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1 **Do functional groups of planktonic copepods differ in their ecological niches?**

2
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12
13
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30 **Abstract**

31 **Aim**

32 To assess the degree of overlap between the environmental niches of marine planktonic
33 copepods and test if the distribution of copepod functional groups differs across environmental
34 gradients.

35

36 **Location**

37 The Mediterranean Sea.

38

39 **Methods**

40 Functional groups were defined based on clustering of functional traits in 106 marine copepod
41 species using a multivariate ordination analysis. Functional traits included maximum body
42 length, feeding mode, spawning strategy and trophic group. Simultaneously, the global
43 distribution of the species was used to model their environmental niches with six environmental
44 variables. For each of these predictors, four niche parameters were derived from the univariate
45 response curve of each species, to summarise their environmental preferences and ordinate the
46 species in niche space through a PCA. Finally the differences in the position in niche space of
47 functional groups were tested with variance analysis.

48

49 **Results**

50 We identified seven copepod functional groups with different distributions along the
51 environmental gradients covered by our study. While carnivorous functional groups were
52 affiliated with oligotrophic and tropical conditions, large and small current-feeding herbivores
53 are associated with colder, more seasonally-varying and productive conditions. Small cruising
54 detritivores and other small current-feeding herbivores were not affiliated with specific
55 conditions as their constituting species were scattered in niche space.

56

57 **Main conclusions**

58 Since copepod functional groups occupy distinct ecological niches, ecosystem processes related
59 to these groups are expected to vary across environmental gradients. Conditions favouring large
60 current-feeding herbivores should allow for enhanced fluxes of energy and nutrients through
61 Mediterranean Sea ecosystems, while such fluxes should be weakened where large carnivores
62 and small passive ambush feeding copepods dominate. Our study supports the development of
63 trait-based zooplankton functional groups in marine ecosystem models.

64 **Introduction**

65 Zooplankton play a key role in the functioning of marine ecosystems. They actively transport
66 particles to the deeper ocean through vertical migration (Jónasdóttir, Visser, Richardson &
67 Heath, 2015), and produce rapidly sinking fecal pellets after grazing on primary producers in the
68 euphotic layer (Turner, 2002). They participate in the remineralisation of organic matter by
69 feeding on particle aggregates (Alldredge, 1972; Nishibe et al., 2015), and are thus involved in
70 nutrient cycling and in the biological carbon pump (Turner, 2015). Additionally, they represent a
71 pivotal link between the basis of the food web and the upper trophic levels (Beaugrand, Brander,
72 Lindley, Souissi & Reid, 2003; Beaugrand & Kirby, 2010). Zooplankton are subdivided into
73 different size classes, among which the mesozooplankton (organisms ranging between 200 μm
74 and 2 mm; Sieburth, Smetacek & Lenz, 1978) have received most attention because of their high
75 biomass (Verity & Smetacek, 1996). In terms of both abundance and diversity, mesozooplankton
76 are dominated by copepods in many regions of the global ocean (Kjørboe, 2011a). Changes in
77 copepod diversity can be indicative of climate variability impacts on ecosystem functioning
78 (Hooff & Peterson, 2006).

79 To assess the vulnerability of marine ecosystems to climate change, global biogeochemical
80 models have been developed to describe the processes controlling ocean biogeochemistry and
81 ecosystem functioning. At first, such models summarized pelagic ecosystems using only a few
82 compartments but they have evolved towards capturing greater ecological complexity, and
83 therefore improved the quantification of ecosystems responses and biogeochemical fluxes (e.g.
84 Le Quéré et al., 2016). However, to depict variations in zooplankton biomass, most ecosystem
85 models still rely on a limited number of size classes from micro-, and meso- to
86 macrozooplankton (Kishi et al., 2007; Le Quéré et al., 2016) so they still only poorly capture the
87 variety of zooplankton life-histories and traits (Kjørboe, 2011a; Litchman, Ohman & Kjørboe,
88 2013).

89 An alternative trait-based approach for describing pelagic ecosystem dynamics is to define
90 plankton functional types based on groups of species with similar functional traits (Pomerleau,
91 Sastri & Beisner, 2015; Benedetti, Gasparini & Ayata 2016). Functional traits are phenotypic
92 attributes that impact the fitness of a species and its contribution to ecosystem functioning
93 (Violle et al., 2007). The appearance of functional traits is governed by the expression of genes
94 within organisms, and trait expression, in turn, governs the organisms' fitness under different
95 biotic and abiotic conditions (Barton et al., 2013). A functional trait can also emerge from the
96 interactions between other traits (trade-offs; Kjørboe, 2011b) and environmental conditions,
97 leading to certain trait combinations being favoured under certain conditions. For zooplankton,
98 Litchman et al. (2013) proposed a comprehensive set of traits, encompassing multiple types (i.e.
99 life-history, morphological, physiological and behavioural) and life missions (i.e. feeding,
100 survival, growth and reproduction). However, zooplankton traits have been described
101 exhaustively for a few taxa only, and are mostly the results of laboratory experiments (Hébert,
102 Beisner & Maranger, 2016). Consequently, depicting zooplankton functional diversity at the
103 community level often requires information about many species and remains possible only for

104 few well-studied regions and/or a limited number of groups. For instance, Pomerleau et al.
105 (2015) described the temporal evolution of zooplankton functional diversity in the north-eastern
106 Pacific using time series data, and Benedetti et al. (2016) identified functional groups of
107 copepods in the Mediterranean Sea. Brun, Payne & Kiørboe (2016) identified strong spatial and
108 seasonal variations of body and offspring sizes, myelination rates and feeding modes for
109 planktonic copepods in the North Atlantic. Copepods have therefore emerged as an interesting
110 model to study marine functional biogeography (Barton et al., 2013).

111 Understanding and quantifying the distribution of zooplankton functional groups along
112 environmental gradients is critical to (i) develop more realistic marine ecosystem models, (ii)
113 better understand the underlying environmental drivers of community structure, (iii) unravel how
114 climate impacts the rate and amplitude of processes mediated by functional types, and (iv)
115 predict how the three above-mentioned aspects may evolve in a global change context.

