

## Research

### Geographic signatures in species turnover: decoupling colonization and extinction across a latitudinal gradient

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High latitude communities have low species richness and are rapidly warming with climate change. Thus, temporal changes in community composition are expected to be greatest at high latitudes. However, at the same time traits such as body size can also change with latitude, potentially offsetting or increasing changes to community composition over time. We tested how zooplankton communities (copepods and cladocerans) have changed over a 25–75 year time span by assessing colonization and extinction rates from lakes across an 1800 km latitudinal gradient, and further tested whether species traits predict rates of community change over time. Lake-level dissimilarity, measured with Sorenson distance, decreased at higher latitudes. This decrease was due to higher colonization rates of cladocerans in lower latitude lakes and consistent extinction rates across the latitudinal gradient. At the species level, colonization increased with regional occupancy, and tended to be higher for smaller bodied, locally abundant, species. Local extinction rates were negatively correlated with local abundance and regional occupancy, but were not influenced by body size. None of these species-specific characteristics changed predictably with latitude. Contrary to our expectations, low-latitude zooplankton communities changed more rapidly than high-latitude communities by becoming more species rich, not by losing species that were historically present. Moreover, colonization and extinction trends suggest that lakes have become increasingly dominated by species with smaller body sizes and that are already common locally and regionally. Together, these findings indicate that rates of species turnover in freshwater lakes across a latitudinal gradient are not predicted by rates of temperature change, but that turnover is nonetheless resulting in trait-shifts that favour small, generalist species.

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#### Introduction

Changes in species composition through time have long fascinated ecologists, with classic theories positing that local and biogeographical properties of communities determine these rates (Elton 1958, MacArthur and Wilson 1967, May 1973). Recently, there has been renewed interest in the factors that promote changes in composition, or temporal turnover (Wolkovich et al. 2014, Tonkin et al. 2017). Classic work on

species–time relationships suggest that turnover dynamics are partially the consequence of island biogeography or metapopulation processes (Rosenzweig 1998, Nuvoloni et al. 2016); whereas more recent research has focussed on how global climate change is modifying the latitudinal ranges of many species, thereby altering the composition of communities (Chen et al. 2011, Burrows et al. 2014). Species dynamics in the anthropocene are increasingly influenced by a mixture of metapopulation and anthropogenic processes (Helmus et al. 2014). As a result, determining patterns of species turnover through time and across broad spatial scales is increasingly important for conservation and basic ecology (Wolkovich et al. 2014).

Temporal turnover is the outcome of a variety of dynamic processes that result in two changes to local diversity: gain of species through new colonization events and loss of species through local extinction events (Anderson 2007). Island biogeography and metacommunity theory highlight how the relative importance of colonization and extinction may differ across regional gradients (MacArthur and Wilson 1967, Leibold et al. 2004, Viana et al. 2016). Although these theories make general predictions about characteristics of patches and species that may lead to qualitatively different patterns of diversity and turnover, empirical patterns are often far more complex than suggested from these models (Matthews and Pomati 2012, Jones et al. 2015). The observed complexity is due to an incredible variation in the importance of dispersal limitation, local interactions, environmental predictability and species–environment relationships among ecosystems that make predictions of turnover for any particular community difficult (Shurin et al. 2007, Bennett et al. 2010, Matthews and Pomati 2012, Jones et al. 2015, Tonkin et al. 2017). This challenge is particularly difficult for studies across latitudinal gradients, because there is a simultaneous change in three determinants of turnover: environmental conditions, species and the composition of communities (James 1970, Parmesan 2006, Jones and Gilbert 2016).

Latitudinal gradients in environmental conditions and anthropogenic change suggest that there will be spatial differences in changes to community composition over time. In North America, mean temperatures decline northward along a latitudinal transect and long-term data indicates that during the last 100 years, temperatures have increased more in northern regions (IPCC 2013, Environment Canada 2014). As a result, mean temperature and temperature increases are negatively correlated across a latitudinal gradient. Consequently, high latitude sites can be more vulnerable to the effects of climate change (Smol et al. 2005). However, geographic gradients in other aspects of global change suggest that the opposite pattern could occur, with polar regions being less vulnerable compared to temperate sites. Specifically, larger human populations and urbanization characterize lower latitude regions. This increased anthropogenic pressure has led to land use changes at lower latitudes, such as higher road density and increased recreational use of natural areas (Gayton 2007, Ministry of Forests Mines and Lands 2010), which have increased connectivity among discrete habitats

such as lakes (Kelly et al. 2012). Given the more pronounced temperature changes at high latitudes and the increased anthropogenic pressure at southern latitudes, the resulting effect of these global changes on colonization–extinction dynamics across latitudinal gradients remains unknown.

In aquatic communities, two species characteristics are hypothesized to drive colonization and extinction dynamics of zooplankton: body size and the local abundances of species. Local abundances reflect a suite of traits that determine the impacts of intra- and inter-specific interactions and resource specialization, and are often broadly defined as species carrying capacities (Carpenter et al. 2009). From a metapopulation or meta-community perspective, high local abundance buffers against local extinction, and also provides more propagules that can disperse to other lakes (Hanski 1994), and thus is commonly related to occupancy, or the proportion of sites where a species is found (Hanski et al. 1993). Likewise, body size affects both local and regional distributions. Locally, body size may structure competitive asymmetries among species (Gliwicz 1990), increase trophic position (Woodward et al. 2005) and influence species susceptibility to predation (Dodson and Brooks 1965). Body size can also indirectly impact local success if larger body sizes are associated with smaller population sizes or slower growth rate (Savage et al. 2004). Apart from these local effects, body size directly influences colonization dynamics in passively dispersed organisms such as aquatic zooplankton, which are dispersed via wind, water or animals (Vanschoenwinkel et al. 2008). For these species, dispersal distance can be negatively associated with body size (Soons et al. 2008, De Bie et al. 2012), with smaller individuals travelling further and more frequently. Allee effects are subsequently important for successful colonization, with species that are obligately sexual suffering from lack of mate availability when few individuals disperse (Baker 1955, Kramer et al. 2008, Henriques-Silva et al. 2016). The associations between body size, dispersal and reproductive mode for plankton suggest that traits conferring competitive dominance locally may come at the expense of dispersal among lakes but that some larger species may offset poor dispersal through asexual reproduction, making the overall impact of body size difficult to predict in a regional context. Moreover, body size is a trait that often changes with latitude. Bergmann's rule and James' rule, for example, describe how body size within and among species increases in cooler regions, and thus increases with latitude (Bergmann's rule summarized in James 1970). Because body size–latitude relationships in ectotherms can be highly variable (Shelomi 2012), it is important to quantify the joint and independent effects of latitude and body size on species turnover to understand proximate and ultimate causes of diversity patterns with latitude.

Differences in species diversity across latitudes are also predicted to impact patterns of turnover. Higher latitude regions contain fewer species on average (Shurin et al. 2007, Jones and Gilbert 2016), although some components of community diversity may not show strong relationships (Henriques-Silva et al. 2016, Supplementary material

Appendix 1 Fig. A1), low diversity is expected to be associated with high rates of temporal turnover. This prediction arises from two hypotheses in community ecology. First, because species diversity is positively correlated with phenotypic variation, elevated diversity could reduce opportunities for new species to establish even when they are no longer limited by climate (Elton 1958). Second, diversity is predicted to stabilize community composition by increasing the number of weak interactions in food webs, which reduce large fluctuations in predators and their prey (McCann et al. 1998). When considered in terms of latitudinal patterns of diversity, these competitive and food web models predict larger compositional changes (higher turnover, lower stability) in high latitude communities.

In this paper, we investigate temporal turnover in freshwater zooplankton communities from across an 1800 km

latitudinal gradient in western Canada that has shown typical shifts in temperature over the past 70 years (Fig. 1a–b). Zooplankton are ubiquitous ectothermic animals in freshwater lakes and display a latitudinal gradient in species diversity and composition typical of many organisms (Fig. 1c–d). We resampled zooplankton communities that were originally sampled fifty years ago on average, and asked the following five questions: 1) is there evidence for a latitudinal trend in species turnover? 2) How do colonization and local extinction events within lakes structure this temporal turnover? 3) Does the reproductive mode of plankton (obligately sexual versus facultatively parthenogenic) influence these results? 4) Are body size, local abundance and occupancy predictive of species' colonization and local extinction rates? And, 5) do body size and local abundance change predictably with latitude?

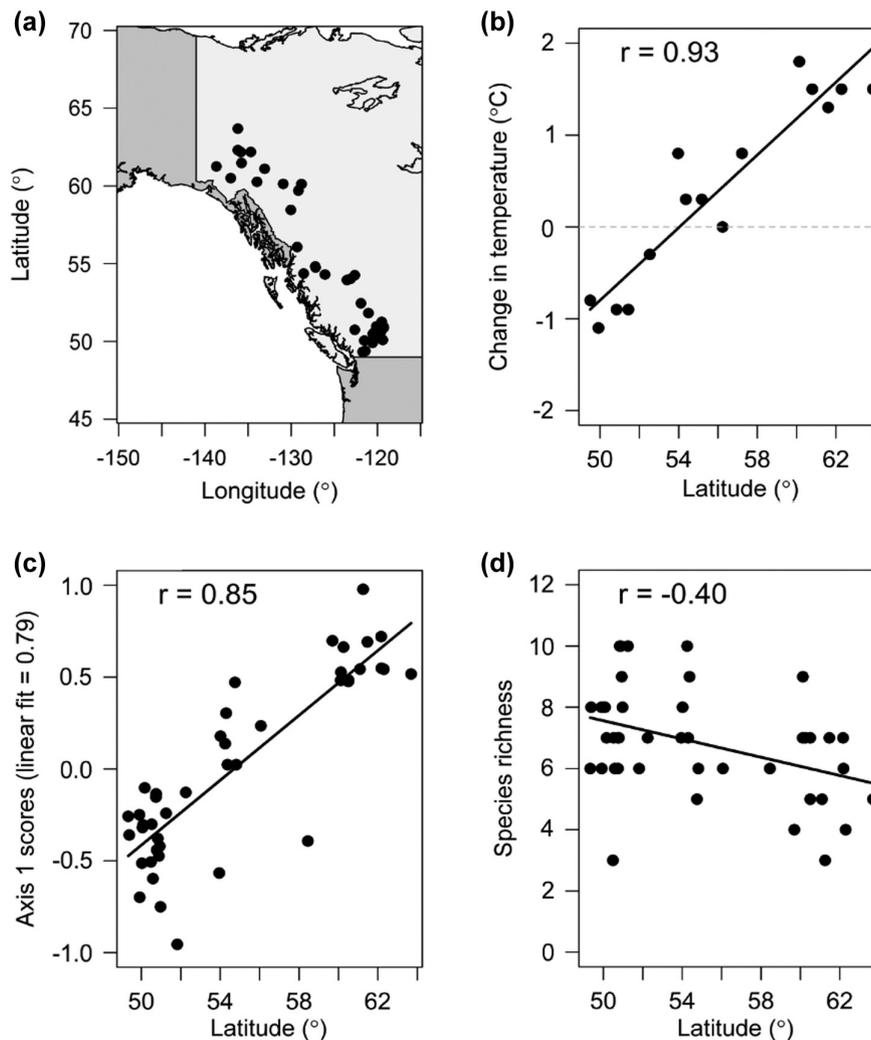


Figure 1. Latitudinal patterns of diversity and temperature change. (a) Locations of the 43 lakes used in this study; (b) the change in air temperature over 70 years, based on differences (present – past) of 30 years means: 1971 to 2000 – 1901 to 1930; (c) species composition of zooplankton (first axis from a nonmetric multidimensional scaling with a 2D solution [stress=0.19] based on Sorenson dissimilarity), illustrating that closer sites are more compositionally similar; and (d) zooplankton species richness with latitude. Data used in (c) and (d) pooled species in historic and current samples for each lake. Lines display the model fit if the relationship was significant at  $\alpha = 0.05$ .

## Material and methods

### Study system and species sampling

This study was conducted in freshwater lakes across a ~1800 km latitudinal gradient in Canada, ranging from southern British Columbia to the middle of the Yukon Territory (Fig. 1a). Long-term temperature averages indicate there is a positive relationship between latitude and the magnitude of temperature warming across our study sites over 70 years (early to late 1900s that encompassed much of the period between sampling periods; Fig. 1b). Lakes that are closer together have more species in common (Fig. 1c) and species richness declines at higher latitudes (Fig. 1d).

Using data from Patalas et al. (1994), we systematically selected 43 lakes that were originally sampled between 1939–1986 (details on how we accounted for differences in time between historic and contemporary samples are given in the Data analysis section). We chose lakes that spanned the latitudinal gradient and had similar levels of known environmental variables (phosphorus, nitrogen, turbidity, etc.), such that there were no relationships between environmental variables and latitude (following Jones and Gilbert 2016, Supplementary material Appendix 1 Fig. A1). All lakes sampled contain fish, because fish are important predators of zooplankton that alter the size structure of those communities (Symons and Shurin 2016). We followed the original collection methods of Anderson (1974), Lindsey et al. (1981) and Patalas et al. (1994), and sampled in the same season (4 July – 28 July 2011, Supplementary material Appendix 1 Table A1). To control for any confounding effects of species succession throughout the growing season, we began sampling in the southern portion of the latitudinal gradient, sampling some lakes as we moved north along the transect, and others as we returned south. Plankton communities were collected by hauling a Wisconsin net (mouth diameter 24 cm, net mesh 76  $\mu\text{m}$ ) through the water column, beginning from near the lake bottom, at the approximate center of each lake. Two vertical tows per lake were taken and zooplankton were immediately preserved in 70% ethanol.

We combined the two replicate tows and haphazardly took 1 ml subsamples, identifying zooplankton following the taxonomy of Thorp and Covich (2010), Sandercock and Scudder (1994) and additional keys as needed, until we had identified at least 500 adult individuals. We also scanned samples to capture rare species. Of the zooplankton, 80% were identified to the species level. Some morphologically similar species could not be differentiated (e.g. *Bosmina longirostris* versus *Eubosmina longirostris*); in those cases, we decreased the taxonomic resolution to the generic or family level (5/25 species, e.g. *Bosmina*). Critically, lumping morphologically similar species is unlikely to bias our results because we used the same approach for all lakes, regardless of their latitudinal origin, and there were species that could not be identified to the species level across the latitudinal gradient we sampled. Moreover, if multiple species within a genera were present, we would not include an unknown from the same genera as

this could inflate estimates of community change (i.e. *Daphnia* sp. was only included if there were no other Daphniids identified to the species level in that lake). This resulted in a consolidated species list, with 25 taxa (species/genera), making our estimate of turnover relatively conservative. For simplicity we refer to each grouping as a ‘species’ throughout the manuscript. We categorized species reproductive mode based on their taxonomic affiliation; copepod reproduction is obligately sexual, while cladocerans are facultatively parthenogenic.

We measured the body size of the first 30 adults of each species for a subset of 19 lakes across the latitudinal gradient. Body size of cladocera was measured from the centre of the eye to the base of the tail spine (Gliwicz 1990, Yurista and O’Brien 2001), while we measured the length of the prosome for copepods (Breteler and Gonzalez 1988, Ban 1994). The historical relative abundance of zooplankton species was available for 31 lakes. We estimated local abundance by averaging the abundance of each species across all the lakes they were present in the historical sampling dataset (Anderson 1974, Lindsey et al. 1981, Patalas 1990). In total, we had both body size and local abundance estimates for 14 species (Supplementary material Appendix 1 Table A2). Finally, we determined historic occupancy for each species (hereafter simply ‘occupancy’) as the proportion of lakes historically occupied relative to all the lakes that fall within the latitudinal range of that species (see range explanation in description of colonization below).

We selected lakes to minimize differences in local abiotic factors, which can also impact diversity patterns (Dodson 1992, Hessen et al. 2006), so that differences in community composition could be attributed primarily to latitude, but because this study considers natural lakes, there is some variation in environmental conditions (Supplementary material Appendix 1 Fig. A2). We quantified chlorophyll a (a measure of productivity) measurements mid-lake using a YSI 6-series multiparameter water quality sonde (Integrated Systems and Services). We used published estimates of elevation lake size and depth from the literature (Anderson 1974, Lindsey et al. 1981).

### Data analysis

To test how zooplankton communities have changed since the historical survey, we transformed the zooplankton species abundance matrix into a presence–absence data matrix for both time periods, then calculated two measure of community change: the total change in species richness and the Sorenson dissimilarity. This was accomplished for all metrics by separating copepods and cladocerans, then developing a single measure for each lake (i.e. species richness in resurvey – species richness in historical sample in each lake, and Sorenson distance between resurvey and historical sample for each lake). We further partitioned Sorenson dissimilarity into its two components of turnover: nestedness and replacement. Nestedness quantifies the fraction of turnover that is due to

the addition or loss of species, where the historical sample is a subset of the contemporary sample. Replacement quantifies the component of turnover that is due to the addition of new species and the loss of previous species across the latitudinal gradient we sampled, i.e. the degree to which species are 'replaced' by new colonizers. Because we observed heterogeneity in variance, we used generalized least squares (GLS) with the weights function (varExp with weights changing by latitude) in the nlme package in R (<[www.r-project.org](http://www.r-project.org)>, Pinheiro et al. 2016) to determine how the total change in species richness and Sorensen dissimilarity (and its nestedness and replacement components) changed across a latitudinal gradient and if these patterns differ between copepods and cladocerans. We first accounted for changes to community composition that could be related to time since the historic sample, as not all historic samples were collected in the same year. We considered the effects of time in two ways. First, we verified that there is no latitudinal bias in sampling date by testing for a correlation between sampling date and latitude and, second, we accounted for differences in time between historic and contemporary samples by including historic sampling date as a covariate in community-level models. There was no correlation between sampling date and latitude (Supplementary material Appendix 1 Fig. A3), and the inclusion of time did not significantly improve model fits, except in the replacement analysis (Supplementary material Appendix 1 Table A3, Fig. A4); however, we included time in all final models because of the known species–time relationship (Adler and Lauenroth 2003).

Next, we determined how colonization and local extinction contributed to different components of turnover. We define colonization in a lake as the proportion of species in the contemporary survey that were not present in the historic survey, and extinction as the proportion of species present in the historic survey that were absent in the contemporary survey. This approach allowed us to account for differences in the species richness among the lakes, which showed a latitudinal trend (Fig. 1d, Supplementary material Appendix 1 Fig. A1).

To account for seasonal succession in zooplankton taxa during the summer growing season we analyzed all data as presence–absence data to ensure that differences in peak abundance did not influence our estimates of compositional change (Jackson and Harvey 1997). Latitudinal variation in colonization and extinction was analyzed with a generalized linear model (GLM) using a quasibinomial error distribution to account for over-dispersion in variance and a logit link function. For eight lakes we had 2–3 historical samples; all samples for each lake were included in the analysis (Supplementary material Appendix 1 Table A1) and, to account for non-independence among samples from the same lake, the lake was included as a random effect. For these analyses, the response variables were colonization frequency and local extinction frequency and the explanatory fixed effects were latitude, taxa (copepod or cladoceran) and years between samples.

We determined how body size, local abundance and occupancy influenced colonization and extinction. In this case, the denominator for colonization and extinction were calculated for each species. For colonization, we extracted the latitudinal range of each species from Patalas (1994) and created a potential colonization data-frame by summing the number of times a species was not historically present in a lake that occurs within the maximum and minimum latitudinal distribution of that species – colonization was defined as the proportion of these potential lakes that were colonized in the contemporary sample. Occupancy was defined as the proportion of lakes within a species' latitudinal distribution where it was found in the historical sample. Extinction was calculated as the proportion of lakes where a species was present in the historical sample and absent in the contemporary sample. Both colonization and extinction were analysed using GLM's with a quasibinomial error distribution to account for over-dispersion. We conducted separate analyses to test whether body size and local abundance changed predictably with latitude and to test for a correlation between occupancy and local abundance. Because we only had body size estimates for four species of copepods, we did not formally test how reproductive life history influences these relationships.

Finally, we used linear mixed models to confirm that patterns in temporal turnover were not driven by four environmental factors that can also impact diversity patterns: elevation, lake size, lake depth and a measure of productivity (chlorophyll a) (Hessen et al. 2006).

## Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.1411n>> (Jones and Gilbert 2017).

## Results

We found a significant effect of latitude on turnover; the change in species richness of cladocerans (Fig. 2a; Latitude  $\times$  Taxa interaction,  $p=0.044$ ) declined northward along the latitudinal gradient and, thus, Sorensen distance also declined with latitude, but in this case for both copepod and cladoceran communities (Fig. 2b; Taxa,  $p=0.001$ ; Latitude,  $p=0.064$ ; Supplementary material Appendix 1 Table A3). When turnover was partitioned into nestedness and replacement, we found that nestedness, not replacement, drove this latitudinal decline (Fig. 2c; Latitude,  $p=0.021$ ; Fig. 2d; Supplementary material Appendix 1 Table A3), but that consistent with the species–time relationship, species were being replaced as time since the original sample was collected increased (Supplementary material Appendix 1 Fig. A4,  $p=0.024$ ). That is species turnover at low latitude sites was the consequence of new species being present in low latitude contemporary sites. We confirmed this result by

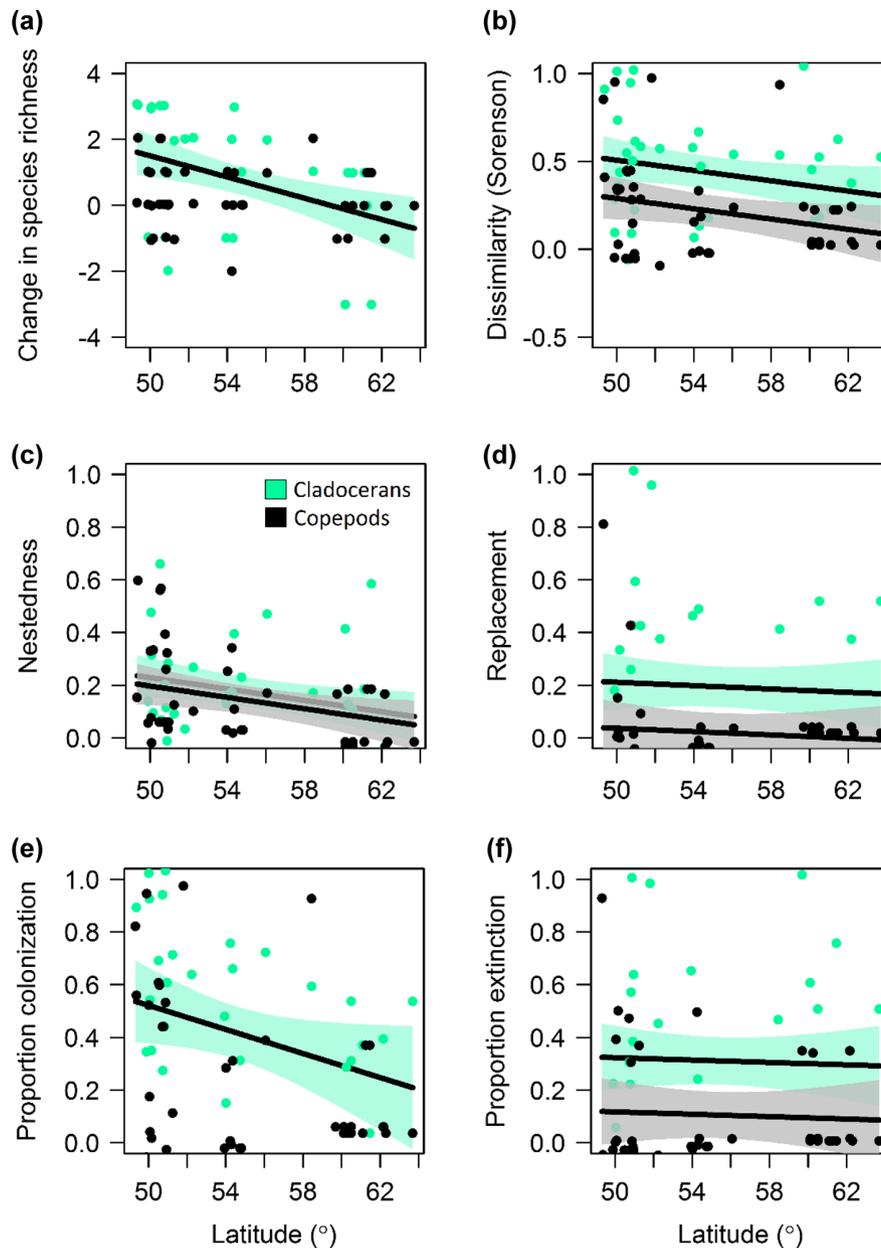


Figure 2. Species temporal turnover with latitude. The relationship between latitude and (a) the change in species richness, (b) Sorensen dissimilarity metric, (c) nestedness, (d) replacement, (e) the proportion of new species per lake, and (f) the proportion of species that went locally extinct. All graphs compare historic zooplankton samples with contemporary samples (temporal turnover), with the total number of species summed for the eight lakes that had more than one historical sample if applicable (see methods). In (e) colonization = the number of species that colonized the lake / the contemporary species richness. In (f), extinction = the number of species that were locally extirpated / the historical species richness. Lines display the model fit if the relationship was significant (latitude, taxon or their interaction) at  $\alpha < 0.05$ . Shaded areas display 95% confidence intervals. The statistical tests for (a–d) were done using generalised least squares to account for error heteroscedasticity, while a generalised linear model with a quasibinomial error distribution was used for (e) and (f).

isolating patterns of species gains and losses across the latitudinal gradient and found that colonization in the southern portion of the latitudinal gradient by cladocerans was significantly higher (Fig. 2e,  $p=0.001$ ) and no latitudinal pattern for local extinction rates (Fig. 2f,  $p=0.576$ ). Body size, local abundance and regional occupancy influenced the frequency of colonization and local extinction among species, but in

different ways (Supplementary material Appendix 1 Table A4, Fig. 3). Colonization rates were highest for species that had high occupancy historically (Fig. 3c;  $p=0.03$ ), and tended to be higher for small-bodied zooplankton (Fig. 3a;  $p=0.051$ ), and species with high local abundance (Fig. 3b;  $p=0.061$ ). Body size had no relationship with local extinction rates (Fig. 3d;  $p=0.38$ ). However, locally abundant species and

those with high historical occupancy were extirpated less often (Fig. 3e,  $p=0.003$ ; Fig. 3f,  $p<0.0001$ ). Unfortunately, low species richness estimates of copepods ( $n=4$ ) precluded us from formally testing if the relationship between body size, abundance and occupancy differed between copepods and cladocerans.

We tested for a correlation among species attributes (body size, local abundance and occupancy) and between these attributes and latitude to determine whether any correlations were influencing latitudinal trends. We detected no correlation between body size and local abundance (Pearson correlation test,  $r=0.17$ ,  $p=0.52$ ; Supplementary material Appendix 1 Fig. A5), suggesting that, for this group of aquatic zooplankton, larger bodied species do not have larger population sizes on average. There was, however, a strong relationship between occupancy and local abundance of species ( $r=0.70$ ,  $p=0.002$ ; Supplementary material Appendix 1 Fig. A6). The average body size of crustacean zooplankton communities did not change across a latitudinal gradient (Supplementary material Appendix 1 Fig. A7a;  $p=0.60$ ),

and there was no relationship between average local abundance and latitude (Supplementary material Appendix 1 Fig. A7b;  $p=0.60$ ). Overall, these relationships show that species traits influence colonization and extinction rates independent of latitude, and suggest that local abundance or regional occupancy reflect a common suite of species traits that influence colonization and extinction rates.

To ensure that our selection of lake environments (other than temperature) was successful, we tested the relationship between community change and elevation, lake size, maximum lake depth and productivity. None of these were significant (all  $p > 0.05$ , Supplementary material Appendix 1 Table A5).

## Discussion

Our study finds an inconsistency between temperature change and species turnover, and highlights how considering colonization and extinction leads to a richer understanding

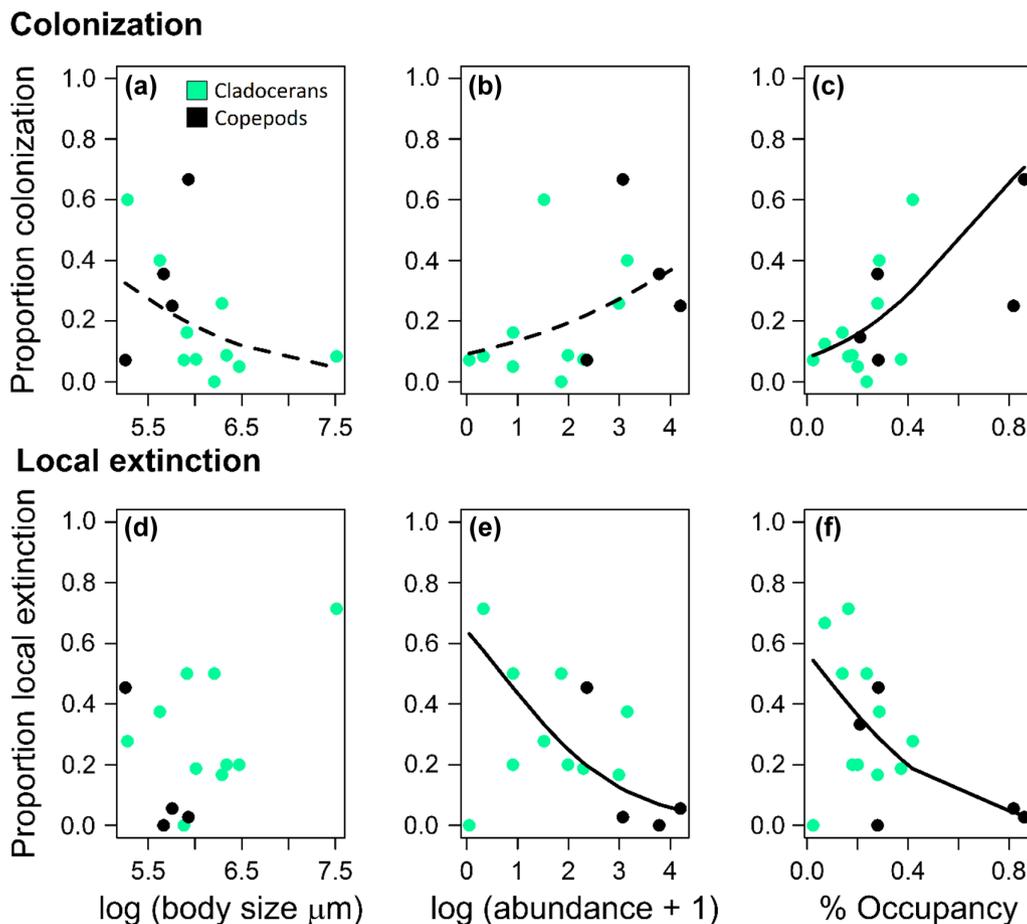


Figure 3. Species traits influence colonization and extinction rates. The relationship between colonization and (a) zooplankton body size, (b) local abundance, and (c) occupancy. (d–f): the relationship between extinction and (d) zooplankton body size, (e) local abundance, and (f) occupancy. Local abundance is a species' mean abundance when present, and occupancy is the proportion of lakes that a species historically occupied within its latitudinal range. Lines display the model fit if the relationship was significant (solid lines;  $p < 0.05$ ) or marginal (hashed lines;  $0.05 < p < 0.10$ ).

of the causes of latitudinal gradients in species turnover. We found that higher latitudes had lower turnover (Fig. 2), a trend that has been observed in shorter-duration studies across latitudinal gradients (Shurin et al. 2007, Korhonen et al. 2010, but see Soininen et al. 2004). However, by decomposing turnover into nestedness and replacement, we were able to show that species are being replaced over time, as predicted by the species–time relationship (Adler and Lauenroth 2003), and attribute the spatial signature in compositional change to elevated colonization events in the southern portion of the latitudinal gradient. These results are consistent with recent work that demonstrated reproductive life history influences macroecological patterns in that facultatively parthenogenic cladocerans had higher colonization rates (Henriques-Silva et al. 2016). Moreover, our results suggest that species-specific patterns of turnover can be partially explained by ecologically important species attributes: body size, local abundance and regional occupancy. Together, these biogeographical and species-specific perspectives on colonization and extinction provide insights into the directions and rates of change in ecological communities across latitudes.

The latitudinal patterns of colonization and extinction that we document in this study may be important for understanding how climate influences community changes more generally. Although arctic and subarctic lakes are often considered to be “sentinels of climate change” (Adrian et al. 2009), our results did not support the hypothesis that communities in high latitude lakes are more likely to show compositional shifts (Fig. 2). This result was surprising, given that these lakes have experienced larger changes in temperature (Fig. 1b), and support less diverse assemblages of species (Fig. 1d). The apparent compositional stability of subarctic zooplankton communities through time may arise from several factors that together slow change in high latitude communities. First, relatively extreme seasonal fluctuations in environmental conditions may prevent new species from colonizing those sites directly by causing a higher variation in population growth rates (Lande 1988) and by creating a shorter seasonal window in which colonization is possible. Second, shorter growing seasons may slow absolute population growth over the season, again increasing chances of stochastic extinction in newly establishing species or generating longer lags between colonization of sites and detection of species in high latitude lakes. Third, many zooplankton have long-lived dormant stages, which may buffer species from extinction across the latitudinal gradient (Jones and Gilbert 2016). Finally, these lakes thermally stratify in the summer months, but zooplankton species are distributed throughout the water column in the pelagic zone. Zooplankton may avoid extreme fluctuations by capitalizing on refugia below the thermocline, where cool waters persist throughout the summer months.

Instead of greater species turnover in northern lakes, our study shows a clear pattern of higher colonization in southern lakes. Interestingly, this increase arose without the addition of new species to the study area, and thus suggests that

lakes were either in disequilibrium in early surveys, or that the non-equilibrium dynamics observed have resulted from increased rates of colonization between surveys (~50 years). Cladocerans had a higher incidence of colonization, suggesting that because they do not suffer from mate limitation they establish at a greater rate than sexual species. Although we cannot isolate the causal mechanism driving this pattern, the association between latitude and colonization events may reflect an increase in connectivity in lower latitude lakes. The southern portion of the latitudinal gradient in our study occurs in regions with relatively high anthropogenic influences, such as higher road density (Ministry of Forests Mines and Lands 2010) and larger human populations (Gayton 2007). As a result, dispersal limitation may be relaxed in those areas due to inadvertent movement via boats and bait fish with water (Kelly et al. 2012), facilitating the introduction of zooplankton into new lakes. An increase in diversity is predicted by metapopulation and island biogeography theory in such cases, so long as local abiotic and biotic conditions do not prevent recruitment (Shurin 2000). The geographic distribution of many passively dispersed aquatic invertebrates is limited by dispersal (Bohonak and Jenkins 2003), therefore altered connectivity among lakes may be an important component of the anthropocene, altering the diversity of local communities.

By linking body size, local abundance and regional occupancy to colonization and extinction dynamics, our results illustrate how trait-based approaches are useful for predicting turnover and metacommunity dynamics (De Bie et al. 2012, Jones et al. 2015). Body size is important for passively dispersed organisms, and our results support previous work which has shown that for passive organisms, larger individuals tend to colonize fewer sites (but see Louette and De Meester 2005). This is in contrast to active dispersers, where larger individuals normally sequester more resources and disperse farther (Shurin et al. 2009). The observation that temperature increases during the last 100 years has caused a reduction in the average body size of many organisms (Daufresne et al. 2009) raises the intriguing possibility that the direct effect of temperature on body size could indirectly increase dispersal rates for passively dispersed species.

Our results also support a growing number of studies that show a positive association between local abundance and occupancy (Soininen and Heino 2005, but see Thompson et al. 1998). A number of mechanisms have been put forth to explain why this pattern persists across distantly related species (reviewed by Gaston et al. 2000). Although no single mechanism has emerged as the sole explanation for this pattern, the association between regional occupancy and colonization–extinction dynamics has important implications for predicting species range expansion and extinction. Specifically, if the proportion of inhabitable lakes a species occurs in is known, detailed abundance data may be unnecessary to estimate how vulnerable that species is to local extinction or the likelihood that it will colonize new lakes (Gaston et al. 2000).

An important question for communities facing global changes is whether patterns of diversity are at an equilibrium or, alternately, if they are shifting over time (Nuvoloni et al. 2016). When communities and species' are at equilibrium in a landscape, both are expected to show equal rates of colonization and extinction on average. Our results highlight two important non-equilibrium trends that are shifting lake communities. First, non-equilibrium dynamics in southern communities are causing an increase in diversity, whereas more northern communities appear to be in equilibrium in terms of species richness (Fig. 2a). Interestingly, many studies of turnover do not explicitly consider non-equilibrium colonization–extinction dynamics as drivers of turnover (but see Matthews and Pomati 2012, Nuvoloni et al. 2016). Second, we observed different non-equilibrium dynamics among species, with these dynamics predicted by species traits (Fig. 3). These trends suggest that relatively small, and locally abundant species that are widespread are becoming even more common. For example, *Bosmina* sp. is the second smallest species we considered and its colonization to extinction ratio was 3:1, having successfully colonized 15 sites while being extirpated from five sites (Supplementary material Appendix 1 Table A2). On the other hand, species with low abundance are disappearing from lakes at a greater rate than they are establishing elsewhere. *Daphnia galeata* is one relatively large, low abundance species that colonized two lakes but was extirpated from three lakes over the same period. In other words, these species-level non-equilibrium dynamics suggest that conditions over the past several decades are causing directional shifts in the traits of species by favouring small, common species to a greater degree than they were historically favoured.

