2-2017

# Increased Habitat Connectivity Homogenizes Freshwater Communities: Historical and Landscape Perspectives

Angela L. Strecker
*Portland State University*, strecker@pdx.edu

Jeffrey Thomas Brittain
*Portland State University*, jtbrittain@gmail.com

### Citation Details

Strecker, A. L. and Brittain, J. T. (2017), Increased habitat connectivity homogenizes freshwater communities: historical and landscape perspectives. Journal of Applied Ecology

1 **Increased habitat connectivity homogenizes freshwater communities: historical and**

2 **landscape perspectives**

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4 Angela L. Strecker[1] and Jeffrey T. Brittain[2]

5 Department of Environmental Science and Management, Portland State University, Portland,

6 OR, USA

7

8 [1] strecker@pdx.edu

9 [2] jbritt2@pdx.edu

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11 Running Head: Connectivity Homogenizes Communities

12

13    **Summary**

14    1. Increases in habitat connectivity can have consequences for taxonomic, functional, and genetic

15    diversity of communities. Previously isolated aquatic habitats were connected with canals and

16    pipelines in the largest water development project in US history, the Columbia Basin Project

17    (eastern Washington, USA), which also altered environmental conditions; however, the

18    ecological consequences are largely unknown.

19    2. Using a historical dataset, we examined long-term patterns in zooplankton communities, water

20    chemistry and clarity, testing the hypothesis that increased connectivity will result in taxonomic

21    homogenization.  Further, we tested contemporary drivers of communities using a

22    comprehensive set of environmental and landscape variables.

23    3. Waterbodies were sampled for zooplankton community composition as well as physical and

24    chemical variables inside and outside the Columbia Basin Project using methods consistent with

25    historical studies.

26    4. We found significant declines in salinity inside the Columbia Basin Project, whereas changes

27    in water clarity were prevalent across all waterbodies.  Increased connectivity via canals

28    homogenized zooplankton communities over time, as well as increasing regional richness.  Other

29    long-term changes in zooplankton communities may be related to climate change, invasive

30    species, and land-use changes.

31    5. *Synthesis and applications.* Though canals may offer species spatial refugia, homogenization

32    may decrease resilience to environmental stressors.  These new hybrid aquatic landscapes, or

33    hydroscapes, should be considered carefully in future water development, including specific

34    plans for monitoring of species and environmental conditions, as well as mitigation of

35    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

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 $\beta_{sim}$ 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 $\beta_{sim}$ index

176 (CS = 1 - $\beta_{sim}$). 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

218    *Objective 2: Analyses of contemporary drivers*

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 ($\Delta$CS = -0.079, $CS_{contemporary}$ = 0.487, $CS_{historical}$ = 0.566),

274    whereas sites inside the CBP experienced a 13.2% increase in compositional similarity ($\Delta$CS =

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 $\Delta$CS 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 $\pm$ 0.19SD, outside: $\beta_{sim}$ = 0.32 $\pm$ 0.24SD) (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

| parameter | contemporary | | historical | |
|---|---|---|---|---|
| | **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 $25^{th}$ and $75^{th}$

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 ($\gamma$) diversity of the

603     time period, while light gray boxes represent $\gamma$ 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

inside CBP

a)
environment
space 0.01
0.09 0.12
residual = 0.78

b)
environment
space
0.15** 0.17**
residual = 0.68

outside CBP

c)
environment
space
0.02 0.03 0.10*
residual = 0.85

d)
environment
0.13**
residual = 0.87

Figure 3

Figure 4

a)

*inside CBP*

environment

space

0.18** 0.04 0.06*

residual = 0.72

b)

