Climate, history and life-history strategies interact in explaining differential macroecological patterns in freshwater zooplankton

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ABSTRACT

Aim We investigated how freshwater microcrustaceans with different susceptibilities to Allee effects differ in the distribution of their geographical range size (GRS) and diversity along latitudinal gradients, evaluating the importance of climatic and historical factors in explaining these differences. We hypothesized that sexual copepods would have a smaller GRS and that their distribution would be linked to historical processes due to mate-finding Allee effects during colonization. Given that cyclic parthenogenetic cladocerans avoid these Allee effects, we predicted that they would exhibit a larger GRS and their distribution would be related to climatic factors rather than dispersal limitation.

Location Canadian watersheds, North America.

Methods We used a database containing the presence–absence of freshwater zooplankton across 1665 Canadian lakes along a latitudinal gradient of 40°. We computed GRS using minimum convex polygons encompassing all lakes in which each species was present. We pooled the diversity of lakes within watersheds, and computed linear regressions models between watershed diversity and average GRS with the average latitude, distance from a glacial refugium and environmental variables of the watershed. All analyses were performed separately for cladocerans and copepods.

Results Cladocerans exhibited, on average, a GRS 70% larger than that of copepods. We found a strong relationship between diversity (negative) and average GRS (positive) with latitude for cladocerans but not for copepods. Cladoceran macroecological patterns were mainly explained by climatic factors, whereas the lack of latitudinal gradients in copepods was potentially due to the influence of a northern glacial refuge and dispersal limitation.

Main conclusions Our results show that Allee effects are strongly and negatively associated with GRS, influencing the relative importance of environmental filtering and dispersal limitation on species diversity patterns. We suggest that studies should avoid lumping species with large differences in their susceptibility to Allee effects in order to better disentangle the multiple processes affecting large-scale patterns.

Keywords
Allee effect, cladocerans, copepods, latitudinal diversity gradient, Rapoport's rule, temperate lakes.

INTRODUCTION

One of the oldest and most recognized patterns in macro-ecology is the latitudinal diversity gradient (LDG), i.e. increasing species diversity from the poles to the equator. Despite its generality across taxa and habitat types (Hillerbrand, 2004), determining the mechanisms that underlie the LDG has been challenging (see Mittelbach *et al.*, 2007, for a review of more than 30 hypotheses). Notably, climatic conditions have been often invoked, given that temperature, precipitation and productivity are well correlated with species richness patterns (Francis & Currie, 2003; Hawkins *et al.*, 2003). Historical hypotheses have also been put forward, suggesting that past environmental conditions and/or geographical barriers, which have shaped speciation and extinction rates as well as dispersal processes, may have longstanding effects on present-day species richness (Dynesius & Jansson, 2000; Baselga *et al.*, 2012). Disentangling these processes is difficult because present-day environments are often correlated with past ones, and both are likely to have played a role shaping current diversity patterns (Hortal *et al.*, 2011).

Evaluating how different groups of species (or species attributes) vary along latitudinal gradients can provide valuable information on the relative importance of these drivers (Marquet *et al.*, 2004). Notably, one species attribute that has been shown to vary in a predictable manner across latitudinal gradients is their geographical range size (GRS): the average GRS of species increases from southern to northern latitudes, a pattern known as Rapoport's rule (Rapoport, 1975; Stevens, 1989). As diversity is a property arising from the overlap of species geographical ranges within a region, analysing the spatial variation in GRS may improve our understanding of the processes underlying the LDG (Gaston, 2009; Blanchet *et al.*, 2013). Geographical range is shaped by both ecological and evolutionary forces and represents the expression of a species' realized niche in space (Gaston, 2009; Kubisch *et al.*, 2014). Species spread to new geographical locations when individuals disperse into new areas and are able to tolerate the local abiotic and biotic environment, generally requiring either pre-adaptation or *in situ* adaptation (Sexton *et al.*, 2009). Given that most invasions start with a few individuals, they are subjected to Allee effects, which is a decrease in the average fitness of individuals when populations are at low densities (Courchamp *et al.*, 1999). In sexual organisms, mate finding is one of the most common sources of Allee effects and is known to slow down range expansion and even promote range contraction via local extinction (Kramer *et al.*, 2008; Shaw & Kokko, 2015). Another challenge in the range expansion of sexual species is the dispersal of maladapted individuals from core populations to the range border (Lenormand, 2002; Holt & Barfield, 2011). Such immigrants, when mating with resident individuals, may swamp out the effects of local adaptation with maladapted genes, a process known as migration load (Lenormand, 2002). Conversely, species that perform autonomous reproduction (e.g. selfing, parthenogenesis) may have a higher

potential associated with range expansion because they avoid both migration load and Allee effects. However, asexual species lack mechanisms that increase the genetic variability of populations such as recombination and crossing over, potentially hindering their capacity for local adaptation (Holt & Barfield, 2011; Kubisch *et al.*, 2014). Thus, species mating strategies are likely to play an important role in regulating both GRS and large-scale diversity patterns.

In this context, it would be interesting to contrast the spatial variation of the GRS and diversity of taxa that are subject to similar abiotic and biotic conditions but have contrasting mating strategies. One group of organisms that allows such comparison is freshwater microcrustaceans (Allan, 1976; Leibold *et al.*, 2010). Cladocerans reproduce almost invariably through cyclic parthenogenesis, in which many phases of asexual reproduction with no genetic recombination are alternated with sexual reproduction, while all copepods are obligate sexual species (Allan, 1976; De Meester *et al.*, 2002). Recent evidence in plants shows that outcrossing species have a much smaller GRS than selfing species (i.e. autonomous reproduction). The authors concluded that, despite having higher genetic variability, sexual species are subjected to Allee effects and are not able to expand their ranges as well as autonomously reproducing species (Grossenbacher *et al.*, 2015). In their system it was not possible to evaluate the unique contribution of Allee effects to GRS because outcrossing species are also subject to migration loads. In contrast, in freshwater zooplankton, one can partially control for it because cladocerans and copepods perform sexual reproduction, which implies that both groups may be subject to migration loads from maladapted immigrants. However, cladocerans remain somewhat less subject to this effect given that they tend to reproduce asexually and due to their ability to prevent gene flow through niche pre-emption by established clonal populations (De Meester *et al.*, 2002). Nevertheless, the ability to reproduce through parthenogenesis suggests that cladocerans have higher dispersal rates than copepods because they evade mate-finding Allee effects during the colonization phase (see Table 1 for a review of the evidence). Therefore, freshwater microcrustaceans provide a strong system to test for the contribution of Allee effects to GRS and latitudinal gradients.

