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1 **Biotic and abiotic drivers of aquatic plant communities in shallow pools and wallows on**
2 **the sub-Antarctic Iles Kerguelen**

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11

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23

24 **Author contributions statement**

25 AKB, FMB, LS, DR, and CS conceived and designed research. AKB and PD collected the
26 data. FV performed the chemical analyses of the samples. AKB, PED, and SD analysed data.
27 All authors contributed to the writing and approved the manuscript.

28 **Abstract**

29 In the sub-Antarctic region, climate change is particularly rapid, while their freshwater
30 ecosystems, such as ponds, host plant species with limited spatial distributions. These
31 particular systems and their plant communities remain however poorly known and the context
32 of their changing habitat calls for deeper insights into these systems. We performed an
33 extensive survey of 45 ponds over three locations of the Iles Kerguelen during the winter and
34 summer seasons of two years, which included the measurement of 12 abiotic parameters and
35 the assessment of the plant community composition. Overall, our results showed that Iles
36 Kerguelen ponds are shallow freshwater ecosystems harboring species-poor plant
37 communities with high evenness, of which structure did not vary among the sampled
38 locations. Three different habitats were identified among ponds in relation with nutrient
39 supply by marine animals, which ultimately influenced plant community structure and cover.
40 We highlight that these habitats are mostly determined by water depth, nutrients, and
41 temperature (mean and variance). Present plant community composition was more strongly
42 correlated with plant community composition in the previous year than with abiotic
43 conditions. Overall, this study provides new knowledge on the aquatic plant communities and
44 the functioning of Iles Kerguelen freshwater ecosystems, which can serve as a basis for future
45 studies dealing with the impact of climate change in the sub-Antarctic region.

46

47 **Keywords**

48 Aquatic plants; Ponds; Seasonality; Plant community structure; Habitat; Spatio-temporal
49 variability.

50 **Introduction**

51 There is now ample evidence that climate change affects a broad range of organisms (see e.g.
52 [Walther et al. 2002](#)), with severe effects for plant species in freshwater habitats ([Lacoul and](#)
53 [Freedman 2006](#)). In polar regions, including the sub-Antarctic region, climate change is
54 particularly rapid ([Lebouvier et al. 2011](#); [Leihy et al. 2018](#)), calling for deeper insights into
55 sub-Antarctic ecosystems, characterized by species with restricted spatial distributions ([Frenot](#)
56 [et al. 2001](#); [van der Putten et al. 2010](#); [Chau et al. 2021](#)). This seems especially true for
57 freshwater ecosystems harboring aquatic plant species. Indeed, to our knowledge, their
58 ecology remains poorly known, probably because of technical difficulties associated with
59 sampling in harsh climatic conditions and remote locations.

60 Freshwater ecosystems of the sub-Antarctic region include numerous rivers and lakes,
61 but aquatic plants preferentially colonize shallow and lentic systems of small sizes, *i.e.* ponds
62 ([Hennion et al. 1994](#)) including elephant seal wallows. So far, most works dealing with sub-
63 Antarctic aquatic plants have focused on their morphological ([Hennion et al. 1994](#); [Hennion](#)
64 [and Walton 1997](#)) and genetic variations ([Siljak-Yakovlev et al. 2020](#); [Chau et al. 2021](#)),
65 while no study has considered community assembly mechanisms. Nevertheless, two main
66 processes, dispersal and environmental filtering, often play key influences on plant
67 community assembly through space and/or time ([Vellend 2010](#)). Yet, the actual influence of
68 these processes in sub-Antarctic ponds has never been tested. Dispersal and environmental
69 filtering in sub-Antarctic ecosystems should be strongly modulated by the specific traits of
70 aquatic plants, and by the harsh environmental conditions encountered by the species.
71 Dispersal in the sub-Antarctic aquatic plant species appears limited, as they do not display
72 specific adaptations to zoochory, and seem alternatively prone to hydrochory ([Hennion and](#)
73 [Walton 1997](#)). Dispersal limitation usually results in spatial differentiation in plant
74 communities. Specificities of climate and ecosystem functioning in the sub-Antarctic region

75 suggest that temporal (*i.e.* seasonal) variations in abiotic parameters may differ from what is
76 usually observed in regions and habitats from lower latitudes (Smith 1985). In particular,
77 Hennion et al. (1994) reported that alternating periods of evaporation and heavy precipitation
78 (seasonality) resulted in frequent and sometimes drastic fluctuations in the water depth of
79 ponds of the sub-Antarctic Iles Kerguelen. It is thus likely that these seasonal variations of the
80 pond habitat characteristics ultimately result in temporal modifications of the plant
81 community composition.

82 Seasonal variations of water depth should therefore shape pond habitat *per se* or by
83 modulating other physical and chemical parameters (Lacoul and Freedman 2006). Ponds are
84 small water bodies, and as such, their physical and chemical characteristics would highly
85 differ from larger sub-Antarctic water bodies, such as lakes (see e.g. Camacho 2006; Saunders
86 et al. 2008). Changes in water temperature, which are linked to pond size (Bornette and
87 Puijalon 2011), should be especially critical in the rapidly warming sub-Antarctic region
88 (Lebouvier et al. 2011). Water temperature influences not only plant metabolism (Bornette
89 and Puijalon 2011) but also microbial processes involved in nutrient cycling (MacKay et al.
90 2009; Biddanda 2017; Velthuis et al. 2017), as well as the concentrations of dissolved gasses
91 (Bornette and Puijalon 2011). Additionally, ponds are enriched by nutrients conveyed by
92 marine animals, with these enrichments being temporarily variable depending on animal
93 migrations (Smith and Froneman 2008). Characterizing water depth, water temperature, and
94 nutrient availability within these freshwater ecosystems is thus crucial to improve our
95 understanding of the drivers of the assembly of aquatic plant community through time.

96 The current lack of knowledge on the sub-Antarctic aquatic biodiversity combined
97 with recent works demonstrating that sub-Antarctic plants are already strongly affected by
98 climate change (Le Roux et al. 2005; Frenot et al. 2006; Le Roux and McGeoch 2008;
99 Bergstrom et al. 2015) call for scrutinizing how variations in abiotic and biotic characteristics

100 of ponds drive plant community assembly. Indeed, there is now ample evidence of climate
101 change across the sub-Antarctic region. In the Iles Kerguelen and Marion Island, temperatures
102 have increased while annual precipitation is strongly reduced (Lebouvier et al. 2011;
103 McClelland et al. 2018). In Macquarie Island, however, summers and winters become
104 respectively drier and wetter (Bergstrom et al. 2015). Given that under harsh environmental
105 conditions, the abiotic filter is known to be a strong driver of plant community composition,
106 in particular within sub-Antarctic terrestrial ecosystems (Bazzichetto et al. 2021; Momberg et
107 al. 2021), it is critically important to characterize and monitor the main abiotic parameters that
108 are known to affect the physiological status, and thus survival, of aquatic plants like
109 *Ranunculus* species (Hennion et al. 2012; Labarrere et al. 2019).

110 A preliminary large field prospection performed during the Austral summer 2017,
111 together with the existing literature (Hennion et al. 1994), indicated that the ponds located
112 along the shore are the main habitat for aquatic plant species at the Iles Kerguelen. Thus, in
113 this study, we surveyed the aquatic plant communities of 45 ponds over three locations across
114 the shore of the main island of the Iles Kerguelen over two years. We expected that (i) pond
115 plant communities should vary both through time (season, year) and space (location) in the
116 Iles Kerguelen because of the stochastic impacts of marine animals on nutrient dynamics in
117 ponds, and the low dispersal ability of aquatic plant species, reducing potential community
118 homogenization among ponds; (ii) water depth, water temperature, and nutrient availability
119 should be major parameters characterizing ponds habitat; and (iii) under the harsh climatic
120 conditions of the archipelago, abiotic characteristics of ponds should prevail over biotic ones
121 (past plant community composition), in determining the present plant community
122 composition.

123

124 **Materials and methods**

125 *Study area*

126 This study was conducted on the main island of the Kerguelen archipelago (hereafter referred
127 to as ‘Kerguelen’) located in the sub-Antarctic region (South Indian Ocean) (48°30’00” to
128 50°00’00” S, 68°27’00” to 70°35’00” E). The climate is characterized by cool temperatures
129 (annual mean of 4.6 °C with little variation over the year, from 2.1 °C to 7.7 °C) (Frenot et al.
130 2001, 2006; Lebouvier and Frenot 2007), and low to abundant precipitations *i.e.* ranging from
131 500 mm to 3200 mm per year along an East-West gradient (Frenot et al. 1998). However,
132 Kerguelen currently experiences rapid climate change with increasing mean and variability of
133 temperatures, and strongly reduced precipitation (Lebouvier et al. 2011). Overall, this leads to
134 harsh environmental conditions for species adapted to cold and stable temperatures.