*outside CBP*

environment

space

0.20** 0.06*
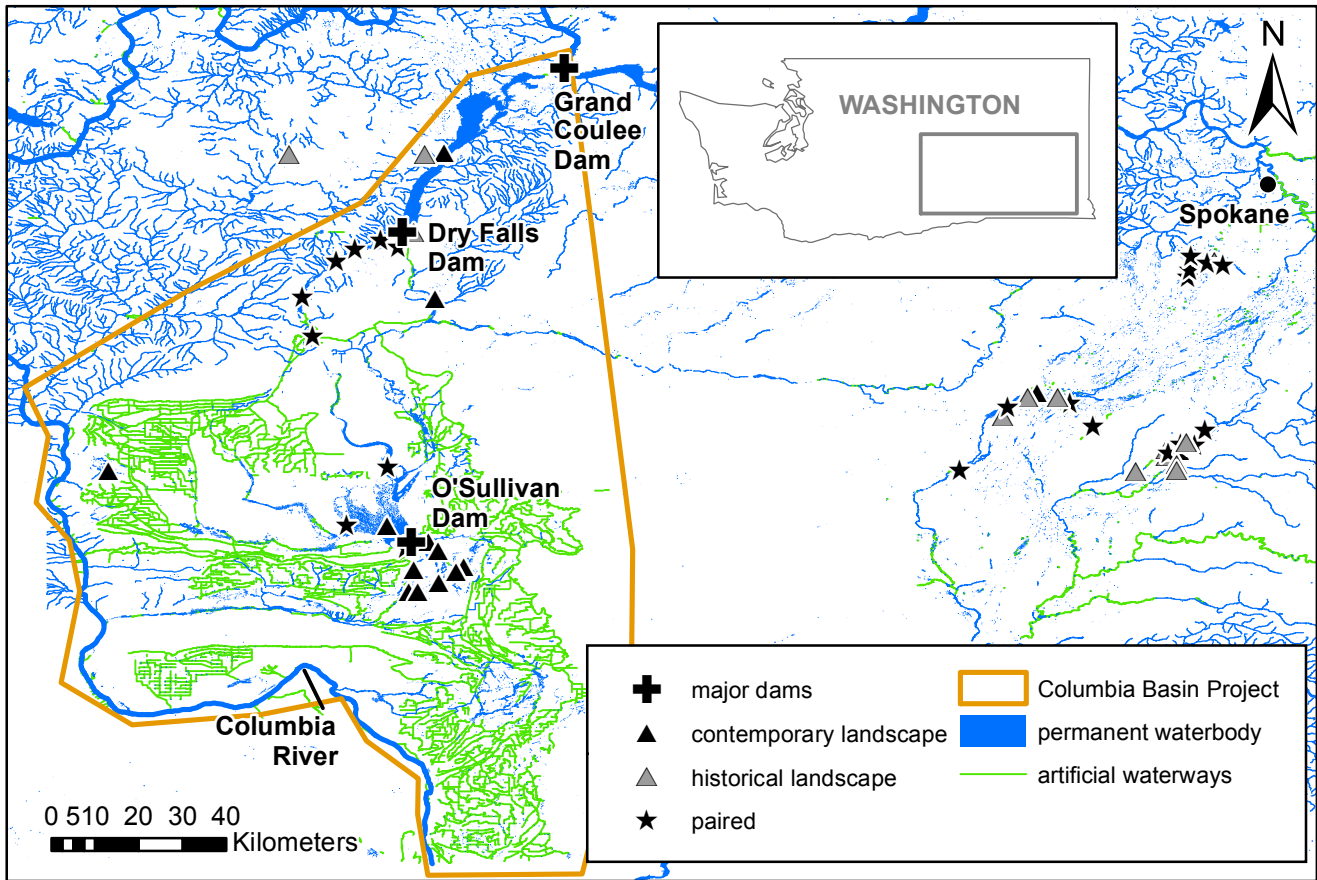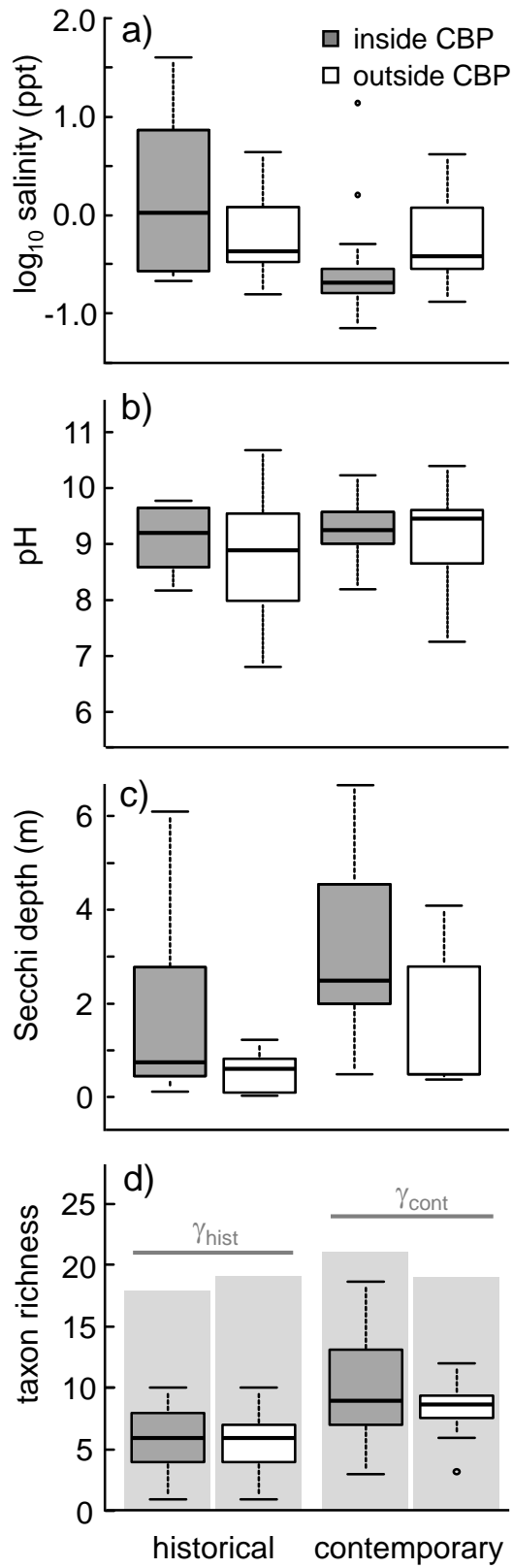
residual = 0.74

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.

