



## Article

# Seeking a Hideout: Caves as Refuges for Various Functional Groups of Bryophytes from Terceira Island (Azores, Portugal)

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**Abstract:** Caves represent sites of great geological and biological interest. For most taxonomic groups, caves represent one of the most challenging ecosystems due to their extreme conditions. However, these places are rich in biodiversity, and some groups, such as bryophytes, can take advantage of these conditions. Bryophytes from twelve caves on Terceira Island (Azores archipelago) were sampled and compared in terms of species richness, abundance, and composition. The results revealed a high species richness of bryophytes, with one-fifth of the species being threatened and one-third endemic. Moreover, the dominance of bryophyte species, as determined by different functional groups, varies depending on the sampled cave and, consequently, the environmental variables. This is evident from the high  $\beta$ -diversity values obtained, demonstrating significant dissimilarities in species composition among the surveyed caves. Both macro- and microclimatic variables significantly influenced the richness and abundance of bryophyte species in different ways, depending on the functional group studied. Highlighting bryophyte diversity in cave environments, this study points to the need for effective management strategies to preserve and protect these unique and ecologically significant communities. These places can serve as refuges for some species, even for bryophytes, a taxonomic group with a long-distance dispersal strategy.

**Keywords:** mosses; liverworts; Macaronesia;  $\beta$ -diversity; phylogenetic groups; life strategy



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## 1. Introduction

Caves represent a unique category of geological formations, hosting exceptionally distinct ecosystems. Cave habitats are characterised by factors such as limited light penetration, minimal temperature fluctuations, elevated humidity levels, and scarce organic matter. These conditions make it challenging for most organisms to survive and reproduce [1]. Consequently, the specialised ecological niches found within caves are often classified as extreme habitats [2], because the organisms inhabiting cave environments are exposed to intense environmental stresses. However, caves are paradoxically rich in biodiversity, with cave-dwelling organisms playing a significant role in overall biodiversity [3]. Therefore, due to their distinctive and uncommon natural characteristics, cave environments have emerged as ideal natural laboratories for studying biodiversity [1,4].

Although caves are biodiversity hotspots, they receive minimal attention and lack appropriate management from governmental authorities [3,5]. Disruptions caused by agriculture, visitors, tourism development, and alterations in water flow can lead to severe consequences for the organisms inhabiting caves [6]. Therefore, the preservation and restoration of caves demand the engagement of both researchers and governmental agencies [7].

Caves are ecosystems that offer limited survival opportunities for many organisms. The scarcity or absence of light in caves renders them largely unsuitable for sustaining plants, as they are critically dependent on light availability. Consequently, biodiversity research in cave habitats has predominantly focused on animals [8] and microbes [9]. However, while some species are compelled to evolve and adapt [8], numerous bryophyte species can survive due to the consistently stable humidity and temperature [1,10–14], emerging as the dominant plant species in these habitats [1]. Bryophytes do not exhibit a high level of endemism due to their high dispersal ability. Nevertheless, some rare species with restricted distributions may find a refuge for their survival in these environments [1]. Furthermore, different caves can host a distinct richness and species composition of bryophytes [1].

The bryophytes, a basal lineage of land plants [15,16], constitute the second most diverse group of land plants after flowering plants [17]. They inhabit nearly every terrestrial ecosystem globally, displaying a broader distribution and a more extensive elevational range compared to vascular plants [18]. Their distribution spans from tropical to polar regions and from sea level to mountain summits [19]. Moreover, due to their poikilohydric nature, susceptibility to environmental shifts, and close association with substrates, bryophytes can be effective indicators of the quality and integrity of ecosystems [20–22]. Consequently, numerous studies employ the functional categorization of these organisms to interpret their sensitivity to environmental change (e.g., [23,24]). Using this approach in ecological studies yields accurate insights (e.g., [25–29]). Among the most studied traits are the growth form [30], the life form [31], and the life strategy [32]. In some ecological studies conducted in caves using bryophytes, they have also been categorised into other functional groups based on their water requirements, light requirements, and pH tolerance (e.g., [29,33]).

The Azores, located in the Macaronesian region, harbour a highly diverse fauna and flora with a wealth of endemic species. However, across the islands, the past 600 years of colonisation have led to a progressive substitution of native forests with pastureland and non-indigenous forests [34–36]. This transformation has been demonstrated to impact the island's species diversity, particularly in the case of arthropods [34,37]. Despite the islands being highly transformed, bryophytes manage to find suitable places for their development. This is attributed to the Azores' extensive range and diversity of habitats, owing to the variety of microhabitats and available substrata, as well as the lack of pollution and the hyper-humid conditions available [38]. Caves have been much less altered than the other habitats, and there are already a few studies on these ecosystems [39–41]. Notably, caves constitute the primary descriptions and exclusive habitats for certain animal species [42–45]. Within the Azorean cave flora, bryophytes have been a particular focus [46–50], but no studies have been published over the last decade regarding their diversity or addressing the environmental variables that influence their presence and abundance.

The following questions were addressed in this research: (1) What is the richness and composition of bryophytes in the 12 caves studied in Terceira? (2) How dissimilar are the bryophytes among these caves, regarding taxonomic and functional diversity? (3) What is the influence of environmental variables on the richness, abundance, and composition of bryophyte species among the different caves? (4) How important are caves to conserve the biodiversity of bryophytes?

## 2. Materials and Methods

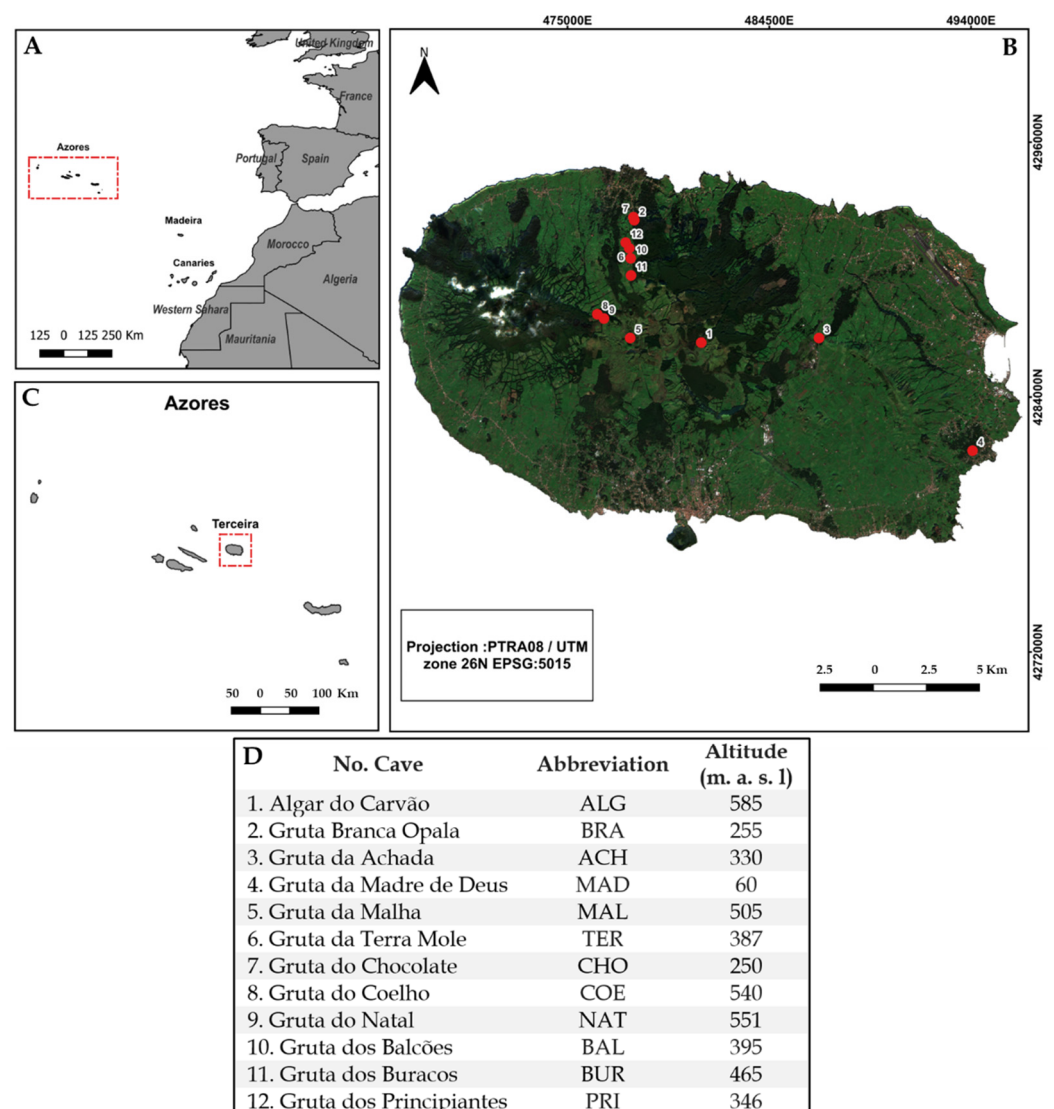
### 2.1. Study Area

The Azores are a volcanic archipelago comprising nine islands aligned on a WNW–ESE axis between 37° and 40° N and 25° and 31° W. Spanning 615 km, the archipelago is located approximately 1300 km west of mainland Portugal, 1600 km east of North America, and 800 km northwest of Madeira Island. The islands are grouped into a western cluster of two islands (Flores and Corvo), a central cluster of five islands (Faial, São Jorge, Graciosa, Pico, and Terceira), and an eastern cluster of two islands (São Miguel and Santa Maria).

Terceira Island is the third oldest island, with an age of 3.52 million years, and the third largest among the Azores archipelago ( $27^{\circ}2' \text{ W}$ ,  $38^{\circ}7' \text{ N}$ ) [51]. Covering an area of 402 km<sup>2</sup> and reaching an elevation of 1021 m above sea level [52]. The island exhibits a mild oceanic climate, characterised by high relative humidity, regular rainfall, and prevailing winds typically originating from the SE and NW sectors.

