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Functional changes across marine habitats due to ocean acidification

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Abstract

Global environmental change drives diversity loss and shifts in community structure. A key challenge is to better understand the impacts on ecosystem function and to connect species and trait diversity of assemblages with ecosystem properties that are in turn linked to ecosystem functioning. Here we quantify shifts in species composition and trait diversity associated with ocean acidification (OA) by using field measurements at marine CO_2 vent systems spanning four reef habitats across different depths in a temperate coastal ecosystem. We find that both species and trait diversity decreased, and that ecosystem properties (understood as the interplay between species, traits, and ecosystem function) shifted with acidification. Furthermore, shifts in trait categories such as autotrophs, filter feeders, herbivores, and habitat-forming species were habitat-specific, indicating that OA may produce divergent responses across habitats and depths. Combined, these findings reveal the importance of connecting species and trait diversity of marine benthic habitats with key ecosystem properties to anticipate the impacts of global environmental change. Our results also generate new insights on the predicted general and habitat-specific ecological consequences of OA.

1 | INTRODUCTION

Global environmental change is causing rapid changes in biodiversity and shifts in community structure (Arneth et al., 2020; Blowes et al., 2019; Díaz et al., 2019). Understanding how changes in biodiversity alter ecosystem function and the ability of ecosystems to deliver services remains a central challenge in ecology (Chacón-Labella et al., 2023; Gallagher et al., 2020; Lavorel & Garnier, 2002; McGill et al., 2006). Accounting for species traits in studies of biodiversity loss (e.g., morphological, physiological, or behavioral characteristics of organisms) has increasingly been recognized as a fundamental approach to unravel how the impacts of global change affect species, communities, and ultimately, ecosystem functions (Mouillot et al., 2013; Streit & Bellwood, 2023; Violle et al., 2007). Among the many escalating threats to Earth's ecosystems, ocean acidification (OA) is expected to profoundly alter the diversity and functioning of marine ecosystems (Doney et al., 2020; Gattuso et al., 2015). However, major uncertainties remain, and most research to date has focused on single species and controlled laboratory settings, with a limited understanding of ecosystem-level responses. Here, we propose a trait-based approach to advance our understanding of the ecological effects of OA across different habitats and depths, and utilize key functional traits as proxies to predict future properties of marine ecosystems.

Trait-based analyses can provide insight into the ecological relevance and roles of species and community assembly (Chacón-Labella et al., 2023; Mouillot et al., 2021; Streit & Bellwood, 2023), allowing a novel understanding of how diversity changes affect key ecosystem properties, by examining the interplay between species, traits, and ecosystem functioning (Brandl et al., 2019; de Bello et al., 2010; Streit & Bellwood, 2023). Trait-based approaches quantify differences among species by assessing the ecological traits that affect their responses to environmental factors and influence ecosystem processes and functions (Lavorel & Garnier, 2002; Violle et al., 2007). Ecosystem function refers to the movement or storage of energy or material within an ecosystem, including primary production and nutrient cycling (Bellwood et al., 2019; Brandl et al., 2019; Díaz & Cabido, 2001). Traits are used to estimate the diversity and distribution of ecological components in an assemblage such as trait diversity (e.g., the breadth of species' ecological traits), trait redundancy (e.g., the number of species sharing similar traits), and trait vulnerability (e.g., loss in trait diversity following the loss of species) (Díaz & Cabido, 2001; Mouchet et al., 2010; Streit & Bellwood, 2023). Analyses of shifts in community trait composition can advance our understanding of how global environmental change affects fundamental ecological strategies from individuals to species assemblages across high-diversity marine communities (Bellwood et al., 2019; McWilliam et al., 2020).

Quantifying how global environmental change will affect trait diversity and ecological functioning in the future is inherently difficult due to the logistical challenges associated with exposing diverse, intact marine communities to future conditions. Natural analogues (environmental settings with similar characteristics as the future environment) overcome this limitation by providing an opportunity to characterize shifts in the structure and trait diversity of whole communities in response to key environmental drivers (Coni et al., 2021; Harvey, Allen, et al., 2021; Kroeker, Micheli, et al., 2013; Teixidó et al., 2018). Natural volcanic CO_2 vents cause local acidification of seawater and are used as natural analogues to assess species and whole-ecosystem responses to future ocean acidification conditions (Fabricius et al., 2011; Hall-Spencer et al., 2008; Kroeker, Micheli, et al., 2013; Linares et al., 2015). At these high pCO_2 environments, the conditions in low pH zones are used to represent future climatic conditions with a decrease in surface pH from −0.16 to −0.44 pH under SSP1-2.6 and SSP5-8.5 (Gattuso et al., 2015; Kwiatkowski et al., 2020). While these high pCO_2 settings provide powerful insights into ocean acidification scenarios, they are not perfect proxies for the future global ocean, as they lack other environmental stressors. Furthermore, our ability to generalize from studies using these natural high pCO_2 settings is limited. Context is key for forecasting the ecological effects of OA, and studies spanning a wide range of habitats are crucial to improving generalizations. To address this limitation, a former ecosystem-scale review highlighted OA's role in mediating biodiversity shifts through structural complexity changes across different ecosystems, including coral reefs, mussel beds, macroalgal habitats, and seagrasses (Sunday et al., 2017). Complementary, in a recent study using trait-based approaches on a single habitat CO_2 vent, Teixidó et al. (2018) showed how trait diversity and functional entities (e.g., unique combination of species traits) decreased along natural CO_2 gradients in shallow rocky reef habitats. Here, we expand on these previous studies by studying natural analogues of CO_2 vents spanning different rocky habitats and community types to contribute to broadening the scope of the ecological effects of OA on marine ecosystems as well as addressing shifts in ecosystem properties using trait-based approaches. We addressed the following questions: (i) what are the impacts of OA on taxonomy and trait diversity?; (ii) what are the impacts of OA on selected traits and their relation to ecosystem properties?; and (iii) are impacts generalizable across habitats? Our hypotheses were designed to identify a pattern of trait diversity change, independent of species composition across habitats, and anticipate variable responses in ecosystem properties. To answer these questions, we conducted comprehensive benthic species censuses in recently discovered natural analogues of CO_2 vents spanning four habitats across different depths in the Mediterranean Sea, including shallow rocky reefs, semi-submerged caves, reefs and deep reefs (see Section 2). We quantify shifts in species composition and

trait diversity associated with an increase in acidity. We then assess how shifts in some species' traits coincide with changes in predicted future ecosystem properties.

2 | MATERIALS AND METHODS

2.1 | Study sites

The study sites are located along the coast of Ischia Island (Italy) across water depths of 0.5 to 48 m (Figure S1). We characterized the physical and chemical parameters and assessed changes in rocky benthic communities in four CO_2 venting sites (vent 1 to vent 4) and eight reference sites with ambient pH with no venting activity (two reference sites for each CO_2 vent). The CO_2 vent sites span four rocky habitats typical of Mediterranean coastal ecosystems: a shallow rocky reef (hereafter: Shallow Reef, local name: Castello Aragonese, vent 1, CO_2 gas bubbles were emerging from the seafloor at 0.5–3 m depth, and benthic surveys were performed at the same depth range); a semi-submerged cave (hereafter: Cave, local name: Grotta del Mago, vent 2, CO_2 gas bubbles were emerging from the seafloor at 5 m depth, and benthic surveys were performed at ~3 m depth); a rocky reef (hereafter: Reef, local name: Chiane del Lume, vent 3, CO_2 gas bubbles were emerging from the seafloor at 11 m depth, and benthic surveys were performed at ~10 m depth); and a coralligenous outcrop (hereafter: Deep Reef, local name: Madonnina, vent 4, CO_2 gas bubbles were emerging from the seafloor at 48 m depth, and the benthic surveys were performed at ~40 m depth). See Supplementary Text for a detailed description of the study sites. Studies using the shallow volcanic CO_2 vent system near the Castello Aragonese have generated key insights on the direct and indirect effects of ocean acidification on the surrounding ecosystems (Foo et al., 2018; Hall-Spencer et al., 2008; Kroeker et al., 2011; Teixidó et al., 2018). Briefly, water carbonate chemistry and *in situ* monitoring of seawater pH delineated a pH gradient along the Castello Aragonese with three carbonate chemistry zones (ambient, low and extreme low pH) caused by spatial variability in CO_2 venting intensity (Hall-Spencer et al., 2008). For this study, we selected two pH zones at this Shallow Reef habitat (moderate venting activity and low pH, $pH_T = 7.8 \pm 0.31$) and ambient pH zone (non-visible vent activity and ambient pH, pH_T ~8.0–8.1), and we excluded the extreme low pH zone (high venting activity, and extreme low pH, pH_T ~6.6–7.2). The criterion was to unify the sampling design with the other three habitats, as the three new CO_2 vent sites presented moderate venting activity and low pH conditions (pH_T ~7.74 to 7.96, ~983–538 pCO_2, see Section 3 and Table 1 for detailed values). For the present study, species and trait diversity data of the Shallow Reef habitat come from Teixidó et al. (2018). Then, for each of the four habitats, two reference sites with ambient pH (ambient site a, ambient site b) were carefully chosen according to the following criteria: (i) they have similar habitat, light exposure, and depth as the CO_2 vent site, and (ii) no venting activity was evident. The use of two reference sites with ambient pH was intended to detect clear ecological differences resulting from the comparison between the natural variability of benthic communities at the ambient pH sites (control

