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Large-scale geographic patterns of diversity and community structure of pelagic crustacean zooplankton in Canadian lakes

Bernadette Pinel-Alloul^{1,2*}, Adrien André^{1,4}, Pierre Legendre^{1,2},
Jeffrey A. Cardille^{1,3**}, Kasimierz Patalas⁵ and Alex Salki⁵

¹GRIL, Groupe de Recherche Interuniversitaire en Limnologie et en Environnement Aquatique, Université de Montréal, C.P. 6128, Succ. Centre-ville, Montréal, QC, Canada, H3C 3J7, ²Département de sciences biologiques, Université de Montréal, C.P. 6128, Succ. Centre-ville, Montréal, QC, Canada, H3C 3J7, ³Département de géographie, Université de Montréal, C.P. 6128, Succ. Centre-ville, Montréal, QC, Canada, H3C 3J7, ⁴Département des sciences et génie de l'environnement, Faculté des sciences, Université de Liège, 15 Allée du 6 août, B-4000, Liège, Belgique, ⁵retired, formerly of Freshwater Institute, Department of Fisheries and Oceans, 501 University Crescent, Winnipeg, MA, Canada R3T 2N6

*Correspondence: Bernadette Pinel-Alloul, GRIL, Groupe de recherche Interuniversitaire en Limnologie et en Environnement Aquatique, Département de sciences biologiques, Université de Montréal, C.P. 6128, Succ. Centre-ville, Montréal, (QC), Canada, H3C 3J7.
E-mail: bernadette.pinel-alloul@umontreal.ca
**Present address: Jeffrey A. Cardille, Natural Resource Sciences and McGill School of Environment, McGill University, 2111 Lakeshore Road, Ste. Anne de Bellevue, (QC), Canada, H9X 3V9.
E-mail: jeffrey.cardille@mcgill.ca

ABSTRACT

Aim We tested the energy and metabolic theories for explaining diversity patterns of crustacean zooplankton in Canadian lakes, and evaluated the influence of regional and local environments on community structure.

Location The 1665 studied lakes are distributed across Canada in 47 ecoprovinces.

Methods Our database included the occurrence of 83 pelagic crustacean species. The regional species richness in each ecoprovince was estimated using the average local species richness per lake and the first-order jackknife diversity index. Using a principal component plot and forward selection in a multiple regression we identified the most important predictors of regional species richness estimates. We tested the predictions of the species richness-energy hypothesis using climatic variables at regional scale, and of the metabolic theory using the inverse of air temperature. To evaluate the influence of regional and local environmental drivers, we carried out a redundancy analysis between crustacean species occurrences and regional climate and lake environmental factors on a subset of 458 lakes.

Results Estimates of pelagic crustacean species richness in Canadian ecoprovinces varied from 3 to 10 species per lake (average local species richness) or 8 to 52 species per ecoprovince (Jackknife diversity index). Our study fully supports the species richness-energy hypothesis and partially the metabolic theory. Mean daily global solar radiation was the most important regional predictor, explaining 51% of the variation in the regional species richness among ecoprovinces. Together, regional climate and local lake environment accounted for 31% of the total variation in community structure. Regional-scale energy variables accounted for 24% of the total explained variation, whereas local-scale lake conditions had less influence (2%).

Main conclusions The richness-energy theory explains diversity patterns of freshwater crustacean zooplankton in Canadian ecoprovinces. Solar radiation is the best predictor explaining regional species richness in ecoprovinces and community structure of pelagic crustaceans in Canadian lakes.

Keywords

Canada, community structure, continental scale, diversity, ecoprovinces, lakes, Large-scale patterns, pelagic crustacean zooplankton.

INTRODUCTION

Since the eighteenth century, species distribution patterns have been of primary interest in the fields of biogeography, evolutionary biology, and ecology. Exploring how and why species are currently distributed in their geographical range are two fundamental issues in ecology and biogeography (Gaston, 2000; Lomolino *et al.*, 2010). Perhaps the most interesting property of species diversity is its organization through space or beta diversity (Whittaker *et al.*, 2001; Legendre *et al.*, 2005). Beta diversity is a key concept for understanding the function of ecosystems, for the conservation of biodiversity, and for ecosystem management (Legendre *et al.*, 2005). It can tell us which species are habitat generalists or specialists, which ones present similar or different competitive ability, and how species composition varies between sites or regions in response to environmental changes (Tuomisto & Ruokolainen, 2006). Thus, understanding the mechanisms controlling spatial patterns in species richness and community structure will help efforts to conserve biodiversity and functions of ecosystems in the face of climate change and increased human disturbances.

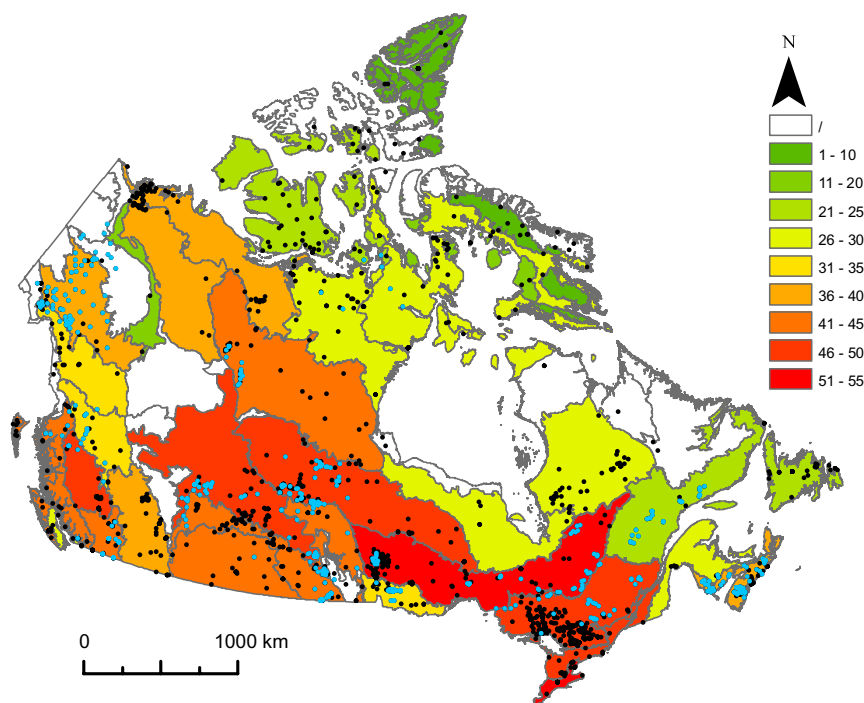
The multiple meanings of beta diversity have been discussed recently (Anderson *et al.*, 2011; Legendre & Legendre, 2012). Beta diversity studies can focus on two aspects of community structure. The first one is *turnover*, or the change in community composition between adjacent sampling units, explored by sampling along a spatial, temporal, or environmental gradient. The second is a non-directional approach to the study of community variation through space; it does not refer to any specific gradient but centres on the *variation in community composition among the study units*. In the present paper, we focused on the second approach, where spatial variation in species richness and community structure among lakes at the scale of Canadian ecoprovinces (beta diversity) will be analysed (in the statistical sense) through linear models involving regional and local environmental variables.

