The structure and diversity of freshwater diatom assemblages from Franz Josef Land Archipelago: a northern outpost for freshwater diatoms

Sergi Pla-Rabés, Paul B Hamilton, Enric Ballesteros, Maria Gavrilo, Alan M. Friedlander, Enric Sala

We examined diatom assemblages from 18 stream and pond samples in the Franz Josef Land Archipelago (FJL), the most northern land of Eurasia. More than 216 taxa were observed, revealing a rich circumpolar diatom flora, including many undescribed taxa. Widely distributed taxa were the most abundant by cell densities, while circumpolar taxa were the most species rich. Stream and pond habitats hosted different assemblages, and varied along a pH gradient. *Diatoma tenuis* was the most abundant and ubiquitous taxon. However, several circumpolar taxa such as *Chamaepinnularia gandrupii*, *Cymbella botellus*, *Psammothidium* sp. and *Humidophila laevissima* were also found in relatively high abundances. Aerophilic taxa were an important component of FJL diatom assemblages (*Humidophila* spp., *Caloneis* spp. and *Pinnularia* spp.), reflecting the large and extreme seasonal changes in Arctic conditions. We predict a decrease in the abundance of circumpolar taxa, an increase in local (α-) freshwater diatom diversity, but a decrease in regional diversity (circumpolar homogenization) as a result of current warming trends and to a lesser extent the increasing human footprint in the region.

1 **The structure and diversity of freshwater diatom assemblages from Franz Josef Land**

2 **Archipelago: a northern outpost for freshwater diatoms**

3 Sergi Pla-Rabès[1], Paul B. Hamilton[2], Enric Ballesteros[3], Maria Gavrilo[4], Alan M. Friedlander[5,6] and Enric
4 Sala[6]

7 [1] Centre for Ecological Research and Forestry Applications (CREAF), Campus UAB, Edifici C, 08193
8 Cerdanyola del Vallès, Barcelona, Spain
9
10 [2] Canadian Museum of Nature, Research and Collections, P.O. Box 3443, Station D, Ottawa, K1P 6P4,
11 Canada
12
13 [3] Centre d'Estudis Avançats de Blanes-CSIC, Acc. Cala Sant Francesc 14, 17300 Blanes, Girona, Spain.

14 [4] National Park Russian Arctic, Sovetskikh kosmonavtov pr., 57, Archangelsk, 163000, Russia

15 [5] Fisheries Ecology Research Laboratory, University of Hawaii, Honolulu, Hawaii, USA

16 [6] National Geographic Society, Washington, DC, USA

19 Corresponding Author:

20 Sergi Pla-Rabés

21 Campus UAB, Edifici C, 08193 Cerdanyola del Vallès, Barcelona, Spain

22 Email address: sergiplarabes@gmail.com

24 **Abstract**

26 We examined diatom assemblages from 18 stream and pond samples in the Franz Josef Land

27 Archipelago (FJL), the most northern land of Eurasia. More than 216 taxa were observed,

28 revealing a rich circumpolar diatom flora, including many undescribed taxa. Widely distributed

29 taxa were the most abundant by cell densities, while circumpolar taxa were the most species rich.

30 Stream and pond habitats hosted different assemblages, and varied along a pH gradient. *Diatoma*

31 *tenuis* was the most abundant and ubiquitous taxon. However, several circumpolar taxa such as

32 *Chamaepinnularia gandrupii, Cymbella botellus, Psammothidium* sp. and *Humidophila*

33 *laevissima* were also found in relatively high abundances. Aerophilic taxa were an important

34 component of FJL diatom assemblages (*Humidophila* spp., *Caloneis* spp. and *Pinnularia* spp.),

35 reflecting the large and extreme seasonal changes in Arctic conditions. We predict a decrease in

36 the abundance of circumpolar taxa, an increase in local (α-) freshwater diatom diversity, but a

37 decrease in regional diversity (circumpolar homogenization) as a result of current warming

38 trends and to a lesser extent the increasing human footprint in the region.

Introduction

39

40

41 The Arctic is warming faster than any other region on the globe, which imposes new challenges

42 to the resilience of this region and its diversity. Freshwater ecosystems are particularly sensitive

43 to global and local stressors such as climate change, atmospheric pollution, alien species

44 introductions, and resource development, which can all alter biogeochemical cycles. Much of the

45 Arctic is still poorly explored, hence little is known about the impact of climate change on

46 northern freshwater and marine ecosystems (e.g. Chernova et al. 2014). There is on-going

47 international interest in expanding monitoring programs on climate change, particularly in the

48 polar regions (UNESCO 2009; AMAP 2015). This will become increasingly more important as

49 resource development and tourism in the Arctic is expected to increase dramatically in the

50 coming decades.

51 Arctic ponds and lakes can be considered as sentinels of the changing Arctic (Williamson et al.

52 2008). Their freshwater living biota, mainly diatoms (Bacillariophyceae) and cyanobacteria, are

53 the most abundant and diverse photosynthetic groups found in these habitats. Paleolimnological

54 studies using freshwater diatoms across the Arctic have documented past climatic changes (e.g.

55 Smol et al. 2005). The most striking change, which is still on-going, has been the expansive

56 increase in diatom productivity and diversity since the 1950s (Gajewski et al. 1997). Despite

57 these rapid changes, we have a limited understanding of the stability (i.e. fluctuations in the

58 occurrence and abundance of species through time) of these freshwaters systems. In addition to

59 changing climate, the expanding human footprint in the Arctic has resulted in increased

60 contamination by heavy metals such as mercury and arsenic (Chetelat et al. 2014). Questions

61   about biological stability, including native species loss and introduction of invasive species have

62   yet to be addressed.

63   The Franz Josef Land (FJL) Archipelago is the most northerly land in the Arctic region of

64   Eurasia. All islands in the archipelago belong to the specially protected area of Franz Josef Land

65   state federal wildlife refuge (corresponding IUCN category IV) and are managed by the Russian

66   Arctic National Park. High Arctic exploration, mining, fishing, and tourism, particularly to the

67   remote northern islands, has always been limited due to logistical constraints. Consequently,

68   little is known about the ecology and distribution of the FJL freshwater diatom flora.

69   Nevertheless, at the end of the 19th century, the Austro-Hungarian Tegetthoff expedition (1872-

70   1874), sampled marine bottom sediments and Grunow (1884) noted several diatom species in his

71   monograph, but only a few freshwater diatoms were reported. Later in that century the Jackson–

72   Harmsworth Expedition to FJL (1894–97) collected about 20 samples, mainly from Cape Flora,

73   but also from Cape Neal and Bell Island, including a mud sample from an off-shore drifting ice-

74   floe (Cleve 1898). A total of 101 diatom morphotypes were observed, including 27 freshwater

75   taxa identified in the ice-floe sample. During the first half of 20th century, Peter Shirshov (1935)

76   sampled four lakes in FJL and compared their algal flora with lakes at Novaya Zemlya, a large

77   Russian island ~ 500 km to the southeast of FJL. Diatom floras from the high Arctic (FJL,

78   Spitsbergen, Beeren Island, Jan Mayen and East and West Greenland) differed from floras in the

79   lower Arctic region (e.g. Siberia and Lapland) (Cleve, 1898).

