1 **Circumpolar patterns of Arctic freshwater fish biodiversity: A baseline for**

2 **monitoring**

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37 **Summary**

38 1. Climate change, biological invasions, and anthropogenic disturbance pose a threat to the

39 biodiversity and function of Arctic freshwater ecosystems. Understanding potential changes

40 in fish species distribution, richness, and additional biodiversity components is necessary,

41 given the importance of fish to the function of freshwater ecosystems and as a resource to

42 humans. However, large information gaps limit large-scale studies and our ability to

43 determine patterns and trends in space and time. This study takes the first step in determining

44 circumpolar patterns of fish species richness and composition, which provides a baseline to

45 improve both monitoring and conservation of Arctic freshwater biodiversity.

46 2. Information on species presence/absence was gathered from the Circumpolar Biodiversity

47 Monitoring Program's Freshwater Database, and used to examine patterns of freshwater fish

48 gamma, alpha, and beta diversity across 240° of longitude in the Arctic. The metrics of

49 diversity provided information on species richness and composition across hydrobasins,

50 ecoregions, and Arctic zones.

51 3. In analyses of all available fish data, circumpolar patterns of fish species biodiversity varied

52 with latitude, isolation, and coarse ecoregion characteristics; patterns were consistent with

53 historic and contemporary barriers to colonization and environmental characteristics. Gamma

54 diversity was reduced in the high Arctic compared to lower latitude zones, but alpha diversity

55 did not decline with increasing latitude below 71°N. Alpha diversity was reduced to a single

56 species in ecoregions farther north where gamma diversity was lowest. Beta diversity

57 indicated little variation in the composition and richness of species across the High Arctic;

58 but at lower latitudes, ecoregions contained additional fish species whose composition turned

59 over across large spatial extents.

60 4. In an analysis of five ecoregions around the Arctic, isolation, area, and topography were

61   identified as strong drivers of gamma, alpha, and beta diversity. Physical isolation reduced

62   the gamma and alpha diversity, and changes in beta diversity between adjacent locations

63   were due mainly to losses in species richness, rather than due to differences in species

64   composition. Heterogeneity of habitats, environmental gradients, and geographic distance

65   likely contributed to patterns of fish dissimilarity within and across ecoregions.

66 5. This study marks the first attempt to document large-scale patterns of freshwater fish

67   biodiversity in the circumpolar Arctic. However, information gaps in space, time, and among

68   taxonomic groups remain. Working towards inclusion of extensive old and new data will

69   allow future studies to test for changes in the observed patterns of biodiversity. This is

70   important given the potential impacts of climate change, land use, and biotic exchange on

71   Arctic fish biodiversity in the future.

72

73

Introduction

74

75   Global change threatens the biodiversity and functions of all ecosystems (Sala et al.,

76   2000), and Arctic ecosystems are no exception (Meltofte, 2013). Maintenance of freshwater

77   biodiversity is crucial to the healthy function of Arctic ecosystems and to the preservation of

78   ecosystem services provided to humans (Culp et al., 2012; Socolar, Gilroy, Kunin, Edwards,

79   2016; Wrona et al., 2013). However, Arctic freshwater ecosystems are vulnerable to multiple

80   pervasive and localized stressors, including climate warming, biological invasions and direct

81   anthropogenic disturbance (Rolls et al., 2017; Wrona et al., 2013). Scenarios of changing

82   biodiversity show that Arctic ecosystems are currently overwhelmingly influenced by climate

83   change when compared to other factors (e.g., land use, biotic exchange, carbon dioxide and

84   nitrogen deposition), but this may change as global economic interests increase in Arctic regions

85   (Hovelsrud, Poppel, van Oort, & Reist, 2011; Huntington et al., 2007). The effects of each of

86   these stressors alone and in combination, though often difficult to determine (Hayden,

87   Myllykangas, Rolls, & Kahilainen, 2017; Schindler & Smol, 2006; Wrona et al., 2006), may

88   impact the fishes that live in Arctic streams and lakes; and ongoing and future changes in climate

89   and land use will likely have profound effects on fish species biodiversity (Rolls et al., 2017;

90   Wrona et al., 2006).

91   Understanding potential changes to fish species distribution and richness is highly

92   relevant to monitoring and conservation efforts because of the importance of fish to humans

93   (Berkes & Jolly, 2002; Hu, Laird, & Chan, 2017) and because fish contribute to the structure and

94   function of Arctic aquatic food webs (Eloranta et al., 2015; Reist et al., 2006; Thomas, Harrod,

95   Hayden, Malinen, & Kahilainen, 2017; Wrona et al., 2006). Large information gaps exist,

96   however, in our knowledge of Arctic freshwater fish distribution and ecology, and patchy

97   collections of species data limit relevant studies on large-scale biodiversity, compromising the

98   ability of managers to assess patterns and trends in biodiversity (Christiansen et al., 2013;

99   Comte, Buisson, Daufresne, & Grenouillet, 2013; Stendera et al., 2012). However, understanding

100   the relationship between locally-collected data and regional biodiversity patterns is critical for

101   effective and efficient conservation and monitoring of Arctic freshwater fish (Kraft et al., 2011;

102   Leprieur et al., 2011; Socolar et al., 2016).

103   Fish biodiversity is affected by landscape factors that act at multiple spatial and temporal

104   scales (Hewitt, 2000; Poff, 1997; Tonn, 1990). Species distribution, richness, and compositional

105   patterns are controlled by both contemporary and historic environmental features of climate,

106   geology, and morphometry (Dias et al., 2014; Hugueny, Oberdorff, & Tedescco, 2010).

107   Compositional change is often strongly influenced by isolating variables (April, Hanner, Dion-

108   Côté, & Bernatchez, 2013; Leprieur et al., 2011; Mangerud et al., 2004) such as glacial retreat

109   and development, which are responsible for many of the distribution patterns influencing

110   present-day biodiversity. Interestingly, increased dispersal between paleo-connected drainage

111   basins during the last glacial maximum has resulted in higher present-day compositional

112   similarity for regions that were historically linked (Dias et al., 2014). Northern watersheds are

113   generally inhabited by highly migratory species with broad geographic distributions

114   (Christiansen et al., 2013; Griffiths, 2006), because strong dispersal abilities of cold-water

115   salmonids promoted rapid recolonization in deglaciated regions in Europe and North America

116   (e.g., Fennoscandia and northeast Canada) (April et al., 2013; Christiansen et al., 2013; Griffiths,

117   2006, 2010; Koljonen, Jansson, Paaver, Vasin, & Koskiniemi, 1999).

118   Dispersal processes and opportunities are an important factor in the geographic

119   distribution and spatial patterns of gamma diversity (i.e., regional species richness), alpha

120   diversity (i.e., local species richness) and beta diversity (i.e., variation in species composition

121   among locations) in Arctic freshwater fishes (Dias et al., 2014; Heino, 2011). Fish communities

122   should be less similar at greater geographic distances because of species identities change along

123   broad spatial gradients (Abell et al., 2008; Anderson et al., 2011; Beisner, Peres-Neto,

124   Lindström, Barnett, & Longhi, 2006; Soininen, McDonald, & Hillebrand, 2007). When

125   communities are not identical, all similarity patterns can be described using two processes –

126   species replacement and loss (Baselga, 2010). These components of beta diversity are commonly

127   referred to as species turnover and nestedness (Baselga, 2010; Koleff, Gaston, & Lennon, 2003).

128   Turnover is the replacement of some species by others along a spatial or environmental gradient,

129   while nestedness refers to a non-random loss (or disaggregation) of species from the richest

130   locality (Baselga, 2010).

131   Understanding the processes that govern beta diversity is important for determining the

132   mechanisms responsible for maintaining biodiversity (Baselga, 2010; Socolar et al., 2016).

133   However, beta diversity patterns are complicated by spatial heterogeneity and spatial extent

134   (Heino, 2011; Leprieur et al., 2011); accordingly, if community comparisons are made across a

135   wide geographic region (e.g., the circumpolar Arctic), spatially structured variation in species

136   composition should be greater than environmental controls (Heino, 2011; Kraft et al., 2011).

137   That is, large-scale effects of continental drift, orogeny, and glaciation would have more

138   influence over patterns in beta diversity than local-scale factors such as habitat area, resource

139   availability, or biotic interactions.

140   Beta diversity studies, which rely on numerous local-scale community investigations (i.e.,

141   alpha diversity studies), provide a method for scaling up local patterns to improve management

142   and conservation of regional or continental species biodiversity (i.e., gamma diversity) (Leprieur

7

143 et al., 2011; Socolar et al., 2016). At continental scales, studies of Arctic fish species diversity

144 show similar patterns of species richness radiating outwards from historic glacial refugia, which

145 resulted in a general decline in species richness to the north and west on both the North

146 American and European continents (Griffiths, 2006, 2010). According to the Arctic Biodiversity

147 Assessment, however, large-scale studies of fish diversity across latitudinal and longitudinal

148 gradients in the Arctic are lacking (Christiansen et al., 2013). The current collection of species

149 richness assessments (e.g., Griffiths, 2006, 2010) and compositional lists (e.g., Christiansen et

150 al., 2013) are valuable, but they do not specifically address spatial patterns of alpha and beta

151 diversity in fishes across the circumpolar region.

152   This study provides a baseline for future monitoring efforts recommended by the Arctic

153 Biodiversity Assessment (CAFF, 2013). Our aim was to evaluate biodiversity patterns in

154 freshwater fish species for the circumpolar Arctic in an effort to determine gamma, alpha, and

155 beta diversity patterns that will inform future monitoring plans. We firstly focused on broad

156 scales and evaluated patterns across the spatial extent of available data. With increasing latitude,

157 we expected a decline in fish species richness, so we hypothesized that both gamma and alpha

158 diversity would decline with latitude; and that alpha diversity would depend on gamma diversity.

