

# Reconstructing the "push" and "pull" of climate and its impacts on subsistence cultures using paleolimnology

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# Abstract

Climate variability has influenced settlement and cultural activities of human populations for millennia, and our knowledge of the context of environmental drivers of migration can be inferred using paleolimnological techniques. We present a systematic map of literature to understand the breadth of paleolimnological research that exists on environmental change and its impact on subsistence cultures. We aim to illustrate how the "push" and "pull" of climate influenced human society over the late-Holocene. A systematic search found 68 unique relevant studies that discussed topics of human settlement and migration, stressors on the environment, and (or) ecological monitoring with respect to changes in climate using paleolimnological methods. We identified three primary themes: where people live, how people live, and how people will continue to live. Most studies took place in North America, within the last decade, and had a focus on diatoms, sediment characteristics, and climate. Topics ranged from reconstructions of changes in climate, human presence, human influence on the environment, subsistence strategies, and the importance of monitoring. We demonstrate the value of paleolimnological methods in understanding the timing of events, revealing long-term ecological trends, and providing baseline conditions for effective remediation and management purposes.

Key words: systemic map, paleolimnology, subsistence, climate, adaptation, management

# Introduction

Changes in the natural environment challenge the resilience of societies, as environmental stress can promote or inhibit adaptation to change (Diamond 2005). Food and livelihood security, in particular, can be threatened by unforeseen and gradual environmental changes that influence cultural health and continuity should adaptation to new conditions not take place within communities (Davies 1993; Newell et al. 2020). Adaptation can be defined as both short-term coping strategies as well as long-term transformations in relation to environmental changes (Davies 1993). Climate change is often a driving force that affects the suitability or practicality of a region that can either "push" human groups to leave some regions or "pull" them to move to others (Friesen et al. 2020). For example, Carto et al. (2009) suggested large-scale changes in climate during the last glacial cycle created inhospitable conditions in Africa that led to one of the earliest migrations of humans into other regions of the world. Smaller-scale changes in climate can also have push and pull effects that influence the resilience of cultural practices and the ability to adopt new strategies (Van Aalst et al. 2008); small fluctuations in precipitation, like those observed in Amazonia for example, allowed for the onset of

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agricultural practices (Bush et al. 2000). The lasting effect from a push or pull of climate is felt globally and is especially pertinent for northern regions where polar amplification of warming can amplify the influence of climate on cultural development (Wooller et al. 2018; Friesen et al. 2020).

Hunter-gatherer (subsistence) and sharing economies have been a fundamental component of the culture, identity, and sustainability of human society throughout the history of the Pleistocene era (Stutz 2012). Various economies were based on hunting, fishing, and gathering from the land, which is inherently built upon knowledge of weather processes and a resilience to disturbances to the environment. As such, unexpected changes to the environment can impact the core of the sharing economy and its dependent community (Dinero 2013). For example, warming during the time of Late Dorset presence in the Arctic (500–1500 AD) is suggested to have strongly influenced the ability to practice subsistence activities (Temple and Stojanowski 2018). Temple and Stojanowski (2018) suggested a loss in sea ice reduced walrus populations and consequently altered hunting practices and shifted diets. Presently, we are in the midst of observing warming in the Arctic that is fundamentally altering the functionality of the landscape, the ecosystem services it supports, and ultimately the activities that can be performed by Northern communities (Williamson et al. 2009). Newell et al. (2020) noted the link between health of modern Inuit and health of the landscape, as the ability to hunt and perform cultural activities is imperative for positive mental health and cultural continuity. Understanding how the Arctic has changed, and may be further affected, is therefore critical to facilitate cultural continuity in a changing environment (Chambers et al. 2004; Newell et al. 2020).

