Delayed postglacial colonization of *Betula* in Iceland and the circum North Atlantic

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DEDICATION

This study is dedicated to the memory and scientific legacy of Prof. Sarah E. Crump (1987-2022).

ABSTRACT

As the Arctic continues to warm, woody shrubs are expected to expand northward. This process, known as "shrubification", has important implications for regional biodiversity, food web structure, and high-latitude temperature amplification. While the future rate of shrubification remains poorly constrained, past records of plant immigration to newly deglaciated landscapes in the Arctic may serve as useful analogues. We provide one new postglacial sedimentary ancient DNA (*sed*aDNA) record of vascular plants from Iceland and place a second Iceland postglacial *sed*aDNA record on an improved geochronology; both show Salicaceae present shortly after deglaciation whereas Betulaceae first appears more than 1000 years later. We find a similar pattern of delayed Betulaceae colonization in eight previously published postglacial sedaDNA records from across the glaciated circum North Atlantic. In nearly all cases, we find that Salicaceae colonizes faster than Betulaceae and that Betulaceae colonization is increasingly delayed for locations farther from glacial-age woody plant refugia. These trends in Salicaceae and Betulaceae colonization are consistent with the plant families' species diversity, environmental tolerances, seed sizes, and soil preferences. As these reconstructions capture the migration of vascular plants during a past period of high latitude warming, a slow response of some woody shrubs to ongoing warming may delay Arctic shrubification and future changes in the structure of tundra ecosystems and temperature amplification.

INTRODUCTION

As the planet warms, the Arctic is warming at 2 to 4 times the global rate (Rantanen et al., 2022). This warming is impacting Arctic ecosystems through a process known as 'shrubification', or the northward expansion and increased height and density of deciduous woody vegetation (Tape et al., 2006; Myers-Smith et al., 2011; Elmendorf et al., 2012; Sweet et al., 2015). Arctic shrubification alters the structure of tundra ecosystems, its regional biodiversity, food web structure, and nutrient availability (Elmendorf et al., 2012; Fauchald et al., 2017; Collins et al., 2018). Arctic shrubification also has implications for the climate system by reducing surface albedo (Sturm et al., 2005) and increasing atmospheric water vapor (Pearson et al., 2013) – both positive feedbacks that amplify high latitude warming (Thompson et al., 2022). However, large uncertainties remain regarding the rate of future shrubification, such that the magnitude of these positive feedbacks is poorly constrained in predictive earth system models. One way to reduce future climate uncertainties is through the analysis of well-constrained paleoenvironmental records dating to warmer-than-present periods in Earth's recent history (e.g., Tierney et al., 2020).

Traditionally, macrofossils and pollen have formed the backbone of Quaternary paleovegetation reconstructions (Birks, 2018). However, macrofossils are not consistently preserved in sedimentary records, and pollen production is restricted to seed-bearing taxa, which can be obscured by long-distant transport from sources 1000s of km away (Hyvärinen, 1970; Birks, 2003; Crump et al., 2019). For example, in Iceland, exotic tree pollen from taxa never reported as macrofossils since the Miocene and Pliocene (i.e., *Pinus*, *Quercus, Corylus, Alnus,* and *Ulmus*, Denk et al., 2011a, b) are found in Early Holocene sedimentary records following retreat of the Icelandic Ice Sheet (Caseldine et al., 2006; Eddudóttir et al., 2015). Hence, the first appearance of pollen need not reflect local colonization of a given taxon. Recent analytical advances in

sedimentary ancient DNA (*sed*aDNA) allow for more reliable vegetation reconstructions (e.g., Capo et al., 2021). Taxa identified by DNA in lake surface sediment closely match those in catchment vegetation surveys, confirming the local origin of DNA in lake sediment and improved reliability for taxa presence compared to pollen (Sjögren et al., 2017; Alsos et al., 2018). Past records of vascular plant *sed*aDNA can provide new insight into postglacial colonization patterns (Crump et al., 2019; Alsos et al., 2022) as well as the magnitude of vegetation response to temperature changes in prior warm periods (Clarke et al., 2020; Crump et al., 2021; Huang et al., 2021).

In this study, we examine *sed*aDNA records from ten North Atlantic lakes that track local vegetation assemblages since deglaciation, with particular attention to postglacial colonization patterns of two woody plant families, Salicaceae and Betulaceae. Of ten total lake records, we present one new Icelandic record and modify the age model of a second previously published record from Iceland. For these two lakes, we also compare existing pollen and *sed*aDNA datasets from the same locations to highlight the power of *sed*aDNA in pinpointing each taxon's first appearance. Collectively, the North Atlantic vascular plant DNA data sets demonstrate that Salicaceae colonized deglaciated lands quickly, whereas Betulaceae was delayed by up to several thousand years. As these colonization patterns occurred during a period of high latitude warming, our datasets suggest that ongoing warming may also lead to different northward expansion rates of woody shrubs. As a result, the biosphere's role in future high latitude temperature amplification may be delayed.

RESULTS AND INTERPRETATION

Stóra Viðarvatn, Iceland

Stóra Viðarvatn (#4, Table 1, Figure 1) is a large lake (surface area: 2.4 km^2, depth: 48 m) in northeast Iceland, with no pre-existing records of Holocene vegetation change. In winter 2020, we recovered sediment core 20SVID-02 from 17.4 m water depth near the center of the lake. The core contains 893 cm of sediment. The basal 20 cm are laminated, clay-rich sediment, transitioning to organic gyttja by 873 cm depth, which characterizes the remainder of the record with periodic tephra (volcanic ash) deposits (Figure S1). The chronology of the Early to Middle Holocene portion of the record is based on 5 tephra layers (see Materials and Methods), of which the lowest, at 886.5 cm depth, is identified as the Askja S tephra (10830 ± 57 BP, Bronk Ramsey et al., 2015), and the highest, at 334 cm depth, as Hekla 4 (4200 ± 42 BP, Dugmore et al., 1995). Because the sedimentation rate between the six tephra layers is essentially linear, we extrapolate that rate from the Askja S tephra layer to the base of the sediment core at 893.5 cm depth, which provides a minimum deglaciation age of ~10950 BP (Figure S2A).

