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Taxonomic and functional diversity of subtidal benthic communities associated with hard substrates at Crozet archipelago (sub-Antarctic, Southern Ocean)

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Sub-Antarctic coastal marine ecosystems harbor rich and diverse benthic communities. Despite their ecological uniqueness and vulnerability to global changes, studies on benthic communities remain limited. Using underwater video-imagery, we investigated the taxonomic and functional diversity of benthic communities associated with hard substrates at *Baie du Marin* (*Ile de la Possession*, Crozet archipelago). The *Baie du Marin* species richness and diversity were additively partitioned to evaluate spatial patterns of species through the following spatial scales: within images, among images within transects, and among transects. We analyzed imagery data from seven transects located at different sites inside *Baie du Marin* and covering contrasting natural rocky habitats and underwater artificial cable substrates. A total of 50 faunal (mainly represented by Echinodermata and Porifera phyla) and 14 algae (mainly represented by Rhodophyta phylum) taxa were identified. Rocky substrates were dominated by high densities of the polychaetes *Parasabella* sp. and *Lanice marionensis*, whereas submarine cables were dominated by high densities of the bivalve *Kidderia* sp. attached to macroalgae. Our results show contrasted distribution patterns in the faunal and algal assemblages within the *Baie du Marin*, with significant ecological differences between submarine cables and natural rocky substrates. Larger spatial scale (i.e., among transects) accounted for most of the bay richness and diversity, highlighting a high-level of habitat heterogeneity within the bay. Through a trait-based approach, our findings revealed that Crozet benthic communities are characterized by low functional richness, evenness, and redundancy, highlighting a potential vulnerability to current and future natural and anthropogenic changes. This study provides a novel bentho-ecological baseline for future assessments of

natural and anthropogenic impacts on the marine environment of the Crozet archipelago; and for the conservation management of these remote habitats that make part of the French Southern Territories Marine Protected Area, recently inscribed on the UNESCO World Heritage list.

1 Introduction

Benthic ecosystems of sub-Antarctic islands host a unique and diverse biodiversity, characterized by high-level endemism (Branch et al., 1993; Chown et al., 2001; Barnes et al., 2006; Freeman et al., 2011; Hogg et al., 2011; Clark et al., 2019). While marine ecosystems of these isolated territories are of high conservation value (Chown et al., 2001), they remain understudied and vulnerable to multiple anthropogenic threats, including climate change (Hogg et al., 2011), biological invasion (Smith, 2002; Hogg et al., 2011; McCarthy et al., 2019), and increasing maritime traffic (i.e., fisheries, tourism activities and scientific research). These synergistic threats can lead to a shift in benthic communities caused by: (i) the loss of a wide range of habitats and associated diversity (including species subject to conservation measures) (Saucède et al., 2017); (ii) altered food web structure (Ehrenfeld, 2010; Kortsch et al., 2015); (iii) modified biotic interactions (Montoya and Raffaelli, 2010); and (iv) formation of a new range of habitats available for benthic and potentially alien species (McCarthy et al., 2019). Biodiversity loss and/or any substantial alteration of benthic assemblages can potentially impair whole ecosystem functioning and alter its properties (e.g., ecosystem services) (Cardinale et al., 2012). Shedding light on the taxonomic and functional diversity of polar nearshore marine benthic communities is therefore needed to provide a baseline for future conservation strategies.

Many studies on coastal marine ecosystems, encompassing those in sub-Antarctic and Antarctic regions, have reported a significant influence of substrate on the composition and distribution of benthic communities (Barnes et al., 2006; Freeman et al., 2011; Clark et al., 2019), and the potential relevance of substrate in conservation management. Hard substrates and habitat-forming species promote habitat heterogeneity and structural complexity, enhancing species diversity (MacArthur and MacArthur, 1961; Levin et al., 2010). Rocky habitats allow the development of benthic communities by providing an additional colonizing space, nutrient source or a protection against predation and unfavorable environmental conditions (Levin et al., 2010). Artificial hard substrates can act as a reef for benthic species by providing new habitats (Langhamer, 2012). The influence of submarine cables on benthic assemblages is subject of

controversy; several studies have highlighted short term or minor ecological effects on benthic communities (Andrulewicz et al., 2003; Kogan et al., 2006; Dunham et al., 2015; Sherwood et al., 2016), whereas other studies have reported major effects including biological invasion risks due to new habitats provided by artificial structures (Connell and Glasby, 1999; Glasby et al., 2007). The characterization of hard substrate benthic communities is thus essential to assess the contribution of different habitat types to the regional diversity and to investigate the potential ecological effects of these artificial structures on these environments.

Diversity studies are fundamental for examining the structure of sub-Antarctic coastal marine ecosystems, particularly in addressing functional diversity for conservation management (Bremner, 2008; Cardinale et al., 2012; Lindegren et al., 2018). Ecosystem function is not directly linked to taxonomic richness, but is dependent on species characteristics – functional traits – that express these species (Hooper et al., 2005). In this regard, trait-based approach – defined as any morphological, physiological or phenological feature measurable at the individual level (Violle et al., 2007) – is a powerful tool to better comprehend the response of benthic diversity to environmental changes and how these translate to ecosystem functioning (Mason et al., 2005; Villéger et al., 2008; Laliberté and Legendre, 2010; Mouchet et al., 2010). Species functional traits are considered as suitable proxies of the ecological functions supported by an ecosystem (Villnäs et al., 2018). Trait-based approaches have previously proven to be efficient in understanding different ecological mechanisms that underlie the local diversity in a wide range of benthic ecosystems, including intertidal seagrass and subtidal maerl beds (Boyé et al., 2019), soft-sediment habitats (Hewitt et al., 2008), and estuarine systems (van Der Linden et al., 2012). A functional trait approach can illuminate ecosystem productivity, functional stability or resilience, and the application to polar regions could estimate the potential effects of biological invasion, climate change, and other stressor factors on ecosystem functions (Hewitt et al., 2016; Degen et al., 2018; Robinson et al., 2022).

Underwater imagery is a non-invasive method which is increasingly used to conduct diversity studies and investigate communities and habitats in polar sensitive environments (Foveau et al., 2017). Imaging techniques provide valuable

quantitative and qualitative information on benthic communities and are an effective tool for monitoring species assemblages and ecosystem functioning (Friedlander et al., 2023). Whereas physical sampling provides point-based data, video-imagery allows for the acquisition of a large amount of ecological data over broader sampling regions with less sampling effort (Solan et al., 2003). Underwater imagery is a powerful method for designating the diversity of coastal benthic habitats, including algal (Amsler et al., 1995; Berov et al., 2016) and faunal communities of natural hard (van Rein et al., 2011; Almond et al., 2021) and artificial substrates such as submarine cables (Dunham et al., 2015; Taormina et al., 2020). Image-based techniques have continually proven their value in a wide range of scientific endeavors of marine ecosystems; such as the assessment of spatial pattern distribution of Antarctic benthic communities (Amsler et al., 1995; Teixidó et al., 2002; Gutt et al., 2019), characterizing sub-Antarctic nearshore marine communities (Clark et al., 2019), and examining species richness in kelp forests (Bravo et al., 2023; Friedlander et al., 2023). Alongside the increasing use of image-based techniques, the development of image and video annotation software, specific to benthic ecology, have increased the efficiency of marine imaging data analysis (Teixidó et al., 2011; Trygonis and Sini, 2012; Langenkämper et al., 2017; Zurowietz and Nattkemper, 2021). Therefore, underwater video-imagery analysis is a suitable approach to conservation studies and for monitoring the sub-Antarctic diversity of nearshore marine ecosystems.

The maritime domain surrounding the Crozet archipelago is managed as a nature reserve, which is part of the French Southern and Antarctic Lands Marine Protected Area (French Government, Decree No. 2016-1700), recently classified on the UNESCO World Heritage list. In 2016, a hydroacoustic monitoring station (HA04) was installed by the "*Preparatory Commission for the Comprehensive Nuclear-Test-Ban Treaty Organization*" (CTBT0) at *Baie du Marin* (*Ile de la Possession*, Crozet archipelago), requiring impact study of the benthic communities. In this context, the contract "Nearshore cable inspection and environmental survey at IMS hydroacoustic station HA04 Crozet, France", was signed between the CTBTO and French Southern and Antarctic Lands (TAAF) for the inspection of submarine cables and ecological surveys of nearshore marine habitats in the *Baie du Marin*, which had never been studied before and for which our knowledge is currently limited. The present study aims (i) to describe and quantify the structure and composition of faunal and algal communities associated with hard substrates (rocky substrate *vs.* HA04 station submarine cables) at *Baie du Marin*; (ii) to investigate and compare the faunal taxonomic and functional diversity; and (iii) to assess the relative contribution of different spatial scales (α-diversity corresponding to the mean diversity within individual images; β_1-diversity the compositional change among images within transects; and β_2-diversity the compositional change among transects within the bay) to *Baie du Marin* richness and diversity.

2 Materials and methods

2.1 Study site

The Crozet archipelago (45°48'S – 46°26'S; 50°14'E – 52°15'E) consists of five main volcanic islands located in the Southern Ocean at 2400 km north of the Antarctic Continent and 2400 km southeast from the South African coast. These islands are divided into two groups with (*i*) a western group including *Île aux Cochons*, *Îlots des Apôtres* and *Île des Pingouins*; and (*ii*) an eastern group about 110 km away comprising the two largest islands of the archipelago, *Île de l'Est* and *Île de la Possession*. *Ile de la Possession* (46°25'S; 51°45'E) is the largest island of the Crozet archipelago – approximately 18 km wide by 15 km long – with a total surface area of ~156 km^2 and elevation of 934 m above sea level (a.s.l.) (*Pic du Mascarin*) (Figure 1A). The image-based sampling was focused on the *Baie du Marin*, a site located on the eastern coast of *Île de la Possession*.

The *Baie du Marin* (BDM; 46°25'54"S; 51°52'11"E) is a narrow inlet of c. 200 m width and 500 m length in its shallowest part (< 20 m depth) and opens to the ocean in a larger embayment of about 2 km wide at 40 m depth (Figures 1B–D). Due to the site geomorphology, the bay is exposed to ocean swell from the north. The coast is mainly composed of a rocky shore with a sandy beach located at the back of the bay. In general, the seabed is composed of coarse sand sediments, sometimes covered in organic detritus. In the inner inlet, down to 10 m depth, the bottom is a mix of coarse sands, pebbles and boulders. Rock and pebble areas are occasionally covered in stands of the giant kelp *Macrocystis pyrifera*, which are developed into loose patches along the shore between 10 and 20 m depth. *Baie du Marin* is characterized by the presence of a large colony of over 10,000 king penguins *Aptenodytes patagonicus* (Miller, 1778) and elephant seals *Mirounga leonina* (Linnaeus, 1758).

2.2 Imagery acquisition and data processing

Imagery acquisition took place from aboard the R/V Marion Dufresne II during the OP03-2021 and OP03-2022 logistical rotations conducted by TAAF (French Southern and Antarctic Lands) in response to Contract No. 2021-0882 with the CTBTO (Comprehensive Nuclear-Test-Ban Treaty Organization) for "Nearshore Cable Inspection and Environmental Survey at IMS Hydroacoustic Station HA04 Crozet, France" from 4th November to 9th November 2021 and 23rd November to 24th November 2022, respectively. Video-transects were recorded using a setting composed of three cameras, two GoPro HERO9® (5K video and 20-megapixel photos resolution; 80% field overlap) and an underwater camera Paralenz® Vaquita (4K resolution). The setting was also equipped with two lights and three 10 cm scaling lasers (spaced to 15 cm in 2022 setting) in order to estimate the
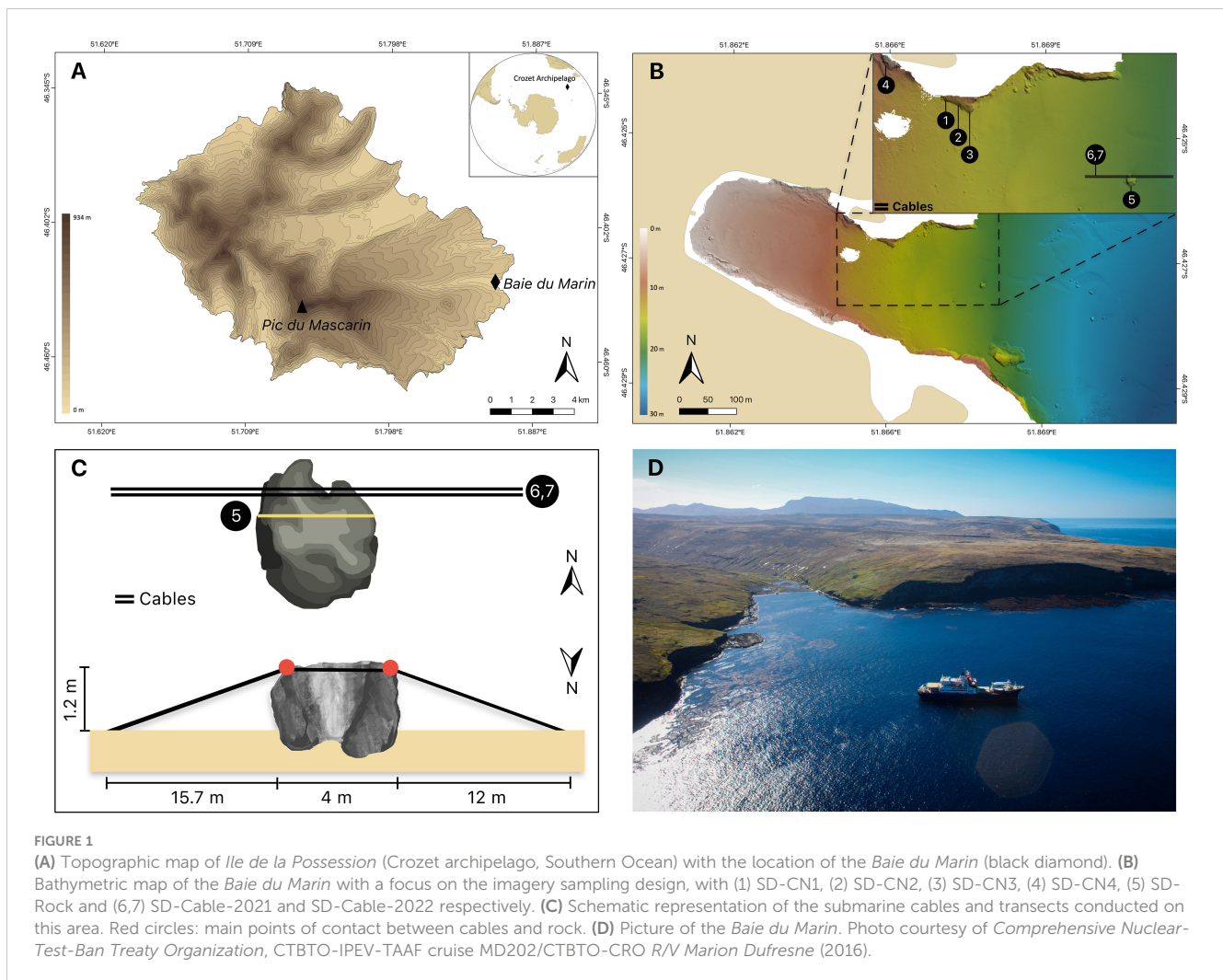
FIGURE 1
(A) Topographic map of *Ile de la Possession* (Crozet archipelago, Southern Ocean) with the location of the *Baie du Marin* (black diamond). **(B)** Bathymetric map of the *Baie du Marin* with a focus on the imagery sampling design, with (1) SD-CN1, (2) SD-CN2, (3) SD-CN3, (4) SD-CN4, (5) SD-Rock and (6,7) SD-Cable-2021 and SD-Cable-2022 respectively. **(C)** Schematic representation of the submarine cables and transects conducted on this area. Red circles: main points of contact between cables and rock. **(D)** Picture of the *Baie du Marin*. Photo courtesy of *Comprehensive Nuclear-Test-Ban Treaty Organization*, CTBTO-IPEV-TAAF cruise MD202/CTBTO-CRO *R/V Marion Dufresne* (2016).

