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Hydrological intermittency drives diversity decline and functional homogenization in benthic diatom communities

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Abstract: Over the last decades, the combined effects of global climate changes and severe land use modifications have been exacerbating river hydrological alterations and habitat fragmentation in many Mediterranean rivers. This trend is predicted to intensify, with expected significant impacts on taxonomic and functional diversity of benthic communities in the next future.

The present research aims at investigating the long-term combined effects of flow intermittency, climate and land use changes on benthic diatom communities, by analysing data collected over 11 years in Mediterranean streams of the NW-Italy.

We demonstrated that the ongoing global changes and local environmental pressures determined a significant decline in diatom species diversity at both local and regional scales. More in detail, flow intermittency affected both diatom diversity and life history traits, with communities of intermittent reaches taxonomically and functionally different and less heterogeneous than assemblages characterizing perennial ones. Communities inhabiting intermittent sections showed high percentages of small, mainly stalked and pioneer taxa belonging to the low profile guild, highlighting the strong environmental pressure exerted by the hydrological alterations. Conversely taxa colonizing permanent reaches were bigger, belonging to the high profile guild and able to produce colonies, denoting environmental stability.

The results we obtained could be ascribed to the long-term effects of drying in Mediterranean streams and, as first in the literature, we highlight that diatoms are able to provide long-term responses to environmental changes caused by water stress, when hydrological disturbance is persistent.

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To the attention of
the editor of Science of the Total Environment
July 20th, 2020

Dear Editor,

we would be grateful if you would consider the possibility of including our contribution entitled **“Hydrological intermittency drives diversity decline and functional homogenization in benthic diatom communities”** in a forthcoming issue of Science of the Total Environment.

We are confident that our manuscript fulfills the aims and scope of the journal, being an interdisciplinary study that investigates the environmental impacts of climate and land use changes on freshwater ecosystems in the Mediterranean basin and, thus, potentially having a high international relevance.

Over the last decades, the combined effects of global climate changes and the local land use changes have been exacerbating the natural flow intermittency and habitat fragmentation in many Mediterranean rivers worldwide. And this trend is predicted to intensify with expected significant biodiversity and functional losses in a next future. In order to highlight the impacts of these phenomena on lotic ecosystems, here we investigated the taxonomic and functional response of the benthic diatom communities experiencing climate- and land use-driven exacerbation of flow intermittency over the last 11 years in a Mediterranean region of the NW-Italy.

By comparing the environmental parameters and diatom communities in permanent and intermittent reaches, we demonstrated that diatom communities are highly impacted by flow intermittency and that hydrological differences are due to the combined effects of the ongoing climate change and local environmental pressures. We highlighted a significant decline of diatom species at both local and regional scales due to the extinction of rare species and the increase of few dominant species in intermittent reaches. When considering community composition, we demonstrated a taxonomic change and a functional homogenization of the diatom communities inhabiting intermittent reaches, which were dominated by low profile, pioneer taxa, typical of disturbed conditions. Although flow intermittency is part of the natural hydrological cycle of Mediterranean rivers, its climate- and land use-driven exacerbation represents a threat to diatom benthic communities. These results are extremely alarming considering that Mediterranean rivers represent a biodiversity hotspot and provide fundamental ecosystem services worldwide.

This manuscript describes original work and is not under consideration by any other journal. All authors approved the manuscript and this submission.

Thank you for receiving our manuscript and considering it for review. We appreciate your time and look forward to your response.

Sincerely Yours,

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Hydrological intermittency drives diversity decline and functional homogenization in benthic diatom communities

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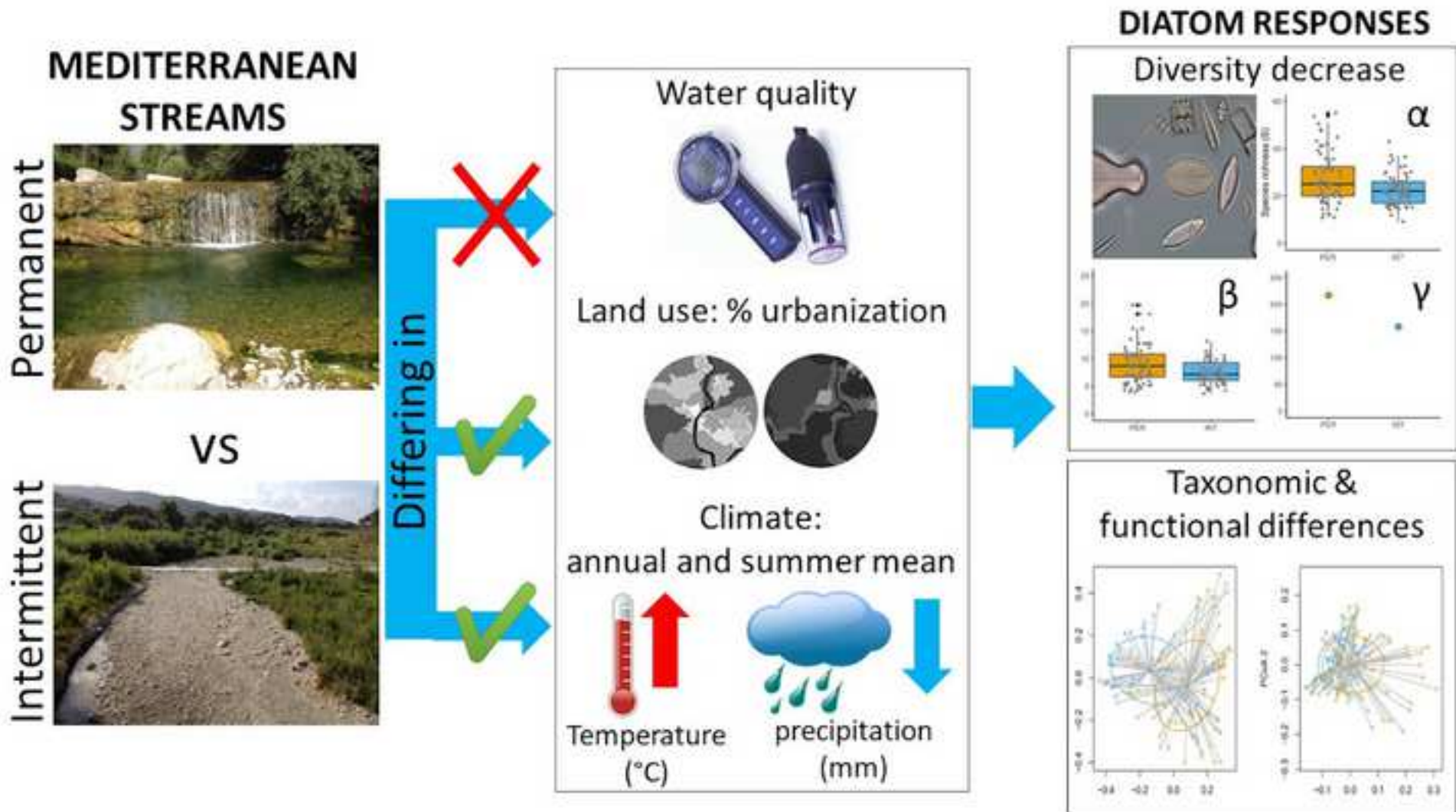
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Running Title: Flow intermittency affects diatom communities

Keywords: Bacillariophyceae, climate change, diversity partitioning, non-flow, functional traits, Mediterranean rivers



Highlights

- Climate and land use changes exacerbate flow intermittency in Mediterranean rivers
- We studied long-term effects of flow intermittency on diatom communities
- Diatom diversity is lower in intermittent than perennial reaches at several scales
- Flow intermittency changed diatom assemblages and reduced functional heterogeneity

1 **Hydrological intermittency drives diversity decline and functional homogenization in benthic diatom**
2 **communities**

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16

17 **ABSTRACT**

18 Over the last decades, the combined effects of global climate changes and severe land use modifications have been
19 exacerbating river hydrological alterations and habitat fragmentation in many Mediterranean rivers. This trend is
20 predicted to intensify, with expected significant impacts on taxonomic and functional diversity of benthic communities
21 in the next future.

22 The present research aims at investigating the long-term combined effects of flow intermittency, climate and land use
23 changes on benthic diatom communities, by analysing data collected over 11 years in Mediterranean streams of the
24 NW-Italy.

25 We demonstrated that the ongoing global changes and local environmental pressures determined a significant decline in
26 diatom species diversity at both local and regional scales. More in detail, flow intermittency affected both diatom
27 diversity and life history traits, with communities of intermittent reaches taxonomically and functionally different and
28 less heterogeneous than assemblages characterizing perennial ones. Communities inhabiting intermittent sections
29 showed high percentages of small, mainly stalked and pioneer taxa belonging to the *low profile* guild, highlighting the
30 strong environmental pressure exerted by the hydrological alterations. Conversely taxa colonizing permanent reaches
31 were bigger, belonging to the *high profile* guild and able to produce colonies, denoting environmental stability.

32 The results we obtained could be ascribed to the long-term effects of drying in Mediterranean streams and, as first in the
33 literature, we highlight that diatoms are able to provide long-terms responses to environmental changes caused by water
34 stress, when hydrological disturbance is persistent.

