Relationships between species feeding traits and environmental conditions in fish communities: a three-matrix approach

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Abstract. Understanding the relationships between species biological traits and the environment is crucial to predicting the effect of habitat perturbations on fish communities. It is also an essential step in the assessment of the functional diversity. Using two complementary three-matrix approaches (fourth-corner and RLQ analyses), we tested the hypothesis that feeding-oriented traits determine the spatial distributions of littoral fish species by assessing the relationship between fish spatial distributions, fish species traits, and habitat characteristics in two Laurentian Shield lakes. Significant associations between the feeding-oriented traits and the environmental characteristics suggested that fish communities in small lakes (displaying low species richness) can be spatially structured. Three groups of traits, mainly categorized by the species spatial and temporal feeding activity, were identified. The water column may be divided in two sections, each of them corresponding to a group of traits related to the vertical distribution of the prey coupled with the position of the mouth. Lake areas of low structural complexity were inhabited by functional assemblages dominated by surface feeders while structurally more complex areas were occupied by mid-water and benthic feeders. A third group referring to the time of feeding activity was observed. Our work could serve as a guideline study to evaluate species traits × environment associations at multiple spatial scales. Our results indicate that three-matrix statistical approaches are powerful tools that can be used to study such relationships. These recent statistical approaches open up new research directions such as the study of spatially based biological functions in lakes. They also provide new analytical tools for determining, for example, the potential size of freshwater protected areas.

Key words: ecological niche; feeding traits; fish communities; fourth-corner method; functional group; habitat; lake; Laurentian Shield lakes, Quebec, Canada; littoral zone; spatial scale; three-matrix approach.

Introduction

Assessing the habitat characteristics required by fish to complete their life cycles is of primary importance in the prediction of the effect of habitat perturbations or losses on fish communities and the identification of the environmental conditions that should be protected for conservation purposes. Differences in the species composition of fish communities among systems and variations in the response of fish species to environmental conditions are major obstacles to the development of habitat models that may be applied to many fish species in many ecosystems (Olden and Jackson 2002). Functional classification of fish species in which fish that share common traits are grouped together represents an alternative to individual species–environment

models and may circumvent these obstacles (McGill et al. 2006). According to Austen et al. (1994), groups of traits form operational units that respond to environmental changes in a more predictable way than individual species, thereby improving the predictive capabilities of habitat models in comparison to models developed at high levels of taxonomic resolution (i.e., species level). Grouping species according to traits is also a way of identifying functional groups of species to assess "key" functions of an ecosystem: this is an essential step in assessing functional diversity within and between ecosystems (Mouillot et al. 2006, Brind'Amour et al. 2009).

Habitats have long been argued as acting as templates on which evolution forges phenotypic attributes (Southwood 1977, 1988). Habitat characteristics can be viewed as filters imposed on species gene pools to select traits suited to a particular set of environmental conditions (Díaz et al. 1998). These concepts notably refer to the "niche filtering hypothesis" and suggest that species sharing similar traits form functional groups that may likely occupy similar habitats (Tonn et al. 1990,

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Zobel 1997). Grouping species according to traits, such as morphology or behavior, is one way to simplify species-rich communities and thus increase the transferability of habitat models among ecosystems (Angermeier and Winston 1998). For instance, traits referring to the beta niche of species (i.e., the type of resources used by species or their mode of acquisition; Ackerly and Cornwell 2007) have been used recently to describe the ecological processes generating species interactions along an altitudinal gradient (Mason et al. 2007). Conclusions from Mason et al. (2007) as well as from early studies (Keast and Webb 1966) suggest that feeding-oriented traits may represent good descriptors of fish communities and can be used to classify species into functional categories.

The relationship between species traits and the environment is commonly assessed indirectly using a two-step analysis. Fish abundances are first linked to environmental conditions and species responses to environmental variation are then related to the biological and/or physiological traits of species. In such analyses, the relationship between the environment and the species traits is thus assessed indirectly (Thuiller et al. 2004, Santoul et al. 2005). Certain authors sacrifice some information at the species level and compute a traits–sites matrix weighted (or not) by the abundances, which they link directly to the environment (Richards et al. 1996, Poff 1997). Although the latter approach may be called a direct functional analysis, the loss of information may be penalizing (Dray and Legendre 2008). Direct assessment of the traits–environment relationships, which keeps all the available ecological information, is rarely done because it requires a statistical method that takes into account simultaneously the information stored in three tables to link fish traits and environmental conditions through fish responses. Among the three-matrix approaches allowing such analyses to be carried out, the RLQ analysis and the fourth-corner method are two complementary approaches. RLQ analysis (Dolédec et al. 1996) is an extension of co-inertia analysis that produces ordination results that can be used to identify the group members of species, species traits, and environmental variables. The fourth-corner method was first developed by Legendre et al. (1997) to statistically test the significance of the correlations between species traits and environmental conditions using a matrix of species traits, a matrix of presence/absence of the species obtained by sampling a series of sites, and a matrix of environmental conditions observed at the sites. Dray and Legendre (2008) have recently revised this method, suggesting new testing procedures and allowing the analysis of the species abundances (instead of presence/absence only) observed at the sampling sites. The modified version of the fourth-corner method is particularly appealing in ecosystems in which generalist species may be present in nearly all sampling sites and for which emerging patterns may

only be observable with species abundance data. On the other hand, being recently published, this revised version has been used in very few studies (Tall et al. 2006) and its usefulness still needs to be assessed.

Our study addresses the issue of understanding species and trait relations to habitat using the two complementary three-matrix approaches cited above. Since feeding is considered one of the major processes structuring lacustrine fish communities (Gatz 1979a, Pierce et al. 1994, Norton 1995, Piet 1998, Mason et al. 2007), we focused mainly on feeding-oriented traits. The objective was to assess whether feeding-oriented traits determine the multiscale distributions of littoral fish species in lakes. It was tested using two lakes from the same watershed, sharing similar geological and biological characteristics. More specifically we (1) define functional groups of species based on feeding-oriented traits, (2) assess the relationships between the feeding-oriented traits and the environmental conditions, and (3) investigate the scale dependency of the feeding-oriented traits and environment correlations.

The latter objective (i.e., scale dependency) was inspired from recent findings on the effect of scale and habitat patchiness on the structure of fish assemblages in lakes (Poizat and Pont 1996, Johnson et al. 2004, Brind'Amour et al. 2005, Stoffels et al. 2005, Brind'Amour and Boisclair 2006). These studies showed that the nature and strength of the relationships between the species abundances and the environmental variables may vary with the scale at which the analysis is conducted. Scale-dependent functional relationships have been extensively investigated in lotic ecosystems (Poff 1997, Angermeier and Winston 1998, Lamouroux et al. 2002, Goldstein and Meador 2004, Higgins 2009) but the concept remains poorly studied in lacustrine ecosystems at the scale of a whole lake (Irz et al. 2007, Eros et al. 2009). This is perhaps because of the river continuum concept (Vannote et al. 1980) and its derived theoretical framework (e.g., "landscape filter framework"; Poff 1997), which offers a predictive spatial support to study the structure and functional relationships of fish species in lotic systems. For instance, Goldstein and Meador (2004) developed functional hypotheses using the "landscape filter framework" to predict the relationships between categories of species traits and the size of streams. In lakes, the concept of "hierarchical filters" was introduced by Tonn et al. (1990). That framework is similar to the one suggested by Poff (1997) in which fish communities are "environmentally filtered" as we move from the continental scale to the lake scale. Unfortunately, that framework cannot be used in the present study to develop functional hypotheses because the filters are not assessed at the same spatial scales as the ones in our study; we are positioned under the finest scale studied by Tonn et al. (1990) and other recent papers (Irz et al. 2007, Eros et al. 2009).
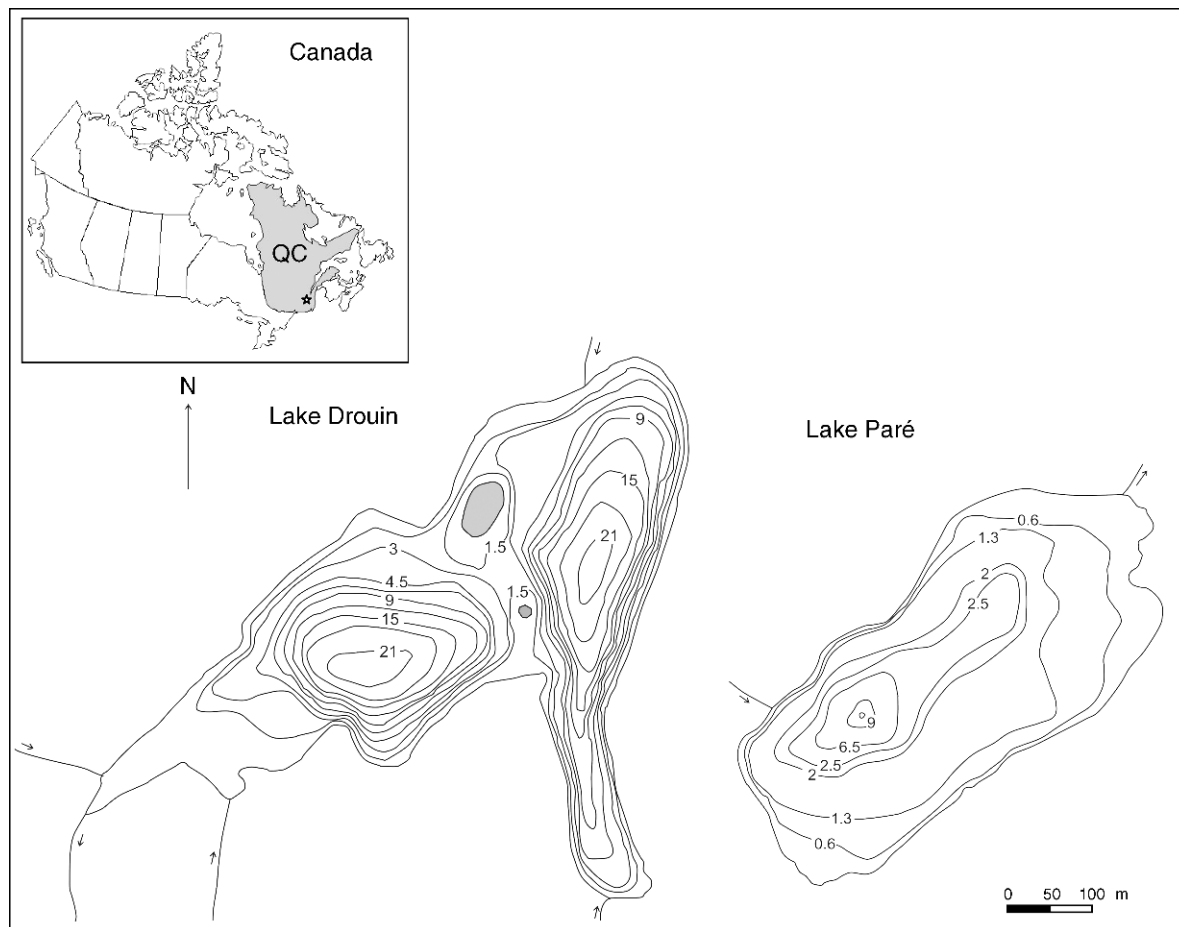
FIG. 1. Bathymetric maps of the two study lakes on the Laurentian Shield in Quebec (QC), Canada. Depth contour values are in meters. Arrows identify inflow and outflow.

METHODS

Study lakes

The fish communities of Lake Drouin and Lake Paré were analyzed in this study. The two lakes are located in the same watershed on the Laurentian Shield in the province of Quebec, Canada (Fig. 1). Lake Drouin (46°09′ N, 73°55′ W) has a surface area of 31 ha, a maximum depth of 22 m, and a perimeter of 4.8 km (calculation based on the sum of the linear lengths of our sampling units). Lake Paré (46°08′ N, 73°54′ W) has a surface area of 23 ha, a maximum depth of 9 m, and a perimeter of 3.1 km. Both lakes present a littoral zone with woody debris, rocky substrate, sandy beaches, and patches of macrophytes of mixed species such as *Brasenia schreberi* Gmelin, *Eriocaulon aquaticum* (Hill) Druce, *Myriophyllum spicatum* L., and *Nymphaea odorata* Aiton. The two lakes are mesotrophic with similar limnological and geomorphological characteristics. During the period of thermal stratification (May to October), surface water temperatures ranged from 15°C to 26°C and bottom temperatures from 4°C to 8°C. The thermoclines formed at 4.5 m depth in mid-June and

broke down in early October (A. Brind'Amour, *unpublished data*).