Samples for *sed*aDNA analysis were taken from 75 equi-spaced depths throughout core 20SVID-02. Of these, 73 yielded amplifiable vascular plant DNA using the trnL P6 loop primer. The two samples that failed (810 and 856.5 cm depth) were sampled adjacent to tephra layers and likely diluted by minerogenic sediment. Following data filtering (see Materials and Methods), the trnL dataset yields 16,073,415 total reads, with an average of 214,312 reads per sample. qPCR cycle threshold (C_T) values, which reflect PCR efficient and the quantity of suitable target sequences for amplification, average 32.1 across samples. While there is inter-sample variation in DNA reads and C_T values, linear regressions show nearly stable temporal trends (Figure S3), which indicates that the availability of DNA to PCR amplification is consistent throughout the record. As

PCR amplification results in sequence read abundances that may not reflect original relative abundances in a sample (Nichols et al., 2018), we focus our discussion on taxa presence/absence. We identified 53 taxa throughout Stóra Viðarvatn's lake sediment record. Of the key woody shrub taxa, Salicaceae is present at the base of the core (892.5 cm depth, 10850 BP) and is present nearly continuously through the core. Betulaceae first appears ~2300 years later (701.5 cm depth, 8560 BP), and has a sporadic presence in samples above that level (Figure 2A).

Torfdalsvatn, Iceland

Torfdalsvatn (#3, Table 1, Figure 1) is a small lake (surface area: 0.41 km^2, depth: 5.8 m) in north Iceland from which sediment cores have been analyzed since the early 1990s to create paleoecological records from proxies such as pollen and macrofossils (Björck et al., 1992; Rundgren, 1995, 1998), and *sed*aDNA (Alsos et al., 2021). The paleovegetation records derived from pollen/macrofossils and *sed*aDNA were constructed from separate sediment cores that have independent age models derived from radiocarbon and tephra layers of known age. To temporally compare the two sediment records, radiocarbon ages need to be calibrated using the same calibration curve, correlative tephra layer ages must agree, and age model construction requires a common method (i.e., linear interpolation vs. Bayesian). For the pollen/macrofossil records (Rundgren 1995, 1998), this required calibrating the radiocarbon ages using IntCal20 (Reimer et al., 2020) and application of a Bayesian age modeling approach that informs sediment rate changes with prior information (Blaauw and Christen, 2011) (see Geirsdóttir et al., 2020). For the *sed*aDNA record (Alsos et al., 2021), only a revision of tephra ages was required to ensure that the two age models were in close agreement (see Methods and Materials).

Our revised age model for the Early Holocene portion of the pollen/macrofossil record (Figure S2B, Geirsdóttir et al., 2020) sets the timing of deglaciation, inferred from the onset of organic sedimentation at 801 cm depth, to 11800 BP. For the *sed*aDNA record, we adjust the age of the Saksunarvatn Ash/G10ka Series tephra layers (10400 to 9900 BP) following the recent dating of these layers in Iceland (Harning et al., 2018, 2019; Óladóttir et al., 2020) and apply the same basal age of 11800 BP as determined in the pollen/macrofossil record. In doing so, the *sed*aDNA record features a linear sedimentation rate and is now synchronized to the pollen record by the G10ka Series tephra layers (Figure S2C).

While the newly synchronized age models for the pollen/macrofossil and *sed*aDNA records feature common tephra layers, variable resolution between the two records increases uncertainty when comparing the timing of proxy changes. Therefore, differences on the order of centuries between the pollen/macrofossil and *sed*aDNA records may be artifacts of chronological uncertainty. Pollen of both woody shrubs, Salicaceae (*Salix spp.*) and Betulaceae (*Betula spp.*), first appear by ~11800 BP (Figure 3, modified from Rundgren, 1995). The oldest *B. nana* macrofossil dates to ~9300 BP, similarly to macrofossils of *S. herbacea* (~9400 BP) and *S. phylicifolia* (~9300 BP) (modified from Rundgren, 1998). The trnL *sed*aDNA data indicate that Salicaceae did not colonize Torfdalsvatn's catchment until ~10300 BP, whereas Betulaceae arrived later at ~9500 BP (modified from Alsos et al., 2021, Figure 2A).

Resolving Icelandic records of woody taxa colonization

Based on the original age model, Torfdalsvatn pollen records were interpreted to capture ecological changes associated with the abrupt climate oscillations between the Bølling-Allerød (14700 to 12900 BP) and Younger Dryas periods (12900 to 11700 BP) (Björck et al., 1992;

Rundgren, 1995). However, calibration of the radiocarbon ages in the Torfdalsvatn cores (Geirsdóttir et al., 2020) suggest that the organic-rich portion of the record began less than 11800 years ago (Figure S2B). While there is sediment at deeper levels, it is described as silty clay (Björck et al., 1992) with sand and gravel (Rundgren, 1995). These characteristics suggest that the sediment likely originates from a rapidly deglaciating environment, perhaps with lingering ice sheet meltwater in the catchment and a rapid sediment accumulation rate that is difficult to constrain without secure age control. Therefore, we suggest that the minimum age for the final retreat of the Icelandic Ice Sheet from Torfdalsvatn's catchment, when organic-rich sedimentation began, is ~11800 BP, several thousand years later than previously proposed. We use the updated age models to improve the history of plant colonization in Iceland.

We observe differences in taxa presence/absence between the *sed*aDNA and pollen records from Torfdalsvatn, which may reflect different mechanisms of transport. *Sed*aDNA for both Salicaceae and Betulaceae from Torfdalsvatn shows a colonization lag relative to deglaciation, whereas pollen from both taxa are present, albeit in low abundance, in the oldest sediment samples (Figure 3). This is most likely explained by the local catchment origin of *sed*aDNA (Sjögren et al., 2017), versus pollen, which can be transported by wind from 1000s of km away (Caseldine et al., 2006; Eddudóttir et al., 2015). Therefore, the occurrence of low pollen counts prior to the corresponding identification with *sed*aDNA (Alsos et al., 2021) likely reflects long-distance transport from southern sources rather than local establishment in the catchment – an inference supported by a lack of *Salix* and *Betula* macrofossils during this interval (Figure 3, Rundgren, 1998). While poor preservation could explain the delay in *sed*aDNA as well, the corresponding sediment is rich in clay (Rundgren, 1995), which preferentially binds with and stabilizes DNA (Kanbar et al., 2020), making poor preservation unlikely. Moreover, other vascular plants are

identified by DNA before Salicaceae and Betulaceae DNA appear, suggesting adequate DNA preservation for PCR amplification (Alsos et al., 2021). Therefore, we conclude that the colonization of Salicaceae and Betulaceae were delayed by 1700 and 2500 years, respectively, after local deglaciation of Torfdalsvatn's catchment.