While both oral and written history provides us with an account of adaptation over a time scale of centuries, knowledge of how cultures have been affected by environmental change over millennia is more difficult to ascertain with a conventional historical review. Paleolimnological methods can extend our knowledge of past environments, and the societies that were supported, at a millennial scale. Paleolimnology is a science that relies on indicators deposited in lacustrine sediments through time (Walker 2001) and has successfully been used to understand long-term perspectives of interactions between people and the environment (Brenner et al. 2002). Millennial-scale change is inferred from chemical, physical, and biological indicators (Brenner et al. 2002), giving insight on key climatic periods such as the Mid-Holocene (6000 years ago) and the Last Glacial Maximum (21 000 years ago). Paleolimnological evidence has also complimented archaeological studies (Hadley et al. 2010) that have linked large-scale climate forcing and human migration (Friesen et al. 2020).

As the depositional environment of lakes incorporates aspects of the atmosphere and terrestrial catchment through time, lakes have often been referred to as sentinels of environmental change (Schindler 2009; Williamson et al. 2009). This methodology is therefore a powerful tool that can be used to gain insight into aspects of human societies in regions where lakes exist. Here, we undertake a systematic mapping exercise to identify how paleolimnological studies are valuable in the reconstruction of cultural groups in the face of environmental change. We aim to illustrate the ability for methods in paleolimnology to understand how human society has been influenced, and continues to be influenced, by (*i*) the push and pull of climate and its influence on migration (where people live), (*iii*) the push and pull of climate and its influence of environmentate the importance of paleolimnological research in tandem with traditional historical reviews for understanding the influence of environmental change.

### Methods

Our research topic was informed by town hall discussions held with the community of Coral Harbour, Nunavut, on 15–20 March 2019. Through community-led engagement on understanding the influence of climate change on subsistence practices, the need to synthesize and mobilize



knowledge behind the influence of climate on human society was identified. We therefore used a systematic mapping approach (Haddaway et al. 2018) to outline and synthesize how methods in paleolimnology are used in research pertaining to the impact of climate change on cultural groups. Trends in the extent, range, and nature of literature were used to identify gaps that exist in the context of research on reconstructing human settlement and subsistence activities. Our systematic process included: (*i*) the identification of the extent of research associated with both paleolimnology and human activity through a Boolean key word search, (*ii*) systematically extracting articles relevant to our identified research themes, and (*iii*) summarizing key themes in publications to identify common approaches as well as potential gaps in knowledge.

### Search strategy

Three peer-review indexes were used in the systematic mapping process: The Web of Science, PubMed, and Scopus. A string of search terms was generated to capture the research themes (Table 1); paleolimnology (paleolimnolog\* OR palaeolimnolog\*, and pal\*limnolog\* for search strings in Web of Science), human activity (settle\*, migration\*, subsist\*, hunt\*, human activity), climate (climat\*), and response (stress\*, adapt\*). Duplicated results between the three indexes were removed. The searches were restricted to articles published between 1990 and 12 December 2020 when the search was completed, the consistency of decisions was reviewed 4 May 2021.

### Inclusion criteria

Inclusion criteria were determined in advance to validate the relevance and eligibility of search results; articles needed to be a primary source and needed to employ methods in paleolimnology. Articles using similar methods (such as paleoecology) were also included as these methodologies are often used in similar contexts. Articles that simply mentioned paleolimnology (or related methods) but did not include it as part of their methodology were not included. Articles were also required to relate

Table 1. Boolean search criteria for peer-reviewed research articles relating to methods in paleolimnology applied to infer subsistence and human migration published and indexed from the Web of Science, Scopus, and PubMed databases since 1990.