135 We focused on the shallow freshwater ponds located near the eastern shoreline,
136 including elephant seal wallows. These ponds are supplied with water largely by rainfall, and
137 with nutrient inputs from marine animal (mostly elephant seals and birds) (Smith and
138 Froneman 2008). These specific habitat conditions are comparable to those found in Spit Bay
139 seal wallows of Heard Island (Bergstrom and Selkirk 2000).

140 Overall, the Kerguelen are characterized by a low species richness, hosting 22 native
141 Angiosperms only (van der Putten et al. 2010). Based on the literature (Schotsman 1961;
142 Lourteig 1952, 1964; Hennion and Couderc 1992; Hennion et al. 1994), six perennial plant
143 species were expected to occur in the ponds, although aquatic plant communities of the
144 Kerguelen have never been thoroughly described so far. These six aquatic plant species were:
145 *Limosella australis* R.Br. (Scrophulariaceae), *Callitriche antarctica* Engelm (Plantaginaceae),
146 *Juncus scheuchzerioides* Gaudich. (Juncaceae), and three species of Ranunculaceae:
147 *Ranunculus biternatus* Smith, *R. pseudotrullifolius* Skotts., and *R. moseleyi* Hook.f.
148 Individuals of these six species are able to horizontally propagate through clonal growth (van
149 Groenendael et al. 1996). Due to water depth fluctuations, we also anticipated that additional

150 non-aquatic plant species (*i.e.* species that usually colonize terrestrial habitat) would colonize
151 ponds from their edges.

152

153 *Field survey*

154 Sampling was conducted from the Austral summer 2018 to the Austral summer 2020, at three
155 locations on the main island of the Kerguelen archipelago. The locations were distributed
156 along the sea shore at low altitudes, and described a West-East gradient: Molloy, Isthme Bas,
157 and Cap Ratmanoff (Table 1, Fig. S1). Location flatness and proximity to the sea shore allows
158 the presence of sea animals. At each location, fifteen ponds were randomly selected to
159 describe a gradient of pond size (Table 1, Fig. S2). Size was variable among ponds but also
160 within ponds, due to important fluctuations of water depth (Hennion et al. 1994). GPS
161 coordinates (precision of 1 m) of pond positions were recorded at each location. These
162 positions were then used in GIS (QGIS 3.20.3) to calculate the distances between ponds and
163 the sea shore as a proxy for the frequency of visitation by marine animals.

164 Within each pond and at each sampling date, we randomly positioned three to five 1
165 m²-quadrats to measure a range of biotic and abiotic parameters. The number of quadrats
166 depended on the pond size: five quadrats were realized for ponds whose surface was >5m²,
167 while three to four quadrats were used for ponds <5m². At each sampling date, quadrat
168 positions and size allowed to sample both ponds' edges and centers. To characterize the
169 composition of pond plant communities, the abundance (*i.e.* percentage of quadrat surface
170 covered) of the different species, and of bare soil, were estimated for each quadrat. All these
171 abundances were recorded twice a year, once in November, and another time in May, which
172 correspond to the beginning and to the end of the vegetation growth season, respectively. This
173 growing season (November-April) will hereafter be referred as to summer, while the rest of
174 the year (May-October) will corresponds to winter (Bergstrom et al. 2015). In addition,

175 physical and chemical parameters were measured every three months, in November,
176 February, May, and August over the two consecutive years of the study. Within each quadrat,
177 we measured the mean water depth (based on three measurements), pH, specific conductance,
178 and mean dissolved oxygen concentration (calculated from three measurements performed
179 near the surface, in the middle of the water column, and at the bottom of the pond; HQ20,
180 HACH_{TM}, Dusseldorf, Germany). At each pond, one 30 mL-water sample, and one 50 mL-
181 sediment sample were also collected for further nutrient analyses in the lab. For these two
182 samples, water and sediments were collected from several points within the pond to account
183 for possible heterogeneity in nutrient distribution.

184

185 *Nutrient analyses*

186 After collection, water and sediment samples were stored at 6 °C and brought within 24h to
187 the laboratory. Water samples were further filtered through Whatman GF/F filters (pore size:
188 0.7µm, Cytiva, Amersham, United Kingdom). All samples (water and sediments) were then
189 stored at -20 °C for several weeks before chemical analyses. N-NH₄⁺, N-NO₃⁻ and P-PO₄³⁻
190 concentrations were determined based on standard colorimetric methods ([Grasshoff et al.](#)
191 [1983](#)) using a sequential analyzer (SmartChem200, AMS Alliance, Frépillon, France).

192 Nitrogen and organic carbon concentrations in sediments were measured following the
193 “capsule” method ([Brodie et al. 2011](#)). Specifically, an amount of five mg (± 10%) of
194 homogeneous sediment was acidified with 2M HCl in silver capsules to eliminate carbonates.
195 Liquids were then evaporated on a 65 °C hot plate for 12 hours, before the entire drying out of
196 capsules at 80 °C for a few days. Carbon and nitrogen analyses were then performed using an
197 elementary analyzer (FlashEA 1112 NC Analyzers®, Thermo Fisher Scientific, Waltham,
198 Massachusetts, USA). Following [Ni et al. \(2016\)](#), available organic phosphorus was extracted
199 from 50 mg of dry sediment samples with 5 ml of NaOH (1 M). After extraction during 16

200 hours on a rotatory shaker at room temperature, the supernatant was collected, and its pH was
201 stabilized at 7 with addition of HCl (4 M). The extracted P that has been converted into
202 orthophosphate was quantified using the molybdate/ascorbic acid blue method (Murphy and
203 Riley 1962), and results were reported in mg of available P (phosphorus available to plant
204 growth) per g of dry sediment.

205

206 *Water temperature simulation*

207 Water temperature was recorded every half hour (HOBO Pendant MX2202, ONSET™, Cape
208 Cod, Massachusetts, USA) from September 2020 to October 2021, in the middle of the water
209 column of each pond. We performed linear regression analyses to determine the relationship
210 between water temperature within each pond and air temperature recorded at the
211 meteorological station of the Kerguelen (Météo France 2020-2021 records, Port-aux-
212 Français), after confirming normality of the distribution of model residuals. All relationships
213 between air and water temperatures were significant ($R^2 \geq 0.55$; $P < 0.05$), with the exception
214 of two ponds. These relationships were then used to infer water temperature occurring during
215 the whole study period (summer 2018-2020) based on Météo France 2018-2020 records.

216 From these estimated data, we calculated the mean and the variance (square of
217 standard deviation) of daily water temperatures over a period of three months *i.e.* between two
218 dates separating other abiotic parameters measurements.

219

220 *Data analyses*

221 Before statistical analyses, abiotic parameters and plant species abundances recorded from
222 different quadrats per pond were averaged for each sampling date. We used plant species
223 abundances to calculate their relative frequencies *i.e.* proportion of vegetation cover occupied
224 by the species. Species richness, Shannon diversity, and evenness (Pielou index) of plant

225 community were calculated using the *vegan* R package (Oksanen et al. 2016). Pairwise
226 correlations between these indexes were tested using non-parametric Spearman's rank
227 correlation tests. Species richness and evenness were not correlated while Shannon diversity
228 was strongly correlated with the two other indexes ($r > 0.75$, and $P < 0.05$). We therefore
229 removed Shannon diversity from subsequent analyses.

230 We tested the effects of year, season, and location (Molloy, Isthme Bas, and Cap
231 Ratmanoff) on the two community indexes using general mixed-effect models with pond as
232 random factor (Bolker et al. 2009). Richness index was square-rooted to satisfy normal
233 distribution of residuals. The statistical significance of the fixed factors and their interactions
234 was determined through type II ANOVA. Calculation of marginal and conditional R^2
235 associated to the model was performed with the *performance* R package (Nakagawa et al.
236 2017).

237 We further used Between-Classes Principal Component Analysis (BCA-PCA;
238 Dolédec and Chessel 1987) as implemented in the *ade4* R package (Dray et al. 2007;
239 Thioulouse et al. 2018) to quantify the amount of variance delivered by time (season, year)
240 and space (location, pond) and explaining plant community composition (*i.e.* relative
241 frequencies of plant species in each pond at each sampling date). BCA-PCA belongs to the
242 constrained analysis techniques (ter Braak and Verdonschot 1995) and is a particular case of
243 PCA in which the sample grouping (e.g. in time or space) is accounted for in the analysis. The
244 index characterizing the effect of time (or space) is quantified by between-class variance,
245 which represents the ratio of the amount of variance explained by the sample grouping and the
246 total variance among samples. Between-class variance was tested against simulated values
247 obtained after 9,999 permutations of the rows of the plant species composition tables and
248 allowed to assess the significance of the effects of year, season, location, and pond on plant
249 community composition.

