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Paleobiodiversity and Paleoecology Insights from a New MIS 5e Highstand Deposit on Santa Maria Island (Azores Archipelago, Portugal)

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Academic Editor: María Fernanda Sánchez Goñi

Received: 28 July 2025
Revised: 9 September 2025
Accepted: 22 September 2025
Published: 30 September 2025

Citation: Moreno, S.; Doukani, M.A.; Hipólito, A.; Madeira, P.; Pérez, S.P.; Dalmau, L.S.; Ávila, G.C.; Silva, L.; Martins, G.M.; Martín-González, E.; et al. Paleobiodiversity and Paleoecology Insights from a New MIS 5e Highstand Deposit on Santa Maria Island (Azores Archipelago, Portugal). *Quaternary* **2025**, *8*, 53. https://doi.org/10.3390/quat8040053

Abstract

During the last two decades, the Macaronesian archipelagos have been the focus of multiple studies targeting the abundant and diversified fossil record from late Neogene and Quaternary deposits. This record of past biota, ecosystems and climates is crucial for understanding the impact of glacial–interglacial cycles on Atlantic littoral marine organisms. Coupled with ongoing studies on the factors responsible for global climate change and associated sea-level variations, they contributed decisively towards the development of the modern marine island biogeography theory. Our current knowledge of the evolutionary and biogeographic history of the past and extant, shallow-water marine organisms from the Macaronesian geographic region relies on detailed analysis of many individual fossiliferous outcrops by means of quantitative and qualitative methodologies. Here, we focus on the fossil record of a newly studied MIS 5e outcrop at Pedra-que-pica (PQP), on Santa Maria Island (Azores Archipelago, Portugal). This multidisciplinary work integrates geology, paleontology and biology, providing the first detailed description of the sedimentary facies and stratigraphic framework of the PQP MIS 5e sequence that, coupled with the documentation of the biodiversity and ecological composition of PQP molluscan assemblages, allows us to produce a paleoecological reconstruction and to compare PQP with other last interglacial outcrops from Santa Maria Island. Our results increase the number of the

Azorean MIS 5e marine molluscs to 140 taxa (116 Gastropoda and 24 Bivalvia). *Ervilia castanea* (Montagu, 1803) is the most abundant bivalve, while *Bittium nanum* (Mayer, 1864) and *Melarhaphe neritoides* (Linnaeus, 1758) are the most abundant gastropod species. In addition, this work emphasizes the crucial importance of complementing quantitative collecting with qualitative surveys of the fossiliferous outcrops, because nearly 42% of the bivalve species and 28% of the gastropod taxa would be missed if only quantitative samples were used. Derivation of Hill numbers and rarefaction curves both indicate that the sampling effort should be increased at PQP. Thus, although Santa Maria Island is recognized by the scientific community as one of the best-studied islands regarding the last interglacial fossil record, this study emphasizes the need to continue with similar efforts in less known outcrops on the island.

Keywords: Pleistocene; last interglacial episode; Mollusca; Pedra-que-pica; systematics; checklist

1. Introduction

The fossil record from highstand sediments deposited in the Macaronesian archipelagos during the last interglacial, especially through its warmer period, the Marine Isotope Stage (MIS) 5e, has a dual significance. First, they can be used to trace past geographic range expansions of tropical fauna towards higher latitudes [1–5] and to infer coeval sea-level temperatures [6]; second, they can be used to test evolutionary and biogeographic theories [7–9]. Elsewhere, field evidence of MIS 5e sea levels has been the subject of several investigations [10–15]. For example, Uranium-series (U-series) dating of mollusc shells and corals from Mallorca established two distinct sea-level highstands in the western Mediterranean at ~135 ka and ~117–120 ka [10]. In North America, U-series evidence from Hawaii and Bermuda suggest a prolonged highstand from approximately 134 to 113 ka, associated with the widespread northward expansion of tropical marine taxa [11]. In the Macaronesia geographic region, raised marine terraces in the Canary Islands and Cabo Verde Archipelago likewise record complex relative sea-level records influenced by vertical land movements, which provide evidence of alternating highstands during MIS 5e [13,16,17]. Along the Spanish Mediterranean and Atlantic coasts, well-preserved Pleistocene marine terraces, combined with geomorphological and sedimentological analyses, indicated submillennial sea-level variations [12,18,19]. These regional records show that rather than a simple global curve, local sea levels reflect a patchwork of eustatic and isostatic processes [20].

In the North Atlantic, high-resolution marine sediment deposits reveal rapid fluctuations in sea-surface temperatures and associated sea levels during MIS 5e, indicating dynamic interactions between ice sheets and ocean circulation [21]. For instance, planktonic foraminiferal stable isotope records from the Norwegian Sea demonstrate a late MIS 5e temperature peak around 118–116 ka, followed by abrupt cooling events [22]. Global syntheses have identified at least six different sea-level intervals during MIS 5e, including a prolonged +2–3 m stillstand (132–125 ka ago), a mid-interglacial regression, a second rise to +3–4 m (124–122 ka ago), and a final highstand of +6–9 m (121–119 ka ago), before a rapid fall into MIS 5d [20,23]. Episodic loss of mass from the Greenland and West Antarctic ice sheets may be the cause of these pulses, demonstrating that even a limited warming (about 1–2 °C) may cause multi-meter sea-level rises over centenary intervals [14,24].

The Azores (36–40° N, 24–31° W) is the northernmost of the Macaronesian archipelagos (Figure 1). It is located in the North Atlantic Ocean, at about 1380 km west of mainland

Portugal. It is composed of nine volcanic islands, Santa Maria (36° 59′ N, 25° 05′ W) being the easternmost and geologically oldest island. Its complex tectonic history [25] resulted in a sequence of uplifted marine terraces [26] and well-preserved fossiliferous deposits [27–29] that provide an exceptional archive of Pleistocene environment and sea-level changes [30–36]. In the Azores Archipelago, the last interglacial (MIS 5e; about 130,000–116,000 years ago) is well represented at Santa Maria Island by a series of geomorphological benchmarks (e.g., wave-cut notches, marine terraces, sea-level highstand fossiliferous deposits) within a range of 3–10 m above present mean sea level (apsl). The fossiliferous deposits span from the Pliocene through the Quaternary (for a review see [37–39] and references therein). Early work by [40,41] first documented the diverse marine fauna preserved in the Quaternary terraces of Praia and Prainha, two MIS 5e outcrops, recording numerous gastropods and bivalves that suggested warm-water conditions. García-Talavera [27] later confirmed tropical affinity, with several species indicating that thermophilic fauna occasionally invaded the northern latitudes during interglacial periods. Callapez and Soares [28] correlated the fossil molluscs' composition of two MIS 5e outcrops (Prainha and Lagoinhas), highlighting a mix of Atlantic–European and tropical taxa. Their results also supported northern expansions of warm-water species during the MIS 5e highstands.

Within this context, Santa Maria's MIS 5e deposits have been investigated extensively over the past two decades, with new outcrops being discovered on a regular basis, and new fossil records steadily increasing the relevance of the island's paleontological heritage [1–3,42–44].

Despite published information regarding the MIS 5e deposits at Prainha (PRA), Vinha Velha (VVE) and Lagoinhas (LAG; cf. Figure 1B) that integrate detailed faunal taxonomy, sedimentary facies analysis and paleoecological interpretations, other MIS 5e outcrops remain under-investigated on the island, such as Ponta do Cedro, Ponta do Castelo and Pedra-que-pica (PQP). The study of these new MIS 5e outcrops would help to constrain the timing of local deposition relative to global sea-level intervals and also provide new insights about the response of faunal communities to changing environments in a mid-Atlantic volcanic context. One of the last outcrops discovered at Santa Maria Island was a small MIS 5e deposit located west from the remarkable Pliocene coquina of Pedra-que-pica (for a review see [45–48]). Hence, we take this opportunity to (1) describe the sedimentary facies and stratigraphic framework of the PQP MIS 5e sequence (Figure 2); (2) document the biodiversity and ecological composition of its molluscan assemblages; and (3) correlate local depositional events with the PRA, LAG and VVE outcrops. Through these goals, we aim to improve regional sea-level reconstructions, evaluate biogeographic affinities within Macaronesia and contribute to a better understanding of the different paleoecological environments in the Azores during the last interglacial episode.

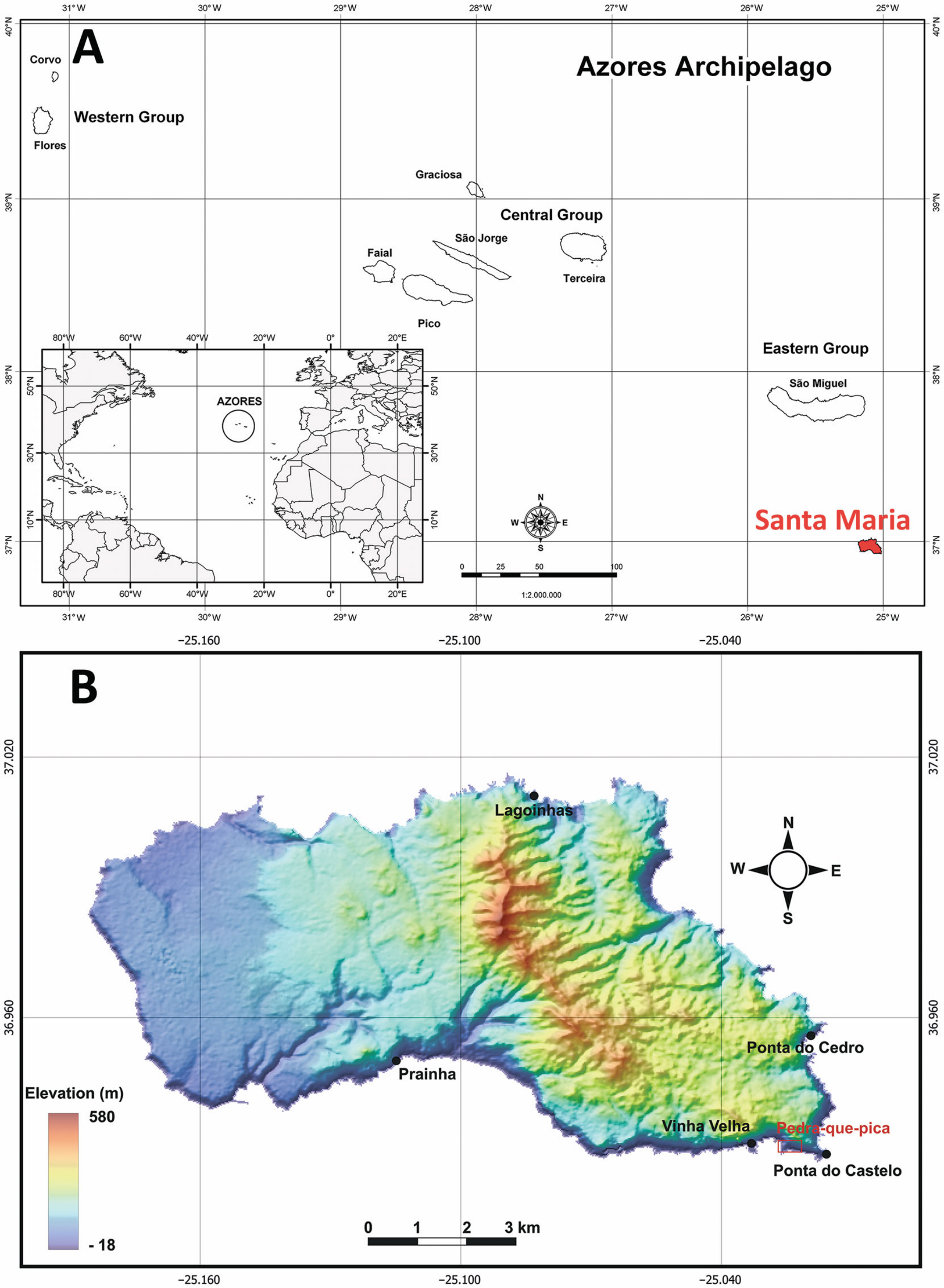

Figure 1. Location maps. (**A**)—Location of the Azores Archipelago within the NE Atlantic (insert) and Santa Maria (highlighted in red) within the Azores Archipelago. Coastline delimitation from the Portuguese Hydrographic Institute free data (https://www.hidrografico.pt/op/33 (accessed on the 9 May 2025)). (**B**)—Map of Santa Maria Island modified from [2], with the location of the MIS 5e deposits known from Santa Maria Island. Red rectangle shows the location of the Pedra-que-pica MIS 5e deposit. Underlying digital elevation model from the 1:5000 scale digital altimetric database.