Biologists have studied large-scale diversity patterns in macroorganisms for centuries, leading to many insights on the biogeography of terrestrial species (Allen *et al.*, 2002; Hawkins *et al.*, 2003a, 2007a). In recent decades, large-scale patterns of beta diversity have been widely assessed for trees and plants (Jiménez *et al.*, 2009; Blach-Overgaard *et al.*, 2010), mammals and birds (Badgley & Fox, 2000; Hawkins *et al.*, 2003b; Melo *et al.*, 2009), and insects (Kerr & Currie, 1999). Many hypotheses have been proposed to explain large-scale diversity patterns of terrestrial species. For decades, the *richness-energy hypothesis* has provided a strong explanation related to productivity-diversity relationships (Chase & Ryberg, 2004). Energy (temperature or solar radiation) or water-energy (precipitation or evapotranspiration) variables typically drive diversity patterns of terrestrial organisms (Hawkins *et al.*, 2003a; Currie *et al.*, 2004). Areas with higher energy and water inputs are able to support higher species richness because productivity is strongly affected by the quantity of energy and water coming into terrestrial ecosystems. The *spatial heterogeneity hypothesis* can provide a supplemental explanation for plants for which diversity patterns also reflect

heterogeneity in habitat and topography (Jiménez *et al.*, 2009). Another important theory is the physiologically-oriented *metabolic theory* (Allen *et al.*, 2002; Brown *et al.*, 2004; Hawkins *et al.*, 2007a,b). According to this theory, large-scale diversity patterns result from the dependence of the metabolism of terrestrial ectotherms to the ambient solar radiation that controls their body temperature. Because species diversity of ectotherms is strongly influenced by metabolic processes, much of the variation in species diversity is due to air temperature, and higher species richness is expected in warmer areas. This hypothesis predicts that log-transformed species richness is linearly associated to the inverse of annual air temperature, and that the slope of the relationship varies between -0.55 and -0.75 . This theory has received support from many studies conducted in terrestrial ecosystems (Algar *et al.*, 2007), though it has also been criticized (Hawkins *et al.*, 2007b).

In contrast to macroorganisms, the field of microbial biogeography is currently immature (Fierer, 2008). There is still debate as to whether microorganisms also exhibit biogeographical patterns, and whether established ecological theory can explain spatial diversity patterns of microbial communities (Fontaneto *et al.*, 2006; Martiny *et al.*, 2006). Microorganisms are expected to show weak geographic variation in diversity compared to macroorganisms because of their small size, high abundance, fast population growth and higher dispersal rates. However, recent reviews have shown that spatial diversity patterns do exist for free-living microorganisms in soil and waters (Martiny *et al.*, 2006; Fontaneto, 2011). Strong biogeographic patterns in plankton biodiversity were observed at global scale in Northern America (Vyverman *et al.*, 2007; Stomp *et al.*, 2011) and in Europe (Hessen *et al.*, 2006, 2007; Ptacnik *et al.*, 2010); they were related to environmental gradients in productivity, habitat area and temperature as observed for terrestrial macroorganisms. However, there is no consensus on the importance of the *species-richness theory* for the regulation of diversity patterns of microorganisms in aquatic systems, where the water environment can buffer the effects of temperature and solar radiation. Air temperature and energy-related factors were found the major determinants of large-scale latitudinal pattern of crustacean species richness in Norwegian lakes (Hessen *et al.*, 2007) and of copepods in the Atlantic and Pacific Oceans (Rombouts *et al.*, 2009). However, Stomp *et al.* (2011) did not find a positive effect of water temperature on large-scale diversity patterns of freshwater phytoplankton. Also, the *metabolic theory* is not universally well supported in aquatic systems. It has little predictive power for the metabolism of lacustrine plankton (De Castro & Gaedke, 2008), and it weakly explains zooplankton species richness pattern in Norwegian lakes (Hessen *et al.*, 2007). Support to the *spatial heterogeneity theory* came from studies on zooplankton diversity patterns, which are driven by multiple regional and local processes (*the multiple force hypothesis*) acting differently across spatial scales (Pinel-Alloul, 1995; Pinel-Alloul *et al.*, 1995; Pinel-Alloul & Ghadouani, 2007). However, it is difficult to disentangle the effects of energy-related variables from that of local environmental variables, because they are all correlated to

Figure 1 Distribution of the 1665 lakes used for describing lake crustacean diversity pattern across Canadian ecoprovinces. Colors of ecoprovinces are ranged according to increasing regional species richness based on the Jackknife diversity index. The localisation of the 458 lakes subset are indicated by light blue dots. Blank color (/): ecoprovinces having 5 or less than 5 sampled lakes.



geographical gradients. A better prediction of the patterns of aquatic biodiversity and its environmental drivers is a fundamental issue for ecologists and may be the most important scientific challenge to face in the twenty-first century (Willig & Bloch, 2006). This is especially important given current concerns about the loss of biodiversity in freshwater ecosystems due to the multiple stressors of climate changes, watershed land use, alteration of nutrient cycles, invasion of exotic species, and overexploitation of halieutic resources. Our ability to detect the effects of those stressors on biodiversity is often low, in part because of poor knowledge of baseline data on biodiversity patterns and their environmental drivers.

In Canada, lakes are a dominant feature of the landscape, but knowledge of biodiversity of freshwater microorganisms and its environmental control is still in its infancy. Our study provides the first comprehensive model relating diversity patterns of pelagic crustaceans across Canada to environmental gradients along a wide range of physiographic, climatic and lake environments. The aims of the study are fourfold: (1) document the spatial pattern of diversity, community structure and species distribution of lake crustacean zooplankton in Canadian ecoprovinces, (2) test the main predictions of the diversity-energy and metabolic ecological theories for large-scale diversity patterns of freshwater microorganisms, (3) determine the environmental drivers of spatial variation in crustacean diversity at regional scale across Canadian ecoprovinces, and (4) evaluate the relative influence of regional climatic features and local lake environmental factors on crustacean community structure.

