

EVIDENCE FOR THE PRESENCE OF MESIC HERBACEOUS SHRUB TUNDRA WITH  
ISOLATED STANDS OF TREES IN SOUTH CENTRAL BERINGIA DURING GLACIAL

STAGES 2 - 16

By

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## Abstract

Palynological analysis of assemblages from the Integrated Ocean Drilling Program (IODP) Expedition 323, Bering Sea Expedition, site U1343, located in deep water adjacent to the Bering Sea shelf edge, permit reconstruction of the terrestrial vegetation of the southern margin of central Beringia. Previous research done by Rachel Westbrook on marine isotope stages (MIS) 1-6 indicates that the southern coast of central Beringia was a glacial refugium for boreal forest vegetation.

This study extends and augments Westbrook's research by analyzing additional samples from IODP site U1343 spanning the last 258 - 615.3 kya, during glacial stages 8, 10, 12, 14, and 16. Grass (Poaceae) and sedge (Cyperaceae) pollen dominate the assemblages with small but persistent amounts of boreal forest taxa, such as alder (*Alnus*), birch and dwarf birch (*Betula* and *Betula nana*), and spruce (*Picea*). A set of modern surface samples forming a transect from the southwestern margin of the Bering Sea shelf to Nome, AK were obtained and analyzed as potential modern analogs for the palynofloral assemblages from site U1343. Low percentages of boreal forest taxa in nearshore samples from this Bering Sea shelf transect reflect the vegetation of the coastal Seward Peninsula and the Yukon/Kuskokim delta, regions dominated by herbaceous tundra with isolated stands of trees. Comparison of modern and fossil assemblages via canonical community ordination indicates that the IODP samples from site U1343 and modern samples from the Bering Sea shelf are most similar to surface samples from lakes and bogs surrounded by moist herbaceous/shrub tundra. These data suggest that boreal forest taxa persisted throughout MIS 8, 10, 12, 14, and 16 on the southcentral Beringian coast, where the vegetation was primarily moist herbaceous/shrub tundra with intermittent stands of trees.



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## Chapter 1: Introduction and background

### *1.1 Expanding on previous work*

Palynological research on MIS stages 2, 4, and 6 from IODP core U1343 was completed by Rachel Westbrook in 2014. Her research used a preliminary, unpublished age model for site U1343 and did not contain palynological analysis of assemblages from glacial stages that preceded MIS 6. This study extends her research and lengthens the palynological record for IODP core U1343 in order to compile a record of vegetation changes on the Bering Sea shelf during MIS 8, 10, 12, 14, and 16. I also recalibrated all of the palynological data with Asahi et al.'s (2016) current age model which places some of the previously analyzed assemblages in different marine isotope stages.

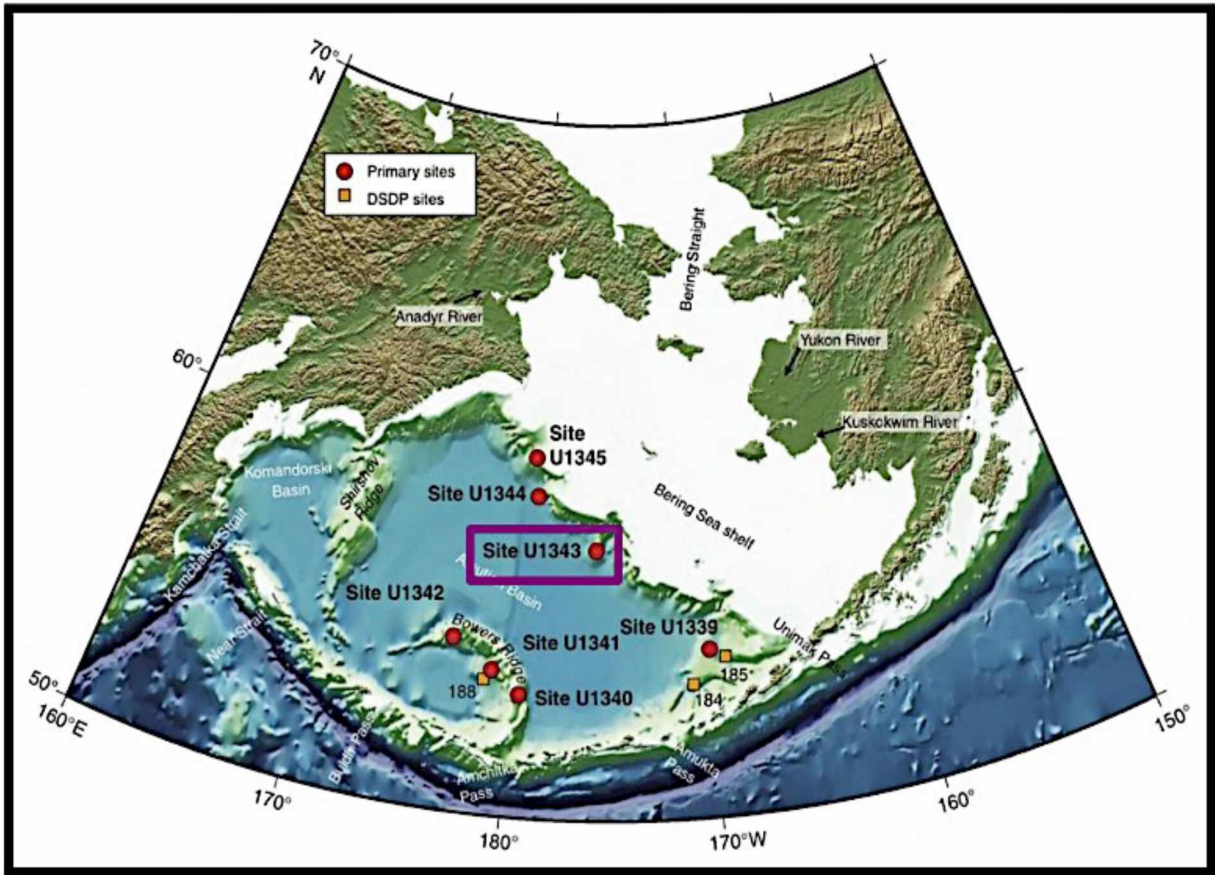
Westbrook's (2014) research indicates that a glacial refugium existed during MIS 2, 3, 4, and 6, as suggested by the presence of tree pollen such as birch, spruce, and alder. Based upon the abundance of fern spores in samples from MIS 1 through 6, she determined that the southern margin of central Beringia remained relatively humid during glacial stages, with a vegetation cover of herbs, forbs, and isolated stands of trees and shrubs (Westbrook, 2014). This differs from reconstructions of eastern and western Beringia, which according to Elias and Crocker (2008) consisted of arid steppe vegetation. However, evidence of increasing humidity at sites proximal to the modern coast suggest that the vegetation of central Beringia may have been more mesic (Elias and Crocker, 2008). In continuing the study of IODP core U1343, my research explores MIS 8, 10, 12, 14, and 16 to determine whether boreal trees and shrubs persisted throughout 676 kya to 243 kya or were present only during the most recent glacial stages. Combined with Westbrook's (2014) data, palynological analysis of the

older glacial stages presented herein provides a record of vegetation changes on the southern margin of central Beringia throughout the last ~600 thousand years (kya).

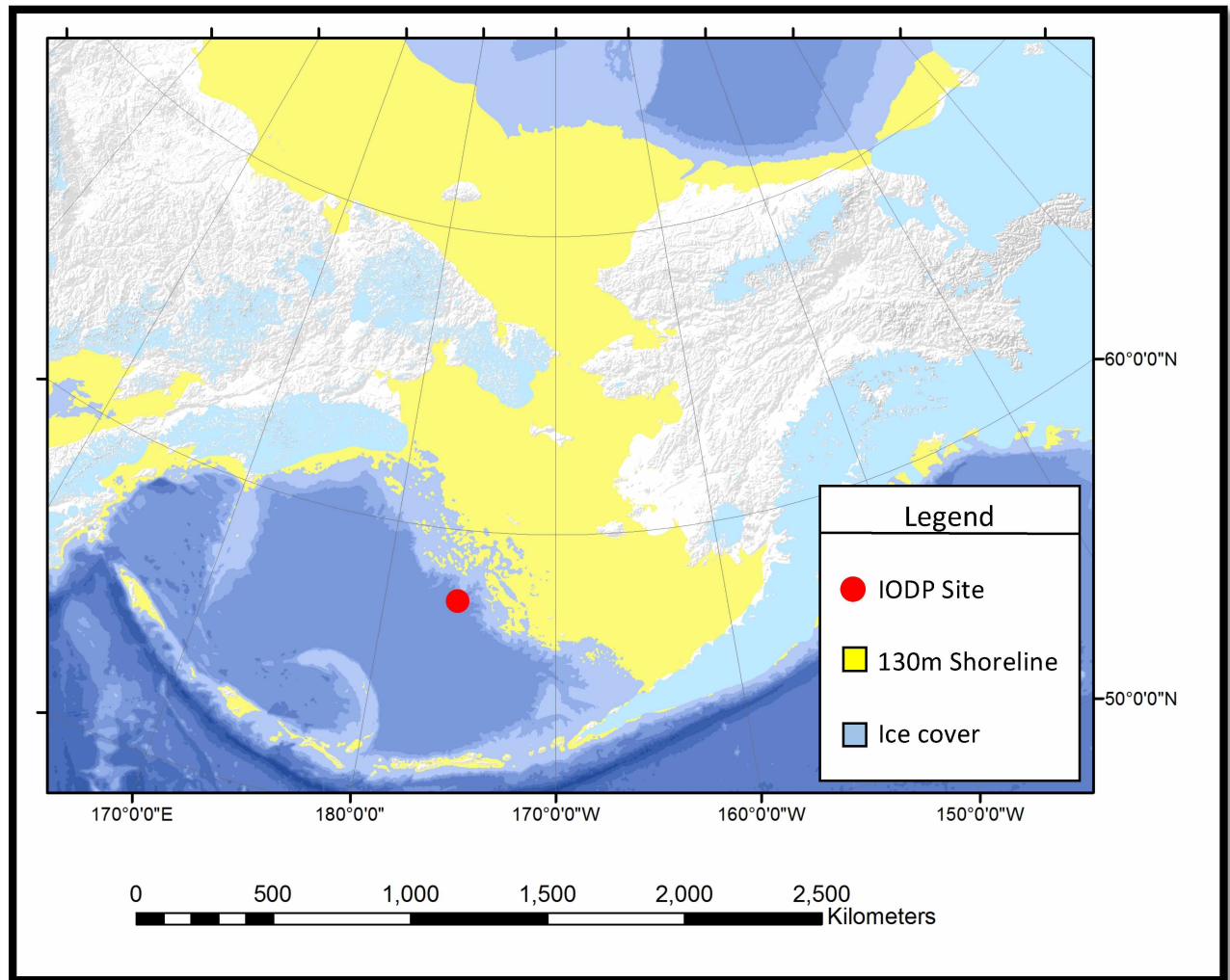
### *1.2 Statement of problem, research questions and hypothesis*

In 2009, through efforts of IODP Expedition 323, seven sites were drilled in the Bering Sea (Expedition 232 Scientists, 2010; Takahashi et al., 2011). Site U1343 is located off the edge of the Bering Sea shelf, about 700 km from today's coastline (Takahashi et al., 2011). During glacial maxima, when sea level was ~130 m lower than modern (Lambeck et al., 2014), this site would have been approximately 100 - 200 km from the paleoshoreline (Figure 1 and Figure 2). Therefore, this site would have been adjacent to the Bering Land Bridge (BLB) during glacial stages and likely received terrestrial runoff, including sediment and plant material, from estuarine and deltaic systems (Heusser and Balsam, 1977; Expedition 323 Scientists, 2010). Therefore, I assume that terrestrial sediment, with constituent pollen and spores, was delivered to this site from the continental margin during glacial stages, when sea level would have been much lower and the site more proximal to shoreline.

In 2010, sediment samples from site U1343 were obtained by Dr. Sarah Fowell for palynological analysis. In 2014, Westbrook completed analysis of selected samples in order to reconstruct the vegetation and climate of the BLB during glacial stages represented by MIS 2, 4, and 6. I am continuing this research and expanding it with the addition of samples from MIS 8, 10, 12, 14, and 16, juxtaposed with a transect of modern surface samples (Bering Sea transect) from sites located between Nome, AK and the western edge of the Bering Sea shelf (Figure 1).



**Figure 1:** IODP Location map with sample site locations. IODP sites are denoted with a red circle and site U1343 is highlighted with a purple box. (Modified from: Westbrook, 2014).



**Figure 2:** Map of Beringia with recreated paleo shorelines (Modified from Ehlers et al., 2011 and Amante and Eakins, 2009).

This palynological research aims to test the following hypotheses, which are based on Westbrook's (2014) prior results:

- 1) The lowlands of central Beringia provided an ice age refugium for boreal trees and shrubs during MIS 8, 10, 12, 14, and 16.
- 2) The ice age vegetation of the southern margin of Beringia was broadly similar from MIS 2 through 16.
- 3) Throughout the last 600 kya, glacial vegetation of southcentral Beringia can be characterized as moist herbaceous tundra with stands of trees, similar to the modern vegetation in the vicinity of the Yukon-Kuskokwim Delta.

### *1.3 Background*

#### *1.3.1 Beringia*

Beringia was a thousand-mile-wide landmass that joined present day Alaska and eastern Siberia during periods of sea level regression during glacial stages throughout the Pleistocene (Martinson et al., 1987; Savva, K., 2014) (Figure 2). Today, Beringia is defined as the land and maritime area bounded on the west by the Lena River in Russia; on the east by the Mackenzie River in Canada; on the north by 72 degrees north latitude in the Chukchi Sea; and on the south by the tip of the Kamchatka Peninsula (National Park Service, 2018). During glacial maxima sea level was at its lowest, up to 130 meters below present day sea level (Lambeck et al., 2014), and Beringia was at its maximum extent. During such glacial maxima, glaciers were located in the Brooks Range and Alaska Range; however, the interior of Alaska and the lowlands of Central Beringia remained ice free (Hamilton et al., 1986; Manley, 2012). IODP site U1343 is adjacent to the southern edge of the continental shelf and therefore it is assumed to contain a record of the

vegetation present on central Beringia's coastal lowlands. Reconstructing the vegetation of the BLB will enhance understanding of the response of tundra and boreal forest plants to past climate changes and the role of central Beringia as a filter bridge for floral and faunal migrations. Because humans are among the migrants, these results also have archeological significance; the paleoenvironment of the BLB determined the resources available to human inhabitants during dispersal into North America (Wooller et al., 2018).

### *1.3.2 Modern Alaskan pollen spectra*

The frequencies of plant taxa in pollen spectra do not coincide with their frequencies in the vegetation cover, for a variety of reasons. Wind-pollinated taxa and grains with thicker walls tend to be overrepresented in pollen spectra, while taxa with vector pollination, thinner exines, or vegetative reproduction are underrepresented (Faegri and Iversen, 1989; Traverse, 2007; Moore et al., 1991). Nevertheless, analysis of surface sediment from 101 lakes in northern Alaska reveals consistent differences in the modern pollen rain in lakes surrounded by Alaskan boreal forest, forest-tundra, and tundra vegetation and (Anderson and Brubaker, 1986). Pollen spectra from the boreal forest contained the highest amounts of spruce and birch, whereas forest-tundra samples had the highest frequencies of alder, and tundra samples contained the highest amounts of grass and sedge (Anderson and Brubaker, 1986).

### *1.3.3 Marine Oxygen Isotope Stage (MIS) notation*

Marine isotope stages (MIS) are determined by changing oxygen isotope ratios that provide evidence for former glacial and interglacial oscillations and serve as a proxy for global climate changes (Lowe, 2014). The ratio of the stable isotopes  $^{18}\text{O}$  and  $^{16}\text{O}$  in the oceans is determined by the amount of  $^{16}\text{O}$  bound up in glaciers. These isotopes are preserved and recorded in foraminifera (forams), amoeboid marine protists with calcium carbonate tests. Once

dated, foram tests can be analyzed for stable isotopes to determine the ratio of  $^{18}\text{O}$  and  $^{16}\text{O}$  present in the oceans in which they lived. Tests from odd numbered stages (e.g. MIS 1, 3, and 5) have low  $\delta^{18}\text{O}$  values and represent the periods of warming (i.e. interglacial stages). Likewise, tests from forams that lived during even numbered stages (e.g. MIS 2, 4, and 6) have relatively high  $\delta^{18}\text{O}$  values, which are representative of glacial stages (Martinson et al., 1987).

#### 1.3.4 Glacial refugia

A glacial refugium is an area that facilitates the growth and survival of select species during glacial episodes when conditions are adverse or unfavorable. Species in refugia survive in small populations during glacial stages and expand their range during interglacial stages, when conditions are more favorable (Holderegger and Thiel-Egenter, 2009).

The presence of refugia in Alaska has been heavily debated, but genetic evidence supports the presence of isolated Alaskan populations. For example, Beatty and Provan (2010) found evidence for genetic isolation in Alaskan specimens of *Orthilia secunda*, an herbaceous taxa found in Alaska and Canada. If plants from southern Canada recolonized Alaska after deglaciation of the Laurentide Ice Sheet, then mutations specific to Canadian *Orthilia* species should be present in Alaskan species as well. However, Alaskan species have different regionally-specific mutations. This suggests a period of genetic isolation in glacial refugia prior to expansion and integration of the Alaskan and Canadian *Orthilia* populations during the Holocene (Beatty and Provan, 2010).

