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Large-scale multi-trophic co-response models and environmental control of pelagic food webs in Québec lakes

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Environmental heterogeneity plays a fundamental role in driving species distributions by, for one, fostering niche dimensionality. Within lake ecosystems, species distributions and concordance patterns are driven by both local and regional heterogeneity, though their relative importance across trophic levels has rarely been explored. We developed a statistical framework to compare responses of taxa from different trophic levels to abiotic factors and determine how this affected multi-trophic network structures. In particular, we used multi-species concordance modelling (concordance analysis and RV coefficient) to determine species associations and correlations within and among three trophic levels (phytoplankton, zooplankton and fish communities sampled across 49 southern Québec lakes, covering eight hydrological regions). We then used multiple factor analysis, latent variable modelling and local contributions of sites to beta diversity to assess the relative importance of major environmental gradients in structuring species co-responses and species interaction turnover across the landscape. Our analyses confirmed that concordant species within each trophic level varied jointly or segregated into different pelagic food webs in Québec lakes where important acidification and eutrophication took place. Some keynote species were indicators of different food web compartments and distinguished groups of lakes along multiple environmental niche dimensions. Among the three trophic levels examined, zooplankton depicted the highest proportion of species concordance and appeared to act as a trophic linkage between phytoplankton and fish. Ultimately, the losses or gains in species richness and species interactions were strongly driven by environmental gradients. This study provides for the first time a combined analysis of the effects of environmental heterogeneity on ecological communities belonging to three trophic levels sampled near simultaneously across an 800 km broad lacustrine landscape. The new framework developed in this study has a great potential to better understand the complex response of aquatic ecosystems in a world increasingly affected by multiple, cumulative stressors.

Keywords: aquatic communities, latent variable model (LVM), local contributions to beta diversity (LCBD), multiple factor analysis (MFA), multitrophic species associations, neutral interaction networks

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Introduction

Environmental heterogeneity is fundamental to the structure and dynamics of communities under the control of multiple generative processes varying with scales from microhabitats to large landscapes or ecozones (Levin 1992, Legendre 1993, Pinel-Alloul and Ghadouani 2007). Exploring how species are distributed across their geographical ranges, and whether they vary jointly or segregate along environmental gradients, are two fundamental issues in macroecology and metacommunity theory (Gaston 2000, Liebold et al. 2004). However, this is a difficult question to grasp, measure and demonstrate, because of the large number of ecological processes that determine patterns in species distributions and interactions, such as natural selection by environments, ecological drift of populations, speciation due to isolation between ecosystems, and dispersal processes such as immigration and colonisation (Vellend and Orrock 2009, Anand et al. 2010, Vellend 2010). Understanding these complex dynamics, and whether their relative importance vary across multiple scales and trophic levels, would require a landscape wide study of species interactions in natural communities (Skrondal and Rabe-Hesketh 2004, Warton et al. 2015, Legendre 2019).

Lakes are relevant model ecosystems in macroecology and community ecology for studying spatial distribution patterns and multi-level community networks in relation to local (environmental filters within lakes) and regional (environmental heterogeneity across the lacustrine landscape) processes (Liebold and Norberg 2004, Norberg 2004, Hortal et al. 2014, Anas et al. 2017). Indeed, according to metacommunity theory (Liebold et al. 2004), large organisms such as fish and crustacean zooplankters are expected to be more constrained by regional dispersal predictors (e.g. overland and watercourse distances among lakes) than by local factors related to abiotic conditions (lake chemical and physical conditions) compared to small organisms such as phytoplankton and bacteria. This was confirmed by work examining the relative roles of local environmental conditions and spatial processes in structuring lake communities from bacteria to fish, independently for each trophic level (Beisner et al. 2006). Others (Pinel-Alloul et al. 1995) documented the relative role of abiotic (water chemistry, lake morphometry) and biotic (phytoplankton, fish) environmental factors, and spatial distances among lakes (geographic coordinates) in structuring zooplankton communities, using different types of variation partitioning approaches. The latter concluded that broad-scale geographical gradients in abiotic factors related to water chemistry represented the main ecological process explaining zooplankton community spatial variation, whereas local-scale variation in phytoplankton and fish communities had a minor influence. However, by considering zooplankton communities as the sole dependent component, this work did not assess the joint responses of multi-trophic species networks to large-scale environmental gradients. Although the roles of local and regional processes in controlling the spatial distribution and concordance of species have been assessed and compared among different freshwater communities (Shurin et al. 2000, Cottenie 2005), until now no study has provided a combined analysis of the effects of environmental heterogeneity on communities belonging to multiple trophic levels sampled simultaneously across a lacustrine landscape.

The present study offers a multi-trophic perspective that complements these prior studies. We have developed a new, original framework (Fig. 1 for analysis plan) for understanding the role of environmental filtering in structuring multitrophic species distributions in lake food webs. In particular, we examined a unique dataset where three trophic levels (phytoplankton, zooplankton and fish) were sampled simultaneously across 49 boreal lakes in 1982, thus capturing information on a historical peak in acid precipitation, to explain food web species distribution patterns along an 800 km longitudinal geographic gradient in southern Québec. We first described patterns of species associations and distributions across space by quantifying species correlations within and among trophic levels using multi-species concordance modelling (Kendall *W* concordance analysis and RV coefficient). We then employed multiple factor analysis (MFA) and latent variable modelling (LVM) to assess whether the concordance among species may be induced by environmental gradients. These analyses allowed us to evaluate the relative importance of major abiotic environmental drivers in structuring large-scale spatial patterns of species concordance, and how this may be indicative of joint variation and/or niche segregation (Skrondal and Rabe-Hesketh, 2004, Hui et al. 2014, Letten et al. 2015, Warton et al. 2015, 2016). Finally, we evaluated the consequences of the multi-species joint variation patterns on beta diversity (turnover) across multiple trophic levels by quantifying the local contributions of lakes to species beta diversity (LCBD) and species interaction beta diversity (LCBD-interaction), and how these metrics were related to environmental gradients. Together, this framework allowed us to identify 1) patterns of species correlations, indicating concordant species within and among trophic levels, 2) keynote indicator species networks distinguishing groups of lakes that reflect species niche separation and their response to the main environmental gradients and 3) how the different responses of species and trophic groups to abiotic gradients determined the distribution of species and their interactions (beta diversity) along environmental gradients.

Material and methods

Study area, sampling and taxonomic analysis

Fifty-four Canadian Shield lakes were sampled throughout southern Québec, north of the St. Lawrence River and south of latitude 52°N, during summer 1982. The lakes are distributed along an 800 km south–west to north–east longitudinal geographical range (78°–63°W) and cover eight hydrographical regions (Fig. 1 in Pinel-Alloul et al. 1990a, b, reported in the Supporting information in this paper). The lakes are located on the Canadian Shield mostly characterized by

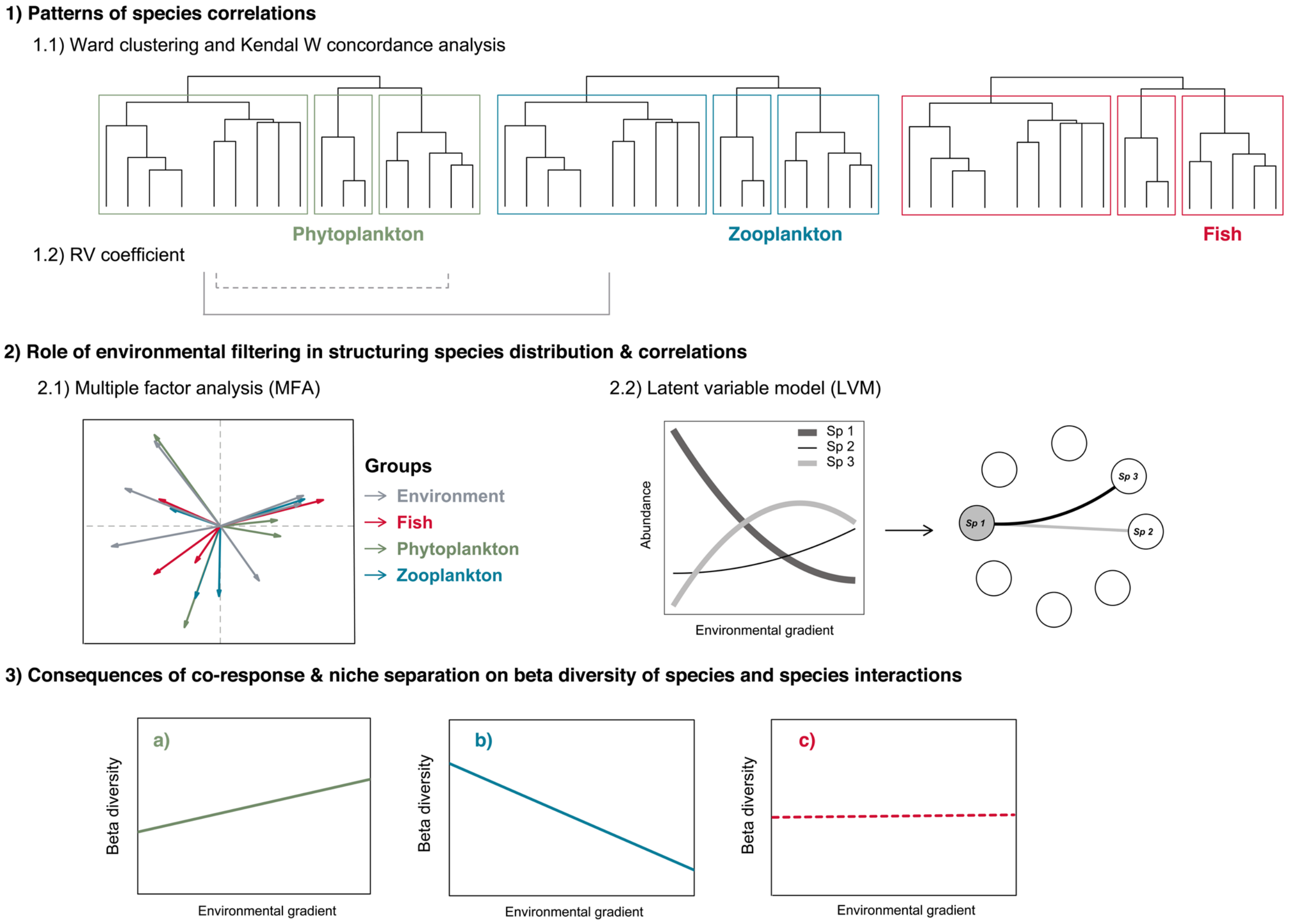

Figure 1. Schematic summary of statistical framework, which consisted of three main steps. Step 1) quantifying patterns of species correlations, where 1.1) Ward hierarchical clustering and Kendall *W* concordance analysis were used to identify subgroups of correlated species within each trophic level, and 1.2) a multivariate correlation (RV coefficient) then helped determine whether certain subgroups were correlated with subgroups pertaining to other trophic levels. Step 2) identifying the role of environmental filtering in structuring the species correlations, where 2.1) a multiple factor analysis (MFA) explored the correlations among dominant species and environmental factors to identify strong correlations among all data matrices, and 2.2) a latent variable model (LVM) examined the linear and nonlinear fitted responses of all species to the main environmental dimensions. For the latter, the fitted responses of the species pairs were correlated, and significant correlations were then represented in network diagrams; negative correlations were interpreted as niche separation, positive correlations as co-responses. Lastly, step 3) explored the consequences of niche separation and co-responses on species and species-interaction turnover. Here, the local contributions of sites to beta diversity (LCBD indices) were calculated and regressed against environmental gradients to test whether site uniqueness in species composition and species interaction (a) increased, (b) decreased or (c) was unrelated to environmental factors.

