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Title: Cladoceran diversity dynamics in lakes from a northern mining region: responses to multiple stressors characterized by alpha and beta diversity

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Abstract

The lakes surrounding the iron-ore mining region of Schefferville, Québec, Canada sit within a landscape of historical disturbances, two of which have been relatively well documented over time: metal contamination and nutrient loading. Based on the analysis of sediment cores, we used cladoceran zooplankton subfossil assemblages from two lakes located in Schefferville to track both alpha and beta diversity over the last 100+ years. We showed that high metal concentrations were correlated with decreased cladoceran diversity and that the site that experienced both direct wastewater input and atmospheric metal loading (Lake Dauriat) had the greatest declines in cladoceran richness. In both lakes, turnover in cladoceran assemblages was highest in the mining period. During the period of mine closures and improvement of wastewater treatment, some decreases in metal enrichment in the sediments and increases in cladoceran richness were observed in Lake Dauriat. Overall, a combined use of species richness and beta diversity metrics showed alpha and beta diversity are not always congruent and that there are various ways to interpret scenarios of temporal beta diversity in northern freshwater systems.

Keywords: beta diversity, biodiversity, Cladocera, mining, paleolimnology, pollution

Introduction

Perturbation of freshwater systems is of general concern because of their importance in providing ecosystem services (Limburg 2009), their role as biodiversity hotspots (Strayer and Dudgeon 2010), and the global prevalence of water insecurity (Vörösmarty et al. 2010). Many studies have addressed how ecological communities have undergone discrete changes in response to anthropogenic stressors (e.g., pre- and post- industrialisation comparison using historical and surface sediments in the field of paleolimnology; Dixit et al. 1999); however, it is also important to understand the processes by which communities change and the degree of temporal species turnover. While many investigators have analysed alpha diversity trends (often measured as the number of species, or richness, in each lake), beta diversity is emerging as a more sensitive diversity metric as it characterizes the degree of change in species composition that may occur even without changes in the total number of species present. Of studies that have addressed alpha diversity responses to multiple stressors (e.g. Heugens et al. 2001), the impacts of multiple disturbances on local biodiversity patterns are often context-dependant, varying by the types of stressor and the local setting. For example, Yan et al. (2004) observed differential diversity responses in zooplankton communities across sites that were exposed to distinct combinations of metal contamination and acidification. Recent studies applying beta diversity metrics to evaluate responses to multiple stressors in aquatic systems have shown great insight. An illustrative example was conducted by Passy and Blanchet (2007) who examined algal community beta diversity responses to anthropogenic impacts (habitat degradation) and showed that spatial beta diversity was lower in degraded systems than in more pristine systems.

The mining region surrounding Schefferville, Québec (Canada) has experienced an intense history of multiple stressors, through iron-ore mining and the development of associated

infrastructure. While many mining regions around the world have experienced large-scale acidification of their surface water bodies (such as the well-studied nickel mining region of Sudbury-Killarney; Dillon et al. 1987), the sedimentary rock geology of the Labrador Trough has prevented acidification of aquatic systems around Schefferville (Aebischer et al. 2013; Aebischer et al. 2015). The sedimentary rock acts like a buffer, helping to neutralize the acidic effect that mining emissions would normally have on water bodies. Therefore, Schefferville presents a relatively unique system for studying the long-term impacts of metal and nutrient contamination in the North, in the absence of acidification. However, the town of Schefferville is similar to many other communities developed around extractive industries, where the infrastructure needed to manage town and (in some cases) industrial wastewater has not necessarily kept pace with its rapid development. Indeed, wastewater treatment facilities were not installed in Schefferville until 1975, despite the founding of the town site in the early 1950s (Adams 2007; Aebischer et al. 2015). Increased nutrient and metal inputs have varied through time and across the Schefferville landscape (especially between the lakes within the town), arising not only from mining sites, but also from commercial infrastructure and residential development to support the mining sector (Laprire et al. 2008; Aebischer et al. 2015).

Laprire et al. (2008) were among the first to demonstrate an effect of mining and mining-related development on the aquatic structure and diversity of Lake Dauriat (previously named Lake Pearce). Their study emphasized that, while the majority of mining activities occurred between the mid-1950s and late 1970s, the legacy effects of these activities were still occurring in Lake Dauriat, more than 20 years later. For the Schefferville region, long-term effects are important to consider, as there was a resurgence of various mining activities in 2009 and 2011, though mining activities have presently slowed again in this region. As such, these

focal lakes provide an opportunity to better understand the effects of metal pollution and increased nutrient inputs on cladoceran diversity in a boreal mining region, without the compounding effect of acidification; especially as the interactions of stressors may be lessened when one stressor has an omnibus effect (such as pH) (Burton and Johnston 2010).

Our study aims to quantify temporal and spatial patterns of alpha- and beta-diversity of cladoceran zooplankton in response to historical metal and nutrient disturbance in the Canadian boreal subarctic (Schefferville, QC, Canada). To do this, we focused on two lakes with different ecological histories with respect to metal contamination and nutrient loading. While one lake experiences only metal loading from atmospheric sources (Lake Knob), the other lake received both metals and nutrients via untreated wastewater loading (Lake Dauriat). The goals of our study were to: 1) characterize the effect of metal contamination on cladoceran species richness and composition in the presence and absence of anthropogenic eutrophication, and 2) examine the extent to which patterns in cladoceran community species richness through time are congruent or not with temporal beta diversity. We hypothesized that metal loading would decrease cladoceran species richness in these lakes as metal-sensitive species are pushed toward tolerance limits and owing to direct toxicity effects. However, there could be site-specific differences in cladoceran responses because the study lakes vary in their metal and nutrient loading histories. For example, greater water column production as a result of enhanced nutrient loading could lessen the impact of metal contamination as cladocerans would have access to more food and the concentration of metals adsorbed onto any one phytoplankton cell would be diluted (Pickhardt et al. 2002). Additionally, the examination of temporal beta diversity (i.e. the turnover in assemblages, measured over multiple time points in a sediment record) to quantify

cladoceran responses to mining has the potential to help us understand different scenarios under which alpha and beta diversity patterns could be congruent.

