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# The vulnerability paradox in Atlantic marine caves: A multiscale mechanistic explanation from wave exposure to cave gradients

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A B S T R A C T

High-diversity ecosystems are often presumed to be resilient. Yet, marine caves, along with other high-diversity systems, have proved highly sensitive to both climate change and anthropogenic stressors. This study seeks to resolve the underlying causes of this apparent paradox by investigating the functional resilience of marine caves ecosystems. We investigated nine Atlantic marine caves to identify key environmental drivers at landscape, local, and within-cave scales of sessile community structure and assess their functional resilience. Using hierarchical sampling (414 photoquadrats, 126 taxa), biological trait analysis (six traits), and statistical modelling (RLQ–Fourth Corner, GLMs, GAMMs), we assessed trait–environment relationships. Wave energy was the dominant driver among seascape and local-scale factors, explaining 34.5% of trait–environment associations, followed by depth range (7.7%). Four functional syndromes reflected major ecological trade-offs, such as autotrophs *vs.* active sponge feeders. Despite high regional taxonomic diversity (Shannon H' = 3.6) and functional richness (1.93), 57% of functional entities were represented by single taxa revealing low functional redundancy and thus low resilience potential. Functional vulnerability decreased and redundancy increased with spatial scale, with semi-dark zones being the most vulnerable cave sector (81%). Overall, wave exposure and depth shaped functional structure and resilience potential at a seascape scale in marine caves. The decoupling between taxonomic diversity and functional redundancy suggests that this vulnerability paradox may be a common pattern in high-diversity systems, as demonstrated in coral reefs and tropical forests, partially explaining their unexpected fragility under global change.

## 1. Introduction

Marine caves are unique "natural laboratories" for ecological and biogeographic research. Their pronounced environmental gradients, from well-lit entrances to dark inner sections, and strong spatial confinement create habitat mosaics that filter species and shape community structures (Bianchi and Morri, 1994; Bussotti et al., 2006). Considerable inter-cave variability in geomorphological characteristics further contributes to community distinctness, making these habitats ideal model systems for testing fundamental theories of species distribution and environmental influences on community assembly (Gerovasileiou et al., 2017).

Moreover, they have proved highly sensitive to environmental change and anthropogenic stressors, and their capacity to recover from disturbance has been proposed to be limited (Nepote et al., 2017; Montefalcone et al., 2018; 2023; Harmelin et al., 1985), which is

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particularly intriguing given that their high taxonomic diversity would suggest a high resilience potential. However, neither their resilience nor the reasons underlying this sensitivity are well understood.

From a mechanistic perspective, understanding how environmental processes shape communities and their functionality would provide crucial insight into this resilience; however, this requires moving beyond species lists toward functional-trait approaches (Bellwood et al., 2019; Stuart-Smith et al., 2013). Adopting a Biological Trait Analysis (BTA) perspective offers a mechanistic link between environmental gradients and the functional assembly of sessile communities (Mouillot et al., 2013; Violle et al., 2007). This approach focuses on performance attributes such as growth form, feeding type, and sociability, which determine how organisms cope with hydrodynamic stress, resource acquisition, and spatial competition (Gerovasileiou et al., 2017; Montefalcone et al., 2018, 2023). Variation in trait distributions reflects how organisms respond to local conditions, linking individual strategies to community structure and emergent processes, such as benthic-pelagic coupling (McGill et al., 2006; Violle et al., 2014). Such trait–environment perspective has been proposed as a route to predictive and comparative community ecology that integrates local gradients with biogeographic issues, with an emphasis on oceanic archipelagos such as the Canary Islands, where strong oceanographic contrasts may reorganise trait composition and function.

The ability of ecosystem functions to persist despite environmental changes or disturbances depends on two components: resistance (capacity to withstand disturbance) and resilience (capacity to recover from disturbance) (Holling, 1973; Mouillot et al., 2013). In this context, functional resilience emphasises the maintenance of ecosystem functions, even when species composition changes, and provides a more robust indicator of ecosystem health than taxonomic diversity alone (Bellwood et al., 2019; Mouillot et al., 2014). However, assessing functional resilience requires specific indicators to species loss. Functional vulnerability (the proportion of unique trait combinations represented by single species), functional redundancy (FRed; the number of species per unique trait combinations), and functional originality (FO; the uniqueness of species' functional roles) serve as complementary indicators of the potential for functional resilience (Biggs et al., 2020; Brandl et al., 2016; Gladstone-Gallagher et al., 2019; Mouillot et al., 2014), with high vulnerability, low redundancy, and high originality indicating a reduced capacity to maintain ecosystem functions under species loss.

However, traditional approaches based on single functions often overestimate functional resilience by assuming that species performing similar individual functions provide redundancy. Mouillot et al. (2014) demonstrated that this assumption is misleading because species with distinct combinations of traits can sustain multiple, non-substitutable roles within an ecosystem. Accordingly, the functional entity approach, which identifies unique combinations of traits, recognises that the loss of a species with a singular trait profile can have disproportionate effects even when its individual functions appear redundant. This framework therefore provides a more realistic assessment of an ecosystem's ability to withstand species loss by accounting for the multiple roles that species perform.

In marine caves, which are typically heterotrophic environments that are dependent on external energy sources, sessile suspension feeders play a pivotal role in the transfer of organic matter from the water column to the benthos (Fichez, 1990; Rastorgueff et al., 2015). Therefore, suspension feeders constitute an ideal model community for assessing the functionality of marine cave ecosystems, enabling the quantification of their vulnerability to anthropogenic and climate-related stressors.

Environmental drivers of caves are characterised by steep light gradients, complex water flow patterns, and variable nutrient availability (Bianchi and Morri, 1994; Harmelin et al., 1985; Pérès and Picard, 1964; Riedl, 1966). These factors drive zonation of communities along the cave axis, particularly among sessile species confined to specific environmental conditions. Although a general pattern of decreasing taxonomic diversity from the entrance to the interior is commonly observed, the trajectory of this decline may vary considerably among individual caves (Balduzzi et al., 1989; Bell, 2002; Gerovasileiou et al., 2017; Harmelin, 1985a; Martí et al., 2004), suggesting interacting processes. More broadly, each cave possesses a unique geomorphological signature that directly affects its internal environmental patterns and, therefore, the structure of communities. Although geomorphological influences on taxonomic structure are well documented (e.g., Pouliquen, 1972; Gerovasileiou et al., 2017; Digenis et al., 2022), their effects on functional structure are not well explained. Moreover, other physical drivers, such as wave exposure, are surprisingly understudied despite their well-known impacts on other marine ecosystems (Denny, 1985; Lange et al., 2021).

Despite their ecological importance, knowledge of marine cave ecosystems is geographically biased. Most studies have been conducted in the Mediterranean Sea, where pioneering studies began in the late 1950s (e.g., Pérès and Picard, 1964; Riedl, 1966). However, regional species distribution, community structure, and environmental drivers remain poorly understood in most parts of the world, particularly in oceanic archipelagos (Gerovasileiou et al., 2016; Gerovasileiou and Bianchi, 2021). The Canary Islands archipelago, located in the subtropical northeast Atlantic, represents an exceptional natural laboratory for testing environmental effects on marine cave communities. More than 200 marine caves have been catalogued to date within the Archipelago (Hernández-González et al., unpublished results) and the region exhibits pronounced orientation-driven gradients in wave exposure and to storm swells, with the northern and western coasts receiving higher energy (mean annual wave power = 18–24 kW/m) than the eastern and southern coasts (mean annual wave power = 12 kW/m) (Chiri et al., 2013). Within this context, this study seeks to resolve an apparent paradox: how can highly diverse marine ecosystems such as marine caves present alarming fragility? The guiding question is: what ecological mechanisms underlie this discrepancy? Our objectives were twofold: (a) to evaluate the functional resilience potential and conservation priorities of marine caves through assessments of vulnerability, redundancy, and originality; (b) to identify how environmental filtering shapes functional resilience and community assembly across spatial scales (seascape, local, within-cave). This study also provides the first comprehensive taxonomic and functional characterisation of marine cave ecosystems in the Canary Islands, establishing a baseline for future monitoring and conservation efforts.

## 2. Methodology

### 2.1. Study area and sampling design

Nine marine caves across four Canary Islands (El Hierro, La Palma, Tenerife, and Gran Canaria), were selected to represent variation in wave exposure, depth range ($<10$ m or $>10$ m), submersion level (submerged or semi-submerged caves), and morphology (blind-ended or tunnel-shaped caves) (Fig. 1; Table 1). Wave exposure was categorised using a regional classification established by Chiri et al. (2013): with north and west coast caves assigned strong exposure ($\geq$18 kW/m) and east and south coast caves assigned reduced exposure ($\leq$12 kW/m). Despite increased wind energy potential over recent decades, wave energy has not shown a comparable increase, indicating a decoupling of wind and wave trends (Ulazia et al., 2023). This pattern reflects the dominance of remote North Atlantic swell around the Canary Islands, resulting in a stable spatial distribution of wave exposure, with persistent high exposure along the north and west coasts and sheltered conditions along the east and south coasts due to island shadowing and limited fetch (Christie et al., 2023; Semedo, 2018). As a result, this categorical distinction is independent of temporal changes in local wind intensity, ensuring the validity of our classification regardless of climate change trends. Moreover, all caves were located in Special Areas of