Relative to Torfdalsvatn, the catchment of Stóra Viðarvatn deglaciated ~1000 years later at ~10850 BP (Figure 2A). Based on our new *sed*aDNA record, Salicaceae colonized the catchment rapidly, as it was identified in the lowermost sample at ~10850 BP, whereas Betulaceae does not appear in the record until 8560 BP, more than 2000 years later. Considering C_T values are relatively stable throughout the entire Holocene record (Figure S3), the delayed appearance of Betulaceae does not likely result from preservation bias. While Stóra Viðarvatn does not have any independent paleovegetation records, a pollen record from a nearby peat section Ytra-Áland in Thistilfjörður (Karlsdóttir et al., 2014), ~12 km to the east, provides a useful cross-examination of woody shrub colonization patterns. In the Ytra-Áland record, *Salix* pollen is found in high counts well above the mean in the lowermost sample dated to 10400 BP, suggesting bona fide presence (Figure 4). For *Betula*, there is limited to no pollen present until ~8000 BP (Figure 4). Despite the coarser resolution of Ytra-Áland's age model, which only has two tephra layer dates bounding the timing of first appearance of these taxa (10400 BP and 7050 BP, Karlsdóttir et al., 2014), there is remarkable agreement between lake and peat records for the arrival of Salicaceae and Betulaceae in northeast Iceland. Based on the *sed*aDNA records from TORF and SVID, we find that as the Icelandic Ice Sheet receded and exposed new land Salicaceae colonized the landscape 0 to 1700 years after inferred deglaciation, whereas Betulaceae colonization was further delayed by several thousand years. The earlier presence of low concentrations of Salicaceae and Betulaceae pollen is most likely derived from long distance wind dispersal.

DISCUSSION

Postglacial *sed*aDNA records from the circum North Atlantic

Eight additional records of vascular plant *sed*aDNA from lake sediments located around the North Atlantic that were glaciated during the Last Glacial Maximum are available to compare with the Icelandic data (see Material and Methods for details). These include records from Baffin Island (*n*=1, Crump et al., 2019), northern Greenland (*n*=1, Epp et al., 2015), Svalbard (*n*=2, Alsos et al., 2016; Volstad et al., 2020), northern Norway (*n*=3, Rijal et al., 2021; Alsos et al., 2022), and southern Norway (*n*=1, ter Schure et al., 2021) (Figure 1). All eight records have age control derived from calibrated radiocarbon ages. Except for Baffin Island, we infer minimum ages of deglaciation based on the age of the oldest sediment.

Baffin Island: Lake Qaupat (#1, Figure 1) is a small lake (surface area: 0.08 km^2, depth: 9.2 m) situated at 35 m asl on southern Baffin Island. Cosmogenic ^{10}Be exposure dating of Lake Qaupat's impounding moraine constrains the timing of deglaciation to 9100 ± 700 BP (Crump et al., 2019). Lake Qaupat and most of its catchment were below sea level until 7700 ± 300 BP, when postglacial isostatic recovery raised the basin above the rising postglacial ocean and its catchment was available for vascular plant colonization. Salicaceae are present in the record at that time, but no vascular plants are documented by *sed*aDNA in the older marine sediment. The first appearance of Betulaceae *sed*aDNA occurs at 5900 BP, more than 1000 years after Salicaceae and 2000 years after the lake and its catchment were above sea level (Crump et al., 2019).

Greenland: Bliss Lake (#2, Figure 1) is a small lake (depth: 9.8 m) situated at 17 m asl on the northern coastline of Greenland (Peary Land). Bliss Lake initially deglaciated by 11000 BP (Olsen et al., 2012) and the first tentative appearance of Salicaceae *sed*aDNA is found at 10800 BP, albeit with a low read count (Epp et al., 2015). Between 10480 and 7220 BP, the lake was

inundated by marine water (Olsen et al., 2012). The ultimate timing of Salicaceae colonization is conservatively interpreted from the onset of larger read counts at 7400 BP as sea level regressed and isolated the lake from the ocean (Epp et al., 2015).

Svalbard: Jodavannet (#5, Figure 1) is a small lake (depth: 6.4 m) situated at 140 m asl on the east coast of Wijdefjorden on northern Spitsbergen. Regional cosmogenic exposure dating suggests the area began to deglaciate between 14600 and 13800 BP (Hormes et al., 2013), although the base of Jodavannet's sediment record suggests a minimum timing of lake deglaciation by 11900 BP (Volstad et al., 2020). Salicaceae *sed*aDNA is first found at 9800 BP in Jodavannet, whereas Betulaceae was not detected with *sed*aDNA metabarcoding (Volstad et al., 2020). Lake Skartjørna (#6, Figure 1) is a small lake (surface area: 0.10 km^2, depth: 7.5 m) situated at 65 m asl on the west coast of Spitsbergen. As sea level fell due to glacial isostatic adjustment, Lake Skartjørna likely became isolated from the sea at ~13000 BP (Landvik et al., 1987), although the base of the recovered sediment record, which provides a minimum deglaciation age, is dated to 8600 BP (Alsos et al., 2016). Salicaceae *sed*aDNA is identified in Lake Skartjørna's basal sample at 8600 BP and Betulaceae is first identified at 7000 BP (Alsos et al., 2016).

Norway: Langfjordvannet (#7, Figure 1) is a small lake (surface area: 0.55 km^2, depth: 34.8 m) situated at 66 m asl on the coast of northern Norway (Rijal et al., 2021). Langfjordvannet deglaciated by 16150 BP, Salicaceae is first identified in *sed*aDNA by 15500 BP, and Betulaceae by 10000 BP (Alsos et al., 2022). Eaštorjávri South (#8, Figure 1) is a small lake (surface area: 0.06 km^2, depth: 5.4 m) situated at 260 m asl near the coast of northern Norway (Rijal et al., 2021). Eaštorjávri South deglaciated by 11060 BP, with Salicaceae *sed*aDNA identified in the basal sample at 11060 BP and consistently present above that level. Betulaceae is identified, albeit with low read counts, in the basal sample as well, but not identified in the overlying sample. Since

Betulaceae *sed*aDNA is not present with substantial read counts until 9950 BP (Alsos et al., 2022), we conservatively set this as Betulaceae's first appearance in Eaštorjávri South. Nordvivatnet (#9, Figure 1) is a small lake (surface area: 0.05 km^2, depth: 13.3 m) situated at 82 m asl on the coastline of northern Norway (Rijal et al., 2021). Nordvivatnet deglaciated by 12880 BP, with Salicaceae *sed*aDNA identified in the basal sample. Betulaceae *sed*aDNA is identified in the basal sample as well but below our cut-off for taxa presence (see Materials and Methods). The first sample with high read counts indicative of Betulaceae presence is at 12080 BP (Alsos et al., 2022), which we conservatively set as the timing of the taxa's first appearance in Nordvivatnet. Finally, Lake Ljøgottjern (#10, Figure 1) is a small lake (surface area: 0.02 km^2, depth: 18 m) situated at 185 m asl in southeastern Norway. Lake Ljøgottjern deglaciated by 9300 BP and both Salicaceae and Betulaceae *sed*aDNA were first detected by 7900 BP (ter Schure et al., 2021).

