Running title: Land use effects on stream diversity

LOCAL AND REGIONAL DRIVERS OF TAXONOMIC HOMOGENIZATION IN STREAM COMMUNITIES

ALONG A LAND USE GRADIENT

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1 **LOCAL AND REGIONAL DRIVERS OF TAXONOMIC HOMOGENIZATION IN STREAM**

2 **COMMUNITIES ALONG A LAND USE GRADIENT**

3

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6

7

8 **ABSTRACT**

9 Aim: The interaction of land use with local vs. regional processes driving biological

10 homogenization (β-diversity loss) is poorly understood. We explored: i) stream β-diversity

11 responses to land cover (forest vs. agriculture) in terms of physicochemistry and

12 physicochemical heterogeneity, ii) whether these responses were constrained by the regional

13 species pool, i.e. γ-diversity, or local assembly processes through local (α) diversity, iii) if local

14 assembly operated through the regional species abundance distribution (SAD) or intraspecific

15 spatial aggregation, and iv) the dependency on body size, dispersal capacity, and trophic level

16 (producer vs. consumer).

17

18 Location: United States of America, Canada, and France

19

20 Time Period: 1993-2012

21

22 Major Taxa Studied: Stream diatoms, insects, and fish

23

24   Methods: We analyzed six datasets totaling 1,225 stream samples. We compared diversity

25   responses to eutrophication and physicochemical heterogeneity in forested vs. agricultural

26   streams with regression methods. Null models quantified contribution of local assembly to β-

27   diversity (β-deviance, β_{DEV}) for both land covers and partitioned it into fractions explained by the

28   regional SAD (β_{SAD}) vs. aggregation (β_{AGG}).

29

30   Results: Eutrophication explained homogenization and more uneven regional SADs across

31   groups, but local and regional biodiversity responses differed across taxa. β_{DEV} was insensitive to

32   land use. β_{SAD} largely exceeded β_{AGG} and was higher in agriculture.

33

34   Main Conclusion: Eutrophication but not physicochemical heterogeneity of agricultural streams

35   underlay β-diversity loss in diatoms, insects and fish. Agriculture did not constrain the

36   magnitude of local vs. regional effects on β-diversity, but controlled the local assembly

37   mechanisms. While the SAD fraction dominated in both land covers, it further increased in

38   agriculture at the expense of aggregation. Notably, the regional SADs were more uneven in

39   agriculture, exhibiting excess common species or stronger dominance. Diatoms and insects

40   diverged from fish in terms of biodiversity, SAD shape, and β_{DEV} patterns, suggesting an

41   overriding role of body size and/or dispersal capacity compared to trophic position.

42

43   **Key words:** β-diversity, biodiversity loss, taxonomic homogenization, diatoms, fish, insects,

44   land use, local assembly, spatial aggregation, species abundance distribution

INTRODUCTION

Landscape transformations from continuous undeveloped expanses to agricultural fields and urban sprawls have accelerated the global biodiversity decline (Newbold, Hudson, Hill, Contu, Lysenko et al., 2015). Human land use (hereafter land use) underlies declines in both regional richness, i.e. γ-diversity (Barlow, Lennox, Ferreira, Berenguer, Lees et al., 2016), and dissimilarity among biological communities, i.e. β-diversity, resulting in taxonomic homogenization across space and time (Petsch, 2016). Biodiversity losses from land use stem from habitat loss, fragmentation, eutrophication, and physicochemical stress, altogether considered among the primary threats facing global biodiversity (Sala, Stuart Chapin, Iii, Armesto, Berlow et al., 2000; Devictor, Julliard, Clavel, Jiguet, Lee et al., 2008). Preventing biodiversity losses and mitigating subsequent homogenization remain a top priority because both can translate into decreased biological integrity and ecosystem resilience (de Juan, Thrush & Hewitt, 2013; Socolar, Gilroy, Kunin & Edwards, 2016). Therefore, it is critical from a conservation planning standpoint to continue investigating how land use affects ecological processes underlying global diversity in order to mitigate the ongoing biodiversity crisis.

Land use effects on biodiversity occur across scales, operating either in a top-down or bottom-up fashion or both (Flohre, Fischer, Aavik, Bengtsson, Berendse et al., 2011). Top-down mechanisms function through the regional species pool (γ-diversity), which is a product of speciation and extinction, large-scale dispersal, climate, and evolutionary, geological, and land use history (Zobel, 2016). Bottom-up mechanisms include local-level assembly processes, e.g. environmental filtering, interspecific interactions, and small-scale dispersal (Márquez & Kolasa, 2013), which constrain local (α) diversity and subsequently affect site-to-site community dissimilarity. Studies across terrestrial and freshwater systems have reported a general decline in

68   γ-diversity because of land use, but divergent patterns of α-diversity, including decreased α-

69   diversity, owing to losses of sensitive and endemic species, and stable, or even increased α-

70   diversity, owing to greater rates of species invasion and colonization (Vellend, Baeten, Myers-

71   Smith, Elmendorf, Beauséjour et al., 2013; Newbold *et al.*, 2015; Gonzalez, Cardinale,

72   Allington, Byrnes, Arthur Endsley et al., 2016). Thus, land use likely exerts differential impact

73   on the species pool and local assembly processes that may cause γ- and α-diversity, respectively,

74   to vary at different rates, which in turn influences β-diversity response (Kraft, Comita, Chase,

75   Sanders, Swenson et al., 2011).

76   β-diversity is usually treated as a scalar linking average α-diversity with γ-diversity, thus

77   reflecting spatial or temporal differences among localities. One can then measure the influence of

78   α- and γ-diversity as proxies of local and regional drivers of β-diversity, respectively.

79   Specifically, null models that constrain the observed species pool variation (i.e., γ-diversity) can

80   assess the role of local assembly by calculating a β-diversity measure (β_{DEV}) corresponding

81   solely to α-diversity variation (e.g., Kraft *et al.*, 2011) (Fig. 1a). β_{DEV} can be further decomposed

82   into fractions reflecting roles of intraspecific spatial aggregation (i.e., the spatial clumping

83   pattern of individuals within species) and the regional species abundance distribution (SAD,

84   vector of species abundances) (Xu, Chen, Liu & Ma, 2015) (Fig. 1b). Intraspecific spatial

85   aggregation results from dispersal, competitive, and environmental mechanisms that cluster

86   individuals of species across fewer sites, thus bolstering β-diversity (Veech, 2005). However,

87   regional SADs influence β-diversity because rare species are less likely to be locally sampled

88   due to low regional abundance (He & Legendre, 2002). Although examined across latitudes, the

89   two fractions of local assembly have not been studied in other contexts and it is unknown

90   whether these components are responsive to strong ecological influences (e.g., land use).