Key words	Web of Science	Scopus	PubMed
paleolimnolog* OR palaeolimnolog* AND settle*	135	191	7
paleolimnolog* OR palaeolimnolog* AND settle* AND adapt*	4	5	0
paleolimnolog* OR palaeolimnolog* AND settle* AND climat* AND stress*	13	11	0
paleolimnolog* OR palaeolimnolog* AND subsist*	5	8	0
paleolimnolog* OR palaeolimnolog* AND hunt*	10	14	3
paleolimnolog* OR palaeolimnolog* AND "human activity"	68	250	3
paleolimnolog* OR palaeolimnolog* AND "human activity" AND adapt*	2	4	0
paleolimnolog* OR palaeolimnolog* AND "human activity" AND climat*AND stress*	2	13	0
paleolimnolog* OR palaeolimnolog* AND migration*	36	66	4
paleolimnolog* OR palaeolimnolog* AND migration* AND climat*	22	31	1

Note: A total of 148 articles (bold text) were fully analysed.



to the subthemes of our review (human/subsistence activity, change, resilience, and vulnerability). Lastly, only articles published in English were included.

### Article selection process

Articles were screened for relevance by means of their key words and the inclusion criteria. If the inclusion of paleolimnology or human/subsistence activity was not clear from the title or abstract, the full article was screened for key terms to determine the context. Articles that were found to fit the inclusion criteria and contained content relevant to paleolimnology and human/subsistence activity were included. Excluded articles, and reasons for exclusion, can be found in **Supplementary Table S1**. Initial search and data extraction was done by A. Covert, and consistency of decisions was checked by A. Medeiros.

### Analysis

The focus of this review was on how paleolimnology has been applied to study components of cultural activities pertaining to the subsistence economy of human populations in the late-Holocene and to map the range in which this research is covered in the literature. Meta-data were extracted from each article, including the year of publication, region of the study, notable features (themes), and the type of paleolimnological methodology employed. Once the articles from our key word search were narrowed down to those containing relevant information based on the inclusion criteria and selection process, a key word query with NVivo 12 PRO was performed. This extracted the top 100 words used in the articles to create a word cloud and identified primary themes represented in the literature. Relevant articles were relevant in more than one topic and were placed in multiple categories. Organizing the articles from our key word search based on content helped understand the context in which this area of research is available in the literature. While this is not a fully complete collection of articles that discuss this area of research, our results can help determine the range of themes that exist in the literature.

### Results

A total of 148 articles were identified using the Boolean search strategy (**Table 1**) applied to the three selected databases. Only one article was found in the search that was not accessible. Among all search criteria, 45 articles were selected from Web of Science (11 unique), 58 from Scopus (23 unique), and 2 from PubMed (0 unique). Two articles overlapped among all three databases, and 34 articles overlapped between Web of Science and Scopus. Some articles resulted from more than one combination of key words within a database and were identified in more than one Boolean search process (e.g., Web of Science counted the article by Kusimba (1999) twice, once in results for paleolimnolog\* OR palaeolimnolog\* AND subsist\* and once in results for paleolimnolog\* OR palaeolimnolog\* AND hunt\*). In these instances, articles were only counted once in the total of unique papers. We then applied the article selection and exclusion criteria to these 148 articles, which resulted in 68 unique and relevant articles that included paleolimnological (or similar) methods and subsistence practices (Supplementary Fig. S1).

When sorted by publication date, all articles were found to be published between the year 1996 to 2020, with noticeable gaps in the years 1997, 1998, and 2000 (Fig. 1a). The largest number of articles (10) were published during the year 2020. Forty-three of the 68 articles (~63%) were published in the last decade (between 2011 and 2020). When sorted by geographic region (Fig. 1b), of the 68 articles, one studied Oceania, two studied South America, three studied Central America, seven studied Africa, eight studied Asia, 19 studied Europe, and 28 (41.18%) studied North America. The Canadian Arctic was the most studied region (30% of articles).

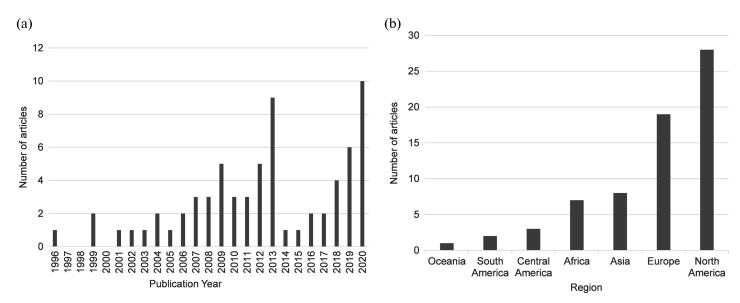


Fig. 1. The number of relevant articles identified during our systematic review process (a) organized by year of publication and (b) organized by region of study.

