A network approach to identify bioregions in the distribution of Mediterranean amphipods associated with Posidonia oceanica meadows

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Although amphipods are key components of the macro-fauna associated with *Posidonia oceanica* meadows, to date no studies focused on the structure and diversity of their assemblages across the whole Mediterranean Sea. Here, we applied a network approach based on modularity on a dataset mined from literature to identify biogeographic modules and to assess the biogeographic roles of associated localities. We also correlated the patterns evidenced with the biogeographic distribution of amphipod groups by means of a multivariate analysis. Modularity analysis highlighted four biogeographic modules bounded by the main Mediterranean biogeographic divides and evidenced a decrease in species diversity along a NW-SE gradient. Assemblages associated with Central-Western Mediterranean and, to a lesser extent, Tunisian modules showed the highest species richness and were identified as hubs, characterized by species with regional distributions that behave as source in a biogeographic context. The paleogeographic history of the host seagrass and the ecology of associated amphipods, both suggest the joint effect of species persistence and post-Last Glacial Maximum expansion in explaining the pattern of amphipod distribution in the Mediterranean Sea.

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ABSTRACT

Although amphipods are key components of the macro-fauna associated with *Posidonia oceanica* meadows, to date no studies focused on the structure and diversity of their assemblages across the whole Mediterranean Sea. Here, we applied a network approach based on modularity on a dataset mined from literature to identify biogeographic modules and to assess the biogeographic roles of associated localities. We also correlated the patterns evidenced with the biogeographic distribution of amphipod groups by means of a multivariate analysis. Modularity analysis highlighted four biogeographic modules bounded by the main Mediterranean biogeographic divides and evidenced a decrease in species diversity along a NW-SE gradient. Assemblages associated with Central-Western Mediterranean and, to a lesser extent, Tunisian modules showed the highest species richness and were identified as hubs, characterized by species with regional distributions that behave as source in a biogeographic context. The paleogeographic history of the host seagrass and the ecology of associated amphipods, both suggest the joint effect of species persistence and post-Last Glacial Maximum expansion in explaining the pattern of amphipod distribution in the Mediterranean Sea.

INTRODUCTION

The Mediterranean Sea represents only 0.3% of ocean waters, yet it is a recognized hot-spot of biodiversity hosting about 17,000 species (Coll et al., 2010; Bianchi et al., 2012). This high diversity stems from a combination of oceanographic, ecological and biogeographic features allowing the coexistence of species of Atlantic origin with temperate and subtropical organisms (Coll et al., 2010). Latitudinal clines of environmental variables (mainly temperature and salinity) combined with marine currents resulted in a generalised latitudinal gradient of both primary production and species richness, decreasing from north-eastern to south-western regions (Coll et al., 2010; Lejeusne et al., 2010). Accordingly, biogeographic sectors were identified within the Mediterranean Sea, each characterized by both different biota and ecological parameters (Bianchi et al., 2012).

Although general patterns of biodiversity distribution within the Mediterranean Sea have been well described (Coll et al., 2010; Bianchi et al., 2012), studies concerning patterns and mechanisms of species co-occurrence across the whole Mediterranean basin are restricted to a relatively small number of organisms (e.g., Arvanitidis et al., 2002; Gerovasileiou & Voultsiadou, 2012). Moreover, geographically widespread and ecologically broadly adapted groups have been only seldom studied according to habitat-related subdivisions (Sevastou et al., 2013). In this work, we focused on amphipod crustaceans associated with *Posidonia oceanica* (L.) Delile, 1813 meadows, since they represent one of the most relevant components of the vagile fauna of this key seagrass, endemic to the Mediterranean Sea.

Posidonia oceanica plays a fundamental role in ecosystem engineering along the Mediterranean coasts, providing important ecosystem functions, including oxygen production, food and shelter for associated species, as well as reduction of coastal erosion (Boudouresque, Mayot & Pergent, 2006). The complexity of this multi-layered and three-dimensional habitat allows a great variety of associated fauna to live into the canopy, rhizomes and mattes, making the meadows a strikingly biodiversity-rich habitat within the Mediterranean (Buia, Gambi & Zupo, 2000). Among the vagile fauna associated with meadows, amphipod crustaceans are one of the dominant groups, showing high abundance and diversity of species (Mazzella, Scipione & Buia, 1989; Gambi et al., 1992; Sturaro et al., 2015). Amphipods are key ecological components of seagrass habitats, due to their role in transferring energy across the system, and represent an important trophic resource for higher predators such as fish (Pinnegar & Polunin, 2000; Zakhama-Sraieb, Ramzi-Sghaier & Charfi-Cheikhrouha, 2011; Michel et al., 2015; Bellisario et al., 2016). Amphipods associated with *P. oceanica* meadows feed preferentially on macroepiphytes, algae and associated detritus (Michel et al., 2015), establishing a sort of facilitative interaction with the host plant by promoting the seagrass growth and obtaining protection against predation (Valentine & Duffy, 2006).

Despite the importance of amphipods in seagrass systems, a comprehensive study on their biogeographic patterns at the whole Mediterranean scale is still lacking. Available data include mainly check-lists and local studies based on classical diversity index (Gambi et al., 1992;

72 Diviacco, 1998; Como et al., 2008; Scipione & Zupo, 2010; Bedini et al., 2011; Zakhama-Sraieb,
73 Ramzi-Sghaier & Charfi-Cheikhrouha, 2011; Sturaro et al., 2015), which can foster
74 biogeographic studies using innovative approaches.
75   Recently, specific metrics rooted in network analysis have been successfully applied in a
76 biogeographic context, outperforming classic approaches as clustering methods in the
77 identification of bioregions (Carstensen & Olesen, 2009; Vilhena & Antonelli, 2015; Bloomfield,
78 Knerr & Encinas-Viso, 2018). In particular, modularity (i.e., the tendency of a network to
79 subdivide in densely connected modules or clusters) has proved powerful in detecting groups of
80 areas and/or species closely connected together (i.e., biogeographical modules, *sensu* Carstensen
81 et al., 2012; 2013). This approach also provides relevant insights into the processes driving the
82 assembly of communities by evaluating the importance of each local assemblage (represented by
83 nodes) in terms of network connectivity (Bloomfield, Knerr & Encinas-Viso, 2018). Specific
84 metrics related to the number of links within and between biogeographic modules can be used as
85 indirect estimators of richness and endemism and provide information on the source/sink role of
86 localities (Carstensen et al., 2012; 2013; Bloomfield, Knerr & Encinas-Viso, 2018).
87   In this work, we mined data from literature on the distribution of amphipods associated with *P.*
88 *oceanica* meadows along the Mediterranean basin. We then used a network approach based on
89 modularity: 1) to detect biogeographic structure; 2) to correlate the patterns evidenced with the
90 current knowledge on the biogeographic distribution and ecological features of amphipod
91 groups; 3) to compare amphipods diversity with the paleogeographic history of Mediterranean
92 Sea and biogeographic history *P. oceanica* seagrass. The results obtained are discussed with the
93 aim to provide insights on the patterns of amphipod diversity and distribution across the
94 Mediterranean basin.