Sampling protocol

The fish community and the environmental variables were quantified at 90 (Lake Drouin) and 60 sites (Lake Paré) that covered the complete perimeter of the littoral zones of the lakes. The sampling sites were defined as an area that possessed fairly homogenous attributes with respect to a combination of environmental variables (i.e., substrate, macrophyte density). Mid-water buoys delimiting the beginning and the end of each site were anchored. The surface area of individual sampling sites ranged from 162.4 to 268.8 m^2 (average size 215.6 m^2) in Lake Drouin and from 109.2 to 390.8 m^2 (average size 207.6 m^2) in Lake Paré. The width of a sampling site (5–10 m) was determined as the distance from the shore to the 3-m depth isobath. The limit of 3 m was adopted because it corresponded to the depth at which all fish observed could be correctly counted and identified to species while snorkeling. The mean width of a site was 10.5 m (range: 9–12 m) for the two lakes. Geographical

TABLE 1. Classification of the fish species into functional groups in Lake Drouin (Laurentian Shield, Quebec, Canada) obtained by K-means partitioning on the species feeding-oriented trait matrices (i.e., matrix **B**).

| | Functional group of species (G_s) | | |
Species	Lake Drouin, very broad	Lake Drouin, broad	Lake Paré
Ameiurus nebulosus	G_s3	G_s3	present
Catostomus commersoni	G_s3	G_s3	present
Couesius plumbeus	absent	absent	present
Fundulus diaphanous	G_s1	G_s1	absent
Lepomis gibbosus	G_s2	G_s2	present
Notemigonus crysoleucas	G_s1	G_s1	absent
Perca flavescens	G_s2	G_s2	present
Semotilus atromaculatus	G_s2	G_s2	present

Notes: No functional relationships were found in Lake Paré. Abbreviations are: G_s1, surface feeders; G_s2, mid-water feeders; G_s3, bottom feeders. For a definition of spatial scales, see *Methods: Analytical framework*.

coordinates were determined at each site using a global positioning system (Garmin GPS 12, Garmin, Olathe, Kansas, USA) with a precision of ± 10 m.

Fish community.—The sites from both lakes were surveyed three times (i.e., on three consecutive days between 09:00 and 15:00) between 25 July and 4 August 2001. The data for the three days were then averaged within homologous sites of the lake. This procedure was done to minimize the effects of daily variations of fish community characteristics at each site. The detailed justification for this procedure is given in Web Appendix 1 of Brind'Amour et al. (2005). Survey of the fish community was done using a modified version of the visual survey technique described by Harmelin-Vivien et al. (1985). The technique and its sampling efficiency are fully detailed in Brind'Amour and Boisclair (2004). It requires two observers who snorkel at the water surface performing zigzags over the complete length and width of a sampling site following a trajectory that is parallel to shore. During such sampling, the distance between the two observers was 4 m. The observers covered nearly 90% of the total area of each sampling site. They maintained a constant swimming speed of 10 m/min to minimize fish disturbance (Eklöv 1997). Data were recorded on PVC cylinders that the snorkellers wore around one forearm. Snorkellers identified the species, the relative abundance, and the approximate size (i.e., small, medium, large) of the fish observed as they progressed along their respective transect. Preliminary identification of fish species and relative size had been conducted prior to the study in order to normalize the sampling protocol.

We recorded a total of nine species in the two lakes (Table 1): eight in Lake Drouin and six in Lake Paré. Pumpkinseed (*Lepomis gibbosus*) represented 51% of the fish surveyed, whereas seven species represented each <20% of the observations: golden shiner (*Notemigonus crysoleucas*), creek chub (*Semotilus atromaculatus*),

banded killifish (*Fundulus diaphanus*), brown bullhead (*Ameiurus nebulosus*), yellow perch (*Perca flavescens*), lake chub (*Couesius plumbeus*), and white sucker (*Catostomus commersoni*). The fathead minnow (*Pimephales promelas*), which accounted for <0.5% of the observations, was excluded from the analyses. This was done because it was impossible to assess whether the low abundance observed for *P. promelas* was due to its rarity or to methodological limits.

Environmental variables.—The sampling sites were characterized by 10 environmental variables (Table 2). All environmental variables, with the exceptions of density of macrophytes and fetch, were surveyed at the end of May 2001. The density of macrophytes was estimated on 29 July in Lake Drouin and 27 July in Lake Paré. The density of macrophytes at each site was estimated by two snorkelers using four randomly selected quadrats of 1 m^2 (a 1-m^2 frame was thrown from the center of the sampling site in different directions within each site). The number of stems of emergent and submersed species was counted in the 1-m^2 frame. The average number of stems from the four replicates was used in the statistical analyses. The percent cover, mainly composed of a dense decaying weed bed of *M. spicatum* and/or unidentified species, was estimated and used as the "bottom cover" variable. Fetch was calculated on each sampling day as the distance to the shore in the direction of the dominant wind.

Environmental complexity index (ECI).—We developed an index to estimate the environmental complexity of the littoral zone of the studied lakes. That index, which we called the environmental complexity index (ECI), sums the squared pairwise dissimilarities (Gower distances) between the sites of each lake that we then divide by the number of sites to make the indices comparable. The ECI measures the total environmental variation captured in the Gower dissimilarity matrix. Greater variability in the matrix of sites × environmental characteristics leads to greater dissimilarity among the sites and, thereby, to greater ECI. Details concerning the computation of that index are found in Appendix A.

Analytical framework

We tested the hypothesis that morphological and behavioral traits determine the spatial distributions of the littoral fish species in the two lakes, using the fourth-corner method (Legendre et al. 1997). This approach requires multiple data taking the form of three input matrices (**R**, **L**, and **Q**) and computes species traits–environment correlations in a fourth matrix (**D**; Fig. 2). This section presents the information contained in each matrix used in fourth-corner analysis and describes the field methods used to collect that information.

*Matrix **L**: abundance of the fish species.*—The first matrix (**L**: $m \times k$) contained the abundances of the k species at the m sampling sites. It was composed of seven species at 90 sampling sites in Lake Drouin and six

TABLE 2. Description of the codes, numerical resolutions, and characteristics of the environmental variables estimated in Lake Drouin and Lake Paré, Quebec, Canada.

Environmental variable	Code	Resolution	Drouin	Paré
Mean littoral slope	Litt	quantitative	0.29 (0.17)	0.14 (0.09)
Mean depth	Z	quantitative	1.66 (0.58)	1.28 (0.34)
Macrophytes				
Mean density of emergent	Emerg	quantitative	7.49 (12.70)	13.95 (21.03)
Mean density of submersed	Subm	quantitative	3.43 (4.62)	10.99 (16.45)
Bottom cover (M. spicatum)	Cover	percentage	26.36 (22.06)	71.08 (38.52)
Fetch (m)	Fetch	quantitative	303.63 (406.63)	2.964 (3.62)
Distance to tributary (m)	Trib	quantitative	596.76 (401.94)	785.86 (455.89)
Surface of a sampling site (m^2)	Size	quantitative	215.60 (52.84)	207.60 (80.93)
Riparian slope	Rip	presence/absence	24.44	35.00
Substrates (by particle size)				
Sand (<2 mm)	Sand	presence/absence	17.78	10.00
Rock (60–250 mm)	Rock	presence/absence	41.11	14.44
Boulders (>250 mm)	Boulder	presence/absence	16.67	0.00
Bedrock	Bedrock	presence/absence	1.11	0.00
Woody debris	Woody	presence/absence	3.33	1.11
Riparian use				
Cottage/brick wall	Cott	presence/absence	62.22	61.67
Forest	Forest	presence/absence	46.67	30.00
Beach		presence/absence	5.56	10.00
Bush		presence/absence	26.67	21.67
Riparian trees	Tree	presence/absence	24.44	43.33
ECI			4.02	2.38

Notes: Values in columns Drouin and Paré are either percentages of occurrence or means with SD in parentheses. The environmental complexity index (ECI) represents the sum of the pairwise distances between the sites (for the formula, see Appendix A).

species at 60 sampling sites in Lake Paré. The abundance data were square-root transformed to reduce the influence of the dominant species in the analysis of community structure (Sokal and Rohlf 1995).

Matrix **Q**: *morphological and behavioral traits.*—The second matrix (**Q**: $k \times n$) described n morphological or behavioral traits of the same k species. Data (i.e., the eight traits) in this matrix were obtained from several studies providing information on the fish species present in the two lakes (Scott and Crossman 1973, Becker 1983, Carlander 1997, Ultsch et al. 1999, Robb and Abrahams 2002). The species were described using eight feeding-oriented and behavioral traits (Table 3) that had been found to be significantly associated with the environmental conditions in other studies. Some of the traits were not mutually exclusive; a species could be coded as feeding on several types of prey and in different parts of the water column (water surface, mid-water, or bottom).

Matrix **R**: *environmental variables.*—The third matrix (**R**: $m \times p$) displayed information about the p environmental variables at the m sampling sites. As our third objective was to investigate the scale dependency of the feeding-oriented traits and environment correlations, we assessed the link between the species traits and the environmental variables over multiple spatial scales by modeling spatially the environmental variables at four spatial scales (see next paragraph for details). Therefore, we created four matrices, **R**$_{VB}$, **R**$_B$, **R**$_M$, and **R**$_F$ ($m \times p$), one for each spatial scale,

containing the spatially modeled environmental variables.

The spatial modeling of the environmental variables was done using principal coordinates of neighbor matrices (PCNM; Borcard and Legendre 2002, Borcard et al. 2004). PCNM eigenvectors represent a spectral decomposition of the spatial relationships among the sampling sites and describe all spatial scales that can be accommodated in the sampling design (Dray et al. 2006). They were obtained by principal coordinate analysis (PCoA) of a truncated geographic distance matrix among the sites, as explained in the above-mentioned papers (Borcard and Legendre 2002, Borcard et al. 2004; step 1 in Fig. 2). In the present study, all distances larger than the distance between the centers of adjacent sites were replaced by four times that value, before PCoA. The resulting principal coordinates, which are called PCNM variables or eigenvectors, were then used as spatial predictors to analyze the spatial variation of the environmental variables. The PCNM variables corresponded to a series of vectors maximizing the spatial autocorrelation measured by Moran's I and constitute a model of spatial structures at multiple scales (Dray et al. 2006). Only the PCNM eigenvectors modeling positive spatial correlation, as verified by the computation of Moran's I statistics, were included in the next step of variable selection in a multiple regression analysis. A forward selection was then done to identify the significant PCNMs (26 for Lake Drouin and 21 for Lake Paré) explaining the environmental variability
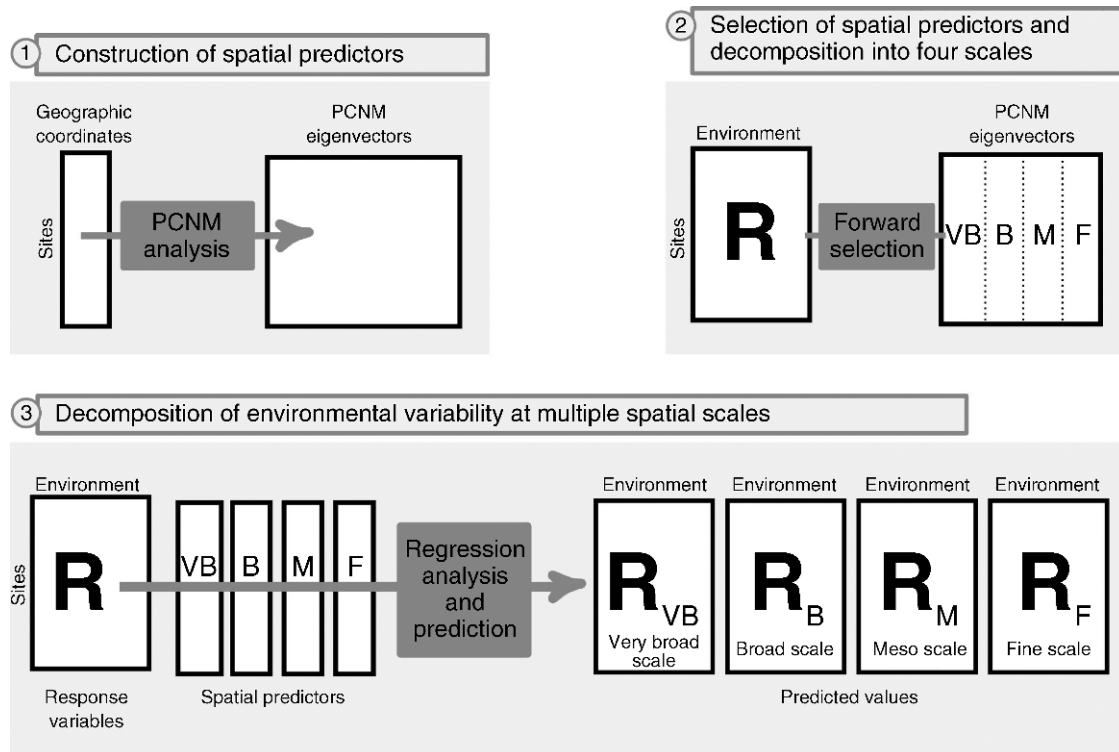
Fig. 2. Schematic flow diagram of the statistical framework used in the present study. Environmental variables were spatially modeled (steps 2 and 3) at multiple spatial scales (very broad, VB, to fine, F) prior to the analyses using principal coordinates of neighbor matrices (PCNM) (constructed in step 1). The fourth-corner and RLQ analyses were then conducted in parallel to assess the multi-scale species traits–environment relationships (step 4). The fourth-corner method was used to test statistically each combination of species traits and environmental variables and estimate the total inertia (matrix trace). RLQ analysis was used for its graphical representations of the species traits and environment ordinations (hyperspaces), which facilitated the ecological interpretation of the results.

