

1 **Determinants of different facets of beta diversity in Mediterranean marine amphipods**

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11

12 **Abstract**

13

14 Relying on a purely taxonomic view of diversity may ignore the fact that ecological
15 communities can be constituted of species having both distinct evolutionary histories and
16 functional characteristics. Thus, considering how the multiple facets of diversity vary along
17 environmental and geographic gradients may provide insights into the role of historic
18 processes and current environmental conditions in determining the distribution of species,
19 lineages and functions across space. By using distributional, taxonomic-distance and traits
20 information, we explore the role of spatial/environmental gradients and of biogeographic
21 subdivision of Mediterranean Sea on the different facets of beta diversity components in
22 seagrass amphipods. Beta diversity partitioning and correlation analyses showed a nearly
23 equal contribution of the replacement and richness components on total beta diversity for all
24 facets, although the influence of environmental and geographic distance differs among
25 components. While the replacement was mainly related to a pure spatial gradient, both the
26 environmental and geographic distance were correlated with the richness component of beta
27 diversities. Our results are in line with the complex paleobiogeographic history of the
28 Mediterranean Sea, with the replacement component likely to be related to the progressive
29 substitution of species of Atlantic origin with Mediterranean endemics along the west-east
30 geographic gradient, and the richness component to the marked environmental difference
31 between different basins. Moreover, the influence of biogeographic partition on the richness
32 components suggests the role of spatially structured gradients at biogeographic level in
33 determining the net loss/gain of species, lineages and functions, possibly influencing the
34 assembly processes of passive dispersal organisms.

35

36 **Introduction**

37

38 Understanding the patterns and mechanisms of species distribution is a central goal in
39 community ecology, having important outcomes for biodiversity conservation. Although
40 classical approaches focused mainly on the quantification of the difference in the number of
41 species across sites and/or time, recent findings have shown the weakness of considering
42 taxonomic diversity (TD, i.e., species richness) as the unique building block of diversity
43 (Flynn et al. 2011; Cadotte et al. 2012; Craven et al. 2018). Indeed, by using TD as main
44 descriptor of natural communities, one often ignores that the different evolutionary history of
45 species (i.e., their phylogenetic diversity, PD) and the diverse array of functional traits (i.e.,
46 their functional diversity, FD) constitute not negligible and complementary facets of diversity
47 (Webb et al. 2002; Petchey and Gaston 2006; Graham and Fine 2008). For instance, distinct
48 communities may be characterized by a high divergence in species composition although
49 showing high levels of functional convergence, signalling the replacement of species
50 performing similar functions across sites (Carvalho et al. 2019). Similarly, functional and
51 phylogenetic diversity may be unrelated as the first usually reflects ecological processes
52 acting at local scales, while the latter is traditionally interpreted as due to the effects of
53 ancient events as biogeographic history (Ramm et al. 2018). Biodiversity investigation taking
54 into account phylogenetic and trait-based analyses can thus help disentangling the
55 mechanisms of community assembly, since differences in their patterns may reveal the
56 signature of processes acting at different spatial and temporal scales.

57 Beta diversity is a core concept in ecology, aimed at determining the degree of dissimilarity
58 in the assemblage of communities along gradients (Whittaker 1960; Anderson et al. 2011; but
59 see Legendre 2019 and reference therein for a temporal definition of beta diversity). Beta
60 diversity can be decomposed into two additive components of dissimilarity, replacement (or
61 turnover, i.e., the substitution rate of species along the gradient) and richness (i.e., the net
62 difference in species number), each reflecting different processes acting on communities. For
63 instance, the replacement along a given gradient can be interpreted as due to environmental
64 niche filtering (Saladin et al. 2019), while the richness differentiation of assemblages may be
65 due either to the competitive loss of species or dispersal limitation (Si et al. 2016).

66 Recently, the beta diversity concept has been extended to include other dimensions of
67 diversity besides taxonomical, namely phylogenetic and functional (Graham and Fine 2008;
68 Leprieur et al. 2012; Cardoso et al. 2014). As the total beta diversity and its components may
69 respond differently to ecological and spatial gradients, knowledge of their correlates provides

70 useful information on the factors shaping biodiversity variation (Rocha et al. 2019; Heino et
71 al. 2019). When the effect of pure spatial distance is dominant, differences in community
72 composition are thought to follow neutral models driven by dispersal limitation alone
73 (Hubbel, 2001). Conversely, in case of strong environmental signals, deterministic models
74 based on the ecological responses of species to their surrounding environment (i.e.,
75 environmental filtering) should shape beta diversity patterns (Cornwell et al. 2006). However,
76 taxonomic, phylogenetic and functional dissimilarity may result from the joint effect of both
77 geographic and environmental constraints, as environmental variables are intrinsically
78 spatially structured (Legendre and Legendre 2012). Under this circumstance, it can be
79 expected that beta diversity is driven by spatially structured environmental gradients, rather
80 than pure environmental ones (Zhang et al. 2019).

