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A new perspective on Quaternary land cover in central Alaska

by

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ABSTRACT

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A NEW PERSPECTIVE ON QUATERNARY LAND COVER IN CENTRAL ALASKA

Emma-Jayne Hopla

In the high northern latitudes vegetation is already responding to increasing global temperatures, with shrubs expanding poleward in a process called "greening". In light of increasing global temperatures, past climate-driven shifts in vegetation can be used as analogues for future warming scenarios. This study addresses vegetation change in Alaska throughout the late glacial and Holocene, specifically how the accuracy of vegetation composition can be improved over current reconstructions.

The Landscape Reconstruction Algorithm (LRA, Sugita 2007a, b) is a two-step framework for quantitative reconstruction of land cover across various spatial scales. The model REVEALS estimates regional vegetation abundance from pollen records from large lakes, which is then incorporated into the model LOVE to arrive at local estimates of vegetation (using pollen records from small lakes). Pollen productivity estimates (PPEs) are one of the major parameters used in the LRA. The first pollen productivity estimates for the dominant forest and tundra taxa in Interior Alaska are presented in this study. The taxonomic ranking of high and low pollen producers are comparable with Europe. PPEs were used with the REVEALS model to obtain quantitative reconstructions of regional vegetation in north-central Alaska. The effectiveness of the LRA approach was then assessed in the landscape of the south Brooks Range at two small lakes, Ruppert and Lake 3. Results indicate that small lakes in Alaska produce the same pollen signal as large lakes and that REVEALS provides similar results as LOVE as the local vegetation is very similar to the regional mean vegetation.

Several key insights and prospects arise from the application of REVEALS: i) after its late glacial expansion, *Betula* may not have been as dominant as previously thought, but rather co-dominant with *Salix*; ii) deciduous, *Populus* woodland may have been extensive in the early Holocene; and iii) The LRA in Alaska needs further testing and validation in the tundra with 3 small lakes and 1 large lake, and would provide an opportunity to further assess the reliability of the new Alaskan PPEs.

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DECLARATION OF AUTHORSHIP

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

A new perspective on Quaternary land cover in central Alaska

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
5. I have acknowledged all main sources of help;
6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
7. None of this work has been published before submission.

Signed: ....

Date:...

Definitions and Abbreviations

1/d	Stepwise inverse distance-weighting
$1/d^2$	Stepwise inverse square distance-weighting
^{14}C	Carbon-14 (radiocarbon)
A.D.	*Anno Domini*
AMS	Accelerator mass spectrometry
AP	Arboreal pollen
C	Carbon
Cal yr BP	Calendar years before present
Cc	Canopy component
Cg	Gravity component
CHAR	Charcoal accumulation rate
CHAR:FF	Charcoal accumulation rate : Fire frequency ratio
CORINE	Coordination of information of the environment
Cr	Long distance component via precipitation
Ct	Trunk space component
Cw	Runoff component
DWPA	Distance weighted plant abundance
ERV	Extended R-value
FF	Fire frequency
FRI	Fire return interval
FSP	Fall speed of pollen
GIS	Geographical Information System
HF	Hydrofluoric acid
HUMPOL	Suite of programs for modelling pollen dispersal (Hull University)
ITRAX	High resolution X-ray analysis of sediment cores
Ka	Thousand
LAC	Lakes and the Arctic Carbon Cycle
LANDCLIM	The past LAND cover – CLIMate Interactions in Europe

LFS	Likelihood function score
LGM	Last Glacial Maximum
LOVE	LOcal Vegetation Estimates
N2	Atmospheric nitrogen
NAP	Non-arboreal pollen
NSAP	Necessary source area of pollen
PAR	Pollen accumulation rate
PAZ	Pollen assemblage zone
PCQ	Point centred quartered
PFT	Plant functional type
PPE	Pollen productivity estimates
POLERV	ERV analysis program (Hull University)
POLLSCAPE	Pollen simulation framework
R	Software for statistical computing and graphics
R^2	R-squared coefficient (coefficient of determination in Regression Analysis
REVEALS	Regional Estimates of VEgetation Abundance from Large Sites
RSAP	Relative source area of pollen
TLP	Total land pollen
µm	microns
XRF	X-ray fluorescence

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“All we have to decide is what to do with the time that is given us”

J.R.R. Tolkien

The Fellowship of the Ring

“It always seems impossible until it’s done”

Nelson Mandela

Chapter 1: Introduction

1.1 Project Background

The Arctic is sensitive to climate change and it is predicted that the region will experience rapid changes with future global warming (Solomon *et al*, 2007). Vegetation is already responding to increasing global temperatures, with shrubs expanding northwards in the Arctic in a process called "greening" (Jia *et al*, 2009). Lakes are important features within these changing landscapes, and use of dated sediment archives can reveal how both vegetation and lake ecosystems responded to climate change in the past.

The state of Alaska contains over 3 million lakes and these have been the focus of palaeoecological studies, particularly vegetation reconstructions from pollen analysis. The region remained largely unglaciated during the Last Glacial Maximum (LGM, 26,500-16,800 cal yr BP) and therefore long records are available extending back to the cold, dry period of the LGM. This provides an opportunity to follow the full development of lake and vegetation systems from the late glacial herb tundra to deciduous woodland as the region became warmer and wetter with the transition to the early Holocene (Anderson *et al*, 2004). In light of increasing global temperatures, past climate-driven shifts in vegetation can be used as analogues for future warming scenarios (Ruess *et al*, 2010)

1.1.1 Lakes and the Arctic Carbon Cycle

This project is linked to the Lakes and the Arctic Carbon Cycle (LAC) Project funded by NERC Arctic Research Programme (NE/K000349/1). LAC aims to understand the interactions between Arctic landscape ontogeny and aquatic biogeochemical cycling at the landscape scale. Lakes are a key component of terrestrial carbon cycling in the Arctic (Cole *et al*, 2007) and production and C sequestration is assumed to increase with climate warming (Smol *et al*, 2005). Catchment vegetation can alter nutrient cycling in soils but little is known about the effect of shifts in vegetation types on lake ecosystems. *Alnus* (alder) for example, can fix atmospheric nitrogen (N_2) and it is assumed that the introduction of this genus into the catchment will have an effect on the availability of nitrogen and lake productivity. For instance, sediment biogenic silica increased with the expansion of alder at Grandfather Lake (south-western Alaska), indicating an increase in diatom productivity due to the fixation of N_2 in the surrounding soils (Hu *et al*, 2001).

In LAC, regionally replicated palaeo records from small sets of lakes in Greenland, Norway and Alaska are being used to evaluate the effect of changing abundances of Plant Functional Types (PFTs) on aquatic diversity and nitrogen and carbon cycling. Catchment vegetation can alter nutrient cycling in soils, including nitrogen and carbon cycling, and any modelling of carbon production by lakes requires input of accurate catchment vegetation cover values. Thus, the accurate reconstruction of vegetation cover around a lake is vital for understanding these long-term lake ecosystem processes. A further aim of LAC was to assess the reproducibility of the signals in records from different sites within a region.

This thesis is linked to LAC as it specifically addresses shifts in vegetation types in Alaska throughout the late glacial and Holocene, particularly how vegetation composition can be reconstructed quantitatively. The LAC study focuses on two small lakes within the central Brooks Range in Alaska; Ruppert Lake and Lake 3 (1-2km apart). Pollen assemblage zones (PAZs) have been identified using pollen analysis from the end of the last Glacial Maximum through the Holocene from pre-existing data from Ruppert Lake (Higuera *et al*, 2009). The approach used in this thesis work involves the following: i) establishing pollen productivity estimates (PPEs) for key pollen taxa in Alaska; ii) applying and assessing the regional land-cover reconstruction program REVEALS (Sugita 2007a) to large lakes and groups of smaller lakes; iii) testing the applicability of the local land-cover reconstruction program LOVE (Sugita 2007b) on a series of test sites; and iv) applying the land-cover reconstructions at Ruppert and Lake 3 to provide what should be a more accurate quantitative representation of how key PFTs have changed through time at these sites.

In addition, catchment fire disturbances have been recorded via a new charcoal record at Lake 3 and are compared with the charcoal data from Ruppert Lake (Higuera *et al*, 2009) to strengthen the current understanding of fire histories in the region, to investigate how replicable these records are, and to link changes in fire regimes to changes in vegetation and nutrient cycling.

1.1.2 Quantitative Reconstructions of Vegetation

The majority of vegetation reconstructions have been based on percentage representations of taxa in samples as a way to deduce the landscape vegetation. Pollen diagrams illustrate changes in the percentages of pollen taxa in samples, and these are then used to interpret changes in taxon abundance (Prentice and Webb, 1986). However, pollen percentages do not reflect a linear correlation with percentage abundance of vegetation (Prentice and Webb, 1986). Pollen spectra are known to be biased towards taxa with high pollen productivity and/or slow deposition from the atmosphere (Prentice, 1985). Pollen accumulation rates (PARs) have been used as way to attempt to obtain quantitative reconstructions of vegetation cover. However, PAR estimates from different lakes are not directly comparable with each other and cannot be used as a direct measure of plant abundance (Davis, 2000).

Developing new methodologies to reconstruct the vegetation quantitatively in terms of actual land cover is increasingly at the forefront of palaeoecology, as quantitative reconstructions can describe more accurately features such as past land use. Given the need to understand how future climate change will unfold, an accurate description of past vegetation dynamics can be used in process models (such as vegetation models) and earth-system models to assess the effects of land-cover change on feedbacks to climate via the surface energy balance and greenhouse gas fluxes (Trondman *et al*, 2015). The Landscape Reconstruction Algorithm (LRA, Sugita, 2007 a, b) has been a fundamental step forward in deriving a quantitative estimate of vegetation and land cover based on the theories of pollen production and dispersal. The LRA has been successfully validated in Europe (e.g. Hjelle *et al*, 2015) but there has been no testing of quantitative landscape reconstruction models to date, in Alaska.

1.2 Aims and Objectives

The main aim of this thesis is to gain a better understanding of what the land cover was in Alaska from the late glacial and throughout the Holocene, particularly with respect to treeless versus forested and deciduous versus coniferous vegetation. Assessing how accurate pollen-based vegetation reconstructions are, and in particular what is the best way to reconstruct catchment vegetation around lakes currently in the boreal forest zone of Alaska will be addressed though four linked aims:

- Obtaining Pollen Productivity Estimates for Interior Alaska (Chapter 3)

Pollen productivity is simply a measure of the amount of pollen released for transport per unit area of pollen-producing vegetation (Bunting *et al*, 2013b), but it is a critical parameter used to make quantitative estimates of land cover from palaeodata. In order to arrive at reliable estimates of regional and local vegetation for any given region, Shinya Sugita (*pers comm, Nov 2015*) suggests that the PPEs used in the LRA should be obtained from that region whenever possible. There are currently no PPEs derived from Alaskan taxa. PPEs were obtained for the dominant forest and tundra taxa in Interior Alaska for use within the Landscape Reconstruction Algorithm.

- Obtain quantitative reconstructions of regional vegetation in north-central Alaska, including the central Brooks Range (Data Chapter 4)

The Landscape Reconstruction Algorithm (LRA) is a two-step framework for quantitative reconstruction of vegetation which corrects the non-linearity of pollen percentage data (Sugita, 2007a). The first step is the model REVEALS which estimates the regional vegetation abundance from large sites. However, recent reconstructions using REVEALS in Europe (Hjelle *et al*, 2015) have also shown that multiple smaller sites can be used in the absence of a large lake for the region. Figure 1.1 illustrates all the study sites used in this thesis from data Chapters 4 -6. REVEALS was applied to large and small lakes in the foothills of the south-central Brooks Range to assess how reconstructions of mean regional vegetation cover alters our current understanding of regional Holocene vegetation trends in Alaska. The reconstructions from this Chapter also provide the regional input data for Chapter 6, where the second step of the LRA (the LOVE model) is applied to Ruppert Lake and Lake 3.

- Test the effectiveness of the LRA for small sites in Alaska (Data Chapter 5)

The second step of the LRA is the model LOVE, which incorporates the regional REVEALS estimates to calculate the background pollen and then applies this to the reconstruction of the local vegetation composition. Validation and testing of the LRA on modern assemblages in different vegetation and climatic regions is vital for producing reliable reconstructions. The effectiveness of the LOVE approach was tested on modern lake surface samples from three small lakes in the tundra along the Richardson and Denali Highway, and at Smith Lake, located in the Interior boreal forest. Vegetation cover around these lakes was recorded and was the baseline for comparison. This exercise also allows the validity and the robustness of the new Alaskan PPEs obtained in Chapter 3 to be assessed.

- Apply the best approach (as identified by the work outlined above) to reconstruct catchment vegetation for the integrated lake studies at Ruppert Lake and Lake 3 in the south-central Brooks Range (Data Chapter 6)

The Landscape Reconstruction Algorithm was applied to reconstruct the vegetation cover at the LAC study lakes, Ruppert and Lake 3. This Chapter assesses the effectiveness of the LRA approaches (REVEALS and LOVE) in the landscape of the southern Brooks Range. The degree of palaeoecological congruence between two sites in the same area with different types of catchment was examined. The charcoal records and fire-history reconstructions in these two lake catchments were compared, and the late-Quaternary fire regime reviewed in light of revised vegetation cover estimates.

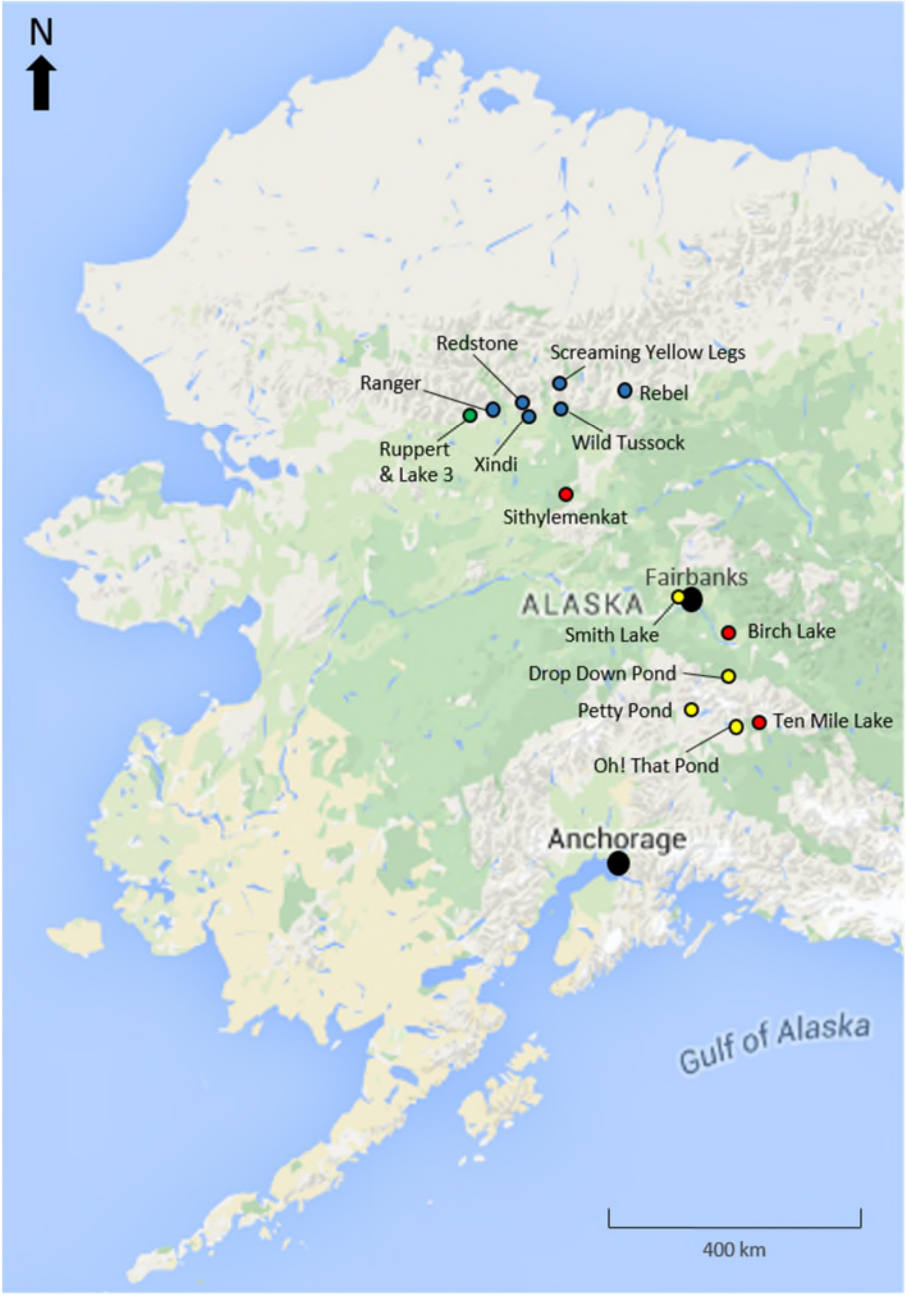


Figure 1.1: *Location map of all study sites used in thesis.*

KEY:RED = Large regional lakes used in REVEALS (Chapters *4, 5 and 6), BLUE = small lakes used in REVEALS* (Chapters *4, 5 and 6), YELLOW = small lakes used in LRA validations* (Chapter *5), GREEN = small lakes used with LOVE reconstructions* (Chapter *6)*

Chapter 2: Literature Review

2.1 Alaskan modern vegetation

2.1.1 Vegetation of Alaska overview

(adapted from Viereck and Little, 2007)

The vegetation varies from the coastal rainforests to the south and the boreal forests of the Interior to the subarctic and arctic tundra. Figure.2.1 illustrates the distribution of the main vegetation functional types. The coastal forests occupy a narrow band (160km) stretching from Alexander Archipelago to the Prince William Sound and Kodiak Island (WWF, 2015). The forests are dominated by *Tsuga heterophylla* (Western hemlock) and *Picea sitchensis* (Sitka spruce), with *Tsuga mertensiana* (Mountain hemlock) and *Chamaecyparis nootkatensis* (Alaska cedar). *Alnus rubra* (Red alder) grows along the streams, with *Populus trichocarpa* (Black cottonwood) along the floodplains and rivers (Viereck and Little, 2007).

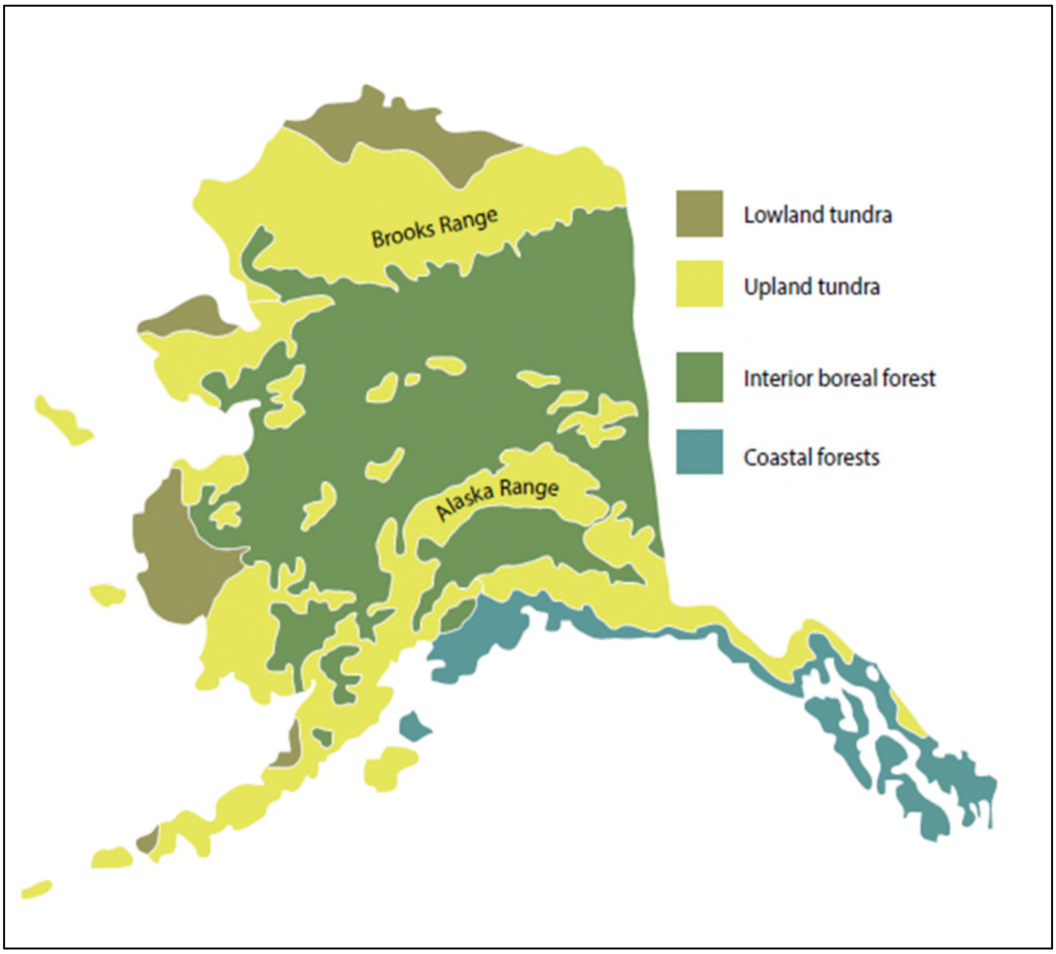


Figure 2.1: *Vegetation Map of Alaska (Source: adapted from Viereck et al, 1992)*

The coastal forests give way to the boreal forests of the interior as the climate becomes colder. The boreal forests cover around 32% of Alaska and extend up to the foothills of the Brooks Range, eastwards across into Canada and out westwards towards the coast. Northwards past the Brooks Range tundra dominates the landscape. Tundra is also extensive across the mountain ranges, the Seward and Alaska peninsulas, the Aleutian Islands and the south-western coastal areas. The transition zone is where the boreal forests and the alpine tundra communities meet, also referred to as the forest-tundra (Payette *et al*, 2001). The transition is often observed as a transition from forest, through an area dominated by forest with patches of tundra, to tundra with patches of forest, to a treeless tundra (Callaghan *et al*, 2002). In this zone tree species have reduced growth and development due to severe climatic conditions (Sirois, 1992). Viereck and Little (2007) discuss seven main forest types and three tundra types for Alaska and these are summarised in Table 2.1. The study regions discussed in subsequent Chapters lie within the boreal forest and tundra biomes and these are discussed in further detail below.

Vegetation Type	**Distribution**	**Trees**	**Common shrubs**
Coastal Forests	Southeast coastline	*Picea sitchensis* (Sitka spruce) *Tsuga heterophylla* (Western hemlock) *Tsuga mertensiana* (Mountain hemlock) *Chamaecyparis nootkatensis* (Alaska cedar) *Alnus rubra* (Red alder) *Populus trichocarpa* (Black cottonwood)	*Alnus sinuate* (Sitka alder) *Gaultheria* shallon (Salal) *Salix sitchensis* (Sitka willow)
Boreal Forests White Spruce Type	Warm, dry, south-facing hillsides, adjacent to rivers	*Picea glauca* (White spruce) *Betula neoalaskana* (Alaskan paper birch) *Populus balsamifera* (Balsam poplar)	*Arctous rubra* (Bearberry) *Empetrum nigrum* (Crowberry) *Rosa acicularis* (Prickly rose) *Salix alaxensis* (Felt-leaf willow) *Salix arbusculoides* (Little-tree willow) *Salix bebbiana* (Bebb willow)
Boreal Forests Recent Burns	Throughout the Interior	Following a fire, it is common for shrubs to colonise the area first.	*Ledum decumbens* (Narrow-leaf Labrador tea) *Rosa acicularis* *Salix arbusculoides* *Salix bebbiana* *Salix scouleriana* (Scouler willow)
Boreal Forests Quaking Aspen Type	South-facing slopes (often replaced by spruce)	*Populus tremuloides* (Quaking aspen) *Picea glauca* *Picea mariana* (Black spruce)	*Rosa acicularis* *Salix bebbiana* *Salix scouleriana* (Scouler willow)

			Shepherdia canadensis (Buffaloberry)
Boreal Forests Paper Birch Type	Common invading tree after fire on east and west-facing slopes	*Betula neoalaskana* *Picea glauca* *Picea mariana*	*Ledum decumbens* *Ledum groenlandicum* (Labrador tea) *Vaccinium vitis-idaea* (Mountain cranberry) *Salix barclayi (Barclay willow)* *Salix bebbiana* *Salix scouleriana*
Boreal Forests Balsam Poplar Type	Floodplains, near altitudinal and latitudinal tree limits	*Populus balsamifera* *Populus trichocarpa* *Picea glauca*	*Alnus fructicosa* (Siberian alder) *Alnus sinuate* *Alnus tenuifolia* (Thin-leaf alder) *Salix arbusculoides* *Salix alaxensis*
Open Spruce Forests	North-facing slopes and poorly drained lowlands	*Picea mariana* *Larix laricina* (Tamarack/Larch) *Betula neoalaskana* *Picea glauca*	*Arctos rubra* *Empetrum nigrum* *Ledum groenlandicum* *Salix*
Moist tundra	Foothills of Alaska Range, Seward and Alaska peninsula The Aleutian Islands	**Common Shrubs**	
		Alnus fruticosa, Betula glandulosa (Resin birch), *Betula nana* (Dwarf arctic birch), *Cassiope tetragona* (Four-angled cassiope), *Salix arctica* (Arctic willow), *Salix barclayi, Salix barrattiana* (Barratt willow), *Salix chamissonis* (Chamisso willow), *Salix commutata* (Under-green willow), *Salix fuscescens* (Alaska bog willow), *Salix reticulata* (Net leaf willow)	
Wet Tundra	Coastal marshes of southern Alaska, Coastal plain north of Brooks Range	*Betula glandulosa*, *Betula nana, Ledum decumbens, Salix fuscescens, Salix reticulata, Salix ovalifolium* (Arctic seashore willow), *Vaccinium uliginosum* (Bog blueberry), *Vaccinium vitis-idaea*	
Alpine Tundra	Mountain ranges , southwestern coastal areas	*Betula glandulosa*, *Betula nana, Salix, Cassiope lycopodioides (*Alaska cassiope*), Cassiope mertensiana (*Mertens cassiope*), Cassiope tetragona, Dryas octopetala (*White mountain avens*), Dryas integrifolia (*Entire-leaf mountain avens*), Empetrum nigrum, Ledum dedcumbens, Salix, Vacciunium uliginosum, Vaccinium vitis idaea,*	
Other types: Treeless Bogs, Coastal Alder thickets, Floodplain thickets			

Table 2.1 *: Seven main forest types and three tundra types for Alaska (source: Viereck and Little, 2007)*

2.1.2 Boreal Forests

The boreal forest biome is considered to be one of the earth's most significant terrestrial ecosystems in terms of their potential for interaction with other global scale systems, such as climate (Shugart *et al*, 2005). Boreal Forests cover 10% of the ice-free terrestrial surface of the

Earth (Chapin *et al*, 2006), approximately an area of 14.7 million km^2 (Kasischke *et al*, 2000) and contribute to around 30% of terrestrial carbon stocks (Apps *et al*, 1993). The distribution of the world's boreal forests includes vast parts of Europe, Russia, Asia and North America. The composition of boreal forests is dependent on local climate, physiography, landform, soil, permafrost and fire regime (Bourgeau-Chavez *et al*, 2000) and they have fewer vascular plants than any other forested biome (Pastor and Mladenoff, 1992).

The boreal forests of Alaska dominate the interior up to the foothills of the Brooks Range. The floristic composition has remained fairly stable for the past 5,000 years, with the main conifer species *Picea glauca* (white spruce) and *Picea mariana* (black spruce) and *Larix laricina* (larch). The deciduous woodland trees are *Populus tremuloides* (quaking aspen), *P. balsamifera* (balsam poplar) and *Betula neoalaskana* (paper birch) along with shrubs of *Salix* and *Alnus* (Chapin *et al*, 2006). The interior of Alaska contains only the three species of conifers and the three species of deciduous trees (Chapin *et al*, 2006) and around 400 herbaceous species (Jorgenson *et al*, 1999). Figure 2.2 illustrates the three main controlling factors on vegetation distribution around Fairbanks, Interior Alaska; microclimate, soils, hydrology and ecosystem processes (Chapin *et al*, 2006). *Picea mariana* forests are widespread on poor drained soils lying on top of permafrost. *Picea glauca* is better represented on well-drained upland sites with *Populus balsamifera* common along the major rivers (Van Cleve and Viereck, 1981). This region is one of the most flammable areas in the boreal biome (Kelly *et al*, 2013).

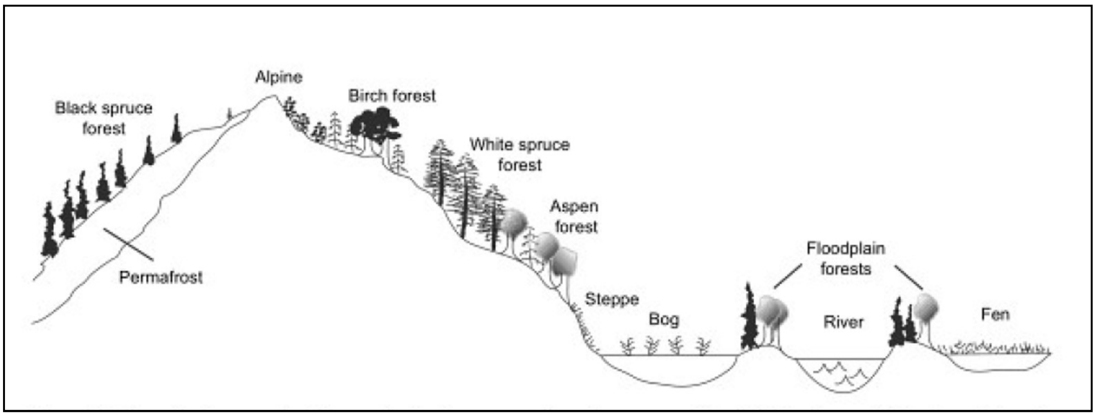


Figure 2.2 *Generalised cross-*Section *of topography, landforms, vegetation and parent material in the Fairbanks area with location of the major vegetation types. Source: Chapin et al (2006) adapted from Viereck et al (1983) and (Jorgenson et al, 1999).*

2.1.3 Tundra

The tundra is the coldest biome on Earth and is often defined as a treeless landscape due to predominantly cold climates (Murray, 1978). Tundra vegetation is therefore beyond the latitudinal (polar tundra) or altitudinal (alpine tundra) limits of tree growth (Callaghan and

Emanuelsson, 1985). The cold climatic conditions means that tundra is often dominated by permafrost. Permafrost is defined as ground (soil or rock including ice or organic material) that remains below zero degrees for two or more years (IPA, 2015). Some shrubs, forbs, mosses and lichens are better adapted to survive in these conditions than arboreal species.

There are three main types of tundra in Alaska as defined by Viereck and Little (2007): moist tundra, wet tundra and alpine tundra. Moist tundra is the dominant vegetation type in the foothills and lower elevations of the Alaska Range. *Eriophorum* species (cottongrass tussocks) are common along with dwarf shrubs. Typical shrubs include *Alnus fructicosa* (Siberian alder), *Betula glandulosa* (Resin birch), *Betula nana* (Dwarf arctic birch), *Cassiope, Dryas* and *Salix* species. Wet tundra type is most prevalent on the coastal plain north of the Brooks Range, but also occurs in some coastal areas to the south. Permafrost is often near the surface and standing water in the summer is a common feature on the landscape. Typical shrubs include *Betula glandulosa, Betula nana, Salix species, Vaccinium* species. Alpine tundra is extensive across all of the mountain ranges. *Dryas octopetala* (white mountain avens) dominates slopes in the Alaska Range with grasses, sedges and herbs. Ericaceous plants (heaths) include *Vaccinium uliginosum* (Bog blueberry) and *Vaccinium vitis idaea* (Mountain cranberry). Other typical shrubs include *Betula glandulosa, Betula nana, Diapensia lapponica (Diapensia), Cassiope*, and *Salix* species.

Figure 2.3: *Tundra landscape along the Denali Highway, Alaska (E.Hopla)*

2.1.4 Brooks Range

The Brooks Range is the focus of the regional vegetation reconstructions discussed in Chapter 4. The study sites of Ruppert and Lake 3 are located in the southern foothills of the Brooks Range

(Chapter 6). The Brooks Range is an east-west trending mountain range that rises to 2,700m above sea level (asl). It separates the Arctic region from the interior and spans 1,000km across northern Alaska (Oswald *et al*, 2012). Scattered small glaciers lie above 1,800m and all soils, except for a few south-facing slopes, are underlain by permafrost (Alaska Department of Fish and Game, 2006). The climate of the Brooks Range is similar to the arctic coastal plains with a mean daily maximum summer temperature of 16°C recorded at Anaktuvuk Pass (WWF, 2015) and winter temperatures as low as -60°C (US Forest Service, 2014).

The lower mountain slopes on the northern side are covered by mixed shrub-sedge tussock tundra (Alaska Department of Fish and Game, 2006), dominated by *Eriophorum vaginatum*. Sparse boreal forest, mainly *Picea glauca* and *Betula neoalaskana* (Hultén, E., 1968) occurs on the south slopes. The treeline in Alaska is often mapped as the limit of *P.glauca* along the south slope of the Brooks Range (Viereck, 1979). The Brooks Range Mountains give way to the Arctic Foothills, where the terrain varies in elevation from 180m at the northern edge to over 1050m (Walker *et al*, 1994). Tussock sedge communities are common in the Arctic foothills and low shrubs including *Alnus crispa* (green alder), *Salix pulchra* (tea leaf willow) and *Salix alazensis* (felt leaf willow) populate the river valleys (Walker *et al*, 1994). This region is generally treeless, but *Populus balsamifera* does occur in small groves near the treeline limit north of the Brooks Range (Viereck and Little, 2007).

2.1.5 The Tanana Valley

The Tanana Valley is a lowland in central Alaska between the foothills of the Brooks Range and the Alaska Range (see Figure 2.4). The study sites used to obtain the PPEs for the dominant boreal forest taxa (Chapter 3) are located within this region along with Birch Lake, which provides the regional vegetation discussed in Chapter 5. The Tanana River is 379km long and its drainage is the second largest tributary system of the Yukon River (State of Alaska, 2014). The region experiences winter lows often below -45°C and summer highs of 32°C (Ager, 1975). The majority of the region is covered by boreal forest with tree species of *P. glauca, Picea mariana, B. neoalaskana, Populus tremuloides, Populus balsamifera* (balsam poplar) and *Larix laricina* (Ager, 1975). Closed *P.glauca/P. balsamifera* forests (also including *Alnus* and *Salix spp*. occur on the floodplains of the Tanana River with open *Picea* hardwood forests widespread on the lowlands (Ager, 1975).

2.2 Vegetational History of Alaska

2.2.1 Overview

The state of Alaska contains over 3 million lakes. Lakes can provide important sedimentary archives for palaeoenvironmental studies and have been the focus of palaeoecological studies, particularly vegetation reconstructions from pollen analysis. Palynological studies in Alaska were pioneered by Livingstone in the 1950s. He proposed a three-zone pollen chronology from the Last Glacial Maximum (LGM) through to the mid-Holocene for the Brooks Range (Livingstone, 1955). The LGM is characterised by an herbaceous zone, followed by a *Betula* zone (late glacial) and an *Alnus* zone (Early/mid-Holocene). These zones still hold over much of the region, however advances in palaeoecological research has identified spatial and temporal variations which are discussed in further detail below. Firstly, a broad overview of the time-transgressive events will be outlined from the Last Glacial Maximum through the Holocene in Alaska, which follows Anderson *et al* (2004). This is followed by a detailed account of the vegetation histories in the study regions of the Brooks Range and the Tanana Valley. The locations of the sites discussed in this Section are shown in Figure 2.4.

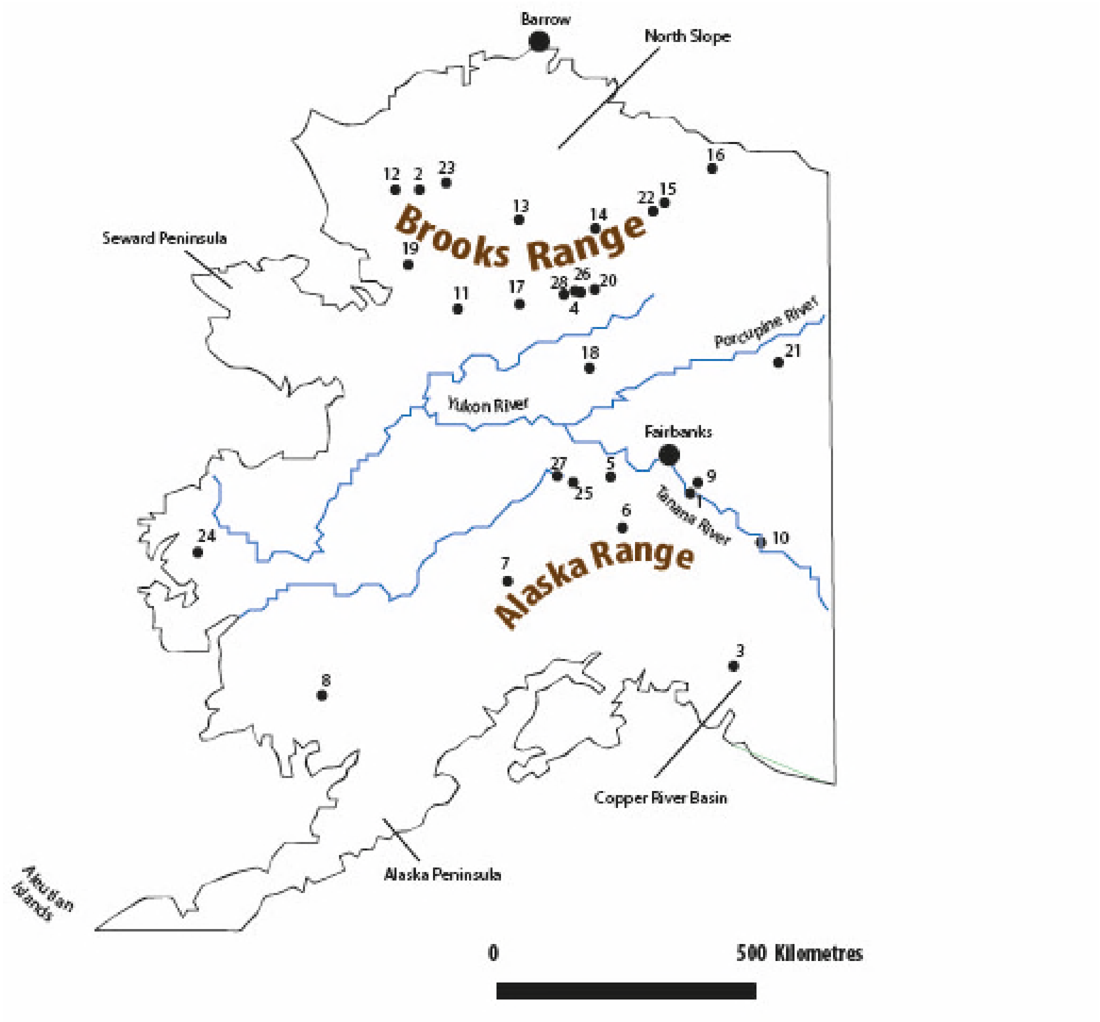


Figure 2.4: *Locations of sites discussed in text*

Birch Lake (2) Burial Lake (3) Chokasna and Moose Lakes (4) Code Lake (5) Dune Lake (6) Eightmile Lake (7) Farewell Lake (8) Grandfather Lake (9) Harding Lake (10) Jan Lake (11) Joe Lake (12) Kaiyak Lake (13) Lake of the Pleistocene and Etivlik (14) Meli Lake (15) Oil Lake (16) Okpilak Lake (17) Ruppert Lake (18) Sithylemenkat Lake (19) Squirrel Lake (20) Tangled Up Lake (21) Tiinkduhl Lake (22) Toolik Lake (23) Tukuto Lake (24) Tungak Lake (25) Wien Lake (26) Wild Tussock (27) Windmill Lake (28) Xindi Lake

2.2.2 The Last Glacial Maximum (26,500-16,800 cal yr BP) and late glacial (16,800-13,000 cal yr BP)

Initial interpretations suggested that much of Alaska was covered in herb tundra (similar to the current high arctic tundra) during the Last Glacial Maximum (LGM), as the majority of pollen diagrams were dominated by species such as Cyperaceae (sedges), *Salix,* Poaceae (grasses), Chenopodiaceae (goosefoots) and *Artemisia* (wormwood) (Ager, 1975; Anderson, 1985).

However, these interpretations have been challenged by some Quaternary mammalian specialists (Guthrie, 1982; 2001) initiating the "steppe-tundra" debate (Anderson *et al*, 2004). Guthrie (1982) suggests that some of the mammals that were present during this period would have required nutritional needs than could not have been provided by tundra alone. The presence of steppe vegetation is further supported by Coleoptera assemblages (Ashworth, 2004).

More recent approaches in palynological studies have adopted the use of plant functional type (PFT) groups (Bigelow *et al*, 2003). The LGM pollen taxa was assigned to PFTs and most were classified as either prostrate shrub tundra or Poaceae-forb tundra. This approach was applied in conjunction with LGM pollen data along with an atmospheric general circulation model (Kaplan *et al*, 2003) and the results support the initial interpretations of a tundra dominated landscape. This interpretation is further supported by plant macrofossils which were preserved under 1m of tephra deposited 18,00014C BP (21,500 cal yrs BP) in the Beringia National Park on the Seward Peninsula. The results indicate vegetation dominated by Cyperaceae, Poaceae and forbs with the occasional occurrence of *Salix* (Goetcheus and Birks, 2001). The presence of arboreal taxa is generally very low during this period in Alaska, although the occurrence of small amounts of tree and shrub pollen is widespread (Brubaker *et al*, 2005).

Towards the end of the LGM rises in *Betula* are recorded at many sites (Anderson *et al*, 2004) as the vegetation transitioned into shrub tundra. The establishment of shrub vegetation was recorded at Lake of the Pleistocene and Oil Lake in the Brooks Range around 15,500-14,700 cal yr BP (Mann *et al*, 2002). The Tungak lake record in south western Alaska indicates that *Betula* was first recorded around 16,700 cal yr BP however; it was not prevalent in the interior until 14,000 cal yr BP (Anderson *et al*, 1994, Hu *et al*, 1993, Edwards and Brubaker, 1986). The replacement of herb tundra by shrub *Betula* was a steady process over several thousand years. The spread of *Betula* towards the end of the late glacial has been attributed to the shift in climate to increased moisture and precipitation (Mann *et al*, 2002, Anderson and Brubaker, 1994). The variations in timing of the development in shrub tundra across Alaska have been largely assigned to the east-west moisture gradient proposed by Barnosky *et al*, (1987).

2.2.3 The Holocene

The major trends in vegetation are broadly similar across most of Alaska during the Holocene. Variations are time and space transgressive depending on landscape features and climate influence on vegetation composition (Carlson and Finney, 2004). The transition from the late glacial into the early Holocene is characterised by the development of deciduous woodland. *Populus balsamifera* was widespread across interior Alaska and present alongside *Betula* and *Salix*

(Anderson *et al*, 2004). *Populus* woodland is thought to have replaced some of the *Betula* shrubland at Joe Lake, northwestern Alaska during this period (Anderson *et al*, 1994) and was established on south-facing slopes and river valleys between 11,000 and 9,000 cal yr BP in the north central region (Anderson and Brubaker, 1994). The first palynological evidence that *Populus* extended above its modern limit around 9,000 cal yr BP and into the western Arctic foothills came from records from Tukuto and Etivlik Lakes (Oswald *et al*, 1999).

The occurrence of thermophilous trees such as *Populus* in the early Holocene has led many palaeoecologists to interpret the climate of this period with warmer than present summer temperatures (Brubaker *et al*, 1983; Edwards and Barker, 1994). The extent to which *Populus* forest was prevalent in central Alaska varies (Anderson *et al*, 2004). Some researchers suggest that the forest was restricted to slopes and floodplains, whereas others indicate a dense cover on lower elevations (Ager, 1983; Brubaker *et al*, 1983; Hu *et al*, 1993). Ritchie *et al* (1983) review pollen records from the uplands surrounding the Mackenzie delta (north-western Canada) which indicate maximum summer warmth centred on 10,000 cal yr BP. Data from Twin Tamarack lake further illustrates an expansion of *Betula nana* (dwarf birch) and *Populus* c.10,000 cal yrs BP which is attributed to climate warming (Ritchie, 1984). Evidence for this early Holocene warming period is absent from sites in central and eastern North America and Ritchie *et al* (1983) suggest that the Alaska-Yukon-Mackenzie delta area record these vegetation responses due to their location upstream of the Laurentide ice sheet. Their position would have made them more sensitive to changes in net solar radiation based on the Milankovitch theory of global climatic change (Berger, 1984). However, chironomid-based temperature reconstructions from three lakes in central and southern Alaska suggest the climate was not as warm as previous studies have suggested (Clegg *et al*, 2011). The results show a nonlinear response of summer temperatures to Holocene insolation radiative forcing with temperatures between 10,000-5,500 cal yr BP lower than modern values. As the climate became cooler and moisture increased, *Populus* declined. However, it has also been suggested that the development of organic soils would have resulted in the decline in *Populus* (Cwynar, 1982, Anderson *et al*, 2004).

Following the decline in *Populus*, the broad pattern across much of Alaska is the establishment of *Alnus* followed by the expansion of *Picea mariana*. The first appearances of *Alnus* are from Kaiyak Lake ~10,000 cal yr BP (Kotzebue Sound, Anderson, 1985) and Toolik Lake ~10,500 cal yr BP (Brooks Range, Bergstrom, 1984). A rapid rise in *Alnus* has been dated to c. 8,000-7,000 cal yr BP at Grandfather Lake, south-western Alaska (Hu *et al*, 1995). Many pollen records from the south-western region encounter higher percentages and accumulation rates than elsewhere in Alaska (Hu *et al*, 2001). A general trend in records from the mid to late Holocene show a final transition to boreal forests as *Picea* expands.

Precise dating of the arrival of *Picea* has been difficult to establish in Alaska due to variable dating methods (outlined below). The general picture is that *Picea glauca* was present c. 9000 cal yr BP in the major river valleys and later in the upland sites (Edwards and Barker, 1994). Abbott and Stafford (1996) discuss the importance of dating methods; with particular reference to bulk dating of sediment which can be contaminated with older carbon. This has caused significant problems when trying to provide a confident chronology for the *Picea* migration as many palaeoecological records have used bulk dating in the past (Carlson and Finney, 2001). There are debates about whether *Picea* was present in refugia during the LGM. Macrofossils occur pre- and post-LGM in eastern Beringia, where the landscape was unglaciated, but there is limited palynological evidence (Edwards *et al*, 2014). Edwards *et al* (2014) argue that refugial populations are likely in eastern Beringia despite the lack of palynological evidence. However, the extent to which refugial populations expanded or were replaced by in-migration is unknown. *Picea glauca* decreases in the mid-Holocene before the arrival of *P. mariana*. The pattern starts in north-central Alaska around 4,500 cal yr BP moving south west and across into the south-west Brooks Range (Anderson *et al*, 2004).

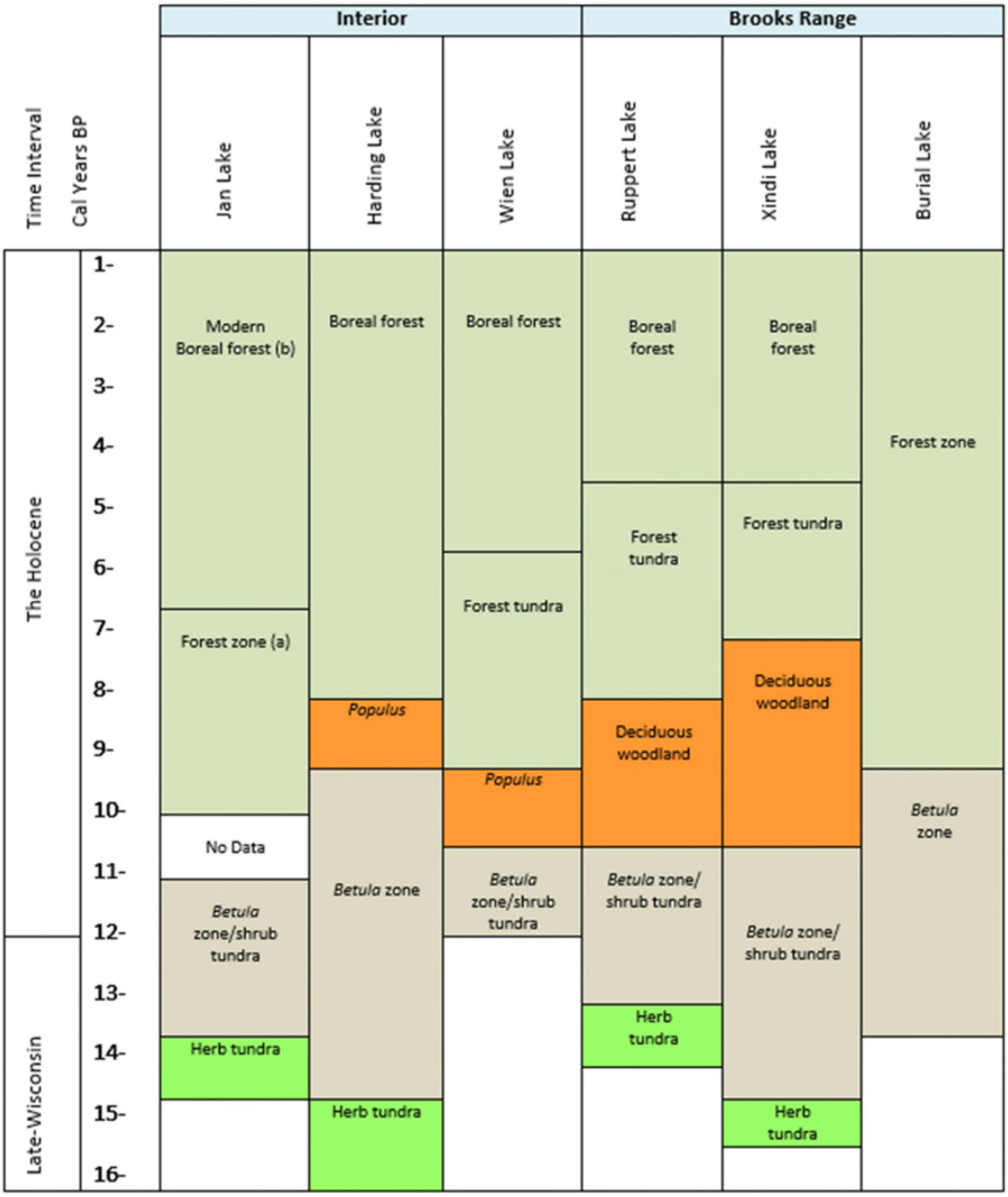


Figure 2.5: *Comparison Chart of PFT zones in the Brooks Range and Interior Alaska (adapted from Ager, 1985)*

2.2.4 The Brooks Range

The LGM pollen record from the Arctic Foothills around Tukuto Lake are characterised by Poaceae and Cyperaceae (Oswald *et al*, 1999). *Salix* and Cyperaceae expanded with an associated decline in Poaceae around 15,500 cal yrs BP. The transition into shrub tundra in the west central Brooks Range has been dated to 15,500-14,700 cal yr BP (Mann *et al*, 2002). More recent advances in AMS dating have placed the rise in *Betula* later than previously thought in this region. AMS 14C dates from Burial Lake record the *Betula* rise to 13,900 cal yr BP which is consistent with Tukuto Lake (Abbott *et al*, 2010) which was dated by AMS 14C measurements on macrofossils (Oswald *et al*, 2005). Abbott *et al* (2010) proposed that these new dates for the birch rise suggest synchronous vegetation change and that this is likely a response to atmospheric circulation readjustment. The Laurentide ice sheet would have still covered a substantial area in the late glacial (14-10,000 cal yr BP) and this along with a cool North Pacific Ocean would have presented cooler than present summer temperatures (Bartlein *et al*, 1991). The dates from Kaiyak, Squirell and Joe Lakes (Anderson, 1985, 1988) place the *Betula* rise 1000-1500 earlier than Tukuto and Burial Lakes and this has been attributed to the use of bulk radiocarbon dating rather than the AMS (Abbott *et al*, 2010).

Records from the southern foothills of the Brooks Range at Ruppert Lake and Xindi Lake place the onset of the transition to shrub tundra to 13,500 and 14,300 cal yr BP respectively (Higuera *et al*, 2009). The expansion of *Betula* is dated later in the upland northeastern region between 11,600-8,500 cal yr BP at Okpilak Lake (Oswald *et al*, 2012). The pattern indicates that the *Betula* rise started in the southern foothills and spread northwards during the transition from the late glacial into the early Holocene.

The arrival of *Populus* on the North Slope is characterised by scattered occurrences, restricted to the floodplains and low-elevations (Mann *et al*, 2002, Oswald *et al* 1999). Dates from macrofossils indicate that *Populus* expanded twice beyond its present range limits, once between 13,500-12,900 cal yrs BP and again between 11,200 and 8,000 cal yrs BP (Mann *et al*, 2002). Mann *et al* (2002) attribute this to the development of stabilized gravel bars during periods of stream aggradation, creating an environment suitable for *Populus* growth. Unlike other northern Alaskan records, no *Populus* subzone was recorded at Burial Lake. Abbott *et al* (2010) attributed this to the high and exposed position of the site. The transition to deciduous woodland in the southern Foothills is dated to c. 10,300 cal yr BP at Ruppert and Xindi Lakes (Higuera *et al*, 2009). This is thought to include both *P. balsamifera* and *P. tremuloides* based on wood macrofossils from east Beringia (Edwards *et al*, 2005) alongside *Betula* and *Salix*.

As *Populus* and *Salix* declined into the Holocene, *Picea* starts to increase in many pollen records throughout the Brooks Range. Percentages increase (<10%) at Ruppert Lake as forest tundra becomes established c. 9600 cal yr BP. As mentioned above, the first occurrences of *Picea* are thought to have been *P.glauca*, with *P.mariana* expanded during the mid-Holocene. The migration of *Picea* at sites in the Brooks Range, and northern foothills of the Alaska Range, lag slightly behind central Alaska (Edwards and Barker 1994), discussed below. The earliest evidence for *Alnus* is dated to ~10,000 cal yrs BP at Kaiyak Lake (Anderson, 1985) and Toolik Lake ~10,500 cal yr BP (Bergstrom, 1984). The shrub was not fully established in the southern Foothills until around 7250-7500 cal yr BP (Higuera *et al*, 2009). *Betula* declined during this period but was still present in the catchment with pollen percentages c. 40% (Higuera *et al*, 2009). *Alnus* had spread to Tukuto and Etvilik lakes in the North Slope by 7500 cal yr BP (Oswald *et al*, 1999).

The mid-Holocene is characterised by a second expansion of *Picea*, particularly *P. mariana* around 6000 cal yr BP (Anderson and Brubaker, 1994). The development of the modern boreal forest is dated to 5500 cal yr BP Ruppert, Xindi, Code and Wild Tussock (Higuera *et al*, 2009). *Alnus* had also reached its maximum abundances ~5800 cal yr BP in the southwestern and south-central Brooks Range (Anderson *et al*, 2004), which suggests higher precipitation (Hu *et al*, 1995) and/or lower summer temperatures (Anderson and Brubaker, 1994; Anderson *et al*, 1991). Oxygen isotope records from Meli and Tangled Up Lake indicate the climate at this time began to cool with increased moisture to modern levels (Anderson *et al*, 2001).

2.2.5 The Tanana Valley

The Tanana Valley is characterised by the same pollen assemblage zones as the Brooks Range (see Figure 2.6). The expansion of shrub tundra is dated to 15,500 to 16,700 cal yr BP (based on bulk radiocarbon dates) at Eightmile and Birch Lake (Ager, 1975, 1983). However, more recent AMS radiocarbon dates from Harding Lake (Finkenbinder *et al*, 2014) place the birch rise in this region just shortly before 14,600 cal yr BP and around 13,700 cal yr BP at Windmill Lake (Bigelow and Edwards, 2001).

The expansion of *Populus* has been dated to around 10,500 cal yr BP at Windmill Lake (Bigelow and Edwards, 1993) and Wien Lake (Hu *et al*, 1993) in the west of the region. *Populus* woodland was widespread across the Tanana Valley in the early Holocene (Ager and Brubaker, 1985; Hu *et al*, 1993; Bigelow and Edwards, 2001). The exact interpretation of forest varies from small populations along floodplains to extensive, dense forests (Ager, 1983; Brubaker *et al*, 1983; Hu *et al*, 1993). *Alnus* and *Picea* start to appear between 8,600 and 7500 cal yr BP, with a second increase in *Alnus* at 7,000 cal yr BP at Harding Lake indicating warm and wet conditions

(Finkenbinder *et al*, 2014). The *Alnus* rise is dated between 7,000 and 8,000 cal yr BP at Dune Lake (Lynch *et al*, 2002).

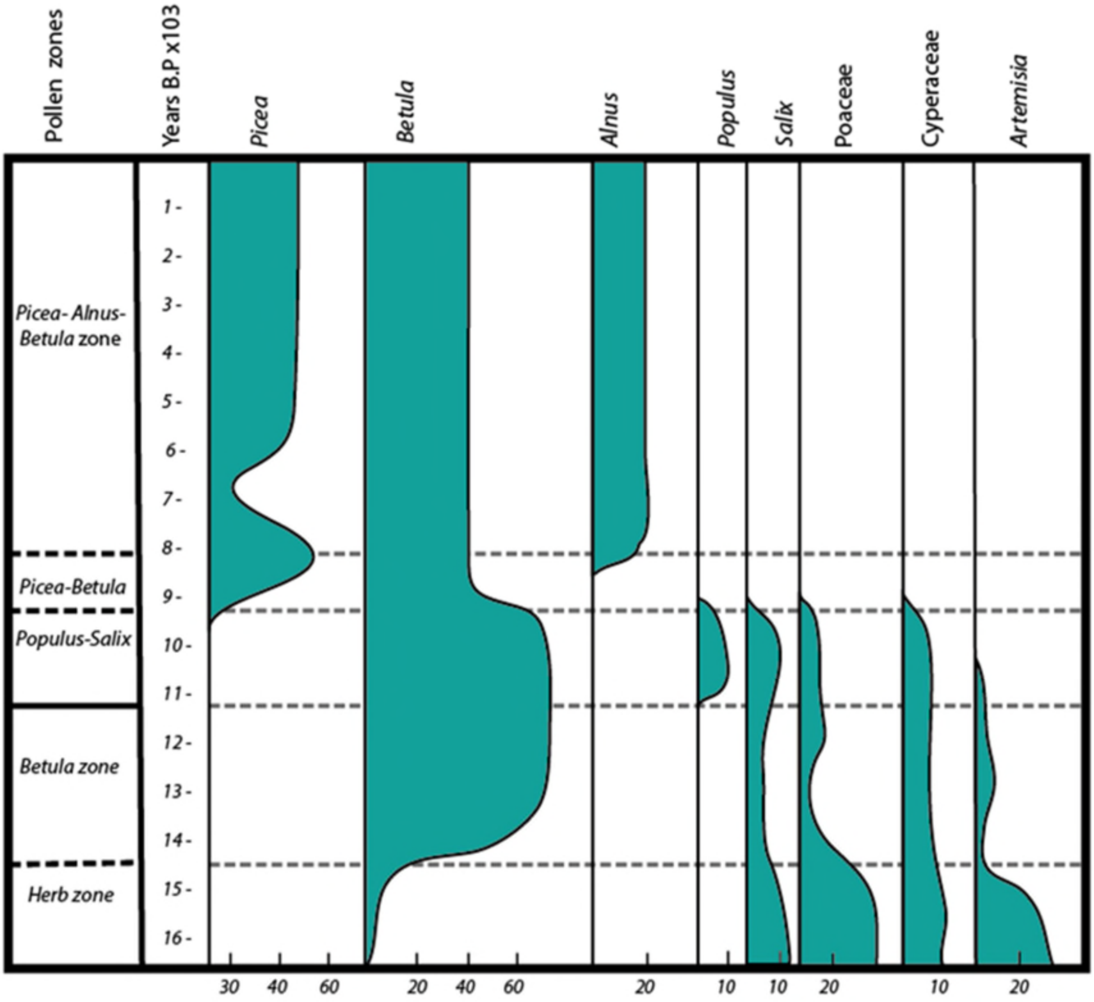


Figure 2.6: *Tanana Valley Pollen percentage Diagram (composite summary) adapted from Ager and Brubaker (1985)*

Many pollen diagrams from central Alaska record a decline in *Picea glauca* prior to the rise in *Picea mariana* and the development of the modern boreal forest in the mid-Holocene (Carlson and Finney, 2004). However, the record from Jan Lake (Carlson and Finney, 2004) illustrates a different pattern which is consistent with Wein Lake (Hu *et al*, 1993). In these records *P. glauca* declines slightly but recovers to full abundance before the arrival of *P. mariana*. This has challenged previous hypotheses that the transition from *P. glauca* to *P. mariana* was due to edaphic changes and successional forcing (eg Brubaker *et al*, 1983). Carlson and Finney (2004) discuss the alternative hypothesis of climate forcing put forward by Hu *et al* (1993) as a more likely explanation. As *P. glauca* declines and then recovers prior to the full establishment of *P.*

mariana it seems unlikely that soil changes can be responsible for both events and therefore climatic cooling is deemed a more likely account for the decline in *P. glauca*.

The development of the modern boreal forest is dated to 7500 cal yr BP at Wien Lake (Hu *et al*, 1993), 5600 cal yr BP at Harding Lake (Finkenbinder *et al*, 2014) and 5500 cal yr BP at Dune Lake (Lynch *et al*, 2003) in central Alaska. The difference in timing is attributed to local, edaphic conditions rather than climate (Hu *et al*, 2006b). The much later arrival at Dune Lake is probably a result of extensive sandy dry soils at the site that delayed soil paludification to initiate the establishment of *P.mariana* (Hu *et al*, 2006b). The general picture indicates an east to west spread of the modern boreal forest from the Tanana Valley to the Brooks Range (Anderson *et al*, 2004, Brubaker *et al*, 2001). The boreal forest was already established when these two records commenced, with *Betula* still an important component of the woodland.

2.3 Fire History and Fire Regimes

Fire is the main disturbance in the boreal forest (Payette, 1993); however, the long-term interactions between fire, climate, and vegetation are currently not well understood (Lynch *et al*, 2003). Understanding these interactions is crucial in light of the predicted increase in boreal forest wildfire activity in response to future climate change (Kelly *et al*, 2013). Knowledge of fire regimes provides the basis for understanding the temporal and spatial patterns of fire behaviour and effects on ecosystems (Sommers *et al*, 2011). A variety of controlling factors contribute to a regions fire regime, including climate at regional to continental scales (Marlon *et al*, 2009; Caracaillet *et al*, 2001a) and local, site specific factors at decadal to millennial scales (Gavin *et al*, 2006; Ali *et al*, 2009). Fire regime terminology used throughout this text is outlined in Table 2.2.

Crown Fire	A fire that burns through the upper tree or shrub canopy. In most cases the understory vegetation is also burned. Depending on species, a crown fire may or may not be lethal to all dominant vegetation. An example of this would be many shrub and broadleaf tree species that sprout from roots, root crowns or stem bases after their tops are killed. A crown fire may be continuous or may occur in patches within a lower severity burn
Fire Frequency	The number of times that fires occur within a defined area and time period
Fire Return Interval	The time between fires in a defined area, usually at the scale of a point, stand or relatively small landscape area
Fire rotation (interval)	The time required to burn an area equal to a defined area of the landscape. The entire area may not burn during this period; some sites may burn several times and others not at all. This is the same as fire cycle
Fire severity	Impact of fire on the ecosystem; degree of mortality, depth of burn, fuel consumption etc.

Table 2.2 : *Fire Regime Terminology (Source: Sommers et al, 2011)*

2.3.1 Fire Ecology and Vegetation

The behaviour of fire can have a variety of effects on the flora, from stand structure and composition (Payette, 1992) and the effects of soil burn severity on tree recruitment (Johnstone and Chapin, 2006), to plant nutrient uptake (Shenoy *et al*, 2013). Some species of trees in the boreal forest are more susceptible to burning and some have adapted to survive in high fire frequency regions, such as *Picea mariana. P.mariana* grow in densely packed stands (Lynch *et al*, 2004b) and the abundant mosses and lichens associated with this tree facilitate fire ignition and spread (Viereck, 1973). *P.mariana* has fine branches which are susceptible to burning (Kershaw and Rouse, 1976). They are, however, adapted to survive fire with a high resin content (Viereck *et al*, 1986) and semi-serontinous cones enable reseeding following fires (Lynch *et al*, 2004b). *Picea glauca*, however, is low in flammability and often increases Fire Return Intervals (FRIs) (Drury and Grissom, 2008). Following a fire, early successional deciduous woodland colonises the burnt area which can cause a negative feedback to additional burning due to low flammability (Viereck, 1973) and slow conifer recovery (Kelly *et al*, 2013). Deciduous woodland particularly favours soils of severely burnt sites where large amounts of the surface organic layer have combusted (Johnstone *et al*, 2010).

2.3.2 Charcoal Analysis

2.3.2.1 Fire Proxy

Charcoal records from lake sediments can be used to reconstruct past fire histories. Charcoal accumulation rate (CHAR) analysis is widely recognised as an indicator for fire occurrence and can be used to infer total biomass burning (Marlon, 2009) and this has recently been directly verified in Alaska by Kelly *et al* (2013). Combined with palynological data, the effect of vegetation on fire regimes and post fire succession can be deduced. Charcoal records are often complex with a variety of processes affecting the composition including rate of burning, charcoal production, charcoal delivery, taphonomy and deposition (Higuera *et al*, 2010).

2.3.2.2 Charcoal Taphonomy

Understanding the taphonomic processes associated with dispersal, deposition and preservation of charcoal is important when interpreting the palaeo-fire record and there are several papers which outline these processes in detail (Clark *et al*, 1998; Blackford 2000; Ohlson and Tryterud 2000; Gardner and Whitlock 2001). Regional, Extra-local and Local charcoal are incorporated in lake sediments and this can also consist of Primary (material deposited during or shortly after the fire) and Secondary (deposited during non-fire years) charcoal sources (see Figure 2.7, Whitlock and Larsen, 2001). It is assumed that most macroscopic charcoal falls close to its source (Higuera *et al*, 2007) and is a signal of local fires (see Section 4.3.4 below). A Gaussian plume model approach was applied by Clark (1988) who suggested that macroscopic charcoal is deposited within 101-103 m of the fire. High intensity fires can also produce large charcoal particles (Ward and Hardy, 1991) and temperature can also affect the density of wood fractions (Vaughn and Nichols, 1995). Secondary charcoal can further complicate the interpretation of fire records as the incorporation of secondary charcoal can come from a number of sources. These can include fallen trees near a lake, surface run-off following several years after a fire (Whitlock and Larsen, 2001) or charcoal deposited on the shorelines of lakes (Whitlock and Millspaugh, 1996). However, the current assumption is that secondary deposits do not obscure the signal from primary deposits (Higuera *et al*, 2007; Lynch *et al*, 2004a).

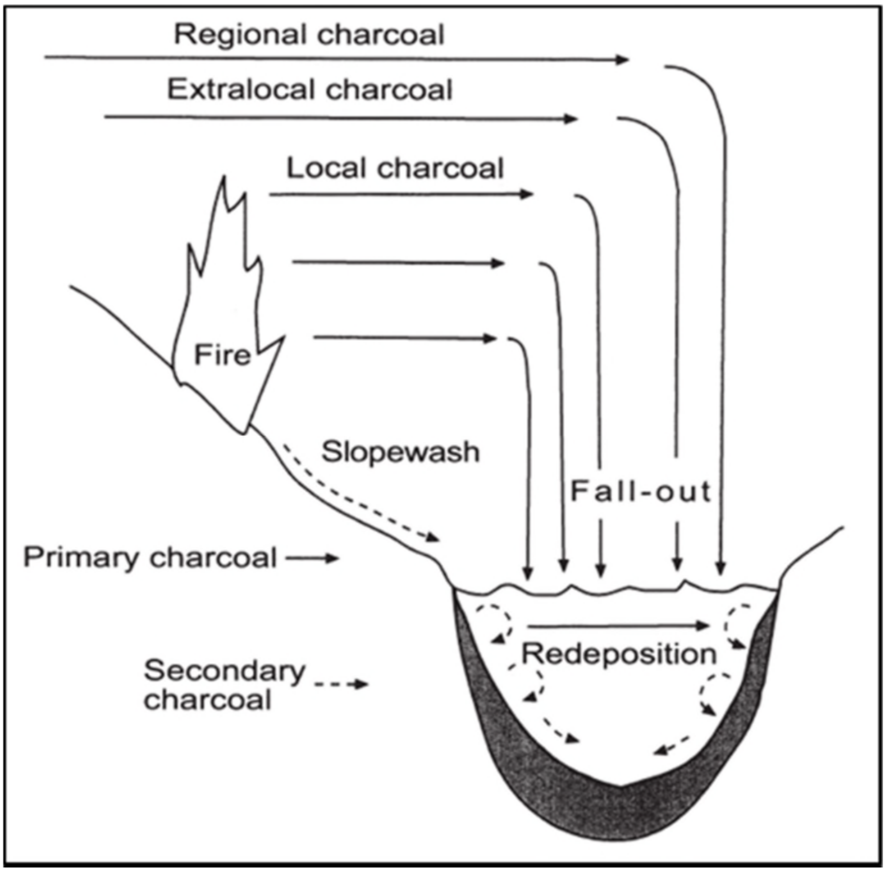


Figure 2.7: *Schematic diagram illustrating the sources of primary and secondary charcoal in a watershed (source: Whitlock and Larsen, 2001)*

2.3.2.3 Microscopic Charcoal

Whitlock and Larsen (2001) have highlighted the lack of a standardised methodology in fire-history studies. There are two analytical approaches used: microscopic and macroscopic. Microscopic charcoal fractions (<100 µm) are preserved in palynological samples and the number or area of charcoal is expressed as an accumulation rate. This was a popular approach in the 1970s and 80s and adopted by many palaeoecologists as an aid to reconstruct fire histories (eg, Swain, 1973, 1978, Cwynar, 1978, and Patterson *et al*, 1987). The advantage of this method is that charcoal is processed and counted alongside pollen, but the particles can often break during pollen preparation (Clark, 1984), creating an exaggerated representation (Whitlock and Larsen, 2001). The approach largely represents regional fire signals as microscopic charcoal can be dispersed over large areas (Clark and Royall, 1995; Carcaillet *et al*, 2001b).

2.3.2.4 Macroscopic Charcoal

In the 1990s, the use of macroscopic charcoal as a technique to reconstruct local fires started to emerge using petrographic thin-Sections (Clark, 1990, Clark and Royal, 1995), which is particularly favoured for varved records (Whitlock and Larsen, 2001). Millspaugh and Whitlock (1995) and Whitlock and Millspaugh (1996) were the first to pioneer the method of macroscopic sieving. This involves analysing contiguous 1cm slices through a core to provide a contiguous record of charcoal accumulation. Particles over 150-200 µm are recognised to represent the local fire component of the charcoal record (Carcaillet, 2007). Both of these methods provide high resolution palaeoenvironmental records which can be used for time series analysis of charcoal accumulation rates (CHAR). CHAR analysis can be used to provide estimates of fire return intervals (FRIs) (Higuera *et al*, 2009); CHAR has two fundamental components; Background CHAR and Peak CHAR. Background CHAR can be assigned to secondary deposition, regional fire signals or changes in fuel accumulation (Whitlock and Larsen, 2001). Analysis of the peaks can then be used to identify individual fire events (Gavin *et al*, 2007; Higuera *et al*, 2010). Combining CHAR and local Fire Frequency (FF) can be used together to produce a CHAR:FF ratio, which is a reflection of fire size (Ali *et al*, 2012). However, Kelly *et al* (2013) suggest CHAR:FF ratio actually reflects fire severity and cautions that this approach combines uncertainty in both CHAR and FF.

2.3.3 Fire History Records from Alaska

Reconstructions of fire histories from palaeoenvironmental records are relatively sparse in Alaska, although they are starting to receive more attention in light of the predicted increase in boreal forest wildfire activity in response to future climate change (see Kelly *et al*, 2013). The focus of most of the charcoal records has concentrated on mid-Holocene fire regimes, and the development of the boreal forest; little is known or understood about the late glacial shrub tundra or the early Holocene deciduous woodland zone. Higuera *et al* (2009) identified that this is a gap in knowledge that requires more research from this region and "*understanding the interactions between climate, vegetation and fire in the deciduous woodland zone remains an important goal of future research*". Higuera *et al* (2009) used CHAR from four lakes in the south-central Brooks Range; Ruppert, Xindi, Code and Wild Tussock to provide estimates of fire return intervals (FRIs) which were linked to the Plant Functional Type (PFT) zones identified through pollen analysis. Fire activity increased at Ruppert and Xindi following the expansion of *Betula* and an increase in temperatures (but cooler than present) between 13,000 -14,300 cal yr BP. More frequent fire events are attributed to the spread of the flammable *Betula glandulosa* species. The shift to *Populus*-dominated deciduous woodland appeared to lengthen the FRIs despite the warmer, drier summers than present (Abbott *et al*, 2001, Anderson *et al*, 2001). This is most likely a result of less available flammable fuels as the *Populus* biomass is not as flammable as *Betula*. Small, low intensity, infrequent fires are also evident during this period at Dune Lake in Interior Alaska (Lynch *et al*, 2002).