96 **MATERIALS & METHODS**

97

98 **Study area and starting dataset**

99

100 An extensive survey of the literature was conducted to obtain all available information on the
101 presence of amphipods from *P. oceanica* meadows across different regions of the Mediterranean
102 Sea. We filtered the available literature to obtain comparable data in terms of sampling season,
103 depth and methods (see Supplemental Materials & Methods S1), so recovering data from 11
104 papers (Diviacco, 1988; Scipione et al., 1996; Scipione, 1998; Sanchéz-Jerez et al., 2000;
105 Zakhama-Sraieb et al., 2006, 2010; Bedini et al., 2011; Sturaro et al., 2014, 2015; Bellisario et
106 al., 2016, Camisa et al., 2017). Data were checked for possible taxonomic issues by updating
107 species nomenclature according to WoRMS, so that species names reported in Table S1
108 correspond to present day taxonomic assignment (see Supplemental Materials & Methods S1 for
109 further explanations). The final dataset (available as Supporting Dataset in Supplemental
110 Materials & Methods) included 147 amphipod species from 28 localities: nine located in Tunisia,
111 16 in Italy (Tyrrhenian, Adriatic and Ionian Sea), two in Spain and one in Corsica (France). The
112 literature source for each locality and each species is listed in Supplemental Materials &
113 Methods S1. Available data covered a large portion of the Mediterranean basin (Fig. 1), and were
114 distributed in regions characterized by different geographic, hydrological and geological
115 features, as well as by differences in the potential connectivity due to the general circulation
116 models (Bianchi & Morri, 2000; Bianchi, 2007; Berline et al., 2014).
117 Information about the biogeographic distribution of observed amphipods were obtained from
118 Bellan-Santini & Ruffo (2003), which classified over 400 species of Mediterranean benthic
119 amphipods in twelve macro-categories on the basis of their current distribution: WM, West
120 Mediterranean; EM, East Mediterranean; Adr, Adriatic Sea; ME, Mediterranean endemics; Afr,
121 African coasts from Ceuta to Cap Vert; Ib, Iberian coasts; Fr, French coasts; Br, British coasts;
122 Norw, Norwegian coasts; Arct, Arctic Sea; Ind-P, Indo-Pacific Ocean; Cosm, Cosmopolitan.
123 Here, species with an Atlantic distribution were clumped in two main categories from the five
124 proposed by Bellan-Santini & Ruffo (2003): ATL, Atlantic Sea (Iberian, French and British
125 coasts) and NATL, North Atlantic Sea (Norwegian and Arctic regions), so that our final
126 distribution comprised nine different categories.

127

128 **Network analysis**

129

130 To provide insights into the biogeographic distribution of amphipod assemblages, a thresholding
131 approach was used to identify groups of localities having stronger similarity in terms of
132 community composition (Kivelä, Arnaud-Haond & Saramäki, 2015).
133 Data were ordered as a species/incidence matrix, whose entries represent the presence of
134 species (rows) at each locality (columns). A weighted network, where localities represent nodes
135 and links the strength of connections, was built using the Jaccard index on the species/incidence

136   matrix, to derive a similarity distance matrix of species co-occurrence. Values ranged from 0,
137   when two localities were identical in amphipod composition, to 1, when they shared no taxa, so
138   that links with higher weights indicated low similarity between localities, and vice versa. The
139   thresholding approach was then applied to identify closely related localities by finding the
140   critical value describing the threshold similarity among pairs (i.e. percolation network).
141   Percolation networks are becoming increasingly used in ecological studies since they allow
142   identifying relationships among nodes (i.e., populations, species, critical scales in landscape
143   ecology) with the advantage of not requiring any *a priori* knowledge of a threshold value
144   (Rozenfeld et al., 2008; Fletcher et al., 2013; Bellisario, 2018). This value was measured by
145   removing distances in decreasing order (i.e., most dissimilar localities), until the network reached
146   the threshold value beyond which it becomes fragmented into disconnected clusters. The
147   identification of this value is obtained by calculating the average cluster size $<L>$ that is, the
148   average number of localities belonging to an l-size cluster, as a function of the last threshold
149   distance value beyond which links were removed (Stauffer & Aharony, 1992):
150
151    $$<L>\ =\frac{1}{N}\Sigma_{l<l_{max}}l^2n_l$$
152   (1)
153
154   where N is the total number of localities not included in the largest cluster (l_{max}) and n_l is the
155   number of clusters containing l localities. Basically, each time a distance value is removed from
156   the network, localities are redistributed in clusters of different sizes, from largest to smallest.
157   This procedure is therefore iterated until the critical threshold is identified in the transitional
158   region characterized by a strong decrease in $<L>$ where the network becomes disconnected
159   (for more information about percolation theory, refer to Stauffer & Aharony, 1992). Here, we
160   used the methodology described in Rozenfeld et al. (2008) and implemented in the package
161   'sidier' (Muñoz-Pajares, 2013) of R (R Development Core Team, 2018).
162
163   **Modularity**
164
165   After identifying the minimum set of pairwise similarities between localities, we tested for the
166   presence of a significant pattern of aggregation between localities, and if this pattern reflected a
167   geographic component. To this end, we measured the modularity (Q), which is defined as the
168   degree to which a network can be subdivided in aggregated sets of nodes (i.e., modules), where
169   the within-module links are significantly higher than between-module ones (Newman & Girvan,
170   2004; Fortunato, 2010). Modularity provides a formal description of the pattern of aggregation
171   between species, populations or communities, being able to identify critical scales in specific
172   ecological and evolutionary processes (Fletcher et al., 2013).
173   Modularity was measured by using the equation originally described by Newman and Girvan
174   (2004):