116 Modelling the environmental niche of each species, and then assessing differences between
117 functional groups, on the basis of their constituent species, enables to explore the biogeography
118 of functional groups (Brun et al., 2015). Field observations of species occurrences can be
119 combined with environmental predictors to build environmental niche models (ENMs) that
120 enable the characterization of the environmental preferences of a species (Colwell & Rangel,
121 2009). In spite of the recent development of global open access plankton occurrence databases
122 (O'Brien, 2005; Buitenhuis et al., 2013), relatively few studies have used ENMs to investigate
123 plankton biogeography (Robinson et al., 2011). For mesozooplankton, most studies have mined
124 the Continuous Plankton Recorder (CPR) data to model past and future range variations of
125 copepod species, and changes in ocean surface layer community composition (Reygondeau &
126 Beaugrand, 2011; Chust et al., 2014; Villarino et al., 2015; Brun, Kiørboe, Licandro & Payne,
127 2016; Benedetti, Guilhaumon, Adloff & Ayata, 2017) but they ignored functional aspects of
128 biodiversity. Hence, the link between trait and species biogeography is currently underexplored.

129 In particular, it remains to be tested how different combinations of morphological traits (e.g.
130 body length) and life history traits (e.g. feeding mode, spawning strategy) are distributed along
131 environmental gradients. Are scanning-current feeders restricted to more productive regions
132 where larger phytoplankton cells emerge (Kiørboe, 2011b; Benedetti et al., 2016)? Are passive
133 ambush-feeding species more tightly affiliated to stable and oligotrophic environments where
134 food availability is limited and mortality rates high (Paffenhöfer, 1993; Kiørboe, 2011b)? Do
135 large herbivorous species thrive in the same conditions as large carnivorous predators, or are
136 they affiliated to very different niches? As ecosystem processes are mediated by such functional
137 traits (*sensu* Hébert, Beisner et al., 2016), assessing how the latter are expressed under varying
138 conditions is a prerequisite for understanding ecosystem functioning under climatic changes.

139 In this study, we attempt to bridge this gap through an investigation of the level of congruence
140 between the environmental niches of species belonging to different copepod functional groups
141 (FGs). We aim to (1) model the environmental niches of copepod species, (2) define relevant
142 FGs based on species functional traits, and (3) test whether species with similar combinations of
143 functional traits inhabit similar environmental niches.

144

145 **Material and Methods**

146 *Species selection and data.*

147 Copepod species most commonly found in the Mediterranean Sea and their trait values were
148 taken from Benedetti et al. (2016). Multiple regional datasets were combined to obtain the
149 geographical distribution of the copepod species. As none of the species is endemic to the
150 Mediterranean Sea (Razouls, de Bovée, Kouwenberg & Desreumaux, 2005-2017), species niches
151 must be calibrated at the global scale in order to avoid truncated response curves, and therefore
152 biased niche estimates (Thuiller, Brotons, Araùjo & Lavorel, 2004). Among the 193 species
153 initially described by Benedetti et al. (2016), only those with more than 50 observations at the
154 regional scale, and with at least 15 additional occurrences at the global scale (OBIS;
155 <http://www.iobis.org/>; accessed on December 11, 2014) were retained. Our final list
156 encompasses 106 copepod species. Our list of 106 species gathers the most commonly observed
157 ones in the epipelagic layer, including those representing most of the mesozooplankton biomass
158 in the Mediterranean Sea (Siokou-Frangou et al., 2010; Razouls et al., 2005-2017). The average
159 sampling depth of the presence data (for the 99.94% of the records for which sampling depth was
160 available) was 58 ± 119 m. The presence data was resampled at a resolution of $1 \times 1^\circ$ grid cells, to
161 match the resolution of the environmental layers (see below). The final data set contained 76 366
162 gridded presence points.

163

164 *Functional groups from species functional traits.*

165 Four functional traits were extracted from Benedetti (2015): maximum body length (mm),
166 trophic group (carnivore, omnivore, omnivore-carnivore, omnivore-herbivore, omnivore-
167 detritivore), feeding mode (ambush, cruise, scanning current, or mixed), and egg-spawning
168 strategy (broadcast-spawner, sac-spawner).

169 These traits were selected because of their ready availability in the literature (Brun, Payne &
170 Kiørboe, 2017). Other important traits such as resting stages and physiological rates are still
171 lacking for the majority of the taxa studied. However, the present traits cover different important
172 ecological functions and can influence ecosystem processes (Hébert, Beisner et al., 2016). Body
173 size is a “master trait” that transcends and scales with a variety of traits related to ecosystem
174 processes such as carbon cycling, secondary productivity or nutrient transfer (Hébert, Beisner et
175 al., 2016). Trophic group describes the primary food source of a species and therefore its role in
176 food-web dynamics (Pomerleau et al., 2015). Though nearly all copepods are omnivorous, many
177 species are known to have preferential food sources (Benedetti, 2016). While omnivores target
178 phytoplankton, detritus or smaller zooplankton, carnivores prey upon earlier life stages, smaller
179 adult copepods or microzooplankton and thus contribute to the top-down control on zooplankton.
180 Omnivore-herbivorous copepods are known to primarily graze upon phytoplankton when
181 available and are therefore involved in the energy transfer from the autotrophs to fishes.
182 Omnivore-detritivores are associated with marine snow or carcasses, so they contribute to the
183 recycling of organic matter. Feeding mode has strong implications for prey selection, energy

184 allocation or nutrient cycling (Litchman et al., 2013; Hébert, Beisner et al., 2016). For instance,
185 ambush feeders that target motile preys are characterized by lower energy expenditure than
186 active feeders, resulting in lower mortality but also a lower feeding efficiency. Similarly,
187 spawning strategy shapes energy allocations. Species developing sacs to place their eggs in
188 invest less energy in growth and survival (Litchman et al., 2013).