Similar results are derived from a study of white spruce trees, which provides evidence for boreal forest refugia in Alaska. Anderson et al.'s (2006) study used spruce chloroplast DNA to evaluate genetic isolation of Alaskan white spruce during the last glaciation. By comparing the genetic diversity of the white spruce from Alaska with that of Canada, they found that Alaskan



populations shared few DNA haplotypes with the Canadian white spruce populations. This suggests that some trees survived in isolation in Alaska throughout the last glacial maximum (LGM). Subsequent range expansion mixed their genetic material with the Canadian variety of white spruce during the current interglacial.

### *1.3.5 Palynological evidence for Beringian refugia*

Brubaker et al. (2005) examined mapped patterns of pollen percentages to determine whether six boreal tree and shrub taxa (*Populus*, *Larix*, *Picea*, *Pinus*, *Betula*, and *Alnus/Duschekia*) survived harsh glacial conditions within Beringia. Maps of pollen percentages from 149 sites plotted at 1000-year intervals from 21,000 to 6000 cal. yrs. BP support the survival of these taxa within Beringia during the LGM. Although abundance records for each taxon are unique, all display rapid increases in pollen percentages at sites deep within Beringia following the LGM. These rapid comebacks suggest that populations remained local rather than migrating long distances, as the spatiotemporal patterns do not support recolonization by northward migration after the ice sheets receded. Rapid increases in pollen percentages in response to post-glacial warming suggest that *Populus* survived in the western Brooks Range. *Larix*, *Pinus*, and *Alnus/Duschekia* persisted in western Beringia, modern day Siberia, *Picea* survived in eastern Beringia, modern day Alaska, and *Betula* trees or shrubs were present in restricted refugia throughout Beringia (Brubaker et al., 2005).

It is possible that Beringia was bisected by a north-south belt of relatively mesic climate that could have allowed flora in the lowlands of central Beringia to survive harsh glacial conditions. Guthrie (2001) hypothesizes such a phenomenon, conjecturing that maritime cloud cover over central Beringia's lowlands could have created wetter and more humid conditions, forming a "mesic belt" between regions of otherwise arid steppe vegetation. Subsequently, Elias

and Crocker (2008) compiled and analyzed data, based on beetle assemblages, from 13 sites in western and eastern Beringia which supports Guthrie's (2001) hypothesis. Their paleoclimate reconstructions indicate that the lowlands of central Beringia were dominated by shrub tundra, indicative of a more mesic environment. In contrast, higher elevation sites in eastern and western Beringia contained a steppe-tundra signature, indicating a relatively dry environment (Elias and Crocker, 2008).

Recent evidence from St. Paul Island, near the southern edge of the Bering Sea shelf, provides additional evidence for drier conditions at higher elevations (Wang et al., 2017). Palynological assemblages and sedimentary ancient DNA (sedaDNA) indicate that St. Paul has been covered by graminoid-forb tundra with prostrate shrubs for the last 18,000 years. Although pollen of *Picea*, *Betula*, and *Alnus* are present, the combination of low abundances ( $\leq 5\%$  for *Picea*) and maximum frequency during intervals of minimum influx is consistent with long-distance transport. Furthermore, sedaDNA analyses do not support the local presence of these taxa.

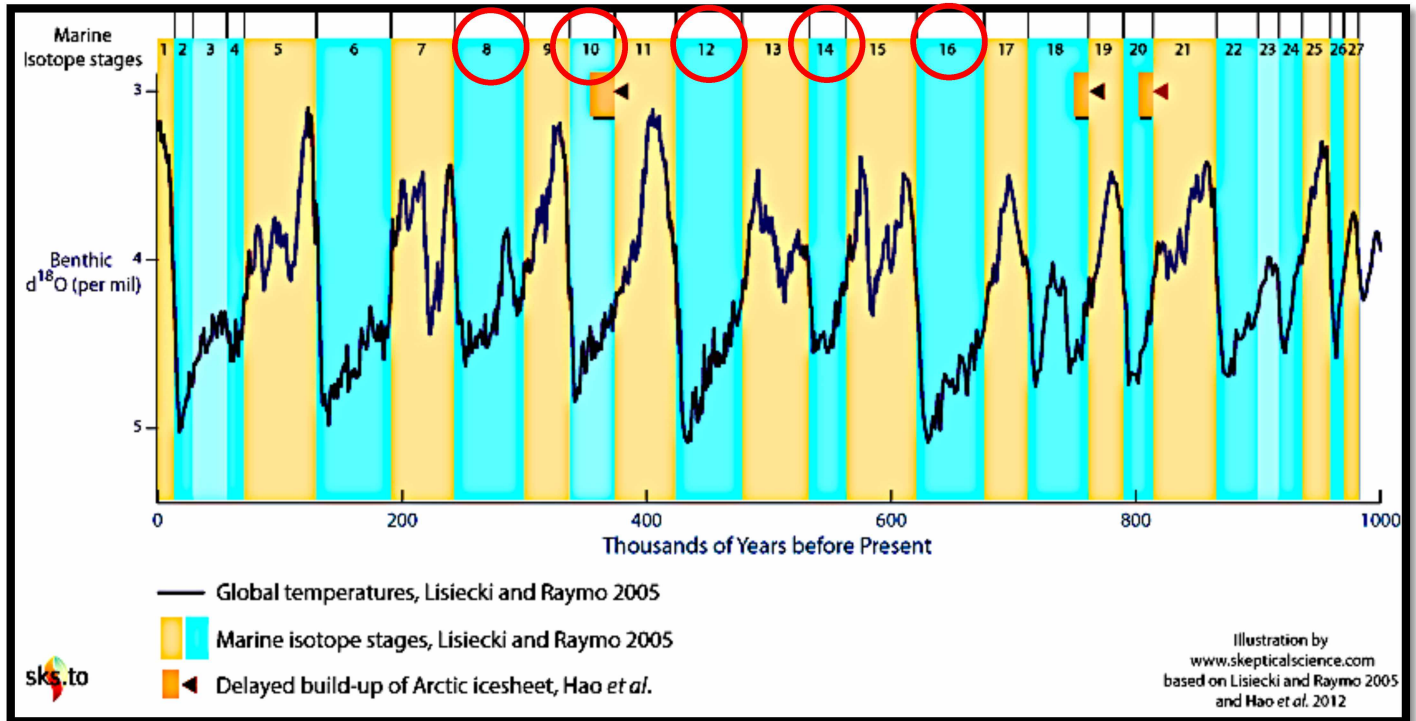
Wang et al., 2017 conclude that if the island of St. Paul did not serve as a glacial refugium for woody taxa, then by implication there were no refugia elsewhere on southern coastal Beringia during the LGM. However, the higher elevation of St. Paul Island compared to the lowlands of surrounding central Beringia is an alternative explanation for these results. Changes in plant taxa with elevation are driven by related changes in temperature, wind, precipitation, and soil chemistry (Harsch and Bader, 2011). Whereas Wang et al. (2017) did not consider the temperature difference resulting from an estimated additional 130 m of elevation on St. Paul to be too small to prohibit colonization by woody taxa, they also do not consider the effects of precipitation. If Guthrie's (2001) hypothesis is correct and maritime clouds and fog

kept central Beringia relatively moist, it is possible that the site on St. Paul Island was above clouds, excluding it from the mesic belt.

### *1.3.6 Significance of offshore pollen records*

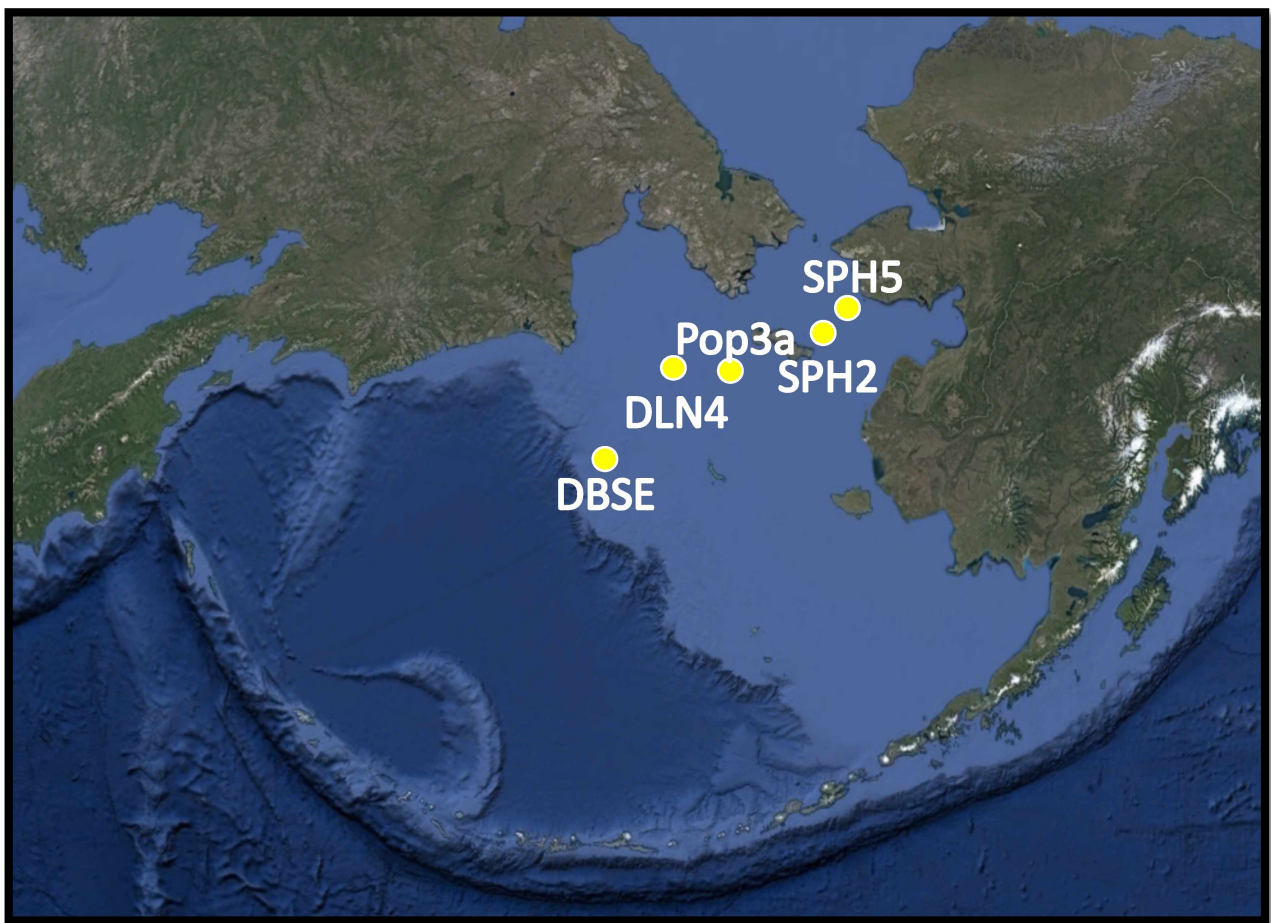
During Quaternary glaciations sea level was significantly lower than today, leaving central Beringia, the Bering Land Bridge between Alaska and Russia, exposed as dry land (Figure 2). Eustatic changes during interglacial periods flooded central Beringia. Through the efforts of IODP Expedition 323 Scientists (2010), cores have been obtained from a site beyond the edge of the Bering Sea shelf, near Zhemchug Canyon (Figure 1). IODP site U1343 is located about 700 km from today's coastline, but this area was approximately 100-300 km offshore, during past glacial maxima. Previous research indicates ocean currents transport terrestrial materials from coastal discharge areas, such as rivers and deltas, to sites of deposition in marine basins (Heusser and Balsam, 1977). Therefore, it is feasible that the majority of the spores, pollen, and terrestrial sediment delivered to site U1343 during glacial stages was derived from the adjacent continental margin. Thus, palynological assemblages from these cores permit reconstruction of the terrestrial vegetation on the southern margin of adjacent southcentral Beringia.

Samples obtained for palynological analysis from site U1343 span MIS 1 to 19, as characterized by Lisiecki and Raymo (2005) (Figure 3). Samples from site U1343 have been dated using benthic foraminiferal oxygen isotope analysis (Asahi et al., 2016). Asahi et al.'s (2016) model employed inter-species calibration of benthic foraminiferal  $\delta^{18}\text{O}$  values to revise and refine a previous age model, changing the ages of some palynomorph assemblages previously analyzed by Westbrook (2014).



**Figure 3:** MIS stages at maximum glaciation, modified image from Lisiecki and Raymo (2005) showing MIS stages at maximum glaciation based upon global benthic  $\delta^{18}\text{O}$  stack data, red circles are the glacial maximums being studied at site U1343.

Samples from the Bering Sea shelf transect (Figure 4) allow comparison between pollen assemblages in marine surface samples and the vegetation of adjacent islands and coastlines. If assemblages from surface samples proximal to the Seward Peninsula and Yukon-Kuskokwim Delta are comparable to the modern pollen rain in these areas, there is additional support for the assumption that fossil pollen assemblages from the IODP sit U1343 reflect the coastal vegetation of southcentral Beringia.



**Figure 4:** Locations of Bering Sea transect sample sites.

## Chapter 2: Methods

### *2.1 Age model*

An updated, orbitally-tuned age model was constructed by Asahi et al. (2016) specifically for IODP site U1343. An inter-species calibration was used to produce a composite benthic foraminiferal  $\delta^{18}\text{O}$  record. Comparison to the composite global benthic  $\delta^{18}\text{O}$  stack curve LR04 (Lisiecki and Raymo, 2005) established a highly refined age model for the past 1.2 million years. By adjusting for small offsets in the  $\delta^{18}\text{O}$  values of different species of benthic foraminifera, this model allowed for a continuous composite  $\delta^{18}\text{O}$  record. Correlation with the global stack curve assumes that the timing of the glacial and interglacial cycles is globally uniform: any deviation from this uniformity would result in a lag between the reported glacial and interglacial events and their occurrence (Asahi et al., 2016). Linear interpolation was employed to estimate the ages of samples from horizons located in between stage boundaries identified and dated by Asahi et al.'s (2016) age model.

In order to reconstruct the coastal vegetation of Beringia during glacial stages, I selected samples from MIS 8, 10, 12, 14, and 16 for processing. Due to the use of a preliminary age model (Asahi, pers. comm. with Fowell and Westbrook, 2014) some of the samples initially selected from MIS 16 were found to fall within MIS 15 once the updated age model was applied. In addition, sample ages previously provided by Westbrook (2014), are herein revised based on Asahi et al.'s (2016) published age model. This changed the ages and, in some case, the stages represented by Westbrook's (2014) samples. For example, 6 of the samples that were presumed to be from MIS 6 were found to be from MIS 5 when the updated age model was applied.

## *2.2 Sample processing*

Samples from MIS 1 through 6, 8, 10, and 12 were processed by Rachel Westbrook and Susana Salazar Jaramillo prior to 2014 (Westbrook, 2014). Processing employed a modified version of the methods outlined by Heusser and Stock (1984), and residues were mounted in silicone oil. However, the silicone oil was too fluid, making it difficult to examine and relocate grains, as they would move freely about the slide.

Processing of samples from MIS stages 14, 15, and 16 also employed a modified version of the methods described by Heusser and Stock (1984) (Figure 5). However, the average sample volume was ~ 2 cc, as determined by water displacement, rather than the 5cc used by Heusser and Stock (1984). Marine sediment typically has lower pollen concentrations than terrestrial sediment due to grains being transported farther from the source. Therefore, a larger sample size would have been optimal, but only 2 cc were available. I processed these samples in three separate batches: batch one consisted of six samples from MIS stages 14 and 15, batch two consisted of six samples from MIS 15 and 16, and batch three consisted of two samples from MIS 16 and five samples from the Bering Sea shelf surface transect.

Sample batches one, two, and three all contained a substantial amount of clay, and samples from MIS 15 and the modern Bering Sea shelf transect contained a large amount of diatoms, both of which obscured palynomorphs on test slides. To remedy this, clay was removed through a series of water washes followed by brief centrifugation for approximately 60 seconds, leaving the clay in suspension. Washing and centrifugation continued until the decanted liquid was completely clear. Two additional hydrofluoric acid washes were added to remove abundant diatoms tests.