250 To characterize the habitat of plant species, we performed Principal Component
251 Analysis (PCA) on the pond abiotic parameters using the *FactoMineR* R package (Lê et al.
252 2008), followed by Hierarchical Clustering on PCA scores (Ward method based on Euclidean
253 distances) to discriminate pond clusters based on abiotic parameters. The mean of each abiotic
254 parameter was then compared between clusters through ANOVA tests based on general linear
255 models, and significant differences between clusters were assessed through Tukey HSD *post-*
256 *hoc* tests ($P < 0.05$). A similar procedure was applied to determine the relationships between
257 clusters and (i) the plant community indexes, and (ii) the total vegetation cover within the
258 pond. The parameter values were log or arctan transformed when necessary, to satisfy the
259 assumption of the normal distribution of residuals.

260 To investigate the relationships between plant community composition and abiotic
261 parameters across seasons, we used the STATICO method (Simier et al. 1999; Thioulouse et
262 al. 2004). The method has been shown to be useful to investigate the temporal dynamics of
263 the relationship between environment and diatoms (Mendes et al. 2009), Copepods (Marques
264 et al. 2011), and macroinvertebrate assemblages (Shieh and Chi, 2010). This method allows
265 the simultaneous analysis of several pairs of tables in one run. In our case, we had four tables
266 *i.e.* two seasons (for each season, we averaged the measurements of two dates) across two
267 years, from summer 2018 to winter 2020 (see Fig. S3). This multivariate method combines
268 the potential of (i) co-inertia analysis that allows matching two tables providing a new table
269 (cross-covariance table), which describes the covariance between each environmental variable
270 and each plant species (Dolédec and Chessel 1994; Dray et al. 2003), and (ii) partial triadic
271 analysis allowing the simultaneous analysis of several tables in one run with the aim of
272 depicting their similarity (Thioulouse and Chessel 1987), *i.e.* in our case, across seasons and
273 years. In practice, the first step (co-inertia analysis) crossed the two tables (*i.e.* the physical
274 and chemical parameters and the plant community composition) associated to each season of

275 each year. This step ended up with the production of four cross-covariance tables depicting
276 the covariance between each environmental variable and each plant species, at each season of
277 each year. In a second step, the series of cross-covariance tables (one per season and per year)
278 were analyzed with partial triadic analysis, looking for temporal variations in the species-
279 environment relationships. The strengths of these relationships between plant communities
280 and abiotic parameters across seasons were then assessed using the Rv -coefficient, which is a
281 multidimensional equivalent of the ordinary correlation coefficient between two variables
282 (Robert and Escoufier 1976). We further evaluated the statistical significance of each of the
283 four computed Rv -coefficients by a random permutation test using 999 replicated matches of
284 two tables (after random permutations of array rows), and we compared the observed Rv -
285 coefficient and the distribution of values obtained from permutations.

286 Finally, to assess the relative contributions of biotic (plant community composition of
287 preceding seasons) vs. abiotic (physical and chemical parameters of preceding seasons)
288 characteristics of ponds to the variability of the plant community composition observed at a
289 given date, we used the analysis proposed by Townsend et al. (2003) and used by de Castro et
290 al. (2017). This analysis was performed between the plant community composition recorded
291 in summer 2020 (at the end of the survey), and the biotic and abiotic characteristics of ponds
292 from summer 2018 to summer 2020. Let $PCPi$ and $PCCi$ denote respectively the physico-
293 chemical parameter table and the plant community composition table at the i th sampling date,
294 and consider PCC_{S20} as the plant community composition table in summer 2020. Assuming
295 that the physico-chemical parameters at the i th sampling date would be a more efficient driver
296 of the plant community composition in summer 2020 than the plant community composition,
297 we tested the null hypothesis $Rv(PCPi, PCC_{S20}) = Rv(PCCi, PCC_{S20})$ against the alternative
298 $Rv(PCPi, PCC_{S20}) > Rv(PCCi, PCC_{S20})$ and we performed bootstraps on the statistics $t =$
299 $Rv(PCPi, PCC_{S20}) - Rv(PCCi, PCC_{S20})$ using 999 replicates. We assessed the statistical

300 significance of the observed difference between pairs of Rv -coefficient by comparing it to the
301 distribution of the simulated values. We used this approach for the 36 pairs of potential
302 differences between the four physical and chemical parameters and the four plant community
303 composition tables.

304 All data simulations and statistical analyses were performed using R 4.1.2. ([R Core](#)
305 [Team 2021](#)).

306

307 **Results**

308 *Description of plant communities within ponds at Kerguelen*

309 Pond plant communities of the Kerguelen were characterized by a low species richness (S),
310 and a high evenness (E). On average, ponds provide a habitat for five to six plant species,
311 while evenness was on average > 0.7 suggesting that plant species displayed similar relative
312 frequencies. Marginal R^2 indicated that year and season explained a very low percentage of
313 species richness and evenness variance respectively, while these indices did not vary with
314 location (Table 2). However, pond explained a large percentage of variance of both indices
315 (conditional R^2 , Table 2). Species richness was higher in the second sampling year
316 ($S_{\text{summer2019}}=5.77 \pm 1.27$; $S_{\text{winter2020}}=5.64 \pm 1.26$) as compared with the first one
317 ($S_{\text{summer2018}}=5.45 \pm 1.33$; $S_{\text{winter2019}}=5.22 \pm 1.57$), while evenness slightly increased in winter
318 ($E_{\text{winter2019}}=0.81 \pm 0.14$; $E_{\text{winter2020}}=0.79 \pm 0.12$) compared to summer ($E_{\text{summer2018}}=0.76 \pm 0.15$;
319 $E_{\text{summer2019}}=0.72 \pm 0.16$).

320 Analyzing the composition of plant communities showed that relative frequencies of
321 aquatic species varied from 0.00 to 0.35 across all locations and dates of sampling (Figs. 1,
322 S4). Overall, the most abundant aquatic species was *Juncus scheuchzerioides* while the rarest
323 ones were *Limosella australis* and *Ranunculus moseleyi*. *R. moseleyi* was almost absent from
324 the three sampled locations during the two winter periods, suggesting that the species was

325 sensitive to seasonal variations in environmental factors. Non-aquatic species altogether [*i.e.*
326 *Poa annua*, *Acaena magellanica*, *Agrostis magellanica*, and *Montia fontana*] generally
327 dominated pond communities with mean relative frequencies ranging from 0.20 to 0.55 (Figs.
328 1, S4).

329 The first three axes of the BCA-PCA performed on the mean relative frequencies of
330 plant species, explained 49.3% of total inertia. Permutation tests revealed that the season had
331 no significant effect on plant community composition in ponds (between-class variance =
332 0.011; *simulated-P* > 0.05), while the year and the location respectively explained only 1.0%
333 (between-class variance = 0.010; *simulated-P*=0.046) and 7.1% (between-class variance =
334 0.070; *simulated-P*=0.001) of their variation. In contrast, a high proportion of variation in
335 plant community composition (*i.e.* between-class variance= 0.595; *simulated-P*=0.001) was
336 explained by differences among ponds, suggesting that mechanisms driving plant community
337 structure operated at the local scale of the pond.

338

339 *Physical and chemical characteristics of ponds*

340 Kerguelen ponds appeared as shallow freshwater ecosystems (mean water depth < 16cm,
341 although they can easily exceed 30 cm in depth depending on rain supply) with highly
342 variable availability in nutrients (Tables 3, S1). pH was very close to neutral on average but
343 its range indicated strong variation between ponds of the same location (Table 3). Water
344 temperature was cool and overall stable among days (mean temperature and temperature
345 variance, Tables 3, S1) but variations in pond size and water depth could cause strong within-
346 day variation (up to ± 10 °C, A.-K. Bittebiere - field observation). Locations and time (year,
347 season) affected all these physical and chemical parameters with varying strengths (Tables 3,
348 S1, S2), either alone or in interactions, with no general pattern in the observed responses. For
349 instance, all abiotic parameters varied with the sampling year except NH_4^+ , and this response

350 additionally depended on the season (mean and variance of water temperature, specific
351 conductance, dissolved oxygen, C/N, N_{tot}) and/or the location (temperature variance,
352 dissolved oxygen, PO_4^{3-}). Yet, most of the variance in physical and chemical parameters was
353 explained by ponds (Table S2).

