Hydrobiologia

Habitat differences filter functional diversity of low dispersive microscopic animals (Acari: Halacaridae)

--Manuscript Draft--

Manuscript Number:	HYDR-D-20-00789R3
Full Title:	Habitat differences filter functional diversity of low dispersive microscopic animals (Acari: Halacaridae)
Article Type:	Primary research paper
Keywords:	Functional originality; meiofauna; Halacaridae; Posidonia oceanica; n-dimensional hypervolumes; trait ecology
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Funding Information:	H2020 Marie Skłodowska-Curie Actions (882221) — Dr. Stefano Mammola
	Comunidad de Madrid (ES), Research Talent Attraction Program (Research Talent Attraction Program 2019-T2/AMB-13328) — Dr. Nuria Sánchez
	Erasmus+ mobility fellowship (OLS ID 641798) — Mr Guillermo García-Gómez
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Response to Reviewers:	We have now replace Garcia-Gomez et al. submitted by Sánchez-Jerez et al. 1999. Sánchez-Jerez, P., Cebrián, C. B., & Esplá, A. A. R. (1999). Comparison of the epifauna spatial distribution in Posidonia oceanica, Cymodocea nodosa and unvegetated bottoms: importance of meadow edges. Acta Oecologica, 20(4), 391-405

Habitat differences filter functional diversity of low dispersive microscopic animals (Acari, Halacaridae)

Running head: environment affects distribution of mites

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Abstract

We are starting to appreciate that microscopic animals are not as widespread as previously thought, but we still ignore to what extent and through which mechanisms the environment selects for specific communities or traits in microscopic animals. We here analyse the functional diversity of marine mite communities living in a seagrass meadow across two habitats: the leaves and the matte. The strictly benthic lifestyle and the conserved morphology of mites allow for unambiguous characterization of their functional traits, while the discrete nature of the two habitats alleviates the uncertainty in their ecological characterization. Our results show that habitat filters the distribution of certain traits favouring a higher diversity, dispersion, and evenness of functional traits in the matte than in the leaves. We further observed temporal variations in the functional diversity of communities, following the changes in biomass and structure of seagrass leaves. However, despite the stark differences between the two habitats, the filtering effect is partial and affects mostly relative species abundances. Our study emphasises the need of moving from a taxonomical toward a functional view of ecological studies of microscopic organisms. This integrative approach is key to achieve a mechanistic understanding of their habitat and distribution patterns.

KEYWORDS: Functional originality; meiofauna; Halacaridae; Posidonia oceanica; n-dimensional hypervolumes; trait ecology

Introduction

It is unlikely to see a whale gliding in the sky (Adams, 1984) or a bovid grazing on the surface of the ocean (Kavcic et al. 2020). However, as the body size of animals decreases, the probability increases of encountering them in places where *they are not supposed to be*. This is because the realised niche of microscopic animals—namely, where they are actually found—can extend well beyond the set of abiotic conditions that allow positive population growth rates (fundamental niche). These broad ecological ranges are more frequent amongst microscopic animals possessing traits that facilitate long distance dispersal such as dormancy, long-term viability, and parthenogenesis (Fontaneto & Hortal, 2013, Fontaneto, 2019). Similar traits are found, for example, in many species of nematodes (Fonseca & Netto, 2015), rotifers (Fontaneto *et al*. 2008), and tardigrades (Bartels *et al*., 2020; Kaczmarek et al., 2015). In comparison, some lineages of microscopic organisms are specialised to thrive within narrow ranges of environmental conditions like caves (Mammola et al., 2020a), mountain summits (Hoschitz & Kaufmann, 2004), hydrothermal vents (Zeppilli et al., 2018), and deep terrestrial subsurface habitats (Borgonie et al., 2011). Many of these animals evolved distinct and often convergent traits for these specific conditions. Quintessential examples are microscopic annelids and copepods specialised to feed in the chemocline of certain aquatic caves (Martínez et al., 2019; Worsaae et al., 2019); or mouthless species of nematodes and flatworms living in strict association to prokaryotic symbionts in anoxic marine sediments (Ott et al., 1982).

The corollary of these examples is that not only the microscopic body size, but also the presence of certain traits and the interaction between them and the environment, determines the ecological range of microscopic organisms. This is nothing new, as this idea was already grasped in the original formulation of the "*everything small is everywhere*" paradigm, which included the postil "*...but the environment selects*" (Baas-Becking, 1934; Bass & Boenigk, 2011). So we now stand to a point where we know that even broadly distributed and apparently generalist species may not be actually so widespread and tolerant when their habitat preferences are taken into account (or, in other words, that the density of individuals across the distribution range of a given species is not homogeneous as it varies across habitats). But, unfortunately, this filtering effect has proven difficult to quantify, partly due to the lack of data on the relevant traits of many microscopic animals (Giere, 2009) and partly due to the intrinsic problem of measuring relevant environmental variables at appropriate resolutions (Levin, 1992; Potter, Arthur Woods, & Pincebourde, 2013),

therefore making it unclear to identify the differences between realized and fundamental niches (Soberón & Nakamura, 2009). These issues have challenged all community-level studies that have so far attempted to directly link functional traits of microscopic animals and their distribution patterns at the relevant scale (Fontaneto 2011). In other words, we know that the environment affects taxonomic and functional diversity in microscopic animals but we ignore to what extent and through which mechanisms the environment selects for specific communities and their traits (e.g. More et al., 2015, Pusceddu et al., 2016; Minor et al., 2017, Semprucci et al., 2018).

We here set to examine the effect of habitat on the distribution of microscopic animals by comparing the multidimensional functional space (Blonder et al., 2014; 2018) of assemblages of mites dwelling on a meadow of seagrass [*Posidonia oceanica* (L.)]—a marine plant with a well-studied architecture and growth pattern (Molenaar et al., 2000)—in the Mediterranean. Due to their strictly benthic life mode and easy-to-measure external traits with a clear functional meaning, marine mites are an excellent model system for a similar analysis (Pfingstl et al. 2020). Furthermore, the patchy distribution of seagrass within meadows provides independent replicates of discrete habitats, the leaves versus the matte (i.e., the grid formed by rhizomes, roots, and trapped particles). Because these two habitats present different hydrodynamic regimes (Matteo et al., 1997; Folkard, 2005) and availability of food (Mabrouk et al., 2011; Boudouresque et al., 2016), we expect that they will filter different mites from the pool of species resident in the meadow. We expect that this filter will be evidenced in the community traits, favouring the dominance of more specialised phytophagous or epiphytes feeder species in the leaves, and limiting the presence of generalist detritivores species to the matte. We therefore hypothesise that i) at the community level, there should be higher diversity, dispersion, and evenness of functional traits in the matte than in the leaves. As a corollary of the previous hypothesis, we also expect that ii) at the species level, the higher diversity of traits in the matte will be reflected by the presence of more functionally original species. Furthermore, the annual phenological changes due to the seasonal renovation and decay of seagrass leaves affect nutrient availability (Drew, 1978; Zupo et al., 1997). So, we also hypothesize that iii) differences in functional diversity of mite communities could be related to phenological variation in biomass and structure of *P. oceanica,* particularly on the leaves.