In the present study we used a large dataset of freshwater microcrustaceans distributed along a latitudinal gradient spanning 40° across Canada (Pinel-Alloul *et al.*, 2013) to evaluate how the difference in susceptibility to Allee effects of cladocerans and copepods may affect their GRS as well as the steepness of their latitudinal gradients in diversity and range size (Rapoport's rule). Like other freshwater organisms, the diversity of zooplankton in Canadian lakes is mainly the result of a recent (<15,000 years) post-glacial range expansion of species located in glacial refugia across the United States during the melting of the glacial sheet (Hebert & Hann, 1986). By restricting our analysis to within Canada, the potential effects of clade age on species GRS should not affect our results because both clades were well established

Table 1 Empirical evidence showing that cladocerans have better dispersal capacity than copepods.

Evidence	Reference
Under low dispersal (i.e. low propagule pressure), copepods are less likely to establish in acidified lakes than cladocerans (i.e. interaction between the local environment and the Allee effect)	Gray & Arnott (2012)
After the removal of fish from historically fishless lakes in which their introduction led to the extinction of large-bodied copepods and cladocerans, only cladocerans were able to recover. This occurred despite the presence of copepod egg banks in these lakes, showing evidence for the Allee effect due to mate-finding difficulties	Kramer *et al.* (2008)
Both parthenogenetic cladocerans and rotifers had higher colonization rates than sexual copepods in newly constructed ponds	Frisch *et al.* (2012)
Most cladocerans produce an ephippia egg, which is much more resistant to desiccation and freezing than normal diapausing eggs (calanoids) or diapausing copepodid stages (cyclopoids)	Havel & Shurin (2004)

long before the melting of the Pleistocene ice sheet, given that the oldest fossil record for both groups dates to the Carboniferous (see Sun *et al.*, 2016, and references therein). Note that one high-latitude region in North America remained unglaciated (i.e. the Beringian refugium in Alaska; Hebert & Hann, 1986), potentially influencing the steepness of latitudinal gradients if many species were able to recolonize northern regions from this refugium. Given that both zooplankton groups had equal time to recolonize Canada after the Pleistocene glaciation, we make the following predictions: (1) cladocerans should exhibit a larger GRS than copepods because the former have a greater colonization ability; (2) the diversity and GRS distribution of cladocerans should be more influenced by climate (i.e. environmental filtering) given that they are not dispersal limited, while copepods should respond mostly to historical factors (i.e. dispersal limitation); (3) the differential response to environmental filtering and dispersal limitation between the two groups should translate into contrasting patterns in LDG and Rapoport's rule between these groups.

MATERIAL AND METHODS

Dataset

The dataset used in this study is based on a long-term sampling programme (1961–91) carried out by the Freshwater Institute of Fisheries and Oceans Canada. It contains the presence–absence of 83 crustacean zooplankton species distributed across 1665 lakes along the entire mainland of Canada (42–80° N and 52–139° W) (Fig. 1). Sampling took place once during mid-summer, near the centre of the lakes (therefore only pelagic species were sampled). As with any long-term large-scale dataset, sampling effort was not equal across lakes, ranging from a single site in most lakes to as many as 50 sites in very large lakes. The sampling method was similar across all lakes: zooplankton were collected with a Wisconsin plankton net (diameter 25 cm, mesh size 53–77 mm) by vertical hauls from the lake bottom to the surface, or from a depth of 50 m in the deepest lakes [see

Patalas (1990) and Patalas *et al.* (1994) for information on the sampling design]. While sampling might have missed some species because it did not cover the entire growing season, it has been shown recently that mean annual species richness is strongly correlated with zooplankton diversity estimated on a daily basis (Shurin *et al.*, 2007). Further, variation in per-lake sampling effort may bias analyses performed at a local scale, especially given that lake zooplankton diversity is influenced by factors that either operate at small and less predictable spatio-temporal scales or by relatively more stable and predictable large-scale factors (Pinel-Alloul, 1995; Pinel-Alloul & Ghadouani, 2007). Given that our interests are in the long-term processes that shaped more stable large-scale patterns, we considered regional variation (i.e. across watersheds; Fig. 1) rather than small local variation at the lake level. In order to pool the lake data (e.g. species occurrence, climatic factors) into watersheds, we downloaded watershed shape files from the global hydrographic dataset HYDRO1K (USGS, 2012; available at https://lta.cr.usgs.gov/HYDRO1K). The drainage basins delineated in the HYDRO1K database consist of a hierarchical structure of six levels of increasingly smaller polygons based on topographic relief and direction of hydrological flow related to elevation. For the analysis reported here, we used secondary watersheds and retained only those that had at least 20 lakes surveyed because it has been shown that over 90% of the species found in a region were usually found by sampling at least 20 lakes (Patalas, 1990). In total, 1500 lakes belonging to 26 watersheds were retained for analysis (Fig. 1). Given that large-scale diversity patterns may be scale dependent (Rahbek, 2005), we tested the consistency of our results by evaluating the LDG and Rapoport's rule using tertiary watersheds (i.e. a finer spatial grain) from the HYDRO1K database. Due to a greater degree of spatial subdivision, fewer lakes (928 in total) across 25 tertiary watersheds were analysed. We also performed another set of analyses by lowering the threshold to a minimum of 10 lakes per watershed, which retained 1219 lakes across 47 tertiary watersheds. In all analyses we removed any species from the dataset with fewer than three occurrences