sites) and the low pH conditions at the CO_2 vents (impact sites). Only one CO_2 vent per habitat was found along the coast off Ischia, resulting in an unbalanced statistical design (Underwood, 1992). These four rocky habitats occur within a moderate coastal depth range, from 1 to 40 m depth. They exhibit large variations in community composition and dynamics (Garrabou et al., 2002): shallower communities are dominated by macroalgae due to well-lit conditions, as those found in Shallow Reefs and Reefs in this study, while deeper communities (or occurring in dim-light conditions) are characterized by the dominance of encrusting calcareous algae and invertebrates, as those in Caves and Deep Reefs in this study. Although the study sites experienced similar seawater temperature conditions from late autumn to winter (marked by the breakdown of the seasonal thermocline after summer), they exhibit distinct temperature conditions in spring and summer when the thermocline develops, typically around depths of 15–25 m. Consequently, temperatures ranged from 25.5°C to 26.7°C at 5 and 10 m above the thermocline in shallow habitats and below 19°C at depths greater than 25 m in July and August (the warmest period) (Figure S2). Overall, the CO_2 vent systems locally acidify the seawater with gas comprising 92%–95% CO_2 (no sulphur) (Table S1) and do not elevate temperature. The mean carbonate chemistry in the ambient pH zones corresponds to current average conditions, whereas the low pH sites are most comparable with values predicted for the year 2100 with a decrease in surface pH from −0.16 to −0.44 pH units under SSP1-2.6 and SSP5-8.5 (Kroeker et al., 2011; Kwiatkowski et al., 2020; Teixidó et al., 2018). Initial investigations of these CO_2 vent systems and reference sites started in 2016 and 2017. Preliminary environmental and ecological data were used to plan subsequent field samplings. The fieldwork was carried out from May 2018 to June 2018 and May 2019 to October 2019.

2.2 | Gas characterization

Gas samples were collected in 200 mL glass bottles and analyzed using gas chromatography (Agilent 7890B combined with a Micro GC analyzer-INFICON, held at a constant temperature of 80°C). The mean composition of the bubbling gas was predominantly CO_2 (92%–95%, with undetectable levels of sulphur gas <0.0002%) (Table S1), and the venting did not elevate the temperature at any site (Table 1), resulting in seawater acidification. Vent activity was sampled by counting the number of vents in randomly placed 0.25 m^2 quadrats ($n = 10$–15) in the CO_2 vent sites, with approximately 5 vents/0.25 m^2 (see Table S1 for composition of gases at the vent sites).

2.3 | pH_T time series, pH_T variability, and pH sensor calibration

SeaFET™ Ocean pH sensors (Satlantic) were deployed to quantify variation in pH at the CO_2 vents and their corresponding ambient pH sites at the same depths where benthic surveys were

TABLE 1 Measured and estimated seawater physiochemical parameters at the study sites for salinity (S), temperature (T), total alkalinity (A$_T$), dissolved inorganic carbon (C$_T$), pH$_T$, pCO$_2$, calcite (Ωc), and aragonite (Ωa) saturation. Values are means ± SD, with 25th and 75th percentiles between parentheses. Calculated concentrations of C$_T$, pCO$_2$, Ωc, and Ωa are shown. (a) Parameters measured from discrete water samples; (b) parameters measured with in situ sensors; and (c) parameters measured by Kroeker et al. (2011). Habitat: Shallow Reefs (0.5–3 m); Caves (3 m); Reefs (10 m); Deep Reefs (40 m). pH conditions: Vent system (Vent 1, 2, 3, 4); ambient pH (2 sites for each habitat).

Habitat	pH conditions	S	T (°C)	A$_T$ (µmol kg^{-1})	C$_T$ (µmol kg^{-1})	pH$_T$	pCO$_2$ (µatm)	Ωc	Ωa
Shallow Reefs	Vent 1, low pH	37.7[c] ±0.2 n=4–10	17.5[c] ±2.8 n=1503–3162	2560[c] ±7 n=4–10	2318[c] ±99 n=4–10	7.8[c] ±0.3 n=1503–3162	1581[c] ±2711 n=1503–3162	3.00[c] ±1.31 n=1503–3162	1.95[c] ±0.85 n=1503–3162
Shallow Reefs	Ambient pH (A1a)	37.6[c] ±0.3 n=4–10	19.6[c] ±1.5 n=1503–3162	2563[c] ±2 n=4–10	2281[c] ±73 n=4–10	8.1[c] ±0.1 n=1503–3162	440 ±192 n=1503–3162	5.11[c] ±0.67 n=1503–3162	3.33[c] ±0.44 n=1503–3162
Shallow Reefs	Ambient pH (A1b)	37.9[c] ±0.3 n=3	23.4[c] ±0.7 n=604	2563[c] ±3 n=3	1768[c] ±96 (n=3)	8.0[c] ±0.1 n=604	567[c] ±100 n=604	4.75[c] ±0.53 n=604	3.13[c] ±0.35 n=604
Caves	Vent 2, low pH	37.8[a] ±0 n=7	21.8[b] ±2.1 (19.8, 23.8) n=1841	2541[a] ±20 (2533, 2550) n=7	2352±89 (2289, 2389) n=1841	7.74[b] (7.74, 7.93) n=1841	983±868 (590, 978) n=1841	3.56±1.05 (2.96, 4.39) n=1841	2.33±0.69 (1.94, 2.88) n=1841
Caves	Ambient pH (A2a)	37.3[a] ±0 n=3	17.3[b] ±0.4 (17.0, 17.6) n=1331	2618[a] ±15 (2607, 2633) n=14	2338±20 (2324, 2350) n=1331	8.05[b] (8.03, 8.07) n=1331	448±42 (417, 471) n=1331	4.80±0.30 (4.61, 5.01) n=1331	3.11±0.19 (2.98, 3.24) n=1331
Caves	Ambient pH (A2b)	37.4[a] ±0 n=3	19.4[a] ±0 n=3	2275[a] ±1 n=3	2610±2 n=3	8.03[a] n=3	375±1 n=3	5.77±0.01 n=3	3.82±0.01 n=3
Reefs	Vent 3, low pH	37.9[a] ±0 n=3	16.8[b] ±0.4 (16.6, 17.1) n=1326	2532[a] ±16 (2522, 2545) n=25	2324±47 (2292, 2341) n=1326	7.91[b] (7.89, 7.99) n=1326	626±311 (497, 643) n=1326	3.69±0.61 (3.43, 4.13) n=1326	2.39±0.39 (2.22, 2.67) n=1326
Reefs	Ambient pH (A3a)	37.6[a] ±0 n=3	26.4[b] ±1 (25.9, 27.0) n=1691	2642[a] ±17 (2629, 2659) n=17	2324±21 (2310, 2338) n=1691	7.97[b] (7.94, 8.00) n=1691	556±57 (513, 597) n=1691	5.53±0.32 (5.31, 5.75) n=1691	3.67±0.22 (3.53, 3.82) n=1691
Reefs	Ambient pH (A3b)	37.8[a] ±0 n=3	20.9[a] ±0 n=3	2239[a] ±4 n=3	2561±4 n=3	8.01[a] n=3	409±1 n=3	5.50±0.01 n=3	3.64±0.01 n=3
Deep Reefs	Vent 4, low pH	37.9[a] ±0 n=3	17.0[b] ±0.57 (16.6, 17.4) n=2692	2519[a] ±10 (2514, 2522) n=27	2292±30 (2273, 2305) n=2692	7.96[b] (7.95, 8.00) n=2692	538±100 (480, 563) n=2692	3.94±0.41 (3.75, 4.22) n=2692	2.55±0.26 (2.43, 2.73) n=2692
Deep Reefs	Ambient pH (A4a)	37.9[a] ±0 n=3	18.2[b] ±0.7 (17.7, 18.7) n=1825	2528[a] ±8 (2522, 2532) n=13	2272±4 (2270, 2275) n=1825	8.00[b] (7.99, 8.01) n=1825	486±19 (472, 500) n=1825	4.38±0.05 (4.34, 4.42) n=1825	2.84±0.03 (2.82, 2.87) n=1825
Deep Reefs	Ambient pH (A4b)	37.9[a] ±0 n=3	16.3[a] ±0 n=3	2249[a] ±5 n=3	2541±3 n=3	7.96[a] n=3	381±7 n=3	5.03±0.05 n=3	3.32±0.04 n=3

performed from May 2019 to October 2019 (see below). Before deployment, the SeaFETs were calibrated with ambient pH water in the aquarium facilities at the Ischia Marine Center (Ischia, Italy) (for full details of pH sensor calibration, see Supplementary Text). The mean offset between calibration samples and calibrated SeaFET pH was ±0.006 units ($n=44$ water samples), indicating a high-quality pH dataset (Figure S3). The pH sensors were deployed in each of the recently discovered CO_2 vents (Vent 2, Vent 3, Vent 4) and in one of the corresponding reference areas with no visible vent activity during the same period (ambient 2a, ambient 3a, ambient 4a). The pH and seawater physicochemical parameters for Shallow Reef habitats (site Castello Aragonese) are originally reported in Kroeker et al. (2011). The pH measurements in the three new vents and ambient pH sites were taken every 15 min for ~15 to 28 days ($n=1326$ to 2692 measurements). See Table S2 for deployment dates and statistics.

