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Meiofaunal Dynamics in Oceanic Islands: Insights From Spatial Distribution, Substrate Influence and Connectivity

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ABSTRACT

There is an apparent contradiction between the sedentary lifestyle and direct development of meiofaunal organisms and their widely observed distribution. This study is situated within the theoretical framework of ecological connectivity, metacommunities, and the impact of substrate type, particularly in the unique context of oceanic islands, offering a crucial perspective to unravel the complexities of meiofaunal dispersal and connectivity. We here studied the spatial distribution of meiofauna on natural and artificial beaches of an oceanic island, that is, Gran Canaria (Canary Is., NE Atlantic Ocean). The results revealed higher abundance and richness of meiofauna on artificial substrates compared to natural ones, with nematodes, copepods, and annelids being the dominant groups. The meiofaunal community composition differed significantly between natural and artificial beaches, suggesting colonisation of artificial beaches by natural beach communities. Notably, certain species were exclusively found on artificial beaches. The study highlighted the importance of substrate type in influencing meiofaunal composition, with artificial beaches providing new ecological niches and resources for meiofauna. The dissimilarity between beaches was attributed to morphospecies exclusive to either artificial or natural substrates, emphasising the role of dispersal mechanisms. These findings contribute to understanding the metacommunity dynamics of meiofauna in oceanic islands and call for further research on dispersal potential and biogeography.

1 | Introduction

Movement of organisms is key to understand how nature is connected (Fang et al. 2018). A network with different ecological connectivity will emerge from movement (Tischendorf et al. 2000; Pelorosso et al. 2016; Bishop et al. 2017). These are influenced by environmental and ecological processes between ecosystems and within the same ecosystem (Fang et al. 2018). Species seek optimal conditions for survival, such as a place with abundant food sources, an area with suitable environmental conditions for reproduction or less competition among others (Gaines et al. 2007). Depending on its dispersal degree, its distribution range will change accordingly (Davidson, Crook, and

Barnes 2004; Srivastava and Kratina 2013). Once one species has been settled, it can generate populations in areas with connection among them (Wilson 1992).

The isolation of oceanic islands from continental areas serves as natural laboratories for the study of metacommunities (Leibold et al. 2004). This is because the ocean will act as a barrier to the organisms residing on them and they will be more isolated from the mainland depending on their degree of dispersal (Mehranvar and Jackson 2001). Meiofauna have a limited dispersal potential because they have a direct developmental cycle and, therefore, as they do not have a pelagic larval stage like zooplankton, they are not expected to

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have a large spatial distribution (Thomas and Lana 2011). Despite these limitations, many species were first described as widely distributed, which became known as the meiofaunal paradox (Giere 1993). However, over time, part of the paradox was resolved as molecular advances differentiate cryptic species (Andrade, Norenburg, and Solferini 2011; Leray and Knowlton 2015; Struck et al. 2018; Tulchinsky, Norenburg, and Turbeville 2012). Meiofauna have a limited dispersal capacity due to various factors, regardless the type of dispersal, that is, active or passive (Palmer 1988). Passive dispersal refers to the transportation of these organisms through drifting substrates (such as sea turtles, algae, previously eroded sand, etc.) within the water column (Ingels et al. 2020; Palmer 1988). When meiofauna respond to changes in biotic and abiotic factors by colonising various substrates, it is considered an instance of active dispersal (Boeckner, Sharma, and Proctor 2009).

The present study uses the origin of beaches on an oceanic island as a model to investigate potential differences in meiofaunal communities between artificial and natural beaches. The primary objective of this research is to assess and compare the meiofauna composition on four sandy beaches along the southwest coast of Gran Canaria (Canary Islands, NE Atlantic Ocean). Two of the sampled beaches are artificial (human-made), while the other two are of natural origin. Our hypothesis is that the meiofaunal composition in artificial beaches is similar to that in the surrounding natural beaches.

2 | Material and Methods

2.1 | Study Area and Sampling Design

The sampling area was located on the southwest coast of Gran Canaria. Samples were taken in early 2022 (January to March). The four beaches selected were Amadores, Mogán, Taurito and El Cura (Figure 1). Beaches were close to each other, and their length was similar, except for Amadores (ca. 500 m) (Table 1).

