelle des Iles Canaries*, volume 2(2). Paris: Béthune. p. 117.

Ordonez, A. & Svenning, J.-C. (2016) Functional diversity of North American broad-leaved trees is codetermined by past and current environmental factors. *Ecosphere*, 7(2), e01237.

Pallary, P. (1900) Coquilles marines du littoral du département d'Oran. *Journal de Conchyliologie*, 48(3), 211–422.

Pallas, P.S. (1766) Elenchus zoophytorum sistens generum adumbrationes generaliores et specierum cognitarum succintas descriptiones, cum selectis auctorum synonymis. *Fransiscum Varrentrapp, Hagae*, 451.

Pearson, T. & Rosenberg, R. (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environments. *Oceanography and Marine Biology Annual Review*, 16, 229–311.

Petchey, O.L. (2003) Integrating methods that investigate how complementarity influences ecosystem functioning. *Oikos*, 101, 323–330.

Petchey, O.L. & Gaston, K.J. (2002) Extinction and the loss of functional diversity. *Proceedings of the Royal Society of London. Series B*, 269, 1721–1727.

Petchey, O.L., Hector, A. & Gaston, K.J. (2004) How do different measures of functional diversity perform? *Ecology*, 85, 847–857.

Poli, J.X. (1791) Testacea utriusque Siciliae eorumque historia et anatome tabulis aeneis illustrata. *Ex Regio Typographeio, Parmae*, Vol. 1, i–lxxiii.

Poli, J.X. (1795) *Testacea utriusque Siciliae eorumque historia et anatome tabulis aeneis illustrata*. Parma: Regio Typographeio Vol. 2: i–xlix, [1–2], 75–264, pls 19–39.

Powell, M.G. & Kowalewski, M. (2002) Increase in evenness and sampled alpha diversity through the Phanerozoic: comparison of early Paleozoic and Cenozoic marine fossil assemblages. *Geology*, 30, 331–334.

Quartau, R., Madeira, J., Mitchell, N.C., Tempera, F., Silva, P.F. & Brandão, F. (2016) Reply to comment by Marques et al. on "The insular shelves of the Faial-Pico Ridge (Azores archipelago): a morphological record of its evolution". *Geochemistry, Geophysics, Geosystems*, 17(2), 633–641.

R Core Team. (2024) *R: a language and environment for statistical computing. Version 4.4.2 (2024-10-31)*. Vienna, Austria: R Foundation for Statistical Computing.

Ramalho, R.S., Helffrich, G., Madeira, J., Cosca, M., Thomas, C., Quartau, R. et al. (2017) Emergence and evolution of Santa Maria Island (Azores)—the conundrum of uplifted islands revisited. *Geological Society of America Bulletin*, 129, 372–390.

Rang, S. (1828) Notice sur quelques mollusques nouveaux appartenant au genre Cléodore, et etablissement et monographie des sous-genre Créseis. *Annales des Sciences Naturelles*, 13, 302–319.

Rasmussen, T.L., Thomsen, E., Kuijpers, A. & Wastegård, S. (2003) Late warming and early cooling of the sea surface in the Nordic seas during MIS 5e (Eemian Interglacial). *Quaternary Science Reviews*, 22, 809–821.

Rebelo, A.C., Rasser, M., Riosmena-Rodríguez, R., Neto, A.I. & Ávila, S. (2014) Rhodolith forming coralline algae in the Upper Miocene of Santa Maria Island (Azores, NE Atlantic): a critical evaluation. *Phytotaxa*, 190(1), 370–382.

Rebelo, A.C., Rasser, M.W., Kroh, A., Johnson, M.E., Ramalho, R.S. & Melo, C. et al. (2016) Rocking around a volcanic island shelf: pliocene rhodolith beds from Malbusca, Santa Maria Island (Azores, NE Atlantic). *Facies*, 62(3), 1–31.

Rebelo, A.C., Rasser, M.W., Ramalho, R.S., Johnson, M.E., Melo, C.S., Uchman, A. et al. (2021) Pleistocene coralline algal build-ups on a mid-ocean rocky shore—insights into the MIS 5e record of the Azores. *Palaeobiogeography, Palaeoclimatology, Palaeoecology*, 579, 110598.