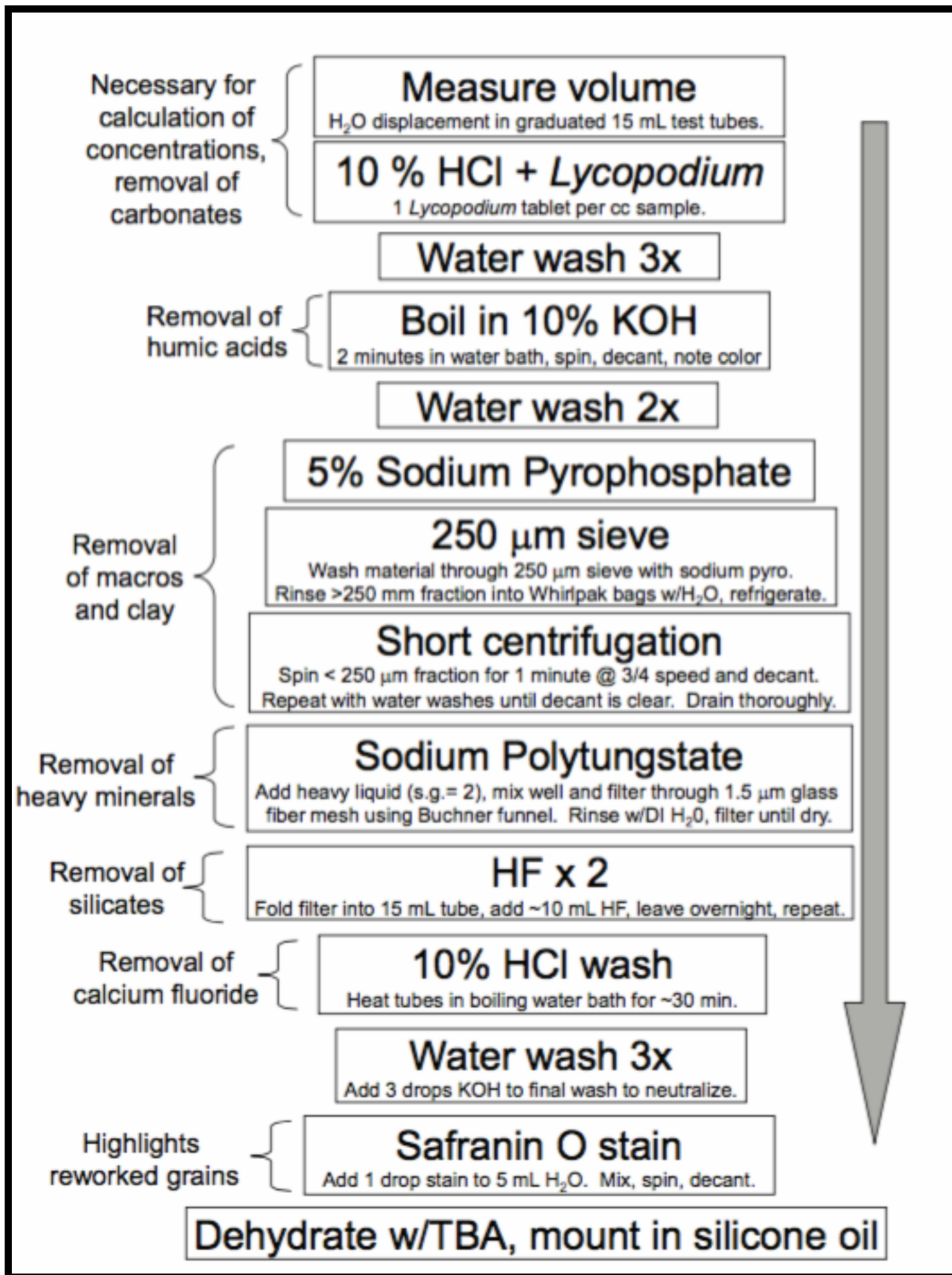


Figure 5: Methods for pollen sample processing by Heusser and Stock (1984).



Prior to mounting, samples were stained with safranin O in order to highlight reworked grains (Brubaker et al., 2005). Rather than use the low viscosity silicon oil, samples from batch one were mounted in glycerin jelly. Samples in batches two and three were mounted 6 months later in a batch of silicon oil with a higher viscosity than that available during batch one processing. As a result, samples in batches two and three were dehydrated with tert-Butyl alcohol to remove water before staining with safranin O and mounting in silicone oil. Silicone oil is preferentially used in these samples so that the pollen and spores can be flipped and rotated to facilitate identification.

### 2.3 Microscopy

Palynomorphs were counted using an Olympus CX41RF microscope at 400X – 1000X magnification. A minimum of 300 grains of terrestrial pollen and spores was counted on each slide, excluding added exotic *Lycopodium*, fungal spores, and aquatic taxa. Identification of pollen grains and spores was facilitated by comparison with type slides located at the University of Alaska Fairbanks Paleoecology Laboratory and photographic plates in Traverse (2007) and Moore et al. (1991).

When counting bisaccate pollen grains such as *Picea* (spruce) and *Pinus* (pine), the individual air bladders were counted individually, and the resulting number was divided by two to determine the total number of bisaccate pollen grains. In addition, the number of bisaccate pollen that were whole versus fragmentary (individual air bladders) was tracked to assess the likelihood of reworking or long distance transport. *Betula* (birch) pollen was differentiated from *Betula nana* (shrub birch) based upon a ratio of the grain diameter (D) and pore depth (P). If the D/P ratio was greater than 9, the grain was categorized as *Betula nana*; if it was less than 9, the

grain was simply categorized as *Betula* (Clegg et al., 2005). In the event that a birch grain was flattened at an oblique angle or damaged such that the pore depth could not be measured, it was categorized as *Betula*. Therefore, the percentages of *Betula nana* reported herein are minimum values. Cyperaceae and Poaceae pollen grains were classified at the family level with no attempt to differentiate genera, because the same pollen morphology is produced by many different genera (Moore et al., 1991). Spores were categorized as monolete, trilete, fungal spores, and *Sphagnum*, but they were not subdivided into species based upon ornamentation or structure because most lacked the diagnostic perine.

#### 2.4 Calculating pollen concentrations, percentages, and paludification index

Pollen concentrations were calculated using the following equation from Traverse (2007):

$$\text{Total Fossil Pollen} = \frac{\text{Fossil Pollen Counted} \times \text{Exotic Spike Added}}{\text{Exotic Spike Counted}}$$

Pollen diagrams are based on identification of at least 300 grains per sample. The basic pollen sum is the total of all identified pollen grains and spores excluding: fungal spores, aquatics, marine palynomorphs, and unknown/indeterminate grains. It is calculated by adding the total numbers of tree, shrub, and herb pollen to the total numbers of monolete and trilete spores and used as the denominator for calculating percentages of taxa that belong to these groups. A separate pollen sum was used to calculate percentages of groups excluded from the basic pollen sum (fungal spores, aquatics, marine palynomorphs, and unknown/indeterminate grains) by adding the total number of grains for the group in question to the basic pollen sum

(Figure 6). The percentage of ripped versus whole bisaccate pollen grains was calculated by dividing the number of ripped sacci by the total number of sacci found and multiplying by 100.

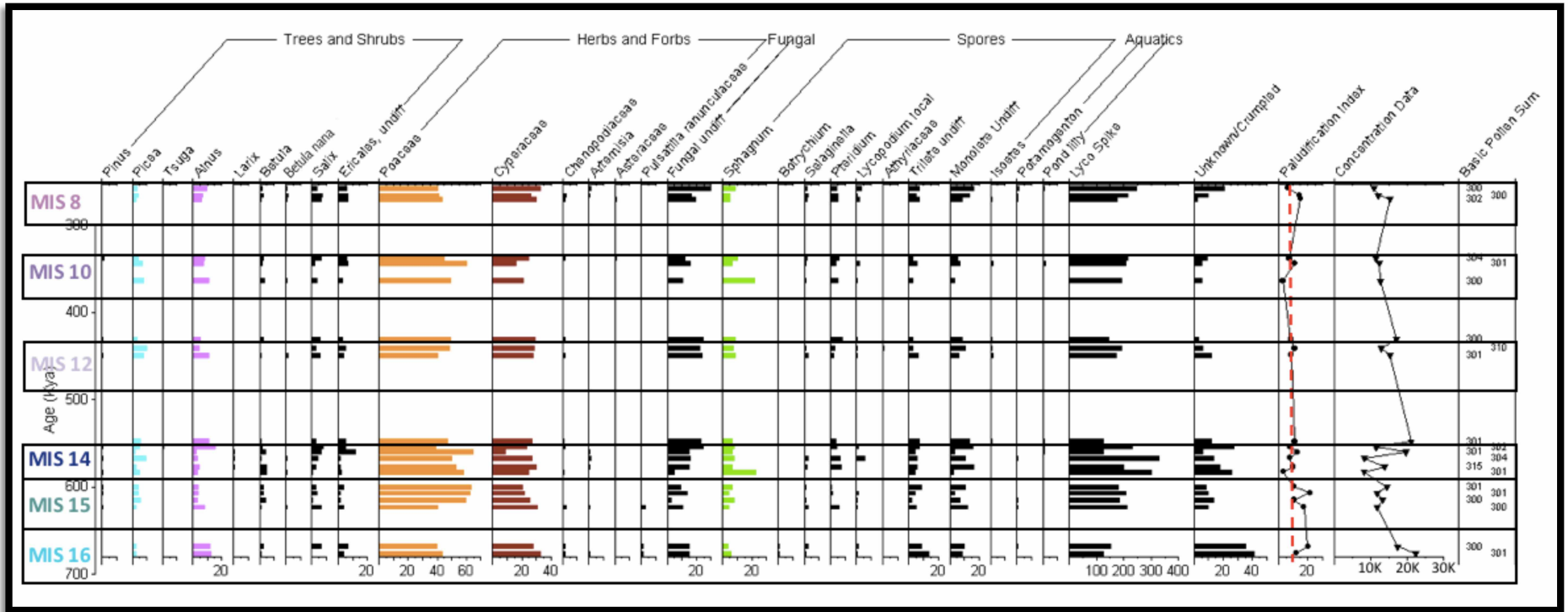
A paludification index  $P_{est}$  (angiosperm pollen / *Sphagnum* spores) constitutes a proxy for saturated organic matter (Figure 6). Values less than 10 correspond to wet conditions and greater paludification (White et al., 1977).

### *2.5 Bering Sea transect*

Modern surface samples that form a transect across the Bering Sea shelf are located between 82 km and 775 km from the modern coast of Alaska (Figure 4). A reference point (Nome Airport: 64.5099N, 165.4435W) is used to estimate the distance from the modern coastline to the sample locations. The transect is used to determine the representation of modern pollen taxa in relation to modern coastal vegetation, serving as a basis for inferences regarding pollen transport and survival in the marine environment (Figure 6 and 7). The transect was assembled from two scientific cruises on the US Coast Guard icebreaker Healy (HLY061 and HLY0702) conducted across the Bering Sea shelf. Five of 35 available modern surface samples were strategically chosen from the two cruises based upon availability and distance from the current shoreline in order to have samples representative of nearshore (SPH5 and SHP2), mid-shelf (POP3a and DLN4), and the shelf edge (DBSE) (Figure 4).

### *2.6 Principal component analysis of modern and fossil samples*

To identify modern analogs, IODP samples were compared with modern surface samples from locations across Alaska and the Bering Sea shelf (Figure 8). Terrestrial surface sample datasets were provided by palynologists Drs. Thomas Ager, Patricia Anderson, and Linda Brubaker. Ager analyzed palynomorphs from 120 sites in western and southern Alaska (59.6°N



**Figure 6:** Abundance (percent total identified) for IODP site U1343. Including total concentration data, which includes terrestrial taxa and spores.

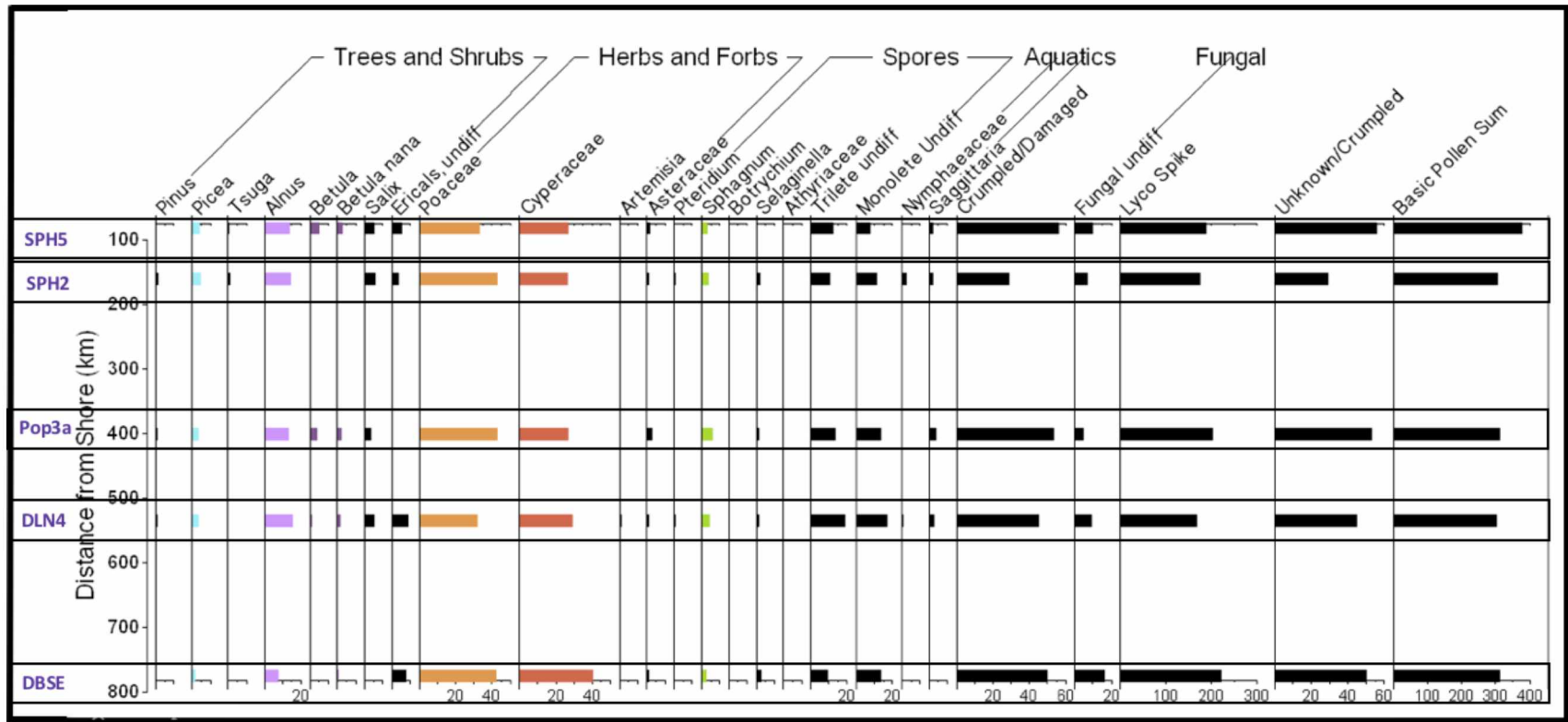
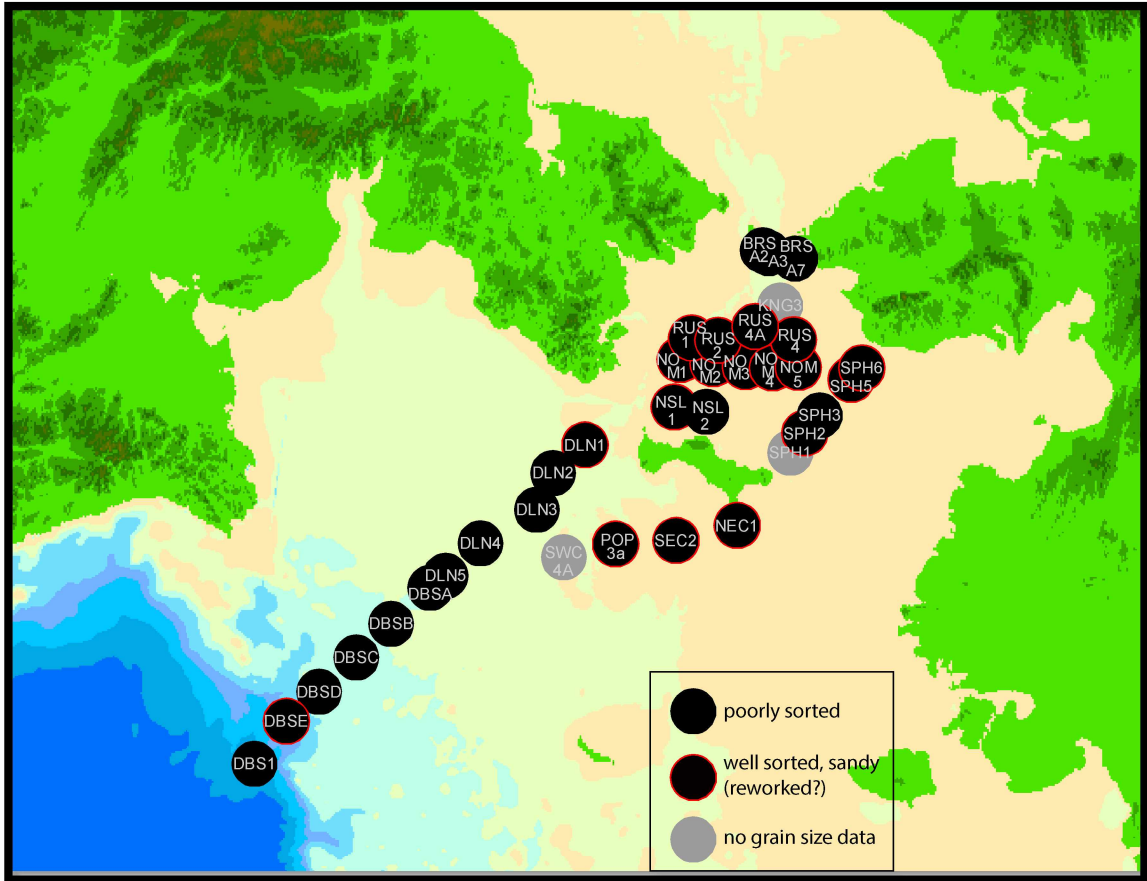


Figure 7: Abundance (percent total identified) for Bering Sea transect.