Figure 1 Map of Canada with the 26 watersheds retained for the analysis (numbered and colored). The dashed line represents the maximum extent of the ice cover during the Last Glacial Maximum (LGM) (modified from Blanchet *et al.*, 2013). The arrows represent the two extreme latitudes of Canada: southern arrow, Point Peele, ON; northern arrow, Cape Columbia, Ellesmere Island, NU.
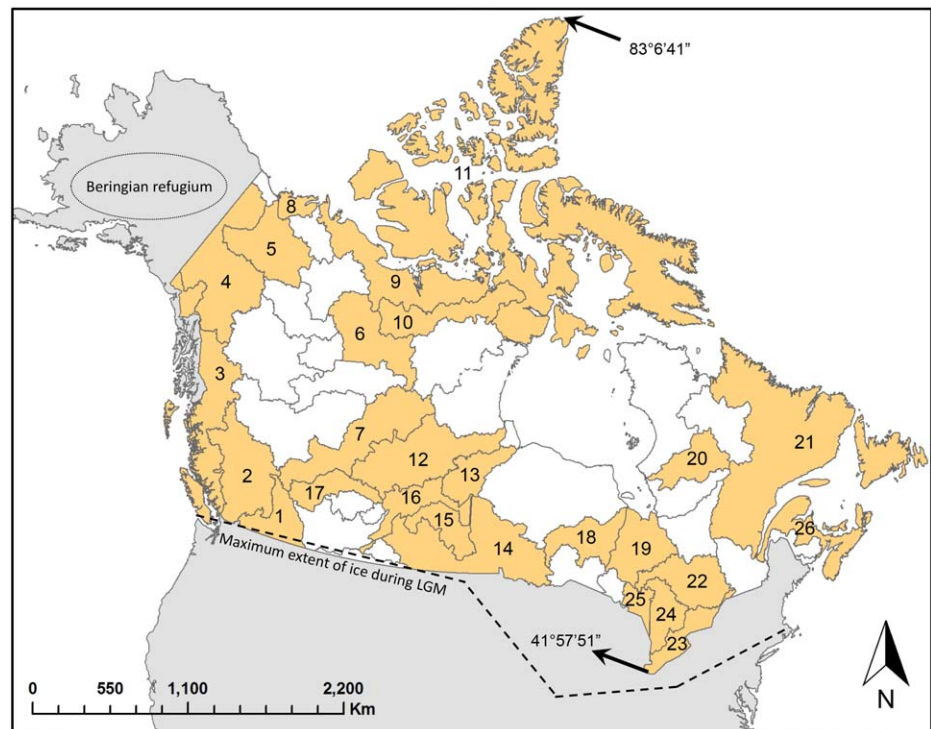
(a total of eight species) because the metric used to compute geographical range needs at least three data points (see 'Diversity and geographical range size metrics' below for more details). In total, 75 species were retained for the main analyses. Note that for the analyses based on tertiary watersheds additional species were removed (three for the 20 lakes rule and one for the 10 lakes rule) because all lakes in which they occurred were eliminated from the dataset.

Climatic and historical factors

Environmental data and geographical coordinates for each lake were obtained from Pinel-Alloul *et al.* (2013): growing season length (days), growing degree days above 10 °C, effective growing degree days above 5 °C, mean elevation (m), annual potential evapotranspiration, total annual precipitation (mm), mean daily global solar radiation, mean duration of bright sunshine (hours), mean annual air temperature, maximum annual air temperature (°C), mean annual vapour pressure (°C), latitude and longitude. To obtain values at the watershed level, we averaged variables across lakes within each watershed. Descriptive statistics for each variable are presented in Appendix S1 in the Supporting Information. Furthermore, we computed the Euclidean distance between Alaska's centroid to each watershed as a variable to account for the potential historical effects of the Beringian refugium on current patterns of zooplankton diversity and GRS (see Fig. 1).

Diversity and geographical range size metrics

Species richness for each zooplankton group (copepods and cladocerans) in any given watershed was defined as all species found within its sampled lakes. To verify potential sampling biases across watersheds, we computed the first-order jack-knife richness index (Palmer, 1990), $S_{EST} = S_{OBS} + x(n - 1)/n$, where S_{OBS} is the total number of species in the watershed, n is the number of lakes and x is the number of species that are present in only one lake (i.e. singletons; see also Pinel-Alloul *et al.*, 2013). We then calculated the Pearson correlation between watershed richness and the first-order jack-knife richness index. Correlation coefficients were extremely high for both groups ($r = 0.97$ for cladocerans and $r = 0.95$ for copepods), suggesting that any sampling differences among watersheds across groups should not affect our results. The dataset contained different numbers of species for cladocerans ($n = 30$) and copepods ($n = 45$). As suggested by Baselga *et al.* (2012), we standardized the species richness of each group for all watersheds to avoid any bias in the regression slopes of the latitudinal diversity:

$$S_{STD} = \frac{S_i}{S_{MAX}} \times 100$$

where S_i is the species richness in the ith watershed and S_{MAX} is the maximum richness value of the corresponding group recorded across all 26 watersheds.

The GRS of each species (see Appendices S2 & S3) was estimated as the area of the minimum convex polygon (km^2) that encompasses all the lakes (independently of watersheds) in which a species was found to be present using the function *earth.poly* in the R package 'fossil' (Vavrek, 2011). This metric has been shown to correlate quite well with other common measures of GRS (Quinn *et al.*, 1996) and was highly correlated with maximum latitudinal extent (r = 0.93)

in our dataset. We obtained a GRS value for each watershed by averaging the range size values of all its constituent species.