MATERIALS AND METHODS

Study sites, zooplankton sampling, and database

A long-term sampling program (1961–1991) carried out by the Freshwater Institute of Fisheries and Oceans Canada and an extensive literature review (1891–1990) provided a large database of crustacean species occurrence in the pelagic zone of nearly 2000 lakes across the entire mainland of Canada (42–80° N and 52–139° W) (Patalas *et al.*, 1994). The studied lakes are distributed across the 15 Canadian terrestrial ecozones and in 47 of Canada's 53 ecoprovinces (Fig. 1). Ecozones and ecoprovinces represent high- and intermediate-level divisions of the Canadian land mass according to climatic and vegetation patterns (Marshall & Schut, 1999). They are useful geographic units for general national reporting (<http://atlas.nrcan.gc.ca>) and for placing Canada's ecosystem diversity assessment in an ecologically meaningful context (McMahon *et al.*, 2004).

The number of lakes sampled during the long-term field survey varied widely among ecoprovinces, from 326 lakes in the Southern Boreal Shield to a single lake in the Sverdrup Islands in the Northern Arctic, and the Whale River Lowland in the Taiga Shield (Appendix S1). Zooplankton sampling took place during mid-summer near the centre of each lake; per-lake sampling effort ranged from a single site in small lakes to 30 to 50 sites in large lakes. Zooplankton was collected with a Wisconsin plankton net (25 cm in diameter, mesh size of 53–77 µm) by vertical hauls from the lake bottom to the surface, or from a depth of 50 m in the deepest lakes. Zooplankton were preserved in 4%

	Minimum	Maximum	Median	Mean
Total number of species	7	44	29	27
Average local species richness	3	10	5	6
Jackknife diversity index	8	52	36	34
Ecoprovince area (km ² 10 ⁴)	1.9	62.6	15.8	23.2
Number of lakes	6	326	32	47
Growing season length (day)	19.4	258.8	163.1	144.8
Growing degree days above 10 °C	0.0	1199.9	423.2	435.5
Effective growing degree days above 5 °C	7.6	2133.2	1117.1	1042.6
Mean elevation (m)	36.1	1624.9	349.2	499.2
Total annual precipitation (mm)	101.2	2258.2	494.9	636.9
Mean daily global solar radiation (megajoules/m ² /day)	8.3	13.6	11.4	11.2
Mean duration of bright sunshine (hrs)	1487.6	2338.0	1873.2	1879.3
Minimum annual air temperature (°C)*	−22.1	5.1	−5.6	−6.8
Maximum annual air temperature (°C)*	−15.6	13.8	6.0	3.0
Mean annual air temperature (°C)*	−18.8	9.4	0.3	−1.8
Mean annual vapour pressure	0.4	1.0	0.7	0.7
Annual potential evapotranspiration**	135.0	864.4	493.5	467.4
Longitude	−132.61	−64.09	−99.75	−100.22
Latitude	42.82	80.80	54.80	57.02

*Over the entire year.

**Penman method.

Table 1 Minimum, maximum, median and mean values of regional species richness estimates (total number of species, averagelocal species richness, Jackknife diversity index) and environmental descriptors in 35 ecoprovinces across Canada ($n = 1665$ lakes)

formalin, and analysed for species identification (see Patalas, 1990; Patalas *et al.*, 1994).

Given the opportunistic nature of the survey and changing technology over the sampling period, we encountered a considerable range of precision and accuracy for lake positional data. The locations of lakes sampled during the earlier decades in the survey were not reported clearly whereas those sampled during the later decades were referenced with relatively clear positional information. Thus, we applied modern techniques to determine the location of each lake in the data set, as accurately as possible. Using their descriptions in the original 2000-lake data set, the GeoNames database (<http://www.geonames.org>) to convert text descriptions to potential latitude-longitude positions, and Google Earth (<http://earth.google.com>) to verify and choose among proposed locations, we relocated 1665 of the lakes with enough precision to be included in the analysis.

Regional and local environmental data

Regional environmental data on climate and precipitation were collected for the 1951–1980 period from the Ecological Framework of Canada website (<http://ecozones.ca>), and from the Climate Atlas of Canada (Environment Canada, 1986; Phillips, 1990). The selected regional environmental descriptors were the growing season length in days, the number of growing days above 10 °C, the effective growing degree days above 5 °C, the mean elevation, the total annual precipitation, the mean daily global solar radiation, the mean duration of bright sunshine, the daily air temperatures (mean, minimum, maximum) estimated over the entire year, the mean annual vapour pressure, the

annual potential evapotranspiration, and the ecoprovince area (Table 1). Using ArcGIS (ESRI software, 2009), we estimated the values of regional environmental descriptors for each lake by intersecting them with the sampled points in the lake-zooplankton database. We also calculated the area-weighted mean for each regional environmental descriptor in each ecoprovince using the values in each polygon.

Our lake survey covered a wide range of regional climatic conditions across most of the Canadian ecoprovinces (Table 1). In addition to regional descriptors, we used previous reports (Salki & Patalas, unpublished data) to obtain local descriptors of the lake environments (July air temperature, lake area and depth, total dissolved solids, Secchi depth) in 458 lakes among the 1665-lake data set. The lakes of this subset were distributed across Canada and covered the same broad range of physiographic, climatic and limnological conditions as the 1665-lake dataset (Fig. 1, Appendix S5).

Biodiversity patterns, community structure, and species distribution

The survey provided us with a unique database on the occurrence of 83 crustacean species (Patalas *et al.*, 1994) in 1665 lakes distributed across Canada. To document biodiversity patterns, local species richness was estimated as the total number of crustacean species found in each lake, and averaged within each ecoprovince. Because sampling effort varied among ecoprovinces, we also calculated the first-order jackknife estimator of species richness, $\hat{S} = S_{\text{obs}} + r(n-1)/n$, where S_{obs} is the number of species observed in n lakes and r is the number of species present

in only one lake, to estimate regional species richness within each ecoprovince, as recommended by Palmer (1990) and Arnott *et al.* (1998). We were able to calculate the two estimates of species richness for 35 of the 47 ecoprovinces. The 12 ecoprovinces, which had five or fewer than five sampled lakes, were excluded (Appendix S1). Community structure was established on information about the presence or absence of each species in each lake. Occurrence of crustacean species across Canada was illustrated by a rank-frequency diagram. We produced distribution maps of each species in ArcGIS using the KML format in ET GeoWizards extension of the Google Earth Web software.

