

Genetic legacies of past climate change on Arctic species: how past responses shape future impacts

Maria Dance

Wolfson College

University of Oxford



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Supervised by:

Professor Marc Macias-Fauria

Professor Erin Saupe

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Abstract

Major ecosystem changes are under way in the rapidly warming Arctic region. Sea ice loss and tundra shrub expansion are leading to ecological impacts across multiple biological, spatial, and temporal scales. The distribution and population dynamics of reindeer/caribou (*Rangifer tarandus* L.) — the most numerous and widespread large herbivore in the Arctic — and the dwarf birches (*Betula nana* L. and *Betula glandulosa* Michx.) — dominant tundra shrubs — will be affected. Understanding how these species responded to rapid and large-scale climate and sea ice changes in the past will increase our understanding of the long-term ecological and evolutionary implications of anthropogenic climate change. The impacts of past climate change on species leave genetic imprints in their living descendants, which, in turn, influence their genetic variation and capacity to adapt to future changes.

In this thesis, I aim to uncover how climate fluctuations in the Quaternary period (2.6 million years ago - present) shaped the population history of reindeer and the dwarf birches, to improve our understanding of ecological and evolutionary responses to past climate change. I analyse the contemporary genetic variation of these panarctic species in a phylogeographic approach. I model their population history and compare timings of inferred population events with those of climate and environmental changes using paleoenvironmental data. I then explore how the genetic legacies of past climate change impact responses to ongoing climate change in the dwarf birches, in the form of vegetation greening trends associated with the expansion of tundra shrubs. The thesis addresses this aim in three studies presented as research papers.

The first paper, '**Retracing the response of reindeer to postglacial climate change in Arctic islands**', compares reindeer population history and role of sea ice and ice sheet dynamics in postglacial island colonisation across two regions in the Arctic: the North American islands, and the Barents Sea islands. Using extant reindeer genetic variation, I modelled past population dynamics and tested hypotheses of glacial locations and postglacial dispersal. From the best supported models, I compared the timings of population isolation (genetic divergence) and connectivity (genetic admixture) with reconstructed and modelled changes in sea ice cover, glacial ice sheet dynamics, and other records of past environmental change.

I found that the best supported model suggested postglacial dispersal onto deglaciated Arctic islands from continental glacial locations, with modelled divergence times broadly in agreement with fossil data. Sea ice changes often coincided with population events, with differing impacts in the two geographically different systems. The compiled evidence suggests that ice sheet retreat, sea ice concentration, and ocean currents appear to be important influences on postglacial reindeer history and genetic structure in Arctic islands.

The second paper, '**Molecular footprints of Quaternary climate fluctuations in the circumpolar tundra shrub dwarf birch**', uses similar phylogeographical methods to the first paper, but with a novel genome-wide genetic dataset compiled across the geographical range of the dwarf birches. I compared the timing of population divergence and admixture with the ice sheet configuration obtained from published reconstructions, and used published pollen, macrofossil, and sedimentary DNA (sedaDNA) records to externally evaluate the demographic events inferred from the dwarf birches' present genetic configuration. The best supported model suggested a Mid-Quaternary origin of the dwarf birch species complex, likely in response to the global cooling and associated large climatic changes of the Mid-Pleistocene Transition. The results identified two distinct genetic groups in *Betula glandulosa* for the first time, which likely reflect glacial isolation north and south of the North American ice sheets. Population events were coeval with major climatic transitions, with interactions between ice sheet changes, climatic and environmental conditions in ice-free areas, and geographical constraints likely resulting in a complex population history. The results suggest that tundra shrubs such as the dwarf birches may have had more nuanced responses to past climatic changes than previously suggested, with implications for future eco-evolutionary responses to anthropogenic climate change.