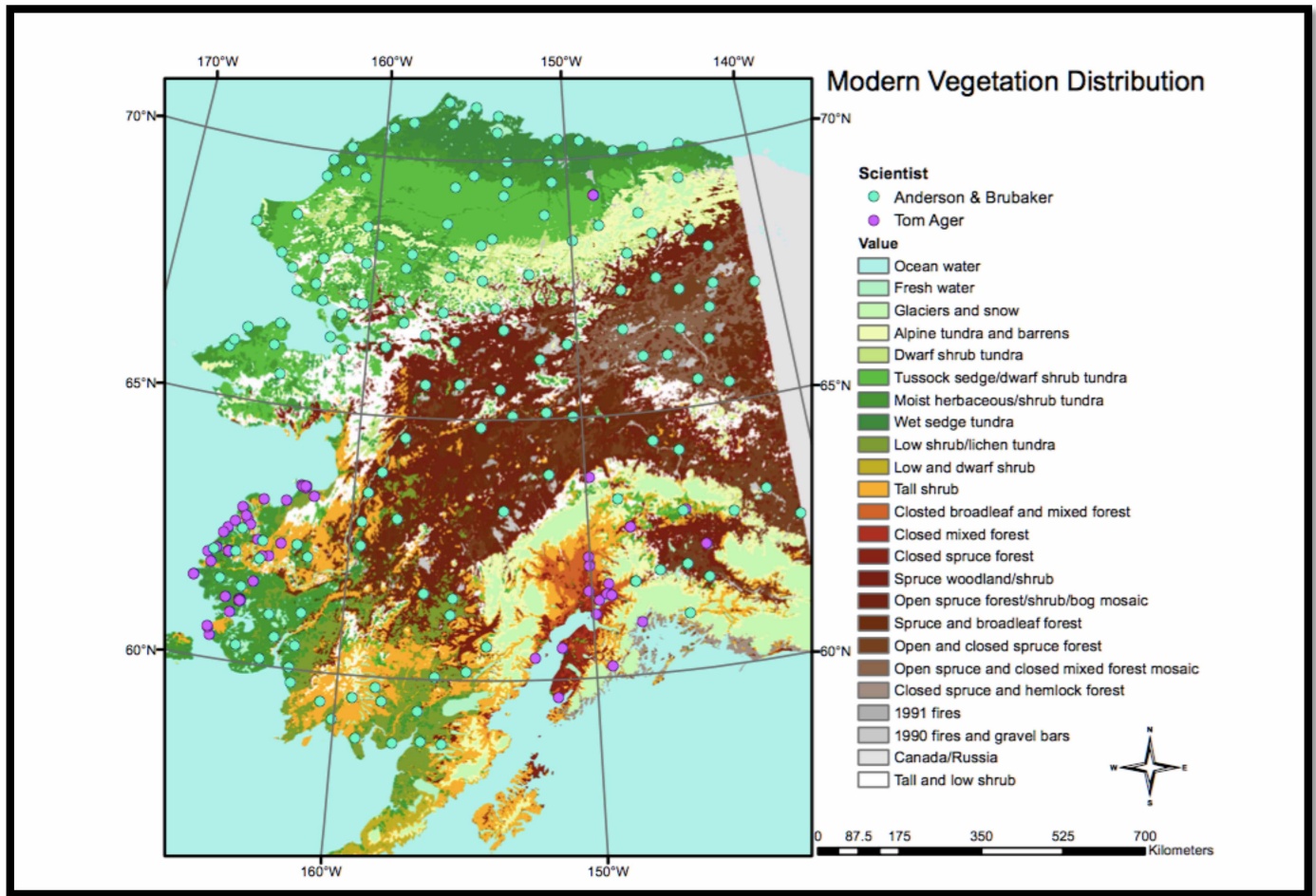


**Figure 8:** Map of modern surface samples taken on the Bering Sea shelf from two cruises HLY061 and HLY0702.

to 69.25°N and -144.65°W to -166.17°W) (Ager, 2003) while Brubaker and Anderson collected and analyzed surface pollen samples 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, 1986; Bigelow et al., 2003).

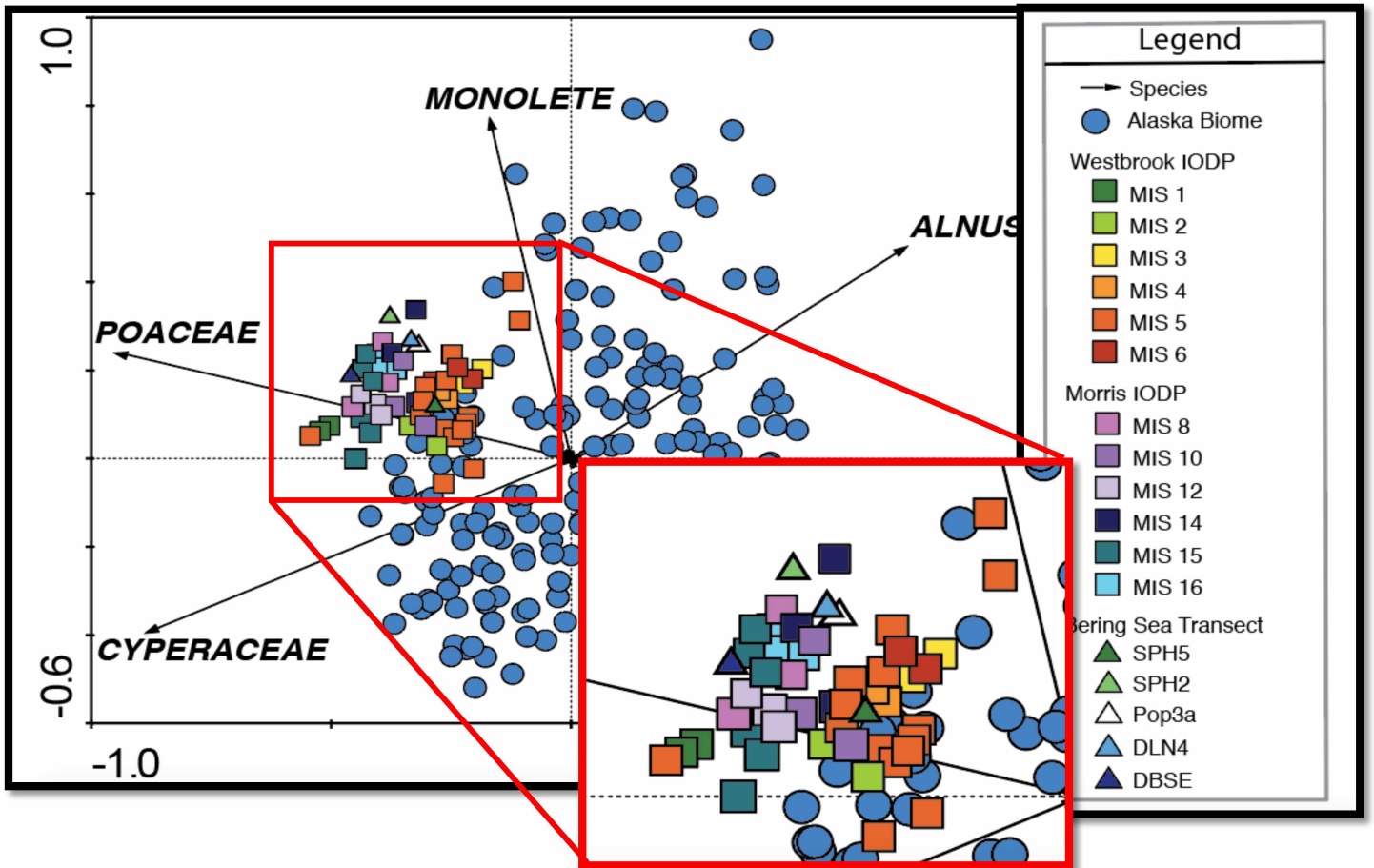
The original datasets from Ager, Anderson and Brubaker varied in their descriptions of the local vegetation at the sample sites. In order to standardize the vegetation descriptions, Westbrook (2014) plotted their site localities onto a modern vegetation distribution map of Alaska developed by Michael Fleming (Figure 9), 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. 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 (Westbrook, 2014).

To facilitate identification of modern analogs, assemblages from IODP samples were compared to 220 surface pollen spectra and spectra from five marine surface samples using canonical community ordination (CANOCO 4.5) software, augmenting Westbrook's (2014) prior analyses (Figure 10). Initially, Westbrook (2014) conducted a detrended correspondence analysis (DCA) to determine the gradient lengths of the first axis. If the gradient length is less than 4 standard deviations, then a linear response model such as principal component analysis (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 PCA characterized by a linear response model with an indirect gradient analysis was applied. I followed typical PCA methodology and



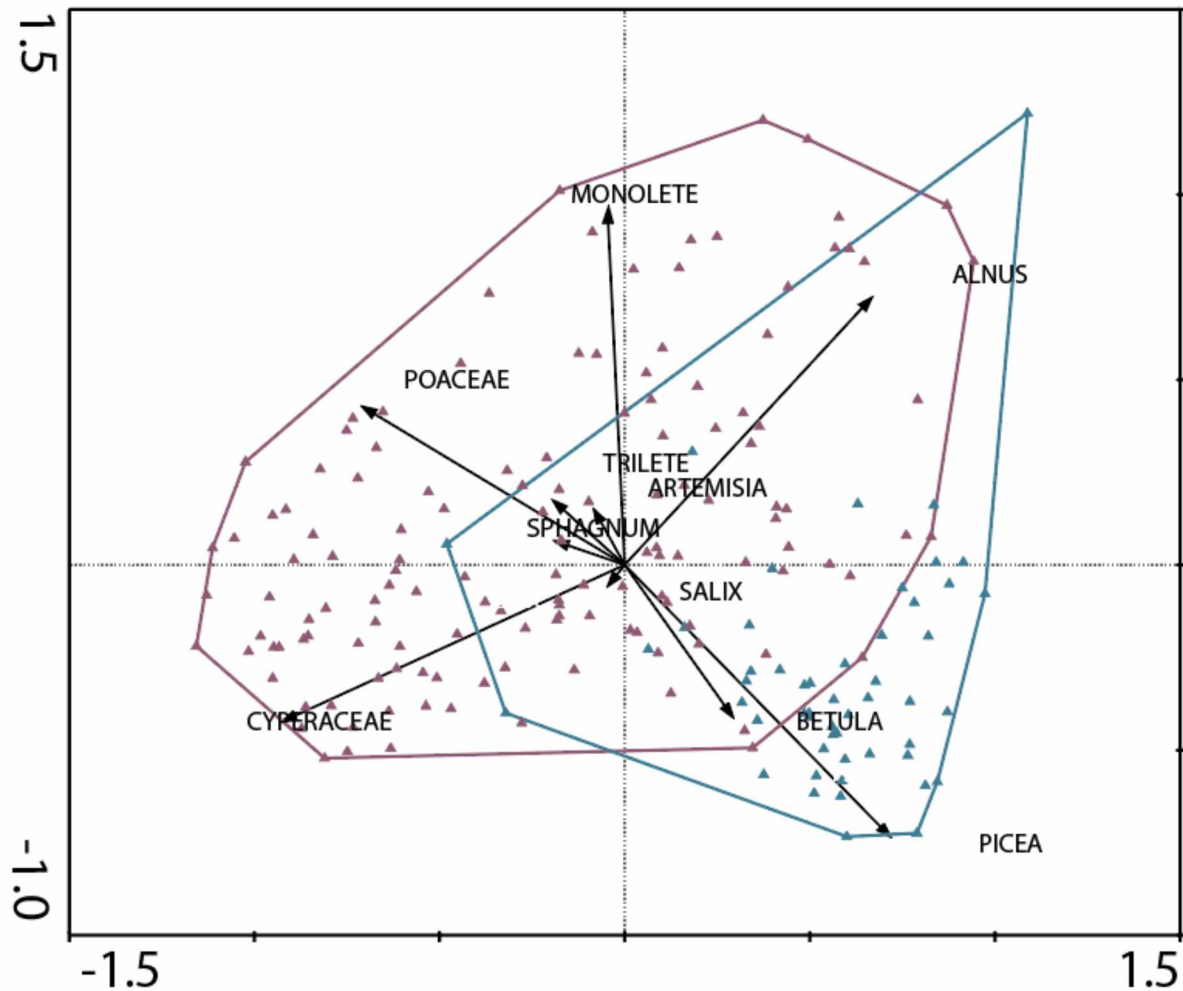
**Figure 9:** Modern vegetation distribution map of Alaska including 24 classes total, 19 of which are vegetative. Surface sample data provided by Tom Ager (indicated by purple circles), and Pat Anderson and Linda Brubaker (indicated by green circles). (Modified from: Fleming, 1998). Modified from Westbrook, 2014.



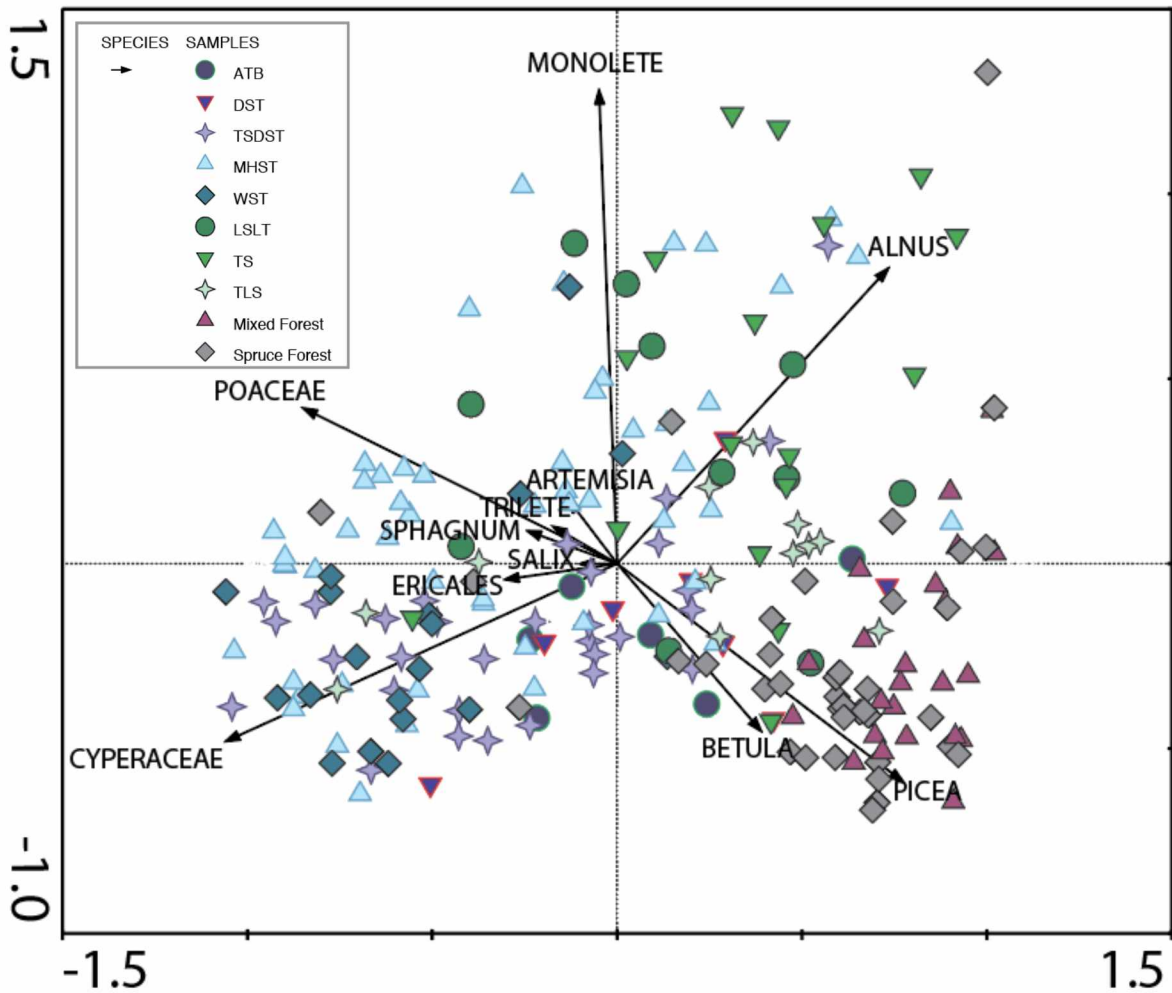


**Figure 10:** Simple ordination plot using Principal Components Analysis (PCA) showing U1343 samples (Westbrook IODP, Morris IODP) plotted with modern surface samples (Alaska Biome) and the Bering Sea transect samples. Plotting indicates IODP and Bering Sea transect samples plot with herbaceous tundra taxa quadrant.

Westbrook's (2014) approach by basing results on 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 (Figure 10). Ordination plots group the samples according to the proportions of constituent taxa, such that similar assemblages appear closer together. The results highlight various aspects of the modern samples, including lake vs. peat, tundra vs. forest, and tundra biome vs. forest biome (Figures 11 and 12) and allow quick visual identification of the closest modern analogs for the IODP assemblages (Figure 10).