Methods

Description of study site and field sampling

The Labrador Trough region, which straddles Québec and Labrador (Fig. 1a), has long been part of the traditional territory of both the Naskapi and Innu (Innu-Montagnais) peoples (Boutet 2012). The Iron Ore Company of Canada (IOC) began ramping up mining operations between 1939 and 1947 (Laperrière et al. 2008; Aebischer et al. 2015) and the town of Schefferville was built in 1954 by the IOC. The first official shutdown of mining operations occurred between 1977 and 1982 (Laperrière et al. 2008; Aebischer et al. 2015). A timeline of both town development and mining activities in the region is shown in S1.

Our two study lakes, Lake Dauriat and Lake Knob, are situated within the town site of Schefferville (Fig. 1b; Table 1). Lake Knob is upstream (southeast) of the town site and serves as the drinking water source for Schefferville. A small outflow from Lake Knob connects it to Lake Dauriat, which is situated northwest and downstream of the town site. Lake Dauriat received raw sewage effluent from the town from its inception until 1975 when a water treatment plant was built, and continues to receive both treated wastewater and surface runoff during rain events (note that historical records of sewage discharge volumes are not available). Laperrière et al. (2008) used sediment cores from Lake Dauriat in the centre of Schefferville to show paleolimnological evidence for negative effects of both mining activities and the discharge of sewage directly into this ecosystem. They found pronounced changes in diatom community composition and increases in diatom-inferred total phosphorus (DITP) from the 1940s to late

1970s (which partly overlapped a monitoring record from the lake (Choulik & Moore 1991)), followed by partial recovery.

Based on analyses of epiphytic lichens growing on trees in the area, as well as sediment cores taken from Lake Dauriat and a lake farther from the town (Lake Oksana), Aebischer et al. (2015) showed that the concentration of Pb decreases linearly (and significantly) with increased distance from both the Schefferville town site and active mining sites. This work demonstrated that lakes have received significant metal loading from both mining projects as well as the town itself, in addition to a background loading of elements like Pb from distant sources via atmospheric deposition (e.g. leaded gasoline in the past, distant smelter activities). Furthermore, this same study used variation in stable isotope ratios for lead, iron and zinc to delineate separate sources of metal loading to the Schefferville lakes. They found four distinct sources of metal loading (for Pb, Fe and Zn) to the lakes: geogenic (occurring prior to mining in this region), town development (corresponding to the mining period), town development after the mining period (which though was also related to town development, had a distinct signature from that of development during the mining period), and long distance atmospheric transport. Note that the last source provides important information about metal loading sources in the region, in the absence of a full understanding of wind regime.

Field sampling occurred between 24-30 July 2012 and 4-14 September 2013. In July 2012, we collected an approximately 40 cm long (diameter = 6.5 cm) sediment core from both Lakes Dauriat and Knob using a Maxi-Glew gravity corer, at the deepest observed part of each lake. We sectioned these cores at 0.25 cm intervals and froze these samples for transport back to the laboratory. The use of 0.25 cm intervals is common practice in paleolimnology (Smol 1992) and especially in studies from northern systems due to relatively lower sedimentation rate than

temperate systems. In September 2013, we used a gravity corer to collect a sediment core from the centre (observed $Z_{\max}$). These cores were sectioned at 2 cm intervals and frozen. The 2012 cores were used for radiometric dating, heavy metal geochemistry and isolation and enumeration of cladoceran subfossils. The 2013 cores were used for the isolation and enumeration of cladoceran ephippia.

Radiometric dating and heavy metal geochemistry

The 2012 cores from Lakes Dauriat and Knob served as references for chronology and geochemical analyses. We first freeze-dried these cores and then measured magnetic susceptibility on each of the 0.25 cm sample slices by subsampling a constant volume. We then selected 15 evenly spaced intervals in each core for radiometric dating (^{210}Pb), and sent these to the GEOTOP facility at the University of Québec at Montreal. The selection of age models based on ^{210}Pb , ^{226}Ra , and ^{137}Cs activity is outlined in S2.

An additional 15 intervals were selected for geochemical analyses (again evenly spaced and adjacent to the 15 intervals selected for dating). These dried samples were analyzed at a commercial laboratory, Actlabs (Ancaster, Ontario, Canada). Using inductively coupled plasma-optical emission spectrometry (ICP-OES), concentrations of the following heavy metals were obtained for each interval: Ag, Al, Ba, Be, Bi, Ca, Cd, Co, Cr, Cu, Fe, Ga, Hg, K, Li, Mg, Mn, Mo, Na, Ni, P, S, Sb, Sc, Sr, Te, Ti, U, V, W, Y, Zn, and Zr. Mercury concentrations were obtained through cold vapour Flow Injection Mass Spectrometry (FIMS). Total organic carbon (TOC) was quantified for these samples using a Carbon-Sulphur combustion analyzer.