80   Since the 1950s numerous surveys have increased our knowledge on the rich Arctic diatom flora

81   (Foged 1953; Foged 1955; Foged 1958; Foged 1964; Foged 1973; Foged 1974; Foged 1977;

82   Foged 1981; Lange-Bertalot & Metzeltin 1996; Metzeltin & Witkowski 1996; Lange-Bertalot &

83 Genkal 1999; Antoniades et al. 2008), but there is only one recent study on diatoms from FJL

84 (Zauer 1963).

85 New species are frequently described as locally endemic (i.e. Van De Vijver et al. 2004), but are

86 quite often later reported from other Arctic localities. Hence, several studies support the idea of a

87 circumpolar diatom distribution (Lange-Bertalot & Metzeltin 1996; Metzeltin & Witkowski

88 1996; Lange-Bertalot & Genkal 1999; Antoniades et al. 2008). Drifting icebergs and ice-floes

89 may act as vectors in the circumpolar distribution of microorganisms (Cleve 1898). In addition,

90 the ability of some diatoms to survive aerial voyages by wind and bird transportation are also

91 possible dispersal mechanisms (Kristiansen 1996). Consequently, there is a need to explore more

92 Arctic sites to understand the biogeography of circumpolar microorganisms.

93 The objective of this research is to document parts of the diatom flora of FJL, a poorly studied

94 region in the high Arctic in order to establish a baseline for future studies. We also examine

95 biogeographical connections with Greenland, Siberia, Spitsbergen, and northern Canada. Finally,

96 we propose a hypothesis driven theoretical framework on the effects of recent and past climate

97 warming scenarios on species richness for future studies and investigate future scenarios for

98 conservation of circumpolar biodiversity.

99

100 **Methods**

101 ***Study area and sites***

102 FJL is a large archipelago that occupies an area of 16,000 km^2 and consists of 192 islands. The

103 archipelago was formed together with the Spitsbergen Archipelago by the uplift and broken

104 margin of the Barents Shelf (Solheim et al. 1998). FJL is basically a remnant of the basaltic

105   plateau fractured by tectonic faults and covered by glaciers (over 85%), with the highest

106   elevation at ca. 600 m. Most of the islands are small, only nine exceed 500 km^2 with large ice-

107   free areas of 80 - 500 km^2 on only four islands.

108   FJL lies within the high arctic climatic zone, with an average annual air temperature of -13.2°C.

109   July and August are the only two months with average air temperatures above zero (+ 0.7°C and

110   + 0.1°C, respectively) (VNIIGMI-MCD data accessed at http://oopt.aari.ru). Periods with above

111   freezing average daily temperatures last from 2 months in the southern portion of FJL to 1.5

112   months in the north. Rainfall averages 250 - 300 mm year^{-1} with only 40 mm during warm

113   months. On average, FJL is much colder than Spitsbergen, which has an annual air temperature -

114   7°C, and four months with air temperatures above zero (Førland et al. 2011), warmer than the

115   Canadian high Arctic islands (e.g. average annual air temperature in Eureka, Nunavut -19.9 °C,

116   additional data can be found in http://www.eureka-nt.climatemps.com/temperatures.php).

117   The hydrographical network of FJL is not well developed; most of the streams are temporal,

118   while all rivers are completely frozen in winter. There are over 850 lakes and ponds in FJL but

119   only 10 of them are deeper than 1 m (i.e. not frozen to the bottom M. Gavrilo field observation).

120   Principal water sources are melting snow and glaciers. Thus, most of freshwater habitats are very

121   harsh, having short growing season and are only temporary.

122   Approval to conduct field studies was granted by the Russian Federation Ministry of Education

123   and Science Approval Ref. No. 14-368 of 06.05.2013 permission to the Russian Arctic National

124   Park.

125   ***Diatoms analysis***

126   During the 2013 National Geographic Pristine Seas expedition to FJL, 18 samples from

127   freshwater habitats (2 lakes, 7 ponds, and 9 streams) were sampled from different islands across

128   the archipelago (Fig. 1, Table 1). Scrapings were done on rock surfaces, which consisted of a

129   mixture of mosses and cyanobacteria biofilm. In the field, samples were fixed and preserved in

130   3% formaldehyde.

131   Diatom samples were processed by hot digestion using hydrogen peroxide (33% H_2O_2) and HCL

132   (2 ml 1M). Through a series of dilutions, the peroxide and acid were removed. Subsequently, the

133   samples were dried onto cover glass and mounted in Naphrax® (R.I.=1.7, Brunel Microscopes

134   Ltd., UK) on a microscope slide following the method described in Battarbee et al. (2001). Five

135   hundred diatom valves per slide sample were identified and counted across random transects at

136   1,000x magnification using a Zeiss Axio Imager A1 microscope (Carl Zeiss Inc., Germany)

137   equipped with a 100x objective (Zeiss Plan-Apo 1.4 numeric aperture) and differential

138   Interference contrast optics. Scanning electron micrographs were taken using a FEI Quanta

139   2000-F-SEM (10 kV, WD 10 mm).

140

141   Diatom identifications were based on contributions by Lange-Bertalot & Metzeltin (1996);

142   Metzeltin & Witkowski (1996); Lange-Bertalot & Genkal (1999); Krammer (2000); Lange-

143   Bertalot (2001b); Lange-Bertalot (2001a); Krammer (2002); Krammer (2003); Van De Vijver et

144   al. (2004); Antoniades et al. (2008); Kulikovskiy et al. (2010); Zimmermann et al. (2010);

145   Lange-Bertalot et al. (2011); Levkov (2013).

146   ***Data analysis***

147   Detrended correspondence analysis (DCA) was conducted to estimate the length of the gradient

148   on the square-root-transformed diatoms abundance data. Due to the large length of the gradient

149   (> 5 SD), a Principal Coordinates Analysis (PCO) was used based on Hellinger distances to

150   reveal the structure among the sampled diatom assemblages (Legendre & Legendre 1998). Only

151   diatoms with abundances >1 % in at least one sample were included in the PCO, which was

152   performed using CANOCO 5.0 (ter Braak & Šmilauer 2012).

153   Diatom assemblage diversity was calculated in terms of species richness (S) and the exponential

154   of Shannon's entropy [exp(H)], which is more appropriate than classical diversity indices for

155   assessing statistically independent measures of alpha (α) and beta (β) diversity (Jost 2007). For

156   each habitat type (lentic and lotic), diversity (D) was partitioned into α, β, and gamma (γ; total

157   diversity) components following Jost (2007). Beta diversity was used as a measure of the

158   differences in the species composition between habitat types. Evenness was calculated using two

159   diversity orders. The first, of order 1, is based on Shannon entropy (EF_1) and the second, of order

160   2 (EF_2) is based on Simpson's diversity metric (Jost 2010). Hence, EF_2 is an approach to the

161   proportion of the dominant species in the assemblage, whereas EF_1 also takes into account all the

162   common species in the assemblage.