## 2.2. Sampling Method and Functional Group Categorisation

Twelve caves from Terceira Island were sampled from January to August of 2019 (Figure 1). All bryophytes were collected in newspaper bags with reference to the place and date of collection, substrate, and different observations concerning the ecology of the plant and microclimatic conditions. A total of 165 bryophyte samplings (30 cm × 30 cm) were collected among the 12 caves. The abundance of each bryophyte species was estimated according to a five-level scale from 1 to 5, as follows: 1 (very rare; 1 or 2 shoots); 2 (rare; less than 10% cover); 3 (common; 10–49% cover); 4 (abundant; 50–75% cover); 5 (dominant; more than 75% cover). Most of the samples were taken from soil and rock, but a small quantity was also collected from trees, wood, and leaves found in the caves.



**Figure 1.** Location of Azores archipelago (A), Terceira Island (B), sampling sites (C), and description of each cave (D).

Bryophyte samples were air-dried in a dark room. The specimens were identified in the “Azores BryoLab” of the School of Agriculture and Environment (FCAA), University of the Azores. Nomenclature follows Hodgetts et al. [53], while information on life strategies, life forms, growth forms, and Ellenberg Indicator Values (EIV) for moisture, light, and reaction/acidity follows Van Zuijlen et al. [54] and Dierssen [55].

Although EIV regarding the ecological preferences of bryophytes includes nine levels [55], they were simplified into three levels in this work. For moisture, xerophytics (including EIV 1, 2 and 3), mesophytics (including EIV 4, 5 and 6) and hygrophytics (including EIV 7, 8 and 9); for light, sciophytics (including EIV 1, 2 and 3), photosciophytics (including EIV 4, 5 and 6) and photophytics (including EIV 7, 8 and 9); for reaction/acidity, acidophytics, pH < 5, (including EIV 1, 2 and 3), mesoacidophytics-subneutrophytics, pH between 5–7, (including EIV 4, 5 and 6), and basiphytics with pH > 7, (including EIV 7, 8 and 9). In cases where the species could thrive across a broad range of humidity, light, or pH conditions, the lowest value was recorded as the extreme for that species.

### 2.3. Studied Variables

For each cave, the CIELO model was used to obtain macroclimate factors [56–58]. This is a layer model based on the transformations experienced by an air mass crossing over a mountain, simulating the evolution of an air parcel’s physical properties, starting from the sea level up to the mountain top [59]. The model allowed us to obtain climatic drivers such as annual mean temperature (TEMP), relative humidity (REHU), annual mean precipitation (PREC), and elevation (ELEV).

For each quadrat, the following ecological and environmental parameters were recorded: (i) exposition (EXPO), measured with a compass in degrees, taken from the lowest edge of the quadrat; (ii) slope (SLOP), the estimated angle of the quadrat from the horizontal, in degrees; (iii) distance from the soil (DSOI), measured with a tape measure, in centimetres. Qualitative scales, ranging from 1 (minimum) to 5 (maximum), adapted from Gabriel and Bates [39], were used to estimate microclimatic conditions such as brightness (BRIG), moisture (MOIS), and substrate roughness (ROUG). For brightness: 1, deeply shaded, more than 200 cm from cave entrance/skylight; 2, shaded, more than 100 cm and less than 200 cm from cave entrance/skylight; 3, more than 50 cm and less than 100 cm from cave entrance/skylight; 4, less than 50 cm from cave entrance/skylight; 5, fully exposed to light. For moisture: 1, only indirect water; 2, water only during rain, substrata not adjacent to soil; 3, water available for a short period after rain, mostly tree trunks or well-drained soil; 4, water available for a longer period after rain, mostly soil with an impermeable layer at low depth; 5, water permanently available. For substrate roughness: 1, very smooth surfaces, plane; 2, smooth surfaces, gradients less than 0.5 cm; 3, surfaces with gradients from 0.5 cm to 5 cm; 4, rough surfaces, gradients from 5 cm to 10 cm; 5, very rough surfaces, gradients of more than 10 cm. Furthermore, each sampling event included notes on the overall cover of bryophytes from 1 to 100% and some ecological observations.

All variables were correlated with the richness and abundance of each functional group to analyse their influence on the bryophyte species found inside the caves.

### 2.4. Alpha ( $\alpha$ ) and Beta ( $\beta$ ) Diversity and Sampling Completeness

Traditional measurements of  $\alpha$ -diversity encompass the number of species (S, or total species richness) and other indices that consider the proportional abundance of each species [60]. Currently, the widely accepted method for quantifying abundance-based species diversity involves the use of effective numbers of species, commonly known as Hill numbers [61,62]. Hill numbers consist of a set of indices distinguished by a single parameter  $q$ , where a higher value indicates greater sensitivity of the index to species relative abundances. The conversion of Shannon entropy and the Simpson index to the Hill series involves exponentiating Shannon and taking the reciprocal of Simpson, ensuring the use of the same units as species richness [61]. At  $q = 1$ , the relative abundances of all species are equally weighted, while at  $q = 2$ , the most abundant species are favoured

(inverse Simpson), targeting dominance in diversity measurement or the “effective number of dominant or very abundant species in the assemblage” [60]. An increase in the number of species or higher homogeneity of abundances leads to diverse Hill number values. Hence, Hill numbers organise a diversity profile into four orders ( $q$ ): (1) total species richness ( $S$ ) ( $q = 0$ ), representing the number of species in a specific site; (2) exponential Shannon–Wiener ( $H'$ ) ( $q = 1$ ) [63]; (3) the inverse of Simpson’s concentration index ( $D$ ) ( $q = 2$ ); and (4) Berger–Parker’s index ( $d$ ) ( $q = 3$ ) [64]. Hill numbers amalgamate information on species richness, species rarity (relative abundances), and species dominance [60,65]. These four Hill levels were used in each of the studied caves for the total bryophyte richness species, as well as separately for mosses and liverworts.

$\beta$ -diversity assesses how communities are different in terms of species composition. The lower the number of common species among different communities, the higher the  $\beta$ -diversity [66]. Dissimilarity distances of  $\beta$ -diversity between pairs of sites can be done by comparing communities in qualitative or quantitative ways [67,68]. This  $\beta$ -diversity index varies from zero (no dissimilarity) to 1 (maximum dissimilarity).

Before comparing diversity across assemblages, the sample completeness of a biological survey and the extent of undetected diversity should first be quantified [68]. Sampling completeness was assessed using a non-asymptotic standardisation approach via coverage-based rarefaction and extrapolation. This approach aims to compare diversity estimates for equally complete samples, where sample completeness is measured by sample coverage [68], determining the percentage of observed richness in comparison to the estimated non-asymptotic richness following Chao et al. [69] and Hsieh et al. [70]. This concept has been used to objectively quantify sample completeness in many biodiversity studies and has been standardised to compare diversity among assemblages [71,72].

## 2.5. Data Analysis

Taxa not identified at the species level were not included in the analysis due to a lack of knowledge about these species. In the same way, *Alophosia azorica*, hornworts, cladocarpous taxa, and annual taxa were not included due to the presence of only one species in each group in the study area. The total number and cover species were calculated for each sampling and cave site in each studied functional group. Spearman correlations were done to evaluate the correlation between the richness and cover of bryophyte functional groups with all environmental and ecological drivers. An indicator species analysis (ISA) was carried out, comparing the composition of bryophytes in each cave. Spearman correlations could be done thanks to the statistic software Jamovi [73,74]. ISA analysis was made using “indicspecies” [75], “vegan” [76], and “permute” packages [77], sampling completeness was evaluated using the iNEXT package [70],  $\alpha$  and  $\beta$  diversity analyses were made using the “BAT” package [78], bar plots and curve graphs using “ggplot2” [79], and the “metbrewer” package [80] in the statistic package of RStudio (v. 3.4.3). Total species richness for each functional group was represented using a barplot with colorblind-friendly palettes [80]. Three Principal Coordinates Analyses (PCoA) were conducted to evaluate changes between caves according to the species composition using a Bray–Curtis dissimilarity matrix. As a result, a general PCoA and two more PCoAs according to each phylogenetic study group were done. Additionally, sample score values obtained in the PCoA analyses were correlated with the macro- and microclimatic drivers and biotic factors to understand which drivers significantly determine the distribution of plots along the gradients. These ordination analyses were performed using CANOCO v4.5 for Windows [81], and the Bray–Curtis distance matrix was done in the PrCoord programme [82].

## 3. Results

### 3.1. Species Inventory

A total of 98 species from 66 genera were identified across all the studied caves (see Table A1, Appendix A), which corresponds to 27% of all bryophytes known to Terceira Island and a fifth of the total richness from the Azores [83]. These included one hornwort, 43 liverworts (35 foliose

and eight thallose), and 54 mosses (27 acrocarpous, 26 pleurocarpous, and one cladocarpous). The most specious genus was *Fissidens* (10 species), followed by *Cololejeunea* (4 species). Thus, the families containing the most species were Fissidentaceae (10 species), followed by Lejeuneaceae (nine species) and Brachytheciaceae (five species). The most frequently encountered mosses in the caves were *Tetrastichium fontanum*, *Heterocladium flaccidum*, *Kindbergia praelonga*, and *Fissidens luisieri*, while among the liverworts, dominant species included *Jubula hutchinsiae*, *Riccardia chamedryfolia*, *Dumortiera hirsuta*, and *Conocephalum conicum*.

A fifth of the identified species ( $n = 21$ ; 9 mosses and 12 liverworts) are considered conservation concern species by the IUCN, with 10 taxa classified as near threatened (NT), 6 as vulnerable (VU), and 5 as endangered (EN) [84]. From the distribution point of view, almost a third ( $n = 31$ ; 15 mosses and 16 liverworts) presented some degree of endemism: 14 were European endemics, four were Ibero-Macaronesian endemics, 11 were Macaronesian endemics, and two were Azorean endemic species (Table 1).

