

# Benthic communities across recent and historical volcanic lava flows of an oceanic island

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## Research Article

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# Abstract

Volcanic eruptions create new marine substrates that serve as natural laboratories for examining benthic ecological succession over time. Benthic community assembly was examined across three lava flows of different ages (<1 year, 73 years, 473 years) at Playa del Arco (28.609141° N, 17.923526° W), La Bombilla (28.592422° N, 17.919193° W) and Puerto Naos (28.584996° N, 17.910301° W), and on La Palma Island (Spain). Fieldwork was conducted in August 2022. Using underwater photoquadrats, microinvertebrate settlement collectors, and microinvertebrate sampling from rocks at two depths (10 and 20 m), distinct successional trajectories were identified for macroalgae, early microinvertebrate settlers, and benthic microinvertebrates. Macroalgal richness was lowest in the youngest flow, peaked in the 73-year-old flow dominated by *Lophocladia trichoclados* and *Canistrocarpus cervicornis* and slightly declined in the oldest substrate. Early settlers increased in richness from the youngest to the 73-year flow, with families such as Caprellidae, Cerithiidae, and Alpheidae driving community differentiation, and later stabilized at 473 years. Benthic microinvertebrates showed the strongest successional shift, with peak richness and taxonomic uniqueness at 73 years, followed by dominance of specialized or predatory taxa such as some Cirratulids, and *Alpheus macrocheles* in the oldest flow. The ratio of larval arrivals to successfully settled species decreased with substrate age, indicating intensified post-settlement filtering. These findings demonstrate a unimodal diversity peak at intermediate successional stages and underscore the role of substrate stability, macroalgal structure, and biotic filtering in shaping benthic community assembly on volcanic coasts.

## 1. INTRODUCTION

Volcanic islands represent dynamic environments where geological and biological processes interact across both short and long temporal scales (Ramalho et al. 2013). Volcanic eruptions, while often perceived as purely destructive, dramatically reshape coastal and marine landscapes by depositing fresh lava flows that create new substrates and alter existing habitats. These events provide unique natural laboratories for studying primary ecological succession, as they effectively “reset” local ecosystems, eliminating established biological communities in some areas and exposing entirely new, uncolonized surfaces (Del Moral and Grishin 1999; Jewett et al. 2010).

The Canary Islands constitute a volcanic archipelago that has formed progressively over the past 60 million years (Carracedo and Troll 2016). Throughout this period, at least 17 eruptions have been documented across different islands, continuously reshaping both terrestrial and submarine landscapes (Longpré and Felpeto 2021). Volcanic activity remains ongoing, as exemplified by the 2011 Tagoro submarine eruption near El Hierro Island and the 2021 Tajogaite eruption in La Palma Island. The Tagoro event, in particular, deposited large volumes of new material that buried preexisting benthic communities, initiating a new phase of ecological succession characterized by the colonization of pioneering organisms, including annelids, crustaceans, cnidarians, and mollusks (Sotomayor-García 2019; Mendoza et al. 2020).

The island of La Palma has experienced eight documented eruptions, the earliest recorded event being the Tacande eruption in 1430 (Klügel et al. 1999; Carracedo et al. 2022). The most recent event was the Tajogaite eruption, occurred between September and December 2021, dramatically reshaped both terrestrial and marine environments. As lava entered the sea along the southern coast of Tazacorte municipality, it gave rise to two new lava deltas: one smaller delta extending ~ 0.5 km from the original shoreline, and a larger southern delta spanning ~ 1.2 km, partially overlapping deposits from the 1949 San Juan eruption (Fraile-Núñez et al. 2021). These new formations buried preexisting habitats and extended the coastline seaward, altering local hydrodynamics and sediment regimes. Prior to the eruption, the seabed comprised shallow rocky substrates transitioning into sandy bottoms (García et al. 2009). At the delta fronts, lava-seawater interactions produced transient perturbations in carbonate chemistry, including acidification plumes and altered alkalinity profiles (González-Santana et al. 2022). Furthermore, the newly formed basaltic substrates constitute highly heterogeneous and dynamic bottoms, influencing colonization pathways and taxonomic turnover in benthic assemblages (Sangil et al. 2024).

These conditions on La Palma Island offer a unique opportunity to examine the formation and development of marine benthic communities on newly created volcanic substrates. Moreover, the island's recurrent volcanic activity has produced seafloor habitats of markedly different ages coexisting within a relatively small geographic area. In addition to the recent lava flows generated during the 2021 Tajogaite eruption, older submarine substrates shaped by the Jedey eruption approximately 73 years ago and the San Juan eruption around 473 years ago are also present. This chronological gradient of substrate ages constitutes a natural ecological timeline, enabling direct comparisons of benthic community assembly across different successional stages from the initial colonization of bare rock to the development of mature and stabilized assemblages.

Ecological succession is a dynamic process characterized by increasing biomass, biodiversity, and ecological complexity, shaped by the interplay of biotic interactions and abiotic factors (Margalef 1977). In marine environments, colonization tends to occur more rapidly than on land, facilitated by ocean currents and the high dispersal potential of many marine organisms (Valiela 1995; Cowen and Sponaugle 2009). This promotes the swift arrival of pioneering species and the subsequent formation of nascent communities, as observed in post-eruption environments such as Kasatochi Island and Vailulu'u seamount (Jewett et al. 2010; Herrera et al. 2023). The first colonizers often include microbial mats and microalgae, which are soon followed by copepods, amphipods, and early crustaceans such as brachyuran and galatheid crabs (Lutz 2001; Danovaro et al. 2017). These species are typically characterized by low competitive ability but high demographic plasticity, exhibiting traits such as physiological tolerance to extreme conditions (e.g., temperature and salinity), broad dietary flexibility, rapid reproduction, and strong dispersal capacity (Connell and Slatyer 1977; Lee 2015; Turner 2015). By modifying the habitat, these early colonizers facilitate the arrival and establishment of additional species, thereby enhancing local abundance and functional complexity.

In the intermediate successional stage, diversity often peaks due to the coexistence of pioneer species and later-arriving taxa (Tilman 1985). Conditions such as increased organic matter, substrate stabilization, and moderate hydrodynamics enable the development of larger, more structurally complex macroalgae. Species like *Dictyota humifusa* and *Sargassum* spp. exemplify this stage, as they require stable substrates and elevated nutrient availability to sustain their canopy-forming morphologies (Cronin and Hay 1996). As succession advances, the community structure shifts from generalist, fast-reproducing taxa to more specialized or competitively dominant organisms (Odum 1969; Connell and Slatyer 1977). This transition reflects increasing ecological complexity and niche partitioning, where late-successional species exhibit slower growth, narrower habitat preferences, and superior abilities to compete for space and resources. Ultimately, the community may reach a relatively stable “climax” state, often characterized by lower diversity but higher specialization and structural integrity (Margalef 1977). Crucially, these transitions are shaped not only by initial settlement but also by post-settlement processes, including what is termed the “settlement filter”. This concept describes the selective establishment of species based on biotic interactions, habitat suitability, and prevailing environmental conditions (Caley et al. 1996). In this context, species considered “competitive” are those capable of thriving in mature, stable environments due to traits such as superior resource acquisition, effective space occupation, and ecological specialization, which distinguish them from the generalist strategies typical of early colonizers.