163   In order to recognize a discontinuous subset of samples, a K-means clustering with the optimal

164   number of groups chosen according to the Calinski-Harabasz pseudo-F-statistic was performed

165   (Legendre & Legendre 1998). The ecological indicator values for each diatom taxon were

166   identified to assess the ecological preferences of individual species for each of the clusters. The

167   Indval-index was employed to control the effects of unequal size of groups (De Cáceres &

168   Legendre 2009).

169 All analyses of diversity metrics were performed using the R statistical program (R v. 3.0.2.;

170 http://www.r-project.org/) and additional functions from the R-packages "vegetarian" v. 1.2 ,

171 "vegan"v. 2.2-1 and "indicspecies" v. 1.7.4 to calculate Indval-index.

172

Results

174 A total of 216 benthic diatom taxa belonging to 44 genera were identified from the 18 samples

175 from FJL. Seventy-two taxa occurred only in lentic (ponds/lakes) environments, 42 occurred

176 only in lotic (streams) environments, while the remaining taxa were found in both habitats. The

177 checklist of all taxa with their means, highest abundances, and biogeographic distributions

178 (circumpolar versus widely distributed) are found in Appendix 1. Widely distributed species, or

179 those with broader distribution than circumpolar, dominated the samples by cell numbers, but

180 more circumpolar taxa dominated species richness (Appendix 1). In lotic ecosystems, the

181 following widely distributed taxa were dominant: *Diatoma problematica, Fragilaria capucina*

182 (complex), *Rossithidium petersenii, Diatoma tenuis, Eucocconeis laevis, Psammothidium*

183 *marginulatum, Nitzschia homburgensis, Meridion circulare, Achnanthidium minutissimum* sensu

184 lato*, Psammothidium kryophilum* and *Hannaea arcus*. Taxa such as *P. marginulatum* and *A.*

185 *minutissimum* sl. are composed of a mix of widely distributed and circumpolar taxa. Four other

186 circumpolar taxa had abundances > 9%: *Encyonema fogedii* (complex)*, Cymbella botellus,*

187 *Psammothidium* sp1*,* and *Cymbella cleve-eulerae*. Several widely distributed taxa showed high

188 abundances in lentic environments, including: *Nitzschia alpina, Tabellaria flocculosa,*

189 *Encyonema silesiacum, Naviculadicta digitulus*, and *Humidophila gallica*. In contrast,

190 circumpolar taxa such as *Chamaepinnularia gandrupii, Fragilaria* cf. *perminuta, Nitzschia* cf.

191 *sublinearis*, and *Hippodonta arctica* had lower abundances in lentic habitats (Fig. 2). Two

192 widely distributed taxa showed similar patterns of dominance in both lotic and lentic habitats:

193 *Diatoma tenuis* and *Hygropetra balfouriana*. A number of taxonomically unidentified forms

194 were also observed (Appendix 1).

195 Ponds supported 82 circumpolar taxa and streams 62. Mean taxa richness per sample was 41 (±

196 12 sd) for ponds and 33 (± 16 sd) for streams, although this difference was not significant (t-

197 test=1.20, p > 0.05). A similar pattern was observed for diversity metrics (Fig. 3). β-diversity

198 showed large differences between stream and pond habitats (β-diversity of order 1; $H_\beta^1 = 3.4$ for

199 streams and $H_\beta^1 = 2.8$ for ponds). Stream samples showed higher variability compared to ponds

200 (Fig. 4).

201 One stream sample from Cape Flora was dominated by *Diatoma problematica* (80% of the

202 assemblage), and was removed for further analysis (FJ03, table 1, Fig. 2). K-means cluster and

203 PCO analysis showed five main assemblages (excluding FJ03 sample). The first PCO component

204 explained 18.9% of the variability, and showed some overlap between ponds/lake and stream

205 diatom assemblages. On the negative end of this first component, the species with higher

206 correlation were *R. petersenii, P. marginulatum* and *Cymbopleura stauroneiformis* (Fig. 4);

207 *Caloneis holarctica, Nitzschia* cf. *sublinearis*, and *Stauroneis subgracilis* were at the positive

208 end of Component 1 (Fig. 4). Additionally, stream diatom assemblages were separated in two

209 groups along the second PCO axis, which explained an additional13.6% of diatom assemblage

210 variability (Fig. 4). Negative scores were mainly associated with northern sites (Nansen, Wilton,

211 and Kuhn islands), with *Eunotia bilunaris, Neidium bisulcatum, Humidophila ingeiiformis*, and

212 *H. laevissima* showing the highest correlation. On the positive end of PCO 2, the species with the

213 highest correlation were *Amphora copulata, E. fogedii* (complex)*, Psammothidium bioretii,*

214 *Encyonema* cf. *spitsbergense, and E. laevis* (Figs 2, 4). The third PCO axis explained an

215   additional 10.1% of variability, which separated lake samples (cluster 4) from the other habitats.

216   Widely distributed species such as *Encyonema reichardtii, E. silesiacum, Staurosirella pinnata,*

217   *Nitzschia alpina, and N. digituloides* had the greatest influence in the lake cluster.

218   In order to further identify representative species for each cluster, species indicator values

219   (Indval) were applied. Cluster 4 (lakes) was characterised by more widely distributed species,

220   which were highly correlated with PCO axis 3. Cluster 2, which had the highest species richness

221   and diversity, was characterised by aerophilic Arctic species: *Caloneis fusus, Humidophila*

222   *paracontenta, Caloneis fasciata, H. laevissima*, and *Luticola paleoarctica*, as well as a high

223   abundance of *C. gandrupii*. In addition, *Nitzschia homburgensis*, which has a broad

224   biogeographic distribution (Fig. 2), was also found in cluster 2. Cluster 3 was characterized by

225   circumpolar species such as *C. gandrupii, C. holartica, N.* cf. *sublinearis, Nitzschia* sp.A, *and*

226   *Sellaphora rectangularis* sensu lato (Fig. 2). Cluster 5 consisted mainly of *C. stauroneiformis,*

227   *Gomphonema nathortsii, Psammothidium* sp1, and *Eunotia scandiorussica*. Cluster 1 consisted

228   of three cosmopolitan species, *A. copulata, Encyonema laevis*, and *Nitzschia* cf. *acidoclinata*,

229   along with one widely distributed species - *E. fogedii* (complex). In addition, some circumpolar

230   species such as *Gomphonema lapponicum, Amphora dusenii*, and *Amphora spitzbergensis* only

231   occurred in samples from this cluster (Fig. 2).

232   Although, diversity measures did not show significant differences between stream and ponds,

233   statistical differences were observed among clusters. Cluster 2 (Fig. 5) showed the highest

234   diversity and richness per sample. This group consisted of two stream samples (Kuhn and Wilton

235   islands) and three pond samples (Cape Tegetthoff, Cape Flora, and Tikhaya Bay). Measures of

236   equitability showed that higher richness was mainly due to the codominance of "satellite"

237   species rather than the codominance of only dominant ones. This higher richness was significant

238   for EF_1 but not for EF_2 (Fig. 5).