175
176    $Q = 1/2m \sum_{i,j} [A_{ij} - P_{ij}]\delta(C_i, C_j)$ (2)
177
178   where m is the total number of links in the percolation network (see above), A_{ij} is the matrix
179   expressing the degree of similarity between localities i and j, $\delta(C_i,C_j)$ is a matrix indicating
180   whether i and j are members of the same module and P_{ij} is the probability in the null model that a
181   link exists between i and j. The extent to which links are distributed within and among modules
182   was tested against an appropriate null model, to correct the observed value of Q by null model
183   expectation. Here we used a simulated annealing algorithm (SA) to test for the significance of a
184   modular partitioning by generating 1,000 null matrices having the same degree distribution as the
185   original network. Under the SA algorithm, affiliation of nodes to modules has an accuracy of
186   90%, and a significant modular structure was found if the empirical Q value lies above the 95%
187   confidence interval for Q in the randomized networks (Guimerà & Amaral, 2005).
188   Starting from the modular partition, we further assigned the role of each locality in the
189   network by using two topological measures related to the number of species of the local fauna (l,
190   local topological richness) and the distribution of its associated species to other modules (r,
191   regional topological linkage) (Carstensen et al., 2012). The two-dimensional space given by l-r
192   allows the subdivision of localities in: peripherals, few local and regional species; non-hub
193   connectors, few local and many regional species; provincial hubs, many local and few regional
194   species; connector hubs, many local and regional species (revised after Carstensen et al., 2012).
195   Following Carstensen et al. (2012). Non-hub localities (i.e., peripherals and connectors) can be
196   interpreted as sink, able to receive species from source localities both within their own module
197   and of other modules. Conversely, hub-localities (i.e., provincial and connector hubs) can be
198   interpreted as source for both their modules (module hubs) and the entire network (network
199   hubs). As links in our network relate with patterns of similarity between assemblages, the role of
200   localities allowed for a straightforward description of how amphipod diversity could have spread
201   between different areas of the Mediterranean basin.
202
203   **Multivariate analysis**
204
205   To explore to what extent the measured network characteristics (i.e., modularity and nodes
206   topology) were related to the biogeographic distribution of amphipods, we ran a between-group
207   correspondence analysis (BGCA) on the 'sites x species-biogeographic classes' matrix, where
208   groups were given by the identified modules. BGCA performs a classic Correspondence
209   Analysis (CA) of the per-group centers of gravity, providing an ordination of the groups by
210   maximizing the between-group variance (Baty et al., 2006). From the nine species-biogeographic
211   classes derived from the literature (see above), data were aggregated by summing the number of
212   species belonging to each class at a given site.

214 **RESULTS**
215
216 The final dataset obtained from literature showed that 147 amphipod species belonging to 77
217 genera have been identified to date in *P. oceanica* meadows from 28 Mediterranean localities
218 (Supplemental Materials & Methods S1).
219
220 **Modules identification**
221
222 The percolation network showed a co-occurrence similarity threshold of 0.74, which means that
223 sampling sites are expected to share no more than 74% of amphipod species. This leaded to a
224 network structure of 28 localities joined by 104 links, showing a significant modular structure
225 when compared with randomized models ($Q = 0.466 \pm 0.005$, $P < 0.001$). Four distinct modules
226 were identified, characterized by a clear geographic distribution: Central-Western Mediterranean
227 (CWM), Tunisian (TUN), Ionian (ION) and Adriatic (ADR) (Fig. 2a).
228   Eleven localities constituted the Central-Western Mediterranean module (CWM), which
229 spanned from the Spanish to southern Tyrrhenian coasts, including Lampedusa (LAM) and
230 Marettimo (MART) Islands. This module contained the highest number of species (130), of
231 which a high percentage were module exclusives (i.e., present in a single module). Eighty
232 species were exclusively linked (i.e., observed) to the CWM module, which shared 20, 11 and
233 two species with the TUN, ION and ADR modules, respectively, while 14 are in common among
234 all the four modules (Fig. 2b). The CWM module also showed the highest number of
235 Mediterranean endemics (*sensu* Bellan-Santini & Ruffo, 2003) as, for example, species
236 belonging to the genus *Peltocoxa*: *P. gibbosa* (Schiecke, 1977), *P. mediterranea* Schiecke, 1977,
237 *P. marioni* Catta, 1875 (Fig. 2b, Table 1 and Table S1 in Supplemental Materials & Methods
238 S1).
239   The Tunisian module (TUN) comprised all nine localities belonging to the Tunisian coasts and
240 showed both a high number of species and a high percentage of module exclusives, for example
241 the species belonging to the genus *Elasmopus*: *E. brasiliensis* (Dana, 1855), *E. pectenicrus*
242 (Spence Bate, 1862), *E. pocillimanus* (Spence Bate, 1862). This module was also characterized
243 by the lowest number of Mediterranean endemics (Fig. 2b, Table 1 and Table S1 in
244 Supplemental Materials & Methods S1).
245   Both the Adriatic (ADR, three localities) and Ionian (ION, three localities) modules were
246 characterized by having a few species and a low percentage of module exclusives (Fig. 2b and
247 Table 1). The ION module showed some Mediterranean endemics like *Iphimedia minuta* G. O.
248 Sars, 1883 or *Maera pachytelson* Karaman & Ruffo, 1971, while the ADR module showed a
249 high percentage of cosmopolitan species.
250   The topological role of localities has been assessed by modularity analysis (Fig. 2c), so that
251 each locality has been assigned to a category according to the topological linkage, i.e., local or
252 regional. Localities with a few, local (i.e., module exclusive) species are considered as peripheral
253 nodes (R1 in Fig. 2c), while nodes with a high number of species characterized by regional