Diversity-energy relationships

To test the species richness-energy theory, we evaluated the relationships between the estimates of species richness (the average local species richness and the Jackknife diversity index) and regional environmental descriptors at the scale of the ecoprovinces using data from the 1665 lakes and the 35 selected ecoprovinces. First, a Principal Component Analysis (PCA) was computed to identify and illustrate groups of correlated variables among the standardized regional environmental descriptors. The average local species richness and the Jackknife diversity index were added to the plot by passive ordination (Legendre & Legendre, 2012). Forward selection in multiple regression analysis was also used to determine which environmental variables were the best predictors of the species richness estimates in the 35 ecoprovinces. We then computed linear regressions between the species richness estimates and selected energy or water-energy related descriptors (mean daily solar radiation, effective growing degree days above 5 °C, mean daily air temperature over the entire year, annual potential evapotranspiration and mean duration of bright sunshine) and tested their significance. Finally, acknowledging the fact that the energy variables were collinear, we used forward selection in linear regression to show which energy-related variables contributed significantly to explain the variation of the species richness estimates.

To test the metabolic theory, we related the log-transformed estimates of species richness to the inverse of annual temperature (in Kelvin) multiplied by the Boltzmann constant, using linear regressions. Then, as suggested by Algar *et al.* (2007), we tested whether this relationship was best fitted by a linear or a curvilinear model using the Akaike Information Criterion (AIC).

Relationships between regional and local environments and community structure

To test the hypothesis of multiple forcing of the crustacean community structure by regional and local environmental drivers (Pinel-Alloul, 1995; Pinel-Alloul *et al.*, 1995), we used the subset of 458 lakes for which local environmental descriptors were available. The regional factors were represented by climatic features of the ecoprovinces whereas the local environmental factors featured morphometric and water quality lake

variables. Both local and regional environmental variables were used to construct third-degree polynomial equations, for a total of forty-eight monomials. The quadratic and cubic monomials enabled us to model nonlinear relationships between the environmental descriptors and each species presence-absence variable (Legendre & Legendre, 2012). We performed a redundancy analysis (RDA) of the species occurrence matrix with forward selection of the significant monomials. The species data had previously been transformed using the Hellinger method (Legendre & Gallagher, 2001). We produced a RDA biplot of the crustacean species with the five most important environmental descriptors retained by forward selection. We then used variation partitioning to assess the relative contributions of the regional and local descriptors (Borcard *et al.*, 1992; Peres-Neto *et al.*, 2006). The statistical analyses were performed using software available in the VEGAN and PACKFOR packages in the R language (R Development Core Team, 2012).

RESULTS

Species richness and distribution patterns

Among the 83 crustacean species recorded in the 1665 lakes, the most diversified groups were the Calanoida (33 species) and the Cladocera (33 species), followed by the Cyclopoida (17 species) (Appendix S2). Only nine species were found in more than 25% of the lakes (Fig. 2). *Bosmina longirostris* was the most common species, found in almost half of the lakes. The other common species found in more than 25% of lakes were: *Holopedium gibberum*, *Diacyclops thomasi*, *Mesocyclops edax*, *Leptodiatomus minutus*, *Daphnia mendotae*, *Cyclops scutifer scutifer*, *Daphnia longiremis*, and *Diaphanosoma leuchtenbergianum*. Two thirds of the species (54/83) were present in less than 5% of the sampled lakes.

The total number of crustacean species found in Canadian ecoprovinces varied from 7 to 44, with the median and mean values respectively of 29 and 27 species; the average local species richness per lake ranged from 3 to 10 species (median: 5; mean: 6) while the Jackknife index ranged from 8 to 52 species (median: 36; mean: 34) (Table 1). Species-rich lakes were typically located in the ecoprovinces of the Boreal Shield and Plains and in the Hudson-Erie and the Great Lakes-Saint Lawrence Plains, whereas the species-poor lakes were found in the northern and arctic ecoprovinces (Fig. 1). Distribution maps of each crustacean species across Canada are available in the KML format compatible with Google Earth Web software: (<https://sites.google.com/site/canadianzooplankton/maps/distribution>).

Regional environment and diversity-energy relationships

The first two axes of the PCA ordination accounted for 73% of the observed variance in regional environmental descriptors among the ecoprovinces (Fig. 3). The first axis (61%) showed strong positive correlations with air temperature, the energy- and water-energy related descriptors, and an inverse correlation