Renz, O., Bernoulli, D. & Hottinger, L. (1992) Cretaceous ammonites from Fuerteventura, Canary Islands. *Geological Magazine*, 129(6), 763–769.

Ricchi, A., Quartau, R., Ramalho, R.S., Romagnoli, C., Casalbore, D., Ventura da Cruz, J. et al. (2018) Marine terrace development on reefless volcanic islands: new insights from high-resolution marine geophysical data offshore Santa Maria Island (Azores Archipelago). *Marine Geology*, 406, 42–56.

Ricchi, A., Quartau, R., Ramalho, R.S., Romagnoli, C., Casalbore, D. & Zhao, Z. (2020) Imprints of volcanic, erosional, depositional, tectonic and mass-wasting processes in the morphology of Santa Maria insular shelf. *Marine Geology*, 424, 106163.

Richards, H.G. (1962) Studies on the marine Pleistocene: the marine Pleistocene of the Americas and Europe; the marine Pleistocene mollusks of eastern North America. *Transactions of the American Philosophical Society*, 52(3), 1–148.

Rivadeneira, M.M. & Nielsen, S.N. (2017) Diversification dynamics, species sorting, and changes in the functional diversity of marine benthic gastropods during the Pliocene-Quaternary at temperate western South America. *PLoS One*, 12(10), e0187140.

Rivadeneira, M.M. & Nielsen, S.N. (2018) Correction: Diversification dynamics, species sorting, and changes in the functional diversity of marine benthic gastropods during the Pliocene-Quaternary at temperate western South America. *PLoS One*, 13(1), e0191525.

Rohling, E.J., Grant, K., Hemleben, C., Siddall, M., Hoogakker, B.A.A., Bolshaw, M. et al. (2008) High rates of sea-level rise during the last interglacial period. *Nature Geoscience*, 1, 38–42.

Rojas, A., Zaffaroni, J.C. & Martínez, S. (2018) New molluscan records and palaeoecology of the late pleistocene marine assemblage from La Coronilla (Rocha, Uruguay). *Journal of Sedimentary Environments*, 3(4), 220–233.

Sacchetti, C., Landau, B. & Ávila, S.P. (2023) The Lower Pliocene marine gastropods of Santa Maria Island, Azores: taxonomy and palaeobiogeographic implications. *Zootaxa*, 5295(1), 1–150.

Serralheiro, A., Alves, C.A.M., Forjaz, V.H. & Rodrigues, B. (1987) Carta Vulcanológica dos Açores. Ilha de Santa Maria na (folhas 1 e 2): Ponta Delgada, Serviço Regional de Protecção Civil dos Açores, Universidade dos Açores and Centro de Vulcanologia, scale 1:15,000.

Scheltema, R.S. (1977) Dispersal of marine invertebrate organisms: paleobiogeographic and biostratigraphic implications. In: Kauffmann, R. & Hazel, G.J.E. (Eds.) *Concepts and Methods of Biostratigraphy*. Stroudsburg, Pennsylvania: Dowden, Hutchinson Ross, pp. 73–108. xiii + 658 pp.

Scheltema, R.S. (1989) Planktonic and non-planktonic development among prosobranch gastropods and its relationship to the geographic range of species. In: Ryland, J.S. & Tyler, P.A. (Eds.) *Reproduction, Genetics and Distribution of Marine Organisms*. Fredensborg, Denmark: Olsen & Olsen, International Symposium Series, pp. 183–188.

Sibrant, A.L.R., Hildenbrand, A., Marques, F.O. & Costa, A.C.G. (2015) Volcano-tectonic evolution of the Santa Maria Island (Azores): implications for paleostress evolution at the western Eurasia-Nubia plate boundary. *Journal of Volcanology and Geothermal Research*, 291, 49–62. Available from: https://doi.org/10.1016/j.jvolgeores.2014.12.017

da Silva, G.H. (1956) Contribution à la connaissance de la faune fossile de Porto Santo. Memórias e Notícias. *Publicações do Museu e Laboratório Mineralógico e Geológico da Universidade de Coimbra*, 42, 26–28.

Soja, C.M. (1992) Potential contributions of ancient oceanic islands to evolutionary theory. *Journal of Geology*, 100, 125–134.