35

36 1. INTRODUCTION

37 Over the last decades, the combined effects of global climate changes and the growing human demand for water and
38 other ecosystem services have been exacerbating flow intermittency in many areas (IPCC Core Writing Team, 2014).
39 This trend is predicted to intensify, causing a global increase of drought frequency and the spatial and temporal extent
40 of intermittent reaches in rivers worldwide (Datry et al., 2017a; b). Indeed, climate change-runoff models forecast
41 future decreases in runoff patterns in mid-latitude regions coupled with an increase of air temperatures (Kundzewicz et
42 al., 2008; Larned et al., 2010). This is particularly evident in the Mediterranean region, where an annual precipitation
43 reduction up to 20% and a contemporary intensification of the extreme events have been observed during the last
44 century (García-Ruiz et al., 2011). Although intermittent rivers are widely distributed in the Mediterranean region
45 (Bonada & Resh, 2013), their number and extension is predicted to rapidly increase (IPCC Core Writing Team, 2014)
46 and changes in air temperature and precipitation patterns can affect water temperature and the duration of the wet and
47 dry phases that naturally characterizes their hydrological cycle during summer (Giorgi & Lionello, 2008). In addition,
48 the local land use changes have been recognized to cause habitat fragmentation and to reduce habitat heterogeneity
49 worldwide (Sala et al, 2000). More in detail, the conversion of natural land uses into agricultural and urban areas led to
50 changes in hydrology, water chemistry and morphological conditions of rivers (Newall & Walsh, 2005; Medeiros et al.,
51 2020; Song et al., 2020), likely exacerbating the negative effects of increasing flow intermittency on the lotic biota.

52 Under this scenario, Mediterranean freshwater ecosystems are expected to face a huge species loss (Chiu et al., 2017),
53 due to the harsh environmental conditions induced by both hydrological alterations and habitat fragmentation, which act
54 as a filter and select for species displaying specific traits that enhance their survival in these extreme environments
55 (Datry et al., 2017c). In particular, drying up of the streambed causes longitudinal, lateral and vertical habitat
56 fragmentation, limiting the recruitment of new individuals, which drift from upstream or colonizing the riverbed from
57 lateral refugia, such as pools, or from the hyporheic zone, with consequences on species distribution and abundances
58 (Tolonen et al., 2019). Focusing on diatom communities, it has been recently demonstrated that droughts in
59 Mediterranean streams can led to a significant decrease of endangered species (Falasco et al., 2016a), thus reducing
60 species diversity at both local and regional scale, and to changes in community functional traits (Elias et al., 2014; B-
61 Béres, et al., 2019; Novais et al., 2020). For instance, the genera *Cymbella* and *Gomphonema* are able to face
62 desiccation by embedding cells within a mucilage-protective layer (Sabater et al., 2017), while motile taxa, such as
63 *Navicula*, *Nitzschia* and *Surirella*, can actively move on the substrate towards refugia or simply penetrate the biofilm
64 toward deeper layers (Falasco et al., 2016b; 2018a). Flow intermittency also changes diatom community composition

65 throughout the year, with shifts from lotic- to lentic-adapted species up to aerophilous ones during the lentification and
66 the drying up of the riverbed respectively (Datry et al., 2017a). Thus, species surviving during the lentification phase
67 can often represent both a taxonomic and functional subset of those typical of the wet phase (Tolonen et al., 2019). In
68 addition, modifications in river physical elements (such as river banks, channel morphology, substrate composition and
69 riparian canopy) induced by land use changes can play an important role as drivers of diatom composition (Kutka &
70 Richards, 1996; Hill et al., 2000; Hlúbiková et al., 2014) and can furtherly lead to a decrease in species richness (Bona
71 et al., 2008).

72 Beside species richness, another important biological response to environmental changes is the degree of compositional
73 variation in communities across space or in time, namely β -diversity (Soininen, 2010). Larned et al. (2010) hypothesises
74 a conceptual model aimed at exploring diversity patterns at different scale in temporary rivers, by predicting maximum
75 β -diversity when the effect of additional aquatic patches is balanced by the homogenising effect of patch connection. In
76 other words, β -diversity reaches its maximum when the connectivity and dispersal among the patches, created by
77 hydrological variations, is intermediate. Thus, β -diversity is mainly driven by habitat heterogeneity and can be used to
78 assess the loss of environmental quality, through a measure of community composition (Piano et al., 2017a). However,
79 results on the existing relationship between β -diversity and habitat heterogeneity are often controversial and, concerning
80 diatom communities, not well documented (Jyrkänkallio- Mikkola et al., 2016).

81 The present research aims at investigating the long-term effects of the combined pressure of both flow intermittency and
82 land use changes in a Mediterranean region of NW-Italy (namely Liguria), by analysing benthic diatom communities
83 collected over a period of 11 years. In particular, we analysed data obtained during the routine biomonitoring programs
84 carried out by the Environmental Protection Agency (ARPAL) in Liguria (NW-Italy) in the framework of the WFD
85 (2000/60/CE) and covering a temporal range of 11 years, from 2008 to 2019. In this region, summer precipitations
86 follow a downward trend, suggesting that this region is becoming drier (Deitch et al., 2017). In addition, the land use is
87 profoundly modified by anthropogenic activities, with high urban coverage especially along the coast, where most of
88 the intermittent reaches are located. We compared communities inhabiting permanent and intermittent reaches during
89 baseflow, in order to highlight differences in terms of diatom taxonomic diversity at multiple scales and in terms of
90 taxonomical and functional community composition. In fact, a deep understanding of the existing relationships between
91 hydrological alterations and benthic communities at different levels still represent an important scientific gap that
92 urgently need to be filled (Wu et al., 2019).

93 We hypothesised that cumulative effects of non-flow events, determined by the ongoing climate change coupled with
94 strong changes in river hydromorphology related to urbanization of the sampling sites, would result in diatom (i)
95 species loss at both local and regional scales and (ii) taxonomic and functional homogenization. We also hypothesised
96 that (iii) diatoms colonizing permanent and intermittent reaches would show different functional traits, measured in
97 terms of class size, growth forms and ecological guilds. In particular, we expected bigger sized diatoms, which are
98 known to be adapted to stable flow conditions (i.e. high profile diatoms, characterized by stalked growth forms and
99 possibly producing colonies, Rimet & Bouchez, 2012), in the permanent reaches, while pioneer communities, composed
100 of smaller sized taxa and thus likely adapted to unstable environments (i.e. low profile diatoms, characterized by adnate
101 growth form, Rimet & Bouchez, 2012), in the intermittent ones.

102

103 **2. MATERIALS AND METHODS**

104 *2.1 Study area*

105 In total, we selected 55 sampling sites characterized by different flow regimes in Liguria, a NW-Italian region with a
106 surface area of about 5400 km² (Figure 1). More in detail, we chose 25 sites with permanent flow (hereafter PER),
107 classified as M4 according to the WFD (i.e. small and medium Mediterranean rivers flowing in the mountains), and 30
108 sites characterized by intermittent flow and experiencing drying during summer (hereafter INT), classified as M5
109 according to the WFD (i.e. Mediterranean temporary rivers). To mitigate potential confounding factors related to water
110 quality, we excluded a priori all the sites with an ecological status “poor” or “bad” according to the historical data
111 provided by ARPAL and assuring a comparable ecological status between the two groups of sites. The PER sampling
112 sites were located between 1 and 649 m a.s.l, with a distance from the source ranging from 22.4 and 62.3 Km and
113 catchment surface ranging from 150 to 675 Km². Streambed in the permanent reaches was generally natural and
114 heterogeneous among the stations, mainly composed of rocks, boulders and cobbles with some gravel and sand. The
115 INT sampling sites were located between 1 and 446 m a.s.l, with a distance from the source ranging from 6 and 41.5
116 Km and catchment surface ranging from 8 to 285 Km². Streambed in the intermittent reaches was mostly natural, but a
117 significant number of sampling sites resulted somehow artificial, characterized by streambed and banks modifications.
118 However, in most of the reaches, the streambed composition was heterogeneous and composed mainly of boulders,
119 cobbles and gravel but also sand and silt (see Table SM1 for more details on the environmental characterization of PER
120 and INT sites).

121 2.2 Diatom samples

122 Epilithic diatoms were collected following the monitoring program of the ARPAL (see Table SM2), for a total of 144
123 samples, among which 72 samples were collected in PER sites and 72 samples were collected in intermittent sites.
124 According to the standard procedure, in each reach we chose five cobbles from the main flow and we collected
125 periphyton by scraping their upper surface by means of a toothbrush (European Committee for Standardization, 2003).
126 Samples were fixed with ethanol (70%) and transported to the laboratory, where they were treated with H₂O₂ (30%) and
127 HCl (European Committee for Standardization, 2003). Permanent slides for the light microscope analysis were mounted
128 by means of Naphrax®. Diatom identification was based on several diatom floras and monographies, as well as recent
129 taxonomic papers (Krammer and Lange-Bertalot, 1986–1991a,b; Lange-Bertalot and Metzeltin, 1996; Krammer,
130 1997a,b; 2002; 2003; Reichardt, 1999; Lange-Bertalot, 2001; Werum and Lange-Bertalot, 2004; Blanco et al., 2010;
131 Hofmann et al., 2011; Bey and Ector, 2013; Falasco et al., 2013; Ector et al., 2015). As required by the standard
132 procedure, we identified at least 400 valves in each sample. For each species, we compiled a list of functional traits
133 focusing on class size, ecological guilds and growth forms, defined according to Rimet and Bouchez (2012).

