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RESEARCH ARTICLE

Seepage, depth, and oxygen as drivers of heterogeneity and resilience of carbonate macrofauna at methane seeps

Olívia S. Pereira[1,2,]*, Greg W. Rouse[1], Erik E. Cordes[3], Jorge Cortés[4], and Lisa A. Levin[1]

Much of the variability in methane seep macrofaunal communities has been attributed to seepage activity (i.e., fluid flux regime); however, more attention is needed to other environmental factors that might be playing a role in structuring methane seep communities. A primary goal was to understand how depth and bottom-water dissolved oxygen concentration affect the influence of seep activity on the diversity and trophic structure of carbonate macrofauna and their recovery and resilience. We conducted mensurative and manipulative experiments on the Costa Rican Pacific margin at three seep locations with varied hydrographic conditions: (1) Quepos Landslide, at 400 m deep, within the oxygen minimum zone (OMZ); (2) Mound 12, at 1,000 m deep, just below the OMZ; and (3) Jaco Scar, at 1,850 m deep, well below the OMZ. Within locations, experiments were conducted at active, transition, and background seep habitats. Habitat was the main factor influencing macrofauna at the deeper seeps, where chemosynthetic production supplies the primary food source. Seep-specialist species found in active habitats exhibited faster responses to colonization and transplant experiments mimicking seep activation than species found in transition habitats. Species in transition habitats, relying on both photo- and chemosynthetic production, appeared to have higher recovery and resilience rates in experiments mimicking seep cessation than seep specialists. Within the OMZ, low oxygen conditions overrode the effects of habitat, yielding low densities and low diversity to the point of limiting colonization and community retention, as observed through manipulated changes in seep habitat. Our study highlights how environmental factors (i.e., seep habitat, depth, and oxygen concentration) promote macrofaunal heterogeneity on carbonates at methane seeps and might control resilience. With the expansion of OMZs and seeps due to ocean deoxygenation and warming, respectively, an understanding of how environmental factors affect the resilience and recovery of these communities is important.

Keywords: Methane seep, Carbonate, Macrofauna, Environmental gradients, Diversity, Trophic diversity

1. Introduction

Since the initial discovery of methane seeps (Paull et al., 1984), they have been found on continental margins worldwide in many geological and environmental settings (Sibuet and Olu, 1998), from 60 m to 7,326 m deep (Fujikura et al., 1999; Vedenin et al., 2020), including within oxygen minimum zones (OMZs; Levin et al., 2015; Seabrook et al., 2024). More than 100 seeps have been found along the Pacific margin of southern Nicaragua and Costa Rica (Sahling et al., 2008), where a well-developed OMZ is formed at 300–700 m (Levin et al., 2015). Seeps are often associated with authigenic carbonate rocks, a by-product of microbial anaerobic oxidation of methane, that represent an important carbon reservoir globally, contributing to methane and CO_2 sequestration (Boetius and Wenzhöfer, 2013, Marlow et al., 2014). These carbonates provide substrate, food access, settlement cues via biofilm, and refuge for diverse macrofaunal communities (Levin et al., 2015; Pereira et al., 2021).

The environmental conditions supporting this chemosynthesis-based ecosystem also drive patterns of benthic community structure, and the biological and geochemical influence of the seep extends into surrounding, background habitats (Levin et al., 2016; Ashford et al., 2021). Along the eastern Pacific, seep macrofauna exhibit distinct community traits under different seepage activities (i.e., methane and sulfide flux regimes; Levin et al.,

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[1] Scripps Institution of Oceanography, University of California, San Diego, CA, USA

[2] Current address: Monterey Bay Aquarium Research Institute, Moss Landing, CA, USA

[3] Department of Biology, Temple University, Philadelphia, PA, USA

[4] Centro de Investigación en Ciencias del Mar y Limnología, Universidad de Costa Rica, San José, Costa Rica

* Corresponding author:
Email: ospereir@ucsd.edu

2015; Pereira et al., 2021; Seid et al., 2025). Active habitats, which are characterized by higher fluid flux and chemosynthetic microbial activity and the formation of carbonate rocks, support dense, gastropod-dominated communities with seep-specialist species on the carbonate rocks (Levin et al., 2015; Pereira et al., 2021). Even though the rocks sit atop the sediment, the macrofauna on the rocks are still exposed to methane released by bubbles or diffusion and sulfide generated by chemosynthetic microbes within the rocks that continue to carry out anaerobic oxidation of methane (Marlow et al., 2014). In surrounding, background habitats, lacking seepage and carbonate formation, the community resembles “typical” deep-sea environments, dominated by crustaceans, cnidarians, and ophiuroids (Levin et al., 2015). Between active and background habitats, a transition habitat is created, hosting both chemosynthesis-based species (i.e., seep specialists found at active habitats) and photosynthesis-based species (i.e., species found at background habitats surrounding the seep and dependent on the flux of surface-derived photosynthetic material; Ashford et al., 2021; Pereira et al., 2021).

In addition to this increased heterogeneity driven by seepage and substrate availability, hydrographic features such as depth and oxygen gradients can also shape benthic community structure (Levin et al., 2001; Carney, 2005). Regarding ocean depth, high species richness has been reported for benthic assemblages at intermediate depths of 1,000–3,000 m (Rex, 1981; Rex and Etter, 2010; De Leo et al., 2017), and the delivery of surface-derived photosynthetic material into the deep ocean declines with depth as the organic matter is consumed by midwater organisms (Rex et al., 2005). Low oxygen conditions within OMZs (below 0.5 mL L^{-1}) reduce invertebrate diversity, density, and biomass (Levin, 2003), often homogenizing assemblages by favoring a limited number of species tolerant to low oxygen (Levin et al., 2000; Guilini et al., 2012).

Notably, most community studies of patterns driven by depth and oxygen come from soft sediment at photosynthesis-based ecosystems. The presence of hard substrates and chemosynthetic production increases ecosystem complexity and may enhance diversity and alter community structure (Lacharité and Metaxas, 2017). As chemosynthetic ecosystems are less reliant on surface productivity, typical patterns in deep-sea abundance, biomass, and diversity are often absent (Cordes et al., 2025). Understanding natural dynamics and resilience of such communities to environmental changes is essential to predicting changes in distribution patterns under future climate scenarios (Venturelli et al., 2018). As the ocean warms and deep-sea oxygen levels decline (Schmidtko et al., 2017), temperature-driven gas hydrate destabilization could increase methane seepage (Ketzer et al., 2020; Li et al., 2023), while ocean deoxygenation will expand OMZs (Stramma et al., 2008; Levin, 2018), affecting benthic communities, including those at methane seeps.

Here, we examined macroinvertebrate diversity, density, composition, trophic structure, and biological traits on carbonate rocks across three methane seeps with different depths and bottom-water dissolved oxygen concentrations along the Costa Rican Pacific margin. We analyzed naturally occurring macrofaunal communities on carbonate rocks, conducted colonization experiments, and examined recovery and resilience through transplant experiments, with the aim of understanding how the influence of habitat on carbonate community dynamics is affected by hydrographic conditions. Specifically, we asked: Are macrofaunal responses to seep habitat affected by depth and bottom-water oxygen concentration? How are colonization and resilience patterns affected by habitat, depth, and bottom-water oxygen concentration? Which taxa and traits confer good colonization ability and resilience? We hypothesized that macrofaunal diversity and trophic structure are influenced by depth and bottom-water oxygen concentration, with increasing reliance on chemosynthetic production with increasing depth and reduced diversity under low-oxygen conditions. We also expected rapid macrofaunal recovery at active habitats, particularly by microbe-grazing fauna, but that resilience would be constrained by low oxygen.

2. Methods

2.1. Study area

The convergent margin of Costa Rica in the Pacific Ocean, where the Cocos Plate subducts beneath the Caribbean Plate (Kimura et al., 1997), hosts hundreds of seeps at depths of 400–2,400 m (Sahling et al., 2008), with new ones continually being discovered. These seeps have been found associated with mounds, faults, subduction scars, and landslides, and almost all rock samples from previous studies were methane-related authigenic carbonates (Sahling et al., 2008). Here, we examined macrofaunal invertebrates on carbonate rocks from three bathyal seeps that span from within to below the Costa Rica OMZ ($[O_2] <22$ µM threshold; **Figure 1**, **Table 1**):

Quepos Landslide is a shallow seep located at 389–400 m within the OMZ, with average bottom-water oxygen concentration of 4.25 µM. It was formed from a slide caused by seamount subduction, with a headwall height of 160 m and head at approximately 400 m deep (Harders et al., 2011). Fluids may originate from buried hydrates within the gas hydrate stability zone along the slide toe (Steeb et al., 2015). Microbial mats are common, covering the sediment, with a few carbonate and mudstone rock outcrops (Karaca et al., 2014). Tuna crabs (*Grimothea monodon*) are abundant megafauna at the seep (**Figure 1**), commonly seen at more inshore shelf and slope sites off the seep (Seid et al., 2025). Smaller invertebrates previously reported include sabellid annelids, anthozoans, and patellid limpets on carbonates (Levin et al., 2015; Seid et al., 2025).

Mound 12 is located at 990–1,000 m water depth (Mau et al., 2006), just below the OMZ, with an average bottom-water oxygen concentration of 27.1 µM (Levin et al., 2015). It is a mud volcano, where methane, geofluids, and mud ascend to the seafloor along faults (Niemann et al., 2013). Intercalated mudflows and slope sediment layers indicate alternating high- and low-seepage activity phases (i.e., higher and lower fluid fluxes) within 12 months (Mau

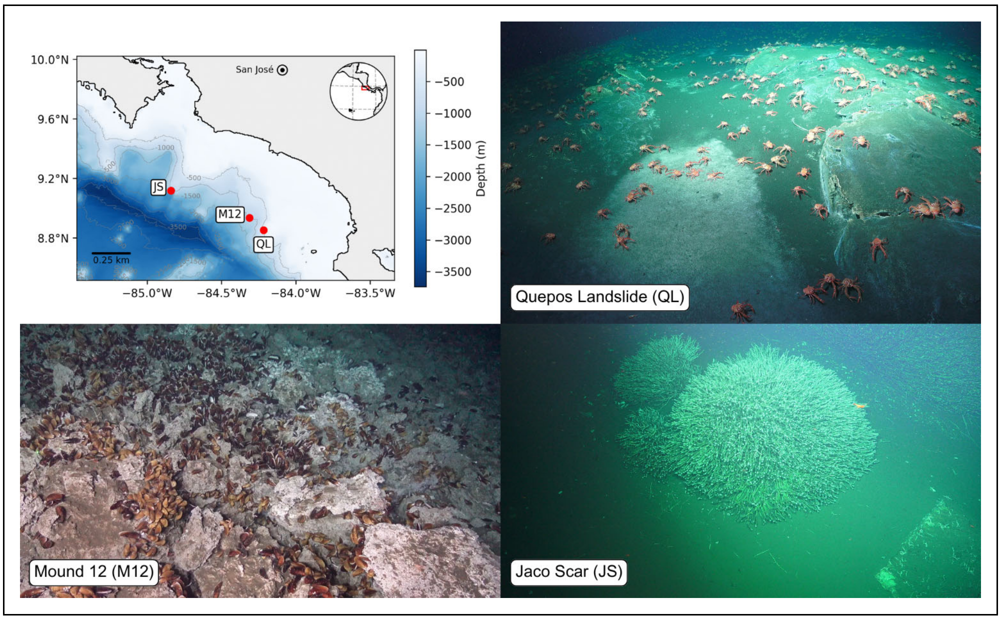

Figure 1. Sampling location and images. Location and representative images of the three methane seeps off the Pacific margin of Costa Rica, Central America: Quepos Landslide (QL), Mound 12 (M12), and Jaco Scar (JS). Tuna crabs (*Grimothea monodon*) can be seen in the image of Quepos Landslide, bathymodioline mussels *Bathymodiolus earlougheri* and *Bathymodiolus nancyshneiderae* and yeti crabs *Kiwa puravida* at Mound 12, and siboglinid tubeworms *Lamellibrachia barhami* and *Escarpia spicata* at Jaco Scar.