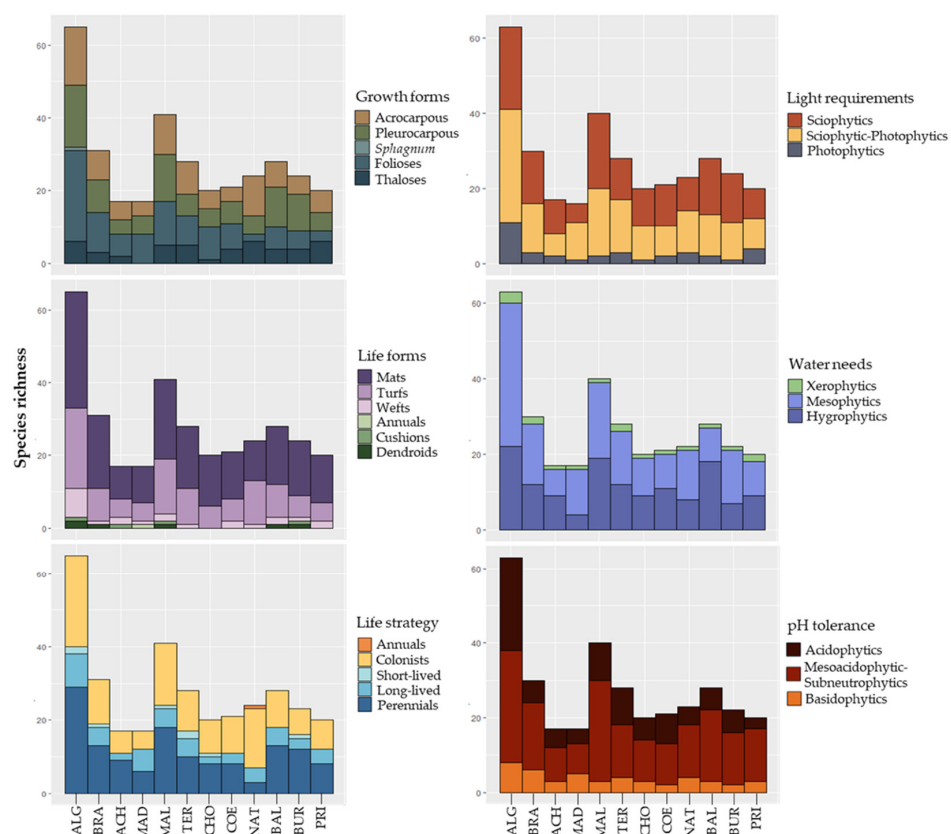
**Table 1.** Conservation concern species according to the IUCN [84] and endemic species found in the sampled caves. Distribution categorisation followed: AZOR (Azores archipelago), MAC (Macaronesian region), IBER-MAC (Ibero-Macaronesian region), EUR (Europe), EUR-AFR (Europe and Africa), AMER-AZOR (America and Azores archipelago), and COSM (cosmopolitan distribution).

Species	IUCN	Distribution
Liverworts		
<i>Acrobolbus azoricus</i>	EN	AZOR
<i>Asterella africana</i>	VU	EUR-AFR
<i>Calypogeia azorica</i>	EN	MAC
<i>Cololejeunea azorica</i>	LC	MAC
<i>Cololejeunea schaeferi</i>	VU	MAC
<i>Cololejeunea sintenisii</i>	EN	COSM
<i>Dumortiera hirsuta</i>	NT	COSM
<i>Frullania acicularis</i>	NT	AZOR
<i>Heteroscyphus denticulatus</i>	NT	MAC
<i>Lejeunea eckloniana</i>	LC	EUR
<i>Marchesinia mackaii</i>	LC	EUR
<i>Plagiochila longispina</i>	EN	AMER-AZOR
<i>Porella canariensis</i>	LC	IBER-MAC
<i>Radula carringtonii</i>	NT	EUR
<i>Radula holtii</i>	NT	EUR
<i>Radula wichurae</i>	NT	MAC
<i>Scapania gracilis</i>	LC	EUR
<i>Telaranea europaea</i>	LC	EUR
Mosses		
<i>Alophosia azorica</i>	NT	MAC
<i>Andoa berthelotiana</i>	VU	MAC
<i>Cyclodictyon laetevirens</i>	LC	EUR
<i>Epipterygium atlanticum</i>	LC	EUR
<i>Fissidens luisieri</i>	LC	MAC
<i>Heterocladium flaccidum</i>	LC	EUR
<i>Hypnum uncinulatum</i>	LC	EUR
<i>Myurium hochstetteri</i>	LC	EUR
<i>Philonotis rigida</i>	VU	EUR
<i>Pseudisothecium prolixum</i>	VU	MAC
<i>Pseudotaxiphyllum laetevirens</i>	NT	IBER-MAC
<i>Tetrastichium fontanum</i>	VU	IBER-MAC
<i>Tetrastichium virens</i>	NT	IBER-MAC
<i>Thamnobryum maderense</i>	NT	MAC
<i>Thamnobryum rudolphianum</i>	EN	AZOR

The categorization according to life strategies includes 41 taxa as perennial, 32 as colonists, 18 as long-lived shuttle, five as short-lived shuttle, and one as annual shuttle. Regarding the life forms, one species was categorised as annual, three as cushions, three as dendroids, 44 as mats, 37 as turfs, and 10 as wefts. According to the environmental factors, using the Ellenberg Indicator Values [54,55], 32 species were grouped as sciophytic, 46 as sciophytic-photophytic, and 15 as photophytic, while regarding water, four species

were categorised as xerophytic, 55 as mesophytic, and 34 as hygrophytic. Reaction values allowed the grouping of 33 species as acidophytic, 51 as mesoacidophytic-subneutrophytic, and nine as basidophytic.

Bar plots illustrating the distribution of various functional groups concerning each surveyed cave may be observed in Figure 2. It is evident that each functional group and the cave studied present different patterns/profiles. In terms of growth forms, foliose species prevailed in Algar do Carvão, Branca Opala, Gruta do Chocolate, Madre de Deus, Gruta da Achada, and Gruta do Coelho. Pleurocarpous species dominated in Gruta da Malha, Gruta dos Balcões, and Gruta dos Buracos, while acrocarpous mosses were predominant in Gruta do Natal and Gruta da Terra Mole. Regarding life forms, mats dominated in all caves except Gruta do Natal, where turfs took precedence. The study of life strategies revealed a dominance of perennial species in six of the 12 studied caves: Algar do Carvão, Gruta Branca Opala, Gruta da Achada, Gruta da Malha, Gruta dos Balcões, and Gruta dos Buracos, while colonist species prevailed in Gruta da Terra Mole, Gruta do Chocolate, Gruta do Coelho, and Gruta do Natal. Sciophytic species prevailed in most cases, while sciophytic-photophytic species dominated in Algar do Carvão, Gruta da Madre de Deus, Gruta da Terra Mole, and Gruta do Natal. Mesophytic species dominated in all caves, except in Gruta da Achada, Gruta do Coelho, and Gruta dos Balcões, where hygrophytic species held dominance. Regarding pH requirements, mesoacidophytic-subneutrophytic species consistently dominate in all caves.



**Figure 2.** Bar plots with each of the studied functional groups found in each sampled cave.

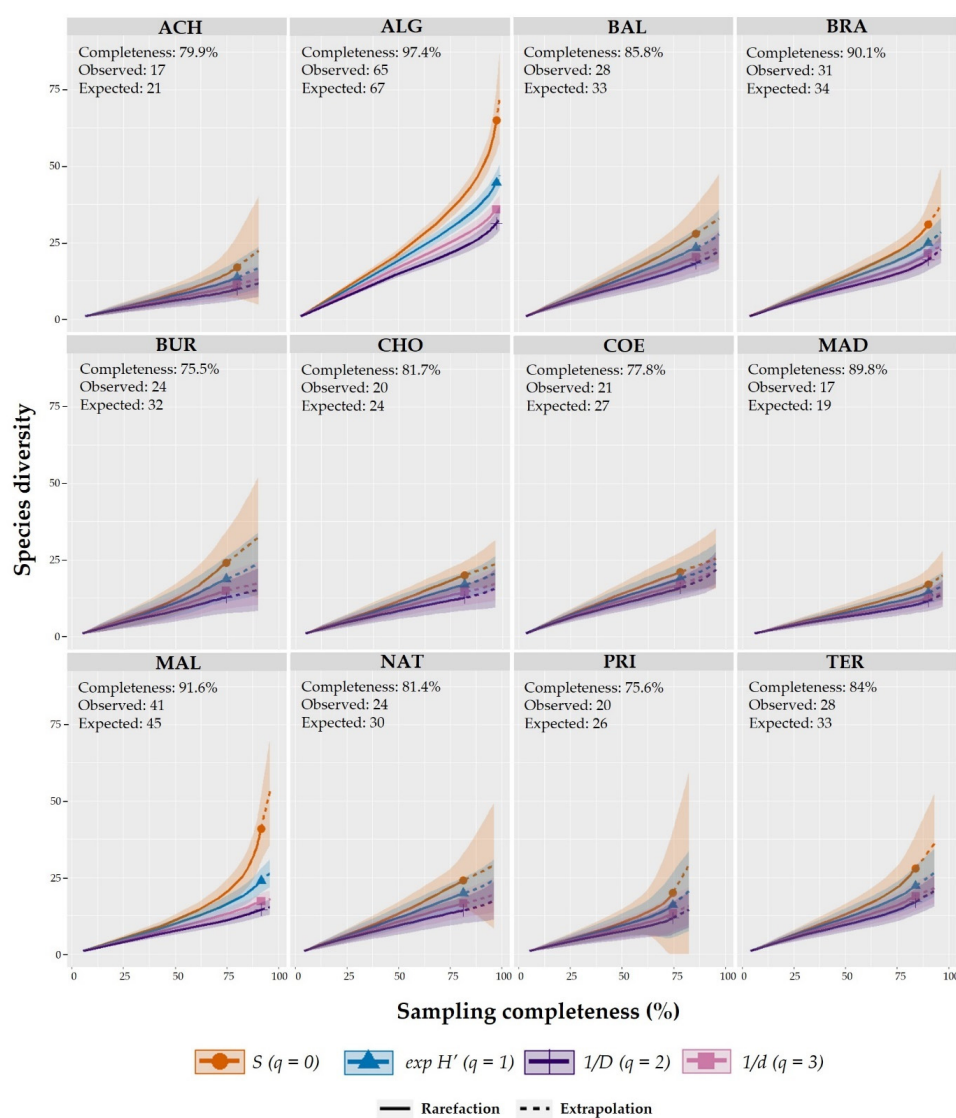
### 3.2. Sampling Completeness, Alpha ( $\alpha$ ), and Beta ( $\beta$ ) Diversity Richness across Caves

The completeness of bryophyte samplings along the twelve caves tended to be high, with the minimum values found for Gruta dos Buracos and Gruta dos Principiantes (75%) (Figure 3). When considering the two taxonomic groups separately, the lowest value was found for liverworts in Gruta do Chocolate (54%). All other completeness values

were higher than 74%, reaching 97% in Algar do Carvão for both liverworts and mosses (see Table A2, Appendix B).