189 FGs for the 106 selected species were defined by performing a Multiple Correspondence
190 Analysis (MCA; Husson, Lê & Pagès, 2010; Fig. 2) on the four functional traits to represent
191 underlying structures in the species characteristics in a reduced functional space (Benedetti et al.,
192 2016). MCA is an ordination method for the multivariate analysis of categorical variables.
193 Maximum body length was thus transformed into four size classes (SC1: 0.5-1.2 mm; SC2: 1.3-
194 1.8 mm; SC3: 1.9-3.0 mm; SC4: 3.4-8.2 mm) using hierarchical agglomerative clustering based
195 on the Euclidean distance and a synoptic aggregation link (Husson et al., 2010; Legendre &
196 Legendre, 2012). Trophic groups were also transformed into binary data because this allows the
197 optimization of their description in functional space. For example, omnivore-herbivores were
198 considered as both “omnivores” and “herbivores” and not just “omnivore-herbivore” as if it was
199 an independent trophic group. Kaiser-Guttman’s criterion (Guttman, 1954) was used to select the
200 significant MCA axes that constitute the functional space. The species are positioned along each
201 MCA axis according to their combination of trait values. The coordinates of the species along the
202 retained MCA axes were used to compute the inter-species Euclidean distance matrix.
203 Hierarchical agglomerative clustering using Ward’s aggregation method (Legendre & Legendre,
204 2012) was performed on this matrix to produce a functional dendrogram. Several cutting-levels
205 along this dendrogram were examined, and the one leading to FGs that are ecologically relevant
206 was kept. The final cutting-level was chosen to ensure groups were functionally homogeneous
207 (i.e. not too large) while also attempting to avoid functional redundancies between the groups
208 (i.e. not too small and numerous).

209 The sensitivity of our FGs to the choice of trait definition and clustering method was tested in
210 additional analyses. Our analysis was repeated using Gower’s distance with the UGPMMA linkage
211 method to draw the functional dendrogram (Mouchet et al., 2008). The absolute values of
212 maximum body size were kept, since Gower’s distance can mix quantitative and qualitative data.
213 The FGs defined using this method were very similar to those found with the initial methodology
214 (cophenetic correlation coefficient between the original and the alternative dendrogram was
215 equal to 0.80; Rohlf & Fisher, 1968).

216

217 ***Choice of the environmental predictors for niche modelling.***

218 Monthly data on 27 environmental predictors thought to be ecologically and physiologically
219 relevant for copepods were considered (Helaouët & Beaugrand, 2007; Beaugrand, Mackas &
220 Goberville, 2013). These variables comprised sea surface temperature (SST), sea surface salinity
221 (SSS), mixed layer depth (MLD, defined according to three different criteria), surface
222 chlorophyll-a concentration (Chla), bathymetric depth, surface photosynthetically active
223 radiation (PAR) and PAR integrated over the MLD (MLPAR; Brun et al., 2015), surface

224 dissolved oxygen concentration, sea surface wind speed and sea level anomalies (Appendix S1).
225 To avoid the use of variables that are too highly correlated, when two predictors showed an
226 absolute Spearman's rank correlation coefficient ($|\rho| \geq 0.7$, one of them was removed (Dormann
227 et al., 2012). The final set of variables consisted of SST, the seasonal range of SST values
228 (Δ SST), SSS, MLD based the temperature criterion (de Boyer Montégut, Madec, Fischer, Lazar
229 & Iudicone 2004), MLPAR (based on the same MLD product), and the logarithm of surface
230 chlorophyll-a concentration (logChla). Subsequently, multivariate and univariate ENMs were
231 fitted for each species using the six selected predictors (Fig. 1).

232

233 *Species niche characteristics.*

234 Various types of algorithm exist to model environmental niches from species observations
235 matched with environmental predictors (Merow et al., 2014). Here, General Additive Models
236 (GAMs) were chosen because they can be tuned to produce unimodal response curves, while
237 allowing skewed response curves (Fig. 1). This type of response to environmental gradients is
238 expected for copepods (Bonnet et al., 2005; Helaouët & Beaugrand, 2007).

239 Since GAMs require absence data that are not available at the global scale, pseudo-absences
240 were simulated for each species. The method employed for drawing pseudo-absences impacts
241 ENMs quality, and should be chosen in light of the ecological characteristics of the species
242 studied (Chefaoui & Lobo, 2008; Barbet-Massin, Jiguet, Albert & Thuiller, 2012).
243 Mesozooplankton are ectotherms whose population dynamics are tightly coupled to climate
244 (Hays, Richardson & Robinson, 2005), and whose individuals are passively dispersed over very
245 large spatial scales during relatively short time periods (Jönsson & Watson, 2016). Therefore,
246 pseudo-absences were generated using an environmental and geographical weighting method
247 (Hengl, Sierdsema, Radović & Dilo, 2009; Hattab et al., 2013; Fig. 1). This method locates the -
248 absences in regions of low habitat suitability for the species (i.e. in environments that are the
249 most dissimilar to the ones where presences are located) and that are relatively far from the
250 observed presences. The weighting procedure is based on a presence-only envelope niche model,
251 the Ecological Niche Factor Analysis (Hirzel, Hausser, Chessel & Perrin, 2002), which provides
252 a Habitat Suitability Index (HSI) from 0 to 1 for each species as a function of the six chosen
253 environmental predictors. Together with the presences, the HSI is then used to produce a
254 probability distribution τ for locating the pseudo-absence following Hengl et al. (2009):

$$\tau(x) = \left[\frac{d(x) + (100 - HSI(x))}{2} \right]^2$$

255

256 with d being the distance between the geographic cell and the presence points normalized by the
257 maximum distance, so that d varies between 0 and 100. Thus, τ is used as a probability density
258 function to select pseudo-absences at random away from known presences and in regions of
259 unsuitable conditions (according to the actual presences). For each species, pseudo-absences
260 were drawn from the monthly subsets of occurrence data to ensure they follow the same
261 temporal variability as the presences. Repeating the pseudo-absence generation procedure

262 (leading to a different set of randomly chosen pseudo-absences), or increasing the number of
263 pseudo-absences, had very little impact on model quality and predictions (Benedetti et al., 2017),
264 so only one set of monthly pseudo-absences was generated per species.

265 Multivariate and univariate GAMs were fitted using the logit link function (binomial response),
266 and the parameter controlling the degree of smoothness was reduced ($k = 5$). ENMs were
267 evaluated by cross-validating 80% of the presence and pseudo-absence data against the
268 remaining 20%. A threshold-dependent metric of the overall performance of each model was
269 computed: the true skill statistic (TSS; Allouche, Tsoar & Kadmon, 2006). TSS ranges from -1 to
270 +1, with 0 indicating that an ENM does not perform better than random. For each species and
271 predictor variable, five cross-validation runs were performed and the mean TSS was calculated
272 to evaluate the predictive power of the selected variables. The five univariate response curves
273 derived from each cross-evaluation run were averaged to provide the univariate response curve
274 of each species.