Statistical analysis

To determine the strength of the latitudinal gradients in richness and range size, we computed linear regressions between log-transformed watershed diversity (S_{STD}) and average GRS (*Range*) for each microcrustacean group on the mean latitude of lakes within a watershed (*Lat*). Additional regression models for latitudinal gradients were performed for tertiary watersheds (see map in Appendix S4) to evaluate if results were scale dependent (see Appendices S5 & S6). We verified the potential effect of the Berigian glacial refuge by regressing log-transformed GRS and diversity for each group on the distance from the refugium (*BER*). Finally, to estimate the importance of different environmental factors in explaining patterns of both diversity and GRS for cladocerans and copepods, we computed multiple linear regression models with all environmental variables (see 'Climatic and historical factors') using a forward selection procedure proposed by Blanchet *et al.* (2008) through the R package 'packfor'; variables were selected on the basis of a significance level of 0.05 and probability values of partial contributions were estimated on randomization tests using 999 permutations (see Blanchet *et al.*, 2008, for more details). In all regression models we included log-transformed watershed area (*A*) as a covariate to control for size differences among watersheds. We tested residual normality by performing the Kolmogorov–Smirnov test with the Lilliefors correction using the R package 'nortest' (Gross, 2015) and residual homoscedasticity through the Breusch–Pagan test using the R package 'lmtest' (Hothorn *et al.*, 2014). Results from these tests are presented in Appendix S7. One model failed the residual homoscedasticity test (cladoceran GRS $\sim$ *BER* + *A*) and therefore we corrected it for heteroscedasticity by the Huber–White method using the R package 'car' (Fox & Weisberg, 2011). In order to better understand how the diversity gradients of cladocerans and copepods are structured across space, we used the beta-diversity metric based on the Sørensen index family developed by Baselga (2010), which decomposes the variation in species composition (i.e. total beta-diversity, β_{sor}) into spatial assemblage turnover (β_{sim}) and differences in species composition due to differences in richness (i.e. nestedness, β_{nes}). These metrics were computed across secondary watersheds in order to have a global measure of beta diversity using the R library 'betapart' (Baselga & Orme, 2012).

Note that populations of the *Daphnia pulex* complex (*D. pulex*, *D. pulicaria* and *D. middendorffiana*) in northern latitudes switched their mating system from cyclic parthenogenetic to obligate asexuality (Decaestecker *et al.*, 2009). Given that we aimed to compare cyclic parthenogenetic cladocerans with obligate sexual copepods to account for the effect of migration load, we repeated all the analyses without the species from the *D. pulex* complex to verify if these species could

have affected our results. Results from these analyses did not affect our main conclusions and are presented in Appendices S8–S10. Finally, to further evaluate the robustness of our results to sampling effort variation (see 'Dataset'), we also performed a resampling technique to test how the relationship between diversity and latitude changed between the two groups if a subset of lakes were selected randomly from each watershed. Details and results from this analysis are presented in Appendix S11, and they show that the striking differences found between the two groups were not affected by potential issues around sampling effort.

RESULTS

On average, cladocerans exhibited a GRS 1.72 times larger than copepods ($t = 2.8699$, $P = 0.0054$). While the cladoceran GRS distribution was almost uniform (skewness = 0.1087), showing a similar number of species with small and large GRS (Fig. 2b), copepod GRS distribution was heavily left skewed (skewness = 0.7750), with most species exhibiting a small GRS (Fig. 2a). Our third prediction was also supported because we found large differences in the steepness of latitudinal gradients for both watershed diversity and average GRS between cladocerans and copepods (Fig. 3, Table 2). The diversity of cladocerans was strongly negatively related to latitude [$b_{LAT} = -0.034$; adjusted R^2 (adj-R^2) = 0.617; $P < 0.001$] while the same relationship was not statistically significant for copepods (adj-$R^2 = -0.012$; $P = 0.442$; Table 2). The same pattern was found for average GRS, where the average GRS for cladocerans was strongly and positively related to latitude ($b_{LAT} = 0.014$; adj-$R^2 = 0.706$; $P < 0.001$) but the average copepod GRS was unrelated to latitude (adj-$R^2 = 0.069$; $P = 0.167$; Table 2). The second set of analyses performed without the *D. pulex* complex did not change our results (Appendix S5). If anything, the pattern became stronger as the adj-R^2 for the diversity–latitude relationship increased its R^2 from 0.61 to 0.69 ($b_{LAT} = -0.037$; $P < 0.001$) while the adj-R^2 for the average GRS–latitude decreased by only 1% ($b_{LAT} = 0.015$; adj-$R^2 = 0.691$; $P < 0.001$).

Regression models between these two variables and the distance from the Beringian refugium (*BER*) showed no significant relationship with either cladoceran richness (adj-$R^2 = 0.001$; $P = 0.37$) or average GRS ($P = 0.07$; Table 3). In contrast, the average GRS of copepods was positively related to the distance from the refugium ($b_{BER} = 0.002$; adj-$R^2 = 0.19$; $P = 0.032$; Table 3), meaning that watersheds near the refugium had smaller-range copepod species compared with watersheds further east (Fig. 3d). However, the diversity of copepods was unrelated to *BER* (adj-$R^2 = 0.029$; $P = 0.27$; Table 3), thus only partially supporting our second prediction regarding the relationship between copepods and cladocerans with historical factors (i.e. dispersal limitation). The analysis performed for cladocerans without the *D. pulex* complex showed no significant changed in either diversity ($P = 0.118$) or average GRS ($P = 0.0636$; Appendix S6).
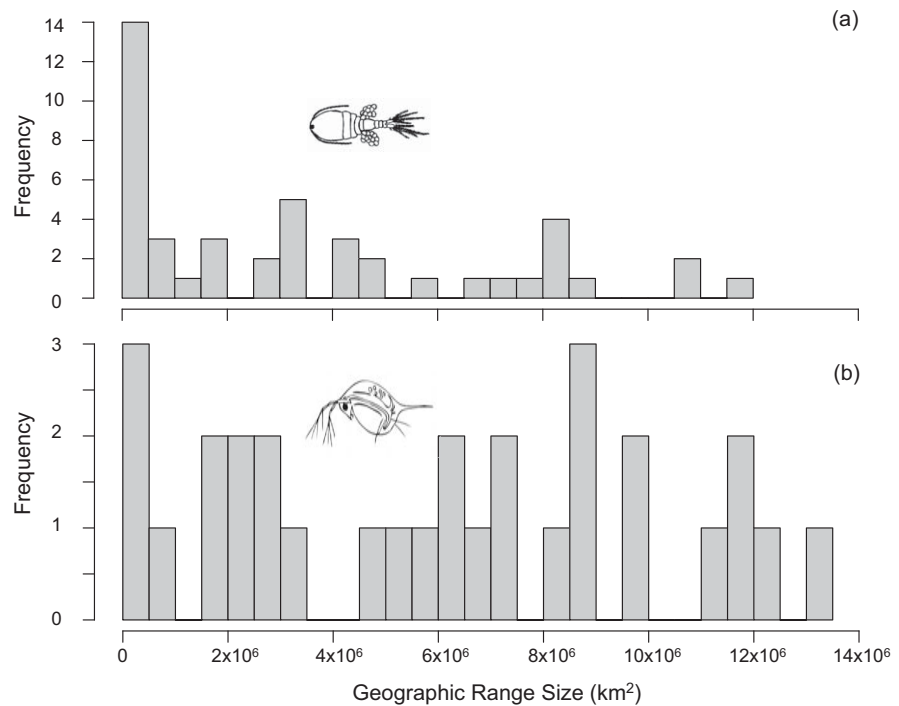
Figure 2 Frequency distribution of geographical range size for (a) copepods and (b) cladocerans. Note that the scale of the y-axis is different for each histogram.