By examining lava substrates of different ages on La Palma Island (< 1 year, 73 years, and 473 years), this study reconstructs successional trajectories across a temporal gradient following volcanic disturbance. We combined in situ surveys of macroalgal and benthic microinvertebrate communities (i.e., defined here as invertebrates between 1 mm and 1 cm associated with algal surfaces, rocky substrates, or biofilm layers) with settlement traps designed to record larval arrivals and early post-settlement stages. This dual approach allowed us to document both the composition of established communities and the initial colonization dynamics. Our objective was to determine how benthic assemblages evolve from pioneer stages toward more complex communities, and to identify the ecological mechanisms that shape this progression. We hypothesized that species richness would follow a unimodal trend across the successional gradient, peaking at intermediate substrate age due to the coexistence of early colonizers and later-arriving taxa. Additionally, we expected that post-settlement filtering processes would intensify with community maturity, favoring more specialized and competitively dominant taxa in the oldest lava flow.

## 2. MATERIAL AND METHODS

### 2.1. Study area

The sampling was conducted at three sites along the coast of La Palma (Canary Islands), each representing volcanic rocky substrates of different ages. To minimize environmental variability related with the orientation of the island to the main trade winds and currents, all sites were selected with the same coastline orientation, the southwest. This is also the orientation with the best representation of

lava flows of different ages that reached the sea. The oldest sampled area corresponds to the Jedey lava flow (Puerto Naos; (28.584996° N, 17.910301° W), produced by a Strombolian eruption that began in May 1585 and lasted several weeks (Carracedo et al. 2001). The intermediate-aged substrate is the San Juan lava flow (La Bombilla; 28.592422° N, 17.919193° W), resulting from a fissural eruption in June 1949 that persisted for 42 days (Carracedo et al. 1992). The most recent substrate stems from the 2021 Tajogaite eruption (Playa del Arco; 28.609141° N, 17.923526° W), also fissural in nature, which erupted in September 2021 and continued for two months and 24 days. This last event reached the sea, creating two new land formations measuring approximately 5.05 ha (northern area) and 43.46 ha (southern area) (Fig. 1).

## 2.2. Sampling

Sampling was conducted by a team of three divers in August 2022 at each selected location and at two depths: 10 and 20 meters. The sampling design encompassed three complementary approaches. To assess the algal community, standardized 25 × 25 cm photoquadrats (Fig. 2a) were randomly deployed across all three volcanic substrates, using an OLYMPUS TG6 underwater camera. A total of 20 photoquadrats were taken at each depth per site during two sampling dives, resulting in 40 photoquadrats per lava flow and 120 in total across all sites. These images provided a non-invasive record of algal composition and coverage, which were later analyzed to identify and quantify species presence, percent cover, and community structure.

To study the earliest colonization stages and early microinvertebrate settlement processes, five early settlement collectors were deployed at a depth of 10–15 m per lava-flow and left *in situ* for 30 days (Fig. 2b). Upon retrieval, the collectors were carefully rinsed in the laboratory, and the retained material was preserved in 95% ethanol at 4°C until laboratory processing. A subsequent examination and sorting of these samples focused on the identification of larvae and early settlers of all available taxa.

Lastly, to delve deeper into the benthic microinvertebrate fauna, five rocks, measuring 15 to 20 cm, were carefully collected from each site and placed in plastic bags, yielding a total of 15 rock samples (Fig. 2c). These rocks were photographed from all faces, including those attached to the substrate, as some taxa tend to occupy less exposed microhabitats on the underside of stones. Subsequent laboratory examination allowed for the identification and quantification of microinvertebrates, contributing detailed insights into the community composition, abundance, and demographic structure of species less easily captured by photographic methods.

## 2.3. Laboratory work

Laboratory processing of the samples was done at two stages. The percentage of cover of all macroalgae species in each photoquadrant was obtained using the open-source image processing ImageJ 1.53m program (Schneider et al. 2012) and the results were displayed in m<sup>2</sup>. To minimize differences between lava flows and prevent misidentifications, some species were aggregated into general or, corresponding to morphological classifications, turf-forming species, crustose coralline algae

(CCA), geniculate coralline algae (GCA) and cyanobacteria, according to Littler and Littler (1980). We defined turf-forming species as sparse to thick mats of diminutive and juvenile algae that are < 2 cm tall (Littler and Littler 2011). The literature (Alfonso-Carrillo and Sanson 1989) was used to help on the identification.

For the early microinvertebrate settlement analysis, organisms were carefully extracted from the collectors upon retrieval. Following identification, specimens were counted and photographed. It is important to note that, due to the small size and early developmental stages of many settlers, taxonomic resolution was limited in several cases to the order and family level. While this represents a methodological constraint, it does not compromise the broader patterns observed. Finally, for the study of the epifauna each collected rock was placed in a tray and all organisms were carefully removed using fine forceps. These specimens were then examined under a stereomicroscope (Leica EZ4) and identified using relevant taxonomic literature (González 1995) and the online identification guide provided by REDPROMAR (<http://www.redpromar.com/app/guide>, accessed in 2024).

## **2.4. Statistical analysis**

Statistical analyses were performed using PRIMER v7 with the PERMANOVA + add-on (Anderson 2008). To examine patterns of biodiversity and community structure across lava flows of different ages (< 1 year, 73 years, and 473 years), both univariate and multivariate analyses were conducted for three benthic groups: (1) macroalgae, (2) early-stage settlers on artificial collectors, and (3) benthic microinvertebrates.

To assess species richness, a univariate approach was applied. PERANOVA tests were conducted using a design that included lava flow age and depth (10 m and 20 m levels) as fixed factors, and replicates as a random factor. Boxplots were generated to visualize differences in richness across lava flows and depths for each significant grouping.

To evaluate differences in community composition and abundance, abundance data were square-root transformed and Bray-Curtis similarity matrices were constructed. For each group, a PERMANOVA was applied using the same experimental design. Significant differences ( $p < 0.05$ ) were followed by pairwise post-hoc comparisons. Non-metric multidimensional scaling (nMDS) plots were generated to visualize similarities among samples. Additionally, SIMPER (Similarity Percentage) analyses identified the species contributing most to differences between lava flows

## **3. RESULTS**

### **3.1. Macroalgae community**

Macroalgal richness varied significantly across lava flows of different ages. The PERANOVA revealed a strong effect of substratum age on the number of algal taxa (PERANOVA,  $F = 18.352$ ,  $P = 0.0002$ ). Post-hoc pairwise comparisons indicated that richness was significantly lower on the youngest lava flow (< 1

year) compared to both the 73-year-old (post-hoc pairwise test,  $P = 0.0002$ ) and 473-year-old flows (post-hoc pairwise test,  $P = 0.0002$ ), while no significant differences were found between the intermediate and oldest flows (post-hoc pairwise test,  $P = 0.3386$ ). These patterns are illustrated in the boxplot (Fig. 3A), with richness peaking in the 73-year flow and declining slightly in the oldest flow, suggesting that algal diversity increases with time since disturbance but may stabilize or decrease in later successional stages.

Macroalgal community composition and percent cover also differed significantly among lava flows. The PERMANOVA showed a significant effect of lava flow age on macroalgal assemblages (PERMANOVA,  $F = 7.1728$ ,  $P = 0.0047$ ), confirming that succession is accompanied by shifts in species identity and abundance. Depth was not a significant factor (PERMANOVA,  $F = 2.9139$ ,  $P = 0.0657$ ), nor was the interaction between flow age and depth (PERMANOVA,  $F = 0.87483$ ,  $P = 0.5633$ ), indicating that community differences were primarily driven by the age of the substrate rather than vertical zonation.

