# Coprophilous fungi as paleo indicators for moose presence after introduction to Newfoundland

by
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# Abstract

To study the non-native moose (*Alces alces*) population on Newfoundland, successfully introduced in 1904, a paleolimnological approach was used: coprophilous fungal spores were isolated in two $^{210}$Pb-dated lake sediment cores to compare with historical abundance numbers for moose. We predicted that, as commonly practiced with megafauna, coprophilous spores would correspond with abundance data. Cores from two ponds were sectioned at 0.25 cm intervals resulting in ~3-4 years in each slice of sediment from ~1850 to 2021. The counts were numerically treated for each spore type and the spore total by two different methods in 24 samples from each core: 1) as a percent of the tracer *Lycopodium* present and 2) as an accumulation rate. Coprophilous spores counted in this study include *Podospora*, *Sordaria*, *Sporomiella*, *Arnium*, *Coniochaeta*, *Ascodesmis*, and *Delitschia*. Results corresponded between moose abundance and spores for Little Crow Pond, but were less promising for Pitcher Pond, possibly due to dating error. Our prediction was supported by the similar trends of coprophilous spore abundance and moose population estimates through time, serving as a validation of these spores as a proxy for large herbivores. With further research, this method may be applicable to the native caribou (*Rangifer tarandus*).



**Keywords:** coprophilous spores, moose, large herbivores, paleolimnology, Newfoundland

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I would like to respectfully acknowledge the territory in which this study took place as the ancestral homelands of the Beothuk, and the island of Newfoundland as the ancestral homelands of the Mi’kmaq and Beothuk.

# Table of Contents

# List of Tables

# List of Figures

# List of Acronyms

| | |
|---|---|
| cf. | *conferre* |
| CIC | constant initial concentration |
| CRS | constant rate of $^{210}$Pb supply |
| KOH | Potassium hydroxide |
| LC | Little Crow Pond |
| PP | Pitcher Pond |
| NPP | Non-pollen palynomorph |
| *sed*aDNA | sedimentary DNA |
| SPT | sodium polytungstate |

# List of Appendices

# Chapter 1: Introduction and thesis overview

## *1.1 Ecosystem services provided by large herbivores*

Populations of large herbivores are declining worldwide without a thorough understanding of their role in ecosystems (Forbes et al., 2019). Anthropogenic activities paired with slow birth rates, expansive ranges, and high-energy requirements have largely contributed to the decline of large mammals (MacDonald et al., 2013). This is concerning, given the few studies demonstrating the vital roles large herbivores play in ecosystems globally, such as resistance and species resilience to environmental change (Forbes et al., 2019), plant regeneration after grazing (Forbes et al., 2019; Ellis & Leroux, 2016; Zhong et al., 2014), and nutrient cycling (Doughty et al., 2016; Bump, 2018; Forbes et al., 2019; Benbow et al., 2020), including influencing the carbon cycle (Leroux et al., 2020; Schmitz & Leroux, 2020).

### *1.1.1 Resistance and resilience*

Although the loss of large herbivores can be detrimental to the populations of some species (Bump, 2018; Huntzinger et al., 2004), there are other species, often non-native species, whose populations increase (Strong & Leroux, 2014; Wardle et al., 2011). Gains and losses of species are generally studied separately, even though both affect ecosystem functioning and often occur simultaneously (Wardle et al., 2011). For example, in Newfoundland, there has been, independently of each other as they have different dietary niches, an increase in the introduced moose population, and a decrease in native woodland caribou (*Rangifer tarandus terra-novae*). Therefore, while many other areas worldwide are losing large herbivore populations, Newfoundland is experiencing a rapid growth in large herbivore numbers over the 20$^{th}$ century,

much like white-tailed deer (*Odocoileus virginianus*) in continental North America with the loss of top predators (Weiskopf et al., 2019).

One of the clearest examples of the web of interactions between predators, prey, and plant assemblages was the result of the reintroduction of wolves to Yellowstone National Park, which led to the recovery of quaking aspen (*Populus tremuloides*) as the presence of wolves decreased the elk (*Cervus canadensis*) population, which had been browsing intensely on young aspen (Painter et al., 2015). As wolves decreased the population size of elk, which had foraged heavily on aspen, the aspen recovred (Painter et al., 2015). This is one of two competing hypotheses, that predators (wolves) have a consumptive effect through consuming prey (elk), thus impacting non-consumptive effects, like foraging, by prey (elk) (Pessarrodona et al., 2019). The interplay between elk and aspen also involves, but is not limited to fire regimes, increasing bison population, warming climate, land use, and hunting outside the park (Painter et al., 2015). Relations between these species also illustrates the dynamic that species gains (elk) and loss (wolves) can have on other species (aspen), and on an ecosystem as a whole.

### *1.1.2 Role in plant regeneration*

Browsing and grazing by large herbivores can promote plant defensive responses (Huntzinger et al., 2004; Forbes et al., 2019; Nosko et al., 2020) whereas in their absence these morphological (Huntzinger et al., 2004; Massey et al., 2007) and chemical (Huntzinger et al., 2004; Lev-Yadun & Gutman, 2013; Fabisch et al., 2019) responses may decline. For example, Huntzinger et al. (2004) found that after a year of protection from grazing, whistling-thorn acacia trees (*Acacia drepanolobiom*) decreased both their chemical, morphological, and mutualistic defenses (Huntzinger et al. 2004). Such decreases in plant defenses, can have far reaching

ecosystem consequences. For example, Palmer et al. (2008) found that African savannah ant and whistling-thorn acacia tree mutualism declined with the removal of herbivores over 15 kg. Also, in the ant-Acacia mutualistic relationship, ants bite browsers, and the tree provides food (nectar) and shelter (domatia). In the absence of browsing by large herbivores, the trees produce less food and shelter for the ants, and with the protection of less ants, trees were invaded by boring beetles which limited their growth and increased mortality rate (Palmer et al., 2008). Thus, large herbivores can mediate complex interactions between plants, their mutualists, and other herbivores.

Other mechanisms by which large herbivores mediate plant community level interactions include preferential browsing and grazing, trampling via migrations, and impacts general life cycle (from seed germination to removal by trampling) (Forbes et al., 2019). For example, seeds and seedlings are assisted by large herbivores that suppress small mammals that consume them, and therefore increase seed germination rates (Forbes et al., 2019). Large herbivores can preferentially consume nutrient-rich species, resulting in an alteration of the species composition in an area, as well as nutrient cycling (Ellis & Leroux, 2016). Moose (*Alces alces*) in Newfoundland, for example, have changed the understory compositions of forests by preferentially consuming juvenile Balsam fir (*Abies balsamea*), producing post-disturbance regeneration issues that results in the replacement of Balsam firs with the growth of tree species that can sprout from stumps, and are shade intolerant (McLaren et al., 2009a). While preferential browsing by herbivores can lower plant diversity, the removal of species can then generate beneficial conditions for other species (Zhong et al., 2014). For example, preferential browsing of conifers by moose benefits spruce species (*Picea* spp.), creating moose-spruce savannas, and other species that prefer more open habitats (Gosse et al., 2011).

### *1.1.3 Nutrient Cycling*

*Megafauna*

The importance of large mammals as drivers in ecosystem nutrient cycling is evident from examining evidence of their role in ecosystem processes prior to the Quaternary extinctions (Doughty et al., 2016). With the loss of megafauna, models predicted a ~5% decline in terrestrial and an ~8% decline in oceanic nutrient cycling (Doughty et al., 2016). For example, phosphorus cycling was predicted to be decreased by 77% from previous estimates due to a decrease in large marine mammals that moved nutrients upward within oceans (Doughty et al., 2016). Oceanic megafauna also played a role in nutrient cycling through carcass deposition on the seafloor which has been found to be significant (Benbow et al., 2020). Undoubtedly, large herbivores today are important for nutrient cycling within ecosystems like past megafauna, and population fluctuations including introductions, growth, and declines, will affect ecosystem nutrient transformations and availability. These effects of large animals on nutrient cycling have prompted some to advocate for trophic rewilding to restore animals and the functions they facilitate (Schmitz et al., 2023).

*Moose*

Moose are biotic vectors that contribute to nutrient cycling by moving nitrogen from aquatic to terrestrial ecosystems through consumption of aquatic macrophytes and excretion in terrestrial areas (Bump, 2018). Moose are subject to a variety of mortality factors including predation by predators such as wolves (*Canus lupis*), mountain lions (*Puma concolor*), and juveniles by coyotes (*Canus latrans*), as well as disease and abiotic mortality factors (e.g. fire, starvation, or very deep snow) (Bump, 2018). For example, in 2012, the northeastern Minnesota,

USA moose population of 3,500 to 4,000 was extirpated in part due to warming temperatures of 2-3˚C (Bump, 2018). The absence of moose in this area lead to a decrease in nutrient repletion in aquatic-terrestrial environments (Bump, 2018). In contrast, when natural predators of herbivores are removed (e.g., wolf extirpation), large herbivores can over forage leading to a decrease in nutrient cycling (Bump, 2018; Forbes et al., 2019).

*Carbon cycling*

Effects of large herbivores on carbon cycling varies widely among ecosystems and species and it has been demonstrated that higher trophic levels impact ecosystem functioning (Forbes et al., 2019; Leroux et al., 2020; Schmitz & Leroux, 2020). This is because on a pyramidal ecosystem structure, animals can have top-down direct and indirect effects on the carbon cycle (Schmitz & Leroux, 2020). For example, large herbivores can impact the carbon cycle through selective foraging, feces, and urine deposition, trampling, and their carcasses (Leroux et al., 2020). These actions and processes directly influence carbon cycling by affecting nutrient storage, plant growth and plant composition. Through browsing, large herbivores such as moose, can impact carbon sequestration and temperatures at the same time. For example, with decreased tree biomass due to browsing, less carbon is stored in trees, and albedo is increased because of reflectivity of solar energy (Salisbury et al., 2023). Large herbivores directly influence soil by compaction through trampling and forest vegetation communities by selective feeding (Leroux et al., 2020). With a warming climate, the question of the importance of large herbivores in ecosystem carbon sequestration becomes vital since they have been thought to be an impediment to carbon storage due to the space they require for feeding (Schmitz et al., 2018).

### *1.2 Temporal changes in large herbivore populations across North America*

Generally, large herbivore populations have been declining in recent years, due to climate warming and habitat transformation (which are related to one another as well). These changes have decreased biodiversity, including that of large herbivores (McGill et al., 2015). Changing herbivore abundances are largely based on short-term monitoring windows that have been gathered over a few surveys within the last 100 years. A crucial part of understanding ecosystem services provided by large herbivores and thus potential losses and changes in ecosystem nutrient cycling is understanding historical population sizes and distributions.

With increasing temperatures and habitat fragmentation, barren ground caribou (*Rangifer tarandus*) populations have declined more than the variability of natural traditional fluctuations allow, by ~57% in their ranges in Alaska, Canada, Greenland, Scandinavia, and Siberia (Vors & Boyce, 2009). Caribou are the last remaining species of large ungulates to migrate in the Northern hemisphere, since bison (*Bison bison*) and saiga antelope (*Saiga tatarica*) no longer migrate due to anthropogenic land use (Vors & Boyce, 2009). Caribou are a vital species to the Inuit, for ecological, emotio-social, and cultural reasons, as well as a food source (Borish et al., 2021). Caribou are part of the nitrogen cycle in the tundra of Canada, and with declining populations this may impact nutrient turnover, as well as species richness (Vors & Boyce, 2009). Past caribou abundances prior to the 1970's are estimated from Indigenous leaders' recollections, the traditional names of places for areas with higher or lower abundances, and hoof scars present on spruce tree roots (Gunn, 2011). While these yield population estimates, longer-term population data would provide a fuller picture of natural fluctuations and potential drivers of population dynamics.

30 million American bison used to roam and migrate across tallgrass prairies of the North American plains but change in use of land for farms has ended the great migrations of bison and limited their range. Bison numbers drastically decreased in the late 1800's after genocide by American settlers for food, hides, to clear land for railroads and farms, and to prevent natives from hunting them (Barnard, 2020). Today, there are ~400,000 bison, only ~30,000 of those being wild while the rest are privately owned (Barnard, 2020). Past abundances have been estimated from the fossil record and using dated sites, which has inaccuracies due to incorrect taxonomic identification and geologic processes of erosion, weathering, and depositional gaps in the record (Wendt et al., 2022). A newer method by Martin et al. (2023) has combined multiple fields including archaeology, paleontology, and ecology that incorporates the fossil record, first-hand accounts, online data, and literature in a metadata set to complete an estimate of bison abundance. Bison are an example of how large herbivores are ecosystem engineers through wallowing, which decreases arthropod abundance while active, but afterwards increases abundance and diversity of arthropods (Nickell et al., 2018). Furthermore, bison grazing and wallowing have positive effects on bird species, by increasing arthropods, an important food source for birds (Nickell et al., 2018). The importance of bison on tallgrass prairie ecosystems underscores the importance of managing them, and possibly reintroductions.

As can be seen from caribou and bison in North America, they play specific key roles in ecosystems that are irreplaceable. Caribou are culturally important to Indigenous people and cannot be replaced by deer, and bison wallow while cattle do not (Borish et al., 2021; Nickell et al., 2018). Therefore, it is important to conserve these species as their numbers are declining. A vital tool in properly managing abundances of large herbivores is accurate population or

abundance data that allows for understanding of past population drivers that can be applied as populations decrease, temperatures increase, and landcover and diversity changes.

### *1.3 Paleolimnology*

A lake is an enclosed body of water that is surrounded by land, and through depositional processes sediments accumulate on a lakebed (Cohen, 2003). Paleolimnology uses lake sediment cores to reconstruct past environmental conditions based on biological and chemical information deposited and preserved in the lake sediments over time (Smol, 2017; Smol, 2022). This relies on the Law of Superposition, that older sediments are buried beneath younger ones, thus yielding a core column that has the youngest material on top and oldest on the bottom (Smol, 2017). Various inputs result in the accumulation of sediments and other materials, like feces, microfossils, spores, and pollen, that can be extracted and quantified from a sediment core (**Figure 1.1**). These inputs are used as proxies, which indicate specific conditions at the time of deposition. While past environments are reconstructed from core samples, they are by no means complete or infallible, and are very closely linked to the temporal resolution of the sediment core gained from a chronology.

In the past, lake sediments were dated using varves (annual laminations of sediment) when present, or sedimentary markers like pollen or diatoms to determine age (Schelske et al., 1994). Today, common sediment core dating methods for recent sediments, 0-150 years, include using the radioisotope $^{210}$Pb, which has a half-life of 22.5 years and is part of the $^{238}$U decay series. It decays from $^{226}$Ra and is deposited in lakes from the atmosphere through precipitation or dry deposition (Appleby, 2001). A timeline or chronology is determined from $^{210}$Pb activities using models like CRS (constant rate of ($^{210}$Pb) supply) and CIC (constant initial ($^{210}$Pb)

concentration) (Appleby, 2001). The CRS model works best with uninterrupted sediment accumulation rates and is the most commonly used sediment core dating method (Appleby, 2001). Additionally, the artificial fallout radionuclides $^{137}Cs$ and $^{241}Am$ can be used as reference points that allow confirmation of the $^{210}Pb$ chronology (Appleby, 2001). Artificial fallout radionucleotides are the result of nuclear weapons testing, and therefore can act as markers for the height of nuclear weapon testing in North America in the early 1960s, or nuclear accidents as with Chernobyl in 1986 (Appleby, 2001).

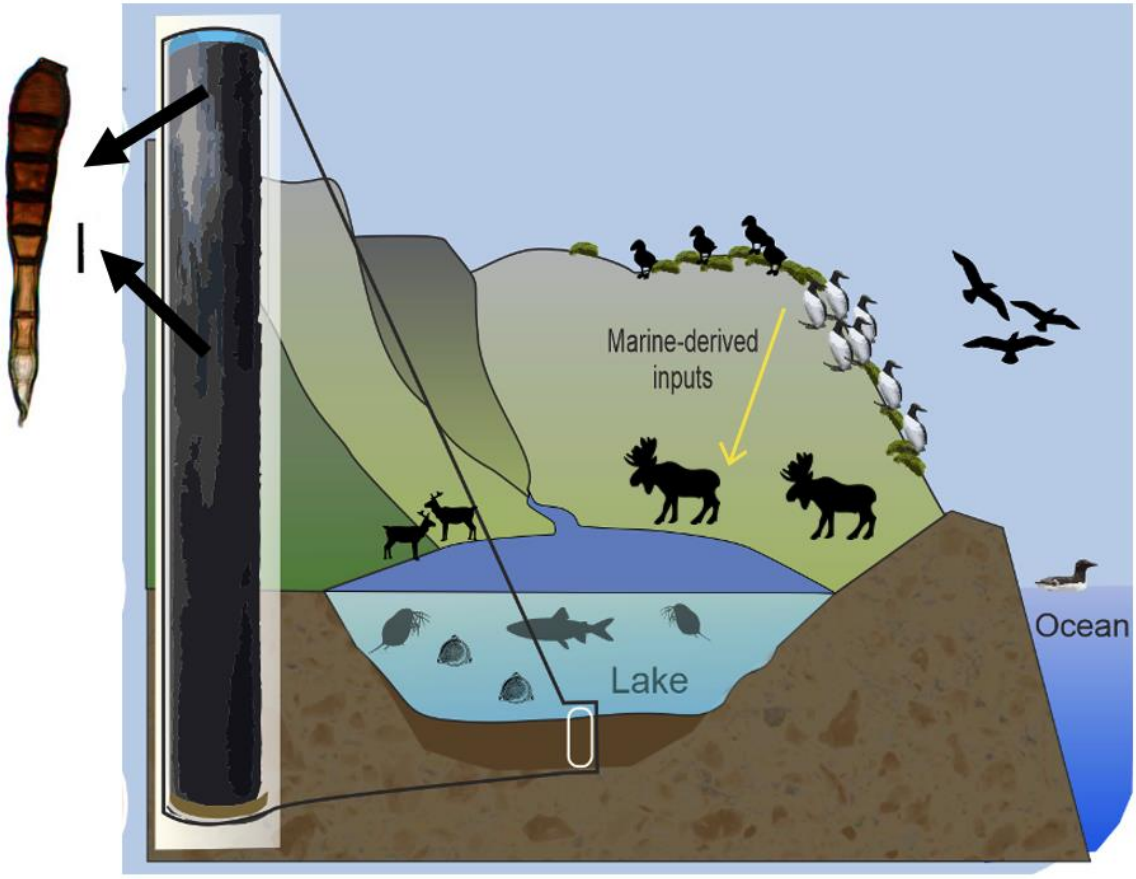



**Figure 1.1.** Fungal spores and other inputs from animals and the surrounding environment are deposited into sediments within lakes. Sediment cores, shown on the left, are collected from the pond bottom. From these sediments, coprophilous spores, like the one pictured on the far left, can be extracted. Organisms in the figure are not drawn to scale. (Courtesy of and adapted from Kathryn Hargan and Gelorini et al., 2012).

Paleolimnological sediment proxies are commonly used to reconstruct herbivore populations (**Table 1.1**). There is no "perfect proxy" as they all come with different pros and cons, which must be considered with respect to the study's research questions and objectives. Thus, more studies are incorporating multiple proxies to further validate their results (Gill et al., 2009; Graham et al., 2016; Rozas-Davila et al., 2021). For example, dung beetles are both trace fossil indicators for climate conditions and indicative of large herbivores. With a higher abundance of beetles, it is assumed that more dung was present in the past indicating a higher abundance of herbivores (Sanchez et al., 2010). Diatom assemblages are used as indicators of past environmental conditions and can corroborate other proxies used in multi-proxy studies tracking ecosystem changes which may have impacted large herbivores (Graham et al., 2016). They are not, however, directly linked to large herbivores. Fecal lipids are an emerging paleo proxy that allows for the tracking of specific species abundances over time (Gallant et al., 2020). They are limited by pre-screening to differentiate species present, as well as requiring a time consuming and precise processing method. Pollen assemblages are commonly used as past climate indicators, and therefore are not directly tied to herbivore presence (Graham et al., 2016). The use of pollen is also limited by species preserved and identified and requires a lengthy processing method and counting. Like fecal lipids, *sed*aDNA is another emerging paleo proxy that can track changes in species over time. This proxy is limited by contamination, limited taxonomic resolution, and a lack of taphonomic understanding (Edwards, 2020). Sub-fossilized bones indicate the presence of species but can be sparce and do not provide abundance numbers, and therefore provide limited data beyond that (Baker et al., 2013). Coprophilous spores will be discussed at length in the next section.

**Table 1.1.** Paleolimnological sediment proxies for tracking large herbivores back in time.

| Proxy | Uses | Pros | Cons |
|---|---|---|---|
| Dung beetles | Trace fossil indicator for herbivores in specific climates (Sanchez et al., 2010) | Size can indicate herbivore size<br>Abundance of beetles reflects abundance of herbivores (Sanchez et al., 2010) | Not always preserved due to taphonomical processes<br>Lack of preservation due to weathering<br>Unfavorable environmental conditions (Sanchez et al., 2010) |
| Coprophilous spores | Indicate past large herbivore presence (Baker et al., 2013) | Relatively easy to identify<br>Preserved well due to cell walls (van Asperen et al., 2021) | Reliant on transport mechanisms<br>Identification still developing<br>Little taphonomy understanding<br>Lack of quantitative reconstructions (Baker et al., 2013) |
| Diatoms | Indicate past climate conditions & ecosystem changes (Graham et al., 2016) | Assemblages indicate temperature and ice-cover (Hargan et al., 2016)<br>Abundant, preserve well, common across all ecosystems | Not directly linked to herbivores |
| Fecal lipids | Usable for tracking the colonization, extinction, or spreading of species (Gallant et al., 2020) | Source/species specific (Gallant et. al., 2020) | Pre-screening to differentiate species to only those present (Harrault et al., 2019)<br>Time consuming and precise processing required |
| Pollen | Indicate past climate conditions (Graham et al., 2016) | Indicate climate conditions (Schroeter et al., 2020) | Limited to preserved and identifiable species<br>Processing & ID time consuming<br>Not directly linked to herbivores |
| *sed*aDNA | Track changes in species over time by examining biological matter (Duda et al., 2021) | Includes full range of taxa (Edwards, 2020) | Sample contamination<br>Limited taxonomic resolution<br>Lack of taphonomic understanding (Edwards, 2020) |
| Sub-fossilized bones | Indicate past large herbivore presence (Baker et al., 2013) | Direct evidence of specific species present (Baker et al., 2013) | Does not allow for estimates of population, distribution range, or exact dates of colonization/extinction/spreading (Baker et al., 2013)<br>Can be scarce |

### *1.4 Coprophilous spores*

The sub-fossil remains of 'non-Pollen Palynomorphs' (NPPs), were first used in 1968 by the Hugo de Vries-Laboratory with Quaternary sediments and was furthered by Bas van Geel in 1972 (Miola, 2012). Non-pollen palynomorphs are so named because they are sub-fossils often encountered on microscope slides prepared for pollen analysis, yet they are not pollen. There are now more than 1300 described NPPs that include fungi, cyanobacteria, invertebrates, and algae (Miola, 2012). One group of NPPs are the spores from fungi that grow on animal dung, commonly called coprophilous spores or dung fungal spores, which have traditionally been used as a proxy for estimating the abundance of large herbivores or megafauna (see review by van Asperen et al., 2020). Dung fungal spore abundances are usually represented as a percentage of total pollen sum and is the basis for herbivore abundance estimates (van Asperen et al., 2020).

Spores are produced as part of the sexual reproduction of the fungus and "…serve as vehicles for transmitting spores through space and time" (Watkinson et al., 2015). There are three fungal phyla that are coprophilous: *Ascomycota*, *Basidiomycota*, and *Zygomycota*, but only *Ascomycota* are large enough to be easily identified and more strongly prefer dung as a growth substrate (van Asperen et al., 2021). Coprophilous fungal spores are relatively easy to identify, and they tend to be well-preserved due to their thick walls, making them a reliable paleolimnological proxy as they persist in lake sediments over hundreds to thousands of years (van Asperen et al., 2021). Spore cell walls are made of the same material as the body of the fungus: glucans, which are polymers of glucose, and glycoproteins, which are cell wall proteins (Watkinson et al., 2015). Herbivores will ingest dung fungal spores as they graze, spores will pass through the digestive tract, and then are excreted in the feces, where the spores then

germinate, fruit, and release their own spores, and the cycle thus repeats (**Figure 1.2**) (Perotti & van Asperen, 2019).

Coprophilous spores as paleo proxies began with megafauna. The cause and subsequent aftereffects for the disappearance of megafauna around the world in the late Quaternary, the Pleistocene and Holocene, is still contested (Meltzer, 2020; Seersolm et al., 2020; Stewart et al., 2021). Decreases in megafauna populations were more intense in the Americas, Australia and Oceanic islands, and less so in Africa, Asia, and Europe (Comandini & Rinaldi, 2004). Either rapid changes in climate, largely decreases in global temperatures (Stewart et al., 2021), or over hunting by humans, or a combination of both, lead to their disappearance (Comandini & Rinaldi, 2004). Many studies noted that as megafauna abundances decreased, so did the frequency of the coprophilous spore *Sporomiella* in lake sediments (Parker & Williams, 2012).

Studies supporting coprophilous fungal spores as reliable megafauna indicators lead to the question whether this same method is applicable to recent sediments and modern-day large herbivore species. The influx of studies using coprophilous spores as large herbivore indicators (**Table 1.2**) shows support for this proxy and its application. Baker et al. (2016), for example, found that there was a direct correlation between large herbivore (cattle, deer, geese, and horses) biomass, measured weekly over 5 years, and dung fungal spores, specifically *Sporomiella*, *Podospora*, and *Sordaria*, from modern pond sediments. To date, no relatively modern sediment cores have been used to track large herbivores that are not livestock.

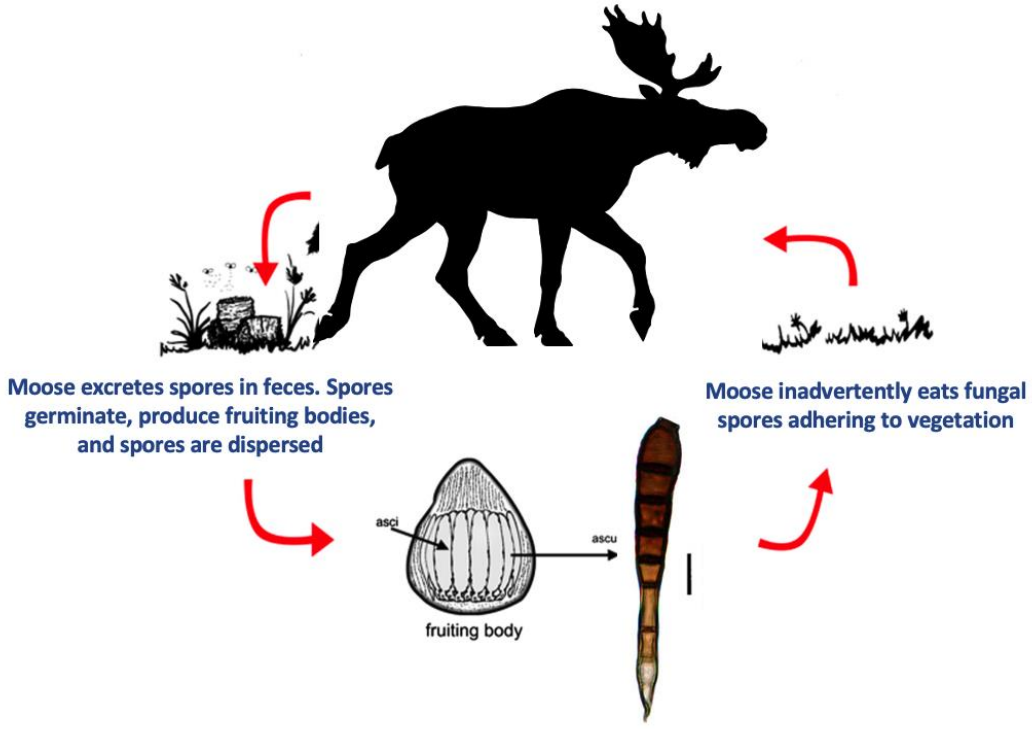



**Figure 1.2.** Circular lifecycle of dung fungal spores and moose, in which the moose consumes the fungal spores, they pass through the digestive tract and are then excreted out, where the fungus then germinates and releases spores for the process to be repeated (based on van Asperen et al., 2021 and Gelorini et al., 2012).