134 2.3 Environmental data

135 Water quality data. Water samples for the physical and chemical analyses were collected together with diatom
136 samplings. In total, over the whole sampling period (2008-2019), we collected 144 water samples. In both PER and INT
137 reaches we measured the chemical and physical parameters required by the WFD, namely ammoniacal nitrogen (N-
138 NH₃), nitrate nitrogen (N-NO₃), total phosphorous (P_{tot}), conductivity (COND), dissolved oxygen (DO, both in mg L⁻¹
139 and %), pH and water temperature (TEMP), by using standard method procedures

140 Land use data. We defined the land use of each sampling site on digital maps in QGIS (Quantum Gis Development
141 2020) in a buffer defined as a circle of 500 m radius with the sampling site as the centre. Land use was obtained from
142 regional data (<http://www.cartografia.regione.liguria.it/>) and we calculated the % of the following five land use
143 categories: urban areas, agricultural areas, woods, open areas and water bodies.

144 Climatic data. Climatic data were obtained from the WorldClim website (www.worldclim.org). We analysed data on
145 monthly precipitations (mm) and monthly minimum and maximum air temperature (°C) from 2008 to 2018, with a
146 spatial resolution of 2.5 minutes. Data from 2019 were not included as they were not available on the website yet. More
147 in detail, by using the function “extract” from the package *raster* in the R software (R Core Team, 2020), for each
148 sampling site, we extracted the value of precipitations, maximum and minimum air temperatures for each month in the

149 considered timeframe. We then averaged the obtained values for (i) all months (hereafter annual climatic data) and (ii)
150 for only June, July and August months (hereafter summer climatic data), which represent the drought period for the
151 study area, to obtain a mean value of all climatic data for each sampling site.

152 *2.4 Statistical analyses*

153 All statistical analyses were performed with the R statistical software (R Core Team, 2020).

154 Environmental data. We first performed data exploration following Zuur et al. (2010) by visually checking the
155 distribution of environmental data and the presence of outliers with dotplots. Nutrients (were then log-transformed to
156 achieve a homogeneous distribution). In order to explore possible differences between PER and INT sampling sites in
157 terms of environmental and physical-chemical conditions we performed three Principal Component Analyses (PCA),
158 one for each environmental database: i) physical and chemical data (Temp = temperature; %DO = dissolved oxygen
159 saturation; Cond = conductivity; log_Ptot = log-transformed total phosphorous concentration; log_N-NO₂ = log-
160 transformed nitrate concentration; log_N-NH₃ = log-transformed ammonia concentration; ii) land use data; and iii)
161 climatic data (annual climatic data: year_prec = year precipitations, year_tmin = year minimum temperature, year_tmax
162 = year maximum temperature; summer climatic data: summer_prec = summer precipitations, summer_tmin = summer
163 minimum temperature and summer_tmax = summer maximum temperature). We separately analysed these datasets
164 because we were interested in highlighting which environmental components, namely physical-chemical parameters,
165 land use or climatic data, could better explain differences among PER and INT sites. A Permutational Multivariate
166 Analysis of Variance (PERMANOVA, Anderson, 2001) was then applied to the three environmental dissimilarity
167 matrices based on Euclidean distances to test for differences between PER and INT sites with the function “adonis”
168 from the *vegan* package (Oksanen et al. 2019). Statistical significance was tested via 999 random permutations. We
169 then performed a two-sample t-test to check for differences between PER and INT sites for each environmental variable.

170 Diversity partitioning. To investigate for differences among PER and INT sites in terms of taxonomic diversity, we
171 partitioned the total diversity at the regional scale (γ) into its local diversity components, namely the average local taxa
172 richness of each site (α), and the variation among sites (β) for both site categories. Variation in taxa composition among
173 local communities (β -diversity) was calculated with the Whittaker’s multiplicative formula as the ratio between γ - and
174 α -diversity (Jost, 2007; Anderson et al., 2011), which expresses the number of times by which the richness at regional
175 level increases compared to the richness at local level. Differences in taxa richness among PER and INT sites were
176 tested with a randomization procedure, whereby we permuted samples over the two hydrological categories 999 times
177 (McGlinn et al., 2018), using the function “get_mob_stats” in the package *mobr* (Xiao et al., 2018). We estimated

178 significant differences between treatments by comparing the observed value of the taxa richness to the null expectation
179 of randomly distributed taxa across sites (Legendre & Legendre, 1998). Diversity partitioning was performed on
180 observed taxa richness (S) and other two diversity metrics, namely rarefied richness (S_n), and effective number of
181 species (S_{PIE}). In particular, S_n controls species richness for the number of individuals among treatments, while S_{PIE}
182 represents evenness (McGlenn et al., 2018). Rarefied species richness (S_n) and evenness (S_{PIE}) are obtained from
183 individual-based rarefaction curves that were either calculated at the level of individual samples (α -level) or by pooling
184 all individuals across samples (γ -level). Evenness was calculated as the probability of intraspecific encounter (PIE) and
185 transformed into an expected number of equally abundant species (S_{PIE}) to obtain an easier interpretation (McGlenn et
186 al. 2018). In a second step, we decomposed total beta diversity, here intended as the dissimilarity between communities
187 in PER and INT sites (β_{total}) into its turnover (β_{repl}) and nestedness (β_{rich}) components with the function beta in the *BAT*
188 package (Cardoso et al., 2020). We then tested for differences between PER and INT sites in terms of all β -diversity
189 components with a t-test.

190 Taxonomic and functional composition. We performed a Principal Coordinate Analysis (PCoA) to visually inspect
191 possible differences in terms of both taxonomical (Bray-Curtis distance) and functional (Gower distance) composition
192 among diatom samples collected in sites with different water regime and land-use (i.e. PER vs INT). Possible
193 dissimilarity in taxonomical and functional composition of diatom communities collected in INT and PER sites was
194 tested through a PERMANOVA (Anderson, 2001) applied on distance matrices, by using the function “adonis” in the
195 package *vegan* (Oksanen et al., 2019). To investigate taxonomic differences, the taxonomic matrix, with the relative
196 abundance of each recorded taxon in each sample, was converted into a site-by-site distance matrix using the Bray-
197 Curtis distance with the function “vegdist” of the *vegan* package (Oksanen et al., 2019). The distance of each site to its
198 associated group multidimensional median was calculated and differences among such site distances were tested by
199 means of multivariate analogue of the Levene’s test for homogeneity of variance with 9999 permutations to determine
200 whether the dispersions between the two groups were different. The same procedure was repeated on the functional
201 matrix, containing trait abundances for each sampled site. To generate the functional matrix, we first created a species-
202 by-trait matrix that was multiplied by the species-by-site matrix to obtain the site-by-trait matrix with the function
203 “functcomp” in the package *FD* (Laliberte et al., 2014), in which each entry corresponds to the sum of the relative
204 abundances of all the species present in a site that have a particular trait state. Functional traits considered for
205 generating the functional matrix were class size, life-forms and ecological guilds (Rimet & Bouchez, 2012). To test
206 whether flow regime and land use changes cause biotic homogenization in both taxonomic and/or functional structure
207 of diatom communities we performed the test of homogeneity for multivariate dispersion (Anderson et al., 2006)

208 following the procedure proposed by Brice et al. (2017) and with the PERMANOVA, with the package *vegan* (Oksanen
209 et al., 2019) by using the functions “betadisper and “adonis” respectively. Finally, to check whether functional
210 differences between PER and INT reaches were due to selective environmental filtering of some functional traits, we
211 compared the two categories by performing a t-test on each functional trait.

212

213 **3 RESULTS**

214 *3.1 Environmental data*

215 When considering the water quality parameters, all the investigated sites were characterized by a good or elevated water
216 quality status going from “moderate” to “high” (Table 1). According to the PCA performed on water quality
217 parameters, PER and INT sites broadly overlap (Figure 2a). The first axis explained 26.2% of the total variance and was
218 negatively correlated with log_Ptot (-0.537), while the second axis explained 19.1% of the total variance and was
219 positively correlated with pH (0.570) and log_N-NH₃ (0.509). The similarity among PER and INT sites was confirmed
220 by the results of the PERMANOVA, which detected no significant differences in terms of physical-chemical parameters
221 ($F_{1,143} = 3.17$, $P = 0.064$). Although the PERMANOVA did not highlight significant differences among the two
222 hydrological categories, the results of the two-sample t-tests showed significant differences in terms of nitrate and total
223 phosphorous concentrations (Table 1). In particular, the former was higher in INT sites, whereas the latter was higher in
224 PER sites. However, as shown in Table 1, observed values were always included in the first or second water quality
225 class following the Italian water quality standards (D. Lgs 152/2006).

226 Conversely, from the visual inspection of the PCA performed on land use (Figure 2b), we could clearly distinguish two
227 groups of sites, corresponding to PER and INT reaches. The observed pattern was confirmed by the PERMANOVA,
228 which showed significant differences between the two hydrological categories ($F_{1,143} = 32.2$, $P = 0.001$). PC1 explained
229 35.7% of the total variance and was positively correlated with urban areas (0.697), while PC2 explained 25.1% of the
230 total variance and was negatively correlated with agricultural land use (-0.806). The results of the two-sample t-tests
231 showed significant differences among the two site categories, in terms of wood areas (with higher percentages in PER
232 sites) and urban areas (with higher percentages in INT sites), while no differences were detected in terms of agricultural
233 areas, open areas and water bodies (Table 1).