**Figure 11:** Simple ordination plot using PCA denoting surface samples classifications, separating classes into tundra vs. forest biomes with envelopes (Modified from Westbrook, 2014).



**Figure 12:** PCA orientation plot 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 (Modified from Westbrook, 2014).



## Chapter 3: Results

### 3.1 *Palynomorph assemblages from MIS 8, 10, 12, 14, 15, and 16*

IODP site U1343 samples ranging in age from 243 to 676 kya and were selected for proximity to glacial maxima as identified by Lisiecki and Raymo (2005) (Figure 3). High percentages of grass (Poaceae) and sedge (Cyperaceae) are present in both glacial and interglacial assemblages. Boreal forest taxa including birch (*Betula* and *Betula nana*), alder (*Alnus*), and spruce (*Picea*), are consistently present in varying abundances. Spores of *Sphagnum* and ferns are also consistently present and commonly abundant.

#### 3.1.1 *MIS 16 (676 - 621 kya)*

Three samples from MIS 16 were analyzed (Figure 6), with estimated ages ranging from 676.1 – 623.5 kya. Grass (Poaceae 39.3 – 43.6%) and sedge (Cyperaceae 27.7 – 32.6%) dominate the assemblages with percentages far greater than that of tree or shrub taxa. Tree pollen is present in low percentages, including birch (*Betula* 1 – 2.3% and *Betula nana* 0 - 0.7%), alder (*Alnus* 8 – 12%), and spruce (*Picea* 2.2 – 2.3%). Small quantities of willow (*Salix* 0 - 6%) and Ericales (Ericaceae 3.7 – 6.3%) pollen are also present. Spore abundances (monolete and trilete spores, excluding *Sphagnum*) are 29.7%, 26.3%, and 30% at 623.5, 668.5, and 676.1 kya, respectively. *Sphagnum* is present in abundances ranging from 3.7 – 5.8%. Sage (*Artemisia* 0.7%) is present in one of the three samples, at 623.5 kya.

#### 3.1.2 *MIS 15 (621 - 563 kya)*

Six samples from MIS 15 were analyzed (Figure 6), with estimated ages ranging from 615.3 – 567.7 kya. Grass (Poaceae 50.1 – 63.1%) and sedge (Cyperaceae 20.6 – 29.5%) dominate the assemblages. Trees and shrubs are present but relatively uncommon, including birch (*Betula* 1.3 – 5% and *Betula nana* 0 - 1%), alder (*Alnus* 2.6 - 4%), and spruce (*Picea* 2.5 –

8.9%). Willow (*Salix* 0.7 – 4.3%) and Ericales (Ericaceae 1.3 - 4%) are also present. Spore abundances (monolete and trilete spores, excluding *Sphagnum*) are 39%, 37.9%, 30%, 27.8%, 14.8%, and 18.3% at 567.7, 577.6, 583.8, 600.1, 607.5, and 615.3 kya, respectively. *Sphagnum* is present in abundances ranging between 4 and 22.8%. Sage (*Artemisia* 1 – 1.3%) is also present in two of the six samples, from approximately 567 and 577 kya.

### 3.1.3 MIS 14 (563 - 533 kya)

Three samples from MIS 14 were analyzed (Figure 6), with estimated ages ranging from 560.8 – 548.4 kya. Grass (Poaceae 39.1 – 64.5%) and sedge (Cyperaceae 8.3 - 27%) again dominate the assemblages. Tree and shrub taxa include birch (*Betula* 1.3 – 3.7%), alder (*Alnus* 2.3 – 15.3%), spruce (*Picea* 2 – 5.5%), willow (*Salix* 2.3 - 8%) and Ericales (Ericaceae 5.3 - 12%). Abundances of monolete and trilete spores, excluding *Sphagnum*, are 24.9%, 27.9%, and 31.6% at 548.4, 554.4, and 560.8 kya, respectively. *Sphagnum* is present in abundances ranging between 6.1 and 8%. One grain of larch (*Larix* 0.7%) is present in one sample at 560.8 kya; sage (*Artemisia* 0.3%) is also present in this sample.

### 3.1.4 MIS 12 (478 - 424 kya)

Three samples from MIS 12 were analyzed (Figure 6), with estimated ages ranging from 449.9 – 431.6 kya. Grass (Poaceae 40.3 - 49%) and sedge (Cyperaceae 27.3 – 29.3%) dominate. Tree and shrub taxa include birch (*Betula* 0.6 – 2.7% and *Betula nana* 0 – 1.7%), alder (*Alnus* 4.2 - 11%), and the highest percentages of spruce (*Picea* 3.3 – 9.7%) recovered from samples included in this analysis. Willow (*Salix* 2.6 – 5.7%) and Ericales (Ericaceae 2.7 – 5.2%) are also present. Spore abundances (monolete and trilete spores, excluding *Sphagnum*) are 27.9%, 31.6%, and 38% at 431.6, 441.2, and 449.9 kya, respectively. *Sphagnum* is present in abundances ranging from 6.8 – 8.5%. One grain of larch (*Larix* 0.3%) is also present at 441.2 kya.

### 3.1.5 MIS 10 (347 - 337 kya)

Three samples from MIS 10 were analyzed (Figure 6), with estimated ages ranging from 364.8 – 338.4 kya. Grass (Poaceae 44.5 – 59.8%) and sedge (Cyperaceae 15.6 – 24.4%) are present in percentages far greater than that of woody taxa. Tree and shrub taxa include birch (*Betula* 2 – 3.3% and *Betula nana* 0 – 1%), alder (*Alnus* 7.3 – 11%), spruce (*Picea* 3.7 – 7.3%), willow (*Salix* 1.7 – 6.3%) and Ericales (Ericaceae 3.3 – 6.6%). Spore abundances (monolete and trilete spores, excluding *Sphagnum*) are 26.6%, 27.6%, and 35.2% at 338.4, 344.5, and 364.8 kya, respectively. *Sphagnum* is present in abundances ranging from 6.5 – 21.8%.

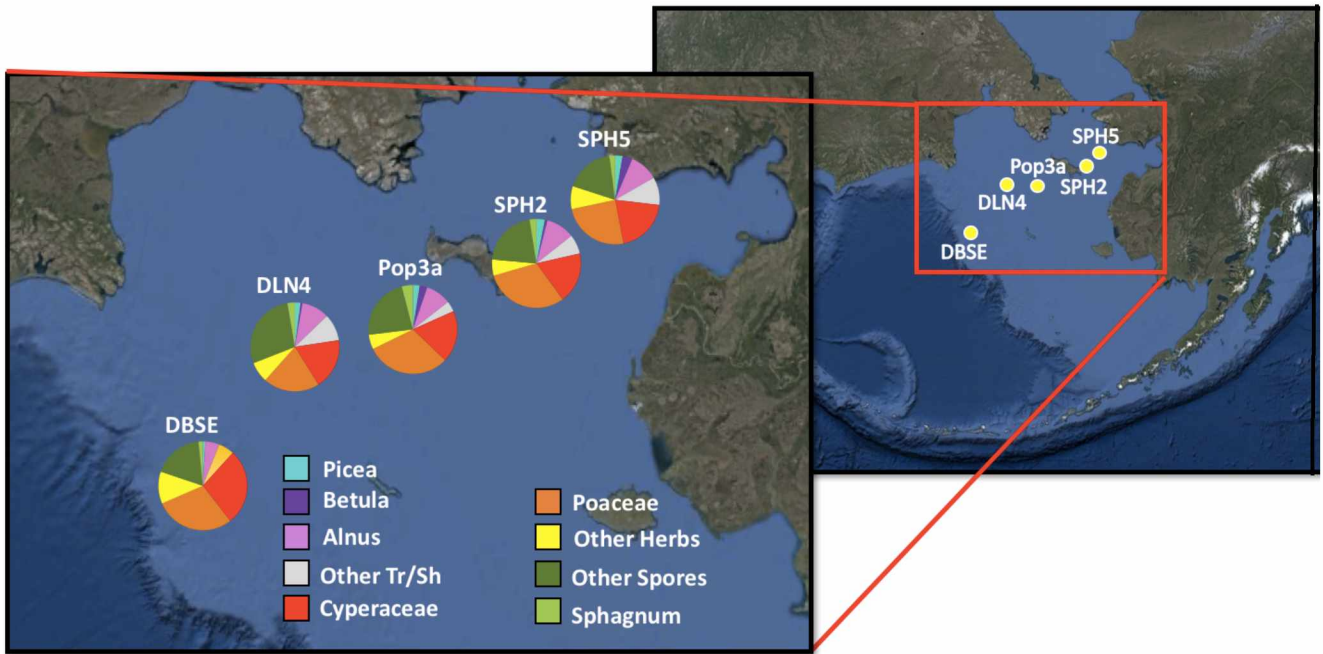
### 3.1.6 MIS 8 (300 - 243 kya)

Three samples from MIS 8 were analyzed (Figure 6), with estimated ages ranging from 272.6 – 260.7 kya. Grass (Poaceae 40.7 – 43.4%) and sedge (Cyperaceae 26.3 – 32.7%) dominate. Tree and shrub taxa include birch (*Betula* 1.3 – 2.7% and *Betula nana* 0.7 – 1.7%), alder (*Alnus* 5.6 – 9.7%), spruce (*Picea* 2.3 – 4.3%), willow (*Salix* 3.3 - 7%) and Ericales (Ericaceae 5.7 - 7%). Spore abundances (monolete and trilete spores, excluding *Sphagnum*) are 42.7%, 31.7%, and 30.4% at 260.7, 266.9, and 272.6 kya, respectively. *Sphagnum* percentages range from 4.6 - 8.6%. Sage (*Artemisia* 0 - 1.7%) is also present in two of the three samples, at approximately 258 and 266 kya.

## 3.2 Bering Sea transect

The Bering Sea shelf samples contain high percentages of grass (Poaceae) and sedge (Cyperaceae), with lower and variable abundances of boreal forest taxa, including birch (*Betula*), alder (*Alnus*), and spruce (*Picea*) (Figure 13). Spores of *Sphagnum* and ferns are consistently present and commonly abundant in these assemblages.





**Figure 13:** Bering Sea transect sample sites with pollen and spore percentages.

3.2.1 Near shore: samples SPH5 and SPH2 (82 - 160 km from shoreline, respectively)

Samples SPH5 and SPH2 are located 82 km and 160 km from the shoreline reference point, respectively. Grass (Poaceae 33.1 and 42.8%) and sedge (Cyperaceae 26.9 and 26%) percentages are greater than that of the boreal forest taxa birch (*Betula* 4.8 and 0%; *Betula nana* 2.7 and 0%), alder (*Alnus* 13.9 and 14.5%), and spruce (*Picea* 3.7 and 4.3%). Willow (*Salix* 5.3 and 5.9%) and Ericales (Ericaceae 5.3 and 3.3%) are also present. Spore abundances are 24.4% and 29%. Hemlock (*Tsuga* 0.3 and 0.7%) and pine (*Pinus* 0 and 1.2%) are also present in very small quantities.

3.2.2 Mid-shelf: samples POP3a and DLN4 (401 - 545 km from shoreline respectively)

Samples POP3a and DLN4 are located 401 km and 535 km from the shoreline reference point, respectively. Grass (Poaceae 42.9 and 31.8%) and sedge (Cyperaceae 26.5 and 28.5%) percentages are greater than birch (*Betula* 3.9 and 1%; *Betula nana* 1.9 and 1.3%), alder (*Alnus* 12.9 and 15.6%), and spruce (*Picea* 3.5 and 3.3%). Willow (*Salix* 3.5 and 5.3%) and Ericales (Ericaceae 0 and 8.6%) are also present. Spore abundances are 34.5% and 41.9%. A very small quantity of sage (*Artemisia* 1%) is also present in sample DLN4.

3.2.3 Shelf edge: sample DBSE (775 km from shoreline)

One sample (DBSE) from the shelf edge was located 775 km from the shoreline reference point. Grass (Poaceae 42%) and sedge (Cyperaceae 40.1%) dominate the sample. Minor percentages of birch (*Betula nana* 0.6%), alder (*Alnus* 7.4%), spruce (*Picea* 1.3%) and Ericales (Ericaceae 7.7%) are also present, but willow (*Salix*) is not represented. The abundance of spores in this sample is 28.6%.



## Chapter 4: Discussion

### *4.1 Potential bias in pollen analysis*

Palynological analysis is subject to limitations, the most significant of which is the reworking of grains. Any and all pollen and spores are potentially subject to reworking (Traverse, 2007). Reworked grains can be identified by reduced absorption of safranin O stain. Due to their differing thermal histories, reworked grains will appear brown or dark yellow as opposed to the pink or red appearance of unaltered, stained grains (Brubaker et al., 2005). However, Brubaker et al. (2005) found such reworked grains to be relatively rare, less than 20 of every 300 counted.

The IODP samples from glacial stages did not display much color variation, with most grains being light yellow to pink. However, specimens that fell closer to or within interglacial stages exhibited more color variation, ranging from pink to dark brown. This is probably due to reworking and mixing of grains with different thermal histories as grains were transported across the shelf to the deposition site.

Another indicator of reworking or long-distance transport is grain appearance: grains that have undergone mechanical damage during long-distance dispersal (i.e. fluvial transport) are likely to be torn or broken. This is especially true of bisaccate grains, such as pine (*Pinus*) and spruce (*Picea*). These grains are relatively large and have two mesh-filled air sacks that are susceptible to mechanical damage (Egberts, 2012). Therefore, sacci that are ripped away from the body or broken at the attachment point are potential indicators of reworking or transport over long distances. Bisaccate pollen grains from site U1343 and the Bering Sea shelf transect show little evidence of mechanical damage during glacial stages. 90% of total bisaccate grains from

MIS 8, 10, 12, 14, and 16 were found to be intact, with both sacchi attached to the body. Comparatively, 76% of total bisaccate grains from interglacial stage MIS 15 were found intact. Due to the intact condition of the majority of bisaccate grains recovered from glacial stages, it seems unlikely that these specimens were reworked from prior stages. The higher percentage of damaged bisaccate grains present in MIS 15 may be the result of long distance fluvial transport across the submerged Bering Sea shelf.

Another potential limitation of palynological analysis in the Arctic is that plants may reproduce vegetatively rather than pollinate during unfavorable conditions, such as cold and/or dry glacial stages (Faegri and Iverson, 1989; D. Mann, pers. comm., 2017). This could lead to underrepresentation of tree species such as spruce. However, all glacial stage samples from IODP site U1343 contain spruce pollen, with percentages ranging from 2.0 to 9.7%. Although the percentages of *Picea* from glacial stages are low, few are broken. Mechanical damage may be a result of long distance transport or reworking from prior interglacial stages, yet the majority are intact and in good condition. Therefore, I find it doubtful that all of these grains are reworked. Instead, I consider the undamaged grains to be strong evidence for local or regional climatic conditions, such as a warmer or more humid climate on the coast of southcentral Beringia, that allowed boreal taxa to persist and continue to pollinate.

A final limitation of palynological analysis, as it pertains to these samples, is human error or analytical bias. Analyst error could affect the total numbers of each taxon identified within a sample. I counted all of the IODP samples from MIS 8-16 and the five Bering Sea shelf transect samples, using the same protocols and resources to minimize error. Samples from MIS 1-6 discussed herein were counted by Westbrook (2014), using the same type collections and photographic atlases. In both cases, pollen grains that were crumpled, crushed, or damaged

beyond identification were tallied separately and not included in per taxon abundances (see Crumpled/damaged column: Figures 6 and 12).

#### 4.2 Pollen transport to UI343

According to Heusser and Balsam (1977) coastal vegetation is primarily transported to marine settings via river systems. Based on pollen spectra for marine sediment samples collected on the continental slope and rise of the Northeastern Pacific Ocean they found a relationship between distance from shoreline and abundances of most taxa, with taxa numbers decreasing the farther they travel from shore. They noted a strong correlation between vegetation of the nearby coast and pollen abundances of taxa such as western hemlock (*Tsuga heterophylla*), spruce (*Picea*), alder (*Alnus*), oak (*Quercus*), redwood (*Sequoia*), and the daisy/dandelion family (Asteraceae) (Heusser and Balsam, 1977). The correlation between distance from shore and decreasing abundance is present, with two exceptions, pine (*Pinus*) and ferns spores. These increase in number as with distance from the shoreline. Heusser and Balsam (1977) hypothesized that this may be due to greater buoyancy of these grains. While pine (*Pinus*) and spruce (*Picea*) share a similar bisaccate morphology, with a body and two lateral air bladders, they are not identical. Spruce (*Picea*) grains are heavier and tend to be deposited shorter distances from the source than those of their bisaccate counterpart, pine (*Pinus*) (Traverse, 2007).