granitic and metamorphic bedrock, with small calcareous soil in the south–west region (Pinel-Alloul et al. 1990a). In general, the lakes are located upland in unperturbed watersheds, deeper than 4 m, and without vegetation in the littoral zones at the time of sampling. Lakes of the region are considered sensitive to anthropogenic acidification and eutrophication due to sulfate deposition and higher nutrient load towards the west, and natural acidification due to the granitic bedrock to the east. The present study was restricted to 49 lakes with complete data for a suite of morphometric, physical, chemical and biotic variables, including three trophic levels (phytoplankton, zooplankton and fish communities). Plankton and fish communities were sampled during July and August 1982, thus capturing a key period of anthropogenic acidification and consequently one of the strongest spatial gradients in natural and anthropogenic lake acidity experienced in the region. To minimize the effect of the seasonal development on plankton communities, sampling started at successive times in the eight regions following the west-to-east geographic and climatic axis gradient over a period of 1 month. Phytoplankton species counts (87 species across all sites) were expressed as cells ml^{-1} (Pinel-Alloul et al. 1990a); zooplankton species counts (34 species) were expressed as numbers of individuals m^{-3} and converted to biomass (mg m^{-3}) using specific dry mass relationships (Pinel-Alloul et al. 1990b); fish counts (18 species) were expressed in abundances (catch per unit effort). Environmental variables examined herein provided information on the geography (latitude, longitude and altitude), morphometry (lake and catchment areas, lake order, maximum and relative depths, length, width and volume) and water quality (pH, ions, metals, alkalinity, alkalinity: sulfate ratio, organic and inorganic carbon, conductivity, transparency, colour and the morphoedaphic index) of each study site. For additional details on species and environmental variables examined herein see Supporting information.

Statistical analyses

Species associations within trophic groups and correlations among subgroups

Ward clustering and Kendall W concordance analysis

To first identify which groups of species were in positive correlation with one another, we conducted a hierarchical clustering combined with a concordance analysis (Legendre 2005) on each of the three trophic levels (phytoplankton, zooplankton and fish) separately (Fig. 1: 1.1).

Kendall's coefficient of concordance, *W*, belongs to the family of the rank correlation coefficients. It measures the agreement among several descriptors, which are the species in our study (in columns) over a set of sites (in rows). The species abundances are first independently transformed into ranks across the sites. The ranks are summed in each row (site) and the variance of these row sums is computed. The variance is divided by the maximum possible value the variance can take. This maximum variance occurs when all descriptors (species) have identical rank vectors; they are then in total agreement and the sum of the ranks has maximum variance (Legendre and Legendre 2012). Statistic *W* is closely related to the Spearman correlation coefficient; it is bounded between 0 and 1, with the value 1 indicating perfect concordance.

Concordance analysis should not be applied to the original community composition matrices containing all species in a trophic group. The paper describing the search for species associations by concordance analysis (Legendre 2005) recommends starting the search for significant associations after a cluster analysis (hierarchical clustering or *K*-means partitioning) is conducted to identify groups of species that are fairly correlated to one another. The criterion for deciding when an appropriate clustering level has been reached is to examine the means of the Spearman correlations of individual species with all the other species in a group. A negative mean indicates that a species does not belong to that group and the group should be split further. The test of the *W* statistic should be computed on groups of species that do not contain species with negative means of their correlations with the other species in the group. This is usually not the case for the initial group containing all species in an analysis.

Species concordance was conducted in two steps. First, a global test of concordance of each tentative group was conducted using the *kendall.global* function of the {vegan} R package (Oksanen et al. 2019), which tests the null hypothesis (H_0) of independence of all species in the group. If this hypothesis is rejected at the 5% significance level (after correction for multiple testing), the test indicates that at least two species are concordant, i.e. in positive rank correlation with one another across the landscape. One can then test the significance of the contribution of individual species to the concordance of their group using another test available in the function *kendall.post* of {vegan}. These a posteriori tests identify the species that form the hard core of a species group identified by clustering; the null hypothesis of that test is that a given species is monotonically independent of all other species in its subgroup (Legendre and Legendre 2012). That function also provides information about the means of the Spearman correlations of individual species with all the other species in their group.

To help identify the optimal number of subgroups in the community composition matrix of each trophic level, we conducted a Ward hierarchical cluster analysis (*hclust* function, {stats} package in R with argument method = 'ward. D2'; <www.r-project.org>) (Legendre and Legendre 2012). Beginning with two subgroups, we tested whether species within each cluster were mostly concordant (global concordance test with the *kendall.global* function), and which species contributed significantly to the group's concordance (a posterior test using the *kendall.post* function, {vegan} package). We also examined whether negative correlations among species were observed in a given subgroup following the procedure proposed by Legendre (2005) and described in a previous paragraph. That is, if negative Spearman means were observed, we further partitioned the community in three or more subgroups, until all species in a given subgroup were in positive correlation. For each trophic level and each corresponding concordance analysis, we tested which transformation among the chord, Hellinger or log–chord maximized the above criteria (Legendre and Borcard (2018) for details on the Box–Cox–chord transformation). We present the final species subgroups with dendrograms, highlighting (bold font and asterisk) the species that contributed significantly to their group's concordance (Supporting information). In particular, significance was tested using a permutational probability based upon 9999 random permutations as well as a Holm adjustment of the p-values for multiple testing; the Holm correction has been shown to be more powerful than the Bonferroni adjustment (Wright 1992, Legendre and Legendre 2012).

RV coefficient

Once the optimal number of subgroups was determined within each trophic level, we examined whether these subgroups were correlated among trophic levels using the RV coefficient (Fig. 1: 1.2) (Borcard et al. 2018). The RV coefficient is a squared multivariate generalization of the Pearson correlation coefficient, bounded between 0 and 1, where values closer to one indicate a greater proximity between two datasets (Legendre and Legendre 2012). We tested the significance of RV coefficients between pairs of subgroups using the *coeffRV* function of the {FactoMineR} package in R.

Taken together, the clustering and concordance analysis helped identify subgroups of concordant species, while the RV coefficient further examined how certain species that were concordant at one trophic level were correlated to groups of concordant species from other trophic levels. This helped provide a first glimpse at bottom–up or top–down species associations across lakes.

Species co-responses to environmental factors

Multiple factor analysis (MFA)

To examine whether the correlations identified by the species association analyses were due to common relationships with environmental variables, we conducted a correlative MFA (Escofier and Pagès 1994) on the phytoplankton, zooplankton, fish and environmental data (Fig. 1: 2.1); the analysis involved the four matrices and, using the function *MFA* from the {FactoMineR} R package (Le et al. 2008), projected sites, species and environmental data on a global PCA, allocating equal weights to each data matrix. Here, weighing is done by first running a PCA on each data matrix individually, and then dividing the variables in each matrix by the square root of the first eigenvalue obtained from their respective PCA (Borcard et al. 2018). The weighted data tables are then regrouped and submitted to a global PCA.

Given the large number of variables, we restricted the MFA to species and environmental variables identified as important by Pinel-Alloul et al. (1990a, b) as well as in our own analyses. That is, for each species matrix, we conducted a principal component analysis (PCA with scaling 1), and calculated the circle of equilibrium contribution (*cleanplot.pca.R* function; Borcard et al. 2018); any species projection vector longer than the radius of the equilibrium contribution circle on the first two PCA axes was interpreted as contributing more than average and was retained as a dominant species for the MFA. The same approach was used for the environmental matrix (PCA and circle of equilibrium contribution); however, to build on prior work, we further reduced the list of environmental variables by retaining only those related to the seven VARIMAX factors presented in Pinel-Alloul et al. (1990b). This eliminated manganese, potassium, iron, DIC and TIC, which had greater than average contributions to the environmental PCA conducted herein, but low factor loadings in Pinel-Alloul et al. (1990b). Reducing the number of species and environmental variables helped improve the readability of the MFA graphs. For each species matrix, we tested which transformation (chord, Hellinger or log–chord) captured the greatest proportion of variance explained (Borcard et al. 2018) and retained this transformation, whereas the environmental variables were standardized to control for differences in measurement units.

To explore any spatial patterns in the different MFA dimensions, we plotted the contributions of sites to the significant dimensions by colour coding them cool to warm according to their factor loadings. We complemented this with a variation partitioning that tested the role of purely spatial effects (latitude, longitude and fine-scale spatial structures based on distance-based eigenvector maps; db-MEMs; Borcard and Legendre 2002, Legendre and Legendre 2012) in structuring all three trophic levels (Supporting information). This also allowed us to quantify what proportion of the variation explained by the environmental factors was jointly explained by space, as well as the scale at which the environment is structured (broad, intermediate or fine), thus controlling for any spatial autocorrelation in the community–environment patterns observed in the MFA.

Latent variable models (LVMs)

Since the MFA was based on a subset of species and was restricted to linear covariances and correlations among variables, we used LVMs to examine linear and nonlinear co-responses (both positive and negative) among all species to the main abiotic environmental gradients of the study region using the *boral* function of the {boral} package in R (Fig. 1: 2.2) (Hui et al. 2016, 2018). We used LVMs to regress species abundance (Hellinger, chord or log–chord transformed) versus degree one (linear) and two (quadratic) polynomials of the environmental gradients to test the concept that species have a niche in environmental space that they tend to occupy. In contrast to the MFA (based on a subset of raw environmental variables), we used the first five orthogonal environmental dimensions of a PCA run on all environmental variables as predictor variables in the LVMs; these five PCA axes were similar to the seven VARIMAX dimensions identified in Pinel-Alloul et al. (1990a, b). The use of these five PCA axes reduced the number of computed LVMs (one for each predictor variable) and controlled for collinearity among predictors (all PCA axes are orthogonal and thus represent different and complementary environmental gradients or niche space axes).