Material and methods

Model organism

The model organisms selected for this study are marine mites of the family Halacaridae (subsequently referred to as marine mites), a lineage of microscopic arachnids that colonized the ocean from a terrestrial ancestor around 270 million years ago, radiating in different types of marine habitats (Pepato et al., 2018). Due to this terrestrial origin, the body plan of the group is constrained, all forms being restricted to benthic habitats. The impossibility of marine mites to swim or move by any other means than crawling in direct contact with the substrate ensures that the species found in each sample belong to the local community. This feature places marine mites among those animals with a realised niche that is smaller than the fundamental niche, even if they are microscopic: not all available habitats in an area are actually colonised, and the animals are not found in habitats that cannot sustain viable populations. Furthermore, the presence of a hard, hydrophobic cuticle allows for a precise measurement of morphological traits even in fixed material, reducing measure errors. Finally, the conserved morphology of marine mites ensures unequivocal homology assessment of the functional traits. These three properties—movement exclusively by crawling, hard cuticle, and conserved morphology—make marine mites ideal candidates for quantifying the effect of habitat filtering on the distribution and functional diversity of microscopic animals (e.g. Mori et al., 2015, Minor et al., 2017, Pfingstl et al., 2020).

Importantly, marine mites are typical and abundant inhabitants of *Posidonia oceanica* meadows (Mari & Morselli, 1990; Durucan, 2018; Durucan & Boyacı, 2018), thriving especially in the vegetated patches (Sánchez-Jerez et al., 1999). This makes it easier to obtain enough specimens for ecological analyses.

Sampling design

As a study area, we selected the exposed seagrass meadow of Cala del Cuartel, in Santa Pola, south-eastern Spain (38° 12' 34.04" N, 0° 30' 19.12" W, WGS84 reference system), consisting of numerous patches at 4–7 m depth separated by bare sandy tongues. Marine mites dwelling in *P. oceanica* meadows thrive in seagrass patches and are rarely found in the adjacent bare sand (Sánchez-Jerez et al., 1999). So, in relation to the size and dispersal capabilities of the marine mites, each patch represents a discrete and independent replica of the same habitat within a larger

area. The fact that all the patches are within the same bay limits the confounding effect of depth, temperature, salinity, or different exposition to currents.

Each patch consists of two compartments representing the two different habitats, the leaves and the matte (Figure 1A). The leaves are exposed to turbulence (Folkard, 2005) and predators (Hovel *et al.*, 2002; Hovel & Fonseca, 2005), as well as affected by changes in length and thus of abundance of epiphytic algae and epifauna (Mabrouk et al., 2011), which potentially represents the main source of food for the mites (Pugh & King, 1985a). In contrast, the matte is a sheltered habitat offering a high and constant availability of detritus throughout the year (Mateo et al., 1997).

We performed four sampling campaigns between December 2015 and August 2016. In each campaign scuba divers sampled these two habitats (leaves and matte) in six randomly selected patches of 400 cm^2 of *Posidonia oceanica* (4 sampling campaign x 6 patches x 2 habitats, totalling 48 samples). In each patch, leaves were collected first by cutting them at the ligulae level, while the surface of the underlying matte was collected by scraping the upper 2 cm layer into a separate container.

Meiofauna from each sample was extracted combining the magnesium chloride and the 'bubble and blot' decantation techniques to ensure the recovery of all species of marine mites (Higgins & Thiel, 1988; Sørensen & Pardos, 2008). The selected mesh size was 62 μm to collect both juveniles and adult forms. Each sample was bulk fixed using 7% formaldehyde in the field. All studied material has been deposited at the Laboratory of Meiofauna at the Universidad Complutense de Madrid.

For each leaves sample, as a proxy for food availability, we measured the average length of the leaves, calculated as the distance from the ligula to the apical end of all the complete leaves. Length of the leaves is known to correlate with the abundance of epiphytic organisms (Malbrouk et al., 2011). For each matte sample, as a proxy for food availability, we directly measured the percentage of organic carbon using the approach by Walkley & Black (1934). Furthermore, we inferred habitat availability as the dry weight of leaves or matte divided by the total volume of the habitat, which varied in the leaves (Average leave length * 20 cm x 20 cm) and was constant in the matte (2 cm x 20 cm x 20 cm).

Species identification and morphological traits measurement

Mites were sorted using a MOTIC® SMZ-168 stereoscope, whole-mounted in a modified Hoyer's medium (Mitchell & Cook, 1952), and assigned to species and developmental stages by inspecting relevant morphological characters with a light microscope equipped with Nomarski optics and an Olympus DP70 camera. We used the keys by André (1946) and Green and MacQuitty (1987), as well as the available literature (Bartsch, 1991, 2000, 2001; Morselli, 1980).

For each species, we examined 13 morphological traits related to body size and shape, the ability to withstand the water currents, and trophic specialisation (Table 1). Body size and shape measures were taken on all 502 well-preserved specimens from our samples (Table 2). The traits were estimated separately from adults and juveniles (larval or nymphal stages), as different life stages exhibit different ecological preferences and dispersal capabilities even within the same species (Bartsch, 2002; Somerfield & Jeal, 1995; 1996). The other traits, species-specific and not changing between individuals of different ages, were assigned at the species level.

Functional space characterization

We performed functional analyses following the general protocol proposed in Mammola et al. (2020c). We expected the properties of the functional space to vary between the two different habitats, reflecting the habitat filtering effect in sorting the mite communities according to the presence of certain traits. Furthermore, we expected variations in the functional space in relation to the phenological changes of the *P. oceanica* meadow through the four sampling campaigns.

We represented the functional space of mite communities in the two habitats and across sampling campaigns with geometrical *n*-dimensional hypervolumes (Blonder et al., 2014, 2018). Since some of the functional traits considered here are categorical, we applied a Gower dissimilarity measure to the complete trait matrix and extracted orthogonal morphological axes through principal coordinate analysis (Carvalho & Cardoso, 2020; Mammola & Cardoso, 2020). We delineated hypervolumes with the package '*hypervolume'* (Blonder & Harris, 2018) of the R software (R Core Team, 2020) using a gaussian kernel density estimate (Blonder et al., 2014, 2018), the first four principal coordinate axes (cumulatively 60% variance explained), a default bandwidth for each axis, and species abundances. A gaussian kernel density estimation was selected as it allows a probabilistic rather than a binary characterization of the functional space (Mammola & Cardoso, 2020). Five samples with one or no species were removed from the

analyses. We analysed the properties of the hypervolumes with specific indices (Mammola & Cardoso, 2020) implemented in the R package 'BAT' (Cardoso et al., 2015, 2020). For each set of analyses, we expressed functional diversity as the total volume of the functional space. We verified if communities in matte and leaves and across sampling campaigns were subjected to different filtering processes by calculating the dispersion of the functional space with the *kernel.dispersion* function and the 'divergence' method (Mammola & Cardoso, 2020). The regularity of traits distributions within the total functional space expresses evenness as the overlap between the input hypervolume and a theoretical hypervolume whose traits and abundances are evenly distributed within their possible range, using the *kernel.evenness* function (Mammola & Cardoso, 2020).

We inspected whether certain assemblages of mite species act as indicators of the two habitats, and which species contribute most original traits to each habitat (i.e., functional outliers; Violle et al., 2017). In particular, we expect the distribution of the originality values to have a smaller variation in the leaves than in the matte, reflecting the stronger filtering effect exerted by this habitat compared to the matte. We calculated the functional originality of each species in each community with the function *kernel.originality*, weighting originality by species abundance (Mammola & Cardoso, 2020). We expressed originality as the average distance between each species to a sample of 10% stochastic points within the boundaries of the hypervolume. For each habitat, we expressed the total originality of a species as the average originality of the species across all communities in which it was present. Also, in this analysis, we considered the stages of the same species separately.