81 The Mediterranean Sea has physical, chemical and historic features that make it particularly
82 suitable to study the effects of geographic and environmental gradients on beta diversity. It is
83 a concentration basin, where global oceanographic conditions allow for differences in
84 evaporation regime between different portions (higher in the easternmost part), ultimately
85 determining strong environmental gradients mostly related to differences in temperature and
86 salinity (Coll et al. 2010). Moreover, surface circulation coupled with local meteorology and
87 bathymetry, allow for a complex spatial environmental heterogeneity and the development of
88 very steep gradients localized at the boundaries of the main circulation divides (Berline et al.
89 2014). Such complexity results in well-defined spatial patterns of diversity, generally
90 decreasing from north-western to south-eastern regions, determined by the dispersal ability of
91 species and the selection by local environmental conditions (Coll et al. 2010; Berline et al.
92 2014).

93 Within this context, marine benthic amphipods represent a well-suited group of species to
94 test specific hypotheses relating the complementary role of geographic and environmental
95 constraints on the structuring of ecological communities within the Mediterranean Sea. The
96 lack of planktonic larval stages limits the dispersal ability of amphipods, suggesting relatively
97 small distribution ranges, high endemism and a robust biogeographic pattern (Arfianti and
98 Costello 2020). Understanding the determinants of amphipods distribution over large scales is
99 fundamental, as they represent a key trophic level in benthic ecosystems, being also
100 extremely sensitive to environmental alterations (Pinnegar et al. 2000; Kumagai 2008; Michel
101 et al. 2015). Beta diversity may thus provide useful information on how environmental and/or
102 geographic factors affect the distribution of species, lineages and functions in Mediterranean
103 marine amphipods.

104 In this paper, we aim to test for the relative contribution of geographic and environmental
105 constraints on the taxonomic, phylogenetic and functional beta diversity. We used
106 distribution data of amphipods associated with *Posidonia oceanica* (L.) Delile, 1813 mined
107 from literature, including information on a selected array of functional traits having important
108 outcomes for the community assembly process: body size, living habit and trophic group.
109 Localities were characterized by using data on the occurrence of *P. oceanica* seagrass habitat
110 and information on specific environmental features (i.e., sea surface temperature and
111 salinity), known to have a direct influence on the distribution of biota in the Mediterranean
112 Sea (Coll et al. 2010). Moreover, as rates of trait evolution and speciation may differ among
113 biogeographic regions (Arnan et al. 2017), we used a previously identified biogeographic
114 partition of the same dataset (Bellisario et al. 2019), to understand the importance of
115 biogeographic barriers with respect to geographic distance and environmental gradients in
116 structuring beta diversity.
117

118 **Material and methods**

119

120 **Study area**

121

122 We used data on the presence/absence of 147 amphipod species from *P. oceanica* meadows
123 in 28 sampling localities across the Mediterranean Sea (Fig. 1). The dataset was reconstructed
124 from different sources mined from literature, all selected by comparable data in terms of
125 sampling season, depth and survey methods (see Bellisario et al. 2019 and reference therein).
126 The study area covered a large portion of the Mediterranean Sea, characterized by different
127 geographic, hydrological and geological features, as well as differences in the potential
128 connectivity due to general circulation models (Bianchi 2011; Berline et al. 2014). In a
129 previous work (Bellisario et al. 2019), a network approach based on modularity was applied
130 on the same data set to identify the bioregional partition of local assemblages, identifying
131 four main bioregions corresponding to the main divides of the Mediterranean basin (Fig. 1).

132

133 **Environmental and habitat characterization**

134

135 We used the Sea Surface Temperature (SST) and Sea Water Salinity (PSU) values as main
136 determinants of the environmental characteristics of sites, since they are both known to co-
137 vary geographically and so influencing the pattern of species diversity throughout the
138 Mediterranean basin (Coll et al. 2010). Data were downloaded from the COPERNICUS
139 Marine Environment Marine Service (CMEMS, <https://marine.copernicus.eu>), which
140 provides an easy way to access a variety of data from multiple sources (e.g., satellite
141 observations and *in situ* sensors) encompassing different spatial and temporal resolution. SST
142 and PSU were extracted from the Mediterranean Sea Physics Reanalysis, a hydrodynamic
143 model supplied by the Nucleus for European Modelling of the Ocean (NEMO), with a
144 resolution matching the seasonal (Spring/Summer), temporal (1987-2014) and depth
145 coverage (5-20m) of the original papers from which community data were extracted (see
146 Data availability statement section). This model has a variational data assimilation scheme
147 (OceanVAR) for temperature and salinity vertical profiles and satellite sea level anomaly
148 along track data, with an horizontal grid resolution of ~1 km. Reanalysis has been initialized
149 with a gridded climatology for temperature and salinity computed from *in situ* data sampled
150 before 1987, and released as monthly mean (more information about models and data

151 processing can be found at [http://marine.copernicus.eu/services-portfolio/access-to-](http://marine.copernicus.eu/services-portfolio/access-to-products/)
152 products/).