Using the {boral} R package, we assessed the degree of co-response between any two species by first retaining the fitted values from the regression of each species versus a given environmental gradient, and then calculating the correlation between the fitted values of any two species using the *get.enviro.cor* function. Note that in a model without trait variables (as in the present study), the correlation coefficient provided by *get.enviro.cor* is a simple Pearson correlation (or the variance/covariance matrix as presented in Pollock et al. 2014). This provided a correlation matrix of similarities in the response among all possible pairs of species, where the sign and strength of the correlations among species-pairs fitted values are an indication of the degree of co-response (positive correlation among fitted values) or niche separation (negative correlation among fitted values) of the two species to the selected environmental gradient (Warton et al. 2015, 2016).

Co-response metrics were assessed for species within and among trophic levels. For the metrics calculated within a trophic level, we presented the significant negative and positive correlations among fitted values across all species using circular network diagrams (Letten et al. 2015 for details on R code adopted herein), where the strength of the correlation is represented by the thickness and darkness of the lines (grey scale) (Fig. 1: 2.2). For the metrics calculated among trophic levels, we summarized the proportion of significant negative and positive correlations among fitted values in histograms. This allowed us to compare how the proportion of significant correlations differed for LVMs conducted among trophic levels (i.e. phytoplankton-to-zooplankton, phytoplankton-to-fish and zooplankton-to-fish) from those conducted within (i.e. phytoplankton-to-phytoplankton, zooplankton-to-zooplankton and fish-to-fish).

Regarding LVM parameterization, due to the relatively small sample size and large amount of variability associated with the regression coefficients (graphically explored using the *coefsplot* function; not shown), and that we were working with sparse community ecology data, we considered weakly informative priors to stabilize MCMC sampling (arguments: prior.control = list (type = c ('cauchy', 'cauchy', 'cauchy', 'halfcauchy'), hypparams = c(2.5^2, 2.5^2, 2.5^2, 2.5^2)). A normal distribution was assumed and tested throughout all LVMs (family = 'normal'). The determination of significance of environmental correlations was based on the highest posterior density (HPD) intervals (Bayesian estimation approach for model fitting), where the environmental correlations across all MCMC samples are first calculated, and then 95% (default) HPD intervals are constructed for each correlation. Correlations are then deemed significant only if the intervals do not contain zero. Latent variables were also included (argument: num.lv=2) to account for other factors at play, such as missing covariates or biotic interactions. Including latent variables is also recommended to reduce the strength of positive co-responses to the environmental variables (that is, when latent variables are omitted, the model attempts to use the explanatory variables to explain all variance, whereas the inclusion of random effects (latent variables) can help diminish the importance of those fixed effects; Francis K. C. Hui, pers. comm.). As noted elsewhere (Letten et al. 2015, Warton et al. 2015), the selection of two latent variables offered a good compromise between model complexity, which increases rapidly with each additional latent variable, and sufficient characterization of species co-response patterns unaccounted by the environmental variables tested.

Structure of interactive networks

The final part of our statistical framework focused on the consequence of the differential responses of species to environmental gradients. That is, we tested for changes in species composition and species interactions among lakes, quantified which lakes had unique species composition and interactions, and whether this was related to their positions within the environmental landscape (i.e. are the sites located at the extremes of environmental gradients depleted in species and interactions?). To consider the effect of isolation both in terms of site remoteness and position within the hydrological network, we also explored the relationship between site uniqueness and altitude, latitudinal position and finer-scale spatial structuring (Supporting information).

Neutral interaction network

To estimate species interactions within each trophic level, we created a neutral interaction matrix, or network, based on species occurrence vectors. The interaction matrix was obtained by transforming a species abundance matrix into presence–absence (occurrence) data and multiplying the occurrences of species pairs at each site (Hadamard product of two species occurrence vectors; Canard et al. 2014). Thus, if two species co-occurred in one site, their Hadamard product will be 1 at that site. Overall, as neutral theory assumes that two species have a higher probability of interacting if they are both present at a given location, the interaction matrix effectively provides an indication of the possible interaction between any two species due to their random-chance co-occurrence.

Local contributions to beta diversity (LCBD) analysis

Total beta diversity (BD_{total}) was estimated as the variance of Hellinger-transformed community composition matrix (Legendre and Gallagher 2001) and the Ochiai-transformed species interaction matrix, computed as described in the previous paragraph. The BD_{total} index produces values in the [0, 1] range for Hellinger-transformed data (Legendre and De Cáceres 2013). To identify unique contributions of sites both in terms of their species composition and their species interactions, we calculated the local contributions of the site to BD_{total} of the community matrix (LCBD, Legendre and De Cáceres, 2013) and of the species-interaction matrix (LCBD-interactions, Poisot et al. 2017), respectively. To identify what made sites unique (higher or lower than average richness), we regressed the LCBD and LCBD-interaction indices on species richness and species interaction richness, respectively. Lastly, to help explain why certain sites were more unique in their contributions to beta diversity of species composition and/or species interactions, we regressed the LCBD and LCBD-interaction vectors of the sites against the main environmental dimensions (five environmental PCA axes) (Fig. 1: 3). The importance of site isolation was tested by regressing the LCBD vectors against lake altitude, latitude and distance-based eigenvector maps (Supporting information).

Results

Species associations within trophic groups and correlations among subgroups

The partition in two clusters, determined by Ward hierarchical clustering, was our starting point for the test for concordance in each trophic level. Subgroups were refined and we ultimately found that partitions in three (fish) and four (phytoplankton and zooplankton) subgroups were optimal (i.e. increased the number of species contributing significantly to their subgroup's concordance while reducing the number of negative correlations among species within any subgroup; Supporting information). Among the different transformations tested, the chord transformation provided the highest number of species with significant contributions in all trophic levels; these results are presented here.

For the phytoplankton, a large number of species contributed significantly to their subgroup's overall concordance (with 59, 67, 79 and 75% of species contributing significantly to their subgroup's concordance; Supporting information). However, given the large number of phytoplankton species, many of these contributions became non-significant following the Holm correction for multiple tests (down to 10, 0, 29 and 10%). Concordance analysis of the zooplankton community identified a slightly greater proportion of species with significant contributions than was observed for phytoplankton, with 71, 82, 86 and 67% of species contributing significantly to their subgroup's concordance (Supporting information); however, the Holm correction once again greatly reduced these percentages to 29, 18, 43 and 11%. For the fish, 60, 71 and 17% of the species contributed significantly to their subgroup's concordance (Supporting information). Following the Holm correction, the proportion of significant contributors fell to 20, 29 and 0%. Overall, among the three trophic levels examined, and after correction for multiple testing, the concordance among species was proportionately highest among zooplankton, but comparable among phytoplankton and fish.

When examining the multivariate correlations among the concordant subgroups from the three trophic levels (RV coefficients; Table 1), we noted that some subgroups had significant correlations across all trophic levels. In particular, fish species belonging to the second subgroup (Fish 2) were correlated with both phytoplankton (Phyto 1 and Phyto 3 subgroups) and zooplankton (Zoop 1 subgroup) species. In contrast, certain subgroups only displayed correlations with neighboring trophic levels. For instance, species from the zooplankton subgroup Zoop 4 were exclusively correlated to phytoplankton species from subgroup Phyto 2, and fish species belonging to the Fish 1 subgroup were correlated exclusively to species from zooplankton subgroups Zoop 1, Zoop 2 and Zoop 3.

Species co-responses to environmental factors

Species and subgroups of species found to be correlated to one another in the species association analysis (previous section) were also found to be correlated to the same environmental variables, as illustrated by the MFA (Fig. 2). For instance, fish and zooplankton species with the strongest contributions to the first MFA dimension (the brook charr – SAFO, *Salvelinus fontinalis* and a rotifer – COCO, *Conochilus unicornis*), were correlated to the same environmental conditions (co-inhabiting deep, large lakes in eastern Québec; Supporting information), and were likewise assigned to correlated subgroups (subgroups Zoop 1 and Fish 2; Table 1, Supporting information). The MFA also distinguished a cyanobacterial species (APNI, *Aphanothece nidulans*) and the common pike (ESLU, *Esox Lucius*), which tended to inhabit shallow, productive lakes in western Québec (sharing the MFA-1 niche space), but separated the second MFA dimension (MFA-2) driven mostly by lake alkalinity/hardness versus acidity (Fig. 2, Supporting information). Correspondingly, these two species belonged to uncorrelated subgroups (Phyto 2 and Fish 3; Table 1, Supporting information). Other species with strong negative contributions to MFA-2, a cyanobacteria (MEMI, *Merismopedia minima*) and two rotifers (KETA, *Keratella taurocephala* and POVU, *Polyarthra vulgaris*), tended to co-inhabit more acidic lakes, and were all classified in correlated subgroups (Phyto 4 and Zoop 3; Table 1, Supporting information). The remaining, significant MFA axes (MFA 3–5; Supporting information) showed further clustering of lakes according to differences in community composition and environmental conditions (Supporting information), such as species inhabiting humic (DOC and TOC) and acidic (Al, H) waters versus species that preferred clearer, more alkaline waters.

The MFA dimensions likewise separated lakes spatially (Supporting information), consistently with their hydrographic region designation (Fig. 1 in Pinel-Alloul et al. 1990a for a map of hydrographic regions). For instance, the first few dimensions separated sites from north-to-south and east-to-west (Supporting information), while the fifth dimension separated sites according to finer scale differences (e.g. lakes 210C and 201C had higher than average DOC and TOC concentrations whereas lakes 33A, 53 and 224A had lower than average DOC and TOC concentrations; Supporting information). Though the role of the purely spatial effects was deemed non-significant in shaping the zooplankton community in a prior variation partitioning (Pinel-Alloul et al. 1995), we provide an updated version of this analysis, considering

Table 1. RV coefficients (lower triangular) and p-values (upper triangular) among groups pertaining to different trophic levels, identified by concordance analysis (Kendall *W*). Grey text corresponds to non-significant correlations ($p > 0.05$). Boxes highlight significant correlations among groups pertaining to different trophic levels. (Note: boxes are mirrored in the upper and lower triangular sections of the matrix.)