filmed surface. Video-imagery was performed by scuba divers who maintained a regular swimming velocity, with the camera oriented parallel to the bottom at an average distance of 50 cm. Seven transects were conducted on different parts of the *Baie du Marin* (Figures 1B, C, 2, Supplementary Material 1). The first transect, SD-Rock, recorded benthic communities on the rock parallel to the cables at 19 m depth (Figure 2A). The following two transects (SD-Cable-2021 and SD-Cable-2022) recorded the suspended section of submarine cables to assess the potential influence of cables as substrate for benthic communities (Figures 2B, C). Finally, four transects – SD-CN1, SD-CN2, SD-CN3 and SD-CN4 – were recorded along the rock wall on the northern coast of the bay for approximately 200 m of the cables (Figures 2D–F). Amongst these four transects, three were carried out in 2022 (SD-CN1, SD-CN2 and SD-CN3) and one in 2021 (SD-CN4).

Video-transects were divided in their entirety into individual images. All combined transects, a total of 161 images (representing c. 100 m^2) were manually analyzed using the online open-source platform BIIGLE 2.0 (Benthic Image Indexing and Graphical Labelling Environment) (Langenkämper et al., 2017). For each image, all faunal organisms were scored and their counts were transformed into density (number of ind m^{-2}), and algae cover was

measured (m^{-2}). In agreement with the taxonomists, organisms were identified to the lowest possible taxonomic level, by (i) submitting collected materials and macro-photography pictures captured during transect imaging acquisition; and (ii) through a systematic review of the images analyzed in BIIGLE 2.0.

2.3 Sampling effort, diversity metrics and benthic communities' variation across transects

Diversity metrics, corresponding to Hill's number of order q, were calculated for fauna and algae for each image of each transect and averaged in order to investigate the spatial variability of these indices across transects, with: species richness (q=0), Shannon diversity (q=1) and Simpson's inverse (q=2) (Jost, 2006). In addition, Piélou's evenness and "rare" species, defined as those represented by less than 1% of total species abundance, were also estimated. For each diversity metrics, non-parametric Kruskal-Wallis followed by Dunn's *post-hoc* pairwise tests were conducted to test for significant differences among the seven transects at the image scale, and *p*-values were adjusted with a Bonferroni
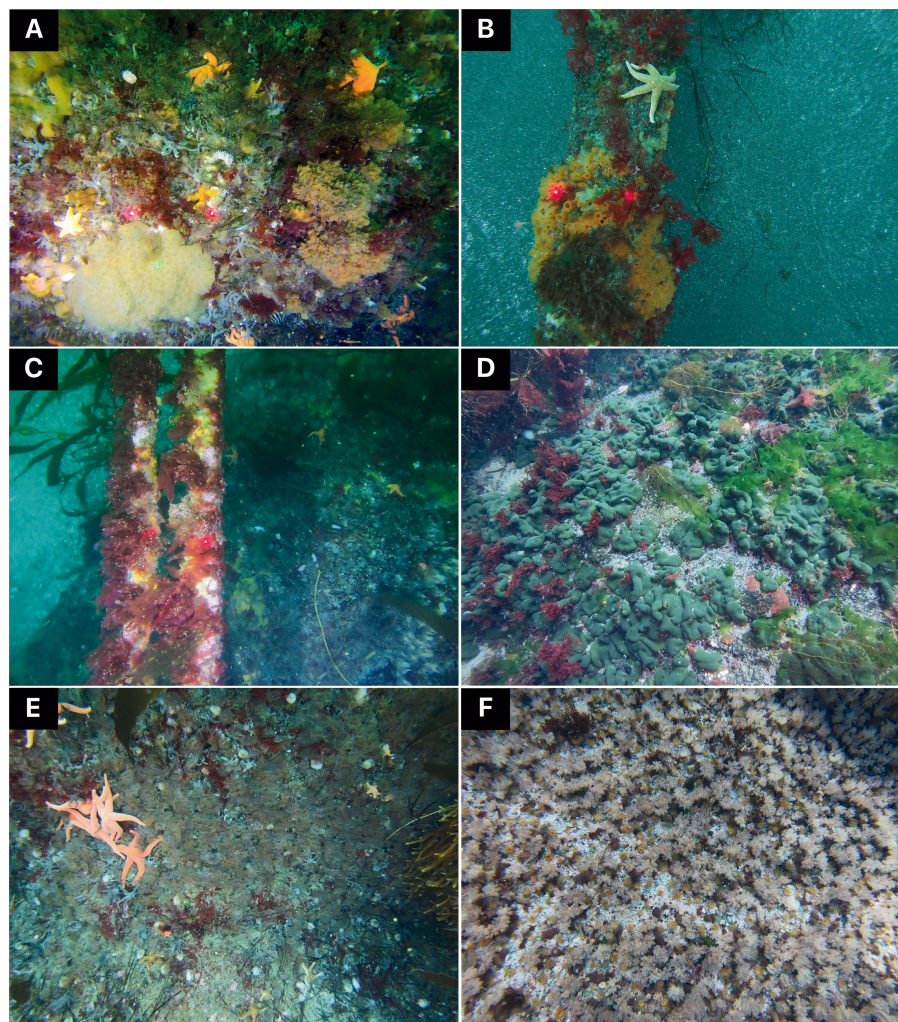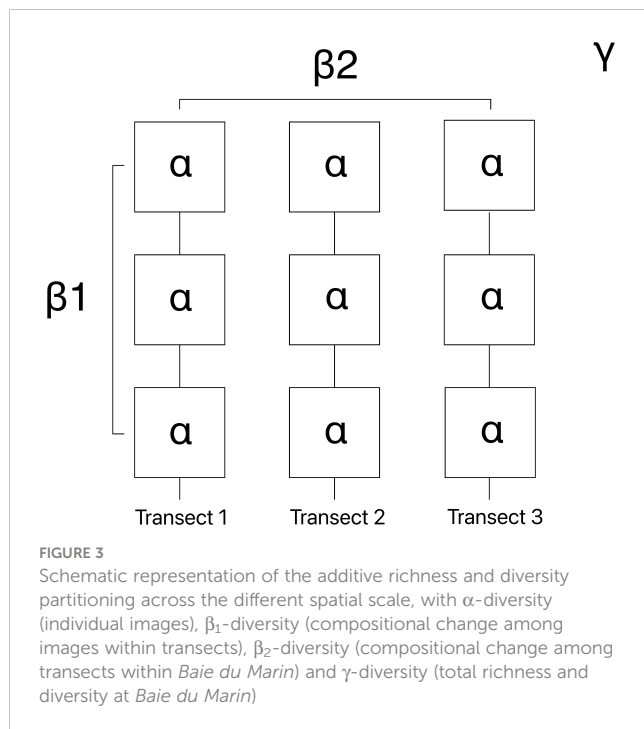
FIGURE 2
Benthic communities associated with hard substrates at different imagery sampling areas of the *Baie du Marin*, with: **(A)** rock located at the center of the bay; **(B, C)** submarine cables and **(D–F)** rocks located on the northern coast of the bay. Laser beams are 15 cm spaced for photos **(A, C, D)** and 10 cm spaced for photos **(B, E, F)**. [©] Proteker.

correction. To assess the sampling effort and to further explore how variation of diversity at the scale of the images scale-up at the scale of whole transects or the whole bay, rarefied diversity were computed from individual-based rarefaction curves for faunal communities (rarefied to the lowest number of individuals among transects: 1446 individuals) and image-based rarefaction curves for algal communities (rarefied to the lowest number of images among transects: 6 images). To investigate variation in benthic community composition across images and between transects, two Principal Coordinates ordination Analysis (PCoA) based on Hellinger-transformed data at the scale of the images were carried out on faunal and algal communities, respectively. Due to the absence of faunal taxa, eight images were excluded from the analyses (5 images of the SD-Cable-2021 transect and 3 of the SD-CN4 transect). A Redundancy Analysis (RDA) was carried out on these Hellinger-transformed data to ascertain how algal cover influences the distribution of faunal species. The Hellinger transformation was applied to minimize the greater weight given to rare species

(Legendre and Gallagher, 2001). All statistical analyses were performed using R software (version 4.2.0, R Core Team, 2022). Rarefaction curves and diversity metrics were conducted using the package *iNEXT* (Hsieh et al., 2016). PCoA and RDA were realized using the package *vegan* (Oksanen et al., 2020).

2.4 Bay richness and diversity partitioning across spatial scales

The *Baie du Marin* (γ-diversity) faunal and algal richness (q=0) and diversity (q=1 and q=2) were additively partitioned to investigate spatial patterns of species through three hierarchical spatial components: (i) alpha (α-diversity) corresponding to the mean diversity within individual images; (ii) beta-1 (β_1-diversity) the compositional change among images within transects; and (iii) beta-2 (β_2-diversity) the compositional change among transects within the *Baie du Marin* (Figure 3). The significance of each spatial

FIGURE 3
Schematic representation of the additive richness and diversity partitioning across the different spatial scale, with α-diversity (individual images), β₁-diversity (compositional change among images within transects), β₂-diversity (compositional change among transects within *Baie du Marin*) and γ-diversity (total richness and diversity at *Baie du Marin*)

component was computed by comparing observed values to values draw from null distributions obtained by randomization (9999 permutations) of the original community matrix. The additive diversity partitioning analysis (Crist et al., 2003) was conducted using the *PARTITION* package available in *GitHub*.

2.5 Functional trait collection and analyses

The trait-based functional approach was focused on faunal taxa. Functional traits were gathered for the lowest taxonomic level possible and inferred from species of the same genus when data was missing. This ecological information was compiled from peer-reviewed literature, taxonomic expertise, and sample collection of the *Université de Bourgogne*. Traits were selected to reflect a wide array of ecological processes and therefore constituted suitable proxies of ecosystem functioning (Table 1). Faunal taxa were assigned 11 traits, which were divided into 37 modalities (Table 1, Supplementary Material 2.1 and 2.2). Taxa were scored for each trait modality based on their affinity using a fuzzy coding procedure (Chevenet et al., 1994), with a score ranging from 0 (no affinity) to 4 (exclusive affinity). This method allows for the integration of species plasticity towards certain traits (e.g., reproduction or feeding), and

TABLE 1   Description of the functional traits and their modalities used to characterize faunal communities associated with hard substrate habitats and estimate their functional diversity.

Trait	Modalities	Definition	Labels	Functional significance
Maximal size (cm)	Very small (<1)	Very small size	VS	Competitive ability, habitat heterogeneity, growth rate, productivity, trophic interactions
	Small (1-3)	Small size	Small	
	Medium (3-6)	Medium size	Medium	
	Large (6-9)	Large size	Large	
	Very large (>9)	Very large size	VL	
Substrate position	Infaunal	Species living under the water-sediment interface	Inf	Living environment, habitat heterogeneity
	Epibenthic	Species living at the surface of the seabed	Epi	
Mobility	Burrower	Moving in a burrow	Burrow	Substrate colonisation, dispersal, trophic and biotic interactions
	Attached	Adherent to a mineral or organic substratum	Att	
	Tube-dweller	Living within a tube	Tube	
	Crawler	Moving on the substratum via muscles, legs, appendages	Crawler	
	Encrusting	Encrusting to the substrate	Enc	
Feeding method	Passive suspension feeder	Using natural flow to bring particles in contact with feeding structures	PSF	Indicator of hydrodynamic conditions, food acquisition and nutrient cycling, biotic interactions
	Active suspension feeder	Using cilia or muscles for pumping water and create feeding currents	ASF	
	Grazer	Feeding by scraping, either on algae, sessile animal or bacteria	Graz	
	Scavenger	Feeding on dead organic material	Scav	
	Deposit feeder	Feeding sediment	Dep	

(Continued)

TABLE 1 Continued

Trait	Modalities	Definition	Labels	Functional significance
	Predator	Feeding on active prey	Pred	
Food size	Microphage	Feeding on very small preys or particles	Micro	Food acquisition, nutrient cycling
	Macrophage	Feeding on large preys or particles	Macro	
Sociability	Solitary	Living alone	Sol	Social behaviour, dispersal
	Gregarious	Living in groups or clusters	Greg	
	Colonial	Organisms produced asexually which remain associated with each other	Col	
Habitat creation ability	3D-structure	Species creates a physical structure that other species benefit	Eng_3D	Habitat heterogeneity, foundation species, ecosystem resilience
	None	No engineering ability	N_3D	
Bioturbation	Surface deposition	Surface deposition of particles	SD_Bioturb	Nutrient and biogeochemical cycles, organic matter redistribution
	Conveyer belt transport	Translocation of sediment within the sediment, deep-top	C_Bioturb	
	Reverse conveyer belt transport	Subduction of particles from surface to some depth	R_Bioturb	
	None	No bioturbation ability	NB	
Sexual differenciation	Gonochoric	Having separate sexes	Gono	Recovery dynamics, dispersal
	Hermaphrodite	Producing ova and spermatozoa either at the time	Herma	
Development mode	Asexual	Development from budding, fragmentation, fission	Asex	Recovery dynamics, dispersal
	Direct	Development without a larval stage	Direct	
	Indirect lecithotrophic	Feeding on internal resouces put in the egg by the female	Lecito	
	Indirect planktotrophic	Feeding on material captured from the plankton	Plankto	
Reproductive frequency	Semelparous	Breeding only once during life	Semel	Recovery dynamics, dispersal, community and ecosystem resilience
	Iteroparous	Breeding repeatedly during life	Itero	

therefore the incorporation of the intra-specific variability in functional analysis.