Pairwise comparisons revealed significant differences in macroalgal composition between the youngest flow and both the 73-year (post-hoc pairwise test,  $t = 3.3667$ ,  $P = 0.0317$ ) and 473-year flows (post-hoc pairwise test,  $t = 2.4162$ ,  $P = 0.0292$ ). In contrast, assemblages on the 73- and 473-year flows did not differ significantly (post-hoc pairwise test,  $t = 1.4618$ ,  $P = 0.1496$ ). These patterns are visualized in the non-metric multidimensional scaling (nMDS) plot (Fig. 3B), where samples from each flow cluster separately, particularly distinguishing the youngest flow from the other two.

SIMPER analysis confirmed that the greatest compositional dissimilarity occurred between the youngest and 73-year-old lava flows (SIMPER, average dissimilarity = 81.7%). This contrast was mainly driven by the higher abundance of *Lophocladia trichoclados* and epiphytic taxa in the intermediate flow, which were nearly absent on the youngest substrate. Comparisons between the youngest and oldest flows also showed high dissimilarity (SIMPER, average dissimilarity = 74.43%), with increased abundance of e.g. *L. trichoclados*, *Canistrocarpus cervicornis*, *Cottoniella filamentosa*, and *Pseudotetraspora marina* in the 473-year assemblage. The comparison between the 73- and 473-year flows revealed the lowest dissimilarity (SIMPER, average dissimilarity = 50.59%), reflecting a more mature and compositionally similar community. Slight shifts in abundance explained this difference, with moderate reductions in e.g. *L. trichoclados* and epiphytes and increases in e.g. *C. cervicornis* and e.g. *P. marina* in the oldest lava flow.

## 3.2. Microinvertebrates early-stage settlement

Species richness of early invertebrate settlers differed significantly among lava flows (PERMANOVA,  $F = 18.955$ ,  $P = 0.0011$ ; Fig. 4A). Richness peaked at the intermediate-aged flow (73 years), followed by the oldest flow (473 years), while the youngest site (< 1 year) exhibited the lowest values. Pairwise comparisons confirmed that richness in the youngest flow was significantly lower than in both the 73-year-old (post-hoc pairwise test,  $t = 5.5$ ,  $P = 0.004$ ) and the 473-year-old (post-hoc pairwise test,  $t = 4.82$ ,  $P = 0.0027$ ) flows. No significant difference was detected between the two older flows (post-hoc pairwise test,  $t = 1.67$ ,  $P = 0.1415$ ).

The analysis of early settler abundances revealed significant compositional differences across flows (PERMANOVA:  $F = 5.1545$ ,  $P = 0.0002$ ), with depth showing no significant effect. Pairwise tests indicated significant differences between the youngest flow and both the 73-year-old (post-hoc pairwise test,  $t = 1.9361$ ,  $P = 0.0452$ ) and 473-year-old (post-hoc pairwise test,  $t = 2.4646$ ,  $P = 0.0036$ ) flows, as well as between the two older flows (post-hoc pairwise test,  $t = 2.2833$ ,  $P = 0.0052$ ). These patterns are visually supported by the nMDS plot (Fig. 4B), which shows partial overlap but also distinct clustering by flow age.

The highest dissimilarity was observed between the 1-year and 473-year-old flows (SIMPER, average dissimilarity = 28.93%), mainly due to reduced abundances of copepods (*Thalestridae* sp.) and Tanaidacea in the older assemblage, and increased representation of Alpheidae, Cerithiidae, and Caprellidae. Similarly, the 1-year vs. 73-year comparison showed an average dissimilarity of 27.95, driven by comparable taxonomic shifts, including a decrease in copepods and Tanaidacea, and increases in Caprellidae, Isopoda, and mollusks (Cerithiidae). The 73- vs. 473-year comparison yielded the lowest dissimilarity (SIMPER, average dissimilarity = 23.35%), reflecting more gradual compositional changes such as increased abundance of Alpheidae and Syllidae in the oldest flow, along with subtler variations across Caprellidae, Sipunculida, Isopoda, and Pycnogonida.

### 3.3. Microinvertebrates benthic community

Species richness of sessile and slow-moving benthic microinvertebrates differed significantly across lava flows of different ages (PERMANOVA:  $F = 17.408$ ,  $P = 0.002$ ), with the highest values observed in the 73-year-old flow (Fig. 5A). Pairwise comparisons revealed that richness in this intermediate-aged flow was significantly higher than in the youngest (post-hoc pairwise test,  $t = 7.13$ ,  $P = 0.0007$ ) and the oldest (post-hoc pairwise test,  $t = 4.55$ ,  $P = 0.0036$ ) flows. In contrast, no significant difference was detected between the youngest and oldest sites (post-hoc pairwise test,  $t = 0.65$ ,  $P = 0.5528$ ), indicating a unimodal pattern of richness along the successional gradient.

In terms of community composition, PERMANOVA results showed that “lava flow age” had a significant effect on the structure of microinvertebrate assemblages (PERMANOVA:  $F = 3.7913$ ,  $P = 0.0009$ ) (Pseudo- $F = 3.7913$ ,  $P\text{-perm} = 0.0009$ ), while no interaction with depth was detected. Pairwise comparisons confirmed significant differences between all lava flow pairs: <1 vs. 73 years (post-hoc pairwise test,  $t = 2.1512$ ,  $P = 0.0427$ ), <1 vs. 473 years (post-hoc pairwise test,  $t = 1.9422$ ,  $P = 0.0364$ ), and 73 vs. 473 years (post-hoc pairwise test,  $t = 2.5693$ ,  $P = 0.0371$ ). These patterns were supported by the nMDS plot (Fig. 5B), which visually highlighted distinct clustering of samples according to flow age.

The highest average dissimilarity was found between the 73- and 473-year-old flows (SIMPER, average dissimilarity = 49.38%), driven primarily by a sharp reduction in the abundance of *Bittium incile*, *Bittium latreilli*, *Metavermlia multicristata*, and few species of the family Syllidae, along with the loss of several taxa present only in the 73-year assemblage, such as *Ophioderma longicaudum*, *Amphipholis squamata*, and *Caprella equilibra*. The comparison between the youngest and the 473-year-old flows (SIMPER, average dissimilarity = 44.38%) revealed a similar pattern: early colonizers like e.g. *M. multicristata*, e.g.

*B. latrelli*, Bryozoans and Gammaridae species declined, while *V. quadrata* and Cirratulidae became more prominent. Lastly, dissimilarity between the youngest and the 73-year-old flows (SIMPER, average dissimilarity = 41.76%) still reflected clear successional turnover, marked by greater abundance and richness in the intermediate flow, including several species absent from the youngest site, such as e.g. *O. longicaudum*, e.g. *A. squamata*, and hermit crabs of the family Diogenidae.

### 3.4. Successional pattern

The successional gradient represented by the three lava flows revealed distinct shifts in species composition across macroalgae, early invertebrate settlers, and benthic microinvertebrates. These patterns reflect progressive stages of ecological succession, from pioneer colonization in the youngest flow to more structured assemblages in the oldest.

In the youngest lava flow (< 1 year), benthic communities included among the macroalgae *Asparagopsis taxiformis*, *Cottoniella filamentosa*, *Canistrocarpus cervicornis*, *Pseudotetraspora marina*, and *Corallina* spp. The early invertebrate settlers comprised annelids (Serpulidae, Syllidae), gammarid amphipods, some tanaidaceans, and brachyurans (*Lophozozymus incisus*, *Xantho poressa*). The benthic microinvertebrate community was characterized by *Bittium latrelli*, *Metavermilia multicristata*, Bryozoans, and some Gammaridae species (Fig. 6\_ left picture).

