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Increased Habitat Connectivity Homogenizes Freshwater Communities: Historical and Landscape Perspectives

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Citation Details

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2 **landscape perspectives**

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11 Running Head: Connectivity Homogenizes Communities

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Summary

1. Increases in habitat connectivity can have consequences for taxonomic, functional, and genetic diversity of communities. Previously isolated aquatic habitats were connected with canals and pipelines in the largest water development project in US history, the Columbia Basin Project (eastern Washington, USA), which also altered environmental conditions; however, the ecological consequences are largely unknown.

2. Using a historical dataset, we examined long-term patterns in zooplankton communities, water chemistry and clarity, testing the hypothesis that increased connectivity will result in taxonomic homogenization. Further, we tested contemporary drivers of communities using a comprehensive set of environmental and landscape variables.

3. Waterbodies were sampled for zooplankton community composition as well as physical and chemical variables inside and outside the Columbia Basin Project using methods consistent with historical studies.

4. We found significant declines in salinity inside the Columbia Basin Project, whereas changes in water clarity were prevalent across all waterbodies. Increased connectivity via canals homogenized zooplankton communities over time, as well as increasing regional richness. Other long-term changes in zooplankton communities may be related to climate change, invasive species, and land-use changes.

5. *Synthesis and applications.* Though canals may offer species spatial refugia, homogenization may decrease resilience to environmental stressors. These new hybrid aquatic landscapes, or hydroscapes, should be considered carefully in future water development, including specific plans for monitoring of species and environmental conditions, as well as mitigation of undesirable conditions and/or non-native species.

36 **Key-words:** biotic homogenization, canals, Channeled Scablands, Columbia Plateau, habitat

37 connectivity, freshwater communities, metacommunities, salinity, taxonomic homogenization

38

39 **Introduction**

40   Despite widespread interest in the ecological effects of habitat fragmentation, much less

41 is known about the consequences of increased habitat connectivity. Globalization of commerce

42 has moved vast numbers of invasive species around the globe, which, in combination with losses

43 of native and endemic taxa, can lead to taxonomic, functional, and genetic homogenization of

44 previously distinct communities (Olden *et al.* 2004). By contrast, the effects of increased

45 connectivity for native taxa at more regional, intermediate spatial scales is poorly understood

46 (Rahel 2007). The current paradigm is that connectivity amplifies species movement, thereby

47 increasing species diversity, and ultimately facilitating adaptation to local conditions (Urban *et*

48 *al.* 2008). Yet, if dispersal is high enough, communities can be homogenized via mass effects

49 (Mouquet & Loreau 2003), where species are rescued from local extinction by immigration in

50 metacommunities (Leibold *et al.* 2004). These high rates of dispersal will overwhelm species

51 sorting, where taxa match the environment when dispersal is moderate (Leibold *et al.* 2004).

52 Critically, the consequences of increased connectivity are likely to be significant for freshwater

53 organisms that are constrained to live in or near water, where habitats are typically discontinuous

54 (Rahel 2007).

55   Aquatic ecosystems have been irreversibly altered by dams and irrigation projects, with

56 significant effects on connectivity. For instance, canals and pipelines can greatly increase

57 structural connectivity (sensu Tischendorf & Fahrig 2000). Despite the potential importance of

58 this widespread increase in connectivity, the ecological effects are poorly understood. For

59   instance, a review of human-created aquatic habitats found that the ability of canals to support

60   native biodiversity is equivocal (Chester & Robson 2013). A neutral model of community

61   assembly suggested that increasing connectivity via water transfers could result in common

62   mobile species spreading relatively easily, increasing local richness, with a decrease in total

63   system richness (Grant *et al.* 2012). Critically, by definition this model failed to consider the

64   influence of environmental conditions, which likely has at least some effect on communities.

65   Water development projects can alter the surrounding surface and groundwater. Leakage

66   from canals and reservoirs is highly correlated with wetland water levels and chemistry via

67   changes in groundwater and interactions with soils (Sueltenfuss *et al.* 2013). Additionally,

68   salinization of surface and groundwater is a common byproduct of irrigation (Lemly, Kingsford

69   & Thompson 2000). Thus, water development represents a type of 'natural experiment,' where

70   the spatial and environmental mosaic of aquatic metacommunities is altered by human activities.

71   However, the consequences of increased connectivity may be intertwined with changes in

72   environmental conditions, making it difficult to disentangle their relative importance for

73   community diversity and similarity (i.e., homogenization). Here, we describe a system in which

74   to test hypotheses about the independent effects of connectivity and environmental change on

75   community structure.

76   The Columbia Basin Project (CBP) in eastern Washington, USA built six dams and >480

77   kilometers of canals for irrigation, flood protection, and power production (Figure 1). The CBP

78   was one of the earliest (~1945) and remains the single largest irrigation project in the country;

79   therefore, it is a useful case study for understanding ecological changes. A study conducted

80   prior to the construction of the CBP showed waterbodies ranging across broad gradients of

81   salinity, seasonality, and productivity, with distinctive invertebrate communities (Whittaker &

82   Fairbanks 1958). Edmondson (1969) showed that hydrologic alterations changed salinity and

83   species composition in two lakes; however, landscape-level effects are unknown and may be

84   variable due to erratic groundwater changes (Whiteman *et al.* 1994). Canals in the CBP have

85   increased the structural connectivity between some lakes, while others have remained isolated,

86   thereby creating differences in connectivity across the landscape and therefore, differences in

87   dispersal opportunities for organisms. Zooplankton are known to be effective colonists,

88   dispersing at scales of <1 to 1000s of kilometers (Havel & Shurin 2004). Thus, waterbodies

89   within the CBP represent a gradient of relevant dispersal distances for zooplankton.

90   Given the changes documented above, our question is this: do changing connectivity and

91   environmental conditions act to homogenize zooplankton communities in freshwater

92   ecosystems? *Objective 1*: Examine long-term changes in water chemistry, clarity, and

93   zooplankton community metrics (richness, turnover, homogenization) using a historical dataset

94   dating back >65 years with sites inside the CBP (~treatment) and outside the CBP (~reference).

95   *Objective 2:* Test contemporary mechanisms affecting zooplankton richness and community

96   composition in waterbodies inside and outside the CBP using a full suite of physical, chemical,

97   landscape (i.e., land use) variables, as well as variables representing spatial connectivity. We

98   predict that there will be no differences in physicochemical and community metrics by region

99   (inside vs. outside CBP) for the historical period before water development, but that there will be

100   significant differences between regions in contemporary times. We hypothesize that increased

101   connectivity via water development will greatly increase dispersal opportunities and therefore,

102   simulate the mass effects metacommunity perspective and homogenize contemporary

103   communities (Mouquet & Loreau 2003). As a result, spatial variables will be more important

6

104 than environmental variables in the contemporary period in determining zooplankton community

105 composition.

106

107 **Materials and methods**

108 *Study Area and Sampling*

109   The study area was located in the arid Channeled Scablands of southeast Washington, a

110 vast area of geological significance containing large coulees spotted by ponds and lakes

111 (Whittaker & Fairbanks 1958). Waterbodies in the region range from oligotrophic to eutrophic,

112 freshwater (<3 ppt) to mesosaline (20 – 50 ppt), and neutral to pH >10 (Whittaker & Fairbanks

113 1958; Edmondson 1969).

114   In July and August 2012, we revisited 24 of the 40 waterbodies that were sampled by

115 Whittaker & Fairbanks (1958), which we call '*paired sites*' (Figure 1). Some of the historically

116 sampled waterbodies no longer exist due to inundation by reservoirs, whereas others were

117 inaccessible or dry, thus the remaining sites were not sampled. Waterbodies were identified by

118 site descriptions in Fairbanks (1950). An additional 17 sites were sampled in summer 2012 and

119 2013 to increase the spatial coverage of the study, especially of sites that experienced an increase

120 in connectivity. We refer to these additional sites as '*contemporary landscape sites*', thus paired

121 and landscape sites are two different subsets of the entire set of samples. To increase spatial

122 coverage, we also included data on 14 historical sites that were not resampled, which were called

123 '*historical landscape sites*'. Thus, we had 24 paired sites (i.e., the same 24 sites in both

124 historical and contemporary periods), 41 total contemporary sites, and 38 total historical sites.

125 Contemporary sites included reservoirs, canals, lakes, and ponds, whereas historical sites

126   included just lakes and ponds. Ponds were defined as sites that were <10 ha in size and <2 m

127   deep. Site characteristics are summarized in Table 1 (details in Appendix S1).

128   Waterbodies were sampled for physical, chemical, and biological parameters between

129   0900 and 1500. At all sites, temperature, dissolved oxygen, specific conductance, salinity, pH,

130   and nitrate were measured using a YSI ProPlus and an Orion 290A pH meter. For deeper lake

131   sites, temperature and dissolved oxygen profiles were taken at 1-m intervals at the deepest spot,

132   and the remaining variables were measured at the surface and 1 m. At shallower sites, a grab

133   sample was taken from ~0.5-m depth, which was immediately measured for the aforementioned

134   physicochemical variables.

135   Using a 2.5-cm diameter tube, an integrated water sample was taken from the epilimnion

136   (determined from temperature profiles) of lakes for total phosphorus, which was analyzed

137   following APHA (2005). At shallower pond sites and canals, a grab sample was taken from

138   ~0.5-m depth. Secchi measurements were taken in all waterbodies using a black and white 20-

139   cm diameter disc. Fairbanks (1950) measured Secchi depth with a 10-cm all-white disc. Studies

140   have found that disc colour and size do not significantly affect the measurement (Holmes 1970;

141   Jones & Bachmann 1978). Epilimnetic (deep lakes) or surface (shallow) water was filtered

142   through glass fiber filters (pore = 1.2 μm) to estimate phytoplankton biomass using chlorophyll

143   *a*. Filters were frozen and analyzed using a Turner Designs fluorometer (Arar & Collins 1997).

144   To maintain consistency between historical and contemporary sampling, both open-water

145   pelagic and shoreline tows were performed for zooplankton in larger waterbodies, whereas only

146   shoreline tows were taken from shallow waterbodies. Zooplankton tows were taken with a 80-

147   μm mesh net (25-cm diameter, 1.2-m length). Pelagic tows were taken at the deep spot, from the

148   bottom of the lake (less 2m for the net) to the surface. Shoreline tows were taken by towing the

149 net horizontally through the water 1-2x (depending on the size of the waterbody) for ~2-3 m,

150 sampling a similar volume as in Fairbanks (1950). Zooplankton samples were preserved at a

151 final concentration of 70% ethanol.

152 Zooplankton were enumerated on a Nikon dissecting microscope by a regional expert and

153 identified using taxonomic keys and a protocol designed to target rare species (Appendix S2).

154 As a result of likely differences in identification over time and between different taxonomists,

155 species that were present and relatively prevalent at the landscape scale (>12%) in one time

156 period, but completely absent from the other time period, were removed from ordinations in

157 which species identity is important. In order to test the sensitivity of our results to these actions,

158 we performed additional analyses in which: 1) all taxa were grouped at the genus level; and 2) all

159 taxa were included (Appendix S3). It is noteworthy that several of the species found in the

160 contemporary but not the historical period were completely new genera, as well as being quite

161 distinctive and not easily confused with other species (e.g., *Eubosmina coregoni* Baird).

162

163 *Objective 1: Analyses of long-term changes in waterbodies*

164 Taxon richness was compared from historical and contemporary time periods for the

165 subset of paired sites and the full set of sites (paired + landscape). Gamma, or regional, richness

166 was the sum of all zooplankton taxa in each study period in each region. Within-lake beta

167 diversity, i.e., turnover across time, was examined in paired sites using the β_{sim} index, which

168 controls for differences in richness (Lennon *et al.* 2001):

169 (eq 1) $\beta_{sim} = \frac{1}{n}\sum_{i=1}^{n}(1 - S_{2i}); S_{2i} = \frac{a_i'}{a_i' + min\,(b_i', c_i')}$

170 where a' is the total number of taxa present in both samples, b' is the number of taxa present only

171 in sample one, and c' is the number of taxa present only in sample two, with $\beta_{sim} = 0$ indicating

172   complete similarity and $\beta_{sim} = 1$ indicating complete dissimilarity. As many of the paired sites

173   did not experience changes in connectivity, taxonomic homogenization was evaluated by

174   comparing between-lake beta diversity, or compositional similarity (CS), across the full set of

175   sites for contemporary and historical periods for all zooplankton taxa, also using the β_{sim} index

176   (CS = 1 - β_{sim}). Pairwise CS values were averaged within a time period and then compared

177   using: $\Delta CS = CS_{contemporary} - CS_{historical}$ (Olden & Rooney 2006). Regions were tested separately

178   to test the hypothesis that homogenization has occurred as a result of water development.