The differences in community change across latitude that we observed suggest that space-for-time substitutions are inappropriate for predicting changes with climate in temperate and northern aquatic communities. Space-for-time substitution is often used to replace temporal replication and can be a powerful tool for predicting community and population level responses to climate change (Dunne et al. 2004, Blois et al. 2013). However, smaller changes in northern lakes relative to southern lakes, despite greater temperature change in the north, indicates that temperature alone is a poor predictor of changes to community composition, at least for lakes over the timescale of this study (approximately 50 years). Regardless of whether these differences are mainly due to larger anthropogenic influences in temperate lakes, higher seasonal variation in northern lakes, or other mechanisms, failing to incorporate this greater complexity into climate change studies will lead to erroneous predictions for biological communities (Jones and Gilbert 2016).

In conclusion, by decoupling community responses across a latitudinal gradient, we could demonstrate colonization and extinction dynamics that depend on geographic location and species attributes. Lakes are particularly vulnerable to the effects of global change because they are naturally fragmented and often heavily exploited (Woodward 2009). By testing

species-level changes within lake communities across an 1800 km gradient, we could refute the hypothesis that high latitude aquatic zooplankton communities exposed to greater temperature increases will change at a faster rate. Our evidence that species attributes, such as reproductive mode, body size and local abundance, predict colonization and extinction rates also highlight a systematic shift in the distribution of these attributes within communities. These results provide a first step towards informing ecologists about species turnover across latitudes and within communities, and offer new insights into the proximate drivers of this turnover.

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## References

- Adler, P. B. and Lauenroth, W. K. 2003. The power of time: spatiotemporal scaling of species diversity. – *Ecol. Lett.* 6: 749–756.
- Adrian, R. et al. 2009. Lakes as sentinels of climate change. – *Limnol. Oceanogr.* 54: 2283–2297.
- Anderson, R. S. 1974. Crustacean plankton communities of 340 lakes and ponds in and near the National Parks of the Canadian Rocky Mountains. – *J. Fish. Res. Board Can.* 31: 855–869.
- Anderson, K. J. 2007. Temporal patterns in rates of community change during succession. – *Am. Nat.* 169: 780–793.
- Baker, H. G. 1955. Self-compatibility and establishment after “long-distance” dispersal. – *Evolution* 9: 347–349.
- Ban, S. H. 1994. Effect of temperature and food concentration on postembryonic development, egg-production and adult body-size of calanoid copepod *Eurytemora affinis*. – *J. Plankton Res.* 16: 721–735.
- Bennett, J. R. et al. 2010. Broad-scale environmental response and niche conservatism in lacustrine diatom communities. – *Global Ecol. Biogeogr.* 19: 724–732.
- Blois, J. L. et al. 2013. Space can substitute for time in predicting climate-change effects on biodiversity. – *Proc. Natl Acad. Sci. USA* 110: 9374–9379.
- Bohonak, A. J. and Jenkins, D. G. 2003. Ecological and evolutionary significance of dispersal by freshwater invertebrates. – *Ecol. Lett.* 6: 783–796.
- Breteler, W. C. M. K. and Gonzalez, S. R. 1988. Influence of temperature and food concentration on body size, weight and lipid content of two Calanoid copepod species. – *Hydrobiologia* 167–168: 201–210.
- Burrows, M. T. et al. 2014. Geographical limits to species-range shifts are suggested by climate velocity. – *Nature* 507: 492–495.
- Carpenter, S. R. et al. 2009. *The Princeton guide to ecology*. – Princeton Univ. Press.
- Chen, I. C. et al. 2011. Rapid range shifts of species associated with high levels of climate warming. – *Science* 333: 1024–1026.