The results from the forward selection procedure showed a strong relationship between both cladoceran diversity (positive) and average GRS (negative) with variables related to temperature and productivity (Table 4). The only variable selected to explain cladoceran richness was mean annual temperature (MAT; $b = 0.044$; adj-$R^2 = 0.718$; $P < 0.0001$). Cladoceran GRS (adj-$R^2 = 0.7376$) was negatively and strongly related to mean daily global solar radiation (MDGSR; $b = -0.067$; $P < 0.0001$) and weakly related to total annual precipitation (TAP; $b = -0.0001$; $P = 0.0278$). When removing the *D. pulex* complex, the latitude–GRS relationship did not change and the same variables were selected in the forward-selection procedure. The diversity–latitude relationship changed slightly, as growing season length (GSL) and MDGRS were selected instead of MAT (Appendix S7). However, both these variables are strongly correlated with temperature, generating a similar interpretation. For copepods, richness was positively but weakly related to mean duration of bright sunshine ($b = 0.0006$; adj-$R^2 = 0.17$; $P < 0.0001$) whereas mean elevation was strongly negatively related to average GRS ($b = -1763.2$; adj-$R^2 = 0.50$; $P = 0.0001$). Overall, these results support our second prediction regarding environmental filtering, which posited a strong relationship to climatic factors for cladocerans but not copepods. Finally, none of the regression models suggested a relationship with watershed area (Tables 2–4, Appendices S5–S7), indicating that the results were not an artefact of the species–area relationship. Finally, the beta-diversity analysis (see Appendix S12) showed that the overall beta diversity (β_{sor}) was slightly higher for copepods (0.86) than cladocerans (0.81), but the partitioning revealed important differences: 94% of the variation in copepod beta diversity was due to pure spatial turnover ($\beta_{sim} = 0.81$) and only 6% to nestedness ($\beta_{nes} = 0.05$), whereas variance in cladoceran beta diversity was decomposed into 83% spatial turnover ($\beta_{sim} = 0.67$) and 17% nestedness ($\beta_{nes} = 0.14$).

DISCUSSION

As predicted, cyclic parthenogenetic cladocerans exhibited a much greater GRS than obligate sexual copepods, with an average difference of 70% between the two mating systems. We have thus added important evidence that mate availability can be a limiting factor during range expansion, as previously established in plants by Grossenbacher *et al.* (2015). Further, these groups differed strongly in how they respond to historical (i.e. the Beringian refuge) and climatic factors (Tables 3 & 4), probably due to their contrasting life histories. Cladoceran richness and GRS had an opposite relationship with temperature, where watersheds with warmer climates contained more species with smaller GRS than colder regions, suggesting that environmental filtering is an important structuring factor for cladocerans at macroecological scales. Furthermore, dispersal limitation seems not to affect their distributional patterns, especially given that the Alaska glacial refuge had no effect on either their diversity or GRS (Fig. 3c,d). The strong influence of climate on cladocerans may explain the steep relationship between their richness and average GRS with latitude (i.e. the LDG and Rapoport's rule; Fig. 3a,b). These results persisted even when we removed the *D. pulex* complex (Appendices S5–S7), populations of which are known to have switched to being obligately asexual (i.e. and therefore are not affected by migration load) in northern latitudes (Dufresne & Hebert, 1997; Decaestecker *et al.*, 2009). In contrast, copepod
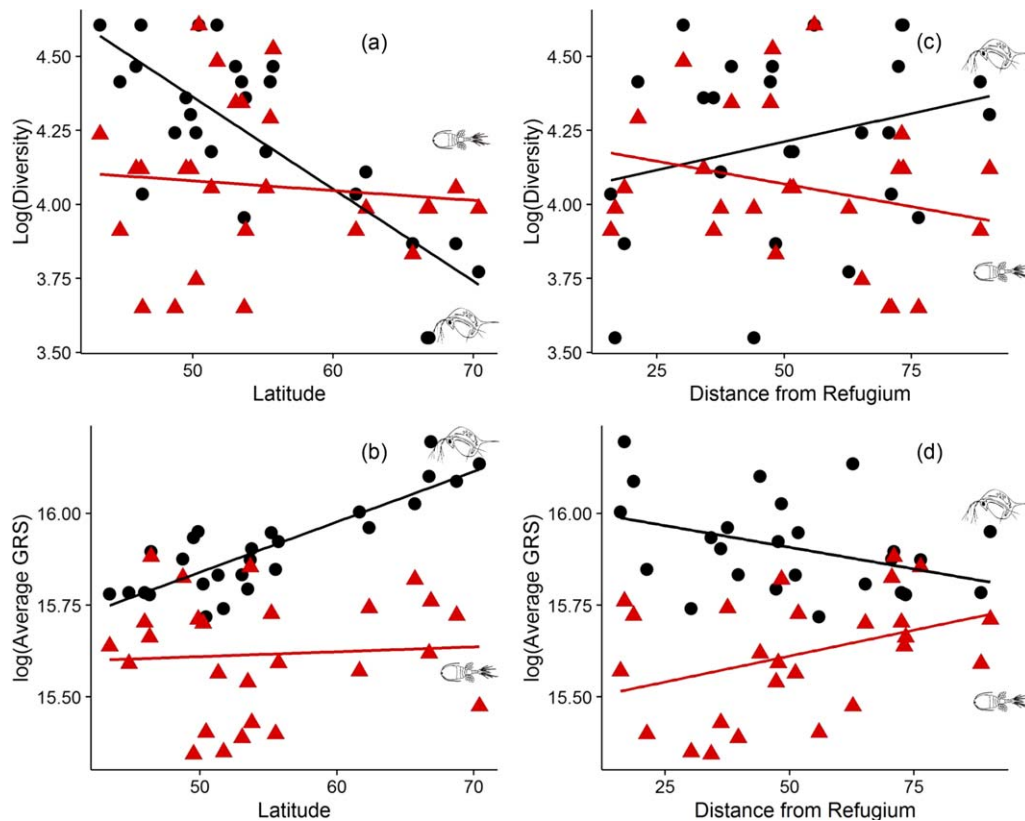
Figure 3 Relationship between watershed latitude and (a) its diversity or (b) average geographical range size (GRS) for copepods and cladocerans. Relationship between watershed distance from the Beringian refugium and (c) its diversity or (d) average GRS for copepods and cladocerans. Circles represent cladoceran data while triangles represent copepod data. Each data point represents a watershed. Regression results for these slopes are presented in Tables 2 & 3.

