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

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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 characterisation of their functional traits, while the discrete nature of the two habitats alleviates the uncertainty in their ecological characterisation. 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 towards 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.

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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 among 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 (Kaczmarek et al., 2015; Bartels et al., 2020). 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 et al., 2013), therefore making it unclear to identify the differences between realised 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 et al., 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. Mori 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 (Mateo et al., 1997; Folkard, 2005) and

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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 hypothesise 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.

Materials 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 colonised 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 & Boyaci, 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, southeastern 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 (Fig. 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, 1985). 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 cm² of *Posidonia oceanica* (4 sampling campaign × 6
patches × 2 habitats, totalling 48 samples). In each patch, leaves were collected first by cutting them at the ligula 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 (Mabrouk 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 * 20 cm) and was constant in the matte (2 cm * 20 cm * 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).

| 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 colonisation of habitat consisting of narrow spaces. Indeed, slender shaped mites are often found among 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 inhabiting aquatic habitats, claws are essential to withstand physical stress, whether large (Pfingstl et al. 2020) or structural complex claws (Pugh et al., 1987; Bartsch, 2006). We here include four 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 |
| (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 | |
| (10) Number of legs with combs | Number of pairs of legs whose claws bear combs | Lamella are present mostly in species that occur in sediments (Bartsch, 2006) |
| (11) Lamella | Categorical, reflecting the presence/absence of cerotegumental or cuticular lamella on legs | Specialised legs for feeding (Green & Macquitty 1987; Bartsch, 2006) |
| (12) Pincer | Categorical, reflecting the presence of a first pair of legs modified as a pincer | |
### 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)

| Species name                           | Stage  | N    |    |    |    |    |    |    |    |    |    |    |
|----------------------------------------|--------|------|----|----|----|----|----|----|----|----|----|----|
| Agaue cf. abyssorum (Trouessart, 1896) |        |      |    |    |    |    |    |    |    |    |    |    |
|                                        |        |      |    |    | 1  | 2  | 3  | 4  | 5  | 6  | 7  | 8  |
|                                        | Juvenile| 394.58 ± NA | 323.52 ± NA | 242.92 ± NA | 71.06 ± NA | 1.33 ± NA | 0.18 ± NA |
|                                        | 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 |
| Agaue panopae (Lohmann, 1893)          |        |      |    |    |    |    |    |    |    |    |    |    |
|                                        |        |      |    |    | 5  | 6  | 7  | 8  | 9  | 10 | 11 | 12 |
|                                        | 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 |
|                                        | 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 |
| Agauopsis brevipalpus (Trouessart, 1889)|        |      |    |    |    |    |    |    |    |    |    |    |
|                                        |        |      |    |    | 3  | 4  | 5  | 6  | 7  | 8  | 9  | 10 |
|                                        | 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 |
|                                        | 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 |
| Agauopsis microrhyncha (Trouessart, 1889)|        |      |    |    |    |    |    |    |    |    |    |    |
|                                        |        |      |    |    | 9  | 10 | 11 | 12 | 13 | 14 | 15 | 16 |
|                                        | 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 |
|                                        | 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 |
| Arhodeoporus gracilipes (Trouessart, 1889) |        |      |    |    |    |    |    |    |    |    |    |    |
|                                        |        |      |    |    | 4  | 5  | 6  | 7  | 8  | 9  | 10 | 11 |
|                                        | 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 |
|                                        | 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 |
| Arhodeoporus labronicus (Morselli, 1981)|        |      |    |    |    |    |    |    |    |    |    |    |
|                                        |        |      |    |    | 5  | 6  | 7  | 8  | 9  | 10 | 11 | 12 |
|                                        | 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 |
|                                        | Adult   | 303.75 ± NA | 245.66 ± NA | 130.81 ± NA | 58.09 ± NA | 1.88 ± NA | 0.19 ± NA |
| Copidognathus lamelloides (Bartsch, 2000)|        |      |    |    |    |    |    |    |    |    |    |    |
|                                        |        |      |    |    | 2  | 3  | 4  | 5  | 6  | 7  | 8  | 9  |
|                                        | 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 |
|                                        | 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 |
| Copidognathus latisetus (Viets, 1940)  |        |      |    |    |    |    |    |    |    |    |    |    |
|                                        |        |      |    |    | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 |
|                                        | 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 |
|                                        | 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 |
| Copidognathus magnipalpus (Police, 1909) |        |      |    |    |    |    |    |    |    |    |    |    |
|                                        |        |      |    |    | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 |
|                                        | 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 |
| Copidognathus oculatus (Hodge, 1863)   |        |      |    |    |    |    |    |    |    |    |    |    |
|                                        |        |      |    |    | 8  | 9  | 10 | 11 | 12 | 13 | 14 | 15 |
|                                        | 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 |
|                                        | 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 |
| Copidognathus quadricostatus (Trouessart, 1894) |        |      |    |    |    |    |    |    |    |    |    |    |
|                                        |        |      |    |    | 1  | 2  | 3  | 4  | 5  | 6  | 7  | 8  |
|                                        | Adult   | 382.72 ± NA | 301.41 ± NA | 212.16 ± NA | 81.31 ± NA | 1.42 ± NA | 0.21 ± NA |
|                                        | Juvenile| 249.17 ± NA | 198.32 ± NA | 113.43 ± NA | 50.85 ± NA | 1.75 ± NA | 0.20 ± NA |
Table 2 continued

