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Research article

The swash zone selects functionally specialized assemblages of beach interstitial meiofauna (Platyhelminthes, Proseriata)

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Life is not a beach for those animals that survive in the rough ecological conditions found in marine sandy beaches – and yet, microscopic animals thrive on them. We explore the drivers for meiofaunal diversity in beaches by analysing taxonomic and functional patterns of 348 flatworm communities across 116 reflective beaches in the western Mediterranean, totalling 152 species (61.2% new to science). First, we confirm that species richness does not differ between beach hydrodynamic levels (swash, shoaling and surf) but rather depends on the characteristics of each beach. Second, we demonstrate that species composition across those levels depends on the species traits, in addition to geographical and abiotic factors. Third, we highlight that the species functional space has a lower richness than expected and a lower redundancy in the wave-exposed swash level compared to the shoaling and subtidal levels, suggesting a trait-based ecological filtering. Finally, we show that those differences depend on the higher frequency of hydrodynamics-related traits in the species of the swash level. Our results suggest that the rough hydrodynamic conditions in the swash level favour a unique combination of species traits, which might be linked to ecological speciation in flatworms but also in other interstitial animals.

Keywords: biodiversity, endemism, functional diversity, habitat filtering, Platyhelminthes, Proseriata, soft-bodied meiofauna

Introduction

Life is not a beach for those animals that survive in the rough ecological conditions found in marine sandy beaches. Early beach ecologists categorized beaches amongst the harshest aquatic ecosystems on Earth (McLachlan et al. 1993), and even dubbed beaches as ‘marine deserts’ of sand and salt water (McLachlan 1983). Beaches, as ecotones between the ocean and the land, indeed represent steep environmental gradients largely defined by exposure to tides and waves (Brown and McLachlan 2010, Brazeiro 2001). Temporally dynamic changes of waves and level of exposure on the one hand,



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and beach morphology on the other hand, affect each other, driving the morphodynamic evolution of a beach over cycles that might extend for long temporal scales, ultimately influenced by changes in regional climate, sea level, tidal regime and long-term geological processes (McLachlan et al. 2018). Beach morphodynamic stages range from dissipative (waves break far from the coast, favouring progressive profiles and flatter slopes) to reflective (waves directly reach the beach front producing short and steep slopes) (Short and Wright 1983, Short 1996). Because energy is released progressively on dissipative beaches, environmental conditions are more benign in them, and become harsher as the reflective condition increases (McLachlan et al. 1993, 1995). As a result, the number of species, as well as density, abundance, and biomass of fauna, increases from reflective beaches to dissipative beaches (McLachlan et al. 2018). In addition, within each beach, the number of species is known to be lower in the wave-incidence zone (McLachlan et al. 1981, 1993, 1996, McLachlan 1990, 1996, Jaramillo et al. 1995), with a pattern that seems to be robust at global scale for large, macrofauna species (McLachlan and Dorvlo 2005, Defeo and McLachlan 2005). Such a pattern is considered to arise from the congruent but independent responses of different species living on the beach to the harsh physical environmental conditions of the wave-incidence zone of beaches (Noy-Meir 1979, McLachlan 1990).

Yet, sandy beaches might look deserted at the first glance because most of their biodiversity is represented by small meiobenthic organisms, which take advantage of the habitat available in the small spaces amongst the sand grains (McLachlan and Defeo 2017). Meiofauna, defined as a heterogeneous group of small animals passing through a sieve of 0.5 mm mesh (Giere 2009), is a crucial component of beach ecosystems, not only in terms of number of species and abundances, but also because of its role in carbon cycling, sediment transportation, and interstitial water circulation (Schratzberger and Ingels 2018). Therefore, in contrast to their minute size, the importance of meiofaunal organisms is larger than their size would suggest, as meiofauna is involved in many processes directly linked to the ecosystem services that beaches provide to human societies (Harris and Defeo 2022), mostly by shaping biogeochemical processes (Bonaglia et al. 2014, 2020, Bonaglia and Nascimento 2023). Understanding the responses of meiofauna to different environmental stressors is then crucial not only from a theoretical perspective, but also to design strategies to preserve those services upon local and global anthropogenic perturbations (Defeo et al. 2021). And here things get interesting, because in contrast to macrofauna, meiofaunal organisms exhibit a wider range of responses to beach environmental parameters (Moens et al. 2013, Venekey et al. 2014, Maria et al. 2018), with some species even preferring areas of strong hydrodynamic disturbance. Counterintuitively, meiofauna, in contrast to macrofauna, is generally more diverse and abundant in reflective than in dissipative beaches (Gheskiere et al. 2005, McLachlan et al. 2018). In reflective beaches, there are even species that prefer the hydrodynamic turmoil of the reflective

wave-incidence zone than deeper and far less agitated subtidal areas (Di Domenico et al. 2009, 2013). Problematically, incongruent species-specific responses across many meiofaunal groups may hamper any attempt to identify changes in taxonomic diversity patterns across beaches or beach levels, thereby masking the overall effect of stressors on beach meiofaunal communities. This may occur even if, for example, hydrodynamical gradients might exert ecological filtering on meiofauna similarly to what is known to occur on macrofaunal species (Moreno et al. 2006, Albuquerque et al. 2007, Sevastou et al. 2011). These difficulties in understanding meiofaunal responses to stress are increased by the lack of trained taxonomists as well as the large number of undescribed species and the conserved morphology that many meiofaunal lineages exhibit (Jörger and Schrödl 2013, Fontaneto et al. 2015). Altogether, the role of environmental stressors on beach communities might be better characterized using functional metrics, which attempt to identify and quantify the traits that explain each species' differential response across levels, in addition to and/or regardless of the species identity (Martínez et al. 2021a).

A quick browse over the pictures and drawings in any specialized identification guide (Schmidt-Rhaesa 2022) immediately highlights that taxonomical diversity metrics might only capture a small part of the diversity of meiofauna. Meiofaunal species, far from representing a bunch of small worm-like creatures, exhibit a remarkable diversity of shapes, sensory structures, reproductive organs, and swimming capabilities, even within a single family or genus. Descriptions of different species-specific adaptations to interstitial lifestyle in meiofauna populate the specialized zoological literature (Jörger et al. 2009, Polte and Schmidt-Rhaesa 2011, Martínez et al. 2013, 2015, Herranz et al. 2019, 2021) sometimes experimentally proved in model species (Boaden 1963, 1968, Armonies 1988). What remains to be quantified is how the frequency of different traits might affect the ecological response of meiofaunal communities across beach hydrodynamic gradients. This is challenging, not only because very different structures might perform the same function across meiofaunal phyla, but also because many meiofaunal groups need to be studied alive, making any multi-taxon study across a large geographical area very complicated (Leasi et al. 2018, Martínez et al. 2020). These problems can be alleviated by targeting a model group of organisms with enough taxonomic and functional diversity, focusing on a habitat that maximizes hydrodynamic gradient but reduces other confounding environmental factors.