richness was only weakly influenced by temperature. Together, these results suggest that environmental filtering is not an important structuring factor for copepod macroecological patterns. Note, however, that our results do not mean that the environment is not important for distributions of individual copepod species. Different species may have particular affinities for different portions of the environmental gradient, but the environment in itself do not explain the variation in the number of copepods species across space. Further, average copepod GRS was related to elevation, and this may be an indirect effect of the proximity of the Rocky Mountains to the Beringian refugium as we found a significant positive effect of distance from the Beringian refugium on GRS for copepods (Fig. 3d; Table 3). This suggests that some copepod species colonized north-western watersheds from this northern refuge, but due to their poor dispersal ability (see Table 1) they were unable to expand their ranges across eastern or southern Canada, particularly given that they are absent from these regions. Indeed, some copepod species may rely on surface waters for dispersal (Stemberger, 1995) and species that survived the Pleistocene glaciation in the Beringian refugium were never in direct contact with the ice-front lakes that formed along the southern ice sheet (Stemberger, 1995). Moreover, dispersal by migrating waterbirds from the Beringian refugium towards north-eastern

watersheds is limited because migratory routes are mainly along a south–north direction. As a consequence, many copepod species in the north exhibit small geographical ranges. For instance, 5 out of 14 copepod species present in the Arctic Archipelago (11 in Fig. 1) were found solely in this watershed or distributed in only two other watersheds (Appendix S3). This may explain the absence of both Rapoport's rule and a LDG in this group (Fig. 3). The regional beta-diversity analysis (Appendix S12) also supports these results, with most of the spatial variation in copepod species composition being unrelated to richness but rather to species ranges that do not overlap (i.e. high spatial turnover, β_{sim}). In contrast, cladoceran beta diversity is partially driven by species loss (i.e. higher β_{nes}), with a clear decrease in species diversity from southern watersheds towards the Arctic (Fig. 3a).

The striking differences found among macroecological patterns in cladocerans and copepods are to an important degree due to their mating systems. We can exclude differences in biogeographical history (e.g. one group colonizing preferentially from northern refugia while the other colonizes preferentially from southern refugia) between the two groups given that many studies have shown that they both colonized Canada from southern (e.g. Mississippian and Atlantic) and northern (e.g. Berigian) glacial refugia (Hebert & Hann, 1986; Stemberger, 1995; Figuerola *et al.*, 2005; Jeffery *et al.*,

Table 2 Results from linear regression models between latitude and log-transformed watershed diversity (S_{STD}) and average geographical range size (GRS) with watershed area (A) as a covariable.

Group	Cladocera		Copepoda	
Response	S_{STD}	GRS	S_{STD}	GRS
F	21.14	31.1	0.846	1.936
Global P	**<0.00001**	**<0.00001**	0.442	0.167
adj-R^2	0.617	0.706	−0.012	0.069
Intercept	5.27	15.16	3.39	16.34
P_{INTER}	**<0.00001**	**<0.00001**	**0.00022**	**<0.00001**
b_{LAT}	−0.034	0.014	−0.006	0.004
P_{LAT}	**<0.00001**	**<0.001**	0.411	0.352
b_A	0.065	−0.002	0.082	−0.078
P_A	0.199	0.91	0.235	0.064

Global P, global probability; P_{INTER} probability for the intercept; P_{LAT}, probability for latitude; P_A, probability for watershed area; b_{LAT}, coefficient for latitude; b_A, coefficient for watershed area. Significant P-values under $\alpha = 0.05$ are given in bold.

2011). We acknowledge that cladocerans and copepods differ in a number of factors other than mating system, such as environmental tolerances, the capacity of their propagules to disperse (e.g. ephippia eggs versus diapausing eggs; Havel & Shurin, 2004) and diet niche overlap (Barnett *et al.*, 2007). Therefore, one cannot exclude the possibility that these differences may also have played a role in shaping the differences in macroecological patterns between the two groups. Nevertheless, mating system may be a critical factor because it influences many processes, such as the susceptibility to Allee effects during earlier stages of colonization (Courchamp *et al.*, 1999; Kramer *et al.*, 2008; Gray & Arnott, 2012), the rapidity of adaptation to local conditions and monopolization of resources (De Meester *et al.*, 2002; Urban & De Meester, 2009) and the number of generations needed during the growing season to produce diapausing eggs. With a few exceptions (Shurin *et al.*, 2000; Leibold *et al.*, 2010), research involving large-scale patterns in diversity and distribution of freshwater microcrustaceans has often neglect the potential effects of these fundamental life-history differences (e.g. Hessen *et al.*, 2007; Mazaris *et al.*, 2010; Pinel-Alloul *et al.*, 2013). For instance, Mazaris *et al.* (2010) could not find either spatial or environmental predictors that accounted for large-scale compositional patterns in zooplankton, and we suspect that it might be because they pooled both cladocerans and copepods in the same analysis. In contrast, Leibold *et al.* (2010) demonstrated that cladocerans respond more to local-scale environmental factors in lakes (e.g. limnological variables) while the distribution of calanoid copepods is related to biogeographical events. Our results corroborate their findings, and show that even at broader scales, cladocerans continue to respond strongly to the environment (e.g. large-scale climatic variables) because they are not dispersal

limited while copepod diversity seems to be more driven by historical factors (e.g. the Beringian refugium).