	Phyto 1	Phyto 2	Phyto 3	Phyto 4	Zoop 1	Zoop 2	Zoop 3	Zoop 4	Fish 1	Fish 2	Fish 3
Phyto 1		0.484	0.764	0.889	0.102	0.714	0.660	0.434	0.564	**0.019**	**0.002**
Phyto 2	0.08		0.493	0.167	0.191	**0.014**	0.094	**0.027**	0.686	0.714	0.063
Phyto 3	0.05	0.06		0.088	**0.026**	0.870	0.851	0.724	0.642	**0.00002**	0.278
Phyto 4	0.07	0.10	0.12		**0.016**	0.625	**0.001**	0.744	0.656	0.097	0.063
Zoop 1	0.09	0.06	**0.11**	**0.13**		**0.0004**	0.067	0.517	**0.001**	**0.005**	0.377
Zoop 2	0.07	**0.15**	0.04	0.06	**0.22**		0.139	0.201	**0.007**	0.405	0.068
Zoop 3	0.08	0.12	0.04	**0.21**	0.10	0.10		0.653	**0.038**	0.135	0.085
Zoop 4	0.06	**0.13**	0.02	0.04	0.03	0.07	0.04		0.127	0.520	0.205
Fish 1	0.07	0.05	0.05	0.06	**0.22**	**0.16**	**0.14**	0.08		0.075	0.472
Fish 2	**0.12**	0.02	**0.26**	0.08	**0.16**	0.04	0.08	0.02	0.08		**0.00001**
Fish 3	**0.19**	0.11	0.07	0.12	0.04	0.10	0.11	0.06	0.05	**0.30**	

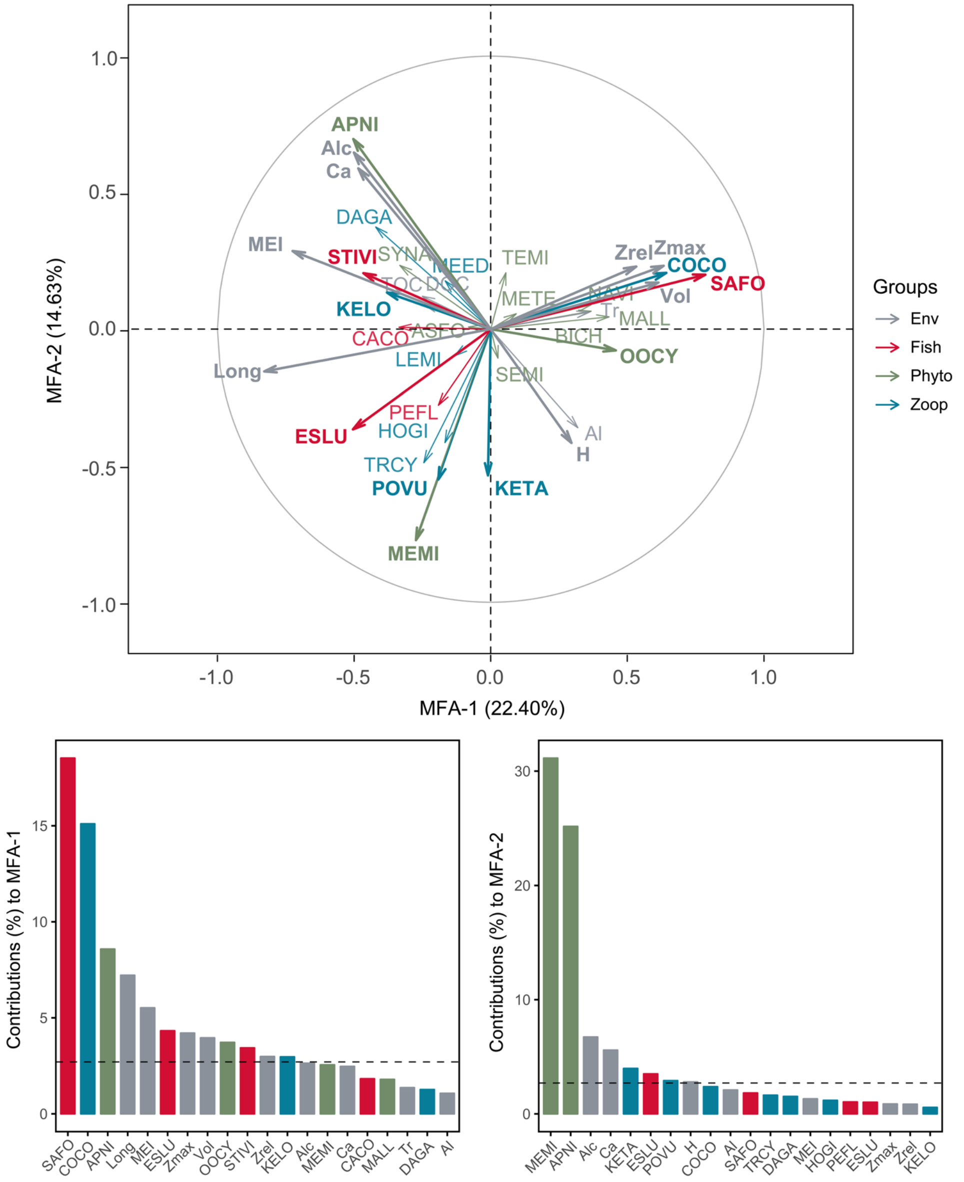

Figure 2. Multiple factor analysis (MFA) of the dominant phytoplankton, zooplankton, fish species and environmental variables. Ordination of quantitative variables on the first two MFA axes. Associated barplots show the % contributions of the variables to the variances of MFA axes 1 and 2; important variables have contributions higher than the dashed lines, which represent the expected values under the hypothesis of equality of the contributions. The chord transformation of the phytoplankton and zooplankton communities and the Hellinger transformation of the fish community explained the largest fractions of variance; they are presented here, though comparable results were obtained when either the chord, Hellinger or log–chord transformations were applied to the three matrices.

all three trophic levels as well as fine-scale spatial structures (db-MEMs), to account for potential spatial autocorrelation in the present dataset (Supporting information). As observed in the earlier study however, variation partitioning failed to identify a strong effect of spatial structuring and autocorrelation, to the exception of a very broad-scale trend (latitude and longitude) in the community data.

When analyzing the similarity or dissimilarity in the co-responses of all species to the five, orthogonal environmental dimensions (PC1–PC5; Fig. 3, Supporting information) using LVMs, we noted that a greater number of phytoplankton species separated (Fig. 4a) or shared (Supporting information) the five niche dimensions than did the zooplankton (Fig. 4b; Supporting information) or fish (Fig. 4c; Supporting information) species. With respect to niche separation (Fig. 4), the first and dominant environmental dimension (PC1), representing an alkalinity/hardness to natural acidity gradient (Fig. 3), displayed the greatest number of significant negative correlations among fitted responses for all three trophic levels (Fig. 4). Phytoplankton and zooplankton species separated additional environmental dimensions related to the physico-chemical and morphometric niche space of lakes (e.g. PC3:

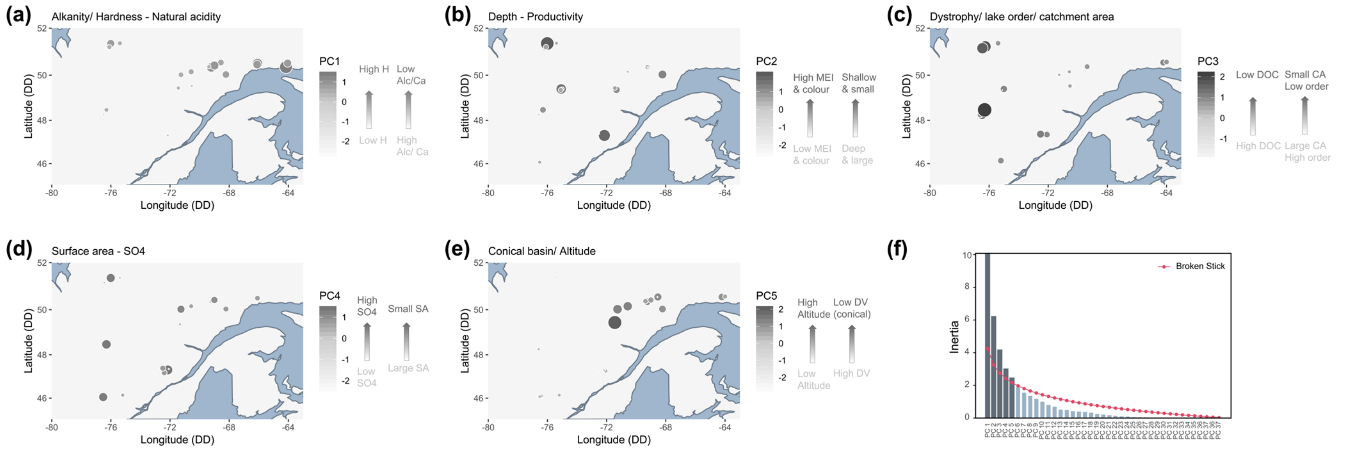

Figure 3. (a–e) Maps of the five environmental dimensions (principal component axes from the PCA run on all environmental variables) used as predictor variables in LVMs analysis. In each panel, point size and shade represent the position of the lake along the given PCA axis, where the two arrows are explanatory variables highly correlated to the PCA axis shown. DV = development of lake volume, where a low DV corresponds to a basin whose 3-dimensional shape approaches that of a cone. (f) Scree plot of eigenvalues (shown in decreasing order of importance) and broken stick model predictions illustrating that only the first five axes of the PCA were significant (i.e. have eigenvalues larger than pieces of a randomly broken stick of length 1).

dystrophy, lake order and catchment area, PC4: lake surface area, PC5: altitude and lake shape and PC2: lake depth, volume, water turbidity and MEI; Fig. 4a–b). Variability in lake morphometry (PC2) and productivity (MEI; PC4) were also important niche dimensions for fish (Fig. 4c).