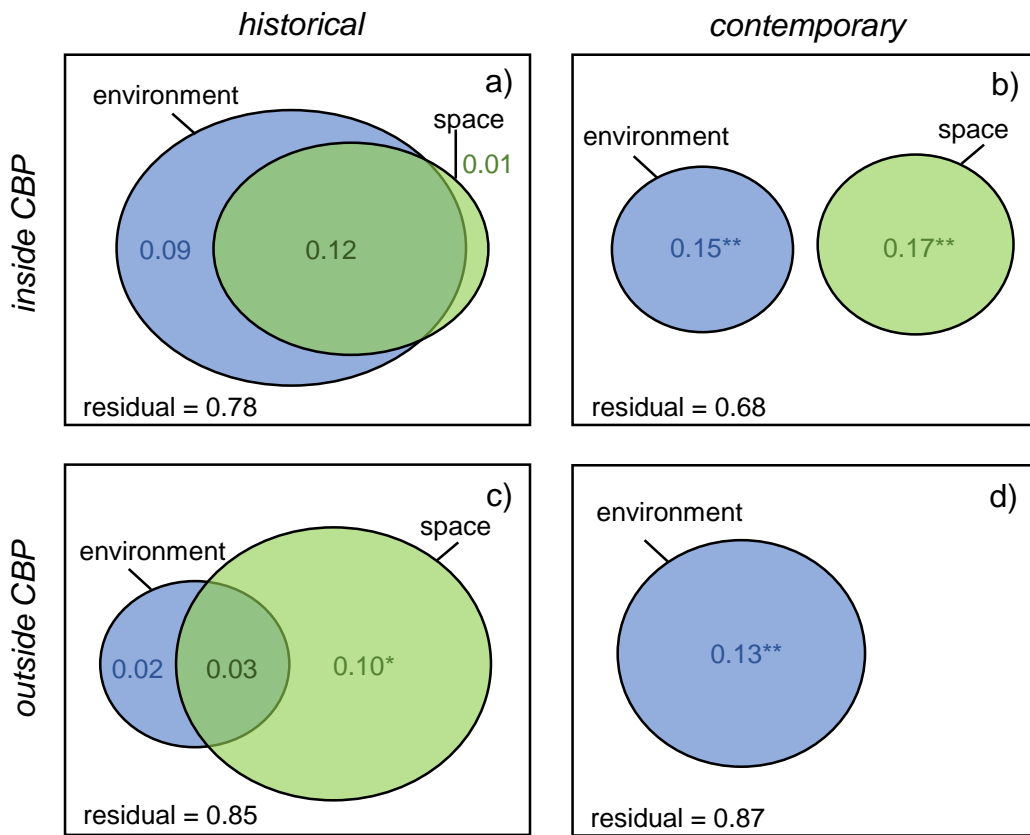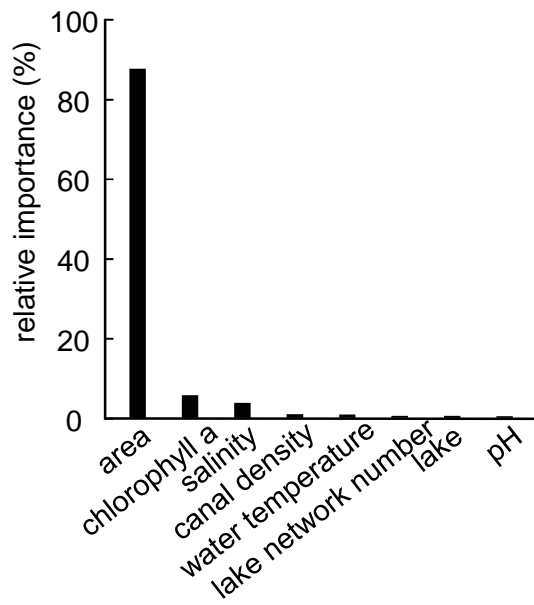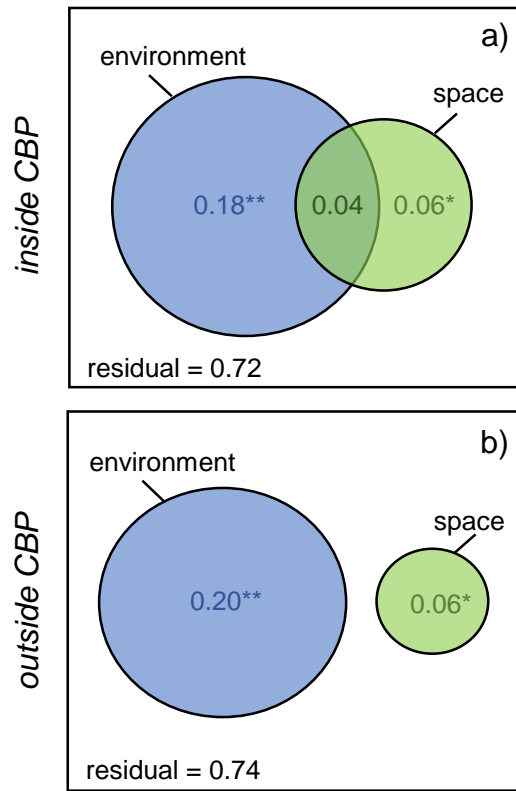| waterbody name (W&F 1958 name) | category | type | surface area (ha) | $Z_{max}$† (m) | surface temperature (°C) | elevation (m) | Secchi (m) | boat ramp‡ | permanence* | latitude (°N) | longitude (°W) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Folsom (Three Inch) | paired | pond | 48.6 | 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 ($\mu S \cdot cm^{-1}$) | total phosphorus ($\mu g \cdot L^{-1}$) | nitrate ($mg \cdot L^{-1}$) | chlorophyll *a* ($\mu g \cdot L^{-1}$) |
|---|---|---|---|---|---|---|
| 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)

