Spatial and environmental correlates of fish community structure in Canadian Shield lakes[1]

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Abstract: We used data on fish species biomass from 38 lakes of the Canadian Shield (Québec) to determine the contribution of environmental (lake and watershed morphometry) and spatial (e.g., hydrographic connectivity and geographic coordinates) variables on fish community structure. By using a combination of multivariate analyses, we show that nearly half of the variation in the fish community structure is explained by the independent contributions of spatial and environmental factors. Walleye (*Sander vitreus*) and lake whitefish (*Coregonus clupeaformis*) were significantly associated with the absence of beaver (*Castor canadensis*) dams, whereas northern pike (*Esox lucius*) was positively correlated with beaver dam presence. Altitude and longitude, but not current patterns in lake connectivity, were the main explanatory spatial variables accounting for the observed pattern in fish community structure. Large piscivorous fish were associated with a reduced richness and biomass of small prey, suggesting that predation is a structuring factor in these lakes. By showing that geographic coordinates and altitude are better descriptors of fish community structure than hydrographic connections, our study suggests that past colonization routes are relatively more important than current ones in structuring fish communities at the landscape level. This interpretation is supported by recently published genetic data.

Résumé : Nous avons utilisé des données de biomasse des espèces de poissons dans 38 lacs du bouclier canadien (Québec) pour déterminer la contribution des variables environnementales (morphométrie du lac et du bassin versant) et spatiales (p. ex. connectivité hydrographique et coordonnées géographiques) sur la structure des communautés de poissons. En utilisant différentes analyses multivariables, nous avons montré que presque la moitié de la variation dans la structure des communautés de poissons est expliquée par une contribution indépendante de facteurs spatiaux et environnementaux. Le doré jaune (*Sander vitreus*) et le grand corégone (*Coregonus clupeaformis)* étaient significativement associés à l'absence de barrages de castor (*Castor canadensis*), alors que le grand brochet (*Esox lucius*) était corrélé directement avec la présence de barrages de castor. L'altitude et la longitude, mais pas les patrons actuels de connectivité entre les lacs, étaient les principales variables qui expliquaient les patrons observés dans la structure des communautés de poissons. Les grands piscivores étaient associés à une richesse spécifique et une biomasse réduites des petits poissons proies, suggérant que la prédation est un facteur structurant dans ces lacs. En montrant que les coordonnées géographiques et l'altitude sont de meilleurs descripteurs de la structure des communautés de poissons que les connexions hydrographiques, notre étude suggère que les anciennes voies de colonisation sont relativement plus importantes que les voies actuelles dans la structuration des communautés des poissons au niveau du paysage. Des données génétiques publiées récemment supportent cette hypothèse.

Introduction

Limnetic fish communities show patterns that can be explained in terms of biogeographic factors and physical–chemical gradients (Tonn and Magnuson 1982; Rahel 1984; Jackson et al. 2001). Although the fish communities of both small, physically unstable lakes (e.g., with strong seasonal variations in dissolved oxygen) (Tonn and Magnuson 1982; Tonn et al. 1992) and larger, more stable lake systems (Jackson and Harvey 1989; Paszkowski and Tonn 2000; Olden et al. 2001) have been the object of quantitative surveys, comparatively few studies have explicitly considered the role of spatial factors such as hydrographic patterns in lake connectivity (e.g., Olden et al. 2001), and only rarely have studies assessed it at large scales (e.g., Legendre and Legendre 1984). Yet, spatial patterns can be important in explaining the possible colonization routes and (or) the variation in both biotic and abiotic factors among lakes and thus may determine fish community structure by multiple pathways (Jackson et al. 2001).

Here, we examine relationships between attributes of lake fish communities and both environmental and spatial factors

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in an area larger by one order of magnitude than that studied by Olden et al. (2001). We used data from a survey of fish communities in 38 Canadian Shield lakes to determine (*i*) which environmental and spatial variables best account for patterns in fish community structure and (*ii*) the relative contribution (and statistical significance) of each of these components to the explained variation.

Even though fish species richness and community structure are predictable along large gradients of lake area and mean depth (Marshall and Ryan 1987; Matthews 1998), we do not expect that these factors will be important in structuring fish communities in this study because the study lakes are relatively homogeneous in morphology. In contrast, because the study lakes are distributed over an area of 30 000 km^2, it is likely that other environmental and geographic factors will influence fish communities. For example, we expect that spatial factors such as patterns of lake connectivity will be important structuring factors (Olden et al. 2001). Other potential structuring factors could be the presence of beaver (*Castor canadensis*) dams (Collen and Gibson 2001) and piscivorous fish (Chapleau et al. 1997), both of which varied among the study lakes. It has been shown that beaver dams can affect the community structure of freshwater fish (Collen and Gibson 2001) by their effects on the aquatic habitat and by the creation of barriers to fish migration, whereas predation by piscivores might be responsible for the extinction of prey species in lakes (Chapleau et al. 1997). The statistical approach we used should help to identify the relationships between these factors and fish community structure.

Materials and methods

Study lakes and fish sampling

Thirty-eight thermally stratified headwater lakes were selected on the basis of comparable size (fetch greater than 1 km), basin morphometry (maximum depth exceeding 5 m), and catchment properties (<6% of catchment occupied by wetlands) (Table 1; for more details, see Carignan et al. 2000). The lakes were accessible only by plane and are located within a 30 000 km^2 area surrounding the Gouin Reservoir, Québec, Canada (48°50′N, 75°00′W; Fig. 1). The landscape is typical of the Canadian Shield, with low relief and numerous lakes and wetlands. Our study lakes are larger than those studied in Wisconsin and Alberta by Tonn and Magnuson (1982), Rahel (1984), and Robinson and Tonn (1989) but are similar in size to those studied in Ontario and Alberta by Hinch et al. (1991) and Paszkowski and Tonn (2000). These Québec lakes are part of three major watersheds (the Outaouais, Saguenay, and Saint-Maurice rivers) that ultimately drain into the St. Lawrence River (Fig. 1).

Lake catchments experienced only limited disturbance until 1995, when nine of them experienced forest fires and nine others were logged by forestry companies. The effects of the forest fires and logging were studied on these lakes for the 3 years following the perturbation (between 1996 and 1998). Carignan et al. (2000) showed that fire and logging increased the concentrations of nutrients and major ions in these lakes through increased runoff from the watershed. Planas et al. (2000) found significant effects of the perturbations on the biomass of both benthic and pelagic algae, which increased in logged and burned lakes between 1996 and 1998. Furthermore, Patoine et al. (2000) found that the biomass of small-sized zooplankton (mostly rotifers) increased in burned-watershed lakes, whereas larger zooplankton (mostly calanoids) decreased in logged-watershed lakes. Between 1996 and 1997, St-Onge and Magnan (2000) found some negative effects of these perturbations on the abundance of the smallest size classes of both yellow perch (*Perca flavescens*) and white sucker (*Catostomus commersoni*), but they did not observe any effect at the population level. Therefore, because of the short-term nature of these perturbations and the fact that they did not have any detectable effects at the population level (St-Onge and Magnan 2000), it is unlikely that these perturbations biased our analyses. To verify this assumption and control for the potential undetected effects of these perturbations on community structure, we included the percent area of watershed logged or burned as an independent variable in our statistical analyses. To avoid collinearity problems, physicochemical and plankton variables, which were clearly affected by the watershed perturbations, were not included in our analysis.