(step 2 in Fig. 2). The significant PCNMs were divided into four groups corresponding to the four spatial scales; see Brind'Amour et al. (2005) for details. We described the spatial scales as patches or sections corresponding to a percentage of the lake perimeter. For instance, the very broad scale (R_{VB}) corresponded to patches of nearly 40% of the total perimeter of each lake, i.e., 1900 m and 1200 m for Lakes Drouin and Paré, respectively; the broad scale (R_B) to sections of 10–20% of the total perimeter; the meso scale (R_M) to sections of 5–10% of the total perimeter; and the fine scale (R_F) to sections smaller than 5% of the total perimeter. Associations between the environmental variables and the groups of PCNMs at the four spatial scales were computed using either multiple regressions for the quantitative continuous variables or logistic regressions for the binary variables (step 3 in Fig. 2). The predicted values (for the quantitative variables) or the probabilities (for the binary variables) at the sampling sites, which represented the relevant information, were used to form four matrices, R_{VB}, R_B, R_M, and R_F. Therefore, these matrices were composed of the environmental conditions predicted at each spatial scale, thereby corresponding to the spatially modeled environmental conditions. The multiple and logistic regressions were computed using the free software R 2.6.1 (R Development Core Team 2005).

Species traits–environment relationships (step 4 in Fig. 2).—Matrix **D** ($n \times p$) contained the results obtained after conducting the fourth-corner analysis. It was composed of correlations of the n morphological or behavioral traits (matrix **Q**) crossed with the p environmental variables (matrix **R**). For each lake, we conducted the analysis four times, one for each spatial scale (i.e., using the four different matrices, R_{VB}, R_B, R_M, and R_F) leading to four matrices D_{VB}, D_B, D_M, and D_F. The analyses were performed using the function "fourthcorner" of the ade4 package (Dray and Dufour 2007) in the R language. We considered species abundances instead of presence/absence data in matrix **L**, the latter being the only type of data used in the original fourth-corner method of Legendre et al. (1997). The correlations obtained in individual cells (d_{ij}) of the **D** matrices were tested using 999 permutations, thereby producing P values. Two permutation models were used (permutation of entire rows and entire columns) and their probabilities combined to test the null hypothesis (H_0) stating that the species traits (matrix **Q**) are not
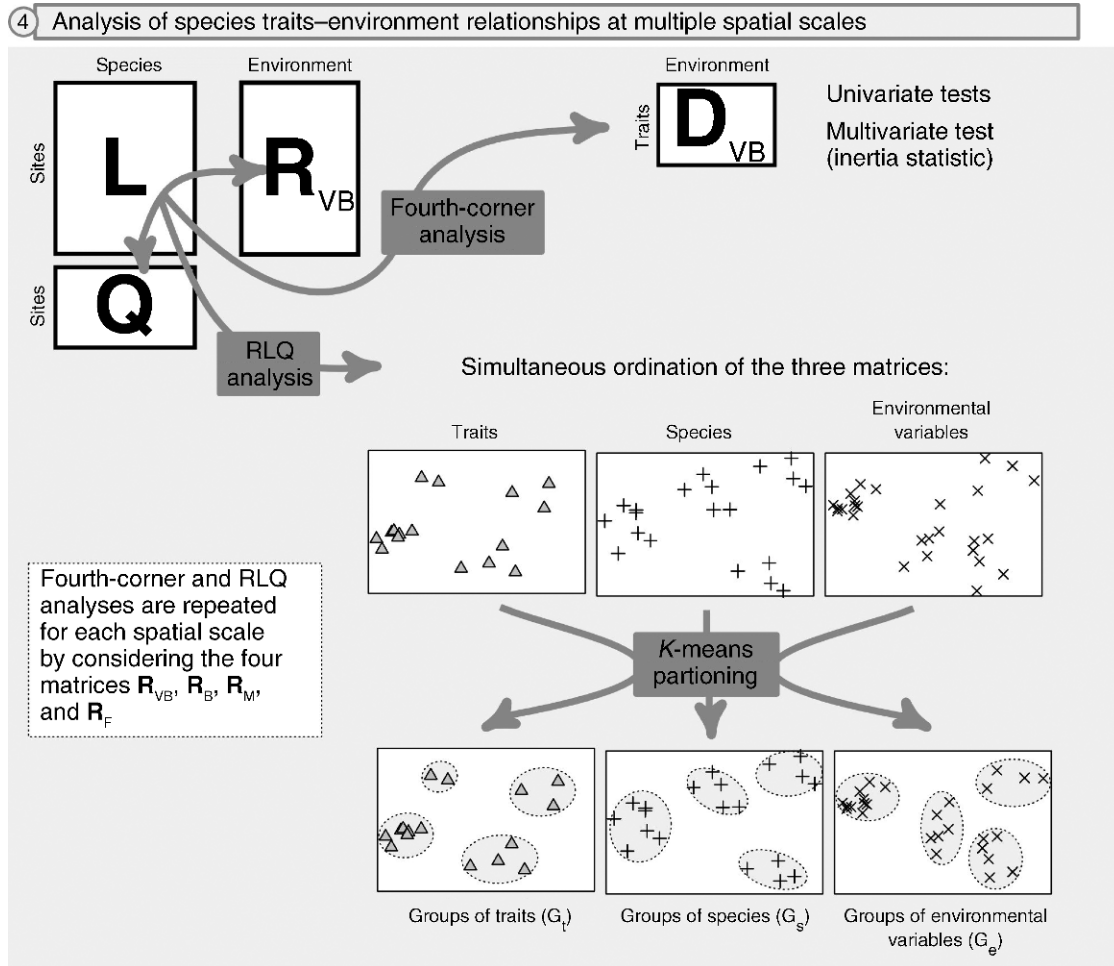
FIG. 2.   Continued.

related to the environmental variables (matrix **R**). According to Dray and Legendre (2008), the rejection of H_0 (**R** $\leftrightarrow$ **Q**) requires two conditions (or hypotheses): (1) the rejection of the absence of a link between species abundances and species traits (i.e., H_{01}: **L** $\leftrightarrow$ **Q**) and (2) the rejection of the absence of a link between species abundances and environmental variables (i.e., H_{02}: **L** $\leftrightarrow$ **R**). The two hypotheses were tested using different permutation models: (1) permutation of entire rows (H_{01}: positions of species assemblages are independent of the environmental characteristics of the sites; model type 2) and (2) permutation of entire columns (H_{02}: distribution of species is independent of their biological traits; model type 4). Rejection of H_0 at significance level $\alpha = 0.05$ required the rejection of the two hypotheses at significance levels $\alpha_1 = \alpha_2 = 0.2236$; in that way, $\alpha = \alpha_1\alpha_2 = 0.05$. Only the correlations that remained significant at the 0.05 level after the α adjustment of Holm's procedure for multiple testing (Holm 1979) and α correction ($\alpha_1\alpha_2$) were used for ecological interpretation. According to Dray and Legendre (2008), combining results from the two

hypotheses seems the only way to test properly the whole link between species traits and environmental variables mediated by the abundances of species. A multivariate statistic (inertia or trace of matrix **D**), which measures the overall link between the variability of the species traits and the variability of the environmental conditions, was also computed at each spatial scale. That statistic, computed by the R function "fourthcorner2" of ade4, was tested using permutations.

RLQ analyses (Dolédec et al. 1996) were computed using the "rlq" function of the "ade4" package. RLQ is an extension of co-inertia analysis that simultaneously finds linear combinations of the variables of table **R** and linear combinations of the variables of table **Q** of maximal covariance weighted by the data in table **L** (Dray et al. 2003). It graphically summarizes and represents the main co-structure in the three tables **R**, **L**, and **Q**. The RLQ and fourth-corner analyses were jointly used to identify the species and the environmental conditions corresponding to the groups of traits. Graphical representations of the outputs of RLQ analysis (e.g., scores of the species traits and environ-

TABLE 3. Description of the species morphological and behavioral traits used in this study.

Species traits	A. nebulosus	C. commersoni	C. plumbeus	F. diaphanous	L. gibbosus	N. crysoleucas	P. flavescens	S. atromaculatus
Type of diet								
Plant (1)	0	0	1	1	0	1	0	0
Zoobenthos (2)	1	1	0	0	1	0	1	1
Zooplankton (3)	0	1	1	1	1	1	0	0
Insect larvae (4)	1	1	1	1	1	0	0	1
Fish (5)	0	0	1	0	0	0	1	1
Feeding strata								
Benthic (6)	1	1	0	0	1	0	1	1
Water column (7)	0	0	1	1	1	0	1	0
Surface (8)	0	0	0	1	0	1	0	0
Body morphology								
Fusiform (9)	0	0	1	1	0	0	1	1
Compressed (10)	0	0	0	0	1	1	0	0
Cylindrical (11)	1	1	0	0	0	0	0	0
Migration								
Daily (12)	0	1	0	0	0	1	1	0
Seasonal (13)	0	1	1	0	0	0	1	0
Mouth position								
Inferior (14)	1	1	0	0	0	0	0	0
Superior (15)	0	0	0	1	0	1	0	0
Terminal (16)	0	0	1	0	1	0	1	1
Temperature								
1: 10–15°C (17)	0	0	1	0	0	0	0	1
2: 15–20°C (18)	0	1	0	1	1	1	0	1
3: 20–25°C (19)	1	0	0	1	0	0	1	0
Dissolved oxygen								
1: 7–8 mg/L (20)	0	1	1	0	1	1	0	1
2: 5–7 mg/L (21)	0	1	1	1	0	1	1	1
3: <2 mg/L (22)	1	0	0	1	0	0	0	0
Activity								
Diurnal (23)	0	0	0	1	1	1	1	1
Nocturnal (24)	1	1	1	0	0	0	0	0

Notes: Numbers in parentheses are codes for the species traits used in Fig. 4. The numbers in the cells represent qualitative coding of the species traits: a trait characterizes (1) or does not characterize (0) the species. Some of the traits are not mutually exclusive; a species could be coded as feeding on several types of prey and in different parts of the water column (water surface, mid-water, or bottom). See Table 1 for full species names.

mental variables) were used for interpretation purposes. The groups of species (G_s), species traits (G_t), and environmental variables (G_e) were obtained by K-means partitioning applied to the tables of species scores, trait scores, and environmental scores of RLQ analysis, respectively. K-means partitioning searches for the groups that minimize the total within-group or "error" sum of squares (TESS), or, equivalently, the total intra-cluster variation. The Calinski-Harabasz criterion, which is a pseudo-F statistic as in ANOVA, was used to assess the best number of groups identified by K-means partitioning (Calinski and Harabasz 1974, Milligan and Cooper 1985).

RESULTS

The global multivariate statistic (inertia of **D**) of the fourth-corner analyses indicated that the overall link between the species traits and the environmental variables displayed similar patterns across spatial scales in Lake Drouin and Lake Paré (Fig. 3). Although the values from the two lakes cannot be directly compared, both lakes displayed low values at finer spatial scales (Lake Drouin, 0.48; Lake Paré, 0.68) and high values at broader scales (Lake Drouin, 2.21 at very broad scale; Lake Paré, 1.72). This suggests either that the environmental variables used in this study explained a lower proportion of the species traits variance at finer scales than at larger scales or that traits other than feeding-oriented traits are associated with the distribution of species at the finer scales. Permutation tests conducted on the overall statistics indicated that only the very broad and broad spatial scales in Lake Drouin displayed global significant correlations between the traits and the environment (i.e., matrices **D**). Therefore, only the traits–environment relationships in Lake Drouin at these two spatial scales are further described. For simplicity, we present hereafter a summary of the fourth-corner results found in matrices **D**. Complete results (i.e., correlation statistics in matrices **D**) can be found in Appendix B.

The relationship between species traits and environmental conditions varied widely between the very broad and broad spatial scales. When comparing the significant correlations at the very broad and broad spatial scales (matrices **D** in Appendix B), we observe that only 6% of the statistically significant correlations were between the same species traits and environmental conditions at the two spatial scales. Graphically, these associations can be observed in Fig. 4 where similar positions of the points relative to the origin in both plots indicate associations between environmental variables and species traits.