234 From the PCA performed on climatic data (Figure 2c), we could again clearly distinguish two groups of sites,
235 corresponding to PER and INT reaches. The PC1 explained most of the variance (76.2%) and was negatively correlated

236 with year_tmin (-0.453) and summer_tmin (-0.451), while PC2 explained 18.7% of the total variance and was positively
237 correlated with summer_tmax (0.727). PERMANOVA highlighted significant differences between the two categories in
238 terms of climatic features ($F_{1,143} = 16.1$, $P = 0.001$). According to the results of the two-sample t-tests performed on
239 climatic data, permanent reaches were characterized by higher annual and summer precipitations than INT sites, while
240 INT sites showed higher minimum and maximum air temperatures, all over the year and during summer, in comparison
241 to PER sites (Table 1).

242 3.2 Taxonomic responses to different water regimes

243 In total we recorded 240 species of diatoms (see Table SM3 for a complete list of the recorded species). The results of
244 the diversity partitioning showed that species richness (S) was significantly different between PER and INT sites in
245 terms of all the diversity components (α - β - and γ -diversity) (Figure 3a-c). PER sites were characterized by a higher
246 number of taxa at both local ($\alpha = 27.6 \pm 10.6$) and regional ($\gamma = 217$) scale than INT reaches ($\alpha = 22.6 \pm 6.44$; $\gamma = 158$).
247 Moreover, the variation of species richness among sites (i.e. β - diversity) was significantly higher in PER ($\beta = 9.11 \pm$
248 3.66) than INT sites ($\beta = 7.57 \pm 2.31$), highlighting a higher heterogeneity in terms of species richness in PER reaches.
249 When considering rarefied richness (S_h) (Figure 3d-f), we observed significant higher values of α - and γ -diversity in
250 PER ($\alpha = 23.0 \pm 8.87$; $\gamma = 198$) than INT sites ($\alpha = 19.1 \pm 5.60$; $\gamma = 146.3$), but not of β -diversity (PER = 2.87 ± 1.15 ;
251 INT = 2.56 ± 0.814). Regarding evenness (S_{PIE}) (Figure 3g-i), we denoted a higher dominance of few taxa in INT than
252 PER reaches at both local (PER: $\alpha = 6.32 \pm 3.96$; INT: $\alpha = 4.39 \pm 2.37$) and regional scale (PER: $\gamma = 15.2$; INT: $\gamma =$
253 6.99), as well as in terms of variation of dominant species (PER: $\beta = 3.48 \pm 2.32$; INT: $\beta = 2.04 \pm 1.03$). When
254 analysing the community dissimilarity, we observed that total β -diversity and its turnover and nestedness components
255 were significantly higher in PER than in INT sites (Table 2). In both groups, patterns of diatom community composition
256 were mainly explained by the turnover component of dissimilarity, while nestedness played a much minor role (Figure
257 4).

258 We then analysed whether the observed differences between the two hydrological categories could also be mirrored in
259 the taxonomic and functional composition of the diatom communities. Visual inspection of the PCoA ordination
260 performed on the taxonomic matrix (Figure 5a) depicted a clear difference in terms of taxonomic composition between
261 PER and INT reaches, which was confirmed by the PERMANOVA ($F_{1,143} = 4.67$, $P = 0.001$). Results of the test of
262 homogeneity for multivariate dispersion highlighted a significant homogenization of diatom communities in the INT
263 reaches in comparison to PER ones, in terms of species composition ($F_{1,143} = 15.5$, $P = 0.001$). When considering the
264 diatom functional matrix, the PCoA showed that communities characterizing the INT reaches were not only

265 functionally different from those found in PER sites but they could be considered a subgroup of those colonizing the
266 PER sites (Figure 5b). Results of the PERMANOVA and of the test of multivariate dispersion demonstrated that diatom
267 communities inhabiting INT sites were functionally different (PERMANOVA: $F_{1,143} = 7.94$, $P=0.001$) and more
268 homogeneous ($F_{1,143} = 9.70$, $P = 0.002$) than those in PER reaches.

269 When analysing the response of diatom functional metrics, we detected significant differences in terms of class size,
270 life-forms, ecological guilds and relative abundance of pioneer species among the two site categories (Table 2; Figure
271 6). When considering class size, we observed significant higher values in PER than INT sites, dropping from an average
272 value of $2.35 \mu\text{m}^3$ in PER sites to $2.16 \mu\text{m}^3$ in INT sites. Regarding life-forms, we observed significant higher relative
273 abundances of pad attached diatoms in PER than INT sites, as well as of colonial diatoms, mainly due to the higher
274 abundance of zig-zag and ribbon forming colonies in PER than INT sites. Contrarily, stalked taxa were significantly
275 more abundant in INT than PER sites. Focusing on ecological guilds, we found significant higher abundances of the
276 high profile guild in PER than INT sites, whereas the low profile guild was more abundant in INT than PER sites.
277 Finally, pioneer species were significantly more abundant in INT than PER sites.

278

279 4. DISCUSSION

280 Although hydrological intermittency is part of the natural hydrological cycle in many Mediterranean streams, the
281 indiscriminate use of the water resources coupled with global climate changes has been exacerbating this phenomenon
282 (Datry et al., 2017a). In addition, over the last decades, land use alterations and increased urbanization strongly
283 contributed to the physical disruption of the river habitat (Romano et al., 2017). Since from our analysis the two groups
284 of sites broadly overlapped in terms of water quality (see Figure 2), here we could highlight that the combined effect of
285 the flow intermittency and urbanization negatively affects diatom communities in Mediterranean streams, both in terms
286 of diversity and composition.

287 Indeed, when considering diatom community diversity, we observed a significant species loss (S) in intermittent
288 reaches, both at local and regional scales, in accordance with other studies (B-Béres et al. 2019; Stubbington et al.,
289 2017). In addition, by partitioning the effective species richness (S_n) and the evenness (S_{PIE}), we could demonstrate that
290 this phenomenon is due to both the reduction of species in the regional pool and by the increase in the relative
291 abundance of few dominant species. This may be due to the strong environmental filter generated by flow intermittency
292 that favours the dominance of few opportunistic taxa to the detriment of less competitive organisms (Richardson &

293 Sato, 2015; Várbró et al., 2020). This hypothesis is furtherly corroborated by the lower β -diversity observed in
294 intermittent than permanent reaches for both total richness (S) and evenness (S_{PIE}), which suggests that diatom
295 communities experiencing flow intermittency are more homogeneous than those found in perennial streams. In addition,
296 when analysing β -diversity as dissimilarity among communities we could show that diatom assemblages are more
297 similar among each other in intermittent than in permanent sites, due to a lower contribution of both turnover and
298 nestedness components.

299 Similar results were observed when analysing the community structure, as we observed significant differences between
300 permanent and intermittent reaches from both the taxonomic and functional point of view. In particular, we observed a
301 taxonomic and functional homogenization of diatom communities inhabiting the intermittent reaches, which appeared
302 simpler and less heterogeneous than those characterizing stations with permanent flow, confirming the results obtained
303 by B-Béres et al. (2019). In addition, diatom communities of intermittent reaches represented a subset of those located
304 upstream, similarly to what observed by Larned et al. (2010). Other biological groups, such as macroinvertebrates and
305 fish, showed similar responses as communities inhabiting sites experiencing prolonged fragmentation (e.g. intermittent
306 rivers) often represented a highly nested subsets of communities living in connected habitats (Datry et al., 2014; 2017c;
307 Miyazono and Taylor, 2015). This is in agreement with the *habitat templet theory* (Southwood 1977, 1988; Townsend
308 and Hildrew 1994), which states that strong environmental filters, such as flow intermittency, are expected to
309 differentially affect species from the regional pool by either favouring species that can tolerate drying conditions and/or
310 disfavoring species lacking resistance or resilience mechanisms to the disturbance (Wu et al., 2019). This selection
311 process is thus expected to favour particular traits (Webb et al. 2010; Luck et al. 2012) conferring resistance (i.e. set of
312 traits that enable organisms to survive during non-flow periods) and/or resilience (set of traits that enable organisms to
313 recolonize and recruit after non-flow events).

314 In this framework, the analysis of functional traits further corroborates this assumption, as we could demonstrate that
315 intermittent sites are characterized by higher percentages of small sized pioneer species, both features reflecting high
316 reproductive rates and conferring great resilience (Lange et al., 2016), confirming previous observations (B-Béres et al.,
317 2014, 2016; Stenger-Kovács et al., 2013). Conversely, permanent sites are inhabited mainly by higher percentage of
318 high profile taxa, characterized by bigger size and pad attached growth forms, reflecting a good environmental stability,
319 confirming the results of Várbró and colleagues (2020). In our research, permanent reaches favoured also the
320 establishment of colonial species, and in particular those forming zig-zag and ribbon colonies. This was indirectly in
321 accordance with Novais et al. (2020), who observed that most of the species characterizing Portuguese intermittent
322 rivers were solitary. Moreover, our result confirmed the conclusions reached by other researches stating that colonies

