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1 **Assembly rules of helminth parasite communities in grey mullets: combining components**
2 **of diversity**

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10 Note: Supplementary data associated with this article.

11 **Abstract**

12 Organisms associate themselves in ecological communities. It has been widely debated whether
13 these associations are explained by deterministic or, in contrast, random processes. The answer
14 may vary depending on the level of an organisational scale (α , β and γ) and the facet of diversity
15 considered: Taxonomic (TD), Functional (FD) and Phylogenetic (PD). Diversity at the sampling
16 unit (i.e. host individual) is the α diversity; β diversity represents the extent of dissimilarity in
17 diversity among sampling units (within a level of an organisational scale, β_1 ; between levels of
18 an organisational scale, β_2); and the total diversity of a system is γ diversity. Thus, the
19 combination of facets and levels of scale may be useful to disentangle the mechanisms driving
20 the composition of a parasite community. Using helminth parasite TD, FD, and a Proxy of PD
21 (PPD) of three species of grey mullets (Teleostei: Mugilidae) from the Mediterranean Sea, we
22 show that random and deterministic processes of different nature explain the assemblage of
23 parasite communities. The parasite community at a host individual (α) was invariably a random
24 subset of the total diversity in the community for the three facets of diversity. At β_1 level, TD
25 was lower than expected by chance, whereas FD and PPD were random. At β_2 , diversity
26 patterns suggested environmental filtering of the parasite assemblage: species, trait, and
27 phylogenetic compositions of parasite communities seem to depend primarily on the species of
28 host, but also on the locality and season. Our study shows that parasite communities are not
29 totally understood if any of the components (i.e. facets and levels) of diversity is neglected.

30

31 **Keywords**

32 diversity; ecological communities; environmental filtering; helminths; limiting similarity;
33 random processes

34 **1. Introduction**

35 Understanding the processes governing the distribution and assembly rules of biological
36 diversity is one of the major challenges in biogeography and macroecology, and a prerequisite
37 for successfully predicting global change impacts on biodiversity (Guisan and Rahbek, 2011).
38 However, due to the extreme complexity of communities and ecosystems, we are still far from
39 achieving this goal. The current state of affairs can be described as a schism between ecological
40 and historical biogeography, which stems from the unresolved debate about the nature of the
41 mechanisms governing community assembly. This divide, known as the Clements-Gleason
42 controversy, has pervaded ecological thought for nearly a century. Whereas the Clementsian
43 ecologists view ecological communities as tightly integrated entities consisting of
44 interdependent species (the community-unit concept), the Gleasonians posit that species co-
45 occur largely according to the individualistic response of each species to variable environmental
46 conditions (the individualistic concept) (Liataud et al., 2019). Accordingly, species would
47 simply coexist because they tolerate the same habitat (Götzenberger et al., 2012; Liataud et al.,
48 2019). To a large degree, the latter view has prevailed in the last decades, based largely on
49 empirical evidence of community composition along environmental gradients, and has
50 eventually led to postulate the “disintegration of ecological community” (Ricklefs, 2008). Under
51 this paradigm, species distributions would be mostly, if not exclusively, constrained by local
52 environmental conditions, historical large-scale events, and dispersal capacity of the species.
53 However, recent evidence suggests that community structure cannot be fully understood without
54 taking into consideration deterministic processes, such as environmental filtering or limiting
55 similarity (Pavoine and Bonsall, 2011).

56 Stochastic processes can affect diversity, influencing speciation, extinction,
57 colonisation, or dispersal to a new community, and these can finally cause a random assemblage
58 of diversity. On the other hand, deterministic processes can lead to either clustering (i.e.
59 convergence) or overdispersion (i.e. divergence) of diversity (not to be confused with spatial
60 clustering and overdispersion, Götzenberger et al., 2012). A clustering pattern of diversity
61 assembly is interpreted as evidence of environmental filtering structuring the diversity of the

62 community, because abiotic factors select individuals with particular environmental tolerances,
63 and it results in similar life strategies converging in a community (Pavoine and Bonsall, 2011).
64 In contrast, the opposite pattern, i.e. overdispersion, would reflect a limiting similarity process,
65 in which biotic forces tend to limit the coexistence of very similar life strategies (Pavoine and
66 Bonsall, 2011; Götzenberger et al., 2012). Nonetheless, environmental filtering and limiting
67 similarity are not the only potential deterministic processes acting on communities and
68 alternative processes can lead to similar patterns of diversity dispersal. For instance,
69 competition due to biotic interactions excluding the less competitive strategies can also result in
70 diversity overdispersion or clustering depending on the species affected in each situation
71 (Mayfield and Levine, 2010).

72 The understanding of the processes that drive biological communities can be examined
73 for the multiple components of diversity to get a complete resolution of communities. Diversity
74 encompasses multiple levels (e.g. α , β , γ) nested in organisational scales (e.g. spatial scales) and
75 it has been argued that the importance of ecological processes is probably scale dependent.
76 From the lowest to the highest of level of an organisational scale, three diversity levels are
77 classically defined: α diversity or diversity at the sampling unit; β diversity or extent of
78 dissimilarity in diversity among sampling units (within a level of an organisational scale, β_1 ;
79 between levels of an organisational scale, β_2) and γ diversity or total diversity (Pavoine et al.,
80 2016). Moreover, it includes multiple facets, such as the variety in species, traits, or
81 evolutionary units (Pavoine and Bonsall, 2011). Regardless of the level considered, diversity
82 has been studied under three facets: Taxonomic Diversity (TD, richness and abundance of
83 taxonomic entities in a community), Functional Diversity (FD, richness and abundance of
84 functional traits in a community) and Phylogenetic Diversity (PD, richness and abundance of
85 genetically different entities in a community) (Pavoine and Bonsall, 2011). Traditionally,
86 ecologists have considered TD as the single measure of diversity. This fact caused a continuous
87 loss of ecological (FD) and evolutionary (PD) information, since TD considers that all the
88 species in a community are equally similar and does not take into account the uniqueness of the
89 functions or the phylogenetic distinctness of each species (Pavoine and Bonsall, 2011).

90 Parasite communities offer excellent models to study the assembly rules of the facets of
91 diversity at different levels of organisation. The sampling unit (i.e. host individual) can be
92 precisely defined (as required by Götzenberger et al., 2012) and it is often relatively easy to
93 sample a large number of communities to eventually get strong statistical conclusions (Poulin
94 and Valtonen, 2001). Although pioneering studies exist (e.g. Mouillot et al., 2005; Krasnov et
95 al., 2014, 2015, 2016), up to now little is known about the mechanisms driving the different
96 facets of diversity at different organisational scales of an entire parasite community. In studies
97 of free-living organisms, assembly mechanisms of diversity can hierarchically be assessed at
98 different spatial levels (e.g. local communities, regions, continents) or even temporal levels (e.g.
99 years, decades, centuries) (Pavoine et al., 2009a). The study of parasite communities provides
100 an additional organisational scale, the host, which also shapes parasite diversity. For example,
101 parasite diversity can be examined at host taxonomic levels (i.e. species, genus, family, and so
102 on).

103 Here, we will investigate the assembly mechanisms (deterministic vs stochastic
104 processes) of the helminth adult parasite communities of grey mullets (Teleostei: Mugilidae)
105 from the Western Mediterranean Sea under the influence of host and environmental factors.
106 This model is appropriate because, first, these parasite communities include parasite species
107 from distant phylogenetic origins and are functionally disparate. Second, it comes from three
108 out of the six sympatric grey mullet species that coexist in this area of the Mediterranean
109 (Blasco-Costa, 2009. Taxonomy of the Haploporinae Nicoll, 1914 and Bunocotylineae Dollfus,
110 1950 (Digenea) from Mediterranean mullets (Teleostei): morphological and molecular
111 approaches. Doctoral dissertation, University of Valencia, Valencia, Spain) and from localities
112 that vary in their environmental parameters. This allows us to test whether the different facets of
113 helminth diversity provide congruent results and whether host factors (phylogenetic proximity
114 and similarity in life strategies) and/or environmental factors (geographical location and habitat
115 conditions) select for different parasitic life strategies. Particularly, two of the host species,
116 *Chelon auratus* and *Chelon ramada*, are phylogenetically closer to each other than to *Mugil*
117 *cephalus* (Durand et al., 2012), whereas *M. cephalus* and *C. ramada* show greater similarities in

118 their life strategies between them than with *C. auratus* (Cardona, 2001; Cardona, 2006).
119 Additionally, our samples are from three coastal localities that differ in their habitat conditions
120 (two marine: Ebro Delta, Sea - EDS and Santa Pola, Sea - SPS; and one brackish lagoon: Santa
121 Pola, Lagoon - SPL) and in their geographical proximity (SPS and SPL are very close, ~10 km
122 apart; whereas EDS is more distant from the other two, ~290 km). Finally, our nested sampling
123 design allows us to measure and compare diversity at the sampling unit (α diversity or parasite
124 diversity at the host individual) and among sampling units within and between levels of a factor
125 (i.e. parasite diversity within (β_1) or between (β_2) host individuals of a host species or locality).