159 We further expected that variation in species composition would decline at higher latitudes,

160 where species richness is expected to be lower; and we expected variation in species composition

161 to increase with distance between locations. We hypothesized that beta diversity would decline

162 with latitude, and increase with increasing distance between locations. Furthermore, given that

163 species richness and compositional patterns are often controlled by contemporary and historic

164 environmental features, we hypothesized that alpha, beta, and gamma diversity would differ

165 across regions of differing characteristics. We also anticipated that location and geography

166   would affect regional and local richness, and that reduced regional species richness in isolated

167   and mountainous areas would also limit local richness. Relying on regions with robust data sets,

168   we hypothesized that gamma and alpha diversity would be reduced or species composition

169   would differ for ecoregions of higher elevation (i.e., mountain regions) relative to low elevation

170   regions, and that gamma and alpha diversity would be reduced for isolated regions (i.e., islands)

171   compared to connected regions (i.e., mainland). Finally, we hypothesized that beta diversity

172   would differ regionally, and that variation would arise from both change in species richness and

173   composition.

174

175   **Methods**

176   *Study Area*

177   Ecologically, the circumpolar Arctic often refers to all of the land north of the treeline

178   (Meltofte, 2013). The region is characterized by short, cool summers with periods of 24-hour

179   sunlight that vary in length depending on latitude. Summer marks a short period of productivity

180   in Arctic aquatic ecosystems (Rautio et al., 2011). Conversely, winters are long and cold with

181   periods of polar darkness, and when a seasonal reduction in resources limits species persistence

182   it may ultimately act as a critical factor determining community composition (Hayden, Harrod,

183   Sonninen, & Kahilainen, 2015; Shuter, Finstad, Helland, Zweimüller, & Hölker, 2012). Much of

184   the terrestrial environment is underlain by permafrost. Freshwater habitats are varied, ranging

185   from small streams to large rivers and including small thermokarst ponds and large lakes (Wrona

186   et al., 2013). For the purpose of this paper, we considered the circumpolar Arctic as the area

187   bounded by the subarctic boundary or the Conservation of Arctic Flora and Fauna (CAFF)

188   boundary, for the most inclusive data set (Meltofte, 2013). Collected fish data spanned 234°

189   longitude from Alaska, across the northern Atlantic, to western Siberia and covered 23° of

190   latitude, across all Arctic zones (high, low, and subarctic; Meltofte, 2013) (Figure 1A).

191

192   *Data processing*

193   We extracted fish data from 3168 stations where the assemblage of fish was assessed

194   (Table S1), rather than surveys focused on single species or commercial fishing. Fish data

195   originated from national monitoring databases, government data reports, academic research

196   programs, and industry monitoring programs. The data included 67% lotic stations (n = 2111)

197   and 33% lentic stations (n = 1057). Multiple stations may occur within a single river or lake

198   because multiple studies may have been conducted in the same waterbody, which then used

199   different sites or identifiers, or multiple station arrays may have been designated within a

200   waterbody (e.g., longitudinal stations along upstream-downstream river gradients). Fish data

201   were included for any station using broadly selective gear types (e.g., electrofisher or fyke net) or

202   multiple gears that sampled different components of the assemblage (e.g., hook and line, minnow

203   traps, and gill nets). Because data were collected by different sampling methods across stations,

204   we converted all data to presence/absence to avoid false inferences about abundance differences

205   that were a result of methodological bias. We included all stations that sampled fish using

206   multiple-mesh gill nets because they are commonly used for monitoring (Appelberg, 2000; CEN,

207   2015); however, we acknowledge that some small-bodied fishes (e.g., Gasterosteidae) are not

208   susceptible to gill nets, and that false absences may occur for small-bodied fishes at some

209   stations. When sampling occurred over multiple years, the fish assemblage for a station resulted

210   from consolidating all recorded presences as a binary indicator: present (1) or absent (0). This

211   may obscure temporal changes in species diversity for those stations that are sampled more than

212   once (32% of stations; Table S1).

213   Stations corresponded to three landscape groupings that provided spatial context for

214   analysis. At the largest, circum-Arctic scale, stations occurred in one of four latitudinal zones –

215   the three Arctic zones (Meltofte, 2013) and an additional "boreal" zone that allowed us to retain

216   all stations south of the predefined Arctic zones (Figure 1). At the regional scale, stations were

217   classified by ecoregion according to the Terrestrial Ecoregions of the World (TEOW; Olson et

218   al., 2001), which defines global ecoregions based on distinct assemblages and environmental

219   conditions including climate. The Arctic's TEOW are related to climatic conditions and provide

220   the necessary connection between landscape features (e.g., geology, temperature, precipitation)

221   and the freshwater ecosystem. TEOWs are smaller than the flow-based Freshwater Ecoregions of

222   the World (Abell et al., 2008), which allows for a more detailed view of how geography may

223   influence diversity. For example, five TEOW, including the Arctic Desert [Svalbard], Kola

224   Peninsula Tundra, Scandinavian and Russian Taiga, Scandinavian Montane Birch Forest, and

225   Northwest Russian-Novaya Zemlya Tundra exist within the Barents Sea Drainages Freshwater

226   Ecoregion, yet each of these TEOW have unique landscapes factors that influence freshwater

227   biota (e.g., climate, geology, elevation; Poff, 1997; Tonn, 1990). At the local scale, stations were

228   grouped into hydrobasins, which are global catchments standardly-derived at different spatial

229   scales (Lehner & Grill, 2013). Hydrobasin scales range from level 01, which is at the continent

230   scale, to level 12 at the smallest sub-basin scale. Stations were classified for small-scale analysis

231   based on the intersection of level 07 hydrobasins (mid-scale sub-basins) and Arctic TEOW (level

232   07 hydrobasin × TEOW intersection, hereafter, hydrobasins), to ensure grouping based on both

233   drainage basin and climatic conditions (Figure S1). All station classifications (zone, ecoregion,

234   and hydrobasin) were assigned using geographic information systems (ArcGIS version 10.3,

235   Esri, Redlands, CA).

236

237   *Circumpolar diversity*

238   Over the spatial extent of the gathered data, we assessed the total number and identities of

239   fish species from literature and expert knowledge (Christiansen et al., 2013; Ponomarev, 2017;

240   Mecklenburg, Mecklenburg & Thorsteinson, 2002; Muus & Dahlström, 1993; Scott &

241   Crossman, 1973). We determined the number and identities of species in the Arctic (high and

242   low zones), the subarctic, and in the ecoregions with sampled stations. We acknowledge that

243   intraspecific diversity is common in Arctic regions (e.g., Siwertsson et al., 2010; Woods et al.,

244   2012); however, it was not considered in this analysis. Species found in each of the individual

245   ecoregions represent the regional species pool or gamma diversity of that ecoregion.

246   Alpha diversity was calculated by averaging species richness of each station within the

247   hydrobasin boundary ($\alpha_{basin} = \overline{\alpha}_{station}$; Whittaker, 1972). With the hydrobasin as our unit of

248   interest, we included both lentic and lotic communities in our estimates of alpha diversity. We

249   found that this was appropriate – to include fishes from both ecosystem types in a single

250   diversity analyses – given the large spatial scale of the study, and the added benefit of preserving

251   sample sizes within ecoregions. Mean alpha diversity of ecoregions was determined; and we

252   assessed relationships between alpha diversity and hydrobasin area, alpha diversity and latitude

253   (hydrobasin centroid), and between alpha diversity and ecoregion gamma diversity using least-

254   squares linear regression. Model parameters were log-transformed when necessary to meet

255   assumptions of the analyses.

256   Beta diversity (i.e., the variation in species composition among/between sites) and its

257   turnover and nestedness components were determined across latitudinal zones and ecoregions

258   using dissimilarity matrices (*betapart*, R package version 1.5.0; Baselga, Orme, Villeger, De

259   Bortoli & Leprieur, 2018). Total beta diversity, calculated as β_{sor}, the Sørensen dissimilarity

260   index (Baselga, 2010), encompasses both spatial turnover and differences in species richness

261   (Koleff et al., 2003). It can be broken into component parts of turnover (β_{sim}), and nestedness

262   (β_{nes}), given the additive relationship: $\beta_{sor} = \beta_{sim} + \beta_{nes}$, where β_{sim} is the Simpson dissimilarity

263   index and β_{nes} is the nestedness-resultant dissimilarity (Baselga, 2010; Lennon, Koleff,

264   Greenwood, & Gaston, 2001). For total diversity, a value of one indicates there are no species in

265   common between a pair of sites, while a value of zero indicates that all of the species are shared

266   between sites.

267   In each ecoregion and in each zone (including: boreal, subarctic, low Arctic, and high

268   Arctic) we calculated beta diversity using multiple-site dissimilarities. Multiple-site dissimilarity

269   calculations (β_{SOR}, β_{SIM}, and β_{NES}) allowed us to quantify the heterogeneity of species

270   composition across all stations within a hydrobasin, because beta diversity depends on species

271   co-occurrence patterns across all sampled locations (Baselga, 2013). Using hydrobasin estimates

272   of β_{SOR}, β_{SIM}, and β_{NES}, we were able to estimate the mean values and standard deviation of beta

273   diversity components across hydrobasins within an ecoregion and zone. Because we wished to

274   maintain as many hydrobasins as possible in the analysis, beta diversity differences across

275   ecoregions and between zones could not be directly compared due to differences in sample sizes

276   (i.e., unequal number of stations), which influences richness data (Gotelli & Colwell, 2001).

277   Therefore, we limit discussion of multiple-site dissimilarity to whether turnover or nestedness

278   contributed equally to ecoregion and zone beta diversity; differences were determined by

279   comparing values of β_{SIM} and β_{NES} using two-tailed, paired Student's t-tests (R package version

280   3.4.1).

281   In each ecoregion and latitudinal zone, we calculated beta diversity using pairwise

282   dissimilarities of hydrobasins. Pairwise dissimilarities allowed us to examine spatial patterns in

283   diversity and correlations between geographic distance and total diversity, turnover, and

284   nestedness. Pairwise dissimilarities (β_{sor}, β_{sim}, and β_{nes}) were calculated from species

285   presence/absence matrices, with species arranged in columns and sites (i.e., hydrobasin

286   identifiers) in rows. Beta diversity dissimilarity matrices were modeled as a function of pairwise

287   spatial distances between hydrobasins using Mantel tests (vegan, R package version 2.4-6;

288   Oksanen et al., 2018), after deriving pairwise distances between hydrobasin centroids

289   (geosphere, R package version 1.5-7; Hijmans, 2017).