Subfossil cladocera

For each interval selected, slides of cladoceran subfossils were prepared following a procedure adapted from Korhola and Rautio (2001). Approximately 0.1 g (this mass was

increased for intervals with low subfossil abundance) of sediment was digested in 50 mL of potassium hydroxide (KOH) for 30 minutes at 65 °C. The solution was manually stirred every few seconds. The solution was removed from heat and 5 mL of 10% hydrochloric acid (HCl) was added to eliminate carbonates, before sieving through a 36 µm mesh. Sediments were washed for 15 minutes to remove any remaining dissolved organic matter and transferred to a Falcon tube using as little water as possible for a total volume between 5 and 10 mL. Permanent slides were then prepared by pipetting 0.05 mL of cleaned slurry material, which was then fixed with glycerine-safranin jelly. Kurek et al. (2010) established that a minimum of 70 to a 100 individuals must be counted to reliably represent a cladoceran assemblage, though it was also noted that 50 individuals may be an appropriate count number in species-poor lakes to record the majority of taxa with relative abundance over 1% of the total assemblage (Kurek et al. 2010). As such, while we attempted to reach a minimum of 70 individuals per interval, some low abundance intervals were only counted to 50 individuals.

Cladoceran remains typically preserved in lake sediments are the chitinized body parts: carapaces, post-abdomens, post-abdominal claws, head shields and mandibles (Korhola and Rautio 2001). For each species or species group, subfossil remains were counted and the most frequently occurring subfossil was used to calculate species abundance for each interval. However, there were some cases where we were unable to resolve subfossils to species. For example, in some samples we found *Bosmina* spp. carapaces and head shields with their pore location covered and therefore could not resolve these individuals to species. In these cases, we split this aggregated count between *Bosmina longirostris* and *Eubosmina longispina* based on the proportion of individuals from these species that had already been accurately identified in that sample. In the same way, carapaces of large *Alona* species that could not be separated were split

between *Alona affinis* and *Alona quadrangularis*. Poorly preserved *Chydorus* spp. individuals were also split proportionately between the identified chydoriids (Chydoridae) in a sample. Identifications were based on the following taxonomic guides: Frey (1959 and 1962), Megard (1967), Sweetman and Smol (2006), Szeroczynska and Sarmaja-Korjonen (2007), and Korosi and Smol (2012 [a and b]).

Statistical analyses

Taxa richness

All statistical analyses were completed in R version 3.1.2 (R Core Team 2014). We calculated rarefied taxon richness for each interval to determine richness standardized by the minimum number of individuals counted in any of the intervals, using *rarefy()* in *vegan* (Oksanen 2015).

Beta diversity

We quantified temporal beta diversity between each time interval within each lake core, computing temporal beta diversity directionally such that the oldest time point was compared to the second oldest time point; the second oldest time point compared to the third oldest and so on. We used the R function *TBI()* (Legendre 2015), to produce a measure of assemblage differentiation between each of the intervals based on the relative abundances of taxa recorded at each interval. We used the percentage difference option in the *TBI()* function which computes dissimilarity using the quantitative (not presence-absence) form of the Sørensen index, also called a Bray-Curtis index (Legendre 2015). We also extracted the proportion of total temporal beta diversity that was explained either by the loss or gain of species' abundances (Legendre and Salvat 2015), to better understand mechanisms behind the temporal differentiation of assemblages. For example, a comparison where total temporal beta diversity was explained

mostly by a loss component would mean that the assemblage change occurring between time intervals at that point is mostly the result of individual species experiencing decreased relative abundance.

Linear mixed effect models

To test the effect of metal loading on cladoceran taxa richness, we employed a mixed effect modelling approach to allow lake identity to be included as random factors in the model. This meant that we pooled the data from both lakes to test the relationship between metals and cladoceran assemblages. The response variables considered for these models were rarefied taxa richness, as well as the first principal component (PC1) scores from a Principal Components Analysis (PCA) of the cladoceran relative abundance data. We Hellinger-transformed relative abundance values for the cladoceran assemblages and performed a PCA using *rda()* in *vegan*. We used *scores()* (*vegan*) to extract the “site” scores for the first principal axis for this PCA, though these represent scores for each individual interval (lake/time combination) as opposed to individual sites.

The explanatory variables for these models were either a total metal enrichment factor (EF) or the PC1 from a PCA of heavy metal concentrations. We calculated an EF for each heavy metal using the following formula (from Bhuiyan et al. 2010):

$$\frac{([Element]_{Sample\ X} / [Al]_{Sample\ X})}{([Element]_{Background} / [Al]_{Background})}$$

where each element’s EF is calculated with reference to aluminum concentrations, and ‘Background’ refers to the oldest interval in a core. After calculating each element’s individual EF, we then summed the EFs to result in total EFs, keeping the background EF as a constant. We performed a PCA on heavy metal data for the following elements: Ag, Al, As, Ba, Be, Bi, Ca, Cd, Co, Cr, Cu, Fe, Ga, Hg, K, Li, Mg, Mn, Mo, Na, Ni, P, Pb, S, Sb, Sc, Sr, Te, V, Y, Zn, and

Zr (standardized by aluminum). We again extracted “site” scores from the PCA to represent scores for each individual sample (interval).

We tested the relationship between metal loading and enrichment on cladoceran taxa richness with the models outlined in S3, using *lmer()* in the R package *lme4* (Bates et al. 2015). We then assessed each model via Akaike information criteria *AICc()* from the package *AICcmodavg* (Mazerolle 2015). Because the observations from our two cores have the potential to be significantly autocorrelated (samples are from the same cores but different time points), we used the method outlined in Simpson and Anderson (2009) to test for autocorrelation amongst our intervals. In particular, we constructed linear models using *gls()* in *nlme* (Pinheiro et al. 2015), including one model with the CAR1 correlation structure (based on year estimates for each interval). We then used an ANOVA to test for significant differences between the linear model without the autocorrelation structure included and the model with autocorrelation structure.