323 need a particularly stable environment to settle down and develop (Elias et al., 2014; Várбірó et al., 2020). Although we
324 observed higher abundances of stalked diatoms in intermittent sites, this life form has been usually classified as
325 sensitive to the hydrological variations (Elias et al., 2014, but see Sabater et al., 2017, who defined species belonging to
326 the genera *Cymbella* and *Gomphonema* as particularly resistant to drought). However, it should be noticed that the
327 group of the stalked diatoms is extremely heterogeneous and includes several different genera, such as those with
328 simple (i.e. *Achnanthydium* spp.) or arbuscular (i.e. *Gomphonema* spp. Or *Cymbella* spp.) stalks, characterized by
329 different sensitivity to physical disturbance. For instance, *Achnanthydium* is known to be one of the most resistant genus
330 to physical disturbance, due to its morphological features and the position occupied within the biofilm (i.e. the inner
331 layers) (Passy 2007). On the contrary, the arbuscular diatoms are secondary colonisers, which develop upon the basal
332 layers taking advantage of light but, at the same time, being more exposed to shear stress and hydrological variations
333 (Rimet and Bouchez, 2012). The great heterogeneity of this group likely explains the contrasting results observed in
334 literature when analysing the pattern of stalked diatoms in response of the hydrological variations. Another important
335 driver of stalked diatom pattern is the strong control that grazers exert on this growth form. It is already well known that
336 herbivory is an important factor regulating the biomass and community structure of benthic algae in streams (Stevenson
337 et al., 1996). It is also known that macroinvertebrate scrapers are generally favoured by rheophilous microhabitats with
338 coarse mineral substrates (Piano et al. 2019) and, at the same time, stalked diatoms are more subject to scrapers'
339 pressure than other growth forms (Holomuzuli et al, 2010). We can hypothesize that the adverse environmental
340 conditions found in intermittent reaches disfavoured the presence of macroinvertebrate scrapers (see Piano et al., 2019b
341 for an example in intermittent Alpine streams) and altered their grazing efficiency, indirectly favouring the development
342 of stalked diatoms. Therefore, although the trait-based approach, which reflects both dispersal capability and
343 environmental adaptability of the species, has been often invoked as a suitable and reliable tool for the hydrological
344 disturbance assessment (B-Béres et al., 2019; Wu et al., 2019; Novais et al., 2020; Várбірó et al., 2020), the response of
345 stalked diatoms to flow intermittency should be interpreted with caution in future work.

346 When comparing the response of diatom communities between Mediterranean and Alpine intermittent streams, results
347 are surprisingly different. In particular, in a previous study (Piano et al., 2019a) we observed that diatoms inhabiting
348 recently intermittent reaches were taxonomically and functionally comparable to the permanent sections located
349 upstream. Therefore, our results seem to contradict the *natural flow regime paradigm*, which states that the structure
350 and function of a lotic ecosystem, and the adaptation of its constituent aquatic species, are determined by the pattern of
351 temporal variation in river flows (Poff et al. 1997; Lytle and Poff 2004). This apparent contradictory result could be

352 explained in light of three main factors: i) the intensity of the flow intermittency; ii) the diatom community
353 composition; and iii) the combined effect of the land use.

354 From one hand, based on our experience (Falasco et al., 2016a,b; 2018a), water retreat is faster in the Mediterranean
355 area than in the Alpine regions, due to the higher air temperatures characterizing the Mediterranean summers and the
356 consequent higher evaporation rates. A slow and gradual water retreat allows biological communities to activate
357 resistance mechanisms to face the drought, such as producing resting forms (Souffreau et al., 2013) or simply moving
358 toward more suitable conditions (Falasco et al., 2016a; 2018a). In addition, a higher amount of humidity can be retained
359 by the biofilm, and organisms colonizing the lowest layers can survive (Sabater et al. 2016). Moreover, a slow water
360 retreat allows the creation of refugia (i.e. residual pools or hyporheic zone) where individuals can survive during harsh
361 conditions (Falasco et al., 2016b) and favouring the recolonization processes after water returns. Conversely, the fast
362 water retreat occurring in Mediterranean streams hampers the activation of resistance and resilience mechanisms. In
363 addition, drought lasts longer and the extension of dry reaches is higher in the Mediterranean than in the Alpine areas.

364 On the other hand, resilience mechanisms are likely influenced by both species composition during the pre-drought
365 event and the composition characterizing assemblages in the upstream sections which serve as source during the
366 recolonization process (Falasco et al., 2018b). When comparing the composition of diatom assemblages in Alpine and
367 Mediterranean rivers, we observed how low profile taxa dominates in the fast-flowing Alpine streams (around 75% in
368 the permanent sections sampled in Piano et al., 2019), while this same guild represents on average only 48% of the
369 communities in the permanent sites of the Mediterranean area. As it is already well known that species belonging to the
370 low profile guild possess a higher resilience than the others, we can suggest that communities dominated by low profile
371 species can easily recover compared to more heterogeneous other communities.

372 Third, it should also be noted that in the present study intermittent reaches are also highly urbanized compared to those
373 examined in the Alpine area. In fact, most of the intermittent reaches included in this research were located in the core
374 of urban contexts, particularly overexploited by tourists during summer, and they showed widespread habitat
375 modifications, with artificial banks and streambeds, a significant presence of weeds, no canopy coverage nor riparian
376 vegetation. All these features led to a further increase of river habitat fragmentation and connectivity loss in the
377 intermittent sections of the Mediterranean area, which likely exacerbate the effects of flow intermittency on diatom
378 communities.

379 **5. CONCLUSIONS**

380 By analysing multiple aspects of benthic diatom communities in permanent and intermittent reaches in Mediterranean
381 streams, here we demonstrated that the combined effects of the ongoing climate change and local environmental
382 pressures have been significantly altering diatom biodiversity in the last 11 years. The results we obtained could be
383 ascribed to the long-term effects of drying in Mediterranean streams and, as first in the literature, we highlight that
384 diatoms are able to provide long-term responses to environmental changes caused by water stress, when disturbance is
385 persistent. Indeed, diatoms are usually considered useful indicators to short-time stresses (i.e. a couple of weeks)
386 probably due to their short life cycles (Karaouzas et al., 2018). Although Mediterranean benthic communities are
387 naturally exposed to intermittency and showed a certain degree of adaptation to drying, our results highlighted that
388 these communities should be still considered fragile and threatened, especially in a global climate change scenario
389 exacerbated by local anthropogenic disturbance (Smeti et al., 2019). In addition, when considering the trophic food
390 web, the alteration of diatom communities in intermittent reaches could affect the river autotrophic processes, leading to
391 a decrease of primary production and diatom chlorophyll a (Piano et al., 2017b). Hydrological intermittency could
392 promote river heterotrophy and alter the fatty acid composition of the biofilm thus reducing grazing efficiency of the
393 macroinvertebrate scrapers, hence their ecological niche (Piano et al., 2019). In this framework, it is mandatory to
394 deepen our knowledge on the potential effects of droughts on river biological communities and, at the same time, to
395 improve and adapt biological indices to assess the water quality of intermittent rivers.

396

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403 **CONFLICT OF INTEREST**

404 The authors declare no conflict of interests.

405 **Data sharing and data accessibility**

406 The data that support the findings of this study are available from the corresponding author upon reasonable request.

407

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642 **CAPTIONS**

643 Table 1 – Average values (\pm SD) of water quality, land use and climatic data in PER and INT sites and results of the
644 two-sample t-tests. Significant results are reported in bold.

645 Table 2 - Average values (\pm SD) of the β -diversity components and functional traits in PER and INT sites and results of
646 the two-sample t-tests. Significant results are reported in bold.

647 Figure 1- Map of the sampling sites located in Liguria (NW-Italy). PER = orange circles; INT = light blue squares.

648 Figure 2 - results of the PCA performed on: (a.) water quality parameters; (b.) land use coverage measured at each
649 sampling site; and (c.) climatic variables —annual and summer average precipitation amount, minimum and maximum
650 air temperatures. Points represent each single sample while arrows represent the loadings of each environmental
651 variable included in the analysis. Ellipses represent standard deviations around the centroids of the two groups (PER =
652 orange circles; INT = light blue squares).

653 Figure 3 - Partitioning of species richness (S , first row), rarefied species richness (S_n , second row) and evenness (S_{PIE} ,
654 third row) into local diversity (α -diversity, left panel), variation among local communities (β -diversity, central panel)
655 and total diversity at the regional scale (γ -diversity, right panel). P-values above each graph depict the significance of
656 differences between PER (orange) and INT (light blue) reaches.

657 Figure 4 - Partitioning of total β -diversity into its nestedness (dark grey) and turnover (light grey) components in PER
658 and INT reaches.

659 Figure 5 - Ordination of the taxonomic (left panel) and functional (right panel) dissimilarity matrices according to the
660 first two PCoA axes (Orange circles = PER sites; light blue squares = INT sites). Ellipses represent standard deviations
661 around the centroids of the two groups.

662 Figure 6 - Boxplots representing differences in diatom functional traits between PER (orange) and INT (light blue)
663 sites.