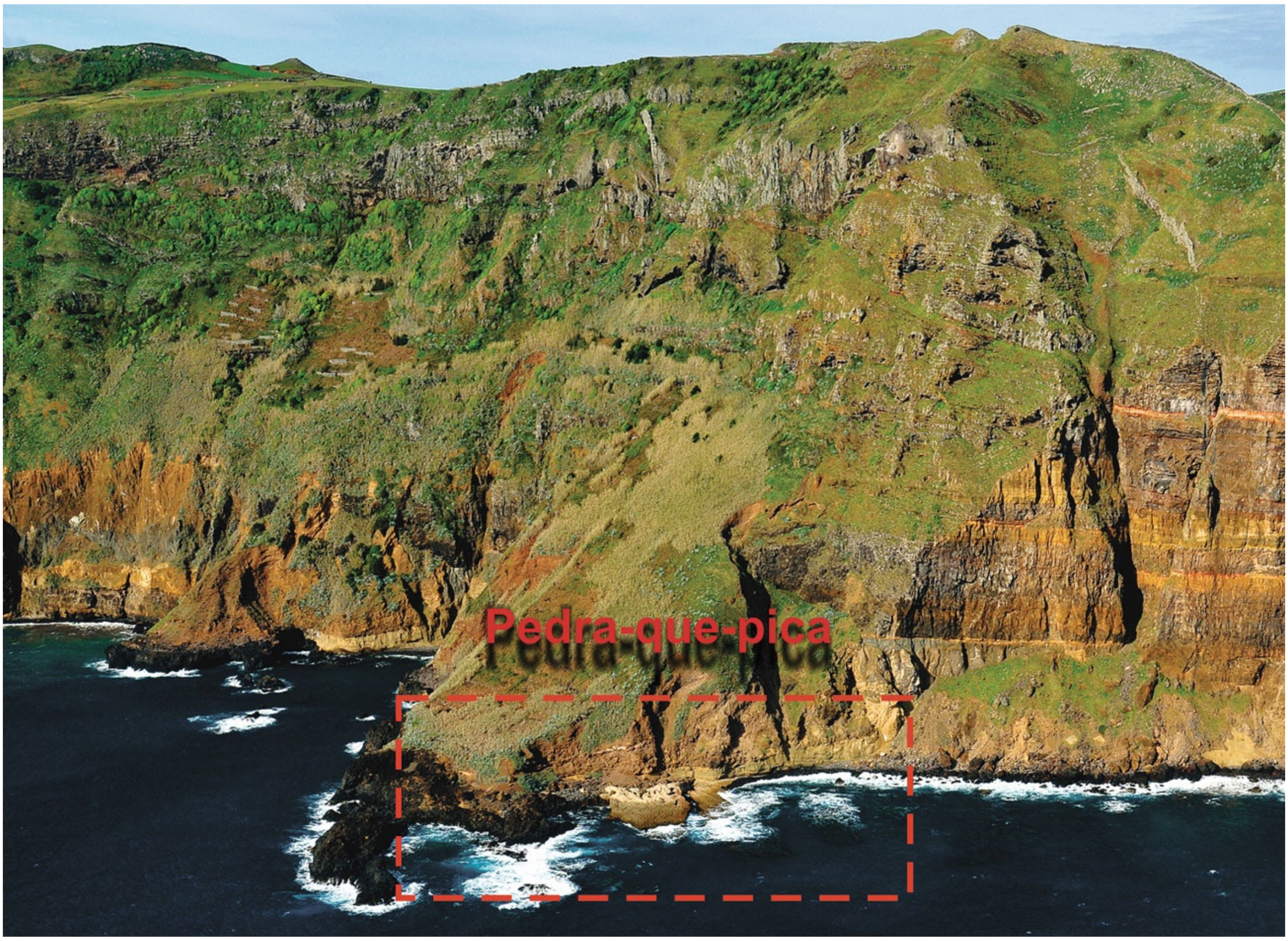

Figure 2. Eastern sector of Baixa do Sul at Santa Maria Island. The dashed red line indicates the location of the of Pedra-que-pica outcrop. Here, two fossil deposits are documented: the oldest and best-known Pliocene (Zanclean) coquina of Pedra-que-pica, described by [45] (see also [34,46,49–55]; and the MIS 5e outcrop of Pedra-que-pica herein first described.

2. Material and Methods

2.1. Stratigraphical, Sedimentological and Paleontological Characterization

The MIS 5e outcrop at PQP was studied in detail to reconstruct the overall structure, geometry and field relations between the sedimentary deposit and the underlying/overlying volcanic sequences (Figure 3). Three cross-sections were compiled along the entire MIS 5e deposit of PQP (Figure 4) showing the arrangement, internal structures and erosional contacts: log 1 was made on the western section of the sequence (Figure 5); log 2 was recorded in the beginning of the Pliocene deposit and shows the MIS 5e erosional terrace; and log 3 was taken in the middle of the Pliocene deposit of Pedra-que-pica. Strip logs for stratigraphic sections represent the variability and facies succession found at this outcrop (Figure 5). Special care was taken to record the geometry and dimensions of observed sedimentary structures, lateral and vertical continuity of facies, and the position and taphonomical aspects of fossil content.

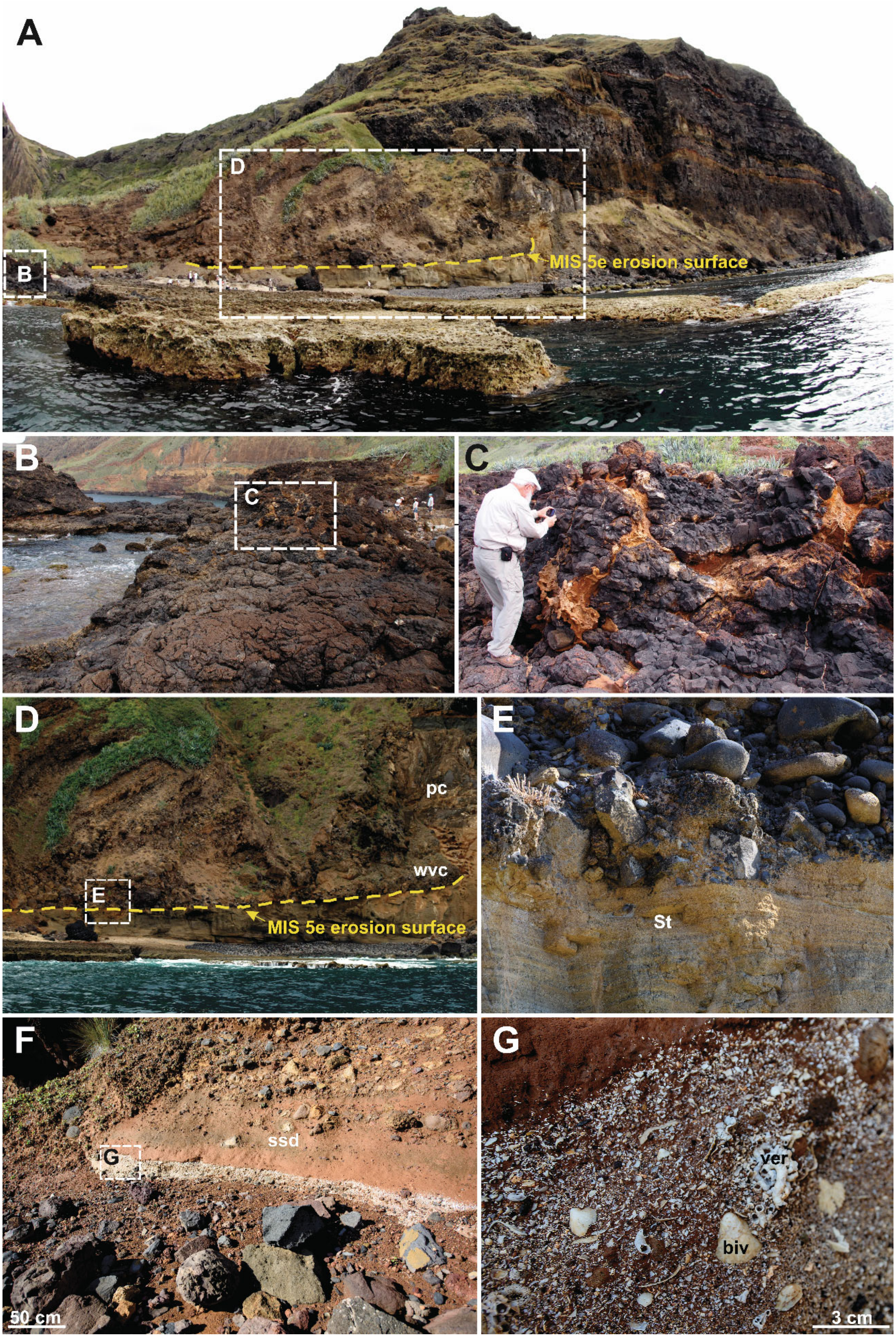

Figure 3. General aspects of the MIS 5e outcrop at Pedra-que-pica. (**A**)—Frontal view of the outcrop from the sea. Yellow dashed line indicates the erosional MIS 5e marine terrace carved on the surtseyan tuff that encapsulated the Pliocene coquina of Pedra-que-pica (see [45]). (**B**)—Detail of the rocky spur that protected the Pliocene coquina of Pedra-que-pica against wave erosion during the early stages of the last interglacial. (**C**)—Pliocene sandstone pockets, composed of fine-grained, light gray calcarenites, infill the spaces in between the pillow lavas. Vertically oriented trace fossils belonging to *Macaronichnus segregatis* Clifton and Thompson, 1978, are abundant in these calcarenites

and record fluctuations of the coastal groundwater mixing zone (see [34]). (**D**)—General view of the MIS 5e erosional surface on top of the Pliocene sediments of Pedra-que-pica. Note the wave cut notch (wvc) and the paleocliff (pc). (**E**)—Detail of the erosional contact zone between the Pliocene surtseyan tuff (St) and the conglomerates and boulders that form the base of the MIS 5e sedimentary section. (**F**)—The MIS 5e lenticular sandy sediments are located west of the Pliocene Pedra-que-pica outcrop and covered by subaerial slope deposits (ssd). (**G**)—Macro-photograph of the surface of the MIS 5e sediments, where abundant bivalve (biv) and gastropod shells [e.g., vermetids (ver)] are visible.

