Meta-community processes supersede leaf subsidy effects on lake aquatic communities

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Abstract

There is a growing consensus that cross-ecosystem fluxes significantly influence the structure and stability of aquatic communities. What remains unclear, however, is the relative importance and potential interactions of those fluxes to/with other well-studied factors affecting aquatic community structure such as local environmental parameters or regional-scale influences related to connectivity or habitat size. In this study we compare those different hypotheses by investigating their individual and combined influence on the functional structure of littoral benthic invertebrates' communities in 7 temperate Canadian lakes (total of 23 sites) located in a semi-protected area. At each site, we sampled macro-invertebrates, we measured C, N, P content of both benthic litter and terrestrial leaves, and we recorded several standard local (pH, dissolved oxygen, turbidity, conductivity, temperature) and regional -scale (perimeter to area ratio, lake connectivity) parameters. We then used a combination of model selection and ordination approaches to disentangle the relative importance of local, regional, and cross-ecosystem factors and their interactions. When considered alone, we found that local factors related to water quality performed best at explaining variations macro-invertebrate community structure. When in combinations, models with both water quality and regional scale variables related to connectivity performed best. However, some functional groups like predator abundances were well correlated to C:N and N:P ratio in sediments (of terrestrial origin). Overall, those results suggest that if stoichiometry (i.e. nutritional quality) of particulate terrestrial subsidies can have some effects on lake benthic communities, local and regional factors still dominate in explaining invertebrate biodiversity patterns, at least in lakes without steep human land-use gradients. Closing knowledge gaps on cross-ecosystem subsidy effects is important to improve our understanding of how communities and functioning may change under human and/or climate driven changes in watersheds.

Introduction

It is becoming increasingly apparent that ecological systems, even distant ones, are linked to one another through a wide range of fluxes (Gounand et al. 2018; McCann et al. 2021; Polis, Anderson, and Holt 1997). From atmospheric deposition of particles, organic and inorganic nutrient diffusion to long range animal migrations, these exchanges of energy, matter and organisms mean that changes in a single system may propagate to adjacent systems (Gravel et al. 2010; Harvey, Gounand, Little, et al. 2017; McCann et al. 2021). Whether reciprocal, unidirectional, regular, asynchronous or asymmetric, these energy transfers can be major drivers of ecosystem function for the receiving systems (Gounand et al. 2020; Marcarelli et al. 2011; Richardson et Sato 2015; Yang et al. 2008). The meta-ecosystem framework is increasingly adopted by ecologists for its capacity to bridge important gaps in our understanding of the regulation of biodiversity and ecosystem function in space (Gounand, Harvey, Little, et al. 2017; Richardson et Sato 2015). However, many challenges remain in the application of those frameworks (Gounand, Harvey, Little, et al. 2017). Among those challenges, it is still unclear how important those cross-ecosystem exchanges are relative to other well-studied local and regional drivers of community structure. Past studies on meta-communities have focused on the relative importance of local (abiotic factors) versus regional (dispersal constraints) drivers among same type habitats (i.e., aquatic to aquatic, terrestrial to terrestrial, Gounand et al., 2017), while cross-ecosystem subsidy research has focused solely on isolating the effect of specific sources of subsidy among different habitat types (e.g., aquatic-terrestrial, for a review see Richardson & Sato, 2015). However, the ecological significance of cross-ecosystem subsidy is likely contingent on local and regional conditions (Collins et al. 2016; Zhang et Richardson

2011). Thus, developing an integrative understanding of when cross-ecosystem subsidies are ecologically relevant and by how much is essential to eventually predict how alterations to those pulse dynamics (via human-induced perturbations such as harvesting, mining or climate change - (Harvey, Gounand, Ward, et al. 2017) will propagate across ecosystem boundaries.

Freshwater ecosystems such as lakes are especially relevant to address those questions given the extensive amount of research previously done on the relative importance of local environmental filtering and regional scale factors in driving biodiversity patterns (for a review see Heino et al., 2021). Interestingly, despite past pioneer studies showing that coarse terrestrial carbon sources (leaf falls) could constitute a significant part of lake metabolism (France et Peters 1995; Gasith et Hosier 1976) and trophic energetic pathways (Cole et al. 2006; Scharnweber et al. 2014), a lot of the work on cross-ecosystem subsidy (excluding dissolved organic carbon, see Prairie, 2008) have focused on river ecosystems (Richardson et Sato 2015). Thus, there is a clear gap in our understanding of how sensitive lakes are to particulate cross-ecosystem subsidy (compared to rivers) and of how important those cross-ecosystem fluxes are relative to local and regional drivers. This knowledge is necessary to develop an accurate “meta-system” view of lake ecosystems (*sensu* Heino et al., 2021). Known for their sensibility to local abiotic factors, freshwater benthic macro-invertebrates are often used as proxies of water quality as their diversity and richness is linked to pH, dissolved oxygen saturation and other physico-chemical processes (Heino 2005; Jacobsen 2008). These organisms are also in close contact with terrestrial particulate organic matter (e.g. leaf litter) in aquatic systems and are key to the decomposition, recycling and integration of terrestrial carbon (Wetzel 2001), making them a suitable focal group for investigating terrestrial to aquatic linkages.