2.4 | Carbonate chemistry and nutrients

Discrete water samples were collected using Niskin bottles at the vent and reference areas with ambient pH to measure: (i) the carbonate system parameters during the pH sensor deployment, and (ii) the dissolved inorganic nutrients. Salinity was measured using a CTD (CTD Sea-Bird Electronics SBE 19 Plus Seacat). Discrete water samples for total alkalinity (A_T) were collected within 0.25 m of the pH sensors using standard operating protocols (for full details, see Supplementary Text). The HCl (0.1 M) titrant solution was calibrated against certified reference materials distributed by A.G. Dickson (CRM, Batches #153, #171, and #177). Precision of the A_T measurements of CRMs was <2 µmol kg^{-1} from nominal values. A_T and pH$_T$ along with in situ temperature and depth were used to determine the remaining carbonate system parameters for each sampling period using the R package seacarb v3.2.12 (Gattuso et al., 2023) (for constant details, see Supplementary Text). Dissolved inorganic nutrients (nitrite NO_2, nitrate NO_3, ammonium NH_4^+, phosphate PO_4, and silicate $Si(OH)_4$) were determined using a colorimetric method (for more information see Supplementary Text; Table S3).

2.5 | Sampling design of benthic surveys

Percent cover of 215 benthic species was quantified using two approaches with scuba diving: (i) visual census techniques in Shallow Reef (benthic surveys were performed from 0.5 to 3 m depth) and Reef habitats (benthic surveys at ~10 m depth) dominated by algae and (ii) photographic surveys in Caves (benthic surveys at ~3 m depth) and Deep Reef habitats (benthic surveys at ~40 m depth) dominated by sessile invertebrate animals. The criteria for using these two approaches were based on previous research suggesting best practices for adequate and reliable estimates of percent cover for these different habitat types (algae versus

invertebrate-dominated habitats) (Sala & Ballesteros, 1997; Teixidó et al., 2013). For visual censuses, 12 quadrats (25 × 25 cm) were haphazardly placed at Vent 1 and Vent 3 and the two corresponding ambient pH sites ($n=3$ sites per habitat, $n=36$ quadrats for Shallow Reefs and Reefs, respectively). For photographic surveys, 48–54 and 24 photoquadrats (25 × 25 cm) were taken at Vent 2 and Vent 4 and the two corresponding reference sites with ambient pH for each habitat ($n=3$ sites per habitat, $n=144$ photographic quadrats for Caves and $n=72$ photographic quadrats for Deep Reefs, respectively) (see Figure S4; Table S4 for more information). The optimal sampling effort for Deep reefs is represented by the sampling unit of 24 photoquadrats (Kipson et al., 2011; Teixidó et al., 2013), whereas we sampled the main chambers of the caves to account for the unique characteristics and variability found in these habitats, resulting in 48–50 photoquadrats. The photographs were taken with a Nikon D70S digital SLR camera fitted with a Nikkor 20 mm DX lens (3000 × 2000 pixel resolution) and housed in Subal D70S housing. Lighting was achieved using two electronic strobes (Ikelite) fitted with diffusers. Collections of voucher specimens were performed to help with species identification, primarily based on the photographs, but also through visual censuses. Both types of quadrats (visual censuses in the field and photographs in the lab) were divided into a grid of 25 squares (5 × 5 cm each). Percentage cover was quantified by counting the number of squares filled in the grid by the species and expressing the final values as relative percentages (Teixidó et al., 2018). We identified a total of 215 benthic taxa: 67 algal species (19 Chlorophyta, 19 Phaeophyceae, 29 Rhodophyta); 1 algal turf species group; and 147 invertebrate species (57 Porifera, 17 Cnidaria, 22 Bryozoa, 1 Foraminifera, 1 Plathelminta, 11 Polychaeta, 7 Crustacea, 7 Echinodermata, 11 Mollusca, and 13 Tunicata). 198 species (out of 215) were identified at the lowest taxonomic level (see species list and % cover in Data S1).

2.6 | Sampling effort homogenization

To unify sampling efforts across habitats and between pH conditions, we performed a set of randomizations. First, we tested whether species cover differed between the two ambient pH sites within each habitat using permutational multivariate variance analysis (PERMANOVA) with Bray-Curtis distance. These preliminary analyses did not reveal any significant differences between the two ambient pH sites for each habitat (all tests $p > .05$). Then, we randomly selected 12 quadrats per habitat and pH conditions (low pH and ambient pH), resulting in 24 quadrats per habitat, with a total of 96 quadrats across the entire study (12 quadrats × 4 habitats × 2 pH conditions). We repeated the randomized selection process 100 times to increase the robustness of our analysis, which resulted in 100 matrices of 215 rows (species) and 8 columns (a combination of the four habitats and two pH conditions). We finally averaged our 100 randomized datasets as a unique dataset to perform all the analyses. Finally, our dataset consisted of 96 quadrats, with 215 species, and 74 Functional entities (FEs, see below).

2.7 | Trait characterization of benthic species

The trait diversity of benthic assemblages was assessed using seven traits, which were chosen to provide an overview of each species' ecological strategy. The traits were: (A) Morphological form, consisting of 4 categories: (a) encrusting, (b) filaments, (c) massive, and (d) tree-like; (B) feeding, consisting of 6 categories: (a) autotroph, (b) filter feeders, (c) herbivores/grazers, (d) carnivores, (e) detritivores, and (f) parasites; (C) growth rates, consisting of three categories: (1) extreme low (<1 cm/year), (2) moderate (1–5 cm/year), (3) high (>5–10 cm/year); (D) calcification, consisting of two categories: (a) without and (b) with calcareous structures; (E) mobility, consisting of two categories: (a) sessile and (b) vagile; (F) age at reproductive maturity, consisting of two categories: (1) <than 1 year, (2) >than 1 year; and (G) chemical defenses, consisting of two categories: (1) no and (2) yes (see Table S5 for a detailed description of the seven traits and categories). Trait values for the 215 species were obtained from the expertise of the team members and also from Teixidó et al. (2018). See Data S2 for species×traits table. Functional entities (FEs) were defined as groups of species sharing the same combination of trait values (Mouillot et al., 2021). In total, the 215 benthic species were classified into 74 different FEs (mean=2.9, max=14 species per 29 FEs). Twenty-nine FEs (39.2%) contained only one species (i.e., no functional redundancy).

2.8 | Measuring changes in taxonomic and trait diversity due to ocean acidification

We quantified whether ocean acidification reduced taxonomic and trait diversity across the four habitat types in the Mediterranean Sea. We built a multidimensional trait space according to the values of the seven traits for all FEs. We applied the framework of Maire et al. (2015) using the function *quality.fspaces* from the R package *mFD* (Magneville et al., 2022). We first calculated pairwise trait distances between species pairs based on the seven traits using the Gower metric, which allows mixing different types of variables while giving them equal weight. Then, we computed principal coordinates analysis (PCoA) based on this Gower dissimilarity matrix. Finally, we selected the number of PCoA axes to build an accurate trait space (convex hull) according to the mean absolute-deviation index (mAD) computed between the initial Gower distance among FEs (based on trait values) and the final Euclidean distance in the trait space. Trait space with four dimensions had the lowest mAD (0.074), and this low value ensures the 4D space faithfully represents trait-based differences between species. We computed convex hulls of each trait category within the trait space to examine the distribution of species according to their trait combinations. For each of the 96 assemblages (e.g., quadrats), we calculated: (i) Species Richness as the number of species; (ii) FE richness as the number of FEs present; (iii) the Trait Richness (V), which is computed as the volume within the convex hull shaping the FEs in the four dimensions space, and (iv) the functional dispersion

(FDis), which is the cover-weighted average distance to the average position of species in the four dimensions space (Laliberté & Legendre, 2010).

2.9 | Shifts in benthic cover of functional traits and ecosystem properties to ocean acidification

We used Bayesian models to predict the probability of a species' cover belonging to a specific trait category across habitats and between pH conditions (see Bayesian model below). First, we selected four traits that are linked to process related to ecosystem functioning including: morphological form, feeding activity, growth rate, and calcification (see Data S3 for the likelihood prediction of benthic cover). Second, we compared how community and ecosystem functions shifted in response to ocean acidification at the CO_2 vents. Third, for ecosystem function analysis, we estimated the shift of six categories within three traits as proxies for ecosystem functions performed by benthic species. The six trait categories and their proxies were autotrophs for the primary production of macroalgae, filter feeders as a proxy for benthic-pelagic coupling and nutrient cycling, herbivore/grazer as a proxy for herbivory, massive and tree-like forms as important characteristics of habitat-forming species for habitat complexity, and the presence of calcifiers for calcification (see Table S6 for functional trait categories and their relation to ecosystem functions). We adopted this criterion to link some categories of species traits to ecological processes with a clearer mechanistic connection from traits to ecosystem functions: primary production, herbivory, filter feeding, habitat provision, and calcium carbonate dynamics (Table S6) (Bellwood et al., 2019; Brandl et al., 2019; Chacón-Labella et al., 2023; Streit & Bellwood, 2023). The rationale behind selecting these categories is to use them as proxies for ecosystem functions and scale up from traits to higher-order ecological processes (Chacón-Labella et al., 2023; Streit & Bellwood, 2023). Fourth, we then quantified the loss in cover generated from the multinomial Bayesian model by calculating the difference between the predicted benthic cover in ambient pH conditions and the predicted benthic cover in low pH conditions for the corresponding functional trait categories. Thus, this analysis helps to highlight species that may be favored ("winners") or negatively impacted ("losers") in response to acidification across habitats. Finally, for community analysis, we quantified whether the observed values of total species richness, functional entity richness, and functional dispersion shifted from ambient to low pH conditions across habitats. Then, these three variables were expressed as the relative percentage of change in biodiversity.