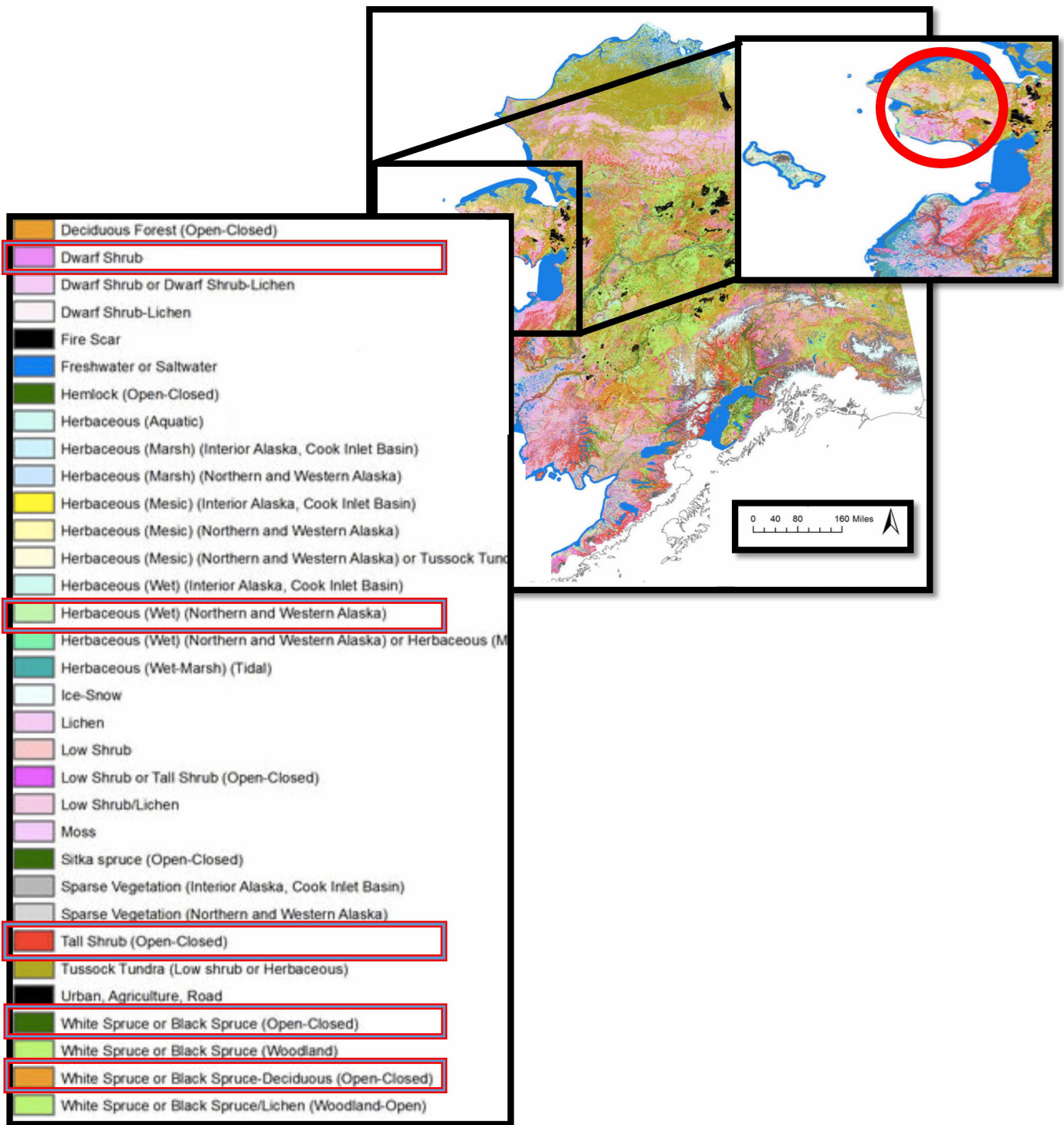
Pine occurs in only 9 of the 21 IODP samples that I analyzed. Where present, the concentrations are very low, less than 2%. The grains are generally in poor condition, with 76% of the air bladders ripped from the body. This is not surprising, as these grains probably came from southeast Alaska or eastern Russia, where pine grows today. Because pine is the most common pollen type to travel long distances (Heusser and Balsam, 1977), and there is little pine

pollen in the IODP samples, there is little evidence of significant contributions from distance sources at site U1343. The spruce grains that are present in the IODP samples are largely in good condition. Therefore, the majority of the IODP samples are assumed to be representative of the regional coastal vegetation.

#### *4.3 Bering Sea shelf transect as potential modern analogs*

The Bering Sea shelf transect extends from just off the coast of the Seward Peninsula to the outer continental shelf east of U1343. The transect samples were analyzed to determine the abundances of boreal tree and shrub taxa relative to the distance from a coastline where stands of woody plants are found. The modern coastal vegetation of Alaska's Seward Peninsula is composed of intermixed herbaceous tundra and dwarf shrubs, with intermittent stands of spruce trees (Boggs et al., 2014). If surface samples ~160 km off the coast of the Seward Peninsula are representative of the modern coastal vegetation, then glacial stage assemblages from site U1343, approximately 100 – 200 km from the coast of emergent central Beringia, could be expected to be representative of the vegetation on the paleo-coastline.

The Alaskan vegetation map from the Alaska Center for Conservation Science, Figure 14, shows a transition across the Seward Peninsula (Boggs et al., 2014). The western side, around Nome, is dominated by herbaceous wet tundra with dispersed dwarf shrubs; further east, towards the village of White Mountain, intermittent groves of cottonwood (*Populus balsamifera*) and black and white spruce (*Picea mariana* and *P. glauca*) are present in the lowlands (Figure 14, Hultén, 1968). If the pollen spectra from the modern nearshore or mid-shelf samples are similar to the assemblages from site U1343 (Figure 6), we could infer that the vegetation of the adjacent coast was also similar.



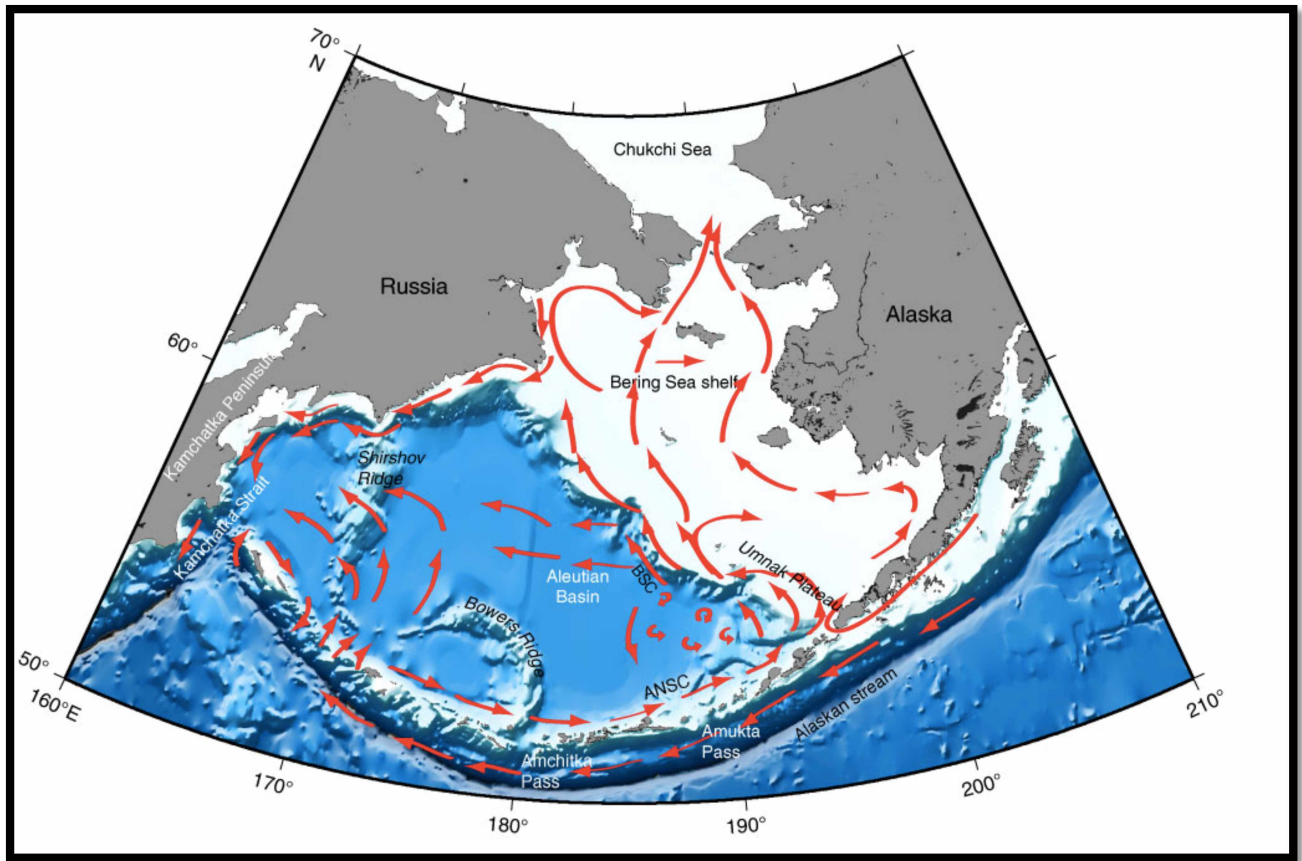
**Figure 14:** Vegetation map of Seward Peninsula from the Alaska Center for Conservation Science (Landcover Mapping, 2016).



At 82 km and 160 km from shore, respectively, Bering Sea transect samples SPH5 and SPH2 are located roughly the same distance from the modern coastline of the Seward Peninsula as IODP site U1343 was from the paleo-coastline of southcentral Beringia during past glacial maxima. Therefore, these samples are potential modern analogs for the effects of offshore transport on palynomorph assemblages, assuming past transport processes and pollen-vegetation relationships were similar to those today. However, there are multiple variables, such as marine currents, wind directions, and adjacent island vegetation that could affect the modern pollen spectra.

The prevailing travel direction for water currents in the Bering Sea is south to north, toward the Bering Strait (Figure 15, Expedition 323 Scientists, 2010; Stabeno et al., 1999). The prevailing winds in this area are southerly in the summer months and northeasterly in the winter months (Figure 16, Alaska Energy Authority, 2005).

Islands between the shoreline and the edge of the Bering Sea shelf that could contribute significantly to the regional modern pollen rain include St. Lawrence and St. Matthew. Both are barren at higher elevations, with lowlands that consist of dwarf shrub, mesic sedge, and wet herbaceous tundra (Fleming, 1998). The Pribilof Islands and Nunivak Island are about 400 km from the transect and thus are expected to be lesser contributors to the modern pollen rain. The vegetation of Nunivak is predominantly moist herbaceous shrub tundra, with areas of tall shrub, wet sedge, and alpine tundra (Fleming, 1998). The Pribilofs are covered by a mix of tall shrub, low shrub, wet sedge, and alpine tundra (Fleming, 1998). *Betula nana* is found on St. Lawrence, St. Matthew, and Nunivak islands, but not on the Pribilof Islands. None of these islands fall within the modern range of *Picea*, *Alnus*, or other species of *Betula* (Hultén, 1968). Based on a recent study by Wang et al. (2017), St Paul, one of the Pribilof Islands, was likely never a



**Figure 15:** Bering Sea current directions (from Expedition 232 Scientists, 2010 and Stabeno et al., 1999).

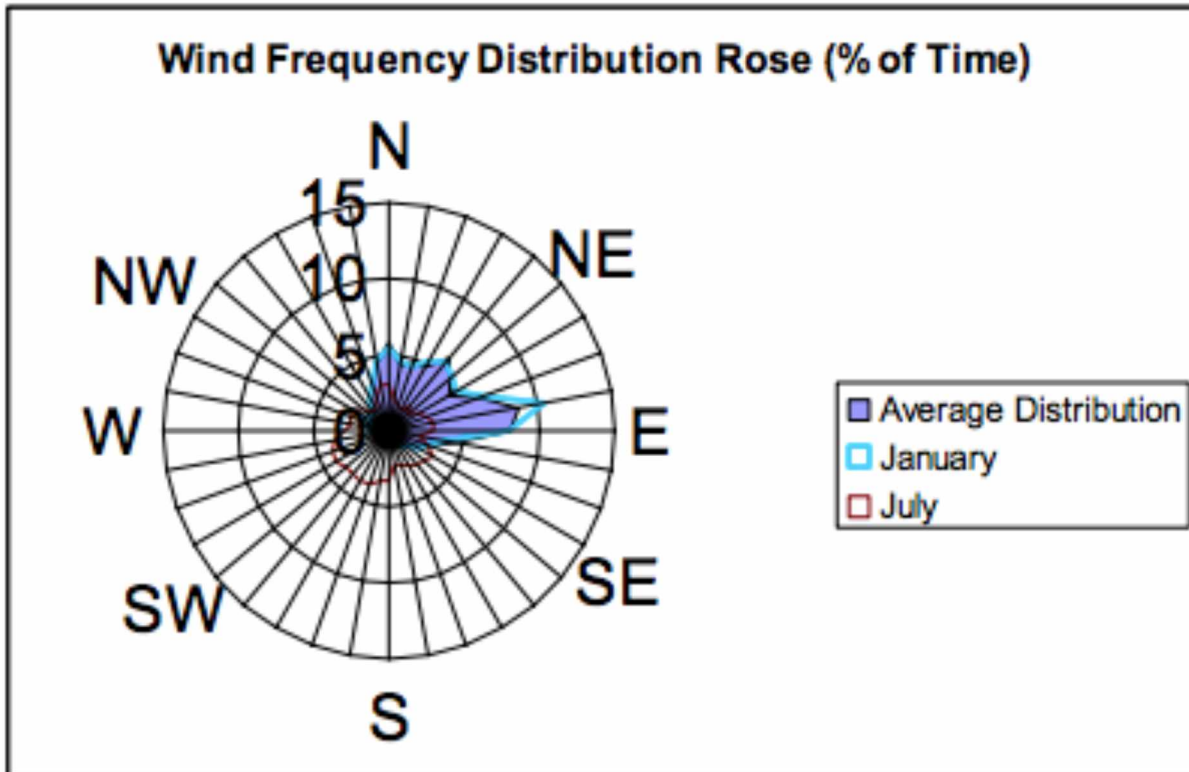


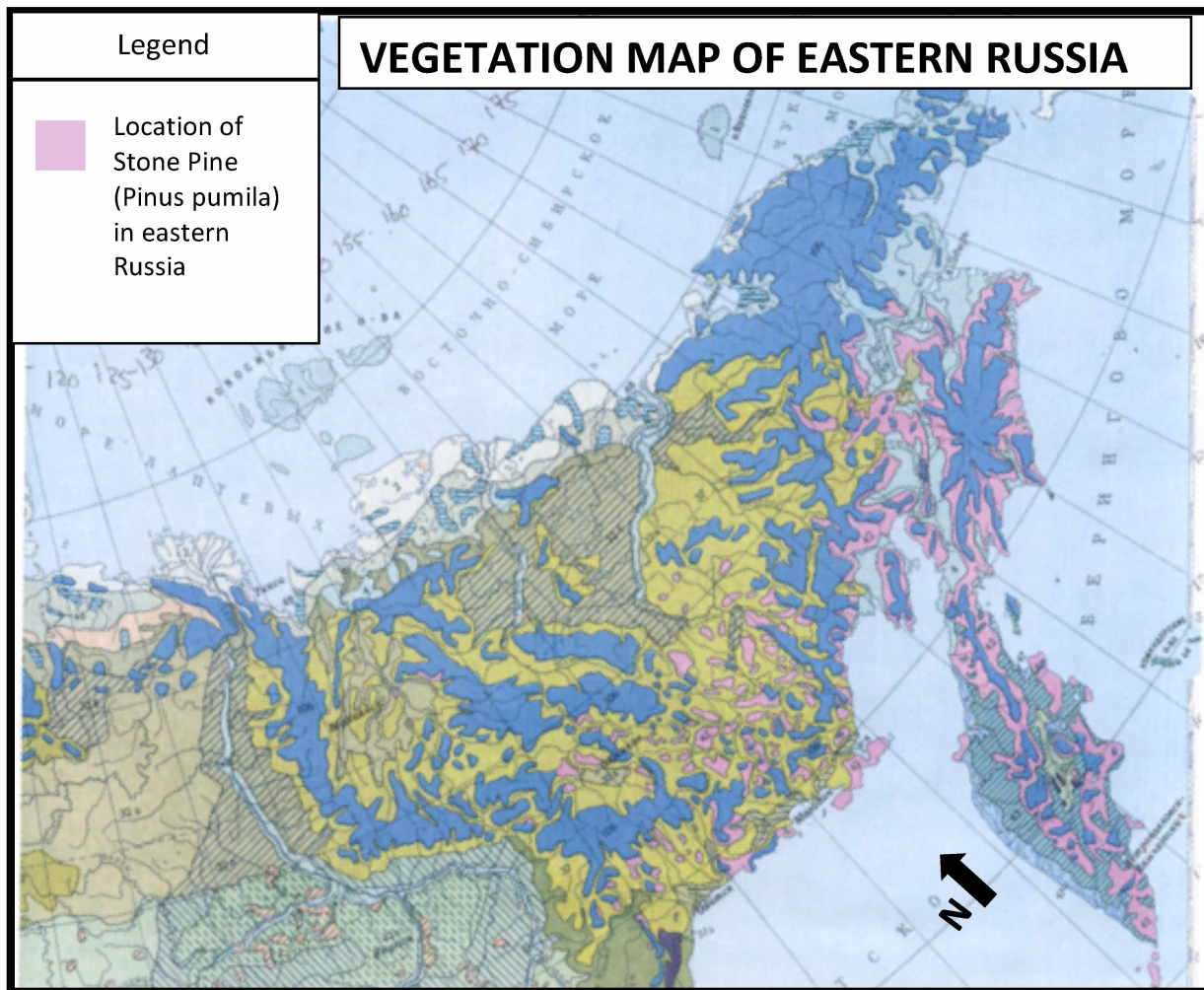
Figure 16: Wind frequency distribution rose (from Alaska Energy Authority, 2005).

refugium for these woody taxa. Records of sedaDNA indicate absence of these genera throughout the last 18,000 years, and palynological assemblages record little change between the modern and paleovegetation.