During the mid-late Holocene, evergreen boreal forests developed with the increase of *Picea* in the landscape. Moisture increased and the climate became cooler during this period. This would usually be associated with a decrease in fire frequencies, but FRIs decreased at many sites with the expansion of the flammable *Picea mariana*. (Figure 2.8). Examples of this pattern occur at Ruppert, Xindi, Code and Wild Tussock Lakes (Higuera *et al*, 2009) in the Brooks Range and Low Lake (Lynch *et al*, 2004c) in Interior Alaska. At Dune Lake (Lynch *et al*, 2002), fire is identified as an important ecological process during this vegetation zone, with increased charcoal accumulation and reflecting the change in fuel availability. Hu *et al* (1993, 1996) recorded elevated numbers of charcoal particles during the *Picea mariana* zone at Wien (west Tanana Valley) and Farewell (northwestern Alaska Range) Lakes. The increase in fire at Farewell Lake may have also contributed to soil erosion. The collective results emerging from the *Picea* zone in Alaska illustrate the importance of vegetation composition on fire activity, which can often override the influence of climate.

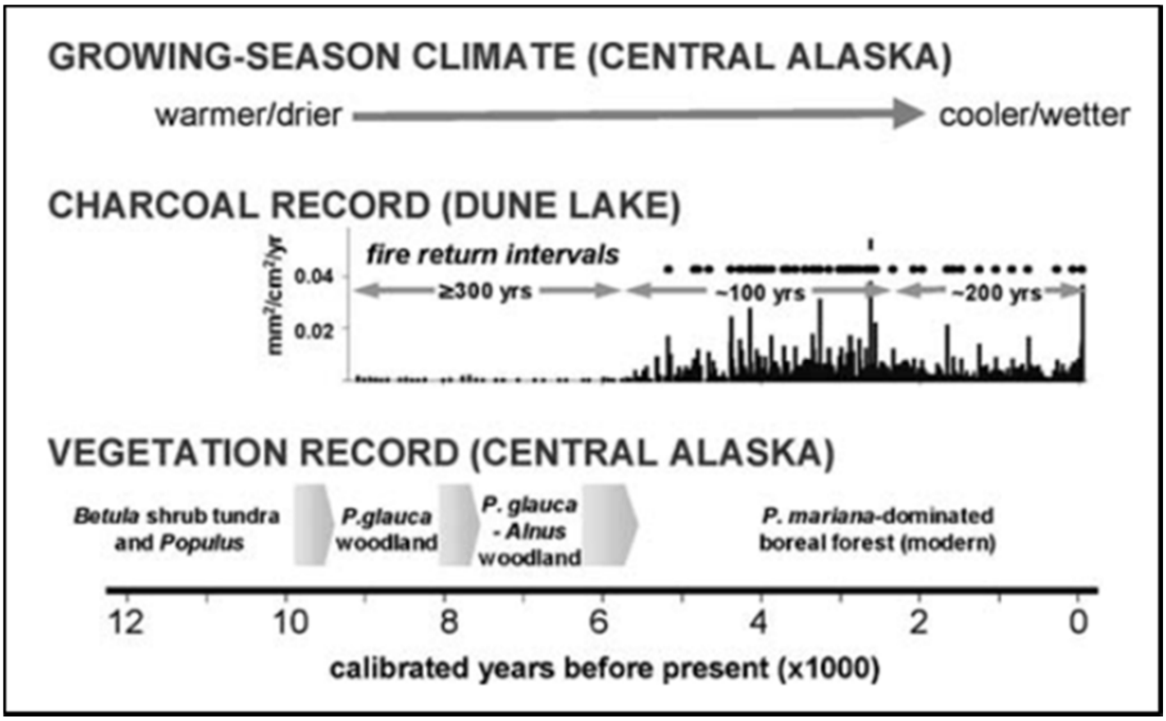


Figure 2.8: *Holocene changes in climate, vegetation and fire regime in central Alaska. The MFI of ≥300 years before the establishment of Picea mariana forests, is based on charcoal data from Dune Lake (Lynch et al, 2003) as well as Low (Lynch et al, 2004c) and Ruppert (Higuera et al, 2004) Lakes. Source: Hu et al (2006)*

Complex spatial patterns emerged when records were compared from four lakes (Dune, Low, Moose and Chokasna) in south-central Alaska (Hu *et al*, 2006b). Fire frequencies increased at all sites with the expansion of *P. mariana*, but the temporal patterns of fire frequency change. The results indicate a lack of statistical synchrony and the authors imply that site-specific factors (e.g. topography, local vegetation, ignition rates) might have exerted a stronger influence on fire regimes than climate, although climate cannot be ruled out as a contributing factor.

Brubaker *et al* (2009) applied modelling techniques to the data from Higuera *et al* (2009). ALFRESCO (ALaskan FRame based EcoSystem Code, Rupp *et al* 2000) was applied to simulate fire dynamics under a variety of changing parameters (i.e. climate, species composition). This approach of combining both palaeoecological records and ecological models allowed for several causes of fire-regimes to be examined. The controlling factors can change through time and space. Barrett *et al* (2013) addressed this by evaluating the role of both climate and landscape features in the spatio-temporal dynamics of fire regimes in the Copper River Basin, south-central Alaska. CHAR analysis and peak analysis was applied to identify individual fire events along with spatial analysis of land form and land use cover. Variations in fire occurrence were spatially and temporarily variable over the last 7000 years. The statistical relationship between climate and biomass burning was deemed not significant prior to 3000 yrs BP, where local site factors exerted dominance, compared with a strengthening of the relationship after 3000 yrs BP. Peak CHAR values were recorded during the Medieval Climate Anomaly (MCA) followed by a decline during the Little Ice Age (LIA).

These results are consistent with composite records from 14 sites in the Yukon Flats region (Kelly *et al*, 2013). *Populus* is a major component of post-fire vegetation in Alaska today and it also reached its highest values between 1000-500 cal yr BP (during the MCA) since the early Holocene in the Yukon Flats during a period of when fire severity was maximal (Kelly *et al*, 2013). Kelly *et al* (2013) suggest that severe fires favoured less-flammable deciduous woodlands, which reduced the fire frequency despite climate conditions more favourable for fire. This work highlights the need for landscape factors such as topography, vegetation composition and biomass abundance to be incorporated in forecasting the impacts of climate change on fire regimes.

Patterns are starting to emerge from the palaeoenvironmental work, particularly about the expansion of *Picea mariana* and the effect on FRIs. Fire records are becoming better understood at the millennial scale, but still little is known about the interactions and relationships between fire-vegetation and climate at the decadal-centennial scale. The approach adopted by Kelly *et al* (2013) in the Yukon Flats offers an opportunity to address fire regimes dynamics at the decadal scale and put this into context of natural millennial scale variation. This approach could be applied to the Brooks Range utilising pre-existing records within the region and comparing data between regions.

2.4 Quantitative Vegetation Reconstructions

2.4.1 Overview

Palynology is one of the most widely used methods in Quaternary environmental reconstructions (Faergi and Iversen, 1989; Moore, Webb and Collinson, 1991). Lennart Von Post introduced the discipline in his lecture entitled ‘Forest-tree pollen in south-Swedish peat layers’ in Oslo and he presented the first pollen diagram in 1916 (Fries, 1967). The majority of reconstructions have been based on percentage representations of taxa in samples as a way to deduce the landscape vegetation. Pollen diagrams illustrate changes in the percentages of pollen taxa in samples which are then used to interpret changes in taxon abundance (Prentice and Webb, 1986). Early studies looked at the relationship between arboreal pollen and non-arboreal pollen as an indicator of openness in the landscape (Firbas, 1934; Andersen and Berglund, 1994). These still remain important and commonly used approaches. However, pollen percentages do not reflect a linear correlation with percentage abundance of vegetation (Prentice and Webb, 1986). Developing new methodologies to reconstruct the vegetation quantitatively in terms of actual land cover is increasingly at the forefront of the discipline.

Determining quantitative vegetation cover around a lake for example is vital for understanding the long-term lake ecosystem processes. Firstly, catchment vegetation can alter nutrient cycling in soils, including carbon cycling. Secondly, any modelling of carbon production by lakes requires input of accurate catchment vegetation cover. In the next Section, an overview of pollen analysis will be outlined, focusing on pollen dispersal and pollen-vegetation relationships. This is followed by a discussion of recent estimates of pollen productivity (PPEs) and the current models used to reconstruct vegetation quantitatively.

2.4.2 Pollen Analysis

2.4.2.1 Pollen dispersal and transfer

In order to interpret percentage pollen diagrams an understanding of how pollen is dispersed and transported is required. Tauber (1965) proposed four main transport pathways; rainout (Cr), canopy (Cc), trunk space (Ct) and surface runoff (Cw) (see Figure 2.9). This model pioneered the recognition of biases in pollen production and dispersal, and it is the understanding of these biases that forms the basis of quantitative reconstructions (Bunting and Middleton, 2009; Sugita, 2007a), as discussed below. Further experimental investigations were carried out by Tauber over a forest lake in Zealand, Denmark looking at pollen transfer over a full growing season (Tauber, 1967). Pollen samplers (traps) were placed in a variety of locations in and around the lake during flowering and non-flowering seasons. The samplers placed above the ground in the trunk space were placed to only collect pollen from this transport component. The number of pollen grains collected in the trunk space contributed to over 40% of all pollen grains from the basin. This paper demonstrates the significance of pollen transport in the trunk space and filtration in the vegetation; however this is not taken forward into later models as a significant contribution to pollen transport, as discussed below.

The size of the basin will also influence the size of the area of vegetation represented in the pollen assemblage. Jacobson and Bradshaw (1981) related basin size to the relative proportions of pollen originating from different areas around the site (Figure 2.10). The larger the basin, the larger the area of surrounding vegetation is represented, therefore larger basins reflect a regional picture of vegetation, rather than a local picture (Jacobsen and Bradshaw, 1981). They also state that when streams enter the basin, additional pollen will be transported through the streams and surface runoff component (Cw), which was not considered an important component in Tauber's earlier model. Jacobsen and Bradshaw (1981) define local pollen as originating from plants growing within 20m of the edge of the sampling basin, extralocal pollen as coming from plants growing between 20 and several hundred meters of the basin, and regional pollen as derived from plants at greater distances.

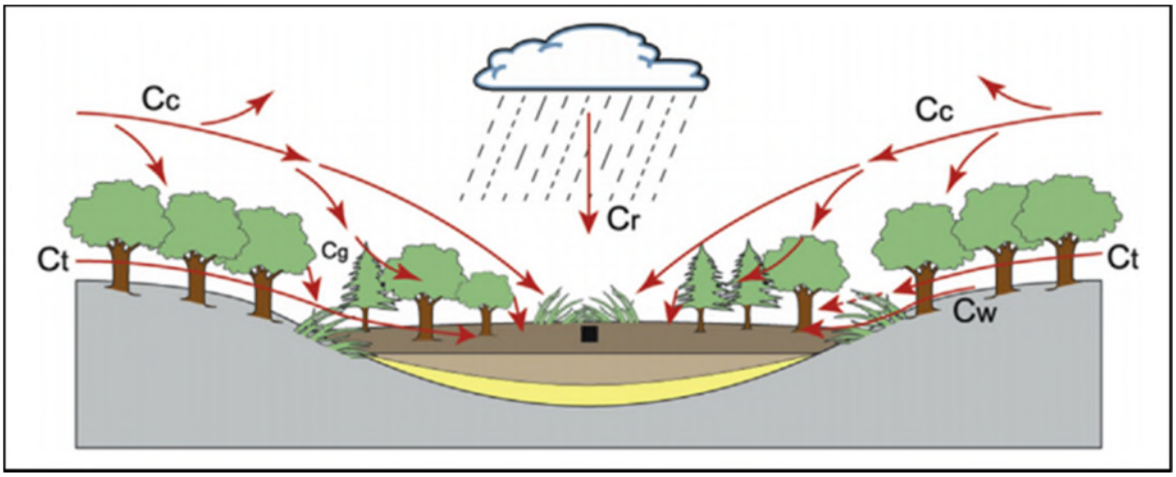


Figure 2.9: *The Tauber model of pollen taphonomy into a surface sample in a mire. Cr = long distance component delivered by precipitation, Cc = canopy component, Ct = trunk space component, Cw = runoff component, Cg = gravity component (after Tauber, 1965, source: Bunting et al, 2013)*

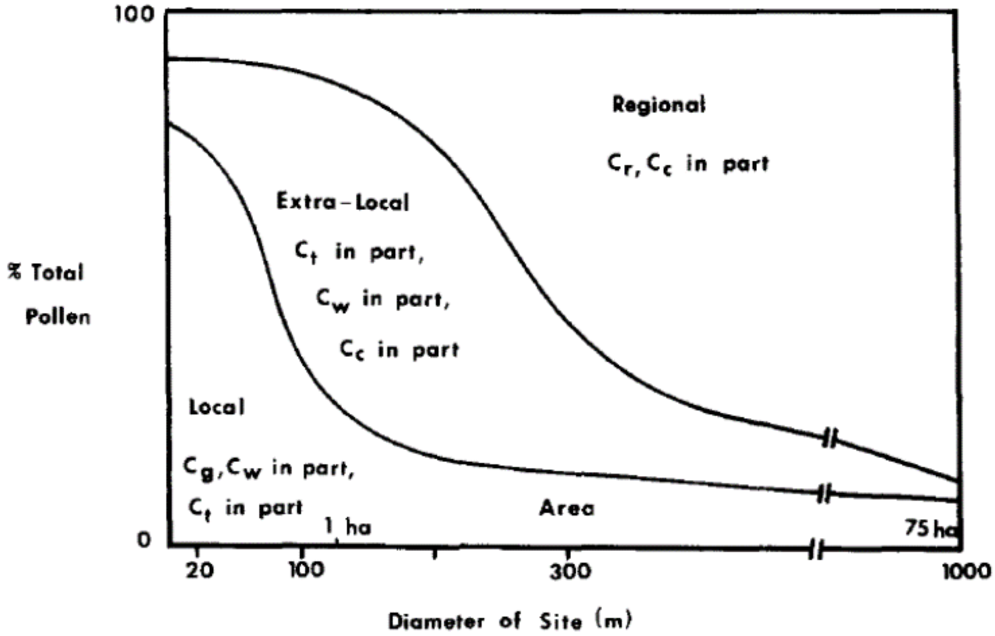


Figure 2.10: *Relationship between the size of a site that has no inflowing stream and the relative proportions of pollen originating from different areas around the site (source: Jacobson and Bradshaw, 1981)*

Additional biases include production (how much pollen is produced) and dispersal differences among species (Gregory, 1973), where the shape and size of pollen grains affect the distance they can travel. The size of the sedimentary basin will have an effect on the amount of pollen deposited (Berglund, 1973) and the area of surrounding vegetation reflected in the pollen assemblage (Sugita, 1994). The further away the source plants, the lower the amount of their pollen that will be deposited, therefore generally the larger the basin the lower the amount of pollen deposited at the centre of it (Prentice, 1985, 1988). Pollen influx is a calculation of the number of pollen grains falling on a unit area of sediment in a given time (Davis, 1969). This can be particularly useful where pollen dispersal of long distances is strong and influx can help deduce the presence or absence of a species at a site (Hicks, 1994, Hicks and Hyvärinen, 1999). Pollen influx for lakes can be more complicated than surfaces of mires. As well as pollen rain falling onto the surface of the lake, there is also likely to be pollen from surface run off and in some cases inflowing waters (Davis, 1968; Davis and Brubaker, 1973). Mixing of pollen in lakes also occurs prior to deposition (Sugita, 1993). A pollen deposition model has been developed for these sites (Sugita, 1993) and is discussed in further detail below.

Prentice (1985, 1988) developed Tauber's model, focusing on the wind above the canopy as the dominant controlling factor and not including the trunk space component of pollen transport. Prentice (1985) states "*the model in its present, admittedly simplistic form correctly predicts known characteristics of pollen assemblages; there is no advantage in adding new parameters unless empirical tests can show that they are needed*". This model has been deemed the most comprehensive and was developed further by Sugita (1993). Prentice's model (1985) calculates pollen loading at a point in the centre of the basin, and Sugita's model (1993) modifies this further to estimate mean pollen loading over the entire basin surface. An assumption is that pollen does not move once deposited on the surface of mires, unlike pollen deposited on lake surfaces which can be subject to mixing.

Sugita (1993) compares the results and concludes that the pollen source radius for an entire lake surface is 10-30% smaller than the source radius for pollen deposited at a point in the centre of a basin (i.e. a mire). Sugita (1993) suggests that pollen records from lakes may provide different spatial resolution compared with a bog of similar size. This is due to pollen loading over the entire surface being more strongly influenced by nearby pollen sources than pollen deposition at the centre. The basic assumptions of both models are the same: (1) the sampling basin is a circular opening in the canopy; (2) wind is even in all directions; and (3) the dominant components of pollen transport are wind above the canopy and gravity below.

The basis of these models is that Pollen loading (pollen input on surface of a basin), of a given species *i* at site *k* depends on pollen productivity (α_i) (discussed below), mean plant abundance at distance *z* from the centre of a basin, the radius of a basin (*R*) and a pollen deposition function (function describing the proportion of pollen deposited at distance x from a point source of species *i*). Definitions are listed in Table 2.3. The Prentice-Sugita model can be presented in its simplest linear form for pollen loading (PL) $Y_{i,k}$ and the distance-weighted plant abundance (DWPA) within a given distance Z_c $(Z_c \geq R)$,

$$Y_{i,k} = \alpha_i \cdot \psi_{i,k} + \omega_{i,k}$$

where $\psi_{i,k}$ is DWPA of species i within Z_c and $\omega_{i,k}$ the amount of pollen coming from beyond Z_c (Sugita, 1994).

R	Radius of a lake or a bog (m)
Y_i	Pollen loading of species *i* on a lake or bog surface (grains) for total pollen loading on a lake (grains m^{-2}) for mean pollen loading on a lake
Z_c	Distance from centre of a lake or bog, within which plant abundance is compared with pollen representation (m)
α_i	Pollen productivity of species i (grains (unit basal area)$^{-1}$), (grains (unit foliage mass or unit foliage area)$^{-1}$),(grains (unit biomass)$^{-1}$), etc
ψ_i	Distance-weighted plant abundance (DWPA) of species *i* within distance Z_c (basal area etc), for total pollen loading on a lake (basal area m^{-2} etc), for mean pollen loading on a lake
ω_i	The portion of pollen loading of species I, coming from beyond distance Z_c (grains) for total pollen loading on a lake (grains m^{-2}) for mean pollen loading on a lake

Table 2.3: *List of symbols used in the linear form of the Prentice-Sugita Model (source: Sugita, 1994)*

As previously mentioned, pollen percentages do not reflect a linear relationship with percentage abundance of vegetation (Prentice and Webb, 1986). This nonlinear relationship can be complex depending on the site and taxa present (Fagerlind, 1952) and this concept is known as the 'Fagerlind effect'. Various models have been developed looking at the pollen-vegetation relationship (Davis, 1963; Andersen, 1970; Jacobson and Bradshaw, 1981). Extended R-value (ERV) models were developed by Parsons and Prentice (1981) and Prentice and Parsons (1983) to incorporate the fact that pollen percentages are nonlinear in relation to actual plant abundance by using distance-weighted data (discussed in detail in Section 2.5.3.3).

The models discussed above are based on the assumption of homogeneous vegetation, and although they provide an important basis for understanding the processes involved in pollen transportation and deposition they are not a true representation of the real world, which can be patchy and complex. In order to improve the accuracy of qualitative and quantitative vegetation reconstructions an understanding of these processes in heterogeneous vegetation scenarios and the Relevant Source Area of Pollen (RSAP) is required, which is a new concept of Shinya Sugita. The RSAP is defined as the area around the basin beyond which the correlation between pollen and vegetation does not improve (Sugita, 1994), which will be discussed in further detail below.

2.4.3 Pollen Productivity Estimates (PPEs)

Pollen productivity is one of the major parameters used in quantitative pollen-vegetation models (Sugita, 2007a) and obtaining accurate measurements is vital for reliable reconstructions. Pollen productivity is simply a measure of the amount of pollen released for transport per unit area of pollen-producing vegetation (Bunting *et al*, 2013b). PPEs can be calculated from modern pollen and vegetation data using Extended R-value (ERV) models (Parsons and Prentice, 1981; Prentice and Parsons, 1983; Sugita, 1994).

Absolute pollen productivity estimates are the ideal measurement of units (grains m-2yr-1; Sugita *et al*, 2010a). To obtain absolute PPEs long-term monitoring records are required to evaluate the variations in annual pollen production and deposition as used by Sugita *et al* (2010a) in Finland. This is difficult to measure and long term monitoring records are not always available for a region. Most PPEs use pollen collected in moss polsters (discussed below) and are expressed as a dimensionless value relative to a reference taxon, for which the pollen productivity is set to 1 (Anderson, 1970; Broström *et al*, 2008). Poaceae is often used as the reference taxon in PPE studies, particularly across Europe, as it is widespread, abundant in fossil and modern assemblages and is an intermediate pollen producer (Broström *et al*, 2008). Other taxa have been used in some studies such as *Quercus* (oak) in a study in England (Bunting *et al*, 2005), *Juniperus* (juniper) in southern Sweden (Sugita *et al*, 1999) and *Pinus* in Germany (Matthias *et al*, 2012) as they were well represented in both the vegetation composition and the pollen counts in these study areas. This is an important factor when considering the reference taxon. Most of the studies discussed below have been recalculated relative to Poaceae for comparisons to be made between regions (Broström *et al*, 2008; Mazier *et al*, 2012).

Broström *et al* (2008) discuss a range of factors that can influence the pollen productivity of species (see Figure 2.11). Physical and biological factors (climate, soil, topography, species interactions, age classes of plants, growth forms) can affect pollen production (Sugita *et al*, 2010a) along with vegetation structure (von Stedingk *et al*, 2008). *Betula* is often a high pollen producer; however low PPEs were recorded in northern Finland (Räsänen *et al*, 2007) and central Sweden (von Stedingk *et al*, 2008). Broström *et al* (2008) have suggested that climate could be a strong contributing factor for their low PPEs of *Betula*, as species close to their climatic range limits, such as *Juniperus* and *Calluna* in northern subalpine areas also have lower PPEs (von Stedingk *et al*, 2008) compared with other values obtained in Europe (see Section 2.4.4).

Methodological factors include problems of identification of pollen taxa which comprise more than one species and differences in vegetation surveys (discussed in further detail below). Hjelle and Sugita (2012) also discuss the potential importance of size and shape of sampling basins from where pollen data are obtained for estimates of PPEs and RSAP (see below). ERV analysis (discussed in detail below) assumes the basins to be circular and of similar size (Sugita, 1994). This can be a problem when using lake sediment samples compared with moss polsters as it can be difficult to collect samples from lots of similarly sized lakes in a region (Soepboer *et al*, 2007). Hjelle and Sugita (2012) found that if lake size followed a highly skewed or random around the mean distribution then the PPE and RSAP estimates were not reliable. These factors make measuring accurate PPEs a challenge and it is therefore vital to understand the climate constraints on taxa in the study area and plan a robust methodology prior to undertaking fieldwork.

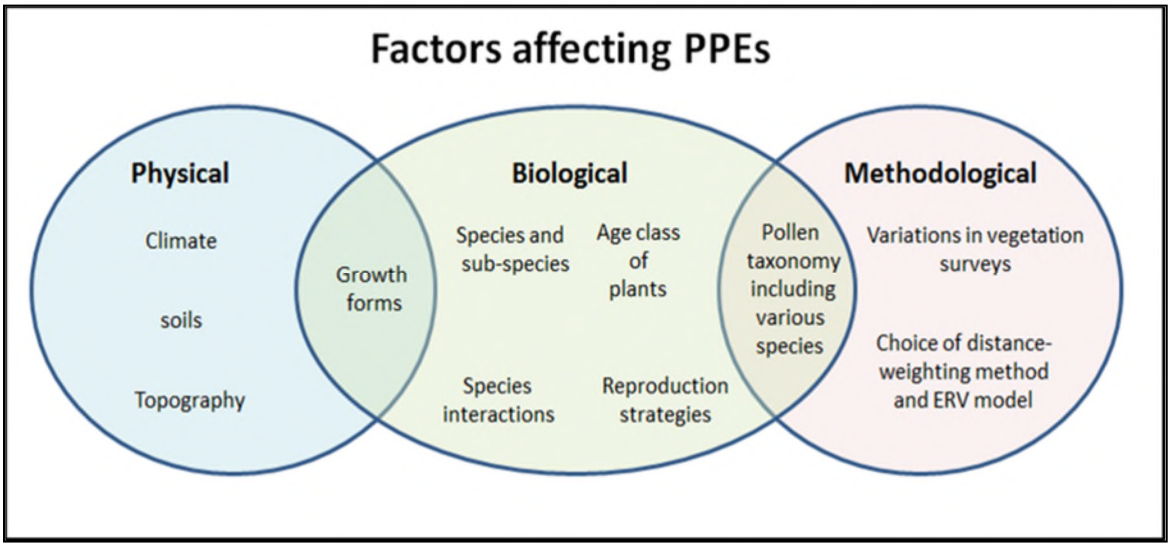


Figure 2.11: *Physical, biological and methodological factors affecting pollen productivity estimates*

2.4.3.1 Relevant Source Areas of Pollen (RSAP) and background pollen

The spatial scale of the source area of pollen needs to be clearly defined otherwise pollen-based reconstruction and interpretation does not make sense (Sugita, 1994; 1998). The relevant source area of pollen (RSAP) is defined as the area around the basin beyond which the correlation between pollen loading and distance-weighted plant abundance does not improve (Sugita, 1994). Theoretically, the RSAP is the smallest spatial unit of vegetation that can be detected using pollen assemblages from similarly sized sites in a given region (Hjelle and Sugita, 2012). Therefore, the survey area of vegetation should include the RSAP to record the local variations of vegetation, irrespective of the amount of pollen coming from beyond that distance (Sugita, 1994). RSAP and background pollen can be derived using Extended R-value (ERV) models (discussed in detail in Section 2.4.3.3). Establishing the RSAP is an important early step in both qualitative and quantitative vegetation reconstruction (Bunting *et al*, 2004) as PPEs are most reliable if they are calculated at, or beyond, this distance (Sugita, 1994; 1998). RSAP is strongly linked to basin size (Sugita, 1994) and vegetation structure (Bunting *et al*, 2004; Galliard *et al*, 2008; Hellman *et al*, 2009a and b). It has been estimated in a variety of landscapes from pollen spectra taken from moss polsters and small lakes using simulation and empirical approaches (e.g. Calcote, 1995; Bunting, 2003; Broström *et al*, 2005; see Table 2.4). It must be noted that moss polsters and small lakes are, however, different basin sizes. The radius of the RSAP can vary from a radius of a few metres up to 7km. The RSAP of 500m calculated at the forest-tundra ecotone in Sweden compared with 50-75m obtained in closed forests (Calcote, 1995) is attributed to lower local pollen production and the openness of the vegetation structure (von Stedingk *et al*, 2008).

Pollen originating from outside of the RSAP is referred to as background pollen. Background pollen is consistent among similarly sized sites in a region, even with patchy vegetation and landscapes (Sugita *et al*, 2007). Differences in pollen loading at similarly sized sites can therefore represent differences in plant abundance within the RSAP at individual sites, superimposed on constant background pollen (Sugita, 1994; 1998; 2007b). The background pollen in the forest-tundra ecotone in Sweden is similar to the background pollen calculated in the North American closed forests (Calcote, 1995), around 60% despite the large difference in RSAP. Von Stedingk *et al* (2008) attribute this to tree taxa having high pollen productivity and a small RSAP leading to a large background pollen component. In the open landscape of the forest-tundra where pollen productivity within the RSAP is low, despite the RSAP being larger which results in a larger pollen loading from background pollen.

The high RSAP of 7km from lakes in Brandenburg, Germany (Matthias *et al*, 2012) is large compared with lakes of similar size in Switzerland for which a RSAP of 800m was estimated

(Soepboer *et al*, 2007). Matthias *et al* (2012) attributed this to the landscape structure, consisting of large units shaped during the last glaciation and distribution of vegetation types in the study region. The glacial sediments of sands, clays and tills are several hundreds of meters thick in study region of Brandenburg. The nutrient poor plains only support *Pinus*, nutrient rich soils are cleared for agriculture and terminal moraines are often dominated by *Fagus*. These three units dominate the landscape and vegetation type (Matthias *et al*, 2012) with larger, extensive forests units compared with that of Switzerland (Soepboer *et al*, 2007) or Estonia (Poska *et al*, 2011) which may lead to the larger RSAP.

Landscape	**RSAP**	**Reference**
Dwarf shrub dominated heathland (moss polsters)	A few metres	Bunting, 2003 Bunting and Hjelle (2010)
Closed forests in Michigan and Wisconsin, USA (forest hollows)	50-75m	Calcote, 1995
Open and semi-open landscapes, southern Sweden (moss polsters)	~400m	Broström *et al*, 2005
Sweden (lakes and bogs)	1000-2500m (50m radius lake) 1200-3000m (25-250m radius basin) 2000-3000m (250m radius basin)	Hellman *et al* (2009 a and b)
Forest-tundra ecotone, Sweden (moss polsters)	~500m	von Stedingk *et al*, 2008
Lakes in Switzerland	800m	Soepboer *et al* (2007)
Danish lakes around AD 1800	~1700m	Nielsen and Sugita (2005)
Lakes in Estonia	1,500-2,000 m	Poska *et al* (2011)
Lakes in eastern Germany	7km	Matthias *et al* (2012)

Table 2.4: *Current estimates of Relevant Source Area of Pollen*

2.4.3.2 Methodology and vegetation surveys

Pollen productivity estimates can be calculated from modern pollen and vegetation data using Extended R-value (ERV) models (Parsons and Prentice, 1981; Prentice and Parsons, 1983; Sugita, 1994). These models enable calibration between pollen percentage data and vegetation (Broström *et al*, 2008). Reliable PPEs are obtained only if the spread in proportions of the taxon in both vegetation and pollen is large enough (Broström *et al*, 2004). As discussed above PPEs are also most reliable if they are calculated at, or beyond, the RSAP (Sugita, 1994; 1998). Therefore, the area of vegetation survey needs to be at least as large as the RSAP (Broström *et al*, 2004). Broström *et al* (2008) outlined a list of recommendations based on a review of PPE studies. The three recommendations discussed below relate to the vegetation survey.

Recommendation 1: *Choice of taxa*

First taxa of interest should be selected, which can be more than the number of taxa for which PPEs will finally be obtained. This involves some prior knowledge of the modern vegetation and the fossil pollen records in the area as the taxa need to be common in both. If the taxa are abundant in the vegetation, but not in the pollen samples, it is unlikely they will be able to be included in subsequent analysis.

Recommendation 2: *Site number, selection and type of pollen sample*

Calculating PPEs requires collecting samples (usually moss polsters or lake sediment surface samples) from sites for modern pollen data analysis along with a detailed vegetation survey of each site. The number of sites selected should be at least double the number of taxa chosen in Recommendation 1 as this is a mathematical constraint of the ERV models (S.Sugita, *pers comm, Nov 2015*). However, Twiddle *et al* (2012) suggest that their dataset from Inshriach, Scotland illustrates that as long as the number of samples meets the ERV model constraints then the quality of the data set and the strength of the pollen-vegetation relationship is more important than the quantity of samples for reliable PPEs (discussed in Section 2.4.3.3). Sites should be randomly distributed, and if this is not possible care should be taken to ensure a large spread of values in vegetation cover for the taxa selected (Broström *et al*, 2008).

Moss polsters are found in a variety of environments and the pollen is easy to extract for analysis; they are therefore often used as the sample of choice in PPE studies. Generally, it has been understood that they trap 1-10 years of pollen depending on type and species (Boyd, 1986; Cundill, 1986) but more recent studies have indicated as little as 1-2 years of accumulation (Räsänen *et al*, 2004). Therefore, it is important to use samples which contain more than 1 year pollen accumulation as pollen production can be highly variable throughout the seasons (Hicks, 2001). Baker *et al* (2016) addressed this issue by sampling mosses forming thick mats and sampling both the green and brown parts. Some studies have collected a single moss sample from the centre of a site (Bunting and Hjelle, 2010) and others have amalgamated multiple samples (Broström *et al*, 2004).

Recommendation 3: *Vegetation Survey*

There have been various methods adopted for collecting vegetation survey data but one of the main requirements is that the survey area should include the RSAP. The data should be distance weighted to create more reliable PPEs as the Prentice-Sugita model assumes the further a plant is from the sampling point the less significant the pollen contribution is to the assemblage.

The measure of vegetation needs to be recorded in a way that it can be distance weighted. The most detailed survey occurs within Zone A which is usually a 10m radius around the sampling point, but can vary from 5m (Sugita *et al*, 1999; Bunting *et al*, 2005) to 20m (Jackson and Kearsley, 1998). For this zone, previous methods have involved a detailed approach of cover estimates in concentric rings around the sampling point (Broström *et al*, 2004; Mazier *et al*, 2008) as well as cover estimates at varying distances from the centre point (Bunting, 2003), mapping communities and random quadrats (von Stedingk *et al*, 2008) (see Figure 2.12). Zone B (10-100m) and Zone C (100-1,000m+) are usually characterised by a combination of field mapping of vegetation communities, aerial photography and satellite imagery (discussed below).

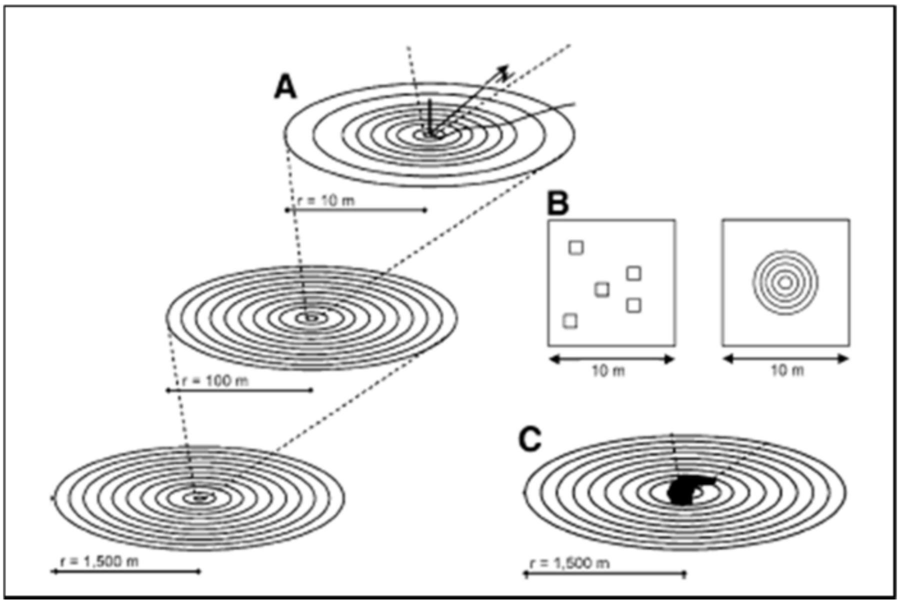


Figure 2.12: *Vegetation sampling design for a) moss polster sites in southern Sweden (Broström et al, 2004) and the Swiss Jura (Mazier et al, 2008). Vegetation in the inner 10m radius from the sampling point is recorded in detail in 1m wide concentric rings by percentage of cover, vegetation communities are mapped in the field for 10-100m and 100-1500m communities are mapped using aerial photography b) moss polster sites in Norway (Hjelle, 1998) and England (Bunting et al, 2005). Vegetation surveys in Norway are conducted using random square metre plots within an area 10 x 10 m2. In England vegetation is recorded in concentric rings c) lake sites in Denmark (Nielsen, 2004) and on the Swiss Plateau (Soepboer et al, 2007). Lake surface sediment samples were taken and the surrounding vegetation was surveyed in concentric rings up to 1000-2000m. Source: Broström et al (2008)*

Bunting and Hjelle (2010) compared different vegetation survey methods on heathland in Norway. The results illustrated the effect that survey design can have on estimates of pollen productivity. Three field methods were compared; the rooted frequency method (Hjelle, 1998) which uses a $1m^2$ quadrat (sub-divided into a grid of 25 smaller squares) on the central point and in four cardinal directions adjacent to the central quadrat; the estimate of cover method (Bunting, 2003) which estimates cover within $1m^2$ quadrats located at a range of distances along four cardinal axes (referred to as 'cover' in this study) and cover estimates in concentric rings (Broström, 2002). The cover estimates in concentric rings method is where concentric rings are established around a central point and plant cover is estimated by eye for each full ring and referred to as 'rings' in this study. The survey methods are illustrated in Figure 2.13.

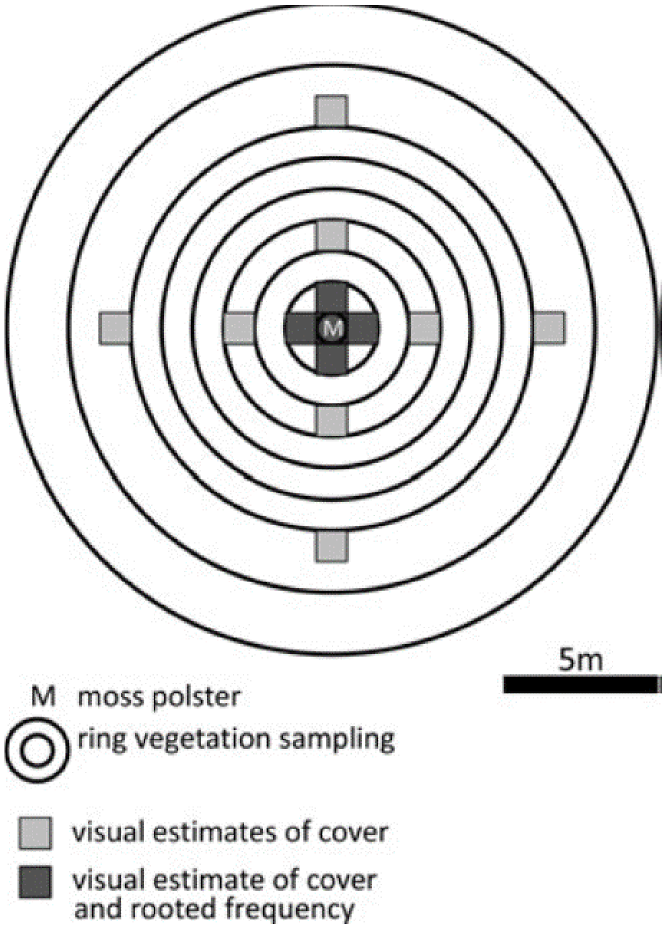


Figure 2.13: *Schematic diagram showing the layout of vegetation recording points around each moss polsters sampled for the three vegetation survey methods (source: Bunting and Hjelle, 2010).*

Each survey produced differences in distance-weighted plant abundance within 1.5m of each sample point. The cover and ring data produced similar results which were dominated by one species, but abundances of species were more equal using the frequency method. The results for the estimations of PPEs are shown in Figure 2.14. The results suggest that the main difference in PPEs is the vegetation method used rather than DWPA or ERV model, with the ring method producing the highest PPEs. Bunting and Hjelle (2010) suggest that this is possibly due to different growth forms of the plants. An example is that shrubs like *Calluna* are better represented in the cover method compared with *Potentilla*. Bunting and Hjelle (2010) suggest that the cover method is the most time efficient and appropriate method based on the likelihood function scores (discussed below). They conclude that PPEs from the literature should only be combined for land-cover reconstructions where the vegetation survey method is identical. The survey method had very little effect on the estimations for RSAP.

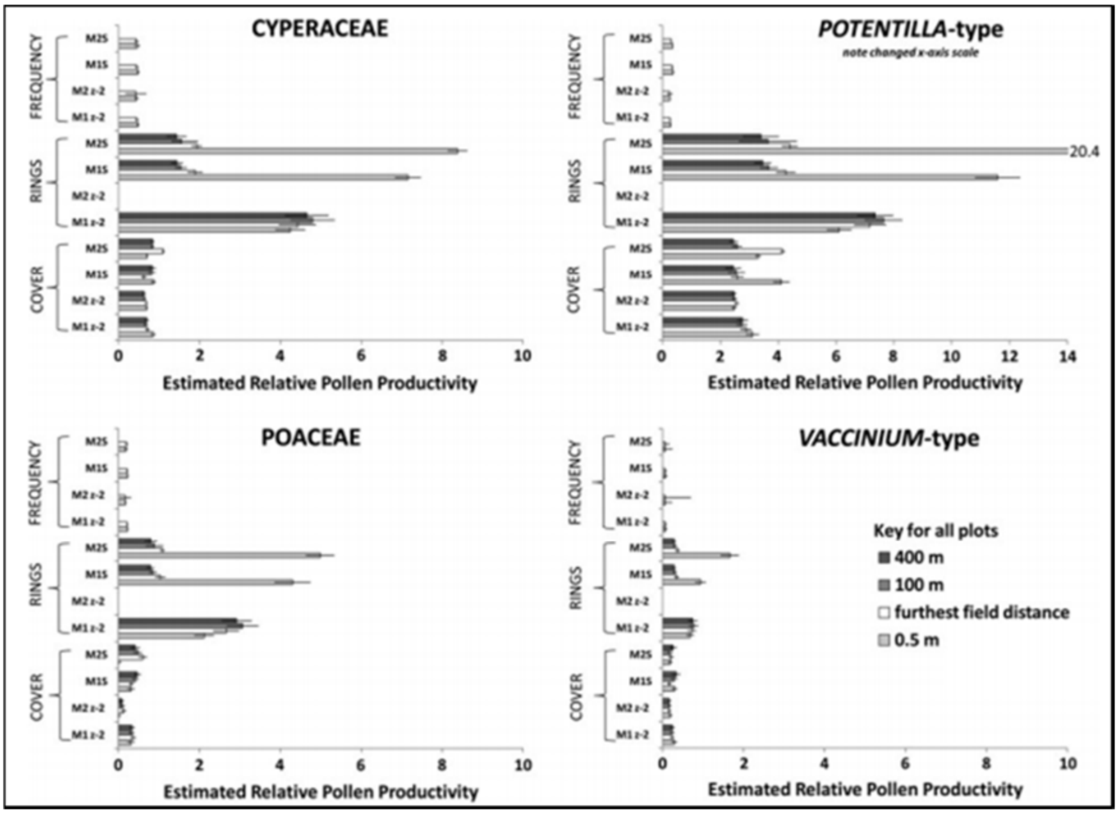


Figure 2.14: *The results from Bunting and Hjelle (2010) illustrating the estimated relative pollen productivity plotted against four distances from the sample point for Cyperaceae, Vaccinium-type, Poaceae and Potentilla-type. Calluna vulgaris was used as the reference taxon. The furthest field distance is 1.5m for the rooted frequency method, 7.5m for the cover method and 10.5m for the ring method. Higher PPEs are produced for all taxa when the ring method is used.*

Matthias *et al* (2012) conducted the first investigations into the influence of vegetation survey in forested landscapes in Germany. Forests are complex environments to conduct PPE studies in as they are multi-layered and trees produce pollen at different flowering ages (Matthias *et al*, 2012). This study in north-eastern Germany utilised the existing forest inventory data, which provided information on canopy structure that cannot be obtained from aerial photography alone. Trees were only included if they had reached flowering age, which affected the estimations of abundance of some taxa. *Betula* and *Alnus* reach flowering age quickly so this had little effect on their abundance, but the constraint of flowering age reduced the abundance of *Picea* (Matthias *et al*, 2012). The results illustrated the importance of forest structure for slow growing trees like *Fagus* (beech) and *Carpinus* (hornbeam). Flowering age is an important factor for fast growing trees like *Fraxinus* (ash) and *Picea*, where flowering age is reached late.

Matthias *et al* (2012) also discuss the variations in the PPEs obtained for *Alnus* from lake sediments compared with moss polsters. Their estimates agree well with lakes from Estonia (Poska *et al*, 2011); however, they identify that *Alnus* PPEs are lower from samples collected from moss polsters (Broström *et al*, 2004; Abraham and Kozáková, 2012). They suggest that the omission of trunk space as a transport component in the current Prentice-Sugita pollen-vegetation model could be the cause of these differences. Bunting *et al* (2013a) discuss the methodological issues associated with vegetation recording in closed canopy areas in relation to the current models of the pollen-vegetation relationship (discussed in Section 2.5.2.1). Currently, the trunk-space component of Tauber's (1965) model is not included in the Prentice-Sugita model of pollen dispersal and deposition (Prentice, 1985; Sugita, 1993; 1994; 2007a; 2007b).

Bunting *et al* (2013a) reviewed the assumptions and methods underpinning current models of pollen dispersal and deposition (discussed above in Section 2.4.2.1) and presented an ideal approach to the vegetation survey methodology. They suggest 21 quadrats in Zone A (0-10m), visually estimating the ground cover from above. The presence of canopy species are also recorded in addition to quadrat data in woodlands. An earlier study (Bunting and Hjelle, 2010) suggested that the estimates of cover method using quadrats at a variety of distances was the most suitable survey method, however the 21 quadrat sampling approach was tested again against full cover estimates in concentric rings and statistically it produced the same results. Zone B (10-100m) is usually defined by mapping the communities in the field or using aerial photographs or existing forestry data if available. Bunting *et al* (2013) combined national mapping with aerial images to define the community boundaries and these were then matched with the communities recorded in the field. Some studies have used a combination of the two methods (Bunting *et al*, 2005) or measured basal area for tree species along transects (Twiddle *et* *al*, 2012). Bunting *et al* (2013a) suggest mapping the vegetation communities in the field and recording their composition. Zone C (100-1000m, or up to the RSAP) is mapped from aerial photographs or satellite imagery. The community boundaries are firstly defined then matched with those recorded in the field.

2.4.3.3 Data Analysis and Extended R-Value (ERV) models

Field data are often digitised in GIS (eg. ArcGIS) to create georeferenced vegetation maps, and vegetation communities can then be distance-weighted. Distance-weighted vegetation data create more reliable PPEs; however the PPEs derived from some earlier studies (Andersen, 1970; Sugita *et al*, 1999; Hjelle, 1998) did not use distance weighted vegetation, and caution must be taken when using these values (Broström *et al*, 2004). GIS approaches to digitising and distance weighting vegetation are time consuming and require the user to have a detailed knowledge of GIS. The result also creates a product with a high spatial precision in relation to the uncertainties of other aspects of the PPE protocol (discussed above). Vegetation Survey Manager v 2.0 (Middleton, unpublished) is an application available from the University of Hull to simplify the storage of spatial vegetation survey data compared with complex GIS software. It also allows the user to distance-weight the vegetation data. However, this program is only designed for the input of data under the vegetation survey protocol outlined in Bunting *et al* (2013a) and if the field survey methodology varies greatly from the sampling methodology in Bunting *et al* (2013a) then this program may not be useful.

There are various different stepwise distance-weighting methods where the plant abundance is weighed and averaged at various increasing distances from the sample (Soepboer *et al*, 2007). It is advised to try several methods as each can have an effect on the resulting PPE values obtained (Poska *et al*, 2011, discussed below).

1) Stepwise inverse distance-weighting (1/d) where d is the distance from a point at the centre of the pollen site (Prentice and Webb, 1986)

2) Stepwise inverse square ($1/d^2$) distance-weighting (Webb *et al*, 1981; Calcote, 1995). The 1/d and $1/d^2$ methods do not consider pollen transport for individual species, which is incorporated into the taxon-specific method. It should be noted that Sugita (*pers comm*) no longer advises $1/d^2$ as an appropriate distance-weighting method.

3) Stepwise taxon-specific distance-weighting (Prentice, 1985; Sugita, 1994; Calcote, 1995). This option incorporates both the distance between the source plant and the sampling area along with fall speeds of pollen types and wind speed (Broström *et al*, 2004).

The distance-weighted vegetation data and the pollen counts from the moss polsters are combined in an Extended R-Value model to produce a PPE value relative to a reference taxon and to estimate background pollen. ERV models were developed to correct the earlier linear model (see Section 2.5.2.1 above) and incorporate the fact that pollen percentages are nonlinear in relation to actual plant abundance by using the distance-weighted data. The linear equation used in the Prentice-Sugita model (Section 2.5.2.1) also forms the basis of the ERV model proposed by Parsons and Prentice (1981) and Prentice and Parsons (1983). The basic assumption is that pollen loading (PL) of taxon *i* at site *k* is linearly related to the distance-weighted plant abundance (DWPA) of taxon *i* around site *k*:

$$PL_{i,k} = \alpha_i \cdot DWPA_{i,k} + \omega_i$$

Where α_i is the pollen productivity and ω_i is the background pollen loading for species *i*, assumed constant among sites in the region (Sugita, 1994). The slope α_i represents the pollen productivity of an individual taxon and the intercept ω_i represents pollen loading coming from beyond the RSAP. There are two Sub-models within the ERV model (models 1 and 2) and Sugita (1994) proposed a further Sub-model, Model 3 (see Table 2.5). Model 1 and 2 are expected to give similar results if the background components are small for all taxa (Prentice and Webb, 1986). A maximum likelihood method is used in all ERV models and as the goodness-of-fit between pollen and vegetation data improves, the likelihood function score decreases. The RSAP can be identified when the score reaches an asymptote, and estimates of slope and intercept provide the pollen productivity and background pollen (Sugita, 1994).

ERV sub model	Assumptions	Authors
1	The 'background model' Assumes a species-specific constant background in pollen proportion	Parsons and Prentice, 1981
2	Assumes a species-specific constant background in the ratio of pollen loading to total plant abundance for all the taxa involved	Prentice and Parsons, 1983
3	Assumes constant background pollen loading between sites. This model relates pollen percentages to absolute plant-abundance data, where ERV models 1 and 2 use vegetation proportions.	Sugita, 1994

Table 2.5: *Summary of assumptions of the three ERV* Sub-models*. Source: Adapted from Broström et al, 2004 and Nielsen and Sugita, 2005.*

Different combinations of ERV Sub-models and distance weighting methods will produce variations in PPEs within sites. Räsänen *et al* (2007) found the strongest linear relationship between relative pollen loadings and absolute vegetation proportion obtained by Sub-model 3. This has been the preferred choice in some studies because of this (Broström *et al*, 2004; Bunting *et al*, 2005). A recent study in Estonia (Poska *et al*, 2011) demonstrated little variation in PPEs between the three ERV Sub-models, but the distance-weighting methods chosen strongly influenced the PPE outcomes. Poska *et al* (2011) found that choice of distance weighting method has a significant effect on the PPE values for *Alnus, Betula, Picea, Salix* and Cerealia. The distance-weighting method had a particular effect on *Picea* and Cerealia as they have heavy, large pollen grains. As inverse distance weighting methods do not take pollen dispersal into consideration, this can often lead to an underestimation of PPE for taxa with heavy grains (Poska *et al*, 2011). This will be something to consider when calculating the *Picea* PPEs for Alaska.

2.4.4 Current Pollen Productivity Estimates

Obtaining pollen productivity estimates can be time consuming and expensive and the majority of efforts to date are concentrated in temperate Europe. However, studies are now being extended further to regions such as the African savannah (Duffin and Bunting, 2008), Kansas, USA (Commerford *et al*, 2013) and China (Li *et al*, 2011). Initially PPE studies within Europe were concentrated in cultural landscapes where human impact at varying scales is evident across the landscape. Little work had been in the higher altitudes and past the extent of the treeline until von Stedingk *et al*'s (2008) study in west central Sweden. Table 2.6 shows the current PPEs for selected taxa in Europe that will be directly compared with future Alaskan PPE values. Mazier *et al* (2012) produced different sets of PPEs using the mean of available PPE values from Europe. The taxa relevant for this study are included in Table 2.6, with the full list illustrated in Table 2.7. It will be useful for the European data to be compared with the Alaskan data obtained in our study, particularly as some of the European PPEs were obtained in the tundra and boreal forest biomes. As previously discussed in Section 2.1.2, the boreal zone extends across Northern America, Europe, Russia and Asia. Although arboreal species differ within this zone, the same genera occur across many of the continents. For example *Picea mariana* and *P.glauca* are widespread across parts of North America, whereas *P.abies* (Norway spruce) is the dominant *Picea* species across Scandinavia (Larsen, 1980). All of the PPEs are expressed relative to a reference taxon, usually Poaceae, and values should now be assumed to be $\text{PPE}_{\text{Poaceae}}$ unless otherwise indicated.

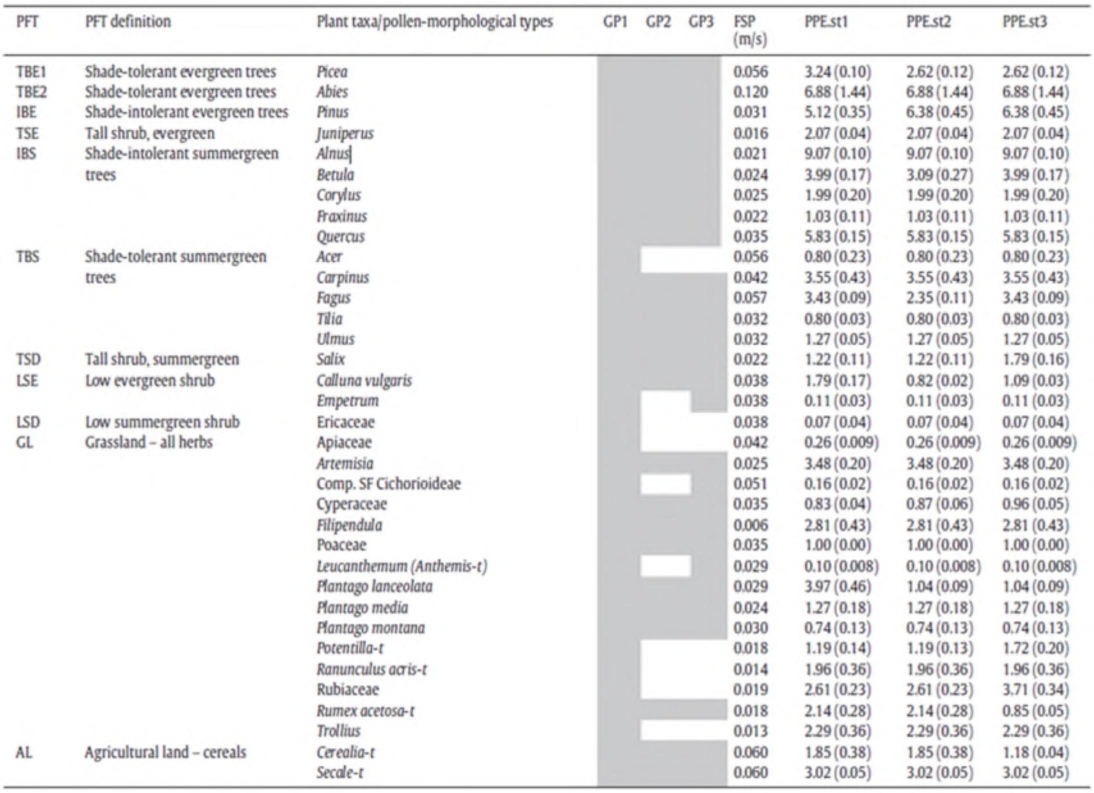
Broström *et al* (2008) reviewed the then existing estimates of pollen productivity for key taxa across Europe and observed some general similarities in trees and herbs, which are high and low pollen producers, respectively, but also some contrasts between regions. The high arboreal pollen producers are *Alnus, Betula, Quercus, Pinus* and *Abies* (fir), with *Fraxinus* (ash), *Salix, Tilia* (lime) and *Ulmus* (elm) having lower PPEs. The PPEs for Salix in particular are in fairly good agreement between studies with values of 1.30 in southern Sweden, 1.37 in England and 1 in recent studies in Greenland (Bunting *et al*, 2013b). The herb high producers were generally *Plantago lanceolata* (ribwort plantain), *Potentilla*-type (cinquefoils/tormentils), *Ranunculus acris*-type (buttercup), Rubiaceae (bedstraws) and *Rumex acetosa* (common sorrel) with *Empetrum* (crowberry), Ericaceae (heaths) and *Vaccinium* producing lower values. Mazier *et al* (2012) is considered an update of Broström *et al* (2008), but the high and low pollen producer trends are still the same. The results from a recent study in Estonia (Poska *et al*, 2011) show fairly similar results to other studies in England, Denmark and Sweden, with *Alnus* and *Quercus* producing high PPEs.

Taxon 🟥 High producers 🟦 Low producers	**Pollen Productivity Estimates**	**Region**
🟥 *Alnus*	18.00	Estonia
	11.40	England
	9.07	PPE.st2 (LANDCLIM)
	4.2	Norway (2)
	3.22	Central Bohemia
	2.56	Southern Sweden
🟥 *Betula*	8.9	Southern Sweden
	8.06	England
	4.60	Finland
	4	Greenland (*B.pubsecens*)
	3.09	PPE.st2 (LANDCLIM)
	2.5	Scotland
	2.24	West Central Sweden
	2	Greenland (*B.glandulosa*)
Calluna	0.30	West central Sweden
	4.7	Southern Sweden
	1.07	Norway (1)
	1.61	Denmark
	2.1	Scotland
	0.82	PPE.st2 (LANDCLIM)
	0.87	Norway (2)
Cyperaceae	1.37	Norway (2)
	1	Southern Sweden, Greenland
	0.89	West Central Sweden
	0.87	PPE.st2 (LANDCLIM)
	0.68	Swiss Jura
	0.29	Norway (1)
	0.002	Finland
🟦 *Empetrum*	0.11	PPE.st2 (LANDCLIM)

	0.07	Finland
Ericaceae	4.7 0.87 0.11 0.07 0.01	Southern Sweden (*Calluna*) Norway (2) (*Calluna*) West Central Sweden (*Empetrum*) West Central Sweden/ PPE.st2 (LANDCLIM) Finland (*Vaccinium* spp.)
Picea	7.10 4.80 2.8 2.62 1.8 1.20 1 0.57	Swiss Jura Estonia West Central Sweden PPE.st2 (LANDCLIM) Southern Sweden Norway (2) Scotland Swiss Plateau
Populus	0.87, 1.23 0.47	Kansas (ERV Sub-model 1 and 3) Germany
Salix	2.31 1.37 1.3 1.22 1 0.62 0.09	Estonia England Southern Sweden PPE.st2 (LANDCLIM) Greenland Norway (2) West Central Swed

Table 2.6 : *PPE values for selected taxa in Europe (Source: Broström et al, 2008). England (Bunting et al, 2005), Scotland (Twiddle et al, 2012), Denmark (Nielsen, 2004), Finland (Räsänen et al, 2007), Greenland (Bunting et al, 2013b; Bunting and Hjelle, 2010), Swiss Jura (Mazier et al, 2008), West Central Sweden (von Stedingk et al, 2008), Southern Sweden (Broström, 2002; Broström et al, 2004; Sugita et al, 1999), Estonia (Poska et al, 2011), Norway (1) (Hjelle, 1998), Norway (2) (Hjelle and Sugita, 2012), Central Bohemia (Abraham and Kozáková, 2012, Germany (Matthias et al, 2012), PPE.st.2 (LANDCLIM) (Mazier et al, 2012)*

Mazier *et al* (2012) produced different sets of PPEs using the mean of available PPE values from Europe when testing different parameter settings on the model REVEALS (Sugita, 2007a, discussed in detail in Section 2.5.6.2). Table 2.7 shows the different combinations of PPEs used in this study. Standard 1 (PPE.st1) calculated the mean PPE value using all PPE values available for that taxon. PPEs that were excluded included values that were not significantly different from zero and values deemed uncertain in the original publications and these were also removed from st2 and st3. Standard 2 (PPE.st2) calculated the mean PPE when (1) 5 or more estimates of pollen productivity (N≥5) are available for a pollen type the largest and smallest values were removed (outliers), (2) when N=4 the most deviating value was excluded and (3) when N≤3 the mean is based on all values available. Standard 3 (PPE.st3) calculated the mean PPE excluding values that are outliers and assumed unreliable based on the authors' knowledge. When looking at the means of PPE values obtained from various studies across Europe the patterns of high and low producers are still the same with *Alnus, Abies* and *Pinus* producing the highest values for the arboreal taxa followed by *Quercus* and *Betula. Ulmus, Salix, Fraxinus* and *Tilia* produce the lowest values. *Artemisia* and *Filipendula* produce the highest PPE values for the herbaceous taxa with Ericaceae and *Empetrum* very low.



PFT	PFT definition	Plant taxa/pollen-morphological types	GP1	GP2	GP3	FSP (m/s)	PPE.st1	PPE.st2	PPE.st3
TBE1	Shade-tolerant evergreen trees	*Picea*	▨	▨	▨	0.056	3.24 (0.10)	2.62 (0.12)	2.62 (0.12)
TBE2	Shade-tolerant evergreen trees	*Abies*	▨	▨	▨	0.120	6.88 (1.44)	6.88 (1.44)	6.88 (1.44)
IBE	Shade-intolerant evergreen trees	*Pinus*	▨	▨	▨	0.031	5.12 (0.35)	6.38 (0.45)	6.38 (0.45)
TSE	Tall shrub, evergreen	*Juniperus*	▨	▨	▨	0.016	2.07 (0.04)	2.07 (0.04)	2.07 (0.04)
IBS	Shade-intolerant summergreen trees	*Alnus*	▨	▨	▨	0.021	9.07 (0.10)	9.07 (0.10)	9.07 (0.10)
		Betula	▨	▨	▨	0.024	3.99 (0.17)	3.09 (0.27)	3.99 (0.17)
		Corylus	▨	▨	▨	0.025	1.99 (0.20)	1.99 (0.20)	1.99 (0.20)
		Fraxinus	▨	▨	▨	0.022	1.03 (0.11)	1.03 (0.11)	1.03 (0.11)
		Quercus	▨	▨	▨	0.035	5.83 (0.15)	5.83 (0.15)	5.83 (0.15)
TBS	Shade-tolerant summergreen trees	*Acer*	▨			0.056	0.80 (0.23)	0.80 (0.23)	0.80 (0.23)
		Carpinus	▨	▨	▨	0.042	3.55 (0.43)	3.55 (0.43)	3.55 (0.43)
		Fagus	▨	▨	▨	0.057	3.43 (0.09)	2.35 (0.11)	3.43 (0.09)
		Tilia	▨	▨	▨	0.032	0.80 (0.03)	0.80 (0.03)	0.80 (0.03)
		Ulmus	▨	▨	▨	0.032	1.27 (0.05)	1.27 (0.05)	1.27 (0.05)
TSD	Tall shrub, summergreen	*Salix*	▨	▨	▨	0.022	1.22 (0.11)	1.22 (0.11)	1.79 (0.16)
LSE	Low evergreen shrub	*Calluna vulgaris*	▨	▨	▨	0.038	1.79 (0.17)	0.82 (0.02)	1.09 (0.03)
		Empetrum	▨		▨	0.038	0.11 (0.03)	0.11 (0.03)	0.11 (0.03)
LSD	Low summergreen shrub	Ericaceae	▨			0.038	0.07 (0.04)	0.07 (0.04)	0.07 (0.04)
GL	Grassland – all herbs	Apiaceae	▨			0.042	0.26 (0.009)	0.26 (0.009)	0.26 (0.009)
		Artemisia	▨	▨	▨	0.025	3.48 (0.20)	3.48 (0.20)	3.48 (0.20)
		Comp. SF Cichorioideae	▨		▨	0.051	0.16 (0.02)	0.16 (0.02)	0.16 (0.02)
		Cyperaceae	▨	▨	▨	0.035	0.83 (0.04)	0.87 (0.06)	0.96 (0.05)
		Filipendula	▨	▨	▨	0.006	2.81 (0.43)	2.81 (0.43)	2.81 (0.43)
		Poaceae	▨	▨	▨	0.035	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)
		Leucanthemum (Anthemis-t)	▨		▨	0.029	0.10 (0.008)	0.10 (0.008)	0.10 (0.008)
		Plantago lanceolata	▨	▨	▨	0.029	3.97 (0.46)	1.04 (0.09)	1.04 (0.09)
		Plantago media	▨	▨	▨	0.024	1.27 (0.18)	1.27 (0.18)	1.27 (0.18)
		Plantago montana	▨	▨	▨	0.030	0.74 (0.13)	0.74 (0.13)	0.74 (0.13)
		Potentilla-t	▨			0.018	1.19 (0.14)	1.19 (0.13)	1.72 (0.20)
		Ranunculus acris-t	▨			0.014	1.96 (0.36)	1.96 (0.36)	1.96 (0.36)
		Rubiaceae	▨			0.019	2.61 (0.23)	2.61 (0.23)	3.71 (0.34)
		Rumex acetosa-t	▨	▨	▨	0.018	2.14 (0.28)	2.14 (0.28)	0.85 (0.05)
		Trollius	▨			0.013	2.29 (0.36)	2.29 (0.36)	2.29 (0.36)
AL	Agricultural land – cereals	*Cerealia-t*	▨	▨	▨	0.060	1.85 (0.38)	1.85 (0.38)	1.18 (0.04)
		Secale-t	▨	▨	▨	0.060	3.02 (0.05)	3.02 (0.05)	3.02 (0.05)

Table 2.7: *Plant functional types (PFTs) and corresponding pollen morphological types used in the study by Mazier et al (2012) to test the effect of different selections of data and parameter inputs on REVEALS estimates. Three data sets of pollen morphological types (GP1, GP2, and GP3) and three data sets of PPEs (PPE.st1, PPE.st2, and PPE.st3) GP1 (all taxa), GP2 (all entomophilous taxa excluded), and GP3 (entomophilous taxa seldom found excluded) include 35, 25 and 28 taxa, respectively. FSP= Fall speed of pollen and means of PPEs for standards 1, 2 and 3 (with their SE). Source: Mazier et al (2012)*

2.4.4.1 PPE estimates in the tundra and boreal biomes

Von Stedingk *et al* (2008) were the first to produce estimates for the forest/tundra ecotone. They discovered strong variations between the alpine forest and the cultural landscape of lowland Sweden and attributed this to the ecological ranges of the taxa represented. For example, *Betula* produced lower PPEs and this is thought to be as a result of a different sub-species in this region (*Betula pubescens* spp. *czerpanovii*, mountain birch). The low PPE for *Betula* was attributed to mountain birch having a lower pollen production that *Betula pubescens* and *Betula pendula* in southern Sweden. Von Stedingk *et al* (2008) suggest that this likely reflects the fact that mountain birch is growing near the range of tree growth in this study. The proximity to range limits is an important factor in regions where pollen production is sensitive to climate. The PPE for *Salix* obtained in the forest-tundra ecotone is also lower than that of southern Sweden (Broström *et al*, 2004). As with *Betula, Salix* growing further south is the tree *Salix caprea* compared with the *Salix* shrub species further north.

The PPE for *Betula* in forest-tundra ecotone is 2.24 (von Stedingk *et al*, 2008) but dwarf birch was not separated from tree birch in this study. Bunting *et al* (2013b) obtained PPEs for tree birch and dwarf birch at 3.7 and 1.4 respectively in Greenland, but when they removed tree birch from the data set they obtained a value of 2.3 similar to the value at the forest-tundra ecotone in Sweden. This could raise issues with the PPE estimates in Alaska as the birch, poplar (*P.balsamifera* and *P.tremuloides*) and spruce (*P.mariana and P.glauca*) will most likely not be palynologically separated. A higher value of 4.6 was obtained for *Betula* from the northern boreal forests in Finnish Lapland (Räsänen *et al*, 2007), but this is still lower compared with a PPE value of 8.9 in southern Sweden (Sugita *et al*, 1999).

The PPE values obtained for *Picea* in west central Sweden (von Stedingk *et al*, 2008) were slightly higher than the southern regions (Broström *et al*, 2004). Von Stedingk *et al* (2008) discuss a variety of issues which complicate the picture when estimating pollen productivity for this tree. *Picea* pollen production is linked to climate and concentrated in specific years (Hicks, 1999). Hicks (1999) monitored pollen traps over 16 years in Finland and also noted that early frost days during the period of pollen formation can also lead to less pollen produced. Von Stedingk *et al* (2008) suggest that the slightly higher than expected value for *Picea* could be attributed to a warmer climate during the last decade which has led to a higher pollen production for this tree. Increased July temperatures in the region saw higher pollen production for *Picea*, with major production in 1998 and 2002 in the Jämtland province. This suggests that the period of pollen deposition represented in the moss polsters contained two major flowering years, rather than one which would be the average for any given 7 year period in the last four decades (von Stedingk *et al*, 2008).

PPE values for *Picea* in Europe have been generally lower compared with other coniferous species such as *Pinus* and *Abies*. PPE values from the Swiss Jura did however produce a value of 7.10 similar to *Pinus*. This high value for the Jura Mountains could be due to favourable climatic conditions for *Picea abies* (Broström *et al*, 2008). Mazier *et al* (2008) also highlight the effect of distance-weighting methods and size of increments which can affect PPEs, especially for heavy pollen types such as *Picea* and *Abies*.

Another possible explanation for the higher PPE values in the forest-tundra compared with the southern lowlands is the age of the stands. Flowering age has been shown to be an important factor for fast growing trees like *Fraxinus* (ash) and *Picea*, where flowering age is reached late (Matthias *et al*, 2012). In regions where human disturbance is high or woodlands are managed, flowering age might not be reached in all woodlands covered in PPE studies. Matthias *et al* (2012) suggest that this could result in the lower PPEs.

Pollen production is known to be lower in the tundra due to climatic factors (Hicks, 1999). The values for dwarf shrubs in Finland produced low values of 0.07 for *Empetrum* and 0.01 for *Vaccinium* (Räsänen *et al*, 2007). The PPE for *Empetrum* (0.11) and Ericaceae (0.07) in the west central Sweden are equally low; however, they do not show linearity in the pollen-vegetation relationship, which von Stedingk *et al* (2008) suggest could be due to the openness of the local vegetation. The authors also note that the Ericaceae group is broad, with species present in both tundra and forest floor communities. Therefore, there could be variation between individual species, a distinction that is lost in the grouping into a single taxon.

2.4.4.2 PPE studies in temperate forests and cultural landscapes

The majority of PPE studies across Europe have been conducted in cultural landscapes where human impact at varying scales is evident across the landscape. It was unknown the extend this would affect PPEs for arboreal species and how applicable current PPEs would be for reconstructing landscapes such as old-growth forests or ancient landscapes with vegetation cover relatively untouched by human impacts (Baker *et al*, 2016). Calcote (1995) conducted the first PPE study in closed forests dominated by hemlock-northern-hardwood forests and old-growth forests dominated by hemlock (*Tsuga canadensis*) or sugar maple-basswood (*Acer saccharum-Tilia americana)* in Michigan, USA. Although these forests are largely dominated by species which are not comparable with the European PPE data set and the reference taxon was sugar maple, Calcote (1995) did obtain PPEs for *Betula*. The PPE for *Betula* in Sylvania, where yellow birch dominated, was 9.4 and 7.5 for Wisconsin where paper birch dominated. Despite the difference in reference taxon and species of *Betula*, these values are fairly high and consistent with some of the values for *Betula* from other regions in Europe (Bunting *et al*, 2005; Broström, 2002), confirming that *Betula* is a high pollen producer.

Baker *et al* (2016) obtained the first PPEs from a closed-canopy old-growth forest in Europe with minimal human impact in Białowieża National Park in Poland. The aim of this study was to assess the difference in pollen productivity between closed forests and more open landscapes. Their results show that the ratio between high pollen producers (*Pinus sylvestris* and *Quercus robur*) and low producers (Poaceae, *Corylus avellana*) is six times greater compared with other European studies. They conclude that light and canopy structure is one of the main reasons for this difference. They suggest that the low pollen producers in their data set (*Corylus*, Poaceae and *Tilia*) do not receive sufficient light in the closed canopy forest for optimal pollen production compared with more open cultural landscapes.

A second reason for differences in pollen production which is not discussed in any other PPE study is nitrogen availability. The presence of dead wood composition can increase the availability of nitrogen for trees, and an increase in nitrogen has been linked to an increase in pollen productivity (Pheonix *et al*, 2012). Long term manipulation field experiments by Pheonix *et al* (2012) have shown that pollen production can increase up to three times in woody plants with added nitrogen. Baker *et al* (2016) also highlight methodological issues raised by Bunting *et al* (2013b) when comparing their *Quercus* and *Alnus* PPEs with other studies. Baker *et al* (2016) only collected samples which contained *Quercus robur* (English or pedunculated oak) but other studies included both *Q. robur* and *Q. petraea* (sessile oak) (Soepboer *et al*, 2007; Theuerkauf *et al*, 2012). Baker *et al* (2012) suggest that PPEs from cultural landscapes should be used alongside PPEs from old growth forest when using landscape reconstruction models. They suspect that the PPEs obtained from the Białowieża National Park will result in higher estimations of open land in past landscapes in Europe.

Betula produced PPEs on the Swiss Plateau (Soepboer *et al*, 2007) of 4.39 (ERV Model 1), 4.73 (Model 2) and 2.42 (Model 3). All of these values are fairly low in comparison to southern Sweden (8.9), England (8.06) and Estonia (6.80). Low values for *Picea* (0.35, model 2 and 0.57, model 3) on the Swiss Plateau is attributed to *Picea* contributing to a large proportion of the background pollen, as *Picea* and *Pinus* are most frequently found at higher latitudes surrounding the Plateau (Soepboer *et al*, 2007). Soepboer *et al* (2007) discuss the difficulties with making direct comparisons of PPEs between regions. The Swiss Plateau for instance is hilly in comparison to lowland areas of Sweden and variations in topography could add further uncertainties (eg wind direction) when estimating PPEs.