Groups of traits

The *K*-means analyses, applied to RLQ scores, identified three groups of species traits in Lake Drouin at very broad (Fig. 4A) and broad spatial scales (Fig. 4B). Comparison of the composition of these groups indicates that 75% of the significant species traits were similarly grouped at the two spatial scales. The first group of traits (G_t1) included fish having a superior mouth, feeding mainly on invertebrates associated with plants or located near the water surface (surface feeders; Fig. 4A; triangles). Two species, *N. crysoleucas* and *F. diaphanus*, were associated with this group (Table 1). The second group of traits (Gt2) included the highest number of species traits and was composed of species with a terminal mouth having mid-water (zooplankton) or benthic (zoobenthos) feeding habits (Fig. 4A, circles). This group was represented by *L. gibbosus*, *P. flavescens*, and *S. atromaculatus* at both spatial scales (Table 1). The third group of traits (G_t3) was based on the time of day at which feeding is expected to occur and, more specifically, was composed of nocturnally active species with cylindrical bodies and inferior mouths (Fig. 4A; circles). Fish species associated with this third group were also the same at the two scales: *C. commersoni* and *A. nebulosus* (Table 1). The sums of the species abundances associated with each group of traits indicated that G_t1, G_t2, and G_t3 represented respectively 17.60%, 78.63%, and 3.77% of the total fish species abundances.

Traits–environment relationships

The RLQ analyses identified three groups of environmental variables at very broad (Fig. 4C) and broad spatial scales (Fig. 4D). The structure of the RLQ analyses is such that these three groups comprise environmental variables that have the highest correlations with the three groups of species traits for each of these spatial scales. At the very broad spatial scale (Fig. 4C), the first group of environmental variables (G_e1), which refers to the presence of boulders and bedrock, corresponded to the environmental conditions that have the highest correlations with the species traits found in the first group of traits (G_t1), which represents the traits associated with species defined as surface feeders. The
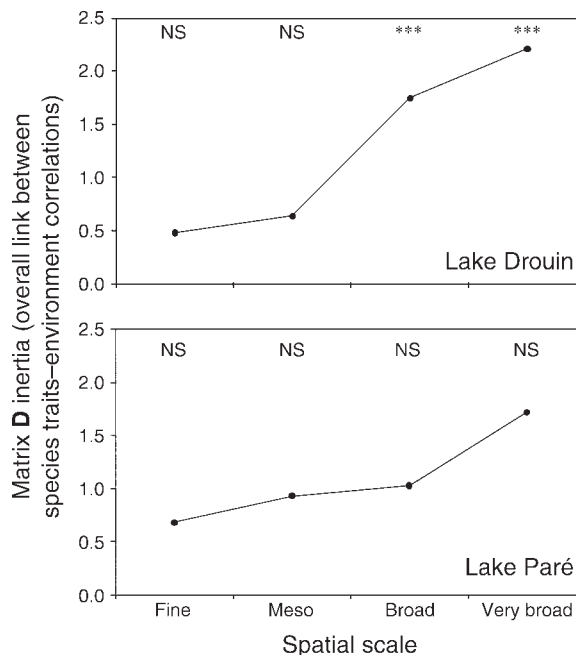
FIG. 3. Inertia between the species traits and the environmental variables at the four spatial scales in Lake Drouin and Lake Paré.
*** $P \leq 0.001$; NS, relationship not significant.

G_e2 group was defined by gentle slopes (Litt, Rip) and sandy bottoms with submerged macrophytes (Subm). This group of environmental variables was best correlated with the species traits that characterized fish described as mid-water/benthic feeders (G_t2). Finally, G_e3 was mainly composed of deep sites (Z) exposed to the action of the wind (Fetch) containing structures such as woody debris, high macrophyte cover of *M. spicatum* (Cover), emergent macrophytes (Emerg), and rocks. This group of sites was inhabited by nocturnally active fish species with cylindrical bodies and inferior mouths (G_t3). At the broad spatial scale (Fig. 4D), G_e1 is expected to represent the group of environmental variables best correlated with traits of surface feeders (G_t1) at that scale. This situation is consistent with the similarity between the species trait groupings obtained at the very broad and broad spatial scales. However, at the broad scale, G_e1 was characterized by a gentle riparian slope (Rip) and rocks as substrate and not, as found for the G_e1 group at very broad scale, by boulders and bedrock. The G_e2 group was mainly associated with the type of substrates (Boulder, Bedrock, Woody) and the littoral slope or variables related to the spatial organization of the sites, such as wind exposition (Fetch), tributaries (Trib), the size of the sites, and the riparian use (Cott). The G_e3 group was defined by high average depth (Z), high abundances of macrophytes (Emerg or Subm), and sandy bottoms (Fig. 4D).
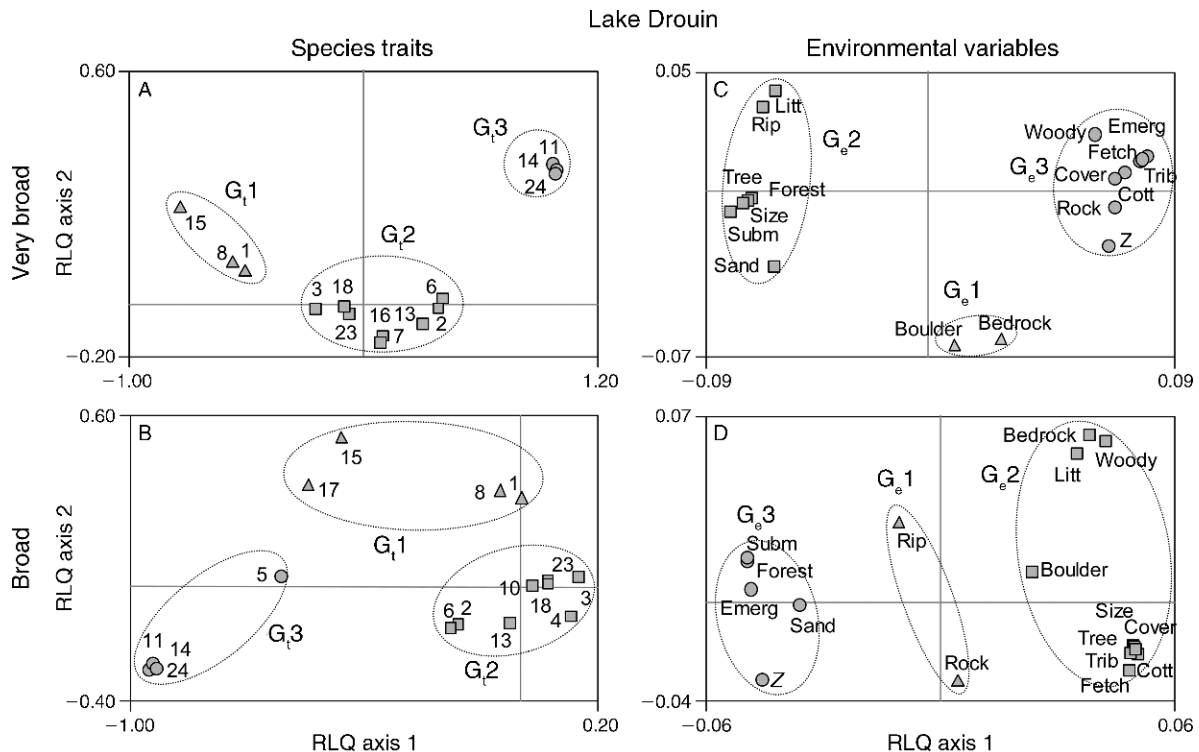
FIG. 4.   Results of the RLQ analysis indicating the scores of species traits along the two RLQ axes for Lake Drouin (A) at very broad spatial scale and (B) at broad spatial scale, and the scores of environmental variables (C) at very broad spatial scale and (D) at broad spatial scale. Positions of the points relative to the origin indicate relative contributions to RLQ axes. Ellipses delineate groups of traits (G_t) and groups of environmental variables (G_e) identified by *K*-means partitioning; see *Methods* for details. Species traits are identified by numbers defined in Table 3. To simplify the interpretation, only the traits that tested significant at the 0.05 level after the α adjustment of Holm's procedure for multiple testing and α correction ($\alpha_1\alpha_2$) using the fourth-corner analyses are displayed. See *Methods* for more details.

DISCUSSION

We intended to assess whether feeding-oriented traits determine the spatial distribution of littoral fish species in lakes. The associations between the feeding-oriented traits and the environmental characteristics at different spatial scales suggest that the fish community, in at least one of the two lakes, was spatially structured along the vertical (strata in the water column) and horizontal (habitats or environmental conditions) dimensions.

Three functional groups, two spatial scales, one significant lake

In Lake Drouin, the positive associations among the feeding-oriented traits indicated the presence of three groups of species (sensu Gatz 1979*b*). These groups were mainly characterized by the vertical distribution of the prey, the position of the mouth (see Plate 1), and the time or period of their feeding activity. The groups agreed with early studies that stated that functional groups of species in lakes are likely founded on the criteria of where and how resources are used by species within the water column (Schutz and Northcote 1972, Gatz 1979*b*). The constancy of the groups of feeding traits across the spatial scales, notwithstanding the

environmental variability at these scales, emphasizes the idea that feeding traits are major functional drivers in structuring fish communities in lakes.

At the two broader spatial scales, the significant correlations between the species traits forming the functional groups and the environmental variables highlighted the influence of environmental characteristics on the organization of fish communities. Water depth and macrophyte density are expected to play an important role in habitat segregation among the littoral fish species (Beauchamp et al. 1994, Weaver et al. 1997, Grenouillet and Pont 2001). At the very broad scale in Lake Drouin, we observed that, as the environmental conditions shifted from areas of low structural complexity such as sites with either boulders or bedrock as substrates to shallow areas with fine sediments and high density of submersed macrophytes (i.e., high habitat complexity), the functional assemblages shifted from surface feeders (G_t1) to mid-water and benthic feeders (G_t2). Concurrently, the habitat of greater complexity (i.e., G_t2 habitat) was also the one in which we observed the highest number of functional traits (see Fig. 3) and the highest relative abundance (G_t1, 17.60%; G_t2, 78.63%). Several studies showed that the diversity and
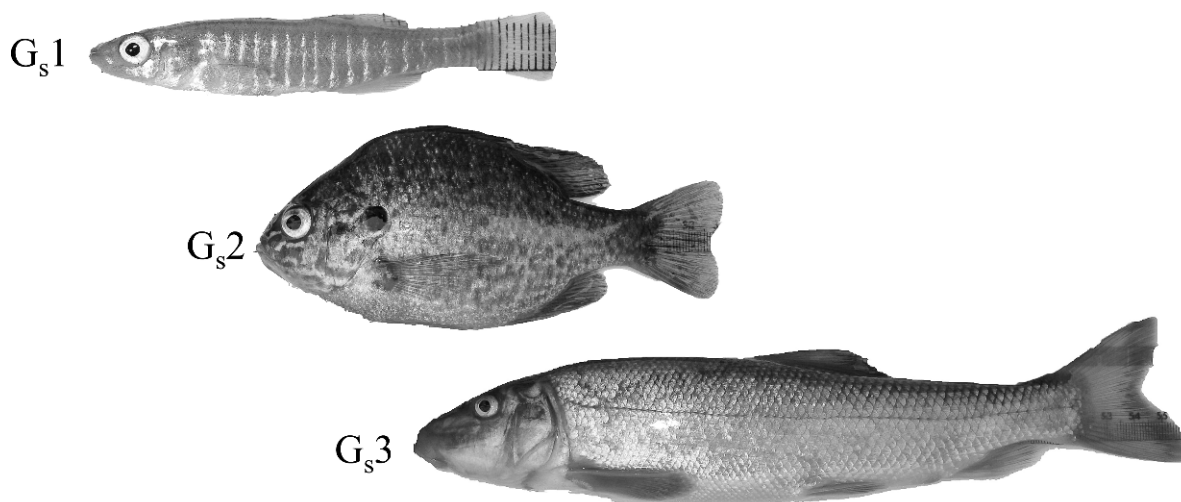
PLATE 1. Species representatives of the three functional groups: G_s1, species with superior mouth, feeding mainly on invertebrates associated with plants or located near the water surface; G_s2, species with a terminal mouth having mid-water (zooplankton) and/or benthic (zoobenthos) feeding habits; and G_s3, nocturnal active species with cylindrical bodies and inferior mouth. Photo credit: J.-M. Chamberland. Special thanks to D. Kopp for photo manipulations.

abundance of invertebrate food associated with near-shore macrophytes allow the coexistence of species having multiple dietary specializations (Werner et al. 1977, Grenouillet and Pont 2001). The abundance of microcrustaceans varies widely between emergent and submersed macrophytes and with habitat depths (Paterson 1993), whereas insect larvae (odonata and chironomids), which are the preferred prey of the mid-water and benthic groups (G_s2), are typically abundant in fine, organic sediments (James et al. 1998, Weatherhead and James 2001). Direct functional association, such as prey items available to fish or consumed by them, have not been surveyed during our study. Yet our interpretation is mostly based on earlier findings and theoretical hypotheses on niche partitioning and habitat complexity stating that the more structurally complex the habitat is, the greater diversity of functional traits it can support (Gorman and Karr 1978, Ross 1986, Higgins and Strauss 2008). Hori et al. (2009) recently described the relationship between groups of fish appearing at the surface of, inside, and along a gradient of habitat complexity defined by the canopy height of seagrass beds in coastal areas. They showed that fish found inside the seagrass (similar to our mid-water group) preferred structurally complex habitat with high seagrass biomass and high three-dimensional structure, whereas the group of surface feeders preferred a less complex habitat with low seagrass biomass and high three-dimensional structure.

