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

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1 **Habitat differences filter functional diversity of low dispersive microscopic animals**

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23
24
25
26 **Author contribution statement**

27
28 AM, GGG, AGH, and NS planned the sampling design. GGG, AGH, and NS sampled, sorted, and
29 identified animals and collected traits. AM and SM planned the statistical approach and performed
30 analyses. FP provided facilities and support. AM, GGG, and SM wrote the first draft. All authors
31 contributed to the writing to additions and comments to the text.

32
33
34
35 **Data availability statement**

36
37 Raw data and R script to generate the analyses will be deposited in a public repository upon acceptance.

41 **Abstract**

42

43 1. Whereas the study of patterns of distribution of microscopic animals has long been dominated by the
44 ubiquity paradigm, we are starting to appreciate that microscopic animals are not as widespread as
45 previously thought and that habitat preferences may have a strong role in structuring their patterns of
46 occurrence. However, we still ignore to what extent and through which mechanisms the environment
47 selects for specific communities or traits in microscopic animals. This gap is partly due to the lack of data
48 on the relevant traits of many species, and partly because measuring environmental variables at an
49 appropriate resolution may be problematic.

50 2. We here overcome both issues by analysing the functional space of marine mite communities living in
51 a sea-grass (*Posidonia oceanica*) meadow across two habitats: the leaves and the matte. The strictly
52 benthic lifestyle and the conserved morphology of mites allow for unambiguous characterization of their
53 functional traits, while the discrete nature of the two habitats alleviates the uncertainty in their ecological
54 characterization.

55 3. Our results show that habitat filters the distribution of certain traits favouring a higher diversity,
56 dispersion, and evenness of functional traits in the matte than in the leaves. We further observed temporal
57 variations in the functional diversity of communities, potentially following the seasonal renovation and
58 decay of seagrass leaves. However, in spite of the stark ecological differences between the two habitats
59 and across seasons, the filtering effect is partial and affects mostly relative species abundances.

60 4. We conclude that in other microscopic organisms, habitat filtering might appear even more subtle
61 especially if they are capable of long distance dispersal or occur in ecological systems where
62 environmental variables vary continuously or fluctuate through time. Our study therefore emphasises the
63 need of moving from a merely taxonomical toward a functional view of ecological studies of microscopic
64 organisms if we want to achieve a mechanistic understanding of their habitat and distribution patterns.

65

66 **Keywords:** Functional originality; meiofauna; Grinnellian niche; n-dimensional hypervolumes; trait
67 ecology

68

69 **Introduction**

70

71 It is unlikely to see buffaloes grazing on the sea surface or whales gliding in the sky (Adams, 1984).
72 However, as the body size of animals decreases, the probability increases of encountering them in places
73 where *they are not supposed to be*. This is because the realised niche of a microscopic animal—namely,
74 where it can be actually found—can extend well beyond the set of abiotic conditions that allow positive

75 population growth rates (Grinnellian niche). These broad ecological ranges are more frequent amongst
76 microscopic animals possessing traits that facilitate long distance dispersal such as dormancy, long term
77 viability, and parthenogenesis (Fontaneto & Hortal, 2013, Fontaneto, 2019). Similar traits are found, for
78 example, in many species of nematodes (Fonseca & Netto, 2015), rotifers (Fontaneto, Barraclough, Chen,
79 Ricci, & Herniou, 2008), and tardigrades (Bartels, Kaczmarek, Rozkowska, & Nelson, 2020; Kaczmarek,
80 Michalczyk, & McInnes, 2015). In comparison, some lineages of microscopic organisms are specialised
81 to thrive within narrow ranges of environmental conditions like caves (Mammola et al., 2020), mountain
82 summits (Hoschitz & Kaufmann, 2004), hydrothermal vents (Zeppilli et al., 2018), and deep terrestrial
83 subsurface habitats (Borgonie et al., 2011). Many of these animals evolved distinct and often convergent
84 traits for these specific conditions. Quintessential examples are microscopic annelids and copepods
85 specialised to feed in the chemocline of certain aquatic caves (Martínez et al., 2019; Worsaae et al.,
86 2019); or mouthless species of nematodes and flatworms living in strict association to prokaryotic
87 symbiont in anoxic marine sediments (Ott, Rieger, Rieger, & Enderes, 1982).

88 The corollary of these examples is that not only the body size but also the presence of certain
89 traits and the interaction between them and the environment determines the ecological range of
90 microscopic organisms. This is nothing new, as this idea was already grasped in the original formulation
91 of the “*everything small is everywhere*” paradigm, which included the postil “*...but the environment*
92 *selects*” (Baas-Becking, 1934; Bass & Boenigk, 2011). So we now stand to a point where we know that
93 even broadly distributed and apparently generalist species may not be actually so widespread and tolerant
94 when their habitat preferences are taken into account (or, in other words, that the density of individuals
95 across the distribution range of a given species is not homogeneous as it varies across habitats). But,
96 unfortunately, this filtering effect has proven difficult to quantify, partly due to the lack of data on the
97 relevant traits of many microscopic animals (Giere, 2008) and partly due to the intrinsic problem of
98 measuring relevant environmental variables at appropriate resolutions (Levin, 1992; Potter, Arthur
99 Woods, & Pincebourde, 2013) overestimating the Grinnellian niche (Soberón & Nakamura, 2009). These
100 two issues have challenged all community-level studies that have so far attempted to directly link
101 functional traits of microscopic animals and their distribution patterns at the relevant scale (Fontaneto et
102 al. 2011). In other words, we ignore to what extent and through which mechanisms the environment
103 selects for specific communities and their traits.