Betulaceae colonization lags Salicaceae in the circum North Atlantic

Following deglaciation, the timing of postglacial Salicaceae and Betulaceae colonization varies across the North Atlantic regions, with first-appearance dates ranging from 15500 BP in Norway to 5900 BP on Baffin Island (Figure 5). Salicaceae appears immediately after inferred deglaciation at 4 out of 10 sites, while colonization dates for the other 6 locations range from 200 to 2100 years after deglaciation and exhibit no clear spatio-temporal pattern (Figure 6). For Betulaceae, colonization times range from 800 to 6150 years after deglaciation, with sites closest to source refugia having generally shorter colonization delays (Figure 6), consistent with seedling viability having a higher probability of success with shorter distance from refugia source (Nathan, 2006). The one exception is Langfjordvannet, in northern Norway (site #7, Figure 1, Alsos et al., 2022), which deglaciated at 16150 BP (Figure 5). Considering that Betulaceae only arrives during the

Holocene Epoch (last 11700 years) across all North Atlantic sites, the anomalously long delay of Betulaceae to Langfjordvannet suggests that this taxon may have required the Holocene's relatively stable climate, as reflected by Greenland oxygen isotope records (Figure 5, Seierstad et al., 2014), to successfully establish itself. In contrast, Salicaceae appears to have been an efficient colonizer to Langfjordvannet during the less stable climate of the preceding Late Glacial period (Figure 5, Seierstad et al., 2014). Finally, except for Lake Ljøgottjern in southern Norway (site #10, Figure 1) where Betulaceae and Salicaceae apparently colonize at the same time (ter Schure et al., 2021), all other sites show that Betulaceae colonization is delayed by 800 to 5500 years relative to Salicaceae colonization dates (Figure 5).

Several possibilities may explain the delay in Betulaceae colonization compared to Salicaceae colonization. First, species diversity is greater for the Salicaceae family compared to Betulaceae family in the North Atlantic, and conventional DNA metabarcoding techniques cannot identify *sed*aDNA to the species level. Iceland, for example, has four native Salicaceae taxa (*S. herbacea, S. phylicifolia, S. lanata,* and *S. arctica*) and only two Betulaceae (*B. nana* and *B. pubescens*) (Kristinsson, 2008). The suite of Salicaceae taxa can collectively tolerate a wider range of environments than Betulaceae, including disturbed and nutrient limited substrate characteristic of deglacial environments (e.g., *S. herbacea,* Beerling, 1998). Second, Betulaceae seeds are generally heavier than Salicaceae seeds (dry mass, *B. nana* = 0.12 to 0.30 mg, de Groot et al., 1997; *S. herbacea* = 0.07 to 0.14 mg, Beerling, 1998). This mass difference would provide a higher probability of long-distance wind dispersal for Salicaceae compared to Betulaceae. Third, modern studies tracking the migration of Salicaceae and Betulaceae in the forefields of retreating glaciers and to new islands show a rapid and faster colonization of Salicaceae compared to Betulaceae (Whittaker, 1993; Magnússon et al., 2009; Burga et al., 2010; Synan et al., 2021). As an example,

following the formation of the volcanic island Surtsey in 1964 CE, Salicaceae (*S. herbaceae, S. lanata* and *S. phylicifolia*) colonized between 1995 and 1999 CE and Betulaceae has yet to arrive (Magnússon et al., 2009). Complimentary studies tracking soil and nutrient development at proglacial sites in the North Atlantic (Vilmundardóttir et al., 2014) suggest that Salicaceae is environmentally unconstrained (Whittaker, 1993; Glausen and Tanner, 2019), whereas Betulaceae requires more developed soil for its ultimate viability (Synan et al., 2021). Collectively, these studies demonstrate that Salicaceae is a more efficient pioneer than Betulaceae, particularly in newly deglaciated landscapes.

Dispersal mechanisms

Coupling the timing of postglacial woody shrub colonization in the North Atlantic with genetic approaches provides a valuable opportunity to identify probable dispersal mechanisms (e.g., wind, sea ice, driftwood, and birds) for long-distance transport. Previously, Alsos et al. (2015) compared amplified fragment length polymorphism (AFLP) data from living plants from Iceland, Greenland, Svalbard, the Faroe Islands, and Jan Mayen to AFLP data from the same species from potential source regions. Genetic distances suggest that *Betula* (*sp. nana* and *pubescens*) and *Salix herbacea* populations in most locations descend from ancestors in a western European Last Glacial Maximum (LGM) refugia (Alsos et al., 2009; Eidesen et al., 2015), and that each taxa underwent a broad-fronted and rapid migration to newly deglaciated regions (Alsos et al., 2015). *B. nana* on Svalbard likely descends from a Russian source (Alsos et al., 2015), and populations on Baffin Island and western Greenland originated from North America (Alsos et al., 2009). However, the relative roles of wind, sea ice, driftwood, and birds as transport vectors remain an open question.

Sea ice has been suggested to be a likely dispersal mechanism for postglacial vascular plants in the Arctic (Alsos et al., 2016). While sea ice persisted throughout the Holocene around Svalbard (Pieńkowski et al., 2021) and northern Greenland (Syring et al., 2020), general ocean circulation patterns require source populations of vascular plants in Arctic Siberia, from which sea ice is dominantly exported, for sea ice to be a viable vector. Considering that *B. nana* on Svalbard likely descends from a Russian refugia (Alsos et al., 2015), sea ice stands as a reasonable transport mechanism for this location. However, genetic data from Salicaceae (*S. herbacea*) on Baffin Island, Greenland, and Svalbard suggest that these populations descend from source populations in either mid-latitude North America or western Europe (Alsos et al., 2009; Eidesen et al., 2015), and neither region exports sea ice. This leaves wind and birds as likely mechanisms for *S. herbacea* transport to Baffin Island, Greenland, and Svalbard during the Holocene. North of Iceland, proxy evidence shows that sea ice disappeared by ~11200 BP (Figure 2B, Xiao et al., 2017) when surface ocean currents were established bringing warm Atlantic waters to the North Iceland Shelf (Figure 2C, Eiríksson et al., 2000; Sha et al., 2022), nearly 500 years before the colonization of the first woody taxon on the island (Figure 2A). With the absence of sea ice around Iceland's coastline during woody plant colonization, wind and/or birds remain the likeliest dispersal mechanisms for Iceland.

