**University of Southampton**

Faculty of Environmental and Life Sciences

Geography and Environmental Science

# Analysing structural ecosystem change in high latitude lakes

by

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Thesis for the degree of Doctor of Philosophy (Ph.D.)

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## Abstract

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High latitude freshwater lakes are highly sensitive to climate change with numerous lake ecosystems already indicating signs of being impacted by the stress of global warming. With the current trajectory of climate change, it is anticipated that these impacts will continue and increase over the coming decades. Climate change is thought to be a likely driver of nonlinear response and abrupt transitions in ecosystems. Therefore, understanding lake ecosystem response to increasing climate stress is a complex issue yet is critical to forecasting ecosystem trajectories and predicting the vulnerability of lake ecosystems to abrupt ecological transitions. The majority of research surrounding nonlinear responses, tipping points, and critical transitions has focused on an approach centred on regime shifts from one community state to another over time. One element of this approach is the idea of early warnings signals within the frequency domain that may anticipate ecosystem instability prior to transitions between states. However, identifying early warning signals has been limited because of difficulties in detecting clear ecosystem shifts and valid statistical signals in time series data. As an alternative approach, research has recently expanded to consider testing ecosystem stability in the spatial domain, through analysing taxonomic organisation and connectivity within biotic networks.

The thesis tests the effectiveness of structural metrics as parameters of lake ecosystem stability using climatically and environmentally sensitive chironomids (Diptera: Chironomidae), a key macroinvertebrate component of freshwater ecosystems. Chironomid ecosystem structure is analysed over spatial temperature gradients, periods of past known abrupt high-magnitude and gradual low-magnitude climate change, and in response to modern (c. 200 years) climate warming. Model-simulated datasets are used to test metric expectations of community composition and structural change across temperature gradients and through network development. The work demonstrates the effectiveness of four ecological metrics, taxon richness, beta diversity, compositional disorder and network skewness, as indicators of chironomid community composition and structure in response to climate change.

Analyses indicate that chironomid assemblages in high latitude locations were likely to be experiencing some level of structural stress due to climate extremes. Climatic warming may have a two-fold effect on high latitude lakes. First, initial warming may allow ecological release and promote increased biological productivity, thus expanding the diversity of lake habitats and

chironomid assemblages. This was recognised in North American and Norwegian datasets through increased beta diversity, compositional disorder and network skewness values. Second, further temperature stress, often with the additional effects of secondary drivers, may cause ecological degradation through habitat homogenisation and increased breakdown of existing network structures. Chironomid communities at the warmest end of the temperature gradients in North American and Norwegian datasets showed decreased beta diversity, compositional disorder and network skewness values.

Evaluation of palaeoecological chironomid records spanning the Late Glacial and Holocene suggested that climate, as an exogenous stress, requires abrupt, high-magnitude change to alter aquatic community structures. Chironomid records spanning the abrupt, high-magnitude climate change at the Bølling-Allerød - Younger Dryas transition exhibited high magnitude changes in taxon richness and beta diversity. However, changes in the ecosystem structure, represented by °disorder and skewness, were smaller. This suggested some functional resilience within the chironomid communities, perhaps through the replacement of the same functional-type taxa in the network structure. Chironomid records spanning the Holocene indicated low taxonomic turnover in association with low levels of climate change, with little indication of climate-driven structural change. Changes within the chironomid assemblages suggested that other environmental factors were having a greater influence on the chironomid assemblages during this period of lower climatic stress.

Recent changes within the chironomid community composition in three subarctic Alaskan lakes indicated signs of climate stress, with increased beta diversity associated with increased lake biological productivity. Small changes in chironomid community structure suggested some resilience within the structure of the chironomid communities to the current levels of climate and environmental change.

Overall, changes in structural metrics for macroinvertebrate assemblages can provide insight into ecosystem stability and resilience. Ecosystems with impacted structures, as indicated by lower compositional disorder and network skewness values, are likely to be less resilient to increasing stress, and thus more vulnerable to system-wide transitions. Wider use and application of structural metrics may help identify reduced ecosystem resilience and vulnerability to potential tipping points in other major assemblages and ecosystems.

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# Research Thesis: Declaration of Authorship

Print name: Roseanna Jane Mayfield

Title of thesis: Analysing structural ecosystem change in high latitude lakes

I declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
5. I have acknowledged all main sources of help;
6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
7. Parts of this work have been published as:

**Paper 1**: Mayfield, R.J., Langdon, P.G., Doncaster, C.P., Dearing, J.A., Wang, R., Nazarova, L.B., Medeiros, A.S. and Brooks, S.J., 2020. Metrics of structural change as indicators of chironomid community stability in high latitude lakes. Quaternary Science Reviews, 249, p.106594. https://doi.org/10.1016/j.quascirev.2020.106594

**Paper 2**: Mayfield, R.J., Langdon, P.G., Doncaster, C.P., Dearing, J.A., Wang, R., Velle, G., Davis, K.L., Brooks, S.J. 2020. Late Quaternary chironomid ecosystem structure shaped by rate and magnitude of climate change. *Manuscript in review at Journal of Quaternary Science.*

**Paper 3**: Mayfield, R.J., Langdon, P.G., Doncaster, C.P., Dearing, J.A., Wang, R., 2020. Structural stability of lake communities during recent climatic and environmental change. *Manuscript in preparation.*

Signature: ....................................................................................... Date:...........................

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There are so many people who I would like to thank for their support over the course of my PhD. Here is just a short list, with further acknowledgements included at the end of each paper presented in this thesis.

Firstly, to my supervisors, Profs. Pete Langdon, John Dearing and Patrick Doncaster, thank you for your support, guidance and enthusiasm, for reading countless drafts, and answering all my questions and emails over the years. A special thank you to Pete for his endless encouragement and positivity.

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To all the laboratory staff, colleagues and friends over the years who have supported my laboratory work and made the experience that much more fun, thank you. You made long days of picking chironomid head capsules bearable! To all the staff and students in the School of Geography and Environmental Science, thank you for making Building 44 such a friendly and inspiring place to work.

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# Chapter 1 Introduction

## 1.1 Preamble

The Earth is warming at an unprecedented rate (Smith *et al.*, 2015; Post *et al.*, 2019), with the Arctic warming almost twice as fast as the global average (Walsh *et al.*, 2017; IPCC, 2018). Freshwater systems are highly vulnerable to climate change, with climate-driven changes recognised in abiotic and biotic factors; including changes in water chemistry and stratification (Holm *et al.*, 2011; Roberts *et al.*, 2017), lake size (Carroll *et al.*, 2011; Roach *et al.*, 2013), and algae (Rühland *et al.*, 2015; Lehnherr *et al.*, 2018), invertebrate (Luoto *et al.*, 2016; Klobucar *et al.*, 2018), fish (Murdoch and Power, 2013; Laske *et al.*, 2016), and bird (Lameris *et al.*, 2018) communities. High latitude lakes provide a diverse range of habitats for cold-adapted taxa and migrating birds (Vincent *et al.*, 2008), as well as providing important resources for local communities, such as drinking water and fisheries (Sjolander, 2011). Thus, understanding the pressures and changes high latitude freshwater ecosystems are experiencing is imperative for the prevalence of both ecological (Post *et al.*, 2009; Woelders *et al.*, 2018) and human (Hayden *et al.*, 2017) communities.

Anticipating changes in ecosystems under increasing climatic stress is a complex issue, yet it is critical for forecasting ecosystem trajectories and predicting the vulnerability of lake ecosystems to abrupt ecological transitions. Previously, 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 high resolution records, across the period prior to and during changes, which can be difficult and expensive to obtain. This thesis investigates the applicability of using structural analyses to understand how stress drives ecosystem change; as theory suggests that ecosystem resilience is strongly influenced by the organisation of taxa within the ecosystem structure (Strogatz, 2001; Scheffer *et al.*, 2012). Increasing our understanding of how freshwater ecosystems have responded to recent climate change improves our ability to anticipate conditions for future ecosystem stability.

In this thesis, the effectiveness of structural metrics as parameters of lake ecosystem stability is investigated using temperature and environmentally sensitive chironomids (Diptera: Chironomidae), a key macroinvertebrate component of freshwater ecosystems. Chironomid community structure is explored through space and time (Figure 1.1). Paper 1 (thesis chapter 3) analyses the effects of temperature-induced changes in taxonomic richness and compositional turnover in space using North American, Norwegian and Russian chironomid datasets. Paper 2 (thesis chapter 4) quantifies the ecosystem structural response of chironomids to high-magnitude climate change during the Late Glacial (14,700 – 11,700 yr cal BP) in Scotland and low-magnitude climate change during the Holocene (11,700 yrs cal BP to present) in Norway. Paper 3 (thesis chapter 5) analyses the current state of Subarctic Alaskan lake ecosystems, using chironomids as indicators of ecological stability, in response to modern (c. 200 years) climate warming and increased anthropogenic stresses.

Considering the existing wealth of chironomid datasets available within the scientific community, this thesis uses a combination of existing datasets and new records. Published datasets that have been presented in this thesis include the North American (Fortin et al. 2015), Norwegian (Brooks and Birks, 2001; 2004) and Russian (Nazarova *et al.*, 2011; 2015) chironomid calibration datasets, and temporal chironomid records from Ashik (Brooks *et al.*, 2012b), Abernethy (Brooks *et al.*, 2012b) and Muir Park (Brooks *et al.*, 2016) in Scotland, and Bjornfjelltjønn (Brooks, 2006b) and Holebudalen (Velle *et al.*, 2005a) in Norway. Four new chironomid records were produced as part of this thesis; one full Holocene sequence from Arctic Norway and three c. 200 year records from Subarctic Alaska.

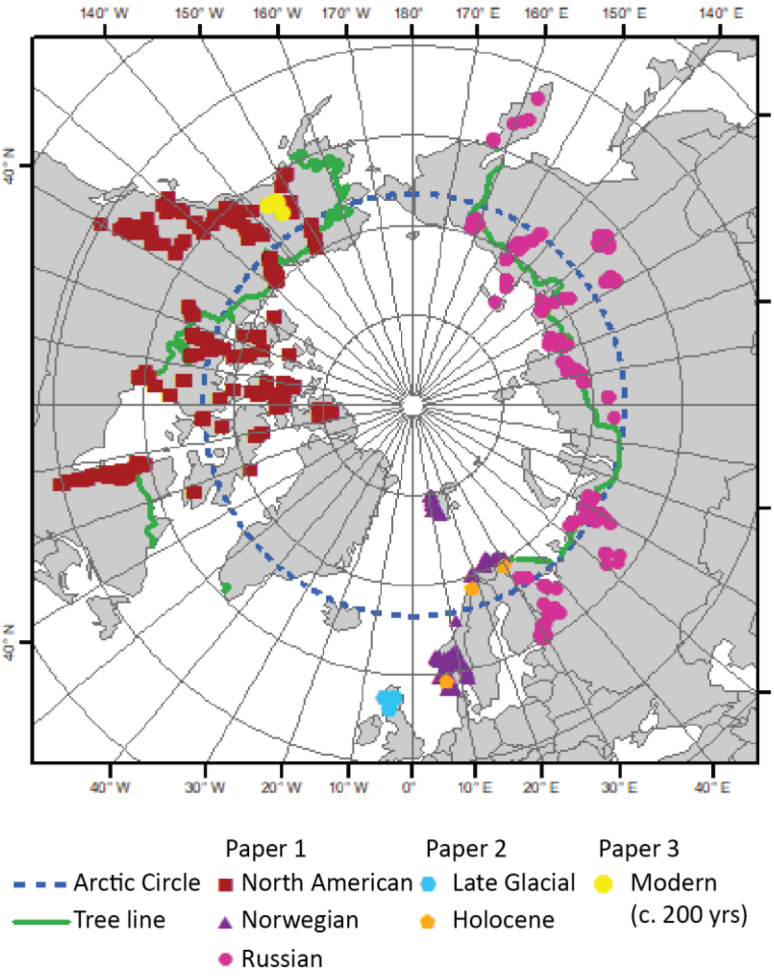

Figure 1.1 The records used in this thesis span a range of Arctic and Subarctic locations and time periods. Paper 1 (thesis chapter 3) analyses the effects of temperature-induced changes in taxonomic richness and compositional turnover in space using the North American, Norwegian and Russian chironomid calibration datasets. Paper 2 (thesis chapter 4) quantifies the ecosystem structural response of chironomids to high-magnitude climate change during the Late Glacial in Scotland and low-magnitude climate change during the Holocene in Norway. Paper 3 (thesis chapter 5) analyses the current state of Subarctic Alaskan lake ecosystems, using chironomids as indicators of ecological stability, in response to modern (c. 200 years) climate warming and increased anthropogenic stresses.

## 1.2 Research aims and objectives

The primary aim of this thesis was to investigate the utility of structural metrics as an indicator of lake ecosystem stability. The effect of climate change on high latitude lakes was used as a case study of ecosystem change. This aim was addressed through the following objectives:

- Evaluate taxon richness, beta diversity, compositional disorder and network skewness as metrics of chironomid assemblage change
- Analyse changing taxonomic richness and compositional turnover across spatial and temporal chironomid datasets
- Examine the effect of high and low magnitude climate change as a driver of assemblage structural change
- Investigate the combined effects of current climate and anthropogenic environmental change on chironomid assemblages

## 1.3 Thesis structure

This thesis is presented through the "3 paper thesis" approach, with three research papers designed and written to expand our scientific knowledge and understanding of ecosystem structural change in response to climate change. The main body of the work is presented as three papers; paper 1 is published in Quaternary Scientific Reviews (Mayfield *et al.*, 2020), paper 2 is in review at the Journal of Quaternary Science (Mayfield *et al.*, *in review*), and paper 3 is in the pre-submission stage of the publication process, with the aim of submitting the manuscript to The Holocene.

**Chapter 1** outlines the rationale for the primary research aims and objectives for this thesis.

**Chapter 2** reviews the relevant literature, providing background theory and evaluating previous methods for anticipating non-linear change in biological systems. This chapter highlights research gaps which have led to the creation of this work, and a brief overview of climate change in high latitude regions. Specific research questions are developed following the literature review (p. 22).

**Chapter 3** (paper 1) analyses the likely effects of temperature-induced changes in taxonomic richness and compositional turnover of chironomids across temperature gradients in North America, Norway and Russia. Taxon richness, beta diversity, compositional disorder and network skewness were discussed and applied to simulated and empirical chironomid datasets. Simulated chironomid taxa presence-absence data was generated to produce null expectations of community composition and structural change across temperature gradients and to assist with the interpretation of the empirical dataset trends.

**Chapter 4** (paper 2) quantifies ecosystem structural response of chironomids to high-magnitude climate change during the Late Glacial and low-magnitude change during the Holocene. Ordination, taxon richness, temporal beta diversity, compositional disorder and network skewness analyses were applied to temporal chironomid datasets to assess changes in the composition and structure of chironomid assemblages following the abrupt, high-magnitude climate change at the Bølling-Allerød – Younger Drays transition and the relatively slower and lower magnitude change between the early and mid-late Holocene. To distinguish true pattern from random noise in the ecological datasets, principles from Telford and Birks (2011) were followed for minimising the likeliness of drawing conclusions from spurious correlations.

**Chapter 5** (paper 3) evaluates the current ecosystem stability in three Subarctic lakes, using chironomids as indicators of ecological stability, in relation to climatic and anthropogenic drivers of stress. Model simulations were used to assess the informative power of taxon richness, temporal beta diversity and network skewness in analysing changing network structure and taxon connectivity. Taxon richness, temporal beta diversity and network skewness analyses were applied to temporal chironomid datasets to assess changes in the composition and structure of chironomid communities over the recent c. 200 years. Ordination and generalized additive models (GAMs) were used to assess the influence of recent climate and environmental change on chironomid community composition and structure.

**Chapter 6** provides a synthesis of the findings from the three papers and summarises how this work has added to the scientific knowledge of climate-driven ecosystem change. Limitations and avenues for further research are discussed.

## 1.4 Three papers

The following three papers are presented in this thesis.

### 1.4.1 Paper 1

This paper is published as:

Mayfield, R.J., Langdon, P.G., Doncaster, C.P., Dearing, J.A., Wang, R., Nazarova, L.B., Medeiros, A.S. and Brooks, S.J., 2020. Metrics of structural change as indicators of chironomid community stability in high latitude lakes. Quaternary Science Reviews, 249, p.106594.

https://doi.org/10.1016/j.quascirev.2020.106594

This work has been presented as (selected examples):

Mayfield, R.J., Langdon, P.G., Doncaster, C.P., Dearing, J.A. 2019. Exploring lake ecosystem resilience in a warming (sub)arctic through ecosystem structural changes. *20th Congress of the International Union for Quaternary Research (INQUA)*. Dublin, Ireland. 27th July. Oral Presentation.

Mayfield, R.J., Langdon, P.G., Doncaster, C.P., Dearing, J.A., Dyke, J.G. 2017. Lake ecosystem response to climate forcing. *QRA Short Discussion Meeting – Developments in Quaternary Entomology and Environmental Reconstruction*. National History Museum, London, UK. 01st June. Oral Presentation.

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.

### 1.4.2 Paper 2

This paper has been submitted to Journal of Quaternary and is currently under peer-review:

Mayfield, R.J., Langdon, P.G., Doncaster, C.P., Dearing, J.A., Wang, R., Velle, G., Davis, K.L., Brooks, S.J. 2020. Late Quaternary chironomid ecosystem structure shaped by rate and magnitude of climate change.

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. R. Wang provided the original MATLAB network skewness code. R.J. Mayfield adapted the above codes and ran all analyses on the empirical data. R.J. Mayfield was part of the coring team at Horntjernet, and processed and identified the Horntjernet chironomid samples at the University of Southampton. P.G. Langdon and S.J. Brooks provided assistance with chironomid identification. Other chironomid data was provided by S.J. Brooks, K.L. Davies, and G. Velle. R.J. Mayfield wrote the draft manuscript, on which all co-authors commented.

### 1.4.3 Paper 3

This paper is currently in the pre-submission stage of the publication process:

Mayfield, R.J., Langdon, P.G., Doncaster, C.P., Dearing, J.A., Wang, R., 2020. Structural stability of lake communities during recent climatic and environmental change. *Manuscript in preparation.*

Author contributions:

R.J. Mayfield, P.G. Langdon, C.P. Doncaster, and J.A. Dearing discussed the research conceptualization and outcomes. R.J. Mayfield and P.G. Langdon discussed potential coring sites. R.J. Mayfield was part of the fieldwork team and collected sediment and water samples. R.J. Mayfield processed the $^{210}$Pb, LOI, bulk density, and chironomid samples. R.J. Mayfield identified the chironomid samples with assistance from P.G. Langdon. R. Wang provided the original MATLAB network skewness code. R.J. Mayfield wrote the network simulation code. R.J. Mayfield adapted the skewness code and ran all analyses on the simulated and empirical data. R.J. Mayfield analysed all data outputs. R.J. Mayfield wrote the draft manuscript, on which all co-authors commented.

# Chapter 2 Literature Review

This literature review is divided into two parts; the first section provides background information on tipping point theory and methods for detecting tipping points, ecological thresholds, and critical transitions in ecosystems. Much of the original work on tipping points refers to detecting system change within the frequency domain; using time-series data to identify fundamental shifts from one community state to another over time. Tipping point theory is reviewed, with reference to applications, limitations, and examples from the frequency domain. Theory for detecting ecological shifts in the spatial domain is introduced. Specific theory and background information for detecting ecological shifts in the spatial domain, and the principal methods (taxon richness, beta diversity, compositional disorder and network skewness) are discussed further in the individual papers (chapters 3 – 5). The second part of this literature review provides a brief introduction to climate change as a driver of lake ecosystem change in high latitude regions.

## 2.1 Anticipating abrupt change in ecosystems

Systems are continuously subjected to a combination of external drivers, and internal processes, forces, and feedback mechanisms (Williams *et al.*, 2011; Scheffer *et al.*, 2012). Ecosystems can respond gradually and linearly to these forces, allowing internal mechanisms and biological communities to adapt to the changing conditions (Young and Collier, 2009; Feher *et al.*, 2017). Alternatively, ecosystems can shift disproportionally in response to a driver, across a threshold, and transition into an alternative state, known as a critical transition (Scheffer *et al.*, 2001; Scheffer, 2009; Ditlevsen and Johnsen, 2010; Scheffer *et al.*, 2012). While critical transitions are often portrayed as abrupt and dramatic, such transitions can occur slowly and imperceptibly once a threshold has been passed (Hughes *et al.*, 2013). Strong feedback mechanisms are often an integral factor in the tipping point process (Scheffer and Carpenter, 2003; Lenton, 2013).

What causes systems to transition into different states is not a new concept; it has been studied previously under the identity of “catastrophe theory”, the notion that spatio-temporal structures can undergo discontinuous (abrupt) shifts due to a continuous change in a variable which has a control over the system (Holling, 1973; Thom, 1975). The question has persisted and an evolved theory has developed, advancing the methods of detecting and anticipating critical transitions, for example in Scheffer *et al.* (2001) and Scheffer *et al.* (2012). Detecting, or anticipating, tipping points is valuable for ecosystem management (Litzow and Hunsicker, 2016); often new ecosystem states are undesirable; for example, the local extinction of species (Scheffer *et al.*, 2001; Drake and Griffen, 2010) and eutrophication (Wang *et al.*, 2012). Thus, research into the non-linear dynamics of ecosystems has grown in recent years. Research has developed two avenues for detecting tipping points: changes in the time-series of key variables (the frequency domain) and changes in the system structure (the spatial domain), which are reviewed further below. A large proportion of recent work has focused on freshwater lakes and tipping points relating to eutrophication; such studies are referred to as examples in this review.

### 2.1.1 Tipping point definitions, theory and real world examples

Tipping points, a concept coined by Gladwell (2000), describe the point at which systems abruptly shift from one steady state to another once an internal threshold has been passed (Lenton *et al.*, 2008; van Nes *et al.*, 2016). A threshold refers to an upper limit of an exogenous driver, which triggers a transition into an alternative state (Groffman *et al.*, 2006; Dearing *et al.*, 2014). Thresholds can be difficult to quantify (Muradian, 2001), possibly because thresholds are likely to be individual to ecosystems, depending on lake size, catchment, and starting ecology. A critical transition is the process in which a system moves from one steady state into an alternative state, once a threshold has been passed (Scheffer *et al.*, 2009). Critical transitions are frequently hysteretic (i.e. experience hysteresis), meaning that the driving stress must be substantially reduced, below the level which initiated the transition, for the system to return to its original state (Scheffer *et al.*, 2001). The term regime shift signifies that the system has undergone a critical transition (Folke *et al.*, 2004; Lees *et al.*, 2006). Ecosystem resilience is defined as the capacity of an ecosystem to absorb disturbance and retain the same ecological function, without shifting into an alternative state (Holling, 1973; Folke *et al.*, 2004; Walker *et al.*, 2004).

Ecosystem response to stress can be gradual and linear, where a system has a small response to a small change in the stressor (Figure 2.1 A); or abrupt and non-linear, where the system experiences a disproportionally large response to a small increase in a stressor (Figure 2.1 B - D) (Scheffer *et al.*, 2009; Scheffer *et al.*, 2012). Linear responses are often more predictable, and/or manageable, as ecosystem state changes proportionally to the level of stress (Young and Collier, 2009). Non-linear responses are common across a wide range of ecosystems; including lake (Carpenter *et al.*, 1999), marine (Lees *et al.*, 2006), coastal (Hewitt *et al.*, 2016) and terrestrial (Holmgren *et al.*, 2012) ecosystems. Non-linear ecosystem transitions can occur in many complex dynamical systems (Scheffer *et al.*, 2009), however, a threshold must have been crossed for a critical transition to have occurred (Figure 2.1 D) (Ditlevsen and Johnsen, 2010). This threshold can be crossed due to multiple interconnecting drivers, by a single pressure if it is strong enough, or by a force amplified through feedback mechanisms (Veraart *et al.*, 2011).

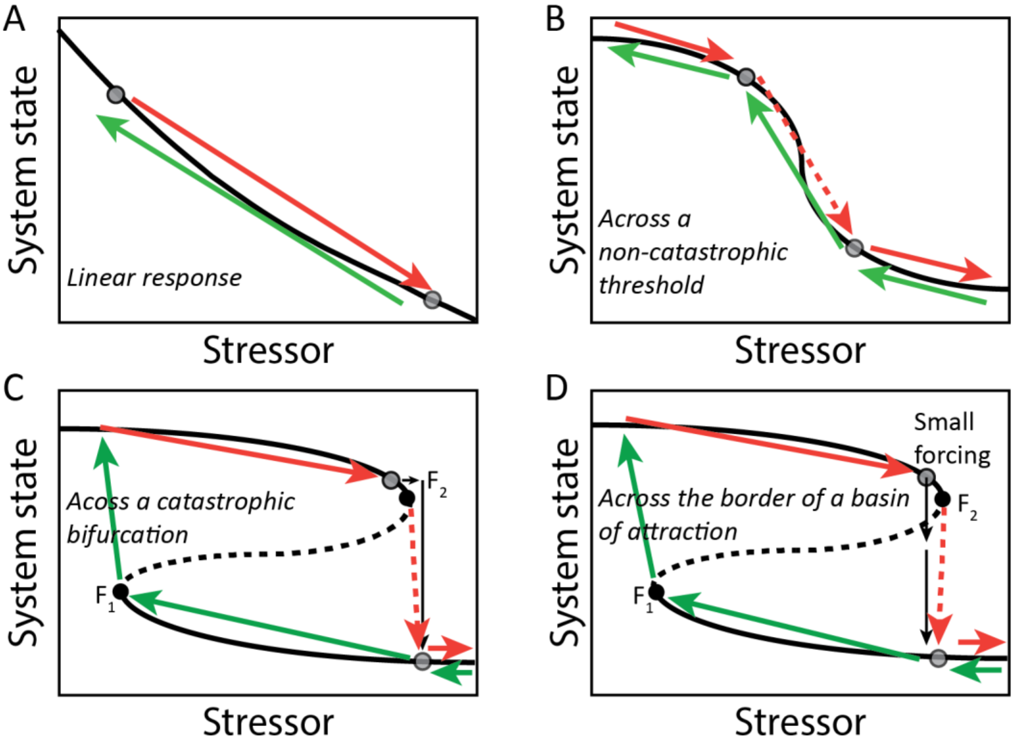

Figure 2.1 Understanding system response (y axis) to stress (x axis). As a stressor increases, a system (black line) may have a small response, i.e. a linear response (A), or a disproportionally large response, i.e. a non-linear response (B - D). System B experiences a non-hysteretic shift i.e. the reverse trajectory (green arrow) follows the same path as the outward trajectory (red arrow). Systems C and D can operate in two alternative stable states, with intermediate, unstable states (dashed line). As systems C and D approach thresholds ($F_2$), a small perturbation can cause a disproportionately large shift in the system (i.e. the system moves to the bottom curve). In some circumstances, system D, this small perturbation can cause the system to shift into an alternative steady state. Systems C and D show hysteretic changes; for the systems to return to their previous states, the external forcing must be substantially reduced below the background conditions. Diagram adapted from Scheffer *et al*. (2009).

Positive feedback loops can reinforce processes, drive evolutionary change or reduce stability within ecosystems (Crespi, 2004; Reyer *et al.*, 2015), and are frequently key components in the tipping point process (Nosil *et al.*, 2017). The breakdown of existing, and/or development of new positive feedbacks can help advance a system over a critical threshold, or propel the system forward towards an alternative state once the threshold for change has been passed (Scheffer and Carpenter, 2003; Angeli *et al.*, 2004). For example, in low-nutrient, clear-water lake conditions, positive feedbacks may exist between plants and plankton; plants provide shelter for the zooplankton, which feed on phytoplankton (algae), keeping the water clear (Sayer *et al.*, 2010). However, increased nutrient input can cause a growth of algae, restricting the sunlight from reaching the plants and diminishing the plants (Ferreira *et al.*, 2011). Fewer plants mean fewer zooplankton available to regulate the algal population, and algal populations increase. The original feedback loop that kept the water clear has diminished, and a new feedback loop can develop in its place; more algae means less plants and less zooplankton and hence more algae (Sunda *et al.*, 2006).

Critical transitions are frequently hysteretic; meaning for the system to return to its original state, the driving force must be reduced considerably below the level at which the transition occurred (Figure 2.1 C - D) (Scheffer *et al.*, 2001). Theoretically critical transitions can be reversed, with disruption to the ecosystem (Dearing *et al.*, 2014), however the practicality of an ecosystem returning to its previous state is low in real world systems. For example, the development of new and resilient positive feedback loops (Carpenter, 2005) or changes in environmental conditions (e.g. climate) (Dakos *et al.*, 2008) can substantially reduce the likelihood of a system returning to its previous steady state. Alternatively, evolutionary changes in species traits may prevent ecosystems from recovering (Dakos *et al.*, 2019), or the driving stressors may change at a faster rate than the ecosystem can recover (Peters *et al.*, 2012). Some studies proposed that there is a window of opportunity following a transition, in which a system may revert to safer conditions before the change becomes permanent (Biggs *et al.*, 2009; Hughes *et al.*, 2013). For example, in a purposely-manipulated lake experiment it was demonstrated that eutrophic lake conditions could be reversed by continually measuring the enrichment levels with sensory data loggers and ceasing the input of nutrients at a pre-determined level (Pace *et al.*, 2016). Others argued that despite model simulations suggesting reversals are possible, e.g. models indicated that the irreversibility of sea ice loss is erroneous (Armour *et al.*, 2011), once environmental conditions have changed and new feedback mechanisms have developed, there is very little chance of a reversal (Hughes *et al.*, 2013). Considering critical transitions can be difficult to reverse in real world scenarios, it is likely easier to prevent than reverse critical transitions (Hansen *et al.*, 2013).

### 2.1.2 Identifying tipping points in the frequency domain

Research has shown that, theoretically, critical transitions can be anticipated by Early Warning Signals (EWS) (Scheffer *et al.*, 2009). Mathematically, EWS arise as systems approach a bifurcation point (tipping point; Ashwin *et al*., 2012) and are relatively simple to formulate (Kuehn, 2011). However, observing EWS in real world systems is complex (Langdon *et al.*, 2016). Work to develop methods of detecting EWS and anticipating tipping points has accelerated as there is huge potential in understanding the drivers and mechanisms behind these sudden shifts to allow early prediction of impending transitions, avoid ecological “surprises” and aid ecosystem service management (Litzow and Hunsicker, 2016). There has been a considerable amount of research focusing on identifying EWS in the frequency domain, investigating changes in the system state prior to critical transitions; such phenomena include critical slowing down, skewness and flickering (Figure 2.2) (Scheffer *et al.*, 2012).

Critical slowing down describes the decreasing rate of recovery following perturbations; often as a system becomes more stressed in the approach to a threshold, the system becomes slower to respond to stress (Figure 2.2 F, Figure 2.3) (Scheffer *et al.*, 2009). This slowing down links to the decline and development of feedback mechanisms as the system loses resilience and re-structures; following an impact there is less strength in the balancing processes to stabilise the system. Therefore, this EWS acts as a proxy for internal re-structuring. Critical slowing down can be identified through two fundamental ways: autocorrelation and variability. Autocorrelation, the rate of change within the system, decreases as the system nears a critical transition (Figure 2.2 H) (Scheffer *et al.*, 2009; Kéfi *et al.*, 2013). The variability of the system (i.e. the time needed for the system to recover and shift between alternate states) increases as the system nears a tipping point (Figure 2.2 G, Figure 2.3 B) (Carpenter and Brock, 2006). Thus, autocorrelation and variability indicate that the system is slower to react to stress and are indicative of critical transitions (Scheffer *et al.*, 2009).

Skewness refers to the asymmetry of the system fluctuations prior to a bifurcation or tipping point (Guttal and Jayaprakash, 2008). As a system approaches a tipping point, it becomes slower to recover from perturbations, meaning that the system will linger in the vicinity preceding the unstable state, until the tipping point is reached and the system abruptly transitions into the new state. Thus, the skewness of the system fluctuations acts as an indicator of resilience and the loss of resilience suggests that the system is nearing a tipping point (Guttal and Jayaprakash, 2008; Scheffer *et al.*, 2009).

Flickering is a phenomenon which occurs in highly stochastic (unpredictable) systems and is thought to be driven by exogenous forces (Wang *et al.*, 2012). Strong stochastic forcing can move the system back and forth between stable states before a permanent shift occurs (Figure 2.2 G) (Scheffer *et al.*, 2009; Scheffer *et al.*, 2012). Flickering can be detected from a rise in variance corresponding with a reduction in autocorrelation and skewness (Wang *et al.*, 2012).

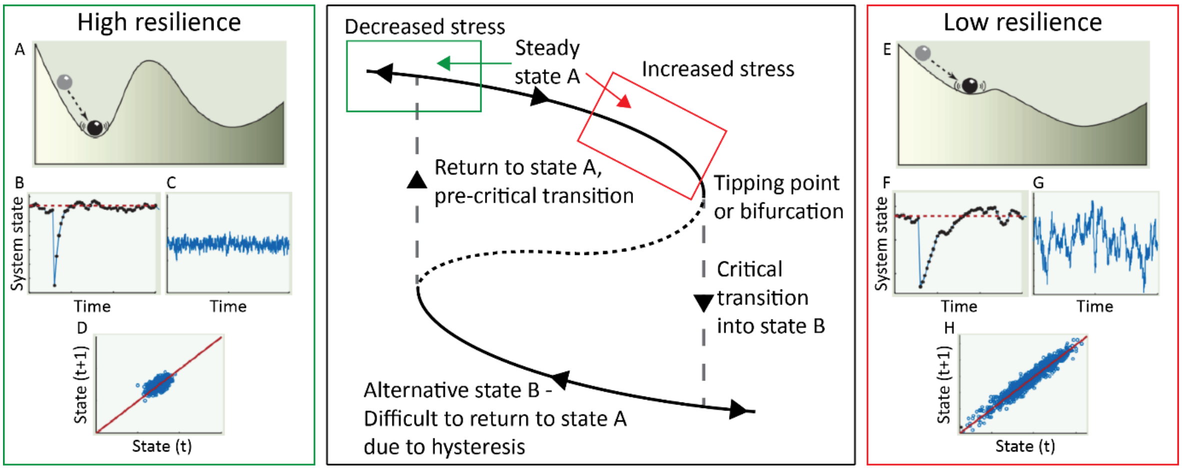

Figure 2.2 Early Warning Signals (EWS) are phenomena which occur before a tipping point is reached and indicate that a system is in distress and likely to experience a regime shift. Under decreased stress conditions, systems tend to have higher resilience (A), a faster recovery rate to perturbations (B), decreased variance (C) and a reduced lag in autocorrelation (D). As a system becomes increasingly stressed and moves towards a tipping point or bifurcation, systems tend to have lower resilience (E), a slower recovery rate to perturbations (F), flickering between system states due to increased variance (G) and a higher first-lag autocorrelation (H). Central bifurcation diagram drawn by R.J. Mayfield, EWS inset diagrams taken from Scheffer *et al*. (2012).

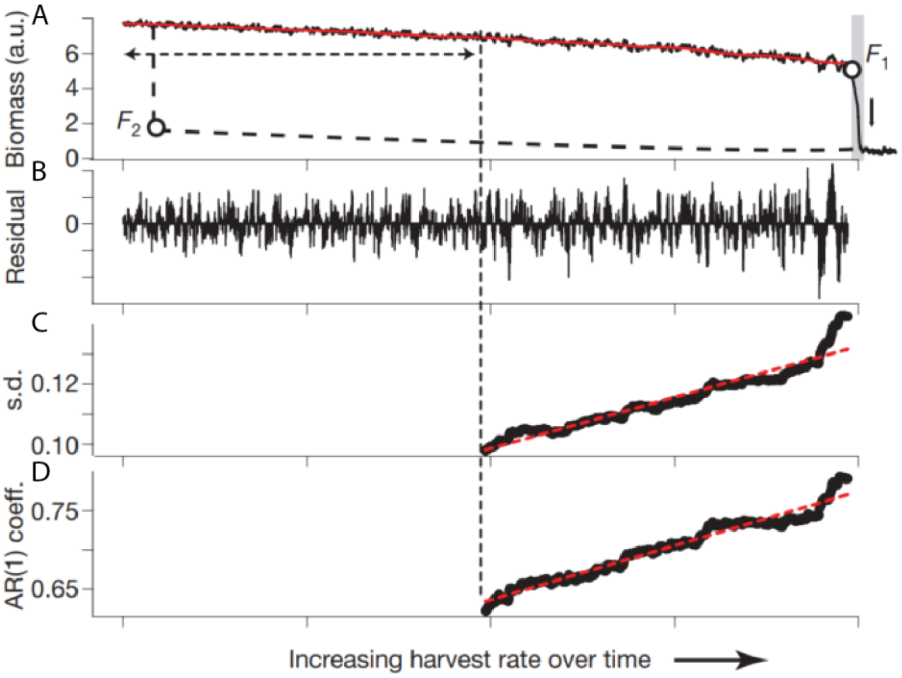

Figure 2.3 EWS for a critical transition in a biomass time series data. Plot (A) shows the trajectory of the time series data towards a critical transition (the grey band). As the system nears the critical transition, the amplitude of fluctuations increase (B), as indicated by the standard deviation (s.d., plot C) and lag-1 autoregression (AR(1) coeff., plot D). Diagram from Scheffer *et al.* (2009), see original publication for methodology.

EWS of ecosystem collapse have been identified in laboratory-controlled (Drake and Griffen, 2010), whole lake (Carpenter *et al.*, 2011), and computer simulated (Dakos *et al.*, 2013) experiments. However, detecting EWS in natural, real-world ecosystems has proved challenging. Evidence of flickering was detected within diatom assemblages prior to an eutrophication-driven collapse (Wang *et al.*, 2012) and an increase in skewness was identified prior to a regime shift in a Saharan dataset (Guttal and Jayaprakash, 2008). However, issues remain, for example in data resolution (Wang *et al.*, 2012), transitions with no EWS (Hastings and Wysham, 2010), false-negative or false-positive EWS (Kéfi *et al.*, 2013; Burthe *et al.*, 2016), and long, equidistant time series are required (Dakos *et al.*, 2012; Litzow and Hunsicker, 2016). Other studies had a mixture of success and failure; successfully detecting increasing variability 1 - 4 years before fishery collapse, but failing to detect increases in skewness prior to collapse (Litzow *et al.*, 2013). Mixtures of successes and failures are perhaps not surprising when applying predictions derived from simple models to complex real world systems (Scheffer *et al*., 2015).

Difficulties in detecting clear ecosystem shifts and EWS has led to growing criticisms; e.g. Mac Nally *et al.* (2014), Capon *et al.* (2015), Montoya *et al.* (2018) and Hillebrand *et al.* (2020), and calls for greater unification in theory, definitions, and applications (Capon *et al.*, 2015; Munson *et al.*, 2018; Klose *et al.*, 2020). In particular, criticisms arose regarding the lack of threshold-driven change or alternate states recorded in empirical systems (Montoya *et al.*, 2018; Hillebrand *et al.*, 2020) and the lack of evidence of linear recovery following a reduction of stress (Jeppesen *et al.*, 2007; Capon *et al.*, 2015). Issues with the application of methods have highlighted the need for meaningfully distinguished background variations (Rudnick and Davis, 2003; Spears *et al.*, 2017), and high temporal resolution and long-term datasets (Dakos *et al.*, 2014; Spears *et al.*, 2017) to fully ascertain current and previous ecosystem states. Such issues emphasize the need for long-term monitoring of freshwater systems and a consensus of measurable quantities that capture the relationship between the trajectories of ecosystems and their stressors (Mac Nally *et al.*, 2014; Capon *et al.*, 2015). It is such issues in detecting ecosystem shifts and EWS in the temporal domain that has led to exploration of ecosystem change in the spatial domain.

### 2.1.3 Ecosystem structure as an indicator of ecosystem stability

The spatial domain may provide greater potential for understanding how stress drives ecosystem change through understanding and analysing ecosystem structure, using network theory. Network theory describes systems as networks of inter-connected units called nodes (Barabási and Albert, 1999; Barabási and Bonabeau, 2003). Virtually all dynamical systems can be defined as networks, regardless of scale or subject; including cells, financial markets or lake ecosystems (Scheffer, 2009). Scheffer *et al*. (2012) summarise and discuss fundamental ideas from network theory, identifying two key types of system structure based on the organisation and connectivity of nodes. These systems are comprised of homogeneous (similar) or heterogeneous (diverse) networks of nodes (Figure 2.4) (Scheffer *et al*., 2012). Nodes can be strongly connected (i.e. have many connections) or weakly connected (i.e. have few connections) (Barabási and Albert, 1999; Barabási and Bonabeau, 2003). In networks of weakly connected, heterogeneous nodes, the systems tend to respond to stress linearly, as individual nodes can change (leave or join the network) as necessary under stress (Figure 2.4 A) (van Nes and Scheffer, 2005; Scheffer *et al*., 2012). In contrast, strongly connected networks of homogeneous nodes have an initial resistance to change; the network can retain its structure until the stress becomes too great (i.e. a threshold is reached) and the network experiences a system-wide shift in nodes (i.e. a critical transition) (Figure 2.4 B) (Dunne *et al.*, 2002; van Nes and Scheffer, 2005; Scheffer *et al.*, 2012). This second type of network has an initial resilience to stress, as the effects of local perturbations can be minimised or counterbalanced by subsidiary inputs from the broader system (Scheffer *et al*., 2012).

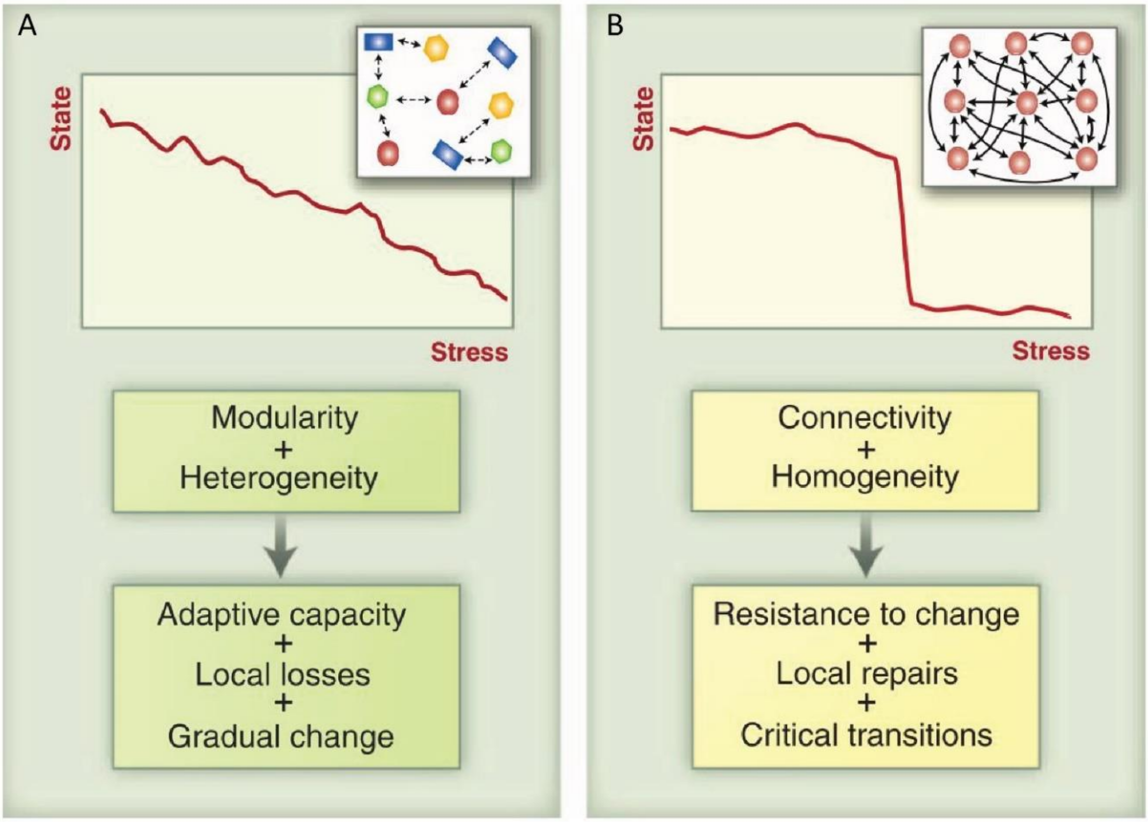

Figure 2.4 Scheffer et al. (2012) hypothesise two fundamental types of system architecture; weakly connected, heterogenic (A) and strongly connected, homogeneous (B) systems. The organisation of these structures is thought to affect how systems respond to stress. Diagram from Scheffer et al. (2012).

Theory suggests that ecosystem resilience is strongly influenced by the structural changes in taxa associations (Strogatz, 2001; Scheffer *et al.*, 2012). Network theory can be applied to ecosystems, with nodes representing taxa and inter-specific associations representing connections. Self-organisation theory states that under low stress conditions, taxa will self-organise into their preferred microhabitats, where the majority of taxa will be weakly connected and a few taxa will be strongly connected (Strogatz, 2001; Doncaster *et al.*, 2016). In Lotka-Volterra competition dynamics, weakly connected taxa can be compared to poorly-competitive and slow self-replicating ‘canary’ taxa, which are the first to disappear (become locally extinct) under increased exogenous stress (Doncaster *et al.*, 2016). Strongly connected taxa are compared to strongly-competitive and weakly self-replicating ‘keystone’ taxa (Figure 2.5, A) (Doncaster *et al.*, 2016). A predominance of weakly connected taxa produces a positively skewed distribution of connectedness (Figure 2.5, B). When a system becomes disturbed canary taxa decline first, while the strongly connected keystone taxa initially prevail distorting the system distribution (Figure 2.5 A(ii), C). As the system becomes increasingly degraded, keystone taxa regress giving competitive release to faster replicating, subordinate weedy taxa (Figure 2.5, A(iii)) (Doncaster *et al.*, 2016). Weedy taxa tend to be eurytopic, thus increasing their probability of interacting with other taxa, causing a negative skewness in connective frequency (Figure 2.5, D) (Darling *et al.*, 2012; Doubleday and Connell, 2018). Thus, theoretically, the structural organisation of an ecosystem can indicate the stability of its lake (Wang *et al.*, 2019).

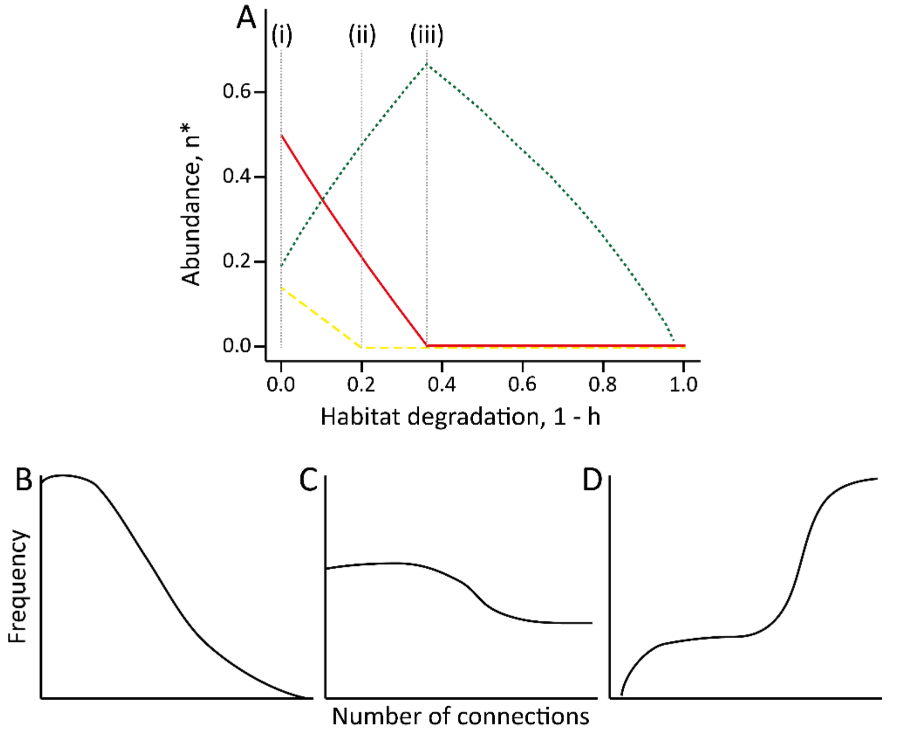

Figure 2.5 Stages of extinction under increasing habitat degradation *h* (A). Initially (i), keystone taxa prevail (red solid line), while “canary” taxa (yellow dashed line) become extinct (ii). As degradation increases (iii), ephemeral “weedy” taxa (green dashed line) reach their peak abundance while keystone taxa become extinct. Diagram A is from Doncaster *et al*. (2016), see the original publication for the Lotka-Volterra equations used produce the curves. Self-organised networks are comprised of a large number of weakly connected taxa and small number of highly connected taxa, producing a positively skewed distribution of taxa connections (B). As the system becomes disturbed, the number of weakly connected taxa declines, while highly connected taxa initially prevail, changing the degree distribution (C). As stress continues and the system degenerates further, the network becomes dominated by faster replicating weedy taxa, which experience competitive release following the loss of keystone taxa (D).