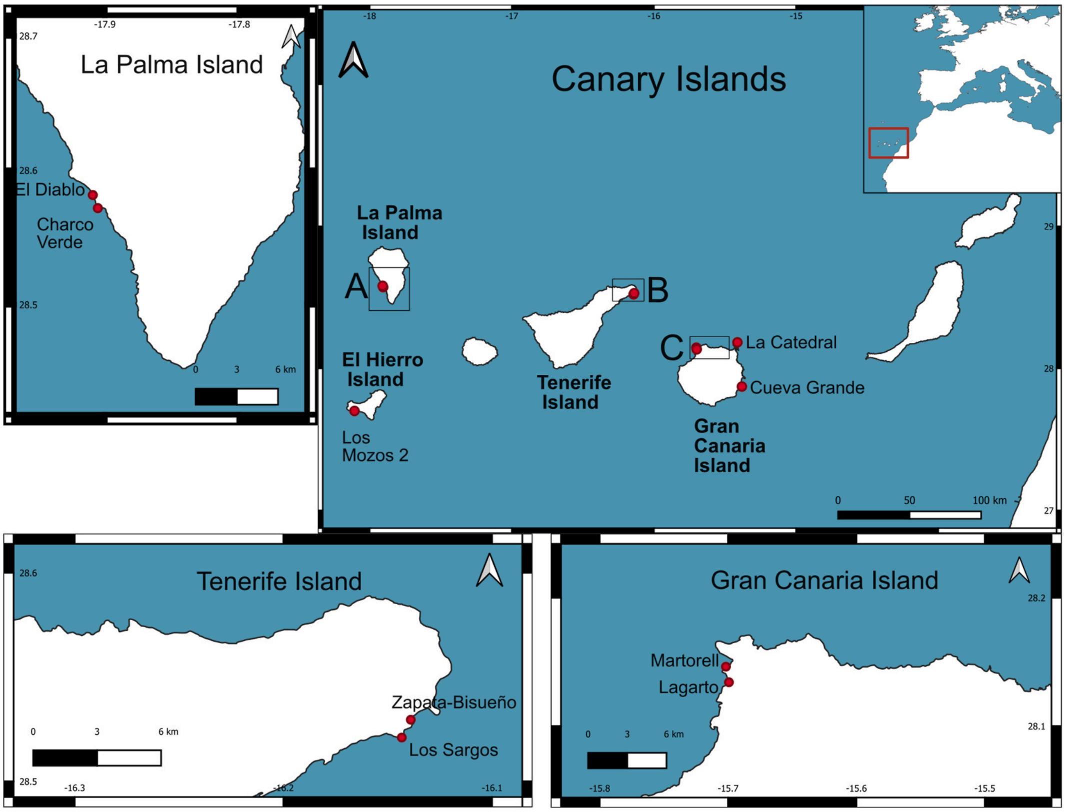


**Fig. 1.** Marine caves surveyed on The Canary Islands. (A) Close-up of two caves in (A) La Palma, (B) Tenerife and (3) Gran Canaria islands.

**Table 1**
Characteristics of surveyed marine caves. Fields include cave name, island, cave type (submerged or semi-submerged), cave morphology (blind-ended or tunnel-shaped), cave depth range, storm-wave-generated energy, and coastal orientation.

| Cave name | Island | Type | Morphology | Depth range | Wave exposure | Coastal orientation |
|---|---|---|---|---|---|---|
| Los Mozos 2 | El Hierro | Semi-submerged | Blind-ended | <10 m | Reduced | South |
| Charco Verde | La Palma | Submerged | Tunnel-shaped | >10 m | Strong | West |
| Cueva del Diablo | La Palma | Semi-submerged | Blind-ended | <10 m | Strong | West |
| Los Sargos | Tenerife | Submerged | Blind-ended | <10 m | Reduced | South-east |
| Zapata–Bisueño | Tenerife | Semi-submerged | Tunnel-shaped | <10 m | Reduced | South-east |
| Martorell | Gran Canaria | Submerged | Tunnel-shaped | <10 m | Strong | North-west |
| Lagarto | Gran Canaria | Semi-submerged | Blind-ended | <10 m | Strong | North-west |
| La Catedral | Gran Canaria | Submerged | Tunnel-shaped | >10 m | Strong | North |
| Cueva Grande | Gran Canaria | Submerged | Blind-ended | >10 m | Reduced | South-east |

Conservation within the European Natura 2000 network and were investigated for the first time.

Planes of cave entrances were predominantly oriented parallel to the coastline, meaning that coastal orientation served as a proxy for cave entrance orientation with respect to dominant wave direction. While this approach captures the main gradient in wave exposure across the archipelago, we acknowledge that fine-scale variation in cave orientation, aperture size, and connectivity with the open sea may influence local hydrodynamic conditions within individual caves. These factors were not explicitly quantified in this study and represent potential sources of unexplained variability. In addition to wave exposure, orientation may also affect light levels within caves (Ballesteros, 2006; Gerovasileiou and Bianchi, 2021). For example, rocky surfaces or cave entrances facing north or northwest generally receive less light than those facing south or southeast. Of course, this is a rather general statement and varies with latitude.

For the wave exposure analysis, caves with entrance depths >5 m were excluded, because wave orbital velocities attenuate significantly beyond this depth, limiting wave influence on benthic communities (Denny, 2006; Wiberg and Sherwood, 2008). Similarly, to isolate the effect of depth range, semi-submerged caves were excluded to avoid confounding effects of strong hydrodynamics, and La Catedral Cave (Fig. 1) was removed to achieve a balanced design.

Surveys were conducted over two years, 2022 and 2023. However, the Largato and La Catedral caves (both in Gran Canaria) were not resampled in 2023 due to logistical constraints. The sampling followed a hierarchical design: stations nested within caves, caves nested within islands, and islands nested within the archipelago. Each cave included to 6-9 fixed stations placed along standard sections (for tunnel-shaped caves: entrance 1, medial, and entrance 2 sections; and for blind-ended caves: entrance, medial, and distal sections) (Fig. S1). In the submerged caves, the stations were positioned on the left, right, and ceiling walls, whereas the semi-submerged caves lacked ceiling stations All stations were permanently marked by drilling the rock and subsequently screwing 3D-printed durable plastic markers into it, as part of the long-term monitoring design (Fig. S2). Each station was assigned to an ecozone (entrance, semi-dark, or dark), based on the sessile taxonomic composition *sensu* Pérès and Picard (1964). This approach is widely used in marine cave studies to account for environmental variation in the absence of direct measurements (Digenis et al., 2022, 2025) and provides a biologically meaningful framework for understanding environmental filtering effects. At each station, four standardised photoquadrats (25 × 25 cm) were captured as replicates at a distance of 25 cm from the centre of the permanent marker in the four cardinal directions to reduce potential spatial autocorrelation.

All surveyed caves were formed in volcanic rock, reflecting the geological homogeneity of the Canary Islands archipelago. While surface geological maps exist for the islands, detailed submarine geological surveys of individual caves are lacking, and the specific rock types (e.g., basalt, phonolite, trachyte) could not be determined for each cave. Although minor differences in rock composition may influence substrate texture and colonisation patterns, the overall volcanic nature of all caves provides a relatively homogeneous geological context compared to regions with mixed lithologies (e.g., Mediterranean caves formed in limestone, sandstone, or volcanic substrates).

### 2.2. Data collection and processing

Benthic communities were surveyed using standardised photoquadrats on vertical, subvertical, and ceiling surfaces (Bohnsack, 1979). Sessile taxa were identified to the lowest taxonomic level and quantified based on percentage of substrate coverage. The abiotic categories used as indicators of ecosystem processes included bare rock, non-living biogenic substrate (clearly dead shelled animals), and a combined biotic turf–sediment category (Montefalcone et al., 2023). In addition, 47 biological samples of the taxa observed in the photoquadrats were collected and analysed to aid in identifications. Details regarding sample conservation, processing, and analyses, as well as the bibliography used, are provided in section *Detailed Biological Sampling Analyses* of the Supplementary Material. The sessile cover was quantified using the PhotoQuad software (Trygonis and Sini, 2012) by overlaying 100 stratified points per quadrat. In total, 414 photoquadrats were annotated across the nine caves over the two years of sampling.

### 2.3. Statistical analyses

We examined how environmental processes shape community structure by distinguishing between seascape-scale factors (wave exposure and depth range) and local geomorphological factors (submersion level, and cave morphology), as well as ecozones representing within-cave conditions. These sets of variables were treated as environmental predictors. The analytical framework is presented in Fig. S3.

**Taxonomic and Functional Diversity Indices.** We calculated the percent cover of 11 major taxonomic groups and computed species richness (S), Shannon diversity (H′), and Pielou's evenness (J′) at the station level and aggregated accordingly using the "vegan" package (Oksanen et al., 2025).

Trait selection was based on their ability to describe the response of sessile communities to environmental conditions (response traits). Specifically, six species traits were selected, ecosystem engineering, maximum coverage, sociability, and stratification, as described by Gerovasileiou et al. (2017), and feeding type and growth form as described by Montefalcone et al. (2023). Trait modalities were obtained from Gerovasileiou et al. (2017) when available; otherwise, we used functional trait databases such as BIOTIC (Biological Traits Information Catalogue) (Marine Life Information Network MarLIN, 2006). For taxa not identified at the species level, trait modalities for growth form, maximum coverage in photoquadrats, and stratification were derived from the data, whereas information for the remaining traits was obtained from higher taxonomic levels.

For each station-year community, we computed functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv) following Villéger et al. (2008); functional dispersion (FDis) following Laliberte and Legendre (2010); Rao's quadratic entropy (RaoQ) following Rao (1982) via the "FD" package (Laliberte and Legendre, 2010; Laliberté et al., 2014). Functional originality (FOri) was calculated following Brandl et al. (2016) using the "mFD" package (Villéger et al., 2022). Following Mouillot et al. (2014), we quantified functional redundancy (FRed), functional over-redundancy (FOR), and functional vulnerability (FVul) using custom functions, based on functional entities (FEs), which represent unique combinations of trait modalities. All diversity indices were calculated at the station level and then aggregated to the required level of analysis (e.g., cave, cave type) for each year.

A multidimensional functional space was constructed using principal coordinate analysis (PCoA) of pairwise distances among taxa, calculated using Gower's coefficient (Gower, 1971) and PCoA with Cailliez correction applied to remove negative eigenvalues (Cailliez, 1983), retaining m = 2 axes (Mouillot et al., 2011; Villéger et al., 2008). This functional space was fixed once ("locked basis") and reused in all subsequent models to prevent numerical artifacts.

**Functional Space Plots for Temporal Dynamics.** To gain a deeper understanding of the temporal dynamics within each ecozone, we performed a functional space composite PCoA on raw data for each year × station aggregated to the ecozone level, including only stations resampled in 2023, to ensure temporal consistency (Villéger et al., 2008).