The intermediate lava flow (73 years) supported the highest species richness and taxonomic complexity across all groups. The macroalgal assemblage included *Laurencia trichoclados*, *Porolithon onkodes*, *Zonaria tournefortii*, and various epiphytic species. Early invertebrate settlers in this flow showed higher diversity and included Caprellidae, Alpheidae, Cerithiidae, Syllidae, and Gammaridae. Benthic microinvertebrates included *Bittium incile*, *B. latrelli*, Syllidae, and unique taxa such as Cirratulidae, Terebellidae, *Pachygrapsus marmoratus*, *Paracentrotus lividus*, *Amphipholis squamata*, and *Ophioderma longicaudum* (Fig. 6\_central picture).

In the oldest lava flow (473 years), the macroalgal community included *Dictyota humifusa*, *Zonaria tournefortii*, *Lophocladia trichoclados*, and *Porolithon onkodes*. Early settlers included Alpheidae, Cerithiidae, and Syllidae, with reduced abundance of Copepoda (Thalestridae) and Tanaidacea. The benthic microinvertebrate community was dominated by *Verticordia quadrata*, Syllidae, e.g. *B. incile*, e.g. *B. latrelli*, Cirratulidae, e.g. *M. multicristata*, and *Alpheus macrocheles*. Additional taxa such as *Percnon gibbesi*, *Macropodia longicornis*, and Diogenidae were also present (Fig. 6\_right picture).

## 4. DISCUSSION

The temporal gradient of lava flow age provided a natural framework to explore how benthic communities assemble over time following volcanic disturbances. Our findings reveal a clear successional trajectory in which species richness and community structure respond differently across taxonomic groups such as macroalgae and invertebrates. The intermediate-aged flow (73 years) consistently supported peak richness and compositional complexity across macroalgae, early

microinvertebrates settlers, and benthic microinvertebrates, suggesting it represents a transitional stage where early colonizers coexist with more specialized taxa. In contrast, the youngest flow (< 1 year) was dominated by opportunistic species adapted to unstable conditions, while the oldest flow (473 years) showed signs of competitive exclusion and post-settlement filtering, particularly among microinvertebrates (Fig. 6). This pattern suggests that initial community expansion is followed by compositional refinement and competitive restructuring over time, as predicted by Margalef (1977).

Macroalgae represent the first stage in colonization on newly formed volcanic lava flows, initiating benthic community development, as observed by Sangil et al. (2024). Their contribution to substrate stabilization and trophic support makes them essential for the establishment of subsequent invertebrate communities (Gibbons and Quijón 2023; Vieira et al. 2024). Although the dominant species identified differ between our study and Sangil et al. (2024), both coincide in showing that early colonization was led by fast-growing opportunistic algae. These discrepancies may reflect the fact that the surveys were conducted during different phases of the very early succession, as well as the strong microhabitat heterogeneity of the lava substrate. In addition, methodological differences are relevant, since our study focused on 10–20 m depth whereas Sangil et al. (2024) covered the full range from the intertidal to 20 m. All together, these factors likely explain the taxonomic differences observed while reinforcing the functional consistency of early successional patterns.

Among the species detected in our survey, some display well-documented adaptive traits that may explain their success as pioneers. For instance, *Asparagopsis taxiformis* and *Cotoniella filamentosa* are red algae that have been shown to have genetic adaptations providing them with high resilience and adaptability to live in a wide range of environments, such as those formed after volcanic eruptions (Htay and Soe-Htun 2010; Cho et al. 2023). After several studies in tropical and subtropical environments, it has been observed that the calcification process of calcareous algae as *Corallina* spp. gives them an advantage as colonizers. This provides them with a rigid structure that can protect them from predators and adverse environmental conditions, also aiding in adherence to various surfaces, facilitating colonization in new habitats (De Carvalho et al. 2022). Additionally, areas with good solar exposure, as in this case, also support their settlement in new habitats, as it improves their proliferation (Tâmega and Figueiredo 2019). Brown algae, including *Canistrocarpus cervicornis*, have advantages such as high dispersal and colonization capacity (García-Gómez et al. 2021). The case of e.g. *C. cervicornis* is special because it was one of the first colonizers and continued to have a high presence in the oldest lava flow. This is not surprising since it is one of the most common algae in the Canary Island (Sangil et al. 2021). Finally, *P. marina* is a green alga (phylum Chlorophyta), and it has been shown to proliferate optimally when water temperature significantly increases, exactly what happens after a volcanic eruption, which could be a key factor for its rapid settlement (Sangil et al. 2012). Recent studies have demonstrated that they exhibit physiological responses that counteract environmental stressors typically associated with recent volcanic disturbances such as elevated temperatures, altered salinity regimes, reduced nutrient availability, and high solar irradiance providing them with a significant advantage in colonizing newly formed substrates (Mikami et al. 2021).

As the lava flows mature and the substrate becomes more stable and biologically enriched, communities tend to converge towards more complex and diverse macroalgae assemblages. Accordingly, the 73 and 473-year-old flows exhibited high similarity in macroalgal composition, suggesting that many of the key structural and ecological conditions necessary for macroalgal development were already established by the intermediate successional stage. The absence of new species in the youngest lava flow, in contrast to their presence on the 73-year-old flow, can be attributed to the ecological succession process and to the specific ecological requirements of these taxa such as substrate stability, nutrient levels, or the presence of biotic precursors which are further discussed below. In early successional stages, pioneer species dominate due to their ability to colonize unstable substrates with minimal competition (Margalef 1977). As the substrate stabilizes and organic matter accumulates, conditions become more suitable for species like *Dictyota humifusa* and *Sargassum* spp., which require higher nutrient availability and a more stable environment to thrive (Cronin and Hay 1996). Indeed, chemical analyses conducted by González-Santana et al. (2022) showed that the 2021 Tajogaite eruption released vast quantities of iron into coastal waters reaching up to  $\sim 1900 \text{ nmol L}^{-1}$ , with soluble forms  $\sim 10$ -fold higher than typical Atlantic levels thereby fertilizing the marine environment and enhancing nutrient availability for macroalgal colonization. This increased nutrient availability and habitat stabilization may also explain the later appearance of species with more specific substrate requirements. *Porolithon onkodes*, a calcifying coralline alga, may appear later due to its potential reliance on specific substrate characteristics and stability that develop over time. Unlike other coralline algae present in the newly formed flow, e.g. *P. onkodes* is known for its contribution to reef-building processes and the consolidation of benthic substrates (Yang et al. 2021). Its establishment is often associated with substrates that have already developed biofilms and initial biological conditioning, which facilitate its adhesion and growth. Moreover, once established, e.g. *P. onkodes* actively contributes to further substrate stabilization through its calcified structure, enhancing the durability and complexity of the benthic habitat. The difficulties related to get definitive taxonomic identification for all pioneer corallines in the youngest flow prevents a full understanding of the competitive or facilitative interactions that might delay the establishment of e.g. *P. onkodes*. Similarly, *Zonaria tournefortii* and small epiphytes, which often grow on other macroalgae, reflect a more diverse and structured community where species interactions, such as epiphytes, become more prominent in a subsequent successional stage (Montañés et al. 2003). The delayed appearance of these species highlights their reliance on the changes brought about by early colonizers, which modify the substrate and create conditions conducive to the establishment of more specialized taxa. This result aligns with established theories of ecological succession in marine benthic ecosystems, where later successional stages are characterized by increased species richness, habitat complexity, and trophic interactions (Steele 1974; Margalef 1977).