153 To describe the habitat characteristic at sites, we used the probability of *P. oceanica*
154 occurrence (PPOMed), downloaded from the EMODnet Seabed Habitat portal
155 (<https://www.emodnet-seabedhabitats.eu>) with a spatial resolution of ~1km and values
156 ranging in the 0-1 interval. PPOMed expresses the probability of seagrass occurrence from
157 the collation and integration of available habitat distribution models at Mediterranean scale,
158 derived by applying a Machine Learning technique (i.e., Random Forest) to train on data
159 from regions where information was available and then used to predict the probability of
160 occurrence of *P. oceanica* (more information can be found in Cameron and Askew 2011).

161 To derive a meaningfulness measure of the environmental and habitat characteristics, we
162 performed a geostatistical analysis by superimposing a vector of sampling data points to the
163 SST, PSU and PPOMed rasters in a Geographic Information System (QGIS Development
164 Team 2019) and derived the average (\pm SD) values within a 1km search radius centred on
165 sampling localities.

166

167 **Amphipod traits and phylogenetic data**

168

169 We included information on body size, living habit and trophic groups, which are considered
170 key functional traits determining the competitive ability and community assembly processes
171 of seagrass amphipods (Best et al. 2013; Scipione 2013; Best and Stachowicz 2014; Lürig et
172 al. 2016). Traits information were extracted from available literature on Mediterranean
173 marine amphipods (Ruffo 1982; 1989; 1993; 1998; Scipione 2013) and nomenclature was
174 updated following the World Register of Marine Species (WoRMS, last access 22/02/2021).

175 Body size was quantified using the maximum body length (measured from the anterior
176 margin of the head to the posterior end of the telson, in mm) in accordance with the fast-
177 seasonal growth cycle of seagrass amphipods (Spring/Summer breeding period, Best and
178 Stachowicz 2014). Since a certain degree of sexual body size dimorphism may exist in
179 amphipods (Longo and Mancinelli 2014), values were taken as the average maximum body
180 length between male and female specimens.

181 Information on living habits and trophic groups were extracted to the highest possible
182 taxonomic level (i.e., species) and, in case of missing information at species level, we used
183 families as the upper limit for classification. Traits were coded as not available (NA) if no
184 information was available at family level. Following Scipione (2013), each species was thus

185 classified to four living habit categories (epifaunal free-living, epifaunal domicolous, infaunal
186 free-burrowing and infaunal tube-building) and 10 trophic groups (suspension feeders,
187 deposit feeders, carnivores, commensals, herbivores, plant detritus feeders, omnivores,
188 deposit-suspension feeders, deposit feeders-carnivores and herbivores-deposit feeders). Traits
189 distance between species was measured with the Gower distance (Pavoine et al. 2009), which
190 allows for missing trait values and the use of both quantitative (body size) and qualitative
191 (living habit and trophic group) data, by means of the function ‘gowdis’ in the FD package of
192 R (Laliberté and Legendre 2010; R Development Core Team 2018).

193 Since a true phylogenetic tree was currently unavailable for all amphipod species recorded
194 in our study, we used a taxonomic distance measure based on the average path lengths in the
195 taxonomic tree (Ricotta et al. 2012; Cardoso et al. 2014). Although the amount of
196 approximation provided by surrogate measures for phylogeny poses serious limits when used
197 for answering strict evolutionary questions (Cardoso et al. 2014), their use is found to be
198 valid in large-scale metacommunity studies (Heino and Tolonen 2017; Hill et al. 2019).
199 Taxonomic information were retrieved from WORMS by using the function ‘classification’
200 in the package ‘taxize’ (Chamberlain and Szocs 2013) of R and the taxonomic distance was
201 calculated by using equal branch lengths between seven taxonomic levels (Species, Genus,
202 Family, Superfamily, Parvorder, Infraorder, Suborder), by using the function ‘taxa2dist’ in
203 the ‘vegan’ package of R (Oksanen et al. 2019).

204

205 **Beta diversity estimates**

206

207 The Jaccard dissimilarity index was chosen as a beta diversity metric reflecting the variation
208 in amphipod assemblage along gradients. Total beta diversity (β_{Tot}) was further decomposed
209 into relativised additive fractions of species replacement (β_{Repl}) and richness (β_{Rich})
210 components for taxonomic, phylogenetic and functional diversity. Here, we followed the
211 approach proposed by Cardoso et al. (2014), which uses trees as common representation for
212 taxonomic, phylogenetic and functional diversity, according to which part of a global tree is
213 shared by or unique to the compared communities. Traits and phylogenetic distance matrices
214 were converted to trees and then used to quantify the taxonomic (TD β), phylogenetic (PD β)
215 and functional (FD β) beta diversity and its replacement and richness components, by using
216 the package ‘BAT’ of R (Cardoso et al. 2015).