The consequences of experiencing a critical transition can be severe for ecosystems, fundamentally changing the ecosystem structure and causing ecological, economic or conservation issues (Scheffer *et al*., 2001); for example, eutrophication can cause fish stocks to deplete altering the lake food-web and reducing food sources (Scheffer *et al*., 2009). Thus, examining ecosystem structure may provide increased insight into ecosystem resilience and likely responses to stress. Analysing network structure changes over time may indicate whether a system has suffered stress, the response of the ecosystem to stress, and whether an ecological threshold was crossed. A number of researchers have started to develop structural metrics to analyse the organisation of taxa and their interactions, to detect structural stability in aquatic communities. Doncaster et al. (2016) used compositional disorder, a measure of nestedness, as an indicator of instability prior to ecosystem collapse; under increased stress, decreased compositional disorder indicated a decline in taxonomic turnover as aquatic communities became more nested. Wang et al. (2019) used network skewness, a measure of taxonomic connectivity, as a parameter of structural stability, indicating that aquatic ecosystems experienced a loss of structure under growing human pressure due to habitat homogenisation. Note, network skewness (i.e. the proportion of strongly and weakly connected taxa) is a measure of network structure, and differs to the frequency domain EWS skewness used to measure the asymmetry of system fluctuations prior to a bifurcation (p. 11). From this point onwards in the thesis, skewness refers to the structural metric, network skewness.

### 2.1.4 Testing for ecosystem change in empirical systems

Palaeoecological archives can provide opportunities to ascertain how far existing systems may have drifted from historical states and identify potential alternative ecosystem states (Willis *et al.*, 2010). Spatial patterns of ecosystem structures may provide insight into the current state of lakes across a broader area; modern datasets of ecological proxies can provide insight into climate change effects across regions, covering large climate gradients (Larocque *et al.*, 2001). Space-for-time substitution is a long-standing technique for investigating process changes, especially where instrumental data is sparse or palaeorecords are unavailable (Pickett, 1989). Regional studies can also reveal patterns within regional change, for example, coastal or mountainous parts of the Arctic might be changing at different rates. Both spatial and temporal studies have their limitations, for example, ecological processes may not develop in the same manner over space and time (Damgaard, 2019), and time series analyses often focus on a small number of sites, samples are often not equidistant in time, and have age model uncertainties (Franke and Donner, 2019). However, both techniques have the potential to expand our understanding of how ecosystem structure may be changing under climatic stress, thus both spatial and temporal datasets are explored in this thesis.

## 2.2 The Arctic and Subarctic: ecologically sensitive regions under threat of climate change

High latitude regions, namely the Arctic (> 66° N latitude) and Subarctic (c. 50° – 70° N), are typically cold and climatically dry (Wielgolaski and Inouye, 2003). High latitude ecosystems face a number of challenges; flora and fauna must be adapted to endure freezing temperatures, limited food availability, and short growing seasons (Lannig *et al.*, 2003; Cooper *et al.*, 2011; Sheriff *et al.*, 2012; Peterson, 2014). Thus, these environments are highly ecologically sensitive (Smol *et al.*, 2005), often with low-diversity ecosystems (Wall, 2007), in which many species are living at their tolerance limits

(Langdon *et al.*, 2011). While such ecosystems can be stable in their natural states (Dunbar, 1973; Jonasson *et al.*, 1999), they are often more vulnerable to stress, and small perturbations are more likely to test, or pressurise, the resilience of these ecosystems (Smol *et al.*, 2005).

Current climate change is occurring at an unprecedented rate (Smith *et al.*, 2015), with the Arctic warming almost twice as fast as the global average (Graversen *et al.*, 2008; Bekryaev *et al.*, 2010; IPCC, 2018) due to amplification effects (Pithan and Mauritsen, 2014). A wide variety of climate-related changes have already been recognised across the Arctic and Subarctic, including permafrost thawing (Jorgenson *et al.*, 2006), peat desiccation (Yurganov *et al.*, 2011), greening (Elmendorf *et al.*, 2012), lake shallowing (Smol and Douglas, 2007a) and increased nitrogen deposition from migrating bird colonies and guano deposits (Griffiths *et al.*, 2009). High latitude freshwater lake ecosystems are highly vulnerable to climate change, subjected to increases in temperature, atmospheric $CO_2$, droughts and nutrient influxes (Woodward *et al.*, 2010), and changes in seasonality and precipitation regimes (Medeiros *et al.*, 2017). Climate-driven changes in lake assemblages have already been recorded in Arctic and Subarctic locations (Smol and Douglas, 2007a; Rosén *et al.*, 2009), including changes in chironomid and diatom assemblages and green-algae blooms (Smol *et al.*, 2005; Rühland *et al.*, 2013; Woelders *et al.*, 2018).

Freshwater lakes and ponds are a common feature across the Arctic, spanning a diverse range of environments, including tundra, permafrost and glacial landscapes (Vincent *et al.*, 2013). Lakes provide natural archives of past climatic and environmental change with good potential for fossil preservation, long records and high resolution (Cohen, 2003; Dearing *et al.*, 2015), making them ideal systems for research. Given the high sensitivity of high latitude ecosystems (Smol *et al.*, 2005) and the trajectory of future climate change (Walsh *et al.*, 2017; IPCC, 2018), it is possible that non-linear changes in high latitude ecosystems will increase in likeliness (Lenton, 2012; Adams, 2013; Clark *et al.*, 2013). Thus, this thesis uses high latitude lakes to investigate the utility of structural metrics as indicators of ecosystem stability under climate change.

### 2.2.1 Chironomids

Chironomid (Diptera: Chironomidae; non-biting midges) larvae are a common environmental indicator as they are stenotopic (have narrow ecological optima), ubiquitous (exist in a large range of aquatic biotopes), species-rich (with many taxa sharing similar habitats), highly sensitive (rapidly responding to environmental changes), and extremely abundant (Brooks *et al.*, 2007). Temperature is thought to be the strongest influential variable on chironomid assemblages as it directly affects the organisms' physiological and biochemical processes; including development, growth, and respiration (Eggermont and Heiri, 2012). Thus, it is thought that the abundance and distribution of chironomids are strongly related to summer temperatures (van Asch *et al.*, 2012). Chironomids can also be influenced by a range of environmental factors, such as glacial meltwater influx, pH, nutrient inwash, dissolved oxygen levels, lake depth, and salinity (Quinlan and Smol, 2001; Brooks, 2006b; Brooks *et al.*, 2007; Engels and Cwynar, 2011; Eggermont and Heiri, 2012). As chironomids are directly influenced by lake conditions, they are thought to make reliable indicators of lake ecosystem changes. Chironomid larval head capsules preserve well in sediments, especially late Quaternary deposits, and are identifiable to genus or species-morphotype level (Brooks *et al.*, 2007). Thus, chironomids are valuable and useful indicators of past climatic change (Walker *et al.*, 1991; Brooks, 2006b), including in the Arctic (Larocque *et al.*, 2001; Velle *et al.*, 2005a; Engels and Cwynar, 2011; Eggermont and Heiri, 2012; Axford *et al.*, 2017).

Climate change is thought to alter chironomid communities directly through physiology and indirectly through phenology, seasonality and taxonomic interspecific interactions (Harley, 2011; Klobucar *et al.*, 2018). Chironomids are a fundamental part of the macroinvertebrate component of food webs (Jones and Grey, 2004; Ólafsson and Paterson, 2004), thus, changes in the abundance or distribution of chironomids can have repercussions throughout the ecosystem (Quinlan *et al.*, 2005; Pearce-Higgins, 2010; Klobucar *et al.*, 2018). Under recent climate change, chironomid abundance and diversity has increased across the Arctic (Quinlan *et al.*, 2005; Luoto *et al.*, 2014). It is possible that chironomids continue to increase in diversity with climate warming, as cold-stenothermic taxa become replaced by warm-preferring taxa (Engels *et al.*, 2020). Climate and anthropogenic stresses are known to impact ecosystem richness and turnover, however, less is known about how such stressors can impact ecosystem structures. There is a growing interest into the changing trends in aquatic compositional diversity (Luoto *et al.*, 2016; Engels *et al.*, 2020) and community structure (Doncaster *et al.*, 2016; Wang *et al.*, 2019) to help predict lake ecosystem change under continued climatic warming. It is thought that by improving our understanding of chironomid community sensitivity and structural change under climatic stress, this thesis can contribute to the wider understanding of climate-related lake ecosystem resilience and stability.

## 2.3 Research questions

This thesis is motivated by concerns that ecosystem critical transitions will increase in likeliness under the projected climate change. Issues in detecting ecosystem shifts and EWS in the temporal domain have led to the examination of methods for detecting ecosystem change in the spatial domain. This thesis aims to build on the research summarised in this literature review, by answering the following questions:

1. Can structural metrics indicate ecosystem stability in relation to temperature change?
2. How do ecosystem structures respond to different rates and magnitudes of climate change?
3. What is the current extent of ecosystem structural stability, under present levels of climate and anthropogenic stress?

# Chapter 3 Paper 1: Metrics of structural change as indicators of chironomid community stability in high latitude lakes

## 3.1 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 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

## 3.2 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 signals (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) summarised and discussed 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 undergone additional stress from climate change or secondary drivers.

## 3.3 Materials and methods

### 3.3.1 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 microhabitats. 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.

### 3.3.2 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 affect 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.

### 3.3.3 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 ($\beta_{SOR}$) as a measure for total beta diversity (Dice, 1945; Sørensen, 1948). The turnover (taxa replacement) component was calculated using Simpson’s dissimilarity index ($\beta_{SIM}$) (Simpson, 1943) and the nestedness-type (taxon loss) component was calculated using Sørensen’s dissimilarity ($\beta_{SNE}$) (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 3.1); the 10-sample window provided the best balance of accuracy, which depends on window size, and sensitivity to change, which depends on window frequency for 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).

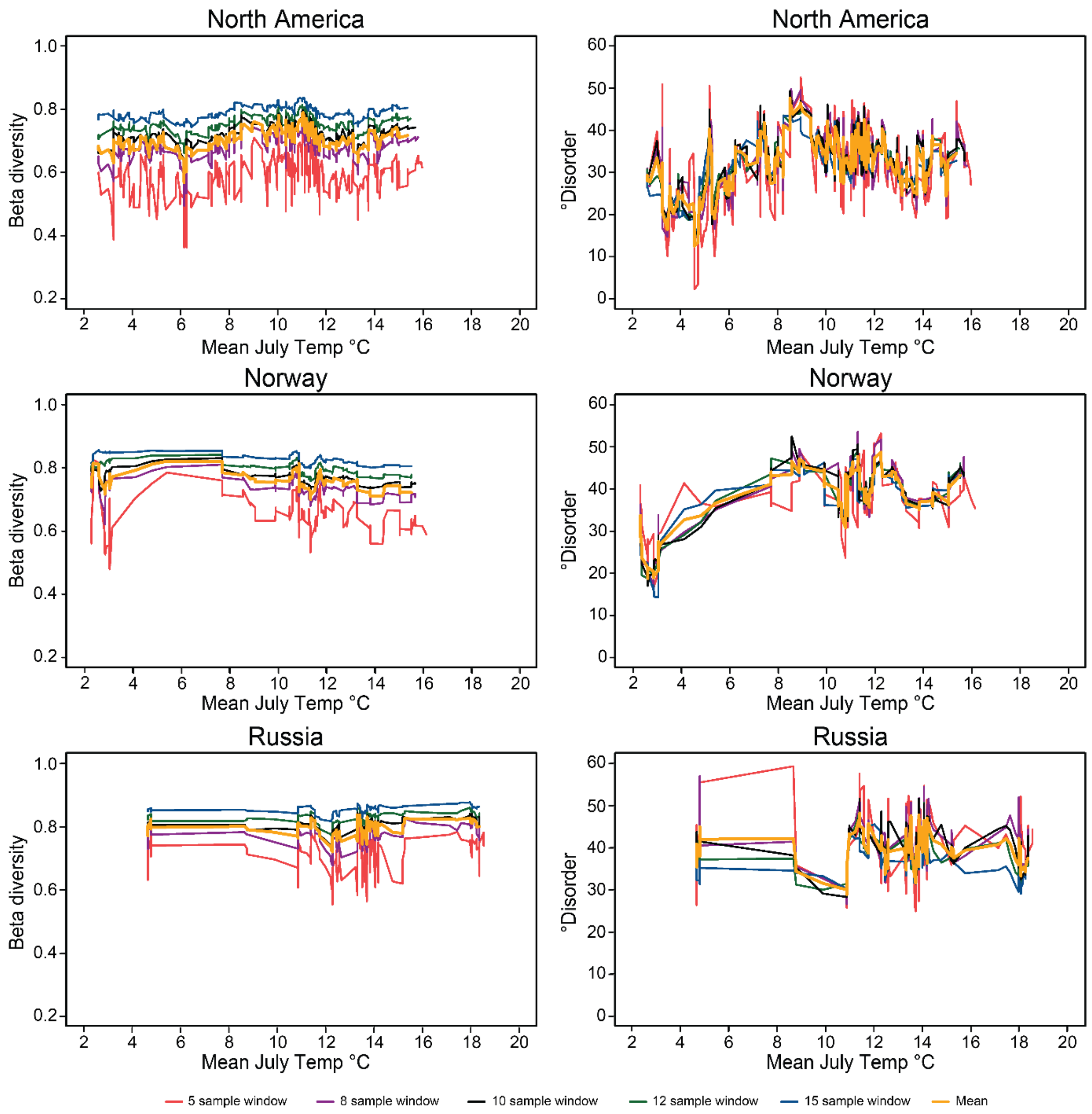

Figure 3.1 Comparison of window sizes for the calculation of beta diversity and °disorder. Multi-site dissimilarity compares the assemblage similarity between sites. °Disorder quantifies the orderliness of compositional change in an assemblage, based on the amount of same-type taxa present in consecutive 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.

### 3.3.4 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 3.2, Table 3.1). 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 3.3). 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.

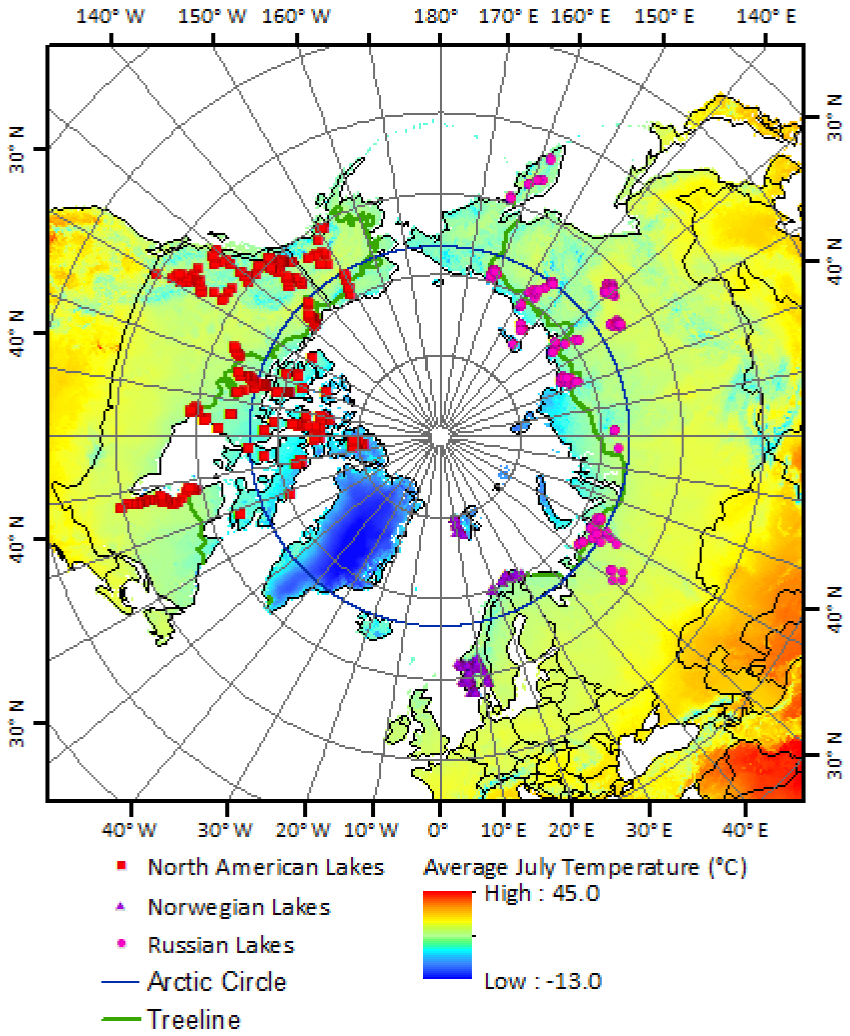

Figure 3.2 The North American (red squares), Norwegian (purple triangles) and Russian (pink circles) chironomid datasets span the Arctic and Subarctic, including island and mainland locations. The Norwegian dataset includes lakes on the Svalbard archipelago, which lies north of continental Norway in the Barents Sea between 10° and 3° E and 74° and 81° N. Background colour denotes mean July Temperature for the period 1970 – 2000 CE. Temperature data from World Clim version 2 (Fick and Hijmans, 2017).

Table 3.1 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 3.3).

| | **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) |

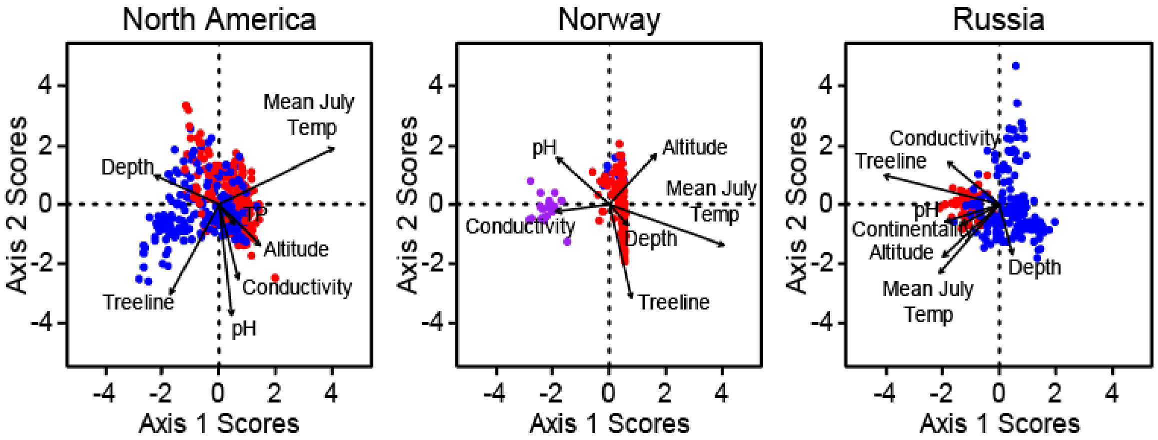

Figure 3.3 Canonical correspondence analyses (CCA) indicate which environmental variables help explain the variance within the datasets, and thus provides indication of which variables were likely to be important drivers of assemblage change. Blue dots indicate above-Arctic Circle lakes, red dots below-Arctic 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 CE for the North American and Russian datasets, and 1971 - 2001 CE 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 CE indicated that the majority of the lakes in this study had experienced warming since the beginning of the twentieth century (Figure 3.4). 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.

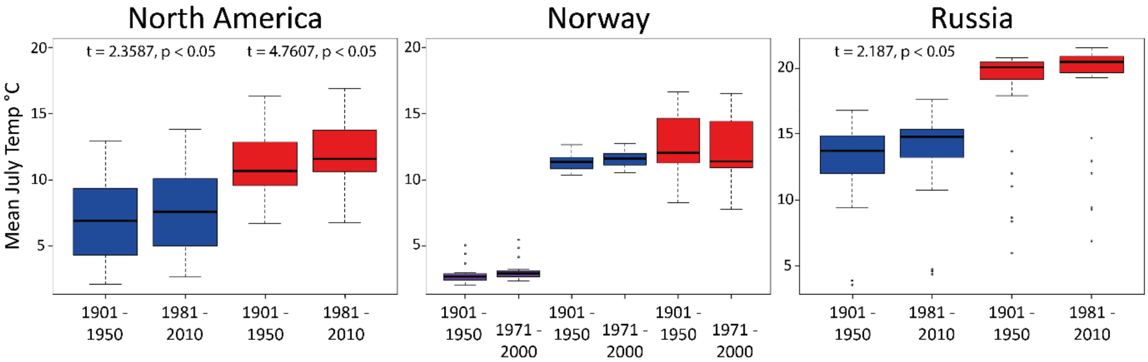

Figure 3.4 Boxplots displaying the change in mean July temperature from 1901 - 1950 CE to 1981 - 2010 CE (North America and Russia) and 1971 - 2000 CE (Norway) datasets. Blue boxes indicate above-Arctic Circle lakes, red boxes below-Arctic Circle lakes, purple boxes (Norway) Svalbard lakes. Significant 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 CE. 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.

## 3.4 Results

### 3.4.1 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 3.5). Here, we describe the general trends and key findings from the models.

Scenario 1 (Figure 3.5.1): 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 3.5.2): 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 3.5.3): 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 3.5.4): 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 skewness 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.

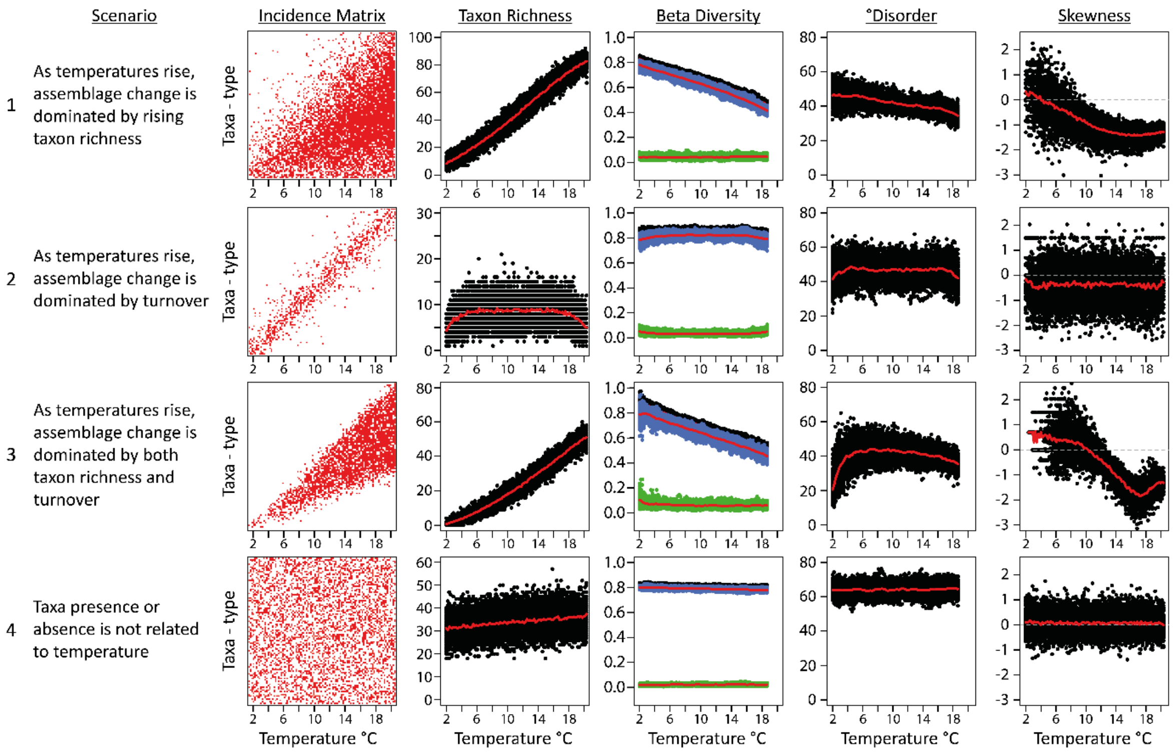

Figure 3.5 The relationship between temperature and taxa presence in four hypothetical scenarios, as described by an incidence matrix (column 1: red dots) and measured using four community structure metrics (columns 2-5) taxon richness, beta diversity, °disorder, and skewness in 100 simulations (black, 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.

### 3.4.2 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 3.6), with some similarities and variations from the simulated models.

#### 3.4.2.1 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 3.7); 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 3.6). 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 3.6). 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.

#### 3.4.2.2 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 3.6). 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 3.7). 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 3.6). 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 c. 12 ° C perhaps indicating the relative loss of weakly connected nodes at higher temperatures as seen in modelled scenarios 1 and 3.

### 3.4.2.3 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 noticeably 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 3.7). 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.

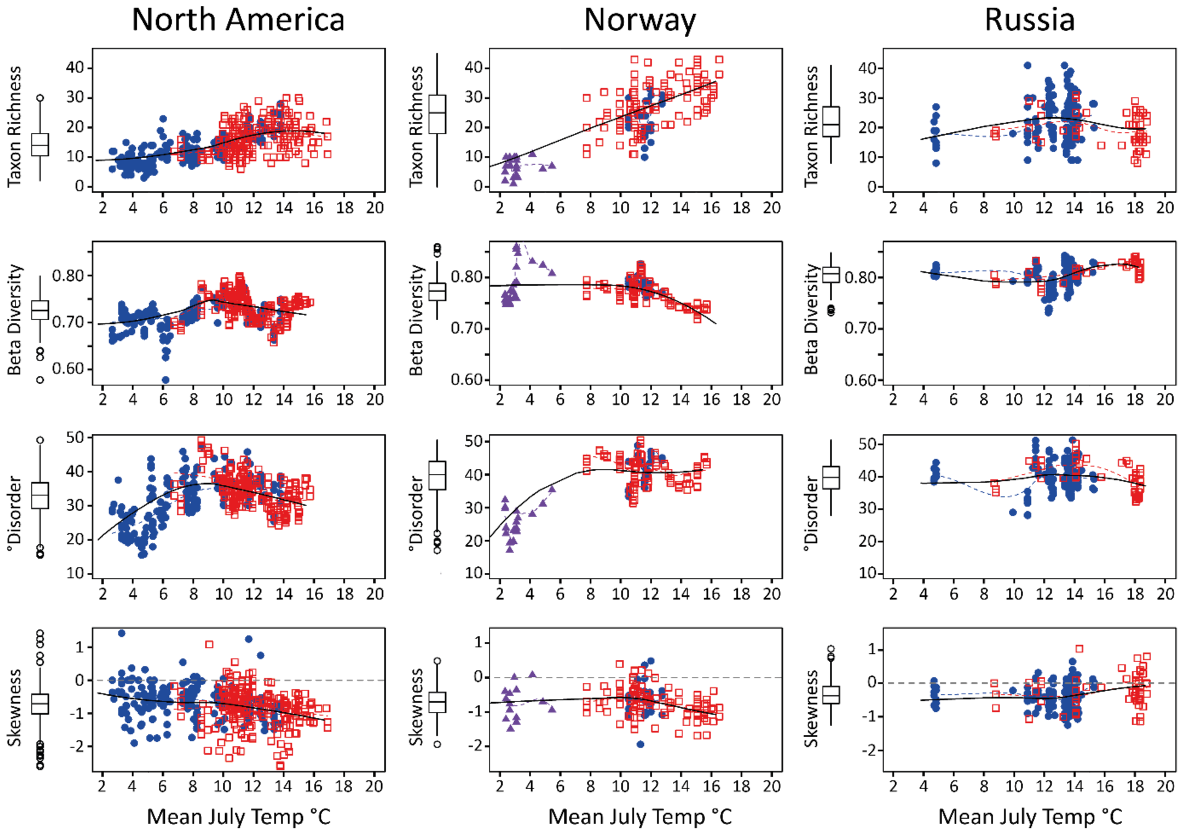

Figure 3.6 Relationships between mean July temperatures and community structure metrics (taxon richness, beta diversity, °disorder, and skewness) in the North American, Norwegian and Russian chironomid datasets. Lake sites above the Arctic Circle (66.56° N) are represented by blue circles and lakes below 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.

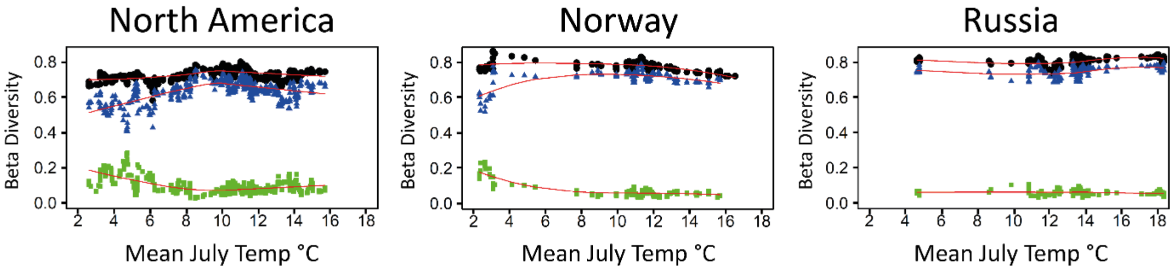

Figure 3.7 Relationships between July temperature and total beta diversity for the North American, Norwegian and Russian datasets. Individual values (black) can be attributed to changes in taxon turnover (blue) and taxon loss (green). Turnover is the most dominant component in all three datasets but 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.

## 3.5 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 3.4). 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.

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

#### 3.5.1.1 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 3.7) 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).

#### 3.5.1.2 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 3.7); 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).

#### 3.5.1.3 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 3.3) 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 number 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.

### 3.5.2 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.*, 2012a), even at the current levels of taxonomic resolution.

### 3.5.3 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.

## 3.6 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.

## 3.7 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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# Chapter 4 Paper 2: Late Quaternary chironomid ecosystem structure shaped by rate and magnitude of climate change

## 4.1 Abstract

Much is known about how climate change impacts ecosystem richness and turnover, but we have less understanding of its influence on ecosystem structures. Here, we use ecological metrics (beta diversity, compositional disorder and network skewness) to quantify the community structural responses of temperature-sensitive chironomids (Diptera: Chironomidae) during the Late Glacial (14,700 – 11,700 cal a BP) and Holocene (11,700 cal a BP to present). Analyses demonstrate high turnover (beta diversity) of chironomid composition across both epochs; however, structural metrics stayed relatively intact. Compositional disorder and skewness show greatest structural change in the Younger Dryas, following the rapid, high-magnitude climate change at the Bølling–Allerød - Younger Dryas transition. There were fewer climate-related structural changes across the early to mid-late Holocene, where climate change was more gradual and lower in magnitude. The reduced impact on structural metrics could be due to greater functional resilience provided by the wider chironomid community, or to the replacement of same functional-type taxa in the network structure. These results provide insight into how future rapid climate change may alter chironomid communities and could suggest that while turnover may remain high under a rapidly warming climate, community structural dynamics retain some resilience.

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

## 4.2 Introduction

Current climate change is occurring at an unprecedented rate that will continue over the coming decades (Smith *et al.*, 2015). The rate and magnitude of climate change affects the capacity of ecosystems to absorb climate shocks (Overpeck *et al.*, 1991; Skelly *et al.*, 2007; Grimm *et al.*, 2013). A fast rate impacts the abilities of organisms to respond effectively and efficiently to changes (Shayegh et al., 2016), while a high variability influences the extent of ecosystem response (Stireman *et al.*, 2005). The nature of community-level response to climate-induced stress will depend on the structural organisation and connectivity of taxa within the ecosystem (Dunne *et al.*, 2002; van Nes and Scheffer, 2005; Scheffer *et al.*, 2012). Structure and connectivity shape both resilience to stress and type of response to the stressor, whether smooth (linear) or abrupt (nonlinear: Burkett *et al*., 2005; Scheffer *et al*., 2012). Here we aim to improve our understanding of how community structures respond to different rates and magnitudes of climate change by compositional and network analyses of micro-faunal datasets in lake sediments spanning major climate cycles over the last 15,000 years. The payoff for understanding how community structures have responded to recent climate change is an improved ability to anticipate the conditions for future ecosystem stability.

Climate is thought to drive changes in ecosystems through two mechanisms: directly through physiological stress; and indirectly by changing taxonomic interspecific interactions, and thus the ecosystem structure (Harley, 2011). Climate change is projected to drive taxon richness and biodiversity loss (Thomas *et al.*, 2006; Foden *et al.*, 2013), with the extent of changes in the ecosystem depending on functional diversity (Chapin *et al.*, 2000). Functional diversity means the number and range of functions that taxa have within the ecosystem (Petchey and Gaston, 2006). Thus, the loss of a taxon can have a different effect on ecosystem structure depending on the connectivity and function of the taxon within the ecosystem (Dunne *et al.*, 2002). A number of studies have started to evaluate the effect of losing functional groups of taxa on community structure. For example, Doncaster *et al.* (2016) and Wang *et al.* (2019) explored the effect of taxon-type losses from aquatic communities, suggesting that the early loss of less-common, weakly-interconnected taxa may leave a predominance of more strongly-interconnected taxa defining a more rigid structure prone to abrupt collapse. The ability of a taxon to persist within an ecosystem relates to its tolerance levels, with greater magnitudes of stress often driving greater assemblage change (Cao and Hawkins, 2005). Thus, investigating how biodiversity, taxonomic interactions and community structure are influenced by different magnitudes of climate change is fundamental to understanding future ecosystem functioning and stability.

Here, we seek to detect signals of compositional change in response to past large-scale temperature changes. We focus on two periods: the relatively rapid, high magnitude climate change during the Last Glacial - Interglacial Transition (LGIT), and the more gradual, relatively low magnitude climate change experienced during the Holocene. The LGIT was a period of rapid, high-amplitude climatic instability (Hoek, 2001). It was composed of two millennial-scale oscillations; the Bølling-Allerød interstadial, a period of abrupt and significant warming (c. 14,700 - 12,800 cal a BP) (Dansgaard *et al.*, 1993; Buizert *et al.*, 2014; Rosen *et al.*, 2014), and the Younger Dryas stadial, an abrupt return to cool, glacial conditions (c. 12,800 – 11,700 cal a BP) (Dansgaard *et al.*, 1993; Tarasov and Peltier, 2005). In contrast, the Holocene climate has been relatively stable (Wolff *et al.*, 2010). Here, we divide the Holocene into two sections; the early Holocene (11,700 cal a BP to 8,200 cal a BP) and mid-late Holocene (8,200 cal a BP to present). The early Holocene (11,700 cal a BP to 8,200 cal a

BP) experienced initial rapid climatic warming following deglaciation (Birks and Birks, 2008; Aarnes *et al.*, 2011). The mid-late Holocene (8,200 cal a BP to present) was less climatically changeable, with weakened orbital forcing during the northern hemisphere summers (Wanner *et al.*, 2008), particularly in high latitude regions (Balascio and Bradley, 2012). While there were a number of widely recognised climatic events during the mid-late Holocene, the timing of such events, e.g. the Holocene Thermal Maximum and neoglaciation, was time transgressive (Kaufman *et al.*, 2004; McKay *et al.*, 2018), variable across high latitude regions (Renssen *et al.*, 2009; 2012; Briner *et al.*, 2017; Geirsdóttir *et al.*, 2019), and spanned the mid-late Holocene boundary in some regions (Miller *et al.*, 2005; Salonen *et al.*, 2011; Badding *et al.*, 2013). We therefore group the “mid” and “late” Holocene sections.

We focus on temperature-sensitive chironomid (Diptera: Chironomidae; non-biting midges) records from Northern Europe (Norway and Scotland) as indicators of the effect of temperature on aquatic ecosystems. Chironomid records have frequently been used as palaeoecological proxies of past temperature changes (Brooks and Birks, 2001; Brooks, 2006b; Axford *et al.*, 2017), thus it is thought that such records may provide a greater insight in to the complex relationships between climatic variability and ecosystem response (Willis *et al.*, 2010; Birks *et al.*, 2016). We test for differences in the ecological response to the relatively rapid, high magnitude climate change at the Bølling–Allerød - Younger Dryas transition and the more gradual, relatively low magnitude climate change experienced at the early – mid Holocene transition. We employ a suite of ecological metrics to compare the assemblage composition before and after the climatic change, including ordination, taxon richness, beta diversity, compositional disorder and skewness. These metrics have previously been used to assess chironomid structural change within spatial datasets (Mayfield *et al.*, 2020); here we use them to assess changing chironomid community structure in temporal records for the first time. To assess how the assemblages may have changed under continued Bølling–Allerød and early Holocene climatic conditions, we test for evidence of departures from a status quo with ARIMA forecasts. We test for a response in chironomid assemblage structure to changing climate by comparing the ecological metrics with the NGRIP 15,000 year isotope record trends and fluctuations. To distinguish true pattern from random noise in ecological datasets, we follow principles in Telford and Birks (2011) for minimising the likelihood of drawing conclusions from spurious correlations. Our criterion for detecting non-random pattern in empirical datasets is that the observed metric must explain more of the variation in a response than is explained by application of the metric to randomised datasets, in at least 95% of 10,000 randomisations. We expect to see a greater response in the ecosystem metrics from the rapid, large magnitude change in the Bølling–Allerød - Younger Dryas, if the chironomid assemblages were responding to climate change. For example, if the rapid, abrupt change in climate drives a faster and greater magnitude change in taxon presence, this could have a greater effect on the organisation and functionality of the ecosystem. In contrast, the more gradual, lower magnitude change between the early and mid-late Holocene should produce smaller scale changes in the ecosystem metrics. For example, under lower stress conditions, the ecosystem may have greater capacity to adjust with the changing boundary conditions, thus any potential changes in taxonomic composition were likely to have a lesser effect on the ecosystem structure.

## 4.3 Methods

### 4.3.1 Quantifying climate change

Oxygen isotope ($\delta^{18}O$ ‰) records from the NGRIP Greenland ice core were used to provide an independent record of relative air temperature for the recent glacial-interglacial period (Wolff *et al.*, 2010) (Figure 4.1, upper panel). To assess the extent of temperature change across the Late Glacial and Holocene epochs, median $\delta^{18}O$ (‰) values were calculated for the Bølling-Allerød and Younger Dryas, and early and mid-late Holocene periods. Median $\delta^{18}O$ (‰) values indicate a relatively large difference in temperature between the Bølling-Allerød (-38.61) and Younger Dryas (-40.77). The Holocene, in contrast, has been relatively more climatically stable (Figure 4.1, upper panel) (Wolff *et al.*, 2010), with little difference between the median $\delta^{18}O$ (‰) values for the early (-34.95) and mid-late (-35.07) Holocene subsections. To ascertain whether the magnitude of change between the observed medians exceeded the expectations for random noise, the observed differences in the medians were compared to differences in median metrics obtained from 10,000 randomised replications of the Late Glacial and Holocene isotope record sections. The randomised datasets were created by randomly re-ordering the isotope record sections. Each randomised dataset was partitioned into the corresponding Bølling-Allerød and Younger Dryas and early and mid-late Holocene subgroups. Median values were calculated for the randomised subsets. Differences between the medians were calculated to produce 10,000 differences in median values. These differences were ranked, along with the observed difference in median values. For the Late Glacial, the observed difference in medians fell in the lower 2.5 % of the ranking, indicating that the observed difference had less than 5 % chance of random occurrence (Appendix A, Figure A. 1). For the Holocene, the observed difference in medians did not fall outside the upper or lower 2.5 % of the ranking, indicating that the observed difference for the Holocene isotope medians was not discernible from random occurrence (Appendix A, Figure A. 1).

To quantify the different rates and magnitudes of climate change during the Late Glacial and Holocene periods, we calculated the cumulative deviation from the long term mean (Dugmore *et al.*, 2007). To do this, long-term rolling mean values were calculated over periods of 200 years (10 samples) (Appendix A, Figure A. 2). The gradient of the slope indicated the relative velocity of the climate change and the amplitude of the curve indicated the magnitude of the climate change. The greatest changes in the rate and magnitude of the isotope trend occurred at the start of the Bølling-Allerød and Younger Dryas periods, with smaller magnitude fluctuations within each period (Figure 4.1, lower panel). In the Holocene record, the $\delta^{18}$O (‰) record showed the greatest difference in cumulative deviation from the long-term mean at the start of the Holocene. The cumulative deviation from the long-term mean gradually decreased through the early Holocene, indicating a slower rate of change. There were rapid, small magnitude changes in the cumulative deviation trend in association with the Preboreal Oscillation, 9.3 ka and 8.2 ka events. There were few substantial cumulative changes in the isotopic trend throughout the mid-late Holocene, with little change in association with the Holocene Thermal Maximum (HTM, c. 9 - 5 ka in Greenland, (Kaufman *et al.*, 2004)), neoglaciation (c. 4 - 3 ka in Greenland, (Briner *et al.*, 2017), Medieval Climate Anomaly (MCA, 950 - 1250 CE, (Mann *et al.*, 2009) or Little Ice Age (LIA, c. 1400 - 1700 CE, Mann *et al.*, 2009)), indicating relative climatic stability throughout the mid-late Holocene.

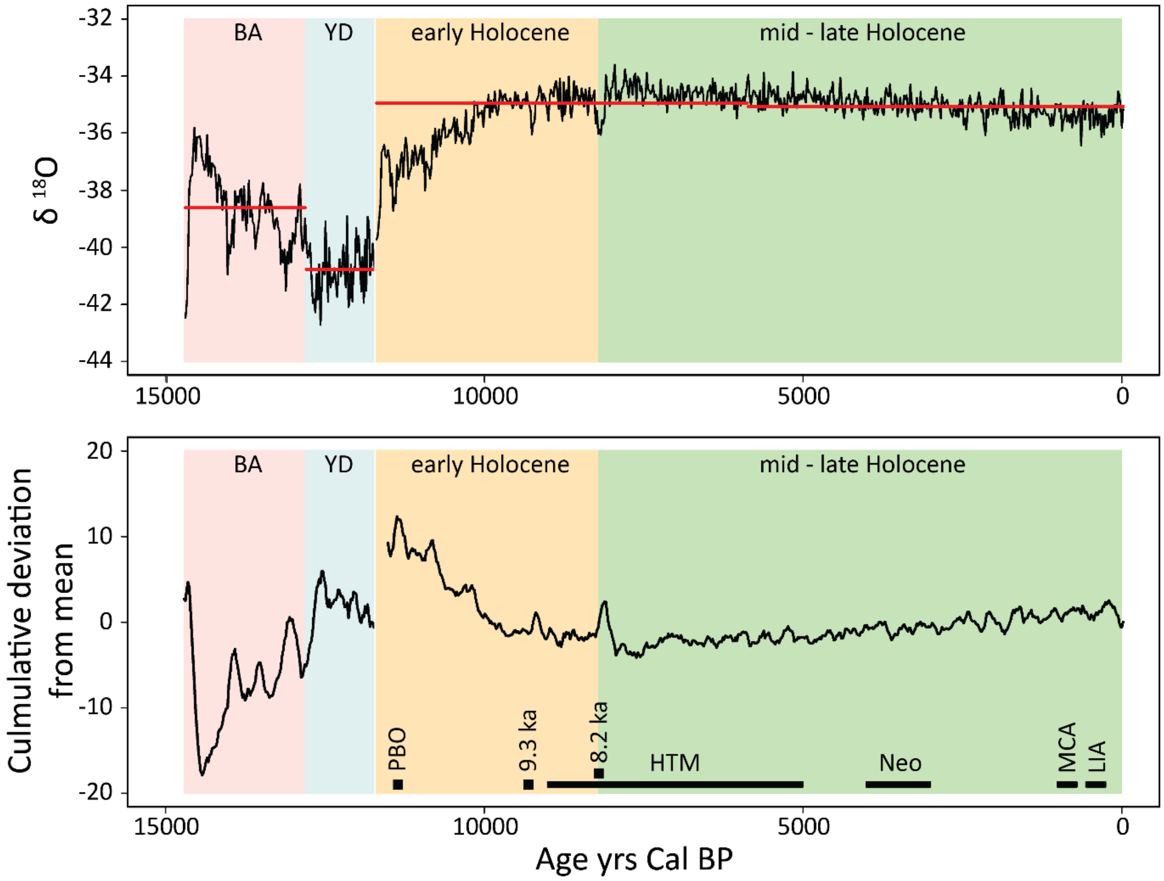

Figure 4.1 Oxygen isotope records from the NGRIP record in Greenland spanning the LGIT and Holocene (upper panel) (Wolff *et al.*, 2010). Lower isotopic values are indicative of lower temperatures. Dates have been corrected to cal a BP from yrs B2K, following Wolff *et al.* (2010). Mean isotopic values are indicated by horizontal red lines. The rate of change, calculated as the cumulative deviation from the rolling long term (200 years) mean (lower panel), indicates a greater rate and magnitude of isotopic change at the onset of the Bølling-Allerød (BA), Younger Dryas (YD) and early Holocene.

### 4.3.2 Empirical chironomid datasets

Larval chironomid assemblages were used here as indicators of ecological stability through time from European datasets (Figure 4.2). The authors of the chironomid datasets are indicated in Table 4.1. Taxa were identified to genus or species-morphotype level using standardised subfossil taxonomy (Brooks et al. 2007). While there are a large number of chironomid records available spanning Late Glacial and Holocene time periods, the records for this study were selected based on high sampling resolution, consistency of taxonomic resolution, and age model quality to allow comparison among sites.

The Late Glacial chironomid records used were from Scotland, UK: Ashik and Abernethy (Brooks *et al.*, 2012b) and Muir Park (Brooks *et al.*, 2016). These lakes span a range of environments, including coastal and inland locations, and varying proximities from the Loch Lomond ice limits (Chandler *et al.*, 2019; Lowe *et al.*, 2019). Age models were available for the Ashik and Abernethy records from the original publications; however, no age model was available for the Muir Park record beyond the tephras (with associated dates) found within the stratigraphy. Estimated ages were calculated for the Muir Park record in this paper (Appendix A, Figure A. 3), based on the tephrochronology, to establish a broad chronostratigraphy. The age-depth model for the Ashik record was also based solely on tephrochronology, using the Borrobol and Penifiler tephras and age estimates derived from the Abernethy Forest age-depth model (Brooks, 2006b; Pyne-O'Donnell, 2007; Matthews *et al.*, 2011).

The Holocene chironomid records used were from Norway and span a latitudinal gradient, covering arctic, coastal and alpine locations; Horntjernet from Finnmark, Arctic Norway (this paper), Bjornfjelltjønn on the northwest coast of Norway (Brooks, 2006b) and Holebudalen in Southern Norway (Velle *et al.*, 2005a). Age models for the Bjornfjelltjønn and Holebudalen records were provided by the original authors. The age model for the Horntjernet record was provided by (Rijal *et al.*, 2020).

To assess the comparability of the fossil records, detrended correspondence analyses (DCA) were used to plot the records in ecological space, using vegan (Oksanen *et al.*, 2013) in R statistical software v. 3.6.0 (R Core Team, 2019). The relative positions of the Bølling-Allerød and Younger Dryas samples and the early and mid-late Holocene samples indicated whether the assemblages were responding similarly to environmental stressors. *Timetrack* (Simpson and Oksanen, 2019) and *ordisurf* (Oksanen *et al.*, 2013) were used to passively plot the temporal records onto the ecological space of the Norwegian calibration set (Brooks and Birks, 2001; 2004) to determine the influence of mean July temperature on the fossil chironomid records in R statistical software v. 3.6.0 (R Core Team, 2019). To further test whether the Norwegian calibration set was an appropriate fit for the fossil datasets, a goodness of fit analysis was performed using squared residual distance (Juggins and Birks, 2012) (Appendix A, Figure A. 4 - 5).