From an applied perspective, human activities such as logging or farming are modifying the exports of matter and energy from the terrestrial system to the aquatic system (Canham et al. 2004; Little et Altermatt 2018) and we know that these subsidies can modify community stability and productivity in streams (Wallace et al. 1997). Freshwater systems receive large quantities of low-quality subsidies from their terrestrial matrix, as dissolved organic carbon (DOC) and (to a lesser extent) as fallen leaves when in forested area. This important import of carbon drives up microbial production and ecosystem respiration rate (Marcarelli et al. 2011). Beyond purely quantitative effects, it has been proposed that the stoichiometry (i.e. nutritional value) of subsidies may also be an important factor in community structure and ecosystem functions (Bartels et al. 2012; Marcarelli et al. 2011; Sitters et al. 2015). While terrestrial carbon subsidies tend to push freshwater systems toward heterotrophy, it is unclear if the stoichiometry (or nutritive value) of allochthonous materials varies enough naturally to drive difference in community structure. It is likely that context-dependency in subsidy effects is caused by interactions occurring among factors acting at different scales (water quality and/or subsidy quality and/or spatial variables).

With this study, we aimed to untangle the effects of leaf subsidy quality (i.e. stoichiometric ratio of C, N and P) on community structure of lake littoral benthic invertebrates, its relative importance and its potential interactions with other factors such as environmental parameters, spatial connectivity, or habitat size. To achieve this, we compared models based on the competing hypotheses that A) subsidy quality drives community structure (classic ‘cross-ecosystem subsidy’ perspective), B) water quality drives community structure (local drivers), C) spatial parameters (regional drivers) drive community structure. We tested those competing views alone and in combination. Subsidy quality was characterized as sediment stock and leaf subsidy C:N and N:P ratios; water quality metrics included pH, Oxido-reduction potential (ORP), specific conductance, turbidity, and dissolved oxygen (DO); spatial parameters considered were perimeter to area ratio as a proxy of land to water linkages and lake connectivity within the watershed. Thus, our study integrates both cross-ecosystem subsidy and meta-community perspectives, which are usually studied independently (Gounand, Harvey, Little, et al. 2017) into a more explicit meta-ecosystem view. Based on the limited evidence available on the effect of particulate subsidy in lake ecosystems (France et Peters 1995; Gasith et Hosier 1976; Scharnweber et al. 2014), we expected that local and regional drivers would dominate, but that the inclusion of subsidy stoichiometry would significantly enhance the models and that higher nutritional value would lead to higher richness and diversity.

Methods

Site Location and Selection:

The sampling for this project was done at the University of Montreal’s research station in the meridional Laurentians mountains, approximately 75 kilometers north-west of Montreal. Sampling was done in 7 lakes with low human influence (mostly from research projects), during the spring (May) and summer (July) of 2021. During each campaign, 23 sites were sampled with 20 sites repeating in both sampling campaigns. Three sites sampled in spring were abandoned and replaced because of logistical difficulties. Prior to sampling, the area and perimeter of all lakes were measured using satellite imagery and Google Earth Pro (Google, LLC). To determine sampling effort, lakes were binned together based on their perimeter. Four size categories were generated. Smallest lakes were sampled at 2 different locations with larger lakes being sampled up to 5 times. Perimeter was chosen over area as a measure of size due to its closer relation to terrestrial subsidies and littoral habitats.

Sampling:

Sampling of invertebrates was based on the Ontario Benthos Biomonitoring Network's protocol (Jones et al. 2007). At every site, invertebrates were sampled in three 1.25m transects perpendicular to shoreline, using a rectangle 500 micrometer mesh hand-held net with a collection cup. Material captured by the net was transferred into sieves (2mm, 1mm and 0.5mm) and abundantly rinsed with water. Material caught by the wider mesh sieve (>2mm) was sorted on site using a white tray to increase contrast. Sorted invertebrates were preserved in 95% ethanol and stored in cool and dark containers. The remaining coarse material (i.e. coarse sediments sorted from the larger invertebrates) was kept in sealed plastic bags for stoichiometry analyses, some of these samples were sub-sampled as material volume was too big. The remainder of the net samples (0.5mm < 2mm, unsorted) were preserved in 95% ethanol, in a 1L container to be sorted later.

For each site, measures of water quality (i.e. pH, turbidity, conductivity, temperature ORP and dissolved oxygen) were taken using a YSI ProDSS handheld multiparameter probe (YSI Inc/Xylem Inc.). Three measures were taken at every site and averaged.