Future outlook

As the planet continues to warm, glacier and ice sheet mass loss is accelerating (Hugonnet et al., 2021), providing new territory for woody shrubs to colonize. Global warming will also allow woody plants to migrate poleward across unglaciated Arctic terrain (e.g., Myers-Smith et al., 2011). This process of "Arctic Greening" will feature positive feedbacks on Arctic warming

through reduced seasonal albedo and increased flux of water vapor into the atmosphere. However, the rate at which these migrations will occur is poorly constrained but is essential to inform climate and ecological predictions for policymakers. In this study, we demonstrate that while Salicaceae will probably migrate rapidly into warming habitats whereas Betulaceae may lag by millennia – an observation previously suggested for some regions of the Arctic (Davis and Shaw, 2001; Crump et al., 2019). While the causes and rates of present-day climate change are fundamentally different from the warming that followed the Last Glacial Maximum (e.g., Tierney et al., 2020), the factors driving the colonization patterns that we identify (i.e., environmental tolerance, seedling size, and soil development) are relevant in both scenarios. Therefore, it is likely that some woody shrubs will colonize recently deglaciated landscapes more efficiently than others, although the ability of these taxa to successfully follow the rapid pace of ongoing range shifts in non-glaciated tundra remains an open question (e.g., Davis and Shaw, 2001; Thuiller et al., 2009). As a result, circum North Atlantic shrubification may be prolonged – ultimately dampening the rate of changes in regional biodiversity and food web structure, as well as high-latitude temperature amplification.

MATERIALS AND METHODS

Lake sediment cores and age control

Stóra Viðarvatn (66.24°N, 15.84°W) is a large (2.4 km^2), deep lake (48 m) located at 151 m asl in northeast Iceland (Figure 1, Axford et al., 2007). In winter 2020, we recovered a composite 8.93 m long sediment core (20SVID-02, Fig. S1) from 17.4 m water depth using lake ice as a coring platform. The sediment was collected in 7 drives of ~150 cm each. The core sections were subsequently stored at 4 ºC before opening for sediment subsampling. The chronology of 20SVID-02 is based on 5 marker tephra layers (volcanic ash) of known age: Askja S, G10ka Series,

Kverkfjöll/Hekla, Kverkfjöll, and Hekla 4 tephra layers, with ages of 10830 ± 57 BP (Bronk Ramsey et al., 2015), 10400 to 9900 BP (Óladóttir et al., 2020), 6200 BP (Óladóttir et al., 2011), 5200 BP (Óladóttir et al., 2011) and 4200 ± 42 BP (Dugmore et al., 1995), respectively (see Supplemental Information). A Bayesian age model was generated using the R package rbacon and default settings (Blaauw and Christen, 2011) (Figure S2A).

Torfdalsvatn (66.06°N, 20.38°W) is a small (0.4 km^2), shallow (5.8 m) lake located at 52 m asl in north Iceland (Figure 1, Rundgren et al., 1997). Paleovegetation records from this lake are based on pollen, macrofossil assemblages (Björck et al., 1992; Rundgren, 1995, 1998; Rundgren and Ingólfsson, 1999), and *sed*aDNA (Alsos et al., 2021). Sediment cores from Torfdalsvatn were also recovered by a joint Colorado-Iceland team in 2004, 2008, 2012, and 2020. In modifying the lake sediment core chronologies, we use the recently calibrated age model (Figure S2B, Geirsdóttir et al., 2020) for the pollen/macrofossil records (Björck et al., 1992; Rundgren, 1995). We note that the ~12000 BP Vedde Ash has been previously identified in this record based on major oxide composition (Björck et al., 1992). However, the age of the Vedde Ash is stratigraphically too old for the radiocarbon-based chronology, suggesting that this tephra layer likely represents ash from a separate and subsequent volcanic eruption that produced the Vedde Ash, of which several possible correlations have been identified in Iceland and mainland Europe (e.g., Pilcher et al., 2005; Kristjánsdóttir et al., 2017; Matthews et al., 2011; Geirsdóttir et al., 2022). For the *sed*aDNA record, the Early Holocene portion of lake sediment core (Alsos et al., 2021) features two age control points, the so-called „Saksunarvatn Ash“ (10267 ± 89 BP) and a graminoid radiocarbon age (6620 ± 120 BP, Alsos et al., 2021). To better compare with the pollen/macrofossil record, we generated a new age model for the *sed*aDNA record (Alsos et al., 2021), using the lowermost radiocarbon age and the upper and lower limits of the main ~20 cm thick G10ka

414 Series/Saksunarvatn tephra unit (10400 to 9900 BP, e.g., Óladóttir et al., 2020). The new Bayesian
415 age model was generated using the R package rbacon and default settings (Blaauw and Christen,
416 2011) with the IntCal20 calibration curve (Reimer et al., 2020) (Figure S2C).
417
418 **DNA metabarcoding**
419 We subsampled the Stóra Viðarvatn sediment core halves immediately upon splitting in a
420 dedicated clean lab facility with no PCR products in the Trace Metal Lab, University of Colorado
421 Boulder. All surfaces and tools were treated with 10% bleach and 70% ethanol before use.
422 Personnel wearing complete PPE took a total of 75 samples using clean metal spatulas. Samples
423 were then stored in sterile Falcon tubes at 4°C until DNA extraction and metabarcoding. Sampling
424 resolution was based upon a preliminary age model with a sample estimated every 150 years.
425 We performed sample extraction and processing in a dedicated ancient DNA laboratory at
426 the Paleogenomics Lab, University of California Santa Cruz. All instruments and surfaces were
427 UV irradiated and treated with 10% bleach and 70% ethanol before use. For each subsample of
428 the core, we extracted two 50 mg replicates according to Rohland et al. (2018) using Binding
429 Buffer D. We pooled extraction replicates prior to subsequent experiments and included one
430 extraction control (containing no sample) for every 12 samples processed to assess the presence of
431 external contaminants or cross contamination.
432 We performed quantitative PCR (qPCR) to determine the ideal dilution of extract to add to
433 the metabarcoding PCR, as well as the ideal number of PCR cycles. We added 2 µl of neat or
434 diluted extract to wells containing 1X Qiagen Multiplex master mix, as well as a final
435 concentration of 0.16 µm of the forward and reverse trnL primer and 0.12X SYBR Green I Dye.
436 Cycling conditions were as follows: a 15 min 95C activation, followed by 40 cycles of 94C for 30

437 sec, 57C for 30 sec, and 72C for 60 sec. We tested 1:10 and 1:100 dilutions of extract to water
438 alongside neat extract. We used cycle threshold (C_T) values to compare PCR efficiency between
439 dilutions and determined the ideal cycle number for the metabarcoding PCR as the number of
440 cycles at which the PCR curve reached the plateau phase.