Figure 3 shows the  $\alpha$ -diversity of species across the four mentioned richness levels (see Table A3, Appendix B). The richest cave in bryophyte species was Algar do Carvão ( $n = 65$  species), followed by Gruta Malha ( $n = 41$ ), Gruta da Branca Opala ( $n = 31$ ), Terra Mole, and Gruta Balcões ( $n = 28$  each). Similarly, Hill numbers showed that the caves that exhibited greater sensitivity to diversity loss were the two richest in species (Algar do Carvão and Gruta Malha). The Gruta da Madre Deus proved to be the cave with the greatest differences in the relative abundance of bryophyte species, showing the least decrease in its values across different  $\alpha$ -diversity levels.

Total  $\beta$ -diversity among caves revealed high dissimilarity indices across the studied caves (Table 2). On one hand, Gruta da Madre Deus appeared to be the most unequal in species diversity (0.96), followed by Algar do Carvão (0.89), Gruta do Natal, and Gruta da Achada (0.83). On the other hand, caves with lower dissimilarity were Terra Mole (0.72) and Gruta dos Balcões (0.73). However, all caves exhibited values above 0.70, indicating a substantial dissimilarity in species diversity.



**Figure 3.** Species accumulation curves by rarefaction and extrapolation for bryophytes from the studied caves on the different scales of species diversity according to Hill numbers. Sampling completeness values and the number of observed and expected species are also reported.

**Table 2.** Total  $\beta$ -diversity differences between sampled caves.

	ALG	BRA	ACH	MAD	MAL	TER	CHO	COE	NAT	BAL	BUR	PRI
<b>BRA</b>	0.86											
<b>ACH</b>	0.93	0.75										
<b>MAD</b>	0.97	0.93	0.96									
<b>MAL</b>	0.66	0.74	0.88	0.99								
<b>TER</b>	0.87	0.61	0.74	0.94	0.76							
<b>CHO</b>	0.94	0.68	0.81	0.89	0.90	0.70						
<b>COE</b>	0.92	0.73	0.74	0.99	0.83	0.60	0.73					
<b>NAT</b>	0.93	0.84	0.90	0.96	0.85	0.74	0.89	0.77				
<b>BAL</b>	0.89	0.67	0.77	0.98	0.73	0.60	0.79	0.65	0.71			
<b>BUR</b>	0.93	0.77	0.83	0.97	0.82	0.69	0.77	0.67	0.83	0.66		
<b>PRI</b>	0.93	0.75	0.81	0.97	0.85	0.62	0.80	0.68	0.72	0.62	0.73	
<b>Total</b>	0.89	0.76	0.83	0.96	0.82	0.72	0.81	0.76	0.83	0.73	0.79	0.77

### 3.3. Influence of Drivers on the Richness and Abundance of Bryophyte Species

The Spearman correlations between the studied variables and the main functional groups are presented in Table 3. Total richness and average bryophyte cover exhibited correlations with temperature, precipitation, elevation, slope, brightness, and evaporation. The cover also displayed a significant correlation with relative humidity, roughness, and moisture. The richness and cover of liverworts were correlated with temperature, brightness, and evaporation. Furthermore, liverwort richness correlated with slope, while cover correlated with relative humidity, precipitation, elevation, and moisture. Moss richness and cover were correlated with temperature, precipitation, elevation, slope, brightness, roughness, and evaporation.

The richness and abundance of foliose species showed correlations with temperature, relative humidity, brightness, roughness, and evaporation. Thallose species richness and abundance were correlated with temperature, relative humidity, precipitation, elevation, and roughness. Thallose richness also exhibited a correlation with slope, while abundance correlated with moisture. Acrocarpous moss richness was correlated with slope, brightness, and evaporation, and abundance was correlated with relative humidity, slope, brightness, and roughness. Pleurocarpous moss richness and abundance were correlated with temperature, precipitation, elevation, slope, and evaporation. Additionally, pleurocarpous moss abundance showed correlations with relative humidity and roughness. Colonist species richness and abundance were correlated with slope and brightness, while abundance also showed correlations with precipitation and roughness. Short-lived shuttle species richness and abundance were correlated with brightness and evaporation. Long-lived shuttle species richness and abundance were correlated with relative humidity, brightness, and evaporation, and abundance also showed correlations with roughness. Perennial species richness and abundance were correlated with temperature, precipitation, elevation, brightness, roughness, and evaporation. Abundance also showed a correlation with relative humidity. Mat species richness was correlated with relative humidity, precipitation, slope, brightness, evaporation, and moisture, while abundance was correlated only with temperature and moisture. Turf species richness and abundance were correlated with temperature, precipitation, elevation, slope, brightness, and roughness, with evaporation playing an important role in abundance. Weft species richness and abundance were correlated with all studied variables except moisture. Cushion species richness and abundance are correlated with elevation, brightness, roughness, and evaporation. Finally, dendroid species richness and abundance were correlated with temperature, precipitation, elevation, evaporation, and moisture.

**Table 3.** Spearman correlation index between richness and cover of the main functional groups and studied variables: annual mean temperature (TEMP), relative humidity (REHU), annual mean precipitation (PREC), elevation (ELEV), slope (SLOP), brightness (BRIG), substrate roughness (ROUG), evaporation (EVAP), and moisture (MOIS). Significant correlations are indicated in different tones of grey:  $p < 0.05$  (light grey);  $p < 0.005$  (medium grey);  $p < 0.0001$  (dark grey). Non-significant values are not shown.

	TEMP	REHU	PREC	ELEV	SLOP	BRIG	ROUG	EVAP	MOIS
<b>Total richness</b>	−0.39	-	0.200	0.241	−0.268	0.355	-	0.326	-
Liverworts	−0.371	-	-	-	−0.202	0.309	-	0.329	-
Mosses	−0.338	-	0.238	0.285	−0.265	0.315	−0.161	0.280	-
Foliose	−0.310	−0.278	-	-	-	0.367	−0.194	0.431	-
Thallose	−0.165	0.312	0.293	0.281	−0.258	-	0.184	-	-
Acrocarpous	-	-	-	-	−0.225	0.337	-	0.156	-
Pleurocarpous	−0.445	-	0.241	0.322	−0.207	-	-	0.223	-
Colonist	-	-	-	-	−0.308	0.239	-	-	-
Short-lived	-	-	-	-	-	0.211	-	0.162	-
Long-lived	-	−0.219	-	-	-	0.174	-	0.229	-
Perennial	−0.550	-	0.235	0.334	-	0.301	−0.206	0.372	-
Mat	-	0.163	0.170	-	0.183	−0.240	-	−0.254	0.169
Turf	−0.173	-	0.270	0.236	−0.215	0.335	−0.218	0.214	-
Weft	−0.251	0.193	0.215	0.242	−0.178	0.378	−0.222	0.312	-
Cushion	-	-	-	0.173	-	0.189	−0.201	0.165	-
Dendroid	−0.357	-	0.324	0.383	-	-	-	0.278	0.193
<b>Mean cover</b>	−0.481	0.204	0.394	0.904	−0.256	0.585	−0.182	−0.495	0.329
Liverworts	−0.428	0.191	0.274	0.243	-	0.223	-	−0.267	0.274
Mosses	−0.296	-	0.242	0.270	−0.270	0.290	−0.215	−0.250	-
Foliose	−0.381	−0.232	-	-	-	0.258	−0.206	0.312	-
Thallose	−0.202	0.308	0.349	0.299	-	-	0.172	-	0.266
Acrocarpous	-	−0.172	-	-	−0.206	0.313	−0.176	-	-
Pleurocarpous	−0.431	0.190	0.257	0.330	−0.225	-	−0.188	0.199	-
Colonist	-	-	0.190	-	−0.236	0.238	−0.236	-	-
Short-lived	-	-	-	-	-	0.208	-	0.158	-
Long-lived	-	−0.184	-	-	-	0.160	0.160	0.186	-
Perennial	−0.553	0.162	0.278	0.377	-	0.236	−0.242	0.303	-
Mat	−0.337	-	-	-	-	-	-	-	−0.180
Turf	−0.173	-	0.285	0.243	−0.239	0.298	−0.219	-	-
Weft	−0.220	0.182	0.185	0.223	−0.183	0.371	−0.232	0.335	-
Cushion	-	-	-	0.174	-	0.186	−0.198	0.162	-
Dendroid	−0.345	-	0.316	0.374	-	-	-	0.276	0.184

### 3.4. Species Composition

ISA analyses revealed significant differences among the studied caves (Table 4). Of the twelve sampled caves, nine hosted indicator species. Among these, Algar do Carvão and Gruta da Madre de Deus are the caves with the highest number of indicator species, primarily due to significant differences in their bryophyte compositions. The presence of some rare and/or endemic species exclusively in certain caves is noteworthy. For instance, *Plagiochila longispina* only appeared in Algar do Carvão, while *Radula wichurae*, *Cololejeunea schaeferi*, and *Marchesinia mackaii* were only found in Gruta da Madre de Deus. The species composition of Gruta dos Buracos is also remarkable. It was the sole location where the endemics *Thamnobryum maderense* and *Alophosia azorica* were observed. According to the taxonomic group, a somewhat homogeneous distribution is discernible regarding indicator species of mosses and liverworts. Nevertheless, in terms of life strategies, some variations can be observed. For instance, Algar do Carvão exhibited long-lived indicator species, mostly perennials, in contrast to Gruta do Natal, where short-lived indicator species (colonists and annuals) were dominant.