The Pedra-que-pica MIS 5e outcrop was first explored during the 4th "Palaeontology in Atlantic Islands" workshop, on 20 June 2007. At that time, the outcrop was sampled based on standardized 1 kg samples (Table 1). A preliminary search revealed that fossils were only abundant in unit 7 (cf. Figure 5), with unit 6 yielding just a few shells of *Patella* sp.; therefore, sampling was performed on fresh material, obtained after the removal of weathered residues. In total, three 1 kg samples were herein surveyed from PQP. No batteries of sieves were used, thus allowing for the hand-picking of all determinable remains of the macrobenthos (including fragments down to a size of 0.1 mm). Quantitative analysis was restricted to the molluscs. Samples were sorted and all mollusc specimens collected were identified to the lowest possible taxonomic level and counted (Figure 6). The best-preserved specimens were photographed, including the new records for the MIS 5e of Santa Maria.

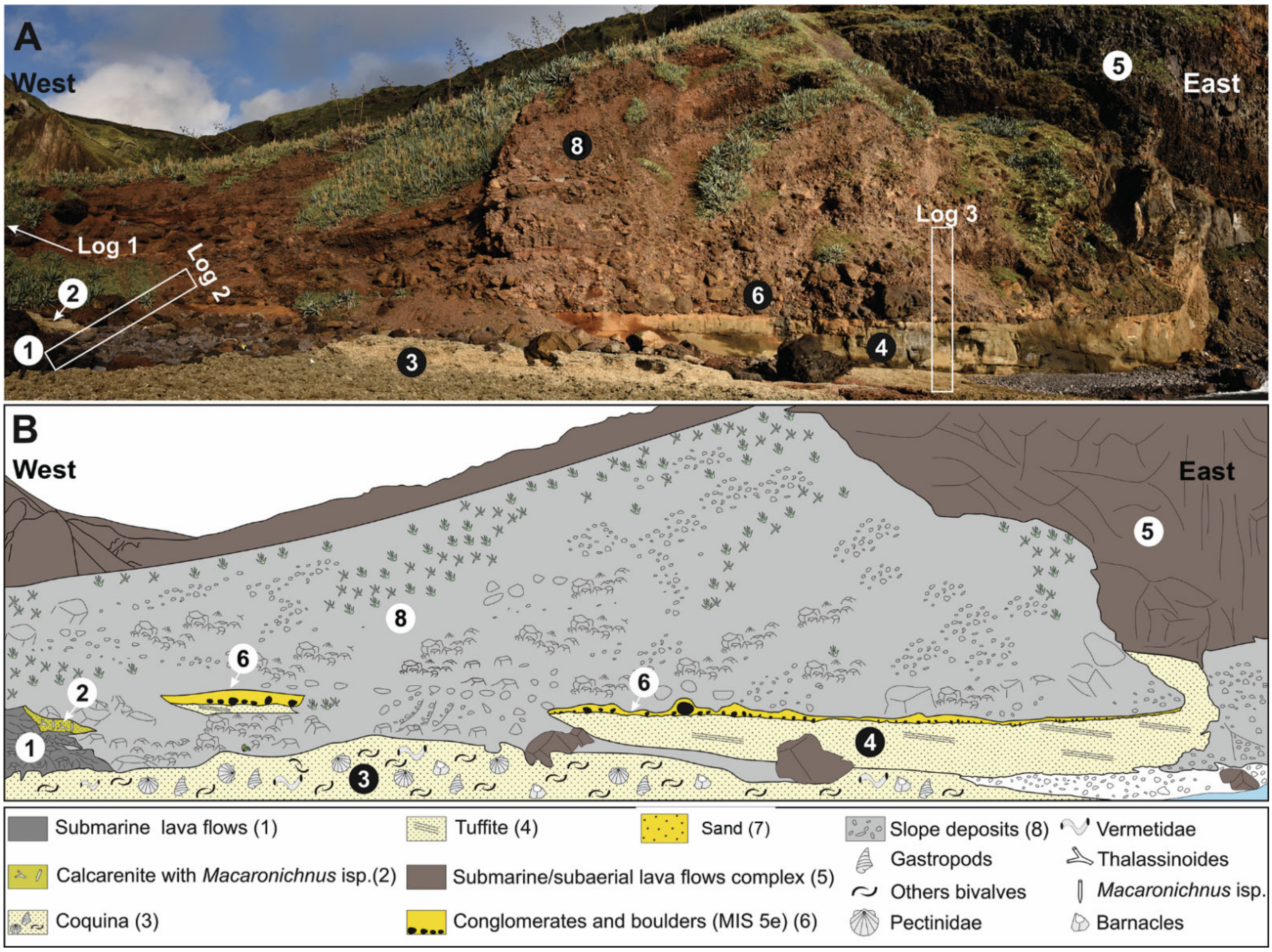

Figure 4. General view (**A**) and schematic representation (**B**) of the Pedra-que-pica Pliocene and MIS 5e outcrops displaying the location and spatial arrangement of the three logs.

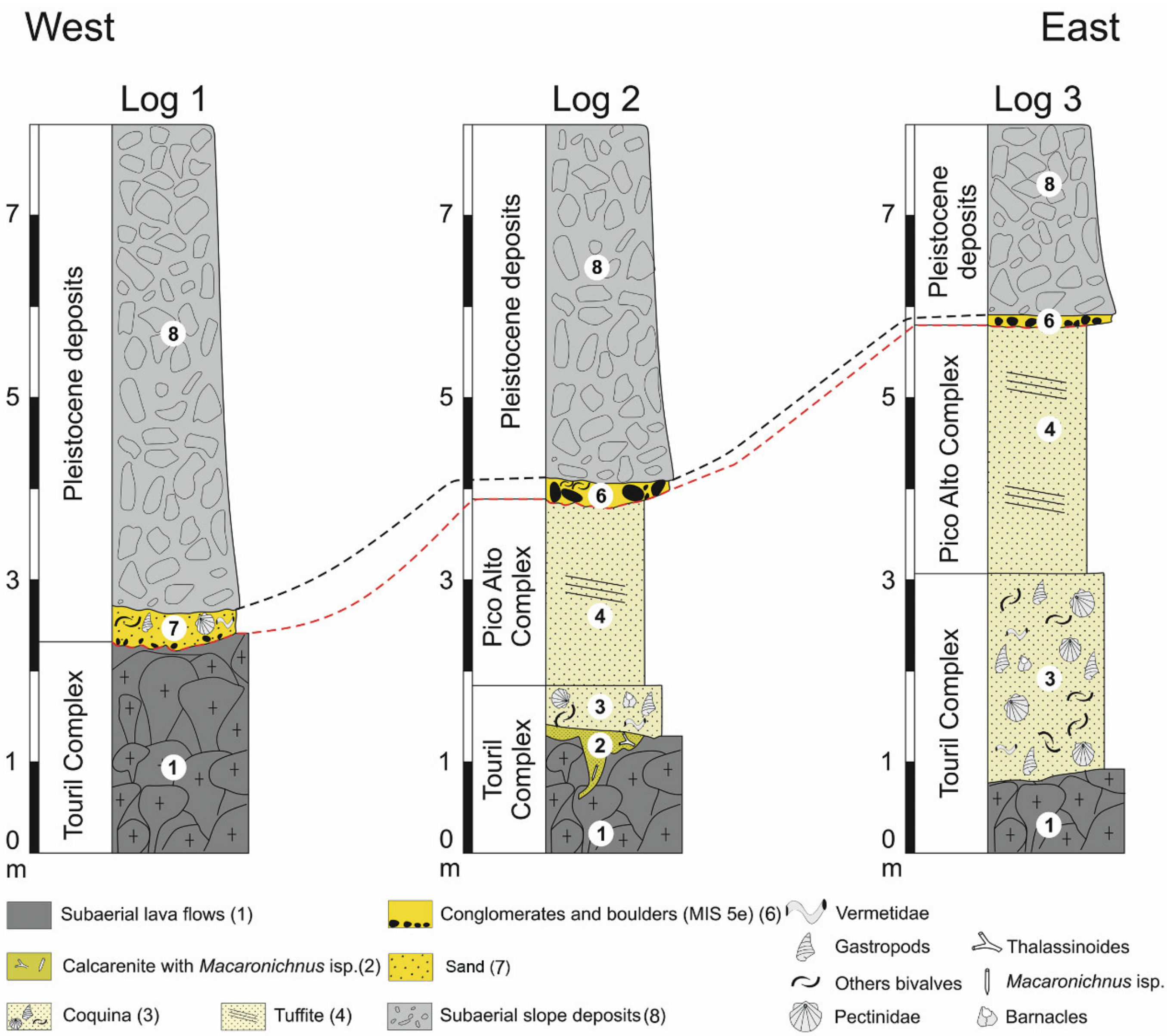

Figure 5. Simplified strip logs of the Pedra-que-pica MIS 5e outcrop, representing main lithologies, sedimentary structures, contacts and fossiliferous content. Numbers correspond to the depositional units described in the main text. For the location of each log in the outcrop, please refer to Figure 4. The three MIS 5e quantitative samples (each of 1 kg) were collected in unit 7.

The invertebrate nomenclature follows that adopted in the "Molluscabase" database (https://www.molluscabase.org/ (last accessed on the 10 May 2025)) for the fossil taxa and WoRMS database (http://www.marinespecies.org/ (last accessed on the 21 June 2025)) for the extant species. 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 1055, 1057-1 and 1057-3.

Table 1. Most frequent species of molluscs (expressed as % of bivalves and % of gastropods) at the MIS 5e outcrops of Santa Maria Island.