Regional variations across Europe are particularly high for *Alnus*, for which estimates were calculated at 18.00 in Estonia (Poska *et al*, 2011) and 3.22 in Norway (Hjelle and Sugita, 2012). The PPE in Norway is slightly lower, but broadly comparable to 4.2 in southern Sweden (Broström *et al*, 2004). The estimate for *Alnus* from England (Bunting *et al*, 2005) is also very high at 11.4. Bunting *et al* (2005) attribute this to the location of taxa growing in or at the edge of the fen carr, where competition is less than it would be in a predominantly dry woodland. This means that the canopy cover for this tree is larger than in dry woodlands and can result in higher pollen percentages.

Populus is an important taxon in our study as it is a dominant species in some boreal forest communities in Alaska (see Section X). More interestingly, the increase in *Populus* pollen in many Alaskan paleo records marks the onset of the development of deciduous woodland in the early Holocene. There is currently only one PPE study which included *Populus* in Europe (Matthias *et al*, 2012) which produced a value of 0.47 when using ERV sub model 3. The forest data used to obtain this value was only included if the flowering age of the tree or shrub had been reached. A value has also been obtained from the tallgrass prairies of Kansas, North America (Commerford *et al*, 2013). A value of 0.87 was obtained from ERV sub model 1 and 1.23 from ERV sub model 3.

2.4.4.3 Summary of factors affecting current PPEs

Factors affecting PPEs can vary from vegetation sampling design (Bunting and Hjelle, 2010; Matthias *et al*, 2012; Bunting *et al*, 2013a), to choice of distance-weighting method (Poska *et al*, 2011) and pollen taxonomy (Bunting *et al*, 2013b; Baker *et al*, 2016). Bunting *et al* (2013a) argue that a lack of a standard methodology of vegetation survey in PPE studies is the main reason for differences in estimations. However, Baker *et al* (2016) suggest that canopy structure and changes in the prevailing environmental settings can be the dominant factor leading to variability in PPEs in forested landscapes. The literature illustrates that the factors affecting PPEs are complex and often coincide with each other complicating the picture. This can make it difficult to assess which are the overriding factors contributing to high or low PPEs in different regions.

Little work has been done in the high latitude regions which will hinder the amount of direct comparisons with the Alaskan PPEs. In light of this and the current greening process occurring in the Arctic, the Alaskan PPEs will contribute an important dataset for future vegetation reconstructions in this region. Southern Sweden has generally produced higher PPEs than other European regions. Broström *et al* (2008) suggest the small spread of values in the vegetation data and some outliers with high pollen proportions as the contributing factor for high PPEs in Sweden. The contrasts between the regions within Europe alone illustrate the importance for more detailed work in other areas of the world in order to more accurately reconstruct vegetation.

2.4.5 Approaches to Quantative Vegetation Reconstructions

Determining quantitative vegetation cover on regional and local scales can address questions on past land use, responses of vegetation to climate change and biodiversity. In light of future climate change, understanding past vegetation dynamics will impact our understanding of processes which should be included in future environmental models (Trondman *et al*, 2015).

Earlier work on pollen-based reconstructions of vegetation focused on the ratio between arboreal pollen (AP) and non-arboreal pollen (NAP). Detecting patterns of landscape openness in the past has implications for the interpretation of archaeological sites. Berglund *et al* (1991) used AP-NAP ratios to quantify land use changes and land cover in Europe. However, as discussed above pollen percentages are not linearly related to vegetation abundance. AP-NAP relationships are therefore also not linearly related to vegetation composition and landscape patterns and do not take into account differences in pollen dispersal and spatial structure of vegetation (Sugita *et al*, 1999; Sugita 2007a, Bunting *et al*, 2004). NAP types are also generally under-represented which can lead to an underestimation of landscape openness (Hellman *et al*, 2009). Studies in southern Sweden (Gaillard *et al*, 1998 and Broström *et al*, 1998) found that the relationship was even more complex with NAP percentages lower in forested area compared with more open areas despite similar percentage cover of open land taxa.

Various approaches have been adopted over the past several decades to interpret pollen data and reconstruct vegetation including indicator species approaches (Behre, 1986), the use of plant functional types and biomization (Prentice *et al*, 1996) and simulation models for pollen dispersal and deposition which include HUMPOL (Bunting and Middleton, 2005) and POLLSCAPE (Sugita, 1994, Sugita *et al*, 1999). Despite advances in theoretical studies of the pollen-vegetation relationship, there still lacked a theoretical framework to incorporate our understanding of the mechanisms and factors into reconstruction of past vegetation (Sugita, 2007a).

2.4.6 The Landscape Reconstruction Algorithm (LRA)

The Landscape Reconstruction Algorithm (LRA, Sugita 2007a and b) is a two-step framework for quantitative reconstruction of vegetation across various spatial scales. The first step is the model REVEALS (**R**egional **E**stimates of **VE**getation **A**bundance from **L**arge **S**ites) which reconstructs vegetation composition in $10^6 – 10^7$ ha ($10^4 – 10^5$ km^2). Studies have shown that pollen assemblages are similar among large sites in a given region (Bradshaw, 1981, Sugita, 1994) and therefore, in theory any large lake in a region can be used to estimate the mean regional vegetation (Sugita, 2007a). Once the regional vegetation is known, estimates of the RSAP and background pollen coming from beyond the RSAP can be made (Sugita, 1994). Background pollen is not included in the REVEALS model as this is not necessary for regional reconstructions. The LRA takes into account the changes in background pollen by estimating the regional vegetation composition (Sugita 2007a,b) and this is incorporated in step two of the LRA (LOVE). Figure 2.15 illustrates the research framework for the LRA. The assumption of REVEALS is that pollen loading is likely related to the mean regional vegetation.

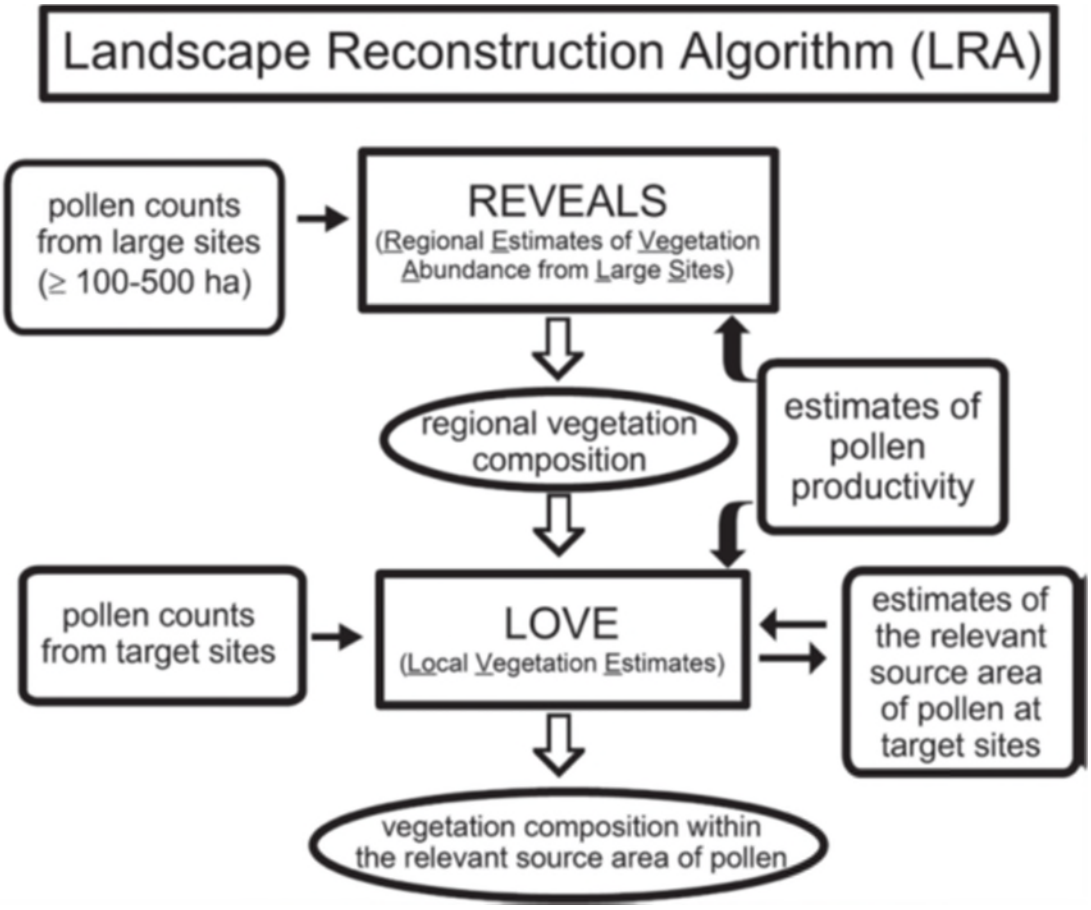


Figure 2.15: *Framework of the LRA (source: Sugita et al, 2007)*

The equation for the REVEALS model is:

$$\hat{V}_i = \frac{n_{i,k} \,/ \hat{\propto}_j \;\; K_i}{\sum_j^m = 1 \;(n_{i,k}/\hat{\propto}_j \, K_j\;)}$$

Where $\hat{V}_i$ is the estimate of mean regional vegetation composition for taxon i, $n_{i,k}$ is the pollen count for taxon i at site K, $\hat{\propto}_j$ is the pollen productivity estimate (PPE) for taxon i, relative to a reference taxon, m is the total number of plant taxa used for reconstruction, and K_i is the "pollen dispersal-deposition coefficient" of taxon i, defined as $\int_R^{Z_{max}} g_{i\ (z)} \cdot \mathrm{d}z$. R represents the radius (m) of a large lake, Z_{max} the spatial extent (m) of the "regional" vegetation within which most of the pollen comes from, z is the distance (m) from the centre point of the lake and $g_{i\ (z)}$ is a pollen dispersal function for taxon i. REVEALS uses Sugita's (1993) model of pollen dispersal and deposition on the entire surface of a basin (Soepboer *et al*, 2010).

The second step in the LRA is the LOVE model (**LO**cal **V**egetation **E**stimate). The LOVE model estimates local vegetation composition within the relevant source area of pollen (RSAP). The model quantifies and then subtracts background pollen (i.e., pollen coming from beyond the relevant source area) in order to arrive at a quantitative reconstruction of local vegetation (Sugita, 2007b). The parameters required to run LOVE are pollen counts from small sites, the RSAP, pollen productivity estimates and the regional vegetation composition.

Assumptions that apply to both large and small sites used in both steps of the LRA (Sugita 2007a and b):

1) The sedimentary basin is a circular opening in the vegetation canopy

2) Wind is the sole agent of pollen transport and comes from all directions

3) PPEs are taxon-specific and constant in space and time

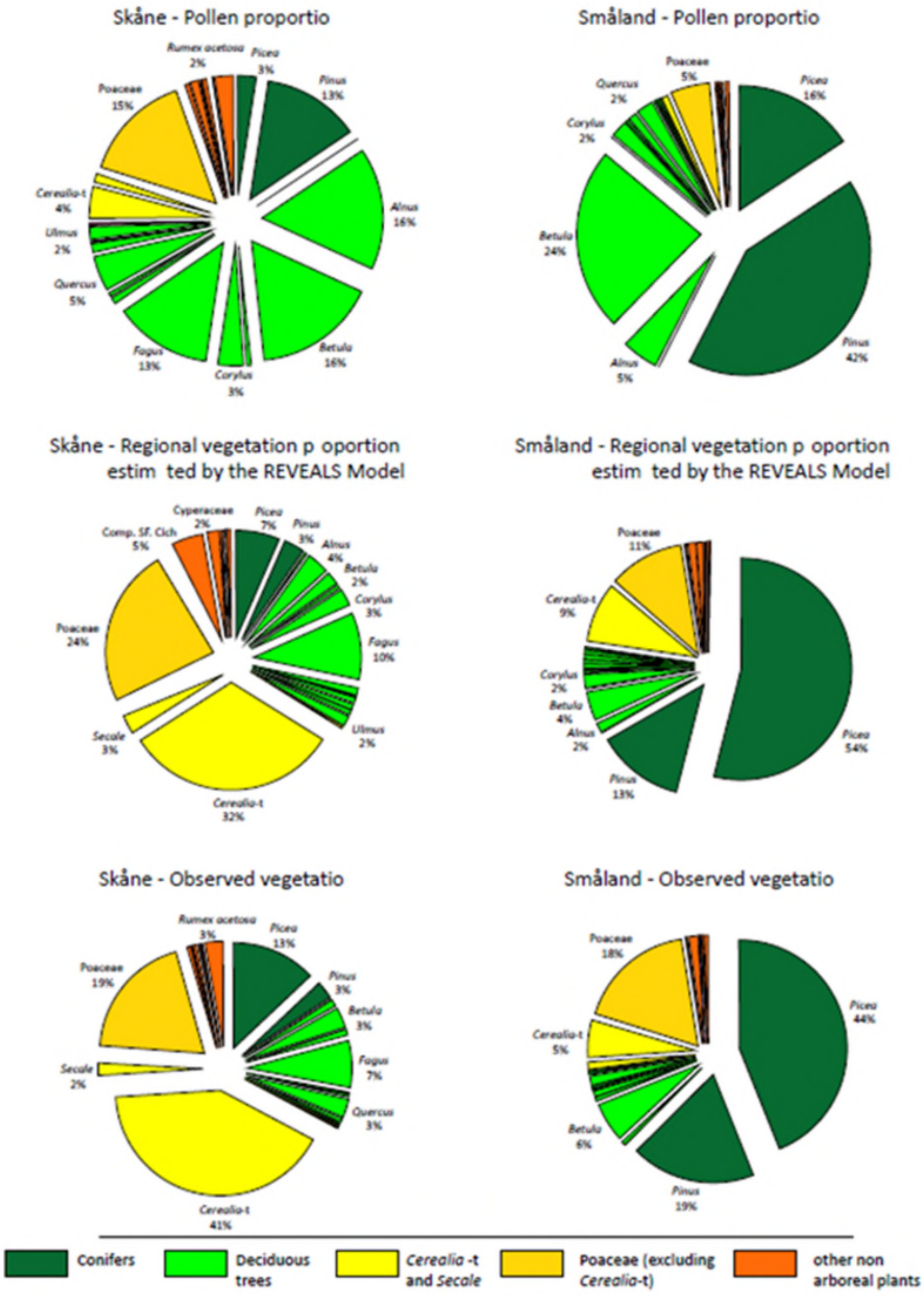
4) Wind speed and atmospheric conditions are constant over time of pollen dispersal

5) Pollen deposited on water surface is well mixed before sedimentation, and the inter-taxonomic differences in pollen preservation in sediments are negligible.

2.4.6.1 Testing and Validation of the LRA

The LRA has been tested and validated at several sites across Europe and in the U.S. and has so far been more successful at estimating observed modern vegetation composition compared with pollen percentages (e.g. Hellman *et al*, 2008a,b; Soepboer *et al*, 2010; Sugita *et al*, 2010b). The REVEALS model was first validated empirically in Sweden (Hellman *et al*, 2008a). REVEALS was used to estimate the regional vegetation in the provinces of Skåne and Småland, two distinctly different vegetation regions. The modern vegetation was recorded using a combination of satellite data, forest and vegetation inventories, crop statistics and aerial photographs within a 104 km^2 area to establish the percentage cover of the modern vegetation. This data was then compared with REVEALS estimates of vegetation from surface pollen samples from ten lakes in the regions. Hellman *et al* (2008a) found that REVEALS was more successful than pollen percentages at predicting the percentage cover of large vegetation units such as total tree, broad-leaf trees, conifers or open land (Figure 2.16). The study was seen as a successful move forward from AP/NAP ratios.

They did, however, find that REVEALS was slightly less successful at estimations of cover for individual taxa. *Picea* was best corrected Småland and *Alnus* was well corrected at both sites, but best in Skåne. in Hellman *et al* (2008a) suggested that the discrepancies between single taxa estimates could possibly be attributed to PPEs, sources of vegetation data or origin of pollen violating the assumptions of the model. The importance of vegetation data sources were discussed further by Hjelle *et al* (2015). They found that when testing REVEALS with CORINE (Coordination of Information on the Environment) data (Aune-Lundberg and Strand, 2010), REVEALS worked well at estimating forest cover but less well at estimating specific groups such as deciduous and conifer trees. They suggested that in, order to assess the LRA at the site-specific scale, land resource maps would be more appropriate than CORINE data. It will be vital to test the new Alaskan PPEs for *Alnus* and *Picea* in particular prior to applying the LRA on Ruppert and Lake 3 to ensure a reliable reconstruction.



Skåne - Pollen proportio

Småland - Pollen proportio

Skåne - Regional vegetation p oportion estim ted by the REVEALS Model

Småland - Regional vegetation p oportion estim ted by the REVEALS Model

Skåne - Observed vegetatio

Småland - Observed vegetatio

Figure 2.16: *Validation of the REVEALS model in southern Sweden, provinces of Skåne (left) and Småland, (right): comparison of pollen percentages, REVEALS estimates, and actual vegetation for 26 taxa. Only taxa represented by ≥ 2% are named. REVEALS was run with the pollen productivity estimates from southern Sweden (Broström et al., 2004). Note the underrepresentation in pollen percentages of cereals (yellow), Poaceae (orange) and other non-arboreal taxa (herbs and shrubs; red), and the overrepresentation of deciduous trees (light green), Betula and Alnus in particular,* compared with *the share of these taxa in the actual vegetation and in REVEALS estimates. Pinus is dominant among conifers (dark green) in the pollen assemblage, while Picea is dominant in the vegetation and REVEALS estimates. (Sources: Gaillard et al, 2010; Hellman et al, 2008a,b)*

Hellman *et al* (2008b) tested existing sets of PPEs on the same regions of Skåne and Småland. They assumed that the best fit between the modern pollen assemblage and the actual vegetation should indicate which set of PPEs were most reliable. Shinya Sugita (*pers comm, 2014*) suggested that PPEs used in the REVEALS reconstruction for a region should be obtained from the region whenever possible. Hellman *et al* (2008b) however, showed that a combination of PPEs was best in southern Scandinavia with PPEs from Denmark providing the best fit for cereals, *Calluna*, *Plantago lanceolata* and *Rumex*. As previously outlined in Section 2.5.3 there are various factors which can affect PPEs and their reliability. It is not just the region but the environmental setting where the PPEs were estimated. Mazier *et al* (2012) used the Czech Quaternary Palynological Database to test different parameter settings on REVEALS. They used the mean of available PPE values from Europe to evaluate the extent to which selection of a set of PPE values influences the REVEALS reconstruction (see Section 2.4.4 above, Table 2.7). They found that when testing PPEs on grid based REVEALS estimates of Plant Function Types (GB REVEALS PFTs) PPE datasets did not affect the rank orders of the GB REVEALS PFTs. Depending on the scale, taxa and research questions, as highlighted by Hellman *et al* (2008b) it is advisable to test more than one set of PPEs when using the LRA.

Further investigations into sampling design in this study in Sweden (Hellman *et al* 2008a and b) illustrated that multiple sites were more reliable than one large lake for regional reconstructions as there can be variation in pollen assemblages. Trondman *et al* (2016) however, found that one large lake was appropriate for a REVEALS reconstruction if the regional vegetation is characterised by a regular, large-scale mosaic of vegetation patches (discussed in further detail below). Hellman *et al* (2008b) suggest that if pollen records are only available from one large lake in the region the regional vegetation should be estimated at regularly spaced intervals (100-300 years) and use at least 3-5 samples per interval.

In the absence of a large lake for the region, studies have shown that medium-sized or small lakes can be used for regional reconstructions of vegetation but the error estimates will be higher (Sugita, 2007b; Hjelle *et al*, 2015; Trondman *et al*, 2016). Hjelle *et al* (2015) demonstrated that 28 small lakes in Norway from modern samples showed comparable results to 1 large lake but the error estimates were higher. Error estimates will be higher when using pollen data from small sites as they exhibit between site differences and variability in the pollen assemblages (Sugita, 2007b). Trondman *et al* (2016) tested how appropriate pollen records from small sites were for REVEALS in southern Sweden. They also agreed with the observations by Hjelle *et al* (2015) that when taking into account the standard errors there were similar results when using several small lakes compared with one large lake. However, they also concluded that they cannot recommend a minimum number of sites for REVEALS runs.

There are various variables which need to be taken into account when deciding on the size and number of sites including 1) the size of the pollen counts for each records 2) type of site 3) vegetation type (mosaic, patch sizes, distribution of vegetation) and 4) area of reconstruction (Hjelle *et al*, 2015). Abraham *et al* (2014) performed simulation experiments, varying different parameter settings when using REVEALS. They found that adjusting the site radius for all taxa substantially influences the REVEALS estimates for very heavy or light pollen grains. They also adjusted the wind speed setting and found that estimates of *Abies* (heavy grain) improved when compared with the modern vegetation. Trondman *et al* (2015) discuss the factors which affect the reliability, accuracy and precision of REVEALS. The following five points to consider are highlighted as the most important particularly when using grid-based REVEALS estimates:

- The type (bog or lake) and size (large or small) of the sites
- The number of pollen records used and their distribution in each grid cell
- The accuracy of the pollen records' chronologies
- The past regional vegetation (homogenous or heterogeneous) in each grid cell
- The applicability and reliability of the available PPEs in the study region.

Nielsen *et al* (2010) tested the performance of the LOVE model on 9 lakes in Denmark before applying the LRA on 3000 year old lake sequences. The 9 lakes were split into 2 regional groupings as the vegetation in the two areas was highly affected by soil types. The LOVE reconstructed vegetation from pollen samples dating to A.D 1800 was compared with distance-weighted vegetation composition extracted from historical maps from this period. REVEALS was unable to be tested during this particular study as there were no regional historical maps available. The general patterns show that the LOVE reconstructions were more comparable with vegetation cover than using the pollen proportions alone. The proportion of tree cover was slightly underestimated at woodland rich sites which was also the case when the model was tested on a small forest hollow in Denmark by Overballe-Petersen *et al* (2013). However, the overestimation is still smaller than the overestimation of tree cover at woodland poor sites through pollen percentages. Poaceae was overestimated by LOVE and Nielsen *et al* (2010) attribute this to the occurrence of wetland grasses such as *Phragmites australis* around their study lakes.

Cui *et al* (2015) tested the performance of the LRA to quantify past landscape changes using historical maps and written sources along with the LRA to gain a better understanding of the origin of landscape diversity and recent loss of species diversity over three centuries (AD 1700 –

2010) in Southern Sweden. Estimates of percentage cover of major taxa was obtained using the LRA reconstructions and the modern and historical maps provided the percentage cover of major land-use/landscape/vegetation units (LuVs). Comparison of the LRA-LuVs and map-LuVs suggested that the LRA performed reasonably well. Mazier *et al* (2015) examined local variability of land-use history in the South Swedish Uplands over 200 years. The LRA approach did overestimate grassland cover by 10-30% between AD1769-1823 and 1837-1895, but the generally the reconstructed estimates were also in good agreement with the historical maps and aerial photographs.

Hjelle *et al* (2015) tested LOVE on 26 small lakes in Norway. Vegetation data from a radius of 2000m around each site was obtained based on digital land resource maps, along with field surveys and aerial photographs. Two sets of PPEs were used to evaluate which were most suitable for this study. LOVE based estimates and distance-weighted plant abundances (dwpa) were compared with pollen percentages taken from modern lake surface samples. The relationship between LOVE estimates and dwpa was an improvement compared with pollen percentages alone, particularly for common and abundant taxa like *Pinus* and Poaceae (Figure 2.17). The relationship is also improved for *Alnus*; however, there were large variations in the LOVE estimates. Hjelle *et al* (2015) suggest that the uncertainty of the PPEs could be a possible cause as there are large differences in the two PPE values used for this taxa (9.07 and 3.22). *Fraxinus* and *Picea* are underestimated by LOVE. The underestimation of *Picea* is likely attributed to the maturity of the trees in the region as the majority have not matured to flowering in many of the plantations (Hjelle *et al*, 2015; Matthias *et al*, 2012). This will affect the PPEs and ultimately the LOVE estimations of cover. As previously discussed the vegetation data choices can also affect the estimates produced by the LRA. Hjelle *et al* (2015) used land resource maps for their site-specific scale along with vegetation surveys. The surveys were not detailed enough to account for some solitary trees such as *Fraxinus* which may have been missed and this may account for the underestimation of this taxa.

Testing of the LOVE model proved to be useful step prior to the vegetation reconstruction in both Denmark, southern Sweden and Norway. The LRA reconstruction demonstrated the landscape openness was at a higher degree than previously thought during the past 3000 years despite the underestimation of woodland and overestimation of Poaceae in Denmark. The interpretation of the LRA results were more reliable in both regions following the results obtaining during the validation process. These studies highlight the importance of testing the LRA models in the study region landscapes where reconstructions will be undertaken.

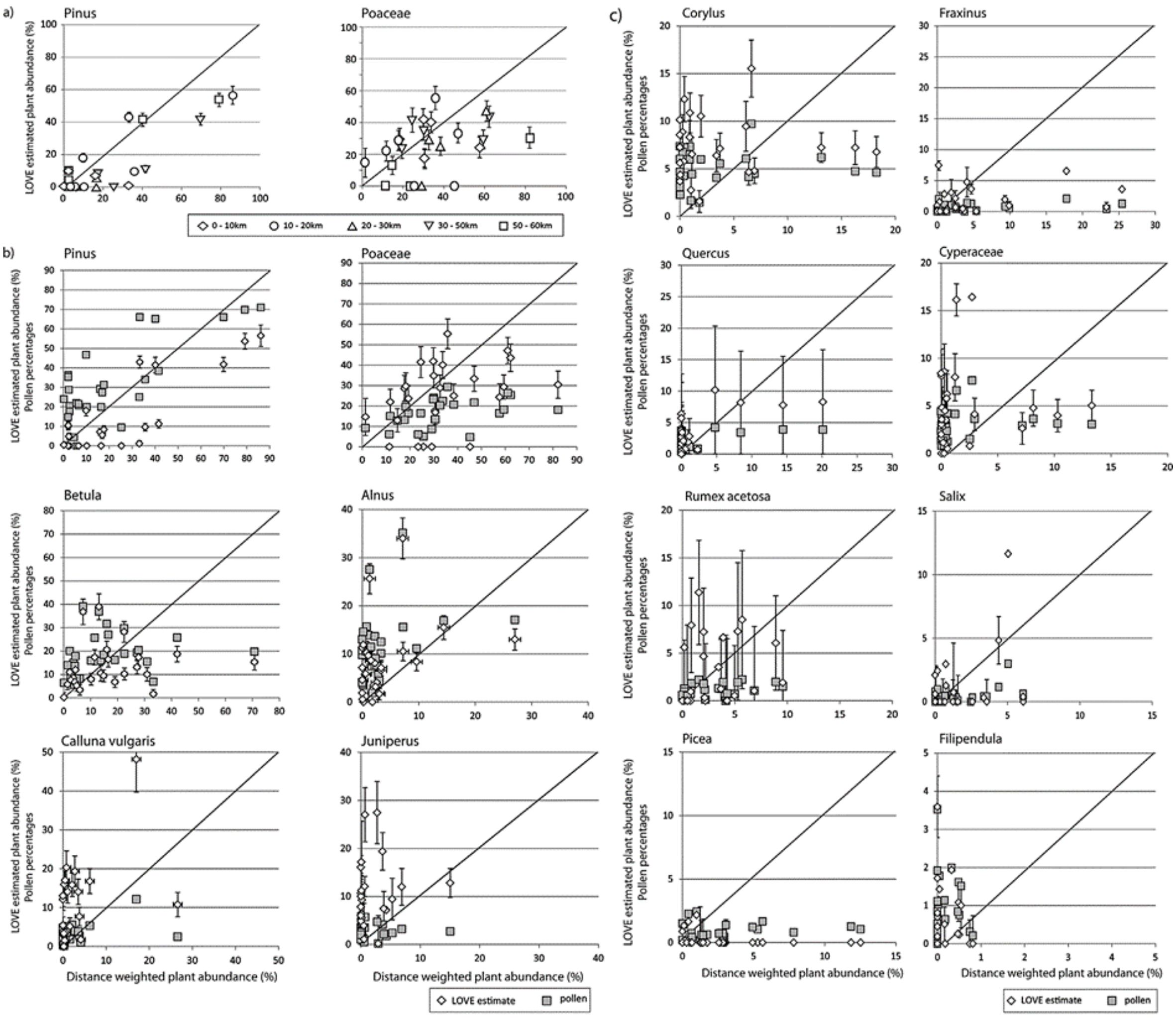


Figure 2.17: *Results from the validation test of the LOVE model in Norway using modern data. LOVE-based plant abundance estimates and pollen percentages plotted against distance-weighted plant abundance for 26 lakes. (a) LOVE-estimated plant abundance for Pinus and Poaceae plotted against dwpa at individual lakes; (b,c) Pollen percentages and LOVE-based plant abundance estimates plotted against dwpa. Note the different scales (source: Hjelle et al, 2015).*

2.4.6.2 LRA Reconstructions

The majority of the current vegetation reconstructions using the LRA have focused on Europe as that is where most PPEs have been estimated. REVEALS has also been applied in studies which mainly address questions on landscape openness and cultural activity on varying scales from subcontinental (Nielsen *et al*, 2012; Fyfe *et al*, 2012; Mehl *et al*, 2015; Marquer *et al*, 2014; Trondman *et al*, 2015) to landscape (Cui *et al*, 2013; Poska *et al*, 2014). Mazier *et al* (2015) and Marquer *et al* (2014) highlight the fact that due to restrictions on the taxa which can be included in the application of the LRA (PPEs available), taxonomic richness is currently beyond the scope of REVEALS and LOVE. However, there are PPEs available for most of the major common taxa in

Europe and applying the LRA can provide new insights into past spatio-temporal dynamics of vegetation composition change (Marquer *et al*, 2014).

The first REVEALS reconstruction was carried out in southern Sweden (Sugita *et al*, 2008). The results show that the proportion of open land was underestimated by pollen percentages at both Skåne and Småland throughout the Holocene (Figure 2.18). Poaceae, in particular, is under-represented in the pollen record and with conifers over-represented.

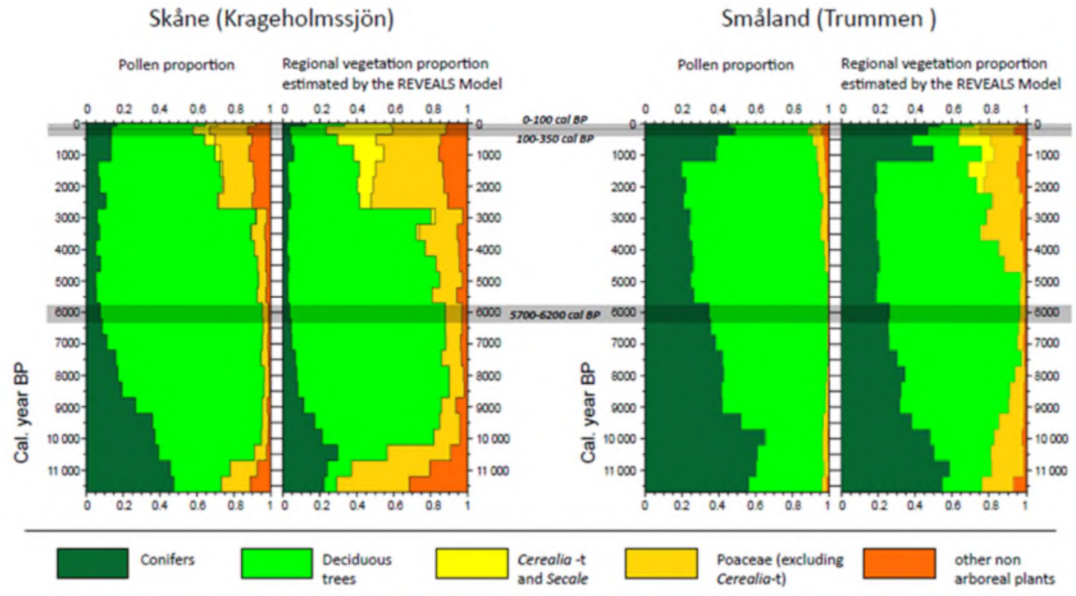


Figure 2.18: *REVEALS reconstructions of Holocene vegetation changes (right in each panel) in southern Sweden based on the pollen records (left in each panel) from Kragehomssjön (province of Skåne, left) and Lake Trummen (province of Småland, right) (from Sugita et al., 2008, modified). The selected three major time-windows studied in the LANDCLIM project are indicated. REVEALS was run with 24 pollen taxa with the pollen productivity estimates from southern Sweden (Broström et al., 2004). The taxa included in the groups "conifers", "deciduous trees", "Cerealia-t" (cereals, rye excluded) and "other non-arboreal plants" (herbs and shrubs) are the same as in Fig. 6. Secale=rye; Poaceae=grasses. (Source: Gaillard et al, 2010)*

REVEALS has been used to address large subcontinental questions particularly through the LANDCLIM project (Gaillard *et al*, 2010). The main objective of the LANDCLIM (LAND cover-CLIMate interactions in NW Europe during the Holocene) was the study of land cover-climate interactions from 6k to modern time (Strandberg *et al*, 2014). This would feed into existing vegetation and climate models (LPJ-GUESS; Smith *et al*, 2001 and RCA3; Kjellström *et al*, 2005) and be compared with palaeoclimatic data. The study region covers northwestern and western Europe north of the Alps. The main time windows of interest were 100-350 BP (Little Ice Age), 350-700 BP (Black Death), 2700-3200 BP (Late Bronze Age), and 5700-6200 BP (Early Neolithic).

They used 24 pollen taxa and the mean of all PPEs available for that taxon in the study region were used.

As part of the LANDCLIM project, 73 pollen datasets were used to reconstruct regional vegetation composition across Britain and Ireland (Fyfe *et al*, 2013). Large lakes and mires were used and where that was not possible they opted for groups of small to medium sized sites. REVEALS was run using 500 year time windows across each region. The results illustrated that landscape openness was more profound than previously thought across Britain and Ireland, particularly during the early Holocene when REVEALS estimations were compared with pollen percentages. More landscape openness was evident in Southwest England (Figure 2.19) but these pollen records were largely from coastal sites and therefore reflect the cover of these environments (Fyfe *et al*, 2013).

Although this study supports the use of REVEALS to estimate regional vegetation cover there are some spatial biases of sites used in the analysis. Fyfe *et al* (2013) acknowledge that the majority of the sites used across were largely from wetlands and uplands. Heather is also a significant component of the regional vegetation in some upland regions which wouldn’t necessarily be the case across the Midlands where there are a lack of available sites (Figure 2.19). The degree of openness may therefore be reasonable for these landscapes but not necessarily a true reflection of vegetation cover in other regions (Fyfe *et al*, 2013).

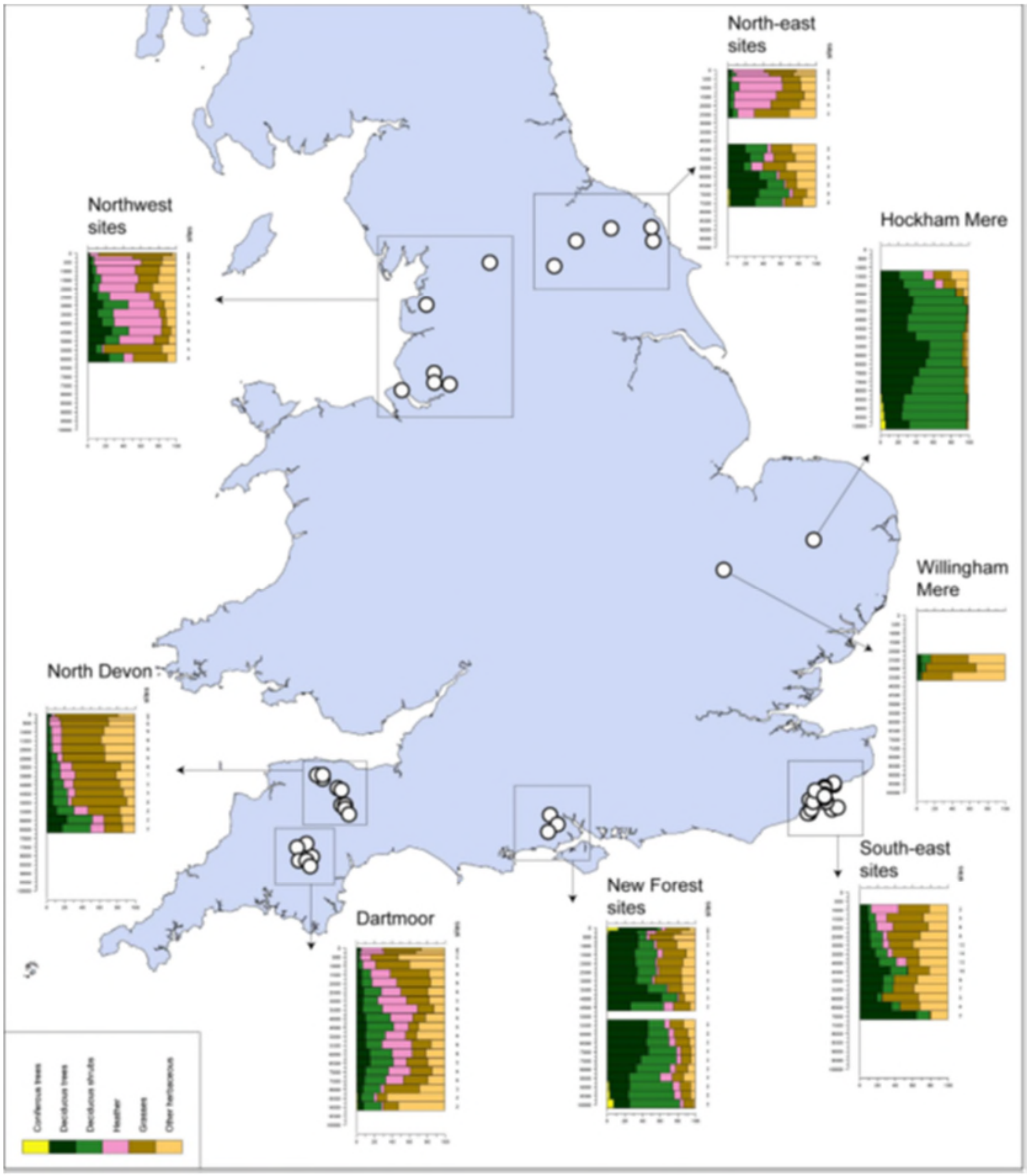


Figure 2.19: *Estimated Holocene regional vegetation cover types for England derived from REVEALS model as part of the LANDCLIM project (source: Fyfe et al, 2013)*

Trondman *et al* (2015) collated all the 636 pollen records used in the LANDCLIM project from 17 countries across north-western, western and eastern Europe. Twenty-five taxa were used and grouped into 10 plant functional types and 3 land cover types (evergreen, summer green and open). Five-hundred-year time windows were used, which were reduced around the time periods of interest outlined above (0.5k, 0.2k and 0.05k BP). The REVEALS model was run on one or more sites located within each cell of a common 1° x 1° grid. Open land was again shown to be much higher in this study compared with pollen percentages, which fit with other REVEALS studies (Gaillard *et al*, 2010; Marquer *et al*, 2013). This was particularly evident during the last 1000 years where NAP percentages reached a maximum of 40% in Germany and 50% in Britain, whereas REVEALS estimates this could actually have been as high as 60-80%.

They also found that the relationship between *Pinus* and *Picea* was inverted when using REVEALS compared with pollen percentages. When *Pinus* was dominate in the pollen percentages over *Picea* this was reversed and visa-versa when using REVEALS. This is attributed to a higher PPE for *Pinus* combined with a fall speed that is half of that of *Picea*. This leads to an under-representation of *Picea* in the pollen record. The representation of *Picea* will be important in Alaska as the increase in *Picea mariana* around 5000 cal years BP marks the development of the modern boreal forest. Understanding the extent of *Picea* cover in relation to past climate warming will also be important for future boreal forest fire projections. Trondman *et al* (2015) conclude that the application of REVEALS not only alters the views of the degree of openness across Europe during the Holocene but also the ratio of conifers and deciduous trees, which can strongly influence the interpretation of land-cover climate interactions.

The application of REVEALS to smaller landscape scale studies and has also proven to be more effective than using pollen percentages alone. Cui *et al* (2013) used LOVE to reconstruct the woodland composition throughout the Holocene to explore the relationship between vegetation-climate-fire-humans. They found between site variations in the woodland composition with *Pinus sylvestris* dominant in woodlands of Storasjö throughout the Holocene. However, *Betula* dominant at Stavsåkra during mid-Holocene and *Corylus avellana* L. during late Holocene. They compared the LOVE results with other proxies and found the reconstructions corroborated well with the plant macrofossil and beetles records. The results of the LRA at Ruppert Lake in Alaska can also be compared with the plant macrofossil record from the LAC project which will also be useful when comparing the charcoal records at Ruppert and Lake 3. This study was highlighted by the authors for having particular implications for biodiversity in the region. The dominance of *Pinus* woodland throughout the Holocene at Storasjö enabled the maintenance of floristic diversity though frequent fires. Fire regimes in the region have been heavily monitored since the nineteenth century, which has led to several species disappearing.

Reitalu *et al* (2013) used REVEALS on 18 sites in Estonia to look at the drivers of forest composition in the boreonemoral region, particularly focusing on human and climatic drivers during the late Holocene (5150-50 cal yrs BP). They compared REVEALS estimates with simulated temperatures based on palaeoclimatic models and stable isotope records as well as the landscape openness inferred from the archaeological and existing pollen records. They found that climate explained about 4 times more variation in forest composition in Estonia than human impact with climate the dominant driver in the beginning of the study period and human impact dominating following agricultural expansion. Results from Germany and Denmark suggest that the main driver of landscape openness prior to the introduction of agriculture was soil conditions and degree of continentality (Nielsen *et al*, 2012). Although human impact will not be something I will be exploring in this thesis, the results of these studies in particular illustrate the potential of combining REVEALS with palaeo and archaeological records. Reitalu *et al* (2013) also found that late Holocene cooling had a negative effect on deciduous trees such as *Tilia, Corylus, Ulmus*, *Quercus, Alnus* and *Fraxinus* and facilitated the expansion of boreal trees such as *Betula, Salix, Picea* and *Pinus.* Applying REVEALS to large lakes in Alaska may change the current understanding of the degree to which key species such as *Betula, Alnus* and *Picea* expanded during the late glacial and Holocene.

Mehl *et al* (2015) used both REVEALS and LOVE to explore and compare the local vegetation and cultural landscape development in Norway on a west-east gradient. They used one large lake for the REVEALS-based regional vegetation estimates and 3 small lakes (outer coast, inner coast and inner fjord) for the local estimates of vegetation. They found that the use of one large lake may not have been totally appropriate for this study as the landscape varied from coast to inland. The representation of some of the taxa in the regional record may have led to an over or underestimation in the local record. Poaceae for example may have been overestimated in the local diagram from the inner fjord in response to an estimation that was too low in the regional record. The results from the LRA reconstructions show a strong west-east gradient with local site specific variations which is more pronounced than in the pollen diagrams. This suggests that it is important to use several small sites to address questions within a region of varying topography (Mehl *et al*, 2015).

2.4.6.3 Summary

The application of the LRA in Europe has so far proven to be useful at exploring and re-evaluating theories of cultural activities, landscape change and development, particularly throughout the Holocene. On large sub-continental scales, REVEALS is challenging the general picture of widespread closed woodlands in the early Holocene in Europe with increasing evidence for a higher level of landscape openness. This could potentially affect the interpretation of the late glacial *Betula* rise in Alaska and the extent to which deciduous woodland developed during the early Holocene.

Trondman *et al* (2015) note that REVEALS is an approximation and does not reflect the exact actual past vegetation. Pollen productivity estimates are one of the main input parameters to the model and they are only currently available for the main plant taxa. As highlighted by Hellman *et al* (2008b) it is important to test several sets of PPEs with the LRA. Testing LOVE on small lakes in

Alaska be a way to test the reliability and robustness of the new Alaskan PPE dataset. REVEALS has also shown to be most effective at estimating cover types than individual taxa. Pollen is also only a proxy of past vegetation and pollen percentages only represent a sample of the vegetation that was present in the past. Therefore, estimates of cover maybe more useful than estimates of individual taxa cover (Trondman *et al*, 2015).

Chapter 3: Pollen Productivity Estimates

3.1 Introduction

Pollen productivity is one of the major parameters used in quantitative vegetation models (Sugita, 2007a) and obtaining accurate measurements is vital for reliable reconstructions. Absolute pollen productivity estimates are the ideal measurement of units (grains m-2yr-1; Sugita *et al*, 2010a). This is difficult to measure and long term monitoring records are not always available for a region. The majority of Pollen Productivity Estimates (PPEs) use pollen collected in moss polsters (discussed in Section 2.4.3.2) and are expressed as a dimensionless ratio relative to a reference taxon (Anderson, 1970; Broström *et al*, 2008).

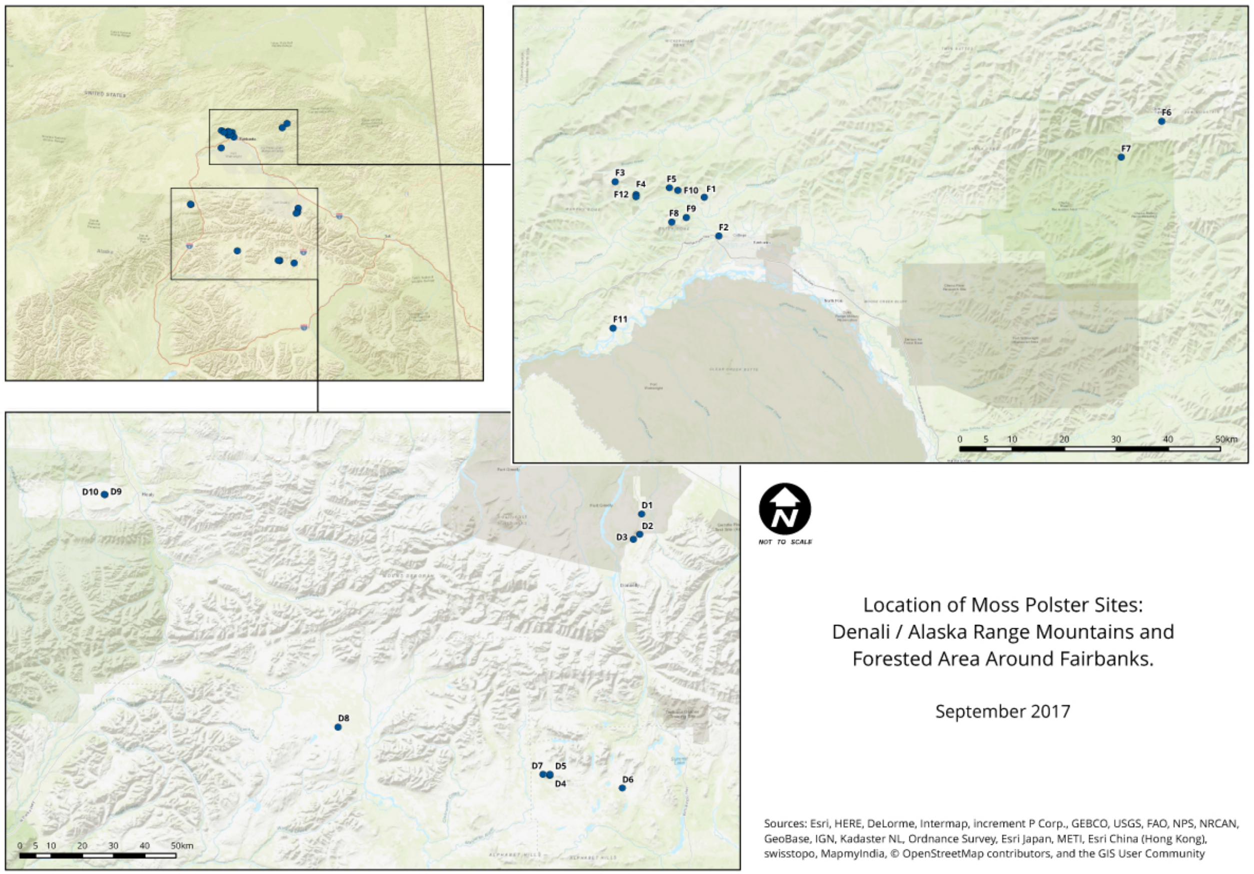
Shinya Sugita (*pers comm, Nov 2013*) suggested that PPEs used in REVEALS and LOVE reconstructions for a region should be obtained from that region whenever possible. The majority of PPE studies to date have focused on Europe and it is likely that these values are not totally suitable for the boreal forests of Alaska. This Chapter describes the first Relative Pollen Productivity Estimates for the dominant forest and tundra taxa in Interior Alaska so that they can be used within the Landscape Reconstruction Algorithm.

3.2 Methods

3.2.1 Vegetation Survey

Nine taxa (listed below) were initially chosen for PPE analysis and include several species which are found in a range of environments in Alaska. The decision was made to survey two separate biomes, mountain tundra and boreal forest. A total of 22 moss polster plots were surveyed in the summer field season of 2014. Ten plots were located in the tundra around the Alaska Range region and twelve plots were located within the interior boreal forest in and around Fairbanks (see Figure 3.1). The vegetation survey followed a combination of the protocols outlined in Bunting *et al* (2013a), von Stedingk *et al* (2008) and Twiddle *et al* (2012). The number of sites selected should be at least double the number of taxa chosen for PPE analysis, as this is a mathematical constraint of the ERV models (S.Sugita, *pers comm, June 2014*). The initial nine taxa were chosen for PPE analysis based on their occurrence and significance in many Alaskan palaeo vegetation records (discussed in Section 2.2). They were *Picea, Betula, Alnus, Salix, Populus*, Poaceae, Cyperaceae, *Artemisia* and Ericaceae.

Randomly distributed sampling across the landscape was not possible due to many areas being inaccessible. Site selection was a compromise between time, safety and suitable data collection. Sites were selected along road networks and plots were also no further than 500m from the road for safety. Stratified random sampling was adopted. The sites were chosen to represent a range of tundra and forest types that included the key taxa in the study in different mixtures (see Table 2.1 for examples). The survey was divided into 3 Sections; Zone A (10m radius around sampling point), Zone B (10-100m) and Zone C (100-1500m) according to Bunting *et al* (2013). The most detailed survey occurred in Zone A as the Prentice-Sugita model assumes the further a plant is from the sampling point the less significant the pollen contribution is to the assemblage (see Section 2.4.2.1). All identifiable species were recorded in the field and later harmonised to the same taxonomic resolution achieved in pollen analysis. Zone C was recorded and mapped using aerial photography (USGS, 2012) and Google Earth. The survey protocol carried out at each site is listed in Appendix A, Table A.1.



Location of Moss Polster Sites:
Denali / Alaska Range Mountains and
Forested Area Around Fairbanks.

September 2017

Sources: Esri, HERE, DeLorme, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, © OpenStreetMap contributors, and the GIS User Community

Figure 3.1: *Location of moss polster sites. Bottom left – 10 sites along the Denali and Richardson Highways. Top right – 12 sites around the Interior forest around Fairbanks (courtesy of Kit Allen, Atkins)*

3.2.1.1 Tundra Plots

A suitable patch of moss was identified within the plot, within the middle of a recognisable vegetation community (Figure 3.2) and a central point was located. Five samples of moss were taken from within a 50cm radius of the central point, placed in zip lock sample bags, labelled and doubled bagged. Photographs were taken of each central sampling point along with four landscape photographs looking N, S, E and W. Four quadrats were placed around the centre of the sampling point (Figure 3.3) and percentage cover for each plant species was recorded, along with cover of non-pollen producing surfaces. If the ground flora was particularly rich an additional 1-2 random quadrats were thrown in each vegetation community present.

Figure 3.2: *An example of a moss patch within a shrub Salix vegetation community (Plot D5)*

A tape measure and flags were used to map out 8 transects (10m) from the sampling point extending out in each cardinal and inter-cardinal direction (Figure 3.3). Ground flora present was recorded at points every 1-2m (depending on floristic diversity) along each transect. The 8 transects set out in Zone A were extended out to Zone B (10-100m). Vegetation community changes were recorded along each transect in addition to individual trees or shrubs.

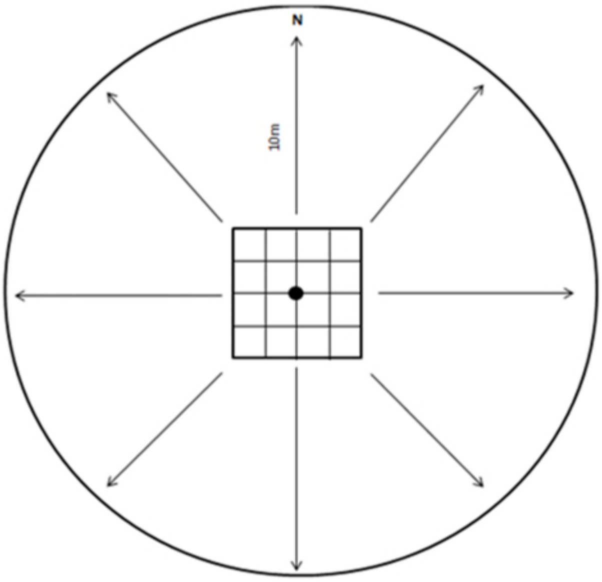


Figure 3.3: *Sampling strategy for Zone A (0-10m radius)*

3.2.1.2 Forest Plots

The survey protocol for the selection of moss, photography and recording vegetation cover around the central point was identical to that undertaken at the tundra plots. At some of the forest plots it was only possible to collect samples from pleurocarpous mosses on branches and the forest floor, therefore the samples contained an unknown number of year's collection of pollen. The pollen-vegetation models currently only take into account wind above the canopy as the main mode of pollen transport within forested landscapes and do not account for trunk space transport. The recording methodology for ground flora was therefore modified at each plot. If the ground flora was particularly rich then it was recorded in the same way as the tundra plots. If diversity was particularly low or leaf litter was the dominant ground cover, ground flora was only recorded in each cardinal direction from the sampling point.

As canopy cover was deemed the most important in the forest plots, the point centred quartered (PCQ) method (Cottam and Curtis, 1956) was adopted to record the arboreal component of the vegetation and to gather basal density data. PCQ was carried out at a distance of 5m from the sampling point in each inter-cardinal direction. Using a compass the four quarters were identified (N-E, E-S, S-W and W-N). The nearest tree (minimum circumference 14cm) was located in each quarter. The tree species, distance from the sampling point (surveyor) and diameter at breast height (DBH) was recorded to the nearest decimal point. A total of 16 trees were recorded in Zone A.

Four transects were set out from 10-100m (see Figure 3.4). The PCQ method was used along each transect with a spacing suitable for the stand density. Initially the sampling spacing was set to 20m, 40m, 60m, 80, and 100m but this was too time consuming with only two surveyors in the field so the spacing was reduced to 20m, 40m and 75m. This spacing was continuously monitored in the field and any obvious changes in community composition were also recorded. As the vegetation is distance weighted and less weighting is given to trees and plants further away from the sampling point this sample spacing was deemed suitable.

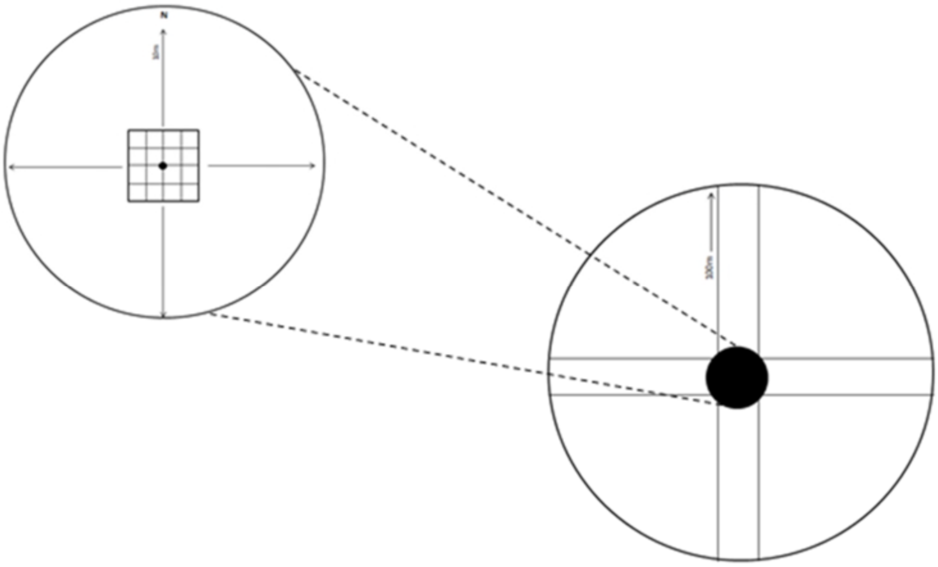


Figure 3.4: *Sampling strategy for Zone A (0-10m) and Zone B (10-100m) in the forest plots (adapted from Twiddle et al, 2012)*

The raw vegetation data were entered into Excel and prepared for later use with applications in the HUMPOL suite (see Section 3.2.3). Percentage cover of species in rings was calculated from the quadrat and count data for the 10m zone in Denali dataset. Zone B (100m) was entered as presence of vegetation community every 1m along each cardinal and inter-cardinal transect. This data were then used to create a hand drawn map of the community changes along each transect.

For the forest plots the ground flora data were calculated as percentage cover in case it was needed at a later stage but it was not included in Survey Manager (see Section 3.2.2) for PPE calculations. Calculations carried out on the PCQ data are shown in Table 3.1. Basal area is related to canopy cover in the same manner that the vertical crown projection of an individual tree is a function of its stem diameter at breast height (DBH) (Smith *et al*, 1992). Percentages of basal area were calculated for each species within each ring and this was then used to assume canopy cover.

Mean distance per tree	Σ all distances recorded / *n* of trees
Mean area per tree	Mean distance^2
Density per ha	(1/*n* of trees)*10000
Basal area of individual trees	$\frac{\sqrt{tC}}{4\ x\ 3.142}$
Basal area per tree	Σ all basal areas / *n* of trees
Basal area per ha	BA per tree x density per ha
Basal area in 10m plot	BA per ha x (314/10000) Plot area 314cm^2
Basal area in 10-30m ring	area of 2513m^2 (BA per ha x (2514/10000)
Basal area in 30-50m ring	area of 5027.2 m^2 (BA per ha x (5027.2/10000)
Basal area in 50-100m ring	area of 23565 m^2 (BA per ha x (23565/10000)

Table 3.1: *Point centred quartered (PCQ) calculations for the Forest sites*

3.2.2 Vegetation Analysis

Vegetation Survey Manager v.2.0 (Middleton, unpublished program) is an application available from the University of Hull to simplify the storage of spatial vegetation survey data up to 100m radius compared with a complex GIS application. It also allows the user to distance-weight the vegetation data. In Survey, Zone A is characterised by 21 fixed quadrats. The survey protocol in Alaska differed from that outlined in Bunting *et al* (2013) slightly so the data had to be adapted to fit the input format for Survey Manager. The percentage data of vegetation cover in rings was used instead of individual quadrat data for the tundra sites (apart from the central quadrat which could remain the same). The percentages of the species from the PCQ basal area calculations were entered into the first four quadrats around the central quadrats for the forest sites. The original ring script (distance of quadrats from centre point) was adjusted to account for the sampling distances used at the tundra and forest sites (Appendix A, Table A.2). The community map for Zone B was firstly hand drawn in fine black pen and then scanned at 100dpi greyscale and saved as a .bmp file. Communities are assigned to the uploaded map to create a community grid. Survey Manager calculates the distance-weighted plant abundances up to 100m. Fall speeds are required to define the Stepwise taxon-specific distance-weighting (Sutton-Prentice). Fall speeds were taken from existing literature (Table 3.2).

Pollen taxon	**Fall speed of pollen *vg***	**Source**
Picea	0.056	Binney *et al* (2011)
Betula	0.024	
Alnus	0.021	
Populus	0.025	
Salix	0.022	
Poaceae	0.035	
Cyperaceae	0.035	
Ericales	0.038	
Larix	0.126	Eisenhut (1961)
Asteraceae	0.051	Crackles Project (J.Bunting)
Artemisia	0.019	
Caryophyllaceae	0.053	
Epilobium	0.098	
Potentilla	0.018	
Fall speeds were not available from the literature for the taxa listed below and fall speeds could not be calculated using Stokes' Law (Gregory, 1973) for some of the taxa as a reference collection was not available for all the taxa and some taxa were also not present in the collected samples. 0.025 was set for all of these taxa as advised by J.Bunting. *Viburnum*, *Mertensia*, *Valariana capitat*, *Linnaea borealis*, *Sedum*, *Cornus canadensis*, *Diapensia lapónica*, *Shepherdia canadensis*, *Equisetum arvense*, *Pedicularis capitata*, *Polygonium bistorta*, *Aconitum delphinifolium*, *Anemone*, *Delphinium*, Rosaceae, *Rosa acicularis*, *Rubus*-type, *Rubiaceae*, *Geocaulon lividum*, *Viola*		

Table 3.2: *Fall speeds of pollen*

Aerial photographs of each of the 22 sites was downloaded from the US Geological Survey Earth Explorer online suppository (USGS, 2012). Google Earth was used to map the 1500m radius around each site and the vegetation communities were hand traced from the aerial photographs. The communities assigned to all of the 22 plots in Zone C are listed in Appendix A, Table A.3. The species percentage in each community was assigned from a combination of comparable communities surveyed in the field, expert local knowledge (M. Edwards *pers comm, July 2014*) and confirmation of dominant species from the Alaskan Vegetation Classification (Viereck *et al*, 1992). The map was marked up in fine black pen and scanned at 100dpi greyscale and saved as a .bmp file. Each map was uploaded into Community Map Builder (Middleton, unpublished program) along with grid extents for georeferencing and communities assigned. The output files are in IDRISI format for the use in the HUMPOL applications discussed below.

3.2.3 HUMPOL

HUMPOL (Hull Method of POLlen simulation) is a suite of applications for modelling pollen dispersal and deposition (Bunting and Middleton, 2005). Using Sutton's equation for the diffusion of small particles from a ground level source (Prentice, 1985; Sutton, 1953) the suite models pollen dispersal from vegetation sources and pollen deposition at a sampling location. There are four aspects of the modelling approach encoded in HUMPOL, outlined in Bunting and Middleton (2005):

(1) A cellular source approach is used rather than a ring source approach used in previous modelling approaches (POLLSCAPE, Sugita, 1994). This allows pollen sources to be treated as two-dimensional rather than one-dimensional.

(2) Vegetation maps define the landscape. Maps can vary with extent and resolution 'nested' together allowing for variation in vegetation composition at a variety of scales to be incorporated into the simulation.

(3) Variable windroses can be included in the simulation as the application allows for an additional weighting factor to be applied to each source cell, varying according to its orientation relative to the deposition target.

(4) The amount of pollen reaching a lake surface is computed by taking the centre of each cell if the water surface as a deposition target. The application (PolFlow and PolLake) produces two outputs based on the pollen dispersal models developed by Prentice (1985) and Sugita (1993), see Section 2.4.2.1.

Four applications were used from the HUMPOL application suite to create the distance-weighted plant abundance data for the 1500m radius (Zone C) and PPEs; PolSack, PolFlow_4, PolLog and PolERV (see Table 3.3). A more recent version of PolFlow is available from the University of Hull (PolFlow_0, 2011); however, there were unknown errors occurring with the input files created through Community Map Builder and PolSack when using this version. It was therefore decided that PolFlow_4 would be used for any subsequent analysis.

Application	Description
PolSack	The HUMPOL data collection editor. Each HUMPOL data collection is divided into seven Sections: TAXA COMMUNITIES SAMPLE POINT SETS RINGS WIND ROSES SCRIPTS METADATA The output is a .hum file which can used with Survey Manager and PolFlow.
PolFlow_4	PolFlow allows for the simulation of pollen assemblages at single points. When a data collection is loaded along with a community grid, sets of rings can be defined. Once the data is loaded various parameters can be calculated including pollen loading, community composition and percentage of each taxon within each ring. Output is to a “log” text file which can be used for later analysis in PolLog.
PolLog	PolLog organises the output from PolFlow for use with other applications in the suite. PolLog allows for the selection and display of different parts of the PolFlow file. This data can then be extracted into Excel to calculate cumulative distance weighted plant abundances for each taxon at each site.
PolERV	PolERV carries out ERV analysis using the same calculation routines as S.Sugita used in erv-v6.exe. All the data for the analysis is entered in a single file which contains all the distance-weight plant abundances and pollen counts for each site within that dataset.

Table 3.3: *Components of the HUMPOL application suite used to create distance weighted plant abundances for the 1500m radius (Zone C) and Pollen Productivity Estimates (Bunting and Middleton, 2005 and Middleton, unpublished)*

3.2.4 Laboratory Analysis

Five moss polsters samples (within 0.5m basin size) were taken from the centre of each of the 22 plots. Approximately one third of the moss from each of the 5 bags collected at each site was amalgamated to create one representative sample for the plot. The remainder of the moss was double bagged, sealed and stored at 4°C for further analysis if required. Each amalgamated sample was thoroughly mixed in a large beaker of distilled water prior to sieving. The sample was washed through a 180µm sieve and centrifuged at 3000rpm as many times as required to remove the water. 1cm^3 of sediment was sub-sampled from each sample for pollen analysis. The sieved residue was placed into small sample bags and stored at 4°C. Pollen preparation following standard methods (Moore *et al*, 1991) including sieving, HF treatment and acetolysis. The residues were mounted in silicon oil. Pollen was counted using a Nikon Eclipse 80i and a Nikon Eclipse E200 microscope. A minimum of 1000 total land pollen (TLP) grains were counted where possible, including *Alnus* and Cyperaceae as these taxa were to be included in subsequent pollen productivity estimations, but excluding aquatics and spores. Some of the samples contained very high pollen counts for *Betula*. In order to assess if less productive taxa had been swamped by *Betula* pollen, additional top up counts were carried out on D2, D3, D9, F1, F2, F5 and F9 where pollen counts for *Betula* were extremely high.

3.2.5 Pollen Data Analysis and ERV Models

Scatterplots were created in Excel to assess the goodness of fit between the pollen and vegetation data. This was done for all sites in the Denali and Forest datasets and raw pollen counts were plotted against distance weighted plant abundance (dwpa) at 1500m for all three distance weightings. Regression analysis was carried out and the data was screened to determine which taxon groups would be included in the ERV analysis.

Estimates of pollen productivity and the RSAP were obtained using POLERV. The pollen counts and the dwpa (25m increments) from each site provided the input to run ERV Sub-models 1, 2 and 3. Cyperaceae was used as the reference taxon for the Denali dataset and *Picea* was used as the reference taxon for the Forest dataset. These two taxa where chosen as they produced a good spread in both the pollen and plant abundance data. The ERV models estimate the linear relationship between pollen and vegetation data. They differ in terms of how background pollen is defined (Sugita, 1994; see Section 2.4.3.3). The outputs of each ERV run consist of likelihood function scores, alpha (α) and *z* values. Likeihood function scores (LFS) represent the goodness of fit of vegetation to pollen data at each ring distance (25m) from the sample point (Parsons and Prentice, 1981; Prentice and Parsons, 1983; Sugita, 1994). These scores were plotted against distance and the graph was visually inspected to decide the point at which an asymptote was reached. This is the distance at which the relationship no longer improves and the RSAP is reached (Sugita, 1994). Once the ERV models have adjusted the vegetation (ERV sub model 1) or the pollen proportions (ERV sub models 2 and 3), a new adjusted relationship between the vegetation and pollen is produced. The alpha values produced by the ERV sub model at each distance represent the slope (PPEs) and the *z* values represent the intercept (background component) of this linear relationship. Pollen Productivity Estimates are taken from the RSAP as the pollen-vegetation relationship in theory does not improve past this point. At this distance PPE values do not change significantly (Broström *et al*, 2008). To account for any variation which may occur, the mean was taken of all alpha values from this distance to the extent of the survey area for the final PPE values.

3.3 Results

3.3.1 Pollen Analysis

Twenty-six taxa were recorded in total across all 22 sites; 6 arboreal taxa (including both tree and shrub species), 1 shrub and 19 herb taxa. The full counts are listed in Appendix A, Table A.4. Figures 3.5 and 3.6 show the pollen percentages for the nine taxa chosen for the initial ERV analysis.

The majority of the samples from the Denali dataset are dominated by *Betula* and *Alnus. Betula* percentages are particularly high in samples from D1, D2 and D3 accounting for over 60% at each site, followed by D6, D9 and D10 with values between 40-50% (Figure 3.5). *Betula glandulosa* shrub was most common at these sites within the 100m survey zone and well recorded within the communities in the 1500m zone. *Betula* pollen was not only present in every sample in the Denali data set but fairly high percentages were recorded at D7 and noticeable values at D4 and D5. *Betula* was not recorded in the vegetation survey at any of these sites and it was not identified as a community in the 1500m zone. This was also the case with *Alnus* at D1, D4, D5 and D6. *Alnus* is recorded over 40% at D4 which is a very high value when it was not recorded in the vegetation. *Alnus* reaches its highest values of 55% at D7 but it is only recorded as a minor component in the wider 1500m and absent from the 100m survey.

Picea is recorded at low values in each sample <10% and peaks in D1 where it was recorded most frequently in the 100m survey. *Populus* pollen is absent from most sites with occasional grains occurring at D4, D5, D8 and D10. *Salix* and Ericaceae are present but in low values across most sites with a peak in Ericaceae at D8. Artemisia values spiked at D5 and it was recorded most frequently in the 100m radius at this site. All other herbs were recorded at low values at most sites.

The majority of the Forest dataset is dominated by *Betula* pollen. Values over 60% are recorded at F1, F2, F4, F5, F9 and F12 and between 25 and 55% at F6, F7, F8, F10 and F11. *Betula* was well represented in the vegetation and recorded in the 100m radius at every site apart from F3. Here the pollen sample is also completely dominated by *Picea* at 85%. This was to be expected at this site since *Picea mariana* was recorded at over 90% vegetation cover in the 100m zone. What is surprising is the representation of *Alnus* in the Forest dataset compared with Denali. *Alnus* was better represented in the vegetation in the Forest, but with the exception of F1, F8 and F11 pollen percentages were generally lower. All other trees, shrubs and herbs are recorded at low values across all of the Forest sites.

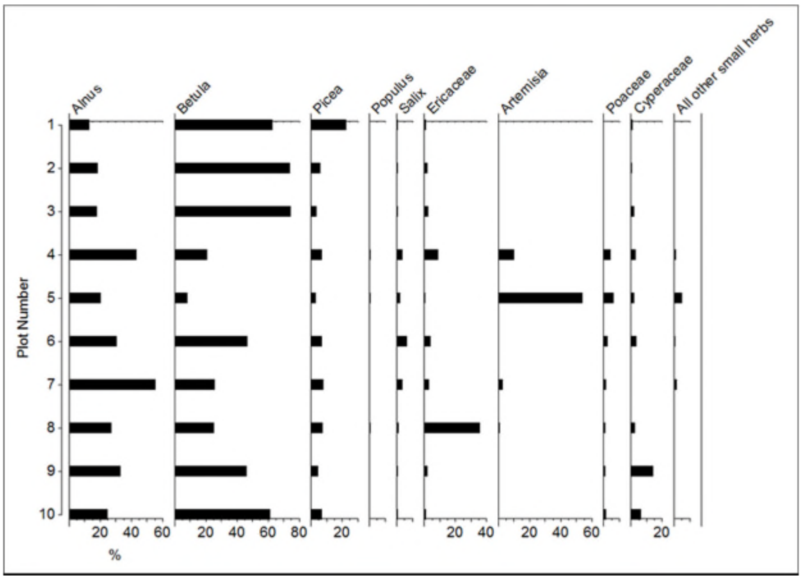


Figure 3.5: *Pollen Percentages from the Denali moss polster sites of the initial 10 taxa chosen for ERV Analysis*

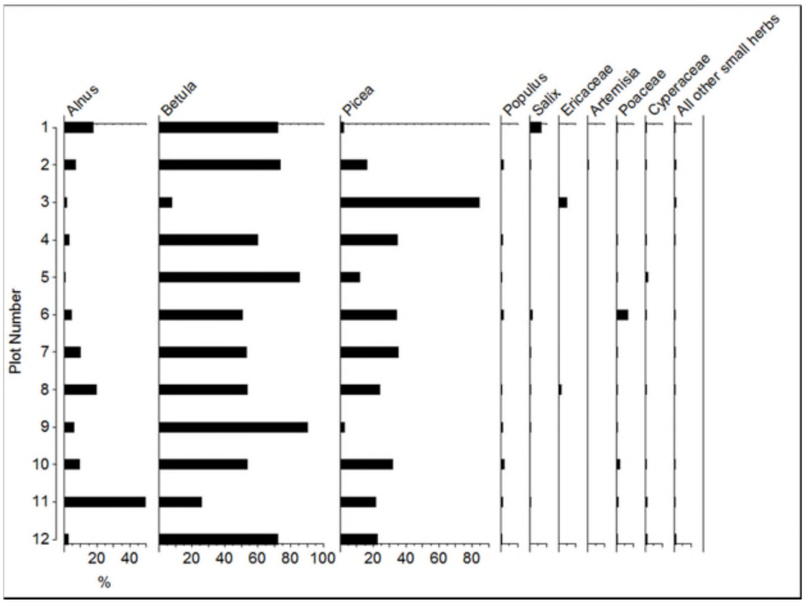


Figure 3.6: *Pollen Percentages from the Forest moss polster sites of the initial 10 taxa chosen for ERV Analysis*

3.3.2 Pollen-Vegetation relationship

Figures 3.7 and 3.8 show the scatterplots for all Denali and Forest sites when using Sutton-Prentice distance weighting. Appendix A, Table A.4 shows the results of regression analysis carried out in Excel from all the raw pollen-vegetation scatterplots.