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Table 1

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	Variables	PER	INT	Two-sample t-test
Water quality data	N-NH ₃ (mg L ⁻¹)	0.050 (±0.078)	0.037 (±0.054)	$t = 1.05; P = 0.295$
	N-NO ₃ (mg L ⁻¹)	0.460 (±0.502)	0.737 (±0.384)	$t = -3.81; P < 0.001$
	Ptot (mg L ⁻¹)	0.074 (±0.092)	0.042 (±0.043)	$t = 2.68; P = 0.008$
	Cond (µS cm ⁻¹)	322 (±119)	345 (±107)	$t = -1.24; P = 0.215$
	DO (%)	102 (±12.0)	105 (±12.1)	$t = -1.43; P = 0.154$
	pH	8.26 (±0.310)	8.27 (±0.396)	$t = -2.55; P = 0.012$
	Temp (°C)	15.4 (±3.16)	17.1 (±4.48)	$t = -0.145; P = 0.885$
Surrounding land use (%)	Urban areas	21.2 (±18.0)	48.3 (±25.3)	$t = -7.41; P < 0.001$
	Agricultural areas	27.1 (±15.3)	23.7 (±22.8)	$t = 1.047; P = 0.287$
	Woods	35.4 (±25.3)	11.8 (±14.4)	$t = 6.89; P < 0.001$
	Open areas	4.81 (±7.91)	3.18 (±5.87)	$t = 1.42; P = 0.159$
	Water bodies	11.5 (±7.08)	13.0 (±7.69)	$t = -1.25; P = 0.212$
Climatic variables	year_prec (mm)	78.8 (±24.5)	71.0 (±13.4)	$t = 2.39; P = 0.019$
	year_tmax (°C)	17.7 (±1.27)	19.4 (±0.55)	$t = -10.2; P < 0.001$
	year_tmin (°C)	9.93 (±1.99)	12.6 (±1.34)	$t = -9.66; P < 0.001$
	summer_prec (mm)	41.7 (±15.4)	33.0 (±9.58)	$t = 4.11; P < 0.001$
	summer_tmax (°C)	26.8 (±1.10)	27.7 (±0.46)	$t = -5.69; P < 0.001$
	summer_tmin (°C)	17.7 (±2.08)	20.0 (±1.29)	$t = -8.19; P < 0.001$

Table 2

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	Component	PER	INT
	β_{tot}	0.77 (\pm 0.15)	0.66 (\pm 0.18)
	β_{repl}	0.70 (\pm 0.17)	0.62 (\pm 0.19)
	β_{rich}	0.07 (\pm 0.08)	0.04 (\pm 0.06)
	Trait	PER	INT
	Size class	2.35 (\pm 0.56)	2.16 (\pm 0.59)
	Pioneer	0.19 (\pm 0.17)	0.36 (\pm 0.22)
GROWTH FORMS	Adnate	0.09 (\pm 0.11)	0.12 (\pm 0.17)
	Pad	0.17 (\pm 0.18)	0.08 (\pm 0.10)
	Stalk	0.41 (\pm 0.27)	0.50 (\pm 0.23)
	Colonial	0.20 (\pm 0.17)	0.12 (\pm 0.11)
	Mucous	0.04 (\pm 0.07)	0.04 (\pm 0.06)
	Filament	0.004 (\pm 0.01)	0.002 (\pm 0.01)
	Zig-zag	0.06 (\pm 0.12)	0.03 (\pm 0.06)
	Rosette	0.006 (\pm 0.013)	0.006 (\pm 0.012)
	Ribon	0.08 (\pm 0.14)	0.03 (\pm 0.07)
	Arbuscular	0.006 (\pm 0.008)	0.008 (\pm 0.015)
	ECOLOGICAL GUILDS	High profile	0.22 (\pm 0.18)
Low profile		0.47 (\pm 0.28)	0.57 (\pm 0.24)
Motile		0.28 (\pm 0.25)	0.28 (\pm 0.23)
Planktonic		0.02 (\pm 0.07)	0.01 (\pm 0.01)

Figure 1
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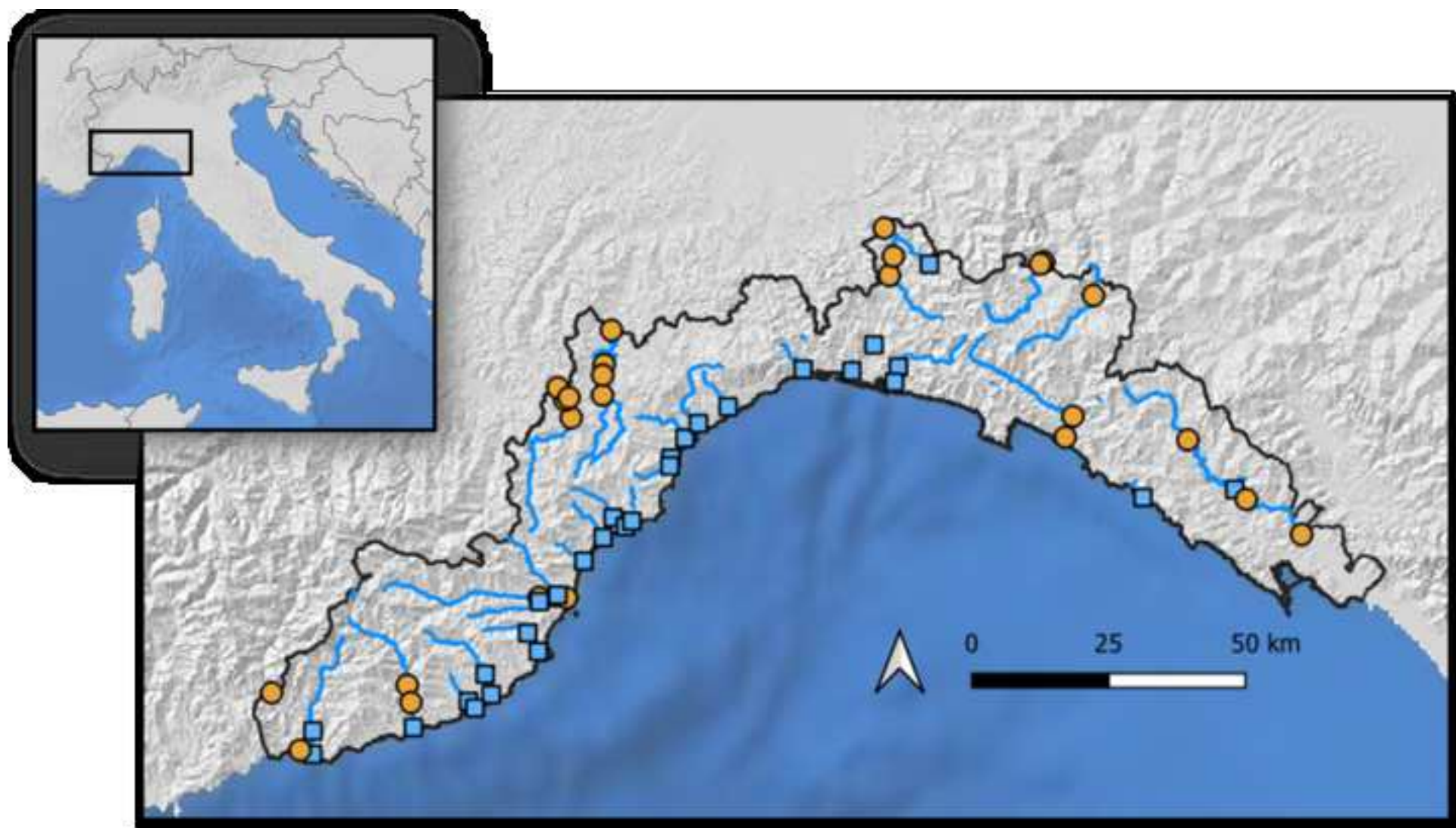


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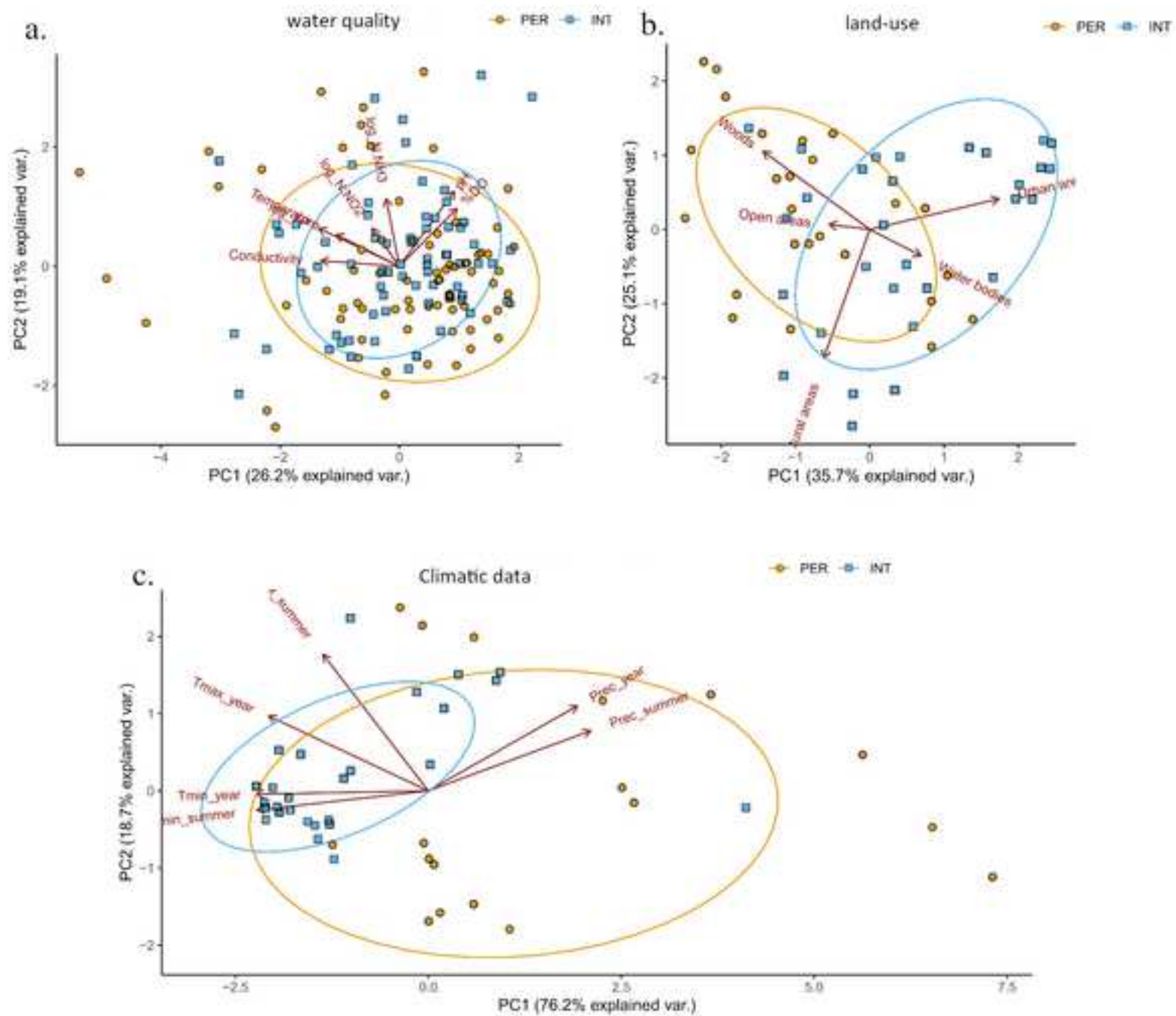