Our goal here is to quantify the response of meiofauna to beach hydrodynamic gradients, using communities of proseriate flatworms in 116 western Mediterranean reflective beaches. Proseriate flatworms exhibit a remarkable diversity in beaches in terms of number of species as well as morphological and behavioural characters, some of which have been proposed as functionally important to cope with turbulence and hydrological stress (Reise 1988). Even before the first studies on beach morphodynamics (Wright and Short 1982), the upper, swash level of reflective beaches was known as the

‘Otoplanen-zone’, due to the abundance of proseriates, and particularly *Otoplana* species, which dominates the swash level of Atlantic–Mediterranean beaches (Gerlach 1953, Ax 1956). We here focused on reflective beaches, so we can establish a comparable zonation across all sampled beaches, avoiding the confounding factors introduced by different hydrodynamic stages due to reefs, barriers, or progressive slopes. By selecting the western Mediterranean Sea, we not only delineate a common pool of species for the study, but we also avoid the confounding effect introduced by ample tidal fluctuations of beaches on open oceans. Our overall hypothesis is that species responses to hydrodynamics depend on the presence of certain traits, with the main rationale included in the four alternative scenarios, depending on whether the environmental condition of the swash zone affects species richness or not; whereas it selects for specific combination of species traits (Fig. 1). In order to select amongst these four scenarios, we first investigate the drivers for species richness, specifically testing whether the number of species differs across beach levels. Then, we explore the drivers for species composition, focusing on whether species composition across beach levels depends on species traits. Third, we compare the properties of the functional space of each beach level, under the assumption that the swash zone exhibits a lower functional richness

and higher species functional contributions than the shoaling and subtidal levels. Finally, we aim to explain these overall differences by the presence of a higher frequency of traits related to hydrodynamics in the species in the swash level.

Material and methods

Data collection

We sampled 116 reflective beaches in the western Mediterranean marine province, across Spain (22 beaches, including Mallorca), France (25 beaches, including Corsica), Italy (63 beaches, including Sardinia, Sicily and Lampedusa), and Tunisia (6 beaches). All sampled beaches were microtidal, wave dominated, and exhibit a reflective morphodynamics stage. In each beach, we collected three samples at three levels corresponding to the wave-breaking zone, the shoaling, and the subtidal level. The wave-breaking zone in reflective beaches corresponds to the swash + surging breaking zone (thereafter referred to as swash level, for simplicity) (McLachlan and Defeo 2017) (Supporting information). Total meiofauna were extracted from each sample using the magnesium chloride decantation methods and a minimum

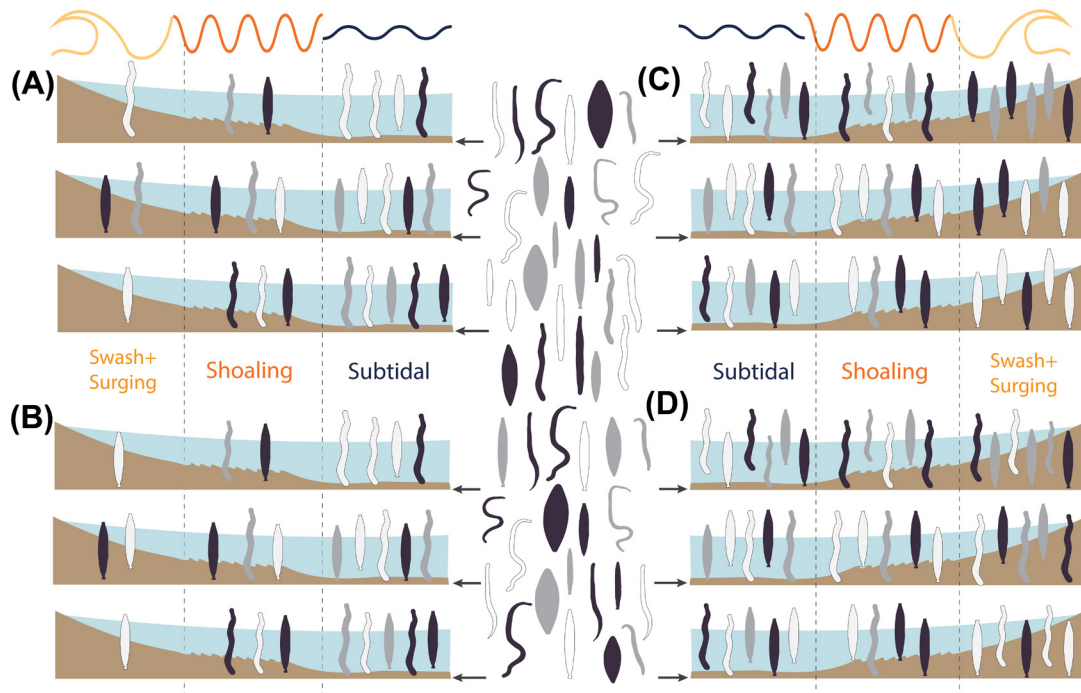


Figure 1. Summary of the four scenarios tested in this study, which differ on how the colonization of the swash zone affects taxonomic and functional diversity. (A) In scenario 1, the conditions of the swash level select for a subset of the species that live in the shoaling and subtidal levels, with differences in species composition across beach levels explained by differences in species richness. (B) In scenario 2, this subset of species found in the swash level is not random, but depends on the presence of specific traits. (C) In scenario 3, if species respond differently to the conditions in the swash level according to their traits, differences in diversity across beach levels will be mostly explained by species functional traits, for example with a higher proportion of adhesive and burrowing species found in the swash level. (D) Scenario 4 is neutral and neither functional nor taxonomic diversity is affected by the conditions in the swash zone. The silhouettes in the central part represent the potential species pool; the silhouettes in each level represent their actual occurrence, with repeated silhouettes in one level representing different species within the same genus.

mesh size of 0.0063 mm. From each sample, 100–150 proseriates were then sorted into different genera under the stereomicroscope and identified to species using a compound microscope. Animals belonging to undescribed species were assigned to the same taxonomic unit using consistent codes. For each individual, we examined 14 morphological traits for each species, focusing on body size and shape, ability to withstand turbulence by adhering to or digging into the sediments, trophic specialization, and the reproductive structures (Fig. 2A, Supporting information).