2.10 | Bayesian Dirichlet-Multinomial model (DMM)

Bayesian modelling effectively handles the inherent uncertainties in ecological systems and for this study, it captures the uncertainty

in species-trait associations, offering a nuanced understanding of how different species contribute to various trait categories. We applied a Bayesian Dirichlet-Multinomial model (DMM) to analyze benthic cover for the four functional traits (morphological form, feeding activity, growth rate, and calcification) using the *brms* package (Bürkner, 2017). We used this Bayesian model as it considers multiple possibilities, for example the trait morphology has four possibilities (categories: encrusting, filaments, massive, and tree-like forms). In this Bayesian analysis, model parameters are random variables, but they require careful specification of prior probability distributions that reflect a priori knowledge about the uncertainty in these parameters. These prior distributions are then combined with observed data using the likelihood, resulting in updated posterior probability distributions for all model parameters (i.e., the posteriors) (van de Schoot et al., 2021). Each model takes as input a matrix of counts (X). The rows of this matrix correspond to different quadrats from each habitat ($\overrightarrow{x_i}$) and the columns correspond to the group of species of the quadrat. Each count $x_{i,j}$ in this matrix corresponds to the jth group of species (of n group of species in total) in the composition observed in the ith quadrat, and quadrats are grouped into k groups, corresponding to pH conditions. Counts in each row of the matrix are multinomially distributed:

$$\overrightarrow{x_i} \sim \text{Multinomial}\left(\overrightarrow{p_i}, N_i\right).$$

Each value $p_{i,j}$ in $\overrightarrow{p_i}$ is the probability of observing a particular species j in quadrat i and $\overrightarrow{N_i}$ is a vector of the total counts in each quadrat. The prior probability for the vector of the group of taxon cover ($\overrightarrow{p_i}$) is a Dirichlet distribution, with non-informative parameters, identical in this case to the kth group of quadrats:

$$\overrightarrow{p_i} \sim \text{Dirichlet}\left(\overrightarrow{\pi_k}, \theta_k\right),$$

$$\theta_k \sim t\,(3, 0, 2.5),$$

$$p_k \sim \text{Uniform}\left(^-\infty, ^+\infty\right),$$

where π_k parameters correspond to the expected proportions of each of the n taxon in group k, and θ is an intensity parameter that is shared among all taxon. We ran each DMM with two chains, 3000 draws per chain, and a warm-up period of 1000 steps, thus retaining 4000 draws to construct posterior distributions. Finally, we verified chain convergence with trace plots and confirmed that $\hat{R}$ (the potential scale-reduction factor) was equal to 1 (Gelman & Rubin, 1992).

2.11 | Statistical analysis

Seawater carbonate chemistry and statistical analyses were performed using the software packages R (www.r-project.org) v.4.2.1 using the libraries seacarb (Gattuso et al., 2023), mFD (Magneville et al., 2022), vegan (Oksanen et al., 2022), ecole (Smith, 2021) and brms (Bürkner, 2017).

3 | RESULTS

3.1 | Carbonate chemistry of the CO_2 vent systems

The CO_2 vent systems occur at 0.5–3 m depth at Vent 1 (type of habitat: Shallow Reef), 5 m depth at Vent 2 (type of habitat: marine Cave), 11 m depth at Vent 3 (type of habitat: Reef), and 48 m depth at Vent 4 (type of habitat: Deep Reef) (Supplementary Text; Figure S1). Each of these sites is compared to two control sites without venting at a similar depth (hereafter described as ambient pH). Venting at these CO_2 vent sites does not elevate temperature, and bubbling of gas from the seafloor is ~93%–96% CO_2 with undetectable levels of sulfur gas <0.0002% (Table 1; Table S1). Water samples for carbonate chemistry characterization and *in situ* monitoring of seawater pH_T (pH on the total scale) revealed decreases in mean pH_T at each CO_2 vent system associated with increased variability in pH_T caused by the venting (Figure 1; Table 1; Figure S5; Table S2). Mean pH_T measured at the same depths of benthic surveys were (mean with 25th and 75th percentiles): 7.8 (7.5, 8.1) at Vent 1 (Shallow Reef); 7.7 (7.74, 7.93) at Vent 2 (Cave), 7.9 (7.89, 7.99) at Vent 3 (Reef), and 7.9 (7.95, 8.00) at Vent 4 (Deep Reef), respectively (see Table 1; Table S2 for detailed pH statistics). The characterization of these new CO_2 vents across different habitats expands upon previous research focused on single habitats exposed to naturally elevated pCO_2 and allows us to assess whether community patterns are generalizable or context-specific. At Vent 1 (Shallow Reef) and Vent 2 (Cave), 31% and 34% of the pH_T measurements were below 7.8 (projected average global sea surface pH value for the year 2100 with the high emission scenario RCP8.5) (Kwiatkowski et al., 2020), respectively (Figure S5; Table S2). The percentage declined to 9% and 0% at Vent 3 (Reef) and Vent 4 (Deep Reef), respectively (Figure S5; Table S2). Vent 1 (Shallow Reef) and Vent 2 (Cave) also experienced the greatest pH_T variability (calculated as the difference between 25th and 75th percentiles of measured pH_T) with 0.3 and 0.2 pH_T units, and the highest number and duration of extreme pH events during the pH sensors deployment (defined as the pH value of 0.4 units less than the mean pH for each CO_2 vent system) (Figure S5; Table S2; Table S7). Reductions in seawater pH_T at the vents were driven by higher pCO_2 concentrations at relatively constant total alkalinities (A_T) and dissolved inorganic carbon concentrations (C_T) (Table 1). Mean pCO_2 ranged from $538 \pm 100\,\mu$atm at Vent 4, to $626 \pm 311\,\mu$atm at Vent 3, to $983 \pm 868\,\mu$atm at Vent 2, and $1581 \pm 2711\,\mu$atm at Vent 1 (Table 1). The saturation states of aragonite (Ωa) and calcite (Ωc) were consistently higher than 1 at the CO_2 vents (Table 1). In the ambient sites across the four habitats, the mean pH_T ranged from 7.97 to 8.1, pCO_2 from $440 \pm 192\,\mu$atm to $567 \pm 100\,\mu$atm, and Ω_a from 2.84 ± 0.03 to 3.67 ± 0.22 (Table 1). The vent systems exhibit high temporal variability in seawater pH due to varying CO_2 venting intensity from the seabed, mixing, and dissolution due to depth variations in the seawater column and fundamental thermodynamic processes central to the carbonate system (Takeshita et al., 2015). The conditions in these zones are comparable with the IPCC projections for near future acidification scenarios (RCP2.6 and RCP8.5), which project a decrease in
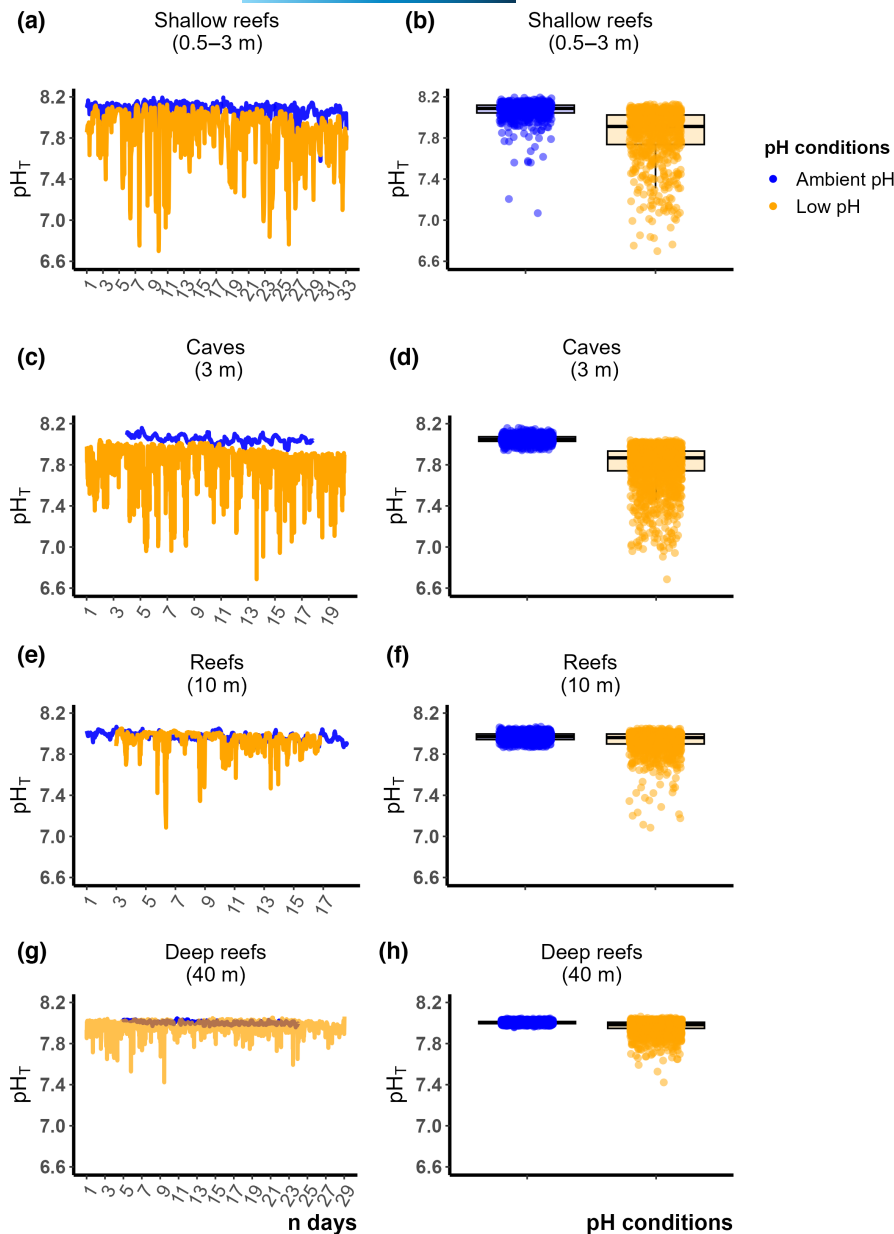
FIGURE 1 Time series (a, c, e, g) and pH_T (total scale) variability (b, d, f, h) at the CO_2 vent sites with low pH (orange) and reference sites with ambient pH conditions (blue). Measurements were taken every 15 min using SeaFETs pH sensors for a period of ~15–28 days. $N = 1326$ to 2692 measurements.