The distinct macroalgal assemblages characterizing each successional stage appeared to play a pivotal role in shaping the composition of early invertebrate colonizers. Previous studies have shown that macroalgae can affect early settled invertebrates' recruitment through structural and biochemical properties that facilitate or inhibit settlement (Dean and Connell 1987). All flows were dominated by species capable of providing essential habitat features, such as structural complexity and surfaces

suitable for biofilm development, which are critical for early settlement (Dobretsov and Rittschof 2020). This could provide valuable information on the behavior and settlement preferences of a wide variety of invertebrates in the Canary Islands. It should be noted that some species were established in a similar way in the three lava flows, such as, *Pagurus anachoretus*, *Lophozozymus incisus* and species of Gammaridae and Cumacea families. Concerning the settling relationships with algae in each lava flow, the following was observed. In the most recent lava flow, the algae was characterized by their rapid colonization ability and filamentous or branching structures, likely created a dynamic but less stable habitat, that may attract species such as *Xantho poressa*, *Lophozozymus incisus*, and Tanaidacea (Gan et al. 2019). The complexity of these algae may provide shelter and surfaces for biofilm development, favoring detritivores and small crustaceans (Paulós 2024). In the 73-year-old lava flow, the structural and chemical diversity of this algal community likely contributed to the settlement of invertebrate species, such as *Arbacia lixula* and *Cronius ruber*. However, *Porolithon onkodes*, as a calcifying alga, provides a stable and durable substrate for attachment, while the branched structures of *Lophocladia trichoclados* and *Zonaria tournefortii* enhance habitat complexity, supporting a wider range of invertebrates (Paulós 2024; Vizon et al. 2024). The presence of epiphytic algae further increases resource availability, attracting predators like e.g. *C. ruber* and omnivores as e.g. *A. lixula* (Gestoso et al. 2012). Finally, in the 473-year-old lava flow, the leathery and robust structures of these algae community provide long-term habitat stability, which may explain the prevalence of species such as e.g. *P. anachoretus*, *Alpheus macrocheles*, and *Percnon gibbesi* (Rojas-González et al. 2004). These invertebrates are known for their competitive abilities and adaptability to environments where resources are more evenly distributed, but competition is higher (Margalef 1977). The calcifying algae present, although less predominant, still contributes to substrate consolidation, thereby supporting species that require firm attachment points (O'Leary et al. 2017).

These habitat-mediated dynamics appear to follow different temporal trajectories for macroalgal and invertebrate communities. Our results suggest that macroalgal assemblages may reach a compositional equilibrium earlier, as no significant differences were detected between the 73- and 473-year-old flows. In contrast, invertebrate communities exhibited distinct shifts across all stages, suggesting a slower and more variable stabilization process likely influenced by habitat complexity and macroalgal structure. Species richness peaked in the intermediate-aged lava flow, which also supported a broader range of functional traits. This included pioneer taxa typically associated with early colonization and r-selected strategies, as well as more specialized organisms adapted to mature environments. These patterns underscore the transitional importance of intermediate successional stages, where both colonization opportunities and competitive interactions shape community assembly.

Understanding the functional contributions of different taxa within this framework is essential to elucidate how benthic communities expand and stabilize over time. The role of macroalgae as primary settlers extends beyond their direct contribution to substrate stabilization and nutrient cycling; they also create essential microhabitats that support the colonization of other organisms, starting with the invertebrates (Vieira et al. 2024). Small benthic invertebrates' community is typically associated with rocky substrates and various algal species, comprising a diverse array of small invertebrates from

multiple taxonomic groups. It includes arthropods, such as isopods, amphipods, and tanaidaceans, as well as small decapods, mollusks, polychaetas, and some echinoderms (Hawkins et al. 2021). These organisms belong to the same taxonomic groups reported in other studies of colonization following volcanic eruptions, such as those conducted on Kasatochi Island (Jewett et al. 2010).

Among the early colonizers, gastropods of the genus *Bittium* (e.g. *B. incile* and e.g. *B. latrelli*) stand out due to their high adaptability and capacity to exploit novel environments for feeding, which has been linked to successful settlement in post-disturbance habitats (Castejón-Silvo and Terrados 2017). Similarly, bivalves like *Verticordia quadrata*, although less studied, possess generalist traits such as filter feeding and protective shells that can facilitate early establishment on unstable substrates (Dame 2011). Certain brachyuran crabs, including *Lophozozymus incisus* and *Xantho poressa*, also exhibit ecological traits favorable to pioneering roles, such as thermal tolerance, high predatory efficiency, and osmoregulatory capacity, which may allow them to colonize dynamic or nearshore environments effectively (Lee 2015; Turner 2015).

For other taxa such as syllids, gammarids, and bryozoans, specific competitive advantages are less documented; however, their functional traits offer insight. These groups often rely on detritus or suspended particles as primary food sources (Somma et al. 2023), and their trophic plasticity may facilitate rapid colonization of nutrient-rich but structurally simple habitats. Gammarids can function as detritivores or filter feeders, syllids primarily consume detritus, and bryozoans are effective suspension feeders traits that support their early establishment in freshly formed substrates (Giangrande et al. 1977; Winston 1981; MacNeil et al. 1997;).

As the substrate matures, greater species richness and the emergence of exclusive taxa appear to result from improved habitat complexity and resource availability (Romoth et al. 2023). However, in later successional stages, competitive interactions likely intensify, potentially leading to declines in diversity through niche filtering or exclusion, as predicted by classical successional theory (Margalef 1977). In the most mature community, we observed a shift towards species exhibiting traits of competitive dominance and niche specialization, such as e.g. *A. macrocheles* that is a predator known for its asymmetrical snapping claw, which produces a powerful cavitation bubble used to stun prey a trait that enhances both foraging efficiency and defense (Hatcher and Trewhella 2021). Similarly, *Macropodia longirostris* exemplifies cryptic adaptation; its capacity to camouflage within algae and substrates not only reduces predation risk but also improves its success as an ambush predator (Bedini et al. 2003). In addition, the consistent presence and dominance of e.g. *P. gibbesi* in the oldest flow may reflect its well-documented competitive strength. Originally introduced into the Mediterranean, where it is considered an invasive species, e.g. *P. gibbesi* has demonstrated high adaptability, environmental tolerance, and success in outcompeting native species in mature rocky environments (Deudero et al. 2005; Cannicci et al. 2008). Its ability to establish and thrive in the complex, resource-saturated habitat of the 473-year-old lava flow suggests that similar competitive advantages may be at play in this system.

These observations prompt broader ecological questions regarding the trajectory and stability of successional outcomes in volcanic marine environments. An additional insight emerges when comparing the species arriving as larvae with those ultimately found as settled invertebrates across the three lava flows. In the newly formed flow, the number of settled species was slightly lower than the number of early settled invertebrates' arrivals, suggesting a modest post-settlement filtering effect. In the 73-year-old flow, this relationship appeared nearly balanced, indicating that the habitat provided favorable conditions for most arriving species to successfully establish. In contrast, in the 473-year-old flow, a marked reduction was observed in the proportion of species that transitioned from arrival to recruitment. This suggests that more mature communities may exert stronger post-settlement selection pressures, likely driven by increased competition, predation and habitat structuring.

While not a primary objective of this study, these results suggest that post-settlement filtering may intensify with community maturity and underscore the importance of future investigations focused on recruitment success and habitat filtering in late successional stages. Similar dynamics have been reported in other marine systems, such as kelp forests, where even after habitat stabilization, communities can diverge significantly from their initial composition due to stochastic colonization, altered species interactions, and disturbance legacies (Bui et al. unpublished data). These parallels reinforce the broader ecological relevance of understanding long-term successional processes in active volcanic coastal environments.

## Declarations

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**Conflict of Interest:** The authors declare that they have no competing interests that could have appeared to influence the work reported in this paper.