Each site was revisited in the Fall, after leaf fall, to sample fallen leaves. Three 0.25m^2 quadrats were deposited in the water upon arrival on site, on top of the collection transects, and leaves within the quadrats were collected and stored in sealed plastic bags. Only recognizable leaves were collected as we presumed these were only recently fallen onto the sites.

Processing samples:

The fine material (< 2mm) that was collected by the net was sorted using a stereoscopic microscope. The volume of material varied a lot ranging from around 200mL to over 1L. The sorting was limited to 150mL (randomly collected from the 1L container) for each site, to keep the task manageable while reducing size bias in the sample. Identification of invertebrates was done using *An Introduction to the Aquatic insects of North America* (Merritt, Cummins, et Berg 2009) and *Guide d'identification des principaux macroinvertébrés benthiques d'eaux douces du Québec* (Moisan 2010), as well as online resources such as www.macroinvertebrates.org for images and additional information on groups. Individuals were identified at the family level, except for Annelids that were identified at the phylum. The resulting dataset includes about 19 000 organisms divided into 79 taxonomic groups. We attributed each taxonomic group to one of seven functional groups (i.e. filterers, gatherers, macrophyte piercers, parasites, predators, scrapers and shredders) based on Merritt, Cummins and Berg 's grouping from *An Introduction to the Aquatic insects of North America,* with Annelids being ignored because of the higher degree of incertitude concerning their identification.

Stoichiometry:

To measure spatial variation in the quality of terrestrial subsidy, carbon, nitrogen and phosphorus content were extracted from i) coarse material sampled with the collection net (littoral sediment) and ii) leaves collected in the Fall. The coarse material sampled with the net served as a proxy of terrestrial (CN ratios all higher than 15; Ishiwatari & Uzaki, 1987; Prahl et al., 1994) resource stocks in the littoral zone, while freshly fallen leaves represented the yearly pulse of terrestrial resources.

Coarse (>2mm) material sorted on site was shredded before being freeze-dried and ground to a fine powder. Collected leaves were identified to the genus level (when possible) and dried in an oven at 40 Celsius for 12 hours. Dried leaves were then weighed before being grinded.

Carbon and Nitrogen content were measured by gas chromatography and electro-thermal detection using a Thermo Fisons EA1108 elemental analyser (Thermo Fisher Scientific, U.S.A).

Concentration of phosphorus was measured using a colorimetry method (Murphy et Riley 1962) on a solution of digested material (Wilson, Braithwaite, et Brian Pyatt 2005). Analysis was conducted using Environment Canada’s TH-2 Standard for phosphorus, with an average extraction efficiency of 88.6% ±0.73%.

Data analysis:

db-RDA Models

To untangle the effects of subsidy stoichiometry on spatial variations in community structure, we built several multivariate models to compare their fit. Explanatory variables were split into four categories. Each category was based on a generic hypothesis concerning determination of community structure. The first category included variables relating to the stoichiometry of the collected material (first hypothesis; cross-ecosystem subsidy), it included: C:N ratio of sediments, N:P ratio of sediments, C:N ratio of leaf subsidy, N:P ratio of leaf subsidy. The second category included variables relating to water quality (second main hypothesis; local parameters) captured by the multiparameter probe, it included : specific conductance (μS/cm), turbidity (FNU), pH, oxidation-reduction potential (ORP, mV), optical dissolved oxygen (ODO, mg/L). Category 3 (perimeter to area ratio) and 4 (lake degree connectivity) represented our third main hypothesis (spatial drivers) but they were split for conceptual clarity because they represent different spatial processes. Perimeter to area ratio is a proxy for lateral connectivity with the terrestrial matrix and relates to inputs of dissolved organic carbon from the watershed. Lake degree connectivity represents longitudinal connectivity among lakes and thus represents limitations in the exchange of organisms (dispersal) and matter. All possible combinations of one, two, three or all four categories were tested (n=15). All models included sampling season (Spring or Summer) to factor in the effect of time on community variations. All 15 models were compared using adjusted-R^2. Unlike with linear models, an Akaike Information Criterion score cannot be calculated on multivariate models. However, similarly to AIC, adjusted-R^2 imposes a penalty on each variable addition. Models were constructed using *vegan*'s *capscale()* function (Oksanen et al. 2022). A Hellinger transformation was applied to community data and explanatory variables were scaled and centered around means to make variables of different scales and units comparable. We used a bray-curtis dissimilarity to emphasize changes in community composition and relative abundances (Anderson et al. 2011). Ordination of these db-RDA models were done with weighted-average scores because these scores are less sensitive to environmental noises (Oksanen 2020) and scaling 2 was used to illustrate correlation between variables/vectors (Legendre and Legendre 2012).

Linear Models

Using the same methodology to construct models, we compared 15 linear models of species richness and Shannon-Wiener diversity index based on their AIC scores. We included a null linear model to this comparison.