global mean surface pH from −0.14 to −0.4 pH units by 2100 relative to 1870 (Gattuso et al., 2015; Kwiatkowski et al., 2020). Estimates of mean pH and its variability found across the CO_2 vents are comparable with the range of natural variation observed in other CO_2 vent systems, with fluctuations' ranging from 0.6 to 0.7 pH units in coral reefs (Agostini et al., 2018) and temperate reefs in Panarea (Prada et al., 2017), respectively. Interestingly, as the mean pH decreased, their variability and the percentage of pH_T measurements registered below 7.8 units increased in Vent 1 (Shallow Reef) and Vent 2 (Cave). In contrast, pH was higher and less variable in the deeper CO_2 vents (Vent 3: Reef and Vent 4: Deep Reef). The volume of seawater likely plays a key role in controlling the spatial and temporal patterns of pH and pCO_2. CO_2 gas dilution at these two CO_2 vent systems (Vent 3 and Vent 4) may be higher as they occur in open waters between 10 and more than 40 m depth.

3.2 | Ocean acidification causes loss of taxonomic and trait diversity across benthic habitats

Surveys of benthic assemblages detected a total of 215 species (Data S1). The ecological characteristics of all species were described using seven traits (form, feeding, growth rates, calcification, mobility, age at reproductive maturity, and chemical defenses) (Table S5), which resulted in a total of 74 functional entities (FEs, unique combinations of trait values) (Data S2). We built a four-dimensional trait space using principal coordinates analysis (PCoA) based on the Gower distance between FEs (Figure 2; Figure S6). The greatest number of species (species richness, SR) and FEs in ambient pH conditions were found at the Deep Reef (SR=68, FEs=46) and Cave habitats (SR=58, FEs=32), whereas Shallow Reef and Reef habitats had the lowest SR (42 and 43, respectively) and FEs (both 26) (Figure 2; Figures S6 and S7).

Acidification significantly reduced taxonomic and trait diversity and redundancy in all habitats except for the Reef habitat. Total Species richness (SR) decreased by 24%, 60%, and 53%, and total FE richness (number of FEs) decreased by 27%, 44%, and 43% in the reduced pH environments for Shallow Reef, Cave, and Deep Reef habitats, respectively. Interestingly, the vulnerability of FEs (i.e., the fraction of FEs including only one species) increased markedly with acidification within these three habitats due to a decrease in the fraction of species that share similar combination of traits: from 7 to 0 for Shallow Reefs, 14 to 5 for Caves, and from 14 to 9 for Deep Reefs. In addition, the trait richness (V, the volume inside the convex hull surrounding the FEs of an assemblage in the 4-dimension trait space) decreased by 62%, 62%, and 18% for Shallow Reef, Cave, and Deep Reef habitats, respectively (Figure 2). Trait dispersion (FDis, defined as the weighted deviation to the center of gravity of species in the assemblage) also decreased between the paired ambient and low pH zones within the same three habitats (Figure S7). Mean FDis significantly decreased by 20% at the Cave, whereas it decreased by 5% and 6% at the Shallow Reef and Deep Reef in the CO_2 vents, respectively (see Figure S7; Table S8). Overall, these three habitats in ambient pH conditions showed the highest occupancy of the trait space, and the dominance of FEs (a key aspect of trait redundancy) was more equally distributed compared to the paired low pH sites (Figure 2; Figure S6). In contrast, there was an increase of 28% and 15% in SR and FEs, and 36% in the trait volume in the reduced pH environments associated with the Reef habitat (Figure 2; Figure S6). The vulnerability of FEs slightly changed within this habitat (from six FEs having one species in ambient pH to five in low pH conditions). Interestingly, this habitat is characterized by a large number of filamentous algae, which may be favored by higher pCO_2.

OA affected the distribution of the benthic species in the trait space (Figure 3), and the reduction of the trait richness in each habitat caused by OA was paired with shifts in trait categories of the overall space across habitats. There was a reduction of volume with acidification across habitats for massive (20%) and tree-like forms (100%), autotrophs (26%), organisms characterized by slow growth (6%), calcification (30%), sessile species (11%), and organisms with a late age of reproductive maturity (40%). In contrast, there was an increase in volume for filamentous forms (14%) and organisms with early age of reproduction maturity (30%).

3.3 | Ocean acidification causes shifts in functional traits across habitats

Considering the key roles of morphological form, feeding activity, growth rate, and calcification in benthic assemblages and their ecosystem properties (see Section 2 for details), we performed a more detailed examination of these important functional traits across habitats. To do this, we computed a Bayesian multinomial model with these key traits to specifically focus on the shifts due to OA across habitats (Figure 4; Data S3). We did not find evidence for multiple traits changing consistently across the four habitats due to OA. Instead, models highlighted habitat-specific patterns. Our prediction

of the benthic cover of calcifying species tended to decline in low pH conditions (% absolute change) primarily in Caves (−37%), in Reefs (−26%), and in Shallow Reefs (−14%), and to a lesser extent in Deep Reefs (−2%) (Figure 4). There was a tendency for the following categories to decline with acidification (Figure 4): massive (−6% in Caves and −15% Deep Reefs) and tree morphological forms (−1% in Caves and −12% Deep Reefs); filter feeding (−8% in Caves and −40% Deep Reefs), and moderate growth rates (−12% in Shallow Reefs and −19% in Caves). Conversely, there was an increase in cover for filamentous forms (+21% in Deep Reefs), photosynthetic autotrophy (+39% in Deep Reefs), and fast growth rates (+9% Shallow reef, +5% Deep Reef) (Figure 4). Combined, these predictions of change in the cover of different traits suggest that responses of these traits to OA are variable and habitat-specific, leading to heterogeneous patterns of change in algal and invertebrate benthic cover.