126 We asked whether diversity patterns differ between the facets of parasite diversity and
127 across two hierarchical scales (i.e. locality and host), and which are the factors (i.e. host
128 phylogeny vs life strategies; habitat conditions vs geographic proximity) related to such
129 variation. Based on evidence from free-living organisms (Cavender-Bares et al., 2006; Kraft and
130 Ackerly, 2010), and previous studies of our host-parasite system (Blasco-Costa, 2009.
131 Taxonomy of the Haploporinae Nicoll, 1914 and Bunocotylinae Dollfus, 1950 (Digenea) from
132 Mediterranean mullets (Teleostei): morphological and molecular approaches. Doctoral
133 dissertation, University of Valencia, Valencia, Spain; Blasco-Costa et al., 2012; Míguez-Lozano
134 et al., 2012; Sarabeev et al., 2013), we hypothesise that both host phylogeny and host life
135 strategy will influence the parasite community, whereas habitat conditions will be a stronger
136 determinant of the parasite communities than the geographic distance. Parasite communities
137 will be overdispersed at low organisational levels (within a locality or a host species) since
138 similar life strategies will be limited (i.e. not able) to coexist. In contrast, at higher levels, we
139 expect that clustering will be the driver of the parasite community, because the environment
140 filters (i.e. selects for) certain life strategies.

141

142 **2. Material and methods**

143 *2.1. Data*

144 Fish were obtained from local harbour markets and surveyed for parasites as described in
145 Blasco-Costa (2009. Taxonomy of the Haploporinae Nicoll, 1914 and Bunocotylinae Dollfus,

146 1950 (Digenea) from Mediterranean mullets (Teleostei): morphological and molecular
147 approaches. Doctoral dissertation, University of Valencia, Valencia, Spain). Adults of helminth
148 parasites were identified following Yamaguti (1958), Gaevskaya and Dmitrieva (1992) and
149 Blasco-Costa (2009. Taxonomy of the Haploporinae Nicoll, 1914 and Bunocotylinea Dollfus,
150 1950 (Digenea) from Mediterranean mullets (Teleostei): morphological and molecular
151 approaches. Doctoral dissertation, University of Valencia, Valencia, Spain) for 18 trematode
152 species; Paperna (1964), Euzet and Combes (1969) and Sarabeev et al. (2013) for 9
153 monogenean species; Orecchia and Paggi (1987) for one nematode species; and Orecchia et al.
154 (1988) and Tkach et al. (2014) for two acanthocephalan species. The dataset includes 272 host
155 individuals and 30 parasite species from three seasons (two autumns and one spring) of two
156 years (2004 and 2005) (Table 1). The Supplementary Material Table S1 contains the prevalence
157 of the parasite species in each host species, locality, and season. Data analysis was entirely
158 performed in R (R Core Team, 2019. R: A language and environment for statistical computing.
159 R foundation for statistical computing, Vienna, Austria).

160

161 2.1.1. *Data accessibility*

162 Parasite abundance, functional traits and phylogenetic-like data analysed in this study and a
163 step-by-step manual of the code, functions and packages used to analyse data and display
164 figures are stored in DOI ##### (<https://github.com/crisLB/diversity>). Thus, we expect to
165 favour the reproducibility of our analyses and the expansion studies of parasite communities and
166 to make future studies comparable under this framework.

167

168 2.2. *The multiple facets of diversity*

169 2.2.1. *Functional trait information*

170 The number of functional traits (i.e. features measurable at individual level which impacts the
171 fitness of individuals and reflects their performance in ecosystems) that can potentially be
172 assessed in any organism is large, but our ability to measure functional traits of parasites is often
173 limited. This is mainly due to technical impediments or lack of knowledge about the

174 relationship between life-history information of the parasites and the components of fitness.
175 Functional traits considered in this study conform to the definition of functional trait currently
176 accepted in ecology (see above) and are susceptible to affect parasite fitness depending on
177 environmental factors (see Table 2 in Llopis-Belenguer et al., 2019).

178 Here, we used five functional traits based on the framework and core list developed by
179 Llopis-Belenguer et al. (2019): attachment organ, type of life cycle, body mass, egg size and
180 number of eggs. We extracted information of categorial functional traits (i.e. attachment organ
181 and type of life cycle) from direct observations, whereas, we obtained information of continuous
182 functional traits (i.e. body mass, egg size and number of eggs) from species descriptions or as
183 the mean value measured from a varying number of individuals of each species. To estimate
184 individual body mass, we resorted to indirect methods “Area by Depth by Density” (for
185 flatworms: trematodes and monogeneans) and “Volume of Revolution by Density” (for
186 organisms with subcircular transversal section along their bodies: acanthocephalans and
187 nematodes) (Llopis-Belenguer et al., 2018). Mass of a parasite species was computed as the
188 mean mass of a range of individuals (mean number of individuals per species 9; range 2-12).
189 Egg size was estimated as the mean maximum egg length and mean width from species
190 descriptions when these measures were available. Otherwise, we measured these features from 3
191 to 20 eggs (mean 10) from a varying number of individuals from each species. Then egg volume
192 (μm^3) was estimated assuming an ellipsoid shape (i.e. depth equal to width). For the number of
193 eggs of monogeneans and trematodes, we counted eggs from 1 to 20 (mean 9) individuals per
194 species mounted on slides. Since acanthocephalans and nematodes possessed too many eggs to
195 be counted directly, the number of eggs was estimated as follows: 10 females of each species
196 were dissected individually, and their eggs diluted in 1 ml of saline solution each. Then the total
197 number of eggs was estimated from aliquots of 0.1 ml from each specimen. Regardless of the
198 method used, we performed the procedure twice to obtain the mean number of eggs for each
199 individual. Finally, we log-transformed data of continuous traits.

200 We built a functional trait (columns) by parasite species (rows) matrix with the `dist.ktab`
201 function from package `ade4` (Thioulouse et al., 2018) and calculated the Gower’s distance

202 (Gower, 1971) between species. This distance allows combining several types of traits
203 (continuous and categorical as described above) and incorporating observations with missing
204 data (4% in our dataset). Then, we transformed the Gower matrix of pairwise distances into
205 Euclidean pairwise distances (function `lingoes` in `ade4`) and divided the resulting matrix by its
206 maximum to bound values between 0 and 1 (Pavoine et al., 2009b).

207

208 2.2.2. *Proxy of phylogenetic diversity*

209 Since we did not have a complete phylogeny of the parasite species in the community, we used
210 a Proxy of Phylogenetic Diversity (PPD) to estimate the phylogenetic pairwise distance between
211 parasite species. The PPD can be seen as a measure of the length of the path connecting two
212 species traced through a Linnaean classification of the full set of species in the community
213 (Clarke and Warwick, 1998). We created a Euclidean pairwise distance matrix between parasite
214 species by means of the `taxa2dist` function from `vegan` (Oksanen, J., Blanchet, F.G., Friendly,
215 M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L.,
216 Solymos, P., Stevens, M.H.S., Szoecs, E., Wagner, H., 2019. `vegan`: Community Ecology
217 Package. R package version 2.5-5) applied to a classification table with parasite species at rows
218 and taxa of such species at higher levels (genus, subfamily, family, suborder, order, class,
219 phylum, in our case) at columns. We divided the resulting distance matrix by its maximum to
220 bound the cell values between 0 and 1.

221

222 2.2.3. *Correlation between functional trait and taxon-level distances*

223 We assessed the correlation between the matrix of pairwise functional distances and the matrix
224 of pairwise phylogenetic distances to study the relationship between the evolutionary history
225 and ecological processes behind community assembly (Pavoine and Bonsall, 2011). We tested
226 such correlation by means of the Mantel test (`mantel` function in `vegan`).

227

228 2.3. *Diversity analyses*

229 Our samples were organised by three key factors: host species, locality, and season (Table 1).
230 Since *C. auratus* does not naturally occur in SPL, we evaluated the effect of the host species and
231 the locality by splitting the diversity analyses into two case studies. In Case 1, we assessed the
232 influence of host species on the three facets of diversity. To that end, we analysed and compared
233 TD, FD and PPD of the helminth parasite communities from the three host species, at SPS in
234 two autumn surveys (2004 and 2005). In Case 2, we evaluated the effect of locality and season
235 survey on the parasite communities. To that end, we analysed and compared TD, FD and PPD
236 of the helminth parasite communities from *M. cephalus* at the three localities surveyed in spring
237 and autumn 2005.