290

291   *Regional diversity comparisons*

292   In Alaska, Iceland, and Fennoscandia, data collected from the CBMP-freshwater database

293   were sufficiently robust to permit a direct comparative analysis of gamma, alpha, and beta

294   diversity across individual ecoregions. We used data from five ecoregions: Arctic Coastal

295   Tundra, Brooks-British Range Tundra, Iceland Boreal Birch Forest and Alpine Tundra,

296   Scandinavian and Russian Taiga (Fennoscandia only; stations west of 30.8°E longitude), and

297   Scandinavian Montane Birch Forest and Grasslands. Gamma diversity (i.e., the regional species

298   pool) was determined using the data available in the database, rather than extracting information

299   from the literature. This provided an accurate assessment of species encountered in the

300   hydrobasins where sampling took place, rather than inferring from published range distribution

301   maps.

302   Estimates of gamma diversity were standardized for comparison among ecoregions by

303 using sample-based rarefaction to determine the number of species (S_{rare}) at the lowest common

304 sample size within the subset of ecoregions. Data at the sample level (within stations) were used

305 to increase the number of samples used in this analysis and improve accuracy of diversity

306 estimates. Individual sampling events at each station were used in randomization tests that

307 compared sample-based rarefaction curves (*rareNMtests*, r package version 1.1; Cayuela &

308 Gotelli, 2014). Comparisons of gamma diversity across adjacent ecoregions (e.g., in Alaska)

309 were based on the ecological null hypothesis, from Cayuela, Gotelli, and Colwell (2015), that

310 two or more samples were drawn randomly from the same species pool; any differences in

311 species composition or richness would be minimal and the result of random chance or rare

312 species. Comparisons of gamma diversity across regions (e.g., Arctic Coastal Tundra in Alaska

313 to Scandinavian and Russian Taiga in Fennoscandia) were made based on the biogeographical

314 null hypothesis from Cayuela, Gotelli, and Colwell (2015), that two or more samples were drawn

315 from assemblages that share species richness profiles (i.e., species accumulation curves are the

316 same); species richness would be similar across regions even when species composition differs.

317   We calculated alpha diversity (species richness at the hydrobasin scale) and beta diversity

318 in all hydrobasins with 10 or more stations. Using sample-based rarefaction (*rareNMtests*, r

319 package version 1.1; Cayuela & Gotelli, 2014), we determined alpha diversity (α_{rare}) as the

320 number of species encountered at 10 stations in each hydrobasin. The mean α_{rare} was calculated

321 and compared across ecoregions using an Analysis of Variance (ANOVA) with a *post hoc*

322 pairwise t-test comparison using a false discovery rate (FDR) correction. We determined

323 ecoregion total beta diversity and its component parts of turnover and nestedness using multiple-

324 site dissimilarity calculations (β_{SOR}, β_{SIM}, and β_{NES}) by randomly resampling (n = 100) the data

325 from a subset of 10 stations in each hydrobasin (*betapart*, R package version 1.5.0; Baselga et

326 al., 2018; Baselga & Orme, 2012). Randomly resampling 10 stations (standardizing the number

327 of sites) allowed us to make comparisons of beta diversity across ecoregions. Hydrobasin means

328 of β_{SOR}, β_{SIM}, and β_{NES} were determined for each ecoregion and compared among ecoregions

329 using Analysis of Variance (ANOVA) with a *post hoc* pairwise t-test comparison using a FDR

330 correction. We also determined which component of beta diversity was underlying the patterns

331 found in each ecoregion by using a paired, one-tailed *t*-test for each ecoregion to compare

332 average values of β_{SIM} and β_{NES}.

333

334 **Results**

335 *Circumpolar diversity*

336   Station distribution was not uniform across the sampled area (Figure 1A), with large

337 differences in the number of stations sampled among the 25 ecoregions (median = 8 stations,

338 range = 2 – 1385 stations; Table S1); the majority of stations included in the database were found

339 in Alaska, Iceland, and Fennoscandia (included in regional diversity analysis, below). Based on

340 data collection, literature, and expert knowledge, we found that gamma diversity varied from one

341 to 47 species, with lower richness in high latitude ecoregions (e.g., High Arctic Tundra and

342 Kalaallit Nunaat High Arctic Tundra) and on islands of the north Atlantic Ocean (e.g., Arctic

343 Desert and Iceland Boreal Birch Forests and Alpine Tundra; Figure 1B). In total, we identified

344 100 fish species that represented 15 families in the study region; the composition of species

345 turned over across the longitudinal gradient (Figure 2, Table S2). Twenty-nine fishes are found

346 in North America, and 50 different fishes are found in Fennoscandia and Russia. Seventeen

347 species (families: Anguillidae, Esocidae, Gadidae, Gasterosteidae, Osmeridae, and Salmonidae)

348   occur across continents; four salmonid species were introduced from North America to Iceland,

349   Fennoscandia, or Russia (Table S2). In Greenland, Iceland, and on other islands of the North

350   Atlantic, only 10 species occur; six of these occur in other regions. The majority of species ($n =$

351   77) occur as far north as the high and low Arctic zones, while 23 (11 Cyprinidae) occur only in

352   subarctic or boreal zones below the low Arctic boundary. Of the 100 fish species known to the

353   study area, only 56 species appeared in the CBMP database and were included in the biodiversity

354   analyses (Table S2).

355   Using only presence/absence records from the database, we determined whether alpha

356   diversity related to area, latitude, and gamma diversity. Log-transformed alpha diversity was

357   unrelated to hydrobasin area (slope = $-1.00\times10^{-5} \pm 5.09\times10^{-6}$, intercept = 0.89 ± 0.05, $r^2 = 0.01$,

358   df = 287, $p = 0.05$), nor did it steadily decline with latitude (Figure 3A). There was, however, an

359   abrupt loss in alpha diversity at latitudes above 70.7°N, where records indicated Arctic charr

360   *Salvelinus alpinus* only. Below 70.7°N, the log-transformed alpha diversity increased slightly

361   with latitude (slope = 0.06 ± 0.01, intercept = -3.08 ± 0.99, $r^2 = 0.05$, df = 285, $p < 0.001$), which

362   translated to an average alpha diversity increase of 1.3 species over 10° of latitude (from 60 to

363   70°N). Log-transformed alpha diversity increased with gamma diversity (slope = $0.03 \pm$

364   2.57×10^{-3}, intercept = 0.15 ± 0.06, $r^2 = 0.37$, df = 296, $p < 0.001$; Figure 3B). Therefore, in high

365   latitude ecoregions with low gamma diversity (e.g., Arctic Desert, High Arctic Tundra, and

366   Kalaallit Nunaat High Arctic Tundra; Figure 1B) alpha diversity was also low (Table 1). Little

367   variation in alpha diversity occurred among low gamma diversity ecoregions ($\gamma \leq 5$), where alpha

368   diversity increased 0.13 species given a four species increase in gamma diversity. However, in

369   ecoregions with higher gamma diversity ($\gamma \geq 43$), alpha diversity increased 0.38 species given a

370   four species increase in gamma diversity.

371   Multiple-site dissimilarity calculations provided insight into the underlying beta diversity

372   patterns for ecoregions and latitudinal zones. Turnover of species was identified as the

373   underlying beta diversity process in five ecoregions (Figure 4A; Table S3): Arctic Coastal

374   Tundra ($t(14) = 2.39$, $p = 0.031$), Arctic Foothills Tundra ($t(9) = 3.85$, $p = 0.004$), Brooks-British

375   Range Tundra ($t(6) = 5.499$, $p = 0.002$), Scandinavian and Russian Taiga ($t(54) = 5.63$, $p <$

376   0.001), and Scandinavian Montane Birch Forest and Grasslands ($t(31) = 2.7$, $p = 0.010$). The

377   nestedness component of beta diversity was prevalent only in the Iceland Boreal Birch Forests

378   and Alpine Tundra ecoregion ($t(24) = -2.79$, $p = 0.010$). In two ecoregions, the Arctic Desert (n

379    $= 2$) and the High Arctic Tundra ($n = 4$), beta diversity was determined to be zero (Figure 4A). In

380   16 ecoregions, we could not determine differences between the beta diversity component

381   dissimilarities ($\beta_{SIM} \approx \beta_{NES}$; Figure 4A; Table S3), and in three ecoregions there was insufficient

382   data to determine the components of beta diversity. Turnover and nestedness component values

383   were not different from one another in either the subarctic ($t(70) = -0.67$, $p = 0.50$) or high

384   Arctic zones ($t(16) = 1.82$, $p = 0.09$), although there was relatively high dispersion and skew in

385   the β_{SIM} estimate for the high Arctic zone (Figure 3B). Turnover was the dominant beta diversity

386   component when compared to nestedness in the boreal ($t(51) = 5.97$, $p < 0.001$) and low Arctic

387   zones ($t(57) = 5.02$, $p < 0.001$; Figure 3B).

388   Weak spatial patterns of beta diversity were evident in three of 25 ecoregions (Table 2):

389   the Iceland Boreal Birch Forests and Alpine Tundra, the Interior Alaska-Yukon Lowland Taiga,

390   and the Scandinavian and Russian Taiga. In the Iceland Boreal Birch Forests and Alpine Tundra,

391   the nestedness component of beta diversity contributed to differences across space, given that

392   values of β_{nes} were positively correlated with geographic distance. Conversely, the turnover

393   component of beta diversity, β_{sim}, was positively correlated with geographic distance between

394   pairs of hydrobasins in the Interior Alaska-Yukon Lowland Taiga and the Scandinavian and

395   Russian Taiga. Beta diversity and its component parts of nestedness and turnover were not

396   correlated with geographic distance in 12 of the 25 ecoregions, and in the remaining 10

397   ecoregions, correlations could not be determined due to limited data or lack of variance in

398   richness between hydrobasins (Table 2).

399   Spatial patterns of beta diversity varied by zone (Table 2). In the boreal and subarctic,

400   where the maximum distance between hydrobasins was greatest, total beta diversity was weakly

401   positively correlated with distance between hydrobasins. In these two zones, the dissimilarity

402   between hydrobasin species assemblages across the spatial extent arose primarily from the

403   turnover component of beta diversity, which was also positively correlated with spatial distance.

404   The nestedness component of beta diversity was not significantly correlated with spatial

405   distance, though correlation coefficients were similar in magnitude to those found for total

406   diversity. In the low Arctic and high Arctic, no correlation was found between hydrobasin

407   assemblage dissimilarity and spatial distance for total beta diversity, the turnover component of

408   beta diversity, or the nestedness component of beta diversity.