The third paper, '**Arctic greening patterns reflect genetic legacies of glacial refugia and past climate change**' used the ongoing tundra shrub expansion trends, as measured by remotely sensed vegetation greening, as an opportunity to test whether the impacts of past climate change on the genetic structure of the dwarf birches may be influencing their response to contemporary climate change. I tested the association between population-level dwarf birch genetic diversity and genetic admixture, time since glacial ice sheet retreat, contemporary climate, and regional greening trends of the Arctic tundra and high latitude treeless areas. By modelling the relative importance of these factors, I was able to determine that

landscape history and genetic diversity in the form of historical genetic admixture are important but previously neglected components of high latitude vegetation greening trends. The relationship between greening trends and genetic diversity suggests that Arctic shrub expansion may be an adaptive response to climate change, and that future evolutionary potential may therefore be modulated by responses to past climate change.

Overall, this thesis demonstrates that postglacial climate change and glacial cycles influenced the evolution and population history of reindeer and the dwarf birches. Climatic fluctuations variously drove population isolation and connectivity. The impacts of these processes included driving allopatric speciation, generating diverse genetic lineages in different regions, enabling dispersal into deglaciated areas, and restoring connectivity between divergent lineages. Species responses were complex, with similar climatic processes resulting in different effects depending on geographical and temporal context. Finally, Arctic species responses to past climate change may impact their future population dynamics and evolution by influencing their contemporary genetic structure and adaptive potential, as illustrated by the link between the population history, genetic structure of the dwarf birches, and their response to ongoing climate change in the form of tundra vegetation greening. Reconstructing past species dynamics in relation to paleoclimatic changes is a useful aid for helping us understand the long-term ecological and evolutionary impacts of environmental change.

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List of Abbreviations

ABC: Approximate Bayesian computation

AFLP: Amplified Length Polymorphism

BIC: Bayesian Information Criterion

BLB: Bering Land Bridge

BSI: Barents Sea islands

CAA: Canadian Arctic Archipelago

Cal BP: calibrated years before the present

CAVM: Circumpolar Arctic Vegetation Map

cpDNA: chloroplast DNA

CTAB: Cetyltrimethyl ammonium bromide

DNA: Deoxyribonucleic acid

EVI: Enhanced vegetation index

EVI2: 2-band Enhanced vegetation index

EVI2_{max}: Maximum summer 2-band
Enhanced vegetation index

HadCM3: Hadley Centre Coupled Model,
version 3

ka: Thousands of years ago

LDA: Linear discriminant analysis

LDD: Long-distance dispersal

LGM: Last Glacial Maximum

MDS: Multidimensional scaling

mtDNA: Mitochondrial DNA

mya: Millions of years ago

MSE: Mean Square Error

NAAI: North American Arctic Islands

NDVI: Normalised difference vegetation
index

NDVI_{max}: Maximum summer Normalised
difference vegetation index

NGS: Next-generation sequencing

PCA: Principal Components Analysis

PCR: Polymerase Chain Reaction

RADSeq: Restriction site-associated
sequencing

sedaDNA: Sedimentary DNA

SML: Supervised machine learning

SNP: Single nucleotide polymorphism

TPD: Transpolar Drift

UPGMA: Unweighted Pair Group Method
with Arithmetic Mean

Chapter 1: Introduction



1.1 Overview

This thesis investigates historical species' responses to environmental change in the Arctic to provide insight into current changes through a phylogeographical approach (i.e., by studying contemporary genetic variation). The thesis focuses on two ecologically key panarctic organisms, reindeer/caribou (*Rangifer tarandus* L.) and dwarf birches (*Betula nana* L. and *Betula glandulosa* Michx.), which have been influenced by past climate change (Crump et al., 2019; Eidesen et al., 2015; Taylor et al., 2021; Yannic et al., 2014) and are currently being affected by ongoing climate change (Mallory, 2019; Mekonnen et al., 2021). The thesis aims to bridge these two, often disparate, research areas of ecological responses to past and present environmental change.

As an introduction to this research, in this chapter I will review the following concepts:

- a) Modern environmental changes in Arctic ecosystems and potential ecological and evolutionary consequences,
- b) The role of past climatic changes and sea ice conditions on the formation and biogeography of Arctic ecosystems, and
- c) Genetics as a tool to infer species responses to past (and future) climate change.