238

239 2.3.1. *Influence of one factor on diversity*

240 In both case studies, we measured diversity in two different ways. First, we used the Double
241 Principal Coordinate Analysis (DPCoA) (Pavoine et al., 2004), that is a combined version of the
242 Rao index of diversity (Rao, 1982) and the Weighted Principal Coordinate Analysis (Gower and
243 Legendre, 1986). DPCoA allows comparing the partitioning of diversity at different levels of an
244 organisational scale and the different facets of diversity. It is based on the matrix of pairwise
245 distances (functional or phylogenetic) between species in a sample and an abundance matrix of
246 such species. When the scope of the analysis is TD, all cells of the distance matrix are defined
247 as 1. Hence, all species are considered equally and maximally distant, and Rao's index becomes
248 equal to the Simpson's index of diversity, i.e. equals to the probability that any two individuals
249 randomly drawn from a community are of different species (Pavoine et al., 2004). Furthermore,
250 the ordination of species according to the previous two matrices (i.e. pairwise distances and
251 abundance) assembles species in a multivariate space related with the decomposition of
252 diversity in organisational levels (Pavoine et al., 2004). Since the DPCoA only allows studying
253 one factor at a time, we analysed the databases by season survey to avoid crossed factors.

254 Under the DPCoA framework we measured α diversity with function `dpcoa` in `ade4`. In
255 order to examine the relationship between α diversity (i.e. parasite community in a host
256 individual) and the factors host species (Case 1) or locality (Case 2), we used function `lm.rppp`

257 of package RRPP (Collyer and Adams, 2018) that performs a linear model by residual
258 randomisation and provides empirical sampling distributions for further ANOVAs. Following
259 Collyer and Adams (2018), univariate α values were log-transformed. Then, we performed
260 ANOVAs (type I of sums of squares) using random distributions of the F-statistics (Collyer and
261 Adams, 2018) for TD, FD and PPD, independently. When differences between samples from
262 different host species or localities were significant, we ran posteriori pairwise comparisons of α
263 TD, FD and PPD between host species or localities using function pairwise in RRPP.

264 We calculated β diversity at two different organisational levels under the context of the Rao
265 index of diversity. β_1 represents dissimilarity in parasite diversity among sampling units (hosts)
266 within the same host species or locality. To calculate β_2 , one must group together parasite
267 communities of hosts of the same species or from the same locality and then, calculate
268 dissimilarities in the parasite communities between different host species or localities. In both
269 cases, we calculated β diversities under the equivalent number approach (Ricotta and Szeidl,
270 2009) using the third proposition of the Rao index of diversity in Pavoine et al. (2016) (EqRao
271 function in adiv (Pavoine, S., 2018. adiv: Analysis of diversity. R package version 1.2)). Indeed,
272 this proposition is specifically developed for unbalanced samplings. Furthermore, we compared
273 each of the TD, FD and PPD β_1 and β_2 diversities with 999 randomly simulated β_1 and β_2
274 values (rtestEqRao function in adiv) in order to establish whether the observed values
275 significantly differ from those randomly simulated ($p < 0.05$). When significant, we compared
276 observed and simulated results to determine whether the observed β_1 or β_2 were greater or
277 lower than expected at random. This allows determining whether parasite communities from
278 fish of the same species or locality (β_1) or of different fish species or locality (β_2) are more
279 similar (the observed value is lower than simulated values) or more dissimilar (the observed
280 value is greater than simulated values) to each other than expected by chance. Finally, we used
281 the standardised β_1 and β_2 given by EqRao function and defined as follows: (observed β – mean
282 of randomly simulated β s)/standard deviation of randomly simulated β s. This standardisation
283 enables us to infer if the parasite species, traits or the phylogenetic proxy are overdispersed

284 (negative standardised β) or clustered (positive standardised β) (Head et al., 2018) within a level
285 of a factor (β_1) or between levels of a factor (β_2).

286

287 2.3.2. *Influence of two crossed factors on diversity*

288 To evaluate and disentangle the effect of crossed factors on diversity, we used crossed-DPCoA
289 (Pavoine et al., 2013a). In both case studies, we analysed the effect of two crossed factors
290 simultaneously: host species (Case 1) or locality (Case 2), and season. The crossed-DPCoA is
291 grounded on the DPCoA. It analyses the effect of two crossed factors at the same time. Thus, it
292 distinguishes the proportional contribution of the sampling unit, each factor individually and the
293 effect of the interaction of both factors on the diversity of the community.

294 The crossed-DPCoA consists of three consecutive analyses. Following Pavoine et al.'s
295 (2013a) terminology, each parasite community is associated with a component of the factor A
296 (hosts species or locality) and a component of a factor B (season). The main version of the
297 crossed-DPCoA plots the parasite species, the sampling units, and the variables of the main
298 factor A, without taking into account seasonal differences (factor B), in a DPCoA space. Then,
299 the first version of the crossed-DPCoA removes the amount of diversity among sampling units
300 due to the sole effect of factor B, but retains combined effects of factors A and B (i.e. the
301 interaction between factors A and B). Finally, the second version of the crossed-DPCoA
302 eliminates any influence of the factor B on the factor A (including the interaction term). Thus, it
303 provides diversity exclusively under the light of the main crossed-factor, factor A (host species
304 or locality). We carried out the main, the first and the second versions of the crossed-DPCoA
305 with functions `crossdpcoa_maineffect`, `crossdpcoa_version1` and `crossdpcoa_version2` in `adiv`,
306 respectively.

307

308 **3. Results**

309 Parasite functional and phylogenetic-like pairwise distance matrices were highly correlated
310 (Mantel test, $F = 0.79$, $p < 0.001$).

311

340 the first axis separated the parasite communities of the two coastal-related grey mullets (*C.*
341 *ramada* and *M. cephalus*) from the marine-related *C. auratus*, although those of *C. ramada*
342 were always in an intermediate position. The parasite communities of the three host species
343 showed an overlap in the parasite functional trait and phylogenetic-like spaces. However, host
344 species was still a significant predictor for trait and phylogenetic diversity of the parasite
345 communities (Fig. 2).

346

347 3.2. *Case 2: parasite communities of Mugil cephalus from spring and autumn*
348 *(2005) overlapped in TD, FD and PPD of marine localities (Ebro Delta Sea,*
349 *Santa Pola Sea) but were separated from those of the lagoon (Santa Pola*
350 *Lagoon)*

351 The statistical analyses of α TD, FD and PPD did not show congruent results. In spring,
352 localities did not differ in the composition of the parasite species (TD in Table 2) but did in FD
353 and PPD. This was due to SPL being significantly less diverse than the other two localities in
354 terms of FD and than EDS in terms of PPD (Table 2; Supplementary Table S3 A and B; Fig. 3:
355 spring 2005). In the autumn survey (Fig. 3: autumn 2005), SPL had significantly lower TD than
356 the other two localities (Supplementary Table S3 C). As for FD, the three localities differed
357 significantly (Supplementary Table S3 D). For PPD, SPS had significantly higher diversity than
358 the other two localities (Supplementary Table S3 E).

359 At β_1 level, the dissimilarity in diversity of the parasite communities from hosts within
360 the same locality tended to be lower than expected by chance only for TD in both season
361 surveys (Table 5, Supplementary Fig. S3 A-C and Fig. S4 A-C). The standardised observations
362 with negative values indicated that parasite species, traits and the phylogenetic proxy were
363 overdispersed within hosts from the same locality, except for “PPD - autumn” (Table 5). At β_2
364 level, differences in parasite diversity between localities always differed significantly from
365 randomness (Table 5) and were always greater than expected (Supplementary Fig. S3 D-F and
366 Fig. S4 D-F). The positive values of the standardised β_2 reflected that parasite species, traits and
367 phylogeny were clustered at this level of the organisational scale.

368 When we considered the crossed factors simultaneously, diversity within each host
369 individual constituted the highest proportion of the parasite diversity in the whole community
370 (58% for TD, 54% for FD and 52% for PPD), followed by the crossed effect of locality and
371 season, the locality and the season, for the three facets of diversity (Table 4). The graphical
372 representation of the second version of the crossed-DPCoA displayed similar patterns for TD,
373 FD and PPD (Fig. 4). The first axis slightly separated the diversity of parasite communities of
374 the two marine localities (SPS and EDS) from the lagoon locality (SPL). Furthermore, both
375 marine localities (EDS and SPS) overlapped substantially in the species (TD), trait (FD) and
376 phylogenetic-like (PPD) spaces (Fig. 4).