Some environmental variables were structurally significant for different functional groups at different spatial scales. This was notably the case for the fetch and the cover of *M. spicatum*, which were both associated with G_t3 at the very broad spatial scale but were linked to G_t2 at the broad scale. This result could

be explained by the roles played by the environmental conditions at different scales. For instance, at the very broad spatial scale (i.e., large parts of the lake), exposed sites with dense cover of *M. spicatum* may represent good refuges for nocturnally active species during the day, whereas at the broader spatial scale (i.e., habitat patches of ~500 m), the fetch may enhance benthic productivity serving as resource areas for mid-water and benthic feeders (G_t2) (Mittelbach 1981, Werner et al. 1983, Tabor and Wurtsbaugh 1991, Gafny et al. 1992, Diehl 1993). These causal links were not properly tested in our study. We can only hypothesize on the scale dependency of some traits–environment correlations that may reflect different processes operating at different scales in lakes.

Scale-dependent relationships between species biological traits and potential processes in lakes have been recently observed by Irz et al. (2007) and Eros et al. (2009). These two studies tested the functional convergence of three reproductive traits and four trophic traits of fish species between 75 French and 168 lakes of northeastern United States (Irz et al. 2007) and characterized the congruence between taxonomic and six trait-based fish assemblages in 125 Finnish boreal lakes (Eros et al. 2009). They both found that reproduction-related traits (i.e., spawning habitat and period) were major drivers of fish assemblages, showing indeed strong intercontinental convergence. Trophic-related traits, omnivores and benthivores, were to a lesser extent associated with lake area (in North American and Finnish lakes) and depth (in Finnish lakes). It is, however, difficult to overstep the results of the two aforementioned studies as they are both focusing on spatial scales much broader than ours.

There were no significant relationships between the feeding-oriented traits and the environmental characteristics at the two finer spatial scales (<10% of the total perimeter of a lake) in Lake Drouin and none at any of the studied scales in Lake Paré. Owing to the nature of the data in the **R**, **L**, and **Q** matrices, the two nonsignificant results could be due to different causes. Four hypotheses could notably explain the lack of significant relationships between the fish traits (biological/physiological) and the environment conditions at a single (e.g., fine scale in Lake Drouin) or multiple scales (Lake Paré). The first hypothesis refers to the low species trait variability among the species present in the community to explain the lack of significant relationship in Lake Paré. In our study, that hypothesis can be easily refuted by comparing the species richness and their related traits in each lake. The two lakes shared five of nine species and the species present from one lake had similar biological traits to the species present in the other lake. This suggests that the variability of the species traits in Lake Paré could not likely explain the lack of traits–environment relationship in that lake. As for the lack of significant relationships at finer spatial scales in Lake Drouin, it could be due to the fact that the feeding-oriented traits used in the study are not structurally important at finer spatial scales: species traits other than feeding-oriented traits might be significant at these scales.

The second hypothesis refers to the lack of spatial variability in the species abundances. This could be the case for ubiquitous species, such as *L. gibbosus*. Brind'Amour et al. (2005) showed, however, that the species abundances in the two lakes displayed spatial variability at multiple spatial scales.

The third hypothesis refers to the random spatial distribution of the species in the studied lakes. As mentioned in the previous paragraph regarding the second hypothesis, spatial analyses conducted on the same fish communities found significant spatial patterns in both lakes, indicating a nonrandom distribution of the fish species in the two lakes.

The fourth hypothesis is the one that may explain the lack of significant relationships in Lake Paré; it refers to the lack of variability in the environmental conditions. Given that the anthropogenic development surrounding the two studied lakes is comparable (Drouin, 62.12% of the lake perimeter; Paré, 61.60%), that the two lakes display similar species composition (Table 1), and that they also display similar geological/morphological characteristics, the only difference between the two lakes lies in the variability of their environmental characteristics (Table 2). The lack of significant species traits–environment relationship at any spatial scale in Lake Paré may hence be attributable to the lower structural diversity of the environmental conditions in its littoral zone than in Lake Drouin, thus providing several habitats at multiple spatial scales in that lake. The environmental complexity in Lake Drouin (ECI = 4.06)

is greater than in Lake Paré (ECI = 2.38). This is particularly apparent for environmental variables (Table 2) such as fetch, depth, and woody debris, which are major environmental drivers structuring the littoral fish communities in lakes (Keast et al. 1978, Brosse et al. 1999a, b, Vono and Barbosa 2001, Brind'Amour and Boisclair 2006).

The absence of a significant species traits–environment relationship in Lake Paré could also be due to the greater power of the fourth-corner correlation test in the lake in which more sites have been surveyed (Lake Drouin, 90 sites; Lake Paré, 60 sites). However, sensibility and power analyses of the fourth-corner to the number of sampling sites have been tested using simulations in Dray and Legendre (2008). According to their results, 60 sites would not be a shortcoming of the fourth-corner approach.

Testing the reliability of the fourth-corner approach

The fourth-corner method has been recently published but its effectiveness has been rarely evaluated using field data (Tall et al. 2006). Dray and Legendre (2008) used simulated data to measure the influence of several parameters (species richness, sample size, levels of alpha and beta diversities) on the efficiency of the method. They showed that the power of the method (i.e., its ability to detect ecological patterns when they exist) increases with the number of sites and the number of species.

Species richness in the two studied lakes may be considered low (six and seven species for Lake Paré and Lake Drouin, respectively). However, it is still comparable to the species richness found in North American lakes, where species richness ranges between 1 and 22 and the mean species richness equals 6.35 (Randall et al. 1995). Dray and Legendre (2008) showed that increasing the sampling size is a way to counterbalance the effects of low species richness. In our study, several significant associations have been detected by the fourth-corner approach, suggesting that the sampling effort is sufficient to detect significant traits–environment relationships in these two lakes. However, increasing the sampling effort would probably help detect other significant associations. In a more general context, this study is quite "encouraging" as we know that the fourth-corner method would be more powerful in richer ecosystems, but it is still able to detect significant traits–environment relationships in a species-poor ecosystem if the sampling size is sufficient.

The fourth-corner correlation statistic differs greatly from the classical bivariate Pearson's r as it measures the relationship between two variables (trait and environmental variable) recorded on different sampling units (species and sites); its computation thus requires the consideration of an extra table of species abundances. Hence, the distribution of fourth-corner correlation statistics is unknown, but experience shows that statistically significant values are much lower than in

ordinary correlation studies (Dray and Legendre 2008). Moreover, the sampling distribution would probably be influenced by the number of sites or the species richness (i.e., dimension of the table **L**) considered in the analysis. Hence, correlations obtained by the fourth-corner method should not be compared between studies (if the dimensions of **L** vary) or to correlation values obtained in the classical bivariate case. For instance, the maximum value reached by the significant correlations in our study was 0.14. Low values could have been favored by the indirect way the information about the fish species traits was gathered. Fish traits were not estimated specifically for the two study lakes but were extracted from the literature, just as in the fish study of the fourth-corner paper of Legendre et al. (1997). Several studies observed that, beside ontogenetic shifts, fish morphology may be affected by spatial and temporal variations in abiotic and biotic factors (Taylor 1999). The underlying assumption that species traits obtained from the literature may adequately represent the fish traits in our study lakes may have weakened our traits–environment relationships. Therefore, we suggest using direct measurements of the functional traits or at least measurements gathered in the same ecosystem or geographic region than the one from which the species come, whenever possible.

New research directions and potential implications for lake management

The present work showed that in small lakes displaying low species richness, species traits can be spatially structured. It also indicated that three-table statistical approaches, such as the fourth-corner analysis coupled with RLQ analysis, are powerful tools to assess such relationships. Approaches like the one we applied here open up a new research direction: the study of spatially based biological functions in lakes and in other ecosystems. To our knowledge, this research field is growing in marine ecosystems (Bremner et al. 2003, Frid et al. 2008) but is still in its infancy in lacustrine ecosystems. For instance, spatial patches of high functional diversity or spatial distribution of essential ecological functions, such as nursery areas, have been recently identified in estuaries (Islam and Tanaka 2006). Determination of biological traits identified as indicators of key aspects of functioning in potential marine protected areas (MPA) have also been recently tested and suggested by Frid et al. (2008). Studies, such as the ones cited above, are all incorporating functional aspects (assessed by species biological traits) into the designation and protection of marine habitats (McLeod et al. 2009).

Freshwater protected areas (FPA; Suski and Cooke 2007) are the freshwater counterpart of MPAs. As in MPAs, the success of FPAs relies notably on their spatial design, i.e., the spatial arrangement and the appropriate size to optimize the exchange between productive (or functionally diverse) areas (Pauly et al. 2002). An analytical approach such as the one used here could help determine the dominant spatial scales (i.e., geographic ranges) at which functional groups of species are varying, thereby identifying habitat patches of high biological (or functional) diversity (i.e., potential FPA sizes).

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APPENDIX A

Computation of the environmental complexity index (ECI) (*Ecological Archives* A021-021-A1).

APPENDIX B

Assessment of the relationships between species traits and environmental conditions for littoral fish communities using the fourth-corner method (*Ecological Archives* A021-021-A2).

***Ecological Application Archives* A021-021-A1**

Computation of the Environmental Complexity Index (ECI)

First, we calculated a distance matrix [D^2_{hi}] among the pairs of sites using Gower's dissimilarity coefficient on the sites-environment matrix. This coefficient was chosen because it can be used with mixed variable types (quantitative, categorical, and binary) and missing values (Legendre and Legendre 1998, eq. 7.20; Podani and Schmera 2006).

From this distance matrix, we computed the index of environmental complexity (ECI) as the sum of the squared distances among the pairs of sampling sites (i, j) divided by the number of sampling sites (n_m) in each lake:

$$\text{ECI} = \left[\sum_{h, i = 1}^{n_m} D^2_{hi} \right] / n_m$$

This equation produces a generalized form of sum-of-squares representing the total variation in the Gower dissimilarity matrix (Legendre and Legendre 1998, eq. 8.6).

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APPENDIX B

Ecological Application Archives A021-021-A2

Assessment of the relationships between species traits and environmental conditions for littoral fish communities using the fourth-corner methodAppendix B: Assessment of the relationships between species traits and environmental conditions for littoral fish communities using the fourth-corner method