91   Studying how local assembly and regional species pool processes interplay is an ongoing

92   area of research in terrestrial systems because it may explain how β-diversity varies with land

93   use (Socolar *et al.*, 2016). Surprisingly, little attention is focused on freshwater systems, even

94   though freshwater biodiversity is more vulnerable to land use relative to terrestrial systems,

95   particularly through habitat modification (Sala *et al.*, 2000; Wiens, 2016) and eutrophication

96   from agriculture (Withers, Neal, Jarvie & Doody, 2014). Although primary productivity in

97   agricultural streams could increase with eutrophication, forest streams, which are usually low in

98   nutrients and have more shading, tend to harbor higher biodiversity stemming from greater

99   physical and environmental heterogeneity that translates into greater ecosystem complexity

100   (Penaluna, Olson, Flitcroft, Weber, Bellmore et al., 2017). Agriculture probably causes changes

101   in physicochemical heterogeneity as well, but this subject is poorly explored. Thus, the scarcity

102   of data, especially for aquatic taxa, has inhibited general understanding of how land use

103   influences local and regional processes driving β-diversity.

104   Impacts of agricultural eutrophication on β_{DEV} are not understood, although null models

105   have been used to assess environmental disturbance (e.g., Myers, Chase, Crandall & Jiménez,

106   2015). We hypothesize β-diversity response to eutrophication, including variation in β_{DEV},

107   depends on trophic level, body size, and dispersal capacity. For example, many unicellular

108   producers, like diatoms, have high nutrient demands and may benefit from increased nutrients

109   (Passy, 2008; Soininen, Jamoneau, Rosebery & Passy, 2016). Diatom microscopic size, high

110   local abundance, and broad geographic distributions, allowing both in-stream and overland

111   passive dispersal (Finlay, 2002), may result in weak β-diversity and β_{DEV} response to agriculture.

112   Smaller bodied macroscopic organisms, such as aquatic insects, may be more constrained in

113   active dispersal capacity during larval stages but exhibit greater overland mobility during winged

114   adult life stages, which could offset some harmful agricultural effects. In contrast, larger

115   consumers with more limited geographic dispersal capacity, such as fish, may be negatively

116   affected by eutrophication due to ammonia toxicity, loss of suitable habitat, and lower quality

117   food sources (Allan, 2004).

118   In this study, we compared spatial patterns of biodiversity and abundance in streams with

119   watersheds dominated by agriculture vs. forest. Our objectives were to determine: i) how β-

120   diversity and related biodiversity properties respond to agriculture (through nutrient enrichment

121   or physicochemical heterogeneity), ii) if agriculture alters the relative contribution of local

122   assembly effects to β-diversity, iii) whether agriculture differentially constrains the fractions of

123   local assembly explained by spatial aggregation vs. the SAD, and iv) if the relationships outlined

124   in i) to iii) vary across organismal groups (Table 1).

125

126   **MATERIALS AND METHODS**

127   *Data sources and site selection*

128   Our datasets (six in total) comprise stream organisms sampled from the US, France, and Canada

129   (Fig. 2). Each dataset included community data and physicochemistry from watersheds

130   dominated by either forest or agriculture. Only streams with ≥ 50% of their upstream watershed

131   belonging to one of the two land cover categories were included in our analyses. We examined

132   biodiversity patterns across three US datasets (diatoms, insects, and fish), two French datasets

133   (diatoms and fish), and one Canadian dataset (diatoms), constructed as follows.

134

135

136

137   *United States*

138   US community data, spanning 19 latitudinal degrees and 55 longitudinal degrees, were obtained

139   from the National Water-Quality Assessment (NAWQA) Program of the United States

140   Geological Survey and the National Rivers and Streams Assessment (NRSA) of the United

141   States Environmental Protection Agency. Communities were collected in the warm months

142   during low flow conditions (July through September) to constrain seasonal succession and

143   variation in temperature and flow. NAWQA communities (diatoms, insects, and fish) were

144   sampled between 1993-2010, whereas NRSA communities (fish), between 2011 and 2012.

145   Diatoms were collected from the richest-targeted habitats, encompassing hard substrates or

146   macrophytes. Depending on available substrate, a defined area of 25 cobbles, 5 woody snags or 5

147   macrophyte beds was sampled within a stream reach and the samples were composited. Diatoms

148   were identified generally to species in counts of 400-800 cells. Benthic insects (class Insecta)

149   were composed of combined sieved samples taken from the richest-targeted habitats (i.e., riffles,

150   main-channel, and natural-bed instream habitats). Insects were identified to the lowest possible

151   category (order to species) in counts of 400-800 individuals. Both NAWQA and NRSA fish were

152   generally identified to species in counts of 400-950 individuals taken from riffle, pool, and run

153   habitats using electrofishing equipment with seines.

154   Land use and cover data were generated by the NAWQA and NRSA using National Land

155   Cover Datasets 1992 and 2006, 30 m resolution. We selected 400 streams for diatoms and 126

156   streams for insects split equally between both land cover categories. Since fish communities and

157   environmental data in both the NAWQA and NRSA data were sampled with similar methods, we

158   combined both fish datasets into a single dataset comprising 231 streams (116 agricultural and

159   115 forested streams).

160   *France*

161   French diatom data were sourced from a national dataset including field collections of 200

162   streams from 2011. Algae were collected from stones during the low flow period in June

163   through September with a standardized sampling method (Afnor, 2007). Diatoms were identified

164   generally to species in counts of about 320-475 cells. The French fish dataset was collected by

165   the French National Agency for Water and Aquatic Environments (ONEMA) during low flow

166   periods between May and October 2011. The dataset comprised 200 streams with fish identified

167   to species in counts of 10-3300 individuals sampled with electrofishers. For both French

168   datasets, we used 100 agricultural and 100 forest streams, spanning 8 latitudinal and 14

169   longitudinal degrees. Land use cover data were obtained from the CORINE land cover database

170   (European Environment Agency, 2013)

171

172   *Canada*

173   Canadian diatom data included 46 stream samples (23 streams in both land cover categories)

174   collected in August to September during the low flow period between 2002 and 2009 (Lavoie,

175   Campeau, Zugic-Drakulic, Winter & Fortin, 2014) spanning 3 latitudinal and 6 longitudinal

176   degrees. Samples were composites of rock scrapes (5-10 rocks) per stream reach, targeting riffles

177   and runs. Diatoms were mainly identified to species in counts of at least 400 valves. Land use

178   cover data were compiled from government GIS databases, including the Ecoforestry

179   Information System, Annual Crop Inventory, and the Insured Crop Database.

180

181   *Environmental data*

182   All datasets had associated physicochemical and coordinate data (i.e., GCS coordinates re-

183   projected with Lambert Conformal Conic). Environmental variables in our analyses included

184   water temperature, air temperature, nitrite + nitrate (or total nitrogen when absent), ammonia,

185   orthophosphate, total phosphorus, specific conductance, and pH (Appendix 1, Table S1.1 in

186   Supplemental Information). Environmental data for the US datasets consisted of the average for

187   the month of sample collection. Environmental data for French diatoms included the median of

188   measurements obtained 30 days before and 15 days after the diatom sample date. The French fish

189   environmental data represented the average of 12 monthly measurements prior to fish sampling.