Exploratory study of cladoceran ephippia in sediment cores

We were interested in whether additional information regarding temporal cladoceran dynamics could be gleaned from examining ephippial cases and diapause resting stages left in the sediment record. Using the 2013 sediment cores, we completed a preliminary study of cladoceran ephippia isolated from the sediment. We sieved wet sediments from 2 cm intervals (~10 g at a time) from one core from each lake, examined sediments under a dissecting scope and manually removed all observed ephippia. We noted whether each ephippia removed was an empty casing or whether it still contained eggs and whether the ephippia contained (or would have contained) one, two or more eggs.

Results

Geochemical loading to the four study lakes

Dauriat and Knob lakes showed contrasting histories in terms of metal loading and other abiotic drivers (see raw plots in S4 for details). Metal loading to Lake Dauriat varied greatly through time, with the elements iron, aluminum, copper, cobalt and nickel showing both pronounced peaks and troughs during pre-mining and during mining time periods. Metal concentrations in the Lake Dauriat sediments generally exceeded both International Quality Guidelines for the Protection of Aquatic Life (ISQG) as well as Probable Effect Levels (PEL) (Canadian Council of Ministers of the Environment 2014) (Table 2). Temporal variation in specific metals measured from the Lake Dauriat core, combined with relatively constant background levels of other elements (such as arsenic, cadmium, mercury and zinc), resulted in considerable variation in the scores from the 1st axis of the PCA of metal concentrations. Metal enrichment in Lake Dauriat record peaked in the 1950s/1960s, followed by the second highest peak in the 1980s when compared to historical conditions (Fig. 2a). Metal loading in Lake Knob was less pronounced, despite the presence of the regional metal stressors (Fig. 2b). The majority of heavy metals measured in Lake Knob remained fairly constant through time with the exception of manganese, which showed peaks in recent intervals. Metal concentrations in the Lake Knob sediments generally exceeded ISQG levels, but did not always exceed PELs.

Biodiversity

Across the two lakes, we enumerated a total of 37 taxa. However, many of these taxa were relatively rare and once we removed taxa that did not make up at least 5% of a sample's assemblage in at least one interval in two lakes, we were left with 14 taxa (Figs. 3 and 4). In Lake Dauriat, cladoceran species richness showed considerable fluctuations through time, with a

fairly extensive reduction in rarefied richness circa 1960s (Fig. 2a). Species richness then increased, but only the most recent sediment interval came close to the pre-mining values. In comparison to Lake Dauriat, cladoceran species richness trends from Lake Knob were relatively stable, even during the mining period (Fig. 2b). Species richness in the Lake Knob record was highest at the start of extraction activities, followed by fluctuations in richness during and after the mining period. Estimated sedimentation rates were considered constant through time in both Lake Knob and Lake Dauriat because of the selection of a Constant Initial Concentration age model, and as such, cladoceran species richness could not be correlated to estimates of sedimentation rate.

The community assemblages of the two lakes were different and remained so through time. In Lake Dauriat, Bosminids (*Bosmina longirostris* and *Eubosmina longispina*) maintained their relative abundances throughout the mining period, whereas taxa such as *Alona circumfimbria* and *Alona* spp. became much more abundant after the main mining period (Fig. 3). In Knob, *B. longirostris* and *E. longispina* were also quite abundant, with other species present in low relative abundances throughout the core profile (Fig. 4). *Chydorus* cf. *sphaericus* was found in intervals throughout the Lake Dauriat and Lake Knob records, although it was generally more abundant during the mining period in both lakes. In comparing both records with a PCA, we observed that the earliest Lake Dauriat assemblages (1920/1930s) were most similar to the Lake Knob assemblages, with more recent Lake Dauriat assemblages differing substantially from Lake Knob by the prevalence of *Alona* spp., and *A. circumfimbria*. Lake Knob assemblages tended to be characterized by taxa such as *Alona affinis* and *Acroperus harpae*. The PCA also demonstrated that there was less variation in cladoceran assemblages through time in the Lake Knob record relative to that of Lake Dauriat. Furthermore, we found a noticeable

difference in the resting egg bank of Lake Dauriat compared to Lake Knob in our preliminary analysis, whereby there was a greater ratio of unhatched: empty cladoceran ephippial cases in Lake Dauriat relative to Lake Knob (Fig. 5). The abundance of both intact ephippia and cases were also generally higher in Lake Dauriat. The most pronounced changes in temporal beta diversity were observed in the Lake Dauriat record compared to Lake Knob (Fig. 6). However, beta diversity reached peaks during the period of mining and town construction in both lake records (from the late 1930s to the 1970s). In both lakes Dauriat and Knob, changes in total beta diversity were largely explained by a loss of species (i.e., the loss component which measures the changes in abundances on a species by species basis).

Cladoceran response to metal loading

The best fit model for the relationship between cladoceran species richness and metal loading was the simple linear model of $\text{Clad_S}_i \sim \text{Metal EF}_i + \epsilon$ without lake included as a random factor (lowest AIC as well as the highest explained variation ($\text{Adj. } R^2 = 0.69$)) amongst the null linear models; Table 3; Fig. 7a). The second lowest AIC values were from the following models: 1) $\text{Clad_S}_{ij} \sim \text{Metal EF}_i + \text{Lake}_j + \epsilon$ with lake included as a random factor (Fig. 7b). For both these latter models, the slope for the mixed effect model was significantly different from zero, as indicated by the range of upper and lower confidence intervals (i.e., did not include zero: varied between -0.05 and -0.08). Although we found that measurements on adjoining sediment intervals were autocorrelated ($\phi = 0.6$), we failed to detect a significant difference based on an ANOVA of the linear model run with autocorrelated structure, and the model run without accounting for this autocorrelation. The set of models with cladoceran richness as a response and metal PC1 as an explanatory variable had higher AIC and a lower $\text{Adj. } R^2$ value than the models with metal EF as an explanatory variable (Table 3). Linear models with cladoceran PC1 as a

response variable explained very low amounts of variation (Adj. $R^2 = 0.09$ with metal EF as an explanatory variable and 0.02 with metal PC1 as an explanatory variable).