Our samples were collected in the intertidal zone, at the lowest tide level. The tidal height ranged from 1.2 m in January 2022 to 0.8 m in March 2022 and the swell was nil because the working area is sheltered from trade winds due to the relief of the island and consequently will favour the settlement of meiofauna (Miller and Sternberg 1988). Oceanographic conditions are similar among the studied beaches as they are all situated along the southern coast of the island, which faces the same hydrodynamics conditions. During the sampling months (January to March), the prevailing current along the coastline flows south-east. In this region, the average current velocity ranges between approximately 24 and 35 cm s⁻¹. The consistent orientation and current patterns ensure that the hydrodynamic forces affecting these beaches are relatively uniform (Port Oceanographic database, <https://www.puertos.es/es-es/oceanografia/Paginas/portus.aspx>).

Natural beaches are El Cura and Taurito whose sediment is mostly of volcanic origin and artificial beaches are Amadores and Mogán were of organic and calcareous origin (Morales 2018). The studied beaches were dominated by fine sands, with a grain size diameter ranging from 0.15 to 0.25 mm,

and exhibited low organic content (<0.9%), as reported by the Departamento de Costas (Ministerio para la Transición Ecológica y el Reto Demográfico 2000, <https://www.miteco.gob.es/es/costas/temas/proteccion-costa/ecocartografias/ecocartografia-laspalmas.html>).

Three sampling stations were established at each beach: two at the ends and one in the middle (Figure 2). From each station, six samples were collected, resulting in a total of 18 samples per beach and 72 samples for the entire study. All samples were collected for faunistic identification. Unfortunately, no replicates were collected for sediment variables such as grain size or organic matter content.

2.2 | Sampling Procedures

Samples were collected using PVC cores at a depth of 35 cm, a methodology that has previously proven successful in the intertidal zone of the study area (Riera, Núñez, and Brito 2012; Riera, Núñez, Brito, and Tuya 2012). The sediment was stored in zip bags where it was preserved in 70% ethanol. In the laboratory, the sediment was decanted through a 2-L graduated cylinder and then poured through a 63- μ m sieve, without separating macrofauna from meiofauna. This approach follows previous studies (e.g., Riera et al. 2011) due to the limited representation of the larger fraction in core sediment samples from the study region. Once the meiofauna was separated from the sediment, they were sorted into the 4 most abundant groups (Nematodes, copepods, annelids, and minor taxa) using a binocular stereo microscope.

Organisms were identified to the morphospecies level for the three main taxonomic groups (Nematodes, Copepods, and Annelids) using either an optical microscope or a stereo microscope. For nematode identification, specimens were initially fixed using a permanent preparation of jelly glycerine. Subsequently, nematode morphologies were further visualised and examined using an optical microscope. The remaining groups were identified to morphospecies using a binocular stereo microscope. Finally, they were identified using taxonomic guides (e.g., Platt, Warwick, and Furstenberg 1985) and scientific contributions close to our study area (e.g., Packmor 2013; Packmor and George 2018; Packmor and Riedl 2016; Riera et al. 2011; Riera, Núñez, Brito, and Tuya 2012). Once identified, the data were transferred to an Excel spreadsheet for further statistical analysis.

2.3 | Data Analysis

To visualise the abundance and richness of the organisms considering different factors, boxplots were used. A nonmetric multidimensional scaling (nMDS) analysis was employed to visualise the spatial dissimilarity or similarity between the studied communities in a two-dimensional space. Two separate nMDS analyses were conducted to compare meiofauna assemblages on different substrates and across different beaches. To further elucidate the observed differences in meiofaunal composition between artificial and natural beaches, as well as among the sampled beaches (Amadores, Mogán, Taurito,



FIGURE 1 | Location of the beaches sampled in the Southwest of Gran Canaria.

TABLE 1 | Type and size of sampled beaches in the Southwest of Gran Canaria (Morales 2018).

Beach	Substrate	Length (m)	Width (m)
Amadores	Artificial	490	30
El Cura	Natural	250	0–50
Mogán	Artificial	215	15–55
Taurito	Natural	220	0–60

Note: Beaches are categorised by substrate type (Artificial or Natural) and include length (m) and width (m) dimensions.

El Cura), a permutational multivariate analysis of variance (PERMANOVA) was conducted. For this analysis, data were not transformed. This analysis provided the F -value and associated probability ($p < 0.05$) to assess the significance of differences. Additionally, the similarity percentage (SIMPER) analysis was utilised to identify the percentage contribution of each morphospecies (or morphological group) to the Bray–Curtis dissimilarity between the different substrates (artificial and natural).

The analyses were carried out using RStudio, namely the *vegan*, *ggplot2*, *flextable* and *readxl* packages (Gohel and Skintzos 2022; Oksanen et al. 2022; Wickham 2016; Wickham and Bryan 2023).