The alpha functional diversity of faunal communities in each transect was characterized through complementary indices calculated using a subset of Principal Coordinates ordination Analysis axes (9 PCoA axes that accounted for 94% of the total variance of the functional/trait space) based on Euclidean distance of the standardized species-trait abundance matrix (Villéger et al., 2008; Laliberté and Legendre, 2010): (i) the functional richness (FRic) that corresponds to the amount of functional space – measured by the convex hull volume (Cornwell et al., 2006) – filled by the faunal community; (ii) the functional evenness (FEve) that describes the regularity of abundance distribution among species within the functional space and the functional distance between species; (iii) the functional divergence (FDiv) that measures the species abundances distribution in relation to the centroid of the functional space. FDiv indicates if abundant species are located close to the centroid (functional convergence) or in the external part of the functional space defined by the whole community (functional divergence); (iv) the functional dispersion (FDis), independent of species richness and defined as the mean-weighted distance of individual species in the functional space to the centroid (Laliberté and Legendre, 2010). High FDis values describe a high functional diversity within the community; (v) Rao's quadratic entropy (RaoQ) which represents a combination between functional richness and divergence that is closely related to FDis (Laliberté and Legendre, 2010) and is equivalent to Simpson's diversity index when all species are maximally different from each other (Botta-Dukát, 2005); and (vi) functional redundancy (FR), defined as the portion of functional traits shared by the species within a community or ecosystem. The functional space underlying these indices, and the distribution of species within it, was visualized using Principal Component Analysis (PCA).

Finally, functional beta diversity was explored through a PCA on the Hellinger-transformed trait modality densities. For that

TABLE 2 Abundance (Ab.), relative abundance (% Ab.) and mean density (D in indiv m^{-2}; mean $\pm$ standard deviation) of faunal taxa, as well as total surface cover (TS; m^{-2}), relative surface cover (% S) and mean surface per square metre (S; m^{-2}; mean $\pm$ standard deviation) of algal taxa identified at *Baie du Marin* using imagery transects.

Taxa	SD-Rock			SD-Cable-2021			SD-Cable-2022			SD-CN1			SD-CN2			SD-CN3			SD-CN4		
	Ab.	% Ab.	D	Ab.	% Ab.	D	Ab.	% Ab.	D	Ab.	% Ab.	D	Ab.	% Ab.	D	Ab.	% Ab.	D	Ab.	% Ab.	D
Fauna																					
Annelida																					
Polychaeta																					
Arenicolidae gen. indet. (Johnston, 1835)	6	< 0.1	0.4 ± 0.68	0	0	0	0	0	0	2	< 0.1	0.06 ± 0.17	0	0	0	0	0	0	1	< 0.1	0.05 ± 0.29
Lanice marionensis (Branch, 1998)	2412	27.1	149.24 ± 108.05	0	0	0	0	0	0	41	0.9	1.27 ± 2.54	19	0.5	2.51 ± 4.52	1	0.1	0.19 ± 0.67	6	< 0.1	0.17 ±0.7
Parasabella sp. (Bush, 1905)	2884	32.4	183.28 ± 146.14	273	16.2	61.78 ± 118.99	59	0.63	45.07 ± 139.9	3336	75.4	105.67 ± 203.95	3245	82.7	481.82 ± 416.1	654	45.2	46.24 ± 58.92	1803	17.2	66.84 ± 207.02
Serpulidae gen. indet. (Rafinesque, 1815)	0	0	0	74	4.4	20.19 ± 72.14	1150	12.33	418.62 ± 1148.54	0	0	0	0	0	0	0	0	0	0	0	0
Thelepus spectabilis (Ehlers, 1897)	1	< 0.1	0.03 ± 0.13	0	0	0	0	0	0	120	2.7	3.63 ± 7.57	98	2.5	17.72 ± 26.16	113	7.8	7.54 ± 12.14	3	< 0.1	0.14 ± 0.47
Arthropoda																					
Malacostraca																					
Halicarcinus planatus (Fabricius, 1775)	2	< 0.1	0.2 ± 0.6	0	0	0	0	0	0	1	< 0.1	0.03 ± 0.09	2	< 0.1	0.26 ± 0.4	3	0.2	0.26 ± 0.49	1	< 0.1	0.06 ± 0.32
Isopoda fam. gen. sp. (Latreille, 1816)	0	0	0	1	< 0.1	0.23 ± 1.51	0	0	0	0	0	0	0	0	0	6	0.4	0.77 ± 0.28	8	0.1	0.43 ± 1.43
Spinoserolis latifrons (White, 1847)	0	0	0	0	0	0	0	0	0	0	0	0	3	0.1	0.44 ± 0.77	4	0.3	0.66 ± 2.01	1	< 0.1	0.08 ± 0.46
Brachiopoda																					
Rhynchonellata																					
Aerothyris kerguelensis (Davidson, 1878)	4	< 0.1	0.32 ± 0.69	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

(Continued)

TABLE 2 Continued

Taxa	SD-Rock			SD-Cable-2021			SD-Cable-2022			SD-CN1			SD-CN2			SD-CN3			SD-CN4		
	Ab.	% Ab.	D	Ab.	% Ab.	D	Ab.	% Ab.	D	Ab.	% Ab.	D	Ab.	% Ab.	D	Ab.	% Ab.	D	Ab.	% Ab.	D
Chordata																					
Ascidiacea																					
Aplidium variabile (Herdman, 1886)	3	< 0.1	0.24 ± 0.55	0	0	0	0	0	0	51	1.2	1.8 ± 2.17	26	0.7	3.7 ± 2.36	49	3.4	3.92 ± 4.56	156	1.5	6.56 ± 14.53
Morchellium cf. *giardi* (Herdman, 1886)	0	0	0	1	0.1	0.32 ± 2.05	0	0	0	25	0.6	1.87 ± 2.78	14	0.4	1.72 ± 2.68	49	3.4	3.47 ± 4.95	2	< 0.1	0.05 ± 0.27
Sycozoa cf. *gaimardi* (Herdman, 1886)	4	< 0.1	0.19 ± 0.37	5	0.3	1.1 ± 5.31	2	< 0.1	2.44 ± 15.84	0	0	0	1	< 0.1	0.13 ± 0.31	0	0	0	2	< 0.1	0.05 ± 0.2
Synoicum sp. (Phipps, 1774)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	< 0.1	0.1 ± 0.59
Cnidaria																					
Anthozoa																					
Actiniaria fam. gen. sp.1 (Hertwig, 1882)	5	0.1	0.42 ± 1.28	0	0	0	0	0	0	8	0.2	0.3 ± 0.37	34	0.9	6.81 ± 11.95	8	0.6	0.85 ± 1.41	5	< 0.1	0.25 ± 1.19
Actiniaria fam. gen. sp.2 (Hertwig, 1882)	0	0	0	0	0	0	0	0	0	0	0	0	2	< 0.1	0.29 ± 0.45	1	0.1	0.11 ± 0.37	0	0	0
Actiniaria fam. gen. sp.3 (Hertwig, 1882)	10	0.1	0.56 ± 0.96	0	0	0	0	0	0	0	0	0	3	0.1	0.49 ± 0.75	1	0.1	0.09 ± 0.29	0	0	0
Actiniaria fam. gen. sp.4 (Hertwig, 1882)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.1	0.11 ± 0.37	0	0	0
Actiniaria fam. gen. sp.5 (Hertwig, 1882)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.1	0.13 ± 0.44	0	0	0
Actiniaria fam. gen. sp.6 (Hertwig, 1882)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1625	15.5	129.03 ± 295.46
Alcyonium cf. *antarcticum* (Wright & Studer, 1889)	0	0	0	0	0	0	0	0	0	1	< 0.1	0.03 ± 0.1	1	< 0.1	0.13 ± 0.31	0	0	0	0	0	0
Hydrozoa																					
Hybocodon sp. (L. Agassiz, 1860)	4	< 0.1	0.27 ± 0.81	52	3.1	11.58 ± 33.23	67	0.72	36.28 ± 137.86	0	0	0	0	0	0	0	0	0	0	0	0

(Continued)

TABLE 2 Continued

Taxa	SD-Rock			SD-Cable-2021			SD-Cable-2022			SD-CN1			SD-CN2			SD-CN3			SD-CN4		
	Ab.	% Ab.	D	Ab.	% Ab.	D	Ab.	% Ab.	D	Ab.	% Ab.	D	Ab.	% Ab.	D	Ab.	% Ab.	D	Ab.	% Ab.	D
Echinodermata																					
Asteroidea																					
Anasterias antarctica (Lütken, 1857)	3	< 0.1	0.22 ± 0.54	0	0	0	1	< 0.1	0.46 ± 2.97	1	< 0.1	0.03 ± 0.09	1	< 0.1	0.13 ± 0.31	3	0.2	0.37 ± 0.94	10	0.1	0.54 ± 1.46
Diplasterias meridionalis (Perrier, 1875)	3	< 0.1	0.11 ± 0.25	1	0.1	0.32 ± 2.05	0	0	0	2	< 0.1	0.12 ± 0.27	1	< 0.1	0.13 ± 0.31	2	0.1	0.23 ± 0.78	0	0	0
Glabraster antarctica (E. A. Smith, 1876)	2	< 0.1	0.15 ± 0.45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	< 0.1	0.06 ± 0.34
Henricia sp. (Gray, 1840)	4	< 0.1	0.25 ± 0.51	0	0	0	0	0	0	2	< 0.1	0.07 ± 0.2	7	0.2	1.12 ± 1.07	3	0.2	0.18 ± 0.35	0	0	0
Leptychaster kerguelenensis (E. A. Smith, 1876)	10	0.1	0.81 ± 1.45	0	0	0	0	0	0	2	< 0.1	0.07 ± 0.2	1	< 0.1	0.13 ± 0.31	1	0.1	0.09 ± 0.29	9	0.1	0.28 ± 0.97
Neosmilaster sp. (Fisher, 1930)	44	0.5	3.07 ± 3.14	0	0	0	1	< 0.1	0.41 ± 2.68	81	1.8	4.36 ± 2.87	65	1.7	8.99 ± 4.96	57	3.9	3.51 ± 3.64	41	0.4	2.23 ± 5.99
Odontaster sp. (Verrill, 1880)	0	0	0	0	0	0	0	0	0	1	< 0.1	0.03 ± 0.1	0	0	0	0	0	0	0	0	0
Smilasterias triremis (Sladen, 1889)	146	1.6	9.25 ± 5.88	0	0	0	1	< 0.1	0.28 ± 1.83	9	0.2	0.37 ± 0.47	9	0.2	1.31 ± 0.82	1	0.1	0.06 ± 0.21	11	0.1	0.46 ± 1.69
Echinoidea																					
Pseudechinus sp. (Mortensen, 1903)	2	< 0.1	0.12 ± 0.35	0	0	0	0	0	0	0	0	0	2	< 0.1	0.28 ± 0.44	0	0	0	3	< 0.1	0.08 ± 0.44
Holothuroidea																					
Echinopsolus splendidus (Gutt, 1990)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6292	60.2	537.27 ± 1300.81
Pentactella sp. (Verrill, 1876)	190	2.1	12.63 ± 16.25	1	0.1	0.19 ± 1.24	3	< 0.1	1.59 ± 6.13	135	3	4.43 ± 11.17	90	2.3	13.48 ± 12.05	1	0.1	0.09 ± 0.29	14	0.1	0.45 ± 1.67
Ophiuroidea																					
Ophionotus hexactis (E. A. Smith, 1876)	51	0.6	4.03 ± 5.43	0	0	0	0	0	0	10	0.2	0.31 ± 0.61	1	< 0.1	0.13 ± 0.31	1	0.1	0.03 ± 0.1	4	< 0.1	0.2 ± 0.67

(Continued)

TABLE 2 Continued

Taxa	SD-Rock			SD-Cable-2021			SD-Cable-2022			SD-CN1			SD-CN2			SD-CN3			SD-CN4		
	Ab.	% Ab.	D	Ab.	% Ab.	D	Ab.	% Ab.	D	Ab.	% Ab.	D	Ab.	% Ab.	D	Ab.	% Ab.	D	Ab.	% Ab.	D
Ophiosabine vivipara (Ljungman, 1871)	1140	12.8	67.11 ± 31.74	0	0	0	2	< 0.1	0.57 ± 3.67	226	5.1	7.09 ± 14.5	139	3.5	19.26 ± 18.57	23	1.6	1.66 ± 2.52	174	1.7	6.03 ± 17.26
Ophiuroglypha brevispinosa (H.L. Clark, 1915)	4	< 0.1	0.49 ± 1.49	0	0	0	0	0	0	4	0.1	0.12 ± 0.25	3	< 0.1	0.49 ± 0.75	0	0	0	1	< 0.1	0.05 ± 0.29
Mollusca																					
Bivalvia																					
Gaimardia trapesina (Lamarck, 1819)	619	7	36.86 ± 22.97	37	2.2	4.29 ± 10.16	32	0.3	18.9 ± 64.44	0	0	0	8	0.2	1.55 ± 2.76	0	0	0	0	0	0
Kidderia sp. (Dall, 1876)	1162	13.1	72.06 ± 68.19	922	54.59	207.57 ± 418.52	7854	84.18	3256.85 ± 4969.44	184	4.2	13.86 ± 22.03	68	1.7	9.58 ± 6.55	376	26	33.96 ± 60.85	146	1.4	7.88 ± 26.1
Gastropoda																					
Aeolidiidae gen. indet. (Gray, 1827)	45	0.5	2.52 ± 2.92	0	0	0	0	0	0	2	< 0.1	0.13 ± 0.38	4	0.1	0.52 ± 0.61	4	0.3	0.32 ± 0.75	0	0	0
Margarella violacea (P. P. King, 1832)	9	0.1	0.6 ± 1.57	0	0	0	0	0	0	143	3.2	7.33 ± 6.01	70	1.8	10.52 ± 6.76	77	5.3	10.01 ± 13.42	82	0.8	4.06 ± 6.06
Nacella delesserti (R. A. Philippi, 1849)	0	0	0	19	1.12	3.19 ± 11.09	0	0	0	34	0.8	1.36 ± 1.88	0	0	0	5	0.3	0.57 ± 0.9	46	0.4	5.25 ± 16.07
Porifera																					
Demospongiae																					
Clathria sp. (Schmidt, 1862)	95	1.1	5.23 ± 3.91	7	0.41	3.24 ± 15.29	11	0.12	3.39 ± 11.96	6	0.1	0.21 ± 0.44	5	0.1	0.74 ± 1.26	1	0.1	0.09 ± 0.29	0	0	0
Crella sp. (Gray, 1867)	0	0	0	41	2.43	10.34 ± 31.61	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Halichondria sp. (Fleming, 1828)	2	< 0.1	0.12 ± 0.33	1	0.1	0.19 ± 1.21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haliclona sp. (Grant, 1841)	0	0	0	9	0.53	1.73 ± 6.97	5	0.1	1.26 ± 5.96	0	0	0	0	0	0	0	0	0	0	0	0