Table 4.1 Metadata for the chironomid datasets spanning the Late Glacial and Holocene. Mean summer (June, July and August) temperatures are shown for the period 1970 – 2000 CE, calculated using temperature data from World Clim version 2 (Fick and Hijmans, 2017).

| Site | Country | Time period | Latitude (°N) | Longitude (°E) | Altitude (m asl) | Mean summer temperature | Reference |
|---|---|---|---|---|---|---|---|
| Ashik | Scotland | Late Glacial | 57.24 | -5.83 | 50 | 12.6 | (Brooks *et al.*, 2012b) |
| Abernethy | Scotland | Late Glacial | 57.24 | -3.71 | 340 | 12.5 | (Brooks *et al.*, 2012b) |
| Muir Park | Scotland | Late Glacial | 56.10 | -4.43 | 210 | 13.9 | (Brooks *et al.*, 2016) |
| Horntjernet | Norway | Holocene | 69.35 | 29.49 | 88 | 10.9 | This paper |
| Bjornfjelltjønn | Norway | Holocene | 68.43 | 18.07 | 510 | 8.6 | (Brooks, 2006b) |
| Holebudalen | Norway | Holocene | 59.84 | 6.99 | 1144 | 10.9 | (Velle *et al.*, 2005a) |

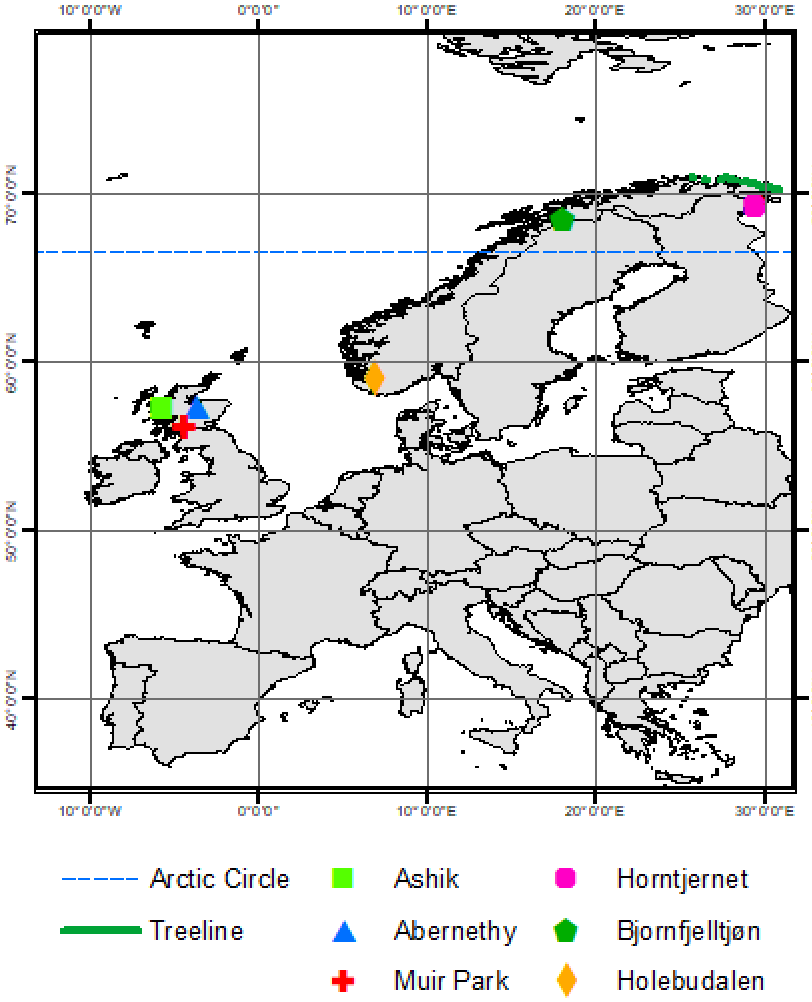

Figure 4.2 Chironomid records analysed in this study. Three lake records spanned the Late Glacial: Ashik, Abernethy (Brooks *et al.*, 2012b) and Muir Park (Brooks *et al.*, 2016), from Scotland, UK. Three lake records covered the Holocene: Horntjernet (this paper), Bjornfjelltjønn (Brooks, 2006b), and Holebudalen (Velle *et al.*, 2005a) from Norway.

### 4.3.3 Metrics of structural change

Four ecological metrics, taxon richness, beta diversity, compositional disorder, and network skewness, were selected as indicators of ecosystem change for the temporal empirical chironomid assemblages. Beta diversity, compositional disorder, and network skewness reflect ecosystem structural change, through taxonomic turnover and taxon organisation (Baselga, 2010; Doncaster *et al.*, 2016; Wang *et al.*, 2019; Mayfield *et al.*, 2020). Palaeoecological datasets often have irregular time series (Glew *et al.*, 2001), including the records analysed here. Our approach in this paper is to sample changes from one climatic period to the next, rather than change over continuous time, thus the records were not corrected for temporal resolution.

Taxon richness has long been used as a measure of the number of taxa present in a sample; however, it is simplistic and does not account for taxon abundance, rarity or ecosystem structure (Veech, 2018; Wang *et al.*, 2019). It was used here as a simplistic characterisation of assemblage change (total number of taxa per sample) over time and during climatic stress. Taxon richness can be affected by specimen preservation and taxonomic resolution (Velle and Larocque, 2008); in attempt to account for this, the records analysed here were screened for taxonomic consistency. All records had a minimum of 50 head capsules per sample (Heiri and Lotter, 2001; Quinlan and Smol, 2001), with the exception of Muir Park, where some samples with a low head capsule concentration had a minimum of 35 capsules per sample, see Brooks *et al.* (2016).

Beta diversity, a measure of variation in taxonomic composition (or turnover) (Legendre and De Caceres, 2013), was used to indicate the similarity of assemblages in consecutive time slices. Beta diversity was calculated for each sample following the variance partitioning framework of Legendre and De Caceres (2013), using the *beta.div* function and “Hellinger” method in the *adespatial* package (Dray *et al.*, 2019) in R statistical software v. 3.6.0 (R Core Team, 2019). The taxon assemblage data were transformed by the “Hellinger” method within the *beta.div* function. This method was selected because a diversity value is calculated for each time slice, as opposed to pairwise site comparisons, which are normally used for spatial datasets. Higher beta diversity values indicate greater variation (or turnover) between assemblages. As assemblages gradually change over time, beta diversity should be low and constant, as there is a high degree of taxonomic overlap. Abrupt changes in the ecosystem composition should cause a sudden rise in beta diversity as the assemblage experiences greater taxonomic turnover.

Compositional disorder, a measure of nestedness, can be used as a proxy for unpredictability in community composition. Compositional disorder is expressed as degree of disorder (°disorder) and measured on a scale from 0° (perfectly nested sequences) to 100° (perfectly disordered sequences) using subsets of 10 consecutive samples (Doncaster *et al.*, 2016; Mayfield *et al.*, 2020). A higher value indicates that the sample was less predictable from previous samples, due to greater dissimilarity between the assemblage compositions. Under low stress conditions, taxa should continually arrive and exit the ecosystem in response to fluctuating environmental variables; this should produce a constant level of °disorder with little directional change (Doncaster *et al.*, 2016; Mayfield *et al.*, 2020). Sudden changes in ecosystem composition should produce an abrupt change in °disorder. As taxa rapidly appear, the proportion of common taxa between samples is likely to diminish, causing greater unpredictability between samples and increasing °disorder values. A sudden decline in taxon abundance is more likely to produce a nested assemblage of core, common taxa, producing a decline in °disorder and signifying greater predictability.

Network skewness measures the hierarchical distribution of nodal degree, i.e., the number of interspecific interactions attributable to each species (termed species degree) (Wang *et al.*, 2019). Network skewness was calculated in MATLAB (ver. R2017b) following the method developed by Wang *et al.* (2019). This method requires a calibration dataset to identify frequently co-occurring chironomid taxon pairs. In this study, we used the Norwegian calibration dataset (Brooks and Birks, 2001; 2004); as goodness of fit analyses confirmed that the Norwegian calibration dataset was an appropriate fit (using squared residual distance (Juggins and Birks, 2012), Appendix A, Figure A. 4 - 5). The most-frequently co-occurring chironomid taxon pairs were identified as the pairs occupying the upper two quartiles of positive values for Cramér's association coefficient (Q2 of V+) in the Norwegian calibration dataset (Brooks and Birks, 2001; 2004). Species degree was calculated for each fossil assemblage based on the co-occurrences of taxa in the Norwegian calibration set. Network skewness was measured as the skewness of the frequency distribution of species degree; see Wang *et al.* (2019) for further details. A positive skewness value indicates a large proportion of taxa with few interspecific interactions and a small number of taxa with many interactions. Environmental degradation may reduce or change the availability of micro-niches, causing the taxa to re-organise structurally, hence increasing the number of taxon interactions (Albert et al., 2000). This creates a larger proportion of highly connected taxa, producing a less positively skewed distribution of taxonomic interactions (Wang *et al.*, 2019). A prerequisite and limitation of this method is that the taxa in the fossil assemblages must be present in the calibration set. Thus, the chironomid datasets were selected and filtered with this in mind, with some sub-categories of taxa being grouped to genus. These filtered datasets were used for the skewness analyses. Comparisons between the filtered and full datasets indicated that the filtering process had a limited effect on the taxon richness, beta diversity and compositional disorder analyses (Appendix A, Figure A. 6 - 7).

### 4.3.4 Testing structural change across high and low magnitude climate change

We tested the magnitude of structural change in the chironomid assemblages in the Late Glacial, between the Bølling-Allerød and Younger Dryas periods, and Holocene, between the early and mid-late Holocene periods. Differences in the median metric values between the periods were calculated for taxon richness, beta diversity, °disorder and skewness. To test whether the magnitude of change between the observed medians exceeded the expectations for random noise, repeat analyses were run on 10,000 randomised datasets (Appendix A, Figure A. 8 - 9).

To test whether the assemblages in the later sections of the records (Younger Dryas and mid-late Holocene) were on a different trajectory to the earlier sections of the records (Bølling-Allerød and early Holocene), an autoregressive integrated moving average (ARIMA) model was applied to the Bølling-Allerød and early Holocene observed metric values, using the R function arima (p, d, q), in which *p* was the autoregressive order, *d* was the degree of differencing, and *q* was the moving-average order (Hyndman *et al.*, 2020). If the observed Younger Dryas and mid-late Holocene metric values fell outside the 95 % confidence interval of the ARIMA forecasts, the chironomid assemblage structure had undergone substantial change between the Bølling-Allerød to Younger Dryas and the early to mid-late Holocene subsections.

To establish the relationship between the chironomid assemblage structure and climate, we assessed the correlation between the ecological metrics and the Greenland NGRIP ice core isotope record. Isotopic values were calculated for the chironomid sample dates using the *predict* function in R statistical software v. 3.6.0 (R Core Team, 2019) (Appendix A, Figure A. 10). To assess the correlation between the metric and isotope trends, Pearson's correlation coefficient was obtained from the association of the calculated isotopic values with each of the metric outcomes for the empirical datasets. To test the correlation between the metrics and isotope fluctuations, Pearson's correlation coefficient was obtained from the association between the detrended fluctuations in the ecological metrics and isotope record, using the first differences in the metric outcomes and isotopic values, obtained with the *diff* function in R statistical software v. 3.6.0 (R Core Team, 2019). To test for non-random correlation, observed magnitudes were ranked within the set of 10,000 repeat analyses run on randomised datasets (Appendix A, Figure A. 11 - 14).

## 4.4 Results

### 4.4.1 Changes in chironomid community structure during the Late Glacial

The Late Glacial chironomid records indicated similar ecological trends, as indicated by the Detrended Correspondence Analyses (Figure 4.3, upper panel). The large degree of variation (c. 3 σ) on axis 1 indicated large taxon turnover, from the Bølling-Allerød to the Younger Dryas. The Late Glacial chironomid assemblages plotted within the Norwegian calibration dataset (Figure 4.3, lower panels), indicating that the Norwegian calibration dataset has good analogues for the fossil datasets. Goodness of fit analyses demonstrated that for the Ashik record 95.6 % of samples had a good fit, for the Abernethy record 88.7 % of samples had a good fit, and for Muir Park 93.0 % of samples had a good fit (< 95 % of calibration-set squared residual distances; Appendix A, Figure A. 4). The Late Glacial samples plotted across the temperature contours calculated from the Norwegian calibration (Figure 4.3, lower panels), suggesting that these chironomid records had been influenced by a range of temperatures over the record.

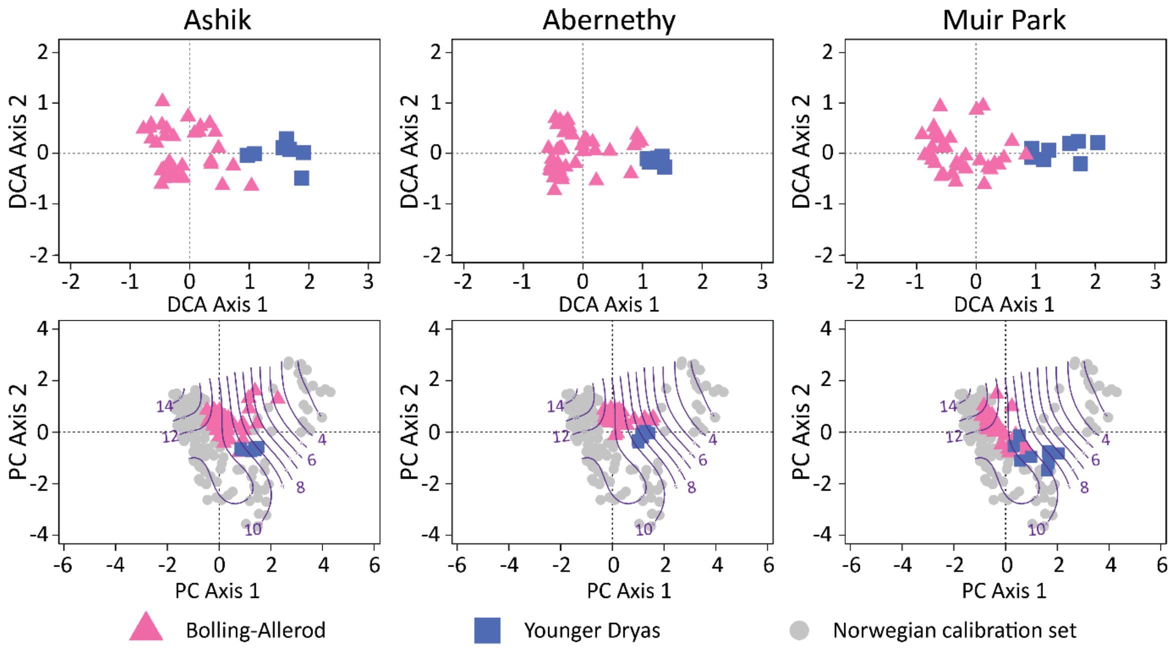

Figure 4.3 Assemblage change in ecological space for the Late Glacial chironomid records. Detrended correspondence analyses (upper panel) of chironomid samples from the Bølling-Allerød (pink triangles) and Younger Dryas (blue squares). The fossil records were passively projected on to the ordination of the Norwegian calibration dataset (lower panel, grey circles). Temperature contours (purple lines, °C), calculated from the Norwegian calibration dataset, are plotted over the chironomid samples.

Taxon richness, beta diversity and network skewness revealed similar changes in assemblage structure across the Bølling-Allerød and Younger Dryas in the Late Glacial records (Figure 4.4). All three sites showed decreases in taxon richness and increases in beta diversity and skewness from the Bølling-Allerød to Younger Dryas. °Disorder indicated a mixed response, decreasing in Ashik, increasing in Abernethy, and not changing detectably in Muir Park.

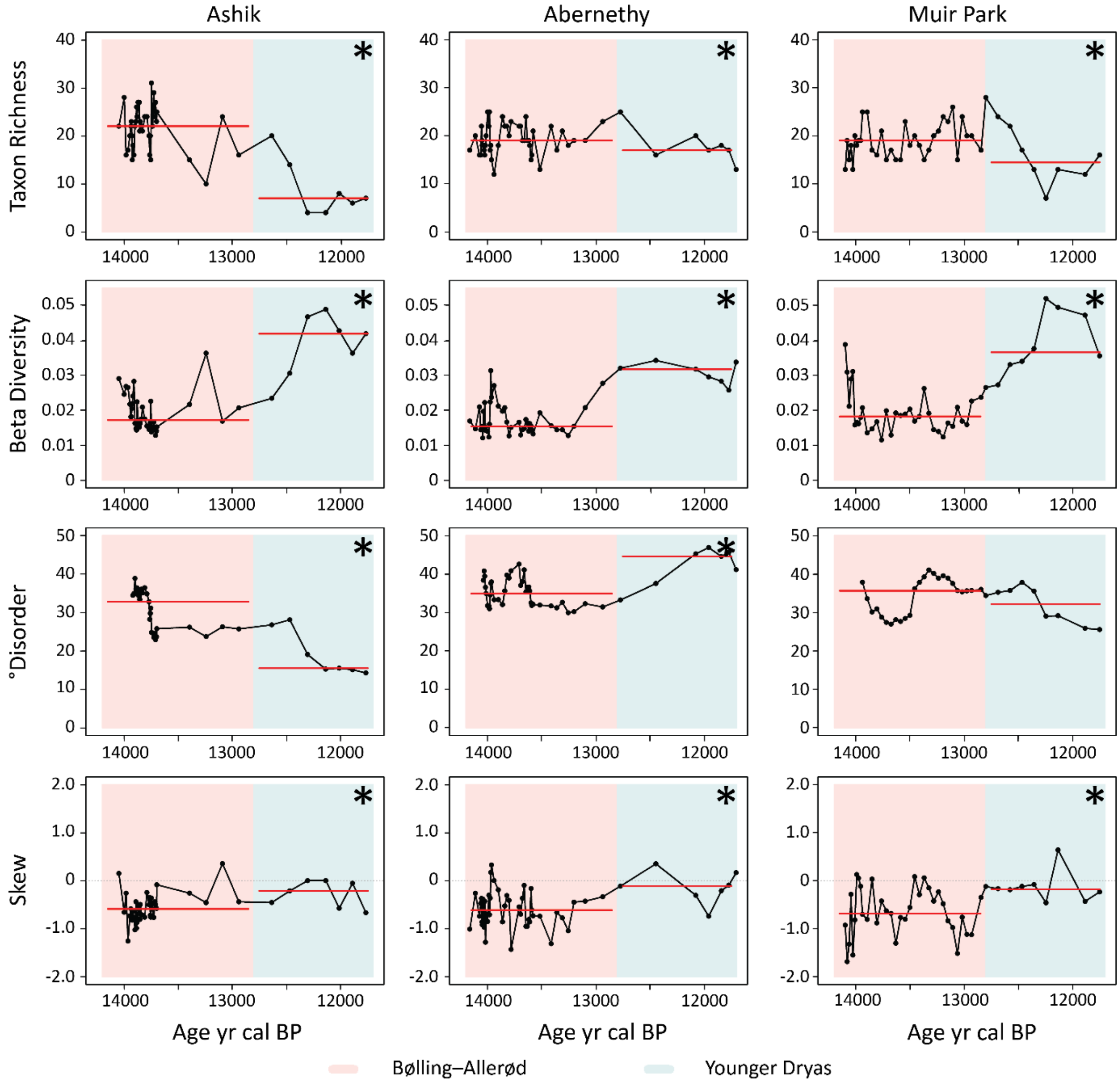

Figure 4.4 Structural metric trends (black lines) of the chironomid records during the Late Glacial. Median values (red lines) were calculated for the Bølling-Allerød and Younger Dryas. An asterisk denotes differences in median metrics ≥ 95 % of median differences obtained from the randomised chironomid records.

ARIMA forecasting indicated whether trends in ecological metrics for the Younger Dryas were predictable from the Bølling–Allerød trends (Figure 4.5). Taxon richness decreased at the start of the Younger Dryas in the Ashik and Muir Park records. Beta diversity increased in all three records. °Disorder decreased during the Younger Dryas in the Ashik and Muir Park records, however remained within the lower boundary of the 95 % prediction interval. In the Abernethy record, °disorder increased during the Younger Dryas, remaining largely within the upper boundary of the 95 % prediction interval. Skewness remained predominantly within the 95 % prediction interval for all three records.

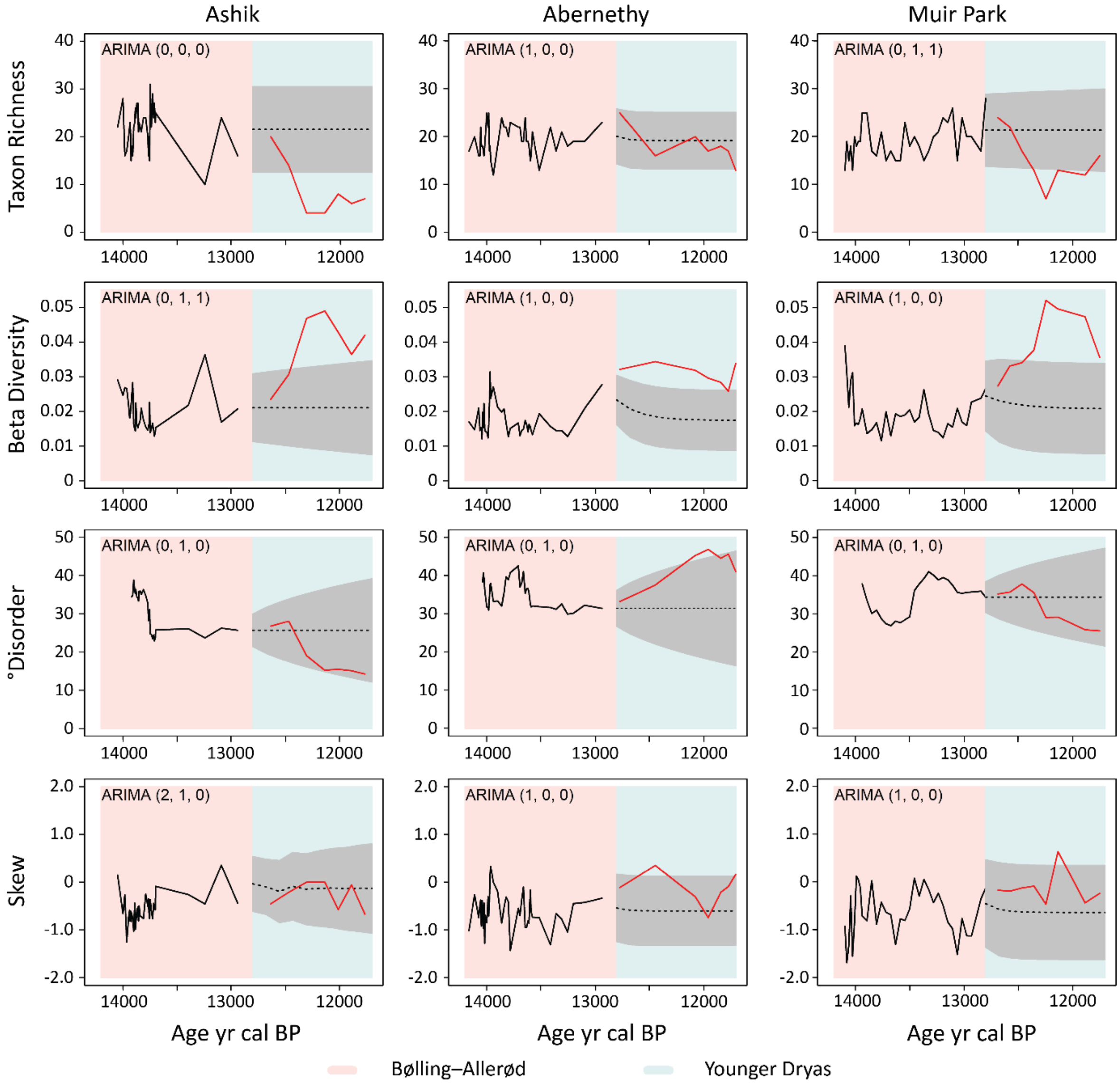

Figure 4.5 ARIMA forecasts for Younger Dryas metrics based on Bølling-Allerød data: Bølling-Allerød metric trends (solid black lines), mean predicted Younger Dryas metric outcomes (dotted black lines), 95 % prediction intervals (grey band), empirical Younger Dryas metric outcomes (red line).

Some records indicated correlations between the ecological metrics and NGRIP isotope record trends (Figure 4.6). Taxon richness at Ashik correlated positively with the isotope record. Beta diversity in all three records was negatively correlated with the isotope record. °Disorder did not correlate with the isotope trend in any record. Skewness in the Ashik and Abernethy records correlated negatively with the isotope record. None of the detrended datasets showed evidence of correlation between the ecological metrics and NGRIP isotope record (Appendix A, Figure A. 15).

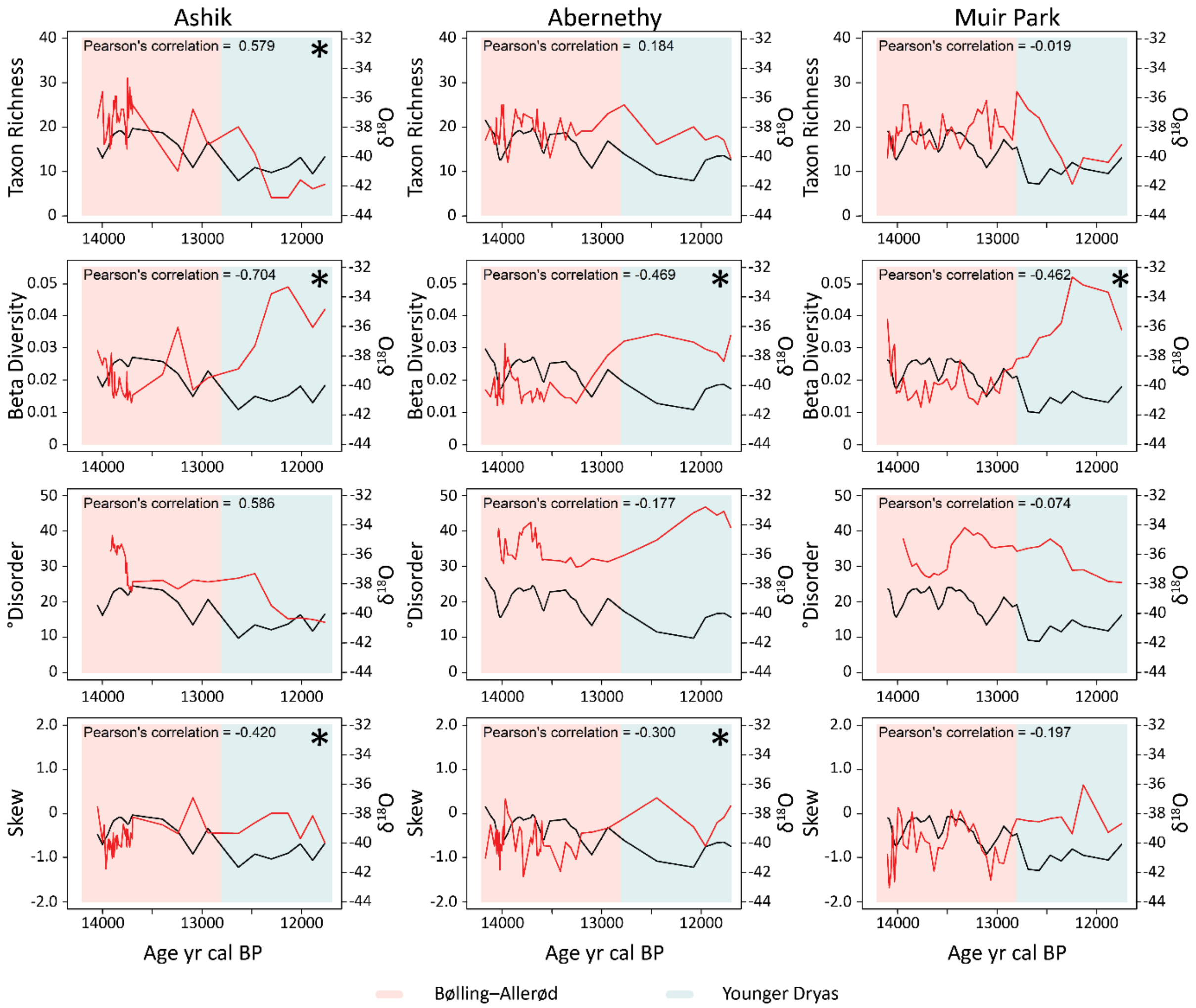

Figure 4.6 Correlation between the NGRIP isotope trends (black) and the chironomid ecological metrics (red) in the Late Glacial. Calculated isotopic values are shown for the same ages as the chironomid samples. Person's correlation coefficients indicate the correlated trends between each metric and the isotopic values. An asterisk denotes trends where the observed correlation trend exceeded the random expectation (p ≤ 0.05), when compared to the 10,000 randomised replicate datasets.

### 4.4.2 Changes in chironomid community structure during the Holocene

Detrended Correspondence Analyses of the Holocene records are shown in Figure 4.7 (upper panel). There was a large degree of variation across axis 1 (c. 2.5 σ) in the Horntjernet record, suggesting the primary driver, likely temperature, explained a large proportion of the assemblage change from the early and mid-late Holocene assemblages. The Bjornfjelltjønn and Holebudalen records showed less variation across axis 1 indicating that the primary driver was less influential on these assemblages. Some of the early Holocene samples in the Horntjernet and Bjornfjelltjønn records plotted separately to the bulk of the samples, suggesting other drivers may have influenced the assemblages at this time. The Holocene chironomid assemblages plotted within the Norwegian calibration dataset (Figure 4.7, lower panels), indicating that the Norwegian calibration dataset had good analogues for the fossil datasets. Goodness of fit analyses demonstrated that for the Horntjernet record 84.5 % of samples had a good fit, for the Bjornfjelltjønn record 98.9 % of samples had a good fit, and for Holebudalen 96.2 % of samples had a good fit (< 95 % of calibration-set squared residual distances; Appendix A, Figure A. 5). The chironomid records plotted across a small number of the temperature contours calculated from the Norwegian calibration (Figure 4.7, lower panels), suggesting that the assemblages experienced a lower magnitude of temperature change than the Late Glacial assemblages. The Horntjernet record plotted across a larger number of temperature contours suggesting that temperature had a greater influence on the Horntjernet record, than the Bjornfjelltjønn or Holebudalen records.

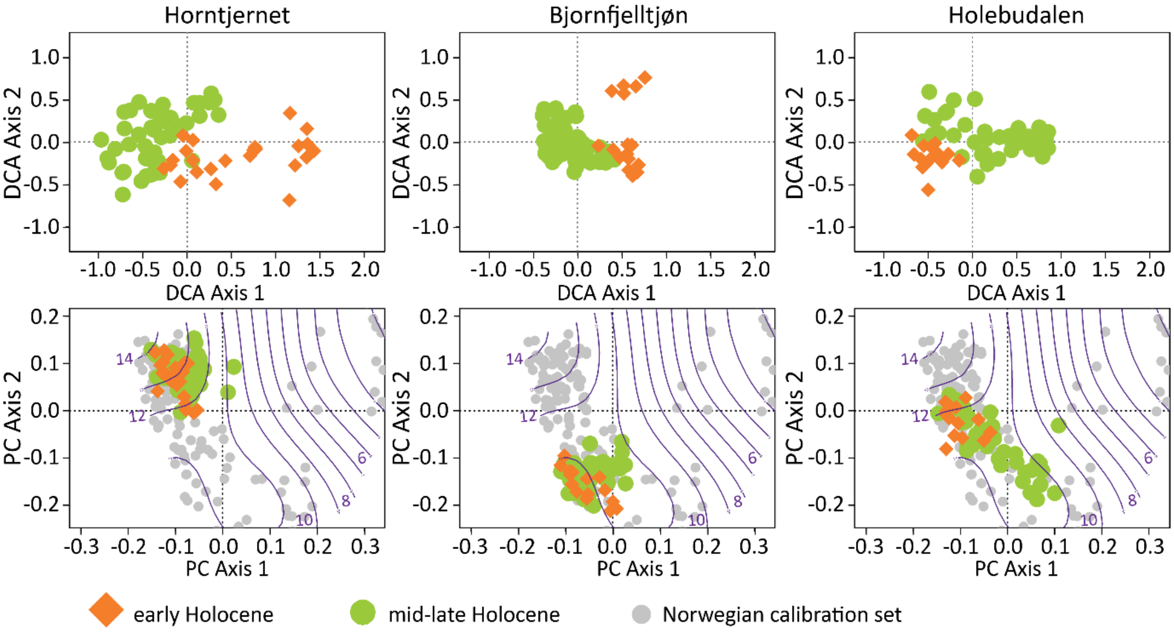

Figure 4.7 Assemblage change in ecological space for the Holocene records using detrended correspondence analyses (DCA) (upper panel), early Holocene (orange diamonds), mid-late Holocene (green circles). The fossil records are passively projected on to the ordination space of the Norwegian calibration dataset (lower panel, grey circles). Temperature contours (purple lines, °C) calculated from the Norwegian calibration dataset are plotted over the chironomid samples.

Taxon richness, beta diversity, °disorder, and skewness revealed fewer detectable trends across the Holocene than during the Late Glacial (Figure 4.8). Taxon richness decreased from the early to mid-late Holocene in the Horntjernet and Holebudalen records. Beta diversity decreased in the mid-late Holocene in the Horntjernet and Bjornfjelltjøn records. °Disorder increased in the Bjornfjelltjøn record. Skewness did not change in any of the records.

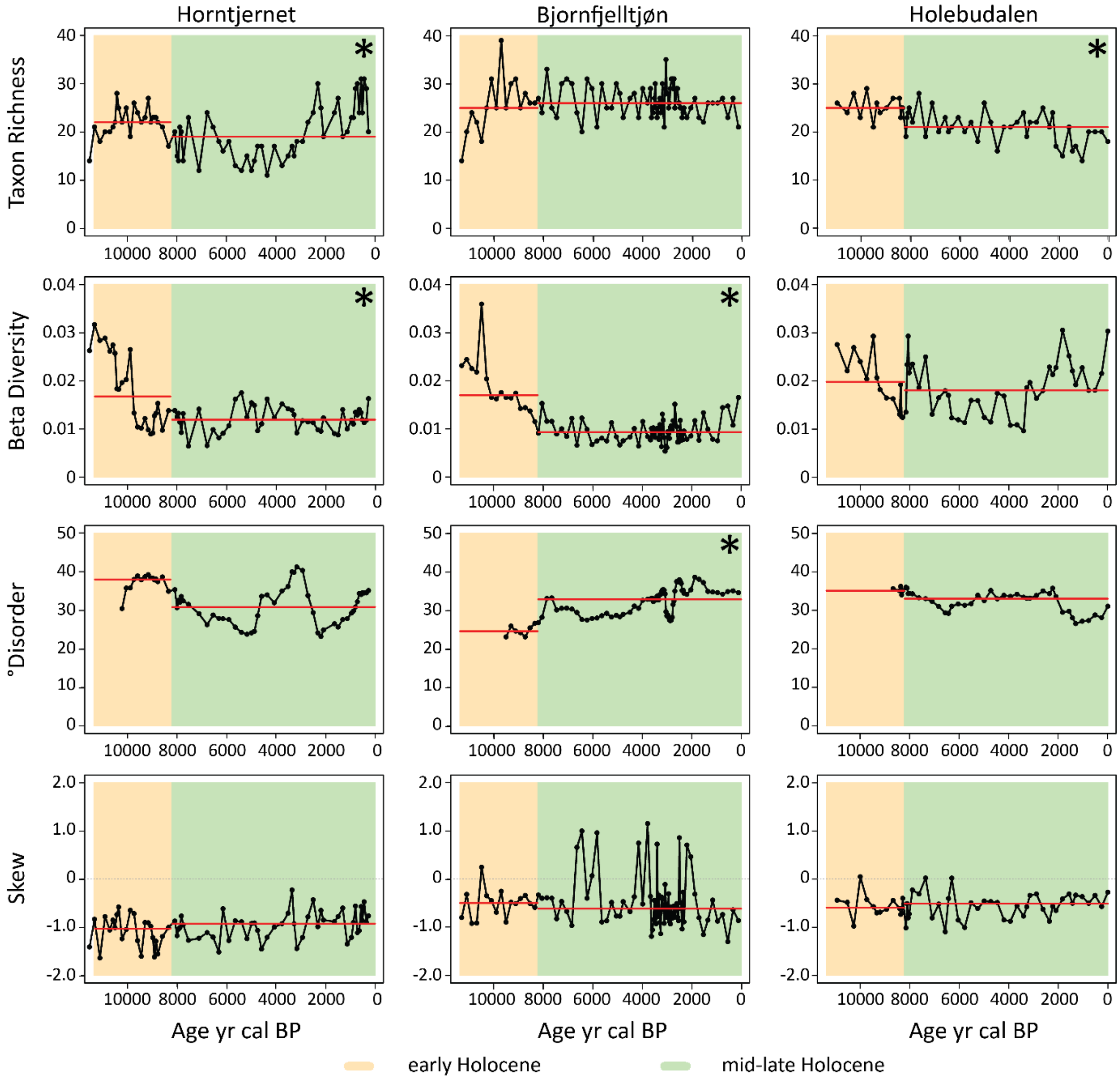

Figure 4.8 Structural metric trends (black lines) for the chironomid assemblages during the Holocene. Median values (red lines) were calculated for the early and mid-late Holocene. An asterisk denotes trends with differences in median metrics ≥ 95 % of median differences obtained from the replicated randomised chironomid records.

The ARIMA forecasting models indicate that trends in ecological metrics in the mid-late Holocene were mostly predictable from the trends in the early Holocene. The majority of the taxon richness, beta diversity, and skewness values for the mid-late Holocene fell within the prediction boundaries from the early Holocene (Figure 4.9). °Disorder exceeded the predicted values in all three records. This inference from the statistical analysis is, however, influenced by the small amount of data available in the early Holocene (due to the requirement for a sample window in which to calculate °disorder).

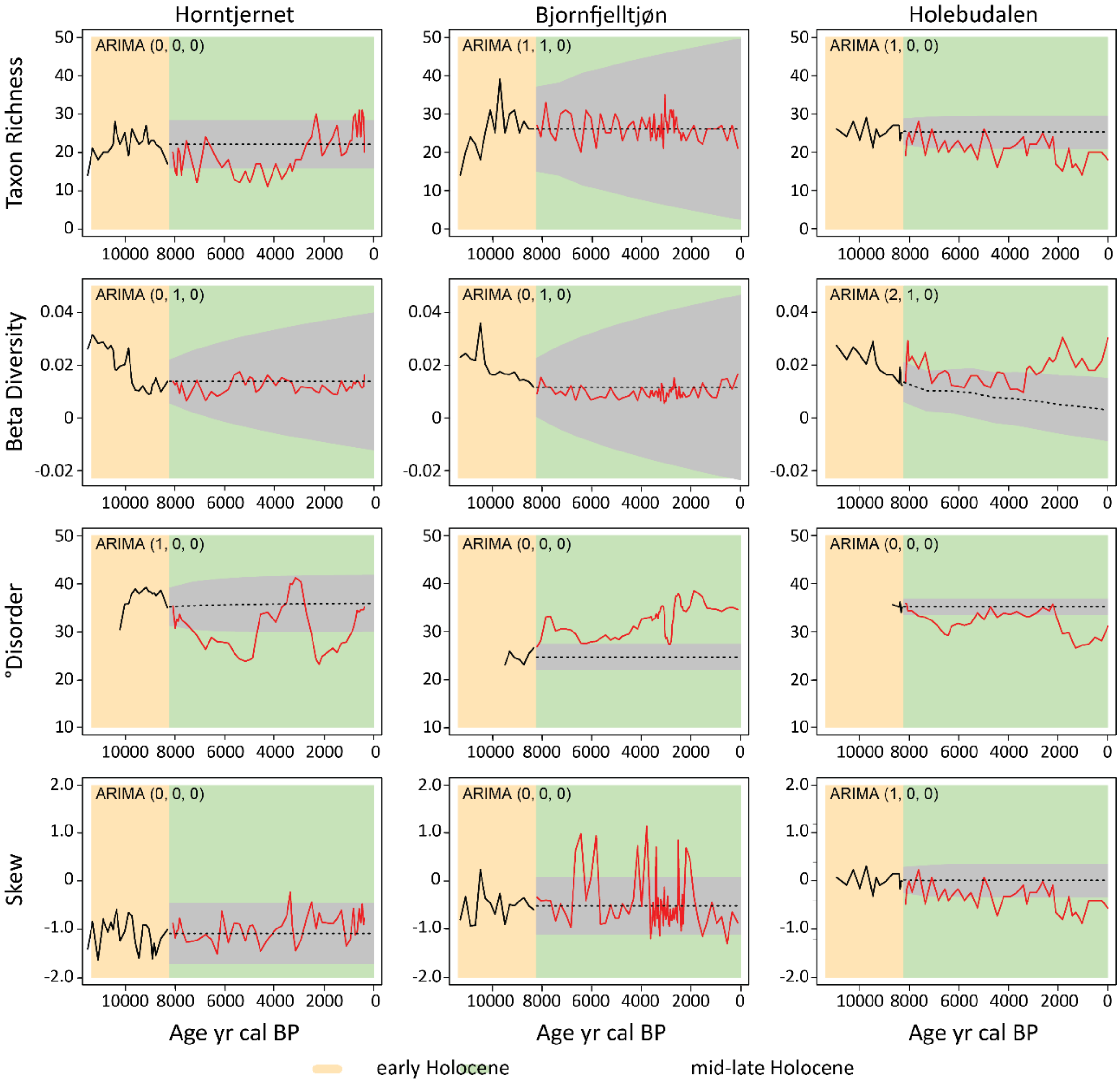

Figure 4.9 ARIMA forecasts for the mid-late Holocene metrics based on early Holocene data: early Holocene metric trends (solid black lines), mean predicted mid-late Holocene metric outcomes (dotted black lines), 95 % prediction intervals (grey bands), and empirical late Holocene metric outcomes (red lines).

Evidence for biometrics tracking the NGRIP isotope trend varied between metrics and locations in the Holocene (Figure 4.10). Taxon richness correlated negatively with the NGRIP isotope record in the Horntjernet record and positively in the Bjornfjelltjønn record. Beta diversity in all three datasets negatively correlated with the NGRIP isotope trend. °Disorder correlated negatively with the NGRIP isotope trend in the Bjornfjelltjønn record. Few of the datasets indicated correlation between the detrended ecological metrics and NGRIP isotope records (Appendix A, Figure A. 16).

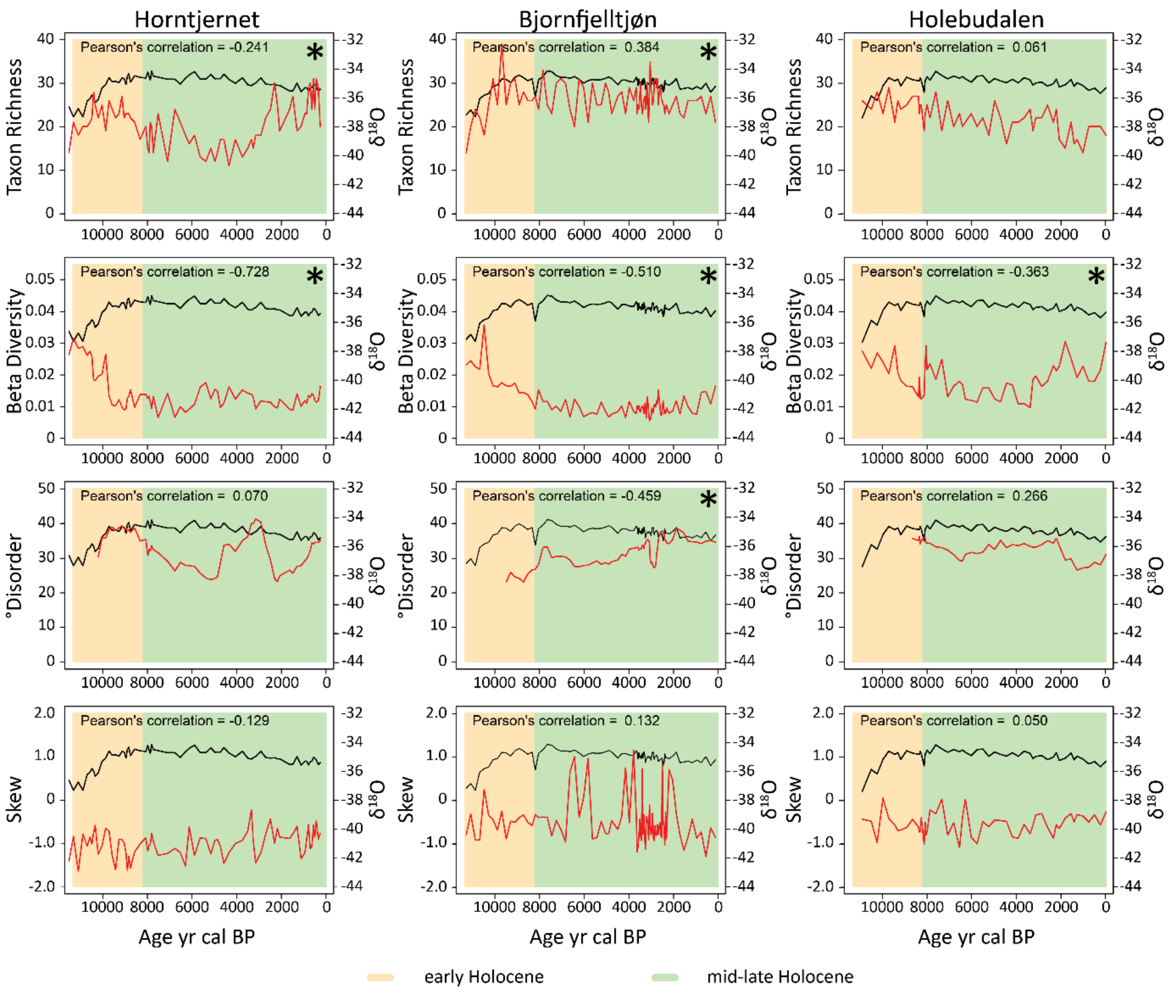

Figure 4.10 Correlation between the NGRIP isotope trends (black) and the chironomid ecological metrics (red) for the Holocene records. Calculated isotopic values are shown for the same ages as the chironomid samples. Person's correlation coefficients indicate the correlated trend between each metric and the isotopic values. An asterisk denotes trends where the observed correlation trend exceeded the random expectation (p ≤ 0.05), when compared to the 10,000 randomised replicate datasets.

## 4.5 Discussion

Ecosystem resilience and adaptability in the face of environmental change are affected by the rate and/or magnitude of the change experienced (Overpeck *et al.*, 1991; Skelly *et al.*, 2007; Grimm *et al.*, 2013). The different rates and magnitudes of the climatic changes within the Bølling-Allerød - Younger Dryas transition and Holocene were reflected in the chironomid assemblage responses. At the Bølling-Allerød - Younger Dryas transition, the chironomid records underwent declines in taxon richness and increases in beta diversity and network skewness. °Disorder, however, showed inconsistent trends. In the Holocene chironomid records, there were some decreases in taxon richness and beta diversity at the early and mid-late Holocene transition. °Disorder and skewness exhibited few discernible changes.

### 4.5.1 Ecosystem structural change during rapid, high-magnitude climatic change

The chironomid assemblage compositions and structures changed in response to the abrupt, high-magnitude climate change at the Bølling-Allerød - Younger Dryas transition (Rasmussen *et al.*, 2006; Golledge, 2010). This was evident in all four metrics, i.e., taxon richness, beta diversity, °disorder and skewness. However, the extent of the response was variable across the metrics. There were large changes in the taxon richness (at Ashik and Muir Park) and beta diversity (all three records) trends, unpredicted by the ARIMA models, suggesting that the changes in composition were unlikely without external forcing. The correlation between the beta diversity and NGRIP ice core isotope trends suggests that the taxon turnover was not independent of climate change. While it is logical that turnover should occur in response to climate change as chironomids are highly temperature sensitive (Brooks *et al.*, 2007), these analyses confirm that high-magnitude changes in stress can drive high-magnitude responses in taxonomic composition.