	Pedra-que-pica		**Prainha**		**Lagoinhas**		**Vinha Velha**	
Class	**Species**	**%**	**Species**	**%**	**Species**	**%**	**Species**	**%**
Bivalvia	*Ervilia castanea*	97.24	*Ervilia castanea*	92.03	*Ervilia castanea*	100.00	*Ervilia castanea*	97.56
Bivalvia	*Cardita calyculata*	2.17	*Lucinella divaricata*	4.10			*Cardita calyculata*	2.18
			Bosemprella incarnata	1.63			*Lucinella divaricata*	0.26
	Total	**99.42**	**Total**	**97.76**	**Total**	**100.00**	**Total**	**100.00**
Class	**Species**	**%**	**Species**	**%**	**Species**	**%**	**Species**	**%**
Gastropoda	*Bittium nanum*	42.96	*Bittium nanum*	50.44	*Bittium nanum*	41.50	*Melarhaphe neritoides*	31.42
Gastropoda	*Rissoa guernei*	26.14	*Alvania mediolittoralis*	11.70	*Alvania mediolittoralis*	21.76	*Bittium nanum*	17.73
Gastropoda	*Jujubinus pseudogravinae*	4.57	*Rissoa guernei*	10.01	*Rissoa guernei*	12.51	*Cingula trifasciata*	15.68
Gastropoda	*Manzonia unifasciata*	4.48	*Melarhaphe neritoides*	5.62	*Alvania sleursi*	6.91	*Vermetidae*	14.44
Gastropoda	*Alvania sleursi*	2.89	*Anachis avaroides*	3.42	*Melarhaphe neritoides*	3.72	*Alvania mediolittoralis*	8.20
Gastropoda	*Alvania angioyi*	2.65	*Jujubinus pseudogravinae*	2.89	*Cingula trifasciata*	2.92	*Anachis avaroides*	2.18
Gastropoda	*Melarhaphe neritoides*	2.56	Triphoridae	2.55	Triphoridae	1.93	*Alvania sleursi*	1.59
Gastropoda	*Crisilla postrema*	2.19	*Manzonia unifasciata*	2.02	*Manzonia unifasciata*	1.75	*Jujubinus pseudogravinae*	1.58
Gastropoda	*Alvania mediolittoralis*	2.07	*Patella aspera*	1.75				
Gastropoda	*Setia subvaricosa*	2.07						
Gastropoda	*Cingula trifasciata*	1.37						
	Total	**93.97**	**Total**	**90.39**	**Total**	**93.00**	**Total**	**92.83**

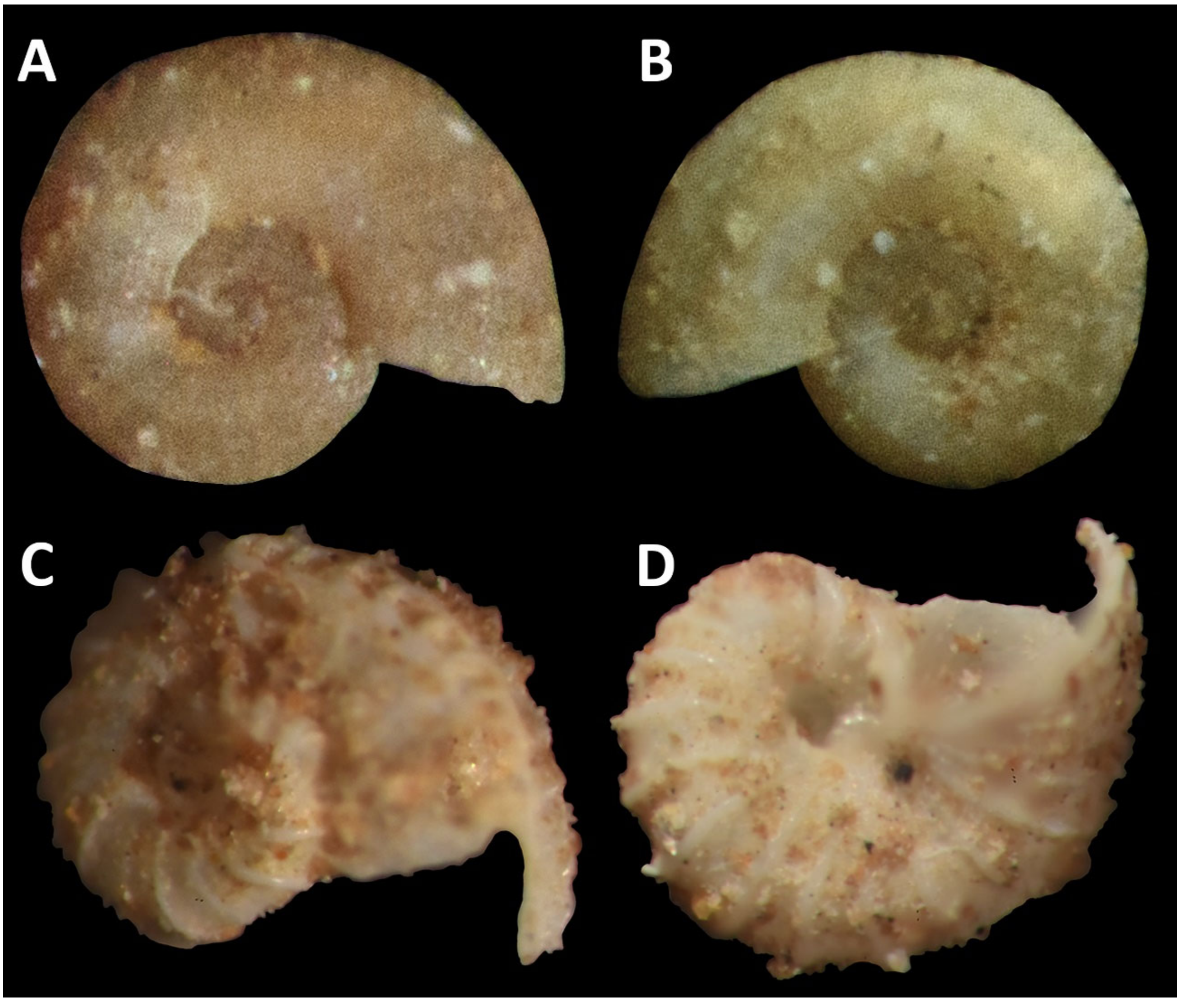

Figure 6. Gastropods first cited for the fossil record of Santa Maria Island (**A**,**B**), and for the world fossil record (**C**,**D**). (**A**,**B**)—*Omalogyra atomus* (R. A. Philippi, 1841), 0.2 mm, DBUA-F 1057-3, collected at the MIS 5e deposit of Pedra-que-pica at the 20 June 2007 by Sérgio P. Ávila. (**C**,**D**)—*Scissurella lobini* (Burnay & Rolán, 1990), 0.3 mm, DBUA-F 1057-1, collected at the MIS 5e deposit of Pedra-que-pica at the 20 June 2007 by Sérgio P. Ávila.

2.2. Statistical Analysis

The quantitative data extracted from the three fossiliferous sand samples from Pedra-que-pica, each ~1 kg was compared with similar data from Prainha ([56]; 8 kg samples), Lagoinhas ([2]; 10 kg samples) and Vinha Velha ([43]; 6 kg samples; cf. Table 2) and a table was compiled (see Supplementary Table S1).

Table 2. Species richness (SpRic) and abundance (N, number of individuals) of molluscs per replicate (1 kg bulk sample). PQP: Pedra-que-pica. LAG: Lagoinhas. PRA: Prainha. VVE: Vinha Velha.

Sample	SpRic	N
PQP-01	36	5895
PQP-02	34	909
PQP-03	36	1628
LAG-01	23	888
LAG-02	27	2780
LAG-03	22	1101
LAG-04	34	4757
LAG-05	25	2150

Table 2. *Cont.*

Sample	SpRic	N
LAG-06	22	1380
LAG-07	22	2503
LAG-08	23	1471
LAG-09	27	2736
LAG-10	23	1555
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	29	1941
VVE-02	27	1559
VVE-03	31	2708
VVE-04	31	2100
VVE-05	24	2186
VVE-06	31	2885

We used Hill numbers (q = 0 for species richness, q = 1 for the exponential of Shannon's entropy index and q = 2 for the inverse of Simpson's concentration index) to estimate diversity of samples using the hillR.package in R (cf. Table 3 and Figure 7). The number of individuals among our samples ranged between 215 and 5895 (cf. Supplementary Table S1). As species richness counts are highly sensitive to the number of individuals sampled [57], we applied extrapolation and rarefaction techniques based on 50 permutations to estimate the numbers of species in a sample of 50 individuals (ES_{50}) using the iNEXT.package in R, thus making comparisons among samples more realistic. Statistical analysis was performed at the scale of the individual samples and at the scale of the location, the latter obtained by pooling data from all samples together within each location.

Table 3. Results of generalized linear models comparing Hill's series (diversity indices) among outcrops. Remaining abbreviations as in Table 2.

Source	Hill q = 0			Hill q = 1			Hill q = 2		
	Estimate	***z***	**v**	**Estimate**	***Z***	***p***	**Estimate**	***z***	***p***
Intercept	3.56	36.70	<0.001	1.82	7.84	<0.001	1.36	4.66	<0.001
LAG	−0.40	−3.38	<0.001	0.03	0.13	>0.05	0.06	0.18	>0.05
PRA	−0.11	−1.03	>0.05	0.05	0.19	>0.05	−0.01	−0.04	>0.05
VVE	−0.23	−1.92	>0.05	0.25	0.89	>0.05	0.33	0.97	>0.05
Null deviance		40.12			12.02			9.29	
Residual deviance		25.08			10.51			7.09	

The Chao estimator was used to account for potentially under-sampled species richness at PQP. 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 (Figure 8).

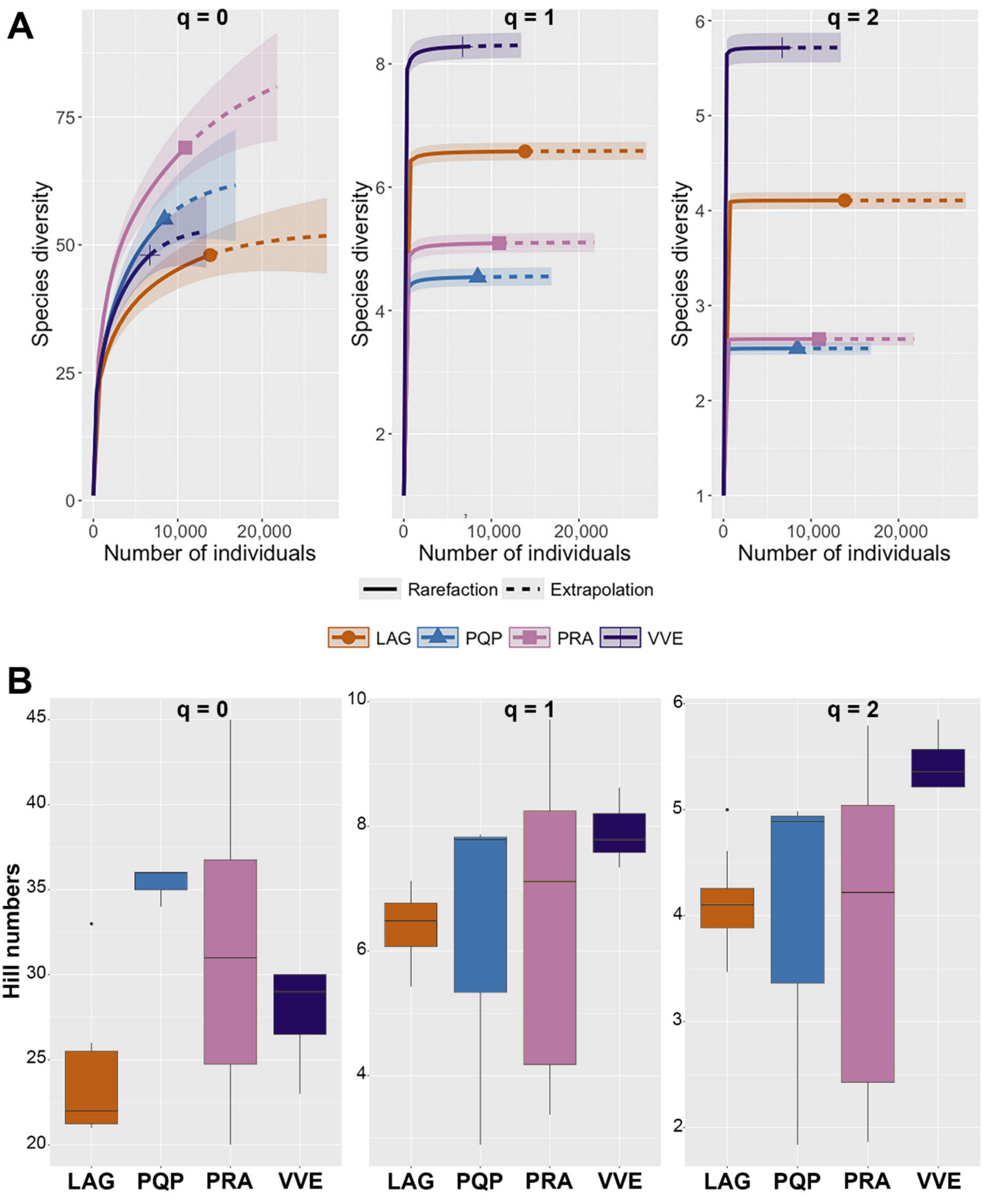

Figure 7. (**A**): Relation between the number of individuals and the estimated number of species (samples pooled by outcrop). Hill numbers (q = 0 for species richness, q = 1 for the exponential of Shannon's entropy index and q = 2 for the inverse of Simpson's concentration index) were used to estimate 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 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. PQP: Pedra-que-pica. PRA: Prainha. VVE: Vinha Velha.