For logistic reasons, 21 lakes were sampled in 1996 and 17 in 1997. This might have introduced some noise in the data owing to interannual differences in fish community structure, but it is unlikely that it biased our results because the choice of sampling a lake in a given year was made randomly. Each lake was sampled once between June and August. Fish were captured with experimental monofilament gill nets (102.3 m long × 2.7 m high) and had stretched mesh panels of 20, 24, 33, 36, 50, 60, 76, 90, and 100 mm (filament diameter of 0.17, 0.20, 0.20, 0.20, 0.20, 0.32, 0.32, 0.32, and 0.32 mm, respectively). Gill nets were set perpendicular to the shore, with small and large meshes alternating from the shore among gill nets. The nets were set at regular intervals around the lake, with the first net location being randomly located on aerial photographs. The fishing effort was six nets per night for <50 ha lakes, eight nets per night for 50–100 ha lakes, 10 nets per night for 100–150 ha lakes, and 12 nets per night for >150 ha lakes. The nets fished on average for 18 h 26 min ± 00 h 32 min (minimum–maximum: 17 h 13 min – 19 h 30 min), covering the period between 1600 and 1030. For all fish captured, total length (±1 mm) and mass (±0.1 g) were noted.

A total of 23 taxa were found in the study lakes (Table 2). Species determination was difficult in the field for cyprinids, and given the remoteness of our study area, it was not possible to bring specimens to the lab for more accurate identification. Unidentified cyprinids, if any, were used only as members of the "prey group" (see next section) and not used separately in the analyses.

Dependent variables

Fish species abundance has been shown to be a more sensitive response variable for studying community patterns than presence–absence data, even though the latter are in general less noisy (Rahel 1990). To select the most sensitive matrix of dependent variables in our analyses, we explicitly compared the sensitivity of relative abundance vs presence–absence data as descriptor variables of community structure. We first built matrices of relative abundance (biomass per unit of effort, BPUE) and presence–absence data to compare

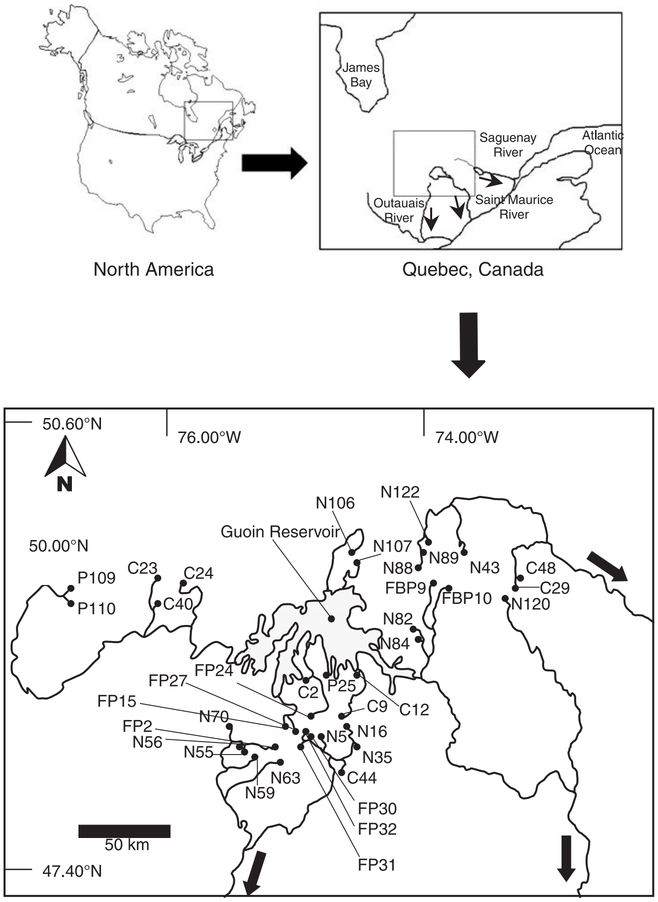
Table 1. General characteristics of the study lakes.

Variable	Mean ± SD	Range
Lake area (km^2)	0.46±0.36	0.15–2.31
Altitude (m)	450±40	391–558
Maximum depth (m)	13.8±6.1	5.0–34.0
Mean depth (m)	4.8±1.8	2.1–10.0
Watershed area (km^2)	3.7±3.8	0.61–21.7
Residence time (years)	1.6±1.1	0.3–5.6
Lake slope (%)	7.6±3.5	3.0–18.3
Lake volume (m^3 × 10^6)	2.2±1.7	0.4–8.5
Epilimnion depth (m)	2.8±0.9	1.3–4.7
Epilimnion–hypolimnon ratio (volume)	1.4±1.5	0.29–8.3
Littoral area (%)[a]	29.4±10.6	11.6–54.9
Chlorophyll *a* (μg·L^{-1})[b]	1.9±0.5	0.9–3.2
Total phosphorus (μg·L^{-1})[b]	7.0±1.9	4.9–11.8
Total nitrogen (μg·L^{-1})[b]	233.1±41.1	158.3–332.1
Dissolved organic carbon (mg·L^{-1})[b]	5.1±1.3	2.8–9.2
Secchi depth (m)[b]	4.0±1.0	2.2–6.0
Fish species richness	4.6±1.8	1–9

[a] Defined as the area between the 0 m and 2 m isobaths.

[b] Only physicochemical data relative to unperturbed lakes are presented.

Fig. 1. Location of the study lakes. The close-up represents the location of the sampling sites within the three major watersheds draining into the St. Lawrence River: the Saguenay, Saint Maurice, and Outaouais rivers. Arrows indicate the direction of water flow.



the sensitivity of these variables as descriptors of community structure. Moreover, because it has been shown that gillnets underestimate the abundance of small-bodied fish (e.g., Olin and Malinen (2003) and references therein), we expect data on small-bodied species to be more affected by noise than data on larger ones. To verify this assumption, we ran the analyses both by including all species and by pooling small-bodied ones into a single "prey fish" group (see Table 2). We expect the prey fish group (composed mostly of cyprinids and gastrosteids) to be more sensitive to environmental factors (e.g., biotic ones) than individual small-bodied species and thus help in identifying patterns in fish community structure. Thus, we considered four matrices of dependent variables: presence–absence and BPUE fish data with all the individual species (hereafter "all species" matrix) or with small-bodied species pooled into the "prey fish" category (hereafter "main species" matrix). We then compared the amount of variation in each of these four matrices of dependent variables that was explained by the independent variables (see below) to estimate the performance of these fish community descriptors. The descriptor with the best performance was used in all subsequent analyses.