Fungal spores were first compared by Mead et al. (1986) in mammoth (*Mammuthus primigenius*) dung from Bechan Cave in Utah, USA with dung found in Siberia and China, establishing that the dung of these megafauna had been preserved. Davis (1987) observed the presence of *Sporomiella* on the dung of caribou, deer, elk, moose, and sheep and noted that these spores had also been found on the preserved dung of mammoths. To further corroborate this observation, Aptroot & van Geel (2006) found the coprophilous spore *Sporomiella* in the colon of the Yukagir mammoth that had been preserved in the Sakha Republic in permafrost, and dated to 18,560 BP.

Following the initial studies with coprophilous fungal spores, there have been many more using them as proxies (**Table 1.2**), a few of them are highlighted here. Schofield et al. (2011) used coprophilous spores to study a Norse settlement in Greenland, finding that *Sporomiella*-type and *Sordaria*-type indicated an increase in herbivore dung, aligning with domestic stock brought with the settlers. The study was also able to correlate a decrease of spores with abandonment of the settlement. Gill et al. (2009) used coprophilous fungi to analyze the slow collapse of megafauna, as decreasing abundance of spores correlates with a reduction in megafauna numbers. A combination of different coprophilous spore taxa and the presence of charcoal was used to indicate pastoral activity near a lake by humans in the Late-Holocene on Madagascar (Razanatsoa et al., 2022). Three different dung fungal spores, *Sporomiella*, *Podspora*, and *Sordaria*, and radiocarbon dated bone fragments were used to indicate megafauna extinctions in Alaska in the late Quaternary (Conroy et al., 2020).

Despite the growing use of coprophilous fungal spores as a proxy in paleoenvironmental studies, there have been few validation studies and poor geographical spread. For example, there have been few validation and/or paleoenvironmental studies in eastern North America, and no paleoenvironmental or dung fungal diversity studies in Canada (**Fig. 1.3**). There has been only one validation study in Canada in Nova Scotia by Graf & Chmura (2006) that focused on modern sediments in a dykeland in the Bay of Fundy, using pollen assemblages to determine grassland types, and coprophilous fungal spores to determine farmed dykeland land use. The authors encountered *Chaetomium*-type, *Cercophora*-type, *Podospora*-type, *Sordaria*-type, *Sporomiella*-type, and *Tripterospora*-type. While this study is labeled as a validation study for modern sediments (Baker et al., 2013), it only uses the spores as an indicator of large herbivores, showing more spores where grazing had occurred, but not correlating herbivores and spores.

**Table 1.2.** Coprophilous spore types shown to be indicative of large herbivores, including spore type, animal tracked, timeframe the spore was used for, and study location. This table adapted and expanded on those of Miola (2012) and Baker et al. (2013) by including studies done since those synthesized in these reviews* Denotes a validation study. Bold spores are those observed in this study.

| Spore | Animal tracked | Timeframe (ya) | Location | Publication |
|---|---|---|---|---|
| ***Sporomiella*-type** | Megaherbivore | 12,000 | Western USA | Davis (1987) |
| | Moose | Modern | Sweden | Nyberg & Persson (2002)* |
| | Large herbivores | 2,000 | Madagascar | Burney et al. (2003) |
| | Pastoral herbivores | Modern | The Netherlands | van Geel et al. (2003) |
| | Megaherbivore | 12,000 | Utah, USA | Davis & Shafer (2005) |
| | Megafauna | 11,000 | Madagascar | Robinson et al. (2005) |
| | Large herbivores | 25,300 | Canada | van Geel et al. (2007) |
| | Livestock | Modern | Italy | Menozzi et al. (2010) |
| | Megafauna | 13,900 | Ohio, USA | Gill et al. (2012) |
| | Bison | 12,000 | Kansas, USA | Gill et al. (2013) |
| | Cattle, horses, deer | Modern | Netherlands | Baker et al. (2016) |
| | Mammoth | 12,000 | Alaska, USA | Graham et al. (2016) |
| | Megafauna | 140,000 | Australia | Johnson et al. (2016) |
| | Megafauna | 25,000 | Andes | Rozas-Davila (2016) |
| | Rhinoceros | Modern | India | Basumatary & McDonald (2017)* |
| | Megafauna | 12,000 | Pilauco, Chile | Pino & Astorga (2019) |
| | Large herbivores | Modern | United Kingdom | van Asperen et al. (2019)* |
| | Megafauna | 13,000 | Alaska, USA | Conroy et al. (2020) |
| | Megafauna | 40,000 | Australia | Hocknull et al. (2020) |
| | Large herbivores | Modern | Africa | Goethals & Verschuren (2020)* |
| | Megafauna | 42,000 | Guatemala | Rozas-Davila (2021) |
| | Horses, sheep, yak | Modern | China | Wei et al. (2021) |
| | Megafauna | 60,000 | Central Europe | Sirocko et al. (2022) |
| ***Sordaria*-type** | Moose | Modern | Sweden | Nyberg & Persson (2002)* |
| | Large herbivores | 25,300 | Canada | van Geel et al. (2007) |
| | Livestock | Modern | Italy | Menozzi et al. (2010) |
| | Wild & domestic herbivores | 200 | Africa | Gelorini et al. (2012) |
| | Mammoth | Modern | Netherlands | Baker et al. (2016) |
| | Rhinoceros | 12,000 | Alaska, USA | Graham et al. (2016) |

| | | | | |
|---|---|---|---|---|
| | Large herbivores | Modern | India | Basumatary & McDonald (2017)* |
| | Cattle, horses, deer | Modern | United Kingdom | van Asperen et al. (2019)* |
| | Large herbivores | Modern | Africa | Goethals & Verschuren (2020)* |
| | Horses, sheep, yak | Modern | China | Wei et al. (2021) |
| | Megafauna | 60,000 | Central Europe | Sirocko et al. (2022) |
| ***Podospora*-type** | Moose | Modern | Sweden | Nyberg & Persson (2002)* |
| | Pastoral herbivores | Modern | The Netherlands | van Geel et al. (2003) |
| | Large herbivores | 25,300 | Canada | van Geel et al. (2007) |
| | Cattle, horses, deer | Modern | Netherlands | Baker et al. (2016) |
| | Mammoth | 12,000 | Alaska, USA | Graham et al. (2016) |
| | Rhinoceros | Modern | India | Basumatary & McDonald (2017)* |
| | Large herbivores | Modern | United Kingdom | van Asperen et al. (2019)* |
| | Large herbivores | Modern | Africa | Goethals & Verschuren (2020)* |
| | Megafauna | 42,000 | Guatemala | Rozas-Davila (2021) |
| ***Apiosordaria*-type** | Livestock | Modern | Italy | Menozzi et al. (2010) |
| ***Ascodesmis*-type** | Rhinoceros | Modern | India | Basumatary & McDonald (2017)* |
| *Cercophora*-type | Pastoral herbivores | Modern | The Netherlands | van Geel et al. (2003) |
| | Livestock | Modern | Italy | Menozzi et al. (2010) |
| | Rhinoceros | Modern | India | Basumatary & McDonald (2017)* |
| | Large herbivores | Modern | Africa | Goethals & Verschuren (2020)* |
| | Megafauna | 42,000 | Guatemala | Rozas-Davila (2021) |
| ***Coniochaeta*-type** | Pastoral herbivores | Modern | The Netherlands | van Geel et al. (2003) |
| | Rhinoceros | Modern | India | Basumatary & McDonald (2017)* |
| | Horse, sheep, yak | Modern | China | Wei et al. (2021) |
| ***Arnium*-type** | Pastoral herbivores | Modern | The Netherlands | van Geel et al. (2003) |
| | Moose | Modern | Sweden | Nyberg & Persson (2002)* |
| ***Meliola*-type** | Rhinoceros | Modern | India | Basumatary & McDonald (2017)* |

| | | | | |
|---|---|---|---|---|
| | Horse, sheep, yak | Modern | China | Wei et al. (2021) |
| *Gelasinospora*-type | Rhinoceros | Modern | India | Basumatary & McDonald (2017)* |
| ***Delitschia*-type** | Livestock | Modern | Italy | Menozzi et al. (2010) |
| | Large herbivores | 200 | Africa | Gelorini et al. (2012) |
| | Large herbivores | Modern | Africa | Goethals & Verschuren (2020)* |
| *Pleospora*-type | Horse, sheep, yak | Modern | China | Wei et al. (2021) |
| ***Saccobolus*-type** | Moose | Modern | Sweden | Nyberg & Persson (2002)* |
| | Rhinoceros | Modern | India | Basumatary & McDonald (2017)* |
| ***Nigrospora*-type** | Rhinoceros | Modern | India | Basumatary & McDonald (2017)* |

### *1.5 Newfoundland*

Newfoundland is a 108,860 $km^2$ island off the coast of Atlantic Canada (47º44'N, 59º28'W to 51º44'N, 52º38'W) (Bastille-Rousseau et al., 2013). It is the northeastern most island in a chain known as the Appalachian Orogen that is the result of ocean opening 600 million years ago, then the North American plate colliding with the African plate 300 million years ago, followed by ocean opening that began 250 million years ago (Williams, 2003). During the last glacial maximum, Newfoundland was covered by the Laurentide Ice Sheet. After the ice sheet melted, the island was inhabited on and off for millennia by different indigenous groups, including the Maritime Archaic, Palaeoeskimo, and Beothuk (Duggan et al., 2017). Newfoundland was colonized in the late 15$^{th}$ century by European settlers, whom the indigenous Beothuk avoided by moving further inland, eventually all dying (Duggan et al., 2017).

The island of Newfoundland is in the boreal region of Canada because of the climate made by the surrounding cold waters of the Labrador current. This current brings ice, including icebergs, near the island for four months of the year (Brown MacPherson, 1995). Growing seasons are short and cool, with an annual precipitation ranging from 600 mm in the north where it is the driest, to 1200 mm in the south-east where the island is the wettest (gov.nl.ca). There are also regions of bogs throughout forests, and the south-eastern portion of the island is largely covered by barrens, with forested mountains to the west.

Newfoundland now has as many non-natives as native terrestrial mammal species (Strong & Leroux, 2014). Non-native species introduction can occur naturally over time, especially with warming global temperatures expanding the ranges of species as more northern areas become warmer. This natural mode of species introduction is not as problematic as the introduction of species by humans. Newfoundland, as an island, is more susceptible to changes caused by the

introduction of new species. There are 1,180 non-native species in the boreal zones of Canada, most of which are plant species, and many are in Newfoundland and the southern most areas of Quebec and Ontario (Langor et al., 2014). The boreal region has been most impacted by non-native earthworms, vertebrate pathogens, and large vertebrates, including moose and white-tailed deer (Langor et al., 2014). In Newfoundland, many non-native species were introduced by Europeans settlers, with further movement and non-native introductions, non-native species were able to spread over time and as technology advanced to cars and airplanes (Langor et al., 2014; Strong & Leroux, 2014). Non-native species have complex interactions with native species (Strong & Leroux, 2014). For example, the extinction of skink species by the Small Asian Mongoose (*Urva auropunctata*) in the Caribbean islands led to the extinction of native species, whereas the recovery of the American marten (*Martes americana*) in Newfoundland is thought to be facilitated through the introduction of southern red-backed voles (*Myodes gapperi*) as a new food source is less common (Strong & Leroux, 2014).

### *1.6 Introduction of moose to Newfoundland*

In many cases non-native species were not purposefully introduced (e.g., several common weeds) whereas in several cases species were purposefully introduced by European settlers, moose being one such species. The most successful way to manage non-native species is to prevent introduction in the first place; however, moose were introduced to Newfoundland intentionally by the government for hunting purposes, both as food security for inhabitants and sport for tourists. Moose from New Brunswick, Canada were introduced to Newfoundland for hunting twice, first unsuccessfully in 1878 and successfully in 1904 with the introduction of two mating pairs being released into what is now Gros Morne National Park (McLaren et al., 2004).

Moose slowly spread across the island, reaching the Avalon and Northern peninsulas in the 1950's (Mercer & McLaren, 2002).

Since their introduction, moose have rapidly increased from the initial 4 to over 125,000 in 1999 (**Figure 1.4**) (McLaren et al., 2004). After the extirpation of wolves (*Canus lupis beothucus*) in 1932, adult moose no longer had non-human predators, and the population continued to increase with abundant resources until the late 1950's (McLaren et al., 2009b**)**. The decline following 1958 was caused by high hunting success rates. In 1973 hunting license regulations were initiated (which were the first island-wide management regulations and reduced license issue through a computerized draw by 50%) and led to a recovery period (Mercer & McLaren, 2002). The increase in the 1980's was likely due to continued low license issue (Mercer & McLaren, 2002). Additionally, the combination of spruce budworm (*Choristoneura fumiferana*) outbreak in the 1970's-1980's and increased forest harvesting in the 1980's resulted in large areas of new growth and excellent food sources for moose (Noonan et al., 2021). The decline in the 1990's was caused by increased hunting season length (Mercer & McLaren, 2002). Numbers are difficult to estimate due to accessibility and continuity of moose range, thus reports from hunters and mandible data are used, since some areas are unreliable to count aerially due to vegetation (Pimlott, 1959).

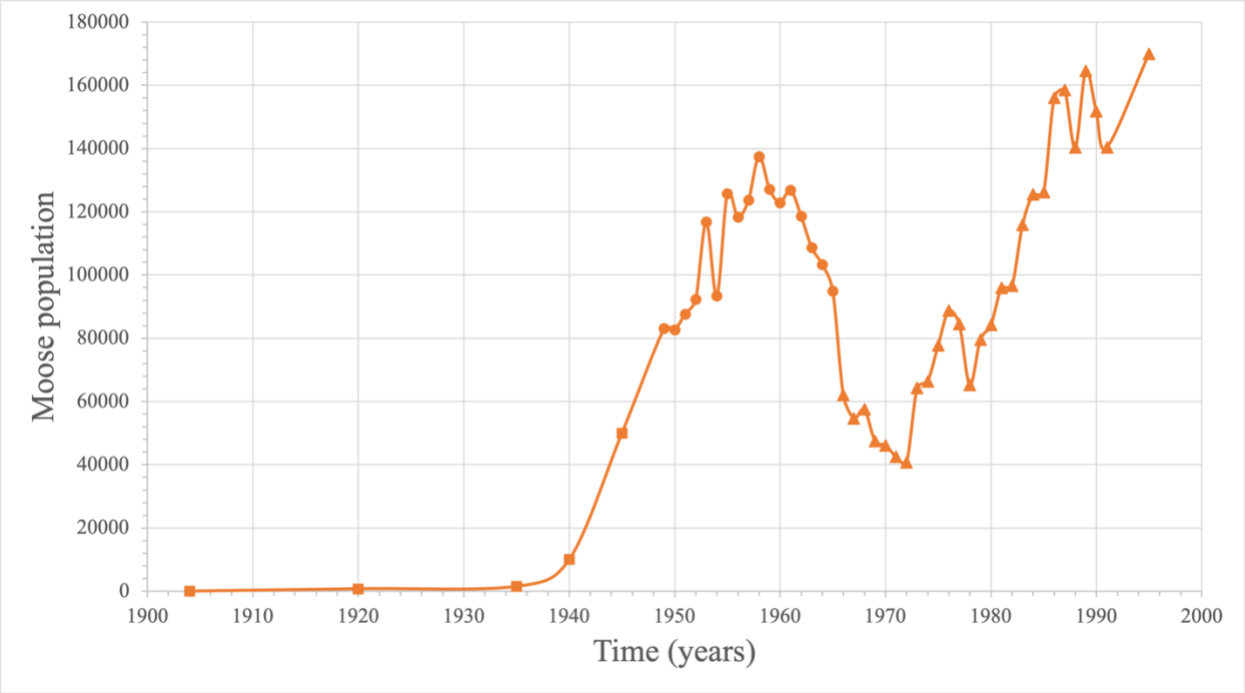



**Figure 1.3.** Total moose population on Newfoundland. Moose were introduced to Newfoundland in 1904 and the population began rapidly growing in ~1930, when wolves were extirpated, with a noticeable drop in the late 1960's due to high hunting success rates. Squares are estimated data, circles are hunter success rates, and triangles are data from hunters (Data from: McLaren et al., 2004).

### *1.7 Economic benefits and costs of moose to Newfoundland*

Moose are both economically beneficial, through trophy hunting and as a food source for Newfoundlanders (Condon & Adamowicz, 1994), and an economic cost, primarily through moose-vehicle collisions (Tanner et al., 2017) and some crop predation (Bird, 2018). There can be contentious issues when there is sharing of land between agriculture, livestock, and wild herbivores that thus far have no clear resolution (Pozo et al., 2021). In July 2020, the government of Newfoundland changed provincial wildlife regulations to issue special permits to shoot moose eating crops after dark (https://www.gov.nl.ca/releases/2020/flr/0709n01/). Moose also have no natural predators or diseases on Newfoundland, so their population is only kept in check through

big game hunting and hunting as a source of food (Gosse et al., 2011). Environmental management, including considering human interactions with large herbivores, is key to keeping a balance in ecosystems and large herbivore populations (Gordon et al., 2004).

Licenses for moose on Newfoundland are issued through a tiered and computerized drawing process, with increasing opportunity for those that have not been drawn recently (https://www.gov.nl.ca/hunting-trapping-guide/2022-23/general-information-for-all-hunters/big-game-licence-application-and-draw-process/). The cost for Newfoundland residents is $52.00, seniors $33.80, and non-residents $502.00. For the 2022-23 hunting season, there have been 27,665 total licenses for moose allotted: 9,360 males only, 17,850 either sex, and 455 for Not-for-profit (https://www.gov.nl.ca/hunting-trapping-guide/2022-23/licence-fees/). This is a decrease from the previous year in 13 different Moose Management Areas, and an increase in 3 areas (https://www.gov.nl.ca/hunting-trapping-guide/2022-23/new-for-2022-23/) (**Figure 1.5**). The license requires hunters to submit moose jawbones with a tag designating sex to drop off locations. Jawbones can be used to age the animal by counting layers of growth in the teeth, which is called the Cementum age. The ages are used to produce data on the health of the moose population. It is thought that many jawbones from older moose indicates a declining population, as hunters prefer yearling and two-year-old moose (https://www.gov.nl.ca/hunting-trapping-guide/2022-23/new-big-game-jawbone-collection-program/).

### *1.8 Ecosystem consequences of the introduction of moose*

Moose alter the natural landscape in Newfoundland by producing open areas due to their preferential consumption of young balsam fir (*Abies balsamea*) and white birch (*Betula papyrifera*) that prevents regeneration (McLaren et al., 2004). With the removal of balsam fir

and white birch, spruce species (*Picea* spp.) can thrive, resulting in more open areas (McLaren et al., 2004). Further compounding the over-browsing by moose, non-native red squirrels (*Tamiasciurus hudsonicus*), introduced in 1963 (Strong & Leroux, 2014), and conifer eating insects consume pre-dispersal seeds of balsam fir, reducing seeds for reestablishment (Gosse et al., 2011). This is especially evident in Gros Morne National Park and Terra Nova National Park, in which hunting was not permitted by Parks Canada until 2011, as well as in central Newfoundland where access is difficult (Gosse et al., 2011). Because of the effect of moose on birch and aspen regeneration in central Newfoundland management district 15 (**Figure 1.5**), in 1960-61 hunting licenses for moose were incentivized by $5 license fees, transportation and accommodation provided, and a bag limit of three moose (Bergerud et al., 1968). As moose densities were also high in the Gros Morne and Terra Nova National Parks due to no hunting, limited hunting was introduced in both parks in 2011, issuing 530 licenses for each park (https://www.gov.nl.ca/hunting-trapping-guide/2022-23/hunting-seasons-and-zones/island/moose-population-reduction-in-national-parks/).

Landscape changes by moose have had detrimental effects on other taxa including lichens (i.e. *Erioderma pedicellatum*), woodland caribou (*Rangifer tarandus terra-novae*), and birds (Goudie et al., 2011; McLaren et al., 2004). Woodland caribou are the only native ungulate on Newfoundland, and prefer to consume lichens, grasses, and shrub leaves and, as such, there is little competition with moose that consume trees and aquatic vegetation (Woodland Caribou-boreal population, 2023; McLaren et al., 2004). Ellis & Leroux (2017) and Swain et al. (2023) studied the impacts of moose browsing in Newfoundland and concluded that while moose negatively impacted the height of trees and litterfall biomass, they did not directly impact soil or the decomposition of litter. Other studies of ecosystem effects of moose in Newfoundland,

moose exclosure experiments, suggested that excluding moose promoted the regeneration of Balsam fir (Nosko et al., 2020; Leroux et al., 2021,). Moose exclosures have been carried out in multiple studies and are a reliable method to observe the impact of preventing browsing by ungulates (McLaren et al., 2004; Zhong et al., 2014; Ellis & Leroux 2016; Nosko et al., 2020; Salisbury et al., 2023).

The winter diet of moose in Newfoundland consists of up to 90% Balsam fir as opposed to the 1-17% Balsam fir in the rest of North America. Despite the chemical defenses of the tree, the winter diet of moose in Newfoundland largely consists of Balsam fir and its indigestible fiber, likely as it is more digestible than boreal conifers such as white spruce (*Picea glauca*) or black spruce (*Picea mariana*) (Nosko et al., 2020). The effects of moose over browsing Balsam fir and white birch can take up to two decades to recover as was demonstrated in moose exclosure studies (McLaren et al., 2009a). McLaren et al. (2009b) found that despite the impacts of high moose densities in the Parks, moose were not food limited. However, they did find that through browsing and tromping moose lead to the spread of both invasive plants and native grasses that replace native tree species. Models by Noonan et al. (2021) suggest that the best way to restore Newfoundland boreal forests is through management of herbivore population by hunting, replanting over browsed species, and expanding exclosures where herbivore populations have not been sufficiently reduced.

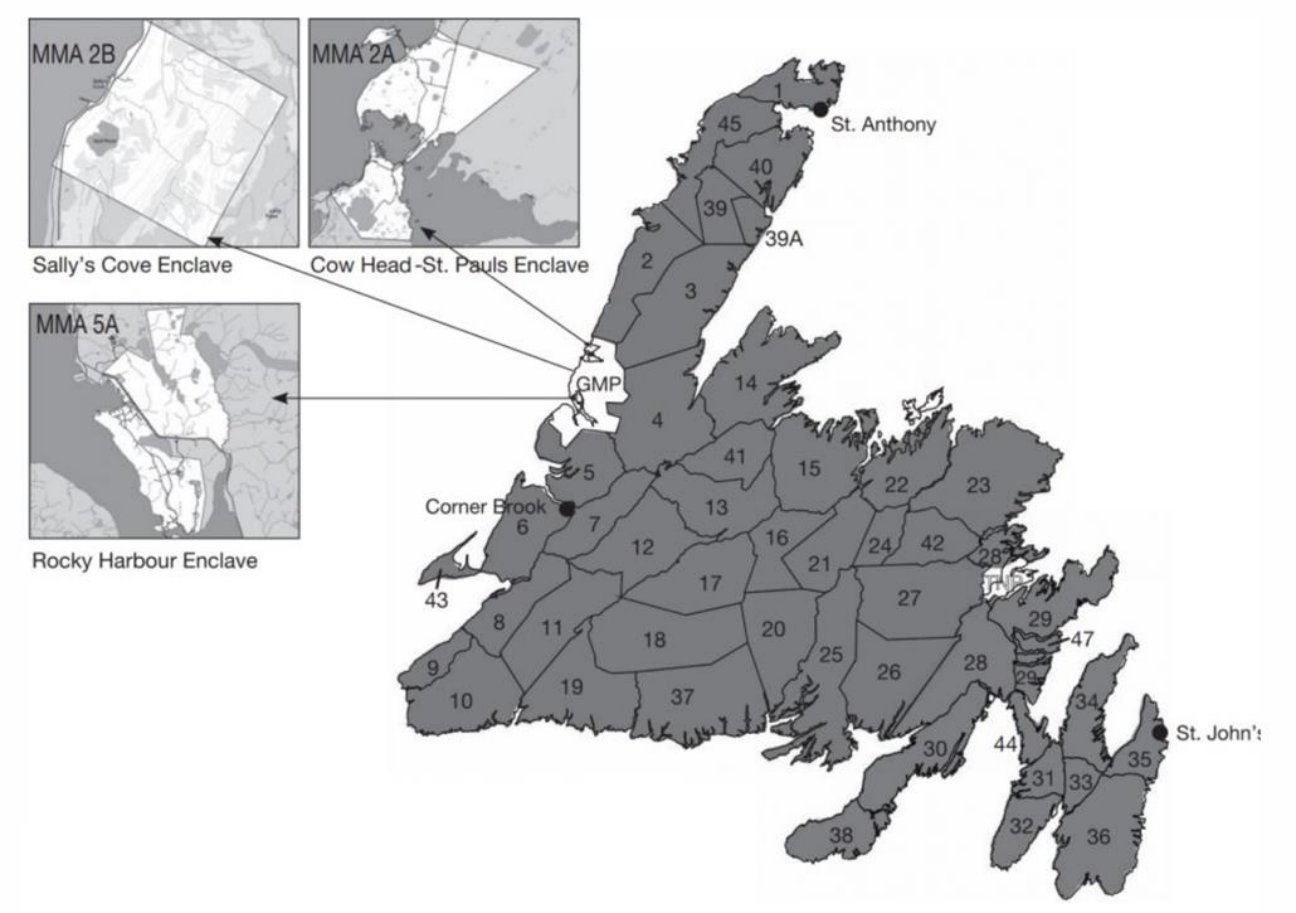



**Figure 1.4.** Moose management areas of Newfoundland (https://www.gov.nl.ca/hunting-trapping-guide/2022-23/hunting-seasons-and-zones/island/moose/). Little Crow Pond is in management area 29-Bonavista Peninsula and Pitcher Pond is in area 33-Salmonier.

### *1.9 Thesis objectives, rationale, and overview*

Since moose are a non-native species on Newfoundland and an important source of revenue, they are subject to management. Management began in 1945, and more recently centers on an ecosystem-based focus (McLaren et al., 2004). There has been a lack of monitoring data on moose after introduction, so it is unclear what has caused their population fluctuations (Mercer & McLaren, 2002). Furthermore, Newfoundland has areas that are largely inaccessible by road, making accurate counts difficult, and temporal information on moose density across the

province is lacking. If drivers for changes in moose population, both spatially and temporally, can be determined and understood, then better management decisions could be made regarding moose.

This is a proof-of-concept study. To date, coprophilous fungal spores have mainly been used to track ice-age megafauna and regional livestock introductions (**Table 1.2**), and validation studies remain sparse, especially in North America (Baker et al., 2013). Clearly, we have no recorded population data for ice-age megafauna and so the validity of using these spores for tracking abundance changes in extant herbivores has rarely been properly tested. In this study, we have a record of moose introduction to Newfoundland and moose population estimates to compare to coprophilous fungal spores, providing the first opportunity to test the spores for temporally tracking a megaherbivore over the past 120 years. Furthermore, caribou were locally extirpated across regions of Newfoundland at the turn of the 19$^{th}$ century, yielding areas void of abundant, large herbivores.

The main goal of this research is to examine and scrutinize the use of coprophilous spores as a paleolimnological proxy for tracking abundant, large herbivores (i.e., moose). Chapter 1 encompasses a short summary on the role of large herbivores in ecosystems, an introduction and review of current paleolimnological methods for tracking herbivores, the interactions of moose in ecosystems, and a short history of species introductions in Newfoundland. Chapter 2 outlines our main methods, Chapter 3 presents spore abundance and accumulation data from sediment cores collected in two distinct regions of Newfoundland (and thus possibly with historically different moose densities), and Chapter 4 provides a discussion of the results and future directions including a comparison to fecal biomarkers and *sed*aDNA left by moose that can be preserved within lake sediments. As coprophilous spores have not been studied in Newfoundland

sediments, I produced a coprophilous spore plate of my own images and identifications, supported by images from various studies, which is in this thesis for future reference. This plate can be used to support spore taxonomy in further studies on the island. The spore data from each core was processed using two numerical treatment methods (percentages and concentrations) and compared to historical moose abundance data for Newfoundland collected since moose introduction. Additionally, our two study lakes are similar in size and depth, but located in very different regions of Newfoundland, which may result in varying moose abundance reconstructions.