409

410   *Regional diversity comparisons*

411   Rarefied (*n* samples = 921) fish species richness, as an estimate of gamma diversity at the

412   ecoregion scale, was highest, with a richness of nearly 20 species in the Scandinavian and

413   Russian Taiga and Arctic Coastal Tundra (Figure 5A; Table 3). Fish species richness in the

414   Scandinavian Montane Birch Forest and Grasslands and Brooks-British Range Tundra were 18

415   and 54 per cent lower, respectively, than their neighboring, lower elevation ecoregions. The

416   rarefied richness in the Iceland Boreal Birch Forests and Alpine Tundra was reduced compared

417   to all of the other ecoregions on mainland continents, with a richness of three species.

418   Comparisons between the Arctic Coastal Tundra and the Brooks-British Range Tundra in

419   Alaska, and between the Scandinavian and Russian Taiga and the Scandinavian Montane Birch

420   Forest and Grasslands using the ecological null hypothesis – that two or more samples were

421   drawn randomly from the same species pool (Cayuela et al., 2015) – was tested using rarefaction

422   curves. Rarefaction curves between the Arctic Coastal Tundra and the Brooks-British Range

423   Tundra differed (n_{iter} = 750, Z_{obs} = 9419, p = 0.001), suggesting that there were differences in

424   either species composition or richness. Rarefaction curves from the Scandinavian and Russian

425   Taiga and the Scandinavian Montane Birch Forest and Grasslands were similar (n_{iter} = 750, Z_{obs} =

426   3447, p = 0.569), suggesting differences in species richness or composition between stations in

427   the two ecoregions were no greater than what would be anticipated from random sampling of the

428   same species pool.

429   When comparing rarefaction curves across distant ecoregions, we failed to reject the

430   biogeographical null hypothesis – that two or more samples were drawn from assemblages that

431   share species richness profiles (Cayuela et al., 2015) – in one of seven pairs. There was no

432   significant difference between the rarefaction curves in the Scandinavian and Russian Taiga and

433   the Arctic Coastal Tundra (n_{iter} = 200, Z_{obs} = 254, p = 0.560). The rarefaction curves for the

434   Iceland Boreal Birch Forests and Alpine Tundra, which had the smallest species pool and only

435   three represented species, differed greatly from those for other ecoregions (i.e., higher values of

436   Z_{obs}). The curves for the Iceland Boreal Birch Forests and Alpine Tundra and for the

437   Scandinavian Montane Birch Forests and Grasslands could not be assessed given the low species

438   richness in both of those ecoregions.

439   Mean alpha diversity was highest in the Scandinavian and Russian Taiga at about 8

440   species, with similar mean alpha diversity in the Arctic Coastal Tundra, and Brooks-British

441   Range Tundra (Table 3; Figure 6A). Mean alpha diversity in the Scandinavian Montane Birch

442   Forest and Grasslands was reduced by two species compared to the adjacent Scandinavian and

443   Russian Taiga ecoregion (Figure 5B). Overall, alpha diversity was reduced in the high-elevation

444   ecoregions (Brooks-British Range Tundra and Scandinavian Montane Birch Forest and

445   Grasslands) when compared to that of adjacent low-elevation ecoregions (Figure 5B). Among

446   the five ecoregions, mean hydrobasin alpha diversity was lowest in the Iceland Boreal Birch

447   Forests and Alpine Tundra, with only 3 species.

448   Using multiple-site dissimilarity calculations we found that beta diversity was greatest in

449   the Arctic Coastal Tundra, the Brooks-British Range Tundra, and the Fennoscandian area of the

450   Scandinavian and Russian Taiga (Table 3). Beta diversity was lower in the Scandinavian

451   Montane Birch Forest and Grasslands and lowest in the Iceland Boreal Birch Forests and Alpine

452   Tundra (Figure 6B). Average β_{SOR} differed significantly between all ecoregions (ANOVA

453    $F(4,5995) = 303$, $p < 0.001$, all pairwise tests $p < 0.003$; Table 3). Comparisons of the turnover

454   and nestedness components revealed higher values of β_{SIM} compared to β_{NES} in the Arctic Coastal

455   Tundra ($t(799) = 35.37$, $p < 0.001$), Brooks-British Range Tundra ($t(399) = 18.39$, $p < 0.001$),

456   Scandinavian and Russian Taiga ($t(2799) = 37.27$, $p < 0.001$), and the Scandinavian Montane

457   Birch Forest and Grasslands ($t(1499) = 24.41$, $p < 0.001$; Figure 5C). Beta diversity in the

458   Iceland Boreal Birch Forests and Alpine Tundra exhibited the opposite pattern, where

459   dissimilarity from nestedness was greater than the dissimilarity from turnover ($t(499) = -20.59$, p

460   < 0.001, Figure 6B).

461

Discussion

By examining the spatial patterns of gamma, alpha, and beta diversity, we provide the

first baseline for understanding processes that govern fish community assembly and species

richness in the circumpolar Arctic. Because community richness and composition depend upon

the dispersal abilities of the fishes, historic and contemporary barriers to colonization, and

environmental characteristics that influence occupancy (Griffiths, 2015; Oswood, Reynolds,

Irons, & Milner, 2000; Tonn, Magnuson, Rask, & Toivonen, 1990), broad-scale patterns of fish

species alpha, beta, and gamma diversity varied with latitude, isolation, and coarse ecoregion

characteristics (e.g., elevation or area). Our evaluation of these biodiversity patterns provides

information on community regulation (i.e., factors that control richness, abundance, or

composition) that can improve monitoring and assessments of biodiversity change or persistence

in the future (Gotelli et al., 2017).

Gamma diversity was reduced in the highest latitude ecoregions (i.e., Middle Arctic

Tundra and High Arctic Tundra in Canada, Kalaallit Nunaat High Arctic Tundra in Greenland,

and Arctic Desert in Svalbard), because limited connections to glacial refugia, time since

glaciation events, harsh environmental conditions, and species dispersal abilities limit species

richness with increasing latitude (Griffiths, 2015; Schleuter et al., 2012). Recent warming of

marine and freshwaters in the Arctic may facilitate the range expansion of species, which could

lead to compositional change (Reist et al., 2006). In fact, climate change now facilitates the

northward movement of many fishes previously constrained by low temperatures in high Arctic

environments. Anadromous fish species, which are fairly common in northern areas, may ascend

non-natal watercourses to colonize new freshwater localities in high Arctic islands. For example,

threespine stickleback *Gasterosteus aculeatus* recently appeared in surveys of freshwaters at

485   Zackenberg, Greenland in Kalaallit Nunaat High Arctic Tundra (Nielsen, Hamerlik, &

486   Christoffersen, 2012), and on Svalbard in the remote Arctic Desert (Svenning, Aas, &

487   Borgstrøm, 2015).

488   Many of the fish species in high latitudes of Canada and Europe are found in both

489   historically unglaciated and glaciated regions, suggesting northward (in Europe, north and west)

490   movement of fishes from a colonizing source after glacial retreat (Griffiths, 2015; Koljonen et

491   al., 1999). In contrast, the Beringia refugia provided protection for freshwater fishes during the

492   most recent Pleistocene glaciation event (Christiansen et al., 2013; Oswood et al., 2000), which

493   has resulted in increased species richness at high latitudes (about 70.3°N) of Alaska (Oswood et

494   al., 2000), where gamma diversity was as high as 26 fish species. Eighty-one per cent of the

495   fishes found in northern Alaska (i.e., Arctic Coastal Tundra and the Arctic Foothills Tundra)

496   persisted in the Beringian refugia (Oswood et al., 2000). Northernmost Scandinavia, which was

497   re-colonized from an eastern refuge, showed higher fish species diversity than Scandinavian

498   Mountain Birch Forests regions (Hewitt, 2000; Nesbø, Fossheim, Vøllestad, & Jakobsen, 1999;

499   Østbye Bernatchez, Næsje, Himberg, & Hindar, 2005). These studies support our finding that the

500   Scandinavian Montane Birch Forests and Grasslands ecoregion had reduced alpha diversity

501   compared to the adjacent low elevation ecoregion, indicating the importance of barriers to

502   colonization at higher altitudes. It should also be noted that current ecoregion definitions are not

503   always ideal for the study of fish diversity and distributions, which have been influenced by

504   historical conditions including a complex suite of melting channels, ice-dammed lakes, and

505   watercourse alterations (e.g., Mangerud et al., 2004). Perhaps constructing additional geographic

506   regions, such as palaeo-drainage basins (see Dias et al., 2014), would benefit biodiversity

507   analyses of fish communities that formed over thousands of years.

508   Due to the refuge provided during the last glacial advance, fish species richness does not

509 decline northward in hydrobasins of the Arctic Coastal Tundra. Instead, species richness

510 increases slightly from the south to north, which corresponds with the additional presence of

511 anadromous fishes at the Beaufort Sea coast (Craig, 1984; Laske et al., 2016). Among all

512 stations, alpha diversity was relatively consistent from 60–70 °N, a pattern that may result from

513 the overwhelming proportion of sites in Alaska's high Arctic and the region's biogeography and

514 glacial history. Because of the sampling imbalance across countries and a lack of stations in

515 swaths of the subarctic (e.g., Canada and Russia), we cannot clearly determine whether the

516 pattern of alpha diversity with latitude occurs uniformly across the circumpolar Arctic.

517   In Arctic Canada, freshwaters extend to roughly 83°N and species richness declines with

518 latitude are evident, but declines are also strongly associated with lack of connectivity among

519 freshwater habitats in the Canadian Archipelago (Christiansen et al., 2013). The abrupt loss in

520 alpha diversity at latitudes above 71°N likely relates directly to the lack of landmass, which

521 includes only parts of Siberia, Greenland, the Canadian Archipelago, and northern Arctic islands

522 (e.g., Svalbard). Lack of freshwater connectivity to Greenland, the Canadian Archipelago, and

523 northern Arctic islands limits colonization to only anadromous species (Christiansen et al.,

524 2013). However, limited data, particularly on continental Eurasia, may be preventing a clear

525 interpretation of our results. At least seven species of freshwater/anadromous fish occur in the

526 high Arctic from the Ural Mountains east to the Indigirka River in Siberia (Novikov et al., 2000),

527 but their latitudinal distribution patterns are unclear.