Interesting patterns emerged from these LVMs that built on the previous analyses (RV coefficients and MFA). For instance, among the species required to maintain negative co-responses within each community (grey circles; Fig. 4), niche separation was predominantly among species belonging to different concordance analysis subgroups (phytoplankton: n = 79 or 96%; zooplankton: n = 42 or 98%; and fish: n = 8 or 100%; Supporting information). There was a small portion of species from the same concordance analysis subgroup that showed negative co-responses to the same environmental dimension (phytoplankton: n = 3 or 4%; zooplankton: n = 1 or 2%), however, these pairs typically included one species that was only weakly associated to its concordance subgroup (e.g. SCEN, a significant contributor to subgroup Phyto 4, separated the PC3 niche space with METE, a non-significant contributor to subgroup Phyto 4; Supporting information). We also found that species identified as important species in the MFA ordination (Fig. 2) displayed some of the most pronounced niche separations (Fig. 4). That is, phytoplankton species with greater than average contributions to the MFA (OOCY, MEMI, BICH, ASFO, APNI, MALL and METE; Fig. 5) presented the most important niche separations in response to the main abiotic factors (Fig. 6). Likewise, zooplankton species (especially the rotifers KELO, COCO, KETA, KECO, the cladocerans HOGI, DASC, DAGA, BOLO, and the copepods LEMI, MEED, CYCS) and most fish species (SAFO, STIVI and ESLU) that contributed greatly to the MFA showed significant negative co-responses to the environmental niche space (Fig. 4, 5, Supporting information).

When comparing the proportion of positive and negative LVM co-responses among trophic levels versus the proportion within the same trophic level (Supporting information), we noted that the patterns of niche separation (black bars) among zooplankton and phytoplankton (phyto-zoop) were most similar to the niche separation patterns among zooplankton and fish (fish-zoop), lacking a separation along the PC2 (or lake productivity and depth) niche dimension.

Consequence on the structure of interaction networks on diversity patterns

As a result of the niche separations identified above, we found that lakes varied in their species composition and estimated number of species interactions. Regionally, the total number of species (gamma diversity) was greater for the phytoplankton community (n = 87 species) than the zooplankton (n = 34 species) or fish (n = 18 species) communities. Similarly, the estimated number of species interactions was greater for phytoplankton (67 species interacting) than for zooplankton (30 species) and fish (6 species), though relatively to the total number of species within each trophic level, zooplankton had the largest proportion of species involved in neutral-theory based interactions (involving 89% of all zooplankton species, versus 77% and 35% of the phytoplankton and fish species that were involved in species interactions, respectively).

Across lakes, the turnover in species composition (beta diversity; BD_{total}) was greater for phytoplankton and fish ($BD_{total} = 0.61$ and 0.70, respectively, representing mid to high end of the [0–1] BD_{total} range for Hellinger transformed data), than zooplankton ($BD_{total} = 0.45$) (Fig. 7a–c; Supporting information). The turnover in species interactions was overall more dynamic than that of species composition, and greater for phytoplankton (BD_{total}-interaction = 0.81) than fish (BD_{total}-interaction = 0.68)

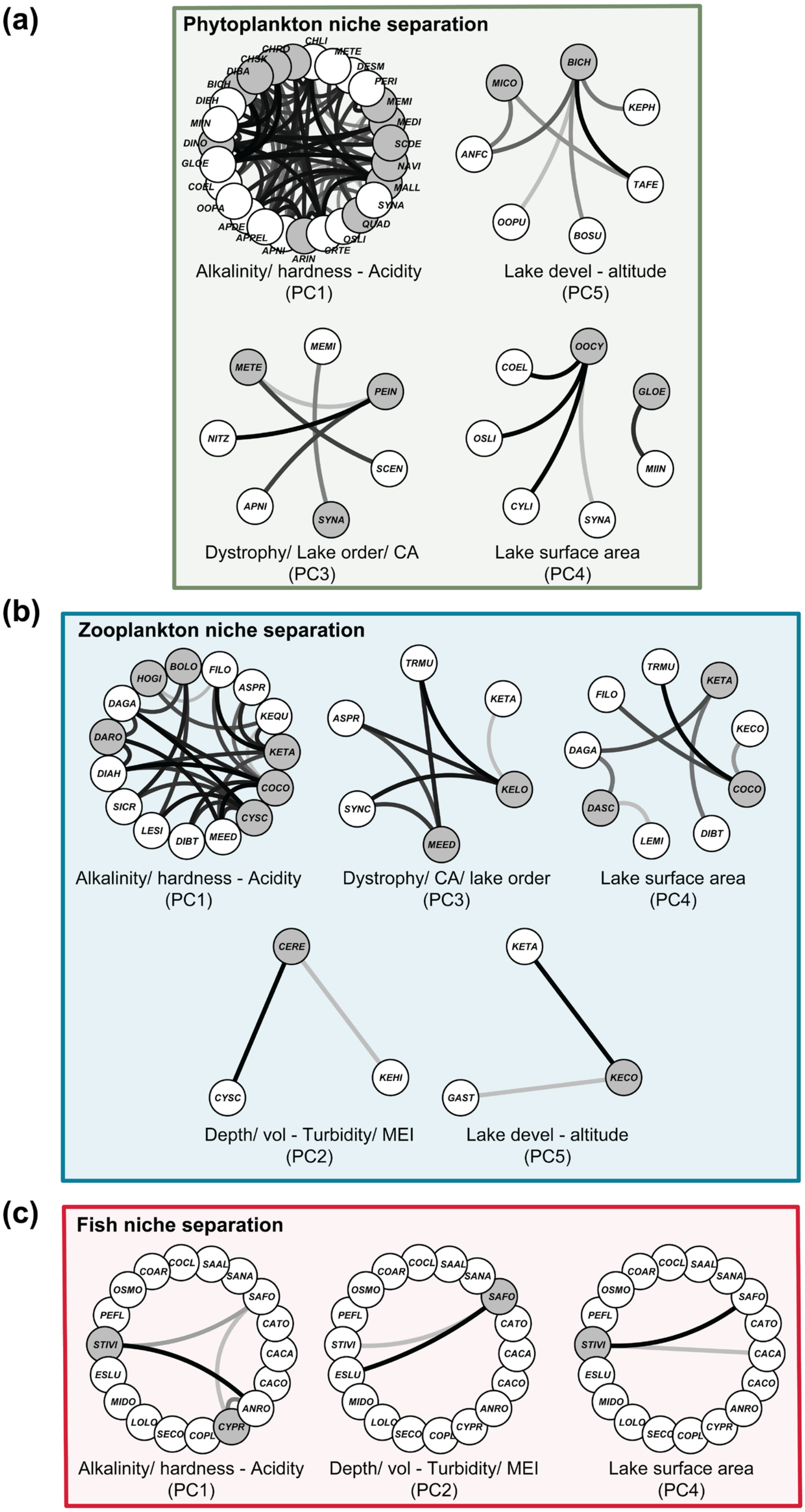

Figure 4. Significant negative pairwise species co-responses of (a) phytoplankton, (b) zooplankton and (c) fish to the environmental dimensions (five principal component axes) derived from single-predictor LVMs (i.e. niche separation). Connecting lines between nodes indicate significant negative correlations between the species responses fitted to an environmental dimension (PCs 1–5). Line thickness and grey scale indicate the strengths of the negative correlations between vectors of fitted values. Grey-filled nodes indicate the minimum vertex cover; that is, the smallest combination of species that need to be removed to break all negative associations in a graph.

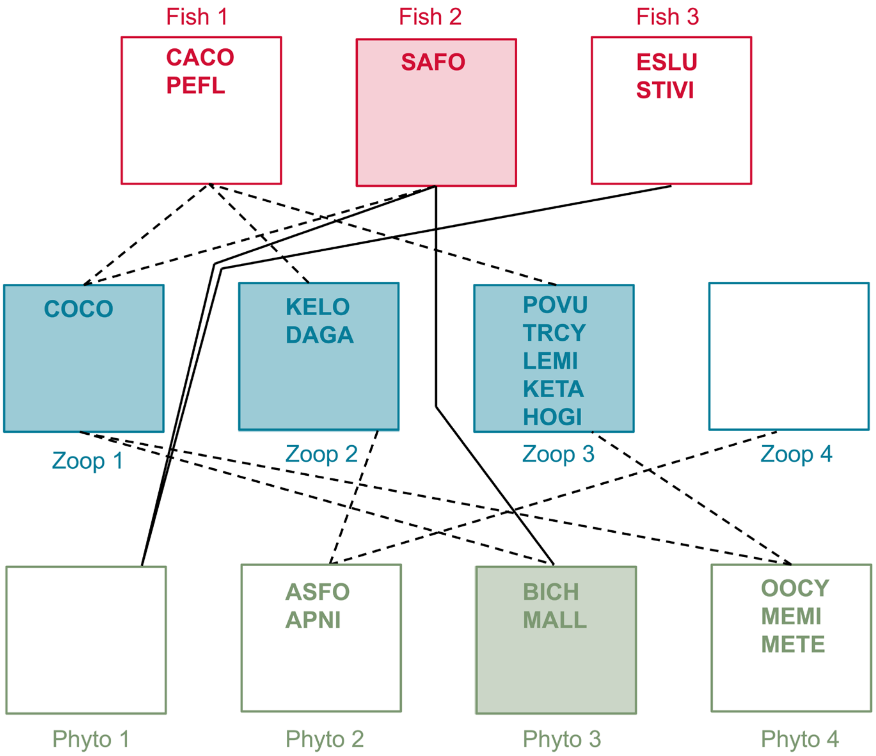

Figure 5. Summary diagram of the RV and MFA analyses. Boxes indicate the phytoplankton (Phyto 1–4), zooplankton (Zoop 1–4) and fish (Fish 1–3) subgroups identified by the concordance analysis. Black lines connecting boxes summarize the significant RV correlations among subgroups from different trophic levels (boxed in cells in Table 1). Full black lines represent significant RV correlations among subgroups that skip one trophic level (i.e. between phytoplankton and fish), whereas dashed black lines represent significant RV correlations between subgroups in neighbouring trophic levels (i.e. between zooplankton and fish, or between phytoplankton and zooplankton). Filled-in boxes (i.e. Fish 2, Zoop 1, Zoop 2, Zoop 3 and Phyto 3) represent subgroups with significant RV correlations with all trophic levels. Species names within each box identify the species with greater than average contributions to MFA dimensions 1–5 (Fig. 2, Supporting information).

and zooplankton (BD_{total}-interaction = 0.69; Fig. 7d–f, Supporting information).

Although lakes were generally more diverse in their species interactions (BD_{total}-interaction ranging from 0.68 to 0.81) than in species compositions (BD_{total} ranging from 0.45 to 0.70), the metrics were related; as a site's uniqueness (or local contribution to species beta diversity; LCBD) increased, so did its contribution to species interactions diversity (LCBD-interaction), notably so for phytoplankton ($r = 0.56$, $p < 0.0001$) and zooplankton ($r = 0.53$, $p = 0.0001$). Thus, not surprisingly, a unique species composition (high LCBD) tended to generate unique interactions among species (high LCBD-interaction). The LCBD and LCBD-interaction were not significantly correlated for the fish community due to an order magnitude lower LCBD-interaction in twelve sites; these sites only had one fish species (thus, no interaction possible). By removing these twelve sites, we noted that LCBD-interaction likewise increased with species LCBD for the fish ($r = 0.50$; $p = 0.002$). The rate of increase in LCBD-interaction per unit increase in species LCBD was overall comparable among all three trophic levels (Δ of 0.29, 0.23 and 0.24 for phytoplankton, zooplankton and fish, respectively).