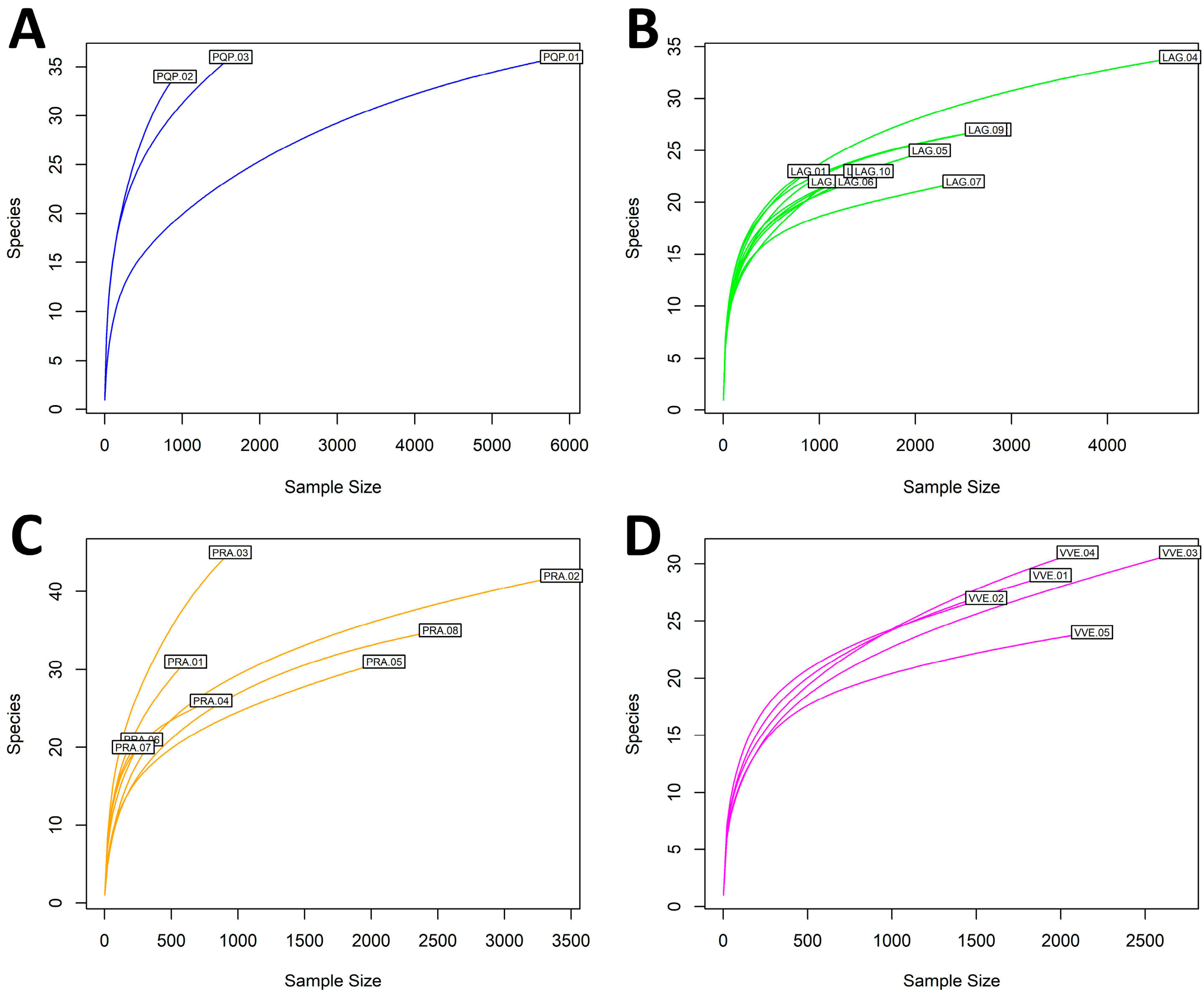

Figure 8. (**A**–**D**): Species count estimates with the Chao estimator for the quantitative samples of the four MIS 5e outcrops in Santa Maria Island. (**A**): Pedra-que-pica. (**B**): Lagoinhas. (**C**): Prainha. (**D**): Vinha Velha. Rarefaction curves were computed using the total sum of individuals per 1 kg bulk sample (individual rarefaction). Remaining abbreviations as in Figure 7.

A number of data transformation and standardization procedures and different association measures were tested. Similarly, multiple clustering methods were explored. After preliminary analysis and considering the values for cophenetic correlation, we opted for using log-transformed species abundances, Bray–Curtis dissimilarity and Ward's minimum variance clustering. We applied Silhouette graph and Mantel statistics to define the optimal number of clusters. A heatmap and a dendrogram (Figure 9) were employed to represent the relationships between sites and samples.

Finally, an indicator species analysis was used to compare the four deposits (PQP, PRA, LAG and VVE). In order to determine the possible association between species and the different sites, based on species abundance, we used the R package "Indicspecies", version 1.8.0, available through Cran (http://cran.r-project.org/web/packages/indicspecies/ (accessed on the 13 June 2025)). This package is a refinement of the IndVal method originally developed by [58] and was elaborated by [59]. This algorithm defines both fidelity (i.e., restriction to a site or group of sites) and consistency (consistent species occurrence among sites within site groups), providing a statistic (IndVal) and the respective p-value (Table 4).

A redundancy analysis (RDA) based on the IndVal was used to project the species and the samples simultaneously (Figure 10). This method was successfully applied in the comparison of recent and paleocommunities' marine ostracods [60,61] and molluscs in the Azores [43].

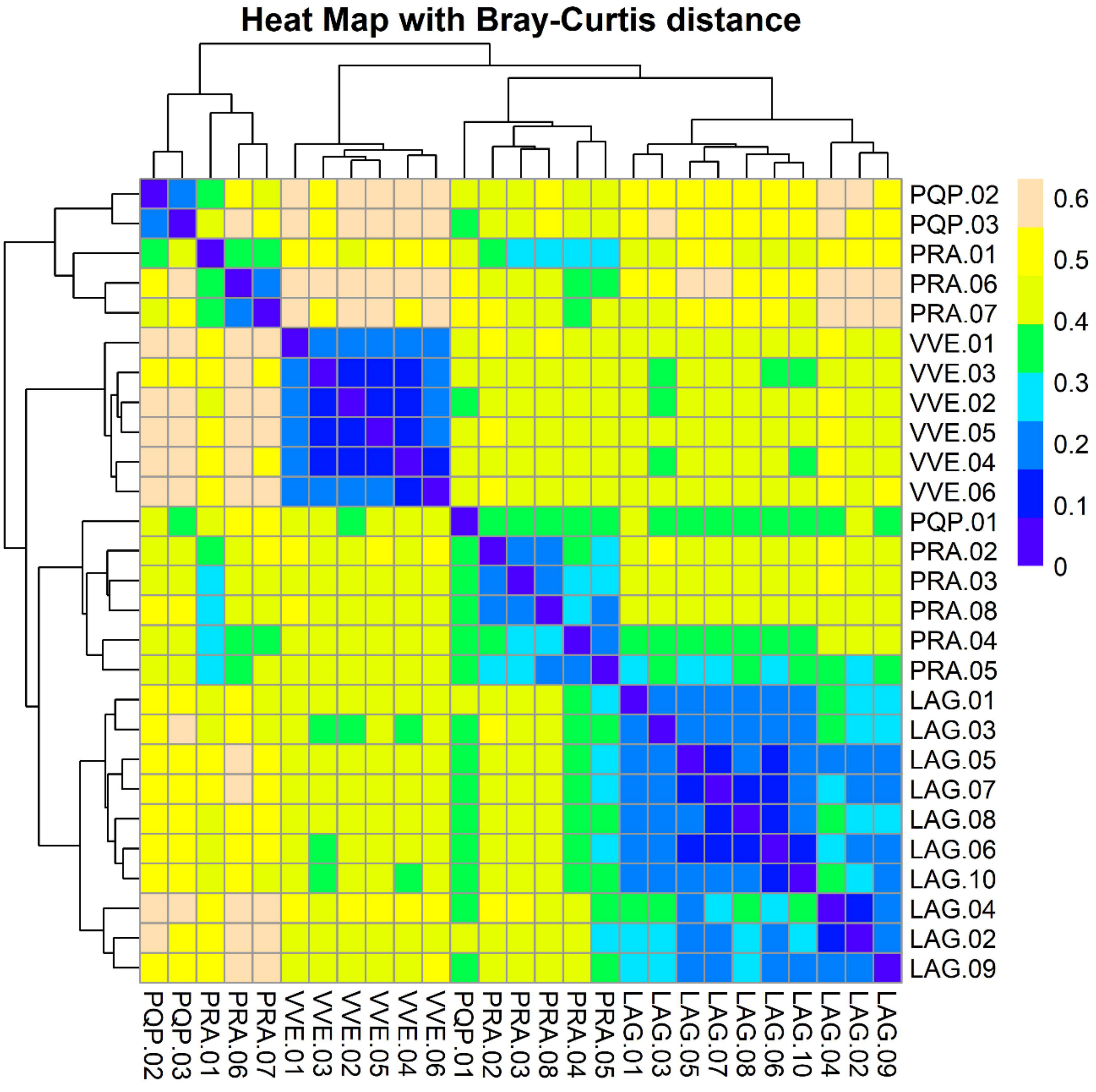

Figure 9. Heatmap based on log-transformed species abundances and Bray–Curtis dissimilarities of the paleocommunities found at the four outcrops. Dendrogram based on Ward's clustering of a matrix of Bray–Curtis dissimilarities. Both the analysis of silhouette width and Mantel statistic suggested an optimal number of four groups. Remaining abbreviations as in Figure 7.

Table 4. Results of indicator species analysis using IndVal. From a total number of 98 species, 28 were selected as having indicator value: 17 species were associated to one group; 7 species were associated to two groups and 4 species were associated to three groups. IndVal (*I*) and probability value (*p*). Significance codes for *p*-values: ** (0.01), * (0.05). Remaining abbreviations as in Table 2.