Simple Regressions

To further investigate apparent correlations shown by the db-RDA ordination, we constructed simple linear regressions of vectors that had similar direction (angles between vectors reflect correlation in ordination scaling 2 (Legendre & Legendre, 2012).

Results

Our primary objective was to disentangle the relative influence of meta-ecosystem (i.e. cross-ecosystem subsidy) and meta-community (i.e. local and regional) drivers on community structure and biodiversity. The results from our multivariate model comparison indicated that the model including all parameters was the best and most parsimonious at explaining variations in community structure (adj.-R^2= 0.644, see Table 1). When looking at one-way models, the model including only variables related to local water quality performed the best (adj.-R^2 = 0.330, which corresponds to more than half of the explained variance by the full model). Among the different model comparisons, any models combining local water quality and regional connectivity variables performed better than models excluding either (Table 1). Models with terrestrial subsidy attributes explained less community variation than other models, except when in combination with water quality and connectivity metrics. Our results showed evidence of interactions among parameter sets. For instance, the adj.-R^2 of the two-way models including water quality and terrestrial subsidy stoichiometric variables did not correspond to the sum of the corresponding one-way models, suggesting that the effect of terrestrial subsidy varies depending on local water quality attributes (Table 1).

Figure 1 presents the ordination for the best model, combining all variables. Overall, a centroid-to-centroid permutation analysis revealed that lakes differed significantly in functional group composition (F=4.2196, p-value=0.0001), but had similar intra-group variance (no difference in beta-diversity, F=1.1592, p-value=0.3494). A marginal test of significance on the db-RDA (at p=0.05) identified perimeter to area ratio, lake connectivity, specific conductance, turbidity and sediments N:P ratio to be the most important variables to the model. The ordination showed several apparent correlations between functional groups abundance and explanatory variables that we further tested with linear regression analyses. Among these, scrapers abundance increased with increasing specific conductance (R^2=0.48, Figure 2); predator abundance declined with higher C:N ratios (R^2=0.29, Figure 2, middle panel); and gatherer abundance declined with increasing pH (R^2=0.24, Figure 2 bottom panel). Phosphorus concentrations were excluded from the db-RDA analysis due to collinearity concerns, but nonetheless it had significant influences on some functional group abundances. Notably its concentration in sediments was positively correlated to predator abundance (R^2=0.44) and shredder abundance (R^2=0.12). Interestingly its concentration in sediments (positive relation, R^2=0.3) and leaves (negative relation, R^2=0.11) had opposite effects on gatherer abundance (see Appendix S1, Figure S1).

All linear models of macro-invertebrate species richness (range = 6 to 26 species) scored similarly or above the null model. (as expressed by AICc, see Table 1). Therefore, none of the considered variables seemed to have any effect on species richness. On the other hand, variation of diversity indexes (range = 0 :4.37, the latter being the theoretical maximum since 79 taxonomic groups were considered) was best explained by a two-way model. The best model combined water quality related factors and lateral connectivity (perimeter to area ratio). Adding stoichiometry of terrestrial subsidies did not enhance the model fit. Analysis of variance showed perimeter to area ratio, turbidity and pH be the significant terms.

Discussion

Our main objective was to disentangle the relative influence of cross-ecosystem subsidy and meta-community related drivers on lake macroinvertebrates community structure and biodiversity. Comparison of multivariate models showed that, when considered separately, local water quality best predicted macro-invertebrate community structure. Nutritional quality of subsidies and spatial variables, on their own, explained significantly less variation. However, adding among-lake connectivity to water quality led to an important gain in explanatory power (adj.-R^2 of 0.470 vs. 0.330), suggesting that longitudinal connectivity can interact with local water quality in driving benthic community structure. The addition of both spatial variables (longitudinal and lateral connectivity) leads to an even greater gain in explanatory power (adj.-R^2=0.533). The inclusion of terrestrial material nutritional quality in the models did increase predictive power marginally (adj.-R2=0.354 vs. adj.-R2=0.330). Nutritional quality of leaf subsidy does seem to affect species abundances and community structure to some degree, but the increase in predictive power is especially important when also including longitudinal connectivity (adj.-R^2=0.567). The complete model, including all variables, scored the highest adjusted-R^2 (0.644). Marginal testing of its variables indicates that among-lake connectivity (longitudinal connectivity) and lake perimeter to area ratio (lateral connectivity) were among the most important variables. These regional factors scored lowest when considered alone, but this result underlines the interacting influence of spatial drivers on local ones and highlights the importance of considering space in studying communities (and meta-communities), and especially their interacting influence.