254   distribution (i.e., shared among many modules) are considered as connector hubs (R4 in Fig. 2c).
255   Localities in the ADR and ION modules were all classified as peripherals or non-hub connectors
256   (R1 and R2 in Fig. 2c), meaning that amphipod assemblages in these localities are composed by
257   few local species and by a higher (although not very consistent) number of species having a
258   regional distribution (see Materials & Methods). Localities in the CWM and TUN modules were
259   classified mainly as hubs, subdivided between provincial and connector hubs (R3 and R4 in Fig.
260   2c). More than half (54%) of localities in the CWM module can be considered connector hubs,
261   characterized by many local and regional species, while most of localities in the TUN module
262   were classified as provincial hubs, so having a larger number of local than regional species (Fig.
263   2c). The highest values of species diversity are found in hub localities (R3 and R4), while the
264   lowest values of diversity were found in peripheral localities (R1 and R2) together with some
265   hubs, as the 9 TUN localities (Fig. 2c).
266
267   **Multivariate pattern**
268
269   The first two principal dimensions of the BGCA accounted for almost 80% of the total inertia
270   (Fig. 3), showing that some biogeographic groups of species concur in explaining the observed
271   pattern of between-modules variance (Fig. 3). Mediterranean endemic species (ME) accounted
272   for almost 50% of the total variance explained by the first dimension of the BGCA, which was
273   associated with the pattern of distribution of assemblages in the CWM module. Indo-Pacific
274   (INDP) and African (AFR) species accounted for more than 30% of variance along the first
275   dimension (Fig. 3), providing a clear differentiation of the TUN module from all others.
276   Cosmopolitan species (COSMP) accounted for 20% of the between-module variance explained
277   by the second dimension of the BGCA, characterizing the pattern of ordination of the ADR
278   module (Fig. 3). With respect to the biogeographic role of localities, provincial and connector
279   hubs seemed to be characterized by both Mediterranean endemics (ME) and species of Indo-
280   Pacific distribution (INDP), while peripheral localities were characterized mainly by
281   cosmopolitan species (COSMP), although the overall pattern was not sharply defined (Fig. 3).

283 **DISCUSSION**

284

285 **Modules are biogeographically based**

286

287 Our findings showed that amphipod assemblages are heterogeneous throughout the
288 Mediterranean area, with a maximum of 74% of species shared among localities, and that these
289 differences lay on a geographical base. Despite the network approach does not relay on spatial
290 information, the identified modules correspond to four geographic regions of the Mediterranean
291 Sea: Central-Western Mediterranean (CWM), Tunisian (TUN), Ionian (ION) and Adriatic
292 (ADR). Each region is delimited by well-known barriers, such as the Almeria-Oran Front, the
293 Sicily Channel and the Strait of Otranto (highlighted as n. 2, 5 and 6 in Fig. 1). All these barriers
294 have been pointed out as the most relevant in accounting for by ecological and biogeographic
295 heterogeneity across the Mediterranean Sea, and all of them set a quite abrupt change in salinity
296 and temperature regimes of adjacent basins.
297   The Almeria-Oran Front (AOF) is the western boundary of the Central-Western module
298 (CWM), corresponding to the range boundary of the Mediterranean endemic *P. oceanica*, unable
299 to tolerate the low temperature and salinity of the Alboran Sea (Boudouresque, 2004).
300 Circulation patterns and changes in temperature and salinity across the Sicily Channel, both
301 concur in partially preventing the dispersal of a number of species across the threshold of the
302 Siculo-Tunisian Straits (Robinson et al., 1992; Coll et al., 2010). In our study, this is the divide
303 between the CWM and TUN modules, with this latter grouping the localities along the Tunisian
304 coasts characterized by the presence of the jet-like Algerian Current and Atlantic Ionian Stream
305 (Pinardi & Masetti, 2000). The Strait of Otranto delimits the Adriatic Sea, a semi-enclosed basin
306 where several factors, as winds, tides and freshwater runoff from rivers, all determine peculiar
307 low salinity and low winter temperatures (Falco et al., 2000; Lejeusne at al., 2010). This is the
308 boundary between the ADR and ION modules, which moderately exchange water mass through
309 the Albanian side of the Strait of Otranto (Orlic, Gacic & Laviolette, 1992).
310   The boundaries between modules are represented by the most effective Mediterranean barriers,
311 in agreement with the geographic patterns highlighted in other organisms studied at the whole
312 basin scale. The areas corresponding to the Western and Eastern Mediterranean and to the
313 Adriatic Sea have been historically considered as different biogeographic provinces, hosting
314 differentiated species assemblages of macrophytes, diatoms and many animal groups (Ignatiades
315 et al., 2009; Gambi, Lampadariou & Danovaro, 2010). Among invertebrates, an analysis of the
316 Mediterranean sponge regional diversity showed distinct assemblages from CW Mediterranean,
317 Tunisia, Adriatic and Ionian Sea (Gerovasileiou & Voultsiadou, 2012). Similar results were
318 reported for benthic polychaetes, showing different assemblages in the Western and Central
319 Mediterranean basins and in the Adriatic Sea (Arvanitidis et al., 2002), while deep-sea
320 megafauna showed dissimilar community compositions in Western Mediterranean and Ionian
321 basins (Tecchio et al., 2010).