The criteria adopted for screening the taxa was dependent on the results from the scatterplots and regression analysis. If the taxon was present in less than 7 out of 10 of the pollen or vegetation data it was excluded from any further analysis. This left *Betula, Salix*, Ericaceae, Cyperaceae and Poaceae to go forward for ERV analysis in the Denali dataset. *Betula* shows the best correlation between pollen and vegetation and produced the highest R^2 value and a P value <0.05. *Salix* displays some variation and was better represented in the vegetation than the pollen and this was also the case for Poaceae with a single high pollen outlier in each of the datasets. It was not possible to obtain a significant relationship for all taxa to the P=0.05 level without removing sites. In order to run POLERV, all taxon groups are required to run simultaneously, therefore any outliers existing in one taxon group would therefore have to be excluded from all taxon groups (Duffin and Bunting, 2008). As there were only 10 sites in this dataset it was decided that only taxa would be removed from the screening process and not sites.

The same criteria were adopted for the forest dataset. Three taxa (*Artemisia*, Cyperaceae and Ericaceae) were removed that were present in less than 70% in both pollen and vegetation (8 out of 12 sites). This left *Alnus, Betula, Picea, Populus, Salix* and Poaceae for further analysis. *Betula* again showed a particularly good correlation in the pollen and vegetation data, followed by *Picea* and *Populus*. It was not possible to obtain a significant relationship for all the taxa to the P=0.05 level. However, significant relationships were produced by *Betula, Picea, Populus* and *Salix* for all three distance weighting methods (Appendix A, Table A.5).

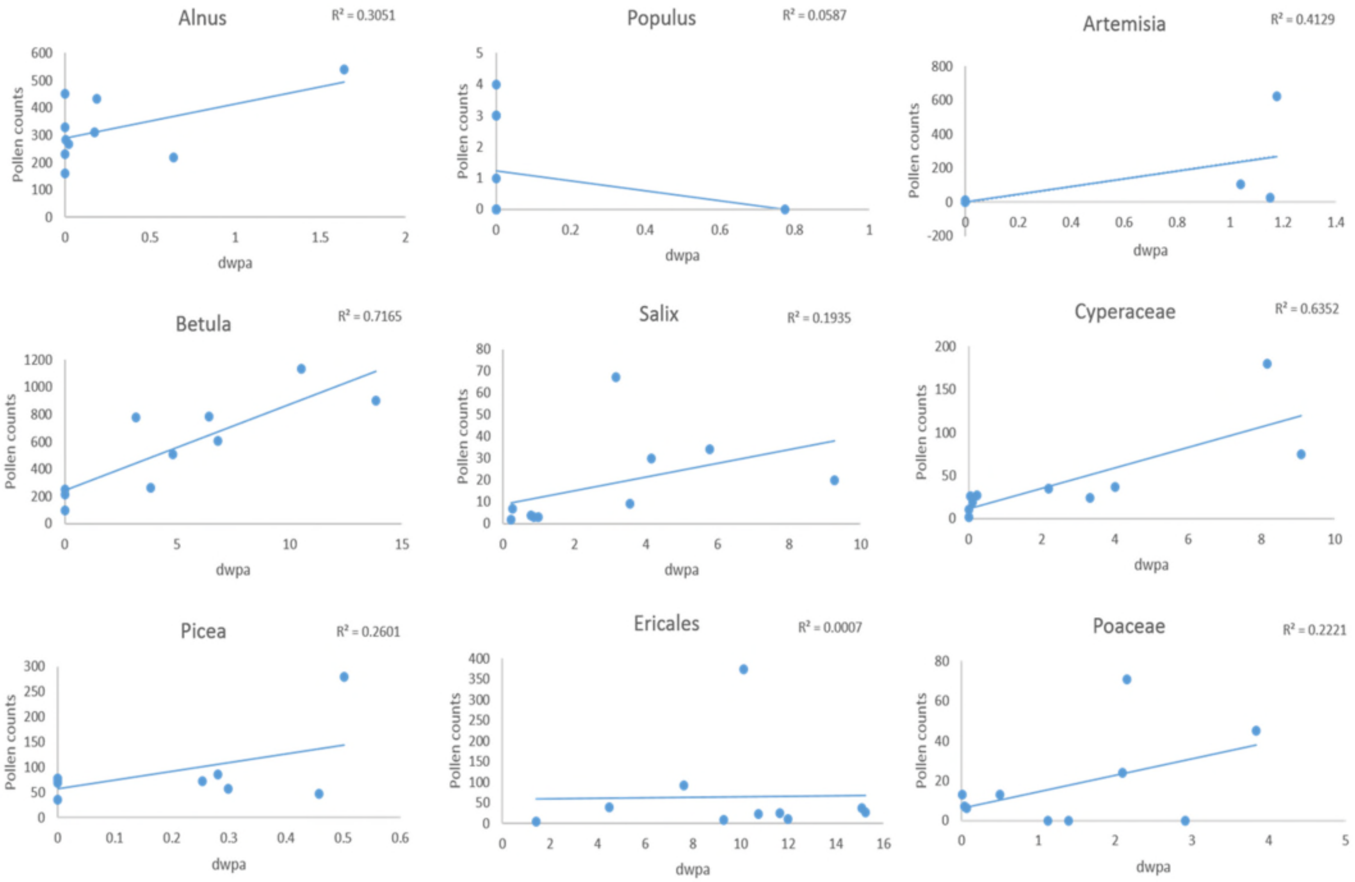


Figure 3.7: *Scatterplots of pollen and distance weighted plant abundance (DWPA) at 1,500m from the pollen sampling site for the Denali sites using Sutton-Prentice distance weighting method. R*^{2} *values are included.*

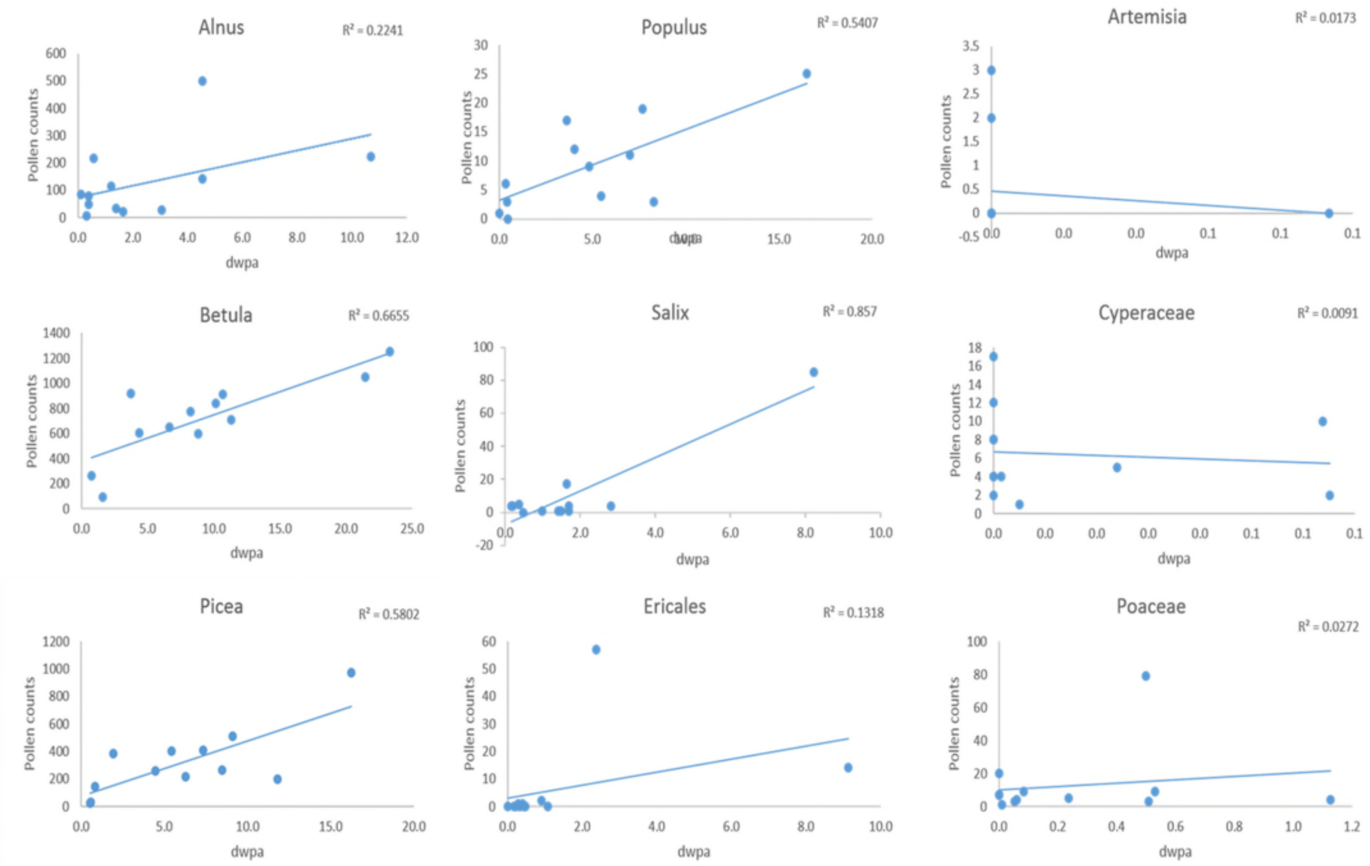


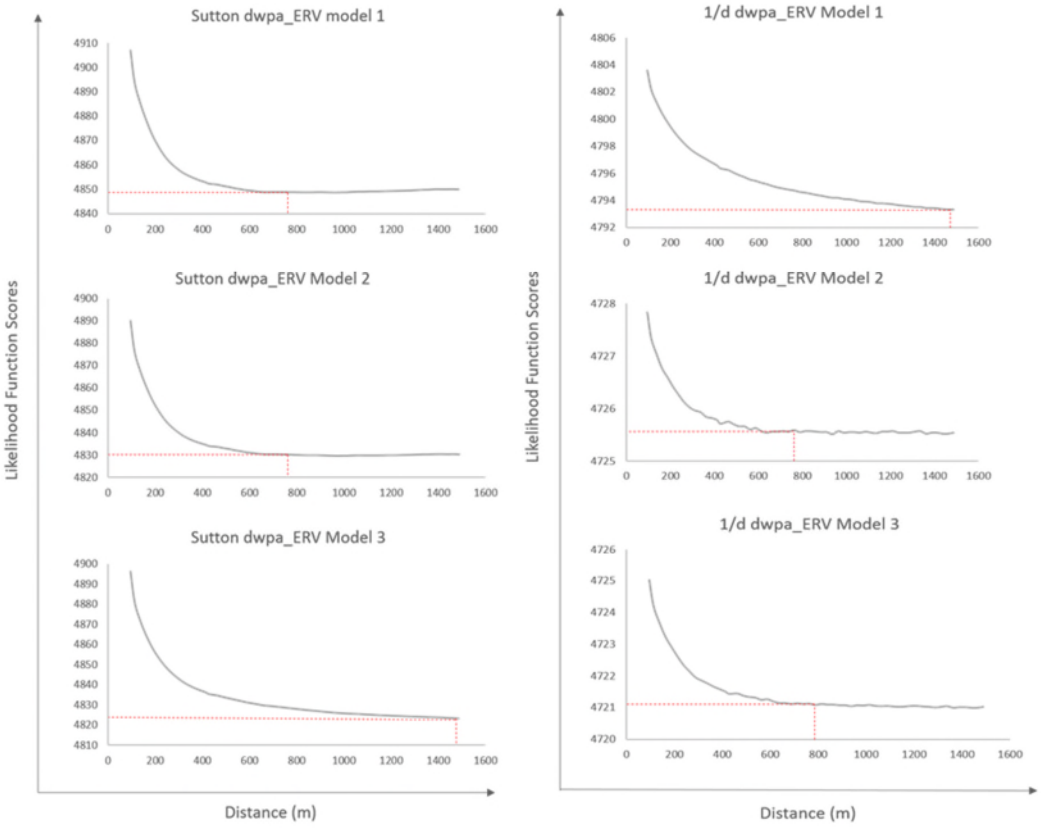
Figure 3.8: *Scatterplots of pollen and distance weighted plant abundance (DWPA) at 1,500m from the pollen sampling site for the Forest sites using Sutton-Prentice distance weighting method.* R^2 *values are included.*

3.3.3 Relevant Source Area of Pollen

The RSAP is defined as the area around the basin beyond which the correlation between pollen loading and distance-weighted plant abundance does not improve (Sugita, 1994). Theoretically, the RSAP is the smallest spatial unit of vegetation that can be detected using pollen assemblages from similarly sized sites in a given region (Hjelle and Sugita, 2012). ERV analysis was run for the Denali and Forest datasets using each of the three distance-weighting methods using ERV Sub-models 1, 2 and 3. The likelihood function scores (LFS) for each model run were plotted against distance (Figures 3.9; 3.10; 3.11 and 3.12). The point at which the curves reach an asymptote is where the RSAP has been reached.

3.3.3.1 Denali RSAP

Figure 3.9 (a, b) show the graphs produced using Sub-models 1, 2 and 3 for Sutton-Prentice and 1/d distance-weighting methods for the Denali dataset. The LF scores reach an asymptote between 750-800m for Sub-models 1 and 2 when using the Sutton-Prentice distance-weighting. Sub-model 3 shows a gradual decline out to 1500m. When 1/d distance-weighting is applied Sub-model 2 and 3 reach an asymptote c. 800m. Sub-model 1 shows a steady decline out to 1500m. Using $1/d^2$ distance-weighting the LF scores did not reach an asymptote with any of the ERV sub models and this distance-weighting method was deemed not appropriate for the Denali dataset. (Figure 3.10). In theory the lower the likelihood function scores, the higher the probability of obtaining a good fit between the data and model (Sugita, 1994). Sub-model 1 produces the highest scores in all three distance-weighting methods and gives the worst fit of the model to the data. Sub-model 3 with 1/d distance-weighting produces the lowest likelihood function scores.



(a) *(b)*

Figure 3.9: *Likelihood Function Scores for the pollen-vegetation data where (a) Sutton-Prentice distance weighting is applied and (b)1/d distance weighting for the Denali dataset. All three ERV Models are used and dotted red lines mark the visual interpretation on the RSAP.*

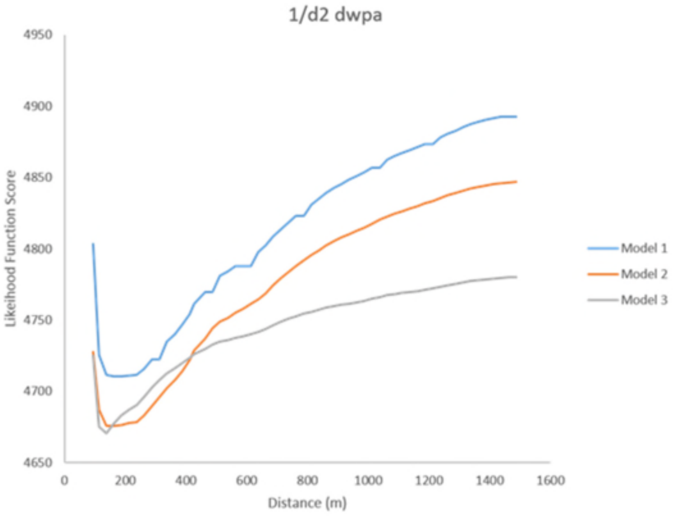


Figure 3.10: *Likelihood Function Scores for the pollen-vegetation data where 1/d^2 distance weighting is applied for the Denali dataset.*

3.3.3.2 Forest RSAP

Figure 3.11 shows the graphs produced for Sub-models 1, 2 and 3 using the Sutton-Prentice distance-weighting method. The LFS curves do not show the same gradual pattern of reaching an asymptote as they do with the Denali dataset and there was no clear asymptote reached. The curves for all three distance-weighting methods produce a rapid decline within the first 100m. However, the LFS reach the minimum 100-200m using Sub-models 1, 2 and 3 with the Sutton-Prentice distance-weighting method. The rapid decline could be an artefact of vegetation sampling design, discussed in detail below. Sub-model 1 produces the highest scores in all three distance-weighting methods and gives the worst fit of the model to the data. The likelihood function scores did not reach a clear asymptote when using 1/d or 1/d^2 distance-weighting methods (Figure 3.12 a, b). The LF scores reach a minimum between 800-1000m with 1/d distance-weighting. The curves produced using Sutton-Prentice distance-weighting suggest this method as the best fit for the Forest dataset. 1/d and 1/d^2 distance-weighting methods were not used in any further analysis.

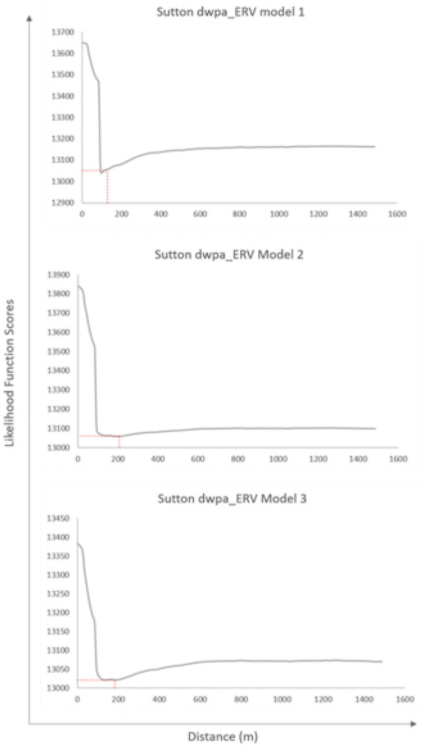
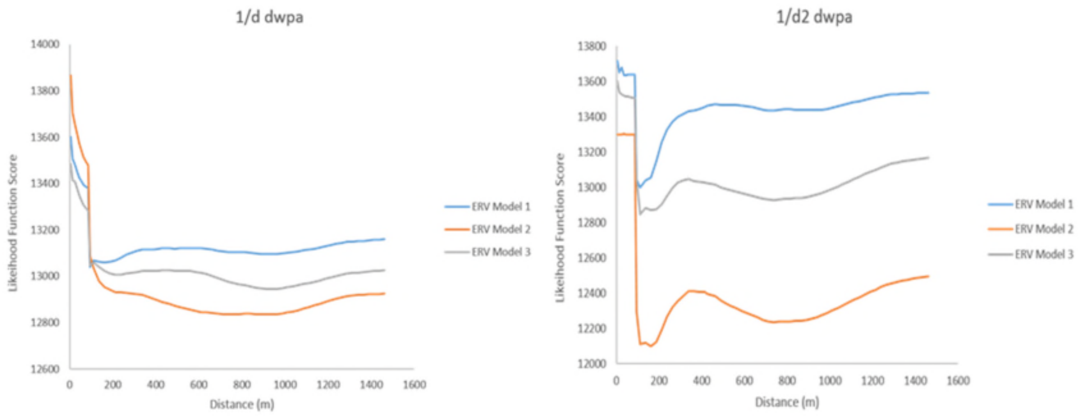


Figure 3.11: *Likelihood Function Scores for the pollen-vegetation data where Sutton-Prentice distance weighting is applied for the Forest dataset. All three ERV Models are used and dotted red lines mark the visual interpretation on the RSAP.*



(a) *(b)*

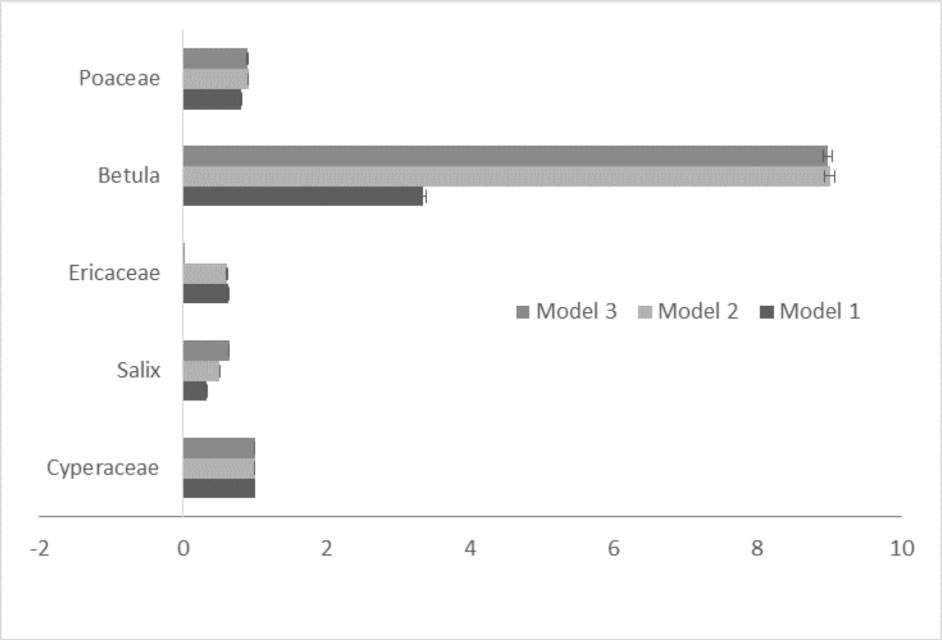
Figure 3.12: *Likelihood Function Scores for the pollen-vegetation data where (a) 1/d distance weighting is applied and (b)1/d^2 distance weighting for the Forest dataset.*

3.3.4 Pollen Productivity Estimates

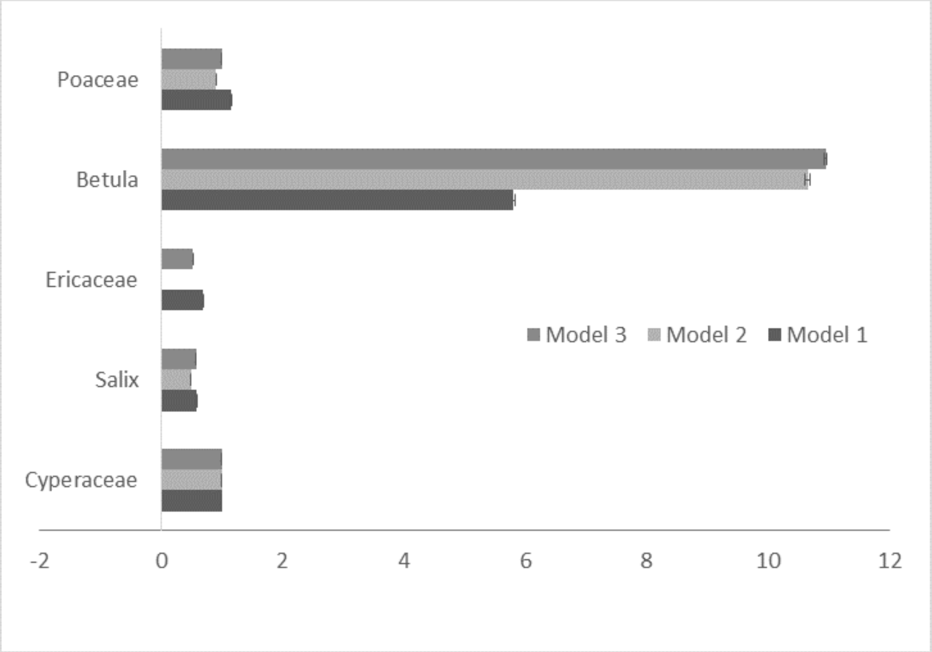
The first iteration of PPEs discussed below are in relation to the reference taxon used in the original analysis using POLERV. Cyperaceae is used as the reference taxon for the Denali dataset and *Picea* as the reference taxon for the Forest dataset.

3.3.4.1 Denali PPEs First Iteration

The PPEs for the Denali dataset are shown in Figure 3.13. As a RSAP was not reached using 1/d^2 distance-weighting, this method was excluded from any further analysis. All of the PPE results from the ERV analysis are listed in Table 3.4 along with standard deviations. The PPEs are fairly similar when comparing the distance-weighting methods used. PPEs are slightly higher when using 1/d for most of the taxa, but particularly *Betula* where values differ from 3.35 (Sutton-Prentice) and 5.81 (1/d) using ERV sub model 1. The values produced for *Betula* are much lower when sub model 1 is used compared with sub models 2 and 3 where estimated values double using both weighting methods. Overall *Betula* produced the highest PPEs in this dataset. Poaceae produced consistent PPEs with all three ERV sub models with values close to 1. Ericaceae and *Salix* values are all low and estimated below 1.



(a)



(b)

Figure 3.13: *Pollen Productivity Estimates for Denali using (a) Sutton-Prentice distance-weighting and (b) 1/d distance-weighting methods, calculated using all 3 ERV Models. Cyperaceae is set to unity, and the PPE values are related to Cyperaceae. Standard deviation is indicated by the error bars.*

3.3.4.2 Forest PPEs First Iteration

The PPEs for the Forest dataset are shown in Figure 3.14 using the Sutton-Prentice distance-weighting method. The PPEs between the ERV sub models are fairly comparable with the exception of *Betula*. The PPEs for *Betula* are lower using all three sub models compared with the values produced in the Denali dataset. *Populus, Salix* and Poaceae values are low and estimated below 1 with all 3 models. *Alnus* PPEs are surprisingly low (around 1) compared with other values produced across Europe.

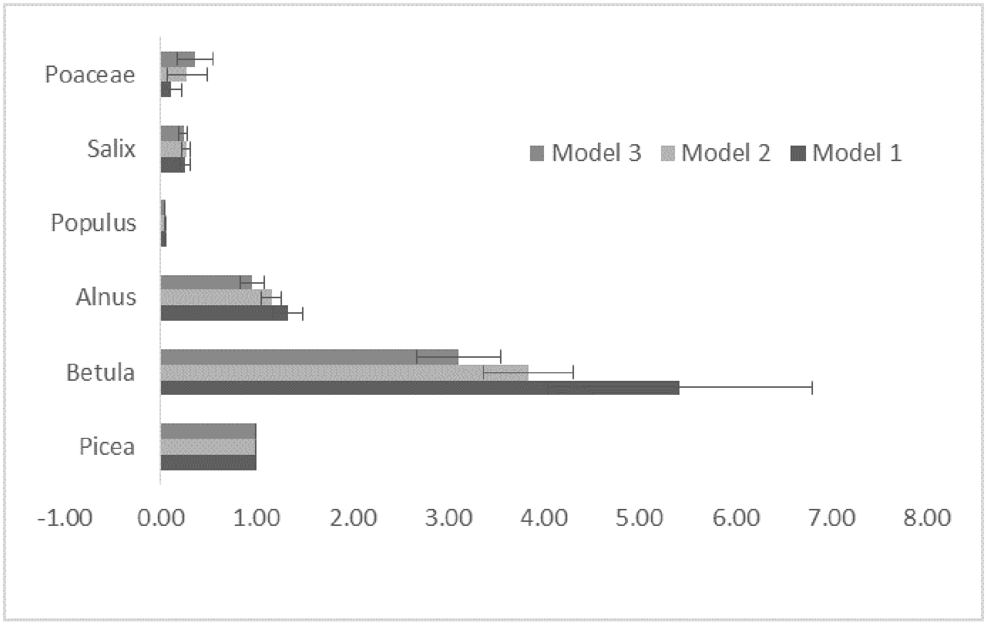


Figure 3.14: *Pollen Productivity Estimates for the Forest using Sutton-Prentice distance-weighting, calculated using all 3 ERV Models. Picea is set to unity, and the PPE values are related to Picea. Standard deviation is indicated by the error bars.*

dwpa	Taxa	ERV Model 1	s.d	ERV Model 2	s.d	ERV Model 3	s.d
DENALI							
Sutton-Prentice	*Betula*	3.35	0.04	9.02	0.07	8.98	0.07
	Salix	0.33	0.01	0.51	0	0.64	0.01
	Ericaceae	0.63	0.01	0.61	0.01	0	0
	Poaceae	0.81	0.01	0.91	0.01	0.90	0.01
	Cyperaceae	1.00	0	1.00	0	1.00	0
1/d	*Betula*	5.81	0.03	10.65	0.04	10.95	0.02
	Salix	0.59	0.00	0.49	0.00	0.58	0.00
	Ericaceae	0.70	0.00	0	0.00	0.53	0.00
	Poaceae	1.16	0.01	0.91	0.01	1	0.07
	Cyperaceae	1.00	0	1.00	0	1.00	0
FOREST							
Sutton-Prentice	*Betula*	5.42	1.38	3.85	0.47	3.12	0.44
	Salix	0.26	0.05	0.27	0.04	0.24	0.04
	Alnus	1.33	0.15	1.16	0.10	0.96	0.12
	Picea	1.00	0	1.00	0	1.00	0
	Populus	0.06	0.01	0.05	0	0.04	0
	Poaceae	0.11	0.11	0.28	0.21	0.36	0.18

Table 3.4: *Pollen Productivity Estimates for Denali and Forest datasets. Shading = the combination of models and distance-weighting method that achieved the lowest likelihood function scores for that dataset.*

The second iteration of PPEs discussed below have been recalculated to be related to Poaceae (reference taxon = 1) for dataset comparison and to make comparisons with European values (Table 3.5). The values for Denali stayed the same using ERV Model 3 as the PPE for Poaceae was already set to 1 using this model outputs of alpha values. The PPE values for the Forest taxa have all increased and these are discussed further below.

DENALI		ERV model 3	s.d
1/d	*Betula*	10.95	0.02
	Salix	0.58	0.00
	Ericaceae	0.53	0.00
	Poaceae	1.00	0.07
	Cyperaceae	1.00	0
FOREST			
Sutton-Prentice	*Betula*	8.7	0.44
	Salix	0.67	0.04
	Alnus	2.7	0.12
	Picea	2.8	0
	Populus	0.11	0
	Poaceae	1.00	0.18

Table 3.5: *Pollen Productivity Estimates for Denali and Forest datasets recalculated to relate to Poaceae (reference taxon = 1)*

3.4 Discussion

3.4.1 Relevant Source Area of Pollen

The RSAP for the Denali dataset is c.800m compared with the Forest (100-200m). RSAP has been strongly linked to vegetation structure (Bunting *et al*, 2004; Matthias *et al*, 2012) so a difference between the two datasets is not surprising. Comparing the three distance-weighting methods applied in the Denali dataset, Sutton-Prentice and 1/d produced fairly similar graphs patterns. $1/d^2$ distance-weighting emphasises the weight on the plants nearer to the source more heavily than the other two methods. The shape of the graphs produced and the fact that an asymptote was not reached indicated that this weighting method was not appropriate for the Denali dataset.

$1/d^2$ distance-weighting also produced larger variation between the ERV sub models when run on the Forest dataset. Fall speeds are accounted for within the Sutton-Prentice distance-weighting method and this produced the best-fit for the Forest dataset. Calcote (1995) found that $1/d^2$ was the most appropriate weighting method for the closed forest in Wisconsin. However, recent considerations by Shinya Sugita (*pers comm, 2016*) now suggest that $1/d^2$ is not an appropriate distance-weighting method for ERV-based analysis. It was therefore decided that based on the results produced in both of the datasets presented here that $1/d^2$ would not be used in any further analysis.

The dramatic decline of the LF scores in the first 100m of the Forest dataset could be an artefact of sampling design. The vegetation survey data in the tundra utilised all 21 quadrat data entry points in Zone A (10m radius of sampling point) in Survey Manager, whereas the forest only used five. However, the ring scripts were adjusted accordingly to account for this as the vegetation composition did not show any variation within this zone (see Section 3.2.2 and Appendix A; Table A.2). Ground flora data were also only accounted for in the central quadrat as wind above canopy is the major transport component accounted for in the pollen-vegetation models (Sugita, 1993). In the tundra the vegetation data also produced community maps in the 100m (Zone B) similar to those produced for Zone C. As PCQ data was used to characterise the vegetation in Zone B of the Forest plots the community maps produced were rings of similar community compositions rather than diverse patches. However, the community map for Zone C in the Forest (from 100m) did detect more complex spatial patterns within the vegetation. This transition point could account for the rapid decline in LF scores. The RSAP of 200m for the Forest dataset is between the estimate of 50-75m from closed forests in Wisconsin and Michigan (Calcote, 1995) and 500m at the forest-tundra ecotone in west central Sweden (von Stedingk *et al*, 2008). Despite possible methodological problems, a RSAP of c.100-200m seems reasonable for moss polsters in this environment.

3.4.1.1 Differences in RSAP

There have been significant differences in the estimations of the RSAP in different environmental settings. Basin size has been shown to be a strong influence on RSAP (Sugita, 1994) with larger estimates resulting from lake studies between 600 and 1700m (Sugita, 1994; Nielson and Sugita, 2005) and even up to 7km (Matthias *et al*, 2012) compared with some moss polster studies. The large RSAP in Denali could be attributed to the location of some of the tundra plots near treelines and with extensive patches of *Picea* and *Betula* present in the wider landscape. Sugita (1994) discusses the differences in RSAP estimations with simulations from small lakes and suggested that a large population of pine 50km away for example may affect and increase estimations of the ‘relevant’ source distance of pollen and the parameters for the linear pollen-plant abundance relationship.

Patch size simulations in open landscapes in southern Sweden (Sugita *et al*, 1999) produced larger RSAP estimates than closed forests (Calcote, 1995) and that is attributed to more patch types that were infrequent. Sugita *et al* (1999) ran various simulations with different frequencies of taxa occurrence. They suggest that infrequent taxa or communities in the landscape can increase the

RSAP as the ‘regional’ composition values will be reached at greater distances. However, simulations by Bunting *et al* (2004) show that the occurrence of infrequent taxa did not necessarily lead to higher estimation of RSAP. They varied the rarity of *Betula* anticipating that when the ratios between the modelled taxa were most uneven that the RSAP would decrease. However, they found that the estimated RSAP actually increased when the taxa ratios were more even. Bunting *et al* (2004) concluded that it was the size of the patches in the landscape that were the major controlling factor on RSAP estimates.

A modelling approach using the POLSCAPE was adopted in southern Sweden to estimate the RSAP in past hypothetical landscapes of the Middle and Late Holocene (Hellman *et al*, 2009). They concluded that the most controlling factor on RSAP was also patch size and more importantly the spatial distribution of taxa and patches in the landscape. They state that “*an increase in patch size or an increase in the number of infrequent taxa/patches in the landscape can lead to an increase in RSAP, but only if these changes imply at the same time differences in spatial patch/taxa distribution over the landscape from more or less even to very uneven”*. This was also the case using empirical data from Denmark (Nielsen and Sugita, 2005).

The RSAP of 800m for the tundra was also estimated on the Swiss Plateau (800m: Soepboer *et al*, 2007) where the vegetation was largely agricultural and fairly open, with areas of *Picea, Abies* and *Fagus* (beech) woodland, with patch sizes similar to those in Denali. However, this study was conducted using lakes and not moss polsters. As demonstrated by Sugita *et al* (1999), infrequent taxa or communities in the landscape can also increase the RSAP. This is certainly the case in Denali with greater variation in taxa occurrence and diversity in the landscape along with more complex community patterns than the Forest dataset. The RSAP of 800m for this dataset therefore seems reasonable.

3.4.2 PPEs in Alaska

The chosen PPE taxa that went forward for analysis in both the Denali and the Forest datasets all show good variation in vegetation abundance (Figures 3.7 and 3.8) which is a requirement for reliable PPEs (Broström *et al*, 2004). PPEs were fairly consistent throughout the first iteration using 1/d and Sutton-Prentice distance-weighting in the Denali dataset with all 3 ERV sub models. The only large variation was with *Betula*. PPEs for *Betula* were consistently lower using sub model 1 regardless of the distance-weighting method applied. ERV sub model 1 assumes background pollen loading is a constant proportion of the total pollen loading (Prentice and Parsons, 1983).

This assumption is questioned when there is a large variation in the total pollen loading among sites (Räsänen *et al*, 2007). *Betula* pollen is very high in some of the samples within the Denali and Forest datasets. This could be a likely source of violation for sub model 1 assumptions (Shinya Sugita *pers comm, 2015*). The results from ERV sub model 1 have therefore been rejected for use to estimate pollen productivity estimates in Alaska.

ERV sub model 2 assumes that background pollen loading is constant relative to total plant abundance around sites. Violations to this model occur if total plant abundance varies greatly between sites (Räsänen *et al*, 2007). The landscape of the tundra sites around Denali is scattered with lakes and areas of bare ground but these are relatively small patches and do not form large extensive areas non-pollen producing areas. In the Forest some of the sites contain residential plots but these too are relatively small isolated patches apart from F2 which encompasses the University of Alaska Fairbanks campus. This aside, the total plant abundance within each dataset does not vary greatly and therefore there is no major violation to the assumptions of sub model 2.

ERV sub model 3 was the model of choice used by Räsänen *et al* (2007) in the boreal forests in Finnish Lapland as this model utilises the absolute vegetation abundance data available and has the most basic assumption about the regional background component of the pollen signal. Räsänen *et al* (2007) found that ERV sub model 3 worked best with their dataset as the study area was a mosaic of forest, mire, lakes and treeless mountain tops and heaths which could lead to variations in species composition, productivity and total plant abundance. There are no major violations to sub model 2 with our dataset, however, sub model 3 produced the lowest likelihood function scores with both Denali and the Forest datasets, indicating that this model was the best fit for the Alaskan data.

3.4.2.1 Dataset comparison

Betula, Salix and Poaceae are present in both the Denali and Forest datasets. In order to compare the datasets, the PPEs from the second iteration are discussed here. The value for *Betula* is higher in Denali than the Forest. There are several possible reasons for this including species variations, vegetation and pollen abundance and vegetation survey methodology. The *Betula* species present in Denali was *Betula glandulosa* compared with *Betula neoalaskana* in the Forest.

Betula was better represented in the vegetation in the Forest compared with Denali. *Betula* pollen was also high in D7 with noticeable counts in D4 and D5 but was not recorded in the vegetation survey at these sites. This is also likely to lead to higher PPE values in the Denali dataset. The abundance of *Salix* in the vegetation and pollen is also lower in the Forest compared with Denali. Even though the PPE is slightly higher in the Forest, the values between the Forest and Denali are directly comparable.

The vegetation survey methodology was different in the forest compared with the tundra which could cause some discrepancies with the PPEs values. The methodologies adopted in each region were chosen and modified to represent the 'pollen eye view' of the vegetation as discussed in Section 2.5.3.2 and Bunting *et al* (2013). The vegetation survey for the forest was modified accordingly to reflect the Prentice-Sugita distance-weighting method (Prentice, 1985; Sugita, 1993, 2007a, 2007b) and that wind above the canopy is the dominant transport pathway (see Section 2.5.3). Any changes in community composition and boundaries were also closely monitored particularly in the Forest as there 20m spacing gaps between each PCQ measurement. The surveyors were also the same which promoted consistency and minimised inter-recorder error and bias (Bunting *et al*, 2013) and it is unlikely that this is a major cause for differences between the datasets.

The survey methodology in the Forest may account for the dramatic decline in the LF scores; however, the alpha values did not vary significantly at and beyond 200m. The standard deviations are larger in the Forest which could be due to the fit between the pollen and vegetation data in this dataset, which is illustrated in the scatterplots and lower R^2 values. Site outliers were also not removed during this study which could contribute to larger standard deviations.

3.4.3 Comparisons with Europe

Table 3.6 illustrates the PPE results from Alaska ranked alongside current PPEs from a selection of other studies for each taxon. The PPEs listed from the Denali dataset were estimated using 1/d distance-weighting with ERV Sub-model 3 and using Sutton-Prentice distance-weighting with ERV Sub-model 3 for the Forest dataset as these combinations produced the lowest LF scores. The reference taxon used in all of the other studies in Europe was Poaceae and the PPEs discussed in this Section from Alaska have also been recalculated relative to Poaceae (second iteration).

Betula shows the largest variation across all datasets from Europe. The PPEs from Denali and the Forest datasets are, however, in the upper range and broadly comparable. Various factors have been suggested for such large variations across Europe including climatic and methodological (Broström *et al*, 2008). The high PPE value from Denali is broadly comparable to estimates in southern Sweden (*B.pendula*) and England (*B.pubescens*), compared with the PPE from Greenland (2) which was the same species, *B.glandulosa* and estimated from a similar environmental setting of open dwarf shrub heath. Von Stedingk *et al* (2008) attributed their lower value for *Betula* (2.24) compared with that of southern Sweden (8.9) to climatic factors with *Betula pubescens* spp. *czerpanovii* (mountain birch) growing near the range of tree growth in their study. In relation to previous studies at higher latitudes which might imply that the PPE for *Betula* in the tundra would be lower, the PPE produced in this study suggests that *Betula glandulosa* in the Denali tundra is highly productive compared with other taxa. The slight discrepancy between values could be attributed to differences in methodological approaches between studies.

Alnus was excluded from the Denali dataset, therefore, only the Forest dataset is available for comparisons of *Alnus*. *Alnus*, like *Betula*, shows a large variation in PPE values across Europe but has generally shown to be a high pollen producer (Broström *et al*, 2008). The Forest dataset value of 2.7 is relatively low compared with the European mean average of 9.07. The value of 2.7 is however directly comparable with central Bohemia and southern Sweden. Brostöm *et al* (2008) discuss the discrepancies between the PPE values for *Alnus* across Europe and suggest a possible taphonomic bias between lake samples and moss polsters. For example, vegetation growing in the littoral zone around a lake may be over-represented in lake sediments. Another more plausible reason they suggest is the underestimation of the taxa in the vegetation survey outside the lakes' direct vicinity. Although lakes were not used in this study, there is a chance that *Alnus* is underestimated in the vegetation survey.

Taxa	PPE	Region
Alnus	18.00 11.40 9.07 4.2 3.22 **2.7** 2.56	Estonia England PPE.st2 (LANDCLIM) Norway (2) Central Bohemia **Alaska (Forest)** Southern Sweden
Betula	**10.95** 8.9 **8.7** 8.06 4.60 4 3.09 2.5 2.24 2	**Alaska (Denali)** Southern Sweden **Alaska (Forest)** England Finland Greenland (*B.pubsecens*) PPE.st2 (LANDCLIM) Scotland West Central Sweden Greenland (*B.glandulosa*)
Cyperaceae	1.37 **1** 1 0.89 0.87 0.68 0.29 0.002	Norway (2) **Alaska (Denali)** Southern Sweden, Greenland West Central Sweden PPE.st2 (LANDCLIM) Swiss Jura Norway (1) Finland
Ericaceae	4.7 0.87 **0.53** 0.11 0.07 0.07 0.01	Southern Sweden (*Calluna*) Norway (2) (*Calluna*) **Alaska (Denali)** West Central Sweden (*Empetrum*) West Central Sweden/ PPE.st2 (LANDCLIM) Finland (*Empetrum*) Finland (*Vaccinium* spp.)
Poaceae	**1** **1** 1	**Alaska (Denali)** **Alaska (Forest)** Reference taxon used in most European studies
Populus	0.87, 1.23 0.47 **0.11**	Kansas (ERV Sub-model 1 and 3) Germany **Alaska (Forest)**
Picea	7.10 4.80 2.8 **2.8** 2.62 1.8 1.20 1 0.57	Swiss Jura Estonia West Central Sweden **Alaska (Forest)** PPE.st2 (LANDCLIM) Southern Sweden Norway (2) ScotlandScotland Swiss Plateau
Salix	2.31 1.37	Estonia England

	1.3	Southern Sweden
	1.22	PPE.st2 (LANDCLIM)
	1	Greenland
	0.67	**Alaska (Forest)**
	0.62	Norway (2)
	0.58	**Alaska (Denali)**
	0.09	West Central Sweden

Table 3.6: *PPE results from Alaska (second iteration) ranked with current PPEs from other studies for each taxon. PPE.st2 was used from the LANDCLIM project (Mazier et al, 2012) as a comparison rather than st1 and st3 as the authors (Mazier et al, 2012) considered the rules and assumptions for that set to be more objective and straightforward than st1 and st3. Source: Broström et al, 2008). England (Bunting et al, 2005), Scotland (Twiddle et al, 2012), Finland (Räsänen et al, 2007), Greenland (Bunting et al, 2013b; Bunting and Hjelle, 2010), Swiss Jura (Mazier et al, 2008), West Central Sweden (von Stedingk et al, 2008), Southern Sweden (Broström, 2002; Broström et al, 2004; Sugita et al, 1999), Estonia (Poska et al, 2011), Norway (1) (Hjelle, 1998), Norway (2) (Hjelle and Sugita, 2012), Central Bohemia (Abraham and Kozáková, 2012), Germany (Matthias et al, 2012)*

Patches of *Alnus* may have been missed using the PCQ method or not recorded due to trunk diameter size. Zone C was characterised using aerial photographs along with PCQ data and the Alaska Vegetation Classification (outlined in Section 3.2). However, not every community was visited and surveyed due to time constraints which could lead to an underrepresentation of some taxa. However, an underestimation of *Alnus* in the vegetation survey should increase the PPEs for this taxon. *Alnus* was better represented in the vegetation in the Forest compared with the Denali plots, but with the exception of F1, F8 and F11 pollen percentages were generally lower. Some moss samples taken in the Forest were taken from pleurocarpous mosses on branches and the forest floor with an unknown number of year's collection of pollen. This could lead to a bias in the representation of taxa in the pollen sample. If the vegetation survey data is correct and the pollen percentages are not showing any bias to one taxon then these results could suggest that *Alnus* pollen production in the boreal forest of Interior Alaska is very low. This is unlikely compared with PPE results for *Alnus* in other regions. The pollen-vegetation scatterplots do not show a particularly good spread in the data for *Alnus* in the forest. One site has a particularly high pollen outlier and another site produced lower pollen counts with a higher dwpa value. A likely source of the issues found with the *Alnus* PPE value is that no outliers were removed from the analysis.

The PPE values for *Salix* are comparable between the Alaska datasets and across Europe, with both the Alaskan values in good agreement with other high latitude regions. *Populus* (including both P.*balsamifera* and *P.tremuloides*) produced a predictably low PPE value in the Forest of 0.04. There are currently no values for *Populus* from the boreal biome. A study in Germany produced the first PPE value for *Populus (P. alba*) using ERV sub model 3 (0.47). Recent studies in Kansas (Commerford *et al*, 2013) produced PPE values for *Populus deltoids* from the tallgrass prairies. The results from this study also produced low values for *Populus* but still higher than the German and Alaskan value. It is likely that different species in different ecological range limits will produce different PPE values but the results presented here confirm that *Populus* is likely to be a low pollen producer.

Picea was used as the reference taxon in the Forest and a value was for this taxon was not produced using the Denali dataset. PPE values for *Picea* in Europe have been generally lower compared with other coniferous species such as *Pinus* and *Abi*es. PPE values from the Swiss Jura did however produce a value of 7.10 similar to *Pinus*. This high value for the Jura Mountains could be due to favourable climatic conditions for *Picea abies* (Broström *et al*, 2008). Mazier *et al* (2008) also highlight the effect of distance-weighting methods and size of increments which can affect PPEs, especially for heavy pollen types such as *Picea* and *Abies*.

A PPE value of 0.53 was obtained for Ericaceae from Denali which was is comparable with other species within this group in Europe. Ericaceae contains several different local species in Alaska. The PPE value of 0.07 from West Central Sweden also includes all ericaceous taxa apart from *Calluna* and *Empetrum*-type. This is the first and only PPE for this taxa. Studies for *Calluna* in Europe have so far produced higher PPE values compared with Ericaceae and *Empetrum*, with the highest value of 4.7 in southern Sweden. There is no *Calluna* in Alaska, therefore the PPE of 0.53 is comparable with the low values for *Ericales* in Europe.

Herbaceous taxa generally produced less pollen than tree taxa (Broström *et al*, 2004; Anderson, 1970). Cyperaceae was used as the reference taxon in Denali for the first iteration and was not included in the Forest data set analysis. The value of 1 produced in Denali when adjusted to relate to Poaceae in the second iteration dataset is comparable with Norway and Sweden and the European mean from the LANDCLIM project which suggests this is a reliable PPE.

3.5 Conclusions

Pollen Productivity Estimates used in REVEALS and LOVE reconstructions for a region should be obtained from that region whenever possible (Shinya Sugita, *pers comm, 2015*). This ensures the most reliable reconstruction for the study area. This Chapter has presented the first PPEs for the dominant forest and tundra taxa in Interior Alaska.

- Previous studies in the Nordic countries (e.g. Hellman *et al*, 2009; Galliard *et al*, 2008; Sugita *et al*. 1999) have demonstrated that the more open the landscape, the larger the RSAP estimates when using moss polsters. Therefore, an estimate of 800m for the Denali dataset seems reasonable.

- The dramatic decline in LF scores may be an artefact of sampling design but the RSAP in the Forest was expected to be lower than the open landscape of the tundra and also seems reasonable.

- *Betula* is a very high pollen producer and *Salix* is a low pollen producer in the Denali tundra.

- *Betula* is again the highest pollen producer in the forest but significantly lower compared with the tundra. *Alnus* is low compared with some other studies in Europe and this could be attributed to the type of moss collected and an underrepresentation of this taxa in the pollen assemblage.

- Site outliers were not removed from the Denali or the Forest datasets and this could be affecting the PPEs, particularly in the Forest where standard deviations are higher.

- Trends of high and low pollen producers seem comparable with Europe. There are some noticeable differences particularly with *Betula* and *Alnus* which supports the reasoning for obtaining PPEs from the specific region of study.

Chapter 4: The Landscape Reconstruction Algorithm: REVEALS

4.1 Introduction

Determining quantitative vegetation cover on regional and local scales can address questions on past land use, responses of vegetation to climate change and biodiversity. Various approaches have been adopted in an attempt to quantitatively estimate past land cover (e.g. Prentice *et al*, 1996; Sugita, 1994; Sugita *et al*, 1999; Bunting and Middleton, 2005). The Landscape Reconstruction Algorithm (LRA, Sugita 2007a; b) is a two-step framework for quantitative reconstruction of vegetation across various spatial scales (outlined in Section 2.4.6). The first step is the model REVEALS which reconstructs the regional composition and is the focus of this Chapter. The LRA has been successfully validated (e.g. Hellman *et al*, 2008 a,b; Soepboer *et al*, 2010; Hjelle *et al*, 2015) and applied to palaeo pollen records (e.g. Nielsen *et al*, 2012; Fyfe *et al*, 2012; Trondman *et al*, 2015) in Europe.

This Chapter describes the first application of REVEALS in Alaska using the pollen productivity estimates described in Chapter 3. Existing pollen records are used to characterise the vegetation in the Brooks Range from the late glacial through to the modern day. The REVEALS estimates of vegetation cover described in this Chapter provide the regional input data for Chapter 6, where the second step of the LRA (the LOVE model) is applied to Ruppert Lake and Lake 3.

4.2 Methods

4.2.1 Study region and site selection

Studies have shown that pollen assemblages are similar among large sites in a given region (Bradshaw, 1981, Sugita, 1994) and therefore, in theory any large lake in a region can be used to estimate the regional vegetation (Sugita, 2007a). Studies have shown that using several large lakes in a region (>100ha) improves the accuracy of the reconstruction (Sugita, 2007a). Recent reconstructions using REVEALS in Europe (Hjelle *et al*, 2015) have also shown that multiple smaller sites can be used in the absence of a large lake for the region but the error estimates will be higher (discussed previously in Chapter 2).

The study sites of Ruppert Lake and Lake 3 are located within the foothills of the Brooks Range (Chapter 6). Existing lake pollen records for REVEALS were selected based on their location to

Ruppert Lake and Lake 3, their vegetation history and chronologies. Large lakes were initially identified and pollen records were assessed to see if they were suitable. As previously discussed in Section 2.2, vegetation change is not only complex across Alaska, but within each region. Patterns of vegetation change and PFT transitions within each potential regional record needed to be on a similar time scale to those identified at Ruppert Lake and Lake 3. The final site selection had to be a compromise between location and timing and arrival of the key taxa during the study period.

4.2.1.1 Sithylemenkat Lake

Sithylemenkat is the largest lake near to Ruppert and Lake 3 (see Figure 4.1) with a high resolution pollen record dating back to 15,461 cal years BP with similar vegetation changes and PFT transitions. Sithylemenkat is located 164km south east of Ruppert Lake in the Kokrines-Hodzana Highlands bordering the Kanuti Flats of north-central Alaska. The lake is 707 ha with a radius of 1500m. The modern vegetation around the lake is characterised by *Picea mariana* muskeg on the poorly drained lowlands to the north east with *Picea glauca* on well-drained warmer sites. *Betula papyrifera* and *Populus tremuloides* are present in post fire areas and common shrub species include *Betula glandulosa, Alnus incana* and *Salix* (Anderson *et al*, 1990).

The majority of the vegetation history of Sithylemenkat is similar to other south-central Brooks Range sites (Anderson *et al*, 1990). The *Betula* rise is dated to 13,830 cal yr BP which is comparable with other dated sequences in the region (Brubaker *et al*, 1983; Edwards *et al*, 1985). Between 14,000 and 13,500 yr BP the Sithylemenkat record contains unusually high amounts of *Picea*, *Betula* and *Alnus* pollen which differs from other records in the herb zone during this period. Anderson *et al* (1990) point out that the combination of tundra and boreal taxa between 14,000 and 13,500 yr BP and the dissimilarity to vegetation inferred for other Brooks Range sites at Sithylemenkat makes the interpretation more difficult. This needs to be considered when using this lake as a regional analogue for vegetation for this period. From 13,500 cal yr BP the vegetation history becomes similar to the rest of the southern Brooks Range sites (Anderson *et al*, 1990). The main PFT transitions of interest at Ruppert Lake are from this date into the Holocene so the vegetation patterns from 13,500 cal yr BP at Sithylemenkat are deemed suitable for REVEALS reconstructions. At around 10,000 cal yr BP, *Populus* pollen increases in the record followed by the *Picea glauca* around 9,000 cal yr BP. *Alnus* appears around 8000 cal yr BP and expands to values over 40%. *Picea* declines and expands again around 5000 cal yr BP which is consistent with the vegetation pattern at Ruppert Lake, with this second expansion likely dominated by P*icea mariana* and the development of the modern boreal forest.

4.2.1.2 Smaller lakes in the Brooks Range

Simulation studies (Sugita, 2007a) have shown that the higher the pollen counts in each sample the more reliable to the reconstruction will be using REVEALS. Hjelle *et al* (2015) outline the various variables which need to be taken into account when deciding on the size and number of sites including 1) the size of the pollen counts for each records 2) type of site 3) vegetation type (mosaic, patch sizes, distribution of vegetation) and 4) area of reconstruction (Hjelle *et al*, 2015). Simulations by Sugita (2007a) assume that the pollen counts at each site are 1000 grains. As he points out, most pollen analysts perform a total count of 300-500 grains per sample and therefore standard errors could be up 10-20% larger than those illustrated in this simulation study. The original total land pollen counts at Sithylemenkat are even lower averaging around 200 grains per sample. This is reduced further when only looking at the 8 key taxa with Alaskan pollen productivity estimates; *Alnus, Betula, Picea, Populus, Salix*, Poaceae, Cyperaceae and Ericaceae with sample counts ranging from 71 to 240 grains.

There were no other suitable large lakes in the region and therefore six smaller lakes were identified in the southern foothills of the Brooks Range with similar vegetation histories to Ruppert which could be used alongside Sithylemenkat to strengthen the regional reconstruction of vegetation. The six lakes are Ranger (Brubaker *et al*, 1983), Rebel, Redstone and Screaming Yellow Legs (Edwards *et al*, 1985), Wild Tussock and Xindi (Higuera *et al*, 2009). Figure 4.2 illustrates the pollen diagrams for the chosen lakes and Table 4.1 summarises the lake locations, ages and size.

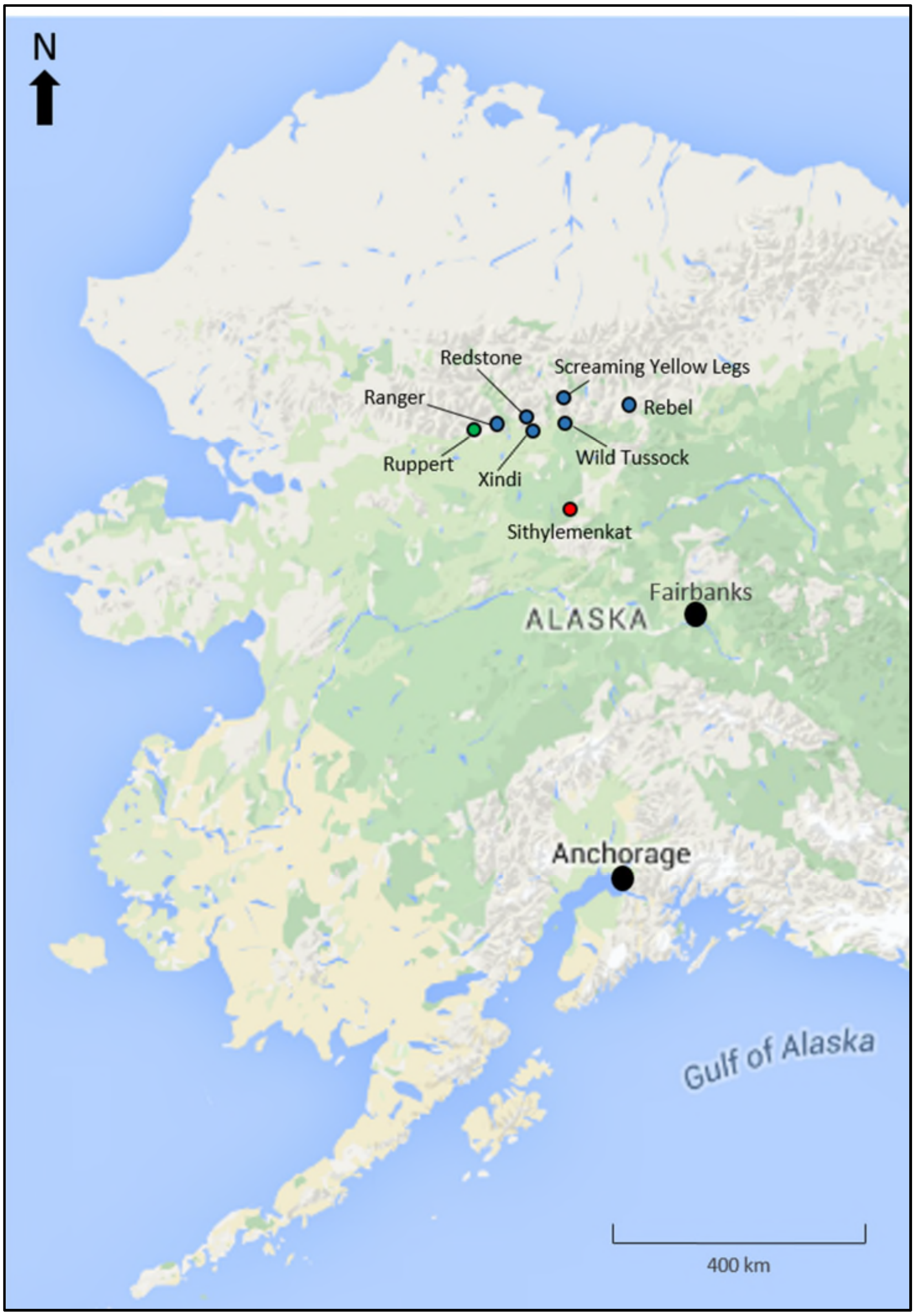


Figure 4.1: *Location of lakes used in REVEALS* (*Google*)

KEY: Red = Large regional lake (Sithylemenkat), BLUE = small lakes, GREEN = Small lake used in LOVE reconstruction (Chapter *6)*

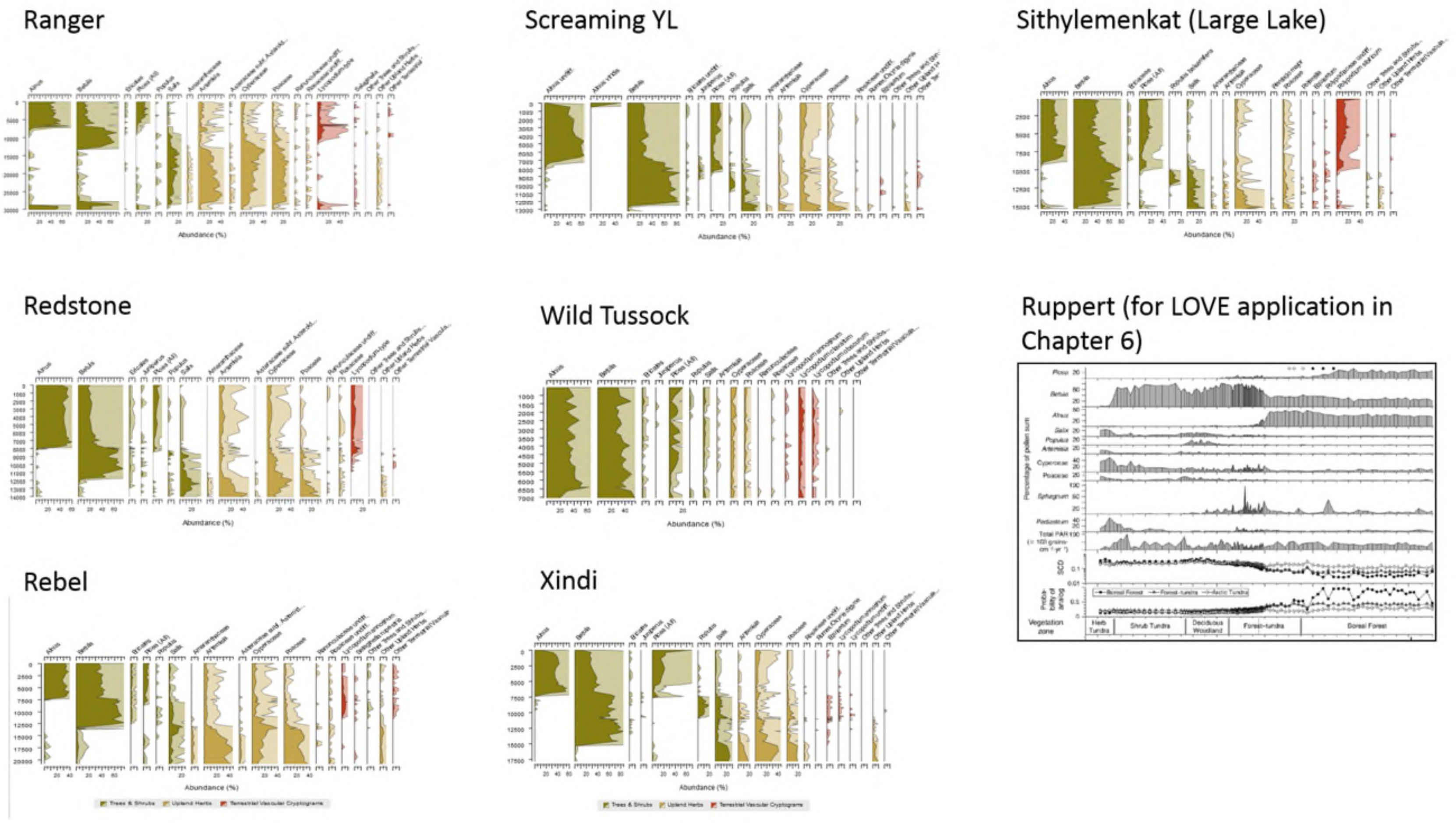


Figure 4.2: *Pollen diagrams for Sithylemenkat (large regional lake) and the six small Brooks Range lakes selected for REVEALS (generated using the Neotoma Database) and Ruppert Lake pollen diagram (Higuera et al, 2009) used for the LOVE reconstructions in* Chapter *6*

Lake	Latitude	Longitude	Date (years BP)	Radius (m)
Sithylemenkat	66.76667	-157.216667	15,461	1500
Rebel	67.41667	-149.8	14,430	250
Screaming Yellow Legs	67.58	-151.42	13,260	250
Xindi	67.11124	-152.491385	15,500	150
Redstone	67.25	-152.6	14,000	80
Ranger	67.14722	-153.65	30,000	178
Wild Tussock	67.12777	-151.381944	7,056	218

Table 4.1: *Brooks Range Lakes used in REVEALS (Latitude, Longitude, Date and Radius)*

4.2.2 The REVEALS model

REVEALS reconstructs vegetation composition in $10^6 – 10^7$ ha ($10^4 – 10^5$ km^2) using pollen records from lakes and bogs. REVEALS is the first step in the LRA, but also works as an independent model to estimate regional changes of vegetation and land cover (Sugita *et al*, 2008). The equation and assumptions of the REVEALS model are outline in Section 2.4.6. Z_{max} is the spatial extent (m) of the "regional" vegetation within which most of the pollen comes from and REVEALS assumes the majority of pollen comes from within this distance (Soepboer *et al*, 2010). For this study Z_{max} was set to 100km. Mazier *et al* (2012) tested the effect of the parameter settings on REVEALS-model estimates using the Czech Quaternary Palynological Database (PALYCZ) and found that altering the values of Z_{max} (50, 100, 200km) did not affect the REVEALS estimates using the PALYCZ data. Parameters required for REVEALS are pollen productivity estimates (PPEs), fall speed of pollen V_g (m sec $^{-1}$), pollen counts from multiple sites, size of each size (mean radius in m) and errors of pollen productivity estimates (the variance and covariance of pollen productivity estimates α's).

4.2.3 Pollen Productivity Estimates

One of the key parameters for the REVEALS model is pollen productivity estimates (PPEs). PPEs have been shown to affect the REVEALS estimates (Hellman *et al*, 2008a). As discussed in Chapter 2 and 3, there can be a marked difference in the PPE values for different taxa between regions and within regions. Hellman *et al* (2008) suggested that it would be advisable to test more than one set of PPEs when using the LRA. The Alaskan PPEs obtained for the nine taxa discussed in Chapter 3 have also shown strong variations between PPE Set 1 and PPE Set 2. In order to test the effect that different PPEs had on the REVEALS reconstructions in Alaska 3 sets of PPEs were used were used for REVEALS model runs 1-13 (Table 4.2). The first set comprised predominantly PPEs derived from the first iteration Denali dataset. PPE Set 2 was predominantly PPEs derived from the first iteration Forest dataset and PPE Set 3 were taken from PPE.st2 from the LANDCLIM project (Gaillard *et al*, 2010). The European PPEs are mean values of all the alpha values obtained across Europe for that taxa and have been tested using REVEALS and the Czech Quaternary Palynological Database (Mazier *et al*, 2012).

Taxa	Fall speed of pollen ($m\ s^{-1}$)	PPE Set 1 Predominantly Denali		PPE Set 2 Predominantly Forest		PPE Set 3 European (LANDCLIM)	
		Pollen productivity estimate	Standard error	Pollen productivity estimate	Standard error	Pollen productivity estimate	Standard error
Betula	0.024	10.95	0.00421	3.12	0.06118	3.09	0.0723
Alnus	0.021	0.96	0.01715	0.96	0.01715	9.07	0.0105
Salix	0.022	0.58	0.00029	0.24	0.00575	1.22	0.0115
Picea	0.056	1	0	1	0	2.62	0.0151
Populus	0.025	0.04	0.00038	0.04	0.00038	-	-
Poaceae	0.035	0.1	0.00062	0.36	0.02534	1	0
Cyperaceae	0.035	1	0	1	0	0.87	0.0037
Ericaceae	0.038	0.53	0.00023	0.53	0.00023	0.07	0.0016

Table 4.2: *PPEs used in the REVEALS scenario runs. Denali PPEs taken from 1/d ERV sub model 3 and Forest PPEs taken from Sutton Prentice ERV sub model 3. European LANDCLIM PPE.st2 (Gaillard et al, 2010; Mazier et al, 2012)*

Following a closer inspection of runs 1-13 (discussed below), it became clear that it was not appropriate to combine the PPEs from the first iteration Denali dataset with the first iteration Forest dataset. As these PPEs had not been adjusted to the same reference taxon, they were being treated as absolute values by combining the first iteration sets which would lead to unreliable REVEALS outputs. Therefore, PPE Sets 4 and 5 were introduced to REVEALS model run 14 which were adjusted to Poaceae. PPE Set 4 comprised predominantly PPEs derived from the second iteration Denali dataset and PPE Set 5 was predominantly PPEs derived from the second iteration Forest dataset (Table 4.3).

Taxa	Fall speed of pollen (m s^{-1})	PPE Set 4 Predominantly Denali		PPE Set 5 Predominantly Forest	
		Pollen productivity estimate	Standard error	Pollen productivity estimate	Standard error
Betula	0.024	10.95	0.00421	8.7	0.06118
Alnus	0.021	2.7	0.01715	2.7	0.01715
Salix	0.022	0.58	0.00029	0.67	0.00575
Picea	0.056	2.8	0	2.8	0
Populus	0.025	0.11	0.00038	0.11	0.00038
Poaceae	0.035	1	0.00062	1	0.02534
Cyperaceae	0.035	1	0	1	0
Ericaceae	0.038	0.53	0.00023	0.53	0.00023

Table 4.3: *PPEs used in the REVEALS scenario run 14. Denali PPEs taken from 1/d ERV sub model 3 and Forest PPEs taken from Sutton Prentice ERV sub model 3 and adjusted to Poaceae.1*

4.2.4 REVEALS model runs

The raw pollen count files must be converted to LRA ready files prior to running REVEALS. *File.format.conversion.forLRA.win64.exe* (Sugita, unpublished) was used which requires raw pollen counts organised in chronological order and a csv file of specified time windows. Pollen counts from all samples in a given time window are combined and the file conversion program produces a single LRA ready file for use with REVEALS. The time windows in this study were split into 500 year time slots for the first two windows (0-500 years and 500-1000 years) and then every 1000 years until 16,000 cal years BP. Some of the pollen records exceeded 16,000 cal years BP but a timeframe needed to be considered by this study. The decision was therefore made to look at major plant functional shifts from the late glacial through the Holocene and as the *Betula* rise occurs after this date the cut off was made to 16,000 years.

Crucial parameters include PPEs and standard errors along with site radius (m) and fall speed of pollen (FSP, m $s^{-1)}$. These together with the raw pollen counts converted into time windows for each site provide the input required by REVEALS. *REVEALS v.5.exe* (Sugita, unpublished) was used for this study and neutral atmospheric conditions and wind speed of 3 m.s^{-1} were assumed. The combinations of lakes and PPEs used are listed in Table 4.4.

Model Run	**Lake combinations**	**PPEs used**	**Figure / Appendix**
1	Sithylemenkat	Set 1	4.3
2	Sithylemenkat	Set 2	4.3
3	Sithylemenkat	Set 3	4.6
4	Small lakes	Set 1	4.8
5	Small lakes	Set 2	4.8
6	Small lakes	Set 3	Appendix A, Figure A.1
7	Sithylemenkat and small lakes	Set 1	4.10
8	Sithylemenkat and small lakes	Set 2	4.10
9	Sithylemenkat and small lakes	Set 3	Appendix A, Figure A.2
10	Sithylemenkat	Set 1 during the LG and Set 2 during the Holocene	4.12
11	Sithylemenkat	Set 1 during the LG and Set 2 during the Holocene (using *Alnus* PPE value from Europe)	4.12
12	Sithylemenkat and small lakes	Set 1 during the LG and Set 2 during the Holocene	4.14
13	Sithylemenkat and small lakes	Set 1 during the LG and Set 2 during the Holocene (using *Alnus* PPE value from Europe)	4.14
14	Sithylemenkat and small lakes	Set 4 during the LG and set 5 during the Holocene	4.16

Table 4.4: *REVEALS model runs/scenarios*

4.3 Results

The results discussed in this Section from REVEALS runs 1-13 used combined PPE Sets from the first iteration of Denali and Forest PPEs. However, as discussed above, it would have been more appropriate to readjust all PPEs to the same reference taxon before combining them. The adjusted PPEs to Poaceae are discussed in Run 14 (Figure 4.16).

4.3.1 Sithylemenkat (using PPE Set 1 and 2)

The pollen proportions of the eight taxa used in the REVEALS analysis for Sithylemenkat are illustrated in Figure 4.3 a. *Betula* dominates the majority of the sequence during the late glacial and into the early Holocene alongside Salix, Poaceae and Cyperaceae. *Betula* percentages rise during the time window 14,000-15,000 cal years BP to 55% and peak at 81% between 9,000-

10,000 cal years BP. *Alnus* appears at the beginning of the record accounting for 10% of the total land pollen but declines throughout the late glacial and does not recover until the Holocene. The start of the Holocene is characterised by the expansion of *Populus* which occurs between 10,000 and 12,000 cal years BP. *Populus* declines during the 9,000-10,000 cal years BP time window along with Salix. The first *Picea* (*P.glauca*) rise is recorded during this time window with proportions recorded at 10%. The *Alnus* rise occurs between 8,000 and 9,000 cal years BP followed by a second expansion of *Picea* (*P.mariana*) between 5,000-6,000 cal years BP.