179   The influence of time period (historical, contemporary) and region (inside CBP, outside

180   CBP) on environmental (salinity, Secchi, pH) and zooplankton community metrics (richness,

181   turnover) were assessed using generalized least squares (GLS) and linear mixed effects (LME)

182   models. Period, region, and their interaction were considered fixed effects, while lake was a

183   random effect. AIC was used to determine the most parsimonious model. If transformations of

184   variables could not achieve randomly distributed residuals, a generalized linear mixed model

185   (GLMM) was used (Zuur *et al.* 2009) with a Poisson distribution for counts (i.e., richness) and a

186   gamma distribution for continuous variables (i.e., salinity). If overdispersion was detected, a

187   negative binomial distribution was used. All analyses were performed with libraries *lme4,*

188   *glmmADMB*, and *MASS* in R version 3.1.3 (R Development Core Team 2013).

189   In order to compare changes in community composition across time, we performed a

190   two-step multivariate analysis on zooplankton in historical and contemporary periods from the

191   full set of sites, as site identity is less important for these tests. Presence/absence data were used

192   because abundances were not available for all taxa historically. Step one was to use a

193   permutational MANOVA to test for statistical differences over time in communities (Anderson

194   2001). The strength of this approach is that it can simultaneously test the significance of period

195   (historical, contemporary) and region (inside CBP, outside CBP) on community composition (*n*

196   = 9999 permutations). Step two used constrained ordination (redundancy analysis: RDA) and

197   variation partitioning techniques to examine the influence of environmental and spatial variables

198   on community composition (Appendix S4). Time periods and regions were tested in separate

199   RDAs to understand relative changes in variable importance; it was not possible to test periods

200   simultaneously because spatial predictors changed over time due to the increased connectivity

201   via canals.

202   Environmental variables that were available for both time periods included salinity, pH,

203   Secchi depth, and surface temperature. The effects of spatial scale and connectivity on

204   zooplankton community composition were determined by constructing spatial variables that

205   modeled the processes of overland dispersal or spatial proximity (Euclidean distance, "as the

206   crow flies") and passive dispersal via natural or human-altered water-courses (watercourse

207   distance, "as the fish swims") (Appendix S4), referred to as spatial variables hereafter. A

208   significant effect of watercourse distance on community composition without a corresponding

209   effect of Euclidean distance would support our hypothesis that increased connectivity via water

210   development is influencing zooplankton over broad distances.

211   Though fish can influence zooplankton, it is unknown whether fish were present

212   historically. Fish are currently present in nearly all the lakes; however, it is unknown whether

213   fish exist in the ponds, where logistics precluded sampling. Because of this uncertainty,

214   categorical variables for *lake* and *pond* were included in all of the analyses that included

215   predictors (e.g., RDA), which should capture unmeasured environmental variables, like fish

216   presence.

217

Objective 2: Analyses of contemporary drivers

218

219   In order to test contemporary mechanisms affecting zooplankton richness and community

220 composition in waterbodies inside and outside the CBP, a suite of landscape variables was

221 created for all sites. Lake network number is an integer representing lake chain number that was

222 used to assess the influence of landscape position and connectivity, with 1 representing a

223 headwater lake, 2 representing the next lake downstream, and so on (Martin & Soranno 2006).

224 Waterbodies completely isolated from a stream/lake network were assigned 0. Lake network

225 number is unaffected by the density of upstream waterbodies. Lake network number and the

226 density of canals and pipelines ($km·km^{-2}$) within watersheds was derived from the National

227 Hydrography Dataset (USGS 2015). To assess the influence of watershed activities on

228 zooplankton communities, the National Land Cover Database was used to determine % wetlands,

229 % urban, % agriculture, and % natural lands (Multi-Resolution Land Characteristics 2011)

230 within 12-digit hydrologic units (USDA 2015). The aforementioned variables could not be

231 constructed for the historical period because of incomplete information. The presence of a boat

232 ramp and waterbody permanence (Appendix S1) were also used in analyses on zooplankton

233 communities. These landscape variables were combined with the physical and chemical

234 variables measured in 2012/13; hereafter, these are referred to as environmental variables.

235   The effects of environmental variables on species richness were examined using boosted

236 regression trees on all contemporary sites. Boosted regression trees use two algorithms

237 (regression trees, boosting) to build many trees that clusters sites into end nodes, which

238 sequentially improve on previously fitted trees (Elith, Leathwick & Hastie 2008). Boosted

239 regression trees were fit with a learning rate of 0.01 and a tree complexity of 3, which provided

240 ~1700 trees, exceeding the minimum recommended by Elith, Leathwick & Hastie (2008). We

241 report D^2 (deviance explained) to evaluate model performance. Ten-fold cross-validation was

242 used to evaluate predictive performance. Boosted regression tree were fit using the R library

243 *dismo*.

244 Finally, we performed an in-depth analysis of the contemporary drivers of zooplankton

245 community composition in each region using the larger suite of environmental variables (i.e.,

246 physical, chemical, landscape) (Appendix S1). RDAs and variation partitioning were run using

247 the same methods as in Objective 1 (Appendix S4), contrasting the relative influence of both sets

248 of spatial variables (Euclidean, watercourse) with environmental variables on zooplankton

249 composition.

250

251 **Results**

252 *Objective 1: Long-term changes in waterbodies*

253 The water clarity and chemistry of sites was compared from historical to contemporary

254 periods for two data sets: 1) paired sites (same site over time), and 2) all sites (paired +

255 landscape). Given the similarity in results, only the full set of sites are shown (paired sites in

256 Appendix S5). There was a significant interaction of time period and region for salinity, where

257 concentrations have declined inside the CBP over time, but have not changed outside the CBP

258 (GLMM: $Z = -3.450$, $P < 0.001$, $n = 79$; Figure 2a). There was no effect of region (GLMM: $Z = -$

259 0.220, $P = 0.830$, $n = 77$) or time period on pH ($Z = -0.371$, $P = 0.710$, $n = 77$) (Figure 2b).

260 Water clarity increased significantly over time, 1.5 m on average (GLMM: $Z = -2.030$, $P =$

261 0.043, $n = 69$; Figure 2c). Water clarity was also significantly different between regions, with

262 waterbodies inside the CBP having significantly higher clarity compared to waterbodies outside

263 the CBP (average difference 1.8 m) ($Z = -2.511$, $P = 0.012$, $n = 69$; Figure 2c).

264   Richness was significantly higher in the contemporary period across all sites (LME: t_{22} =

265 -4.101, $P < 0.001$), but there was no effect of region (t_{53}= -1.430, $P = 0.159$), or an interaction of

266 period and region ($t_{22} = 0.886$, $P = 0.385$) (Figure 2d). Total regional, or gamma, richness also

267 increased over time, from 21 to 24 taxa (Figure 2d), likely from newly introduced non-native

268 species (i.e., *Eubosmina coregoni*) and detections of native species new to the area (i.e.,

269 *Hesperodiaptomus nevadensis* Light*,* which is known from several western states; Reid and

270 Williamson (2010)).

271   We observed evidence of taxonomic homogenization inside the CBP, in contrast to sites

272 outside the CBP, which diversified over time. Sites outside the CBP experienced a 14.0%

273 decrease in compositional similarity (ΔCS = -0.079, $CS_{contemporary} = 0.487$, $CS_{historical} = 0.566$),

274 whereas sites inside the CBP experienced a 13.2% increase in compositional similarity (ΔCS =

275 0.066, $CS_{contemporary} = 0.562$, $CS_{historical} = 0.496$). Sensitivity analyses to test for the effects of

276 potential changes in taxonomy over time or different taxonomists showed that ΔCS was

277 consistent in direction but generally greater in magnitude compared to the results above,

278 suggesting that the trends that we have observed are robust and likely conservative estimates of

279 community change (Appendix S3). Within-lake beta diversity, or temporal turnover for paired

280 lakes, indicated that turnover in zooplankton communities in individual lakes did not differ

281 inside vs outside the CBP (inside: $\beta_{sim} = 0.24 \pm 0.19$SD, outside: $\beta_{sim} = 0.32 \pm 0.24$SD) (LME: t_{22}

282 = 0.970, $P = 0.343$).

283   We hypothesized that there would be significant changes in community composition in

284 the contemporary period compared to the historical period. We found significant effects of

285 period (permutational MANOVA: $F_{1,75} = 2.320$, $P = 0.044$) and region ($F_{1,75} = 3.765$, $P = 0.001$)

286 on community composition, in addition to a nearly significant interaction of period and region

287   ($F_{1,75}$ = 2.018, P = 0.077). To understand this interaction further, we analyzed time periods

288   separately: as predicted, region was not significant in the historical period ($F_{1,36}$ = 1.392, P =

289   0.233), but was significant in the contemporary period ($F_{1,36}$ = 4.528, P = 0.004) in explaining

290   zooplankton community composition. The sensitivity analyses indicated that the results from the

291   permutational MANOVA were not qualitatively different when all species were included

292   (Appendix S3).

293   We examined relationships between zooplankton community composition, environmental

294   variables, and spatial connectivity via watercourses in the full set of sites with RDA. In

295   historical communities, salinity and the categorical variable *lake* were significant environmental

296   drivers inside the CBP and *lake* was significant outside the CBP (Appendix S5). Variation

297   partitioning indicated that spatial structure explained some variation in historical zooplankton

298   communities (inside CBP: R^2_{adj} = 0.01, P = 0.359; outside CBP: R^2_{adj} = 0.10, P = 0.010).

299   Environmental variables failed to explain significant variation in historical community structure

300   after controlling for the effects of spatial variation (Figure 3a,c), suggesting that spatially-

301   structured environmental gradients were likely influencing communities, explaining an

302   additional 12% and 3% of variation inside and outside the CBP, respectively (the shared fraction

303   cannot be tested for significance) (Figure 3a,c).

304   Contemporary zooplankton communities inside the CBP were influenced by the

305   categorical variables *reservoir, canal*, and *pond*, whereas Secchi depth was a significant variable

306   outside the CBP (Appendix S5). The importance of spatial variation increased inside the CBP in

307   the contemporary period compared to the historical period: spatial variables explained significant

308   variation in zooplankton communities inside the CBP (R^2_{adj} = 0.17, P = 0.001), but spatial

309   variables were not significant outside the CBP (R^2_{adj} = 0.00, P = 1.000) (Figure 3b,d).

310   Environmental factors explained a significant portion of variance in both regions (Figure 3b,d).

311   Spatially-structured environmental gradients did not explain any additional variation. The results

312   obtained when using Euclidean distance to generate spatial variables only showed a moderately

313   significant trend outside the CBP in the historical period (Appendix S5).

314

315   *Objective 2: Contemporary Drivers*

316   We examined the influence of environmental and landscape factors on contemporary

317   species richness using boosted regression trees. Boosted regression trees explained 18% of the

318   deviance in contemporary species richness across all sites (cross-validated residual deviance =

319   9.100, total deviance = 11.131). The most important variables included surface area, chlorophyll

320   *a*, salinity, and canal density (Figure 4, Appendix S5). Finally, our in-depth analysis of the

321   factors that influence contemporary zooplankton communities indicated that pH, Secchi depth,

322   surface temperature, % agriculture, and total phosphorus were significant environmental

323   predictors inside the CBP, with % agriculture and the presence of a boat ramp significant

324   predictors outside the CBP (Appendix S5). Using variation partitioning, we found that spatial

325   variables constructed using watercourse distance explained significant variation in contemporary

326   zooplankton communities in both regions (inside CBP: $R^2_{adj} = 0.06$, $P = 0.013$; outside CBP: R^2_{adj}

327     $= 0.06$, $P = 0.022$) (Figure 5). Additionally, spatial variables constructed from Euclidean

328   distances were significant predictors of zooplankton communities outside the CBP only (inside

329   CBP: $R^2_{adj} = 0.00$, $P = 1.000$; outside CBP: $R^2_{adj} = 0.150$, $P = 0.002$) (Appendix S5). This

330   suggests that the natural riverine connections that connect waterbodies outside the CBP have an

331   influence on community structure, but that the effect is localized and related to spatial proximity

332   (i.e., high proportion of variation explained by Euclidean distance). By contrast, the lack of

333 significant community variation explained by Euclidean distance inside the CBP suggests that

334 the connectivity created by water development projects is having an effect at broad spatial scales.