In general, lakes that were unique in species composition (high LCBD) and interaction (high LCBD-interaction) had lower than average richness (Fig. 8). That is, species richness (phytoplankton range: 8–39, zooplankton range: 4–18; fish range: 1–6) was negatively related to LCBD values, and the richness in species interactions (phytoplankton range: 28–741; zooplankton range: 6–153; fish range: 1–15) was also inversely related to LCBD-interaction values. In terms of relationship with anthropogenic impact, we noted that low species richness in some lakes, and its effect on species interactions, was related to extreme environmental conditions. For phytoplankton, LCBD indices increased (weakly; R^2-adj = 0.09, $p = 0.046$) with the alkalinity-to-acidity dimension (PC1) (Fig. 9a). Thus, lakes with unique phytoplankton assemblages tended to be more acidic and had few phytoplankton species (low richness). Several phytoplankton species were also found to separate this niche dimension (i.e. displayed negative correlations among their fitted response; Fig. 4a). In contrast, the LCBD-interaction for phytoplankton was not related to the alkalinity-to-acidity dimension (Fig. 9d) nor to any of the other four dimensions. For zooplankton, LCBD indices decreased with the alkalinity-to-acidity dimension (PC1) (Fig. 9b). Thus, in contrast to phytoplankton, sites with more unique zooplankton assemblages (high LCBD, low richness) were more alkaline. Zooplankton richness was greater in naturally acidic lakes (eastern part of Québec).

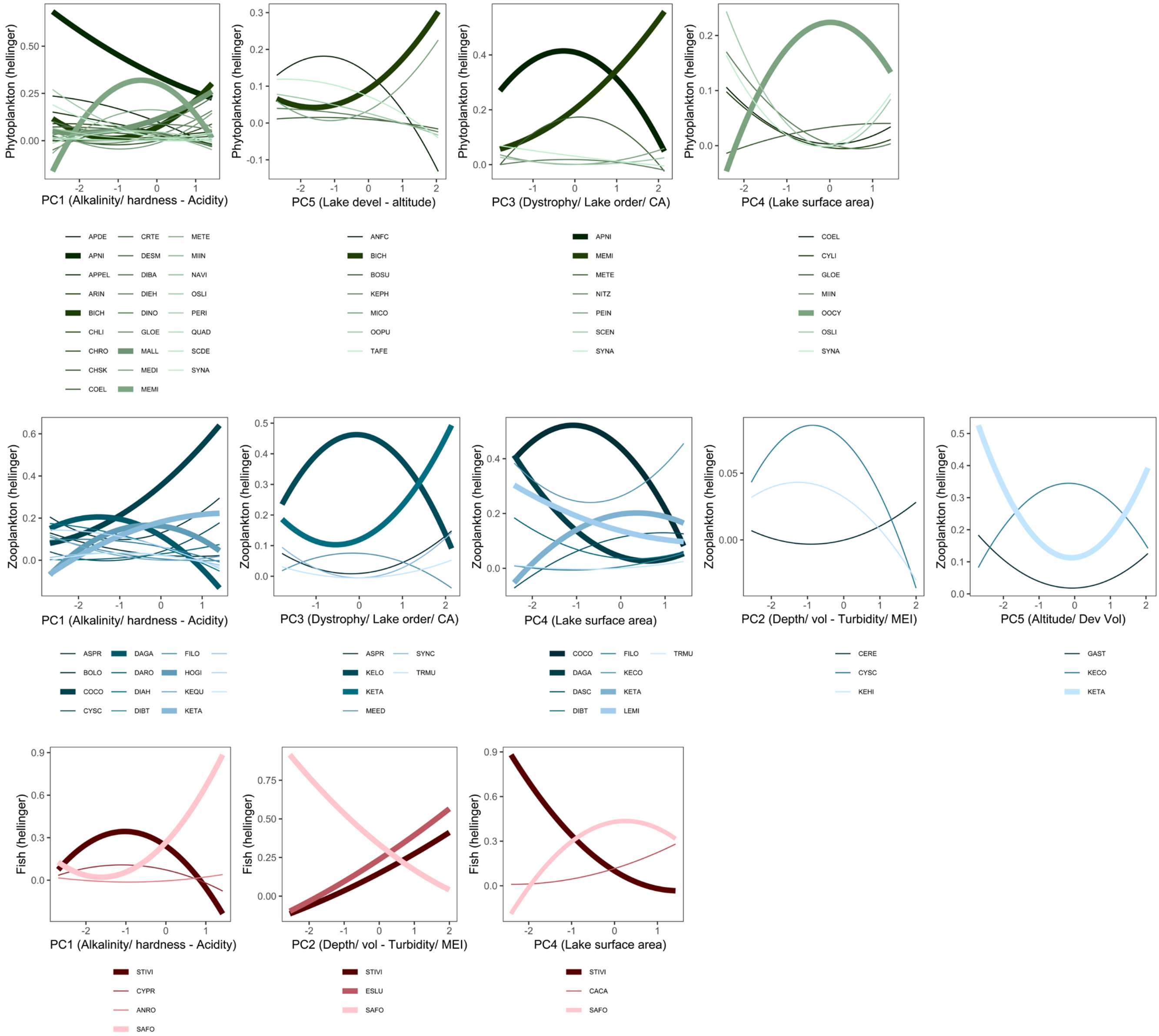

Figure 6. Nonlinear (quadratic polynomial) relationships illustrating the significant niche separation of phytoplankton, zooplankton and fish species identified by the LVM analysis (Fig. 4). That is, for each panel, only species with significant niche separation are shown. Bold lines highlight the species identified by MFA as having a greater than average contribution to the MFA axes 1–5 (Fig. 2, Supporting information).

LCBD-interaction for zooplankton was related to two environmental dimensions (R^2-adj = 0.54, $p < 0.0001$): greater in more alkaline lakes (– association with PC1) (Fig. 9e) and high elevation, and in conical lakes (+ unimodal association with PC5) (not shown). Fish LCBDs were not related to any of the five environmental dimensions (Fig. 9c).

In terms of site isolation, we failed to identify a significant relationship between the LCBD metrics and lake altitude, while latitude was only important for the zooplankton community (Supporting information). However, zooplankton richness (high uniqueness) decreased towards the south–west and increased towards more remote northern sites. The relationship between the LCBD metrics and longitude, or finer spatial structuring, strongly mirrored those of the environmental gradients (e.g. the increase in zooplankton LCBD-interaction towards the south–west, and importance of db-MEM2 and db-MEM4, followed the PC1 and PC5 gradients, respectively; Fig. 3, Supporting information).

Discussion

By examining a unique dataset (three trophic levels sampled simultaneously across 49 boreal lakes), sampled during a key anthropogenic period (1980s acidification), and combining for the first time novel and complementary statistical

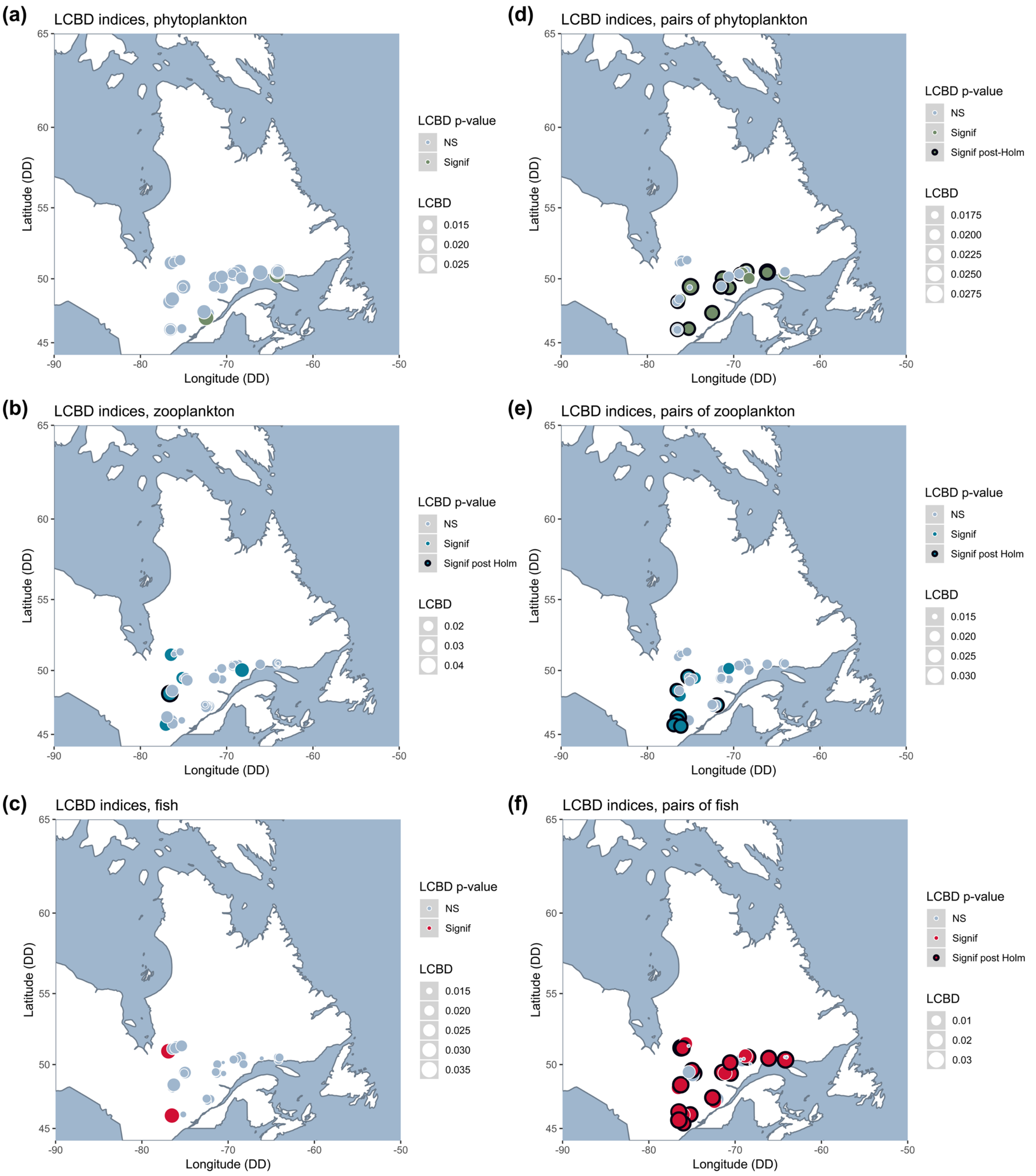

Figure 7. Maps of local contributions of species and species interactions to beta diversity (LCBD and LCBD-interactions) for each site and trophic level. Point sizes correspond to the LCBD and LCBD-interaction values, where significant LCBDs are shown in green (phytoplankton), blue (zooplankton) and red (fish) filled points. LCBDs that remained significant after Holm correction have points with black borders. Sites with non-significant LCBD and LCBD-interactions are shown in slate grey. Note: some closely clustered sites have been slightly moved on the panel maps to allow visualization of all points.