I also introduce the focal taxa of the thesis: reindeer/caribou and the dwarf birches, and review research and knowledge gaps on the use of contemporary genetic variation to infer responses to past climate change, and how these may affect adaptive potential to current climate change. Finally, I outline detailed aims and objectives and structure of the thesis where I state the hypotheses and how they were tested.

1.2 Changing Arctic ecosystems

The Arctic region is dominated by a large, ocean basin with seasonal and perennial sea ice, almost completely encircled by landmasses (**Figure 1.1**). The Arctic can be defined in geophysical terms as the area north of the Arctic Circle at 66°33'N: the latitude at which the sun does not set on the midsummer solstice and does not rise on the winter solstice. One ecological definition for the Arctic is the land north of the tree line, where the mean temperature of the warmest month is below 10-12°C (CAFF, 2013). The region contains varied marine and terrestrial ecosystems: lowland tundra, wetlands, mountains, polar

deserts, shallow marine shelves and deep ocean basins, large terrestrial ice sheets, glaciers, and ice shelves. The Arctic has also been the homeland of many peoples and nations for millennia (CAFF, 2013).

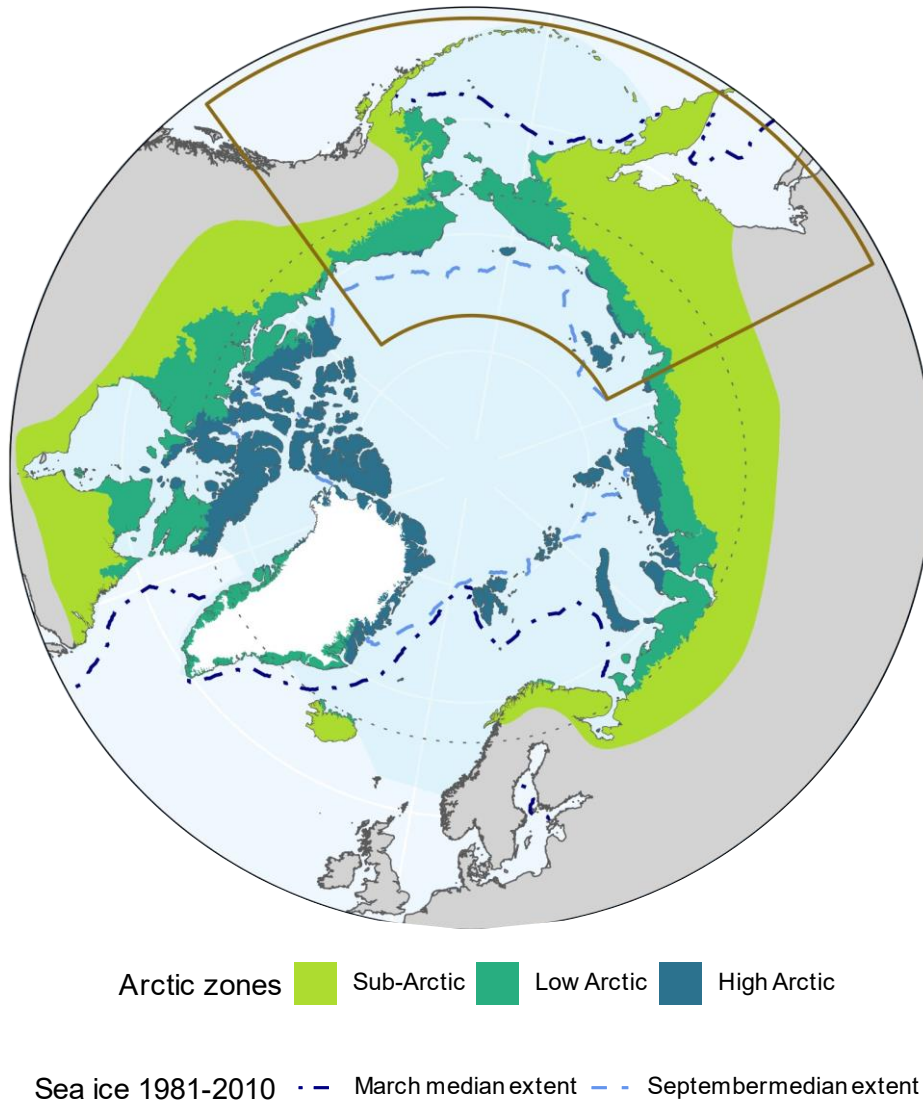


Figure 1.1. Overview of the Arctic region. The main bioclimatic zones of the Arctic and the sub-Arctic zone are mapped along with the Arctic circle at 66°33'N (fine dotted grey line) and maximum (March) and minimum (September) annual sea ice extents (dot-dash and dashed blue lines, respectively) for the climatological period 1981-2010. The sub-Arctic or forest tundra region is loosely delineated as the northernmost part of the boreal forest zone: the area between the timberline and the treeline (Meltofte et al., 2013). The Arctic zones are north of the treeline where the mean temperature of the warmest month is below 10-12°C. The separation between Low Arctic and High Arctic follows the boundary between bioclimatic sub-zones C (mean temperature of the warmest month 5-7°C) and D (mean temperature of the warmest month 7-9°C) of the Circum-Arctic Vegetation Map, approximately (Raynolds et al., 2019). The Arctic Ocean and adjacent marginal and gateway seas (Christiansen et al., 2013) are highlighted in a darker shade of blue. The Beringean refugial region (Hultén, 1937) is outlined in gold.