To define the degree to which a given species was characteristic to one habitat or the other, we further calculated the Δ Originality by subtracting to the value of originality of each species in the matte the value of originality of the same species in the leaves. When a species was absent in a habitat, we assigned its originality in this habitat to zero. We visualized Δ Originality values as histograms centred to the value of zero, where positive values indicate species that are more original in the matte than in the leaves, and negative values *vice versa*. We estimated and visualized the theoretical density of values with the R package 'ggplot2' (Wickham, 2016), by computing a kernel density estimate with a default bandwidth through the data.

To ease the interpretation of our findings, we finally calculated the probability of recovering a given trait within each habitat as the community weighted mean with the *cwm* function in 'BAT'. For categorical traits, we calculated instead the probability of finding each state

of the trait in each habitat using a function developed *ad hoc* for this study—see R code uploaded alongside this submission.

Statistical analyses

We performed analysis of variance (ANOVA) to evaluate the significance of the differences observed in functional diversity, dispersion, and evenness between the matte and the leaves samples (Hypothesis 1). Then, we verified whether the originality values of species in the leaves were significantly different than those in the matte using a null modelling approach (Hypothesis 2). We performed 99 permutations of the species between the two habitats, keeping fixed the original abundance values. For each run, we recalculated the hypervolumes and the originality values and estimated how many species in the leaves had higher originality than the species in the matte. As in Mammola et al. (2020b), the null hypothesis of random sorting of species between the two habitats was rejected if the observed value was higher than the 97.5 percentile or lower than the 2.5 percentile of the 99 randomizations. For each permutation, we estimated the standard effect size and associated p-value.

In order to address Hypothesis 3, we explored the variation of functional metrics across sampling campaigns within each habitat using linear models (LMs). The response variables were the functional metrics richness, dispersion, and evenness calculated for the mite communities in each sample. As environmental predictors, we selected four variables: two of them, the length of the leaves and the organic matter content in the matte, were used as proxies of food availability in each habitat; the other two, the density of leaves and the density of matte, were used as proxies of habitat availability. Prior to the analyses, we checked collinearity among predictors with Pearson's *r* correlations, setting the threshold for collinearity at $|r| > 0.7$ (Zuur et al., 2010). We log-transformed each independent variable in order to capture their biological effect on the mite communities, which is expected to change logarithmically, *i.e.*, a difference of 1 cm in the leave length is expected to have a stronger effect on the mite communities when the leaves are short than when they are long. To facilitate model convergence, we further scaled all independent variables. Finally, to take into account the dependency structure in our data due to sampling campaigns, we included the variable sampling campaign as a fixed factor in all the models, because we could not include it as a random effect due to the presence of only four levels, which are considered too few to be used as a random effect (Gelman & Hill, 2006).

Given that the environmental predictors are different between the matte and the leaves, we fitted separate regressions for the two habitats. All analyses were performed in R. Following Zuur & Ieno (2016), we validated models by checking the normality of model residuals, the plot of residuals versus fitted values, normal Q-Q plots, and Cook's distances, using the R package 'performance' (Lüdecke et al. 2020). The outputs of the results are presented as type-II analysis-of-variance tables for model objects obtained with the R package 'car' (Fox & Weisenberg, 2018).

Results

We successfully reconstructed the hypervolumes for the 43 communities (that is, all those with more than one species). As we expected on our Hypothesis 1, we observed a clear polarization of the trait space according to the two habitats (Figure 1). Properties of the functional space of the community in the two habitats were significantly different: the communities in the matte were functionally more diverse (ANOVA: $F_{(1,41)} = 26.94$, $p < 0.001$), more dispersed ($F_{(1,41)} = 20.93$, $p < 0.001$), and more even ($F_{(1,41)} = 74.75$, $p < 0.001$) than those in the leaves (Figure 2A, Table 3).

Contrary to our Hypothesis 2, the distribution of the total functional originality values was similar in both habitats (Figure 3A). According to the null modelling analysis, the number of species more original in the leaves than in the matte was not lower than what is expected from a random sorting of species across habitats (Standard effect size = –0.41, p-value = 0.06). Regarding the values of Δ Originality, we found a set of distinct species in the two habitats, allowing us to differentiate the leaves and matte communities according to the functional traits of few indicator species (Figure 3B).

The environmental predictors for each habitat were not collinear (for leaves: length *vs.* density of the leaves, r = –0.003; for matte: organic matter *vs.* density of the matte, r = –0.48) and were thus retained in the statistical models. Richness, dispersion, and evenness of the mite communities in the leaves were only marginally negatively affected by the length of the leaves, with dispersion and evenness different between sampling campaigns (Figure 2G–I; Table 4). No significant effects were detected in the matte (Table 4). These results partially support our Hypothesis 3, although the effect of the environment in the leaves was nonetheless weak.

Discussion

Habitat patterns in functional diversity

Our analyses confirmed our first hypothesis that mite communities in matte habitat had a significantly higher functional richness, dispersion, and evenness than those in the leaves. Analytically, this means that, on average, the functional space in the leaves is significantly less voluminous (*i.e.* trait diversity is lower) and observations are less dispersed (*i.e.* species have traits that are more similar amongst them) and less even (*i.e.* the traits hypervolume is not homogenous indicating that certain combinations of traits are more common than others) than in the matte. Biologically, this suggests that the selective conditions in the leaves exert a stronger filtering effect upon the traits present in the colonizing species, whereby only a small subset from all the pool of traits present in the seagrass meadow allows mites to thrive in the leaves. This habitat filtering is reflected in the distribution of mites between habitats: even if the habitats are physically connected, communities in the leaves consist of a subset of the species present in the matte. Furthermore, this pattern was consistent through the different sampling campaigns, despite the stark phenological changes experienced by the *Posidonia* meadow throughout the year. The leaves are the habitat in which it is more likely to find individuals bearing specialised traits (Supplementary Material Figure S1). These traits are chiefly specialised claws (Figure S1d, S1e), which might aid in clinging to the leaf's surface and thereby withstand turbulence (e.g. Pfingstl et al., 2020; but see Pugh et al., 1987) and a larger body size (Figure S1g). In contrast, the assemblages in the matte consist of species bearing these traits, as well as species with more slender bodies (Figure S1i) and a longer and pointier gnathosoma (Figure S1j). Whereas the slender body presumably aids this species to crawl in the tighter habitat spaces in the matte, as observed in most interstitial microscopic species (Giere 2009), it is more difficult to interpret the functional meaning of the elongation of the gnathosoma. We here speculate that it might aid this species in reaching food particles accumulated in the tight spaces such as detritus and deposits of organic matter, but more in-depth studies would be needed to corroborate this assumption. A third group of species, presumably consisting of predators feeding on mites (Bartsch, 1989; Green & MacQuitty, 1987), are found occasionally in some of the samples, occurring stochastically both in the leaves and the matte as they wander around in the meadow searching for their prey.