104 We here set to examine the effect of habitat on the distribution of microscopic animals by
105 comparing the multidimensional functional space (Blonder, Lamanna, Violle, & Enquist, 2014; Blonder
106 et al., 2018) of assemblages of mites dwelling on a seagrass [*Posidonia oceanica* (L.)] meadow in the
107 Mediterranean—a marine plant with a well-studied architecture and growth pattern (Molenaar,
108 Barthélémy, De Reffye, Meinesz, & Mialet, 2000). Due to their strictly benthic life mode and easy-to-

109 measure external traits with a clear functional meaning, marine mites are an excellent model system for a
110 similar analysis. Furthermore, the patchy distribution of seagrass within meadows provides independent
111 replicates of discrete habitats, the leaves versus the matte (i.e., the grid formed by rhizomes, roots, and
112 trapped particles). Because these two habitats present different environmental conditions and availability
113 of food, we expect that they will filter different mites from the pool of species present in the meadow. We
114 expect that this filter will be evidenced in the community traits, favouring the dominance of more
115 specialised phytophagous or epiphytes feeder species in the leaves, and limiting the presence of
116 generalistic detritivorous species to the matte. We therefore hypothesise that i) at the community level,
117 there should be higher diversity, dispersion, and evenness of functional traits in the matte than in the
118 leaves. As a corollary of the previous hypothesis, we also expect that ii) at the species level, the higher
119 diversity of traits in the matte will be reflected by the presence of more functionally original species.
120 Furthermore, the annual phenological changes due to the seasonal renovation and decay of seagrass
121 leaves affects nutrient availability (Drew, 1978; Zupo, Buia, & Mazzella, 1997). So, we also hypothesize
122 iii) temporal variations in the functional diversity of mite communities following the annual cycle of *P.*
123 *oceanica*, particularly on the leaves.

124

125 **Material and Methods**

126

127 *Model organism*

128 The model organisms selected for this study are marine mites of the family Halacaridae (subsequently
129 referred to as marine mites), a lineage of microscopic arachnids that colonized the ocean from a terrestrial
130 ancestor around 270 million years ago, radiating in different types of marine habitats (Pepato, Vidigal, &
131 Klimov, 2018). Due to this terrestrial origin, the body plan of the group is constrained, being all forms
132 strictly restricted to benthic habitats. The impossibility of marine mites to swim or disperse by any other
133 means than crawling in direct contact with the substrate, ensures that the species found in each sample
134 belong to the local community. This feature places marine mites among those with a realised niche that is
135 smaller than the potential Grinnellian niche, even if they are microscopic: not all available habitats in an
136 area are colonised, and the animals are not found in habitats that cannot sustain viable populations.
137 Furthermore, the presence of a hard, hydrophobic cuticle allows for a precise measurement of
138 morphological traits even in fixed material, reducing measurement errors. Finally, the conserved
139 morphology ensures unequivocal homology assessment of the functional traits. These three properties—
140 dispersal exclusively by crawling, hard cuticle, and conserved morphology—make marine mites ideal
141 candidates for quantifying the effect of habitat filtering on the distribution and functional diversity of
142 microscopic animals.

143

144 *Habitats and sampling design*

145 As a study area, we selected the exposed seagrass meadow of Cala del Cuartel, in Santa Pola, south-
146 eastern Spain (38° 12' 34.04" N, 0° 30' 19.12" W, WGS84 reference system), consisting of replicated
147 patches at 4–7 m depth separated by bare sandy tongues. Marine mites prefer the *P. oceanica* patches and
148 are rarely found in the sand (García-Gómez et al., submitted). So, in relation to the size and dispersal
149 capabilities of the marine mites, each patch represents a discrete and independent replica of the same
150 habitat within a larger area. The fact that all the patches are within the same bay limits the confounding
151 effect of depth, temperature, salinity, or different exposition to currents.

152 Each patch consists of two compartments representing the two different habitats, the leaves and
153 the matte (Figure 1A). The leaves are exposed to turbulence and affected by seasonal changes in length
154 and growth of epiphytic algae and epifauna, which potentially represents the main source of food for the
155 mites (Pugh & King, 1985a). In contrast, the matte is sheltered and offers a high and constant availability
156 of detritus throughout the year.