322

323   **Modules diversity and species distribution**
324
325   The differentiation among the four modules depends on different aspects of assemblage diversity
326   and composition. The assemblages characterized by higher diversity were all from the CWM
327   module, and in particular were located in the Central Tyrrhenian area (e.g., CHIA, MOR, GIAN,
328   TAV; Fig. 2b). Localities from ADR and ION modules showed the lowest diversity values,
329   together with a few localities from CWM (MART, MED) and TUN (ZAP, RAF). A decreasing
330   gradient in species richness from north-west to south-east is a generalized pattern in the
331   Mediterranean Sea, with an overall animal species diversity 100% greater in the western than in
332   the eastern basin in both vertebrates and invertebrates (Boudouresque, 2004; Coll et al., 2010).
333   As an example, the diversity of deep-sea nematode assemblages decreases with depth but, when
334   similar depths are compared, a longitude effect appears, with diversity decreasing eastward
335   (Danovaro et al., 2008). A similar pattern was detected in deep-sea foraminifers, whose species
336   richness decreases from western to eastern Mediterranean, likely mimicking the longitudinal
337   cline of organic matter availability on the deep seafloor (Danovaro et al., 2010).
338   The biogeographic role of localities showed how assemblages differ among and within
339   modules, by identifying hubs *vs.* peripheral localities. Localities with assemblages having a high
340   number of species characterized by regional distribution (i.e., shared among many modules) are
341   considered as connector hubs and are supposed to behave as source in a biogeographic context.
342   On the opposite, localities where assemblages contain few, local species are labeled as peripheral
343   nodes, and considered as sinks. Interestingly, nearly all the localities of CWM and TUN modules
344   are classified as hubs, meaning that they share a large proportion of species with many other
345   localities belonging to other modules, besides a relevant number of species among each other.
346   On the contrary, all the localities from ADR and ION modules are considered as peripherals or
347   ultra-peripherals, so having assemblages very similar at intra-module level and highly
348   differentiated with respect to localities belonging to other modules. Both modules are
349   characterized by a small number of module exclusive species, together with a sub-set of species
350   found either in the whole basin or in the hub localities of the CWM module.
351   The identified modules differ not only in species richness and biogeographic roles of their
352   associated localities, but also in the biogeographic distribution of the species found in various
353   assemblages. The pattern recovered links species' richness and distribution, with low-richness
354   modules characterized by species having wider distributions and vice-versa, which can be
355   explained in the light of biogeographic considerations. For instance, Indo-Pacific and African
356   species associated with warm waters typify the rich Tunisian assemblages, as for example those
357   belonging to the genus *Elasmopus* (Fig. 3). Mediterranean endemics and, to a lesser extent,
358   North-Atlantic species characterize the high diversity of CWM. *Apherusa chiereghinii* Giordani-
359   Soika, 1949, *Cressa cristata* Myers, 1969, *Gammaropsis crenulata* Krapp-Schickel & Myers,
360   1979, and the species belonging to the genus *Peltocoxa* are examples of Mediterranean endemics
361   of the CWM module, while some species belonging to the genus *Ampelisca*, like *A.*
362   *serraticaudata* Chevreux, 1888 and *A. tenuicornis* Lilljeborg, 1855, represent an example of

363 temperate species of Atlantic origin inhabiting also the western part of the Mediterranean Sea.
364 This pattern is due to the well-known paleogeographic history of the basin, with particular regard
365 to the most recent cycles of Plio-Pleistocene glaciations (Coll et al., 2010). These climatic
366 oscillations induced temperate Atlantic species to periodically enter the Mediterranean Sea
367 where they originated vicariant endemic species as a result of geographic isolation and local
368 adaptation. Examples are species belonging to the genera *Apherusa*, *Tritaeta* and *Tmetonyx*,
369 which represent the cold component of the Mediterranean amphipod fauna (Bellan-Santini &
370 Ruffo, 2003). For these reasons the Mediterranean Sea is considered as a 'diversity pump' from
371 the Atlantic and the identification of its biogeographic provinces largely rely on the distribution
372 of Mediterranean endemics (Bianchi & Morri, 2000; Bianchi et al., 2012). Similarly, it has been
373 shown that species originated from warm faunas prevail in the south-eastern part of the
374 Mediterranean basin (Lejeusne et al., 2010). Accordingly, the presence of warm species as a
375 representative of the Tunisian coasts has been signaled for other invertebrates, e.g., sponges
376 (Gerovasileiou & Voultsiadou, 2012).
377 Assemblages in the geographically confined ADR module are characterized mainly by widely
378 distributed species with cosmopolitan range. This observation, and the fact that only few species
379 are found exclusively in this module, both suggest that this area may be particularly difficult to
380 be colonized and behave as a sink, as shown by modularity analysis (Fig. 3c). This difficulty can
381 be related to both extreme environmental conditions and geographic isolation, so that only vagile
382 and tolerant species may enter and establish in this basin. Indeed, the Adriatic Sea is
383 characterized by low salinity and winter temperatures, together with a moderate water mass
384 exchange with the neighbouring Ionian Sea through the Strait of Otranto (Orlic, Gacic &
385 Laviolette, 1992; Falco et al., 2000). Moreover, the Adriatic basin was largely dried during the
386 Last Glacial Maximum (LGM, 23K-19K years ago; Rohling et al., 2010), so that a significant
387 part of the Adriatic fauna has only recently re-colonized this basin. Within the poorly vagile
388 group of amphipods, which are brooding species lacking a pelagic larval stage, cosmopolitan
389 species are generally euryhaline, eurytherm and more prone to passive dispersal (Bellan-Santini
390 & Ruffo, 2003), thus having the highest probability to reach and settle in the Adriatic habitat.
391 Accordingly, a recent checklist of opisthobranch Adriatic fauna signaled that the great majority
392 of species had an Atlantic-Mediterranean range, while only few were Mediterranean endemics
393 (Zenetos et al., 2016).
394
395 **Amphipod diversity and paleogeographic history of *Posidonia oceanica***
396
397 Populations of *P. oceanica* inhabiting the western and eastern parts of the Mediterranean Sea are
398 genetically differentiated, with those from the central Mediterranean around the Siculo-Tunisian
399 Strait characterized by a higher genetic diversity (Arnaud-Haond et al., 2007; Serra et al., 2010).
400 This pattern was interpreted as the result of a secondary contact zone between the western and
401 eastern forms, each one originated by vicariance in glacial refugia during the Last Glacial
402 Maximum (LGM) (Serra et al., 2010). A more recent study has superimposed Ecological Niche