Due to the prevailing southeasterly summer winds, it is unlikely that wind transported modern pollen to sites west and south of St. Lawrence and St. Matthew islands. Whereas the vegetation on both islands consists of dwarf shrub, mesic sedge, and wet herbaceous tundra, I would expect to find more pollen from dwarf shrubs and sedges in the Bering Sea transect samples if the islands were the primary contributors to the modern pollen rain. Instead, the presence of pollen from tree and shrub taxa such as birch (*Betula*), spruce (*Picea*), and alder (*Alnus*), suggests that mainland Alaska is the primary source, as none of these taxa except shrub birch (*Betula nana*) are present on these islands (Hultén, 1968).

In addition to wind, marine currents could have transported pollen from coastal vegetation to sites on the Bering Sea shelf. The presence of pine (*Pinus*) in several samples suggests that some grains may have travelled all the way from Southeast Alaska, as *Pinus* is currently found only in the southeastern part of the state (Hultén, 1968). The other potential source of *Pinus* in the Bering Sea is eastern Russia, which also involve long distance transport, presumably by currents in the North Pacific (Figure 17). Very little *Pinus* is found in Bering Sea transect samples; it occurs in only 3 of the 5 samples at low frequencies (0.3 – 1.2%). Consistent with expectations for grains that have travelled long distances, the few grains present are in poor condition, many with the sacchi ripped from the body.

Located south or east of the Bering Sea sample sites, the Yukon-Kuskokwim Delta region may be a significant contributor of modern palynomorphs. There, two major rivers empty into the Bering Sea, and the vegetation is primarily moist herbaceous/shrub and tall shrub tundra with



**Figure 17:** Vegetation map of eastern Russia to show the location of stone pine (from Gerasimov, 1964).

stands of spruce and broadleaf trees (Fleming, 1998). Vegetation from the Yukon-Kuskokwim Delta are similar to those seen in the surface assemblages from the Bering Sea (Figure 10 and 14), indicating substantial similarities. Marine currents could have transported grains delivered by the Yukon and Kuskokwim rivers to sites SPH2 and SPH5 to the north. Whereas prevailing southeasterly winds would have carried pollen to the northwest, away from sites in the Bering Sea, there is some variation in the wind directions during the summer, with winds occasionally blowing from the northeast (Figure 16). Therefore, I infer that the pollen rain at the Bering Sea transect sites is derived primarily from the coastal vegetation of western Alaska and transported to sites of deposition by periodic northeasterly winds and/or marine currents.

The ordination diagram generated in CANOCO 4.5 is broken up into 4 quadrants, each dominated by different taxa. Samples from the Bering Sea shelf transect and site U1343 all plot in the same quadrant, which is populated by modern terrestrial samples derived primarily from moist herbaceous/shrub tundra with isolated stands of trees (Figures 9, 10, and 11) (Westbrook, 2014). Assemblages with more spruce (*Picea*) and birch (*Betula*) plot closer to the center of the ordination diagram. In general, DBSE, DLN4, SPH2, and Pop3a plot further from the center of the diagram, in the vicinity of IODP samples from glacial stages 8-16 and interglacial stage 15. The Bering Sea shelf sample located closest to modern shoreline, SPH5, plots closer to the center, near IODP samples from stages 3, 4, and 5 and some of the samples from stage 10 (Figure 10).

Despite minor variations in the proportions of trees, grass, sedge, and monolet spores, most of the IODP samples from glacial stages 1-16 plot adjacent to or between samples from the modern Bering Sea shelf transect (Figure 10). Therefore, I concur with Westbrook (2014) and tentatively conclude that the southcentral coast of emergent central Beringia was covered by

vegetation similar to that found today on the Seward Peninsula and in the Yukon-Kuskokwim Delta region: moist herbaceous/shrub tundra with intermittent stands of trees.

#### *4.4 Vegetation reconstruction from MIS 8, 10, 12, 14, 15, and 16*

Due to the lack of sage (*Artemisia*) pollen, the IODP samples from glacial stages are not indicative of a steppe tundra environment (Westbrook, 2014) such as those recovered from the margins of eastern Beringia (Elias and Crocker, 2008). Steppe tundra environments are characterized by the presence of sage (*Artemisia*) which thrives in arid climates, such as those found at high latitudes in modern day Russia and Greenland (Elias and Crocker, 2008). Instead, the IODP assemblages contain small, but persistent amounts of tree and shrub pollen, including *Betula*, *Alnus*, and *Picea*. Whereas percentages of individual taxa are typically less than 10%, total percentages of tree and shrub pollen range from 20% to 37%. Based on these results, I infer that scattered spruce trees and tall shrubs, such as birch and alder, occupied coastal refugia in central Beringia during glacial stages.

According to White et al. (1977), there is a correlation between site paludification and temperature, with less saturation during colder 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. Samples from MIS 8, 14, 15, and 16 have peak values of  $P_{est}$  ( $>10$ ), indicating dryer conditions during these MIS stages (Figure 6). In the case of MIS 15, an interglacial stage, it seems likely that factors other than temperature and sea ice affected the humidity. One such factor suggested by Guthrie (2001) is the influence of clearer skies in upland areas, this would increase moisture loss, creating a drier environment. Conversely, the presence of cloud cover, at lower elevations in central

Beringia (Guthrie, 2001), may explain data for greater paludification during MIS 8, 14, and 16.

#### *4.4.1 MIS 16*

According to the ordination diagrams, samples from MIS 16 are indicative of moist herbaceous/shrub tundra (Figures 9 and 11). However, minor amounts of woody boreal forest taxa could indicate the presence of glacial refugia. Samples from MIS 16 plot between the Bering Sea shelf samples DBSE and Pop3a/DLN4. Sample DBSE is located farthest from the present day shoreline and Pop3a/DLN4 are located mid-shelf. The three MIS 16 samples have ages of 623 kya, 668 kya, and 676 kya; the other two samples were deposited earlier in MIS 16 (Figure 3) during times of relatively high or fluctuating sea level (Lisiecki and Raymo, 2005). The youngest sample from MIS 16 plots closest to DBSE, suggesting that it may also have been relatively far from shore. It is possible that deposition of this sample occurred near the end of MIS 16, during deglaciation.

#### *4.4.2 MIS 15*

Bering Sea transect sample DBSE is the closest modern analog for three of the pollen assemblages from MIS 15 (Figure 10). It is also the sample farthest from the present day coastline, very near the shelf edge, which is compatible with the premise that sea level was higher during interglacial stages, and the paleocoastline was much farther away from the sample site. As previously stated, the samples from MIS 15 needed secondary processing with hydrofluoric acid in order to dissolve numerous diatoms. Diatom abundance has been linked to increased biological marine productivity during interglacial periods (Nair et al., 2015).

Overall, the pollen and spore assemblage reflects the same mesic herbaceous shrub tundra environment as MIS 8, 14, and 16 but with lower percentages of tree and shrub taxa (15 – 21%). It must be noted, however that samples from MIS 15 have the most conclusive evidence



for both reworking and long distance transport. Four of the five samples analyzed from MIS 15 contained large amounts (50+ individual grains) of total broken or damaged pollen grains, many of which were damaged to the point that they could not be identified. Both color variability and the proportion of damaged grains are more common in samples from MIS 15, possibly due to the increased biological activity (from marine organisms like zooplankton and phytoplankton), higher sea level, and increased travel distance from shoreline to the sample site. Because these samples exhibit the largest variation in the color of the grains, ranging from brownish to bright pink, I argue that these samples are likely to contain reworked grains from prior assemblages. Thus the evidence suggests that it is the interglacial assemblages, rather than the glacial assemblages, that contain higher proportions of grains reworked from prior stages.

Whereas the total percentages of tree pollen are significantly lower (15 – 21%) than in the samples from glacial stages, this is not generally true of interglacial assemblages. Samples analyzed by Westbrook (2014) from MIS 1 and 5 contain greater proportions of tree taxa and plot closer to the center of the diagram (Figure 10). Either woody taxa were present in lower abundances during MIS 15, or woody taxa were present in similar abundances, and the differences are a result of selective transport across the shelf or varying degrees of reworking from prior glacial stages.

#### *4.4.3 MIS 14*

Two MIS 14 samples plotted closest to DLN4 and Pop3a (Figures 9), the two samples from the Bering Sea transect that are located mid-shelf. The other MIS 14 sample plotted closer to SPH2. The implication is that MIS 14 may have been a milder glaciation, leaving sea level higher and placing IODP site U1343 farther from the shoreline than usual during glacial stages.

This is supported by Lisiecki and Raymo (2005) (Figure 3) who found evidence for higher sea levels during MIS 14 compared to the preceding and subsequent glacial stages.

Due to the undamaged condition of the spruce (*Picea*) grains, which have all of their sacci attached, and the lack of notable color differences, there is no clear evidence for the presence of reworked grains in the MIS 14 samples.

#### *4.4.4 MIS 12*

Samples from MIS 12 plot closely together on Figure 10, and some overlap with assemblages from MIS 8, 10, and 15. The overlapping MIS 12 samples plot closest to DBSE, the Bering Sea sample farthest from shore. The proximity of these samples indicates that the palynological assemblages from MIS 12 and 10 are very similar and potentially travelled similar distances from the paleoshoreline during their respective glacial stages.

#### *4.4.5 MIS 10*

Samples from MIS 10 have a particularly large spread on Figure 10. One sample plots near SPH5, the Bering Sea shelf sample closest to the shoreline. A second MIS 10 sample lies between SPH5 and DBSE, and the third plots near DLN4 and Pop3a. The variability in the MIS 10 samples could be caused by the delayed build-up of glacial ice at the MIS 10/11 boundary (Figure 3), as determined by Lisiecki and Raymo (2005). Delayed ice buildup would result in higher sea levels and longer distance transport via ocean currents. Therefore, part of the variability in MIS 10 samples may be attributed to differences in temperature, sea level and transport distance. Additional evidence for variable environmental conditions throughout MIS 10 are provided by the paludification index. A  $P_{est}$  value of 3 at 364 kya indicates relatively humid conditions at the transition from MIS 11 to MIS 10. A subsequent increase to a  $P_{est}$  of 11 at 335 kya signifies drier conditions later in MIS 10, when temperatures were presumably cooler and

sea ice more extensive. This is also seen in Figure 10, where the two older MIS 10 samples plot closer to the center of the diagram than the youngest sample.

#### *4.4.6 MIS 8*

Samples from MIS 8 plot closest to DBSE, the sample located farthest from shore on the Bering Sea shelf, or lie between DBSE, SPH2, and DLN4/Pop3a (Figure 10). There is also overlap between samples from MIS 8, 14, and 16, which could indicate similar coastal vegetation cover and possibly a similar distance from the paleoshoreline.

#### *4.4.7 Westbrook IODP samples*

As previously stated, the ages of Westbrook's (2014) samples have been adjusted to conform to the updated age model provided by Asahi et al. (2016). All of the data from Westbrook's samples, the IODP samples presented herein, and the Bering Sea transect were included in the CANOCO 4.5 PCA and ordination diagrams (Figure 10). Westbrook's samples plotted in the same quadrant as my IODP samples and the Bering Sea transect, indicating mesic herbaceous/shrub tundra. However, the majority of Westbrook's samples contained less grass (Poaceae) and therefore plotted closer to the center of the graph. Most of Westbrook's samples surround Bering Sea shelf sample SPH5, located closest to the modern shoreline.

Westbrook's interglacial samples have a larger spread in the quadrant than any of the glacial samples, similar to my samples from MIS 15. The samples that plot adjacent to SPH5 are from MIS 2, 3, 4, 5, 6, and 10. However, three of the interglacial samples, two from MIS 1 and one from MIS 5, are grouped together close to Bering Sea shelf sample DBSE, which is located farthest from the shoreline. Two other MIS 5 interglacial samples are outliers that plot far away from all other IODP and Bering Sea transect samples, though still in the same quadrant. These samples contain more spores and less grass than any of the other samples, which pulls them

toward the monolete spore axis and away from the bulk of the samples. The increased presence of spores is indicative of a wetter environment during stage 5 (Westbrook, 2014). These outliers are due to sampling an earlier, and consequently warmer period of MIS 5.

#### *4.5 Modern analogs*

Based upon the PCA and ordination diagrams (Figures 9, 10, and 11, and Westbrook, 2014), all of the IODP and the Bering Sea shelf samples plot in the quadrant populated by modern terrestrial samples collected from sites surrounded by mesic herbaceous/shrub tundra. This indicates that the paleovegetation was similar to the modern vegetation type in the vicinity of the Yukon-Kuskokwim Delta and Seward Peninsula, which is classified as moist herbaceous/shrub tundra with stands of trees (Fleming, 1998).

Each of the individual Bering Sea shelf samples is a close modern analog for at least one of the IODP samples (Figure 10). The sample furthest from shore, DBSE, is the closest modern analog for samples from MIS 1, 8, 12, and 15, while samples from MIS 2, 3, 4, 5, 6, and 10 are most similar to assemblages from SPH5; MIS 14 is most similar to assemblages from SPH2. DLN4 and Pop3a are most similar to samples from MIS 8, 10, and 14. However, glacial samples from intervals of lowest sea level do not all plot near to SPH5. Evidently, distance from shoreline is not the only variable influencing the composition of the IODP assemblages in Figure 10. Additional sources of variation include selective transport, due to prevailing wind and water currents, or minor differences in the source vegetation driven by changes in temperature and humidity.

#### 4.6 *Refugium hypothesis*

Consistent amounts of tree and shrub taxa (19 to 37%) are present throughout the IODP samples from glacial stages, and the majority are unbroken and well preserved. Thus glacial stages 8, 10, 12, 14, and 16 all contain evidence of glacial refugia for woody plant taxa on the southern coast of central Beringia. This is consistent with the findings of Brubaker et al. (2005), who suggested that minor but consistent abundances of spruce, birch, and alder at sites in eastern Beringia suggest that these trees and shrubs survived MIS 2 within Beringia.

These results contradict Wang et al. (2017), who conclude that woody refugia were absent from southern coastal Beringia. Although their pollen spectra also indicate low but persistent percentages of *Picea*, *Betula*, and *Alnus*, coincidence of greater abundance with intervals of minimal influx are interpreted as evidence of long-distance transport to the coring site on St. Paul Island (Wang et al., 2017). Although influx calculations were not performed due to uncertainties in the sedimentation rate, no correlation between abundance and concentration (Figure 6) is evident in the data presented herein. Instead, the percentages of woody taxa recovered from glacial assemblages appear to be independent of pollen concentrations. Samples with low concentrations do not correlate with higher percentages of woody taxa. Taken together with the preponderance of unbroken *Picea* pollen grains, I find that the concentration data favors a local source over long-distance transport for spruce and other woody plant taxa.

Slightly lower abundances of tree and shrub taxa (14 to 20%) are present in samples from MIS 15 compared to the samples from glacial stages. These interglacial samples were presumably transported from the coast of eastern Beringia. Higher percentages of damaged and unidentifiable grains are consistent with long-distance transportation across the submerged shelf.

In addition, greater color variability within these assemblages indicates a greater proportion of reworked grains compared to the assemblages from glacial stages. This is also consistent with transportation across a previously vegetated shelf.



## Chapter 5: Conclusions

### 5.1 Key points

Palynological analysis, PCA and community ordination diagrams of assemblages from IODP Expedition 323 site U1343, in conjunction with modern terrestrial and marine assemblages from Alaska and the Bering Sea shelf, support the following conclusions:

1. Based upon the presence of minor amounts of well-preserved woody taxa in assemblages from glacial stages 2-16, the lowlands of Central Beringia provided an ice age refugium for boreal trees and shrubs, including birch (*Betula*), alder (*Alnus*), and spruce (*Picea*).
2. The vegetation recorded in the IODP pollen assemblages is similar throughout glacial stages 2-16 (Figure 10). Surprisingly, interglacial samples from MIS 15 contain lesser amounts of pollen from tree taxa and higher proportions of damaged grains. These assemblages also exhibit greater variation in grain color, indicative of reworking. Therefore, samples from interglacial stage 15 appears to contain a greater number of reworked grains than samples from glacial stages 8-16.
3. Identification of modern analogs indicates that the paleovegetation was similar to the modern vegetation type in the vicinity of the Yukon-Kuskokwim Delta and Seward Peninsula, which can be classified as moist herbaceous/shrub tundra with stands of trees.