441 We performed metabarcoding PCR on each extract using the best dilution as determined
442 by qPCR and versions of the trnL primer set that contained attached truseq adapters (Table 2). We
443 used five replicate PCRs for each primer set and for each sample, with reaction conditions as
444 follows: 2 µl of diluted or undiluted extract in 1X Qiagen Multiplex Mix and a 0.16 µM
445 concentration of each primer at a total volume of 25 µl. Thermocycling began with 15 min at 95C,
446 followed by a number of cycles (as determined by qPCR) at 94C for 30 sec, 50-57C for 90 sec,
447 72C for 60 sec. We used one negative control PCR (no sample) alongside every 16 samples to
448 assess the possibility of contamination during the PCR set up. Extraction controls also underwent
449 metabarcoding. We cleaned reactions using SPRI select beads and eluted them into a final volume
450 of 20 µl.

451 We then used indexing PCR to attach the full truseq adapter and unique identifier. We
452 added 5 µl of cleaned PCR product from the metabarcoding PCR to 1X Kapa Hifi master mix and
453 dual-unique truseq style indices at a concentration of 0.4 µM. Thermocycling began with an
454 activation step at 98C for 3 min, followed by 8 cycles of 98C for 20 sec, 65C for 30 sec, 72C for
455 40 sec, and a final extension at 72C for 2 min. We cleaned reactions using SPRI select beads and
456 quantified DNA concentration using the Nanodrop 8000 Spectrophotometer. We pooled PCR
457 replicates from all samples in equimass ratios prior to sequencing on an Illumina Nextseq 550
458 sequencing platform using v3 chemistry and generating paired-end 76 bp reads.

We processed raw fastq files and performed taxonomic assignment using the Anacapa Toolkit (Curd et al., 2019) and the ArcBorBryo library, which contains 2280 sequences of Arctic and boreal vascular plants and bryophytes (Sønstebø et al., 2010). To minimize the chance of false positives, we retained only sequences that: 1) were not detected in negative controls, 2) had 100% match to sequences in the library, 3) had a minimum of 10 reads per PCR replicate and occurred in a minimum of two of five PCR replicates, and 4) had a minimum of 100 reads across all PCR replicates. We verified non-native taxa identified by this pipeline by comparison against the NCBI nucleotide database using BLAST (http://www.ncbi.nlm.nih.gov/ blast/) and removed these due to the low likelihood of correct taxonomic assignment.

Published *sed*aDNA datasets

To place the Icelandic plant *sed*aDNA datasets in the context of the circum North Atlantic, we compiled all existing lake *sed*aDNA records of vascular plants from this region that were formally glaciated during the Last Glacial Maximum (Figure 1, Table 1). These include records from Baffin Island (n=1, Crump et al., 2019), northern Greenland (n=1, Epp et al., 2015), Svalbard (n=2, Alsos et al., 2016; Volstad et al., 2020), northern Norway (n=3, Rijal et al., 2021; Alsos et al., 2022), and southern Norway (n=1, ter Schure et al., 2021). To ensure that all records were comparable, we excluded 7 records from northern Norway: Sandfjorddalen, Horntjernet, Gauptjern, Jøkelvatnet, Kuutsjärvi, Nesservatnet, Sierravannet (Rijal et al., 2021; Alsos et al., 2022). Nesservatnet and Sierravannet contained only Late Holocene records and thus do not capture local postglacial colonization patterns. A lack of supporting proxy records (e.g., carbon content) for Sandfjorddalen and Horntjernet meant it was unclear whether these two records capture the complete postglacial period. For Gauptjern, the inferred basal age (8776 BP) is inconsistent with the reconstructed

timing of deglaciation (~11000 BP, Hughes et al., 2016), which suggests the initial postglacial interval may be missing. Finally, both Jøkelvatnet and Kuutsjärvi were impacted by glacial meltwater during the Early Holocene when woody taxa are first identified (Wittmeier et al., 2015; Bogren, 2019), and thus the inferred timing of plant colonization is probably confounded in this unstable landscape by periodic pulses of terrestrial detritus. Unless otherwise specified, the timing of deglaciation at each site is inferred from the basal age of the sediment record.

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COMPETING INTERESTS

The authors declare that they have no competing interests.

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865 **TABLES AND FIGURES**

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867 Table 1: *Lake site information.*

Site #	Lake name	Region	Latitude (º)	Longitude (º)	Reference
1	Lake Qaupat	Baffin Island	63.68	-68.20	Crump et al. (2019)
2	Bliss Lake	Greenland	83.52	-28.35	Epp et al. (2015)
3	Torfdalsvatn	Iceland	66.06	-20.38	Alsos et al. (2021)
4	Stóra Viðarvatn	Iceland	66.24	-15.84	This study
5	Jodavannet	Svalbard	77.34	16.02	Volstad et al. (2020)
6	Lake Skartjørna	Svalbard	77.96	13.82	Alsos et al. (2016)
7	Langfjordvannet	Norway	70.15	20.54	Alsos et al. (2022)
8	Eaštorjávri South	Norway	70.43	27.33	Alsos et al. (2022)
9	Nordvivatnet	Norway	70.13	29.01	Alsos et al. (2022)
10	Lake Ljøgottjern	Norway	60.15	11.14	ter Schure et al. (2021)

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870 Table 2. *Primer Sequences used in metabarcoding and qPCR experiments.*

Primer	Sequence 5'-3'
truseq_trnL_g	ACACTCTTTCCCTACACGACGCTCTTCCGATCTGGGCAATCCTGAGCCAA
truseq_trnL_h	GTGACTGGAGTTCAGACGTGTGCTCTTCGATCT TTGAGTCTCTGCACCTATC