Table 1. Environmental settings of the three methane seep study sites off the Pacific margin of Costa Rica

Seep Location	Latitude (N)	Longitude (W)	Water Depth Sampling Range (m)	Average Bottom Water Temperature (°C)	Average Bottom Water Salinity	Average Bottom Water Oxygen (μM)
Quepos Landslide	8°51.051′	84°12.984′	308–399	11.31	34.79	4.25
Mound 12	8°55.827′	84°18.757′	991–1,003	4.91	34.56	27.10
Jaco Scar	8°05.389′	84°49.620′	1,708–1,887	2.48 (approximately 6 in certain seeping areas)	34.71	79.07

et al., 2007; Niemann et al., 2013). Carbonates are abundant; they host the Costa Rican yeti crab *Kiwa puravida* (Thurber et al., 2011; Azofeifa-Solano et al., 2022), two recently described species of bathymodioline mussels *Bathymodiolus earlougheri* and *Bathymodiolus nancyshneiderae* (McCowin et al., 2020) that form large beds (Sahling et al., 2008; **Figure 1**), and the siboglinid tubeworm *Lamellibrachia donwalshi* (McCowin and Rouse, 2018) forming bushes. Neolepetopsid limpets and provannid snails are found on the carbonates and within the mussel beds and tubeworm bushes (Levin et al., 2015; Pereira et al., 2021; Betters et al., 2024; Seid et al., 2025).

Jaco Scar is located at 1,850 m, well below the OMZ, with an average bottom-water oxygen concentration of 79.07 μM. It is a large landslide scar caused by seamount subduction, and is considered a hydrothermal seep due to warm fluid at the active seeping area (averaging 6°C, with some areas reaching up to 8°C), hosting both hydrothermal vent and seep-specialist species (Levin et al., 2012). It exhibits constant fluid flow with higher methane concentration than at Mound 12 (Mau et al., 2014). Siboglinid tubeworms *Lamellibrachia barhami* and *Escarpia spicata* form large spherical bushes (1–2 m in diameter; **Figure 1**) supporting bathymodioline mussels, including *Bathymodiolus earlougheri* and the hydrothermal vent species *B. thermophilus* (McCowin et al., 2020). Lepetodrilid limpets are abundant, and zoarcid fishes nest among the tubes (Levin et al., 2012; Frable et al., 2023). Additional microhabitats include dense beds of the clam *Archivesica gigas* and frenulate worms (*Siboglinum* sp.; Levin et al., 2012; Seid et al., 2025).

These three seep locations were visited during two research cruises aboard the R/V *Atlantis* (AT37-13, May to June 2017, and AT42-03 in October 2018) with the human-occupied vehicle (HOV) *Alvin*, and during a third research cruise aboard R/V *Falkor* (FK190106 in January 2019) with the remotely operated vehicle (ROV) *SuBastian*.

2.2. Experimental design and sample processing

2.2.1. Unmanipulated carbonate rocks

With the goal of understanding how the influence of seep habitat on community dynamics is affected by depth and

Table 2. Number of carbonate rocks collected at each seep by experiment and sampling year[a]

Seep or Experiment	Quepos Landslide 2017	Quepos Landslide 2018	Quepos Landslide 2019	Mound 12 2017	Mound 12 2018	Mound 12 2019	Jaco Scar 2017	Jaco Scar 2018	Jaco Scar 2019
Unmanipulated rocks									
Active	5	1	0	7	9	0	6	8	1
Transition	6	1	0	8	8	0	4	3	1
Background	0	0	0	0	0	0	2[b]	1[b]	0
Colonization experiments									
3 months active[c]	0	0	5	0	0	5	0	0	5
17 months active[d]	0	4	0	0	0	0	0	0	0
7 years active[e]	0	0	0	0	4	0	0	0	0
7 years transition[e]	0	0	0	0	4	0	0	0	0
Transplant experiments (17 months)[f]									
Active to transition	0	4	0	0	10	0	0	0	0
Active to background	0	0	0	0	5	0	0	5	0
Transition to active	0	3	0	0	5	0	0	5	0
Transition to background	0	0	0	0	5	0	0	0	0
Background to active	0	0	0	0	0	0	0	5[b]	0

[a] For experimental rocks, sampling year indicates year rocks were recovered at the end of the experiment.

[b] These rocks were sedimentary, not carbonate.

[c] Rocks deployed in October 2018, recovered in January 2019.

[d] Rocks deployed in May 2017, recovered in October 2018.

[e] Rocks deployed in January 2010, recovered in May 2017.

[f] Rocks deployed in May 2017, recovered in October 2018.

bottom-water oxygen concentrations, naturally occurring carbonate rocks (hereafter called "unmanipulated") were taken from the three seep locations in 2017, 2018, and 2019 at different seep habitats. The sampling effort is summarized in **Table 2**. Seep habitats (active, transition, and background) were defined visually by the presence or absence of seep specialists and microbial mats, which are fueled by methane and hydrogen sulfide produced by anaerobic oxidation of methane (Marlow et al., 2014; Levin et al., 2015, Ashford et al., 2021). Active habitats exhibited microbial mats, methane bubbles or seep megafauna (bathymodioline mussels, vesicomyid clams, and/or siboglinid tubeworms). Background habitats lacked seep megafauna and microbial mats but supported occasional deep-sea megafauna (e.g., paralomid crabs, *Scotoplanes* sea cucumbers), as in the typical deep-sea habitat that surrounds the seep. Transition habitats were characterized by carbonates and a mix of seep and background species, representing an ecotone between the active and background habitats (see Ashford et al., 2021). Although carbonates are formed mainly at active habitats by microbial activity (mostly anaerobic methanotrophic archaea ANME-2 and associated sulfate-reducing bacteria), some can be found at transition habitats hosting viable methanotrophic microbes (mostly ANME-1; Marlow et al., 2014). At Jaco Scar a few sedimentary rocks were collected at background habitats for comparisons with seep communities.

Rocks were collected using HOV *Alvin* and ROV *SuBastian* manipulators. Each rock was placed separately into an individual compartment inside Delrin bioboxes on the vehicle basket, which were sealed closed during recovery to avoid loss and damage of fauna and cross contamination between samples. Upon recovery, rocks were kept in the cold room at 4°C, and taken out one by one for processing. Rocks were photographed intact, and macrofauna were removed manually. Tissue samples were collected from at least three specimens of each species on each rock for stable isotope analyses and frozen at -20°C. The rocks were wrapped in aluminum foil to determine the approximate rock surface area later in the laboratory by dividing the total weight of the foil used to wrap the rock by the average weight of a 1 cm^2 piece of foil (Pereira et al., 2021; Pereira et al., 2022). Rocks were left overnight in a bucket with filtered seawater at room temperature to induce additional infauna to crawl out, as is known to happen with temperature stress. The next day, the water in the buckets with the remaining fauna was sieved through a 300 µm mesh, with the retained macrofauna preserved in 95% ethanol in Nalgene bottles for community composition analysis. In the laboratory on shore, these samples were re-sieved using a 300 μm mesh and sorted in freshwater at 12× magnification under a dissecting microscope. Specimens were identified to species level with the help of taxonomy experts and the faunal inventory from Costa Rica seeps (Seid et al., 2025), and counted. Counts of specimens removed at sea for isotope analyses were added to the laboratory total counts.

To constrain nutritional sources, particulate organic matter (POM) samples were collected from surface (0–5 m) and near-bottom waters (<15 m above the seafloor) at each seep location using Niskin bottles on CTD-Rosette casts. For each sample, 2–4 L were filtered through a pre-combusted 0.7 μm pore size, 47 mm diameter glass microfiber filter. The filter with retained material was frozen at −20°C.

In the laboratory onshore, POM samples and faunal tissue collected for stable isotope analyses ($\delta^{13}C$ and $\delta^{15}N$) were processed as in Pereira et al. (2021; 2022). Samples were sent to Washington State University for stable isotope measurements using a Costech elemental analyzer coupled to a Micromass Isoprime isotope ratio mass spectrometer. Precisions for $\delta^{13}C$ and $\delta^{15}N$ analyses were ±0.02‰ and ±0.05‰, respectively (standard deviation of 10 replicate organic standards).

2.2.2. Carbonate rocks for colonization and transplant experiments

The unmanipulated rocks described in Section 2.2.1 served as control samples for colonization and transplant experiments. To examine the dynamics and colonization rate of carbonate-dwelling macrofauna at the different seep locations and habitats, we performed colonization experiments for various periods of time using other carbonate rocks. These rocks had been collected at Mound 12 and the fauna removed, following the same sampling and processing methods described above, during a prior cruise in January 2010. These rocks were stored at room temperature at Scripps Institution of Oceanography for 7–8 years and were fully dried by the time they were deployed. At Quepos Landslide and Jaco Scar, rocks were deployed at active habitats for 3 months (October 2018 to January 2019; **Figure 2A** and **G**) and for 17 months (May 2017 to October 2018). At Mound 12, rocks were deployed at active habitats for 17 months (May 2017 to October 2018) and at active and transition habitats for 7 years (January 2010 to May 2017). We compared the communities on colonization rocks to the communities on unmanipulated rocks, collected from the same habitat in the same year when the colonization rocks were recovered, to analyze whether the colonization community achieved the patterns of unmanipulated communities. Numbers of colonization rock samples are summarized in **Table 2**.

To compare biological patterns and dynamics of carbonate macrofauna, the rates of community response, and the effects of hydrographic conditions on such dynamics, we performed transplant experiments at the three seep locations. Rocks with all fauna attached were moved by the HOV to a different habitat during a single dive without bringing them back to the ship. They remained on the seafloor for 17 months (transplanted in May 2017, recovered in October 2018; **Figure 2**). Rocks were moved from active habitats to transition or background habitats and from transition or background habitats to active habitats (summarized in **Table 2**). In Sections 3 and 4, we refer to the habitat from which the rocks were moved as the "start habitat," and the habitat to which they were moved as the "end habitat." We compared the communities on the transplanted rocks to communities on unmanipulated rocks collected at the start and end habitats in 2017 and 2018, respectively. The assumption is that the unmanipulated rock communities collected from the start habitat represent the communities on the transplanted rocks before they were moved in 2017.

Although performing identical experiments at all seep locations was not feasible, efforts were made to standardize the approach as much as possible across locations. Experimental rocks were recovered and processed for community and trophic analyses following the same methods described above for the unmanipulated rocks.

2.3. Data synthesis and statistical analyses

The 17-month and 7-year colonization experiments at Mound 12 and the 17-month transplant experiment at Mound 12 were reported previously in Pereira et al. (2021). However, the invertebrate communities were described and discussed only at the family and order levels. Since then, knowledge of the species associated with these seep locations has improved considerably, and a faunal inventory based on genetics and morphology has been published (Seid et al., 2025). Here, we reassess data from Mound 12, after carrying out identifications to species level, and add data from Quepos Landslide and Jaco Scar to examine patterns and dynamics at seeps under different hydrographic conditions.

Densities of invertebrate communities on unmanipulated and experimental rocks were standardized to number of individuals per 200 cm^2, the average size of a rock that can be collected with the submersible or ROV, following previous methodology (Levin et al., 2015; Pereira et al., 2021), allowing for comparisons across rocks of different sizes. PERMANOVA analysis was performed to check for variability in densities among seep locations across all habitats, habitats across all seep locations, and sampling year within seep locations for unmanipulated communities. To compare densities between these communities and experimental communities (both colonization and transplant), Kruskal-Wallis tests followed by Dunn's tests using the Benjamini-Hochberg adjustment (Benjamini and Hochberg, 1995) were used for datasets with three factors or more, and Wilcoxon tests for datasets with two factors.