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## Appendix

### A.1 Tables

#### T.1 MIS boundaries of IODP samples

Sample Name	Old MIS	New MIS	New Ages (kya)
U1343E_1H02	1	1	10.7
U1343E_1H03	1	1	13.7
U1343E_1H04	2	2	18.7
U1343E_1H05	2	2	23.8
U1343E_2H03	3	3	47.5
U1343E_2H04	4	3	54.8
U1343E_2H05	4	4	59.8
U1343E_3H01	5	4	69.2
U1343A_3H04	5	5	73.9
U1343E_3H03	5	5	77.7
U1343A_3H05	5	5	78.1
U1343E_3H04	5	5	82
U1343A_3H06	5	5	82
U1343A_4H02	5	5	89
U1343A_4H03	5	5	92.9
U1343E_4H02	5	5	96.6
U1343A_4H04	5	5	96.7
U1343A_4H05	6	5	100.7
U1343A_4H06	6	5	104.8
U1343E_4H05	6	5	109
U1343E_4H06	6	5	116
U1343E_4H07	6	5	123
U1343E_5H02	6	5	129
U1343E_5H03	6	6	137
U1343E_5H04	6	6	146
U1343E_5H05	6	6	152
U1343A_9H03	N/A	8	258
U1343A_9H04	N/A	8	266
U1343A_9H05	N/A	8	270
U1343A_11H05	N/A	10	335

Sample Name	Old MIS	New MIS	New Ages (kya)
U1343A_11H06	N/A	10	344
U1343A_12H03	N/A	10	364
U1343A_14H02	N/A	12	431
U1343A-14H03	N/A	12	441
U1343A_14H04	N/A	12	449
U1343A_17H04	N/A	14	548
U1343A_17H05	N/A	14	554
U1343A_17H06	N/A	14	560
U1343A_20H02	N/A	15	567
U1343A_18H04	N/A	15	577
U1343A_18H05	N/A	15	583
U1343E_21H02	N/A	15	600
U1343E_21H03	N/A	15	607
U1343E_21H04	N/A	15	615
U1343E_21H05	N/A	16	623
U1343E_22H02	N/A	16	668
U1343E_22H03	N/A	16	676

*T.2 Raw data counts of IODP samples from Tilia with concentrations*

<b>IODP Sample Names</b>	<b>U1343 A_9H0 3</b>	<b>U1343 A_9H0 4</b>	<b>U1343 A_9H0 5</b>	<b>U1343 A_11 H05</b>	<b>U1343A _11H06</b>	<b>U1343A _12H03</b>	<b>U1343A _14H02</b>	<b>U1343A -14H03</b>
Pinus	0	0	0	3.5	0	0	1	0
Picea	10	13	7	11	20	22	10	30
Tsuga	0	0	0	0	0	0	0	0
Alnus	29	20	17	25	22	33	15	13
Larix	0	0	0	0	0	0	0	1
Betula	6	8	4	8	6	10	8	2
Betula nana	2	5	3	1	0	3	0	0
Salix	10	21	19	19	5	11	17	8
Ericales, undiff	17	20	21	18	20	10	8	16
Poaceae	122	124	131	135	180	148	147	151
Cyperaceae	98	79	91	74	47	63	88	88
Chenopodiaceae	1	8	6	6	0	0	6	1
Artemisia	5	1	0	0	0	0	0	0
Asteraceae	0	1	3	3	1	0	0	0
Pulsatilla ranunculaceae	0	0	0	0	0	0	0	0
Fungal undiff	128	60	73	42	56	35	97	89
Sphagnum	45	21	20	41	27	101	36	28
Botrychium	0	0	0	0	0	0	0	0
Selaginella	10	12	9	7	5	4	3	3
Pteridium	24	21	23	24	15	25	33	11
Lycopodium local	19	2	7	0	9	3	3	1
Athyriaceae	0	0	0	0	0	0	0	2
Trilete undiff	35	22	32	12	24	13	12	10
Monolete Undiff	88	59	37	24	28	14	35	44
Isoetes	3	2	4	2	7	3	3	4
Potamogenton	5	2	1	0	0	0	0	0
Pond lilly	3	0	0	0	5	0	0	0
Crumpled/ Damaged	19	10	2	7	4	3	3	4
Unknown	2	0	0	2	1	2	0	2
LycO Spike	248	216	174	215	207	192	143	192
Concentrations	11031	12056	15322	11625	12542	12796	17072	13038

<b>IODP Sample Name</b>	<b>U1343 A- 17H04</b>	<b>U1343 A- 17H05</b>	<b>U1343 A- 17H06</b>	<b>U1343 A- 20H02</b>	<b>U1343 A- 18H04</b>	<b>U1343 A- 18H05</b>	<b>U1343 E- 21H02</b>	<b>U1343 E- 21H03</b>
<b>Pinus</b>	0	1.5	0	1.5	0	1	1	1
<b>Picea</b>	16.5	15	6	27	8	13.5	11	11.5
<b>Tsuga</b>	0	2	1	0	0	1	0	0
<b>Alnus</b>	33	46	7	8	15	9	11	12
<b>Larix</b>	0	0	2	3	2	0	0	0
<b>Betula</b>	4	6	11	4	14	15	7	7
<b>Betula nana</b>	0	0	0	2	0	3	0	0
<b>Salix</b>	7	24	18	13	8	2	7	11
<b>Ericales, undiff</b>	16	16	36	5	5	6	12	5
<b>Poaceae</b>	141	118	194	152	166	174	190	188
<b>Cyperaceae</b>	81	69	25	82	93	74	62	65
<b>Chenopodiaceae</b>	2	4	0	1	1	2	0	0
<b>Artemisia</b>	0	0	1	4	3	0	0	0
<b>Asteraceae</b>	0	0	0	1	0	0	0	0
<b>Pulsatilla ranunculaceae</b>	0	0	0	0	0	0	0	0
<b>Fungal undiff</b>	90	98	53	57	55	16	31	46
<b>Sphagnum</b>	27	39	23	39	31	98	28	14
<b>Botrychium</b>	0	0	0	0	0	0	0	1
<b>Selaginella</b>	2	3	0	13	8	2	4	2
<b>Pteridium</b>	15	22	0	32	36	0	2	5
<b>Lycopodium local</b>	0	4	0	26	0	0	0	3
<b>Athyriaceae</b>	0	0	0	0	0	0	0	0
<b>Trilete undiff</b>	31	36	15	27	30	17	36	15
<b>Monolete Undiff</b>	59	78	12	54	84	12	44	11
<b>Isoetes</b>	5	3	0	3	3	0	2	1
<b>Potamogenton</b>	0	0	0	3	0	0	0	0
<b>Pond lilly</b>	4	4	3	0	0	0	0	0
<b>Crumpled/ Damaged</b>	11	27	5	9	18	25	8	8
<b>Unknown</b>	1	0	1	4	0	1	0	2
<b>Lycospike</b>	124	231	125	327	198	302	181	207
<b>Concentrations</b>	21094	11558	19778	8212	13817	8199	14601	11887



<b>IODP Sample Name</b>	<b>U1343E-21H-4</b>	<b>U1343E-21H-5</b>	<b>U1343E-22H-2</b>	<b>U1343E-22H-3</b>
Pinus	0	1	0	0
Picea	16	7	7	6.5
Tsuga	0	0	1	0
Alnus	10	25	36	38
Larix	0	0	0	0
Betula	12	4	7	3
Betula nana	0	2	0	0
Salix	2	18	18	0
Ericales, undiff	4	11	19	11
Poaceae	178	122	118	131
Cyperaceae	76	91	83	98
Chenopodiaceae	1	8	6	6
Artemisia	0	2	0	2
Asteraceae	1	0	1	0
Pulsatilla ranunculaceae	0	9	4	5
Fungal undiff	8	35	54	52
Sphagnum	28	17	15	25
Botrychium	0	0	2	2
Selaginella	3	10	9	5
Pteridium	1	26	0	0
Lycopodium local	1	2	5	2
Athyriaceae	0	0	0	0
Trilete undiff	8	21	35	60
Monolete Undiff	26	51	41	35
Isoetes	0	0	0	0
Potamogenton	1	1	3	0
Pond lilly	2	2	0	0
Crumpled/Damaged	12	10	30	41
Unknown	1	0	5	0
Lycospike	183	211	153	124
<b>Concentrations</b>	<b>13298</b>	<b>11937</b>	<b>17374</b>	<b>22531</b>

*T.3 Percentage data of IODP samples from Tilia*

IODP Sample Name	U1343 A_9H 03	U1343 A_9H0 4	U1343 A_9H0 5	U1343A _11H05	U1343A _11H06	U1343A _12H03	U1343A _14H02	U1343 A_14H 03
Alnus	9.7	6.7	5.6	8.2	7.3	11	5	4.2
Artemisia	1.7	0.3	0	0	0	0	0	0
Asteraceae	0	0.3	1	1	0.3	0	0	0
Athyriaceae	0	0	0	0	0	0	0	0.5
Betula	2	2.7	1.3	2.6	2	3.3	2.7	0.6
Betula nana	0.7	1.7	1	0.3	0	1	0	0
Botrychium	0	0	0	0	0	0	0	0
Chenopodiaceae	0.3	2.7	2	2	0	0	2	0.3
Crumpled/ Damaged	19	10	2	7	4	3	3	4
Cyperaceae	32.7	26.3	30.1	24.4	15.6	21	29.3	28.4
Ericales, undiff	5.7	6.7	7	5.9	6.6	3.3	2.7	5.2
Fungal undiff	29.9	16.7	19.5	12.2	15.7	10.4	24.4	22.3
Isoetes	0.6	0.5	0.9	0.5	1.7	0.6	0.7	1
Larix	0	0	0	0	0	0	0	0.3
Lycospike	248	216	174	215	207	192	143	192
Lycopodium local	3.6	0.5	1.6	0	2.2	0.6	0.7	0.2
Monolete Undiff	16.8	13.4	8.5	5.8	6.7	3	8.2	10.7
Picea	3.3	4.3	2.3	3.6	6.6	7.3	3.3	9.7
Pinus	0	0	0	1.2	0	0	0.3	0
Poaceae	40.7	41.3	43.4	44.5	59.8	49.3	49	48.7
Pond lilly	1	0	0	0	1.6	0	0	0
Potamogeton	1.6	0.7	0.3	0	0	0	0	0
Pteridium	4.6	4.8	5.3	5.8	3.6	5.4	7.8	2.7
Pulsatilla ranunculaceae	0	0	0	0	0	0	0	0
Salix	3.3	7	6.3	6.3	1.7	3.7	5.7	2.6
Selaginella	1.9	2.7	2.1	1.7	1.2	0.9	0.7	0.7
Sphagnum	8.6	4.8	4.6	9.9	6.5	21.8	8.5	6.8
Trilete undiff	6.7	5	7.4	2.9	5.8	2.8	2.8	2.4
Tsuga	0	0	0	0	0	0	0	0
Unknown	2	0	0	2	1	2	0	2

IODP Sample Name	U1343A_14H04	U1343 A_17H 04	U1343 A_17H 05	U1343 A_17H 06	U1343 A_20H 02	U1343 A_18H 04	U1343 A_18H 05	U1343 E_21H 02
Alnus	11	11	15.3	2.3	2.6	4.8	3	3.7
Artemisia	0	0	0	0.3	1.3	1	0	0
Asteraceae	0	0	0	0	0.3	0	0	0
Athyriaceae	0	0	0	0	0	0	0	0
Betula	1	1.3	2	3.7	1.3	4.4	5	2.3
Betula nana	1.7	0	0	0	0.7	0	1	0
Botrychium	0	0	0	0	0	0	0	0
Chenopodiaceae	2	0.7	1.3	0	0.3	0.3	0.7	0
Crumpled/Damaged	11	11	27	5	9	18	25	8
Cyperaceae	27.3	27	22.9	8.3	27	29.5	24.6	20.6
Ericales, undiff	3.7	5.3	5.3	12	1.6	1.6	2	4
Fungal undiff	23.8	23	24.5	15	15.8	14.9	5.1	9.3
Isoetes	1.4	1.1	0.6	0	0.6	0.6	0	0.5
Larix	0	0	0	0.7	1	0.6	0	0
Lycos Spike	172	124	231	125	327	198	302	181
Lycopodium local	0.5	0	0.8	0	5.2	0	0	0
Monolete Undiff	6.2	13.4	16	3.4	10.9	16.6	2.8	10.6
Picea	7.5	5.5	5	2	8.9	2.5	4.5	3.7
Pinus	0.3	0	0.5	0	0.5	0	0.3	0.3
Poaceae	40.3	46.9	39.1	64.5	50.1	52.7	57.9	63.1
Pond lilly	0.7	1.3	1.3	1	0	0	0	0
Potamogenton	0	0	0	0	1	0	0	0
Pteridium	1.9	3.4	4.5	0	6.4	7.1	0	0.5
Pulsatilla ranunculaceae	0	0	0	0	0	0	0	0
Salix	5.3	2.3	8	6	4.3	2.5	0.7	2.3
Selaginella	2.9	0.5	0.6	0	2.6	1.6	0.5	1
Sphagnum	8.4	6.1	8	6.6	7.8	6.1	22.8	6.7
Trilete undiff	6.5	7.1	7.4	4.3	5.4	5.9	4	8.6
Tsuga	0	0	0.7	0.3	0	0	0.3	0
Unknown	1	1	0	1	4	0	1	0

IODP Sample Name	U1343E_21H0 4	U1343E_21H0 5	U1343E_22H0 2	U1343E_22H0 3
Alnus	3.3	8.3	12	12.6
Artemisia	0	0.7	0	0.7
Asteraceae	0.3	0	0.3	0
Athyriaceae	0	0	0	0
Betula	4	1.3	2.3	1
Betula nana	0	0.7	0	0
Botrychium	0	0	0.5	0.5
Chenopodiaceae	0.3	2.7	2	2
Crumpled/Damaged	12	10	30	41
Cyperaceae	25.3	30.3	27.7	32.6
Ericales, undiff	1.3	3.7	6.3	3.7
Fungal undiff	2.6	10.4	15.3	14.8
Isoetes	0	0	0	0
Larix	0	0	0	0
Lycospike	183	211	153	124
Lycopodium local	0.3	0.5	1.2	0.5
Monolete Undiff	7.1	11.9	10.1	8.1
Picea	5.3	2.3	2.3	2.2
Pinus	0	0.3	0	0
Poaceae	59.3	40.7	39.3	43.6
Pond lilly	0.7	0.7	0	0
Potamogeton	0.3	0.3	1	0
Pteridium	0.3	6.1	0	0
Pulsatilla ranunculaceae	0	3	1.3	1.7
Salix	0.7	6	6	0
Selaginella	0.8	2.3	2.2	1.2
Sphagnum	7.6	4	3.7	5.8
Trilete undiff	2.2	4.9	8.6	14
Tsuga	0	0	0.3	0
Unknown	1	0	5	0

*T.4 Raw data counts of Bering Sea transect samples from Tilia with concentrations*

Bering Sea Transect Sample Name	SPH5	SPH2	POP 3a	DLN4	DBSE
Pinus	0	3.5	1	2	0
Picea	14	13	11	10	4
Tsuga	1	2	0	0	0
Alnus	52	44	40	47	23
Betula	18	0	12	3	0
Betula nana	10	0	6	4	2
Salix	20	18	11	16	0
Ericals, undiff	20	10	0	26	24
Poaceae	124	130	133	96	131
Cyperaceae	101	79	82	87	125
Chenopodiaceae	9	1	5	6	0
Artemisia	0	0	0	3	0
Asteraceae	6	3	9	2	3
Pteridium	0	1	0	3	0
Fungal undiff	40	23	15	31	59
Sphagnum	14	15	27	22	10
Botrychium	0	0	0	0	0
Selaginella	1	8	8	7	11
Isoetes	1	1	0	0	2
Lycopodium local	6	9	2	0	4
Athyriaceae	0	0	0	0	0
Trilete undiff	61	44	63	96	40
Monolete Undiff	38	47	63	88	58
Nymphaeaceae	1	7	0	2	0
Sagittaria	8	5	11	8	0
Crumpled/Damaged	56	29	53	45	50
Stratiotes aloides	0	0	0	10	0
Diphasiastrum	0	0	0	2	0
Lycy Spike	187	173	201	168	221
Concentration data	24908	22063	21284	28417	19147

*T.5 Percentage data of Bering Sea transect samples from Tilia*

Bering Sea Transect Sample Name	SPH5	SPH2	POP 3a	DLN4	DBSE
Pinus	0	1.2	0.3	0.7	0
Picea	3.7	4.3	3.5	3.3	1.3
Tsuga	0.3	0.7	0	0	0
Alnus	13.9	14.5	12.9	15.6	7.4
Betula	4.8	0	3.9	1	0
Betula nana	2.7	0	1.9	1.3	0.6
Salix	5.3	5.9	3.5	5.3	0
Ericals, undiff	5.3	3.3	0	8.6	7.7
Poaceae	33.1	42.8	42.9	31.8	42
Cyperaceae	26.9	26	26.5	28.8	40.1
Chenopodiaceae	2.4	0.3	1.6	2	0
Artemisia	0	0	0	1	0
Asteraceae	1.6	1	2.9	0.7	1
Pteridium	0	0.2	0	0.6	0
Fungal undiff	9.6	7	4.6	9.3	15.9
Sphagnum	2.8	3.5	5.7	4.2	2.3
Botrychium	0	0	0	0	0
Selaginella	0.2	1.9	1.7	1.3	2.5
Isoetes	0.2	0.2	0	0	0.5
Lycopodium local	1.2	2.1	0.4	0	0.9
Athyriaceae	0	0	0	0	0
Trilete undiff	12.3	10.3	13.3	18.5	9.2
Monolete Undiff	7.7	11	13.3	16.9	13.3
Nymphaeaceae	0.3	2.2	0	0.6	0
Sagittaria	2.1	1.6	3.4	2.5	0
Crumpled/Damaged	56	29	53	45	50
Stratiotes aloides	0	0	0	3.1	0
Diphasiastrum	0	0	0	0.4	0
Lycospike	187	173	201	168	221