(Continued)

TABLE 2 Continued

Taxa	SD-Rock			SD-Cable-2021			SD-Cable-2022			SD-CN1			SD-CN2			SD-CN3			SD-CN4		
	Ab.	% Ab.	D	Ab.	% Ab.	D	Ab.	% Ab.	D	Ab.	% Ab.	D	Ab.	% Ab.	D	Ab.	% Ab.	D	Ab.	% Ab.	D
Hemigellius sp. (Burton, 1932)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	< 0.1	0.03 ± 0.15
Hymedesmia sp. (Bowerbank, 1864)	21	0.2	1.52 ± 3	17	1.01	3.71 ± 6.93	17	0.18	8.73 ± 26.82	0	0	0	0	0	0	0	0	0	0	0	0
Hymeniacidon sp. (Bowerbank, 1858)	3	< 0.1	0.09 ± 0.34	2	0.1	0.37 ± 2.42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mycale sp.1 (Gray, 1867)	0	0	0	120	7.1	28.41 ± 44.61	120	1.29	59.56 ± 120.01	0	0	0	0	0	0	0	0	0	0	0	0
Mycale sp.2 (Gray, 1867)	0	0	0	94	5.57	21.33 ± 44.78	4	< 0.1	3.75 ± 24.29	0	0	0	0	0	0	0	0	0	0	0	0
Tetillidae gen. indet. (Sollas, 1886)	0	0	0	12	0.71	4.49 ± 16.39	1	< 0.1	0.02 ± 0.11	0	0	0	0	0	0	0	0	0	1	< 0.1	0.03 ± 0.15
Algae	TS	% S	S	TS	% S	S	TS	% S	S	TS	% S	S	TS	% S	S	TS	% S	S	TS	% S	S
Ochrophyta																					
Phaeophyceae																					
Desmarestia chordalis (J.D.Hooker & Harvey, 1845)	0	0	0	10.8	20.6	0.49 ± 1.17	3.7	10.5	0.22 ± 0.91	0	0	0	0	0	0	< 0.1	0.3	< 0.1	6.9	45	0.49 ± 1.17
Desmarestia confervoides (M.E.Ramírez & A.F.Peters, 1993)	0.2	9.8	< 0.1	2.2	4.2	< 0.1	11.6	32.9	1.06 ± 1.14	1.4	13.8	< 0.1	< 0.1	0.9	< 0.1	0.9	11.2	< 0.1	0.3	1.9	< 0.1
Macrocystis pyrifera ((Linnaeus) C.Agardh, 1820)	0.8	30.7	< 0.1	2.8	5.3	0.56 ± 1.68	1.2	3.4	0.55 ± 1.21	0.8	7.8	< 0.1	1	33.9	0.16 ± 0.15	0.3	3.6	< 0.1	0.3	1.9	< 0.1
Chlorophyta																					
Ulvophyceae																					
Chlorophyta fam. gen. sp. (Pascher, 1914)	0.4	14.1	< 0.1	0.4	0.7	< 0.1	0.2	0.6	< 0.1	0	0	0	< 0.1	< 0.1	< 0.1	0	0	0	0	0	0
Codium adhaerens (C.Agardh, 1822)	0	0	0	0	0	0	0	0	0	1.5	14.7	< 0.1	0.4	12.6	< 0.1	1.6	19.4	0.18 ± 0.25	5.3	34.6	0.27 ± 0.39
Ulva sp. (Linnaeus, 1753)	0	0	0	< 0.1	0.1	< 0.1	< 0.1	< 0.1	< 0.1	1.3	12.2	< 0.1	0.1	4.7	< 0.1	1.1	12.9	0.14 ± 0.19	0.2	1.2	< 0.1

(Continued)

TABLE 2 Continued

Taxa	SD-Rock			SD-Cable-2021			SD-Cable-2022			SD-CN1			SD-CN2			SD-CN3			SD-CN4		
	TS	% S	S	TS	% S	S	TS	% S	S	TS	% S	S	TS	% S	S	TS	% S	S	TS	% S	S
Rhodophyta																					
Florideophyceae																					
Corallinales fam. gen. sp. (P.C. Silva & H.W. Johansen, 1986)	< 0.1	0.2	< 0.1	0.5	1	< 0.1	0.2	0.7	< 0.1	< 0.1	0.3	< 0.1	< 0.1	0.1	< 0.1	< 0.1	0.1	< 0.1	0.9	5.7	< 0.1
Delesseriaceae gen. indet. (Bory, 1828)	1.1	45.2	< 0.1	35.7	68.2	1.4 ± 1.41	17.2	48.9	1.63 ± 1.04	0	0	0	0	0	0	0	0	0	0	0	0
Falklandiella harveyi ((J.D.Hooker) Kylin, 1956)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	1.9	< 0.1	< 0.1	< 0.1	< 0.1
Heterosiphonia berkeleyi (Montagne, 1842)	0	0	0	< 0.1	< 0.1	< 0.1	0	0	0	0	0	0	0	0	0	0.1	0.7	< 0.1	0.9	6.1	< 0.1
Phycodrys quercifolia ((Bory) Skottsberg, 1922)	0	0	0	0	0	0	0	0	0	2.5	23.7	< 0.1	0.4	13.4	< 0.1	3	36.2	0.13 ± 0.18	0.2	1.3	< 0.1
Rhodophyta fam. gen. sp.1 (Wettstein, 1901)	0	0	0	0	0	0	0	0	0	2.9	27.2	0.18 ± 0.23	1	34.4	0.12 ± 0.17	1.1	13.1	< 0.1	0.3	2.3	< 0.1
Rhodophyta fam. gen. sp.2 (Wettstein, 1901)	0	0	0	< 0.1	< 0.1	< 0.1	< 0.1	0.1	< 0.1	0	0	0	0	0	0	0	0	0	0	0	0
Schizoseris sp. (Kylin, 1924)	< 0.1	0.1	< 0.1	< 0.1	< 0.1	< 0.1	1	2.8	0.24 ± 0.54	< 0.1	0.4	< 0.1	0	0	0	0.1	0.7	< 0.1	0	0	0

purpose, a species-trait abundance matrix was obtained by multiplying the faunal community matrix (abundances of the species within transects) with the species-trait matrix, containing the relative expression of trait modalities by species after standardization of scores to 1 for each trait and species. This procedure gives a weight at each modality in order to ensure that each trait has equal weight in the underlying functional analyses, regardless of the number of associated modalities. Functional analyses were conducted using the *FD* package (Laliberté et al., 2014) and PCA using the package *vegan* (Oksanen et al., 2020).

3 Results

3.1 Imagery sampling effort

A total of 50 faunal (representing 40,157 individuals) and 14 algal taxa were identified across the seven transects (Table 2). The *Baie du Marin* rarefaction curves (all transects combined) of the faunal and algal diversity show that a plateau is reached at about 50 taxa and 14 taxa, respectively, giving a fair representation of the benthic diversity in hard substrates along transects conducted at *Baie du Marin* (Figure 4; black curves). At the transect level, faunal rarefaction curves show that the sampling effort tends to reach an asymptote (with the exception of SD-CN3 and SD-Cable-2021 transects), indicating that enough images were collected to capture faunal diversity within transects (Figure 4A). For algal taxa, rarefaction curves at the transect level tend to reach a plateau, indicating sufficient sampling from images for algal diversity (Figure 4B).

3.2 Crozet benthic communities' description

The most diversified faunal phyla were Echinodermata (with 8 Asteroidea, 3 Ophiuroidea, 2 Holothuroidea and 1 Echinoidea) and Porifera (with 10 Demospongiae); and the most represented algal phylum was Rhodophyta (with 8 Florideophyceae). A high level of rare faunal taxa was found among transects, ranging from 50 to 82.4% (74.2 ± 10.6%) of the species (Table 3). Rare algal taxa were fewer, ranging from 10 to 60% (33.3 ± 15.5%). More specifically, the SD-Rock transect was dominated by the polychaetes *Parasabella* sp. (183.3 ± 146.1 ind m^{-2}; 32.4%) and *Lanice marionensis* (149.2 ± 108.1 ind m^{-2}; 27.1%), the bivalve *Kidderia* sp. (72.1 ± 68.2 ind m^{-2}; 13.1%) and the ophiuroid *Ophiosabine vivipara* (67.1 ± 31.7 ind m^{-2}; 12.8%). As for macroalgae, this transect was dominated by Delesseriaceae gen. indet. (45.2%), *Macrocystis pyrifera* (30.7%) and Chlorophyta sp. (14.1%). On the northern coast of BDM, the transect SD-CN1 was dominated by the high density of polychaete *Parasabella* sp. (105.7 ± 204 ind m^{-2}; 75.4%), and to a lesser extent by the ophiuroid *O. vivipara* (7.1 ± 14.5 ind m^{-2}; 5.1%) and the bivalve *Kidderia* sp. (13.9 ± 22 ind m^{-2}; 4.2%), while algae were mainly represented by Rhodophyta sp.1 (27.2%), *Phycodrys quercifolia* (23.7%) and *Codium adhaerens* (14.6%). The SD-CN2 transect was highly dominated by the polychaete *Parasabella* sp. (481.8 ± 416.1 ind m^{-2}; 82.7%), and to a lesser extent by the ophiuroid *O. vivipara* (19.3 ± 18.6 ind m^{-2}; 3.5%) and the polychaete *Thelepus spectabilis* (17.7 ± 26.2 ind m^{-2}; 2.5%); and by Rhodophyta sp.1 (34.4%), *M. pyrifera* (33.9%) and *P. quercifolia* (13.4%). Like the SD-CN1 and SD-CN2 transects, SD-CN3 was dominated by the polychaete *Parasabella* sp. (46.2 ± 58.9 ind m^{-2}; 45.2%), the

Rarefaction curves for **(A)** faunal and **(B)** algal communities within the seven transects at *Baie du Marin*. Black lines in the inset figures represent the rarefaction curve at the *Baie du Marin* scale considering all transects combined.
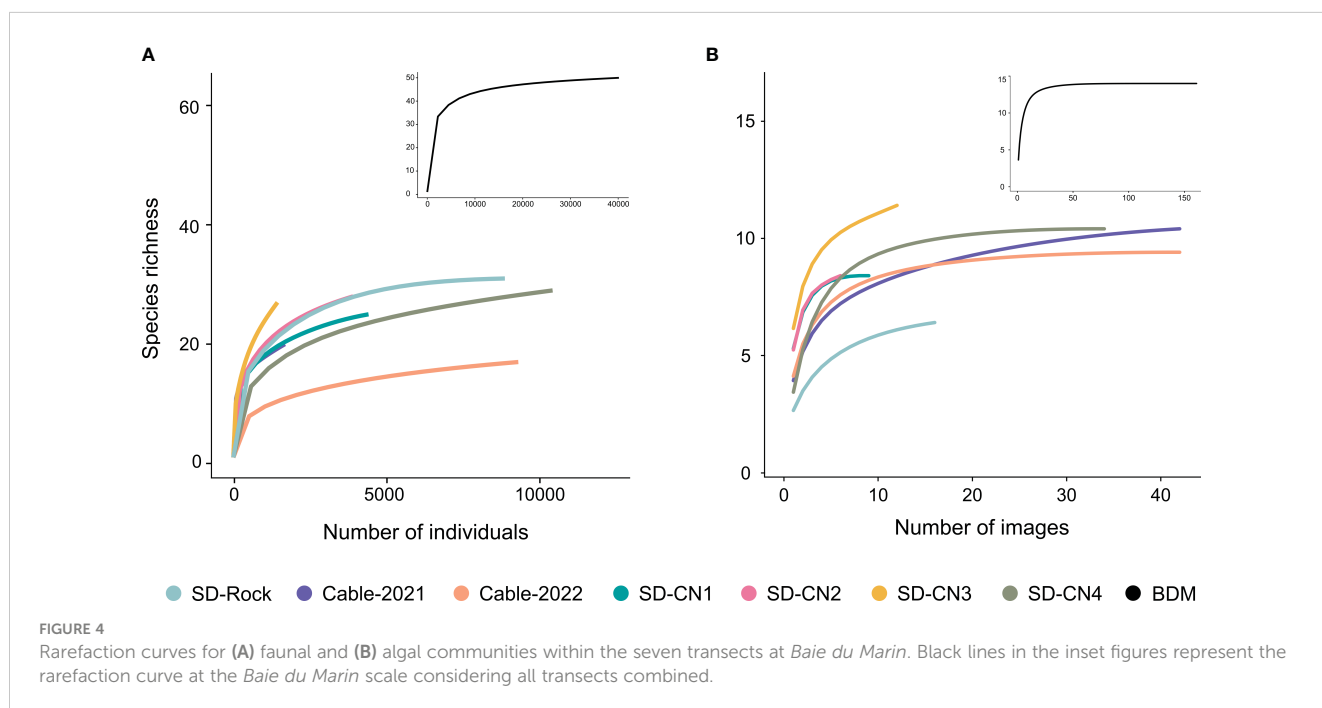
TABLE 3 Diversity indices of faunal and algal communities for each transect and for Baie du Marin (all transects combined). Diversity indices are taxonomic richness (R), rarefied taxonomic richness (R_{rar}), mean taxonomic richness by image (R_m), Shannon diversity (N), rarefied Shannon diversity (N_{rar}), mean Shannon diversity by image (N_m), Simpson diversity ($1/\lambda$), rarefied Simpson diversity ($1/\lambda_{rar}$), mean Simpson diversity by image ($1/\lambda_m$), Piélou's evenness (J'), rarefied Piélou's evenness (J'_{rar}), mean Piélou's evenness by image (J'_m) and percentage of rare species (% Rar). The sampling effort is also provided with the number of images analyzed (n_{image}), transect total surface (TTS) and the mean image surface (S_m). Significance is given by asterisks: (***) p-value $\leq$ 0.001.