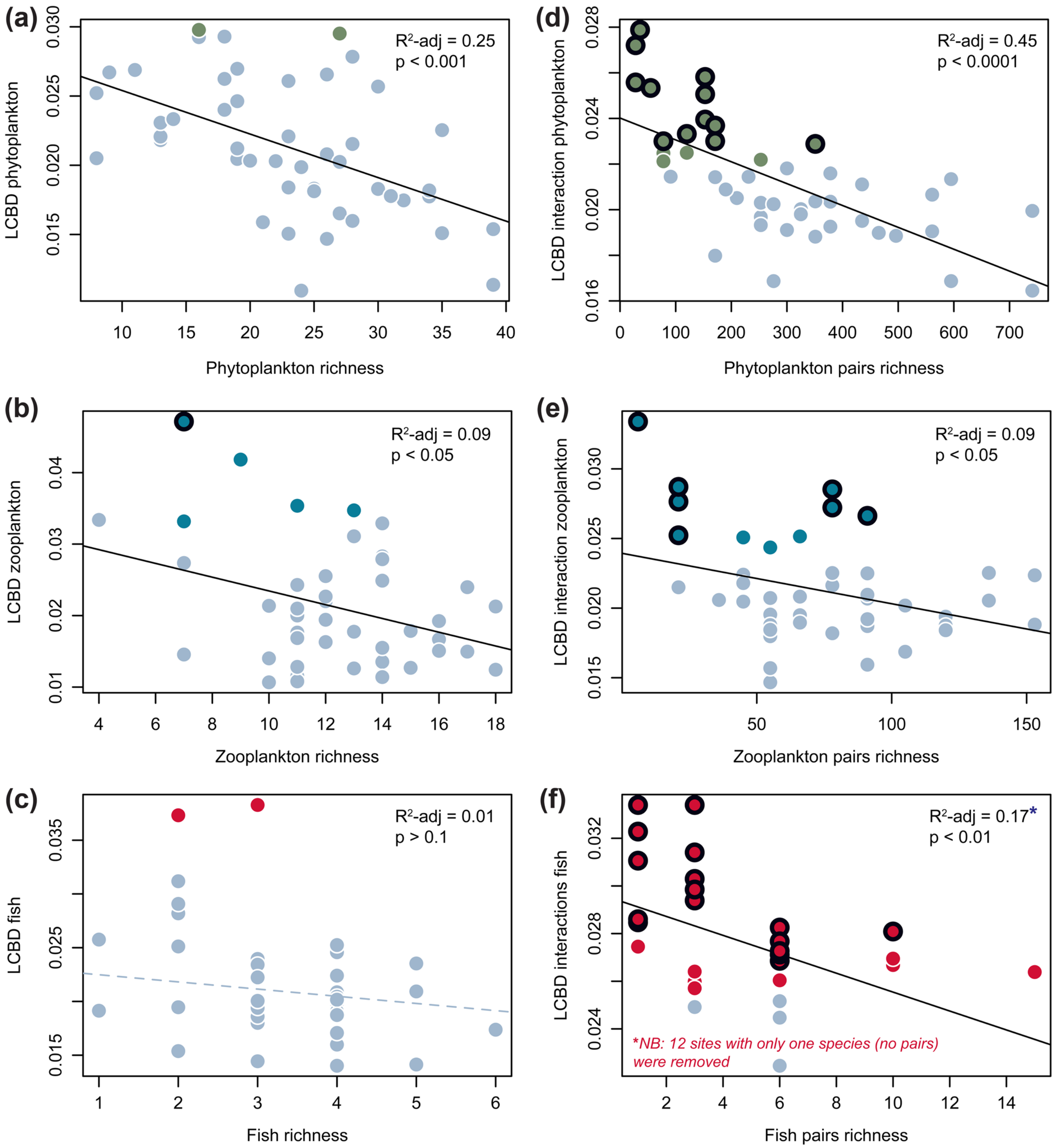

Figure 8. Relationships between the local contributions of sites to beta diversity (LCBD) and richness. (a–c) LCBD for species abundance data versus species richness. (d–f) LCBD-interactions versus interaction richness. Significant LCBDs are shown in green (phytoplankton), blue (zooplankton) and red (fish) filled points. LCBD values that remained significant after Holm correction have points with black borders. Sites with non-significant LCBD or LCBD-interaction values are shown in slate grey.

approaches (concordance analysis, RV coefficient, MFA, LVM and LCBD analysis on neutral interaction networks), we provided a thorough overview of the distribution patterns and food web interactions of communities belonging to three trophic levels in relation to a broad-scale environmental gradient. In particular, our framework helped show that certain phytoplankton, zooplankton and fish species were significantly correlated within and among trophic levels

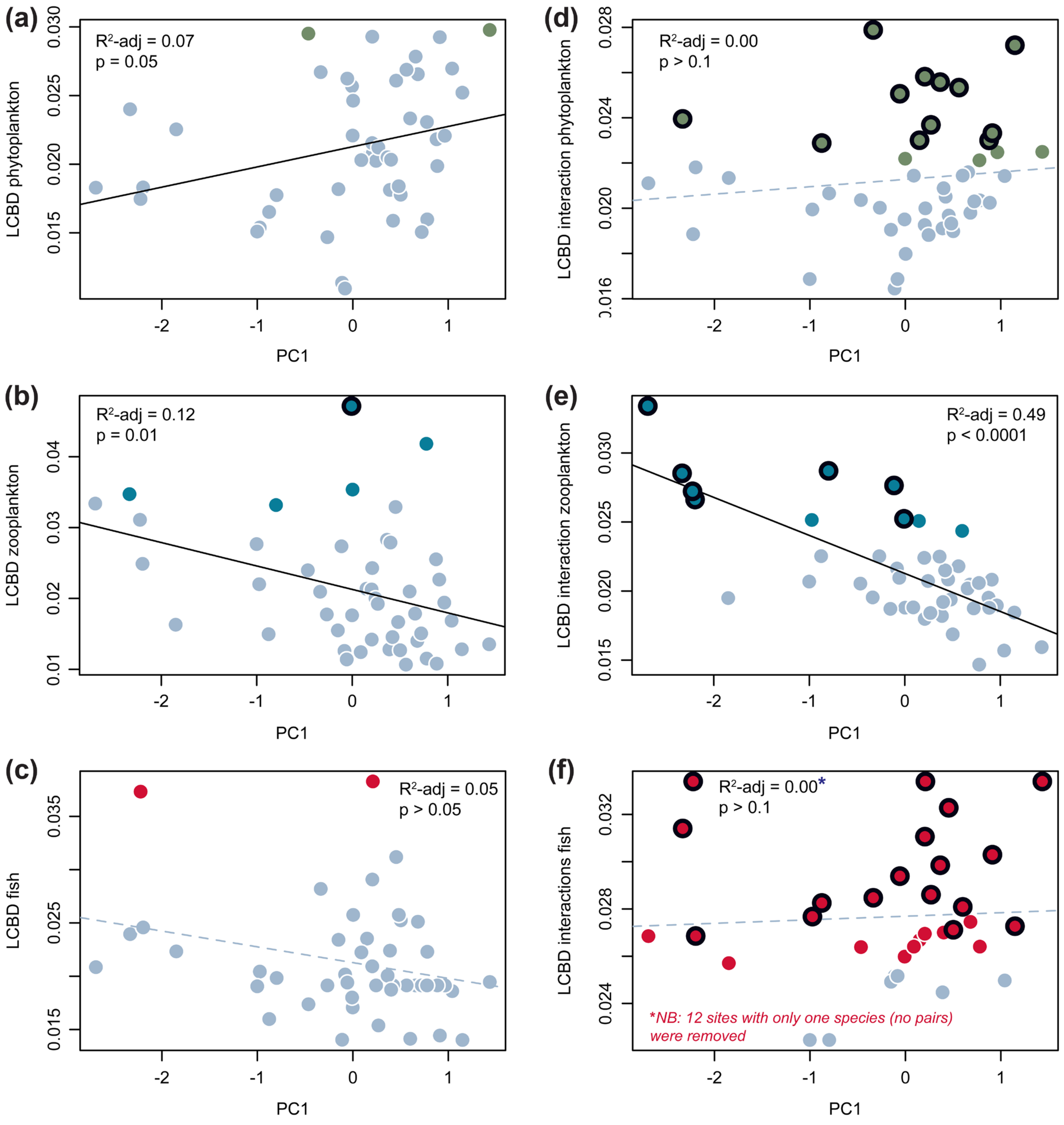

Figure 9. Relationships between local contributions of sites to beta diversity (LCBD) and PC1 representing an environmental gradient from high to low alkalinity and low to high natural acidity (Fig. 3, Supporting information). (a–c) LCBD species versus PC1 and (d–f) LCBD-interactions versus PC1. Significant LCBD values are shown in green (phytoplankton), blue (zooplankton) and red (fish) filled points. LCBD values that remained significant after Holm correction have points with black borders. Sites with non-significant LCBD and LCBD-interaction values are shown in slate grey.

(concordance analysis and RV coefficient) and that these species were also correlated to the same environmental conditions (MFA). We then tested the hypothesis that these strong and dominant biotic and abiotic correlations gave way to niche partitioning among dominant and sub-dominant species by examining how niche dimensions within multispecies communities responded to environmental gradients (LVM). This showed that groups of positively associated species apportioned the environmental dimensions with other groups of positively associated species. In turn, the opposing response of multispecies communities to environment heterogeneity had important consequences on the structure of interaction networks, whereby lakes located at environmental extremes displayed the highest dissimilarity in species composition and species interactions, as well as lower richness, relative to other lakes. This observed multi-trophic co-occurrence at local scales (within a lake) constrained by similar environmental spatial heterogeneity at regional scales (among lakes) does not, however, imply direct causality, but suggests a phenomenon underlying mass-effect dynamics (Liebold et al. 2004).