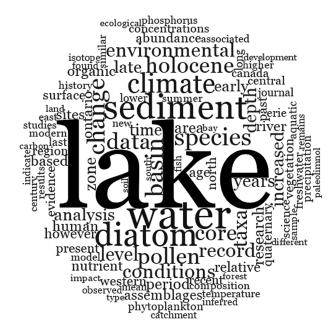


Fig. 2. Word cloud displaying the top 100 key words (>3 letters) used among relevant articles identified in our systematic mapping process.

The top 100 key words (>3 letters) common across the 68 articles identified in our systematic mapping process identified key commonalities between the studies (Fig. 2). The five most common words used were: lake, water, diatom, sediment, and climate. We then collated three thematic areas to form the scope of our discussion: where people live, how people live, and how people will continue to live (Table 2). Studies that focused on where people live included reconstruction of large-scale

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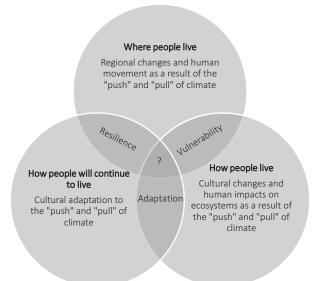


Fig. 3. Thematic areas identified in the literature that utilize paleolimnological methods to examine how environmental change impacts human society.

changes in climate and the effect on human occupation and migration. Studies that focused on how people live included reconstructions of changes in ecosystems as a result of subsistence activities, changes in the environment as a result of anthropogenic stressors, impacts of both climate and anthropogenic stressors on human activities, cultural changes due to environmental change, and the onset of new subsistence strategies. Studies that focused on how people will continue to live used paleolimnological methodologies to examine water management, wildlife management, and vegetation history reconstructions. A variety of physical, chemical, and biological indicators were used in the studies included in our systematic map (see **Supplementary Material**). Most articles focused on reconstructing change—climate patterns, human activities, or identifying the need for paleolimnology to examine change in the context of a sustainable future (Fig. 3).

### Discussion

Informed by our systematic mapping process, we discuss how paleolimnology, and similar methodologies, have provided context to our knowledge of the push and pull of climate and its impacts on human society. We focused on articles identified in our results and also highlight future implications, applications, and insights on the use of paleolimnological methodology for increasing our understanding of how climate variability may affect human society in a warming future.

### The push and pull of climate over the past millennia

Climate change is a key factor in the spread of human populations across the globe, influencing environments that have predicated the migration of both species and peoples; migration is often an adaptive response to the push and pull factors of climate (Marr 2015). Large-scale changes in climate, such as significant warming and cooling periods, have been well researched through paleo-inferences of isotopic geochemistry and biological indicators in lacustrine sediments (Reheis 1999; Stefanova et al. 2003; Lozhkin and Anderson 2013; Adams et al. 2019). Twenty-six of the relevant 68 articles from our key word search studied large-scale changes in climate using geochemical and (or) biological indicators. Paleoenvironmental reconstruction of glacial change (Vegas-Vilarrúbia et al. 2013),



Table 2. Key themes identified by thematic coding of relevant articles from the systematic mapping process

Theme	Papers
Where people live—the push and pull of climate over the past millennia	
Large-scale changes in climate	26
Human occupation	18
Early human migration	12
How people live—how the push and pull of climate has influenced culture	68
Ecosystem changes resulting from anthropogenic stressors	36
The impact of both climate and anthropogenic stressors	23
Cultural changes resulting from environmental change	9
How people will continue to live—the use of paleolimnological methods to anticipate impacts	34
Water management	23
Wildlife management	6
Vegetation history reconstructions	5