Discussion

A common approach across the Québec landscape has been a focus on restoration of sites post-mine closure, as opposed to proactive planning for the mitigation of effects on biodiversity (Hamilton et al. 2015). An improved understanding of biodiversity responses to mining in the Schefferville landscape through time could contribute to more proactive planning in the future. Both Lake Dauriat and Lake Knob are situated within the limits of the same town site and are exposed to the same sources of atmospheric metal deposition. Despite this similarity, peaks in heavy metals and metal enrichment varied between the lakes, with Dauriat experiencing higher sediment metal concentration enrichment values compared to background conditions (where T = 0, bottom of sediment core). Based on isotopic analyses, Aebischer et al., (2015) have recently shown that the sediments of Lake Dauriat indicate pollution sources arising from mining activities, as well as municipal waste and sewage. However, the extent of metal enrichment derived from mining sources in both focal lakes appears to be ecologically important, even in Lake Knob where atmospheric deposition dominated, as numerous sediment intervals had metal concentrations above quality guidelines for aquatic life. Consistent with our hypothesis, we found that periods of higher metal loading were associated with decreased cladoceran richness in both lakes. This relationship was most evident in Lake Dauriat that received both metal and nutrient inputs, though we do not have evidence for a strong lake effect in our study. Secondly, we revealed that the contribution of loss and gain components to temporal beta diversity differed through time and between lakes. To further advance knowledge concerning responses to metal

contamination, we explored the interpretation of alpha richness and temporal beta diversity trends together.

The approach taken by this study was to use paleolimnology to examine biodiversity dynamics through time. The field of paleolimnology has been championed as an ideal way to study biodiversity dynamics (Gregory-Eaves and Beisner 2011). Furthermore, based on recent studies by Levi et al. (2014) and Winegardner et al. (2015), we now have evidence that paleolimnological approaches can draw similar conclusions regarding environmental and spatial drivers of diversity as studies using a contemporary ecological approach. However, this is not always the case: Kurek et al. (2011) used paleolimnology to show that environmental factors were more important than spatial variables in cladoceran communities of lakes in Ontario, Canada. More of these kinds of comparative studies are needed to understand the context-dependency of such results.

Alpha richness and temporal beta diversity can be interpreted relative to each other in a number of ways to provide new insight based on our observation of cladoceran assemblages in response to multiple stressors. This is because high temporal beta diversity indicates strong gain or loss components individually or in combination. Thus, if the gain component of beta diversity (pseudo species replacement) dominated during a stressful event, then temporal beta diversity (increasing) would not track alpha diversity (decreasing due to a metal stress; Fig. 8a). However, if the dominant explanatory component of temporal beta diversity was loss, then reductions in alpha richness should occur, as species are lost between intervals (including via reduced abundances which make species extirpations more likely demographically; Fig. 8b). Conversely, if the dominant explanatory component of temporal beta diversity was a strong taxa gain component, this could be associated with either no net change of richness between intervals (if

species abundances for those already present increased, as opposed to new species being added), or an increase in richness as new species colonized over time (Fig. 8c). In our study, temporal beta diversity was highest during time periods of maximum (or near maximum) metal enrichment while cladoceran alpha richness was declining. Consideration of alpha richness and beta diversity in this way is important, as it will improve understanding of biodiversity trends that can be masked when only considering alpha diversity.

Metal contamination had an overarching effect on local cladoceran species richness in our study lakes. A simple linear negative relationship between cladoceran species richness and metal enrichment factor was the most robust model and is consistent with the sensitivity of zooplankton to increased heavy metal concentrations in many laboratory toxicity studies (e.g., Biesinger and Christensen, 1972; Bossuyt and Janssen 2005, among others). Reduced cladoceran species richness under conditions of metal contamination from mining and smelting is a common occurrence across aquatic systems, from the subarctic to temperate regions. While the acute toxicity responses of aquatic invertebrates to different metals can vary in magnitude (Canadian Council of Ministers of the Environment 2014), the negative effects on cladoceran diversity and abundance have been demonstrated using paleolimnological studies across many different types of metal mining. For example, extreme increases in arsenic and other heavy metals from gold mining and roasting activities at Yellowknife's Giant Mine in the Northwest Territories, Canada resulted in a functional absence of cladocerans from nearby lakes during mining operations (Thienpont et al. 2016). In another example, smelting of copper, zinc and silver sulphide in Flin Flon, Manitoba, Canada resulted in significant decreases in cladoceran abundances in surrounding lakes (Doig et al. 2015). In the region around Sudbury, Ontario, Canada, nickel mining and the accompanying acidification and metal contamination has also seen severe

reductions in invertebrate communities, with cladocerans slower to recover than copepod species (Keller et al. 2002; Yan et al. 2004). Indeed, the extent of mining, processing (e.g. smelting, roasting etc.) and associated activities (construction, waste discharge etc.) might be more important to cladoceran diversity than the actual metal type itself as mining activities introduce a whole suite of multiple stressors to a system.