**Modelling Environmental Effects.** Generalized additive mixed models (GAMMs) were used to assess diversity patterns across environmental factors using "mgcv" package (Wood, 2004, 2011, 2016). The distribution families implemented—negative binomial, Gaussian, and Beta—were selected individually for each diversity index according to its statistical properties (see Table S2 for details). Depth was modelled using a smooth function (k = 5) to balance model complexity and avoid overfitting, with random intercepts for islands, caves, and stations. The fixed effects included year and either ecological zone or other environmental factors, and significance was assessed using likelihood ratio tests. The detailed methodology is provided in section SM1 of the Supplementary Material.

**Controlling for Cave-Specific Characteristics.** The hierarchical structure of our GAMMs explicitly accounts for cave-specific characteristics, including morphological variability (e.g., volume, entrance size, internal complexity), and random intercepts for island, cave (nested within island), and station (nested within cave). This approach partitions the variance attributable to differences among caves from the variance explained by the fixed effects (ecozone, wave exposure, depth range). Consequently, the reported effects of seascape-scale drivers and within-cave gradients are adjusted for morphological differences among caves, ensuring that our inferences are not confounded by unmeasured cave-specific attributes.

**RLQ and Fourth-Corner Analysis.** A two-step trait-based approach was used in this study. First, RLQ analysis (Dolédec et al., 1996) was used to identify significant environmental variables shaping community functional structure. Then a fourth-corner analysis (Dray and Legendre, 2008; Dufrene and Legendre, 1997) was tested for specific statistical associations between individual environmental variables and trait modalities (e.g., whether particular growth forms are significantly associated with high wave exposure). Both analyses were implemented with "ade4" (Dray and Dufour, 2007). Together, these complementary approaches identified the most relevant environmental drivers and the specific traits they select.

**Functional syndrome identification.** Functional syndromes, defined as coordinated combinations of traits representing fundamental ecological trade-offs, were identified using hierarchical clustering of trait loadings from RLQ axes, cutting the dendrogram to obtain clusters representing distinct trait combinations using the Ward's method (Ward, 1963).

**Multivariate Community Analysis:** To complement trait-based analyses with species-level inference, we applied the manyglm function from the "mvabund" package (Wang et al., 2012), modelling taxon-specific abundances using a negative binomial distribution because of overdispersion. The model included ecozone and local environmental predictors with year as a fixed effect. Predictor significance was assessed using the Wald statistics and 999 stratified permutations. We applied a shrinkage estimator to stabilise the species correlation matrix. Due to numerical instability in the Generalized Linear Models (GLMs) from manyglm, caused by quasi-complete separation in the sparse dataset, the coefficient magnitudes (β) and associated p-values were unreliable. Therefore, we focused on the sign and approximate range of the coefficients as stable indicators of trend direction, without interpreting their exact effect sizes. The wave exposure factor was adjusted independently of the other local environmental variables in other model by excluding caves deeper than 5 m to avoid bias from caves unaffected by wave action. The detailed methodology for RLQ, fourth-corner, functional syndromes and multivariate community analysis are provided in section SM2 of the Supplementary Material.

**Triangulation Approach:** To improve inference and identify the taxa most influenced by trait–environment relationships, we combined the GLM models' beta coefficients ranks, which indicate the taxa most affected by each environmental predictor, with fourth-corner analyses, which identify the trait modalities most influenced by those same predictors. Coefficient signs and ranks were used to infer taxon responses, which were cross-referenced with statistically significant trait–environment data to identify the environmentally responsive taxa.

**Indicator Taxa.** Indicator taxa for each ecozone were identified using the IndVal.g index (De Cáceres et al., 2012; Dufrene and Legendre, 1997) calculated with the "indicspecies" package (De Cáceres and Legendre, 2009), which selects taxa with high specificity and fidelity to particular environmental conditions.

All analyses were performed using (R core Team, 2025).

## 3. Results

### 3.1. Diversity patterns

#### 3.1.1. Regional characterisation

Across the nine studied caves, 126 sessile taxa (distributed across 11 major taxonomic groups) were identified, with 69 taxa identified at the genus or species level (Table S3). The regional species pool exhibited high taxonomic diversity (Shannon H' = 3.6) and moderately high evenness (Pielou's J' = 0.75; indices by year in Table S4). Porifera dominated the assemblages, with 60 taxa and 38.2 ± 3.2% (mean ± SD) relative cover, followed by Algae (24.6 ± 4.6%), Bryozoa (18 ± 1.8%) and Polychaeta (9.7 ± 0.9%). The most prevalent taxa across all caves were crustose coralline algae, Serpulidae polychaetes, and the sponge *Merlia normani*, with values of 8.2 ± 16.4%, 7.8 ± 7.7%, and 7 ± 11.5%, respectively. Nevertheless, 82% of the taxa showed a prevalence of less than 1%. The annual diversity indices for the region are listed in Table 2.

#### 3.1.2. Diversity patterns along cave axis

Marine cave communities exhibited a clear taxonomic diversity gradient along the entrance-dark zone gradient (Fig. 2B). Although raw data displayed high variability and overlap between the entrance and semi-dark zones in boxplots, GAMM analysis revealed higher species richness (S) at the entrance (18 ± 1) (emmeans + SD) and semi-dark zones (17 ± 1) than in the dark zone (11 ± 1) ($p < 0.001$), indicating a 39% species loss toward the interior of the caves. Shannon diversity (H′) followed the same pattern (2.07 ± 0.14–2.1 ± 0.14 *vs.* 1.65 ± 0.16), whereas evenness (J') remained stable (0.74 ± 0.03–0.75 ± 0.03–0.72 ± 0.04).

Regarding functional diversity indices (Fig. 2D–L), richness (FRic) mirrored the taxonomic gradient, with entrance and semi-dark zones occupying a markedly larger functional space than dark zones with a 30% reduction. In contrast, other indices showed divergent responses. Dispersion (FDis) remained relatively stable across ecozones, whereas redundancy (FRed) increased toward dark zones and was lowest in the semi-dark zones. Originality (FOri) was highest in the entrances and semi-dark zones but lowest in the dark zones. The evenness (FEve) was relatively stable. Rao's quadratic entropy (RaoQ) exhibited a hump-shaped trend, peaking in semi-dark zones and declining in dark zones.

#### 3.1.3. Temporal dynamics

Temporal analysis revealed pronounced interannual variations in functional indices, superimposed on the spatial patterns introduced across ecozones. FRic peaked in the semi-dark zone in 2022 but shifted to the entrance in 2023 (Fig. 3). The aggregated raw data showed that the entrance and dark zones gained functional richness (+2.2% and +11.6%, respectively), whereas evenness declined (−1.6% and −0.5%, respectively). Semi-dark zones lost both richness (−6%) and dispersion (−5.8%), but gained evenness (+10.8%).

The PCoA topology reinforced this variability; the functional spatial structure varied over time, as reflected by the interannual variability of the raw functional index values (Fig. 3). Minimum spanning trees (MST) showed longer branch lengths in dark zones, indicating functional gaps, reduced evenness, and dominance by peripheral specialists defined by rare functions. In GAMMs, all taxonomic or functional diversity indices remained stable between years ($p > 0.05$) at the overall cave scale despite temporal shifts at the ecozone scale. Furthermore, convergence in the functional space toward the inner sectors is shown in Fig. 3, with overlapping entrance and semi-dark zones, whereas dark zones occupy a nested reduced trait space, reflecting strong filtering.

### 3.2. Functional resilience potential assessment

The analyses of functional vulnerability, redundancy, and originality revealed patterns related to functional resilience. Despite the high taxonomic diversity, the functional structure of the communities revealed a significant vulnerability to species loss. At the regional scale, 57% of the 53 unique functional entities were sustained by a single taxon. Conversely, 43% exhibited over-redundancy, while an average of 2.3 ± 2.8 taxa (emmeans ± SD) were grouped into each functional entity, representing identical combinations of traits. At the cave scale, the average vulnerability was higher than that at the regional scale (68 ± 0.07%), and over-redundancy was lower (21 ± 0.04%). At the ecozone scale, the average vulnerability reached a maximum of 74 ± 0.07%, whereas over-redundancy was minimal (17 ± 0.02%). Across the ecozones, the semi-dark zone was the most vulnerable (81 ± 0.05%) and taxa identified as highly original (Table S5) were predominantly concentrated in the entrances and semi-dark zones. Conversely, the dark zone was the least vulnerable, and exhibited the highest redundancy (Fig. 2; GAMM results in Table S6). Despite having the highest number of functions and being the less stressed sector, 81 ± 0.05% of the FEs in the semi-dark zone were performed by a single taxon, revealing low redundancy, with the most functionally diverse sector being the most vulnerable.