This general pattern further emerges from the analysis of originality values, a metric that averages the distance between each observation to a sample of stochastic points within the boundaries of the hypervolume. It thereby measures how unique the position of individual

observations is in the trait hyperspace, as the distances are expected to increase as the species' combination of traits becomes unique (Mammola & Cardoso, 2020). Therefore, we expected more functionally original species in the matte, because species in the leaves need special adaptations presumably to cope with turbulence and feed on specialised food sources. The same adaptations are not required in the matte, where the presence of shelters and more diverse sources of food might relax the filtering effect on species and traits. This might result in a more functionally heterogeneous assemblage in which the probability of finding a given species is less dependent upon their traits. Our results, however, did not support this assumption given that originality values in the leaves did not differ significantly from those in the matte (Figure 3a). This might be the case because the species with the highest values of originality—such as *Pelacarus aculeatus*, *Agaue panopae*, *Agauopsis microrhyncha*, or *Agaue abyssorum*; Table S1—typically consisted of large rare species with uncommon traits that facilitate predation upon other microscopic animals, including mites (Bartsch, 1989; Green & MacQuitty, 1987). These species also occur in low abundances and their distribution is scattered across the meadow, being found stochastically in one habitat or the other. In fact, these species can be considered functional outliers (*sensu* Violle et al., 2017) in that they take extreme values of Δ Originality (Figure 3b), as they only occur in low numbers in either habitat, thus indicating that the filtering may act at another spatial or temporal scale on them. However, we acknowledge that further studies on the feeding biology of marine mites would be needed to fully understand the biological mechanisms behind the ecological patterns we documented.

Phenological changes and functional diversity

Our results partially corroborate our third hypothesis, as we found weakly significant variations in the functional diversity of mite communities in the leaves following the phenological changes of biomass of *Posidonia oceanica,* specifically the change in the length of the leaves. These changes permeate all metrics, which surprisingly were negatively affected by the length of the leaves, used as a proxy for food availability.

The end of the summer is characterized in the Mediterranean by an increase of the rainfall and primary production, which favours a rapid growth of *P. oceanica* in winter reaching a peak in the biomass in the seagrass meadow in spring (Champenois & Borges, 2014). A large number of epiphytes colonize the leaves, which get densely populated by diverse epiphytic communities

(Mabrouk et al., 2011; Piazzi et al., 2016), as they enlarge. Food resources are hence more abundant in the leaves at their peak of production in spring, which might feedback positively the mite populations in this habitat. However, instead of favouring an increase of functional diversity driven by a higher abundance of resources, our results suggested the opposite, as they show a marginally significant reduction of the functional dispersal and evenness in the leaves when the leaves are longer. We speculate that the higher abundance of epiphytes might provide an advantage to those mites that are better adapted to feed on them, increasing their relative abundance to other species and favouring the homogenization of the trait space in the leaves. Furthermore, the basal parts of long leaves are less exposed to hydrodynamics, as leaves themselves provide shelter from the current towards the bottom (Folkard, 2005). This favours presence of a larger number of macrofaunal organisms, such as fish and decapod juveniles, which find shelter in the leaves for larger macrofaunal predators (Hovel *et al.*, 2002; Hovel & Fonseca, 2005), preying on the most conspicuous and less specialized meiofaunal organism that colonize the leaves (Zupo and Stübing, 2010). We acknowledge that these explanations are tentative given our current data. Only further functional ecological approaches will be able to address our hypotheses, obtaining a more holistic picture of ecosystem functioning.

In contrast, the matte does not experience similar pronounced phenological changes and we can speculate that this is the reason for which no significant changes were observed in the functional diversity of mite communities in the matte.

Conclusions

Being the first study using hypervolumes to define functional properties of meiofauna communities, our study highlights a potential role of the environment in affecting the distribution of microscopic animals between connected habitats by filtering them according to the presence of certain traits. Remarkably, this filtering effect was relatively weak, as most species were found in both habitats and the filtering was mostly reflected by their relative abundances. One may argue that our results of filtering effects between connected habitats might not be applied to all microscopic animals more widely and that mites in seagrass meadows might represent only a specific case. Habitat filtering effects might be even more subtle in other microscopic animal groups, especially the soft-bodied ones, for which the functional interpretation of morphological traits is often obscure and trait measurements subjected to strong artefacts due to post-mortem

contraction, fixation, and other bias (Higgins & Thiel, 1988). Furthermore, most microscopic animals have a high probability to be passively dispersed to suboptimal habitats (Armonies, 1988; Hagerman & Rieger, 1981; Hauspie & Polk, 1973), increasing the uncertainty associated with habitat characterization at a small scale relevant for their biology, thus overestimating both their functional and realized niches. Interestingly, our results add an extra value to the *Posidonia oceanica* meadows: on top of their indisputable importance as a reservoir of biological diversity (e.g., Mazzella & Spinoccia, 1992; Kalogirou et al. 2010; Urra et al., 2013; Piazzi et al, 2016) and the many services that they provide (Boudouresque et al., 2017; Vacchi et al., 2017), they may also represent important model systems to explore research questions in ecology and evolution, such as distribution patterns of microscopic fauna.

It is not surprising that in studies on the distribution of microscopic animals, such distribution might appear either uniform or random, simply as a consequence of the high uncertainty associated with measurements and morphological interpretation at the small spatial scales. In other words, 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.* Exploring the distribution of small animals through the lens of functional ecology, targeting traits with clear functional meaning related to habitat occupation, is crucial to overcome some of these biases (Violle et al., 2014). Our study therefore emphasises the need of moving from a merely taxonomical toward a functional view of ecological studies of microscopic organisms (Green et al., 2008). Further steps in this direction will warrant a better mechanistic understanding of their habitat and distribution patterns.

Acknowledgements

The authors want to thank Dr Alfonso Ramos-Esplá (CIMAR) for the logistical assistance during the sampling campaigns in Santa Pola. We also thank Dr Sergio Pérez and Nuria Rico for the help with the samplings. We gratefully acknowledge Dr Ilse Bartsch for her invaluable help with the identification of halacarid species. We also thank Dr Dolores Trigo and María Isla for the facilities and their useful assistance in the laboratory of soil chemistry of the Zoology Department (UCM). SM was supported by the CAWEB project "Testing macroecological theory using simplified systems", funded by the European Commission through Horizon 2020 Marie Skłodowska-Curie Actions (MSCA) individual fellowships (Grant no. 882221). GGG was supported by an Erasmus+

mobility fellowship, OLS ID 641798. NS was funded by the Research Talent Attraction Program (Regional Government of Madrid and University Complutense of Madrid) (2019-T2/AMB-13328). We also want to thank Iacopo Bertocci and two anonymous referees for their very useful comments, which have improved the final version of this manuscript.

AUTHOR CONTRIBUTION STATEMENTS

AM, GGG, AGH, and NS planned the sampling design. GGG, AGH, NS and AIM collected the samples; GGG, AGH and NS sorted the latter samples for animals of interest and measured the environmental variables, whereas GGG identified animals and collected traits. AM and SM planned the statistical approach and performed analyses. FP provided facilities and support. AM, GGG, and SM wrote the first draft. All authors contributed to the writing to additions and comments to the text.

DATA AVAILABILITY STATEMENTS

Raw data and R script to generate the analyses will be deposited in a public repository upon acceptance.

SUPPLEMENTARY MATERIALS ONLINE

Figure S1. Probability of finding each state of discrete traits **(a–f)** and community weighted mean of continuous traits **(g–k)** for mite communities in the leaves and matte.