Despite the potential for interaction between multiple stressors in the Schefferville system, nutrient loading in Lake Dauriat did not appear to mitigate or exacerbate the effect of metal contamination, as we did not find strong support for lake-specific declines in richness to metal enrichment. This is interesting as local knowledge as well the lithology of the Lake Dauriat cores indicates an anoxic period from the 1950s to 1970s. During this period, one might have expected metal deposition to Lake Dauriat to have had an amplified impact on biodiversity because eutrophication and subsequent deepwater anoxia may have altered redox reactions within the sediments, making metals in the sediments more soluble, enabling more diffusion into overlying waters (e.g. Jacobs and Emerson 1982) and thus exposing cladoceran repeatedly, or to a more toxic form. However, in our study, the simple relationship between metal concentration and cladoceran richness appears to be the most supported model. In addition, while changes in sedimentation rates may also have affected these results, we do not believe that these results are artefactual (as per Smol 1981) because the best age model for Lake Dauriat was one where sedimentation rate was held relatively constant. Even when a different age model was used (i.e. CRS), we still failed to find a significant effect of sedimentation rates on cladoceran species richness. In future, it would be helpful to conduct a chironomid analysis of sediment records from Lakes Dauriat and Knob to gain some insight into the severity and spatial extent of hypolimnetic anoxia. With richer information on the nutrient loading stressor (i.e. volume of

sewage inputs; not available for this site unfortunately) it might also be possible more accurately characterize the extent of multiple stressors in Lake Dauriat.

While the response of cladoceran diversity to metal enrichment was similar in both lakes, there are some key differences with respect to biotic and abiotic lake characteristics. The magnitude of metal contamination was much higher in Lake Dauriat, and it experienced more drastic reductions in taxon richness. Additionally, the preliminary investigation of the cladoceran resting egg banks showed other potential differences. For example, we found evidence for a greater ratio of unhatched: empty cladoceran ephippial cases in the resting egg bank of Lake Dauriat than in Lake Knob. A dominance of empty cases could indicate a greater hatching success from Lake Knob sediments with less severe contamination, although other mechanisms cannot be ruled out (e.g., poorer preservation of eggs in Lake Knob). A reduced hatching success in the presence of multiple stressors (metal-contamination and eutrophication in Lake Dauriat) is supported by work by Rogalski et al. (2015), where metal contamination negatively affected the hatching of *Daphnia ephippia* from lake sediments. More experimental work could be insightful to evaluate the support for different potential mechanisms and might elucidate eco-evolutionary dynamics via the rapid adaptation of cladoceran species to metal stressors (e.g. Turko et al. 2016).

Community composition in our two study lakes showed some similar response to those observed in other mining regions. The dominance of *Bosmina longirostris* and *Eubosmina longispina* observed in both lakes is similar to reports from other metal-contaminated lakes in northern Russia and eastern Canada (Lukin et al. 2003; Korosi et al. 2012; Labaj et al. 2015). Bosminid dominance has generally been attributed more to their heightened ability to withstand acidification but with some indications for a tolerance of metals (Doig et al. 2015). We also

observed a consistent presence of *Chydorus* cf. *sphaericus*, a species that is generally associated with macrophytes and mud (Chen et al. 2010) or moderately acidified waters (Belyaeva and Deneke 2007). Our results indicated that this species can also survive some degree of metal-contamination, without accompanying acidification, but this remains to be verified experimentally. On the other hand, *Holopedium gibberum* has commonly been observed in metal-contaminated and acidified lakes of the nickel-mining region of Sudbury (Canada; Valois et al., 2011). However, Yan et al. (2004) found that *H. gibberum* was twice unsuccessful in colonizing a previously acidified and metal contaminated Sudbury lake, even after remediation through liming. While we also observed *H. gibberum* in one of our samples from Lake Knob (during the mining period), it was present only at very low relative abundances (less than 5% of the total assemblage), suggesting that it is not tolerant of the disturbance conditions in our focal lakes. It is also important to note that *H. gibberum* is historically rare in the region and generally not broadly distributed across northern Québec (at least in historical research; Carter et al. 1979). Here again, experimental research would help to elucidate the tolerance of this taxon to heavy metal and acidification stressors.

Temporal beta diversity varied throughout the history of both cores and consistently showed peaks during the mining period. These peaks were mostly attributable to loss in abundance on a taxon-by-taxon basis in both lakes, with one exception in Lake Knob. In Lake Knob, two incidences of higher total beta diversity occurred during the mining period (during the 1960s and 1970s): the first explained predominantly by taxa gain, and the second predominantly by taxa loss (Fig. 6); both taxa gain and taxa loss in this case were mainly related to changes in *Bosmina* sp. taxa. This switching in explanatory components can be explained by (i) a lag in cladoceran taxon response, or (ii) the creation of new niches for metal- and disturbance-tolerant

taxa during early mining activities in Lake Knob, before metal-sensitive taxa were affected. As mining activities continued however, increasing disturbance should have reduced relative abundances of non-metal tolerant species and perhaps also of generalist taxa as observed in Lake Dauriat. This taxa loss would have sustained a high temporal beta diversity, via taxa loss (Fig. 6). Such “switching” between dominance of taxa loss and gain components in temporal beta diversity has been demonstrated in at least one other study of mollusc communities (Legendre and Salvat 2015). Thus, variation in the main explanatory component of temporal beta diversity provides insight into the richness dynamics of a community as we observed for Lake Knob.