3.4 | Ocean acidification causes shifts in ecosystem properties

To capture the shifts in ecosystem properties, we quantified the losses or gains of species and trait diversity (using all seven traits) and investigated the changes in selected functional trait categories (see Table S6 for trait categories and relation to ecosystem functions). Biodiversity in an ecosystem (including the number of species and species traits) and ecosystem function (ecological processes) collectively refer to as ecosystem properties. They define and maintain ecosystem identity and influence how ecosystems respond to environmental changes (Bellwood et al., 2019; Keith et al., 2022). A key outcome of the changes at the CO_2 vents was the shifts observed in both species and trait diversity within benthic habitats due to OA, with important consequences for key ecological functions (Figure 5; Table S9). The magnitude of change for both diversity (species and traits) and predicted cover of trait categories were partly related to the combination of CO_2 vent intensity and pH variability, but varied also with habitat type, possibly as a result of differences in community composition and species vulnerabilities. For example, Shallow Reef and Cave vents had the lowest pH values and highest variability. The Shallow Reef habitat showed over 25% declines in Species richness (SR) and FE richness, Cave and Deep habitats suffered the most consistent losses (~60% and 53% in SR and 44% and 43% in FE richness, respectively) (Figure 5). Interestingly, the cover of herbivores (~0.1%) also slightly decreased due to the loss of sea urchins (herbivores/grazers). Our results also reveal the negative effects of OA on habitat-forming species in Cave and Deep Reef vents, with declines greater than 25% in benthic cover at Deep Reefs, due to reductions in massive and tree morphological forms. This strong reduction of habitat-forming species aligns well with the decrease in filter feeders (~40%). The predicted reduction of calcifiers in response to OA was evident across habitats (37%, 26%, 14%, and 2% loss of cover in Cave, Reef, Shallow Reef, and Deep Reefs, respectively). Furthermore, we found positive gains in autotrophs under low pH at Deep Reefs (39%), which was associated with the losses of habitat-forming species and filter feeders (Figure 5).
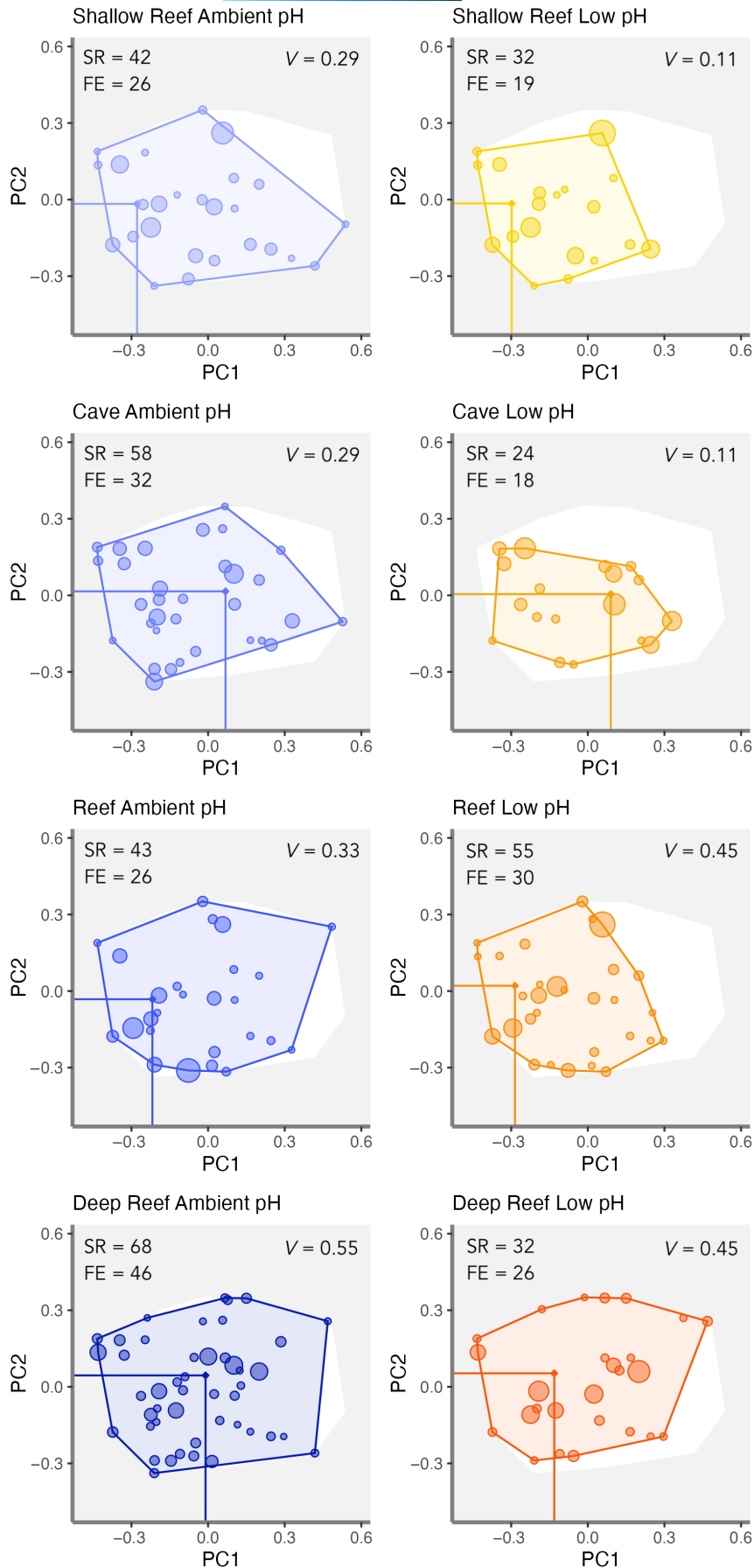
FIGURE 2 Shifts in trait diversity between pH zones (low and ambient pH) and across habitats. Trait space for the global pool of 215 benthic species and 74 functional entities (FEs) after averaging 100 randomized datasets to a unique dataset. Axes (PC1–PC2) represent the first two dimensions of the 4D trait space. The number of species (SR), the number of FEs, and the trait volume (V) for pH conditions and each habitat are indicated in each plot's upper left and right corners. The global convex hull is filled in white for all four habitats and pH conditions. The size of the circles is proportional to the relative cover of the species belonging to a certain functional entity. The intersection of vertical and horizontal lines is the centroid, the mean distance to the center of gravity for each habitat and pH condition. Habitats: Shallow Reefs (0.5–3 m depth), Caves (3 m depth), Reefs (10 m depth), and Deep Reefs (40 m depth).
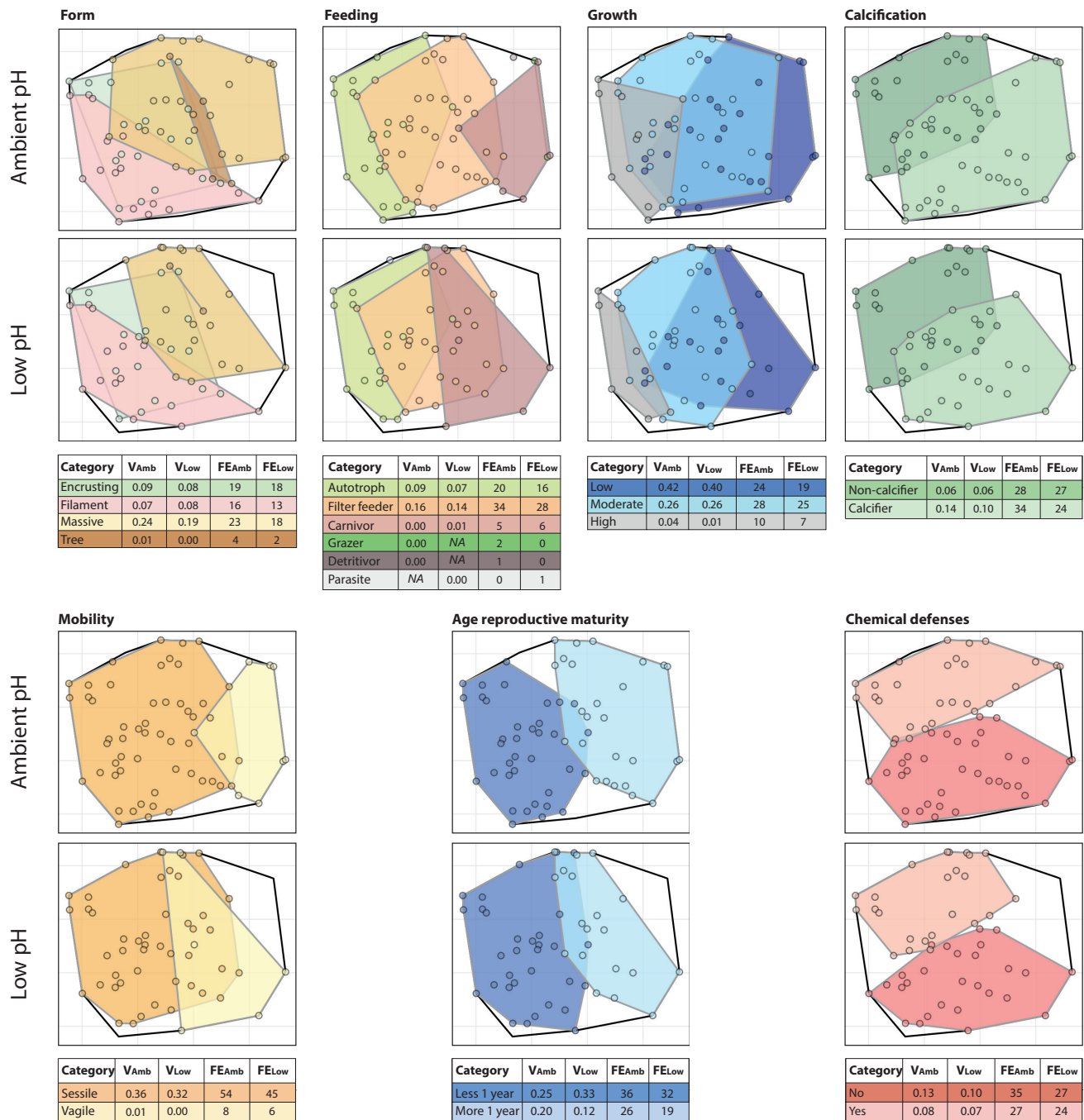
Form

Category	VAmb	VLow	FEAmb	FELow
Encrusting	0.09	0.08	19	18
Filament	0.07	0.08	16	13
Massive	0.24	0.19	23	18
Tree	0.01	0.00	4	2

Feeding

Category	VAmb	VLow	FEAmb	FELow
Autotroph	0.09	0.07	20	16
Filter feeder	0.16	0.14	34	28
Carnivor	0.00	0.01	5	6
Grazer	0.00	NA	2	0
Detritivor	0.00	NA	1	0
Parasite	NA	0.00	0	1

Growth

Category	VAmb	VLow	FEAmb	FELow
Low	0.42	0.40	24	19
Moderate	0.26	0.26	28	25
High	0.04	0.01	10	7

Calcification

Category	VAmb	VLow	FEAmb	FELow
Non-calcifier	0.06	0.06	28	27
Calcifier	0.14	0.10	34	24

Mobility

Category	VAmb	VLow	FEAmb	FELow
Sessile	0.36	0.32	54	45
Vagile	0.01	0.00	8	6

Age reproductive maturity

Category	VAmb	VLow	FEAmb	FELow
Less 1 year	0.25	0.33	36	32
More 1 year	0.20	0.12	26	19

Chemical defenses

Category	VAmb	VLow	FEAmb	FELow
No	0.13	0.10	35	27
Yes	0.08	0.07	27	24

FIGURE 3 Impact of OA on trait categories. For each trait, panels show the distribution of trait categories across the two first dimensions of the trait space for ambient and low pH conditions, respectively. Points are functional entities (FEs) and color polygons are the convex hulls shaping all FE having each category for each condition. The black polygon is the global convex hull. The functional volume (computed in 4D) and number of FEs for each trait category and pH conditions are indicated at the bottom of each plot. The two axes (PC1 and PC2) represent the first two dimensions of the 4D trait space as in Figure 2.