275 Following Brun et al. (2015), niche characteristics were summarized by four statistics derived
276 from the mean univariate response curve (Fig. 1). The median of the mean curve was used to
277 estimate the univariate niche centers, and quantile ranges between the 10th and the 90th
278 percentiles were computed to estimate niche breadths (i.e. relative species tolerance ranges). The
279 predictor values at the 10th and 90th percentiles served as estimates of lower and upper niche
280 boundaries. These four niche parameters were used to test the differences in the environmental
281 preferences of FGs (next section). Confidence intervals for TSS values and each univariate niche
282 parameter were obtained by applying a bootstrapping procedure on the species occurrences
283 (presences and pseudo-absences) which generated 200 replicates of every univariate model and
284 niche characteristic.

285 The multivariate models could have been used to derive response curves but this possibility was
286 discarded because multivariate models generate response curves that are much harder to interpret
287 (Irwin, Nelles & Finkel, 2012; Brun et al., 2015). The response curve of a multivariate model is
288 generated through the variation of one predictor, while setting the value of the other predictors to
289 their average. Even though this corrects for the effect of the other variables in the response, it can
290 flatten parts of the response due to variable collinearity, even if patterns exist (Brun et al., 2015).
291 Furthermore, the identity of misrepresented variables varies between species, making it even
292 harder to compare species niche characteristics. This is why the univariate GAMs were selected
293 over multivariate ones to depict the species niches.

294 TSS values for the 106 multivariate GAMs show that the six selected variables lead to a fair
295 modelling of the species distribution (Appendix S2). The average TSS for all the multivariate
296 models is 0.82 (± 0.11), and species mean TSS ranges between 0.46 (*Oithona decipiens*) and
297 0.97 (*Labidocera wollastoni*). The univariate models differ greatly in their performance
298 (Appendix S2): the best performing variables are SST (mean TSS = 0.57), SSS (mean TSS =
299 0.64) and Δ SST (mean TSS = 0.63), while the other three variables obtained significantly lower
300 average TSS values (pairwise Wilcoxon tests, p -value < 0.05). MLD (mean TSS = 0.39)
301 performs slightly better than logChla (mean TSS = 0.34) and MLPAR which displays the lowest

302 average performance score (mean TSS = 0.291).

303

304 ***Functional groups and functional traits in niche space.***

305 The niche characteristics of each species were used in a scaled Principal Component Analysis
306 (PCA; Legendre & Legendre, 2012) to ordinate them according to their environmental
307 preferences in a reduced space (hereafter “niche space”; Fig. 1). We assess the similarity
308 between the niche characteristics of species by comparing their coordinates along the retained
309 Principal Components (i.e. their position in niche space). To create a parsimonious niche
310 space, Spearman’s rank correlation coefficients were used to examine the correlation
311 between the univariate niche characteristics. When two niche parameters displayed $|\rho|$
312 ≥ 0.7 , one of them was removed. From the correlation matrix (Appendix S3), the
313 following eleven niche characteristics were kept to create the niche space: SST center
314 and breadth (as center is correlated to both lower and upper boundaries), SSS niche
315 center (negatively correlated to breadth and lower boundary), upper and lower
316 boundaries of Δ SST (as SST breadth is highly correlated to Δ SST breadth), MLD center
317 (which summarizes all other 3 MLD characteristics), all MLPAR parameters but the
318 lower boundary (highly correlated to SST and MLPAR centers), and both logChla center
319 and breadth (logChla niche center summarises the two boundaries). Kaiser-Guttman’s
320 criterion was used to select the number of significant PCs that will generate the niche
321 space (Fig. 1).

322 In order to test for the differences between the niches of species pertaining to different FG, the
323 central positions of the groups in niche space were computed as the average coordinates of the
324 constituting species. Kruskal-Wallis variance analysis (Kruskal & Wallis, 1952) was performed
325 to test whether FGs differed significantly in their positions in niche space. Similarly, variations
326 between the positions in niche space of each functional trait were tested (for instance, between
327 the different trophic groups) in order to explore whether some are more closely linked to certain
328 environmental conditions. All statistical analyses were conducted with R v.3.4.0 (R Core Team
329 2017). The *biomod2* package (Thuiller, Georges & Engler, 2013) was used to develop the niche
330 models and extract the response curves. The *FactoMineR* package (Husson, Josse, Lê & Mazet,
331 2017) was used for the multivariate analyses.

332

333 **Results**

334 ***Copepod functional groups.***

335 The first separation in the functional dendrogram (Fig. 2) distinguishes carnivorous species (FG
336 1 and 2) from the non-carnivorous ones (FG 3 to 7). Among the latter, the next cutting level
337 distinguishes egg-broadcasters (FG 3 and 4) from sac-spawners (FG 5, 6 and 7). Further down on
338 the dendrogram, trophic groups and size classes drive the composition of the FGs. Hence, all
339 traits contribute to the structure of the functional space, with carnivorous diet being the primary
340 discriminative trait.

341 Given that the 106 species were classed into different FGs on the basis of a dendrogram resulting
342 from a cluster analysis of four different traits, some species were assigned to a FG when they
343 differ in one particular trait with respect to other species because they present similar values of
344 the other traits considered. FG 1 is composed of large sac-spawning carnivores that either feed
345 by cruising or through a scanning current, but five of the ten species constituting this FG lack
346 information on their feeding strategy. FG 2 is defined by 15 smaller and strictly carnivorous
347 species that mainly feed through ambush tactics. The spawning strategy is equally divided
348 between broadcasters and sac-spawners. Most of them inhabit the epi- and mesopelagos, and are
349 thought to exhibit weak to no diel vertical migration (DVM) behaviour. FG 3 is defined by eight
350 scanning current-feeding species belonging to the largest size class. All but two species
351 (*Eucalanus hyalinus* and *Pleuromamma abdominalis*) are usually considered herbivores. The
352 group's main spawning strategy is broadcasting. Some of them are established as strong migrants
353 in the Mediterranean Sea (*Calanus helgolandicus*, *P. abdominalis* and *Neocalanus gracilis*),
354 while the remainder have rarely exhibited any DVM behaviour. FG 4 is the largest group (n =
355 27) and gathers smaller (compared to FG 3) scanning current-feeding herbivores and omnivores
356 displaying mixed feeding strategies. Like FG 3, the copepod species are all broadcasters, thus
357 size class was the factor dividing these two FG. Most of the species in FG 4 preferentially inhabit
358 the epipelagos and are known to exhibit weak to no DVM behaviour. FG 5 is the second largest
359 group (n = 21) and clusters the small sac-spawning detritivorous species together. The dominant
360 feeding strategy is cruising, as only 4 species rely on a scanning current to capture their food.
361 Additionally, 4 species of this group are small cruise-feeders. Most of these species are known to
362 occur within a broad depth range. Small ambush-feeding omnivores belonging to the *Oithona*
363 genus constitute FG 6, together with three species (*Haloptilus longicornis*, *Isias clavipes* and
364 *Lubbockia squillimana*) for which information about feeding strategy was lacking, but that are
365 characterized by similar sizes and trophic groups. FG 7 gathers small herbivores that feed either
366 by cruising or a scanning current. They are separated from the herbivores of FG 4 because they
367 are sac-spawners and not broadcasters. The corresponding species are known to mainly occur in
368 the epipelagos.