217

218 **Statistical analyses**

219

220 The Mantel and partial Mantel tests (Legendre and Legendre 2012) were used to measure the
221 correlation between the different facets of beta diversity components and between these latter
222 with environmental and geographic variables.

223 The environmental distance was measured by computing the euclidean distance of
224 PPOMed, SST and PSU between sampling localities. Pairwise geographic distances were
225 calculated with a least-cost paths approach, by using land areas (masked using the European
226 Environment Agency coastline polygon 1:100000) as a barrier in distance calculation. This
227 method allows for a more realistic evaluation of the effective spatial separation than the more
228 commonly used Great Circle or euclidean distances due to the complex geometry of
229 coastlines in the Mediterranean basin (Ratray et al. 2016). We also considered the
230 biogeographic (aka modular) partition already derived from our previous study (Bellisario et
231 al. 2019) to account for the biogeographic-level effects in determining the patterns of
232 dissimilarity. We therefore assigned a numeric code to each site corresponding to the
233 bioregion it belonged (Fig. 1), and then calculated the dissimilarity matrix by means of the
234 euclidean distance. This matrix was used as covariates in the partial Mantel test to account for
235 the biogeographic-level effect on explanatory variables. Data and codes are available from
236 the Data availability statement section.

237

238 **Generalized dissimilarity modelling**

239

240 We used Generalized Dissimilarity Modelling (GDM, Ferrier et al. 2007) to model the
241 relationship of TD β , PD β and FD β components with environmental variables. GDM is a
242 statistical regression technique able to accommodate for nonlinearity in eco-geographical
243 datasets, where the compositional dissimilarity provided by beta diversity estimates is
244 modelled as a nonlinear function of the environmental distance between pairs (Ferrier et al.
245 2007). Moreover, GDM is known to be robust to multicollinearity among predictor variables
246 (e.g., Glassman et al. 2017), facilitating the understanding of the variation in beta diversity
247 along actual environmental gradients.

248 Here, we discarded the geographic distance provided by latitudinal and longitudinal
249 coordinates as poorly representative of the real geographic distance in our system. Thus, we
250 fitted GDMs using three predictor variables, PPOMed, SST and PSU and plot the I-splines
251 (i.e., monotone cubic spline functions) to assess the impact of predictor variables on the total,
252 replacement and richness components of taxonomic, phylogenetic and functional

253 dissimilarity matrices. The slope of the I-splines curves indicates the rate of dissimilarity
254 while the maximum height represents the total amount of dissimilarity associated with the
255 variable, holding all other variables constant. Variable's importance was estimated from the
256 sum of each I-spline coefficient. Here, we used the default setting of three I-splines for each
257 predictor, using the package 'gdm' of R (Manion et al. 2018).

258

259 **Results**

260

261 **Beta diversity patterns**

262

263 Assemblages of Mediterranean seagrass amphipods showed relatively high values of total
264 beta diversity for $TD\beta$, slightly lower for $PD\beta$ and exhibited the lowest value for $FD\beta$
265 ($TD\beta_{Tot} = 0.799 \pm 0.014$; $PD\beta_{Tot} = 0.624 \pm 0.011$; $FD\beta_{Tot} = 0.509 \pm 0.009$). The replacement
266 and richness components accounted for by a nearly equal contribution for all beta diversity
267 facets ($TD\beta_{Repl} = 0.418 \pm 0.007$, $TD\beta_{Rich} = 0.381 \pm 0.006$; $PD\beta_{Repl} = 0.298 \pm 0.005$, $PD\beta_{Rich} =$
268 0.326 ± 0.006 ; $FD\beta_{Repl} = 0.232 \pm 0.004$, $FD\beta_{Rich} = 0.277 \pm 0.005$). As expected, we found
269 significant and positive correlations between the different facets and components of beta
270 diversity ($R^2 > 0.8$ and $p < 0.001$ for all cases). Correlations between the components of $PD\beta$
271 and $FD\beta$ still remained significant, although lower, after controlling for $TD\beta$ ($R^2 > 0.45$ and p
272 < 0.001 for all cases) (Fig. SM1 in Supplementary Materials).

273

274 **Correlates of beta diversity**

275

276 Mantel and partial Mantel tests did not show substantial differences between the total beta
277 diversity of different facets, which resulted to be always positively correlated with both
278 environmental and geographic distances, even after controlling for the biogeographic
279 partition (Table 1). Conversely, the replacement and richness components showed different
280 patterns with respect to the environmental and geographic gradients.

281 The replacement component of all beta diversity facets was correlated with geographic
282 distance and such correlations were robust enough even after partialing out, with the only
283 exception of $FD\beta_{Repl}$, which showed no correlation with the geographic distance after
284 controlling for the biogeographic partition (Table 1). No correlation was detected with
285 environmental distance, signalling that the replacement was not influenced by the
286 environment (Table 1). The richness component of beta diversities was correlated with both

287 the environmental and geographic distance, although this latter lacked a correlation when
288 considering the effect of either the environment or biogeography (Table 1). Conversely, the
289 environmental distance still remained significantly correlated when accounting for the
290 geographic and biogeographic distance (Table 1).