PQP	***I***	***p***
Alvania angioyi	0.952	0.005 **
Skeneopsis planorbis	0.907	0.005 **
Odostomia lukisii	0.839	0.005 **
Vitreolina philippi	0.816	0.025 *
Crisilla postrema	0.799	0.015 *
Retusa truncatula	0.763	0.030 *
Tectura virginea	0.749	0.035 *
Volvarina sp.	0.722	0.025 *
Botryphallus ovummuscae	0.709	0.035 *
Lasaea adansoni	0.706	0.030 *

PRA	***I***	***p***
Bosemprella incarnata	0.935	0.005 **
Laevicardium crassum	0.707	0.040 *
Tetrarca tetragona	0.707	0.015 *

LAG	***I***	***p***
Alvania abstersa	0.684	0.040 *

VVE	***I***	***p***
Myosotella myosotis	1.000	0.005 **
Coralliophila meyendorffii	0.935	0.005 **
Patella candei	0.933	0.005 **

PQP + PRA	***I***	***p***
Papillicardium papillosum	0.739	0.005 **
Parvicardium vroomi	0.719	0.040*

PQP + VVE	***I***	***p***
Vermetidae	0.938	0.005 **
Paludinella globularis	0.794	0.015 *

LAG + PRA	***I***	***p***
Tectonatica prietoi	0.707	0.045 *

LAG + PQP	***I***	***p***
Cerithiopsis sp.	0.884	0.005 **

PRA + VVE	***I***	***p***
Lucinella divaricata	1.000	0.005 **

LAG + PQP + PRA	***I***	***p***
Manzonia unifasciata	0.974	0.005 **
Rissoa guernei	0.972	0.010 **
Claremontiella nodulosa	0.787	0.020 *

PQP + PRA + VVE	***I***	***p***
Cardita calyculata	1.000	0.005 **

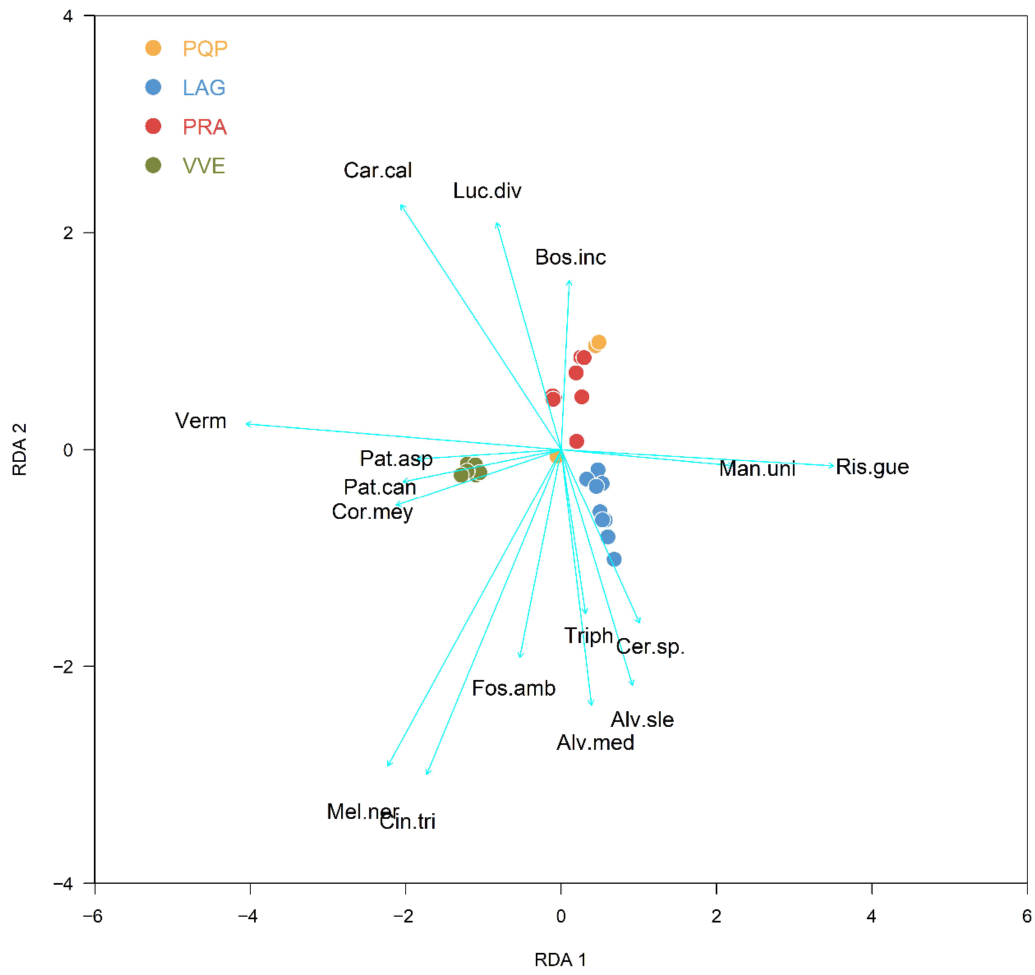

Figure 10. Redundancy analysis based on the IndVal, with species and samples projected in a 2D space. Alv.med: *Alvania mediolittoralis*. Alv.sle: *Alvania sleursi*. Bos.inc: *Bosemprella incarnata*. Car.cal: *Cardita calyculata*. Cer.sp: *Cerithiopsis* sp. Cin.tri: *Cingula trifasciata*. Cor.mey: *Coralliophila meyendorffii*. Fos.amb: *Fossarus ambiguous*. Luc.div: *Lucinella divaricata*. Man.uni: *Manzonia unifasciata*. Mel.ner: *Melarhaphe neritoides*. Pat.asp: *Patella aspera*. Pat.can: *Patella candei*. Ris.gue: *Rissoa guernei*. Verm: Vermetidae.

3. Results

3.1. Stratigraphical and Sedimentological Characterization

The Pliocene sedimentary succession at Pedra-que-pica (which is part of the Touril Complex and of the Pico Alto Complex; cf. Figure 5), was described in detail by [45]. Pillow lavas (facies 1; Figures 4 and 5) form the base of the volcano-sedimentary sequence. Thin neptunian dikes filled in with light gray calcareous sand (Figure 3C) occur in between the pillow lavas, and traces of *Macaronichnus segregatis* (Clifton and Thompson, 1978) are locally abundant in the sediments in these dikes (facies 2, Figures 4 and 5). These calcarenites are truncated by an erosional surface and covered by a 3–4 m thick coquina, which is very rich mostly in disarticulated bivalves, with fewer barnacles, echinoids, brachiopods, bryozoans, calcareous-algae-forming rhodoliths and small stony-corals (facies 3; Figures 4 and 5). Teeth of bony fishes and sharks are also present [32,52]. Moulds of the large gastropod *Tethystrombus coronatus* (Defrance, 1827) are rare [52,55], while whale bones are extremely rare [38,62].

As a result of a surtseyan eruption that occurred nearby Pedra-que-pica, the coquina was covered by a thick unit of vitric ash to lapilli tuff (facies 4; Figures 4 and 5). These tuffs are overlain by a lava-delta sequence of submarine lavas and hyaloclastites and subaerial flows (facies 5; Figure 4).

The Pleistocene MIS 5e sedimentary succession at Pedra-que-pica either truncates the pillow lavas of the Touril Complex (see log 1, facies 1; Figure 5), or the tuffaceous sequence of the Pico Alto Complex (facies 4 in logs 2 and 3; Figure 5). The resulting erosional shore platform increases in height from the west to the east (Figure 3D). The boulder beach conglomerate (unit 6, Figures 4 and 5) that covers this erosion surface (Figure 3E) has a maximum thickness of about 1 m, and ends against a visible shore angle, which is well exposed in the eastern end of the outcrop, forming a wave cut notch (Figure 3D). A small MIS 5e deposit is present (unit 7; Figure 5), appearing west of the volcanic spurs that now protect the coquina from storm damage, consisting of volcano-bioclastic, unconsolidated, very fossiliferous reddish sands (Figure 3F,G). These sediments show a lateral extension of about 4 m and a thickness of less than 30 cm. No internal structure (e.g., cross-lamination) is visible, and the grain-size distribution of these sands is dominated by the 250–500 µm fractions. The entire MIS 5e deposit, including the conglomerates and boulders (unit 6) present in logs 2 and 3 (cf. Figures 4 and 5) and the sandy layer (unit 7) present in log 1 (cf. Figures 3G and 5) is topped by a wedge-shaped terrigenous talus deposit (colluvium; unit 8), consisting predominantly of boulder breccias, with over 20 m in thickness (Figures 4 and 5).

3.2. Paleobiodiversity

In total, 55 taxa of molluscs were recovered from the quantitative samples collected at the MIS 5e PQP deposit: 49 gastropod taxa and 6 bivalve species (cf. Supplementary Table S1). Considering all the MIS 5e quantitative samples from Santa Maria Island, thus including the four Pleistocene (MIS 5e) outcrops (PQP, PRA, LAG and VVE), a total of 98 marine mollusc species are reported, comprising 14 bivalve species (14.3%) and 84 gastropod taxa (85.7%). A total of 54,019 specimens were counted and identified across the four outcrops, including 26,364 bivalves (48.8%) and 27,655 gastropods (51.2%) (cf. Supplementary Table S1).

Table 1 illustrates the most frequent species of bivalves and gastropods at each outcrop, expressed as a percentage of the total number of specimens for each of the mollusc classes. Across all outcrops (PQP, PRA, LAG and VVE), *Ervilia castanea* (Montagu, 1803) is the most abundant bivalve, ranging from 92% of all the specimens of bivalves at PRA to 100% at LAG. No other bivalve species was found in the quantitative samples collected at LAG, although two additional species (*Leiosolenus aristatus* (Dillwyn, 1817) and *Tetrarca tetragona* (Poli, 1795) [43]) have been reported in the literature from qualitative samples at this site. Of the 24 bivalve species presently known from the MIS 5e sediments at Santa Maria Island, six occur at PQP, that compares with 20 bivalve species reported from PRA, eight from VVE, and three from LAG (cf. Supplementary Table S1).

Bittium nanum (Mayer, 1864) is the dominant gastropod in most of the MIS 5e outcrops studied, representing 43% at PQP, 51% at PRA, 42% at LAG and nearly 18% at VVE. It is worth noting that the most abundant gastropod species at VVE is *Melarhaphe neritoides* (Linnaeus, 1758), accounting for over 31% (Table 1). *Rissoa guernei* Dautzenberg, 1889 (26% at PQP), *Alvania mediolittoralis* Gofas, 1989 (22% at LAG), *Cingula trifasciata* (J. Adams, 1800) (16% at VVE) and Vermetidae (14% at VVE) are also abundant species in the MIS 5e outcrops of Santa Maria Island.

Table 2 summarizes species richness (SpRic) and the total number of individuals (N) per replicate at each MIS 5e outcrop. A total of 27 quantitative 1 kg bulk samples were collected and analyzed. Pedra-que-pica (PQP, $n = 3$), had the highest single-sample abundance (5895 specimens in PQP−01) with a total abundance of 8432 individuals and a species richness of 34–36 species per sample. Lagoinhas (LAG, *n* = 10) showed a total abundance of 21,321, with relative abundances between 888 (LAG-01) and 4757 specimens (LAG-04), and richness ranging from 22 (LAG-03) to 34 species (LAG-04). Prainha (PRA, *n* = 8) spanned 215 to 3428 specimens per sample, with a total abundance of 10,888 individuals and a species richness ranging from 19 (PRA-07) to 44 (PRA-03). Vinha Velha (VVE, *n* = 6) recorded 1559 to 2885 individuals per sample, a total abundance of 13,379 specimens and a richness of 24 to 31 species. Overall, Prainha represents the highest species richness, while the sample PQP-01 had the highest abundance.

This work adds two new gastropod species to the MIS 5e record from Santa Maria Island: the heterobranch *Omalogyra atomus* (R. A. Philippi, 1841), and the vetigastropod *Scissurella lobini* (Burnay & Rolán, 1990) (cf. Figure 6).