354 We performed a PCA on all abiotic parameters measured in the ponds. The first-
355 three axes explained 46.7% of total variance (Fig. 2). The first axis described the trophic
356 status of ponds based on water and sediment nutrient concentrations, and dissolved oxygen
357 concentration (Fig. 2a), while the second and third axes were related to physical parameters,
358 (temperature variance and water depth on the one hand, mean temperature and pH on the
359 other hand; Fig. 2b). We detected three different pond clusters regardless of time (year,
360 season), and locations (Table S3). Cluster 1 corresponded to ponds with a high variance in
361 water temperature together with high concentrations of dissolved oxygen, low concentrations
362 of phosphorus (bioavailable P in sediments and PO_4^{3-}) and nitrogen (N_{tot} in sediments, NH_4^+ ,
363 NO_3^-) (Fig. 2c). Cluster 2 was characterized by the deepest water, low temperature variance,
364 and intermediate concentrations of phosphorus (bioavailable P and PO_4^{3-}) (Fig. 2c). Cluster 3
365 was related to occasionally extreme values in nutrient concentrations in water and sediments
366 (NH_4^+ , NO_3^- , PO_4^{3-} , and bioavailable P), high water temperature and low dissolved oxygen.

367 We detected a significant difference in pond distance to sea shore among pond
368 clusters (ANOVA, $F_{2/332}=25.4$, $P < 0.001$; Fig. 3a). Ponds of clusters 2 and 3 were
369 significantly closer to sea shore than ponds of cluster 1. In addition, the total vegetation cover
370 significantly changed with the pond cluster (ANOVA, $F_{2/164}=13.8$, $P < 0.001$; Fig. 3b).
371 Indeed, ponds of cluster 1 had significantly lower vegetation cover than those of cluster 2,
372 while cluster 3 showed intermediate vegetation cover. Regarding plant community structure,
373 species richness did not depend on the pond cluster (ANOVA, $X_{1/165}=1.7$, $P > 0.05$; Fig. 3c),

374 while evenness was respectively the highest and the lowest in ponds of cluster 2 and 1, those
375 of cluster 3 displaying an intermediate evenness (ANOVA, $F_{2/164}=8.0$, $P < 0.001$); Fig. 3d).

376

377 *Abiotic and biotic drivers of plant community composition*

378 The composition of the plant community was significantly related to the physical and
379 chemical parameters of ponds with a slightly stronger response in summer compared to winter
380 (Table 4). No strong covariation of relative frequencies was detected among aquatic plant
381 species (Figs. S5a, c, e, g). The plant community composition was similar in summers 2018
382 and 2019 (Figs. S5a, e), and more seasonally stable during the second sampling year in
383 comparison with the first year (Figs. S5a, c, e, g). In addition, plant community composition
384 was very similar between locations of sampling (Figs. S6a, c, e, g). Importantly, regardless of
385 the sampling season and year, bioavailable P (P_{bio}) and total N (N_{tot}) in the sediments, together
386 with the variance of daily water temperature were the strongest drivers of the plant
387 community composition unlike mean water temperature (Figs. S5b, d, f, h). Ponds with higher
388 water temperature variance among days were preferentially inhabited by *Juncus*
389 *scheuchzerioides* (summer 2018-2019 and winter 2020; Figs. S5a, e, g). During winter, the
390 importance of abiotic parameters for plant community composition was more variable across
391 sampling years, but nitrogen availability in water and sediments seemed determinant (N_{tot} ,
392 and NO_3^- or NH_4^+) (Figs. S5d, h). Sampling locations were mostly differentiated by the
393 abiotic parameters especially along the second STATICO axis (Fig. S6) *i.e.* by the specific
394 conductance of water (winter 2019 and summer 2019, Figs. S5d, f), and by the availability in
395 NH_4^+ (winter 2020, Fig. S5h).

396 Most tested relationships between the present (summer 2020) and past (summer-
397 winter 2018-2020) physical and chemical parameters and plant community composition, and
398 the present plant community composition (summer 2020; Table 5) were statistically

399 significant, indicating the influence of past physical and chemical parameters (in winter and
400 summer 2019 only), and of all past plant community compositions on present plant
401 community composition. The differences in R_V -coefficients between plant community
402 composition and physical and chemical parameters were all negative when significant (Table
403 S4), indicating that the relationships between present and past plant community compositions
404 were overall stronger than the relationships between present plant community composition
405 and present and past physical and chemical parameters. In addition, plant community
406 composition of the two preceding seasons (winter 2020 PCC_{M20} and summer 2019 PCC_{N19})
407 similarly influenced present plant community composition (summer 2020). Indeed,
408 differences in the strengths of the relationships between present plant community composition
409 and PCC_{M20} on the one hand, and PCC_{N19} on the other hand, were not significant (Table S4).

410

411 **Discussion**

412 In this study, indices of plant community structure mostly varied between ponds with an
413 additional low effect of time (either season or year depending on the index). Water depth,
414 water temperature, and nutrient availability were the major parameters differentiating sub-
415 Antarctic ponds habitat. Surprisingly, and contrary to our hypothesis, abiotic characteristics of
416 ponds did not prevail over biotic characteristics in determining the plant community
417 composition.

418

419 *Pond habitats and their plant communities through space and time*

420 The studied ponds were shallow freshwater ecosystems characterized by intermediate level of
421 specific conductance and dissolved oxygen concentration, which were consistent with rainfall
422 supply. Indeed, [Voisin et al. \(2018\)](#) showed that specific conductance of urban wetlands
423 receiving stormwater runoff ranged from 50 to 200 $\mu\text{S}\cdot\text{cm}^{-1}$. Nutrient availability in the water

424 was highly variable, and pH was on average close to neutral (*i.e.* softwater habitat; see [Lacoul](#)
425 [and Freedman 2006](#)) although the maximal and minimal values indicate heterogeneity among
426 the ponds, likely reflecting different levels of photosynthetic activity (e.g. [Buapet et al. 2013](#)).
427 At similar latitudes, equivalent mean values of pH were recorded within lakes of the
428 Macquarie and Kerguelen islands ([Tyler 1972](#)), and of South Georgia ([Hansson et al. 1996](#)).
429 However, these ecosystems display higher specific conductance and lower phosphate
430 concentration ([Hansson et al. 1996](#)) than that observed in our studied ponds. Phosphorus
431 appears to be the limiting nutrient as usually observed in freshwater systems ([Toivonen and](#)
432 [Huttunen 1995](#); [Sarneel et al. 2011](#)). Indeed, the mean N:P atomic ratio in the water column
433 (using N-NH₄⁺, N-NO₃⁻ and P-PO₄³⁻ concentrations reported on Table 3) was strongly higher
434 (55:1) than the Redfield N:P ratio of 16:1, suggesting that P was a more limiting nutrient for
435 primary producers than N ([Geider and La Roche 2002](#)). Mean daily temperature of water was
436 about 4.7 °C, and was similar on average among consecutive days, albeit strong within days'
437 variations were recorded.

438 Location and time (year, season) affected all of the considered physical and chemical
439 parameters measured from the ponds with varying strengths, either alone or in interaction.
440 Although we could not detect any general pattern in the observed changes through location
441 and time, we evidenced that pond explain a large part of the variability in most physical and
442 chemical parameters. These complex patterns may result from factors such as variations in
443 pond morphometry (pond size, depth) ([Hanson et al. 2007](#); [Nõges 2009](#)) and climatic
444 conditions (air temperatures, rainfall) ([Dodds et al. 2019](#)) interacting through space and time,
445 although this hypothesis remains to be thoroughly tested.

446 The studied ponds were poorly colonized by plants, with only five to six species being
447 present, which is consistent with former studies performed at high latitudes on aquatic
448 ecosystems ([Lacoul and Freedman 2006](#); [Heino and Toivonen 2008](#)). Field observations also

449 reveal the presence of algae and cyanobacteria in these systems (AK. Bittebiere, field
450 observations). Plant species like *Poa annua* and *Acaena magellanica* colonized ponds from
451 their edges, likely benefiting from more frequent decrease in water depth related to rainfall
452 reduction (Casanova and Brock 2000). These species even became the most frequent,
453 although not dominant (high evenness), probably because they display faster expansion rate
454 than the aquatic species like *Ranunculus biternatus* and *R. pseudotrullifolius* (Chapuis et al.
455 2004). Different mechanisms were suggested to explain high evenness of aquatic plant
456 communities in the literature, such as low pressure of vegetative propagules, high water level
457 (Li et al. 2015), or disturbance (e.g. through grazing, reducing the dominance of the most
458 abundant species) (Wood et al. 2012). In the shallow ponds of Kerguelen, as all species are
459 clonal, we can hypothesize that disturbance, probably by sea animals, is the mechanism
460 preventing species from becoming dominant.