377

378 **4. Discussion**

379 We examined the mechanisms driving the helminth parasite assemblages of grey mullets. Four
380 main findings can be extracted from our results. First, the three facets of diversity (i.e. TD, FD
381 and PPD) did not always show congruent results among them, which is unsurprising and
382 follows the general trend reported for diverse groups of free-living organisms (e.g. Devictor et
383 al., 2010; Hevia et al., 2016). However, these results have been hardly reported for parasite
384 communities. Thus, conclusions of a parasite community study might be biased if any of the
385 facets of diversity is overlooked (Jarzyna and Jetz, 2016). Second, the diversity of the parasite
386 communities shows at least two opposed patterns (i.e. overdispersion and clustering). These
387 patterns are found at different levels (β_1 and β_2 , respectively) of the two organisational scales
388 (i.e. host species or locality). Third, the diversity of the two organisational scales is influenced
389 by several variables. Fourth, the phylogenetic-like signal on functional traits suggested that
390 functional traits are, at least, constrained by phylogeny. However, these two facets of diversity
391 did not always display the same results, which suggests that the FD of this parasite community
392 is not a surrogate of PPD (see Pavoine et al., 2013b).

393 At the lowest organisational level (α diversity), the most notable case of incongruences
394 among the three facets of diversity was the spring survey at SPL (Fig. 3), which was the richest
395 in terms of number of species (highest TD) mainly because of trematodes. However, SPL

396 displayed the lowest mean for α FD and α PPD probably because trematode species are
397 redundant (sensu Carmona et al., 2016) in terms of FD and PPD. At the α level as well, we
398 found that host individual explains for most of in its the three facets (~50% of the total diversity,
399 crossed-DPCoA results), regardless of the case study considered. This strongly suggests that the
400 parasite community found at each host individual (α TD) is a random subset of a larger pool of
401 parasite species within a host species or locality (Poulin, 1996). However, it also highlights that
402 the parasite community found at this level is to a large extent a random subset of a larger pool of
403 parasite ecological (FD) and evolutionary (PPD) strategies. This can be explained as α being
404 product of random events (Poulin, 1996) or as result of several forces acting simultaneously in
405 different directions in the development of parasite communities at α level (Poulin, 2005).
406 However, it has been recently shown that α TD of parasite communities is determined by host
407 age-class like an ecological succession of communities of free-living organisms. Thus, if hosts
408 of different age-classes were analysed together it could mask an actual deterministic pattern of
409 parasite community assemblage (Espínola-Novelo et al., 2020). Nonetheless, we consider that
410 this is not a likely scenario in this study since parasite communities were mainly sampled from
411 fish of two consecutive age-classes out of nine (classes 3 and 4 according to those described for
412 *M. cephalus* in Espínola-Novelo et al., 2020).

413 In the case of β_1 diversity (within a host species or locality), differences among host
414 individuals of the same species were less important than differences between host individuals of
415 the same locality to determine the variation of the parasite communities (Table 4). In other
416 words, host species is more determinant of the parasite community than locality, at least for TD
417 since the parasite communities from different host species (Fig. 2) and localities (Fig. 3) are
418 overlapped in FD and PPD spaces. In fact, the parasite community of grey mullets, especially
419 monogeneans of genus *Ligophorus* (Dactylogyridae), tend to be host-species specific while they
420 are not so geographically constrained within the Mediterranean Sea (e.g. Sarabeev et al., 2013).

421 In addition, the negative standardised value of β_1 TD indicated that diversity of parasite
422 species were overdispersed within hosts from the same species, which may indicate that parasite
423 species sharing the same resources are limited to coexist (e.g. Krasnov et al., 2005a).

424 Nonetheless, parasite FD and PPD were randomly distributed among host individuals (Table 3
425 and 4). A similar result was found by Krasnov et al. (2005b). These authors proposed that when
426 the number of parasite species infecting a host species becomes saturated, a random assemblage
427 in PPD suggests that all the parasite species are ecologically interchangeable and contribute
428 equally to the saturation. Here we show that FD and PPD are random assemblages. This would
429 indicate that parasite species are functional and phylogenetic interchangeable entities.
430 Furthermore, the span of the boxes (Fig. 1 and 3) and the size of the ellipses (Fig. 2 and 4)
431 reflect the heterogeneity in infection among host individuals from the same species or locality.
432 This could result from the almost universal observation of parasite aggregation among host
433 individuals (Poulin, 2007a). Unfortunately, it is difficult to interpret the causes of parasite
434 aggregation in host individuals in our system because we do not have enough data about
435 inequality in environmental pressures among host individuals (Thieltges and Reise, 2007), host
436 genetic background (Poulin, 2007a), host traits (Timi and Poulin, 2003) or parasite
437 characteristics (such as dispersal ability) (Poulin, 2007b).

438 At β_2 level (between host species or localities), the positive standardised observations
439 indicated that species, traits and the proxy of the phylogeny were clustered, i.e. the species, trait,
440 and phylogenetic compositions of parasite communities depend on the species host and the
441 locality. Both environmental filtering and competition can be responsible for these patterns
442 (Cadotte and Tucker, 2017). Moreover, intrahost speciation has also been pointed out as a cause
443 of clustering in parasites (Krasnov et al., 2014). Parasite species competition is difficult to
444 demonstrate (Mideo, 2009). However, the filtering of parasite species has received much more
445 attention, particularly after the framework developed by Combes (2001). Due to the strong
446 association between parasite and host species (Fig. 2), we consider that environmental (host)
447 filtering is an important driver in these communities. As for intrahost speciation, it has been
448 suggested for some *Ligophorus* spp. in our system (Blasco-Costa et al., 2012). Consequently,
449 intrahost speciation could be an additional mechanism accounting for the clustering of such
450 species. As for geographical differences in parasite assemblages, the overlap in the three spaces
451 of diversity of the two marine localities was considerable (Fig. 4). This suggests that habitat

452 condition (marine vs lagoon) is perhaps a stronger driver than geographical distance of the
453 parasite communities. The environmental characteristics of the lagoon together with the high
454 site fidelity of *M. cephalus* to lagoons (Chang et al., 2004) might eventually determine the
455 slightly differentiated parasite community from SPL (Fig. 4). These results are indicative of
456 environmental filtering in the parasite facets of diversity, which conforms with previous
457 evidence only reported for TD of parasite communities of fish populations (e.g. Levy et al.,
458 2019).

459 Finally, the season survey had a moderate effect on the parasite diversity of the host
460 species and localities (crossed-DPCoA results). However, the capacity to differentiate parasite
461 communities from different localities might be seasonal-dependent. Since freshwater effluents
462 widely vary in EDS seasonally, and, thus, the parasite diversity in EDS and SPL localities could
463 be more similar in some seasons than in others (Míguez-Lozano et al., 2012).

464 To sum up, our study supports the idea that the assembly rules driving parasite
465 communities depend on the level of the analysis and the facet of diversity considered.
466 Particularly, communities at host individual level appear to represent a random subset of
467 parasite species of a larger pool of species, traits, and phylogeny of parasites. At intermediate
468 levels, similar parasite species are limited to coexist, whereas at higher levels, the environment
469 filters the parasite diversity, since a joint influence of host phylogenetic origin (*Chelon* vs
470 *Mugil*) and environmental preferences (marine-related vs coastal-related) might drive the
471 parasite TD, FD and PPD. Although this was less clear for the last two facets of diversity.
472 Finally, the habitat conditions of the locality seem to be more determinant not only of the TD,
473 but also of FD and PPD than geographic distance. The fact that diversity in these parasitic
474 communities are subjected to random and deterministic processes simultaneously, but at
475 different organisational levels, brings together Clements and Gleason ideas. These can be seen
476 as two polar cases along a single deterministic-stochastic continuum of community organisation
477 outcomes (Götzenberger et al., 2012; Liautaud et al., 2019). Clearly, parasitologists should pay
478 attention to patterns of diversity at different facets and organisational levels.

