EVIDENCE FOR A GLACIAL REFUGIUM IN SOUTH-CENTRAL BERINGIA USING MODERN ANALOGS: A 152.2 KYR PALYNOLOGICAL RECORD FROM IODP EXPEDITION 323 SEDIMENT

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A

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Abstract

Palynological assemblages from Integrated Ocean Drilling Program (IODP) Expedition 323 (Bering Sea Expedition) site U1343, on the edge of the Bering Sea Shelf, permit reconstruction of the terrestrial vegetation of the southern margin of central Beringia. Previous research indicates that central Beringia was a glacial refugium for boreal vegetation, which expanded into eastern and western Beringia as glaciers retreated. This hypothesis has been difficult to test because sampling has been largely restricted to eastern and western Beringia and islands in the Bering Sea. Pollen grains and spores preserved in core samples from site U1343 provide a record of central Beringian vegetation over the past 152.2 kyr at a resolution of ~10 kyr. Grass (Poaceae $\geq$ 17.4%) and sedge (Cyperaceae $\geq$ 17.1%) pollen dominate the assemblages, indicating the presence of graminoid tundra. Lower abundances of spruce (*Picea* $\leq$ 8.5%), birch (*Betula* $\leq$ 19.9%), and alder (*Alnus* $\leq$ 27.7%) pollen are consistently present throughout glacial/interglacial cycles, suggesting that trees and shrubs remained in central Beringia during glacial maxima. *Sphagnum* spores (3.4-10.9%) in all samples indicate locally or regionally mesic conditions during marine oxygen isotope stages (MIS) 1-6. Minimum site paludification during MIS 2, indicated by high ratios of angiosperm pollen to *Sphagnum* spores, coincides with the lowest shrub/herb ratios in our record, suggesting that conditions were drier and woody plants were sparse during the last glacial maximum.

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Chapter 1: Introduction and Background

1.1 Statement of problem, research questions and hypotheses

In 2010, the Integrated Ocean Drilling Program (IODP) Expedition 323 drilled seven sites in the Bering Sea. Of these seven sites, site U1339 and U1343 were proposed for palynological analysis by Dr. Sarah Fowell and Dr. Nancy Bigelow in order to reconstruct the vegetation and climate of the emergent Bering Land Bridge. Expedition 323's scientific objectives applicable to this palynological research include:

1) To elucidate a detailed evolutionary history of climate and surface ocean conditions since the earliest Pliocene in the Bering Sea, where amplified high-resolution changes of climatic signals are recorded.
2) To characterize the history of continental glaciations, river discharge, and sea ice formation in order to investigate the link between continental and oceanic conditions in the Bering Sea and on adjacent land areas (Expedition 323 Scientists, 2010).

Sites U1343 and U1339 are located at the edge of the Bering Sea shelf (Figure 1). This area was adjacent to the emergent Bering Land Bridge (BLB) during glacial stages and may have received terrestrial material from estuarine and deltaic systems that delivered sediments to the continental shelf (Expedition 323 Scientists, 2010; Heusser and Balsam, 1977; Faegri and Iverson, 1989). Site U1343 is currently ~700 km from shore, but it was approximately 100-200 km offshore during glacial maxima, whereas site U1339 is ~900 km from shore and was ~100 km offshore during glacial stages. Due to the inaccessibility of sites U1339 and U1343 (i.e. their submersion in the Bering Sea), palynological and paleoclimatic research has not previously been conducted in this area. It is probable that the majority of the spores, pollen, and terrestrial sediment delivered to these sites during low sea level stands (i.e. glacial stages) were derived from the adjacent continental margin. Oceanic currents transport terrestrial materials from the coast across the continental shelf to sites of deposition in marine basins (Heusser and Balsam, 1977). Pollen taxa from sites U1339 and U1343 provide a 152.2 thousand year (kyr) record of

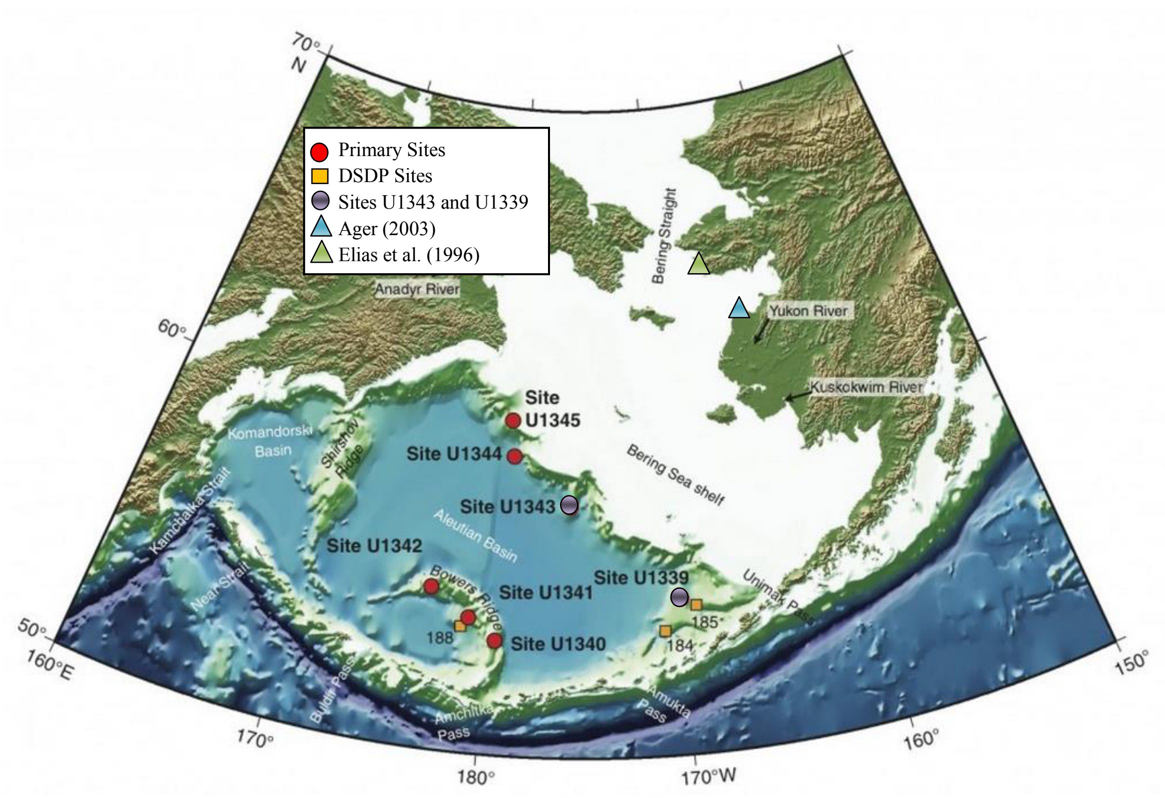

Figure 1. Location map showing sites mentioned in text. Red circles indicate IODP sites; purple circles highlight sites U1343 and U1339. Triangles indicate previously studied sites: Blue= Ager (2003), Green= Elias et al. (1996) (Modified from: Expedition 323 Scientists, 2010).

the terrestrial vegetation of south-central Beringia, permitting me to address the following questions: 1) Was the climate of the emergent BLB more humid than that of eastern and western Beringia? 2) How did the vegetation respond to local climatic changes near the continental margin? 3) Did the lowlands of central Beringia provide an ice age refugium (Guthrie, 200l; Brubaker et al., 2005) for boreal trees and shrubs?

1.2 Background

1.2.1 Climate, Vegetation, and Palynomorphs

Plant species distribution is primarily controlled by climatic factors (Thompson et al., 2006). For instance, the ranges of trees and shrubs in Alaska, such as *Picea* (spruce), *Alnus* (alder), *Betula* (birch) and *Salix* (willow), are limited by temperature and precipitation. *Picea* grows in conditions where the mean July temperature is warmer than 9.2°C and the annual precipitation is between 195mm and 3,615mm. *Alnus* survives in mean July temperatures warmer than 6.7°C with an annual precipitation of 195mm to 3,615mm. *Betula* is present in environments with an annual precipitation of 145mm to 2,635mm. Tree birch (*Betula papyrifera*) grows where the mean July temperature is more than 9.2°C while shrub birch (*Betula nana*) grows in areas where the mean July temperature is greater than 4.5°C. Finally, *Salix* (willow) is found where the mean July temperature is greater than 3.1°C and the annual precipitation is 130mm to 3,715mm. It is evident that tree birch and spruce require warmer summer temperatures compared to shrub birch, willow and alder (Thompson et al., 2006). Therefore, changes in vegetation composition through time can be used to infer changes in temperature and/or precipitation. The concentrations and relative abundances of pollen taxa from the Expedition 323 core sites provide a proxy for terrestrial climate of south-central Beringia.

If pollen samples are collected from a variety of sites in a modern setting, the composition of pollen assemblages can be compared to the vegetation classification. Assuming that Holocene and Pleistocene relationships between palynomorph assemblages and vegetation classes are similar to modern relationships (Jackson and Williams, 2004), then fossil palynomorph assemblages can be used to infer vegetation classifications based on modern analogs (Jackson and Williams, 2004). The same reasoning can be applied to the relationship between vegetation and climate. However, in order to interpret the relationship between modern pollen and vegetation, it is important to recognize under- and over-represented pollen taxa. Taxa that are under-represented in the pollen record include plants that pollinate underwater (i.e. seagrass and horned pondweed), plants that are self-pollinating (i.e. garden tomatoes and miner's lettuce) and plants that are pollinated by birds, bats and insects (i.e. fireweed, blackberries and clover) (Faegri and Iverson, 1989). Over-represented taxa are wind-pollinated plants such as gymnosperms (i.e. *Pinus* (Pine) and *Picea*) and spore-producing plants (Faegri and Iverson, 1989). Therefore, percentages of pollen and spores from under- and over-represented taxa may not be good indicators of the frequency of the plants in the vegetation cover. Pollen assemblages within sediments are biased towards vegetation with high pollen productivity and pollen transported by wind (Jackson and Williams, 2004). Despite the pitfalls, pollen diagrams based on over-represented taxa can be compared in order to identify relative changes in vegetation and climate across time and space (Faegri and Iverson, 1989).

Pollen and spores are used as proxies of climate and vegetation because of their pervasiveness, durability, and abundance. Palynomorphs can be found in sedimentary rocks of late Precambrian to modern age and occur in both terrestrial and aquatic (freshwater and marine) environments. Pollen is the reproductive product of a seed plant's life cycle (i.e. the male gametophyte) while spores are haploid reproductive cells of seedless plants (Moore et al., 1991). Both are products of brief life cycles; usually weeks or months elapse between development within the anther or sporangium and production of a new sporophyte (Faegri and Iversen, 1989). The resistant outer wall (exine) of a pollen grain or spore is composed of sporopollenin, a naturally occurring, inert chemical compound. Fossil pollen and spores are destroyed when the exine degrades. Exine can be destroyed by oxidation, high temperatures and pressures, high alkalinity and formation of mineral crystals. Therefore, palynomorphs are not well preserved in clean limestone, weathered rocks, evaporate deposits, re-crystallized rocks (like dolomite) or red bed deposits, and diagenetic environments with extremely high temperatures and pressures destroy the exine of pollen grains more quickly than shallow burial in a marine setting. When present in sediment, spores and pollen are typically more abundant than other microfossils (Faegri and Iversen, 1989).

Some spores and pollen grains can only be identified to the family or genus level (Traverse, 2007). This is unfortunate because various pollen species from the same genus can have different ecological implications. For instance, within the family Poaceae, *Poa arctica* is adapted for moist-mesic environments while *Poa glauca* grows in relatively dry conditions (Swanson, 2005). Therefore, Poaceae pollen can be an indicator of either mesic or arid environments.

1.2.2 Marine Oxygen Isotope Stage (MIS) notation

Marine isotope stages (MIS) are used as a timescale for the IODP samples. MIS are based on oxygen isotope data (i.e. the ratio of stable isotopes ^{18}O and ^{16}O), which record warm and cold periods within Earth's Plio-Pleistocene oceans. Odd-numbered stages (e.g. MIS 1, 3, and 5) have low levels of δ^{18}O values and represent periods of relative warmth, while even-numbered stages (e.g. MIS 2 and 6) have relatively high δ^{18}O values indicative of cooler periods during which glaciers and ice sheets expanded (Martinson et al., 1987).

1.2.3 Beringia

Beringia was a thousand-mile-wide landmass that intermittently joined present-day Alaska and eastern Siberia during the Pleistocene (Figure 2). Sea level repeatedly transgressed and regressed throughout MIS 1-6, periodically exposing the lowlands of central Beringia. For instance, sea level was ~125m below modern sea level during MIS 6. During MIS 5, sea level rose 6-8m above modern sea level and then dropped to ~110-105m below modern level during MIS 4 and 3. During MIS 2, sea level in the Bering Sea dropped approximately 130m below modern levels during the last glacial maximum (LGM, ~20 kya) (Martinson et al., 1987; Chappell et al., 1996). The southern margin of central Beringia was emergent during ice ages when ice sheets covered most of the

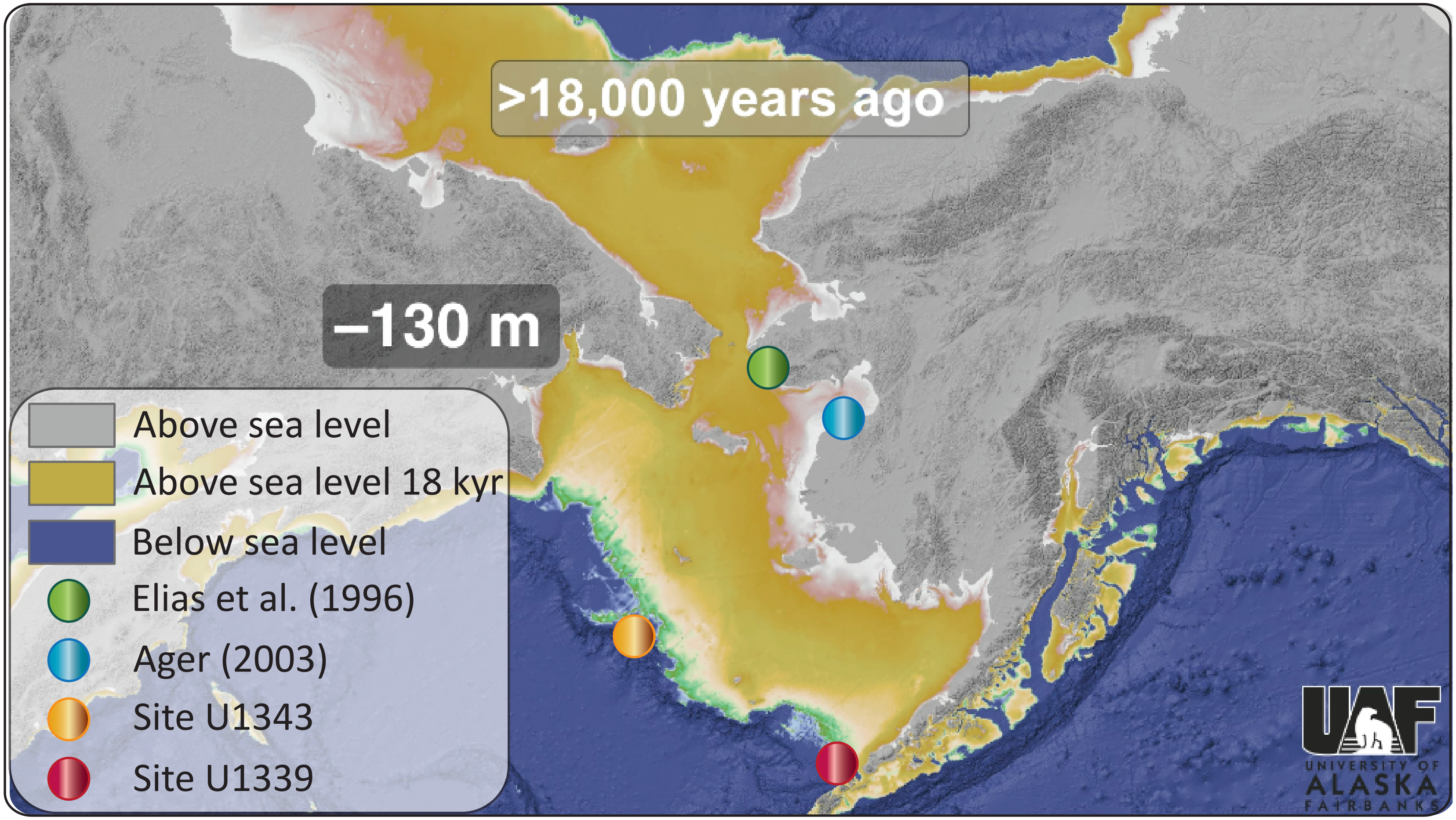

Figure 2. Coast line of Beringia at 18,000 calibrated yrs. B.P. (Modified from: Sam VanLaningham, 2012).

northern United States and Canada. While glaciers formed in the Brooks Range and Alaska Range, the interior of Alaska and lowlands of central Beringia, located on the modern Bering Sea shelf, remained ice free (Hamilton., 1994; Hamilton et al., 1986; Manley and Kaufman, 2002). Sites U1343 and U1339 are adjacent to this continental shelf and therefore proximal to the central Beringian lowlands. The Bering Strait last opened between 11.3-12.4 kya, indicated by flooding of Hope Valley (north of the Bering Strait). According to Keigwin et al. (2006), sea level was 55m below modern and the Bering Land Bridge (BLB) was submerged at this time. By 10.7-9.8 kya, the Bering Strait was completely open (England et al. 2009).

1.3 Significance of offshore pollen records

Heusser and Balsam (1977) analyzed palynomorphs from core tops from the continental shelf of the northeast Pacific Ocean to examine the taphonomy of pollen in modern marine sediments. They conclude that pollen from coastal areas is transported into marine environments largely by rivers and then transported across the shelf along with fine sediment. It is reasonable to assume that similar transport processes occurred in the past (Smith and Pun, 2006). Heusser and Balsam (1977) also found that the pollen frequency in marine sediments reflects the vegetation distribution on the adjacent coast and hydraulic sedimentation on the shelf. For example, boreal taxa such as *Alnus* and *Picea* are common in temperate conifer forests of western Washington, while Compositae stands are located off southern California. In marine surface samples, *Alnus* and *Picea* pollen are more prevalent north of 45°N while Compositae pollen are dominant south of 40°N. Percentages of *Alnus*, *Picea*, and Compositae all decrease with distance from shore, but *Pinus* pollen percentages increase from 10% on the shelf to over 50% on the abyssal plain, indicating long-distance transport by submarine currents. Like *Pinus*, fern spores (Polypodiaceae) are also subject to long-distance submarine transport and are concentrated in more distal settings.