Species diversity × lake matrices were also built as dependent variables describing our fish communities. Because different measures of diversity–evenness can differ in their ability to discriminate among sites (Magurran 1988), we compared three different diversity indices: species richness (*S*), Shannon diversity (*H*), and evenness (Pielou's *J*) (Magurran 1988).

Independent variables

The matrix of environmental variables included variables that we expected might affect fish community structure and species diversity, such as shoreline development, percent of littoral area, epilimnion to hypolimnion ratio (Matthews 1998), the presence of a beaver dam at the lake outlet (Collen and Gibson 2001), and the percent area of the water-

Table 2. Occurrence of the fish species (and their code names) in the study lakes.

			Occurrence	
Common name	Scientific name	Code	No. of lakes	Percentage of lakes
White sucker	*Catostomus commersonii*	caco	31	81.6
Northern pike	*Esox lucius*	eslu	27	71.1
Yellow perch	*Perca flavescens*	pefl	25	65.8
Lake whitefish	*Coregonus clupeaformis*	copl	11	28.9
Fallfish	*Semotilus corporalis*	seco	10	26.3
Walleye	*Sander vitreus*	savi	9	23.7
Pearl dace[a]	*Margariscus margarita*	mama	7	18.4
Brook trout	*Salvelinus fontinalis*	safo	7	18.4
Burbot	*Lota lota*	lolo	7	18.4
Golden shiner[a]	*Notemigonus crysoleucas*	nocr	5	13.2
Lake chub[a]	*Couesius plumbeus*	copl	5	13.2
Finescale dace[a]	*Phoxinus neogaeus*	phne	5	13.2
Lake trout	*Salvelinus namaycush*	sana	2	5.3
Northern redbelly dace[a]	*Phoxinus eos*	pheo	2	5.3
Atlantic rainbow smelt[a]	*Osmerus mordax mordax*	osmo	2	5.3
Spottail shiner[a]	*Notropis hudsonius*	nohu	2	5.3
Ninespine stickleback[a]	*Pungitius pungitius*	pupu	1	2.6
Trout-perch[a]	*Percopsis omiscomaycus*	peom	1	2.6
Logperch[a]	*Percina caprodes*	peca	1	2.6
Blacknose shiner[a]	*Notropis heterolepis*	nohe	1	2.6
Common shiner[a]	*Luxilus cornutus*	luco	1	2.6
Brook stickleback[a]	*Culaea inconstans*	cuin	1	2.6
Cyprinid spp.[a,b]		cysp	8	21.1

[a] Species included in the "prey fish" group.

[b] Species not included in the analyses based on all species.

shed that was burned or logged. Lake morphometry and catchment properties (including the presence of a beaver dam at the lake outlet) were determined from 15–25 echosounder transects and aerial photographs (see methodological details in Carignan et al. 2000). Although we tried to reduce the variation in both lake area and maximum depth by selecting morphologically similar lakes, some variation for these variables was still present in our data set (Table 1). To control for this residual variation, lake area and maximum depth, which are considered key factors in determining fish species richness and composition at larger scales (Matthews 1998; Dodson et al. 2000; Amarasinghe and Welcomme 2002), were included in the analysis. A total of seven environmental variables were thus considered in the analyses.

To estimate the influence of hydrographic spatial structure on species assemblages, six different matrices were constructed. We compared their ability to extract patterns from the fish data in order to select the most effective one in subsequent analyses. The hydrographic network mapping the connections among lakes was first built using both paper and digital maps with scales from 1:20 000 to 1:250 000 (Fig. 1). Each branching point represents a node and a number was assigned to each node (Magnan et al. 1994). Then, a lake-by-node matrix (NODE) was constructed by assigning, for each lake, a value of one to all nodes connecting it to the origin or "root" and a value of zero to all other nodes. This procedure results in a hydrographic tree in which each lake is classified by a row vector of binary values (0 or 1) (for examples, see Magnan et al. 1994; Angers et al. 1999). Hydrographic trees estimate the isolation between any two lakes by determining the number of streams that a fish encounters when dispersing from one lake to another, but they do not measure distances between lakes.

Two additional matrices were built by measuring the watercourse distance (in kilometres) between each pair of lakes (WC1) and between each lake and each node (WC2). These two alternative measures of lake isolation should give better measures than the first approach (NODE) regarding the distances that a fish might have to travel from one lake to another. The watercourse distances were obtained by processing the information contained in digital maps with MapInfo software.

The last two isolation measures were obtained by integrating both watercourse distances (i.e., WC1) and differences in altitude between lakes. The matrix of differences in altitude between lakes (D_ALT) was built by calculating the average differences in altitude between the lakes and the closest hydrographic node connecting them. This measure reflects the altitude difference experienced by fish when moving from one lake to another via the hydrographic network. We then used WC1 and D_ALT to produce two orthogonal isolation measures (D_ELEV1 and D_ELEV2) following the method proposed by Olden et al. (2001). This approach starts by unfolding both of these 38 × 38 distance matrices (i.e., WC1 and D_ALT) from a triangular form into a continuous vector (for an example, see Legendre and Legendre 1998, p. 560). A matrix of 741 × 2 (i.e., the (38 ×

37)/2 + 38 rows and two columns) was created by combining the two vectors side by side. The two columns of this matrix were then used as variables in a principal component analysis (PCA) to construct D_ELEV1 and D_ELEV2, which are obtained from the first two axes of the PCA. The first PCA axis summarized the relationship between interlake watercourse distance and elevation difference. This set of 741 observations was then converted back into a triangular matrix of interlake distances (D_ELEV1), which corresponds to an integrated measure of the overall distance, both by water and elevation, between any two lakes. The second PCA axis is a stream gradient measure as it represents the relative change in elevation compared with distance by water (Olden et al. 2001). In a similar way, the 741 observations from axis II were converted back into a triangular distance matrix (D-ELEV2) (Olden et al. 2001).