291 GDMs showed substantial differences between the components of each beta diversity facet
292 when considering environmental predictors, being relatively higher for the total beta diversity
293 and showing a negligible contribution on the replacement component with respect to the
294 richness one (Table 2). $TD\beta_{Tot}$ was mostly impacted by salinity (Table 2), which showed a
295 linear relationship and then exhibited a sudden increase approximately around 38 PSU, after
296 which the species compositional variation increased rapidly (Fig. 2c). The same trend was
297 observed for $PD\beta_{Tot}$ and $FD\beta_{Tot}$, although the contribution of PSU was comparable to that of
298 other predictors (Table 2), and the shape of relationship showed the same pattern observed
299 for $TD\beta_{Tot}$, although less marked (Fig. 2c). About the replacement component, none of beta
300 diversity facets was impacted by PPOMed (Table 2 and Fig. 2d). SST had a relatively high
301 impact on $FD\beta_{Repl}$, while PSU impacted most $TD\beta_{Repl}$, and both had a relatively similar effect
302 on $PD\beta_{Repl}$ (Table 2). For both $FD\beta_{Repl}$ and $PD\beta_{Repl}$, a sharp increase was observed within a
303 narrow range of temperature between 17-18 °C, followed by a slow increase for higher
304 temperatures, while the impact on $TD\beta_{Repl}$ was mostly linear with a moderate slope (Fig. 2e).
305 Both taxonomic and phylogenetic replacement showed a curvilinear response to PSU, while
306 $FD\beta_{Repl}$ exhibited a linear relationship (Fig. 2f). Considering the richness component,
307 PPOMed provided the highest impact on all the facets, all showing a curvilinear relationship
308 followed by a plateau (Fig. 2h). SST had a minor impact on all facets (Fig. 2i), while PSU
309 showed a more pronounced impact characterized by no effect until the threshold of about 38
310 PSU, beyond which the taxonomic, phylogenetic and functional richness component of beta
311 diversity showed a sudden increase (Fig. 2l).

312

313 Discussion

314

315 In this study, we focused on the beta diversity of Mediterranean seagrass amphipods to
316 disentangle the role of environmental and geographic gradients on taxonomic, phylogenetic
317 and functional facets of diversity. $FD\beta$ showed the lowest value of total beta diversity with
318 respect to both $TD\beta$ and $PD\beta$, but a nearly equal contribution of both the replacement and
319 richness components was found for all the three facets considered. However, environmental
320 and geographic gradients influenced differently the components of each facet. Geographic
321 distance was the only determinant of the replacement component, while environmental
322 distance and, to a lesser extent, spatial distance, mainly influenced the richness component.
323 Moreover, the not negligible role of biogeographic partition found for the richness
324 components suggest the role of spatially structured gradients in determining the net loss/gain
325 of species, lineages and functions in Mediterranean seagrass assemblages.

326 Taxonomic and phylogenetic beta diversity are usually associated with events occurring on
327 wide scales and over long time, typically within a biogeographic frame. The same vision
328 interprets functional beta diversity as mainly, although not exclusively, due to local
329 ecological processes such as environmental filtering (Ramm et al. 2018; Pavoine and Bonsall
330 2011). Accordingly, different factors might have driven the dynamics of current distribution
331 of species and lineages in seagrass amphipods to produce the observed patterns, mainly
332 related to both the complex paleogeographic history and the marked biogeographic structure
333 of the Mediterranean Sea (Bianchi et al. 2011). About the Mediterranean history, it is well
334 known the role of geological events occurred during the Tertiary and the climatic fluctuations
335 during the Quaternary (especially the most recent cycles of Plio-Pleistocene glaciations; Coll
336 et al. 2010) in determining the distribution of biota in the basin (Bianchi et al. 2011).

337 Moreover, the turbulent geological history of the basin allowed for the creation of a great
338 variety of climatic and hydrologic conditions in fairly isolated sub-basins, subdividing the
339 Mediterranean Sea in many biogeographic sectors characterized by different environmental
340 and habitat features (Bianchi et al. 2011). This allowed species of different biogeographic
341 origin to enter and settle within the basin, contributing to the high level of α -diversity and
342 endemism rate designating the Mediterranean Sea as one of the world's biodiversity hotspots
343 (Lejeune et al. 2010; Bianchi et al. 2011).