369

370 ***Species position in niche space based on the niche characteristics.***

371 A PCA based on individual species niche parameters was used to summarize the species' relative
372 position in environmental space. The first three PCs were retained, accounting for 72.27% of the
373 total variance. The first PC (PC1, 35.68%; Fig. 3) separates species affiliated with oligotrophic
374 conditions (warm SST, higher SSS and low seasonality) from those affiliated with more
375 productive conditions (colder and less saline waters, often characterized by higher seasonality).
376 The species with higher values of SST centers, SSS centers, MLPAR centers and upper MLPAR
377 boundaries have positive coordinates on PC1. Meanwhile, species displaying
378 higher logChla centers and upper Δ SST boundaries are located on the negative
379 side of PC1. The second PC (PC2, 21.74%; Fig. 3) distinguishes species with
380 broader tolerance to variations in SST and in chlorophyll-a concentrations

381 (positive coordinates) from species affiliated to habitats of lesser seasonal
382 variability (i.e. characterized by higher values of lower Δ SST boundaries). So,
383 copepod species with positive PC2 coordinates can endure colder temperatures
384 and seasonally varying environments. Meanwhile, species that present positive
385 coordinates on PC1 and negative coordinates along PC2 are specialized in more
386 oligotrophic conditions. The PCA reveals that species show distinct co-
387 variations between their niche characteristics, thus demonstrating that they have
388 different environmental preferences. The values of the species niche parameters
389 are given in the Appendix S2.

390

391 ***Do functional groups occupy distinct environmental niches?***

392 The FGs were represented in niche space after the mean position of each group was computed to
393 assess if different FGs occupy distinct environmental niches (Fig. 4). The PC1 coordinates of the
394 species differ significantly between FGs (Kruskal-Wallis test, p-value = 0.007, H-value = 17.52),
395 which indicates that species between FGs present distinct environmental niches. No significant
396 differences were found between the FG coordinates along PC2: the niche characteristics
397 structuring this PC do not differ between FGs. The groups gathering carnivorous species (FG 1
398 and 2) were on average located on the positive side of PC1 while FG 3 (large scanning current-
399 feeding herbivores), FG 6 (small ambush-feeding omnivores), and FG 7 (small sac-spawning
400 herbivores) were on the negative side. This supports the hypothesis that there are differences in
401 the environmental niches between groups: FG 1 and 2 are affiliated to warmer, saltier, more
402 stable and less productive conditions in the open ocean; meanwhile, FG 3, 6 and 7 are associated
403 with conditions of stronger seasonal variations, colder temperatures, lower salinities and higher
404 chlorophyll-a concentrations. The mean positions of FG 4 (small broadcasting scanning current-
405 feeding herbivores) and FG 5 (detritivores) were predominantly central in the environmental
406 niche space. Therefore, these two FGs are composed of species that are spread out in niche
407 space. With regard to the distribution of functional traits in niche space, only the mean position
408 of each trophic group (Carnivores vs. Omnivores vs. Herbivores vs. Detritivores) showed
409 significant differences along PC1 (Kruskal-Wallis test, p-value = 0.023, H-value = 11.38).

410

411 **Discussion**

412

413 ***Mediterranean copepod functional groups differ in their niches.***

414 The main finding of our study is that, on average, the environmental niches of the species within
415 a FG differ from those of species constituting another FG (Fig. 4). Under the more tropical
416 conditions where FGs 1 and 2 are favoured, we expect the Mediterranean zooplankton food-web
417 dynamics to be dominated by top-down processes. The small passive ambush-feeding taxa
418 (Corycaids and some *Oithona* species) benefit from a metabolism that is well adapted to food-
419 depleted conditions where competition and predation are high (Landry, 1985; Kiørboe, 2011a).

420 When these small species dominate, we also expect size-related ecosystem fluxes (e.g. secondary
421 productivity, nutrient recycling, excretion or carbon transfer etc.) to be weakened (Hébert,
422 Beisner et al., 2016), which is the case in the ultra-oligotrophic eastern Mediterranean Sea
423 (Siokou-Frangou et al., 2010; The MerMex Group, 2011). Larger predatory copepods (FG 1)
424 may also occur, as they are able to feed on smaller copepods but also larger gelatinous
425 zooplankton like Doliolids or Appendicularia (Ohtsuka & Onbé, 1989; Takahashi et al., 2013).
426 Under the colder, more variable and more productive conditions where FGs 3 and 7 are
427 favoured, we expect Mediterranean zooplankton food-web dynamics to be dominated by bottom-
428 up processes, as these functional entities thrive on phytoplankton of different size classes. The
429 larger current-feeding taxa (FG 3) are able to feed on the larger phytoplankton and we expect
430 those species to mediate stronger energy fluxes from the surface to the deeper ocean (Jónasdóttir
431 et al., 2015; Visser, Grønning & Jónasdóttir, 2017). Rates of secondary productivity, nutrient
432 recycling and carbon transfer should be enhanced in the communities where such species
433 dominate (Hébert, Beisner et al., 2016). These FGs are known to be more abundant in the coldest
434 and most productive regions of the Mediterranean Sea: the northwestern regions (Gulf of Lion
435 and Ligurian Sea), the northern Adriatic and Aegean Sea (Siokou-Frangou et al., 2010; The
436 MerMex Group, 2011). Regarding small ambush-feeding generalists (FG 5), the positioning of
437 *O. similis* at the extreme negative end of the niche space (Fig. 3) skews the average position of
438 FG 5, whereas most of the species constituting this group are located at the opposite side of the
439 niche space. *O. similis* is known to reach high abundances and biomass in colder environments
440 (Gallienne & Robins, 2001; Castellani, Licandro, Fileman, Di Capua & Mazzocchi, 2016), but it
441 has been frequently misidentified with *O. helgolandica* and is sometimes even considered as a
442 conglomerate of cryptic species (Razouls et al., 2005-2017). Based on the present results, we do
443 not expect cruise-feeding detritivorous species to be favoured under any particular conditions in
444 the Mediterranean Sea.