Three-way ANOSIM and SIMPER analyses were performed on Primer v.7 using Bray-Curtis dissimilarity matrices of species density values, after fourth-root transformation, to assess variability in community composition among seeps, habitats, and sampling years. One-way ANOSIM and SIMPER analyses were performed on Primer v.7 to assess differences in community composition between unmanipulated rocks and experimental rocks, for both transplant and colonization experiments. Cluster and

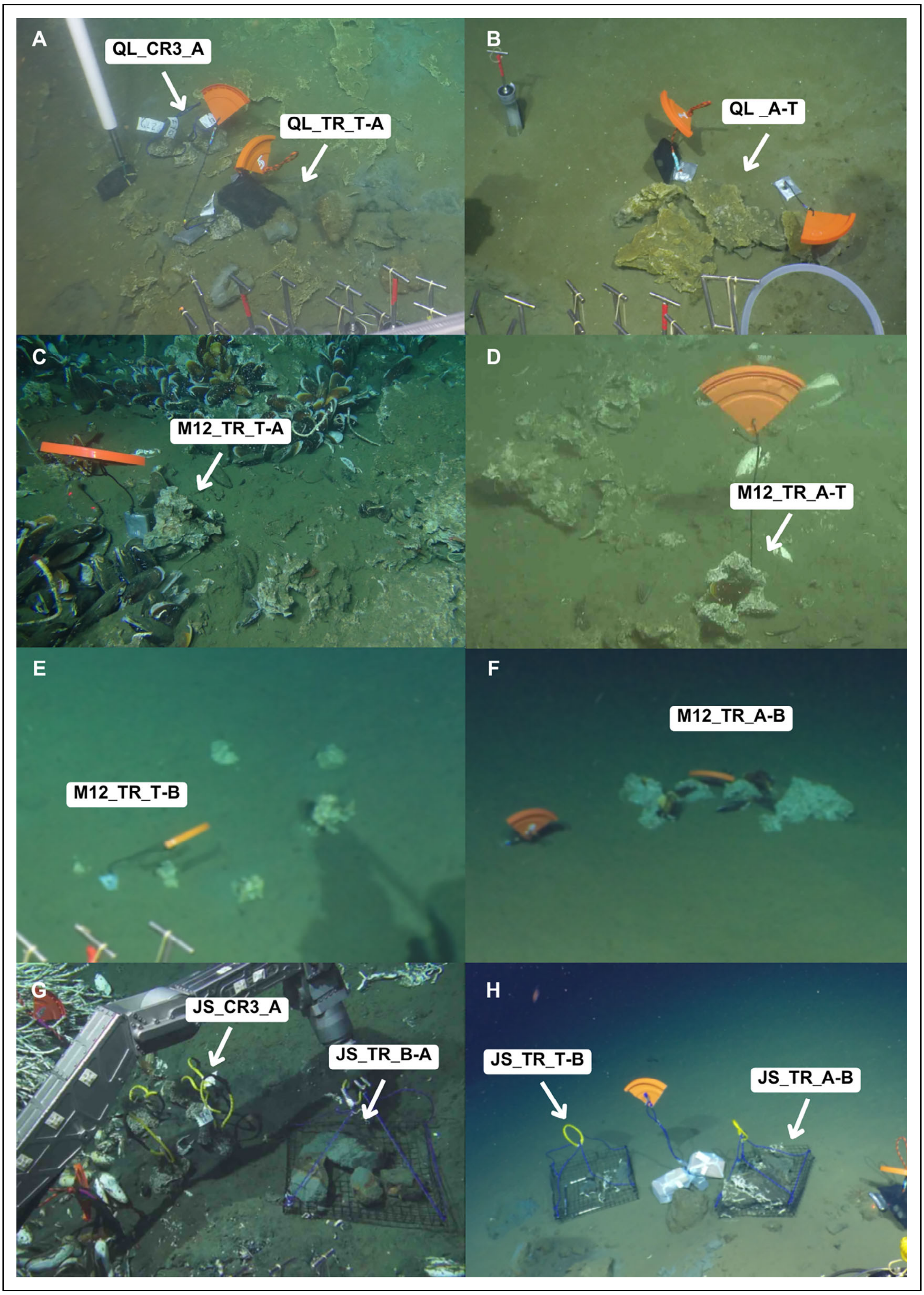

Figure 2. Representative images of experimental rocks in situ. Transplant (TR) and colonization (CR) experiments were conducted at three methane seeps: (A, B) Quepos Landslide (QL), (C–F) Mound 12 (M12), and (G,H) Jaco Scar (JS). For the transplant experiments, rocks were moved from transition to active habitats (T–A), active to transition habitats (A–T), transition to background habitats (T–B), active to background habitats (A–B), and background to active habitats (B–A). Rocks were moved to sites from which other rocks were moved; for example, transplanted rocks moved to the active site in panel A were moved from the transition site in panel B, and vice versa. Colonization experiments were carried out for 3 months (CR3), shown here in active habitats at (A) QL and (G) JS, and for 17 months and 7 years (not shown). See **Table 2** for the complete sampling effort; unmanipulated rocks were collected at the same sites to serve as controls.

non-multidimensional scaling (nMDS) analyses were also performed on Primer v.7 with the same dataset to provide a visualization of the results.

Shannon-Wiener diversity (H′), Pielou's evenness (J), richness (S), and rarefaction curves were calculated using the R package "vegan" for the seeps and different habitats, including for unmanipulated and experimental communities, by pooling total counts of all samples at each seep or habitat. The same data set was used to calculate functional diversity as Rao's quadratic entropy (FD_Q; Alfaro-Lucas et al., 2020) and functional redundancy (FD_R) using the R package "SYNCSA" after characterizing species in body size categories (small, >0.3–2 mm; medium, 2–5 mm; large, >5 mm), feeding guilds (filter feeder, microbial grazer, surface-deposit feeder, subsurface deposit feeder, carnivore, omnivore, chemosynthesis via symbionts, parasitic), lifestyles (tube builder, burrower, errant, sessile, parasitic), mobility (motile, discretely motile, sessile), and calcification categories (heavy, light or partial, none; Levin et al., 2017).

Where multiple individuals of the same species were sampled from a single rock, an average isotope value of all individuals on that rock would be biased toward the value of that species. Thus, mean isotope values of each species were calculated for each rock, and then rock values were averaged by seep, habitat, and experiment to avoid this sampling bias. PERMANOVA tests were performed to check for variability in isotopic composition among seep locations, habitats, and sampling years for unmanipulated communities. To compare isotopic values between unmanipulated communities and experimental communities (for both colonization and transplant experiments), Kruskal-Wallis tests followed by Dunn's tests using the Benjamini-Hochberg adjustment (Benjamini and Hochberg, 1995) or Wilcoxon tests were used as described above. Community-level metrics (Layman et al., 2007) were calculated using the "SIBER" package in R (Jackson et al., 2011), following Pereira et al. (2021; 2022; 2024). Trophic diversity was assessed using standard elliptical area corrected for sample size (SEAc) in $\delta^{13}C$ and $\delta^{15}N$ biplots. Pairwise trophic overlap based on Bayesian posterior estimates of ellipses was calculated between unmanipulated and experimental rocks using two chains of 20,000 iterations with a burn-in of 1,000 and thinning of 10, as previously done in Pereira et al. (2022; 2024).

3. Results

3.1. Macrofaunal communities on unmanipulated carbonate rocks

Densities of macrofaunal invertebrates on carbonate rocks varied among seep locations (**Figure 3A–C**); Jaco Scar showed the highest densities (mean ± standard error of 173 ± 33 individuals per 200 cm^2, n = 18 rocks), followed by Mound 12 (105 ± 23 individuals per 200 cm^2, n = 23 rocks), and lastly Quepos Landslide (27 ± 12 individuals per 200 cm^2, n = 13 rocks; PERMANOVA, $R^2 = 0.21$, $p < 0.001$). When analyzing macrofauna on unmanipulated carbonates from all seeps together, densities were the highest at active habitats (130 ± 25 individuals per 200 cm^2, n = 25 rocks), followed by transition habitats (98 ± 24 individuals per 200 cm^2, n = 25 rocks), and background habitats (26 ± 4 individuals per 200 cm^2, n = 2 rocks; $R^2 = 0.08$, $p = 0.01$). However, within Quepos Landslide there was no significant difference in densities with habitat (Kruskal-Wallis, $\chi^2_3 = 1.51$, $p = 0.70$). There was also no significant interannual difference in densities at all seeps ($R^2 = 0.01$, $p = 0.39$). The effect of seep location on densities did not vary across habitat across all seeps ($R^2 = 0.03$, $p = 0.33$).

Community composition was also different among seep locations (three-way ANOSIM, Global R = 0.72, p = 0.001; **Table 3**), habitats (Global R = 0.35, p = 0.002; **Table 4**), and sampling years (Global R = 0.39, p = 0.01; **Figures 4A–C**, **5A**, and S1–S4). Among seeps, Jaco Scar macrofaunal communities showed the highest dissimilarity to those at the other seeps (JS vs. QL: R = 0.77, p = 0.001; JS vs. M12: R = 0.74, p = 0.001), and Mound 12 and Quepos Landslide showed lower dissimilarity, although still high (R = 0.74, p = 0.001; **Figures 5A** and S1). Jaco Scar was dominated by the tanaids *Parakanthophoreus* sp. 1 and *Typhlotanoides* sp. 1 (27%), annelids Chrysopetalidae n. sp. and *Laminatubus paulbrooksi* (23%), and the snail *Provanna goniata* (13%). The tanaids and *L. paulbrooksi* contributed the most (14%) to the dissimilarity between Jaco Scar and Quepos Landslide (SIMPER, average dissimilarity = 96.97). The five most abundant species at Jaco Scar were also the species that contributed the most (17%) to the dissimilarity between Jaco Scar and Mound 12, together with the snail *Provanna laevis*, which was more abundant at Mound 12 (SIMPER, average dissimilarity = 86.73). In addition to the abundance of *P. laevis* (19%), Mound 12 was dominated by Chrysopetalidae n. sp. (15%) and the limpets *Lepetodrilus ovalis* (8%), Neolepetopsidae (6%), *Pyropelta musaica* (3%), and *Pyropelta wakefieldi* (3%). *Provanna laevis* and *L. ovalis* contributed 10% of the dissimilarity between Mound 12 and Quepos Landslide (SIMPER, average dissimilarity = 92.87). Finally, Quepos Landslide was dominated by a species in the hydrozoan order Anthoathecata (27%).

At all seeps together, based on species-level community composition, communities at active habitats were different than at background habitats (R = 1.00, p = 0.033), and somewhat similar to communities at transition habitats (R = 0.27, p = 0.002). In general, active habitats were dominated by *Provanna goniata* (16%) and *P. laevis* (12%). Transition habitats were dominated by Chrysopetalidae n. sp. (24%) and *Parakanthophoreus* sp. 1 (12%). Surprisingly, background habitats were dominated by *Laminatubus paulbrooksi* (18%). The predominant species and major taxa within habitat varied among seep locations (**Table 4**, **Figure 4A–C**).

Finally, there was a shift in community composition from 2017 to 2018 (R = 0.39, p = 0.001), especially at active habitats (SIMPER, average dissimilarity = 84.15) and at Mound 12 (SIMPER, average dissimilarity = 85.51%), where seep-specialist species (e.g., *Provanna laevis*, *Lepetodrilus ovalis*, *Lepetodrilus* sp., *Pyropelta musaica*, *P. wakefieldi*, and *Kiwa puravida*) were more abundant in 2017.