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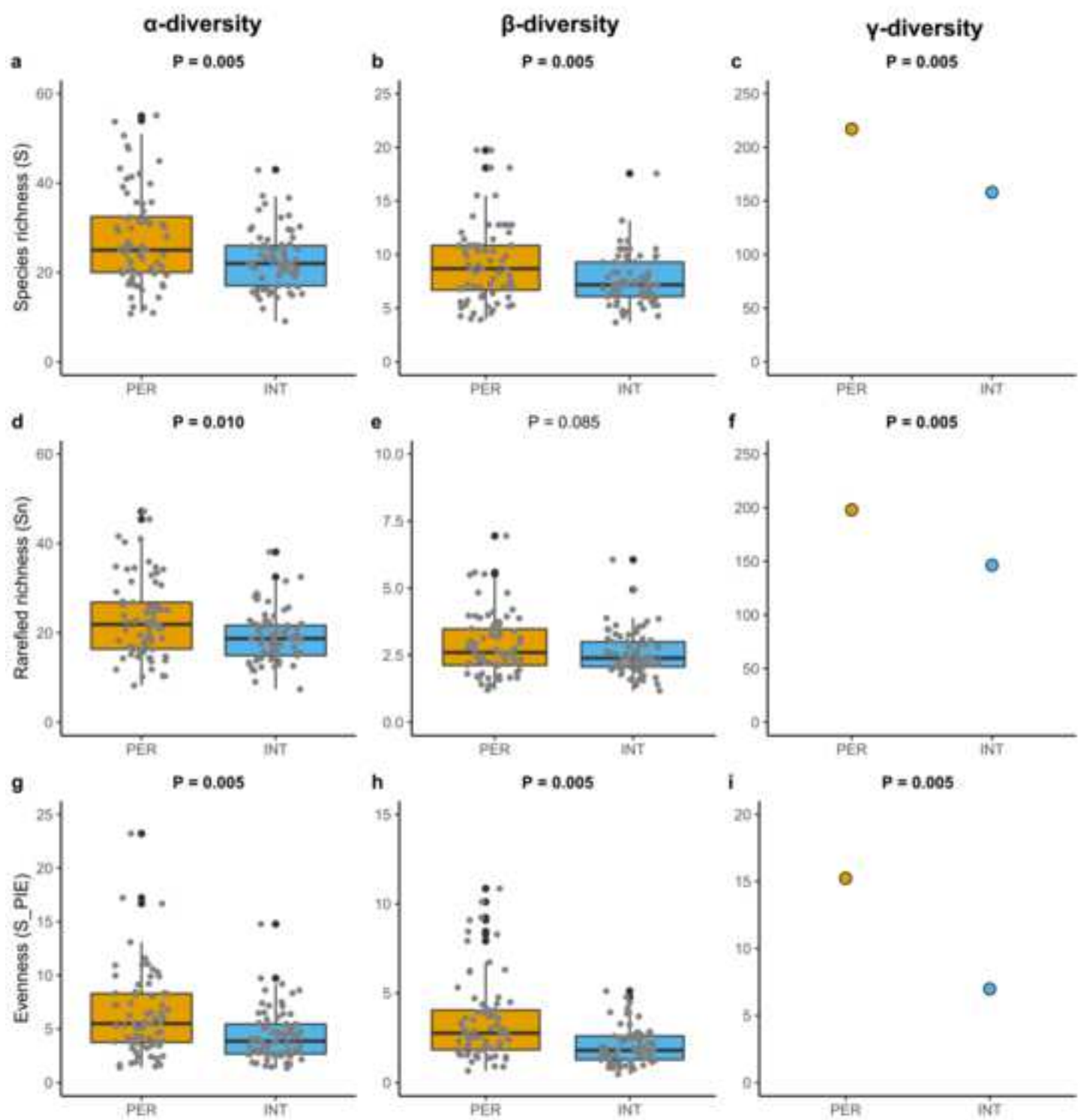


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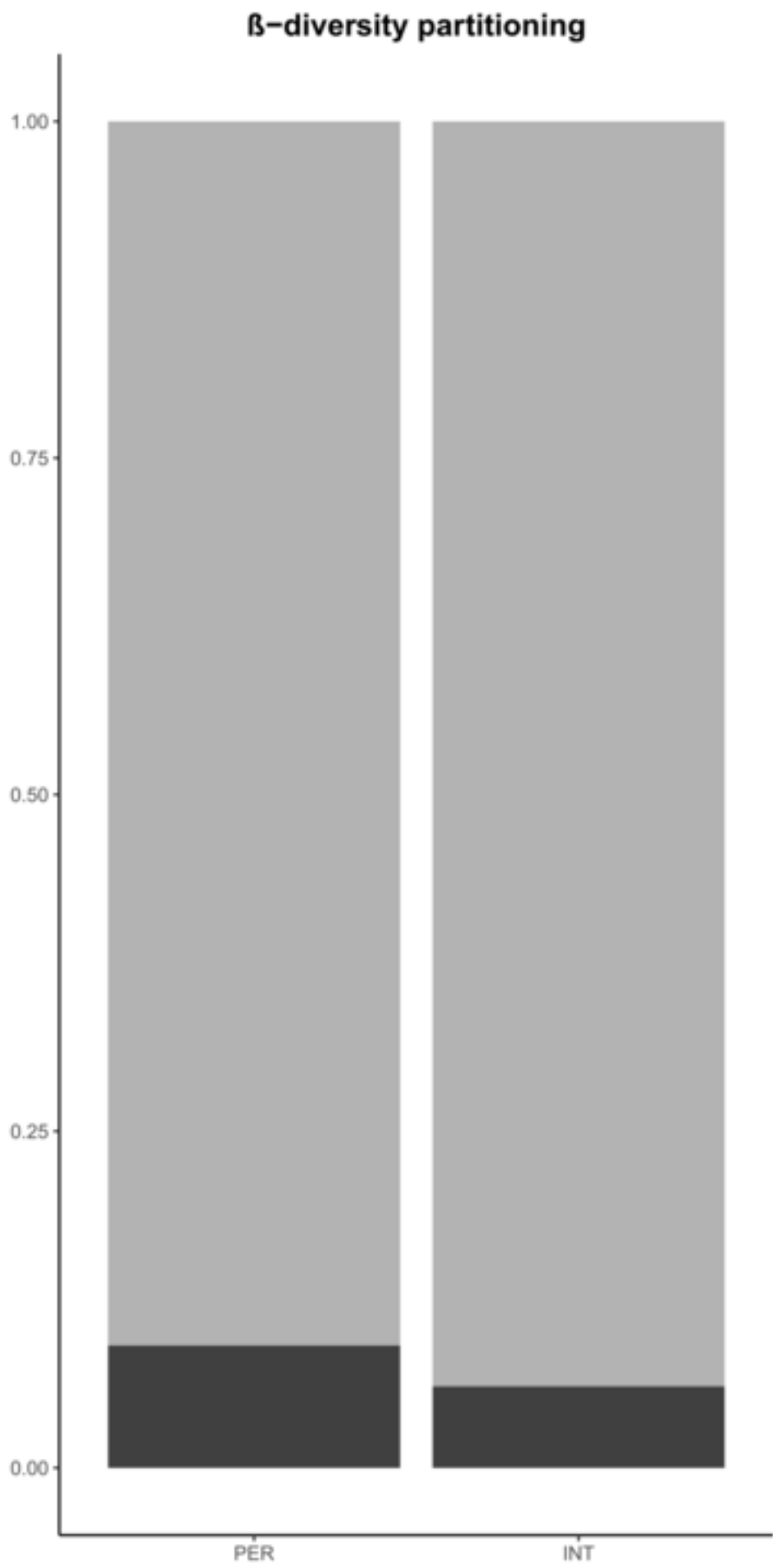