°Disorder and skewness were used here to indicate changes within the ecosystem structure, specifically taxonomic organisation and connectivity (Doncaster *et al.*, 2016; Wang *et al.*, 2019; Mayfield *et al.*, 2020). In the Late Glacial records, °disorder displayed inconsistent trends, decreasing in Ashik, increasing in Abernethy, and indicating no clear change in Muir Park. A rise in °disorder values indicates greater unpredictability between samples, i.e. fewer taxa in common, while a decrease in °disorder suggests greater predictability, i.e. more taxa in common (Doncaster *et al.*, 2016). Therefore, these records indicate that changing assemblages, with decreased richness and increased turnover, can produce different outcomes in °disorder. Doncaster *et al.* (2016) theorised that the ordered or disordered turnover of an assemblage corresponds to the functional type of the taxa gained or lost from the assemblage. For our sites, this suggests that the functional types of the taxa lost, or gained, was different between the Ashik and Abernethy records, causing the opposing changes in °disorder values. For example, the Ashik and Abernethy records had similar assemblage compositions during the Younger Dryas, with assemblages dominated by cold-stenothermic *Micropsectra radialis*-type (Chase *et al.*, 2008; Rolland *et al.*, 2008), however, the two lakes had different Bølling-Allerød assemblages (Brooks *et al.*, 2012b). In the Ashik record, *Microtendipes pedellus*-type and *Corynocera ambigua* dominated the assemblage during the Bølling-Allerød indicating relatively warm, mesotrophic conditions (Brodersen and Lindegaard, 1999; Watson *et al.*, 2010), and the possible presence of aquatic macrophytes as suggested by the presence of *Dicrotendipes nervosus*-type (Brodersen *et al.*, 2001; Watson *et al.*, 2010). In the Abernethy record, the Bølling-Allerød assemblages were more diverse, with the continued presence of cool-adapted taxa and the arrival of more phytophilic taxa, such as *Psectrocladius* and *Tanytarsus glabrescens*-type (Brodersen *et al.*, 2001; Heiri and Lotter, 2010). This indicates that the lakes had different lake habitats, and thus different assemblages, prior to undergoing the Younger

Dryas climatic cooling, perhaps explaining the different responses within the °disorder metric. This also highlights the importance using long-term palaeoecological records to understand the historical contingencies of communities, in order to anticipate future responses to climate and environmental change (Hawkes and Keitt, 2015).

Skewness rose in all three Late Glacial records, possibly as a result of reduced interspecific competition indicated by the low taxon richness (Eurich *et al.*, 2018). A more positive skewness indicates a greater proportion of weakly connected taxa (Wang *et al.*, 2019). It is thought that undisturbed networks are positively skewed, indicating stable, highly evolved, self-organised, complex states, where the majority of taxa are weakly connected, with a small number of highly connected taxa (Albert and Barabási, 2002; Scheffer *et al.*, 2012). This structure provides a degree of resilience to taxonomic loss and network fragility, assuming that the weakly connected taxa are lost first (Albert *et al.*, 2000; Sole and Montoya, 2001; Dunne *et al.*, 2002). The majority of the chironomid samples in this study produced negative values, suggesting that the communities were prevented from developing a more complex structure. The lack of positive skewness in chironomid communities could relate to unstable environmental conditions, or non-analogue communities when comparing past conditions with modern assemblages (Velle *et al.*, 2005b). However, the lack of positive skewness could also be a limitation of the analytical method as the absolute skewness values are sensitive to statistical procedures. Mayfield *et al.* (2020) also reported a predominance of negatively skewed chironomid communities in their study of structural change in chironomid communities across high latitude regions, thus, here we focus on the relative trends as a guide to structural change.

There was a relatively small rise in positive skewness during the Younger Dryas, however, the increase in skewness values did not fall outside the prediction intervals of the ARIMA model. This suggests that, despite the large compositional turnover, the change in ecosystem structure was relatively small. This may relate to the ecological function of the lost taxa within the ecosystem. Gallagher *et al.* (2013) found that loss of taxa does not necessarily lead to impairment of ecosystem function as the remaining taxa may still occupy all the available niches, while Obertegger and Flaim (2018) found that functionally similar ecosystems can exist in large and small communities, at different levels of diversity, based on resource use. Furthermore, many chironomid taxa have relatively large trait variability or plasticity (Serra *et al.*, 2017), and depending on availability of food resources, taxa can display generalist or opportunistic feeding behaviours (Reuss *et al.*, 2013; Lee *et al.*, 2018), thus, increasing the ability of different chironomid taxa to substitute functions within an ecosystem and reducing the effect of taxon loss on the ecosystem functionality (Brown et al., 2001). At genus level, there is an overlap in food and habitat preferences within Orthocladiinae and Chironominae (sub-tribes *Chironomini*, *Tanytarsini* and *Pseudochironomini*) (Serra *et al.*, 2016). The assemblages at Loch Ashik, Abernethy and Muir Park primarily consisted of these *Chironomidae* genus-types, thus the temperature-driven assemblage changes may have had a subdued effect on ecosystem functionality.

### 4.5.2 Additional drivers influence ecosystem structure during periods of low climatic change

In the Holocene, the change in beta diversity was relatively gradual, reflecting the lower magnitude changes in the NGRIP record (Wanner *et al.*, 2008). There was a rise in °disorder in the Bjornfjelltjønn record indicating a rise in composition dissimilarity with the changing climate. Skewness indicated little ecosystem structural stability. Theoretically, skewness should become more positive during long, stable periods, such as the Holocene, as habitats develop and micro-niches diversify (Wang *et al.*, 2019). The lack of clear trends in the Holocene records is likely an effect of non-climate factors as discussed below.

As the climate stabilised in the mid-late Holocene (Wolff *et al.*, 2010), other environmental drivers may have become prominent, such as edaphic factors, paludification, vegetation change, and more recently anthropogenic drivers including increased nutrient loading (Velle *et al.*, 2010). Such drivers can also cause changes in ecosystem structure and functionality; for example, through eutrophication and acidification (Heiri and Lotter, 2003; Ilyashuk *et al.*, 2005; Velle *et al.*, 2010). While ecosystem stability may be ultimately controlled by climate (Birks and Ammann, 2000; Brooks *et al.*, 2012b), our study suggests that localised factors may have a greater influence on assemblage structure in times of low climatic stress, as also suggested by Velle *et al.* (2005a) and Brooks (2006b). Inspection of the chironomid assemblages supports this: Horntjernet, situated at the current boreal ecotone boundary in arctic Norway, was exposed to post-glacial environments, paludification and afforestation during the Holocene (unpublished data). Landscape change and increased dissolved organic carbon possibly caused the large change in °disorder trend at c. 5,000 to 2,000 a cal BP. Bjornfjelltjønn, a low-alpine lake, was subjected to the increased influence of cold melt-waters during the early Holocene and acidification during the later Holocene in response to vegetational succession and soil development (Brooks, 2006b). Plant macrofossils indicated a change in landscape vegetation at c. 3,800 a cal BP (Brooks, 2006b), possibly causing the brief decrease in °disorder in the chironomid record around this time. Holebudalen, a low-alpine lake, also experienced acidification during the Holocene most likely due to local forest or bog development (Brooks *et al.*, 2012a). Velle *et al.* (2005a) identify a shift in chironomid composition at c. 2,000 a cal BP, attributing this change to an increase in thermophilic and eutrophic taxa. Thus, a change in the chironomid assemblage to taxa more sensitive to water quality may have caused the changes in the °disorder metric. Comparisons with proxies of landscape dynamics and water quality, such as pollen or diatoms, would help clarify the driver of these assemblage changes and provide greater insight into changing lake ecosystem structure; for example, as done by Rosén *et al.* (2001), Langdon *et al.* (2004), and Velle *et al.* (2005b). This emphasises the importance of constructing detailed, multiproxy analyses of lake records to enable full comprehension of the changes preserved in the records.

### 4.5.3 Timescales and magnitude of change

To better understand changes within ecosystem structures, timescale should be considered. The selected proxy and sampling resolution must have the appropriate sensitivity to record the magnitude of change and the response of a system to a driver of stress (Lenton, 2011; Lenton *et al.*, 2012). The records used in this study span millennial timescales, with variable temporal resolution; the time between adjacent samples represented between c. 3 – 163 years during the Bølling-Allerød and c. 43 – 369 years in the Younger Dryas. Similarly, in the Holocene, the temporal resolution varied between c. 44 and 415 years in the early Holocene and c. 36 – 430 years in the mid-late Holocene. While these temporal resolutions were comparable, changes in °disorder and skewness were identified in the Late Glacial records, but not in the Holocene records. This indicates that rapid, high-magnitude climate change can drive ecosystem structural change, as seen at the Bølling-Allerød - Younger Dryas transition, however, the slower, lower-magnitude, climate change between the early and mid-late Holocene was not great enough to influence the ecosystem structure. Furthermore, the metrics did not indicate substantial changes in the trends in association with rapid, higher-magnitude Holocene climatic events, such as the Preboreal Oscillation, 9.3 ka and 8.2 ka events (Alley *et al.*, 1997; Rasmussen *et al.*, 2007) or rapid, lower-magnitude events such as the MCA and LIA (Massé *et al.*, 2008; Mann *et al.*, 2009) (Appendix A, Figure A. 17). Previous studies have indicated changes in chironomid assemblage composition and associated chironomid-inferred temperature reconstructions with these Holocene climatic events (Axford *et al.*, 2008; Larocque-Tobler *et al.*, 2010; Paus *et al.*, 2011; Porinchu *et al.*, 2019). Thus, this suggests that while chironomid assemblages can be sensitive enough to record taxonomic changes in association with such events, it is possible that these resulting assemblage changes had limited effect on the ecosystem structure, or community structural changes were not detectable in the temporal resolutions presented here. Other environmental stressors have been seen to drive structural change at shorter time-scales; Doncaster et al. (2016) and Wang *et al.* (2019) found high magnitude changes in °disorder (for chironomids and diatoms) and skewness (diatoms) in lakes experiencing high magnitude shifts in total phosphorus that drove large changes in chironomid and diatom assemblage structure on a sub-decadal timescale. This reaffirms that the sampling resolution must have the appropriate sensitivity to record the magnitude of change and the response of a system to a driver of stress (Lenton, 2011; Lenton *et al.*, 2012). Analysing records with a higher temporal resolution spanning rapid climatic events could provide greater insight into the ability of rapid climate events to drive structural change.

### 4.5.4 Future possibilities of ecosystem structural analysis

The records analysed here provided insight into the influence of past millennial-scale climatic changes on the structure of chironomid communities, yet to fully understand how ecosystem structures may respond to future rates and magnitudes of climate change, we need to consider how ecosystems have responded to stress in the more recent past. Chironomid communities have already experienced changes in composition in relation to recent 20th century warming (Porinchu *et al.*, 2007), however, finding lakes without additional environmental or human-derived stress is increasingly unlikely, even in the Arctic (Smol *et al.*, 2005). Considering that the Holocene records studied here appear to be influenced by multiple-interacting factors, this further emphasises the importance of investigating the effect of combined environmental stressors. Thus, we propose that analysing high-resolution lake records spanning the more recent past may further our understanding of the combination of ecosystem drivers that lakes currently are facing and the effects such drivers have on lake ecosystem structures; for example, see Ilyashuk *et al.* (2015), Nevalainen *et al.* (2015) and Engels *et al.* (2020).

Macroinvertebrates, such as chironomids, are a fundamental component of freshwater ecosystems (Jones and Grey, 2004; Ólafsson and Paterson, 2004), and changes in the abundance or distribution of the invertebrate component of a food web can have repercussions throughout the ecosystem (Petchey *et al.*, 1999). Multi-tropic scale ecosystems are at risk from climate change (Beier, 2004; Pecl *et al.*, 2017), and analysis of the interactions between tropic levels has indicated that low trophic levels can indicate the level of deterioration in food-web stability (Kuiper *et al.*, 2015; Kivilä *et al.*, 2019). It is thought that chironomids can improve biomonitoring approaches and increase understanding of lake ecosystem change (Nicacio *et al.*, 2015; Czechowski *et al.*, 2020). It is hoped that through improving our knowledge of chironomid community sensitivity to environmental change with this study, we can contribute to the wider understanding of lake ecosystem resilience and stability.

## 4.6 Conclusions

This study evaluated the effect of rate and magnitude of climate change on chironomid community structure using two periods of past climatic change; the relatively rapid, high magnitude climate change at the Bølling-Allerød - Younger Dryas transition, and the more gradual, relatively low magnitude, climate change during the early - mid-late Holocene transition. The Late Glacial records exhibited high magnitude changes in taxon richness and beta diversity, however, changes in the community structure, represented by °disorder and skewness, were smaller. This was perhaps due to the functional resilience of the chironomid community through the replacement of same functional-type taxa within the network. The Holocene records indicated low taxonomic turnover in association with low levels of climate change, with little indication of climate-driven structural change during the Holocene. It is likely that other environmental factors were having a greater influence on the chironomid assemblage at this time. Overall, this study illustrates that beta diversity is sensitive to compositional change driven by high and low magnitude temperature change. High magnitude changes are required to cause structural change within chironomid community, as seen in the Late Glacial records. The lack of changes in °disorder and skewness in the Holocene records suggest that low-magnitude climate change is not a key driver of structural change. We emphasise that a greater understanding of how combined environmental stresses may influence ecosystem community is important for understanding current and future lake ecosystem change.

## 4.7 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. R. Wang provided the original MATLAB network skewness code. R.J. Mayfield adapted the above codes and ran all analyses on the empirical data. R.J. Mayfield was part of the coring team at Horntjernet, and processed and identified the Horntjernet chironomid samples at the University of Southampton. P.G. Langdon and S.J. Brooks provided assistance with chironomid identification. Other chironomid data was provided by S.J. Brooks, K.L. Davies, and G. Velle. R.J. Mayfield wrote the draft manuscript, on which all co-authors commented.

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# Chapter 5 Paper 3: Structural stability of chironomid communities during historic climatic and environmental change in subarctic Alaska

## 5.1 Abstract

Understanding the current levels of lake ecosystem resilience in the face of increasing environmental and anthropogenic stress may increase our ability to anticipate future ecosystem stability. Here, we assess historic ecosystem stability using network simulations to inform empirical zoobenthos chironomid (Diptera: Chironomidae) reconstructions from three Subarctic Alaskan lakes. We measured ecosystem richness, taxonomic turnover and assemblage structure using taxon richness, beta diversity and network skewness respectively. These three metrics were applied to model-simulated taxonomic networks to establish the sensitivity of the ecological parameters to structural change. The empirical datasets, spanning the last 200 years, indicated a rise in beta diversity, with differing trends in taxon richness and network skewness over time. Increased lake productivity, likely driven by climate change, was associated with changes in community composition and turnover. Trends in taxon richness and network skewness suggest that these chironomid community structures have not fully been impacted by the current levels of climate and environmental change, however, changes within the taxa present suggest these communities may become further impacted as the climate continues to warm.

**Keywords**: Chironomids, ecosystem structure, beta diversity, network skewness, Alaska

## 5.2 Introduction

The world is warming at an unprecedented rate (Smith *et al.*, 2015), with high latitude regions warming almost twice as fast as the global average (Walsh *et al.*, 2017; IPCC, 2018). High latitude freshwater ecosystems are particularly vulnerable to climate change, with recent climate-driven changes in lake assemblages already recorded in Arctic and Subarctic locations (Smol and Douglas, 2007a; Rosén *et al.*, 2009). Combined with growing anthropogenic stresses (Smol *et al.*, 2005; Vilmi *et al.*, 2017), such as increased recent nutrient influx (e.g. from sewage inputs), high latitude lakes have also experienced a rise in nutrient levels (Antoniades *et al.*, 2011; Gallant *et al.*, 2020). High latitude lakes are important resources for local communities, providing drinking water and fisheries (Sjolander, 2011), thus changes in lake ecosystem state have both ecological (Post *et al.*, 2009; Woelders *et al.*, 2018) and human (Hayden *et al.*, 2017) consequences. Climate and anthropogenic stresses are known to impact ecosystem richness and turnover, but less is known about how such stressors can impact ecosystem structures. Here we aim to improve our understanding of current aquatic ecosystem stability, under increasing climatic and anthropogenic stress, through compositional and network analyses of micro-faunal datasets in lake sediments spanning the last c. 200 years.

Climate-driven increases in the abundance and diversity of chironomid taxa have been recorded across the Arctic over the last c. 200 years (Quinlan *et al.*, 2005; Luoto *et al.*, 2014). Warmer temperatures can increase lake microhabitat heterogeneity and biological productivity; for example, through increased macrophyte presence, which in turn can increase microhabitat and faunal diversity (Langdon *et al.*, 2010; Lau *et al.*, 2020). However, combined effects of climate and other environmental pressures, such as bird habitats, can have detrimental effects on chironomid distribution (Luoto and Ojala, 2018). Changes in the abundance or distribution of aquatic invertebrates can have repercussions throughout the ecosystem (Quinlan *et al.*, 2005; Pearce-Higgins, 2010), such as altering ecosystem function and corresponding food web structures (Chapin *et al.*, 2000; Wrona *et al.*, 2006). As such, climate can indirectly influence assemblage structure through changing taxonomic interspecific interactions (Harley, 2011), which can alter the resilience of an ecosystem (Smol *et al.*, 2005; Grimm *et al.*, 2013). Here, we use temporal beta diversity to inform on taxonomic turnover (Legendre and Gauthier, 2014) and ecosystem organisation (Soininen *et al.*, 2007; Heino *et al.*, 2012). Community turnover under exogenous stress is often influenced by the loss of sensitive species (Pound *et al.*, 2018). Considering the large degree of sensitive, cold-adapted chironomid taxa within the Arctic (Medeiros *et al.*, 2011; Eggermont and Heiri, 2012); beta diversity should effectively indicate climate-driven ecosystem change. However, we propose that analysing chironomid community structure, in addition to community composition, may provide increased insight into the stability of lake ecosystems.

Biotic communities are comprised of networks of inter-connected taxa (Bruder *et al.*, 2019). Under low stress conditions, ecosystems are often spatially heterogeneous, with the majority of taxa self-organising into their preferred microhabitats (Van de Meutter *et al.*, 2005; Kouamé *et al.*, 2011), reducing the number of interactions or co-occurrences between taxa (i.e. these taxa are weakly connected) (Dunne *et al.*, 2002; van Nes and Scheffer, 2005). A few taxa may have a large number of interactions or co-occurrences (i.e. they are strongly connected) (Strogatz, 2001; Doncaster *et al.*, 2016; Wang *et al.*, 2019). This produces a network of predominantly weakly connected taxa. Networks with a high proportion of weakly connected taxa have a greater capacity to change gradually to external stressors, as individual taxa can change (leave or join the network) as necessary (Dunne *et al.*, 2002; van Nes and Scheffer, 2005; Scheffer *et al.*, 2012). Increased stress can cause environmental homogenisation and a loss of microhabitats increasing the number of interactions between taxa. This re-organisation of taxa causes an increase in the proportion of strongly connected taxa. In networks of strongly connected taxa, the fate of each individual taxon depends on the fates of its many other interconnected taxa. High connectivity can provide a local resilience to stress, however, also increases the likelihood of systemic critical transitions; a sudden and system-wide shift in taxa (Dunne *et al.*, 2002; van Nes and Scheffer, 2005; Scheffer *et al.*, 2012). Thus, measuring community structure, i.e. the distribution of taxa and their connections, can indicate the level of stress a community might be experiencing (Wang *et al.*, 2019).

In this paper, we investigate the current ecosystem stability of temperature- and environmentally-sensitive chironomid (Diptera: Chironomidae; non-biting midges) communities from three lakes in Subarctic Alaska, an area that has experienced climate warming (Figure 5.1 A - B) (Hinzman *et al.*, 2005) and human population growth (Figure 5.1C) (World Population Review, 2020) over the last *c*. 100 years. Taxon richness, beta diversity and network skewness were used to inform on ecosystem richness, taxonomic turnover and assemblage structure. To assess the informative power of the metrics, taxon richness, beta diversity and network skewness were applied to simulated taxonomic networks with changing taxonomic connectivity. Chironomid assemblage reconstructions were created for three lakes spanning the last c. 200 years. Ordination was used to assess the influence of environmental variables on the chironomid assemblages. Sedimentological and geochemical records were used to identify changes in the lake catchment and in-lake processes, and temperature observations covering the last c. 100 years were used as an indicator of recent climate change. We hypothesise that if the chironomid communities have been affected by recent climatic warming, taxonomic richness and beta diversity (turnover) are likely to have increased. Network skewness should indicate whether this warming had a positive or negative effect on the community structure. For example, if the chironomid communities were experiencing temperature stress, we may expect to see a loss of weakly connected taxa as the most vulnerable (cold stenothermic) taxa disappear from the assemblages.

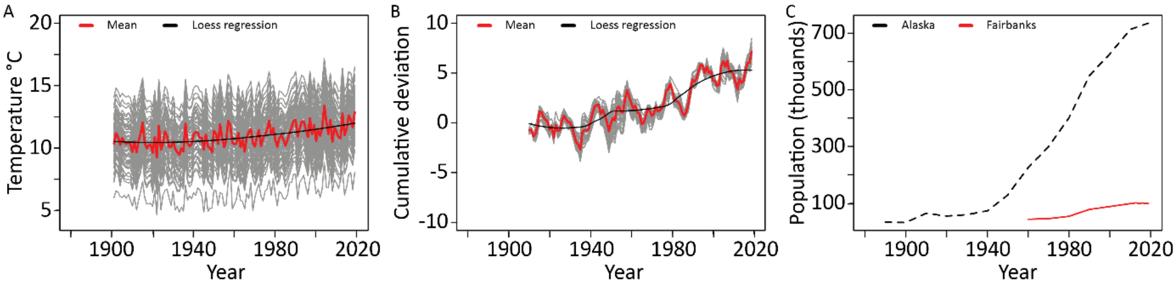


Figure 5.1 Over the last c. 100 years Alaska has experienced climate warming and population growth. (A) Mean summer ambient temperatures (June, July and August) across Alaska (grey lines, see Appendix B, Figure B. 1A for temperature site locations), with mean (red) and smoothed regression (black) curves. Temperature data are from the CRU TS4 Google Earth interface (Harris *et al.*, 2020). (B) To indicate the rate and magnitude of climate change, the cumulative deviation from the long term mean was calculated for each temperature location (grey lines), following Dugmore *et al.* (2007). The long term mean was calculated over periods of 10 years (10 samples). Mean cumulative deviations (red) and smoothed regression (black) curves are also shown. (C) Human population data are shown for the whole of Alaska (black dashed line) and the Fairbanks North Star Borough (solid red line). Population data are from the World Population Review (2020).

## 5.3 Methods

### 5.3.1 Changing taxon connectivity in hypothetical networks

Theory indicates that increased environmental stress can increase taxonomic connectivity (i.e. the number of connections a taxon has) causing structural re-organisation (Wang *et al.*, 2019). To assess the informative power of taxon richness, beta diversity and network skewness in detecting changes in taxonomic connectivity, the metrics are applied to simulated taxonomic networks with changing taxonomic connectivity. Connectivity is defined as the associations of taxa co-occurring in the same microhabitat (Wang *et al.*, 2019; Mayfield *et al.*, 2020). Hypothetical models have previously been used to produce null expectations of community composition and structural change across temperature gradients in Mayfield *et al.* (2020), however, those models did not account for the connectivity between taxa. Here we test the effect of changing connectivity on the metrics.

Networks with a scale-free distribution, i.e. a large proportion of weakly connected taxa and a small proportion of strongly connected taxa (Barabási and Bonabeau, 2003), were generated to represent a single lake community under low stress conditions. Networks were generated using the *barabasi.game* function from the *igraph* package (Csardi and Nepusz, 2006) for R statistical software v. 3.6.0 (R Core Team, 2019). Taxa correspond to a species-morphotype and connections refer to undirected, unweighted taxon co-occurrences within lake microhabitats. Changing taxon presence is likely to occur as environmental conditions change under exogenous stress and taxa leave or join the community network within a lake, however, the type of environmental stress driving the taxon change is not discussed in these model scenarios. The effect of changing taxon connectivity under taxon loss, gain and replacement were tested using scenarios of decreasing and increasing taxonomic richness and taxon turnover (Table 5.1). At each iteration, the model randomly selected the number of taxa (1 or 2) to change within the network. Starting network graphs of 100 taxa were generated for the taxon loss (scenarios 1 - 3) and replacement (scenarios 7 - 11) scenarios. Starting graphs of 10 taxa were generated for the taxon gain scenarios (scenarios 4 - 6). Each model had 50 iterations, with each iteration representing a time step. 50 iterations were selected to show the general trends of changing taxon presence and maintain a manageable network size. The end product was a presence-absence matrix indicating the changing presence of taxa, and their number of connections (called taxon degree), within the network over time. Taxa with zero connections were removed from the network, ensuring that all taxa had at least one connection to another. The network could become fragmented or additional taxa could be lost as a consequence of the removal of a taxon with multiple connections. Each scenario was repeated 100 times to create 100 output matrices. All analyses were run in R Studio v. 3.6.0 (R Core Team, 2019).

In scale-free networks, the distribution of taxon degrees follows a power law (Barabási and Albert, 1999). Under linear preferential attachment, taxa joining a network have a greater likelihood of connecting with strongly connected taxa. A power law of 1, for linear preferential attachment, was used to calculate the new degree distribution as taxa were added in scenarios 4, 5, and 7 - 10. In scenarios 6 and 11, a power law of 0 was used to enable newly arrived taxa to join a random node within the network. Taxa were removed from the existing networks using the *delete_vertices* function and added to the networks using the *sample_pa* function from the *igraph* package. The *sample_pa* function requires an algorithm to generate the new network structure. The 'bag' algorithm was used for scenarios 4, 5, and 7 - 10; 'bag' works by placing the applicable taxa into a multiset the same number of times as their (in-)degree plus one, and by drawing the required number of cited vertices from the bag, with replacement (Csardi and Nepusz, 2006). Under this method, multiple edges between the same two taxa could be generated. Multiple connections between taxa were removed from the networks using *simplify*. The 'bag' algorithm cannot work with a power law of zero, thus, the 'psumtree' algorithm was used for scenarios 6 and 11. The 'psumtree' algorithm uses a partial prefix-sum tree to generate the new network structure (Csardi and Nepusz, 2006).

Table 5.1 Scenarios for testing the effect of taxon connectivity and taxonomic loss, gain, and replacement on three ecological metrics; taxon richness, beta diversity and network skewness. For the taxon replacement scenarios, taxa were removed or added to the network at alternate iterations.

| | | |
|---|---|---|
| Taxon loss | Scenario 1: | Weakly connected (1 – 2 connections) taxa were removed from the network |
| | Scenario 2: | Strongly connected taxa were removed from the network. The three most strongly connected taxa could be selected for removal |
| | Scenario 3: | Taxa were removed from the network, irrespective of the number of connections |
| Taxon gain | Scenario 4: | Weakly connected (1 – 2 connections) taxa were added to the network |
| | Scenario 5: | Strongly connected taxa were added to the network. A newly added taxon could have the same number of connections as one of the 3 most strongly connected taxa within the existing network. This meant that the number of connections the new taxa had was proportion to the existing network |
| | Scenario 6: | Taxa were added to the network with a random number of connections (1 - 24 connections) |
| Taxon replacement | Scenario 7: | Weakly connected (1 – 2 connections) taxa were replaced with other weakly connected (1 – 2 connections) taxa |
| | Scenario 8: | Strongly connected taxa were replaced with other strongly connected taxa. The three most-connected taxa could be selected for removal, while taxa added to the network could have the same number of connections as the remaining three most strongly connected taxa |
| | Scenario 9: | Weakly connected (1 – 2 connections) taxa were replaced with strongly connected taxa. The taxa added to the network could have the same number of connections as the 3 most strongly connected taxa |
| | Scenario 10: | Strongly connected taxa were replaced with weakly connected (1 – 2 connections) taxa. Removed taxa were randomly selected from the three most strongly connected taxa |
| | Scenario 11: | Taxa were randomly removed and added to the network, irrespective of number of connections |

Taxon richness, beta diversity and network skewness were calculated on the simulated output matrices. Taxonomic richness was calculated as the sum of taxa present in each network iteration. Beta diversity was calculated using the variance partitioning framework by Legendre and De Caceres (2013), using the *beta.div* function and ‘Hellinger’ method in the *adespatial* package in

*R* (Dray *et al.*, 2019). To measure skewness, first the frequency distribution of connections between the taxa in the network was calculated, then the skewness of the frequency distribution was calculated using the *skew* function, from the *psych* package for *R* (Revelle, 2016).

### 5.3.2 Chironomid community change in three Alaskan lakes

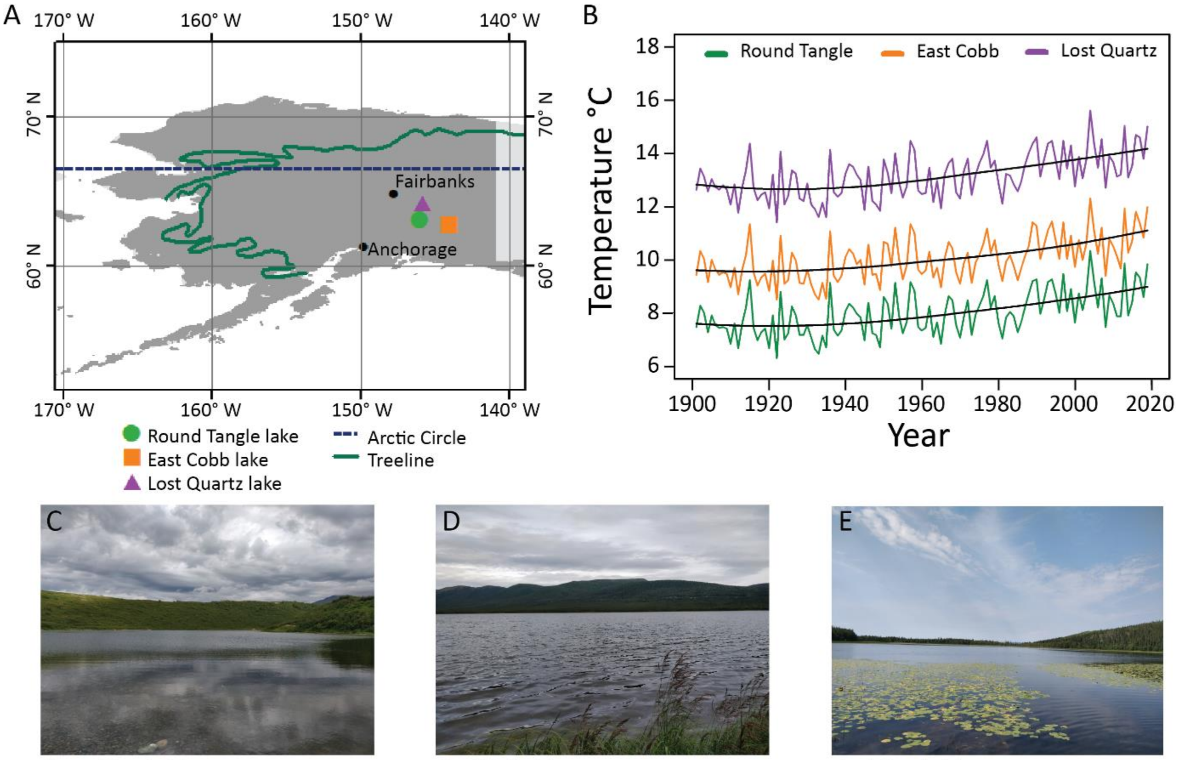
#### 5.3.2.1 Site selection and descriptions

Three lakes from Subarctic Alaska were sampled and analysed to ascertain the current ecosystem stability of environmentally sensitive chironomid communities (Figure 5.2A, Table 5.2). The lakes are part of the North American chironomid calibration dataset (Fortin *et al.*, 2015) and have previously been sampled by Barley *et al.* (2006). The lakes were originally selected for their small size, shallowness, and lack of disturbance, including little or no inflow, to ensure the chironomid assemblage reflected local environmental and limnological conditions (Barley *et al.*, 2006). Lakes for this study were selected based on location, accessibility, lack of disturbance and comparable environmental conditions. The lakes are located within the boreal and discontinuous permafrost zones of Alaska (Brandt, 2009; Wang *et al.*, 2018) and situated on unconsolidated Quaternary surficial deposits (Wilson *et al.*, 2015). The lakes have experienced climatic warming (Figure 5.2B), with comparable rates of change (Appendix B, Figure B. 2) during the last c. 100 years. All three lakes have comparable temperature trends for the last c. 100 years. The differences between the microclimates may relate to altitude; Round Tangle is located at the highest altitude, while Lost Quartz lake has the lowest altitude (Table 5.2).

Round Tangle lake is part of a chain of lakes (c. 26 km long) connected by streams. Samples were taken from the smaller (c. 0.03 km$^2$), shallower southwest embayment, located by the campground. The surrounding catchment was largely comprised of shrub tundra, dominated by dwarf birch (*Betula glandulosa*), various willow (*Salix*) species and scattered white spruce (*Picea glauca*).

East Cobb lake is a shallow, c. 1 km$^2$, lake situated just off the Glen Highway, near the small settlement of Slana (population: c. 150 as of the 2010 census, World Population Review, 2020). The catchment vegetation is dominated by white spruce (*Picea glauca*), Alaska birch (*Betula neoalaskana*), green alder (*Alnus viridis*), balsam poplar (*Populus balsamifera*) and various willow (*Salix*) species. The lake edges were lined with grasses. Pondweeds (*Potamogeton*) and mollusc shells were visible in the shallower sections of the lake.

Lost Quartz lake is a small, c. 0.3 km$^2$, fishing lake, next to the larger Quartz Lake, situated in the Quartz Lake State Recreation Area, c. 10 miles north of Delta Junction. The catchment vegetation is dominated by white spruce (*Picea glauca*), with some Alaska birch (*Betula neoalaskana*), grey alder (*Alnus incana*) and various willow (*Salix*) species. Yellow (*Nuphar lutea*) and white (*Nymphaea alba*) water lilies were present within the lake.



Round Tangle lake

East Cobb lake

Lost Quartz lake

Figure 5.2 Surface cores were collected from three lakes, Round Tangle, East Cobb, and Lost Quartz, in Subarctic Alaska during summer 2018 (A). Mean summer ambient temperatures (June, July and August) were plotted for the 0.5 x 0.5 latitude-longitude grids in which the three lakes are located (B). Temperature data was downloaded from the CRU TS4 Google Earth interface (Harris *et al.*, 2020). Lake images (C - E).

Table 5.2 Metadata for the Alaskan lakes. Mean annual and summer (June, July and August) temperatures were calculated from the CRU TS4 Google Earth interface for the period 1989 – 2018 (Harris *et al.*, 2020). Near-surface water samples were collected for chemical analysis. Water chemical analyses were carried out by Shane Billings, Lab Manager and Building Coordinator at Water and Environmental Research Center (WERC), University of Alaska Fairbanks. For Lost Quartz and East Cobb lakes, there were no detectable levels of fluoride, nitrite, nitrate, bromide, phosphate, iron or manganese. Water chemistry was not available for Round Tangle Lake.

| | Round Tangle | East Cobb | Lost Quartz |
|---|---|---|---|
| Latitude (°N) | 63.05536 | 62.70349 | 64.19979 |
| Longitude (°E) | -146.00697 | -144.06845 | -145.84511 |
| Altitude (m a.s.l.) | 877 | 716 | 303 |
| Depth (m) at coring location | 3.7 | 1.6 | 2.7 |
| pH | 7.5 | 6 | 5.5 |
| Mean annual temperature °C | - 6.0 | - 3.9 | - 2.4 |
| Mean summer temperature °C | + 8.7 | + 10.7 | + 13.9 |
| Conductivity (uS/cm) | NA | 337 | 173 |
| Chloride (ppm) | NA | 3.387 | 3.39 |
| Sulphate (ppm) | NA | 7.544 | 7.47 |
| Calcium (ppm) | NA | 33.7 | 16.0 |
| Magnesium (ppm) | NA | 12.2 | 8.3 |
| Sodium (ppm) | NA | 6.02 | 2.99 |
| Potassium (ppm) | NA | 2.16 | 4.34 |

#### 5.3.2.2 Core collection and analysis

Surface sediment cores were collected from the lakes, summer 2018, using a percussion gravity corer and polycarbonate tubes. A single-beam echo sounder was used to ascertain the deepest part of the lakes. Two parallel cores were collected from each lake at the deepest part. For each site, one of the cores was processed for $^{210}$Pb dating (alpha spectrometry was used to aid dating precision, however, this process is destructive causing a loss of sediment), loss on ignition and bulk density. The second core was processed for chironomid assemblage composition, loss on ignition, bulk density, magnetic susceptibility and XRF sediment analysis. Loss on ignition and bulk density were used to connect the parallel cores and correlate the $^{210}$Pb dating profile and chironomid assemblage composition (see Appendix B, Figure B. 3 - 5).

$^{210}$Pb dating was used to establish a chronology for the lake cores. Analysis was carried out at GAU-Radioanalytical, Ocean and Earth Science, University of Southampton. Freeze dried sediment samples were treated using acid digestion (Aqua Regia) with added $^{209}$Po as a recovery tracer. The extracted $^{210}$Po/$^{209}$Po were plated onto silver disks using auto electrodeposition from a diluted HCl solution. The alpha spectrometric sources were counted using ORTEC Octete spectrometers equipped with PIPS semiconductor detectors. Spectra were analysed using Maestro software. Raw $^{210}$Pb dates were calculated using the Constant Rate of Supply Model (Appleby and Oldfield, 1978). This assumes a constant rate of supply of unsupported $^{210}$Pb to the lake sediments.

To understand the influence of catchment dynamics and in-lake processes on the chironomid assemblage, the minerogenic and geochemical composition of the lake sediment cores was analysed using magnetic susceptibility and elemental X-ray fluorescence (XRF) spectroscopy at the British Ocean Sediment Core Facility (BOSCORF), National Oceanography Centre, Southampton. Magnetic susceptibility measurements were taken at 0.5 cm resolution using a Multi-Sensor Core Logger-Standard (MSCL-S). Geochemical analysis was measured at 200 µm resolution using an ITRAX Energy Dispersive X-Ray Fluorescence (ED-XRF) core scanner (Croudace *et al.*, 2006). To account for changes in core density, surface topography and water content, the elemental data (counts per second, cps) were normalised using the total kilo counts per second (kcps) (Croudace, 2015): *normalised elemental data = cps / kcps.*

Loss on ignition (LOI) and bulk density analyses were carried out in the Geography and Environmental Science laboratories, University of Southampton. LOI was used to indicate the sediment organic matter content (Heiri *et al.*, 2001) and bulk density was used to measure the compactness of the sediment matrix (Mukhopadhyay *et al.*, 2019). For LOI (%) and bulk density (g/cm$^3$), 0.5 cm$^3$ (v) samples were subsampled at a 0.5 cm resolution and dried over night at 105 °C and weighed for the dry sediment mass (α). The samples were incinerated at 550 °C for two hours and weighed for the ash sediment mass (β) (Howard and Howard, 1990). Organic carbon content was calculated using the equation: $LOI\,\% = ((\alpha - \beta) / \alpha) * 100$. Bulk density was calculated as the dry sediment mass (α) divided by the sample volume (v): $bulk\ density = \alpha / v$. For magnetic susceptibility, LOI, bulk density and ITRAX records see Appendix B, Figure B. 6 - 8.

Chironomid assemblage reconstructions were carried out at the Geography and Environmental Science laboratories, University of Southampton. Sediment samples were taken at

0.5 cm resolution to span the past c. 200 years. Samples were deflocculated using 10% KOH for 18 minutes at c. 70 °C and passed through 180 and 90 µm sieves. Chironomid head capsules were picked individually from the residues using Bogorov sorting trays and a mounted pin, air-dried and mounted in Euparal. The specimens were identified to genus or species-morphotype level using standardised subfossil taxonomy (Wiederholm and Eriksson, 1977; Brooks *et al.*, 2007). For Round Tangle, all samples had > 75 head capsules, for East Cobb lake all samples had > 75 head capsules, with the exception of 1 sample (6.0 - 6.5 cm, 71.5 head capsules) (Appendix B, Table B. 1). For Lost Quartz, all lake samples had a minimum of 50 head capsules (lowest count 53.5) (Heiri and Lotter, 2001; Quinlan and Smol, 2001). Chironomid assemblage diagrams were created in *R* using the *rioja* package (Juggins, 2017). Shifts in the chironomid assemblages were identified from dissimilarity indices, using the *vegdist* function in Vegan (Oksanen *et al.*, 2013). Dendrographs were added to the assemblage diagrams to indicate zones of differing taxonomic composition. For assemblage diagrams, see Appendix B, Figure B. 9 – 11.

#### 5.3.2.3 Calculating community change

To identify key gradients within the chironomid assemblages, detrended correspondence analysis (DCA) was used to plot the chironomid records in ecological space. Canonical correspondence analysis (CCA) was used to indicate key influential environmental variables on the chironomid assemblages. Ordinations were run using vegan (Oksanen *et al.*, 2013). Taxonomic richness was calculated as the sum of taxa present in each sample. Beta diversity was calculated using the *beta.div* function and ‘Hellinger’ method in the *adespatial* package (Dray *et al.*, 2019). The assemblage data was transformed by the ‘Hellinger’ method within the *beta.div* function. The above analyses were run in R Studio v. 3.6.0 (R Core Team, 2019).

Network skewness was calculated in MATLAB (ver. R2017b) following Wang *et al.* (2019). To calculate skewness values for temporal assemblages, a modern calibration dataset is required to identify the most-frequently co-occurring chironomid taxa pairs occupying the upper two quartiles of positive values for Cramér’s association coefficient (Q2 of V+). Then, taxon degree (number of connections) was calculated for the fossilised datasets based on the co-occurrences of taxa in the calibration set. Network skewness was measured as the skewness of the frequency distribution of taxon degree. Here, skewness was calculated for the fossilised datasets using both the North American (Fortin *et al.*, 2015) and Norwegian (Brooks and Birks, 2001; 2004) chironomid calibration datasets, as the datasets have different degrees of taxonomic resolution. To test the appropriateness of the calibration sets, non-metric multidimensional scaling (NMDS) was used to ordinate the temporal chironomid records and calibration datasets simultaneously, using the *Timetrack* function in *R* (Simpson and Oksanen, 2019) (Appendix B, Figure B. 12). The fossil samples plotted within the calibration datasets, suggesting that both calibration datasets had good analogues for the fossil records. Goodness of fit analyses, performed using squared residual distance (Juggins and Birks, 2012), also indicated that both calibration datasets were appropriate (Appendix B, Figure B. 13). As required by this method of skewness, the temporal chironomid assemblages were filtered to match the taxa identified in the calibration sets, with some sub-categories of taxa being grouped to genus-type. Taxon richness and beta diversity were calculated on the filtered datasets for comparison. Pearson's correlation indicated strong correlation between the taxon richness and beta diversity trends for the full and filtered datasets. Pearson's correlation did not indicate detectable correlations between the skewness trends for the filtered datasets (Appendix B, Figure B. 14).

Differences in the median metric values were calculated for taxon richness, beta diversity, and skewness for the assemblage zones (identified by the assemblage dendrographs). To test whether the magnitude of change between the observed medians exceeded the expectations for random noise, repeat analyses were run on 10,000 randomised datasets, following Telford and Birks (2011) (Appendix B, Figure B. 15).

Compositional disorder has previously been used as an indicator of unpredictability in chironomid assemblage composition (Mayfield *et al.*, 2020; *in review*), however, the calculation of compositional disorder requires a sample window (Doncaster *et al.*, 2016; Mayfield *et al.*, 2020). The records studied in in this paper cover a relatively short period of time (c. 200 years), and thus, were relatively short in length (n = 10 to 30). Due to the shortness of these records, compositional disorder was not calculated on these records.

#### 5.3.2.4 Environmental drivers of ecosystem change

To assess the relationship between key environmental variables and the chironomid ecological metrics (taxon richness, beta diversity and skewness), generalized additive models (GAMs) were used. LOI, magnetic susceptibility, Fe and Ca were used as predictor variables. Fe and Ca were identified as key elemental variables by performing a Principal Component Analysis on the XRF data (Appendix B, Figure B. 16). Due to the difference in sampling resolution, geochemical values were calculated for the chironomid sample dates using the *predict* function in *R* (Appendix B, Figure B. 17). The relationship between mean July temperature and the chironomid ecological metrics were estimated using GAMs for the period 1901 – 2018. Local historical (mean July) temperature observations were available from 1901 – 2018 from the CRU TS4 dataset to the nearest latitude-longitude half degree grid (Harris *et al.*, 2020). Temperature values were calculated for the chironomid sample dates using the *predict* function in *R* (Appendix B, Figure B. 18). GAMs were run using the *gam* function from the *mgcv* package in *R* (Wood, 2011; Wood *et al.*, 2017). For full model outputs, see Appendix B, Table B. 3 – 19.

## 5.4 Results

### 5.4.1 Simulated changes in taxon connectivity

Taxon richness clearly distinguished between taxon loss, gain, and replacement (Figure 5.3, left-hand columns). However, the metric indicated little sensitivity to structural change as simulated by changes in taxonomic connectivity. Taxon richness did not show unique signatures for non-random change in connectivity to distinguish from random change.

Under taxonomic loss, beta diversity demonstrated more sensitivity to structural change than taxon richness or skewness (Figure 5.3, scenarios 1 – 3). Beta diversity increased in all three scenarios indicating a rise in dissimilarity with taxon loss. Beta diversity became more variable with the loss of weakly connected taxa as the networks decreased in size (scenario 1). The loss of strongly connected taxa produced a gradual increase in beta diversity (scenario 2), distinct from the loss of randomly connected taxa. The random loss of taxa, irrespective to connectivity, produced the greatest increase and variation in beta diversity (scenario 3).

Under taxonomic gain, skewness indicated more sensitivity to structural change than taxon richness or beta diversity (Figure 5.3, scenarios 4 - 6). The gain of weakly connected taxa had a unique signal, with a small, abrupt decrease in skewness after which skewness remained relatively unchanging (scenario 4). The gain of strongly connected and randomly connected taxa produced large decreases in skewness. There was a small rise in skewness as strongly connected taxa continued to join the network (scenario 5). Skewness continued to decline gradually as randomly connected taxa continued to join the network (scenario 6).

Under taxonomic replacement, both beta diversity and skewness were required to see the unique signatures of the type of structural change (Figure 5.3, scenarios 7 - 11). Beta diversity increased and skewness experienced a small decrease as weakly connected taxa joined the network structure (scenarios 7 and 10). As existing taxa were replaced with strongly connected taxa, beta diversity was highly variable, with little directional trend, and skewness strongly decreased (scenarios 8 and 9). In the random replacement scenario, beta diversity was most variable at the ends of the model run, and skewness decreased with taxon replacement (scenario 11), most similar to the replacement of weakly connected taxa with strongly connected taxa (scenario 9).

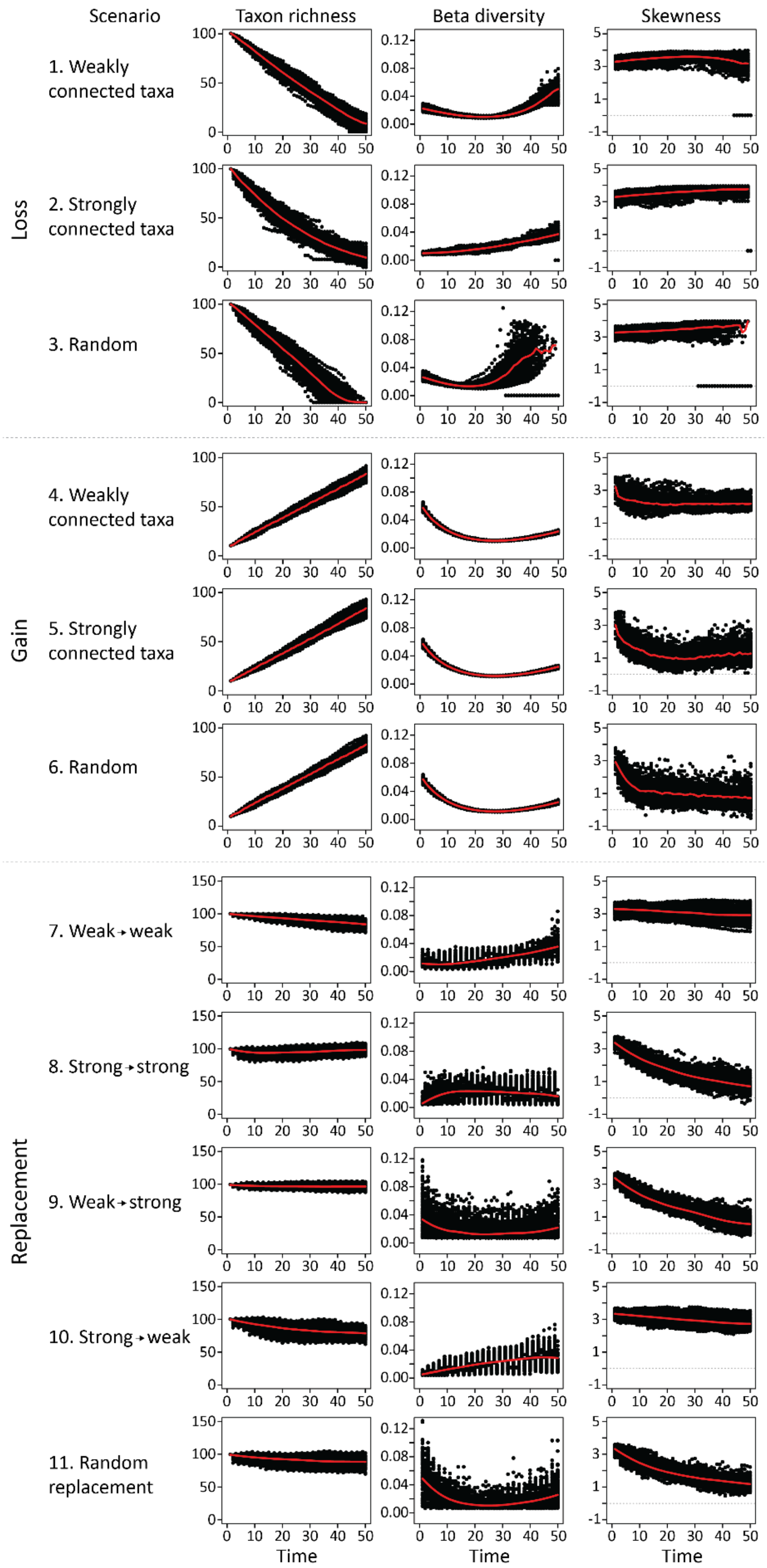


Figure 5.3 Responses of ecological metrics to alternative scenarios of changing taxa connectivity with decreasing and increasing community richness and community turnover. Changing community composition is measured using taxon richness, beta diversity and skewness in 100 simulations (black dots). Mean values are used to highlight the general trend (red lines).