The research questions of this study were: (1) can paleolimnological data track moose arrival and subsequent population variation in Newfoundland?; (2) how do trends in fungal spores compare among the ponds from which cores were taken in tracking moose abundances in Newfoundland over the past hundred years? I predicted that coprophilous spore abundance data collected from lake sediment cores would closely track past moose population data collected through census reporting. This prediction is despite the mismatch in scale between spore abundance data representing the moose population of the local region where the lake is located versus the moose population data being representative of the entire province of Newfoundland. I further predicted that fungal spores in the core from Little Crow Pond would more accurately align with abundance data in part due to location, having a lower population of humans and housing nearby, as well as higher hunting quotas. Little Crow Pond is in management area 29-Bonavista Peninsula (**Figure 1.5**) and allows for 500 moose to be harvested with a 2018 success rate of 57.4%, while Pitcher Pond is in area 33-Salmonier and allows for 350 moose with a lower success rate of 35.4% (https://www.gov.nl.ca/hunting-trapping-guide/2020-21/hunting-seasons-and-zones/island/moose/). Due to the management of moose, permits issued are based on moose

abundance in a management area, and therefore it is likely that the more licenses issued in an area is indicative of higher moose abundance. For success rates, however, there is no indication that this is related to abundance of moose as percentage of success could be related to many other factors (accessibility, skill, etc.) besides the amount of moose present. Furthermore, to aid our interpretations of spore data and exclude long-term changes in precipitation as factors influencing spore abundances in lake sediments, we examined historical temperature and precipitation data for Newfoundland.

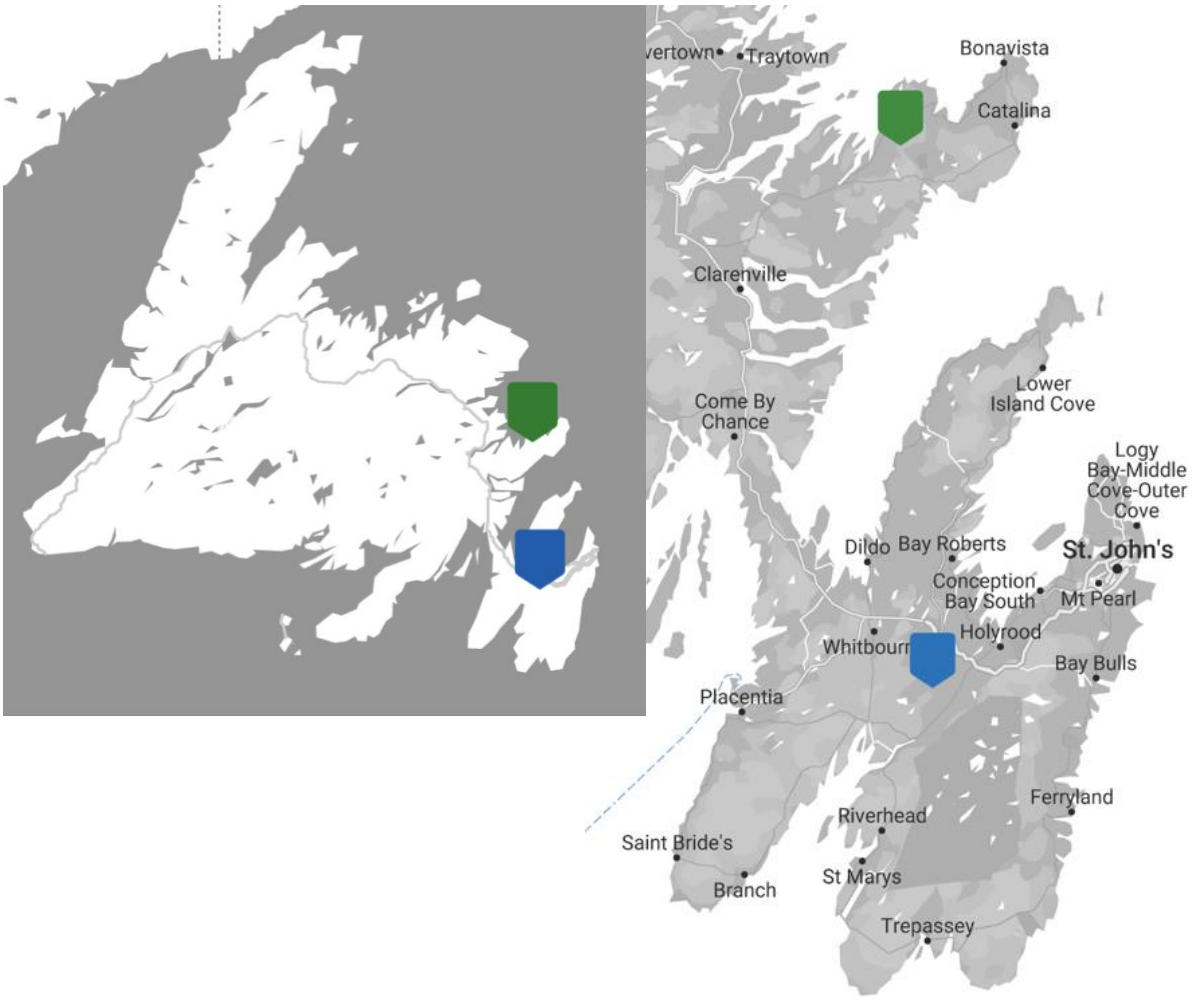



**Figure 1.5.** Map of Newfoundland with the two study site locations for Little Crow Pond (green) and Pitcher Pond (blue).

# Chapter 2: Methods

### *2.1 Study sites*

Two ponds were chosen for this study on the eastern side of Newfoundland. The first pond is located on the Bonavista Peninsula (~3.5-hour drive from St. John's), named Little Crow Pond due to its proximity to Crow Pond (**Figure 2.1**). Approximately one third of the pond is covered by emergent macrophytes (e.g., *Nuphar variegata* and *N. odorata*) and it is 261.5 meters across and ~3 m deep (**Table 2.1**). This area is a Boreal Shield ecozone, and it belongs to the Atlantic mid-boreal ecoclimate and the North Shore Forest ecoregion of Newfoundland (http://www.ecozones.ca/english/region/113.html). Vegetation consists of an understory of feathermoss (e.g., *Pleurosium schreberi*, *Hylocomium splendens*), black and white spruce, and balsam fir, while mire vegetations consists of *Sphagnum* mosses and various Ericaceous plants such as *Kalmia* spp., and *Rhododendron* spp., etc. The Bonavista weather station mean temperature is 4.95ºC, and the average annual precipitation is 1164 mm (https://climate.weather.gc.ca/historical_data/). Little Crow Pond lies on Paleozoic strata, with granitic intrusions that form hills in the area (http://www.ecozones.ca/english/region/113.html).

The second study pond was named Pitcher Pond (**Figure 2.3**) by the researchers, and is located off Tower Road, northeast of Salmonier Nature Park on the Avalon Peninsula (~1 hour drive from St. John's). This pond is in the curve of the road, approximately 5 meters below the road, teardrop in shape, and surrounded by trees (**Table 2.4**). It is 126 meters across, and ~5 meters deep in the center where the sediment core was collected. Macrophytes, including lily pads (*Nuphar variegata* and *N. odorata*) and pitcher plants (*Sarracenia purpurea*), were located around the perimeter of the pond. Other vegetation of the area includes balsam fir, white birch, and yellow birch (*Betula lutea*), and an understory of wood ferns (*Dryopteris* spp.), feathermoss,

heath moss (*Rhacomitrium lanuginosum*) (https://www.gov.nl.ca/ecc/files/publications-parks-ecoregions-island-5-avalon-forest.pdf). The St. John's weather station average mean annual temperature is 4.91$^{o}$C, and annual precipitation is 1434 mm (https://climate.weather.gc.ca/historical_data/). This area is a Boreal Shield ecozone, but also falls in the Avalon Forest ecoregion of Newfoundland (http://www.ecozones.ca/). Geology of the area consists of late Precambrian sedimentary conglomerates, sandstones, and shales, as well as some younger volcanic rocks (http://www.ecozones.ca/english/region/115.html).

### *2.2 Sediment core collection*

The core from Little Crow Pond was collected previously by MSc students Courtney White and Johanna Bosch in the fall of 2021 from an inflatable boat using a push corer (**Figure 2.2, right**) (Glew & Smol, 2016). The core for Little Crow Pond was sectioned into 0.25-centimeter increments for the entirety of the core using a core extruder (Glew, 1988). A lake sediment core was collected from Pitcher Pond in July 2022 (**Figure 2.4, right**) using the same methods as for Little Crow Pond. The Pitcher Pond core was sectioned next to the lake into 0.25 increments for the first 10 centimeters, and 0.5 cm increments after that. Each section for both ponds was stored in a labelled plastic bag which was stored in a refrigerator at the lab.

**Table 2.1.** Little Crow Pond and Pitcher Pond site and morphometric data.

| | Little Crow | Pitcher Pond |
|---|---|---|
| Latitude | 48$^{o}$28'24" N | 47$^{o}$17'39'' N |
| Longitude | -53$^{o}$26'49" W | -53$^{o}$20'39" W |
| Core Length | 42 cm | 36.5 cm |
| Core Section resolution | 0.25 cm | 0.25 cm to 0.5 cm |
| Max Pond Depth | 3 m | 5 m |
| Max Pond width | 261.5 m | 120.6 m |
| Surface Area | 19, 204 m$^2$ | 97, 587 m$^2$ |
| Elevation | 103 m.a.s.l. | 166 m.a.s.l |

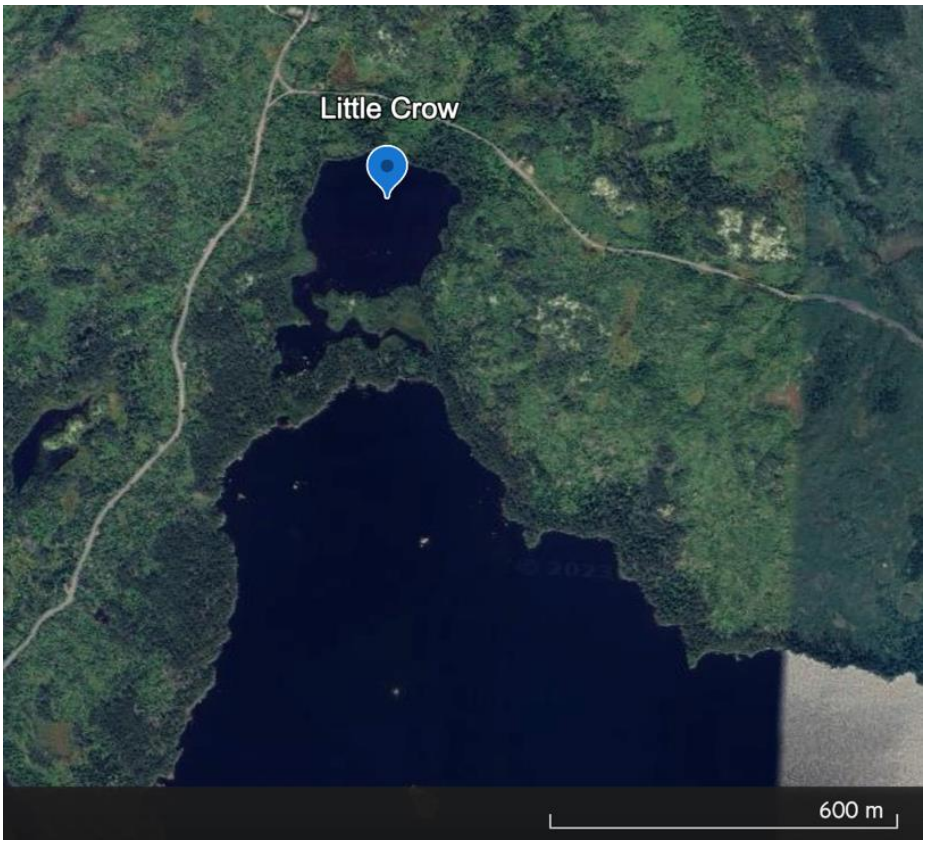



**Figure 2.1.** Google earth image of Little Crow Pond (July 12, 2021).

**Figure 2.2.** Left: Little Crow Pond on day of sediment core collection, October 6, 2021. Right: Sediment core collected from Little Crow Pond with tape measure for scale.


**Figure 2.3.** Google earth image of Pitcher Pond (May 25, 2020).

**Figure 2.4.** Left: Pitcher Pond during sample collection, July 22, 2022. Right: Sediment core collected from Pitcher Pond with a tape measure for scale.

### *2.3 Sediment core dating*

To date each sediment core, radioisotopes ($^{210}$Pb, $^{137}$Cs, $^{214}$Pb) were quantified by gamma counting with an EG&G Ortec High Purity Germanium Gamma Spectrometer. Sediments were freeze-dried and ~0.5-1.0 g of dry sediment was sealed in labelled gamma tubes with 2-ton epoxy. The constant rate of supply (CRS) was used to determine dates for each interval due to the uniformity of sample deposition (Scheleske et al., 1994; Appleby 2001).

### *2.4 Spore extraction*

The goal when processing sediment samples with spores is to retain as much pollen and non-pollen palynomorphs (NPPs) as possible. Therefore, less treatment and gentler methods (i.e., less caustic chemicals) are preferred (Pound et al., 2021). The isolation methods of Pound et al. (2021) and van Asperen et al. (2016) were modified and used in combination to extract and concentrate spores from the sediment, with the density of sodium polytungstate (SPT) powder modified based on van den Bos et al. (2020). Methods used from van Asperen et al. (2016) were Methods C [*Lycopodium* tablets, volumetric sampling, heating samples with 10% KOH, sieving out the fraction >125 μm, density separation with swirling dish, sieving out the fraction <6 μm, treatment with 10% HCl] and D [*Lycopodium* tablets, volumetric sampling, sieving out the fraction >125 μm, sieving out the fraction <6 μm] as shown in Table 2 of their paper. Samples were heated with potassium hydroxide (KOH) as in Method C, but not treated with hydrochloric acid (HCl) due to its damaging effects on fungal spores. Also, samples were not sieved a second time using a sieve with a mesh size <6 μm as in both methods (we wanted to limit treatment steps and potential loss of sample), and density separation was performed with SPT rather than a swirling dish. Acetolysis was not performed on the samples since it can damage the coprophilous

spores *Sporomiella, Sordaria*, and *Podospora* (van Asperen et al., 2016). In preparation for processing, one tablet of *Lycopodium* spores, a pollen standard (https://www.geology.lu.se/services/pollen-tablets), was added to a centrifuge tube with 15 mL distilled water and centrifuged for 3 minutes at 3500 rpm.

To isolate the spores from sediment in the sample, ~0.1 g of dry sample (~1.0 g when wet) was added to 15 mL beakers. A 10% KOH solution was then added to ~15 mL mark on the beaker. The beakers were then placed in a hot water bath heated to 90ºC. Samples were left in beakers in the hot water bath for 10 minutes, stirring occasionally with a glass rod to encourage sediment separation and deflocculation. The beakers were then removed and allowed to cool before sieving.

Samples were filtered using a 180 μm mesh sieve. The sieve was placed on a plastic funnel that was inserted into a 125 mL Erlenmeyer flask. The sample in the KOH solution was then poured from the beaker over the sieve and flowed into the flask. Distilled water was used to rinse out the beaker and poured again into the sieve. The sieve was then rinsed further with distilled water until it ran clear, and there was ~50-75 mL of filtered sample in the flask. The funnel was then rinsed to ensure all the sample was in the flask. The sample was then added to the centrifuge tube containing a *Lycopodium* tablet and stirred. Samples were vortexed and centrifuged for 3 minutes at 2200 rpm. They were then decanted, and the supernatant discarded. More sample from the flask was added to the centrifuge tube, and it was again vortexed and centrifuged for 3 minutes at 2200 rpm. The process was repeated until no more sample was left in the flask. Additionally, the flask was rinsed with distilled water and emptied into the centrifuge tube. To isolate and clean the samples further, they were stirred, vortexed, and then centrifuged for 3 minutes at 2200 rpm. The supernatant was discarded, the tube refilled with

distilled water, and the process repeated until the supernatant was clear. This averaged between 5-6 rounds.

After centrifuging, the sample was separated further using heavy liquid density separation with SPT powder. The use of such separation allows for pollen and spores to float and, therefore, be further separated from denser organic and mineral matter that will sink and form a pellet (van den Bos et al., 2020). It is common for lake sediment cores to have differing compositions, and therefore for different SPT densities to be used for best results. Too high of a density will remove more spores than desired, while too low will not remove enough organic and mineral matter. For the Little Crow Pond samples, 56 g of SPT was weighed into a 125 mL Erlenmeyer flask and 44 mL distilled water was added to create a solution with a density of 1.27 $g/cm^3$. Pitcher Pond had denser matter present in soil samples, which could possibly be due to the location of Pitcher Pond partly circled by a road and at the bottom of a steep catchment. To consider the soil composition of Pitcher Pond samples, a denser solution was used to retain more sample and spores. 80 g SPT powder was weighed into an Erlenmeyer flask and 40 mL distilled water was added to produce a 2.0 $g/cm^3$ solution (van den Bos et al., 2020). Once the SPT powder was swirled and mixed into the distilled water, a pipette was used to add 5 mL of the SPT solution to the centrifuge tube containing the sample. The tubes were centrifuged for 18 minutes at 1800 rpm. While waiting, new centrifuge tubes were labeled. If after 18 minutes there was a pellet at the bottom of the tube and some sediment floating at the top, this sediment was carefully pipetted into the new tube. If there was not sediment floating, the tube would be centrifuged again for 9 minutes at 1800 rpm until there was sediment floating. The new tube with the floating sediment was filled to the 10 mL mark with distilled water, and then centrifuged for 10 minutes at 3500 rpm. If no pellet was formed after this, and sediment was floating, it was then again transferred

into a new tube and centrifuged. Once a pellet formed, the supernatant was discarded. The tube was filled to 10 mL with distilled water and centrifuged for 5 minutes at 3500 rpm. The supernatant was discarded. Samples were stained with a drop of safranin dye added to the pellet in the tube. The tube was filled with 10 mL distilled water and vortexed, then centrifuged for 3 minutes at 3800 rpm. The supernatant was discarded.

The samples were next dehydrated with alcohol and tert-butanol. First, 8 mL 100% alcohol (ethanol) was added to the tubes. They were then vortexed and centrifuged for 3 minutes at 3800 rpm. Supernatant was then discarded, and 8 mL tert-butanol was added. The tubes were vortexed and centrifuged again for 3 minutes at 3800 rpm and the supernatant discarded. Less than 1 mL silicon oil was added to the tubes. They were then stirred with a wooden stick and left open overnight so that any water left in the tubes could evaporate.

Now extracted, cleaned, and further isolated, the samples were mounted on labeled microscope slides so they could be counted with a light microscope. The samples were stirred in the centrifuge tubes, and more silicon oil was added if needed. Using a pipette, 50 μL was placed on the slide and a coverslip placed on top. Bubbles were removed by gently pressing on the coverslip with a glass stir rod. Corners were secured with clear nail polish placed on the corners of the coverslip. They were placed on a hot plate and dried for one to two hours.

### *2.5 Spore identification and counting*

Taxa were learned by looking at multiple plates of coprophilous fungal spores for comparison, since no guide exists for Newfoundland or Atlantic Canada. Sources used for this include reference plates from: Basumatary & McDonald (2017), Cugny et al. (2010), Lee et al., (2022), Perrotti, & van Asperen (2018), van Asperen et al. (2020), van Asperen et al. (2021), and

van Geel et al. (2007). Coprophilous spores were counted using both Nikon and Zeiss light microscopes. Images were taken using Zen Lite software through the Zeiss microscope; 10 µm scale bars were stamped onto each photo. All coverslips were scanned using a 40x lens, further magnified by a 10x within the eyepieces for a total 400x magnification. No oil or further magnification was used as touching the coverslip moved the medium.

Spores observed were compared to images in the reference plates listed above. If unsure whether what was observed was a certain spore, it was recorded as *conferre* (*cf.*). All coprophilous spores, whether exclusively found on dung, or not, were counted and recorded. Several unknowns were recorded, identified, and categorized as "unknowns". Fungal hyphae were counted and recorded as well. Overall, of the coprophilous spores, *Arnium*, *Sporomiella*, and *Sordaria* were present in the largest amounts, while *Podospora*, *Coniochaeta*, *Ascodemsis*, and *Delitschia* were less abundant. Other coprophilous spores observed include *Meliola*, *Apiosordaria*, *Trichocladium opacum,* cf. *Trichocladium* sp., *Nigrospora*, *Tripsporium elegans*, and *Saccolobus*.

For both Little Crow Pond and Pitcher Pond, 24 sediment intervals were counted (48 samples in total), starting at the surface, 0.0-0.25 cm, and continuing every other quarter interval, until 9 cm deep (~1900 CE). Intervals for 10-18 cm were counted for even centimeter intervals for five intervals. The coprophilous spores and *Lycopodium* were tallied and recorded in Excel. For most slides, counting stopped when 150 *Lycopodium* spores were reached, as this is half the amount present in one tablet of *Lycopodium* spores. Therefore, the use of *Lycopodium* spores allows for comparison of known amount of *Lycopodium* spores to unknown amounts of coprophilous spores, so that not all coprophilous spores have to be counted and a proportion is available across all slides (Stockmarr, 1971). Some slides were sparse, and there were fewer than

150 *Lycopodium* spores. For other slides, the entirety of one coverslip was counted. This variability was accounted for with the calculation of percent *Lycopodium*, discussed further in the next section.

### *2.6 Data analysis*

First, dating of the sediment cores was done to establish our target intervals and resolution for spore analysis and ensure we had good $^{210}$Pb decays, dates, and sedimentation rates to compare spore abundances and concentrations to moose temporal data. There is no universally accepted standard for coprophilous spore numerical treatment, so spore abundance data was calculated in two ways: 1) relative to *Lycopodium* as a percentage and 2) accumulation rate as a concentration. Since this is an emerging methodology, the treatment of data in two different methods allows for a comparison to see which best matches the known moose abundance data. It has been observed that counting spores with tracers as a percentage can be sensitive and skew data, but still provides an insight to spores present (Perrotti et al., 2022).

The number of spores relative to the number of *Lycopodium* spores was calculated for each spore type in every interval by:

$$\frac{number\ of\ spores}{number\ of\ Lycopodium}\ x\ 100$$

This yielded a percentage, referred to as "percent *Lycopodium*", and accounted for counting effort, such that if greater or lesser counting effort was committed there would be a greater denominator (i.e. more *Lycopodium* encountered).

To calculate accumulation rate, wet bulk density was first calculated by:

$$\frac{mass\ of\ sample\ (with\ water)\ (g)}{volume\ of\ whole\ (cm3)}$$

Samples tested for $^{210}$Pb by Queens University also calculated wet bulk density based on the percent water before and after freeze-drying, and the known core tube volume and volume of each sediment slice. This data was used for those samples tested. For samples without this data provided, we interpolated the value based on adjacent intervals.

The sedimentation rate was also calculated by through ScienTissiME, the dating software used at Queen's University. Again, for intervals without a sedimentation rate, one was interpolated based on adjacent intervals.

Accumulation rate was calculated by:

$$\frac{number\ of\ spores}{wet\ bulk\ density\ (g/cm3)}\ x\ sedimentation\ rate\ (\frac{cm}{yr})$$

50 spores/ 1cm$^3$ * cm/yr = X spores/cm$^2$/yr

These two methods were chosen because through comparison they can create a more thorough picture of coprophilous fungal spores present than either one by itself (Wood & Wilmshurst, 2013). Quantifying the spores relative to *Lycopodium* ensured that when more or less than 150 *Lycopodium* were counted (and thus counting effort varied), amounts of spores are still comparable. Changes through time were also examined with spore accumulation rates which can often be most informative because it considers changes in sedimentation rate through time (van Asperen et al. 2021). As estimating accumulation relies on well-established and reliable age-depth models, we first had to assure this was possible. The two cores dated relatively well (close to exponential decay in $^{210}$Pb, discussed in the results) and there was no expected change in sedimentation rate over the last ~150 years. Total pollen assemblage was not used due to its sensitivity to changes in accumulation of total pollen and because the SPT density used to isolate smaller spores may have caused larger pollen to be lost (van Asperen et al., 2021). These

calculations were done in excel and imported into the program C2 (c2prog.com) to produce stratigraphies.

### *2.7 Climate data*

Climate data was gathered from climate.weather.gc.ca for both sites and both precipitation and temperature. Precipitation is the total precipitation for the year, and the yearly average was taken from monthly data for temperature. Years missing four or more months were excluded, and years missing one to three months of data were noted. Little Crow weather was generated from one monthly data file, Terra Nova National Park HQ (1962-1996), and daily data averaged for yearly rates for Terra Nova National Park CS (1997-2022). St. John's data was used for Pitcher Pond, combining St. John's (1874-1941) with St. John's A (1942-2011) and St. John's West Climate (2011-2022).

# Chapter 3: Results

### *3.1 Core Dating*

$^{210}$Pb activity in Little Crow Pond core decayed gradually, almost linearly, between 0 cm and 10.25 cm, with the CRS model identifying 10.25 cm as 1905 CE, with ~23 years of error (**Figure 3.1a**). Radioisotope $^{137}$Cs has several small peaks between 1900 and 2020 and cannot be used to corroborate the CRS model dates. Sedimentation rates between 0 and 10.25 cm ranged from 0.0159 to 0.2581 cm/yr and averaged 0.1097 cm/yr (**Figure 3.2a**). There is also a small increase in $^{210}$Pb activity from 0 cm to 2.13 cm before it decays to background $^{214}$Pb levels. Core dates beyond $^{210}$Pb activity were calculated by extending the CRS model using a 2$^{nd}$ order polynomial equation, for Little Crow Pond is $y = -3.4203x^2 – 2.233x + 2022$ ($R^2 = 0.944$), where x = depth (cm) and y = age.

Pitcher Pond decayed exponentially, with $^{210}$Pb decaying between 0 and 8.13 cm, which dated approximately to the year 1894 CE ±28 years (**Figure 3.1b**). Artificial $^{137}$Cs radioisotope increases gradually towards the surface of the core and cannot be used to confirm the CRS model dates. From 0 to 8.13 cm, the sedimentation rates ranged from 0.031 to 0.181 cm/yr and it averaged 0.1023 cm/yr (**Figure 3.2b**). The 2$^{nd}$ order polynomial equation to extend the CRS model for Pitcher Pond is $y = -0.01x^2 – 7.0935x + 2022$ ($R^2 = 0.9779$), where x = depth (cm) and y = age.