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

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***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 ($\Delta$CS) 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 ($\Delta$CS = change in compositional similarity).

|  | Inside CBP | | Outside CBP | |
|---|---|---|---|---|
| **model** | **$\Delta$CS** | **% change** | **$\Delta$CS** | **% 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 |

**<u>Appendix S4</u>:** *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.

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Borcard, D., Gillet, F. & Legendre, P. (2011) *Numerical Ecology with R*. Springer, New York, USA.
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Legendre, P. & Gallagher, E.D. (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia*, **129**, 271-280.
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.*
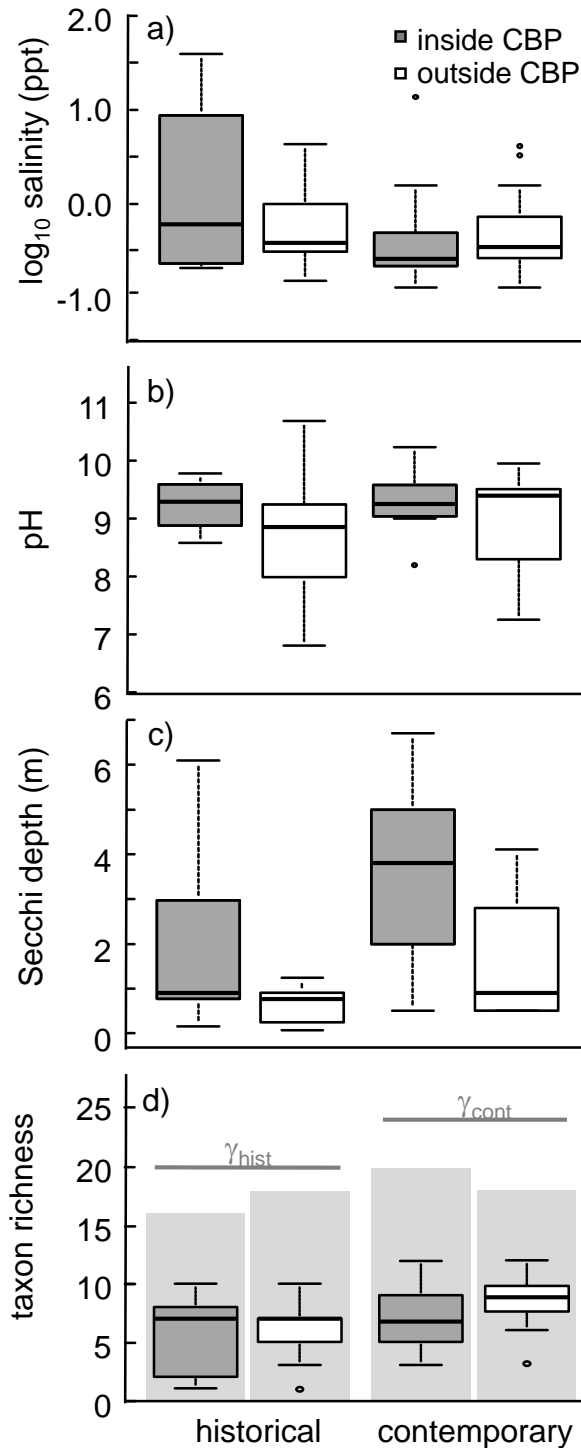