We propose two complementary explanations for the decrease in cladoceran diversity but not copepod diversity across the latitudinal gradient in northern regions. The first is directly related to mating systems whereas the second encompasses other differences in life-history traits. Zooplankton cope with winter conditions by going through a diapausing phase that resists freezing and drying (Havel & Shurin, 2004), providing long-term persistence in highly seasonal environments. However, cyclic parthenogenetic cladocerans only produce diapausing eggs during their sexual phase, meaning that they need at least two generations to produce those eggs. Lakes and ponds located in northern regions have short growing seasons and experience very cold temperatures, in which both cladocerans and copepods have a slower metabolism and take longer to complete their life cycles (Allan, 1976). Northern-latitude conditions might thus exclude some cladoceran species because they are unable to complete their life cycle twice during the short growing season (Hebert & Hann, 1986). Notably, some cladoceran species (e.g. the *Daphnia pulex* complex) lose their ability to reproduce sexually at northern latitudes, becoming completely asexual either through obligate apomictic parthenogenesis (Dufresne & Hebert, 1997) or self-fertilization (Hebert *et al.*, 2007). Evidence shows that many cladoceran populations found in the Canadian High Arctic have switched to an asexual breeding system, while southern populations from the same species still reproduce through cyclic parthenogenesis (Hebert *et al.*, 2007). Therefore, cladoceran

Table 3 Results from linear regressions between the distance from the Beringian refugium (BER) and log-transformed watershed diversity (S_{STD}) and average geographical range size (GRS) with watershed area (A) as a covariable.

Group	Cladocera		Copepoda	
Response	S_{STD}	GRS*	S_{STD}	GRS
F	1.02	–	1.383	3.995
Global P	0.3762	–	0.2709	**0.032**
adj-R^2	0.001	–	0.029	0.1933
Intercept	4.48	15.52	3.44	16.26
P_{INTER}	**<0.0001**	**<0.0001**	**0.000147**	**<0.0001**
b_{BER}	0.003	−0.002	−0.003	0.002
P_{BER}	0.193	0.071	0.20	**0.0435**
b_A	−0.038	0.04	0.06	−0.06
P_A	0.615	0.36	0.31	0.073

Global P, global probability; P_{INTER}, probability for the intercept; P_{BER}, probability for distance from the Beringian refugium; b_{BER}, coefficient for distance from the Beringian refugium; P_A, probability for watershed area; b_A, coefficient for watershed area.
Significant P-values under $\alpha = 0.05$ are given in bold.
*Given that the residuals from this model were not homoscedastic, we applied the Huber–White method, which gives heteroscedastic corrected estimates for the linear model.

Table 4 Result from forward-selection regression models between environmental variables and diversity and average geographical range size (GRS) of watersheds for both cladocerans and copepods.

Group	Cladocera		Copepoda	
Model	S_{STD}	GRS	S_{STD}	GRS
VAR1	MeanAT	MDGRS	MDBS	M_ELE
VAR2	–	TAP	–	–
F	35.82	24.43	3.569	13.73
Global P	**<0.0001**	**<0.0001**	**0.044**	**0.00012**
adj-R^2	0.718	0.7376	0.1705	0.5045
Intercept	3.52	16.76	1.85	16.43
P_{INTER}	**<0.0001**	**<0.0001**	0.0549	**<0.0001**
B_{VAR1}	0.044	−0.0669	0.0006	−0.0003
P_{VAR1}	**<0.0001**	**<0.0001**	**0.023**	**0.0001**
B_{VAR2}	–	−0.000103	–	–
P_{VAR2}	–	0.0278	–	–
b_A	0.06	−0.00168	0.082	−0.05584
P_A	0.166	0.9220	0.1668	0.056

VAR1 and VAR2 refer to the variables selected in the forward-selection procedure. MeanAT, mean annual temperature; MDGSR, mean daily global solar radiation; TAP, total annual precipitation; MDBS, mean duration of bright sunshine; M_ELE, mean elevation; b_{VAR1}, regression slope for the first selected variable; b_{VAR2}, regression slope for the second selected variable; P_{VAR1}, probability for the first selected variable; P_{VAR2}, probability for the second selected variable; b_A, coefficient for watershed area; P_A, probability for watershed area. Significant P-values under α = 0.05 are given in bold.

diversity towards northern latitudes may be limited due to the inability of most species to transition their mating system towards obligate asexuality. In contrast, copepods comprise two groups that have different adaptations to cope with overwintering. Cyclopoid copepods are able to produce resting eggs throughout the growing season and can encyst in the fourth copepodid instar, providing greater insurance to cope with highly seasonal environments (Tash & Armitage, 1967). Calanoid copepods are mostly univoltine species that produce a small number of eggs and may require as long as 3 months before reaching reproductive maturity (Tash & Armitage, 1967); this can make them particularly susceptible to disturbances such as an early onset of winter conditions (Hebert & Hann, 1986). However, diaptomid calanoid copepods (e.g. *Hesperodiaptomus arcticus*) can attain reproductive maturity at greatly reduced body sizes but unchanged generation times in stressful environmental conditions (Anderson, 1971), thus allowing them to cope with environmental conditions at northern latitudes.