335

336 **Discussion**

337 Changes in the connectivity of aquatic landscapes are a prevalent feature of human

338 society, yet there are significant knowledge gaps regarding how increases in structural

339 connectivity may alter ecological communities. Using historical comparisons and measures of

340 landscape connectivity, we suggest that connectivity via canals has homogenized zooplankton

341 communities over time, but that there has been no significant loss of average local or regional

342 taxon richness. Water development can result in unintended and widespread changes in the

343 environment: we found that the Columbia Basin Project (CBP) resulted in significant declines in

344 salinity, but no changes in water clarity or pH compared to reference sites. We also observed

345 changes in zooplankton communities and water clarity over multiple decades that were not

346 linked to water development, suggesting other long-term phenomena may be responsible. The

347 combination of historical and landscape ecology may be a powerful approach to elucidating

348 complex responses to anthropogenic changes in natural ecosystems.

349 Homogenization of flora and fauna has become a signature of human impacts on

350 communities (Olden *et al.* 2004). We observed regional homogenization of zooplankton

351 communities over time inside the CBP, with a ~13% increase in compositional similarity

352 (compared to a 14% decrease in similarity outside the CBP). These rates are substantially higher

353 than values observed in plants and animal communities globally (Baiser *et al.* 2012). These

354 results supported our hypothesis that increasing connectivity would greatly increase dispersal

355 rates and lead to homogenization (i.e., mass effects metacommunity perspective). The

356   mechanisms for this were revealed using watercourse distances as explanatory variables in our

357   multivariate ordinations of zooplankton communities: the increase in the importance of spatial

358   variation over time within the CBP (Figure 3a,b) indicates connectivity had a significant

359   influence on community structure. In contrast, the insignificant variance explained using

360   Euclidean distance in either time period (Appendix S5) suggests that proximity is not driving

361   spatial differentiation of zooplankton communities and thus, that the connectivity created by

362   water development projects is having an effect at broad spatial scales. Additional evidence

363   comes from examining the factors that influence contemporary taxon richness: more highly

364   connected downstream sites and sites near canals had greater richness (Appendix S5).

365   Despite the increase in community similarity over time, we did not observe decreases in

366   local or regional richness – indeed we observed increased local richness in the contemporary

367   period compared to the historical period across both regions (i.e., inside and outside the CBP)

368   and increased regional richness over time inside the CBP, from 18 to 21 taxa, with no

369   corresponding increase outside the CBP (Figure 2d). Grant *et al.* (2012) modeled the effects of

370   inter-basin water transfers and found that increasing connectivity via canals could result in

371   common taxa spreading easily, increasing local richness, but decreasing overall regional richness

372   via homogenization. These results generally align with our findings. In our study, highly

373   connected canals and reservoirs were the most diverse waterbodies, with ~6 more taxa on

374   average compared to other more isolated waterbodies inside the CBP. For instance, the invasive

375   zooplankter, *Eubosmina coregoni*, was present in six waterbodies in the study area, all of which

376   were within the CBP (Smits *et al.* 2013). Anthropogenic waterbodies (e.g., canals and reservoirs)

377   can act as refuges for biodiversity, harbouring endangered species, with community composition

378   similar to natural waterbodies (Chester & Robson 2013 and references therein). The ability of

379 these anthropogenic waterbodies to protect biodiversity may be linked to both local and

380 landscape factors, including providing connectivity to natural waterbodies. Thus, connectivity

381 may be a double-edged sword, capable of promoting diversity but also of homogenizing regional

382 communities and accelerating the spread of invasive species.

383   Changes in connectivity do not occur in isolation of other environmental stressors. We

384 observed significant changes in water clarity and zooplankton richness over time, as well as

385 influences of land use, temperature, and salinity on richness and community composition. Given

386 that agricultural intensification has occurred in the region alongside water development, it was

387 surprising to observe increased water clarity over time. However, erosion control measures

388 begun in the 1970s have likely contributed to this improvement (Ebbert & Roe 1998). Temporal

389 increases in both average alpha and gamma richness across the entire study area (Figure 2d)

390 likely reflect several factors, including the spread of *Eubosmina coregoni* (Smits *et al.* 2013),

391 declining salinity in historically hypo- and meso-saline lakes facilitating the introduction of the

392 moderately saline tolerant *Hesperodiaptomus nevadensis* (Hammer 1986), and climate change

393 facilitating range expansion of warmwater species, particularly at thermal boundaries (Heino,

394 Virkkala & Toivonen 2009). We observed mid-summer near surface temperatures from 14.5 –

395 26.8°C (median = 22.7°C), suggesting that there is a large thermal gradient that exists in the

396 region, potentially fed by cooler groundwater that rose considerably following construction of

397 dams and canals (Whiteman *et al.* 1994). This variable thermal landscape may encourage

398 regional coexistence of both cool- and warmwater species: several of the taxa found in

399 contemporary, but not historical periods, included so-called southern species associated with

400 warmer temperatures (e.g., *Skistodiaptomus oregonensis* Lilljeborg) (Patalas 1990). Importantly,

401 maintaining spatial variability in the abiotic environment may facilitate a diverse regional species

402 pool, with taxa, traits, and genes that can respond to future environmental changes.

403   Studies of this nature face some limitations. We took steps to minimize the influence of

404 inaccuracies in historical data, including pairing the same level of taxonomic identification,

405 enlisting a regional taxonomic expert, harmonizing sampling methods, and excluding species

406 that were present and relatively prevalent in one period, but not present in the other, from

407 multivariate analyses. Sensitivity analyses indicated that these actions did not significantly alter

408 our results (Appendix S3). Total variation explained by multivariate comparisons of historical

409 and contemporary zooplankton communities was generally low (13-32%, Figure 3), which is

410 likely because some key environmental variables were not included in the analysis as a result of

411 limited historical environmental information. Another limitation is that assessing patterns rather

412 than process can limit inference, particularly with unreplicated study regions. For instance, we

413 assumed that canals were the major zooplankton dispersal pathway; however, other dispersal

414 vectors, such as waterfowl or boaters, may be important in moving organisms between

415 waterbodies (Havel & Shurin 2004; Stasko *et al.* 2012). We found no significant influence of

416 boat ramps on communities inside the CBP; additionally, Gray and Arnott (2011) demonstrated

417 that the egg bank and stream connections were the largest contributors of individuals to a lake,

418 which suggests that canals likely outweigh other pathways of dispersal. Though our inference is

419 limited by the lack of independent replicated regions, the similarities between our results and the

420 modeling study of Grant *et al.* (2012) suggests that our findings are valid. Finally, the presence

421 of fish can significantly alter zooplankton communities, but we did not have sufficient data on

422 fish presence. Rather, we used categorical variables to represent lake vs. pond waterbodies,

423 which were significant predictors of community composition (Figure 3). However, the species

424   associated with pond and lake vectors likely do not represent the influence of fish: lakes were

425   typically associated with large-bodied copepods (e.g., *Epischura nevadensis* Lilljeborg), whereas

426   ponds were associated with littoral species (e.g., *Scapholeberis* sp. Schoedler) (Appendix S5).

427   Thus, there was no strong signal of fish predation in our study.

428   In conclusion, we observed significant changes in community structure (i.e.,

429   homogenization) and environmental conditions following the largest water development project

430   in US history, the Columbia Basin Project. Homogenization can have important consequences:

431   more spatially similar communities may be less resilient to widespread environmental stressors

432   through the loss of specialists (Clavel, Julliard & Devictor 2010), and less able to resist invasive

433   species (García-Ramos & Rodríguez 2002). Thus, canals connecting previously isolated lakes

434   may constitute a new type of hybrid aquatic landscape, blending elements of riverscapes with

435   landscape limnology (Fausch *et al.* 2002; Soranno *et al.* 2010). These novel hydroscapes are

436   likely to become more prevalent in the future, as water shortages will intensify demands for

437   higher volume and longer distance water transfers (McDonald *et al.* 2011), heightening the need

438   for better understanding of the ecological consequences of altered hydrologic regimes. By

439   contrast, regions where droughts become more frequent may experience partial or complete

440   losses of connectivity, with negative consequences for aquatic species (Jaeger, Olden & Pelland

441   2014). We recommend that managers and policymakers consider the effects of increased aquatic

442   connectivity and changing surface and groundwater conditions for local freshwater ecosystems

443   prior to initiating new water development projects, with specific plans for monitoring of species

444   and environmental conditions and mitigation of undesirable conditions and/or non-native

445   species.

446

447 **Authors' Contributions**

448 AS conceived the study; AS and JB collected and analyzed the data, and wrote the manuscript.

449 All authors contributed critically to the drafts and gave final approval for publication.

450

457

458 **Data Accessibility**

459 Environmental data included in Appendix S1. Contemporary species data deposited in Dryad

460 Digital Repository, doi:10.5061/dryad.b9h4h.

461

462 **Supporting Information**

463 Additional supporting information may be found in the online version of this article.

464 Appendix S1. Physical, chemical, biological, and landscape characteristics of waterbodies.

465 Appendix S2. Taxonomic information for historical and contemporary species identifications.

466 Appendix S3. Sensitivity analyses.

467 Appendix S4. Detailed methods for redundancy analysis and variation partitioning.

468 Appendix S5. Results from paired sites, redundancy analyses, and variation partitioning.

469

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586

587 **Table 1**. Physical, chemical, and biological parameters of waterbodies from contemporary and

588 historical samples. Historical data from Fairbanks (1950). SD = standard deviation, Z_{max} =

589 maximum depth

	contemporary		historical	
parameter	**median (± SD)**	**minimum – maximum**	**median (± SD)**	**minimum – maximum**
surface area (ha)	40.1 ± 2488	0.1 – 11331.2	43.0 ± 419.8*	0.5 – 2060.0*
Z_{max} (m)	6.4 ± 19.3	1.5 – 106.7	--	--
elevation (m)	366 ± 163.9	216 – 732	--	--
surface temperature (°C)	22.7 ± 2.3	14.5 – 26.8	23.1 ± 4.0	13.5 – 32.2
Secchi (m)	2.1 ± 1.8	0.4 – 6.7	0.7 ± 1.5	0.1 – 6.1
pH	8.78 ± 0.65	6.70 – 9.85	9.12 ± 0.80	7.10 – 10.68
calc pH	9.33 ± 0.65	7.25 – 10.40	--	--
salinity (ppt)	0.28 ± 2.31	0.07 – 14.43	0.62 ± 7.09	0.16 – 38.7
specific conductance ($\mu S \cdot cm^{-1}$)	571.5 ± 3839.1	9.4 – 23838.0	--	--
total phosphorus ($\mu g \cdot L^{-1}$)	58.51 ± 286.53	1.72 – 1746.21	--	--
nitrate ($mg \cdot L^{-1}$)	0.63 ± 0.87	0.13 – 4.20	--	--
chlorophyll *a* ($\mu g \cdot L^{-1}$)	1.63 ± 1.97	0.22 – 7.81	--	--

590 * estimated from maps available at the time

591   **Figure Captions**

592   **Figure 1.** The Columbia Plateau region, with inset showing study location within Washington.

593   Paired sites indicate waterbodies that were originally sampled in the 1940s and were resampled

594   in 2012. Contemporary landscape sites indicate additional waterbodies that were sampled in

595   2012-13; historical landscape sites indicate waterbodies that were sampled in the 1940s but not

596   resampled in the contemporary period.

597

598   **Figure 2.** Comparisons of (a) $\log_{10}$ salinity (ppt), (b) pH, (c) Secchi depth (m), and (d) richness

599   inside and outside the Columbia Basin Project (CBP) in historical and contemporary samples in

600   the full set of sites. Thick inner bar is the median, outer edges of the box are 25th and 75th

601   percentiles, whiskers are the maximum value, unless outliers are present, in which case they

602   represent 1.5x interquartile range. Gray lines above boxes represent gamma (γ) diversity of the

603   time period, while light gray boxes represent γ diversity for each region.

604

605   **Figure 3.** Variation partitioning of species presence or absence in historical (left) and

606   contemporary (right) zooplankton communities (a,b) inside CBP and (c,d) outside CBP.

607   Independent environmental and spatial variation are indicated as the unshared portion of each

608   circle, while the overlap represents spatially-structured environmental variation (the shared

609   fraction cannot be tested for significance). Circles are scaled relative to their importance within

610   each test. $* P < 0.05$, $**P < 0.01$

611

612   **Figure 4.** Relative importance of predictor variables from boosted regression tree model of

613   contemporary species richness.