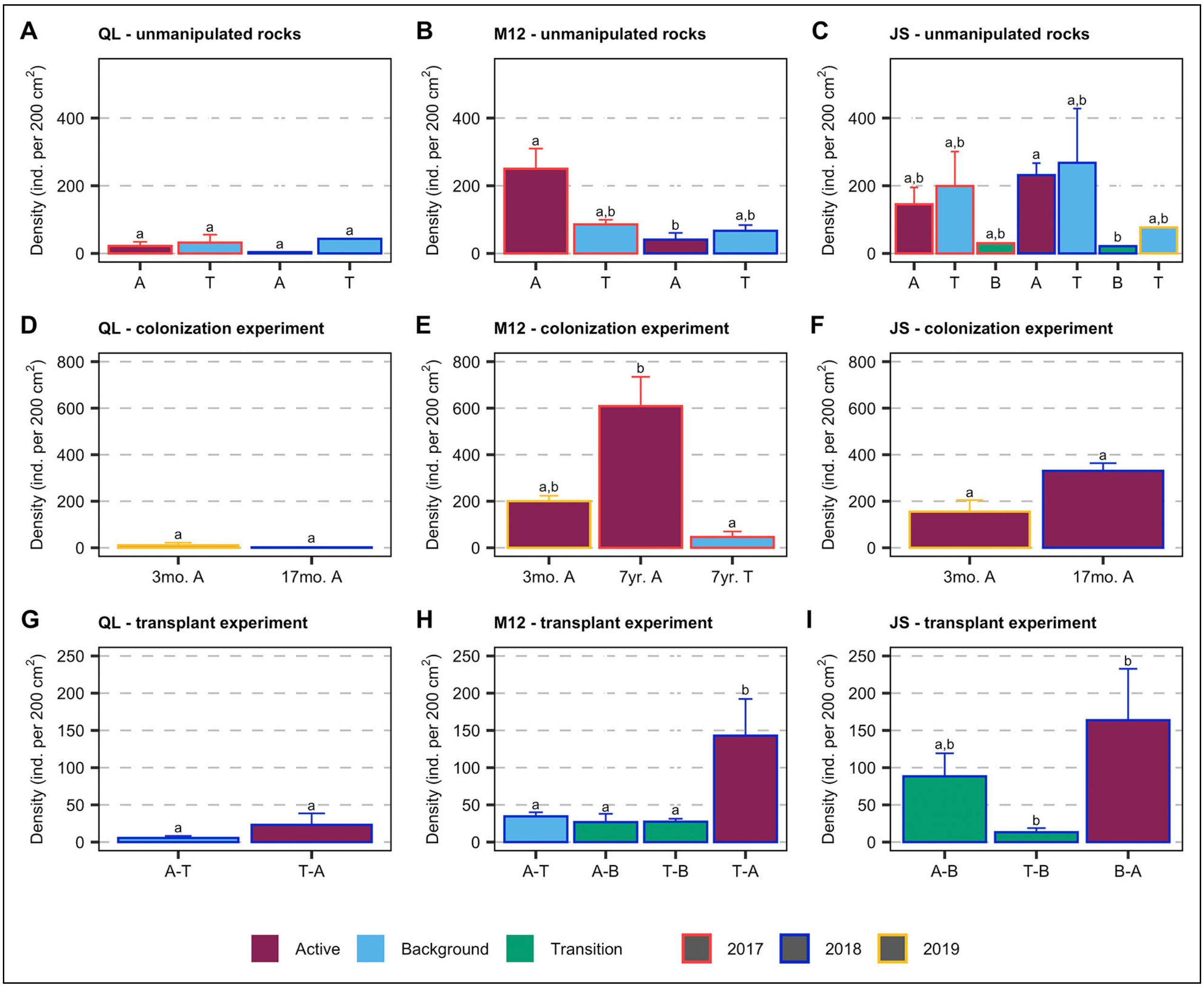

Figure 3. Density of macrofaunal invertebrates on unmanipulated and experimental rocks. Densities were calculated as number of individuals (ind.) per 200 cm^2, the average size of a rock. (A–C) Unmanipulated carbonate rocks, (D–F) colonization rocks, and (G–I) transplanted rocks at Quepos Landslide (QL), Mound 12 (M12), and Jaco Scar (JS). Fill colors indicate seep habitats: active (A), transition (T), and background (B); border colors indicate sampling years: 2017 (red), 2018 (blue), and 2019 (yellow). Letters above bars indicate statistically significant comparisons within subplot.

Table 3. Top 10 most abundant species[a] of macrofaunal invertebrates on carbonate rocks by seep location

Quepos Landslide	**%**	**Mound 12**	**%**	**Jaco Scar**	**%**
Anthoathecata (A+T)	27	*Provanna laevis* (A+T)	19	*Chrysopetallum* sp. (A+T)	17
Eudaronia sp. (A)	8	Chrysopetalidae n. sp. (T)	14	*Parakanthophoreus* sp. 1 (T)	14
Delectopecten sp. (T)	8	*Lepetodrilus ovalis* (A)	8	*Provanna goniata* (A)	13
Pyropelta musaica	8	Neolepetopsidae (A)	6	*Typhlotanoides* sp. 1 (A)	7
Lepidonotopodini sp.	6	*Pyropelta musaica*	3	*Laminatubus paulbrooksi* (B)	6
Serpulidae sp. 1	6	*Pyropelta wakefieldi*	3	*Bispira* sp.	5
Grimothea monodon	6	*Lepetodrilus* sp.	3	*Archinome levinae*	3
Lepetodrilus sp.	6	*Fucaria* sp. 1	3	*Neolepetopsis* sp. 2	2
Parougia sp.	4	*Anguillosyllis* sp.	2	*Neolepetopsis* sp. 3	2
Galatheoidea sp.	4	*Laminatubus joycebrooksi*	2	*Gammaropsis* sp. 2	2

[a] If a species contributed to more than 10% of the community at a given habitat, the habitat is indicated parenthetically: active (A), transition (T), and background (B).

Table 4. Top 10 most abundant species[a] of macrofaunal invertebrates on carbonate rocks by habitat

Active	%	Transition	%	Background	%
Provanna goniata (JS)	16	Chrysopetalidae n. sp. (JS+M12)	24	*Laminatubus paulbrooksi* (JS)	18
Provanna laevis (M12)	12	*Parakanthophoreus* sp. 1 (JS)	12	Chrysopetalidae n. sp.	9
Chrysopetalidae n. sp. (JS)	7	*Bispira* n. sp.	4	Hesionidae	6
Typhlotanoides sp. 1 (JS)	6	Anthoathecata (M12+QL)	3	Ophiuroidea	6
Parakanthophoreus sp. 1	6	*Laminatubus paulbrooksi*	3	*Ophiura* cf. *scutellata*	6
Lepetodrilus ovalis (M12)	6	*Provanna laevis* (M12)	3	*Lepetodrilus* sp.	6
Neolepetopsidae (M12)	5	*Typhlotanoides* sp. 1	3	*Fucaria* sp. 2	6
Laminatubus paulbrooksi	4	*Archinome levinae*	2	Amphinomidae sp. 1	3
Pyropelta musaica (QL)	2	*Gammaropsis* sp. 2	2	*Cirriformia* sp.	3
Pyropelta wakefieldi	2	*Neolepetopsis* sp. 3	2	Phyllodocidae	3

[a] If a species contributed to more than 10% of the community at a given seep location, the location is indicated parenthetically: Jaco Scar (JS), Mound 12 (M12), and Quepos Landslide (QL).

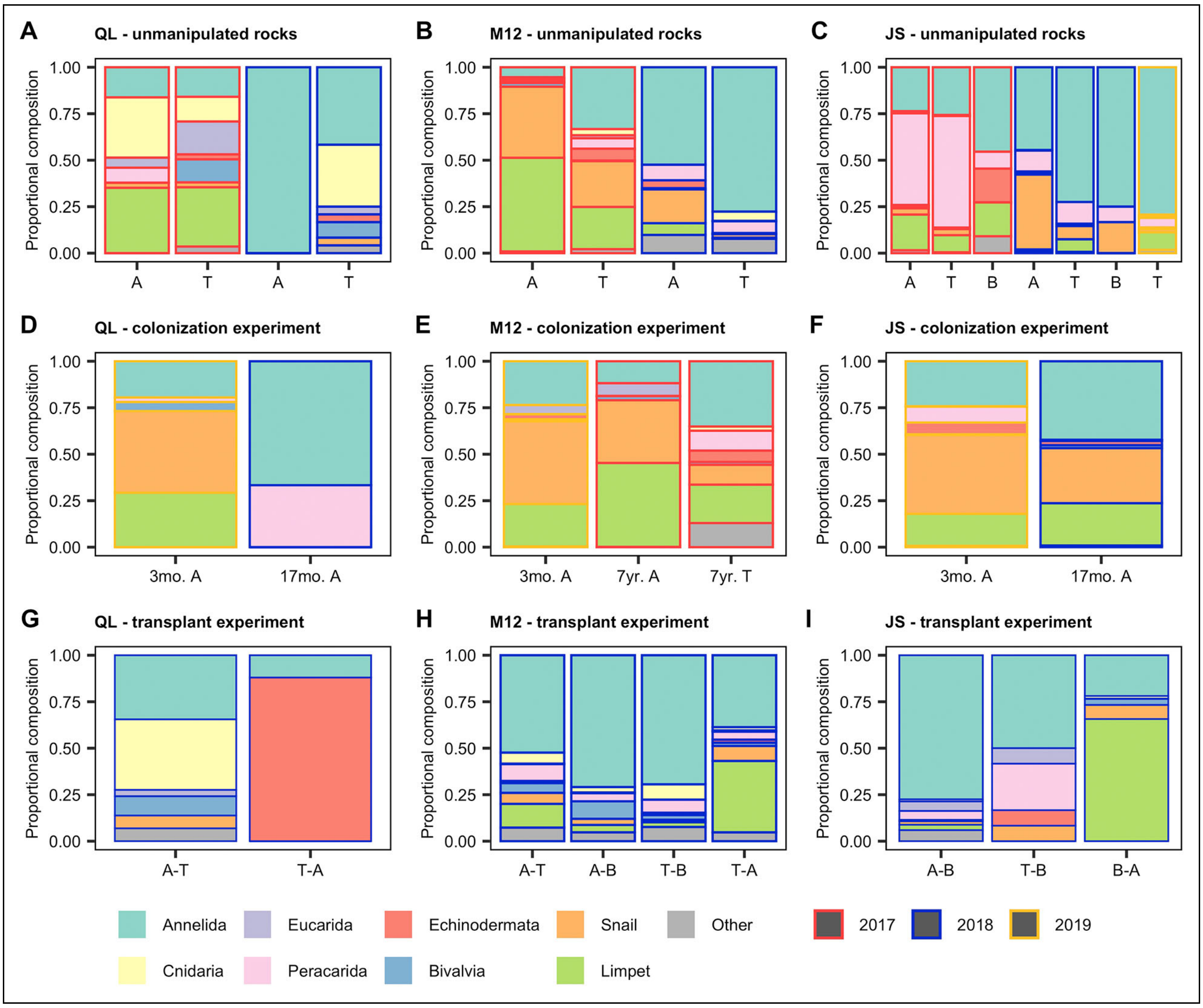

Figure 4. Proportional community composition of macrofaunal invertebrates on unmanipulated and experimental rocks. (A–C) Unmanipulated carbonate rocks, (D–F) colonization rocks, and (G–I) transplanted rocks at Quepos Landslide (QL), Mound 12 (M12), and Jaco Scar (JS) in different seep habitats: active (A), transition (T), and background (B). Fill colors indicate macrofaunal taxa; border colors indicate sampling years: 2017 (red), 2018 (blue), and 2019 (yellow).