479

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487

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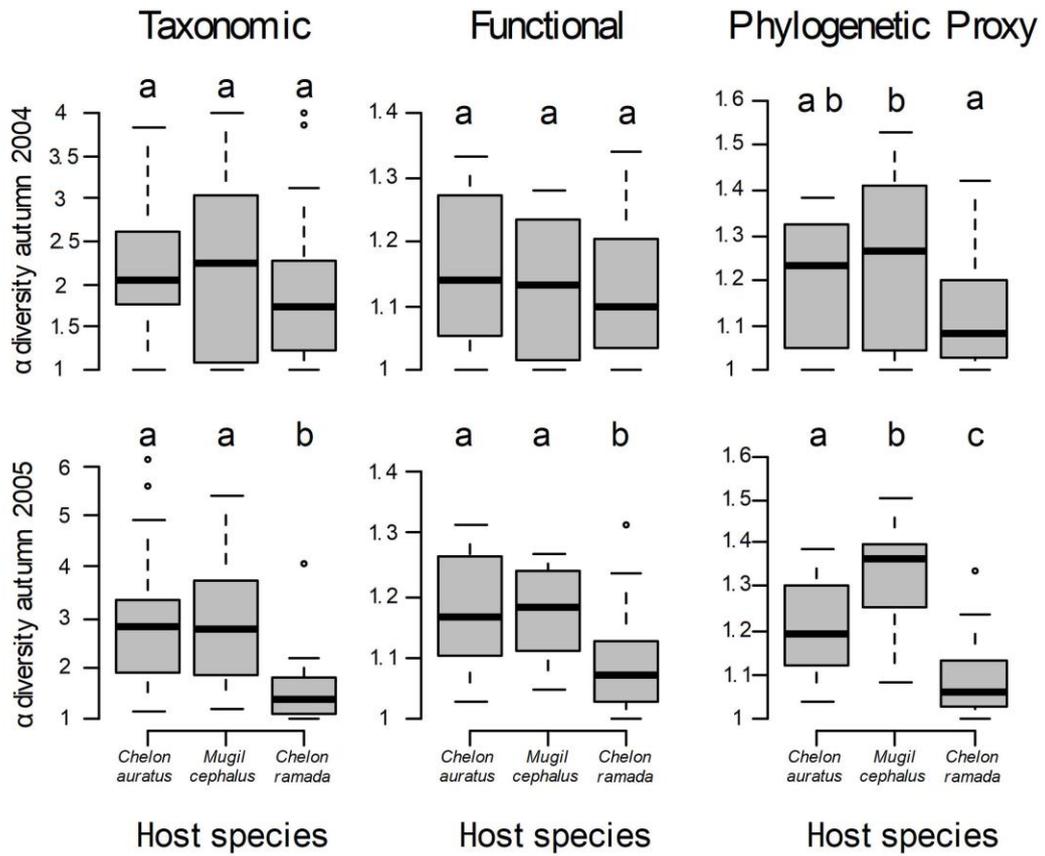
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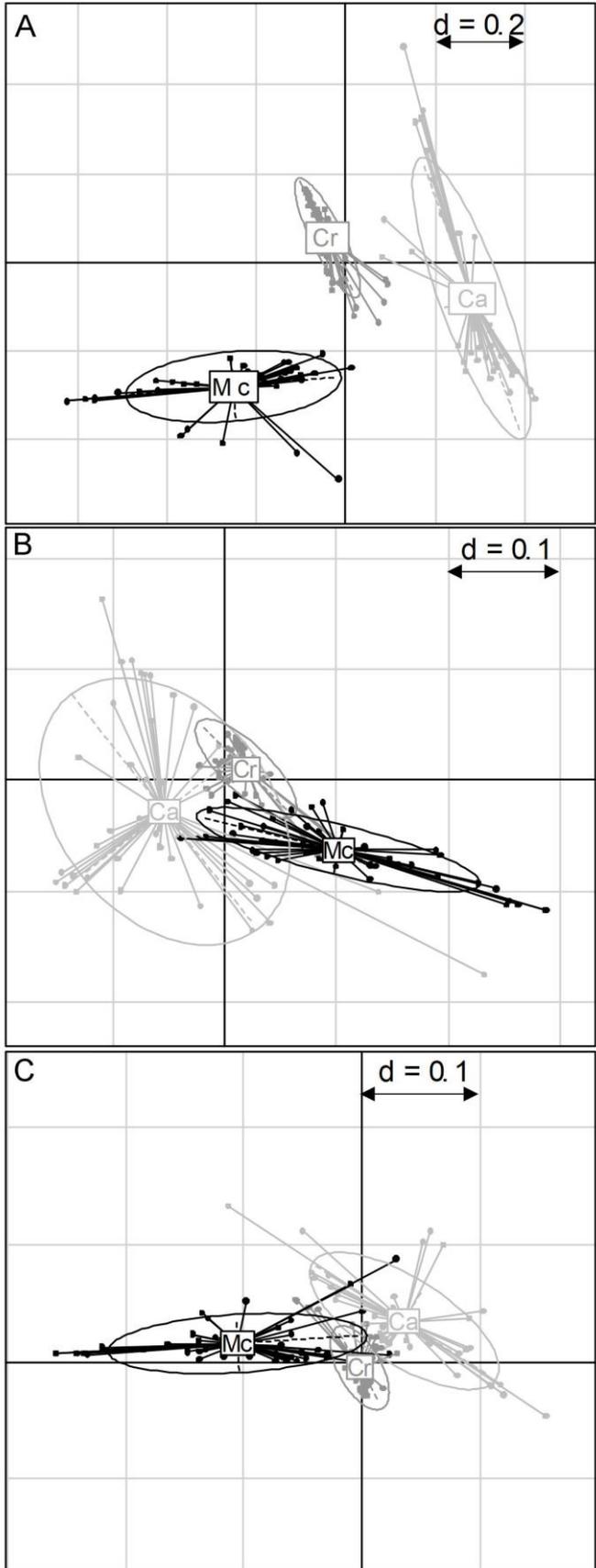


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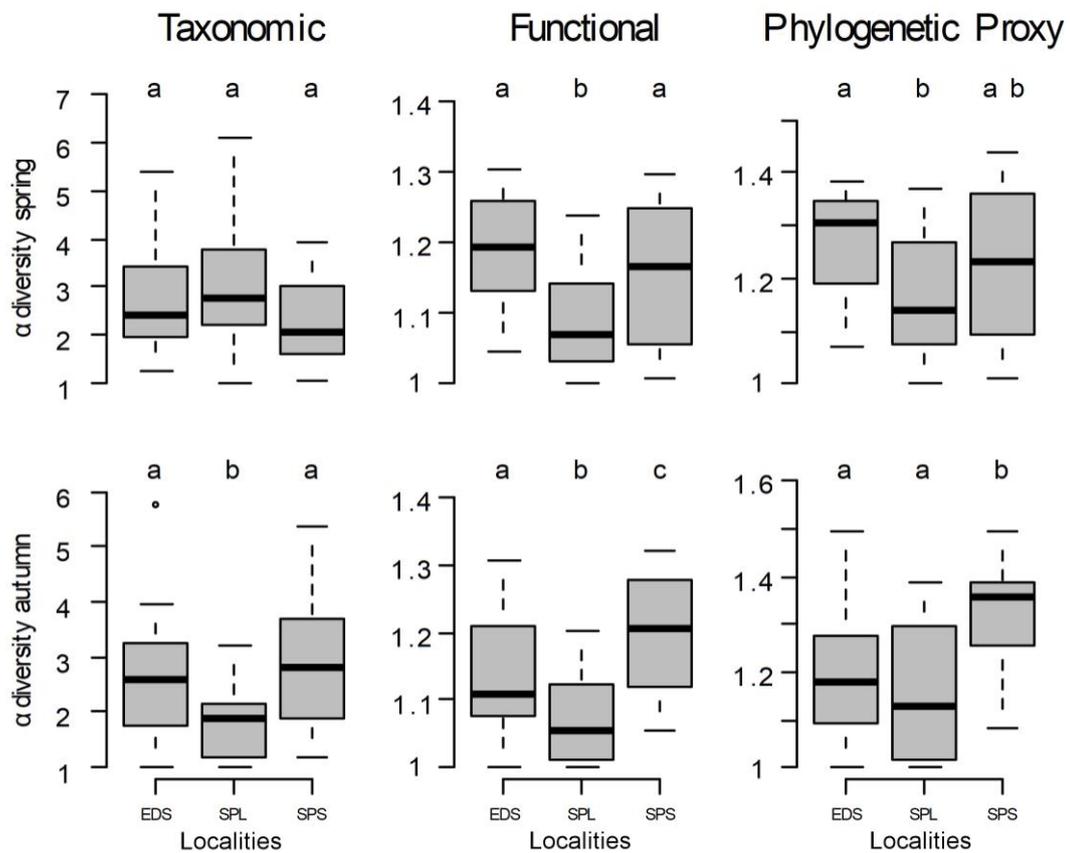
639 **Fig. 1. Parasite α diversity in terms of taxonomic (TD), functional (FD) and a proxy of the**
 640 **phylogenetic (PPD) diversity for each host individual of each fish species (Case 1).**