344 This scenario is compatible with the high level of β -diversity found in seagrass amphipods
345 in our study and with the balanced contribution of its components. Indeed, replacement could

346 be related to the progressive substitution of species of Atlantic origin with Mediterranean
347 endemics along the west-east axis and, to a lesser extent, along the north-south axis (Bianchi
348 et al. 2011) so following a geographic gradient, while the richness difference could be due to
349 the extremely low environmental affinities of the eastern sectors (i.e., Adriatic and Ionian
350 Sea) with the central-western part of the basin. This hypothesis is in line with the reduced
351 occurrence of Mediterranean endemics and number of shared species with other
352 biogeographic sectors observed in the eastern areas (Bianchi et al. 2011; Bellisario et al.
353 2019). Indeed, it has been shown that 95% of the known species of Mediterranean amphipods
354 can be recovered in the Central basin, while only 53% inhabit the Adriatic Sea (Bellan-
355 Santini and Ruffo 2003). Thus, the balanced contribution of the replacement and richness on
356 the overall dissimilarity would stem from the combined action of: i) repeated isolation and
357 contraction of biotas and associated speciation events, which might have contributed to the
358 overall diversity of taxa and the divergence of lineages and, ii) variation in environmental
359 features, able to filter which species can survive in particularly selective environments as, for
360 instance, the Adriatic Sea.

361 This scenario is also suitable for the functional diversity, that however showed a higher
362 influence of the biogeographic subdivision with respect to the geographic cline. Specific
363 features of the Mediterranean circulation and bioregional subdivision can help explain this
364 finding, together with the low dispersal potential of seagrass amphipods. Indeed, a recent eco-
365 regionalization based on the potential connectivity assessed from ensemble Lagrangian
366 simulations provided an in-depth subdivision of the basin in several different regions whose
367 hydrodynamical boundaries can help explain the spatial distribution of passively transported
368 organisms (Berline et al. 2014). Biogeographic boundaries largely match the major
369 discontinuities in variables describing the environment and geographic clines in temperature
370 and salinity characterizing the Mediterranean basin show sharp changes at the main divides,
371 resulting in geographically adjoining but ecologically dissimilar regions (Coll et al. 2011,
372 Berline et al. 2014).

373 Under this scenario, environmental discontinuities among bioregions might be involved in
374 determining the spatial distribution of functional traits, by sorting species according to their
375 environmental and habitat requirements. For instance, significant differences in the body size
376 distribution across bioregions (but not of living habits and trophic groups) have shown how
377 the Adriatic bioregion is composed of species significantly larger than other bioregions (Fig.
378 SM2, Supplementary Materials). Interestingly, body size is considered a key trait related to
379 the community assembly processes of seagrass amphipods, being involved in a series of

380 complex relationships occurring between the abiotic features of surrounding environment and
381 direct and indirect biotic interactions, mainly due to competition and predation avoidance.
382 Body size, temperature and salinity are dominant factors affecting the metabolic rate in
383 amphipods (Poulin and Hamilton 1995; Maranhão and Marques 2003), which may however
384 vary significantly in response to different ecological condition as, for instance, predation
385 pressure (Glazier et al. 2020). Moreover, historical and biogeographic processes, alongside
386 current environmental conditions, may have played a role in determining the distribution and
387 complexity of seagrass habitat (*sensu* Hacker and Steneck 1990), thereby allowing for the
388 functional differentiation of assemblages at bioregional scale as response to an evolved
389 consequence of consistently high predation risk, size-dependent habitat selection and food
390 availability (Kovalenko et al. 2011; Lürig et al. 2016).

391 GDM analysis supports these findings, highlighting the impact of salinity and the presence
392 of a threshold at 38 PSU, beyond which beta diversity metrics showed an exponential
393 increase (Fig. 2). This value corresponds to the southern Adriatic/Ionian Sea surface salinity,
394 and is abruptly reached by crossing the Sicily Channel, a main divide of the Mediterranean
395 Sea. In the case of Adriatic Sea, environmental features are coupled with the presence of the
396 strong barrier represented by the Strait of Otranto, and previous studies have shown that this
397 area is inhabited exclusively by widely distributed amphipod species, mainly cosmopolitan,
398 as a result of both extreme environmental conditions and geographic isolation (Bellisario et
399 al., 2019). Moreover, such threshold sets also the tolerance limit for the activation of
400 osmoregulatory processes that may potentially interfere with the leaf growth, survival and
401 photosynthetic rates of *P. oceanica*, thereby affecting meadow structure and limiting the
402 distribution of the seagrass in the easternmost sectors of the Mediterranean (Sandoval-Gil et
403 al. 2012).

404 In conclusion, our findings show how taxonomic, phylogenetic and functional beta diversity
405 in Mediterranean seagrass amphipods stem from an equal contribution of both the
406 replacement and richness components, which however can be driven by distinct processes
407 with respect to the beta diversity facets analysed. While geographic distance alone is the main
408 constraint determining the replacement, spatially structured gradients at biogeographic scale
409 mainly determine the net loss/gain of species, lineages and functions. Overall, our results
410 corroborate the hypothesis that, although the Mediterranean Sea is largely characterized by
411 wide-basin gradients, biogeographic boundaries may have a strong influence in accounting
412 for biodiversity distribution (Bianchi et al. 2011), by creating marked discontinuities in

413 environmental and spatial gradients, possibly influencing dispersal- and niche-based
414 processes in the community assembly of passive dispersal organisms.
415
416

417 **Declarations**

418

419 **Funding** – The authors did not receive support from any organization for the submitted work.