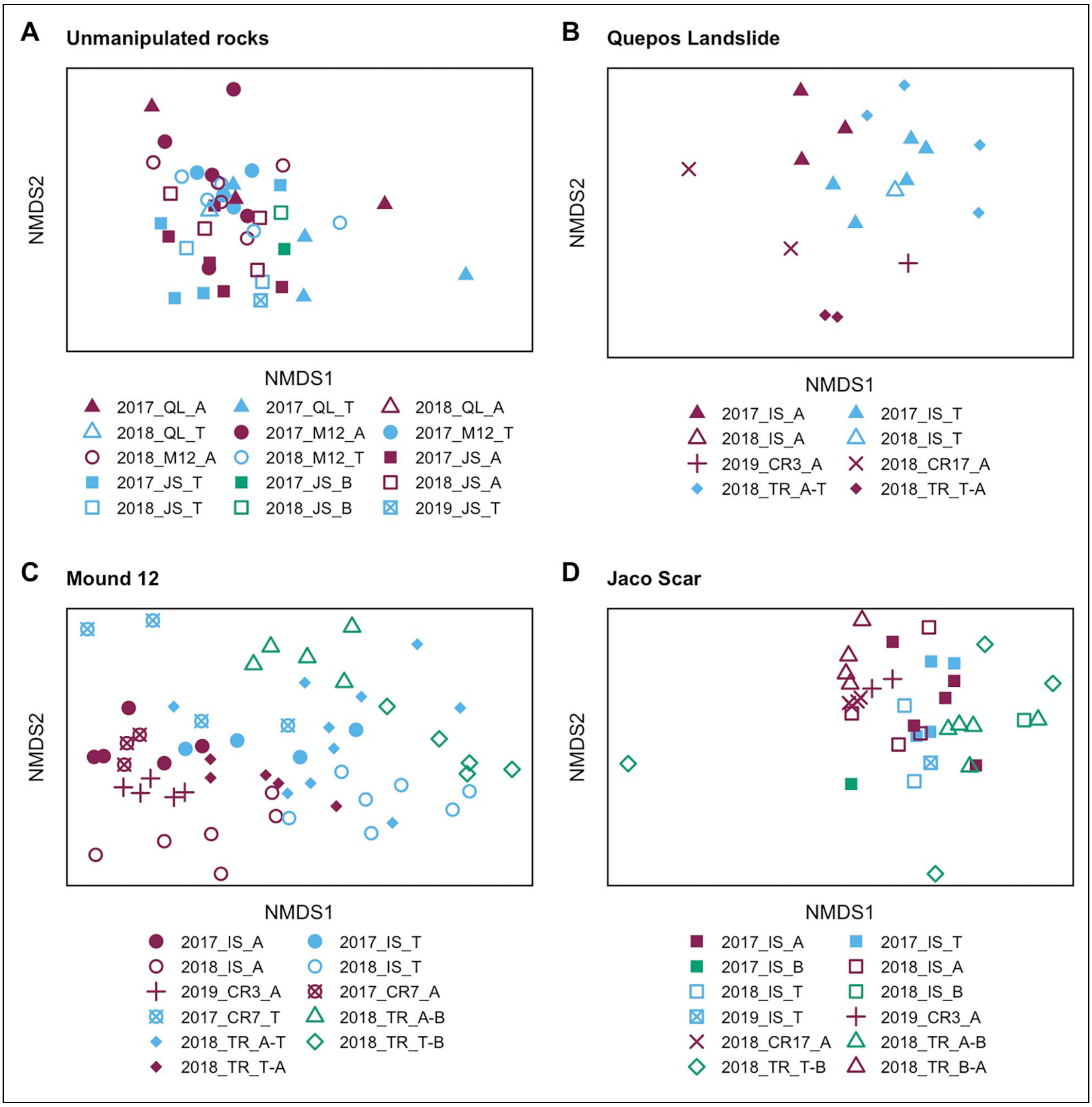

Figure 5. Non-multidimensional scaling analyses of macrofaunal invertebrates on unmanipulated and experimental rocks. (A) Unmanipulated carbonate rocks at all three seep locations: Quepos Landslide (QL, triangles), Mound 12 (M12, circles), and Jaco Scar (JS, squares). Colors represent seep habitats: active (A, maroon), transition (T, blue), and background (B, green). Symbol style represents sample collection year: 2017 (open), 2018 (closed), and 2019 (crossed squares). (B–D) Experimental carbonate rocks at (B) Quepos Landslide, (C) Mound 12, and (D) Jaco Scar, with corresponding unmanipulated (in situ, IS) data from panel A included in these panels. Symbols for seep locations and colors for seep habitats as in panel A. Other symbols are used for duration of colonization experiments: 3 months (plus signs), 17 months (x signs), and 7 years (crossed circles). Diamonds indicate transplant experiments.

Among seeps, Mound 12 (below OMZ) showed the highest Shannon-Wiener diversity and richness, followed by Jaco Scar (well below OMZ), but Quepos Landslide (within OMZ) showed highest evenness (excluding a sample with one specimen; **Table 5**). Jaco Scar had the highest rarefaction diversity (**Figure 6A**). At all seep locations together, Shannon-Wiener diversity and richness were consistently highest at active habitats, lower at transition habitats, and lowest at background, whereas evenness showed the opposite trend (**Table 5**). However, rarefaction diversity was the highest for transition communities (**Figure 6B**). These general patterns of diversity metrics with habitats were also observed within each seep location (**Table 5**, **Figure 6C**). Interestingly, functional diversity showed patterns opposite to Shannon-Wiener diversity; Quepos Landslide showed the highest functional diversity and lowest functional

Table 5. Community diversity, functional diversity, and isotope values of macrofaunal invertebrates by experiment, seep, and habitat

	Community Metrics[a]					Trophic Metrics[b]	
Experiment	**H′**	**S**	**J**	**FD_Q**	**FD_R**	**Mean δ^{13}C (‰)**	**Mean δ^{15}N (‰)**
Unmanipulated rocks by seep location							
Quepos Landslide	2.33	19	0.82	0.65	0.21	−21.6 ± 1.1	6.8 ± 1.3
Mound 12	2.93	62	0.72	0.49	0.37	−35.2 ± 1.3	6.3 ± 0.5
Jaco Scar	2.44	47	0.71	0.58	0.24	−36.8 ± 1.4	5.2 ± 0.6
Unmanipulated rocks by habitat							
Active	2.71	57	0.71	0.52	0.34	−36.1 ± 1.5	4.7 ± 0.4
Transition	2.58	47	0.72	0.59	0.25	−31.5 ± 1.6	7.2 ± 0.5
Background	2.08	11	0.90	0.62	0.19	−27.2 ± 2.7	6.9 ± 3.1
Quepos Landslide transplant experiment—17 months (2017–2018)							
Active to transition	2.04	12	0.82	0.64	0.17	−21.2 ± 0.3	10.2 ± 0.4
Transition to active	0.42	3	0.38	0.18	0.03	−20.6	11.7
Mound 12 transplant experiment—17 months (2017–2018)							
Active to background	3.61	76	0.83	0.72	0.23	−45.3 ± 9.2	6.2 ± 1.2
Active to transition	3.43	66	0.82	0.67	0.27	−35.7 ± 3.2	8.4 ± 0.9
Transition to active	2.88	71	0.68	0.46	0.44	−39.5 ± 2.8	5.4 ± 1.1
Transition to background	3.04	52	0.77	0.66	0.22	−23.1 ± 0.9	10.5 ± 1.7
Jaco Scar transplant experiment—17 months (2017–2018)							
Active to background	2.24	41	0.60	0.63	0.15	−38.4 ± 3.8	7.6 ± 1.1
Transition to background	2.37	11	0.99	0.68	0.22	−37.3 ± 6.6	5.5 ± 2.0
Background to active	2.68	55	0.67	0.39	0.45	−40.8 ± 1.0	2.6 ± 0.6
Colonization experiment—3 months (2018–2019)							
Quepos Landslide active	2.29	15	0.85	0.38	0.47	−22.1	11.1
Mound 12 active	2.63	69	0.59	0.38	0.44	−35.8 ± 0.9	7.5 ± 0.4
Jaco Scar active	2.98	54	0.75	0.44	0.48	−38.5 ± 1.8	6.8 ± 0.6
Colonization experiment—17 months (2017–2018)							
Quepos Landslide active	1.10	3	1.00	0.57	0.10	−33.5	5.5
Jaco Scar active	2.82	87	0.63	0.49	0.38	−39.2 ± 0.8	6.0 ± 0.6
Colonization experiment—7 years (2010–2017)							
Mound 12 active	2.25	43	0.60	0.33	0.50	−34.6 ± 2.5	1.3 ± 0.4
Mound 12 transition	3.41	45	0.90	0.72	0.23	−29.8 ± 1.8	7.4 ± 0.7

[a] Shannon-Wiener diversity (H′), richness (S), Pielou's evenness (J), functional diversity as Rao's quadratic entropy (FD_Q), and functional redundancy (FD_R).

[b] Trophic metrics are mean ± 1 standard error δ^{13}C and δ^{15}N (‰), $n = 1$–8 rocks.

redundancy, followed by Jaco Scar (**Table 5**, Figure S5). Functional diversity was the highest at background habitats, and functional redundancy was the highest at active habitats (**Table 5**, Figure S6).

Stable carbon and nitrogen isotope values of POM near bottom were on average −25.2 ± 0.5‰ and 6.7 ± 0.7‰, respectively ($n = 7$), and were not significantly different among seeps (Kruskal-Wallis tests, $p > 0.05$). The δ^{13}C of POM in surface waters was higher (−23.7 ± 0.3‰) than near bottom ($W = 40$, $p = 0.04$), but δ^{15}N was similar (6.3 ± 0.4‰; $W = 23$, $p = 0.90$, $n = 7$; Figure S7).

Stable carbon isotope values of macrofaunal invertebrates were the lowest at Jaco Scar and highest at Quepos Landslide (PERMANOVA, $R^2 = 32.43$, $p = 0.0001$). Among habitats, δ^{13}C values were the lowest at active habitats and highest at background habitats ($R^2 = 6.39$, $p < 0.001$; **Table 5**, **Figure 7A–C**). There was also a significant interannual difference in δ^{13}C values ($R^2 = 4.99$, $p = 0.007$),

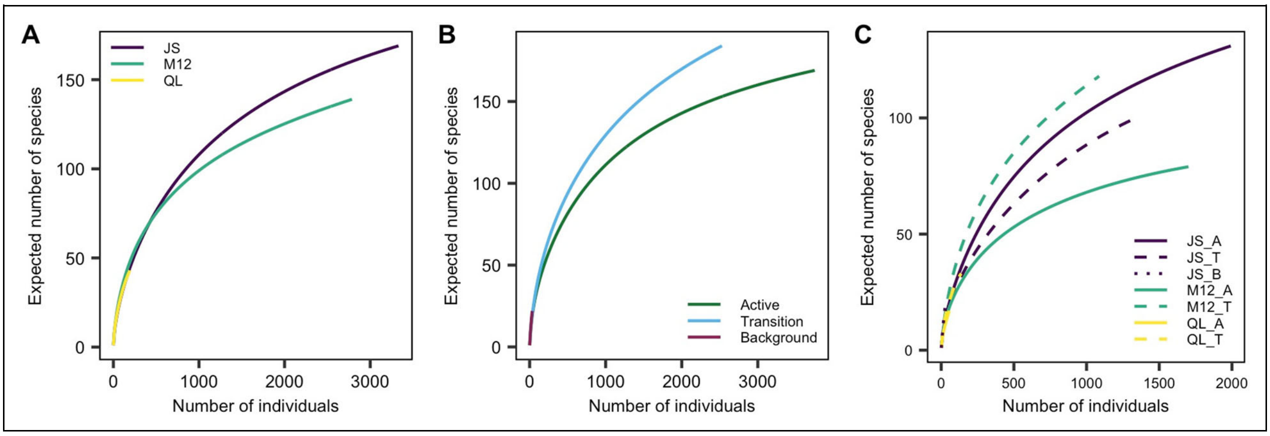

Figure 6. Rarefaction curves of macrofaunal invertebrates on unmanipulated carbonate rocks. By (A) seep location: Quepos Landslide (QL, yellow), Mound 12 (M12, light green), and Jaco Scar (JS, purple); (B) seep habitat: active (A, green), transition (T, blue), and background (B, maroon); and (C) habitat within seep location. Colors for seep location as in panel A. Line types represent seep habitats: active (A, solid line), transition (T, dashed line), and background (B, dotted line).

possibly due to low sample size (two rocks were collected at Quepos Landslide in 2018 and one rock was collected at Jaco Scar in 2019). Macrofaunal $\delta^{13}C$ values were the lowest at Jaco Scar at all habitats and the lowest at active habitats at all seep locations; thus, there was no interaction between seep location and habitat ($R^2 = 0.16$, $p = 0.87$). Similarly, the effect of seep location on $\delta^{13}C$ values did not vary across sampling years ($R^2 = 0.24$, $p = 0.82$). For the stable nitrogen isotopes ($\delta^{15}N$), there was no difference in values of macrofaunal invertebrates across seep location (PERMANOVA, $R^2 = 0.09$, $p = 0.06$), habitat ($R^2 = 0.13$, $p = 0.11$), and sampling year ($R^2 = 0.09$, $p = 0.06$; **Table 5**, **Figure 7A**–**C**). Trophic diversity based on SEAc and trophic niche based on TA were the greatest at active habitats, except at Mound 12 in 2017 when these were higher at transition habitats (**Figure 7A**–**C**).

3.2. Macrofaunal colonization patterns

Invertebrate communities at active habitats on colonization rocks achieved unmanipulated densities in 3 months at Quepos Landslide (3-month colonization density: 11 ± 10 individuals per 200 cm^2, $n = 3$ rocks; $W = 2$, $p = 1.00$) and Jaco Scar (3-month colonization density: 155 ± 50 individuals per 200 cm^2, $n = 2$ rocks; $W = 7$, $p = 0.27$), but not at Mound 12 (3-month colonization density: 200 ± 23 individuals per 200 cm^2, $n = 5$ rocks; $W = 1$, $p = 0.01$; **Figure 3D**–**F**). After 17 months, densities on colonization rocks at active habitats were low at Quepos Landslide (17-month colonization density: 2 ± 1 individuals per 200 cm^2, $n = 4$ rocks; $W = 2$, $p = 1.00$), but increased with time of exposure at Jaco Scar with values 2–4× greater than on unmanipulated rocks, although not significant (17-month colonization density: 330 ± 2 individuals per 200 cm^2, $n = 4$ rocks, $W = 3$, $p = 0.20$). This increase in density on colonization rocks with time of exposure was also observed in the longer-term experiment (7 years) at active habitats at Mound 12, where densities on colonization rocks were 2.5× higher than on unmanipulated rocks (7-year colonization density: 609 ± 126 individuals per 200 cm^2, $n = 3$ rocks; $W = 1$, $p = 0.07$). However, at transition habitats at Mound 12, densities on colonization rocks exhibited unmanipulated values after 7 years (7-year colonization density: 46 ± 24 individuals per 200 cm^2, $n = 4$ rocks; $W = 12$, $p = 0.34$).