528   Location and isolation affected both gamma and alpha diversity; in high Arctic

529 ecoregions and on islands, alpha diversity was constrained by the available species pool. The size

530 of the regional species pool (gamma diversity) is tightly coupled to lower scale processes,

531 including the dispersal and persistence of species within a region (Hillebrand et al., 2018; Rolls

532 et al., 2017). At larger scales, historic and contemporary conditions limit species access to

533 ecoregions. For example, the Brooks-British Range Tundra was glaciated during the last

534 Pleistocene event, and combined with current elevation effects (e.g., stream gradients) the fish

535 fauna of this ecoregion is dissimilar compared with Alaska's other ecoregions (Hershey et al.,

536 2006; Oswood et al., 2000). We found, by comparing rarefaction curves, that the Brooks-British

537 Range Tundra differed either in species richness or composition from the Arctic Coastal Tundra.

538 By examining the identities of fish found in these two ecoregions, differences arose from loss of

539 species across ecoregion boundaries (Mecklenburg et al., 2002). In Iceland, an isolated region

540 with low alpha and gamma diversity, freshwater fish dispersal to the island is limited by distance

541 to mainland freshwaters. As a result, only anadromous species have colonized (Christiansen et

542 al., 2013).

543   While Salmonidae (48–52 species) is a diverse, cold-water adapted and wide-ranging

544 family of fishes (Erkinaro et al., 2019; Siwertsson et al., 2010; Woods et al., 2012), other

545 taxonomic groups (e.g., Anguillidae, Cobitidae, and Umbidae) have limited diversity and

546 geographic distributions in the Arctic (Christiansen et al., 2013). Across the study area, 14% of

547 fishes (excluding introduced species) spanned multiple continents, and the remaining species

548 turned over, or were replaced. The assessment of beta diversity compared diversity at two

549 different scales (the ecoregion – gamma diversity; and the hydrobasin – alpha diversity), with

550 dissimilarities arising from species replacement (i.e., turnover) or loss (i.e., nestedness)

551 (Anderson et al., 2011; Baselga, 2010). We found that in a majority of ecoregions, both

552 replacement and loss of species from hydrobasin to hydrobasin contributed to beta diversity. In

553 ecoregions with robust sampling, however, turnover was the dominant process, suggesting that a

554 change in species composition between basins was more prevalent than losses of species from a

555 primary, species rich location. Turnover may result from directional change in species

556 composition that occur along a predefined spatial or environmental gradients (e.g., temperature;

557 altitude), or from a non-directional change that occurs among sites within a given area (e.g., lake

558 depth; Anderson et al., 2011; Legendre, Borcard, & Peres-Neto, 2005).

559   The virtual lack of beta diversity in northern ecoregions (i.e., Arctic Desert, High Arctic

560 Tundra, Kalaallit Nunaat Low Arctic Tundra) was not surprising given the low richness of

561 regional species pools (Mecklenburg et al., 2002; Muus & Dahlström, 1993; Scott & Crossman

562 1973). The high Arctic zone did not display a strong pattern of species turnover or nestedness,

563 likely because patchy data obscured true beta diversity patterns. Most species in the high Arctic

564 were found in one ecoregion (Arctic Coastal Tundra, 21 spp.), and only one shared species

565 (Arctic charr) was represented in the remaining four ecoregions (High Arctic Tundra, Middle

566 Arctic Tundra, Kalaallit Nunaat High Arctic Tundra, and the Arctic Desert). However, low

567 gamma diversity and consistent fish assemblages, often including Holarctic species (e.g., Arctic

568 charr or threespine stickleback), would limit the amount of possible variation in communities of

569 the high Arctic. Potentially, with increased sampling, patterns of beta diversity in the high Arctic

570 may become apparent. Those sites that are particularly harsh (i.e., isolated, and at high latitudes)

571 may be occupied only by a subset of the richest assemblage, including only species that are

572 either physiologically tolerant or migratory (Griffiths, 2010; Henriques-Silva, Lindo, & Peres-

573 Neto, 2013).

574   We anticipated that the dissimilarity between hydrobasin assemblages would increase

575 with geographic distance (Beisner et al., 2006; Soininen et al., 2007). In other words, distant

576 assemblages would share fewer species than proximate assemblages – either as a result of

577   species replacement (i.e., turnover) or loss (i.e., nestedness). Species turnover was correlated

578   with geographic distance at lower latitudes, in the boreal and subarctic zones, so dissimilarity

579   between distant hydrobasin assemblages arose from replacement of fish species rather than from

580   changes in fish species richness. On a circumpolar scale, patchy distributions of species with

581   more southerly distributions may contribute to turnover, since some families or species are

582   restricted to either the Nearctic (e.g., Catostomidae and Hiodontidae) or the Palearctic (e.g.,

583   Balitoridae and Cobitidae) (Christiansen et al., 2013). Among cyprinid fishes, 38 and 62% of

584   Arctic species occupy freshwaters of the Nearctic and Palearctic, respectively (Christiansen et

585   al., 2013; Muus & Dahlström, 1993; Scott & Crossman, 1973), however, no Cyprinidae are

586   shared between the Nearctic and Palearctic.

587   In the Scandinavian and Russian Taiga, there was little difference in mean alpha diversity

588   across the sampled hydrobasins, but distant sites were dissimilar due to species replacement;

589   hydrobasin assemblages in Sweden and southern Finland differed from those in western Russia.

590   Rapid changes in the identities of species along a spatial gradient may identify ecotones, or the

591   transitional boundary between two biological assemblages (Guerin, Biffin, & Lowe, 2013;

592   Leprieur et al., 2011). This particular terrestrial ecoregion covered a large spatial extent that

593   overlapped two major drainages (Northern Baltic Sea and the Barents Sea), considered as two

594   flow-based Freshwater Ecoregions (Abell et al., 2008). The spatial breadth of the ecoregion had

595   a major impact on our assessment of gamma diversity from literature and in our analyses by

596   adding species either along a longitudinal gradient or with increasing area. Gamma diversity

597   based on rarefaction curves in the Arctic Coastal Tundra and Fennoscandian portion of the

598   Scandinavian and Russian Taiga were similar. Those estimates included 77% (20 of 26 species)

599   of the known species in the Arctic Coastal Tundra and only 43% (20 of 47 species) of the known

600   species in the Scandinavian and Russian Taiga, which may indicate that the freshwaters to the

601   east (in Russia) contain additional species. Each of the other terrestrial ecoregions (Olson et al.,

602   2001) subdivided the Freshwater Ecoregions (Abell et al., 2008), and accounted for additional

603   landscape features such as isolation (e.g., Svalbard) or mountain ranges (e.g., the Brooks Range

604   in Alaska). Community variation was often not associated with geographic distance (83% of

605   ecoregions), however, so other factors such as historical conditions during deglaciation, species

606   co-occurrence, non-spatial gradients, or environmental heterogeneity may underlie the processes

607   of turnover or nestedness (Anderson et al., 2011; Baselga, 2013).

608   At regional scales, environmental heterogeneity across hydrobasins can affect factors that

609   control fish species richness, composition, and community assembly (Gotelli et al., 2017;

610   Magnuson et al., 1998). In our study, patterns of diversity did not always differ in distant

611   ecoregions (e.g., Arctic Coastal Tundra and Scandinavian and Russian Taiga), suggesting that

612   mechanisms of community regulation may operate similarly on dissimilar regional species pools

613   (Kraft et al., 2011; Tonn et al., 1990). In the Arctic Coastal Tundra of Alaska, coastal

614   hydrobasins with large river deltas contained a far greater diversity of species (Christiansen et

615   al., 2013; Craig, 1984; Wrona et al., 2006), including regionally rare species (e.g., sockeye

616   salmon *Oncorhynchus nerka*), anadromous species (e.g., Dolly Varden *Salvelinus malma*), and

617   freshwater species (e.g., longnose sucker *Catostomus catostomus*). Because turnover was the

618   predominant process in the Arctic Coastal Tundra ecoregion, other hydrobasins did not represent

619   disaggregated subsets of the richest location. Instead, species replaced one another along

620   environmental gradients (e.g., distance from major river, isolation) given their individual

621   dispersal abilities (Craig, 1984; Laske et al., 2016; Oswood et al., 2000).

622   Isolation may have profound effects on the distribution of fishes across landscapes, and

623   on our understanding of environmental gradients that effect biodiversity (Brittain et al., 2009;

624   Magnuson et al., 1998; Schleuter et al., 2012). Freshwater habitats on islands (e.g., the Canadian

625   Archipelago, Svalbard, Iceland) are considerably more isolated than freshwater habitats on

626   contiguous land masses (e.g., Eurasian Arctic), and had only a subset of species found elsewhere.

627   In mountainous regions, physical barriers limit species access from adjacent lower elevation

628   ecoregions and promote the creation of discrete fish communities (Degerman & Sers, 1992,

629   Hershey et al., 1999). Lakes of the Brooks-British Range Tundra are occupied by specific

630   communities that turnover along specific geomorphic constraints (Hershey et al., 1999),

631   including channel gradients, altitude, and lake area or depth (Degerman & Sers, 1992; Hershey et

632   al., 2006; Holmgren & Appelberg, 2000). In addition, in many species-poor regions, historical

633   conditions during deglaciation and ecological opportunity have facilitated fish divergence via

634   resource polymorphism and ecological speciation events (Hershey et al., 2006; Siwertsson et al.,

635   2010; Woods et al., 2012) that can have very important trophic consequences within

636   communities (Lucek, Kristjánsson, Skúlason, & Seehausen. 2016; Woods et al., 2012).

637   Across the circumpolar Arctic, fish biodiversity depended upon the historic and modern

638   characteristics of the ecological region or zone where they occurred. However, some of the

639   variability we found among hydrobasins was likely due to differences in sample availability

640   rather than the environment, given that streams and lakes were not sampled in relation to their

641   abundance or with consistency across ecoregions. Additionally, in hydrobasins with fewer

642   sampled stations, we likely missed a greater number of species because of non-detection.

643   Potentially, reduced alpha diversity in hydrobasins with fewer sample stations may be overly

644   influential in our circumpolar analyses where all hydrobasins were considered, reducing average

29

645   alpha diversity and increasing the contribution of nestedness to beta diversity patterns. The effect

646   of area on species diversity at larger spatial scales (i.e., that of the ecoregion) was also difficult to

647   ascertain because of disparities in the distribution and number of hydrobasins with station data.