157 In each season between December 2015 and August 2016, scuba divers sampled these two
158 habitats (leaves and matte) in six randomly selected patches of 400 cm² of *Posidonia oceanica* (4 season
159 x 6 patches x 2 habitats, totalling 48 samples). In each patch, leaves were collected first by cutting them at
160 the ligulae level, while the surface of the underlying matte was scraped into a separate container.

161 Meiofauna from each sample was extracted combining the magnesium chloride and the ‘bubble
162 and blot’ decantation techniques to ensure the recovery of all species of marine mites (Higgins & Thiel,
163 1988; Sørensen & Pardos, 2008). The selected mesh size was 62 µm to collect both juveniles and adult
164 forms. Each sample was bulk fixed using 7% formaldehyde in the field. All studied material has been
165 deposited at the Laboratory of Meiofauna at the Universidad Complutense de Madrid.

166 In each habitat, we estimated a proxy for the availability of food. For each leaves sample, we
167 estimated the average length of the leaves as the distance from the ligula to the apical end of all the
168 complete leaves. Length of the leaves is known to correlate with the abundance of epiphytic organisms
169 (Malbrouk, Hamza & Bradai, 2011). For each matte sample, we directly measured the percentage of
170 organic carbon using the approach by Walkley & Black (1934).

171

172 *Species identification and morphological traits measurement*

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

178 For each species, we examined 13 morphological traits related to body size and shape, the ability
179 to withstand the water currents, and trophic specialisation (Table 1). Body size and shape measures were
180 taken on all 502 well-preserved specimens from our samples. The traits were estimated separately from
181 adults and juveniles (larval or nymphal stages), as different life stages exhibit different ecological
182 preferences and dispersal capabilities even within the same species (Bartsch, 2002; Somerfield & Jeal,
183 1995; 1996). The other traits, species-specific and not changing between individuals of different ages,
184 were assigned at the species level.

185

186 ***Functional space characterization***

187 We expected the properties of the functional space to vary between the two different habitats, reflecting
188 the habitat filtering effect in sorting the mite communities according to the presence of certain traits.
189 Furthermore, we expected seasonal variations in the functional space in relation to the phenological
190 changes of the *P. oceanica* meadow through the year. Therefore, we performed two sets of analyses: one,
191 grouping all the samples from each habitat; and another, in which the samples were separated according
192 to different surveys, each corresponding to a season.

193 We represented the functional space of mite communities in the two habitats and across seasons
194 with geometrical n -dimensional hypervolumes (Blonder et al., 2014, 2018). Since some of the functional
195 traits considered here are categorical, we applied a Gower dissimilarity measure to the complete trait
196 matrix and extracted orthogonal morphological axes through principal coordinate analysis (Carvalho &
197 Cardoso, 2020; Mammola & Cardoso, 2020). We delineated hypervolumes with the R package
198 '*hypervolume*' (Blonder & Harris, 2018) using a gaussian kernel density estimate (Blonder et al., 2014,
199 2018), the first four principal coordinate axes (cumulatively 60% variance explained), a default
200 bandwidth for each axis, and species abundances. A gaussian kernel density estimation was selected as it
201 allows a probabilistic rather than a binary characterization of the functional space (Mammola & Cardoso,
202 2020). Five samples with one or no species were removed from the analyses. We analysed the properties
203 of the hypervolumes with specific indices (Mammola & Cardoso, 2020) implemented in the R package
204 'BAT' (Cardoso, Rigal, & Carvalho, 2015; Cardoso, Mammola, Rigal, & Carvalho 2020). For each set of
205 analyses, we expressed functional diversity with the *kernel.alpha* function as the total volume of the
206 functional space. We verified if communities in mat and leaves and across seasons were subjected to

207 different filtering processes by calculating the dispersion of the functional space with the
208 *kernel.dispersion* function and the ‘divergence’ method (Mammola & Cardoso, 2020). The regularity of
209 traits distributions within the total functional space was verified using the *kernel.evenness* function, which
210 expresses evenness as the overlap between the input hypervolume and a theoretical hypervolume whose
211 traits and abundances are evenly distributed within their possible range (Mammola & Cardoso, 2020).

212 We inspected whether certain assemblages of mite species act as indicators of the two habitats,
213 and which species contribute most original traits to each habitat (i.e., functional outliers; Violle et al.,
214 2017). In particular, we expect the distribution of the originality values to have a smaller variation in the
215 leaves than in the matte, reflecting the stronger filtering effect exerted by this habitat compared to the
216 matte. We calculated the functional originality of each species in each community with the function
217 *kernel.originality*, weighting originality by species abundance (Mammola & Cardoso, 2020). We
218 expressed originality as the average distance between each species to a sample of 10% stochastic points
219 within the boundaries of the hypervolume. For each habitat, we expressed the total originality of a species
220 as the average originality of the species across all communities in which it was present. Also, in this
221 analysis, we considered the stages of the same species separately.

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

230 To ease the interpretation of our findings, we finally calculated the probability of recovering a
231 given trait within each habitat as the community weighted mean with the *cwm* function in ‘BAT’. For
232 categorical traits, we calculated instead the probability of finding each state of the trait in each habitat
233 using a function developed *ad hoc* for this study—see R code uploaded alongside this submission.