614

615   **Figure 5**. Variation partitioning of contemporary zooplankton communities a) inside and b)

616   outside CBP using watercourse distances to generate spatial variables. Symbols as in Figure 3.

Figure 1

Figure 2

historical   *contemporary*

a) inside CBP — environment, space

environment 0.09   0.12   space 0.01

residual = 0.78

b) environment 0.15**   space 0.17**

residual = 0.68

c) outside CBP — environment 0.02   0.03   space 0.10*

residual = 0.85

d) environment 0.13**

residual = 0.87
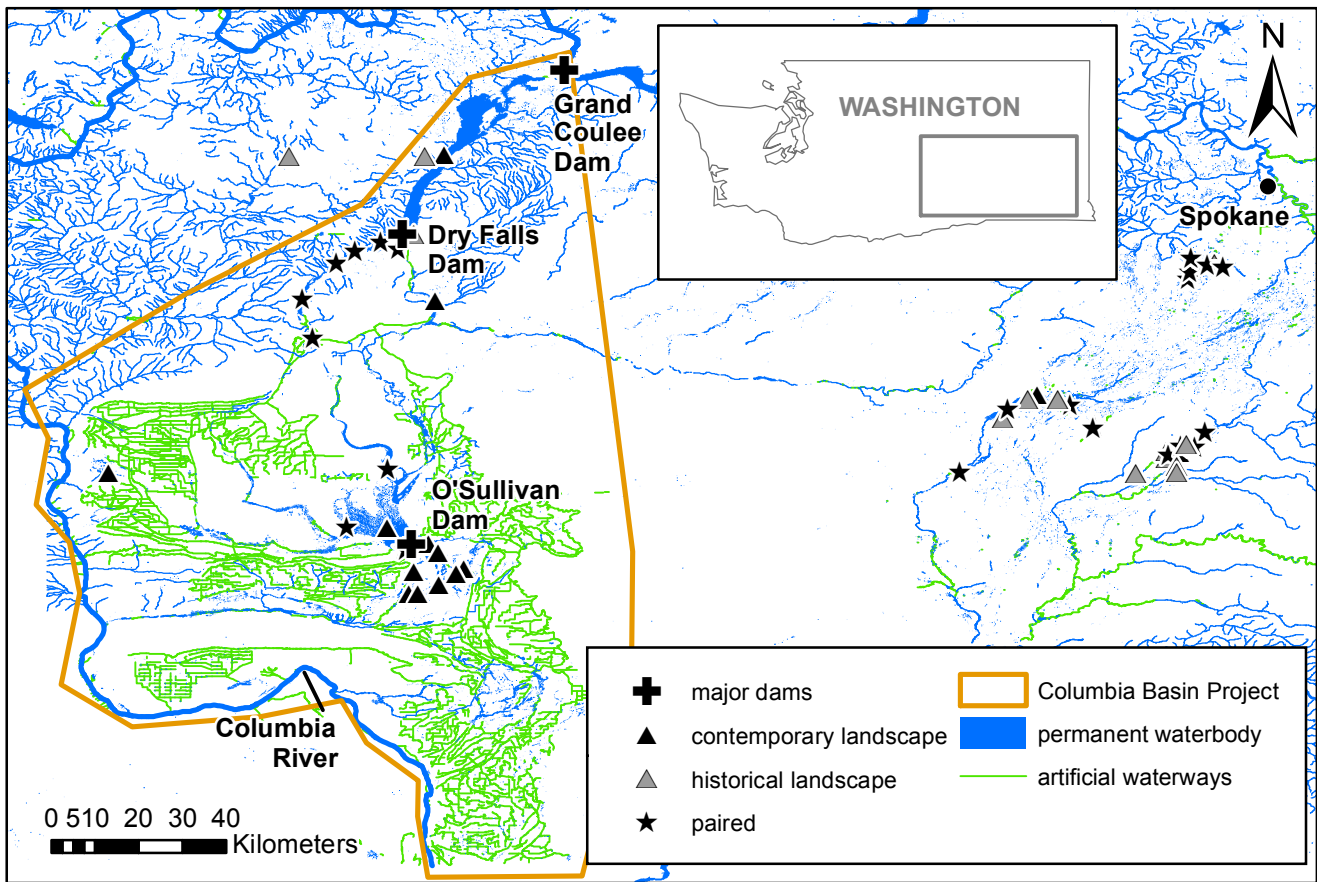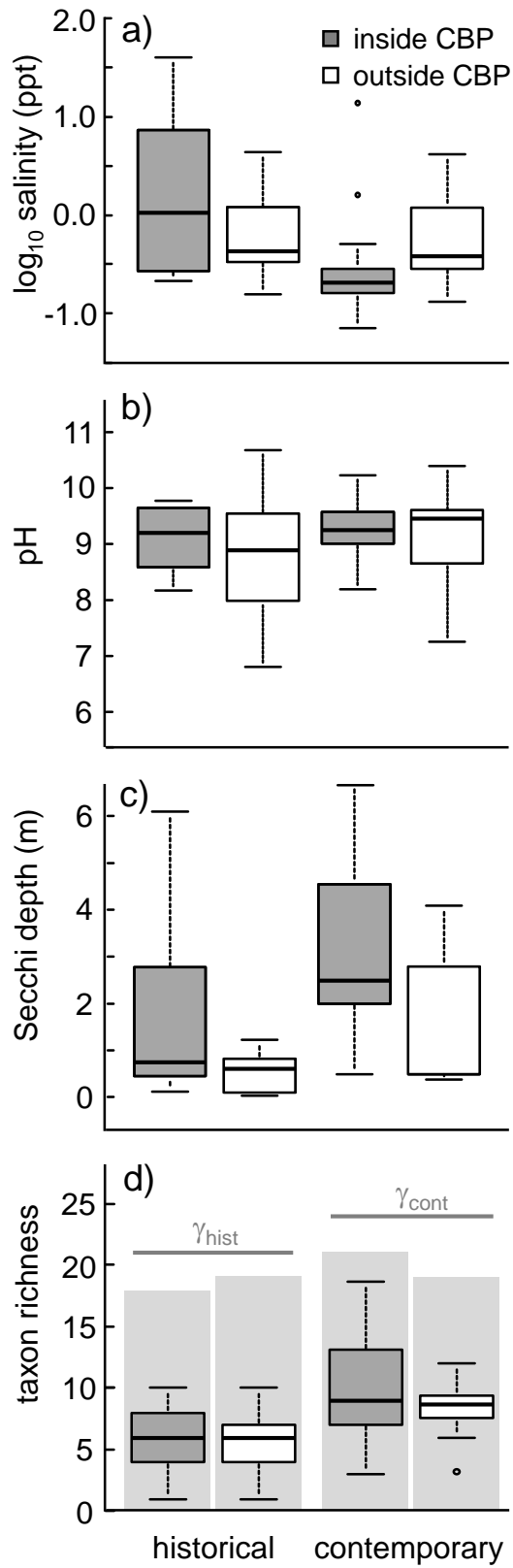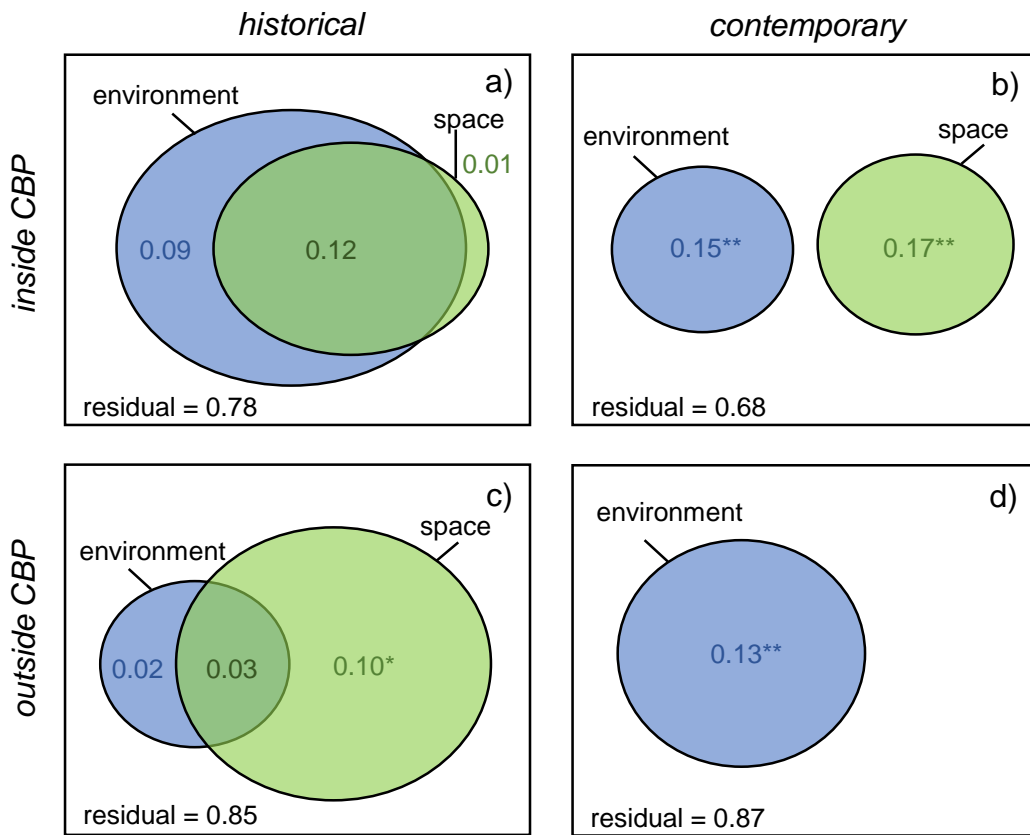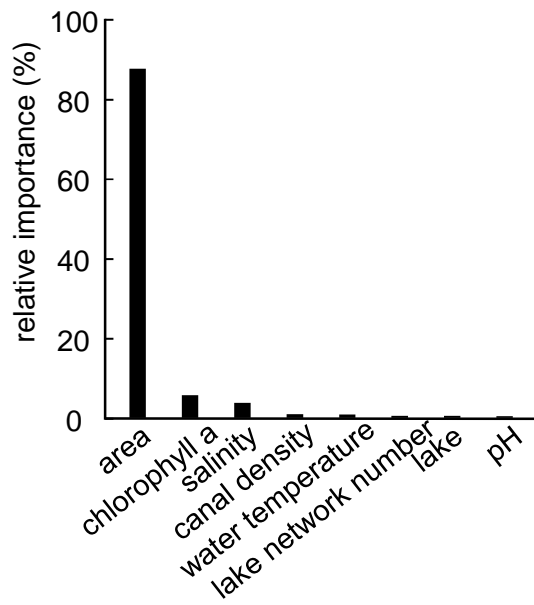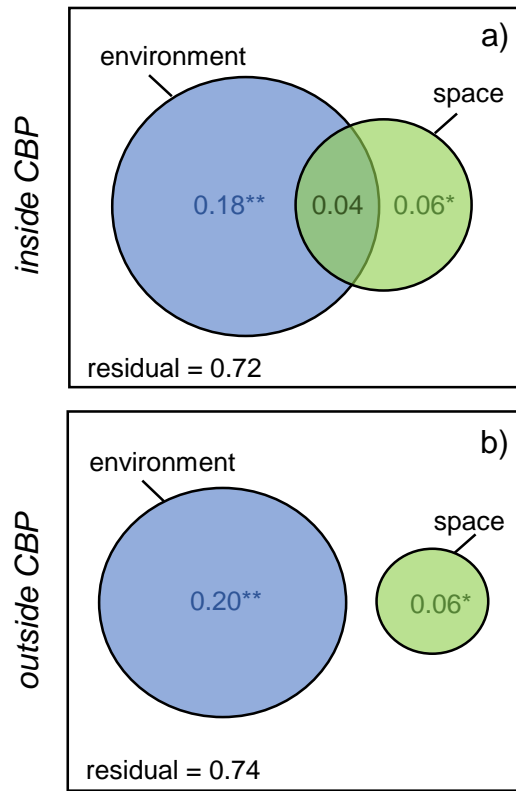
Figure 3

Figure 4

Figure 5

Appendix S1*: Physical, chemical, biological, and landscape characteristics of waterbodies.*

Table S1-1. Physical descriptions of lakes. Geographic Names Information System (GNIS) name is listed, with parentheses following if the waterbody was named differently in Whittaker & Fairbanks (1958). Semi-natural lakes refer to those that existed prior to hydrologic development, but which changed in size following the completion of the Columbia Basin Project.