Colonization rocks at Quepos Landslide recovered community composition of unmanipulated rocks within 3 months ($R = 0.50$, $p = 0.40$) and 17 months ($R = 0$, $p = 1.00$), although SIMPER analyses showed high dissimilarities (100%), which is also apparent in the nMDS and cluster analyses (**Figures 4D**, **5B**, and S2). These analyses could be a result of the low number of animals on the colonization rocks (two 3-month colonization rocks had 0 individuals, and 17-month colonization rocks had 0–1 individuals) which were also species not commonly found on unmanipulated rocks (the annelids *Parougia* sp. and Spionidae sp., and the amphipod *Harpinae* sp.; Table S1). At both Jaco Scar and Mound 12 (**Figures 4E**, **4F**, **5C**, and **5D**), communities on colonization rocks became more similar to unmanipulated communities with time of exposure, but they never fully recovered (ANOSIM tests, $R > 0.3$, $p < 0.01$), even after 7 years at Mound 12 (SIMPER, average dissimilarity = 75.8% and 79.9% within 3 months at JS and M12, respectively, 72.35% within 17 months at JS, and 54.22% within 7 years at M12). Early colonizers (i.e., animals on colonization rocks within 3–17 months of deployment) at Jaco Scar were *Provanna goniata*, *Neolepetopsis* limpets, *Archinome levinae*, and *Fucaria* snails (Table S2). Snails and limpets were also the most successful colonizers at Mound 12 at active habitats both in the short- and long-term, including *P. laevis*, *Lepetodrilus ovalis*, *Pyropelta corymba*, and *P. musaica* (Table S3). These were also the top species that contributed the most to the dissimilarity between colonization rocks and unmanipulated rocks at Mound 12 and Jaco Scar, being more abundant on colonization rocks, in addition to *Laminatubus paulbrooksi* at Jaco Scar, which was more dominant on unmanipulated rocks.

The community metrics of Shannon-Wiener diversity, richness, and Pielou's evenness were higher on colonization rocks at all seep locations than on unmanipulated rocks, but

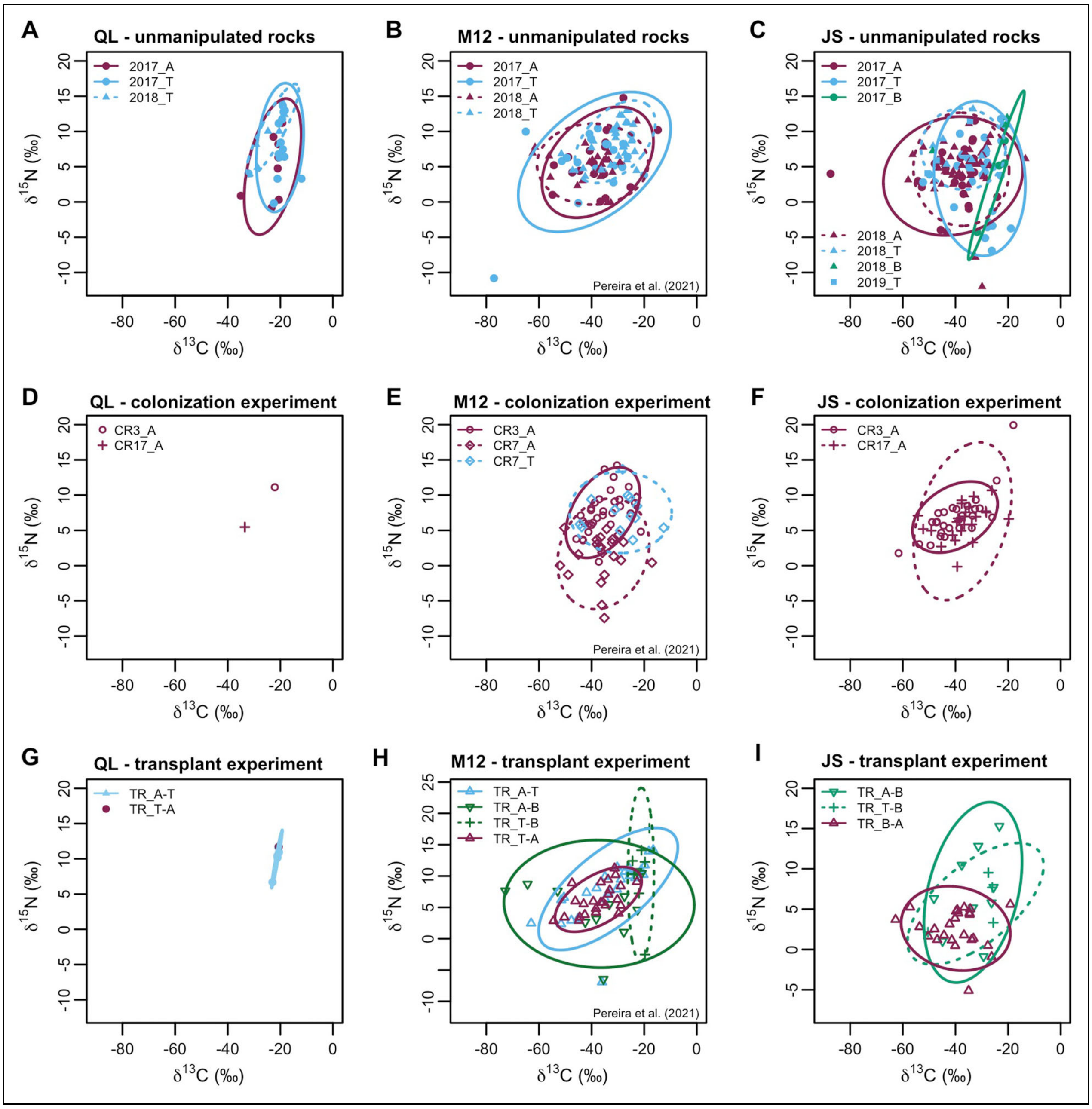

Figure 7. Trophic niche diversity of macrofaunal invertebrates on unmanipulated and experimental rocks. (A–C) Unmanipulated carbonate rocks, (D–F) colonization rocks for 3-month (CR3), 17-month (CR17), and 7-year (CR7) experiments, and (G–I) transplanted rocks at Quepos Landslide (QL), Mound 12 (M12), and Jaco Scar (JS) in the different seep habitats: active (A, maroon), transition (T, blue), and background (B, green). Each point represents the average for one species. Ellipses represent standard ellipse areas corrected by sample size (SEAc). See Table S7 for mean isotope, total niche area, and SEAc values.

Shannon-Wiener diversity and richness decreased with time of exposure, and evenness increased with time of exposure, except at Jaco Scar, where evenness was the highest within 3 months (**Table 5**). At all seep locations, communities on colonization rocks did not recover functional diversity and redundancy, and these metrics were generally lower than on unmanipulated rocks. Functional diversity on colonization rocks was higher with longer colonization exposure from 3 months to 17 months but was lower at 7 years of exposure. Functional redundancy was lower the longer the colonization experiments (**Table 5**).

Communities on colonization rocks achieved similar $\delta^{13}C$ and $\delta^{15}N$ values as communities on unmanipulated rocks at active habitats at Quepos Landslide within 17 months ($\delta^{13}C$: $W = 1$, $p = 0.44$; $\delta^{15}N$: $W = 4$, $p = 1.00$). At Jaco Scar and Mound 12, animals on all colonization rocks achieved similar $\delta^{13}C$ as animals on unmanipulated rocks (pairwise Wilcox tests, $p > 0.05$). However, $\delta^{15}N$ of animals on colonization rocks were 1.1‰ higher within 17 months at Jaco Scar than on unmanipulated rocks ($W = 435$, $p = 0.02$) and 2.4‰ higher within 3 months at Mound 12 ($W = 219$, $p = 0.005$), but 3.3‰ lower

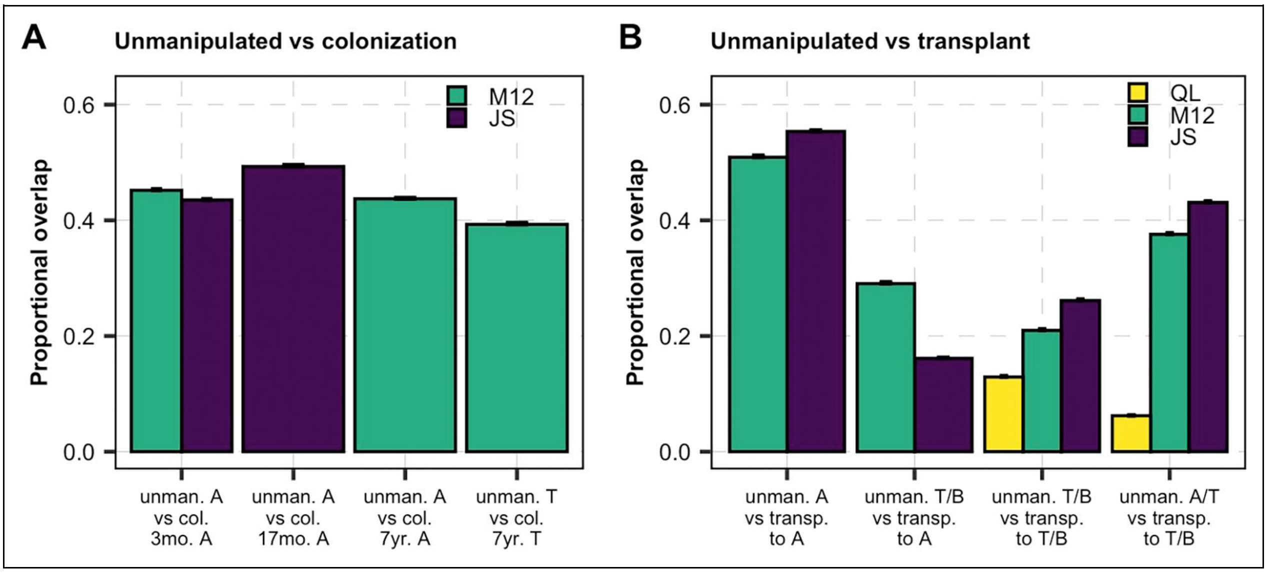

Figure 8. Proportional Bayesian overlap of standard ellipse areas of macrofaunal invertebrates on unmanipulated versus experimental rocks. (A) Trophic overlap between unmanipulated carbonate rocks (unman.) and colonization experiments (col.) at the same seep habitat, for active (A) and transition (T) habitats, at seep locations Mound 12 (M12) and Jaco Scar (JS). Colonization experiments were conducted for 3 months, 17 months, and 7 years. (B) Trophic overlap between unmanipulated carbonate rocks (unman.) and transplanted rocks (transp.), comparing experimental rocks to unmanipulated rocks at the start and end habitats of the transplants for all three seep locations: Quepos Landslide (QL), Mound 12 (M12), and Jaco Scar (JS). Transplant experiments were conducted for 17 months and were combined here for simplicity into two general treatments: rocks transplanted from transition or background habitats (T/B) to active habitats, mimicking seepage activation, and rocks transplanted from active or transition (A/T) habitats to transition or background habitats (T/B), mimicking a decline in seepage. Error bars indicate standard errors; see text for n values and statistical analyses.

within 7 years at Mound 12 ($W = 349$, $p = 0.001$). Animals on colonization rocks did not achieve trophic diversity (based on TA and SEAc; **Figure 7**) and only partially achieved trophic niche space (based on trophic overlap; **Figure 8A**) of unmanipulated communities at both Jaco Scar and Mound 12. Trophic diversity decreased with time of experiment at Jaco Scar (3–17 months) and increased with time of experiment at Mound 12 (3 months to 7 years; **Figure 7**). Similarity in niche space (based on trophic overlap) at active habitats between colonization and unmanipulated communities within 3 months was higher at Mound 12 (45%) than at Jaco Scar (43%; $Z = 22.8$, $p < 0.001$), but it was higher with longer time of exposure at Jaco Scar within 17 months (49% overlap; $Z = 15.6$, $p < 0.001$) and lower at Mound 12 within 7 years (44% overlap; $Z = 11.2$, $p < 0.001$; **Figure 8A**).