234

235

236 **Statistical analyses**

237 We performed analysis of variance (ANOVA) to evaluate the significance of the differences observed in
238 functional diversity, dispersion, and evenness between the matte and the leaves samples (Hypothesis 1),
239 as well as amongst seasons (Hypothesis 3). When there was a significant effect of season, we performed a
240 post hoc Tukey Honestly Significant Difference test to identify significant differences between pairs of

241 seasons, using the R package ‘multcomp’ (Hothorn, Bretz, & Westfall, 2008). We verified whether the
242 originality values of species in the leaves were significantly higher and lower than those in the matte
243 using a null modelling approach (Hypothesis 2). We performed 99 permutations of the species between
244 the two habitats, keeping fixed the original abundance values. For each run, we recalculated the
245 hypervolumes and the originality values and estimated how many species in the leaves had higher
246 originality than the species in the matte. As in Mammola et al. (2020), the null hypothesis of random
247 sorting of species between the two habitats was rejected if the observed value was higher than the 97.5
248 percentile or lower than the 2.5 percentile of the 99 randomizations. For each permutation, we estimated
249 the standard effect size and associated p-value.

250

251 **Results**

252

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

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

265 There was a pronounced seasonal variability in the functional space of leave communities (Figure
266 2B), reflected in the differences in functional diversity ($F_{(3,20)} = 5.146$, $p = 0.008$), dispersion ($F_{(3,20)} =$
267 10.35 , $p < 0.001$), and evenness ($F_{(3,20)} = 7.593$, $p = 0.001$) among seasons. In coincidence with the peaks
268 of production of the meadow (Figure 2B, in-set graph), all three metrics were significantly higher in
269 spring than in autumn and summer (Post-Hoc test: all $p < 0.05$). Functional dispersion and evenness were
270 also significantly higher in winter than in autumn (Post-Hoc test: both $p < 0.05$). All other seasonal
271 comparisons in the leaves were not significant (Post-Hoc test: all $p > 0.05$). In contrast, the seasonal
272 pattern was not significant in the matte, neither for richness (ANOVA: $F_{(3,15)} = 1.33$, $p = 0.303$), nor for
273 dispersion ($F_{(3,15)} = 2.13$, $p = 0.139$) nor evenness ($F_{(3,15)} = 1.32$, $p = 0.306$).

274

275 **Discussion**

276

277 *Spatial patterns in functional diversity*

278 Our analyses confirmed our first hypothesis that mite communities in matte habitat had a significantly
279 higher functional richness, dispersion, and evenness than those in the leaves. Analytically, this means
280 that, on average, the functional space in the leaves is significantly less voluminous (*i.e.* trait diversity is
281 lower) and observations are less dispersed (*i.e.* species have traits that are more similar amongst them)
282 and less even (*i.e.* the traits hypervolume is not homogenous indicating that certain combinations of traits
283 are more common than others) than in the matte. Biologically, this suggests that the selective conditions
284 in the leaves exert a stronger filtering effect upon the traits present in the colonizing species, whereby
285 only a small subset from all the pool of traits present in the seagrass meadow allows mites to thrive in the
286 leaves. This habitat filtering is reflected in the distribution of mites between habitats: even if the habitats
287 are physically connected, communities in the leaves consist of a subset of the species present in the matte.
288 The leaves are the habitat in which it is more likely to find individuals bearing specialised traits
289 (Supplementary Material Figure S1). These traits are chiefly specialised claws (Figure S1d, S1e), which
290 might aid in clinging to the leaf's surface and thereby withstand turbulence (e.g. Pflingstl, Kerschbaumer,
291 & Shimano, 2020; but see Pugh, King, & Fordy, 1987) and a larger body size (Figure S1g). In contrast,
292 the assemblages in the matte consist of species bearing these traits, as well as species with more slender
293 bodies (Figure S1i) and a longer and pointier gnathosoma (Figure S1j). Whereas the slender body
294 presumably aids this species to crawl in the tighter habitat spaces in the matte, as observed in most
295 interstitial microscopic species (Giere 2008), it is more difficult to interpret the functional meaning of the
296 elongation of the gnathosoma. We here speculate that it might aid this species in feeding on detritus and
297 deposits of organic matter accumulated in the tight spaces, but more in-depth studies would be needed to
298 corroborate this assumption. A third group of species, presumably consisting of predators feeding on
299 mites (Bartsch, 1989; J. Green & MacQuitty, 1987), are found occasionally in some of the samples,
300 occurring stochastically both in the leaves and the matte as they wander around in the meadow searching
301 for their prey.