The second likely explanation for the macroecological patterns described in this study is related to the monopolization hypothesis, proposed by De Meester et al. (2002), and lately extended to multiple species (i.e. the community monopolization hypothesis; Urban & De Meester, 2009; De Meester et al., 2016). Here, we extend this idea to macroecological

scales: suppose that a few lakes in northern watersheds were first colonized by a long-distance dispersal event (e.g. diapausing eggs carried in the feathers of waterbirds, a process deemed to be important in zooplankton dispersal; Figuerola et al., 2005). Furthermore, as cladocerans are not affected by mate-finding Allee effects during colonization they can spread across these regions via small-scale dispersal processes much more rapidly than copepods. In addition, rapid population growth rates due to asexual reproduction, together with clonal selection, enable early cladoceran colonizers to adapt quickly to the local environment (De Meester et al., 2002). In contrast, copepod growth rates are slower and they do not undergo clonal selection due to obligate sexual reproduction, and thus have a slower local adaptation process (De Meester et al., 2002). Eco-evolutionary metacommunity models predict that local adaptation from first colonizers enhances priority effects precluding the establishment of later migrants through niche pre-emption (Urban & De Meester, 2009; Fukami, 2015). Indeed, recent experimental work has shown that this process occurs frequently in cladocerans (e.g. Louette & De Meester, 2007; Pantel et al., 2015), especially given that most species in this clade are herbivorous (28 out of 30 in our dataset; Barnett et al., 2007) and exhibit high niche overlap in their resource use (Guisande et al., 2003). Due to the short growing season and low productivity of northern-latitude lakes, the few resources available cannot sustain many cladoceran species (Vogt et al., 2013). Therefore, rapid dispersal, resource monopolization and high food niche overlap may be further reasons underlying the sharp decline in cladoceran diversity across the latitudinal gradient. The fact that cladocerans exhibited a strong Rapoport's rule, in which only species with a large GRS were present in northern watersheds (Fig. 3b), suggests that these regions were only colonized by highly dispersive and/or competitive species. For instance, 6 out of 10 cladoceran species present in the Arctic Archipelago watershed (11 in Fig. 1) were also distributed across 20 or more other watersheds and the remaining 4 were located in more than 12 watersheds (Appendix S2). In contrast, copepods show a much greater variability in diet, containing many omnivorous, carnivorous and some herbivorous species (Barnett et al., 2007), allowing them to consume a much broader range of resources and lessen the strength of competition. Indeed, experimental work evaluating amino-acid composition and the signature of stable isotope has shown that copepods exhibit a much lower food niche overlap than cladocerans (Guisande et al., 2003; Santer et al., 2006). Cyclopoid copepods, for instance, may change opportunistically between resources depending on their relative abundance (Santer et al., 2006). Taken together, the fact that copepods are more dispersal limited (Stemberger, 1995) and use a much broader range of resources might preclude monopolization from a few copepod species and allow later colonizers or weaker competitors to persist in these environments.

Disentangling the main factors underlying species geographical ranges is pressing, especially given the predicted

changes in future climatic conditions and the potential range shift processes that will follow. Most of the literature concerning range dynamics focuses on traits that influence the environmental tolerances and dispersal ability of species (Gaston, 2009; Sexton *et al.*, 2009). The results presented here show that mate-finding Allee effects should also be considered when trying to understand species range dynamics (Courchamp *et al.*, 1999; Shaw & Kokko, 2015). Thus, future studies should also focus on how traits that alleviate Allee effects (e.g. dispersal timing, female sperm storage) may influence how different groups of species will cope with changing environmental conditions. With respect to zooplankton, our results suggest that cladocerans will be less affected by climate change given their broad distribution, resilience to extinction and capacity for adaptation (Van Doorslaer *et al.*, 2009). However, it is possible that completely asexual populations thriving in the Arctic could be replaced by cyclic parthenogenetic phenotypes as temperature and growing season length increase. Moreover, the number of cladoceran species in northern watersheds may also increase, but it will depend on the immigration of other trophic levels (i.e. new species of algae) as well as the strength of resource monopolization from resident species in these lakes. Copepods, however, may face more difficulties, particularly the species restricted to the Arctic region. Given their strong dispersal limitation, they may not have enough time to adapt to the changing conditions and these processes may profoundly modify the trophic networks of Arctic ecosystems.

In conclusion, the present study shows important differences in the macroecological patterns of copepods and cladocerans. Cladoceran species are generally widespread, whereas most copepods have a spatially restricted distribution. Furthermore, cladocerans show the usual decrease in species diversity towards northern latitudes associated with an increase in average GRS (i.e. Rapoport's rule) and are highly influenced by climatic conditions. Conversely, neither copepod diversity nor average GRS show any significant relationship with latitude and are not related to environmental factors, suggesting a stronger role of dispersal limitation and biogeographical events. We hope that our findings will encourage both empiricists and theoreticians to carry out work to better elucidate the effect of mating system and, more generally, Allee effects on these processes.

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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 Descriptive statistics of the variables used in the study.
Appendix S2 Watershed occurrence and geographical range size of cladoceran species.
Appendix S3 Watershed occurrence and geographical range size of copepod species.
Appendix S4 Map depicting the tertiary watersheds selected to investigate the robustness of our main results to a lower hierarchical spatial level.
Appendix S5 Regression models for latitude–diversity and latitude–geographical range size relationships across tertiary watersheds with a minimum of 20 lakes per watershed.
Appendix S6 Regression models for latitude–diversity and latitude–geographical range size relationships across tertiary watersheds with a minimum of 10 lakes per watershed.
Appendix S7 Results from tests on normality and homoscedasticity of residuals from regression models.
Appendix S8 Regression models between latitude with diversity and geographical range size for the cladoceran clade without the *Daphnia pulex* complex.
Appendix S9 Regression models between distance from the Beringian refugium with diversity and geographical range size for the cladoceran clade without the *Daphnia pulex* complex.
Appendix S10 Multiple regression models between environmental variables with diversity and geographical range size for the cladoceran clade without the *Daphnia pulex* complex.
Appendix S11 Resampling protocol for testing the robustness of the main results to variation in sampling effort of lakes.
Appendix S12 Beta-diversity analysis for copepods and cladocerans at the continental scale (i.e. across watersheds).

BIOSKETCHES

Renato Henriques-Silva is a PhD student working at the interface between metacommunity ecology and macroecology, interested in understanding the processes regulating large-scale ecological patterns. He developed the main questions, the analyses and the writing of this manuscript. He was co-supervised by Pedro R. Peres-Neto and Bernadette Pinel-Alloul, who contributed to the ideas and the writing.

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