239   **Discussion**

240   ***Diversity and distribution patterns***

241   The reported number of diatom taxa per sample in our study was similar to previous Arctic

242   surveys (Douglas & Smol 1995; Laing et al. 1999; Weckstrom & Korhola 2001; Antoniades &

243   Douglas 2002; Michelutti et al. 2003; Jones & Birks 2004; Antoniades et al. 2005). However,

244   these surveys also sampled surface sediments, which could have increased the number of

245   observed taxa per sample. Surface sediment samples often integrate a disparity of habitats over

246   time. Our study also found many diatom morphotypes that could not be identified, illustrating

247   that taxa still need to be described, and supporting the recognition of high diversity and richness

248   of freshwater diatoms across the Arctic (Foged 1981; Antoniades et al. 2008; Pinseel et al.

249   submitted). Many species (new Arctic taxa) are presently included within species complexes

250   (e.g. *A. minutissimum*, *N.* cf. *perminuta, E. cf. fogedii, P. marginulatum*) or yet to be described

251   (e.g. *Psammothidium* sp1).

252   The large compositional turnover among samples (5.3 sd in the DCA) indicates large differences

253   in diatom assemblages among sites. The main source of diatom assemblage variability was

254   related to habitat (PCO axis 1; lotic versus lentic). Nevertheless, two clusters (2 and 5; Fig. 4)

255   had samples from both lotic and lentic habitats, similar to findings from Spitzbergen (Pinseel et

256   al. submitted). Small pond assemblages could be largely influenced by the arrival of taxa from

257   streams (Antoniades & Douglas 2002), and conversely streams with low velocity (discharge)

258   could support lentic assemblages. Unfortunately, we do not have stream velocity or water

259   residence time data to confirm these observations. However, characteristic taxa of stream

260 habitats in FJL, such as *R. petersenii* and *F. capucina* (complex), were also common in FJL pond

261 samples. This observation indicates that pond diatom assemblages in FJL may be influenced by

262 streams, as observed in other Arctic regions (Antoniades & Douglas 2002; Pinseel et al.

263 submitted). Therefore, the dominance of stream taxa in pond sample FJ07 suggests a large

264 influence of stream species. The same reasoning can be applied to the pond samples in cluster 2

265 (FJ04, FJ06, and FJ15), but results are less evident. This cluster, showed higher richness and

266 diversity, with a dominance of circumneutral/slightly acidic taxa (pH optima ca. 6.8–7.2) such as

267 *C. gandrupii*, *H. gallica, H. laevissima, P. marginulatum, N. homburgensis*, and *H. balfouriana*

268 (Antoniades et al. 2004; Antoniades et al. 2008). On the PCO biplot, cluster 1 (Fig. 4, with only

269 stream samples), was characterised by the presence of alkaliphilic taxa [optimum pH 8.0–8.3 in

270 Antoniades et al. (2008)] such as*, E. laevis, P. bioretii, E. fogedii* (complex)*, A. copulata*, and *A.*

271 *inariensis*. Therefore, this second axis of diatom variability is likely correlated with a pH

272 gradient, which is a main source of variability for diatom assemblages (Battarbee et al. 2001),

273 with Algers, Mabel, and Wilkzec islands potentially marking alkaline conditions with higher pH.

274 The pH gradient should be, in part, related to the complex archipelago geology with intrusions of

275 basalt between sedimentary bedrocks (Dibner & Fursenko 1998). However, recent deglaciated

276 areas tend to have increased alkalinity and pH in lakes and streams from bedrock and till

277 exposure (Engstrom et al. 2000; Milner et al. 2007). Thus, lake age (Milner et al. 2007) could be

278 an alternative hypothesis to explain the lower pH optima of the characteristic taxa from cluster 2,

279 rather than changes in the site geological settings.

280 Interestingly, the samples from cluster 2 also showed higher diversity metrics, due to the higher

281 equitability among the non-dominant taxa (EF_1). Less stable environments exposed to physical

282 stressors (e.g. current flow) could impact dominance by minimizing the effects of competitive

283   exclusion and promoting species coexistence (Hughes et al. 2007) maintaining species diversity

284   (Chesson 2000). In Antarctic streams, environmental instability (changes in stream velocity and

285   successive periods of freezing and thawing) promote small cell size, maintaining higher diatom

286   richness (Pla-Rabes et al. 2013), with diatom assemblages showing higher resilience (recovery to

287   pre-disturbance conditions; e.g. flood event) (Stanish et al. 2011). There are indicators to suggest

288   that the biology at some FJL sites support high environmental variability. First, cluster 2 samples

289   are characterised by the presence of aerophilic taxa (*H. laevissima, H. paracontenta*, and *C.*

290   *fusus*), which indicate potential periods of lower water availability, and possibly even

291   desiccation. Second, species from cluster 2 showed lower pH optima (6.8–7.2 in Antoniades et

292   al. 2008) compared to cluster 1 (7.9–8.2 in Antoniades et al. 2008), which means lower buffering

293   capacity in cluster 2 sites, and consequently higher environmental variability. Furthermore, lower

294   alkalinity sites would tend to be older (Milner et al. 2007), and consequently have a higher

295   chance of accumulating species (Adler et al. 2005). Interestingly, cluster 2 sites showed large

296   expanses of ice-free areas (Khun and Wilton Islands), and more human influence (Tikhaya Bay,

297   Cape Tegetthoff, Cape Flora). Nevertheless, our data set did not include samples from the largest

298   ice-free areas located on the largest islands in the archipelago (Alexandre Land and Prince

299   George Land), which could potentially be diversity hotspots due to large biogeographic sizes.

300   ***Biogeographical patterns***

301   The general diatom flora observed in FJL is similar to other circumpolar localities (Cleve 1898;

302   Lange-Bertalot & Genkal 1999; Antoniades & Douglas 2002; Stewart et al. 2005; Antoniades et

303   al. 2008). A comparison of photomicrograph documented taxa in this study (Appendix 2) with

304   Antoniades et al. (2008) for the Canadian Archipelago shows that 67% of the taxa observed in

305   FJL were present in both studies. This indicates a circumpolar distribution, along with some local

306   species selectivity due to microhabitats and regions. In an earlier study, Foged (1981)

307   demonstrated that many more species are present in Arctic microhabitats, but often not recorded

308   due to their rare distributions. Interestingly, a small araphid species flock representing

309   *Staurosirella, Staurosira*, and *Pseudostaurosira,* was scarce in FJL, with only *S. pinnata*

310   abundant and characteristic of pond samples in cluster 2. This was also observed in Svalbard

311   (Pinseel et al. submitted). The *Staurosirella, Staurosira*, and *Pseudostaurosira* flocks typically

312   dominate hard substrate habitats in low productivity ponds and lakes across the Canadian and

313   western Russian Arctic (e.g. Metzeltin & Witkowski 1996; Laing et al. 1999; Michelutti et al.