190   Air temperature for French diatom data were not recorded at the time of sampling and were

191   obtained from the WorldClim database (Hijmans, Cameron, Parra, Jones & Jarvis, 2005),

192   whereas air temperatures for French fish streams were measured at the stream. Canadian

193   environmental data were seasonal averages calculated from water samples collected from July to

194   September.

195

196   *Diversity, spatial aggregation, and species abundance distribution*

197   We calculated $\bar{\alpha}$-diversity (average richness across samples), γ-diversity (total richness per land

198   use), and β-diversity of stream samples for both land cover categories for each dataset. We used

199   equation (1) to calculate the observed β-diversity (β_{OBS}),

200    $$\beta_{OBS}= 1 - \frac{\bar{\alpha}}{\gamma} \qquad\qquad (1)$$

201
202   which indicated the average proportion of the species pool absent from a stream.

203   We used the null model framework developed by Xu *et al.* (2015) to quantify i) the

204   magnitude of the local assembly effect on β-diversity after controlling for γ-diversity and ii) the

205   contributions of the SAD vs. intraspecific spatial aggregation to local assembly (Fig. 1b). First,

206   the difference (i.e., β-deviance, β_{DEV}) between β_{OBS} and the expected β-diversity (β_{EXP}, i.e., β-

207   diversity expected assuming completely random sampling, see Appendix S2) was taken to

208   quantify local assembly absent the effect of γ-diversity. β_{DEV} is bounded between 0 and 1, with

209   larger β_{DEV} corresponding to greater local control. Secondly, we calculated β-diversity predicted

210   when intraspecific spatial aggregation is constant across all species (β_{PRED}). Then, the difference

211   between β_{PRED} and β_{EXP} reveals what fraction of β_{DEV} is contributed by the SAD (β_{SAD}), while the

212   remaining fraction of β_{DEV} is attributed to spatial aggregation (β_{AGG}). In this model, β_{SAD} can

213   exceed β_{DEV} if β_{PRED} exceeds $\beta_{OBS.}$ The corresponding aggregation fraction will in turn be

214   negative because the sum of the two fractions, β_{SAD} and β_{AGG}, must equal 1, thus meaning that

215   the pattern is less aggregated than expected by the null model. To test whether the two land

216   covers differ in their magnitude of intraspecific spatial aggregation, we used maximum

217   likelihood methods and calculated the aggregation parameter, k, across samples within each land

218   cover (Appendix S3). Because smaller k corresponded to greater aggregation, we analyzed the

219   reciprocal of the parameter for easier interpretation. In summary, the procedure yielded six

220   measurements: $\beta_{EXP,}$ β_{PRED}, $\beta_{DEV,}$ β_{SAD}, $\beta_{AGG,}$ and $1/k$.

221   Regional SADs for both land cover categories was analyzed by summing abundances of

222   each species across all stream samples and calculating the standard deviation (parameter σ) of

223   the Poisson-lognormal distribution fit of the abundance data using the `sads´ R package (Prado,

224   Mirands & Chalom, 2017). Parameter σ reflects SAD evenness with greater σ values

225   corresponding to increased unevenness. To determine if changes in σ were associated with

226   prevalence of rare vs. common species, we also examined the relationship of σ with the skewness

227   (`skewness´ function from R package `moments´, Komsta & Novomestky, 2015) of the log-

228   transformed regional species abundances for each land cover category. Skewness was

229   significant if skewness divided by the standard error of the skewness (i.e., $(6/n)^{0.5}$, where n =

230   number of species) was greater than 2. Significant positive skew indicates greater prevalence of

231 abundant species, while significant negative skew reveals higher number of rare species

232 compared to the lognormal distribution.

233

234 ***Statistical analyses***

235 *Resampling scheme*

236 Generally, the described procedures in our study typically produced a single value without any

237 estimate of error, which inhibits statistical comparisons between datasets. Therefore, to test for

238 abiotic and biotic differences between land covers, we conducted a resampling procedure where

239 we randomly selected 50% of the streams within each land cover category for each dataset

240 without replacement 999 times. Each loop calculated the median of each physicochemical

241 variable, an estimate of physicochemical heterogeneity, biodiversity ($\bar{\alpha}$-, β-, and γ-diversity),

242 SAD, and null model measures including the null model β-diversity values, and the within group

243 intraspecific aggregation ($1/k$). This procedure generated six new datasets that contained

244 resampled physiochemistry data and biotic measures, which were used further statistical

245 analyses. R scripts are available as supplementary material for online publication only (see

246 Appendices S3 and S4).

247

248   *Eutrophication and physicochemical heterogeneity*

249 We employed principal components analysis with all resampled, standardized median

250 physicochemical variables (mean = 0, standard deviation = 1) to create a synthetic variable

251 corresponding to the major physicochemical trend. The first PCA axis represented a

252 eutrophication gradient and explained between 53.1% (French diatom samples) and 94.3%

253 (Canadian diatom samples) of the variation among samples (Appendix 1, Fig. S1.1).

254	To estimate physicochemical heterogeneity within each land cover, we used

255	permutational analysis of multivariate dispersion on standardized physiochemical data with the

256	`betadisper´ function from R package `vegan´ (Anderson, Ellingsen & McArdle, 2006; Oksanen,

257	Blanchet, Friendly, Kindt, Legendre et al., 2017). In this procedure, physicochemical

258	heterogeneity is calculated as the average distance from a multivariate group median (group =

259	land cover) with larger distances corresponding to greater within-group heterogeneity.

260

261	*Environmental effects*

262	We determined how land use-driven eutrophication and physicochemical heterogeneity affected

263	diversity components using a combination of univariate and multivariate techniques and variance

264	partitioning. For each dataset, we used permutational MANOVA function `adonis´ from package

265	`vegan´ to test for differences in the multivariate mean of the $\bar{\alpha}$-, β-, and γ-diversity between

266	land covers. If the permutational MANOVA was significant, we followed with permutational

267	ANOVA using the `perm.anova´ function provided in `RVAideMemore´ (999 permutations;

268	Herve, 2018) for each dependent variable. We then used RDA-based variance partitioning

269	models (`vegan´ function `varpart´) on each dataset to identify major explanatory factors

270	underlying diversity patterns, with eutrophication, physicochemical heterogeneity, and land

271	cover (coded as dummy variables) as predictors and the diversity measures ($\bar{\alpha}$-, β-, and γ-

272	diversity) as response variables.

273	We employed permutational MANOVA and permutational ANOVA to determine if the

274	resampled β_{DEV}, β_{SAD}, β_{AGG}, $1/k$, σ, and skewness differed between land covers. Because total

275	abundance and γ-diversity influence the shape of the regional SAD, we controlled their

276	influences by regressing parameter σ against total abundance and γ-diversity of the resample and

277   obtaining the residuals, which were then used in subsequent analyses. To further explore if β_{DEV}

278   was sensitive to variation in SAD unevenness (residual σ) and intraspecific spatial aggregation

279   (1/k), we calculated Pearson correlations within both land cover categories for all datasets.

280   Pearson correlations were also used to assess whether residual σ correlated with skewness and

281   1/k. We then implemented variance partitioning to determine if eutrophication, physicochemical

282   heterogeneity, land cover, or their covariance explained the variation in β_{DEV}.

283

284   **RESULTS**

285   ***Eutrophication and Environmental Heterogeneity Effects on Diversity and the SAD***

286   Permutational MANOVA and permutational ANOVAs of environmental data showed that all

287   physiochemistry levels were significantly elevated ($P < 0.05$) in agricultural land use across all

288   datasets. Permutational ANOVAs also indicated greater physicochemical heterogeneity among

289   agricultural streams in all but the Canadian diatom dataset (higher in forest land cover) and the

290   US Fish dataset (no differences, Fig. 3). MANOVA of $\overline{\alpha}$-, β-, and γ-diversity against land use

291   revealed that land use significantly affected the diversity measures across all datasets. Following

292   our first objective, we demonstrated that β-diversity declined with agriculture across all datasets.

293   Gamma diversity usually decreased, whereas $\overline{\alpha}$-diversity often increased with agriculture (Table

294   2). Except for French fish, SADs were generally significantly more uneven for agricultural land

295   use than forest (higher residual σ), although the differences were mainly small (Fig. 4, columns

296   1-3). Intraspecific aggregation (1/k) was always greater in forest than in agriculture and was

297   negatively correlated with residual σ, meaning more even SADs were always associated with

298   higher aggregation (Appendix 1, Table S1.2). Skewness was significantly positive in the insect

299   and all three diatom datasets, but non-significant in the two fish datasets. When positive,

13

300   skewness correlated positively with residual σ regardless of land cover (although weakly for

301   diatoms), indicating that SAD unevenness was generally characterized by greater abundances of

302   more common species.

303   Our first objective was to determine how biodiversity explained by land use,

304   eutrophication, and physicochemical heterogeneity. Variation in all diversity measures was

305   primarily explained by covariance effects, while pure land cover, pure eutrophication, and pure

306   physicochemical heterogeneity contributed minorly (Fig. 5). In general, covariance of

307   eutrophication with land cover explained most of the variation, indicating that land use

308   constrained biotic variability mainly through eutrophication rather than physicochemical

309   heterogeneity. However, the insect dataset differed from the rest in that the covariance fraction of

310   land cover, eutrophication, and physicochemical heterogeneity captured most of the variation.

311

312   *Eutrophication-associated shifts in local assembly across organismal groups*

313   For our second objective, we found local assembly weakly drove diatom and insect β-diversity

314   (β_{DEV} generally less than 0.26 across land covers) but had a relatively greater influence on fish β-

315   diversity (β_{DEV} between 0.38-0.45). β_{DEV} differed significantly between forest and agriculture

316   (permutational ANOVA) in all datasets except insects (no difference). However, the magnitude

317   of the difference in β_{DEV} was usually small (3.49 to 16.04%), with the direction of the difference

318   depending on organismal group and biogeographic region (Fig. 4, column 4).

319

320   *Contribution of the SAD vs. intraspecific spatial aggregation to β_{DEV}*

321   For objective three, the partitioning of β_{DEV} revealed that β_{SAD} generally exceeded 100% and

322   β_{AGG} was negative, regardless of land cover except for the US and French diatom datasets, which

14

323   showed $\beta_{SAD} < 100\%$ and positive β_{AGG} for forest land use (Fig. 4, columns 5-6). As changes in

324   β_{SAD} correspond to equal and opposite changes in β_{AGG}, we focus on β_{SAD} for brevity. β_{SAD}

325   represented nearly all of β_{DEV} regardless of dataset and land cover type (~ 90-110% of total

326   deviance) and was significantly (although marginally) larger in agricultural land use than in

327   forest cover. Further, β_{DEV} was generally negatively correlated with residual σ, regardless of land

328   cover or organismal group, implying that increased SAD unevenness was usually associated with

329   greater contribution of the regional species pool (Appendix 1, Table S2). Variance partitioning of

330   β_{DEV} across datasets showed mixed patterns among and within organismal groups over what

331   effects best explained β_{DEV} (Fig. 6).

332

333   *Variability across organismal groups*

334   Consistent with our fourth objective, we demonstrated that smaller organisms (diatoms and

335   insects) with greater dispersal capacity were more similar in terms of SAD and β_{DEV} patterns, but

336   diverged from fish. However, we also observed divergence in some ecological patterns between

337   datasets within organismal groups (i.e., diatoms and fish) in that $\overline{\alpha}$-diversity, γ-diversity, SAD

338   skewness, and β_{DEV} responses varied between country of origin, which indicated context

339   dependency of our results.

340

341   **DISCUSSION**

342   In this comprehensive study of stream organisms from two continents, agriculture and

343   subsequent eutrophication were generally associated with reduced β- and γ-diversity and

344   increased $\overline{\alpha}$-diversity. First, covariance of land use with physicochemical gradients, rather than

345   with physicochemical heterogeneity, characterized regional biodiversity loss with land use.

346   Second, all datasets showed significant shifts in magnitude of β_{DEV} with eutrophication but the

347   direction (i.e., stronger or weaker local assembly effects) depended on organismal group and

348   potentially biogeographical factors. Third, the regional SAD overrode intraspecific spatial

349   aggregation in explaining β_{DEV} and its influence and unevenness increased with agriculture.

350

351   *Eutrophication and Environmental Heterogeneity Effects on Diversity and the SAD*

352   With respect to objective one, regional biodiversity loss, local diversity gains, and increased

353   community similarity in aquatic taxa were correlated with agricultural land use, consistent with

354   patterns expected for taxonomic homogenization (Petsch, 2016). Recently, Ribiero *et al*. (2015)

355   explored the generality of floral homogenization consequential of agricultural land use and noted

356   that too many studies focus on a single spatial scale or a single taxon. For aquatic taxa,

357   agriculturally-associated changes in β-diversity have been reported, however, we have only

358   begun to examine these changes at broader spatial scales. For example, Winegardner *et al*.

359   (2017) attributed greater temporal β-diversity of diatoms across modified US landscapes to

360   richness gains and losses stemming from disproportionate influence of contemporary vs. past

361   land use, yet observed no changes in spatial β-diversity. In contrast, diatom spatial β-diversity

362   declined with eutrophication in French streams (Jamoneau, Passy, Soininen, Leboucher & Tison-

363   Rosebery, 2018). Our investigation, exploring diatoms, insects, and fish across regional to

364   subcontinental scales, demonstrates that the detrimental effects of agriculture on the regional

365   biodiversity in stream ecosystems are independent of species biology or scale.