Table B1   Correlations from the fourth-corner analysis between the species traits (columns) and the environmental variables (rows) at very broad spatial scale in Lake Drouin. Species trait codes are found in Table 3. Each environmental variable name is followed by a line of fourth-corner correlation coefficients.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Litt	0.110	-0.114	0.031	-0.079	-0.039	-0.114	-0.116	0.110	-0.027	0.029	-0.006	0.068	-0.075	-0.006	0.138	-0.116	0.007	0.047	-0.029	0.029	0.067	0.011	0.006	-0.006
Z	-0.112	0.129	-0.060	0.070	0.054	0.129	0.086	-0.112	0.016	-0.035	0.038	-0.056	0.080	0.038	-0.127	0.086	0.012	-0.067	0.018	-0.018	-0.066	-0.022	-0.038	0.038
Emerg	-0.112	0.143	-0.100	0.044	0.070	0.143	0.026	-0.112	-0.010	-0.039	0.092	-0.023	0.089	0.092	-0.096	0.026	0.033	-0.099	0.001	-0.001	-0.061	-0.040	-0.092	0.092
Subm	0.103	-0.136	0.096	-0.045	-0.070	-0.136	-0.031	0.103	0.004	0.039	-0.081	0.026	-0.082	-0.081	0.093	-0.031	-0.036	0.090	-0.001	0.001	0.056	0.037	0.081	-0.081
cover	-0.097	0.129	-0.088	0.047	0.065	0.129	0.035	-0.097	-0.001	-0.037	0.073	-0.030	0.075	0.073	-0.093	0.035	0.034	-0.083	0.002	-0.002	-0.055	-0.033	-0.073	0.073
Fetch	-0.116	0.147	-0.103	0.043	0.071	0.147	0.023	-0.116	-0.012	-0.039	0.097	-0.021	0.093	0.097	-0.096	0.023	0.032	-0.103	0.000	0.000	-0.063	-0.042	-0.097	0.097
Trib	-0.111	0.145	-0.103	0.043	0.073	0.145	0.025	-0.111	-0.009	-0.040	0.093	-0.022	0.090	0.093	-0.095	0.025	0.036	-0.100	0.000	0.000	-0.060	-0.042	-0.093	0.093
Size	0.097	-0.128	0.087	-0.047	-0.064	-0.128	-0.035	0.097	0.001	0.037	-0.073	0.030	-0.074	-0.073	0.093	-0.035	-0.033	0.082	-0.002	0.002	0.055	0.033	0.073	-0.073
Rip	0.112	-0.122	0.043	-0.077	-0.046	-0.122	-0.106	0.112	-0.023	0.032	-0.019	0.064	-0.078	-0.019	0.136	-0.106	-0.001	0.056	-0.025	0.025	0.068	0.016	0.019	-0.019
S1	0.063	-0.101	0.097	-0.016	-0.062	-0.101	0.022	0.063	0.017	0.032	-0.092	0.000	-0.053	-0.092	0.041	0.022	-0.048	0.080	0.014	-0.014	0.033	0.036	0.092	-0.092
S3	-0.105	0.131	-0.078	0.058	0.061	0.131	0.057	-0.105	0.006	-0.037	0.060	-0.042	0.078	0.060	-0.109	0.057	0.025	-0.077	0.009	-0.009	-0.061	-0.029	-0.060	0.060
S4	-0.056	0.030	0.047	0.063	-0.011	0.030	0.128	-0.056	0.039	-0.003	-0.067	-0.065	0.031	-0.067	-0.100	0.128	-0.044	0.018	0.038	-0.038	-0.038	0.017	0.067	-0.067
S5	-0.079	0.061	0.023	0.074	0.006	0.061	0.134	-0.079	0.038	-0.012	-0.047	-0.071	0.049	-0.047	-0.121	0.134	-0.034	-0.003	0.038	-0.038	-0.051	0.009	0.047	-0.047
S8	-0.075	0.111	-0.096	0.026	0.063	0.111	-0.004	-0.075	-0.013	-0.034	0.088	-0.010	0.060	0.088	-0.058	-0.004	0.044	-0.082	-0.009	0.009	-0.040	-0.036	-0.088	0.088
S9	0.090	-0.120	0.080	-0.048	-0.060	-0.120	-0.039	0.090	-0.002	0.035	-0.064	0.034	-0.067	-0.064	0.091	-0.039	-0.032	0.074	-0.003	0.003	0.052	0.029	0.064	-0.064
U1	-0.103	0.135	-0.093	0.046	0.067	0.135	0.032	-0.103	-0.004	-0.038	0.080	-0.027	0.080	0.080	-0.094	0.032	0.034	-0.089	0.001	-0.001	-0.057	-0.036	-0.080	0.080
U2	0.094	-0.125	0.085	-0.047	-0.063	-0.125	-0.037	0.094	0.000	0.036	-0.069	0.031	-0.071	-0.069	0.092	-0.037	-0.034	0.079	-0.002	0.002	0.053	0.031	0.069	-0.069
Tree	0.095	-0.125	0.086	-0.047	-0.064	-0.125	-0.036	0.095	0.000	0.037	-0.070	0.031	-0.072	-0.070	0.092	-0.036	-0.034	0.079	-0.002	0.002	0.054	0.032	0.070	-0.070

Table B2	Correlations from the fourth-corner analysis between the species traits (columns) and the environmental variables (rows) at broad spatial scale in Lake Drouin. Species trait codes are found in Table 3.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Litt	0.137	-0.102	0.034	0.018	-0.003	-0.102	0.015	0.137	0.067	-0.021	-0.081	-0.035	-0.107	-0.081	0.040	0.015	0.066	0.111	-0.007	0.007	0.077	0.047	0.081	-0.081
Z	-0.038	0.088	-0.130	-0.016	0.089	0.088	-0.035	-0.038	0.000	-0.043	0.082	0.016	0.047	0.082	-0.017	-0.035	0.067	-0.105	-0.002	0.002	-0.012	-0.034	-0.082	0.082
Emerg	0.004	0.042	-0.110	-0.072	0.078	0.042	-0.091	0.004	-0.021	-0.015	0.067	0.071	0.035	0.067	0.057	-0.091	0.066	-0.079	-0.033	0.033	0.023	-0.059	-0.067	0.067
Subm	0.012	0.030	-0.102	-0.098	0.076	0.030	-0.111	0.012	-0.033	-0.001	0.061	0.099	0.042	0.061	0.085	-0.111	0.062	-0.072	-0.049	0.049	0.035	-0.078	-0.061	0.061
cover	-0.011	-0.031	0.102	0.097	-0.076	-0.031	0.110	-0.011	0.032	0.001	-0.061	-0.098	-0.041	-0.061	-0.084	0.110	-0.062	0.073	0.048	-0.048	-0.034	0.077	0.061	-0.061
Fetch	-0.021	-0.021	0.093	0.111	-0.075	-0.021	0.121	-0.021	0.037	-0.008	-0.053	-0.116	-0.045	-0.053	-0.102	0.121	-0.062	0.061	0.061	-0.061	-0.045	0.090	0.053	-0.053
Trib	-0.013	-0.029	0.100	0.100	-0.076	-0.029	0.113	-0.013	0.034	-0.001	-0.060	-0.102	-0.042	-0.060	-0.088	0.113	-0.062	0.071	0.051	-0.051	-0.036	0.080	0.060	-0.060
Size	-0.011	-0.032	0.103	0.095	-0.076	-0.032	0.109	-0.011	0.032	0.002	-0.062	-0.096	-0.041	-0.062	-0.082	0.109	-0.062	0.073	0.047	-0.047	-0.033	0.075	0.062	-0.062
Rip	0.067	-0.043	-0.032	-0.046	0.030	-0.043	-0.050	0.067	0.022	-0.021	0.000	0.040	-0.014	0.000	0.058	-0.050	0.042	0.000	-0.002	0.002	0.059	0.002	0.000	0.000
S1	0.014	0.045	-0.121	-0.048	0.113	0.045	-0.039	0.014	0.039	-0.062	0.047	0.056	0.072	0.047	0.012	-0.039	0.087	-0.073	-0.004	0.004	0.053	-0.043	-0.047	0.047
S3	-0.088	0.031	0.078	0.027	-0.076	0.031	0.018	-0.088	-0.067	0.056	0.015	-0.008	0.030	0.015	-0.032	0.018	-0.092	0.011	-0.014	0.014	-0.070	-0.016	-0.015	0.015
S4	0.017	-0.035	0.033	-0.002	-0.013	-0.035	0.032	0.017	0.027	-0.002	-0.046	-0.004	-0.001	-0.046	-0.005	0.032	-0.024	0.020	0.025	-0.025	0.016	0.022	0.046	-0.046
S5	0.118	-0.105	0.051	-0.020	-0.012	-0.105	0.004	0.118	0.043	0.010	-0.097	0.000	-0.085	-0.097	0.065	0.004	0.032	0.099	-0.016	0.016	0.070	0.020	0.097	-0.097
S8	0.094	-0.114	0.105	-0.024	-0.058	-0.114	-0.003	0.094	0.008	0.043	-0.097	0.016	-0.070	-0.097	0.073	-0.003	-0.019	0.119	-0.027	0.027	0.054	0.011	0.097	-0.097
S9	-0.013	-0.029	0.101	0.100	-0.076	-0.029	0.113	-0.013	0.033	-0.001	-0.060	-0.102	-0.042	-0.060	-0.088	0.113	-0.062	0.071	0.050	-0.050	-0.036	0.079	0.060	-0.060
U1	-0.013	-0.029	0.100	0.100	-0.076	-0.029	0.113	-0.013	0.034	-0.001	-0.059	-0.103	-0.042	-0.059	-0.089	0.113	-0.062	0.071	0.051	-0.051	-0.037	0.080	0.059	-0.059
U2	0.011	0.032	-0.103	-0.095	0.077	0.032	-0.109	0.011	-0.032	-0.002	0.062	0.096	0.041	0.062	0.082	-0.109	0.062	-0.073	-0.047	0.047	0.033	-0.076	-0.062	0.062
Tree	-0.012	-0.031	0.102	0.096	-0.077	-0.031	0.110	-0.012	0.032	0.001	-0.061	-0.098	-0.041	-0.061	-0.084	0.110	-0.062	0.073	0.048	-0.048	-0.034	0.077	0.061	-0.061

Table B3　　　Correlations from the fourth-corner analysis between the species traits (columns) and the environmental variables (rows) at meso spatial scale in Lake Drouin. Species trait codes are found in Table 3.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Litt	0.026	-0.029	0.000	-0.043	-0.007	-0.029	-0.052	0.026	-0.021	0.017	0.006	0.039	-0.014	0.006	0.056	-0.052	-0.001	0.000	-0.015	0.015	0.019	-0.011	-0.006	0.006
Z	0.033	-0.010	-0.045	-0.013	0.026	-0.010	-0.066	0.033	0.016	-0.058	0.080	0.040	0.037	0.080	0.019	-0.066	0.036	-0.023	0.011	-0.011	0.052	0.017	-0.080	0.080
Emerg	-0.017	0.007	-0.027	-0.012	0.014	0.007	-0.012	-0.017	0.015	-0.036	0.040	0.021	0.052	0.040	-0.015	-0.012	-0.016	-0.052	0.043	-0.043	0.012	0.021	-0.040	0.040
Subm	-0.012	0.001	-0.028	-0.019	0.011	0.001	-0.025	-0.012	0.012	-0.036	0.047	0.029	0.052	0.047	-0.005	-0.025	-0.017	-0.054	0.042	-0.042	0.017	0.022	-0.047	0.047
cover	-0.012	0.002	-0.028	-0.019	0.012	0.002	-0.024	-0.012	0.012	-0.036	0.046	0.029	0.052	0.046	-0.006	-0.024	-0.017	-0.054	0.042	-0.042	0.016	0.022	-0.046	0.046
Fetch	-0.015	0.005	-0.028	-0.015	0.013	0.005	-0.017	-0.015	0.014	-0.036	0.043	0.024	0.052	0.043	-0.011	-0.017	-0.016	-0.053	0.042	-0.042	0.014	0.021	-0.043	0.043
Trib	0.011	0.000	0.028	0.020	-0.011	0.000	0.026	0.011	-0.011	0.036	-0.048	-0.031	-0.052	-0.048	0.003	0.026	0.017	0.054	-0.042	0.042	-0.017	-0.022	0.048	-0.048
Size	-0.012	0.001	-0.028	-0.019	0.012	0.001	-0.024	-0.012	0.012	-0.036	0.046	0.029	0.052	0.046	-0.005	-0.024	-0.017	-0.054	0.042	-0.042	0.016	0.022	-0.047	0.046
Rip	0.101	-0.079	-0.011	-0.053	0.006	-0.079	-0.083	0.101	0.013	-0.016	0.007	0.050	-0.042	0.007	0.091	-0.083	0.042	0.027	-0.012	0.012	0.076	0.015	-0.007	0.007
S1	-0.024	0.010	-0.004	-0.041	0.003	0.010	-0.031	-0.024	-0.024	0.014	0.019	0.049	0.046	0.019	0.023	-0.031	-0.023	-0.029	-0.008	0.008	0.002	-0.030	-0.019	0.019
S3	-0.060	0.006	0.043	0.052	-0.058	0.006	0.055	-0.060	0.003	-0.009	0.012	-0.053	0.014	0.012	-0.073	0.055	-0.084	-0.027	0.072	-0.072	-0.051	0.068	-0.012	0.012
S4	-0.051	0.043	0.031	0.019	-0.014	0.043	0.044	-0.051	-0.035	0.055	-0.040	-0.024	-0.007	-0.040	-0.023	0.044	-0.018	0.022	-0.042	0.042	-0.054	-0.048	0.040	-0.040
S5	-0.050	-0.003	0.053	-0.008	-0.069	-0.003	-0.020	-0.050	-0.061	0.049	0.018	0.008	-0.001	0.018	0.010	-0.020	-0.082	-0.012	0.004	-0.004	-0.049	0.006	-0.018	0.018
S8	-0.094	0.028	0.058	0.093	-0.084	0.028	0.087	-0.094	-0.012	0.005	0.013	-0.101	-0.011	0.013	-0.110	0.087	-0.105	-0.029	0.082	-0.082	-0.099	0.087	-0.013	0.013
S9	-0.015	0.004	-0.028	-0.015	0.013	0.004	-0.018	-0.015	0.014	-0.036	0.044	0.025	0.052	0.044	-0.010	-0.018	-0.016	-0.053	0.042	-0.042	0.014	0.022	-0.044	0.044
U1	0.010	0.001	0.028	0.022	-0.010	0.001	0.030	0.010	-0.010	0.036	-0.049	-0.033	-0.052	-0.049	0.001	0.030	0.017	0.054	-0.041	0.041	-0.019	-0.022	0.049	-0.049
U2	0.011	-0.001	0.028	0.020	-0.011	-0.001	0.026	0.011	-0.012	0.036	-0.048	-0.030	-0.051	-0.048	0.004	0.026	0.016	0.054	-0.042	0.042	-0.017	-0.022	0.048	-0.048
Tree	-0.013	0.002	-0.028	-0.018	0.012	0.002	-0.023	-0.013	0.012	-0.036	0.046	0.028	0.052	0.046	-0.007	-0.023	-0.016	-0.054	0.042	-0.042	0.016	0.022	-0.046	0.046