403 Modelling to phylogeographic data, highlighting the southern Mediterranean as the most
404 climatically suitable area during LGM, with particular regard to the central zone. This area was
405 then proposed as the main glacial refugium of the seagrass, thus explaining its higher genetic
406 diversity as due to the long-term persistence in this region (Chefaoui, Duarte & Serrão, 2017).
407   Glacial refugia have been repeatedly pointed out as hot-spots and melting pots of diversity,
408 not only in terrestrial environments but also in marine habitats (Hewitt, 1999; 2004; Maggs et al.,
409 2008). This diversity may concern both genetic lineages and community richness, in agreement
410 with the postulated relationship between habitat stability and community diversity (Hewitt, 2000;
411 Ives & Carpenter, 2007). Within this frame, the high diversity and the hub role of assemblages in
412 TUN module can be explained by their localization in a glacial refuge area, as proposed by
413 Chefaoui, Duarte & Serrão (2017). However, the same pattern characterized the CWM
414 assemblages, which are richer in species and share an even greater percentage of their species
415 with other modules. This finding however may be only apparently in contrast with the lower
416 presence probability of *P. oceanica* in the northern Mediterranean during LGM, if we consider
417 that amphipods living on *P. oceanica* are not exclusively found in this habitat.
418   Indeed, amphipods can actively choose their substratum, and this habitat preference produces
419 differences in their abundance on various seagrasses and other substrates, rather than a
420 presence/absence pattern (Sanchez-Jerez et al., 1999; Vázquez-Luis, Sanchez-Jerez & Bayle-
421 Sempere, 2009). A possible scenario is therefore that the northward seagrass range expansion
422 triggered by climate warming after LGM prompted the migration of part of the associated fauna.
423 At the same time, the north-western Mediterranean was likely already inhabited by a local pool
424 of amphipod species derived from the Atlantic (according to the 'biodiversity pump'
425 mechanism), therefore adapted to temperate climatic conditions and able to survive during LGM.
426 Under this hypothesis, it is expected that the CWM assemblages would include many module
427 endemics represented by species with Mediterranean and/or Atlantic distribution (i.e., ME and
428 ATL according to biogeographic classes). Also, CWM and TUN modules should share a relevant
429 number of species (i.e., those originated in the southern refuge and migrated northward with the
430 seagrass). Our analyses showed that all these expectations were verified, supporting the blending
431 between resident, temperate species with the warm-adapted ones spreading from the south with
432 *P. oceanica* during LGM in explaining the current richness of amphipod fauna in CWM.

434 **CONCLUSIONS**

435

436 To our knowledge, this study is the first trying to assess the pattern of co-occurrence of
437 Mediterranean benthic amphipod assemblages associated with a peculiar habitat, such as *P.*
438 *oceanica* meadows. A network approach based on modularity has proven useful in detecting the
439 biogeographic subdivisions of assemblages and in assessing biogeographic roles of associated
440 localities. Our results provide a new perspective on the less studied southern Mediterranean,
441 which may gain a relevant place in the origin of the basin biodiversity as a LGM refuge, besides
442 confirming the known role of the Central Western Mediterranean area as a 'biodiversity pump'
443 from the Atlantic. Our findings also suggest how the distribution of amphipod diversity in *P.*
444 *oceanica* meadows stems from complex interactions between present and past geographic
445 barriers, local species adaptation, and the biogeography of the host plant.
446   To this end, comparative phylogeographical studies can be used to verify the assumptions
447 made in this study, in order to clarify the history of the biogeographical modules identified. This
448 can open the road to a series of studies aimed at deepening the knowledge of the most common
449 and abundant species shared by modules, to identify the centre of evolution and/or dispersion of
450 amphipods within the Mediterranean. For instance, a comparative phylogeography between
451 congeneric species shared by the TUN and CWM modules but showing different distributions
452 (e.g., species belonging to genera *Apolochus*, *Ampithoe*, *Dexamine*) can help both disentangling
453 the role of the southern basin in the diversity of amphipods and testing for the hypothesis of a
454 convergence between the ecological and evolutionary outcomes of amphipods and seagrass in
455 the Mediterranean basin.

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Figure 1

Overview of the Mediterranean Sea with reference localities

Arrows indicate the main circulation patterns and red lines the main barriers: 1, Gibraltar Strait; 2, Almeria-Oran Front; 3, Ibiza Channel; 4, Balearic Front; 5, Sicily Channel; 6, Otranto Strait. For acronyms, see Supplemental Materials & Methods.