**Figure S5-1.** Comparisons of (a) $\log_{10}$ salinity (ppt), (b) pH, (c) Secchi depth (m), and (d) richness inside and outside the Columbia Basin Project (CBP) in historical and contemporary samples in paired sites (n=24). Thick inner bar is the median, outer edges of the box are 25th and 75th percentiles, 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     |
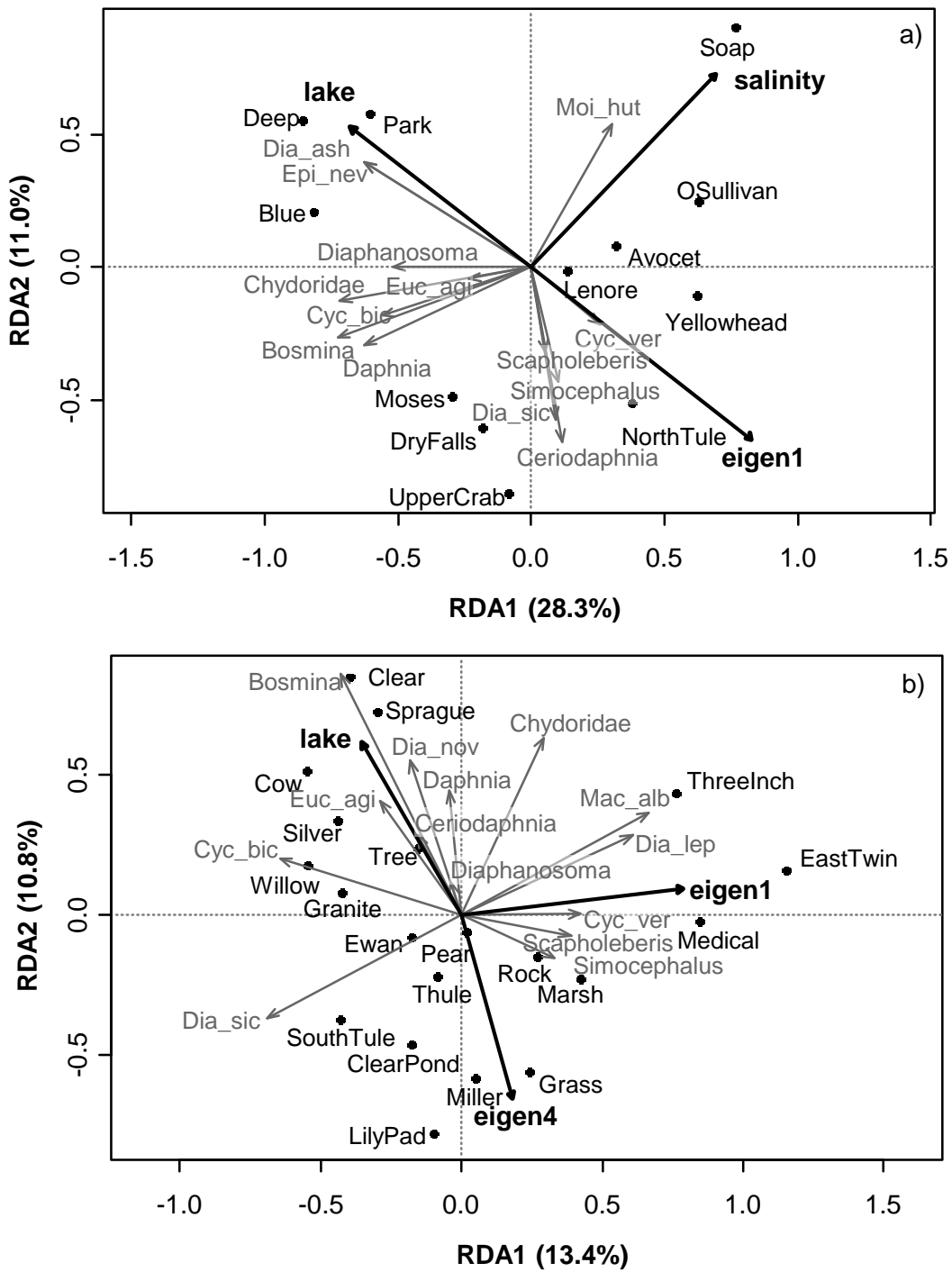
**Figure S5-2.** Redundancy analyses of species presence or absence in historical communities