3.3. Macrofaunal patterns on transplanted rocks

We compared communities on transplanted rocks to those on unmanipulated rocks collected at the start habitat in 2017 (the source of rocks transplanted at the beginning of the experiment) and at the end habitat in 2018 (where rocks were transplanted at the end of the experiment). Differences in densities between transplanted communities and the unmanipulated communities at the start and end habitats were not statistically significant (Kruskal-Wallis and Wilcox tests, $p > 0.05$), but some patterns and trends emerged (**Figure 3G–I**). Densities of macrofaunal invertebrates at Jaco Scar and Mound 12 on transplanted rocks increased within 17 months when rocks were moved to active habitats but decreased when moved to transition or background habitats (in comparison to densities on unmanipulated rocks at the start habitat). At Quepos Landslide, densities always decreased after transplant. At all seeps, transplanted communities did not achieve densities equal to unmanipulated rocks at the end habitat, except at Mound 12, where densities on rocks that were transplanted from transition to active habitats were 3.5× higher than the unmanipulated active community.

Communities on rocks transplanted from transition to active habitats appeared to retain some of their original species, inferred from those present on unmanipulated rocks at transition habitats at Mound 12 (ANOSIM, $R = 0.41$, $p = 0.01$). These transplanted rocks also gained some seep-specialist species that were abundant at active habitats, such as *Pyropelta* limpets, *Neolepetopsis* sp. 1, and *Provanna laevis* (Table S4), resulting in the highest richness of all transplant treatments and similarity, although not significant ($R = 0.23$, $p = 0.06$), to the unmanipulated communities at active habitats. At Jaco Scar, the transplanted community from background to active habitats was less similar to the unmanipulated communities at active habitats ($R = 0.69$, $p = 0.03$) than at Mound 12; however, this community also gained some seep-specialist species including *Neolepetopsis* sp. 2, *Lepetodrilus* sp., and *Provanna goniata* (Table S5). At Quepos Landslide, communities on rocks transplanted from transition to active habitats were different ($R = 0.40$, $p = 0.04$) and with lower diversity metrics than the communities on unmanipulated rocks at the start, transition habitat. They had abundant holothurians not found anywhere else that accounted for 88% of the total individuals and 17% of the dissimilarity between transplanted and unmanipulated communities (SIMPER, average dissimilarity = 90.46%; Table S6). Across all seeps, community diversity metrics (H′, S, and J) on transplanted rocks did not achieve those of unmanipulated communities at the end habitat (i.e., active; **Table 5**), except for richness at Mound 12. Functional redundancy was the highest on rocks transplanted to active habitats compared to other transplant treatments (**Table 5**).

Communities on rocks transplanted from active to transition habitats at Mound 12 partially retained composition of unmanipulated communities at the start habitat (R = 052, p = 0.001) and gained similarity to unmanipulated communities at the end habitat, although the change was not significant (R = 0.16, p = 0.13). At Quepos Landslide, there was no significant difference in community composition between communities on rocks transplanted from active to transition habitats and the unmanipulated communities at the start (R = 0.26, p = 0.08) and end habitats (R = 0.09, p = 0.25). At both seeps, transplanted rocks gained species commonly found at transition habitats, such as hydroids, Lepidonotopodini sp., and *Delectopecten* sp. at Quepos Landslide and peracarid crustaceans, Chrysopetalidae n. sp., and chitons at Mound 12, and retained some seep-specialist species including *Fucaria* sp. 1 and *Kanoia myronfeinbergi* at Quepos Landslide, and *Neolepetopsis* limpets, *Archinome levinae*, and *Bathymodiolus earlougheri* at Mound 12 (Tables S4, S6). In general, diversity metrics following transplant from active to transition habitat increased at Mound 12 but decreased at Quepos Landslide (except for evenness). At both seeps, functional diversity and redundancy increased after transplant from active to transition habitat.

Communities on rocks transplanted to background habitat at Mound 12 did not retain the original community composition when moved from active (R = 0.92, p = 0.008) or transition habitats (R = 0.91, p = 0.008). At Jaco Scar, however, communities transplanted to background habitats partially retained their original species from active (R = 0.55, p = 0.008) and transition (R = 0.49, p = 0.008) habitats. These communities showed more similarity to the unmanipulated communities at background habitats when transplanted from transition (R = 0.46, p = 1.00) than from active habitats (R = 0.72, p = 0.17), although this difference was not significant. Species commonly found at transition and background habitats (e.g., Chrysopetalidae n. sp., dorvilleid and cirratulid annelids, and peracarid crustaceans) colonized these rocks at Jaco Scar. Some seep-specialist species were found on rocks transplanted to background habitats, including *Laminatubus paulbrooksi*, *Amphisamytha fauchaldi*, and *Provanna goniata* at Jaco Scar (Table S5), and *A. fauchaldi*, *Paralepetopsis* sp., *Lamellibrachia donwalshi*, and *Bathymodiolus* spp. mussels at Mound 12 (Table S4). Diversity metrics were higher on the transplanted rocks than on unmanipulated rocks at background habitats but lower than from the communities at the start habitats (i.e., active or transition) at Jaco Scar. At Mound 12, diversity was retained through the transplant to background habitats when coming from active habitats but not when coming from transition habitats. At both Mound 12 and Jaco Scar, communities on rocks transplanted to background habitats showed some of the highest functional diversity and lowest functional redundancy among all transplants and unmanipulated rocks (**Table 5**).

For most transplants there was no significant difference between mean δ^{13}C or δ^{15}N values of communities on transplanted rocks and those of the unmanipulated communities at the start and end habitats (Kruskal-Wallis and Wilcox tests, $p > 0.05$; **Table 5**). Exceptions were communities transplanted from background to active habitats at Jaco Scar, which showed 16.3‰ lower δ^{13}C values than unmanipulated communities at background habitats (Z = 2.97, p = 0.009) but were similar to unmanipulated communities at active habitats (Z = 0.76, p = 0.44), and δ^{15}N values that were 2.3‰ lower than unmanipulated communities at active habitats (Z = 3.58, p = 0.001). Also, communities transplanted from active to transition habitats at Mound 12 showed 1.9–2.2‰ higher δ^{15}N values than unmanipulated communities at active habitats (Dunn's tests, $p < 0.05$), and communities transplanted from transition to background habitats at Mound 12 showed 10.9‰ higher δ^{13}C values (W = 4, $p < 0.001$) and 4‰ higher δ^{15}N values (W = 30, p = 0.02) than at unmanipulated communities at transition habitats. At both Jaco Scar and Mound 12, trophic diversity based on TA and SEAc was highest on rocks transplanted from active to background habitats and lowest on rocks transplanted to active habitats (**Table 5**, **Figure 8B**). Trophic overlap was the highest between rocks transplanted to active habitats and the unmanipulated communities at active habitats (Kruskal-Wallis, $\chi^2_9 =$ 10,096, $p < 0.001$); for these rocks, Jaco Scar showed higher trophic overlap between transplanted rock and end habitat (i.e., active; 55%) than Mound 12 (50%; Z = 5.24, $p < 0.001$), but Mound 12 showed higher trophic overlap between transplanted rock and start habitat (i.e., transition; 29%) than Jaco Scar (16%; Z = −17.74, $p < 0.001$). Jaco Scar also showed the highest trophic overlap among seeps for transplants from active to transition or background habitats versus communities at start (43%) and end habitats (26%), and Quepos Landslide, the lowest overlap (6% and 13%, respectively; Dunn's tests, $p <$ 0.001; **Figure 8B**).

4. Discussion

Much of the local variability in methane seep macrofaunal communities documented previously has been attributed to seepage activity (i.e., fluid flux; Dando et al., 1994; Levin, 2005; Levin et al., 2017). Indeed, here we observed that seep habitats exhibit a strong influence on densities, community composition, diversity metrics, and trophic diversity across different methane seeps on the Costa Rican Pacific margin. However, we see evidence that other environmental variables, specifically depth and oxygen concentration, play a role in shaping faunal and trophic diversities of these communities, as well as their recovery and resilience abilities.

4.1. Seep habitat and depth as drivers of macrofaunal diversity patterns

Higher densities at active habitats are expected due to the increased availability of organic matter by chemosynthetic production compared to the surrounding deep sea (Levin, 2005). Authigenic carbonates at active habitats are generally dominated by grazing gastropods, symbiont-bearing annelids, and bivalves, while rocks at background (i.e., non-seep) habitats are generally dominated by echinoderms (Levin et al., 2015, Rybakova et al., 2022). Here, however, the highest densities occurred at transition habitats at Mound 12 and Jaco Scar (**Figure 3**), where seep-specialist species were not as abundant and background species were well represented. Carbonate macrofaunal densities at Costa Rican seeps were 3–6× higher than at shallower seeps at Hydrate Ridge, Oregon (Levin et al., 2017), 1.3–2.5× higher than at the Amon Mud Volcano and Pockmark areas of the Nile Deep-sea Fan at 1,000–1,700 m (Ritt et al., 2011), and 20–26× higher than at the Del Mar Seep, California, at 1,020 m (Grupe et al., 2015). Compared to 2009 data for Mound 12, densities were 1.4× lower at active habitats but similar at transition habitats (Levin et al., 2015). Interannual shifts in densities, particularly at Mound 12, likely reflected natural fluctuations in methane flux by frequent earthquake activity in the region (Mau et al., 2007; Xie et al., 2020).

Habitat also influenced diversity metrics across all seeps (**Table 4**). The observations of high Shannon-Wiener diversity and species richness peaked at active habitats, while evenness was higher at background habitats—patterns consistent with the dominance of seep specialists at active habitats and lower species dominance at background habitats. Low Shannon-Wiener diversity and richness of sediment macrofauna at active sites from these same Costa Rican seeps (Ashford et al., 2021) highlight the role of carbonate rocks in maintaining diversity at active habitats. High functional diversity has been hypothesized to reduce interspecific competition and facilitate species coexistence at hydrothermal vents (Alfaro-Lucas et al., 2020), which could lead to higher community diversity. Here, while Shannon-Wiener diversity was high at active habitats, high functional redundancy and low functional diversity may reflect the specific ecosystem functioning of chemosynthesis-based communities. Functional diversity, rather than species diversity, may better indicate community resilience, and low functional diversity can signal ecosystem vulnerability (e.g., Bellwood et al., 2003; Douglas et al., 2017; Alvarez et al., 2019).

Diversity also varied with depth among seep locations. Mound 12 showed the highest Shannon-Wiener diversity, but rarefaction diversity was higher at Jaco Scar (**Figure 6C**). These results suggest the presence of more rare species and a more heterogeneous environment at Jaco Scar, where different microhabitats or niches may exist, as reflected in the higher functional diversity and lower functional redundancy compared to Mound 12 (**Table 5**). Jaco Scar had the highest bottom-water oxygen concentration, and higher oxygen has been linked to steeper species accumulation curves in sediment macrofauna (Levin et al., 2010). In turn, Quepos Landslide, within the OMZ, showed the lowest Shannon-Wiener diversity and species richness, as expected (**Table 4**). Low bottom-water oxygen also tends to homogenize benthic communities (Levin et al., 2000), and at Quepos Landslide, fewer animals showed a more even distribution of functional traits (Figure S5), leading to higher functional diversity but lower functional redundancy (**Table 4**). However, in this case, higher functional diversity did not equate to greater resilience, as our experiments revealed community vulnerability at Quepos Landslide (see discussion below).

Finally, densities and community composition differences between Mound 12 and Jaco Scar (**Figures 3** and **4**) likely reflect taxon-specific depth preferences. Jaco Scar, the deepest seep at 1,850 m, had the highest densities, dominated by tanaids and annelids. Tanaids are common in reducing habitats, with several species restricted to seeps, and tend to increase in diversity with depth (Blazewicz-Paszkowycz and Bamber, 2011; Zeppilli et al., 2011; Blazewicz-Paszkowycz et al., 2012). Jaco Scar also showed high abundance of the snail *Provanna goniata*, whereas Mound 12 was dominated by *P. laevis* and other grazing gastropods—a depth-specific pattern also reported for tubeworm and mussel-bed communities at these seeps (Betters et al., 2023).

4.2. Influence of depth and habitat on macrofaunal trophic structure at seeps

Depth indirectly influences trophic structure at seeps; shallow-water seeps receive more photosynthetically derived organic matter due to stronger bentho-pelagic coupling (Levin, 2005), while deeper seeps receive rely more on chemosynthetic production (Dando et al., 1991; Dando et al., 1994; Levin and Mendoza, 2007). Indeed, Quepos Landslide showed the highest macrofaunal $\delta^{13}C$ and $\delta^{15}N$ values, and Jaco Scar, the lowest, reflecting a stronger reliance on chemosynthetic production with increasing depth (**Table 5**). However, $\delta^{15}N$ values of macrofauna at active habitats at Quepos Landslide (Table S7) were still lower than near-bottom POM values and values typical of non-chemosynthesis-based ecosystems (e.g., Levin et al., 2012; Colaço et al., 2013; Pereira et al., 2024), suggesting mixed feeding on both photo- and chemosynthetic production. A similar dietary mix has been reported for other shallow seeps (at approximately 300–500 m; Levin and Michener, 2002; Åström et al., 2019; Bravo et al., 2024).