Multi-species association and trophic interactions across food webs

Among the three trophic levels examined, zooplankton displayed the greatest number of correlations per unit species with other trophic levels, suggestive of the important role of certain zooplankters as a trophic linkage between the phytoplankton and fish communities (Fig. 5). In particular, five species of rotifers (POVU, COCO, TRCY, KELO and KETA), two species of cladocerans (HOGI and DAGA) and one calanoid copepod species (LEMI) were associated with different species of the fish and phytoplankton communities. These same species were previously found to be the most discriminant zooplankters, responding to the main abiotic (acid inputs) and/or biotic (spiny water flea invasion) gradients in lacustrine landscapes in southern Québec, northern Ontario and Wisconsin (USA) (Pinel-Alloul et al. 1995, Rusak et al. 2002, Yan et al. 2008). The keynote zooplankters may also be subjected to top–down effects resulting from competitive interactions between salmonid and catastomid fish. This is most notable when specialized zooplanktivores such as the brook charr (SAFO) are pushed out of the littoral into the pelagic when living sympatrically with more competitive benthivorous fish such as the yellow perch (PEFL) (Magnan 1988, Tremblay and Magnan 1991, Lacasse and Magnan 1992, Bourke et al. 1999). In turn, these biotic interactions could be felt through the trophic pyramid down to the phytoplankton, where a change in the size and structure of the zooplankton community could alter the trophic pathways connecting fish to primary producers. This link may explain why the proportion and pattern of positive and negative co-responses among zooplankton and phytoplankton (phyto–zoop) were comparable to those among zooplankton and fish (fish–zoop) (Supporting information).

Cascading versus contrasting outcomes among trophic levels

The patterns in multi-trophic niche separation among species observed in this study (Fig. 6) indicate that lacustrine environmental gradients, e.g. alkalinity to natural acidity, lake size, productivity, transparency and colour (dystrophic versus clear lakes), along the west-to-east longitudinal geographical gradient, were important drivers of food web structures among boreal lakes in southern Québec, as depicted earlier for the phytoplankton and zooplankton communities (Lachance et al. 1984, Kelso et al. 1986, Pinel-Alloul et al. 1990a, b). The greater importance of abiotic factors, over that of biotic, in controlling broad-scale patterns in lacustrine landscapes would lend support the multiple forces hypothesis, which assumes that across broad-scale environmental gradients, regional changes in abiotic factors associated to climate and lake features (water chemistry, morphology) will have dominant effects on community composition, compared to local changes in biotic factors related to competition and predation processes (Pinel-Alloul 1995, Pinel-Alloul et al. 1995). Similar studies also depicted the importance of abiotic control for structuring phytoplankton communities in Newfoundland and Labrador lakes (Earle et al. 1987) and zooplankton communities in northeastern Ontario lakes (Keller and Pitblado 1984). Furthermore, a previous analysis looking at the relative influences of space, abiotic and biotic factors on the zooplankton community of the set of lakes examined here had shown that the abiotic contribution (physical and chemical factors: 31% of variance explained) was more important in explaining the total variance in zooplankton communities than the biotic contribution (phytoplankton or fish communities: 11% or 16%) when analysing independently each type of factors, and controlling for the spatial structure by a third-degree polynomial of the geographic coordinates used as covariables (Pinel-Alloul et al. 1995). In an additive approach including all spatial and environmental components, this prior variation partitioning analysis had indicated that the environmental contribution (either pure or spatially structured) remained the same independently of the geographic positions of the lakes, and that the purely spatial fraction was not significant. None of these prior studies, however, had developed a multi-trophic perspective, as examined herein. By extending the previous study using concordance and co-responses across multiple trophic levels, we showed important biotic network effects among the phytoplankton, zooplankton and fish. The distribution patterns of keynote species within the abiotic niche space (LVM) characterized by the five environmental dimensions (PC1–PC5) were not easy to interpret and yielded ambiguous results as patterns were evidently not governed solely by the major abiotic factors. Instead, we observed a relatively complex network of multiple abiotic and biotic environmental factors acting differently at regional and local scales. Indeed, food web networks seemingly depended on biotic factors such as competition and predation within and among trophic levels (Fig. 5).

Interestingly, and perhaps as a consequences of these complex interactions, the effect of abiotic gradients differed across trophic levels. That is, although the three trophic levels were constrained by the same environmental drivers and the dominant species from the three trophic groups were correlated (Fig. 2, Supporting information), the importance of each environmental gradient varied among the trophic levels (Fig. 4), as did their effects on species richness and turnover (Fig. 9). In terms of differences in the degree of niche separation, phytoplankton and zooplankton separated several physical, chemical and morphometric niche dimensions, whereas fish only separated three dimensions related to the lake morphometry and the morphoedaphic index (Fig. 4). Furthermore, smaller organisms (phytoplankton), less subject to dispersal limitation, showed a greater number of species with significant niche separation than larger, more constrained organisms (zooplankton and fish) across the lake landscape (Fig. 4). This supports other research suggesting that dispersal ability related to organism size in aquatic ecosystems determines the relative role of environmental filtering (Liebold et al. 2004). When considering each trophic level, a small-scale study also showed that zooplankton and fish are more constrained by dispersal than phytoplankton and therefore more likely operate as metacommunities across the lacustrine landscape in southern Québec (Beisner et al. 2006).

Our analysis also highlighted that although species turnover (LCBD) and species interaction turnover (LCBD interaction) were greater for phytoplankton due to the higher number of species, zooplankton played a crucial role in diversity variation, showing the greatest relative amount of species interactions proportionate to the number of species. In terms of trends and drivers of turnover, we noted a negative correlation between richness and site uniqueness (LCBD) across all three trophic levels. This negative correlation is not a general case for all ecosystems (large LCBDs in some systems indicate rare species combinations; Legendre and De Cáceres 2013), but suggests that lakes with exceptional natural conditions, or subjected to pollution or other man-made alterations, harboured a reduced and different fauna and flora (e.g. proximity to mining towns such as Rouyn-Noranda in Québec). We examined this further by regressing the LCBD metrics against the five environmental PCA axes and found that although the alkalinity to acidity gradient showed the greatest amount of niche separation for all trophic levels, the directional change in beta diversity and species richness with respect to this gradient differed among the three trophic levels (Fig. 9). In particular, phytoplankton species richness decreased whereas zooplankton richness increased in more naturally acid lakes (eastern part of Québec; Fig. 3, Supporting information). Correspondingly, the phytoplankton species that contributed the most to beta diversity (e.g. the cyanobacteria *Aphanothece nidulans*) decreased in more acidic, low-alkalinity lakes, which contrasted the increase in zooplankton species that contributed most to beta diversity (e.g. the rotifers *Conochilus unicornis*, *Kellicottia longispina*, *Polyarthra vulgaris*). The fish species that contributed the most to beta diversity (the brook charr, *Salvelinus fontinalis*) also increased in abundance in more acidic lakes (Fig. 6).

Future outlook

Recently, long-term changes in the spatial patterns of zooplankton assemblages in 73 lakes across the same geographical south–west to north–east range in southern Québec was examined in light of regional and local variations in climate, water chemistry and lake environments, providing a comparison of two years (1982 and 2017) of sampling spanning a 35-year period (Couture et al. 2020). During this time, in spite of a sharp decrease in acidic deposition (based on sulfate concentrations), only minor changes in pH and calcium concentrations were observed in the study lakes. Consequently, no major changes in zooplankton assemblages were detected since the 1980s. The 2017 lake survey in southern Québec supports a multiple forcing of spatial patterns in zooplankton community by large-scale gradients in climatic conditions, lake exposure to acidic deposition and local-scale changes in lake water quality and morphology, as observed in this study for multi-trophic species food web networks. Overall, the examination of long-term changes (1982–2017) of these aquatic communities showed their temporal stability along a large gradient of alkalinity/hardness – acidity, as depicted by the PC1 dimension in our study.

Interactions among competitive and predation processes, and environmental gradients will likely become increasingly complex and multi-directional under future climate change, for which broad-scale food web studies with a thorough examination of multi-trophic responses will be crucial. Notably so given that the effects of natural drivers and anthropogenic stressors on freshwater species richness and community structure were shown, in a recent review (Stendera et al. 2012), to be controlled by different sets of factors (historical, local, regional, abiotic and biotic) depending on the ecosystem and type of organisms. Ultimately, our study developed a new framework to test how ecological processes and abiotic factors affect multi-trophic species richness and interactions in aquatic ecosystems: we showed some relationships between food web structuring, on the one hand and beta diversity on the other. We suggest that our framework has a great potential to help improve our understanding of the complex response of aquatic ecosystems in a world increasingly driven by multiple, cumulative stressors.

Speculations and alternative viewpoints

The co-authors agree that the responses of aquatic food webs to changes in environment conditions along geographical gradients involving climate, watershed geology and water quality of lakes are complex. They also stress the importance of the influence of less well-understood biotic conditions such as competitive and predation interactions, as well as species population features (life-history, induced predation defence, etc.). B. Pinel-Alloul and P. Legendre have explained elsewhere that abiotic geographical gradients are the basic processes controlling community variation among lakes at broad spatial scales while fine changes in biotic processes are controlling fine-scale variation. Similarly, Z. E. Taranu believes that regional drivers synchronise lake responses, while local factors act as filters that lead to more unique and varied responses across the landscape. Z. E. Taranu further suggests that local factors may not only be biotic, but also abiotic (e.g. differences in morphology among neighbouring lakes may generate differences in community composition and thus alter biotic interactions). Although the interaction among local to regional scale factors is complex, the authors believe that appropriate statistical modelling and sampling design can help untangle the contributions of these factors, biotic and abiotic, and explain the heterogeneity observed in lake responses.

Data availability statement

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.vmcvdncrn> (Taranu et al. 2020).

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Conflicts of interest – The authors have no conflicts of interest to declare.

Author contributions

Zofia E. Taranu: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Methodology (equal); Software (lead); Visualization (lead); Writing – original draft (equal); Writing – review and editing (lead). **Bernadette Pinel-Alloul**: Conceptualization (lead); Funding acquisition (equal); Investigation (lead); Project administration (equal); Resources (equal); Supervision (equal); Validation (lead); Writing – original draft (lead); Writing – review and editing (equal). **Pierre Legendre**: Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Funding acquisition (equal); Methodology (equal); Resources (equal); Software (supporting); Supervision (equal); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (equal).

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