Table B4   Correlations from the fourth-corner analysis between the species traits (columns) and the environmental variables (rows) at fine spatial scale in Lake Drouin. Species trait codes are found in Table 3.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Litt	0.002	-0.002	0.007	-0.007	-0.014	-0.002	-0.022	0.002	-0.028	0.025	0.003	0.004	-0.025	0.003	0.024	-0.022	0.001	0.010	-0.025	0.025	-0.012	-0.014	-0.003	0.003
Z	0.036	-0.049	0.000	-0.039	-0.023	-0.049	-0.067	0.036	-0.014	-0.002	0.029	0.035	-0.020	0.029	0.056	-0.067	-0.015	-0.015	0.016	-0.016	0.025	0.028	-0.029	0.029
Emerg	-0.004	0.022	-0.007	-0.023	0.012	0.022	-0.002	-0.004	-0.038	0.061	-0.046	-0.001	-0.048	-0.046	0.035	-0.002	0.025	0.016	-0.063	0.063	-0.031	-0.062	0.046	-0.046
Subm	-0.002	-0.020	0.014	0.024	-0.017	-0.020	0.006	-0.002	0.034	-0.054	0.042	0.000	0.048	0.042	-0.037	0.006	-0.032	-0.014	0.062	-0.062	0.025	0.059	-0.042	0.042
cover	-0.002	-0.020	0.014	0.024	-0.018	-0.020	0.006	-0.002	0.034	-0.054	0.042	0.000	0.048	0.042	-0.037	0.006	-0.032	-0.014	0.062	-0.062	0.024	0.059	-0.042	0.042
Fetch	-0.001	0.021	-0.010	-0.023	0.015	0.021	-0.004	-0.001	-0.036	0.058	-0.044	-0.001	-0.048	-0.044	0.036	-0.004	0.028	0.015	-0.063	0.063	-0.028	-0.061	0.044	-0.044
Trib	-0.004	-0.020	0.016	0.024	-0.019	-0.020	0.008	-0.004	0.032	-0.052	0.040	-0.001	0.048	0.040	-0.037	0.008	-0.035	-0.014	0.061	-0.061	0.022	0.058	-0.040	0.040
Size	-0.002	-0.020	0.013	0.023	-0.017	-0.020	0.006	-0.002	0.034	-0.055	0.042	0.000	0.048	0.042	-0.037	0.006	-0.032	-0.015	0.062	-0.062	0.025	0.059	-0.042	0.042
Rip	-0.037	0.014	0.007	-0.010	0.001	0.014	0.002	-0.037	0.004	-0.018	0.028	0.034	0.081	0.028	-0.022	0.002	-0.037	-0.028	0.023	-0.023	0.008	-0.004	-0.028	0.028
S1	0.037	0.002	-0.034	-0.009	0.056	0.002	0.015	0.037	0.041	-0.025	-0.028	0.007	0.008	-0.028	0.003	0.015	0.059	0.014	-0.014	0.014	0.040	-0.022	0.028	-0.028
S3	-0.003	-0.015	0.008	0.007	-0.006	-0.015	0.009	-0.003	0.029	-0.038	0.021	0.009	0.046	0.021	-0.025	0.009	-0.026	-0.016	0.047	-0.047	0.022	0.037	-0.021	0.021
S4	0.002	0.035	-0.003	0.031	0.050	0.035	0.083	0.002	0.038	0.004	-0.077	-0.035	0.000	-0.077	-0.041	0.083	0.054	0.050	-0.039	0.039	0.002	-0.048	0.077	-0.077
S5	0.001	-0.013	0.025	0.025	-0.051	-0.013	-0.025	0.001	-0.038	0.023	0.025	-0.030	-0.061	0.025	0.011	-0.025	-0.017	0.016	-0.008	0.008	-0.033	0.027	-0.025	0.025
S8	0.050	-0.020	-0.019	0.020	0.015	-0.020	-0.004	0.050	0.030	-0.030	0.002	-0.024	-0.040	0.002	0.003	-0.004	0.048	0.022	0.002	-0.002	0.027	0.026	-0.002	0.002
S9	-0.004	-0.020	0.015	0.024	-0.019	-0.020	0.007	-0.004	0.033	-0.053	0.041	0.000	0.048	0.041	-0.037	0.007	-0.034	-0.014	0.061	-0.061	0.023	0.058	-0.041	0.041
U1	-0.002	-0.020	0.014	0.024	-0.018	-0.020	0.006	-0.002	0.034	-0.054	0.042	0.000	0.048	0.042	-0.037	0.006	-0.032	-0.014	0.062	-0.062	0.024	0.059	-0.042	0.042
U2	0.002	0.020	-0.013	-0.024	0.017	0.020	-0.006	0.002	-0.034	0.054	-0.042	0.000	-0.048	-0.042	0.037	-0.006	0.032	0.014	-0.062	0.062	-0.025	-0.059	0.042	-0.042
Tree	0.002	0.020	-0.013	-0.024	0.017	0.020	-0.006	0.002	-0.034	0.054	-0.042	0.000	-0.048	-0.042	0.037	-0.006	0.032	0.014	-0.062	0.062	-0.025	-0.059	0.042	-0.042

Table B5   Correlations from the fourth-corner analysis between the species traits (columns) and the environmental variables (rows) at very broad spatial scale in Lake Paré. Species trait codes are found in Table 3.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Litt	0.117	-0.108	-0.040	0.039	0.067	-0.108	-0.051	0.089	0.067	-0.091	0.051	0.006	0.034	0.051	0.108	-0.086	0.117	0.005	-0.040	0.040	0.093	-0.007	-0.086	0.086
Z	-0.119	-0.031	0.073	-0.069	-0.047	-0.031	-0.071	-0.132	-0.047	0.001	0.071	0.127	0.132	0.071	0.031	-0.078	-0.119	-0.050	0.042	-0.042	0.016	-0.097	-0.078	0.078
Emerg	0.044	-0.098	-0.004	-0.001	0.037	-0.098	-0.042	0.016	0.037	-0.058	0.042	0.042	0.066	0.042	0.098	-0.074	0.044	-0.019	-0.012	0.012	0.068	-0.049	-0.074	0.074
Subm	0.057	-0.104	-0.008	0.009	0.040	-0.104	-0.072	0.028	0.040	-0.079	0.072	0.053	0.079	0.072	0.104	-0.105	0.057	-0.013	-0.019	0.019	0.087	-0.041	-0.105	0.105
cover	-0.057	0.104	0.008	-0.009	-0.040	0.104	0.073	-0.028	-0.040	0.079	-0.073	-0.054	-0.079	-0.073	-0.104	0.105	-0.057	0.013	0.019	-0.019	-0.087	0.040	0.105	-0.105
Fetch	-0.056	0.104	0.007	-0.008	-0.040	0.104	0.070	-0.027	-0.040	0.078	-0.070	-0.053	-0.078	-0.070	-0.104	0.103	-0.056	0.014	0.019	-0.019	-0.086	0.042	0.103	-0.103
Trib	0.055	-0.104	-0.007	0.007	0.040	-0.104	-0.066	0.026	0.040	-0.075	0.066	0.051	0.077	0.066	0.104	-0.099	0.055	-0.015	-0.018	0.018	0.084	-0.043	-0.099	0.099
Size	-0.057	0.105	0.008	-0.009	-0.040	0.105	0.073	-0.028	-0.040	0.079	-0.073	-0.054	-0.079	-0.073	-0.105	0.105	-0.057	0.013	0.019	-0.019	-0.087	0.041	0.105	-0.105
Rip	-0.048	-0.072	0.043	-0.040	-0.010	-0.072	-0.080	-0.071	-0.010	-0.038	0.080	0.107	0.123	0.080	0.072	-0.101	-0.048	-0.039	0.018	-0.018	0.053	-0.082	-0.101	0.101
S1	0.064	-0.105	-0.012	0.012	0.043	-0.105	-0.068	0.035	0.043	-0.080	0.068	0.047	0.073	0.068	0.105	-0.101	0.064	-0.012	-0.021	0.021	0.087	-0.038	-0.101	0.101
S3	-0.121	0.108	0.042	-0.041	-0.068	0.108	0.049	-0.093	-0.068	0.092	-0.049	-0.003	-0.031	-0.049	-0.108	0.084	-0.121	-0.007	0.041	-0.041	-0.093	0.004	0.084	-0.084
S4	0.170	-0.092	-0.073	0.070	0.087	-0.092	-0.018	0.148	0.087	-0.090	0.018	-0.052	-0.027	0.018	0.092	-0.049	0.170	0.028	-0.059	0.059	0.084	0.038	-0.049	0.049
S5	-0.171	0.092	0.074	-0.071	-0.087	0.092	0.017	-0.149	-0.087	0.090	-0.017	0.053	0.028	-0.017	-0.092	0.048	-0.171	-0.029	0.059	-0.059	-0.084	-0.038	0.048	-0.048
S8	0.176	-0.027	-0.091	0.087	0.080	-0.027	0.042	0.174	0.080	-0.049	-0.042	-0.119	-0.110	-0.042	0.027	0.030	0.176	0.051	-0.061	0.061	0.033	0.090	0.030	-0.030
S9	0.056	-0.104	-0.007	0.008	0.040	-0.104	-0.070	0.027	0.040	-0.078	0.070	0.053	0.078	0.070	0.104	-0.102	0.056	-0.014	-0.019	0.019	0.086	-0.042	-0.102	0.102
U1	0.048	-0.101	-0.005	0.000	0.038	-0.101	-0.047	0.019	0.038	-0.063	0.047	0.044	0.069	0.047	0.101	-0.079	0.048	-0.018	-0.013	0.013	0.072	-0.049	-0.079	0.079
U2	0.056	-0.104	-0.007	0.008	0.040	-0.104	-0.069	0.027	0.040	-0.077	0.069	0.052	0.078	0.069	0.104	-0.102	0.056	-0.014	-0.018	0.018	0.085	-0.042	-0.102	0.102
Tree	-0.100	0.037	0.082	0.007	-0.086	0.037	0.057	-0.092	-0.086	0.112	-0.057	-0.041	-0.050	-0.057	-0.037	0.067	-0.100	0.024	-0.013	0.013	-0.109	-0.023	0.067	-0.067