4 | DISCUSSION

Using benthic field surveys and species-specific traits, we find losses of trait diversity and shifts in ecosystem properties with acidification across different habitats and depths on temperate rocky reefs. A reduction of calcification and calcifying species' cover is one of the most common patterns found under acidified conditions (Doney et al., 2020; Gattuso et al., 2015; Kroeker, Kordas, et al., 2013), and our results reinforce these findings across the habitats studied herein that span different depths. However, we also found that shifts in other trait categories, each associated with key ecological functions—autotrophs, filter feeders, herbivores, and habitat-forming species—were habitat-specific, indicating that OA may produce divergent responses across habitats and depths. Combined,
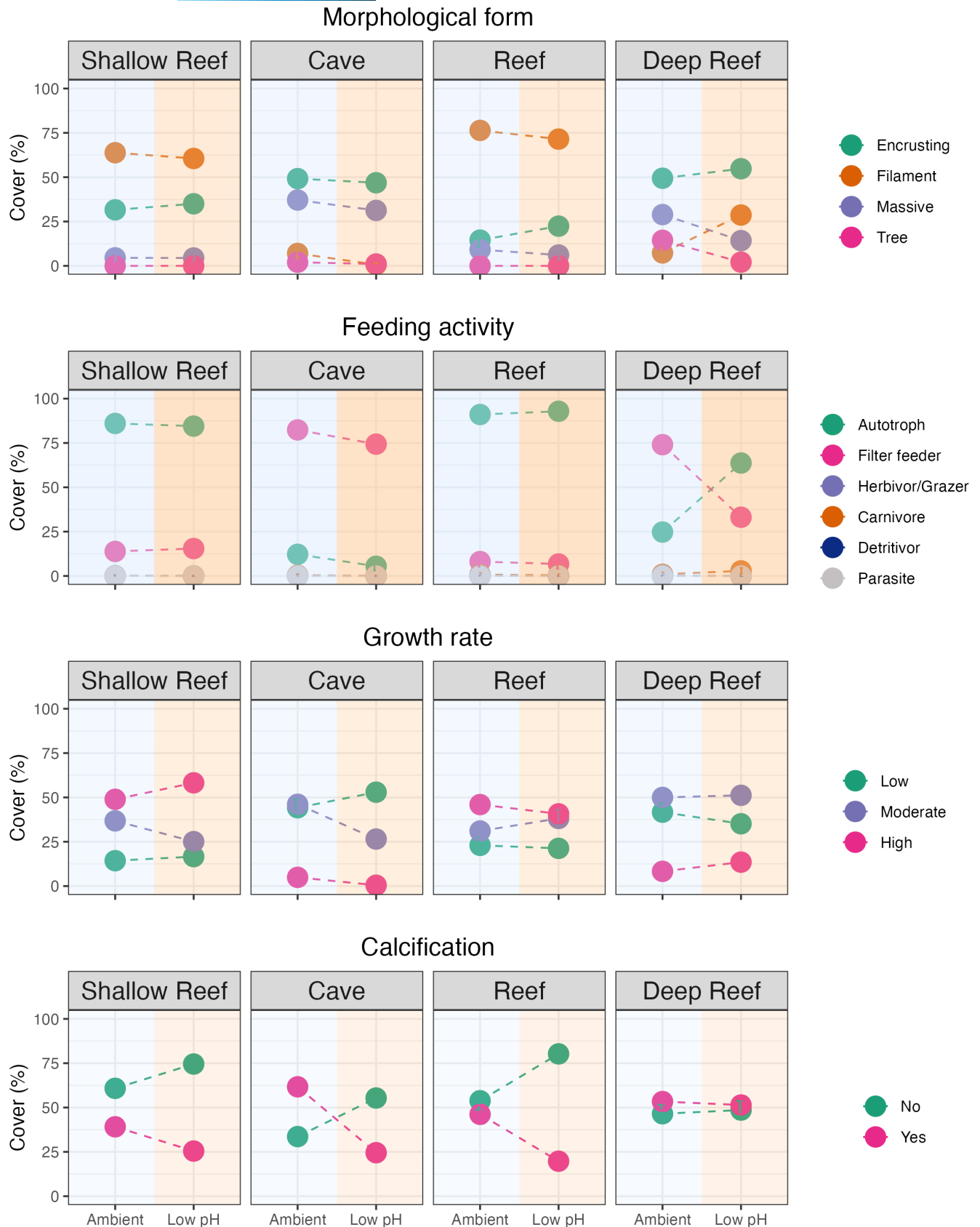
FIGURE 4 Bayesian prediction probability of the likelihood of benthic cover to belong to a functional trait category across habitats and between pH zones. Colors refer to categories for each trait. The functional traits are as follows. Form: (a) Encrusting, (b) filaments, (c) massive, and (d) tree-like; feeding: (a) autotroph, (b) filter feeders, (c) herbivores/grazers, (d) carnivores, (e) detritivores, and (f) parasites; and growth rates: (1) Low (<1 cm/year), (2) moderate (1–5 cm/year) and (3) high (>5–10 cm/year). Habitats: Shallow Reefs (0.5–3 m depth), Caves (3 m depth), Reefs (10 m depth), and Deep Reefs (40 m depth).
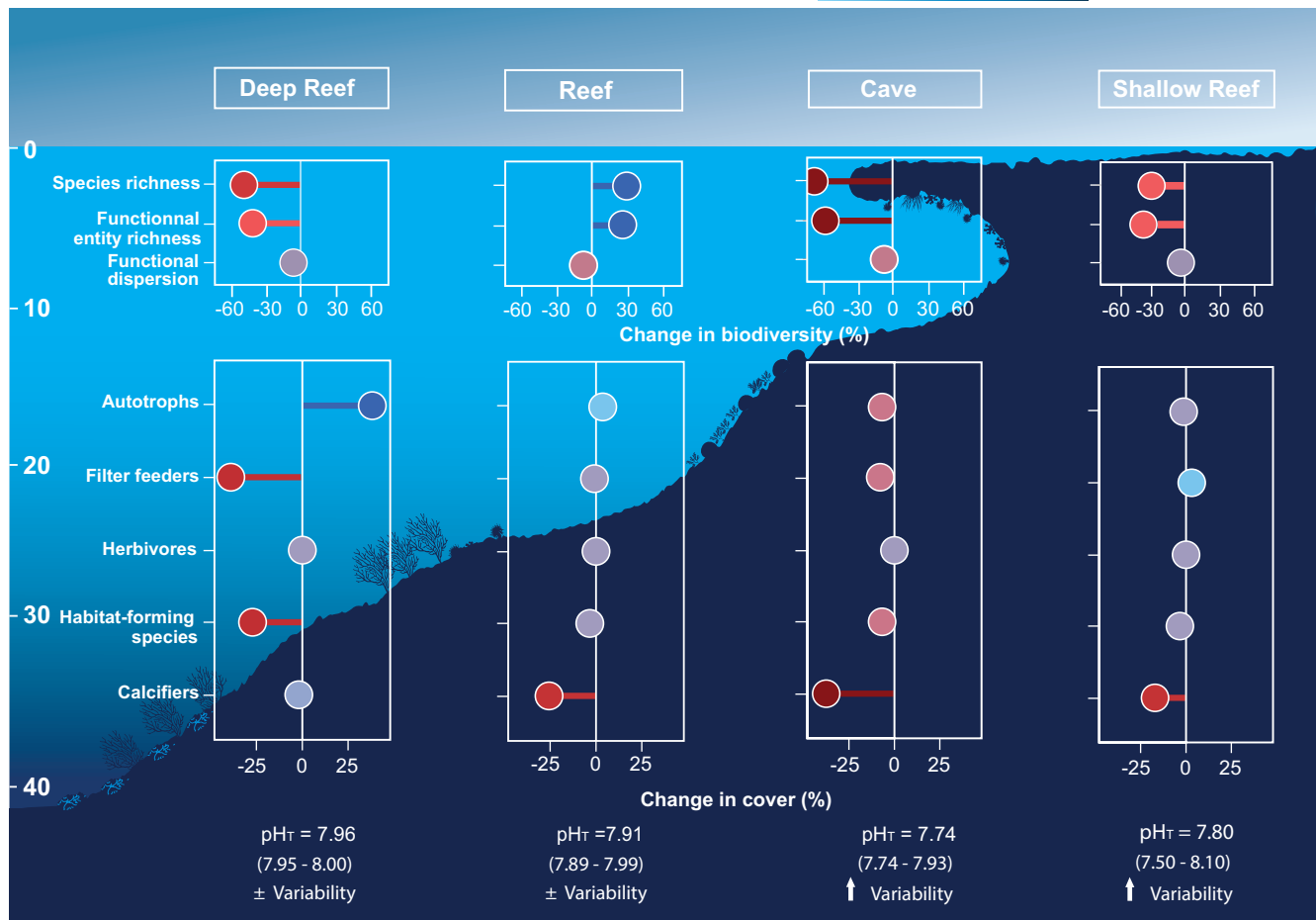
FIGURE 5 Changes (losses or gains) of diversity (species and traits) and predicted benthic cover of some functional traits categories across habitats and between pH zones. Upper panel: Dots indicate changes in species richness, functional entity richness, and functional dispersion between ambient pH and low pH conditions. Data were obtained from the global pool of 215 benthic species and 74 FEs. Lower panel: Dots indicate changes in benthic cover for some selected functional traits calculated from the Bayesian multinomial model between low and ambient pH conditions. Losses are indicated in red and gains in blue. pH_T is the mean with 25th and 75th percentiles between parenthesis and its variability at the CO_2 vent systems.

these findings highlight the importance of connecting species and trait diversity of benthic habitats with key ecosystem properties to anticipate the impacts of global environmental change on marine ecosystems. This approach generates new insights on the predicted ecological consequences of OA, showing that, in addition to the loss in species and trait diversity, estimated key ecological functions, including calcification, habitat provision, and filter feeding, will be negatively impacted. While shifts in trait diversity occur across different habitats and therefore are expected as a general effect of OA, trait and function-specific responses vary across habitats, contributing to further uncertainty on the overall ecological consequences of global environmental change.