Transect	R	R_{rar}	$R_m \pm sd$	N	N_{rar}	$N_m \pm sd$	$1/\lambda$	$1/\lambda_{rar}$	$1/\lambda_m \pm sd$	J'	J'_{rar}	$J'_m \pm sd$	% Rar	n_{image}	TTS (m²)	$S_{mean} \pm sd$ (m²)
Fauna																
SD-Rock	31	21	14.323 ± 3.535	6.033	5.977	5.174 ± 0.816	4.584	4.574	3.934 ± 0.886	0.523	0.587	0.626 ± 0.075	74.2	16	18.14	1.13 ± 0.51
SD-Cable-2021	20	19	3.476 ± 2.856	5.061	5.055	2.060 ± 1.858	2.971	2.971	1.689 ± 1.495	0.541	0.550	0.455 ± 0.366	50	42	13.54	0.32 ± 0.39
SD-Cable-2022	17	10	3.190 ± 1.596	1.791	1.783	1.334 ± 0.805	1.381	1.381	1.181 ± 0.712	0.206	0.251	0.246 ± 0.237	82.4	42	7.56	0.18 ± 0.28
SD-CN1	25	20	8.889 ± 4.314	3.080	3.061	3.405 ± 1.749	1.737	1.737	2.628 ± 1.463	0.350	0.373	0.560 ± 0.239	68	9	22.56	2.51 ± 1.04
SD-CN2	28	22	15 ± 3.899	2.407	2.391	3.488 ± 2.225	1.453	1.453	2.328 ± 1.437	0.264	0.282	0.424 ± 0.245	75	6	7.12	1.19 ± 0.26
SD-CN3	27	27	8.083 ± 3.605	5.413	5.413	3.470 ± 1.215	3.505	3.505	2.492 ± 0.752	0.512	0.512	0.619 ± 0.151	70.4	12	14.18	1.18 ± 0.79
SD-CN4	29	17	3.706 ± 3.564	3.437	3.410	1.711 ± 1.508	2.398	2.396	1.384 ± 1.233	0.367	0.433	0.431 ± 0.360	79.3	34	17.73	0.52 ± 0.26
Baie du Marin	50	-	-	7.720	-	-	5.056	-	-	0.522	-	-	82	161	100.83	1 ± 0.73
Algae																
SD-Rock	6	5	2.250 ± 0.931	3.454	3.797[a]	1.659 ± 0.937	3.047	3.254[a]	1.523 ± 0.870	0.692	0.829	0.625 ± 0.353	33.3	16	18.14	1.13 ± 0.51
SD-Cable-2021	10	7	3.476 ± 1.087	2.614	5.647[a]	1.753 ± 0.674	1.952	4.979[a]	1.488 ± 0.564	0.417	0.890	0.425 ± 0.221	60	42	13.54	0.32 ± 0.39
SD-Cable-2022	9	7	3.714 ± 0.995	3.457	6.034[a]	2.265 ± 0.664	2.770	5.363[a]	2.006 ± 0.662	0.565	0.924	0.621 ± 0.196	44.4	42	7.56	0.18 ± 0.28
SD-CN1	8	8	4.889 ± 1.453	5.723	7.136[a]	2.795 ± 1.234	5.219	6.653[a]	2.265 ± 1.023	0.839	0.945	0.585 ± 0.220	25	9	22.56	2.51 ± 1.04
SD-CN2	8	8	4.5 ± 2.345	4.312	7.272[a]	2.465 ± 1.137	3.715	6.837[a]	2.052 ± 0.873	0.703	0.954	0.600 ± 0.140	37.5	6	7.12	1.19 ± 0.26
SD-CN3	11	10	5.583 ± 1.240	5.729	8.519[a]	2.905 ± 0.983	4.613	7.772[a]	2.343 ± 0.885	0.728	0.930	0.591 ± 0.150	36.4	12	14.18	1.18 ± 0.79
SD-CN4	10	8	2.941 ± 1.632	4.091	6.832[a]	1.399 ± 0.990	3.021	6.052[a]	1.240 ± 0.846	0.612	0.924	0.303 ± 0.286	10	34	17.73	0.52 ± 0.26
Baie du Marin	14	-	-	6.168	-	-	4.178	-	-	0.689	-	-	28.6	161	100.83	1 ± 0.73

[a]Rarefied univariate measures for algae were estimated from presence-absence data.

bivalve *Kidderia* sp. (34 ± 60.9 ind m^{-2}; 26%) as well as the polychaete *T. spectabilis* (7.5 ± 12.1 ind m^{-2}; 7.8%); while algae were mainly represented by *P. quercifolia* (36.2%), *C. adhaerens* (19.4%), Rhodophyta sp.1 (13.1%) and *Ulva* sp. (12.9%). Finally, SD-CN4 fauna was dominated by the holothuroid *Echinopsolus splendidus* (537.3 ± 1300.8 ind m^{-2}; 60.2%), the polychaete *Parasabella* sp. (66.8 ± 207 ind m^{-2}; 17.2%) and the actiniid Actiniaria sp.6 (129 ± 295.5 ind m^{-2}; 15.5%), while algae were represented by *Desmarestia chordalis* (45%), *C. adhaerens* (34.6%), *Heterosiphonia berkeleyi* (6.1%) and Corallinales (5.7%). For submarine cables transects, the SD-Cable-2021 transect was dominated by the bivalve *Kidderia* sp. (207.6 ± 418.5 m^{-2}; 54.6%), the polychaete *Parasabella* sp. (61.8 ± 119 ind m^{-2}; 16.2%) and the sponge *Mycale* sp.1 (28.4 ± 44.6 ind m^{-2}; 7.1%); and algae were represented by Delesseriaceae gen. indet. (68.2%), *D. chordalis* (20.6%) and *M. pyrifera* (5.3%). Finally, the SD-Cable-2022 transect was dominated by a high density of the bivalve *Kidderia* sp. (3256.9 ± 4.969.4 ind m^{-2}; 84.2%) and to a lesser extent by the polychaete Serpulidae (418.6 ± 1148.5 ind m^{-2}; 12.3%) and the sponge *Mycale* sp.1 (59.6 ± 120 ind m^{-2}; 1.3%), while algae were represented by Delesseriaceae gen. indet. (48.9%), *Desmarestia confervoides* (32.9%) and *D. chordalis* (10.5%).

3.3 Taxonomic benthic diversity among and within transects

Baie du Marin hard substrates indicate a high-level of taxonomic richness and diversity for both fauna and algae composition (Table 3). With the exception of SD-Cable-2022, where species richness was low (R_{rar} = 10), the number of species was similar between transects (R_{rar} from 17 to 27 taxa). The highest level of diversity was found for the SD-Rock transect (N_{rar} = 5.977; $1/\lambda_{rar}$ = 4.574), followed by the SD-CN3 transect (N_{rar} = 5.413; $1/\lambda_{rar}$ = 3.505), and to a lesser extent by the SD-Cable-2021 transect (N_{rar} = 5.055; $1/\lambda_{rar}$ = 2.971; Table 3). Diversity values on the rock located at the center of the bay were greater (N_{rar} = 5.977; $1/\lambda_{rar}$ = 4.574) than those estimated from the northern coast (N_{rar} = 3.569 ± 1.3; $1/\lambda_{rar}$ = 2.273 ± 0.912). These patterns at the scale of transects are in line with the average richness and diversity per image. Along submarine cables transects, mean diversity indices per image were relatively low (SD-Cable-2021: R_m = 3.476 ± 2.856; N_m = 2.060 ± 1.858; $1/\lambda_m$ = 1.689 ± 1.595; SD-Cable-2022: R_m = 3.190 ± 1.596; N_m = 1.334 ± 0.805; $1/\lambda_m$ = 1.181 ± 0.712; Table 3). Images of the SD-Rock transect displayed high-levels of average richness and diversity (R_m = 14.323 ± 3.535; N_m = 5.174 ± 0.816; $1/\lambda_m$ = 3.934 ± 0.886), as well as a low spatial variability of these indices (Table 3). With the exception of the SD-CN4 transect, the mean diversity by image of transects conducted on the northern coast of the bay was similar (SD-CN1: N_m = 3.405 ± 1.749; $1/\lambda_m$ = 2.628 ± 1.463; SD-CN2: N_m = 3.488 ± 2.225; $1/\lambda_m$ = 2.328 ± 1.437; SD-CN3: N_m = 3.470 ± 1.215; $1/\lambda_m$ = 2.492 ± 0.752; Table 3). Overall, macrofaunal communities were characterized by low Piélou's evenness values (J'_{rar} = 0.427 ± 0.131), indicating high dominance of certain faunal

taxa (Table 3). For algal communities, species richness was similar between transects and substrates (R_{rar} from 6 to 11 taxa; Table 3). Nevertheless, the highest value of species richness and diversity indices were found at the SD-CN3 transect (R_{rar} = 10; N_{rar} = 8.519; $1/\lambda_{rar}$ = 7.772), while lowest values were found on the SD-Rock transect (R_{rar} = 5; N_{rar} = 3.797; $1/\lambda_{rar}$ = 3.254). Algal diversity metrics were also lower on the submarine cables (N_{rar} = 5.841 ± 0.274; $1/\lambda_{rar}$ = 5.171 ± 0.272) compared to the rocky substrate of the northern coast (N_{rar} = 7.44 ± 0.743; $1/\lambda_{rar}$ = 6.829 ± 0.713; Table 3). Overall, the average richness and diversity by image along transects conducted on the northern coast of the *Baie du Marin* were higher than submarine cables and SD-Rock transects (Table 3). Piélou's evenness values for algal communities were greater than for faunal communities (J'_{rar} = 0.914 ± 0.042), indicating the greater distribution of algal cover across transects.

Taking into account the spatial heterogeneity of diversity metrics within transects (Figure 5), significant differences were identified in faunal species richness between rocky and submarine cables substrates, except for the SD-CN4 transect (Figure 5A). Overall, no significant variations in faunal species richness were detected between rocky substrate transects. However, the SD-Rock transect has shown significant differences of the faunal species richness and Shannon and Simpson diversity indices with submarines cables (SD-Cable-2021 and SD-Cable-2022) and SD-CN4 transects (Figures 5A, C, E). Globally, no significant differences in the Shannon and Simpson diversity indices were observed among transects conducted on the northern coast of the *Baie du Marin* (Figures 5C, E). As for species richness, no significant differences of Shannon and Simpson diversity indices were observed between submarine cables transects. For the algal component, no clear patterns were observed for the algal species richness and diversity between rocky and submarine cables transects (Figure 5). The SD-Rock highlighted significant variations of the algal species richness with submarine cables transects, but no significant differences in the Shannon and Simpson diversity indices (Figures 5B, D, F). On the northern coast of the bay, the algal species richness and Shannon and Simpson diversity indices were similar between the SD-CN1, SD-CN2 and SD-CN3 transects, but significant variations were observed between SD-CN4 with both SD-CN1 and SD-CN3 transects (Figures 5B, D, F).