445 The extent to which our findings apply to the global scale remains to be tested and depends on
446 the representativeness of the Mediterranean copepod fauna relative to the global one. Yet it
447 should be noted that the occurrence data we used here already covers a nearly global latitudinal
448 and environmental range (Appendices S4 and S5). The geographical range of the data used to
449 model the copepod niches is comparable across FGs, with data mainly located in the
450 Mediterranean Sea and its surrounding basins: the North Atlantic and Indian Oceans. A notable
451 exception is FG 6 because of the wider distribution of *Oithona similis* in polar oceans. Similarly,
452 the distribution of the environmental predictors associated with the monthly presence of species
453 largely overlaps between FGs (Appendix S5), suggesting that the differences observed in niche
454 space (Fig. 4) result from the differential segregation of the FG presence data in geographical
455 and/or environmental space.

456 Based on these findings, we anticipate that carnivorous FGs should dominate community
457 composition in tropical conditions, whilst small ambush-feeding omnivores (*Oithona* spp.), large
458 current-feeding herbivores and some smaller current-feeding herbivores should prevail in
459 temperate, subpolar and polar oceans. Our results are in line with those of Woodd-Walker, Ward

460 & Clarke (2002) who found a higher proportion of carnivorous copepods at lower latitudes,
461 relative to herbivorous and omnivorous copepods. Primary production is low in warmer seas, so
462 there is a clear ecological advantage in specializing on food sources other than phytoplankton.
463 Alternatively, species that primarily graze on phytoplankton and store lipids, such as many large
464 Calanoida (Barton et al., 2013) are disadvantaged under tropical conditions. Our results are also
465 in agreement with Atkinson (1998), who observed that the strong seasonality in food availability
466 at high latitudes favours two types of life history strategies: (i) small generalists (typified by
467 *Oithona* spp.) that present extended feeding periods thanks to a wide range of feeding
468 mechanisms and preys (Castellani, Irigoien, Harris & Lampitt, 2005); and (ii) larger herbivorous
469 lipid-storing species (typified by *Calanus* and other large Calanoida) that are able to enter
470 diapause at greater depth for overwintering. This is in line with the association of large current-
471 feeders with colder and more productive conditions.

472

473 ***Implications for ecosystem functions and modelling.***

474 Based on our analyses we recommend the integration of selected, observation-based zooplankton
475 functional groups in regional to global marine ecosystem models to better represent the diversity
476 of plankton and their functional roles in ecosystems (Le Quéré et al., 2016). At present, copepods
477 are represented by the mesozooplankton compartment in most models, a size class that was
478 included due to its important role in the carbon cycle via the formation of particulate organic
479 matter, and its link between phytoplankton and higher trophic levels (Le Quéré et al., 2005). In
480 current models, the mesozooplankton group has a fixed trophic level and comprises groups with
481 different trophic levels and distinct traits. Such a simplistic representation prevents an accounting
482 of food-web dynamics involving multi-trophic interactions and energy transfer from the first
483 trophic level upwards through multiple channels, with potentially different time scales and
484 transfer rates. A recent study demonstrates the importance of zooplankton food web interactions
485 for ecosystem characteristics in a model with higher heterotroph complexity (Le Quéré et al.,
486 2016). The authors suggest that the inclusion of multiple zooplankton taxa at different trophic
487 levels, and with different physiological and behavioral characteristics, may be a promising
488 avenue in order to improve the representation of marine ecosystem dynamics in a more realistic
489 way. Our results confirm these findings and show that even within a single size class, the
490 available functional trait data is now ample enough to inform the observation-based definition of
491 functional groups based on physiological and behavioural characteristics.

492 The delineation of FGs presented here is relevant for Mediterranean and global ecosystem
493 models because FGs (i) play different roles in food webs, (ii) are characterized by different,
494 though overlapping, environmental and physiological requirements, and (iii) impact the
495 abundance of other PFTs and energy and matter transfer patterns within marine food-webs
496 (Hood et al., 2006; Le Quéré et al., 2016). Current-feeding herbivores primarily graze upon the
497 phytoplankton and the protozooplankton and then are preyed upon by predators (i.e. carnivorous
498 copepods or fishes; Lynam et al., 2017). Carnivorous FGs contribute to the top-down control of

499 other FGs. The detritivores graze upon particulate organic matter, therefore affecting its re-
500 mineralization and attenuation at depth (Nishibe et al., 2015).

501

502 ***Caveats and robustness of our study.***

503 In this study, all niche characteristics were derived from GAMs, one of the many existing ENMs
504 (Merow et al., 2014). ENM choice is the primary cause of uncertainty in niche model projections
505 (Diniz-Filho et al., 2009; Garcia, Burgess, Cabeza, Rahbek, Araújo & 2012; Benedetti et al.,
506 2017) and is therefore likely to be the largest uncertainty factor in our niche parameters. We
507 visually compared the response curves with those obtained from generalized linear models
508 (GLMs), maximum entropy (MaxEnt; Phillips, Anderson & Schapire, 2006), flexible
509 discriminant analysis (FDA), multivariate adaptive regression splines (MARS), neural network
510 analysis (ANN), classification tree analysis (CTA), boosted regression trees (BRT) and random
511 forest (RF). Most of these models (GLMs, FDA, MARS and MaxEnt) generated response curves
512 with shapes similar to those obtained from GAMs, while deviations in certain models (CTA,
513 BRT) were explained by methodological reasons, thus suggesting that our results are robust to
514 model choice (Appendix S6) and model set-up.