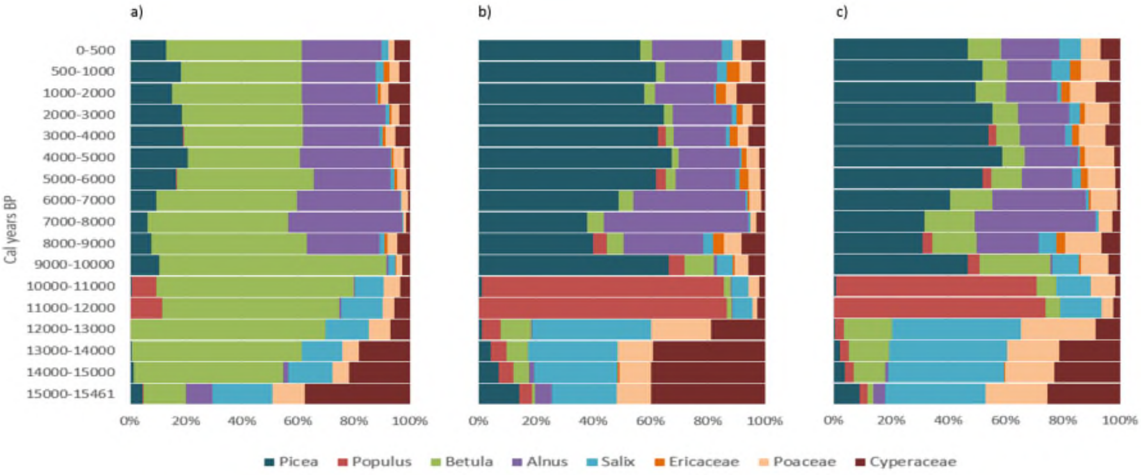


Figure 4.3: *Pollen Proportions and REVEALS estimates for Sithylemenkat Lake a) Pollen proportions b) REVEALS estimates of vegetation cover using* PPE Set *1 c) REVEALS estimates of vegetation cover using* PPE Set *2 (Runs 1 and 2)*

Figure 4.3 b and c illustrates the REVEALS estimates of vegetation proportion using PPE Sets 1 and 2 for Sithylemenkat. The two REVEALS reconstructions show similar patterns with *Salix*, Cyperaceae and Poaceae dominating throughout the late glacial. One of the most striking difference is the dramatic reduction in *Betula* compared with the pollen percentages using both PPE Sets during this time. The REVEALS estimates show a much higher percentage cover of *Populus* (85%) in the early Holocene compared with pollen percentages (~10%). Following the decline in *Populus* and the transition from deciduous woodland into forest-tundra there is an increase in *Picea* in the pollen proportions. Pollen percentages of *Betula* reach up to 81% between 9,000-10,000 cal years BP but the REVEALS estimates do not exceed 25% during this period using either PPE Sets, averaging around 10% throughout the entire sequence. PPE Set 2 produced slightly higher estimated vegetation cover for *Betula* compared with PPE Set 1. The PPE for *Betula* from the Forest dataset was considerably lower at 3.12 compared with 10.95 from Denali which would account for this difference. Alongside the dramatic decrease in *Betula* in the REVEALS estimates is a large increase in *Picea* using both PPE Sets 1 and 2. *Picea* is the dominant arboreal species throughout the Holocene followed by *Alnus*.

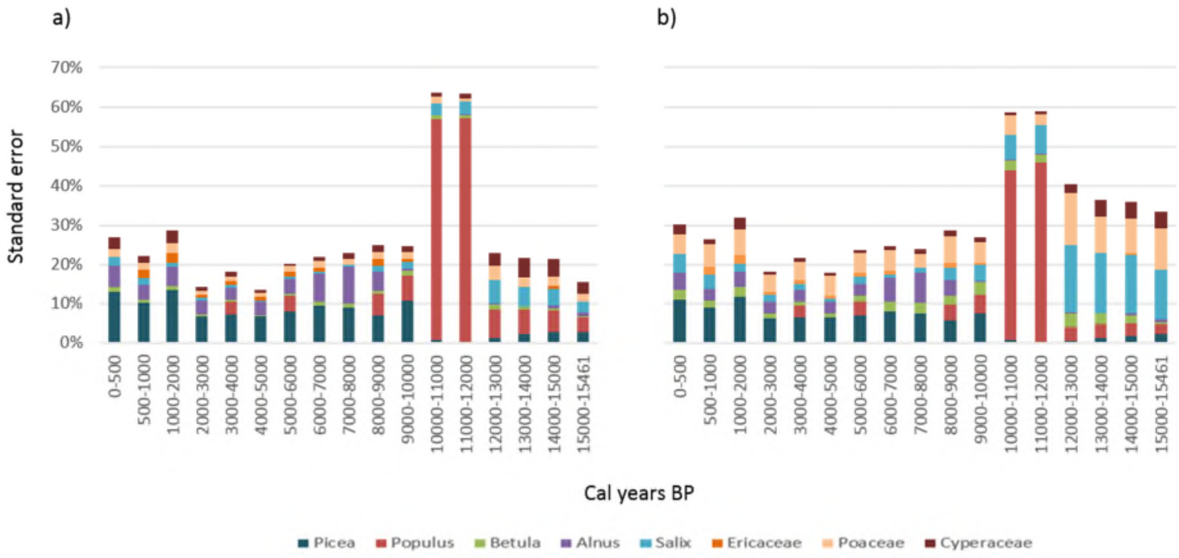


Figure 4.4: *Standard errors REVEALS estimates for Sithylemenkat Lake a) REVEALS run 1 using* PPE Set *1 b) REVEALS run 2 using* PPE Set 2

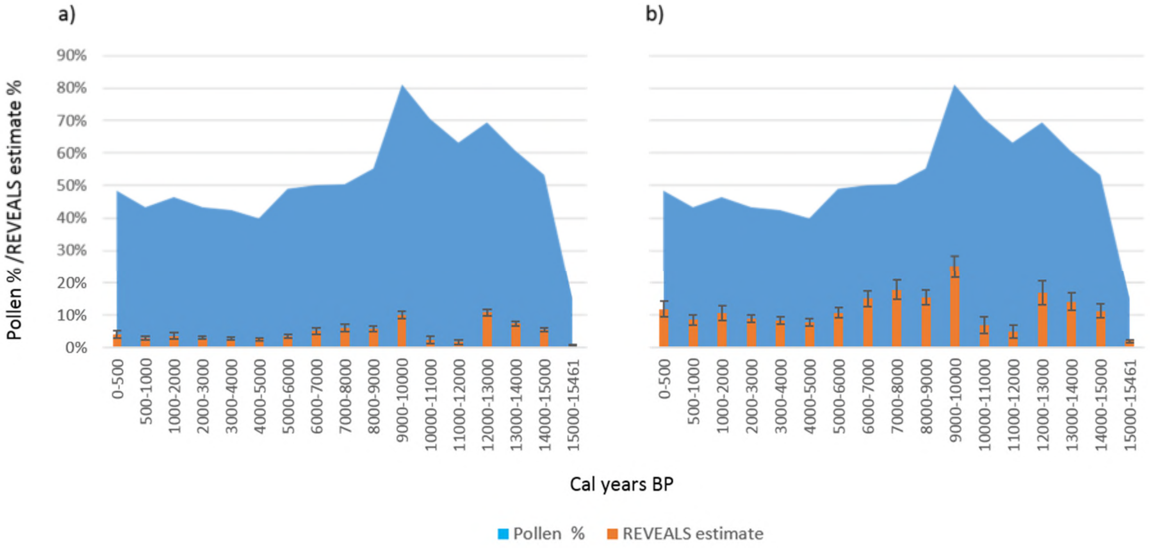


Figure 4.5: *Betula pollen percentages vs REVEALS estimates a)* PPE Set *1 b)* PPE Set *2. Error bars = standard errors on REVEALS estimates*

The standard errors are largest for *Populus*, particularly in the time windows between 10,000 and 12,000 cal years BP (Figure 4.4). Errors for *Salix* and Poaceae are higher using PPE Set 2, but the errors are generally comparable between the two PPE Sets. The overall patterns suggest that *Betula* is the most over represented in pollen percentages (Figure 4.5), followed by *Alnus*. *Populus* and *Picea* are the most under represented, followed by *Salix* and Poaceae.

A third set of PPEs was tested on Sithylemenkat (PPES set 3) which contained only PPEs derived from studies in Europe. As these PPEs are mean values of all the alpha values obtained across Europe for that taxa these will also include taxa which are not present in Alaska. This will have an effect on the REVEALS estimates and may not be appropriate for the study area. The results for are illustrated in Figure 4.6 (Run 3). There is no *Populus* PPE obtained in Europe so comparisons with this taxa could not be made. As this was a test to compare purely PPEs obtained from other regions the decision was made not to include the Alaskan PPE at this stage. This, however, has affected the percentage cover of the other taxa and is probably the likely cause for the increase in *Salix* cover in the early Holocene. The main patterns noticed here are the large increase in Ericaceae and the decrease in *Alnus*. As discussed in Chapter 3 there are various reasons why the low Alaskan PPE may not be totally appropriate. The REVEALS estimates presented here for *Alnus* seem more appropriate and the European value of 9.07 was considered for further analysis in runs 4-13. However, *Alnus* relative to Poaceae (PPE Sets 4 and 5) had a higher value of 2.7 and therefore in run 14 the Alaskan value was kept rather than replacing with European mean.

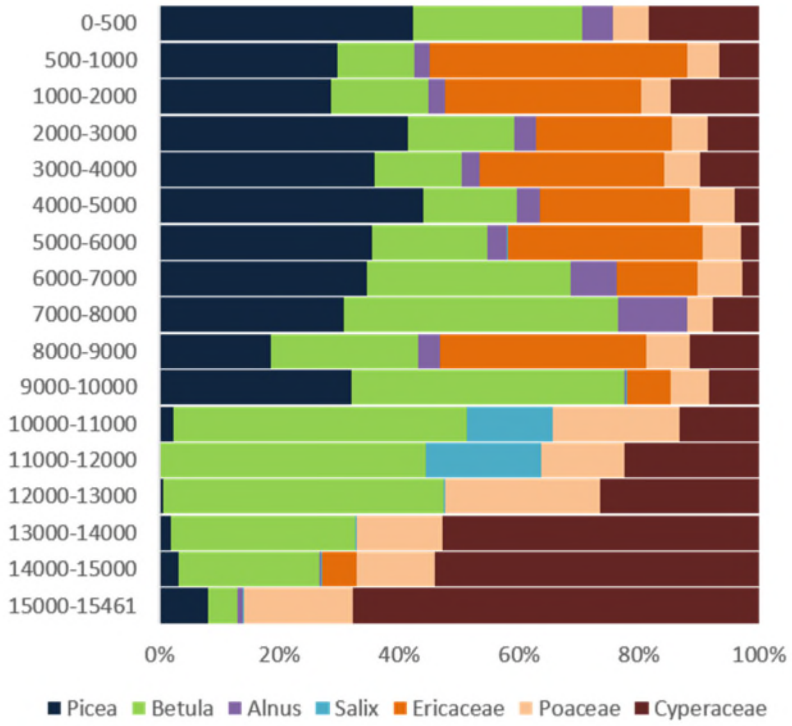


Figure 4.6: *REVEALS estimates for Sithylemenkat Lake using the European LANDCLIM values (*PPE *Set 3, Run 3)*

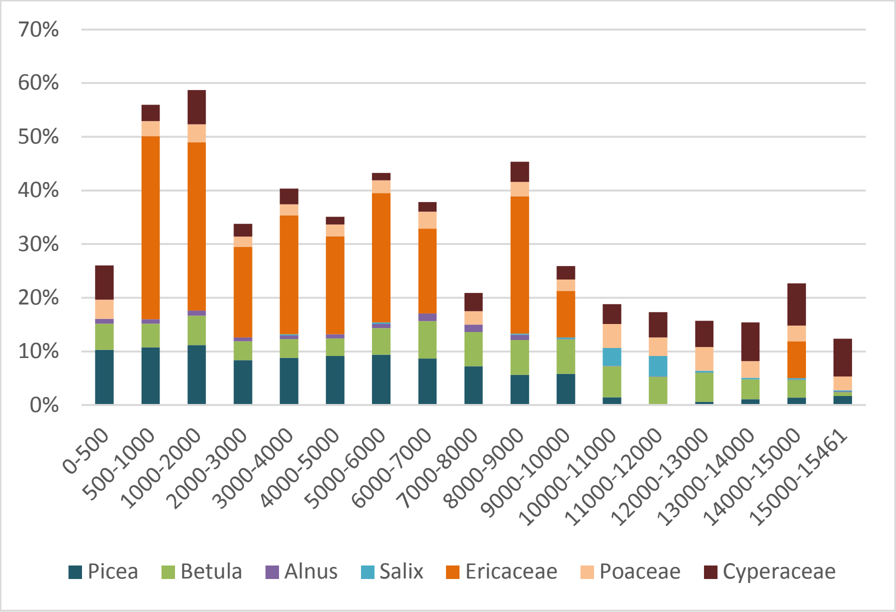


Figure 4.7: *Standard errors REVEALS estimates for Sithylemenkat Lake using* PPE Set *3*

4.3.2 Small Lakes (PPE Sets 1 and 2)

The pollen proportions of the eight taxa used in the REVEALS analysis for the six small lakes are illustrated in Figure 4.8a. The patterns are broadly similar to using Sithylemenkat on its own. *Betula* dominates the majority of the sequence during the late glacial and into the early Holocene alongside *Salix*, Poaceae and Cyperaceae. However, Poaceae and Cyperaceae vegetation estimates are higher using just small lakes. *Betula* percentages also rises during the time window 14,000-15,000 cal years BP to 48% and peak at 71% between 9,000-10,000 cal years BP, which is comparable to the percentages from just using the Sithylemenkat pollen data. *Alnus* appears at the beginning of the record at low values of under 1% and does not increase until the Holocene which differs slightly to the Sithylemenkat record.

The start of the Holocene is characterised by the short-lived expansion of *Populus*. The pollen percentages for *Populus* appear to be different with the *Populus* rise recorded at 10,000-11,000 cal years BP at Sithylemenkat and at lower values. *Populus* declines later during the 7,000-8,000 cal years BP time window along with *Salix*. The first *Picea* (*P.glauca*) rise is recorded earlier during 9,000-10,000 cal years BP but with very low proportions recorded at under 1%. *Alnus* appears between 8,000-9,000 and the rise occurring between 6,000-7,000 cal years BP. This is followed by a second expansion of *Picea* (*P.mariana*) starting between 5,000-6,000 cal years BP.

Figure 4.8 b and c illustrates the REVEALS estimates of vegetation proportion using PPE Set 1 and 2 for the six small lakes. The two REVEALS reconstructions show similar patterns with *Salix*, Cyperaceae and Poaceae dominating throughout the late glacial. As with the previous REVEALS runs on Sithylemenkat, the most striking difference is the dramatic reduction in *Betula* compared with the pollen percentages using both PPE Sets. PPE Set 2 again produced slightly higher estimated vegetation cover for *Betula* compared with PPE Set 1. The REVEALS estimates show a much higher percentage cover of *Populus*, particularly during the early Holocene with values reaching up to 73% using PPE Set 1 and 58% using PPE Set 2. *Populus* declines between 8,000-9,000 cal year BP but REVEALS estimates suggest that *Populus* continued to be an important component of the boreal forest throughout the Holocene. REVEALS estimates also show an increase in *Picea* during the Holocene, but not to the same extent as using Sithylemenkat. PPE Set 3 was also run as a test on small lakes (Appendix A, Figure A.1). The trends in taxon representation are similar to the estimates made when using just Sithylemenkat. Ericaceae appears to be under represented in the pollen record along with Cyperaceae and these two taxa dominate the majority of the record. REVEALS estimates suggest that *Alnus* and *Betula* are over represented.

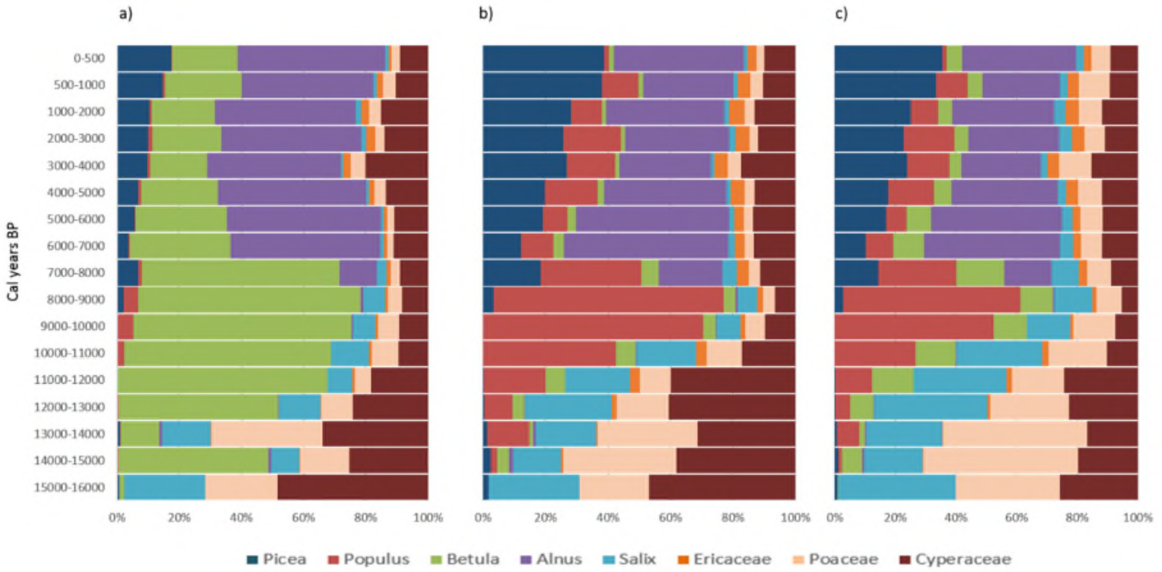


Figure 4.8: *Pollen Proportions and REVEALS estimates for small lakes a) Pollen proportions b) REVEALS estimates of vegetation cover using* PPE Set *1 / run 4) REVEALS estimates of vegetation cover using* PPE Set *2 / run 5*

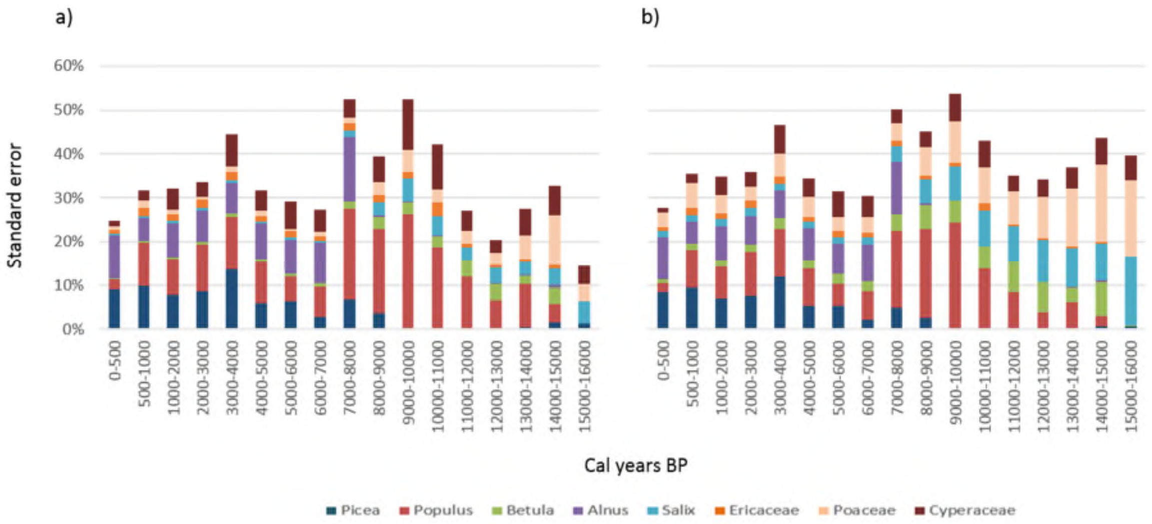


Figure 4.9: *Standard errors REVEALS estimates for small lakes a) REVEALS run 1 using* PPE Set *1 / Run 4 b) REVEALS run 2 using* PPE Set *2 / Run 5*

4.3.3 Sithylemenkat and small lakes (PPE Sets 1 and 2)

The pollen proportions of the eight taxa used in the REVEALS analysis for Sithylemenkat and the small lakes combined are illustrated in Figure 4.10a. The patterns are almost identical to the pollen proportions obtained using just the 6 small lakes on their own. The main noticeable difference is the presence of *Alnus* in the late glacial. In the Sithylemenkat and small lakes combined record *Alnus* is recorded up to 10% between 15,000-16,000 cal years BP and there is also an increase in *Betula* and *Picea* resulting in a decrease in *Salix,* Cyperaceae and Poaceae. Ericaceae is also present at slightly higher values in the late glacial compared with just the small lakes alone.

Figure 4.10 b and c illustrates the REVEALS estimates of vegetation proportion using PPE Set 1 and 2 for Sithylemenkat and the small lakes combined (Run 7 and 8). The two REVEALS reconstructions show the same patterns as the estimates from just the small lakes alone. The higher pollen percentages of *Betula* and *Alnus* between 15,000-16,000 cal years BP are reflected in the REVEALS estimates. A small presence of Ericaceae is not present in just the small lake runs. The REVEALS estimates when using PPE Set 3 are shown in Appendix A, Figure A.2. As expected the results are very similar to the estimates from the six small lakes with Cyperaceae and Ericaceae dominating the record with dramatic decreases in *Betula* and *Alnus* compared with the pollen record. Apart from *Alnus* no other European PPEs were used in further analysis.

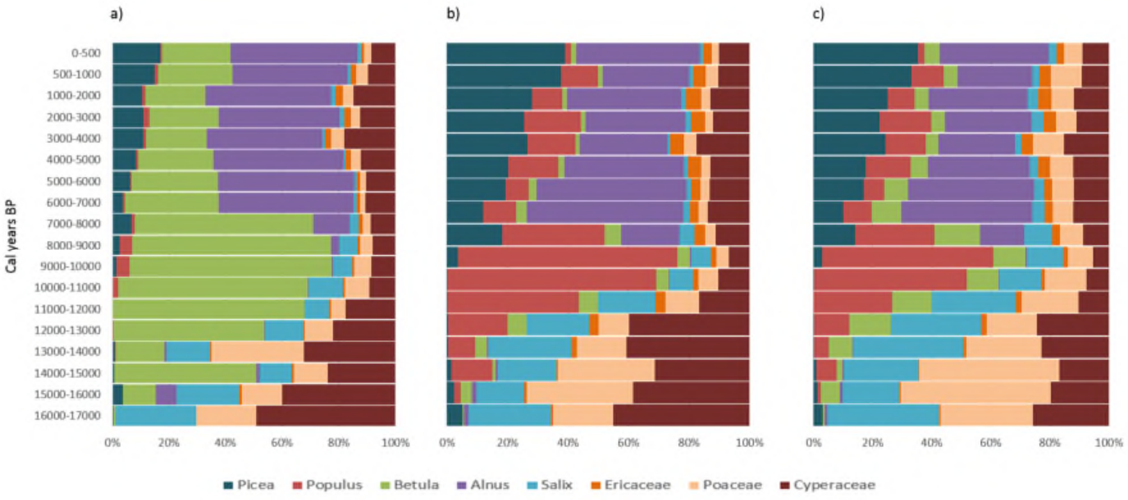


Figure 4.10: *Pollen Proportions and REVEALS estimates for Sithylemenkat and small lakes a) Pollen proportions b) REVEALS estimates of vegetation cover using* PPE Set *1 / run 7 c) REVEALS estimates of vegetation cover using* PPE Set *2 / run 8*

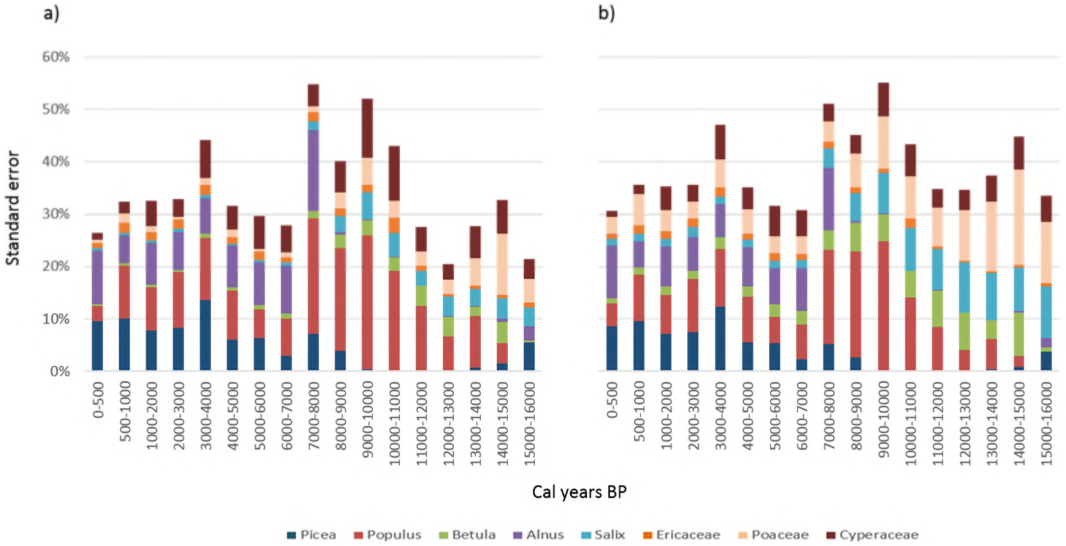


Figure 4.11: *Standard errors REVEALS estimates for Sithylemenkat and small lakes a) REVEALS run 7 using* PPE Set *1 b) REVEALS run 8 using* PPE Set *2*

The standard errors are very similar and do not seem to be affected whether using just small lakes or one large lake and small lakes combined. The large errors on *Populus* are reduced compared with using Sithylemenkat alone, but are still the highest compared with all the other taxa.

4.3.4 Applying different PPE Sets to the late glacial and Holocene (PPE Sets 1 and 2)

The PPEs derived from the Denali dataset include 5 taxa (*Betula, Salix*, Ericaceae, Cyperaceae and Poaceae) from the mountain tundra biome. The six taxa from the Forest dataset (*Betula, Salix, Alnus, Populus, Picea* and Poaceae) are from the boreal forest biome. As discussed in Chapter 3 the differences in the constituent species between the Denali and Forest datasets will produce different PPEs. The results above from REVEALS scenario runs 1-9 illustrate changes in *Betula* and *Salix* when between PPE Set 1 (shrubby species) and 2 (tree species). Shrubby taxa would have been more prevalent during the late glacial and arboreal taxa throughout the Holocene with the development of forest. Therefore, using different sets of PPEs for different time windows would be more appropriate. Although the REVEALS estimates didn't show much variation between small lakes on their own and combining them with Sithylemenkat, in order to keep pollen counts as high as possible in each time window they were not taken forward on their own in any further analysis. Runs on just Sithylemenkat were taken forward in further analysis despite low pollen counts to compare the results from 1 large lake vs combining with small lakes. Various combinations were used on Sithylemenkat and Sithylemenkat plus small lakes to assess the appropriateness of PPEs and the resulting reliability of the REVEALS reconstruction.

4.3.4.1 Sithylemenkat

REVEALS scenario run 10 uses PPE Set 1 throughout the late glacial, as tundra species dominated during this time and PPE Set 2 throughout the Holocene when deciduous woodland and boreal forest dominate the record in this region. The PPE for *Alnus* is discussed in detail in Chapter 3. The Forest dataset value of 0.96 is extremely low compared with the European mean average of 9.07. There are various reasons why the PPE obtained was so low (discussed in Section 3.4.3) and as mentioned above this value may not be entirely appropriate for the regional vegetation reconstruction in the Brooks Range. REVEALS scenario run 11 therefore uses the same PPE Sets as Run 10 but the *Alnus* value was substituted for the European LANDCLIM value of 9.07 from PPE Set 3 for the Holocene.

The results from Run 10 and 11 are illustrated in Figure 4.12. The patterns are the same between these two runs but *Alnus* is drastically reduced when using the value from PPE Set 3. Compared with the original pollen percentages *Picea* is the dominant taxa throughout the majority of the Holocene. *Betula* values have increased slightly in run 11 compared with run 10 but are still much lower than the pollen proportions.

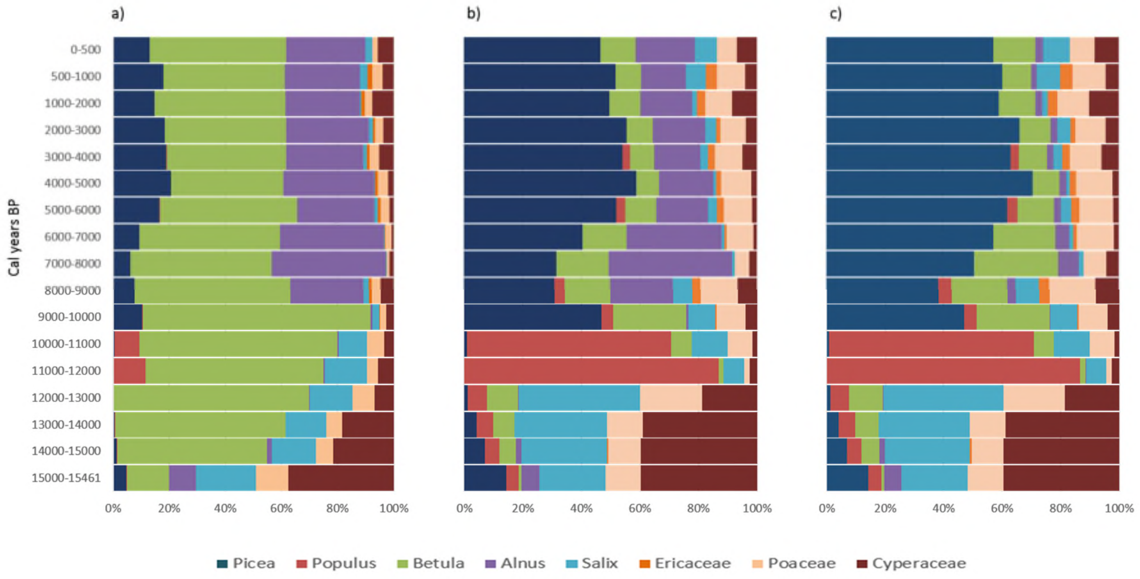


Figure 4.12: (a) *Pollen Proportions from Sithylemenkat and (b) REVEALS estimates of vegetation cover using* PPE Set *1 during the late glacial (15,461-11,000 cal years BP) and* PPE Set *2 during the Holocene (11,000 cal year BP-present day) Run 10 (c)* PPE Set *1 during the late glacial (15,461-11,000 cal years BP) and* PPE Set *2 during the Holocene (11,000 cal year BP-present day) and substituting the Alnus value from* PPE Set *3 for the Holocene (Run 11)*

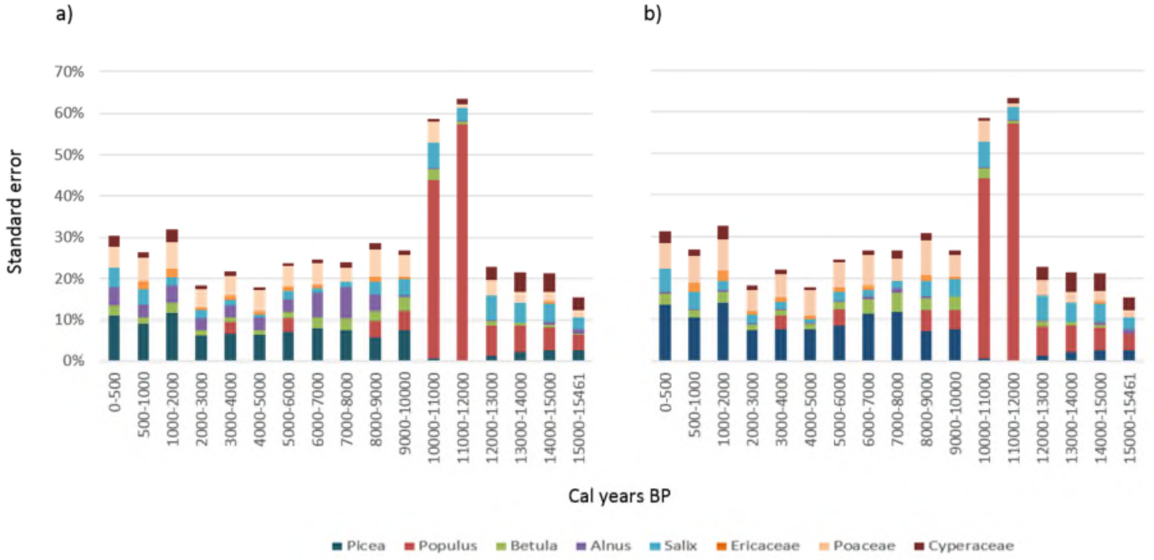


Figure 4.13: *Standard errors REVEALS estimates for Sithylemenkat Lake using (a) the combination of* PPE Set *1 during the late glacial (15,461-11,000 cal years BP) and* PPE Set *2 during the Holocene (11,000 cal year BP-present day) (b)* PPE Set *1 during the late glacial (15,461-11,000 cal years BP) and* PPE Set *2 during the Holocene (11,000 cal year BP-present day) and substituting the Alnus value from* PPE Set *3 for the Holocene*

4.3.4.2 Sithylemenkat and small lakes (PPE Set 1, 2, 4 and 5)

REVEALS scenario run 12 uses PPE Set 1 throughout the late glacial as tundra species dominated during this time and PPE Set 2 throughout the Holocene where deciduous woodland and boreal forest dominate the record in this region. REVEALS scenario run 13 therefore uses the same PPE Sets as Run 10 but the *Alnus* value was substituted for the European LANDCLIM value of 9.07 from PPE Set 3 for the Holocene.

The results from Run 12 and 13 are illustrated in Figure 4.14. Most patterns are the same between these two runs, but *Alnus* is drastically reduced when using the value from PPE Set 3. This was to be expected following the results from Runs 10 and 11. *Picea* values are lower than the estimates using Sithylemenkat Lake on its own, but it is increased from the pollen proportions and an important component of the forest, particularly during the late Holocene. *Betula* values have increased slightly but are still much lower than the pollen proportions. As illustrated in previous runs using a combination of 1 large lake and several small lakes, *Populus* is more visible throughout the record in the Holocene compared with pollen percentages.

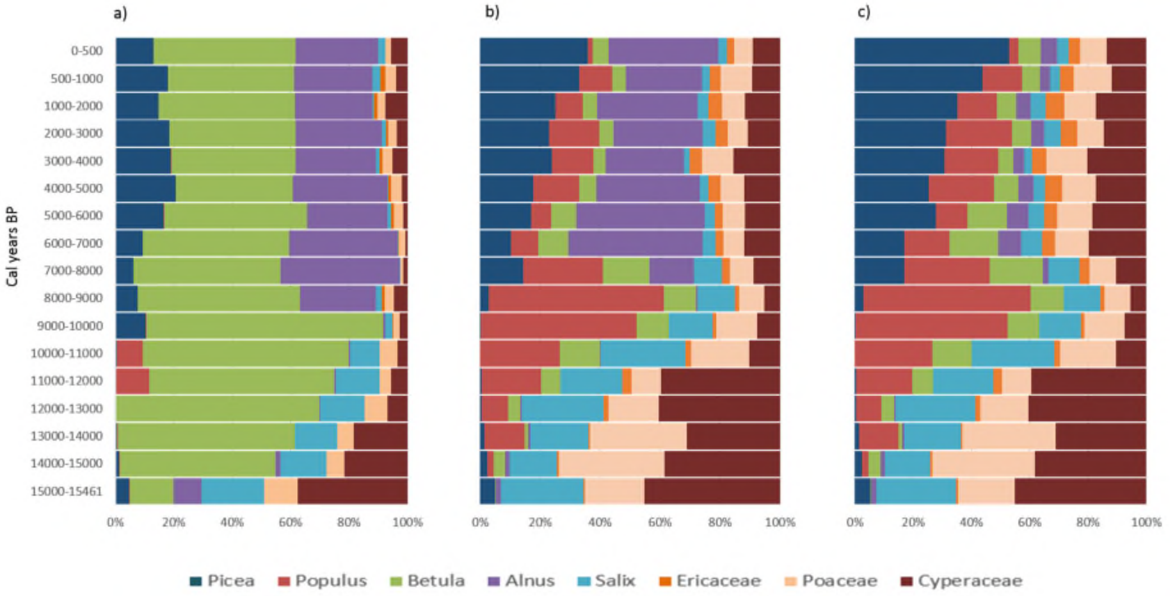


Figure 4.14: (a) *Pollen Proportions from Sithylemenkat and small lakes (b) REVEALS estimates of vegetation cover using* PPE Set *1 during the late glacial (15,461-11,000 cal years BP) and* PPE Set *2 during the Holocene (11,000 cal year BP-present day) Run 12 (c)* PPE Set *1 during the late glacial (15,461-11,000 cal years BP) and* PPE Set *2 during the Holocene (11,000 cal year BP-present day) and substituting the Alnus value from* PPE Set *3 for the Holocene (Run 13)*

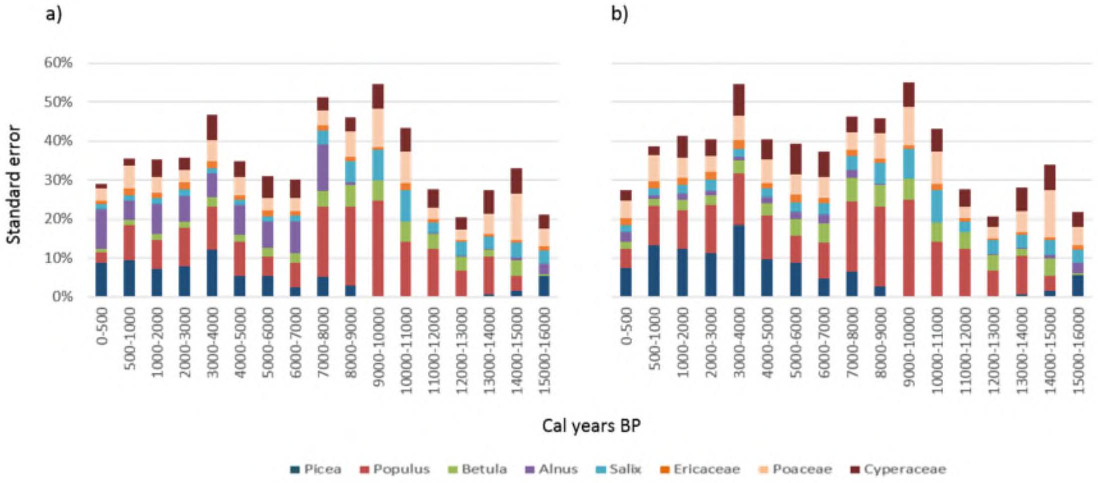


Figure 4.15: *Standard errors REVEALS estimates for Sithylemenkat and small lakes using (a) the combination of* PPE Set *1 during the late glacial (15,461-11,000 cal years BP) and* PPE Set *2 during the Holocene (11,000 cal year BP-present day) (b)* PPE Set *1 during the late glacial (15,461-11,000 cal years BP) and* PPE Set *2 during the Holocene (11,000 cal year BP-present day) and substituting the Alnus value from* PPE Set *3 for the Holocene*

REVEALS scenario run 14 uses PPE Set 4 for the late glacial and PPE Set 5 for the Holocene. These are the same PPE Sets as 1 and 2 and the same scenario as run 12, but the PPEs have been adjusted relative to Poaceae. The results from run 14 are illustrated in Figure 4.16 alongside run 12 results for comparison. The patterns are the broadly the same throughout both sequences, but with the adjusted PPEs in Run 14, Cyperaceae has increased and almost doubled throughout the Holocene to values around 30% and *Alnus* and Ericaceae have decreased.

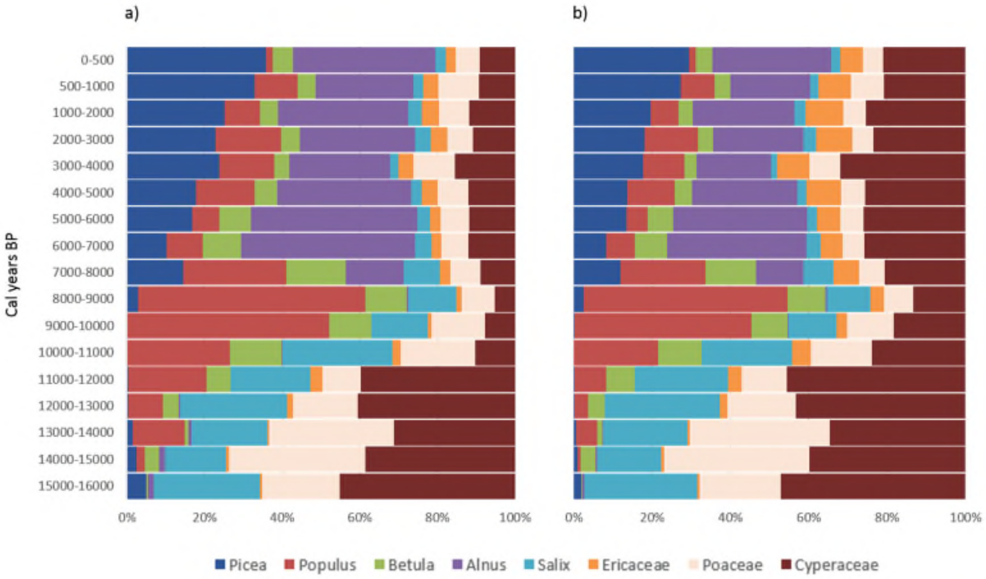


Figure 4.16: (a) *REVEALS estimates of vegetation cover using* PPE Set *1 during the late glacial (15,461-11,000 cal years BP) and* PPE Set *2 during the Holocene (11,000 cal year BP-present day) Run 12 (b) REVEALS estimates of vegetation cover using* PPE Set *4 during the late glacial and* PPE Set *5 during the Holocene (Run 14)*

4.4 Discussion

4.4.1 Methodology

There are various studies which have used a combination of large and small lakes and these have given insights into which provides a more robust and reliable regional reconstruction (e.g. Hjelle *et al*, 2015; Trondman *et al*, 2016). Sugita (2007a) states that several large lakes will provide a more robust reconstruction but where a large lake is not available several smaller lakes can be used but the error estimates will be higher. As several large lakes with robust chronologies were not available for the Brooks Range study region, the decision was made to compare one large lake (Sithylemenkat) with several small lakes.

The REVEALS estimates using 1 large lake (runs 1-2) produced broadly similar patterns to using several small lakes on their own (runs 4-5). The main differences were the representation of certain taxa. *Populus* was present throughout the pollen sequences in all the small lakes, albeit at very low levels but it disappears completely from some time windows at Sithylemenkat. *Populus* is present in the modern boreal forest in the region and it seems unlikely based on other pollen records in the region (e.g. Mann *et al*, 2002; Higuera *et al*, 2009) that it was absent on the landscape for the past 3,000 years. Poaceae and Cyperaceae are also increased in the pollen record when using just the small lakes and this has also resulted in an increase in the REVEALS estimates. This could be due to a stronger pollen signal from local vegetation when using small lakes; which might not be a completely appropriate pollen signal for the regional picture of the region. When the Sithylemenkat record was combined with the smaller lakes (runs 7-8) the results are almost identical to the patterns of estimates shown from just the small lakes. This could indicate that small lakes are producing the same pollen signal as large regional lakes or that the Sithylemenkat signal is being swamped by the small lakes signal.

The error estimates for *Populus* are much higher during the time windows 10,000-11,000 and 11,000-12,000 cal years BP when using just Sithylemenkat than any other scenario/run. However, the overall error estimates for all taxa during the other 15 time windows are lower than the errors produced using a combination of lakes. Hjelle *et al* (2015) and Trondman *et al* (2016) found that several small lakes produced similar results to 1 large lake but with higher error estimates. The results presented here would agree with this pattern observed in other studies, however, there might be more to consider than just the error estimates when deciding on the appropriate data for a regional reconstruction. Trondman *et al* (2016) also found that 1 large lake was appropriate for a REVEALS reconstruction if the regional vegetation is characterised by a regular, large-scale mosaic of vegetation patches.

Trondman *et al* (2015) discuss the factors which affect the reliability, accuracy and precision of REVEALS; these are discussed in detail in Section 2.4.6.1. One consideration is the accuracy of the pollen records' chronologies. As discussed in Chapter 2, Abbot and Stafford (1996) discuss the importance of dating methods. Many Alaskan palaeoecological records have used bulk dating of sediment in the past (Carlson and Finney, 2001) which can be contaminated with older carbon. This can cause problems when trying to provide a confident chronology. This may not be such an issue when using REVEALS in this study as the time windows are quite large (1000 years). The amount of samples per time window could also cause a potential problem. There were some time windows for the small lakes which only used 1 sample. However, these were never run on their own and the minimum number of samples per time window when multiple lakes were run was 5. The only scenario when 1 sample was used was at Sithylemenkat (500-1000 years, runs 1-3).

The most important point to discuss on the methodology is the PPE Sets used. This is also discussed in further detail below, but on reflection the majority of the runs presented in this Chapter could have been improved by using the adjusted PPEs from PPE Sets 4 and 5. PPE Set 1 and 2 were not an appropriate approach and in retrospect the PPEs should have all been adjusted to the same reference taxon before combining.

4.4.2 Pollen Productivity Estimates

Variations in PPEs will have an effect on the reliability and robustness of the REVEALS estimates. Shinya Sugita (*pers comm, 2014*) suggests that obtaining and using PPEs from the study region is best as pollen taxa can contain a variety of species with different ecological niches and, most importantly, different PPEs. However, as discussed in Chapter 2 and 3, PPEs can be affected by a variety of factors, often methodological ones. The *Alnus* PPE obtained in Alaska from the first iteration dataset has been highlighted as a potential taxon which might not be completely reliable and therefore it might be more appropriate to use values from other studies.

The results between the Alaskan PPE Sets 1 and 2 and the European PPEs at Sithylemenkat (Runs 1,2 and 3 for example), show a great deal of variation in the REVEALS estimates. *Betula* is dramatically reduced in the REVEALS estimates across all runs compared with pollen percentages when either of the Alaskan PPE values are used. The estimates for *Betula* are higher when using PPE Set 2 from the Forest compared with the tundra, but this is not surprising as the PPE value is lower than that produced in the tundra. When PPE Set 3 is used on any of the sequences (Sithylemenkat (Run 3), small lakes (Run 6) or Sithylemenkat and small lakes combined (Run 9)) the estimated REVEALS value for *Betula* is increased. What is surprising here is that this PPE value is similar to the value obtained in the Forest (3.12). A potential reason for this could be the exclusion of *Populus* on the runs using European values. As there is no European value for *Populus,* this taxon was not included in PPE Set 3. When *Populus* is included in the pollen sum the REVEALS estimates for this taxon increase dramatically during the early Holocene at Sithylemenkat and throughout the sequence when small lakes are also included. The absence of this taxon is likely to have an effect on the representation of other taxa in the sequence, which could be increasing *Betula* estimates. Equally, the higher PPE value for *Alnus* from Europe has reduced the REVEALS estimates of this taxon which could potentially increase the estimate for *Betula*.

REVEALS estimates for Ericaceae are considerably increased when using the European value (Run 3). The European value is lower but still comparable with Alaska, therefore it could be that this taxon is also experiencing a large increase due to *Populus* being omitted from the record. The reduction in *Alnus*, however, seems more appropriate. The European mean value of 9.07 seems more appropriate than 0.96 obtained in Alaska, but caution should be taken with the interpretation of these results as the *Alnus* value from the first iteration PPEs has not been adjusted to Poaceae (discussed in Chapter 3).

Hellman *et al* (2008) showed that a combination of PPEs was most successful when applying REVEALS in Sweden. They showed that combining PPEs from Denmark provided the best fit for cereals, *Calluna*, *Plantago lanceolata* and *Rumex* compared with the Swedish ones. Various combinations of PPEs were applied to our lakes to assess the variation in REVEALS estimate outcomes. It seems most appropriate to use different PPE Sets in different time windows. The variations in PPEs obtained in Alaska for taxa such as *Betula* is likely to be attributed to different species. Using PPEs obtained from the tundra is more appropriate for the late glacial, when tundra dominated the landscape, and similarly the PPE obtained from the arboreal species is more appropriate for the Holocene, which was dominated by forest. The combination runs (10-13) provide a more reasonable estimation of vegetation cover based on the modern vegetation cover in the southern Brooks Range. However, as *Alnus* is likely to be unreliable, and using the European value within a combination approach (Runs 11 and 13) might provide a more reliable scenario for the regional reconstruction.

The vegetation in the foothills of the southern Brooks Range where the study areas of Ruppert Lake and Lake 3 are located is discussed in detail in Chapter 6. Characterising the regional vegetation which these lakes lie is the primary focus of this Chapter. The modern vegetation in this region is dominated by forests and woodlands on lowlands and hill slopes, with *Picea mariana* muskegs, *P. glauca* and *Populus balsamifera* along riparian area (Higuera *et al*, 2009). *P. glauca*, *Betula papyrifera* and *Populus tremuloides* are frequent on the uplands and south-facing slopes and *Betula glandulosa*, *Alnus* spp. and *Salix* shrub communities occur in the non-forest areas (Nowacki *et al*, 2009). Fire disturbance is also a major controlling factor on vegetation communities within this region (Higuera *et al*, 2009).

Looking at the top time window (0-500 yr) from runs 10-13; *Picea, Betula* and *Populus* proportions seem fairly realistic for this landscape. However, as discussed above the PPE combinations used in these runs are also not entirely appropriate. When PPE Sets 4 and 5 are used the REVEALS estimates for the top time window appear to be a good correlation with the modern vegetation for the arboreal taxa, but Cyperaceae and Ericaceae seem to be slightly over represented. These are the only 2 taxa where the adjusted PPE values did not change from PPE Sets 1 and 2. Further exploration of the data is required into the PPEs produced in Chapter 3. Even though the LFS scores were lower from ERV model 3 and these were taken forward for further analysis, revisiting the data might be an appropriate line of investigation and adjusting the PPEs from ERV model 2 to explore which ERV model is most appropriate.

4.4.3 REVEALS estimations of taxa in the vegetation

REVEALS has been tested and validated at sites across Europe and in the U.S. and has so far been more successful at estimating observed modern vegetation composition compared with pollen percentages (Hellman *et al*, 2008a,b; Soepboer *et al*, 2010; Sugita *et al*, 2010b). Poaceae and other NAP types are generally under-represented and arboreal taxa over-represented in pollen percentages. REVEALS has been shown be successful at predicting the percentage cover of large vegetation units such as total tree, conifers or open land, but less successful at individual taxa in Sweden (Hellman *et al*, 2008a). They found that taxa such as *Picea*, however, which are under -represented in pollen, showed an improvement on the pollen-vegetation cover relationship. This was also found to be the case by Trondman *et al* (2015). REVEALS estimations of cover for *Picea* in Alaska increased over the pollen percentages throughout the Holocene using both the Alaskan and European PPE values and under each scenario/run and using all PPE Sets 1 and 2 and 4 and 5. This would suggest that *Picea* has been under-represented in pollen diagrams.

In the dataset presented here there are few (non-arboreal pollen) NAP types to compare with the European results to test how under represented this type is in pollen diagrams. As discussed above, the small lakes do pose the concern of over representing local vegetation rather than the regional pollen signal. Therefore, taxa such as Poaceae and Cyperaceae might result in an increased estimation of cover in REVEALS from fringing mats of sedge and grass around lakes. This is particularly evident when applying PPE Sets 4 and 5 (run 14) to Sithylemenkat and small lakes. Nielsen *et al* (2010) found that the occurrence of *Phragmites* around the lakes led to an increase in Poaceae in the REVEALS estimates which may not be completely reliable.

REVEALS cannot be validated at this stage in Alaska as a regional cover of modern vegetation (i.e a 100 x 100 km vegetation cover map) was not obtained for the purpose of this thesis. This would be a consideration for further research (discussed in Chapter 7). The second stage of the LRA will be validated in Chapter 5 as detailed vegetation maps were developed as part of the PPE study in Chapter 3. The robustness of the Alaskan PPEs will be tested at this stage. This will rely on some confidence in the REVEALS reconstruction from the first stage of the LRA, however, the results will provide an insight to the appropriateness of the PPEs.

4.4.4 Alaskan Vegetation Reconstructions (PPE Sets 1 and 2 and 4 and 5)

The results presented here (including PPE Sets 4 and 5) from all the various scenarios do suggest that *Betula* was less dominant than previously thought in the late glacial. The high PPE obtained in the tundra will be the main reason for this which was much higher than the PPE from the forest, even when the PPEs were adjusted to Poaceae. As discussed in Chapter 3, the high PPE from Denali is comparable to estimates from southern Sweden (Broström, 2002; Broström *et al*, 2004; Sugita *et al*, 1999) but generally seems higher than PPEs estimated from other studies at higher latitudes. The methodological factors which can affect PPEs have been previously discussed but when validating the LRA in Chapter 5 the high tundra PPE for *Betula* seems reasonable for this landscape. If the high PPE for *Betula* in the tundra is correct and suggesting that *Betula* shrub is very productive then the high percentages obtained in many Alaskan pollen diagrams from the late glacial may not be a true reflection of the vegetation cover.

Coinciding with the decrease in *Betula*, REVEALS estimates show that *Salix* and Poaceae were more dominant on the landscape than previously thought. Anderson and Brubaker (1994) comment that *Salix* pollen in northcentral Alaska prior to the “birch rise” is never abundant, but most common on at southern sites (below the southern Brooks Range into the Yukon River drainage).

The second most striking result from the REVEALS scenarios presented here (including run 14) is that *Populus* appears to be far more dominant in the early Holocene in the Brooks Range than previously thought. Investigations looking at dendrochronological and palynological observations on *Populus balsamifera* on the Alaskan North Slope by Edwards and Dunwiddie (1985) suggested that *Populus* was abundant locally during the late glacial and early Holocene. Modern samples from that study showed that *Populus* can produce abundant pollen but little was found (~5%) >30m from the trees. The low PPE values (0.04 from the first iteration and 0.11 from the second iteration) obtained in the forest suggests that *Populus* is a low pollen producer, however, it is possible that low pollen percentages in the moss polsters could also be that they were located several meters away from the nearest tree. One of the forest sites (F10) was located in the middle of a *Populus* stand (*P.tremuloides*) and this did produce the highest pollen counts (25 grains) but compared with the very high counts of *Betula* and *Picea* this only accounted for 2% of the overall pollen composition. Edwards and Dunwiddie suggest that the high early Holocene pollen values indicate that (a) deposition was occurring from regional vegetation where *Populus* was more common that it is today or (b) that trees were growing in abundance around the site due to higher temperatures in the past.

Edwards and Dunwiddie (1985) demonstrated that *P.balsamifera* has a positive growth response to May temperatures. Bartlein *et al* (2015) suggest that early summer temperatures were likely higher in the late glacial and Early Holocene due to an insolation peak. These warmer temperatures would have been more favourable to *Populus* and facilitated its expansion during this time. Extralimital *Populus* remains from the Arctic slope by Nelson and Carter (1987) also suggest warmer temperatures than today. They suggest that summer temperatures may have lowered the permafrost table and facilitated drainage which may have been responsible for dry summer surface conditions favourable to *Populus*. Bartlein *et al* (2015) used GENESIS V2.01 atmospheric general circulation model (AGCM, Thompson and Pollard, 1995) to run several climate simulation scenarios including vegetation change. They found that this shift from tundra vegetation to deciduous woodland around 11ka was also responsible for additional warming in spring and early summer on top of the insolation peak.

The results presented in this Chapter suggest that REVEALS gives new insights into understanding land cover during the late glacial and the Holocene in the Brooks Range. Reinvestigation of the PPEs presented in Chapter 3 and validating REVEALS in this landscape would be the next step to challenge and test the robustness of the reconstructions presented in this study. As previously discussed in Chapter 2, the patterns of vegetation change across the state are complex and not uniform. Although it would not be appropriate to assume that REVEALS would provide the same cover estimates elsewhere, these results might have implications for the interpretation of pollen records and vegetation change during the late glacial and Holocene in other regions in Alaska.

4.5 Conclusions

- Using different PPEs is most appropriate over different time windows (e.g particularly for the late glacial and Holocene). PPEs obtained from tundra species are most appropriate during the late glacial when tundra dominated the landscape and PPEs obtained from arboreal taxa are most appropriate for the Holocene following the development of deciduous woodland and boreal forest. The next stage for future investigation here would be to use only the new adjusted PPE Set 4 for the late glacial and only PPE Set 5 for the Holocene to assess the appropriateness of combining different PPEs from different biomes.

- Several small lakes in Alaska work just as well for REVEALS as one large lake.

- The *Betula* rise may not have been as expansive in cover as previously thought in the Brooks Range.

- *Salix* may have been more dominant on the landscape during the late glacial and early Holocene.

- *Populus* and the spread of deciduous woodland may have been more extensive than previously thought.

Chapter 5: LRA Validation and modern surface samples

5.1 Introduction

Chapter 4 described the first application of the Landscape Reconstruction Algorithm; REVEALS. The second application is the model LOVE (LOcal Vegetation Estimates) for estimating local vegetation composition within the relevant source area of pollen (Sugita, 2007b, Section 2.5.6). LOVE has been successfully tested on small lakes in Europe (Hjelle *et al*, 2015; Nielsen *et al*, 2010), and both studies highlighted the importance of testing the approach in landscapes where reconstructions will be undertaken. This Chapter describes the testing of LOVE on modern surface samples from small lakes in the tundra along the Denali Highway and the boreal forest around Fairbanks (central Alaska, Figure 5.1) using the pollen productivity estimates from the first iteration described in Chapter 3 and PPE Sets 1 and 2 from Chapter 4 which have not been adjusted to Poaceae.

5.2 Methods

5.2.1 Study Sites

Three small lakes were chosen in the tundra around Denali, each located next to sites where moss polster and vegetation surveys were used to obtain the pollen productivity estimates (Chapter 3). Drop Down Pond was located next to D3; Oh! That Pond was located next to D6 and Petty Pond was located next to D8 (Figure 5.1). Drop Down Pond was located in *Betula* shrub tundra with *Vaccinium* health and *Picea* trees. Oh! That Pond was located in *Salix* and *Betula* shrub tundra with areas of Cyperaceae meadow and Petty Pond was located in *Betula* and *Salix* shrub tundra with patches of *Betula/Vaccinium* heath (Figure 5.2 a-c). One small lake was used in the forest near the University campus in Fairbanks. Smith Lake was located by F2 in *Picea glauca*-dominated forest with over-mature *Populus tremuloides* (Figure 5.1 and 5.2 d). The vegetation around each lake was recorded at a basic level, which involved recording the species present and major plant communities while walking around each lake. The vegetation data used in the analysis for this Chapter were taken from the surveys conducted during the PPE analysis at D3, D6, D8 and F2 (Chapter 3).

Figure 5.1: *Location map of Birch Lake, Ten Mile lake, Drop Down Pond, Petty Pond, Oh! That Pond and Smith Lake (Google)*

Ten Mile Lake (Anderson *et al*, 1994c) was used to obtain the REVEALS regional vegetation composition in the Alaska Range. Ten Mile Lake is located at altitudinal treeline to the south of the Alaska Range (Figure 5.1). *Betula glandulosa* and *Salix* spp. dominate the shrubby vegetation around the lake and Copper River valleys (Anderson *et al*, 1994c). The base of the pollen diagram dates to the late glacial (11540±120, 276-288cm, BETA-42707) and is dominated by *Betula*. The *Picea* rise is dated to around 9000 years followed by *Alnus* around 7000 years (see Figure 5.3).

Birch Lake is located on a high terrace of the middle Tanana Valley, east of Fairbanks (Figure 5.1). Its pollen record was first described by Ager (1975) and a detailed record of late glacial and Holocene vegetation change can be found in Bigelow (1997, pollen diagram shown in Figure 5.4) The site was not glaciated during the Last Glacial Maximum, but the basin was evidently dry or comprised only a few shallow ponds (Abbott *et al*, 2000).

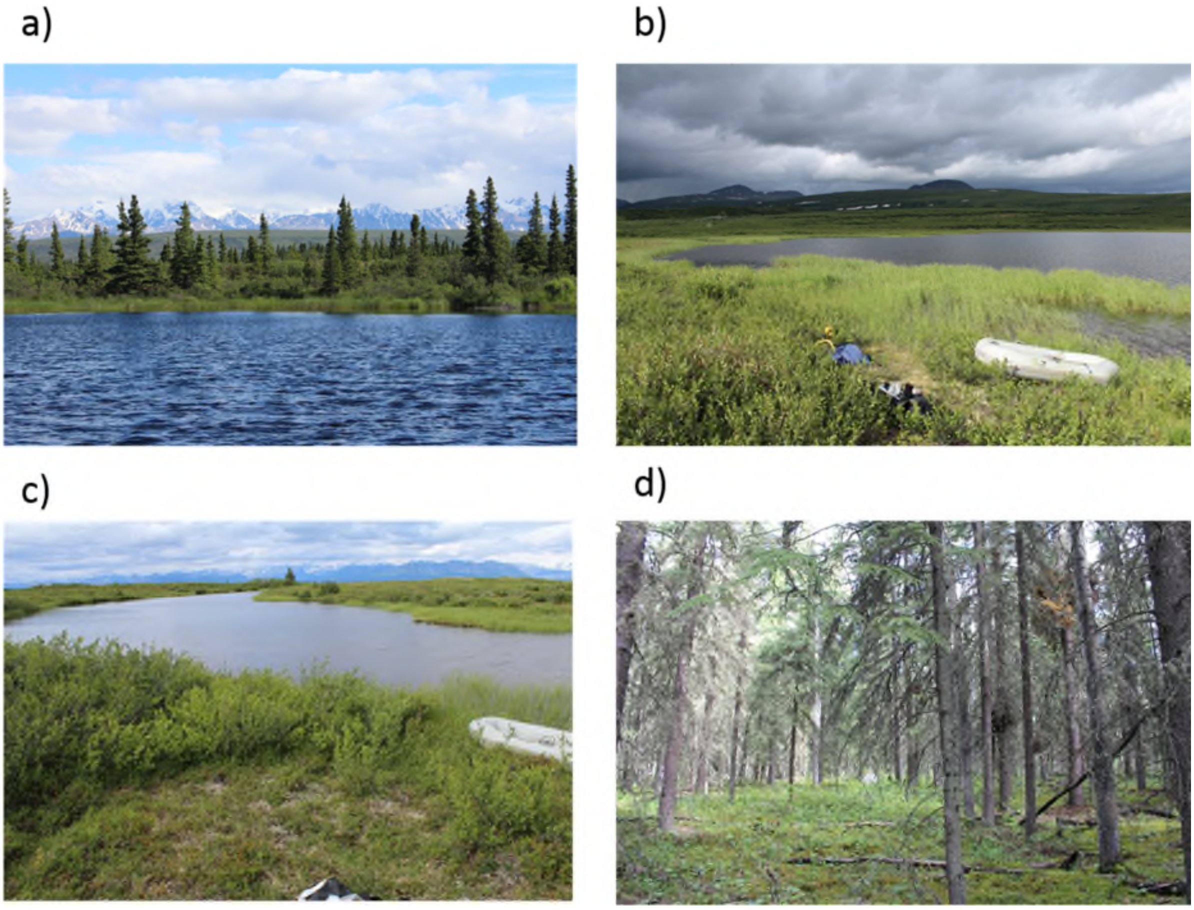


Figure 5.2: *Photos of vegetation around small ponds. a) Drop Down Pond- Betula shrub tundra and Vaccinium health with Picea tress and lake lowland vegetation around the lake; b) Oh! That Pond - Salix and Betula shrub tundra with areas of Cyperaceae meadow; c) Petty Pond - Betula and Salix shrub tundra with patches of Betula/Vaccinium heath and occasional Picea trees; d) The forest surrounding Smith Lake - Picea glauca dominated forest with over-mature Populus tremuloides*

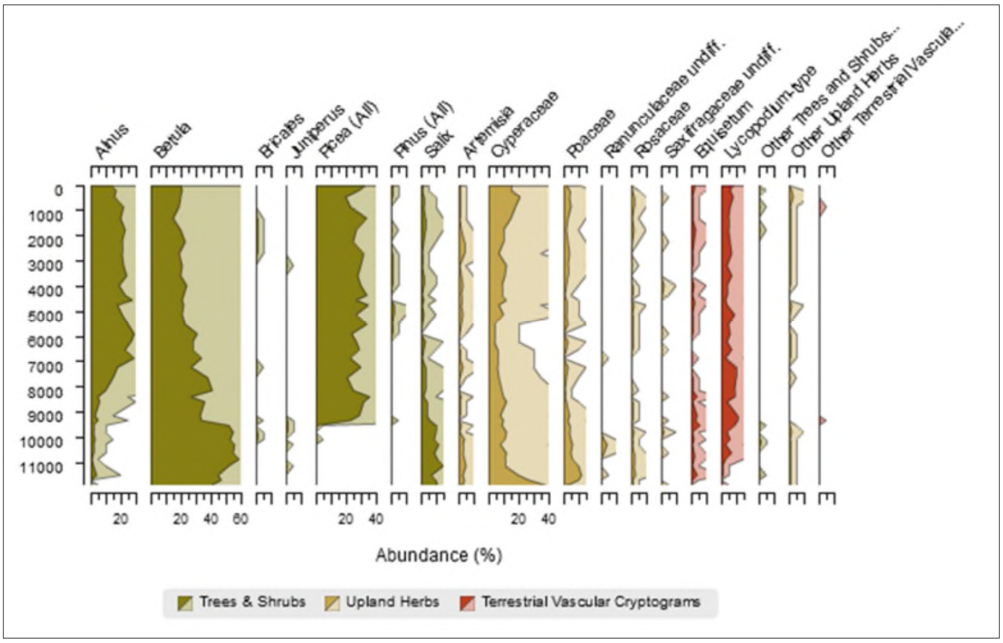


Figure 5.3 : *Ten Mile lake pollen diagram. Ages = years BP (Anderson et al, 1994, generated using the Neotoma Database)*

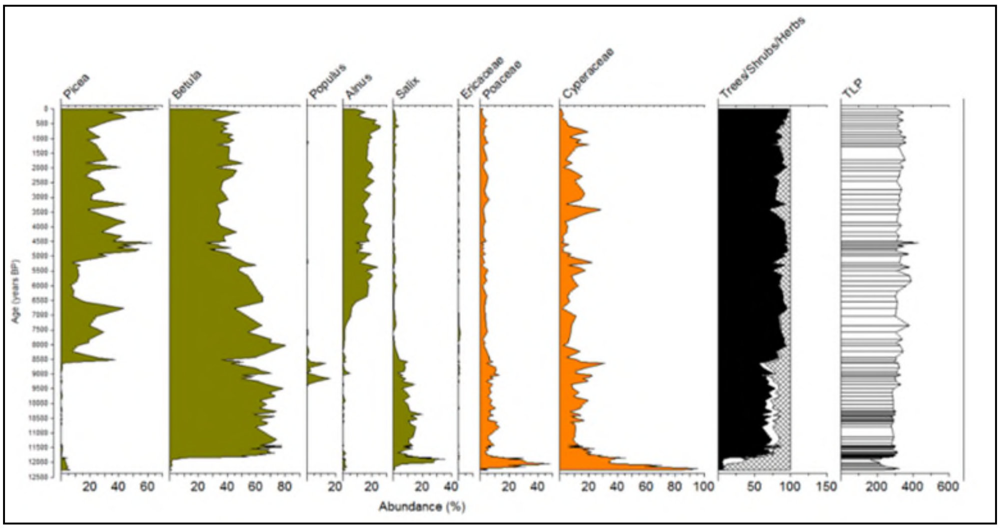


Figure 5.4: *Birch lake pollen diagram. Ages = years BP (Bigelow, 1997) generated using Tilia v.1.7.16 and Tilia Graph, Grimm, 2011*

5.2.2 Surface Samples

The three Denali lakes and Smith Lake were cored using a Uwitech gravity sampler from open water (Figure 5.5) and extruded in the field into 1cm slices. Only the top 0-5cm were retained. The samples were double bagged in Ziploc bags and stored at 4°C.

Figure 5.5: *Collecting surface samples at Drop Down Pond, in the tundra around Denali*

5.2.3 Vegetation Survey and Analysis

The methodology for the vegetation surveys around the moss polsters is outlined in Section 3.2.1. HUMPOL (Bunting and Middleton, 2005) was used to extract the percentage of each taxon within 25m concentric rings out to 1500m and the distance weighted plant abundances were calculated in Excel using 1/d distance weighting (Prentice and Webb, 1986) in Denali and Sutton-Prentice distance (Sugita, 1994) weighting method in the Forest. These distance-weighting methods were chosen based on their suitability during the PPE analysis (see Section 3.3.3).

5.2.4 Laboratory Analysis

Two samples (0-1cm and 1-2cm) were prepared for pollen analysis from each of the lakes. Samples were prepared following standard methods for pollen analysis (Moore *et al*, 1991) including sieving, HF treatment and acetolysis. The residues were mounted in silicon oil. Pollen was counted at x400 magnification using a Nikon Eclipse E200 microscope. A minimum of 300 total land pollen (TLP) grains were counted, including *Alnus* and excluding aquatics and spores. Identifications were made using Alaskan type material held at the University of Southampton.

5.2.5 LOVE and REVEALS models

The LOVE (LOcal Vegetation Estimates) model estimates local vegetation composition within the relevant source area of pollen (RSAP). The model quantifies and then subtracts background pollen (i.e., pollen coming from beyond the relevant source area) in order to arrive at a quantitative reconstruction of local vegetation (Sugita, 2007b). The parameters required to run LOVE are pollen counts from small sites, the RSAP, pollen productivity estimates and the regional vegetation composition. In Chapter 3 the RSAP was evaluated using the Extended R-value model (ERV). Included in LOVE is an inverse modelling approach to estimate RSAP. The inverse model requires that the vegetation composition is expressed as a proportion. The model will try to find a radius within each site where the values reconstructed in LOVE for each taxon lie between 0.0 and 1.0. This is the "the *Necessary Source Area of Pollen* (NSAP)" at each site (Sugita *et al*, 2010b). An iterative process is then used at every 1m or 5m increments to find the solution at each site. The largest estimate of NSAP amount all sites is defined as the LRA-based estimate of RSAP (Sugita, *LOVE user guide*, 2015).

REVEALS v.5.0 (S.Sugita, unpublished program version, 2015) was used to produce the regional vegetation composition for the Denali pond sites using the Ten Mile lake existing pollen record (Anderson *et al*, 1994). The Birch lake pollen record (Bigelow, 1997) was used to produce the regional vegetation composition for the boreal forest in central Alaska. REVEALS was run on the whole pollen sequence from both of these lakes. The results are shown in Figure 5.6 and 5.7 using PPE Set 1 (with the European LANDCLIM value for *Alnus* of 9.07) for Ten Mile Lake and PPE Set 2 (with *Alnus* value of 9.07) for Birch Lake. Combination sets (PPE Set 1 and 2) were not used throughout each sequence (as was the case in the Chapter 4). This is because for the purpose of the validation of LOVE only the top time window (0-500 years) was used for the subsequent analysis rather than the whole of the Late Quaternary period. Therefore, only the PPEs most relevant to the most recent time window were required. The same pollen productivity estimates were used in this study to test the appropriateness of the LOVE model in the tundra and boreal forest of Alaska, i.e., PPE Set 1 (with the European value for *Alnus*) was used for the Denali ponds and PPE Set 2 (with the European value for *Alnus*) was used at Smith Lake in Fairbanks.

The REVEALS output from the top time window at Ten Mile Lake and Birch Lake were then used as the regional vegetation input for each region into LOVE, along with the pollen counts from the small lakes and the PPEs. The three lakes from Denali (Drop Down Pond, Oh! That Pond and Petty Pond) were all run together. LOVE repeatedly failed to run on Smith Lake on its own. As Smith Lake was the only small Lake in the forest that had dwpa data available for this validation exercise two "dummy" lakes were created to run the LOVE program. Pollen counts were created along with a lake radius that was similar to Smith Lake. This, however, did not solve the problem and LOVE repeatedly failed to find a solution for vegetation reconstruction (Appendix A, Table A.6). The pollen counts for the dummy lakes were then adjusted as the previous set might have been too similar in composition and LOVE did find a solution for vegetation reconstruction for some of the taxa at Smith Lake. Due to the complications encountered using LOVE on the Forest data and following the results of LOVE in the tundra discussed below Section 5.3.3); REVEALS was also run on the surface samples of all the small lakes as an experimental validation test for the PPEs obtained in Chapter 3 and this test is further discussed in Section 5.3.4.

5.3 Results

5.3.1 Pollen Analysis

The pollen counts from the surface samples of the small lakes are shown in Figure 5.6. The samples from all three Denali ponds (Oh! That Pond, Petty Pond and Drop Down Pond) produced a similar pollen spectrum. *Betula* produces the highest counts and dominates all the samples followed by *Alnus* then *Picea*. *Populus* is only present at Drop Down Pond (2 grains). *Salix*, Ericaceae and Poaceae have low values at each site with Cyperaceae producing slightly higher counts (between 42-66 grains). Smith Lake also produced similar patterns with *Betula* dominating the sample, followed by *Picea* and *Alnus* at reduced counts compared with the tundra spectra. *Populus* is better represented at Smith Lake (13 grains) but Ericaceae is less well represented in the Forest (1 grain) as this taxa is not a common component of the boreal forest vegetation community.