420 **Conflicts of interest/Competing interests** – The authors declare no conflicts or competing
421 of interest.

422 **Availability of data and material** - Data and codes are available from Supplementary
423 Materials.

424 **Authors' contributions** - BB and RC conceived and designed the paper, wrote the
425 manuscript and approved the final draft; BB analysed the data, prepared figures and tables;
426 FC and CA collected field materials. All authors gave final approval for publication.

427

428 **List of Tables**

429

430 **Table 1** – Results of the (partial) Mantel tests between taxonomic (TD β), phylogenetic (PD β)
 431 and functional (FD β) beta diversity components of Mediterranean seagrass amphipods and
 432 environmental (ENV) and geographic (GEO) distances, while accounting for the
 433 biogeographic-level (BIO) effect (see Fig. 1). Bold is for significant values, with p values
 434 shown in italic.

435

Model	TD β			PD β			FD β		
	Tot	Repl	Rich	Tot	Repl	Rich	Tot	Repl	Rich
ENV	0.312 <i>0.003</i>	-0.097 <i>0.927</i>	0.287 <i>0.001</i>	0.346 <i>0.001</i>	-0.081 <i>0.891</i>	0.299 <i>0.002</i>	0.281 <i>0.005</i>	-0.048 <i>0.768</i>	0.282 <i>0.005</i>
GEO	0.407 <i>0.001</i>	0.182 <i>0.003</i>	0.178 <i>0.001</i>	0.367 <i>0.001</i>	0.165 <i>0.006</i>	0.101 <i>0.001</i>	0.298 <i>0.002</i>	0.168 <i>0.006</i>	0.103 <i>0.001</i>
ENV GEO	0.231 <i>0.007</i>	-0.154 <i>0.985</i>	0.277 <i>0.005</i>	0.276 <i>0.001</i>	-0.131 <i>0.951</i>	0.284 <i>0.003</i>	0.218 <i>0.022</i>	-0.099 <i>0.911</i>	0.266 <i>0.003</i>
ENV BIO	0.326 <i>0.001</i>	-0.112 <i>0.955</i>	0.281 <i>0.002</i>	0.372 <i>0.001</i>	-0.096 <i>0.917</i>	0.293 <i>0.001</i>	0.288 <i>0.001</i>	-0.072 <i>0.872</i>	0.276 <i>0.003</i>
GEO ENV	0.353 <i>0.001</i>	0.217 <i>0.001</i>	0.001 <i>0.472</i>	0.303 <i>0.001</i>	0.194 <i>0.005</i>	0.022 <i>0.385</i>	0.241 <i>0.009</i>	0.189 <i>0.001</i>	0.03 <i>0.32</i>
GEO BIO	0.331 <i>0.001</i>	0.138 <i>0.01</i>	0.046 <i>0.271</i>	0.277 <i>0.001</i>	0.117 <i>0.05</i>	0.055 <i>0.237</i>	0.199 <i>0.031</i>	0.095 <i>0.076</i>	0.067 <i>0.191</i>

436

437

438 **Table 2** - GDM model summary for each facets and component of beta diversity with respect
 439 to environmental variables.

440

	TD β _{Tot}	TD β _{Repl}	TD β _{Rich}	PD β _{Tot}	PD β _{Repl}	PD β _{Rich}	FD β _{Tot}	FD β _{Repl}	FD β _{Rich}
Gradient									
PPOMed	0.551	0	0.444	0.373	0	0.355	0.183	0	0.232
SST	0.646	0.087	0.099	0.31	0.102	0.0877	0.404	0.177	0.078
PSU	1.408	0.282	0.294	0.468	0.12	0.243	0.455	0.0988	0.233
GDM summary									
Model deviance (%)	28.727	79.244	77.411	19.586	56.971	61.931	23.109	53.305	50.268
NULL deviance	44.529	79.759	91.811	28.391	58.374	74.331	34.339	55.672	61.353
Deviance explained (%)	35.481	4.407	15.685	31.011	2.403	16.682	32.701	4.252	18.066