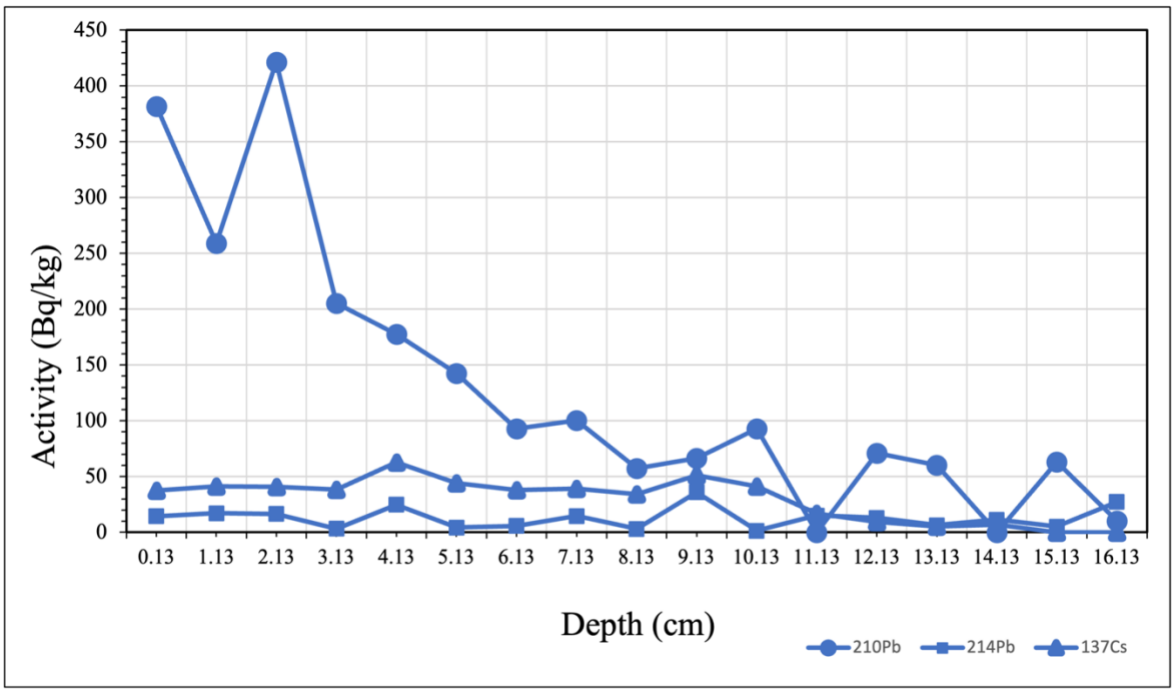
As the focus of our study for both sites falls within the range of $^{210}$Pb dating, the ~150 years half-life of $^{210}$Pb we had to infer very few dates beyond the CRS model. However, it is worth noting that inferred dates beyond the range of $^{210}$Pb are less reliable and should be interpreted with caution. For Little Crow Pond, the 1904 moose introduction date error is ~23 years, for the first moose hunting season in 1930 it is ~21 years, and for moose hunting

regulation changes in 1973 it is ~10.3 years. The error for Pitcher Pond is ~25.4 years, ~21.4 years, and ~7.5 years, respectively. The dating error for these cores is within the expected range for error – increasing from the surface of the core to the turn of the 19$^{th}$ century as $^{210}$Pb activity becomes low approaching background radioisotope activity levels (measured with $^{214}$Pb).

**Table 3.1.** Common Era (CE) dates assigned to sediment core depths using the constant rate of supply (CRS) model with respective depth model error reported for Little Crow Pond (LC) and Pitcher Pond (PP).

| LC Midpoint depth (cm) | LC CRS year (years CE) | LC CRS error (years) | PP Midpoint depth (cm) | PP CRS year (years CE) | PP CRS error (years) |
|---|---|---|---|---|---|
| 0.13 | 2020.3 | 0.12 | 0.13 | 2021.9 | 0.1 |
| 1.13 | 2013.1 | 2.0 | 2.13 | 1984.5 | 7.4 |
| 2.13 | 2001.6 | 3.9 | 4.13 | 1938.1 | 20.4 |
| 3.13 | 1990.9 | 6.0 | 6.13 | 1922.7 | 22.4 |
| 4.13 | 1982.3 | 7.9 | 8.13 | 1894.1 | 28.3 |
| 5.13 | 1973.4 | 10.3 | | | |
| 6.13 | 1963.6 | 13.3 | | | |
| 7.13 | 1953.3 | 16.6 | | | |
| 8.13 | 1942.0 | 20.4 | | | |
| 9.13 | 1932.2 | 21.0 | | | |
| 10.13 | 1905.9 | 23.0 | | | |

a)




b)

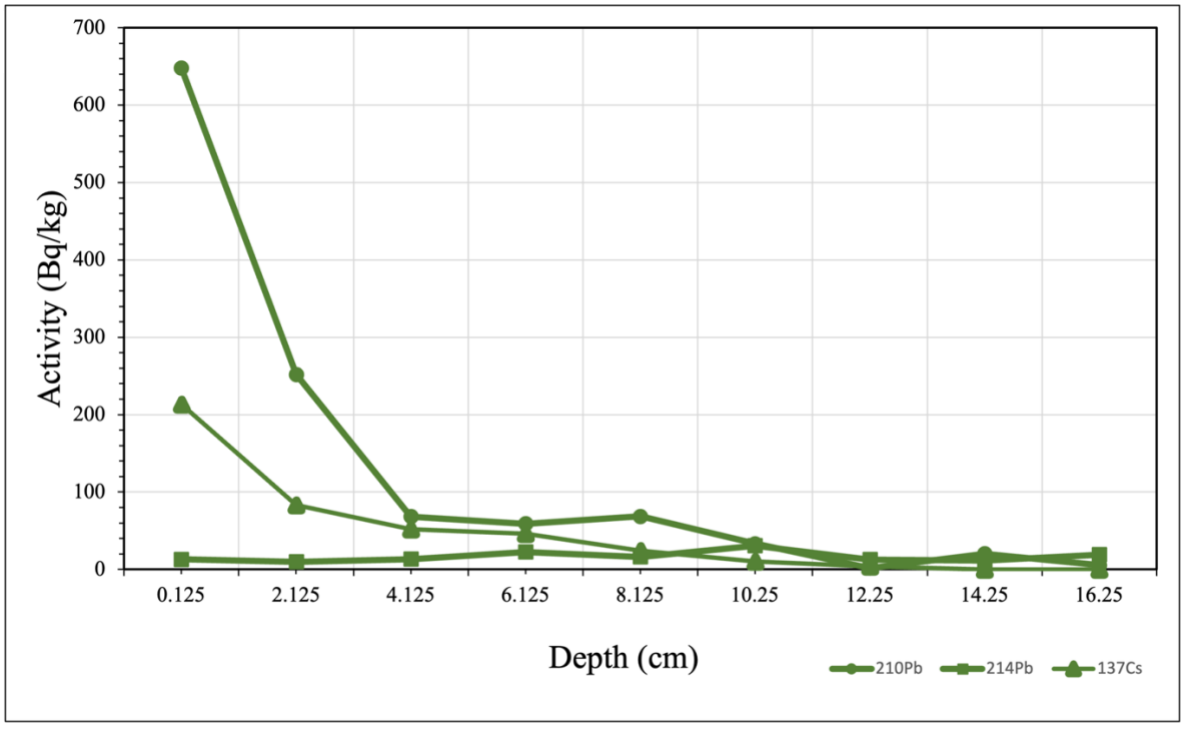
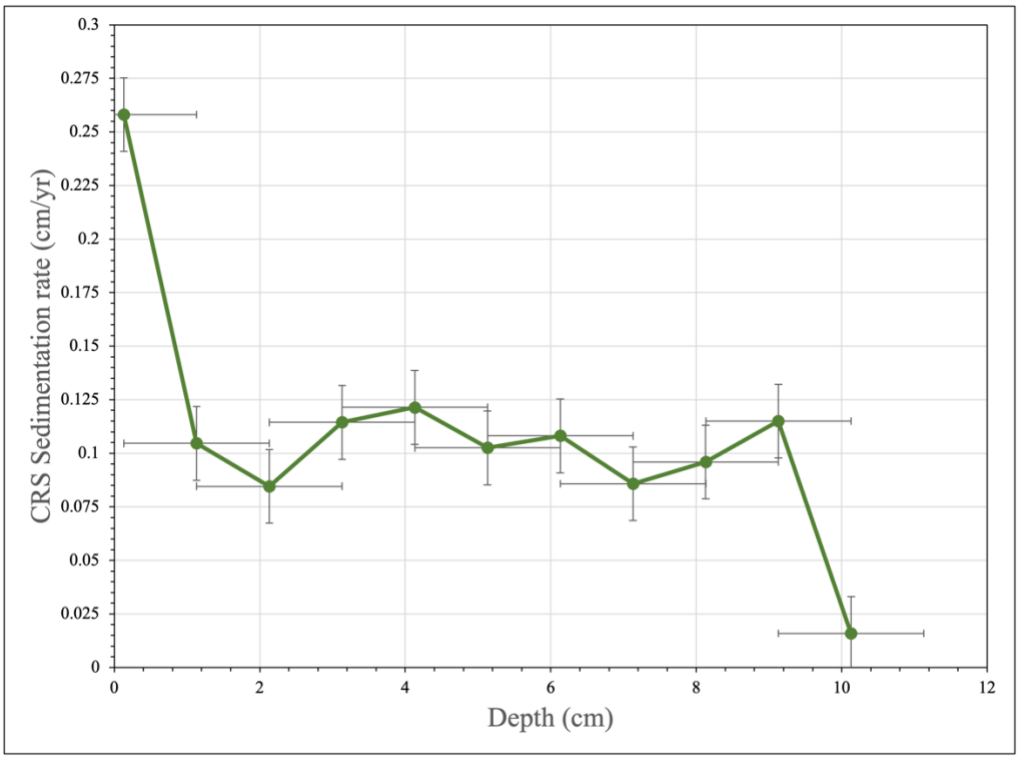



**Figure 3.1.** $^{210}$Pb (circles), $^{214}$Pb (squares), and $^{137}$Cs (triangles) activities for a) Little Crow Pond (blue) and b) Pitcher Pond (green).

a)




b)

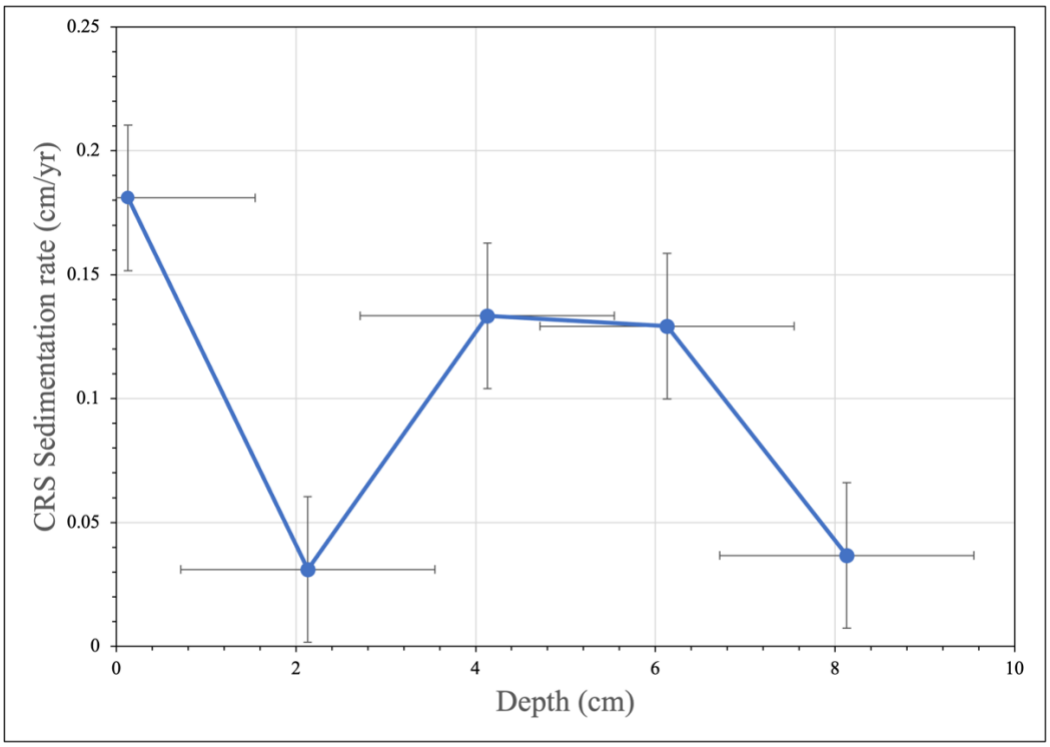



**Figure 3.2.** CRS Sedimentation rate versus depth with standard error bars for a) Little Crow Pond (blue) and b) Pitcher Pond (green).

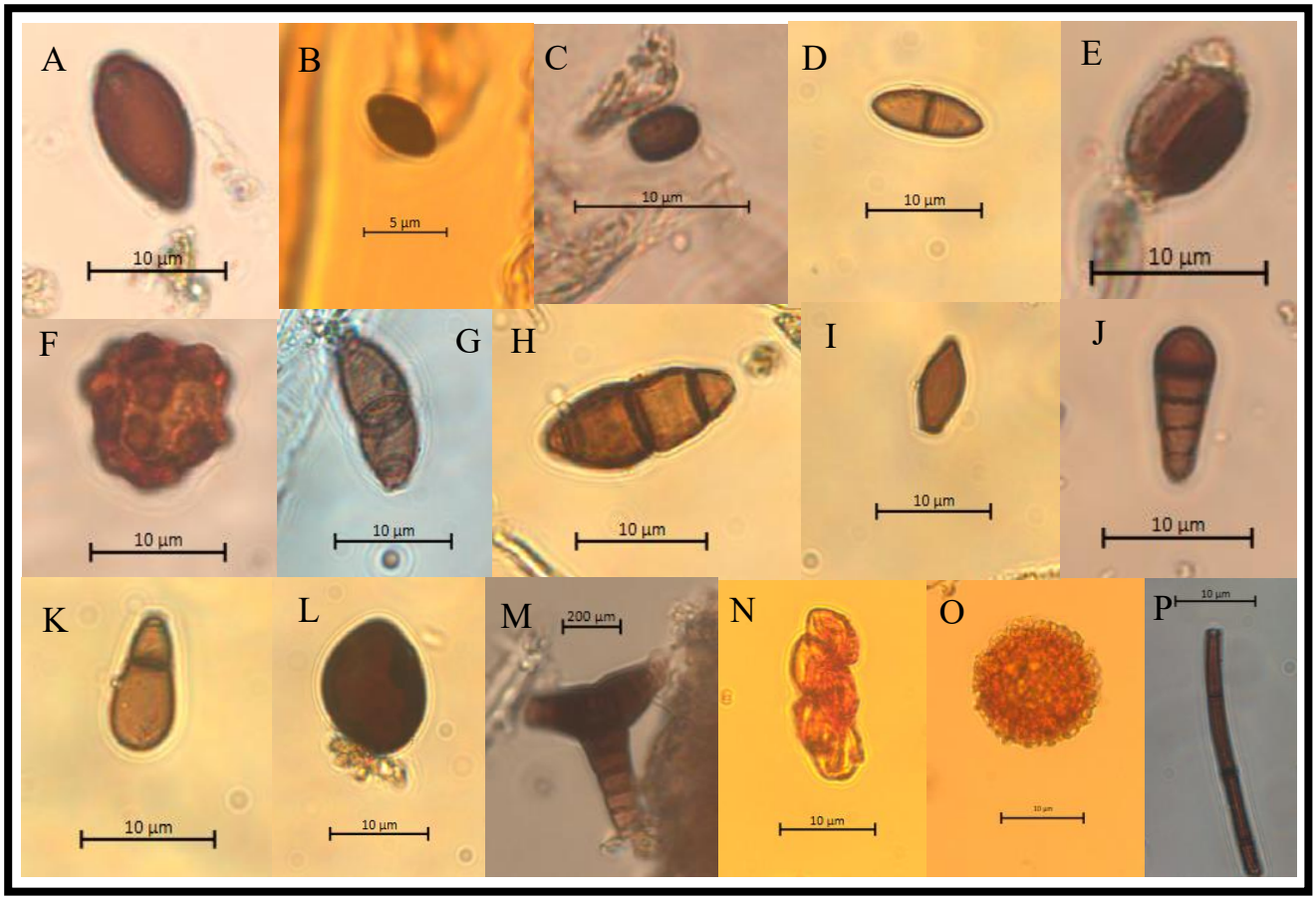



**Figure 3.3.** Non-pollen palynomorphs including coprophilous spores and fungal hyphae identified from both Little Crow Pond (LC) and Pitcher Pond (PP). Also included is a *Lycopodium* spore that was used for relative abundance. A) *Podospora* (LC 2.0-2.25 cm), B) *Sordaria* (PP 3-3.25 cm), C) *Sporomiella* (PP 0.25-0.5 cm), D) *Arnium* (LC (1.0-1.5 cm), E) *Coniochaeta* (LC 2.0-2.25 cm), F) *Ascodesmis* (LC 1.0-1.25), G) *Delitschia* (LC 5.0-5.25), H) *Meliola* (LC 1.0-1.25), I) *Apiosordaria* (LC 1.0-1.5), J) *Trichocladium opacum* (LC 2.0-2.25) K) cf. *Trichocladium* sp. (LC 1.0-1.25) L) *Nigrospora* (LC 1.0-1.25), M) *Triposporium elegans* (LC 9-9.25) N) *Saccolobus* (PP 1.5-1.75), O) *Lycopodium* (PP 8.5-8.75), P) Fungal hyphae (LC 7.0-7.25).

### *3.2 Coprophilous spores*

The coprophilous fungal spores *Podospora, Sordaria, Sporomiella, Arnium, Coniochaeta, Ascodesmis,* and *Delitschia* were present at both Little Crow Pond and Pitcher Pond. These are the coprophilous spores that primarily grow on dung, and occasionally soil, and have been shown to be indicators for large herbivores (van Asperen et al., 2021). *Sporomiella* concentration ranged from 0 to 15 spores per slide, *Podospora* from 0 to 4, *Sordaria* 0 to 10, and *Arnium* from 0 to 35. *Sporomiella* were present as single spores rather than in chains.

In Little Crow Pond, spores were quantified across 24 intervals, with *Arnium* being the most abundant, followed by *Sporomiella*. *Sporomiella* was present in 20 intervals, increasing in number after ~1940 (8 cm) and none found before ~1928 (10 cm), *Sordaria* in 17 intervals with none before ~1928 (10 cm), *Podospora* in 13 intervals very sporadically, and *Arnium* encountered in all 24 intervals.

For Pitcher Pond, *Sporomiella* was present in 16 intervals with none before ~1900 (8.5 cm), *Sordaria* in 19 intervals with none found before ~1780 (10 cm), *Podospora* in 18 intervals with none before ~1670 (14 cm), and *Arnium* in all 24 intervals, dropping in number before ~1780 (10 cm). Other coprophilous spores included in counts that were present sporadically in small numbers were *Ascodesmis, Delitschia,* and *Coniochaeta*.

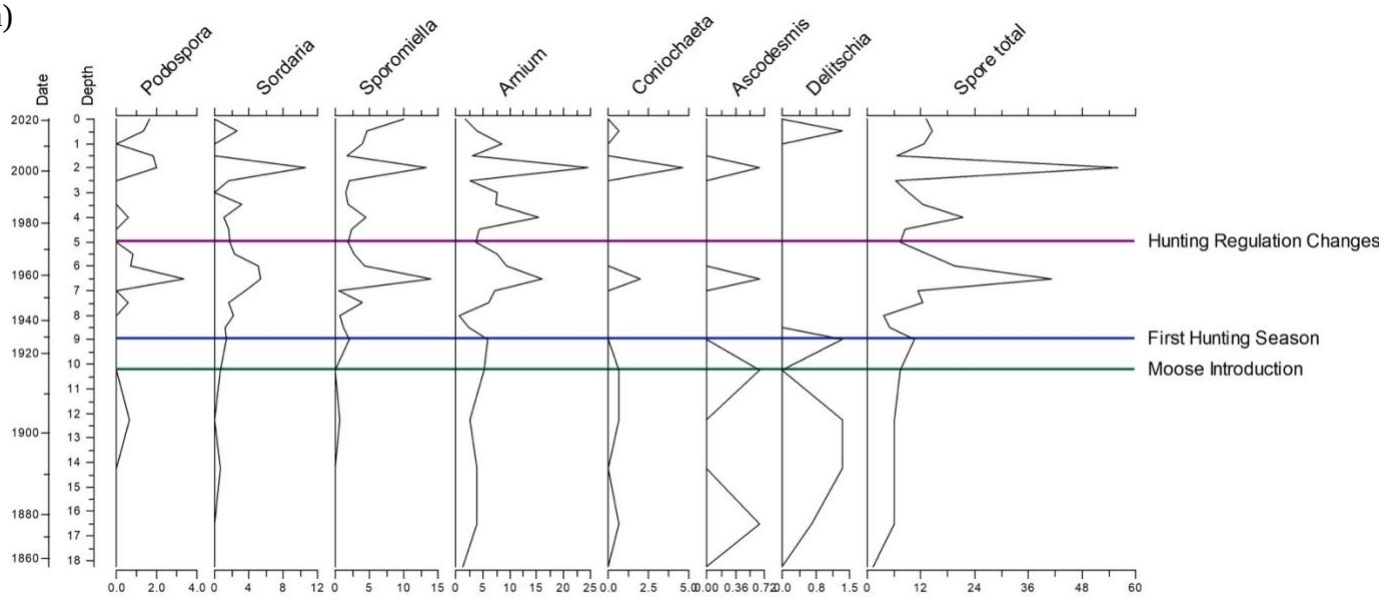
### *3.3 Spore percents (relative to* **Lycopodium** *counted)*

Spores calculated relative to *Lycopodium,* and expressed as a percentage, are low in Little Crow Pond before around 1915 (~10 cm), and increases after 1915 for *Sordaria*, *Sporomiella*, *Arnium*, and *Delitschia* until about 1930 (~9 cm) (**Figure 3.4a**). The highest peak present is 58% for the spore total in 2000 (~2 cm) for all but *Delitschia.* The second highest peak is 45% for

spore total around the year 1960 (~ 6.5 cm). Smaller peaks are present around 24% of the spore total for about 1985 (~3.5 cm) for *Sordaria*, *Sporomiella*, and *Arnium*, and mid 2010's (~1 cm) at 18% spore total, and for all but *Delitschia*. Minima for all spores include down to 6% in the late 1930's (~8.5 cm), 7% in the 1970's (~5 cm), about 6% in the 1990's (~3 cm), and 8% in the early 2010's (1.5 cm).

Pitcher Pond percent *Lycopodium* began without *Podospora*, *Sporomiella*, and *Ascodesmis*. *Sporomiella* appears around 1825 (~9 cm) at less than 1% and begins increasing with all spores around the early 1910's (~7.5 cm) until the 1930's (~5 cm) during which time the spore total increases from 10% to 35% (**Figure 3.4b**). The highest peak is present around 1946 (~4 cm) for all but *Ascodesmis* and *Delitschia* with a spore total of 46%. Subsequent peaks are seen in the early 1970's (~2.5 cm), except for *Coniochaeta*, for a spore total of 25% and the late 2010's (~0.5 cm) except for *Coniochaeta* and *Sordaria*, reaching 30% spore total. The largest decrease is in the 1950's (~3.5 cm) in all but *Ascodesmis*, decreasing to the lowest spore total of 16% since the increase in the 1910's (~7.5 cm). Another decrease is in the 2000's (~1.5 cm) except for *Ascodesmis* and *Delitschia* decreasing to 20%.

a)




b)

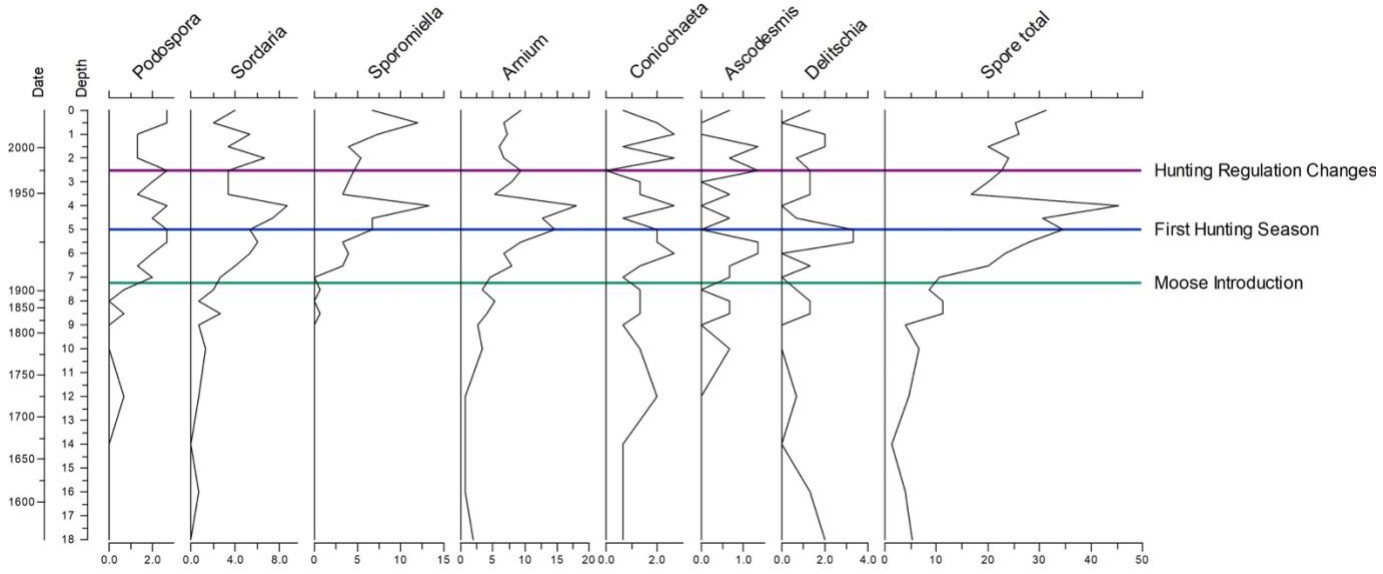


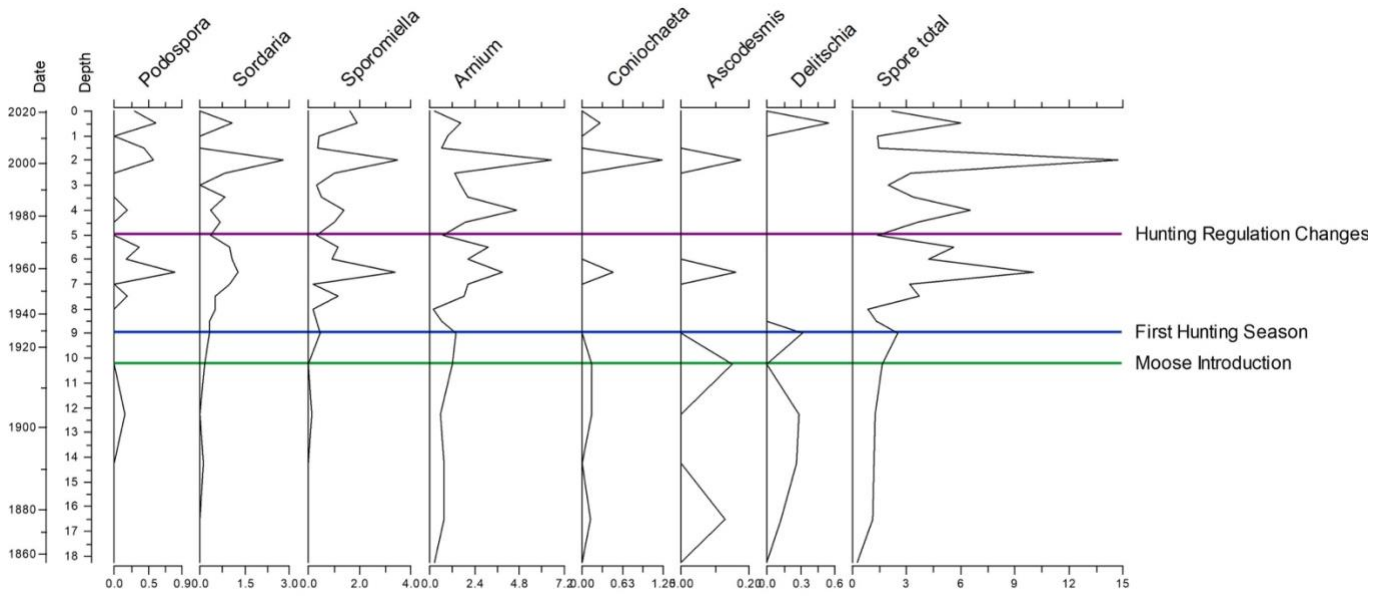

**Figure 3.4.** Coprophilous fungal spores expressed relative *Lycopodium* counted (number of spores divided by the number of *Lycopodium* counted *100), for a) Little Crow Pond and b) Pitcher Pond. Green line is for the introduction of moose in 1904, blue is for the first hunting season in 1930, and purple is for hunting regulation changes in 1973. Depth is in centimeters and date expressed in common era. Spore total is the sum of all 7 spores.