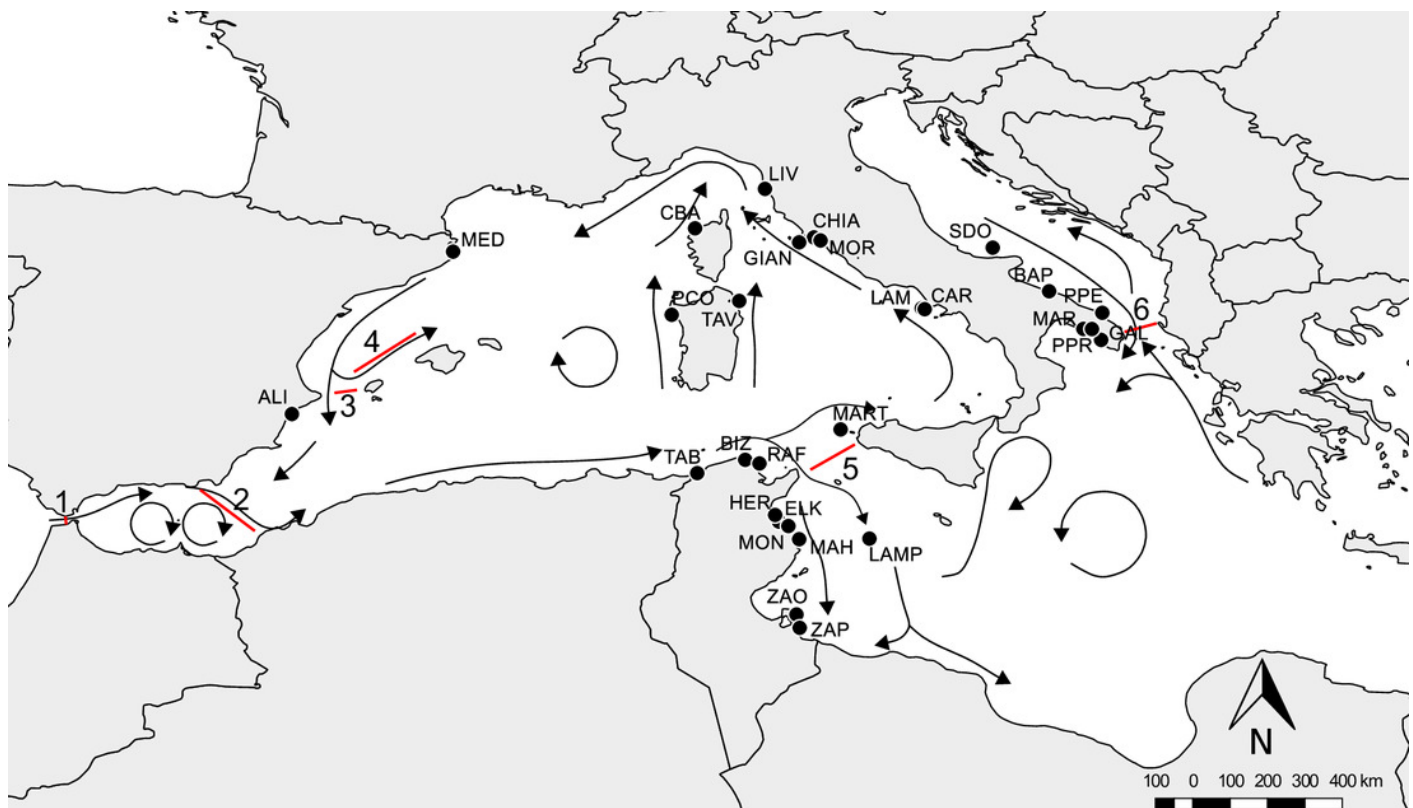



Figure 2

Spatial distribution of modules, network structure and biogeographic roles of localities.

(a) Spatial distribution of the four modules identified: yellow, CWM; blue, TUN; green, ION; red, ADR. (b) Network visualization of biogeographic modules with associated amphipod species (black dots). (c) Plot showing the biogeographic role of localities. Coordinates l and r describe the species richness of localities and the geographical distribution of associated species, respectively. Node size is proportional to species diversity. R1, peripherals: few local and regional species; R2, non-hub connectors: few local and many regional species; R3, provincial hubs: many local and few regional species; R4, connector hubs: many local and regional species (revised after Carstensen et al., 2012). For locality acronyms, see Supplemental Materials & Methods S1.