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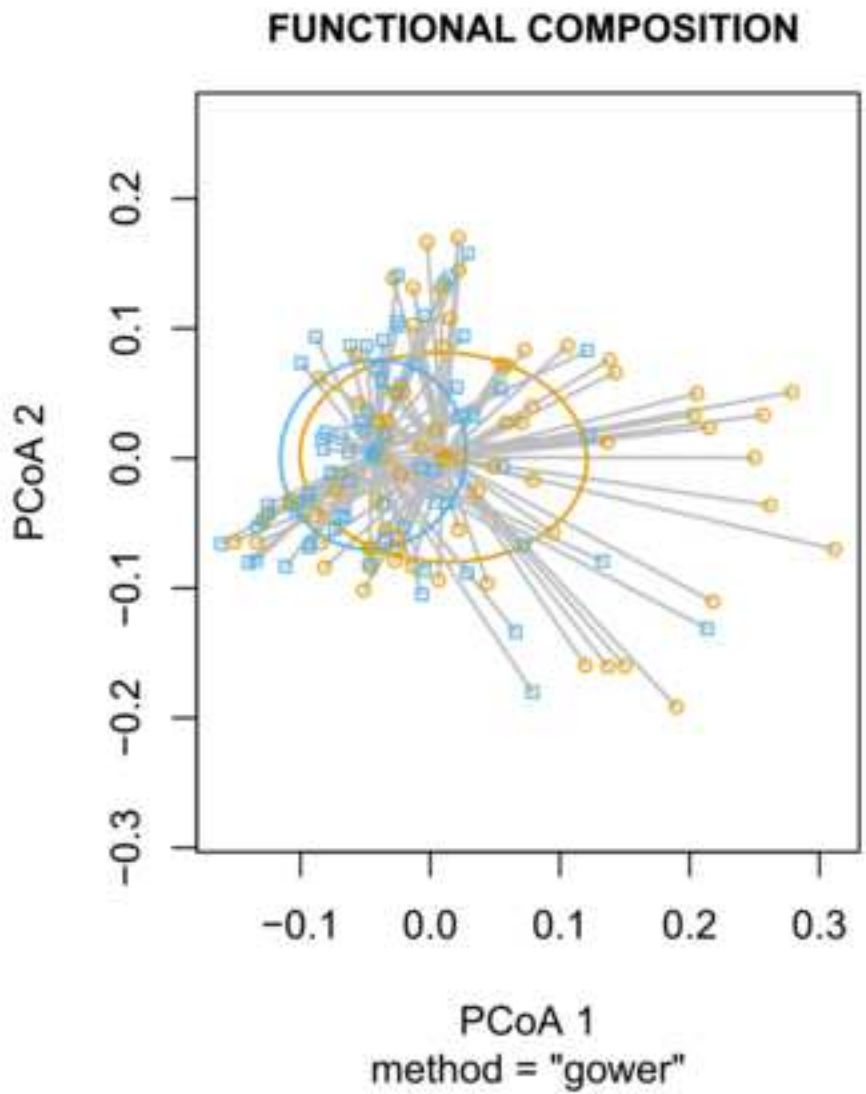
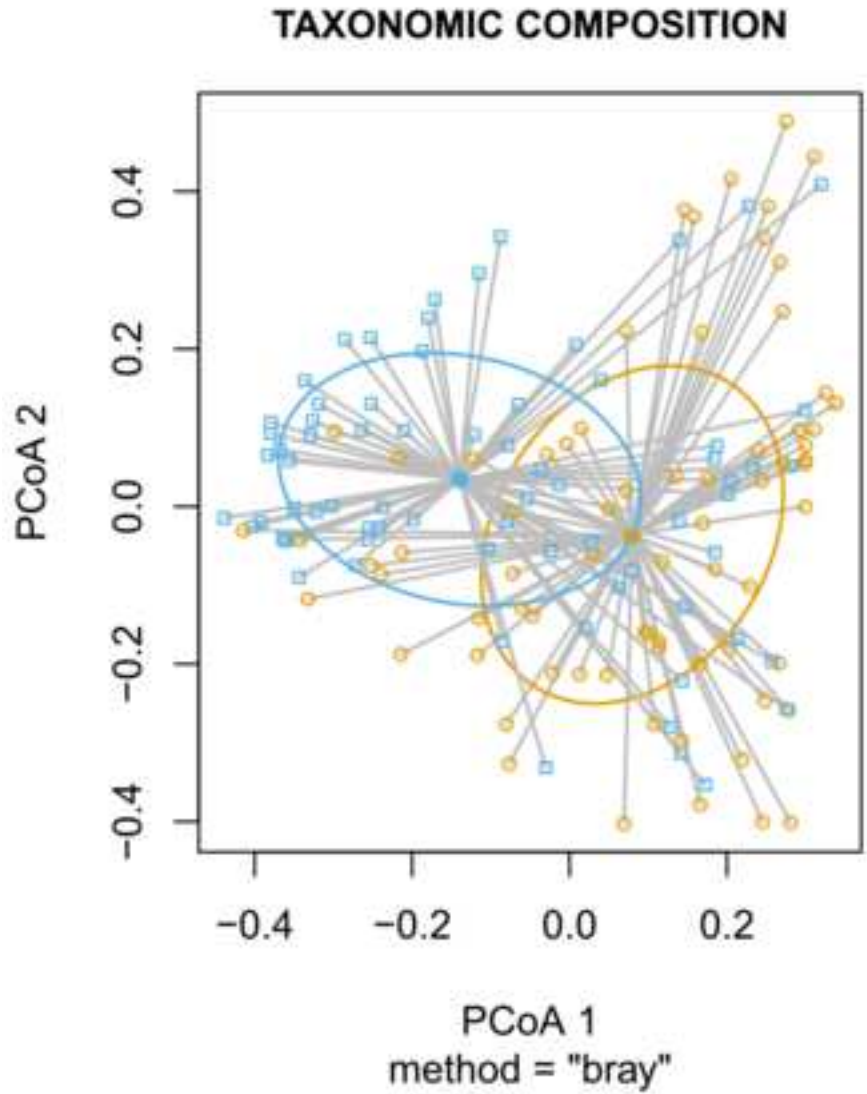
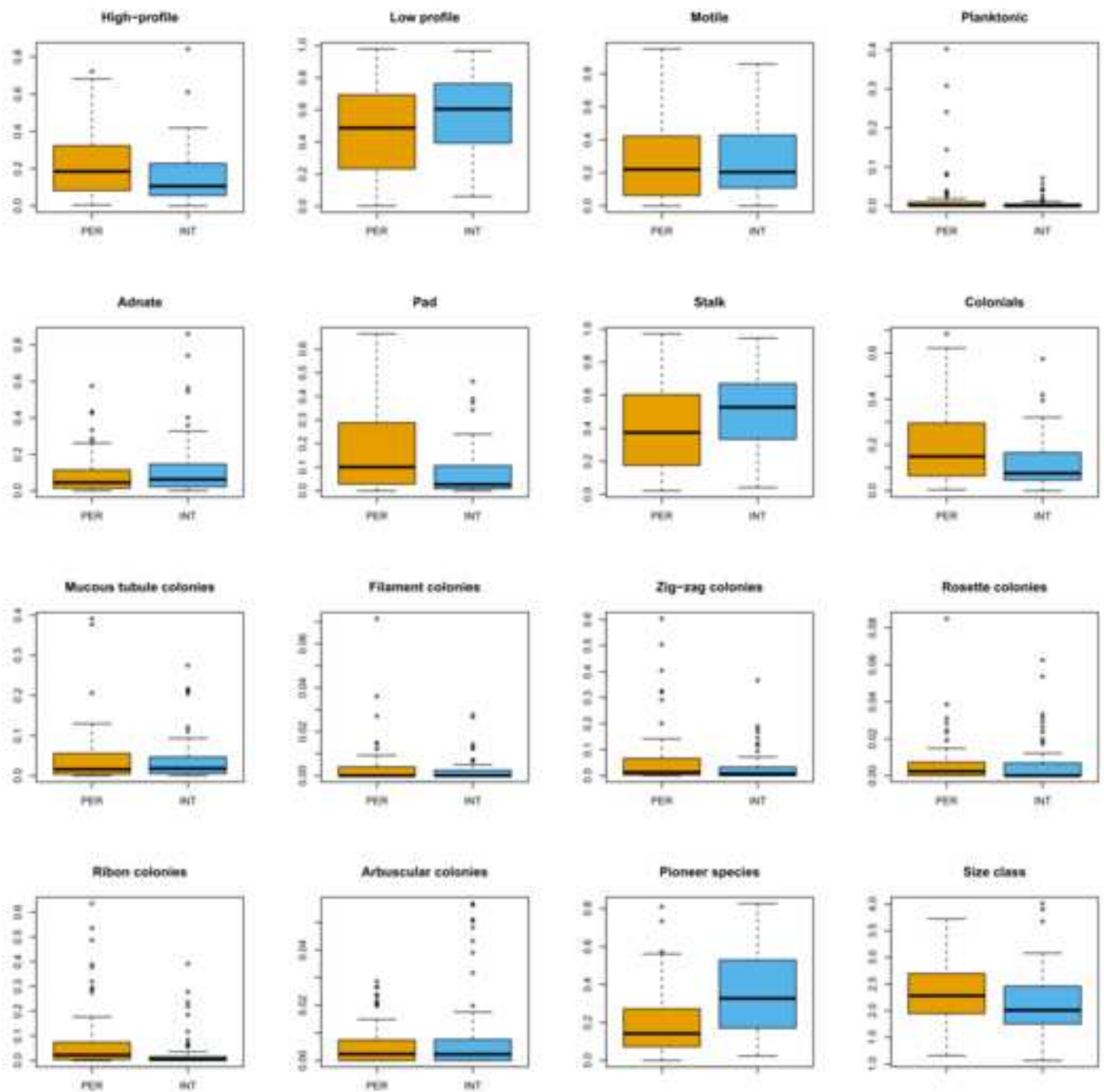


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The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: