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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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Author Biosketch: William R. Budnick is a Ph.D. candidate studying macroecology at the University of Texas at Arlington. His primary research interests lie with the application of cutting-edge numerical and spatial techniques to study and predict how global change forces will affect macroecological patterns particular to aquatic ecosystems. His interests also include integrating basic ecological theory with fisheries science to assist with the global conservation of threatened fish and crayfish fauna.

1 **LOCAL AND REGIONAL DRIVERS OF TAXONOMIC HOMOGENIZATION IN STREAM**
2 **COMMUNITIES ALONG A LAND USE GRADIENT**

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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

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

45 **INTRODUCTION**

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

60 Land use effects on biodiversity occur across scales, operating either in a top-down or
61 bottom-up fashion or both (Flohre, Fischer, Aavik, Bengtsson, Berendse et al., 2011). Top-down
62 mechanisms function through the regional species pool (γ -diversity), which is a product of
63 speciation and extinction, large-scale dispersal, climate, and evolutionary, geological, and land
64 use history (Zobel, 2016). Bottom-up mechanisms include local-level assembly processes, e.g.
65 environmental filtering, interspecific interactions, and small-scale dispersal (Márquez & Kolasa,
66 2013), which constrain local (α) diversity and subsequently affect site-to-site community
67 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 $\geq 50\%$ 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}),

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

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 β_{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: β_{EXP} , β_{PRED} , β_{DEV} , β_{SAD} , β_{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 `RVAideMemoire` (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 $\bar{\alpha}$ -, 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 $\bar{\alpha}$ -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,

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

323 showed $\beta_{\text{SAD}} < 100\%$ 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 $\bar{\alpha}$ -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 $\bar{\alpha}$ -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

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 β_{DEV}*

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

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480 Foundation (grant NSF DEB-1745348) to SIP is gratefully acknowledged.

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-](https://www.epa.gov/national-aquatic-resource-surveys/data-national-aquatic-resource-surveys)
487 [resource-surveys](https://www.epa.gov/national-aquatic-resource-surveys/data-national-aquatic-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 $\bar{\alpha}$ -, 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 $\bar{\alpha}$ -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 physicochemistry 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.

<p>4) Determine if β-deviation (β_{DEV}) is explained by the species abundance distribution (SAD) or intraspecific spatial aggregation.</p>	<p>Null models, Permutational ANOVA</p>	<p>It is unknown how land use may influence the fractions of β_{DEV} explained by the SAD and intraspecific spatial aggregation.</p>	<p>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;</p> <p>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;</p>
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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	${}^1\beta_{\text{OBS}}$
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

$${}^1\beta\text{-diversity} = 1 - \frac{\bar{\alpha}}{\gamma}$$

FIGURE LEGENDS

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 ($\bar{\alpha}$ -, 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

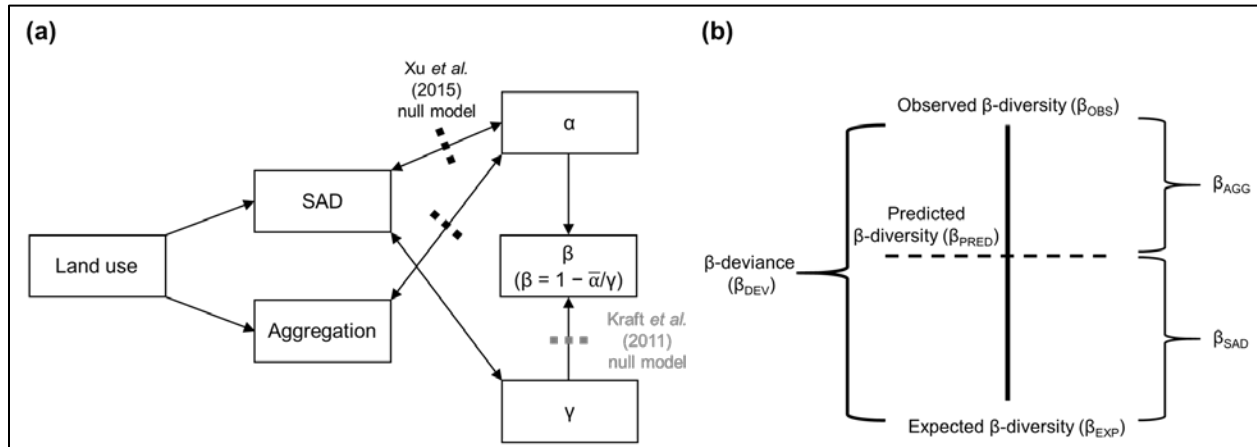


Figure 1

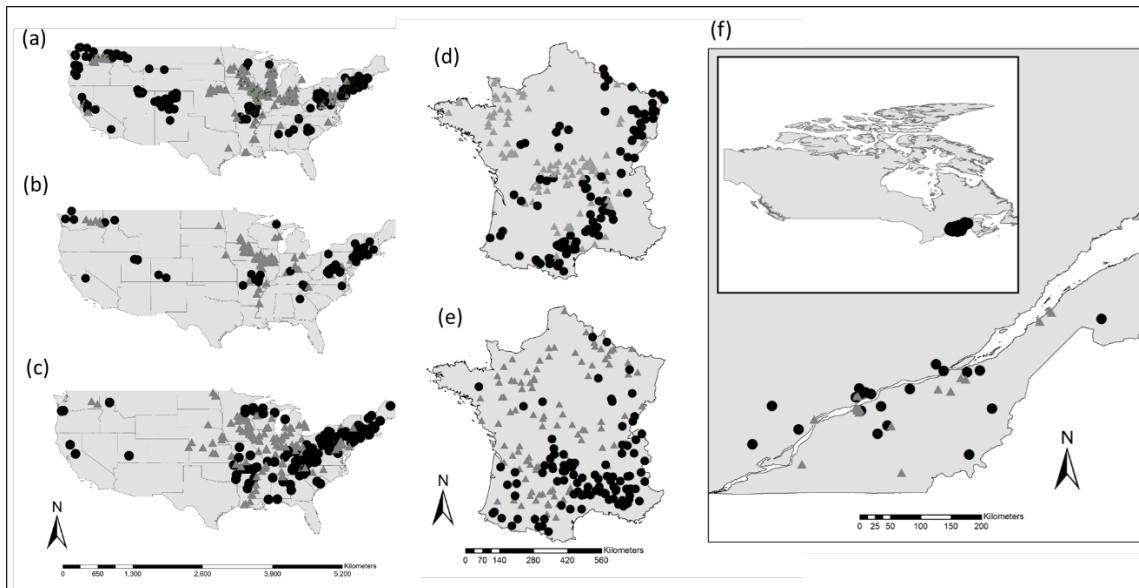


Figure 2

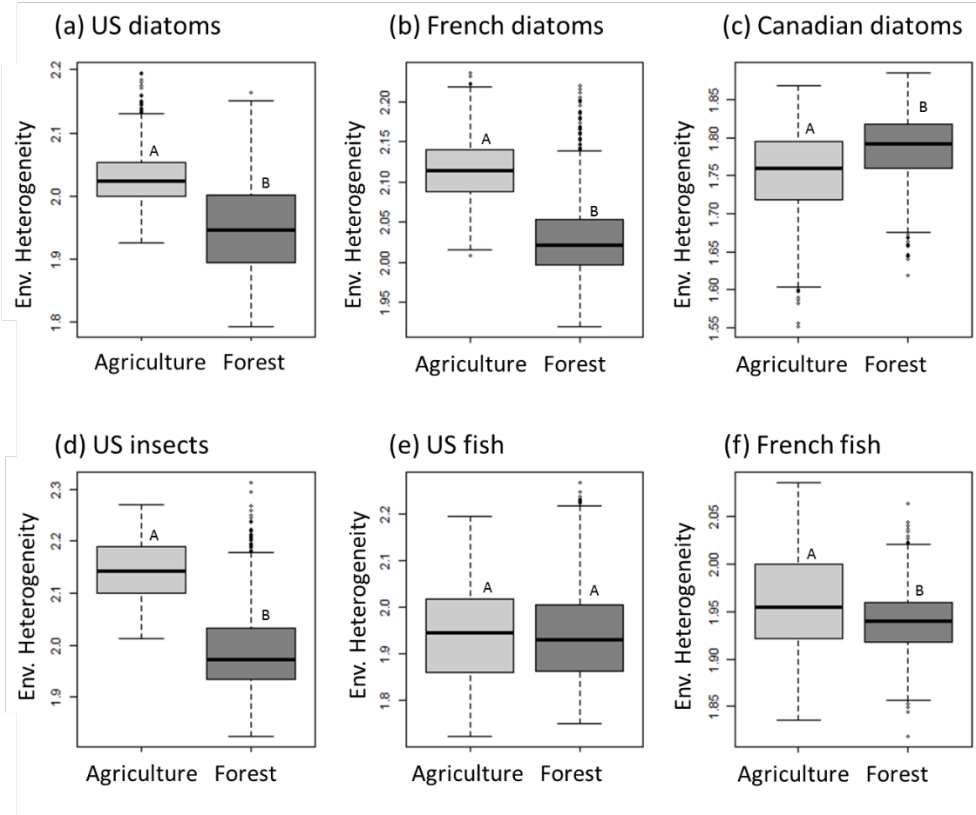


Figure 3

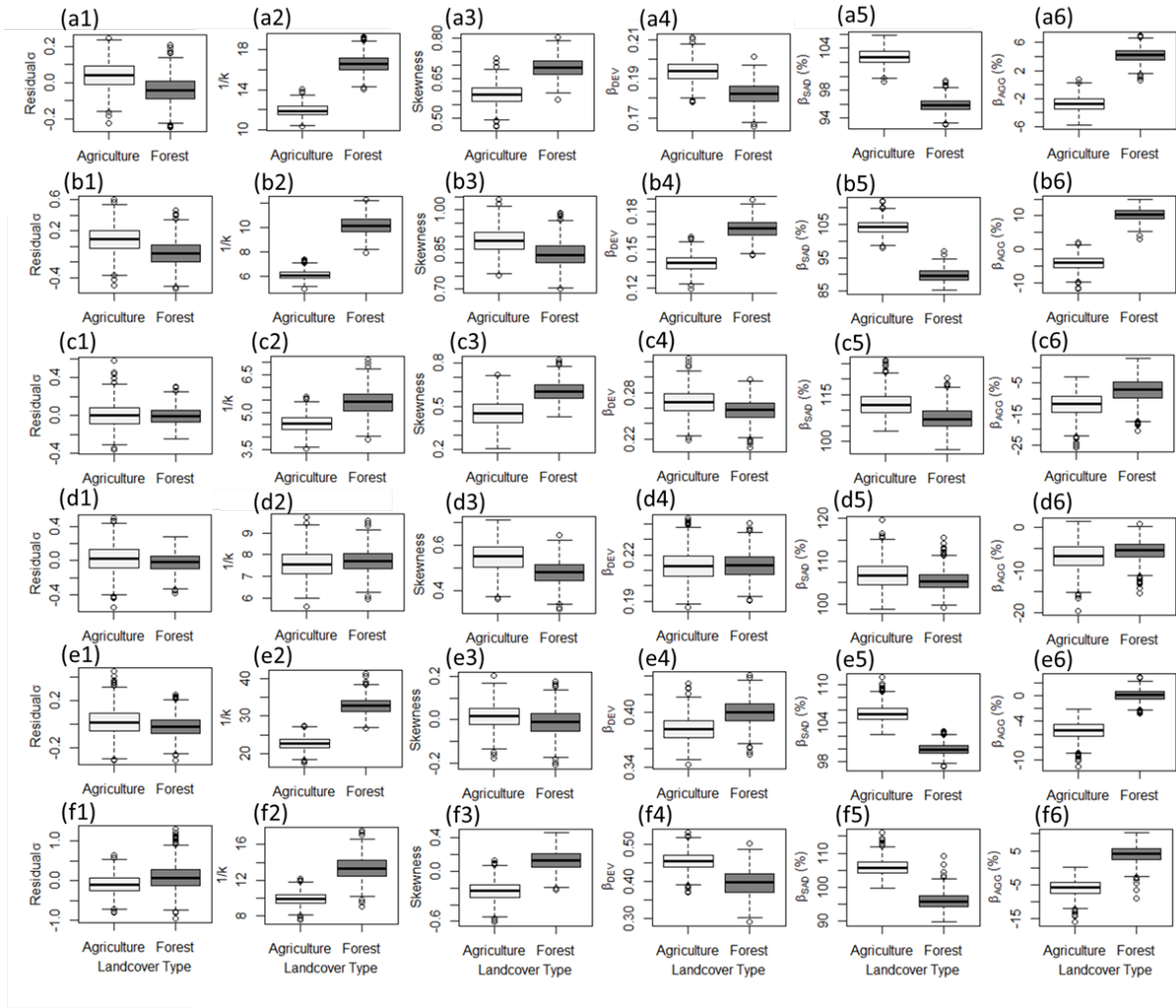


Figure 4

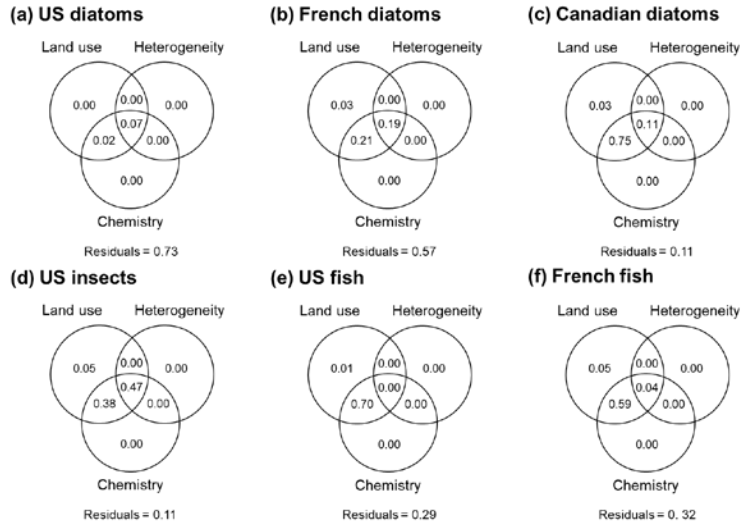