| Species name                      | N  | Stage   | 1    | 2    | 3    | 4    | 5    | 6    | 7    | 8    | 9    | 10   | 11   | 12  |
|-----------------------------------|----|---------|------|------|------|------|------|------|------|------|------|------|------|-----|
| *Copidognathus remipes* (Trouessart, 1894) |    | 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 |
|                                   |    | 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) |    | Adult   | 269.36 ± NA | 225.19 ± NA | 124.03 ± NA | 44.17 ± NA | 1.82 ± NA | 0.16 ± NA | 1 | 1 | 1 | 4 | 1 | 0 |
|                                   |    | 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 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Lohmannella falcata* (Hodge, 1863)  |    | 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 | 1 | 0 | 0 | 0 | 0 | 0 |
|                                   |    | 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 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Pelacarus aculeatus* (Trouessart, 1896) |    | 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 |
|                                   |    | Juvenile| 389.57 ± 61.61 | 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 |    | 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 | 0 | 1 | 0 | 0 | 0 |
|                                   |    | 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 |    | 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)  |    | 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 |
|                                   |    | 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 |

The number for each character and the explanation for the coding are summarised in Table 1

N total number of measured specimens, NA not available
The other traits, species-specific and not changing between individuals of different ages, were assigned at the species level.

**Functional space characterisation**

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 characterisation 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, 2021). 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 visualised 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 visualised 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 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. Then, we verified whether the originality values of species in the leaves were significantly different than those in the

Fig. 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.
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 randomisations. For each permutation, we estimated the standard effect size and associated p value.

To address Hypothesis 3, we explored the variation of functional metrics across sampling campaigns within each habitat using linear models. 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 the 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, 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 & Weisberg, 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 polarisation of the trait space according to the two habitats (Fig. 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 (Fig. 2A, Table 3).

Contrary to our Hypothesis 2, the distribution of the total functional originality values was similar in both habitats (Fig. 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 (Fig. 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 (Fig. 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 among 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 colonising 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 Fig. S1). These traits are chiefly specialised claws (Fig. 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 (Fig. S1g). In contrast, the assemblages in the matte consist of species bearing these traits, as well as species with more slender bodies (Fig. S1i) and a longer and pointier gnathosoma (Fig. 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 (Green & MacQuitty, 1987; Bartsch, 1989), 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

| Table 3 | Summary of the average values (± standard error) of the number of species, number of individuals, and hypervolume metrics for the samples grouped by habitat (leaves and matte) and sampling campaign |
|---------|-------------------------------------------------------------------------------------------------|
| 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 | 13.200 ± 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     |
the distance between each observation to a sample of stochastic points within the boundaries of the hyper-volume. 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 (Fig. 3a). This might be the case because the species with the highest values of originality—such as Pelacarucus 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 $\Delta$ Originality (Fig. 3b), as

| 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 |           |           |

Continuous predictors are log-transformed. Bold values denote significant effects.

df degrees of freedom
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 characterised 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 colonise 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 homogenisation 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 specialised meiofaunal organism that colonise the leaves (Zupo & 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 affected 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 (Hauspie & Polk, 1973; Hagerman & Rieger, 1981; Armonies, 1988), increasing the uncertainty associated with habitat characterisation at a small scale relevant for their biology, thus overestimating both their functional and realised 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 towards 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.

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Author contributions 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, DF, and SM wrote the first draft. All authors contributed to the writing to additions and comments to the text.

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

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