461 Contrary to our expectations, this composition of pond communities did not vary
462 much at the spatial scale, suggesting that aquatic species dispersal was not limited within
463 Kerguelen (Capers et al. 2010). Our observations reveal that most variation of the plant
464 community composition was actually detected among ponds, and not between sites.
465 Mechanisms driving pond community assembly thus operated at local scale, likely involving
466 abiotic and biotic filters (Violle et al. 2012) such as water trophic level (Alahuhta 2015) and
467 species interactions (Sarneel et al. 2011). Based on our results, we argue that future studies of
468 pond systems of the Iles Kerguelen, have to be conducted at this spatial scale.

469

470 *Different pond habitats*

471 Three pond clusters, *i.e.* habitats, related expectedly to water nutrients, water depth, and
472 temperature, could be discriminated across ponds. Importantly, not only the mean
473 temperature, but also its variance, determined pond habitats. These differences could be, at

474 least partially, explained by the distance to sea shore, *i.e.* by the frequency of visitation by sea
475 animals such as elephant seals and penguins. Indeed, inland ponds that were the most distant
476 from the sea shore (cluster 1) displayed the lowest nutrient concentrations. By contrast, ponds
477 close to the sea shore, *i.e.* more easily reachable by sea animals, showed intermediate (cluster
478 2 – coastal ponds) to high concentrations of phosphorus (P bioavailable, PO_4^{3-}) and nitrogen
479 (N_{tot} , NH_4^+ , NO_3^-) leading to eutrophication episodes associated with high water temperature,
480 and involving low dissolved oxygen (cluster 3 - wallows). Differences in nutrient availability
481 between coastal ponds and wallows may have resulted from stochastic visitation of different
482 sea animals. Indeed, penguins and elephant seals may supply pond water into varying source
483 of nitrogen (NH_4^+ , NO_3^- , urea, and uric acid) that can be differentially assimilated by plant
484 species (Erskine et al. 1998). In addition, seasonal variation in feeding habits and use of ponds
485 of sea animals (Cherel et al. 2007) may explain the observed nitrogen dynamics in water and
486 sediments. This interpretation suggests that these ecosystems rely heavily on trophic
487 exchanges with surrounding oceanic waters, as suggested by Smith (2008) and Lebouvier et
488 al. (2011). Similar influence of sea animals that deposit substantial amount of feces, urine,
489 and molted skin or feathers together with carcasses, have been demonstrated in other
490 Antarctic and sub-Antarctic ecosystems such as terrestrial grasslands at Marion Island
491 (Panagis 1985) or larger freshwater ecosystems (lakes) in the Antarctic (Smith 1985).
492 Interestingly, the habitat differentiation that we have highlighted here, occurred within
493 restricted area (at the location scale) along a few hundred meters.

494 Ultimately, changes in pond habitat caused variations in plant community structure
495 and aquatic ecosystem functioning. Coastal ponds (with intermediate level of nutrient
496 availability) had higher vegetation cover and evenness compared to wallows and inland
497 ponds. In plant communities with low evenness, fertilization usually enhances the dominance
498 of already successful competitors, and accelerates local extinction rates (Wilsey and Polley

499 2004). However, in our studied ponds, dominance within plant communities was low and the
500 different species were equally abundant. It has been shown in the literature that sea animal
501 fertilization could enhance species persistence, by increasing population sizes (Hillebrand et
502 al. 2007) and stimulating greater plant growth. Nevertheless, higher fertilization did not seem
503 to benefit to plant cover in the present survey, probably because of eutrophication
504 phenomenon, involving water turbidity that would have limited light availability.

505 Finally, our results reemphasize the tight trophic interaction that exists between
506 marine and terrestrial ecosystems at the sub-Antarctic islands (Smith 1985; Convey and
507 Lebouvier 2009). Elephant seals may additionally structure aquatic plant communities
508 through trampling and soil compaction (Tejedo et al. 2009) although this effect was not
509 considered in our study. To this end, this suggests that decrease in sea animal populations, as
510 observed for example in Macquarie Islands (Hindell et al. 2017), could have serious impacts
511 on the plant community dynamics in ponds (Jenkin 1997; Erskine et al. 1998).

512

513 *Physical and chemical parameters of ponds determine plant community composition*

514 Our result showed how the physical and chemical parameters of ponds could drive plant
515 community composition. This abiotic control appeared slightly stronger in summer, *i.e.* the
516 growing season, than in winter, and was mostly attributed to the availability of nutrients in
517 sediments (P_{bio} , N_{tot}) and to the variance in daily water temperature within ponds, regardless
518 of the sampling season and the year. In Kerguelen, water temperature appears independent
519 from pond area and water depth (Douce et al., 2023). Ponds with higher variation in water
520 temperature among days were preferentially inhabited by *J. scheuchzerioides*, suggesting that
521 this aquatic species could be more tolerant than the five others to the instability of
522 temperatures resulting from climate changes of Kerguelen, although this assertion remains to
523 be tested. This finding additionally raises the question of the ability of the other species to

524 cope with these changes in the upcoming years (Lebouvier et al. 2011). Aquatic plant species
525 found in the sub-Antarctic region have restricted distribution areas (*R. moseleyi* may even be
526 endemic to Kerguelen) (Hennion et al. 1994; Chau et al. 2021), and conservation issues are
527 also of concern in the face of climate change. More widely, since aquatic plants play a major
528 role in the functioning of freshwater ecosystems (Jeppesen et al. 1997; Iacarella et al. 2018;
529 Reitseman et al. 2018; Lürig et al. 2020), the resistance of pond ecosystem to the on-going
530 rising of water temperature is highly questionable.

531 A new finding emanated from our study, which demonstrated that the past abiotic
532 conditions in ponds acted more significantly on the present plant community composition
533 than present abiotic conditions. However, and contrary to our expectations, these abiotic
534 conditions did not prevail on the past plant community composition in determining the present
535 plant community composition. Indeed, it may be expected that under the harsh abiotic
536 conditions of Kerguelen combined to the high variability in pond abiotic parameters observed
537 through years and seasons, abiotic conditions would be the strongest determinant of plant
538 community composition. The effect of past plant community composition in aquatic plants
539 can be explained by two non-mutually exclusive hypotheses related to their clonal properties
540 (as studied communities were dominated by perennials). First, aquatic plants display both
541 ramets and connections of which lifespans exceed the year, ensuring the stability of their
542 population sizes (Winkler and Fischer 2002; Stöcklin and Winkler 2004) within ponds.
543 Connections are in particular involved in resources storing (carbohydrates) through time, to
544 support further individual growth (Stuefer and Huber 1998, 1999). Second, clonal plants are
545 known to integrate their past interactions and adjust their present growth accordingly
546 (Turkington et al. 1991; Bittebiere and Mony 2015), ultimately determining their persistence
547 within the present community (Bittebiere and Mony 2015). This process is based on the
548 availability of resources: ramets share information on resource depletion by neighbors within

549 the clone, depending on the integration distance that mimic the duration of clone memory of
550 the habitat conditions (Louâpre et al. 2012). Therefore, longer term studies are needed to
551 precisely determine the actual duration of the influence exerted by abiotic and biotic
552 parameters on pond plant communities.

553

554 *Conclusions*

555 To our knowledge, this study is the first focusing on pond ecosystems at Kerguelen. It
556 provides new insights on the relationships between the dynamics and functioning of pond
557 plant communities and their habitat, which can serve as a basis for future studies dealing with
558 the impact of climate change within the whole sub-Antarctic region. Indeed, other
559 archipelagos like Prince Edward Islands (Chau et al., 2021), and Heard and MacDonald
560 Islands (Bergstrom and Selkirk 2000) harbor the same aquatic species and pond habitats.

561 In particular, we have demonstrated the importance of past abiotic and biotic
562 parameters on pond plant communities, highlighting the need for long-term studies dedicated
563 to these threatened ecosystems, especially in a context of climatic warming. Our study
564 additionally showed that water temperature variability influences plant community
565 composition and subsequently the whole pond ecosystem. This result motivates for
566 conducting new studies on the mechanisms underlying the responses of aquatic plants to
567 temperature by investigating how thermal stress may affect plant growth (Riis et al. 2012) and
568 physiological strategies (Arbona et al. 2013).