The ordination of the best model showed interesting correlation between specific functional group abundances and variables relating to nutritional quality, local and regional drivers. Specifically, the abundance of scrapers was correlated with water conductance (simple linear regression with a R^2 of 0.48, see Figure 2), which is probably related to the presence of calcium (Ca, among other ions) necessary to snails (the most abundant scraper organisms) for their shells. The abundance of predators was negatively correlated to the C:N and N:P ratio of sediments (a proxy of subsidy accumulation) ($R^2 = 0.29$ and 0.25 respectively, see Figure 2), but positively correlated to phosphorus concentration ($R^2=0.44$, see Appendix). This is interesting because predators do not feed directly off this material, therefore this supports the idea that terrestrial subsidy quality can drive bottom-up trophic cascades (Bartels et al. 2012; Polis et Strong 1996). Results also show that gatherer abundances were negatively associated with pH ($R^2=0.24$, see Figure 2) and concentration of phosphorus in leaves (fresh subsidy, $R^2=0.11$, see Appendix), but positively associated with phosphorus concentration in sediments ($R^2=0.3$, see Appendix). This result could suggest that fresh material does not follow the same energy pathway as sediment material. It would be in line with a recent study showing that initial phosphorus excretion in leaf subsidy mainly feeds the plankton loop (Hirama et al. 2022). Shredder abundances were negatively associated with phosphorus content of sediments ($R^2=0.12$, see Appendix). Overall, our results suggest that subsidy nutritional quality influences the structure of the community by affecting the abundance of specific functional groups. Our study was done in a relatively homogeneous protected area representing a sort of baseline variation and effects of leaf subsidy on communities. Those influences on specific functional groups suggest that perturbations leading to abrupt changes in subsidy quality could potentially lead to more noticeable changes in community structure.

The comparison of linear models of diversity index also shows that water quality and spatial parameters seem of great importance. The best fit (as suggested by AICc) was obtained with the model combining water quality metrics with lateral connectivity. Contrary to our initial hypothesis, we found no relation to species richness and therefore variation in diversity index score seems mostly driven by changes in evenness. As with the multivariate models, the exclusion of local water quality metric significantly lowers model fit. Although regional drivers and to some extent terrestrial subsidy nutritional quality can modify community structure, these results suggest that local drivers are essential to the determination of community.

Our results indicate that natural variation of leaf subsidies stoichiometry is not big enough to drive major differences in macroinvertebrate community structure, in lakes. While terrestrial subsidy nutritional quality did appear to impact community structure as it was correlated to some groups' abundance and increased predictive power of db-RDA models of community structure, the effect of local water quality and spatial connectivity (lateral or longitudinal) supersedes the influence of terrestrial particulate organic matter stoichiometry. Possibly, insects’ dispersion and colonization occur independently from ecosystems subsidy dynamics, and therefore terrestrial leaf nutritional quality would influence communities only after their initial establishment from egg deposition. Hence it appears to modulate groups' abundance and community structure mostly through evenness. All sites were adjacent to forested shorelines and within watersheds dominated by forest cover. Therefore, none of the variation is linked to changes in land-usage. Introduction or exclusion of new tree species through species distribution shifts northwards (Chen et al. 2011) or human intervention may lead to greater variation in riparian plant communities. Whether this would lead to greater variation in benthic communities would need to be investigated, but the results showed here suggest it could be the case. This also has implications for restoration projects targeting riparian habitats, as it suggests the choice of plants used to revegetate will impact functional groups of benthic communities adjacent to these sites. Overall, our results illustrate well the need for more empirical tests of the meta-ecosystem concept and the potential context-dependency of cross-ecosystem subsidy effects on community structure and functioning. This is essential to developing an integrative biodiversity and ecosystem function management framework at landscape extent.

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Authors contributions

GEH and EH designed the research project, GEH conducted the field work, conducted data processing and statistical analyses with support from EH and wrote the first draft of the manuscript. Both authors contributed to further manuscript revisions.

Conflict of interest statement

Authors do not have any conflict of interest to declare.

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Tables

Table 1: Comparison of multivariate and linear models. Comparison is based either on their Adjusted-R^2 or their second order Akaike Information Criterion Score. For all three model types, the better model's score is framed by a black box.

Models	Comparative Criteria	0.Null	1.Terrestrial	2.Water Quality	3.Lateral Connectivity	4.Longitudinal Connectivity	5.Terrestrial + Water	6.Terrestrial + Lat. Co	7.Terrestrial + Lon. Co.	8.Water + Lat. Co.	9.Water + Lon. Co.	10.Lat. Con. + Lon. Co.	11.Terr. + Water + Lat. Co.	12.Terr. + Water + Lon. Co.	13.Terr. + Lat. Co. +Lon. Co.	14.Water + Lat. Co. +Lon. Co.	15.Complete
db-RDA, Funct.Gps.	R^2-ajd.	NA	0.140	0.330	0.059	0.123	0.354	0.161	0.304	0.345	0.470	0.179	0.385	0.567	0.351	0.533	0.644
Linear, Richness	AICc	243.0	247.4	248.2	244.5	245.4	259.4	250.4	250.4	250.9	251.2	246.5	263.4	263.5	253.1	254.3	267.9
Linear, Diversity	AICc	30.8	30.2	28.6	29.4	33.7	31.8	32.3	32.2	23.7	26.6	31.7	30.1	27.7	35.3	26.6	31.7