### 5.4.2 Structural change in chironomid assemblages

All three datasets indicated variation in ecological space across the DCA axis 1 (Figure 5.4, upper panels). Changes in the assemblage composition over time, as indicated by dendrographs (Appendix B, Figure B. 9 - 11), plotted separately across the DCA axis 1 (light toned symbols indicate younger samples and dark toned symbols indicate the older samples). CCA plots indicate that changes in the organic (LOI) and minerogenic content were likely to have influenced the chironomid assemblages (Figure 5.4, lower panels). The historical temperature data corresponded with LOI in a CCA applied to the data covering the period c. 1901 to 2018, suggesting the change in productivity corresponded with changing temperature (Appendix B, Figure B. 19).

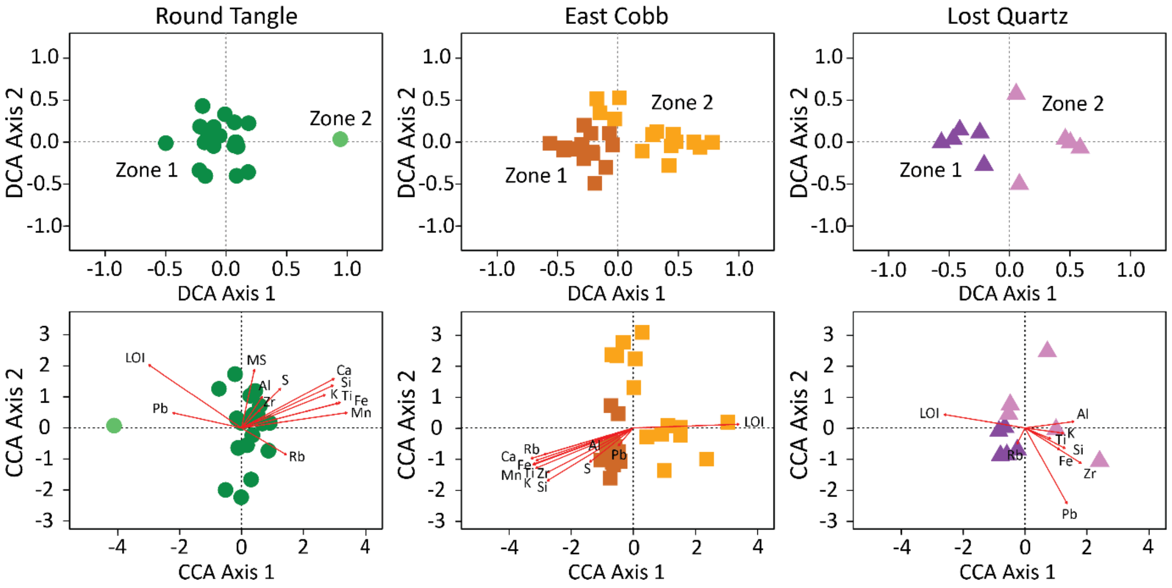


Figure 5.4 Detrended correspondence analyses (DCA) indicated the variation in ecological space for the chironomid samples for each of the Alaskan lakes. Canonical correspondence analyses (CCA) indicated the influence of various sedimentological proxies (organic content (LOI), magnetic susceptibility (MS), and ITRAX elements) on the chironomid samples for each of the Alaskan lakes. The samples are colour coded to correspond with the assemblage zones identified by dendrographs in the assemblage diagrams (Appendix B, Figure B. 9 - 11), with older samples in dark tones (zone 1), and younger samples in light tones (zone 2).

Round Tangle and East Cobb indicated an increase in the taxon richness trend in the upper samples. Lost Quartz showed a decrease in taxon richness in the most recent samples (Figure 5.5). Taxon richness showed no common pattern across the assemblage zones in the three records. There was a detectable decrease in the median richness in East Cobb in the more recent assemblages.

Beta diversity increased in Round Tangle and East Cobb, indicating a rise in turnover in association with the identified assemblage zones (Figure 5.5). GAMs indicated a strong relationship between LOI and beta diversity, with LOI explaining 90.3 % of the deviance in beta diversity in Round Tangle and 63.2% of the deviance in East Cobb (p values < 0.001). A GAM indicated a strong relationship between July temperature and beta diversity in Round Tangle, with July temperature explaining 97.1 % of the deviance in beta diversity for the period 1901 – 2018. In Lost Quartz, beta diversity rose in the mid-section of the record, before decreasing in the uppermost samples. Beta diversity did not change discernibly across the assemblage zones in Lost Quartz.

Round Tangle had the least negative skewness values, with East Cobb and Lost Quartz having more negative skewness values (Appendix B, Figure B. 20). There was little directional change in the skewness values for Round Tangle and East Cobb, although in East Cobb, the Norwegian skewness model suggested a relative decline in the latter half of the record (Figure 5.5). In Lost Quartz, skewness decreased in the recent samples, for both skewness methods.

Skewness trends indicated different fluctuations in all three lakes based on the filtering technique (Figure 5.5, Appendix B, Figure B. 14, 20). Generally, skewness values calculated using the Norwegian calibration dataset were less negative than skewness values calculated using the North American calibration dataset (Appendix B, Figure B. 20). The three records showed little change in assemblage structure in association with the assemblage zones identified by the dendrographs.

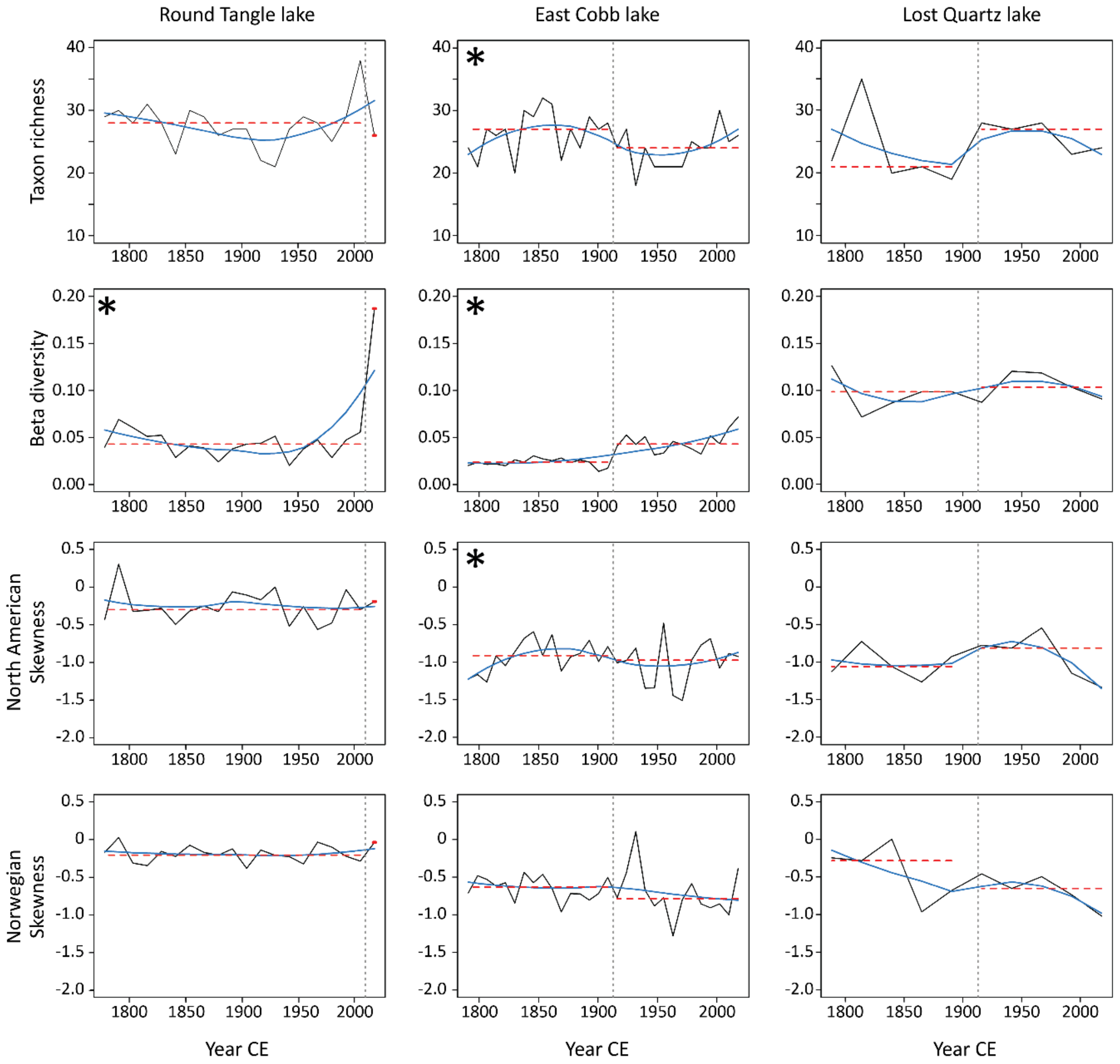


Figure 5.5 Structural metric trends (black lines) for the chironomid records. Smoothed loess regression curves (span = 0.90, blue lines) indicate the general trends. Median values (dashed red lines) were calculated for assemblage zones identified in the assemblage diagrams (Appendix B, Figure B. 9 – 11). An asterisk denotes differences in median metrics ≥ 95% of median differences obtained from the randomised chironomid records.

## 5.5 Discussion

High latitude lakes have been exposed to a wide range of stressors over the recent centuries (Smol *et al.*, 2005), driving changes in freshwater assemblages (Smol and Douglas, 2007b; Woelders *et al.*, 2018). Here, we demonstrated that recent chironomid communities in Subarctic Alaska have experienced compositional change in relation to climatic and environmental stress, however, maintain some degree of structural stability.

### 5.5.1 Network structure as an indicator of ecosystem stability

Network structure can indicate the level of stress a community might be experiencing, through the proportion of strongly and weakly connected taxa (Wang *et al.*, 2019). The network models in this paper suggest that taxa joining a network have a greater influence on the network structure, as indicated by the decline in skewness, with the arrival of weakly connected taxa causing a smaller decrease and the arrival of strongly connected taxa causing a larger decrease in skewness. These trends are evident in the gain and replacement scenarios, suggesting that the arrival of new taxa has greater influence on network structure than the loss of taxa. The loss scenarios support this; the loss of taxa simulated gradual changes in skewness, irrespective of the connectivity of the lost taxa. In the hypothesised models in Mayfield *et al.* (2020) where connectivity was not accounted for, the arrival of taxa also simulated a decrease in skewness values in scenarios where taxon richness increased linearly and where taxon richness increased overall with turnover in taxon-type. The models used in this study suggest that the relative connectivity of the taxa joining a network is key to understanding the effect of the additional taxa on the network structure. It is possible that the connectivity of a joining taxon is determined by the heterogeneity/ homogeneity of the environment the taxon is joining. Under reduced exogenous forcing, systems composed of weakly connected taxa are likely to have relatively high diversity and turnover rates, where individual taxa react to changes in environmental conditions (leave or join the ecosystem) at their own rate (van Nes and Scheffer, 2005; Scheffer *et al.*, 2012). This is unlikely to have a strong effect on the network structure, as suggested by modelled scenario 7. However, increased environmental stress from exogenous forcing has been associated with the increased prevalence of strongly connected taxa in analyses of community nestedness (Doncaster *et al.*, 2016), and lake environmental homogenisation, due to eutrophication, corresponded with abrupt declines in skewness in analyses of diatom communities (Wang *et al.*, 2019). Understanding community structure, through analyses such as network skewness, may provide earlier detection of ecosystem instability, increasing the window of opportunity to manage or reduce shifts in ecological state (Hughes et al., 2013).

Abrupt, high-magnitude climate change has been shown to alter aquatic ecosystem structures (Mayfield *et al.*, *in review*). Current climate change is occurring rapidly (Smith *et al.*, 2015), with climate change already recognised in Alaska (Hinzman *et al.*, 2005), however, the empirical lake records in this study do not indicate discernible changes in community structure. This suggests that the lake assemblages presented here experienced a relatively low magnitude of climate and/or environmental change, compared to abrupt changes measured during periods of past climate change such as the Late Glacial Interglacial Transition (Mayfield *et al.*, *in review*). All three empirical records had primarily negative skewness values, however, it is likely that high latitude aquatic communities, comprised of taxon-poor cold-adapted assemblages, have some degree of structural stress due to the extreme climatic conditions (Mayfield *et al.*, 2020). As the climate warms, taxonomic turnover is likely to occur as cold adapted taxa are lost and more temperate taxa arrive (Engels *et al.*, 2020). Theoretically, the first taxa to disappear from a network are likely to be sensitive, weakly connected taxa, increasing the proportion of highly connected taxa and causing a decline in skewness (Doncaster *et al.*, 2016; Wang *et al.*, 2019). The network models in this paper suggest that the arrival of new taxa may cause a further decline in skewness. Both skewness methods indicate decreases in skewness in the upper samples of the Lost Quartz record. The models suggest that decreasing skewness is associated with an increasing richness or turnover in taxa type. There were small increases in taxon richness and beta diversity in the Lost Quartz record, however, the Lost Quartz record is short (10 samples long), making it difficult to distinguish the trend from background variation. Analysis of the taxonomic composition may provide greater insight into the level of chironomid community change the records have experienced from current climatic and environmental conditions.

### 5.5.2 Relative ecosystem stability in changing Subarctic Alaskan lakes

Beta diversity indicated a rise in turnover in Round Tangle and East Cobb lakes, whereas there was little discernible change in taxon richness and skewness across the lake assemblage zones. Analysis of the lake assemblages and sedimentology in this study suggests these lakes have experienced environmental change. A decrease in cold, oligotrophic taxa such as, *Corynocera ambigua* and *oliveri*-type, and rise in temperate-preferring taxa, such as *Chironomus anthracinus*-type, *Microtendipes pedellus*-type, and *Polypedilum nubeculosum*-type, in East Cobb lake indicated a direct response to temperature change (Brooks *et al.*, 2007) (Appendix B, Figure B. 10). In Round Tangle (Appendix B, Figure B. 9), there was a rise in the presence of littoral taxa, such as *Diplocladius, Limnophyes – Paralimnophyes*, and *Thienemannimyia*, which could indicate lake shallowing (Cranston, 1983; Fittkau and Roback, 1983; Massaferro and Brooks, 2002; Brooks *et al.*, 2007). Lake shallowing and shrinking has been recorded across Subarctic and boreal Alaska, attributed to climate-driven processes, such as increased drainage from permafrost melting and increased evapotranspiration from warmer and longer summers (Riordan *et al.*, 2006; Jepsen *et al.*, 2013). *Thienemannimyia* and *Limnophyes* can also be found in streams (Fittkau and Roback, 1983; Brooks *et al.*, 2007), thus, a rise in these taxa could indicate increased catchment activity or inwash. However, a decrease in concentration of the geochemical composition within the recent sediments at Round Tangle (Appendix B, Figure B. 6), suggest increased inwash was not the primary reason for the increased presence of littoral taxa (Schlolaut *et al.*, 2014; Davies *et al.*, 2015; Plaza-Morlote *et al.*, 2017).

The changes in beta diversity in the lakes were strongly related to changes in biological productivity, likely linked to warmer temperatures (as identified by the CCA and GAM outputs). In Lost Quartz, there was a rise in the abundance of *Dicrotendipes nervosus* and *Ablabesmyia*, which are often associated with macrophytes (Brodersen *et al.*, 2001; Langdon *et al.*, 2010; Watson *et al.*, 2010), and a decrease in *Pagastiella*, which can be sensitive to increases in eutrophication (Moller Pillot and Buskens, 1990). In East Cobb, there was an increase in the abundance of *Dicrotendipes nervosus* (associated with macrophytes) and *Polypedilum nubeculosum*-type, which often occurs in eutrophic lakes (Brooks *et al.*, 2007). Increased lake productivity has been linked with warming in the Arctic (Michelutti *et al.*, 2005). Thus, it is possible that the assemblages in this study, relating to increased productivity and potentially lake shallowing, are showing signs of ecosystem change, indirectly related to climate change.

Skewness was predominately negative across all three lakes, indicating high taxon connectivity. This suggests some degree of community stress; Mayfield *et al.* (2020) found that the majority of high latitude chironomid communities were experiencing structural stress, likely due to their extreme environments. The lack of detectable change in skewness, despite the turnover of taxa, could suggest that the lakes have some degree of relative resilience to the current level of environmental stress. Cold stenothermic taxa are adapted to thrive in harsh environments, perhaps providing Arctic and Subarctic ecosystems with extra resilience to changing conditions (Stewart *et al.*, 2013). Chironomids can have relatively large trait variability or plasticity (Serra *et al.*, 2017) and opportunistic feeding behaviours (Lee et al., 2018), further promoting a degree of resilience within chironomid communities. The lakes studied here experienced a rise in productivity (LOI %) and possibly lake shallowing. The rise in productivity could have increased the availability of microhabitats within the lake, for example through an increase in macrophyte presence (Langdon *et al.*, 2010). Aquatic vegetation was present in all three lakes on sampling. This rise in microhabitat diversity, or heterogeneity, may explain the lack of definitive change in network skewness. Hayden *et al.* (2017) found a peak in macroinvertebrate community in mesotrophic lakes in the Subarctic. The increasing trend of eutrophication in high latitude lakes with climate change (Douglas and Smol, 1999; Antoniades *et al.*, 2011; Hessen *et al.*, 2017), could be indicative of future structural change. Changes in skewness have been recognised in contemporary lake assemblages driven by eutrophication and ecosystem homogenisation (Wang *et al.*, 2019). Lougheed *et al.* (2011) identified a range of climate-associated changes in Alaskan ponds over the last 30 - 40 years, however, commented that the macroinvertebrate communities experienced little change, with the arrival of few new chironomid species, further suggesting chironomid communities may be slow to register recent arctic warming.

### 5.5.3 Taxonomic resolution and network skewness

Skewness requires the use of a calibration dataset for the calculation of the frequently co-occurring chironomid taxa pairs. Here, we used the North American (Fortin *et al.*, 2015) and Norwegian (Brooks and Birks, 2001; 2004) calibration datasets, more commonly used for temperature reconstructions. The North American calibration dataset has a lower taxonomic resolution, due to inconsistencies in taxonomic identification across individual lakes and combining smaller datasets into larger datasets (Fortin *et al.*, 2015). The taxonomic resolution was refined in the Norwegian calibration dataset, increasing the number of morphotypes (Brooks and Birks, 2001), with the primary aim of improving the prediction of subtle climatic changes in fossil records. The taxon richness trends remained largely similar across the empirical records, although the values were lower when filtered using the North American calibration dataset. The differences in taxonomic resolution had reduced effects on the beta diversity trends, indicating that the changes in taxonomic turnover occurred at a higher taxonomic level than species-morphotype.

Skewness produced different trends, based on usage of the North American and Norwegian calibration datasets, with little correlation. This suggests that the filtering of the fossil datasets can affect skewness, most likely because the grouping process obscures the interactions between taxa. In the North American calibration dataset, *Cricotopus-Orthocladius* species-types are grouped and the majority of *Tanytarsini* taxa are combined in a sub-tribe Tanytarsina-other group, including rare/ common taxa and warm/ cold taxa. For example, *Tanytarsus lugens* is a cold-preferring taxon and commonly occurs with other cold-water taxa, while *Tanytarsini glabrescens* is more commonly a warm-indicator taxon (Watson *et al.*, 2010; Brooks *et al.*, 2012b). It is unlikely for these *Tanytarsus* species to occur simultaneously, however, they are grouped in the North American dataset, changing the co-occurrences of these taxa with others and likely effecting skewness. In the Lost Quartz and East Cobb records, changes in skewness were more pronounced when calculated using the Norwegian calibration dataset. The Norwegian calibration dataset has a higher taxonomic resolution, and thus, perhaps provides a more accurate representation of structural change.

## 5.6 Conclusions

This study demonstrates the current chironomid community structure of three Subarctic lakes using taxon richness, beta diversity and network skewness. Beta diversity indicated the greatest change in taxonomic composition, in association with increased lake productivity. Taxon richness and skewness indicated some changes in trends in the most recent samples, however, the lack of substantial changes in assemblage structure suggested that that the lakes maintained a degree of ecosystem structural stability under the current levels of climate and environmental change. We find that beta diversity is a more sensitive ecological metric to current climatic change. We propose that the current levels of climate and environmental change are not great enough to drive structural change, as detected by network skewness. However, the rise in lake productivity and taxon turnover may be indicative of future assemblage change under current climatic and environmental projections. We conclude that high taxonomic resolution is required for skewness to work optimally.

## 5.7 Author contributions

R.J. Mayfield, P.G. Langdon, C.P. Doncaster, and J.A. Dearing discussed the research conceptualization and outcomes. R.J. Mayfield and P.G. Langdon discussed potential coring sites. R.J. Mayfield was part of the fieldwork team and collected sediment and water samples. R.J. Mayfield processed the $^{210}$Pb, LOI, bulk density, and chironomid samples. R.J. Mayfield identified the chironomid samples with assistance from P.G. Langdon. R. Wang provided the original MATLAB network skewness code. R.J. Mayfield wrote the network simulation code. R.J. Mayfield adapted the skewness code and ran all analyses on the simulated and empirical data. R.J. Mayfield analysed all data outputs. R.J. Mayfield wrote the draft manuscript, on which all co-authors commented.

## 5.8 Acknowledgements

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# Chapter 6 Synthesis and Conclusions

## 6.1 Research motive recapitulation

The Arctic has already warmed by 0.75°C in the past decade and by 2° to 3°C in the last century (Post *et al.*, 2019). Climate warming is projected to continue at an unprecedented rate (Smith *et al.*, 2015; IPCC, 2018) and is already having impacts on freshwater aquatic assemblages across the northern hemisphere (Woelders *et al.*, 2018). Scientists have argued that we are edging closer to a cascade of tipping points as the climate continues to warm (Lenton *et al.*, 2019). Thus, there has been an expansion in the number of studies attempting to detect thresholds of change and anticipate potential tipping points. However, detecting thresholds for ecological responses to stress in empirical systems is complex. Difficulties in detecting clear ecosystem shifts and early warning signals (EWS) in time series data, and discrepancies in definitions and applications, has raised doubts in the capability to anticipate abrupt, nonlinear ecological shifts (Capon *et al.*, 2015; Montoya *et al.*, 2018; Hillebrand *et al.*, 2020). Subsequently, a small number of studies have started to investigate ecosystem structure as an indicator of ecosystem stability and resilience under increasing stress, e.g. Doncaster *et al.* (2016) and Wang *et al.* (2019). This thesis sought to test the applicability of such methods to chironomid communities, as a proxy for aquatic ecosystem change, under changing climate conditions.

## 6.2 Thesis aim and structure

The three papers presented in this thesis were designed to address the primary aim of investigating the utility of structural metrics as an indicator of lake ecosystem stability under changing climate. Ecosystem structure and stability were measured using chironomids as the response variable, as they comprise a key component of aquatic ecosystems, through their various feeding strategies, and acting as food for higher trophic levels (Vanni, 2002). Specific research questions (p. 22) were developed to address this aim, following a review of the existing methods of detecting abrupt change in ecological systems and the difficulties arising from these methods.

The research questions addressed in this thesis were:

1) Can structural metrics indicate ecosystem stability in relation to temperature change?
2) How do ecosystem structures respond to different rates and magnitudes of climate change?
3) What is the current extent of ecosystem structural stability, under present levels of climate and anthropogenic stress?

The three papers together form a contribution beyond their individual parts. Each paper presents a step towards greater understanding of the capabilities of structural metrics as indicators of chironomid community structure under changing ambient temperatures. This synthesis section assesses the research outcomes of these papers and their contribution to examining structural metrics as indicators of ecosystem stability. Method limitations and steps to further develop structural metrics as indicators of ecosystem stability are considered.

## 6.3 Structural metrics as indicators of ecosystem stability

High latitude lake ecosystems have already been exposed to climatic warming. Increased temperatures can affect lake community composition through the loss of cold-adapted taxa and the arrival of temperate or eurytopic taxa. The first part of this thesis (Paper 1, Chapter 3, Mayfield *et al*., 2020) analysed the likely effects of temperature-induced changes in taxonomic richness and compositional turnover of environmentally-sensitive chironomids across three regions, northern North America (Fortin *et al.*, 2015), Norway (Brooks and Birks, 2001; 2004), and Russia (Nazarova *et al.*, 2015). Taxon richness, beta diversity, compositional disorder (°disorder) and network skewness were applied to the spatial chironomid datasets to determine whether climate stress had affected ecosystem stability through taxonomic turnover and taxon organisation. Simulated chironomid community data were analysed to produce null expectations of community composition and structural change across temperature gradients. The North American and Norwegian empirical datasets showed comparable trends across the temperature gradient, with lakes at the extreme ends of the gradient indicating greater signs of stress, while the mid-temperature range lakes displayed signs of reduced stress. In the Russian dataset, the chironomid assemblages showed fewer signs of temperature-driven stress. Changes in assemblage composition were primarily influenced by taxonomic turnover, with consistent taxon richness, beta diversity, °disorder and skewness trends across the temperature gradient. These trends were attributed to the wide variance in the environments across Russia, including island, coastal, mountainous and continental locations.

In the North American and Norwegian datasets, lakes existing at the coldest end of the temperature gradient indicated signs of stress in the chironomid communities, with low taxon richness, low dissimilarity (beta diversity), low °disorder (i.e. nestedness) and negative skewness. Nested communities (low °disorder) are more likely to have specialised taxa with narrow ecological tolerances and limited dispersal capabilities (McAbendroth *et al.*, 2005), while negative skewness suggests a higher proportion of highly connected taxa, suggesting habitat homogenisation and fewer available niches (Wang *et al.*, 2019). Cold adapted ecosystems are often ecologically sensitive (Smol *et al.*, 2005), with taxa living at their tolerance limits (Langdon *et al.*, 2011), thus it is perhaps logical that the lakes at the coldest end of the gradient indicated signs of structural stress. This was supported by the modelled scenario outcomes; the simulated assemblages at the coldest end of the temperature gradient also showed structural stress.

Lakes with warmer temperatures should be able to support a greater diversity of life (LeBlanc et al., 2004; Langdon et al., 2010). This was evident in the lakes at the mid-temperature range. These lakes indicated the least amount of structural stress; with the highest beta diversity, °disorder and skewness values, suggesting that the assemblages in this temperature range were more diverse (Wang and Loreau, 2016), with increased habitat diversity and niche development (Wright *et al.*, 2007). The rise in metric values suggested increased ecosystem stability, thus suggesting that a rise in temperature might improve ecosystem conditions. However, the lakes at the warmest end of the temperature gradient indicated an increase in stress; through lower beta diversity, °disorder and skewness values. This could indicate signs of increased temperature stress in the North American dataset, whereas lakes at the warmer end of the temperature gradient in the Norwegian dataset were influenced by bedrock type due to site selection and the purposeful avoidance of areas with human interaction.

From this paper (specifically the North American and Norwegian chironomid datasets), analyses of structural change indicated that, under temperature warming, chironomid assemblages may undergo two stages of structural change. High latitude aquatic communities, comprised of taxon-poor cold-adapted assemblages, are likely to be structurally stressed. Initial warming may provide some ecological release; warmer temperatures may increase biological productivity, increasing lake habitat diversity and, thus, assemblage diversity. However, continued temperature stress, and potentially the addition of secondary drivers of stress, may cause ecological degradation through habitat homogenisation and increased structural stress.

Paper 1 analysed a large number of lakes (n = 784), with a single sample from each lake, representing a snapshot in time. The majority of lakes were negatively skewed. Negative skewness suggests a high proportion of strongly connected taxa, likely from the loss of sensitive, weakly connected taxa under increased environmental stress (Wang *et al.*, 2019). While high connectivity can provide a temporary resilience to stress, there is less capacity for the system to respond gradually to increased stress; individual taxa cannot respond to stress in isolation, but rather in connection with other taxa within the ecosystem (van Nes and Scheffer, 2005; Walther, 2010). This increases the likeliness of systemic critical transitions; a sudden and system-wide shift in taxa (Scheffer *et al.*, 2012). Thus, this paper indicates that high latitude lakes are likely structurally sensitive to changing climatic, or environmental, conditions. However, to ascertain how close these lakes might be to a critical transition, comprehension of how chironomid communities change over time when stressed by climate change is required.

## 6.4 Ecosystem structure response to different rates and magnitudes of climate change

Current climate change is occurring at an unprecedented rate that will continue over the coming decades (Smith *et al.*, 2015). High latitude chironomid communities are likely to be ecologically and structural sensitive to such changes (Smol *et al.*, 2005; Mayfield *et al.*, 2020). The ability of these ecosystems to respond to climate change is likely affected by the rate and magnitude of change (Grimm *et al.*, 2013). Thus, paper 2 (chapter 4, Mayfield *et al*., in review) analysed the effect of different rates and magnitudes of climate change on chironomid community composition and structure, using chironomid palaeoecological records. Two time periods were selected; first the Bølling-Allerød - Younger Dryas transition, a period of past abrupt, high-magnitude climate change, and second, the slower, relatively low-magnitude climate change between the early and mid-late Holocene. A range of ecological and statistical methods were employed to analyse assemblage change across the epochs; including ordination, taxon richness, beta diversity, °disorder, network skewness, and ARIMA forecasting. The Greenland oxygen isotope record was used to test for hemispheric scale climatic influence on the ecological metrics. To distinguish true pattern from random noise in the ecological trends, the observed metric trends were compared to metrics repeated on randomised datasets, following principles from Telford and Birks (2011).

This paper indicated that beta diversity was highly sensitive to climate change, indicating compositional turnover in all records during abrupt, high-magnitude and gradual, low-magnitude climatic stress. °Disorder and skewness indicated structural change in response to the abrupt high-magnitude climate change at the Bølling-Allerød - Younger Dryas transition; however, the metric responses were relatively low magnitude. °Disorder and skewness indicated little structural change in response to the slower, low-magnitude climate change between the early and mid-late Holocene. This suggested that a great amount of exogenous forcing is required to change the structure of chironomid communities, and/or that in other circumstances endogenous changes may dominate. Overall, paper 2 indicated that metrics such as °disorder and skewness can express changes in chironomid community structure over time in response to high-magnitude stress.

During the Late Glacial, the climate experienced a rapid, high-magnitude decrease in temperature (Dansgaard *et al*., 1993; Wolff *et al*., 2010), thus in paper 2 we quantify the effects of climatic cooling on chironomid community structure. Considering that the current climate is warming, a second study testing chironomid structural change from cool to warm climates may be informative; for example, the Younger Dryas to Holocene transition. This was not done as part of this study due to a lack of sample availability. A high sampling resolution was one of the site selection criteria for this paper to ensure there was a wealth of samples to analyse and establish a trend within the climatic epochs. For the Younger Dryas subsections, the number of available samples was small; there were seven samples from the Younger Dryas from Ashik and Abernethy, and eight samples in the Muir Park record. The original authors used a sampling resolution between one to four cm for the Late Glacial records (Brooks *et al.*, 2012b; 2016), with some samples being merged in the Muir Park record due to low head capsule numbers (Brooks *et al.*, 2016). Processing and analysing cores with greater sampling resolution (0.5 cm to 1 cm) during the Younger Dryas - Holocene boundary may provide opportunities to quantify structural change from cool to warm climatic conditions.

## 6.5 Current extent of ecosystem structural stability

Records indicate that the Arctic has already warmed 2° to 3°C in the last century (Post *et al.*, 2019), with climate-driven changes in lake assemblages already recorded in Arctic and Subarctic locations (Smol and Douglas, 2007a; Rosén *et al.*, 2009). Combined with growing anthropogenic stresses (Vilmi *et al.*, 2017; Gallant *et al.*, 2020), and ecosystem sensitivity (Smol *et al.*, 2005; Mayfield *et al.*, 2020), high latitude lakes are at risk of further ecological change. In paper 3 (chapter 5, Mayfield *et al.*, in prep.), the current stability of high latitude aquatic ecosystems was assessed in three Subarctic Alaskan lakes through chironomid community compositional and structural change over the last c. 200 years. Lakes were selected to reflect changes in temperature, with reduced impact from secondary factors, for example, the lakes were in comparable areas of vegetation, permafrost and geology, with minimal human interaction. High-resolution monthly temperature observations are available for the period 1901 – 2018 (Harris *et al.*, 2020), however, the chironomid records were prepared to cover the last c. 200 years to provide increased knowledge of assemblage conditions prior to this known climatic warming. Taxon richness, beta diversity and network skewness were used to analyse chironomid community composition and structure. °Disorder was used as an indicator of unpredictability in assemblage composition in papers 1 and 2. The calculation of °disorder requires a sample window. Window sizes for the °disorder calculation were tested in paper 1, with a 10-sample window providing the best balance of accuracy and sensitivity to change. The records studied in paper 3 covered a relatively short period of time (c. 200 years), and thus, were relatively short in length (number of samples ranged from 10 to 30). Due to the shortness of these records, °disorder was not used in paper 3.

Theory indicates that increased environmental stress can increase taxonomic connectivity (i.e. the number of connections a taxon has) causing structural re-organisation (Wang *et al.*, 2019).

To assess the informative power of taxon richness, beta diversity and network skewness in detecting changes within taxonomic connectivity, the metrics were applied to simulated taxonomic networks with changing taxonomic connectivity. Connectivity was not accounted for in the models in paper 1, where the models were used to demonstrate what metric trends might be expected as assemblages changed over time. Theoretically, the proportion of weakly to strongly connected taxa can indicate assemblage structural organisation, and thus, the stability of the assemblage (Wang *et al.*, 2019). Under rising temperatures, chironomid taxon richness and diversity is likely to increase (Quinlan *et al.*, 2005; Luoto *et al.*, 2014), however the addition of secondary environmental variables may cause taxon loss (Luoto and Ojala, 2018). Thus, in paper 3, network models were generated enabling the controlled loss and/or gain of weakly and strongly connected taxa to distinguish between the informative capabilities of taxon richness, beta diversity and skewness and changing network connectivity. Taxon richness indicated little sensitivity to structural change as simulated by changes in taxonomic connectivity. Under taxonomic loss, beta diversity demonstrated more sensitivity to structural change than network skewness, whereas skewness was more sensitive to structural change under taxonomic gain. Both beta diversity and skewness were required to see the unique signatures of the type of structural change under taxonomic replacement. This highlighted the importance of applying multiple metrics to ecological records to fully comprehend the changes within the assemblages.

The empirical chironomid records indicated assemblage change within the last c. 200 years, likely linked to climate change. Cold, oligotrophic taxa decreased, while more temperate and littoral taxa increased, associated with decreased lake size and increased biological productivity. Beta diversity indicated taxonomic turnover, in association with increased temperature and lake biological productivity. Skewness indicated different trends across the records. Round Tangle lake, which had the lowest ambient summer temperatures, had the least negative skewness values with little directional trend. In contrast, Lost Quartz lake, with the warmest ambient summer temperatures, indicated a decline in skewness in the most recent samples. This could indicate stress; a decline in skewness suggests a loss of weak connected taxa, as the most vulnerable taxa are lost from the network, and a rise in the proportion of highly connected taxa. In the simulated models, a strong decline in skewness was associated with the arrival of strongly connected taxa (scenario 5) and the replacement of either strongly or weakly connected taxa with strongly connected taxa (scenarios 8 and 9). The decrease in skewness in Lost Quartz is most likely to correspond to taxon replacement; there is a small decrease and rise in taxon richness in the uppermost samples. In the most recent samples in Round Tangle and East Cobb lakes, there was a slight rise in taxon richness and beta diversity, suggesting initial changes in assemblage composition. There was a slight decrease in the Norwegian skewness model in East Cobb in the most recent samples, however, generally there was little change in skewness in the Round Tangle and East Cobb records. The lack of change in skewness suggested that the change in composition had not effected the community structure, at the time of sampling (summer 2018). This suggests that climate has a relatively slow influence on assemblage structure, and that the assemblages had some structural stability, and thus resilience, to the current levels of climate warming. However, the projected continual rise in temperature could cause structural change in the future.

## 6.6 Developments in detecting ecological shifts

The majority of previous work has focused on the frequency domain, a more traditional approach that focuses on the process of a system experiencing a fundamental shift from one steady state to another over time. However, there are a number of issues with detecting clear ecosystem shifts and EWS in the frequency domain, as discussed in section 2.1.2 (p.15). Key criticisms include the lack of unification in key terms and applications (Capon *et al.*, 2015; Klose *et al.*, 2020), and lack of evidence of threshold-driven change, alternate states and ecosystem recovery in empirical systems (Capon *et al.*, 2015; Montoya *et al.*, 2018; Hillebrand *et al.*, 2020). Research investigating abrupt ecological change in the spatial domain is relatively new, with methods designed as alternative approaches to detecting ecosystem (in)stability prior to ecosystem change. This thesis applied a range of palaeoecological and statistical tools alongside structural metrics, °disorder and skewness, to detect chironomid community stability. Here, some of the key outcomes from papers 1 - 3 (chapters 3 - 5) are discussed, with reference to issues arising from the frequency domain.

Clarity in the theory, definitions, and applications of EWS research is fundamental for collaborative research (Klose *et al.*, 2020). The work in this thesis, and the associated publications, follow key definitions and theory, as set out in the literature review (section 2.1.1, p.10) for clarity and future comparability to other studies. Definitions, theory, and method descriptions are provided in the individual papers.

Evidence of threshold-driven change and alternate states are fundamental in identifying whether critical transitions have occurred (Hillebrand *et al.*, 2020). In their development and original applications, °disorder and skewness were tested using records from lakes with known ecological transitions. Doncaster *et al.* (2016) applied °disorder to diatom and chironomid records from two lakes in China with high levels of human disturbance and increased algae blooms and phosphorus levels; lake Erhai, Yunnan Province and lake Taibai, Hubei Province. These lakes were considered to have experienced critical transitions (Wang *et al.*, 2012; 2019). A third lake, not thought to have experienced a critical transition, was used as a comparison; lake Loggan, Hubei-Anhui provinces, China. Wang *et al.* (2019) applied skewness to a spatial diatom dataset and five temporal diatom records, from lakes with varying levels of human disturbance as an exogenous stress, from China, including lakes Erhai, Taibai and Loggan. Diatoms were selected as indicators of aquatic stability in these studies as diatoms are sensitive to a range of environmental factors, including nutrient influxes (Battarbee *et al.*, 2002). °Disorder and skewness indicated changes in community structure in the lakes known to have experienced increased exogenous stress, with little or no change in °disorder and skewness in the lakes that did not experience heightened exogenous stress. This provided promising results regarding the ability of these metrics to detect community structure change under nutrient induced stress. In this thesis, datasets were not selected on the knowledge or assumption that critical transitions had occurred; sites were selected on their likeliness of experiencing climatic stress, i.e. high latitude locations and past known climatic events. Furthermore, feedback mechanisms are often an integral factor in the tipping point process (Scheffer and Carpenter, 2003; Lenton, 2013), and feedback mechanisms have not been discussed as part of the papers presented here. The work presented here was designed to preliminarily test the ability of structural metrics to detect changes in chironomid communities under climate change. Analysing palaeorecords of climate change (e.g. during the Lateglacial period), when chironomid communities showed complete turnover, was thought to be the closest comparison to testing lakes with known climatic critical transitions.

Numerous biological proxies can be used as indicators of lake ecosystem state, including ciliates (Pennekamp *et al.*, 2018), phytoplankton and zooplankton (Parparov and Gal, 2016), diatoms (Rühland *et al.*, 2015), chironomids (Langdon *et al.*, 2010), and fish (Jeppesen *et al.*, 2010). The type of proxy used often depends on the type of exogenous forces acting on the lakes, for example, diatoms can be useful indicators of eutrophication as diatoms respond to water quality (Hall and Smol, 1999; Vilmi *et al.*, 2015), however, chironomids are also sensitive to eutrophication (Belle *et al.*, 2017). Doncaster *et al.* (2016) found responses in chironomid and diatom communities to large increases in phosphorus. Often the primary influential variable on chironomids is temperature (in absence of marked nutrient changes), which directly affects the organisms' physiological and biochemical processes (Eggermont and Heiri, 2012). In this thesis, chironomids were used as indicators of lake ecosystem changes as the effect of temperature on aquatic ecosystems was being tested. However, multi-proxy studies often provide increased information on the presence of secondary environmental stress that could influence, amplify, or confound, lake ecosystem stability (Birks and Birks, 2006). Considering the recent increase in lake eutrophication in high latitude areas (Antoniades *et al.*, 2011; Gallant *et al.*, 2020), complementary diatom analyses may provide increased insight in to current, and past, lake ecosystem structural stability and the likelihood of impeding critical transitions. Particularly in sites influenced by climate warming and secondary factors, for example, Luoto and Ojala (2018) found decreased chironomid ecological functioning in relatively nutrient-rich ponds in Svalbard.

High temporal resolution and long-term datasets are required to identify dynamic community conditions and meaningfully distinguish background variations (Spears *et al.*, 2017). In this thesis, the majority of chironomid assemblages had negative skewness values. Paper 1 suggested that high latitude assemblages may exist in a state of disequilibrium with negative skewness due to extreme climatic conditions, and thus, changes in the skewness trend might be more informative. To determine a changing trend in skewness, and thus deviations from background variations, a large number of samples are required. Similarly, the calculation of °disorder requires a sample window, and thus °disorder values are not available for those first samples within the sample window. This further indicates that a large number of samples are required to provide meaningful interpretations about the changing ecosystem stability. Therefore, for now, it is thought that high temporal resolution and long-term datasets are required to indicate changing ecosystem stability in the spatial domain.

## 6.7 Taxonomic resolution

In this thesis, analyses suggest that taxonomic resolution can influence skewness. For the calculation of skewness in temporal datasets, a calibration dataset is required to identify frequently co-occurring chironomid taxa pairs. In paper 2, the Norwegian calibration dataset (Brooks and Birks, 2001; 2004) was selected as the chironomid records were located in Norway and Scotland. However, in paper 3, the records were located in Alaska. The North American calibration dataset (Fortin *et al.*, 2015) has a lower taxonomic resolution than the Norwegian calibration dataset, thus both were applied to the Alaskan records to assess the effect of taxonomic resolution on skewness. Analyses indicated that skewness values were more pronounced and less negative when calculated using the Norwegian calibration dataset. It is thought that the North American calibration dataset had reduced sensitivity regarding skewness due to the grouping of taxa types, e.g. *Cricotopus-Orthocladius* species-types are grouped and the majority of *Tanytarsini* taxa are combined in a sub-tribe Tanytarsina-other group. Taxa in these groups can occupy different microhabitats (especially *Tanytarsini*), and hence reduced taxonomic resolution will influence network generation. This lead to the conclusion that high taxonomic resolution is preferential for skewness to work optimally.

Chironomid identification resolution and uniformity has increased over recent years, with the production of more accessible identification guides, e.g. Rieradevall and Brooks (2001) and Brooks *et al.* (2007). As resolution increases, so does the potential for misidentifications and identification of rare, poorly represented taxa (Heiri and Lotter, 2010). The inclusion of rare taxa may improve structural analyses; rare taxa are often more sensitive to changes in environmental variables and the first to disappear after environmental disturbances (Doncaster *et al.*, 2016; Yang *et al.*, 2016). However, difficulties in taxonomic resolution remain due to the lack of diagnostic characteristics and the fragmentary nature of chironomid head capsules in fossil samples (Brooks and Birks, 2001). For example, the presence of a mandible is a key diagnostic feature for a number of *Tanytarsini* morphotypes (Brooks *et al.*, 2007). There were a large proportion of *Tanytarsini* taxa grouped in to a "*Tanytarini* - no spur" classification in paper 3 due to the lack of mandibles. This leads to a loss of assemblage detail. Wang *et al.* (2019) used diatoms in their study into skewness as an indicator of aquatic assemblage structure. The diatom calibration dataset used a total of 452 diatom species, however, all fossil datasets suffer from challenges, and in some lakes diatom dissolution can inhibit preservation and/or taxonomic identification. In comparison, the North American chironomid training set comprises 78 taxa (Fortin *et al.*, 2015), and the Norwegian chironomid training set contains 141 taxa (Brooks and Birks, 2001; 2004). One hypothesis to be tested could be that calibration datasets with coarser taxonomic resolution are more suited to large-scale, high magnitude events, such as assemblage shifts in the Late Glacial (Mayfield *et al.*, *in review*), while higher taxonomic resolution is required for more subtle assemblage changes (Brooks and Birks, 2001; Heiri and Lotter, 2010).

## 6.8 Expanding research in the spatial domain

This thesis provides the first evidence for the applications of structural metrics as indicators of chironomid community change with changing climates. More research is required to demonstrate if the outcomes presented here are representational of the larger Arctic – Subarctic regions. There is a wealth of existing chironomid datasets in the scientific community; thus, applying °disorder and skewness analyses to more records, spanning a large geographic area, will provide further insight in to the applicability of the metrics and comparability of the outcomes. To ensure comparability between sites, consistency in taxonomic resolution is advised. In this thesis, the records for paper 2 were carefully selected to ensure taxonomic consistency, while R.J. Mayfield identified the records in paper 3 consecutively, with comparison between samples to ensure taxonomic consistency.

Applying structural metrics to a wider range of organisms may increase our understanding of aquatic ecosystem stability. For example, Doncaster *et al.* (2016) and Wang *et al.* (2019) applied °disorder and skewness analyses to diatom records. Considering the rise in eutrophication in high latitude lakes (Antoniades *et al.*, 2011; Gallant *et al.*, 2020), analyses on diatom records may provide further evidence of lake ecosystem stability. In paper 2, the fluctuations in the structural metrics suggested that localised factors might have influenced the chironomid assemblages during times of low climatic stress. Comparisons with other proxies of water quality, such as diatoms, could provide greater insight into changing lake ecosystem stability. Furthermore, analysing proxies from different trophic levels may provide increased insight in to lake stability; for example, indicating whether different trophic levels respond simultaneously or have the same magnitude of response to stress.

Review papers have re-evaluated and tested records in which authors suggested evidence for regime shifts and threshold transgressions e.g. Capon *et al.* (2015) and Hillebrand *et al.* (2020). Applying structural metrics to systems thought to have experienced critical transitions, as identified through the temporal domain may provide a useful test. For example, lake Erhai, China, experienced an observable shift from a low-eutrophic clear state to a hypereutrophic state with large annual algal blooms c. 2001 (Wang *et al.*, 2012). Wang *et al.* (2012) found flickering (an EWS thought to anticipate regimes shifts in the frequency domain, section 2.1.2, p. 13) in a temporal diatom assemblage from Erhai. Wang *et al.* (2019) applied network skewness to the same diatom assemblage, also finding structural change in association with the shift to hypereutrophic water conditions. Applying the structural metrics tested in this thesis to more records, with known and unknown exogenous stresses, will strengthen our understanding of the applicability and usefulness of structural metrics as indicators of ecosystem stability and resilience, and thus, as potential tools for anticipating potential tipping points.

## 6.9 Conclusions

This thesis evaluated the use of taxon richness, beta diversity, compositional disorder and network skewness as metrics of chironomid community composition and structure in response to climate change. Modelled simulations were used in papers 1 and 3 to test metric expectations of community composition and structural change across temperature gradients and through network development.

Analyses indicated that chironomid assemblages in locations with extreme climates are likely experiencing some level of structural stress. Initial climatic warming may provide ecological release; warmer temperatures may increase biological productivity, increasing lake habitat diversity and, thus, chironomid assemblage diversity. Continued temperature stress, and potentially the addition of secondary drivers of stress, may cause ecological degradation through habitat homogeneity and increased structural stress.