1.4 Beringian pollen studies

Previous pollen studies relevant to my findings (sites shown on Figure 3) were conducted along the modern coastline of Alaska (i.e. Seward Peninsula, Togiak Bay,

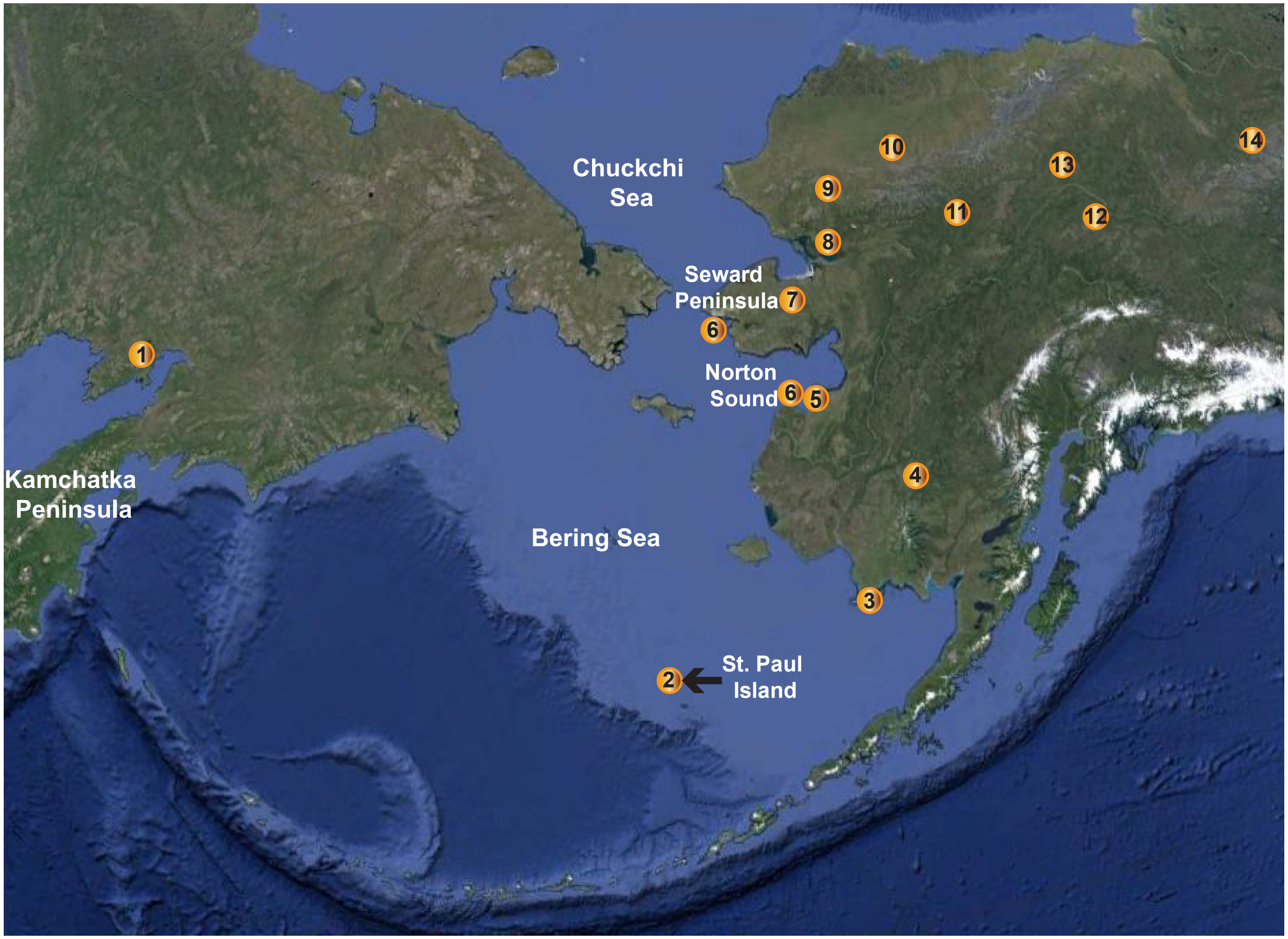

Figure 3. Locations of previous pollen analysis. Previous pollen sites indicated by: (1) Elikchan, (2) Cagaloq Lake, (3) Togiak Bay, (4) Holitna Lowland (5) Zagoskin, (6) Chukchi and Bering Sea (7) Imuruk Lake, (8) Squirrel Lake, (9) Kaiyak, (10) Tukuto, (11) Koyukuk/Ky-11, (12) Birch Creek, (13) Bluefish Basin, (14) Lateral Pond. Site 6 encompasses multiple sites in the general vicinity (Modified from: Google Earth Image, 2013).

Chuckchi Sea) (Colinvaux, 1964; Shackleton, 1982; Schweger and Matthews, 1985; Kaufman et al., 2001; Elias et al., 1996), on St. Paul and St. Lawrence islands in the Bering Sea (Colinvaux, 1981; Colinvaux, 1967), in Norton Sound (Elias et al., 1996) and in eastern Russia (Anderson and Lozhkin, 2001). St. Paul Island, St. Lawrence Island and Zagoskin Lake are the only sites located within the Beringian lowlands (Colinvaux, 1981; Colinvaux, 1967). Few of the eastern Beringian records extend beyond the late Pleistocene (ca. 16-14 kya) because these records are from lakes which formed after the LGM. However, there are exceptions, such as the Zagoskin Lake record which spans MIS 1-3 (Ager, 2003), a record from St. Paul Island that spans MIS 1-2 (Colinvaux, 1981), the Imuruk Lake record from MIS 1-6 (Colinvaux, 1964; Shackleton, 1982; Schweger and Matthews, 1985), the Ky-11 record that spans MIS 1-6 (Bigelow et al., 2014; Schweger and Matthews, 1985) and the Squirrel Lake record which spans MIS 1-5 (Anderson, 1985). Zagoskin Lake, Imuruk Lake and a lake on St. Paul Island contain assemblages indicative of steppe tundra vegetation, suggesting that conditions were drier during glacial stages. On the other hand, ice age assemblages from Squirrel Lake indicate mesic vegetation and thus wetter conditions (Elias and Crocker, 2008).

1.4.1 Palynology of MIS 6

MIS 6, a glacial stage, occurred between 191-130 kya (Lisiecki and Raymo, 2005). The Birch Creek site 200 km northeast of Fairbanks (Figure 3, site 12), Ky-11, approximately 280 km northwest of Fairbanks on the Koyukuk River (Figure 3, site 11), Imuruk Lake on the Seward Peninsula (65°21’36”N, 163°12’W; Figure 3, site 7), and the Holitna Lowland site (61°20’N, 157°10’W; Figure 3, site 4) contain pollen assemblages from late MIS 6. Temperature reconstructions based on insect data from Ky-11 indicate summer temperatures ~4-5°C cooler than modern (Bigelow et al., 2014). Ky-11 palynomorph assemblages contain Cyperaceae (sedge) and Poaceae (grass) with lesser percentages of *Salix* (willow) and ericaceous shrubs (Schweger and Matthews, 1985), while Birch Creek assemblages are dominated by herbs with minor percentages of *Betula* and *Salix* (Edwards and McDowell, 1991). Both sites record vegetation characterized as steppe-tundra or herb-dominated meadow (Bigelow et al., 2014). In addition, invertebrate and plant macrofossil assemblages from Ky-11 suggest that the landscape was shrubby and treeless.

Imuruk Lake, located more than 300m above modern sea level on the Seward Peninsula, contains one of the longest lacustrine records from eastern Beringia (Colinvaux, 1964). However, it is important to note that there are problems with the Imuruk Lake chronology, which was based on bulk dates and includes some puzzling reversals. Traces of graphite found in Imuruk Lake mud indicates the presence of old ^{14}C depleted carbon that would have been taken in by organisms such as algae. This could skew bulk dates, making pollen assemblages seem older than they really are. Additional problems could be the result of slumping sediment and turbidity currents. If the sediment was reworked, it would affect the radiocarbon dates and contaminate pollen samples. Assemblages assigned to MIS 6 by Colinvaux (1964) contain high levels of Cyperaceae (5-40%), Poaceae (>20%) and *Artemisia* (0-~28%) with minor percentages of *Betula* (<20%), *Alnus* (<10%) and *Picea* (<15%), indicating arctic tundra and cold temperatures.

A sample recovered above the Old Crow tephra (OCt) in an exposed bluff along the Holitna River contains large percentages of Poaceae (58.5%) and Filicales (fern) (20.7%) with minor percentages of *Salix* (1%), *Sphagnum* (4%) and *Alnus* (3%) (Waythomas et al., 1993). This pollen assemblage is indicative of mesic graminoid tundra. According to Bigelow et al. (2014), the OCt is 134,000-130,000 years old and marks the end of MIS 6. However, this is contrary to Preece et al. (2010) who suggest the OCt dates to 124 ± 10 kya.

1.4.2 Palynology of MIS 5

MIS 5, the last full interglacial (Sangamonian), occurred between 130 and 71 kya. MIS 5.5, an interval of maximum warmth, occurred at 123 kya (Lisiecki and Raymo, 2005). Further warm intervals within MIS 5 include: 5.4 (109 kya), 5.3 (96 kya), 5.2 (87 kya) and 5.1 (82 kya) (Lisiecki and Raymo, 2005). Summer insolation is the measure of solar radiation impacting the top of the Earth's atmosphere (Berger, 1978). During MIS 5, summer insolation (for the months of May, June and July) was approximately 11%

higher in northern latitudes than it is today (CAPE, 2006). CAPE (Circum-Arctic Paleo Environments) Last Interglacial Project Members reconstructed MIS 5 temperatures from biotic proxies in marine, alluvial, lacustrine and peat deposits as well as isotopic records from ice cores and carbonates. They conclude that, between 130-127 kya, peak Alaskan summer temperatures were 0-2°C warmer than modern temperatures while winters were 1-3°C cooler than modern. They also found evidence of greater moisture in Alaska early in the last interglacial compared to coeval arctic sites in Canada, Europe and Russia (CAPE, 2006).

Assemblages from Ky-11 (Figure 3, site 11) record dominance of *Betula*, *Picea*, *Salix* (willow), and *Alnus*, with lesser amounts of Cyperaceae and forbs (Bigelow et al., 2014; Schweger and Matthews, 1985). These results suggest the presence of boreal forests similar to modern interior Alaskan forests. Birch Creek pollen assemblages from MIS 5 record high percentages of spruce, suggesting that it was more common in forests than today (Edwards and McDowell, 1991; Bigelow et al., 2014). Bigelow et al. (2014) propose that MIS 5 was relatively mesic compared to today based on the abundance of fern spores (Miller et al., 2010; Bigelow et al., 2014). Pollen analysis of MIS 5 samples from the Holitna Lowlands reveals a sedge-grass-birch-dominated mesic tundra. Waythomas et al. (1993) notes that some samples contain high percentages of *Picea* (up to 22%) compared to MIS 6. Waythomas et al. (1993) do not report pollen analyses from MIS 4-1.

Colinvaux (1964) identified pollen assemblages from MIS 5 in samples from Imuruk Lake (Figure 3, site 7). With the above mentioned chronological uncertainties in mind, pollen assemblages from MIS 5 (or zone i_1) indicate that *Betula*, *Alnus* and *Picea* increased while Cyperaceae and Poaceae decreased compared to MIS 6 (or zone H). Colinvaux (1964) suggests that the climate was similar to the modern climate of the Seward Peninsula. Based on alder abundances, he also proposes that the climate was wetter than the arctic climate of his zone H. His pollen analysis is corroborated by Shackleton (1982) who also analyzed Imuruk Lake and noted an increase in abundances of *Picea* (>15%), *Betula* (>~15%) and *Alnus* (>10%) compared to MIS 6, while Cyperaceae (<20%), Poaceae (<30%) and *Artemisia* (<10%) percentages decrease.

Pollen records from Squirrel Lake, north of Kotzebue, Alaska (Figure 3, site 8), display greater abundances of *Betula*, *Picea* and *Alnus* compared to percentages from MIS 4, signaling the presence of the boreal forest (Berger and Anderson, 2000) which extended north and west of the modern forest boundary. Pollen assemblages from a coastal bluff at Togiak Bay, on the northwest end of Bristol Bay (Figure 3, site 3), contain *Alnus* (0-50%), *Betula* (about <20%) and *Picea* (0-10%) with lesser amounts of Cyperaceae (approximately >10%) and Poaceae (about <24%). This site also suggests an expansion of the boreal forest relative to today.

1.4.3 Palynology of MIS 4

MIS 4 occurred between 71-57 kya and is an interstadial event (Lisiecki and Raymo, 2005). Due to dating issues noted above, it is difficult to identify MIS 4 sediment from Imuruk Lake (Figure 3, site 7) based on Colinvaux's (1964) dates. Shackleton (1982) has a better chronology for this site. He noted that zone i_2 (just after MIS 5) contains lower percentages of *Betula* (<10%), *Alnus* (trace levels) and *Picea* (trace levels), while Cyperaceae (~10-40%), Poaceae (>20%) and *Artemisia* (<15%) percentages increase compared to MIS 5. MIS 4 records from Squirrel Lake (Figure 3, site 8) reveal lesser percentages of *Betula* (<15%), *Picea* (<5%) and *Alnus* (<5%) compared to MIS 5 spikes in the abundances of these taxa (*Betula* >60%, *Picea* >55%, *Alnus* about >70%). These data suggest that the extent of boreal forests diminished from MIS 5 to 4 (Berger and Anderson, 2000). Assemblages from Togiak Bay (Figure 3, site 3) contain roughly <20% *Betula*, <5% *Picea* and <10% *Alnus* with higher percentages of Cyperaceae (<70%) and Poaceae (<60%) (Kaufman et al., 2001). Percentages of Cyperaceae and Poaceae increase while *Betula* decreases from MIS 5 to MIS 4.

1.4.4 Palynology of MIS 3

MIS 3 occurred from 57 to 29 kya and is an interstadial event (Lisiecki and Raymo, 2005). It is a complicated interval both in terms of vegetation and climate.

According to paleobotanical data, conditions were drier and cooler than modern (Ager, 2003; Anderson and Lozhkin, 2001). According to Anderson and Lozhkin (2001), the dominant vegetation in most of eastern Beringia consisted of tundra, while *Larix* forests were prevalent throughout western Beringia. During warm intervals of MIS 3, western Beringia was more heavily forested than eastern Beringia. Based on regional changes in vegetation, the greatest warming occurred in far western and eastern areas of Beringia (Anderson and Lozhkin, 2001).

The Zagoskin Lake record spans the last ≥30,000 ^{14}C yr BP (Ager, 2003). This site is located on an island in Norton Sound, 7m above modern sea level, and is one of the few sites located within central Beringia (Figure 3, site 5). The record shows abundant Cyperaceae (>25%), Poaceae (>30%), and *Artemisia* (sage >5%) with smaller quantities of *Salix* and *Betula*. MIS 3 assemblages from Kaiyak Lake also contain abundant Cyperaceae and Poaceae, with *Thalictrum* (a mesic indicator) with some *Salix* (Anderson, 1985). Assemblages from both Kaiyak (Anderson, 1985) and Zagoskin (Ager, 2003) lakes indicate that the vegetation was primarily grassy tundra with sporadic shrub populations.

1.4.5 Palynology of MIS 2

MIS 2 occurred between 29 and 14 kya (Lisiecki and Raymo, 2005). This interval records vegetation associations for which there are no modern analogs. Reconstructing the climate based on no-analog pollen assemblages requires pollen-vegetation-climate modeling, synthesizing available paleoecological data, and reliance upon ecological theories (Jackson and Williams, 2004). Based on the results of previous pollen analyses, Beringia experienced drier conditions during MIS 2 compared to today. However, a subtle regional moisture gradient extended from drier conditions in the east (i.e. Bluefish basin in Canada, Figure 3, site 13) to a more mesic environment in the west (i.e. Elikchan in Russia, Figure 3, site 1). For instance, pollen records from Elikchan, located north of the Okhotsk Sea, record an influx of *Artemisia* with *Thalictrum* and mosses during the LGM (Anderson and Lozhkin, 2001), suggesting relatively mesic conditions compared to sites like Bluefish basin. Bluefish basin, located east of the Alaska/Canada border in the northern Yukon Territory, is dominated by Poaceae (40%), Cyperaceae (>20%) and *Artemisia frigida* (a dry indicator, present on open slopes and disturbed areas) (Zazula et al., 2006). The combination of grass, sedge and *Artemisia* indicates the presence of steppe tundra. Steppe tundra is found in small patches on south-facing slopes at mid-to-high latitudes in Eastern and Western Beringia today. However, during the LGM, steppe tundra was thought to be widespread across Beringia and was associated with cold, dry climatic conditions (Elias and Crocker, 2008).

Elias et al. (1996) analyzed pollen, plant microfossils, and beetles from cores of the Chuckchi Sea (between 69°57'N, 165°21'W and 71°06'N, 167°36'W, Figure 3, site 6). During the LGM, the dominant vegetation consisted of Poaceae (28-44%), Cyperaceae (13-30%), *Betula* (19-28%) and *Sphagnum* (26-58%) with smaller percentages of *Salix* (1-5%) and no evidence of *Artemisia*. Elias et al. (1996) interpret the MIS 2 landscape as birch-graminoid tundra "with small ponds choked with aquatic plants" and found no evidence for a steppe tundra environment (Elias et al., 1996).

Elias's et al. (1996) data is comparable to Anderson (1985), as both suggest the vegetation of MIS 2 consisted of relatively mesic tundra instead of dry steppe tundra. Anderson (1985) analyzed pollen from Squirrel Lake (Figure 3, site 8) and Kaiyak Lake (Figure 3, site 9). Assemblages are dominated by Poaceae (20-50%) and Cyperaceae (10-35%) with *Artemisia* (20%) and smaller percentages of *Betula* and *Alnus* (10%) during the LGM. Anderson (1985) suggests herbaceous tundra was present during the LGM with willow and dwarf shrub birch in more mesic localities.

Comparatively arid conditions are recorded by assemblages from a 14m sediment core recovered from Cagaloq Lake on St. Paul Island in the Beringian lowlands (Figure 3, site 2). Colinvaux (1981) observed abundant Cyperaceae, Poaceae and *Artemisia*, suggesting that St. Paul Island was dominated by herb tundra without trees or shrubs during the LGM. Percentages of trees, shrubs, and *Sphagnum* (<10% each of *Betula*, *Alnus*, *Picea*, and *Sphagnum*), are distinctly different from those reported by Elias et al. (1996) (*Betula* 19-28%, *Sphagnum* 26-58%) and Anderson (1985) (10% each of *Alnus* and *Betula*). According to Colinvaux (1981), dwarf birch was extremely rare and tussock vegetation was lacking; the absence of both indicate a relatively dry environment. Despite Colinvaux's (1981) persuasive data, the ages of the assemblages are based on bulk dates, which are ambiguous because the amount of old carbon in the sample is unknown. Ultimately, the dates might be younger than Colinvaux (1981) reported. There is also uncertainty regarding the elevation of the site. Colinvaux (1981) mentions that St. Paul Island was 150-300m above the BLB during the LGM but does not provide the specific elevation at which the sediment core was taken. Differences in elevation could influence the type of vegetation present (i.e. higher elevations might sustain more dry-adapted species while lower elevation areas might contain more mesic-adapted vegetation).

1.4.6 Palynology of MIS 1

MIS 1 occurred between 14-0 kya (Lisiecki and Raymo, 2005) and includes the cold Younger Dryas (13-11.5 kyr) and the Holocene Thermal Maximum (HTM) between 11.5 kya and 9.1 kya (Kaufman, 2004; Abbott et al., 2000). The Younger Dryas was an abrupt return to near-LGM conditions with high winds and increased aridity (Abbott et al., 2000). The strongest signal for the Younger Dryas occurs in Greenland; it is much weaker in Beringia, as characterized by minor, short-term shifts in vegetation in most locations (Peteet and Mann, 1994). The Younger Dryas, was followed by a period of warming (the HTM). Based on proxy data of 16 terrestrial sites from the western Arctic (i.e. Alaska, Canada, Greenland, Iceland), Kaufman et al. (2004) suggest that HTM temperatures were 1.6 ±0.8°C higher than modern summer temperatures.

Pollen analysis from Zagoskin Lake (Figure 3, site 5) records an increase in *Betula* (<62%) and *Alnus* (<65%) and a minor increase in *Picea* (2-5%) during MIS 1, along with decreases in Poaceae (<30%), Cyperaceae (<30%) and *Artemisia* compared to the same site during MIS 2 (Ager, 2003). From MIS 2 to 1, Poaceae decreased by ~15% and Cyperaceae decreased ~10%, while *Betula* increased by ~30%, *Alnus* by ~50% and *Picea* by ~2%. Increases in *Picea*, *Betula* and *Alnus* together indicate boreal forest conditions. A spike in *Betula* from the end of MIS 2 to the beginning of MIS 1 indicates it was growing at that site (Ager, 2003).

Based on a compilation of 49 pollen records from the Paleoenvironmental Arctic Sciences (PARCS) database from the LGM to the mid-Holocene, Brubaker et al. (2005) report rapid increases in tree and shrub pollen at sites across Beringia early in MIS 1. *Picea* pollen increases throughout eastern Beringia (EB - modern day Alaska) from <2% in MIS 2 to >20% during MIS 1. In western Beringia (WB - modern day Russia) *Picea* pollen increases only slightly, from nearly absent during MIS 2 to up to 2% in sporadic locations during MIS 1. In WB, *Pinus* pollen increased from <2% at many MIS 2 sites to >2% during MIS 1, whereas in EB it increased from nearly absent to trace amounts. In EB, the abundance of *Betula* pollen increases from >10% during MIS 2, reaching >60% at a quarter of the sites during MIS 1. Percentages of *Betula* pollen in WB during MIS 2 are >10%; MIS 1 abundances are variable, exceeding 50% at a few sites. Finally, *Alnus* pollen increases from 5-30% in WB and from <5% in EB during MIS 2 to >30% in EB and WB during MIS 1. These changes represent the spread of boreal forest vegetation across much of EB during the Holocene.