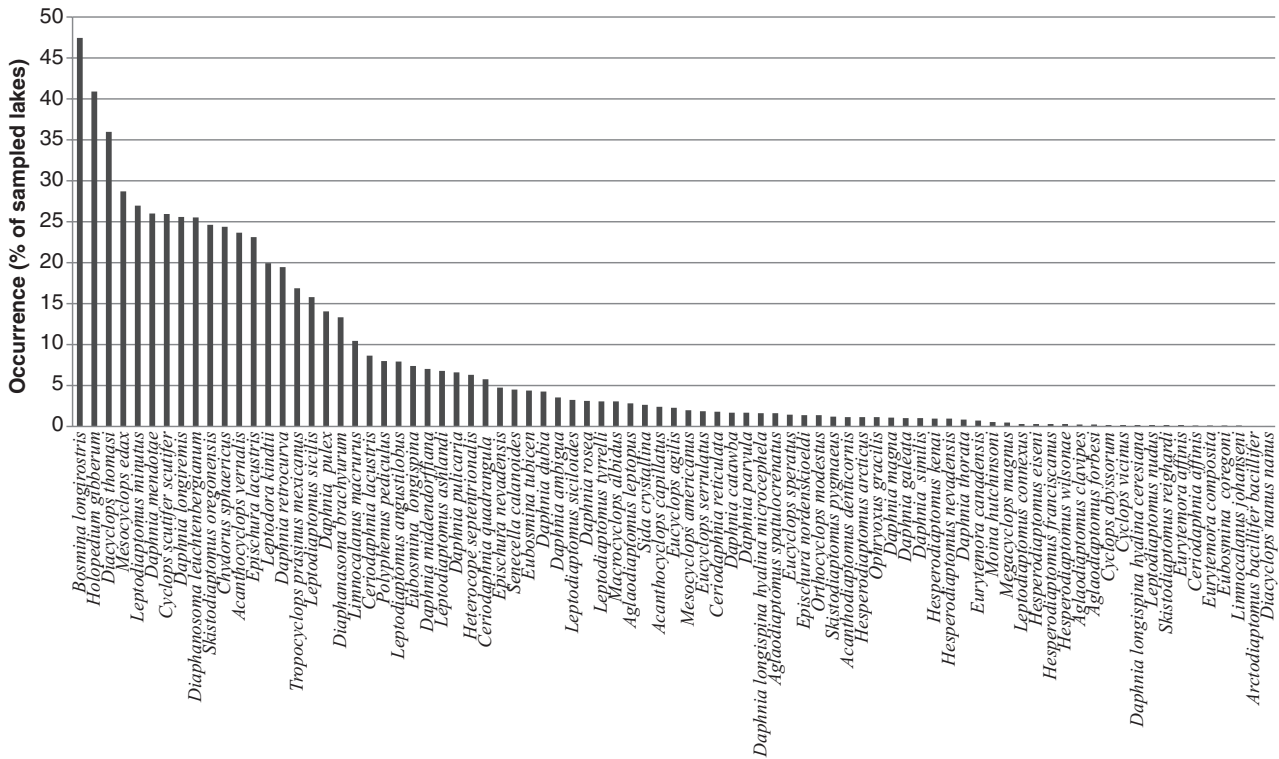


Figure 2 Rank-frequency occurrences of the 83 pelagic crustacean species collected in the 1665 lakes across Canada.

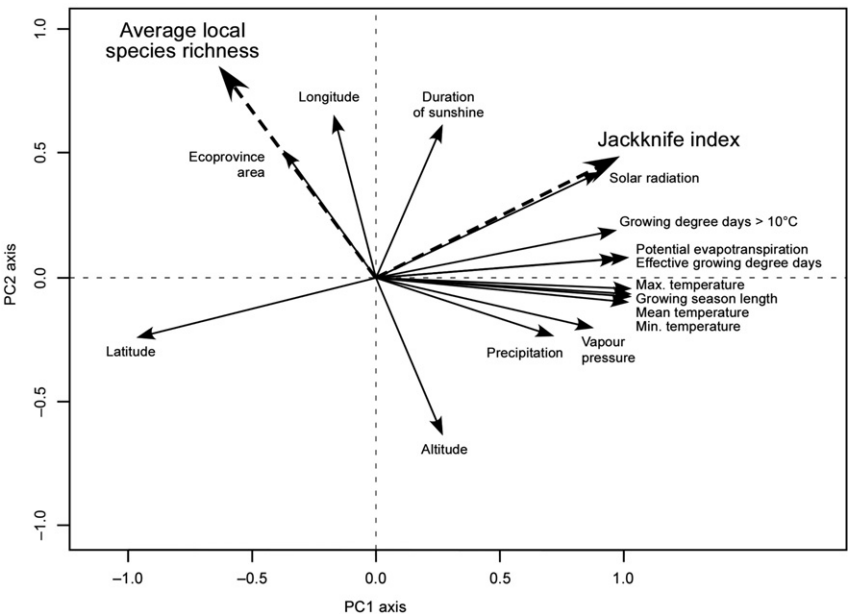


Figure 3 PCA ordination plots of the regional environmental descriptors selected by forward selection and the estimates of regional species richness (Average local species richness, Jackknife index).

with latitude, reflecting the latitudinal gradient of decreasing temperature and solar irradiance. The Jackknife diversity index was strongly and positively associated with this axis. Higher regional species richness was observed in southern ecoprovinces located at lower latitude where mean global daily solar variation was the highest. The second axis (12%) represents the longitudinal and altitudinal gradients and was related to the average local species richness; it opposes species-poor lakes located at

higher altitude in small ecoprovinces in western Canada to species-rich lakes located at low altitude in large ecoprovinces with higher duration of bright sunshine. Forward selection in multiple regression modelling retained four statistically significant regional descriptors (Table 2). It showed that the single energy variable *Mean daily global solar radiation* accounted alone for 52% of the variation of regional species richness among ecoprovinces (Jackknife index) and that

Table 2 Forward selection of regional environmental descriptors in multiple regression analysis of regional species richness (Jackknife diversity index; $n = 1665$ lakes) R^2 : coefficient of multiple determination (unadjusted), R^2_{Cum} : cumulative coefficient of multiple determination; R^2_{adj} Cum: cumulative adjusted coefficient of multiple determination

Regional descriptors – Jackknife diversity index	R^2	R^2_{Cum}	R^2_{adj} Cum	F	P -value
Mean daily global solar radiation (megajoules/m ² /day)	0.52	0.52	0.51	36.09	< 0.001
Ecoprovince area (km ² 10 ⁴)	0.08	0.60	0.58	6.66	0.015
Effective growing degree days above 5 °C	0.12	0.72	0.69	12.84	0.001
Mean duration of bright sunshine (hours)	0.03	0.75	0.72	4.18	0.050

Table 3 Linear regression models between regional species richness (Jackknife diversity index) and selected energy-related regional descriptors and the area of ecoprovinces ($n = 1665$ lakes)

Regional descriptors – Jackknife diversity index	R^2_{adj}	P -value
Mean daily global solar radiation (megajoules/m ² /day)	0.51	< 0.001
Annual potential evaporation**	0.48	< 0.001
Effective growing degree days above 5 °C	0.44	< 0.001
Mean annual air temperature (°C)*	0.41	< 0.001
Mean duration of bright sunshine (hours)	0.32	< 0.001
Ecoprovince area (km ² 10 ⁴)	–	0.28

*Over the entire year.

**Penman method.

two other energy-related variables (*Effective growing degree days above 5 °C*, and *Mean duration of bright sunshine*) also contributed significantly to explain the spatial variation of regional species richness. The ecoprovince area was also included as a significant regional descriptor of crustacean species richness in multiple regression modelling; however, its contribution was weak as suggested by the lack of correlation detected with the PCA ordination. The adjusted R-square (R^2_{adj}) of the combined effect of these four variables on the Jackknife index was 0.72 (Table 2). In contrast, no energy variable was related to the variation of the average local species richness among ecoprovinces which was significantly explained by the latitude, altitude, and area of ecoprovinces ($R^2_{\text{adj}} = 0.40$) (Appendix S3A).