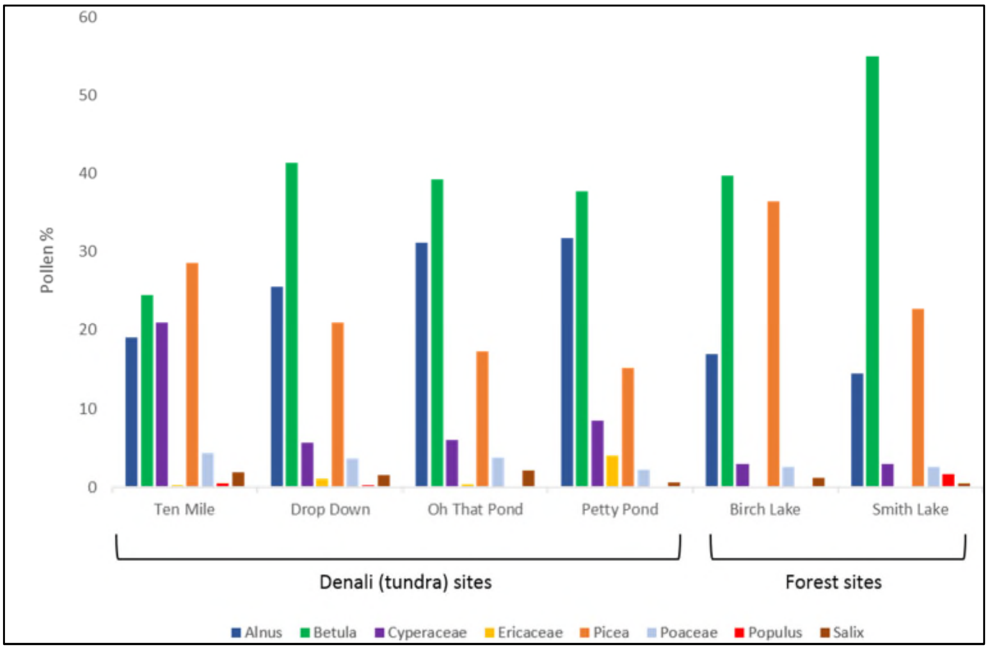


Figure 5.6: *Pollen counts from small lake surface samples in Denali (Drop Down, Oh That Pond and Petty Pond (0-1cm and 1-2cm combined counts) compared with Ten Mile (0-500 years top time window pollen counts and pollen counts from Smith lake surface sample and the top time window (0-500 years) from Birch Lake*

5.3.2 REVEALS – Regional Vegetation Compositions

The results from running REVEALS on Ten Mile Lake using the 8 taxa with PPEs (*Picea, Populus, Betula, Alnus, Salix*, Ericaceae, Poaceae and Cyperaceae) is illustrated in Figure 5.77. The vegetation composition changes quite dramatically from the pollen percentages when using the PPE Set 1 with the European value for *Alnus*. *Picea* completely dominates the sequence during the Holocene with *Betula* and *Alnus* vastly reduced. *Populus* also increases, particularly in the early Holocene (10,500-9,500 years BP). Poaceae and *Salix* increase during the late glacial but remain at similar values to the pollen percentages throughout the Holocene. Cyperaceae also increases during the late glacial but decreases slightly during the Holocene, although still maintaining values between 10-20% of the vegetation composition. Ericaceae values remain low throughout. The top time window (0-500 years) which was used for the subsequent LOVE analysis is dominated by *Picea* up to 70%.

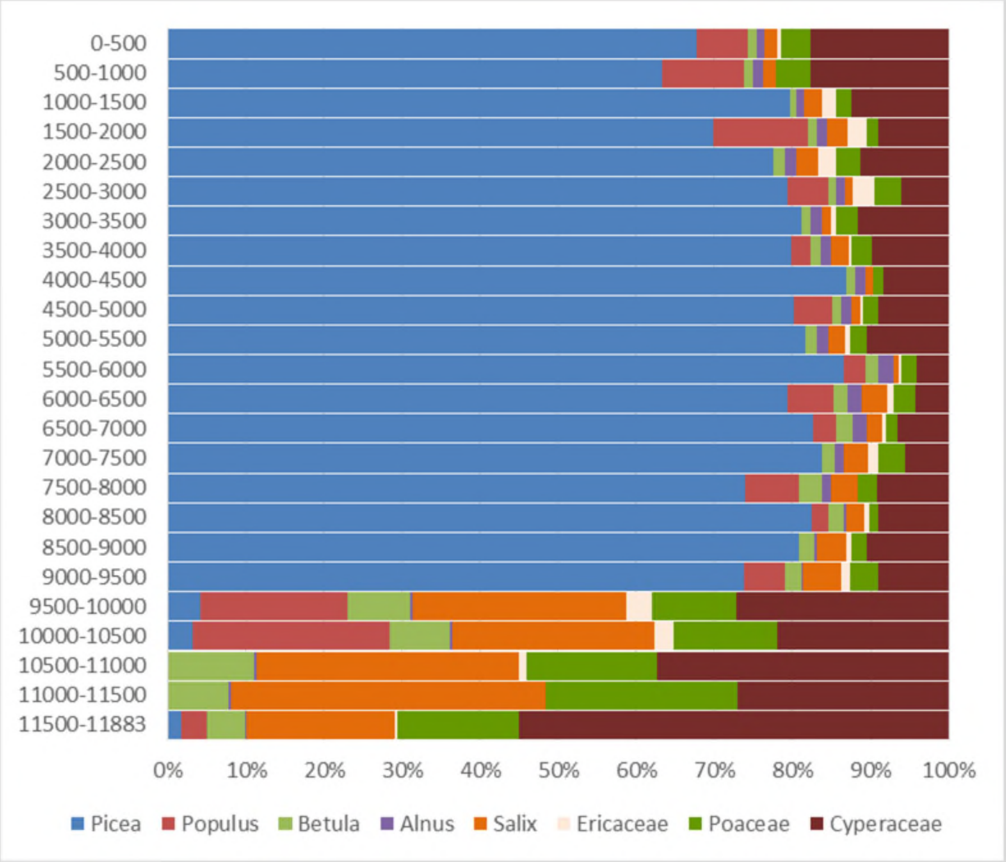


Figure 5.7: *REVEALS regional vegetation composition at Ten Mile Lake*

The REVEALS regional vegetation composition from Birch Lake is illustrated in Figure 5.8. Using PPE Set 2 with the European value for *Alnus* has also dramatically changed the vegetation proportions compared with the pollen percentages. *Picea* dominates the sequence throughout the Holocene, which leads to a large decrease in *Alnus* and *Betula*. The patterns are not dissimilar to Ten Mile Lake, despite Ten Mile being at treeline and thus surrounded by part-tundra and part-forest vegetation. *Salix*, Poaceae and Cyperaceae all increase from the pollen percentages in the late glacial. The increased pollen percentages for Cyperaceae might be due to fringing sedge around the lake rather than a true reflection of the regional vegetation cover. *Populus* increases between 10,000-8,000 years BP with a decrease in *Salix* and *Betula*. The top time window (0-500) is dominated by *Picea* (80%).

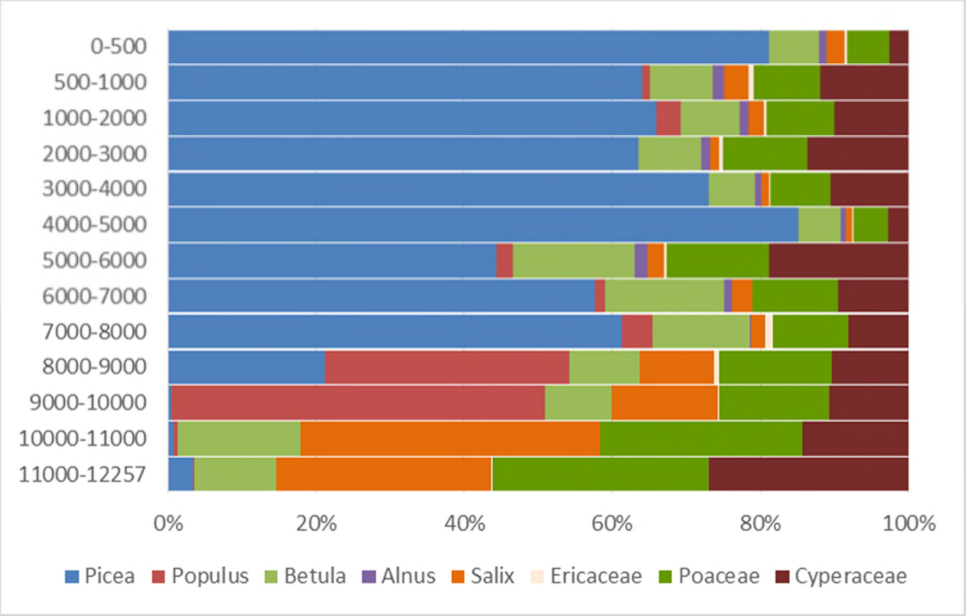


Figure 5.8: *REVEALS regional vegetation composition at Birch Lake*

5.3.3 LOVE on small lake surface samples

5.3.3.1 LOVE in the tundra

LOVE estimated the RSAP at 175m when considering all the NSAP at Drop Down Pond, Oh! That Pond and Petty Pond. When estimated local abundance is <0.0 or >1.0 after the RSAP evaluation the final results are expressed as 0.0 (S.E=0.0) and 1.0 (S.E=0.0) respectively. Vegetation proportion for each taxon is then recalculated in such a way that the total sum at each site becomes 1.0 (Sugita, 2015). The dwpa had been calculated at each site in Chapter 3. The dwpa was taken from the incremental ring nearest the LOVE estimated RSAP for comparison with the LOVE estimates of local vegetation abundance (162.5m, the closest dwpa ring to the LOVE estimated RSAP of 175m) and was recalculated to be expressed as a percentage. The LOVE proportions were also recalculated as percentages for ease of comparison. The results along with the pollen percentages at each site are shown in Figures 5.9 – 5.11.

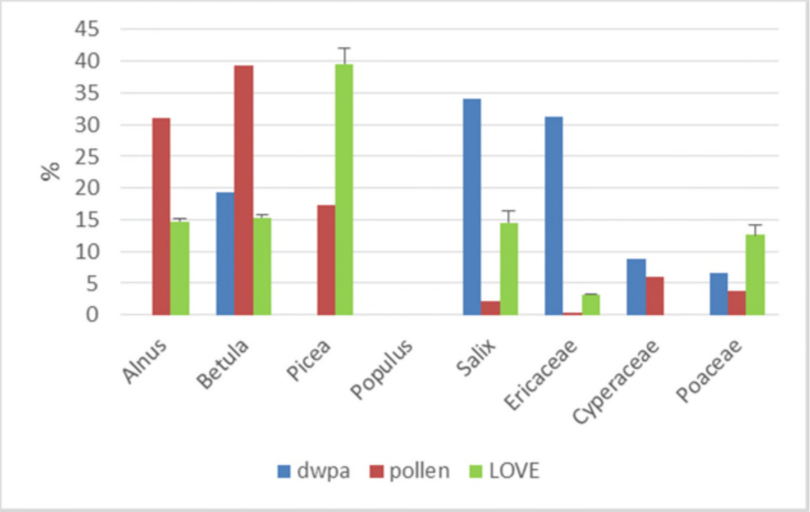


Figure 5.9: *LOVE estimates of local vegetation proportions, pollen percentages and dwpa at Oh! That Pond*

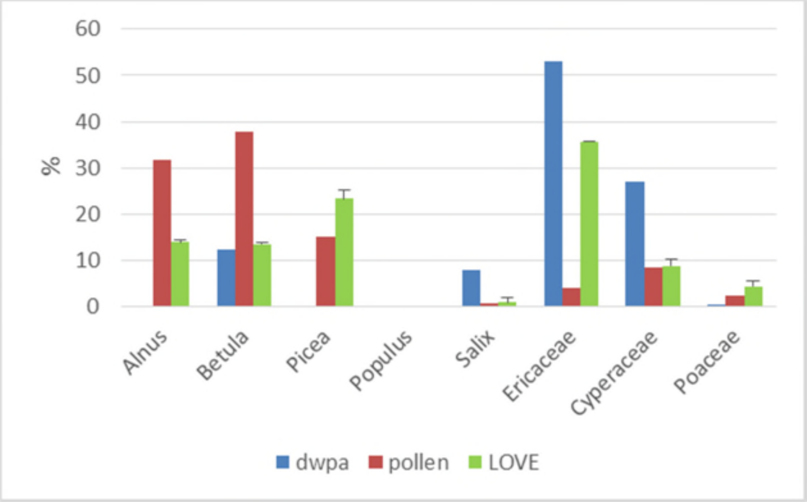


Figure 5.10: *LOVE estimates of local vegetation proportions, pollen percentages and dwpa at Petty Pond*

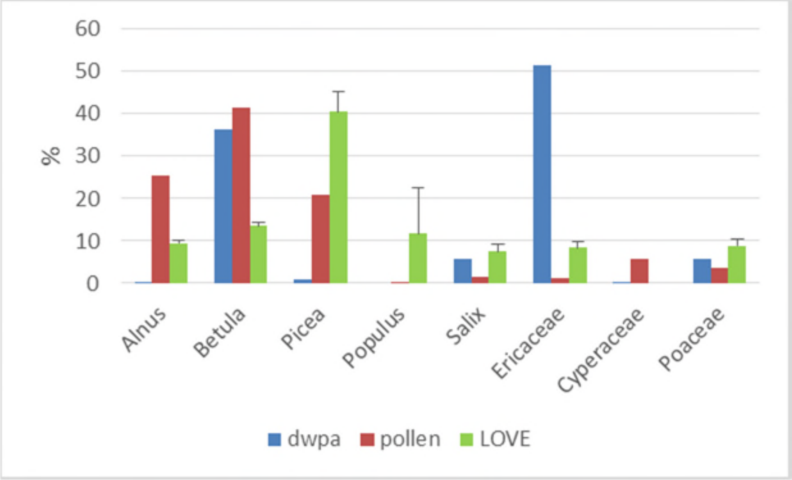


Figure 5.11: *LOVE estimates of local vegetation proportions, pollen percentages and dwpa at Drop Down Pond*

The results show many differences between the LOVE estimates and dwpa. LOVE shows a better correlation with dwpa for *Betula* at Oh! That Pond and particularly Petty Pond compared with pollen percentages, which are much higher. However, this is not the case at Drop Down Pond, where the pollen percentages correlate better with the dwpa. *Picea* has the largest mismatch, as it has very little presence on the local landscape at all three ponds but contributes to over 20% of the LOVE estimates of local vegetation at Petty Pond while dominating the LOVE estimates at Oh! That Pond and Drop Down Pond (up to 40%). The pollen percentages fall in between dwpa and LOVE estimates at each site for *Picea*. The pollen percentages for *Alnus* exceed both the LOVE estimates and the dwpa at each site. The LOVE estimates partly correct for the over representation of *Alnus* pollen but still over represent the taxon compared with the actual vegetation. *Populus* is not present in the local vegetation around any of the sites and is also not present in the pollen at Oh! That Pond and Petty Pond. Pollen is present in the surface sample at Drop Down Pond albeit at a very low value of 0.27%. This has increased the LOVE estimate of *Populus* to 11% which is not a true representation of the local vegetation.

Salix varies between dwpa and LOVE estimates at all three sites. *Salix* dominates the local vegetation at Oh! That Pond along with Ericaceae. However, these two taxa are poorly represented in the pollen record. LOVE estimates have increased *Salix* values, but the estimations are still half of the dwpa while they are only 10% for Ericaceae. The relationship between LOVE estimates for *Salix* and dwpa improve at Drop Down Pond but LOVE vastly underestimates Ericaceae. The pollen counts are very slightly higher at Petty Pond for Ericaceae and the LOVE estimates have increased to over 35%.

LOVE overestimates Poaceae at all three sites. There is little variation in the values between dwpa, pollen percentages and LOVE estimates at Petty Pond and Drop Down Pond where all values are under 10%. At Oh! That Pond LOVE estimates are double that of the actual local vegetation. This is the opposite of Cyperaceae for which LOVE found no solution for the vegetation reconstruction despite Cyperaceae being present in the vegetation and in the pollen record, this was also the case at Drop Down Pond. LOVE estimates for Cyperaceae are half of the dwpa at Petty Pond and are more similar to the pollen percentages.

A further test was applied by removing *Picea* from the regional REVEALS reconstruction (Appendix A, Figure A.3). The top time window (0-500 years) at Ten Mile Lake is dominated by *Picea* and this is not a true reflection of the regional vegetation at the treeline as much of the *Picea* pollen is likely to have travelled up slope to the site (discussed in further detail below). This could be a contributing factor to the differences shown in the results between dwpa and LOVE estimates of the local vegetation. However, this produced a reconstruction where the majority of the

Holocene was dominated by *Populus* and Poaceae which is not a likely scenario for this landscape. To remove any other woody taxa which may have an impact on the local reconstruction would result in removing some of the dominant taxa in this landscape. It was therefore decided to keep the original regional reconstruction from REVEALS for Ten Mile Lake, and consider the limitations of using sites at treeline which are discussed below.

5.3.3.2 LOVE in the Forest

LOVE was run in the Forest with the same taxa as in the tundra but PPE Set 2 and PPE Set 2 with the European value for *Alnus* were used. As discussed above, no solution for vegetation reconstruction was found for any of the taxa at Smith Lake when using two dummy lakes with similar pollen counts. LOVE did find a solution for some of the taxa when the pollen counts were adjusted for the dummy lakes to show greater variation between the taxa (Appendix A, Table A.6). LOVE estimated the RSAP at 145m considering all the NSAP at Smith Lake, Dummy Lake 1 and Dummy Lake 2. The dwpa was taken at 138m (the closest dwpa ring to the LOVE estimated RSAP of 145m) and was recalculated as an expression of percent. The LOVE proportions were also recalculated as percentages for ease of comparison. The results along with the pollen percentages at Smith Lake are shown in Figure 5.12.

LOVE failed to find a solution at Smith Lake for *Picea* despite a fairly significant count (176 grains (22%) see Figure 5.6). A solution was also not found for *Salix*. *Salix* did have low counts (4 grains) at Smith Lake but a solution was found for Ericaceae with only 1 grain present in the sample. Possible reasons for this are discussed in below. Generally LOVE performed well for *Betula*, which was also the case in the tundra particularly at Oh! That Pond and Petty Pond. LOVE estimates for Poaceae and Ericaceae are low and consistent with dwpa. No dwpa was recorded at Smith Lake for Cyperaceae, but the pollen counts are likely from fringing sedge around the lake that was not necessarily recorded from the aerial photographs. LOVE overestimates *Populus* by a significant amount. *Populus* and *Picea* are important components of the local vegetation around Smith Lake and such major discrepancies between *Picea* and *Populus* estimates suggest that LOVE may not be the most useful approach in this landscape. The possible reasons for this are discussed below.

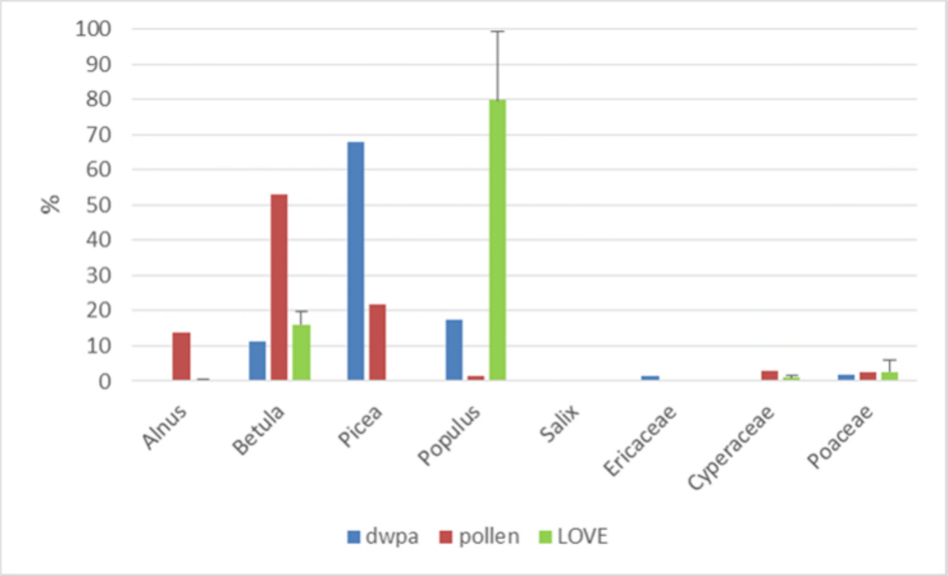


Figure 5.12: *LOVE estimates of local vegetation proportions, pollen percentages and dwpa Smith Lake*

5.3.4 REVEALS on small lake surface samples

5.3.4.1 REVEALS in the tundra

REVEALS was run on the surface samples at Drop Down Pond, Oh! That Pond and Petty Pond as a test of the appropriateness of the PPEs and if small groups of small lakes in the tundra represented the regional vegetation better than the local vegetation. The results are illustrated in Figures 5.13 – 5.15. At Oh! That Pond, REVEALS results align well with REVEALS top time window at Ten Mile Lake, particularly for *Picea*. REVEALS increases *Alnus*, *Betula*, *Salix*, Ericaceae and Poaceae compared with Ten Mile Lake but values are all within 5%. *Populus* values increase at Ten Mile Lake, but *Populus* pollen grains are in the record at Ten Mile and absent from Oh! That Pond. When considering these five taxa, LOVE increases their values a second time, leads to an over representation of *Alnus*, and Poaceae compared with the dwpa. LOVE underestimates *Salix* and Ericaceae but still produces higher estimates than REVEALS. LOVE works well for *Betula* producing estimates nearest to the dwpa and less well for *Alnus*, *Picea*, Ericaceae and Cyperaceae. REVEALS works well for Poaceae and Cyperaceae but less well for *Betula*, *Picea*, *Salix* and Ericaceae.

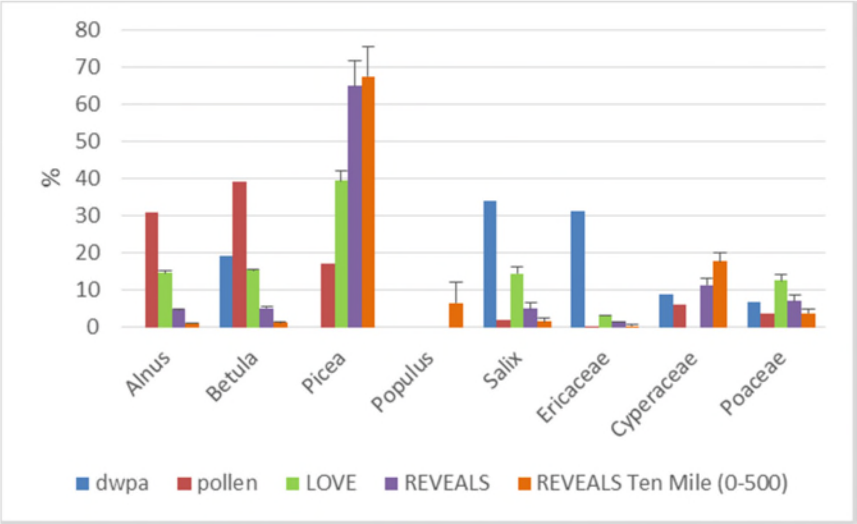


Figure 5.13: *LOVE estimates of local vegetation proportions, REVEALS estimates and REVEALS Ten Mile Lake top time window (0-500), pollen percentages and dwpa at Oh! That Pond*

The patterns at Petty Pond are very similar to Oh! That Pond for *Alnus*, *Betula* and *Picea*. LOVE works better for Ericaceae compared with Oh! That Pond and REVEALS but less well for Cyperaceae. REVEALS at Petty Pond generally produces estimates closer to the top time window at Ten Mile Lake than the dwpa around Petty Pond itself.

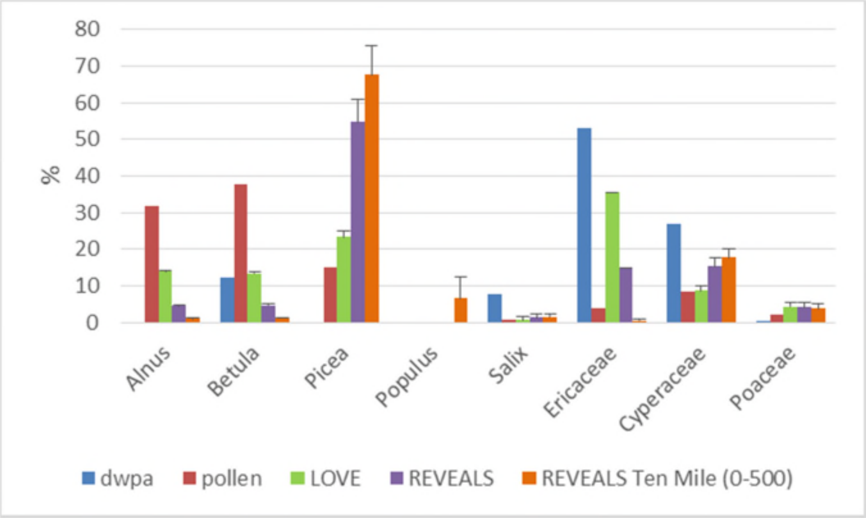


Figure 5.14: *LOVE estimates of local vegetation proportions, REVEALS estimates and REVEALS Ten Mile Lake top time window (0-500), pollen percentages and dwpa at Petty Pond*

The results at Drop Down Pond are fairly similar to the other sites; however LOVE and REVEALS estimates align less well with dwpa for *Betula*, both underestimating this taxon. Ericaceae is underestimated by both LOVE and REVEALS at all three sites, particularly Oh! That Pond and Drop Down Pond. As with the other two sites, REVEALS produces results most similar to those at Ten

Mile Lake. REVEALS generally does not perform that well in the tundra across all three sites, particularly for the main shrubby and woody taxa (*Betula, Salix* and *Picea*). *Populus* is difficult to address in the tundra as it is not always present in the dwpa at each site or the pollen record and this is also the case for *Alnus*. As discussed above, the removal of *Picea* from the regional record (Ten Mile Lake) produced an even more skewed estimate of land cover and was therefore not removed from testing REVEALS on the small lakes here. These results further illustrate the difficulty of using sites at treeline.

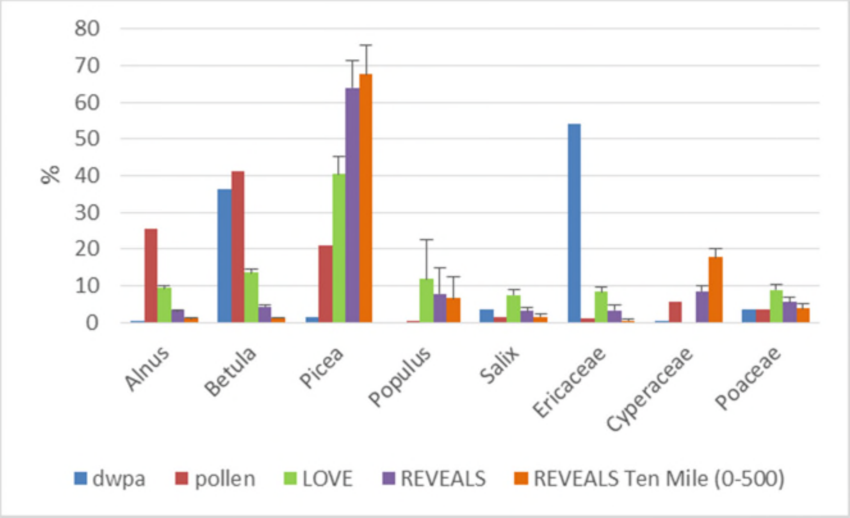


Figure 5.15: *LOVE estimates of local vegetation proportions, REVEALS estimates and REVEALS Ten Mile Lake top time window (0-500), pollen percentages and dwpa at Drop Down Pond*

5.3.4.2 REVEALS in the Forest

The results of running REVEALS on the surface sample at Smith Lake are illustrated in Figure 5.16. REVEALS over estimates *Populus* and underestimates *Betula* and *Picea*, however, the relationship between REVEALS estimates and dwpa is greatly improved compared with pollen percentages alone. The REVEALS estimates are also an improvement for Poaceae. REVEALS overestimates *Alnus*, but reduces the values compared with the pollen percentages. The pollen and dwpa values for Cypercaeae, Ericaceae and *Salix* are all low, between 0 and 7%, and REVEALS estimates also fall within these values. The REVEALS estimates are similar to the top time window for Birch Lake for *Betula*, *Salix*, Cyperaceae, Ericaceae and Poaceae. There is, however, quite a large discrepancy in *Alnus* and *Populus* values; little *Alnus* estimated in the Birch Lake regional record and no *Populus*. *Picea* values are much higher (81%) at Birch Lake than both the REVEALS estimates and pollen percentages at Smith Lake. The results of running REVEALS on the surface sample at Smith Lake do, however, represent the local dwpa much better than using LOVE and give better results than any from the tundra sites. Despite the discrepancies for some of the taxa REVEALS works well in this landscape. Continuous forest with mixed taxa seems to work best for reconstructing past land cover with the LRA and possible reasons why REVEALS is more successful than LOVE are discussed below and in Chapter 6.

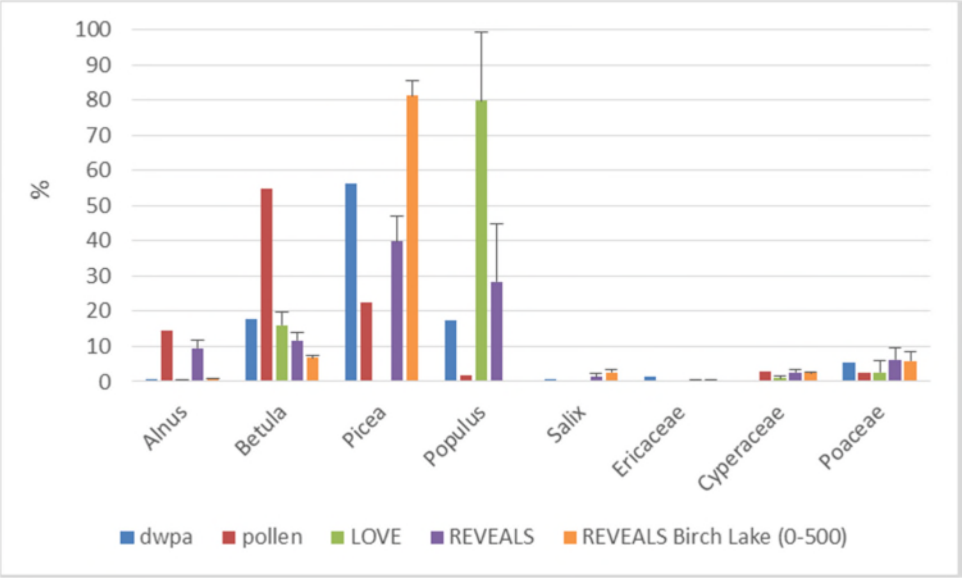


Figure 5.16: *LOVE estimates of local vegetation proportions, REVEALS estimates and REVEALS Birch Lake top time window (0-500), pollen percentages and dwpa at Smith Lake*

5.4 Discussion

5.4.1 Relative Source Area of Pollen

There is a marked difference in the RSAP obtained for the tundra using the ERV model versus LOVE. The RSAP for the tundra moss polster sites using the ERV model 3 was 800m but 175m using the inverse model in LOVE. The RSAP of 800m was deemed reasonable and comparable to similar patch sizes in the Swiss Plateau (Soepboer *et al*, 2007). Many small sites are needed for a reliable RSAP (Sugita, 2007b; Sugita *et al*, 2010). The RSAP of 175m is therefore likely to be unreliable due to only using 3 sites. The estimates of RSAP using the inverse model in LOVE also tend to be sensitive to rare plant taxa in the pollen data (Hjelle *et al*, 2015). The greater the number of rare taxa in the pollen; the larger the RSAP (Hjelle *et al*, 2015; Shinya Sugita *pers comm*). As only a limited number of taxa were used, and few are rare pollen types, this could be another reason for the low RSAP. Patch size is also a contributing factor to RSAP, and the implications of this are discussed further in the Section below.

The RSAP for the forest moss polsters using ERV model 3 was 200m and 145m using the inverse model in LOVE; these values are reasonably comparable. While potential methodological problems with the survey method used in the forest (discussed in Section 3.4.2.1), may have affected the estimates, an RSAP of 200m was deemed appropriate for this landscape based on previous studies (Calcote, 1995; von Stedingk *et al*, 2008, discussed in Section 3.4.1). A previous study from closed forests in Wisconsin and Michigan (Calcote, 1995) produced estimates of RSAP between 50-75m. Therefore, the LOVE estimate of 145m is reasonable for this landscape.

5.4.2 LOVE Validations

The patterns produced for the 8 individual taxa in the tundra are complex and the estimates were seldom close to a true reflection of the modern vegetation. There are various reasons why this might have occurred including the PPEs used (discussed in Section 3.4.4), the vegetation survey, the location of sites in the treeline ecotone and the regional vegetation input. When the local plant composition (dwpa) differs a lot from the mean composition of the constituent taxa in the regional vegetation, the LOVE estimates would deviate greatly from the expected (Shinya Sugita *pers comm,* 2017). The top time window (0-500 years) at Ten Mile Lake is dominated by *Picea*, but this is not an accurate reflection of the regional vegetation at the treeline (see below). *Picea* is over estimated in LOVE and REVEALS in the tundra. LOVE reduces the estimate at each site but it is still much higher than the dwpa. *Picea* pollen is widely dispersed and the pollen percentages at Ten Mile Lake and the Denali ponds is most likely reflect the effects of wind dispersal from *Picea* populations in nearby valleys (Anderson *et al*, 1994). Pollen percentage data is particularly difficult to interpret from treeline regions as wind-pollinated tree species dominate the percentages of pollen assemblages despite the absence of the corresponding tree species at the site (Seppä and Hicks, 2006). *Picea* is therefore probably more over-represented at treeline and into the tundra than in the forest. Therefore, pollen percentages at these sites and at Ten Mile Lake are not an accurate reflection of the vegetation.

The regional and local signals from the pollen are also further complicated by the fact that the vegetation is not homogenous at treeline in the tundra. The sites used for both the regional and local reconstructions are set in a complicated landscape of approximately half forest (at lower elevations) and half tundra (higher elevations). This violates the assumptions of the LRA. REVEALS is assuming that the vegetation is homogenous with 50% tree cover and 50% shrubs and tundra vegetation at any point in the landscape. Figure 5.17 a and b illustrates an example of two sites (Petty Pond and D10; moss polster site used in Chapter 3) which are located in the tundra landscape along the Denali Highway. The vegetation is constructed of large and more irregular areas of shrub and heath around Petty Pond with no *Picea* or forest recorded within the 1500m radius around the site. Large areas of shrub tundra are also evident in the landscape around D10 with occasional dense *Picea* patches.

This scenario is not the case in forested landscapes. In the forest, Smith Lake is producing a similar pollen signal to a larger "regional" lake. In the Interior boreal forest vegetation comprises small-scale patches often formed by homogenous stands. There are few 'gaps' (i.e. open areas) and therefore the pollen signal and dwpa is similar whether looking at a large lake or a small lake. The scenario is different in the tundra as discussed above, with large irregular areas of communities such as *Betula* shrub or tussock tundra with occasional trees (Figure 5.17).

The scale of the mosaic in the boreal forest largely determined by fire patterns, drainage and aspect (M. Edwards *pers comm*, 2017; Lloyd *et al*, 2006; Viereck and Little, 2007). As discussed in Chapter 3, patch size simulations in open landscapes in southern Sweden (Sugita *et al*, 1999) also produced larger RSAP estimates than closed forests (Calcote, 1995) which is attributed to more patch types that were infrequent. Bunting *et al* (2004) concluded that it was the size of the patches in the landscape that were the major controlling factor on RSAP estimates. This is another reason why the RSAP of 145m obtained for the tundra in this study does not seem appropriate for this landscape.

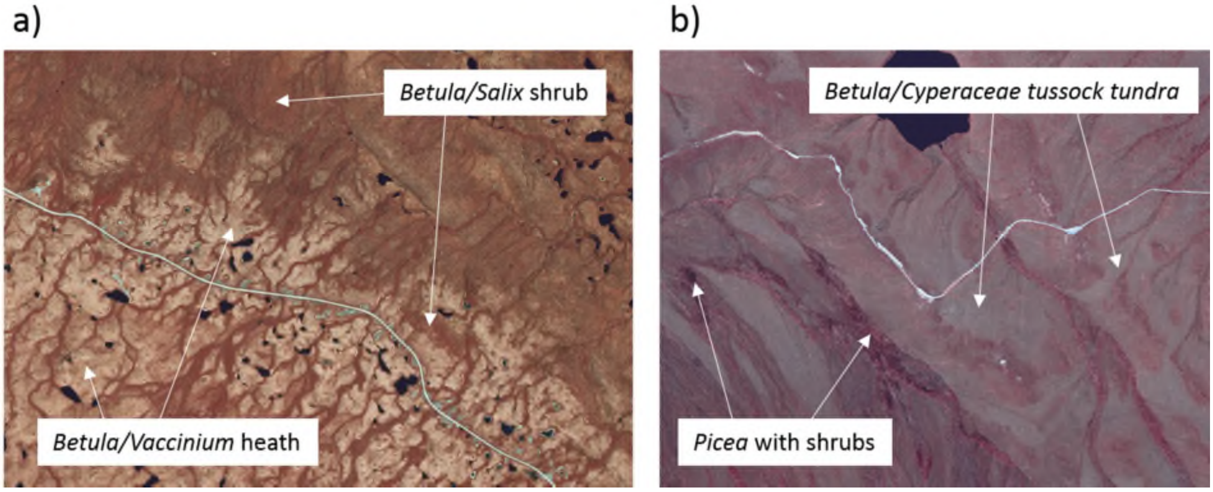


Figure 5.17: *Examples of aerial photographs from the Denali moss polster sites used in* Chapter *3 and 5 a) 1500m landscape around Petty Pond with large areas of Betula/Vaccinium heath and Betula/Salix shrub with no Picea trees recorded b) Vegetation near D10 as an example of treeline sites in this landscape with large areas of Betula/Cyperaceae tussock tundra with occasional Picea patches (USGS)*

Continuous forest with mixed taxa seems to work best for reconstructing past land cover with the LRA. The patch sizes in the interior boreal forest are most likely small enough that several small lakes are just as appropriate to use for REVEALS as a large lake in this landscape. This is also probably why REVEALS also performed well using several small lakes in the Brooks Range (Chapter 4). This is further corroborated when examining REVEALS output at Smith Lake. Here REVEALS produced a better relationship with the local dwpa than the pollen. This could also be a fundamental reason as to why LOVE did not perform as well in the forest. The LOVE model quantifies and then subtracts background pollen to arrive at quantitative reconstructions of local vegetation (Sugita, 2007b). A mismatch with REVEALS estimates can also result in inappropriate LOVE estimates (Shinya Sugita *pers comm*, 2017). However, if the regional background pollen is the same as the local pollen then this could be affecting the LOVE estimates as the model is trying to subtract what is actually part of the local vegetation. Therefore, this is the likely cause as to why the LOVE estimates are providing a worse result.

5.4.3 Pollen Productivity Estimates

As discussed in Chapters 2 and 3, pollen productivity estimates are one of the key input parameters into the LRA. However, PPEs can be affected by a variety of factors, often methodological ones (see Section 2.5.3). Hjelle *et al* (2015) found that the LRA performed well when classifying plant taxa into forest and open land types but the patterns were less clear with individual taxa. They suggest two reasons for this; PPEs and the vegetation survey. Hjelle *et al* (2015) found that the pattern for *Alnus* was complex with some of the LOVE estimations producing a good fit with the dwpa at some sites but an over or under estimation at others. The *Alnus* PPE (0.96) obtained in Alaska has been highlighted potentially unreliable, and therefore the LANDCLIM project European mean value (9.07) was used in this study. However, even using the higher value LOVE over-estimated the taxon values compared with the dwpa. This could potentially suggest that even a value of 9.07 is too low. However, REVEALS estimates at Drop Down Pond (Figure 5.15) produce a better fit with the dwpa. This would suggest that other factors are affecting the LOVE estimations rather than the PPE. There was no *Alnus* recorded in the vegetation at Oh! That Pond and Petty Pond so it is difficult to assess the reliability of records from these sites. REVEALS over estimates *Alnus* at Smith Lake (Figure 5.16) but the values are comparable with the top window (0-500 years) at Birch Lake.

LOVE estimates are an improvement compared with pollen percentages for *Betula* at Oh! That Pond and Petty Pond. This is not the case at Drop Down Pond but *Betula* is abundant in the vegetation and the pollen at Drop Down Pond but has very low estimations in the regional composition at Ten Mile Lake. When the REVEALS estimates vary greatly from the local vegetation composition, the LOVE estimates may not be reliable (Shinya Sugita *pers comm,* 2017). Therefore, it is likely that the under estimation of *Betula* at Drop Down Pond is most likely due to the large differences between local dwpa and the regional vegetation composition rather than an inappropriate PPE value. This applies to most of the taxa in the tundra, and, particularly as REVEALS improves the relationship for Poaceae and Cyperaceae, other factors than PPEs probably cause the discrepancies between LOVE estimates and dwpa. This is further corroborated by the

REVEALS results at Smith Lake where the relationship between REVEALS estimates and dwpa is greatly improved compared with pollen percentages alone.

Reflecting on previous discussions in Chapters 3 and 4, the choice of PPEs used in this Chapter may also be contributing to the LOVE results presented here. The next approach for further exploration of validating the LRA would be to apply the adjusted PPEs from the second iteration data set in Chapter 3. The validation could be improved in Denali by using PPE Set 4 from Chapter 4 on the 3 small ponds and Ten Mile lake as the current PPE Sets used in this Chapter are not all adjusted to the same reference taxon.

5.4.4 Vegetation Surveys and DWPA

The vegetation survey methodology can affect the PPE values and this could also be one of the reasons why the LRA estimates did not always produce a good fit with the dwpa. As discussed in Chapter 3, it seems unlikely that the vegetation survey was a major cause of any discrepancies in the PPE datasets as any changes in community boundaries were closely monitored and surveyors were the same at each site, which promoted consistency and minimised and inter-recorder error or bias (Bunting *et al*, 2013). However, the vegetation recorded between 100m-1500m was taken from aerial photography and the Alaska Vegetation Classification (Viereck *et al*, 1992). The communities were sampled in the field to check vegetation composition but there is a possibility that not all of the communities were correctly assigned from the aerial photography. This could particularly be the case with fringing sedge communities around Smith Lake. Patches of tree cover, particularly *Picea*, are easily identified through aerial photography so it is unlikely that this is the cause for the major discrepancy between LRA estimates and dwpa of *Picea*.

A possible reason for differences between the LRA estimates and dwpa could be cover vs biomass. The vegetation surveys adopted in this study focused on recording estimations of cover. However, if biomass were recorded these values would be different. In the tundra, for example, even if Ericaceae was recorded at 80% cover and *Betula* at 20%, these values could easily be reversed if biomass were estimated. The Ericaceae is also low pollen producers so although this taxon is widespread across the landscape and accounts for a high dwpa at all the tundra sites, it is still being dramatically under estimated by the LRA. Hjelle *et al* (2015) conclude that patterns are less clear for individual taxa or species groups compared than they are for estimations of open or forest cover. They suggest that producing good vegetation data is probably a critical step for testing and validating LRA on a site-specific and taxon-specific scale. Investigations in the boreal forests of Finland have also shown that pollen accumulation rate (PAR) of common tree taxa there directly related to biomass (Seppä *et al*, 2009). Seppä *et al* (2009) also suggest that PAR records provide a potential proxy for quantitative biomass. It might therefore be more appropriate to estimate biomass rather than cover in future studies, or to apply a conversion, if available.

5.5 Conclusions

- There are limitations in using sites at treeline.
  - The pollen assemblages from lakes within this ecotone are not a true reflection of the taxa present within the reconstructed landscape. *Picea* dominates the records as its pollen travels upslope from the forested valleys, but it is not a major component of the vegetation.
  - REVEALS assumes that the vegetation is homogenous, in this case with 50% tree cover and 50% shrubs and tundra vegetation at any point in the landscape, when in fact the landscape comprises half forest and half tundra in large areal blocks.

- In the boreal forest small sites are recording the same vegetation mosaic as large sites. It is possible that LOVE cannot improve on the estimates of REVEALS in this situation. A corollary of this is that, the successful application of LOVE might be restricted to certain landscapes and combinations of lakes.
- The PPEs from the second iteration in Chapter 3 and PPE Set 4 from Chapter 4 would have been more appropriate to use here on the small ponds in Denali so that all the PPEs in the analysis were adjusted to the same reference taxon. This would be the most appropriate next stage for future research to test the LRA in the tundra.

- The next Chapter will apply the LRA using the regional vegetation estimates derived in Chapter 4 and attempt to reconstruct the local vegetation cover around Lake 3 and Ruppert Lake in the southern foothills of the Brooks Range. From the results presented in this Chapter, it seems likely that LOVE will not necessarily perform better than REVEALS in this landscape.

Chapter 6: Vegetation Reconstructions in the Brooks Range

6.1 Introduction

This project was originally linked to the Lakes in the Arctic Carbon Cycle (LAC) Project funded by NERC Arctic Research Programme (NE/K000349/1). LAC aims to understand the interactions between Arctic landscape ontogeny, biodiversity and aquatic biogeochemical cycling at the landscape scale. Regionally replicated palaeo records from small sets of lakes in Greenland, Norway and Alaska are being used to evaluate the effect of changing Plant Function Types (PFTs) on aquatic diversity and nitrogen and carbon cycling over Holocene timescales. Testing reproducibility of the signals in records within regions is a key element of the project. This thesis is linked to LAC as it specifically addresses shifts in vegetation types in Alaska throughout the late glacial and Holocene and particularly how vegetation composition can be reconstructed quantitatively.

The previous Chapters (4 and 5) have addressed the Landscape Reconstruction Algorithm (the LRA) and the testing and validation of this model in Alaska. This Chapter focuses on two small lakes in the south central Brooks Range; Ruppert Lake and Lake 3. Ruppert Lake pollen and charcoal records have previously been studied (Brubaker *et al*, 1983; Higuera *et al*, 2009) and these data, along with new data collected through the LAC project are presented here. This Chapter also presents a new site 1km away from Ruppert Lake; Lake 3, and examines the degree of palaeoecological congruence between two sites in the same area with different catchments. New data from Lake 3 include high resolution pollen and charcoal records. The Landscape Reconstruction Algorithm was applied to quantitatively reconstruct the vegetation cover in the region and to re-assess the charcoal records and the interpretation of the fire histories in these two lake catchments in light of revised vegetation cover estimates.

6.2 Study Sites

6.2.1 Ruppert Lake

Ruppert Lake and Lake 3 are kettle lakes on a terminal moraine located in the foothills of the south-central Brooks Range. Forests and woodlands dominate the lowlands and hillslopes of this region, with *Picea mariana* muskegs and *Populus balsamifera* in riparian areas, and *P. glauca*, *Betula papyrifera* and *Populus tremuloides* on uplands and south-facing slopes (Nowacki *et al*, 2000). *Salix* spp., *Betula glandulosa* and *Alnus* spp. dominate the shrub communities away from forested areas (Higuera *et al*, 2009; Nowacki *et al*, 2000). Ruppert Lake is located to the east of Walker Lake (67° 04.19 N, 154° 14.40 W) in the south central Brooks Range (Figure 6.1).

Figure 6.1: *Location map of Ruppert Lake and Lake 3 within Alaska. Catchment scale maps are shown in Figures 6.4 and 6.6. (Google)*

The freshwater lake has a small inlet stream coming from the north and an intermittent outlet stream flowing westward into Walker Lake. The vegetation around Ruppert Lake can be seen in Figures 6.2 and 6.3. Fringing sedge mats occur around the lake, with small *Populus tremuloides* trees and *Betula* shrubs occupying adjacent moraine slopes. The main arboreal species near the lake is *Picea mariana* and *Picea glauca* is common on the better drained moraine slopes. The vegetation mosaic has largely been controlled by the fire regime. The most recent fire occurred in 1991 (15, 357 ha; Higuera *et al*, 2009; Alaska Fire Service, 2004). The catchment is much larger (3.1 km^2) than that of Lake 3 (0.06 km^2) (Figures 6.4 and 6.6). The lake: catchment ratio at Ruppert is ca. 1:77.

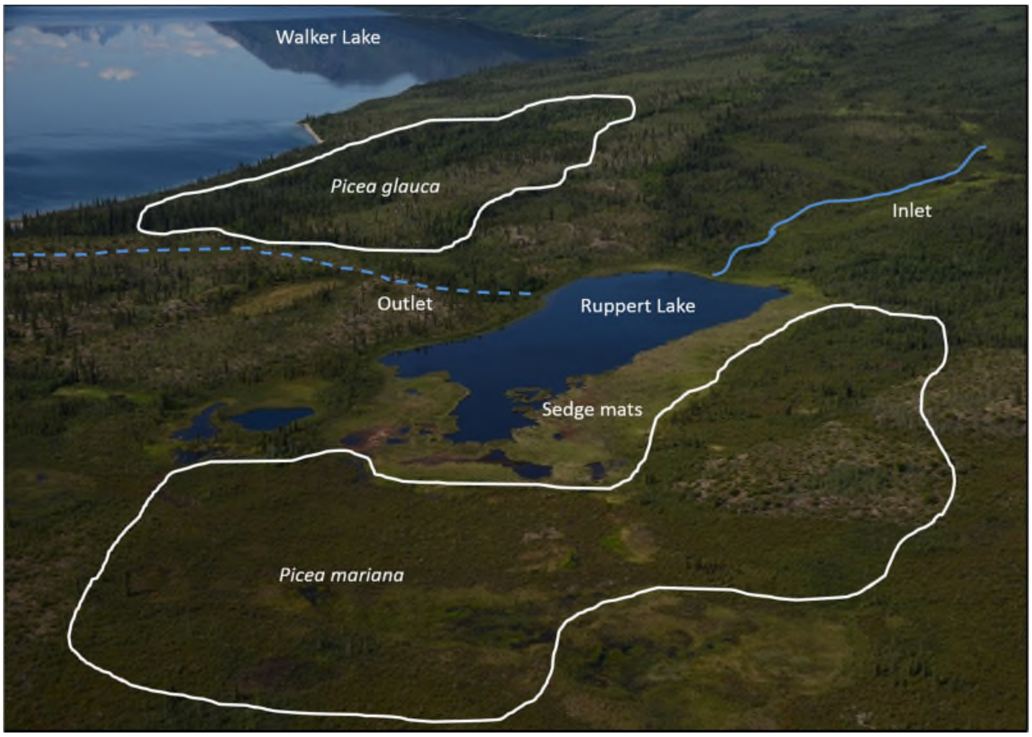


Figure 6.2: *Aerial photograph of Ruppert Lake. Walker Lake to the East (photo credit: Tom Roland, 2013)*

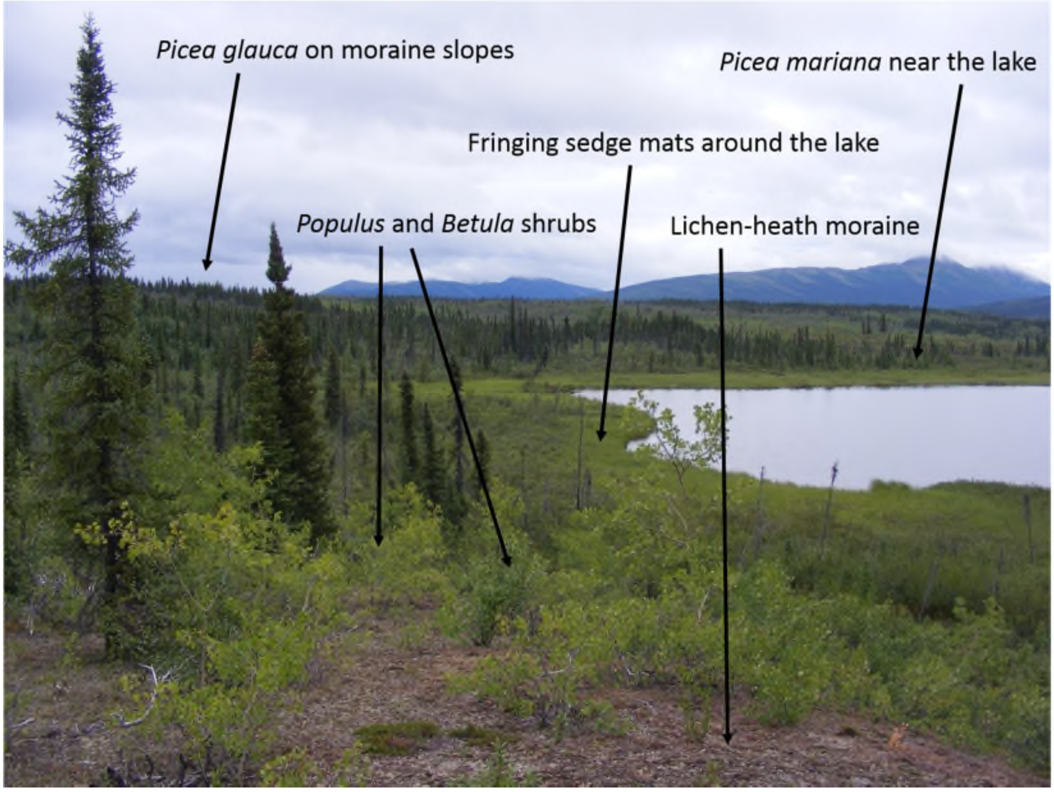


Figure 6.3: *Vegetation around Ruppert Lake (photo credit: M. Edwards, 2013)*

Figure 6.4: *Ruppert Lake catchment (K. Reuss-Schmidt, Google Earth)*

6.2.2 Lake 3

Lake 3 is located approximately 1km north-east of Ruppert Lake and lies east of Walker Lake (67° 04.33 N, 154° 13.53 W). Lake 3 is a freshwater lake with no clear inlet, but it does have an outlet to the east side which connects hydrologically to a neighbouring lake (Figure 6.5). Lake 3 is 0.87ha in area and has a maximum water depth of 4.25m. As with Ruppert Lake, Lake 3 is a kettle lake formed on moraine from the last glacial period. The catchment is smaller than that of Ruppert (0.06 km^2) with a lake: catchment ration of c. 1:9 (Figure 6.6) and is dominated by *Populus tremuloides* and *Betula glandulosa*, with *Picea mariana* near the lake. Lichen-heath is common on the moraine slopes, and small sedge mats occur at the lake edge (Figure 6.5).

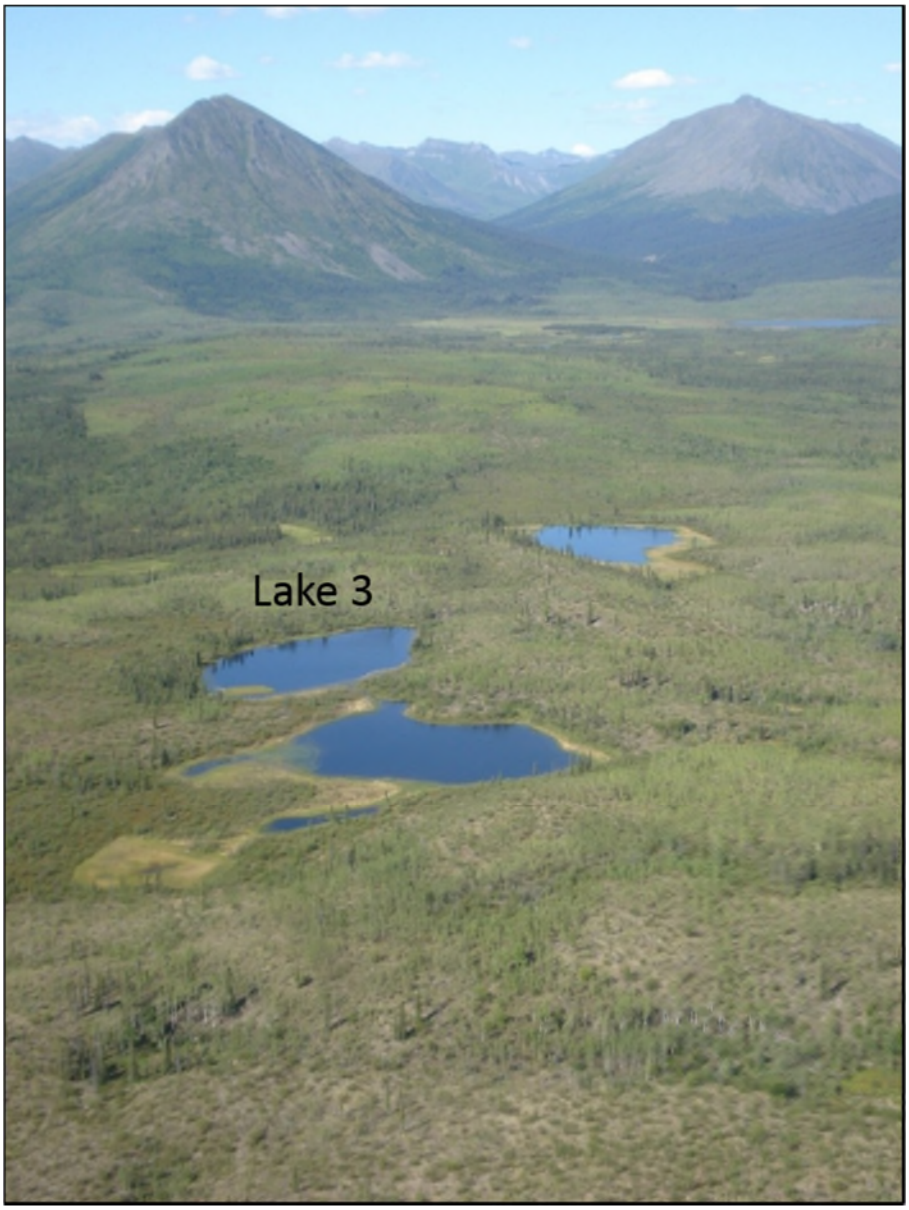


Figure 6.5: *Aerial photograph of Lake 3. (photo credit: Maarten van Hardenbroek, 2013)*

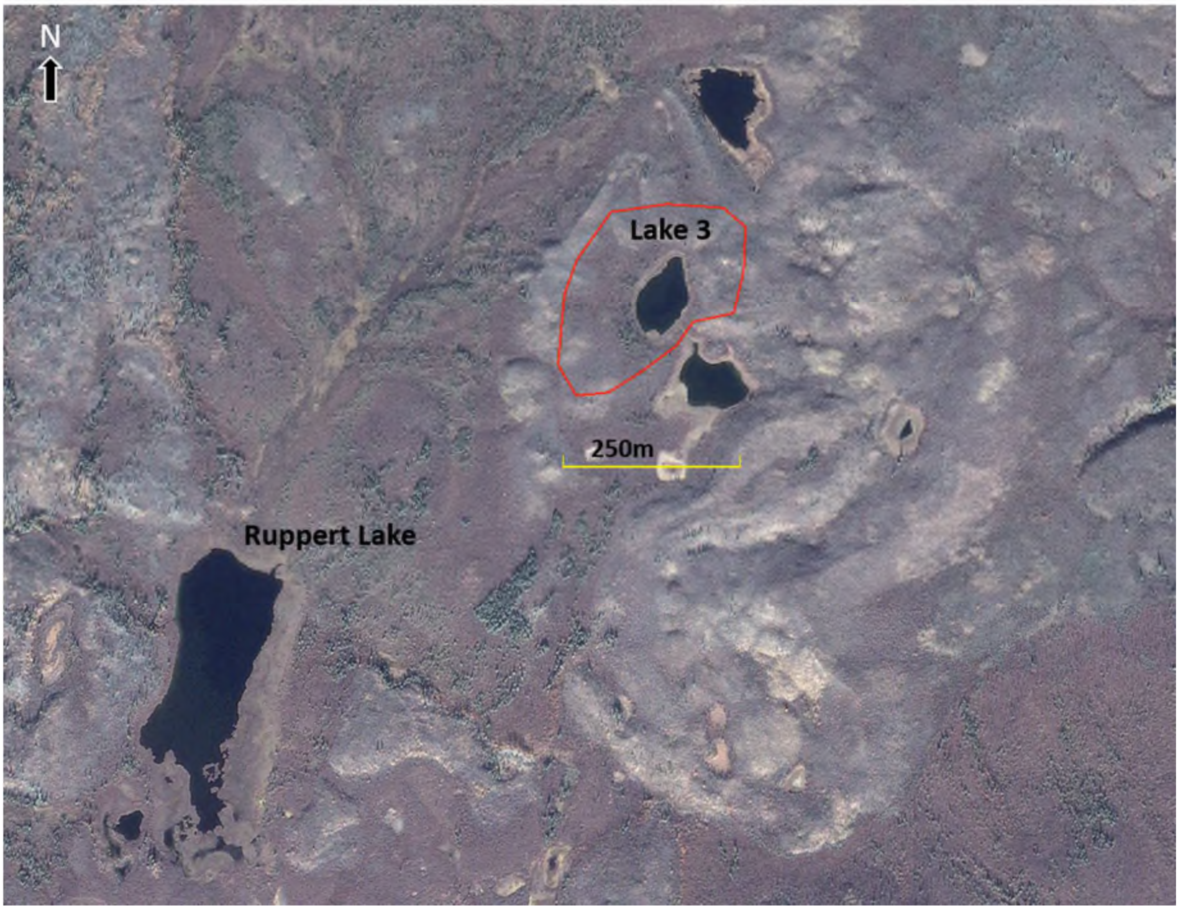


Figure 6.6: *Lake 3 catchment (K. Reuss-Schmidt, Google Earth)*

6.3 Methodology

6.3.1 Core Collection

Fieldwork was undertaken in the summer of 2013 as part of the LAC project. Sediment sequences were collected from the deepest part of each lake using overlapping drives. The water depth at Ruppert Lake was 580 cm and 425 cm at Lake 3. A 73-mm diameter Bolivia corer (LAC Core, University of Minnesota, 2011) was used to collect the uppermost sediments and underlying relatively soft sediments. A meter long, 50mm diameter Livingstone coring system (Wright, 1967) was used to recover the deeper core Sections characterised by stiffer sediments.

Figure 6.7: *Collecting cores from Lake 3 (H. van Hardenbroek, 2013)*

6.3.2 Laboratory sub-sampling

A U-channel was taken from each of the cores prior to sub-sampling. This was then double wrapped in cling film, sealed, labelled and stored in the cold store at 4°C for ITRAX analysis for the LAC project and for archiving. The remainder of the core was sub-sampled at 1cm intervals, and 1cm^3 was taken at 4cm intervals for pollen analysis for Lake 3. Ruppert Lake was not sampled evenly, as it has previously been studied and a high resolution pollen record exists for this lake (Higuera *et al*, 2009). Samples were taken from the new Ruppert core focusing on vegetation transitions that acted as biostratigraphic markers to link the new record with that of Higuera *et al* (2009). The remainder of the cores were stored for subsequent analysis for the LAC project. All sub-samples were placed into small sample bags and stored in the dark at 4°C.

6.3.3 Radiocarbon Dating

Terrestrial plant remains were picked for AMS ^{14}C Dating, but in some instances floating-leaved aquatic macrophytes (*Nuphar lutea* and *Potamogeton*) and unidentified moss were used. The samples were prepared to graphite and analysed at the NERC Radiocarbon Facility, East Kilbride. Very small samples were analysed at the Keck C Cycle AMS Lab, University of California, Irvine. A tephra layer related to the Aniakchak Caldera Forming Event II, dated to 3,595 ± 4 cal BP in Greenland ice cores (Pearce *et al*, 2004; Denton & Pearce, 2008) was identified in Ruppert Lake and Lake 3, and included in the age-depth model (Monteath *et al*, 2017). Ages were calibrated and age-depth models were created using Bacon version 2.2 for Mac, an R package using Bayesian modelling (Blaauw and Christen, 2011) and the IntCal13 calibration curve (Reimer *et al*, 2013) courtesy of Maarten van Hardenbroek.

6.3.4 Pollen Analysis

Fifty samples were prepared from Lake 3 and 43 from Ruppert Lake following standard methods (Moore *et al*, 1991) including sieving, HF treatment and acetolysis and the residues were mounted in silicon oil. Pollen was counted at x400 magnification using a Nikon Eclipse 80i or a Nikon Eclipse E200 microscope. A minimum of 300 total land pollen (TLP) grains were counted possible, including *Alnus* and excluding aquatic pollen and spores. Identifications were made using Alaskan reference material held at the PLUS laboratory at the University of Southampton.

6.3.5 *Picea* measurements

It is difficult to separate *Picea glauca* and *Picea mariana* in the pollen record (Lindbladh *et al*, 2002). Previous studies have shown that morphometric analysis of *Picea* grains can help to distinguish between the two species with *Picea mariana* (e.g. Brubaker *et al*, 1987). Lindbladh *et al*'s (2002) study in North America illustrated the distributions of “total grain size” with *Picea mariana* grains generally being smaller than *Picea glauca* grains. Twenty *Picea* grains were measured from 7 levels throughout the Lake 3 sequence (48cm, 104cm, 120cm, 124cm, 132cm, 136cm, and 148cm). This was to assess approximately when *Picea mariana* expanded and to compare this with the charcoal record to see the effect on the fire history in the area. Five measurements were taken from each grain: (1) overall grain size (2) Sac width at base (3) Sac height (4) Corpus breadth (5) Sac attachment (Figure 6.8). The grains were identified, measured and a selection photographed used a Nikon Eclipse 50i microscope with camera attachment and digital graticule.

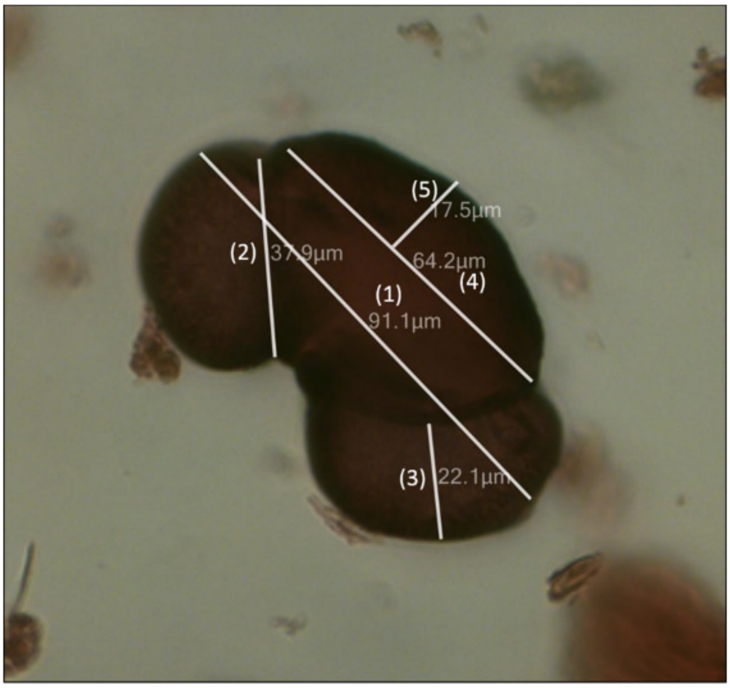


Figure 6.8: *Picea grain measurements: (1) overall grain size (2) Sac width at base (3) Sac height (4) Corpus breadth (5) Sac attachment*

6.3.6 The Landscape Reconstruction Algorithm

REVEALS (run 13 from Chapter 4) was used for the regional reconstruction of vegetation. This run used Sithylemenkat Lake plus small lakes and a combination PPE Sets: PPE Set 1 for the late glacial and PPE Set 2 for the Holocene (set 2 substitutes the Alaskan *Alnus* PPE value for the European value). The regional vegetation was then input into LOVE along with pollen counts from Ruppert Lake (Higuera *et al*'s 2009 data) and Lake 3. After reflection on the application of PPE Sets 1 and 2 in Chapter 4; an additional REVEALS run was also performed using the REVEALS run 14 from Chapter 4 using PPE Set 4 for the late glacial and PPE Set 5 for the Holocene and then this was input into LOVE using the new PPE Sets and pollen counts from Ruppert and Lake 3. As already shown in Chapter 5, various issues arose in the validation of LOVE that led to the decision to use REVEALS to reconstruct the vegetation around the smaller lakes. REVEALS was therefore independently run on Ruppert Lake and Lake 3 to compare the results between REVEALS and LOVE using PPE Set 1 and 2 to assess whether these smaller Brooks Range lakes produced an individualistic signal or the same pollen signal as larger "regional" lakes.

6.3.7 Charcoal Analysis

Macroscopic charcoal analysis was undertaken by Charlotte Clarke (University of Southampton PhD student) as part of the LAC project. Macroscopic (>125 µm) charcoal particles were extracted from 1 cm^3 of sediment at a sampling interval of 0.5 cm. Sediments were deflocculated in 10% tetra-sodium pyrophosphate overnight and later soaked in a 3% hydrogen peroxide solution and heated to 50oC for 48 h to remove or bleach non-charcoal organic matter. Samples were rinsed over a 125 µm sieve mesh to isolate macroscopic particles. Samples were scanned under a stereomicroscope at × 20 magnification for locating fragments, with charcoal identification confirmed at x 40 magnification. All charcoal fragments present in the sample were counted. Macroscopic charcoal concentration (particles/ cm^3) were multiplied by sediment accumulation rate (cm/ yr-1) to obtain charcoal accumulation rate (CHAR; particles cm-2 yr-1).

Char-Analysis v.1.2 software was used to analyse the charcoal time series (Higuera *et al*., 2009). The software distinguishes background influx from peaks by creating a threshold through the time series of charcoal data, and it provides a statistical probability that distinctions are valid. Experimentation with different parameter values assessed the sensitivity of the method to these data. In all runs, the results were fairly similar and robust.

A 10-year initial data interpolation was chosen to create a data set with uniform time steps less than the sampling resolution of the records. We used a 500-year local smoothing window to distinguish charcoal peaks and a 1000-year moving window to estimate fire return intervals (FRI) and its approximate reciprocal, fire frequency.

6.4 Results

6.4.1 Radiocarbon Dates and Age-Depth Model

The sediment core from Ruppert Lake collected for the LAC project in 2013 doesn't capture as much of the late glacial herb zone as that collected by Higuera *et al* (2009). The date at the base of the Higuera (2009) sequence is 14,000 yr BP with a higher resolution pollen diagram. For Ruppert Lake, Higuera *et al*'s (2009) data will be used in this analysis. The base of Lake 3 is dated to ca. 9500 cal yr BP (8564±40, SUERC-50486). The dates discussed in this Chapter for Ruppert Lake and Lake 3 are summarised in Table 6.2.

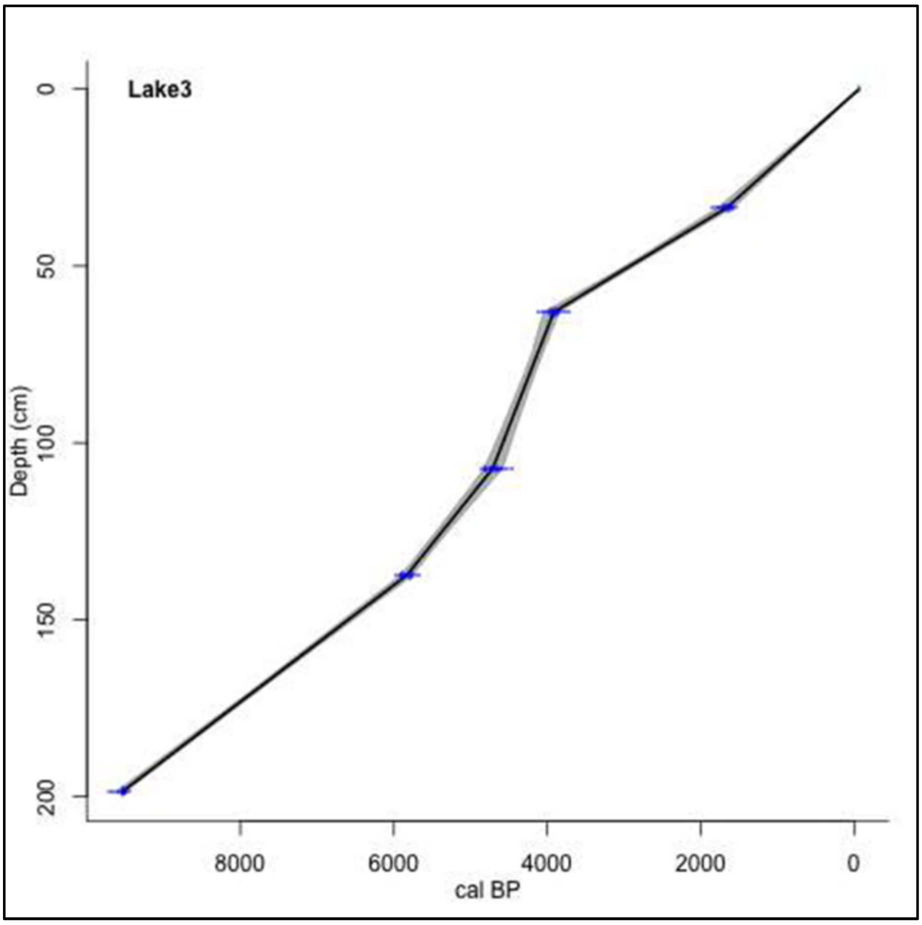


Figure 6.9: *Age-Depth Model for Lake 3 (Maarten Van Hardenbroek)*

6.4.2 Pollen Results

6.4.2.1 Ruppert Lake

A detailed description of the previous pollen records from Ruppert Lake is discussed in Brubaker *et al* (1983) and Higuera *et al* (2009). The detailed pollen diagram from Higuera *et al* (2009) data is shown in Figure 6.10. The pollen diagram of the 43 samples counted for the LAC project along with a summary description of the zones is shown in Appendix A, Figure A.4 and Table A.7 and the pollen counts in Table A.8 The pollen diagrams were zoned by eye and characterized by plant function type shifts or following the introduction of dominant taxa.