366   We further revealed that biodiversity variation between forest and agriculture was mainly

367   driven by land use differences in physicochemistries rather than physicochemical heterogeneity,

368   a result contrary to conventional wisdom that higher environmental heterogeneity brings greater

16

369   turnover. While agriculture may homogenize the landscape, we show that it tended to lead to

370   greater stream physicochemical heterogeneity, possibly due to variability in fertilization and

371   landscape management regimes. Heterogeneity is an important mechanism of co-existence

372   because it offsets competitive exclusion (Tilman & Pacala, 1993). However, we observed that

373   physicochemical heterogeneity poorly explained β-diversity, because eutrophication in

374   agricultural streams may have exceeded the physiological thresholds of sensitive species and

375   decoupled compositional and environmental variability (Bini, Landeiro, Padial, Siqueira &

376   Heino, 2014). The lack of a relationship may also be due to our measure of heterogeneity, which

377   did not incorporate other aspects of heterogeneity, such as variability in substrate size, known to

378   diminish with agriculture (Allan, 2004).

379   Increased prevalence of common species over spatial and temporal scales is a hallmark of

380   taxonomic homogenization (Olden & Rooney, 2006), but our findings are restricted to the spatial

381   dimension. Notably, while across datasets SADs were generally more uneven in agriculture,

382   they were more positively skewed compared to forest only in two datasets, i.e. US insects and

383   French diatoms. In these datasets, homogenization in agriculture was characterized by greater

384   prevalence of common relative to rare species, which has also been observed in terrestrial

385   arthropods (Simons, Gossner, Lewinsohn, Lange, Türke et al., 2015; Komonen & Elo, 2017).

386   However, SADs were more positively skewed in forest cover than in agriculture for two datasets

387   (US and Canadian diatoms), and not skewed for both fish datasets. This suggested that stronger

388   SAD unevenness in agriculture resulted from either buildup of common species or greater

389   regional dominance by a relatively few species. Like recent terrestrial and tropical studies

390   (Vázquez & Gaston, 2004; Lohbeck, Bongers, Martinez-Ramos & Poorter, 2016), we showed

391   that SAD unevenness was associated with agriculturally-driven homogenization. Future research

392   on homogenization should incorporate novel methods and procedures, like we employed, to

393   elucidate how habitat modification and trait distribution contribute to the two forms of

394   unevenness, i.e. asymmetry vs. dominance.

395

396   *Land use-associated shifts in local assembly across organismal groups*

397   Following objective two, we examined how local assembly (β_{DEV}) varied between forested and

398   agricultural streams. In general, β_{DEV} marginally differed between land covers, suggesting that

399   the strength of local vs. regional mechanisms was relatively unaffected by physicochemical

400   stressors, consistent with prior work, reporting that fire disturbance altered β-diversity but not its

401   causes (Myers *et al.*, 2015). Community comparisons revealed that the magnitude of β_{DEV}

402   usually increased with body size, which here was linked with dispersal capacity. Smaller β_{DEV}

403   values in diatoms and insects indicated that the observed species pool exerted greater influence

404   on β-diversity relative to local assembly. These results are corroborated by earlier research

405   showing that diatom and insect communities are unsaturated, whereby local richness is limited

406   by the size of the regional pool as opposed to local interactions (Passy, 2009; Al-Shami, Heino,

407   Che Salmah, Abu Hassan, Suhaila et al., 2013; but see Thornhill, Batty, Death, Friberg &

408   Ledger, 2017). Therefore, it is possible that regional effects play a greater role in structuring

409   local richness and β-diversity of smaller and more dispersive organisms than of larger and less

410   dispersive organisms, and these relationships are not consistently affected by eutrophication.

411   In contrast, β_{DEV} in both fish datasets approaching 0.50 suggested relatively similar local

412   and regional control of β-diversity, in agreement with prior observations of comparable

413   contributions of regional and local factors to fish richness (Angermeier & Winston, 1998).

414   Taxonomic homogenization is a particularly prevalent phenomenon among freshwater fish

415 (Petsch, 2016) and our study elucidated that the possible causes include both local and regional

416 processes.

417   Other nearly uniform patterns, independent of land use, were the negative correlation of

418 residual σ of the regional SAD and the positive correlation of intraspecific aggregation ($1/k$) with

419 β_{DEV}. These correlations indicated that more even regional SADs and increased intraspecific

420 spatial aggregation were associated with stronger local constraints on β-diversity. Recent work

421 has only begun to explore the relationship of SAD evenness with taxonomic homogenization,

422 showing clear links between the two with implications for conservation (e.g., Simons *et al.*,

423 2015; Komonen & Elo, 2017). Our study is novel in that it demonstrates that local and regional

424 processes controlling β-diversity are dependent on SAD evenness—a finding that could guide

425 future stream conservation and management decisions, which need to be scale-explicit. For

426 example, if preserving β-diversity, then adopting practices promoting abundance of less common

427 species may be beneficial, given that SAD evenness is positively correlated with β-diversity.

428

429 ***The contribution of the SAD vs. intraspecific spatial aggregation to βDEV***

430 To our knowledge, we are the first to explore how land use affects partitioning of β_{DEV} into SAD

431 vs. spatial aggregation fractions, i.e. β_{SAD} vs. β_{AGG} (objective three). β_{SAD} accounted for most of

432 β_{DEV}, similar to observations for global tree communities (Xu *et al.*, 2015), but opposite to

433 findings, with a different null model, for Czech forests (Sabatini, Jiménez‑Alfaro, Burrascano,

434 Lora & Chytrý, 2017). We further discovered that β_{SAD} largely exceeded β_{AGG} across organismal

435 groups, datasets, and land cover types. However, β_{SAD} was significantly higher in agriculture

436 compared to forest in all datasets. The two land covers also diverged in β_{AGG}—less spatial

437 aggregation than predicted by the null model ($\beta_{AGG} < 0$) was detected in agriculture across all

438   datasets, while some aggregation ($\beta_{AGG} > 0$) was observed in forest streams in four out of six

439   datasets. These results suggest that although land use did not constrain the magnitude of local

440   assembly effects (β_{DEV}), it did control the mechanisms of local assembly, i.e. land use increased

441   the role of the SAD, but diminished the influence of aggregation.

442

443   ***Organismal and geographic dependencies in biodiversity response to homogenization***

444   In pursuit of our fourth objective, we found that organismal groups responded differently to land

445   use, as reported by other studies (e.g., Angermeier & Winston, 1998; Thornhill *et al.*, 2017). Insects

446   resembled diatoms in biodiversity, SAD shape, and β_{DEV} patterns, which suggested that body

447   size and dispersal capacity may be more important than trophic position (autotroph vs.

448   heterotroph) in predicting ecological responses to agricultural eutrophication. We generally

449   expected consistent responses of these metrics to agriculture, regardless of country of origin (i.e.,

450   diatoms and fish). We reasoned that agriculture, being a major habitat alteration, will override all

451   other influences, yet within both groups, there was divergence depending on region. We ensured

452   that variation in individual counts and mean counts among samples and differences in

453   geographic spread across datasets did not contribute to their dissimilarity (data not shown). Thus,

454   our findings of within-taxon variability with respect to biodiversity and the SAD highlighted the

455   importance of considering context dependency. Histories of land use disturbance among

456   geographic regions can set biodiversity and relative abundance patterns on different trajectories

457   by affecting processes underlying β-diversity (Cramer, Hobbs & Standish, 2008). For example,

458   European fish diversity has been historically depauperate relative to North American fauna

459   owing particularly to differences in glacial influence (Oberdorff, Hugueny & Guégan, 1997).