314   2003; Bouchard et al. 2004; Paull et al. 2008). In our study of the twenty most abundant taxa,

315   *Nitzschia* and *Psammothidium* were the most common genera with no clear associations within

316   species flocks. These genera, along with *Achnanthidium*, are indicative of moss and sediment

317   microhabitats. Moss wetlands have a diverse flora with select genera like *Luticola*, *Humidophila*,

318   and *Eunotia* having unique compositions (Douglas & Smol 1995; Van De Vijver et al. 2003).

319   *Luticola* taxa observed from FJL were similar to the Novaya Zemlya Archipelago (Lange-

320   Bertalot & Genkal 1999), while different from the Canadian Archipelago (Antoniades et al.

321   2008). Some common Arctic stream species, such as *Hannaea arcus*, occurred in low

322   abundance at FJL, which could be related to the absence of specific habitat requirements such as

323   high current velocity (Antoniades & Douglas 2002). Likewise, taxa from the genera

324   *Humidophila* and *Placoneis* appeared to be species rich in FJL, which has also been observed in

325   Svalbard (Pinseel et al. submitted). In locations with more productive freshwater habitats, taxa

326   from the family Cymbellaceae (*Cymbella*, *Cymbopleura*, and *Encyonema*) are noted to be

327   abundant, with greater species richness, and widely distributed across microhabitats (Douglas &

328   Smol 1995; Michelutti et al. 2003). Except for *C. gandrupii*, currently recognized circumpolar

329 taxa do not dominate FJL assemblages, although species richness is clearly linked to circumpolar

330 and regionally endemic taxa (Fig. 2).

331 Geographic dispersal, especially with respect to a potential circumpolar flora, requires

332 mechanisms that are inherently controlled by climate. Freshwater organisms such as diatoms

333 could be dispersed by air as well as organisms such as birds, fishes, or mammals (Kristiansen

334 1996). Interestingly, Nansen (1897) documented a similarity in diatoms and microbes in melt

335 water pools from the Bering Strait and Greenland, and along with other observations, proposed

336 that drifting ice could pass across the North Pole. Cleve (1898) was the first to suggest a

337 potential circumpolar distribution of diatom species. Arctic drift ice has preferential pathways

338 throughout the Arctic region and has been found to transport viable freshwater algae such as

339 diatoms (Cleve 1898; Abelmann 1992; Pfirman et al. 1997). Therefore, drifting ice could be an

340 important mechanism for dispersal, hence the recognition of a circumpolar flora. Additionally,

341 airborne diatoms could also reach different Arctic regions. For example, dust storms routinely

342 transport particulates from northern Asia to western North America (Chin et al. 2007). In this

343 regards, population genetic studies of diatoms across the Arctic can assist in answering questions

344 of biogeographic distribution (Hamilton et al. 2015). Specifically, population genetics may help

345 identify potential vectors of migration like drifting ice trajectories, atmospheric wind patterns,

346 and bird migration pathways.

347 Consequently, the concept of circumpolar diatom species is applicable to a broader region

348 including northern boreal regions from the Palearctic and Nearctic areas. For instance, the

349 presence of *Boreozonacola hustedtii* recently described from a Mongolian peat-bog (Kulikovskiy

350 et al. 2010), has been found in Siberia (Lange-Bertalot & Genkal 1999), Lapland (Lange-Bertalot

351 & Metzeltin 1996), Canada (Zimmermann et al. 2010), the Rocky Mountains USA (Bahls 2010),

352 and in FJL.

353 ***Future scenarios of diversity***

354 Franz Josef Land Archipelago is a "zakaznik" Russian protected area (nature refuge

355 corresponding to IUCN IV). As in Antarctica, climate change and an increasing human footprint

356 are the two main threats for conservation in FJL (Chown et al. 2012). However, due to the poor

357 knowledge of diatom distribution and ecology, it is difficult to predict future changes in

358 productivity and diversity. Current predictions are theoretical using knowledge from other

359 regions and ecological theory.

360 Arctic biodiversity has been exposed to strong selection mechanisms in harsh and fluctuating

361 environments (glaciation/deglaciation periods) for millennia. However, at present we consider

362 rapid climate change as the main factor impacting biodiversity in polar ecosystems (Millennium

363 Ecosystem Assessment 2005). In addition to climate change, increasing human activity (e.g.,

364 shipping, mining, fishing, tourism) in the Arctic are new stressors that need to be assessed, as

365 well as other stressors such as global atmospheric pollution and species invasions, which could

366 push the Arctic ecosystems to unknown scenarios (Larsen et al. 2014). All these threats imply

367 rapid changes in the local environments (habitat change) and associated environment

368 connectivity (dispersal mechanisms); both factors will modify the FJL freshwater ecosystems

369 and communities.

370 Rapid environmental change can lead to a reduction in species richness and diversity (extinction

371 event), which is often followed by a transition to novel communities dominated by generalist

372 species with broader niches (Blois et al. 2013). This scenario represents a possible negative

373   impact on specialized circumpolar taxa, with lower densities in FJL and other Arctic regions.

374   There is a decreasing diversity gradient from the equator to the poles, although it is weaker and

375   patchier for freshwater compared to terrestrial ecosystems (Hillebrand 2004). Paleolimnological

376   records across the Arctic region indicate that recent climate warming has driven diatom

377   compositional changes with an increase in local diatom richness. These changes have been

378   related to an increase in the length of the growing season (ice-free period), which increase habitat

379   availability and the structural complexity of diatom communities (e.g. development of complex

380   of periphytic communities) (Smol et al. 2005; Lim et al. 2008). An increase in air temperature,

381   and consequently an increase in the length of the ice-free season (growing period) would

382   facilitate the establishment of species from warmer regions (i.e. Lapland, low tundra in the

383   Canadian Arctic), as has been observed in other ecosystems (Dornelas et al. 2014). The

384   introduction of species would be accelerated by the expected increase in connectivity among

385   Arctic regions due to an increase in the human footprint. In addition, an increase in temporal

386   climate variability (seasonal and inter-annual) could promote species coexistence by reducing

387   competitive exclusion through fluctuation-dependent mechanisms such as storage effect and

388   relative nonlinearities of competition (Chesson 2000). Our data show that sites with higher

389   diversity are characterized by the presence of slightly acidophilic and aerophilic species (cluster

390   2), which indicate fluctuating environmental conditions.

391   However, to sustain local species diversity, the total surface area of available habitat must be

392   maintained. Despite the lower surface area-taxa richness relationship in high latitude regions and

393   in freshwater ecosystems, it is higher for islands (Drakare et al. 2006). Hence, in the short-term,

394   FJL will increase aquatic freshwater habitats due to melting ice as reported from other similar

395   arctic regions (e.g. Pinseel et al. submitted). In the long-term, the expected decrease of water

396   bodies in the Arctic related to climate warming such as changes in the permafrost (i.e. loss of

397   thermokarst lakes) (Larsen et al. 2014) and a reduction of ice would lower habitat availability,

398   despite the observed pole-ward transport of moisture (Zhang et al. 2012). Consequently, we

399   would expect a short term increase in diversity due to a warmer climate, followed by a decrease

400   due to habitat loss.