Finally, as suggested by Legendre and Legendre (1998), we built a sixth matrix by including all terms of a cubic trend surface polynomial (TREND) based on geographic coordinates (including altitude). Even though this approach does not estimate the among-lake distances that fish experience moving from one lake to another, trend surface analysis is appropriate for describing broad-scale spatial trends in data (Legendre and Legendre 1998). Thus, given the relatively large spatial scale of our study area, we considered that it was informative to compare this approach with the other five presented above. This procedure allows one to estimate parameters of a trend surface regression equation of the form:

$$\mathrm{SR} = b_1X + b_2Y + b_3XY + b_4X^2 + b_5Y^2 + b_6X^2Y + b_7XY^2 + b_8X^3 + b_9Y^3$$

where X is the longitude and Y is the latitude in Cartesian coordinates. Because all of the lakes are headwater, we considered altitude as an indirect measure of lake isolation. Thus, we added the terms $b_{10}Z$ and $b_{11}Z^2$ to the equation, where Z is the altitude in metres above sea level. This equation represents a geographic surface that can be used to describe how a summary measure of the fish community structure (the SR variable, which in this study takes the form of the ordination axis score) varies over the matrix of X–Y–Z coordinates. The corresponding TREND matrix was composed of 38 rows (i.e., lakes) and 11 columns (i.e., the terms of the polynomial). The inclusion of quadratic, cubic, and interaction terms in the equation allowed the modelling of not only simple linear gradient patterns, but also more complex features such as patches or gaps (Borcard et al. 1992).

The selection of spatial variables to be used in subsequent analyses was based on their ability in extracting patterns from fish data. We first ranked the six sets of spatial predictors (i.e., NODE, WC1, WC2, D_ELEV1, D_ELEV2, and TREND) by comparing the amount of variation in fish data explained by each of them separately in canonical correspondence analysis (CCA) (see below). If possible, we partitioned the variation among them (see below) to see if the spatial predictors explained different portions of the variation on the fish data. We retained for further analyses the set of spatial variables explaining the largest part of the variation independently of the others. When they explained similar proportions of the variation and their effect was confounded, we considered them as equivalent. In this case, we selected the simplest set of spatial variables. The six sets were ranked on the basis of increasing construction complexity (i.e., amount of information needed to build them) as follows: TREND, NODE, WC1 and WC2, and D_ELEV1 and D_ELEV2.

Statistical analyses

We used CCA first to relate the matrix of the dependent variables (i.e., fish presence–absence and BPUE) to the six sets of spatial variables. This allowed us to select the matrix of spatial variables to be used in subsequent analyses. CCA was then used to relate the matrix of the dependent variables to two sets of predictor variables separately: environmental (lake and catchment characteristics) and spatial (i.e., the selected matrix). Used in combination with permutation tests, this procedure allowed us to evaluate the magnitude and statistical significance of effects associated with each component (Legendre and Legendre 1998). Explanatory variables were selected using a forward selection procedure, with a cutoff point of $p = 0.10$ (i.e., alpha-to-enter, as in multiple regression analysis), based on 9999 Monte Carlo permutations. The statistical significance of both selected variables and ordination axes ($\alpha = 0.05$) were assessed by means of a Monte Carlo permutation test ($n = 9999$). The collinearity between selected explanatory variables was controlled by eliminating those variables with a variance inflation factor (VIF) greater than 10 (ter Braak and Smilauer 1998). As environmental variables show spatial heterogeneity, the variation explained by environmental and spatial variables may be redundant. To explain this potential redundancy, variations in fish species assemblage were analyzed against the spatial and environmental variables combined, using the method of variation partitioning proposed by Borcard et al. (1992).

The method of variance partitioning uses CCA and partial CCA (i.e., a CCA with covariables) to partition the variation in species assemblage explained by independent variables into different components (see Borcard et al. (1992) for details of computations). In the analysis, the amount of fish community variance explained by independent variables was partitioned into “pure” environmental and “pure” spatial components using CCA and partial CCA. This procedure also allowed us to determine the portion of unexplained variation (Borcard et al. 1992). With this procedure, a part of the pure component explained by the spatial variables could in fact be related to environmental factors that are spatially structured and could thus contain unmeasured environmental gradients.

The significance of the relationship between single explanatory variables and fish taxa ($\alpha = 0.05$) was determined by using Van Dobben circles (ter Braak and Looman 1994). These ordination diagrams are built using the t values of canonical coefficients of the CCA and can be used to easily visualize the relationships between single dependent and independent variables in the analysis.

A correspondence analysis (CA) was used to summarize the fish community structure in a reduced space. For both CA and CCA, BPUEs were log(x + 1)-transformed to reduce the effect of outliers on the ordination. Furthermore, rare species were downweighted by the standard downweighting function of CANOCO to reduce their unduly large influence in the analyses (ter Braak and Smilauer 1998). Finally, both CA and CCA assume a unimodal relationship between the dependent and independent variables. Detrended correspondence analysis (DCA) was used to verify this assumption. The range of the ordination scores obtained by DCA was greater than the threshold of three standard deviations, indicating that the use of unimodal methods was appropriate in this study (Jongman et al. 1995). Geographic coordinates were centred to a zero mean before computing the higher terms of the polynomial to reduce nonessential collinearity when fitting the polynomial. Here, the backward-selection procedure was used to reduce the number of terms in the CCA. This was preferred to the forward-selection procedure because if any of the higher terms had been retained by the forward-selection procedure, all terms of lower order (significant or not) must also have been retained to avoid any deformation of the model (Draper and Smith 1998). Ordinations (CCA, DCA, and Van Dobben circles) were done with the CANOCO program (version 4.02; ter Braak and Smilauer 1998).

We used stepwise multiple regression to determine (*i*) if fish species diversity was related to the above-mentioned environmental variables and the pooled BPUE of main piscivores and (*ii*) if total fish biomass was related to the environmental variables and fish species diversity. Fish species diversity indexes (*S*, *H*, and *J*) were used here as independent variables because it has been suggested that the total biomass in a community can be affected by species diversity (e.g., Loreau 1998). This procedure was applied to both the whole fish community and to “prey fish” only, considered a priori as more sensitive to piscivorous fish predation. Residual scatter plots, normal probability plots, and partial residual plots were used to determine if regression assumptions were satisfied. When these conditions were not fulfilled, the data were log- or square-root-transformed. Collinearity between the independent variables was evaluated by examination of the variance inflation factor (see above). To control for the potential relationships with sampling date and fishing time, these two variables were used as covariates in the analyses and discarded if not significant.

Results

Selection of the spatial variables

The trend surface analysis explained 33.6% ± 2.6% (mean ± standard deviation, SD) (range 33.4%–36.1%) of the variation in the fish data. This represented the largest proportions of variation explained by spatial descriptors, regardless of the dependent matrix used (i.e., presence–absence and BPUE of both the all species and main species matrices). Nine terms of the polynomial trends surface were selected for both analyses conducted on the all species data (presence–absence and BPUE), whereas seven terms were selected for the analyses conducted on the main species data (for details, see Environmental and spatial correlates of fish community structure).