460 Furthermore, French aquatic communities have been impacted by agricultural activities far

461 longer than their North American counterparts (Hahn & Orrock, 2015).

462   In summary, we determined eutrophication is a major driver of β-diversity losses among

463 stream taxa, although the importance of geographic context was shown through the varied

464 biodiversity responses within taxonomic groups. Local assembly generally was weakly affected

465 by agriculture. However, in agriculture the regional SAD became significantly more uneven and

466 its effect on local assembly significantly increased compared to forest, which may be the

467 underlying causes of taxonomic homogenization. Biodiversity, SAD shape, and β_{DEV} depended

468 more strongly on body size and/or dispersal than trophic position. Future research should explore

469 how local and regional processes operate in tandem with the SAD to uncover whether

470 homogenization drivers are specific to organismal groups and the regions from which they were

471 sampled. Although we examined β-diversity loss from a taxonomic perspective, we recommend

472 future investigations on whether agriculture leads to phylogenetic and functional homogenization

473 across space and time. Then, taxonomic, phylogenetic, and functional diversity responses to

474 agriculture could be compared to generate more holistic understandings of the causes and

475 patterns of biotic homogenization.

476

477

481

482

483 **DATA AVAILABILITY STATEMENT**

484 Community and environmental datasets for the US are available for download from the USGS

485 NAWQA Program via the Water Quality Portal (https://www.waterqualitydata.us/contact_us/)

486 and EPA NRSA (https://www.epa.gov/national-aquatic-resource-surveys/data-national-aquatic-

487 resource-surveys) databases. DOI with associated URLs for all community and environmental

488 datasets analyzed for this project will be made freely available for download from Dryad Digital

489 Repository upon publication.

490

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622
623

Table 1. Summary of procedures and analyses performed with corresponding expectations and observations.

Procedures	Analyses	Expectations	Observations

| 1) Determine the differences in physicochemistry and physicochemical heterogeneity between land covers. | PCA, PERMDISP, MANOVA | Land cover would be characterized effectively by physicochemical parameters and potentially by physicochemical heterogeneity. | 1) All analyses clearly separated streams into two groups, corresponding to forest and agriculture; 2) Agricultural streams had elevated nutrient levels, suggestive of eutrophication; 3) Physicochemical heterogeneity was greater among agricultural streams except in the Canadian diatom dataset. |

2) Reveal the responses of $\overline{\alpha}$-, γ-, and β-diversity, SAD evenness, and SAD skewness to physicochemistry and physicochemical heterogeneity.

MANOVA, Variance partitioning

The responses of biodiversity components to physicochemistry and physicochemical heterogeneity may differ depending on body size, dispersal capacity, and trophic level (autotroph vs. heterotroph).

1) In general, β- and γ-diversity were negatively related to eutrophication, whereas $\overline{\alpha}$-diversity increased. SADs tended to be more uneven in agricultural streams due to buildup of common species and/or increased dominance;

2) Covariance of land use with physiochemistry explained most of the diversity variation across datasets, whereas environmental heterogeneity poorly explained diversity;

3) Pure land cover and pure physiochemistry generally explained some additional variation in the diversity components.

3) Determine if land use influences the relative roles of local assembly and the regional species pool in driving β-diversity.	Null models, Permutational ANOVA, Variance partitioning	The contribution of local assembly should be responsive to agricultural land use, however, the magnitude and direction of the response may vary across organismal groups.	1) The role of local assembly was generally weakly affected by land use, and not in a consistent way across datasets, suggesting a potential influence of organismal type and biogeography.

4) Determine if β-deviation (β_{DEV}) is explained by the species abundance distribution (SAD) or intraspecific spatial aggregation.	Null models, Permutational ANOVA	It is unknown how land use may influence the fractions of β_{DEV} explained by the SAD and intraspecific spatial aggregation.	1) The SAD was the dominant fraction of β_{DEV} and this pattern was independent of land use and organismal group. However, the SAD fraction was significantly higher in agriculture across all datasets, which may be the underlying factor of taxonomic homogenization; 2) Intraspecific spatial aggregation fraction was negative for agricultural streams and positive for forest streams, indicating that intraspecific aggregation was lower than expected across disturbed streams;

Table 2. Summary of the impact of agricultural land use on resampled diversity measures as positive or negative percent change relative to forest cover. Significant differences between land covers were detected in all comparisons (permutational MANOVA and ANOVA, $P < 0.05$).

Taxonomic group	Country	% Change from agriculture		
		$\bar{\alpha}$	γ	[1]β_{OBS}
Diatoms	US	+20.71	−3.54	−1.09
	France	+13.33	−7.46	−2.22
	Canada	−12.15	−23.14	−4.64
Insects	US	−20.42	−22.98	−0.59
Fish	US	+9.55	+12.97	−2.29
	France	+54.99	+26.91	−6.41

[1]$\beta\text{-diversity} = 1 - \dfrac{\bar{\alpha}}{\gamma}$

Figure 1. a. Conceptual model depicting the land use effect on the species abundance distribution (SAD) and intraspecific spatial aggregation, which in turn interact with local (α) and regional (γ) diversity. β-diversity is calculated as a function of average α-diversity and γ-diversity. Interactions that were controlled for by the null models of Kraft *et al.* (2011) and Xu *et al.* (2015) are marked with a thick dotted line. **b.** Diagram summarizing the Xu *et al.* (2015) partition of β_{DEV} into fractions explained by the SAD and intraspecific spatial aggregation using an occupancy-abundance based null model procedure. The null model β_{DEV} is taken as the raw difference between expected β-diversity (β_{EXP}) and observed β-diversity (β_{OBS}). The fraction of β_{DEV} explained by the SAD, β_{SAD}, is the difference between predicted β-diversity (β_{PRED}) and expected β-diversity (β_{EXP}), whereas the fraction of β_{DEV} explained by intraspecific aggregation (β_{AGG}) represents the difference between β_{OBS} and β_{PRED}.

Figure 2, a-f. Maps of diatom, macroinvertebrate, and fish sampling localities in the US, France, and Canada. Grey triangles represent agriculture samples, whereas black circles represent forest samples. a = US diatoms, b = US insects, c = US fish, d = French diatoms, e = French fish, f = Canadian diatoms.

Figure 3, a-f. Boxplots showing differences in resampled physicochemical heterogeneity between land covers for each dataset. a = US diatoms, b = French diatoms, c = Canadian diatoms, d = US insects, e = US fish, f = French fish. Points indicate resamples that fall outside

the interquartile range. Different letters denote significant differences in mean heterogeneity (permutational ANOVA, $P < 0.05$).