Arctic ecosystems are among the most rapidly changing on Earth (Isaksen et al., 2022; Post et al., 2019; You et al., 2021), with average warming rates four times greater than other regions over the last half century (Chylek et al., 2022; Rantanen et al., 2022), and even up to seven times greater in the Barents Sea region over the last two decades (Isaksen et al., 2022). Although many stressors affect the Arctic, anthropogenic climate change is the most serious threat to Arctic biodiversity (CAFF, 2013). Climate change has already led to sea ice loss, ice sheet and glacier retreat, changes in snow cover, permafrost thaw, and changes in the ratio of snow to rain, with feedbacks on global climate and on marine and terrestrial Arctic ecosystems (IPCC et al., 2019; You et al., 2021). The abundance and distribution of species is changing across the Arctic, as are ecosystem functions and processes (CAFF, 2013; IPCC et al., 2019).

1.2.1 Tundra shrub expansion (the “Greening of the Arctic”)

Some of the most visible changes are occurring in the Arctic tundra. Climate warming is driving an overall increase in terrestrial vegetation productivity and biomass, detectable as a “greening” signal in remote sensing imagery (Jia et al., 2003; Myneni et al., 1997; Zhou et al., 2001). This greening is largely attributable to the expansion of shrubs in recent decades (Martin et al., 2017; Mekonnen et al., 2021; Myers-Smith, Elmendorf, et al., 2015; Myers-Smith, Hallinger, et al., 2015; Sturm et al., 2001; Tape et al., 2006). A range of experimental and observational evidence at different spatial scales shows increased growth and abundance of woody plants (Mekonnen et al., 2021). *Alnus*, *Salix*, and *Betula* species are implicated in this trend in different regions (Myers-Smith et al., 2011). Shrub expansion occurs as (a) infilling of existing patches, either through lateral growth or recruitment, (b) an increase in an individual’s growth, particularly canopy height, and (c) advancing shrublines into areas previously beyond range limits (Myers-Smith et al., 2011). Shrub growth sensitivity to climate is higher at elevational and northern range limits (Myers-Smith, Elmendorf, et al., 2015), but currently range expansion appears to be mostly elevational (Myers-Smith & Hik, 2018). Expansion beyond current latitudinal limits is, however, predicted (Dial et al., 2016; Myers-Smith & Hik, 2018; Pearson et al., 2013; Reji Chacko et al., 2023).