569

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855

856

857 **Table 1.** Description of the surveyed ponds at the three locations. Means and ranges of pond
 858 size were calculated based on measurements replicated on three consecutive years.

	Molloy	Isthme Bas	Cap Ratmanoff
Latitude, longitude	49.36°S - 70.06°E	49.36°S - 70.24°E	49.32°S - 70.53°E
Mean altitude of ponds above sea (\pm SD, m, $N = 15$)	11.2 (8.4)	3.4 (2.6)	8.8 (3.6)
Mean pond size (\pm SD, m ² , $N = 45$)	58.9 (\pm 56.9)	140.3 (\pm 344.7)	54.0 (\pm 62.9)
Pond size range (min-max, m ² , $N = 45$)	2.4 – 166.5	4.8 – 1,252.2	2.9 – 164.6

859

860 **Table 2.** Variations of plant community indexes in space (location) and time (year, season) assessed with mixed-models and pond as random
 861 factor. The significance of the explanatory variables was determined by ANOVA tests. Marginal R² indicates the percentage of index variance
 862 explained by the fixed effects; Conditional R² indicates the percentage of index variance explained by the whole model (including fixed and
 863 random effects).

	Marginal R ²	Conditional R ²	Year (df=1)		Season (df=1)		Location (df=2)		Year×Season (df=1)		Year×Location (df=2)		Season×Location (df=2)		Year×Season×Location (df=2)	
			X ²	P	X ²	P	X ²	P	X ²	P	X ²	P	X ²	P	X ²	P
Richness	0.07	0.48	6.1	*	1.7	ns	2.8	ns	0.2	ns	2.3	ns	0.5	ns	2.3	ns
□																
Evenness	0.07	0.50	3.3	t	12.8	**	1.2	ns	0.7	ns	2.3	ns	1.0	ns	0.3	ns

864 *Notes: t 0.1 < P < 0.05, * P < 0.05; *** P < 0.001; ns = not significant. □ square-root-transformed.*

865

866 **Table 3.** Mean (\pm SD) abiotic parameters measured in the ponds of Iles Kerguelen depending on the year, season, and location of sampling.

867 Values in italic indicate the maximum and the minimum (*i.e.* the range) recorded for each season per year on each location.

Date	Location	Mean Temp. (°C)	Temp. variance (°C ²)	Water depth (cm)	Conduct. (μ S.cm ⁻¹)	pH	DO (mg.L ⁻¹)	N-NH ₄ ⁺ (μ g.L ⁻¹)	N-NO ₃ ⁻ (μ g.L ⁻¹)	P-PO ₄ ³⁻ (μ g.L ⁻¹)	P _{bio} (mg.g ⁻¹)	C/N	N _{tot} (g.g ⁻¹)
Summer 2018	Isthme	4.55	2.72	16.07	240.23	7.00	7.25	233.27	201.14	24.98	0.88	13.84	0.017
	Bas	(\pm 1.34)	(\pm 2.10)	(\pm 11.75)	(\pm 85.82)	(\pm 0.81)	(\pm 4.73)	(\pm 298.24)	(\pm 268.35)	(\pm 38.97)	(\pm 0.59)	(\pm 2.35)	(\pm 0.007)
		<i>6.34-</i>	<i>7.66-0.57</i>	<i>50.53-</i>	<i>452.00-</i>	<i>8.98-</i>	<i>14.65-</i>	<i>1597.00-</i>	<i>1379.50-</i>	<i>197.85-</i>	<i>2.26-</i>	<i>19.99-</i>	<i>0.032-</i>
		<i>1.82</i>		<i>3.60</i>	<i>142.35</i>	<i>5.88</i>	<i>0.08</i>	<i>76.60</i>	<i>45.50</i>	<i>0.00</i>	<i>0.17</i>	<i>8.95</i>	<i>0.003</i>
	Molloy	4.64	6.03	15.04	155.66	7.04	9.84	566.13	254.30	25.65	0.79	12.63	0.013
		(\pm 1.95)	(\pm 1.48)	(\pm 7.55)	(\pm 51.85)	(\pm 0.56)	(\pm 4.86)	(\pm 1415.07)	(\pm 329.60)	(\pm 54.60)	(\pm 0.56)	(\pm 1.43)	(\pm 0.007)
		<i>6.92-</i>	<i>9.34-3.59</i>	<i>35.11-</i>	<i>336.80-</i>	<i>8.07-</i>	<i>15.90-</i>	<i>7545.00-</i>	<i>1275.50-</i>	<i>221.97-</i>	<i>2.34-</i>	<i>17.32-</i>	<i>0.029-</i>
		<i>1.89</i>		<i>4.22</i>	<i>102.54</i>	<i>6.10</i>	<i>0.15</i>	<i>59.55</i>	<i>28.00</i>	<i>0.00</i>	<i>0.00</i>	<i>10.06</i>	<i>0.002</i>
	Cap Ratmanoff	4.41	4.05	10.66	255.34	6.73	5.77	924.19	236.54	33.95	0.83	11.75	0.021
		(\pm 1.63)	(\pm 1.08)	(\pm 4.86)	(\pm 77.13)	(\pm 0.74)	(\pm 4.16)	(\pm 1677.30)	(\pm 435.32)	(\pm 50.44)	(\pm 0.58)	(\pm 1.25)	(\pm 0.009)
		<i>6.55-</i>	<i>6.02-2.15</i>	<i>27.50-</i>	<i>482.00-</i>	<i>9.09-</i>	<i>17.95-</i>	<i>7840.00-</i>	<i>2341.00-</i>	<i>199.55-</i>	<i>1.95-</i>	<i>13.87-</i>	<i>0.043-</i>
		<i>2.15</i>		<i>1.47</i>	<i>164.46</i>	<i>5.58</i>	<i>0.14</i>	<i>68.10</i>	<i>29.50</i>	<i>0.95</i>	<i>0.01</i>	<i>8.02</i>	<i>0.006</i>
Winter 2019	Isthme	3.31	3.00	14.10	238.10	6.78	8.57	95.48	103.31	31.38	0.70	16.38	0.015
	Bas	(\pm 1.46)	(\pm 2.43)	(\pm 8.83)	(\pm 117.77)	(\pm 1.23)	(\pm 4.39)	(\pm 123.55)	(\pm 39.55)	(\pm 35.80)	(\pm 0.32)	(\pm 2.26)	(\pm 0.006)
		<i>5.17-</i>	<i>9.87-0.52</i>	<i>37.33-</i>	<i>605.20-</i>	<i>10.25-</i>	<i>13.54-</i>	<i>681.50-</i>	<i>198.50-</i>	<i>147.62-</i>	<i>1.24-</i>	<i>21.69-</i>	<i>0.029-</i>
		<i>0.31</i>		<i>2.33</i>	<i>125.86</i>	<i>3.62</i>	<i>0.15</i>	<i>22.10</i>	<i>35.50</i>	<i>1.25</i>	<i>0.15</i>	<i>12.03</i>	<i>0.003</i>
	Molloy	2.66	6.64	14.76	121.07	6.70	10.11	117.56	583.78	13.74	0.72	14.40	0.010
		(\pm 1.91)	(\pm 2.10)	(\pm 8.00)	(\pm 48.22)	(\pm 0.60)	(\pm 4.33)	(\pm 247.10)	(\pm 1085.69)	(\pm 35.39)	(\pm 0.37)	(\pm 1.36)	(\pm 0.005)
		<i>5.04-</i>	<i>12.03-3.25</i>	<i>29.20-</i>	<i>230.34-</i>	<i>7.70-</i>	<i>16.14-</i>	<i>1401.70-</i>	<i>4793.00-</i>	<i>181.17-</i>	<i>1.45-</i>	<i>17.45-</i>	<i>0.022-</i>
		<i>0.30</i>		<i>0.83</i>	<i>66.92</i>	<i>5.28</i>	<i>0.15</i>	<i>8.15</i>	<i>50.50</i>	<i>0.00</i>	<i>0.04</i>	<i>11.49</i>	<i>0.003</i>
	Cap Ratmanoff	2.79	4.46	12.48	184.62	6.63	8.44	112.08	267.74	20.90	0.71	14.05	0.014
		(\pm 1.63)	(\pm 1.49)	(\pm 4.23)	(\pm 53.31)	(\pm 0.38)	(\pm 4.17)	(\pm 111.13)	(\pm 711.41)	(\pm 35.12)	(\pm 0.38)	(\pm 1.76)	(\pm 0.006)
		<i>5.20-</i>	<i>7.76-1.95</i>	<i>22.93-</i>	<i>319.00-</i>	<i>7.55-</i>	<i>15.84-</i>	<i>651.05-</i>	<i>3813.00-</i>	<i>152.66-</i>	<i>1.51-</i>	<i>18.66-</i>	<i>0.025-</i>
		<i>0.33</i>		<i>5.00</i>	<i>116.84</i>	<i>5.70</i>	<i>0.14</i>	<i>29.55</i>	<i>25.00</i>	<i>2.08</i>	<i>0.17</i>	<i>10.89</i>	<i>0.004</i>