302 This general pattern further emerges from the analysis of originality values, a metric that averages
303 the distance between each observation to a sample of stochastic points within the boundaries of the
304 hypervolume. It thereby measures how unique the position of individual observations is in the trait
305 hyperspace, as the distances are expected to increase as the species' combination of traits becomes unique
306 (Mammola & Cardoso, 2020). Therefore, we expected more functionally original species in the matte,
307 because species in the leaves need special adaptations presumably to cope with turbulence and feed on
308 specialised food sources. The same adaptations are not required in the matte, where the presence of

309 shelters and more diverse sources of food might relax the filtering effect on species and traits. This might
310 result in a more functionally heterogeneous assemblage in which the probability of finding a given
311 species is less dependent upon their traits. Our results, however, did not support this assumption given
312 that originality values in the leaves did not differ significantly from those in the matte (Figure 3a). This
313 might be the case because the species with the highest values of originality—such as *Pelacarus aculeatus*,
314 *Agaue panopae*, *Agauopsis microrhyncha*, or *Agaue abyssorum*; Table S1—typically consisted of large
315 rare species with uncommon traits that facilitate predation upon other microscopic animals, including
316 mites (Bartsch, 1989; Green & MacQuitty, 1987). These species also occur in low abundances and their
317 distribution is scattered across the meadow, being found stochastically in one habitat or the other. In fact,
318 these species can be considered functional outliers (*sensu* Violle et al., 2017) in that they take extreme
319 values of Δ Originality (Figure 3b), as they only occur in low numbers in either habitat, thus indicating
320 that the filtering may act at another spatial or temporal scale on them. However, we acknowledge that
321 further studies on the feeding biology of marine mites would be needed to fully understand the biological
322 mechanisms behind the ecological patterns we documented.

323

324 ***Temporal patterns in functional diversity***

325 Our results partially corroborate our third hypothesis, as we found significant temporal variations in the
326 functional diversity of mite communities in the leaves likely following the annual cycle of the *Posidonia*
327 *oceanica*. As above, these changes permeate all metrics, which were significantly higher in spring than in
328 autumn and summer, in coincidence with the spring peaks of production in the meadow. Functional
329 dispersion and evenness were also significantly higher in winter than in autumn.

330 The end of the summer is characterized in the Mediterranean by an increase of the rainfall and
331 primary production, which favours a rapid growth of *P. oceanica* in winter reaching a peak in the biomass
332 in the seagrass meadow in spring (Champenois & Borges, 2014). A large number of epiphytes colonize
333 the leaves, which get densely populated by diverse epiphytic communities (Mabrouk, Hamza, Brahim, &
334 Bradai, 2011; Piazzini, Balata, & Ceccherelli, 2016), as they enlarge. Food resources are hence more
335 abundant and diverse in the leaves at their peak of production in spring, which positively feedbacks the
336 mite populations. Furthermore, the basal parts of long leaves are less exposed to hydrodynamics, as leaves
337 themselves provide shelter from the current towards the bottom (Folkard, 2005). These two factors,
338 increase of food and higher shelter, presumably result in a milder ecological filter, enhancing the
339 possibility for different mites to exploit this habitat and reproduce therein. Indeed, juveniles, which have
340 not developed yet all their adult traits to withstand currents (e.g. smaller body or legs with fewer
341 segments, yet provided with claws as in adults), become dominant in the long leaves exclusively in spring
342 (García-Gómez et al., submitted).

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

346

347 ***Conclusion***

348 Being the first study using hypervolumes to define functional properties of meiofauna communities, our
349 study highlights a potential role of the environment in affecting the distribution of microscopic animals
350 between connected habitats by filtering them according to the presence of certain traits. Remarkably, this
351 filtering effect was relatively weak, as most species were found in both habitats and the filtering was
352 mostly reflected by their relative abundances. Therefore, one may argue that our results of filtering effects
353 between connected habitats might not be applied to all microscopic animals more widely and that mites in
354 seagrass meadows might represent only a specific case. Similar filtering effects might be even more
355 subtle and difficult to isolate in other microscopic animal groups (rotifers, tardigrades, and soft-bodied
356 groups) for which the functional interpretation of morphological traits is often obscure and trait
357 measurements subjected to strong artefacts due to post-mortem contraction, fixation, and other bias
358 (Higgins & Thiel, 1988). Furthermore, most microscopic animals have a high probability to be passively
359 dispersed to suboptimal habitats (Armonies, 1988; Hagerman & Rieger, 1981; Hauspie & Polk, 1973),
360 increasing the uncertainty associated with habitat characterization at a small scale relevant for their
361 biology, thus overestimating their potential Grinnellian niche.

362 Therefore, it is not surprising that in such studies the distribution of microscopic animals might
363 appear either uniform or random, simply as a consequence of the high uncertainty associated with
364 measurements and morphological interpretation at the small spatial scales. In other words, microscopic
365 size may generate uncertainty in a macroscopic observer, on both the definition of traits and the definition
366 of niche even if *the environment did select*. Exploring the distribution of small animals through the lens of
367 functional ecology, targeting traits with clear functional meaning related to habitat occupation, is crucial
368 to overcome some of these biases (Violle, Reich, Pacala, Enquist, & Kattge, 2014). Our study therefore
369 emphasises the need of moving from a merely taxonomical toward a functional view of ecological studies
370 of microscopic organisms (Green, Bohannan, & Whitaker, 2008).