The basal Herb Tundra Zone (14,000-13,000 yr BP) is dominated by Cyperaceae (<25%) and *Salix* (~25%). Poaceae and *Artemisia* are also present between 10-15%. Higuera *et al* (2009) state that these pollen spectra suggest the presence of a discontinuous prostrate shrub tundra and grass and forb tundra (also see Anderson *et al*, 2004). The shrub tundra zone is characterised by the rise in *Betula* (13,000-10,300 yr BP). As discussed in Chapter 2, the high percentages of *Betula* pollen have led many palaeoecologists to interpret the landscape as dominated by birch shurbs (Higuera *et al*, 2009; Anderson and Brubaker, 1993). However, the results from Chapter 4 indicate that this may not have been the case (discussed in further detail below). The transition to deciduous woodland is dated to 10,300-8,500 cal yr BP and is characterised by an increase in *Populus* pollen (10-20%). *Betula* percentages are still high (50-75%) and *Salix* increases slightly (10-15%).

The onset of the forest-tundra (a) zone is dated to 8500 yr BP and is marked by the increase in *Picea* pollen (up to 10%) and the decrease in *Populus* (<10%). *Alnus* pollen also starts to increase in this zone. Forest-tundra (b) is characterised by the sharp increase in *Alnus* pollen (up to 55%). *Populus* is only present at trace values and *Salix* has also declined to <5%. *Betula* also decreases to ~40%. The final zone is the development of the modern boreal forest. This is dated to 5500 yr BP- present and where *Picea* pollen increases (from 20 to 35%). *Alnus* values decrease to ~40% and *Betula* decreases further to ~30%. Only occasional grains of *Populus* occur in this final zone.

6.4.2.2 Lake 3 and Ruppert comparison

The descriptions of pollen zones at Lake 3 are summarised in Table 6.1 and the pollen diagram is shown in Figure 6.11 (pollen counts Appendix A, Table A.9). A summary of the major vegetation transitions and dates are shown in Table 6.2. The record of Lake 3 starts around half way through the deciduous woodland zone and is dated to 8564±40 (9511 yr BP, age-depth model). The birch rise in the late glacial recorded at Ruppert Lake is not present in this sequence. *Populus* pollen is high in the basal sample (30%) with *Betula* (30%), *Salix* (10%) and Cyperaceae (15%). *Populus* pollen declines at the top of this zone to 10%. The start of the forest-tundra zone (a) is dated to 9016 yr BP (from the age-depth model, no radiocarbon date at this depth) and 8500 yr BP at Ruppert Lake. *Picea* pollen occurs for the first time at Lake 3 (<10%) and at trace values at Ruppert. *Betula* pollen increases at both lakes c. 80% in this zone along with a decline in *Populus* to values <5%. *Salix* declines at both lakes but maintains slightly higher values at Ruppert Lake. Cyperaceae is present at both lakes although values are higher (20-40%) at Ruppert than Lake 3 (up to 20%). Other herbs are rare and include occasional grains of *Artemisia* (sagebrush) and Rosaceae (rose family).

Forest-tundra (b) is dated to 7924 yr BP (from the age-depth model, no radiocarbon date at this depth) at Lake 3. This zone begins with the *Alnus* rise, which is also recorded at Ruppert Lake. *Alnus* values increase up to 60% (55% at Ruppert). *Betula* values decrease at both lakes to around 40*%.* *Picea* values are consistent at values under 10% but start to increase towards the top of this zone. *Populus* is absent from this zone at Lake 3 but occasional grains occur at Ruppert. *Salix* is present at trace values at Lake 3 and <5% at Ruppert. Cyperaceae maintains consistent values

<10% at both lakes. The development of the closed boreal forest is dated to 5477 yr BP (age-depth model) and is consistent with the date of 5500 obtained from Ruppert Lake. The rise in *Picea* pollen that marks the beginning of this zone is recorded at both lakes. The *Picea* curve fluctuates slightly though out this zone at both lakes but maintains consistent values around 20-30% for the rest of this zone.

Depths	Dates	PFT Zone	Description
190-200cm	198cm 8564 C^{14} yrs (9502 yr BP)	Deciduous Woodland	*Populus-Betula-Salix* The opening of the basal zone is characterised by *Populus* pollen (up to 30%), *Betula* (ca. 30%), *Salix* and Cyperaceae. Occasional grains of *Juniperus,* Ericaceae and *Artemisia* are also present. *Populus* declines during this zone to 10% and *Betula* starts to increase. Other herbs are rare apart from low frequencies of Poaceae.
172-190cm	190cm (9016 yr BP) 172cm (7924 yr BP)	Forest Tundra (a)	*Betula* This zone is dominated by *Betula* where it reaches its highest frequencies (up to 80%). *Picea* is introduced in this zone with low but consistent values around 5%. *Populus* and Salix are reduced to trace values. Occasional grains of *Alnus, Juniperus* and Ericaceae are present. Herbaceous pollen is low with Poaceae and Cyperaceae (<20%). Other herbs are rare but include occasional grains of *Artemisia*, *Filipendula* and *Rumex acetosella*.
128-172cm	137.5cm 5100 C^{14} yrs (5812 yr BP) 128cm (5477 yr BP)	Forest Tundra (b)	*Alnus-Betula* This zone is distinguished by a marked increase in *Alnus* (up to 60%) with reduced frequencies of *Betula*. *Picea* maintains values similar to the previous zone. *Populus* and *Juniperus* disappear from the record with only occasional grains of *Salix* present. The range and values of herbs are much the same as the previous zone.
0-128cm	107.5cm 4175 C^{14} yrs (4706 yr BP) 63cm 3605 C^{14} yrs (3915 yr BP) 33.5cm 1750 C^{14} yrs (1634 yr BP)	Boreal Forest	*Picea-Betula-Alnus* This zone is characterised by the rise in *Picea* (ca. 40%) and the development of the modern boreal forest. *Alnus* decreases but maintains values of around 30% along with *Betula* throughout the zone. Occasional grains of *Salix* and Ericaceae are present throughout. Herbaceous pollen is low with a similar spectra as the previous zone.

Table 6.1: *Summary description of pollen zones at Lake 3 (Ages in brackets are taken from the clam-based age depth model)*

ZONE	Ruppert (Higuera *et al*, 2009, yr BP)	Lake 3 Depth (cm)	Lake 3 C^{14} Dates	Lake 3 (age-depth model yr BP)
Base of sequence (late glacial herb zone)	13000			
Start of Deciduous woodland	10300			
Base of Lake 3 sequence		198	8564±40 (SUERC-50486)	9511
Start of Forest-tundra (a)	8500	190		9016
Start of Forest-tundra (b)		172		7924
Forest-tundra		165	8000±39 (SUERC-63546)	7524
Forest-tundra		137	5100±30 (UCIAMS-154535)	5821
Start of Boreal forest	5500	128		5477
Boreal forest		107	4175±37 (SUERC-58895)	4727

Table 6.2: *Summary table of dates for the major vegetation transition zones at Ruppert Lake and Lake 3*

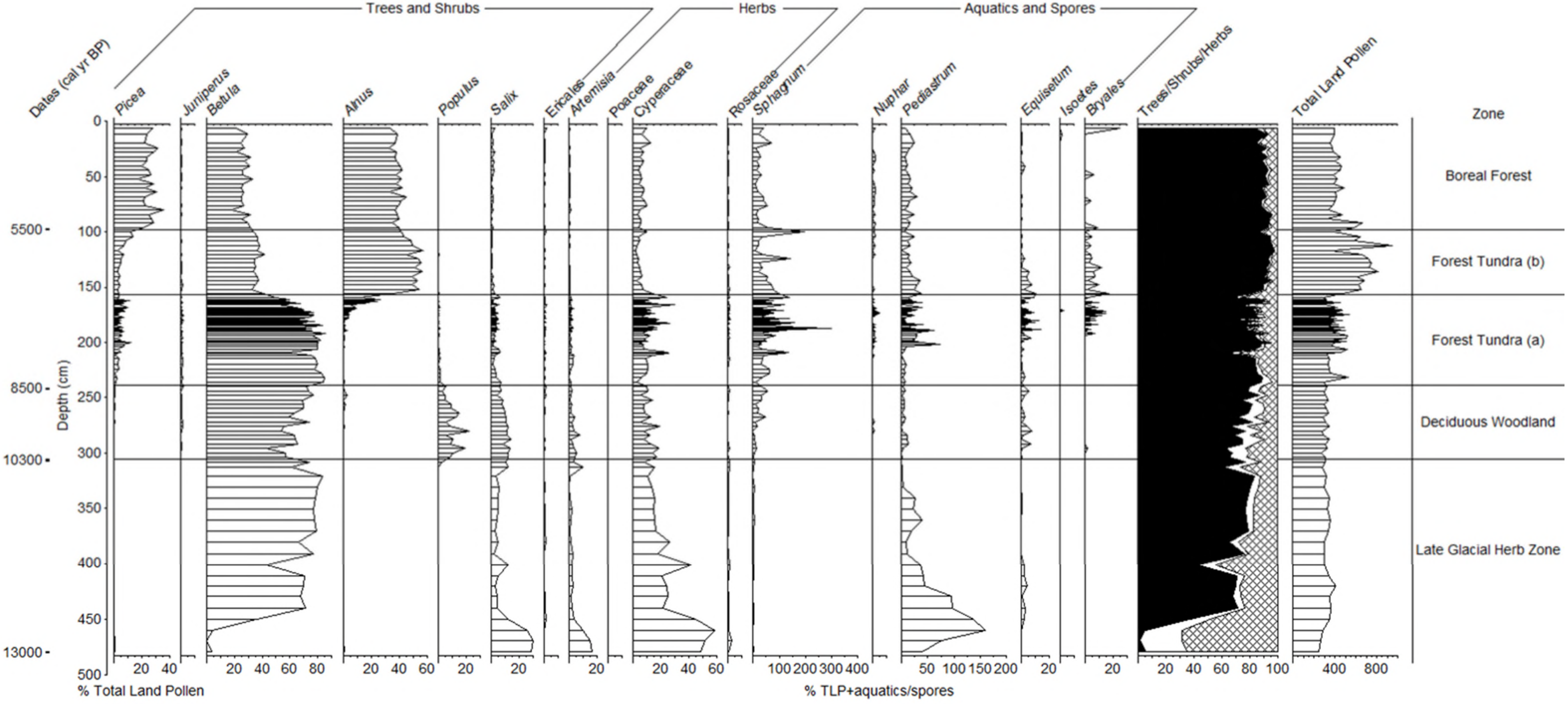


Figure 6.10: *Pollen Diagram for Ruppert Lake from Higuera et al (2009) data (Tilia v.1.7.16 and Tilia Graph, Grimm, 2011)*

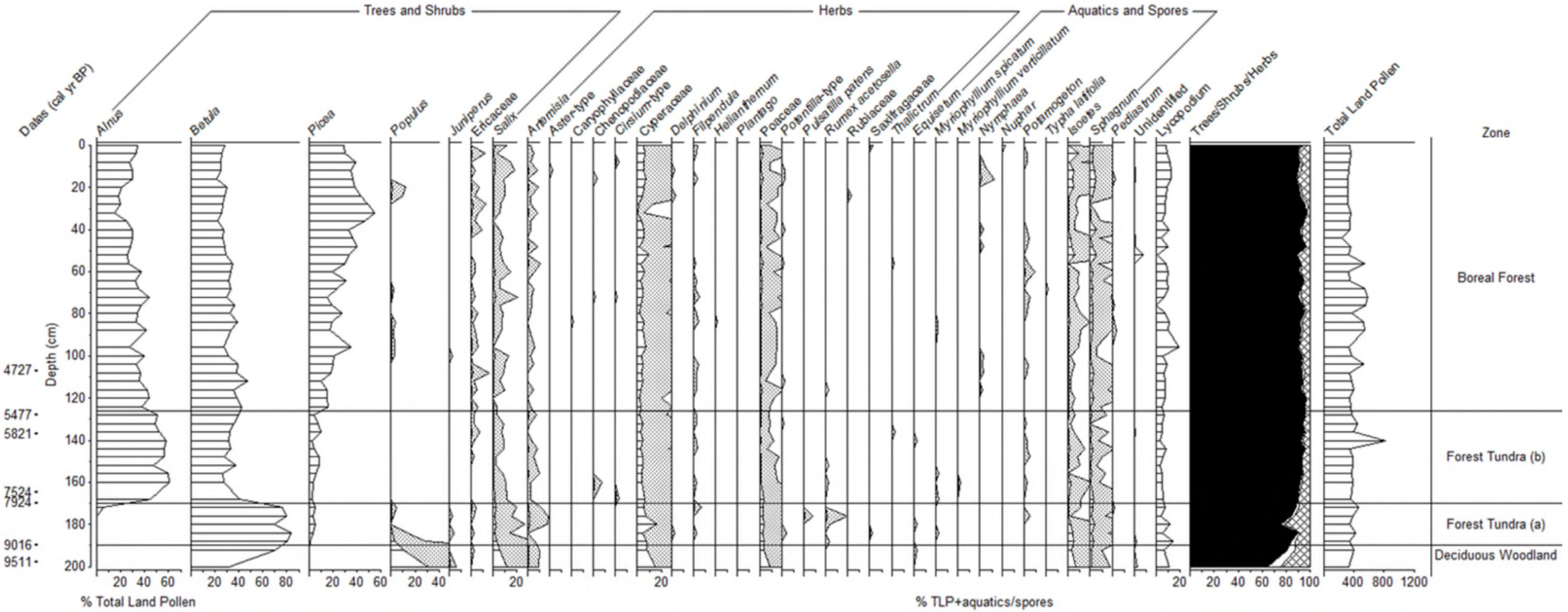


Figure 6.11: *Pollen Diagram for Lake 3 (Analyst E. Hopla; Tilia v.1.7.16 and Tilia Graph, Grimm, 2011)*

6.4.3 *Picea* measurements

The full table of measurements taken from the *Picea* grains is in Appendix A, Table A.10. Figure 6.12 below illustrates the mean of the grain size measurements from each depth. The mean average grain size increases with depth. The onset of the boreal forest development is recorded from 128cm in the pollen record. As samples were only taken from 8 depths throughout the core, the exactly transition cannot be pinpointed but there is a clear reduction in the mean grain size of *Picea* in the upper half of the record when the boreal forest is well established indicating a shift from *Picea glauca* to *Picea mariana*.

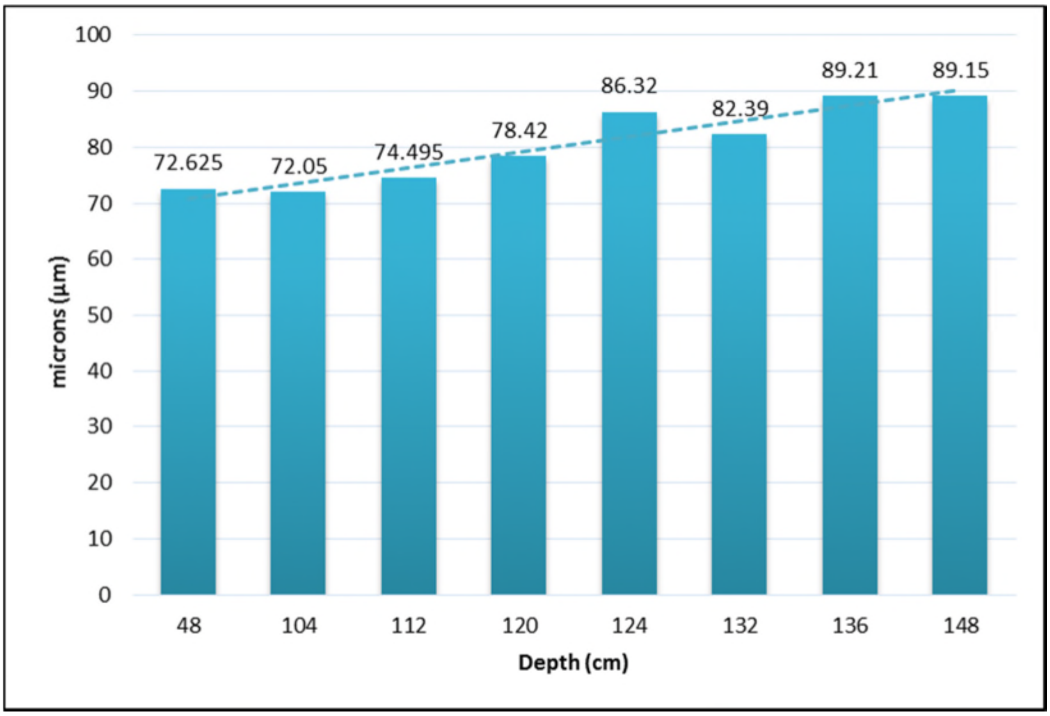


Figure 6.12: *Mean grain sizes of Picea grains measured throughout the core at Lake 3. Numbers above bars are microns (µm)*

6.4.4 LOVE and REVEALS Reconstructions

6.4.4.1 RSAP estimates

As discussed in the previous Chapter, LOVE estimates the RSAP considering all the NSAP for the sites included in the analysis at a given time window. The RSAP that have been estimated at each time window for Ruppert Lake and Lake 3 are listed in Table 6.3. Time windows between 10,000-

13,890 yr BP are only based on Ruppert Lake. The RSAP of pollen has changed over time ranging from 115m between 11,000-12,000 yr BP to 555m at 3000-4000 yr BP.

(a)

Time Window (yr BP)	RSAP (m)
0-500	420
500-1000	360
1000-2000	425
2000-3000	415
3000-4000	555
4000-5000	325
5000-6000	165
6000-7000	285
7000-8000	275
8000-9000	180
9000-10000	185
10000-11000*	310
11000-12000*	115
12000-13000*	410
13000-13890*	280

(b)

Time Window (yr BP)	RSAP (m)
0-500	370
500-1000	220
1000-2000	780
2000-3000	410
3000-4000	220
4000-5000	510
5000-6000	255
6000-7000	650
7000-8000	330
8000-9000	230
9000-10000	385
10000-11000*	580
11000-12000*	190
12000-13000*	570
13000-13890*	235

Table 6.3: (a) *RSAP estimates from LOVE at each time window for Ruppert and Lake 3 using* PPE Set*s 1 and 2 and (b) RSAP estimates from LOVE at each time windown for Ruppert and Lake 3 using* PPE Set*s 4 and 5. *time windows based only on Ruppert Lake*

6.4.4.2 LOVE and REVEALS reconstructions (PPE Sets 1, 2, 4 and 5)

The LOVE and REVEALS estimates for Ruppert Lake using PPE Sets 1 and 2 are illustrated in Figure 6.13. Figure 6.13 (a) shows the pollen proportions for the 8 taxa used in the analysis. The LOVE and REVEALS patterns are fairly similar throughout the majority of the Holocene. The main differences are throughout the late glacial and early Holocene. During the late glacial between 13,000-13,890 yr BP, Cyperaceae and *Salix* values increase compared with the pollen percentages, using both LOVE and REVEALS. LOVE found no solution for Poaceae but REVEALS estimates have increased the values slightly from the pollen. Few solutions are found for vegetation when using LOVE between 12,000-13,000 yr BP; with only *Betula*, Ericaceae and Cyperaceae present during this time window. Cyperaceae dominates this time window when using LOVE and *Salix* disappear completely despite being present in the pollen record and having a low PPE. Thus, the REVEALS estimates seem more realistic as they show an increase in *Salix*. Cyperaceae is then removed completely from LOVE estimates between 11,000-12,000 yr BP. This scenario for the late glacial seems unrealistic as *Salix* and Cyperaceae are not only present in the pollen record but it is also unlikely that major taxa would decline and reappear. *Betula* values have been dramatically reduced when using REVEALS during the late glacial, but values are still high between 11,000-12,000 yr BP when using LOVE.

The early Holocene is dominated by *Populus* in both LOVE and REVEALS estimates. However, LOVE estimates that this is the only taxa in the local vegetation between 9000-10,000 yr BP. REVEALS estimates increase the proportions of *Populus* when compared with the pollen; but *Salix, Betula*, Poaceae and Cyperaceae are also present. *Betula* values decrease dramatically in the early Holocene compared with the pollen when using REVEALS, but no solution for this taxon was found when using LOVE. The remainder of the Holocene is fairly consistent between REVEALS and LOVE. *Alnus* values decrease dramatically compared with the pollen and *Picea* values increase. *Betula* values are higher when using LOVE and *Picea* values are higher when using REVEALS. Where *Populus* is present at trace values and not evident in the pollen proportions (e.g. between 4000-5000 yr BP) REVEALS increases the estimate of this taxon. *Salix* values increase using both LOVE and REVEALS compared with the pollen percentages, with the values slightly higher using LOVE.

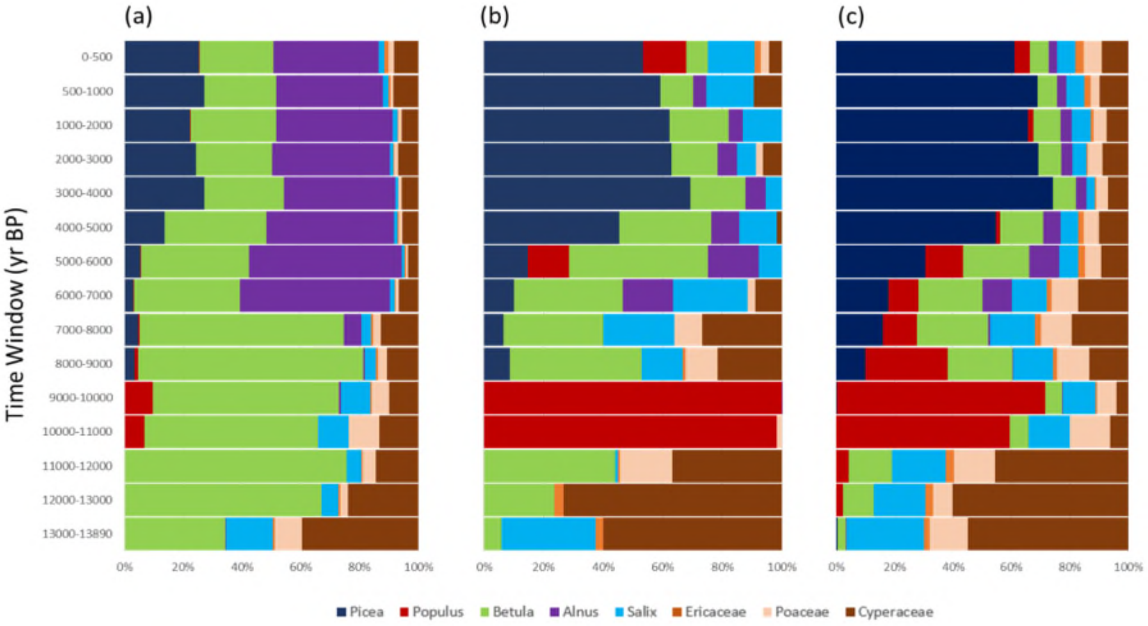


Figure 6.13: *LOVE estimates at Ruppert Lake (a) Pollen proportions (b) LOVE estimates (c) REVEALS estimates*

The LOVE and REVEALS estimates for Lake 3 using PPE Sets 1 and 2 are illustrated in Figure 6.14. Figure 6.14 (a) shows the pollen proportions for the 8 taxa used in the analysis. The patterns between LOVE and REVEALS (as with Ruppert Lake) are fairly similar throughout the majority of the Holocene with the main differences occurring in the earlier part of the record. *Populus* dominates the record in the early Holocene when using both LOVE and REVEALS which is a contrast from the pollen proportions. LOVE estimates that *Populus* is almost the only taxa in the local vegetation between 8000-9532 yr BP and completely removes *Betula, Salix* and Poaceae. This is similar to the patterns produced at Ruppert Lake (Figure 6.13 b). *Betula* values have decreased, particularly when using REVEALS but also when using LOVE throughout the mid-late Holocene. The remainder of the Holocene is fairly consistent between REVEALS and LOVE. *Alnus* values have decreased dramatically from the pollen and *Picea* has increased, which is also consistent with the patterns at Ruppert Lake. *Betula* values are higher when using LOVE and *Picea* values are higher when using REVEALS. Where *Populus* is present at trace values and not evident on the pollen graph. REVEALS increases the estimate of this taxon. *Salix* values increase using both LOVE and REVEALS compared with the pollen percentages, with the values slightly higher using LOVE.

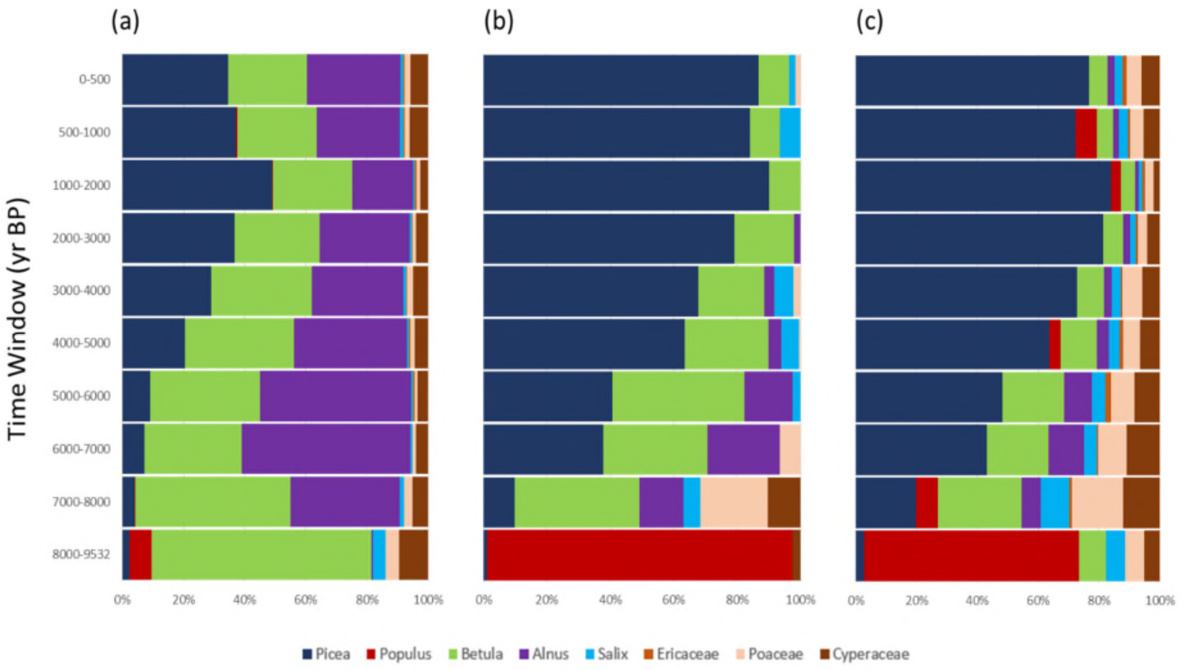


Figure 6.14: *LOVE estimates at Lake 3 (a) Pollen proportions (b) LOVE vegetation estimates (c) REVEALS estimates*

The LOVE estimates for Ruppert Lake using PPE Sets 3 and 4 are illustrated in Figure 6.15. Figure 6.15 (a) shows the pollen proportions for the 8 taxa used in the analysis. The LOVE patterns are fairly similar throughout the majority of the late glacial (patterns discussed above). The early Holocene is dominated by *Populus* in both LOVE reconstructions with slightly increased values for Poaceae and *Salix* using PPE Set 4 and 5. Cyperaceae values are increased using PPE Sets 4 and 5, particularly between 8000-9000 and 7000-9000 yr BP time windows. The dramatic difference between the two LOVE reconstrcutions is from 7000 yr BP onwards where *Alnus* values are much higher using PPE Set 3 and 4 and *Betula* is better represented using PPE Set 1 and 2.

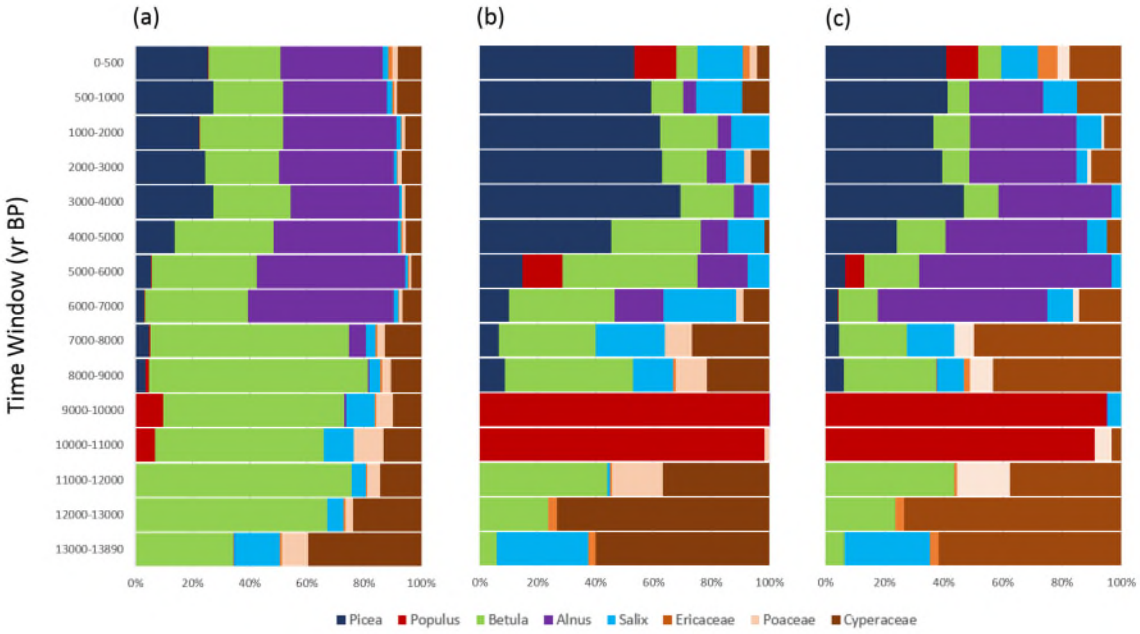


Figure 6.15: *LOVE estimates at Ruppert Lake (a) Pollen proportions (b) LOVE vegetation estimates using* PPE Set *1 and 2 (c) LOVE vegetation estimates using* PPE Set *4 and 5*

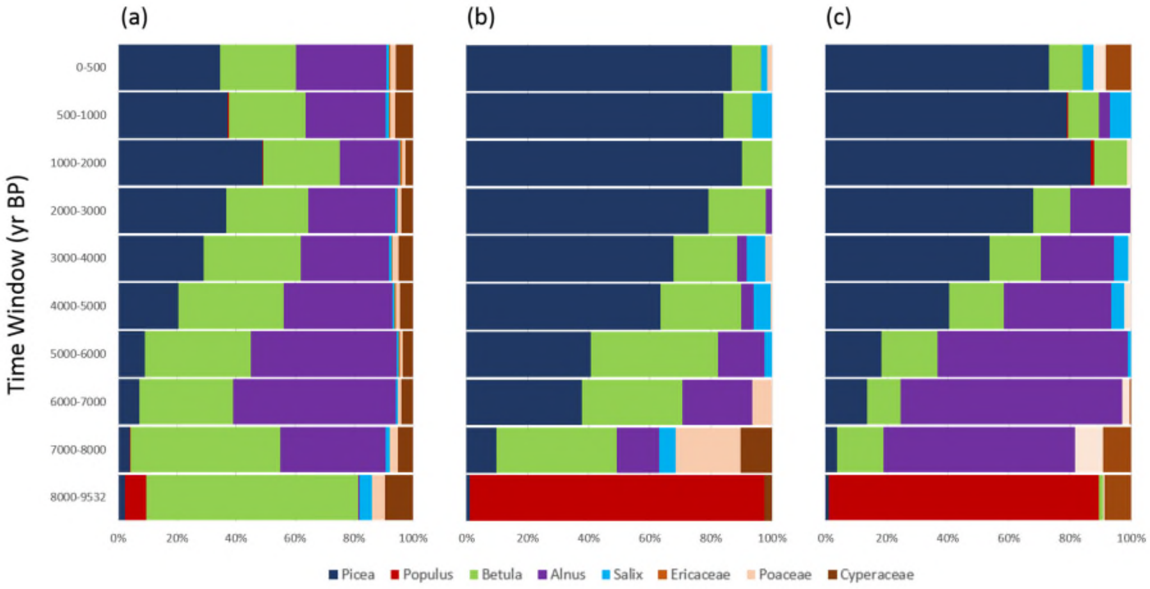


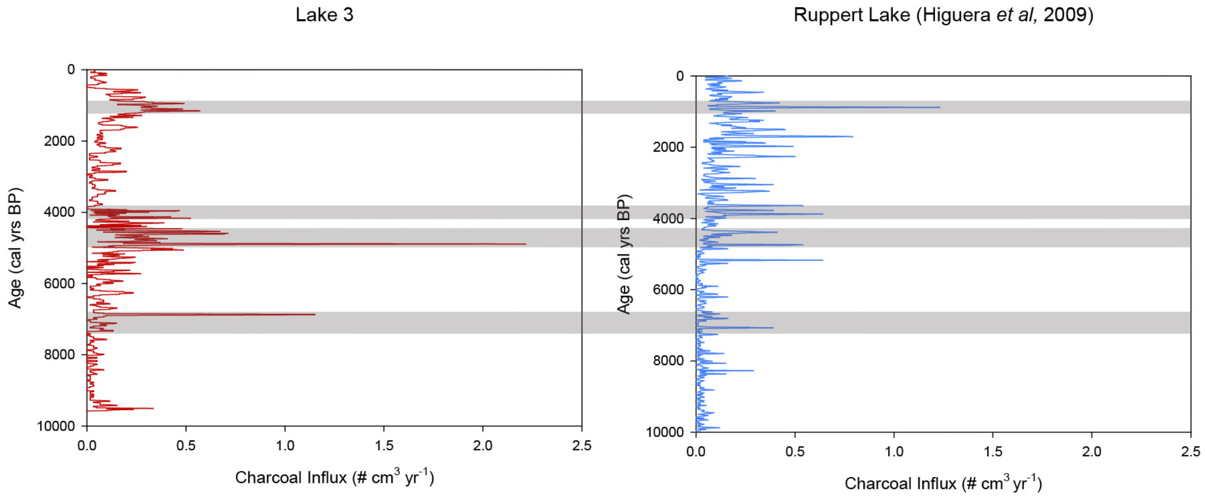
Figure 6.16: *LOVE estimates at Lake 3 (a) Pollen proportions (b) LOVE vegetation estimates using* PPE Set *1 and 2 (c) LOVE vegetation estimates using* PPE Set *4 and 5*

The LOVE estimates for Lake 3 using PPE Sets 4 and 5 are illustrated in Figure 6.16. The early Holocene is dominated by *Populus* in both LOVE reconstructions with slightly increased values for

Cyperaceae using PPE Set 4 and 5. Poaceae and *Salix* values decrease using PPE Set 4 and 5 from 8000 yr BP. *Alnus* values are much higher using PPE Sets 4 and 5 and again, as at Ruppert Lake, *Betula* is better represented using PPE Set 1 and 2.

6.4.5 Charcoal Records

The charcoal influx (charcoal particles deposited per cm^2 per year) for Ruppert and Lake 3 are illustrated in Figure 6.17. There are periods when peaks in charcoal match between each lake and these are indicated by the grey highlighted boxes. However, the magnitudes of the peaks vary considerably between the two lakes. This is likely due to different catchment sizes and different processes of allochthonous input. Lake 3 has no clear inlet, but Ruppert does, which is likely to increase overall sediment flux to Ruppert Lake. When comparing the charcoal influx at Lake 3 with the Titanium input derived from XRF for the LAC project analysis (Figure 6.18), it is clear that there is a large influx of Titanium in the early part of the record which then settles and stabilised around 160cm. This indicates that there is little effect of erosional events and inwash from elsewhere in the catchment for the majority of the record and the charcoal influx to the lake is therefore suitable and reliable for CHAR analysis.


Lake 3

Ruppert Lake (Higuera *et al*, 2009)

Figure 6.17: *Charcoal Influx at lake 3 and Ruppert Lake (C. Clarke)*

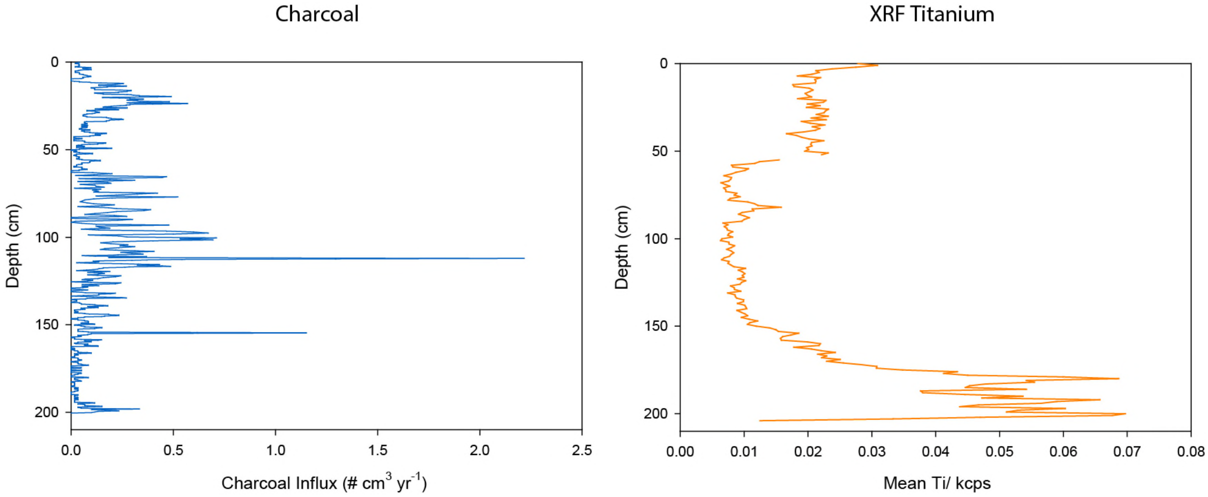


Figure 6.18: *Charcoal Influx at lake 3 and Titanium (mean Ti/kcps) at Lake 3 (C. Clarke)*

CharAnalysis (Higuera *et al*, 2009) was used to statistically decompose or estimate 'background charcoal' versus a true signal of fire events at Lake 3. Background charcoal is the low frequency, but consistent input of charcoal into a lake basin even when no fires have occurred in the catchment or nearby. This is likely due to erosional events and in wash of material (Clark and Patterson, 1997). Figure 6.19 illustrates the charcoal influx values based on raw charcoal counts which are then interpolated to every 10 years. The threshold for background charcoal is shown by the grey line in the top figure. When the charcoal influx is above the level of background charcoal it is considered to be a true signal or 'peak'. The location of peaks are denoted by a '+' and each '+' represents a true positive charcoal peak. Each dot shows samples which failed to pass the peak magnitude test. The red lines show the threshold values for detecting charcoal peaks. Figure 16.19b is the interpolated charcoal influx value (Figure 16.19a) minus the estimated value for background charcoal influx. The results indicate the highest peak frequencies occur between 6,500 and 3,500 cal yrs BP.

When comparing these data with Ruppert Lake (Figure 6.20, Higuera *et al*, 2009), it is clear that there are more identified charcoal peaks at Ruppert Lake. The main difference is that in the early period (cs. 9000-8000 cal yr BP) there are several peaks at Ruppert and virtually none at Lake 3. The data shown here is only covers the period that correlates with the Lake 3 record.

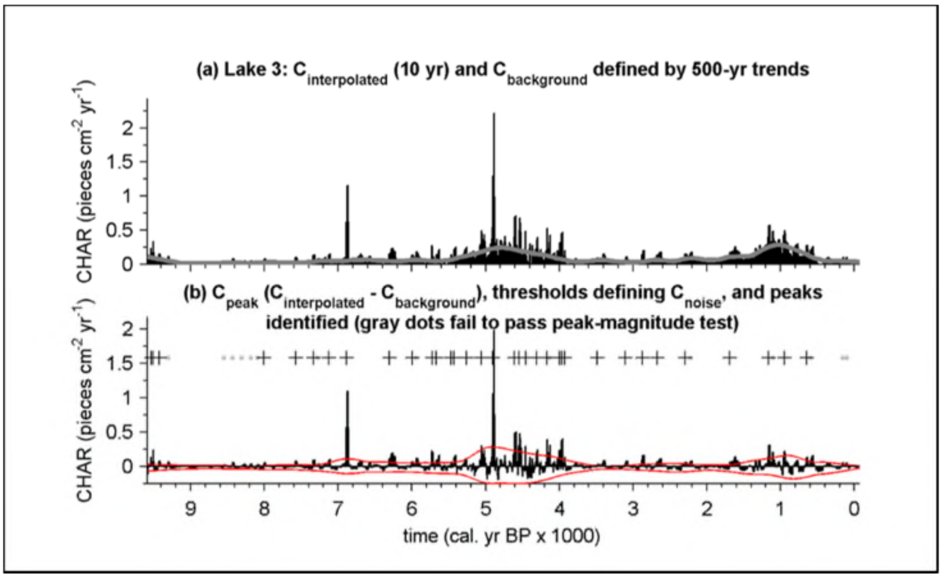


Figure 6.19: *CHAR Analysis at Lake 3 (C. Clarke)*

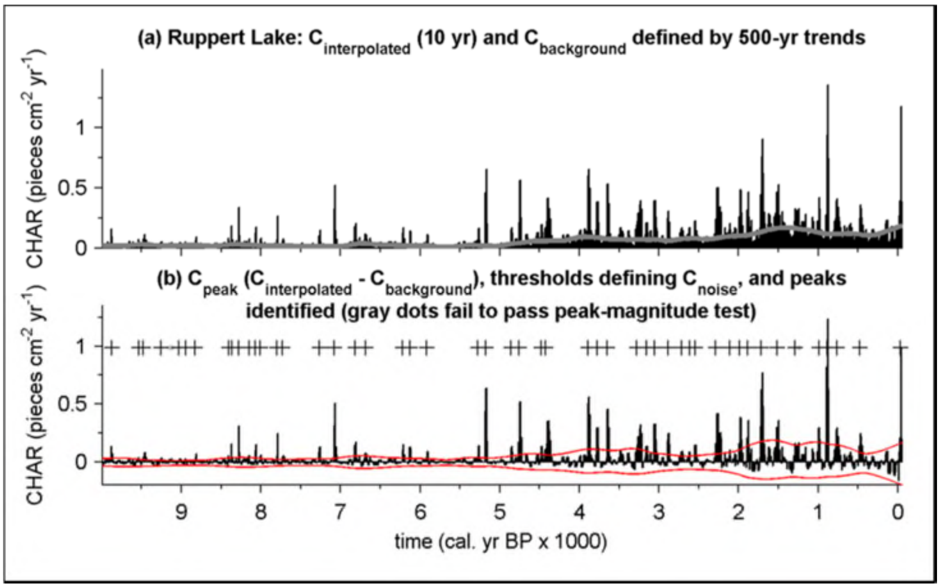


Figure 6.20: *CHAR Analysis at Ruppert Lake (Higurea et al, 2009)*

Figure 6.21 illustrates the peak magnitude, fire return interval (FRI) and fire frequency at Lake 3. The large peaks in the peak magnitude are likely to be fire events, significant peaks are recorded around 7,000 and 5,000 cal yr BP. These do not necessarily represent individual fire events as charcoal from fire events may take several years before finally deposited into the lake (Higuera *et al*, 2010). During the period between 6,500 and 3,500 cal yrs BP the mean FRI is low (150-200 years) indicating that fires were occurring frequently in the catchment during this period.

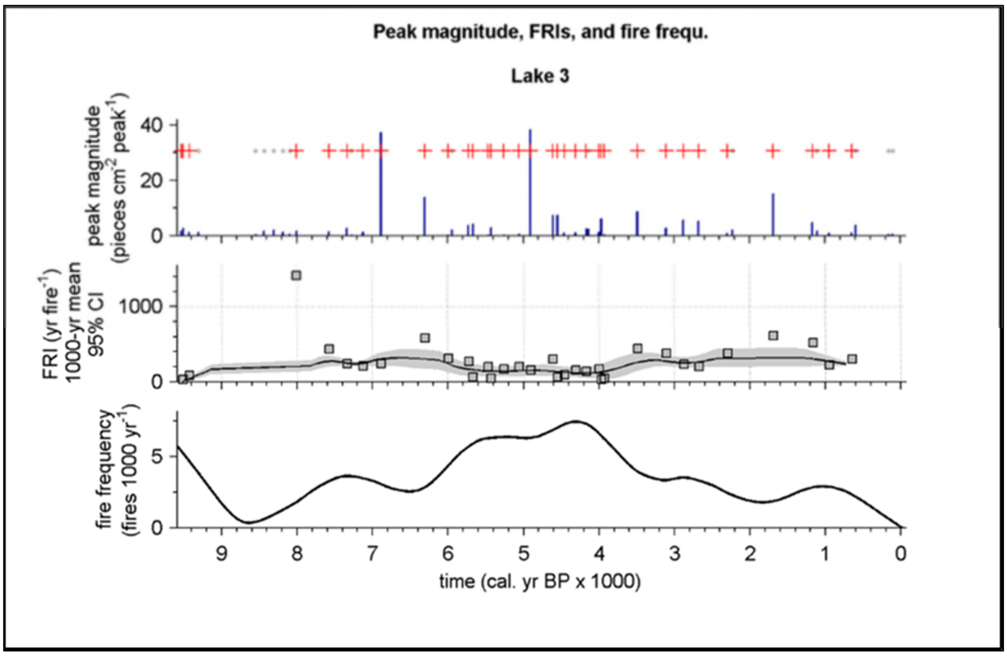


Figure 6.21: *Peak magnitude, Fire Return Intervals (FRIs) and Fire frequency at Lake 3 (C. Clarke)*

6.5 Discussion

6.5.1 Ruppert and Lake 3 pollen records

Ruppert Lake and Lake 3 pollen sequences record the same main shifts in plant functional types and vegetation cover from deciduous trees to evergreen forest-tundra and then to the development of the evergreen boreal forest. One of the main differences is that Lake 3 starts later than Ruppert and does not record the late glacial herb tundra zone. During the late glacial, rises is *Betula* are recorded at many sites (Anderson *et al*, 2004) as vegetation transitioned to shrub tundra from herb tundra. The *Betula* rise is dated to around 13,500 yr BP at Ruppert Lake (Higuera *et al*, 2009). There are some discrepancies between radiocarbon dates from older studies, but this has been attributed to bulk radiocarbon dating methods (Abbott *et al*, 2010). Knowledge of the methods used for dating should be kept in mind when comparing vegetation transitions across the region.

The dates of the broad vegetation transitions at Ruppert and Lake 3 are comparable. The deciduous woodland zone was already developed when Lake 3 sediment deposition began. The date obtained from the base of this sequence is after the onset date of the deciduous woodland zone and before the onset of the forest-tundra in Ruppert and it therefore fits well chronologically. Only the end of the *Populus* zone is captured in the Lake 3 pollen diagram, but similar percentages as Ruppert suggests that this tree was common locally during this period.

Many Alaskan palaeo records record this small *Populus* zone (e.g. Brubaker *et al*, 1983; Anderson and Brubaker, 1994; Hu *et al*, 1993) and the results from Chapter 4 and this Chapter using the LRA suggest that it could have been more abundant than previously thought (discussed below).

The start of the forest-tundra is dated to 8500 yr BP at Ruppert Lake and 500 years earlier (9016 yr BP) at Lake 3. The date at Lake 3 is not from an AMS radiocarbon date, but extrapolated from the age-depth model, which might account for the slightly earlier date. *Betula* rises again in this zone with the decline of *Populus*, but the main occurrence in this zone is the appearance of *Picea* in both records. The general picture is that *Picea glauca* was present c. 9000 cal yr BP in the major river valleys and later in the upland sites (Anderson *et al*, 2004). The mean grain size measurements of *Picea* (Figure 6.12) also suggest that the initial spread of *Picea* was *P. glauca*.

The *Alnus* rise is present in many Alaskan palaeo records and was found across the Brooks Range by the mid-Holocene (Anderson and Brubaker, 1993; Brubaker *et al*, 2001). High pollen percentages (>30%) suggest *Alnus* was abundant in the western and central Brooks Range by 7500 cal yr BP (Anderson and Brubaker, 1994). The expansion of *Alnus* has been viewed by some palaeoecologists as evidence for increased moisture during this period (Anderson and Brubaker, 1993). However, the results from Chapter 4 and this Chapter indicate that it may not have been as abundant as previously thought (discussed below).

The development of the closed boreal forest started around 5500 cal yr BP at Ruppert Lake and Lake 3. This zone sees the second expansion of *Picea* (most likely *Picea mariana*) and this is seen in pollen records across north-central Alaska (Anderson and Brubaker, 1994a). The measurements of *Picea* grains shown in Figure 6.12 also indicate that the mean grain size is smaller in the top half of the record at lake 3 compared with the base which suggests that the second expansion in the mid-Holocene was most likely *Picea mariana*. Higuera *et al* (2009) also record a decrease in fire return in which coincides with the development of flammable *P. mariana*-dominated forests.

6.5.2 The Landscape Reconstruction Algorithm

6.5.2.1 LOVE vs REVEALS

The results from the previous Chapter suggest that REVEALS provided satisfying results compared with LOVE, particularly in forested landscapes, most likely because the vegetation around the small lakes was very similar to the mean regional vegetation. When applying the full 2-step LRA approach to Ruppert and Lake 3 using PPE Sets 1 and 2 in this Chapter we also see some unlikely results, particularly in the late glacial and early Holocene. *Populus* is increased dramatically in both REVEALS and LOVE reconstructions during these periods. However, as discussed above it seems very unlikely that this taxon completely dominated the landscape which is suggested from the LOVE output. LOVE appears to perform well during the later Holocene.

Following considerations on the appropriateness of PPE Sets 1 and 2 in Chapter 4; PPE Sets 4 and 5 were also applied using the LRA in this Chapter. The results shown in Figure 6.15 and 6.16 show some striking differences compared with PPE Sets 1 and 2. The main difference is during the Holocene with the increase in *Alnus* and the decrease in *Betula*. The PPE for *Alnus* in PPE Sets 1 and 2 was substituted for the European mean value. This value is considerably higher the PPE obtained in Alaska in Chapter 3, even with the new value adjusted to relate to Poaceae. This would account for the decrease in the representation of *Alnus* shown using PPE Sets 1 and 2 compared with PPE Sets 4 and 5. The values for *Alnus* are discussed in detail in Section 3.4.3 and there are several reasons for the discrepancies across Europe and for the low value obtained in Alaska. Although the value of 2.7 when adjusted to relate to Poaceae is comparable with values obtained in southern Sweden and central Bohemia, the high LOVE estimates illustrated in Figures 6.15 and 6.16 still seem high for this landscape. REVEALS was not applied to Ruppert and Lake 3 using PPE Sets 4 and 5 in this study. Considering the results from Chapter 5 and this Chapter, it would be an approach for further investigation to apply REVEALS using the more appropriate PPE Sets 4 and 5 to Ruppert and Lake 3. It seems likely that the vegetation around these smaller lakes is very similar to the mean regional vegetation and why REVEALS may provide more satisfying results compared with LOVE. The reasons for the uncertainties with using LOVE are discussed in detail in Chapter 5 but patch size seems to be the most appropriate conclusion (also see below). The results discussed below will therefore focus on the REVEALS estimations of land cover using PPE Sets 1 and 2.

6.5.2.2 Land Cover in the Brooks Range

The results from Chapter 4 illustrated that several small lakes in the Brooks Range produced broadly similar REVEALS estimates to one large lake. When Sithylemenkat Lake was combined with the small lakes the patterns of estimates were almost identical to using just the small lakes on their own. There is a possibility that the Sithylemenkat pollen signal was being swamped by the small lakes or that the small lakes were producing the same pollen signal as large regional lakes. When looking at the results from Chapter 5, particularly in the interior boreal forest, it seems very reasonable that small lakes like Smith Lake are producing a similar pollen signal to a larger ‘regional’ lake. This is most likely due to patches of homogenous forest vegetation in the boreal forest with few ‘gaps’ with small enough patch sizes to suggest that small lakes are just as appropriate for REVEALS as a large lake in this landscape. The modern vegetation in this region is dominated by forests and woodlands on lowlands and hillslopes (Higuera *et al*, 2009) and the pollen record suggests that the foothills of the Brooks Range was forested during the Holocene and this could be why REVEALS performs well here.

Comparing the pollen proportions from Sithylemenkat (Figure 4.12) with Ruppert (Figure 6.13) and Lake 3 (Figure 6.14) the patterns of the main taxa are almost identical. These lakes are 154km apart and Sithylemenkat is 18 times larger than Ruppert and Lake 3. The time windows are quite large (1000 years) during the late glacial and Holocene but this suggests that the timing of vegetation change across the south-central Brooks Range was the broadly synchronous and small lake pollen records do represent the regional signal. This could also suggest that the local vegetation around small lakes did not vary greatly from the regional vegetation. There are some variations when looking at just the small lakes compared with one large regional lake in Chapter 4 (Figure 4.8) Pollen proportions and REVEALS estimates are increased for Poaceae and Cyperaceae, which is not surprising with lake fringing sedge mats present around small lakes today. REVEALS estimates also increase throughout the Holocene for *Populus* as it is present (albeit in small pollen proportions) in more samples in the small lake records suggesting it was locally present.

As discussed in Chapter 4, one of the most striking results from the REVEALS scenarios in the Brooks Range using PPE Sets 1 and 2 was that *Betula* may have been less dominant than previously thought in the late glacial and that Salix and Poaceae were more dominant on the landscape. This is also the case at Ruppert. *Betula* values are drastically reduced in the late glacial at Ruppert Lake when REVEALS is applied and this has been attributed to the high PPE obtained from the tundra dataset. When looking at some of the modern vegetation surveys around the Denali highway (particularly at D6 around Oh, That Pond!) *Salix* is widespread in some of the tundra communities despite very low pollen proportions in the moss polsters. The low PPE obtained for *Salix* suggests that low pollen proportions are misleading in indicating low presence of this shrub in the tundra.

Pollen assemblages from ~13,500 to 9500 cal yr BP have posed a problem for vegetation reconstructions in Beringia with little similarity to modern spectra (Edwards *et al*, 2005). Edwards *et al* (2005) analysed pollen and macrofossil data from Beringia (northeast Siberia, Alaska, and northwest Canada), with a focus on structural and functional features of the vegetation. They discuss the early Holocene vegetation as structurally, and functionally, novel compared with today's vegetation types. The results from the LRA validation and modern cover estimates in Chapter 5 suggest that REVEALS produced reasonable estimations of cover of *Betula* with the PPE Sets 1 and 2 obtained in Chapter 3. This increases the confidence in the REVEALS reconstruction and the interpretation that *Betula* was not as widespread as previously thought during the late glacial and early Holocene, and that the vegetation differed substantially from forest and tundra types today (Edwards *et al*, 2005).

Macrofossil evidence from eastern Beringia (Edwards *et al*, 2005) suggests that shrub taxa reached tree sizes (>2m), and with arboreal taxa, formed open woodlands and deciduous forests dominated by Populus (both *P. balsamifera* and *P. tremuloides*). Opinions about the extent to which *Populus* forest was prevalent in central Alaska vary (Anderson *et al*, 2004). Some researchers suggest that the forest was restricted to slopes and floodplains, whereas others indicate a dense cover on many low-to-mid elevation sites (Ager, 1983; Brubaker *et al*, 1983; Hu *et al*, 1993). Anderson *et al* (2004) discuss that *Populus* density was most likely greatest towards the interior with only scattered populations at sites closer to the present-day coast. Although pollen proportions of *Populus* are low in many of the records presented in this thesis, particularly past 8000 yrs BP at Ruppert and Lake 3, the low PPE obtained in Chapter 3 (from all PEE sets) and the REVEALS estimates produced in this Chapter would suggest the tree was more abundant than previously thought.

With regards to the Holocene, aside from the reduction in *Betula*, the two main taxa which show major changes between pollen proportions and REVEALS estimates are *Picea* and *Alnus*. The introduction of *Picea* (most likely *Picea glauca*) around 9000 cal yr BP is increased in the REVEALS estimates compared with the pollen proportions alone. *Picea* was the reference taxon for the first iteration of the Forest dataset in Chapter 3 and no PPE was produced for this taxon in the tundra. *Picea mariana* was dominant in some of the Forest moss polster plots, but *Picea glauca* was well represented and the vegetation-pollen dataset includes both species. There was also a good spread in the pollen-vegetation scatterplots for *Picea* and, therefore, it was the most appropriate reference taxon. For these reasons there is some confidence that the PPE value used is reliable for the REVEALS reconstruction used for the Holocene time windows in this study for Ruppert and Lake 3.

The increased REVEALS estimates for *Picea* (from 5% in the pollen percentages to between 20-30% in REVEALS estimates) during the early Holocene could modify our interpretation of how dense the *Picea* cover was during this period. The pollen percentages for *Picea* at this time in the Brooks Range are slightly different to Interior Alaska, where percentages are higher (around 20%) at some sites in the interior (e.g. Jan lake; Carlson and Finney, 2004). The expansion of *Picea* forest at Birch Lake has been closely correlated to a rise in lake levels and moisture increase during this time in interior Alaska (Abbott *et al*, 2000). There is the possibility that the soils in the Brooks Range maintained drier for longer as organic soils and permafrost on moraine soils took longer to build up compared with loess soils in the interior. This could be why *Picea* expanded faster in the interior. However, if the REVEALS estimates are correct *Picea* was slightly more widespread in the Brooks Range than previously thought, then the cover of *Picea* in the early Holocene is likely to be increased in the interior. The REVEALS reconstruction at Birch Lake (Figure 5.8) suggests that this might be the case. Although the full sequence at Birch Lake was not used in the analysis of the LRA in Chapter 5 or considered in great deal here, it does illustrate potential considerations for future land cover studies in Alaska.

For the Holocene time windows (11,000 yrs BP to present day) the PPE for *Alnus* (obtained in Chapter 3 from the Forest dataset) was substituted for the higher European mean used in the LANDCLIM project (Mazier *et al*, 2012). The reasons for this have been outlined in Chapter 4 as the PPEs obtained in Chapter 3 was not deemed entirely appropriate or accurate. *Alnus* is dramatically reduced at both Ruppert and Lake 3. Some caution should be taken of the interpretation of this as the PPE used was not obtained from the study region, but *Alnus* is a high pollen producer and it is likely that this taxon was not as abundant on the landscape as has been previously interpreted from pollen diagrams alone. The spread of *Alnus* has been interpreted as evidence for increased moisture during this period (Anderson and Brubaker, 1993). The implications for this new interpretation on the cover of *Alnus* is discussed in more detail in Chapter 7.

Coinciding with the reduction in *Alnus* and *Betula* in the REVEALS estimates compared with the pollen proportions, is the increase in *Picea*. The REVEALS estimates suggest that *Picea* is the dominant taxon in this landscape, particularly during the mid-late Holocene following the expansion of *Picea mariana*. The results from REVEALS at Ruppert and Lake 3 have provided a new insight into nature of the land cover in the south-central Brooks Range and the extent to which this contributes to the interpretation of the fire history for this region is discussed below.

6.5.2.3 Fire History

A detailed fire history of this region is discussed in Higuera *et al* (2009). The focus of most of the charcoal records in Alaska have concentrated on mid-Holocene fire regimes, and the development of the boreal forest. Higuera *et al* (2009) used CHAR from four lakes in the south-central Brooks Range; Ruppert, Xindi, Code and Wild Tussock to provide estimates of fire return intervals (FRIs) which were linked to the Plant Functional Type (PFT) zones identified through pollen analysis. More frequent fire events are attributed to the spread of the flammable *Betula glandulosa* species between 13,000-14,300 cal yr BP. The results from this Chapter indicate that *Betula* was not as widespread as previously thought which could possibly indicate that this species was highly flammable and extensive cover was not required on the landscape to increase fire frequency.

The spread of *Populus*-dominated deciduous woodland in the early Holocene appeared to lengthen the FRIs despite the warmer, drier summers than present (Abbott *et al*, 2001, Anderson *et al*, 2001). Higuera *et al* (2009) attribute this to the presence of less flammable fuels. The REVEALS estimates suggest that *Populus* was more widespread than previously thought during the early Holocene and potentially indicates that a large shift in vegetation cover is required to override the effects of climate. Higher fire frequencies are recorded at many sites across Alaska during the mid-late Holocene following the expansion of *Picea mariana* (Hu *et al*, 1993; 1996; Lynch *et al*, 2002; Higuera *et al*, 2009). *P. mariana* has fine branches which are susceptible to burning (Kershaw and Rouse, 1976) compared with *P. glauca* which is low in flammability and often increases Fire Return Intervals (FRIs) (Drury and Grissom, 2008). The average *Picea* grain sizes (Figure 6.12) indicate that the forest is dominated by *P. mariana* in the upper half of the Lake 3 record and fire frequency is highest at Lake 3 between 6,500 and 3,500 cal yr BP which coincides with the development of the boreal forest and increased REVEALS estimates of *Picea* cover.

Charcoal records were examined in this Chapter, firstly, to explore if two small lakes in close proximity to each other recorded the same fire histories; secondly, to see if new perspectives on land cover at Ruppert Lake and Lake 3 altered the interpretation of the fire records. The interpretations of the fire records has not fundamentally changed with new interpretations of vegetation cover. What is interesting is the comparison of the fire records between the two lakes. In the early Holocene (9000-8000 cal yr BP) they are different, with several peaks at Ruppert and virtually none at Lake 3. Gavin *et al* (2006) examined fire records at two lakes 11km apart in south-eastern British Columbia. Both lakes were located in similar forests and had experienced the same late-Holocene climate changes; as with both Ruppert and Lake 3. They concluded that neighbouring stands with similar modern conditions may have experienced different fire intervals and episodes, most likely driven by local controls outweighing the effect of climate (Gavin *et al*, 2006). Higuera *et al*'s (2009) record could potentially be picking up a regional fire signal as the catchment is larger as well as local fire charcoal records or have higher rates of inwash and erosional events compared with Lake 3. However, following the expansion of the highly flammable *Picea mariana* both Ruppert and Lake 3 charcoal records exhibit peaks confirming that the expansion of *Picea* is most likely the main driver of increased fire frequency at both lakes during the mid-Holocene.

6.6 Conclusions

- Small lakes in the south central Brooks Range 1-km apart with different lake: catchment ratios record the same main shifts in PTFs in their pollen sequences from deciduous trees to evergreen forest-tundra and then to the development of the evergreen boreal forest.

- Ruppert and Lake 3 records exhibit different fire histories in the early Holocene with more charcoal peaks in the Ruppert record compared with Lake 3. The records do, however, show peaks in their charcoal records following the expansion of *Picea mariana*.

- REVEALS provides a more satisfactory result for vegetation reconstructions than LOVE for the small lakes in the Brooks Range; but this is only because the vegetation around the small sites is very similar to the mean regional vegetation. However, it must be stated that REVEALS is not appropriate for reconstructing local vegetation around single small lakes.

- REVEALS has shown the same patterns of cover throughout the Holocene as demonstrated at other lakes in the Brooks Range (Chapter 4) particularly that the *Betula* rise may not have been as expansive as previously thought and the spread of deciduous woodland may have been more extensive than previously thought in the early Holocene.

Chapter 7: Discussion and Conclusions

7.1 Introduction

Developing new methodologies to reconstruct the vegetation quantitatively in terms of actual land cover is increasingly at the forefront of palynology. As discussed in Chapter 2, the majority of reconstructions have been based on percentage representations of taxa in samples as a way to deduce the landscape vegetation. Pollen influx is a calculation of the number of pollen grains falling on a unit area of sediment in a given time (Davis, 1969). This can be particularly useful where pollen dispersal of long distances is strong and influx can help deduce the presence or absence of a species at a site (Hicks, 1994, Hicks and Hyvärinen, 1999). However, pollen influx is not comparable among sites and therefore cannot be used in regional or continental summaries of land cover change.

It has been acknowledged by palynologists for some time that there are disparities between the percentages of species in the present vegetation and the percentages of pollen being deposited (Fagerlind, 1952; Davies, 1963; Faegri and Iversen, 1989). Davies (1963) discusses that this relationship is further complicated by the fact that some species contribute proportionately more pollen than others. One of the first attempts to correct for this was the *R*-value model developed by Davies (1963). This led to various other proposed models attempting to address the pollen-plant abundance relationship (Tauber, 1965; Anderson, 1970; Jacobson and Bradshaw, 1981). Tauber's (1965) model pioneered the recognition of biases in pollen production and dispersal, and it is the understanding of these biases that forms the basis of quantitative reconstructions (Bunting and Middleton, 2009; Sugita, 2007a). Prentice (1985, 1988) developed Tauber's model to focus on the wind above the canopy as the dominant controlling factor of pollen transport. This model was deemed the most comprehensive and developed further by Sugita (1993; 1994).

Various approaches have been adopted over the past several decades to interpret pollen data and reconstruct vegetation including the use of plant functional types and biomization (Prentice *et al*, 1996) and simulation models for pollen dispersal and deposition which include HUMPOL (Bunting and Middleton, 2005) and POLLSCAPE (Sugita, 1994, Sugita *et al*, 1999). Despite advances in theoretical studies of the pollen-vegetation relationship, there still lacked a theoretical framework to incorporate our understanding of the mechanisms and factors into reconstruction of past vegetation (Sugita, 2007a).

The Landscape Reconstruction Algorithm (Sugita, 2007 a; b) has been a fundamental step forward in attempting to a quantitatively estimate vegetation and land cover based on the theories of pollen production and dispersal mentioned above. One of the major inputs into this framework is pollen productivity estimates (PPEs) and the challenges of obtaining these have been discussed in Chapter 2. These range from site selection, vegetation survey methods and regional vegetation cover data available. In order to arrive at reliable estimates of regional and local estimates of vegetation for any given region, Shinya Sugita (*pers comm, Nov 2013*) suggests that PPEs used in REVEALS and LOVE should be obtained from that region whenever possible. Geographical variation in pollen production can be driven by climate and this is particularly important when reconstructing vegetation at treeline sites. Climate can also cause annual variation in pollen production (Hicks, 1999), and pollen production can often be lower at the forest-tundra ecotone (von Stedingk *et al*, 2008).

Chapter 3 described the methods used to obtain the first PPEs for the dominant forest and tundra taxa in Interior Alaska. There are several limitations to this study and Chapter 3 in particular highlights some of the difficulties faced when attempting to collect appropriate vegetation data in remote regions like Alaska. However, despite these challenges this study has produced PPEs for the dominant taxa. The new Alaskan PPEs from the second iteration have shown comparable trends of high and low producers to those obtained in Europe. There are some interesting comparisons to other boreal regions, particularly with *Betula*. The PPE obtained from the Denali Highway tundra was particular high (10.95) compared with other tundra regions such as Greenland (2) and west central Sweden (2.24). However, the PPE value of 8.7 obtained in the interior forest seems very reasonable when compared with the value from southern Sweden (8.9). Although there are broad comparisons with other regions, this study has highlighted the importance of obtaining PPEs from the study region whenever possible.

This work attempted to assess whether the accuracy of vegetation reconstructions can be improved over conventional approaches, and in particular what is the best way to quantitatively reconstruct catchment vegetation around lakes. The limitations are discussed below followed by a critical evaluation of the estimates of regional vegetation cover in the Brooks Range and the implications for current and future research in boreal regions.

7.2 Limitations and challenges

7.2.1 Pollen Productivity Estimates (Chapter 3)

One of the main factors which can affect PPEs is the methodology employed. Site selection should be randomly distributed, and if this is not possible care should be taken to ensure a large spread of values in vegetation cover for the taxa selected (Broström *et al*, 2008). The impracticality of choosing random locations is one of the main limitations faced when working in Alaska. Site selection was a compromise between safety and quality of data collection. Practical issues when working in remote areas need to be taken into consideration, for example distance to the nearest road and potential encounters with wildlife including bears. The decision was made to focus on the Richardson and Denali Highways for the more remote tundra sites. As sampling could not be completely random, a subjective sampling approach was adopted. As the road network in and around Fairbanks was a little more extensive, sampling could be more random as parts of the forest in this area were more accessible. Despite these constraints, every effort was made that the sites reflected a spread of values in the vegetation cover for the selected taxa, and the pollen-vegetation scatterplots (Figures 3.7 and 3.8) reflect that this approach was quite successful. The importance of random sampling is probably landscape dependant, for example in study areas comprising forest and farmland. Therefore, I think other factors discussed below had a greater effect on the PPEs obtained in Chapter 3.

A second limitation with site selection and sampling was the number of sites. Prior to commencing fieldwork the choice of taxa and number of sites was discussed in detail. However, the constraints that a small number of sites might have on the data analysis post-fieldwork was not necessarily fully taken into consideration during the fieldwork planning phase. The number of sites chosen was a compromise between the minimum requirements for PPE studies and time and resources in the field. The number of sites selected should be at least double the number of taxa chosen for PPE analysis as this is a mathematical constraint of the ERV models (Shinya Sugita, *pers comm, June 2014*). Even though the tundra and forest sites just doubled the number of taxa, this left no room for outliers to be removed. To run POLERV all taxon groups are required to run together, therefore removing outliers in one taxon group would require removing that site from all taxon groups. If this was done for every outlier then there would have not been enough sites left for analysis. If more sites had of been used this could have potentially provided a more reliable spread in the pollen-vegetation relationship, reducing outliers or allowing the option for some sites to be removed in the analysis stage. This could be one of the reasons why the Alaskan value for *Alnus* was not entirely appropriate or reliable. However, no major assumptions were violated and the minimum number of sites were used in the ERV analysis which produced reasonable PPEs for the major taxa.

The vegetation survey can often affect PPEs and the results discussed in Chapter 2 by Bunting and Hjelle (2010) in Norway highlight the effect that survey design can have on estimates of pollen productivity. Zone A (0-10m) and zone B (10-100m) was careful planned prior to fieldwork and tested in the New Forest, Hampshire before attempting in Alaska. The methodology was discussed in detail with Shinya Sugita and Jane Bunting (Hull University) and any adaptations made in the field with regards to sampling intervals and time constraints were assessed on a site by site basis and any changes in vegetation composition and boundaries were closely monitored. Sampling intervals were therefore deemed appropriate at each individual plot.

The main issue which may have arisen from the sampling methodology is cover vs biomass. As discussed in Chapter 5, vegetation surveys focused on recording estimations of cover. However, if biomass were recorded these values would be different. An example of this is particularly evident when looking at Ericaceae where the biomass is small compared with trees for example. Even if Ericaceae was recorded at 80% cover and *Betula* at 20%, these values could easily be reversed if biomass was estimated. However, estimations of cover worked particularly well when estimating tree cover.

One consideration that should be mentioned is the choice of vegetation mapping for Zone C (100-1500m). Aerial photographs and google earth images were used to map the communities in this zone. The communities were assigned based on the point-centred quarter method data collected in the field and the Alaskan Vegetation Classification (Viereck *et al*, 1992). Han *et al* (2017) point out that the range and resolution of vegetation maps and aerial photographs are different in different regions (Baker *et al*, 2016; Duffin and Bunting, 2008; Mazier *et al*, 2008) and the different sources of vegetation data amount these studies may affect the accuracy and comparability off PPEs and RSAP (Han *et al*, 2017). Not every community was visited and surveyed in the field in Alaska due to time constraints which could lead to an under or over-representation of some taxa. This could be an area where increasing the number of plots could reduce the uncertainty in vegetation community assignments. With more time and resources it would have been beneficial to survey more of the vegetation communities in the 1500m zone. Even though the Alaskan Vegetation Classification only specified dominance rather than cover data, it was a useful tool for confirming species that are present in certain communities and dominance.

7.2.2 The Landscape Reconstruction Algorithm (Chapters 4 and 5)

A potential limitation to applying REVEALS in the Brooks Range and testing large lakes vs small lakes is the availability of large lakes with pollen records covering the late glacial and Holocene. The extent of vegetation reconstructed by REVEALS was 100km. There were no large lakes with existing pollen records and a robust chronology within this area around Ruppert Lake and Lake 3. Sithylemenkat is approximately 154km away from the study sites. Despite this, the pollen records of all three lakes were very similar for the time period covered. However, simulation studies (Sugita, 2007a) have shown that the higher the pollen counts in each sample the more reliable to the reconstruction will be using REVEALS. Even though the Sithylemenkat pollen record produced a good regional signal for the Brooks Range, pollen counts were particularly low averaging around 200 grains per sample. As diversity was low and Sithylemenkat was also combined with several small lakes, it is unlikely that low counts contributed to any issues with the reconstructions in Chapter 4.

The methods employed in Chapter 5 probably faced the most difficult challenges of the study. To start with the LOVE estimates of the modern vegetation cover relied on confidence of the REVEALS reconstructions at Ten Mile Lake and Birch Lake. The Ten Mile Lake record in particular was not an accurate reflection of the modern vegetation due to the complications of reconstructing vegetation at treeline sites. Anderson and Brubaker (1994) determined that *Picea* pollen values up to 10% typically indicated a location beyond the treeline.