Figure Captions

Figure 1: Ordination of sites community structure, db-RDA model (Adjusted-R^2=0.644). This ordination uses weighted-average scores and scaling 2. It shows sites distanced by their community composition and related to 12 explanatory variables (complete model). Sites were clustered in 7 groups showing the seven lakes that were sampled for this project. Sites were sampled for invertebrates in spring 2021 (n=20) and again in summer 2021 (n=23), each point representing a single invertebrate sample (n=43).

Figure 2: Simple regressions showing linear relations suggested from vectors association of the db-RDA ordination. Top panel shows a strong linear relationship between scraper abundance and specific conductance. Middle panel shows strong linear relationships between predator abundance and nutritional quality of sediments (terrestrial subsidy stock). In red, regression and R^2 for C:N ratio. In blue, regression and R^2 for N:P ratio. Bottom panel shows a good linear relationship of gatherer abundance with pH.

Figure 3: Simple linear regressions of Shannon-Wiener diversity index in relation with the significant variables from the linear model scoring the lowest AIC. Top graph shows the relation of the diversity index with pH (water quality). Middle panel shows the relation between diversity index and turbidity (water quality). Bottom panel shows the relation between diversity index score and lateral connectivity (perimeter to area ratio).

Figures

Figure 1:

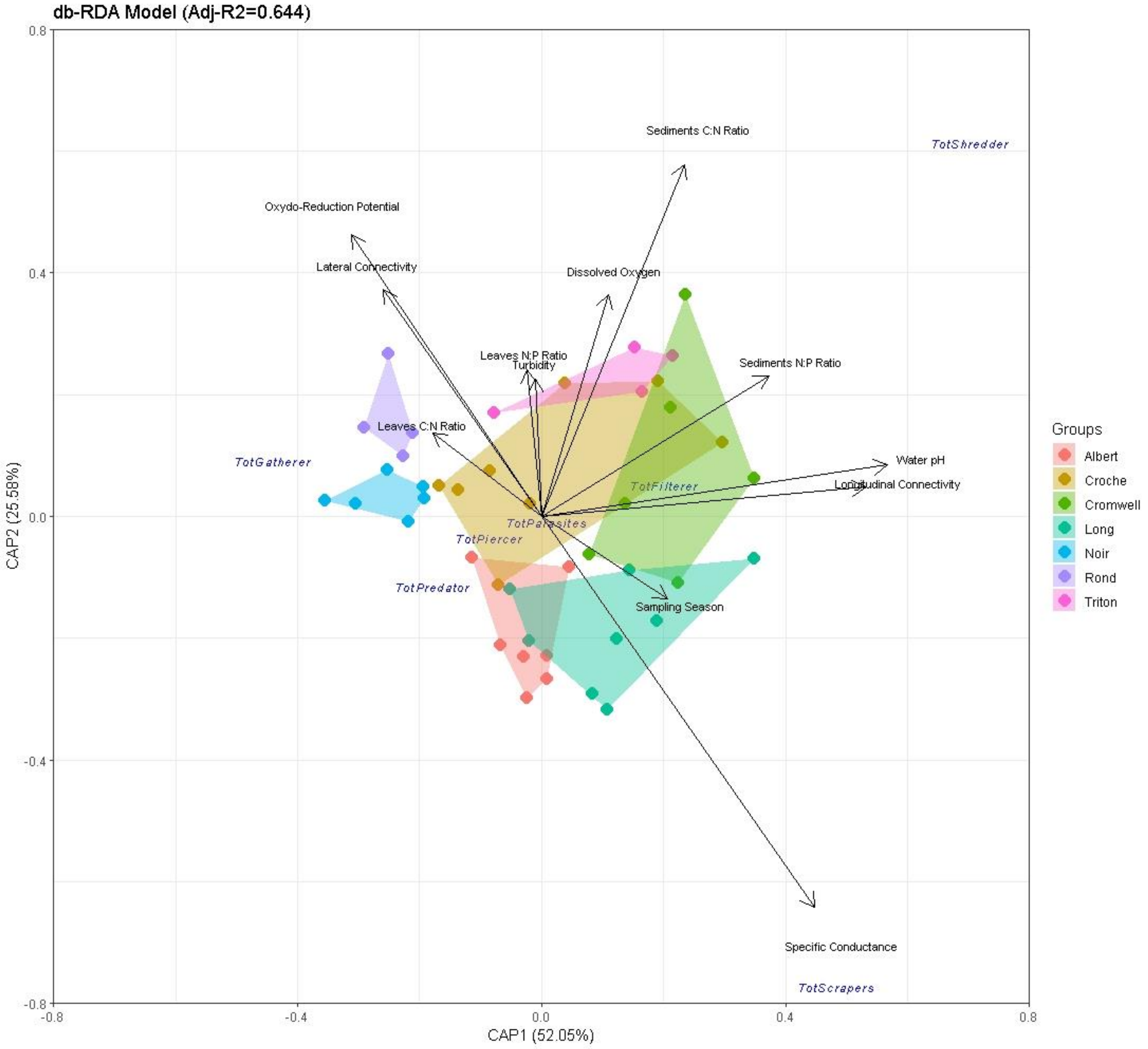


Figure 2:

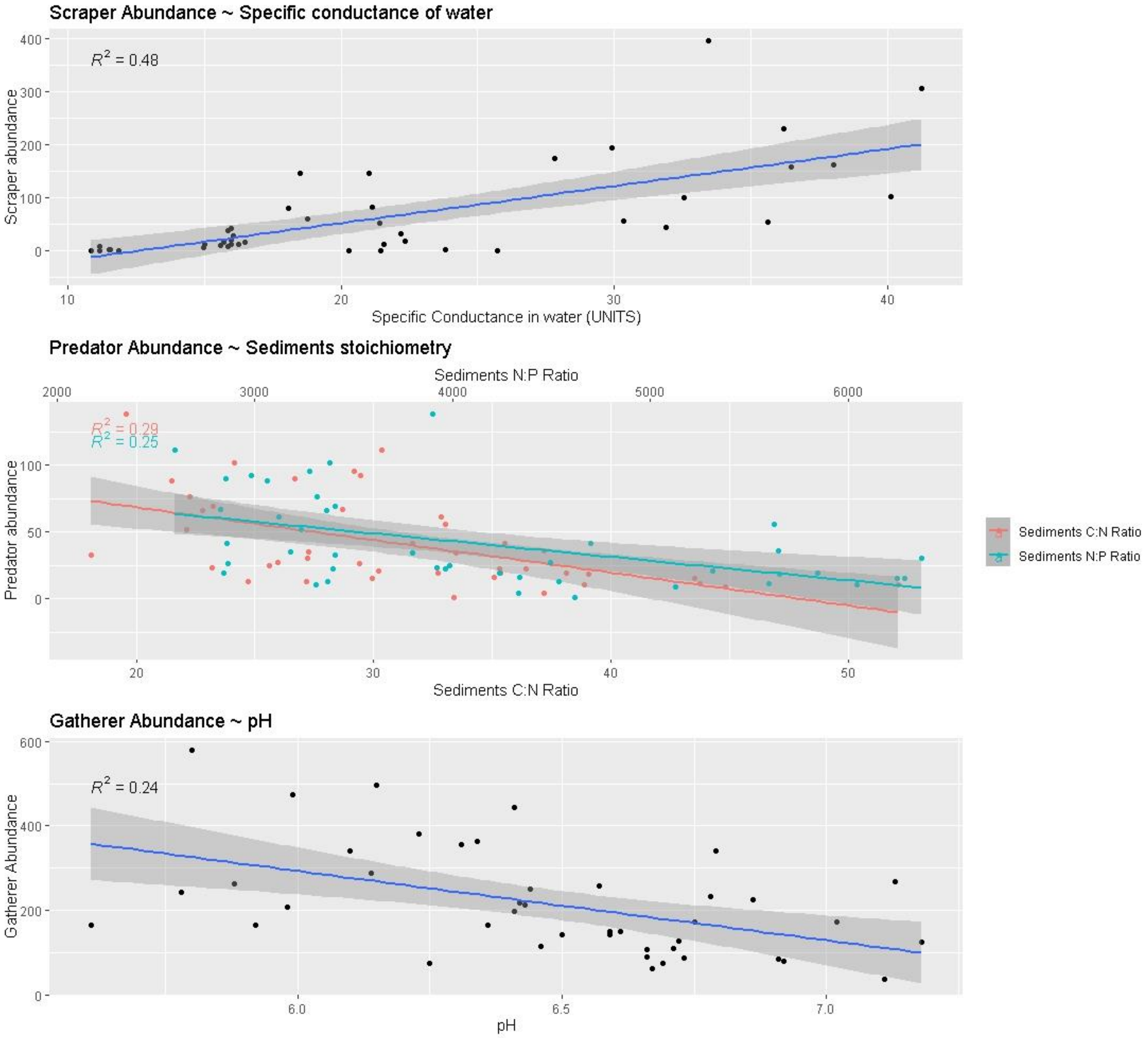
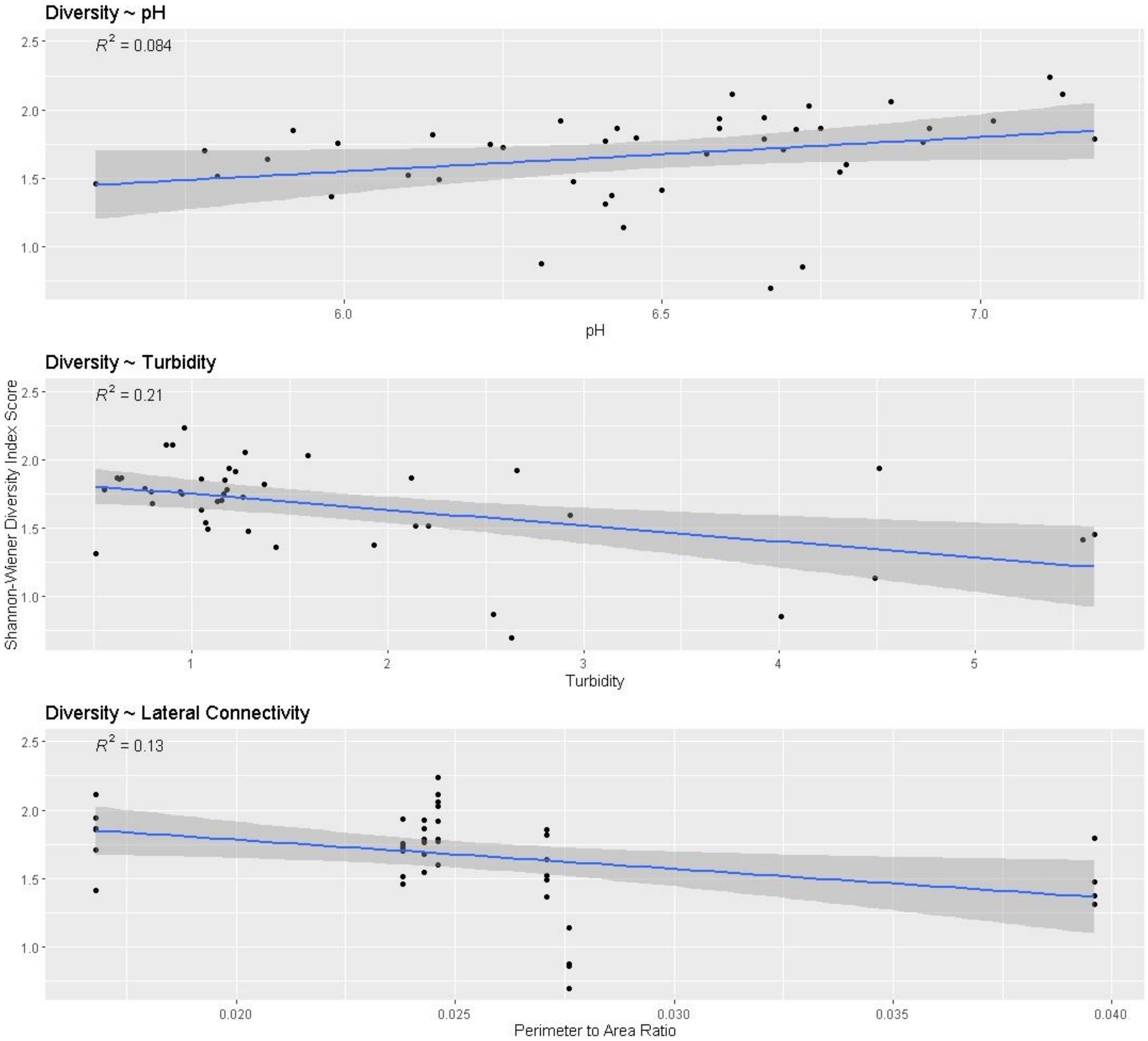

Scraper Abundance ~ Specific conductance of water
R^2 = 0.48
Scraper abundance
400
300
200
100
0
10
20
30
40
Specific Conductance in water (UNITS)
Predator Abundance ~ Sediments stoichiometry
Sediments N:P Ratio
2000
3000
4000
5000
6000
R^2 = 0.29
R^2 = 0.25
Predator abundance
100
50
0
20
30
40
50
Sediments C:N Ratio
Sediments C:N Ratio
Sediments N:P Ratio
Gatherer Abundance ~ pH
R^2 = 0.24
Gatherer Abundance
600
400
200
0
6.0
6.5
7.0
pH

Figure 3:


Diversity ~ pH
R^2 = 0.084
2.5
2.0
1.5
1.0
6.0
6.5
7.0
pH
Diversity ~ Turbidity
R^2 = 0.21
Shannon-Wiener Diversity Index Score
2.5
2.0
1.5
1.0
1
2
3
4
5
Turbidity
Diversity ~ Lateral Connectivity
R^2 = 0.13
2.5
2.0
1.5
1.0
0.020
0.025
0.030
0.035
0.040
Perimeter to Area Ratio