At the ecoprovince level, simple linear regression models computed between the Jackknife diversity index and selected environmental variables indicated significant positive correlations with the energy and water-energy descriptors measured in the ecoprovinces. Higher values of mean daily global solar radiation, annual potential evapotranspiration, effective growing degree days above 5 °C, mean annual air temperature, and mean duration of bright sunshine were all significantly associated with higher values of the Jackknife index of regional species richness (Table 3). However, there was no significant correlation with the area of ecoprovinces considered alone. In comparison, simple linear regression models between the average local species richness and the selected environmental variables were weak (Appendix S3B).

The relationship between the natural logarithm of the Jackknife diversity index in each ecoprovince and the inverse of ambient temperature (in Kelvin) corrected by the Boltzmann

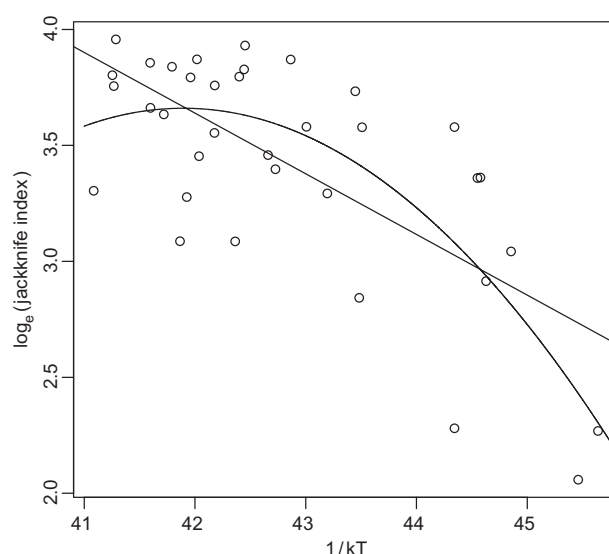


Figure 4 Linear and quadratic regressions between the natural logarithm of estimates of regional species richness (Jackknife index) and the inverse of temperature (in Kelvin) corrected by the Boltzmann constant.

constant supported the first prediction of the metabolic theory (Fig. 4). Both the linear model ($y = 14.63 - 0.26x$; $R^2_{\text{adj}} = 0.46$; P -value: $4.06 \cdot 10^{-8}$, AIC = 18.13) and the quadratic model ($y = -165.91 + 8.09x - 0.096x^2$; $R^2_{\text{adj}} = 0.54$, P -value: $1.39 \cdot 10^{-6}$, AIC = 25.85) were highly significant but AIC, whose minimum indicates the best predictive model, showed that the linear model was best. However, the second prediction of the metabolic theory was not supported: the slope of the linear regression was -0.26 , far out of the range of slopes (-0.55 to -0.75) predicted by the metabolic scaling law for species richness. When using the average local species richness, the relationships with the inverse of ambient temperature were very weak both for the linear ($R^2_{\text{adj}} = 0.10$; P -value: 0.04) and the quadratic models ($R^2_{\text{adj}} = 0.13$; P -value: 0.04) (Appendix S4).

Local and regional control of crustacean community structure

Among the regional descriptors of the ecoprovinces and the local lake descriptors measured on the subset of 458 lakes, 32 monomials were retained as significant predictors of the crustacean community structure (Table 4). Those variables

Table 4 Forward selection in RDA model relating crustacean species community structure to polynomial terms of the regional and local environmental descriptors after a forward regression ($n = 458$ lakes; R^2_{adj} : 0.31, P -value = 0.008)

Regional and local descriptors	R^2	R^2_{adj}		F	P -value
		Cum			
Mean daily global solar radiation 1	0.130	0.128	65.43	0.001	
Mean duration of bright sunshine 1	0.042	0.169	22.09	0.001	
Mean elevation 1	0.026	0.193	14.29	0.001	
Mean annual vapour pressure 1	0.023	0.214	12.67	0.001	
Total dissolved solids 1	0.012	0.224	6.60	0.001	
July air temperature 2	0.008	0.231	4.57	0.001	
July air temperature 1	0.007	0.236	4.16	0.001	
July air temperature 3	0.008	0.243	4.66	0.001	
Mean duration of bright sunshine 2	0.007	0.249	4.25	0.001	
Mean daily global solar radiation 2	0.007	0.254	3.95	0.001	
Mean annual air temperature 2	0.007	0.259	3.99	0.001	
Mean daily global solar radiation 3	0.007	0.265	4.38	0.001	
Secchi depth transparency 1	0.006	0.269	3.54	0.001	
Mean annual vapour pressure 2	0.005	0.273	3.25	0.001	
Mean annual air temperature 1	0.006	0.277	3.60	0.001	
Maximum annual air temperature 3	0.004	0.280	2.59	0.001	
Mean duration of bright sunshine 3	0.004	0.283	2.43	0.001	
Mean annual vapour pressure 3	0.004	0.285	2.50	0.001	
Mean elevation 2	0.004	0.287	2.36	0.001	
Total annual precipitation 1	0.004	0.290	2.40	0.001	
Annual potential evapotranspiration 1	0.003	0.292	2.10	0.003	
Total annual precipitation 3	0.004	0.294	2.27	0.002	
Mean elevation 3	0.004	0.296	2.32	0.001	
Annual potential evapotranspiration 3	0.003	0.298	1.98	0.002	
Growing season length 2	0.004	0.300	2.22	0.001	
Mean annual air temperature 1	0.003	0.301	1.92	0.003	
Secchi depth 2	0.003	0.303	1.91	0.004	
Lake depth 2	0.003	0.304	1.90	0.011	
Lake depth 1	0.004	0.307	2.22	0.001	
Lake depth 3	0.003	0.308	1.92	0.003	
Growing season length 3	0.003	0.310	1.85	0.009	
Effective growing degree day above 5 °C 1	0.003	0.311	1.66	0.008	

accounted together for 31% of the total variation in species assemblages. The most important regional descriptors were the mean daily global solar radiation followed by the mean duration of bright sunshine, mean elevation, mean annual vapour pressure, and mean annual air temperature. Some local descriptors of lake environments such as total dissolved solids, July air temperature, Secchi depth transparency and lake depth were also retained in the RDA model. The first five selected descriptors (4 regional and 1 local) were first-degree monomials, indicating predominance of linear effects. The RDA ordination of the species occurrences by the five most important descriptors ($R^2_{adj} = 0.22$) showed strong associations with species distributions across lakes (Fig. 5). The first canonical axis accounted for 14.3% of the total variation and was mainly driven by higher mean daily global solar radiation and duration of bright sunshine. The second axis was related to gradients of altitude and

productivity (via total dissolved solids) and accounted only for 5.4% of the total variation. Western species such as *Leptodiptomus angustilobus* and *Heteroscoptes septentrionalis* were associated with lakes located at higher altitude, and eastern species such as *Holopedium gibberum*, *Leptodiptomus minutus* and *Tropocyclops prasinus mexicanus* to lakes located at lower elevation. *Mesocyclops edax*, *Bosmina longirostris* and *Diaphanosoma leuchtenbergianum* were associated with lakes receiving the highest solar radiation, and *Skistodiaptomus oregonensis* and *Diacyclops thomasi* to the highest duration of sunshine. Variation partitioning between significant regional and local environmental variables indicated that 24% of the total variation in community structure was due to regional factors, and only 2% to local factors (Appendix S6).