515 Although our traits span diverse types and functions, many other quantitative and qualitative
516 functional traits exist for zooplankton (Litchman et al., 2013). Our choice of traits was limited by
517 the amount of available information for more than 100 species that are representative of
518 Mediterranean planktonic ecosystems. In spite of the growing literature publishing trait tables for
519 zooplankton, physiological rates are still only measured for a small pool of calanoid copepods
520 (Kiørboe & Hirst, 2014; Hébert et al., 2016; Brun et al., 2017). Ultimately, the identified FGs
521 and the covered range of trait values depend on the species pool studied. In the present
522 framework, missing functional trait values have relatively minor impact on the FGs definition
523 because species with more than two missing traits are treated as supplementary objects in the
524 MCA, meaning they are placed in the functional space a posteriori and according to their
525 similarity with the fully-informed species (Benedetti et al., 2016). A species with only one
526 informed trait will deviate from the center of the MCA space only along the dimensions that are
527 scored by this very trait. Ignoring rare species was necessary in our study since those largely lack
528 both trait information and distribution data. The species with several missing trait values studied
529 here are also those less frequently sampled in the Mediterranean Sea (Razouls et al., 2005-2017;
530 Mazzocchi et al., 2014). Apart from the species belonging to the Siphostomatoida order, which
531 are mostly semi-parasitic, it is unlikely that including rare species would add trait combinations
532 that are completely novel compared to the ones covered here. As rarer copepod species are much
533 less abundant in the plankton, it is also unlikely that they play an equally significant role in
534 Mediterranean ecosystem functioning than the species studied here. However, we acknowledge
535 that it remains to be tested how accounting for additional species, or clades, would change the
536 distribution of FGs in niche space.

537 Although copepods represent the largest fraction of biomass and diversity in the Mediterranean
538 zooplankton (Siokou-Frangou et al., 2010), not accounting for other taxa, such as pteropods,

539 chaetognaths, salps and appendicularians, may potentially ignore important ecological functions
540 performed by these other groups. The next step will be to enlarge the species pool to the
541 dominant taxa of other basins to test whether our findings apply to zooplankton communities
542 worldwide.

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793 **Biosketch**

794 **Fabio Benedetti** is currently a post-doc at the Observatoire Océanologique de Villefranche-sur-
795 Mer where he is studying zooplankton trait biogeography at multiple scales. His main research
796 interests focus on the co-variation of biodiversity components with environmental gradients and
797 how these affect ecosystem processes simultaneously.

798 Author contributions: F.B. gathered the biological data and designed the study with M.V. and S-
799 D.A. D.R. provided the environmental layers, and helped in optimizing the methods with F.G.
800 F.B. led the writing of the manuscript that all co-authors contributed to.

801 **Figure Legends**

802 **Figure 1:** Flowchart describing the main steps of the methodology for the present study. From
803 the top to the bottom, the left-hand side shows how the species functional traits table was used to
804 define functional groups from a multivariate functional space. The right-hand side shows how
805 environmental niche modelling was performed to quantify the species' environmental
806 preferences (i.e. niche parameters). The niche parameters were selected according to their
807 correlation in order to perform a parsimonious Principal Component Analysis (PCA) to generate
808 the niche space. Finally (bottom), the position of the functional group (FG) in niche space was
809 assessed and variance analysis was performed to test if different FGs present different niches.

810
811 **Figure 2:** Functional dendrogram showing the ordination of the 106 copepod species according
812 to the combination of functional traits. A Multivariate Correspondence Analysis (MCA) based of
813 the functional traits was performed to ordinate the species in a reduced functional space. The
814 coordinates of the species along the four retained axes of the functional space were used to
815 compute a Euclidean distance matrix. Agglomerative hierarchical clustering was used to draw
816 the functional dendrogram. The chosen cutting-level is shown and the species are coloured
817 according to the seven derived functional groups.

818
819 **Figure 3:** Principal Component Analysis (PCA) based on the selected eleven niche
820 characteristics of the 106 copepod species. The contribution of the eleven niche parameters to the
821 niche space, as well as their correlation (i.e. the angles between the arrows) are evidenced. The
822 abbreviations of the environmental predictors are as follows: sea surface temperature (SST), sea
823 surface salinity (SSS), seasonal range of SST values (Δ SST), mixed layer depth (MLD), active
824 radiation (PAR) integrated over the MLD (MLPAR), and logarithm of surface chlorophyll-a
825 concentration (logChla).

826
827 **Figure 4:** Position of the seven functional groups in niche space. Smaller symbols correspond to
828 the 106 copepod species with the colors and shapes varying according to the functional group
829 they belong to. Larger symbols correspond to the average position of the functional groups,
830 based on the coordinates of the species they comprise. The first principal component (PC1)
831 represents a gradient characterizing oligotrophic conditions on the positive side (higher centers
832 of SST, SSS, MLPAR) and more productive conditions on the negative side (broader SST and
833 SSS niches, and higher MLD and logChla centers). The second principal component (PC2)
834 distinguishes species with broader tolerance to SST, logChla variations (positive side) from
835 species affiliated to habitats of lesser seasonal variability (negative side). The standard error of
836 each FG' coordinates along PC1 and PC2 are illustrated with the error bars. The abbreviations of
837 the environmental predictors are as follows: sea surface temperature (SST), sea surface salinity
838 (SSS), seasonal range of SST values (Δ SST), mixed layer depth (MLD), active radiation (PAR)
839 integrated over the MLD (MLPAR), and the logarithm of surface chlorophyll-a concentration
840 (logChla).

841 **Supporting Information**

842 **Supporting Information S1:** Table describing the set of environmental predictors tested in the
843 present study. The time period covered by the monthly climatologies is given, as well as the
844 corresponding references.

845
846 **Supporting Information S2:** Table summarising for every 106 copepod species: the number of
847 observations (presences at the global scale, after re-sampling on the predictors cell grid); the
848 average TSS value of the multivariate niche models and its standard deviation; the average niche
849 characteristics derived from the univariate models and their associated standard deviations
850 computed thanks to the bootstrapping procedure.

851
852 **Supporting Information S3:** Pair-wise Spearman's correlation coefficient (ρ) values of all the
853 univariate niche characteristics ($n = 24$).

854
855 **Supporting Information S4:** Maps of the sampling effort (i.e. number of species presences) for
856 each of the seven copepod functional group defined in the study. Presences are at a $1^\circ \times 1^\circ$ cell
857 grid resolution after re-sampling the observed occurrences on the cell grid of the environmental
858 predictors.

859
860 **Supporting Information S5:** Distribution of the latitude and the six environmental predictors'
861 values for each of the seven copepod functional groups defined in the study. Values correspond
862 to the environmental monthly data that were fitted on each species monthly occurrence.