Figure 4, a-f. Boxplots of resampled SAD and null model metrics showing the differences between land covers for each dataset. a = US diatoms, b = French diatoms, c = Canadian diatoms, d = US insects, e = US fish, f = French fish. Significant differences were observed in all comparisons (permutational ANOVA, $P < 0.05$) except β_{DEV} for US insects (panel D3, denoted by asterisk).

Figure 5, a-f. Venn diagrams showing output of redundancy analysis-based variance partitioning of diversity measures ($\overline{\alpha}$-, β-, and γ-diversity). Values represent model adjusted R^2 values. Values in intersections represent covariance fractions, whereas values in circles represent pure fractions.
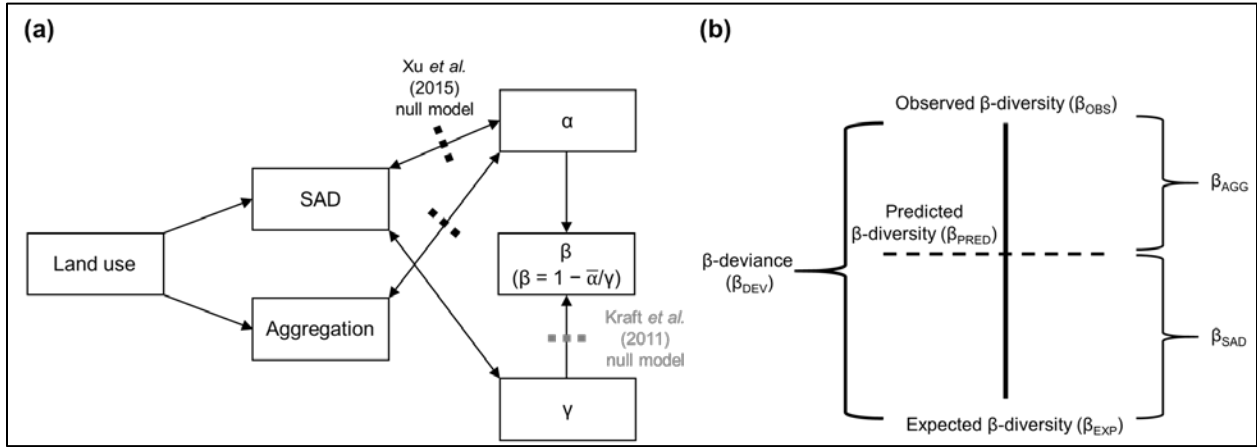