We ecologically characterized each sample measuring its granulometry, and each beach by measuring its length as well as collecting a set of bioclimatic and oceanographic variables from open-access databases (Supporting information).

Statistical analyses

See further details for each section in the Supporting information.

Drivers of species taxonomic richness across beaches and levels

We tested whether number of species was significantly different across beach levels using generalized least squares models (GLS), which allow us to account for the potential effect of various spatial autocorrelation structures, using the *gls* function in the package ‘nlme’ ver. 3.1-153 (Pinheiro and Bates 2023, Supporting information). In each model, we included the number of species at each sample as the response variable and beach level, mean grain size, beach length, as well as all bioclimatic and oceanographic variables as predictors, in addition to a spatial structure. Model assumptions and model fit were assessed for each model with the R package

‘performance’ ver. 0.7.3 (Lüdecke et al. 2021), testing for distribution of residuals, homoscedasticity, multicollinearity and influential observations (Zuur et al. 2010). For the models that included a set of predictors with both categorical and continuous variables, which are not easily summarised as output of GLS, we used type II ANOVA tables using the function *Anova* in the R package ‘car’ ver. 3.0.10 (Fox and Weisberg 2019).

Drivers of species composition across beaches and levels

We first partitioned the variance in species composition due to geographical distances and to the environmental differences included in the previous models as predictors (Borcard et al. 1992, Peres-Neto et al. 2006), using the R package ‘ade4’ ver. 1.7-19 (Dray and Dufour 2007, Bougeard and Dray 2018). Second, we investigated the relationship between species community composition and geographical distances using Mantel test for each separate beach level. Third, we quantified the effect of environmental variables on the community of proseriates using the function *manyglm* in the R package ‘mvabund’ ver. 4.2.1 (Wang et al. 2022). Finally, to specifically address this hypothesis, we used an environment-by-trait fourth-corner interaction by analyses of deviance using the function *anova.traitglm* included in the R package ‘mvabund’. Fourth-corner analyses fit a predictive model for species occurrence as a function of the environmental variables and the species traits. Since most of the functional traits were categorical, we applied a Gower dissimilarity transformation to the complete trait matrix and extracted orthogonal morphological axes through principal component analyses, which we then used to fit the model (Mammola and Cardoso 2020). The selected axes accounted for 79% of the cumulative variance.

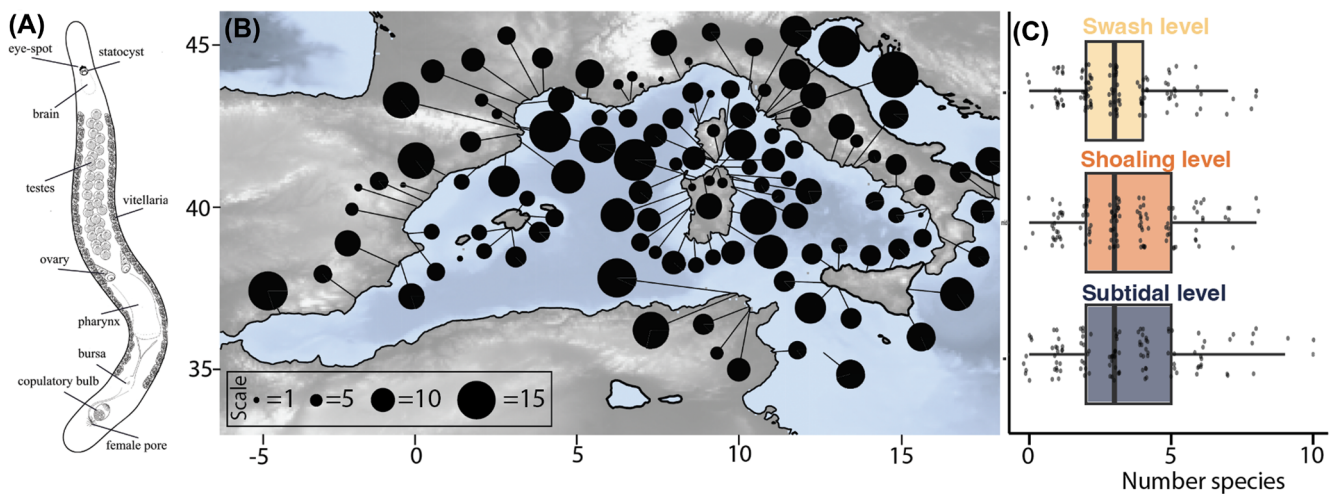


Figure 2. Overview of the data and summary of Hypothesis 1 on differences in species richness across beach levels. (A) Overview of a Monocelididae, as a representation of a typical proseriate flatworm. The main internal and external structures that are considered in the analyses are marked. (B) Distribution of the sampled beaches in the western Mediterranean, with latitude and longitude reported as WGS84 reference coordinates. The size of the circle is proportional to the total number of species found in each beach (see box). (C) Box plot showing the distribution of the number of species in each sample, divided by beach level. Each value is jittered vertically (and to a minimum extent also horizontally) to allow a visualization of sample size. The non-independence of the data is accounted for in the model, and the plot with the identity of the beach for each dot is shown in the Supporting information.

Properties of the functional space significantly across beach levels

We represented the functional space of each beach level using n -dimensional hypervolumes (Blonder et al. 2014, Blonder and Harris 2018), calculated with the function *kernel.build* in the R package 'BAT' (Cardoso et al. 2015, 2022). We used a Gaussian approximation with a default bandwidth, and we weighted each species according to the number of times it has been recorded in each level ('abund' option = TRUE) (see the Supporting information for further details).

As a proxy of the number of functions performed by the species in a given level, we extracted the functional richness of the hypervolume of each beach level using the function *kernel.alpha* (Mammola and Cardoso 2020). We then compared the functional richness observed at each beach level with the average of the functional richness obtained from 1000 combinations of the same number of species randomly sampled from the complete species pool via null modelling. We tested the significance of the differences using standard size effects as implemented by the function *ses* in the R package 'BAT'.