3.4 Faunal and algal community variation among transects

Principal Coordinates ordination Analyses (PCoA) were performed to assess compositional patterns on faunal and algal communities between transects (Figure 6). For faunal communities, the PCoA highlighted distinct communities between natural (rocks) and artificial (submarine cables) hard substrates (Figure 6A). Although a section of the submarine cables goes through the rock, variation in faunal composition was highlighted between rock (SD-Rock) and submarine cables transects (SD-Cable-2021 and SD-Cable-2022). Overall, no clear differences were found
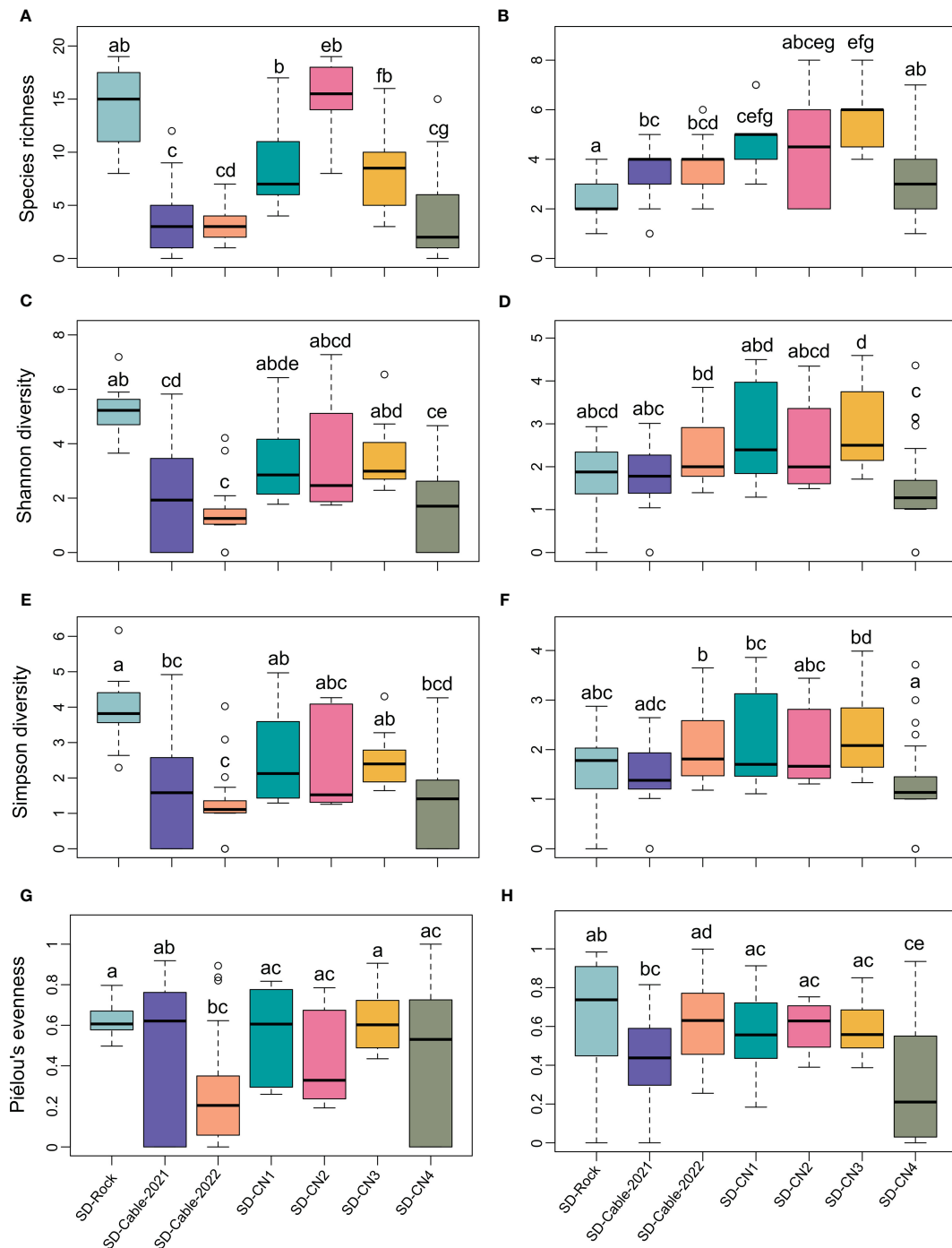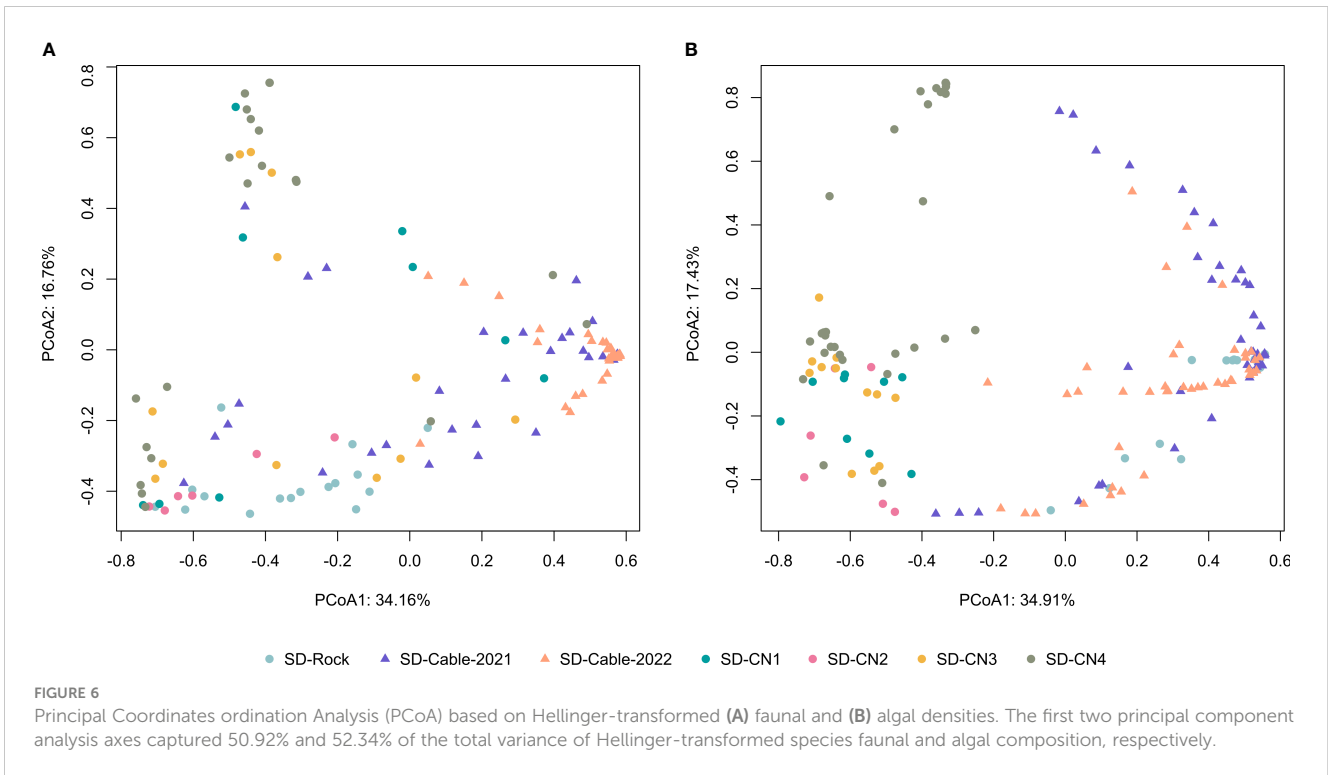
FIGURE 5

Diversity metrics comparison among the seven transects conducted at *Baie du Marin* at the image scale, with: species richness for fauna **(A)** and algae **(B)**; Shannon diversity for fauna **(C)** and algae; Simpson diversity for fauna **(D)** and algae **(E)**; and Piélou's evenness for fauna **(G)** and algae **(H)**, respectively. Each letter denotes a significantly different result according to the Dunn's *post-hoc* pairwise tests.

between the four transects conducted on the northern coast of the *Baie du Marin*. However, faunal communities of the SD-Rock transect have displayed compositional and structural differences from the northern coast and submarine cable transects (Figure 6A). Interestingly, PCoA have shown that transect SD-CN4 harbors two distinct groups of fauna. Similar patterns were observed for algal communities (Figure 6B). With the exception of the SD-Rock, an

important algal community variation was observed between natural and submarine cables substrates. This algal heterogeneity was found between transects from the center of the bay (SD-Rock, SD-Cable-2021 and SD-Cable-2022) and those on the northern coast of the bay (SD-CN1, SD-CN2, SD-CN3 and SD-CN4) (Figure 6B). However, no differences were observed between transects conducted on the northern part of the *Baie du Marin*.

3.5 Influence of algal cover on species diversity within transects

A Redundancy Analysis (RDA) was performed to characterize the influence of algal cover on faunal communities, and the algae distribution across transects (Figure 7). The RDA discerns four groups of co-occurring algae corresponding to: (i) *Schizoseris* sp.,

Rhodophyta sp.2, *Desmarestia confervoides* and Delesseriaceae gen. indet.; (ii) *Macrocystis pyrifera* and Chlorophyta sp.; (iii) *Phycodrys quercifolia*, *Ulva* sp., *Codium adhaerens*, *Falklandiella harveyi* and Rhodophyta sp.1; and (iv) *Heterosiphonia berkeleyi*, *Desmarestia chordalis* and Corallinales. Cables transects were generally characterized by the presence of algae in the group (i). The presence of a high surface cover generated by *D. confervoides* and

FIGURE 8

Observed and expected contribution, expressed in percentage values, of each spatial scale to the *Baie du Marin* richness (q=0) and diversity (q=1 and q=2) for **(A)** faunal and **(B)** algal communities.
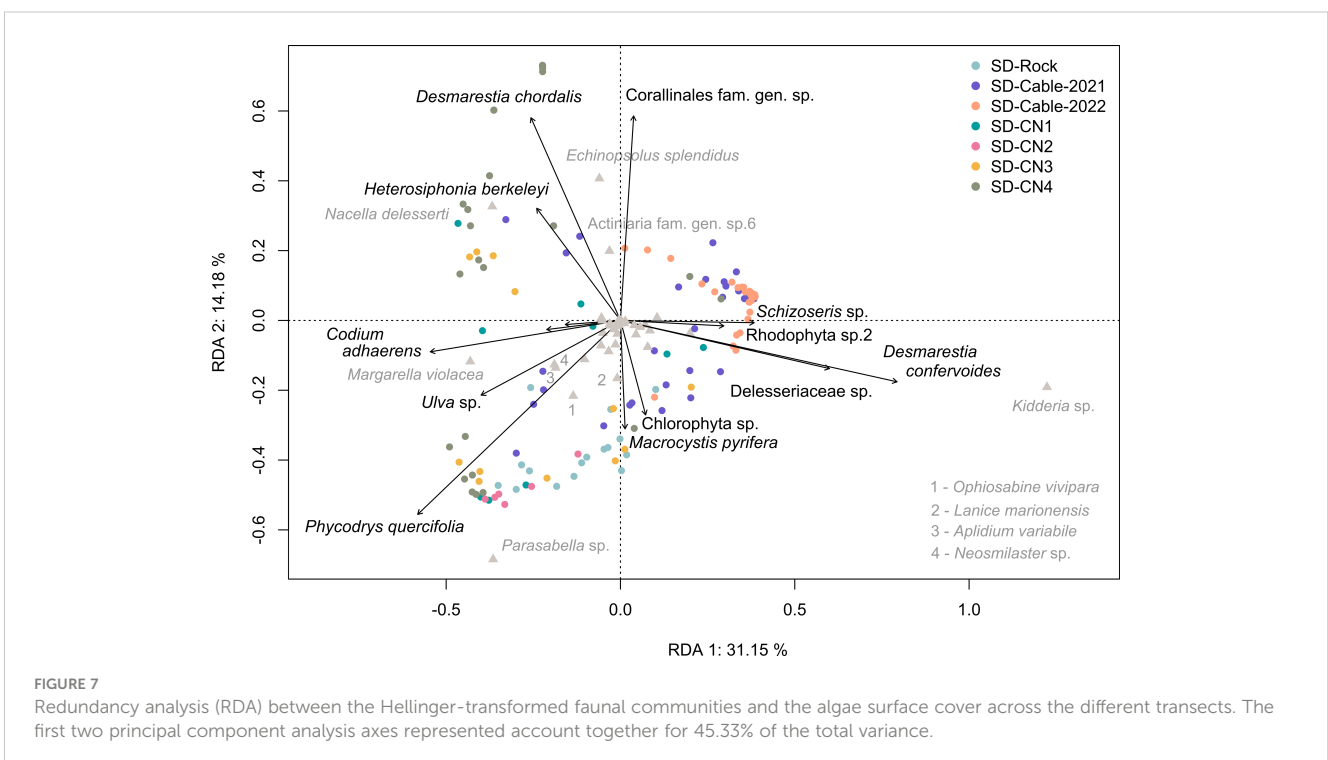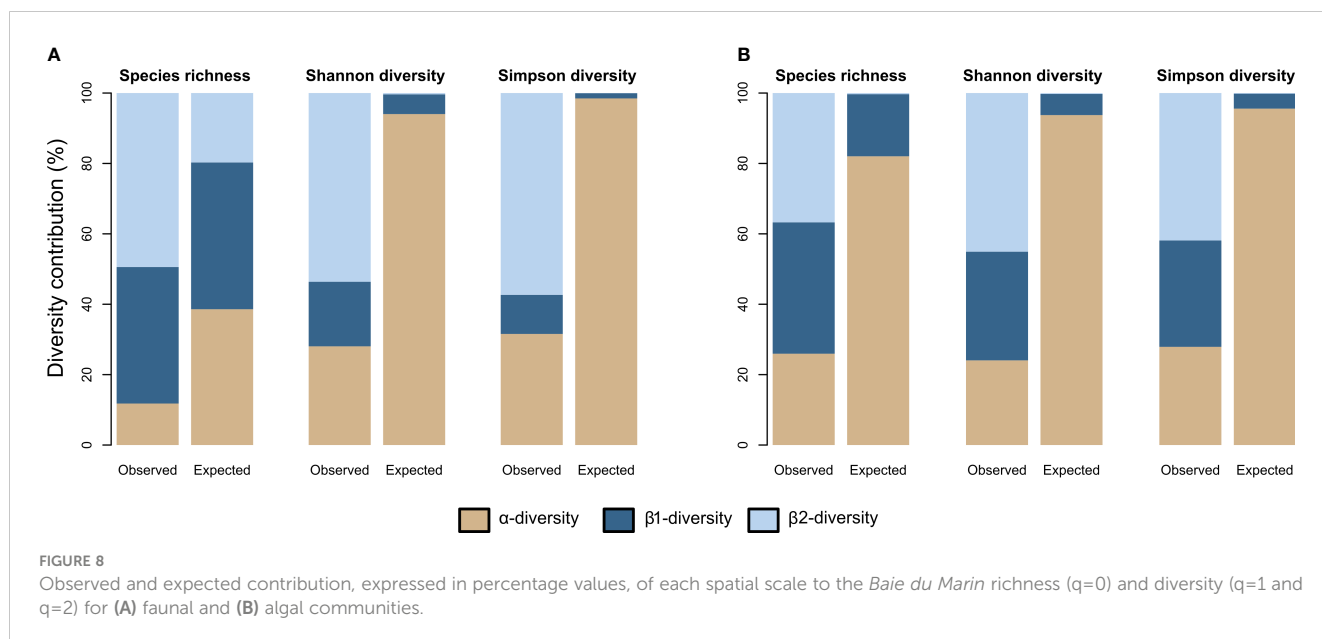
Delesseriaceae gen. indet. was correlated to high densities of the bivalve *Kidderia* sp. The SD-Rock transect, characterized by high densities of the polychaetes *Parasabella* sp. and *Lanice marionensis*, as well as the ophiuroid *Ophiosabine vivipara*, was dominated by algae of the group (ii) and by *P. quercifolia*. Overall, transects conducted on the northern coast of the *Baie du Marin* have a greater levels of algal diversity, and more specifically to algae groups (iii) and (iv). The RDA highlighted that the distribution of the gastropod *Margarella violacea* is associated with the presence of *C. adhaerens*, A section of the SD-CN4 transect exhibited a high surface coverage of *D. chordalis* and Corallinales, while another section was mainly dominated by *P. quercifolia*. Corallinales are associated with the presence of high densities of the holothuroid *Echinopsolus splendidus* and the actiniid Actiniaria sp.6. The occurrence of the gastropod *Nacella delesserti* was also related to the presence of *D. chordalis* and *H. berkeleyi* algae.