waterbody name (W&F 1958 name)	category	type	surface area (ha)	Z_{max}† (m)	surface temperature (°C)	elevation (m)	Secchi (m)	boat ramp‡	permanence*	latitude (°N)	longitude (°W)
Folsom (Three Inch)	paired	pond	48.6	4.3	19.7	597	0.5	0	S	47.2217	-117.8900
Alkali	landscape	pond	9.7	<2	26.8	568	0.5	0	S	47.1680	-117.7120
Banks**	landscape	reservoir	10926.5	25.9	20.2	479	2.5	1	P	47.7820	-119.2260
Billy Clapp**	landscape	reservoir	404.7	33.5	20.7	407	4.8	1	P	47.4820	-119.2450
Blue	paired	lake	214.5	21.0	24.3	335	4.3	1	P	47.5618	-119.4482
Canal #1	landscape	canal	NA	2.0	21.8	305	1.0	0	P	46.9223	-119.1954
Canal #2	landscape	canal	NA	2.0	21.3	308	NA	0	P	46.9804	-119.2583
Canal L.	landscape	lake	24.7	19.8	22.9	300	4.9	1	P	46.9245	-119.1858
Clear	paired	lake	165.9	33.5	24.0	713	3.0	1	P	47.5275	-117.6945
Clear Pothole	paired	pond	0.3	<2	20.5	719	1.5	0	E	47.5430	-117.6903
Clear Sprague	landscape	pond	2.4	<2	23.2	592	0.4	0	S	47.2870	-118.0039
Cow	paired	lake	218.5	6.4	19.5	534	2.8	1	P	47.1299	-118.1639
Deep	paired	lake	44.5	36.6	24.5	376	6.5	1	P	47.5896	-119.3209
Dry Falls	paired	lake	40.1	9.1	24.4	368	3.8	1	P	47.6049	-119.3569
Crooked Knee (East Twin)	paired	pond	48.6	2.7	18.7	597	0.5	0	S	47.2247	-117.8869
Evergreen**	landscape	reservoir	101.2	16.8	23.2	366	2.2	1	P	47.1260	-119.9170
Halfmoon	landscape	lake	10.0	2.0	21.4	250	2.0	0	P	46.8917	-119.2364
Heart	landscape	lake	10.9	19.8	23.7	298	6.2	1	P	46.9305	-119.1859
Hutchinson	landscape	lake	19.8	3.8	23.8	216	1.5	1	P	46.8776	-119.2992
Lake Lenore	paired	lake	526.1	8.2	25.0	330	2.0	1	P	47.4874	-119.5173
Lily Pad	paired	pond	8.4	<2	23.9	568	0.5	0	S	47.1657	-117.7346
Lower Goose	landscape	semi-natural lake	20.2	22.9	22.0	262	3.1	1	P	46.9239	-119.2890

waterbody name (W&F 1958 name)	category	type	surface area (ha)	Z_{max}† (m)	surface temperature (°C)	elevation (m)	Secchi (m)	boat ramp‡	permanence*	latitude (°N)	longitude (°W)
Marsh	paired	pond	0.8	<2	20.8	592	0.5	0	S	47.2676	-117.9377
Medical	paired	lake	64.7	18.3	23.9	730	2.8	1	P	47.5704	-117.6884
Miller (Sunken)	paired	pond	0.6	<2	23.2	607	0.5	0	S	47.2117	-117.6590
Morgan	landscape	lake	14.0	2.0	22.3	250	2.0	0	P	46.8959	-119.2375
Moses	paired	semi-natural lake	2751.9	11.6	23.6	319	3.0	1	P	47.1368	-119.3422
North Teal	landscape	lake	8.8	12.0	22.2	291	3.8	0	P	46.9193	-119.2012
O'Sullivan	paired	pond	0.2	<2	17.2	293	0.5	0	S	46.9705	-119.3089
Park	paired	lake	141.6	25.9	23.7	345	5.0	1	P	47.5847	-119.4094
Pot #1	paired	pond	0.1	<2	23.5	317	0.5	0	S	47.0174	-119.4264
Potholes	landscape	reservoir	11331.2	42.7	21.2	317	2.3	1	P	47.0126	-119.3436
Rock	paired	lake	890.3	106.7	22.1	526	3.8	1	P	47.1819	-117.6799
Shiner	landscape	lake	13.0	3.0	22.7	216	1.0	1	P	46.8786	-119.2799
Silver	paired	lake	198.3	24.4	24.1	714	4.1	1	P	47.5571	-117.6536
Soap	paired	lake	348.0	29.0	25.1	327	6.7	1	P	47.4056	-119.4963
Soda	landscape	reservoir	72.8	36.6	22.0	304	2.1	1	P	46.9630	-119.2384
Sprague	paired	lake	728.4	6.1	22.2	572	1.9	1	P	47.2599	-118.0656
Tule (Ledge)	paired	pond	8.2	<2	21.3	582	0.5	0	S	47.1836	-117.7086
Upper Crab	paired	pond	0.2	<2	14.5	299	0.5	0	S	46.9702	-119.3057
Willow	paired	lake	21.9	1.8	22.7	732	0.9	0	P	47.5537	-117.6223

† maximum depth of ponds was not measured but was defined as <2 m

‡ data from http://wdfw.wa.gov/fishing/washington/lowland.htm

* permanence categories: P = permanent; S = semi-permanent, fluctuating water levels; E = ephemeral, drys annually; A. Strecker, unpublished

** sampled in 2013

Table S1-2. Chemical and biological descriptions of lakes. GNIS name is listed, with parentheses following if the waterbody was named differently in Whittaker & Fairbanks (1958).

waterbody name (W&F 1958 name)	pH	salinity (ppt)	specific conductance (µS·cm⁻¹)	total phosphorus (µg·L⁻¹)	nitrate (mg·L⁻¹)	chlorophyll *a* (µg·L⁻¹)
Folsom (Three Inch)	9.50	1.95	3687.0	1746.2	2.79	0.69
Alkali	9.92	1.41	2738.0	184.4	1.40	0.41
Banks	8.37	0.07	140.7	74.0	0.21*	NA
Billy Clapp	8.21	0.07	140.0	73.0	0.13*	NA
Blue	9.38	0.27	560.0	40.3	0.28	0.36
Canal #1	9.20	0.16	328.8	1.7	0.71	3.35
Canal #2	9.17	0.16	335.9	43.4	0.49	3.21
Canal L.	9.77	0.21	428.7	33.2	0.22	0.58
Clear	9.47	0.41	828.0	39.7	0.82	1.63
Clear Pothole	9.22	0.41	840.0	173.9	1.63	0.28
Clear Sprague	10.40	0.98	1932.0	39.5	1.74	1.87
Cow	9.01	0.21	434.9	61.4	0.53	2.02
Deep	9.18	0.17	361.4	58.5	0.16	0.37
Dry Falls	9.58	0.52	1054.0	40.3	0.57	0.50
Crooked Knee (East Twin)	8.29	0.44	888.0	57.7	0.86	0.59
Evergreen	8.91	0.07	152.0	72.0	0.26*	NA
Halfmoon	9.39	0.30	624.0	82.6	0.73	NA
Heart	9.58	0.35	710.0	78.1	0.63	0.74
Hutchinson	9.26	0.28	585.0	54.7	0.25	2.48
Lake Lenore	9.98	1.69	3248.0	66.2	0.81	1.98
Lily Pad	9.50	0.39	805.0	83.0	0.86	7.81
Lower Goose	9.33	0.10	208.2	55.6	0.15	1.72
Marsh	8.29	0.28	582.0	70.2	0.67	3.67
Medical	9.59	0.76	1512.0	23.8	1.01	1.22
Miller (Sunken)	7.25	0.33	9.4	58.5	0.90	5.06

waterbody name (W&F 1958 name)	pH	salinity (ppt)	specific conductance ($\mu S \cdot cm^{-1}$)	total phosphorus ($\mu g \cdot L^{-1}$)	nitrate ($mg \cdot L^{-1}$)	chlorophyll *a* ($\mu g \cdot L^{-1}$)
Morgan	9.77	0.18	379.0	84.8	0.88	0.86
Moses	9.04	0.13	267.2	99.2	0.23	0.63
North Teal	9.61	0.20	424.3	31.9	0.36	1.34
O'Sullivan	9.00	0.66	1320.0	28.9	1.32	2.29
Park	9.26	0.24	490.4	71.5	0.29	0.22
Pot #1	9.90	0.19	401.7	46.6	0.92	1.79
Potholes	8.84	0.17	364.4	57.8	0.36	1.97
Rock	9.64	0.14	293.0	23.4	2.51	0.69
Shiner	9.25	0.28	574.0	68.5	0.24	5.62
Silver	9.36	0.40	809.0	47.9	0.96	0.41
Soap	10.24	14.43	23838.0	300.9	4.20	0.28
Soda	9.02	0.16	342.3	70.1	0.42	3.65
Sprague	9.44	0.20	412.4	53.8	0.34	5.43
Thule (Ledge)	7.91	0.39	793.0	79.8	0.43	6.91
Upper Crab	8.19	0.28	571.5	70.0	0.58	2.38
Willow	9.95	4.60	8227.0	569.3	3.06	0.28

* total nitrogen

Table S1-3. Landscape characteristics of lakes. GNIS name is listed, with parentheses following if the waterbody was named differently in Whittaker & Fairbanks (1958).

waterbody name (W&F 1958 name)	lake network number*	urban %	natural %	agriculture %	wetlands %	canal density (km·km^{-2})
Folsom (Three Inch)	1	1.1%	72.7%	19.3%	6.9%	0.023
Alkali	0	1.7%	49.5%	37.9%	10.8%	0.033
Banks	1	2.8%	52.4%	43.9%	0.6%	0.001
Billy Clapp	2	1.6%	55.9%	42.4%	0.1%	0.071
Blue	3	1.7%	84.6%	13.2%	0.3%	0.000
Canal #1	8	0.3%	94.8%	4.0%	0.9%	0.195
Canal #2	5	0.3%	94.8%	4.0%	0.9%	0.195
Canal L.	3	0.3%	94.8%	4.0%	0.9%	0.195
Clear	2	6.0%	68.0%	23.8%	2.2%	0.000
Clear Pothole	0	6.0%	68.0%	23.8%	2.2%	0.000
Clear Sprague	0	6.4%	66.5%	14.7%	12.3%	0.029
Cow	10	1.6%	82.4%	5.9%	10.2%	0.023
Deep	1	4.2%	83.4%	11.6%	0.6%	0.051
Dry Falls	1	4.2%	83.4%	11.6%	0.6%	0.051
Crooked Knee (East Twin)	1	1.1%	72.7%	19.3%	6.9%	0.023
Evergreen	3	1.2%	68.6%	29.8%	0.4%	0.229
Halfmoon	6	1.6%	79.7%	14.7%	4.0%	0.296
Heart	0	0.3%	94.8%	4.0%	0.9%	0.195
Hutchinson	8	1.6%	79.7%	14.7%	4.0%	0.296
Lake Lenore	5	2.7%	77.8%	19.1%	0.2%	0.053
Lily Pad	0	3.2%	21.8%	66.1%	8.9%	0.086
Lower Goose	5	1.6%	79.7%	14.7%	4.0%	0.296
Marsh	2	6.4%	66.5%	14.7%	12.3%	0.029
Medical	1	9.5%	68.0%	20.9%	1.6%	0.019
Miller (Sunken)	0	1.7%	49.5%	37.9%	10.8%	0.033
Morgan	5	1.6%	79.7%	14.7%	4.0%	0.296

waterbody name (W&F 1958 name)	lake network number*	urban %	natural %	agriculture %	wetlands %	canal density (km·km⁻²)
Moses	3	15.0%	57.0%	25.5%	2.5%	0.303
North Teal	2	0.3%	94.8%	4.0%	0.9%	0.195
O'Sullivan	0	1.6%	79.7%	14.7%	4.0%	0.296
Park	2	1.7%	84.6%	13.2%	0.3%	0.000
Pot #1	1	9.9%	57.5%	14.9%	17.7%	0.141
Potholes	4	9.9%	57.5%	14.9%	17.7%	0.141
Rock	6	1.7%	49.5%	37.9%	10.8%	0.033
Shiner	7	1.6%	79.7%	14.7%	4.0%	0.296
Silver	1	9.5%	68.0%	20.9%	1.6%	0.019
Soap	1	13.6%	55.9%	30.4%	0.0%	0.357
Soda	6	0.3%	94.8%	4.0%	0.9%	0.195
Sprague	8	6.4%	66.5%	14.7%	12.3%	0.029
Thule (Ledge)	1	3.2%	21.8%	66.1%	8.9%	0.086
Upper Crab	1	1.6%	79.7%	14.7%	4.0%	0.296
Willow	1	9.5%	68.0%	20.9%	1.6%	0.019

* *sensu* Martin and Soranno (2006)

References

Martin, S.L. & Soranno, P.A. (2006) Lake landscape position: Relationships to hydrologic connectivity and landscape features. *Limnology and Oceanography*, **51**, 801-814.