Shrub expansion will have wide-ranging impacts on tundra ecosystems. Taller shrubs can outcompete and displace other vegetation under warmer conditions (Chapin et al., 1995;

Mekonnen et al., 2021). The increase in shrub abundance appears to be at the expense of non-woody herbaceous and non-vascular plants and is associated with declines in tundra diversity (Myers-Smith et al., 2011; Post et al., 2013). The response of shrub species to changing climate (Krab et al., 2018; Saccone et al., 2017) could therefore result in shifts in species assemblages and in biome boundaries (Rees et al., 2020). Shrub expansion is also likely to impact herbivore populations as forage availability changes, with herbivores potentially affecting shrub growth in turn (Christie et al., 2015; Olofsson & Post, 2018). Complex ecosystem-level responses are also expected: changing interactions between soil, shrubs, and atmosphere may alter ecosystem carbon, nutrient, and energy budgets, resulting in climate feedbacks and trophic interactions (Henry et al., 2022; Mekonnen et al., 2021).

1.2.2 Sea ice loss

Sea ice is a key physical, climatic, and ecological feature of the Arctic, with influence over terrestrial and marine ecosystems (Macias-Fauria & Post, 2018a). Sea ice extent, thickness, seasonal duration, and proportion of multiyear ice have all rapidly declined in recent decades as a result of climate warming (Serreze & Meier, 2019), and the Arctic Ocean is predicted to become seasonally ice free this century (Serreze & Meier, 2019; Wang et al., 2021).

The ecological and evolutionary consequences of sea ice loss are uncertain: changes are occurring before we have a complete understanding of how sea ice interacts with biological processes (Gilg et al., 2012; Kovacs et al., 2011; Macias-Fauria & Post, 2018b). It is likely that sea ice loss will affect Arctic biota over multiple taxonomic levels (Grémillet & Descamps, 2023; Macias-Fauria & Post, 2018a):

- Individual level: body condition, survival, and reproduction,
- Population level: dispersal, connectivity, and migration,
- Species level: distribution shifts, abundance, and local extinctions, and
- Community and ecosystem level: species interactions, community composition, and primary productivity.

Species such as the polar bear and ice-breeding pinnipeds that need sea ice to complete their life histories (“ice-obligate” species) will be particularly vulnerable (**Figure 1.2**) (Kovacs

et al., 2011; Laidre et al., 2008; Moore & Huntington, 2008). Sea ice is also important for terrestrial species as a dispersal corridor, and continued loss will reduce across-ice migrations, increase genetic isolation, and reduce evolutionary potential of Arctic mammal populations (Jenkins et al., 2016, 2018; Kutschera et al., 2016; Mallory, 2019; Norén et al., 2011; Peeters et al., 2019). In contrast, population connectivity of some whale and seal species will likely increase, potentially leading to hybridization with sub-Arctic species (Kovacs et al., 2011; O’Corry-Crowe, 2008; O’Corry-Crowe et al., 2016; Post et al., 2013). Sea ice loss can also impact biota indirectly: through its influence on atmospheric and oceanic circulation (McKenna et al., 2017) and biological interactions (Hauser et al., 2018; Iverson et al., 2014; Kerby & Post, 2013).



Figure 1.2. Sea ice is a crucial hunting, breeding, and resting platform for ice-obligate Arctic species. A group of walrus rest on ice floes between feeding excursions for benthic invertebrates in the shallow coastal waters north of Svalbard (Laidre et al., 2008; Moore & Huntington, 2008). Photo: Maria Dance.

Predictions of the ecological impacts of Arctic vegetation changes, tundra shrub expansion, and sea ice decline are usually based on the current observational period and modelled future conditions (Macias-Fauria & Post, 2018a; Mekonnen et al., 2021; Pearson et al., 2013; Post et al., 2013; Reji Chacko et al., 2023). To improve them, we need a better understanding of how Arctic species responded in the past to rapid and large-scale climate and sea ice changes. For this, an appreciation of the major climatic forces that have shaped the biogeography and history of Arctic ecosystems is useful.