### *3.4 Accumulation rate (spores/cm$^2$/yr)*

Accumulation rates for Little Crow Pond are under 2 spores/cm$^2$/yr until 1930 (~9 cm) with a spore total accumulation rate of 2.5 spores/cm$^2$/yr, after which there is a slight dip back under 2 spores/cm$^2$/yr until the late 1940's (~7.5 cm) (**Figure 3.5a**). Other peaks are around 1960 (~6.5 cm) for all spores but *Delitschia*, early 1980's (~3.5 cm) for *Sordaria*, *Sporomiella*, *Arnium*, and *Podospora*, 2000 (~2 cm) for all spores but *Delitschia*, and late-2010's (~1 cm) for all but *Ascodesmis*. There are decreases in all spores in the 1940's (~8.25 cm) 0.85 spores/cm$^2$/yr, and the 1990's (~3.5 cm) 2 spores/cm$^2$/yr. The highest accumulation rate for total spores was 14.7 spores/cm$^2$/yr around the year 2001 (~2 cm), and the lowest accumulation rate was 0.25 spores/cm$^2$/yr for the year 1856 (~3.5 cm).

Pitcher Pond has a small accumulation peak of 1 spores/cm$^2$/yr that occurs roughly around 1625 (~16 cm) for all spores but *Sporomiella*, which was not found until roughly 1825 (~8.5 cm) (**Figure 3.5b**). Besides this peak, accumulation rates are under 1 spores/cm$^2$/yr for all spores until around 1915 (~6.5 cm). There was a peak of 5.3 spores/cm$^2$/yr spore total around 1930 (~5 cm) for all spores but *Ascodesmis*, and then a decrease followed by a slow increase until around 1940 (~4 cm) for all spores but *Ascodesmis* and *Delitschia*. There is a decrease seen overall except for *Ascodesmis* until the 1980's (~2.5 cm) that reaches a low of 0.73 spores/cm$^2$/yr in 1985 (~2.5 cm), and after that there is a slow increase that peaks in the late 2010's at 4.4 spores/cm$^2$/yr (~0.5 cm), for all but *Ascodesmis* and *Delitschia*. For Pitcher Pond spore total, the highest accumulation rate was 6 spores/cm$^2$/yr around the year 1938 (~4 cm), and the lowest was 0.15 spores/cm$^2$/yr around the year 1668 (~14 cm).

a)




b)

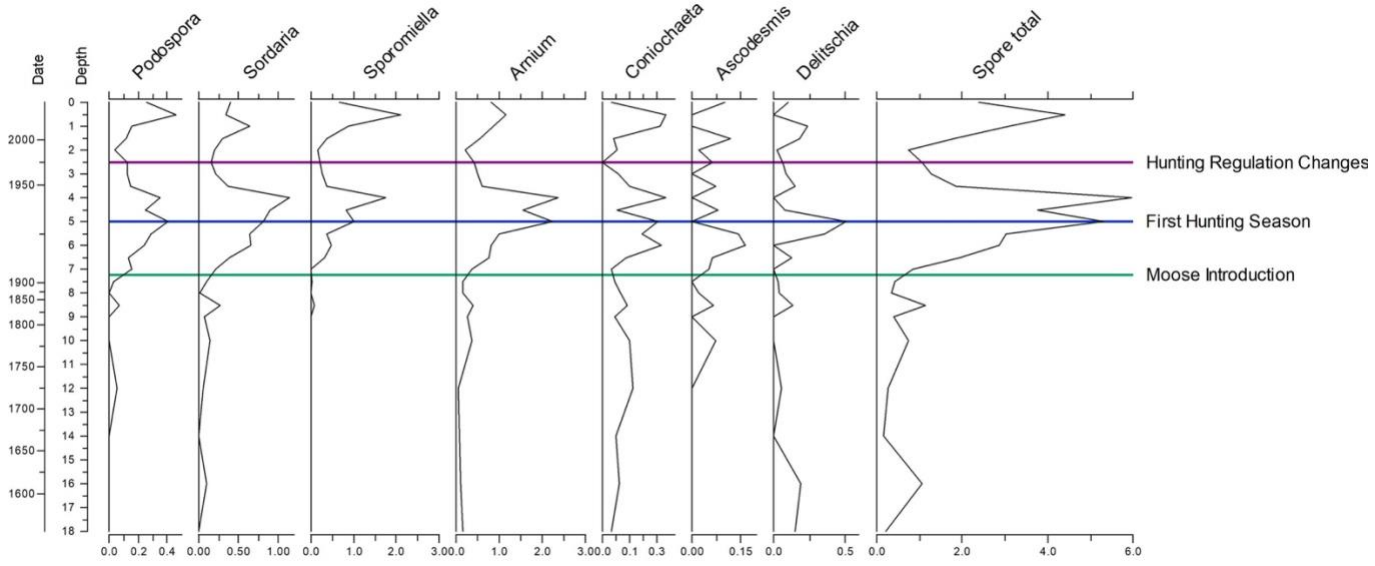
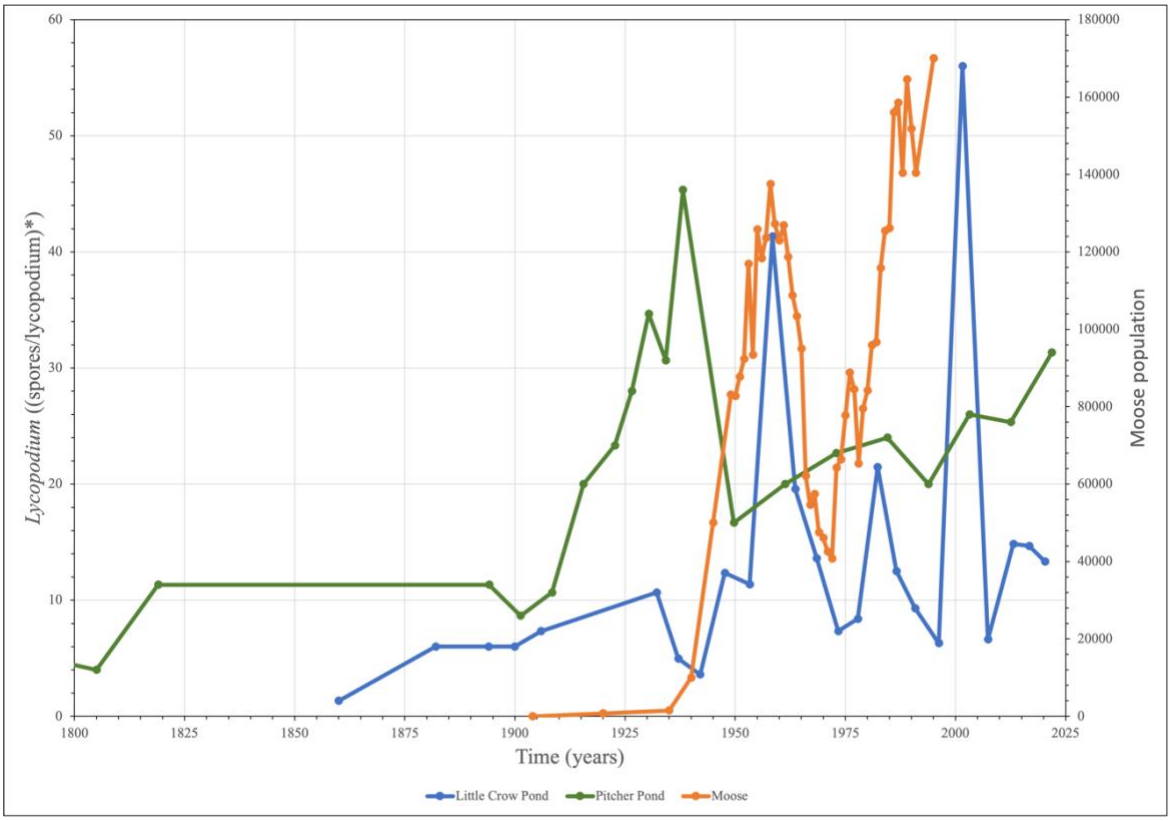



**Figure 3.5.** Accumulation rates (spores/cm$^2$/yr) of most common coprophilous spores for a) Little Crow Pond and b) Pitcher Pond. Green line is for the introduction of moose in 1904, blue is for the first hunting season in 1930, and purple is for hunting regulation changes in 1973. Depth is in centimeters, date is in common era, and spore total is the sum of all 7 spores.

a)




b)

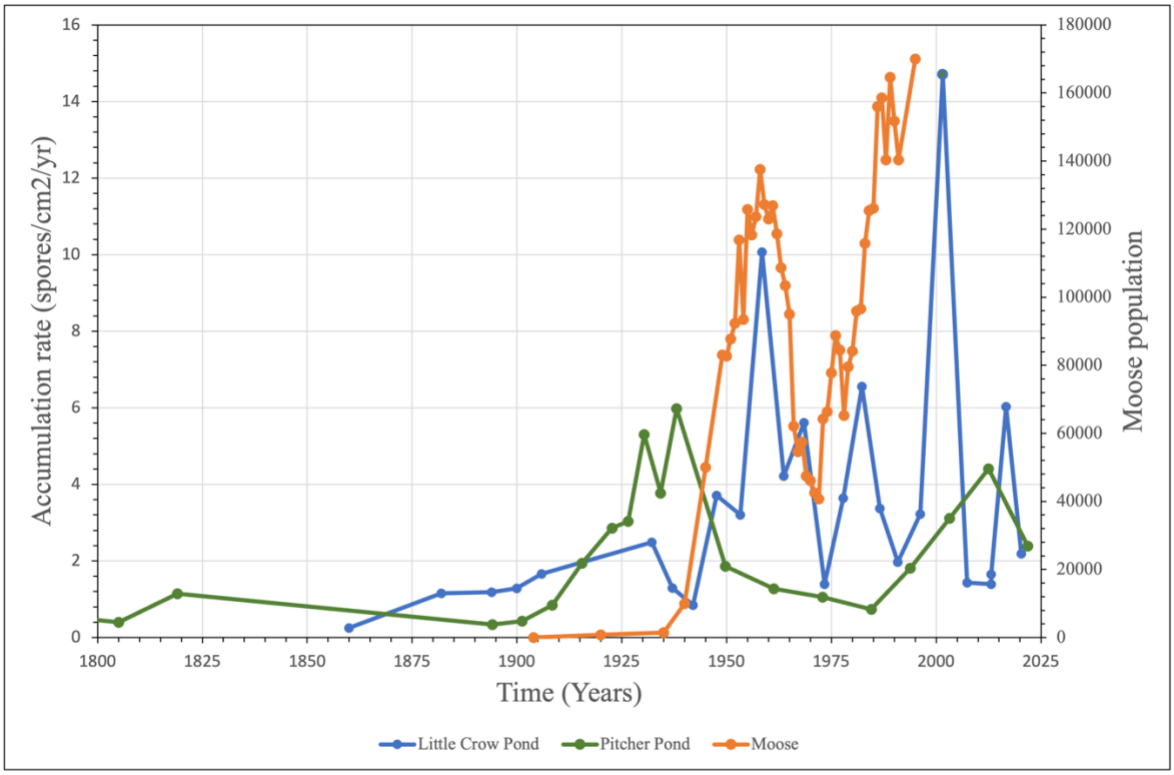



**Figure 3.6.** Comparison of a) lycopodium percents and b) accumulation rates between Little Crow Pond (blue), Pitcher Pond (green), and moose abundance (orange).

### *3.5 Climate Data*

There were no apparent trends seen in annual precipitation (**Figure 3.7**). The two locations have similar precipitation records, but on average, there was more precipitation recorded in St. John's than Terra Nova National Park in all but a few years between 1965 and 2005. After 1900, there were peaks in precipitation in 1905, 1935, 1970, the 1980's, ~1998, and 2010. Dips in precipitation for both locations are in 1915, 1930, 1940's, 1960, 1975, 1990, and ~2002. The average annual precipitation was 1433 mm for Terra Nova National Park and 1164 mm for St. John's.

Temperature also had no overarching trends present; however, unlike precipitation temperatures are higher for Terra Nova National Park then St. John's (**Figure 3.8**). There are annual temperature peaks at both locations in 1910, 1935, 1950, 1970, 1995, 2000, and 2015. Annual temperature lows for both locations are seen in 1975, 1986, and 2002. The highest temperatures for both areas are between 2000-2006, and the lowest from 1975-1985. Average annual temperature for Terra Nova National Park was 4.95$^{o}$C, and 4.91$^{o}$C for St. John's.

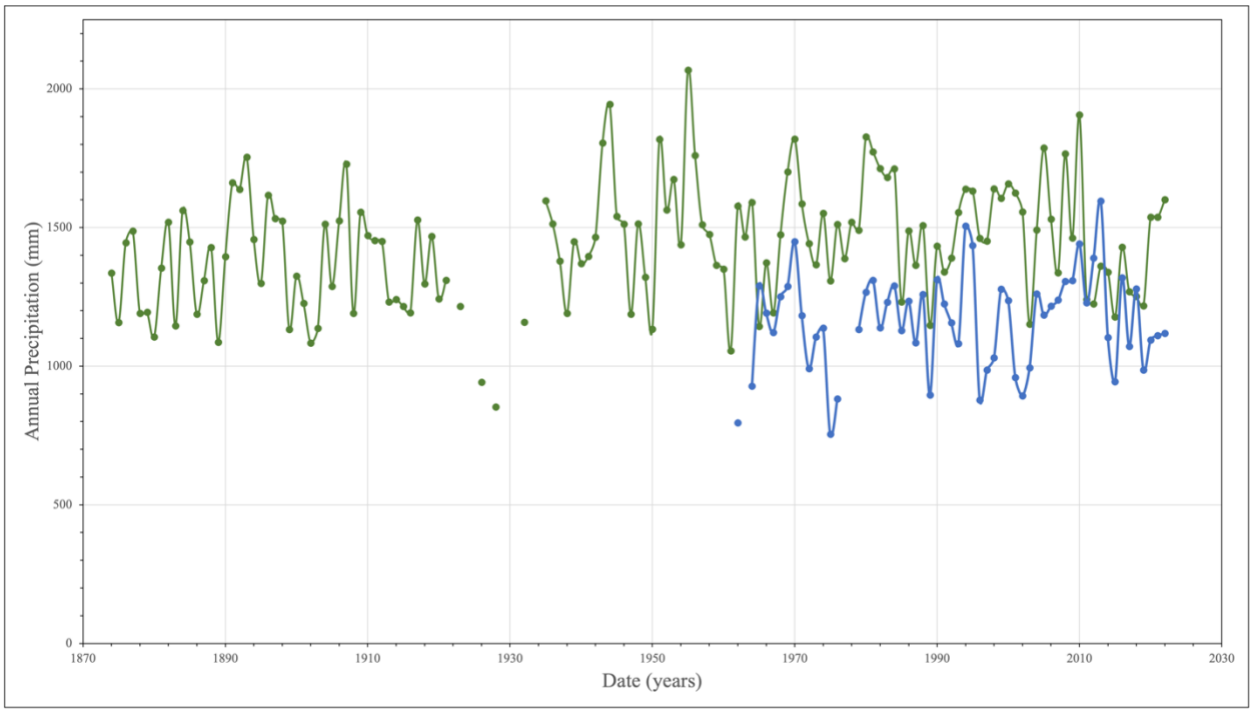



**Figure 3.7.** Total annual precipitation (mm) for Newfoundland stations near the sediment core sample collection sites. Terra Nova NP annual data was used for Little Crow Pond (blue), years 1964, 1975, 1976, 1981, and 1993 were missing 1-3 months data. St. John's annual data was used for Pitcher Pond (green), years 1889, 1895, 1897, 1921, and 2011 were missing one month of data. (Data from: https://climate.weather.gc.ca/historical_data/search_historic_data_e.html).

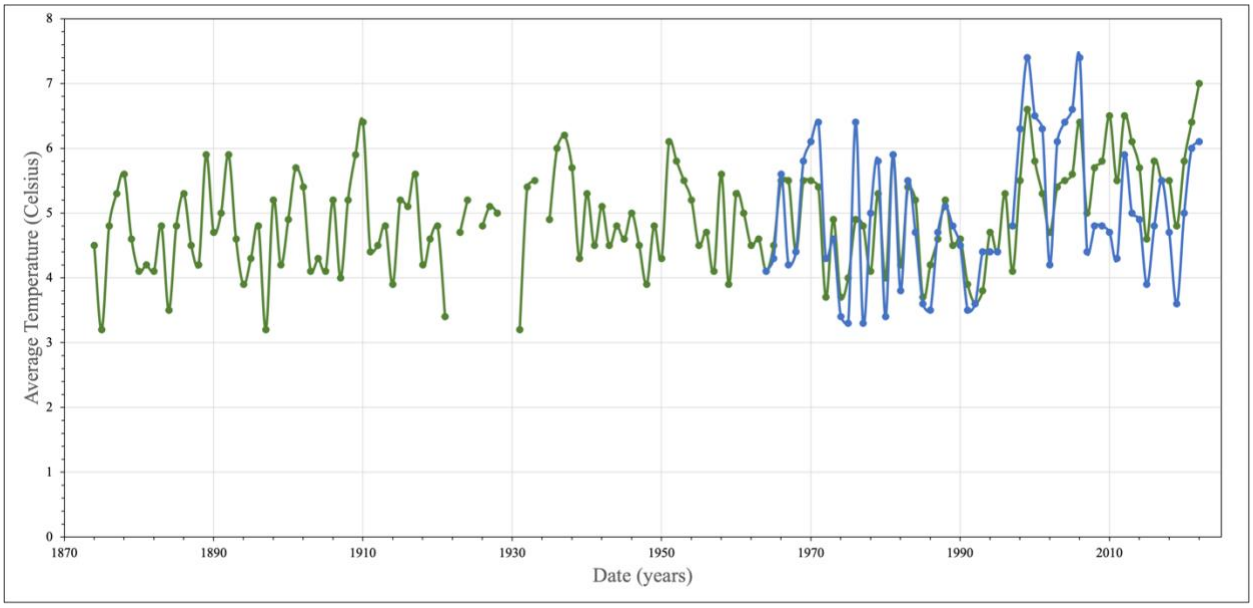



**Figure 3.8.** Average annual temperature (C$^{o}$) for Newfoundland from stations nearest the sediment core collection sites. Terra Nova NP annual data was used for Little Crow Pond (blue), years 1971, 1972, and 1975 missing one month, and 1976, and 1993 missing 3 months of data. St. John's annual data was used for Pitcher Pond (green) years 1889, 1895, 1897, 1921, and 2011 were missing one month of data. (Data from: https://climate.weather.gc.ca/historical_data/search_historic_data_e.html).

# Chapter 4: Discussion & conclusions

Coprophilous fungal spores are increasingly being used to track megafauna (Gill et al., 2012; Rozas-Davila et al., 2016; Conroy et al., 2020; Rozas-Davila 2021; Sirocko et al., 2022), animal husbandry (Cugny et al., 2010; Schofield & Edwards, 2011), and the regional arrival and presence of livestock (van Geel et al., 2003; Raper & Bush, 2009; Menozzi et al., 2010; Parker & Williams, 2012). However, across many islands, the introduction of non-native species to previously herbivore-depauperate ecosystems represents an opportunity to further test and validate fungal spores as proxies for large herbivore abundances. Here, a sharp increase in coprophilous fungal spores in Little Crow Pond sediment cores, for both percent as *Lycopodium* and accumulation rate methods at ~9 cm, corresponds with moose introduction to the island of Newfoundland, and spores roughly track changes in moose abundance. This data supports that fungal spores may act as accurate indicators of the moose population in Newfoundland. Furthermore, the presence of *Sporomiella* and a variety of other coprophilous fungi known to prefer dung increase the likelihood that the source of these spores are large herbivores. Not all dung fungal spores consistently followed moose abundance trends (*Coniochaeta, Ascodesmis*, and *Delitschia*), but many similarities are seen in trends. The Little Crow Pond coprophilous spore record more closely matches the moose population record, whereas the Pitcher Pond sediment record exhibits an increase in coprophilous spores before moose populations were known to exponentially increase across the island after introduction. The following discussion delves into the meaning of this data, and its relevance to the use of spores as a paleo-herbivore proxy, the management of moose, and the possibility of future paleolimnological reconstructions of caribou populations.

### *4.1 Low background levels of coprophilous spores in Newfoundland*

Coprophilous spores, both calculated as a percentage relative to *Lycopodium* and as accumulation rates, capture low background levels of spores prior to moose introduction in 1904, for both Little Crow Pond and Pitcher Pond, which is to be expected. The introduction of moose provides a concrete time after which we anticipate spores to increase, and thus a clear point of comparison for spore abundance before and after that date. *Sporomiella*, *Sordaria*, *Podospora*, *Arnium*, *Ascodesmis*, and *Delitschia* have been found to primarily grow on dung as their preferred growth substrate, which is why they were chosen to be included in this study (Perotti & van Asperen, 2019). A low background level of spores is common, as there are other substrates and herbivore species present that contribute coprophilous spores to forests and lakes catchments. It is not understood but has been observed and studied by some that coprophilous spore types prefer growing on the dung of different herbivore species (Nyberg & Persson, 2002). There are also other substrates that fungi will grow on when their preferred substrate, dung, is not available, which will be discussed later (Perotti & van Asperen, 2019).

Low background spore levels present before moose introduction could be from spores present on caribou feces. Caribou are the only other large herbivore present on Newfoundland, although both their population and range declined at the turn of the 19$^{th}$ century (Newfoundland and Labrador Department of Environment and Conservation, 2016). There are presently small caribou herds in both the Bonavista Peninsula and Avalon Peninsula, that have what appears to be population fluctuations, large populations which are then drastically reduced, that are still not well understood or historically documented (Bastille-Rousseau et al., 2013). If this is a cyclical density-dependent population dynamic with caribou, as some suspect, it was not reflected in spore data prior to moose introduction as counts remain steady in Pitcher Pond (which

encompasses much older spore data) and despite a large increase in caribou abundance in the late 1800's to early 1900's with a heavy decline in the 1920's (no significant increase in spores is seen until after the caribou population would have declined (Newfoundland and Labrador Department of Environment and Conservation, 2016). Also, since spores typically do not travel far due to transport mechanisms (i.e., low wind transport; Baker et al., 2016), spores on caribou dung further away (i.e. outside of the lake catchment by >100 km) would not contribute to these sediment spore records.

Smaller herbivore species could provide fecal sources for different coprophilous fungi to grow on. Two such species are the native Arctic hare (*Lepus arcticus bangsii*) and the Snowshoe hare (*Lepus americanus*), which was introduced to Newfoundland in 1864 (Strong & Leroux, 2014). *Sordaria* and *Sporomiella*-type spores have been found on hare dung (Nyberg & Persson, 2002), and thus the earlier introduction of hare to Newfoundland could contribute to the "background" levels of spores prior to moose introduction. Other possible sources for *Arnium* are cows, horses, and sheep (Nyberg & Persson, 2002); to our knowledge none of these animals are currently kept within the lake catchment. However, horses would have been present as a means of transportation in the ~1900's.

Another possible cause for a low background level of spores is that coprophilous fungi will grow on other substrates when dung is not available (Perotti & van Asperen, 2019). *Sordaria* prefers dung, but will also grow on plant vegetation or soil, and *Coniochaeta* will grow on dung but have been found ineffective in use for indicating herbivore abundance alone (Perotti & van Asperen, 2018). Thus, we thought it best to include multiple coprophilous spores to better corroborate the presence of a large herbivore population. This is becoming a more common

practice as it strengthens the veracity of spores as an indicator (Baker et al., 2016; Graham et al., 2016; Rozas-Davila 2016; Sirocko et al., 2022; van Geel et al., 2007; Wei et al., 2021).

Climatic variables including temperature, humidity, wind, and precipitation all can contribute to differences in spore abundances and accumulation rates over time. Coprophilous fungi, like all fungi, grow best in moist environments so humidity and precipitation are important for growth (Nyberg & Persson, 2002). Baker et al. (2016) noted that most dung fungal spores are deposited in lakes as precipitation runoff, rather than from short- or long-distance transportation by wind, so both variables play a part in deposition. It has been observed from wild yak (*Bos motus*) dung in the Himalayas that there are more coprophilous spores in summer rather than winter, suggesting more growth happens at warmer temperatures (Basumatary et al., 2020). We expect that most of the fungi grew during the spring, summer and fall months and that deposition of spores to the lake in the winter was minimal (especially if lakes are ice-covered). Given the short growing seasons in Newfoundland there may have been limited growth compared to areas with longer growing seasons. However, years with warmer air temperatures during the summer and greater precipitation may result in greater fungal growth and spore release.

There were no directional trends in precipitation over time; however, there were periods of higher precipitation and warmer temperatures corresponding with increases in spore abundances. It appears that the highest period of precipitation, between 1951 and 1955 (1818 to 2067 mm; for the St. John's location, as there is no data for Terra Nova NP at this time) coincides with the initial peak in island moose populations (~140,000) as well as Little Crow Pond spore abundance (42% *Lycopodium*; 10 spores/$cm^2$/yr). Temperatures during this time were above average by 0.4$^o$C. Furthermore, the highest peak in moose and Little Crow Pond spore abundance, ~2000 CE, was during a time of slightly above average precipitation (1433 mm for

Terra Nova NP and 1164 mm for St. John's location), between 1300-1600 mm. Temperature at this time, ~1995-2006, was above average by 1.4°C. During this time, ~2000 CE, there were increases in both the moose population (increase of 30,000) and Little Crow Pond spore abundance (increases of 47% *Lycopodium*; 12 spores/cm$^2$/yr). Shortly after the boom in spores for Little Crow Pond, there was a sharp decrease in abundance. Pitcher Pond spore abundance was increasing at this time (increases of 6% *Lycopodium*; 1.8 spores/cm$^2$/yr). Therefore, it appears that in years with higher precipitation and temperature, more spores were deposited in lake sediments. However, these years of higher precipitation and temperature are also years of high moose abundance, and thus we cannot disentangle the two.

### *4.2 Little Crow Pond coprophilous spore record more closely matches the moose population record*

The number of spores and the abundance of moose was more closely tracked at Little Crow Pond for both numerical treatment methods. Potential reasons for this relatively close association include location and moose abundance, pond morphometric differences, transport mechanisms, and age dating error. While fluctuations in moose abundance and spore abundance and flux are not identical (**Fig. 3.4**), they closely track one another for Little Crow Pond. Pitcher Pond spores peak earlier than the moose population for both numerical treatment methods, and subsequently varies more in spore abundance and concentrations. This is not what we would expect, as Little Crow Pond is located closer to the original site of introduction than Pitcher Pond, so moose should have reached that area sooner. The earlier appearance of spores at Pitcher Pond could be due to local spore transport mechanisms, and/or that the moose population data are estimated for the entire island of Newfoundland, and therefore not representative of local moose abundances. Also, as moose did not reach the Avalon peninsula until the 1950's, we

would also expect there to be a lag from moose introduction to spores increasing (Mercer and McLaren, 2004).

Little Crow Pond is in a less human-populated area, which may correspond to higher moose density. Historical hunting pressure is unknown for both sites, but current hunting pressure is higher with 150 more licenses issued and a 22% higher success rate than Pitcher Pond (https://www.gov.nl.ca/hunting-trapping-guide/2022-23/hunting-seasons-and-zones/island/moose/). Again, hunting pressure in the form of permits issued is largely based on moose density, so the more permits issued the higher the expected moose density for that management area, whereas success rates are not indicative of a higher moose density as there are many variables that contribute to rates. Perhaps the moose density by Pitcher Pond decreased with increasing human activity in the area, as spore accumulation rates increased ~1920's-1940's, after which it decreased again. Deer Park/Vineland Road local service district has 500 properties off a gravel road, and a campground is also close by.

Morphometric aspects of ponds and the impacts they have on spore abundance has not largely been studied, but differences in these aspects of the ponds should be considered. Little Crow Pond is twice the width and slightly deeper (2 m) than Pitcher Pond. Greater pond surface area and a larger catchment would provide a larger "funnel" to capturing spores. Pitcher Pond also has a lower spore accumulation rate than Little Crow Pond, likely representative of the smaller catchment size of Pitcher Pond and the limitations of run-off and wind transport mechanisms of spores into the pond.