DISCUSSION

In total, our records indicate that at least 83 crustacean species inhabit the pelagic zone of Canadian lakes. The variation in species richness of crustaceans in lakes across Canadian eco-provinces is comparable to the range observed in other large-scale and multiple-year surveys in European and American lakes (Arnott *et al.*, 1998; Hessen *et al.*, 2006, 2007; Shurin *et al.*, 2007).

Our study provided the first model of continental-scale distribution patterns of freshwater crustacean species in relation to energy-related gradients in Canadian ecoprovinces. The richness-energy theory is a fundamental process explaining diversity patterns of freshwater zooplankton at the continental scale of Canada. Our results are consistent with monotonically increasing species-energy relationships found in macro-scale studies of fish (Kerr & Currie, 1999) and terrestrial organisms (Hawkins *et al.*, 2003a; Evans *et al.*, 2005). Crustacean species richness per ecoprovince, estimated by the Jackknife diversity index is best predicted by global solar radiation, meaning that in ecoprovinces with higher energy inputs, the lakes support globally more crustacean species. The identification of a pure energy variable (mean daily global solar radiation) as the first predictor of diversity pattern rather than a water-energy (e.g., annual potential evapotranspiration) or a water-only variable (e.g., total annual precipitation) reflects the obvious fact that water availability is not a limiting factor in lake ecosystems. Our results also pointed to the importance of other energy-related variables, mainly the effective growing degree days above 5 °C and the mean duration of bright sunshine, because they are closely correlated with the global solar radiation variable. In contrast, average local species richness in lakes of Canadian ecoprovinces does not vary with energy-related variables as observed by Hessen *et al.* (2007) at the continental scale of Norway. This means that while solar radiation appears to control regional diversity of freshwater zooplankton at large continental scale, it does not control local species richness within a lake. At local scale, zooplankton species richness may be controlled both by abiotic and biotic processes (Pinel-Alloul, 1995; Hessen *et al.*, 2006; Pinel-Alloul & Ghadouani, 2007).

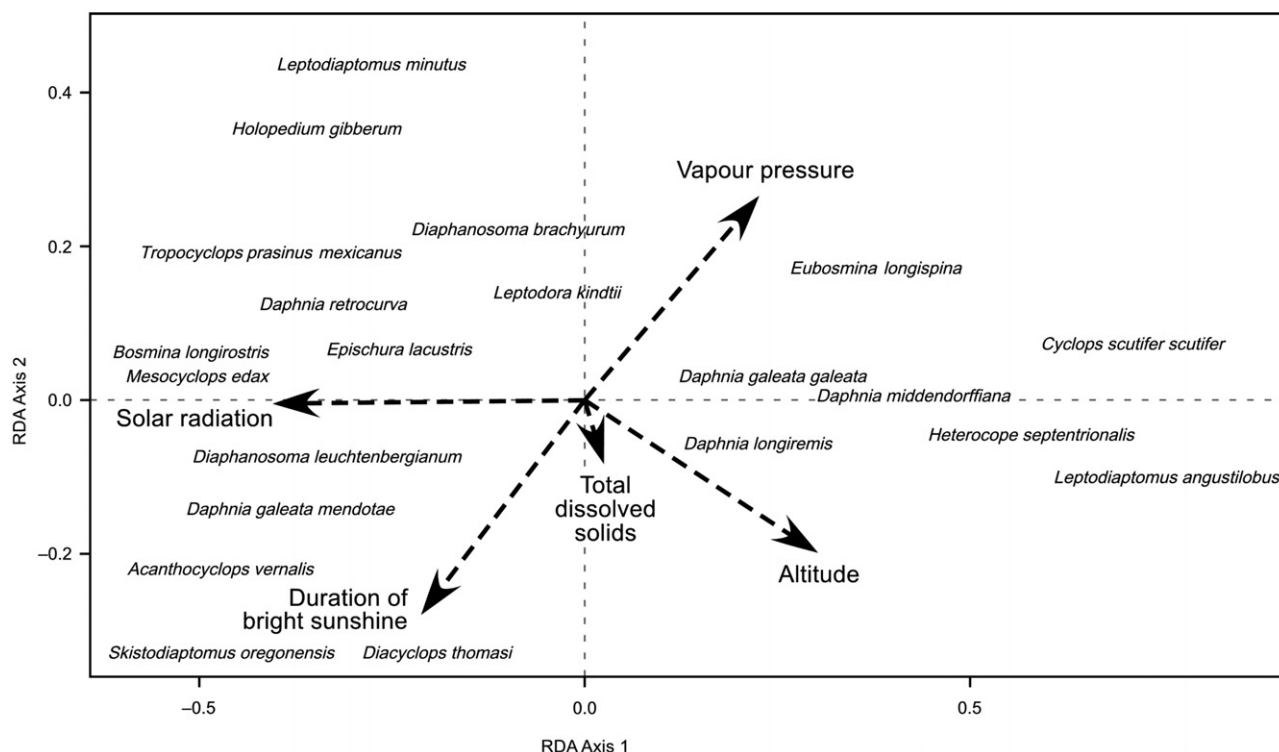


Figure 5 Redundancy analysis (RDA) between the matrix of occurrences of crustacean species in the 458 lakes and the five most important environmental descriptors selected by forward selection at regional and local scales.