1.5 Refugium hypothesis

Brubaker et al. (2005) suggest that rapid increases in pollen from boreal forest taxa, including *Betula*, *Alnus*, *Picea* and *Pinus,* during MIS 1 indicates that these plants survived MIS 2 in refuge populations within Beringia rather than migrating long-distances from south of the ice sheets. If trees and shrubs migrated from locations further south (i.e. modern Washington) into Beringia, pollen production would lag behind climate change. The concurrent increases of tree and shrub pollen with the onset of MIS 1 suggest they did not migrate from southern regions; instead, local populations began to flourish as soon as conditions became more favorable (Ager, 2003). If trees and shrubs did not migrate back into Beringia from regions south of the ice sheets, they must have survived in small populations throughout MIS 2 (Brubaker et al., 2005). It is hypothesized that seed dispersal between these isolated populations of trees and shrubs would have contributed to long-term survival (Brubaker et al., 2005). Despite extreme LGM conditions, Beringia likely experienced varying moisture and temperature conditions which are evident in the disparate pollen presence/absence and percentage data from sites in EB and WB (Brubaker et al., 2005; Guthrie, 2001).

Due to differences in climate and vegetation cover, the exposed BLB could have presented a barrier to migrating flora and fauna during Pleistocene glacial stages. Guthrie (2001), who cites Colinvaux (1964), Anderson and Brubaker (1994) and Elias et al. (1996), hypothesizes that maritime cloud cover over Beringia created a "mesic buckle" within a belt of arid steppe vegetation. He suggests that conditions were more humid in low topographic regions of central Beringia and that a S-N moisture gradient spanned the emergent Bering Strait during the LGM. Southern regions were more mesic while northern regions were more arid. Lower-humidity environments of eastern Russia and western Alaska resulted in different vegetation compared to central Beringia and limited the dispersal of megafauna such as short-faced bears (*Arctodus*), badgers (*Taxus*), camels (*Camelops*), Kiang (*Equus*) and Muskoxen (*Bootherium*) into central and western Beringia. In the Holocene, mesic-adapted species within the refugium radiated from central Beringia into Western and/or Eastern Beringia (Guthrie, 2001).

Elias and Crocker (2008) compiled and analyzed palynological data from 13 sites in WB and EB. Elias and Crocker (2008) also find evidence of a west-east moisture gradient during the LGM. They hypothesize that the lowlands of the BLB were dominated by shrub tundra indicative of a more mesic environment while EB sites contained steppe-tundra indicating a relatively dry environment.

To test whether small populations of spruce trees existed in Alaska during the LGM, Anderson et al. (2006) examined white spruce chloroplast genomes from 24 forest stands along an assumed interior migration route between Alaska and south-central Canada. They found that DNA haplotyes were unique and diversity was high in Alaska compared to Canadian stands. This suggests that white spruce did not migrate into Alaska from southern areas when the Laurentide ice sheet retreated but remained in isolated refuge populations of Alaska during the LGM.

1.6 Site descriptions of U1339 and U1343

Site U1339 is located 54.40°N and 169.58°W on the northwest flank of Umnak Plateau. The plateau is detached from the Bering shelf by an incised canyon. During low sea level stands, this site was presumed to contain more pelagic biogenics compared to terrigenous sediments transported from the adjacent shelf into the canyon below. Three holes drilled at site U1339 reached a maximum age of ~0.74 Ma. Sedimentation rates, determined by an age model based on biostratigraphic datum points, range from 22 to 50 cm/kyr (Expedition 323 Scientists, 2010).

Site U1339 sediment is comprised primarily of biogenic (diatoms), volcaniclastic and siliciclastic sediment with minor amounts of dolomite, pyrite, benthic and planktonic foraminifera (Figure 4). Radiolarians, sponge spicules and calcareous nannofossils are rare. Sediments composed of diatom-rich silt/ashy silt are dark greenish gray while diatom ooze is an olive color. Terrigenous sediments are common and comprised of clay, mica, quartz, feldspar and rock fragments. Dropstones are also apparent, consisting of gravel- to pebble-sized grains. Volcanic ash layers throughout the unit range from ~2mm to ~10cm thick (Expedition 323 Scientists, 2010). My oldest U1339 sample was obtained ~35m CCSF-A (core composite depth below seafloor, appended). IODP scientists use the mudline, or the topmost sediment, as the “anchor” for correlating lithologies from different holes. The acronym CCSF-A refers to the stratigraphic correlation between drilled holes (Expedition 323 Scientists, 2010).

Site U1343 is located 57.33°N and ~175.49°W on a topographic high, detached from the main Bering Sea shelf, at a depth of 1,953m (Takahashi et al., 2011). Expedition 323 scientists assumed the site would collect less reworked terrigenous material from the submerged or emergent continental shelf during interglacial or glacial periods, respectively, compared to locations further down slope (Expedition 323 Scientists, 2010). A composite age model from all five holes drilled at site U1343 shows that sediments

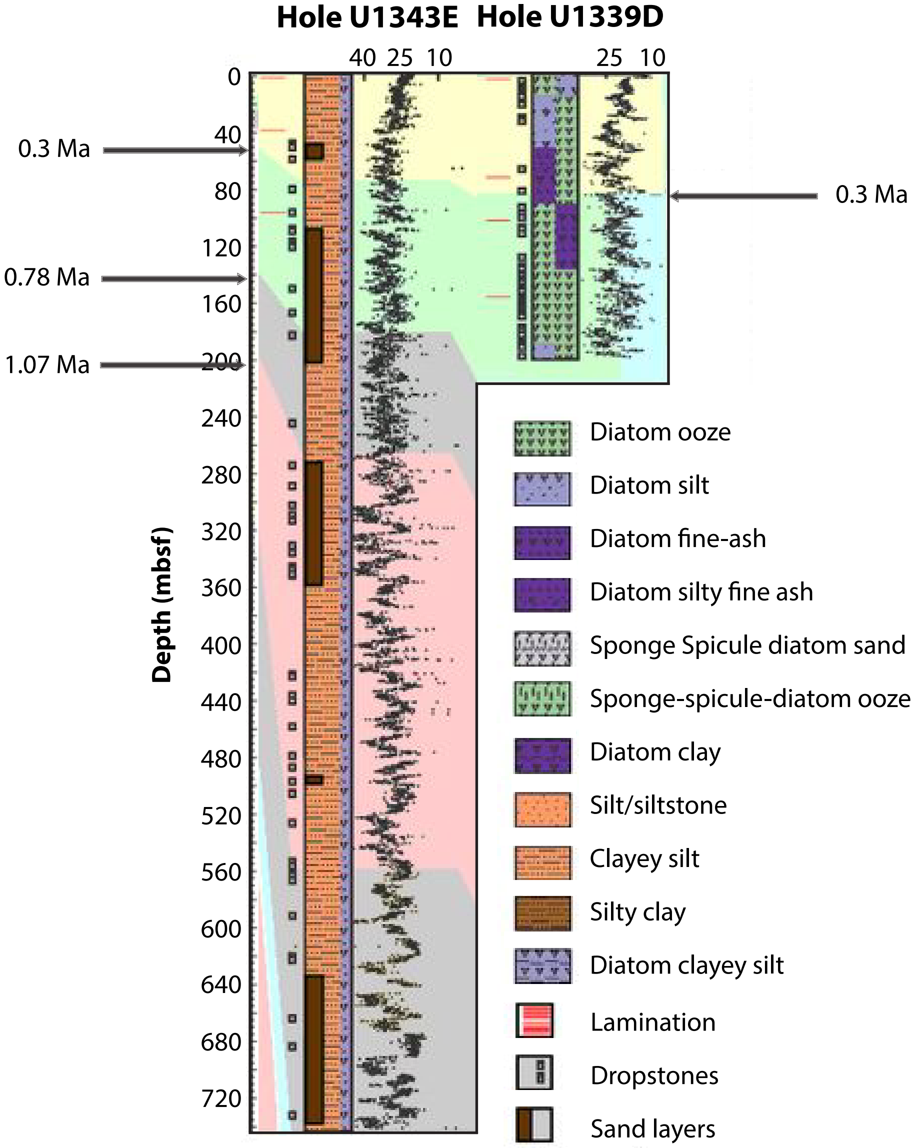

Figure 4. Lithostratigraphic summary of cores U1343E and U1339D. Natural gamma ray data plotted alongside stratigraphy. Background colors indicate temporal correlation between sedimentary sequences from U1343E to U1339D (Modified from: Expedition 323 Scientists,

span the last ~2.2m.y. (Takahashi et al., 2011). In general, high sedimentation rates characterize site U1343. Sedimentation rates are ~26cm/kyr within the uppermost 400m CCSF-A (Takahashi et al., 2011). My oldest IODP sample was collected from U1343E at ~42.2m CCSF-A.

Site U1343 consists largely of silt with variable amounts of clay and diatoms and minor concentrations of ash, foraminifers, sand, sponge spicules (common throughout the core) and calcareous nannofossils (Figure 4) (Takahashi et al., 2011). Sediment appears to be primarily dark greenish gray to dark gray (Takahashi et al., 2011). Sediments are characterized by a high proportion of siliciclastic grains compared to biogenic grains. Clay content tends to be high compared to sites on Bowers Ridge (i.e. U1342, U1341 and U1340). Fine layers of volcanic ash are present due to proximity to the Aleutian arc but are less abundant than in cores from U1339. The degree of bioturbation ranges from slight to average throughout the core, excluding laminated intervals that show no visible bioturbation.

1.7 Age Models

The age model for site U1339 is provided by Mea Cook and Alan Mix (Figure 5). It is based on the $\delta^{18}O$ (‰) values from analyses of benthic foraminifera, which is correlated to a composite record compiled and dated by Lisiecki and Raymo (2005). Five species, including *Uvigerina peregina*, *U. senticosa*, *Elphidium cf. batialis*, *Nonionella labradorica*, and *Globobulimina affinis*, were measured for $\delta^{18}O$ (‰). Two tephra layers (11.1 and 14.6 k cal BP respectively) provide additional age control (Cook, pers. comm., 2013).

The age model (Figure 6) for site U1343 is based on $\delta^{18}O$ (‰) data provided by Hiro Asahi (Asahi et al., 2014). The average sample resolution for this age model is ~1.5 kyr from the core top to MIS 5. Down-core sediment ages were determined by linear interpolation between dated horizons based on the $\delta^{18}O$ (‰) record. Table 1 identifies boundaries of MIS 1-6 as described by (Asahi, pers. comm., 2012).

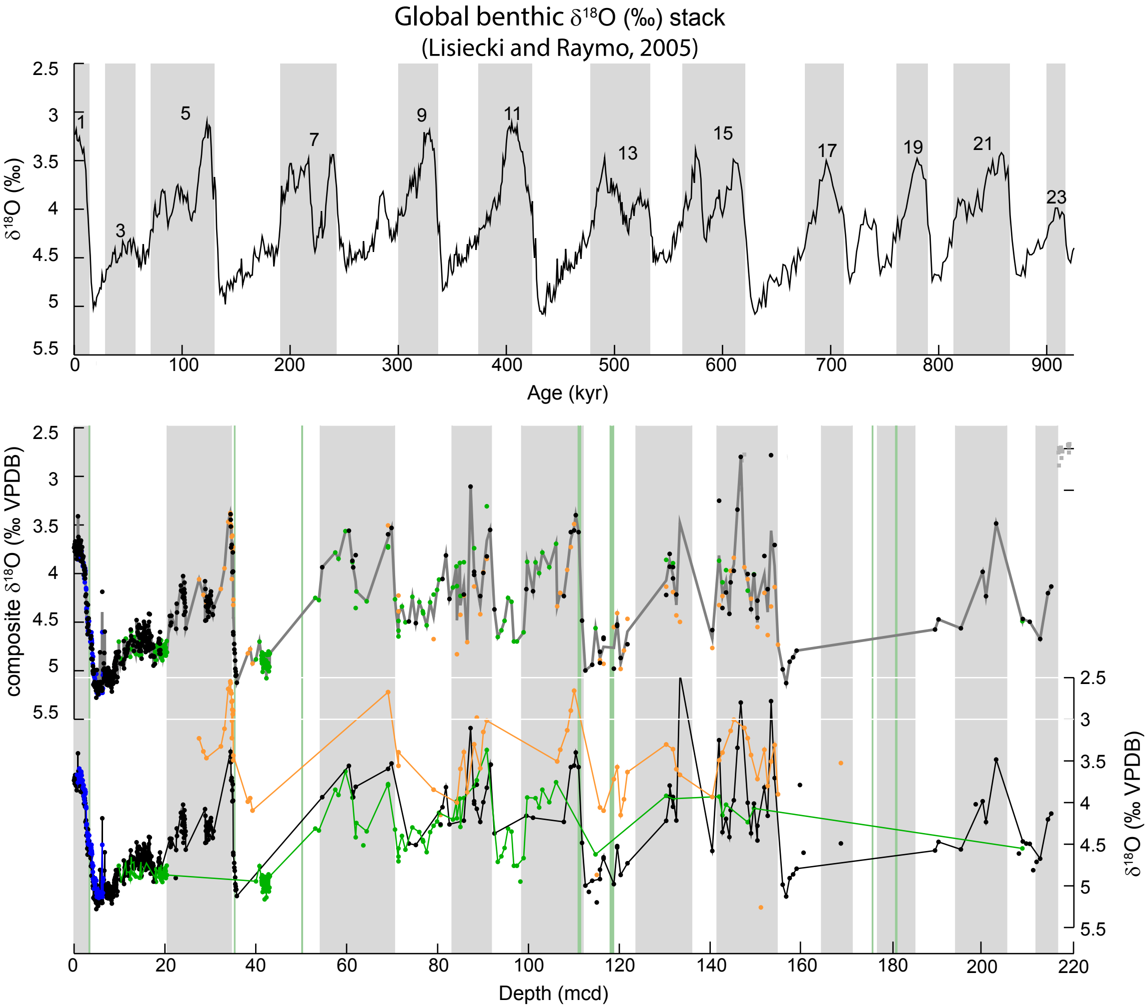

Figure 5. Top panel indicates age model based on global benthic δ18O (‰) stack data for site U1339 provided by Lisiecki and Raymo, 2004. Interglacial periods indicated by grey bars while glacial periods denoted by white sections. Bottom panel shows composite benthic δ18O (‰ VPDB) data from *Elphidium cf. batialis*, *Uvigerina peregrina*, *U. senticosa*, *Nonionella labradorica*. Green bars show positions of laminated sediments (Modified from: Cook et al., 2011).

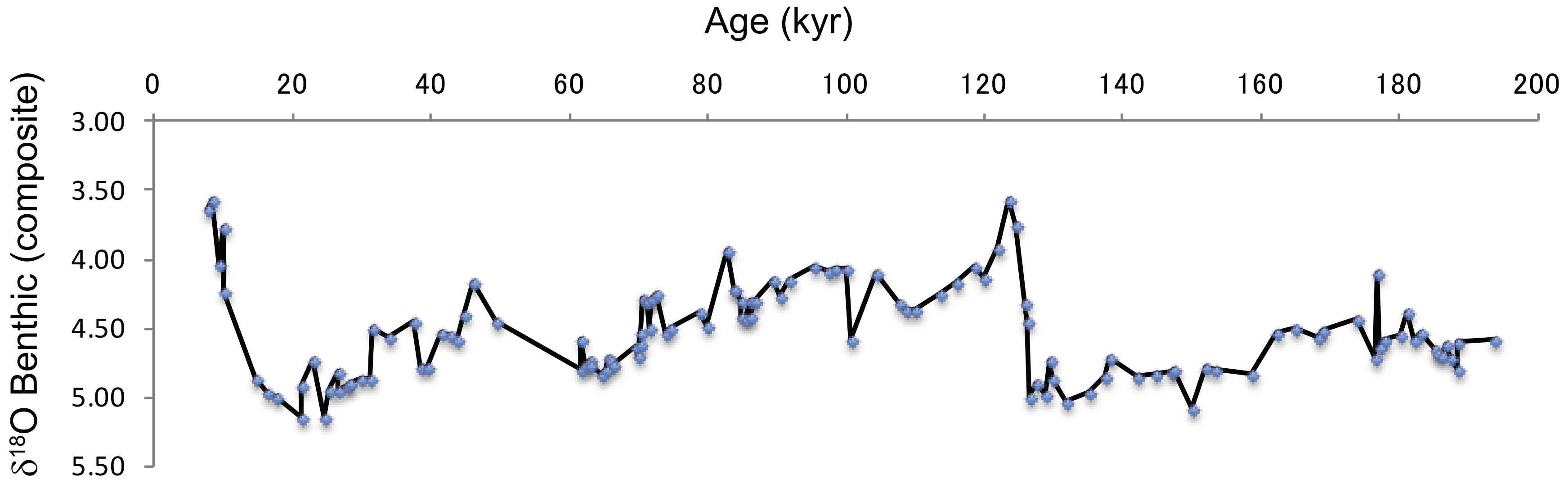

Figure 6. Age model based on δ18O (‰) data from site U1343 provided by Hiro Asahi (Modified from: Asahi pers. comm., 2012).

Table 1. Age boundaries determined by δ18O (‰) data provided by Hiro Asahi (Asahi, pers. comm., 2012).

MIS Boundary	Age (Ma)	Age (kyr)	Depth (m CCSF-A)
	0.0076	7.62	0.010
1/2	0.014	14	3.191
2/3	0.029	29	7.523
3/4	0.057	57	13.158
4/5	0.071	71	18.415
5.1(peak)	0.082	82	22.236
5.2(peak)	0.087	87	25.078
5.3(peak)	0.096	96	28.488
5.4(peak)	0.109	109	32.933
5.5(peak)	0.123	123	35.611
5/6	0.13	130	38.550
6/7	0.191	191	48.766

Chapter 2: Methods

2.1 Processing: IODP Samples

Samples from Expedition 323 sites U1343 and U1339 were requested from IODP and received from the Kochi Core Center. I followed a modified version of the methods described in Heusser and Stock (1984) for laboratory processing of marine sediment (Figure 7). Whereas Heusser and Stock (1984) processed 5cc samples, the samples I received from IODP had volumes ≤2cc as determined by water displacement. Low pollen concentrations are typical of marine sediment compared to terrestrial samples because grains are transported far from source material. A larger sample is ideal if pollen concentrations are low; small sample size increases the probability of low pollen recovery.

I added a *Lycopodium* tablet (15,500 spores per tablet) to each sample in a 15 mL glass test tube in order to calculate the total number of fossil polymorphs present in the sample, following the methods of Stockmarr (1971). Carbonates were removed using a 10% hydrochloric acid (HCl) wash. Samples were washed three times in water and centrifuged for five minutes after each wash to eliminate remaining 10% HCl. Prior to any centrifugation, samples were stirred manually to ensure the material was well mixed. After the washes, samples were heated in 10% potassium hydroxide (KOH) solution for 2 minutes to remove humic acids. The color of the liquid in which the sample was suspended indicates the quantity of humates in the sample (i.e. dark brown or black supernatant indicates high humate content). Two water washes followed the 10% KOH bath.