641 Different lowercase letters indicate significant differences between host species.

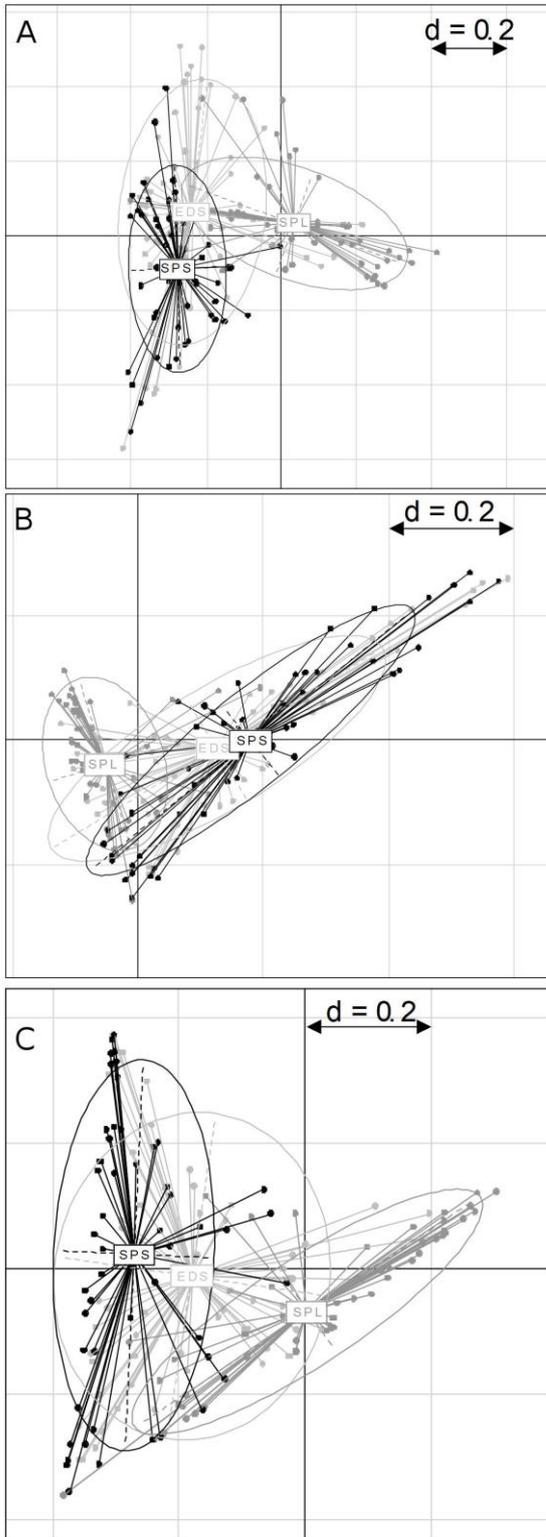
642



644 **Fig. 2. Position of each host individual (dots) in the (A) parasite species space, (B) parasite**
645 **trait space, and (C) parasite phylogenetic-like space (Case 1).** Fish are grouped by host
646 species. Abbreviations: Mc, Cr and Ca represent the centroid of each fish species, and stand for
647 *Mugil cephalus*, *Chelon ramada* and *C. auratus*, respectively. These analyses were carried out
648 with the second version of the crossed-DPCoA. The width and height of the ellipses are given
649 by the variance of the coordinates of the individuals, and the covariance between the
650 coordinates on the two axes gives the slope of the ellipse. “d” (top-right) indicates the length of
651 the side of the grey squares of the background grid.
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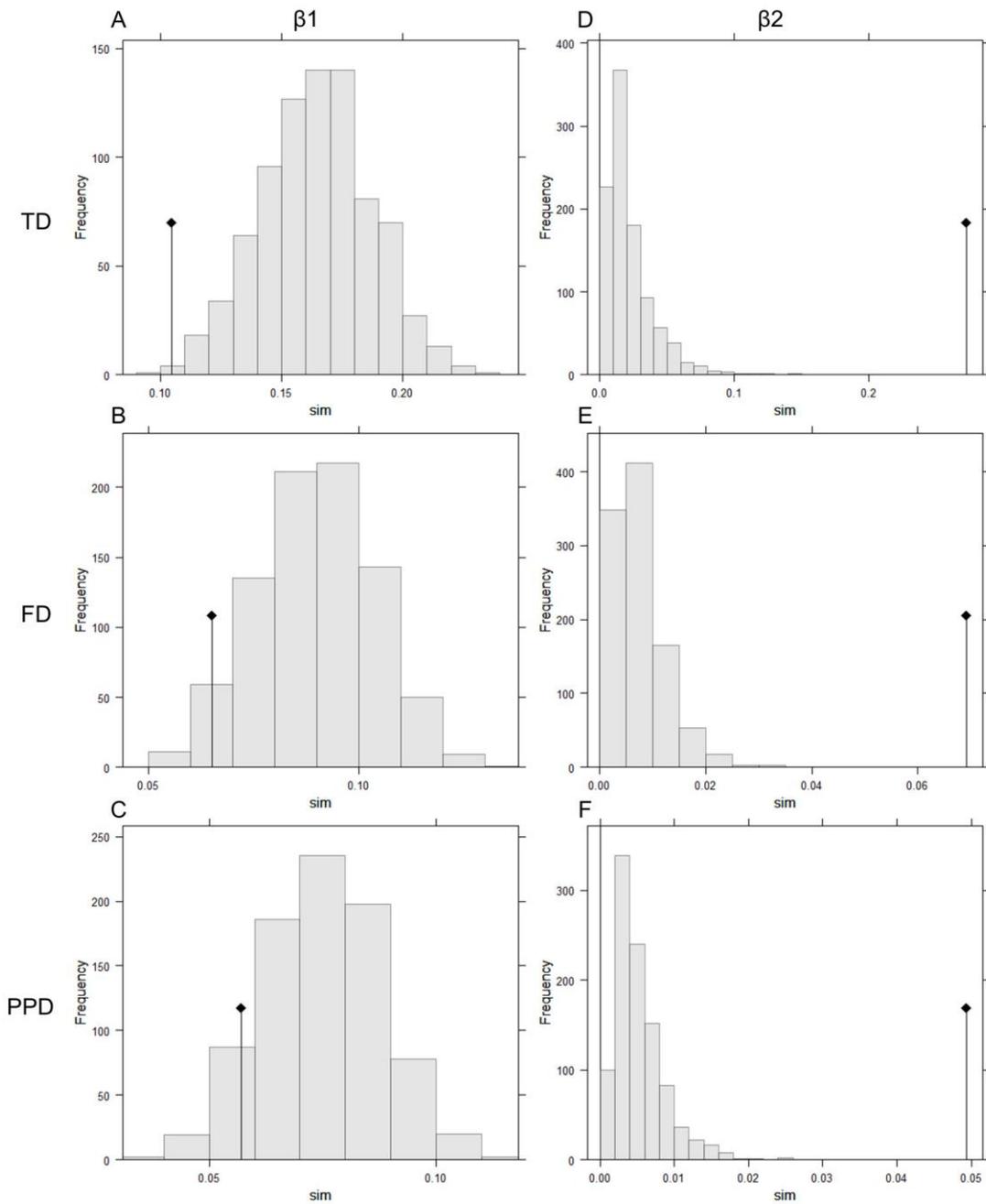
653
654 **Fig. 3. Parasite α diversity in terms of taxonomic (TD), functional (FD) and a proxy of the**
655 **phylogenetic (PPD) diversity for each locality (Case 2).** Different lowercase letters indicate
656 significant differences between localities. Abbreviations: EDS, Ebro Delta Sea; SPS, Santa Pola
657 Sea; SPL, Santa Pola Lagoon.