**Note:** Themes are organized by primary topic (bold text) and their subthemes are identified. Some papers discussed more than one primary theme as identified in our thematic process.

southern oscillation (Rodysill et al. 2012), and hydrologic change (Magyari et al. 2009) all focus on large-scale changes associated with threshold shifts in biological indicators on a millennial scale. Paleolimnological studies have also supported revision of previous estimates of when large-scale changes occurred (Hoelzmann et al. 2001; Wolfe et al. 2012) as well as the amplitude and timing of ecosystem response (Wolfe et al. 1996). This has proven to be important for understanding the impact of climate forcing on biological change, as different biota have different thresholds at which they can tolerate change (Stefanova et al. 2003). Different taxa have differences in their optima and tolerance of environmental conditions in which they operate (Williamson et al. 2009).

While paleolimnological techniques can effectively reconstruct past environments, archaeological evidence is sometimes paired with these inferences to specify the presence of early human populations (Tudryn et al. 2013; Temoltzin-Loranca et al. 2018). Depending on the subsistence strategies employed, a region's climate is known to influence whether the location is suitable for occupation (Liu et al. 2020), but direct evidence of human occupation is less apparent, especially in studies that deploy a single paleolimnological proxy. Paleolimnology has also been used to help confirm previous human occupation dates that were solely dated using archaeological data (Hoelzmann et al. 2001). While 18 of the 68 articles reviewed discussed human occupation, reconstructing human occupation was often not the main topic of focus. Human occupation was often discussed coincidently alongside other historical environmental information. For example, Schmidt et al. (2019) aimed to reconstruct the onset of stable freshwater conditions on Ruben Island, Japan, using multiproxy paleolimnological records, but they also discovered the appearance of the earliest settlement of sedentary hunter-gatherer populations (5000–4000 cal. Years BP).

The movement of early humans can largely be tied to environmental changes, especially when a region is no longer fit for occupation. For example, Inuit who rely on seal hunting are required to migrate further north when the sea ice is too thin to be able to safely hunt (Hadley et al. 2010). Twelve of the 68 articles from our key word search discussed human migration, often using paleolimnological techniques alongside archaeological evidence. For example, Hoelzmann et al. (2001)

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identified four settlement phases around a freshwater in the Eastern Sahara (Africa) during the Holocene epoch using a multi-proxy reconstruction approach of carbonates, oxygen and carbon isotopes, and diatoms, paired with the dates of stone tool remains. The chemical composition of the sediment core allowed for the inference of lake stages throughout history and provided context for why groups settled and abandoned the region in cycles. Indeed, several studies reconstructed the timing of human migration by inferring the timing of abandonment (Hoelzmann et al. 2001; Filippelli et al. 2010; Temoltzin-Loranca et al. 2018). For example, Filippelli et al. (2010) inferred abandonment of a once-continuous human occupation from the recovery of vegetation at the site.

### How the push and pull of climate has influenced culture

A common theme in the field of paleolimnology is how anthropogenic stressors, such as the arrival of settlers or increased human development in lake basins, have led to ecological changes. Climate is often an integral component of understanding ecological stress, as climate factors can influence both the environment as well as human society (Todgham and Stillman 2013). We found that topics relating to how human society was influenced in relation to climate was more commonly covered in the literature than studies relating to where people lived (Table 2). Thirty-six articles from our key word search discussed how people lived and the impacts that they had on the environment. Indigenous cultures in the Canadian Arctic, in particular, have received large amounts of recent attention. This is not unexpected as climate change is significantly impacting the cultural continuity of the Indigenous Peoples of the Canadian Arctic (primarily Inuit) and the sustainability of their subsistence-sharing economy (Hadley et al. 2010; Michelutti et al. 2013). Paleolimnology can also identify impacts by subsistence/anthropogenic stressors in what were once thought to be pristine environments (Zawiska et al. 2013). For example, whaling camps by Thule Inuit impacted the water quality and ecology of high Arctic lakes as a result of constructing their settlements from nutrient-rich whale bones that over time leached nitrogen into freshwater bodies, altering their chemical composition (Douglas et al. 2004). The Thule society's impact continues be evident despite these lakes having been abandoned centuries ago due to the legacy of nutrient enrichment that continues to leach into the water at these sites (Douglas et al. 2004).