To remove clay and macrofossils, I added a 5% sodium pyrophosphate ($Na_4P_2O_7$) dispersant, which kept material from clumping. I then poured the samples through a 250 μm sieve. Material >250 μm was rinsed off from the sieves into Whirlpack bags and refrigerated for possible later analysis. Due to the high clay content in my IODP samples, the sieving procedure differed from that employed by Heusser and Stock (1984). Although they also used sodium pyrophosphate ($Na_4P_2O_7$) as a dispersant, Heusser and

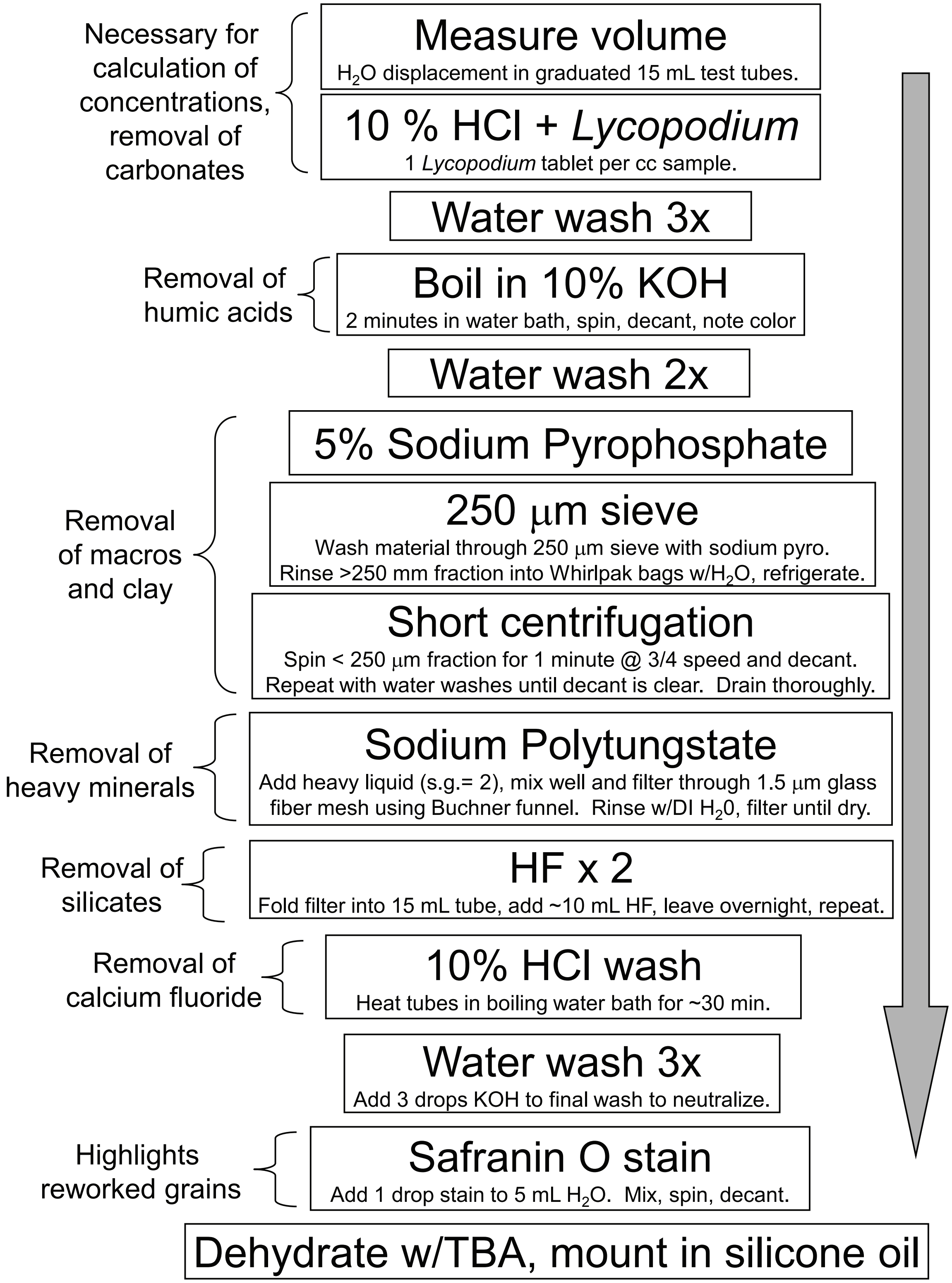

Figure 7. Flow chart of labratory procedure sequence.

Stock (1984) sieved samples through a 150 µm sieve and then 7 µm nylon mesh screen. My IODP samples contained so much clay that fine sieves rapidly became clogged. Instead, I employed the short centrifugation technique described by Traverse (1988). The portion passing the 250 µm sieve (which included the pollen) was poured back into 15 mL test tubes, manually stirred, centrifuged for 1 minute at 1,500-1,750 rpm and then decanted. Centrifuging the sample allows the pollen to sink to the bottom of the test tube, while excess clay remains in suspension and is removed when the liquid is decanted. I continued centrifuging samples for one minute in water until the supernatant was clear. A drop of decanted material was placed on a slide and checked for palynomorphs under a laboratory Olympus CX41RF microscope prior to disposal. In 80% of samples no palynomorphs were found. In the remaining samples, I found isolated grains of exotic *Lycopodium.* If more than three pollen grains were present on the slide, I poured the decanted material into the 15 mL test tube and resumed the short centrifugation process.

Gravity separation employed sodium polytungstate ($Na_6[H_2W_{12}O_{40}]$) mixed to a specific gravity of 2.1. I mixed the samples with the heavy liquid and poured them through a 1.5 µm glass fiber mesh twice using a Buchner funnel. To eliminate silicate minerals, diatoms, and glass fibers, I folded the filter into 15 mL tubes and immersed each sample twice in hydrofluoric acid (HF), adding ~10 mL of HF and leaving the samples overnight at room temperature. Due to the presence of numerous diatoms in addition to the glass from the filters, I found that a second HF treatment was necessary in order to remove all the silica. Heusser and Stock (1984) treated their samples with HF just once, placed them in a hot water-bath for an hour, left them to cool overnight, and reheated them the next day.

After the second HF treatment, I decanted the HF, filled the sample tubes with a 10% HCl wash, placed the samples in a boiling water bath for approximately 30 minutes, and manually stirred them to dissolve any calcium fluoride crystals. Three water washes eliminated remaining 10% HCl. I added three drops of 10% KOH to the final wash to neutralize the pH. I then added 5 mL of water and one drop of 2.5% safranin O stain to help identify reworked grains. Next I dehydrated the samples with a tertiary buytl alcohol (TBA) wash and decanted the residues into 5 mL vials. I placed sample vials, without caps, into a warm drying oven for 24 hours to evaporate excess TBA. Finally, I mounted pollen grains in silicon oil so that they could be rotated and flipped over, making identifications easier.

Heusser and Stock (1984) employed several techniques, including acetolysis, oxidation and a second sieving step that were not necessary in the preparation of my samples. Acetolysis dissolves cellulose material in recent samples, while oxidation was used if "large amounts of amorphous organic matter or charcoal-like particles [were] present" (Heusser and Stock, 1984). Their second and final sieving step uses a 7 µm screen to remove undigested fine particles before dehydrating samples with TBA. My samples did not require these procedures because they were not highly organic, did not contain fine cellulose material, and fine clay particles were eliminated through the short centrifugation procedure.

2.2 Microscopy

Palynomorphs were counted using an Olympus CX41RF microscope at 400-1000X magnification. Pollen grains and spores were compared with type slides in collections housed at the University of Alaska Fairbanks palynology lab, photographic plates in Traverse (1988), and plates and keys in Faegri and Iverson (1989), Hultén (1968), Kapp (1969), McAndrews et al. (1973), Moore et al. (1991), and Moriya (1976). Taxa were identified to family or genus. In addition, I categorized *Alnus* (alder) pollen by the number of pores on each grain (i.e. 4 -pores, 5 -pores or 6 -pores), because this may have stratigraphic or climatic significance. Reinink-Smith (2010) noticed a transition from 4-pored *Alnus* within the Miocene Beluga Formation and Pliocene lower Sterling Formation to 5-, 6-, 7-, and 8-pored *Alnus* within the upper Sterling Formation along Cook Inlet. Reinink-Smith (2010) speculates that this change was caused by a floristic shift in subgenus from *Alnus incana* (4-pored) to cold-adapted *Alnus alnobetula* (>5-pored).

I did not differentiate between species of spruce such as *Picea glauca* (white spruce) and *Picea mariana* (black spruce) because many grains of this genus appeared as a single bladder. To determine the number of spruce pollen grains, I counted the total number of bladders and divided by two. Similarly, *Betula* (birch) pollen from shrub birches was not distinguished from that of tree birches, because it is difficult to differentiate birch subgenera or species based on pollen grains (Edwards et al., 1991). Accurate measurements of grain diameter and pore depth are critical for correctly distinguishing the two types of birch (Clegg et al., 2005); many of the birch grains in my sample were crumpled, making such measurements difficult or impossible. Cyperaceae and Poaceae pollen grains were classified to the family level because the same pollen morphology is produced by many genera.

Spores were categorized as monolete, trilete, or *Sphagnum* but were not subdivided further into genera or species based on wall structure and ornamentation; many were too degraded to make a positive identification. Indeterminate spores and pollen grains were described and photographed with an Olympus DP20-5 camera.

Stain is absorbed by the outer wall, or exine, of a grain. Older, reworked grains have degraded exines and do not absorb stains as readily when compared to younger, non-reworked grains (Faegri and Iversen, 1989). I noted the number of brown or dark yellow grains in each sample an indicator of reworked material relative to pink/red color of the majority of the grains.

2.3 Calculating pollen percentages

Pollen concentrations were calculated by the following equation (from Traverse, 1988):

$$\text{Total Fossil Pollen} = \frac{(\text{Fossil Pollen Counted} \times \text{Total Number Markers})}{\text{Markers Counted}} \div \text{Sample Volume}$$

Due to limited pollen concentrations in U1339, located on Unmak Plateau, my research focuses on site U1343A and E. A total of 26 samples comprises the scope of research. Pollen diagrams are based on identification of at least 300 grains per sample at site U1343. Samples at site U1339 are based on the identification of at least 200 grains per sample. The pollen sum includes all identified pollen grains and spores excluding *Pediastrum* (i.e. green alga). The basic pollen sum is calculated by adding the total number of tree and shrub pollen to herb pollen and spores. Unknown and Indeterminable categories are not included in the basic pollen sum. A paludification index P_{est} (angiosperm pollen / *Sphagnum* spores) constitutes a proxy for saturated organic matter. Values less than 10 correspond to wet conditions and saturation of sedimentary organic matter according to definitions by White et al. (1997).

2.4 PCA of modern and fossil samples

Cores from IODP sites U1339 and U1343 were sampled for palynomorphs at approximately 10 kyr intervals, focusing on the last 150 kyr. The youngest core samples from site U1343 are dated to 10.7 kya. To identify modern analogs, I compared my samples with modern surface samples from various locations in Alaska. Surface sample datasets were provided by palynologists Thomas Ager, Patricia Anderson, and Linda Brubaker. Ager analyzed palynomorphs from 120 sites in western and southern Alaska (59.6°N to 69.25°N and -144.65°W to -166.17°W) while Brubaker and Anderson collected and analyzed pollen percentages from a total of 278 sites throughout mainland Alaska (59.1°N to 71.23°N and -141.07°W to -166.47°W) (Anderson and Brubaker, 1996; Bigelow et al., 2003). The original datasets from Ager, Anderson and Brubaker varied in their descriptions of the local vegetation at the sample sites. In order to standardize the vegetation descriptions, I plotted their site localities onto a modern vegetation distribution map of Alaska developed by Michael Fleming (Figure 8), which employs 23 vegetation classifications (Fleming, 1998). The vegetation distribution map was constructed from a phenology index of the 1991 growing season using Advanced Very High Resolution Radiometer (AVHRR) satellite data (Markon et al., 1995). Vegetation classifications provided by Ager, Anderson and Brubaker were consistent with vegetation descriptions on the distribution map. Table 2 outlines the relevant vegetation types from Fleming’s modern vegetation distribution map of Alaska and provides a description of each type. Viereck and Little's (1972) vegetation map from *Alaska Trees and Shrubs* provided the description of vegetation represented by each type

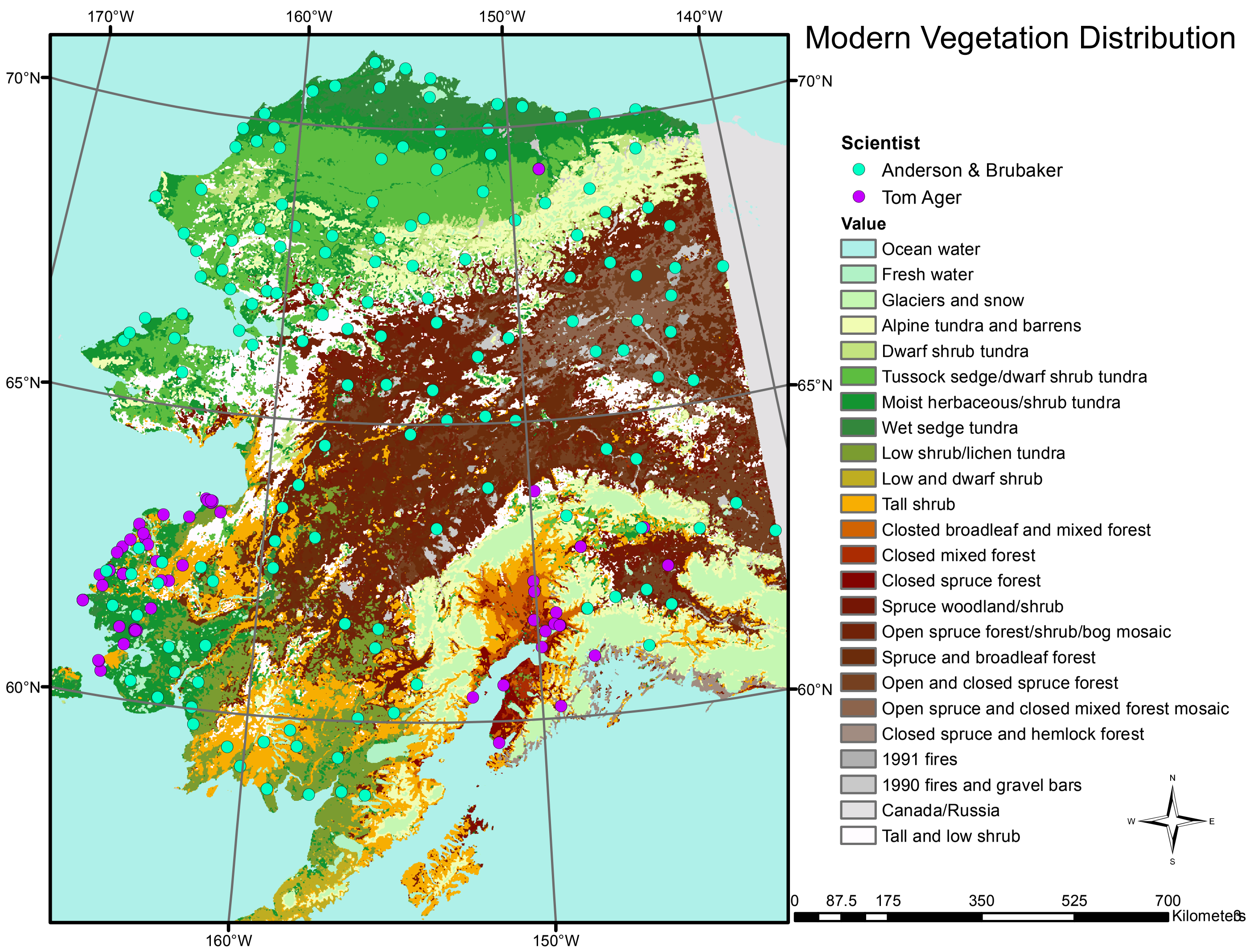

Figure 8. Modern vegetation distribution of Alaska including 24 classes total, 19 of which are vegetative. Surface sample data provided by Tom Ager (indicated by purple cirles), and Pat Anderson and Linda Brubaker (indicated by green circles) (Modified from: Fleming, 1998).

Table 2. Description and grouping of pertinent vegetation classifications constructed from satellite and ground-truthed data (Viereck and Little, 1972; Fleming, 1998). Vegetation descriptions represented by each vegetation type are provided by Viereck and Little (1972) *Alaska Trees and Shrubs*. Vegetation types are described by Felming (1998).

Vegetation Type **(Flemming, 1998)**	**Vegetation Description** **(Viereck and Little, 1972)**	**Grouped Vegetation** **(this study)**
Alpine Tundra and barrens	Consisting of white mountain-avens, low heath shrubs, prostrate willows, and dwarf herbs. Predominantly barren.	**Herbaceous Tundra** (i.e. alpine tundra and barrens, wet sedge tundra)
Dwarf shrub tundra	Consisting of Dryas, willow, sedge, birch, crowberrys, forbs, moss, lichen.	**Shrub Tundra** (i.e. dwarf shrub tundra, tussock sedge/ dwarf/shrub tundra, low shrub/lichen tundra, tall shrub, tall and low shrub)
Tussock sedge/dwarf shrub tundra	Consisting of cottongrass (Eriophorum) sedge, grasses, labrador tea, dwarf birch, moss, willow, forbs (lousewort, heartleaf saxifrage).	**Shrub Tundra**
Moist herbaceous/shrub tundra	Consisting of sedge and grass; typically wet coastal tundra and marsh land.	**Herbaceous shrub Tundra** (i.e. moist herbaceous/shrub tundra)
Wet sedge tundra	Consisting of dwarf birch, labrador tea, sedge, moss, alpine blueberry.	**Herbaceous Tundra**
Low shrub/lichen tundra	Consisting of sedge, lichen, moss and erect dwarf shrub (i.e. lingonberry, cloudberry).	**Shrub Tundra**
Tall shrub	Consisting of sedges, especially in tussocks; scattered willows, dwarf birch and alder. Resemble tundra meadows.	**Shrub Tundra**
Tall and low shrub	Consisting of dwarf birch, alder, willow, myrica, herbs and forbs (i.e. Rosaceae).	**Shrub Tundra**
Mixed Forest	Consisting of paper birch, quaking aspen-balsam poplar, shrubs.	**Mixed Forest** (i.e. closed broadleaf and mixed forest, closed mixed forest)
Spruce Forest	Consisting of white spruce, paper brich, black spruce, quaking aspen, balsam poplar, shrubs.	**Spruce Forest** (i.e. closed spruce forest, spruce woodland/shrub, open spruce forest/shrub/bog mosaic, spruce and broadleaf forest, open and closed spruce forest, open spruce forest and hemlock forest)

(i.e. specified the taxa within vegetation types) on Table 2. Several of the modern surface samples from Ager, Anderson and Brubaker were not included in subsequent analyses due to overlapping locations or redundant vegetation classifications.

Raw pollen counts of selected surface samples and IODP samples were converted to percentage data using Tilia version 1.7.16. The data was exported as an excel file. If a taxon occurred less than three times in a sample and/or the percent of that taxon was <2%, then I excluded the taxon from the sample dataset.

I compared 220 surface pollen spectra to my IODP samples using Canonical Community Ordination (CANOCO) version 4.5. Initially, a Detrended Correspondence Analysis (DCA) determined the gradient lengths of the first axis. If the gradient length is less than 4 standard deviations, then a linear response model such as PCA is an appropriate technique (Ter Braak and Smilauer, 2002). The first axis gradient length of my dataset was 1.868 standard deviations, therefore a Principal Component Analysis (PCA) characterized by a linear response model with an indirect gradient analysis was applied. I followed typical PCA methodology by basing results on species (taxa) only and implementing a square-root transformation that reduces the range in the dataset and generates a more compact plot. I did not weight dominant taxa relative to minor taxa. This means that the dominant taxa are plotted far from the center of the diagram. Ordination plots were generated in CanoDraw to showcase correlations between IODP samples and surface samples highlighting various aspects of the modern samples, including lake vs. peat, tundra vs. forest, and tundra biome vs. forest biome.

Chapter 3: Results

3.1 Pollen in MIS 1-6

Fossil pollen concentrations range from 5,574 to 11,476 per cc at site U1339, while concentrations at site U1343 vary from 3,232 to 25,805 per cc (Table 3). Due to lower average concentrations in samples from U1339, my research focuses on site U1343. I successfully identified at least 300 pollen grains and spores in each of 26 samples (Figure 9) ranging in age from 10.7 to 152.2 kya at approximately 10 kya intervals. Results from site U1343 reveal high percentages of sedge (Cyperaceae ≥ 17.1%) and grass (Poaceae ≥ 17.4%) in glacial and interglacial assemblages. Boreal forest taxa including birch (*Betula* ≤ 19.9%), alder (*Alnus* ≤ 27.7%) and spruce (*Picea* ≤ 8.5%) are consistently present. Spores of *Sphagnum* and ferns also consistently present and commonly abundant (3.4-10.9%). Large differences in the relative abundances of these taxa are not apparent between glacial and interglacial samples; percentages of grass and sedge are always higher than birch, alder and spruce from MIS 6 to MIS 1. The paludification index (P_{est}), which indicates wet versus dry environmental conditions, falls between 6 and 15 for samples from MIS 1, 3, 4, and 5. P_{est} for glacial stages MIS 2 and 6 are higher, ranging from 11-22. MIS 2 records the lowest shrub/herb ratio in the samples.