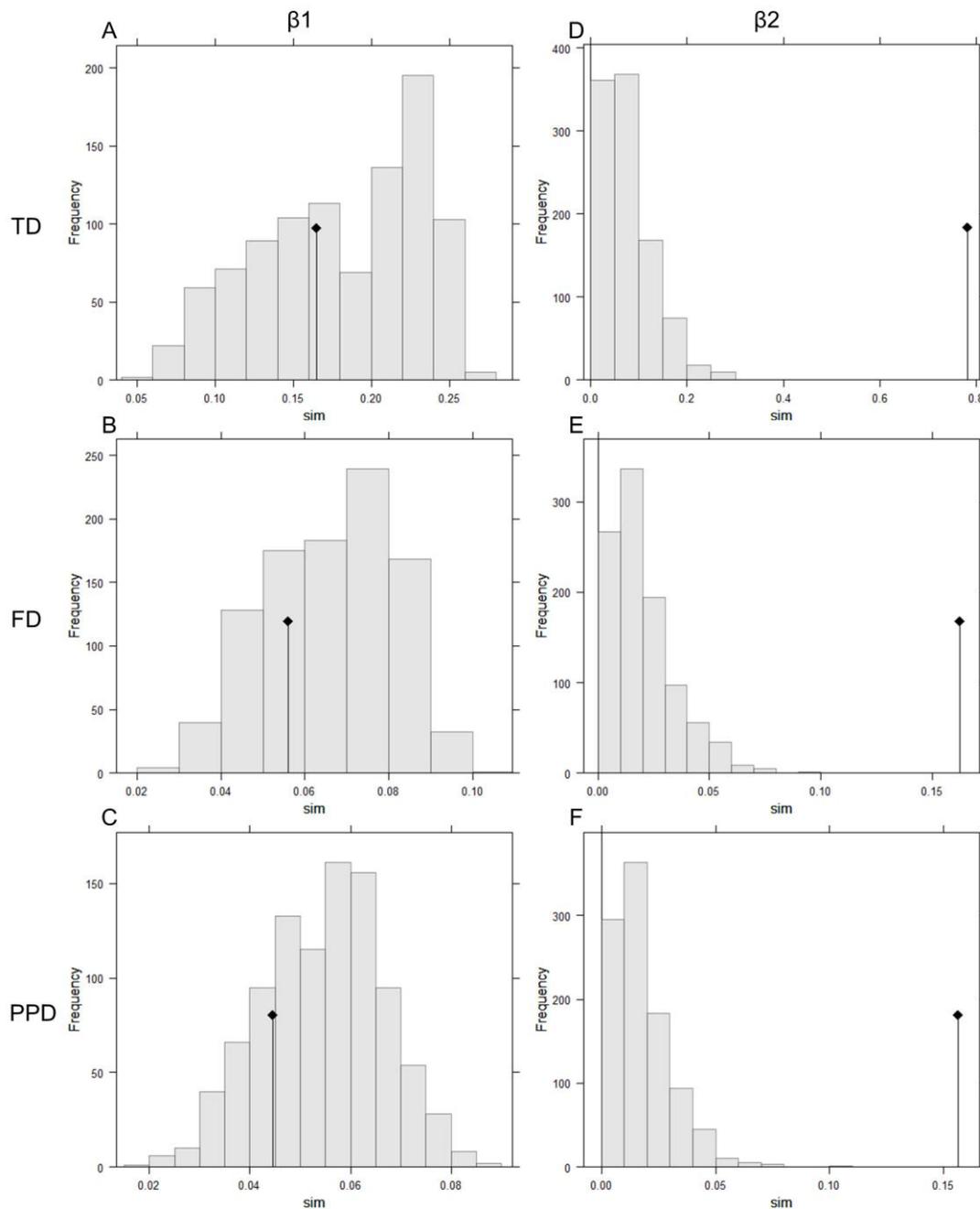
659

660 **Fig. 4. Position of each host individual (dots) in the (A) parasite species space, (B) parasite**
 661 **trait space and (C) parasite phylogenetic-like space (Case 2).** Fish were grouped by
 662 localities. Abbreviations: EDS, SPL and SPS represent the centroid of each locality, and stand

663 for Ebro Delta Sea, Santa Pola Lagoon and Santa Pola Sea, respectively. These analyses were
664 carried out with the second version of the crossed-DPCoA. The width and height of the ellipses
665 are given by the variance of the coordinates of the individuals, and the covariance between the
666 coordinates on the two axes gives the slope of the ellipse. “d” (top-right) indicates the length of
667 the side of the grey squares of the background grid.

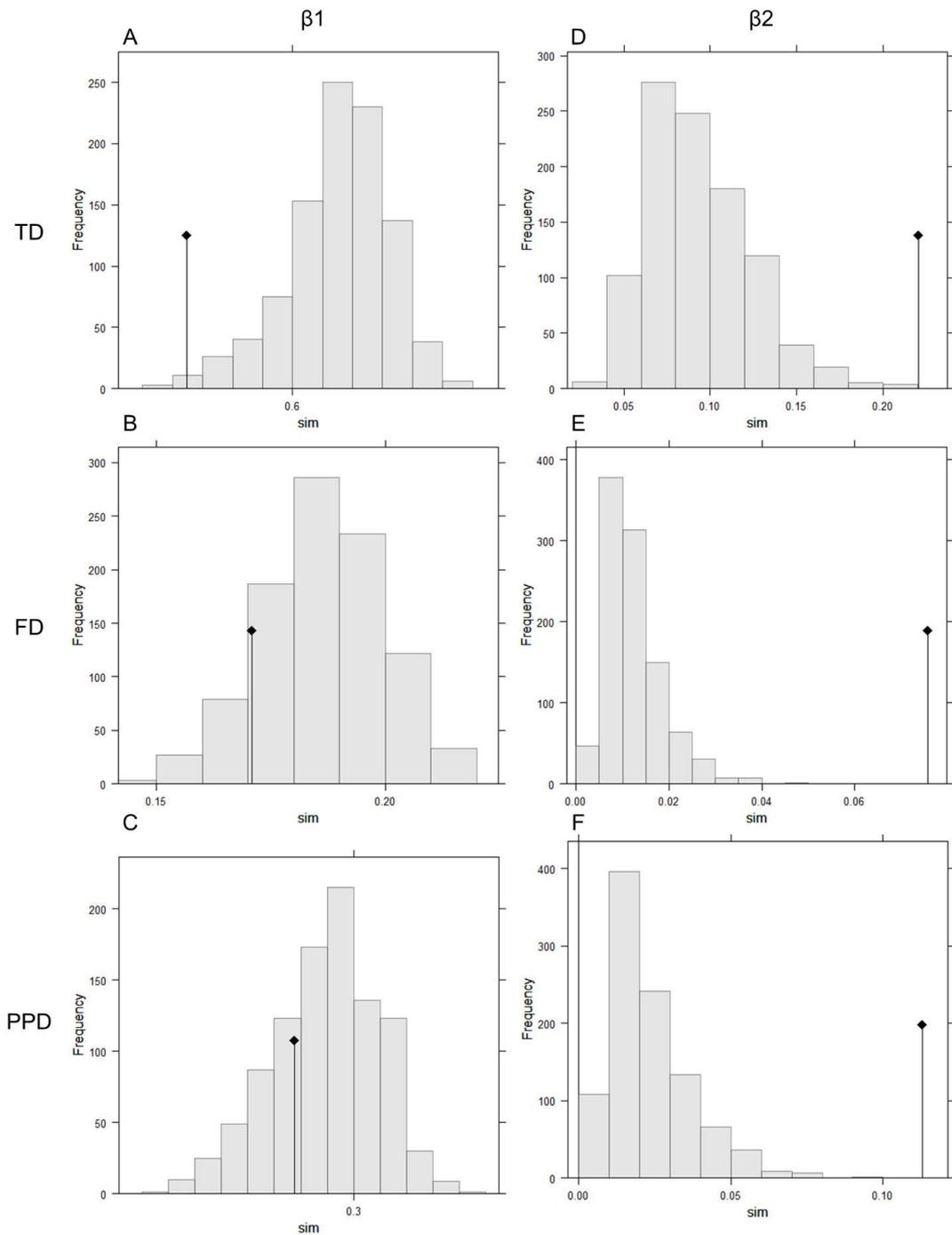


676 Diversity (TD), (B, E) Functional Diversity (FD) and (C, F) the Proxy of Phylogenetic Diversity
 677 (PPD). Samples are from Santa Pola Sea and autumn 2004 (Case 1). Observed β values (black
 678 diamond on the top of the black vertical line) and distribution of the simulated (x-axis: sim) β
 679 values (grey bars).
 680



681
 682 **Supplementary Figure S2. Observed and simulated β diversity values (Case 1: autumn**
 683 **2005). (A, B, C) β_1 diversity or extent of dissimilarity in the diversity of parasite communities**

684 among host individuals within each host species (*Chelon auratus*, *Mugil cephalus* and *Chelon*
685 *ramada*). (D, E, F) β 2 diversity or extent of dissimilarity in the diversity of parasite
686 communities between host species. Diversity was measured in terms of (A, D) Taxonomic
687 Diversity (TD), (B, E) Functional Diversity (FD) and (C, F) the Proxy of Phylogenetic Diversity
688 (PPD). Samples are from Santa Pola Sea and autumn 2005 (Case 1). Observed β values (black
689 diamond on the top of the black vertical line) and distribution of the simulated (x-axis: sim) β
690 values (grey bars).
691



692

693 **Supplementary Fig S3. Observed and simulated β diversity values (Case 2: spring 2004).**

694 (A, B, C) β_1 diversity or extent of dissimilarity in the diversity of parasite communities among