Summer 2019	Isthme	5.68	4.51	17.00	197.00	6.85	10.87	71.61	75.38	28.24	0.70	16.11	0.015	
	Bas	(±2.37)	(±4.02)	(±9.25)	(±29.18)	(±0.70)	(±2.74)	(±61.49)	(±24.59)	(±21.27)	(±0.45)	(±2.13)	(±0.005)	
		9.77- 2.12	16.82-0.62	44.93- 2.80	275.33- 147.86	8.47- 5.41	16.83- 4.40	324.50- 31.00	136.50- 13.50	79.62- 4.30	1.70- 0.23	20.92- 12.25	0.026- 0.004	
	Molloy	6.44	9.99	18.63	141.47	7.21	12.99	629.84	72.15	6.97	0.96	15.23	0.010	
		(±3.50)	(±4.40)	(±6.57)	(±115.35)	(±0.86)	(±2.76)	(±1195.31)	(±54.43)	(±6.72)	(±0.60)	(±2.42)	(±0.005)	
		10.99- 2.20	20.51-3.93	32.73- 8.25	688.00- 73.52	9.53- 6.00	19.03- 6.39	5630.50- 51.00	259.50- 21.50	32.53- 0.00	2.25- 0.09	19.92- 10.63	0.019- 0.002	
	Cap	5.88	6.71	13.84	198.35	6.89	11.91	770.34	380.83	18.62	0.65	14.86	0.014	
		(±2.87)	(±3.05)	(±5.92)	(±81.01)	(±0.48)	(±1.89)	(±1566.66)	(±1121.00)	(±33.20)	(±0.40)	(±1.41)	(±0.006)	
	Ratmanoff	9.27- 2.40	13.22-2.35	28.33- 4.00	411.40- 5.70	8.23- 5.61	17.09- 9.03	7330.00- 31.50	4590.00- 23.00	145.38- 0.00	1.69- 0.11	17.76- 11.19	0.022- 0.003	
	Winter 2020	Isthme	5.04	3.72	22.65	212.45	7.11	10.40	126.34	116.59	49.57	0.59	14.29	0.018
		Bas	(±1.60)	(±3.33)	(±13.93)	(±43.76)	(±0.41)	(±2.19)	(±46.37)	(±102.82)	(±50.71)	(±0.39)	(±1.83)	(±0.007)
7.37- 2.22			13.94-0.51	67.07- 6.43	333.60- 151.18	8.09- 6.39	14.88- 4.62	223.00- 65.50	425.00- 3.00	237.60- 5.01	1.52- 0.01	18.65- 9.72	0.041- 0.004	
Molloy		5.41	8.24	17.41	112.13	6.83	10.97	395.76	180.07	7.04	0.59	13.61	0.011	
		(±2.36)	(±3.68)	(±7.84)	(±54.82)	(±0.46)	(±2.90)	(±804.68)	(±324.14)	(±6.86)	(±0.35)	(±1.48)	(±0.005)	
		8.34- 2.31	16.99-3.21	34.67- 4.00	332.67- 54.94	8.10- 6.08	14.15- 1.70	3334.50- 37.50	1575.00- 3.00	33.61- 0.00	1.65- 0.07	17.47- 11.30	0.027- 0.004	
Cap		5.04	5.54	13.79	192.86	6.80	10.93	299.50	77.70	5.29	0.59	12.48	0.018	
		(±1.95)	(±2.54)	(±6.86)	(±53.34)	(±0.64)	(±3.17)	(±908.52)	(±182.17)	(±4.21)	(±0.37)	(±2.39)	(±0.008)	
Ratmanoff		7.37- 2.48	10.96-1.92	31.33- 4.00	326.00- 120.98	7.68- 4.63	14.38- 3.86	4836.00- 21.00	1030.50- 5.00	21.50- 0.00	1.48- 0.14	16.86- 8.05	0.034- 0.005	

868 Notes: Temp. temperature; Conduct. specific conductance; Pbio: phosphore bioavailable. N = 30.

869 **Table 4.** Relationships between the plant community composition and the physical and
 870 chemical parameters recorded in ponds at each sampling date. Parameters from the
 871 permutation test in STATICO analysis are given with R_v quantifying the strength of the
 872 relationship (on a 0-1 scale), and *simulated-P* as the statistical significance of the observed
 873 R_v .

	R_v	<i>Simulated-P</i>
summer 2018	0.285	***
winter 2019	0.229	**
summer 2019	0.276	***
winter 2020	0.238	**

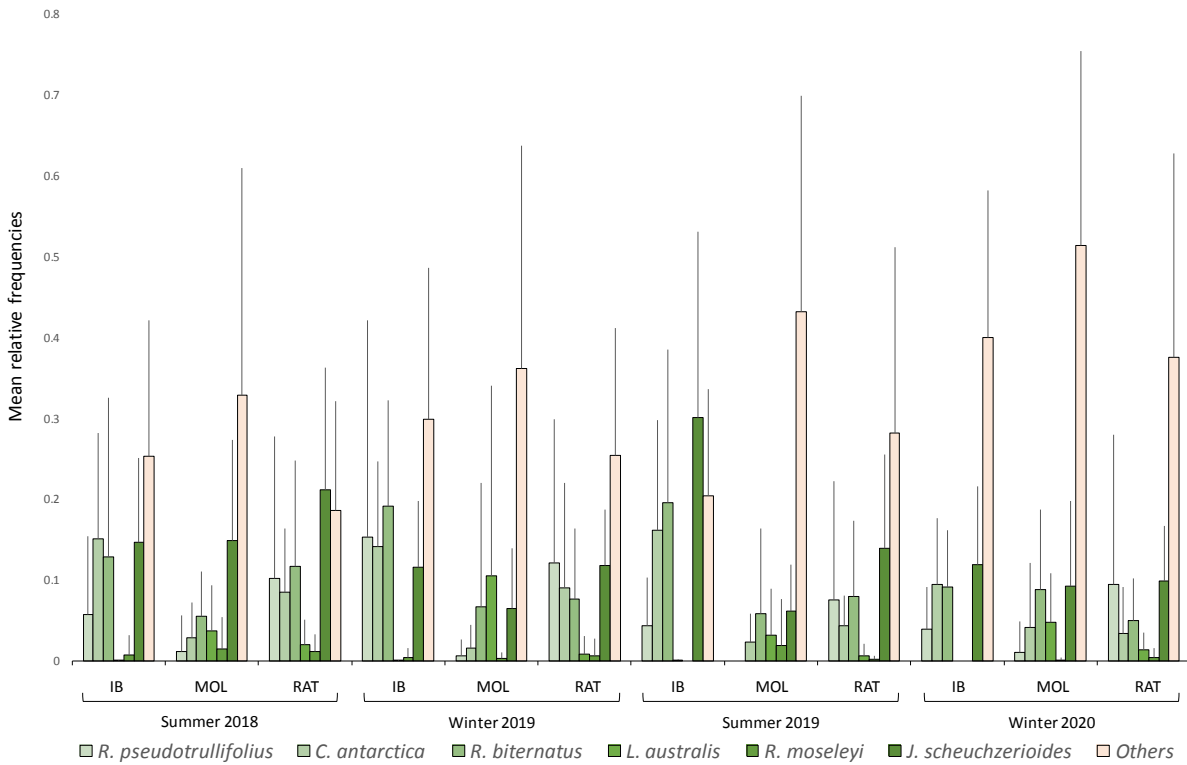
874 *Notes: ** $P < 0.01$; *** $P < 0.001$.*

875

876 **Table 5.** Relationships between present plant community composition *i.e.* recorded during the
877 last campaign of survey (summer 2020), and past plant community compositions (PCC), and
878 past and present physical and chemical parameters (PCP, *i.e.* recorded during summer 2020
879 and the preceding seasons). *R_v*: strength of the relationship; *simulated-P*: statistical
880 significance of the observed *R_v*.