In addition, we calculated the functional contribution of each species to the functional space of each level using the function *kernel.contribution* in 'BAT' (Mammola and Cardoso 2020). Functional contribution was expressed as the difference between the functional richness with and without each of the species in the community (option 'one-out'). Species with high functional contribution can be interpreted as functionally unique, whereas species exhibiting small contribution are more likely functionally redundant. We plotted the distribution of the species contribution in each level with a density plot using the R package 'ggplot2' ver. 3.3.6 (Wickham 2016).

Difference in frequency of traits across beach levels

We evaluated the differences in frequency of five traits related and one trait unrelated to hydrodynamics across beach levels. For each trait, we fitted a generalized linear mixed effect model (GLMM) using the proportion of species that present each trait at each sample as a response variable, the beach level as predictor, and the identity of each beach as a random effect. We selected a binomial(logit) family model to account for proportion data, using the function *cbind*. The GLMM were run with the function *glmer* in the R package 'stats' of the R core team. We tested significance of models for pairwise differences across habitats by comparing marginal means between the three beach levels using a Tukey HSD test as implemented in the functions *glbt* in the R package 'multcomp' ver. 1.8.1-1 (Hothorn et al. 2008). The results were then represented using box plots drawn using the R package 'ggplot2', and type II ANOVA tables from the R package 'car' to produce output tables from GLMM with both categorical and continuous predictors.

A reproducibility checklist for the study (Palacio et al. 2022) including detailed information on sample size, number of traits, and statistical procedures is available in the Supporting information.

Results

We found 152 species, 93 of which still undescribed (61.2%), in 348 samples collected across 116 beaches in the western Mediterranean (Fig. 2B, GBIF dataset: <https://doi.org/10.15468/64xtt9>, Curini-Galletti et al. 2023). Most of the species exhibited very limited distribution ranges, with 58 species limited to a single beach, 22 to two and 12 to three beaches. In contrast, only three species were found in more than 50 beaches: *Coelogynepora gynocotylo* (65 beaches), *Otoplana bosporana* (63 beaches), *Postbursoplana fibulata* (56 beaches). Species richness per sample ranged up to 10 species (totalling up to 17 species per beach) although 59.8% of the samples ranged between 1 and 3 co-occurring species (Supporting information).

Taxonomic richness did not differ significantly across beach levels (Fig. 2C), but was significantly explained by environmental variables: negatively affected by mean grain size, having fewer species with coarser grain size, and marginally affected by eastward horizontal surface velocity, having more species with stronger winds (Table 1). Considering each beach level separately (Supporting information), species richness in the swash level was significantly and negatively affected by northward horizontal surface velocity and precipitation of the coldest quarter; none of the analysed environmental variables affected richness in the shoaling level; richness in the subtidal level was negatively affected by mean grain size and positively by eastward horizontal velocity.

Species traits calculated after the Gower distance matrix were significantly affected by the beach level, as well as by mean grain size (Fig. 3A). The effects of the beach level on trait dissimilarity had different direction in the swash than in the subtidal level. Despite the fact that we detected significant effects of environmental variables, most of the variance in the community matrix remained unexplained (variance partitioning analyses, residuals = 87%), with geography, environment and their interactions explaining only 4, 7 and 2% of the variance respectively (Fig. 3B). Geographical distances were weakly correlated to beta diversity (Mantel test: $r = 0.095$, $p = 0.001$); the correlation was stronger in the shoaling and subtidal levels than in the swash levels, where it was not significant (Fig. 3C–E). Differences in community composition of proseriates were explained by beach level, beach identity, and mean grain size, but not eastward horizontal surface velocity (Table 2). The effect of these variables on each species is summarized in the Supporting information. The species that was most strongly affected by beach level was *Otoplana bosporana* (LRT = 111.6, p -adjusted = 0.001), occurring significantly more often in the swash than in the other two levels.

Properties of the functional space differed across beach levels. Functional richness was significantly lower than the null modelling only in the swash level (observed = 0.040, estimated = 0.057, SES = -2.8, $p = 0.0049$) (Fig. 4) (H3); but not in shoaling (observed = 0.043, estimated = 0.059, SES = -1.6, $p = 0.1002$) and subtidal levels (observed = 0.047, estimated = 0.065, SES = -1.8, $p = 0.0778$) (Fig. 4A–C).

Table 1. Output of the spatially explicit generalised least square (GLS) model with exponential correlation structure to test the effects of the environmental variables on the number of species of Proseriata. The output of a type II ANOVA is reported for the GLS to include both categorical and continuous predictors. Abbreviations: χ^2 =chi-square values, df=degrees of freedom, SE=standard error. p-values and estimates for significant predictors are marked in bold.

	Value	SE	t-value	df	χ^2	p-value
(Intercept)	3.2281	0.1827	17.6728	–	–	0
Beach level	–	–	–	2	0.8723	0.6465
Mean grain size	–0.3486	0.1186	–2.9405	1	7.3340	0.0068
Beach length	–0.1639	0.1312	–1.2496	1	1.5614	0.2115
Salinity	0.0684	0.1735	0.3942	1	0.1554	0.6935
Water temperature	0.1904	0.2348	0.8109	1	0.6576	0.4174
Primary production	–0.0151	0.2144	–0.0703	1	0.0049	0.9440
Nitrate concentration	0.2167	0.2527	0.8577	1	0.7356	0.3911
Northward horizontal surface velocity	–0.3030	0.1682	–1.8006	1	3.2422	0.0718
Eastward horizontal surface velocity	0.3717	0.1720	2.1614	1	4.6716	0.0307
Air temperature	–0.0741	0.2264	–0.3273	1	0.1071	0.7434
Precipitation coldest quarter	–0.1503	0.1611	–0.9328	1	0.8700	0.3509
Air temperature range	0.1984	0.2070	0.9582	1	0.9181	0.3380
Air temperature seasonality	0.0683	0.2007	0.3402	1	0.1158	0.7337

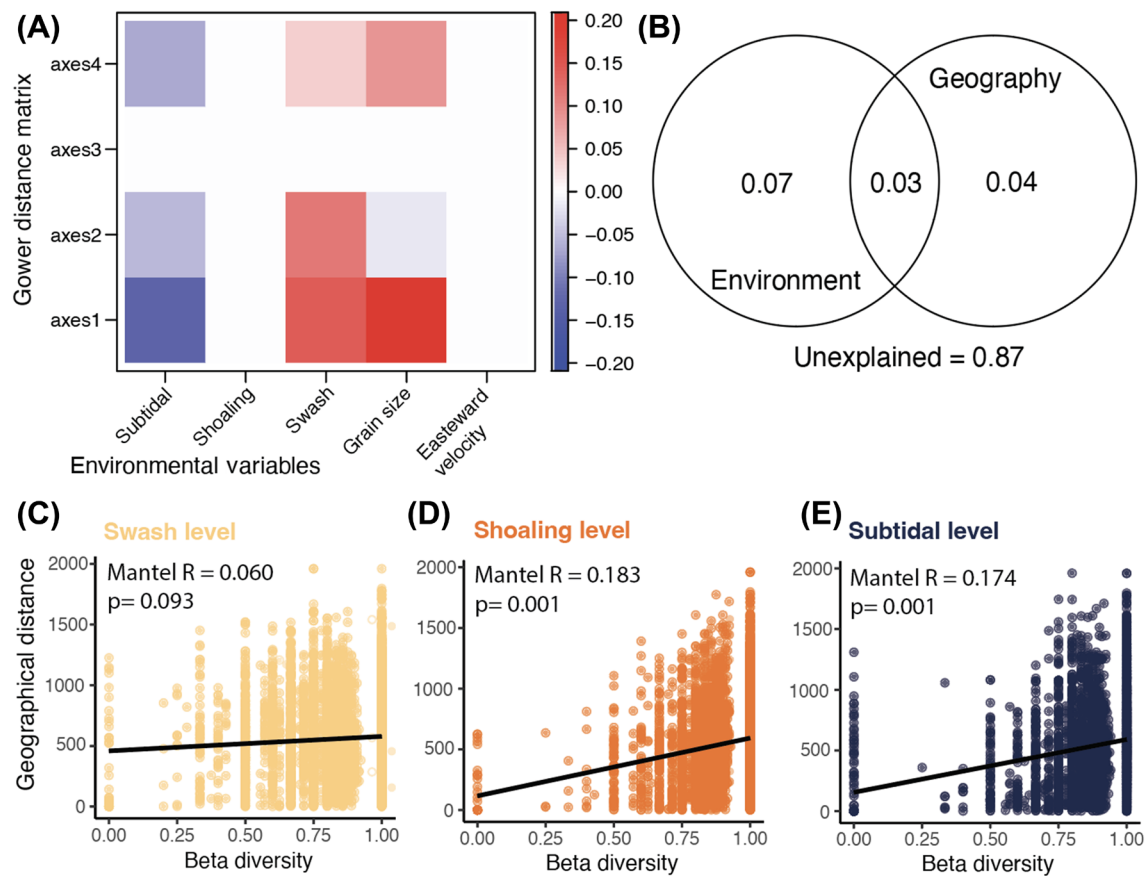


Figure 3. Summary of the results regarding hypothesis 2 on differences in species traits. (A) Representation of the results of the fourth-corner analysis showing the significant relationship between functional traits (represented as the axis of the Gower matrix) and the selected abiotic environmental variables representing beach level (subtidal, shoaling, and swash) and the only two variables affecting species richness. (B) Graphical representation of the variance partitioning analysis, showing the amount of variance explained uniquely by environmental and geographical differences and by their combination, in addition to the unexplained residual variance. (C–E) Relationship between geographical distances and beta diversity calculated for each pair of stations in each beach level. R and p-values shown are from the Mantel test analyses.

Table 2. Model output of the multi-generalized linear models ('mvabund') on the community matrix to test the effects of the environmental variables on species composition of Proseriata. df=degrees of freedom. p-values and estimates for significant predictors are marked in bold.

	Residual df	df difference	Deviance	p-value
(Intercept)	347			
Beach level	345	2	999	0.001
Beach	228	117	4672	0.001
Mean grain size	227	1	107	0.013
Eastward horizontal surface velocity	227	1	0	0.364

Species contributions were mostly negative, but higher in the swash level (contribution average = -12.20 ± 0.23), followed by the shoaling (contribution average = -9.29 ± 0.17) and the subtidal (contribution average = -4.75 ± 0.12) (Fig. 4D).

Finally, our analyses confirmed that those differences were due to the different proportion of traits adapted to hydrodynamics in each beach levels. Specifically, the proportion of species with cephalic sensory area (GLMM: LR $\chi^2 = 16.5$, $p = 0.0003$), brain capsule (LR $\chi^2 = 50.3$, $p < 0.0001$), ventral sole (LR $\chi^2 = 30.5$, $p < 0.0001$), and flat body (LR $\chi^2 = 52.5$, $p < 0.0001$), all exhibit higher proportions in the swash level (Fig. 5, Supporting information). The proportion of species with well-developed adhesive glands (LR $\chi^2 = 20.9$, $p < 0.0001$) was higher in the shoaling, whereas no differences were found regarding species with eversible pharynx (LR $\chi^2 = 2.5$, $p = 0.2873$) (Fig. 5).

Discussion

Our main results are straightforward: the community of proseriates in the swash levels was different from those in the shoaling and subtidal levels mostly due to the presence of certain functional traits related to adaptation to hydrodynamics. This was expected given that the zoological literature highlighted the presence of highly specialized interstitial species in swash levels of reflective beaches, bearing a unique combination of traits, also in other groups of animals (Jörger et al. 2009, Worsaae et al. 2012, Herranz et al. 2019, 2021, Martínez et al. 2021a, b). However, we here support those observations by showing that the proseriate communities in the swash level bear a narrower and non-random combination of traits, compared to those in the shoaling and the subtidal levels. We also quantified how those specialized species shape the taxonomic and functional diversity patterns across beach levels using an extensive dataset. Overall, species taxonomic richness was not affected by differences across beach levels but traits significantly differed across beach levels, leading to differences in the functional richness across levels, explained by differences in the frequency of traits related to hydrodynamics. These results, together, may provide insights into the underlying process related to environmental filtering, at least in beach proseriates.