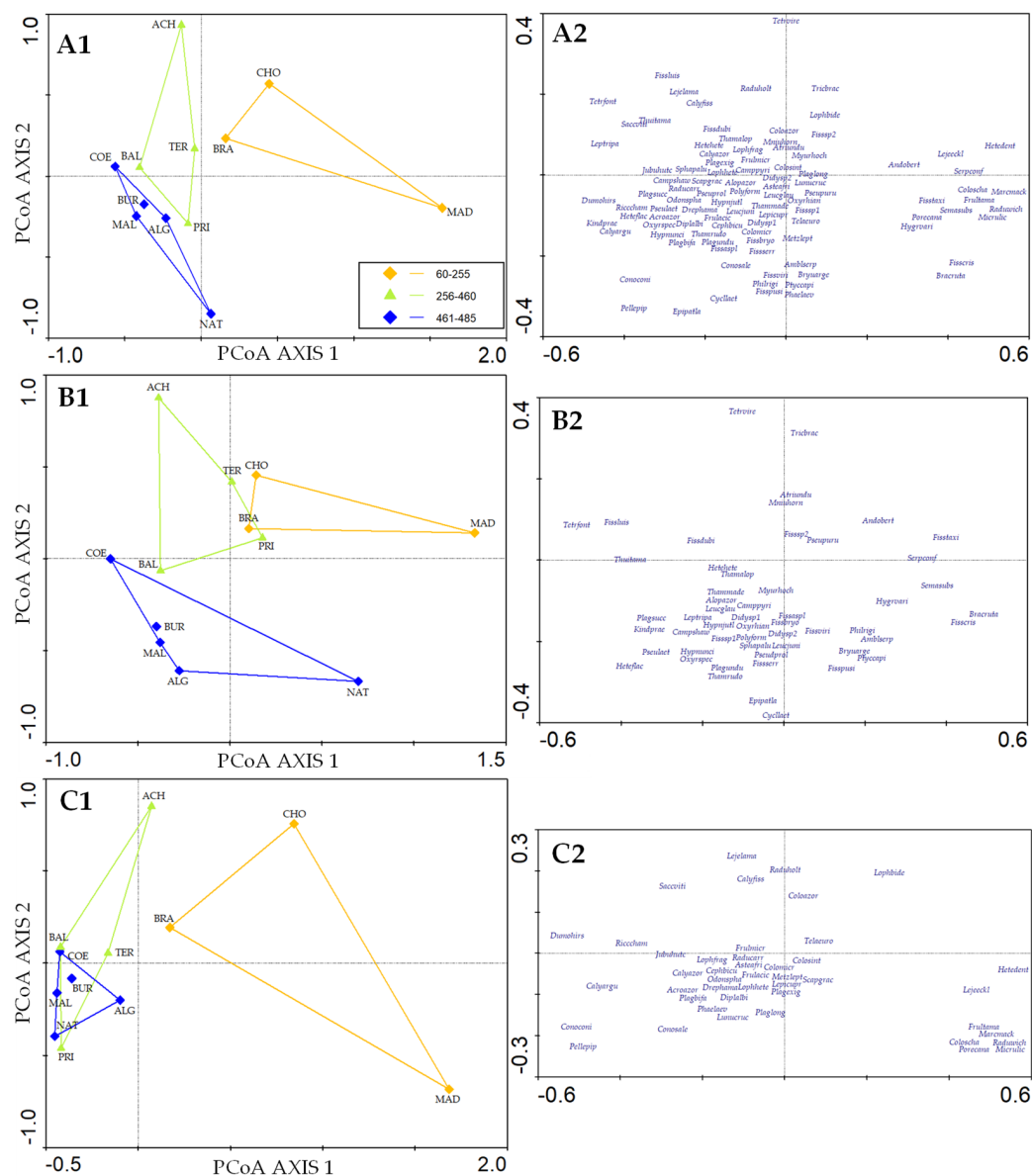
**Table 4.** Indicator species analysis for the species composition in each sampled cave. Taxonomic group, life strategy, and significant indicator value (in asterisks) for each species are presented:  $p < 0.005$ ; (\*);  $p < 0.005$  (\*\*);  $p < 0.0001$  (\*\*\*)

Cave	Species	Taxonomic Group	Life Strategy	Indicator Value
Algar do Carvão	<i>Thamnobryum rudolphianum</i>	Moss	Perennial	0.710 ***
	<i>Sphagnum palustre</i> *	Moss	Long-lived	0.672 **
	<i>Plagiochila longispina</i> *	Liverwort	Perennial	0.648 **
	<i>Plagiommium undulatum</i>	Moss	Perennial	0.570 **
	<i>Leucobryum juniperoideum</i> *	Moss	Perennial	0.508 *
	<i>Lepidozia cupressina</i> *	Liverwort	Perennial	0.475 *
	<i>Plagiochila exigua</i> *	Liverwort	Perennial	0.475 *
Gruta Branca Opala	<i>Frullania microphylla</i>	Liverwort	Long-lived	0.527 **
	<i>Cololejeunea sintenisii</i>	Liverwort	Short-lived	0.508 **
	<i>Fissidens</i> sp. 2 *	Moss	Colonist	0.471 **
Gruta da Achada	Non-significant species			
Gruta da Madre de Deus	<i>Marchesinia mackaii</i> *	Liverwort	Perennial	1.00 ***
	<i>Radula wichurae</i> *	Liverwort	Long-lived	0.926 ***
	<i>Porella canariensis</i>	Liverwort	Long-lived	0.831 ***
	<i>Lejeunea eckoniana</i>	Liverwort	Perennial	0.807 ***
	<i>Cololejeunea schaeferi</i> *	Liverwort	Long-lived	0.756 ***
	<i>Hygroamblystegium varium</i>	Moss	Perennial	0.706 ***
	<i>Brachythecium rutabulum</i>	Moss	Colonist	0.681 ***
	<i>Fissidens crispus</i>	Moss	Colonist	0.590 **
	<i>Frullania tamarisci</i> *	Liverwort	Long-lived	0.535 **
	<i>Microlejeunea ulicina</i> *	Liverwort	Long-lived	0.535 **
Gruta da Malha	Non-significant species			
Gruta da Terra Mole	<i>Atrichum undulatum</i> *	Moss	Colonist	0.426 **
	<i>Mnium hornum</i> *	Moss	Long-lived	0.426 **
Gruta do Chocolate	<i>Lophocolea bidentata</i>	Liverwort	Perennial	0.696 ***
	<i>Cololejeunea azorica</i>	Liverwort	Short-lived	0.677 ***
Gruta do Coelho	<i>Odontoschisma sphagni</i>	Liverwort	Colonist	0.502 *
Gruta do Natal	<i>Amblystegium serpens</i> *	Moss	Perennial	0.548 **
	<i>Ptychostomum capillare</i> *	Moss	Colonist	0.548 **
	<i>Bryum argenteum</i> *	Moss	Colonist	0.447 **
	<i>Phaeoceros laevis</i> *	Hornwort	Annual	0.447 **
Gruta dos Balcões	<i>Heterocladium heteropterum</i>	Moss	Perennial	0.577 **
	<i>Leptodictyum riparium</i>	Moss	Perennial	0.471 *
	<i>Radula carringtonii</i>	Liverwort	Long-lived	0.459 *
Gruta dos Buracos	<i>Leucobryum glaucum</i> *	Moss	Perennial	0.548 **
	<i>Thamnobryum maderense</i> *	Moss	Perennial	0.548 **
	<i>Alophosia azorica</i> *	Moss	-	0.447 *
	<i>Asterella africana</i> *	Liverwort	Short-lived	0.447 *
Gruta dos Principiantes	Non-significant species			

In the Principal Coordinates Analysis (PCoA) for all bryophyte species, liverworts and mosses showed differences in the cave composition. PCoA conducted for all bryophyte species (Figure 4A) revealed a clear separation of caves based on elevation. Along axis 1, a pronounced gradient emerged, delineated by elevation and precipitation ( $R^2 = -0.634$ ;  $R^2 = -0.583$ ), positioning caves at lower altitudes to the right and those at higher altitudes to the left of the graph. This axis also exhibited correlations with the richness and cover of pleurocarpous mosses ( $R^2 = -0.706$ ;  $R^2 = -0.720$ ), thallose cover ( $R^2 = -0.609$ ), sciophytic cover ( $R^2 = -0.762$ ), and hygrophytic cover ( $R^2 = -0.657$ ). Axis 2 was marked by a brightness and evaporation gradient ( $R^2 = 0.702$ ;  $R^2 = 0.671$ ), where liverwort and moss cover were also correlated ( $R^2 = -0.664$ ;  $R^2 = 0.594$ ).

A congruent pattern with the general dynamics was observed when focusing on the ordination of moss composition (Figure 4B). However, distinctions emerged when scrutinising extant correlations along the gradients. In this context, the richness and cover of sciophytic ( $R^2 = -0.587$ ;  $R^2 = -0.839$ ) and hygrophytic cover ( $R^2 = -0.594$ ) once again displayed influence along axis 1. Nevertheless, moss cover ( $R^2 = -0.594$ ) and the richness and cover of pleurocarpous mosses exhibited a negative impact ( $R^2 = -0.664$ ;  $R^2 = -0.657$ ), while a positive influence emanated from the richness of long-lived shuttle species ( $R^2 = 0.637$ ). Conversely, axis 2 was delineated by the impact of macroclimatic

variables such as elevation and precipitation ( $R^2 = -0.830$ ;  $R^2 = -0.792$ ), coupled with the microclimatic variable of evaporation ( $R^2 = 0.629$ ). The influence of bryophyte species, thallose, and liverwort cover ( $R^2 = 0.615$ ;  $R^2 = -0.623$ ;  $R^2 = -0.769$ , respectively) also surfaced as salient along this axis.