**Table 2**
Taxonomic and functional diversity indices were aggregated at the regional level in 2022 and 2023, respectively. The abundances from all stations within a given year were pooled to create a regional species matrix before calculating each index. Functional indices were based on a consistent trait space to ensure comparability between years.

| Year | S | H' | J' | FRic | FDis | FDiv | FEve | RaoQ | FRed | FOri | FVul | FOR |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2022 | 113 | 3.57 | 0.76 | 1.84 | 1.62 | 0.88 | 0.30 | 2.74 | 0.02 | 2.31 | 0.59 | 0.36 |
| 2023 | 106 | 3.51 | 0.75 | 1.76 | 1.59 | 0.89 | 0.33 | 2.64 | 0.02 | 2.16 | 0.63 | 0.35 |

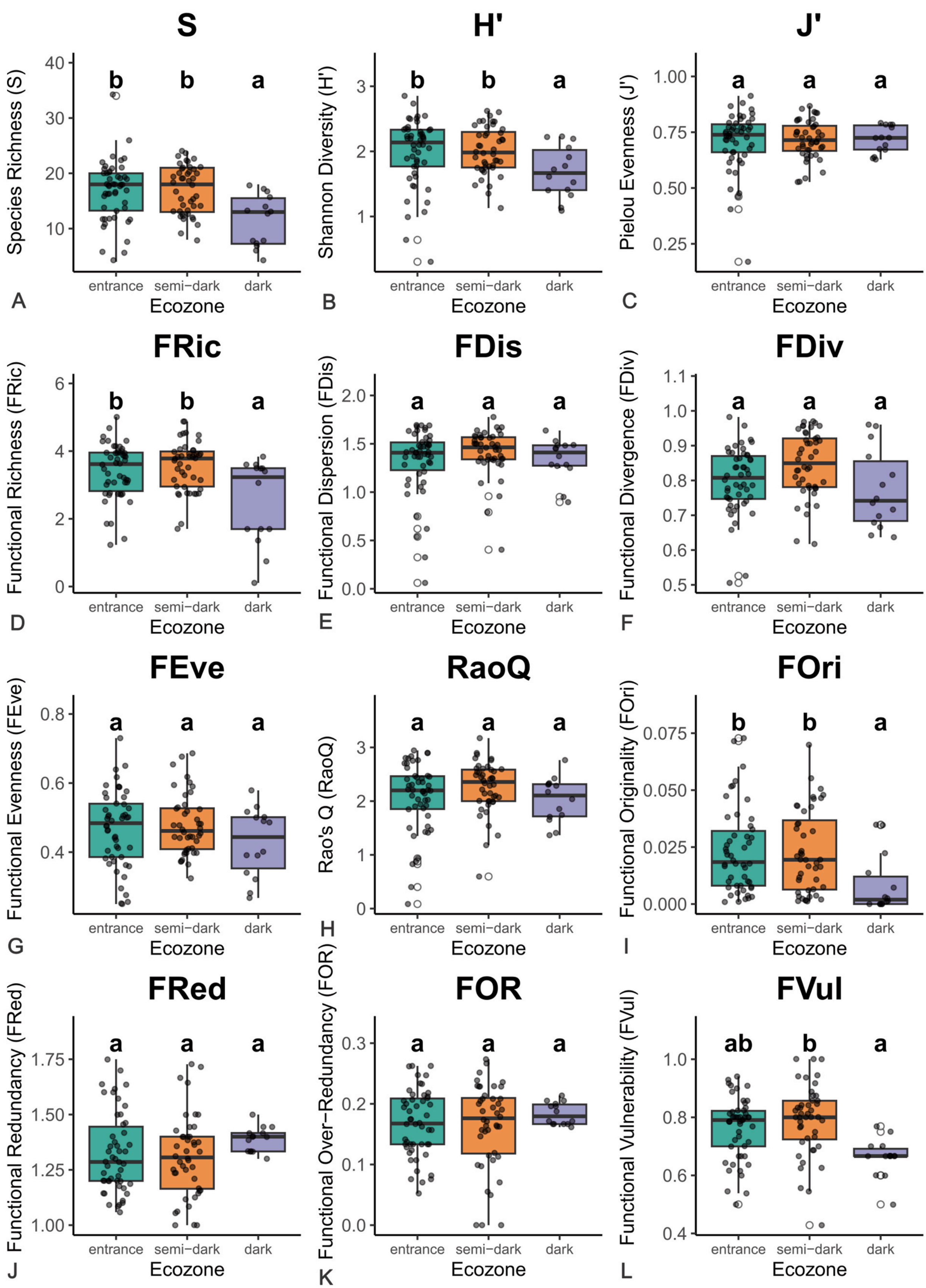


**Fig. 2.** Effects of environmental filtering on taxonomic and functional diversity indices along the ecozone gradient. **A** Taxa richness (S). **B** Shannon diversity (H′). **C** Pielou evenness (J′). **D** Functional richness (FRic). **E** Functional dispersion (FDis). **F** Functional divergence (FDiv). **G** Functional evenness (FEve). **H** Rao quadratic entropy (RaoQ). **I** Functional originality (FOri). **J** Functional redundancy (FRed). **K** Functional over-redundancy (FOR). **L** Functional vulnerability (FVul). Points represented in the boxplots are raw data, whereas different letters indicate statistical differences ($p < 0.05$) from GAMM analyses.

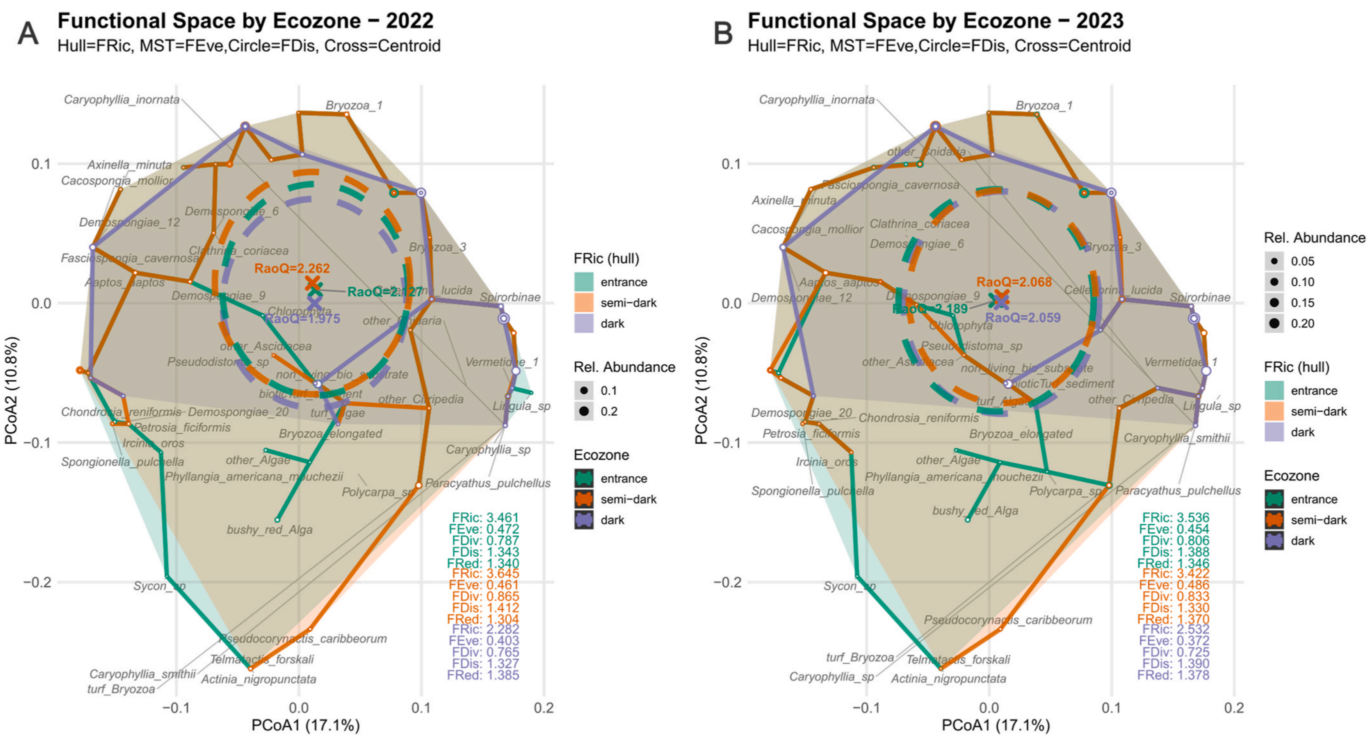


**Fig. 3.** Principal Coordinate Analysis (PCoA) of functional space occupation for **A**: 2022 and **B**: 2023 for each ecozone. The axes represent the first two functional axes (PCoA1 and PCoA2), with their explained variance shown in parentheses. Grey labels indicate the position of each species in the total functional space. Colours distinguish the three ecozones: entrance (green), semi-dark (orange), and dark (purple). Within each ecozone plot, circles represent species, with size proportional to their relative abundance. The coloured polygons (hulls) represent the functional richness (FRic); the crosses (+) show the weighted centroid; the dashed circles represent functional dispersion (FDis); and the solid lines connecting species (Minimum Spanning Tree, MST) represent functional evenness (FEve). Numerical values for FRic, FEve, functional divergence (FDiv), FDis, and functional redundancy (FRed) are provided in the lower right legend for each ecozone. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

### 3.3. Effects of environmental drivers

#### 3.3.1. Effects on traits

The influence of environmental factors on community structure was quantified by assessing trait–environment associations, which exhibited clear hierarchical importance in structuring functional trait composition (Fig. 5). RLQ analysis showed that wave exposure emerged as the single most important environmental driver of functional composition, except

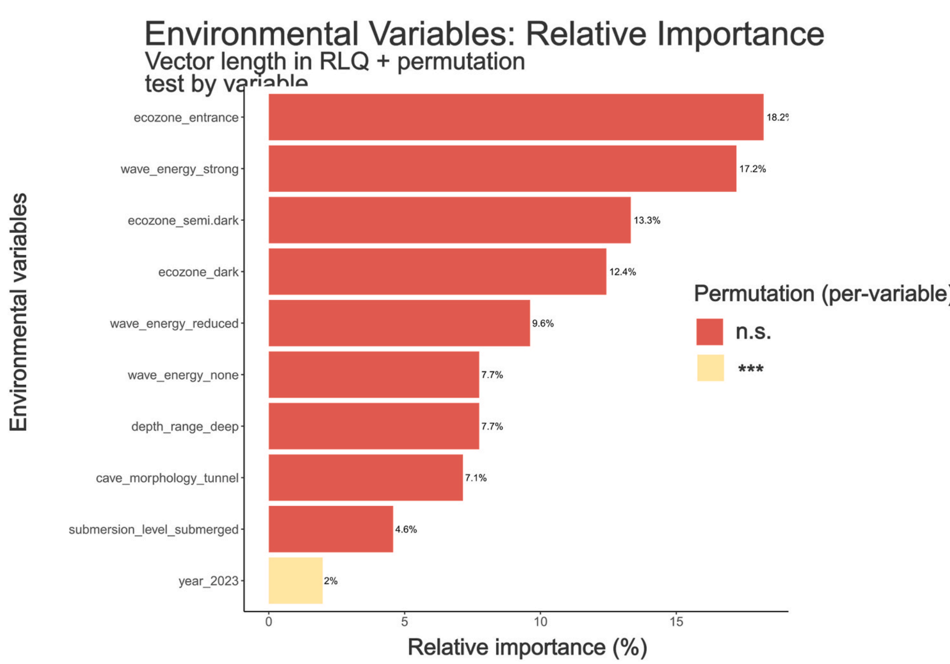


**Fig. 4.** Relative importance of environmental predictors from RLQ analysis. The bars in red indicate that the environmental process statistically affected the community trait structure. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

for ecozone, explaining 34.5% of trait variation, nearly twice the explanatory power of any other factor (Fig. 4). Depth range was the second most important seascape or local factor explaining 7.7% of the variation. Cave morphology accounted for 7.1% and submersion level had the weakest influence (4.6%).