The differences in the overall functional space across beach levels depended on the higher frequency of traits that were previously described as adaptations against hydrodynamic stress, rather than on the presence of fewer species in the swash level. This contradicts the view of sandy beaches, and particularly the swash level, as 'marine deserts' in which few animal species can survive (McLachlan 1983) and, instead, suggests that beach habitats might act as a potential cradle for evolutionary innovation. Based on our results, we hypothesized that selection of specialized adaptive features in the swash level, along with the limited dispersal capability of many interstitial species, might have even favoured processes of ecological speciation and the radiation of certain interstitial lineages. This hypothesis warrants further exploration using appropriated phylogenetic comparative methods (Nosil 2012), given that it is in contrast with previous phylogenetic studies on proseriates. Indeed, proseriate species adapted to the conditions in the swash level belong to different families (Scarpa et al. 2017, Curini-Galletti 2023).

Patterns of taxonomic diversity: many new species but no differences in species richness across beach levels

We did not find significant differences in the number of species across beach levels. The number of species was significantly affected by environmental variables shaping beach as habitats: granulometry and eastward superficial velocity. Granulometry, in addition to determining available space among the sand grains for meiofaunal species, is a proxy for beach exposure, since finer sediments tend to be washed away by strong waves (Remmache et al. 2020). Indeed, granulometry strictly influences the morphodynamic stage of a beach, with its dimensionless fall velocity being correlated to mean grain size in our dataset (Pearson $r = 0.73$). Another significant predictor of species richness of western Mediterranean proseriates, eastward superficial velocity, provides a complementary support for the idea that different types of beaches may host different numbers of species: beaches with coarse or very coarse grain size and stronger winds hosted more species in our dataset.

When looking at other environmental drivers of the differences in species richness separately for each level, the number of species in the swash level was negatively affected by precipitation (Supporting information). This is evidence that richness in marine meiofauna might be negatively affected by freshwater discharge in the upper layer of the beach through precipitation: it makes sense to expect a negative effect of freshwater on a group of marine organisms.

One potential caveat to our estimates of richness can be found in the fact that our species identities were entirely based on morphology. Morphological identifications tend to underestimate the number of meiofaunal species in many groups, given that many meiofaunal lineages present conserved, simplified morphologies with few morphological characters available for species identification (Tang et al. 2012, Jörger and Schrödl 2013). This is somehow different in

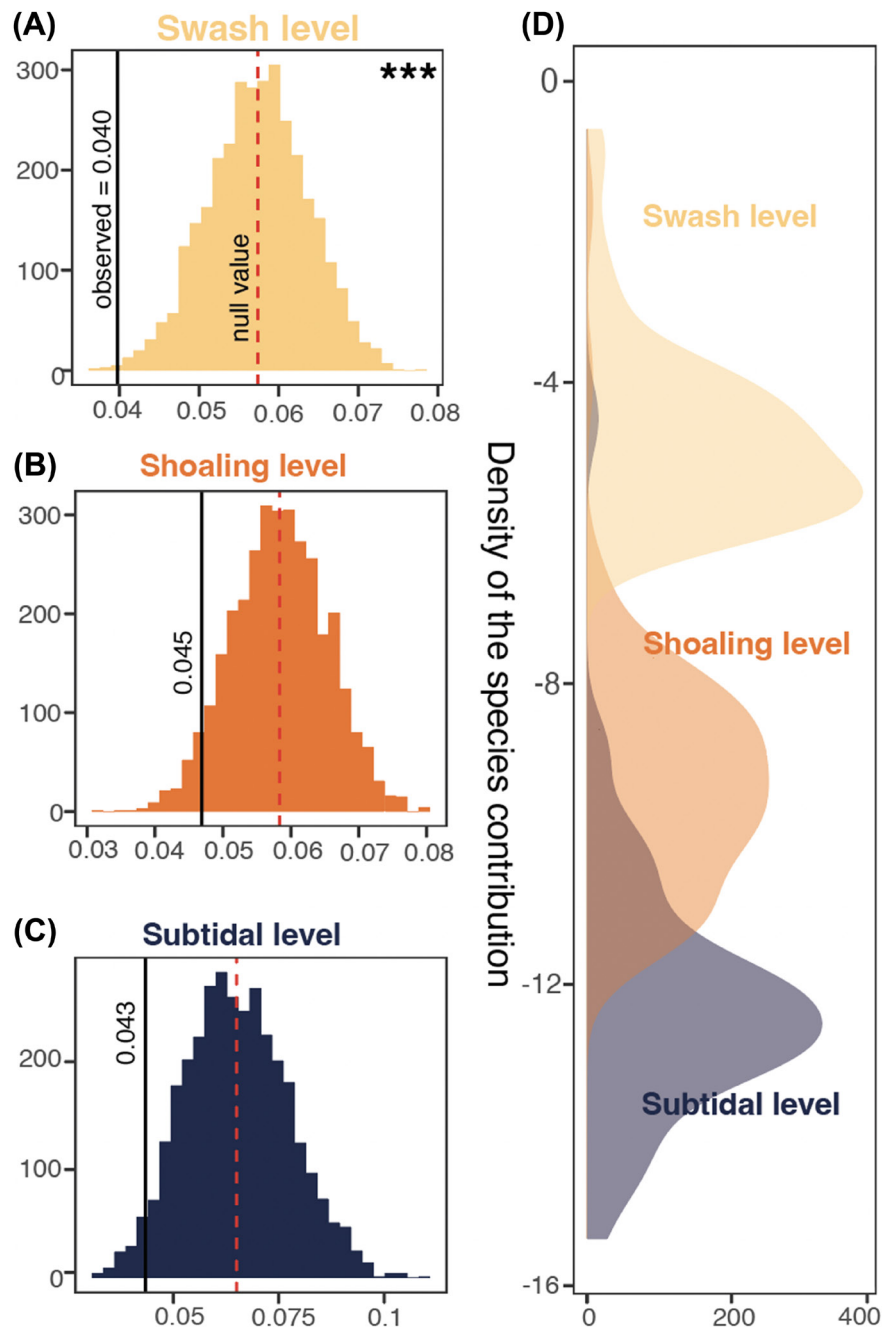


Figure 4. Summary of the results regarding Hypothesis 3 on functional properties. (A–C) Histograms of the distribution of the expected functional richness values for each beach level. The expected average values are shown with a dashed red line. The observed values are shown with a solid, black line. Observed values being significantly different from the expected ones according to the standard size effect test are marked with asterisks (***: $p < 0.001$). (D) Distribution of the species contribution to the overall functional space in each level.