Freshwater lakes are under threat globally from both natural and anthropogenic stress (Mills et al. 2017). As these systems are important for both cultural and subsistence practices, the environment (climate) can have a large influence on settlement and migration. Twenty-three articles from our key word search discussed the impact of both climate and anthropogenic stress on subsistence lifestyles. For example, lake-level is often associated with climate, which can influence agricultural practices as well as the presence of subsistence prey (Sedov et al. 2010). Paleolimnological inferences have documented examples of human society that transitioned from a low-impact nomadic lifestyle to a high-impact and overly consumptive sedentary lifestyle. These transitions frequently depend on the magnitude of the push or pull of climate on the ecosystem or ecological services that cultural activities depend on and the timing of climate events (Junginger and Trauth 2013). Water collection, hunting, fishing, gathering, and agriculture are all environment dependent, and adaptations to these practices are frequently tied to changes in climate, and more recently, technological advancements. While migration is a common response to environmental stress (Shaw 2016), adaptation or the transition to different subsistence practices was discussed in nine articles (Table 2). For example, Feeser et al. (2016) described the transition to animal husbandry inferred with the use of pollen during the Neolithic epoch (7000-4000 BP).

#### The use of paleolimnological methods to anticipate impacts

The context of how lakes have changed from their natural or predisturbed state provides key information for remediation projects and the creation of freshwater management plans. As such,



paleolimnology can ultimately be considered an effective tool to achieve environmental sustainability (Saulnier-Talbot 2016). Environmental managers are better able to understand the trajectory of ecosystem change with a baseline context of the predisturbance state. This knowledge can then be applied to the management of ecosystem services that communities are reliant upon (Sullivan and Charles 1994). The use of paleolimnology to qualify freshwater sustainability was a common theme discussed in the literature, with 23 articles discussing the application of paleolimnological methods in the realm of water management. Popular themes identified focused on the influence of anthropogenic activities and how they have modified lake catchments (Magyari et al. 2009; Shaw Chraïbi et al. 2014), as well as changes in ecological status since the industrial revolution (Kirilova et al. 2009).

The reconstruction of lake trophic structure can be a determining factor for inferences on the population dynamics of wildlife, especially where census data do not exist for a species (Hargan et al. 2019). Similar to the migration of humans, the migration of sensitive species can be tracked through paleolimnological inferences of limnological conditions (Hobbs and Wolfe 2008). Six articles from our key word search discussed the application of paleolimnological methodologies in the realm of wildlife management. A reoccurring theme in these articles was reconstructing limnological conditions to assess and track how habitat conditions of endangered fish species have changed in freshwater lakes (Selbie et al. 2007; Ginn et al. 2008). As ecotones are expected to shift with an anthropogenic warming, employing paleolimnological techniques will be very valuable to understand wildlife population shifts and to better protect species against habitat threats. Ultimately, the history behind the evolution of natural systems is crucial for assessing conservation priorities (Zawiska et al. 2013).

While pollen analysis is commonly used in paleolimnological reconstructions, studies that specifically focus on changes in vegetation that may influence human society were less commonly found in the literature. Five of the 68 articles in our study focused on the application of paleolimnological methodologies for identifying the onset of new species (e.g., the introduction of invasive species), and (or) changes in climate and post-glacial hydrologic change with respect to vegetation cover. Paleolimnological methodologies are also useful to simply reconstruct changes in the dominant types of vegetation (Zhilich et al. 2017), which can ultimately provide reference conditions of a region for restoration projects to keep in mind.