**Ethical Approval:** The authors declare that this study adheres to ethical standards and guidelines. All applicable international, national, and institutional guidelines for sampling, care, and experimental use of organisms were followed.

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# Figures

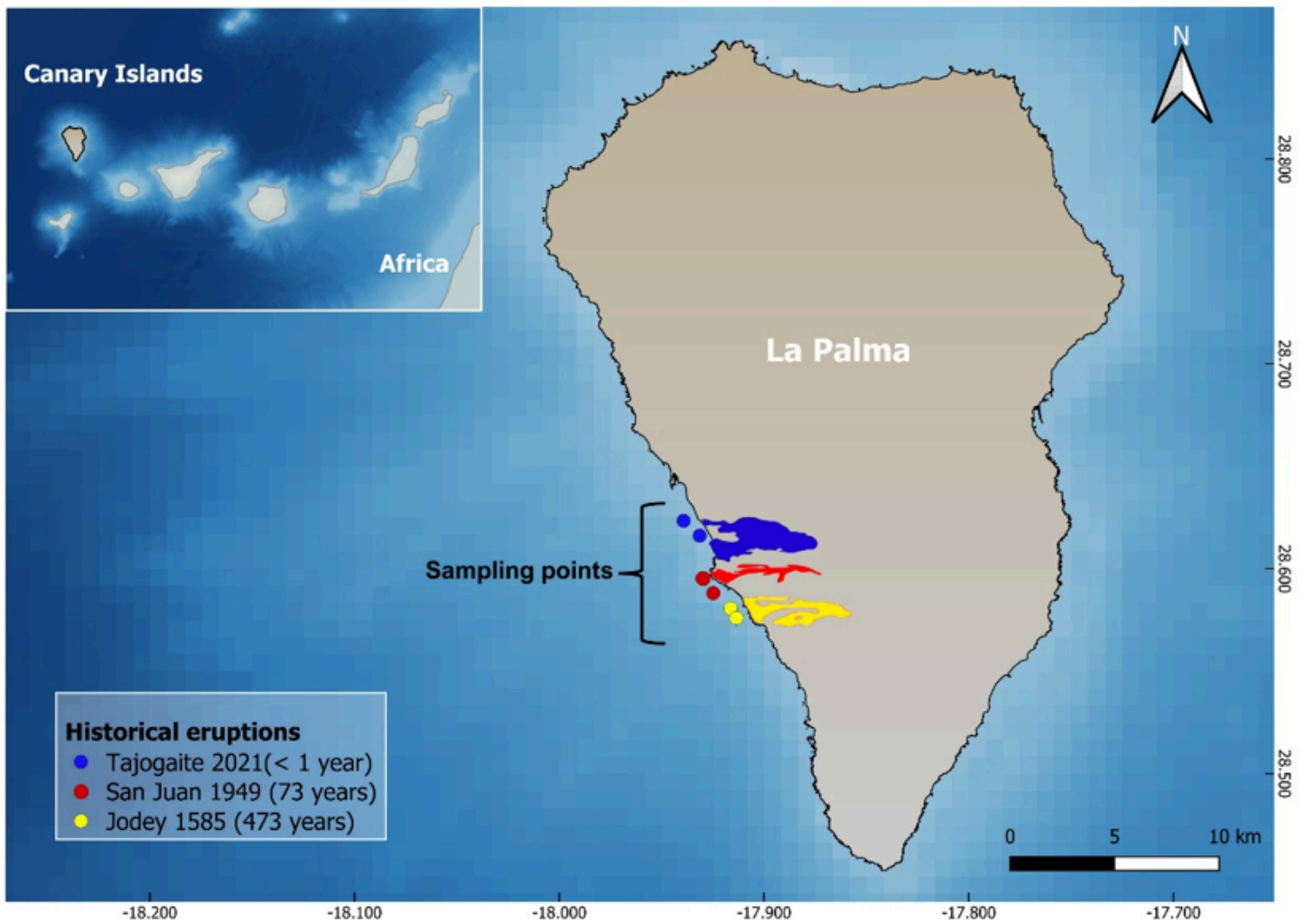


Figure 1

Map of La Palma Island with sampling points, located at the three lava flows studied. Geological data obtained from Instituto Geográfico Nacional (<https://www.ign.es>, accessed in January 2025) and EpData (<https://www.epdata.es/>, accessed in January 2025).

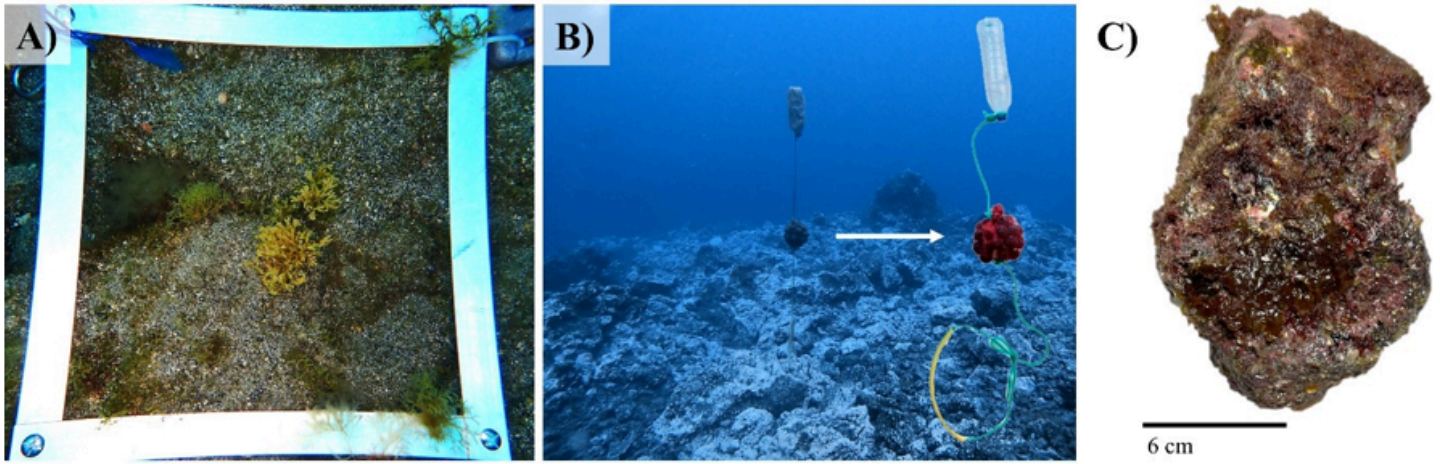


**Figure 2**

Sampling methodologies used in the study. A: Macroalgae cover photoquadrats; B: Larvae settlement collectors; C: Collected rock sample.