The analyses conducted on the D_ELEV1 and D_ELEV2 matrices explained 13.2% ± 4.5% (range 10.2%–19.9%) and 11.8% ± 3.0% (range 7.4%–13.8%) of the variation, respectively. Two variables (distances from lakes N106 and P109) were retained by the forward-selection procedure in the D_ELEV1 matrix in both analyses based on all species (both presence–absence and BPUE). Distances from lakes FP24 and P109 were selected from the D_ELEV1 matrix in the analysis on the presence–absence of main species. Distances from lakes N43, N63, and N82 were selected from the D_ELEV1 matrix in the analysis of the BPUE of main species. The same two variables (stream gradient from lakes FP24 and N106) were selected in the D_ELEV2 matrix in all four analyses.

Twenty-five nodes were determined in the hydrographic tree of interlake connections (Fig. 1). No node was retained in the analysis based on the BPUE of main species or the NODE matrix, and only two nodes were retained by the forward-selection procedure in the other three analyses. The hydrographic node matrix explained a relatively small fraction of the variation in the fish data (6.5% ± 4.5%; range 0%–10.3%), whereas neither matrix of watercourse distances (WC1 and WC2) was significantly related to any of the four fish descriptors. A partial CCA analysis was thus possible only with the first four spatial descriptors. However, most of the partial CCAs, which included all the spatial covariables, were not significant (Table 3). Therefore, it was not possible to partition the variation among the different sets of spatial variables. Only the partial CCA based on the BPUE of main species (dependent variable) and TREND (independent variable) was significant: it explained 21.5% of the variation in the fish data after inclusion of the other spatial descriptors as covariables (i.e., NODE, D_ELEV1, and D_ELEV2) (Table 3). Moreover, partial CCAs using TREND as independent variables and the other spatial descriptors used separately as covariables were significant in most cases and explained a larger proportion of the variation than the CCAs based on the other three spatial descriptors. Therefore, we selected the trend surface polynomial as the simplest and most robust model explaining the largest proportion of the variation in fish data.

Descriptors of fish community structure

The CCA results showed that the amount of variation explained by environmental variables alone was fairly similar among the four matrices of dependent variables (i.e., presence–absence and BPUE of both the all species and main species matrices), ranging from 10.4% to 14.9% (Table 4). Similarly, the comparison of the four sets of models showed that the total amount of variation explained by the spatial descriptors (i.e., TREND) was fairly similar among the four matrices of dependent variables. Variance partitioning was not possible for the presence–absence matrix of all species. In the other cases, it showed that the environment explained on average 11% of the variation, whereas TREND explained on average 31.2%. The total amount of variation explained was in general greater when small-bodied species were grouped in the analysis, but slightly greater when using BPUEs rather than presence–absence data. Therefore, this matrix was considered as the most sensitive and was selected for all our analyses.

Fish community structure

Of 23 fish taxa (Table 2; Appendix A), six species had population biomasses (BPUE) exceeding 1% of the total BPUE averaged over lakes: northern pike (*Esox lucius*),

Table 3. Summary statistics of significant partial CCAs ($\alpha = 0.05$) based on four spatial descriptors explaining the variation in fish data: lake interconnections in the hydrographic tree (NODE), a combined measure of watercourse and elevation distance between lakes (D_ELEV1), stream gradient (D_ELEV2), and trend surface polynomial (TREND).

	NODE (*N*)				D_ELEV1 (*D*1)				D_ELEV2 (*D*2)				TREND (*T*)			
	T[a]	*D*1	*D*2	All	*T*	*N*	*D*2	All	*T*	*N*	*D*1	All	*N*	*D*1	*D*2	All
(*a*) Presence or absence																
All species	ns	9.2	ns	ns	ns	12.2	9.8	ns	8.6	10.3	12.6	ns	28.0	27.6	31.3	ns
Main species	ns	ns	ns	ns	ns	14.6	11.2	ns	ns	12.4	12.9	ns	34.9	28.4	32.0	ns
(*b*) Relative biomass (BPUE)																
All species	ns	9.4	ns	ns	ns	12.2	9.1	ns	8.9	10.6	9.0	ns	30.3	30.5	29.9	ns
Main species	—	—	—	—	ns	—	14.4	ns	ns	—	ns	ns	—	ns	28.8	21.5

Note: The four matrices of spatial descriptors were also used as covariables (individually or jointly) in the different partial CCAs. None of the CCAs based on interlake watercourse (WC1) or lake-node (WC2) distances was significant. Four matrices were used as dependent variables; fish data were expressed as (*a*) presence or absence or (*b*) relative biomass (BPUE) for all fish species or main species only. For each fish data matrix, results are expressed as percent variation explained by the independent matrices after inclusion of the covariables. —, not analyzed because the correspondent CCA was not significant; ns, not significant after inclusion of the covariables.

[a] Covariables.

Table 4. Summary statistics of significant CCAs ($\alpha = 0.05$) explaining the variations in fish data.

	Explained variation (%)		
	ENV	TREND	Total
(*a*) Presence or absence			
All species	10.4	34.2*	34.2
Main species	14.5* (11.8)	32.5* (29.8)	44.3
(*b*) Relative biomass (BPUE)			
All species	11.4* (9.2)	35.5* (33.3)	40.3
Main species	14.9* (12.1)	33.4* (30.6)	45.5

Note: Four matrices were used as dependent variables: fish data were expressed as (*a*) presence or absence or (*b*) relative biomass (BPUE) for all fish species or main species only. For each fish data matrix, results are expressed as the percent variation explained by the two independent matrices: environment (ENV) and trend surface polynomial (TREND). An asterisk (*) indicates those CCAs that remained significant ($\alpha = 0.05$) after the inclusion of the covariables (i.e., partial CCAs). The pure contribution of each independent matrix is shown within parentheses only for significant pairs of partial CCAs. The total variation explained by significant partial CCAs is also shown (right column).

white sucker (*Catostomus commersoni*), lake whitefish (*Coregonus clupeaformis*), walleye (*Sander vitreus*), yellow perch (*Perca flavescens*), and brook trout (*Salvelinus fontinalis*) represented (mean ± SD) 38.7% ± 37.8%, 32.4% ± 33.8%, 8.3% ± 15.6%, 8.0% ± 15.7%, 3.8% ± 13.5%, and 3.6% ± 6.0% of the total BPUE, respectively. These species, along with fallfish (*Semotilus corporalis*) and burbot (*Lota lota*), which had average biomasses lower than 1%, occurred in at least 18% of the lakes. Only one small-bodied species included in the prey group (pearl dace, *Margariscus margarita*) also occurred in 18% of the lakes (Table 2). Among potential piscivores, pike and walleye showed the largest occurrence and biomass (Table 2; Appendix A).