a) inside the CBP and b) outside the CBP. We found significant structure in communities (inside CBP: $F = 1.994$, $P = 0.009$; outside CBP: $F = 2.076$, $P = 0.002$). Dark arrows are significant predictor variables, 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
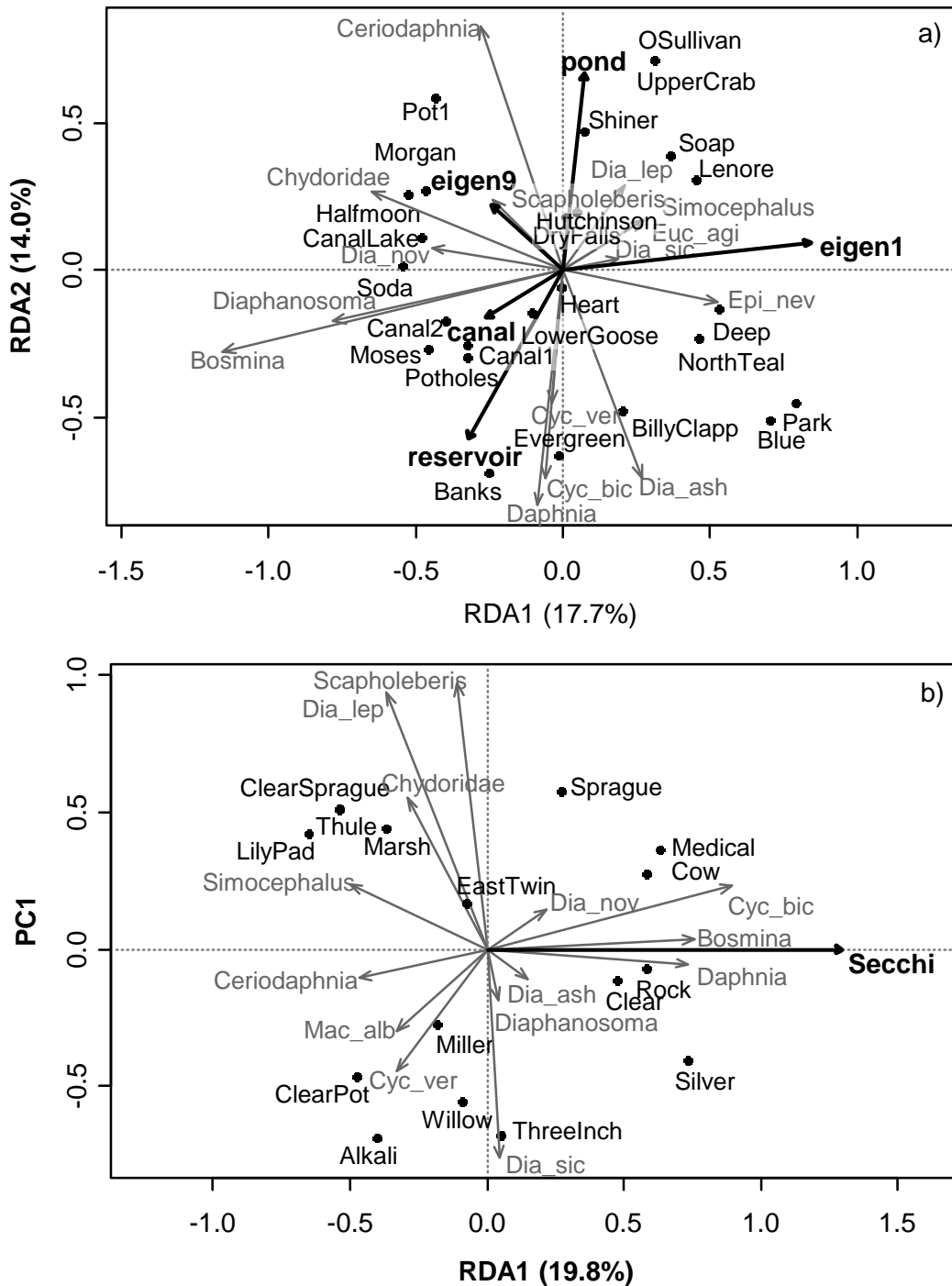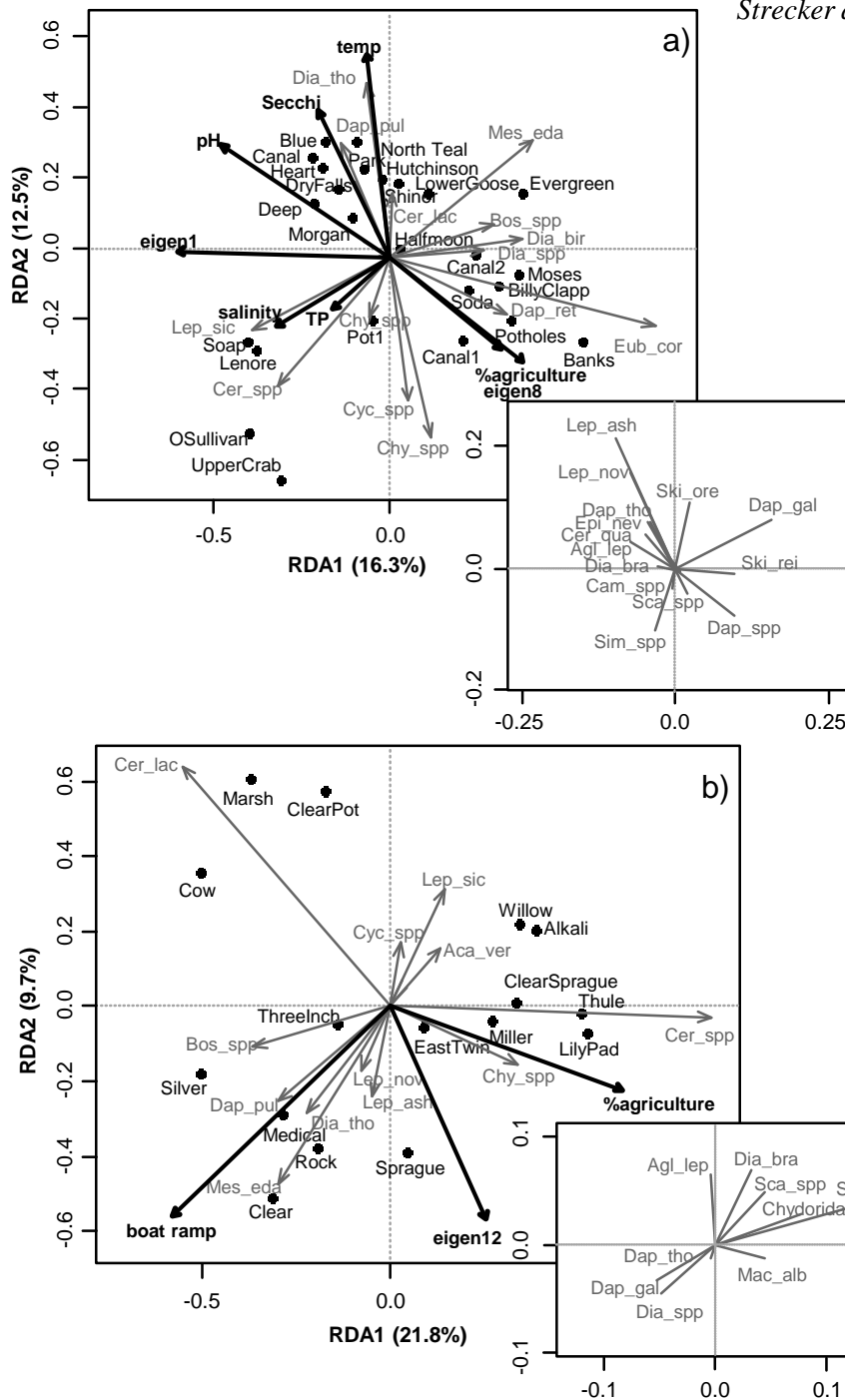
**Figure S5-3.** Redundancy analyses of species presence or absence in contemporary communities a) inside the CBP and b) outside the CBP. We found