Solan, M., Cardinale, B.J., Downing, A.L., Engelhardt, K.A.M., Ruesink, J.L. & Srivastava, D.S. (2004) Extinction and ecosystem function in the marine benthos. *Science*, 306, 1177–1180.

Sowerby, G.B.I. (1844) Descriptions of some new species of Columbella in the collection of H. Cuming. Proceedings of the Zoological Society of London. 1844, 48–53.

Trenhaile, A.S. (2015) Coastal notches: their morphology, formation, and function. *Earth-Science Reviews*, 150, 285–304.

Uchman, A., Johnson, M.E., Ramalho, R.S., Quartau, R., Berning, B., Hipólito, A. et al. (2020) Neogene marine sediments and biota encapsulated between lava flows on Santa Maria Island (Azores, north-east Atlantic): an interplay between sedimentary, erosional, and volcanic processes. *Sedimentology*, 67, 3595–3618.

Uchman, A., Quintino, V., Rodrigues, A.M., Johnson, M.E., Melo, C.S., Cordeiro, R. et al. (2017) The trace fossil *Diopatrichnus santamariensis* nov. isp.—a shell armored tube from Pliocene sediments of Santa Maria Island, Azores (NE Atlantic Ocean). *Geobios*, 50, 459–469. Available from: https://doi.org/10.1016/j.geobios.2017.09.002

Uchman, A., Torres, P., Johnson, M.E., Berning, B., Ramalho, R.S., Rebelo, A.C. et al. (2018) Feeding traces of recent ray fish and occurrences of the trace fossil *Piscichnus waitemata* from the Pliocene of Santa Maria Island, Azores (Northeast Atlantic). *Palaios*, 33(8), 361–375. Available from: https://doi.org/10.2110/palo.2018.027

Villéger, S., Grenouillet, G. & Brosse, S. (2013) Decomposing functional β-diversity reveals that low functional β -diversity is driven by low functional turnover in European fish assemblages. *Global Ecology and Biogeography*, 22, 671–681.

Villéger, S., Mason, N.W.H. & Mouillot, D. (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89(8), 2290–2301.

Villéger, S., Miranda, J.R., Hernández, D.F. & Mouillot, D. (2010) Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecological Applications*, 20(6), 1512–1522.

Villéger, S., Novack-Gottshall, P.M. & Mouillot, D. (2011) The multidimensionality of the niche reveals functional diversity changes in benthic marine biotas across geological time. *Ecology Letters*, 14(6), 561–568.

Warwick, R. & Clarke, K. (1993) Comparing the severity of disturbance: a metaanalysis of marine macrobenthic community data. *Marine Ecology Progress Series*, 92, 221–232.

Watson, R.B. (1873) On some marine mollusca from Madeira, including a new genus of the Muricinae, a new Eulima and the whole of the Rissoa of the group of islands. Proceedings of the Zoological Society of London, 1873, 361–391.

Winkelmann, K., Buckeridge, J.S., Costa, A.C., Dionísio, M.A.M., Medeiros, A., Cachão, M. et al. (2010) *Zullobalanus santamariaensis* sp. nov., a new late Miocene barnacle species of the family Archaeobalanidae (Cirripedia: Thoracica), from the Azores. *Zootaxa*, 2680, 33–44.

Zazo, C., Goy, J.-L., Dabrio, C.J., Soler, V., Hillaire-Marcel, C., Ghaleb, B. et al. (2007) Quaternary marine terraces on Sal Island (Cape Verde archipelago). *Quaternary Science Reviews*, 26, 876–893.

Zazo, C., Goy, J.L., Hillaire-Marcel, C., Dabrio, C.J., González-Delgado, J.A., Cabero, A. et al. (2010) Sea level changes during the last and present interglacials in Sal Island (Cape Verde archipelago). *Global and Planetary Change*, 72, 302–317.

Zbyszewsky, G., Ferreira, O. & da, V. (1961) La faune marine des basses lages quaternaires de Praia et Prainha dans l'ile de Santa Maria (Açores). *Comunicações dos Serviços Geológicos de Portugal*, 45, 467–478.

Zhang, C., Cadotte, M.W., Chiarucci, A., Loreau, M., Willis, C.G., Si, X. et al. (2021) Scale-dependent shifts in functional and phylogenetic structure of Mediterranean island plant communities over two centuries. *Journal of Ecology*, 109, 3513–3523.