Proseriata, given that the species of the group have complex reproductive structures with sclerotized spicules that provide very useful morphological characters for species identification (Curini-Galletti et al. 2023). Indeed, we found 93 new species out of the 152 species recorded in our survey. As impressive as this number might look, considering the taxonomic knowledge available for other ecosystems, it is not so different from numbers obtained in previous meiofaunal surveys

(Curini-Galletti et al. 2012, Martínez et al. 2019, Jörgen et al. 2021). The presence of so many new species might be influenced by some of the species traits potentially connected to low dispersal capability (Curini-Galletti et al. 2001) but most likely reflects the low sampling effort that has been historically performed for most interstitial groups and the little taxonomic knowledge we have on several meiofaunal groups (Fontaneto et al. 2012, Rubio-López et al. 2023).

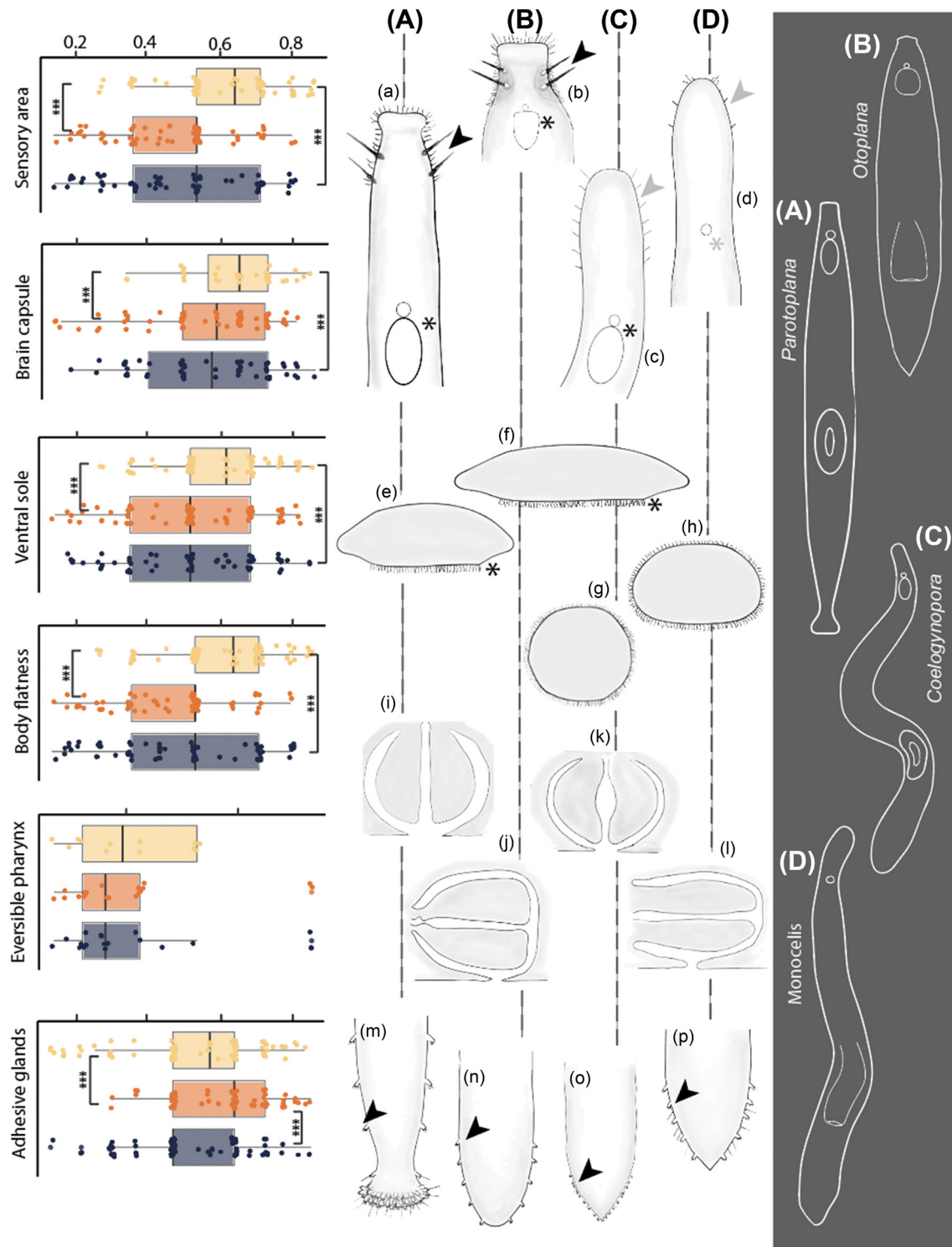


Figure 5. Summary of the results regarding hypothesis 4 on trait frequency. The boxplots on the left graphically show proportion (from 0 to 1) of species with the selected traits across the three beach levels, following the same colour coding of Fig. 1–4 for beach level. Significant differences between pairs of levels after generalized linear models are marked with asterisks (***) ($p < 0.001$) (see the Supporting information for further details). The drawings on the right of the boxplots illustrate the traits in four genera; the silhouettes in the grey box show an overview of the whole animals for the same four genera. Upper-case letters: (A) *Parotoplana* sp., (B) *Otoplana* sp., (C) *Coelogygnopora* sp., (D) *Monocelis* sp. Lower-case letters: (a) typical anterior end of *Parotoplana*, showing cephalic area (black arrowhead) and brain capsule next to the statocyst (black asterisk). (b) Same as (a) for *Otoplana*. (c) Typical anterior end of *Coelogygnopora*, without sensory cephalic area (grey arrowhead) but with brain capsule next to the statocyst (black asterisk). (d) Typical anterior end of *Monocelis*, without cephalic sensory area

Figure 5. (Continued)

(grey arrowhead) and without brain capsule (grey asterisk). (e) Transverse section of *Parotoplana*, showing the flatness of the body and the ventral ciliary sole (black asterisk). (f) Same as (e) for *Otoplana*. (g) Transverse section of *Coelogyropora*, cylindrical and without ciliary central sole. (h) Same as (g) for *Monocelis*. (i) Transverse section of the collar-shaped pharynx of *Parotoplana*. (j) Transverse section of the collar-shaped pharynx of *Otoplana*. (k) Transverse section of the collar-shaped pharynx of *Coelogyropora*. (l) Transverse section of the tubular pharynx of *Monocelis*. (m) Typical posterior end of *Parotoplana* showing the adhesive glands (black arrowhead) in a belt as well as along the body sides. (n) Typical posterior end of *Otoplana*, showing the adhesive glands (black arrowhead) along the rear of the body. (o) Same as (n) for *Coelogyropora*. (p) Same as (n) for *Monocelis*.