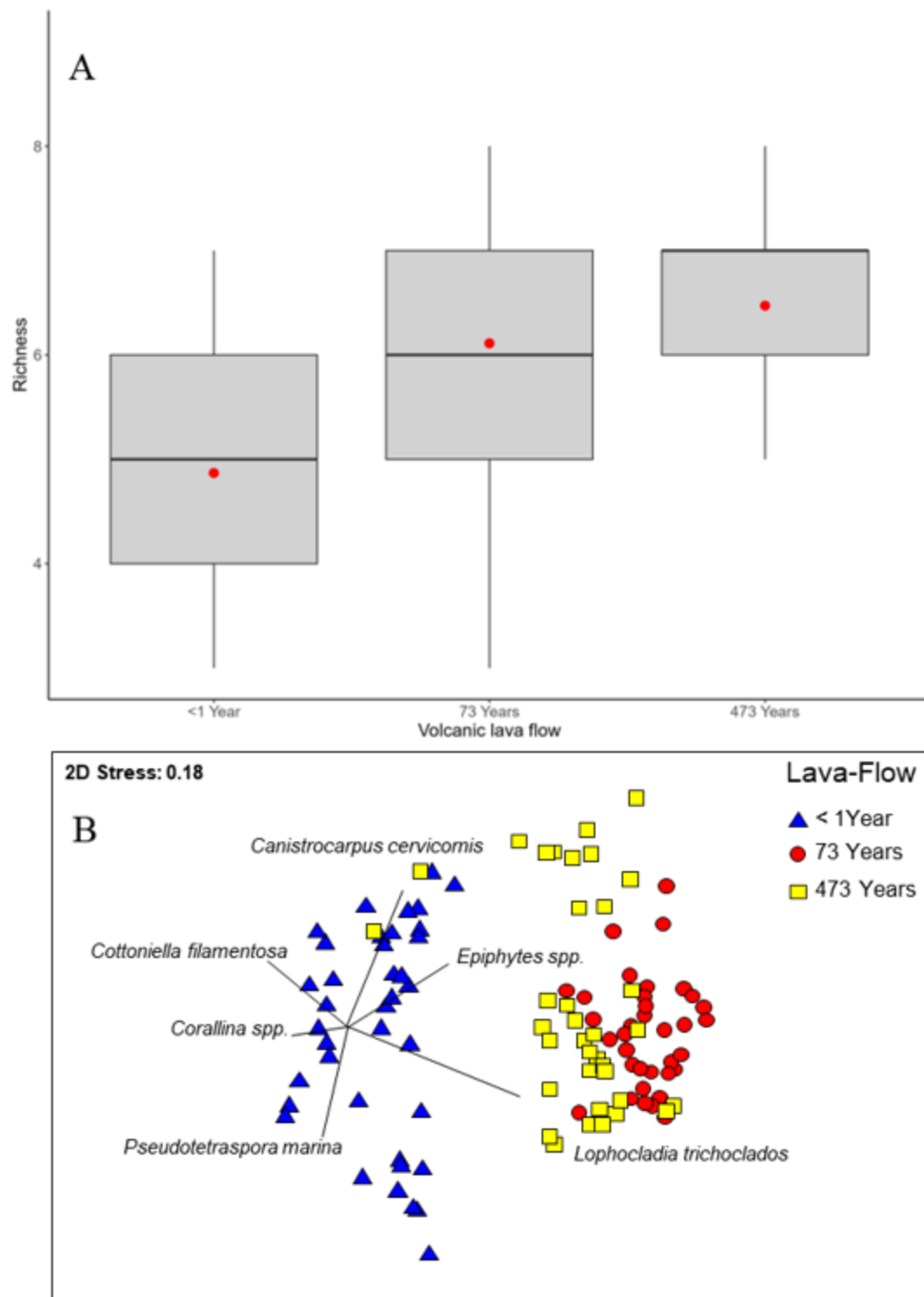


**Figure 3**

Macroalgae community structure and composition across volcanic substrates of different ages (<1 year, 73 years, 473 years). (A) Boxplot of species richness per lava. (B) nMDS based on Bray-Curtis similarity of square-root transformed cover data.

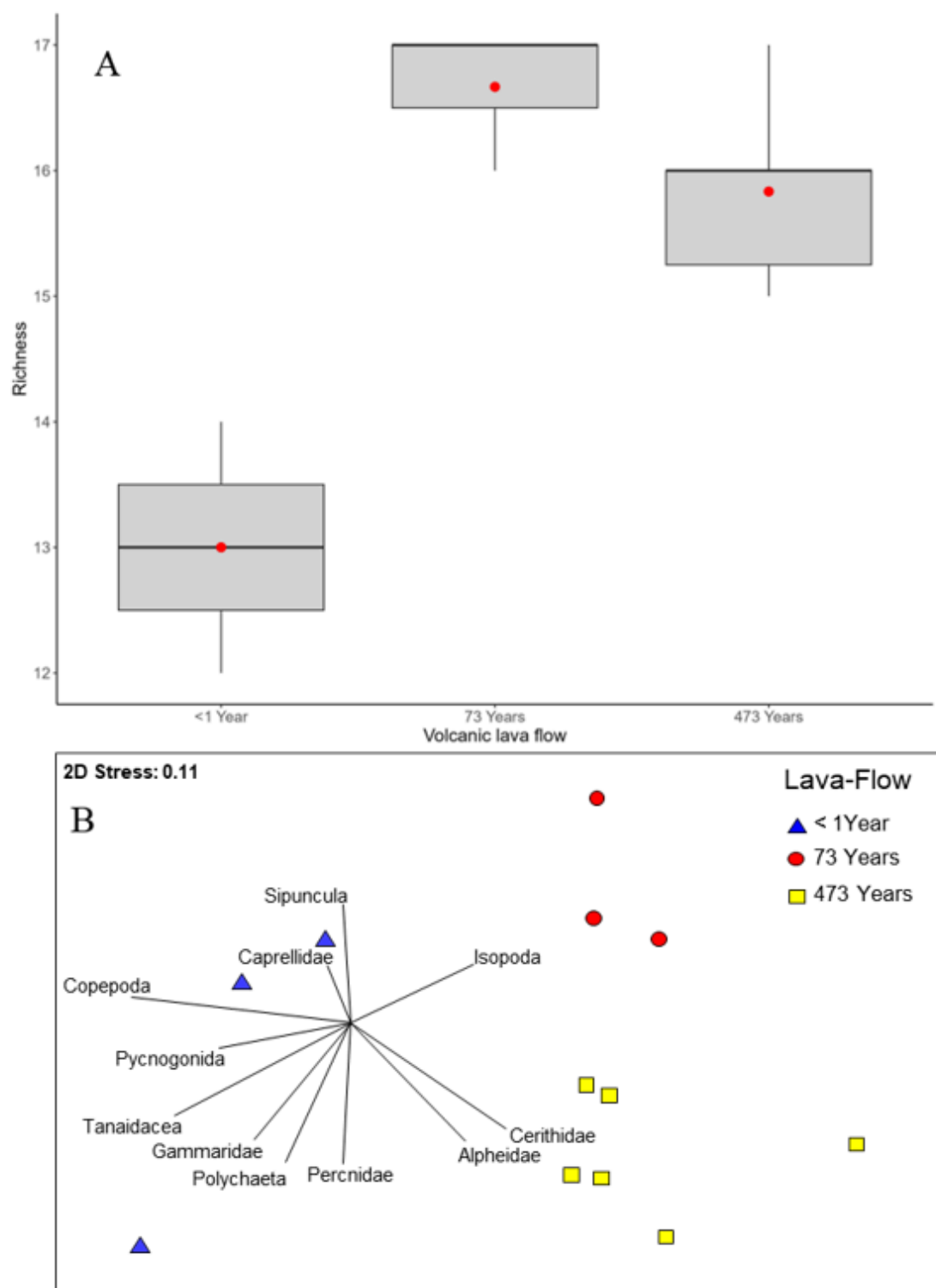


**Figure 4**

Early settled microinvertebrates across volcanic substrates of different ages (<1 year, 73 years, 473 years). (A) Boxplot of species richness per lava-flow. (B) nMDS of collector assemblages based on Bray-Curtis similarity.