3 | Results

A total of 16,787 individuals, belonging to 51 morphospecies were collected in this study. The proportion of the major groups was 48.11% nematodes, 39.04% copepods, 8.85% annelids and 4%

of the remaining taxa that comprised ostracods, isopods, kinorhynchans, acari, amphipods and tanaids. The most abundant species was the nematode *Oncholaimellus calvadosicus* with 10.86% (1368 individuals), followed by the copepod *Cyclopina* aff. *gracilis* with 8.82% (1111 ind.) and the oligochaete Tubificidae sp. with 3.6% (423 ind.).

Mogán was the richest beach (15.44 ± 4.13 taxa), with a high heterogeneity between samples ranging from 8 to 23 morphospecies (Figure 3A). However, the maximum richness was similar in the remaining beaches (16 morphospecies in El Cura and 12 in Amadores and Taurito). The minimum number of morphospecies was uneven (6 morphospecies in Amadores, 5 in Taurito and 3 in El Cura). Artificial beaches were significantly richer than natural counterparts ($F = 31.5050$, $p = 0.0001$) (Figure 3B, Tables 2 and 3).

In terms of the average abundance, higher densities were found on artificial substrates than on natural ones (Table 2). The comparison between beaches showed a greater number of individuals at Mogán beach (270.26 ± 117.79 ind.) than at Amadores (196.56 ± 62.44 ind.), Taurito (110.81 ± 55.26 ind.) and El Cura (122.17 ± 105.58 ind.). The meiofaunal abundance of natural beaches showed a significant variability than in artificial beaches (Figure 3B). However, this variability is mainly due to Mogán beach as the abundance between the 4 beaches is not significant (Table 3).

According to the two types of substrates, there was a great difference between the community composition, with a large disparity between artificial and natural substrates (Figure 4). There was an important difference in meiofauna assemblages between the artificial (Mogán and Amadores) and natural (El Cura and