Whittaker, R.H. & Fairbanks, R.H. (1958) A study of plankton copepod communities in the Columbia Basin, southeastern Washington. *Ecology*, **39**, 46-65.

Appendix S2: *Taxonomic information for historical and contemporary species identifications.*
In order to make historical and contemporary datasets comparable, it was assumed that all
copepods were identified to species and all cladocerans were identified to genus (or family for
Chydoridae) in historical samples (Fairbanks 1950). No juveniles were included in measures of
richness or abundance. Subsamples of a known volume of the sample were taken and a
minimum of 250 individuals were counted. Zooplankton were enumerated with a protocol
designed to target rare species, where 40-50 individuals of the dominant taxa, 40-50 copepodids
per order, and 20-30 nauplii per order were counted. The remainder of the sample was scanned
for rare species. For lakes that had both pelagic and shoreline samples, the shoreline sample was
scanned to note new species. For ponds with just shoreline samples, the regular counting
protocol was followed. Some lakes did not have additional shoreline samples; richness of these
lakes was modelled using linear regression from the samples that had both pelagic and shoreline
samples (*modelled richness* = 1.102*pelagic richness* + 0.999; $r^2 = 0.79$, $p < 0.001$, $n = 13$).
Zooplankton in contemporary samples were identified using the taxonomic keys of Brooks
(1957); Edmondson (1959); Korovchinsky (1992); Kotov, Ishida and Taylor (2009); and Thorp
and Covich (2010). Table S2-1 indicates updates to genus and species names for taxa. The
predatory cladoceran, *Leptodora kindtii* Focke, was also excluded from historical–contemporary
comparisons as it is unknown whether historical samples were scanned for this species in their
entirety.

Table S2-1. Taxonomic updates for crustacean taxa. Historical name refers to the nomenclature of Whittaker & Fairbanks (1958) using resources available at the time of the study (Ward & Whipple 1918).

Historical Name	Contemporary Name
Cyclops bicuspidatus	*Diacyclops thomasi* Forbes
Cyclops varicans	*Microcyclops varicans* Sars
Cyclops vernalis	*Acanthocyclops vernalis* Fischer
Diaptomus ashlandi	*Leptodiaptomus ashlandi* Marsh
Diaptomus leptopus	*Aglaodiaptomus leptopus* Forbes
Diaptomus novomexicanus	*Leptodiaptomus novomexicanus* Herrick
Diaptomus sanguineus	*Onychodiaptomus sanguineus* Forbes
Diaptomus sicilis	*Leptodiaptomus sicilis* Forbes
Diaptomus shoshone	*Hesperodiaptomus shoshone* Forbes

References

Brooks, J.L. (1957) *The Systematics of North American Daphnia*. Yale University Press, New Haven, Connecticut.

Edmondson, W.T. (1959) *Fresh-Water Biology*, Second edn. John Wiley & Sons, New York, USA.

Korovchinsky, N.M. (1992) *Sididae and Holopediidae: (Crustacea: Daphniiformes): Guides to the Identification of the Microinvertebrates of the Continental Waters of the World*. SPB Academic, The Hague, Netherlands.

Kotov, A.A., Ishida, S. & Taylor, D.J. (2009) Revision of the genus *Bosmina* Baird, 1845 (Cladocera: Bosminidae), based on evidence from male morphological characters and molecular phylogenies. *Zoological Journal of the Linnean Society*, **156**, 1-51.

Thorp, J.H. & Covich, A.P. (2010) *Ecology and Classification of North American Freshwater Invertebrates,* Third edn. Academic Press, London, UK.

Ward, H. B. & G. C. Whipple. (1918). *Freshwater Biology*. John Wiley & Sons, New York, USA. 1111 pp.

Whittaker, R. H. & R. H. Fairbanks. (1958). A study of plankton copepod communities in the Columbia Basin, southeastern Washington. *Ecology* **39**:46-65.

Appendix S3: *Sensitivity analyses.*

Sensitivity analyses on changes in compositional similarity (ΔCS) showed that grouping all taxa at the genus level (model 2) or including species that were absent from one time period (model 3) generally increased the degree of homogenization (inside CBP) or the degree of diversification (outside CBP) compared to the original model (Table S3-1). These results were similar when conducting both actions (model 4), indicating consistency with the original model (Table S3-1).

Table S3-1. Sensitivity analyses of homogenization (ΔCS = change in compositional similarity).

	Inside CBP		Outside CBP	
model	**ΔCS**	**% change**	**ΔCS**	**% change**
1) original	0.066	13.2%	-0.079	-14.0%
2) genus-level identification	0.130	22.4%	-0.057	-7.3%
3) including species that were absent in one time period	0.083	17.5%	-0.101	-17.2%
4) both 2) and 3)	0.096	16.7%	-0.146	-18.5%

Sensitivity analyses indicated that the results from the permutational MANOVA (Table S3-2) were not qualitatively different when all species were included. Permutational MANOVA was conducted using the full model, as well as separate tests for each time period.

Table S3-2. Permutational MANOVA results on the full set of species (including species that were absent in one time period).

model	fixed effect	F-ratio	*P*-value
full	region	2.229	0.043
	period	4.752	<0.001
	period * region	1.529	0.173
just historical	region	1.047	0.422
just contemporary	region	2.730	0.037

Appendix S4: *Detailed methods for redundancy analysis and variation partitioning.*

Objective 1

Redundancy analysis (RDA) and variation partitioning techniques were used to examine the influence of environmental and spatial variables on zooplankton community composition. Environmental variables that were available for both time periods included salinity, pH, Secchi depth, and surface temperature – six waterbodies were removed from the historical period because of missing data. All environmental variables were standardized via Z-score prior to analysis. The effects of spatial scale and connectivity on zooplankton community composition were determined by constructing spatial variables distance networks that modeled the processes of overland dispersal or spatial proximity (Euclidean distance, "as the crow flies") and passive dispersal via natural or human-altered water-courses (water-course distance, "as the fish swims"). Distances between sites were calculated in ArcGIS 10.2 using centroids of sample sites and contemporary connectivity via rivers, canals, or pipelines extracted from the National Hydrography Dataset (US Geological Survey 2015). Historical connectivity was mapped using rivers from the National Hydrography Dataset, which were verified by historical topographic maps (US Geological Survey 2016) and site descriptions (Fairbanks 1950). Spatial structure of study sites was extracted using Moran's Eigenvector Maps (Dray, Legendre & Peres-Neto 2006), which generates synthetic variables that represent spatial structure at different scales. This procedure was performed separately for historical sites and contemporary sites. The truncation distance that describes connectivity between sites was calculated as 4 * maximum pairwise distance in the distance matrix (Borcard, Gillet & Legendre 2011), as this value keeps all pairwise sites connected but places a higher weight on sites that are close together. Synthetic variables, or eigenvectors, were retained if they represented positive spatial correlation (Borcard,

Gillet & Legendre 2011). Thus, any variation in community composition explained by these

spatial variables is indicative of positive spatial correlation in communities. These variables are

collectively referred to as spatial variables hereafter.

All taxa that occurred in <5% of sites were excluded to reduce the influence of rare taxa.

Predictor variable correlations and variance inflation factors indicated that there was no evidence

of serious collinearity, therefore all variables were retained. An assumption in testing for spatial

correlation is that the data are stationary (i.e., exhibit the same relationship in all parts of the

system) – thus, species data were detrended using x-y coordinates if non-stationarity was

detected (Borcard, Gillet & Legendre 2011). Permutations tested the significance of RDAs (n =

9999). Adjusted R^2 (R^2_{adj}) values were used when there were multiple significant predictor

variables. Variation explained with RDA was then partitioned into purely environmental, purely

spatial, or spatially-structured environmental variation following Peres-Neto *et al.* (2006). All

analyses were done with libraries *vegan*, *ade4*, and *packfor* in R.

Objective 2

Redundancy analysis (RDA) and variation partitioning techniques were used to examine

the influence of environmental and spatial variables on zooplankton community composition in

the contemporary time period using a broader set of landscape and environmental variables.

Regions (inside vs. outside the CBP) were tested separately. Species abundances were

Hellinger-transformed prior to analysis (Legendre & Gallagher 2001) and species that occurred

in <2 lakes were excluded to reduce the influence of rare taxa. Environmental variables were

drawn from Appendix S1. Highly correlated predictor variables were removed (e.g., nitrate,

specific conductance, elevation), and variables with missing values were also discarded (e.g.,

chlorophyll *a*). All environmental variables were standardized via *Z*-score prior to analysis.

Species data were detrended using x-y coordinates if non-stationarity was detected (Borcard,

Gillet & Legendre 2011). Permutations tested the significance of RDAs (n = 9999). Adjusted R^2

(R^2_{adj}) values were used when there were multiple significant predictor variables. Variation

explained with RDA was then partitioned into purely environmental, purely spatial, or spatially-

structured environmental variation following Peres-Neto *et al.* (2006). All analyses were done

with libraries *vegan*, *ade4*, and *packfor* in R.

References
Borcard, D., Gillet, F. & Legendre, P. (2011) *Numerical Ecology with R*. Springer, New York, USA.
Dray, S., Legendre, P. & Peres-Neto, P.R. (2006) Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling*, **196**, 483-493.
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Peres-Neto, P.R., Legendre, P., Dray, S. & Borcard, D. (2006) Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology*, **87**, 2614-2625.
US Geological Survey (2015) The national hydrography dataset. United States Geological Survey. Accessed on: 26 March 2015. http://nhd.usgs.gov/
US Geological Survey (2016) The National Map: Historical Topographic Map Collection. United States Geological Survey. Accessed on: 2 April 2016. http://nationalmap.gov/historical/

__Appendix S5__: Results from paired sites, redundancy analyses, and variation partitioning.
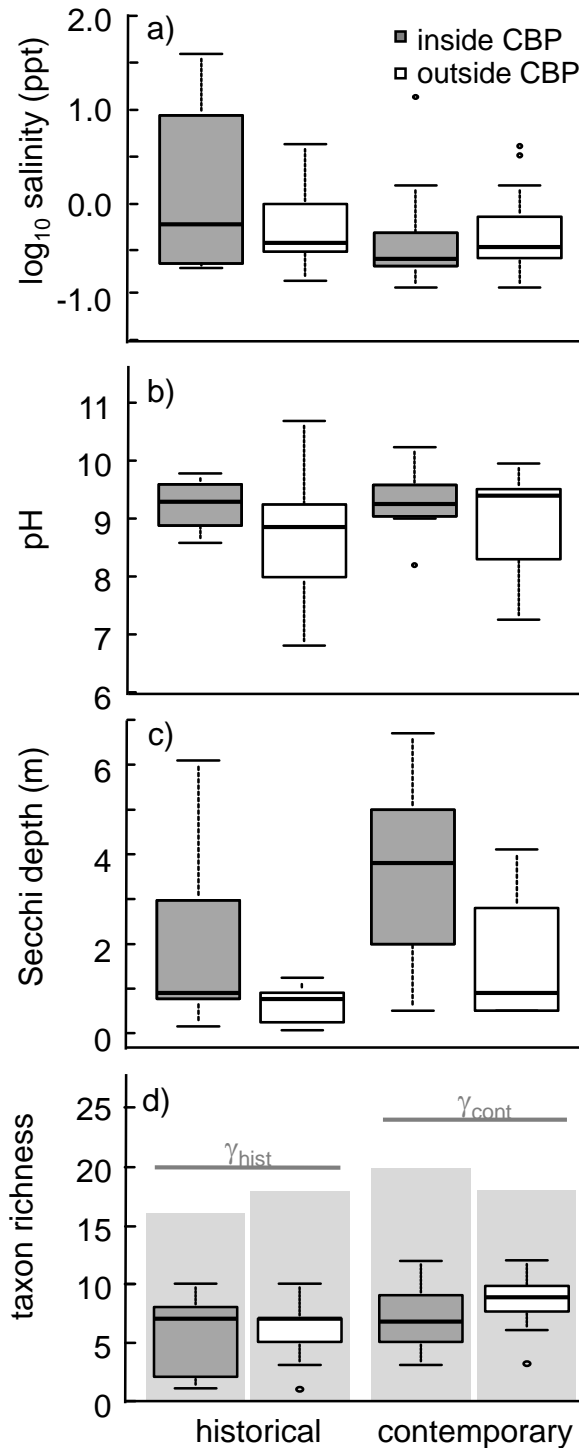

Figure S5-1. Comparisons of (a) $\log_{10}$ salinity (ppt), (b) pH, (c) Secchi depth (m), and (d) richness inside and outside the Columbia Basin Project (CBP) in historical and contemporary samples in paired sites (n=24). Thick inner bar is the median, outer edges of the box are 25th and 75th percentiles, whiskers are the maximum value, unless outliers are present, in which case they represent 1.5x interquartile range. Gray lines above boxes represent gamma (γ) diversity of the time period, while light gray boxes represent γ diversity for each region.