**Figure 4.** Principal Coordinates Analysis (PCoA) showing the distribution of sampled caves by elevation groups (1) according to bryophyte composition (2) with total species ((A), PCoA Axis 1 eigenvalue = 0.300; PCoA Axis 2 eigenvalue = 0.191), mosses ((B), PCoA Axis 1 eigenvalue = 0.284; PCoA Axis 2 eigenvalue = 0.198), and liverworts ((C), PCoA Axis 1 eigenvalue = 0.390; PCoA Axis 2 eigenvalue = 0.188).

The ordination analysis of liverworts revealed greater variations compared to the observed general pattern (Figure 4C). Interestingly, there was considerable heterogeneity in the composition of liverworts among caves at lower altitudes, while two groups of caves at higher altitudes exhibited a certain homogeneity in liverwort species composition. In this instance, macroclimatic variables such as precipitation and elevation positively influenced axis 1 ( $R^2 = -0.732$ ;  $R^2 = -0.644$ ). Additionally, this axis was correlated with abundance and richness variables, including bryophyte species cover ( $R^2 = -0.622$ ), foliose richness ( $R^2 = 0.727$ ), thallose richness and cover ( $R^2 = -0.608$ ;  $R^2 = -0.755$ ), as well as

microclimatic variables such as brightness ( $R^2 = 0.611$ ), evaporation ( $R^2 = 0.825$ ), and humidity ( $R^2 = -0.658$ ). Axis 2 was correlated with the cover of mesophytic and sciophytic species ( $R^2 = -0.608$ ;  $R^2 = -0.699$ ).

## 4. Discussion

### 4.1. Bryophyte Richness Patterns in Caves on Terceira Island

This study, which examines the diversity and species composition of bryophytes in twelve caves on the island of Terceira, provides valuable insights into the diversity, distribution, and ecological preferences of bryophytes in caves, specifically in the Azores archipelago. Nearly a third of the existing species on Terceira Island and about a fifth of the species listed for the Azores archipelago have been found to inhabit these cave environments. The fact that one-fifth of these species are threatened, and one-third are endemic makes the caves a significant reservoir of biodiversity. Other studies conducted in caves in the Azores Islands provide markedly different richness figures [47–49]. However, intra- and inter-island variations, coupled with the extreme conditions of this habitat type, induce changes in species composition patterns. For instance, studies along altitudinal gradients in the Macaronesia region report richness values much higher than those documented here [25,26,85–87]. This is attributed to the broader ecological and climatic range offered by these gradients, thereby enhancing climatic diversity, which is particularly significant for these organisms, especially liverworts [38].

It is noteworthy that the sampling completeness values obtained for the 165 microplots investigated were generally very good, reaching at least 75% (Gruta dos Buracos and Gruta Principiantes), with the highest value recorded in Algar do Carvão (97%), which is attributed to intensive sampling effort. Sampling completeness values exceeding 74% were also obtained for separate taxonomic groups (mosses and liverworts), except for liverworts in Gruta do Chocolate (54%). Attaining a comprehensive sampling of species in biodiversity hotspots for such a diverse plant group can be challenging [85], particularly in caves, where sampling may require climbing equipment and expertise [88]. The overall species richness across the caves exhibited variation, with the maximum diversity observed in the highest-altitude cave (Algar do Carvão, with 65 species) and the minimum diversity in the lowest-altitude caves (Gruta da Madre de Deus and Gruta da Achada, both with 17 species). This diversity is influenced by the occurrence of the Algar do Carvão, an ancient volcanic vent located in the central part of the island and extending vertically to a depth of 90 m [53].

The notable elevation-dependent  $\beta$ -diversity values highlight substantial dissimilarity across the twelve surveyed caves. Specifically, the cave situated at the lowest altitude (60 m a.s.l.) exhibited the highest  $\beta$ -diversity values, ranging from 0.94 to 0.99 when compared to the other caves. Conversely, the cave located at the highest altitude (583 m a.s.l.) follows this trend, demonstrating elevated  $\beta$ -diversity values ranging from 0.86 to 0.94. However, further studies involving caves at higher altitudes are necessary to determine whether a clear altitudinal gradient exists and whether the distribution of  $\alpha$  and  $\beta$ -diversity follows patterns observed in other ecosystems in island archipelagos [25,26,85–87,89].

### 4.2. Bryophyte Composition Patterns in Caves on Terceira Island

Our survey of caves on Terceira Island revealed a rich biodiversity of bryophytes, including noteworthy endemic and threatened species, which clearly found caves a sanctuary for their survival [48,50]. Some rare or uncommon species were identified in these caves. Namely, *Tetrastichium virens* and *T. fontanum* are rare species that find their largest populations within caves, making them among the most abundant bryophyte species in this habitat. The same three bryophyte species were found to be dominant across all the studied caves: *Kindbergia praelonga*, *Fissidens luisieri*, and *Jubula hutchinsiae*. This partially aligns with findings from previously published studies in caves in the Azores [48]. Remarkable among the species found in this system are the liverworts *Cololejeunea schaeferi*, exclusively documented within the Madre de Deus cave in the Azores, and *Asterella africana*, frequently identified in shady humid slopes of ravines [90,91] and in riparian areas in other Macarone-

sian islands [92,93]. However, it is noteworthy that *A. africana* populations from the Azores are situated in cave entrances, which suggests a possible refugium for this species [48,50].

In the current study, the composition of bryophyte species changed depending on each cave, consistent with previous reports [1,27,46–49,94]. The analysis of indicator species highlights a significant variation among the surveyed caves, showcasing species closely tied to specific caves. Examples include the liverworts *Plagiochila longispina* and *Lepidozia cupressina* in Algar do Carvão, or *Marchesinia mackaii* and *Radula wichurae* in Gruta da Madre de Deus. Additionally, certain moss species that are less dependent on water and have a broader distribution also exhibit specificity in caves at intermediate altitudes, as observed with *Atrichum undulatum* or *Leucobryum glaucum*.

According to the ordination analyses, there is a clear influence of elevation on species composition. When examining the overall set of bryophyte species, the composition of the twelve sampled caves was perfectly correlated according to altitude. This pattern was repeated in the moss analysis but not in the case of liverworts. Liverwort ordination analyses showed some species overlap between caves at higher altitudes and those at intermediate altitudes, although the higher-altitude caves exhibited greater heterogeneity in species composition than the intermediate ones. However, the liverwort composition for the lower-altitude gradient exhibited even greater species heterogeneity. This is influenced by the distinct composition of the cave at a lower altitude (Gruta da Madre de Deus), as previously observed in its  $\beta$ -diversity values.

#### 4.3. Influence of Drivers on the Bryophyte Species

Macroclimatic drivers such as temperature, precipitation, and elevation exerted a profound influence on the richness and cover of bryophyte species. However, this influence varied across the diverse functional groups. Specifically, temperature and slope negatively impacted the richness and cover of bryophyte species, while precipitation, elevation, brightness, and moisture exhibited positive influences on the functional groups to which they were correlated. The functional groups least affected by the studied variables were acrocarpous mosses and short-lived shuttle species, likely due to their xerophytic or mesophytic character [95,96]. On the other hand, the functional groups most dependent on the studied variables were the wefts and mosses. This dependence was probably driven by pleurocarpous mosses, forming wefts primarily of the genus *Eurhynchium* s.l. One standout species in our study was *Kindbergia praelonga*, prevalent in all the sampled caves. Moisture was correlated with the richness and cover of dendroid and mat-forming species and the overall cover of bryophytes, liverworts, and thalloles. It is worth noting that dendroid mosses and all liverwort species typically fall within the category of groups most reliant on microclimatic conditions [38]. However, the abundance of mat-forming species was negatively correlated with moisture. This could be explained because of the competition between mat-forming species and dendroid species. Elevation was one of the most important drivers in species composition, as clearly seen when comparing the lowest and highest caves (Gruta da Madre de Deus and Algar do Carvão, respectively). Regarding life forms, thallose liverworts and pleurocarpous mosses were the most dependent on the studied variables. However, they exhibited differences in terms of richness and cover with some of the macro- and microclimatic variables. For instance, relative humidity influenced the richness and cover of thallose species and the cover of pleurocarpous mosses, but not their richness. According to the various observed life strategies, the richness and cover of perennial species appear to be the most dependent on the studied climatic variables. This confirms the greater climatic and ecological stability required for this type of species to thrive, considering their long-life expectancy [21].

## 5. Conclusions

Caves serve as biodiversity laboratories, as their extreme conditions make them ideal places to study factors and processes underlying biodiversity. Studying the richness and

composition of bryophytes in caves may contribute significantly to the current understanding of biodiversity as a whole.

According to the questions originally proposed in this study, it is possible to conclude the following: (1) The richness of bryophytes in the caves of Terceira is quite high, following patterns already observed in other cave studies on islands [48]; (2) The investigated caves host sharply different bryophyte compositions [1], so it is important to ensure protection for all of them; (3) The studied macro- and microclimatic variables influence biotic variables such as bryophyte richness, abundance, and species composition differently, depending on the functional group under consideration.

This research offers one of the most comprehensive accounts of cave bryophytes worldwide, highlighting the remarkable bryophyte flora found in the caves of the Azores. Approximately 35% of Azorean bryophytes are found in these caves [48]. Many of the species thriving in these habitats are endemic and/or endangered, making their populations crucial for the survival of the species in the archipelago. Consequently, these concealed ecosystems need to receive the attention and protection they merit. Conservation management should be taken to mitigate human impacts in these ecosystems [97]. The caves serve as reservoirs of biodiversity, especially for groups with a high microclimate dependence, such as bryophytes. Conserving bryophytes could enhance cave biodiversity and resilience by fostering biological interactions among multiple species and improving ecological functions [95].