3.6 Richness and diversity contributions across spatial scales

The additive partitioning of the *Baie du Marin* faunal richness ($\gamma = 50$) showed that the β_2-diversity had the greatest contribution to total faunal richness (49.4%), followed by β_1-diversity (38.8%) and α-diversity (11.8%) components (Figure 8A). The observed richness per image ($\alpha_{obs}= 5.895$) and among images within transects ($\beta_{1obs} = 19.390$) were different and lower than expected if taxa were randomly distributed (Table 4; Figure 8A). The observed richness among transects was on the other hand, significantly higher than expected ($\beta_{2obs} = 24.714$; $p = 0.001$). For Shannon diversity, β_2-diversity (53.6%) contributed the most to the *Baie du Marin* diversity, followed by α-diversity (28%) and β_1-diversity (18.3%) (Figure 8A). Alpha-diversity was lower than randomly expected by the null model. However, β_1-diversity

TABLE 4   Additive partitioning of the *Baie du Marin* richness and diversity of faunal and algal communities. α-diversity corresponds to the mean value per images, $\beta1$-diversity corresponds to the value among images within transects and $\beta2$-diversity to the value among transects. *P*-values were obtained by comparing observed values to expected values draw from a random distribution (9999 iterations).

Taxa		Species richness			Shannon diversity			Simpson diversity		
		Observed	Expected	*p*-value	Observed	Expected	*p*-value	Observed	Expected	*p*-value
Fauna	α	5.895	19.292	1	2.165	7.259	1	1.596	4.979	1
	β_1	19.39	20.846	0.997	1.415	0.432	0.001***	0.561	0.074	0.001***
	β_2	24.714	9.862	0.001***	4.14	0.029	0.001***	2.899	0.003	0.001***
	γ	50	50	-	7.72	7.72	-	5.056	5.056	-
Algae	α	3.634	11.485	1	1.921	7.485	1	1.558	5.337	1
	β_1	5.224	2.466	0.010***	2.465	0.478	0.010***	1.687	0.236	0.010***
	β_2	5.143	0.049	0.010***	3.599	0.022	0.010***	2.339	0.011	0.010***
	γ	14	14	-	7.985	7.985	-	5.584	5.584	-

(β_{1obs} = 1.415) and β_2-diversity (β_{2obs} = 4.14) were significantly higher than expected (p = 0.001). A similar pattern was observed for Simpson diversity (Table 4). For algal communities, the additive partitioning of the *Baie du Marin* richness (γ = 14) showed a similar contribution of β_1-diversity (37.3%) and β_2-diversity (36.7%), followed by α-diversity (26%) (Figure 8B). The additive partitioning shows that richness among images within transects (β_{1obs} = 5.224) and richness among transects (β_{2obs} = 5.143) were significantly greater than expected (p = 0.010) (Table 4). For Shannon diversity and Simpson diversity, similar patterns were observed with a greater contribution of β_2-diversity (45.1% and 41.9% respectively) to the *Baie du Marin* diversity, followed by the contribution of β_1-diversity (30.9% and 30.2% respectively) and α-diversity (24% and 27.9% respectively; Table 4; Figure 8B). Similar patterns of greater than expected β_1 and β_2 components were observed for both Shannon and Simpson diversity indices (Table 4).

3.7 Functional diversity of benthic faunal communities

The Principal Component Analysis (PCA) illustrated the trait distribution between faunal taxa (Figure 9) and trait densities within transects at *Baie du Marin* (Figure 10). PCA indicates that dominant species are characterized by a suspension-feeding (active

or passive) mode. Active suspension feeders are mainly represented by bivalves and demosponges, while passive suspension feeders correspond to polychaetes and holothuroids (Figure 9). Despite lower abundances, a high diversity of predators, mainly represented by Asteroidea taxa, occurs within faunal assemblages. For trait densities distribution within transects, the PCA showed that submarine cables transects were characterized by attached, active suspension feeders and very small and solitary taxa with a direct development (Figure 10). In contrast, rock and northern coast transects display similar functional traits, dominated by habitat-forming and tube-dwellers taxa with a medium size and passive suspension feeders, as well as gregarious behavior, hermaphrodite reproduction, and lecithotrophic development mode (Figure 10).

Rocky substrate habitats displayed the greatest functional richness values, whereas transects on the submarine cables were characterized by lower levels of functional richness (Table 5; FRic). Faunal abundances were distributed in a similar pattern between transects (similar FEve and FDiv), with clustered abundances (low FEve) and higher abundances at the edges of the trait space (high FDiv) (Table 5; FEve and FDiv). The higher functional dispersion (FDis) and Rao's quadratic entropy (RaoQ) values were found at the SD-CN3 transect, followed by SD-Rock and SD-Cable-2021 transects, whereas lower transect values were found at SD-Cable-2022, followed by SD-CN2 and SD-CN1 transects (Table 5; FDis and RaoQ). Collectively, all transects have shown a low functional
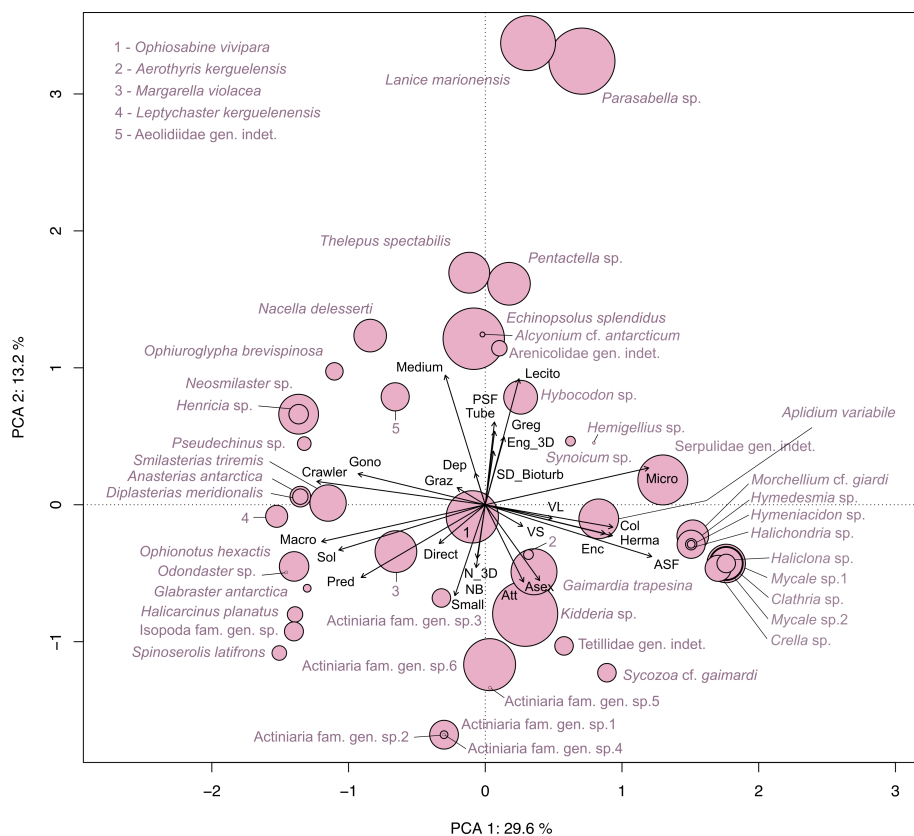

FIGURE 9
Principal Component Analysis (PCA) on functional trait distribution in faunal taxa identified within the *Baie du Marin* weighted by their abundances. The first two PCA axes jointly account for 42.8% of the total variance.
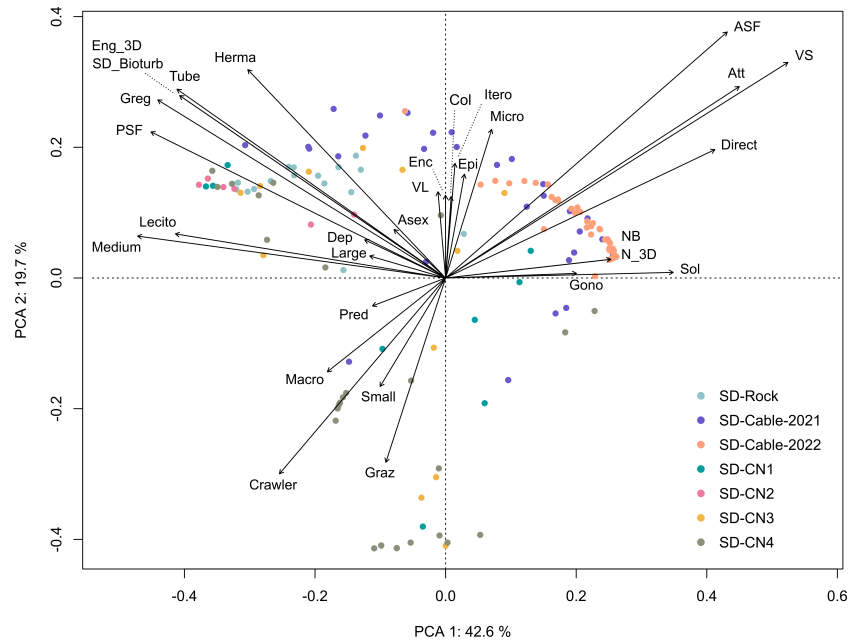
FIGURE 10
Principal Component Analysis (PCA) of the Hellinger-transformed trait modality densities within transects. The first two principal component analysis axes represented account together for 62.3% of the total variance of Hellinger-transformed trait composition.

redundancy (FR), ranging from 0.162 to 0.464 (0.301 ± 0.116) (Table 5; FR).

4 Discussion

4.1 Description of hard substrate benthic communities

Crozet hard substrates have shown high faunal and algal diversity, highlighting the significant ecological value of these

habitats for the preservation of marine polar ecosystems. Similarly to other Antarctic and sub-Antarctic islands (Downey et al., 2012), Demospongiae constitute a dominant component of Crozet marine benthic communities. Sponges provide a high habitat structural complexity and heterogeneity (Thrush et al., 2006), and also act as food resource and substrate for a great variety of faunal species (Gutt and Schickan, 1998; McClintock et al., 2008). The high diversity of echinoderms and more specifically sea stars (Asteroidea) is also characteristic of subtidal Southern Ocean benthic communities, where these organisms play an important role in trophic interactions and ecosystem functioning

TABLE 5 Faunal functional diversity between transects conducted on hard substrates at *Baie du Marin*, with: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), functional redundancy (FR), Rao's quadratic entropy (RaoQ), and their respective geometric representations.

Transect	FRic	FEve	FDiv	FDis	FR	RaoQ
SD-Rock	$8.032*10^{-2}$	0.372	0.992	1.888	0.464	3.97
SD-Cable-2021	$5.939*10^{-6}$	0.337	0.955	1.729	0.369	3.414
SD-Cable-2022	$3.757*10^{-7}$	0.28	0.972	0.666	0.169	0.947
SD-CN1	$1.838*10^{-2}$	0.37	0.978	1.228	0.224	2.425
SD-CN2	$2.252*10^{-2}$	0.415	0.984	0.918	0.162	1.786
SD-CN3	$6.122*10^{-3}$	0.439	0.966	2.033	0.378	4.207
SD-CN4	$1.214*10^{-1}$	0.404	0.994	1.426	0.341	2.576
Baie du Marin	1	0.346	0.987	2.05	0.458	4.236

(McClintock, 1994; Le Bourg et al., 2022). *Baie du Marin* rocky substrates are covered by high densities of tube-dwellers polychaetes such as the terebellid *Lanice marionensis*, on which the Aeolidiidae nudibranchs feed, and the sabellid *Parasabella* sp. Interestingly, high-level densities of the polychaete *Lanice marionensis* were previously reported at Crozet, Marion and Prince Edward islands, but were not encountered at Kerguelen Islands (Sicinski and Gillet, 2002). These high polychaete densities found in Crozet benthic communities are often associated with high densities of the ophiuroid *Ophiosabine vivipara*. This brittle star is common on rocky substrates in the sub-Antarctic region, as reported at Prince Edwards Islands (Branch et al., 1993) and at Saint-Paul and Amsterdam Islands (O'Hara and Thuy, 2022). Important populations of the holothuroid *Echinopsolus splendidus* were also found on rocky substrates at shallow depths on the northern coast of the *Baie du Marin*. This species was also reported in the Antarctic region (O'Loughlin et al., 2011). Although some characteristic groups of sub-Antarctic rocky shores such as barnacles (e.g., genus *Balanus*) and mussels (e.g., genera *Aulacomya* and *Mytilus*) have been reported at Bounty Island (Freeman et al., 2011) and Kerguelen Islands (Arnaud, 1974), they appear to be absent in sampling areas of Crozet. The crab *Halicarcinus planatus*, only member of the Hymenosomatidae family that inhabits shallow subtidal waters of sub-Antarctic islands (Arnaud, 1974; Beckley and Branch, 1992; Branch et al., 1993), was identified at *Baie du Marin*. Extended stands of the giant kelp *Macrocystis pyrifera* are predominant in nearshore subtidal ecosystems of Kerguelen compared to the less widespread beds at Crozet. However, the composition of the marine vegetation identified at Crozet appears to be closely similar to algal taxa reported in coastal waters of the Kerguelen Islands, with a dominance of Rhodophyta species (Féral et al., 2021). As reported from the Beagle Channel at Tierra del Fuego (Adami and Gordillo, 1999), the bivalve *Gaimardia trapesina* is often found attached to the fronds of *M. pyrifera*. This bivalve is an emblematic species of nearshore Antarctic and sub-Antarctic waters. It has already been identified in numerous areas such as Antarctic Peninsula, Tierra del Fuego, Falkland Islands, Magellan Strait, South Georgia, Marion, Prince Edward, Kerguelen and Crozet islands (Dell, 1964; Branch et al., 1991; Adami and Gordillo, 1999; Puccinelli et al., 2018). High densities of the bivalve *Kidderia* sp. occur on fronds of *Desmarestia confervoides* and Delesseriaceae gen. indet. algae at *Baie du Marin*. Finally, *Codium adhaerens* habitat seemed to favor the presence of the grazer gastropod *Margarella violacea*.