Secondly, the dwpa for the small ponds was taken from nearby moss polster sites rather than the small lakes themselves. This was not deemed to be too much of a problem at Smith Lake as the cover of taxa was relatively consistent in this region. This was confirmed when applying REVEALS to Smith Lake surface sample which provided a good fit between the estimates of cover and the dwpa for individual taxa. This could, however, have contributed to the difficulties when applying LOVE at the tundra sites as the vegetation was more diverse and complex over small areas.

On reflection, the location of the tundra sites may not have been entirely appropriate for this exercise and this is the main component of the methodology I would modify if to approach this exercise again. Chapter 5 has highlighted the difficulties of reconstructing vegetation at treeline sites. Biomization was applied in North America by Williams *et al* (2000) and they found that forest tended to be over-represented at the northern treeline and the forest-tundra ecotone. The small lakes along the Denali Highway, along with Ten Mile Lake, were sat in a complex vegetation structure. The pollen proportions were reflecting an assemblage of mixed forest and tundra which is not an accurate reflection of the modern vegetation.

The results presented in Chapter 4 indicate that REVEALS works well when applied to pollen sequences in the Brooks Range. Chapter 4 and 6 strongly suggest that small lakes in Interior Alaska produce the same pollen signal as large regional lakes and therefore REVEALS produces a satisfactory result using small lakes; but this is only because the vegetation around the small sites is very similar to the mean regional vegetation. The application of the LRA has provided new insights into the extent of vegetation cover during the late glacial and early Holocene in the Brooks Range. Obtaining accurate regional cover of the modern vegetation in order to validate REVEALS is needed in this region to fully assess the robustness and reliability of these reconstructions which is discussed below, but the results presented in this thesis have provided a sound basis for further studies in quantitative vegetation reconstructions in Alaska (discussed in further detail below).

7.3 Implications

Despite the challenges that have been encountered in the study, there have been several successful outcomes and positive steps forward for quantitative vegetation reconstructions in Alaska. The chosen PPE taxa in both the Denali Highway tundra and the interior Forest showed good variation in vegetation abundance which is a requirement for reliable PPEs (Broström *et al*, 2004). The trends of high and low pollen producers are comparable with European values as discussed above. There are some noticeable differences particularly with *Betula* and *Alnus* which supports the reasoning for obtaining PPEs from the specific region of study. The RSAP obtained in Chapter 3 also seem very reasonable for each of the study regions and are comparable with similar vegetation biomes in other regions.

Chapter 4 and 6 discuss the results from all the REVEALS reconstructions and new interpretations of Alaskan pollen records. One of the main findings is that the *Betula* rise may not have represented as large an expansion in cover as previously thought and that *Salix* may have been more dominant on the landscape during the late glacial and early Holocene. Anderson and Brubaker (2004) discuss the early *Betula* zone and suggest that herb tundra (including *Salix*) remained common in the eastern Brooks Range until c. 12 ka BP despite high *Betula* pollen percentages. This is inferred from the fact that slight increases in pollen accumulation rates (PARs) can result in a large percentage increase when background pollen productivity is low. Therefore, the percentage increase in *Betula* pollen at 14 ka BP at sites in the eastern Brooks Range could be related to low pollen productivity of sparse herb tundra communities. This is likely the case with the modern tundra species around the Denali Highway, where *Salix* and Ericaceae have been shown to produce low PPEs in this study despite being widespread on the landscape, and why *Betula* pollen percentages are so high when the cover of this shrub in the tundra is less so.

The *Populus* zone has also shown interesting results, indicating that this species was far more dominant in the early Holocene than has been previously interpreted from pollen diagrams. Bartlein *et al* (2015) tested the sensitivity of Beringia's early Holocene climate to regional-scale controls such as the development of thaw lakes and the replacement of tundra by deciduous forest or woodland using a regional climate model (RegCM). The change from tundra to deciduous woodland produced additional warming in spring and early summer. To simulate the vegetation changes around 11Ka they used a biomization approach. Deciduous needleleaf (*Larix*) forest was not present in some of their pollen maps due to low pollen counts and they therefore enhanced *Larix* by a factor of 15 which still did not identify deciduous needleleaf forest at this time. In this study the deciduous woodland zone is reconstructed using REVEALS and no moderations are made for low pollen producers such as *Populus* as *Populus* pollen did have low counts at some sites, but was present enough to be used in the reconstructions. Although REVEALS has most likely over-estimated *Populus* in the early Holocene, the results suggest that deciduous woodland was wide spread in the Brooks Range.

Catchment vegetation can alter nutrient cycling in soils but little is known about the effect of shifts in vegetation composition on lake ecosystems. Sediment biogenic silica increased with the expansion of *Alnus* at Grandfather Lake (south-western Alaska) indicating an increase in diatom productivity possibly due to the fixation of N2 in the surrounding soils (Hu *et al*, 2001). The data emerging from the Lakes in the Arctic Carbon Cycle (LAC) project suggests that species such as *Alnus* do have a large influence on lake ecology through changes in biogeochemical cycling. Figure 7.1 shows the initial pollen and diatom results from Lake 3. Shifts in diatom concentration and algal community composition, driven particularly by a decrease in *S. anceps gracillis* and an increase in *F. construens* in the diatom assemblage, occur alongside the *Alnus* rise at Lake 3 indicating an increase in lake productivity. There could be a possibility that *Alnus* has been underestimated in this study. The PPE value for *Alnus* that was used during the one of the Holocene reconstructions in the Brooks Range from PPE Sets 1 and 2 is the European mean value from PPE.st2 (Mazier *et al*, 2012) this PPE value was deemed more appropriate than the Alaskan values obtained in Chapter 3. Further considerations of the PPE Sets used for the reconstructions are required here though as PPE Sets 1 and 2 are not entirely appropriate. PPE Set 4 and 5 are more appropriate, but the low PPE value in these sets for *Alnus* would need further exploration in the future. The results from Chapter 4 and 6 however, suggest that *Alnus* cover may not have been as extensive in the Brooks Range as previously interpreted from pollen proportions alone.

This will have implications for project such as LAC as this taxon has proven to have a large influence on lake ecology, but this study raises questions regarding the extent of abundance before *Alnus* has an effect on lake productivity.

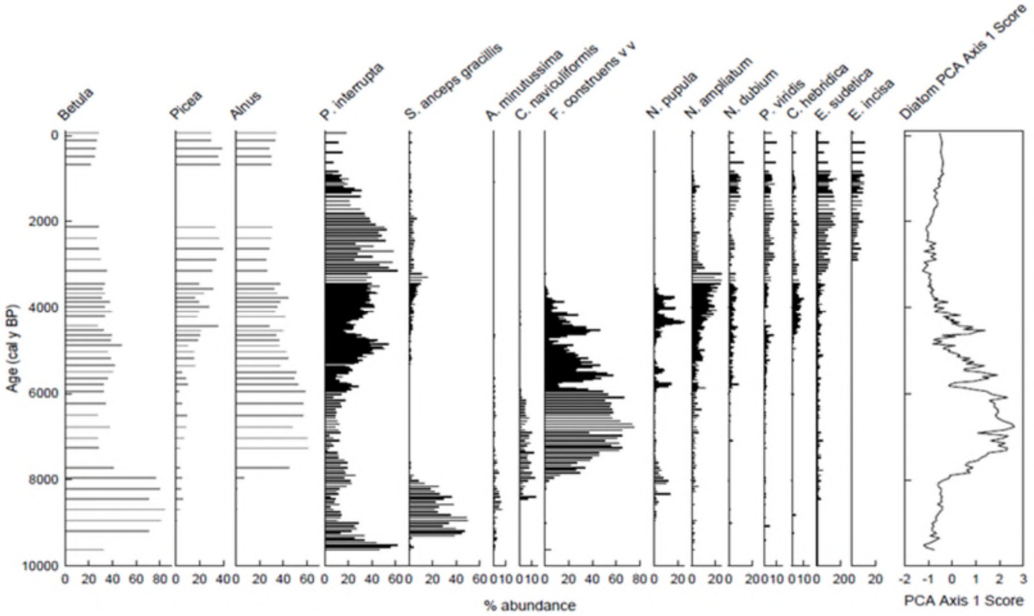


Figure 7.1: *Initial pollen and diatom data from Lake 3 (Erika Whiteford, Emma Hopla)*

7.4 Future research

This study is the first attempt to produce PPEs for the dominant tundra and forest taxa in Interior Alaska. It was of necessity limited in scale, and the next step for PPEs in this region would be to increase the number of sites selected for analysis. The limitations outlined above highlight the need for collection of a larger dataset. More sites would increase the confidence in the pollen-vegetation relationship; for example, with the addition of new sites, the outlier site that probably contributed to the low *Alnus* PPE estimate could be removed.

Validation of the LRA needs greater consideration. The robustness and the limitations of this method require further testing; otherwise the reliability of the PPEs obtained in this study and in the future cannot be further assessed. REVEALS provided a satisfactory result, but only because the local vegetation around the small sites is very similar to the mean regional vegetation. A selection of a set of modern test sites near treeline also clearly played a part in the unsuccessful application of LOVE. As REVEALS ended up being the main focus in the Brooks Range study, obtaining more detailed and reliable data for the regional cover of the modern vegetation, and for cover within one kilometre of sites, would be the obvious next step for validating this model. It would also be beneficial to then test and validate LOVE in a different landscape away from the complications encountered at treeline sites. Although REVEALS produced more satisfactory results at Ruppert Lake and Lake 3, the LOVE reconstructions were not totally unreasonable. A next step might be to test LOVE on more small interior forest lakes as the results from Smith Lake alone are not robust enough to rule out the use of LOVE in this landscape. Further modelling and ordination techniques might also allow a diagnosis as to whether a particular taxa, pollen assemblages, PPE value or the vegetation mosaic, for example, are problematic.

Determining quantitative vegetation cover on regional and local scales can address questions on past land use and responses of vegetation to climate change. A more refined understanding of land cover in the past will be important for paleoclimate models. LandCover6k (PAGES project coordinated by Marie-José Gaillard) addresses land-cover change across the globe that is climate-induced, natural and human-induced. In light of future climate change, understanding past vegetation dynamics will impact our understanding of processes which should be included in future environmental models (Trondman *et al*, 2015). LandCover6k builds on the land-cover reconstructions across Europe by Trondoman *et al* (2015) focussing on, but not limited to, periods of anthropogenic land cover changes such as deforestation. The results from REVEALS reconstructions by Trondman *et al* (2015) suggest that the degree of anthropogenic deforestation at 3k is significantly higher than deduced from pollen percentages.

Particularly for the boreal forest biome, understanding interactions between fire, climate and vegetation is crucial in light of predicted forest wildfire activity in response to future climate change (Kelly *et al*, 2013). Although the application of REVEALS did not drastically alter the interpretation of the fire records at Ruppert Lake and Lake 3, the new perspective on vegetation cover during periods of climatic change in central Alaska is applicable here. Binney *et al* (2005) suggest that climatic warming at high northern latitudes may favour the development of deciduous forest biomes. The results from this project indicate that, although probably over-estimated, *Populus* dominated woodland was probably more extensive in the early Holocene than previously thought. This could potentially increase fire return intervals with a shift to less flammable fuels compared with *Picea mariana* dominated forests. Further PPE studies and modelling will help to address how extensive *Populus* was during this early period across central Alaska and how future warming may cause rapid shifts of the dominant PFTs (Binney *et al*, 2005). The Alaskan PPEs and REVEALS reconstructions presented here have made a positive first step into gaining a better understanding of how vegetation responds to climate change and will help to contribute to the efforts of the LandCover6k project.

7.5 Conclusions

- The pollen productivity estimates suggest that *Betula* is a very high pollen producer and *Salix* is a low pollen producer in the Denali tundra. Therefore,
- The *Betula* rise may not have been as expansive in cover as previously thought and Salix may have been dominant on the landscape during the late glacial and early Holocene.
- Trends of high and low pollen producers seem comparable with Europe.
- The PPE for *Populus* was derived from a strong pollen-vegetation relationship; however, the high level of under-representation means that it plays a disproportionate role in determining the reconstructed vegetation proportions in some cases. However, *Populus* and the spread of deciduous woodland may have been more extensive than previous thought.
- Small lakes in Alaska produce the same pollen signal as large regional lakes.
- There are limitations in using sites at treeline. Pollen assemblages from lakes within this ecotone are not a true reflection of the taxa present within the reconstructed landscape. REVEALS also assumes that the vegetation is homogenous, in this case 50% tree cover and 50% shrubs and tundra vegetation at any point in the landscape.
- REVEALS provides a more satisfactory result for vegetation reconstructions than LOVE for the small lakes in the Brooks Range; but this is only because the vegetation around the small sites is very similar to the mean regional vegetation. However, it must be stated that REVEALS is not appropriate for reconstructing local vegetation around single small lakes.

Appendices

Appendix A

Plot	**Central Plot**	**Additional Quadrats**	**Zone A** **10m walkouts**	**Zone A** **PCQ**	**Zone B** **100m walkouts**	**Zone B** **PCQ**
D1	Quadrat	-	2m intervals		yes	
D2	Quadrat	-	2m		yes	
D3	Quadrat	-	2m		yes	
D4	Quadrat	x 12 (*Cassiope* heath, *Salix* heath, *Vaccinium* heath, *Salix* shrub, *Salix* retic)	2m		yes	
D5	Quadrat	x 7 (*Salix* shrub, moist tundra)	2m		yes	
D6	Quadrat	x 4 (*Salix* shrub)	2m		yes	
D7	Quadrat	x 4 (*Cassiope* heath)	1m		yes	
D8	Quadrat	x 6 (*Betula* shrub heath)	2m		yes	
D9	Quadrat	x 4 (*Betula* Sedge tussock tundra)	1m		yes	
D10	Quadrat	x 4 (*Betula* Sedge tussock tundra)	2m		yes	
F1	Quadrat	-	2m	Every tree		20m, 40m, 60m, 80m, 100m
F2	Quadrat	x 4 (in each quadrant)	-	Every tree		20m, 40m, 75m
F3	Quadrat	x 4 (in each quadrant)	1m (only in each cardinal point)	In each quadrant		20m, 50m (dense PM stand)
F4	Quadrat	x 4 (in each quadrant)	-	In each quadrant		20m, 40m, 75m

F5	Quadrat	x 8 (2 in each quadrant)	2m (only in each cardinal point)	In each quadrant		20m, 40m, 75m
F6	Quadrat	-	1m (only in each cardinal point)	In each quadrant		20m, 40m, 75m
F7	Quadrat	-	1m (only in each cardinal point)	In each quadrant		20m, 40m, 75m
F8	Quadrat	x 4 (in each quadrant)	1m	No-Dominated by herbs so increased the walkouts		20m, 40m, 75m
F9	Quadrat	-	1m	In each quadrant		20m, 40m, 75m
F10	Quadrat	-	1m	In each quadrant		20m, 40m, 75m
F11	Quadrat	-	1m (only in cardinal points)	In each quadrant		20m, 40m, 75m
F12	Quadrat	-	1m	In each quadrant		20m, 40m, 75m

Table A.1: *Vegetation Survey undertaken at each moss polster*

Original Rings (Middleton, 2011)	Adjusted rings	Data from tundra plots to be included	Ring Script
Tundra Sites			
0 to 0.5	0 to 0.5	Central quadrats	qC
0.5 to 1.5	0.5 to 2	2m ring data (or 1 and 2m combined)	qN1*0.25+qE1*0.25+qS1*0.25+qW1*0.25
1.5 to 3	2 to 4	4m ring data (or 3 and 4m combined)	qN2*0.25+qE2*0.25+qS2*0.25+qW2*0.25
3 to 6	4 to 6	6m ring data (or 5 and 6m combined)	qN3*0.25+qE3*0.25+qS3*0.25+qW3*0.25
6 to 10	6 to 10	8 and 10m ring data combined (or 7-10m combined)	qN4*0.125+qE4*0.125+qS4*0.125+qW4*0.125+qNE*0.125+qSE*0.125+qSW*0.125+qNW*0.125
10 to 100	10 to 100	Community map	= every 10
Forest Sites			
	0 to 0.5	Central quadrats	qC
	0.5 to 10	PCQ basal area data used as % cover	qN1*0.25+qE1*0.25+qS1*0.25+qW1*0.25
	10 to 100	Community Map	= every 10

Table A.2: *Ring scripts for Survey*

DENALI			**FOREST**		
Plot	**Community**	**% coverage**	**Plot**	**Community**	**% coverage**
D1	Lichen Heath	27.82	F1	*Betula* dominated	53.29
	Shrubby Lichen Heath	22.34		*Alnus/Salix*	7.8
	Picea	17.95		*Picea* domianted	26.33
	Populus	0.03		Bare Ground	11.32
	Betula Shrub Tundra	28.22		Water	1.26
	Bare Ground	3.64			
D2	*Betula* shrub with *Alnus* and *Picea*	67	F2	Old mixed hardwoods with *Picea*	42.36
	Open Lichen Heath	27.7		*Picea mariana* stands	19.85
	Picea Lichen Woodland	1.63		Crops Fields	11.21
	Donnelly Dome Slopes	2.76		Other Hardwoods	1.8
	Bare Ground	0.91		Bare	23.95
				Water	0.83
D3	*Betula* shrub with trees	72	F3	*Picea mariana* stands	74.22
	Lichen/*Vaccinium* heath with *Picea*	18.83		*Alnus/Salix*	0.51
	Lake Lowland	2.13		Hardwoods	22.57
	Lakes	2.13		Shrub tundra	1.35
	Picea Stand	0.41		Bare	1.35
	Bare Ground	1		Water	0
	Water	3.5			
D4	*Salix* Shrub	35.17	F4	*Picea mariana* stands	46.65
	Tundra	38.72		Hardwoods	51.7
	Shrub/Tundra Mix	14.71		Bare Ground	1.61
	Bare Ground	11.02		Water	0
	Water	0.38			
D5	*Salix* Shrub	28.53	F5	*Populus/Betula*	59.11

	Tundra Shrub/Tundra Mix Bare Ground Water	42.43 15.81 12.35 0.88		*Picea mariana* stands Mixed *Picea* and Hardwoods Bare Water	34.4 3.4 3.09 0
D6	Thick *Salix/Betula* Shrub Sedge Meadow with *Salix/Betula* Lichen/Mixed Heath Pondlets Polygons Water	43.21 47.32 2.94 0.41 1.54 4.58	F6	Mixed hardwoods (and *Picea*) Mountain tundra *Picea mariana* stands Hardwoods Muskeg Bare Water	41.15 10.02 19.03 26.41 0.78 2.42 0
D7	*Salix* Shrub Mixed Heath Lake Lowland lakes Bare Ground	26.43 58.51 0.68 6.18 8.2	F7	Mature *Picea* Forest Hardwoods Muskeg Bare Water	23.26 47.31 26.57 1.02 1.84
D8	*Betula/Salix* shrub with Sedge *Betula/Vaccinium* Heath Lake Lowland Lakes Bare Ground	56.99 0.4058 0.42 1.4 0.97	F8	Forest-tundra treeline *Picea* Mixed Hardwoods and *Picea* Hardwoods Bare Water	29.66 36.6 13.49 17.99 2.27 0
D9	BSTT with *Picea* *Picea* and shrubs Water Bare Ground	78.19 18.86 1.82 1.13	F9 78.19	*Picea* *Populus/Betula* Bare Water	37.03 60.8 2.17 0
D10	BSTT with *Picea*	75.96	F10	*Populus/Betula*	26.77

	Picea and shrubs	18.5		*Picea mariana*	35.88
	Water	4.22		Mixed *Picea* and Hardwoods	32.91
	Bare Ground	1.32		Bare	4.44
				Water	0
			F11	Muskeg	20
				Populus	27.32
				Picea mariana	41.3
				Bare	1.12
				Water	10.26
			F12	*Picea mariana*	41.35
				Hardwoods	56.47
				Bare	2.18
				Water	0

Table A.3: *Communities assigned to the tundra and forest plots in Zone C*

Taxa	D1	D2	D3	D4	D5	D6	D7	D8	D9	D10	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	F11	F12
Alnus	161	219	269	452	232	329	540	284	432	310	224	85	20	34	5	50	143	216	80	114	500	28
Betula	782	903	1136	217	95	509	252	265	607	775	910	918	91	708	1049	600	775	602	1250	649	264	840
Picea	280	72	48	70	35	76	77	77	58	86	24	200	975	411	147	405	512	266	32	385	217	260
Populus	0	0	0	3	4	0	0	3	0	1	1	17	0	9	4	19	3	6	12	25	11	3
Salix	3	4	3	34	20	67	30	9	7	2	85	4	1	1	0	17	4	4	5	1	4	1
Ericales	10	22	37	93	5	40	27	374	24	9	0	0	57	1	0	0	0	14	0	0	2	1
Aconitum	0	1	0	0	29	0	1	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0
Artemisia	0	1	3	102	622	2	26	8	0	1	0	3	0	0	2	0	0	0	0	0	0	0
Apiaceae	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Anemone	0	0	1	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Asteraceae	0	0	0	1	8	0	1	1	0	0	1	0	10	1	0	1	0	0	0	0	0	0
Caryophyllaceae	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
Chamerion angustifolium	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0
Chenopodiaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Cornus	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	3	0	13
Cyperaceae	10	2	27	26	19	37	0	24	180	75	4	8	1	4	17	4	2	5	2	8	10	12
Lactuceae	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0
Viburnum	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Equisetum	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Poaceae	0	0	0	45	71	24	13	6	7	13	7	4	1	7	4	79	9	3	3	20	9	5
Potentilla	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Rubiaceae	0	0	1	3	4	0	1	1	0	0	0	0	0	0	0	1	2	0	0	0	1	0
Rumex	0	1	0	0	2	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rubus arcticus	0	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0
Rosaceae	1	0	1	2	0	0	9	0	0	0	1	1	1	0	0	0	0	3	0	1	1	0
Total	1247	1225	1526	1053	1160	1089	979	1052	1315	1272	1259	1249	1157	1179	1229	1179	1455	1119	1384	1206	1019	1163
Herbs	1	3	6	113	666	7	40	10	0	1	4	13	11	4	3	5	7	3	0	4	2	13

Table A.4: *Pollen counts from moss polster sites*

Taxon Group	***r* values**			**R^2**			***P* value**		
	Sutton	**1/d**	**$1/d^2$**	**Sutton**	**1/d**	**$1/d^2$**	**Sutton**	**1/d**	**$1/d^2$**
DENALI									
Alnus	0.552378	0.49458	0.60653	0.3051	0.24461	0.36788	0.09777	0.24461	0.06301
Betula	0.84645	0.90404	0.89388	0.7165	0.00033	0.79902	0.00201	0.81729	0.00049
Picea	0.50998	0.25648	0.56733	0.2601	0.06578	0.32187	0.13209	0.47442	0.08718
Populus	0.2423	0.24230	0.2423	0.0587	0.05871	0.05871	0.50001	0.50001	0.50001
Salix	0.43992	0.66885	0.51291	0.1935	0.44737	0.26308	0.20329	0.44737	0.12951
Ericaceae	0.0256	0.25107	0.17328	0.0007	0.06304	0.03003	0.94403	0.48411	0.63213
Artemisia	0.64254	0.94932	0.03228	0.4129	0.90120	0.00104	0.04512	0.00003	0.92944
Cyperaceae	0.797	0.70763	0.62692	0.6352	0.50075	0.39303	0.00577	0.02206	0.05239
Poaceae	0.47132	0.78905	0.64832	0.2214	0.62259	0.42032	0.16911	0.00665	0.04261
FOREST									
Alnus	0.47344	0.29861	0.01564	0.2241	0.08917	0.00024	0.12002	0.34579	0.96153
Betula	0.81579	0.83742	0.82556	0.6655	0.70127	0.68154	0.00122	0.00068	0.00094
Picea	0.76170	0.88954	0.93190	0.5802	0.79128	0.86843	0.00399	0.00011	0.00001
Populus	0.73531	0.69340	0.46236	0.5407	0.48080	0.21378	0.00643	0.01240	0.13017
Salix	0.92573	0.85350	0.71475	0.857	0.72846	0.51086	0.00002	0.00041	0.00899
Ericaceae	0.36297	0.32893	0.27777	0.1318	0.10820	0.07716	0.24619	0.29650	0.38204
Artemisia	-0.13172	0.13172	0.13172	0.0173	0.01735	0.01735	0.68324	0.68324	0.68324
Cyperaceae	-0.09546	0.08647	0.08286	0.0091	0.00748	0.00687	0.76791	0.78930	0.79793
Poaceae	0.16482	0.35013	0.31251	0.0272	0.12259	0.09766	0.60873	0.26454	0.32268

Table A.5: *Regression Analysis on raw pollen-vegetation scatterplot data*

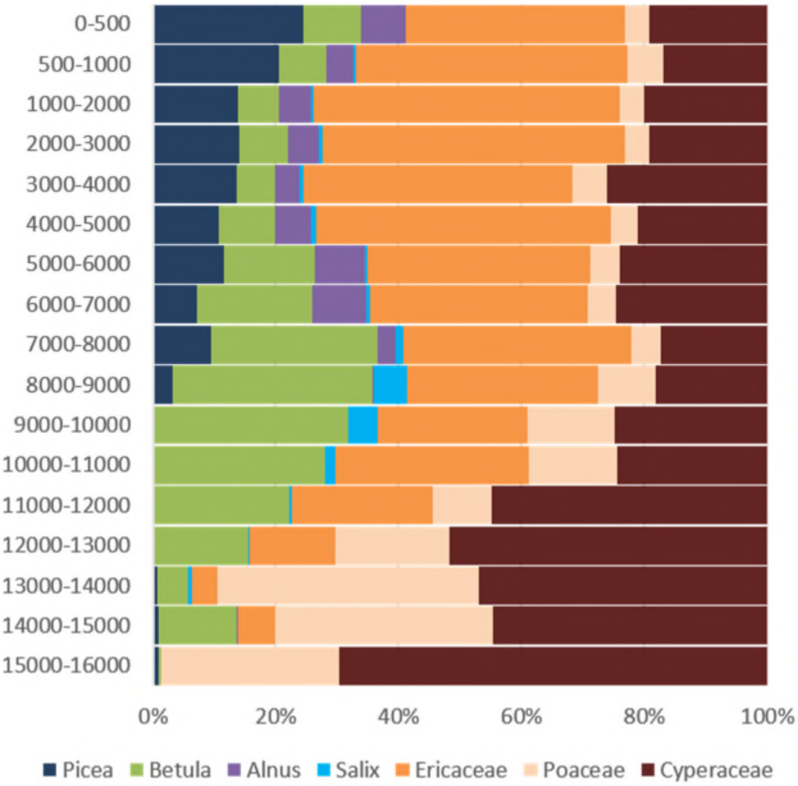


Figure A.1: *REVEALS estimates for small lakes using the European LANDCLIM values (*PPE Set *3/Run 6)*

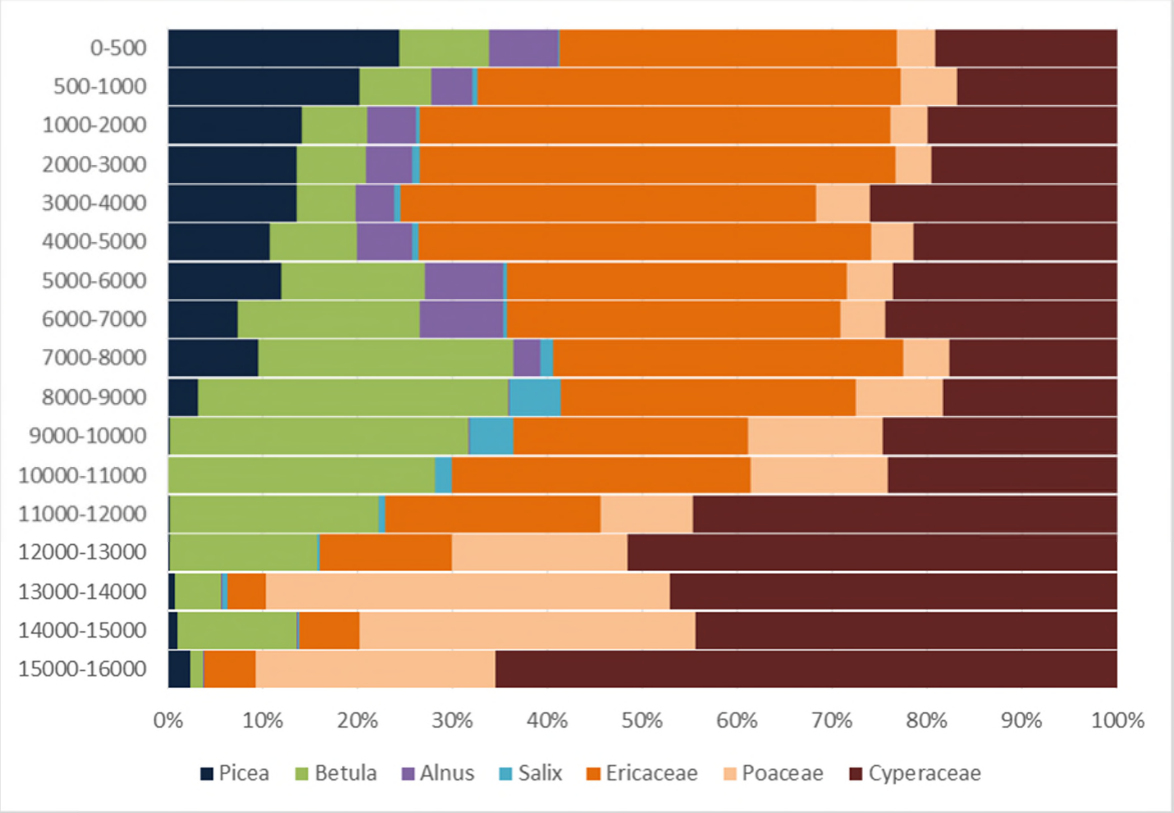


Figure A.2: *REVEALS estimates for Sithylemenkat and small lakes using the European LANDCLIM values* (PPE Set *3/Run 9)*

Smith Lake			**Dummy Lake 1**			**Dummy Lake 2**	
Radius(m)	30		Radius(m)	30		Radius(m)	30
Alnus	112		Alnus	90		Alnus	120
Betula	427		Betula	400		Betula	450
Cyperaceae	23		Cyperaceae	30		Cyperaceae	22
Ericaceae	1		Ericaceae	1		Ericaceae	1
Picea	176		Picea	180		Picea	160
Poaceae	20		Poaceae	24		Poaceae	30
Populus	13		Populus	12		Populus	12
Salix	4		Salix	5		Salix	5
Adjusted Values							
Smith Lake			**Dummy Lake 1**			**Dummy Lake 2**	
Radius(m)	30		Radius(m)	30		Radius(m)	30
Alnus	112		Alnus	40		Alnus	130
Betula	427		Betula	600		Betula	200
Cyperaceae	23		Cyperaceae	30		Cyperaceae	60
Ericaceae	1		Ericaceae	1		Ericaceae	1
Picea	176		Picea	100		Picea	400
Poaceae	20		Poaceae	50		Poaceae	10
Populus	13		Populus	12		Populus	12
Salix	4		Salix	10		Salix	8

Table A.6: *Pollen counts for Smith Lake and dummy lakes*

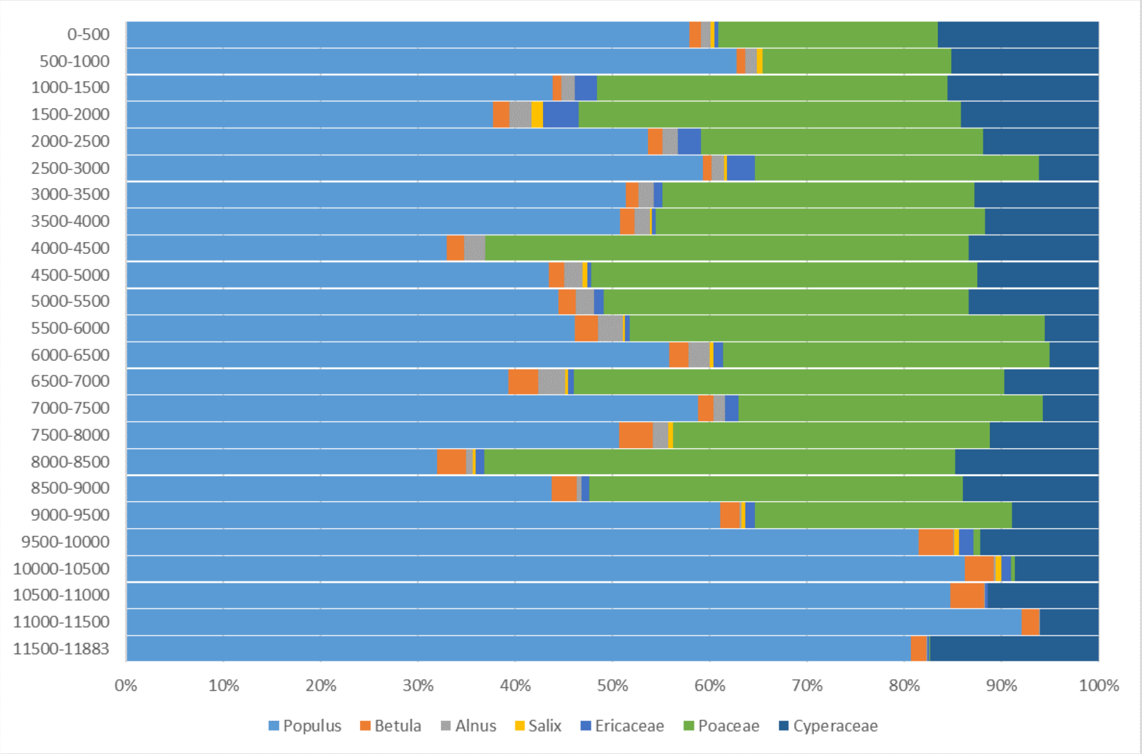


Figure A.3: *REVEALS on Ten Mile Lake (removing Picea)*

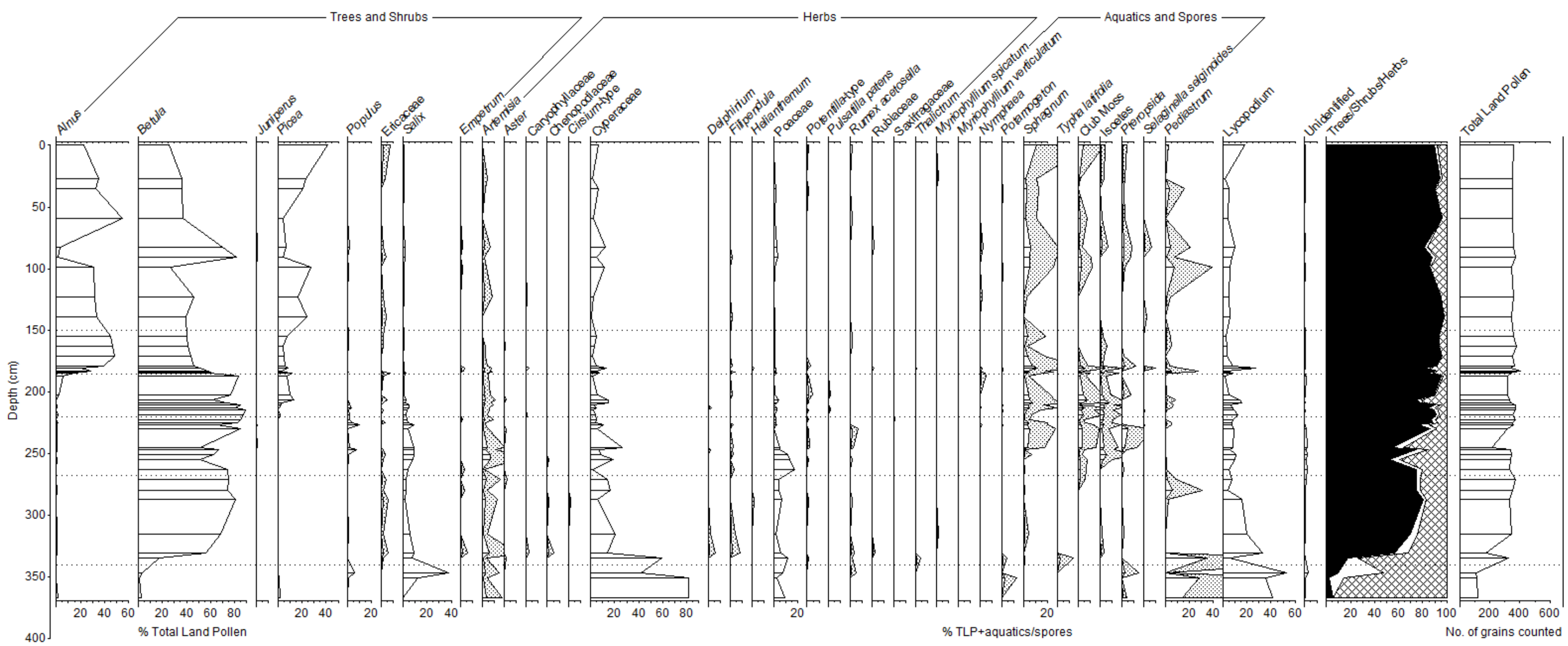
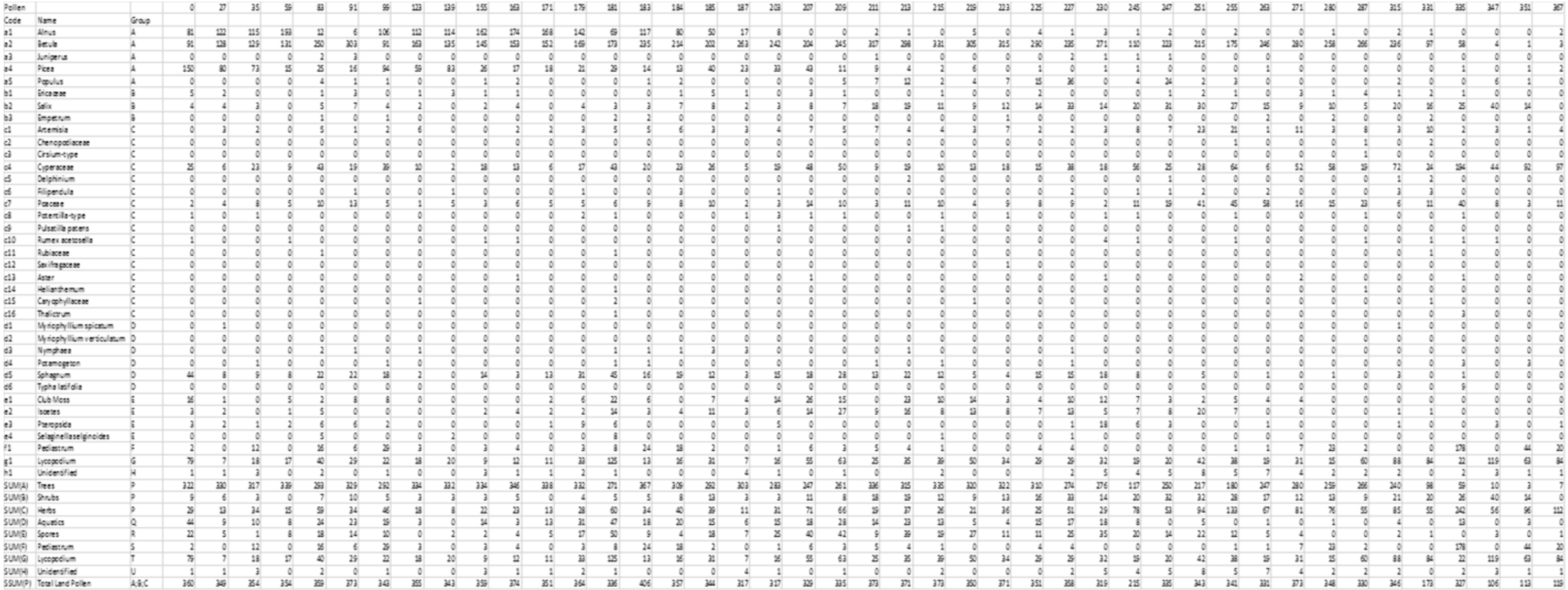


Figure A.4: *Pollen Diagram for Ruppert Lake (Analyst, E.Hopla, Tilia v.1.7.16 and Tilia Graph, Grimm, 2011)*

Depths	PFT Zone	Description
268-340cm	Shrub Tundra	*Betula*-Cyperaceae-Poaceae-*Salix* This zone is characterised by a rise in *Betula* up to 80%. Cyperaceae falls from the previous zone to ca. 20%. Other herbs are rare apart from low frequencies of Poaceae and occasional grains of *Artemisia, Delphinium*, *Filipendula*, *Potentilla*-type, *Rumex acetosella ,*Rubiaceae and *Aster*.
220-268cm	Deciduous Woodland	*Betula*-Cyperaceae-Poaceae-*Salix (Populus)* The opening of the basal zone is characterised by a peak in Poaceae (17%) and a small peak in *Populus* pollen (up to 5%). *Betula* declines slightly and recovers to reach its highest values of 85%. *Salix* increases slightly from the previous zone along with *Artemisia* and Cyperaceae. Occasional grains of Ericaceae and is also present. Other herbs are rare apart from occasional grains of *Filipendula*, *Potentilla*-type, *Rumex acetosella* and *Aster*. Spores increase in the zone with rises in Sphagnum, Isoetes and Pteropsida (monolete) indet.
182-220cm	Forest Tundra (a)	*Betula-Picea* *Picea* is introduced in this zone up to 10%. *Betula* continues to dominate the arboreal pollen spectra. *Populus* disappears from the record with only occasional grains of *Salix* present. Poaceae declines to trace values. Other herbs are rare apart from low frequencies of Cyperaceae and occasional grains of *Filipendula*, *Potentilla*-type and *Pulsatilla patens.*
150-182cm	Forest Tundra (b)	*Alnus-Betula-Picea* This zone is distinguished by a marked increase in *Alnus* (up to 50%) with reduced frequencies of *Betula*. *Picea* maintains values similar to the previous zone. The range and values of herbs are much the same as the previous zone.
0-150cm	Boreal Forest	*Picea-Betula-Alnus* This zone is characterised by the rise in *Picea* and the development of the modern boreal forest. Frequencies peak at the top of the zone to 40%. *Alnus* maintains values of between 30-40% along with *Betula* throughout the zone. There is a peak in *Betula* (83-91cm) where it reaches values up to 80% with an associated drop in *Alnus and Picea*. Occasional grains of *Populus, Salix* and Ericaceae are present throughout. Herbaceous pollen is low with a similar spectra as the previous zone. Cyperaceae increases slightly to values <10%.

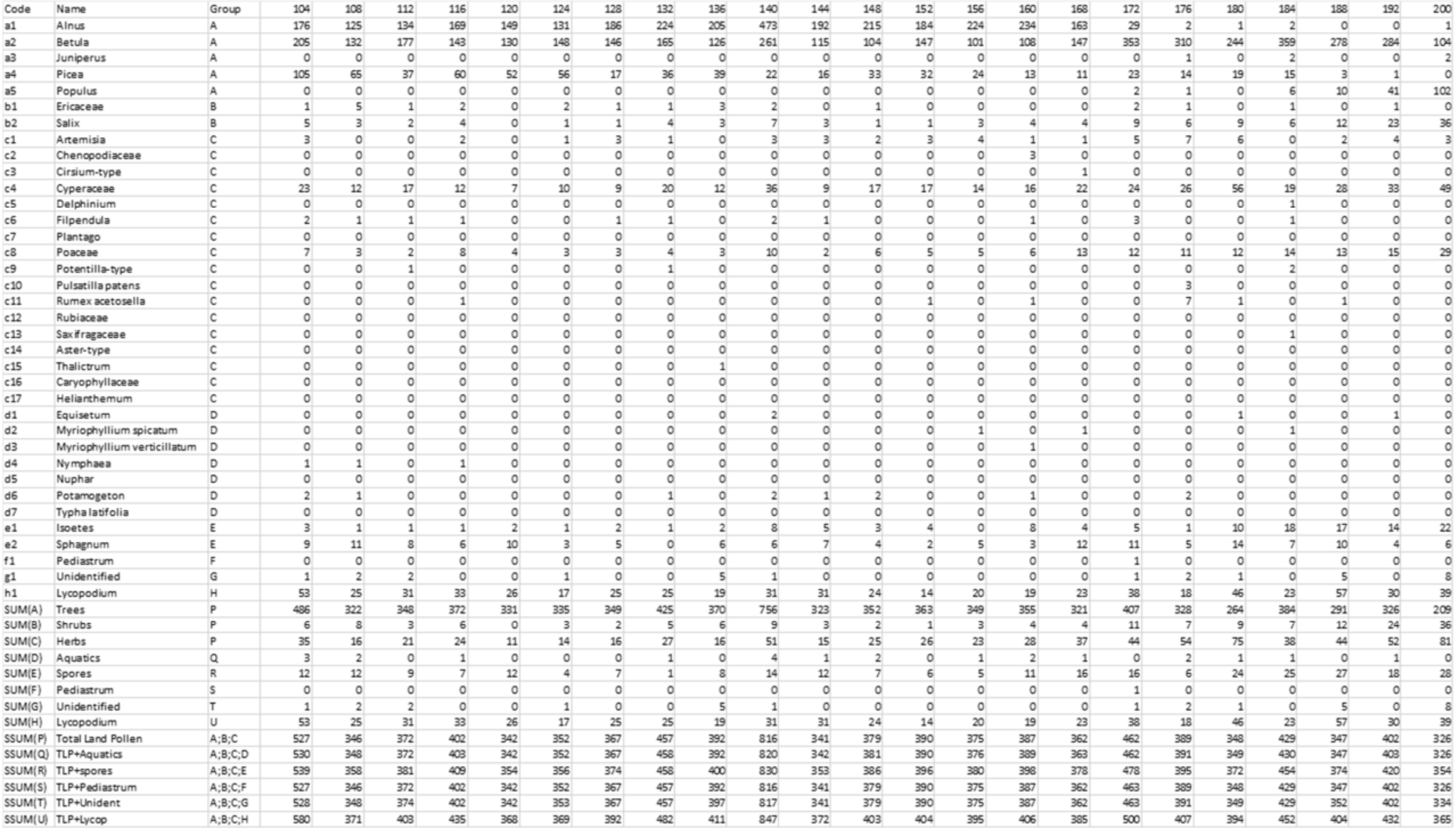
Table A.7: *Summary description of pollen zones at Lake 3 (Ages in brackets are taken from the clam-based age depth model*



Pollen			0	27	35	59	83	91	99	123	139	155	163	171	179	181	183	184	185	187	203	207	209	211	213	215	219	223	225	227	230	245	247	251	255	263	271	280	287	315	331	335	347	351	367
Code	Name	Group																																											
a1	Alnus	A	81	122	115	193	12	6	106	112	114	162	174	168	142	69	117	80	50	17	8	0	0	2	1	0	5	0	4	1	3	1	2	0	2	0	0	1	0	2	1	0	0	0	2
a2	Betula	A	91	128	129	131	250	303	91	163	135	145	153	152	169	173	235	214	202	263	242	204	245	317	298	331	305	315	290	235	271	110	223	215	175	246	280	258	266	236	97	58	4	1	3
a3	Juniperus	A	0	0	0	0	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
a4	Picea	A	150	80	73	15	25	16	94	59	83	26	17	18	21	29	14	13	40	23	33	43	11	9	4	2	6	0	1	0	1	1	0	0	0	1	0	0	0	0	0	1	0	1	2
a5	Populus	A	0	0	0	0	4	1	1	0	0	1	2	0	0	0	1	2	0	0	0	0	5	7	12	2	4	7	15	36	0	4	24	2	3	0	0	0	0	2	0	0	6	1	0
b1	Ericaceae	B	5	2	0	0	1	3	0	1	3	1	1	0	0	0	0	1	5	1	0	3	1	0	0	1	0	0	2	0	0	0	1	2	1	0	3	1	4	1	2	1	0	0	0
b2	Salix	B	4	4	3	0	5	7	4	2	0	2	4	0	4	3	3	7	8	2	3	8	7	18	19	11	9	12	14	33	14	20	31	30	27	15	9	10	5	20	16	25	40	14	0
b3	Empetrum	B	0	0	0	0	1	0	1	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	2	0	0	2	0	0	0	0
c1	Artemisia	C	0	3	2	0	5	1	2	6	0	0	2	2	3	5	5	6	3	3	4	7	5	7	4	4	3	7	2	2	3	8	7	23	21	1	11	3	8	3	10	2	3	1	4
c2	Chenopodiaceae	C	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	0	0	0	0	0	0	0	1	0	0	0	1	0	2	0	0	0	0
c3	Cirsium-type	C	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	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
c4	Cyperaceae	C	25	6	23	9	43	19	39	10	2	18	13	6	17	43	20	23	26	5	19	48	50	9	19	10	13	18	15	38	18	56	25	28	64	6	52	58	19	72	34	194	44	92	97
c5	Delphinium	C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	2	0	0	0	0
c6	Filipendula	C	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	3	0	0	1	0	0	0	0	0	0	0	0	2	0	1	1	2	0	2	0	0	0	3	3	0	0	0	0
c7	Poaceae	C	2	4	8	5	10	13	5	1	5	3	6	5	5	6	9	8	10	2	3	14	10	3	11	10	4	9	8	9	2	11	19	41	45	58	16	15	23	6	11	40	8	3	11
c8	Potentilla-type	C	1	0	1	0	0	0	0	0	0	0	0	0	2	1	0	0	0	1	3	1	1	0	0	1	0	1	0	0	1	1	0	0	1	0	0	0	1	0	0	1	0	0	0
c9	Pulsatilla patens	C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
c10	Rumex acetosella	C	1	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	1	0	0	1	0	0	0	1	0	1	1	1	0	0
c11	Rubiaceae	C	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
c12	Saxifragaceae	C	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	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
c13	Aster	C	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	1	0	0	0
c14	Helianthemum	C	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
c15	Caryophyllaceae	C	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
c16	Thalictrum	C	0	0	0	0	0	0	0	0	0	0	0	0	0	1	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	3	0	0	0
d1	Myriophyllium spicatum	D	0	1	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	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
d2	Myriophyllium verticulatum	D	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	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
d3	Nymphaea	D	0	0	0	0	2	1	0	1	0	0	0	0	0	1	1	1	3	3	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
d4	Potamogeton	D	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0	3	0
d5	Sphagnum	D	44	8	9	8	22	22	18	2	0	14	3	13	31	45	16	19	12	3	15	18	28	13	22	12	5	4	15	15	18	8	0	5	0	1	0	1	0	3	0	1	0	0	0
d6	Typha latifolia	D	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	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0
e1	Club Moss	E	16	1	0	5	2	8	8	0	0	0	0	2	6	22	6	0	7	4	14	26	15	0	23	10	14	3	4	10	12	7	3	2	5	4	4	0	0	0	0	0	0	0	0
e2	Isoetes	E	3	2	0	1	5	0	0	0	0	2	4	2	2	14	3	4	11	3	6	14	27	9	16	8	13	8	7	13	5	7	8	20	7	0	0	0	0	1	1	0	0	0	0
e3	Pteropsida	E	3	2	1	2	6	6	2	0	0	0	0	1	9	6	0	0	0	0	5	0	0	0	0	0	0	0	0	1	18	6	3	0	0	1	0	0	0	1	0	0	3	0	1
e4	Selaginellaselginoides	E	0	0	0	0	5	0	0	0	2	0	0	0	0	8	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
f1	Pediastrum	F	2	0	12	0	16	6	29	3	0	3	4	0	3	8	24	18	2	0	1	6	3	5	4	1	0	0	4	4	0	0	0	0	1	1	7	23	2	0	0	178	0	44	20
g1	Lycopodium	G	79	7	18	17	40	29	22	18	20	9	12	11	33	125	13	16	31	7	16	55	63	25	35	39	50	34	29	29	32	19	20	42	38	19	31	15	60	88	84	22	119	63	84
h1	Unidentified	H	1	1	3	0	2	0	1	0	0	3	1	1	2	1	0	0	0	4	1	0	1	0		2	0	0		2	5	4	5	8	5	7	4	2	2	2	0	2	3	1	1
SUM(A)	Trees	P	322	330	317	339	293	329	292	334	332	334	346	338	332	271	367	309	292	303	283	247	261	336	315	335	320	322	310	274	276	117	250	217	180	247	280	259	266	240	98	59	10	3	7
SUM(B)	Shrubs	P	9	6	3	0	7	10	5	3	3	3	5	0	4	5	5	8	13	3	3	11	8	18	19	12	9	13	16	33	14	20	32	32	28	17	12	13	9	21	20	26	40	14	0
SUM(C)	Herbs	P	29	13	34	15	59	34	46	18	8	22	23	13	28	60	34	40	39	11	31	71	66	19	37	26	21	36	25	51	29	78	53	94	133	67	81	76	55	85	55	242	56	96	112
SUM(D)	Aquatics	Q	44	9	10	8	24	23	19	3	0	14	3	13	31	47	18	20	15	6	15	18	28	14	23	13	5	4	15	17	18	8	0	5	0	1	0	1	0	4	0	13	0	3	0
SUM(E)	Spores	R	22	5	1	8	18	14	10	0	2	2	4	5	17	50	9	4	18	7	25	40	42	9	39	19	27	11	11	25	35	20	14	22	12	5	4	0	0	2	1	0	3	0	1
SUM(F)	Pediastrum	S	2	0	12	0	16	6	29	3	0	3	4	0	3	8	24	18	2	0	1	6	3	5	4	1	0	0	4	4	0	0	0	0	1	1	7	23	2	0	0	178	0	44	20
SUM(G)	Lycopodium	T	79	7	18	17	40	29	22	18	20	9	12	11	33	125	13	16	31	7	16	55	63	25	35	39	50	34	29	29	32	19	20	42	38	19	31	15	60	88	84	22	119	63	84
SUM(H)	Unidentified	U	1	1	3	0	2	0	1	0	0	3	1	1	2	1	0	0	0	4	1	0	1	0	0	2	0	0	0	2	5	4	5	8	5	7	4	2	2	2	0	2	3	1	1
SSUM(P)	Total Land Pollen	A;B;C	360	349	354	354	359	373	343	355	343	359	374	351	364	336	406	357	344	317	317	329	335	373	371	373	350	371	351	358	319	215	335	343	341	331	373	348	330	346	173	327	106	113	119

Table A.8: Pollen counts from Ruppert Lake (Analyst, E.Hopla)

Pollen			0	4	8	12	16	20	24	28	32	36	40	44	48	52	56	60	64	68	72	76	80	84	88	96	100
Code	Name	Group																									
a1	Alnus	A	116	117	95	100	97	66	60	64	54	87	103	71	101	84	143	125	112	189	258	207	126	172	228	94	150
a2	Betula	A	97	92	87	83	70	97	92	86	92	77	95	64	102	97	191	112	110	180	178	205	121	205	183	92	120
a3	Juniperus	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
a4	Picea	A	100	105	135	118	119	123	140	159	195	161	113	87	144	111	163	65	109	127	91	108	102	102	97	118	78
a5	Populus	A	0	0	0	0	0	4	3	0	0	0	0	0	0	0	0	0	0	1	1	0	0	2	1	1	1
b1	Ericaceae	B	0	4	0	1	0	2	1	4	2	1	3	0	0	0	2	1	0	1	2	0	2	1	2	2	0
b2	Salix	B	4	1	5	6	3	3	3	2	2	0	2	2	2	2	5	5	2	3	12	3	3	4	4	0	5
c1	Artemisia	C	1	2	1	3	0	3	1	1	3	1	1	0	3	0	6	2	0	3	2	2	1	0	1	2	1
c2	Chenopodiaceae	C	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
c3	Cirsium-type	C	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
c4	Cyperaceae	C	18	23	18	17	23	18	15	4	2	12	18	12	8	31	17	20	9	26	28	17	9	27	25	24	15
c5	Delphinium	C	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
c6	Filpendula	C	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	3	0	1	2	0	0	0
c7	Plantago	C	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
c8	Poaceae	C	3	9	3	3	9	5	5	2	5	5	4	4	2	5	15	4	7	13	9	11	3	7	8	5	5
c9	Potentilla-type	C	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
c10	Pulsatilla patens	C	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
c11	Rumex acetosella	C	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
c12	Rubiaceae	C	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
c13	Saxifragaceae	C	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
c14	Aster-type	C	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
c15	Thalictrum	C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
c16	Caryophyllaceae	C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
c17	Helianthemum	C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
d1	Equisetum	D	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
d2	Myriophyllium spicatum	D	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
d3	Myriophyllium verticillatum	D	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
d4	Nymphaea	D	0	0	1	2	4	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1
d5	Nuphar	D	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
d6	Potamogeton	D	0	1	1	0	0	0	0	0	0	0	1	1	1	0	2	3	1	0	3	2	1	0	0	0	0
d7	Typha latifolia	D	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
e1	Isoetes	E	2	35	4	19	15	18	3	2	3	2	2	6	11	21	0	3	3	5	3	4	4	10	6	3	1
e2	Sphagnum	E	12	10	9	14	17	12	7	0	2	3	19	2	9	21	4	7	4	13	10	12	9	13	10	2	2
f1	Pediastrum	F	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	2	0	0
g1	Unidentified	G	0	0	0	3	2	0	0	0	0	0	2	2	5	28	3	1	0	0	3	0	0	3	2	1	1
h1	Lycopodium	H	30	36	46	48	45	32	30	26	28	18	40	11	39	2	50	37	34	61	43	0	29	62	62	80	24
SUM(A)	Trees	P	313	314	317	301	286	290	295	309	341	325	311	222	347	292	497	302	331	497	528	520	349	481	509	305	350
SUM(B)	Shrubs	P	4	5	5	7	3	5	4	6	4	1	5	2	2	2	7	6	2	4	14	3	5	5	6	2	5
SUM(C)	Herbs	P	24	35	23	26	35	26	23	7	10	18	24	16	13	36	41	26	17	43	44	30	14	38	34	31	21
SUM(D)	Aquatics	Q	1	1	2	2	4	0	0	0	0	0	2	1	2	0	2	3	1	1	3	2	1	1	1	0	1
SUM(E)	Spores	R	14	45	13	33	32	30	10	2	5	5	21	8	20	42	4	10	7	18	13	16	13	23	16	5	3
SUM(F)	Pediastrum	S	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	2	0	0
SUM(G)	Unidentified	T	0	0	0	3	2	0	0	0	0	0	2	2	5	28	3	1	0	0	3	0	0	3	2	1	1
SUM(H)	Lycopodium	U	30	36	46	48	45	32	30	26	28	18	40	11	39	2	50	37	34	61	43	0	29	62	62	80	24
SSUM(P)	Total Land Pollen	A;B;C	341	354	345	334	324	321	322	322	355	344	340	240	362	330	545	334	350	544	586	553	368	524	549	338	376
SSUM(Q)	TLP+Aquatics	A;B;C;D	342	355	347	336	328	321	322	322	355	344	342	241	364	330	547	337	351	545	589	555	369	525	550	338	377
SSUM(R)	TLP+spores	A;B;C;E	355	399	358	367	356	351	332	324	360	349	361	248	382	372	549	344	357	562	599	569	381	547	565	343	379
SSUM(S)	TLP+Pediastrum	A;B;C;F	341	354	345	334	325	321	322	322	355	344	340	240	362	330	545	334	350	544	586	554	368	525	551	338	376
SSUM(T)	TLP+Unident	A;B;C;G	341	354	345	337	326	321	322	322	355	344	342	242	367	358	548	335	350	544	589	553	368	527	551	339	377
SSUM(U)	TLP+Lycop	A;B;C;H	371	390	391	382	369	353	352	348	383	362	380	251	401	332	595	371	384	605	629	553	397	586	611	418	400



Code	Name	Group	104	108	112	116	120	124	128	132	136	140	144	148	152	156	160	168	172	176	180	184	188	192	200
a1	Alnus	A	176	125	134	169	149	131	186	224	205	473	192	215	184	224	234	163	29	2	1	2	0	0	1
a2	Betula	A	205	132	177	143	130	148	146	165	126	261	115	104	147	101	108	147	353	310	244	359	278	284	104
a3	Juniperus	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	2
a4	Picea	A	105	65	37	60	52	56	17	36	39	22	16	33	32	24	13	11	23	14	19	15	3	1	0
a5	Populus	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	6	10	41	102
b1	Ericaceae	B	1	5	1	2	0	2	1	1	3	2	0	1	0	0	0	0	2	1	0	1	0	1	0
b2	Salix	B	5	3	2	4	0	1	1	4	3	7	3	1	1	3	4	4	9	6	9	6	12	23	36
c1	Artemisia	C	3	0	0	2	0	1	3	1	0	3	3	2	3	4	1	1	5	7	6	0	2	4	3
c2	Chenopodiaceae	C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0
c3	Cirsium-type	C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
c4	Cyperaceae	C	23	12	17	12	7	10	9	20	12	36	9	17	17	14	16	22	24	26	56	19	28	33	49
c5	Delphinium	C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
c6	Filpendula	C	2	1	1	1	0	0	1	1	0	2	1	0	0	0	1	0	3	0	0	1	0	0	0
c7	Plantago	C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
c8	Poaceae	C	7	3	2	8	4	3	3	4	3	10	2	6	5	5	6	13	12	11	12	14	13	15	29
c9	Potentilla-type	C	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
c10	Pulsatilla patens	C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
c11	Rumex acetosella	C	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	7	1	0	1	0	0
c12	Rubiaceae	C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
c13	Saxifragaceae	C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
c14	Aster-type	C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
c15	Thalictrum	C	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
c16	Caryophyllaceae	C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
c17	Helianthemum	C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
d1	Equisetum	D	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	1	0
d2	Myriophyllium spicatum	D	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0
d3	Myriophyllium verticillatum	D	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
d4	Nymphaea	D	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
d5	Nuphar	D	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
d6	Potamogeton	D	2	1	0	0	0	0	0	1	0	2	1	2	0	0	1	0	0	2	0	0	0	0	0
d7	Typha latifolia	D	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
e1	Isoetes	E	3	1	1	1	2	1	2	1	2	8	5	3	4	0	8	4	5	1	10	18	17	14	22
e2	Sphagnum	E	9	11	8	6	10	3	5	0	6	6	7	4	2	5	3	12	11	5	14	7	10	4	6
f1	Pediastrum	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
g1	Unidentified	G	1	2	2	0	0	1	0	0	5	1	0	0	0	0	0	0	1	2	1	0	5	0	8
h1	Lycopodium	H	53	25	31	33	26	17	25	25	19	31	31	24	14	20	19	23	38	18	46	23	57	30	39
SUM(A)	Trees	P	486	322	348	372	331	335	349	425	370	756	323	352	363	349	355	321	407	328	264	384	291	326	209
SUM(B)	Shrubs	P	6	8	3	6	0	3	2	5	6	9	3	2	1	3	4	4	11	7	9	7	12	24	36
SUM(C)	Herbs	P	35	16	21	24	11	14	16	27	16	51	15	25	26	23	28	37	44	54	75	38	44	52	81
SUM(D)	Aquatics	Q	3	2	0	1	0	0	0	1	0	4	1	2	0	1	2	1	0	2	1	1	0	1	0
SUM(E)	Spores	R	12	12	9	7	12	4	7	1	8	14	12	7	6	5	11	16	16	6	24	25	27	18	28
SUM(F)	Pediastrum	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
SUM(G)	Unidentified	T	1	2	2	0	0	1	0	0	5	1	0	0	0	0	0	0	1	2	1	0	5	0	8
SUM(H)	Lycopodium	U	53	25	31	33	26	17	25	25	19	31	31	24	14	20	19	23	38	18	46	23	57	30	39
SSUM(P)	Total Land Pollen	A;B;C	527	346	372	402	342	352	367	457	392	816	341	379	390	375	387	362	462	389	348	429	347	402	326
SSUM(Q)	TLP+Aquatics	A;B;C;D	530	348	372	403	342	352	367	458	392	820	342	381	390	376	389	363	462	391	349	430	347	403	326
SSUM(R)	TLP+spores	A;B;C;E	539	358	381	409	354	356	374	458	400	830	353	386	396	380	398	378	478	395	372	454	374	420	354
SSUM(S)	TLP+Pediastrum	A;B;C;F	527	346	372	402	342	352	367	457	392	816	341	379	390	375	387	362	463	389	348	429	347	402	326
SSUM(T)	TLP+Unident	A;B;C;G	528	348	374	402	342	353	367	457	397	817	341	379	390	375	387	362	463	391	349	429	352	402	334
SSUM(U)	TLP+Lycop	A;B;C;H	580	371	403	435	368	369	392	482	411	847	372	403	404	395	406	385	500	407	394	452	404	432	365

Table A.9: *Pollen counts from Lake 3 (Analyst, E.Hopla)*

Sample	Total grain size (X1)	Saccus width	Saccus Height	Corpus breadth (X2)	Saccus attachment (X8)
Lake 3	82.9			41	7.4
104cm	62.7			42.1	13
	63.4			45.9	11
	87.5			63.5	10.3
	71.5			57.3	14.4
	87.1			51.7	10.7
	91.1			61.7	15
	53.2			41	8
	76.7			53.4	11.4
	66.5			43.1	6.1
	83.3			64.3	13.8
	79.9			58.3	17.9
	84.6			62.4	13.8
	69.4			46.7	7.1
	70.6			52.6	14.3
	78.5			55.5	11
	90.7			66.4	16.4
	80.1			56.3	9.4
	80			57.3	7.1
	75.1			59	12.4
	65.7			45.9	13.1
	74			49.5	12.5
	72.6			58.3	14
	70.3			47	10.6
	99.1			70.8	10.3
	65			51.4	12
	69.9			53.9	10.4
	79.7			54.1	11
	74.2			60.7	16.8
	68			54.3	15.2
	76.1			53.1	11.4
	74.7			52.3	10.9
	73.4			56.2	13.5
	87.6			59.5	12.2
	79.4			57.6	15
	75.8			51.6	13.1
	76.6			59.5	16.9
	54.9			50.7	13.3
	69.2			55.9	15.7
	60.2			41.9	9.8
	70.5			51.7	15.2
	75.9			55.4	12.7
	93.3			60	11.4
	80.8			62.1	16.6
	91.8			68.5	14.3
	58.8			48.2	16.5
	71			64.4	21.1
	70.8			57.4	16

	60.3			51.8	12.5
	72.2			56.2	15.9
48cm	Grain size	Sac width	Sac height	Corpus	Sac attach
	92	39.1	33.4	62	15.9
	68.6	32.7	24.9	43.5	9
	66.3	32	23.8	43.7	14.7
	84	35	30.7	61.3	20.1
	65.4	27.8	23.6	52.8	15.9
	69.7	34	22	44.2	16.6
	73.9	39.1	21.6	48	14.3
	77.2	32.1	21.4	56.7	15.5
	61.6	23.2	19.6	41.1	12.5
	67.1	27.2	16.1	41.3	6.9
	69.5	28	22	48.1	19.5
	75.2	30.9	28.4	56.8	17.2
	70.1	32.5	16.7	53.6	10.5
	67.5	30.6	20.5	50.8	14.5
	66.8	28.8	21.2	55.3	14
	77.1	38.1	22.1	57.2	13.1
	56.7	32	27.4	56.7	15.8
	94.6	40.1	25.6	54.1	14.1
	70.4	29.6	19.9	58.3	18.1
	78.8	34.4	19.2	53.7	13.5
136cm	Grain size	Sac width	Sac height	Corpus	Sac attach
	68.1	31.3	17.8	43.2	12.5
	78.9	41	18	58.1	15.5
	88.6	41.4	24.7	64.9	19.2
	75.9	37.4	21.5	14.3	11.9
	97.1	41.4	29.9	62.7	13.6
	86.8	45.6	20.5	55.3	10.5
	88.6	40.8	23.2	56.9	14.8
	93.5	44.7	20.9	64.0	14.7
	84.2	34	25.5	56.9	14.9
	82.1	34.5	21	56.5	14.5
	87.5	44.7	26.5	51.1	15.7
	91.6	34.1	18.7	64.1	13.8
	105.4	46.7	23.7	65.1	15.7
	77.5	33.2	17.5	61.2	21.3
	100.2	49.3	25.7	58.8	14.2
	91.7	45.9	26.3	52.1	10.8
	100.9	48.9	32.5	59.3	13.1
	96.1	43.6	25.6	58.6	11.1
	97.7	45.2	25	64.3	13.2
	91.8	41.3	28.9	68.3	15.9

120cm	Grain size	Sac width	Sac height	Corpus	Sac attach
	87.5	42.4	27.6	47.6	9.4
	83.6	38.4	25.3	58	11.9
	83.7	40	26.4	51	11
	70.1	27.8	22.5	49.9	12.6
	74.9	28.2	21.3	50.2	10.7
	77.1	34.9	26.1	54.2	9.2
	87.4	38.1	21.8	60.6	13.7
	92.1	46.1	22.9	62.7	15.8
	65.6	31.8	20.8	46.5	11.8
	68.0	29.9	22.9	50.6	14.3
	84.6	36.8	21.7	57.7	15.1
	65.4	28.3	14.9	50.2	14.6
	93.7	40.4	27.3	63.5	13.5
	86.8	30	18.7	50.9	11.7
	50.2	27	22.7	50.2	14.3
	81	40.3	21.6	63.9	21.8
	62.9	29.8	16.7	43.6	13
	76.5	37.3	25.8	49.9	12.2
	74.2	29.2	20.1	59.8	16.9
	103.1	44	25	64.9	13.9
124cm	Grain size	Sac width	Sac height	Corpus	Sac attach
	65.7	27.2	17.1	50	12.3
	95.3	42.4	22.5	58.9	12.2
	93.8	34.4	31.2	57.4	12.1
	83	32.7	23.9	57	13.5
	84.4	37.8	20	61.1	12.3
	84.9	34.2	25.6	64.8	12.6
	91.9	38.9	28	60.5	12.8
	95.8	41.1	23.5	61.1	14.1
	89	38.1	29.2	58.9	10.4
	83.5	31.3	25.6	55	11.9
	79.8	35.3	19.7	49.9	11.4
	105.9	46.8	34.2	76.8	13.8
	97.6	40.5	23.4	66.8	19
	83.2	42.5	24.2	58.6	14.4
	100.4	50.5	28.3	70.5	17.1
	67.7	42.8	21.1	67.7	16.1
	72.3	36.2	22.3	52.5	13.9
	87.3	43	26.2	60.6	11.9
	74.4	59.1	18.2	59.1	16.4
	90.5	39.1	21.9	60.1	11.8
132cm	Grain size	Sac width	Sac height	Corpus	Sac attach
	77.7	40.5	22.3	61.8	11.8
	80.7	37.7	18.6	49.1	10.8
	87.2	38.7	20.2	66.2	19.9

	77	38.5	14.6	49.3	9.3
	84.1	39.2	21.5	60.5	17.3
	76	30.1	19.3	57	17.6
	78.3	39.8	22.2	52.7	13.4
	69.6	31.4	15.9	51.1	10.9
	89.7	30.2	20.1	63.2	12.7
	87.8	37.2	22	63.8	15.7
	78.9	47.8	20.2	64	12.9
	79.5	34.7	20.5	58.3	14.6
	89.8	37.9	26.1	59.4	14.1
	80.7	34.6	21.1	58	13.7
	85.9	35.8	30.9	59	19.1
	75.1	32.4	23.5	53.5	11.1
	87.7	41.4	20.2	63.9	15.1
	82.5	36.5	22	64.2	17
	91.7	38.9	28.1	63.2	12.7
	87.9	35.1	28.4	58.7	17.4
148cm	Grain size	Sac width	Sac height	Corpus	Sac attach
	91.1	37.9	22.1	64.2	17.5
	92.6	44.4	26.9	66.7	16.4
	90.7	41.3	20.1	63.6	16.8
	77.3	35.3	24.6	44.8	7.6
	94.8	41.8	23.9	72.2	17.3
	85.8	43.9	19.6	46.6	9.
	93.3	39.4	23.5	53.9	12.8
	84.3	33.4	21	64.8	17
	76.5	36.3	18.1	55.1	15.4
	88.2	44.7	28.4	57.5	9.9
	95.3	42.2	25.1	68	16.4
	87.5	39.1	23.8	60.8	15.1
	95.9	43.1	21.3	68.6	16.1
	90.2	39	22.1	64.3	16
	93.5	44.7	23.4	72.5	17.2
	90.5	41	20	69.2	21.4
	90.4	42.9	24.6	59.8	14.8
	83.4	35.9	23.2	61.1	9.6
	94.1	37.9	20.5	63.6	10.9
	87.6	45.3	27.3	59.1	12.7
112cm	89.4	44	26.2	62.3	12.6
	62.9	27.7	19	46.7	13.5
	85.2	41.2	23.7	65.6	16
	68.3	28.3	20.7	51	15.1
	68.4	29.8	20.7	55.4	17.9
	68.9	36.3	16	54.6	16.1
	70.4	34.4	18.1	44.5	7.8
	72.7	34.7	18.9	51.4	15.5
	90.7	35.7	26.9	64.7	12.3
	67.3	37.7	17.1	52.4	10.7

	79.4	32.3	25.6	58.6	18
	70.1	28.8	19.1	49.4	13.7
	70.3	30.1	19.6	44.8	10.5
	72.2	40	22.8	49.4	13.6
	71.2	38.5	22.2	47.6	12.6
	69.3	31.3	20.7	47.6	11.5
	71	34.7	21.1	53	13
	69.6	30.3	17	51.6	14.3
	93.7	49.5	25.5	66	13.9
	78.9	35.4	17.8	57.7	15.7

Table A.10: *Picea measurements (Analyst, E.Hopla)*

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