Table S5-1. Comparisons of region (inside vs. outside the Columbia Basin Project), period (historical vs. contemporary), and their interaction for paired sites. LMM = linear mixed model, GLMM = generalized linear mixed model, -- = interaction not tested in model simplification

|	model type	fixed effect	statistic	*P*-value
pH	LMM,	region	-0.796	0.435
	t-statistic,	period	-0.263	0.795
	n=46	period * region	-0.352	0.728
salinity	GLMM,	region	0.170	0.862
	Z-statistic,	period	3.520	<0.001
	n=48	period * region	-2.500	0.013
Secchi	GLMM,	region	-2.790	0.005
	Z-statistic,	period	-3.180	0.002
	n=44	period * region	--	--
richness	LMM,	region	-1.430	0.159
	t-statistic,	period	-4.101	<0.001
	n=48	period * region	0.886	0.385
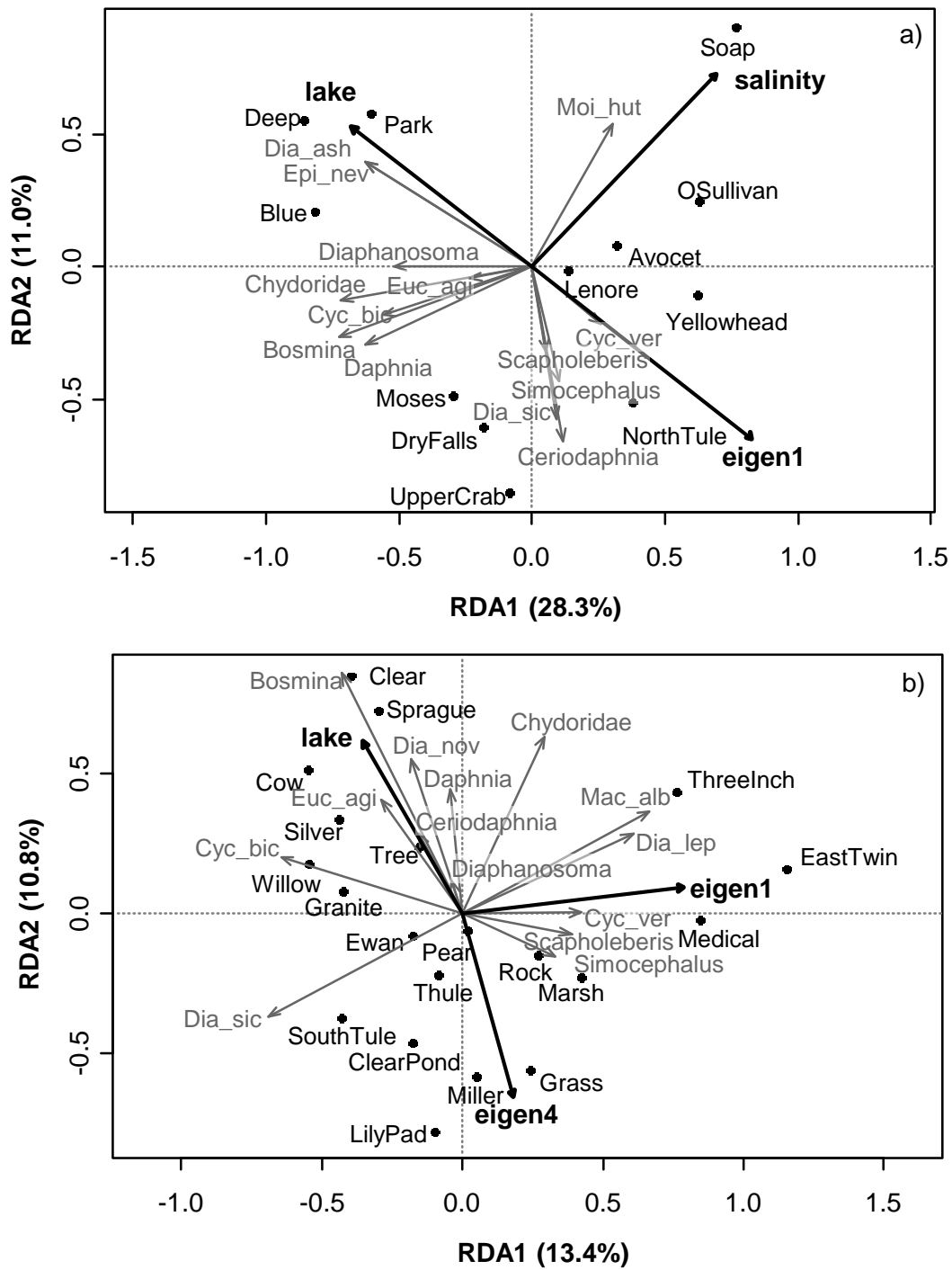
Figure S5-2. Redundancy analyses of species presence or absence in historical communities a) inside the CBP and b) outside the CBP. We found significant structure in communities (inside CBP: *F* = 1.994, *P* = 0.009; outside CBP: *F* = 2.076, *P* = 0.002). Dark arrows are significant predictor variables, grey lines are species scores, and circles are site scores for waterbodies. The prefix *eigen* indicates a significant spatial variable. See Appendix S2 for taxonomy notes. Cyc_bic = *Cyclops bicuspidatus,* Cyc_ver = *Cyclops vernalis*, Dia_ash = *Diaptomus ashlandi*, Dia_lep = *Diaptomus leptopus*, Dia_nov = *Diaptomus novomexicanus*, Dia_sic = *Diaptomus sicilis*, Epi_nev = *Epischura nevadensis*, Euc_agi = *Eucyclops agilis*, Moi_hut= *Moina hutchinsoni*, CBP = Columbia Basin Project
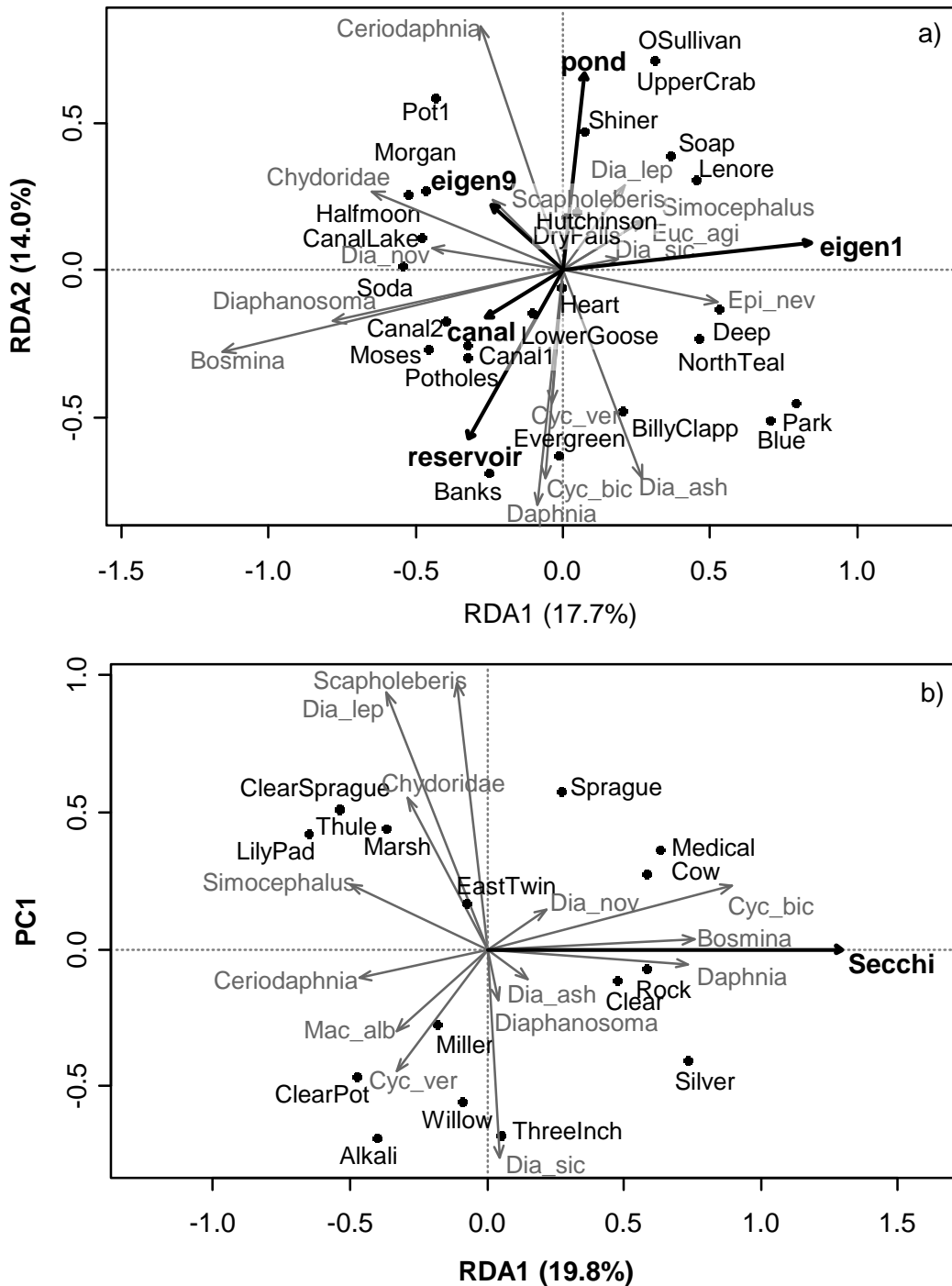
Figure S5-3. Redundancy analyses of species presence or absence in contemporary communities a) inside the CBP and b) outside the CBP. We found significant structure in communities (inside CBP: $F = 3.260$, $P = 0.001$; outside CBP: $F = 3.453$, $P = 0.001$). Dark arrows are significant predictor variables, grey lines are species scores, and circles are site scores for waterbodies. The prefix *eigen* indicates a significant spatial variable. See Appendix S2 for taxonomy notes. Cyc_bic = *Cyclops bicuspidatus,* Cyc_ver = *Cyclops vernalis*, Dia_ash = *Diaptomus ashlandi*, Dia_lep = *Diaptomus leptopus*, Dia_nov = *Diaptomus novomexicanus*, Dia_sic = *Diaptomus sicilis*, Epi_nev = *Epischura nevadensis*, Euc_agi = *Eucyclops agilis*, Mac_alb = *Macrocyclops albidus*, Moi_hut= *Moina hutchinsoni*, CBP = Columbia Basin Project

Table S5-2. Variation partitioning of environmental and spatial variables for zooplankton communities using Euclidean distance for constructing spatial variables. environment | space = independent environmental variation, space∩environment = spatially-structured environmental variation, space | environment = independent spatial variation