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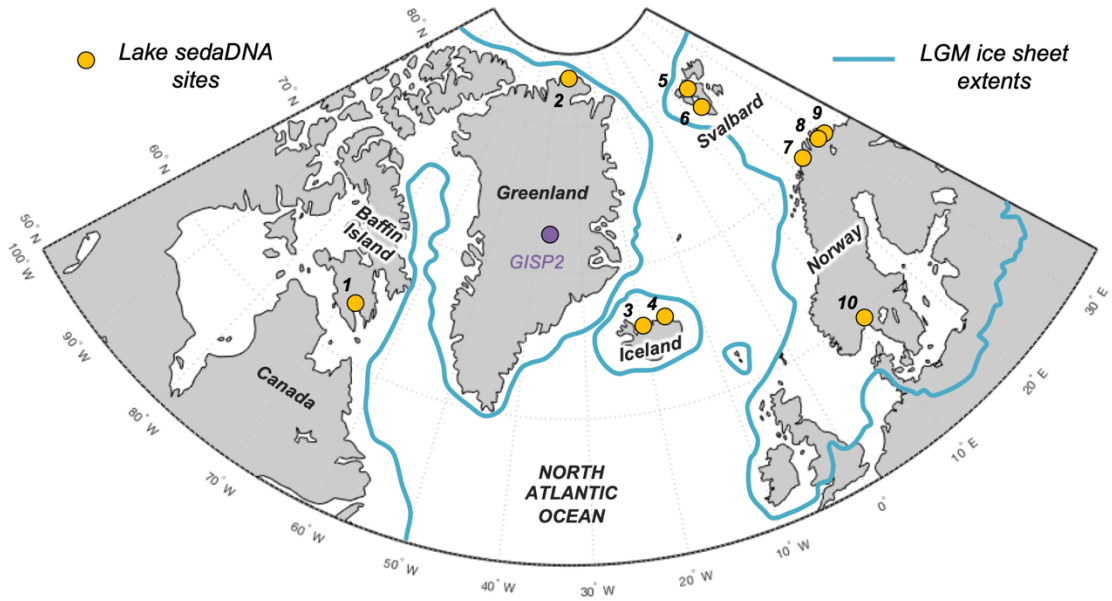

Figure 1: Overview map of the North Atlantic. Lake *sed*aDNA sites with vascular plant histories since local deglaciation shown in yellow (see Table 1 for site information). The extent of the Last Glacial Maximum (LGM) ice sheets is delineated in blue (Batchelor et al., 2019).

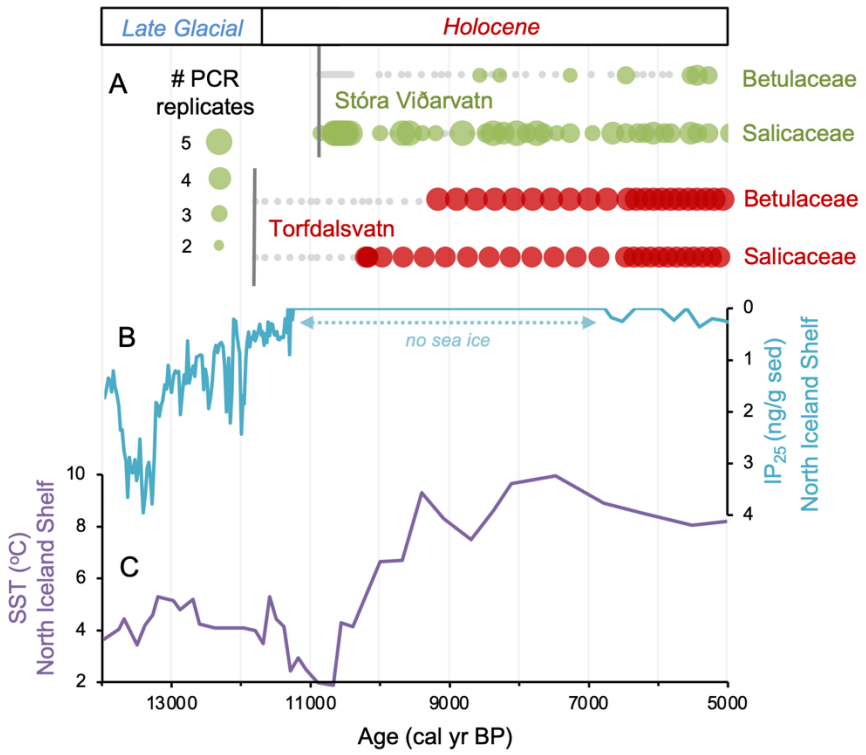

Figure 2: Comparison of paleoclimate and lake *sed*aDNA records from Iceland. A) Presence/absence *sed*aDNA record from Stóra Viðarvatn (green) and Torfdalsvatn (red) for Betulaceae and Salicaceae, where light gray markers denote that no taxa was detected. For Stóra Viðarvatn *sed*aDNA, the bubble size is proportional to the number of PCR replicates, and vertical dark gray lines denote the timing of each lake's deglaciation. B) Biomarker-proxy record of sea ice from the North Iceland Shelf (inverted), where greater concentrations of IP_{25} correspond to more sea ice (Xiao et al., 2017). C) Diatom-based SST record from the North Iceland Shelf (Sha et al., 2022).

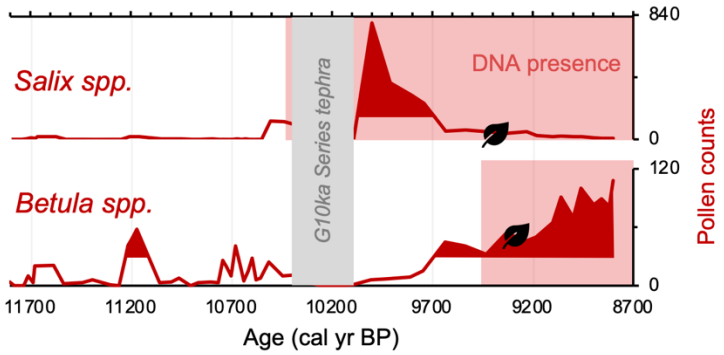

Figure 3: Simplified paleovegetation records from Torfdalsvatn for two taxa: *Salix spp.* and *Betula spp.* Shown are pollen counts (bold red lines), where shaded regions indicate values above the mean (Rundgren, 1995), first occurrence of taxa macrofossils (black leaves, Rundgren, 1998), and DNA presence (light red bars, Alsos et al., 2021).

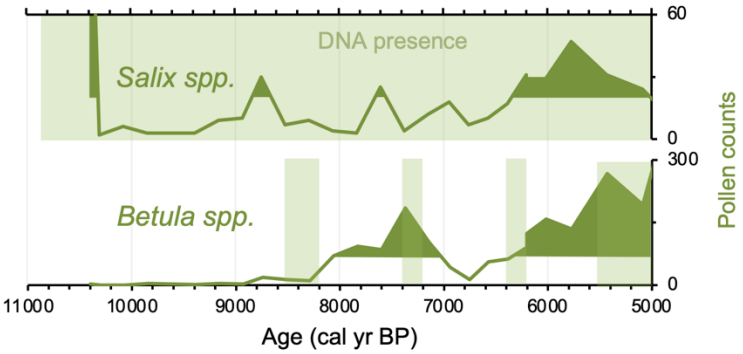

Figure 4: Simplified paleovegetation records from northeast Iceland for two taxa: *Salix spp.,* and *Betula spp.* Shown are Ytra-Áland pollen counts (bold green lines), where shaded regions indicate values above the mean (Karlsdóttir et al., 2014) and DNA presence (light green bars) from Stóra Viðarvatn (this study).