4.1 | Biodiversity shifts across habitats under ocean acidification

Our results reveal that OA transformed the assemblage structure and trait diversity across temperate benthic habitats with

significant consequences for ecosystem function. The overall decrease in species richness and trait diversity in the majority of habitats found here supports previous observations that long-term exposure to ocean acidification at CO_2 vents can have significant impacts on whole community assemblages leading to an overall simplification of the community, dominated by non-calcifying species (Fabricius et al., 2011; Harvey, Allen, et al., 2021; Kroeker, Micheli, et al., 2013; Teixidó et al., 2018). Studies at single-habitat CO_2 vents have reported direct and indirect effects of OA on benthic communities, including a decrease in species richness, biomass, and altered species interactions, with cascading impacts on habitat structural complexity and trophic links (Enochs et al., 2015; Foo et al., 2018; Hall-Spencer & Harvey, 2019; Kroeker et al., 2011; Sunday et al., 2017). In addition to these structural shifts as well as declines in the abundance of calcifying taxa, we found a decrease in trait diversity and redundancy, an increase of vulnerability and a shift in the trait space due to OA. Key traits that shifted across the different habitats included morphological forms, feeding activity, growth rate, and calcification. For

instance, species with massive (e.g., the coral *Cladocora caespitosa*) and tree-like morphologies (e.g., the red gorgonian *Paramuricea clavata*), filter feeders (e.g., the tunicate *Halocynthia papillosa*) and grazing feeding strategies (e.g., the sea urchin *Arbacia lixula*), slow growth rates (e.g., the encrusting calcareous algae *Lithophyllum stictiforme*), and the presence of calcifying structures (e.g., the bivalve *Mytilus galloprovincialis*) decreased from ambient pH to low pH zones. The patterns of trait change found here are similar to the reported regional-scale shifts in the trait diversity of benthic assemblages in temperate and coral reefs that occurred during periods of broad-scale environmental variation, such as marine heatwaves (when temperature is extremely warm for an extended period of time) (Gómez-Gras et al., 2021; Harvey et al., 2022; Hughes et al., 2018). These studies indicate a shift from the dominance of slow-growing and long-lived species that are important for habitat complexity to simplified assemblages characterized by encrusting morphological characteristics with higher growth rates and fast-lived. Combined, these results highlight that across different taxa and different ecosystems, there is a convergence towards similar life history strategies, an overall loss of trait diversity and redundancy along with an increase of vulnerability, which can lead to a decline in the functioning and ultimately affect the long-term resilience of ecological communities to cope with environmental change.

However, our results also revealed an increase in species richness and trait diversity in the Reef habitat at 10 m depth. Interestingly, this habitat is characterized by a large number of filamentous and turfy algal species with seasonal life histories, high growth rate, and a lack of calcified structures, which may be favored by higher $p\mathrm{CO}_2$. Thus, the observed benthic assemblage structure and the abundance of species with these life-history traits confirm that non-calcifying macroalgal species (e.g., *Dictyota dichotoma*, *Halopteris scoparia*) are generally physiologically tolerant to OA and even can exhibit enhanced growth under these conditions (Harvey, Kon, et al., 2021; Koch et al., 2013; Porzio et al., 2011). This tolerance to low pH conditions is explained by the ability of macroalgal species to increase photosynthetic rates, as they benefit from increased $p\mathrm{CO}_2$ and higher availability of dissolved inorganic carbon (DIC) forms under OA conditions (Connell et al., 2013; Cornwall et al., 2017; Kumar et al., 2022).

4.2 | Ecosystem shifts under ocean acidification

Importantly, we show that the characteristics of total benthic cover, species composition, the life history strategies of the species, and trait diversity, which support the overall species assemblages and functioning of benthic communities, experience a marked shift under exposure to OA. Functional traits (with a focus on specific ecological functions and their impact on the ecosystem) have long been understood to drive ecosystem functions such as nutrient cycling, primary production, and habitat provisioning that are fundamental for marine ecosystems, and in turn, to guarantee the

ecosystem services provided to people, ranging from food provisioning, shoreline protection, water quality, climate regulation (carbon sequestration), and intrinsic cultural values (Brandl et al., 2019; Díaz & Cabido, 2001; Hughes et al., 2018; Madin et al., 2016). These shifts in functional traits might be associated with changes in key estimated ecosystem processes, including primary production of algae (through changes in autotrophs), herbivory, as a proxy for trophic interactions, and habitat complexity (through habitat-forming species). These shifts in ecosystem processes suggest different pathways by which OA may impact temperate coastal ecosystems. There were some marked differences regarding the magnitude of the change in ecosystem processes for each habitat. Such differences are probably due to the specific benthic composition of each habitat (invertebrate-dominated habitats for Cave and Deep Reef versus macroalgae-dominated for Shallow Reefs and Reefs). Overall, we found a clear decrease in habitat complexity as well as an increase in primary production driven by the loss of three-dimensional habitat by habitat-forming and long-lived species with massive and three-like morphologies and the increase of seasonal filamentous and low-lying algal communities under low pH conditions at the Deep Reef (40 m). These results align with the indirect effects driven by OA on habitat-forming species (e.g., coral reefs, mussel beds, and macroalgal habitats) and the associated changes in the extent and structural complexity of biogenic habitat (Sunday et al., 2017). The Deep Reef habitat (also named coralligenous outcrops) hosts around 10% of the Mediterranean species and is characterized by high structural complexity and long-lived species, which provide habitat for fish communities, a framework for carbonate accretion, as well as filter-feeding and nutrient cycling (Ballesteros, 2006; Gómez-Gras et al., 2021; Teixidó et al., 2011). Moreover, the increased cover of turf and macroalgae and the homogenization of community composition results in a striking regime shift that changes the structure, habitat complexity, and function of communities at natural CO_2 vents (Agostini et al., 2018; Harvey, Allen, et al., 2021; Sunday et al., 2017). Turf algae and low-lying algal communities are characterized by fast-growing, seasonal strategies with high turnover that tolerate stressful conditions and represent alternative states in temperate rocky reefs (Airoldi, 1998; Benedetti-Cecchi et al., 2019). Ongoing regime shifts in temperate reef communities include the transition from macroalgal forest to turf-dominated assemblages or barrens, devoid of marine vegetation, mass mortalities of sessile species in response to marine heatwaves, species invasions and diseases (Bevilacqua et al., 2021; Pessarrodona et al., 2021; Wernberg et al., 2016). Thus, OA, similar to other climate-driven and local impacts, results in shifts in community composition that fundamentally alter the balance between consumers and resources, suppressing ecological resilience and rendering these marine ecosystems vulnerable to other disturbances.

Over the past decade, studies using natural CO_2 vents as natural analogues for future OA conditions have provided novel insights into the long-term effects on ecosystem properties, functions, and services (Aiuppa et al., 2021; González-Delgado & Hernández, 2018; Hall-Spencer & Harvey, 2019). The relevance

of field studies in these natural systems lies in that the spatial carbonate chemistry gradient mimics the temporal continuum of future CO_2 levels. The low pH zones are most comparable with values predicted for the year 2100 with a decrease of pH from −0.16 to −0.44 pH under SSP1-2.6 and SSP5-8.5 (Gattuso et al., 2015; Kwiatkowski et al., 2020). While these systems have provided crucial information about OA effects, they also present ample opportunities to assess the combined effects of multiple stressors on future global ocean ecosystems. Combining natural carbonate chemistry conditions with different warming scenarios and extreme climatic events, such as marine heatwaves (especially during and after the summer when temperatures peak) or through in-situ manipulation of temperature and oxygen, could provide new insights into future global ocean conditions and may be crucial in determining future ecosystem functions.

Preserving ecosystem functioning and the provision of ecosystem services to humanity are major goals of this century (Bellwood et al., 2019, Tilman et al., 2014). Our study provides novel mechanistic insights into shifts in community patterns and trait diversity due to OA across multiple temperate benthic habitats and water depths. Future studies could clarify crucial questions regarding how shifts in benthic community structure and functional traits affect ecosystem functioning and resilience. These studies could involve directly measuring and linking rates of ecological processes in coral reefs, macroalgal forests and seagrass meadows by using natural analogues found across the ocean. In particular, a better quantitative understanding of how traits link with key ecological functions, including calcium carbonate dynamics, trophic interactions, and nutrient cycling, could provide new insights into future ecosystem functioning and shifts across marine ecosystems in the Anthropocene.

AUTHOR CONTRIBUTIONS

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

All data needed to assess the conclusions in the paper are provided in both the main text or the Supplementary Materials. pH and seawater physiochemical parameters are available through PANGAEA database at https://doi.org/10.1594/PANGAEA.964032. Data for the in situ temperature data analysis (Figure S2) are available from the T-MEDNet network www.t-mednet.org Cover data of benthic species (Data S1), traits codes (Data S2), and outputs from the Bayesian model (Data S3) are available through Dryad database at: https://doi.org/10.5061/dryad.2z34tmps9. The R code used to generate trait analysis and results is available through GitHub-Zenodo repository at https://zenodo.org/doi/10.5281/zenodo.10246135.

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SUPPORTING INFORMATION

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