# New approaches in paleolimnological assessment of the Anthropocene

The use of emerging techniques with an interdisciplinary focus, as well as transdisciplinary methods, have expanded our knowledge of human settlement. For example, the inclusion of zooarchaeological archives along with an analysis of lipid biomarkers and isotopic geochemistry of sediments allowed Connolly et al. (2019) to infer human settlement locations back to the Paleolithic (late Pliocene) era, providing evidence of some of the very first sites of human occupation. Indeed, as Smol (1990) noted, paleolimnology as a method in the realm of aquatic sciences has substantially advanced; we can still see that this holds as true in 2020 as it did in 1990. The number of publications on reconstructing subsistence cultures has increased dramatically in recent years (Fig. 1a). While our systematic mapping approach captured some new and novel approaches (such as Connolly et al. 2019), we undoubtedly missed studies that may have made inferences from lacustrine sediments using different methods deploying different terminology. For example, advances in fecal biomarkers (Guillemot et al. 2015; Zocatelli et al. 2017) and sedimentary DNA (Domaizon et al. 2017) have opened new and interesting opportunities for investigating long-term influences of humans on the environment. Yet, our systematic approach did not capture these studies, as they did not include key words associated with paleolimnology. Studies that are either primarily driven by an archaeological focus (e.g., Zocatelli et al. 2017), or based on former lacustrine sediment archives (Labarca et al. 2020) are particularly difficult



to capture in a review of paleolimnological approaches; while they use lacustrine archives, they do so in a unique way for a completely different discipline. Indeed, our systematic map of literature notes that while paleolimnology can be used to infer the influence of climate on subsistence cultures, these inferences are often only made in a direct way when a combination of discipline-specific methods are deployed (e.g., archaeological evidence). The future of paleolimnological research may actually reside in the ability for researchers to have an interdisciplinary focus and combine innovative approaches to reconstruct past environments.

# Conclusion

We found 68 articles that demonstrated the usefulness of paleolimnological methodologies in reconstructing subsistence lifestyles throughout history using a systematic mapping process. Three key themes were identified and further organized by subtheme: the push and pull of climate over the past millennia; large-scale changes in climate, human occupation, and early human migration, how the push and pull of climate has influenced culture; ecosystem changes resulting from anthropogenic stressors, the impact of both climate and anthropogenic stressors, and cultural changes resulting from environmental change, and the use of paleolimnological methods to anticipate impacts; water management, wildlife management, and vegetation history reconstructions.

Our review revealed that a comprehensive collection of literature exists that demonstrates paleolimnological methods are an effective tool at providing insight into how climate has influenced aspects of the subsistence culture; 63% of the relevant articles from our systemic mapping process were published in the past decade. This suggests that the employment of paleolimnological techniques has become more common in subsistence-related research. These records have changed our perception of subsistence cultures and our transition to modern-day techniques. Paleolimnological methods can also aid in the understanding of the timing of events and baseline/reference conditions for water bodies, wildlife populations, and vegetation types. This knowledge is crucial for effective remediation and management. Of the 10 articles published in the year 2020, all studies explored a unique research scope and topic; a common characteristic found was that paleolimnological methods provide quantitative context for past environments based on physical data. We note that our systematic mapping process has likely missed key studies that use unique and novel approaches, especially those that deploy transdisciplinary approaches to understanding past environments. Ultimately, the future of paleolimnological research likely lies with interdisciplinary research focused on understanding how past societies were either resilient or adaptable to environmental change. This knowledge is essential should we wish to achieve environmental sustainability while we continue to be pushed and pulled by climate.

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# Author contributions

ASM conceived and designed the study. AEC performed the experiments/collected the data. AEC analyzed and interpreted the data. ASM contributed resources. AEC and ASM drafted or revised the manuscript.

# **Competing interests**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability statement

All relevant data are within the paper and in the Supplementary Material.

# Supplementary Materials

The following Supplementary Material is available with the article through the journal website at doi:10.1139/facets-2021-0088.

Supplementary Material 1

Supplementary Material 2

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