The spores of fungi associated with large herbivore dung may vary as a function of the habitat in which the herbivores are living. Nyberg and Persson (2002) studied moose dung in Sweden and the effects different habitats had on coprophilous fungal growth, as well as what

species of fungi was found on which animal dung. They found that there were three times as many spores in pine forests and open mires than in spruce forests. Even though spruce forests have the most moisture, which is beneficial for fungal growth, it was concluded spruce forests had the least number of coprophilous fungal species due to higher insect abundances in the moister environment, as the insects and fungi compete for resources from the dung. This was not observed in this study, as Little Crow Pond has spruce and fir present, and had 119 *Sporomiella* spores from 1900 (~12.75 cm) across 20 intervals, while Pitcher Pond had 94 *Sporomiella* from 1900 (~7.5cm) to present in 15 intervals. Furthermore, there were more *Sporomiella* spores in spruce forests than in the pine forests or open mire. This was true in our findings as well, since Little Crow Pond did have more *Sporomiella* spores than Pitcher Pond. Nyberg and Persson (2002) observed that spores on moose dung were *Sporomiella*-types and *Sordaria*, *Podospora* and *Arnium* were present on cow dung, and one type of *Sporomiella* was present on caribou dung. *Coniochaeta*, *Ascodesmis*, and *Delitschia* were not found by the authors but were found in this study.

As the Pitcher Pond spore abundances and concentrations begin increasing earlier in the record, by ~20 years, it is also possible that the CRS model error for Pitcher Pond sediments at this interval (8.13 cm) needs to be considered. When $^{210}$Pb activity becomes low, approaching background levels (of $^{214}$Pb), CRS model error is greater. Model error at the timing of spore increase in Pitcher Pond is ±28.3 years and thus, when this is considered, the spore increase still falls within the time frame of moose introduction and population increase. The CRS model may be underestimating the age of sediments (i.e. the sediment interval dates are too old currently). For *Lycopodium* as a percent, Pitcher Pond spores peak ~20 years before spore abundance for Little Crow Pond and moose abundance peak in ~1960, which falls in the ±28.3 years error for

that pond. Afterwards, Pitcher Pond has slight peaks that match with moose abundance, but never again reach the same level as it did in ~1940, which again could be due to increasing human activity in the area. As for accumulation rate, this same pattern is observed, with Pitcher Pond spores peaking ~20 years before moose and Little Crow Pond spores, and after which there is little match to moose abundance data as spore abundance for Pitcher Pond falls and does not rise again until ~2015, during which time moose abundance has dropped and peaked. While the first peak in spores and moose abundance are close for Little Crow Pond, it appears that moose abundance begins to precede spore abundance by ~10-15 years starting in ~1970 for both methods. It would be expected to see a lag between moose abundance and spores due to transport and sedimentation mechanisms. The corresponding moose abundances and spore concentration for Little Crow Pond, and possibly Pitcher Pond (if sediment age error is reason for lack of similarities in trends), implies that coprophilous spores can be indicators of large herbivores presence and abundance, especially since spores increased in abundance after moose introduction and were largely absent before.

It is worth noting that in addition to dating error, each sediment slice represents a “window" of time, i.e. several years are captured in one 0.25 cm slice. As we analyze sections deeper into a core, sediment becomes more compacted in each slice, and therefore more time is represented in a window. Thus, the range of time captured by a slice increases from the surface of the core to deeper depths inherently increasing the “error” or dating window making comparisons to moose abundance data increasingly more challenging further back in time.

### *4.3 Abundance vs concentration data*

Moose abundance data and percent *Lycopodium* concentration data for total spores visually, for Little Crow Pond, generally followed similar trends. In Little Crow Pond, percent *Lycopodium* concentration increases as there is an increase in moose abundance after introduction, followed by a decrease after the first hunting season of 1930 (Mercer & McLaren, 2002). There is another peak around 1960, which corresponds with an increase in population from 1953-56 reported by Mercer and McLaren (2002), that was likely due to lack of predators and abundance of food. There was a period of moose abundance decline in the mid to late 1960's, due to localized over-hunting and over-browsing that corresponds with a decrease of spores in the 1970's (Department of Fisheries, Forestry, and Agriculture, 2022). After hunting regulation changes in 1973, because of a declining population which restricted licenses granted, and therefore increased moose abundance, increases in spores can be seen (Mercer & McLaren, 2002). A percent *Lycopodium* peak is seen in 2000, matching up with high moose abundance in the 1990's after decades of hunting restrictions. While *Coniochaeta*, *Ascodesmis*, and *Delitschia* did exist in low numbers before introduction, afterwards they did not follow population trends at Little Crow Pond as *Podospora, Sordaria*, *Sporomiella,* and *Arnium* did, their presence being much more sporadic. Pitcher Pond percent *Lycopodium* had all spores present before moose introduction, but *Sporomiella,* and had an increase in all of them after introduction. Peaks that match up with moose abundance are seen after introduction until the first hunting season and just after hunting regulations in 1973.

Like the percent *Lycopodium* data, accumulation rate data and moose abundances had similar trends, more so for Little Crow Pond. Accumulation rates for Little Crow Pond increase for *Sordaria, Sporomiella, Arnium, Delitschia*, and spore total after moose introduction until the

first hunting season. Other peaks are around 1960, mid-1980's, 2000, as would be expected based on moose abundance trends discussed above. Decreases are in the 1940's, after the first hunting season, and the 1990's, which is when moose abundance was high. Again, for Little Crow Pond *Coniochaeta*, *Ascodesmis*, and *Delitschia* existed in low numbers before introduction and then did not follow population trends. Pitcher Pond accumulation rates do not as closely follow moose abundance as for Little Crow Pond, with most trends appearing to lag. One trend that does align is that all spore types are present before moose introduction in low amounts and show an increase in all of them after introduction. There is a peak when the first hunting season occurred, and then a decrease followed by a slow increase until around 1940. A decrease is seen overall in accumulation rate until 1973, with the hunting regulation changes and the number of licenses were limited.

When comparing the accumulation rates in this small-scale study to that of Etienne et al. (2012), Graham et al. (2016), Conroy et al., (2020), ours are much lower. Etienne et al. (2012) had rates of ~90-115 spores/cm$^2$/yr for ~6,000 sheep over 45 years, and ~40-80 spores/cm$^2$/yr for ~2,000 cows and sheep over 105 years. Our lower rates may be due to the cattle in the study by Etienne et al. (2012) were all directly in contact with the study lake and at a higher density, whereas only a few moose would be expected to be frequenting our study lake catchments, at a much lower density than domesticated herds. Accumulation rates for Graham et al. (2016) cores from a small lake had a maximum of 200 spores/cm$^2$/yr when mammoths were present. Conroy et al. (2020) studied megafauna extinction and large herbivore increases surrounding 4 lakes, estimating population based on bone fossils and spore abundance. Accumulation rates varied 50-100 spores/cm$^2$/yr, for modern to 13,000-year-old sediments for *Bison*, *Alces*, *Ovibos*, *Rangifer*, and *Cervus* species, and up to 200 spores/cm$^2$/yr 13,000 to 24,000-year-old sediments for

megafauna species *Mammuthus*, *Equus*, *Saiga*, *Bison*, *Ovibos*, and *Rangifer*. We had rates of ~1-15 spores/cm$^2$/yr for 0 to 170,000 moose over 150 years. Again, this is a total number for moose present on the island and does not reflect moose density in the area. Historically, large mammal populations also would have been in higher densities relative to contemporary populations that have to deal with humans and all that we do to them and their habitats. Hunting is also more feasible today than in the past due to less limitations (i.e., access to shot guns, higher density of roads and trails, vehicles such as ATV's, refrigeration). More spores present in the megafauna studies could be due to both size of the contributing species (and thus more feces), as well as lake size. The larger the lake catchment the more spores can be deposited.

Based on the results of this study, we found that both numerical treatment methods for Little Crow Pond closely matched up with moose abundance data visually. Accumulation rates are more accurate when the entire sample is counted, but is very time consuming, therefore a percentage is more favorable.

### *4.4 Study limitations and Future Research*

Ideally, there would be multiple sediment core samples collected from various lakes in different locations across Newfoundland, and multiple sediment core samples taken from each location. In the scope of this project that was not possible, and therefore results are limited by the amount of data and variability two cores can provide. Only analyzing two cores could skew data by under- or over-representing spore abundance. It also means that data is not representative of Newfoundland as a whole, but only for the Avalon and Bonavista peninsulas. This is especially important as moose abundance varies spatially. Data was also limited by the number of intervals counted, as so few data points overlapping with moose abundance data hindered correlation tests.

Perhaps the biggest limitation of this study and its validation was that the spore and moose abundance data available was not able to be statistically correlated as there were so few data points overlapping in time. For both ponds, there were few sediment samples that fell in the period with known moose abundances, with Little Crow Pond having 10 samples, and Pitcher Pond with only 5 samples. Unfortunately, this limitation was not able to be remedied even with the application of a running mean for the moose abundance (as moose data is annual and sediment slices represent 3-4 years). The Pearson correlation test was applied for Little Crow Pond spores with running means of 4-7 years of moose abundance data, resulting in positive, but weak correlations. This issue could be solved in future research if more spore intervals were counted and used to compare with moose data.

Some studies have found differences in spores present depending on where in a lake the sediment core was collected, and therefore could be a researched aspect of future studies. In 2009, Raper & Bush studied the correlation between domestic livestock, cows, and the coprophilous spore *Sporomiella* in nearby ponds and found the more cattle livestock present, the more *Sporomiella* there was in lake sediments. They also found that more spores are found closer to shore rather than the center of the pond, as these spores don't disperse aerially and instead are usually deposited with runoff. Another study by Parker & Williams (2012), also with cattle, found that this shoreline-spore abundance effect is only within 20 meters of a shoreline. Etienne et al. (2013) also studied spore distribution in lakes for *Sporomiella* and *Sordaria* from livestock. They, however, found no correlation between spores and shoreline distance, but instead distance from an inlet source; the closer the core sample was to the inlet, the more spores were present. These studies should be considered as the location from where the sample is taken, traditionally from the lakes center and deepest point (how our samples were collected), influences spores.

Management of moose in Newfoundland is vital, and to that end so is abundance data that could be created in future studies. As an introduced species in Newfoundland, moose are economically important for hunting, tourism, and food, but they also are changing the landscape by preferential consumption and a hazard to drivers. Knowing how many moose are on the island, and how they have spread and where they have succeeded with past abundance numbers could lead to more informed management decisions about moose, such as how many licenses should be issued and in which management areas. Surface sediment samples could provide moose population density data in areas in which direct counting of moose is difficult. Another reason for management of moose is the budding awareness of the importance of large herbivores' role in the carbon cycle, and how they can aid in carbon sequestration through trophic rewilding (Schmitz et al., 2023).

In addition to moose abundance data, this methodology also has the potential to be transferable to inferring sensitive caribou populations in Newfoundland and across the subarctic. In a single decade, the caribou population declined by 60%, from 94,000 in the 1990's to 32,000 in 2013, a pattern seen previously in the late 1800's to early 1900's, when there was a caribou population of 100,00 that swiftly declined into the 1920's (Newfoundland and Labrador Department of Environment and Conservation, 2016). While it was concluded this was due to density-dependence and the island's ability to only support so many caribou, population records only go back to the 1890's (Newfoundland and Labrador Department of Environment and Conservation, 2016). This limits data of a pattern of rapid increase followed by sharp decline to two instances, and while it is seen in caribou populations in other parts of eastern Canada, Alaska, and Greenland, historical records that go back further in time would better corroborate such a pattern. Changes in caribou population before humans would indicate climate as the

source, whereas after humans they could serve as a driver in population fluxes (Duda et al., 2021). Historical populations are currently inferred with paleolimnology, dendrochronology, hoof scars, and Indigenous knowledge (Gunn, 2011). On Newfoundland, as of 2019 there is an estimated 30,580 caribou and 120,000 moose, which is the highest concentration of moose in North America (https://www.gov.nl.ca/hunting-trapping-guide/2021-22/labrador-caribou/; https://www.huntingnewfoundlandlabrador.com/species/moose).

As this is an exploratory study, the numerical treatment methodology could be further tested with larger sample sizes to see if there is one that is more accurate for tracking spores and larger herbivore abundance data. There is no universal method in place for paleolimnology, so this could be further studied and determined.

According to van Asperen et al. (2021), coprophilous spores are just one proxy, and with correlation with other paleo proxies the data they provide become more significant through validation, and therefore should be carried out in any future research. In one sedimentary core, multiple proxies are present, and by comparing results of each proxy they become more valid (if they correlate with one another). However, if the proxies rely on linked processes, their validation becomes circumstantial (van Asperen et al, 2021). Graham et al. (2016) applied the use of multiple paleo proxies in their study of wooly mammoths (*Mammuthus primigenius*) extinction on St. Paul Island, Alaska, USA; *sed*aDNA, coprophilous spores (*Sporomiella*, *Podospora*, and *Sordaria*), cladoceran and diatom assemblages, radiocarbon dates from mammoth remains, sediment magnetic susceptibility, and pollen accumulation rate. These methods combined supported one another, together showing the decline and disappearance of mammoth on the island. Therefore, the use of multiple paleo proxies it is future direction of this

study, as the use of and correlation with other proxies would corroborate and validate the results of the coprophilous spores as indicators for larger herbivores.

Further research could include the proxy fecal lipids, an evolving paleolimnology abundance tool. Fecal lipids are fats like cholesterol that are present in feces once they pass through the digestive system of an animal (Harrault et al., 2019). Fecal lipids specifically used for paleolimnology abundance studies are two subgroups called sterols and stanols that are in all eukaryotes at some level (Gallant et al., 2020). 5β-stanols are particularly useful to indicate feces, and are generally well-preserved (Harrault et al., 2019). Based on which sterols and stanols are present in a sample, they can be used as indicators of a species (Ortiz et al., 2018). Schroeter et al. (2020) was able to examine human and herbivore sterols and stanols at the same site by determining percentages present and distinguishing which were human specific or herbivore specific. For herbivores, Harrault et al. (2019) was able to specifically distinguish between moose and caribou fecal lipids, which is not possible with coprophilous spores. Furthermore, sedimentary fecal lipids are becoming more common for tracking animal abundance in lake catchments, and moose on Newfoundland would present a unique opportunity to compare fecal lipids against known population records much like we have done with coprophilous spores.

Sedimentary DNA (*sed*aDNA) is a paleo proxy that has become more widely used in the last 20 years, and thus would be a future tool to use (Edwards, 2020). This proxy has been utilized to track changes in species over time by examining biological matter from animals, plants, and microbes to determine taxonomic groups to a high resolution (Duda et al., 2021). Initially *sed*aDNA was used with plants, but now its uses are expanding to include mammals (Edwards, 2020). The main methods *sed*aDNA is used is shotgun sequencing and

metabarcoding, and the main issue is sample contamination (Edwards, 2020). Lee et al. (2022) further proposed that *sed*aDNA could be used to identify coprophilous spores present that are not as well preserved and identifiable as *Sporomiella*-types.

In summary, future research for moose and caribou on Newfoundland would involve collecting various sediment cores from across the island to fully represent moose abundance and counting more intervals for each core than in this study. Sample sites would include both national parks, Gros Morne and Terra Nova, and the moose management areas, thereby providing data that would be useful to managers. Along with sampling different locations, multiple sediment core samples taken from each location would increase accuracy of abundance data provided by dung fungal spores. Core samples could be taken from the center of the lake, closer to the edge, and close and distant to any inlet sources to compare spore counts and determine if there is a difference as Raper & Bush (2009) and Etienne et al. (2013) did. Numerical treatment methods could both be tested again to see if one is more accurate. Multiple paleo proxies could be used together to further validate any findings.

### *4.5 Conclusions*

Moose were introduced to Newfoundland almost 120 years ago, and since then their population has flourished. *Sporomiella*, and increasingly an array of coprophilous fungal spores, have been used to indicate megafauna and large herbivores through the nature of their life cycle and preservation over time. As hypothesized, one of the ponds, Little Crow Pond, did have a spore record that closely matched moose population data. As expected, the two ponds differed in spore record accuracy. The error in dating could account for this, and if so the Pitcher Pond *Lycopodium* as a percent spore record does match with moose abundance, albeit with

underestimated ages. Overall, I was able to produce a spore record for two ponds using two different numerical treatment methods. These findings offer a validation of the use of dung fungal spores as an indicator for larger herbivores, especially when multiple spores are used.

# References

Appleby P.G. (2001) Chronostratigraphic techniques in recent sediments. In: Last WM, Smol JP (eds) Tracking environmental change using lake sediments. Volume 1: basin analysis, coring, and chronological techniques, vol 1. Kluwer, Dordrecht, pp 171–203

Aptroot, A., & van Geel, B. (2006). Fungi of the colon of the Yukagir mammoth and from stratigraphically related permafrost samples. *Review of Palaeobotany and Palynology*, *141*(1-2), 225–230. https://doi.org/10.1016/j.revpalbo.2005.04.006

Baker, A. G., Bhagwat, S. A., & Willis, K. J. (2013). Do dung fungal spores make a good proxy for past distribution of large herbivores? *Quaternary Science Reviews*, *62*, 21–31. https://doi.org/10.1016/j.quascirev.2012.11.018

Baker, A. G., Cornelissen, P., Bhagwat, S. A., Vera, F. M., & Willis, K. J. (2016). Quantification of population sizes of large herbivores and their long-term functional role in ecosystems using dung fungal spores. *Methods in Ecology and Evolution*, *7*(11), 1273–1281. https://doi.org/10.1111/2041-210X.12580

Barnard, J. L. (2020). The Bison and the Cow: Food, Empire, Extinction. *American Quarterly*, *72*(2), 377–401. https://doi.org/10.1353/aq.2020.0023

Basumatary, & McDonald, H. G. (2017). Coprophilous fungi from dung of the Greater One-Horned Rhino in Kaziranga National Park, India and its implication to paleoherbivory and paleoecology. *Quaternary Research*, *88*(1), 14–22. https://doi.org/10.1017/qua.2017.34

Basumatary, S. K., Singh, H., van Asperen, E. N., Tripathi, S., McDonald, H. G., & Pokharia, A. K. (2020). Coprophilous and non-coprophilous fungal spores of Bos mutus modern dung from the Indian Himalaya; implications to temperate paleoherbivory and paleoecological

analysis. *Review of Palaeobotany and Palynology*, *277*, 104208–. https://doi.org/10.1016/j.revpalbo.2020.104208

Benbow, M. E., Receveur, J. P., & Lamberti, G. A. (2020). Death and Decomposition in Aquatic Ecosystems. *Frontiers in Ecology and Evolution*, *8*. https://doi.org/10.3389/fevo.2020.00017

Bergerud, A. T., Manuel, F., & Whalen, H. (1968). The Harvest Reduction of a Moose Population in Newfoundland. *The Journal of Wildlife Management*, *32*(4), 722–728. https://doi.org/10.2307/3799546

Big Game License and Application Draw. (n.d.) Government of Newfoundland and Labrador. Retrieved from https://www.gov.nl.ca/hunting-trapping-guide/2022-23/new-for-2022-23/

Bird, L. (2018). Moose are eating Newfoundland harvests, says farmers, and provincial laws aren't helping. *CBC News*. Retrieved from: https://www.cbc.ca/news/canada/newfoundland-labrador/moose-eating-harvests-say-nl-farmers-1.5365144

Borish, D., Cunsolo, A., Snook, J., Shiwak, I., Wood, M., HERD Caribou Project Steering Committee, Mauro, I., Dewey, C., & Harper, S. L. (2021). "Caribou was the reason, and everything else happened after": Effects of caribou declines on Inuit in Labrador, Canada. *Global Environmental Change*, *68*, 102268–. https://doi.org/10.1016/j.gloenvcha.2021.102268

Brown MacPherson, J. (1995). A 6 ka BP Reconstruction for the Island of Newfoundland from a Synthesis of Holocene Lake-Sediment Pollen Records. *Géographie Physique et Quaternaire*, *49*(1), 163–182. https://doi.org/10.7202/033035ar

Bump, J. K. (2018). Fertilizing riparian forests: nutrient repletion across ecotones with trophic rewilding. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1761), 20170439–. https://doi.org/10.1098/rstb.2017.0439

Burge, D. R. L., Edlund, M. B., & Frisch, D. (2018). Paleolimnology and resurrection ecology: The future of reconstructing the past. *Evolutionary Applications*, *11*(1), 42–59. https://doi.org/10.1111/eva.12556

Cohen, A., (2003). *Paleolimnology: The History and Evolution of Lake Systems.* Oxford University Press. P. 3-18.

Comandini, O., & Rinaldi, A. C. (2004). Tracing megafaunal extinctions with dung fungal spores. *Mycologist*, *18*(4), 140–142. https://doi.org/10.1017/S0269915X0400401X

Conroy, Baker, A. G., Jones, V. J., Van Hardenbroek, M., Hopla, E. J., Collier, R., Lister, A. M., & Edwards, M. E. (2020). Tracking late-quaternary extinctions in interior Alaska using megaherbivore bone remains and dung fungal spores. *Quaternary Research*, *97*, 99–110. https://doi.org/10.1017/qua.2020.19

Condon, B., & Adamowicz, W. (1995). economic value of moose hunting in Newfoundland. *Canadian Journal of Forest Research*, *25*(2), 319–328. https://doi.org/10.1139/x95-036

Cugny, Mazier, F., & Galop, D. (2010). Modern and fossil non-pollen palynomorphs from the Basque mountains (western Pyrenees, France): the use of coprophilous fungi to reconstruct pastoral activity. *Vegetation History and Archaeobotany*, *19*(5/6), 391–408. https://doi.org/10.1007/s00334-010-0242-6

Davis, O. K. (1987). Spores of the dung fungus Sporormiella; increased abundance in historic sediments and before Pleistocene megafaunal extinction. *Quaternary Research*, *28*(2), 290–294. https://doi.org/10.1016/0033-5894(87)90067-6

Department of Fisheries, Forestry, and Agriculture. (2022). 2022-2026 Newfoundland and Labrador Moose Management Plan.

Doughty, C. E., Roman, J., Faurby, S., Wolf, A., Haque, A., Bakker, E. S., Malhi, Y., Dunning, J. B., & Svenning, J.-C. (2016). Global nutrient transport in a world of giants. *Proceedings of the National Academy of Sciences - PNAS*, *113*(4), 868–873. https://doi.org/10.1073/pnas.1502549112

Duda, M. P., Hargan, K. E., Michelutti, N., Blais, J. M., Grooms, C., Gilchrist, H. G., Mallory, M. L., Robertson, G. J., & Smol, J. P. (2021). Reconstructing Long-Term Changes in Avian Populations Using Lake Sediments: Opening a Window Onto the Past. *Frontiers* in Ecology and Evolution, 9. https://doi.org/10.3389/fevo.2021.698175

Duggan, A. T., Harris, A. J. T., Marciniak, S., Marshall, I., Kuch, M., Kitchen, A., Renaud, G., Southon, J., Fuller, B., Young, J., Fiedel, S., Golding, G. B., Grimes, V., & Poinar, H. (2017). Genetic Discontinuity between the Maritime Archaic and Beothuk Populations in Newfoundland, Canada. *Current Biology*, *27*(20), 3149–3156.e11. https://doi.org/10.1016/j.cub.2017.08.053

Edwards, M. E. (2020). The maturing relationship between Quaternary paleoecology and ancient sedimentary DNA. Quaternary Research, 96, 39–47. https://doi.org/10.1017/qua.2020.52

Ellis, N. M., & Leroux, S. J. (2016). Moose directly slow plant regeneration but have limited indirect effects on soil stoichiometry and litter decomposition rates in disturbed maritime

boreal forests. Functional Ecology, 31(3), 790–801. https://doi.org/10.1111/1365-2435.12785

Etienne, D., Wilhelm, B., Sabatier, P., Reyss, J.-L., & Arnaud, F. (2013). Influence of sample location and livestock numbers on Sporormiella concentrations and accumulation rates in surface sediments of Lake Allos, French Alps. *Journal of Paleolimnology*, *49*(2), 117–127. https://doi.org/10.1007/s10933-012-9646-x

Fabisch, T., Gershenzon, J., & Unsicker, S. B. (2019). Specificity of Herbivore Defense Responses in a Woody Plant, Black Poplar (Populus nigra). *Journal of Chemical Ecology*, *45*(2), 162–177. https://doi.org/10.1007/s10886-019-01050-y

Forbes, E. S., Cushman, J. H., Burkepile, D. E., Young, T. P., Klope, M., Young, H. S., & Brody, A. (2019). Synthesizing the effects of large, wild herbivore exclusion on ecosystem function. *Functional Ecology*, *33*(9), 1597–1610. https://doi.org/10.1111/1365-2435.13376

Gallant, Kimpe, L. E., Hargan, K. E., & Blais, J. M. (2020). Tracking the history of 20th century cultural eutrophication in High Arctic waterbodies. *Anthropocene*, *31*, 100250–. https://doi.org/10.1016/j.ancene.2020.100250

Gelorini, Vanessa & Verbeken, Mieke & Lens, Luc & Eggermont, Hilde & Odgaard, Bent & Verschuren, Dirk. (2012). Effects of land use on the fungal spore richness in small crater-lake basins of western Uganda. Fungal Diversity. 55. 10.1007/s13225-012-0155-z.

Giralt, S., Cabrera, L., & Gierlowski-Kordesch, E. H. (2010). Paleolimnology. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *294*(1), 1–3. https://doi.org/10.1016/j.palaeo.2010.05.030

Glew. (1988). A portable extruding device for close interval sectioning of unconsolidated core samples. *Journal of Paleolimnology*, *1*(3), 235–239. https://doi.org/10.1007/BF00177769

Glew, & Smol, J. P. (2016). A push corer developed for retrieving high-resolution sediment cores from shallow waters. *Journal of Paleolimnology*, *56*(1), 67–71. https://doi.org/10.1007/s10933-015-9873-z

Gill, Williams, J. W., Jackson, S. T., Lininger, K. B., & Robinson, G. S. (2009). Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. *Science (American Association for the Advancement of Science)*, *326*(5956), 1100–1103. https://doi.org/10.1126/science.1179504

Goudie R.I., Scheidegger C., Hanel C., Munier A., Conway E. (2011). New population models help explain declines in the globally rare boreal felt lichen *Erioderma pedicellatum* in Newfoundland. *Endangered Species Res*. 13:181-189. https://doi.org/10.3354/esr00326

Gordon, I. J., Hester, A. J., & Festa-Bianchet, M. (2004). The Management of Wild Large Herbivores to Meet Economic, Conservation and Environmental Objectives. *The Journal of Applied Ecology*, *41*(6), 1021–1031. https://doi.org/10.1111/j.0021-8901.2004.00985.x

Gosse, J., Hermanutz, L., McLaren, B., Deering, P., & Knight, T. (2011). Degradation of Boreal Forests by Non-native Herbivores in Newfoundland's National Parks: Recommendations for Ecosystem Restoration. *Natural Areas Journal*, 31(4), 331–339. https://doi.org/10.3375/043.031.0403

Graf, M.-T., & Chmura, G. L. (2006). Development of modern analogues for natural, mowed and grazed grasslands using pollen assemblages and coprophilous fungi. *Review of Palaeobotany and Palynology*, *141*(1), 139–149. https://doi.org/10.1016/j.revpalbo.2006.03.018

Graham, R. W., Belmecheri, S., Choy, K., Culleton, B. J., Davies, L. J., Froese, D., Heintzman, P. D., Hritz, C., Kapp, J. D., Newsom, L. A., Rawcliffe, R., Saulnier-Talbot, É., Shapiro, B., Wang, Y., Williams, J. W., & Wooller, M. J. (2016). Timing and causes of mid-Holocene mammoth extinction on St. Paul Island, Alaska. *Proceedings of the National Academy of Sciences - PNAS*, *113*(33), 9310–9314. https://doi.org/10.1073/pnas.1604903113

Gunn, A. (2011). *Northern caribou population trends in Canada*. Canadian Councils of Resource Ministers.