Transects undertaken on the northern coast of the *Baie du Marin* highlighted a unique vertical zonation of benthic communities. From 0 to 3 m depth, the bedrock is mostly covered with crustose coralline algae and host high densities of the holothuroid *Echinopsolus splendidus* and actiniid Actiniaria sp.6. Like in the temperate sub-Antarctic islands where these calcifying algae dominate extensive areas with small invertebrates such as anemones and bryozoans (Freeman et al., 2011), or at Marion Island where they are abundant on boulders (Gon and Mostert, 1992), crustose coralline are characteristic of sub-Antarctic subtidal marine communities. From 3 to 7 m depth, the rocky plateau is dominated by a dense bed of canopy-forming *D.*

chordalis, with corallines and *Codium adhaerens* covering the bottom. This canopy formed by algae could be hiding additional levels of benthic diversity, which could not be assessed using imaging techniques. From 7 to 8 m depth, the rock wall is inhabited by high abundance and diversity of faunal species, structurally dominated by high-level densities of the polychaete sabellid *Parasabella* sp. and ophiuroid *Ophiosabine vivipara* to a lesser extent. From 8 to 10 m depth, the rocky shore is mainly inhabited by *C. adhaerens* associated with the gastropod *M. violacea*. An important algal diversity is present in this area, including *Phycodrys quercifolia*, *Ulva* sp. and *Macrocystis pyrifera*. As reported at the Kerguelen Islands (Arnaud, 1974) and along the coastline of the sub-Antarctic Magellan region (Ríos et al., 2007), kelp holdfasts support high species richness and abundance of a wide range of invertebrate taxa compared with the surrounding environment. Approaching to the seafloor, the rocky substrate leaves place to vast sand stretches that are characteristic of the *Baie du Marin*.

4.2 Distribution of taxonomic diversity between transects and substrates

While species richness among rocky transects were substantially similar with each other and greater than transects performed on the submarine cables section, our results show compositional and structural differences between transects and substrates within the bay. High densities of the terebellid polychaete *Lanice marionensis* were found on rock located at the center of the bay. In contrast, benthic communities of the northern coast are dominated by high densities of the sabellid polychaete *Parasabella* sp. The presence of these passive suspension feeders polychaetes in high densities suggests a surrounding habitat rich in food sources, including phytoplankton, resuspended microphytobenthos, bacteria, and/or non-living organic particles (Jumars et al., 2015). We propose that particle capture and sediment deposition provided by these polychaetes could facilitate the presence in high abundance of the deposit feeder ophiuroid *Ophiosabine vivipara*. Structural and compositional differences in benthic communities between these areas could also reflect variation in environmental and hydrodynamic conditions within the bay. The greatest diversity found on the rock (SD-Rock) may also be attributed to the dense aggregations of the tube-building polychaete *L. marionensis*. As reported for *Lanice conchilega* (Rabaut et al., 2007; Van Hoey et al., 2008; Rabaut et al., 2009), this polychaete adds heterogeneity and complexity within the ecosystem, acting as a habitat-structuring species for a wide variety of organisms. In addition, hard substrates between the northern coast and the center of the bay were characterized by distinct macroalgal assemblages. Algae are a key component of benthic ecosystems and contribute greatly to the functioning of marine environments through their involvement in biogeochemical (especially carbon, nitrate and phosphorus) and nutrient cycles, both in water column and sediments. While algal physical characteristics can directly influence local conditions (e.g., light accessibility, oxygen concentration, particle deposition), their metabolism can also act on the ambient environment (Delille et al.,

2009). Through physical structure and metabolism, algae generate important habitat modifications and create a multitude of ecological micro-niches that support high-levels of diversity, by providing a surface for larval settlement and colonization, refuges from predation and physical disturbance, food resources and nursery sites, thereby influencing directly or indirectly the faunal distribution and community structure in Antarctic (Gambi et al., 1994; Amsler et al., 2014) and sub-Antarctic (Graham et al., 2007; Andrade et al., 2016) ecosystems. In light of these results, we suggest that the interaction between rocky substrate and habitat-forming species (e.g., faunal and macroalgae physical architecture), increase habitat complexity and heterogeneity at *Baie du Marin*. This spatial segregation of environmental conditions and nutrient resources within these complex habitats allows for species coexistence and promotes high levels of taxonomic diversity.

Most studies assess the biological effects of cable installation as transient and relatively minor (Andrulewicz et al., 2003; Kogan et al., 2006; Dunham et al., 2015; Sherwood et al., 2016). For instance, in the case of the Acoustic Thermometry of Ocean Climate (ATOC)/Pioneer Seamount cable in the nearshore waters of California, a significant increase in the abundance of sea anemones on the cable was the main biological impact observed (Kogan et al., 2006). However, other studies have reported significant changes in species behavior due to submarine cables (Westerberg and Lagenfelt, 2008; Love et al., 2015; Love et al., 2017). At Crozet, our results show that the composition and structure of submarine cables faunal communities are different from the surrounding environment. Benthic species richness on submarine cables is similar between the two surveyed years. However, images of the suspended cables section in 2022 display a large algal development compared to images taken in 2021, which could explain the differences observed in diversity indices. Polychaetes *Lanice marionensis* and *Parasabella* sp. and ophiuroid *Ophiosabine vivipara* are abundant on the rock where the cables are laid, whereas only a few individuals are found on cables. Similarly to the *Basslink High Voltage Direct Current* (HVDC) cable in south-eastern Australia (Sherwood et al., 2016), a high diversity of sponges had colonized the cable surface. We suggest that suspended cables introduce heterogeneity within the ecosystem and promote the settlement of certain species. In addition to providing a new surface to colonize, we hypothesized that suspended cables are out of the reach for benthic consumers and thus influence biotic interactions by reducing predation pressure compared to the natural substrate on the seabed. This lowered predation pressure could facilitate the establishment of non-native and potential invasive species (Dumont et al., 2011). However, macroalgae diversity was similar between the rock and artificial substrates, but different from the northern part of the *Baie du Marin*. This difference may be explained by the depth variations between these areas. Overall, the suspended cables in the bay promoted the development of epifaunal biota in an area dominated by soft sediments, by providing a new colonization surface. This resulted in a composition and structure of faunal communities that differ from their surrounding environment.

Climate change and anthropogenic activities are major factors increasing the risk of biological invasion in polar marine ecosystems (McCarthy et al., 2019). Many studies have reported that the composition and structure of benthic communities differed between natural and artificial substrates, with a greater number of non-native species on artificial structures (Connell and Glasby, 1999; Glasby et al., 2007; Airoldi et al., 2015). Consequently, artificial structures may constitute a serious threat to the native biodiversity, highlighting the importance of monitoring programs to detect the presence of non-native species and prevent the spread of invasive species.

4.3 Richness and diversity partitioning: a high spatial heterogeneity

The greater contribution of the β_2-diversity (among transects) to the *Baie du Marin* richness and diversity highlights that faunal species composition varied the most among transects. At larger spatial scales, β_2-diversity was greater than expected under the null model, whereas values for finest scales (α and β_1-diversity) were lower. These results indicate that faunal communities are not randomly distributed between transects, and that species distribution within these transects tends to be spatially structured as patches at a very small scale (approximately 1 m^2). This aggregated distribution at fine spatial scales was also observed on Antarctic coastal habitats (Gili et al., 2001; Teixidó et al., 2002; Gutt et al., 2019; Rovelli et al., 2019) and could be the result of multiple ecological processes, including local environmental filtering (e.g., hydrodynamic conditions, bottom topography, substrate nature and inclination, depth) (Gutt et al., 1999; Cárdenas and Montiel, 2015), biotic interactions (e.g., competition, predation, facilitation) (Valdivia et al., 2014), and species biological traits (e.g., gregarious behavior, dispersal limitations). Our study's results call for further studies to investigate the abiotic environment and species biology. In contrast to species richness, α-diversity has also shown a greater contribution to the *Baie du Marin* Shannon and Simpson diversity, which could be the result of the engineer species presence – such as habitat-formers *Lanice marionensis* and *Parasabella* sp. – that enhance species abundance and diversity. In addition to complex substrate micro-topography, biogenic structures provide a greater number of potential microhabitats at finer scales, promoting local variation of environmental conditions and food partitioning, and thus enabling high-level diversity (Jones et al., 1994). Similarly to faunal communities, β_1-diversity and β_2-diversity have shown closely matched and high-level contributions to the *Baie du Marin* algal richness. However, all spatial scales have shown a similar contribution to the *Baie du Marin* Shannon diversity. As reported in other studies (Gering et al., 2003; Valdivia et al., 2014; Gutt et al., 2019), these findings corroborate the importance of accounting for spatial scale in preserving sub-Antarctic habitats and their unique biodiversity for conservation policies. Multi-scale analyses are essential to ensure a better understanding of the local and regional processes that shape benthic assemblages (Lamy et al.,

2018). These results provide useful information for decision-makers to design effective management strategies and sustain benthic diversity, ecosystem health, and resilience (Gering et al., 2003).

4.4 Functional diversity of Crozet benthic ecosystems

The trait-based approach constitutes an ecological bridge between the structure of species assemblages and ecosystem functioning (Mouchet et al., 2010). Faunal communities of Crozet shallow water habitats are dominated by suspension-feeders. This prevalent high diversity of suspension-feeders was also reported at the Kerguelen Islands (Améziane et al., 2011) and could play an important role in the recycling of nutrients in the water column (Orejas et al., 2000). Crozet benthic communities have shown a high number of species that have a lecithotrophic larval stage during development. Such species produce large eggs with rich and great amounts of food resources necessary for the effective embryonic and larval development (Pearse et al., 1991; Pearse and Lockhart, 2004). The predominance of lecithotrophy at Crozet is a life trait shared by many invertebrates in the Southern Ocean and in deep-sea environments (Lau et al., 2020). In addition, Crozet faunal communities show a high number of sessile organisms and if biological information on species lifespan are limited, we presume that these communities are likely characterized by slow growth rates, as reported in Southern Ocean marine ecosystems (Teixidó et al., 2004; Smale and Barnes, 2008). All these functional characteristics make these communities potentially vulnerable to changes in environmental conditions (Degen et al., 2018).

Overall, Crozet benthic communities have low values of functional richness (FRic), even more so for benthic communities located on the submarine cables substrate. Mason et al. (2005) reported that low FRic and low functional evenness (FEve) could indicate that some resources availability may be under- or not used by species. These low indices values, and consequently the dominance of some functional traits, could also be explained by the presence of few resources in sufficient abundance in which benthic communities are specialized (Boyé et al., 2019). While taxonomic results have shown that faunal communities present on the submarine cables differed from natural hard substrates, these functional characteristics could increase the establishment of non-native species and decrease the invasion resistance (Mason et al., 2005). Some recent studies have highlighted that the introduction of artificial substrates could facilitate biological invasions (Glasby et al., 2007; Macreadie et al., 2011; Adams et al., 2014). In addition, the low FEve and high functional divergence (FDiv) found in Crozet benthic communities are characteristic of communities where dominant species share similar traits that are generally different from all other species (e.g., sessile tube dwellers), and that a large part of functional trait space is occupied by rare species with rare traits. Therefore the distinctiveness of rare species functional traits, compared to the species pool, may have a significant role in the ecosystem functioning (Mouillot et al., 2013). The loss of species with distinctive traits may deeply affect ecosystem functioning, and several studies highlight the importance

of considering rare species as a conservation priority (Ellingsen et al., 2007; Mouillot et al., 2013; Boyé et al., 2019). In addition to the low FEve and FDiv, benthic communities at *Baie du Marin* were characterized by low functional redundancy (FR). FR proposes that ecosystems characterized by high degree of species which share similar functional traits, are less susceptible to environmental upheavals or species loss (Schmera et al., 2017). Based on this concept, functional redundancy is a good proxy of ecosystem resilience. The low FEve and FR measured on faunal communities highlight a high vulnerability of the functional stability of Crozet benthic ecosystems. The taxonomic diversity found at *Baie du Marin* is associated with a redundancy of a few functions (e.g., suspension feeders, lecithotrophy), a pattern called functional over-redundancy (Mouillot et al., 2014). Depending on the interplay between species abundance and the rarity of functional traits, this disproportionate grouping of species in few particular functions leaves many ecological functions highly vulnerable (i.e., supported by just one or few species) (Mouillot et al., 2014; Boyé et al., 2019). As reported in the Western Antarctic Peninsula (Robinson et al., 2022), these results show that the functional diversity of Crozet benthic marine ecosystems may be highly vulnerable to species loss due to future environmental changes in sub-Antarctic region, including anthropogenic threats (Campos et al., 2013), biological invasion (McCarthy et al., 2019) and climate change (Auger et al., 2021).

5 Conclusion

This study provides an important description and analysis of the structure and distribution of nearshore subtidal benthic communities associated with hard substrates at *Baie du Marin*, and the first to assess the functional diversity of Crozet archipelago benthic marine ecosystems. Combined taxonomic and biological trait analyses provide a comprehensive understanding of marine ecosystem functioning and community structure. Our results show that the use of a non-destructive method, underwater imagery, is a powerful surveying technique to investigate patterns in marine organism distribution and sub-Antarctic ecosystems functioning. Overall, hard substrates constitute complex habitats harboring a rich faunal and algal diversity, with a high spatial heterogeneity at the *Baie du Marin* scale. The structure and composition of faunal communities on rocky shores were distinct from those of the submarine cables, where high sponge diversity occurs. No algal community differences were found between the rock located at the center of the bay and submarine cables. However, the algal composition of these sites differs from the northern part of the *Baie du Marin*. Further studies of environmental variables and biotic interactions that shape benthic communities would be a valuable contribution to improve our knowledge of the functioning of these ecosystems.

The high sensitivity of sub-Antarctic regions due to accelerating climate change is expected to impact coastal marine habitats of numerous sub-Antarctic islands – including the Crozet archipelago – through the multiple and synergistic effects of factors such as seawater temperature increase, ocean acidification, and extreme

climatic events. Current taxonomic and functional results emphasize the high degree of vulnerability of Crozet marine communities to climate change and biological invasions. The low functional evenness and redundancy of Crozet benthic communities indicate that the functioning of these marine environments is highly vulnerable to diversity loss. These results highlight the need to use taxonomic and functional studies to advise conservation strategies. Future studies on the functioning of sub-Antarctic ecosystems are imperative to support an effective conservation of species and ecosystem functions, and for an enhanced resilience of these isolated territories against the current and future environmental changes.

Data availability statement

The original contributions presented in the study are publicly available. The taxonomical data can be found here: ZooBank with identifier "2BF9D61C-5167-4F2A-B0CD-1A36BB3F7CE7".

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

YL: Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft. LS: Formal analysis, Data curation, Investigation, Methodology, Writing – original draft. TL: Methodology, Formal analysis, Writing – original draft. AB: Methodology, Formal analysis, Writing – original draft. RD: Investigation, Supervision, Writing – original draft. TS: Funding acquisition, Conceptualization, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing – original draft.

Funding

Acknowledgments

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2023.1291038/full#supplementary-material

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