In a review of freshwater ecosystems subjected to a wide variety of anthropogenic stressors, Niemi et al. (1990) documented 150 case studies where aquatic assemblages (from plankton to fish) exhibited resilience to a disturbance. They found that the majority of these trended towards biological recovery in less than three years, as long as, 1) the disturbance or stressor did not physically alter aquatic habitat, 2) there were no residual pollutants remaining from the disturbance, and 3) the system was not isolated, precluding recolonization. In our study, cladoceran communities in Lake Knob changed relatively little prior to the mining period (Fig. 7). For Lake Dauriat, the majority of assemblage turnover occurred during the mining period due to reductions in taxa richness associated with increased metal contamination (Fig. 7). However, the cladoceran assemblages in Lake Dauriat have not returned to their pre-mining state even though mining activities were terminated in this region by the early 1980s; we suggest that the lack of recovery could be because lake sediments are still metal-enriched and continuing to release metals to the water-column. Climate change is an unlikely mechanism for assemblage shifts observed as temperature records show very little change over the study period (Environment and Climate Change 2015). Alternatively, species assemblages may take longer to

recover in a multiple stressor situation, as in Lake Dauriat, if adaptation to one stressor results in an increased susceptibility to other stressors (Moe et al. 2013).

Our study quantified historical patterns in cladoceran species richness and turnover in two northern lakes that were exposed to differences in metal contamination and eutrophication. Understanding both the effect of metal loading on cladoceran assemblage richness in this region, as well as their propensity for turnover through time is important because the extent of mining continues to vary from year to year. As such, biological assemblages that might be considered ‘recovered’ post-mining may still be exposed to evolving stressor combinations via legacy effects and the addition of new stressors. The strength of our study is in our use of a temporal beta diversity lens to quantify cladoceran turnover over a 100-300 year period across a major perturbation event. Cladoceran communities were considerably dynamic, despite a linear negative relationship with metal contamination.

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Draft

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Tables

Table 1: Description of lake size characteristics and surrounding land use for each of the four study lakes.

Lake	Latitude (DD)	Longitude (DD)	Observed maximum depth (m)	Surface area (km ²)	Surrounding land use
Dauriat	54°48'23.73"N	66°49'30.85"W	11	0.56	Town site; hedge row around some of lake; used for raw sewage until 1975.
Knob	54°37'29.13"N	66°48'30.77"W	5.2	2	Town site surrounding part of lake; drinking water source; flow through to Dauriat.

Table 2: Mean and maximum sediment metal concentrations along with sediment quality guidelines for the protection of aquatic life (for freshwater systems). All concentrations are expressed in parts per million (ppm). ‘ISQG’ refers to “International Sediment Quality Guidelines for the Protection of Aquatic Life” and is converted from $\mu\text{g kg}^{-1}$ dry weight (Canadian Council of Ministers of the Environment, 2014). ‘PEL’ refers to “Probable Effect Level”, also converted from $\mu\text{g kg}^{-1}$ dry weight.

Metal	Dauriat mean (ppm)	Dauriat maximum (ppm)	Knob mean (ppm)	Knob maximum (ppm)	ISQG (ppm)	PEL (ppm)
Al	5746	7360	5923	6690	--	--
Fe	13452	18400	8272	9500	--	--
Mn	2176	4270	4087	40900	--	--
Zn	600	1430	144	200	123	315
As	10	21	11	14	5.9	17
Cd	3	6	0.9	2	0.6	3.5
Co	64	121	37	124	--	--
Cr	67	85	72	93	--	--
Cu	159	348	35	52	35.7	197
Hg	3	8	0.9	0.9	0.2	0.5
Ni	105	226	81	158	--	--
Sb	5	5	5	5	--	--

Table 3: Mixed-effect model summaries and model assessment in order of decreasing plausibility. The formula (as used as input in lme4) is shown along with the AIC value for each model. Only models with high amounts of explained variation are shown.

Model	Random factors	AIC value	R^2 (for linear models)
$\text{Clad_S}_{ij} \sim \text{Metal_EF}_i + \varepsilon$	None	85	Adj. $R^2 = 0.69$
$\text{Clad_S}_{ij} \sim \text{Metal_EF}_i + \text{Lake}_j + \varepsilon$	Lake (varying intercept)	88	--
$\text{Clad_S}_{ij} \sim \text{Metal_EF}_i + \text{Lake}_j + \varepsilon$	Lake (varying intercept + slope)	94	--
$\text{Clad_S}_{ij} \sim \text{Metal_PC1}_i + \varepsilon$	None	100	Adj. $R^2 = 0.51$
$\text{Clad_S}_{ij} \sim \text{Metal_PC1}_i + \text{Lake}_j + \varepsilon$	Lake (varying intercept)	102	--
$\text{Clad_S}_{ij} \sim \text{Metal_PC1}_i + \text{Lake}_j + \varepsilon$	Lake (varying intercept + slope)	107	--

Figure captions

Figure 1: Maps showing the location of (a) Schefferville in the Québec landscape and (b) the two study lakes surrounding the town of Schefferville.

Figure 2: Heavy metal enrichment factors and rarefied cladoceran species richness for Lake Dauriat (a) and Lake Knob (b). The Metal EFs depicted represent total metal enrichment factors of 10 heavy metals (Ag, Ba, Cd, Co, Cu, Fe, Hg, Mo, Ni, and Pb).