Hargan, K. E., Nelligan, C., Jeziorski, A., Rühland, K. M., Paterson, A. M., Keller, W., & Smol, J. P. (2016). Tracking the long-term responses of diatoms and cladocerans to climate warming and human influences across lakes of the Ring of Fire in the Far North of Ontario, Canada. *Journal of Paleolimnology*, *56*(2-3), 153–172. https://doi.org/10.1007/s10933-016-9901-7

Harrault L, Milek K, Jarde´ E, Jeanneau L, Derrien M, Anderson DG (2019). Faecal biomarkers can distinguish specific mammalian species in modern and past environments. PLoS ONE 14(2): e0211119. https://doi.org/10.1371/journal. pone.0211119

Huntzinger, M., Karban, R., Young, T. P., & Palmer, T. M. (2004). Relaxation of induced indirect defenses of acacias following exclusion of mammalian herbivores. *Ecology (Durham)*, *85*(3), 609–614. https://doi.org/10.1890/03-3056

Langor, D. W., Cameron, E. K., MacQuarrie, C. J. K., McBeath, A., McClay, A., Peter, B., Pybus, M., Ramsfield, T., Ryall, K., Scarr, T., Yemshanov, D., DeMerchant, I., Foottit, R., & Pohl, G. R. (2014). Non-native species in Canada's boreal zone: diversity,

impacts, and risk. *Environmental Reviews*, *22*(4), 372–420. https://doi.org/10.1139/er-2013-0083

Lee, Claire M., van Geel, Bas & Gosling, William D. (2022). On the Use of Spores of Coprophilous Fungi Preserved in Sediments to Indicate Past Herbivore Presence. *Quaternary*, *5*(3), 30–. https://doi.org/10.3390/quat5030030

Leroux, S. J., Charron, L., Hermanutz, L., & Feltham, J. (2021). Cumulative effects of spruce budworm and moose herbivory on boreal forest ecosystems. *Functional Ecology*, *35*(7), 1448–1459. https://doi.org/10.1111/1365-2435.13805

Leroux, S. J., Wiersma, Y. F., & Vander Wal, E. (2020). Herbivore Impacts on Carbon Cycling in Boreal Forests. *Trends in Ecology & Evolution (Amsterdam)*, *35*(11), 1001–1010. https://doi.org/10.1016/j.tree.2020.07.009

Lev-Yadun, S., & Gutman, M. (2013). Carrion odor and cattle grazing: Evidence for plant defense by carrion odor. *Communicative & Integrative Biology*, *6*(6), e26111–e26111. https://doi.org/10.4161/cib.26111

License Fees. (n.d.) Government of Newfoundland and Labrador. Retrieved from https://www.gov.nl.ca/hunting-trapping-guide/2022-23/new-for-2022-23/

Macdonald, D. W., Boitani, L., Dinerstein, E., Fritz, H., & Wrangham, R. (2013). Conserving large mammals: are they a special case? In *Key Topics in Conservation Biology* (Vol. 2, pp. 277–312). Wiley-Blackwell. https://doi.org/10.1002/9781118520178.ch16

Martin, J. M., Short, R. A., Plumb, G. E., Markewicz, L., Van Vuren, D. H., Wehus-Tow, B., Otárola-Castillo, E., & Hill, M. E. (2023). Integrated evidence-based extent of occurrence for North American bison (Bison bison) since 1500 CE and before. *Ecology (Durham)*, *104*(1), e3864–n/a. https://doi.org/10.1002/ecy.3864

Massey, F. P., Roland Ennos, A., & Hartley, S. E. (2007). Herbivore specific induction of silica-based plant defences. *Oecologia*, *152*(4), 677–683. https://doi.org/10.1007/s00442-007-0703-5

McGill, B. J., Dornelas, M., Gotelli, N. J., & Magurran, A. E. (2015). Fifteen forms of biodiversity trend in the Anthropocene. *Trends in Ecology & Evolution (Amsterdam)*, *30*(2), 104–113. https://doi.org/10.1016/j.tree.2014.11.006

McLaren, Roberts, B. A., Djan-Chekar, N., & Lewis, K. P. (2004). Effects of overabundant moose on the Newfoundland landscape. Alces, 40, 45–.

McLaren, B., Hermanutz, L., Gosse, J., Collet, B., & Kasimos, C. (2009a). Broadleaf competition interferes with balsam fir regeneration following experimental removal of moose. *Forest Ecology and Management*, *257*(5), 1395–1404. https://doi.org/10.1016/j.foreco.2008.12.009

McLaren, B. E., Taylor, S., & Luke, S. (2009b). How moose select forested habitat in Gros Morne National Park, Newfoundland. *Alces*, *45*, 125–.

Mead, J. I., Agenbroad, L. D., Davis, O. K., & Martin, P. S. (1986). Dung of Mammuthus in the arid Southwest, North America. *Quaternary Research*, *25*(1), 121–127. https://doi.org/10.1016/0033-5894(86)90048-7

Menozzi, B. I., Zotti, M., & Montanari, C. (2010). A non-pollen palynomorphs contribution to the local environmental history in the Ligurian Apennines; a preliminary study. *Vegetation History and Archaeobotany*, *19*(5-6), 503–512. https://doi.org/10.1007/s00334-010-0271-1

Mercer, W. E., & McLaren, B. E. (2002). Evidence of carrying capacity effects in Newfoundland moose. *Alces*, 38, 123–141.

of-decision-to-introduce-wolves-at-ilse-royale-national-park.htm

Miola, A. (2012). Tools for Non-Pollen Palynomorphs (NPPs) analysis: A list of Quaternary NPP types and reference literature in English language (1972–2011). *Review of Palaeobotany and Palynology*, *186*, 142–161. https://doi.org/10.1016/j.revpalbo.2012.06.010

Moose/Caribou Jawbone Collection Program. (n.d.) Government of Newfoundland and Labrador. Retrieved from https://www.gov.nl.ca/hunting-trapping-guide/2022-23/new-for-2022-23/

New for 2022-23. (n.d.). Government of Newfoundland and Labrador. Retrieved from https://www.gov.nl.ca/hunting-trapping-guide/2022-23/new-for-2022-23/

Nickell, Z., Varriano, S., Plemmons, E., & Moran, M. D. (2018). Ecosystem engineering by bison (Bison bison) wallowing increases arthropod community heterogeneity in space and time. *Ecosphere (Washington, D.C)*, *9*(9), e02436–n/a. https://doi.org/10.1002/ecs2.2436

Noonan, M., Leroux, S. J., & Hermanutz, L. (2021). Evaluating forest restoration strategies after herbivore overbrowsing. *Forest Ecology and Management*, *482*, 118827–. https://doi.org/10.1016/j.foreco.2020.118827

Nosko, P., Roberts, K., Knight, T., & Marcellus, A. (2020). Growth and chemical responses of balsam fir saplings released from intense browsing pressure in the boreal forests of western Newfoundland, Canada. *Forest Ecology and Management*, *460*, 117839–. https://doi.org/10.1016/j.foreco.2019.117839

Nyberg, Å., & Persson, I.-L. (2002). Habitat differences of coprophilous fungi on moose dung. *Mycological Research*, *106*(11), 1360–1366. https://doi.org/10.1017/S0953756202006597

Ortiz, Sánchez-Palencia, Y., Torres, T., Domingo, L., Mata, M. P., Vegas, J., Sánchez España, J., Morellón, M., & Blanco, L. (2016). Lipid biomarkers in Lake Enol (Asturias, Northern Spain): Coupled natural and human induced environmental history. *Organic Geochemistry*, *92*, 70–83. https://doi.org/10.1016/j.orggeochem.2015.12.005

Painter, L. E., Beschta, R. L., Larsen, E. J., & Ripple, W. J. (2015). Recovering aspen follow changing elk dynamics in Yellowstone: evidence of a trophic cascade? *Ecology (Durham)*, *96*(1), 252–263. https://doi.org/10.1890/14-0712.1

Palmer, T. M., Stanton, M. L., Young, T. P., Goheen, J. R., Pringle, R. M., & Karban, R. (2008). Breakdown of an Ant-Plant Mutualism Follows the Loss of Large Herbivores from an African Savanna. *Science*, *319*(5860), 192–195. http://www.jstor.org/stable/20051975

Parker, N. E., & Williams, J. W. (2012). Influences of climate, cattle density, and lake morphology on Sporormiella abundances in modern lake sediments in the US Great Plains. *Holocene (Sevenoaks)*, *22*(4), 475–483. https://doi.org/10.1177/0959683611425550

Perrotti, A. G., & van Asperen, E. (2019). Dung fungi as a proxy for megaherbivores: opportunities and limitations for archaeological applications. *Vegetation History and Archaeobotany*, *28*(1), 93–104. https://doi.org/10.1007/s00334-018-0686-7

Perrotti, A. G., Ramiadantsoa, T., O'Keefe, J., & Otaño, N. N. (2022). Uncertainty in coprophilous fungal spore concentration estimates. *Frontiers in Ecology and Evolution*, *10*. https://doi.org/10.3389/fevo.2022.1086109

Pessarrodona, A., Boada, J., Pagès, J. F., Arthur, R., & Alcoverro, T. (2019). Consumptive and non-consumptive effects of predators vary with the ontogeny of their prey. *Ecology (Durham)*, *100*(5), 1–13. https://doi.org/10.1002/ecy.2649

Peterson, R. (2019). *North American Moose*. University of Toronto Press. https://doi.org/10.3138/9781487578213

Pimlott, D. H. (1959). Reproduction and Productivity of Newfoundland Moose. *The Journal of Wildlife Management*, *23*(4), 381–401. https://doi.org/10.2307/3796486

Pound, O'Keefe, J. M. K., & Marret, F. (2021). An overview of techniques applied to the extraction of non-pollen palynomorphs, their known taphonomic issues and recommendations to maximize recovery. *Geological Society Special Publication*, *511*(1), 63–76. https://doi.org/10.1144/SP511-2020-40

Pozo, R. A., Cusack, J. J., Acebes, P., Malo, J. E., Traba, J., Iranzo, E. C., Morris-Trainor, Z., Minderman, J., Bunnefeld, N., Radic-Schilling, S., Moraga, C. A., Arriagada, R., & Corti, P. (2021). Reconciling livestock production and wild herbivore conservation: challenges and opportunities. *Trends in Ecology & Evolution (Amsterdam)*, *36*(8), 750–761. https://doi.org/10.1016/j.tree.2021.05.002

Raper, D., & Bush, M. (2009). A test of Sporormiella representation as a predictor of megaherbivore presence and abundance. *Quaternary Research*, *71*(3), 490–496. https://doi.org/10.1016/j.yqres.2009.01.010

Razanatsoa, Gillson, L., Virah-Sawmy, M., & Woodborne, S. (2022). Synergy between climate and human land-use maintained open vegetation in southwest Madagascar over the last millennium. *Holocene (Sevenoaks)*, *32*(1-2), 57–69. https://doi.org/10.1177/09596836211041731

*A report on the Newfoundland caribou: a summary and interpretation of the state of knowledge of the island of Newfoundland's caribou population and key considerations for sustainable management.* (2016). Newfoundland and Labrador Department of Environment and Conservation.

Roy, A., Dash, S. K., & Sathyakumar, S. (2022). A Combination of Cultural Values and Economic Benefits Promote Tolerance Towards Large Mammals in a Hotspot of Human-Wildlife Conflicts in Eastern India. *Human Ecology : an Interdisciplinary Journal*, *50*(2), 321–329. https://doi.org/10.1007/s10745-022-00306-8

Salisbury, J., Hu, X., Speed, J. D. M., Iordan, C. M., Austrheim, G., & Cherubini, F. (2023). Net Climate Effects of Moose Browsing in Early Successional Boreal Forests by Integrating Carbon and Albedo Dynamics. *Journal of Geophysical Research. Biogeosciences*, *128*(3). https://doi.org/10.1029/2022JG007279

Sánchez, M. V., Laza, J. H., Bellosi, E. S., & Genise, J. F. (2010). Ichnostratigraphy of middle Cenozoic Coprinisphaera from central Patagonia: Insights into the evolution of dung beetles, herbivores and grass-dominated habitats. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *297*(3), 633–648. https://doi.org/10.1016/j.palaeo.2010.09.013

Schelske, C. L., Peplow, A., Brenner, M., & Spencer, C. N. (1994). Low-background gamma counting: applications for210Pb dating of sediments. *Journal of Paleolimnology*, *10*(2), 115–128. https://doi.org/10.1007/BF00682508

Scmhitz, O.J., Wilmers, C. C., Leroux, S. J., Doughty, C. E., Atwood, T.B., Galetti, M., Davies, A. B., Goetz, S. J. (2018). Animals and the zoogeochemistry of the carbon cycle. *Science* 362, eear3213

Schmitz, O. J., & Leroux, S. J. (2020). Food Webs and Ecosystems: Linking Species Interactions to the Carbon Cycle. *Annual Review of Ecology, Evolution, and Systematics*, *51*(1), 271–295. https://doi.org/10.1146/annurev-ecolsys-011720-104730

Schmitz, O. J., Sylvén, M., Atwood, T. B., Bakker, E., Berzaghi, F., Brodie, J. F., Cromsigt, J. P. G., Davies, A. B., Leroux, S. J., Schepers, F. J., Smith, F. A., Stark, S., Svenning, J.-C., Tilker, A., & Ylänne, H. (2023). Trophic rewilding can expand natural climate solutions. *Nature Climate Change*, *13*(4), 324–333. https://doi.org/10.1038/s41558-023-01631-6

Schofield, & Edwards, K. J. (2011). Grazing impacts and woodland management in Eriksfjord: Betula, coprophilous fungi and the Norse settlement of Greenland. *Vegetation History and Archaeobotany*, *20*(3), 181–197. https://doi.org/10.1007/s00334-011-0281-7

Schroeter, Lauterbach, S., Stebich, M., Kalanke, J., Mingram, J., Yildiz, C., Schouten, S., & Gleixner, G. (2020). Biomolecular Evidence of Early Human Occupation of a High-Altitude Site in Western Central Asia During the Holocene. *Frontiers in Earth Science (Lausanne)*, *8*. https://doi.org/10.3389/feart.2020.00020

Smol John P. (2017). Paleolimnology, Reference Module in Earth Systems and Environmental Sciences, Elsevier, 2017. 16- Jun-17 doi: 10.1016/B978-0-12-409548-9.10537-8.

Smol John P. (2022) Paleolimnology: Long-Term Reconstructions of Environmental Change. In: Mehner, Thomas and Tockner, Klement, *Encyclopedia of Inland Waters 2nd edition*. vol. 1, pp. 401-409. Oxford: Elsevier.

Special permit allows farmers to shoot problem moose after sunset. (2020). *News Releases*. Government of Newfoundland and Labrador Retrieved from: https://www.gov.nl.ca/releases/2020/flr/0709n01/

Stockmarr, Jens (1971). Tablets with Spores used in Absolute Pollen Analysis. *Pollen et Spores*. 13. 615-621.

Strong J.S., Leroux S.J. (2014). Impact of Non-Native Terrestrial Mammals on the Structure of the Terrestrial Mammal Food Web of Newfoundland, Canada. PLoS ONE 9(8): e106264. doi:10.1371/journal.pone.0106264

Swain, M., Leroux, S. J., & Buchkowski, R. (2023). Strong above-ground impacts of a non-native ungulate do not cascade to impact below-ground functioning in a boreal ecosystem. *The Journal of Animal Ecology*. https://doi.org/10.1111/1365-2656.13993

Tanner, A. L., Leroux, S. J., & Saunders, P. W. (2017). Road Characteristics Best Predict the Probability of Vehicle Collisions with a Non-Native Ungulate. *Écoscience (Sainte-Foy)*, *24*(1–2), 1–11. https://doi.org/10.1080/11956860.2017.1292100

van Asperen, E. N., Kirby, J. R., & Hunt, C. O. (2016). The effect of preparation methods on dung fungal spores: Implications for recognition of megafaunal populations. *Review of Palaeobotany and Palynology*, *229*, 1–8. https://doi.org/10.1016/j.revpalbo.2016.02.004

van Asperen, E., Kirby, J. R., & Shaw, H. E. (2020). Relating dung fungal spore influx rates to animal density in a temperate environment: Implications for palaeoecological studies. *Holocene (Sevenoaks)*, *30*(2), 218–232. https://doi.org/10.1177/0959683619875804

van Asperen, E., Perrotti, A., & Baker, A. (2021). Coprophilous fungal spores: Non-pollen palynomorphs for the study of past megaherbivores. *Geological Society Special Publication*, *511*(1), 245–367. https://doi.org/10.1144/SP511-2020-41

van den Bos, Valerie, et al. (2020). “Density Separation in Pollen Preparation: How Low Can You Go?” *Journal of Paleolimnology*, vol. 63, no. 3, pp. 225–34, https://doi.org/10.1007/s10933-020-00112-6.

van Geel, Zazula, G. D., & Schweger, C. E. (2007). Spores of coprophilous fungi from under the Dawson tephra (25,300 14C years BP), Yukon Territory, northwestern Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *252*(3), 481–485. https://doi.org/10.1016/j.palaeo.2007.04.017

Vors, L. S., & Boyce, M. S. (2009). Global declines of caribou and reindeer. *Global Change Biology*, *15*(11), 2626–2633. https://doi.org/10.1111/j.1365-2486.2009.01974.x

Watkinson, S. C., Boddy, L., & Money, N. (2015). *The Fungi* (Third edition.). Elsevier Science.

Wardle, D.A., Bardgett, R. D., Callaway, Ragan, M., Van der Putten, W. H. (2011). Terrestrial Ecosystem Responses to Species Gains and Losses. WASHINGTON: American Association for the Advancement of Science. *Science*, 332 (6035). 1273-77.

Weiskopf, S. R., Ledee, O. E., & Thompson, L. M. (2019). Climate Change Effects on Deer and Moose in the Midwest. *The Journal of Wildlife Management*, *83*(4), 769–781. https://doi.org/10.1002/jwmg.21649

Wendt, J. A. F., McWethy, D. B., Widga, C., & Shuman, B. N. (2022). Large-scale climatic drivers of bison distribution and abundance in North America since the Last Glacial Maximum. *Quaternary Science Reviews*, *284*, 107472–. https://doi.org/10.1016/j.quascirev.2022.107472

Williams, H. M. (2003). Geologic ancestors to the Atlantic: the geology of Newfoundland. *Newfoundland Quarterly (1971)*, *96*(3), 10–.

Wood, J. R., & Wilmshurst, J. M. (2013). Accumulation rates or percentages? How to quantify Sporormiella and other coprophilous fungal spores to detect late Quaternary megafaunal extinction events. *Quaternary Science Reviews*, *77*, 1–3. https://doi.org/10.1016/j.quascirev.2013.06.025

Woodland Caribou- boreal population. (2023). *Conservation and protection of Canada's forests*. Government of Canada. Retrieved from: https://natural-resources.canada.ca/our-natural-resources/forests/sustainable-forest-management/conservation-and-protection-canadas-forests/woodland-caribou-boreal-population/13201

Zhong, Z., Wang, D., Wang, L., Wang, Z., Zhu, H., & Feng, C. (2014). Positive interactions between large herbivores and grasshoppers, and their consequences for grassland plant diversity. *Ecology (Durham)*, *95*(4), 1055–1064. https://doi.org/10.1890/13-1079.1

# Appendix I: Spore count

# Little Crow Pond

| Spore type | LC 0-0.25 | LC 0.5-0.75 | LC 1-1.25 | | LC 1.5-1.75 | LC 2-2.25 | LC 2-2.25 | LC 2.5-2.75 | LC 3-3.25 | LC 3.5-3.75 | LC 4-4.25 | LC 4.5-4.75 | LC 5-5.25 | LC 5.5-5.75 | LC 6-6.25 | LC 6.5-6.75 | LC 6.5-6.75 | LC 7-7.25 | LC 7.5-7.75 | LC 8-8.25 | LC 8.5-8.75 | LC 9-.25 | LC 10.25-.5 | LC 12.25-.5 | LC 14.25-.5 | LC 16.5-.75 | LC 18.25-.5 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | redo SPT 2 | A | B | | A | SPT 2.0 | A | A | | A | | A | | B | | SPT 2.0 | A | | A | | SPT 2.0 | SPT 2.0 | SPT 2.0 | SPT 2.0 | SPT 2.0 | SPT 2.0 |
| Lycopodium | 60 | 150 | 128 | 127 | 166 | 139 | 150 | 302 | 129 | 160 | 177 | 250 | 109 | 250 | 138 | 178 | 150 | 167 | 225 | 139 | 161 | 150 | 150 | 150 | 150 | 150 | 150 |
| Fungal Hyphae | 20 | 31 | 46 | 70 | 14 | 52 | 51 | 16 | 31 | 9 | 54 | 9 | 22 | 15 | 38 | 9 | 79 | 30 | 10 | 19 | 11 | 59 | 61 | 39 | 43 | 28 | 24 |
| | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Podospora | 1 | 2 | 1 | 0 | 3 | 2 | 3 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 1 | 3 | 0 | 1 | 0 | 0 | | | 1 | | | |
| cf podospora | | | | | | | | | | | | | | | | | 2 | | | | | | | | | | |
| Apiosordaria | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Sordaria | 0 | 3 | 0 | 0 | | 5 | 16 | 5 | 0 | 5 | 2 | 4 | 2 | 6 | 7 | 5 | 6 | 6 | 3 | 3 | 2 | 2 | | | | | |
| cf sordaria | | 1 | | | | | | | | | | | | | | | 2 | | | | | | | 1 | | 1 | |
| Sporomiella | 6 | 5 | 13 | 5 | 3 | 5 | 18 | 6 | 2 | 3 | 8 | 6 | 2 | 7 | 6 | 6 | 15 | 1 | 7 | 1 | 2 | 2 | | | | | |
| cf sporomiella | | 2 | | | | | 2 | | | | | | | | | | 6 | | | | | 1 | | 1 | | | |
| Arnium | 1 | 6 | 5 | 11 | 5 | 18 | 35 | 8 | 10 | 12 | 27 | 11 | 4 | 19 | 13 | 11 | 21 | 12 | 11 | 1 | 4 | 9 | 7 | 3 | 4 | 5 | 2 |
| cf arnium | | | | | | | 2 | | | | | | | | | | 3 | | | | | | 1 | 1 | 2 | 1 | |
| Coniochaeta | | 1 | | | | | 7 | | | | | | | | | | 2 | | | | | | | | | 1 | |
| cf conio | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | |
| Coniochaeta B | | | | | | | | | | | | | | | | | | | | | | | 1 | 1 | | | |
| cf conio B | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Meliola | | 2 | | | | | 1 | | | | | | | | | | 1 | | | | | 1 | 3 | 4 | 2 | 1 | 1 |
| cf meliola | | | | | | | | | | | | | | | | | 4 | | | | | 1 | 2 | 1 | | | |
| Endophragmiella | | | | | | 2 | 1 | 1 | | 2 | | 2 | | 2 | | | | 2 | 1 | | 1 | | | 1 | | | |
| cf endo | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| cf endo B | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | |
| Ascodesmis | | | | | | | 1 | | | | | | | | | | 1 | | | | | | 1 | | | | |
| cf asco | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | |
| Helicoon | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| cf helicoon | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Trichocladium | | | | | | 2 | 7 | | | | | 1 | 1 | 1 | | | | | | | | | | 2 | | 1 | |
| cf tricho | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | |
| cf tricho opacum | | 1 | | | | | 7 | | | | | | | | | | 4 | | | | | 1 | | 1 | | | |
| Delitschia | | 2 | | | | | | | | | | | | | | | | | | | | | | | | | |
| cf delitschia | | | | | | | | | | | | | | | | | | | | | | 2 | | 2 | 2 | 1 | |
| Taper | | | | | | | 4 | | | | | | | | | | 2 | | | | | 2 | 3 | 5 | | 5 | 2 |
| Chain | 8 | 2 | | | 1 | 14 | 13 | 10 | 21 | 9 | 40 | 14 | 9 | | 14 | | 8 | 1 | 8 | 2 | | 5 | 3 | 6 | 6 | 4 | 1 |
| Saccolobus | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| cf gelasinospora | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Nigrospora | | | | | | | | | | | | | | | | | | | | | | 2 | 2 | 2 | 4 | 1 | 2 |
| Triposporum elegans | | | | | | | | | | | | | | | | | | | | | | 2 | 1 | 1 | 1 | | |
| Spore total | 16 | 27 | 19 | 16 | 12 | 48 | 118 | 30 | 13 | 31 | 78 | 38 | 18 | 34 | 41 | 23 | 81 | 22 | 31 | 7 | 9 | 30 | 11 | 32 | 23 | 21 | 8 |
| | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Unknown | 5 | 1 | 10 | 14 | 2 | 25 | 10 | 1 | 5 | 2 | 11 | 1 | 1 | 2 | 5 | 1 | 2 | 6 | 2 | 2 | 1 | 2 | 1 | | 2 | 4 | |
| Covered | 0 | 6 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | | 1 | |
| Damaged | | 4 | | | 2 | 11 | 4 | 7 | 2 | 3 | 6 | 4 | 4 | 5 | 6 | 3 | 3 | 5 | 3 | 1 | 2 | 1 | 1 | 1 | | | |
| Unknown total | 5 | 11 | 10 | 14 | 4 | 35 | 17 | 8 | 7 | 5 | 17 | 5 | 5 | 7 | 11 | 4 | 13 | 11 | 5 | 3 | 3 | 4 | 3 | 2 | 2 | 5 | 0 |