Seascape and local environmental variables dominated, explaining 53.9% of the trait–environment associations. In contrast, the combined ecozone predictors (within-cave scale) accounted for 43.9% of the trait–environment associations. The year predictor did not differ ($p = 0.08$), explaining only 2% of total inertia.

We used fourth-corner analysis to identify specific trait–environment associations (Fig. 5). Under wave exposure, we detected the highest number of significant associations between environmental conditions and functional trait modalities. High-energy conditions favoured mechanical-resistance strategies (e.g., binder engineers, $r = 0.18$, $p = 0.01$) and traits with high energetic demands, such active sponge ($r = 0.21$, $p = 0.006$), and colonial or modular sociability ($r = 0.15$, $p = 0.04$). In contrast, caves with low wave exposure were positively associated with constructor-type ecosystem engineering ($r = 0.16$, $p = 0.002$), active lophophore feeding types ($r = 0.12$, $p = 0.04$), and hemispherical growth forms ($r = 0.13$, $p = 0.04$).

Additionally, trailing (reptant) growth forms showed a positive correlation with strong wave exposure ($r = 0.19$, $p = 0.02$) and a negative correlation with submerged caves ($r = -0.15$, $p = 0.04$), indicating an affinity for highly hydrodynamic environments. Deep caves are associated with maximum cover per quadrat of 3–10% and are negatively associated with the highest cover values (>30%).

Regarding cave morphology, a notable discrepancy emerged between the global significance detected by the RLQ analysis and the absence of associations with specific traits. Although cave morphology exerted a clear global influence on functional composition (RLQ permutation test, $p < 0.001$), it was not linked to individual trait modalities. This suggests that morphological effects operate through diffuse filtering mechanisms rather than through strong selection for particular trait combinations.

### 3.3.2. *Effects on diversity*

Local environmental factors had stronger effects on functional diversity (Fig. 6) than on taxonomic diversity (Fig. S4). When considering all cave sections, neither seascape nor local environmental factors influenced taxonomic diversity, except for depth range, with deep caves exhibiting higher species richness (S: 19 ± 4.3 *vs.* 15 ± 4.72 taxa) (emmeans ± SD) and Shannon diversity (H'; 2.32 ± 0.27 *vs.* 1.82 ± 0.46). Depth also exerted a strong positive effect on functional diversity. Deeper caves (≥10 m) showed higher functional richness (3.65 ± 0.61 *vs.* 3.22 ± 0.78), dispersion (1.48 ± 0.13 *vs.* 1.22 ± 0.34), and Rao's quadratic entropy (2.40 ± 0.29 *vs.* 1.83 ± 0.6) than shallower caves. This pattern indicated unexpectedly greater diversity in deeper, more stable, and oligotrophic systems.

Strong wave exposure increased originality (0.02 ± 0.02 *vs.* 0.007 ± 0.02) and vulnerability (0.87 ± 0.08 *vs.* 0.65 ± 0.12), while reducing redundancy (1.19 ± 0.15 *vs.* 1.43 ± 0.17) and dispersion (1.18 ± 0.41 *vs.* 1.4 ± 0.19). Cave morphology effects were subtle, with tunnel-shaped caves supporting slightly higher functional richness (3.46 ± 0.75 *vs.* 3.34 ± 0.99; $p = 0.57$) and redundancy (1.36 ± 0.17 *vs.* 1.31 ± 0.17; $p = 0.42$) than blind-ended caves. Regarding the submersion level, functional richness was considerably higher in semi-submerged caves than in submerged ones (3.7 ± 0.78 *vs.* 3.14 ± 0.97), where higher disturbance and instability prevailed. However, submersion levels did not affect taxonomic diversity. Conversely, originality (0.012 ± 0.01 *vs.* 0.025 0.02) and evenness (0.45 ± 0.1 *vs.* 0.49 ± 0.1) were lower. All taxonomic indices remained stable between years ($p > 0.05$) for all GAMMs.

### 3.3.3. *Functional syndromes and ecological trade-offs*

Hierarchical clustering of functional traits, based on RLQ co-inertia analysis, identified four functional syndromes: coordinated combinations of traits representing fundamental ecological trade-offs (Lavorel and Garnier, 2002; Raffard et al., 2017), each of which represented distinct trait combinations associated with specific environmental conditions (numbers follow cluster groups in Fig. S5).

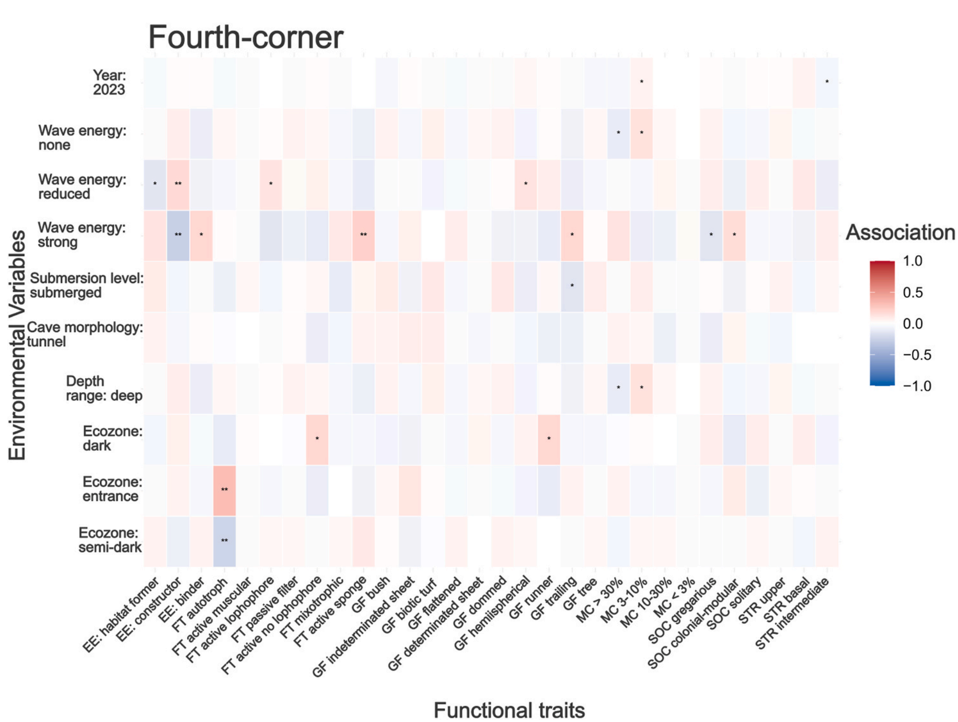


**Fig. 5.** Fourth-corner analysis identifying specific associations between trait modalities and environmental variables. Red indicates positive associations, blue indicates negative associations, and white indicates no association, with colour intensity representing the strength of the relationship. EE: ecosystem engineers; FT: feeding types; GF: growth forms; MC: maximum coverage; SOC: sociability; STR: stratification. P-values: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