Figure 6, a-f. Venn diagrams showing output of regression-based variance partitioning of β_{DEV}. Values represent model adjusted R^2 values. Values in intersections represent covariance fractions whereas values in circles represent pure fractions.
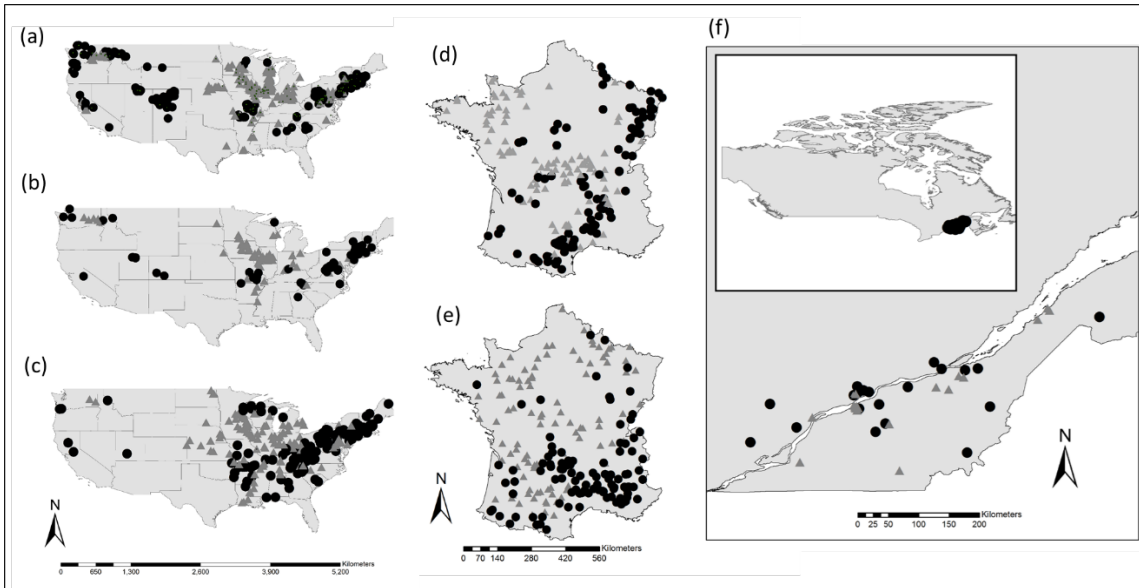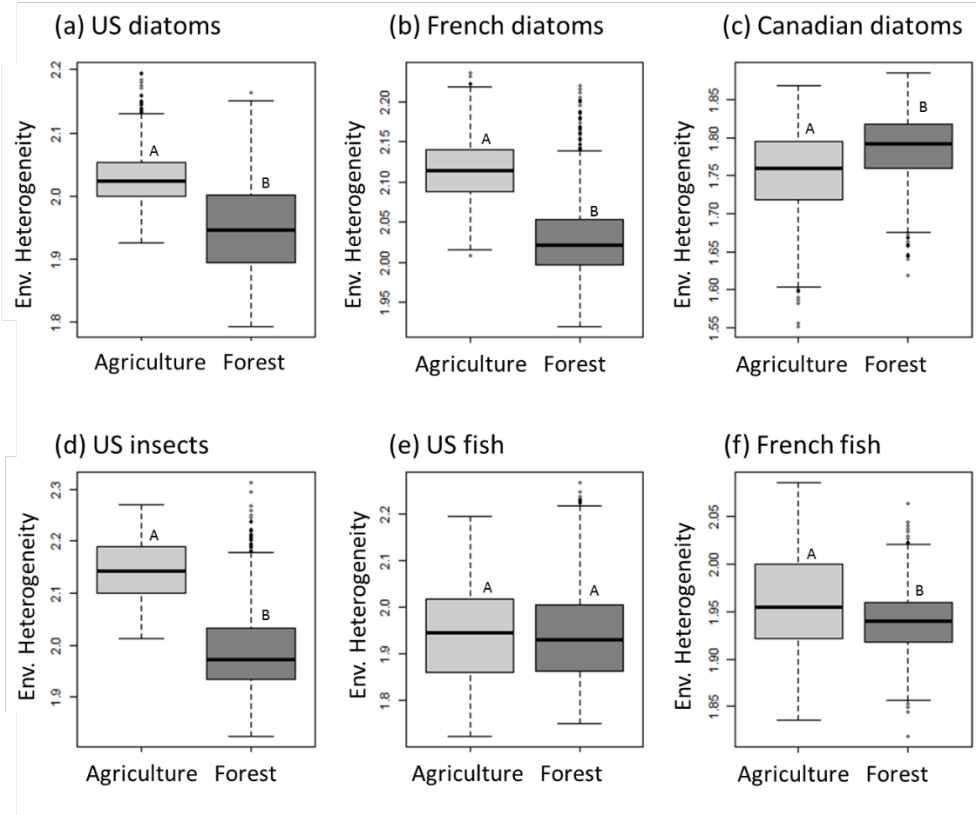
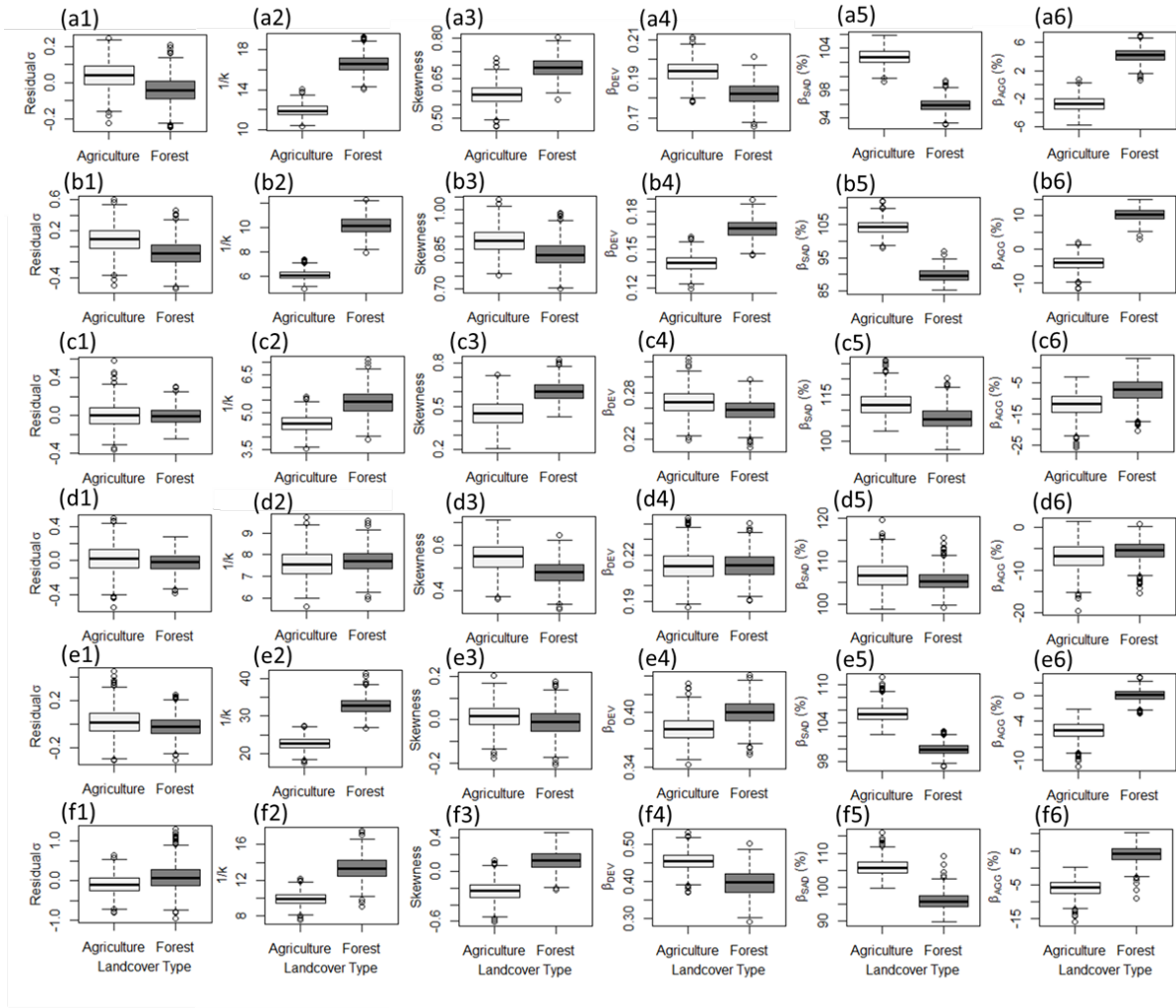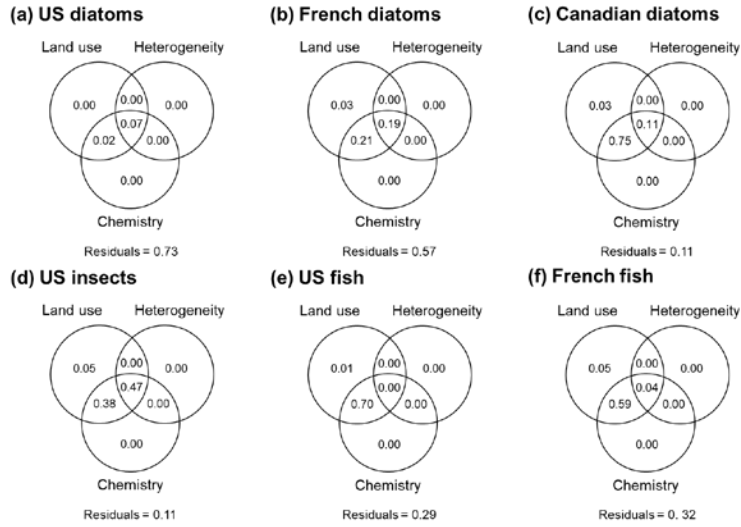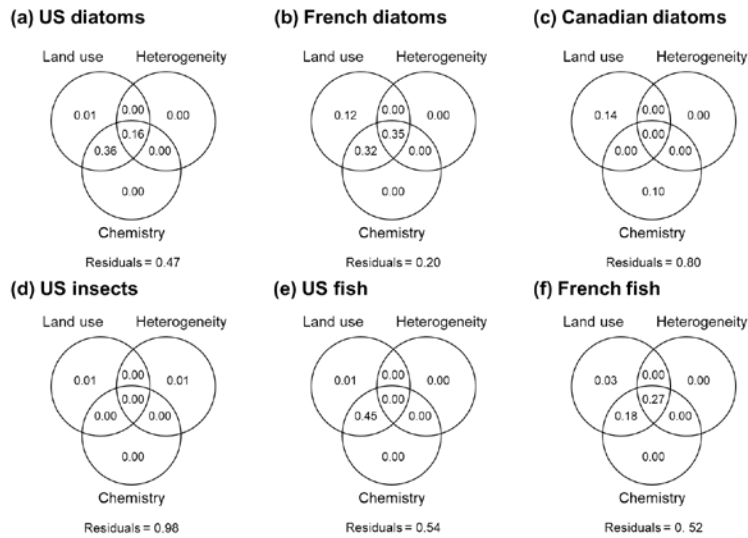# Figures

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

Supporting Information Appendix Short Titles

Appendix 1: Expanded description of environmental data and null model correlation results

Appendix 2: Description of Null Model Machinery

Appendix 3: R-code script for looping procedures

Appendix 4: R-code script for analyses of loop output