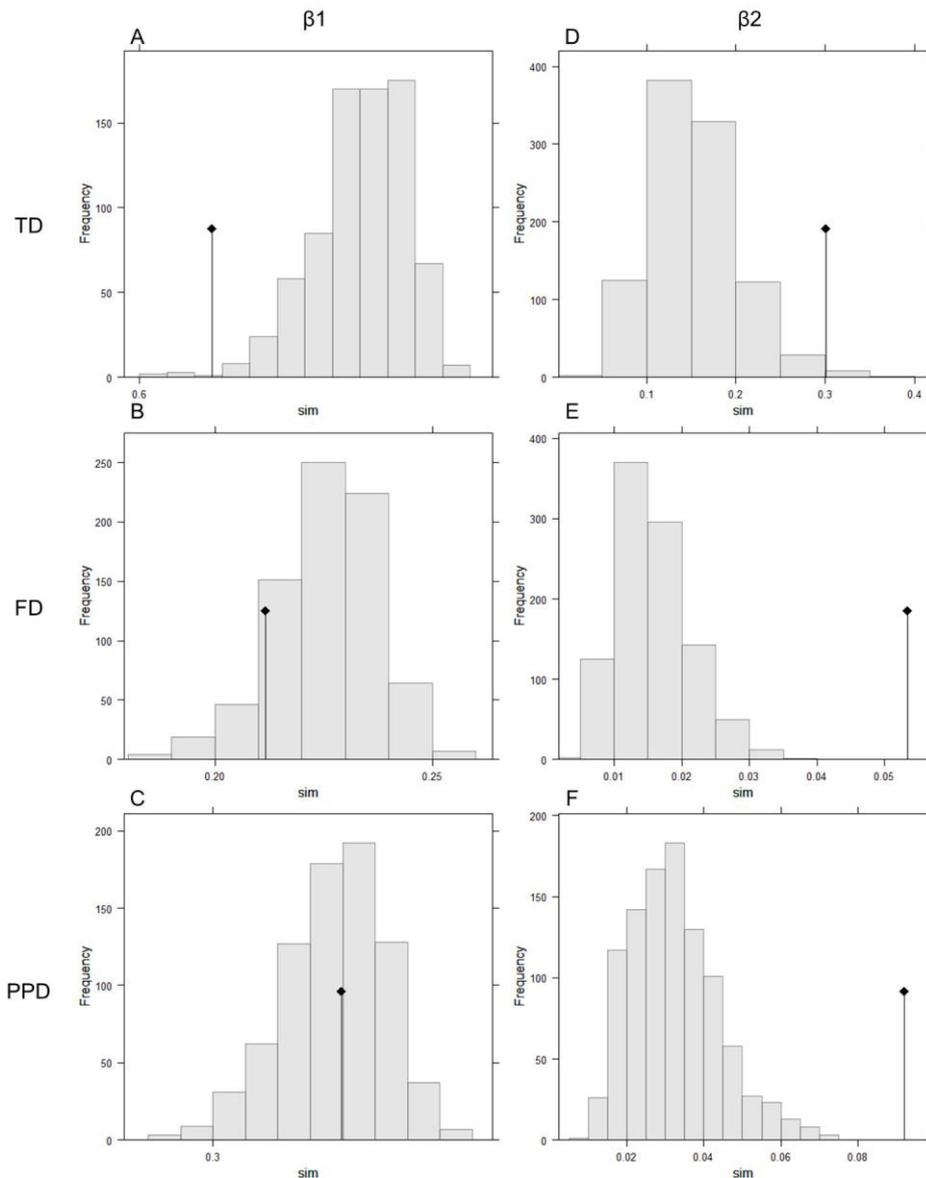
695 host individuals within each locality (Ebro Delta Sea, Santa Pola Lagoon and Santa Pola Sea).

696 (D, E, F) β_2 diversity or extent of dissimilarity in the diversity of parasite communities between

697 localities. Diversity was measured in terms of (A, D) Taxonomic Diversity (TD), (B, E)

698 Functional Diversity (FD) and (C, F) the Proxy of Phylogenetic Diversity (PPD). Samples are of

699 the host species *Mugil cephalus* and from spring 2005 (Case 2). Observed β values (black
 700 diamond on the top of the black vertical line) and distribution of the simulated (x-axis: sim) β
 701 values (grey bars).
 702



703
 704 **Supplementary Fig S4. Observed and simulated β diversity values (Case 2: autumn 2005).**
 705 (A, B, C) β_1 diversity or extent of dissimilarity in the diversity of parasite communities among
 706 host individuals within each locality (Ebro Delta Sea, Santa Pola Lagoon and Santa Pola Sea).
 707 (D, E, F) β_2 diversity or extent of dissimilarity in the diversity of parasite communities between
 708 localities. Diversity was measured in terms of (A, D) Taxonomic Diversity (TD), (B, E)

709 Functional Diversity (FD) and (C, F) the Proxy of Phylogenetic Diversity (PPD). Samples are of
710 the host species *Mugil cephalus* and from autumn 2005 (Case 2). Observed β values (black
711 diamond on the top of the black vertical line) and distribution of the simulated (x-axis: sim) β
712 values (grey bars).

713 **Tables**

714 **Table 1. Sample summary.** Fish (host individuals) sample sizes by host species, seasons, and
 715 localities.

	Santa Pola Sea			Santa Pola Lagoon			Ebro Delta Sea		
	Autumn 2004	Spring 2005	Autumn 2005	Autumn 2004	Spring 2005	Autumn 2005	Autumn 2004	Spring 2005	Autumn 2005
<i>Chelon auratus</i>	12		30						
<i>Mugil cephalus</i>	20	22	30		25	31		28	29
<i>Chelon ramada</i>	30		15						

716

717 **Table 2. Results of Type I ANOVAs of α Taxonomic (TD), Functional (FD) and Proxy of**
 718 **Phylogenetic (PPD) diversity. *P* values are given (significance level $P < 0.05$).**

	Case 1		Case 2	
	Autumn 2004	Autumn 2005	Spring 2005	Autumn 2005
TD	0.447	0.001	0.16	0.001
FD	0.693	0.002	0.001	0.001
PPD	0.023	0.001	0.03	0.001

719

720 **Table 3. Partition of diversity at two organisational levels of the host species factor (Case**
721 **1).** Statistical results of the partitioning of Taxonomic (TD), Functional (FD) and the Proxy of
722 Phylogenetic (PPD) Diversity at two organisational levels (β_1 [among host individuals within
723 host species] and β_2 [between host species]) in comparison to a distribution of 999 random
724 replicates. *P* values are given (significance level $P < 0.05$). Standardised observed values are
725 given in parenthesis. Standardised β is negative when the community structure is overdispersed,
726 and positive when the community structure is clustered.

	β_1			β_2		
	TD	FD	PPD	TD	FD	PPD
autumn 2004	0.007 (-2.6)	0.07 (-1.8)	0.17 (-1.4)	0.001 (14.6)	0.001 (13)	0.001 (13.3)
autumn 2005	0.85 (-0.3)	0.61 (-0.7)	0.42 (-0.8)	0.001 (13.8)	0.001 (10.1)	0.001 (11.2)

727

728 **Table 4. Percentage of diversity associated with each factor.** Taxonomic (TD), Functional
729 (FD) and Proxy of Phylogenetic (PPD) Diversity of parasite communities (A) of three host
730 species and autumn 2004 and 2005 (Case 1); (B) and from three localities and spring and
731 autumn 2005 (Case 2).

A	TD	FD	PPD
Host individual	50.3	50.2	56.3
Host species	31.3	28	20.6
Season	1.6	2.1	1.5
Host species × season	16.8	19.7	21.6
<hr/>			
B			
Host individual	57.9	53.7	52.1
Locality	5.8	12.4	12.1
Season	1.3	0.6	1
Locality × Season	35	33.3	34.8

732

733 **Table 5. Partition of diversity at two organisational levels of the locality factor (Case 2).**
734 Statistical results of the partitioning of Taxonomic (TD), Functional (FD) and Proxy of
735 Phylogenetic (PPD) Diversity at two organisational levels (β_1 [among host individuals within
736 locality] and β_2 [between localities]) in comparison to a distribution of 999 random replicates. *P*
737 values are given (significance level $P < 0.05$). Standardised observed values are given in
738 parenthesis. A standardised β is negative when the community structure is overdispersed, and
739 positive when the community structure is clustered.

	β_1			β_2		
	TD	FD	PPD	TD	FD	PPD
spring 2005	0.01 (-2.9)	0.25 (-1.2)	0.57 (-0.6)	0.001 (4.3)	0.001 (10.2)	0.001 (6.7)
autumn 2005	0.01 (-3.2)	0.2 (-1.2)	0.91 (0.1)	0.01 (3)	0.001 (7)	0.001 (5.2)

740