Higher carbon and nitrogen isotope values of animals at background habitats, more similar to near-bottom POM isotope values, suggest greater reliance on photosynthetic production than animals at active habitats, consistent with other studies at seeps on the Pacific margin (Levin and Michener, 2002; Levin et al., ; 2015; Levin et al., 2017) and for sediment infauna (Åström et al., 2016; Portail et al., 2016; Ashford et al., 2021). However, trophic diversity was higher for macrofauna at active habitats at Mound 12 and Jaco Scar than at transition or background habitats (**Table 4**, **Figure 7**). This finding suggests that although animals at active habitats rely more on chemosynthetic production, they are feeding on a broader variety of food sources (e.g., multiple metabolic types of microbes). At Quepos Landslide, the combined effects of seep habitat and low oxygen (described below) might explain the higher trophic diversity at transition than at active habitats.

4.3. Influence of availability of chemosynthetic production on macrofaunal colonization and resilience

High macrofaunal densities on colonization rocks at active habitats and transplant rocks to active habitats at Jaco Scar and Mound 12 were mainly due to high densities of microbe-grazing gastropods, mainly provannid snails and neolepetopsid limpets, dominant at methane seeps (Levin et al., 2015). Their presence likely impacts the settlement of other animals (Grupe, 2014). For example, tanaids, abundant on unmanipulated rocks at Jaco Scar, were less abundant on experimental rocks, perhaps due to competition for physical space on the rock with the dominant gastropods or limited recruitment caused by direct development limitations (i.e., no larval stage). The response of microbial grazers suggests rapid microbial growth within as little as 3 months, as seen in colonization experiments monitoring seep microbial communities (Case et al., 2015).

Gastropod dominance also appeared to affect macrofaunal trophic structure (**Table 5**, **Figure 7**). Lower trophic and functional diversities of macrofauna on experimental rocks than on unmanipulated rocks at both Jaco Scar and Mound 12 suggest that there was less variability in feeding modes on experimental than on unmanipulated rocks (seen in Figures S8 and S9). However, the relatively higher trophic overlap between communities on colonization and unmanipulated rocks in 3 months suggests that the gastropod-dominated community on the colonization rocks was feeding on similar food sources as animals on unmanipulated rocks. Changes in trophic diversity and overlap over time at both Jaco Scar and Mound 12 reflect successional shifts in community diversity and functional diversity.

For the 17-month experiments at Jaco Scar, trophic overlap with unmanipulated rocks was higher on transplant rocks (moved with the microbial community and all fauna attached) to active habitats than on colonization rocks (deployed after being kept dry for 7–8 years in a storage room following faunal removal), suggesting that establishment of a chemosynthetic microbial community on rocks might be faster when a preexisting microbial community is present. Notably, rocks transplanted from background to active habitats were sedimentary rather than carbonate, reinforcing the idea that the chemosynthetic microbial community can quickly establish on substrates. This observation aligns with earlier incubation experiments showing that chemosynthetic microbial activity can begin within days after the addition of methane into the system (Marlow et al., 2014).

The higher reliance on chemosynthetic production by communities at active habitats may limit their responses to experiments mimicking declines in seepage, as shown by the low retention of species initially present on rocks transplanted to transition or background habitats (**Figures 4** and **8**; **Table 4**). In addition, the transition between habitats is more obvious with increasing depth, as photosynthetic input decreases and chemosynthetic reliance increases at active habitats (Rybakova et al., 2022). This effect of depth could also explain why communities on rocks transplanted from transition to background habitats at Jaco Scar retained greater similarity, both in composition and trophic structure, to unmanipulated communities at background habitats than those transplanted from active to background habitats (**Figures 4** and **8**). Species at transition habitats likely rely more on photosynthetic production and might be more resilient to decreased seepage than seep specialists that rely more on chemosynthetic production.

Still, communities from active habitats showed some resilience when transplanted to background habitats at both Mound 12 and Jaco Scar, maintaining their functional diversity and trophic structure (**Table 4**, **Figure 7**). Chemosynthetic microbes can be active even under low seepage conditions (Marlow et al., 2014), and rocks transplanted from active to background habitats may have retained chemosynthetic microbes, supporting seep-specialist species through the 17 months of the experiment. The recovery of the microbial grazer Chrysopetalidae n. sp. supports this idea. In contrast, provannid snails and pyropeltid limpets were less abundant on the transplanted rocks than on unmanipulated rocks at active habitats. A similar pattern was observed in a 13-month transplant to low-activity habitats at Hydrate Ridge, where provannid snails were hypothesized to feed on a specific microbial taxon that was not recovered on the transplanted rocks (Case et al., 2015; Levin et al., 2017). The absence of provannid snails may explain the lack of *Pyropelta corymba* limpets on transplanted rocks, as these are often found on provannid snails (Warén and Bouchet, 2001; Seid et al., 2025; O.S. Pereira, personal observation).

4.4. Bottom-water oxygen concentration limits macrofaunal diversity and resilience

Community patterns at Quepos Landslide, the shallowest seep studied at 400 m with 4.25 µM O_2, well within the OMZ, were very different from the other seeps. Dominated by hydroids, this seep showed the lowest macrofaunal densities, which did not vary with habitat (**Figures 3** and **4**). Densities were 2.5–5× lower than at low-oxygen seeps at Hydrate Ridge, Oregon, consistent with Quepos Landslide having half the oxygen concentration (Levin et al., 2017). Other shallow seeps (400–600 m) in the Bering Sea also host "hydroid bushes" that thrive on hard substrate and seep-derived food. Notably, hydroid diversity in the North Pacific decreases below 1,000 m (Prudkovsky et al., 2023). Low bottom-water oxygen levels are known to reduce macrofaunal densities at other deep-sea hardground ecosystems (Wishner et al., 1990; Wishner et al., 1995; Levin, 2003). At Quepos Landslide, oxygen levels appear to override the effect of seep habitat and act to lower macrofaunal densities. Moreover, transitions in seepage activity (i.e., fluid flux) are less pronounced at shallow seeps (Seabrook et al., 2024). Predation by the dense community of tuna crabs (*Grimothea monodon*; **Figure 1**) might further influence the macrofaunal community at Quepos Landslide (Sahling et al., 2003).

While depth and active habitat at Jaco Scar and Mound 12 appear to facilitate colonization and resilience through availability of chemosynthetic production, the hydrographic conditions at Quepos Landslide (i.e., shallow depth and low bottom-water oxygen concentration) likely limit macrofaunal colonization. Environmental stressors (e.g., low-oxygen conditions, predation, and environmental changes) can increase mortality and limit recruitment rates (Sahling et al., 2003; Alfaro-Lucas et al., 2020; Seabrook et al., 2024). Some seep-specialist species colonized the rocks in 3 months at Quepos Landslide (e.g., *Provanna goniata*, *Neolepetopsis* sp. 2, and *P. corymba*) but may have been predated upon, considering the high abundance of tuna crabs at Quepos Landslide, or moved away and disappeared from the 17-month colonization rocks.

Alternatively (though unlikely; Section 4.3), the microbial community may not have developed sufficiently within the experimental timeframe to support macrofaunal recruitment (Hadfield, 2011). If microbial growth were the only limiting factor of macrofaunal colonization, we would expect less variation between Quepos Landslide and the other seeps. Hypoxia can be common at seeps due to aerobic microbial respiration and sulfide oxidation depleting oxygen in the benthic boundary layer (Boetius and Wenzhöfer, 2013). Despite high microbial activity and methane emissions, most of Quepos Landslide is covered in microbial mats with fewer exposed carbonate rocks than the other seeps (Karaca et al., 2014). These multiple stressors (i.e., high activity, low oxygen, less exposed hard substrate) may constrain density and diversity of the unmanipulated community, preventing the establishment of well-developed macrofaunal communities capable of colonizing new substrates with new recruits or motile adults.

The transplant experiment at Quepos Landslide was of particular interest, as it simulates a potential future scenario of methane seep expansion (via gas hydrate destabilization) due to ocean warming (Ketzer et al., 2020; Li et al., 2023) and OMZ expansion due to ocean deoxygenation (Stramma et al., 2008; Levin, 2018). The patterns were less clear than at Jaco Scar and Mound 12 (described above). Densities decreased after transplant (**Figure 3**), possibly due to the limited unmanipulated community in the first place, as with the colonization experiments. The dominance of holothurians on the transplants to active habitats remains unexplained, but they likely took advantage of the provision of substrate and chemosynthetic production in the absence of competition.

In contrast, transplants to transition habitats at Quepos Landslide showed patterns more similar to Jaco Scar and Mound 12; some seep-specialist species (e.g., hydroids Anthoathecata) persisted, and species typical of transition habitats (e.g., *Delectoplecten* sp.) appeared. Functional diversity was similar to unmanipulated communities (**Table 5**, Figure S10). We expected higher trophic overlap between the community transplanted to transition habitats and the unmanipulated community at transition habitats at Quepos Landslide than at the other seeps, given the lower reliance on chemosynthetic production and weaker distinction between habitats at shallower depths. However, trophic overlap was the lowest of all transplant experiments (**Figure 8B**). Slightly higher isotope values of animals on rocks transplanted to transition habitats than unmanipulated communities and near-bottom POM indicate even higher reliance on photosynthetic production (**Table 5**). Low oxygen also may have affected the resilience of chemosynthetic microbial communities at Quepos Landslide.

5. Conclusion

We observed high variability of macrofaunal assemblages on unmanipulated and experimental carbonate rocks at three methane seeps with different environmental conditions on the Costa Rican Pacific margin. Active habitats exhibited high species diversity and trophic diversity, highlighting the heterogeneity provided by carbonate rocks. Depth drove changes in macrofaunal communities likely due to faunal depth preferences and increased reliance on chemosynthetic production with depth. Low bottom-water oxygen concentration appeared to override the effect of habitat, creating unique macrofaunal communities with low diversity.

The rapid colonization of seep-specialist species, especially microbial grazers, on experimental rocks at active habitats underscores the role of chemosynthetic production in facilitating colonization and enhancing biodiversity at chemosynthesis-based ecosystems. The persistence of some seep-specialist species and a chemosynthetic trophic structure on transplant rocks mimicking seepage cessation (i.e., to transition or background habitats) indicated that a viable microbial community remained, capable of continued methane consumption. Thus, depth and seep habitat appear to influence the availability and reliance on chemosynthetic production, which can facilitate or limit seep macrofaunal resilience. However, under low bottom-water oxygen concentration, oxygen availability may become the dominant factor, limiting colonization and resilience regardless of habitat or depth. As chemosynthetic production is carried out by chemosynthetic microbes, a question that remains unanswered is whether the observed macrofaunal patterns result solely from environmental drivers or were also shaped by the dynamics and resilience of chemosynthetic microbial communities.

Methane seeps provide many ecosystem services but are threatened by bottom trawling, oil and gas extraction, ocean deoxygenation, and ocean warming (Ramirez-Llodra et al., 2011; Thurber et al., 2014; Levin et al., 2016; Schmidtko et al., 2017; Le et al., 2022). Our findings suggest that seep ecosystems may exhibit resilience, particularly if microbial chemosynthetic communities and key seep-specialist species persist. This potential for ecosystem recovery depends on maintaining a minimum threshold level of integrity. However, as deoxygenation intensifies, low oxygen conditions can be expected to hinder macrofaunal resilience significantly. To protect deep-sea seep communities effectively, conservation and management strategies need to consider oxygen availability and incorporate predictions of oxygen loss.

Data accessibility statement

Datasets were submitted to the BCO-DMO database for public download at the project page: https://www.bco-dmo.org/project/648472.

Supplemental files

The supplemental file for this article can be found as follows:

Tables S1–S7. Figures S1–S10. PDF

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Competing interests

The authors declare that no competing interests exist.

Author contributions

Contributed to conception and design: OSP, LAL.
Contributed to acquisition of data: OSP, GWR, EEC, JC, LAL.
Contributed to analysis and interpretation of data: OSP, LAL.
Drafted and/or revised the article: OSP, GWR, EEC, JC, LAL.
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