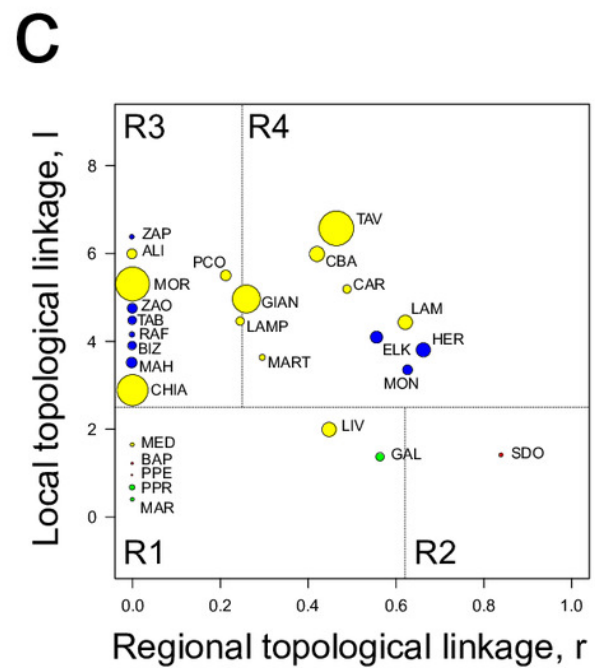
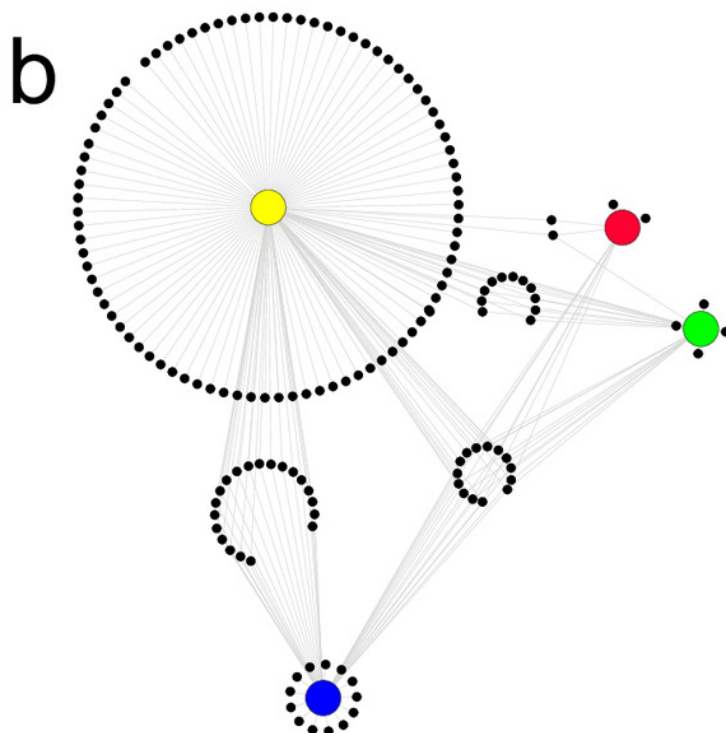
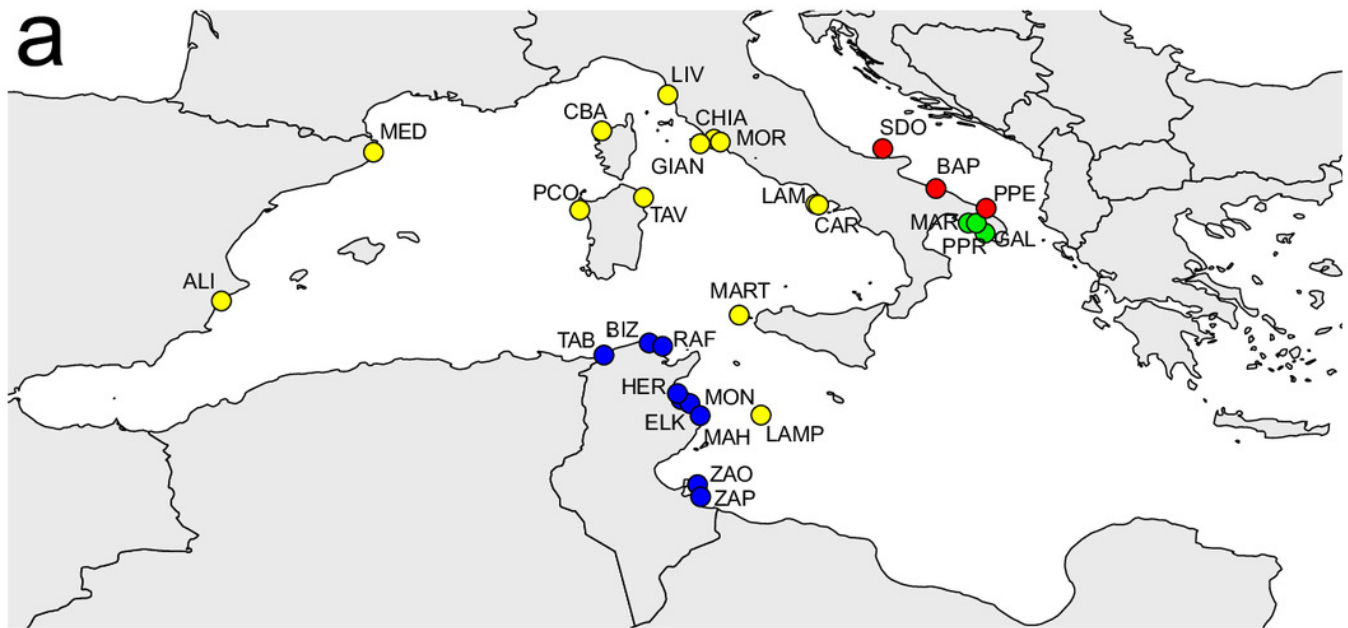
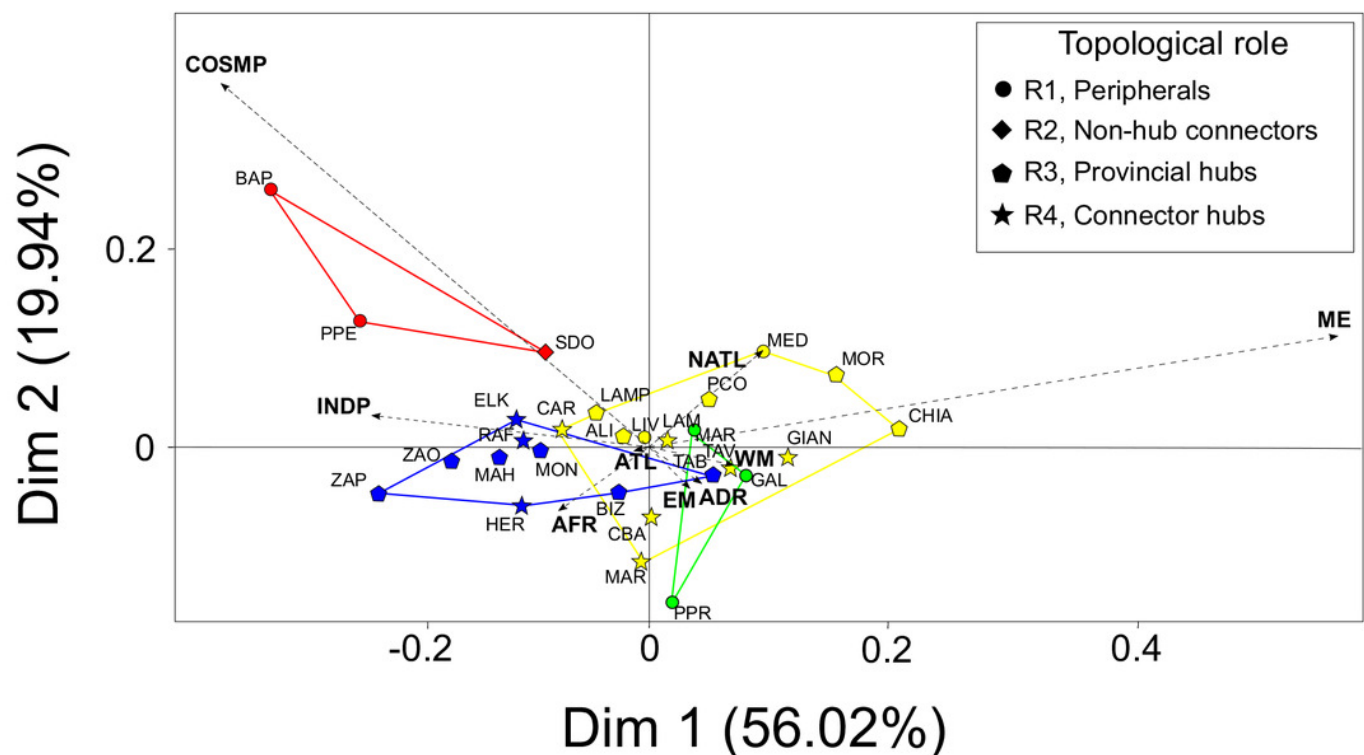



Figure 3

Between-Group Correspondence Analysis (BGCA) of localities based on the nine species-biogeographic classes according to literature.

Colours indicate the identified modules (see Fig. 2a) and different shapes correspond to the biogeographic role of localities (see top-right box). Dashed arrows indicate the nine species-biogeographic classes (revised after Bellan-Santini & Ruffo, 2003): COSMP, Cosmopolitan; INDP, Indo-Pacific; AFR, African coasts from Ceuta to Cap Vert; ATL, Atlantic coasts from Spain to Britain; NATL, North Atlantic from Norway to Arctic Sea; WM, West Mediterranean; EM, East Mediterranean; ADR, Adriatic Sea; ME, Mediterranean endemics. For locality acronyms, see Supplemental Materials & Methods S1.

Modular subdivision of sampling localities.

L is the number of localities in each module;*s* the total number of species. Module exclusive
is the percentage of species exclusively present in a single module; ME and COSMP are the
percentage of species in each module belonging to the Mediterranean Endemics (ME) and
Cosmopolite (COSMP) biogeographic classes (see Supplemental Materials & Methods).

Module	L	s	Module exclusive (%)	Mediterranean endemics (ME%)	Mediterranean cosmopolite (COSMP%)
CWM	11	130	64.7	16.7	4.8
TUN	9	46	27.6	7.3	7.3
ION	3	26	15.4	13	4.3
ADR	3	15	18.4	9	27.3