The first two axes of the CA explained 53.7% of the variation in the BPUE of the main fish species. The first axis explained 36.9% of the variation in the data and separated lakes with northern pike (with or without walleye) from lakes with *Salvelinus* spp. (*S. fontinalis* and (or) *S. namaicush*) (Fig. 2*a*). The second axis explained 16.8% of the variation in the data and separated most lakes with northern pike only from lakes in which northern pike co-occurred with walleye (Fig. 2*b*). Walleye and lake whitefish had a very similar distribution and always occurred with northern pike (Appendix A). Yellow perch co-occurred frequently with northern pike, walleye, and lake whitefish but co-occurred with *Salvelinus* spp. in only two lakes (Appendix A). Fallfish showed a pattern similar to yellow perch but were scarcer. White sucker was present in most of the lakes, and its biomass tended to be associated positively with the first axis (Fig. 2*a*). Burbot was also mostly associated with the positive part of the first axis (Fig. 2*a*). Prey fish were associated with the positive parts of both axes I and II, and their biomass was inversely related to the biomass of large piscivores (Fig. 2). The biomass of prey fish was particularly low when northern pike and walleye co-occurred.

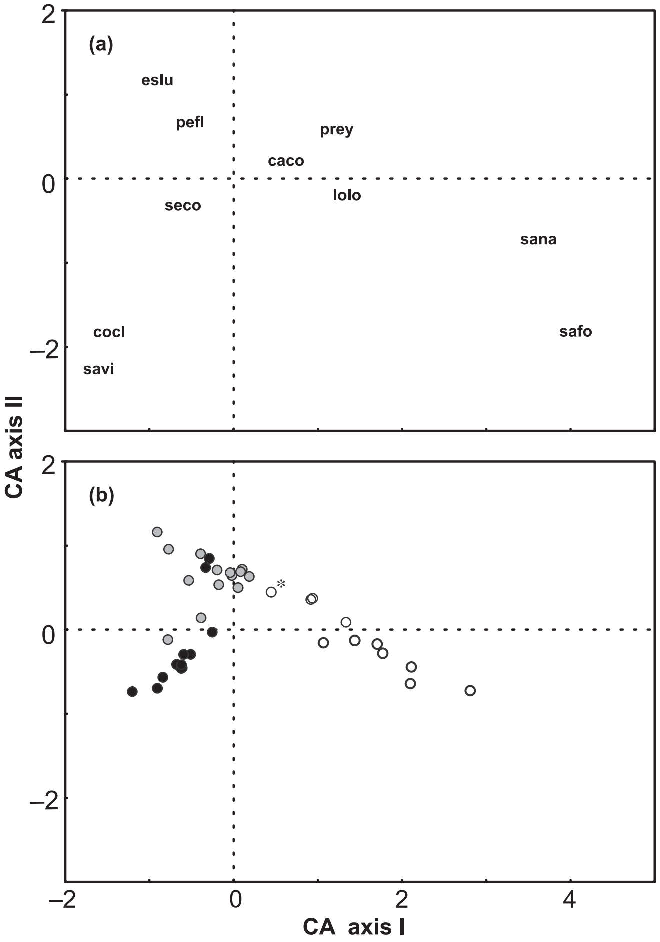
Environmental and spatial correlates of fish community structure

Of the seven environmental variables included in the CCA forward-selection procedure, only lake area and the presence of a beaver dam at the lake outlet were retained (Fig. 3*a*). The CCA model was significant ($P = 0.0029$) and the two first axes together explained 14.9% of the variability in fish community structure (9.9% and 5.0%, respectively) (Fig. 3*a*).

Brook trout, lake trout, and white sucker were significantly associated with lake area, whereas yellow perch and northern pike were only marginally associated (negatively) to this variable. However, the analysis was particularly influenced by lake C48, which had the largest surface area (2.3 km^2) in the sample. When lake C48 was excluded, the effect of lake area disappeared. Walleye and lake whitefish were both significantly associated with the absence of beaver dams, whereas northern pike was positively associated with the presence of a beaver dam. No watershed perturbation variables were retained by the forward-selection procedure.

The best model relating fish community structure to the trend surface polynomial explained 33.4% of the total varia-

Fig. 2. (*a*) Correspondence analysis (CA) ordination diagram of the relative biomass of the main fish species (BPUE). Species codes (Table 2) indicate the approximate locations of species centroids. Eigenvalues: axis 1 = 0.53; axis 2 = 0.27; sum of all unconstrained eigenvalues = 2.12. (*b*) Same as (*a*) but without species centroids and with circles indicating the lakes. Patterns related to the occurrence of selected species are shown, i.e., lakes with *Salvelinus* spp. are indicated by open circles; lakes with northern pike (*Esox lucius*), shaded circles; lakes with both northern pike and walleye (*Sander vitreus*), solid circles. Note that the random jitter option was used to avoid overlapping of data points. Asterisk (*) indicates that brook trout (*Salvelinus fontinalis*) was found in lake P109 in a subsequent sampling.



tion and included seven terms after the backward-selection procedure:

$$\mathrm{SR} = b_1X + b_2Y + b_3XY + b_5Y^2 + b_7XY^2 + b_{10}Z + b_{11}Z^2$$

The first and second axes explained 21.9% and 4.8% of the variance, respectively, in the fish community structure and were mainly associated with altitude and the quadratic term for longitude (Fig. 3*b*, axis 1) and the quadratic altitude term (Fig. 3*b*, axis 2).

Altitude was significantly (positively) associated with brook trout, white sucker, and prey fish and negatively associated with lake trout, creek chub, and lake whitefish. Creek chub was also the only species correlated (negatively) with Z^2 and XY^2. A significant positive correlation was found between Y^2 and lake whitefish. No other terms were correlated with fish taxa. Altitude and longitude were correlated (Pearson's $r = 0.66$, $P < 0.0001$), with elevation increasing

Fig. 3. Canonical correspondence ordination of the biomass of the main fish species (BPUE) and (*a*) environmental variables or (*b*) spatial variables (i.e., TREND) versus the relative biomass of main fish species (BPUE). The species abbreviations (Table 2) indicate the approximate locations of species centroids. Arrows represent the vectors of the selected environmental or spatial variables. In (*a*), the axes scaling is 1 for environmental variables and 0.38 for species. In (*b*), the axes scaling is 1 for spatial variables and 0.66 for species. For clarity, only those terms significantly associated with at least one of the fish taxa are shown. In both (*a*) and (*b*), bold lettering indicates those species significantly related to one of the independent variables, as revealed by *t* plot analysis.