Table B6   Correlations from the fourth-corner analysis between the species traits (columns) and the environmental variables (rows) at broad spatial scale in Lake Paré. Species trait codes are found in Table 3.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Litt	0.001	-0.018	0.051	0.065	-0.045	-0.018	-0.021	-0.004	-0.045	0.029	0.021	-0.035	-0.030	0.021	0.018	-0.026	0.001	0.057	-0.065	0.065	-0.028	-0.009	-0.026	0.026
Z	0.000	-0.020	0.001	0.002	-0.001	-0.020	-0.107	-0.006	-0.001	-0.061	0.107	0.069	0.073	0.107	0.020	-0.108	0.000	-0.011	0.005	-0.005	0.057	0.026	-0.108	0.108
Emerg	0.073	-0.087	0.032	0.086	-0.003	-0.087	0.054	0.049	-0.003	0.034	-0.054	-0.099	-0.074	-0.054	0.087	0.021	0.073	0.065	-0.095	0.095	-0.027	-0.041	0.021	-0.021
Subm	-0.015	0.042	-0.037	-0.045	0.020	0.042	-0.018	-0.003	0.020	-0.029	0.018	0.041	0.030	0.018	-0.042	-0.002	-0.015	-0.039	0.053	-0.053	0.023	0.035	-0.002	0.002
cover	-0.012	0.040	-0.037	-0.043	0.021	0.040	-0.018	-0.001	0.021	-0.030	0.018	0.040	0.029	0.018	-0.040	-0.003	-0.012	-0.037	0.051	-0.051	0.024	0.035	-0.003	0.003
Fetch	0.023	-0.048	0.037	0.052	-0.018	-0.048	0.018	0.010	-0.018	0.027	-0.018	-0.046	-0.033	-0.018	0.048	0.000	0.023	0.043	-0.060	0.060	-0.021	-0.036	0.000	0.000
Trib	0.017	-0.044	0.037	0.047	-0.020	-0.044	0.018	0.005	-0.020	0.029	-0.018	-0.043	-0.031	-0.018	0.044	0.002	0.017	0.040	-0.055	0.055	-0.022	-0.035	0.002	-0.002
Size	-0.010	0.038	-0.037	-0.042	0.022	0.038	-0.017	0.001	0.022	-0.030	0.017	0.038	0.027	0.017	-0.038	-0.003	-0.010	-0.036	0.049	-0.049	0.024	0.034	-0.003	0.003
Rip	-0.042	0.028	0.055	0.032	-0.057	0.028	0.080	-0.035	-0.057	0.099	-0.080	-0.077	-0.083	-0.080	-0.028	0.085	-0.042	0.044	-0.037	0.037	-0.095	-0.023	0.085	-0.085
S1	-0.099	0.051	0.062	-0.005	-0.076	0.051	-0.010	-0.087	-0.076	0.064	0.010	0.008	-0.005	0.010	-0.051	0.009	-0.099	0.008	0.008	-0.008	-0.067	0.012	0.009	-0.009
S3	-0.091	0.083	0.024	-0.041	-0.044	0.083	0.122	-0.069	-0.044	0.112	-0.122	-0.055	-0.075	-0.122	-0.083	0.145	-0.091	-0.014	0.040	-0.040	-0.113	0.003	0.145	-0.145
S4	-0.011	-0.003	0.040	0.036	-0.034	-0.003	0.039	-0.012	-0.034	0.055	-0.039	-0.051	-0.050	-0.039	0.003	0.036	-0.011	0.039	-0.041	0.041	-0.050	-0.025	0.036	-0.036
S5	-0.073	0.057	0.012	-0.053	-0.021	0.057	0.134	-0.059	-0.021	0.098	-0.134	-0.049	-0.062	-0.134	-0.057	0.146	-0.073	-0.028	0.047	-0.047	-0.095	-0.020	0.146	-0.146
S8	0.031	-0.005	-0.051	-0.030	0.047	-0.005	-0.103	0.031	0.047	-0.103	0.103	0.091	0.091	0.103	0.005	-0.099	0.031	-0.036	0.036	-0.036	0.099	0.026	-0.099	0.099
S9	-0.013	0.040	-0.037	-0.044	0.021	0.040	-0.018	-0.001	0.021	-0.030	0.018	0.040	0.029	0.018	-0.040	-0.003	-0.013	-0.038	0.052	-0.052	0.024	0.035	-0.003	0.003
U1	0.034	-0.056	0.035	0.059	-0.015	-0.056	0.018	0.018	-0.015	0.024	-0.018	-0.052	-0.037	-0.018	0.056	-0.002	0.034	0.048	-0.067	0.067	-0.018	-0.037	-0.002	0.002
U2	-0.014	0.041	-0.037	-0.044	0.021	0.041	-0.018	-0.002	0.021	-0.030	0.018	0.041	0.029	0.018	-0.041	-0.003	-0.014	-0.038	0.052	-0.052	0.023	0.035	-0.003	0.003
Tree	0.068	-0.090	0.027	0.075	0.001	-0.090	0.075	0.043	0.001	0.043	-0.075	-0.105	-0.080	-0.075	0.090	0.040	0.068	0.052	-0.083	0.083	-0.037	-0.038	0.040	-0.040

Table B7   Correlations from the fourth-corner analysis between the species traits (columns) and the environmental variables (rows) at meso spatial scale in Lake Paré. Species trait codes are found in Table 3.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Litt	0.147	0.035	-0.123	0.020	0.104	0.035	-0.012	0.162	0.104	-0.103	0.012	-0.018	-0.027	0.012	-0.035	0.001	0.147	0.017	-0.006	0.006	0.094	0.049	0.001	-0.001
Z	0.021	0.029	-0.015	0.023	0.000	0.029	-0.036	0.030	0.000	-0.021	0.036	-0.002	-0.009	0.036	-0.029	-0.024	0.021	0.020	-0.011	0.011	0.014	0.041	-0.024	0.024
Emerg	-0.038	0.012	0.077	0.070	-0.081	0.012	-0.038	-0.036	-0.081	0.052	0.038	-0.030	-0.033	0.038	-0.012	-0.032	-0.038	0.068	-0.067	0.067	-0.054	0.007	-0.032	0.032
Subm	0.000	0.022	0.040	0.068	-0.048	0.022	-0.039	0.007	-0.048	0.021	0.039	-0.030	-0.035	0.039	-0.022	-0.029	0.000	0.066	-0.062	0.062	-0.024	0.016	-0.029	0.029
cover	-0.002	-0.022	-0.039	-0.068	0.047	-0.022	0.039	-0.008	0.047	-0.021	-0.039	0.030	0.035	-0.039	0.022	0.029	-0.002	-0.066	0.062	-0.062	0.024	-0.016	0.029	-0.029
Fetch	-0.001	-0.022	-0.039	-0.068	0.048	-0.022	0.039	-0.008	0.048	-0.021	-0.039	0.030	0.035	-0.039	0.022	0.030	-0.001	-0.066	0.062	-0.062	0.024	-0.016	0.030	-0.030
Trib	-0.007	0.021	0.047	0.068	-0.054	0.021	-0.039	-0.001	-0.054	0.027	0.039	-0.029	-0.034	0.039	-0.021	-0.029	-0.007	0.066	-0.062	0.062	-0.030	0.014	-0.029	0.029
Size	-0.001	0.022	0.042	0.068	-0.050	0.022	-0.039	0.005	-0.050	0.023	0.039	-0.030	-0.035	0.039	-0.022	-0.029	-0.001	0.066	-0.062	0.062	-0.026	0.015	-0.029	0.029
Rip	-0.072	0.046	0.048	0.014	-0.068	0.046	-0.011	-0.060	-0.068	0.057	0.011	-0.015	-0.027	0.011	-0.046	0.006	-0.072	0.015	0.000	0.000	-0.066	0.051	0.006	-0.006
S1	-0.032	0.023	-0.027	-0.052	0.011	0.023	0.036	-0.027	0.011	0.011	-0.036	0.003	-0.003	-0.036	-0.023	0.042	-0.032	-0.056	0.065	-0.065	-0.022	0.058	0.042	-0.042
S3	-0.075	0.084	0.062	0.037	-0.087	0.084	0.050	-0.052	-0.087	0.110	-0.050	-0.072	-0.092	-0.050	-0.084	0.077	-0.075	0.053	-0.029	0.029	-0.115	0.028	0.077	-0.077
S4	0.030	0.008	-0.038	-0.014	0.034	0.008	-0.062	0.033	0.034	-0.068	0.062	0.053	0.050	0.062	-0.008	-0.056	0.030	-0.013	0.016	-0.016	0.066	0.009	-0.056	0.056
S5	-0.078	0.016	0.049	-0.023	-0.046	0.016	0.068	-0.076	-0.046	0.082	-0.068	-0.022	-0.026	-0.068	-0.016	0.070	-0.078	-0.009	0.014	-0.014	-0.077	-0.033	0.070	-0.070
S8	-0.096	0.051	0.048	-0.023	-0.061	0.051	0.053	-0.084	-0.061	0.087	-0.053	-0.020	-0.033	-0.053	-0.051	0.068	-0.096	-0.007	0.024	-0.024	-0.088	0.004	0.068	-0.068
S9	-0.006	-0.024	-0.034	-0.067	0.043	-0.024	0.039	-0.014	0.043	-0.017	-0.039	0.030	0.035	-0.039	0.024	0.029	-0.006	-0.066	0.061	-0.061	0.020	-0.018	0.029	-0.029
U1	0.000	-0.022	-0.041	-0.068	0.049	-0.022	0.039	-0.007	0.049	-0.022	-0.039	0.030	0.035	-0.039	0.022	0.030	0.000	-0.066	0.062	-0.062	0.025	-0.016	0.030	-0.030
U2	-0.001	-0.022	-0.040	-0.068	0.048	-0.022	0.039	-0.007	0.048	-0.021	-0.039	0.030	0.035	-0.039	0.022	0.030	-0.001	-0.066	0.062	-0.062	0.024	-0.016	0.030	-0.030
Tree	-0.071	0.024	0.118	0.092	-0.123	0.024	-0.028	-0.066	-0.123	0.097	0.028	-0.054	-0.059	0.028	-0.024	-0.019	-0.071	0.093	-0.089	0.089	-0.098	0.002	-0.019	0.019

Table B8   Correlations from the fourth-corner analysis between the species traits (columns) and the environmental variables (rows) at fine spatial scale in Lake Paré. Species trait codes are found in Table 3.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Litt	-0.059	0.058	0.024	-0.018	-0.035	0.058	0.010	-0.044	-0.035	0.038	-0.010	0.011	-0.004	-0.010	-0.058	0.029	-0.059	0.004	0.014	-0.014	-0.035	-0.014	0.029	-0.029
Z	-0.017	-0.030	0.033	0.021	-0.029	-0.030	-0.083	-0.027	-0.029	-0.022	0.083	0.039	0.046	0.083	0.030	-0.089	-0.017	0.007	-0.017	0.017	0.019	0.015	-0.089	0.089
Emerg	0.069	-0.083	-0.008	0.046	0.022	-0.083	-0.007	0.046	0.022	-0.025	0.007	-0.037	-0.015	0.007	0.083	-0.036	0.069	0.011	-0.038	0.038	0.021	0.025	-0.036	0.036
Subm	-0.068	0.089	0.007	-0.045	-0.022	0.089	0.015	-0.043	-0.022	0.029	-0.015	0.032	0.009	-0.015	-0.089	0.045	-0.068	-0.007	0.036	-0.036	-0.024	-0.031	0.045	-0.045
cover	0.068	-0.089	-0.008	0.045	0.023	-0.089	-0.014	0.043	0.023	-0.029	0.014	-0.033	-0.009	0.014	0.089	-0.044	0.068	0.007	-0.036	0.036	0.024	0.030	-0.044	0.044
Fetch	-0.067	0.091	0.007	-0.045	-0.021	0.091	0.019	-0.042	-0.021	0.031	-0.019	0.030	0.006	-0.019	-0.091	0.050	-0.067	-0.006	0.035	-0.035	-0.025	-0.034	0.050	-0.050
Trib	0.068	-0.087	-0.008	0.045	0.023	-0.087	-0.011	0.045	0.023	-0.028	0.011	-0.034	-0.011	0.011	0.087	-0.040	0.068	0.008	-0.036	0.036	0.023	0.027	-0.040	0.040
Size	0.067	-0.090	-0.007	0.045	0.022	-0.090	-0.016	0.043	0.022	-0.030	0.016	-0.032	-0.008	0.016	0.090	-0.046	0.067	0.007	-0.036	0.036	0.024	0.032	-0.046	0.046
Rip	-0.072	0.002	0.064	0.007	-0.063	0.002	0.037	-0.073	-0.063	0.080	-0.037	-0.030	-0.030	-0.037	-0.002	0.036	-0.072	0.009	-0.008	0.008	-0.079	-0.008	0.036	-0.036
S1	-0.011	-0.077	0.065	0.066	-0.056	-0.077	-0.032	-0.034	-0.056	0.032	0.032	-0.040	-0.019	0.032	0.077	-0.057	-0.011	0.026	-0.052	0.052	-0.041	0.046	-0.057	0.057
S3	0.033	0.009	-0.011	0.031	0.004	0.009	0.058	0.037	0.004	0.030	-0.058	-0.071	-0.072	-0.058	-0.009	0.058	0.033	0.025	-0.023	0.023	-0.034	0.024	0.058	-0.058
S4	-0.009	-0.015	0.049	0.042	-0.037	-0.015	0.051	-0.014	-0.037	0.065	-0.051	-0.061	-0.056	-0.051	0.015	0.043	-0.009	0.045	-0.052	0.052	-0.057	-0.042	0.043	-0.043
S5	-0.049	0.021	0.041	0.004	-0.042	0.021	0.051	-0.044	-0.042	0.069	-0.051	-0.035	-0.040	-0.051	-0.021	0.056	-0.049	0.015	-0.009	0.009	-0.066	-0.019	0.056	-0.056
S8	-0.100	0.053	0.043	-0.060	-0.038	0.053	0.108	-0.087	-0.038	0.098	-0.108	-0.010	-0.023	-0.108	-0.053	0.121	-0.100	-0.017	0.035	-0.035	-0.082	-0.090	0.121	-0.121
S9	-0.067	0.090	0.007	-0.045	-0.022	0.090	0.016	-0.043	-0.022	0.030	-0.016	0.031	0.008	-0.016	-0.090	0.047	-0.067	-0.007	0.036	-0.036	-0.024	-0.032	0.047	-0.047
U1	0.068	-0.089	-0.007	0.045	0.022	-0.089	-0.015	0.043	0.022	-0.029	0.015	-0.032	-0.008	0.015	0.089	-0.046	0.068	0.007	-0.036	0.036	0.024	0.031	-0.046	0.046
U2	-0.067	0.090	0.007	-0.045	-0.022	0.090	0.017	-0.042	-0.022	0.030	-0.017	0.031	0.007	-0.017	-0.090	0.048	-0.067	-0.007	0.035	-0.035	-0.024	-0.033	0.048	-0.048
Tree	-0.062	0.090	0.003	-0.048	-0.016	0.090	0.028	-0.038	-0.016	0.031	-0.028	0.027	0.004	-0.028	-0.090	0.058	-0.062	-0.007	0.036	-0.036	-0.024	-0.041	0.058	-0.058