3.1.1 MIS 6 (191-130 kya)

Three samples from MIS 6 were analyzed (Figure 9), with estimated ages ranging from 152.2-137.2 kya. Grass (Poaceae 22.2-20.4%) and sedge (Cyperaceae 33.3-50.6%) percentages are greater than birch (*Betula* 9.5-12.7%), alder (*Alnus* 8.9-16.7%) and spruce (*Picea* 3.6-6.2%). Willow (*Salix* 3.6-4.7%) is also present. *Sphagnum* abundances are 6.6%, 5.5%, and 4.7% at 152.2 kya, 146.2 kya and 137.2 kya, respectively. MIS 6 P_{est} values range from 11-17, indicating relatively dry conditions. Total pollen concentrations were generally high: 25,805.85 grains per cm^3 at 152.2 kya, 14,154.96 grains per cm^3 at 146.2 kya, and 20,472.60 per cm^3 at 137.2 kya (Figure 10), whereas influx values are

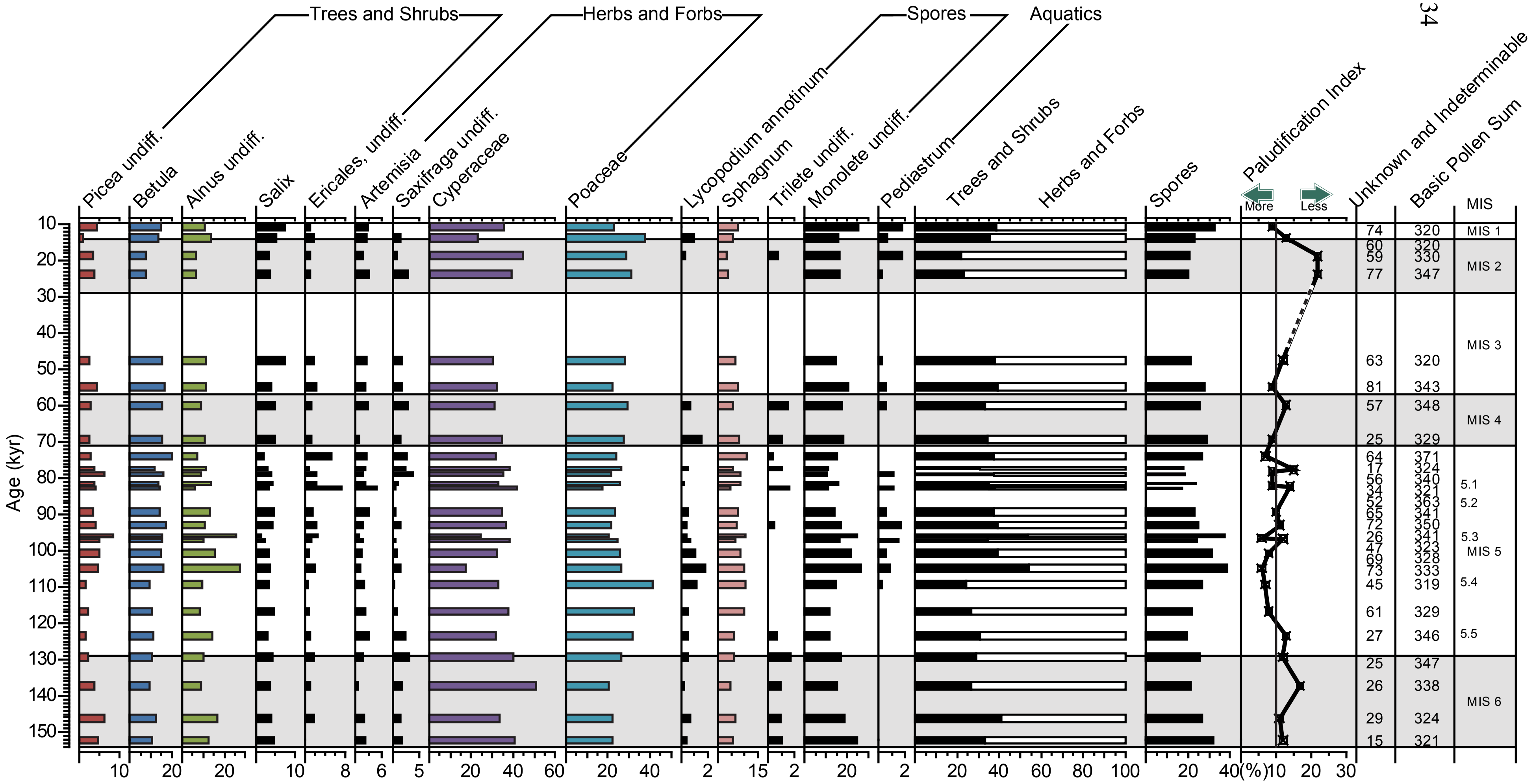

Figure 9. Abundance (percent total identified) of selected taxa from IODP Expedition 323 site U1343 samples. All columns start at zero percent and scales vary. “Unknown and Indeterminable” are presented as raw data of total items encountered in a given sample and are not included in the basic pollen sum. Percentage of tree and shrubs vs. herbs and forbs are based on a different pollen sum that includes these taxa only. Values less than 10 on the paludification index indicate greater saturation.

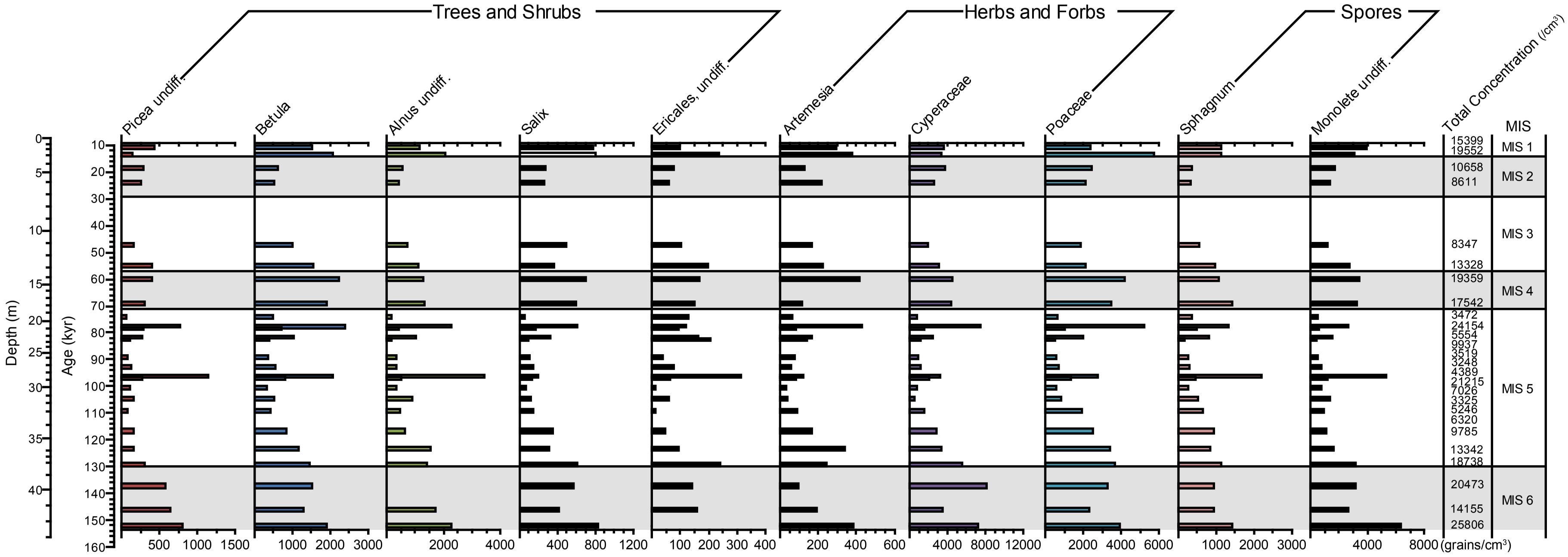

Figure 10. Concentration (grains/cm^3) of selected taxa from IODP Expedition 323 site U1343 samples. All columns start at zero grains/cm^3 and scales vary.

Table 3. Pollen concentrations for sites U1339 and U1343.

Age (kyr)	Core Name U1343	Pollen Concentrations (per cc)
10.7	1343E_1H02	15399.39
13.7	1343E_1H03	19551.67
18.7	1343E_1H04	10657.85
23.8	1343E_1H05	8611.11
47.4	1343E_2H03	8346.95
54.8	1343E_2H04	13327.76
59.8	1343E_2H05	19359.44
69.2	1343E_3H01	17541.46
73.9	1343A_3H04	3471.89
77.7	1343E_3H03	24153.86
78.1	1343A_3H05	5553.72
82	1343E_3H04	9937.41
82.2	1343A_3H06	3518.72
89.3	1343A_4H02	3247.60
92.9	1343A_4H03	4389.46
96.6	1343E_4H02	21214.65
96.7	1343A_4H04	7025.92
101	1343A_4H05	3325.27
105	1343A_4H06	5245.57
109	1343E_4H05	6319.68
117	1343E_4H06	9784.83
124	1343E_4H07	13341.70
129	1343E_5H02	18738.26
137	1343E_5H03	20472.60
146	1343E_5H04	14154.96
152	1343E_5H05	25805.85
	U1339	
21	1339C_1H05	6234.88
28	1339D_2H02	5574.65
58	1339D_3H03	11476.48
89	1339C_4H05	8727.61

relatively moderate, ranging from 434,399 grains/cm^2/yr at 152.2 kya to 236,860 grains/cm^2/yr at 146.2 kya (Figure 11).

3.1.2 MIS 5 (130-71 kya)

Fifteen samples were analyzed from MIS 5. Estimated ages of the samples range from 129.3 kya to 73.9 kya with an average 4 kya between sampled horizons. Grass (Poaceae 17.4-41.1%) and sedge (Cyperaceae 17.1-41.9%) abundances are more variable than those for samples from MIS 6. Percentages of birch (*Betula* 9.4-19.9%), alder (*Alnus* 6.1-27.7%) and spruce (*Picea* 1.4-8.5%) are somewhat higher compared to MIS 6. Willow (*Salix* 1.5-4.6%) is also present in small amounts. *Sphagnum* abundances ranged from 4.6% to 10.9%. Low P_{est} values (7, 6, and 9) correspond to peak warming periods within MIS 5, including stages 5.4, 5.3 and 5.1 (Figure 9). Such low values indicate relatively wet conditions, but stage 5.5 appears to have been relatively dry. With the exception of the samples at 96.6 and 77.7 kya, total pollen concentrations are low compared to MIS 6, decreasing to 3,471.89 grains per cm^3 at the end of MIS 5 (73.9 kya). The lowest concentrations within MIS 5 occur at 89.3 kya with 3,247.60 grains per cm^3. Two peaks in concentrations occur at 96.6 kya (21,214.65 grains per cm^3) and 77.7 kya (24,153.86 grains per cm^3) (Figure 10). The peak at 96.6 kya corresponds to substage 5.3. Influx data resembles concentrations in that values are lower than those for MIS 6, with a peak of 775,451 grains/cm^2/yr at 96.6 kya and another of 840,209 grains/cm^2/yr at 77.7kya (Figure 11).

3.1.3 MIS 4 (71-57 kya)

Two samples were examined from MIS 4. Estimated ages are 69.2 kya and 59.8 kya. Percentages of grass (Poaceae 27.7%, 29.1%) and sedge (Cyperaceae 35%, 31.4%) are less variable than those from MIS 5. Percentages of birch (*Betula* 15.5%, 15.5%) are higher within MIS 4 than in ten of the fifteen samples from MIS 5, but eight samples from MIS 5 have higher percentages of alder than the MIS 4 samples (*Alnus* 10.6%, 8.9%). Percentages of spruce (*Picea* 2.4%, 2.7%) are lower in MIS 4 than in eleven samples from MIS 5. Small quantities of willow (*Salix* 4.9%, 4.9%) are again present.

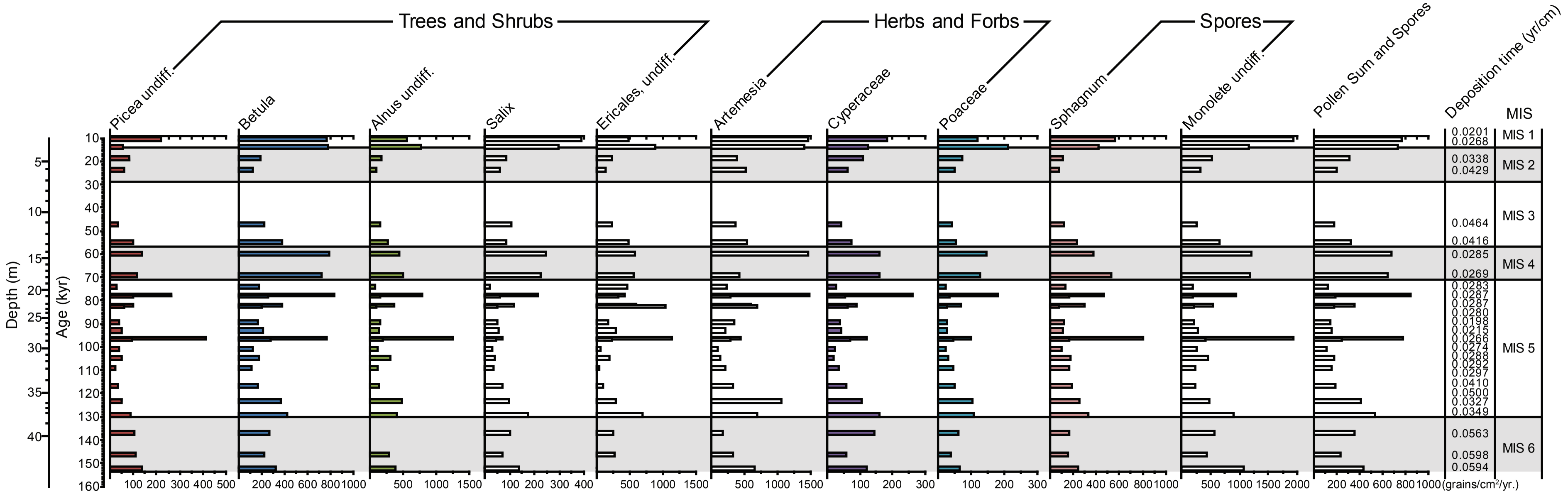

Figure 11. Influx (grains/cm^2/yr) of selected taxa from IODP Expedition 323 site U1343 samples. All columns start at zero and scales vary. All values are divided by 100.

Sphagnum percentages are 8.2% and 5.6%, and P_{est} values vary from 9 at 69.2 kya to 13 at 59.8 kya. Total pollen concentrations were generally high compared to most of MIS 5, ranging from 17,541.46 grains per cm^3 at 69.2 kya and 19,359.44 grains per cm^3 at 59.8 kya (Figure 10). Influx values remain relatively high within MIS 4: 651.398 grains/cm^2/yr at 69.2 kya and 678.656 grains/cm^2/yr at 59.8 kya (Figure 11).

3.1.4 MIS 3 *(57-29 kya)*

Two samples fall within MIS 3. The estimated ages are 54.8 kya and 47.4 kya. Grass (Poaceae 22.2%, 27.9%) and sedge (Cyperaceae 32.4%, 29.7%) abundances are relatively low compared to MIS 4. Birch (*Betula* 16.4%, 15.3%), alder (*Alnus* 11.4%, 11.3%) and spruce (*Picea* 4.2%, 2.3%) are generally more abundant than they are in the MIS 4 samples. Minor percentages of willow (*Salix* 3.8%, 7.5%) are again present. *Sphagnum* percentages are 7.4% and 6.7%. P_{est} values range from 9 at 54.8 kya to 12 at 47.4 kya. Total pollen concentrations are low compared to MIS 4: 13,327.76 grains per cm^3 at 54.8 kya and 8,346.95 grains per cm^3 at 47.4 kya (Figure 10). Influx values also remain relatively low within MIS 3, with 320,189 grains/cm^2/yr at 54.8 kya and 179,702 grains/cm^2/yr at 47.4 kya (Figure 11).

3.1.5 MIS 2 (29-14 kya)

Two pollen assemblages were evaluated from MIS 2, with estimated ages of 23.8 kya and 18.7 kya. Grass (Poaceae 30.9%, 28.8%) and sedge (Cyperaceae 38.7%, 43.9%) percentages increase relative to MIS 3. However, birch (*Betula* 7.5%, 7.6%), alder (*Alnus* 6.3%, 6.7%) and spruce (*Picea* 3.6%, 3.3%) abundances decline. Small quantities of willow (*Salix* 3.8%, 3.3%) were again present. *Sphagnum* abundances were 3.7% and 3.4%, and P_{est} values peak, reaching 22 at both 23.8 kya and 18.7 kya. Total pollen concentrations are generally low compared to MIS 3: 8,611.11 grains per cm^3 at 23.8 kya and 10,657.85 grains per cm^3 at 18.7 kya (Figure 10). Influx values also remain relatively low, with 200,576 grains/cm^2/yr at 23.8 kya and 315,409 grains/cm^2/yr at 18.7 kya (Figure 11).

3.1.6 MIS 1(14-0 kya)

Two samples represent pollen assemblages from MIS 1. The estimated ages are 13.7 kya and 10.7 kya. Grass (Poaceae 37.8%, 22.5%) and sedge (Cyperaceae 22.5%, 35.4%) proportions are low compared to the samples from MIS 2. Meanwhile, percentages of birch (*Betula* 13.8%, 14.7%), alder (*Alnus* 13.8%, 11%) and spruce (*Picea* 0.9%, 4.2%) increase relative to MIS 2. Minor percentages of willow (*Salix* 5.3%, 7.5%) were again present. *Sphagnum* abundances were 5.8% at 13.7 kya and 7.4% at 10.7 kya, corresponding to P_{est} values of 13 and 9, respectively. Pollen concentrations are high relative to MIS 2: 19,551.67 grains per cm^3 at 13.7 kya and 15,399.39 grains per cm^3 at 10.7 kya (Figure 10). Influx values are also high, with 730,499 grains/cm^2/yr at 13.7 kya and 767,403 grains/cm^2/yr at 10.7 kya (Figure 11).

3.2 Pollen in U1339

Four samples from U1339 were examined, with estimated ages of 21.2 kya, 27.7 kya, 58.4 kya and 89.2 kya (Figure 12). Two samples representing MIS 2 (21.2 kya, 27.7 kya) have high grass (Poaceae 19.9%, 27.3%) and sedge (Cyperaceae 30.4%, 33.9%) percentages relative to birch (*Betula* 7.3%, 4.7%), alder (*Alnus* 5.9%, 5.2%) and spruce (*Picea* 4.2%, 1.8%). MIS 2 samples from site U1339 record 1% differences in alder and spruce and 9% differences in sedge compared to MIS 2 samples from site U1343. One sample represents MIS 4 (58.4 kya). Percentages of grass (Poaceae 14.7%) and sedge (Cyperaceae 26.2%) are higher than birch (*Betula* 8.5%) alder (*Alnus* 6.5%) and spruce (*Picea* 2.1%). Site U1339 shows consistently lower percentage values of grass (<14%) than U1343 samples during MIS 4. One sample represents MIS 5 (89.2 kya). Grass (Poaceae 22.3%) and sedge (Cyperaceae 32.2%) proportions are consistently higher than birch (*Betula* 7.1%) alder (*Alnus* 7.1%) and spruce (*Picea* 1.2%). These abundances fall within the ranges recorded for these taxa from site U1343 during MIS 5. However, this correspondence is not surprising, given that I am comparing one sample from U1339 to 15 samples from U1343. Slight differences between abundances of taxa from roughly coeval samples from sites U1339 and U1343 could be due to the number of grains counted for each site (≥300 pollen grains per sample for U1343 and ≥200 pollen grains

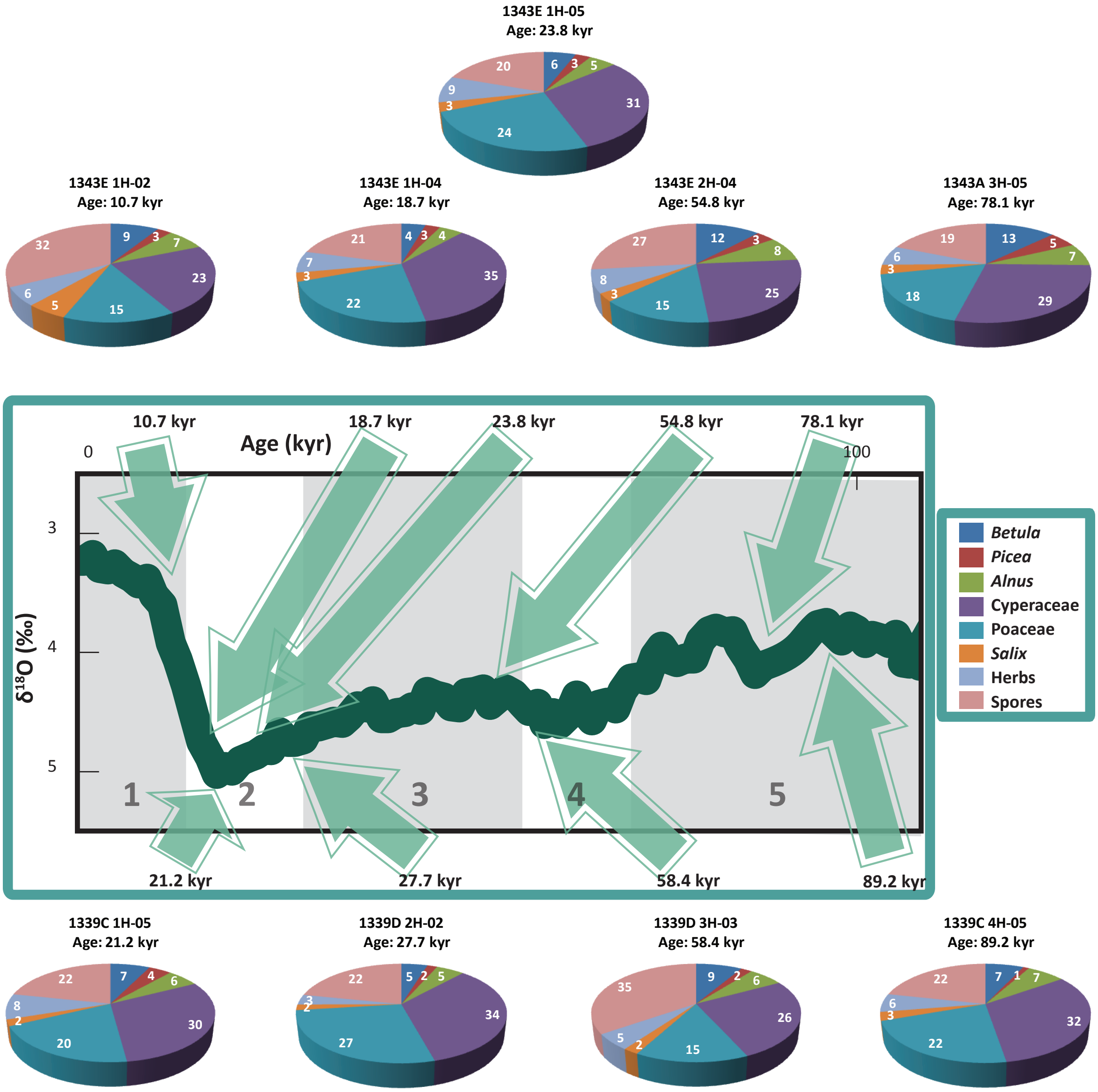

Figure 12. Abundance (percent total identified) of selected taxa from IODP Expedition 323 sites U1343 and U1339. Preliminary results shown here focus on samples from the last 100 kyr. Assemblage data are based on identification of at least 200 pollen grains per sample. The pollem sum includes all identified pollen grains and spores. Lengend on the right denotes selected taxa. Tie points (at 21 kyr, 27-28 kyr and 57-58 kyr) between site U1339 and U1343 indicate similar taxa percentages.

per sample for U1339), differences in the ages of the samples, or differences in pollen influx at the sites (Table 3). In general, both sites record high percentages of sedge and grass and small but persistent frequencies of birch, alder and spruce (Figure 12).

3.3 PCA of modern and fossil samples

I generated four PCA ordination diagrams (Figures 13, 14, 15, and 16) to demonstrate similarities and differences between modern surface assemblages and my IODP samples. The dominant taxa plot far from the center of the diagram; these include Poaceae, Cyperaceae, *Betula*, *Picea*, *Alnus* and monolete spores. For Figures 13-15, Axis 1 is driven by high percentages of *Picea* or Cyperaceae while Axis 2 is influenced heavily by *Alnus*, *Picea* and monolete spores. Figure 13 classifies the modern data by sample site, including lacustrine, peat, moss polster and unclassified sample sites. These categories are indicators of local (i.e. peat and moss polster) versus regional (i.e. lacustrine) sources of pollen and spores. Lacustrine and peat samples do not cluster together, but appear throughout quadrants I, II, III, and IV.

Figure 14 displays modern surface samples classified as forest or tundra according to the biome surrounding the collection site. Samples from forest and tundra biomes are highlighted with envelopes. Forest samples cluster within quadrants II and III. Four outliers, TA021, S176, TA026, and S116, are evident among the forest samples. Samples from the tundra biome can be found in all quadrants, contain high values of Poaceae, Cyperaceae and monolete spores, are influenced to a lesser degree by *Alnus* and *Picea*, and do not include obvious outliers.

Figure 15 categorizes the biome surrounding the modern surface sample sites more precisely as herbaceous tundra, herbaceous shrub tundra, shrub tundra, spruce forest, and mixed forest (i.e. both deciduous and coniferous forest types). Table 2 lists each vegetation classification relevant to my study, provides a brief description of typical taxa found within each, and identifies the biome represented by each vegetation type. Mixed forest and spruce forest samples cluster mainly in quadrant III, indicating high percentages of both *Picea* and *Betula*. Samples from herbaceous tundra fall within quadrants I and IV and are dominated by Cyperaceae and Poaceae, while herbaceous

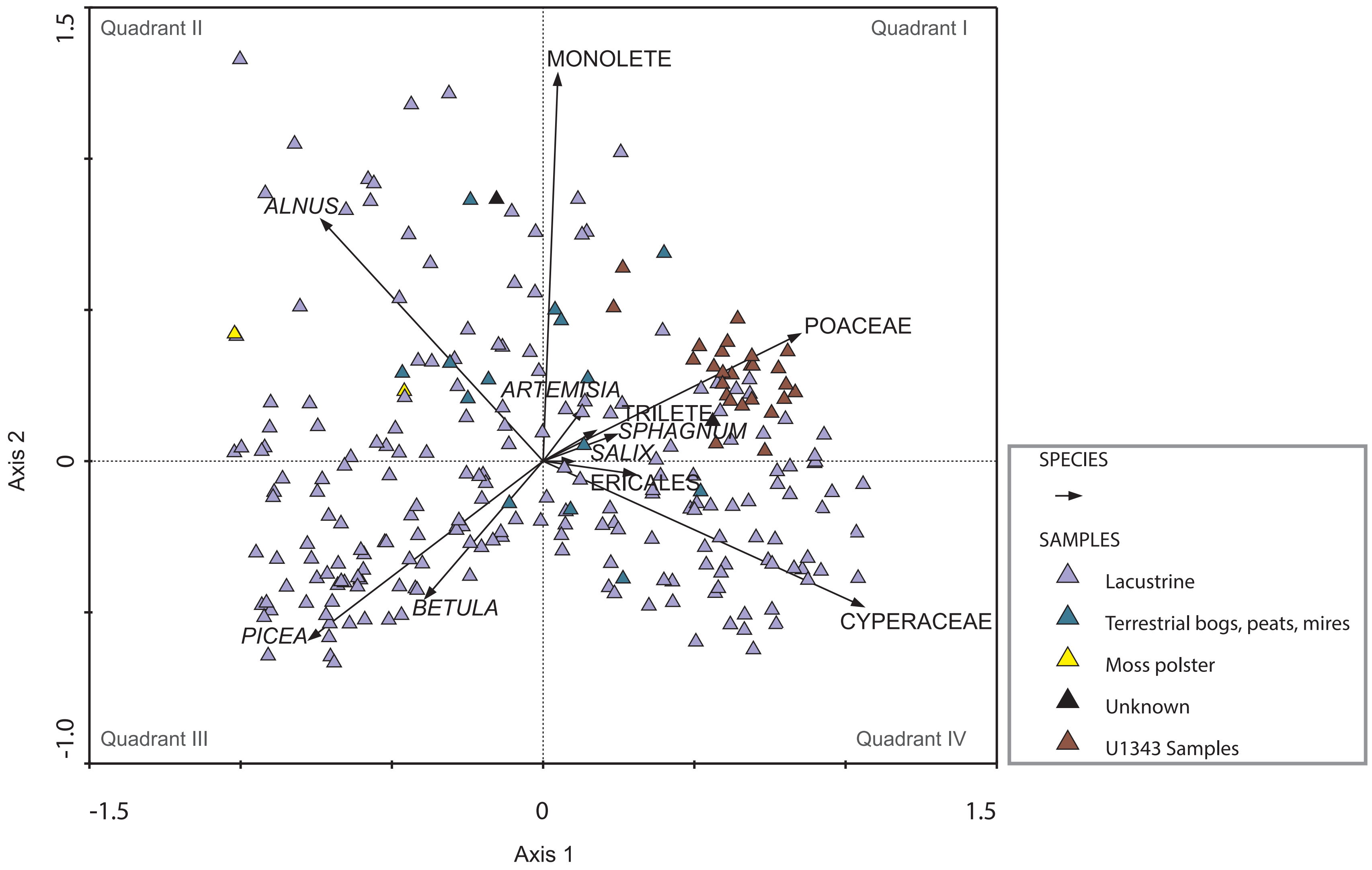

Figure 13. Simple ordination plot using Principal Components Analysis (PCA) showing U1343 samples plotted with modern surface samples classified into lacustrine, and moss polster, and terrestrial bogs, peats, mires, and unknown sites. Relevant taxa marked by arrows.

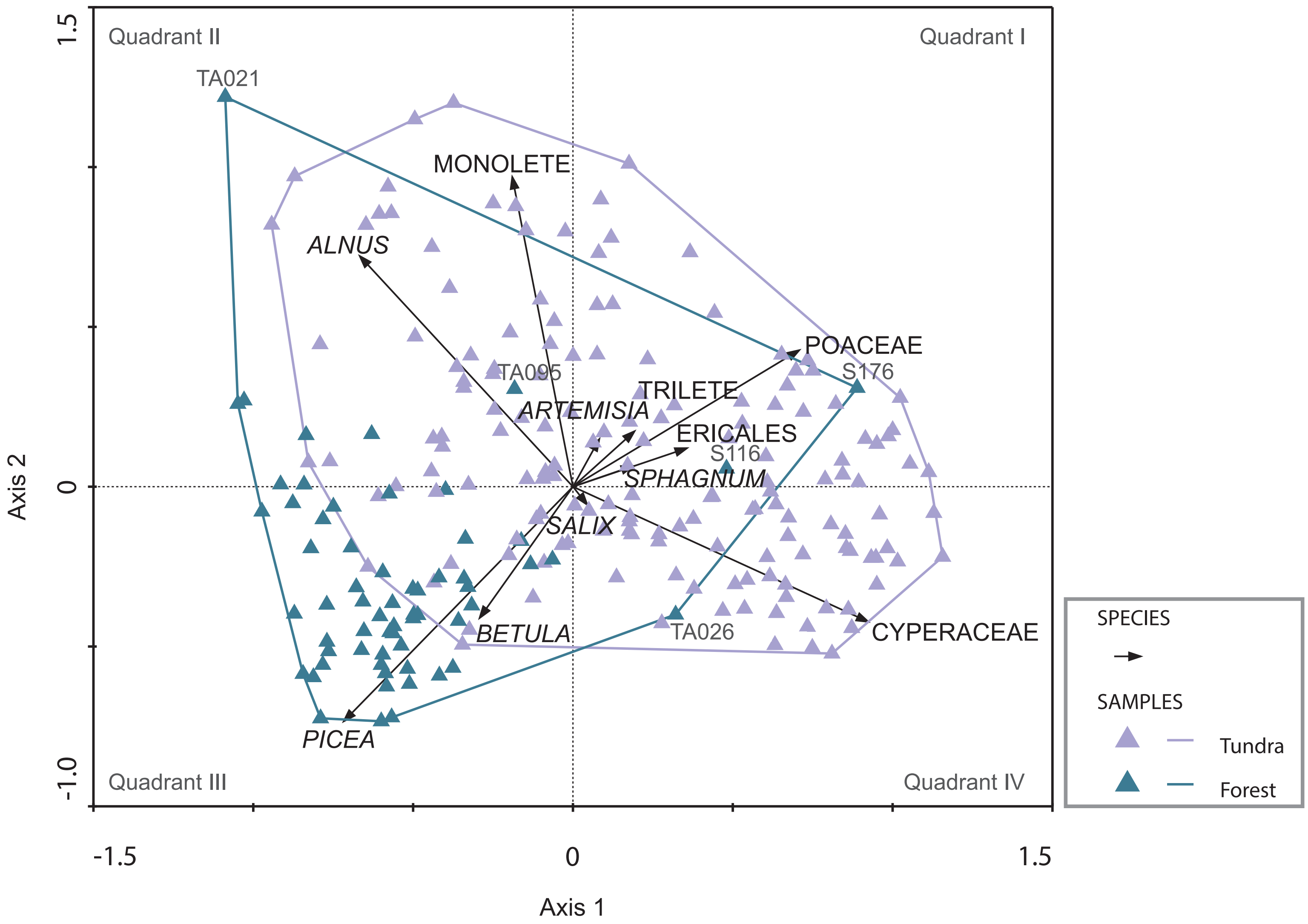

Figure 14. Simple ordination plot using PCA denoting surface samples classified into tundra vs. forest biomes with envelopes. Pertinent taxa designated by arrows. Five samples (i.e. TA021, S176, TA026 and S116) indicated on biplot are all found in or near the forest/tundra ecotone.

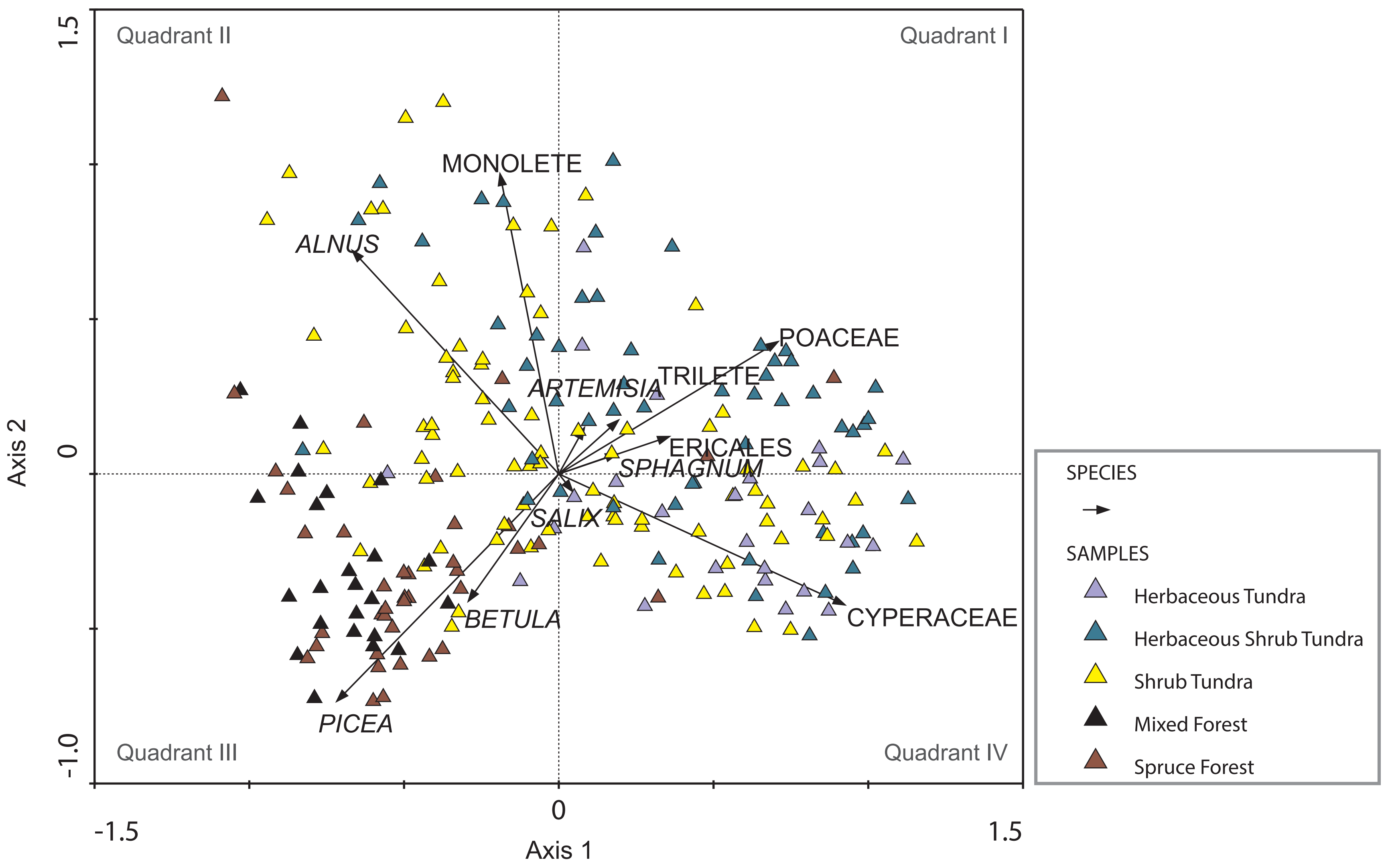

Figure 15. Simple ordination plot using PCA showing surface samples classified into herbaceous, herbaceous shrub, shrub tundra vs. mixed and spruce forest biomes. Selected taxa expressed by arrows.