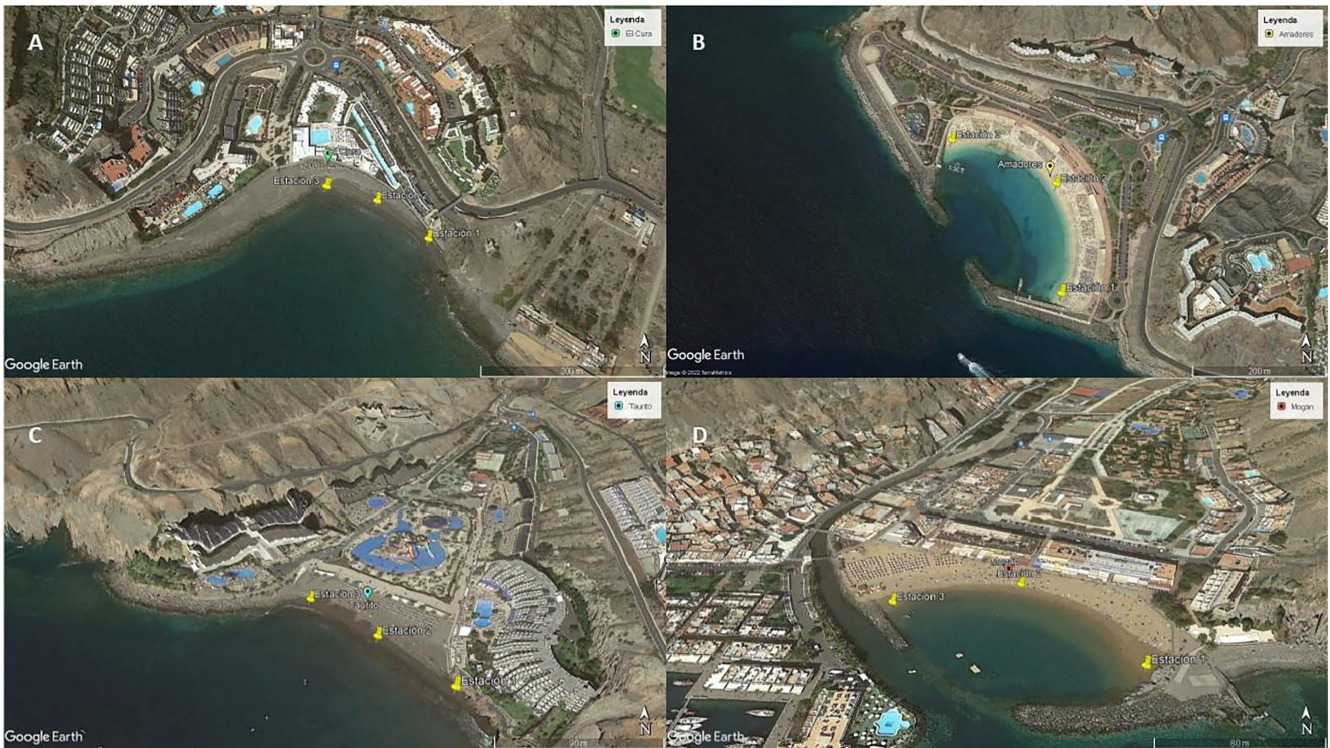


FIGURE 2 | The study beaches with their respective stations: (A) El Cura, (B) Amadores, (C) Taurito, (D) Mogán.

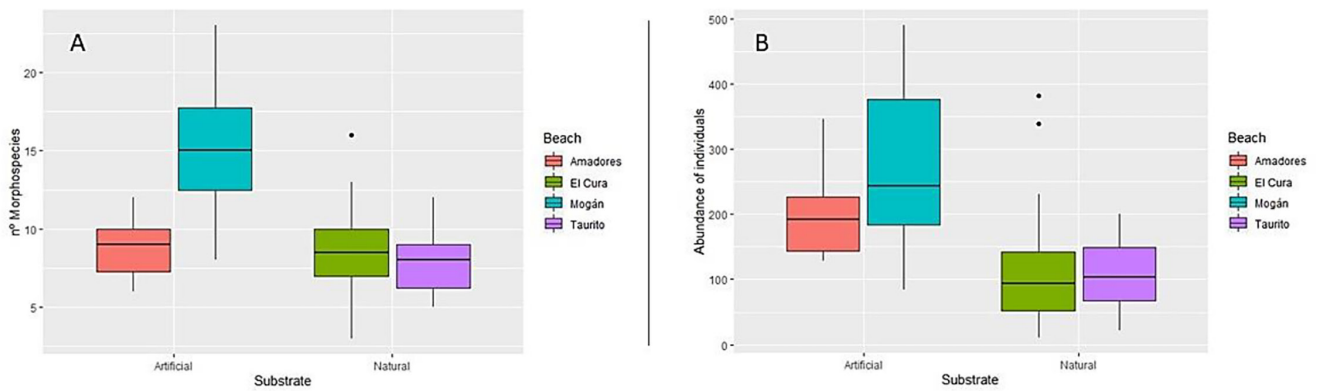


FIGURE 3 | (A) Number of meiofaunal morphospecies considering substrates and beaches. (B) Abundance of individuals considering substrates and beaches.

TABLE 2 | Richness of morphospecies and abundance of organisms at each study beach and substrate type, presented as mean with standard deviation (SD).

Beach	Substrate	Abundance (mean ± SD)	Species richness (mean ± SD)
Amadores	Artificial	196.56 ± 62.44	9.00 ± 1.94
El Cura	Natural	122.17 ± 105.58	8.72 ± 3.25
Mogán	Artificial	270.26 ± 117.79	15.44 ± 4.13
Taurito	Natural	110.81 ± 55.26	7.89 ± 1.78

Taurito) beaches as the dots ordered in space show a great disparity between substrates. In addition, between the artificial beaches (Amadores and Mogán) there was a great disparity between their communities. On the other hand, between the natural beaches (El Cura and Taurito) there was a small similarity in the composition of their meiofaunal communities (Figure 5).

Meiofauna composition showed highly significant differences between artificial and natural substrates ($F=31.5050, p=0.0001$). The studied beaches harboured different meiofauna composition, with significant differences among them ($F=24.9480, p=0.0001$). Meiofaunal community structure varied spatially among the studied beaches regardless the type of substrate (Table 4).

TABLE 3 | PERMANOVAs results of abundance and richness of meiofaunal community with the analysed factors.

	Factor	<i>F</i>	Pr (> <i>F</i>)
Abundance	Substrate	26.03	0.001
	Beach	1.62	0.19
Richness	Substrate	23.96	0.001
	Beach	13.98	0.001

Note: *p*-values <0.05 (bold) denote significant differences.