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649 **TABLES & FIGURES**

650 **Table 1.** Morphological traits considered in the analyses, with hypotheses on their functional
651 meaning

Trait	Variable description	Functional meaning
(1) Total length	Measurement the tip of the gnathosoma to the tip of the idiosome in mm	Proxy of the total biovolume, trophic level and passive resistance of mites against water currents.
(2) Idiosome length	Idiosome dorsal length	Proxy of the hard body length.
(3) Idiosome width	Idiosome dorsal width	Proxy of the hard body width.
(4) Gnathosoma (dorsal) length	Length of the gnathosoma which is not covered by the idiosome and exposed dorsally.	Proxy of the diet. The length of the gnathosoma is adapted to exploit different food resources (Bartsch 2006).
(5) Idiosome length/width	Ratio between idiosome length and width	Proxy of body shape. Wider body shapes limit the colonization of habitat consisting of narrow spaces. Indeed, slender shaped mites are often found amongst fine sediments (Bartsch 2006).
(6) Relative gnathosoma length	Ratio between gnathosoma dorsal length total body length	Proxy of the diet, as a measure of protruding gnathosoma relative to body size.
(7) Number of Accessory teeth	Number of accessory teeth on the claws	In mites, especially those species linked to aquatic habitats, claws are essential to withstand physical stress, whether large (Pfingstl et al. 2020) or structural complex claws (Pugh & Fordy, 1987; Bartsch 2006). We here include four claw
(8) Combs	Degree of comb complexity, where 0 = absence, 1 = fine, 2 = regular, and 3 = large combs	

(9) Median claw type	Degree median claw development, where 0 = absence, 1 = small, and 2 = large median claw	structures to account for different possible combinations that define claw complexity. The combination of these variables provides a proxy of the resistance of each individual to turbulence, as increasing claw complexity means a better grip to the substrate.
(10) Number of legs with combs	Number of pairs of legs whose claws bear combs	
(11) Lamella	Categorical, reflecting the presence/absence of cerotegumental or cuticular lamella on legs	Lamella are present mostly in species that occur in sediments (Bartsch 2006).
(12) Pincer	Categorical, reflecting the presence of a first pair of legs modified as a pincer	Specialised legs for feeding (Green & Macquitty 1987; Bartsch 2006).

652

Table 2. Summary of the species included in this study, number of counted individuals, and coding for the 12 included functional traits in each developmental state (± standard error). The number for each character and the explanation for the coding are summarized in Table 1. Abbreviations: N, total number of measured specimens.

Species name	N	stage	1	2	3	4	5	6	7	8	9	10	11	12
Agaue cf. abyssorum (Trouessart, 1896)	1	juvenile	394.58 ± NA	323.52 ± NA	242.92 ± NA	71.06 ± NA	1.33 ± NA	0.18 ± NA	0	1	0	4	1	0
Agaue panopae (Lohmann, 1893)	7	adult	737.42 ± 61.05	587.59 ± 52.18	366.99 ± 48.21	149.83 ± 17.50	1.61 ± 0.07	0.20 ± 0.02	1	2	1	4	1	0
	5	juvenile	621.77 ± 139.82	480.90 ± 111.47	314.33 ± 91.55	140.87 ± 39.26	1.55 ± 0.12	0.23 ± 0.04	1	2	1	4	1	0
Agauopsis brevipalpus (Trouessart, 1889)	3	adult	483.66 ± 24.32	389.34 ± 4.78	294.59 ± 17.52	94.32 ± 25.56	1.33 ± 0.09	0.19 ± 0.04	1	2	0	3	0	0
	3	juvenile	366.14 ± 52.34	301.28 ± 45.14	231.84 ± 41.69	64.86 ± 7.58	1.30 ± 0.06	0.18 ± 0.01	1	2	0	3	0	0
Agauopsis microrhyncha (Trouessart, 1889)	5	adult	520.87 ± 15.70	487.68 ± 9.70	342.02 ± 27.43	40.13 ± 10.61	1.38 ± 0.02	0.08 ± 0.02	1	3	1	4	0	0
	9	juvenile	376.29 ± 71.24	321.94 ± 39.12	236.68 ± 30.76	33.75 ± 7.61	1.37 ± 0.10	0.10 ± 0.03	1	3	1	4	0	0
Agauopsis minor (Trouessart, 1894)	10	adult	377.19 ± 10.33	340.37 ± 13.98	245.66 ± 10.81	36.82 ± 7.47	1.39 ± 0.05	0.10 ± 0.02	1	2	1	3	0	0
	4	juvenile	267.27 ± 82.22	237.20 ± 70.45	170.28 ± 58.76	30.07 ± 15.04	1.41 ± 0.09	0.11 ± 0.03	1	2	1	3	0	0
Arhodeoporus gracilipes (Trouessart, 1889)	10	adult	353.28 ± 19.15	291.01 ± 16.15	190.17 ± 19.34	62.28 ± 7.48	1.57 ± 0.09	0.19 ± 0.03	1	1	1	4	0	0
	5	juvenile	277.26 ± 48.32	223.23 ± 36.39	145.35 ± 35.27	54.03 ± 13.32	1.56 ± 0.14	0.19 ± 0.02	1	1	1	4	0	0

Arhodeoporus labronicus (Morselli, 1981)	1	adult	303.75 ± NA	245.66 ± NA	130.81 ± NA	58.09 ± NA	1.88 ± NA	0.19 ± NA	1	1	1	3	0	0
	2	juvenile	281.05 ± 33.72	231.54 ± 33.71	132.52 ± 35.11	49.51 ± 0.01	1.78 ± 0.22	0.18 ± 0.02	1	1	1	3	0	0
Copidognathus lamelloides Bartsch, 2000	24	adult	337.40 ± 16.96	280.95 ± 14.69	201.56 ± 12.92	56.44 ± 6.82	1.40 ± 0.05	0.17 ± 0.02	1	1	1	3	1	0
	11	juvenile	242.00 ± 35.00	196.23 ± 32.85	129.10 ± 21.39	45.77 ± 3.84	1.52 ± 0.05	0.19 ± 0.02	1	1	1	3	1	0
Copidognathus latisetus Viets, 1940	15	adult	219.34 ± 6.72	203.85 ± 6.11	122.41 ± 6.42	15.49 ± 3.72	1.68 ± 0.08	0.07 ± 0.02	1	1	1	4	0	0
Copidognathus magnipalpus (Police, 1909)	21	adult	398.95 ± 17.49	339.31 ± 18.23	220.12 ± 17.73	59.64 ± 6.16	1.55 ± 0.08	0.15 ± 0.02	2	3	1	4	0	0
	8	juvenile	291.29 ± 51.78	254.38 ± 48.83	170.00 ± 24.15	46.63 ± 8.59	1.42 ± 0.26	0.16 ± 0.01	2	3	1	4	0	0
Copidognathus oculatus (Hodge, 1863)	30	adult	352.82 ± 14.48	299.28 ± 13.41	176.19 ± 12.48	53.54 ± 9.01	1.71 ± 0.10	0.15 ± 0.02	1	3	1	4	0	0
Copidognathus quadricostatus (Trouessart, 1894)	1	adult	382.72 ± NA	301.41 ± NA	212.16 ± NA	81.31 ± NA	1.42 ± NA	0.21 ± NA	1	1	1	4	0	0
	1	juvenile	249.17 ± NA	198.32 ± NA	113.43 ± NA	50.85 ± NA	1.75 ± NA	0.20 ± NA	1	1	1	4	0	0
Copidognathus remipes (Trouessart, 1894)	13	adult	360.86 ± 10.87	299.25 ± 11.24	175.32 ± 11.91	60.45 ± 7.05	1.71 ± 0.13	0.17 ± 0.02	1	0	1	4	1	0