Further studies involving caves from other islands would contribute to a better understanding of the patterns of richness and abundance that shape these inhospitable ecosystems. This approach would help determine the influence of macro- and microclimatic variables on a larger scale and lead to extrapolatable conclusions for the entire archipelago.

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**Data Availability Statement:** The data presented in this study are available on request from the corresponding author.

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## Appendix A

**Table A1.** List of the bryophytes found across the twelve sampled caves. Nomenclature follows Hodgetts et al. [53] and life strategy to Van Zuijlen et al. [54]. Distribution categorisation followed: AZOR (Azores archipelago), MAC (Macaronesian region), IBER-MAC (Ibero-Macaronesian region), EUR (Europe), EUR-AFR (Europe and Africa), AMER-AZOR (America and Azores archipelago), MEX-AZOR-UK (Mexico, Azores and United Kingdom distribution) and COSM (cosmopolitan distribution). Abbreviation of cave names follows Figure 1D.

	Family	Life Strategy	Distribution	Abbreviation	Occurrence												
					TOTAL	ALG	BRA	ACH	MAD	MAL	TER	CHO	COE	NAT	BAL	BUR	PRI
<b>Div. Antocerothyta</b>																	
<i>Phaeoceros laevis</i> (L.) Prosk.	Notothyladaceae	Annual shuttle	COSM	Phaelaev	1									1			
<b>Div. Marchantiophyta</b>																	
<i>Acrobolbus azoricus</i> (Grolle & Perss.) Briscoe	Acrobolbaceae	Perennial	AZOR	Acroazor	6	4				1			1				
<i>Asterella africana</i> (Mont.) Underw. ex A.Evans	Aytoniaceae	Short-lived shuttle	EUR-AFR	Asteafri	1											1	
<i>Calypogeia arguta</i> Nees & Mont.	Calypogeiaceae	Colonist	COSM	Calyargu	35	1	6			4	5	1	1	2	4	6	5
<i>Calypogeia azorica</i> Bischl.	Calypogeiaceae	Colonist	MAC	Calyazor	17	10	2	2		1					1		1
<i>Calypogeia fissa</i> (L.) Raddi	Calypogeiaceae	Colonist	COSM	Calyfiss	37	16	3	3		5	6	1	3				
<i>Cephalozia bicuspidata</i> (L.) Dumort.	Cephaloziaceae	Colonist	COSM	Cephbici	1					1							
<i>Cololejeunea azorica</i> V.Allorge & Jovet-Ast	Lejeuneaceae	Short-lived shuttle	MAC	Coloazor	4					1	1	2					
<i>Cololejeunea microscopica</i> (Taylor) Schiffn.	Lejeuneaceae	Short-lived shuttle	COSM	Colomicr	3	3											
<i>Cololejeunea schaeferi</i> Grolle	Lejeuneaceae	Long-lived shuttle	MAC	Colosche	3				3								
<i>Cololejeunea sintenisii</i> (Steph.) Pócs	Lejeuneaceae	Short-lived shuttle	COSM	Colosint	4	2	2										
<i>Conocephalum conicum</i> (L.) Dumort.	Conocephalaceae	Long-lived shuttle	COSM	Conoconi	45	16	5			8	5		2	2	3	1	3
<i>Conocephalum salebrosum</i> Szweyk., Buczk. & Odrzyk.	Conocephalaceae	Long-lived shuttle	COSM	Conosale	21	7				7	2			2			3
<i>Diplophyllum albicans</i> (L.) Dumort.	Scapaniaceae	Colonist	COSM	Diplalba	5	4				1							
<i>Drepanolejeunea hamatifolia</i> (Hook.) Schiffn.	Lejeuneaceae	Long-lived shuttle	COSM	Draphama	1					1							
<i>Dumortiera hirsute</i> (Sw.) Nees	Dumortieraceae	Long-lived shuttle	COSM	Dumohirs	47	15	4	4		13	1		2	3	2	2	1
<i>Frullania acicularis</i> Hentschel & von Konrat	Frullaniaceae	Long-lived shuttle	MAC	Frulacic	5	5											
<i>Frullania microphylla</i> (Gottsche) Pearson	Frullaniaceae	Long-lived shuttle	EUR	Frulmicr	3		2			1							
<i>Frullania tamarisci</i> (L.) Dumort.	Frullaniaceae	Long-lived shuttle	COSM	Frultama	1				1								
<i>Heteroscyphus denticulatus</i> (Mitt.) Schiffn.	Lophocoleaceae	Long-lived shuttle	MAC	Hetedent	11		6		2			3					
<i>Jubula hutchinsiae</i> (Hook.) Dumort.	Jubulaceae	Perennial	COSM	Jubahutc	60	20	7			24	3		2		4		
<i>Lejeunea eckloniana</i> Lindenb.	Lejeuneaceae	Perennial	EUR	Lejeecko	16	7	2		6		1	1					
<i>Lejeunea lamacerina</i> (Steph.) Schiffn.	Lejeuneaceae	Long-lived shuttle	COSM	Lejelama	25	8	5	4			2	2	1		1	2	

Table A1. *Cont.*

					Occurrence												
	Family	Life Strategy	Distribution	Abbreviation	TOTAL	ALG	BRA	ACH	MAD	MAL	TER	CHO	COE	NAT	BAL	BUR	PRI
<i>Lepidozia cupressina</i> (Sw.) Lindenb.	Lepidoziaceae	Perennial	COSM	Lepicups	6	6											
<i>Lophocolea bidentata</i> (L.) Dumort.	Lophocoleaceae	Perennial	COSM	Lophbide	4	1	1					2					
<i>Lophocolea fragrans</i> (Moris & De Not.) Gottsche, Lindenb. & Nees	Lophocoleaceae	Perennial	COSM	Lophfrag	8	1	4	1								1	1
<i>Lophocolea heterophylla</i> (Schrad.) Dumort.	Lophocoleaceae	Colonist	COSM	Lophheter	2	1					1						
<i>Lunularia cruciata</i> (L.) Dumort ex. Lindb.	Lunulariaceae	Perennial	COSM	Lunucruc	1												1
<i>Marchesinia mackaii</i> (Hook.) Gray	Lejeuneaceae	Perennial	EUR	Marcmack	6				6								
<i>Metzgeria leptoneura</i> Spruce	Metzgeriaceae	Long-lived shuttle	COSM	Metzlept	3	3											
<i>Microlejeunea ulicina</i> (Taylor) Steph.	Lejeuneaceae	Long-lived shuttle	COSM	Micruclic	1				1								
<i>Odontoschisma sphagni</i> (Dicks.) Dumort.	Cephaloziaceae	Colonist	COSM	Odonspgh	9	7							2				
<i>Pellia epiphylla</i> (L.) Corda	Pelliaceae	Colonist	COSM	Pellepip	42	10				11	4		2	6	5	2	2
<i>Plagiochila bifaria</i> (Sw.) Lindenb.	Plagiochilaceae	Perennial	COSM	Plagbifr	9	7				1						1	
<i>Plagiochila exigua</i> (Taylor) Taylor	Plagiochilaceae	Perennial	COSM	Plagexiq	6	6											
<i>Plagiochila longispina</i> Lindenb. & Gottsche	Plagiochilaceae	Perennial	AMER-AZOR	Plaglong	12	12											
<i>Porella canariensis</i> (F.Weber) Underw.	Porellaceae	Long-lived shuttle	IBER-MAC	Porecana	5	1			4								
<i>Radula carringtonii</i> J.B.Jack	Radulaceae	Long-lived shuttle	EUR	Radicarr	4	3									1		
<i>Radula holtii</i> Spruce	Radulaceae	Colonist	EUR	Radiholt	4	3		1									
<i>Radula wichurae</i> Steph.	Radulaceae	Long-lived shuttle	MAC	Radiwich	5				5								
<i>Riccardia chamedryfolia</i> (With.) Grolle	Aneuraceae	Colonist	COSM	Ricccham	59	27	5	1		13	4	1	3	2	2		1
<i>Saccogyna viticulosa</i> (L.) Dumort.	Saccogynaceae	Perennial	EUR	Saccvita	19	9		2		1	2	1	1		2	1	
<i>Scapania gracilis</i> Lindb.	Scapaniaceae	Perennial	EUR	Scapgrac	1	1											
<i>Telaranea europaea</i> J.J.Engel & G.L.Merr.	Lepidoziaceae	Colonist	EUR	Telaeuro	5	3						1		1			
Div. Bryophyta																	
<i>Alophosia azorica</i> (Renauld & Cardot) Cardot	Polytrichaceae	NA	MAC	Alopazor	1											1	
<i>Amblystegium serpens</i> (Hedw.) Schimp.	Amblystegiaceae	Perennial	COSM	Amblsere	2									2			
<i>Andoa berthelotiana</i> (Mont.) Ochyra	Hypnaceae	Perennial	MAC	Andobert	14		3		2	1	2	3			1	1	1
<i>Atrichum undulatum</i> (Hedw.) P.Beauv.	Polytrichaceae	Short-lived shuttle	COSM	Atriundu	1						1						
<i>Brachythecium rutabulum</i> (Hedw.) Schimp.	Brachytheciaceae	Colonist	COSM	Bracruta	4				3					1			
<i>Bryum argenteum</i> Hedw.	Bryaceae	Colonist	COSM	Bryuarge	1									1			
<i>Campylopus pyriformis</i> (Schultz) Brid.	Leucobryaceae	Colonist	COSM	Camppyri	4	3					1						
<i>Campylopus shawii</i> Wilson	Leucobryaceae	Perennial	MEX-AZ-UK	Campshaw	11	9		1		1							
<i>Cyclodictyon laetevirens</i> (Hook. & Taylor) Mitt.	Pilotrichaceae	Colonist	EUR	Cycllaet	12	6				3				2		1	
<i>Didymodon</i> sp. 1	Pottiaceae	Colonist	COSM	Didysp.1	1	1											

Table A1. Cont.