- Daufresne, M. et al. 2009. Global warming benefits the small in aquatic ecosystems. – *Proc. Natl Acad. Sci. USA* 106: 12788–12793.
- De Bie, T. et al. 2012. Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. – *Ecol. Lett.* 15: 740–747.
- Dodson, S. 1992. Predicting crustacean zooplankton species richness. – *Limnol. Oceanogr.* 37: 848–856.
- Dodson, S. I. and Brooks, J. L. 1965. Predation, body size, and composition of plankton. – *Science* 150: 28–35.
- Dunne, J. A. et al. 2004. Integrating experimental and gradient methods in ecological climate change research. – *Ecology* 85: 904–916.
- Elton, C. S. 1958. *The ecology of invasions by animals and plants.* – Methuen.
- Environment Canada 2014. Canadian climate normals 1971–2000 for Kamloops, British Columbia. – *Natl Clim. Data Inf. Arch.*
- Gaston, K. J. et al. 2000. Abundance–occupancy relationships. – *J. Appl. Ecol.* 37: 39–59.
- Gayton, D. 2007. Major impacts to biodiversity in British Columbia (excluding climate change). – *Biodiversity BC Steering Committee.*
- Gliwicz, Z. M. 1990. Food thresholds and body size in cladocerans. – *Nature* 343: 638–640.
- Hanski, I. 1994. A practical model of metapopulation dynamics. – *J. Anim. Ecol.* 63: 151–162.
- Hanski, I. et al. 1993. Three explanations of the positive relationship between distribution and abundance of species. – In: Ricklefs, R. and Schluter, D. (eds), *Species diversity in ecological communities: historical and geographical perspectives.* Univ. of Chicago Press, pp. 132–148.
- Helmus, M. R. et al. 2014. Island biogeography of the Anthropocene. – *Nature* 513: 543–546.
- Henriques-Silva, R. et al. 2016. Climate, history and life-history strategies interact in explaining differential macroecological patterns in freshwater zooplankton. – *Global Ecol. Biogeogr.* 25: 1454–1465.
- Hessen, D. O. et al. 2006. Extrinsic and intrinsic controls of zooplankton diversity in lakes. – *Ecology* 87: 433–443.
- IPCC 2013. *The physical science basis. Contrib. Working Grp I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* – Cambridge Univ. Press.
- Jackson, D. A. and Harvey, H. H. 1997. Qualitative and quantitative sampling of lake fish communities. – *Can. J. Fish Aquat. Sci.* 54: 2807–2813.
- James, F. C. 1970. Geographic size variation in birds and its relationship to climate. – *Ecology* 51: 365–390.
- Jones, N. T. and Gilbert, B. 2016. Changing climate cues differentially alter zooplankton dormancy dynamics across latitudes. – *J. Anim. Ecol.* 85: 559–569.
- Jones, N. T. and Gilbert, B. 2017. Data from: Geographic signatures in species turnover: decoupling colonization and extinction across a latitudinal gradient. – *Dryad Digital Repository*, <<http://dx.doi.org/10.5061/dryad.1411n>>.
- Jones, N. T. et al. 2015. Dispersal mode mediates the effect of patch size and patch connectivity on metacommunity diversity. – *J. Ecol.* 103: 936–944.
- Kelly, N. E. et al. 2012. Recreational boats as a vector of secondary spread for aquatic invasive species and native crustacean zooplankton. – *Biol. Invas.* 15: 509–519.
- Korhonen, J. J. et al. 2010. A quantitative analysis of temporal turnover in aquatic species assemblages across ecosystems. – *Ecology* 91: 508–517.
- Kramer, A. M. et al. 2008. Allee effect limits colonization success of sexually reproducing zooplankton. – *Ecology* 89: 2760–2769.
- Lande, R. 1988. Genetics and demography in biological conservation. – *Science* 241: 1455–1460.
- Leibold, M. A. et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. – *Ecol. Lett.* 7: 601–613.
- Lindsey, C. C. et al. 1981. Glaciation and the physical, chemical, and biological limnology of Yukon lakes. – *Can. Tech. Rep. Fish. Aquat. Sci.* 996: 1–37.
- Louette, G. and De Meester, L. 2005. High dispersal capacity of cladoceran zooplankton in newly founded communities. – *Ecology* 86: 353–359.
- MacArthur, R. H. and Wilson, E. O. 1967. *The theory of island biogeography.* – Princeton Univ. Press.
- Matthews, B. and Pomati, F. 2012. Reversal in the relationship between species richness and turnover in a phytoplankton community. – *Ecology* 93: 2435–2447.
- May, R. M. 1973. Stability and complexity in model ecosystems. – *Monogr. Popul. Biol.* 6: 1–235.
- McCann, K. et al. 1998. Weak trophic interactions and the balance of nature. – *Nature* 395: 794–798.
- Ministry of Forests Mines and Lands 2010. *The State of British Columbia's Forests*, 3rd edn. – Ministry of Forests Mines and Lands, British Columbia, Canada
- Nuvoloni, F. M. et al. 2016. Species turnover through time: colonization and extinction dynamics across metacommunities. – *Am. Nat.* 187: 786–796.
- Parnes, C. 2006. Ecological and evolutionary responses to recent climate change. – *Annu. Rev. Ecol. Evol. Syst.* 37: 637–669.
- Patalas, K. 1990. Diversity of zooplankton communities in Canadian lakes as a function of climate. – *Verh. Intern. Verein Limnol.* 24: 360–368.
- Patalas, K. et al. 1994. Planktonic crustaceans in lakes of Canada (distribution of species, bibliography). – *Can. Tech. Rep. Fish. Aquat. Sci.* 154.
- Pinheiro, J. et al. 2016. nlme: linear and nonlinear mixed effects models. – R package ver. 3.1-126.
- Rosenzweig, M. L. 1998. Preston's ergodic conjecture: the accumulation of species in space and time. – In: McKinney, M. L. and Drake, J. A. (eds), *Biodiversity dynamics turnover of populations taxa and communities.* Columbia Univ. Press, pp. 311–348.
- Sandercock, G. A. and Scudder, G. G. 1994. *An introduction and key to the freshwater calanoid copepods (crustacea) of British Columbia.* – Dept. of Zool., Univ. of British Columbia, Vancouver, BC, Canada.
- Savage, V. M. et al. 2004. Effects of body size and temperature on population growth. – *Am. Nat.* 163: 429–441.
- Shelomi, M. 2012. Where are we now? Bergmann's rule sensu lato in insects. – *Am. Nat.* 180: 511–519.
- Shurin, J. B. 2000. Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. – *Ecology* 81: 3074–3086.
- Shurin, J. B. et al. 2007. Diversity–stability relationship varies with latitude in zooplankton. – *Ecol. Lett.* 10: 127–134.

- Shurin, J. B. et al. 2009. Spatial autocorrelation and dispersal limitation in freshwater organisms. – *Oecologia* 159: 151–159.
- Smol, J. P. et al. 2005. Climate-driven regime shifts in the biological communities of arctic lakes. – *Proc. Natl Acad. Sci. USA* 102: 4397–4402.
- Soininen, J. and Heino, J. 2005. Relationships between local population persistence, local abundance and regional occupancy of species: distribution patterns of diatoms in boreal streams. – *J. Biogeogr.* 32: 1971–1978.
- Soininen, J. et al. 2004. Benthic diatom communities in boreal streams: community structure in relation to environmental and spatial gradients. – *Ecography* 27: 330–342.
- Soons, M. B. et al. 2008. Small seed size increases the potential for dispersal of wetland plants by ducks. – *J. Ecol.* 96: 619–627.
- Symons, C. C. and Shurin, J. B. 2016. Climate constrains lake community and ecosystem responses to introduced predators. – *Proc. R. Soc. B* 283: 20160825.
- Thompson, K. et al. 1998. Abundance–range size relationships in the herbaceous flora of central England. – *J. Ecol.* 86: 439–448.
- Thorp, J. H. and Covich, A. P. 2010. Ecology and classification of North American freshwater invertebrates. – Elsevier.
- Tonkin, J. D. et al. 2017. Seasonality and predictability shape temporal species diversity. – *Ecology* 98: 1201–1216.
- Vanschoenwinkel, B. et al. 2008. Any way the wind blows – frequent wind dispersal drives species sorting in ephemeral aquatic communities. – *Oikos* 117: 125–134.
- Viana, D. S. et al. 2016. Assembly mechanisms determining high species turnover in aquatic communities over regional and continental scales. – *Ecography* 39: 281–288.
- Wolkovich, E. M. et al. 2014. Temporal ecology in the Anthropocene. – *Ecol. Lett.* 17: 1365–1379.
- Woodward, G. 2009. Biodiversity, ecosystem functioning and food webs in fresh waters: assembling the jigsaw puzzle. – *Freshwater Biol.* 54: 2171–2187.
- Woodward, G. et al. 2005. Body size in ecological networks. – *Trends Ecol. Evol.* 20: 402–409.
- Yurista, M. and Brien, W. J. O. 2001. Growth, survivorship and reproduction of *Daphnia middendorffiana* in several Arctic lakes and ponds. – *J. Plankton Res* 23: 733–744.

Supplementary material (available online as Appendix oik-04590 at <[www.oikosjournal.org/appendix/oik-04590](http://www.oikosjournal.org/appendix/oik-04590)>). Appendix 1.