	5	juvenile	301.05 ± 70.17	248.63 ± 60.69	153.42 ± 37.26	52.42 ± 10.87	1.62 ± 0.09	0.18 ± 0.02	1	0	1	4	1	0
Copidognathus reticulatus (Trouessart, 1893)	1	juvenile	269.36 ± NA	225.19 ± NA	124.03 ± NA	44.17 ± NA	1.82 ± NA	0.16 ± NA	1	1	1	4	1	0
Lohmannella falcata (Hodge, 1863)	5	adult	494.44 ± 28.73	326.74 ± 15.22	257.21 ± 18.69	167.70 ± 19.75	1.27 ± 0.06	0.34 ± 0.02	0	0	0	0	0	0
	3	juvenile	304.25 ± 57.12	210.79 ± 51.87	166.02 ± 41.00	93.46 ± 0.02	1.27 ± 7.64	0.31 ± 0.04	0	0	0	0	0	0
Pelacarus aculeatus (Trouessart, 1896)	2	adult	574.82 ± 118.04	479.31 ± 95.03	401.39 ± 98.56	95.51 ± 23.01	1.20 ± 0.06	0.17 ± 0.01	2	0	1	0	0	0
	2	juvenile	389.57 ± 0.61	313.10 ± 5.27	243.75 ± 10.87	76.48 ± 4.66	1.29 ± 0.04	0.20 ± 0.01	2	0	1	0	0	0
Rhombognathus praegracilis Viets, 1939	110	adult	398.11 ± 26.82	348.55 ± 25.75	237.16 ± 22.80	50.28 ± 8.13	1.48 ± 0.11	0.13 ± 0.02	2	3	0	4	0	0
	172	juvenile	289.88 ± 60.37	246.25 ± 53.94	166.26 ± 37.81	34.84 ± 7.98	1.51 ± 0.10	0.13 ± 0.03	2	3	0	4	0	0
Rhombognathus cf. procerus Bartsch, 1975	1	adult	333.83 ± NA	297.33 ± NA	198.00 ± NA	36.50 ± NA	1.50 ± NA	0.11 ± NA	1	1	0	4	0	0
Simognathus minutus (Hodge, 1863)	5	adult	450.79 ± 20.79	374.39 ± 19.23	202.92 ± 43.67	76.40 ± 6.40	1.93 ± 0.54	0.17 ± 0.01	1	1	2	3	0	1
	7	juvenile	361.95 ± 45.32	298.18 ± 41.61	197.88 ± 41.56	53.03 ± 5.00	1.59 ± 0.13	0.16 ± 0.02	1	1	2	3	0	1

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660 **Table 3**. Summary of the average values (± standard error) of the number of species, number of
661 individuals, and hypervolume metrics for the samples grouped by habitat (leaves and matte) and
662 sampling campaign.
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Habitat	Sampling campaign	Richness	Dispersion	Evenness	Number of species	Number of individuals
leaves	total	0.007 ± 0.002	0.204 ± 0.009	0.076 ± 0.011	6.792 ± 0.481	58.583 ± 13.127
	December	0.001 ± 0.000	0.159 ± 0.005	0.029 ± 0.015	6.667 ± 0.615	146.167 ± 31.584
	March	0.011 ± 0.004	0.225 ± 0.017	0.105 ± 0.018	6.333 ± 1.202	24.333 ± 3.148
	April	0.014 ± 0.004	0.247 ± 0.012	0.124 ± 0.017	7.000 ± 1.033	22.167 ± 2.701
	August	0.003 ± 0.001	0.185 ± 0.013	0.046 ± 0.015	7.167 ± 1.138	41.667 ± 8.053
matte	total	0.026 ± 0.004	0.261 ± 0.008	0.213 ± 0.011	8.000 ± 0.662	15.053 ± 1.822
	December	0.025 ± 0.004	0.262 ± 0.013	0.216 ± 0.023	6.600 ± 1.364	13.2000 ± 3.967
	March	0.019 ± 0.005	0.243 ± 0.016	0.189 ± 0.016	9.400 ± 1.833	20.200 ± 5.305
	April	0.036 ± 0.008	0.285 ± 0.009	0.239 ± 0.022	7.667 ± 0.803	13.000 ± 1.592
	August	0.021 ± 0.01	0.239 ± 0.027	0.194 ± 0.012	8.667 ± 0.882	13.667 ± 0.333

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668 **Table 4**. Results of the linear models between metrics of functional diversity and ecological
669 variables, reported as type-II analysis-of-variance tables. Continuous predictors are log-
670 transformed. Bold values denote significant effects. Abbreviation: df = degrees of freedom
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Habitats	Response variables	Environmental predictors	df	F -value	p-value
Leaves	Richness	density of leaves	1	0.409	0.530
		length of leaves	1	4.543	**0.047**
		sampling campaign	3	2.980	0.059
		residuals	18		
	Dispersion	density of leaves	1	0.268	0.611
		length of leaves	1	4.667	**0.044**
		sampling campaign	3	5.368	**0.008**
		residuals	18		
	Evenness	density of leaves	1	0.001	0.976
		length of leaves	1	5.325	**0.033**
		sampling campaign	3	4.681	**0.014**
		residuals	18		
Matte	Richness	density of matte	1	0.007	0.937
		organic of matter	1	2.416	0.144
		sampling campaign	3	1.256	0.330
		residuals	13		
	Dispersion	density of matte	1	0.392	0.542
		organic of matter	1	1.268	0.280
		sampling campaign	3	1.856	0.187
		residuals	13		
	Evenness	density of matte	1	0.391	0.543
		organic of matter	1	0.026	0.875
		sampling campaign	3	0.676	0.582
		residuals	13		

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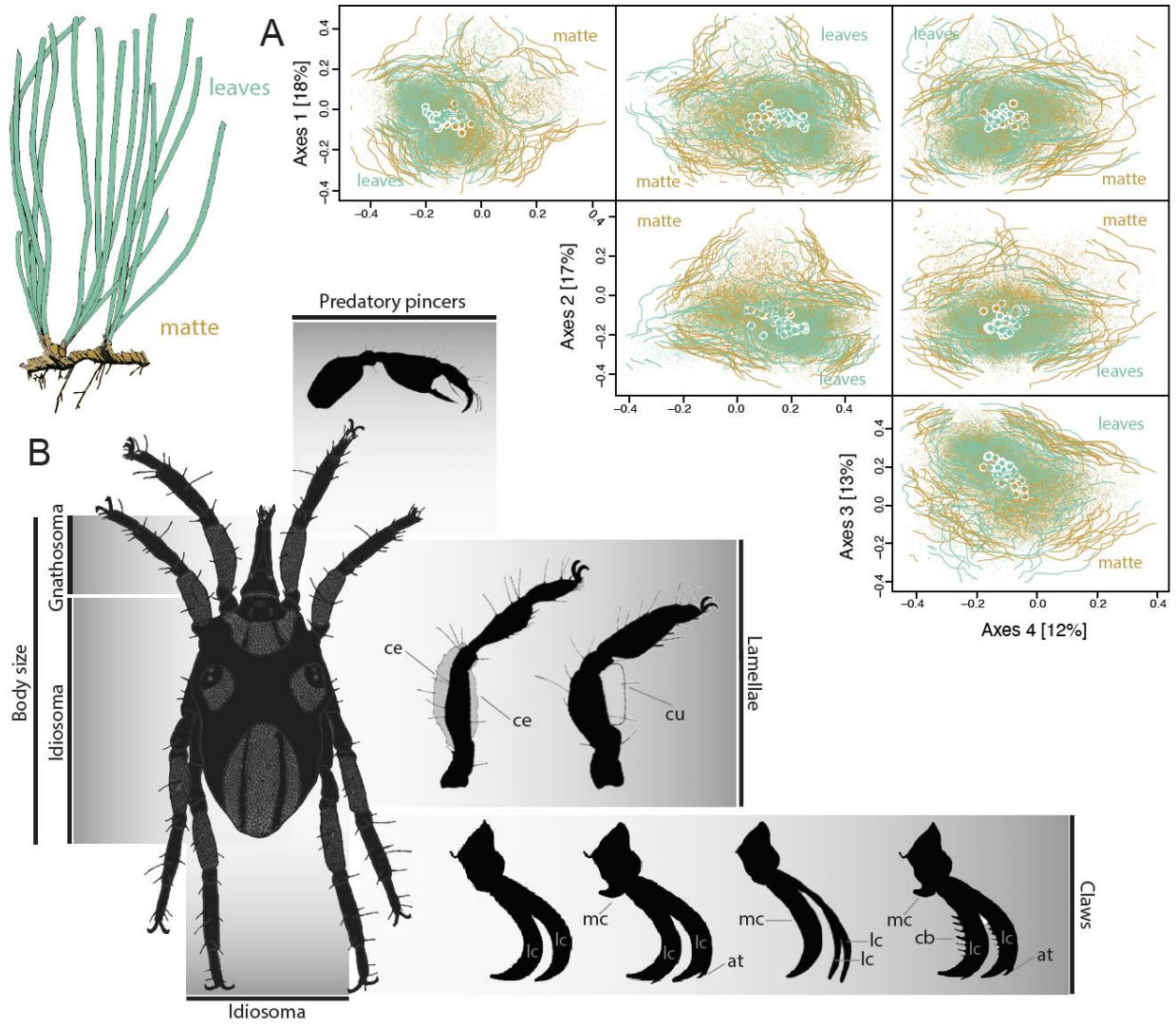