	Family	Life Strategy	Distribution	Abbreviation	Occurrence												
					TOTAL	ALG	BRA	ACH	MAD	MAL	TER	CHO	COE	NAT	BAL	BUR	PRI
<i>Didymodon</i> sp. 2	Pottiaceae	Colonist	COSM	Didysp.2	1					1							
<i>Epipterygium atlanticum</i> Hanusch	Mniaceae	Colonist	EUR	Epiptatla	22	2				7	1		1	4	3	3	1
<i>Fissidens asplenioides</i> Hedw.	Fissidentaceae	Colonist	COSM	Fissaspl	31	11	1			2	3	2	1	1	4		6
<i>Fissidens bryoides</i> Hedw.	Fissidentaceae	Colonist	COSM	Fissbryo	18	5	2			5		1		2	2		1
<i>Fissidens crispus</i> Mont.	Fissidentaceae	Colonist	COSM	Fisscris	4	1			2					1			
<i>Fissidens dubius</i> P.Beauv.	Fissidentaceae	Perennial	COSM	Fissdoub	3			1		2							
<i>Fissidens luisieri</i> P. de la Varde	Fissidentaceae	Colonist	MAC	Fissluis	57	17	9	1		9	5	6	3		2	5	
<i>Fissidens pusillus</i> (Wilson) Milde	Fissidentaceae	Colonist	COSM	Fisspusi	2					1				1			
<i>Fissidens serrulatus</i> Brid.	Fissidentaceae	Colonist	COSM	Fisserr	9	2	1			4				1	1		
<i>Fissidens</i> sp. 1	Fissidentaceae	Colonist		Fissssp.1	1	1											
<i>Fissidens</i> sp. 2	Fissidentaceae	Colonist		Fissssp.2	1		1										
<i>Fissidens taxifolius</i> Hedw.	Fissidentaceae	Colonist	COSM	Fisstaxi	14	2	1	2	4		2	2		1			
<i>Fissidens viridulus</i> (Sw.) Wahlenb.	Fissidentaceae	Colonist	COSM	Fissviri	38	9	3		1	2	6	2	3	6	1	2	3
<i>Heterocladium flaccidum</i> (Schimp.) A.J.E.Sm.	Lembophyllaceae	Perennial	EUR	Heteflac	63	23	5			22	1	2	2	1	4	1	2
<i>Heterocladium heteropterum</i> (Brid.) Schimp.	Lembophyllaceae	Perennial	COSM	Heteheter	1										1		
<i>Hygroamblystegium varium</i> (Hedw.) Mönk.	Amblystegiaceae	Perennial	COSM	Hygrvari	5				3	1						1	
<i>Hypnum jutlandicum</i> Holmen & E.Warncke	Hypnaceae	Perennial	COSM	Hypnjutl	1	1											
<i>Hypnum uncinulatum</i> Jur.	Hypnaceae	Perennial	EUR	Hypnunci	10	8				1						1	
<i>Kindbergia praelonga</i> (Hedw.) Ochyra	Brachytheciaceae	Perennial	COSM	Kindprae	59	22	5	4		7	6		2	3	5	1	4
<i>Leptodictyum riparium</i> (Hedw.) Warnst.	Amblystegiaceae	Perennial	COSM	Leptripa	3					2					1		
<i>Leucobryum glaucum</i> (Hedw.) Ångstr.	Leucobryaceae	Perennial	COSM	Leucglau	2											2	
<i>Leucobryum juniperoideum</i> (Brid.) Müll.Hal.	Leucobryaceae	Perennial	COSM	Leucjuni	7	7											
<i>Mnium hornum</i> Hedw.	Mniaceae	Long-lived shuttle	COSM	Mniumhorn	1						1						
<i>Myurium hochstetteri</i> (Schimp.) Kindb.	Myuriaceae	Perennial	EUR	Myurhoch	10	9	1										
<i>Oxyrrhynchium hians</i> (Hedw.) Loeske	Brachytheciaceae	Colonist	COSM	Oxyrhian	2	2											
<i>Oxyrrhynchium speciosum</i> (Brid.) Warnst.	Brachytheciaceae	Perennial	COSM	Oxyrspec	22	15				5					2		
<i>Philonotis rigida</i> Brid.	Bartramiaceae	Long-lived shuttle	EUR	Philrigi	7									4	2		1
<i>Plagiomnium undulatum</i> (Hedw.) T.J.Kop.	Mniaceae	Perennial	COSM	Plagundu	11	10				1							
<i>Plagiothecium succulentum</i> (Wilson) Lindb.	Plagiotheciaceae	Perennial	COSM	Plagsucc	47	23				11	1		1		5	6	
<i>Polytrichum formosum</i> Hedw.	Polytrichaceae	Perennial	COSM	Polyform	5	5											
<i>Pseudoscleropodium purum</i> (Hedw.) M.Fleisch.	Brachytheciaceae	Perennial	COSM	Pseupuru	1												1
<i>Pseudisothecium prolixum</i> (Mitt.) Ignatova, Fedosov & Ignatov	Lembophyllaceae	Perennial	MAC	Pseuproli	1	1											
<i>Pseudotaxiphyllum laetevirens</i> (Dixon & Luisier ex F.Koppe & Düll) Hedenäs	Plagiotheciaceae	Colonist	IBER-MAC	Pseulaet	16	11	1			2			1			1	
<i>Ptychostomum capillare</i> (Hedw.) Holyoak & N.Pedersen	Bryaceae	Colonist	COSM	Ptyccapi	2									2			

Table A1. Cont.

	Family	Life Strategy	Distribution	Abbreviation	Occurence												
					TOTAL	ALG	BRA	ACH	MAD	MAL	TER	CHO	COE	NAT	BAL	BUR	PRI
<i>Sematophyllum substrumosum</i> (Hampe) E.Britton	Sematophyllaceae	Colonist	COSM	Semasubstr	3	2			1								
<i>Serpoleskea confervoides</i> (Brid.) Schimp.	Amblystegiaceae	Perennial	COSM	Serpconf	5	2	1		1			1					
<i>Sphagnum palustre</i> L.	Sphagnaceae	Long-lived shuttle	COSM	Sphapalu	13	13											
<i>Tetrastichium fontanum</i> (Mitt.) Cardot	Leucomiaceae	Perennial	IBER-MAC	Tetrfont	90	27	5	7		23	5	4	4		6	5	4
<i>Tetrastichium virens</i> (Cardot) S.P.Churchill	Leucomiaceae	Perennial	IBER-MAC	Tetrvire	13		5	1			1	4			2		
<i>Thamnobryum alopecurum</i> (Hedw.) Gangulee	Neckeraceae	Perennial	COSM	Thamalop	2	1	1								1		
<i>Thamnobryum maderense</i> (Kindb.) Hedenäs	Neckeraceae	Perennial	MAC	Thammade	2											2	
<i>Thamnobryum rudolphianum</i> Mastracci	Neckeraceae	Perennial	AZOR	Thamrudo	21	19				2							
<i>Thuidium tamariscinum</i> (Hedw.) Schimp.	Thuidiaceae	Perennial	COSM	Thuitama	13	7		3		1			1		1		
<i>Trichostomum brachydontium</i> Bruch	Pottiaceae	Perennial	COSM	Tricbrac	7	1	1	1	3		1						1

Appendix B

Table A2. Hill numbers for total species, mosses and liverworts in each of the twelve sampled caves.

Hill		ALL	ALG	BRA	ACH	MAD	MAL	TER	CHO	COE	NAT	BAL	BUR	PRI
S (q = 0)	Total	98	65	31	17	17	41	28	20	21	24	28	24	20
	Mosses	55	34	17	9	9	24	15	10	10	16	18	15	11
	Liverworts	43	31	14	8	8	17	13	10	11	8	10	9	9
exp H' (q = 1)	Total	50.46	37.70	21.05	10.72	13.44	19.40	20.22	12.22	16.33	17.22	20.89	17.44	14.55
	Mosses	27.48	20.26	10.56	5.61	7.68	11.47	10.53	7.13	7.28	11.87	13.33	10.66	7.91
	Liverworts	23.01	17.48	10.50	5.74	6.26	8.04	9.95	8.22	9.16	5.57	7.63	7.23	6.73
1/D (q = 2)	Total	35.10	28.86	16.19	7.32	11.56	13.33	16.49	8.29	13.84	13.52	16.73	13.33	11.94
	Mosses	18.57	16.08	7.52	3.99	6.92	7.27	8.63	5.50	5.96	9.69	10.33	8.27	6.48
	Liverworts	16.71	12.79	8.74	4.31	5.56	6.06	8.36	6.75	8.26	4.31	6.77	5.86	5.64
1/d (q = 3)	Total	29.81	24.93	13.61	5.80	10.48	11.15	14.60	6.55	12.36	11.50	14.28	11.20	10.74
	Mosses	15.53	14.23	6.07	3.30	6.49	5.90	7.76	4.65	5.29	8.56	8.72	7.11	5.86
	Liverworts	14.42	10.72	7.82	3.58	5.20	5.25	7.43	5.79	7.76	3.69	6.38	4.99	5.12

**Table A3.** Sampling completeness, observed and expected species for all bryophytes, liverworts and mosses in each of the twelve sampled caves.

	All			Liverworts			Mosses		
	SC (%)	Observed	Expected	SC (%)	Observed	Expected	SC (%)	Observed	Expected
ALG	97.36	65	67	97.24	31	32	97.47	34	35
BRA	90.1	31	34	98.22	13	13	82.77	18	22
ACH	79.88	17	21	84.55	8	9	76.66	9	12
MAD	89.84	17	19	92.88	7	8	87.55	10	11
MAL	91.61	41	45	90.03	17	19	92.95	24	26
TER	83.97	28	33	89.62	13	15	78.67	15	19
CHO	81.73	20	24	54.17	9	17	94.14	11	12
COE	77.83	21	27	82.33	11	13	74.8	10	13
NAT	81.35	24	30	91.39	8	9	76.49	16	21
BAL	85.84	28	33	88.92	10	11	84.6	18	21
BUR	75.48	24	32	74.64	9	12	76.31	15	20
PRI	75.6	20	26	74.86	9	12	76.33	11	14

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