significant structure in communities (inside CBP: $F$ = 3.260, $P$ = 0.001; outside CBP: $F$ = 3.453, $P$ = 0.001). Dark arrows are significant predictor 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 |
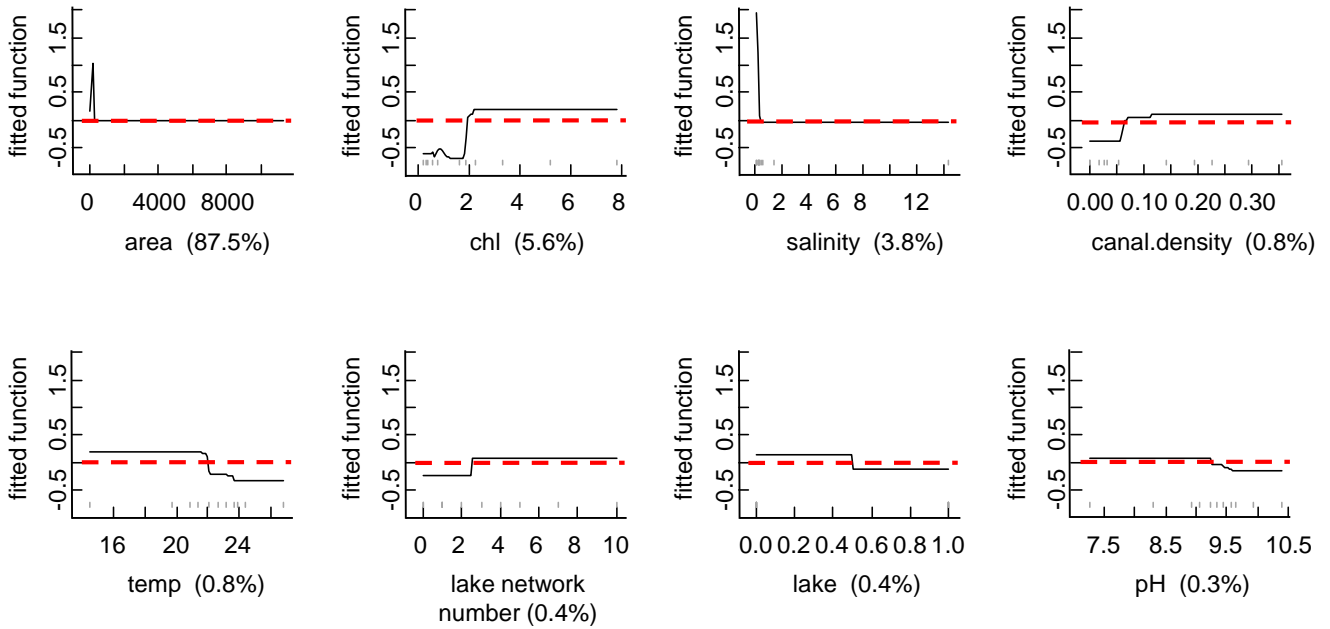
**Figure S5-4.** Partial dependence plots illustrating the influence of the top eight variables on species richness. The y-axis is the logit scale, which is centered around a mean of zero for the data. To interpret these plots, when the black line is above