# *Structural change metrics as indicators of chironomid community stability in high latitude lakes*

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# Abstract

Understanding the effects of climate change on ecosystem structure and stability is challenging, especially in high latitude regions that are predicted to experience the largest increases in ambient temperature. Global warming is likely to be a key driver of ecosystem change in freshwater lakes. Increased temperature can positively or negatively affect lake community composition through the loss of cold-adapted taxa and the arrival of temperate or eurytopic taxa. Here, we analyse the likely effects of temperature-induced changes in taxonomic richness and compositional turnover of environmentally-sensitive chironomids (Diptera: Chironomidae) across three regions - northern North America, Norway, and Russia - using existing datasets. Structural parameters (beta diversity, compositional disorder, and network skewness) were applied to model-simulated and empirical chironomid datasets across a large spatial temperature gradient. The analyses of empirical datasets showed changes in community structure across temperature gradients, suggesting varying states of ecosystem stability or instability. The comparison with null models enabled assessment as to whether these stresses agreed with expected patterns due to covarying summer temperature conditions or whether they deviated from expectations suggesting additional stress on the ecosystems. For the North American and Norwegian datasets, the structural parameters indicated signs of anticipated stress at the coldest end of the temperature gradient and additional stress at the warmest end of the temperature gradient. For the Russian dataset, the ecological metrics were less indicative of stress at the extreme ends of the temperature gradient. For all three regions, lakes in the mid-temperature range showed most evidence of relative ecosystem stability, with greater beta diversity, compositional disorder, and skewness, unanticipated by the modelled simulations. This is most likely due to more diverse habitats across the ecotone boundaries and additional factors that can influence ecosystem structures. Thus, we show that structural changes typical for ecosystem stability can be detected through changes in community structure across temperature gradients. This is important for understanding how lakes may change under current and future climate change.

**Key words:** Chironomids, community structure, beta diversity, compositional disorder, network skewness

# Introduction

High latitude lake ecosystems have already been exposed to global stress, with recent warming driving chironomid- and diatom-assemblage change and green-algae blooms in Arctic lakes (Smol *et al.*, 2005; Rühland *et al.*, 2013; Woelders *et al.*, 2018). Current predictions show that high latitude regions will likely undergo an exaggerated level of warming due to polar amplification processes (Overpeck *et al.*, 1997; Post *et al.*, 2009; Pithan and Mauritsen, 2014). While lakes are frequently subjected to many interacting stressors (Christensen *et al.*, 2006; Yan *et al.*, 2008), it is thought that climate change is one of the most likely drivers of nonlinear responses and abrupt transitions in ecosystems (Grimm *et al.*, 2013). Lakes facing continuous stress may increasingly lose resilience until they are unable to sustain their current ecosystem function (Scheffer *et al.*, 2012) or transition into an alternate state (Wang *et al.*, 2012). Understanding how lake ecosystems respond to increasing climate stress is a complex issue, yet is critical to forecasts of ecosystem trajectory and for predicting the vulnerability of lake ecosystems to abrupt ecological transitions.

Previous studies have predominantly investigated ecosystem stability in the frequency domain using time-series data, an approach that identifies fundamental shifts from one community state to another over time (Wang *et al.*, 2012; Dakos *et al.*, 2014; Holbrook *et al.*, 2016). However, this requires long and detailed records, which can be difficult and expensive to obtain. Early warning signs (EWS) of ecosystem collapse have been identified through studies of variability in laboratory-controlled (Drake and Griffen, 2010), whole lake (Carpenter *et al.*, 2011), and computer simulated experiments (Dakos *et al.*, 2013). However, attempts to detect similar EWS in natural, real-world ecosystems have proved challenging. The frequency domain presents many issues, for example in data resolution (Wang *et al.*, 2012), transitions with no EWS (Hastings and Wysham, 2010), and false-negative or false-positive EWS (Kéfi *et al.*, 2013; Burthe *et al.*, 2016).

The structural domain could provide greater potential for understanding how stress drives ecosystem structural changes as theory suggests that ecosystem resilience is strongly influenced by the structural changes in species associations (Strogatz, 2001; Scheffer *et al.*, 2012). Scheffer *et al.* (2012) summarise and discuss fundamental ideas from network science, identifying key types of network structure in systems based on the organisation and connectivity of nodes. These concepts can be applied to networks of taxa in ecosystems. Systems comprised of weakly connected, heterogeneous nodes (taxa) respond to stress gradually due to the greater independence of the individual nodes; this allows each node to react to stress at their own rate (van Nes and Scheffer, 2005). Weakly connected systems are likely to be characterised by relatively high diversity and turnover rates, and redundancy in taxon functions. As a result, the loss of a single taxon can have little effect on ecosystem function and the response to stress will be linear (Scheffer *et al.*, 2012). In contrast, systems composed of well connected, homogeneous nodes have an initial resistance to stress due to subsidiary inputs from the broader system minimising or counterbalancing the effects of local or short-term perturbations (Scheffer *et al.*, 2012). This gives the perception of stability within the system, as the high connectivity of nodes is likely to reduce the turnover rate. Thus, the loss of a single taxon could have different effects on the wider system, depending on whether the taxon was highly or weakly connected. Under continued stress, an ecosystem is likely to reach a point, or threshold, where the network can no longer resist or counteract the disturbance and the nodes change synchronously causing an abrupt shift throughout the system (Dunne *et al.*, 2002; van Nes and Scheffer, 2005).

Applying network science principles, such as those developed by Barabási and Albert (1999) and Strogatz (2001), to real-world ecosystems poses a number of challenges. Network theory typically assumes that a network starts in a fixed stable state with a singular environmental stress (Gao *et al.*, 2016), whereas, in real-world systems, lakes are long-lived, dynamic systems subjected to continuous stresses. In principle, network theory can model links encompassing a wide range of associations between nodes (Zaheer *et al.*, 2010). Defining such associations, while difficult, is imperative in ecosystems where the variety of connections includes predator-prey, nutrient cycling, and inter- and intra- species links (Quevedo *et al.*, 2009; McCauley *et al.*, 2012; Simões *et al.*, 2012; Prado *et al.*, 2016). However, few studies incorporate taxon interactions in their models when forecasting taxon distribution under future climate scenarios (Wisz *et al.*, 2013; Cavieres *et al.*, 2014; Bulleri *et al.*, 2018).

A small number of studies have started to investigate ecosystem change using structural metrics in order to investigate whether the organisation of taxa and their interactions affects system response to stress. Doncaster *et al.* (2016) used compositional disorder, a measure of nestedness, as an indicator for instability in aquatic communities prior to ecosystem collapse; under increased stress, compositional disorder decreased indicating a decline in taxonomic turnover as the aquatic communities became more nested. In addition, Wang *et al.* (2019) used network skewness as a parameter of structural stability, indicating that aquatic ecosystems experienced a loss of structure under growing human pressure due to habitat homogenisation.

Here, we build on studies of community composition, by investigating whether structural metrics can indicate ecosystem stability in relation to temperature change, using data from modern lakes on temperature-sensitive chironomids (Diptera: Chironomidae; non-biting midges). We begin by generating presence-absence data on simulated chironomid taxa and lakes to produce null expectations of community composition and structural change across temperature gradients using three structural metrics: beta diversity, compositional disorder and network skewness. We then apply these metrics to three empirical datasets of chironomids across regional gradients of ambient temperature from northern North America (Fortin et al. 2015), Norway (Brooks and Birks, 2001; 2004), and Russia (Nazarova *et al.*, 2011; 2015). Comparison of empirical to modelled outcomes reveals deviations from the null expectations, enabling us to assess whether the lakes have under gone additional stress from climate change or secondary drivers.

# Materials and methods

## 2.1. Metrics of structural change

Three ecological metrics were selected as indicators of structural change in hypothesised and empirical chironomid assemblages to determine whether climate stress has affected ecosystem stability in high latitude regions. We chose beta diversity, compositional disorder, and network skewness as they have been used previously as ecological indicators of stress to measure taxonomic turnover (Baselga, 2010; Doncaster *et al.*, 2016; Nazarova *et al.*, 2020) and taxon organisation (Wang *et al.*, 2019), which reflect ecosystem instability.

Beta diversity, originally defined by Whittaker (1960), describes the ratio between regional and local taxonomic diversity and can be used as a measure of taxonomic turnover. The metric is a valuable tool for understanding the processes of change in community composition across ecological gradients (Chave and Leigh, 2002; Soininen *et al.*, 2007; Chase and Myers, 2011). The successful application of beta diversity can inform ecosystem managers of local versus regional ecosystem change (Socolar *et al.*, 2016), local-scale resilience (Vellend *et al.*, 2013; Dornelas *et al.*, 2014) and global widespread extinction (Barnosky *et al.*, 2011). Baselga’s (2010) calculation of beta diversity explores the variation in taxonomic assemblages across spatial datasets. It measures the dissimilarity between assemblages and attributes the changes in the assemblages to turnover (taxon replacement) and nestedness-type patterns (taxon loss). A larger beta diversity value indicates greater dissimilarity, or diversity, between neighbouring assemblages due to turnover and/or taxon loss. Here, beta diversity is used to indicate the dissimilarity of assemblages due to turnover and taxon loss as temperature increases.

Nestedness describes the hierarchical organization of systems, where neighbouring systems are subsets of a parent system (Mariani *et al.*, 2019). It is normally applied to species-site systems and was originally devised from patterns of taxa occurrence across islands with increasing distance from the mainland (Patterson and Atmar, 1987). Each island further away from the mainland was a subset of the previous one, with the most isolated island having the most highly nested community, with low taxon richness and turnover. Doncaster *et al.* (2016) used compositional disorder, a measure of nestedness, as a proxy for unpredictability in community composition through time, to test for declining resilience and early warning of impending ecosystem collapse. Compositional disorder, expressed as degree of disorder (°disorder), indicates whether an assemblage is nested and predictable (low °disorder) from one sample to the next or unnested and unpredictable (high °disorder), on a scale from 0° to 100°. For example, in a highly disordered (weakly nested) community, it is difficult to predict which taxa are present from knowledge only of the composition of neighbouring samples. Here, °disorder is used to measure whether lake assemblages become more ordered and predictable (i.e. more nested with less taxonomic turnover) or more disordered and unpredictable (i.e. less nested with greater turnover) as temperatures warm.

Network skewness measures the distribution of nodes (taxa) and their connections within a network. It is calculated using degree distributions, where the nodal degree is the number of interactions a taxon has with other taxa and the degree distribution is the spread of these degrees over the whole network. Interactions between taxa are assumed to be well represented by associations of taxa co-occurring in the same microhabitat. Network skewness as a metric of system stability is based on the theory that new stresses will modify the distribution of nodal connections away from a theoretically positively skewed distribution produced through emergent, self-organisational processes (Wang *et al.*, 2019). In low stress, heterogeneous environments, taxa self-organise into their preferred microhabitats, where the majority of taxa will have a small number of interactions, i.e. they are weakly connected. A few taxa will have a large number of interactions, i.e. they are strongly connected (Strogatz, 2001; Doncaster *et al.*, 2016). Wang *et al.* (2019) tested the theory further, suggesting that when a lake becomes stressed, the environment becomes more homogenized reducing the number of micro-habitats. This causes taxon loss, with specialist or weakly-connected taxa being more likely to be lost first. As weakly connected taxa are lost, the proportion of highly-connected taxa increases leading to a less positively skewed distribution of taxa associations. Here, network skewness is used to identify relative differences in the community response to temperature stress.

## Hypothetical datasets of structural change across a temperature gradient

Temperature is strongly associated with the distribution of chironomid taxa, with more taxa adapted to warmer temperatures (Eggermont and Heiri, 2012; Engels *et al.*, 2020). Thus, it is thought that taxon richness should increase with temperature (Patalas, 1990; Hawkins *et al.*, 2003), while turnover is also likely to influence taxonomic composition as cold-adapted taxa are lost (Theodoridis *et al.*, 2018). While it is widely accepted that taxon richness and turnover are primary components of community composition change (Buckley and Jetz, 2008; Coelho *et al.*, 2018), how these newly arrived taxa effect ecosystem structure is not fully understood.

Here, four hypothetical null models are developed using different matrix distributions of points to represent taxa existing along a temperature gradient. Each scenario is designed to simulate a plausible response to rising temperatures in a community as taxa become locally extinct or new taxa colonise. These scenarios represent reduced-stress ecosystems, where the modelled communities are in natural, stable states. Temperature change is the only stress driving community change, with no secondary drivers of stress taken into consideration. The model outputs will demonstrate how beta diversity, °disorder, and network skewness represent structural change across controlled temperature gradients. This will allow assessment of empirical chironomid datasets with regards to how the empirical datasets show a characteristic response to temperature rise (i.e. structural change comparable to the hypothetical modelled outputs), or show signs of greater disturbance from natural assemblage change due to additional stress. The following hypothetical scenarios were developed:

Scenario 1: Taxon richness increases linearly with temperature as new taxa arrive. Cold environments often have a lower taxonomic richness (Brodersen and Anderson, 2002; Brooks and Birks, 2004) due to the strong relationship between solar-derived energy and taxonomic richness (Hawkins *et al.*, 2003). This scenario tests the effect of taxon richness, with minimal turnover, on ecosystem structure.

Scenario 2: Taxon richness remains constant with temperature while taxon-type changes. Taxon specialisms and niche adaptation suggest that it is unlikely that the same taxa will be present at all temperature intervals. Temperature directly affects chironomid physiological and biochemical processes such as development, growth, and respiration (Eggermont and Heiri, 2012), and it has long been known that lake surface water temperature affects the distribution of subfossil chironomid assemblages (Brundin, 1949; Thienemann, 1954). This scenario tests the effect of turnover, with minimal increase in taxon richness, on assemblage structure.

Scenario 3: Taxon richness increases overall with temperature, while taxon-type changes. In real-world scenarios, it is likely that both rising taxon richness and taxonomic turnover will occur as temperature increases. This scenario tests the combined effect of rising taxon richness and turnover.

Scenario 4: Taxon presence is random, unaffected by temperature. This scenario is designed as a control; the simulated assemblages change with no reference to temperature.

Taxon presence-absence matrices were simulated for each scenario in R statistical software v. 3.6.0 (R Core Team, 2019). Each matrix comprised a sample from each of 100 lake communities with up to 100 taxa per sample, for lakes distributed over a simulated temperature gradient of 2 to 20 °C. Taxonomic richness and replacement were independently manipulated based on the lake-specific probability of receiving a taxon and the independent probability of availability of each taxon in each lake. The product of these two probabilities gave the incidence probability of each taxon in each lake. The model-generated assemblages assume no temporal change. The model was run 100 times for each scenario. Output matrices were analysed for taxon richness, beta diversity, °disorder, and network skewness.

## Statistical methods

Taxonomic richness was calculated as the sum of taxa present in each network. Beta diversity was calculated using Baselga and Orme’s (2012) betapart package for R statistical software v. 3.6.0 (R Core Team, 2019). Multi-site dissimilarity was calculated using a 10-sample working window along the temperature gradient, with the Sørensen index (*βSOR*) as a measure for total beta diversity (Dice, 1945; Sørensen, 1948). The turnover (taxa replacement) component was calculated using Simpson’s dissimilarity index (*βSIM*) (Simpson, 1943) and the nestedness-type (taxon loss) component was calculated using Sørensen’s dissimilarity (βSNE) (Baselga, 2010). °Disorder was calculated using a 10-sample working window along the temperature gradient, following methods developed by Doncaster et al. (2016) in R statistical software v. 3.6.0 (R Core Team, 2019). Window sizes were tested for beta diversity and °disorder (Figure 1); the 10-sample window provided the best balance of accuracy, which depends on window size, and sensitivity to change, which depends on window frequencyfor both metrics. Network skewness was calculated in Matlab (MATLAB ver. R2017b) following the method developed by Wang et al. (2019). For each dataset, the most-frequently co-occurring taxa pairs were identified as the pairs occupying the upper two quartiles of positive values for Cramér’s association coefficient (Q2 of V+). Taxon degree was calculated for each taxon in an assemblage from the sum of its connected pairings within the assemblage. Network skewness was measured by the asymmetry in the frequency of co-occurrences between taxa (Wang *et al.*, 2019).

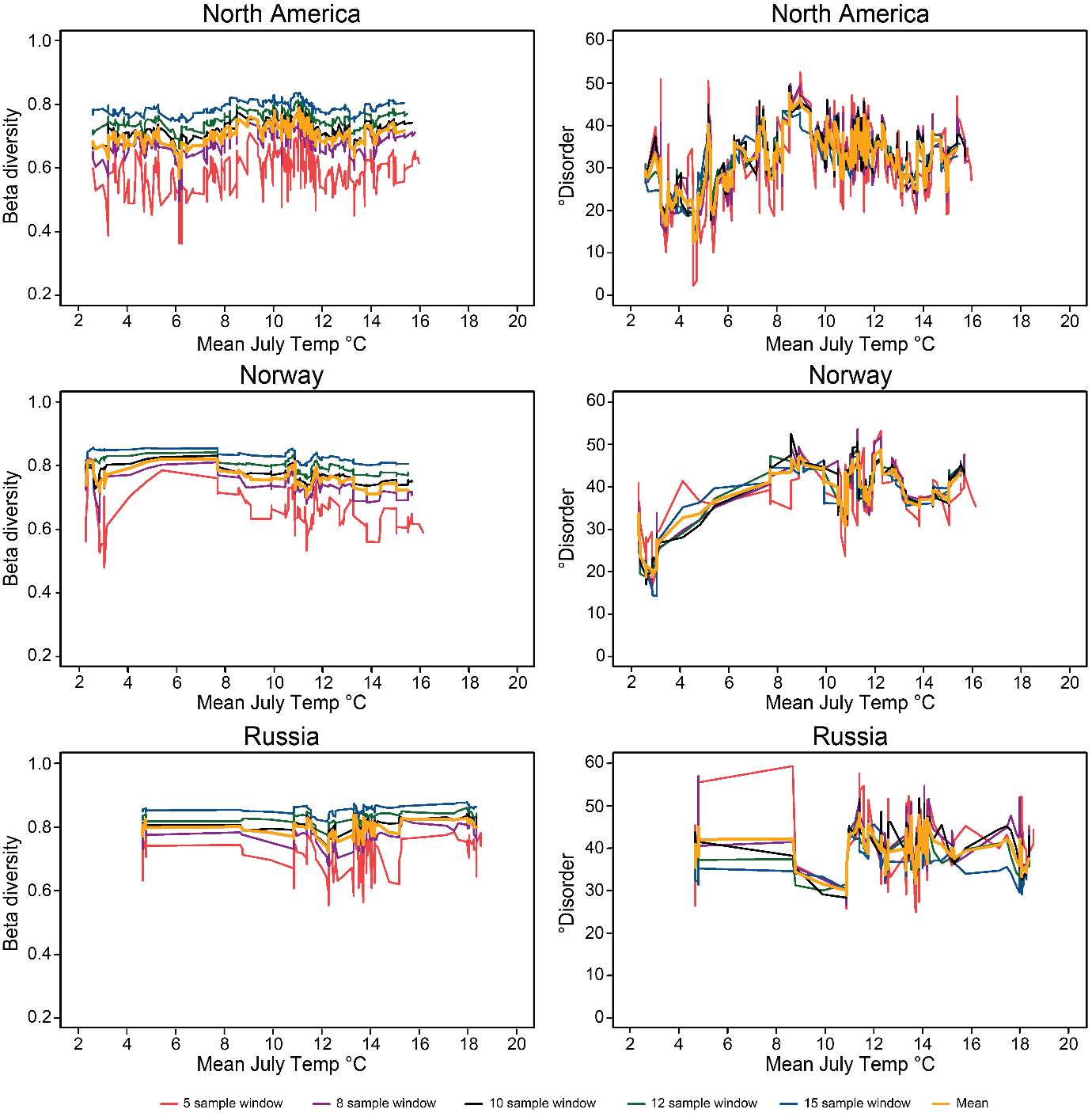


Figure 1 Comparison of window sizes for the calculation of beta diversity and °disorder. Multi-site dissimilarity compares the assemblage similarity between sites. °Disorder quantifies the orderliness of compositional change in an assemblage, based on the amount of same-type taxa present in consecutive samples. Both calculations thus require a window of samples. We considered windows of 5, 8, 10, 12 and 15 samples. All showed comparable trends in beta diversity and °disorder, with smaller window sizes (e.g. 5 or 8 samples) amplifying the changes in the metrics between samples, and larger window sizes (e.g. 12 or 15) smoothing the changes in the metrics around a similar running average.

## 2.4. Empirical chironomid datasets across spatial temperature gradients

Larval chironomid assemblages are used as ecological indicators of stability in three large spatial datasets, spanning North America (Fortin *et al.*, 2015), Norway (Brooks and Birks, 2001; 2004) and Russia (Nazarova *et al.*, 2011; 2015) (Figure 2, Table 1). Chironomid taxa are highly sensitive to mean July temperature and ubiquitous across high latitude regions, with numerous cold-adapted taxa making them a viable proxy in high latitude areas (Brooks, 2006a; Medeiros *et al.*, 2011; Eggermont and Heiri, 2012). There is a growing interest into the power of spatial trends in chironomid diversity to help predict how assemblages might change with continued climatic warming (Engels *et al.*, 2020).

Chironomid assemblage composition was ascertained for each lake surface sediment sample in the original studies of each region, with taxon identified to genus or species-morphotype level using standardised subfossil taxonomy (Brooks et al. 2007). Mean July temperature was identified as the primary influencing factor of taxon presence by the original authors. A canonical correspondence analysis indicated that mean July temperature explained the largest proportion of variance in the North American and Norwegian datasets, suggesting that mean July temperature was likely to be an important driver of taxonomic distribution (Figure 3). Distance from treeline appeared to explain the greatest amount of variance in the Russian dataset, with mean July temperature having the second largest influence on variance. Vegetation-type was also shown to influence cladoceran communities in northeastern Siberia (Frolova *et al.*, 2014), and treeline position has often been shown to be related to climate in non-anthropogenically disturbed areas (MacDonald *et al.*, 1998; 2000; Harsch and Bader, 2011). Distance from treeline data was not included in the original studies and was calculated using treeline location (Brown *et al.*, 1998, revised 2001) in ArcGIS (ESRI, 2011) for this study.

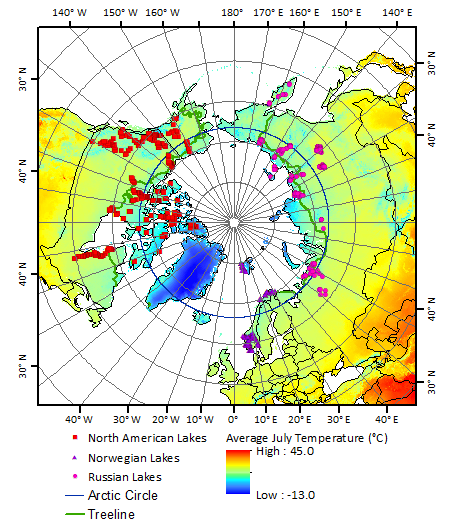


Figure 2 The North American (red squares), Norwegian (purple triangles) and Russian (dark blue circles) chironomid datasets span the arctic and subarctic, including island and mainland locations. The Norwegian dataset includes lakes on the Svalbard archipelago, which lies north of continental Norway in the Barents Sea between 10° and 3° E and 74° and 81° N. Background colour denotes mean July Temperature for the period 1970-2000. Temperature data from World Clim version 2 (Fick and Hijmans, 2017).

Table 1 Metadata for the North American, Norwegian and Russian chironomid datasets. The three datasets span a large geographic area; including arctic, subarctic and island locations. Altitudinal data was not available for all lakes in the North American dataset, thus was calculated using altitude data (EROS, 2014) in ArcGIS (ESRI, 2011) for the whole North American dataset. Key secondary environmental factors were identified by original authors for the North American and Russian datasets. Analyses to identify key secondary environmental factors for the Norwegian dataset were run as part of this study (Figure 3).

|  |  |  |  |
| --- | --- | --- | --- |
|  | **North America** | **Norway** | **Russia** |
| Collection period | mid-1990s to 2007 | 1995 - 1999 | 1998 to 2011 |
| Number of lakes | 434 | 157 | 193 |
| Latitudinal range | 49.8 to 80.83° | 58.08 to 79.8° | 53.03 to 75.4° |
| Longitudinal range | -151.32 to -68.44° | 5.01 to 31.04° | 50.5 to 163.15° |
| Taxon richness range | 3 – 30 | 1 – 43 | 8 – 41 |
| Total number of taxa | 78 | 141 | 174 |
| Altitude range (m a.s.l.) | 1 – 1709 | 5 - 1594 | 1 – 805 |
| Mean July temperature range | 2.6 – 16.9 °C | 2.3 – 16.5 °C | 4.5 – 19.0 °C |
| Other influential environmental factors,  as identified by original authors | August temperature, annual temperature, DOC, water depth, Fe, K, pH, and conductivity | Conductivity, pH, and water depth | Conductivity, pH, and water depth |
| Citation | Fortin *et al.* (2015) | Brooks and Birks (2001), Brooks and Birks (2004) | Nazarova *et al.* (2011), Nazarova *et al.* (2015) |

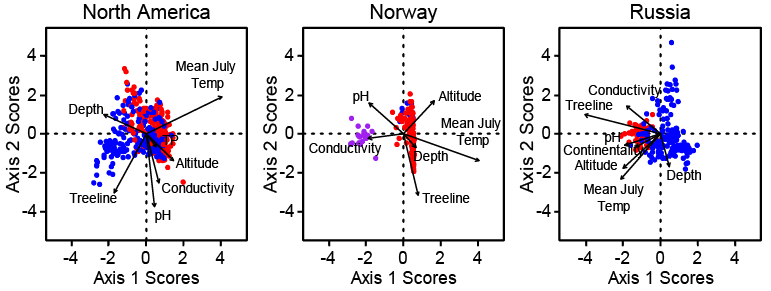


Figure 3 Canonical correspondence analyses (CCA) indicate which environmental variables help explain the variance within the datasets, and thus provides indication of which variables were likely to be important drivers of assemblage change. Blue dots indicate above-Arctic Circle lakes, red dots below-Arctic Circle lakes, and purple dots (Norway) Svalbard lakes. The strength of each variable is represented by the length of arrow. Mean July temperature appears to explain the greatest amount of variance in the North American and Norwegian datasets. However, treeline appears to have the greatest influence on variance in the Russian dataset, with mean July temperature having the second strongest influence on variance.

Modern mean July air temperatures were calculated for each lake using the CRU TS4 Google Earth interface to the nearest half-degree grid (Harris *et al.*, 2014) for the periods 1981˗2011 for the North American and Russian datasets, and 1971˗2001 for the Norwegian dataset. Time periods were chosen to cover the data collection periods. The CRU TS4 dataset accounts for altitude, following New *et al.* (1999); however, in mountainous regions, there may be some error in the predicted temperatures for lakes with considerably lower or higher altitudes. These modern temperature gradients may conflate two processes; a cold to warm temperature gradient from the higher to lower latitudes, both in the present and past that represent natural boundary conditions not stresses, and secondly, incremental rises in temperature superimposed upon the natural gradient caused by global warming, where the higher latitude lakes have received greater warming stress than the lower latitude (i.e. the reverse of the natural gradient). A comparison of the modern 30-year mean July temperatures to mean July temperatures for the period 1901 to 1950 indicated that the majority of the lakes in this study had experienced warming since the beginning of the twentieth century (Figure 4). These modern temperatures are not yet boundary conditions and are more likely to represent stresses or transient conditions. There is also the possibility that the two effects are in some way cancelling each other. Characterisations obtained from the modelled simulations will be used to help interpret patterns seen in the empirical data; however, the matrix models only simulate the natural gradient, thus any variance between the real data and the models could be the effect of global warming or the interactions of other secondary environmental variables.

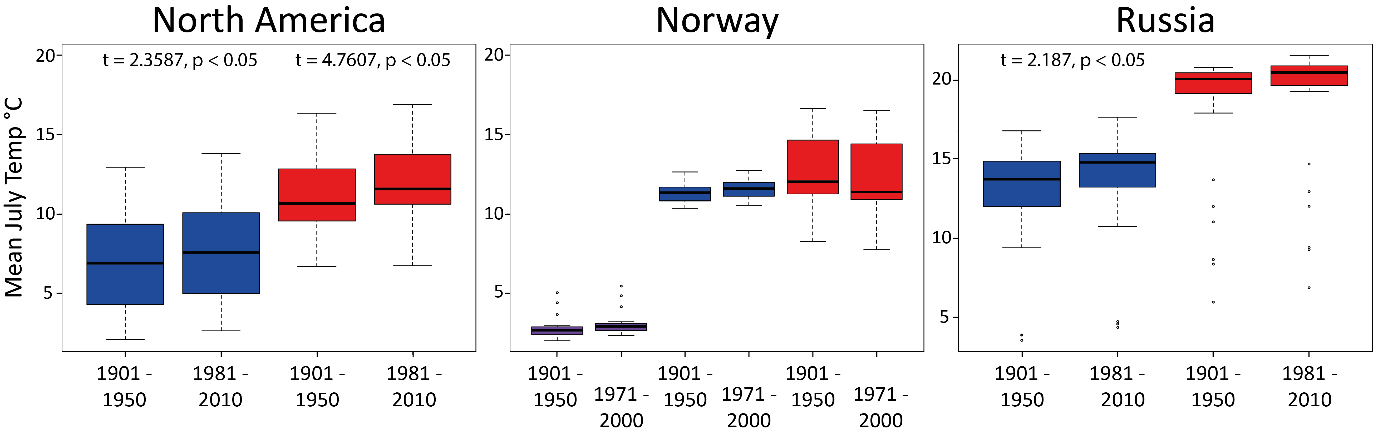


Figure 4 Boxplots displaying the change in mean July temperature from 1901–1950 to 1981-2010 (North America and Russia) and 1971-2000 (Norway) datasets. Blue boxes indicate above-Arctic Circle lakes, red boxes below-Arctic Circle lakes, purple boxes (Norway) Svalbard lakes. Significant differences (p < 0.05) between pairs of data using T-test statistics indicate lakes in North America and above-Arctic Circle lakes in Russia have undergone warming since 1950. All other differences between pairs are insignificant (p < 0.05).

Lake samples were ordered from cold to warm using the calculated CRU TS4 mean July air temperatures within the datasets. Changes in empirical community compositions across the temperature gradients were measured using taxon richness, beta diversity, °disorder, and network skewness, as described previously.

# Results

## 3.1. Simulated structural change in assemblage composition

The simulation models revealed how different scenarios for the interaction of taxon richness with composition can affect ecosystem structure across gradual temperature gradients, where temperature is the only driver of assemblage change (Figure 5). Here, we describe the general trends and key findings from the models.

Scenario 1 (Figure 5.1): constantly rising taxon richness with rising temperature. Beta diversity, °disorder, and network skewness decline in response to rising taxon richness. Declining beta diversity indicates a reduction in turnover as taxon richness increases; however, this could be an artefact of the model, which minimises the effect of turnover. This model demonstrates that in the absence of turnover, increasing taxon richness allows the accrual of common taxa across assemblages, making the warmer lake assemblages more similar to the neighbouring assemblages. This is supported by declining °disorder; as the number of common taxa increase, the lake assemblages become more predictable from neighbouring assemblages. The declining trend in skewness means that as temperature increases and taxon richness rises, the system homogenises by losing weakly connected nodes.

Scenario 2 (Figure 5.2): constant shift in taxon composition with temperature. Generally, the beta diversity, °disorder, and skewness outputs for this scenario are variable with little directional change. Partly as a result of the model setup, taxon richness is lower at the extreme ends of the temperature gradient. This lower taxon richness produces slightly lower beta diversity and °disorder. Focusing on the mid-temperature sections where taxon richness is constant, total beta diversity is high and predominately explained by the turnover component. This is to be expected as the model is purposely simulating taxon turnover. °Disorder is highly variable with no directional change. This suggests that there is little accrual of common taxa and thus assemblages are unpredictable from neighbouring assemblages. However, as the turnover is constant and gradual, there are no sudden changes in the assemblages either, suggesting that the assemblages are not necessarily unstable. The trend in skewness has no directional change meaning a shift in taxon composition alone does not change the distribution of nodal degrees.

Scenario 3 (Figure 5.3): constant shift in taxon composition and rising richness with temperature. Overall beta diversity, °disorder, and network skewness decline. These responses in the metrics are closer to scenario 1 than 2, indicating that the metrics primarily reflect the increasing taxon richness. Beta diversity is highest in the colder end of the gradient, indicating that turnover has a greater influence on the taxon-poorer assemblages. Total beta diversity is predominantly controlled by the turnover component; however, the taxon loss component has a slightly larger influence at the colder end of the gradient. As taxon richness increases, beta diversity declines suggesting that the loss of individual taxa has a lesser impact on larger communities and the increase in common taxa reduces the dissimilarity between the assemblages. °Disorder is lowest (i.e. the assemblages are more nested) at the coldest end of the gradient where taxon richness is also the lowest. As taxon richness increases, °disorder rapidly increases suggesting greater unpredictability and turnover in taxa-type. °Disorder gradually declines with increasing temperature and taxon richness, decreasing the unpredictability as there is an increase in common taxa between the assemblages. The overall declining trend in network skewness indicates losses of weakly connected nodes as taxon richness increases. The upturn in skewness at the end of the temperature gradient might suggest a rise in assemblage stability as the effect of taxonomic turnover diminishes.

Scenario 4 (Figure 5.4): composition and richness independent of temperature. Metrics show little or no directional change; taxon richness has a small increase over the temperature gradient, however beta diversity, °disorder and skwness showed little change. This response is more comparable to scenario 2 than 1, indicating that the metrics primarily reflect turnover. Beta diversity and °disorder are high across the temperature gradient and the stationarity in skewness means that random changes in taxon composition alone do not affect the distribution of taxon nodal degree. All three of the metrics are less variable than in scenario 2.

Overall, within the simulation models the rising taxon richness allows for the accrual of common taxa, reducing the dissimilarity (lower beta diversity) and unpredictability (lower °disorder) of assemblages. Skewness generally declines in positivity with increasing taxon richness. Turnover, with minimal change in taxon richness, creates highly variable assemblages with high dissimilarity (high beta diversity), unpredictability (high °disorder), and stationary skewness. Scenario 3 was designed to represent empirical taxonomic assemblages, where there is an overall increase in assemblage richness and taxon-type changes with temperature, i.e. the cold-adapted taxa are lost as temperatures increased and the assemblage becomes dominated by a greater number of relatively warmer taxa. This produced an overall decline in beta diversity (dissimilarity) and °disorder (unpredictability), and an overall decline in skewness. Thus, if the empirical assemblages are responding primarily to a natural temperature gradient, similar trends in structural metrics would be expected in the empirical datasets.

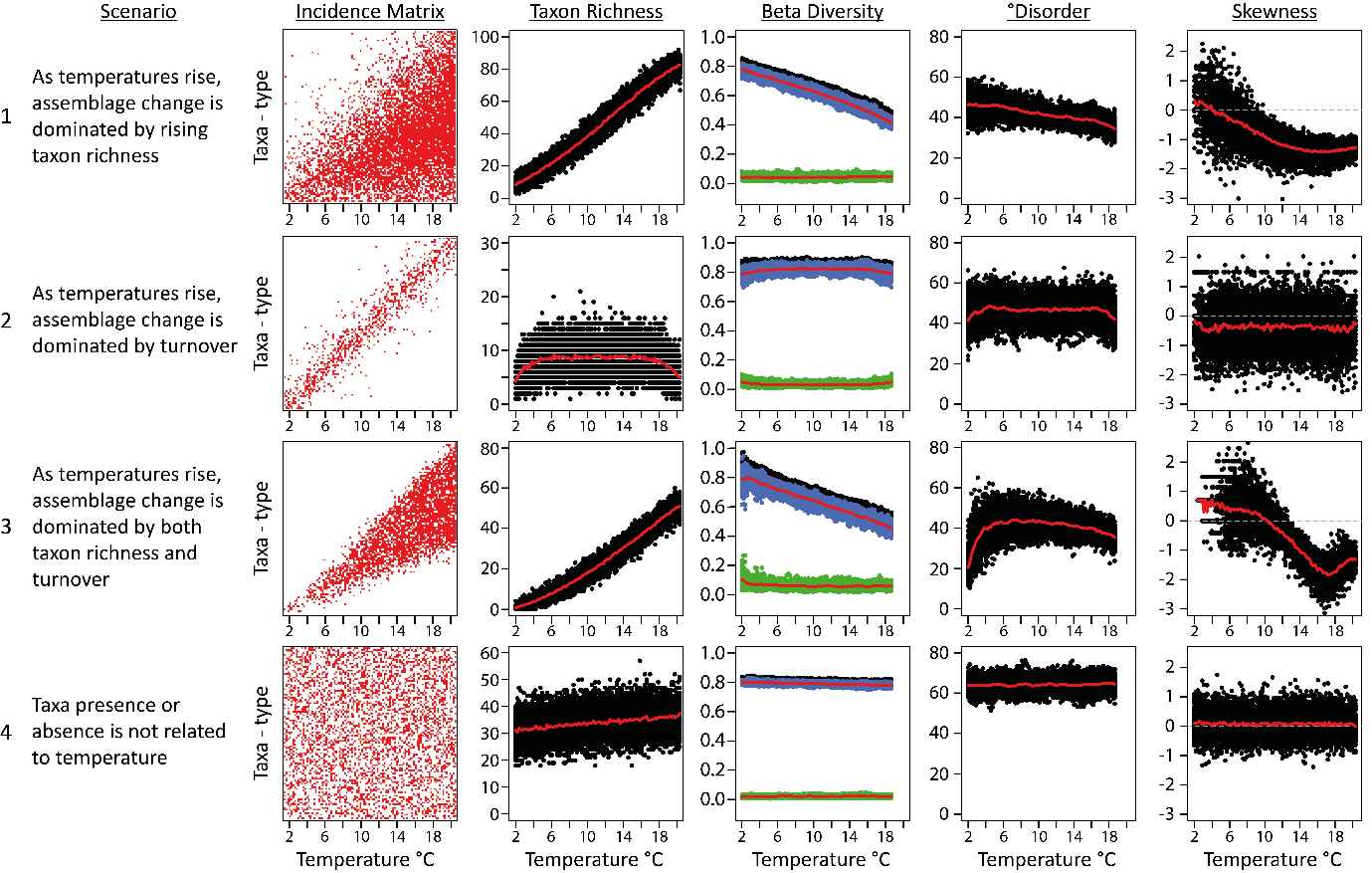


Figure 5 The relationship between temperature and taxa presence in four hypothetical scenarios, as described by an incidence matrix (column 1: red dots) and measured using four community structure metrics (columns 2-5) taxon richness, beta diversity, odisorder, and skewness in 100 simulations (black, blue and green dots). Total beta diversity (column 3) results are shown in black with changes attributed to taxon turnover (blue) and taxon loss (green). Red lines show mean values to illustrate general trends.

## Structural change in empirical chironomid assemblages

The ecological metrics, beta diversity, °disorder, and network skewness, reveal changes in assemblage structure across the empirical datasets (Figure 6), with some similarities and variations from the simulated models.

### North America

In the North American dataset, taxon richness was lowest in the coldest lakes and increased with temperature, comparable to hypothesised scenarios 1, 3 and 4. Beta diversity was lower in the colder lakes, with lakes situated on Victoria and Baffin Island having the lowest beta diversity. This indicates that the cold, taxon poor lakes were less dissimilar (i.e. they had more taxa in common with their neighbouring assemblages) with lower turnover. Beta diversity generally increased up to the mid-temperature range (c. 9 - 13 °C); indicating an increase in turnover, as cold-adapted taxa were lost and more temperate taxa arrived. Beta diversity declined at the warmer end of the temperature gradient (greater than c. 10 °C), suggesting that the lake assemblages were becoming more similar, due to the accrual of common taxa, and the loss or arrival of individual taxa was less influential in the larger assemblages. This second part of the trend is comparable to the pattern seen in hypothesised scenarios 1 and 3. The turnover component was the primary driver of total beta diversity across the temperature gradient (Figure 7); however, taxonomic loss had a larger influence on the cold, taxon poor lakes indicating that the taxa loss of was more influential on these smaller assemblages.

°Disorder presented a comparable trend to beta diversity, with lower °disorder at the cold end of the temperature gradient, a peak in °disorder at the mid-temperature range (c. 9 - 13 °C) and a subsequent gradual decline at the warmer end of the gradient (Figure 6). This pattern was more comparable to the °disorder trend seen in hypothesised scenario 3, suggesting that the changes in °disorder were driven by taxon richness and turnover. The lower °disorder values indicated that the assemblages were more nested and thus more predictable in colder lakes. As temperature and taxon richness increased, the assemblages became more disordered and unpredictable. This rise in °disorder was concurrent with the rise in beta diversity, indicating that taxon richness and turnover were both influencing the changing ecosystem structure. The decline in °disorder at the warmest end of the gradient indicated that the lakes were becoming more predictable as there was an accrual of common taxa and turnover was less influential on the assemblages.

Network skewness was predominately negative across the dataset, with 90.8 % of lakes having a negative value (Figure 6). The lakes show a trend towards more negative values with increasing temperature indicating losses of weakly connected taxa as seen in modelled scenarios 1 and 3 with increased richness.

### 3.2.2. Norway

In the Norwegian dataset, taxon richness was lowest in the coldest lakes and increased with temperature, comparable to hypothesised scenarios 1, 3 and 4. Beta diversity was high in the coldest lakes, which were from Svalbard. The mainland lakes had a higher beta diversity at the colder end of the gradient and beta diversity declined towards the warmest end of the gradient (after c. 12 °C, Figure 6). Beta diversity was lowest in the warmest lakes, where taxon richness was highest and the chance of common taxa was greater. This decline in beta diversity with temperature was comparable to the trends seen in modelled scenarios 1 and 3, where beta diversity was highest in the cold, taxon poor lakes, and lowest in the warmer, more taxon rich lakes. This suggests that the lake assemblages were changing due to taxon richness and turnover. Turnover was the primary driver of total beta diversity (Figure 7). Taxon loss had the greatest influence on total beta diversity in the lakes from Svalbard, due to the lack of common taxa between the lake assemblages.

°Disorder was lowest in Svalbard lakes and highest in the mainland Norwegian lakes (Figure 6). This pattern was comparable to the °disorder trend seen in hypothesised scenario 3 suggesting that the assemblage structure was influenced by taxon richness and turnover. However, scenario 3 indicated a gradual decline in °disorder in the warmest lakes, whereas °disorder remained high in the Norwegian dataset. The Svalbard lakes had the highest beta diversity values and lowest °disorder scores, suggesting these lakes had the most dissimilar yet predictable assemblages. This pattern was seen in modelled scenario 3 and most likely relates to the low taxon richness across Svalbard. The lakes had a limited number of potential taxa (19 taxa present across the 23 lakes from Svalbard) and a richness range of 1 to 11. This reduced probability of multiple Svalbard lakes having the same taxa, making the lakes highly dissimilar (high beta diversity), yet the low pool of taxa (19) meant that the lakes were more predictable (low °disorder). The mainland Arctic and Subarctic lakes were highly °disordered suggesting that the turnover of taxa maintained a high degree of unpredictability between neighbouring assemblages.

Network skewness was predominately negative across the temperature gradient with 88.5 % of having a negative value (Figure 3). The overall flat trend shows some evidence for a reducing trend towards more negative values after ~12 oC perhaps indicating the relative loss of weakly connected nodes at higher temperatures as seen in modelled scenarios 1 and 3.

### Russia

In the Russian dataset, taxon richness was lower in the lakes at both the ends of the temperature gradient. Taxon richness was more variable in the mid-temperature range lakes (c. 11 -15 °C), with some lakes having low richness, while other lakes had the highest taxon richness values of the dataset. Beta diversity was high and constrained at the two temperature extremes. In the mid-temperature range, beta diversity was generally high, but the range in values was greater, with some lakes having noticelably lower beta diversity. Lakes with the lowest beta diversity values were located in the high-Arctic and central Yakutia Republic (eastern Siberia), and just west of the Yakutia Republic - Taymyrsky Dolgano-Nenetsky District boarder (eastern Siberia). High beta diversity values signify greater dissimilarity between lake assemblages suggesting a lack of common taxa. This trend is more comparable to modelled scenarios 2 and 4, which were primarily controlled by turnover. Turnover was the most influential component on total beta diversity (Figure 7). Thus, it is likely that the Russian lake assemblages were more influenced by taxon turnover than rising taxon richness.

°Disorder values were high, with little directional change across the temperature gradient. This is comparable to trends seen in modelled scenarios 2 and 4. High °disorder indicates unpredictability between lake assemblages and high turnover, further supporting the idea that the Russian dataset was controlled by turnover, with little accrual of common taxa.

Network skewness was predominately negative across the temperature gradient with 81.3 % of lakes having a negative value. The overall flat trend shows some evidence for rising values towards less negative values after c.14 °C perhaps indicating the relative increases and stability of weakly connected nodes at higher temperatures as seen in modelled scenarios 3.

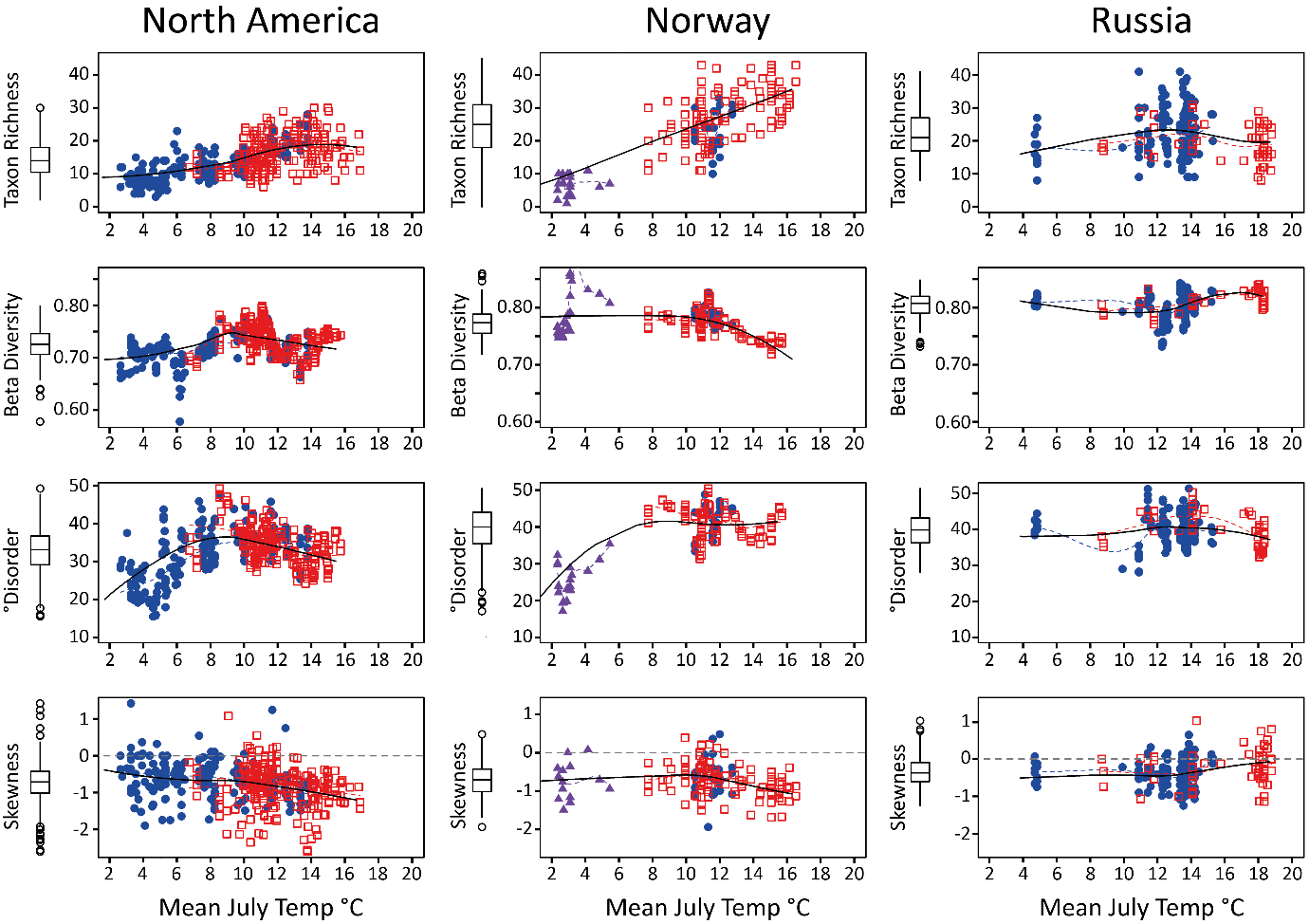


Figure 6 Relationships between mean July temperatures and community structure metrics (taxon richness, beta diversity, odisorder, and skewness) in the North American, Norwegian and Russian chironomid datasets. Lake sites above the Arctic Circle (66.56° N) are represented by blue circles and lakes below the Arctic Circle are displayed as hollow red squares. The Norwegian dataset was divided further, with lakes located on Svalbard shown as purple triangles. Smoothed loess regression curves (span = 0.90) are plotted in black. Regression lines for data subgroups are displayed as corresponding coloured dashed lines. Box and whisker plots (y-axes) show data spread, including data range, mean, interquartile range and outliers.

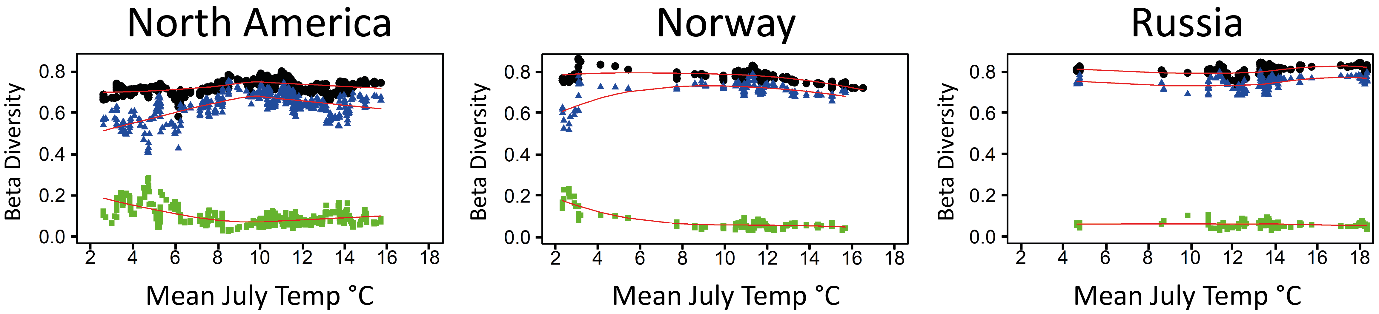


Figure 7 Relationships between July temperature and total beta diversity for the North American, Norwegian and Russian datasets. Individual values (black) can be attributed to changes in taxon turnover (blue) and taxon loss (green). Turnover is the most dominant component in all three datasets but taxon loss had a greater influence on beta diversity at the colder end of the temperature gradient in the North American and Norwegian lakes. Smoothed loess regression curves (span = 0.90) are shown in red.

# Discussion

Climate change has already affected freshwater aquatic assemblages in the northern hemisphere (Woelders *et al.*, 2018) and the majority of the lakes studied here have undergone some degree of temperature stress during the twentieth century (Figure 4). The ecological metrics provide information on assemblage structure at different points on the temperature gradient, indicating whether the assemblages were exhibiting signs of structural stress. The modelled simulations indicate potential changes in assemblage structure as temperatures increased at a gradual pace, with no secondary drivers of stress. There were some comparable and unparalleled trends between the empirical and modelled scenarios. Generally, the North American and Norwegian datasets showed comparable trends to modelled scenarios 1 and 3, suggesting that the changes within these datasets were driven by rising taxon richness and turnover across the temperature gradient. The Russian dataset showed little directional change across the temperature gradient, with the mid-temperature lakes having the largest variation in taxon richness, beta diversity, and °disorder. Some increase in skewness values at higher temperatures indicates relatively more weakly connected taxa and greater heterogeneity of the nodal distributions. These trends were more comparable to modelled scenarios 2 and 4, suggesting that turnover was more influential on the Russian assemblages than taxon richness. The similarities in the metrics between the empirical and modelled datasets could indicate that assemblages were under natural levels of stress expected for different temperature conditions, however, the differences may suggest additional ecosystem stress, possibly from a combination of secondary drivers or external drivers such as global warming. The relative speed of recent warming may be altering the lake ecosystem structures quicker than they would change naturally, and this could be further tested through long-term ecosystem changes from palaeoenvironmental archives in future studies.

## . Ecosystem structure as an indicator of stress in chironomid assemblages

### Lakes in cold, arctic environments

Climate change is predicted to have a greater impact in Arctic regions (Pithan and Mauritsen, 2014), therefore lakes with colder mean July temperatures should show a greater level of disturbance if they are reacting to heightened temperature stress.

In the North American dataset, lakes at the colder end of the temperature gradient (below c. 7 °C) had lower beta diversity and °disorder values; indicating reduced turnover and greater similarity/ predictability between assemblages. Lower beta diversity values were not simulated by the hypothesised models for the colder lakes, whereas scenario 3 did produce low °disorder values in the coldest lakes. Low beta diversity indicates greater similarity between assemblages and lower turnover, and low °disorder suggests more predictable, nested results. These metric outcomes can suggest stressed environments (Wang and Loreau, 2014). Nested communities (low °disorder) are more likely to have specialised taxa with narrow ecological tolerances and limited dispersal capabilities (McAbendroth *et al.*, 2005). This can indicate poor local resilience; with communities being more prone to large shifts in community composition in the face of environmental stress (Okuyama and Holland, 2008; Scheffer *et al.*, 2012). The taxon loss component of beta diversity had higher values at the colder end of the temperature gradient (Figure 7) further suggesting that the loss of taxa between assemblages had a stronger influence on diversity in these lakes (Viana *et al.*, 2016). When low beta diversity and °disorder occurred simultaneously in modelled scenarios 1 and 3, skewness was negative. The lakes at the colder end of the gradient in the North American dataset were predominantly negatively skewed. Negative skewness signifies fewer weakly connected taxa, and therefore suggests stress, due to habitat homogenisation and few available niches (Wang *et al.*, 2019). Thus, all three metrics show indication of assemblage instability, however, the similarities between the modelled and empirical datasets suggest that this instability might be an expected level of stress for cold, taxon-poor environments.

In the Norwegian dataset, the lakes with the coldest mean July temperatures, located in Svalbard, were indicating signs of stress. Taxon richness was low, beta diversity was high, °disorder was low, and skewness was predominantly negative. Low °disorder and negative skewness indicate that assemblages are under greater stress (Doncaster *et al.*, 2016; Wang *et al.*, 2019), whereas high beta diversity can indicate stability (Allan *et al.*, 2011; Wang and Loreau, 2016). In this circumstance, the high beta diversity was likely to be a consequence of the relatively low pool of available taxa (19 taxa) and low taxon richness (1 – 11) across Svalbard reducing the chance of lakes having overlapping assemblages. However, these trends were comparable to modelled scenario 3, where assemblages at the cold end of the gradient were taxon poor and subjected to increasing taxon richness and turnover. This suggests that these lakes were experiencing an expected levels of stress, most likely as a result of Svalbard’s climate.

In the Russian dataset, lakes at the colder end of the temperature gradient (below c. 6 °C) showed signs of reduced stress. Beta diversity and °disorder were high, indicating higher levels of turnover and greater dissimilarity / unpredictability between lake assemblages. High beta diversity and °disorder suggest that lake habitats are heterogenic with a wide variety of niches (Wright *et al.*, 2007), thus theory suggests that taxa should self-organise into their preferred habitats, creating a positive skewness (Wang *et al.*, 2019). However, these lakes were negatively skewed. Negative skewness indicates increased taxonomic interaction, possibly due to greater environmental homogenisation and/or stress. This could suggest that the Russian lakes were reacting to different drivers of stress, as opposed to temperature driven stress. These lakes were located in the high-Arctic and islands in the Yakutia Republic. Most of the lakes in this area were shallow, thermokarst lakes, with a short ice free period, up to 120 days per year (Kumke *et al.*, 2007). Such extreme climate conditions were likely to limit taxa able to survive in these lakes (Self *et al.*, 2011).

### Lakes in the mid-temperature range

Increasing mean July temperatures should create more microhabitats as lake conditions become more favourable for warm-adapted species, e.g. macrophyte presence can be closely associated with certain chironomid assemblages (Langdon *et al.*, 2010). Taxon richness increased in the mid-temperature range for all three empirical datasets, suggesting that the lake environments were able to support greater variety of chironomids, as predicted by the hypothesised models.

Beta diversity and °disorder values were highest in the mid-temperature range lakes in the North American (c. 9 - 13 °C) and Norwegian (c. 11 - 13 °C) datasets, and were most variable (highest and lowest) in the mid-temperature range lakes in the Russian dataset (c. 11 - 15 °C). High beta diversity can indicate stability within ecosystems as communities are more diverse, supporting increased ecosystem functioning (Allan *et al.*, 2011; Wang and Loreau, 2016). The taxon loss component of beta diversity was strongly reduced in these lakes (Figure 7); with cold-adapted taxa likely to have already been lost from the assemblages (Brooks *et al.*, 2007). The turnover component almost entirely explained total beta diversity, suggesting that turnover was more influential on community composition in these lakes, as assemblages adapted to changes in environmental conditions (Viana *et al.*, 2016). Higher beta diversity could also indicate a greater diversity in habitats, for example there was a range of Arctic and Subarctic lakes in the mid-temperature section of the gradient. Variations in the number of ice-free days, water pH or depth between lakes could influence the chironomid assemblages on a local scale (Brooks, 2006b) and increase the beta diversity between lakes on the larger temperature scale. This is supported by the peak in °disorder, which can also represent increased habitat diversity and niche development (Wright *et al.*, 2007). Conversely, in the modelled scenarios, beta diversity and °disorder showed little directional change in the mid-temperature sections, with mid-range values for beta diversity in scenario 1 and 3, mid-range values for °disorder in scenario 1, and a plateauing of °disorder values in scenario 3. Thus, the peaks in beta diversity and °disorder in three empirical datasets were unanticipated from the hypothesised models.

Network skewness was primarily negative in all three empirical datasets, despite the potential for more microhabitats in the warmer environments. Greater niche diversity should allow taxa to self-organise into preferred habitats, reducing interactions and producing positively skewed degree distributions (Wang *et al.*, 2019). There was a small peak in positively skewed lakes in the Norwegian dataset, a few positively skewed lakes in the North American dataset, and a rise in positively skewed lakes in the Russian dataset in these mid-temperature lakes, most likely as a consequence of increased environmental heterogeneity. This could further indicate greater ecosystem stability. In the mid sections of modelled scenarios 1 and 3, network skewness continued to decline, reaching its lowermost values before rising towards the warmest end of the gradient. Thus, the trends seen in skewness in the empirical datasets were also unanticipated from the hypothesised models.

There was little agreement between the metrics for the simulated and empirical lakes in the mid-temperature range. The purpose of the modelled scenarios was to identify what trends could be expected in the ecological metrics as assemblages changed with temperature. Assuming the model scenarios were appropriate, this suggests that mid-temperature range lakes were behaving unexpectedly or were experiencing additional stress. However, there was a mixture of Arctic and Subarctic lakes in these mid-temperature ranges. It is possible that beta diversity and °disorder were superficially increased by comparing lakes with similar mean July temperatures but different physical locations and lake attributes (Luoto *et al.*, 2016). Ecotone transitional zones have also been shown to be more taxon rich and diverse (Nyman *et al.*, 2005). The modelled scenarios only simulated the effect of temperature on taxon richness and turnover, therefore it is possible that the models were too simplistic to replicate the trend seen in the empirical datasets (Merow *et al.*, 2014).

### Lakes in warmer, subarctic environments

Lakes subjected to warmer mean July temperatures should be more productive with the potential to support a greater diversity of life (LeBlanc *et al.*, 2004; Langdon *et al.*, 2010). However, lakes in more southerly or less isolated locations could have increased disturbance from secondary drivers; for example, predation (Mousavi *et al.*, 2002) or proximity to agriculture, urbanisation and pollution (Koperski, 2009; Mackintosh *et al.*, 2015).

In the North American and Norwegian datasets, the lake assemblages indicated signals of ecosystem instability at the warmest end of the temperature gradient. Taxon richness was highest, in fitting with modelled scenarios 1 and 3, and demonstrating that these lakes were able to support a greater variety of taxa. Lower beta diversity was in agreement with hypothesised models 1 and 3, which suggested greater similarity (i.e. more common taxa) between the taxon-richer assemblages. °Disorder decreased in the North American dataset, suggesting the lake assemblages were becoming more nested and predictable, and in agreement with modelled scenarios 1 and 3. Whereas, °disorder remained high in the Norwegian dataset, suggesting more diverse assemblages and greater turnover. Decreased beta diversity and °disorder can indicate ecosystem instability. A decrease in beta diversity can signal a loss of local biodiversity and increased environmental homogenization at a regional scale (Wang and Loreau, 2014; 2016). Doncaster *et al.* (2016) suggest that undisturbed ecosystems should have high °disorder values, derived from the continual turnover of slow-growing and weakly competitive ‘canary taxa’ and a reduced presence of highly competitive ‘keystone taxa’. As an ecosystem becomes stressed, keystone taxa initially prevail at the expense of canary taxa, causing a decrease in °disorder values and decline in turnover. This restructuring increases the proportion of highly connected taxa, producing a less positively (or more negatively) skewed degree distribution, a sign of increased environmental stress (Wang *et al.*, 2019). Skewness became more negative in the warmer lakes in the North American and Norwegian datasets, in accordance with network theory (Wang *et al.*, 2019), indicating increased ecosystem instability. Modelled scenarios 1 and 3 suggested that skewness should rise in the most taxon rich assemblages. This disagreement between the modelled and empirical skewness outputs could suggest that the empirical lake assemblages were affected by additional environmental factors or indicated signs of stress.

Lakes at the warmer end of the temperature gradient in the North American and Norwegian datasets could be indicating signs of increased disturbance due to secondary drivers. There is limited knowledge of the extent of human induced pressure on the dataset lakes and the lakes were purposely selected for their reduced human influence. The CCA (Figure 3) analysis identified water pH and conductivity as secondary explanatory drivers of variance, suggesting these environmental factors may also have had significant influences on the dataset. This could be for a numer of reasons, for example pH, conductivity and DOC concentrations can change considerably in boreal zones due to vegetation change, such as paludification and an increase in coniferous trees (Rosén and Hammarlund, 2007; Pienitz *et al.*, 2018). Changes in pH and conductivity could also indicate a rise in pollution from human inference on the catchment (Kazi *et al.*, 2009). It is possible that these additional stresses could be responsible for the increase in disturbance seen in lakes at the warmer end of the gradient in the North American dataset. However, lakes at the warmer end of the temperature gradient in the Norwegian dataset were more acidic due to bedrock type, and therefore the increased influence of additional environmental factors could be an intrinsic feature of the assemblage data based on sample selection. No secondary drivers of stress were taken in to account in the hypothetical models, therefore there is no comparison as to how secondary drivers may affect the outcomes of the ecological metrics.

Lakes at the warmer end of the temperature gradient in the Russian dataset showed signs of greater stability. Taxon richness was lower in these warmer lakes, contrary to the hypothesised scenarios. Declining taxon richness has previously been used as a sign of environment degradation (McCann, 2000). However, these lakes are located in central Komi and Yakutia where they experience a continental climate with extreme differences between summer and winter temperature and limited precipitation, which is likely to influence which taxa are able to live in such environments (Self *et al.*, 2011; Nazarova *et al.*, 2017). High beta diversity values showed an increase in turnover and diversity, and thus greater stability and ecosystem functioning (Allan *et al.*, 2011). °Disorder values were relatively high, suggesting diverse systems with high turnover, and indicating ecosystem stability (Doncaster *et al.*, 2016). Modelled scenarios 2 and 4 indicate that high beta diversity and °disorder are not unexpected for assemblages largely impacted by turnover. Network skewness was less negative in these warmer lakes, with a number of positively skewed lakes. This trend was not anticipated by modelled scenarios 2 and 4, however, model 3 did predict a rise in skewness in the warmest lakes, in conjunction with higher taxon richness and turnover. The rise in skewness in the Russian dataset corresponded to a decline in taxon richness. Wang *et al.* (2019) indicated that taxon richness should not affect network skewness. Positive skewness occurs when there is a larger proportion of weakly connected taxa, as environmental heterogeneity provides a wider range of niches allowing taxa to self-organise into their preferred habitats (Wang *et al.*, 2019). Thus, these Russian lakes may be demonstrating a stabilisation in community structure.

## Taxonomic resolution

Chironomid larval head capsules recovered from lake sediments are often identified to genus or species-morphotype because a lack of diagnostic characters preclude species-level identification (Brooks *et al.*, 2007). Chironomid taxonomic resolution is a known problem in palaeoenvironmental studies; for example, *Procladius*, *Psectrocladius* *sordidellus*-type and *Chironomus anthracinus*-type can include multiple species. It has been shown that greater taxonomic resolution typically produces more precise environmental and temperature reconstructions (Heiri and Lotter, 2010; Greffard *et al.*, 2011). It is possible that the levels of taxonomic resolution affected the structural metrics in this study. For example, the primarily negative skewness values across the empirical datasets may be a consequence of low taxonomic resolution. Wang *et al.* (2019) found positive skewness values in the reduced impacted lakes in their study, however, there are very few positively skewed lakes in this study. Wang *et al.* (2019) used diatoms as an indicator of lake state; diatoms are highly abundant, sensitive and diverse, enabling the detection of subtle changes in water quality (Battarbee, 1986; Recasens *et al.*, 2015). However, the hypothesised models in the present study also had a large proportion of negatively skewed lakes. Thus, the change in trend of skewness values, or ratio of positive to negative skewed lakes, may be more informative than the values themselves, e.g. the rise/ decline in skewness values at the warmest end of the temperature gradient in the empirical datasets in this study.

Improved taxonomic resolution may benefit structural analyses, such as the ones tested here, however, the potential for misidentification may also increase causing erroneous or confounding results (Heiri and Lotter, 2010). Analyses of chironomid assemblages based on samples of living larvae, rather than on the larval head capsules preserved in lake sediments can provide greater taxonomic resolution (Greffard *et al.*, 2011), although samples of living assemblages suffer in comparison with sediment samples from difficulties in obtaining quantitative data and representative samples of all available habitats. Future development in techniques such as sedimentary DNA analysis may resolve issues such as low resolution or misidentification; for example, sedimentary ancient DNA analyses have increased the resolution of plant taxa identified in palaeoenvironmental studies (Alsos *et al.*, 2016; Clarke *et al.*, 2018). However, such techniques take time to develop (Domaizon *et al.*, 2017). Nonetheless, chironomid studies have frequently been showed to provide valuable insight in to palaeoenvironmental studies (Brooks, 2006b; Brooks *et al.*, 2012), even at the current levels of taxonomic resolution.

## Future trajectories of structural change

Global warming has continued to affect the study locations since sampling and is expected to continue rising (IPCC, 2013). The ecosystem metrics presented here show a time-slice of the chironomid community compositions across space. In reality, ecosystems are dynamic and continually reacting to stress (Crone and Taylor, 1996). The lakes will have been in a state of transition since the sampling dates, some more than twenty years ago, thus it is unlikely that these metric outputs represent the current state of the lakes or document the effects of the most recent climate change. The metrics indicated some signs of expected stress, e.g. in the coldest environments, and some signs of unanticipated stress, e.g. in the mid-temperature and warmest range. As climates continue to warm and anthropogenic activities increase, it is likely that the lakes will continue to react to different types of stress, driving further assemblage changes. Chironomids are ubiquitous and can be found in arctic, temperate and tropical climates (Matthews-Bird *et al.*, 2016; Wu *et al.*, 2016; Chang *et al.*, 2017), and in polluted (Madden *et al.*, 1992; Wright and Burgin, 2009), acidic (Halvorsen *et al.*, 2001; Rees and Cwynar, 2010) and eutrophic (Little *et al.*, 2000; Langdon *et al.*, 2006) lakes. Therefore, there is potential for more taxa to arrive in these high latitude regions, likely causing further structural changes in the lakes. Resampling these lakes (or a sample of these lakes) could provide further understanding of how warming and other environmental drivers can affect existing ecosystems and provide a temporal comparison of structural change between the original sampling dates and present. This could provide greater insight into the current health of high latitude lake ecosystems, indicating their resilience to modern warming and environmental change, and signifying whether they have undergone additional stress-driven structural change. Furthermore, exploring temporal records of assemblage change may increase our understanding of how individual lake assemblages change structurally over time; such as indicating whether assemblages exhibit signs of long-term or short-term stress. This may also enable the examination of the impact of secondary environmental factors on structural metrics; as Smol *et al.* (2005) argue - it is becoming increasingly unlikely to find Arctic lakes unaffected by human activity.

# Conclusions

This study provides a new comparison of three ecological metrics of structural change with the aim of testing whether high latitude lakes have experienced temperature-related stress. Comparison between simulated model outputs and empirical datasets suggested that assemblage changes in the North American and Norwegian datasets were driven by increasing taxon richness and turnover, whereas assemblage change in the Russian dataset was primarily driven by turnover.

In the North American and Norwegian datasets, lakes at the cold end of the temperature gradient showed signs of stress, however the agreement between the hypothetical models and empirical dataset metrics indicated that this could be an expected level of stress for cold environments. The metrics indicated signs of higher ecosystem stability in the mid-temperature range; the higher levels of beta diversity and turnover in these lakes could be due to greater habitat diversity. However, these trends deviated from those predicted by the hypothetical models; this could be a sign of additional stress or model simplicity. Lakes at the warmest end of the temperature gradient also showed some signs of stress. Lower levels of beta diversity could indicate an accrual of common taxa between sites or a loss in local biodiversity, however the simulated models suggested this was not an unexpected trend. Skewness, however, was more negative in the warmest lakes, which is a sign of ecosystem stress and was unpredicted by the modelled scenarios. This could indicate signs of unanticipated stress in warmer lakes, or could suggest the influence of secondary factors, such as site selection limitations or human activity. In the Russian datasets, lakes at the extreme ends of the temperature gradients produced responses in the ecological metrics that were less indicative of temperature-driven stress. Changes in the Russian assemblages appeared to be more driven by turnover, perhaps relating to the large geographic area with greater habitat diversity.

Overall, these analyses showed that changes in community structure, detected by beta diversity, °disorder, and network skewness, can reveal patterns that are indicative of ecosystem stability or instability for chironomid communities. The comparison to null models enabled reflection as to whether these stresses were to be expected of the temperature conditions, or whether there was additional stress on the ecosystems.

# Author contributions

R. J. Mayfield, P. G. Langdon, C. P. Doncaster, and J. A. Dearing discussed the research conceptualization and outcomes. C. P. Doncaster provided the original R code for the compositional disorder calculations and incidence matrix simulation R code used to create the theoretical data. R. Wang provided the original MATLAB network skewness code. R. J. Mayfield adapted the above codes, created the hypothetical datasets and ran all analyses on the simulated and empirical data. Chironomid data was provided by L. B. Nazarova, S. J. Brooks and A. S. Medeiros. New mean July temperatures were calculated for each lake using the CRUTEMP database by R. J. Mayfield, A. S. Medeiros provided some assistance with downloading individual temperature records. R. J. Mayfield generated additional lake data using ArcGIS. R. J. Mayfield wrote the first manuscript draft, on which all co-authors commented.

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