371

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373

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386 **Supplementary materials online**

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388 **Table S1.** Summary traits, number of examined individuals, and originality values per species and life
389 stage. The definition of each trait is included in Table 1.

390

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

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554 **TABLES & FIGURES**

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

Trait	Variable description	Functional meaning
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.
Idiosome length	Idiosome dorsal length	Proxy of the hard body length.
Idiosome width	Idiosome dorsal width	Proxy of the hard body width.
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).
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).
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.
Accessory tooth	Categorical, reflecting the presence/absence of an accessory tooth on claws	In mites, especially those species linked to aquatic habitats, claws are essential to withstand physical stress, whether large (Pfungstl et al. 2020) or structural complex claws (Pugh & Fordy, 1987; Bartsch 2006).
Combs	Degree of comb complexity, where 0 = absence, 1 = fine, 2 = regular, and 3 = large combs	We here include four claw structures to account for different possible combinations

Median claw type	Degree median claw development, where 0 = absence, 1 = small, and 2 = large median claw	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.
Number of legs with combs	Number of pairs of legs whose claws bear combs	
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).
Pincer	Categorical, reflecting the presence of a first pair of legs modified as a pincer	Specialised legs for feeding (Green & Macquitty 1987; Bartsch 2006).

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559 **Table 2.** Summary of the average values (\pm standard error) of the number of species, number of
 560 individuals, and hypervolume metrics for the samples grouped by habitat (leaves and matte) and season.

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Habitat	Season	Richness	Dispersion	Evenness	Number of species	Number of individuals
leaves	total	0.007 \pm 0.002	0.204 \pm 0.009	0.076 \pm 0.011	6.792 \pm 0.481	58.583 \pm 13.127
	autumn	0.026 \pm 0.004	0.261 \pm 0.008	0.213 \pm 0.011	6.667 \pm 0.615	146.167 \pm 31.584
	winter	0.001 \pm 0	0.159 \pm 0.005	0.029 \pm 0.016	7 \pm 1.033	22.167 \pm 2.701
	spring	0.011 \pm 0.004	0.225 \pm 0.017	0.106 \pm 0.018	7.167 \pm 1.138	41.667 \pm 8.053
	summer	0.014 \pm 0.004	0.248 \pm 0.012	0.122 \pm 0.017	6.333 \pm 1.202	24.333 \pm 3.148
matte	total	0.003 \pm 0.001	0.185 \pm 0.013	0.046 \pm 0.015	8.000 \pm 0.662	15.053 \pm 1.822

	autumn	0.025 ± 0.004	0.262 ± 0.013	0.216 ± 0.023	6.6 ± 1.364	13.2 ± 3.967
	winter	0.019 ± 0.005	0.244 ± 0.016	0.189 ± 0.017	7.667 ± 0.803	13 ± 1.592
	spring	0.036 ± 0.008	0.285 ± 0.009	0.239 ± 0.021	8.667 ± 0.882	13.667 ± 0.333
	summer	0.022 ± 0.01	0.24 ± 0.026	0.193 ± 0.013	9.4 ± 1.833	20.2 ± 5.305