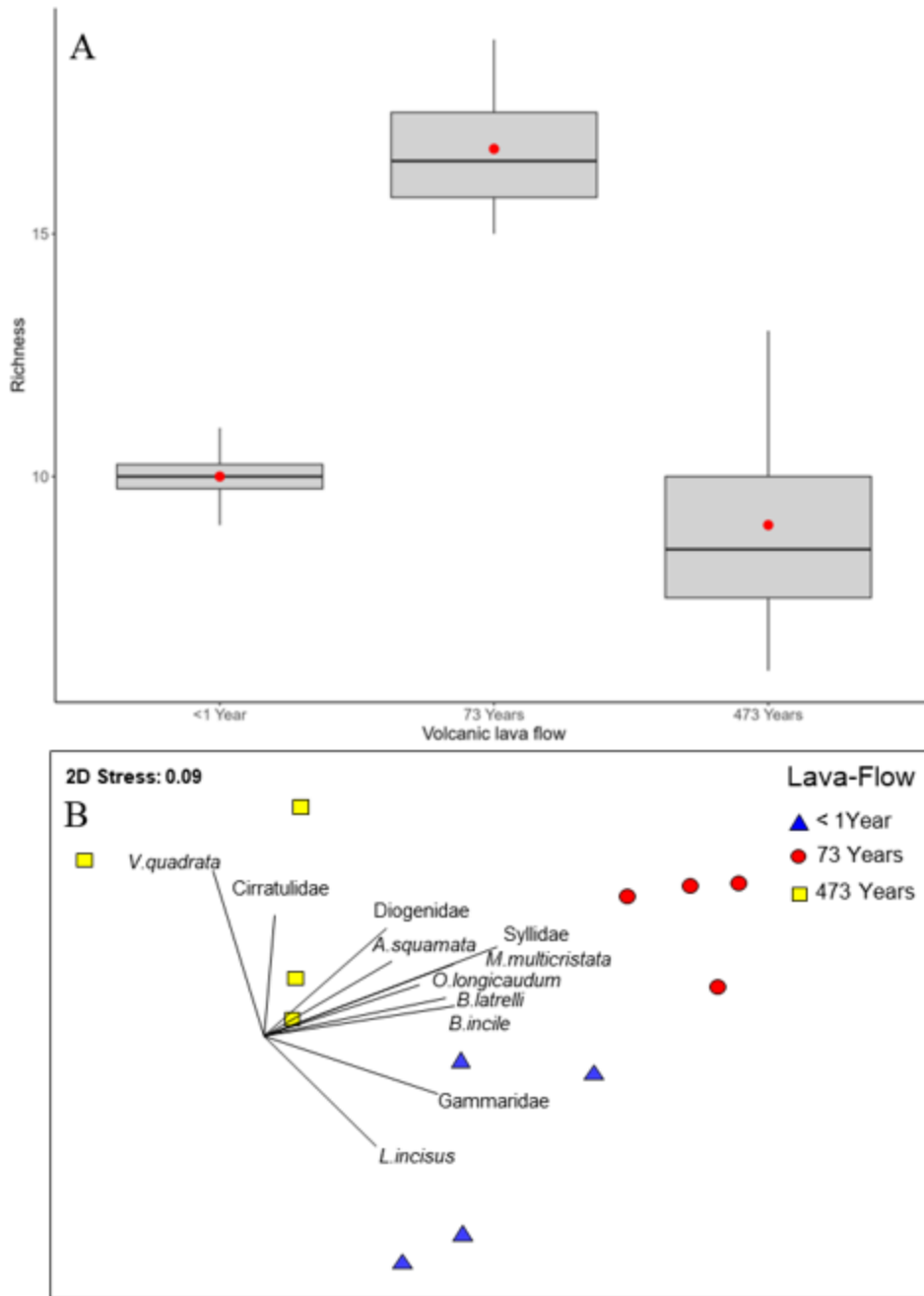


**Figure 5**

Benthic microinvertebrates communities across volcanic substrates of different ages (<1 year, 73 years, 473 years). (A) Boxplot of species richness lava-flow. (B) nMDS based on Bray-Curtis similarity of square-root transformed abundances.

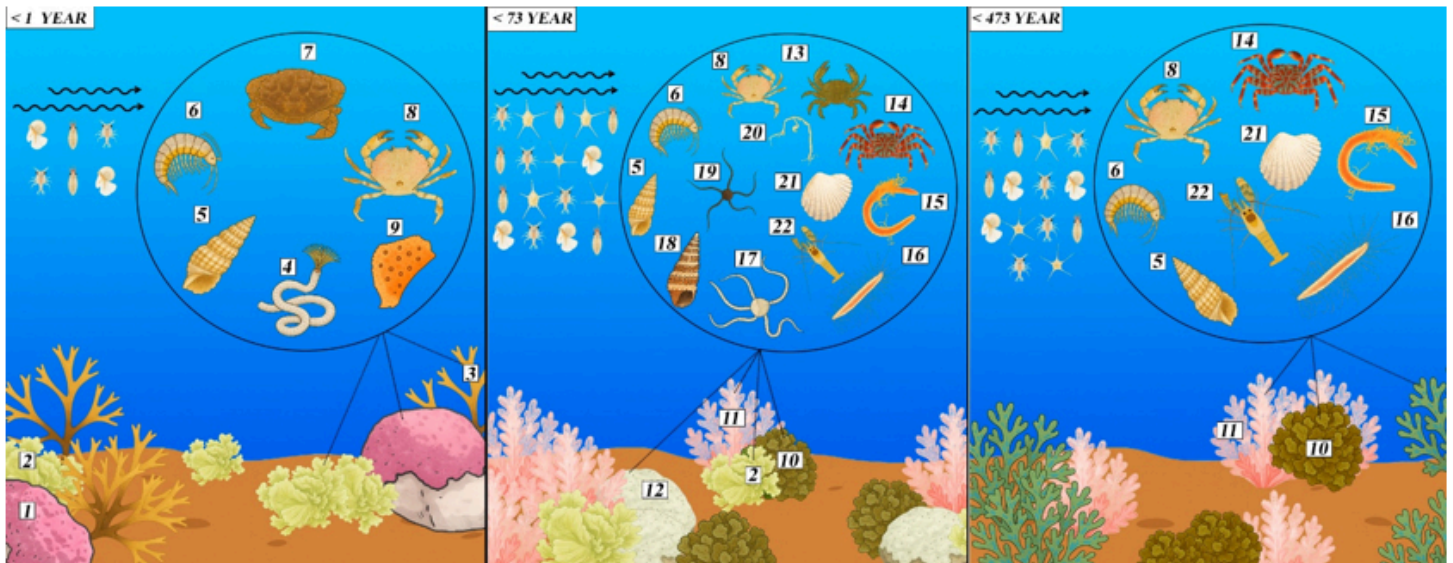


**Figure 6**

Infographic comparing benthic community composition across three volcanic lava flows of different ages (<1 year, 73 years, 473 years) on La Palma Island. Each panel illustrates representative macroalgal species and successfully settled invertebrates observed on the corresponding substrate. Species: 1- *Corallina* spp, 2- *Pseudotetraspora marina*, 3- *Canistrocarpus cervicornis*, 4- *Metavermilia multicristata*, 5- *Bittium latreilliid*, 6- *Gammaridae* sp., 7- *Xantho poressa*, 8- *Lophozozymus incisus*, 9- *Bryozoa* sp., 10- *Zonaria tourneforti*, 11- *Lophocladia trichoclados*, 12- *Porolithon onkodes*, 13- *Pachygrapsus marmoratus*, 14- *Percnon gibbesi*, 15- *Cirratulidae* sp., 16- *Syllidae* sp., 17- *Amphipholis squamata*, 18- *Bittium incile*, 19- *Ophioderma longicauda*, 20- *Caprellidae* sp., 21- *Verticordia quadrata*, 22- *Alpheus macrocheles*, 23- *Dictyota humifusa*.