Our study gave partial support for the metabolic ecological theory for explaining diversity patterns of freshwater crustaceans in Canada. We did find a linear significant relationship ($R^2_{adj} = 0.46$) between the log-transformed Jackknife index and the inverse transformation of annual air temperature, yet the slope (-0.26) was less steep than predicted by the theory (between -0.55 and -0.75). In comparison, the linear relationship with the average local species richness was weak ($R^2_{adj} = 0.10$). In Norwegian lakes, the metabolic theory explained only 21% of the variation in zooplankton local species richness (Hessen *et al.*, 2007), but the slope (-0.78) was in the expected range. Several reasons may account for these differences: (i) our broad-scale study covered a wider air temperature gradient (29° vs 12°), (ii) we used regional species richness per ecoprovince in our Canadian survey whereas local species richness in each lake was used in the Norwegian survey, (iii) the weaker relationships with the local species richness in Norwegian and Canadian lakes suggest that there are other important factors influencing species richness at local scale than at regional scale, (iv) there is still controversy over the value of the slope of the relationship of the metabolic theory, which may vary close to multiples of 0.25. In our large-scale study, we suggested that lake water stratification may buffer the effect of ambient air temperature on metabolism of crustacean zooplankton that can migrate in deeper cold waters. Furthermore, mean daily air temperature over the entire year used as the explanatory variable in our model does not directly correspond to the realized temperature experienced by crustacean species during their life cycle.

Our study of crustaceans in Canadian lakes gave additional support to the spatial heterogeneity theory and the multiple forces hypothesis which stated that abiotic environmental gradients will be the most important drivers of spatial variation in community structure at large scale (Pinel-Alloul, 1995; Pinel-Alloul *et al.*, 1995; Shurin *et al.*, 2000; Pinel-Alloul & Ghadouani, 2007). Indeed, latitudinal gradients in global solar radiation and ambient air temperature were the most important drivers of biodiversity patterns of freshwater crustaceans across Canada. Lakes situated in northern and arctic ecoprovinces experienced almost no light and extremely low temperatures during winter, and with such limiting factors they showed the lowest crustacean species richness. Crustaceans need to develop special physiological or behavioural responses to survive in this kind of environment. In lakes located in southern ecoprovinces, the higher inputs of energy by solar radiation can sustain primary productivity via efficient photosynthesis and carbon fixation of producers. Higher solar radiation can also be responsible for an increased euphotic zone depth. In consequence, a positive bottom-up control of primary producers by solar radiation can promote more abundant consumer populations, and therefore a reduction of the extinction rate which leads to increased species richness (Hessen *et al.*, 2007). Moreover, areas receiving higher energy inputs contain higher abundances of relatively rare resources that are exploited by niche position specialists. This should allow those specialists to maintain larger viable populations, thus increasing species richness. In our study, regional climate was the most important predictor of

both crustacean diversity and community structure, while local factors appear to be poor predictors of the community structure. The weak signal of local predictors may probably be caused by the low number of local variables available in our survey, which reduced our power to detect strong effects at local scale. As in other large-scale studies of zooplankton-environment linkages (Pinel-Alloul *et al.*, 1995; Hessen *et al.*, 2007), more than half of the total variance in crustacean community structure remains unexplained.

As with most large-scale surveys, there are caveats in our study which might limit our conclusions. Sampling did not cover the whole summer growing season and the survey extended through more than 90 years. However, we are confident that our data provide an accurate evaluation of crustacean species richness patterns in Canada: a recent study conducted at spatial and temporal scales on an extensive data set of zooplankton showed that species richness evaluated on a daily basis was linearly related to mean annual species richness (Shurin *et al.*, 2007). Pelagic zooplankton is a key component of food webs in large and deep lakes. However, because littoral crustaceans can make a major contribution to zooplankton species richness in small lakes (Walseng *et al.*, 2006), it is important to note that our study does not assess species richness of crustaceans in littoral habitats of Canadian lakes. Our modelling effort for assessing regional and local control of crustacean assemblages in the subset of 458 lakes was also limited by the unavailability of local descriptors beyond a few morphometric and trophic variables. Other unmeasured descriptors such as nutrients, chlorophyll biomass and fish predation may have important effects on crustacean community structure at local scale (Hessen *et al.*, 2006, 2007).

In the coming years, scientists may well discover that zooplankton species distribution and community structure are changing with climate warming and land use, perhaps at a variety of scales from local lakes to large ecoprovinces. Efforts to compile and modernize existing but disparate records will serve a key role in understanding changes inside lakes. Meanwhile, modern techniques allow the assembly and sharing of such databases for future researchers. In this setting, we created an extensive and modern spatial lake database, addressed it with models built from wide-area environmental data, and tested basic ecological theories at large scales. We hope that our findings on continental-scale distribution of zooplankton can serve as a baseline for understanding potential future departures from current and recent conditions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Estimates of regional species richness (Average local species richness, Jackknife diversity index, total number of species) and number of lakes in each of the 47 ecoprovinces located in the 15 ecozones of Canada (total numbers: $n = 1665$ lakes; $n = 83$ species). Data not calculated for 12 ecoprovinces with total number of species ≤ 10 or total number of lakes ≤ 5 .

Appendix S2 List of crustacean species recorded in the field and literature surveys based on GIS-validated lakes.

Appendix S3 (A) Forward selection of regional environmental descriptors in multiple regression. (B) Simple linear regression

analyses of the Average local species richness in each ecoprovince ($n = 1665$ lakes); the adjusted R^2 is shown when the regression coefficient was significant ($\alpha = 0.05$)

Appendix S4 Linear and quadratic regressions between the natural logarithms of estimates of regional species richness (average local species richness) and the inverse of temperature (in Kelvin) corrected by the Boltzmann constant.

Appendix S5 Minimum, maximum, median and mean values of the local and regional environmental descriptors within ecoprovinces across Canada in the subset of 458 lakes.

Appendix S6 Variation partitioning of the total explained variation (represented by the outside rectangle) of the crustacean community structure between regional (left box, $[a + b]$) and local (right box, $[b + c]$) and environmental descriptors.

BIOSKETCH

B.P.A., P.L. and J.C. are research scientists in the Group for Interuniversity Research in Limnology and aquatic environment (GRIL), a major Canadian research centre in freshwater ecology. They co-supervised the master student (A.A.). B.P.A. research aims at studying patterns and processes of biodiversity and community structure of freshwater zooplankton at multiple scales; she developed the general research questions and hypotheses and led the writing. P.L. develops quantitative methods of spatial analysis in Numerical Ecology; he supervised the statistical analyses and contributed to ideas and writing. J.C. uses GIS applications to study patterns and processes at large spatial scales in the landscape; he supervised the GIS analysis and mapping, and contributed to ideas and writing. K.P. and A.S. provided the database on crustacean species occurrences. A.A. conducted the day-to-day work, validated the lake-zooplankton data, performed GIS and statistical analyses, wrote the initial draft of the article and participated in ideas and final writing and revisions. His contribution was crucial to the completion of the study and he should be considered as the first author of the paper.

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