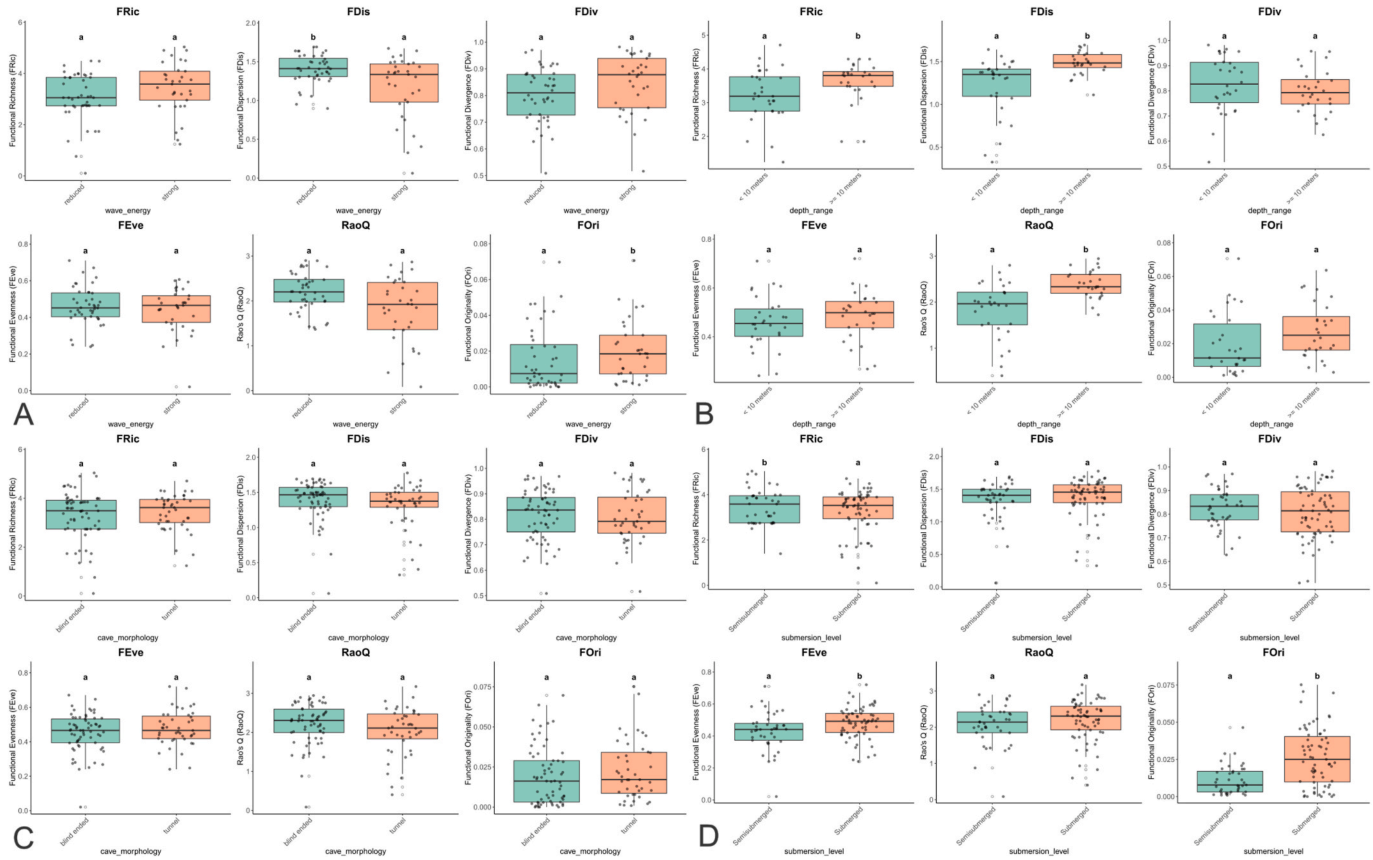


**Fig. 6.** Local environmental processes driving functional diversity patterns through distinct filtering mechanisms. **A** Effects of wave energy on functional indices, reduced vs. strong energy. **B** Effects of depth range, shallow caves (average depth <10 m) vs. deep caves (>10 m). **C** Morphological confinement effects: blind-ended caves vs. tunnel-shaped caves. Maximum entropy (Rao's Q), and originality. **D** Effects of submersion factor submerged vs. semi-submerged caves. Functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv), functional dispersion (FDis), Rao's quadratic entropy (RaoQ), and functional originality (FOri). Box plots show medians, quartiles, and outliers. Different letters indicate statistically significant differences according to GAMM ($p < 0.05$).

Syndrome 4: Photophilic Autotrophic Syndrome. Defined solely by autotrophy, this syndrome occupied an extreme position in functional space occupancy and was restricted to entrance zones ($r = 0.32$, $p < 0.001$), reflecting full dependence on light.

Syndrome 3: Broad-intermediate Syndrome. With the highest trait diversity (14), this syndrome was distributed across all ecozones and represented the functional core of the marine cave communities, showing the broadest environmental tolerance.

Syndrome 1: Encrusting Sciaphilic Syndrome. Associated with semi-dark zones, this syndrome includes traits such as other taxa binding, habitat-forming roles, intermediate stratification, flattened, trailing or indeterminate sheet growth forms, and mixotrophic or active sponge-feeding adaptations to consistent nutrient supply in twilight zones.

Syndrome 2: Dark Habitat Specialist Syndrome. Comprising constructor engineering, runner growth forms, active non-lophophore feeding, and gregarious organisation, this syndrome is restricted to dark zones characterised by the absence of light and low trophic input.

Together, these syndromes demonstrate that functional structure is not random, but rather a direct consequence of fundamental ecological trade-offs along the axes of energy acquisition (autotrophy *vs.* active filter feeder with no lophophore), ecosystem engineering strategies (constructor *vs.* habitat former), and generalist *vs.* specialist strategies.

### 3.3.4. *Indicator Taxa and taxa-environment associations*

Indicator species analysis identified taxa with strong fidelity to specific ecozones (see Table S7). Taxa-environment associations derived from the triangulation method is presented in SM3 and Table S8 in the Supplementary Material. Representative examples of sessile communities are showed in Fig. 7.

## 4. Discussion

### 4.1. *Novel environmental processes: wave exposure and depth range effects*

Our results highlighted the importance of seascape-scale environmental factors, which have been largely overlooked in marine cave studies. Wave exposure was the dominant driver among seascape and local-scale factors. This underscores the ecological importance of wave-driven processes (hydrodynamic stress and nutrient supply) for structuring these communities. Although wave exposure has received little attention in this context, our results align with the broader literature that recognises hydrodynamics as a primary driver across marine ecosystems (Denny, 1985; Lange et al., 2021). This finding elevates hydrodynamics from a local modifying factor to a primary seascape-scale process that shapes the functional biogeography of these species-rich ecosystems, at least in oceanic archipelagos such as the Canary Islands.

Wave exposure operates through two complementary mechanisms. First, it imposes intense physical stress, selecting specific morphological and life history traits. High-energy orientations promote active sponge feeding with binder engineers, modular sociability, and trailing forms, whereas low-energy systems are dominated by constructor ecosystem engineers who create calcium carbonate structures. In high-energy caves, binder engineers with encrusting morphologies are favoured because their low-profile growth forms and increased surface-area-to-volume ratios enhance resistance to mechanical disturbance and

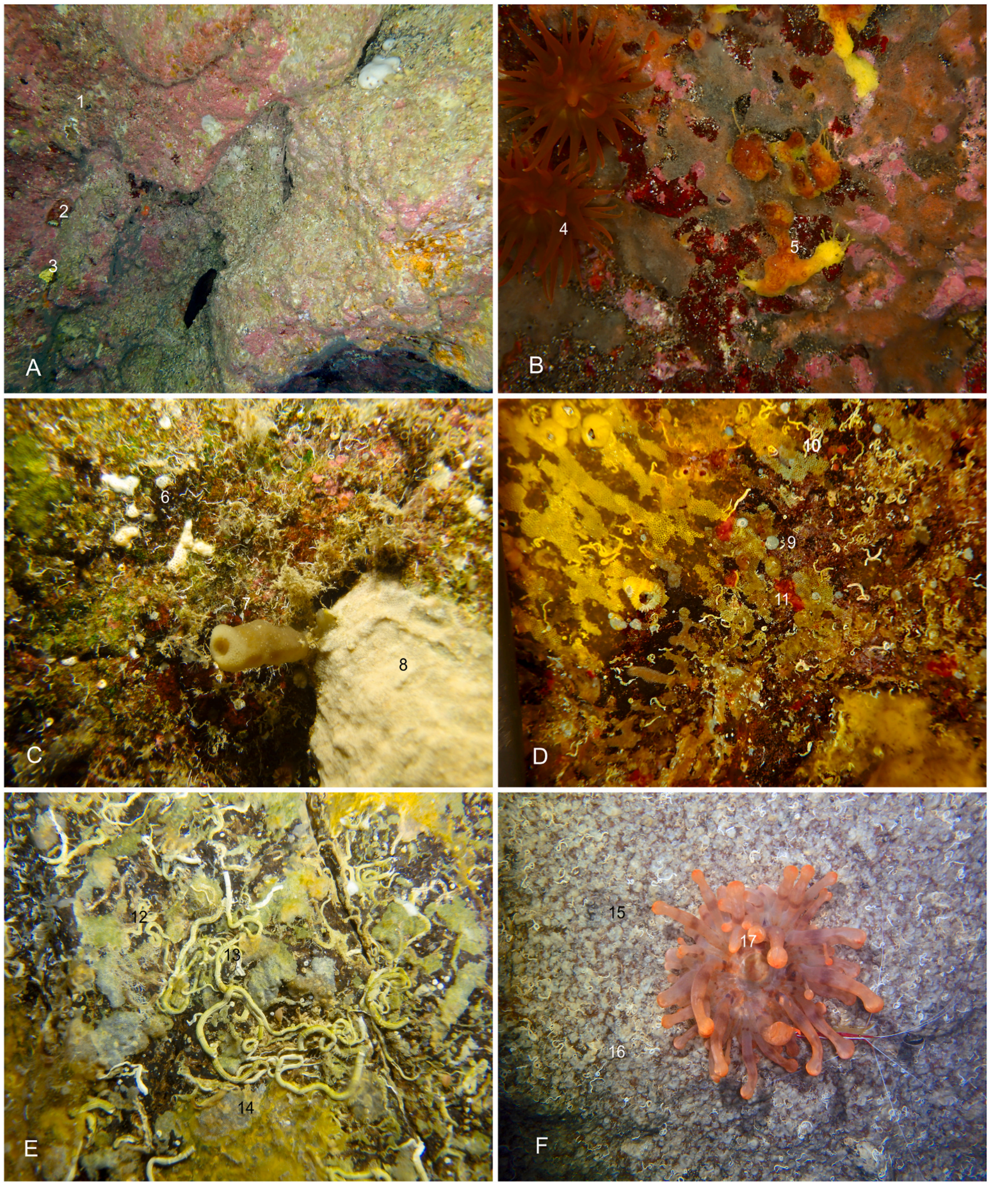


**Fig. 7.** Representative examples of sessile benthic assemblages and taxa from marine caves of the Canary Islands. Images illustrate an example of a typical zonation pattern from light-influenced entrance communities to specialised dark zone assemblages, which is characteristic of the Canary Islands. **A** Entrance zone of Los Sargos cave (Tenerife) showing *Phyllangia americana mouchezii* (1), *Polycarpa* sp. (2), and *Dictyonella madeirensis* (3) (horizontal scale ~2 m); **B** Entrance zone of Zapata–Bisueño tunnel (Tenerife) with *Actinia nigropunctata* (4) and *Aplysina* cf. *aerophoba* (5) (scale ~25 cm); C Semi-dark zone of Cueva Grande (Gran Canaria) displaying *Lissoclinum perforatum* (6), *Spongionella pulchella* (7), and *Parasmittina tropica* (8); **D** Semi-dark zone of Los Mozos 2 cave (El Hierro) featuring *Verruca spengleri* (9), *Antropora granulifera* (10), and Spirorbinae (11) (scale ~8 cm); **E** Dark zone of Cueva Grande cave (Gran Canaria) highlighting *Crassimarginatella crassimarginata* (12), *Vermiliopsis* sp. (13), and *Diplastrella bistellata* (14) (scale ~10 cm); **F** Dark zone of Cueva Grande (Gran Canaria) showing the brachiopod *Novocrania* sp. (15), *Metavermilia multicristata* (16), and *Telmatactis cricoides* (17) (scale ~30 cm). The latter was exceptionally found in a dark zone, likely due to its location at a narrowing cave that increases the chance of predation on observed mysids during their diel migrations. The scales are approximate and given for orientation. Photos by Y. Gonzalez-Marrero.

surge-generated flow (Bell, 2002, 2003; Bell and Barnes, 2000), which support the hypothesis that the effects of turbulent currents on sessile morphologies may extend to innermost sections in shallow caves (Bussotti et al., 2006).