441

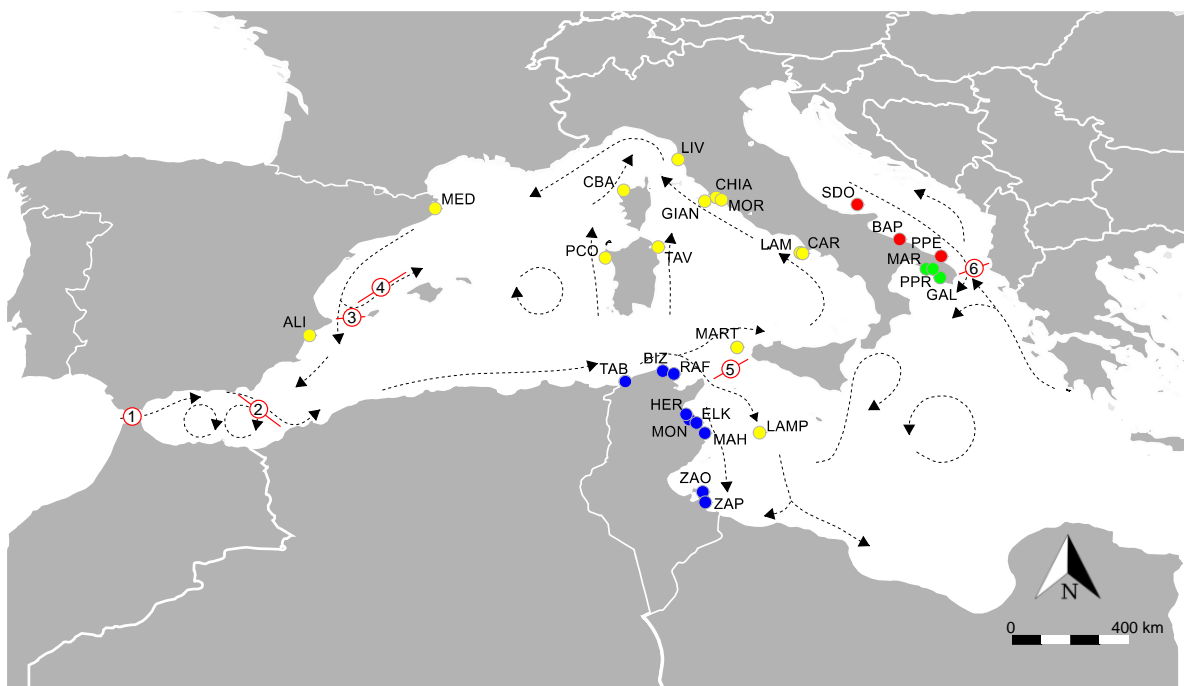
442

443 **List of Figures**

444

445 **Figures 1** – Geographic extension of the study area and sampling localities. Dotted arrows
446 indicate the main circulation patterns and red lines with circles the main barriers: 1, Gibraltar
447 Strait; 2, Almeria-Oran Front; 3, Ibiza Channel; 4, Balearic Front; 5, Sicily Channel; 6,
448 Otranto Strait. Colours correspond to the biogeographic partition: blue, Tunisian (TUN);
449 yellow, Central Western Mediterranean (CWM); red, Adriatic Sea (ADR); green, Ionian Sea
450 (ION). For acronyms, please refer to the Supplementary Materials available in the Data
451 availability statement section.

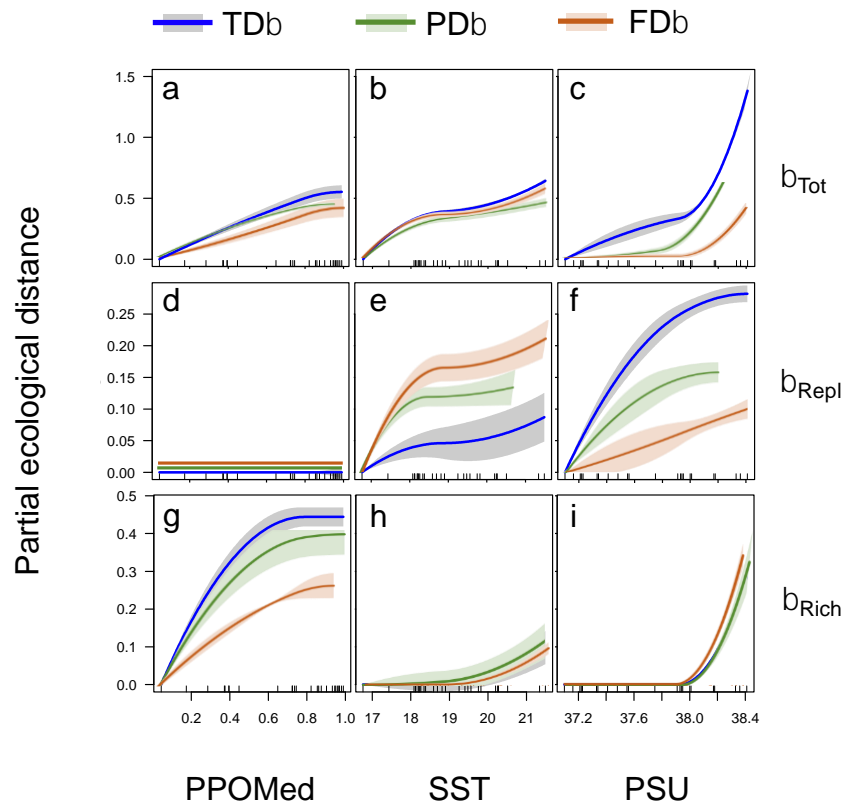
452



453

454

455 **Figure 2** – Plots of I-splines of the environmental predictors and confidence intervals from
456 bootstrapping (shaded colours) for the beta diversity components of different facets.
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460 **References**

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