Climate, as an exogenous stress, requires abrupt, high-magnitude change to alter aquatic community structures. During periods of more gradual, low-magnitude climate change, it is likely that several drivers can influence structural stability.

Recent changes within the chironomid community composition in three Subarctic Alaskan lakes indicated signs of climate stress. However, the community structures indicated a degree of structural stability, suggesting some resilience within the chironomid assemblages to the current levels of climate and environmental change.

Ecosystem stability, as measured by structural metrics, can provide insight into ecosystem resilience to stress. Wider application of such methods may help the anticipation of potential tipping points through identifying systems with reduced structural stability and thus, reduced ecosystem resilience.

# Appendix A Supporting Information: Paper 2

Supporting information and figures are included to augment those in the main text of paper 2.

## A.1 Difference in the median $\delta^{18}O$ (‰) values between the Bølling–Allerød - Younger Dryas and early - mid-late Holocene subsections

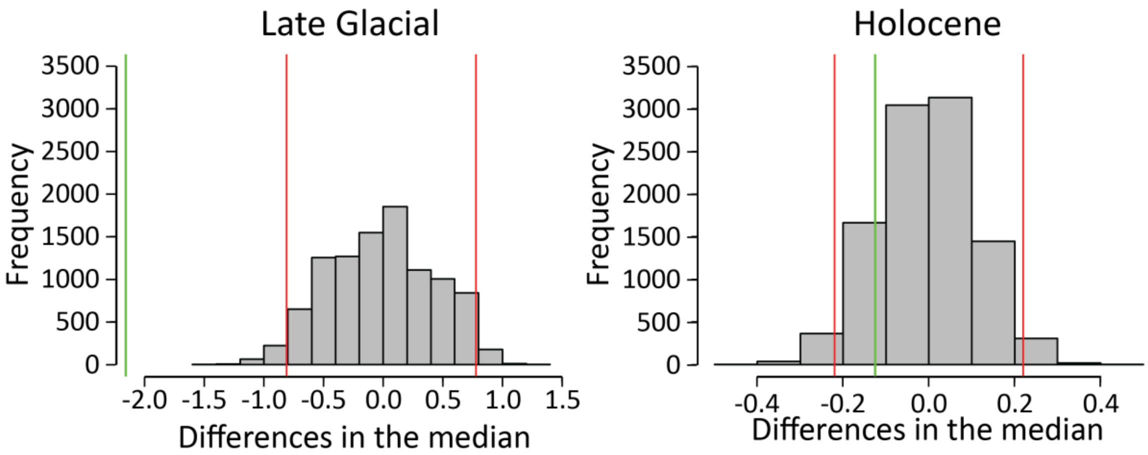

Figure A. 1 To test whether the difference in medians between the Bølling–Allerød and Younger Dryas, and the early and late Holocene were non-random, we compared the empirical difference in medians to differences in medians of subsets of 10,000 replicate randomised records. To do this, the isotopic values for the Late Glacial were randomly re-ordered 10,000 times. These randomised datasets were divided into Bølling–Allerød – Younger Dryas and early – mid-late Holocene subsections. Median values were calculated for each subsection. The difference between the subsections were compared to the differences in the empirical median values. The difference in the Bølling–Allerød and Younger Dryas medians was non-random when compared to the 10,000 replicate datasets, $p < 0.001$. The difference in the early and later Holocene medians was indiscernible from the 10,000 replicate datasets, $p > 0.05$.

## A.2 Testing window sizes for calculating the long term mean

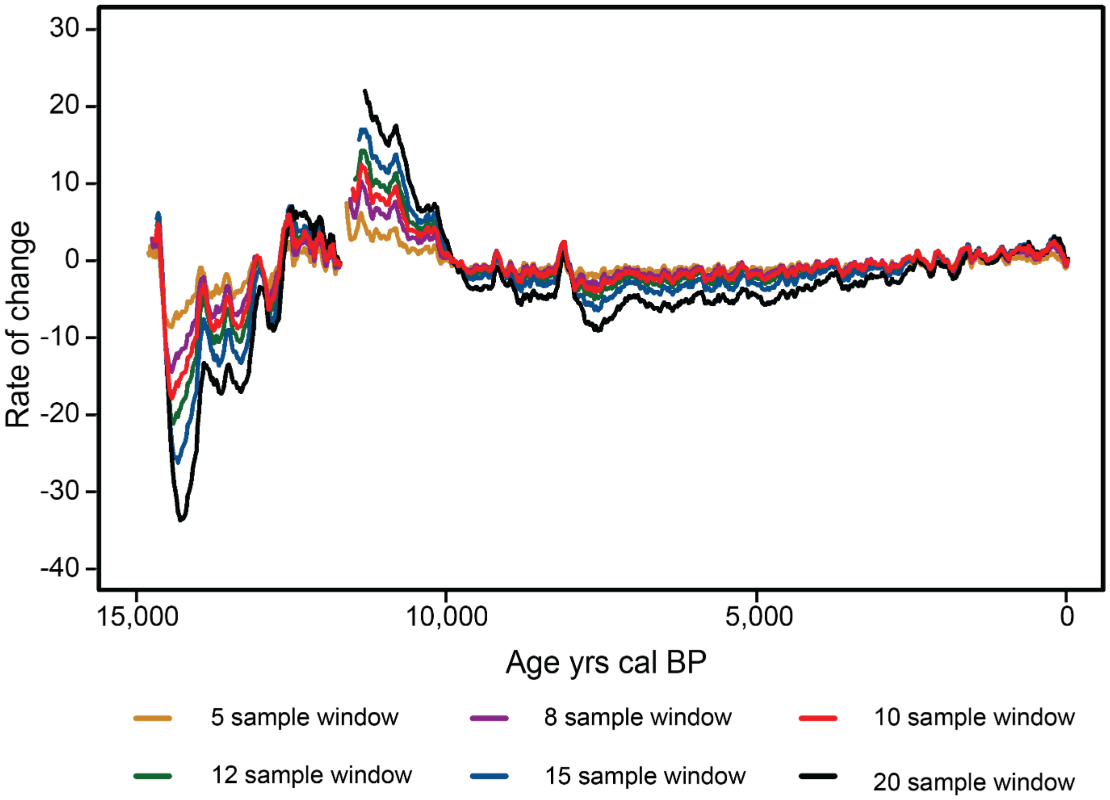

Figure A. 2 Comparison of window sizes for the calculation of $\delta^{18}O$ (‰) cumulative deviation from the long term mean. A rolling mean was used for the long term mean. We considered windows of 5, 8, 10, 12, 15 and 20 samples. Isotopic measurements were available for every 20 years, therefore these window sizes covered 100, 160, 200, 240, 300 and 400 year periods. All of the window sizes showed comparable trends in the cumulative deviation, however, larger window sizes (e.g. 12, 15 and 20 samples) amplified the signal and smaller window sizes (e.g. 5 or 8) reduced the signal.

## A.3 Estimated age-depth model for Muir Park

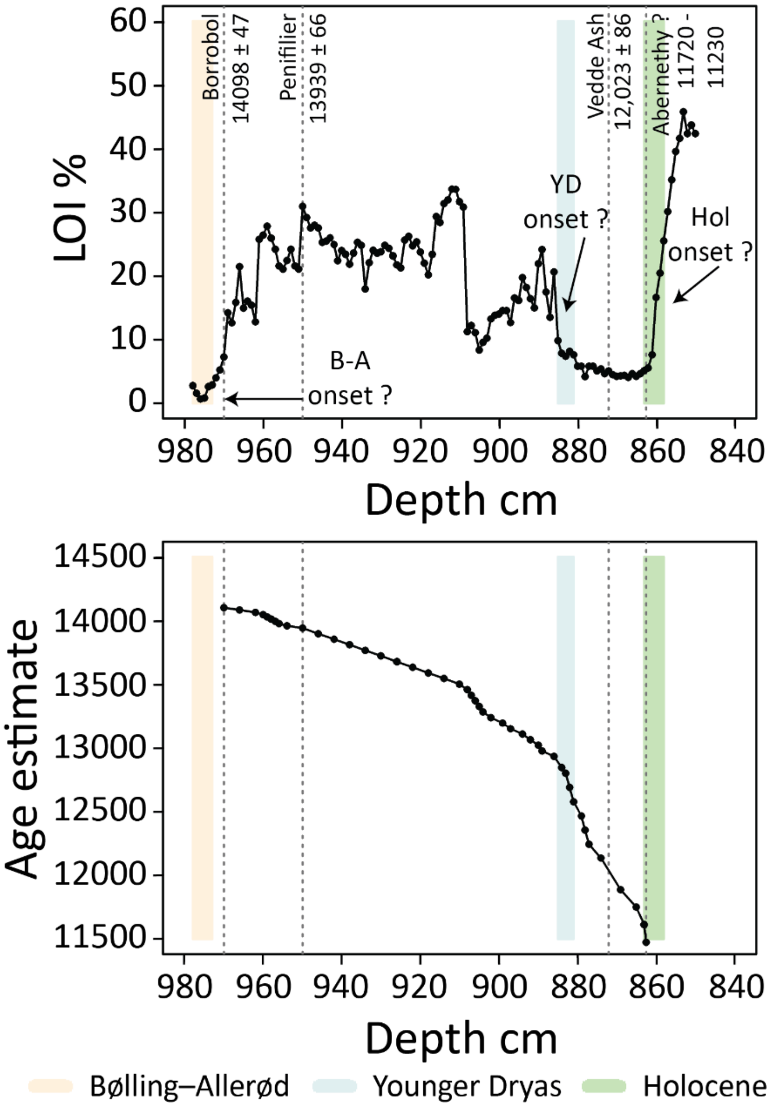

Figure A. 3 No age model was available for the Muir Park record. Three cryptotephra layers were chemically identified by the original authors (Brooks *et al.*, 2016); the Borrobol (14,098 ± 47 a cal BP), Penifiler (13,939 ± 66 a cal BP) and Vedde Ash (12,023 ± 86 a cal BP) (Brooks, 2006b; Pyne-O'Donnell, 2007; Matthews *et al.*, 2011; Bronk Ramsey *et al.*, 2015). A fourth layer was found, speculated to be the Abernethy tephra (11,720 – 11,250 a cal BP, MacLeod *et al.* (2015)), however no chemical analysis was possible due to the low shard count. Shaded bands indicate onset of known climatic events. Age estimates were created using these tephra layers and the changing organic matter content (LOI %). Sedimentation rate was assumed to be linear. These age estimates were used to loosely compare the Muir Park record to the other Late Glacial records and the Greenland isotope record. However, due to the assumptions in these age estimates for Muir Park, these comparisons cannot be made in full confidence.

## A.4 Goodness of fit analyses for the empirical records and Norwegian chironomid calibration dataset

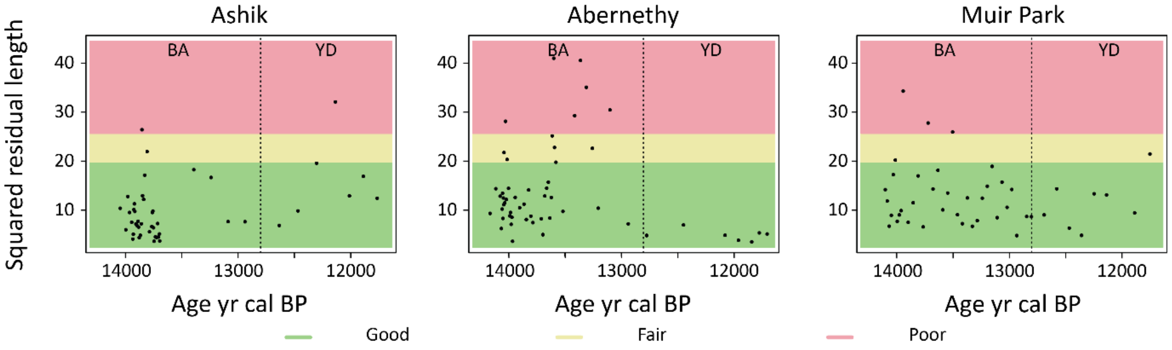

Figure A. 4 Goodness of fit for the Late Glacial fossil samples added passively to the Norwegian calibration set constrained by temperature. Goodness of fit analyses were performed using squared residual distance (Juggins and Birks, 2012).

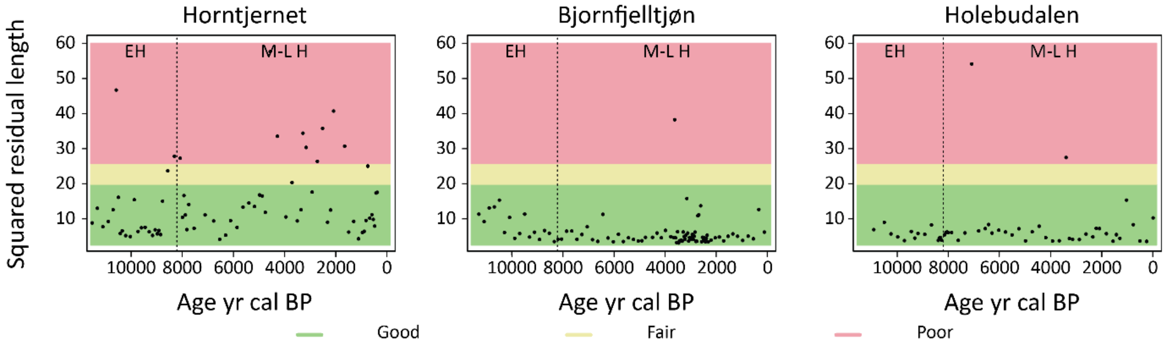

Figure A. 5 Goodness of fit for the Holocene fossil samples added passively to the Norwegian calibration set constrained by temperature. Goodness of fit analyses were performed using squared residual distance (Juggins and Birks, 2012).

## A.5 The effect of filtering on the empirical datasets

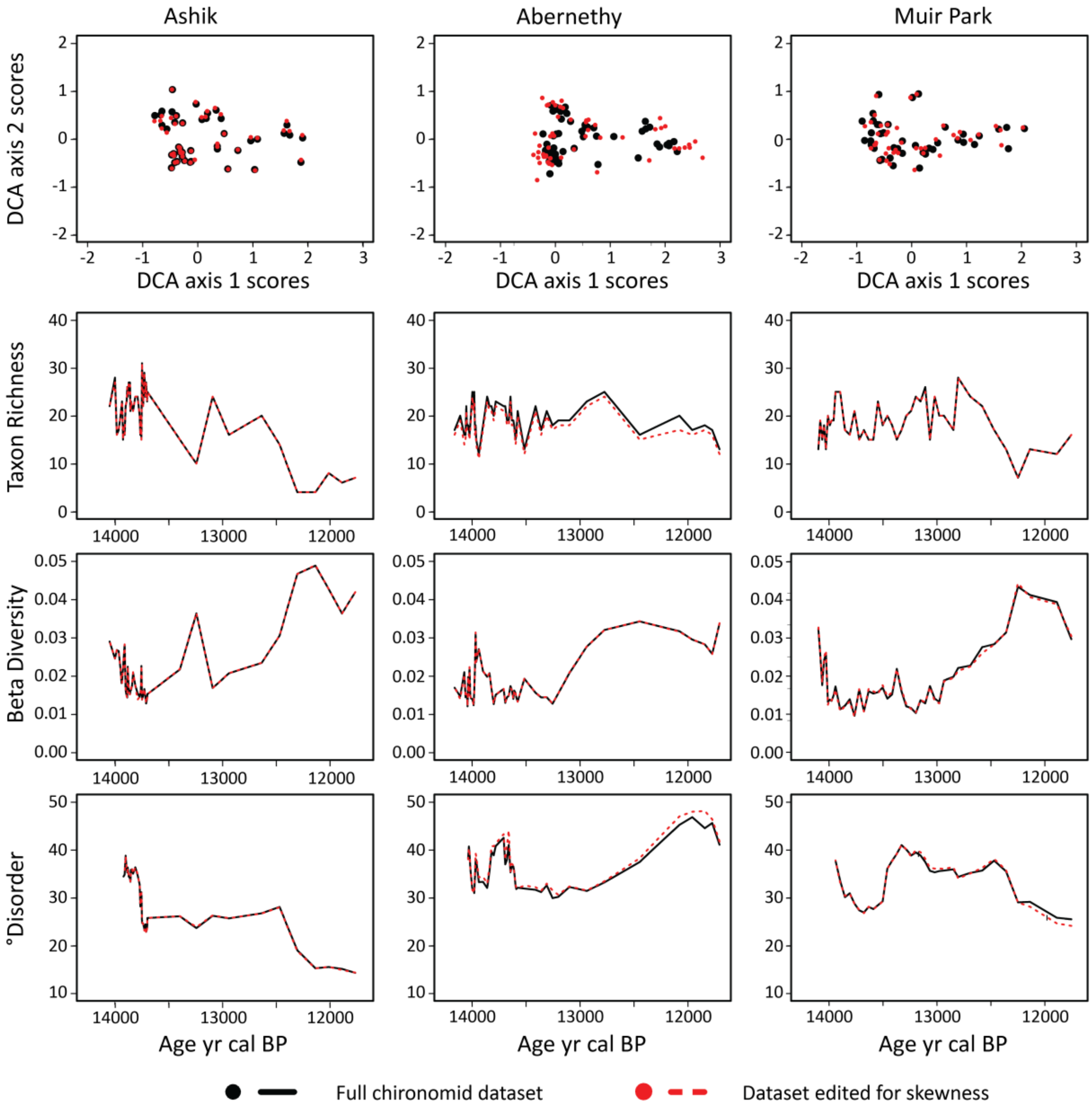

Figure A. 6 Skewness values for the temporal datasets were calculated by using the species degree of co-occurrences in a calibration dataset. In this study, we used the Norwegian chironomid calibration set due to the location of the temporal sites (Brooks and Birks, 2001; Brooks and Birks, 2004). Taxa present in the temporal datasets must be present in the calibration set. The fossil assemblages were cleaned and filtered to ensure the fossil taxa names matched the calibration set. Analyses were performed on the unedited and filtered chironomid datasets to ensure the filtering process required for skewness did not have notable effects on the assemblage structures. The plots here show that there were few differences in the metric outcomes for the unedited (black, solid lines) and filtered (red, dotted lines) in the Late Glacial datasets.

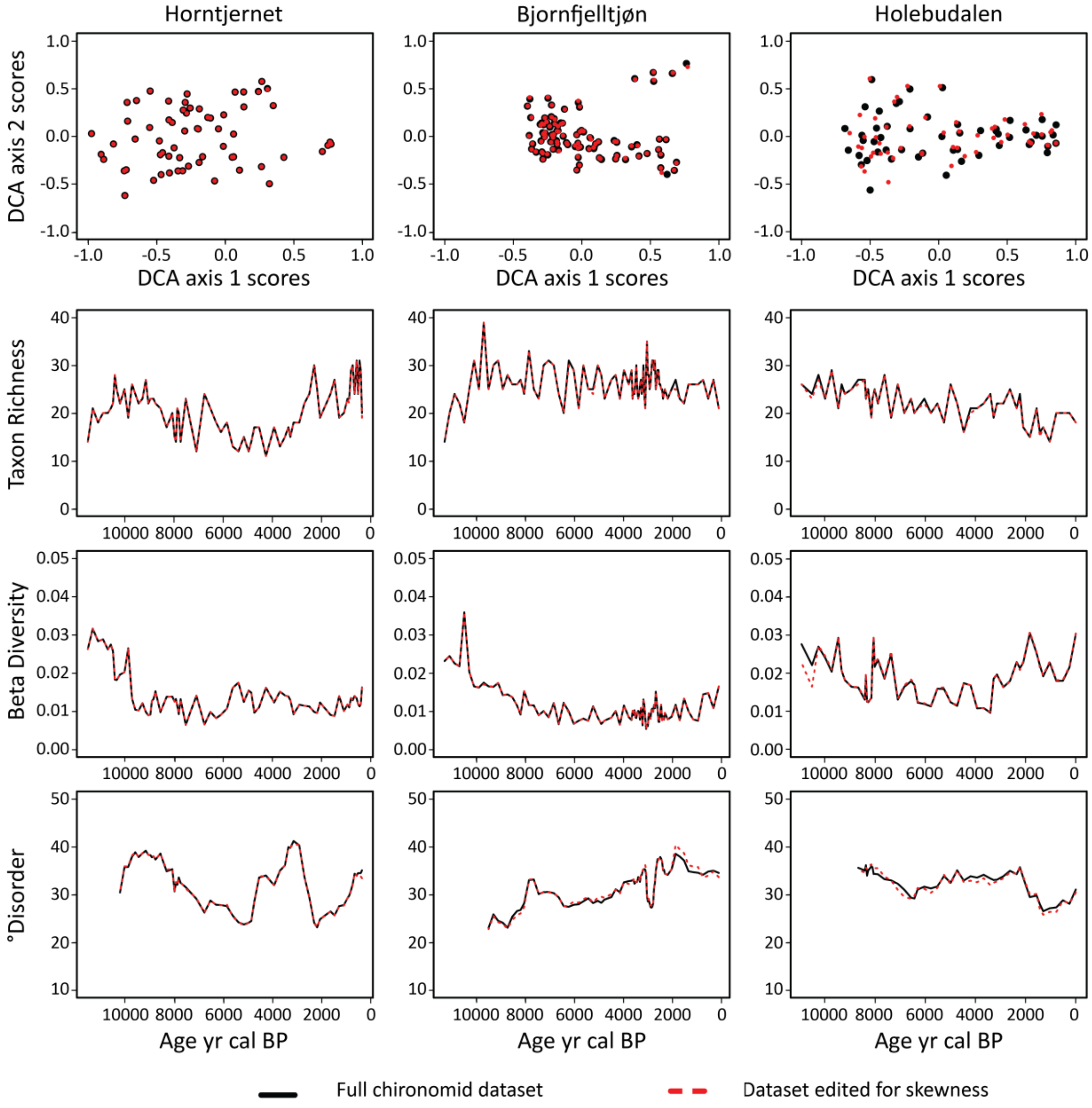

Figure A. 7 Skewness values for the temporal datasets were calculated by using the species degree of co-occurrences in a calibration dataset. In this study, we used the Norwegian chironomid calibration set due to the location of the temporal sites (Brooks and Birks, 2001; Brooks and Birks, 2004). Taxa present in the temporal datasets must be present in the calibration set. The fossil assemblages were cleaned and filtered to ensure the fossil taxa names matched the calibration set. Analyses were performed on the unedited and filtered chironomid datasets to ensure the filtering process required for skewness did not have notable effects on the assemblage structures. The plots here show that there were few differences in the metric outcomes for the unedited (black, solid lines) and filtered (red, dotted lines) in the Holocene datasets.

## A.6 Distinguishing pattern from noise: ecological metric median values

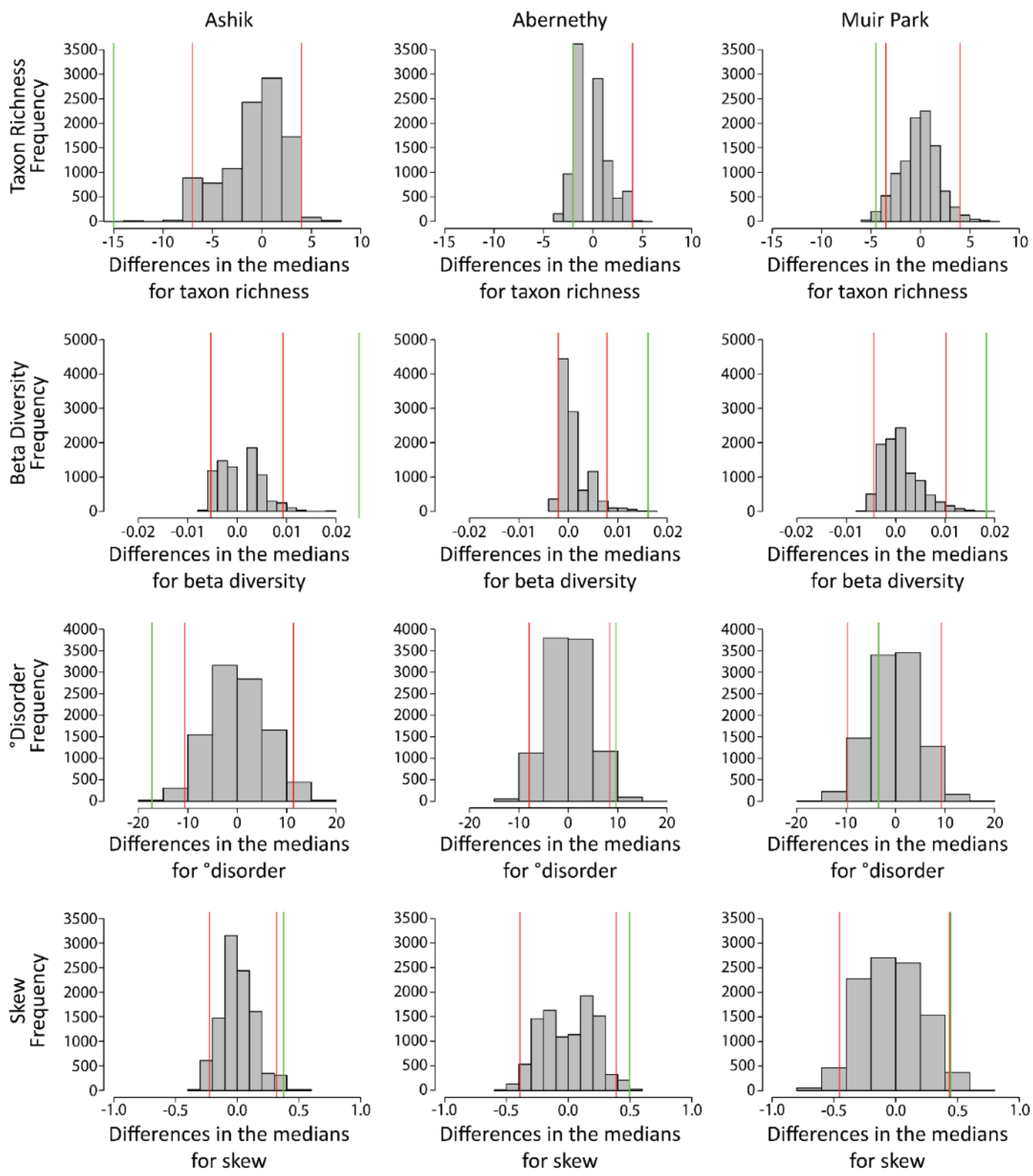

Figure A. 8 Histograms showing the spread of differences in the medians for 10,000 randomised datasets for the Late Glacial sites; Ashik, Abernethy, and Muir Park. 10,000 randomised replications of the observed chironomid datasets were created by randomly re-ordering the full set of observed chironomid records. Taxon richness, beta diversity, °disorder, and skewness were calculated on each of the randomised datasets. The randomised datasets were partitioned into Bølling-Allerød and Younger Drays subsections, to correspond with the empirical records. Median values were calculated for each metric for the randomised subsets. The difference between the medians was calculated to produce 10,000 differences in median values. These differences were ranked, along with the observed differences in median values. The 2.5th and 97.5th percentiles are shown by vertical red lines. The differences in the medians for the empirical datasets are shown in green. If the observed difference in medians fell in the upper or lower 2.5% of the ranking, then the observed difference had less than 5% chance of random occurrence.

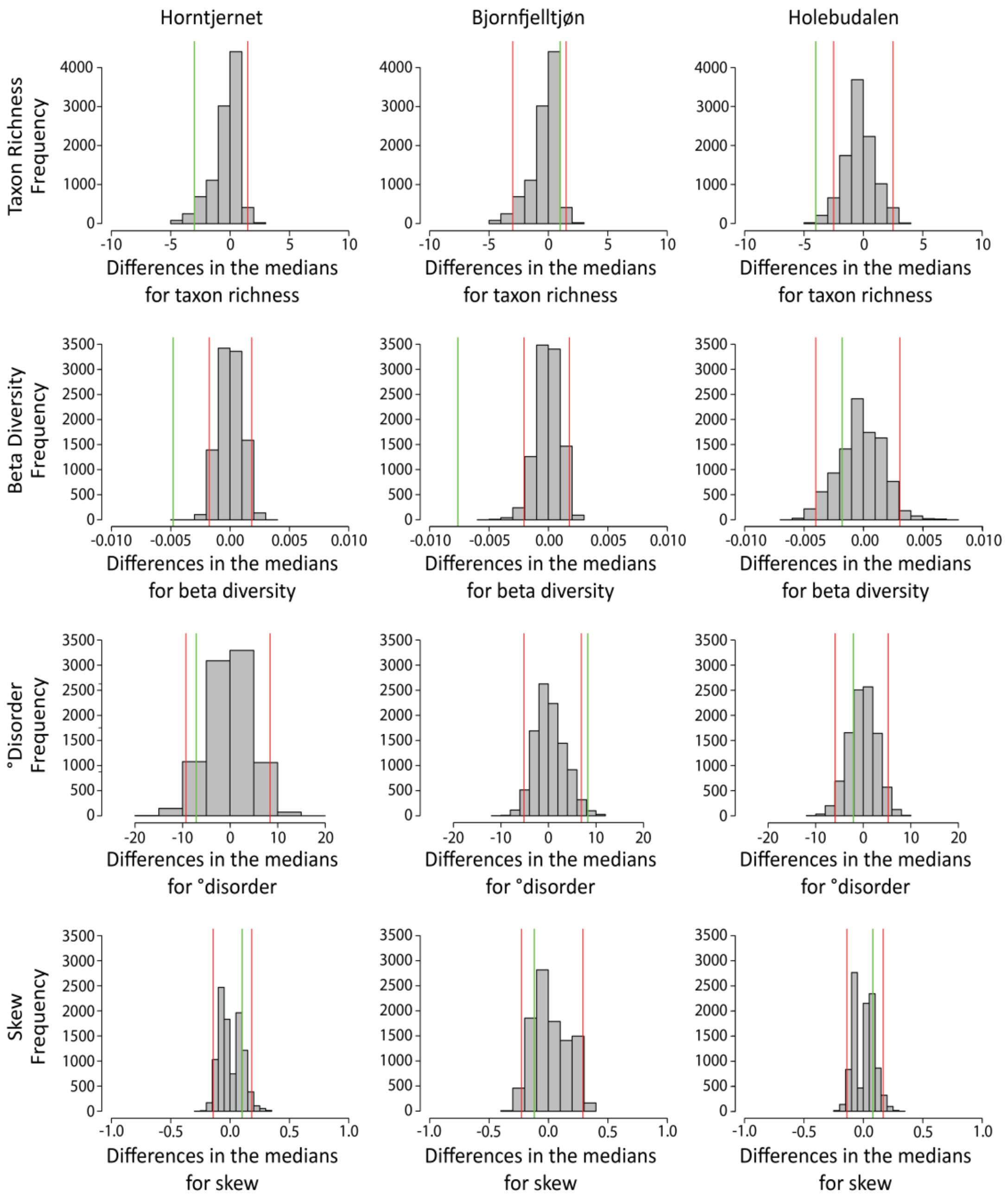

Figure A. 9 Histograms showing the spread of differences in the medians for 10,000 randomised datasets for the Holocene sites; Horntjernet, Bjornfjelltjønn, and Holebudalen. 10,000 randomised replications of the observed chironomid datasets were created by randomly re-ordering the full set of observed chironomid records. Taxon richness, beta diversity, °disorder, and skewness were calculated on each of the randomised datasets. The randomised datasets were partitioned into early and mid-late Holocene subsections, to correspond with the empirical records. Median values were calculated for each metric for the randomised subsets. The difference between the medians was calculated to produce 10,000 differences in median values. These differences were ranked, along with the observed differences in median values. The 2.5th and 97.5th percentiles are shown by vertical red lines. The differences in the medians for the empirical datasets are shown in green. If the observed difference in medians fell in the upper or lower 2.5% of the ranking, then the observed difference had less than 5% chance of random occurrence.

## A.7 Calculated isotopic values

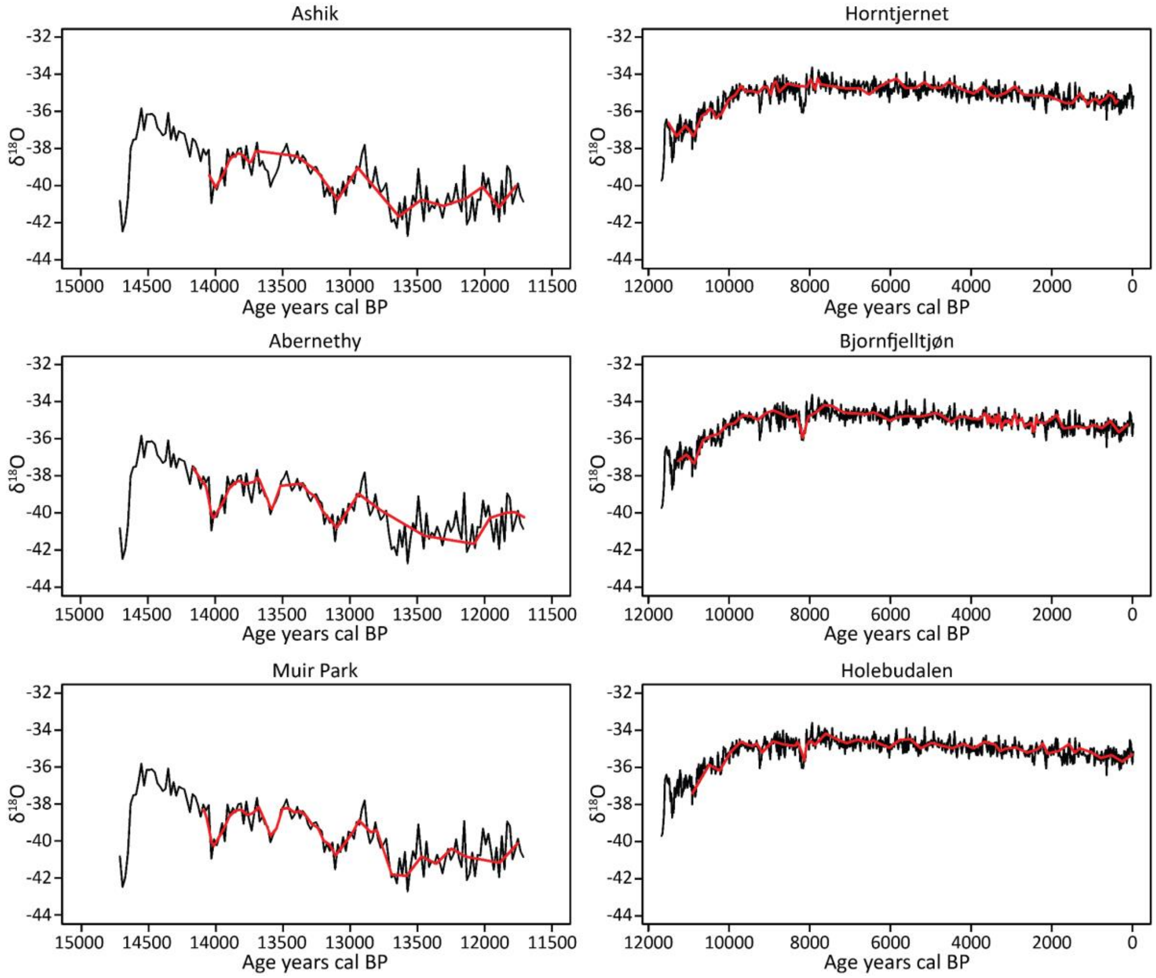

Figure A. 10 Isotopic values were calculated to correspond to the sample ages in the Late Glacial and Holocene chironomid records. The full NGRIP isotopic record is shown in black and the calculated isotope values corresponding to the chironomid sample ages are shown in red. The calculated isotope ages follow the overall trend seen in the full NGRIP isotopic record.

## A.8 Distinguishing pattern from noise: ecological metrics and the Greenland oxygen isotope record

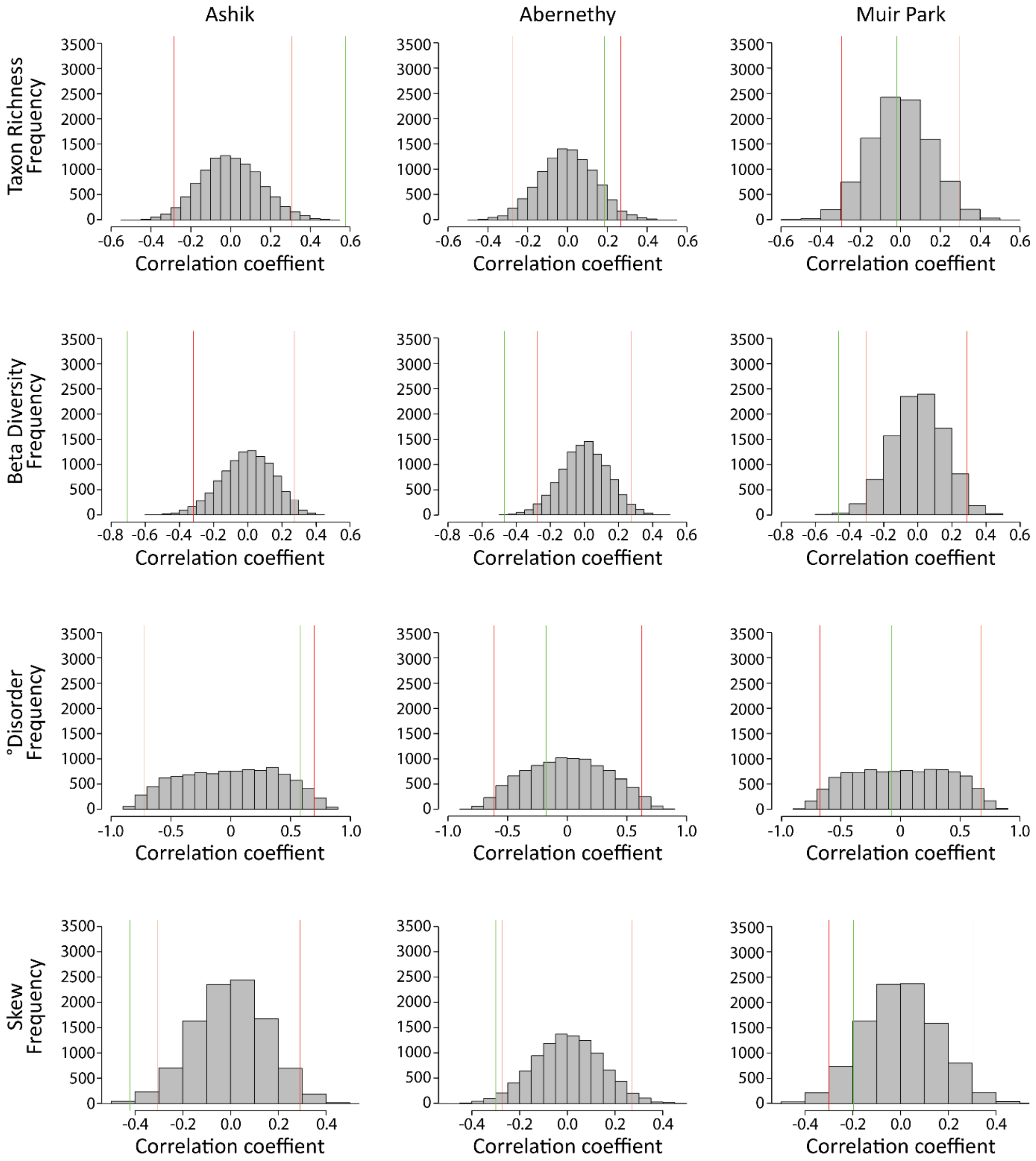

Figure A. 11 Histograms showing the spread of correlation coefficient values between the calculated isotope values and the ecological metrics for 10,000 randomised datasets for the Late Glacial sites; Ashik, Abernethy, and Muir Park. The 2.5th and 97.5th percentiles are shown by vertical red lines. The correlation coefficient values for the empirical datasets are shown in green. The correlated trends in the empirical datasets exceed the random expectation ($p \leq 0.05$), if the empirical correlation coefficient values lie outside of the 2.5th and 97.5th percentiles.

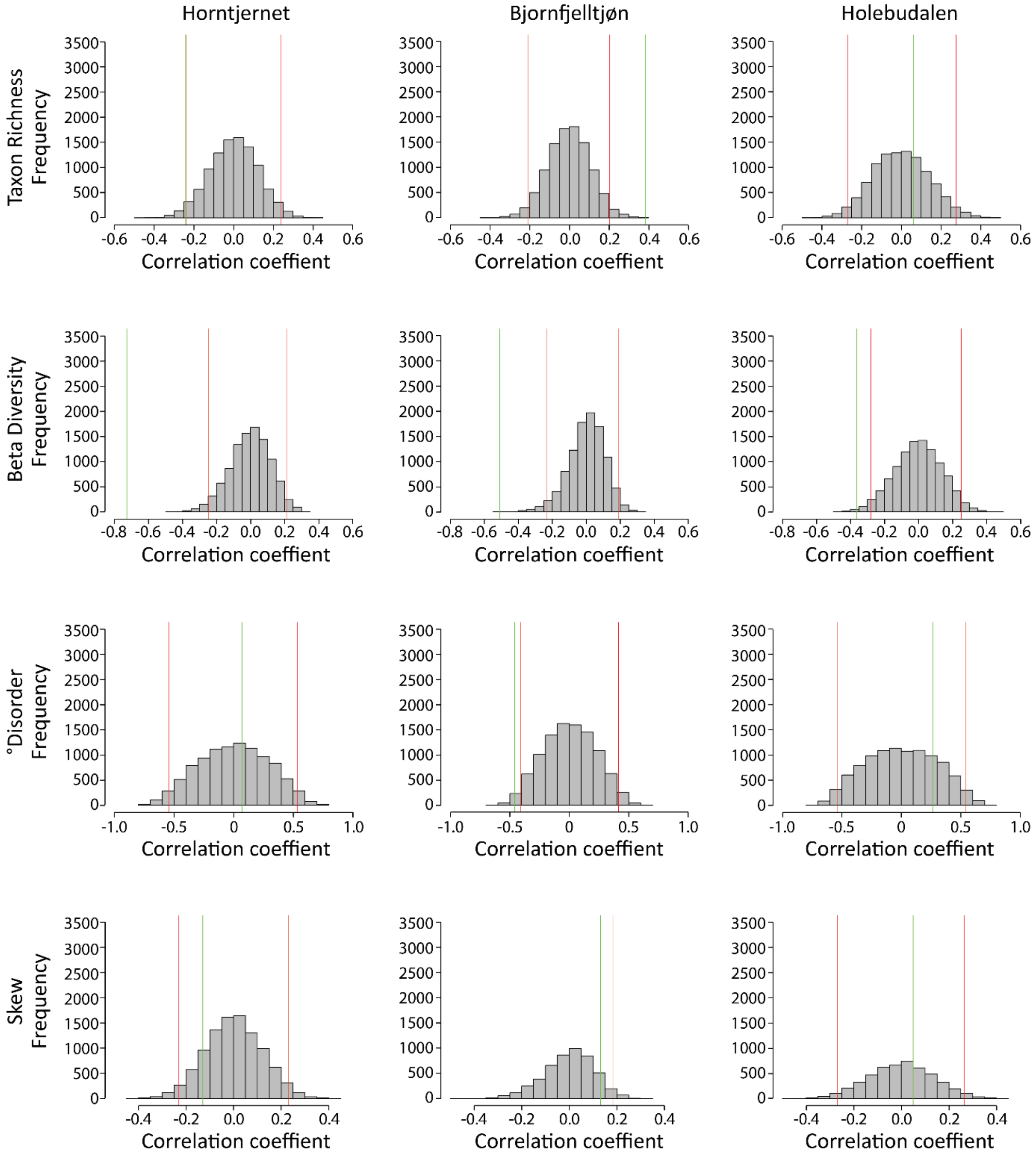

Figure A. 12 Histograms showing the spread of correlation coefficient values between the calculated isotope values and the ecological metrics for 10,000 randomised datasets for the Holocene sites; Horntjernet, Bjornfjelltjønn, and Holebudalen. The 2.5th and 97.5th percentiles are shown by vertical red lines. The correlation coefficient values for the empirical datasets are shown in green. The correlated trends in the empirical datasets exceed the random expectation ($p \leq 0.05$), if the empirical correlation coefficient values lie outside of the 2.5th and 97.5th percentiles.

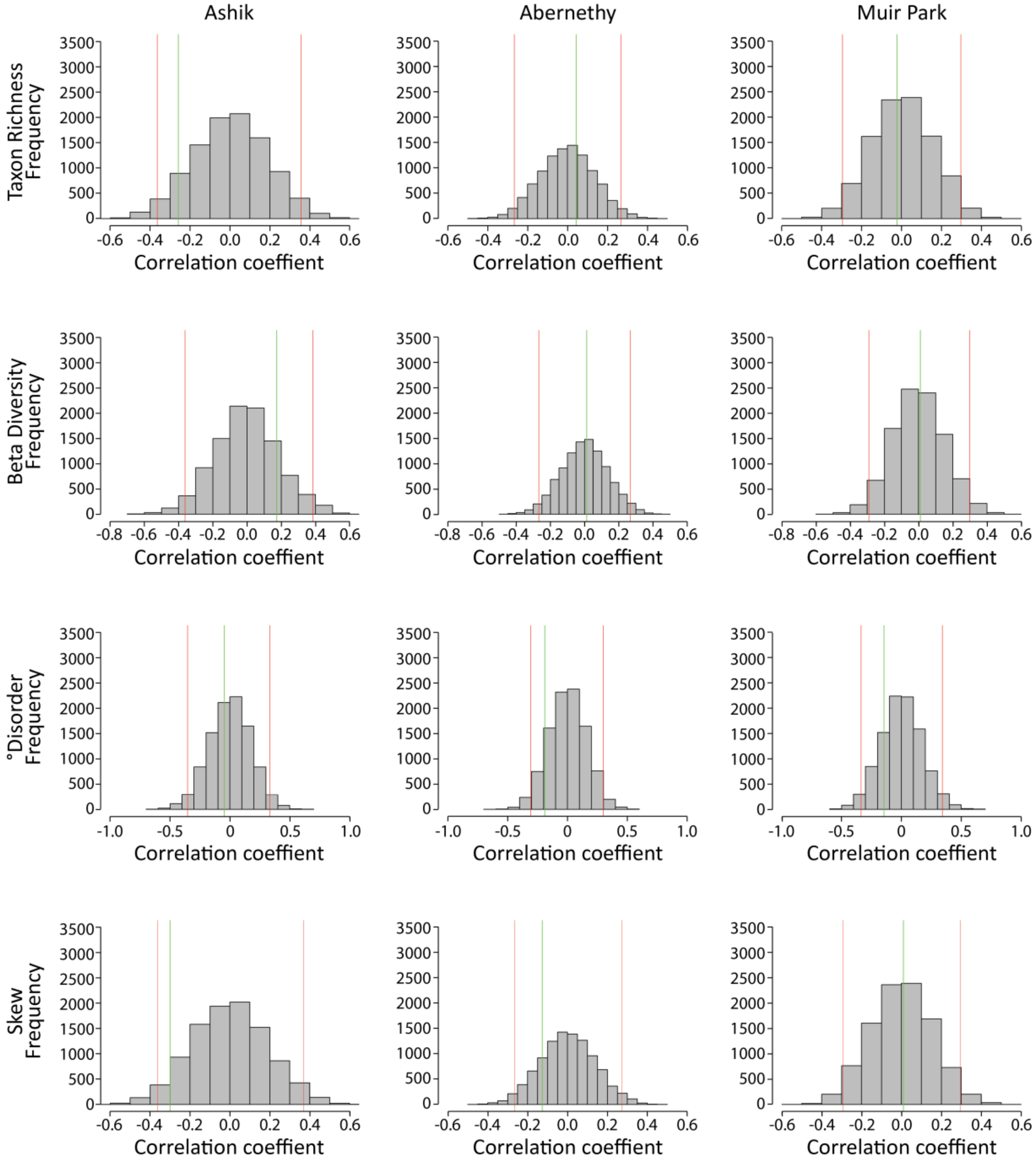

Figure A. 13 Histograms showing the spread of correlation coefficient values between the first differences for the calculated isotope values and ecological metrics for 10,000 randomised datasets for the Late Glacial sites; Ashik, Abernethy, and Muir Park. The 2.5th and 97.5th percentiles are shown by vertical red lines. The correlation coefficient values for the empirical datasets are shown in green. The correlated fluctuations in the empirical datasets exceed the random expectation ($p \leq 0.05$), if the empirical correlation coefficient values lie outside of the 2.5th and 97.5th percentiles.