401   At the global scale there are predicted increases in rates of extinction, particularly in the polar

402   regions (Millennium Ecosystem Assessment 2005). However, there is evidence that biodiversity

403   will remain constant or even increase over time (Vellend et al. 2013; Dornelas et al. 2014),

404   including human impacted areas and isolated oceanic islands (Sax et al. 2002). This apparent

405   contradiction (species loss versus gain) is due to different scales of study and measures of

406   diversity, which need to be taken into account when considering biodiversity patterns (McGill et

407   al. 2015). For instance, an increasing trend in local α-diversity could parallel a decreasing trend

408   in global β-diversity (Sax & Gaines 2003; Dornelas et al. 2014; Magurran et al. 2015).

409   One of the main factors determining β-diversity is regional connectivity and habitat

410   heterogeneity. The general expected increase in human footprint related activities across

411   circumpolar regions (e.g. tourism, polar transport, fishing, and natural resource extraction) would

412   increase the homogenization of communities across the Arctic, therefore reducing β-diversity.

413   Conversely, if drifting sea-ice has been enhancing FJL diatoms α-diversity by facilitating

414   propagule dispersion, then a reduction in sea-ice would increase β-diversity. This change in

415   diversity could be offset by an increase in human visitation. Ice-floe trajectories over FJL

416   archipelago show two main sources: one from the Ob and Yenisei rivers through the Kara Sea,

417   and the other from the Lena River and New Siberian Islands (Novosibirskiye Ostrova

418   Archipelago) through the Láptev Sea (Pfirman et al. 1997). FJL diatoms suggest connections

419   with these northern Siberia areas. The continuous arrival of freshwater diatoms from northern

420   Siberia could also stabilize populations of rare diatom species (low abundance) species, which

421   would otherwise become extinct in a harsh and fluctuating environment.

422   In the short term, the α-diversity of FJL diatoms is expected to increase with climate warming in

423   association with an increase in human activities. In contrast, β-diversity (circumpolar) is

424   expected to decrease due to an increase in circumpolar connectivity resulting from stressors

425   related to an increase in anthropogenic activities. However, in the longer-term, an expected loss

426   of freshwater bodies and habitat diversity could reduce diatom populations and increase

427   competitive exclusions and therefore local species extinctions (decreasing α-diversity; Fig. 6).

428   This process would be worse for rare species, which are mainly of circumpolar distribution or

429   regionally distributed. We could argue that Arctic species have adapted to past climate

430   fluctuations and will be able to persist. However, the human footprint will compound the impact

431   of isolation due to less sea-ice (extension and duration), which has occurred in past warmer

432   periods, consequently producing a net loss in β-diversity (Fig. 6). Therefore, local α-diversity

433   could not be replenished as fast as in previous periods with the return of a new colder climate

434   period in association with a parallel increase in connectivity across the Arctic Ocean.

435   Our discussion is founded on the novelty of the recent warming (habitat change), which parallels

436   an increase in Arctic human activity (dispersal facilitation). However changes in other

437   environmental and dispersal factors such as bird migration pathways, and atmospheric and ocean

438   circulation modes could also affect the distribution of circumpolar diatoms. Furthermore, the

439   sensitivity and adaptability of diatoms to environmental change are also dependent on

440   endogenous factors (e.g. genetic diversity, phenotypic plasticity, species traits, populations

441   density, fitness, dispersal ability, persistence, etc.), which are likely to modulate a disparity in

442   diatom responses to external threats and consequently their vulnerability and future distribution

443   (Dawson et al. 2011).

444   Finally, the low frequency of small araphid species flocks such as *Staurosirella, Staurosira*, and

445   *Pseudostaurosira*, also observed in Svalbard (Pinseel et al. submitted), has interesting

446   biogeographic implications. A better distributional record of these taxa across the circumpolar

447   region is required including the need to explore more freshwater habitats in the FJL Archipelago,

448   such as hard substrate habitats, ponds, and stream that are largely influenced by sea birds

449   colonies, as well as other factors, to characterize the complete diatom diversity of this isolated

450   and northern archipelago.

451   To conclude, there is an urgent need to explore the Arctic to understand, predict, and mitigate

452   future environmental change scenarios to preserve this unique ecosystem. In this regard,

453   monitoring programs and/or paleolimnological approaches using diatoms as environmental

454   indicators could be used as early warnings of environmental changes.

455

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462

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649   **Tables & Figures**

Code	Locality	NN	EE	Habitat	Date	S	ExpH	Simpson	EF-1	EF-2
FJ01	Cape Flora, Northbrook Island	79.9453	50.1295	pond 1	5 August	37	5.8	3.3	0.156	0.089
FJ02	Cape Flora, Northbrook Island	79.9453	50.1295	pond 2	5 August	30	10.3	6.7	0.345	0.224
FJ03	Cape Flora, Northbrook Island	79.9453	50.1295	stream	5 August	9	1.9	1.5	0.212	0.165
FJ04	Cape Flora, Northbrook Island	79.9453	50.1295	pond 3	5 August	35	10.8	7.4	0.307	0.211
FJ05	Cape Flora, Northbrook Island	79.9453	50.1295	pond 4	5 August	34	12.4	8.4	0.365	0.248
FJ06	Tikhaya Bay, Hooker island	80.3362	52.7758	pond 1	31 July	64	26.8	14.1	0.418	0.220
FJ07	Tikhaya Bay, Hooker island	80.3362	52.7758	pond 2	31 July	40	9.4	5.6	0.234	0.139
FJ08	Wilczeck Land	80.6109	61.9859	stream	15 August	18	8.7	7.0	0.483	0.388
FJ09	Mabel Island	80.0193	49.3579	nearshore stream	25 August	31	5.7	3.3	0.183	0.105
FJ10	Mabel Island	80.0193	49.3579	uphill stream	25 August	21	7.1	4.8	0.340	0.227
FJ11	Nansen Island	80.5502	54.1329	glacier stream	23 August	36	13.3	8.7	0.369	0.243
FJ12	Mabel Island	80.0111	49.3791	small lake 1	21 August	36	12.1	6.8	0.337	0.189
FJ13	Mabel Island	80.0111	49.3791	small lake 2	21 August	36	13.5	8.4	0.376	0.234
FJ14	Wilton Island	80.5613	54.3557	stream	23 August	64	25.2	15.0	0.393	0.234
FJ15	Cape Tegethoff, Hall Island	80.0926	58.0584	nearshore pond	11 August	59	30.8	17.3	0.522	0.294
FJ16	Kuhn Island	81.1047	58.3721	small stream	9 August	48	18.2	9.9	0.379	0.206
FJ17	Alger Island	80.3529	56.1413	small stream 1	14 August	36	9.4	5.2	0.261	0.144
FJ18	Alger Island	80.3820	55.7698	small stream 2	14 August	35	11.7	7.8	0.334	0.222

650   **Table 1** Sample localities, geographic coordinates, habitat type and sampling date. NN (latitude N.), EE (longitude E), S (species
651   richness), ExpH (exponential of Shannon Entropy), Simpson (Simpson diversity index), EF-1 evenness of order 1 and EF-2 evenness
652   of order 2 (Jost, 2010).