648   This study takes the first steps in determining large-scale patterns of freshwater fish

649   biodiversity throughout the circumpolar Arctic using a unique data compilation. It is important to

650   evaluate the current biodiversity patterns and to provide a baseline to improve our ability to

651   detect temporal species turnover and spatial dissimilarity (Hillebrand et al., 2018; Socolar et al.,

652   2016). Changes in climate, land use, and biotic exchange will have profound effects on Arctic

653   fish biodiversity and the structure and function of communities and food webs in the future

654   (Hayden et al., 2017; Sala et al., 2000; Wrona et al., 2006). In this respect, freshwaters in the

655   subarctic zone should be monitored intensively, because it is most likely to experience

656   encroachment and expansion of warm-water adapted species from boreal region (Rolls et al.,

657   2017). In future fish diversity assessments, we should look beyond the species level towards

658   intraspecific diversity, which is known to repeatedly occur in many of the studied circumpolar

659   areas (Taylor, 1999), and is an important contributor to freshwater ecosystem structure and

660   function (Power, Reist, & Dempson, 2008; Woods et al., 2012). An underlying question is,

661   should we monitor the richest assemblages or focus on ecosystem gradients or factors that

662   promote the evolution of fish diversity? Thus, future studies examining patterns and drivers of

663   Arctic biodiversity should strive to combine extensive old and new data from the circumpolar

664   regions to test for changes in observed patterns and the consequences of both among- and within-

665   species variation on design and implementation of monitoring frameworks used to preserve

666   freshwater biodiversity.

667

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927 Table 1. Diversity values for all ecoregions where fish data were available. Gamma diversity was based on literature (Ponomarev,

928 2017; Mecklenburg et al., 2002; Muus & Dahlström 1993; Scott & Crossman 1973;) and expert knowledge. Alpha diversity was

929 determined as the average species richness of all sample stations within a hydrobasin; and beta diversity was determined from

930 Sørensen dissimilarities of sample stations within a hydrobasin. The number, n, and the mean and standard deviation (sd) are provided

931 for each ecoregion.

Ecoregion	Gamma	Alpha		Beta	
		n	mean (sd)	n	mean (sd)
Arctic Coastal Tundra	26	19	2.83 (0.43)	15	0.66 (0.32)
Arctic Desert	1	3	1.00 (0)	2	0 (0)
Arctic Foothills Tundra	26	11	1.45 (0.11)	10	0.67 (0.33)
Beringia Lowland Tundra	25	1	1.50 (–)	1	0.33 (–)
Beringia Upland Tundra	26	17	1.82 (0.24)	13	0.47 (0.30)
Brooks-British Range Tundra	19	9	1.65 (0.15)	7	0.78 (0.06)
Faroe Islands Boreal Grasslands	3	1	1.50 (–)	1	0.33 (–)
High Arctic Tundra	2	8	1.00 (0)	3	0 (0)
Iceland Boreal Birch Forests and Alpine Tundra	8	29	1.94 (0.09)	25	0.45 (0.18)
Interior Alaska-Yukon Lowland Taiga	22	9	2.38 (0.31)	7	0.75 (0.15)
Interior Yukon-Alaska Alpine Tundra	17	2	1.75 (0.75)	2	0.10 (0.14)
Kalaallit Nunaat High Arctic Tundra	1	3	1.00 (0)		
Kalaallit Nunaat Low Arctic Tundra	5	18	1.03 (0.03)	10	0.03 (0.10)

932

933 Table 1. Continued.

Ecoregion	Gamma	Alpha		Beta	
		n	mean (sd)	*n*	mean (sd)
Kola Peninsula Tundra	18	5	3.07 (1.24)	2	0.25 (0.35)
Low Arctic Tundra	17	1	3.50 (–)	2	0.27 (0.18)
Middle Arctic Tundra	9	2	1.00 (0)		
Muskwa-Slave Lake Forests	27	2	2.75 (0.25)	1	0.20 (–)
Northern Canadian Shield Taiga	21	3	3.83 (0.44)	3	0.44 (0.18)
Northwest Russian-Novaya Zemlya tundra	45	14	3.96 (0.48)	9	0.56 (0.20)
Northwest Territories Taiga	33	12	2.32 (0.26)	6	0.48 (0.11)
Ogilvie-MacKenzie Alpine Tundra	14	5	1.65 (0.38)	1	0.54 (–)
Scandinavian and Russian Taiga	47	72	4.49 (0.26)	55	0.65 (0.27)
Scandinavian Montane Birch Forest and Grasslands	25	47	2.89 (0.28)	32	0.62 (0.26)
Ural Mountain Forest and Tundra	7	3	2.61 (0.39)	2	0.17 (0.04)
Yamal Gydan Tundra	26	2	9.50 (0.50)		

934

935 Table 2. Correlations of hydrobasin community dissimilarity and geographic distance within ecoregions and latitudinal zones.

936 Mantel's *r* and *p*-values are given for pairwise beta diversity (β_{sor}) and its components turnover (β_{sim}) and nestedness (β_{nes}). The

937 number of hydrobasins (*n*) and maximum distance (Max. dist.) between hydrobasins within ecoregions and zones is provided. Bolded

938 values are significant for an $\alpha = 0.05$.

	n	Max. dist. (km)	Dissimilarity (β_{sor})		Dissimilarity (β_{sim})		Dissimilarity (β_{nes})	
			r	*p*	*r*	*p*	*r*	*p*
Ecoregion								
Arctic Coastal Tundra	19	465	0.05	0.26	0.02	0.38	0.03	0.35
Arctic Desert	3	559						
Arctic Foothills Tundra	11	638	0.14	0.18	0.13	0.19	-0.03	0.58
Beringia Lowland Tundra	1							
Beringia Upland Tundra	17	281	0.01	0.47	-0.01	0.53	0.03	0.34
Brooks-British Range Tundra	9	300	0.07	0.44	0.04	0.51	0.03	0.42
Faroe Islands Boreal Grasslands	1							
High Arctic Tundra	8	218						
Iceland Boreal Birch Forests and Alpine Tundra	29	381	**0.12**	**0.04**			**0.12**	**0.04**
Interior Alaska-Yukon Lowland Taiga	9	441	**0.4**	**0.01**	**0.42**	**0.01**	-0.23	0.92
Interior Yukon-Alaska Alpine Tundra	2	26						
Kalaallit Nunaat High Arctic Tundra	3	1492						
Kalaallit Nunaat Low Arctic Tundra	18	1153	0.02	0.54	0.01	0.6	0.03	0.61
Kola Peninsula Tundra	3	107	-0.43	0.67	-0.43	0.67	0.43	0.67
Low Arctic Tundra	2	898						

939

Table 2. Continued.

	n basins	Max. dist (km)	Dissimilarity (β_{sor})		Dissimilarity (β_{sim})		Dissimilarity (β_{nes})	
			r	p	r	p	r	p
Ecoregion								
Middle Arctic Tundra	3	1698						
Muskwa-Slave Lake Forests	2	73						
Northern Canadian Shield Taiga	3	72	-0.37	0.50	0.57	0.33	-0.99	1
Northwest Russian-Novaya Zemlya Tundra	14	598	0.11	0.14	0.01	0.41	0.18	0.06
Northwest Territories Taiga	12	370	-0.01	0.56	-0.02	0.54	0.02	0.14
Ogilvie-MacKenzie Alpine Tundra	5	364	-0.32	0.77	-0.44	0.90	0.41	0.17
Scandinavian and Russian Taiga	72	2198	0.01	0.44	**0.48**	**<0.001**	-0.19	1
Scandinavian Montane Birch Forest and Grasslands	47	1060	-0.01	0.56	0.01	0.47	-0.01	0.62
Ural Mountain Forest and Tundra	3	50	-0.93	1	-0.93	1	0.93	0.33
Yamal Gydan Tundra	2	64						
Latitudinal zone								
Boreal	67	6441	**0.11**	**0.02**	**0.48**	**<0.001**	–0.19	1
Subarctic	96	5923	**0.20**	**<0.001**	**0.21**	**<0.001**	–0.13	1
Low Arctic	82	5585	–0.03	0.92	–0.02	0.85	<0.01	0.49
High Arctic	28	3931	–0.01	0.41	–0.04	0.75	0.08	0.17

941

942 Table 3. Gamma diversity (S_{rare}), alpha diversity (α_{rare}), multiple-site beta diversity (β_{SOR}) and its components turnover (β_{SIM}) and

943 nestedness (β_{NES}) for a subset of five ecoregions with robust fish species presence-absence data. The number of basins (n) used to

944 determine the mean and standard deviation of α_{rare} and beta diversity estimates based on resampling. Sample size for beta diversity

945 resampling is $100n$.

Ecoregion	n	S_{rare}	α_{rare}		β_{SOR}		β_{SIM}		β_{NES}	
			mean	sd	mean	sd	mean	sd	mean	sd
Arctic Coastal Tundra	8	19.7	7.74	1.09	0.77	0.06	0.54	0.14	0.23	0.11
Brooks-British Range Tundra	4	9.0	5.49	1.38	0.75	0.09	0.53	0.21	0.22	0.13
Iceland Boreal Birch Forests and Alpine Tundra	5	3.0	3.00	0.01	0.57	0.08	0.16	0.17	0.42	0.12
Scandinavian and Russian Taiga	28	19.8	8.64	2.69	0.73	0.07	0.47	0.26	0.26	0.13
Scandinavian Montane Birch Forest and Grasslands	15	16.3	6.60	3.21	0.65	0.22	0.45	0.17	0.21	0.16

946

947

948   Figure 1. Distribution of stations included in the analysis of Arctic freshwater fish biodiversity

949   (A) and the gamma diversity of ecoregions, as quantified by estimates of species richness from

950   reference texts (Mecklenburg et al., 2002; Muus & Dahlström, 1993; Ponomarev, 2017; Scott &

951   Crossman 1973) and expert knowledge (B). The black line indicates the Conservation of Arctic

952   Flora and Fauna (CAFF) boundary of the Arctic. Ecoregions are BU – Beringia Upland Tundra,

953   BL – Beringia Lowland Tundra, IY – Interior Yukon-Alaska Alpine Tundra, IA – Interior

954   Alaska-Yukon Lowland Tundra, AF – Arctic Foothills Tundra, AC – Arctic Coastal Tundra, BB

955   – Brooks-British Range Tundra, NT – Northwest Territories Taiga, OM – Ogilvie-Mackenzie

956   Alpine Tundra, LA – Low Arctic Tundra, MS – Muskwa-Slave Lake Forests, MA – Middle

957   Arctic Tundra, HA – High Arctic Tundra, NC – Northern Canadian Shield Taiga, KH – Kalaallit

958   Nunaat High Arctic Tundra, KL – Kalaallit Nunaat Low Arctic Tundra, I – Iceland Birch Forests

959   and Alpine Tundra, FI – Faroe Islands Boreal Grasslands, AD – Arctic Desert, SM –

960   Scandinavian Montane Birch Forest, SR – Scandinavian and Russian Taiga, KP – Kola

961   Peninsula Tundra, RT – Northwest Russian-Novaya Zemlya Tundra, UM – Ural Montane

962   Forests and Tundra, and YG – Yamal-Gydan Tundra.

963

964   Figure 2. Longitudinal distribution pattern of fish species from Alaska to western Russia. Species

965   occurrences for each ecoregion (x-axis) were determined using reference texts (Mecklenburg et

966   al., 2002; Muus & Dahlström, 1993; Ponomarev, 2017; Scott & Crossman 1973) and expert

967   knowledge. Each value on the y-axis represents a single species, colored by taxonomic family.