Patterns of functional diversity: species traits vary across levels yet a large proportion of the variance remains unexplained

Taxonomic and functional community composition varied across beach levels. The functional space of the swash level had different properties than the functional space of the shoaling and subtidal levels, with differences relying on the different frequency of traits that are linked to beach morphodynamics. Communities in the swash level had a significantly higher proportion of species with flat bodies, ventral ciliary sole, cephalic sensory area, and brain capsule, as expected if proseriate species living in the swash level had to withstand the effect of waves (Curini-Galletti et al. 2023). Species with a more regular arrangement of the adhesive glands along the body, as is achieved by flattening the body, combined with the mucous secretion of the ventral ciliary sole, seems to maximize the adhesion capabilities. The presence of flat bodies, with a ventral ciliary sole, cephalic sensory area, and brain capsule characterizes the species of the genus *Otoplana* (Ax 1956). This genus has been historically highlighted as the most specialized animal occurring in the swash level of sandy beaches in the Atlantic–Mediterranean area: the swash level was called ‘*Otoplanen-zone*’ by early meiobenthologists (Gerlach 1953, Ax 1956).

Adaptations and responses of meiofauna to different beach morphodynamics are known for several groups. A higher taxonomic diversity of annelid taxa was found in reflective than in dissipative beaches (Di Domenico et al. 2009), suggesting that more species of worms could be adapted to the strong action of waves. Studies focusing on a single species of annelids have shown how *Saccocirrus pussicus* probably sticks to the sand grains using the glands in the rear end of the body, and moves along with them across beach morphodynamic zones (Di Domenico et al. 2014). Other species of meiofauna cope with turbulence by digging deeper into the sediments, such as certain kinorhynchs (Herranz et al. 2019, Mello et al. 2019). Moving to deeper sediments is a general response of meiofaunal communities to cope with turbulence in the sea (Moreno et al. 2006).

Notwithstanding such a pattern of relationships between community composition, trait space and environmental variables, when we analysed the relative contribution of environmental factors and geographical distances to explain the variance of community composition, a large proportion of variance remained unexplained. A reason for the unexplained variance might be connected to overlooked relevant environmental predictors: oxygen, depth of the redox zone, or the presence of certain nutrients mediated by bacterial production could have been relevant. Indeed, bacterial communities

have been proposed to determine the presence of certain meiofaunal species, by acting as specific food sources or by providing additional nutrients to the fauna via the excretion products (Gray 1966, 1967). Another reason behind the unexplained variance might be due to the role of species interactions at the community level, either amongst proseriates or with other interstitial species that share the habitat with them. Indeed, the role of species interactions is known to be relevant in structuring community composition (Vieira et al. 2022). Yet, we could not include such additional abiotic and biotic predictors in our analyses because we did not have such information. Early studies have suggested that species interactions might play a negligible role, explaining that the distribution patterns of macrofaunal taxa across the beach gradients instead rely on the integrated response of different species towards multiple environmental drivers, such as granulometry and wave exposure (Brazeiro 2001, Papageorgiou et al. 2006). However, this hypothesis assumes that the environment negatively affects the richness in the swash zone, excluding most species from surviving there. Given that, at least for proseriates, we found a rich community of functionally specialized taxa living in that beach level, we might assume that species interactions might play an important role that remains to be quantified. Indeed, in other ecosystems it has been debated whether it is possible to quantify the effect of ecological filtering, given the confounding factor of competence (Cadotte and Tucker 2017).

Beyond beaches and environmental filtering: functional diversity patterns of microscopic animals across different habitats

Overall, regardless of the processes involved in adaptations to different hydrodynamics, for proseriates from reflective beaches in the western Mediterranean Sea, we demonstrated that the rough hydrodynamic conditions in the swash level shape diversity patterns. Wave incidence selects for species bearing adaptations to cope with turbulence, leading to the presence of highly specialized communities in these areas, compared to those in the deeper shoaling and subtidal levels.

Our results add more support to previous analyses, which highlighted that environment might act in affecting the distribution of microscopic animals in a way comparable to that of larger species. Distribution of microscopic animals might appear either uniform or random, simply as a consequence of the smaller scale, which brings a higher uncertainty associated with measurements and morphological interpretation. As previously suggested, microscopic size may generate uncertainty in a macroscopic observer, on both the definition

of traits and the definition of niche, even if the environment did select. Here again, a functional ecology-based study, in which we selected traits with a clear functional meaning related to habitat occupation, has revealed that the distribution of species within the beach is not random but clearly a response to the turbulence gradient of the beach. Similar processes of ecological filtering in response has been observed in meiofaunal groups dwelling in hard substrate or marine algae and phanerogams exposed to different degrees of turbulence, such as marine mites (Riesgo et al. 2010, Martínez et al. 2021a). In freshwater, a certain degree of trait selection has been demonstrated in the nematode communities dwelling in sediments between intermittent and permanent streams (Majdi et al. 2020), as well as in the communities associated to mosses (Kreuzinger-Janik et al. 2021). However, evidence for ecological selection of traits is also present in other groups, including free-living (Jaturapruerk et al. 2021) and epibiont bdelloid (Fontaneto and Ambrosini 2010) rotifers, as well as Cycliophora (Baker and Giribet 2007). In those cases, though, the effect of the environment was comparatively weak, and could only be seen as differences in the relative abundance of the traits. In the swash zone of a sandy beach, the effect is stronger and can be quantified even if the relative abundance of different species cannot be considered. Those studies collectively emphasize the need for moving from a merely taxonomical towards a functional view of ecological studies of microscopic organisms (Violle et al. 2014). Further steps in this direction will warrant a better mechanistic understanding of their habitat and distribution patterns.

All this evidence collectively suggests that, indeed, environment does select for the presence of different species in meiofauna, suggesting that ecological processes might play an important role in the evolution of new species, also amongst microscopic animals (Nosil 2012).

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Supporting information

The Supporting information associated with this article is available with the online version.

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