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675 **Figure 1. A)** The 4-dimensional hypervolume of the mite communities in the *Posidonia oceanica*
676 leaves (n=24) and matte (n=19). Large points with white borders represent the centroid of each
677 hypervolume (note that due to the proximity of centroids, most points appear superimposed). The
678 shape and boundaries of each hypervolume are defined by 1,000 random points. All points are
679 coloured according to the habitat. **B)** Summary of the morphological traits measured or estimated
680 for each species and developmental stage. Further details on the interpretation of each trait are
681 provided in Table 1 and 2, and the average values of traits across habitats in Figure S1.
682 Abbreviations: *at* accessory tooth, *cb* comb, *ce* ceratogegumental lamellae, *cu* cuticular lamellae,
683 *lc* lateral claw, *mc* median claw.

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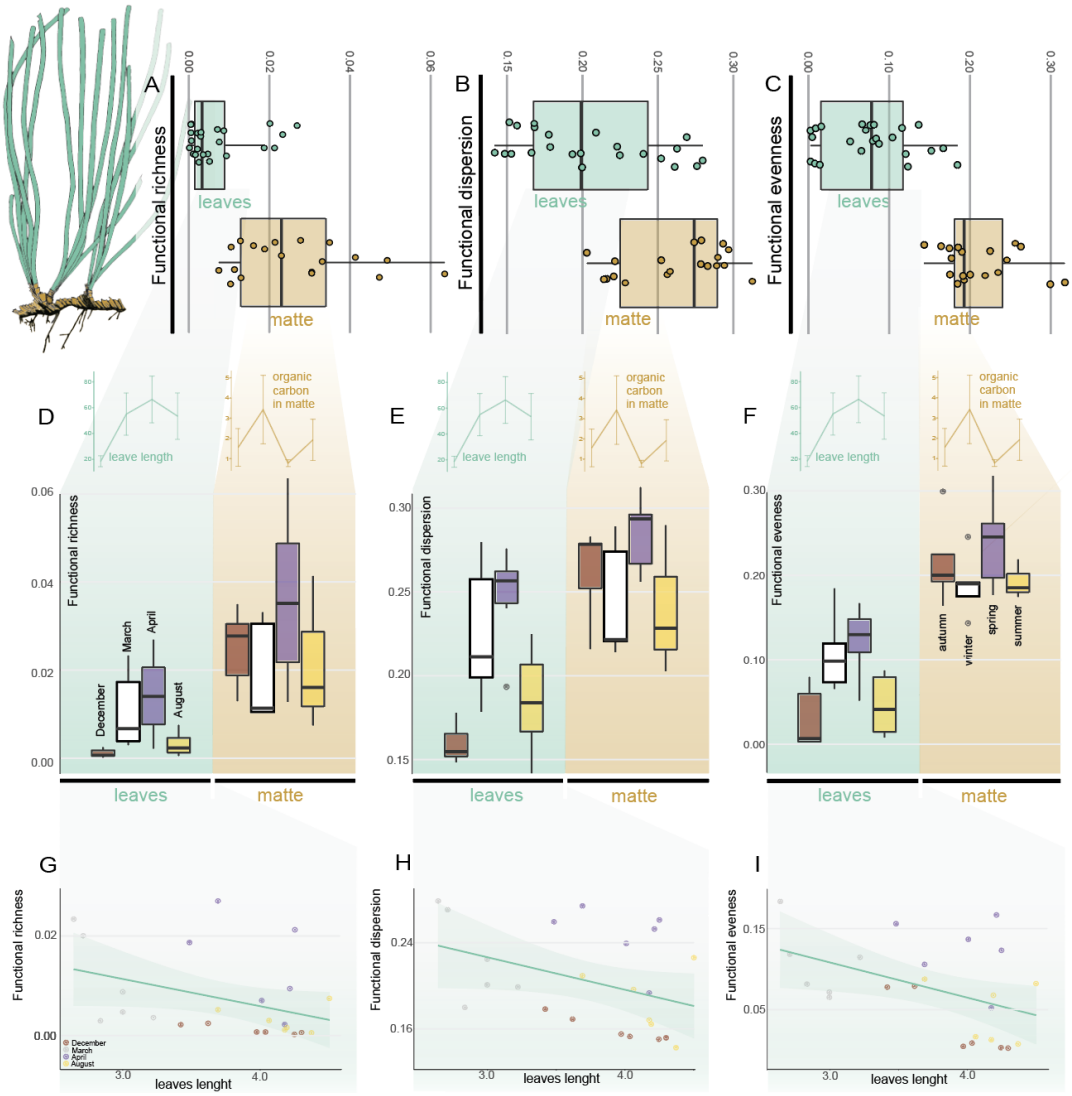

Figure 2. A–C) Overall differences in functional richness (A), dispersion (B) and evenness (C) between mite communities in leaves and matte. **D–F**) Differences in functional richness (D), dispersion (E) and evenness (F) across sampling campaigns. Each sampling campaign corresponds to a different period along the full phenological cycle of *Posidonia oceanica*. Inset graphs in D–F represent the variation in leaves mean length (in cm) for the leaves, and the organic matter content (in %) for the matte, thus reflecting the change in energy inputs due to the regeneration of leaves in the seagrass meadow across the four sampling campaigns. **G–I**) Effect of leaves length on functional richness (G), dispersion (H), and evenness (I); the regression lines together with the 95% confidence intervals are reported, and colours of the dots refer to the four sampling campaigns.