Figure captions

Figure 1 Diatoms samples localities in Franz Josef-Land Archipelago. Orange dots denote stream samples, and green dots pond samples. Numbers are sample codes from table 1.

Figure 2. Dot plot of FJL diatom assemblages for all samples sites and diatoms with higher abundance (> 2%). Species are sorted across PCO axis 2 scores (pH gradient). Samples are sorted across the PCO axis 1 (from ponds to streams). Sites in blue denotes stream habitat. Symbol size indicates the relative abundance of each taxa for each site. Symbols colour indicates *Indval* value for species in each K-means cluster. Symbol shape denotes species geographic distribution.

Figure 3. Stream and pond (including lake) samples diversity metrics boxplots. Evenness-F1 and Evenness-F2 are evenness factor of order 1 and of order 2 following Jost (2010).

Figure 4 PCO results. Ellipses are grouping results of K-means cluster analysis. Only the 25 species with highest correlation with one of the two main axes are showed. Numbers in red denotes K-means cluster. Squares denote stream samples and circles ponds samples. Full species names are reported in Appendix 1.

Figure 5 Diversity metrics boxplots for each k-means clusters (see plot legend). Evenness-F1 and Evenness-F2 are evenness factor of order 1 and of order 2 following Jost (2010).

Figure 6. Hypothetical models on how species richness changes on two different warming scenarios. (A) Past warming periods; a.1) Increasing temperature would promote a rapid increase in FJL α-diversity, but a decrease of circumpolar β-diversity due to biotic homogenization across the arctic. a.2) Shortly, the lower extension and duration of circumpolar sea-ice would increase isolation among circumpolar regions, and different species would be locally selected. This isolation would reverse the previous decreasing trend in β-diversity. a.3) However, later on, an expected generalized loss of freshwater ecosystems and the consequent increase in local competitive exclusion would reduce FJL α-diversity. On the end of a warm period cycle (a.4) a net increase on circumpolar diversity (γ-diversity) would be expected by local speciation. (B) Anthropocene warming scenario. Would be expected similar changes on α-diversity, however, the higher expected human frequentation would increase connectivity, which would cancel out the positive effects of isolation on β-diversity. This expected homogenization of circumpolar diatom flora due to higher connectivity and the expected habitat lost (climate warming) could reduce the overall γ-diversity with a net loss of circumpolar species.