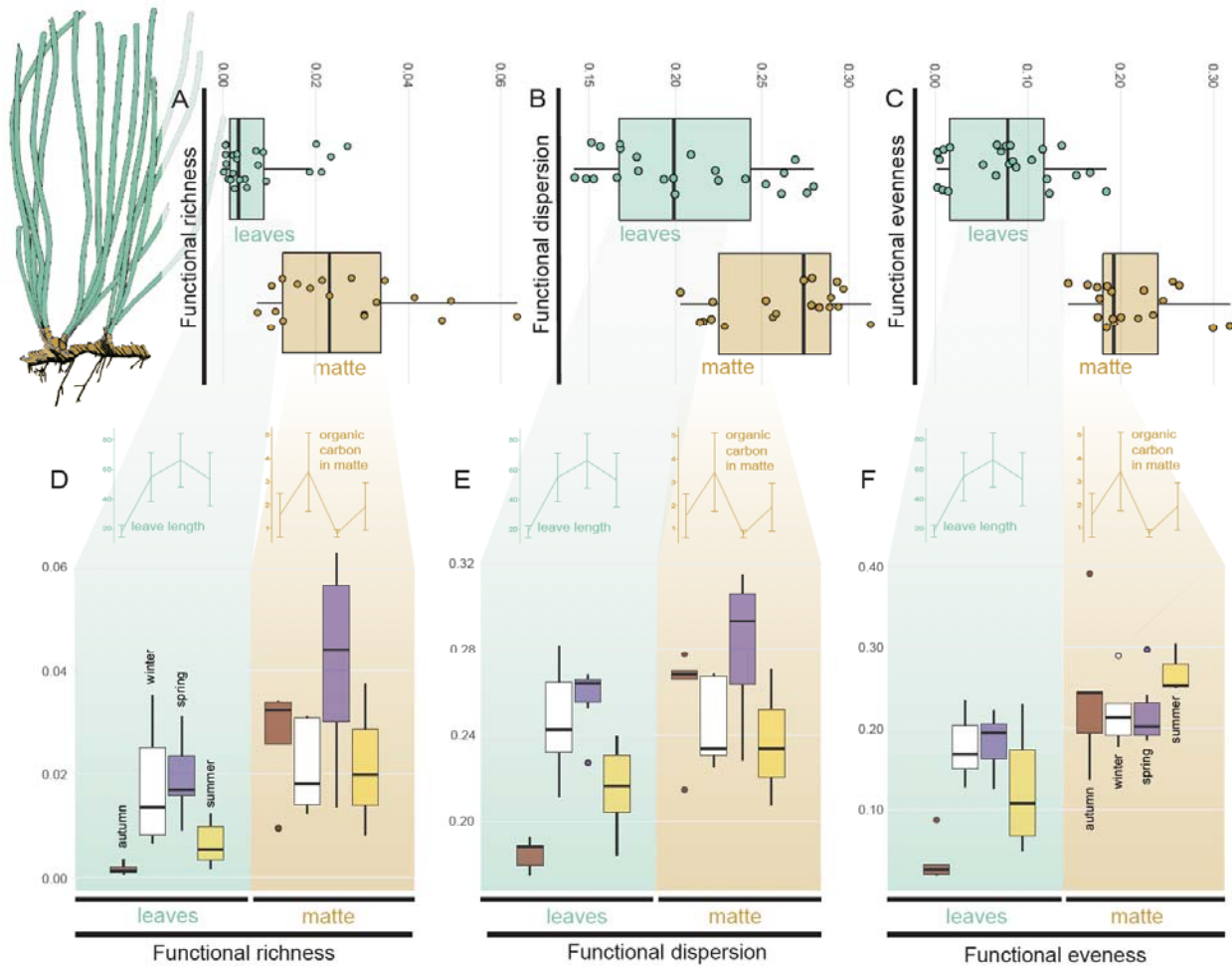
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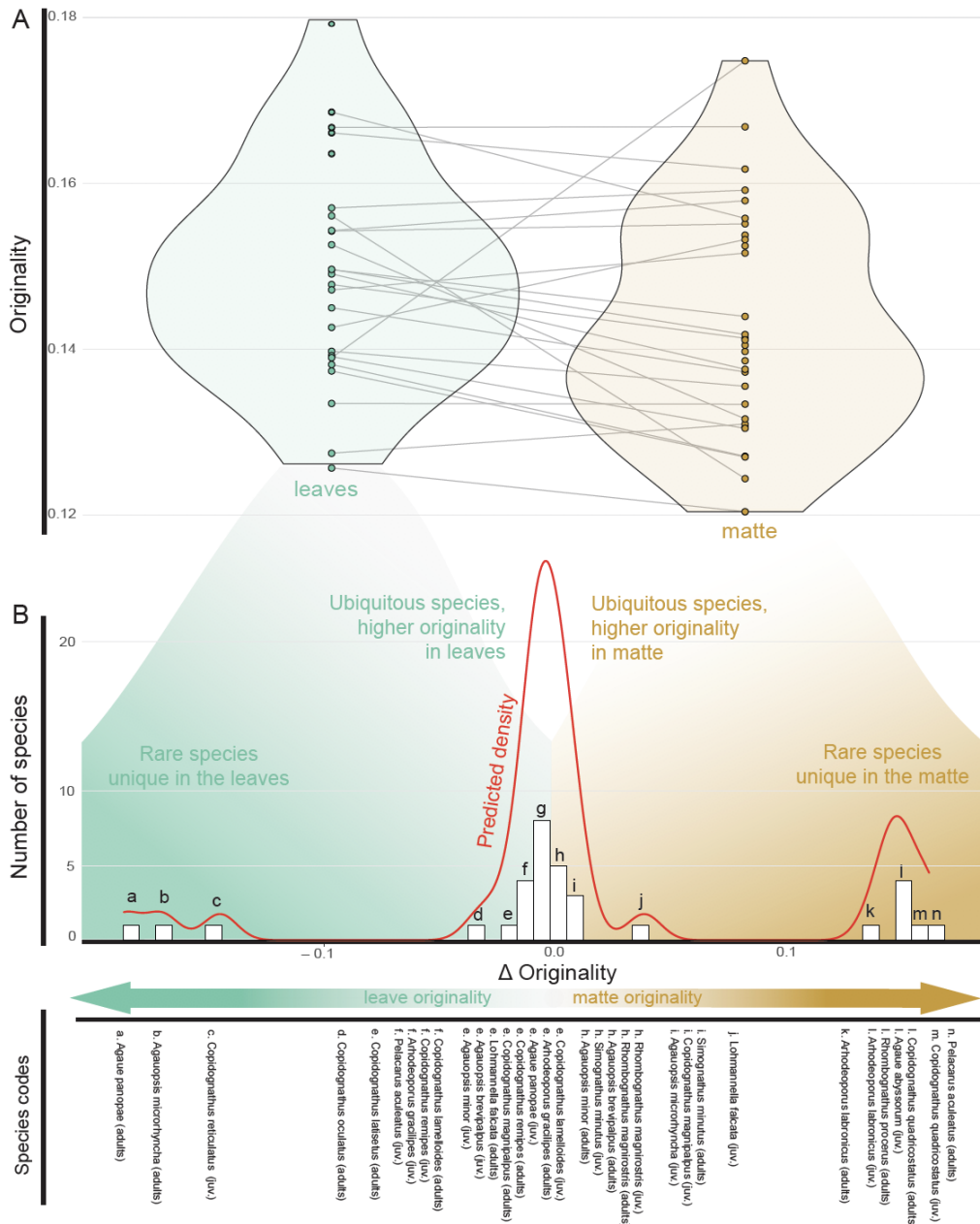
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584 **Figure 2.** A–C) Overall differences in functional richness (A), dispersion (B) and evenness (C) between
585 mite communities in leaves and matte. D–F) Differences in functional richness (D), dispersion (E) and
586 evenness (F) across seasons. Inset graphs in d–f represent the variation in leaves mean length (in cm) for
587 the leaves, and the organic matter content (in %) for the matte, thus reflecting the change in energy inputs
588 due to the regeneration of leaves in the seagrass meadow across the four seasons.
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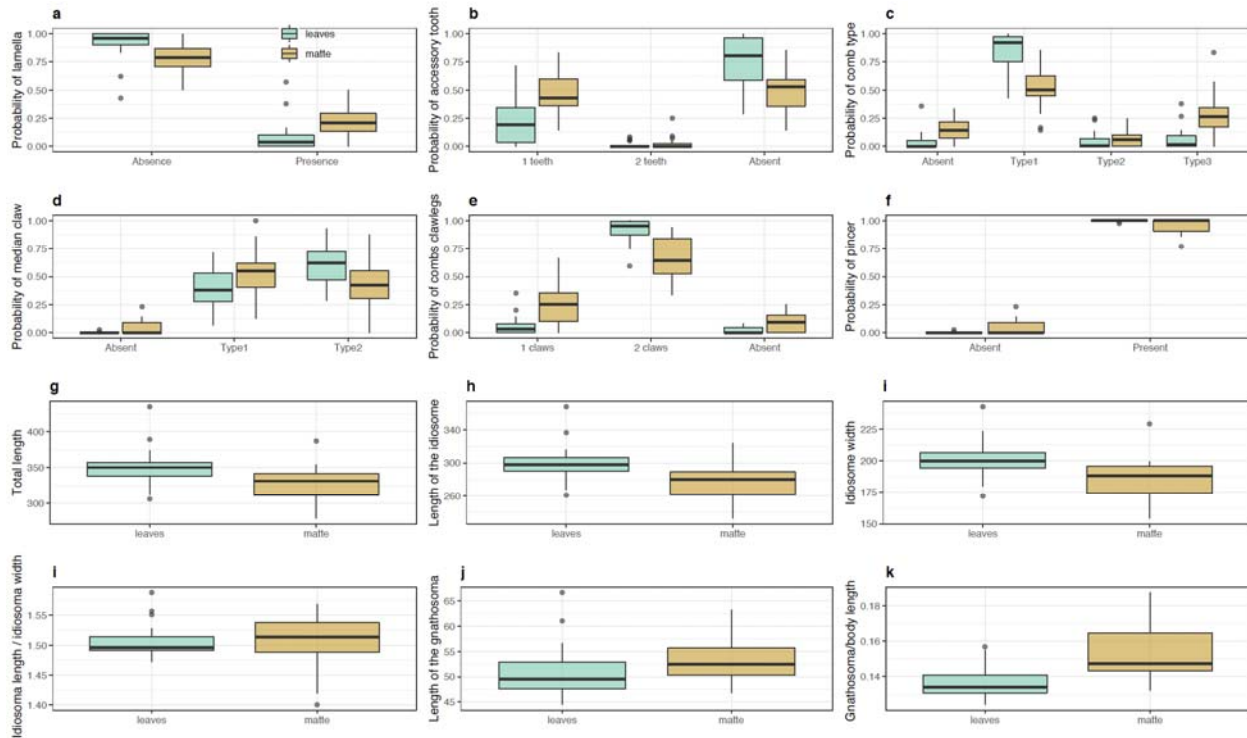


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593 **Figure 3.** **A)** Violin plots showing the distribution of functional originality values of species in the leaves
594 and the mat. Species present in both habitats are connected by grey lines. **B)** Histogram of Δ Originality
595 values between species in the two habitats, calculated by subtracting the value of originality of each
596 species in the leaves to the value of originality of each species in the mat. Orange smoothed lines show
597 the predicted density of values according to a kernel density estimation. The letters above each bar
598 correspond to the species listed at the rear of the figure.

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Supplementary material Figure S1

Habitat differences filter functional diversity of low dispersive microscopic animals



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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.