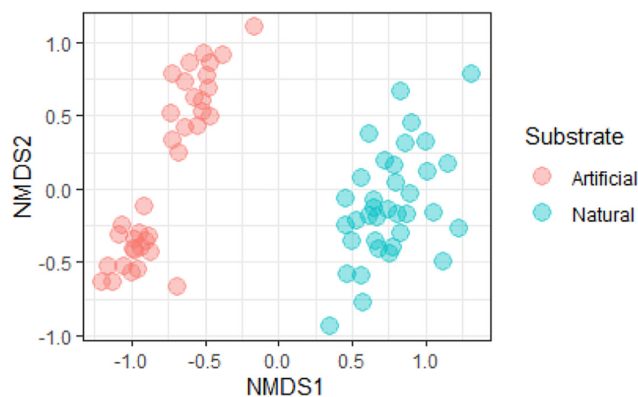


FIGURE 4 | nMDS showing sampling substrates of both beaches (artificial and natural). nMDS, nonmetric multidimensional scaling.

In the studied beaches, several copepod species were dominant, with five taxa from this group accounting for 50% of the dissimilarity observed in the samples (Table 5). Notably, all of these species were exclusively collected on artificial substrates, with the exception of the copepod *Grabroteson scheibeli*, which was solely found on natural substrates. However, the species that showed the greatest dissimilarity was the nematode *Oncholaimellus calvadosicus*. Nematodes were recorded in both substrates, some species were more abundant on natural than artificial ones, for example, the nematode *Enoplolaimus propinquus*, and other species showed the opposite pattern, for example, the nematode *Enoploides delamarei*, with higher abundances on artificial than on natural substrates. Regarding annelids, it was observed that the polychaete *Brania* aff. *arminii* is more frequent in artificial than in natural substrates.

4 | Discussion

The type of substrate (artificial or natural) was of pivotal importance for the meiofaunal composition, with differences in abundance of individuals and the number of species. We observed that the meiofauna abundance in the artificial beaches was higher than in adjacent natural beaches. A higher abundance in artificial beaches may be due to the emergence of new ecological niche for meiofauna (Atilla and Fleeger 2000). These niches generate new resource availability, both in terms of food and unoccupied space, facilitating subsequent colonisation (Ramli and Kassim 2016). The species richness showed the same trend though the artificial beach of Amadores showed similar species richness than the natural studied beaches. Species richness may be influenced by the ecological succession cycle, where pioneer

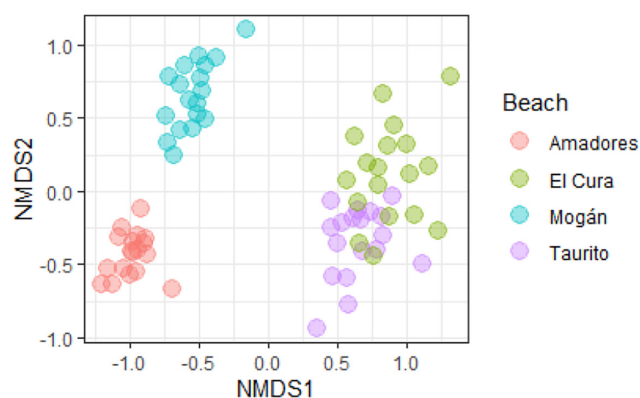


FIGURE 5 | nMDS showing the sampled beaches. nMDS, nonmetric multidimensional scaling.

TABLE 4 | PERMANOVA results for the distribution of the meiofaunal community with the analysed factors.

Factors	<i>F</i>	Pr (> <i>F</i>)
Substrate	31.5050	0.0001
Beach	24.9480	0.0001
Substrate (Beach)	24.9480	0.0001

Note: *F*-values and *p*-values (bold) indicating significant differences (*p* < 0.05) are presented.

species, for example, good swimmers like copepods, are more diverse before equilibrium is established in the community on the artificial substrate (Mirto and Danovaro 2004).

In terms of species composition, the dissimilarity between beaches was mainly explained by morphospecies that were collected exclusively in one substrate (artificial or natural). For example, most copepods, that is, *Cyclopina* aff. *gracilis*, *Canuella perplexa* and *Arenosetella germanica*, prioritise inhabiting artificial substrates. The copepods exhibit an active dispersal mechanism due to their great swimming ability, enabling them to pioneer in artificial substrates with favourable conditions compared to natural beaches, establishing a strong population (Hockin and Ollason 1981; Colangelo and Ceccherelli 1994). While on the other hand both annelids and nematodes inhabit natural and artificial substrates, that is, the nematodes *Oncholaimellus calvadosicus* and *Enoplolaimus propinquus* and the polychaete *Brania* aff. *arminii*. The presence of these two groups in both substrates is primarily attributed to their passive dispersal mechanisms (sediment transport) rather than an active one (Coull and Palmer 1984). If the dispersion were active, a higher prevalence would be expected in the artificial substrate due to greater availability of space and food, as observed with copepods.