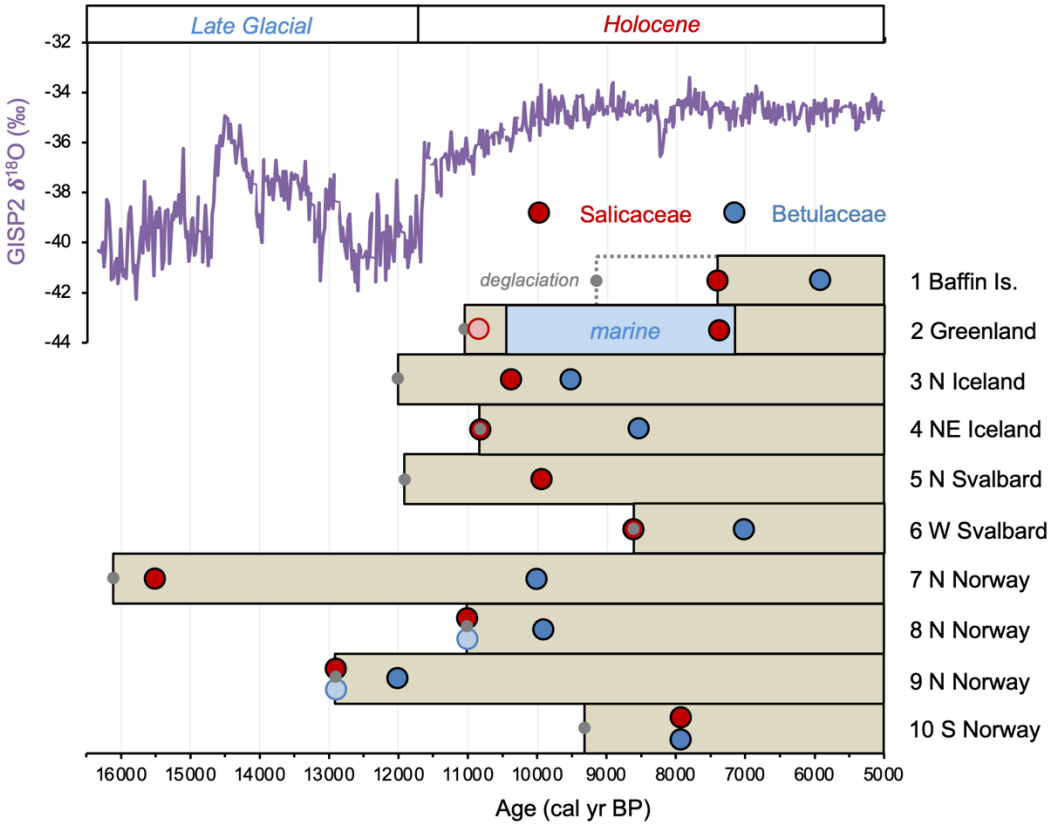

Figure 5: Timing of postglacial Salicaceae and Betulaceae colonization in the circum North Atlantic at 10 locations (see site numbers in Figure 1 and Table 1). A) GISP2 $\boldsymbol{\delta}^{18}$O reflective of regional North Atlantic temperature variability (Seierstad et al., 2014), and B) lake *sed*aDNA records of vascular plants, where the brown boxes reflect the extent of sedimentary record and the red/blue circles denote the first appearance of Salicaceae/Betulaceae (Epp et al., 2015; Crump et al., 2019; Alsos et al., 2016, 2021, 2022; Volstad et al., 2020; Rijal et al., 2021; ter Schure et al., 2021; this study). Light red and blue circles denote the presence of a low number of taxa reads, which we conservatively do not interpret to reflect genuine presence (e.g., Epp et al., 2015). Grey circles denote the minimum timing of local deglaciation inferred from basal core ages, and in the case of Baffin Island, cosmogenic radionuclide dating of the lake's impounding moraine (Crump et al., 2019).

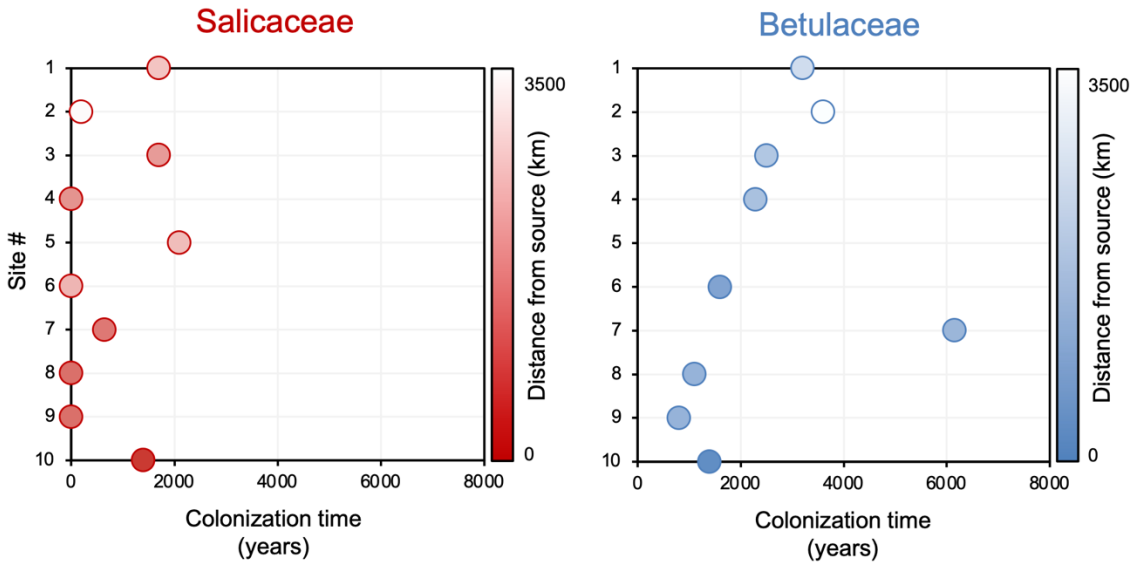

Figure 6: Colonization time after deglaciation for Salicaceae (red) and Betulaceae (blue) for all circum North Atlantic sites (see site numbers in Figure 1 and Table 1). Each point's color is scaled to the distance the lake is from the closest possible source outside the LGM ice sheet margins.