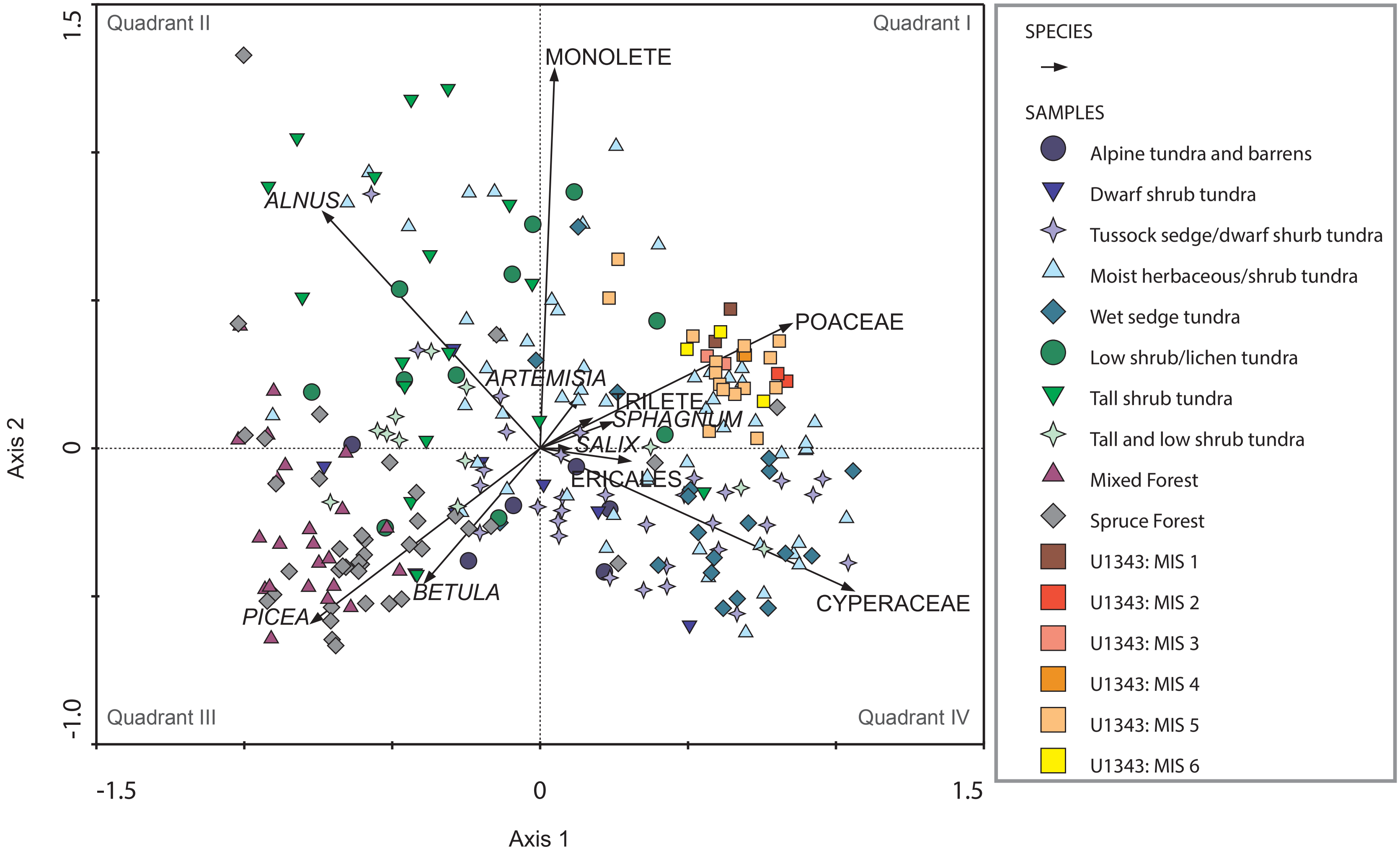

Figure 16. Ordination plot constructed using PCA showing U1343 samples, grouped by marine oxygen isotope stages (MIS), plotted with modern surface samples categorized into eight specific tundra classifications (i.e. alpine tundra and barrens, dwarf shrub tundra, tussock sedge/dwarf shrub tundra, moist herbaceous/shrub tundra, wet sedge tundra, low shrub/lichen tundra, tall shrub, and tall and low shrub) vs. mixed and spruce forest. Relevant taxa designated by arrows.

shrub tundra is located primarily within quadrants I, II and IV, corresponding to high values of Poaceae, *Alnus*, and Cyperaceae, respectively. Samples from shrub tundra span all quadrants, indicating a range of dominant taxa including Poaceae, Cyperaceae, *Betula*, *Picea*, *Alnus* and monolete spores.

Figure 16 plots the surface sample dataset with the U1343 samples. The range of Axis 1 is governed by *Picea* and Cyperaceae while Axis 2 is determined by monolete spores. Cyperaceae and *Betula* are driving the distribution of surface samples categorized as alpine tundra and barrens in quadrants III and IV. Dwarf shrub tundra sites plot near the Cyperaceae, *Alnus* and *Picea* vectors, while tussock sedge/dwarf shrub tundra sites typically have higher percentages of *Alnus* and *Betula.* Cyperaceae, Poaceae and monolete spores dominate surface samples classified as moist herbaceous/shrub tundra. The majority of wet sedge tundra sites contain abundant Cyperaceae and plot in quadrant IV, while samples classified as low shrub/lichen tundra have high percentages of Poaceae, Cyperaceae, monolete, and *Alnus* and plot in quadrants I and II. The distribution of tall shrub tundra sites are determined by high percentages of *Alnus*, monolete spores, *Picea*, and *Betula* and plot primarily in quadrants II and III. Finally, surface samples of tall and low shrub tundra sites have high percentages of both Cyperaceae and *Alnus* and plot in quadrants II, III and IV. U1343 samples cluster within quadrant I due to high percentages of Poaceae and monolete spores. Surface assemblages clustering around U1343 are classified as moist herbaceous/shrub tundra vegetation.

Chapter 4: Discussion

4.1 Possible biases in pollen analysis

This analysis is subject to several limitations, the most significant of which is the presence of reworked grains. All pollen and spores are potentially subject to reworking (Traverse, 2007). Reworked grains with different thermal histories were identified and highlighted through the addition of safranin O stain. Reworked grains did not absorb the safranin O stain and appeared brown or dark yellow, whereas most of the grains were visibly pink and/or red. However, such reworked grains were relatively rare, ≤20 out of >300 total grains. Brubaker et al. (2005) cited several lines of evidence for limited abundances of reworked pollen, including differences in glacial vs. interglacial assemblages and synchronous pollen production. Samples from site U1343 reveal consistent differences between glacial and interglacial stages. For example, samples from MIS 1 and 5 have different abundances of dominant taxa; they contain more *Betula*, *Alnus* and *Picea* and less Cyperaceae and Poaceae than samples from MIS 2. Furthermore, preservation of both herbaceous pollen and tree and shrub pollen indicates simultaneous pollen production. Therefore, I conclude that the majority of grains in my IODP samples are not reworked, and hence the assemblages do not represent mere averages of the Pleistocene vegetation.

Another limitation is the fact that, during unfavorable conditions, vegetation has a propensity not to pollinate (Faegri and Iversen, 1989), reproducing vegetatively instead. For instance, when temperature and/or precipitation conditions become marginal, spruce can reproduce vegetatively and not produce pollen. Therefore, low abundances of spruce pollen can indicate either that spruce is reproducing vegetatively or that spruce trees are not abundant on the landscape (Nienstaedt et al., 1990; Viereck et al., 1990). According to Brubaker et al. (2005), Beringia contained “cryptic refugia” where individual tree and shrub taxa survived marginal conditions in small populations rather than migrating together as forest biomes.

A third limitation is data resolution. The U1343 samples presented herein only capture general vegetation trends at ~10 kyr intervals. A higher resolution data set is necessary to address questions of temporal variability and rates of vegetation change. Brief variations in vegetation could occur between sample sets.

The final limitation of pollen analysis centers on potential operator error. Analyst error will affect the overall count of pollen grains within each sample. I counted all the samples myself, and I was consistent in my counting and identification protocols, thus minimizing the margin of error. Pollen grains that were crumpled, crushed or damaged beyond identification (<50 grains per sample) were tallied separately (see Unknown column in Figure 9). These grains were photographed and later viewed by Dr. Fowell, who was occasionally able to identify a grain, but generally agreed that the grains could not be accurately identified.

4.2 Vegetation reconstruction from MIS 1-6

My samples indicate that graminoid-herb tundra, comprised mainly of grass and sedge, was the dominant vegetation cover on coastal, south-central Beringia during MIS 1-6. Minor but consistent abundances of *Betula*, *Alnus* and *Picea* in all samples suggest that these boreal taxa survived Pleistocene glacial stages in cryptic coastal refugia. Locally or regionally mesic conditions are indicated by the presence of *Sphagnum* (3.4-10.9%), resulting in P_{est} values between 6 and 10 during MIS 1, 3, 4, and 5 (Figure 9). According to White et al. (1997), there is a correlation between site paludification and temperature, with less saturation during colder times. My IODP samples display a similar temperature and paludification relationship; P_{est} values peak during glacial stages (MIS 2 and 6) indicating minimal paludification at these times. Such differences may be the result of changes in the extent of regional sea-ice cover. Sea-ice cover expands as temperatures decrease, limiting regional evaporation (Guthrie, 2001) and decreasing paludification during cold intervals.

4.2.1 MIS 6

My IODP samples indicate the presence of sedge and grass in greater percentages compared to birch, alder and spruce in MIS 6. Also, P_{est} values suggest that south-central Beringia experienced relatively dry conditions during MIS 6, though not as dry as MIS 2 (Figure 9). Evidence for graminoid-tundra vegetation on the BLB differs from the steppe tundra vegetation present around Birch Creek and Ky-11 in interior Alaska. These sites record herb-dominated taxa such as willow, sedge, grass and ericaceous shrubs with trace amounts of trees (Bigelow et al., 2014). These differences may indicate an absence of trees and shrubs in interior Alaska relative to coastal locations on the BLB during this glacial stage.

4.2.2 MIS 5

Compared to MIS 6, abundances of birch, alder and spruce increase during MIS 5 while percentages of grass and sedge are more variable. P_{est} values indicate wetter conditions during peak warming events, particularly 5.4, 5.3 and 5.1 (Figure 9). MIS 5 samples from Squirrel Lake, Imuruk Lake and Ky-11 reveal significant differences (Bigelow et al., 2014; Schweger and Matthews, 1985; Berger and Anderson, 2000). Whereas my assemblages record the presence of *Picea, Betula* and *Alnus* in similar percentages throughout MIS 6 and 5, the abundances of these taxa increase from MIS 6 to 5 at Ky-11 (Schweger and Matthews, 1985). This could be the result of differing site geography. U1343 is a lowland coastal site, while Ky-11 is located at higher elevation in eastern Beringia. It is conceivable that the boreal forest biome was located further inland during MIS 5, just as it is today. Squirrel Lake and Imuruk Lake are also located at higher elevations in eastern Beringia; pollen records from both sites note an increase in *Betula*, *Picea* and *Alnus* during MIS 5 compared to MIS 6 (Berger and Anderson, 2000). At Imuruk Lake, an increase in *Sphagnum* compared to *Artemisia* is also recorded during MIS 5 (Shackleton, 1982). My IODP samples show the same: higher percentages of *Sphagnum* compared to *Artemisia* during MIS 5 indicate relatively mesic conditions.

4.2.3 MIS 4

Grass and sedge increase during MIS 4 compared to MIS 5. Although *Sphagnum* (8 and 10.9%) is more abundant than *Artemisia* (1 and 2%) in both MIS 4 samples, P_{est} values indicate mesic conditions at 47.4 kya and relatively dry conditions at 54.8 kya (Figure 9). Assemblages from Imuruk Lake also record an increase in Cyperaceae and Poaceae, with decreasing *Alnus*, *Picea* and *Betula*, between 71 and 57 kya (zone i_2 of Schakleton, 1982). However, Shackleton (1982) noted an increased presence of *Artemisia* and little evidence of *Sphagnum*. This disparity can be attributed to differences in elevation. Shackleton (1982) was sampling a lake site 300m above modern sea level in mainland central Beringia, whereas site U1343 is located off the coast of south-central Beringia, which lay below modern sea level. Guthrie (2001) hypothesized that low cloud cover over the central Beringian lowlands led to more mesic conditions. As a result of higher elevation, Imuruk Lake lay outside the "mesic buckle" and was subject to drier conditions.

4.2.4 MIS 3

Percentages of sedge and grass decrease while proportions of birch, alder and spruce increase during MIS 3 compared to MIS 4 (Figure 9). In their analyses of cores from the margins of the Bering and Chukchi seas, Elias et al. (1996) report similar results. During MIS 3 (40,000 yr BP) they found abundant Cyperaceae (5-13%) and Poaceae (20-46%), along with substantial percentages of *Betula* (15-20%) and *Sphagnum* (5-20%). The abundance of *Sphagnum* in the interior of central Beringia thus exceeds that recovered at U1343 (3.4-7.4%), off the coast of south-central Beringia. However, the results support more mesic conditions on the emergent BLB, as *Sphagnum* is rare or absent in glacial assemblages from eastern and western Beringia (Ager, 2003; Anderson, 1985; Colinvaux, 1964; Shackleton, 1982), further indicating that differences in humidity are correlated to differences in site elevation. Ager's (2003) findings from pollen analysis of Zagoskin Lake on St. Michael's Island (Figure 3) are of particular interest in this regard. Ager (2003) also records assemblages dominated by grass and sedge, but he reports significant percentages of *Artemisia* with little evidence of *Sphagnum* during the late-middle Wisconsin interstadial (MIS 3). Whereas Zagoskin Lake is located in central Beringia, proximal to sites described in Elias et al. (1996), its higher elevation island location may account for the lower humidity suggested by the relative lack of *Sphagnum*.

4.2.5 MIS 2

Relative abundances of sedge and grass increased during MIS 2 compared to MIS 3, while percentages of birch, alder and spruce decreased. Maximum P_{est} values and the minimum ratios of trees/shrubs to herbs/forbs indicate that the environment was relatively dry (Figure 9). Elias et al. (1996) also found evidence of greater aridity on the glacial landscape of central Beringia. 20 kya beetle fossils indicate the presence of relatively dry tundra heaths or dry meadows (Elias et al., 1996).

MIS 2 assemblages from St. Paul Island, near the southern coast of the BLB, differ from the site U1343 samples by having more *Artemisia* and less *Sphagnum*. Based on the presence of grass, sedge and sage, Colinvaux (1981) suggests that the glacial vegetation of St. Paul Island was herb tundra, which is also indicative of a relatively dry environment. As with Imuruk and Zagoskin lakes, the elevation of Cagaloq Lake could account for differences in vegetation cover compared to site U1343. In addition, Cagaloq Lake is located further inland, while site U1343 probably reflects the vegetation of the adjacent coast. Difference in vegetation between site U1343 and Cagaloq Lake may indicate that the west-east moisture gradient (i.e. mesic in the west and arid in the east), as described by Guthrie (2001) and Elias and Crocker (2008), was discontinuous, consisting of a patchwork of mesic and arid habitats, or that small differences in elevation had a significant impact on vegetation cover, or both.

Samples from site U1343 record minor percentages of birch (~8%), alder (~7%) and spruce (~4%) during MIS 2. In a survey of pollen spectra from EB (modern Russia) and WB (modern Alaska), Brubaker et al. (2005) noted similar results with respect to the presence of boreal trees and shrubs during MIS 2 (21-19 kya). *Betula* is consistently present in EB and WB (exceeding 10% at some sites) from 21-20 kya. *Alnus* pollen is also present during the LGM (<5%) throughout EB. Finally, low percentages (<2%) of *Picea* are present in EB between 21 and 13 kya, but this taxon is absent in WB (Brubaker et al., 2005). Results from site U1343 are thus consistent with other sites across EB with respect to the abundance of these boreal taxa.

Other results from EB reveal that *Populus* (0-2%) is exceedingly rare and *Pinus* and *Larix* are absent. *Populus* is present in minute amounts (<1%) along the Brooks Range but absent in WB. *Populus* grains are fragile, do not preserve well, and degrade with increased distance from parent sources. If grains are present within the sample, *Populus* likely grew close by and the grains are not reworked (Edwards and Dunwiddie, 1985; Faegri and Iversen, 1989). Because site U1343 is located offshore, it is understandable that *Populus* does not appear in my IODP samples. Like *Populus*, *Larix* is also difficult to identify and may be under-represented in the pollen record, but it is present in a few LGM sites in WB. *Pinus* is also extremely rare in EB during MIS 2 while present in small amounts (<2%) within WB. It is, therefore, not surprising that *Pinus* and *Larix* pollen are also absent from site U1343.

4.2.6 MIS 1

Percentages of birch, alder, and spruce increased from MIS 2 to 1, while sedge and grass abundances decreased. Increases in *Betula* (from 7.6% to 13.8%) and *Alnus* (from 6.7% to 13.8%) from the LGM to the early Holocene are consistent with results from other EB sites (Figure 9). According to Ager (2003), *Betula*, *Alnus* and *Picea* percentages increased dramatically during the Holocene. An abrupt increase in *Betula* indicates that it was already growing at the site when conditions became more favorable and the climate warmed (Ager, 2003). My data does not indicate a similar abrupt change in *Betula* because the sample resolution is too coarse.

Brubaker et al. (2005) observe that *Betula*, *Picea* and *Alnus* percentages increase during MIS 1 while *Pinus* and *Larix* remain relatively rare in EB. *Betula* exceeded 40% around 13 kya. *Alnus* increases to >30% by 8 kya throughout EB. *Larix* is rare in EB at

10 kya but increases across WB. From 11-7 kya *Pinus* remained scarce (1-2%) in EB, where it is found primarily in southeast Alaska, while increasing throughout WB. These findings support my hypothesis that pollen deposited at U1343 is derived from south-central Alaska rather than Russia or southeast Alaska due to the absence of *Pinus* and *Larix*. On the other hand, Brubaker et al. (2005) records *Populus* increasing (2-5%) in EB while site U1343 samples do not record any *Populus*. This could indicate that *Populus* was absent from south-central Beringia or that transport to site U1343 destroyed the exine of fragile *Populus* grains.

4.3 Pollen Concentrations from MIS 1-6

In general, pollen concentrations are high within MIS 1, 4, 6 and parts of MIS 5 and low within MIS 2, 3 and most of MIS 5 (Figure 10). Influx values reflect the general trends evident from the concentration data. Relatively high pollen concentrations within MIS 6, 4, and the LGM could be due to low sea levels. During glacial stages, sea level was as much as 125m below modern levels, meaning that site U1343 was closer to the coast, allowing more pollen to reach the site. Low pollen concentrations within MIS 2 relative to MIS 6 may also be the result of harsh environmental conditions, which can cause trees and shrubs to produce less pollen. On the other hand, minimum concentrations within MIS 5 could be a result of higher sea level and greater transport distances. It is not likely that MIS 5 concentrations are indicative of the density of the coastal vegetation due to the variability between samples; MIS 5 records from various regions in Alaska suggest abundant vegetation at this time (c.f. Squirrel, Imuruk, Ky-11, Birch Creek) (Anderson, 1985; Colinvaux, 1964; Shackleton, 1982; Schweger and Matthews, 1985; Bigelow et al., 2014; Edwards and McDowell, 1991). The pollen concentration peak at 96.6 kya corresponds to substage 5.3. However, there is no correlation between concentration values and the paludification index, suggesting that pollen concentrations are not driven by changes in humidity. The high influx at 96.6 kya may represent a combination of greater plant density and transport mechanisms that concentrated the pollen at this level. Finally, MIS 1 samples show an increase in pollen concentrations at 13.7 kya and 10.7 kya. This suggests that conditions became more favorable for pollen production of trees and shrubs.

Pollen concentrations in samples from U1343A are consistently higher than those from U1343E. Samples with higher pollen concentrations have less additional material (i.e. diatoms, radiolarians, sponge spicules) while samples with lower pollen concentrations contain more additional material. Therefore, the differences between U1343A and U1343E could be due to differences in the sedimentation rates.

4.4 Pollen transport to U1343

Heusser and Balsam (1977) examined pollen spectra from marine surface sediment samples collected on the continental slope and rise (between 41°13′N and 59°14′N and between 124°42′W and 144°43′W) of the Northeastern Pacific Ocean. They concluded that pollen from coastal vegetation is primarily transported to marine settings by rivers. Pollen concentrations from the continental slope and abyssal plain are inversely proportional to the distance from shoreline for most taxa, and a strong correlation is apparent between vegetation of the nearby coast and pollen abundances for taxa such as *Pinus, Tsuga heterophylla* (western hemlock)*, Picea, Alnus, Quercus* (oak)*, Sequoia* (redwood) and Compositae (daisy and dandelion family). However, percentages of *Pinus* and fern spores (Polypodiaceae) were found to increase with distance from shoreline, perhaps due to the buoyancy of these grains (Heusser and Balsam, 1977). Although *Picea* and *Pinus* are morphologically similar in that both are bisaccate (i.e. consist of a body and two lateral bladders), *Picea* grains are only found proximal to source areas and do not increase in relative abundance with distance from shore. Heusser and Balsam (1977) suggest that *Picea* is not as hydrodynamic as *Pinus*, thus it provides a more reliable record of the coastal vegetation. Because pollen concentrations are highest in areas where fine-grained terrigenous sediment is delivered to the site by rivers, the authors conclude that pollen distribution in marine environments is affected by fluvial transport as well as bottom topography, surface and subsurface currents, oxidation, and the density and composition of vegetation on the adjacent continent (Heusser and Balsam, 1977).

According to Heusser and Balsam's (1977) findings, *Picea* pollen is not preferentially transported long distances in marine settings. The consistent presence of *Picea* in U1343 samples suggests that it was growing on the adjacent coast of Beringia. Furthermore, the lack of exotic taxa such as pine, which is notoriously susceptible to long-distance transport, suggests that the majority of pollen in my IODP samples was locally derived (Anderson and Brubaker, 1986; Campbell et al., 1999). Today pine is present in southeast Alaska but absent from sites further north. Based on the results of Heusser and Balsam's (1977) research and the absence of pine pollen in samples from site U1343, I think it is reasonable to assume that most of the pollen and spores deposited at the site originated from the proximal southern coast of Beringia and not from more distant locations.