A significant heterogeneity was observed between the two substrates types and among the artificial beaches, whilst natural ones showed higher levels of meiofaunal community similarity. These differences, as also reflected in the composition, could be due to potential cycles of ecological succession when meiofauna colonise an artificial substrate (Atilla, Wetzel, and Fleeger 2003). Another effect in these differences is the sediment sorting process, whether angular or eroded, results in the formation of diverse meiofaunal structures (Conrad 1974). It might also stem

TABLE 5 | Dissimilarity in the composition of morphospecies between natural and artificial substrates, and cumulative species abundance (cumsum & percentage) among the 10 most dominant species.

Morphospecies	Average.Artificial	Average.Natural	Cumsum	%
<i>Oncholaimellus calvadosicus</i> (Nematoda)	0.444	37.55	0.122	12.2
<i>Cyclopina</i> aff. <i>gracilis</i> (Copepoda)	30.865	0	0.238	23.8
<i>Canuella perplexa</i> (Copepoda)	22.170	0	0.313	31.3
<i>Arenosetella germanica</i> (Copepoda)	26.670	0	0.379	37.9
<i>Grabroteson scheibeli</i> (Copepoda)	0	23.95	0.436	43.6
<i>Enoplolaimus propinquus</i> (Nematoda)	1.590	12.14	0.474	47.4
<i>Tryphoema irmgardae</i> (Copepoda)	9.146	0	0.508	50.8
<i>Brania</i> aff. <i>armirii</i> (Annelida)	7.774	0.17	0.540	54
<i>Enoploides delamarei</i> (Nematoda)	8.316	2.33	0.572	57.2
<i>Calytronema</i> sp. (Nematoda)	4.368	9.47	0.603	60.3

from various events causing differences among communities, such as algae or sediment drifting caused by a storm, anthropogenic agent like floating materials or ballast sand brought in by ships or snow marine (Hicks 1988a, 1988b; Shanks and Edmonson 1990). Thus, due to the unknown origins of specific morphospecies within the artificial substrate, the possibility of the meiofauna paradox cannot be dismissed.

The study presents important points regarding the distribution and composition of meiofauna on natural and artificial beaches of Gran Canaria. However, several limitations may have influenced the results and their interpretation. Firstly, the lack of sediment samples, such as granulometry and organic matter content, restricts a comprehensive understanding of the sedimentary environment where meiofauna develop, impacting their colonisation and abundance. Secondly, conducting the study on only four beaches may not represent the diversity of coastal habitats in the region. Lastly, the absence of temporal replication prevents the assessment of seasonal or interannual variations in meiofaunal communities, which could offer a more complete understanding of their dynamics and adaptability to environmental changes. Addressing these limitations in future studies will provide a more robust and detailed understanding of meiofauna ecology on oceanic islands.

Future research should also explore the meiofaunal paradox, focusing on dispersal, settlement, and postsettlement dynamics to improve understanding of cryptic species differences and community connectivity across spatial scales (Cerca, Purschke, and Struck 2018). This will help identify geographic variations and factors affecting meiofauna, particularly in response to environmental changes like global warming (Palmer 1988; Giere 2019).

5 | Conclusions

Current findings revealed differences in meiofauna between the studied substrates, with higher richness and individual abundance observed on artificial substrates. Evidence of colonisation from natural to artificial beaches was apparent, yet distinct morphospecies exclusive to artificial substrates challenge

our understanding. To substantiate these observations, further investigations are warranted, encompassing both temporal and spatial dimensions. Comparative studies involving islands from the Macaronesian region or other geographic areas such as, Hawaii, Iceland, Faroe Islands, among others, would enhance our comprehension. Moreover, exploring species-level analyses, rather than morphospecies, is essential to address the challenge posed by cryptic species. Understanding meiofauna dynamics contributes valuable insights into global connectivity, underscoring the need for comprehensive studies beyond the current scope.

Author Contributions

A.T.-M. and R.R. conceived and designed research. A.T.-M. conducted taxonomic identification and statistical analysis. R.R. supervised identification and analysis. A.T.-M. wrote the first version of the manuscript. R.R. revise the manuscript. Both authors read and approved the manuscript.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the first author, A.T.-M., upon reasonable request.

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