Both the Hill numbers (Figure 7A) and rarefaction curves (Figure 8) indicate that the sampling effort at VVE and LAG is sufficient, but should be increased at PQP and PRA. Table 3 compares the diversity indices obtained from the marine mollusc taxa quantitative data of LAG, PRA and VVE, with those from PQP (each consisting of 1 kg standardized samples). The detected differences are statistically significant when PQP samples are compared with the average values from the other MIS 5e samples from Santa Maria Island ($p < 0.001$ for all Hill numbers used, i.e., for q = 0, q = 1 and q = 2; cf. Table 3). Moreover, LAG stands apart from the remaining MIS 5e outcrops for Hill numbers q = 0, whereas VVE is significantly different from the remaining MIS 5e outcrops for Hill numbers q = 2 (cf. Figure 7B).

3.3. Community Composition and Key Indicator Species

Four groups result from the cluster analysis dendrogram, which are also supported by the heatmap analysis (Figure 9): a first group containing all the six samples of VVE that share a similar number of species and abundance (Table 2); a second group with all ten samples from LAG, denoting a lower homogeneity among samples, which translates into two sub-groups; a third group with five out of the eight samples from PRA that cluster with PQP-01; and finally, a fourth group with three samples from PRA and two samples from PQP.

The results of the indicator-value analysis (*I*) are expressed in Table 4, identifying which taxa are associated with individual outcrops, and which taxa are representative of two (or three) outcrops. From a total number of 98 species, 28 were selected as having indicator value: 17 species were associated to one group; seven species were associated to two groups and four species were associated to three groups. Three diagnostic species characterize PQP (*Alvania angioyi* van Aartsen, 1982; *Skeneopsis planorbis* (O. Fabricius, 1780); and *Odostomia lukisii* Jeffreys, 1859), whereas *Bosemprella incarnata* (Linnaeus, 1758) is diagnostic for PRA; *Alvania abstersa* van den Linden and van Aartsen, 1994, for LAG; and three species characterize VVE: *Myosotella myosotis* (Draparnaud, 1801), *Coralliophila meyendorffii* (Calcara, 1845) and *Patella candei* A. d'Orbigny, 1840. Moreover, Vermetidae and *Paludinella globularis* (Hanley, 1844) are commonly found at PQP and VVE, whereas two bivalves—*Papillicardium papillosum* (Poli, 1791), and *Parvicardium vroomi* van Aartsen, Menkhorst & E. Gittenberger, 1984—typify the bivalve-rich assemblages of PQP and PRA. *Lucinella divaricata* (Linnaeus, 1758) typifies PRA and VVE, while *Cerithiopsis* sp. occurs predominantly at LAG and PQP. Finally, at LAG, PQP and PRA, *Manzonia unifasciata*, *Rissoa guernei* and *Claremontiella nodulosa* are widespread across all outcrops, whereas *Cardita calyculata* occurs in all of the outcrops but LAG.

The redundancy analysis is based on the IndVal and is able to discriminate outcrops along two main axes (Figure 10). Three clusters result from this analysis: all VVE samples cluster together; all LAG also cluster together; and PQP and PRA samples are mixed in the same cluster. While the first axis individualizes two main clusters (VVE, and (PQP+PRA+LAG)), the second axis separates the bivalve-dominated outcrops of PQP and PRA from the gastropod-rich outcrops of LAG and VVE.

4. Discussion

4.1. Paleoenvironmental Reconstruction of Pedra-que-pica and Comparison with Other MIS 5e Outcrops

The newly discovered MIS 5e outcrop at Pedra-que-pica increases the number of last interglacial sites studied at Santa Maria Island to six (cf. Figure 1): Lagoinhas outcrop is located in the northern coast of the island; Ponta do Cedro is in the eastern shores; and four sites are located in the southern shores (Prainha, Vinha Velha, Ponta do Castelo and Pedra-que-pica; cf. Figure 2). All these sites range from 3 to 4 m in elevation registered at PRA and Ponta do Castelo, to 6–7 m reported from LAG [43,63]. These heights are compatible with that of the maximum sea level reported for the MIS 5e at Santa Maria, which is about 10 m at Pedra-que-pica.

The MIS 5e deposit at Pedra-que-pica corresponds to a wave-cut platform carved by a highstand in seas during the maximum warming period of the last interglacial. This erosional feature was produced during a transgressive event, on top of the surtseyan tuffs that cover the prominent Pedra-que-pica Pliocene coquina. The coquina is a paleosite of international relevance [31,38,46,64], first described in detail by [45].

In a similar way, compared with other MIS 5e outcrops on Santa Maria Island (e.g., at PRA and LAG, but not at VVE), the stratigraphic succession at PQP begins with a beach conglomerate with rounded boulders and pebbles (unit 6, Figure 5) that lies on top of a shore platform. This platform extends for about 75 m in a W-E direction (cf. Figure 3A,D). However, at PQP, only a few shells of *Patella aspera* Röding, 1798, were found, whereas at PRA, a total of 14 mollusc species (11 gastropods, including *P. aspera*, and three bivalve species) are reported from the conglomerate basal layer [1,37,56].

A crustose coralline algal buildup is present at PRA [1] and at LAG [2,43] but not at PQP nor at VVE [63]. It is also absent from Ponta do Castelo [65] and from Ponta do Cedro (*personal observation*). Thus, at PQP, the basal conglomerate layer (unit 6, Figure 5) is not consolidated by an algal crust layer as it is at PRA and LAG. The unconsolidated sandy layer (unit 7, Figure 5) that follows up in the sedimentary sequence is common to most of the MIS 5e outcrops known from Santa Maria Island, the exceptions being the outcrops of Ponta do Castelo and Ponta do Cedro (cf. Figure 1B). The MIS 5e sandy layer at Pedra-que-pica was deposited at shallow depths, similarly to other Santa Maria outcrops (e.g., PRA, VVE and LAG), and represents the peak of the last interglacial highstand. The small (1–2 cm) and well-rounded pebbles found in the sandy layer of PQP (unit 7, Figure 5) are also indicative of a generally low hydrodynamic depositional environment. The position of the wave cut notch, at the eastern end of the Pedra-que-pica MIS 5e deposit (cf. Figures 3A,D and 4), at about 10 m apsl, represents the maximum height of sea level during the transgressive episode that characterizes the peak of the last interglacial. Accordingly, we interpret the fossiliferous sandy layer at PQP (unit 7 of Figure 5) as corresponding to the intermediate shoreface of a submerged beach sensu [66], i.e., the deposition of these sediments is estimated to have taken place at a paleodepth of 5 to 10 m. This contrasts with the inferred paleodepth for the fossiliferous sandy layer sediments at PRA and LAG, which were interpreted by [43] as corresponding to a shoreface to foreshore (intertidal) depositional setting. This inference is based on the presence of wave-ripple cross-bedding and cross-lamination, coupled with the presence in both outcrops of a crustose coralline algal buildup with coarse-grained sediments trapped in the structural cavities of the dense and closely superposed algal crusts, all indicating high-energy hydrodynamic settings (cf. also [63]). At VVE, the absence of such structures in the sandy layer probably indicates a paleodepth similar to the one inferred for PQP.

4.2. Paleobiodiversity and Paleoecology

Although Mollusca is the most abundant and diversified marine group present at the MIS 5e deposit of PQP, other accessory marine groups were also found in the quantitative samples, as represented by fragments of echinoderm spines, polychaete annelids and foraminifers. The most recent account by [29] on the number of fossil molluscs from the MIS 5e deposits of Santa Maria Island reported a total of 138 taxa (114 Gastropoda and 24 Bivalvia). This work adds two new species to the Pleistocene (MIS 5e) record of Santa Maria Island: the gastropod *Omalogyra atomus* (R. A. Philippi, 1841) and the vetigastropod *Scissurella lobini* (Burnay & Rolán, 1990). *Scissurella lobini* is reported for the first time to the world fossil record. Thus, these new findings increase the total number of Mollusca cited for the Azorean MIS 5e record to 140 taxa (116 Gastropoda and 24 Bivalvia), and is yet another contribution to address the taxonomic gap in the marine Pleistocene of the Azores.

The most abundant MIS 5e mollusc species at PQP, PRA and LAG (the bivalve *E. castanea* and the gastropod *Bittium nanum*; cf. Table 1) are associated with coarse and fine sand (in the former case) and with coarse and fine sand, as well as with algae (in the latter case). It is worth noticing that not a single shell of *Ervilia castanea* was found preserved with the valves still attached in any of the 27 kg of samples sorted (3 kg from PQP, 10 from LAG, 8 from PRA and 6 from VVE). This number compares with the 25,500 individual valves of *Ervilia castanea* that were counted from the four outcrops studied (Supplementary Table S1). This allows us to conclude that some degree of transport of the bivalve shells must have occurred, and without exception, all fossil samples correspond to allochtonous species in relation to their final depositional setting.

At PQP, most of the gastropods are minute (less than 3 mm in length) and associated with algae (e.g., *Rissoa guernei*, *Manzonia unifasciata*, *Alvania angioyi*, *Alvania mediolittoralis*, *Alvania sleursi*, *Crisilla postrema* and *Setia subvaricosa*). The same occurs at PRA and LAG, with some differences registered for the percentage of each gastropod species (cf. Table 1). At VVE, the most abundant MIS 5e gastropod is *Melarhaphe neritoides* (31.42%), which is associated with wave-exposed areas and hard grounds/bare rocky shores in the supralittoral zone (Table 1). Also, at VVE, the bivalve *Cardita calyculata* (2.18%) and the gastropods *Cingula trifasciata* (15.68%) and Vermetidae (14.44%) are abundant, and all are associated with hard grounds/rocky shores. Our data also supports [63], who suggested that, similar to the present environmental settings, LAG, located in the more exposed windward northern coast of the island, was subjected to higher hydrodynamic conditions compared to the other MIS 5e outcrops in Santa Maria Island, which are located in the more protected southern (PRA, VVE, PQP) or eastern coasts (Ponta do Cedro).

The ecological bathymetrical zonation of recent marine molluscs of the Azores is known in detail (cf. [67–74], allowing to make sound inferences about the probable zonation of the Azorean marine molluscs during the MIS 5e. Thus, and assuming that the present bathymetrical zonation and that of the MIS 5e molluscs found in the four studied outcrops are similar, there is a mix of supralittoral species (e.g., *Melarhaphe neritoides*, which occurs at VVE, PRA and LAG) with mostly intertidal species (e.g., *Cingula trifasciata*, that was found at VVE, LAG and PQP); very shallow species typically found associated with algae and at depths ranging from 0 to 5–6 m (e.g., *Rissoa guernei* and *Manzonia unifasciata*, found at PQP, PRA and LAG; *Alvania angioyi*, found at PQP); and finally, species usually found associated with algae but also in rocky/gravel/coarse sandy environments and at depths ranging from 10 to 30 m (e.g., *Alvania sleursi*, *Setia subvaricosa*, *Anachis avaroides*, *Bittium nanum* and *Jujubinus pseudogravinae*). Taking into account the taphomic signature of the disarticulated valves of *Ervilia castanea* for inferred transport, the level of low breakage in the majority of the shells of bivalves and gastropods, and the diverse bathymetrical zonation of the biological assemblage found in each of the four outcrops, we conclude that all were deposited at depths around or shallower than 10 m, although some difference in the final depositional depth of the fossiliferous sediments is evident (with PRA and VVE being the shallowest and PQP the deepest one).