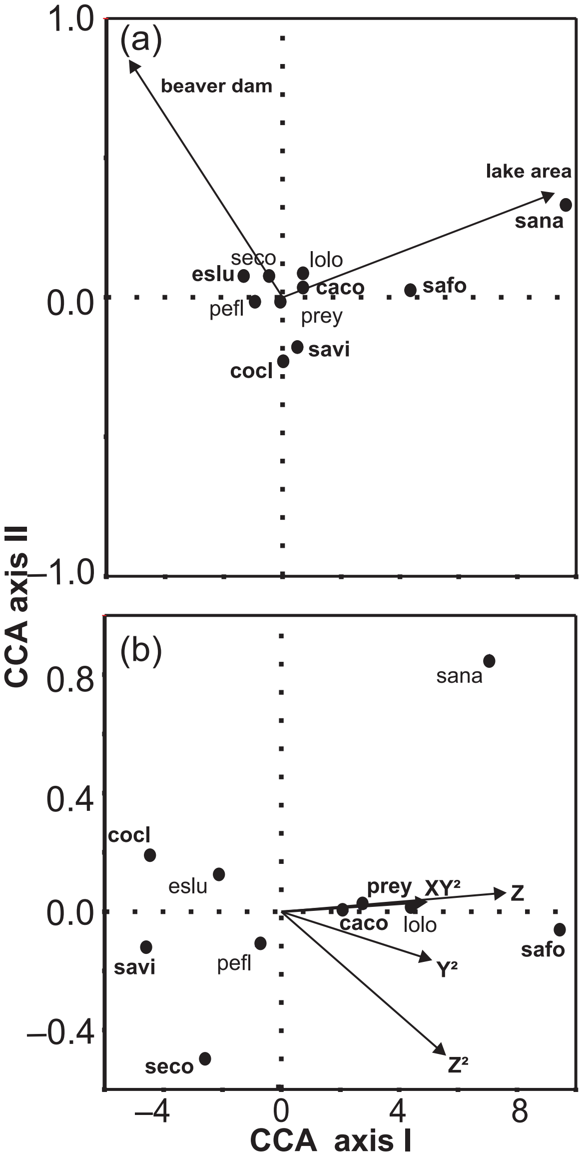


Table 5. Regression models predicting fish species (*a*) richness (*S*), diversity (Shannon *H*), and evenness (Pielou *J*), and (*b*) total fish biomass (BPUE).

Dependent variable	Independent variable	Standardized regression coefficient	Partial R^2	Model R^2_{adj}	Model *P*
(*a*) All species					
S	—	—	—	—	>0.05
H	Beaver dam	–0.37 **	0.11		
	BPUE piscivores	0.51 ***	0.26	0.34	0.0003
J	Beaver dam	–0.39 **	0.15		
	Maximum depth	–0.28 *	0.14		
	BPUE piscivores	0.42 **	0.16	0.39	0.0003
(*b*) All species					
log(BPUE)	*H*	0.54 ***	0.29	0.27	0.0006
(*c*) Prey fish only					
log(*S*)	BPUE piscivores	–0.39 *	0.15	0.14	0.0120
H	—	—	—	—	>0.05
J	—	—	—	—	>0.05
(*d*) Prey fish only					
SQRT(BPUE)	BPUE piscivores	–0.29 **	0.31		
	S prey	0.47 **	0.36		
	H prey	0.27 *	0.04	0.68	<0.0001

Note: In (*a*), the biomass of piscivores (pooled BPUE of walleye and northern pike) was included on the list of independent variables. In (*b*), *S*, *H*, and *J* were included in the list of independent variables. (*c*) and (*d*) are the same as (*a*) and (*b*), respectively, but for the prey fish category only. In (*d*), the biomass of piscivores was included in the set of independent variables. Significance: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

eastward, suggesting that their effects were partly confounded (Fig. 3*b*).

About 45.5% of the total variation in the fish community was explained jointly by environmental and spatial variables. The pure environmental and pure spatial variables accounted for 12.1% and 30.6%, respectively, of the total variation in the BPUEs of the main fish species, with the remaining variation (2.8%) explained by the component shared between the two.

Patterns in fish species diversity and total fish biomass

Fish species richness ranged from one to nine species. None of the explanatory variables was retained by the stepwise procedure to explain the variation in fish species richness (Table 5*a*). In contrast, the stepwise multiple regression revealed that the Shannon diversity index was negatively related to beaver dam presence and positively related to the biomass of large piscivores (Table 5). A similar result was obtained for fish species evenness (Pielou *J* index), but in this case, maximum depth was also included in the model (Table 5). The Shannon diversity index was the only variable retained to explain the variation in total fish biomass (Table 5*b*).

Prey fish species richness ranged from zero to six species. Stepwise multiple regression indicated that prey fish richness was negatively related to the biomass of large piscivores (Table 5*c*), which accounted for 14% of the variation. None of the explanatory variables was retained for either prey fish diversity or evenness (Table 5*c*). The biomass of large piscivores was inversely related to prey fish biomass, whereas prey fish richness and diversity were both directly related to prey fish biomass (Table 5*d*).

Discussion

Although the failure to integrate spatial variables into empirical ecological models can lead to the misinterpretation of spatially structured data (Legendre and Legendre 1998), studies explicitly addressing this issue for aquatic communities are still rare (cf. Jackson et al. 2001). We show here that nearly half of the variation in the fish community structure in a sample of boreal lakes is explained by the independent contribution of spatial and environmental factors. Unlike several previous studies (e.g., Olden et al. 2001), fish community structure was not clearly associated with the hydrographic network. Altitude, longitude, and the presence of beaver dams were the main explanatory variables. More specifically, our results suggest a potential link between the presence of beaver dams at the lake outlet and the absence of species such as walleye and lake whitefish. Beaver dams can be a barrier to fish movement and can dramatically alter stream habitats (Collen and Gibson 2001) such as the lake outlets. Outlets might be key spawning habitats for some species in these headwater lakes, which lack large inlets. Thus, beaver dams might have affected lacustrine fish communities by reducing the access to spawning areas for some species (i.e., neighbouring streams or lakes) (Rasmussen et al. 2002) or by altering the quality of the spawning areas situated in the outlet (Collen and Gibson 2001).

Surprisingly, both measures of watercourse distances used (WC1 and WC2) were unrelated to fish community structure; the hydrographic tree explained only a small portion of the variation in fish data. Only those spatial descriptors including altitude (TREND, D_ELEV1, and D_ELEV2) were successful in explaining a relatively large proportion of the variation in fish data. Moreover, the surface trend polynomial, despite the fact that it did not take into account watercourse distances, had a greater predictive power than both D_ELEV1 and D_ELEV2. This suggests that the predictive power of D_ELEV1 and D_ELEV2 might be due more to the inclusion of altitude differences rather than watercourse distances. Replacing watercourse distances by straight-line distances in the calculation of these two latter descriptors did not change their predictive power (results not shown), corroborating the view that the actual hydrographic network has little power to predict fish community structure in our lakes. These results contrast with those of Olden at al. (2001), who found a good concordance between patterns in interlake connectivity and fish occurrence patterns at a smaller scale.