Figure 3: Relative abundance of Cladoceran assemblages through time in Lake Dauriat as expressed by percentage of the total Cladoceran assemblage. Only taxa with a relative abundance of at least 5% in at least one interval are shown (rare species excluded). Cladoceran taxa are: *Acroperus harpae* (*A. harpae*); *Alona affinis* (*A. affinis*); *Alona circumfimbria*/*Alona guttata* (*A. circumfimbria guttata*); *Alona quandrangularis* (*A. quandrangularis*); *Alona* spp. (*Alona* spp.); *Alonella nana* (*A. nana*); *Chydorus gibbus* (*C. gibbus*); *Chydorus* cf. *sphaericus* (*C. sphaericus*); *Eurycercus* spp. (*Eurycercus* spp.); *Paralona piger* (*P. piger*); *Bosmina longirostris* (*B. longirostris*); *Eubosmina longispina* (*E. longispina*); and *Daphnia longispina* (*D. longispina*). Taxa are labelled as being found in either a littoral or pelagic habitat. Note that *Bosmina* spp. can be found in both open-water littoral as well as pelagic habitat. Black bars for *B. longirostris* and *E. longispina* represent the total number of individuals, grey bars represent the fraction of that total that were determined from indistinguishable *Bosmina* spp., that were then split proportionally between the two species depending on the prevalence of individuals of each species in the sample. The mining period (1939-1977) is marked by dashed lines.

Figure 4: Relative abundance of Cladoceran assemblages through time in Lake Knob as expressed by percentage of the total Cladoceran assemblage. Only taxa with a relative abundance of at least 5% in at least one interval are shown (rare species excluded). Cladoceran taxa are: *Acroperus harpae* (*A. harpae*); *Alona affinis* (*A. affinis*); *Alona circumfimbria*/*Alona guttata* (*A. circumfimbria guttata*); *Alona quandrangularis* (*A. quandrangularis*); *Alona* spp. (*Alona* spp.); *Alonella nana* (*A. nana*); *Chydorus gibbus* (*C. gibbus*); *Chydorus* cf. *sphaericus* (*C. sphaericus*); *Eurycercus* spp. (*Eurycercus* spp.); *Paralona piger* (*P. piger*); *Bosmina longirostris* (*B. longirostris*); *Eubosmina longispina* (*E. longispina*); and *Daphnia longispina* (*D. longispina*). Taxa are labelled as being found in either a littoral or pelagic habitat. Note that *Bosmina* spp. can be found in both open-water littoral as well as pelagic habitat. Black bars for *B. longirostris* and *E. longispina* represent the total number of individuals, grey bars represent the fraction of that total that were determined from indistinguishable *Bosmina* spp., that were then split proportionally between the two species depending on the prevalence of individuals of each species in the sample. The mining period (1939-1977) is marked by dashed lines.

Figure 5: Cladoceran resting stages extracted from sediment intervals from Lake Dauriat (a) and Knob (b). The sediment core number is specified at the top of each panel. ‘Specimen_type’ refers to the type of resting stage material observed in the samples: ‘CAS_1’ refers to an empty casing that would have held a single diapause egg; ‘CAS_2’ refers to an empty casing that would have held two diapause egg; ‘CAS_X’ refers to an empty casing that would have held more than two eggs; ‘CAS_und’ refers to casing where it could not be determined whether it would have held one or two eggs; ‘EPH_1’ refers to a casing with one egg present; ‘EPH_2’ refers to a casing with two eggs present; ‘EPH_X’ refers to a casing with

multiple eggs present. No comment is made on the viability of the observed eggs. Gaps between histogram bars represent intervals where no resting stages were found in the sediment cores.

Figure 6: Beta diversity for (left) Lake Dauriat and (right) Lake Knob, shown through time. Each temporal beta diversity point represents a comparison between two intervals, and the year midpoint of that comparison is shown on the y-axis. “Total_beta” refers to total temporal beta diversity computed between time intervals. “Species_loss” refers to the loss of Cladoceran abundances on a taxa by taxa basis. The mining period (1939-1977) is shaded.

Figure 7: Relationship between cumulative metal enrichment factor and rarefied Cladoceran species richness for the two Schefferville lakes ($n_{\text{interval}} = 27$) using (a) a linear model and (b) mixed effect model with lake as a random factor. For the linear model, the blue line represents Lake Dauriat and the red line Lake Knob. The adjusted $R^2 = 0.7$. For the mixed effect model, the slope of the overall line is -0.071, whereas the upper and lower confidence intervals for this model are -0.0 and -0.08, respectively.

Figure 8: Three hypothetical assemblages of eight species (relative abundance) at each of three time points show ways in which patterns observed using cladoceran richness may or may not be congruent with those observed using temporal beta diversity. Figure 9 shows three hypothetical assemblages (Scenarios A, B, C) where the abundance of eight species (A-H) is recorded at three points in time (Time point 1, 2 and 3). Beta diversity is further represented by either a loss component (hashed bar) or gain component (solid bar). Scenario A and B represent assemblages where species richness has decreased through time (for the context of this study, we will assume that this decrease through time is related to a negative linear relationship with metal contamination), whereas Scenario C shows an assemblage where species richness has stayed constant through time, despite changes in the relative abundances of individual species. In Scenario A, metal tolerant species are able to take advantage of niches opened up in high metal conditions, thus contributing to an increased gain component in temporal beta diversity because these metal tolerant species gain in abundance on an individual basis. Under this scenario, the conclusions drawn about the effect of metal contamination in a system would be different if observing species richness (decreasing) or temporal beta diversity (high gain component). Scenario B demonstrates an example of where both species richness and temporal beta diversity show congruent patterns, where cladoceran species richness decreases with higher metal concentrations and this results in a high loss component making up total temporal beta diversity, as species themselves are lost and remaining species experience losses in abundance. Finally, Scenario C shows a situation where cladoceran richness may increase or stay the same with increased metal concentrations, and this is further echoed by increase in abundances of a species by species basis in terms of temporal beta diversity. As such individual species show gains in abundance, and species richness either stays constant or increases.

Figures

Figure 1

Figure 2

Figure 3

Figure 4

(a)

(b)

Figure 5

Figure 6

Figure 7

Figure 8