968   Species identification numbers are referenced in Table S2. Introduced species are represented by

969   triangles. Ecoregions are arranged longitudinally; ecoregions in Alaska, United States, BU –

970   Beringia Upland Tundra, BL – Beringia Lowland Tundra, IY – Interior Yukon-Alaska Alpine

48

971   Tundra, IA – Interior Alaska-Yukon Lowland Tundra, AF – Arctic Foothills Tundra, AC –

972   Arctic Coastal Tundra, and BB – Brooks-British Range Tundra; in Canada, NT – Northwest

973   Territories Taiga, OM – Ogilvie-Mackenzie Alpine Tundra, LA – Low Arctic Tundra, MS –

974   Muskwa-Slave Lake Forests, MA – Middle Arctic Tundra, HA – High Arctic Tundra, and NC –

975   Northern Canadian Shield Taiga; in the Atlantic, KH – Kalaallit Nunaat High Arctic Tundra and

976   KL – Kalaallit Nunaat Low Arctic Tundra; I – Iceland Birch Forests and Alpine Tundra; FI –

977   Faroe Islands Boreal Grasslands; in Svalbard and other northern islands, AD – Arctic Desert, in

978   Fennoscandia and Russia, SM – Scandinavian Montane Birch Forest, SR – Scandinavian and

979   Russian Taiga, KP – Kola Peninsula Tundra, RT – Northwest Russian-Novaya Zemlya Tundra,

980   UM – Ural Montane Forests and Tundra, and YG – Yamal-Gydan Tundra.

981

982   Figure 3. Response of hydrobasin alpha diversity to latitude (A) and gamma diversity (B). Each

983   point on the plots represents a single hydrobasin. The log-linear relationship between alpha

984   diversity and latitude (± 1 standard error) is shown for latitudes below 70.7°N.

985

986   Figure 4. Dominant components of beta diversity in ecoregions (A) of the circumpolar Arctic

987   characterized as nestedness, turnover, no diversity (none, beta = 0), or similar nestedness and

988   turnover (nest ~ turn). Box and whisker plots of turnover (β_{SIM}) and nestedness (β_{NES})

989   components of beta diversity for each latitudinal zone (B). Statistical differences in turnover and

990   nestedness are indicated with an * above the zone. Boxes span the first to third quartile, the line

991   within the box is the median, and points beyond the whiskers are outliers. Ecoregions are BU –

992   Beringia Upland Tundra, BL – Beringia Lowland Tundra, IY – Interior Yukon-Alaska Alpine

993   Tundra, IA – Interior Alaska-Yukon Lowland Tundra, AF – Arctic Foothills Tundra, AC –

994   Arctic Coastal Tundra, BB – Brooks-British Range Tundra, NT – Northwest Territories Taiga,

995   OM – Ogilvie-Mackenzie Alpine Tundra, LA – Low Arctic Tundra, MS – Muskwa-Slave Lake

996   Forests, MA – Middle Arctic Tundra, HA – High Arctic Tundra, NC – Northern Canadian Shield

997   Taiga, KH – Kalaallit Nunaat High Arctic Tundra, KL – Kalaallit Nunaat Low Arctic Tundra, I –

998   Iceland Birch Forests and Alpine Tundra, FI – Faroe Islands Boreal Grasslands, AD – Arctic

999   Desert, SM – Scandinavian Montane Birch Forest, SR – Scandinavian and Russian Taiga, KP –

1000   Kola Peninsula Tundra, RT – Northwest Russian-Novaya Zemlya Tundra, UM – Ural Montane

1001   Forests and Tundra, and YG – Yamal-Gydan Tundra. The black line indicates the Conservation

1002   of Arctic Flora and Fauna (CAFF) boundary of the Arctic.

1003

1004   Figure 5. Gamma diversity (A), alpha diversity (B), and the primary beta diversity component

1005   for the Alaska Coastal Tundra and Brooks-British Range Tundra in Alaska, the Iceland Boreal

1006   Birch Forests and Alpine Tundra, and the Scandinavian Montane Birch Forest and Grasslands

1007   and Scandinavian and Russian Taiga in Fennoscandia.

1008

1009   Figure 6. Box and whisker plots of ecoregion alpha diversity (A) and fish assemblage

1010   dissimilarity due to the turnover (β_{SIM}) and nestedness (β_{NES}) components of beta diversity (B).

1011   Differences in alpha diversity are indicated by the letters above each box, shared letters indicate

1012   no statistical difference of means. Statistical differences in mean turnover and nestedness are

1013   indicated with an * above the ecoregion. Boxes span the first to third quartile, the line within the

1014   box is the median, and points beyond the whiskers are outliers.
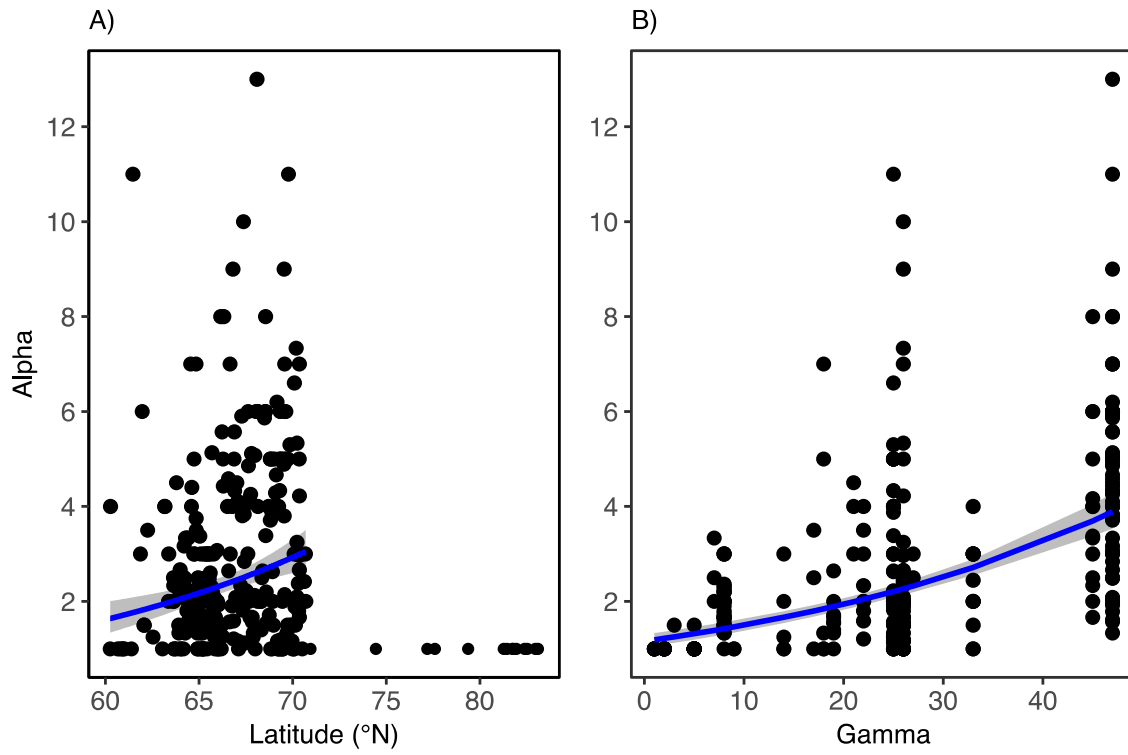
1015