Second, wave action serves as a critical vector for nutrient supply. Increased water motion enhances suspended particulate organic matter flux and facilitates propagule transport, effectively subsidising energy-poor cave interiors (Balduzzi et al., 1989; Benedetti-Cecchi et al., 1997; Fichez, 1991; Harmelin, 1985b; Zabala et al., 1989). This hydrodynamic subsidy may allow active filter-feeding sponges to thrive further into wave-exposed caves. In Atlantic temperate caves, sponge abundance peaks in the range of 10–30 m from the entrance where water flow is sufficiently high (Bell, 2002). Our results, within this range, suggested that increased wave exposure extends this optimal zone further inward than in sheltered caves, consistent with sponge dependence on water flow for feeding (Maldonado et al., 2012).

In contrast, constructor-type engineers were less common in these high-energy caves. This supports the hypothesis of a spatial decoupling between the zone of intense physical disturbance, which is typically restricted to cave entrances, and the zone of optimal food availability, which extends deeper into the cave (Bell, 2002; Gerovasileiou and Bianchi, 2021). This decoupling creates a complex selective environment where mechanically resistant, encrusting taxa predominate at entrances with high hydrodynamics (Bell and Barnes, 2000; Lange et al., 2021; Gerovasileiou and Voultsiadou, 2016), while active filter-feeders are favoured in the more stable, yet still resource-rich, intermediate zones.

Beyond hydrodynamics, depth range emerged as a strong positive predictor of both taxonomic and functional diversity, which is a novel finding. Deeper caves (≥10 m) had approximately 25% higher species richness ($p < 0.001$) and greater functional richness ($p = 0.03$) than did shallower caves. We propose that this pattern may result from three non-exclusive mechanisms: (1) greater environmental stability in deeper zones, which buffers surface disturbances and facilitates the persistence of sensitive taxa (Harmelin et al., 1985); (2) potentially higher connectivity with deep-water species pools, a concept supported by findings of deep-water fauna in Mediterranean caves (e.g. Harmelin et al., 1985; Pisera and Gerovasileiou, 2021; Riedl, 1966; Vacelet et al., 1994; Vasseur, 1974; Zibrowius, 1971), and especially relevant in the Canarian archipelago where great depths are reached at short distances from the shore; and (3) exclusion of some space-dominant vegetal species and their replacement by a more diverse array of less competitive sessile invertebrates, thereby increasing overall biological heterogeneity (Balduzzi et al., 1989). However, Riedl (1966) questioned the bathyal affinity of cave fauna, suggesting alternative origins from coastal hard substrates. Nevertheless, our findings of 18 taxa exclusive to deep caves support our interpretation suggesting that depth provides a unique ecological niche that promotes functional distinctiveness. Direct measurements of larval supply, oceanographic modelling, and spatial autocorrelation studies would be needed to resolve this debate.

Our findings revealed that wave exposure and depth are not independent factors, but instead interact to create a complex environmental matrix. While wave action operates as a dual force of physical stress (Lange et al., 2021) and resource subsidy through enhanced nutrient and propagule transport (Fichez, 1991; Zabala et al., 1989), depth provides stabilising refuge, leading to distinct functional outcomes. These landscape-scale processes structure community composition by selecting for specific trait combinations. Physically resistant binder engineers thrive in high-energy systems (Bell and Barnes, 2000), whereas constructor-type engineers dominate in calmer systems at the cave scale due to the better adaptation of polychaetes, brachiopods and bryozoans to low nutrient conditions. Both processes determine which functional roles are present and how redundantly they are performed, thereby shaping the functional resilience mosaic across the seascape. Although these individual mechanisms have been previously documented in Mediterranean cave systems (Harmelin et al., 1985; Zabala et al., 1989), to our knowledge, this study provides the first quantitative evidence of their combined influence on functional diversity in Atlantic oceanic caves, and demonstrates how wave exposure modulates the spatial extent of hydrodynamic subsidy—a pattern not previously described.

### 4.2. *Influence of cave morphology on functional structure*

While our study highlights seascape-scale drivers and within-cave gradients as primary structuring forces, cave-specific geomorphology undoubtedly contributes to the observed ecological patterns. The nine caves surveyed exhibited a range of morphological complexities, from simple single-chamber systems to multi-entrance tunnels (see Table S1 for details). This variability firstly responds to speleogenesis. The Canary Islands' predominantly volcanic composition (Anguita and Hernán, 2000) contrasts with the mixed carbonate, volcanic, and sedimentary geologies of regions like the Mediterranean (Xanke et al., 2024; Gerovasileiou and Bianchi, 2021), reducing large-scale lithological variability. Within this volcanic context, marine caves can be syngenetic (e.g., lava tubes) or epigenetic (formed by erosion) (López-bedoya and Pérez-Alberti, 2009). Although true anchialine lava tubes are known from the Canaries (Dumpiérrez et al., 2001; Iliffe, 1984), they are scarce and were not included in our dataset.

All nine caves in this study are considered to be of epigenetic marine erosional origin, resulting in relatively simple morphologies compared to karstic systems. However, we hypothesise that Mozos 2 cave, may have a composite origin. Its bubble-like main chamber and smooth rock surfaces suggest a primary pneumatogenic cavity, subsequently opened and enlarged by marine erosion. This unique geomorphology may influence its community structure; for instance, the low rugosity of its bubble walls could favour encrusting growth forms over branching species. However, this cave lies in a high-energy wave zone, where our model predicts that fragile growth forms with vertical development are absent, illustrating the challenge of disentangling broad-scale drivers from cave-specific morphology.

Nonetheless, our hierarchical modelling approach, which included cave identity as a random effect, robustly accounted for this morphological variability. By partitioning the variance attributable to cave-specific characteristics, our model effectively isolated the influence of the broader environmental drivers we aimed to test. This statistical control, combined with the predominantly homogeneous speleogenesis (8 of 9 caves being of erosional origin) reduces potential confounding factors in ecological analyses, strengthening our conclusion that wave exposure and depth are the dominant, predictable drivers of functional structure at the seascape scale. However, future research, could explicitly incorporate quantified morphological variables (e.g., volume-to-entrance ratio, internal complexity indices) to further explore their interaction with large-scale environmental gradients.

### 4.3. *Environmental filtering mechanisms*

Our findings provide strong evidence that environmental filtering plays a central role in structuring marine cave assemblages via functional trait-based processes. The distinct trait compositions observed along the cave axis reflect two fundamental environmental gradients: resource availability (light and food) and physical disturbance (wave action). This spatial pattern, consistent across both years, supports the idea that extreme environments promote trait convergence (Cornwell et al., 2006) and demonstrates universal community assembly patterns shaped by small scale (order of metres) environmental conditions (Bianchi and Morri, 1994; Harmelin, 1985b).

In wave-exposed caves, well-lit cave entrance zones, constant hydrodynamic stress selects for robust, stress-tolerant traits such as encrusting growth forms and strong attachment mechanisms. However, abundant light and high particulate flux create resource-rich conditions that allow diverse functional strategies to coexist (Tilman et al., 1997). The high functional evenness and divergence in these zones reflect a regular, spread-out distribution of traits, characteristic of communities in which multiple functional strategies can be maintained simultaneously.

Conversely, in nutrient-limited dark zones, biotic control through interspecific competition is progressively being replaced by abiotic constraints that impose severe limitations (Harmelin, 1985b; Harmelin et al., 1985). The primary constraint is resource scarcity, that is the absence of light and reduced externally derived food (Bianchi and Morri, 1994; Harmelin, 1985b; Morri et al., 1994; Zabala et al., 1989). This acts as a powerful convergent filter, selecting a narrow range of functional traits adapted to heterotrophy and energy conservation. Functional richness declined by 30% from the semi-dark to dark zones, with communities dominated by suspension feeders lacking lophophores, simple growth forms, and limited habitat-forming capacity. Despite reduced functionality, dark zone communities exhibited the highest specialisation, with traits clustered at functional space edges, suggesting that only limited trait combinations succeed in trophic-limited environments.

Spatial patterns found along the cave axis, may provide a predictive framework for understanding community assembly in other environmentally constrained and resource-limited ecosystems such as deep-sea vents, polar habitats, and cryptic reef environments.

### 4.4. The vulnerability paradox

The coexistence of high taxonomic diversity and high functional vulnerability—and the way community assembly processes operating at different scales (seascape, local, and within-cave) generate this paradox—is the central finding of this study.

Wave exposure shapes vulnerability through contrasting spatial effects. At cave entrances, high-energy conditions lead to the predominance of mechanically resistant functional entities, potentially increasing local redundancy. However, in medial sections, wave-driven resource delivery enables niche partitioning and functional divergence, supporting higher functional richness but lower redundancy. At the cave scale, the subsidy effect dominates: wave-exposed caves exhibited higher functional vulnerability (lower redundancy) than sheltered caves, likely because enhanced nutrient input relaxes competitive constraints and promotes functional differentiation. Consequently, caves across wave exposure gradients exhibit contrasting vulnerability and originality profiles, with exposed caves being both more vulnerable and more original, and therefore possessing lower functional resilience. This pattern has important implications for conservation under changing wave regimes, such as those driven by climate change.

Strong spatial variation in functional vulnerability also emerged across the cave-axis gradient. Semi-dark zones exhibited the highest functional richness (FRic), highest functional vulnerability, and highest percentage of functional roles performed by a single taxon (82%), creating a vulnerability hotspot. The high concentration of functionally original taxa and species with unique trait combinations further elevates vulnerability, as their loss eliminates irreplaceable functional roles (Brandl et al., 2016). Conversely, dark zones showed the lowest functional originality and vulnerability, but the highest redundancy for limited functional entities. Since sessile community regeneration can take decades (Harmelin, 1985b), the recovery potential in dark zones may be constrained by extreme conditions coupled with slow growth rates, severely limiting potential colonisers and leading to longer return times following disturbances.