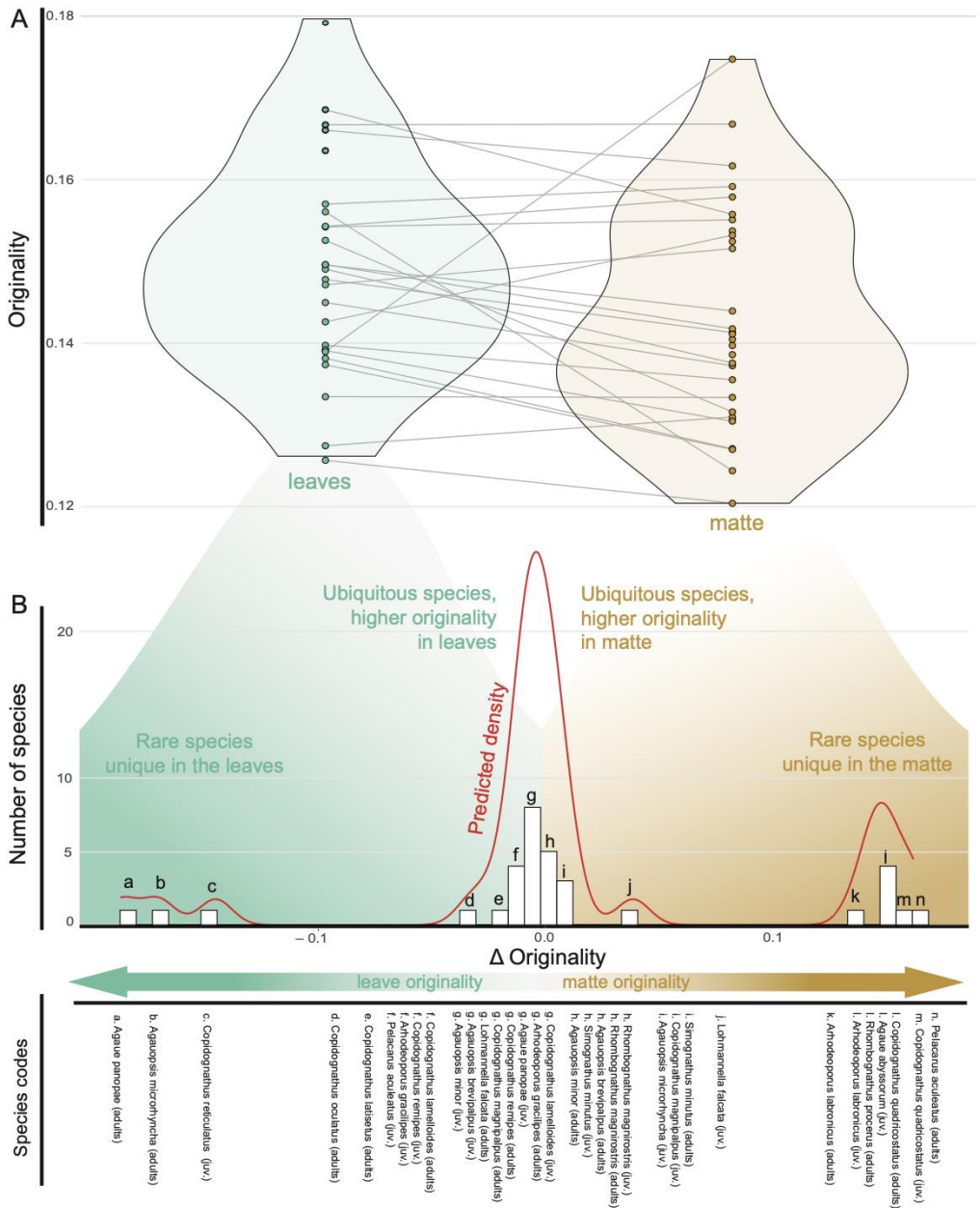

Figure 3. A) Violin plots showing the distribution of functional originality values of species in the leaves and the matte. Grey lines connect species that are present in both habitats. **B**) Histogram of Δ Originality values between species in the two habitats, calculated by subtracting the value of originality of each species in the leaves to the value of originality of each species in the matte. Orange smoothed lines show the predicted density of values according to a kernel density estimation. The letters above each bar correspond to the species listed at the bottom of the figure.

Supplementary material Figure S1

Habitat differences filter functional diversity of low dispersive microscopic animals

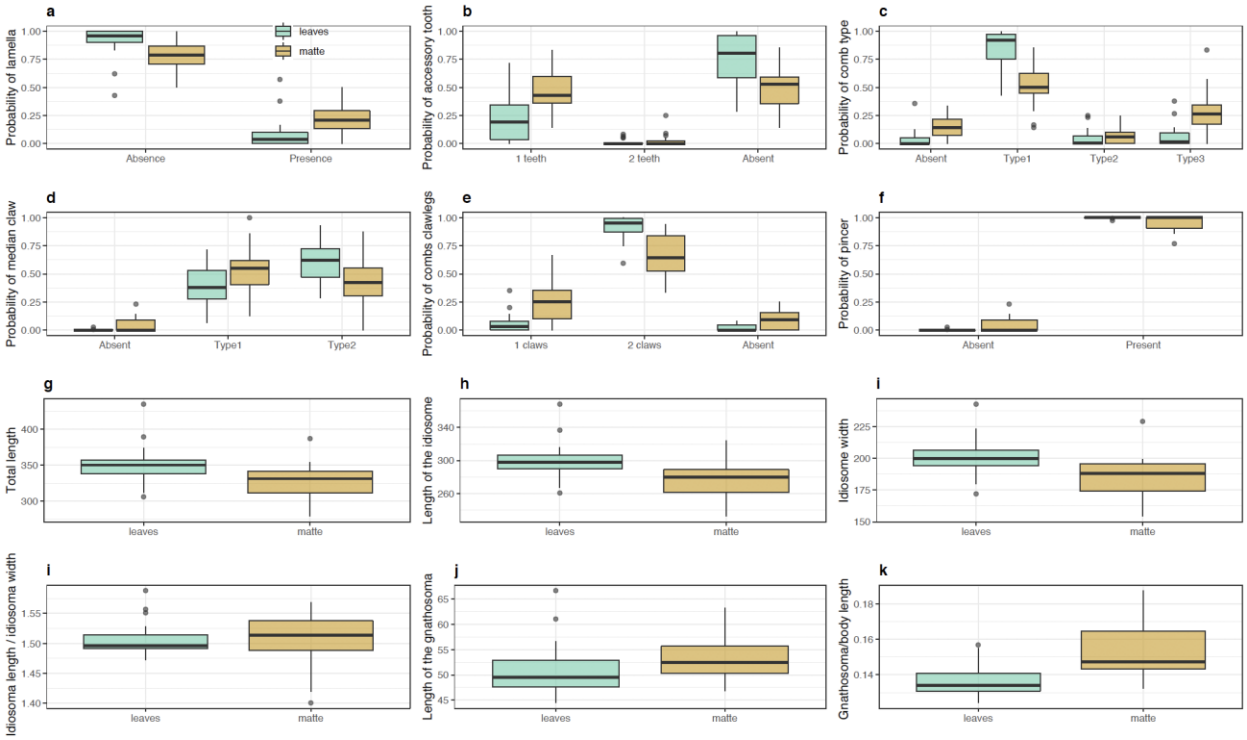

Figure S1. Probability of finding each state of discrete traits **(a–f)** and community weighted mean of continuous traits **(g–k)** for mite communities in the leaves and matte.

Supplementary Table

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Supplementary Material

02_Supplementary_table.xlsx