1016   Figure 1.
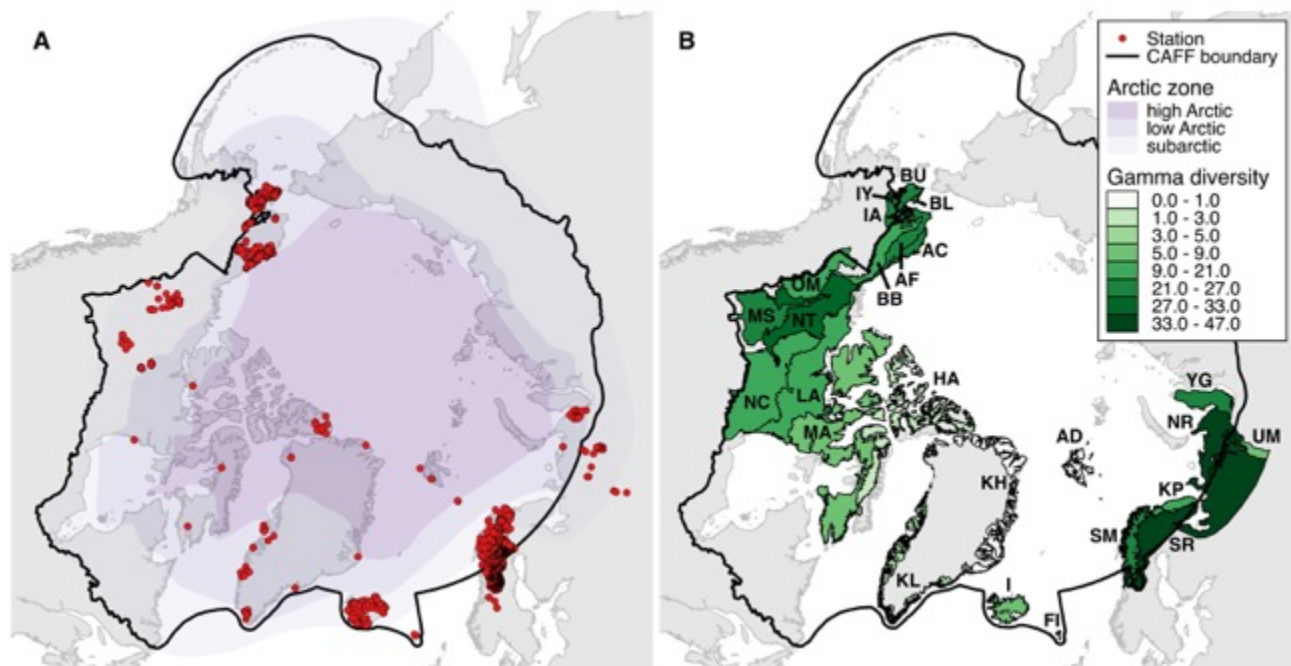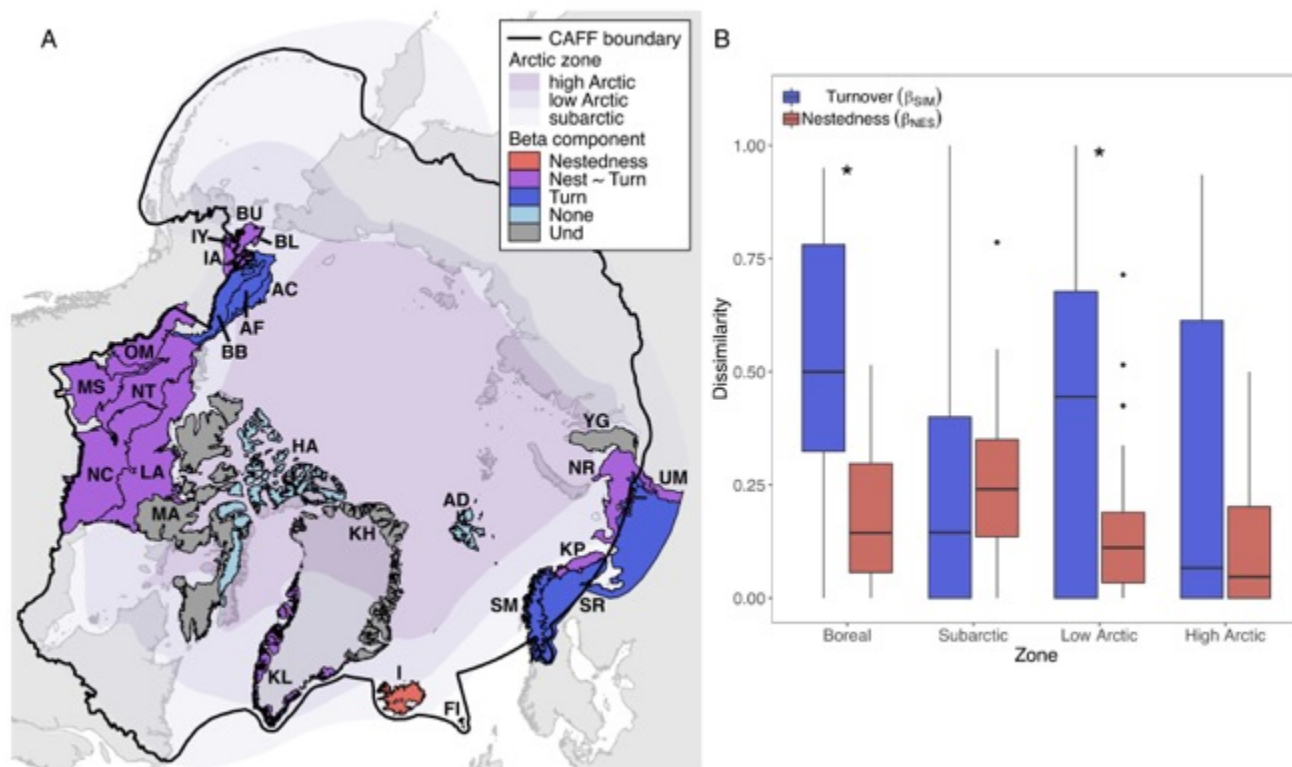

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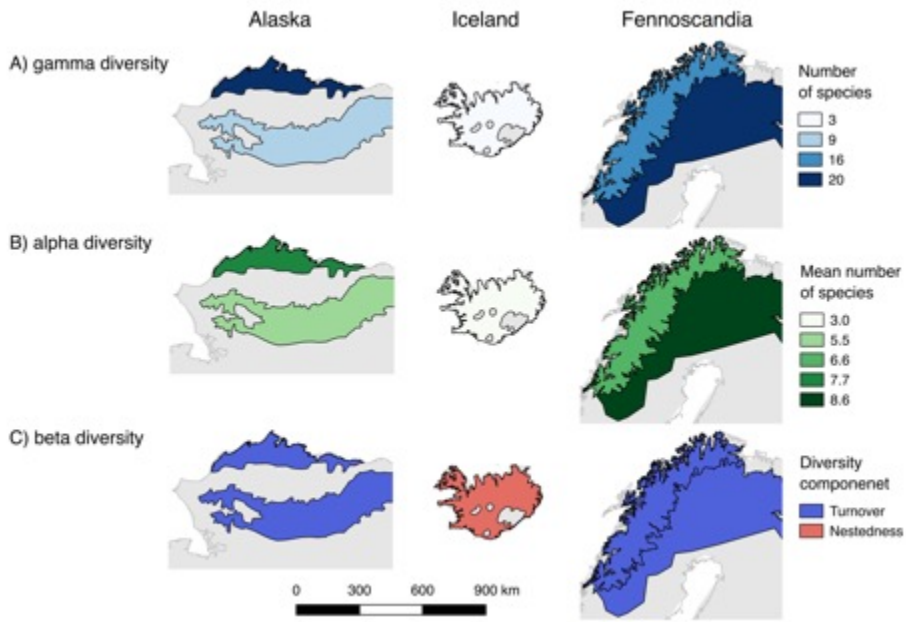1020   Figure 2.

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1023   Figure 3.

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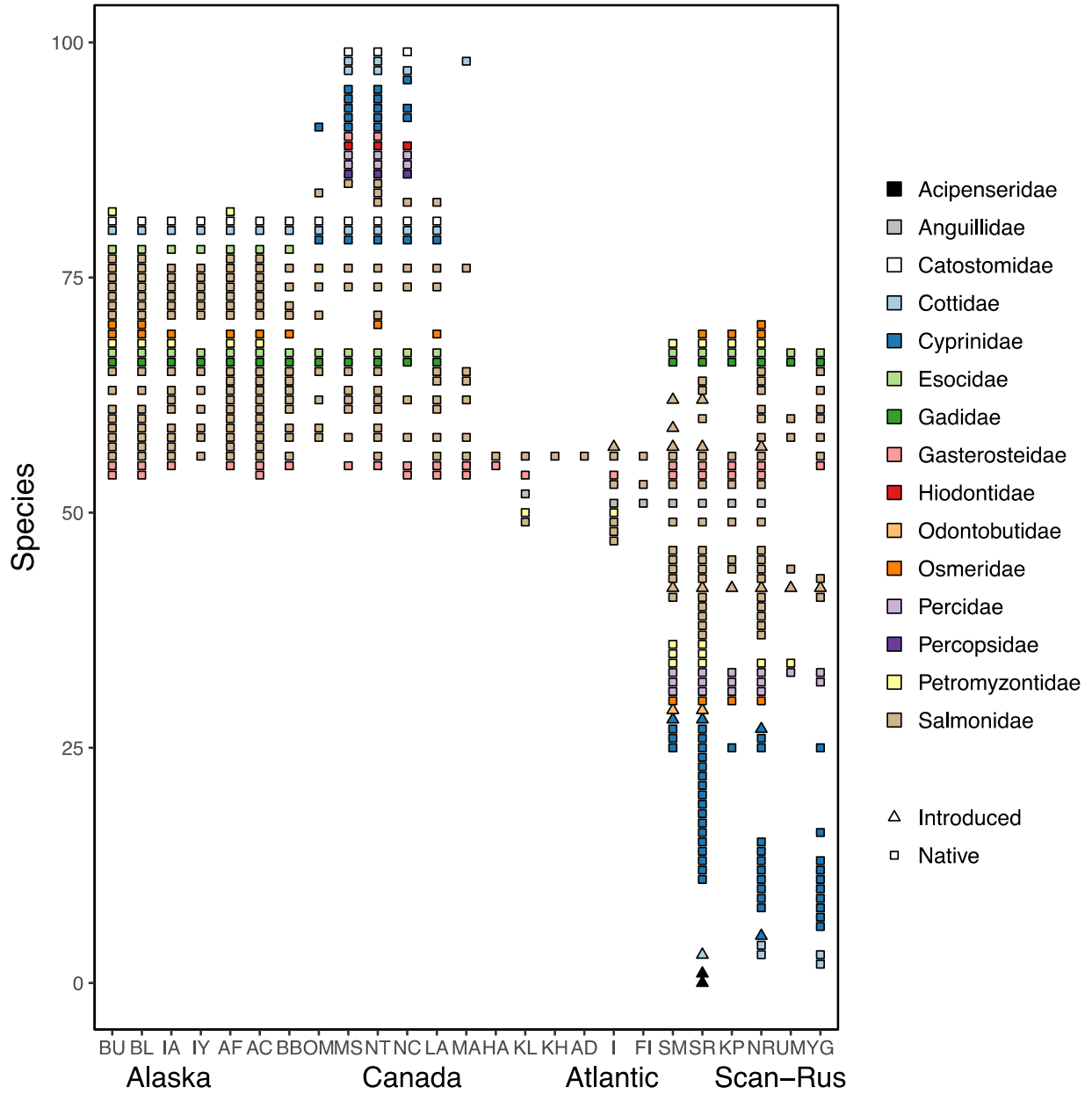
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1031   Figure 6.