The trend surface polynomial built from the lake geographical coordinates accounted by far for the highest proportion of the variation in fish BPUE explained by spatial descriptors. This suggests that a broad-scale spatial phenomenon shaped fish communities in these lakes. A possible mechanism could be linked to the postglaciation dispersion patterns, which were largely linked, at least at the beginning of the dispersal process, to lakes created by ice melt. Present drainage patterns do not necessarily reflect past drainage patterns in such dynamic landscapes, as suggested by large-scale biogeographic studies on the Québec fish fauna (Legendre and Legendre 1984). The genetic study by Gagnon and Angers (2006) supports this interpretation by showing that the genetic differences in four fish species in a subset of our study lakes were consistent with longitude but not with the current drainage system. These authors showed, for example, that northern pike and yellow perch populations situated 100 km apart latitudinally and in distinct watersheds were genetically more similar than populations situated in the same drainage and less than 30 km apart on a longitudinal axis (Gagnon and Angers 2006).

The strong relationship between altitude and fish community structure might be explained by the isostatic rebound that followed the glacier retreat. Isostatic rebound contributed to eliminating immigration routes from lowland into highland areas, and some fishes, particularly species with warm-water preferences (e.g., northern pike and walleye), may have been unable to recolonize highland areas. This could explain why *Salvelinus* spp. occur mostly in lakes with elevations higher than ca. 470 m, whereas the reverse was found for species like northern pike and walleye. According to the differences in the physiological capacities and the ecological preferences of each species, these species are in fact expected to have colonized this area at different times. Thus, despite its reduced range of variation, altitude seemed to be an important spatial factor structuring fish communities of this part the Canadian Shield. Hinch et al. (1991), having found that elevation (200–400 m) was important in explaining fish community composition in their Ontario lakes, came to a similar conclusion.

The negative relationship between the BPUE of large piscivores and both prey fish richness and prey BPUE adds to the growing evidence that the presence of top predators is associated with a reduction in small-bodied fish diversity and (or) abundance in temperate lakes (Chapleau et al. 1997; Findlay et al. 2000). The BPUE of large piscivores was also associated with greater Shannon diversity and Pielou evenness in the fish community, suggesting that piscivory, despite its negative relationship with small-bodied species richness, could contribute to maintaining a relatively high diversity in the fish communities by reducing the biomass of dominant species. *Salvelinus* spp. never co-occurred with large predators, also suggesting an effect of piscivory.

A relatively large part of the variation in the total fish biomass in our study lakes was explained by the Shannon diversity index. Similarly, both prey species richness and diversity were significantly related to prey fish BPUE. It is possible that fish species diversity was related to resource use complementarity, thus leading to higher biomass levels (Loreau 1998; Cardinale et al. 2002). At the level of the top predators, this complementarity could be due to differences in habitat use (in space and time) by walleye and northern pike (i.e., pelagic vs littoral predator with different light regimes), thus leading to an increase in the system's production (Ryder and Kerr 1978). In the case of benthivorous species, the co-occurrence of lake whitefish in lakes containing white sucker could have allowed a better exploitation of deep benthic prey.

The patterns in fish community structure observed in our study lakes are in accordance with the qualitative results of different authors who described the fish communities in lakes of the Canadian Shield (Johnson et al. 1977; Ryder and Kerr 1978; Marshall and Ryan 1987). These authors showed, for example, that northern pike is often the only top predator in these communities, whereas walleye, if present, co-occurs in most cases with northern pike. Our results help in understanding the factors behind these patterns. However, about 50% of the variability in the fish community structure was not accounted for by our analysis. This amount of unexplained variation means that other important factors not considered in our analysis (e.g., water chemistry or lake productivity) are likely to influence fish community structure. Moreover, a more accurate estimation of factors such as beaver dam impact might also have raised the proportion of the explained variation. However, our results show that considering only current connectivity when analyzing the patterns in lake fish communities is a shortcoming. Despite the relative simplicity of this approach, integrating geographic coordinates and elevation as proxies of past dispersion patterns at the landscape level can be highly informative. Olden et al. (2001) criticized such straight-line distance approaches, suggesting that we should consider spatial factors from an "as the fish swims" rather than an "as the crow flies" perspective. However, our results show that spatial factors related to "as the fish swam" are also of primary importance in multivariate approaches aimed at determining the current patterns of distribution of fish.

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Appendix A

Table A1 appears on the next page (p. 2792).

Table A1. Occurrence of fish species in the study lakes.

Lake	caco	eslu	pefl	cocl	seco	savi	mama	safo	lolo	nocr	copl	phne	sana	pheo	osmo	nohu	pupu	peom	peca	nohe	luco	cuin	cysp
C12	×	×	×	×	×	×																	×
C2	×	×	×		×																		
C23		×	×	×		×																	
C24		×	×		×				×	×													
C29	×							×	×		×												
C40		×	×							×													
C44	×	×	×	×	×					×										×			
C48	×							×	×		×	×	×										
C9	×	×	×																				
FBP10	×	×	×				×																
FBP9	×	×			×																		
FP15	×	×	×	×	×	×																	×
FP2	×	×	×	×						×													
FP24		×	×																				
FP27	×								×				×						×				×
FP30	×	×	×	×		×																	×
FP31							×	×															
FP32	×	×	×	×		×	×																
N106	×						×	×			×												
N107	×	×	×																		×		
N120	×		×		×			×	×			×											
N122		×																					
N16	×							×															
N35	×	×	×				×																
N43	×	×	×	×					×														
N5	×										×												×
N55	×	×	×		×					×						×							
N56	×	×									×												
N59		×	×													×							
N63	×	×										×											
N70	×	×	×	×	×	×			×														
N82	×													×									×
N84	×	×	×		×	×																	×
N88	×	×					×																
N89	×	×	×	×		×						×											
P109	×		×				×					×			×								
P110	×		×					×						×	×		×	×				×	×
P25	×	×	×	×		×																	

Note: caco, *Catostomus commersonii*; eslu, *Esox lucius*; pefl, *Perca flavescens*; cocl, *Coregonus clupeaformis*; seco, *Semotilus corporalis*; savi, *Sander vitreus*; mama, *Margariscus margarita*; safo, *Salvelinus fontinalis*; lolo, *Lota lota*; nocr, *Notemigonus crysoleucas*; copl, *Couesius plumbeus*; phne, *Phoxinus neogaeus*; sana, *Salvelinus namaycush*; pheo, *Phoxinus eos*; osmo, *Osmerus mordax mordax*; nohu, *Notropis hudsonius*; pupu, *Pungitius pungitius*; peom, *Percopsis omiscomaycus*; peca, *Percina caprodes*; nohe, *Notropis heterolepis*; luco, *Luxilus cornutus*; cuin, *Culaea inconstans*; cysp, Cyprinid sp.