4.5 Comparison between modern and fossil samples using PCA

I compared modern surface samples with my IODP samples using PCA to identify modern analogs. Surface samples from Ager, Anderson and Brubaker were collected from different environments, including lacustrine and peat deposits (Bigelow et al., 2003). Peat deposits typically contain autochthonous matter (from within the peat deposit), while lake sediments are derived from both allochthonous (outside the boundaries of the lake) and autochthonous material (Moore et al., 1991). Lake deposits thus record a more regional pollen signal while peat deposits contain a more local signal. However, peat deposits receive pollen from various sources, including long-distance wind transport, air currents below the canopy, pollen nucleating around rain droplets, and groundwater. Lakes receive pollen from the same sources as peat deposits, but a greater proportion of material is transported by water either from rivers or surface runoff (Moore et al., 1991). Figure 13 explores possible differences due to site type and area by distinguishing samples from lacustrine and peat deposits. Samples from both types of sites appear in all quadrants, suggesting that the type of site is not a primary influence on these pollen spectra.

Distinguishing modern surface samples from tundra and forest sites (Figure 14) reveals five distinct outliers. These outliers are all found in or near the forest/tundra ecotone, the transitional area where two plant communities converge and integrate. Sites TA021, TA026 and S176 (Figure 14) are all classified as spruce woodland/shrubs on the modern vegetation distribution map (Figure 17) (Fleming, 1998). Although placed within the forest biome, woodlands are more complex systems consisting of low-density forests with an understory of shrubs and herbaceous plants. TA026, located in the Copper River Basin, is the only outlier classified as spruce woodland/shrubs that is enveloped by a forest biome (i.e. open and closed spruce forest). Despite this general classification, TA026 contains abundant Cyperaceae, *Picea* and Poaceae.

TA021 (spruce woodland/shrub) and TA095 (closed spruce forest), from sites on the Kenai Peninsula, can be merged into a broader category of spruce forests. However, TA021 is in proximity to tall shrub stands while TA095 is along the coast of Cook Inlet. Pollen spectra from these two sites are dominated by *Alnus* and monolete spores. These taxa grow in relatively mesic and warm environments. Site S116, located on the northeast edge of the Seward Peninsula, is within open spruce forest/shrub/bog vegetation next to tall and low shrubs. Site S116 thus occupies a transitional zone between dominance of birch and alder vs. grass and sedge.

S176 is a lake site, located along the lower Kuskokwim River (60.58°N and -162.63°W), adjacent to a spruce woodland stand but enveloped by tundra-dominated biomes including moist herbaceous shrub tundra and low shrub/lichen tundra. The pollen spectra from site S176 is very similar to many of the U1343 spectra (Figure 18). Therefore, site U1343 may have received pollen from coastal vegetation consisting of isolated stands of birch, alder and spruce surrounded by grass and sedge tundra during glacial and interglacial stages.

Surface samples from the tundra biome are highly variable, plotting in all quadrants (Figure 15). In order to understand this distribution, I grouped surface samples into five specific biomes that included (1) herbaceous tundra, (2) herbaceous shrub tundra, (3) shrub tundra, (4) mixed forest and (5) spruce forest. The ordination diagram

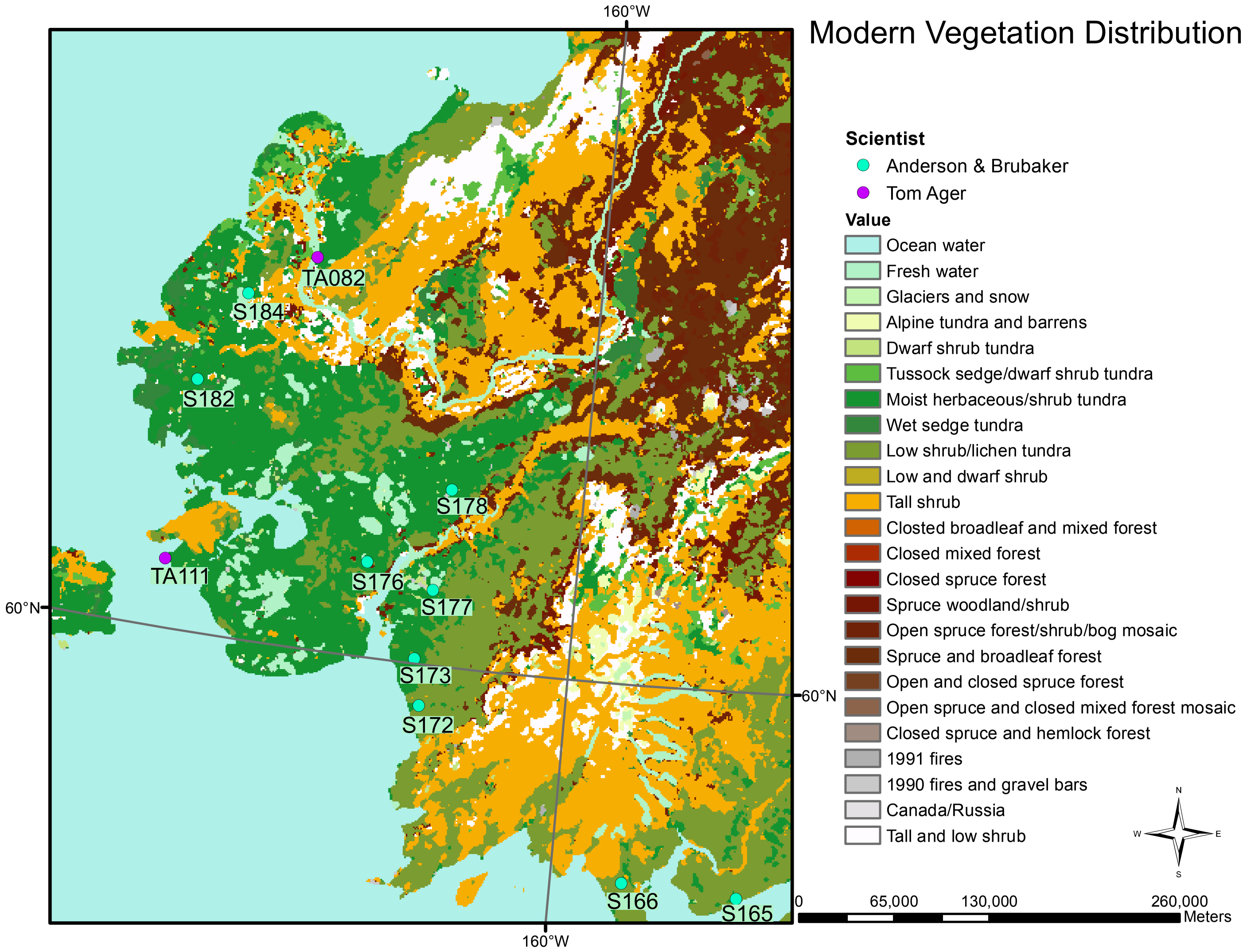

Figure 17. Modern vegetation distribution of Alaska with 11 highlighted surface samples defined as moist herbaceous shrub tundra. Surface sample data is provided by Tom Ager, and Pat Anderson and Linda Brubaker (Modified from: Fleming, 1998).

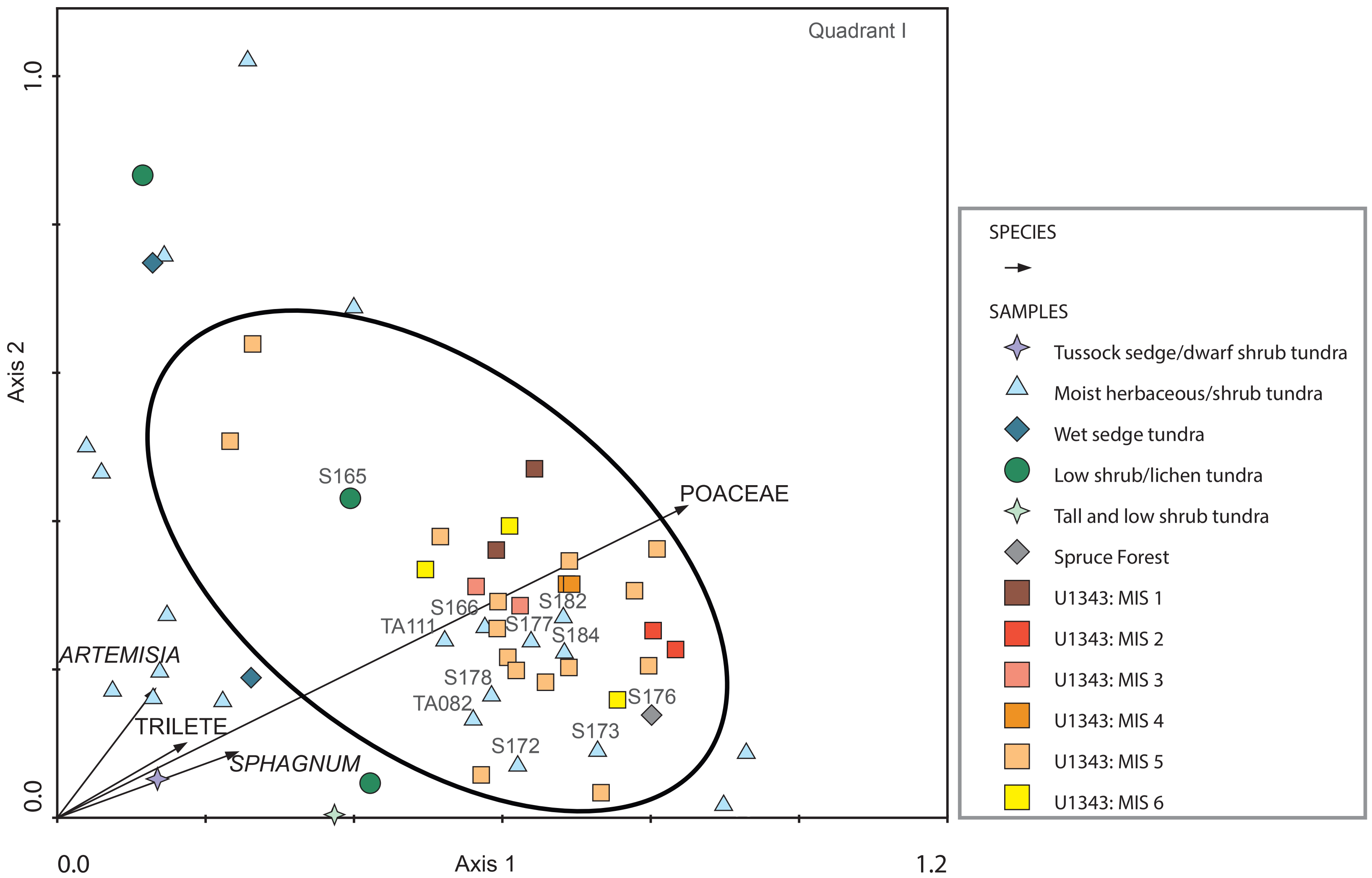

Figure 18. PCA ordination diagram of Quadrant I showing U1343 samples, grouped by MIS, plotted with modern surface samples categorized into eight specific tundra classifications vs. mixed and spruce forest. Circle denotes modern samples that resemble U1343 samples in terms of taxa. Pertinent taxa expressed by arrows.

indicates that shrub tundra is a highly variable biome with an assortment of dominant taxa including Cyperaceae, Poaceae, *Alnus* and monolete spores. More tightly clustered samples, from biomes such as mixed forest and spruce forest, are dominated by *Picea* and *Betula* and contain few tundra taxa such as Poaceae and Cyperaceae.

The modern surface samples capture the variability of the Alaskan vegetation. The best modern analogs for site U1343 samples are from moist herbaceous/shrub tundra (Figures 16 and 18). My IODP samples contain very low percentages of *Picea* and *Betula*. Thus these taxa do not greatly influence the distribution of my samples on the ordination graph. Dominant taxa are Poaceae and Cyperaceae. The U1343 samples all cluster within quadrant I, indicating low variability through time (152.2-10.7 kyr) (Figure 18). This suggests that the vegetation of the southern margin of Beringia during glacial intervals was similar to that of the modern southwestern coast of Alaska during interglacial stages. In addition, Figure 18 reveals no visible gradational relationship between the site paludification index (a proxy for moisture) and dominant taxa. For example, MIS 2 samples indicate relatively dry conditions and cluster together. However, samples that plot nearby specify a relatively wet environment.

I used the ordination plots to identify modern analogs of my IODP samples and plotted these sites on the modern vegetation map of Alaska (Figure 17). Figure 17 suggests that the coastal vegetation proximal to site U1343 was similar to that of modern western Alaska in the Yukon/Kuskokwim drainage, possibly indicating that the majority of palynomorphs were transported to site U1343 by rivers. My IODP samples are thus indicative of a strong coastal signal and fluvial-dominated transport.

4.5.1 Modern climate of the Yukon/Kuskokwim delta

It is possible to make inferences concerning the climate at site U1343 based on the climate of the region where the closest modern analogs are found. The villages of Bethel, Quinhagak, Eek, and Chevak are proximal to modern surface sample sites plotted on Figure 17. Bethel maintains a 30-year climate record (from 1981 to 2010) on the Yukon-Kuskokwim delta. Records indicate a mean annual temperature for Bethel of -

0.7°C, a mean July temperature of 13.4°C and a mean January temperature of -14.11°C. The mean annual precipitation is 470.9mm. Most of the rain falls during the months of July, August and September (59.9mm, 82.5mm and 69.9mm respectively) (The Alaska Climate Research Center, 2013). In Alaska, the distribution of boreal forest taxa (i.e. spruce, birch and alder) appears to be determined primarily by temperature. Shrub birch (*Betula nana*) survives in areas where the mean July temperature is more than 4.5°C (typical of coastal locations), alder appears where the mean July temperature is warmer than 6.7°C and tree birch (*Betula papyrifera*) and spruce grow where the mean July temperature is warmer than 9.2°C (typical of more interior locations of Alaska). Based on the modern climate and vegetation data, it is possible that coastal vegetation proximal to site U1343 contained more alder and shrub birch compared to tree birch and experienced warmer summers and cooler winters compared to other sites along the west coast of Alaska (i.e. St Paul and Cold Bay). The vegetation that contributed palynomorphs to site U1343 also received more annual precipitation than modern sites in interior Alaska (i.e. Fairbanks), consistent with a coastal location. Although there are small but consistent differences between glacial and interglacial samples from site U1343, the modern analogs are very similar, probably because the site records coastal vegetation cover throughout glacial and interglacial cycles.

4.6 Refugium hypothesis and the moisture gradient

Site U1343 contains an abundance of *Sphagnum* (a mesic indicator) along with minor abundances of boreal trees and shrubs (i.e. spruce, birch and alder). These data suggest that the trees and shrubs remained within Beringia during MIS 2 and 6. This result is consistent with the findings of Brubaker et al. (2005) and Elias and Crocker (2008) on boreal refugia. According to Brubaker et al. (2005), minor but consistent abundances of spruce, birch and alder at sites in EB suggest that these trees and shrubs survived MIS 2 within Beringia. Because increases in these taxa during MIS 1 are concurrent with climatic changes (Brubaker et al., 2005), they infer that these taxa did not migrate long distances (south of 50°N) as the ice retreated. Elias and Crocker (2008) suggest that a west-east moisture gradient (more moisture on the lowlands of the BLB and less moisture near interior Alaska) existed across central Beringia during the LGM. Site U1343, located along the southern coast of Beringia, contains *Sphagnum* spores and pollen of boreal trees and shrubs, indicating locally mesic conditions compared to sites in eastern Beringia and sites at higher elevation in central Beringia. These inferences have implications for human migration into North America, DNA evidence suggests that there was a pause in the migration between Siberia and regions south of the ice sheet in North America (Tamm et al., 2007). The pause may have occurred in Beringia, possibly in the region now submerged by the Bering Sea (Hoffecker et al. 2014). If that is the case, the data presented here suggests that southern Beringia, with its mesic and probably woody vegetation, could have supported a long-term human population prior to further southward migration.

Chapter 5: Conclusions

5.1 Key Points

Palynological assemblages from IODP Expedition 323 site U1343 indicate a glacial refugium existed during MIS 2. Pollen and spore analyses suggest:

(1) Trees and shrubs including birch, alder and spruce were probably present on the land bridge throughout glacial stages. However, they were not present in large numbers on the adjacent coast.

(2) During glacial stages, the dominant vegetation along the south central Beringian coast consisted of grass, sedge and spore-producing plants such as *Sphagnum* and ferns.

(3) Significant abundances of ferns in conjunction with minor percentages of tree and shrub pollen are indicative of relatively mesic conditions compared to localities in eastern Beringia.

(4) Minimum site paludification ratios and the lowest shrub/herb ratios indicate that the LGM (MIS 2) was drier, and woody plants were less common.

(5) By comparing surface sample data to U1343 data, it is evident that my IODP samples are similar to samples from modern moist herbaceous/shrub tundra located in the vicinity of the Yukon/Kuskokwim delta (western Alaska).

(6) The lack of exotic taxa subject to long-distance transport by wind (e.g. *Pinus*) indicates that pollen and spores were transported to site U1343 primarily by Alaskan rivers.

(7) Throughout glacial and interglacial stages, the southern margin of central Beringia remained a relatively wet environment with isolated stands of trees and shrubs surrounded by herbs and forbs.

(8) The overall environment of the BLB was a mosaic of mesic and arid adapted vegetation. In the words of Elias and Crocker (2008), “None of us should take the view that the BLB, or any other large geographic region, was completely dominated by a single type of biological community. All ecosystems, past and present, are made up of patches of varied communities”.

5.2 Avenues for future research

Samples from site U1343 presented herein represent snapshots of the vegetation at a resolution of ~10 kyr. A higher resolution dataset with samples from transitional times (i.e. stage boundaries) is needed to increase understanding of the pace and nature of vegetation changes. In addition, there is a gap in the MIS 3 data. Further analysis of this stage could illuminate the Beringian vegetation cover during one of the less understood interstadials (Anderson and Lozhkin, 2001). Furthermore, the youngest sample analyzed from U1343 currently is 10.7 kya. Younger MIS 1 samples could help clarify the relationship between modern vegetation and palynomorphs deposited at site U1343. Unfortunately, surface samples from these sites were sieved, rendering them useless for palynological analyses (C. Zarikian, pers. comm., 2013).

In 2010, IODP cored five sites in addition to U1343 and U1339. It would be particularly beneficial to analyze samples from sites U1345 and U1344, which are located north of site U1343 at the edge of the Bering Sea Shelf, to search for evidence of contributions from WB rivers and vegetation.

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Appendices

A.1 Confirmation letter from Anderson and Brubaker

Request sent by Nancy Bigelow (August 8, 2013)

Dear Linda and Pat,
..… I'm writing to see if it is okay if a student I'm advising (she is cc'ed above) could use your AK surface sample dataset to compare it with her pollen data coming from a Bering Sea core (from just south of the Bering platform, hence the seds are marine). The student's record goes back to early MIS 5, but unfortunately doesn't have anything younger than about 7.5k yr cal. We would like her to compare the Holocene and MIS5e data with the modern AK data, especially from SW Alaska.
I actually have your surface sample dataset on my computer (from the pollen biomising days), so I can just give her the appropriate samples if it is okay with you.
I've attached a pdf of her GSA poster from last Fall. Since then she has filled in some of the gaps and I think the chronology has changed some since then as well.
Cheers,
Nancy

Response sent by Pat Anderson (August 14, 2013)

Hi Nancy:
Sounds fine to me, but of course we will need Linda's input. A lot of work went into that data set so I am happy to see it put to some use. . . . . .
Cheers, Pat

Response sent by Linda Brubaker (August 23, 2013)

Nancy,
I agree. I hope that you and Rachel can make good use of the surface sample data.

A.2 Confirmation letter from Ager

Response sent by Thomas Ager (August 8, 2013)

Hi Nancy,
. . . . .
Of course Rachel Westbrook can use my Alaska surface pollen sample data set for her study, and anyone else is welcome to use it as well. I assumed that once it was used for the biome study, that the entire data set from all sources would be made generally available. But thank you for asking about using the data. . . . .
Best regards,
Tom Ager