Statistical analysis based on Hill numbers highlights the higher number of species at both PRA and PQP, compared to VVE and LAG. Lagoinhas outcrop is located in the north coast of Santa Maria Island (Figure 2) and it is the least diverse of the four MIS 5e outcrops studied (Figure 7A). As demonstrated by [75] for the present times, the north coast of Santa Maria Island sustains more severe sea conditions (e.g., stronger winds, higher waves and swell) compared to the south and the east coast of the island. As it is expected that the current environmental conditions were similar during the MIS 5e period, this is probably the best explanation for the lower LAG diversity.

The results of the heatmap (Figure 9) and redundancy analysis (RDA; Figure 10) are in agreement with the inferred depositional paleodepth of the fossiliferous sediments, revealing two primary paleocommunities: (1) a high diversity assemblage at PQP and PRA, dominated by suspension feeder bivalves (*Ervilia castanea*, *Cardita calyculata*, *Lucinella divaricata*), indicating a fine sediment habitat and a sheltered substrate interspersed with intertidal rocky shores (in the case of PRA); and (2) a lower-diversity (at LAG and VVE) and high-energy community (at VVE), dominated by grazers (*Patella candei*, *Patella aspera*) and Vermetidae, indicating an exposed substrate, typical of rocky environments.

Tables 5 and 6 display the number of bivalve and gastropod MIS 5e species, respectively, that were extirpated from the Azorean shores as a consequence of the last glacial episode (see [8,43,76–78] for a full explanation). These 25 taxa are regarded as "ecostratigraphic indicators" [79–81] for the MIS 5e fossiliferous deposits in the Azores Archipelago [4,5]. Most of the 5 bivalve and 20 gastropod taxa occur at PRA (4 bivalves and 19 gastropods), while only one ecostratigraphic indicator gastropod species—*Claremontiella nodulosa* (C. B. Adams, 1845)—was found at PQP (Table 6).

Table 5. Bivalve species reported from the MIS 5e fossil record of Santa Maria Island (Azores Archipelago) that were extirpated during the course of the last glacial episode. Remaining abbreviations as in Table 2.

Extirpated MIS 5e Bivalve Species	Qualitative + Quantitative Samples				Only Quantitative Samples			
	PQP	PRA	LAG	VVE	PQP	PRA	LAG	VVE
Ensis minor		1						
Glycymeris glycymeris				1				
Laevicardium crassum		1				1		
Leiosolenus aristatus		1	1					
Lucinella divaricata		1		1		1		1
	0	4	1	2	0	2	0	1

Table 6. Gastropod species reported from the MIS 5e fossil record of Santa Maria Island (Azores Archipelago) and that were extirpated during the course of the last glacial episode. Remaining abbreviations as in Table 2.

Extirpated MIS 5e Gastropod Species	Qualitative + Quantitative Samples				Only Quantitative Samples			
	PQP	PRA	LAG	VVE	PQP	PRA	LAG	VVE
Alvania cf. *tesselata*		1						
Claremontiella nodulosa	1	1	1		1	1	1	
Conus sp.		1	1			1	1	
Conus ambiguus		1						
Conus cf. *ermineus*		1						
Conus cf. *miruchae*		1						
Conus cf. *roeckeli*		1						
Conus ventricosus		1						
Conus venulatus		1						
Euspira guillemini		1						
Gemophos viverratus		1	1			1		
Gibberula sp.		1						
Mitrella broderipi		1		1		1		
Polinices lacteus		1	1	1		1	1	
Pseudopusula grohorum		1	1	1		1	1	1
Seila trilineata		1						
Steromphala cf. *umbilicaris*			1				1	
Zebina paivensis		1						
Zonaria picta		1						
Zonaria pyrum		1						
	1	19	6	3	1	6	5	1

4.3. Sampling Methods: Quantitative vs. Qualitative Samples

Tables 5–7 highlight the importance of complementing quantitative, standardized 1 kg samples of fossiliferous sediments, with qualitative samples obtained from careful surveys that fully explore the entire outcrop and its fossiliferous layers. For example, when the number of MIS 5e extirpated species of bivalves found in all the quantitative samples of Santa Maria is compared with the total number (herein including the data from qualitative and quantitative samples) of MIS 5e extirpated species of bivalves, the quantitative samples only yield 40% of the total number of MIS 5e extirpated species of bivalves. The figures are similar (35%) when we compare the numbers for gastropods, with only 7 MIS 5e extirpated species of gastropods being found in the quantitative samples, compared with the 20 MIS 5e extirpated taxa of gastropods found in the combined qualitative and quantitative data (cf. Table 6).

Table 7. Comparison of the total number of mollusc species found in the quantitative samples at each studied MIS 5e outcrop, and the total number of molluscs reported from each of the MIS 5e outcrops at Santa Maria Island. Remaining abbreviations as in Table 2.

Total Number of Molluscs	Only Quantitative Samples				Qualitative + Quantitative Samples				% (Quantitative/ (Quantitative + Qualitative)			
	PQP	PRA	LAG	VVE	PQP	PRA	LAG	VVE	PQP	PRA	LAG	VVE
Bivalvia	6	13	1	7	6	20	3	8	100.0	65.0	33.3	87.5
Gastropoda	48	56	48	42	49	100	48	62	98.0	56.0	100.0	67.7
TOTAL	**54**	**69**	**49**	**49**	**55**	**120**	**51**	**70**	**98.2**	**57.5**	**96.1**	**70.0**

At PQP, the number of species obtained from the quantitative samples is almost identical to that obtained from pooling quantitative and qualitative samples, with 100% and 98% of bivalve and gastropod species, respectively, being found in the quantitative samples (Table 7). This contrasts with LAG, where only 33.3% of the bivalves reported from this site are recovered in the quantitative samples. At PRA, 65.0% and 56.0% of the total number of bivalves and gastropods that are cited for this location, respectively, are found in the quantitative samples (Table 7). When the entire dataset is compared, only 14 MIS 5e bivalve species (58.3%) are found in the quantitative samples when compared with the 24 bivalve species reported from the combined qualitative and quantitative data. For gastropods, the numbers are better, with 84 out of the total 116 gastropod taxa (72.4%) being found in the quantitative samples (Supplementary Table S1).

5. Conclusions

As a result of the combined effort of over 80 marine biologists, paleontologists and geologists over the last two decades, the number of MIS 5e paleosites described and explored on Santa Maria Island has gradually increased from a single outcrop (PRA), reported in the historical works of [40,41], to the current six, i.e., the four herein reported (PQP, PRA, LAG, VVE), plus Ponta do Cedro and Ponta do Castelo. Due to their difficult access (e.g., PQP, VVE and Ponta do Cedro outcrops are only safely accessible by boat), these paleosites had never been explored by researchers before the series of 20 "Palaeontology in Atlantic Islands" organized on Santa Maria Island from 2002 to 2023. A direct consequence of this was the steady increase in the total number of fossil marine species reported for the last interglacial deposits of Santa Maria, from 95 [1] to the current 140 mollusc taxa. Only taking into account the explorations of the MIS 5e deposits on Santa Maria, a total of 13 species of molluscs were first reported for the world fossil record as a result of the works of [43] (10 gastropods), [29] (1 gastropod) and this work (2 gastropod species). Our findings also highlight how integrating biological, paleontological and geological approaches contributes to a more comprehensive understanding of the past ecosystem dynamics and their relationship with long-term environmental processes.

The paleobiodiversity of the MIS 5e fossiliferous sediments at Pedra-que-pica is quite high, compared with that of VVE and LAG, despite the small size of PQP last interglacial deposit. Both the results of the Hill numbers (Figure 7) and of the Chao estimator (Figure 8) suggest that an increase in the sampling and sorting effort at PQP and at PRA will yield new mollusc species for the MIS 5e record of Santa Maria Island. Finally, our results show that quantitative data should be always complemented with a systematic survey of the studied outcrops aiming to collect qualitative data, because restricting the collecting to quantitative methods results in missing up to 66.7% of the bivalve species (e.g., at LAG; cf. Table 7) and up to 44% of the gastropod taxa (e.g., at PRA; Table 7).

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/quat8040053/s1, Table S1. Quantitative data for the studied MIS 5e outcrops of Santa Maria Island. PQP: Pedra-que-pica; LAG: Lagoinhas; PRA: Prainha; VVE: Vinha Velha. * New records for the MIS 5e of Santa Maria Island.

Author Contributions: Conceptualization, S.P.Á.; Data curation, S.M., P.M., G.C.Á., E.M.-G. and S.P.Á.; Formal analysis, S.M., M.A.D., A.H., L.S., G.M.M. and S.P.Á.; Funding acquisition, P.M. and S.P.Á.; Investigation, S.M., M.A.D., A.H., P.M., S.P.P., L.S.D., G.C.Á., E.M.-G., M.E.J. and S.P.Á.; Methodology, L.S., G.M.M. and S.P.Á.; Project administration, S.P.Á.; Resources, P.M. and S.P.Á.; Supervision, S.P.Á.; Validation, S.M., L.S., G.M.M., E.M.-G., M.E.J. and S.P.Á.; Visualization, S.M., M.A.D., A.H., L.S., G.M.M. and S.P.Á.; Writing—original draft, S.M. and S.P.Á.; Writing—review and editing, M.A.D., A.H., P.M., S.P.P., L.S.D., G.C.Á., L.S., G.M.M., E.M.-G., M.E.J. and S.P.Á. All authors have read and agreed to the published version of the manuscript.

Funding: SM was supported by an ERASMUS + grant (2024-1-ES01-KA131-HED-000196755). SPP was supported by an ERASMUS + grant (University of Barcelona ub.edu:EST20556966). SPA and PM acknowledge their contracts with project M1.1. A/INFRAEST CIENT/A/001/2021—Base de Dados da PaleoBiodiversidade da Macaronésia, funded by the Regional Government of the Azores. SPA appreciates his current FCT/2023.07418 CEEECIND research contract with BIOPOLIS (https://doi.org/10.54499/2023.07418.CEECIND/CP2845/CT0001). This work was supported by National Funds through FCT-Fundação para a Ciência e a Tecnologia in the scope of the project UID/50027-Rede de Investigação em Biodiversidade e Biologia Evolutiva. This work also benefited from FEDER funds, through the Operational Program for Competitiveness Factors—COMPETE, and from National Funds, through FCT (POCI-01–0145-FEDER-006821, UIDB/00153/2020, LA/P/0048/2020), as well as through the Regional Government of the Azores (M1.1.a/005/Funcionamento-C-/2016, CIBIO-A; M1.1.A/INFRAEST CIENT/A/001/2021; M3.3.B/ORG.R.C./005/2021, M3.3.B/ORG.R.C./008/2022/EDIÇÃO 1, M3.3.G/EXPEDIÇÕES CIENTÍFICAS/005/2022 and M3.3.G/EXPEDIÇÕES CIENTÍFICAS/004/2022). Finally, this work was also supported by FEDER funds (85%) and by funds from the Regional Government of the Azores (15%) through the Azores 2020 Operational Program under the VRPROTO project: Virtual Reality PROTOtype: the geological history of "Pedra-que-pica": ACORES-01-0145-FEDER-000078, and by M1.1.A/INFRAEST CIENT/A/001/2021—Base de Dados da PaleoBiodiversidade da Macaronésia.

Data Availability Statement: The original contributions presented in this study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author(s).

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

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