zero (i.e., the dashed red line), the variable 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
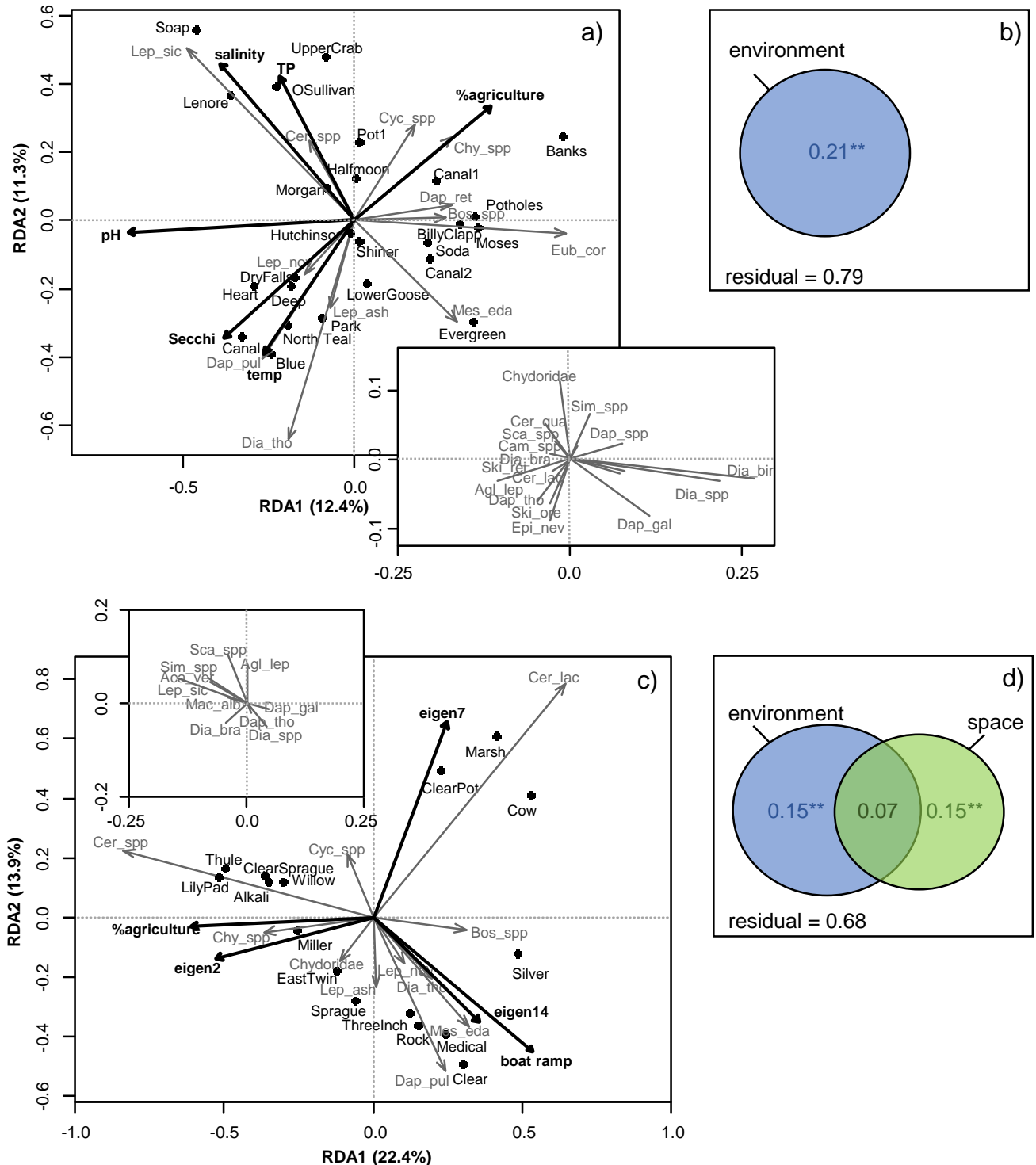
**Figure S5-6.** (left) Redundancy analyses and (right) variation partitioning of species abundance of contemporary zooplankton communities (a,b) inside the CBP and (c,d) outside the CBP using Euclidean distances for spatial predictor variables. Independent environmental and spatial variation are indicated 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).