# Pitcher Pond

| Spore type | 0.0-0.25 | 0.5-0.75 | 1-1.25 | 1.5-1.75 | 2-2.25 | 2.5-2.75 | 3-3.25 | 3.5-3.75 | 4-4.25 | 4.5-4.75 | 5-5.25 | 5.5-5.75 | 6-6.25 | 6.5-6.75 | 7-7.25 | 7.5-7.75 | 8-8.25 | 8.5-8.75 | 9-9.25 | 10-10.5 | 12-12.5 | 14-14.5 | 16-16.6 | 18-18.5 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Lycopodium | 150 | 150 | 150 | 150 | 150 | 150 | 150 | 150 | 150 | 150 | 150 | 150 | 150 | 150 | 150 | 150 | 150 | 150 | 150 | 150 | 150 | 150 | 150 | 150 |
| Fungal Hyphae | 109 | 38 | 110 | 89 | 74 | 82 | 144 | 76 | 102 | 68 | 73 | 62 | 55 | 49 | 51 | 33 | 42 | 33 | 34 | 39 | 16 | 19 | 26 | 25 |
| | | | | | | | | | | | | | | | | | | 0 | | | | | | |
| Podospora | 4 | 4 | 2 | 2 | 2 | 3 | 2 | 1 | 3 | 2 | 4 | 3 | 2 | 1 | 2 | 1 | | 1 | | | 1 | | | |
| cf podospora | 1 | | | | | 1 | 1 | 1 | 1 | 1 | | 1 | 1 | 1 | 1 | | | 0 | | | | | | |
| Apiosordaria | | | | | | | | | | | | | 1 | | | | | 0 | | | | | 1 | 1 |
| Sordaria | 6 | 3 | 8 | 4 | 8 | 4 | 4 | 4 | 10 | 9 | 6 | 7 | 6 | 4 | 3 | 1 | 1 | 2 | 1 | | | | | |
| cf sordaria | 2 | | | 1 | 2 | 1 | 1 | 1 | 3 | 2 | 2 | 2 | 2 | 2 | 1 | 2 | | 2 | | 2 | 1 | | 1 | |
| Sporomiella | 10 | 10 | 8 | 4 | 6 | 5 | 5 | 4 | 13 | 8 | 7 | 4 | 5 | 4 | | 1 | | 1 | | | | | | |
| cf sporomiella | 3 | 8 | 3 | 2 | 2 | 2 | 1 | 1 | 7 | 2 | 3 | 1 | 1 | 1 | | | | 0 | | | | | | |
| Arnium | 14 | 8 | 9 | 7 | 9 | 13 | 8 | 6 | 23 | 17 | 20 | 12 | 9 | 10 | 5 | 5 | 6 | 4 | 2 | 4 | 1 | 1 | 1 | 2 |
| cf arnium | 2 | 2 | 2 | 2 | 1 | 1 | 4 | 2 | 4 | 2 | 2 | 2 | 1 | 2 | 2 | | 2 | 2 | 2 | 1 | | | | 1 |
| Coniochaea | | 2 | 3 | | 4 | | 1 | 1 | 4 | | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 1 | | | | | | |
| cf conio | 1 | 1 | 1 | 1 | | | 1 | 1 | | 1 | 2 | 1 | 1 | | | | 1 | | 1 | | 1 | | | |
| Coniochaeta B | | | | | | | | | | | | | | | | 1 | 3 | 1 | | 2 | 2 | 1 | 1 | 1 |
| cf conio B | | | | | | | | | | | | | | 1 | | | | | | | | | | |
| Meliola | | | | 1 | | | 2 | 1 | | 2 | 1 | | 3 | 1 | | 1 | 2 | | | | 1 | | 1 | 1 |
| cf meliola | | | 1 | 2 | 1 | | 1 | 1 | 15 | | | | | 1 | 1 | 1 | | | | 2 | | | 1 | 1 |
| Endophragmiella | | | | | 1 | | | | | 1 | | | | | | | | | | | | | | |
| cf endo C | | | | | | | | | | | | | | | | | | | | | | | | |
| cf endo B | 1 | | | | | | 1 | | | | | | | | | | | | | | | | | |
| Ascodesmis | 1 | | | 1 | 1 | 1 | | | | | | 1 | | | | | | | | | | | | |
| cf asco | 1 | | | 1 | | 1 | | 1 | | 1 | | 1 | 2 | 1 | 1 | | 1 | 1 | | 1 | | | | |
| Helicoon | | | | | | | | | | | | 1 | | | | | | | | | | 1 | 2 | |
| cf helicoon | | | | | | | | | | | | | | | | | | | | | | 1 | | 1 |
| Trichocladium | | | | | | | 1 | | 2 | | | | 1 | 3 | 3 | 1 | 1 | 2 | | 1 | 1 | | 1 | 2 |
| cf tricho | | | | | | | | | | | | | | 1 | | | | | | 1 | | | | |
| cf tricho opacum | 1 | | 1 | | | | 1 | 1 | | 3 | 7 | 5 | | | | 2 | 2 | 2 | 1 | 1 | 2 | | 1 | 2 |
| Delitschia | 1 | | | 1 | 1 | 2 | 1 | | | | 3 | 4 | | 1 | | 1 | | 1 | | | | | | |
| cf delitschia | 1 | | 3 | 2 | | | 1 | 2 | | 1 | 2 | 1 | | 1 | | | 2 | 1 | | | 1 | | 2 | 3 |
| Taper | 1 | 1 | | | | 1 | 1 | | 1 | | | 1 | | 1 | | | 1 | | | | | 1 | | |
| Chain | 15 | 5 | 7 | 12 | 11 | 7 | 9 | 4 | 18 | 11 | 14 | 6 | 8 | 10 | 11 | 6 | 5 | 8 | 3 | 6 | 5 | 2 | 11 | 4 |
| Saccolobus | | | | 2 | | | | | | | | | 1 | | | | | | | | | | | |
| CF gelasinospora | | | | | | | | 2 | | | | | | | | | | | | | | | | |
| Nigrospora | 5 | 7 | 3 | 3 | 5 | 1 | 3 | 5 | 4 | 4 | 3 | 6 | 1 | 6 | 4 | 4 | 2 | 2 | 2 | 4 | 3 | 1 | 2 | 4 |
| Spore total | 70 | 51 | 51 | 48 | 54 | 43 | 49 | 39 | 108 | 67 | 77 | 61 | 48 | 53 | 35 | 28 | 30 | 30 | 12 | 25 | 19 | 8 | 25 | 23 |
| | | | | | | | | | | | | | | | | | | | | | | | | |
| Unknown | 3 | 10 | 2 | 2 | 4 | 1 | 1 | 1 | 7 | 2 | 1 | 1 | 1 | 1 | 1 | | 1 | 1 | | | | | | 2 |
| covered | 4 | 8 | 2 | 3 | 2 | 4 | 4 | 4 | 12 | 6 | 5 | 5 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 3 | | 2 | 2 |
| damaged | 8 | 3 | 8 | 5 | 6 | 4 | 5 | 4 | 10 | 6 | 8 | 6 | 5 | 6 | 2 | 3 | 2 | 2 | 2 | 1 | | | 1 | |
| Unknown total | 15 | 21 | 12 | 10 | 12 | 9 | 10 | 9 | 29 | 14 | 14 | 12 | 8 | 8 | 4 | 4 | 4 | 4 | 3 | 2 | 3 | 0 | 3 | 4 |

# Appendix II: *Lycopodium* percents

## Little Crow Pond

| Spore type | LC 0-0.26 | LC 0.5-0.75 | LC 1-1.25 | LC 1-1.25 | LC 1.5-1.75 | LC 2-2.25 | LC 2.5-2.75 | LC 3-3.25 | LC 3.5-3.75 | LC 4-4.25 | LC 4.5-4.75 | LC 5-5.25 | LC 5.5-5.75 | LC 6-6.25 | LC 6.5-6.75 | LC 7-7.25 | LC 7.5-7.75 | LC 8-8.25 | LC 8.5-8.75 | LC 9-.25 | LC 10.25-.5 | LC 12.25-.5 | LC 14.25-.5 | LC 16.5-.75 | LC 18.25-.5 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Podospora | 1.66666667 | 1.33333333 | 0.78125 | 0 | 1.80722892 | 2 | 0 | 0 | 0 | 0.56497175 | 0 | 0 | 0.8 | 0.72463768 | 2 | 0 | 0.56179775 | 0 | 0 | 0 | 0 | 0.66666667 | 0 | 0 | 0 |
| cf podospora | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1.33333333 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Apiosordaria | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Sordaria | 0 | 2 | 0 | 0 | 0 | 10.6666667 | 1.65562914 | 0 | 3.125 | 1.1299435 | 1.6 | 1.83486239 | 2.4 | 5.07246377 | 4 | 3.59281437 | 1.68539326 | 2.15827338 | 1.24223602 | 1.33333333 | 0 | 0 | 0 | 0 | 0 |
| cf sordaria | 0 | 0.66666667 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1.33333333 | 0 | 0 | 0 | 0 | 0 | 0.66666667 | 0 | 0.66666667 | 0 | 0 |
| Sporomiella | 10 | 3.33333333 | 10.15625 | 3.93700787 | 1.80722892 | 12 | 1.98675497 | 1.5503876 | 1.875 | 4.51977401 | 2.4 | 1.83486239 | 2.8 | 4.34782609 | 10 | 0.5988024 | 3.93258427 | 0.71942446 | 1.24223602 | 1.33333333 | 0 | 0 | 0 | 0 | 0 |
| cf sporomiella | 0 | 1.33333333 | 0 | 0 | 0 | 1.33333333 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0.66666667 | 0 | 0.66666667 | 0 | 0 | 0 |
| Arnium | 1.66666667 | 4 | 3.90625 | 8.66141732 | 3.01204819 | 23.3333333 | 2.64900662 | 7.75193798 | 7.5 | 15.2542373 | 4.4 | 3.66972477 | 7.6 | 9.42028986 | 14 | 7.18562874 | 6.17977528 | 0.71942446 | 2.48447205 | 6 | 4.66666667 | 2 | 2.66666667 | 3.33333333 | 1.33333333 |
| cf arnium | 0 | 0 | 0 | 0 | 0 | 1.33333333 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0.66666667 | 0.66666667 | 1.33333333 | 0.66666667 | 0 |
| Coniochaeta | 0 | 0.66666667 | 0 | 0 | 0 | 4.66666667 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1.33333333 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.66666667 | 0 |
| cf conio | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.66666667 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Coniochaeta B | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.66666667 | 0.66666667 | 0 | 0 | 0 |
| cf conio B | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Ascodesmis | 0 | 0 | 0 | 0 | 0 | 0.66666667 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.66666667 | 0 | 0 | 0 | 0 | 0 | 0.66666667 | 0 | 0 | 0 | 0 |
| cf asco | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.66666667 | 0 |
| Delitschia | 0 | 1.33333333 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| cf delitschia | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1.33333333 | 0 | 1.33333333 | 0.66666667 | 0 |
| Saccolobus | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Spore total | 13.3333333 | 14.6666667 | 14.84375 | 12.5984252 | 6.62650602 | 56 | 6.29139073 | 9.30232558 | 12.5 | 21.4689266 | 8.4 | 7.33944954 | 13.6 | 19.5652174 | 41.3333333 | 11.3772455 | 12.3595506 | 3.5971223 | 4.9689441 | 10.6666667 | 7.33333333 | 6 | 6 | 6 | 1.33333333 |
| | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Unknown | 8.33333333 | 0.66666667 | 7.8125 | 11.023622 | 1.20481928 | 6.66666667 | 0.33112583 | 3.87596899 | 1.25 | 6.21468927 | 0.4 | 0.91743119 | 0.8 | 3.62318841 | 1.33333333 | 3.59281437 | 1.12359551 | 1.43884892 | 0.62111801 | 1.33333333 | 0.66666667 | 0 | 1.33333333 | 2.66666667 | 0 |
| damaged | 0 | 2.66666667 | 0 | 0 | 1.20481928 | 2.66666667 | 2.31788079 | 1.5503876 | 1.875 | 3.38983051 | 1.6 | 3.66972477 | 2 | 4.34782609 | 2 | 2.99401198 | 1.68539326 | 0.71942446 | 1.24223602 | 0.66666667 | 0.66666667 | 0.66666667 | 0 | 0 | 0 |
| covered | 0 | 4 | 0 | 0 | 0 | 5.33333333 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5.33333333 | 0 | 0 | 0 | 0 | 0.66666667 | 0.66666667 | 0.66666667 | 0 | 0.66666667 | 0 |
| Unknown total | 8.33333333 | 7.33333333 | 7.8125 | 11.023622 | 2.40963855 | 11.3333333 | 2.64900662 | 5.42635659 | 3.125 | 9.60451977 | 2 | 4.58715596 | 2.8 | 7.97101449 | 8.66666667 | 6.58682635 | 2.80898876 | 2.15827338 | 1.86335404 | 2.66666667 | 2 | 1.33333333 | 1.33333333 | 3.33333333 | 0 |
| Taper | 0 | 0 | 0 | 0 | 0 | 2.66666667 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1.33333333 | 0 | 0 | 0 | 0 | 0 | 1.33333333 | 2 | 3.33333333 | 0 | 3.33333333 |
| Chain | 13.3333333 | 1.33333333 | 0 | 0 | 0.60240964 | 8.66666667 | 3.31125828 | 16.279698 | 5.625 | 22.5988701 | 5.6 | 8.25688073 | 0 | 10.1449275 | 5.33333333 | 0.5988024 | 4.49438202 | 1.43884892 | 0 | 3.33333333 | 2 | 4 | 4 | 2.66666667 | 0.66666667 |
| | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| All Spores | 35 | 25.3333333 | 22.65625 | 23.6220472 | 9.63855422 | 90 | 12.5827815 | 15.503876 | 22.5 | 53.6723164 | 17.2 | 21.1009174 | 16.4 | 37.6811594 | 62.6666667 | 19.760479 | 20.2247191 | 7.1942446 | 7.45341615 | 22.6666667 | 9.33333333 | 22.6666667 | 24 | 17.3333333 | 5.33333333 |

## Pitcher Pond

| Spore type | 0.0-0.25 | 0.5-0.75 | 1-1.25 | 1.5-1.75 | 2-2.25 | 2.5-2.75 | 3-3.25 | 3.5-3.75 | 4-4.25 | 4.5-4.75 | 5-5.25 | 5.5-5.75 | 6-6.25 | 6.5-6.75 | 7-7.25 | 7.5-7.75 | 8-8.25 | 8.5-8.75 | 9-9.25 | 10-10.5 | 12-12.5 | 14-14.5 | 16-16.6 | 18-18.5 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Podospora | 2.666666667 | 2.666666667 | 1.33333333 | 1.33333333 | 1.33333333 | 2 | 1.33333333 | 0.66666667 | 2 | 1.33333333 | 2.66666667 | 2 | 1.33333333 | 0.66666667 | 1.33333333 | 0.66666667 | 0 | 0.66666667 | 0 | 0 | 0.66666667 | 0 | 0 | 0 |
| cf podospora | 0.666666667 | 0 | 0 | 0 | 0 | 0.666666667 | 0.666666667 | 0.666666667 | 0.666666667 | 0.666666667 | 0 | 0.666666667 | 0.666666667 | 0.666666667 | 0.666666667 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Apiosordaria | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.666666667 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.666666667 | 0.666666667 |
| Sordaria | 4 | 2 | 5.33333333 | 2.666666667 | 5.33333333 | 2.666666667 | 2.666666667 | 2.666666667 | 6.666666667 | 6 | 4 | 4.666666667 | 4 | 2.666666667 | 2 | 0.666666667 | 0.666666667 | 1.33333333 | 0.666666667 | 0 | 0 | 0 | 0 | 0 |
| cf sordaria | 1.333333333 | 0 | 0 | 0.666666667 | 1.33333333 | 0.666666667 | 0.666666667 | 0.666666667 | 2 | 1.33333333 | 1.33333333 | 1.33333333 | 1.33333333 | 1.33333333 | 0.666666667 | 1.33333333 | 0 | 1.33333333 | 0 | 1.33333333 | 0.666666667 | 0 | 0.666666667 | 0 |
| Sporomiella | 6.666666667 | 6.666666667 | 5.33333333 | 2.666666667 | 4 | 3.33333333 | 3.33333333 | 2.666666667 | 8.666666667 | 5.33333333 | 4.666666667 | 2.666666667 | 3.33333333 | 2.666666667 | 0 | 0.666666667 | 0 | 0.666666667 | 0 | 0 | 0 | 0 | 0 | 0 |
| cf sporomiella | 2 | 5.33333333 | 2 | 1.33333333 | 1.33333333 | 1.33333333 | 0.666666667 | 0.666666667 | 4.666666667 | 1.33333333 | 2 | 0.666666667 | 0.666666667 | 0.666666667 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Arnium | 9.333333333 | 5.33333333 | 6 | 4.666666667 | 6 | 8.666666667 | 5.33333333 | 4 | 15.33333333 | 11.33333333 | 13.33333333 | 8 | 6 | 6.666666667 | 3.33333333 | 3.33333333 | 4 | 2.666666667 | 1.33333333 | 2.666666667 | 0.666666667 | 0.666666667 | 0.666666667 | 1.33333333 |
| cf arnium | 1.333333333 | 1.33333333 | 1.33333333 | 1.33333333 | 0.666666667 | 0.666666667 | 2.666666667 | 1.33333333 | 2.666666667 | 1.33333333 | 1.33333333 | 1.33333333 | 0.666666667 | 1.33333333 | 1.33333333 | 0 | 1.33333333 | 1.33333333 | 1.33333333 | 0.666666667 | 0 | 0 | 0 | 0.666666667 |
| Coniochaea | 0 | 1.33333333 | 2 | 0 | 2.666666667 | 0 | 0.666666667 | 0.666666667 | 2.666666667 | 0 | 0.666666667 | 1.33333333 | 2 | 0.666666667 | 0.666666667 | 0.666666667 | 0.666666667 | 0.666666667 | 0 | 0 | 0 | 0 | 0 | 0 |
| cf conio | 0.666666667 | 0.666666667 | 0.666666667 | 0.666666667 | 0 | 0 | 0.666666667 | 0.666666667 | 0 | 0.666666667 | 1.33333333 | 0.666666667 | 0.666666667 | 0 | 0 | 0 | 0.666666667 | 0 | 0.666666667 | 0 | 0.666666667 | 0 | 0 | 0 |
| Coniochaeta B | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.666666667 | 2 | 0.666666667 | 0 | 1.33333333 | 1.33333333 | 0.666666667 | 0.666666667 | 0.666666667 |
| cf conio B | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.666666667 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Ascodesmis | 0.666666667 | 0 | 0 | 0.666666667 | 0.666666667 | 0.666666667 | 0 | 0 | 0 | 0 | 0 | 0.666666667 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| cf asco | 0.666666667 | 0 | 0 | 0.666666667 | 0 | 0.666666667 | 0 | 0.666666667 | 0 | 0.666666667 | 0 | 0.666666667 | 1.33333333 | 0.666666667 | 0.666666667 | 0 | 0.666666667 | 0.666666667 | 0 | 0.666666667 | 0 | 0 | 0 | 0 |
| Delitschia | 0.666666667 | 0 | 0 | 0.666666667 | 0.666666667 | 1.33333333 | 0.666666667 | 0 | 0 | 0 | 2 | 2.666666667 | 0 | 0.666666667 | 0 | 0.666666667 | 0 | 0.666666667 | 0 | 0 | 0 | 0 | 0 | 0 |
| cf delitschia | 0.666666667 | 0 | 2 | 1.33333333 | 0 | 0 | 0.666666667 | 1.33333333 | 0 | 0.666666667 | 1.33333333 | 0.666666667 | 0 | 0.666666667 | 0 | 0 | 1.33333333 | 0.666666667 | 0 | 0 | 0.666666667 | 0 | 1.33333333 | 2 |
| Saccolobus | 0 | 0 | 0 | 1.33333333 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.666666667 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Copro spore total | 31.33333333 | 25.33333333 | 26 | 20 | 24 | 22.666667 | 20 | 16.666667 | 45.33333333 | 30.666667 | 34.666667 | 28 | 23.3333333 | 20 | 10.666667 | 8.666667 | 11.3333333 | 11.3333333 | 4 | 6.666666667 | 4.666666667 | 1.33333333 | 4 | 5.33333333 |
| | | | | | | | | | | | | | | | | | | | | | | | | |
| Unknown | 2 | 6.666666667 | 1.33333333 | 1.33333333 | 2.666666667 | 0.666666667 | 0.666666667 | 0.666666667 | 4.666666667 | 1.33333333 | 0.666666667 | 0.666666667 | 0.666666667 | 0.666666667 | 0.666666667 | 0 | 0.666666667 | 0.666666667 | 0 | 0 | 0 | 0 | 0 | 1.33333333 |
| covered | 2.666666667 | 5.33333333 | 1.33333333 | 2 | 1.33333333 | 2.666666667 | 2.666666667 | 2.666666667 | 8 | 4 | 3.33333333 | 3.33333333 | 1.33333333 | 0.666666667 | 0.666666667 | 0.666666667 | 0.666666667 | 0.666666667 | 0.666666667 | 0.666666667 | 2 | 0 | 1.33333333 | 1.33333333 |
| damaged | 5.33333333 | 2 | 5.33333333 | 3.33333333 | 4 | 2.666666667 | 3.33333333 | 2.666666667 | 6.666666667 | 4 | 5.33333333 | 4 | 3.33333333 | 4 | 1.33333333 | 2 | 1.33333333 | 1.33333333 | 1.33333333 | 0.666666667 | 0 | 0 | 0.666666667 | 0 |
| Unknown total | 10 | 14 | 8 | 6.666666667 | 8 | 6 | 6.666666667 | 6 | 19.33333333 | 9.33333333 | 9.33333333 | 8 | 5.33333333 | 5.33333333 | 2.666666667 | 2.666666667 | 2.666666667 | 2.666666667 | 2 | 1.33333333 | 2 | 0 | 2 | 2.666666667 |
| Taper | 0.666666667 | 0.666666667 | 0 | 0 | 0 | 0.666666667 | 0.666666667 | 0 | 0.666666667 | 0 | 0 | 0.666666667 | 0 | 0.666666667 | 0 | 0 | 0.666666667 | 0 | 0 | 0 | 0 | 0.666666667 | 0 | 0 |
| Chain | 10 | 3.33333333 | 4.666666667 | 8 | 7.33333333 | 4.666666667 | 6 | 2.666666667 | 12 | 7.33333333 | 9.33333333 | 4 | 5.33333333 | 6.666666667 | 7.33333333 | 4 | 3.33333333 | 5.33333333 | 2 | 4 | 3.33333333 | 1.33333333 | 7.33333333 | 2.666666667 |
| #SPILL! | 41.33333333 | 39.33333333 | 34 | 26.666666667 | 32 | 28.666666667 | 26.666666667 | 22.666666667 | 64.666666667 | 40 | 44 | 36 | 28.6666667 | 25.3333333 | 13.3333333 | 11.3333333 | 14 | 14 | 6 | 18 | 0 | 0 | 0 | 0 |

# Appendix III: Accumulation rates

## Little Crow Pond

| Date | Depth | Podospora | Sordaria | Sporomiella | Arnium | Coniochaeta | Ascodesmis | Delitschia | Spore total |
|---|---|---|---|---|---|---|---|---|---|
| **2020.28** | 0 | 0.27426543 | 0 | 1.64559257 | 0.27426543 | 0 | 0 | 0 | 2.19412342 |
| **2016.7** | 0.5 | 0.54853086 | 1.09706171 | 1.91985799 | 1.64559257 | 0.27426543 | 0 | 0.54853086 | 6.03383941 |
| **2013.12** | 1 | 0 | 0 | 0.43555154 | 0.95821339 | 0 | 0 | 0 | 1.39376492 |
| **2007.355** | 1.5 | 0.39090839 | 0 | 0.39090839 | 0.65151398 | 0 | 0 | 0 | 1.43333076 |
| **2001.59** | 2 | 0.52518761 | 2.80100057 | 3.50125071 | 6.47731381 | 1.22543775 | 0.17506254 | 0 | 14.705253 |
| **1996.22** | 2.5 | 0 | 0.84906926 | 1.01888311 | 1.35851082 | 0 | 0 | 0 | 3.22646319 |
| **1990.85** | 3 | 0 | 0 | 0.3291552 | 1.645776 | 0 | 0 | 0 | 1.9749312 |
| **1986.58** | 3.5 | 0 | 0.84309225 | 0.50585535 | 2.0234214 | 0 | 0 | 0 | 3.37236899 |
| **1982.31** | 4 | 0.17266682 | 0.34533364 | 1.38133455 | 4.6620041 | 0 | 0 | 0 | 6.5613391 |
| **1977.835** | 4.5 | 0 | 0.69366089 | 1.04049133 | 1.90756744 | 0 | 0 | 0 | 3.64171966 |
| **1973.36** | 5 | 0 | 0.34832773 | 0.34832773 | 0.69665546 | 0 | 0 | 0 | 1.39331092 |
| **1968.495** | 5.5 | 0.33021925 | 0.99065776 | 1.15576739 | 3.1370829 | 0 | 0 | 0 | 5.6137273 |
| **1963.63** | 6 | 0.15609423 | 1.09265959 | 0.93656537 | 2.02922496 | 0 | 0 | 0 | 4.21454415 |
| **1958.455** | 6.5 | 0.81186712 | 1.29898739 | 3.4098419 | 3.89696217 | 0.48712027 | 0.16237342 | 0 | 10.0671523 |
| **1953.28** | 7 | 0 | 1.012032 | 0.168672 | 2.024064 | 0 | 0 | 0 | 3.204768 |
| **1947.65** | 7.5 | 0.16882141 | 0.50646423 | 1.18174987 | 1.85703552 | 0 | 0 | 0 | 3.71407103 |
| **1942.02** | 8 | 0 | 0.50691249 | 0.16897083 | 0.16897083 | 0 | 0 | 0 | 0.84485415 |
| **1937.085** | 8.5 | 0 | 0.32434248 | 0.32434248 | 0.64868496 | 0 | 0 | 0 | 1.29736992 |
| **1932.15** | 9 | 0 | 0.31078863 | 0.46618294 | 1.39854883 | 0 | 0 | 0.31078863 | 2.48630902 |
| **1905.89** | 10.25 | 0 | 0.15075976 | 0 | 1.2060781 | 0.15075976 | 0.15075976 | 0 | 1.65835739 |
| **1901.28** | 12.25 | 0.14222201 | 0 | 0.14222201 | 0.56888804 | 0.14222201 | 0 | 0.28444402 | 1.27999809 |
| **1896.67** | 14.25 | 0 | 0.13184268 | 0 | 0.79105611 | 0 | 0 | 0.26368537 | 1.18658416 |
| **1876.485** | 16.5 | 0 | 0 | 0 | 0.76955623 | 0.12825937 | 0.12825937 | 0.12825937 | 1.15433434 |
| **1856.3** | 18.25 | 0 | 0 | 0 | 0.24565987 | 0 | 0 | 0 | 0.24565987 |

## Pitcher Pond

| Depth | Depth | Podospora | Sordaria | Sporomiella | Arnium | Coniochaeta | Ascodesmis | Delitschia | Spore total |
|---|---|---|---|---|---|---|---|---|---|
| **0** | 0 | 0.2539534 | 0.40632545 | 0.66027885 | 0.81265089 | 0.05079068 | 0.10158136 | 0.10158136 | 2.38716199 |
| **0.5** | 0.5 | 0.46391007 | 0.34793256 | 2.08759533 | 1.15977518 | 0.34793256 | 0 | 0 | 4.40714569 |
| **1** | 1 | 0.159849 | 0.63939599 | 0.87916949 | 0.87916949 | 0.319698 | 0 | 0.2397735 | 3.11705546 |
| **1.5** | 1.5 | 0.12063451 | 0.30158628 | 0.36190353 | 0.5428553 | 0.06031726 | 0.12063451 | 0.18095177 | 1.80951765 |
| **2** | 2 | 0.04082263 | 0.20411313 | 0.16329051 | 0.20411313 | 0.08164525 | 0.02041131 | 0.02041131 | 0.73480728 |
| **2.5** | 2.5 | 0.12388139 | 0.15485173 | 0.21679243 | 0.43358485 | 0 | 0.06194069 | 0.06194069 | 1.05299179 |
| **3** | 3 | 0.12740447 | 0.21234079 | 0.25480895 | 0.5096179 | 0.08493632 | 0 | 0.08493632 | 1.27404474 |
| **3.5** | 3.5 | 0.14895743 | 0.37239358 | 0.37239358 | 0.59582972 | 0.14895743 | 0.07447872 | 0.14895743 | 1.86196787 |
| **4** | 4 | 0.35148529 | 1.1423272 | 1.75742646 | 2.37252572 | 0.35148529 | 0 | 0 | 5.97524996 |
| **4.5** | 4.5 | 0.24627079 | 0.90299288 | 0.82090262 | 1.55971497 | 0.08209026 | 0.08209026 | 0.08209026 | 3.77615204 |
| **5** | 5 | 0.40760795 | 0.8152159 | 1.01901988 | 2.24184373 | 0.30570596 | 0 | 0.50950994 | 5.29890336 |
| **5.5** | 5.5 | 0.28869404 | 0.6495616 | 0.36086755 | 1.01042915 | 0.21652053 | 0.14434702 | 0.36086755 | 3.03128745 |
| **6** | 6 | 0.2449226 | 0.65312694 | 0.4898452 | 0.81640867 | 0.32656347 | 0.16328173 | 0 | 2.85743034 |
| **6.5** | 6.5 | 0.12928899 | 0.38786698 | 0.32322248 | 0.77573396 | 0.12928899 | 0.0646445 | 0.12928899 | 1.9393349 |
| **7** | 7 | 0.15881164 | 0.21174885 | 0 | 0.37056049 | 0.05293721 | 0.05293721 | 0 | 0.84699541 |
| **7.5** | 7.5 | 0.03332734 | 0.09998202 | 0.03332734 | 0.16663669 | 0.06665468 | 0 | 0.03332734 | 0.4332554 |
| **8** | 8 | 0 | 0.01989574 | 0 | 0.15916592 | 0.0994787 | 0.01989574 | 0.03979148 | 0.33822757 |
| **8.5** | 8.5 | 0.0673104 | 0.2692416 | 0.0673104 | 0.4038624 | 0.1346208 | 0.0673104 | 0.1346208 | 1.14427681 |
| **9** | 9 | 0 | 0.06580506 | 0 | 0.26322023 | 0.06580506 | 0 | 0 | 0.39483035 |
| **10** | 10 | 0 | 0.14899007 | 0 | 0.37247518 | 0.14899007 | 0.07449504 | 0 | 0.74495036 |
| **12** | 12 | 0.05542266 | 0.05542266 | 0 | 0.05542266 | 0.16626799 | 0 | 0.05542266 | 0.27711332 |
| **14** | 14 | 0 | 0 | 0 | 0.07528147 | 0.07528147 | 0 | 0 | 0.15056294 |
| **16** | 16 | 0 | 0.09584999 | 0 | 0.09584999 | 0.09584999 | 0 | 0.19169997 | 1.05434986 |
| **18** | 18 | 0 | 0 | 0 | 0.15129558 | 0.05043186 | 0 | 0.15129558 | 0.20172744 |