686 **Figure 1**

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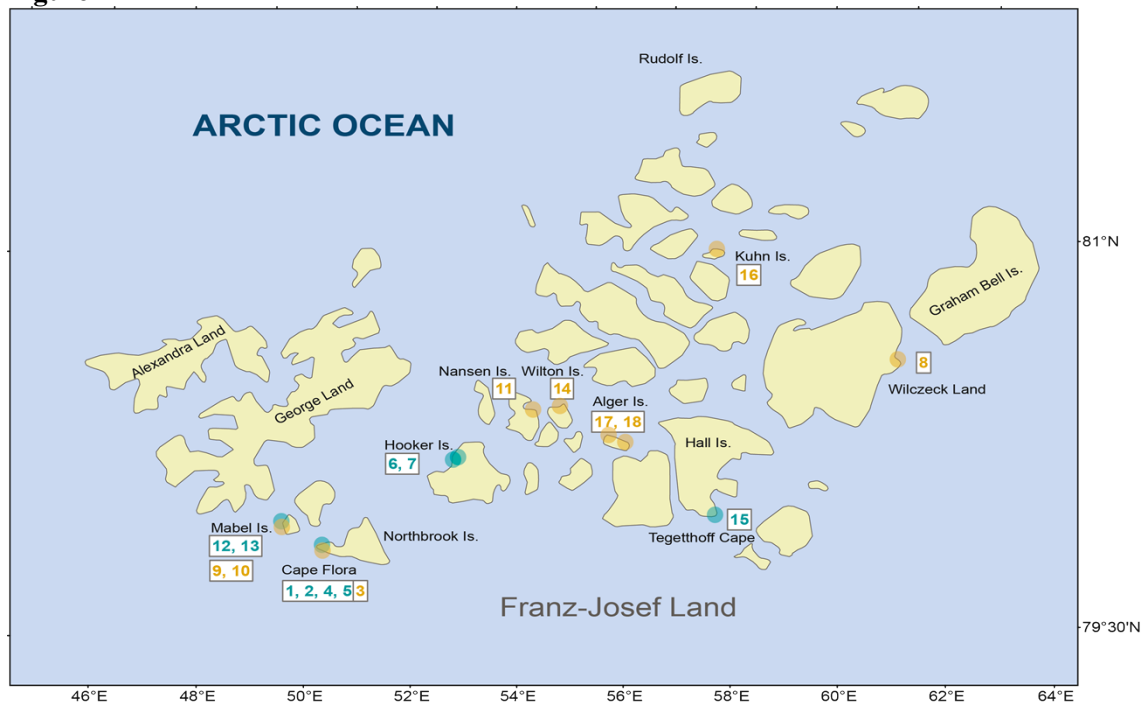
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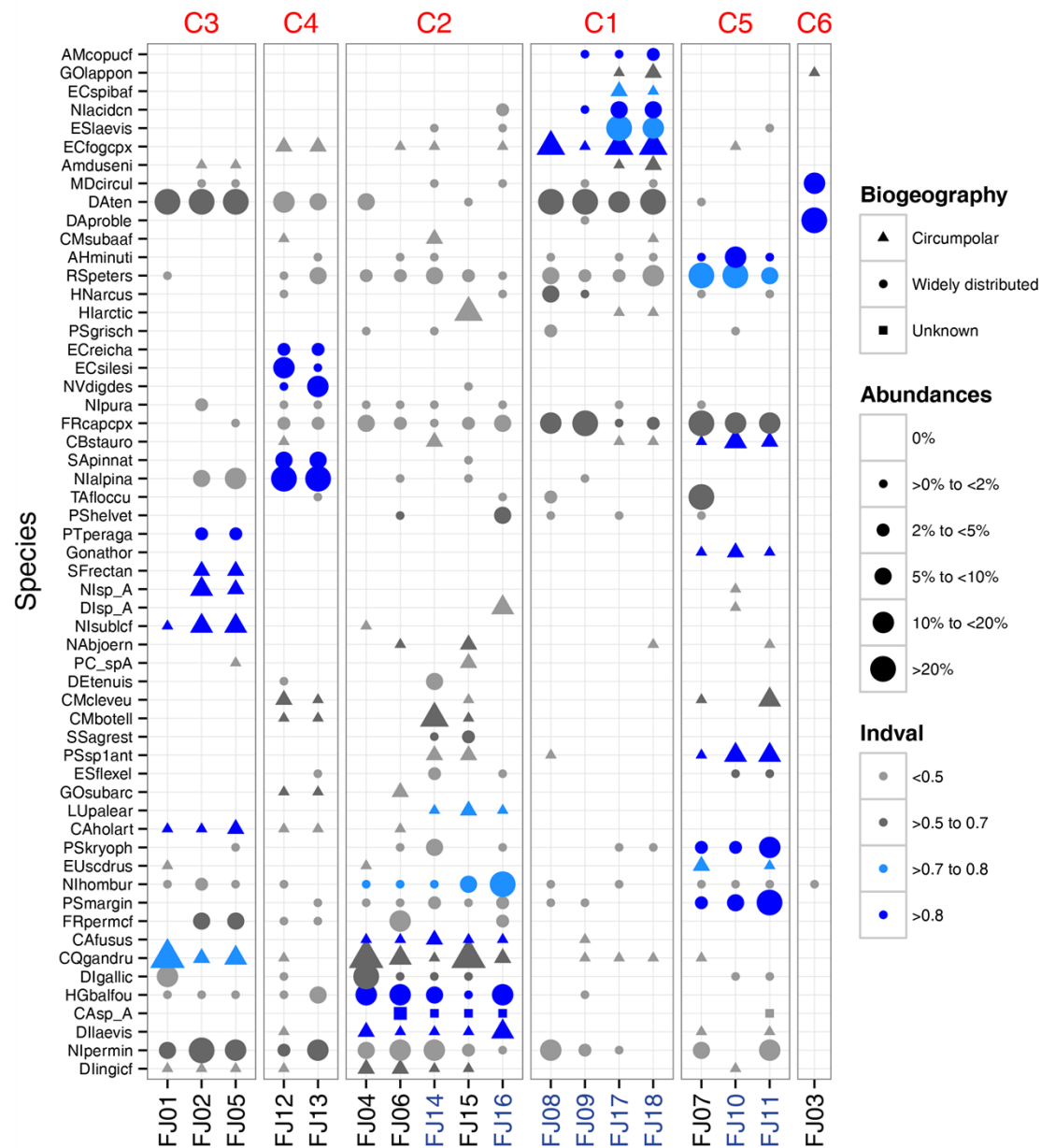
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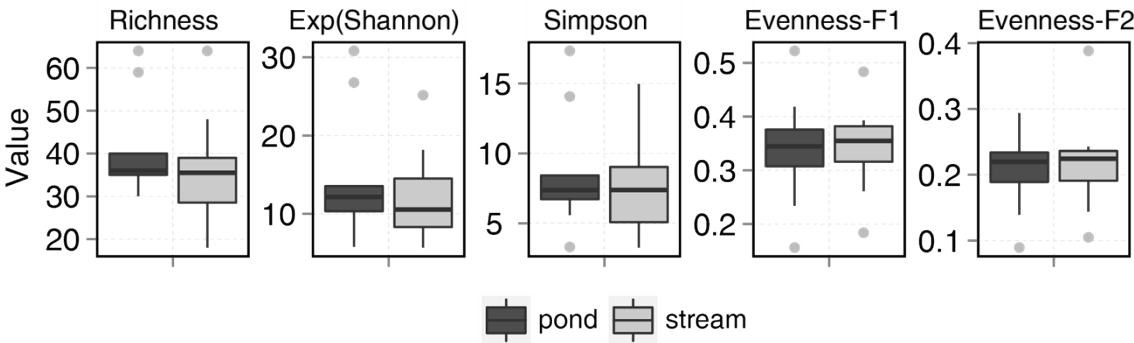
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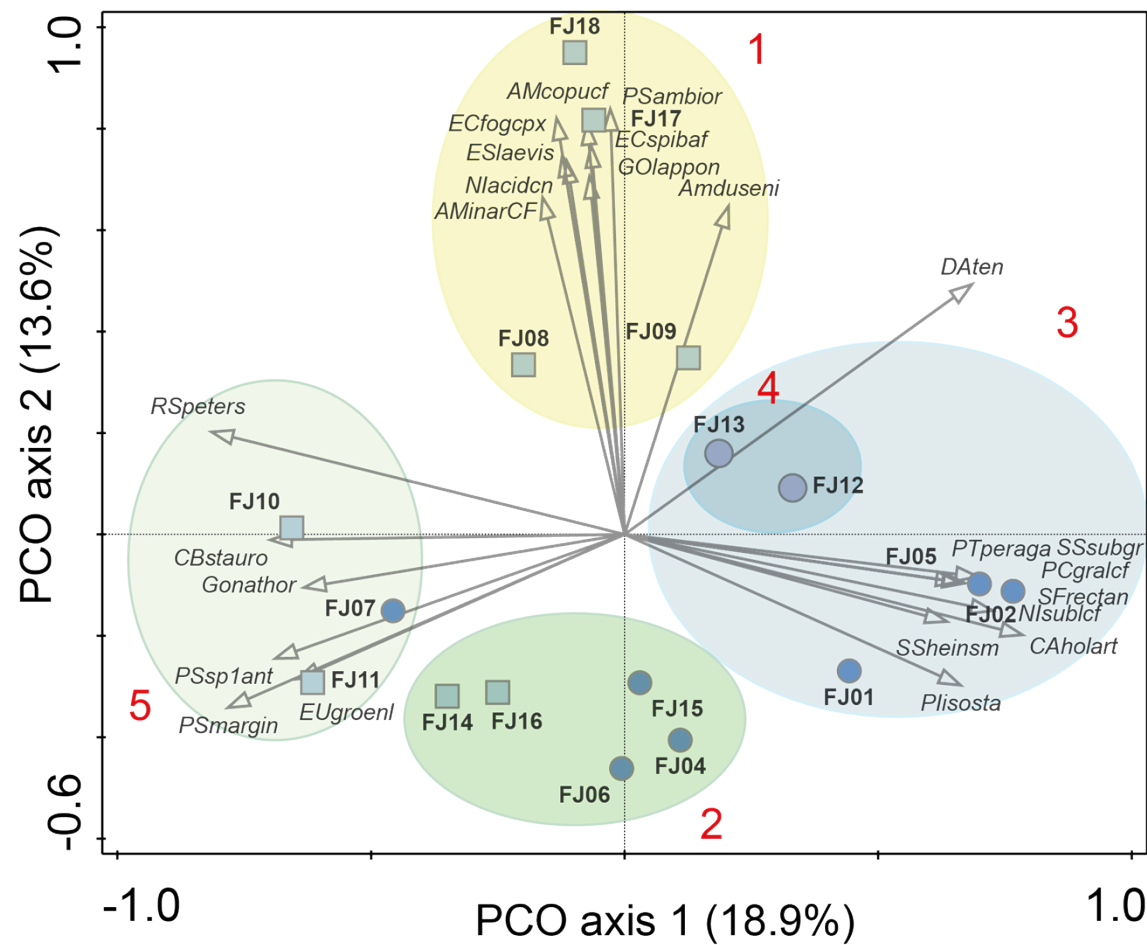
696   **Figure 4**

699 **Figure 5**

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702 **Figure 6**

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