	<i>R_v</i>	<i>Simulated-P</i>
PCC, winter 2020	0.575	<0.001
PCC, summer 2018	0.568	<0.001
PCC, summer 2019	0.553	<0.001
PCC, winter 2019	0.458	<0.001
PCP, winter 2019	0.227	<0.030
PCP, summer 2019	0.216	<0.040
PCP, winter 2020	0.196	ns
PCP, summer 2020	0.191	ns
PCP, summer 2018	0.179	ns

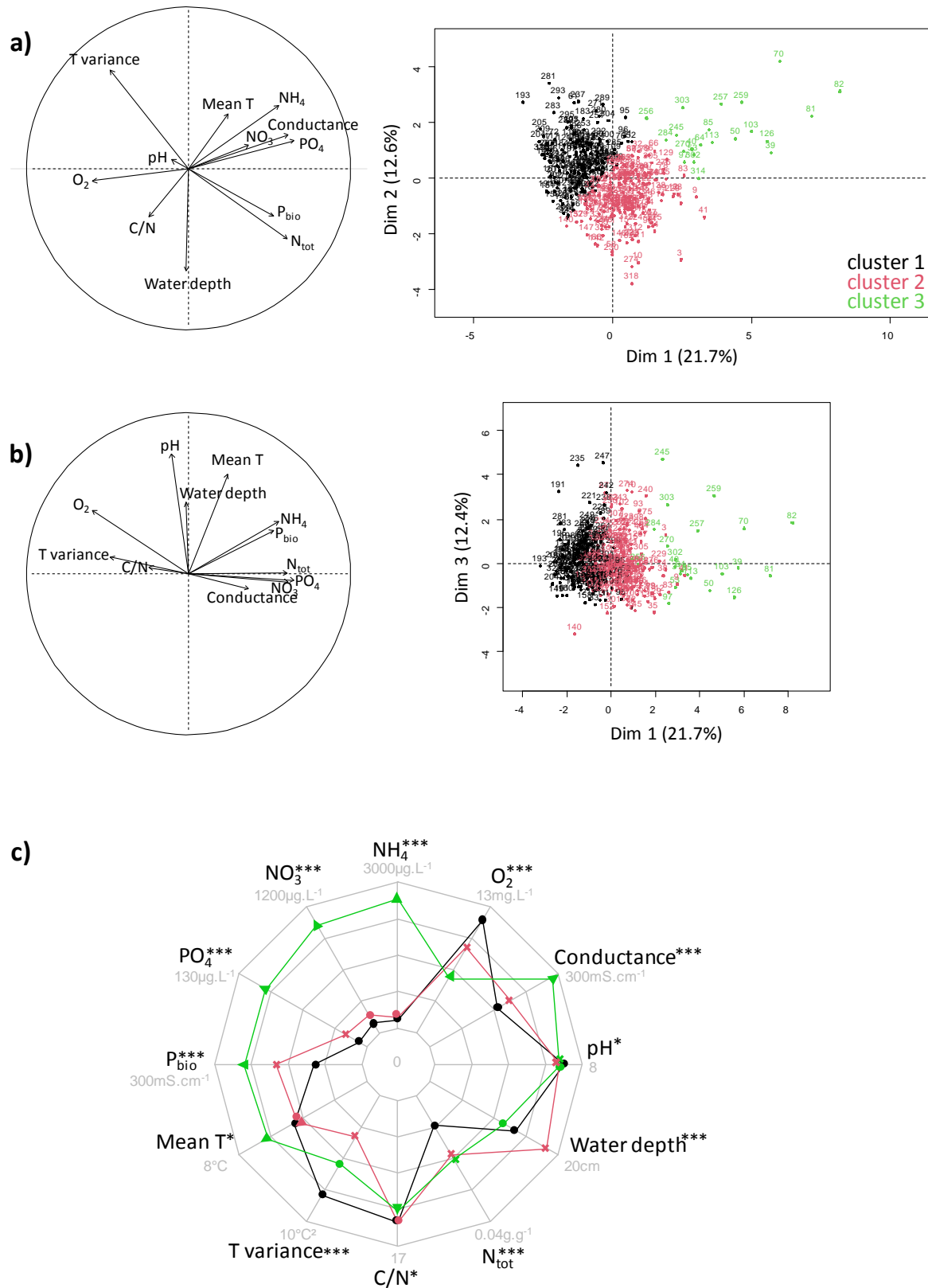
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882

883 **Figure 1.** Mean (\pm SD) composition of pond plant communities depending on the season and
 884 year. Varying shades of green represent different aquatic plant species (see accompanying
 885 legend), while light orange was used to represent relative frequencies of all non-aquatic
 886 species. IB: Isthme Bas, MOL: Molloy, RAT: Cap Ratmanoff.

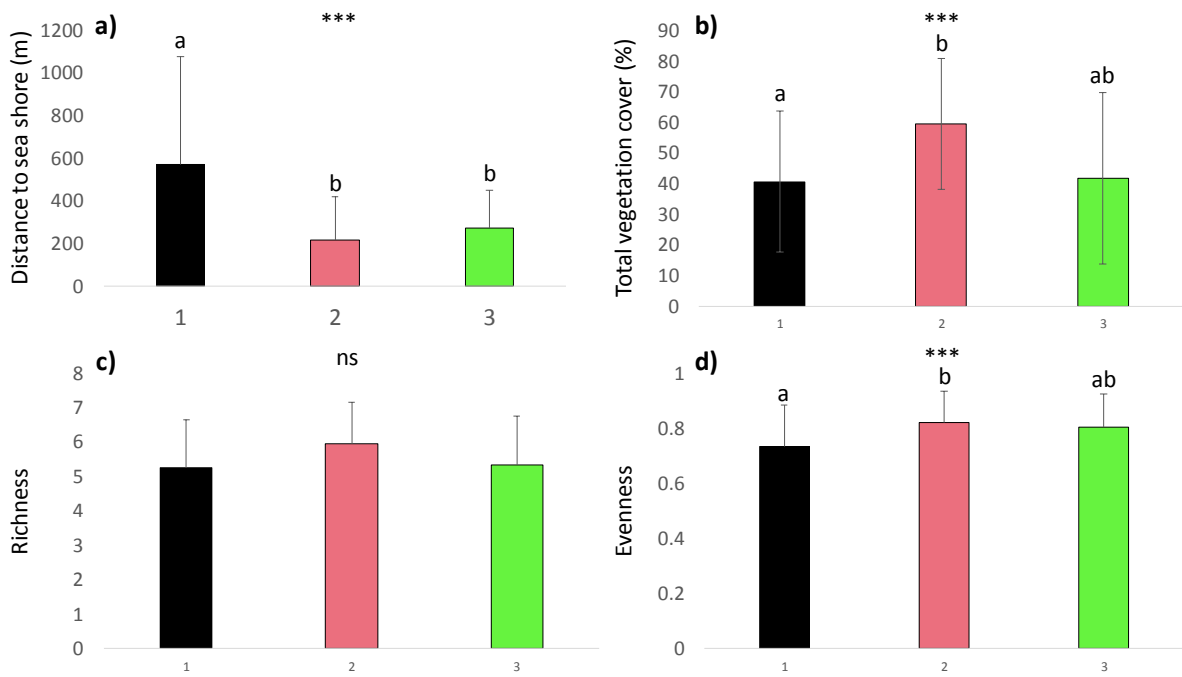
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888

889 **Figure 2.** Principal component analysis and hierarchical clustering performed on the abiotic
 890 parameters of all ponds. Abiotic parameters and pond scores projected along a) axes 1 and 2,
 891 and b) axes 1 and 3. c) Mean abiotic parameters characterizing the clusters shown with

892 different colors). Asterisks indicate significant difference of mean abiotic parameters between
893 clusters (ANOVA tests) *P < 0.05; *** P < 0.001, different symbols indicate different means
894 (Tukey post-hoc tests). Tvariance – temperature variance, mean T – water temperature, O₂ –
895 dissolved oxygen, P_{bio} – bioavailable P. In a) and b) different numbers refers to different
896 ponds at varying dates of sampling, and within different locations (N = 360 in total).
897



898

899 **Figure 3.** Mean (\pm SD) cluster values (labelled from 1 to 3 along the first axis of the PCA
 900 performed on abiotic parameters) for a) distance from sea shore, b) percentage of vegetation
 901 cover within the pond, c) plant community richness, d) plant community evenness. Asterisks
 902 above the figures indicate the significance of the clustering on the response variable (ANOVA
 903 tests), ns $P > 0.05$; *** $P < 0.001$, different letters indicate significant differences in mean
 904 response variable among clusters (Tukey post-hoc tests).

905