Figure 5

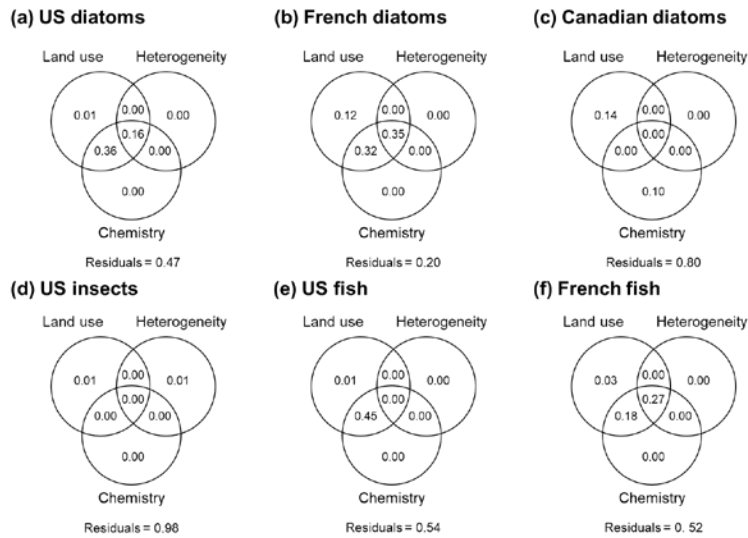


Figure 6

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