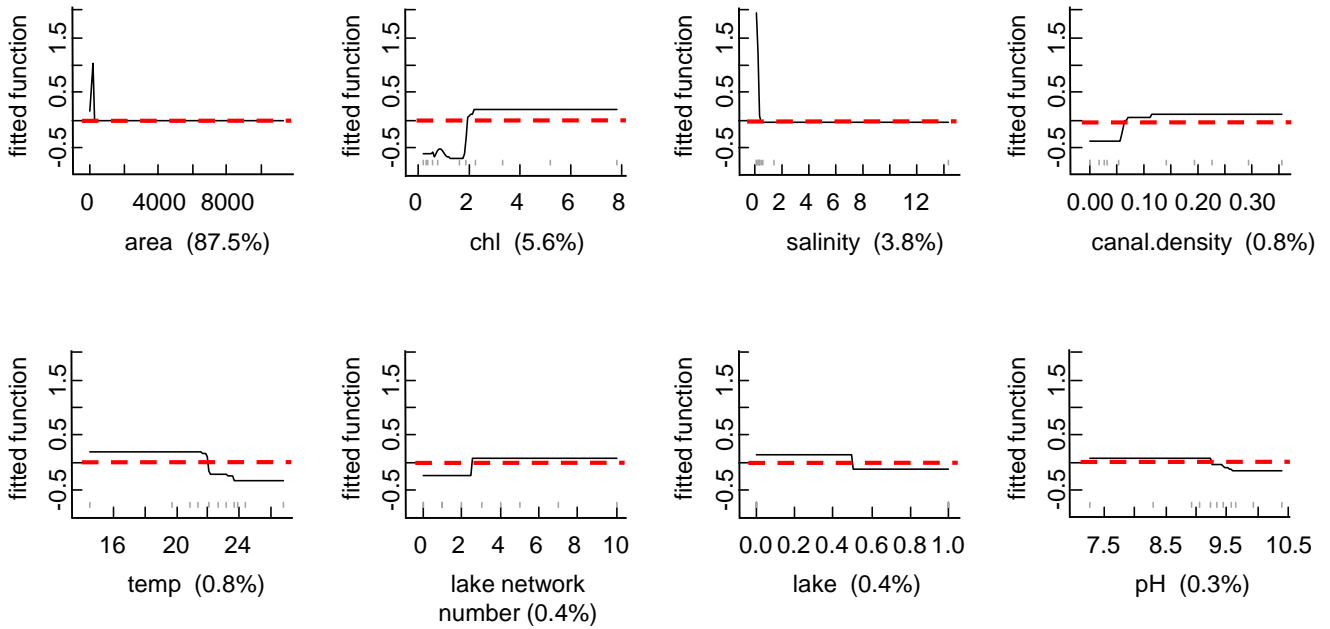| fraction	historical		contemporary	
	R^2_{adj}	*P*-value	R^2_{adj}	*P*-value
inside CBP				
environment | space	0.213	0.009	0.135	0.001
space∩environment	0	n/a	0.011	n/a
space | environment	0	1.000	0.013	0.226
outside CBP				
environment | space	0.400	0.051	0.141	0.001
space∩environment	0.006	n/a	0	n/a
space | environment	0.044	0.033	0	1.000

Figure S5-4. Partial dependence plots illustrating the influence of the top eight variables on species richness. The y-axis is the logit scale, which is centered around a mean of zero for the data. To interpret these plots, when the black line is above zero (i.e., the dashed red line), the variable is having a positive effect on species richness; when the line is below zero, the variable is having a negative effect.
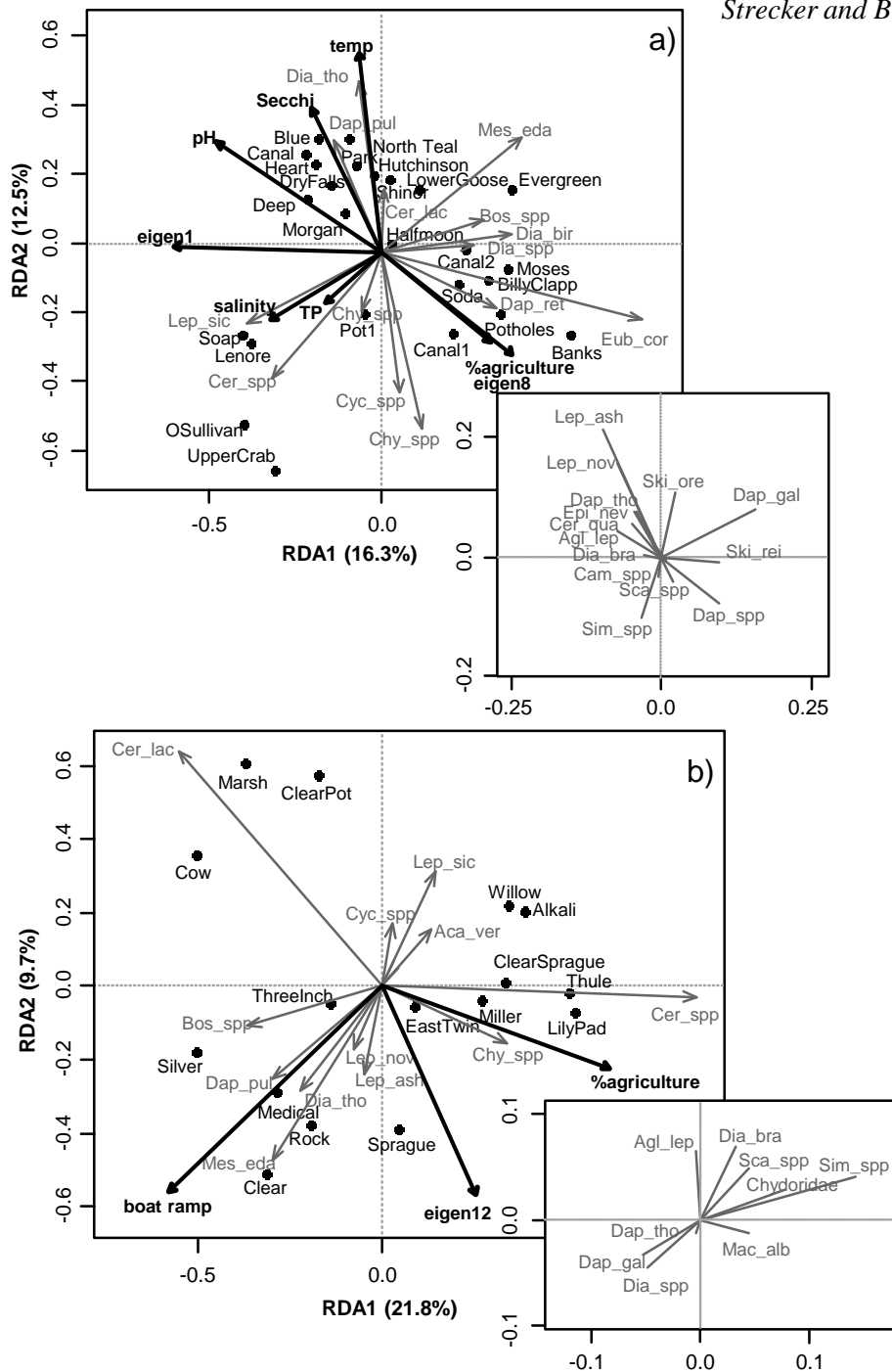
Figure S5-5. Redundancy analyses of species abundance of contemporary zooplankton communities a) inside the CBP and b) outside the CBP using watercourse distances for spatial predictor variables. Dark arrows are significant predictor variables, grey lines are species scores, and circles are site scores for waterbodies. Insets are species near the center of the plot. The prefix *eigen* indicates a significant spatial variable. Aca_ver = *Acanthocyclops vernalis*, Agl_lep = *Aglaodiaptomus leptopus*, Bos_spp = *Bosmina* spp., Cam_spp = *Camptocercus* spp., Cer_lac = *Ceriodaphnia lacustris*, Cer_qua = *Ceriodaphnia quadrangula*, Cer_spp = *Ceriodaphnia* spp., Chy_spp = *Chydorus* spp., Cyc_spp = *Cyclops* spp., Dap_gal = *Daphnia galeata*, Dap_pul = *Daphnia pulicaria*, Dap_ret = *Daphnia retrocurva*, Dap_spp = *Daphnia* spp., Dap_tho = *Daphnia thorata*, Dia_tho = *Diacyclops thomasi*, Dia_bir = *Diaphanosoma birgei*, Dia_bra = *Diaphanosoma brachyurum*, Dia_spp = *Diaptomus* spp., Epi_nev = *Epischura nevadensis*, Eub_cor = *Eubosmina coregoni*, Lep_ash = *Leptodiaptomus ashlandi*, Lep_nov = *Leptodiaptomus novomexicanus*, Lep_sic = *Leptodiaptomus sicilis*, Mac_alb = *Macrocyclops albidus*, Mes_eda = *Mesocyclops edax*, Sca_spp = *Scapholeberis* spp., Sim_spp = *Simocephalus* spp., Ski_ore = *Skistodiaptomus oregonensis*, Ski_rei = *Skistodiaptomus reighardi,* temp = near-surface temperature, TP = total phosphorus
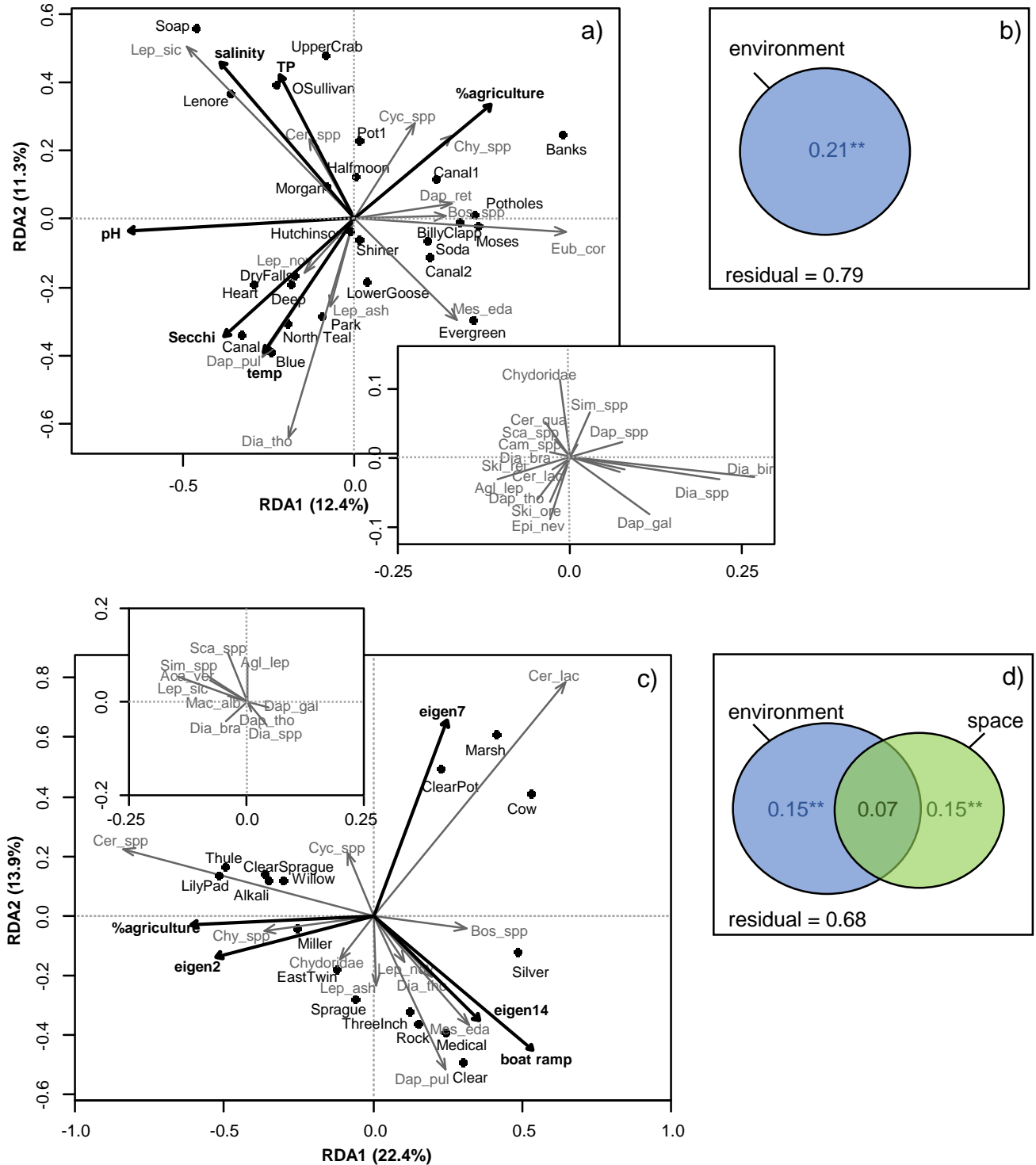
Figure S5-6. (left) Redundancy analyses and (right) variation partitioning of species abundance of contemporary zooplankton communities (a,b) inside the CBP and (c,d) outside the CBP using Euclidean distances for spatial predictor variables. Independent environmental and spatial variation are indicated as the unshared portion of each circle, while the overlap represents spatially-structured environmental variation (the shared fraction cannot be tested for significance). Circles are scaled relative to their importance within each test. * $P < 0.05$, ** $P < 0.01$ Abbreviations and symbols as in Figure S5-5. Note that there were no significant spatial variables in panel a).