We interpret both the wave exposure effects and the within-cave vulnerability gradient as result of interacting processes: resource availability and environmental filtering. Under non-limiting nutrient conditions, high functional diversity arises through niche partitioning as species diverge to exploit different resource pools (Cadotte et al., 2011). Conversely, under severe nutrient limitation, strong filtering constrains communities to a narrow set of stress-tolerant traits, producing functionally similar assemblages with higher redundancy and lower vulnerability (Zobel, 1997).

This framework explains three patterns. First, wave-exposed cave entrances experience high particle flux, promoting niche partitioning and, functional diversification, and consequently lower redundancy and higher vulnerability. Second, entrances and semi-dark zones, also receiving external resource delivery, support functionally diverse but weakly redundant assemblages, thus maintaining elevated vulnerability. Third, dark zones, where nutrient limitation is severe, host functionally homogeneous communities with high redundancy, resulting in lower vulnerability.

At the regional scale, despite high taxonomic diversity (H' = 3.6), marine caves exhibit substantial functional vulnerability: 57% of functional entities are represented by a single species, indicating that ecosystem functions would be at risk if these species were lost.

Scale-dependent decoupling of functional vulnerability and redundancy found in this study can be interpreted as evidence of shifting assembly mechanisms operating at different spatial scales. At broad, regional scales, high taxonomic diversity masks functional vulnerability. However, at fine scales of individual cave ecozones, strong filtering reveals underlying functional fragility, particularly in semi-dark zones where many functional entities are performed by a single, highly functionally divergent species. This pattern is consistent with Giordani et al. (2019), who showed that the decoupling between taxonomic diversity and functional vulnerability is stronger in communities subjected to intense environmental filtering.

In summary, the "vulnerability paradox" seems driven by environmental filtering under a sustained nutrient supply, which promotes functional diversification through resource partitioning. While this process sustains high taxonomic diversity, it simultaneously reduces functional redundancy and thus increases vulnerability to species loss.

Furthermore, the concentration of diverse species strategies into a limited number of viable functional entities reflected by the elevated functional over-redundancy, mirrors patterns documented in other highly diverse ecosystems such as coral reefs' fish fauna and tropical or subtropical forests (Mouillot et al., 2014; Huang et al., 2024; Zhang and Zang, 2021). This suggests that such functional packing may be a widespread feature of species-rich ecosystems. The resulting functional fragility offers a potential explanation for the unexpected vulnerability and recent phase shifts observed globally in ecosystems long assumed to be resilient due to their high species richness.

Together, these findings provide a mechanistic basis for the vulnerability of marine caves reported previously (e.g., Nepote et al., 2017). More broadly, they demonstrate that high taxonomic diversity does not guarantee effective buffering against anthropogenic pressures or climate change; instead, it may obscure substantial functional vulnerability, with important implications for conservation prioritisation in these threatened ecosystems.

Complementary to these spatial patterns, the temporal analysis revealed compensatory dynamics among the three ecozones. Between 2022 and 2023, semi-dark zones showed functional space contraction and increased evenness, contrasting with entrance and dark zones. Moreover, redundancy increased in the entrances and semidark zones whereas for dark zones decreased. These opposing trends suggest that changes in one zone may be linked to changes in adjacent zones, possibly through species redistribution driven by stochastic colonisation–extinction dynamics, interspecific competition, and priority effects during community assembly. Although a two-year period is insufficient to fully capture temporal dynamics, these marked temporal patterns at the ecozone level were not detected in cave-level analyses using GAMMs, highlighting the importance of examining data across multiple spatial scales.

### 4.5. Implications for conservation and management from functional resilience analysis

The findings of this study have important implications for the conservation and management of marine cave ecosystems, particularly regarding functional vulnerability.

The identification of semi-dark zones as the most functionally vulnerable and dark zones that are sensitive to directional pressures (e.g., changes in nutrient-sedimentation regimes or chemical pollution from overlying agricultural seepage) underscores the need for whole-system protection measures that explicitly include often-overlooked deeper and more internal cave compartments.

The dominant role of wave exposure as a structuring force suggests that changes in wave regimes, whether driven by climate change (e.g., increased storm intensity and frequency) or coastal development (e.g., altered exposure levels), could strongly affect the functional composition of assemblages. Therefore, it is imperative to establish a network of protected areas that encompasses a variety of different wave-exposure regimes.

The positive relationship between depth range and functional diversity indicated that deeper caves may serve as refugia for both taxonomic and functional diversity, buffering communities from surface perturbations and rising temperatures. In the context of warming surface waters, these colder caves will become vital. Therefore, protection strategies should include caves located at greater depths ($\geq$10 m) as these systems are more likely to support unique taxa and complex functional assemblages.

The strong temporal dynamics observed at the ecozone level underscores the importance of long-term monitoring at an appropriate spatial resolution. Short-term or single-time-point surveys may overlook natural variability, potentially leading to inaccurate impact assessment. We recommend long-term monitoring (at least three–five years), with data collection at the ecozone level, to adequately capture spatial heterogeneity and temporal fluctuations.

The identification of functionally original taxa, and secondarily, those located at the edges of the functional space (Fig. 3), provide specific targets for conservation. These taxa may contribute disproportionately to functional diversity and should be prioritised for biodiversity assessment and monitoring. Precise management recommendations for marine cave systems are provided in Supplementary Material SM4, and specific actions for the Canary Islands are summarised in Table S9 including diversity indices for each cave and year in Tables S10 and S11.

### 4.6. Study limitations

To the best of our knowledge, this study provides the first functional characterisation of sessile communities in the Atlantic marine caves. However, some limitations should be acknowledged. First, the sampling design excluded the easternmost Canary Islands, whose distinct oceanographic conditions and biogeographic history might have influenced trait distributions. Including these systems in future surveys would allow us to test the generality of the functional patterns observed in this study. Second, comparability with existing studies is constrained by inconsistencies in trait selection, species pools, and functional space construction. To enhance cross-study comparability, we recommend standardising trait frameworks, reporting methodological details, and developing regional baseline datasets. Third, wave exposure was characterised using mean annual wave power data, which does not capture seasonal variability; future studies should incorporate seasonal wave dynamics to better understand temporal variation in environmental filtering (Chiri et al., 2013; Yanes et al., 2006). Fourth, while planes of cave entrances were predominantly oriented parallel to the coastline, allowing coastal orientation to serve as a proxy for wave exposure, fine-scale variation in cave orientation, aperture size, and connectivity with the open sea may influence local hydrodynamic conditions and were not explicitly quantified. Fifth, although all caves were formed in volcanic rock, providing regional geological homogeneity, the specific rock types could not be determined due to the lack of detailed submarine geological surveys—a limitation inherent to underwater cave research. Nevertheless, we expect that minor lithological differences within volcanic substrates have less influence on community structure than in regions with greater geological heterogeneity. These steps are essential for building a cumulative and coherent understanding of functional diversity across marine cave ecosystems.

## 5. Conclusive remarks

This study provides the first comprehensive taxonomic and functional characterisation of marine cave ecosystems in the Canary Islands, revealing a system defined by high functional fragility despite high species richness, a “vulnerability paradox”. Our findings demonstrate how functional resilience is spatially structured and likely modulated by seascape-scale drivers, such as wave exposure and depth, as well as environmental gradients along the cave axis.

Environmental filtering fosters functional diversification by promoting resource partitioning under sustained nutrient supply; however, this mechanism limit functional redundancy, thereby increasing vulnerability. Functional vulnerability was scale-dependent where functional over-redundancy increases and functional vulnerability decreases with increasing spatial scale. The synergy among wave exposure, cave depth and local environmental gradients drives functional resilience, producing a mosaic that supports a taxonomically rich yet functionally fragile ecosystem. Wave exposure has emerged as the dominant environmental driver among seascape and local-scale factors (explaining 34.5% of the variance), revealing an overlooked mechanism. Deeper caves supported higher taxonomic diversity and functional richness, suggesting their potential role as diversity refugia under changing environmental conditions. Environmental filtering acts as a crucial assembly rule, shifting its focus from physical stress in the entrance zones to resource limitation in darker sections. This gradient explains the emergence of distinct functional syndromes. Marine cave communities exhibit substantial temporal dynamics, even over short observation periods. These ecosystems are structured by ongoing colonisation-extinction processes, underscoring the need for long-term monitoring to evaluate their resilience.

We propose that this “vulnerability paradox” is not an isolated phenomenon but may represent a fundamental and widespread pattern in other highly specialised ecosystems, as demonstrated for coral reefs and tropical forests. The ongoing biodiversity crisis, characterised by ecosystem collapses and phase shifts, may be exacerbated by perturbations acting on inherently fragile systems. Consequently, in line with previous studies, we suggest to re-evaluate the perception of highly diverse ecosystems, replacing the long-held assumption of inherent resilience with a recognition of their increasingly evident sensitivity to anthropogenic stressors and global change.

## CRediT authorship contribution statement

**Y. Gonzalez-Marrero:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **A. Canepa-Oneto:** Writing – review & editing, Supervision. **S. Clemente:** Writing – review & editing, Supervision. **J. Cristobo:** Writing – review & editing, Supervision. **C. Hernandez-Gonzalez:** Writing – review & editing, Project administration. **A. Herrero-Perez:** Writing – review & editing, Methodology, Data curation. **M. Adrover-Huesca:** Writing – review & editing, Methodology, Data curation. **V. Gerovasileiou:** Writing – review & editing, Supervision.

## Data access statement

The data that support the findings of this study belong to the Spanish Ministry for the Ecological Transition and the Demographic Challenge (MITECO). Due to the nature of the research agreement (administrative assignment), the authors do not have permission to share the raw data.

## Declaration of Generative AI

During the preparation of this work the author(s) used ChatGPT-4.1 with the aim of refining language and readability. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the publication's content.

## Declaration of competing 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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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2026.107915.

## Data availability

The authors do not have permission to share data.

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