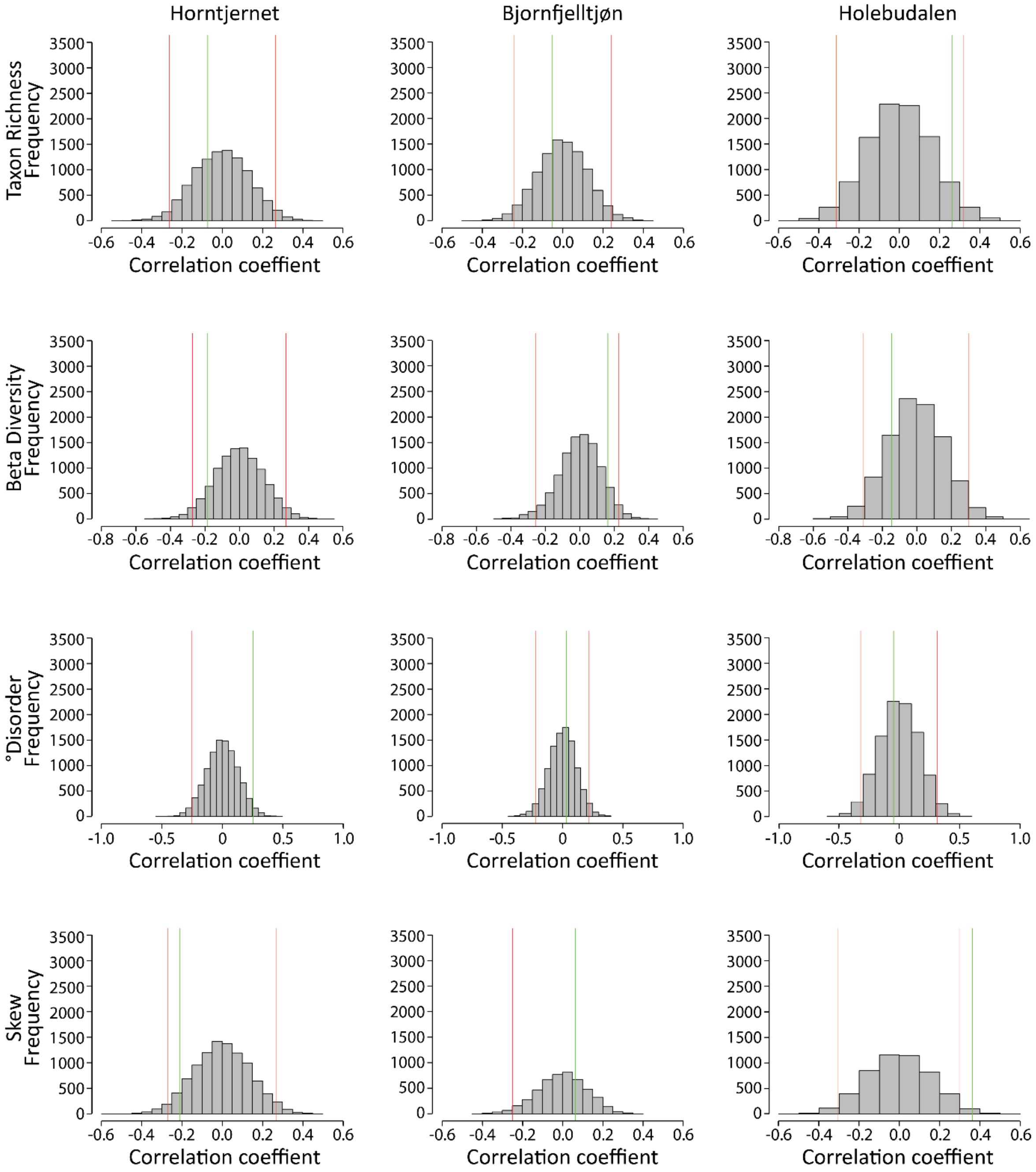

Figure A. 14 Histograms showing the spread of correlation coefficient values between the first differences for the calculated isotope values and ecological metrics for 10,000 randomised datasets for the Holocene sites; Horntjernet, Bjornfjelltjønn, and Holebudalen. The 2.5th and 97.5th percentiles are shown by vertical red lines. The correlation coefficient values for the empirical datasets are shown in green. The correlated fluctuations in the empirical datasets exceed the random expectation ($p \leq 0.05$), if the empirical correlation coefficient values lie outside of the 2.5th and 97.5th percentiles.

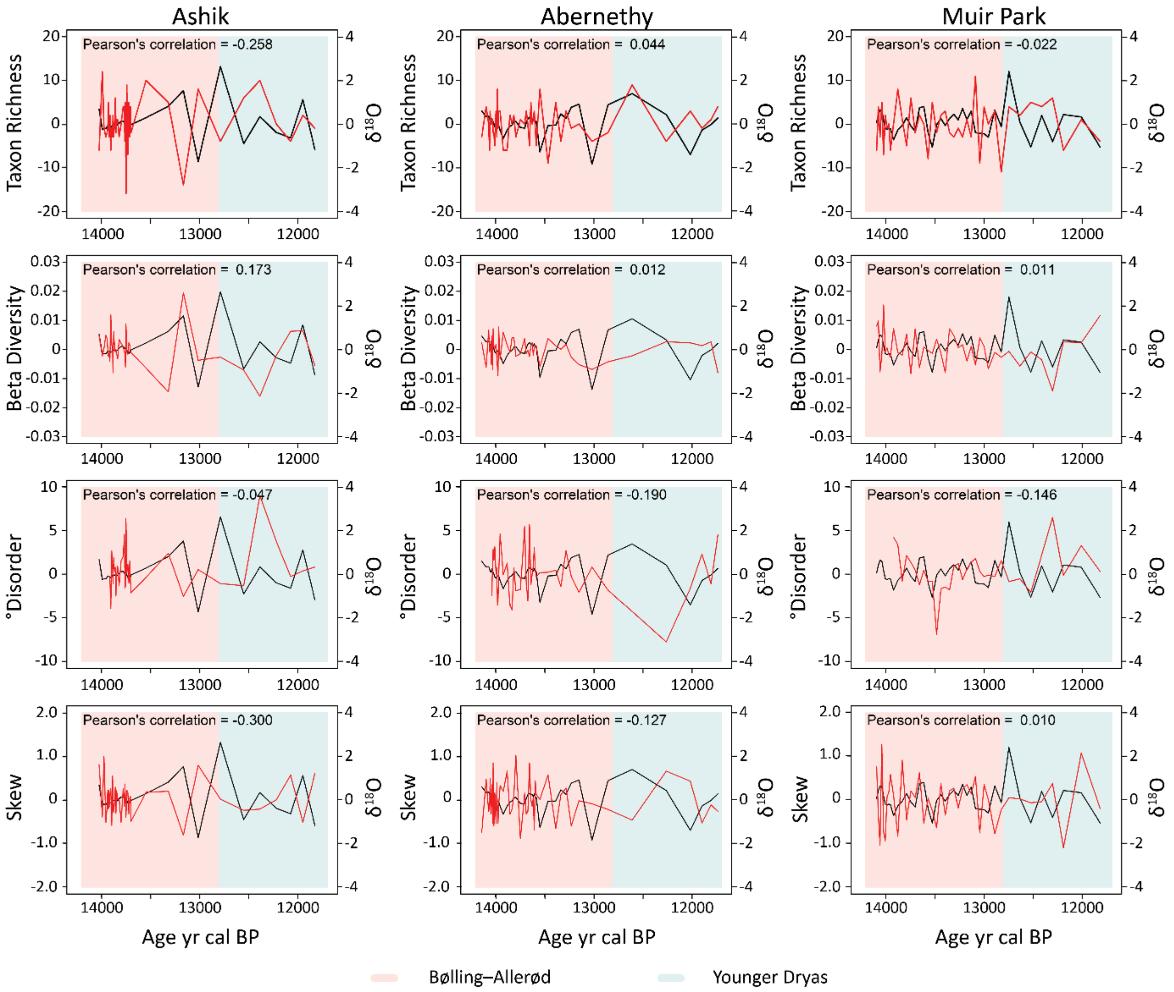

Figure A. 15 Correlation between the first differences for the calculated isotope values (black) and the chironomid ecological metric (red) for the Late Glacial records. Calculated isotopic values are shown for the same ages as the chironomid samples. Person's correlation coefficient indicates the linear correlation between the fluctuations in the ecological metrics and the isotopic values. No relationship is statistically significant (p ≤ 0.05) when compared to the 10,000 randomised replicate datasets.

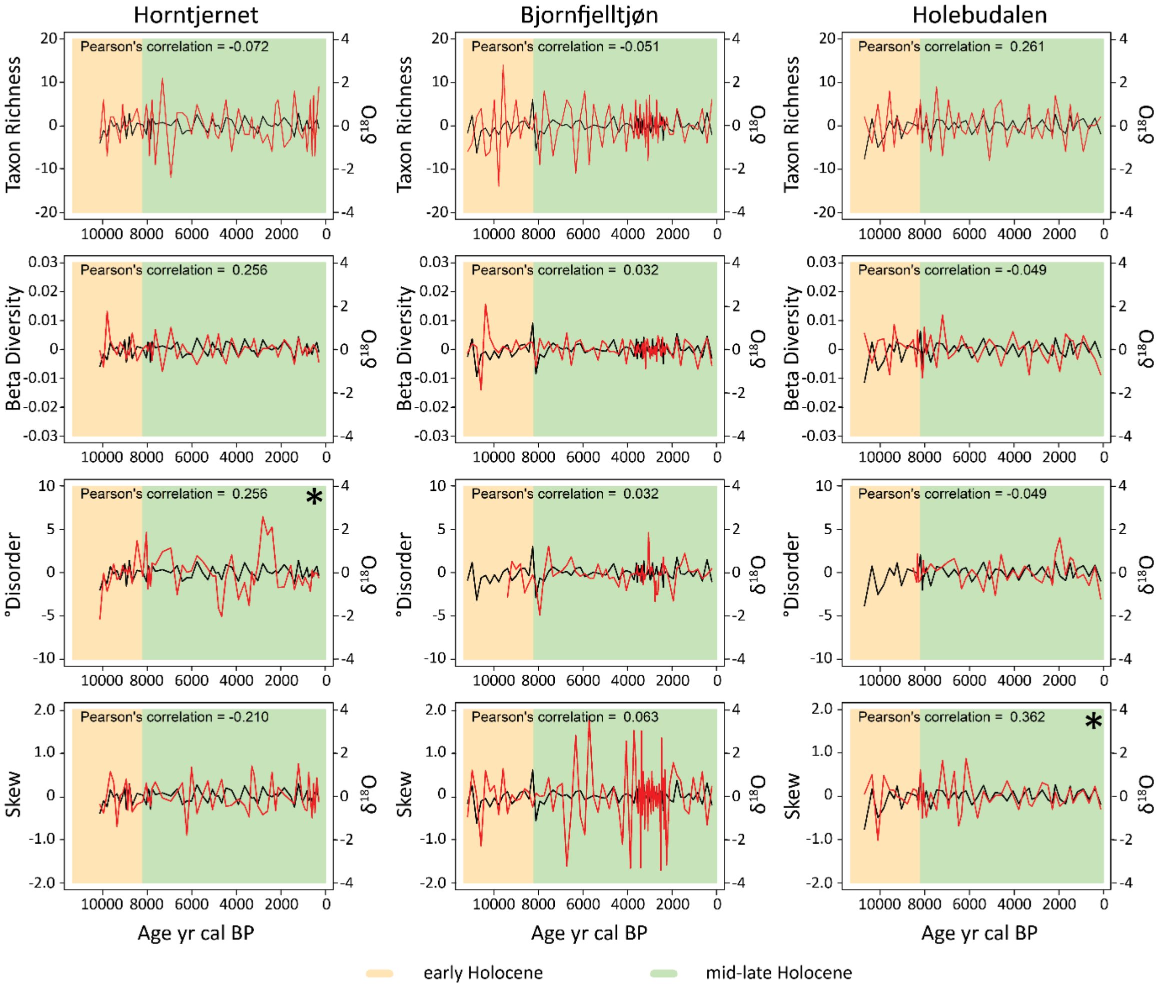

Figure A. 16 Correlation between the first differences for the calculated isotope values (black) and the chironomid ecological metric (red) for the Holocene records. Calculated isotopic values are shown for the same ages as the chironomid samples. Person's correlation coefficient indicates the correlated fluctuations in the ecological metrics and isotopic values. An asterisk denotes trends where the observed correlation trend exceeds the random expectation ($p \leq 0.05$), when compared to the 10,000 randomised replicate datasets. The °disorder first differences correlates positively with the isotope first differences in the Horntjernet record and the skewness first differences correlates positively with the isotope first differences in the Holebudalen record.

## A.9 Key climatic events during the Holocene

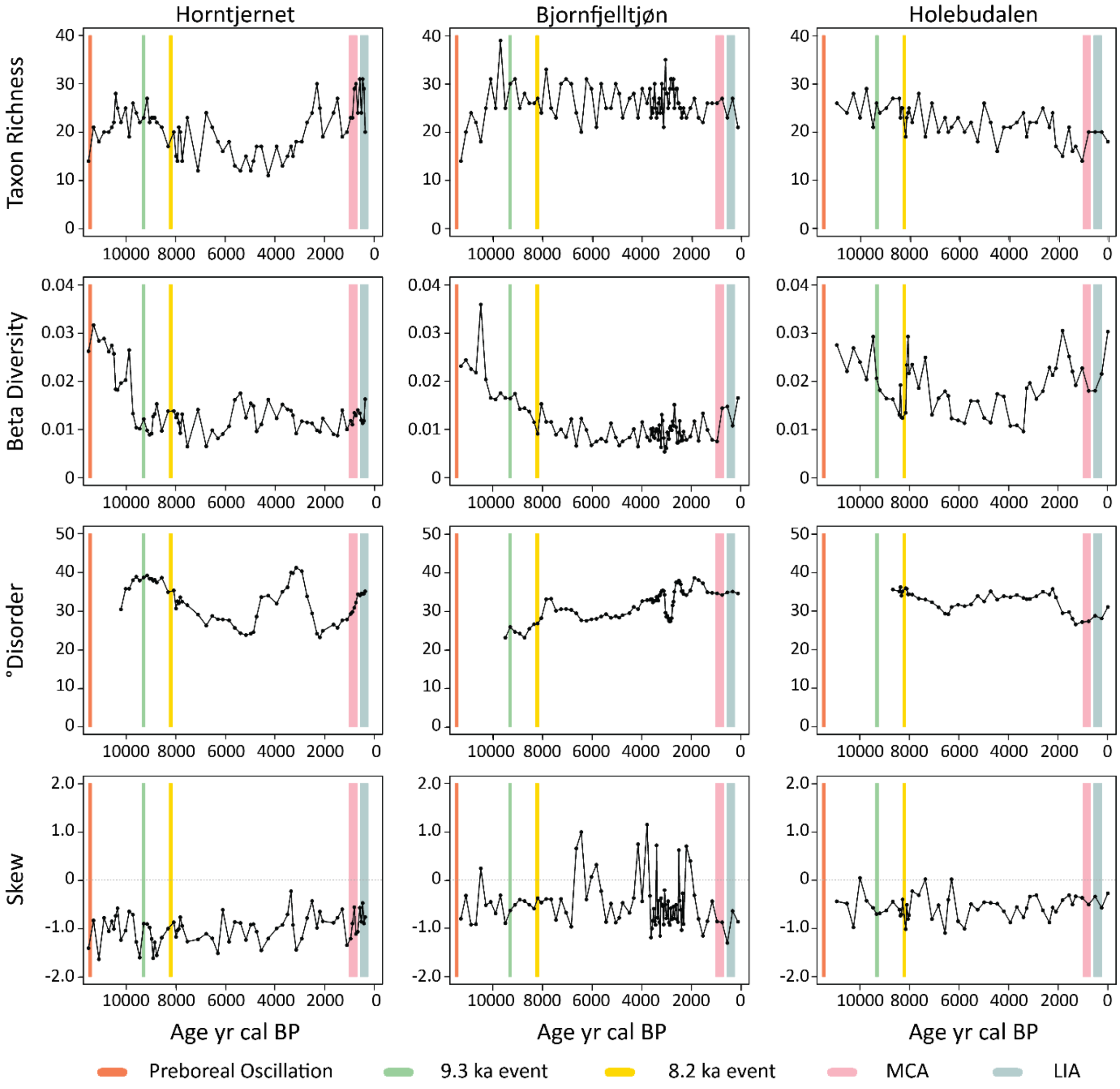

Figure A. 17 Changes within the ecological metrics in association with key climatic events during the Holocene. Fluctuations within the metric trends at times of greater climatic sensitivity did not necessarily have a greater magnitude than other fluctuations within the record.

# Appendix B Supporting Information: Paper 3

Supporting information, tables and figures are included to augment those in the main text of paper 3.

## B.1 Temperature change across Alaska

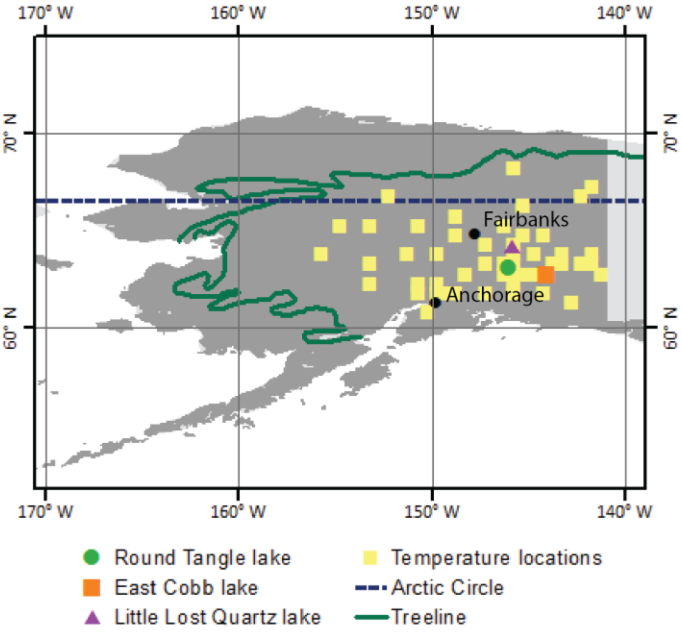

Figure B. 1 Temperature observation locations for the period 1901 – 2018. Temperature data was downloaded from the CRU TS4 Google Earth interface (Harris *et al.*, 2020).

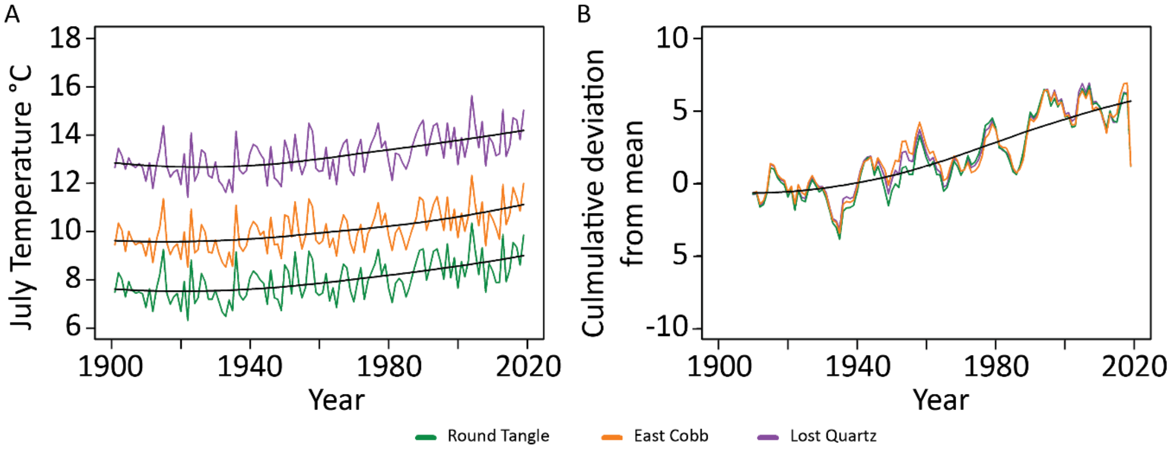

Figure B. 2 Mean summer ambient temperatures (June, July and August) were plotted for the 0.5 x 0.5 grids, in which the three lakes studied here are located (A). To quantify the rate and magnitude of climate change over the past c. 100 years, the cumulative deviation from the long term mean was calculated, following Dugmore *et al.* (2007). The long term mean was calculated over periods of 10 years (10 samples).

## B.2 Core correlation

Parallel cores were taken for each lake to ensure an adequate amount of sediment was available for laboratory analysis. The parallel cores were sampled at the same time from the same location. One core was processed for $^{210}$Pb, loss on ignition (LOI) and bulk density, while the other core was processed for chironomid assemblage composition, LOI, bulk density, magnetic susceptibility and ITRAX sediment analysis. LOI and bulk density were used to correlate the cores (Figure B. 3 - 5). Pearson's correlation was used to correlate the LOI and bulk density profiles.

For Round Tangle Lake cores, there were slight deviances in the LOI and bulk density profiles, however, Pearson's correlation indicated high similarities between the cores. For the East Cobb Lake cores, the LOI and bulk density curves were highly similar, with strong Pearson's correlation r values. Based on the high similarities between the LOI and bulk density profiles for the Round Tangle Lake cores and East Cobb Lake cores, we assume that the ages are the same for both cores. For Lost Quartz Lake cores, there were a number of differences between the profiles, with Pearson's correlation suggesting less similarities between the cores. In the absence of other sedimentary information, we assume the ages correlate to the same depths in the Lost Quartz Lake cores.

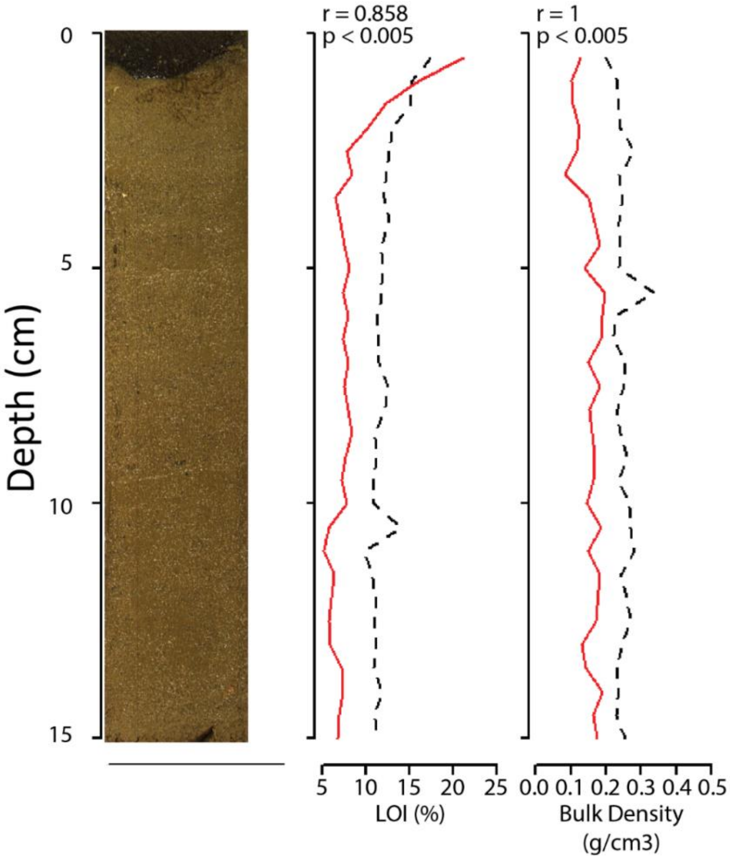

Figure B. 3 Round Tangle Lake: LOI and bulk density profiles for the parallel cores, with core RT4 shown by the dashed black line and core RT3 shown by the solid red line. Pearson's correlation and p values indicate that the profiles have a high correlation.

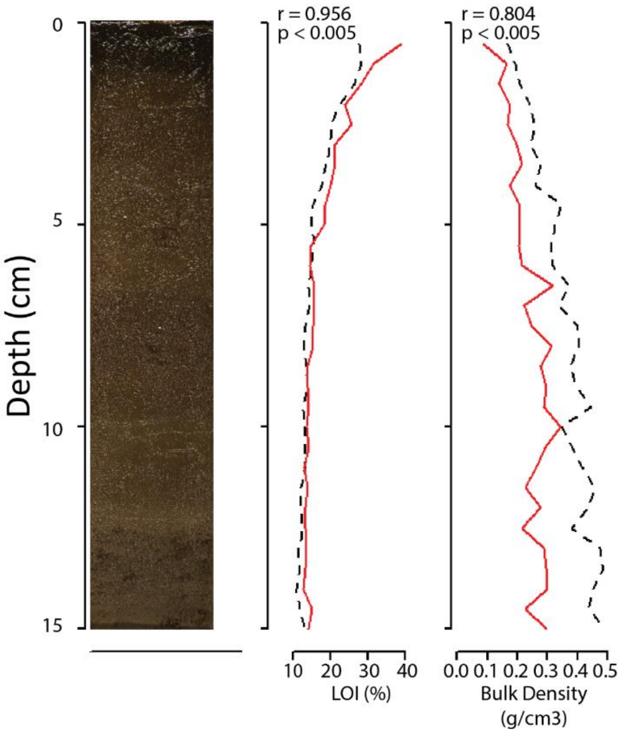

Figure B. 4 East Cobb Lake: LOI and bulk density profiles for the parallel cores, with core ECL2 shown by the dashed black line and core ECL1 shown by the solid red line. Pearson's correlation and p values indicate that the profiles have a high correlation.

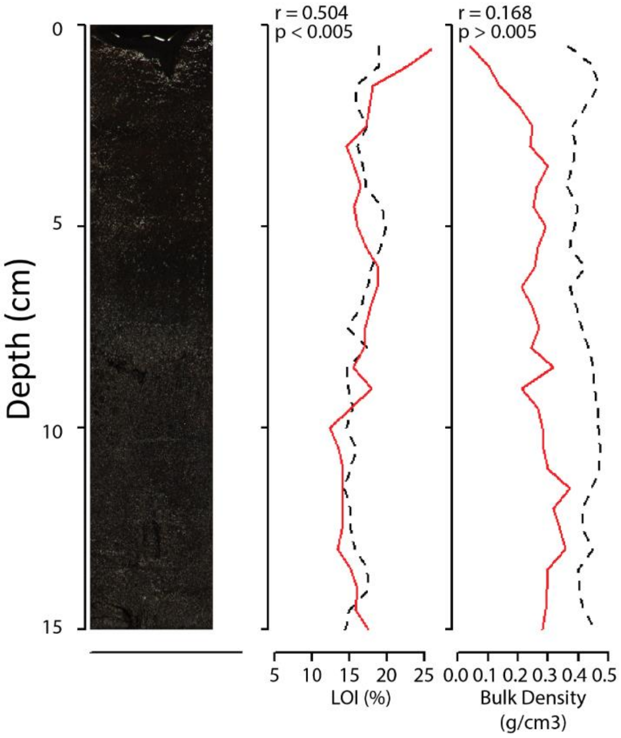

Figure B. 5 Lost Quartz Lake: LOI and bulk density profiles for the parallel cores, with core LQ2 shown by the dashed black line and core LQ4 shown by the solid red line. Pearson's correlation and p values indicate that the profiles have a number of differences.

## B.3 Core sedimentology

The geochemical profiles for the cores indicate various amounts of environmental change in the lake sediments (Figure B. 6 – 8). Magnetic susceptibly was used to designate the magnetic composition of the sediment (Dearing *et al.*, 1996). The XRF spectroscopy indicates lake catchment dynamics, such as variations in run-off (Si, Ti) (Schlolaut *et al.*, 2014; Plaza-Morlote *et al.*, 2017), detrital input (K, Mn, Rb, Si, Zr) (Boës *et al.*, 2011), erosion (Ti, Zr) (Boës *et al.*, 2011), nutrient loading (P) (Correll, 1998), leaching (S) (Olsen *et al.*, 2013) and anthropogenic pollution (Pb, Zn) (Miller *et al.*, 2014), and in-lake process, such as lake level (Ca and S) (Scholz *et al.*, 2007; Brown, 2011; Hodell *et al.*, 2012), and redox conditions (Fe and Mn) (Sugiyama *et al.*, 1992; Fakhraee *et al.*, 2017).

The abrupt decline in element contents at the top of the Round Tangle and Lost Quartz core profiles relates to the un-even sediment–water interfaces (indicated in yellow on the core profiles, Figure B. 6 – 8) and remnants of Zorbitrol (sodium polyacrylate) polymer gel used in the field to absorb excess water within the polycarbonate tubes and preserve the sediment–water interface.

The Round Tangle sediment proxy profiles indicate few large changes; there was a slight rise in organic content (LOI) towards the top of the core and a number of fluctuations with the Al, Si and Pb profiles (Figure B. 6).

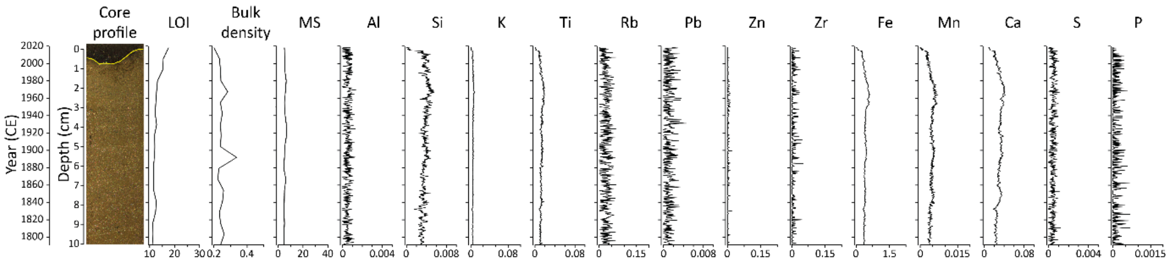

Figure B. 6 Sedimentological analysis of Round Tangle Lake. The sediments were a light brown lake mud, as indicated by the core photo. The sediment-water interface is indicated by a yellow line. The core profile was analysed for organic content (LOI %), bulk density (g/cm$^3$), magnetic susceptibility (MS, SI), and key lithogenic elements Al, Si, K, Ti, Rb, Pb, Zn, Zr, FE, Mn, Ca, S and P (cps / kps).

In East Cobb sediment profiles (Figure B. 7), there was a linear rise in organic content towards the top of the core. There were large fluctuations in the records at c. 1960. There was a decline in Si, K, Ti, Zr, Fe, Mn, and S at the top of the core, while there was an increase in Al, Rb, Pb, and P.

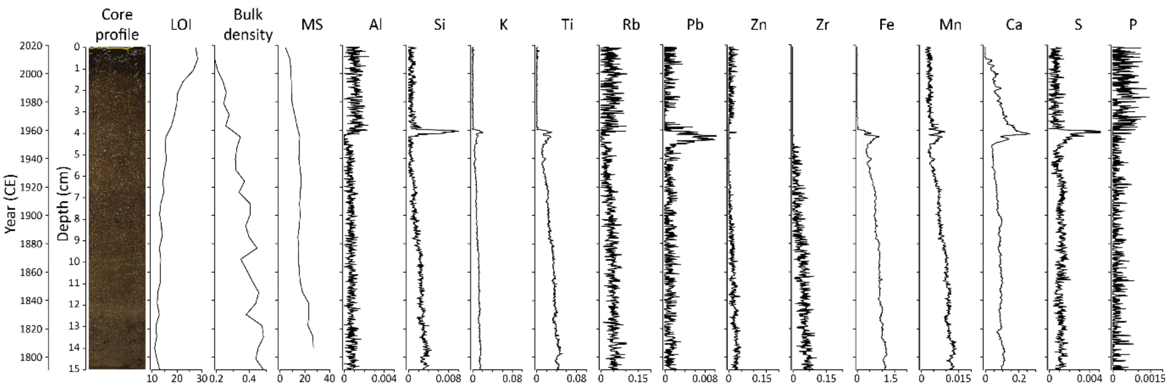

Figure B. 7 Sedimentological analysis of East Cobb Lake. The sediments were a dark brown lake mud with some lighter bands, as indicated by the core photo. The sediment-water interface is indicated by a yellow line. The sediment-water interface is indicated by a yellow line. The core profile was analysed for organic content (LOI %), bulk density (g/cm$^3$), magnetic susceptibility (MS, SI), and key lithogenic elements Al, Si, K, Ti, Rb, Pb, Zn, Zr, FE, Mn, Ca, S and P (cps / kps).

The Lost Quartz sediment proxy profiles indicate a number of fluctuations in the Al, Pb, Zr and S profiles (Figure B. 8).

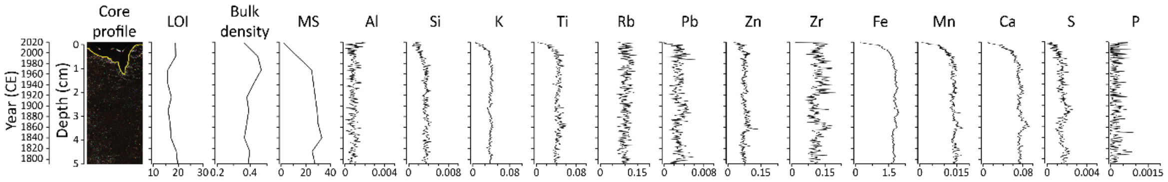

Figure B. 8 Sedimentological analysis of Lost Quartz Lake. The sediments were a dark brown-black lake mud, as indicated by the core photo. The sediment-water interface is indicated by a yellow line. The sediment-water interface is indicated by a yellow line. The core profile was analysed for organic content (LOI %), bulk density (g/cm$^3$), magnetic susceptibility (MS, SI), and key lithogenic elements Al, Si, K, Ti, Rb, Pb, Zn, Zr, FE, Mn, Ca, S and P (cps / kps).

## B.4 Chironomid assemblage information

Table B. 1 Chironomid assemblage record information

| | Round Tangle | East Cobb | Lost Quartz |
|---|---|---|---|
| Sampling resolution (cm) | 0.5 | 0.5 | 0.5 |
| Number of samples | 20 | 30 | 10 |
| Temporal resolution (yrs) | c. 12 | c. 8 | c. 25 |
| Head capsule conc. (per g) | 79.5 – 199.9 | 58.2 – 200.4 | 16.4 – 45.8 |
| Head count - range | 100.5 – 226.5 | 71.5 - 224 | 53.5 – 141.5 |
| Head count - mean | 169.2 | 146.5 | 78.4 |

The chironomid assemblage at Round Tangle lake (Figure B. 9) was dominated by *Sergentia coracina*-type, *Paratanytarsus* undifferentiated, *Tanytarsus* no spur, *Tanytarsini* undifferentiated, *Orthocladius consobrinus*-type, *Paracladius* and *Zalutschia* type B. The dendrograph indicated that the greatest change in taxonomic composition occurred between the most recent sample and the rest of the record. The most recent sample (zone 2) indicated an increase of *Sergentia coracina*-type, *Corynocera oliveri*-type, *Cricotopus cylindraceus*, *Diplocladius*, *Limnophyes - Paralimnophyes*, and *Thienemannimyia*, and a decrease in *Paratanytarsus* undifferentiated, *Cricotopus intersectus*, *Orthocladius consobrinus*-type, *Paracladius* and *Procladius*.

The chironomid assemblage at East Cobb lake was dominated by *Microtendipes pedellus*-type, *Polypedilum nubeculosum*-type, *Corynocera ambigua*, *Tanytarsus* no spur, and *Procladius* (Figure B. 10). The dendrograph identified a shift in taxonomic composition at c. 1915. In the upper assemblage zone (zone 2), *Chironomus anthracinus*-type, *Microtendipes pedellus*-type, *Polypedilum nubeculosum*-type, *Ablabesmyia* increased in abundance and *Thienemannimyia*, and *Corynocera ambigua*, *Corynocera oliveri*-type, and *Zavrelia* decreased.

The chironomid assemblage at Lost Quartz lake (Figure B. 11) was dominated by *Chironomus anthracinus*-type, *Microtendipes pedellus*-type, *Tanytarsus* no spur, *Psectrocladius sordidellus*-type, and *Procladius*. The dendrograph identified a shift in taxonomic composition at c. 1900. There was a decline in *Chironomus anthracinus*-type, *Pagastiella*, *Psectrocladius sordidellus*-type, and *Thienemannimyia* taxa in the upper zone (zone 2), whereas *Dicrotendipes nervosus*, *Corynocera ambigua*, *Tanytarsus pallidicornus*-type, and *Ablabesmyia* increased in abundance.

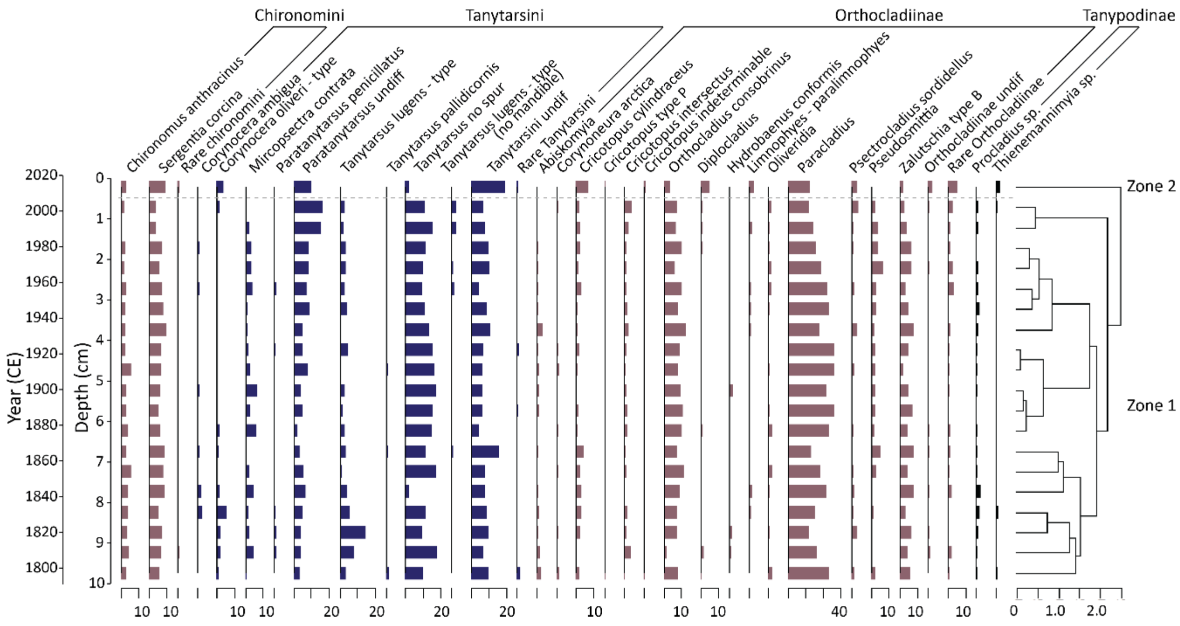

Figure B. 9 Total percentage abundances of the chironomid taxa present in Round Tangle lake. Taxa are grouped by subfamily. Taxa with < 5% abundance are grouped within their subfamily. A dendrograph indicates zones of similar taxonomic composition, with the highest order of dissimilarity indicated by a horizontal grey dashed line.

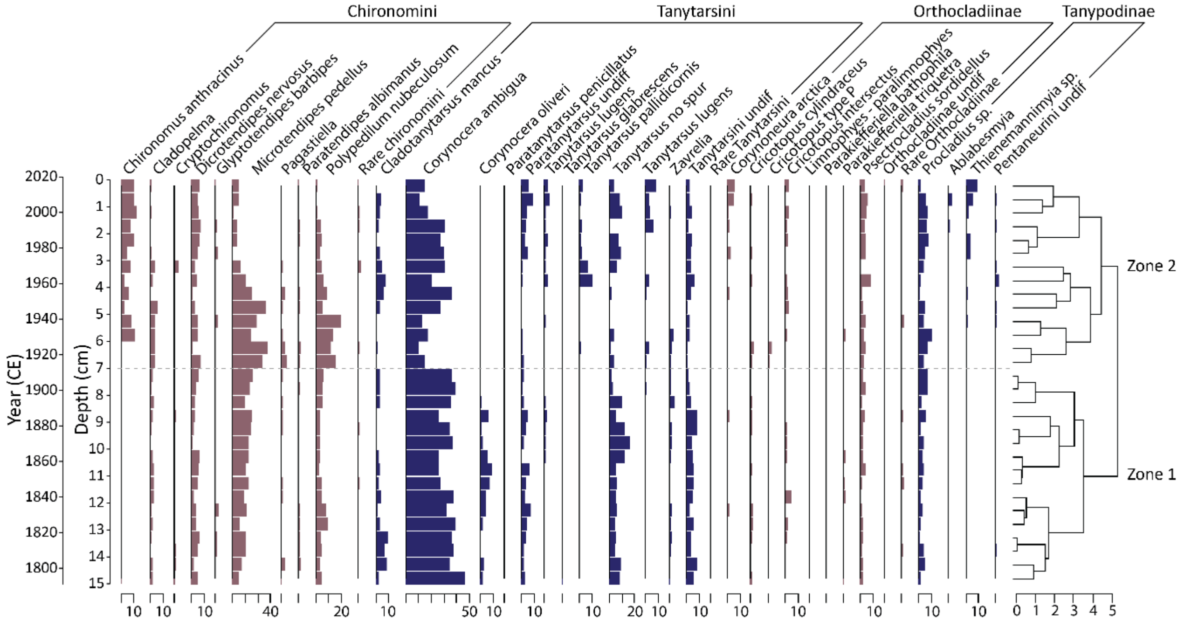

Figure B. 10 Total percentage abundances of the chironomid taxa present in East Cobb lake. Taxa are grouped by subfamily. Taxa with < 5% abundance are grouped within their subfamily. A dendrograph indicates zones of similar taxonomic composition, with the highest order of dissimilarity indicated by a horizontal grey dashed line.

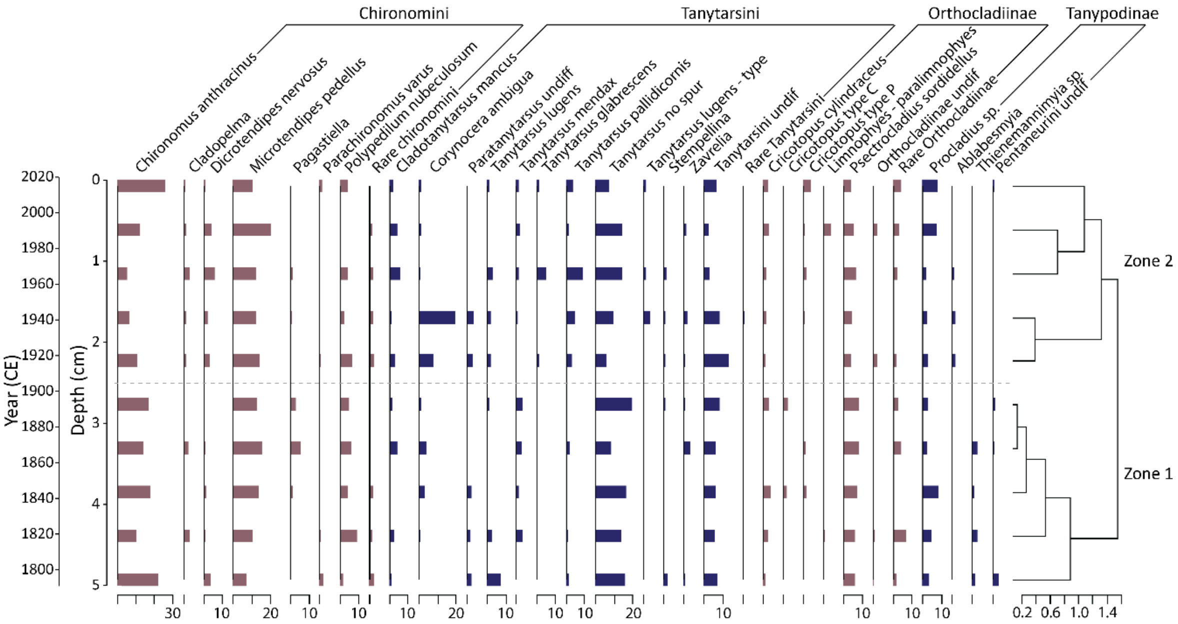

Figure B. 11 Total percentage abundances of the chironomid taxa present in Lost Quartz lake. Taxa are grouped by subfamily. Taxa with < 5% abundance are grouped within their subfamily. A dendrograph indicates zones of similar taxonomic composition, with the highest order of dissimilarity indicated by a horizontal grey dashed line.

## B.5 Analogue testing for the temporal and calibration chironomid datasets

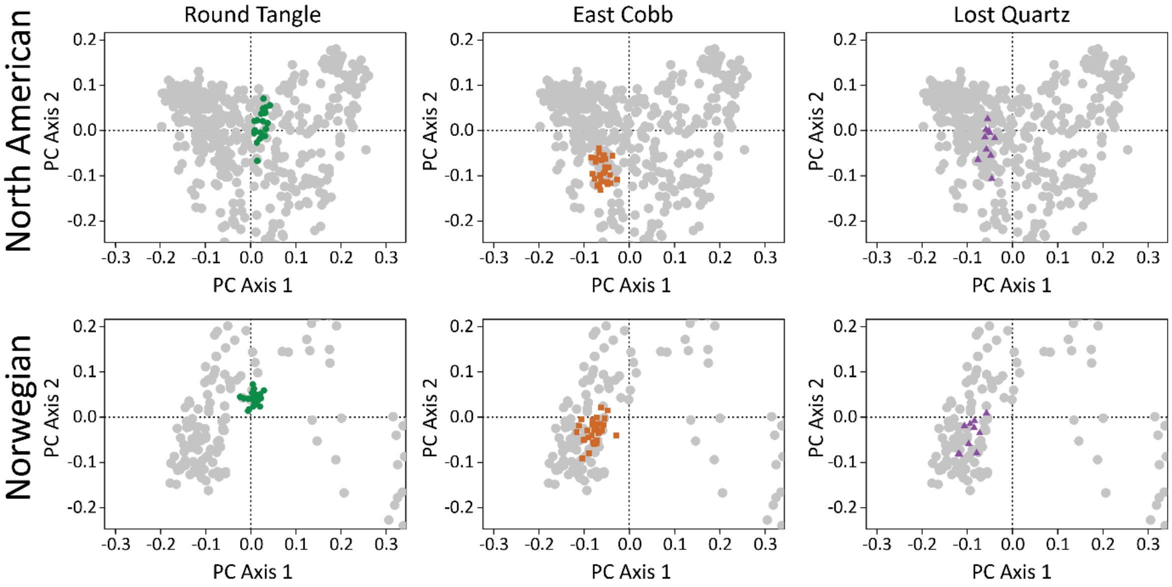

Figure B. 12 The Alaskan lake chironomid samples plotted within the North American and Norwegian calibration datasets, indicating that the calibration datasets have good analogues for the fossil datasets.

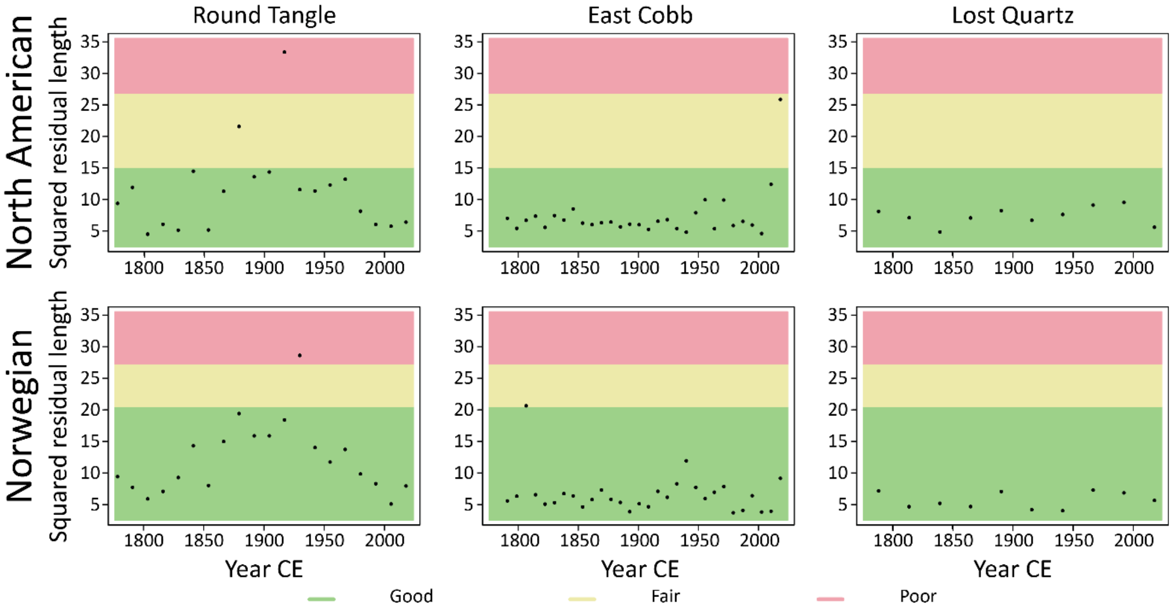

Figure B. 13 Goodness of fit analyses indicated that both the North American and Norwegian calibration sets have good analogues for the Alaskan lakes.

## B.6 The effect of taxonomic resolution on taxon richness, beta diversity and skewness

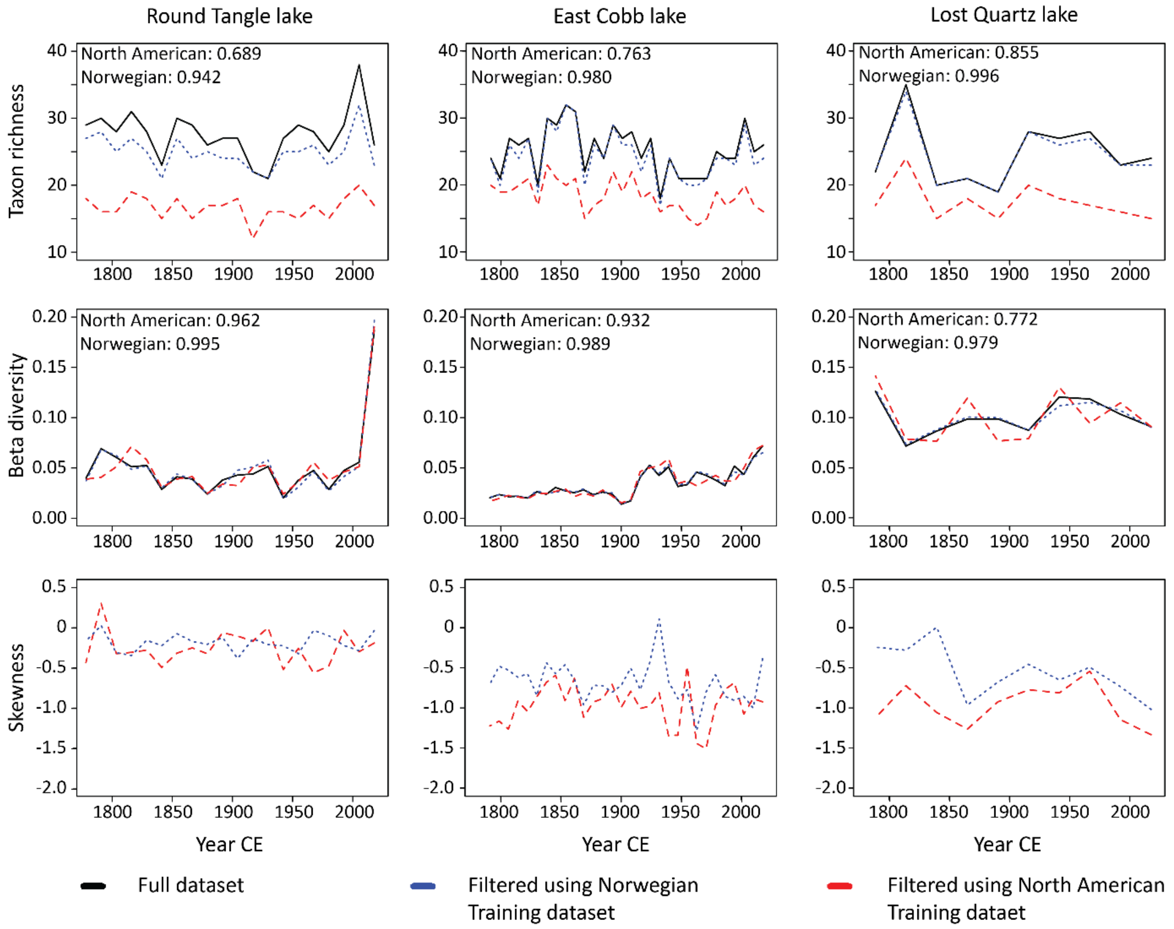

Figure B. 14 The effect of taxonomic resolution on taxon richness, beta diversity and skewness. Solid black lines show taxon richness and beta diversity values for the full chironomid assemblage. The datasets were filtered using the North American and Norwegian datasets for the skewness analysis. Dashed red lines show the taxon richness, beta diversity and skewness for the lake datasets filtered using the North American calibration dataset. Dotted blue lines show the taxon richness, beta diversity and skewness for the lake datasets filtered using the Norwegian calibration dataset. For taxon richness and beta diversity, Pearson's correlation values (3.d.p.) indicate the correlation between the trends for the full dataset and filtered datasets. All correlations had p values < 0.05. For skewness, Pearson's correlation did not indicate detectable correlations between the trends for the filtered datasets (p > 0.05).

## B.7 Distinguishing pattern from noise: ecological metric median values

10,000 randomised replications of the observed chironomid datasets were created by randomly re-ordering the full observed chironomid records. Taxon richness, beta diversity, and skewness were calculated on each of the randomised datasets. The randomised datasets were partitioned into assemblage zone subsections, to correspond with the empirical records. Median values were calculated for each metric for the randomised subsets. The difference between the medians was calculated to produce 10,000 differences in median values (Figure B. 15).

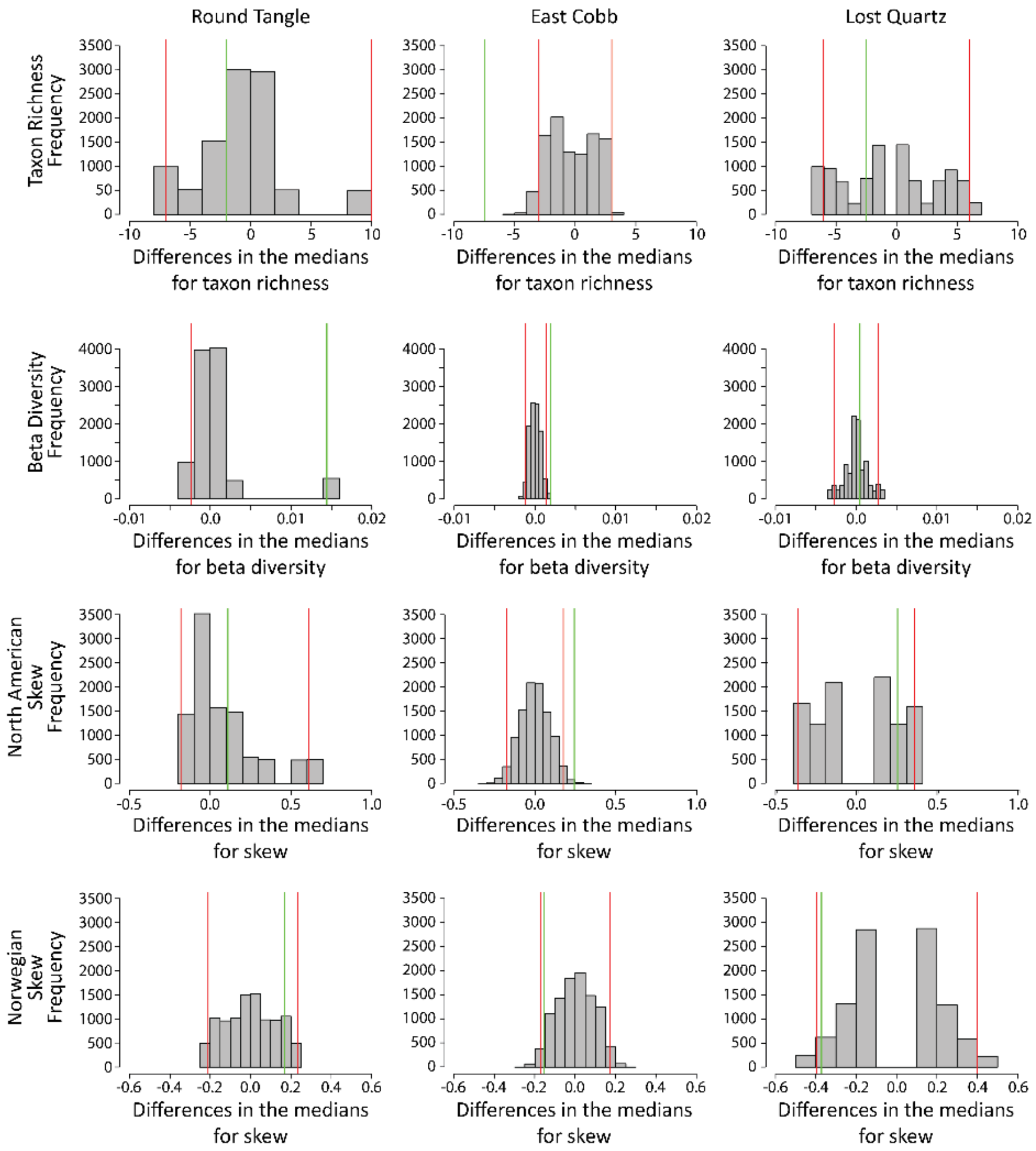

Figure B. 15 Histograms indicate the spread in differences in the medians for 10,000 randomised datasets. The 2.5th and 97.5th percentiles are shown by vertical red lines. The correlation coefficient values for the empirical datasets are shown in green. The correlated trends in the empirical datasets exceed the random expectation ($p \leq 0.05$), if the empirical correlation coefficient values lie outside of the 2.5th and 97.5th percentiles.

## B.8 Key elemental data

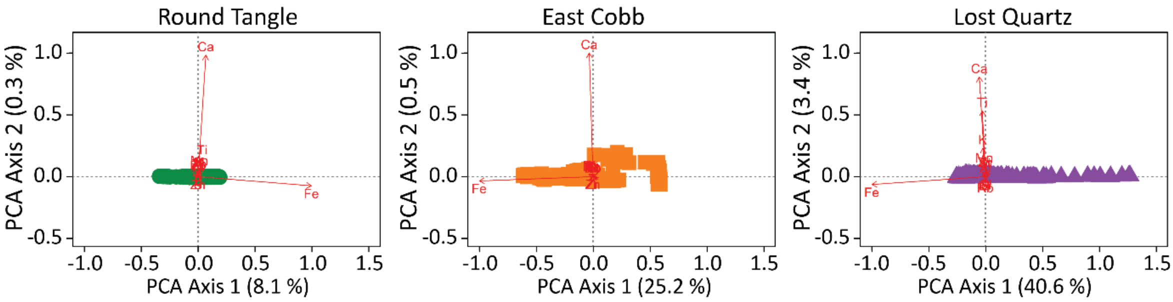

Figure B. 16 Principal components analyses (PCA) indicate that Fe and Ca were the most influential elements. These elements were used in the GAMs. PCAs were performed using the *princomp* function in *R* statistical software v. 3.6.0 (R Core Team, 2019).

## B.9 ITRAX predicted values for GAMs

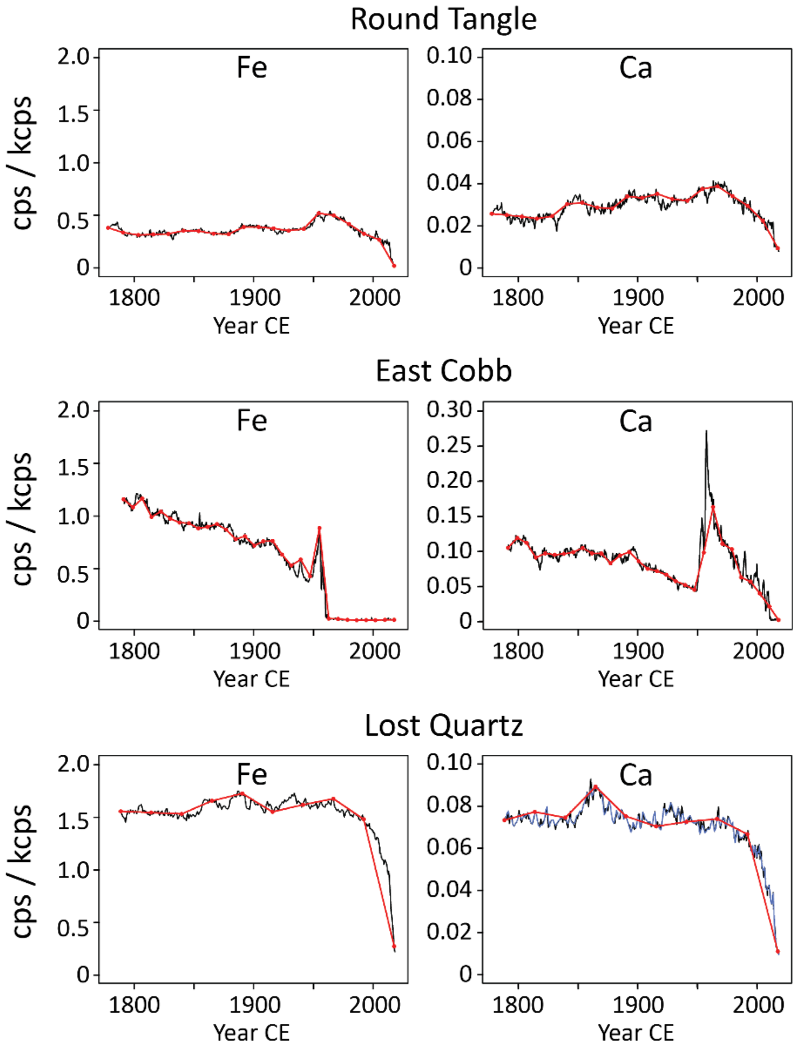

Figure B. 17 Fe and Ca values were calculated to correspond to the chironomid sample ages for Round Tangle, East Cobb and Lost Quartz lakes. The full ITRAX records are shown in black and the calculated ITRAX values corresponding to the chironomid sample ages are shown in red.

## B.10 Temperature predicted values for GAMs and CCAs

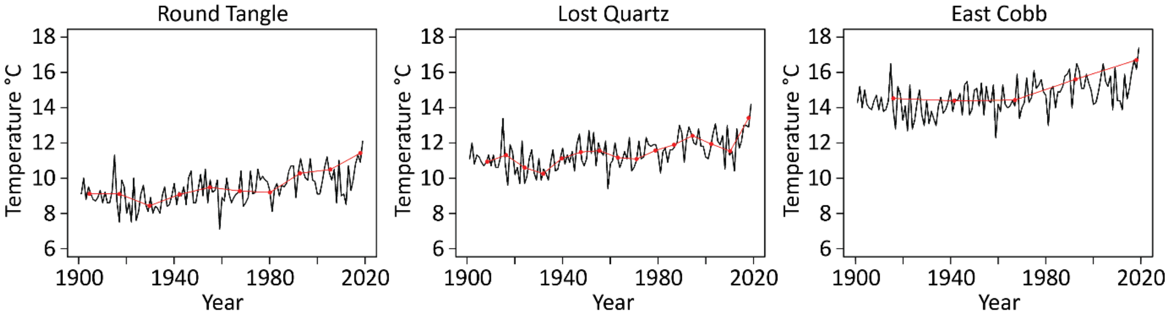

Figure B. 18 Temperature values were calculated to correspond to the chironomid sample ages for Round Tangle, Lost Quartz and East Cobb lakes. The full temperature records are shown in black and the calculated temperature values corresponding to the chironomid sample ages are shown in red.

## B.11 GAM output statistics

### B.11.1 Round Tangle

Table B. 2 Summary of the GAM output used to assess the effect of multivariate drivers on chironomid taxon richness in Round Tangle Lake. Predictor variables included Loss On Ignition (LOI), magnetic susceptibility (MS), Fe and Ca. LOI explained a large proportion of the variance in taxon richness for the full chironomid dataset and the Norwegian-filtered dataset, whereas Fe and Ca explained a greater proportion of the variance in taxon richness for the North American- filtered dataset. Significance codes: *** p ≤ 0.001, ** p ≤ 0.01, * p ≤ 0.05.

| | Predictor variables | edf | Ref edf | F statistic | p-value | significance |
|---|---|---|---|---|---|---|
| Taxon richness | LOI | 3.41 | 3.78 | 3.23 | 0.03 | * |
| | MS | 1.26 | 1.45 | 0.15 | 0.86 | |
| | Fe | 1.00 | 1.00 | 11.71 | 0.01 | ** |
| | Ca | 1.00 | 1.00 | 8.04 | 0.02 | * |
| | Intercept coefficient: 27.65 | | | | | |
| | Deviance explained: 75.7 % | | | | | |
| | LOI | 3.12 | 3.54 | 3.54 | 0.04 | * |
| | Intercept coefficient: 27.65 | | | | | |
| | Deviance explained: 46.5% | | | | | |
| Taxon richness, filtered using the North American dataset | LOI | 1.00 | 1.00 | 3.08 | 0.10 | |
| | MS | 1.00 | 1.00 | 1.84 | 0.20 | |
| | Fe | 1.00 | 1.00 | 4.17 | 0.06 | |
| | Ca | 1.80 | 1.96 | 5.41 | 0.03 | * |
| | Intercept coefficient: 16.65 | | | | | |
| | Deviance explained: 47.9 % | | | | | |
| | Fe | 1.00 | 1.00 | 2.02 | 0.17 | |
| | Ca | 1.00 | 1.00 | 4.22 | 0.06 | |
| | Intercept coefficient: 16.65 | | | | | |
| | Deviance explained: 25 % | | | | | |
| Taxon richness, filtered using the Norwegian dataset | LOI | 3.10 | 3.56 | 2.35 | 0.07 | |
| | MS | 1.00 | 1.00 | 0.75 | 0.40 | |
| | Fe | 1.00 | 1.00 | 8.71 | 0.01 | * |
| | Ca | 1.00 | 1.00 | 7.15 | 0.02 | * |
| | Intercept coefficient: 24.950 | | | | | |
| | Deviance explained: 70.0 % | | | | | |
| | LOI | 3.14 | 3.56 | 3.54 | 0.03 | * |
| | Intercept coefficient: 24.9500 | | | | | |
| | Deviance explained: 47.9% | | | | | |

Table B. 3 Summary of the GAM output used to assess the effect of temperature on chironomid taxon richness in Round Tangle Lake, for the period 1901 – 2018. Significance codes: *** p ≤ 0.001, ** p ≤ 0.01, * p ≤ 0.05.

| | Predictor variable | edf | Ref edf | F statistic | p-value | significance |
|---|---|---|---|---|---|---|
| Taxon richness | Temp | 2.39 | 2.86 | 3.52 | 0.07 | |
| | Intercept coefficient: 27.20 | | | | | |
| | Deviance explained: 65.7 % | | | | | |
| Taxon richness, filtered using the North American dataset | Temp | 1.00 | 1.00 | 2.22 | 0.17 | |
| | Intercept coefficient: 16.40 | | | | | |
| | Deviance explained: 21.8 % | | | | | |
| Taxon richness, filtered using the Norwegian dataset | Temp | 2.23 | 2.71 | 2.02 | 0.16 | |
| | Intercept coefficient: 24.60 | | | | | |
| | Deviance explained: 48.0 % | | | | | |

Table B. 4 Summary of GAM output used to assess the effect of multivariate drivers on chironomid beta diversity in Round Tangle Lake. Predictor variables included Loss On Ignition (LOI), magnetic susceptibility (MS), Fe and Ca. The GAMs were repeated on the filtered datasets. The majority of the variance in beta diversity could be explained by LOI. Significance codes: *** p ≤ 0.001, ** p ≤ 0.01, * p ≤ 0.05.

| | Predictor variables | edf | Ref edf | F statistic | p-value | significance |
|---|---|---|---|---|---|---|
| Beta Diversity | LOI | 1.00 | 1.00 | 0.03 | 0.88 | |
| | MS | 1.00 | 1.00 | 1.39 | 0.26 | |
| | Fe | 1.00 | 1.00 | 0.07 | 0.79 | |
| | Ca | 1.96 | 2.00 | 19.09 | < 0.00 | *** |
| | Intercept coefficient: 0.05 | | | | | |
| | Deviance explained: 93.2 % | | | | | |
| | LOI | 3.43 | 3.78 | 38.00 | < 0.00 | *** |
| | Intercept coefficient: 0.05 | | | | | |
| | Deviance explained: 90.3% | | | | | |
| Beta Diversity, filtered using the North American dataset | LOI | 1.00 | 1.00 | 0.00 | 0.95 | |
| | MS | 1.00 | 1.00 | 0.26 | 0.62 | |
| | Fe | 1.00 | 1.00 | 0.29 | 0.60 | |
| | Ca | 1.97 | 2.00 | 22.48 | < 0.00 | *** |
| | Intercept coefficient: 0.05 | | | | | |
| | Deviance explained: 93.6 % | | | | | |
| | LOI | 3.46 | 3.80 | 34.13 | < 0.00 | *** |
| | Intercept coefficient: 0.05 | | | | | |
| | Deviance explained: 89.3 % | | | | | |
| Beta Diversity, filtered using the Norwegian dataset | LOI | 1.00 | 1.00 | 0.69 | 0.42 | |
| | MS | 1.00 | 1.00 | 2.74 | 0.12 | |
| | Fe | 1.00 | 1.00 | 1.22 | 0.29 | |
| | Ca | 1.96 | 2.00 | 16.31 | < 0.00 | *** |
| | Intercept coefficient: 0.05 | | | | | |
| | Deviance explained: 93.1 % | | | | | |
| | LOI | 3.43 | 3.78 | 33.80 | < 0.00 | *** |
| | Intercept coefficient: 0.05 | | | | | |
| | Deviance explained: 89.2 % | | | | | |

Table B. 5 Summary of the GAM output used to assess the effect of temperature on chironomid beta diversity in Round Tangle Lake, for the period 1901 – 2018. Significance codes: *** p ≤ 0.001, ** p ≤ 0.01, * p ≤ 0.05.

| | Predictor variable | edf | Ref edf | F statistic | p-value | significance |
|---|---|---|---|---|---|---|
| Beta diversity | Temp | 3.36 | 3.71 | 50.38 | < 0.00 | *** |
| | Intercept coefficient: 0.06 | | | | | |
| | Deviance explained: 97.1 % | | | | | |
| Beta diversity, filtered using the North American dataset | Temp | 3.32 | 3.68 | 39.66 | < 0.00 | *** |
| | Intercept coefficient: 0.06 | | | | | |
| | Deviance explained: 96.3 % | | | | | |
| Beta diversity, filtered using the Norwegian dataset | Temp | 3.28 | 3.65 | 38.78 | < 0.00 | *** |
| | Intercept coefficient: 0.06 | | | | | |
| | Deviance explained: 96.2 % | | | | | |

Table B. 6 Summary of GAM output used to assess the effect of multivariate drivers on chironomid skewness in Round Tangle Lake. Predictor variables included Loss On Ignition (LOI), magnetic susceptibility (MS), Fe and Ca. The predictor variables explained little of the variance in skewness. Significance codes: *** p ≤ 0.001, ** p ≤ 0.01, * p ≤ 0.05.

| | Predictor variables | edf | Ref edf | F statistic | p-value | significance |
|---|---|---|---|---|---|---|
| Skewness, filtered using the North American dataset | LOI | 1.00 | 1.00 | 0.33 | 0.58 | |
| | MS | 1.00 | 1.00 | 0.00 | 0.95 | |
| | Fe | 1.00 | 1.00 | 0.79 | 0.39 | |
| | Ca | 1.00 | 1.00 | 0.26 | 0.62 | |
| | Intercept coefficient: -0.26 | | | | | |
| | Deviance explained: 7.68 % | | | | | |
| Skewness, filtered using the Norwegian dataset | LOI | 1.00 | 1.00 | 0.25 | 0.63 | |
| | MS | 1.00 | 1.00 | 0.27 | 0.61 | |
| | Fe | 1.00 | 1.00 | 0.54 | 0.48 | |
| | Ca | 1.57 | 1.82 | 0.92 | 0.50 | |
| | Intercept coefficient: -0.19 | | | | | |
| | Deviance explained: 15.6 % | | | | | |

Table B. 7 Summary of the GAM output used to assess the effect of temperature on chironomid skewness in Round Tangle Lake, for the period 1901 – 2018. Significance codes: *** p ≤ 0.001, ** p ≤ 0.01, * p ≤ 0.05.

| | Predictor variable | edf | Ref edf | F statistic | p-value | significance |
|---|---|---|---|---|---|---|
| Skewness, filtered using the North American dataset | Temp | 1.21 | 1.39 | 0.14 | 0.89 | |
| | Intercept coefficient: -0.26 | | | | | |
| | Deviance explained: 95.3 % | | | | | |
| Skewness, filtered using the Norwegian dataset | Temp | 1.00 | 1.00 | 0.42 | 0.54 | |
| | Intercept coefficient: -0.20 | | | | | |
| | Deviance explained: 4.99 % | | | | | |

### B.11.2 East Cobb

Table B. 8 Summary of GAM output used to assess the effect of multivariate drivers on chironomid taxon richness in East Cobb Lake. Predictor variables included Loss On Ignition (LOI), magnetic susceptibility (MS), Fe and Ca. The GAMs were repeated on the filtered datasets. LOI explained the largest proportion of the variance in taxon richness. Significance codes: *** p ≤ 0.001, ** p ≤ 0.01, * p ≤ 0.05.

| | Predictor variables | edf | Ref edf | F statistic | p-value | significance |
|---|---|---|---|---|---|---|
| Taxon richness | LOI | 2.71 | 2.91 | 5.39 | 0.01 | ** |
| | MS | 1.00 | 1.00 | 4.46 | 0.05 | * |
| | Fe | 1.74 | 1.90 | 1.67 | 0.28 | |
| | Ca | 1.00 | 1.00 | 1.78 | 0.20 | |
| | Intercept coefficient: 25.31 | | | | | |
| | Deviance explained: 52.6 % | | | | | |
| | LOI | 2.50 | 2.98 | 2.96 | 0.06 | |
| | Intercept coefficient: <0.00 | | | | | |
| | Deviance explained: 28.8 % | | | | | |
| Taxon richness, filtered using the North American dataset | LOI | 2.51 | 3.02 | 2.35 | 0.11 | |
| | MS | 1.00 | 1.00 | 0.15 | 0.71 | |
| | Fe | 1.00 | 1.00 | 0.49 | 0.49 | |
| | Ca | 1.73 | 1.90 | 1.77 | 0.26 | |
| | Intercept coefficient: 18.3793 | | | | | |
| | Deviance explained: 48.3 % | | | | | |
| | LOI | 2.73 | 3.21 | 4.27 | 0.02 | * |
| | Intercept coefficient: <0.00 | | | | | |
| | Deviance explained: 38.0 % | | | | | |
| Taxon richness, filtered using the Norwegian dataset | LOI | 2.62 | 3.13 | 2.86 | 0.07 | |
| | MS | 1.00 | 1.00 | 3.41 | 0.08 | |
| | Fe | 1.00 | 1.00 | 0.11 | 0.74 | |
| | Ca | 1.28 | 1.45 | 0.51 | 0.63 | |
| | Intercept coefficient: <0.00 | | | | | |
| | Deviance explained: 38.9 % | | | | | |
| | LOI | 2.26 | 2.72 | 2.29 | 0.16 | |
| | Intercept coefficient: <0.00 | | | | | |
| | Deviance explained: 21.2 % | | | | | |

Table B. 9 Summary of the GAM output used to assess the effect of temperature on chironomid taxon richness in East Cobb Lake, for the period 1901 – 2018. Significance codes: *** p ≤ 0.001, ** p ≤ 0.01, * p ≤ 0.05.

| | Predictor variable | edf | Ref edf | F statistic | p-value | significance |
|---|---|---|---|---|---|---|
| Taxon richness | Temp | 1.00 | 1.00 | 4.74 | 0.05 | * |
| | Intercept coefficient: 23.93 | | | | | |
| | Deviance explained: 26.7 % | | | | | |
| Taxon richness, filtered using the North American dataset | Temp | 1.00 | 1.00 | 0.08 | 0.78 | |
| | Intercept coefficient: 17.33 | | | | | |
| | Deviance explained: 0.62 % | | | | | |
| Taxon richness, filtered using the Norwegian dataset | Temp | 1.44 | 1.76 | 2.07 | 0.12 | |
| | Intercept coefficient: 22.93 | | | | | |
| | Deviance explained: 29.4 % | | | | | |

Table B. 10 Summary of GAM output used to assess the effect of multivariate drivers on chironomid beta diversity in East Cobb Lake. Predictor variables included Loss On Ignition (LOI), magnetic susceptibility (MS), Fe and Ca. The GAMs were repeated on the filtered datasets. Separate models were run for LOI and MS and Fe and Ca due to the small dataset size. The majority of the variance in beta diversity could be explained by LOI and MS. Significance codes: *** p ≤ 0.001, ** p ≤ 0.01, * p ≤ 0.05.

| | Predictor variables | edf | Ref edf | F statistic | p-value | significance |
|---|---|---|---|---|---|---|
| Beta Diversity | LOI | 2.22 | 2.73 | 1.84 | 0.21 | |
| | MS | 1.00 | 1.00 | 1.02 | 0.32 | |
| | Fe | 1.05 | 1.08 | 0.08 | 0.81 | |
| | Ca | 1.86 | 1.96 | 1.96 | 0.04 | * |
| | Intercept coefficient: 0.034 | | | | | |
| | Deviance explained: 77.8 % | | | | | |
| | LOI | 1.21 | 1.39 | 31.45 | < 0.00 | *** |
| | Intercept coefficient: 0.034 | | | | | |
| | Deviance explained: 63.2 % | | | | | |
| Beta Diversity, filtered using the North American dataset | LOI | 3.65 | 4.53 | 3.43 | 0.03 | * |
| | MS | 1.00 | 1.00 | 2.49 | 0.13 | |
| | Fe | 1.20 | 1.34 | 0.13 | 0.77 | |
| | Ca | 1.43 | 1.63 | 3.52 | 0.04 | * |
| | Intercept coefficient: 0.034 | | | | | |
| | Deviance explained: 83.5 % | | | | | |
| | LOI | 5.27 | 6.40 | 13.56 | < 0.00 | *** |
| | Intercept coefficient: 0.034 | | | | | |
| | Deviance explained: 80.0 % | | | | | |
| Beta Diversity, filtered using the Norwegian dataset | LOI | 2.71 | 3.22 | 3.35 | 0.05 | |
| | MS | 1.00 | 1.00 | 2.84 | 0.11 | |
| | Fe | 1.03 | 1.06 | 0.11 | 0.76 | |
| | Ca | 1.82 | 1.95 | 3.21 | 0.07 | |
| | Intercept coefficient: 0.034 | | | | | |
| | Deviance explained: 80.2 % | | | | | |
| | LOI | 3.95 | 4.87 | 13.80 | < 0.00 | *** |
| | Intercept coefficient: 0.034 | | | | | |
| | Deviance explained: 74.8 % | | | | | |

Table B. 11 Summary of the GAM output used to assess the effect of temperature on chironomid beta diversity in East Cobb Lake, for the period 1901 – 2018. Significance codes: *** p ≤ 0.001, ** p ≤ 0.01, * p ≤ 0.05.

| | Predictor variable | edf | Ref edf | F statistic | p-value | significance |
|---|---|---|---|---|---|---|
| Beta diversity | Temp | 1.38 | 1.68 | 4.80 | 0.05 | |
| | Intercept coefficient: 0.04 | | | | | |
| | Deviance explained: 37.0 % | | | | | |
| Beta diversity, filtered using the North American dataset | Temp | 1.00 | 1.00 | 3.06 | 0.10 | |
| | Intercept coefficient: 0.05 | | | | | |
| | Deviance explained: 19.1 % | | | | | |
| Beta diversity, filtered using the Norwegian dataset | Temp | 1.00 | 1.00 | 3.41 | 0.09 | |
| | Intercept coefficient: 0.04 | | | | | |
| | Deviance explained: 20.8 % | | | | | |

Table B. 12 Summary of GAM output used to assess the effect of multivariate drivers on chironomid skewness in East Cobb Lake. Predictor variables included Loss On Ignition (LOI), magnetic susceptibility (MS), Fe and Ca. The predictor variables explained a large proportion of the variance in skewness. Significance codes: *** p ≤ 0.001, ** p ≤ 0.01, * p ≤ 0.05.

| | Predictor variables | edf | Ref edf | F statistic | p-value | significance |
|---|---|---|---|---|---|---|
| Skewness, filtered using the North American dataset | LOI | 1.00 | 1.00 | 0.00 | 0.98 | |
| | MS | 1.00 | 1.00 | 0.02 | 0.90 | |
| | Fe | 2.78 | 2.96 | 4.89 | 0.01 | * |
| | Ca | 1.35 | 1.61 | 0.64 | 0.36 | |
| | Intercept coefficient: -0.96 | | | | | |
| | Deviance explained: 49.0 % | | | | | |
| | Fe | 3.31 | 3.72 | 4.07 | 0.01 | * |
| | Ca | 1.33 | 1.59 | 3.92 | 0.09 | |
| | Intercept coefficient: -0.69 | | | | | |
| | Deviance explained: 48.6 % | | | | | |
| Skewness, filtered using the Norwegian dataset | LOI | 1.00 | 1.00 | 2.36 | 0.14 | |
| | MS | 1.23 | 1.41 | 0.12 | 0.85 | |
| | Fe | 1.00 | 1.00 | 0.14 | 0.72 | |
| | Ca | 1.00 | 1.00 | 7.23 | 0.01 | * |
| | Intercept coefficient: -0.69 | | | | | |
| | Deviance explained: 31.1 % | | | | | |
| | Fe | 1.00 | 1.00 | 5.52 | 0.03 | * |
| | Ca | 1.00 | 1.00 | 4.29 | 0.05 | * |
| | Intercept coefficient: -0.69 | | | | | |
| | Deviance explained: 21.3 % | | | | | |

Table B. 13 Summary of the GAM output used to assess the effect of temperature on chironomid skewness in East Cobb Lake, for the period 1901 – 2018. Significance codes: *** p ≤ 0.001, ** p ≤ 0.01, * p ≤ 0.05.

| | Predictor variable | edf | Ref edf | F statistic | p-value | significance |
|---|---|---|---|---|---|---|
| Skewness, filtered using the North American dataset | Temp | 1.00 | 1.00 | 0.99 | 0.34 | |
| | Intercept coefficient: -1.00<br>Deviance explained: 7.05 % | | | | | |
| Skewness, filtered using the Norwegian dataset | Temp | 2.74 | 3.26 | 3.41 | 0.06 | |
| | Intercept coefficient: -0.71<br>Deviance explained: 53.7 % | | | | | |

### B.11.3 Lost Quartz

Table B. 14 Summary of GAM output used to assess the effect of multivariate drivers on chironomid taxon richness in Lost Quartz Lake. Predictor variables included Loss On Ignition (LOI), magnetic susceptibility (MS), Fe and Ca. Separate models were run for LOI and MS and Fe and Ca due to the small dataset size. The GAMs were repeated on the filtered datasets. LOI and MS explained the largest proportion of the variance in taxon richness. Significance codes: *** p ≤ 0.001, ** p ≤ 0.01, * p ≤ 0.05.

| | Predictor variables | edf | Ref edf | F statistic | p-value | significance |
|---|---|---|---|---|---|---|
| Taxon richness | LOI | 1.88 | 2.05 | 2.43 | 0.28 | |
| | MS | 1.94 | 1.99 | 8.19 | 0.10 | |
| | Intercept coefficient: 24.29 | | | | | |
| | Deviance explained: 91.3 % | | | | | |
| | Fe | 1.00 | 1.00 | 0.33 | 0.60 | |
| | Ca | 1.00 | 1.00 | 0.36 | 0.58 | |
| | Intercept coefficient: 24.286 | | | | | |
| | Deviance explained: 8.31 % | | | | | |
| Taxon richness, filtered using the North American dataset | LOI | 1.48 | 1.74 | 1.79 | 0.40 | |
| | MS | 1.93 | 1.99 | 11.48 | 0.04 | * |
| | Intercept coefficient: 17.00 | | | | | |
| | Deviance explained: 94.3 % | | | | | |
| | Fe | 1.00 | 1.00 | 0.27 | 0.63 | |
| | Ca | 1.04 | 1.08 | 0.53 | 0.52 | |
| | Intercept coefficient: 17.00 | | | | | |
| | Deviance explained: 29.8 % | | | | | |
| Taxon richness, filtered using the Norwegian dataset | LOI | 1.87 | 2.05 | 2.61 | 0.27 | |
| | MS | 1.95 | 1.99 | 10.12 | 0.08 | |
| | Intercept coefficient: 23.86 | | | | | |
| | Deviance explained: 92.7 % | | | | | |
| | Fe | 1.00 | 1.00 | 0.31 | 0.61 | |
| | Ca | 1.00 | 1.00 | 0.30 | 0.61 | |
| | Intercept coefficient: 23.86 | | | | | |
| | Deviance explained: 7.28 % | | | | | |

Table B. 15 Summary of the GAM output used to assess the effect of temperature on chironomid taxon richness in Lost Quartz Lake, for the period 1901 – 2018. Significance codes: *** p ≤ 0.001, ** p ≤ 0.01, * p ≤ 0.05.

| | Predictor variable | edf | Ref edf | F statistic | p-value | significance |
|---|---|---|---|---|---|---|
| Taxon richness | Temp | 1.98 | 2.18 | 13.13 | 0.07 | |
| | Intercept coefficient: 26.00 | | | | | |
| | Deviance explained: 93.8 % | | | | | |
| Taxon richness, filtered using the North American dataset | Temp | 1.00 | 1.00 | 5.05 | 0.11 | |
| | Intercept coefficient: 17.20 | | | | | |
| | Deviance explained: 62.7 % | | | | | |
| Taxon richness, filtered using the Norwegian dataset | Temp | 1.25 | 1.44 | 7.72 | 0.08 | |
| | Intercept coefficient: 25.40 | | | | | |
| | Deviance explained: 78.9 % | | | | | |

Table B. 16 Summary of GAM output used to assess the effect of multivariate drivers on chironomid beta diversity in Lost Quartz Lake. Predictor variables included Loss On Ignition (LOI), magnetic susceptibility (MS), Fe and Ca. The GAMs were repeated on the filtered datasets. Separate models were run for LOI and MS and Fe and Ca due to the small dataset size. The majority of the variance in beta diversity could be explained by LOI and MS. Significance codes: *** p ≤ 0.001, ** p ≤ 0.01, * p ≤ 0.05.

| | Predictor variables | edf | Ref edf | F statistic | p-value | significance |
|---|---|---|---|---|---|---|
| Beta diversity | LOI | 1.96 | 2.22 | 3.79 | 0.15 | |
| | MS | 1.00 | 1.00 | 1.04 | 0.38 | |
| | Intercept coefficient: 0.10 | | | | | |
| | Deviance explained: 78.6 % | | | | | |
| | LOI | 1.85 | 2.11 | 3.72 | 0.12 | |
| | Intercept coefficient: 0.10 | | | | | |
| | Deviance explained: 67.7 % | | | | | |
| | Fe | 1.00 | 1.00 | 0.67 | 0.46 | |
| | Ca | 1.00 | 1.00 | 0.37 | 0.58 | |
| | Intercept coefficient: 0.10 | | | | | |
| | Deviance explained: 25.4 % | | | | | |
| Beta diversity, filtered using the North American dataset | LOI | 1.00 | 1.00 | 0.05 | 0.84 | |
| | MS | 1.00 | 1.00 | 0.16 | 0.71 | |
| | Intercept coefficient: 0.10 | | | | | |
| | Deviance explained: 3.95 % | | | | | |
| | Fe | 1.00 | 1.00 | 0.59 | 0.49 | |
| | Ca | 1.00 | 1.00 | 0.77 | 0.43 | |
| | Intercept coefficient: 0.10 | | | | | |
| | Deviance explained: 18.4 % | | | | | |
| Beta diversity, filtered using the Norwegian dataset | LOI | 2.06 | 2.31 | 3.95 | 0.16 | |
| | MS | 1.00 | 1.00 | 2.41 | 0.22 | |
| | Intercept coefficient: 0.10 | | | | | |
| | Deviance explained: 80.0 % | | | | | |
| | LOI | 1.77 | 2.04 | 2.33 | 0.21 | |
| | Intercept coefficient: 0.10 | | | | | |
| | Deviance explained: 57.0% | | | | | |
| | Fe | 1.00 | 1.00 | 0.61 | 0.48 | |
| | Ca | 1.00 | 1.00 | 0.26 | 0.64 | |
| | Intercept coefficient: 0.10 | | | | | |
| | Deviance explained: 30.3 % | | | | | |

Table B. 17 Summary of the GAM output used to assess the effect of temperature on chironomid beta diversity in Lost Quartz Lake, for the period 1901 – 2018. Significance codes: *** p ≤ 0.001, ** p ≤ 0.01, * p ≤ 0.05.

| | Predictor variable | edf | Ref edf | F statistic | p-value | significance |
|---|---|---|---|---|---|---|
| Beta diversity | Temp | 1.00 | 1.00 | 1.21 | 0.35 | |
| | Intercept coefficient: 0.10 | | | | | |
| | Deviance explained: 28.7 % | | | | | |
| Beta diversity, filtered using the North American dataset | Temp | 1.00 | 1.00 | 0.08 | 0.80 | |
| | Intercept coefficient: 0.10 | | | | | |
| | Deviance explained: 2.5 % | | | | | |
| Beta diversity, filtered using the Norwegian dataset | Temp | 1.00 | 1.00 | 0.81 | 0.43 | |
| | Intercept coefficient: 0.10 | | | | | |
| | Deviance explained: 21.3 % | | | | | |

Table B. 18 Summary of GAM output used to assess the effect of multivariate drivers on chironomid skewness in Lost Quartz Lake. Predictor variables included Loss On Ignition (LOI), magnetic susceptibility (MS), Fe and Ca. The predictor variables explained a large proportion of the variance in skewness. Significance codes: *** p ≤ 0.001, ** p ≤ 0.01, * p ≤ 0.05.

| | Predictor variables | edf | Ref edf | F statistic | p-value | significance |
|---|---|---|---|---|---|---|
| Skewness, filtered using the North American dataset | LOI | 1.00 | 1.00 | 1.26 | 0.33 | |
| | MS | 1.00 | 1.00 | 0.76 | 0.43 | |
| | Intercept coefficient: -0.97 | | | | | |
| | Deviance explained: 56.9 % | | | | | |
| | Fe | 1.00 | 1.00 | 4.79 | 0.09 | |
| | Ca | 1.00 | 1.00 | 3.21 | 0.15 | |
| | Intercept coefficient: -0.97 | | | | | |
| | Deviance explained: 63.3 % | | | | | |
| Skewness, filtered using the Norwegian dataset | LOI | 1.00 | 1.00 | 0.02 | 0.88 | |
| | MS | 1.00 | 1.00 | 2.43 | 0.19 | |
| | Intercept coefficient: -0.72 | | | | | |
| | Deviance explained: 53.0 % | | | | | |
| | Fe | 1.00 | 1.00 | 6.87 | 0.06 | |
| | Ca | 1.00 | 1.00 | 4.65 | 0.10 | |
| | Intercept coefficient: -0.72 | | | | | |
| | Deviance explained: 70.9 % | | | | | |

Table B. 19 Summary of the GAM output used to assess the effect of temperature on chironomid skewness in Lost Quartz Lake, for the period 1901 – 2018. Significance codes: *** p ≤ 0.001, ** p ≤ 0.01, * p ≤ 0.05.

| | Predictor variable | edf | Ref edf | F statistic | p-value | significance |
|---|---|---|---|---|---|---|
| Skewness, filtered using the North American dataset | Temp | 1.00 | 1.00 | 19.69 | 0.02 | * |
| | Intercept coefficient: -0.92 | | | | | |
| | Deviance explained: 86.8 % | | | | | |
| Skewness, filtered using the Norwegian dataset | Temp | 1.00 | 1.00 | 18.49 | 0.02 | * |
| | Intercept coefficient: -0.67 | | | | | |
| | Deviance explained: 86.0 % | | | | | |

## B.12 CCA plots indicating assemblage change over the last 100 years

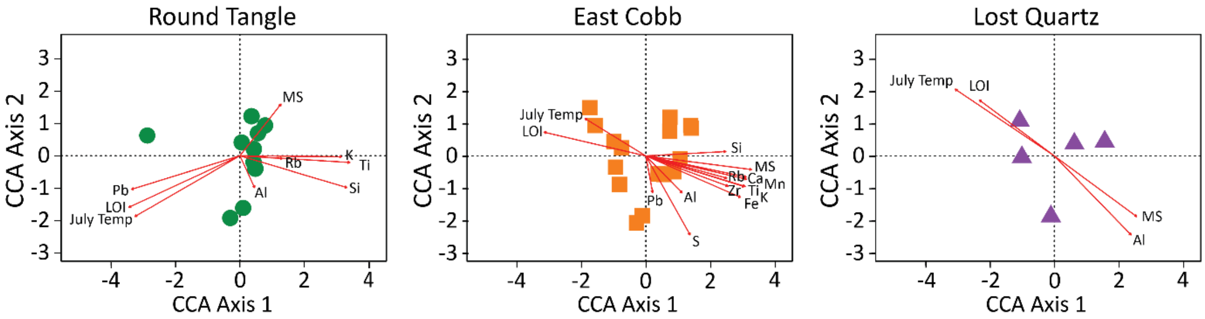

Figure B. 19 Canonical correspondence analyses (CCA) indicated the influence of July temperature and sedimentological proxies (organic content (LOI), magnetic susceptibility (MS), and ITRAX elements) on the chironomid samples, spanning the period 1901 – 2018, for each of the Alaskan lakes.

## B.13 Differences in skewness values

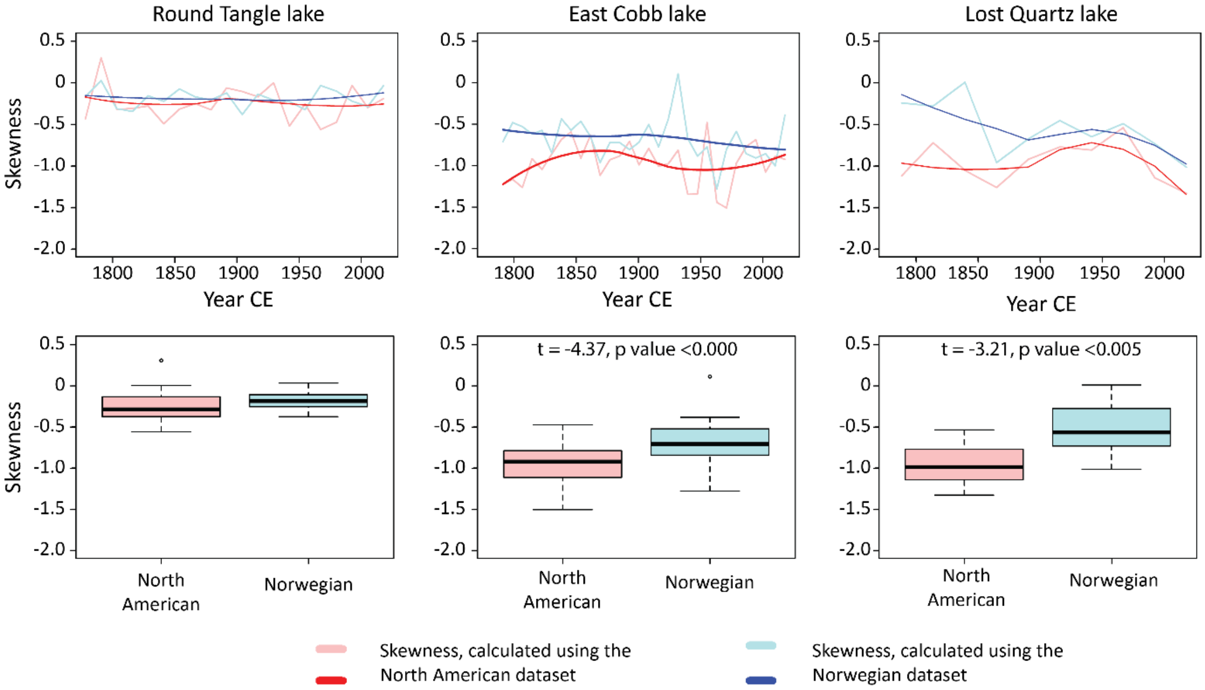

Figure B. 20 Comparing skewness outputs: skewness values were calculated using the North American and Norwegian chironomid calibration datasets. Skewness trends are displayed in the upper panels, with smoothed loess regression curves (span = 0.90). Box plots indicate the spread of values in the lower panels. T test statistics are displayed where $p < 0.05$.

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