863
864 **Supporting Information S6:** Examples of response curves to Sea Surface Temperature (SST)
865 variations for *Calanus helgolandicus*, *Acartia Acartiura clausi* and *Clausocalanus*
866 *mastigophorus*, according to nine different types of environmental niche models (ENMs):
867 Generalized Additive Models (GAM), Generalized Linear Models (GLM), Multi-Adaptive
868 Regression Splines (MARS), Flexible Discriminant Analysis (FDA), Maximum Entropy
869 (MAXENT), Boosted Regression Trees (BRT), Random Forest (RF), Classification Tree
870 Analysis (CTA), and Neural Network Analysis (ANN). Additionally, the niche spaces (based on
871 a Principal Component Analysis (PCA) performed on the chosen eleven niche characteristics)
872 and positions of the seven copepod functional groups according to various parameters of the
873 niche modelling framework designed for the present study: the choice of the ENM, the choice of
874 the Generalized Additive Models (GAMs) smoothing parameter value (k), and the percentage of
875 the species' monthly occurrence data considered to train (and test) the GAMs.

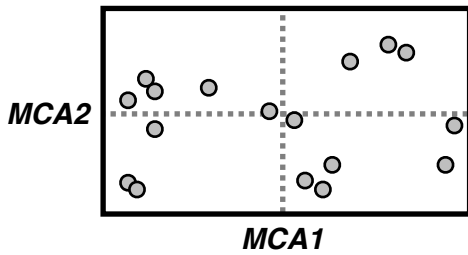
Functional traits and groups

Functional traits table
maximum body length,
feeding mode, spawning
strategy and trophic group
106 species

Categorize
all traits

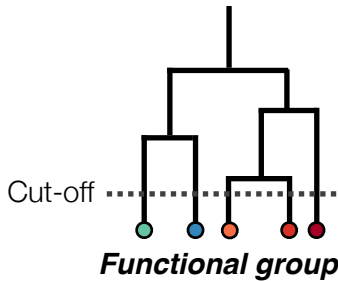
Multiple Correspondance Analysis (MCA)

Functional space



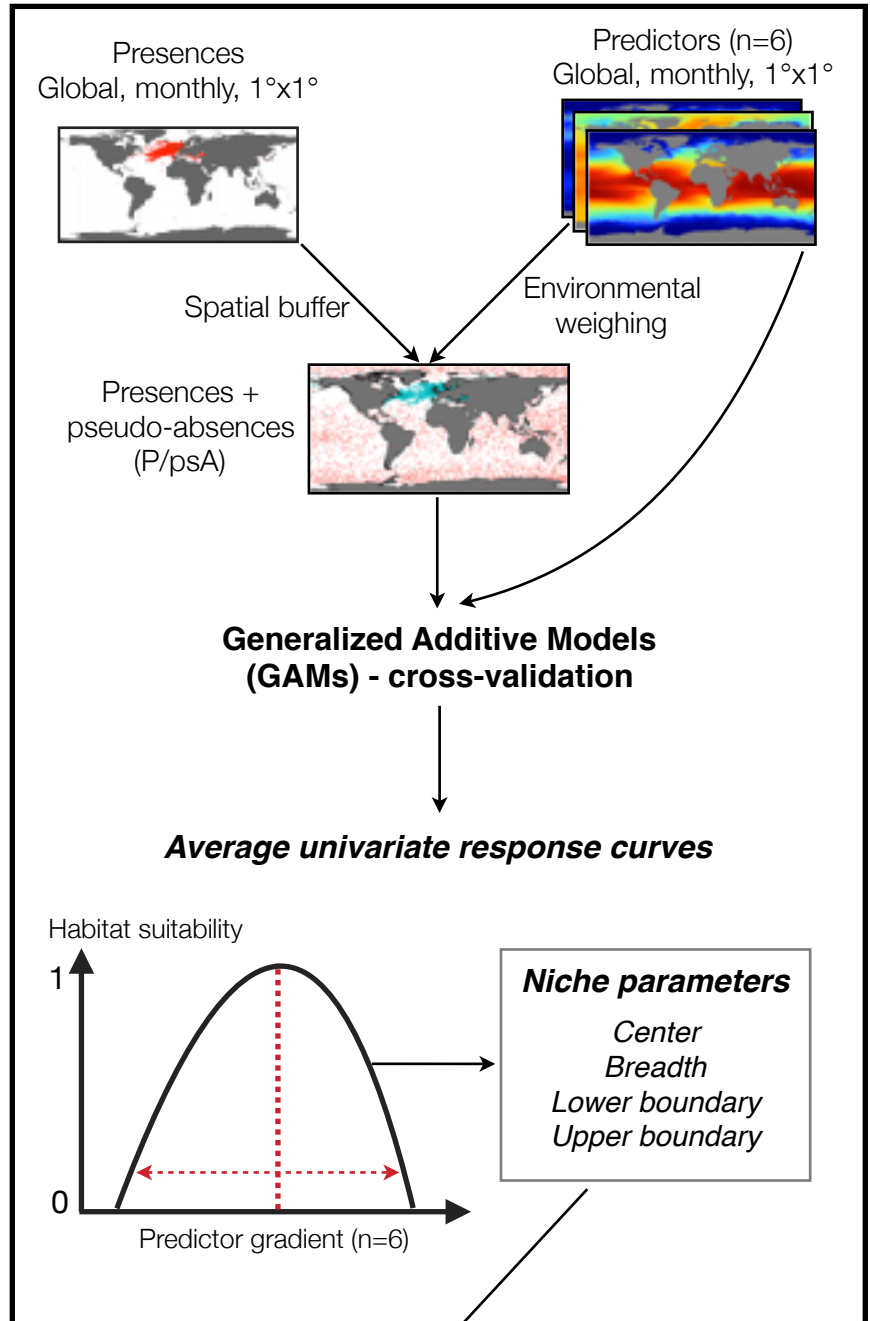
Hierarchical clustering
on MCA coordinates

Functional dendrogram



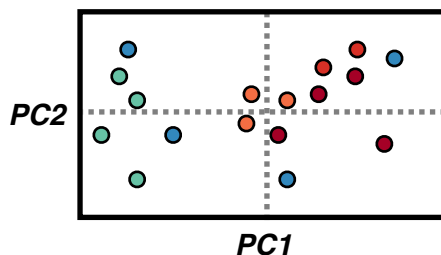
Project functional
groups in niche space

Environmental niche modelling



Principal Component Analysis (PCA)

Niche space



Variance analysis
on PC scores

*Are functional groups
differently distributed
in niche space ?*

Parameter filtering
(Spearman's rank correlation)