1.3 The biogeography of the Arctic

1.3.1 Quaternary climate changes

The modern Arctic ecosystem arose ~3 million years ago in response to global cooling and the onset of Quaternary glaciations (Miller et al., 2010) and is characterised by relatively low biological diversity. High latitude forests gave way to tundra (Matthews & Ovenden, 1990; Murray, 1995) and sea ice became a more persistent and widespread feature of the Arctic ocean (Polyak et al., 2010). The Arctic flora appears to derive from species migrations from mountainous areas in Asia and North America (Hultén, 1937; Murray, 1995), as well as shrubby and herbaceous species from the ancient Arctic forests (Kjær et al., 2022; Murray, 1995).

The Quaternary glaciations had a major impact on the biogeography of the Arctic and the evolution of its flora and fauna (Hewitt, 2004; Shafer et al., 2010). Glacial periods lasting up to 100,000 years (typically characterised by expanding continental ice sheets) were interspersed with shorter and warmer interglacials (Miller et al., 2010). Within these long-term cycles were millennial-scale climatic events (Alley, 2007; Dansgaard et al., 1993; Svensson et al., 2006). Rapid and large fluctuations in climate and ice sheet conditions caused changes in species distribution and abundance (Birks, 2008; Hofreiter & Stewart, 2009). Species' ranges shifted repeatedly in and out of climatically suitable, ice-free areas (refugia) in the terrestrial and marine realms (Abbott, 2008; Hardy et al., 2011; Hultén, 1937; Stewart et al., 2010). Populations within a species may have had varying ability to track the changing climate conditions, meaning that only a subset of populations would make a lasting contribution to species persistence and evolution (Bennett & Provan, 2008; Stewart et al., 2010).

Fossil, molecular, and phytogeographical evidence has shown that the Beringian region (stretching from the Verkhoyansk mountains in Eastern Russia to the Mackenzie River in North America: see **Figure 1**) was an important glacial location and potential refugium for Arctic and boreal plants (Abbott & Brochmann, 2003; Bigelow et al., 2003; Brochmann & Brysting, 2008; Brubaker et al., 2005; Hewitt, 2004; Hultén, 1937; Weider & Hobæk, 2000; Westergaard et al., 2010), and other species (Loog et al., 2020; Weksler et al., 2010; Winker et al., 2023).

Refugia are conventionally described as regions where species' ranges contracted to and persisted in during glaciations (Bennett & Provan, 2008; Hewitt, 1996). However, using "glacial refugia" for cold-adapted and Arctic species may be inaccurate, as they often had more extensive distributions in glacial intervals than in interglacial intervals (Alsos et al., 2009; Bennett & Provan, 2008; Dalén et al., 2004; Lorenzen et al., 2011; Smith et al., 2017; Stewart & Dalén, 2008), and several Arctic animal species have genetic signatures of increased population size at the onset of the last glaciation (Dalén et al., 2004; Fedorov, 1999; Flagstad & Røed, 2003; Louis et al., 2020; Taylor et al., 2021). Nonetheless, the distributions of cold-adapted taxa may have been somewhat restricted and discontinuous during glacial maxima due to ice sheets (Stewart et al., 2010; Yannic et al., 2014). Refugia can therefore be defined as the geographical region(s) inhabited by a species during a glacial/interglacial cycle during the maximum contraction of a species' geographical range (Stewart et al., 2010). This recognises that different species are adapted to different conditions, with cold-adapted species expected to be in refugia during interglacials, and more temperate species expected to be in refugia during glacials (Stewart et al., 2010).

As well as causing changes in species distribution and abundance, past climate change has contributed to the diversification of Arctic biodiversity. The transition to cooler climates at the onset of the Quaternary led to new selection pressures and opportunities for speciation and diversification for cold-adapted organisms (Brochmann & Brysting, 2008; Davis & Shaw, 2001; Kadereit & Abbott, 2021). During glacial cycles, population isolation in refugia was likely an important driver of population and species divergence (Hewitt, 1996). Genetic variation was partitioned across the landscape, and bottlenecks, genetic drift, and mutations resulted in genetic differentiation and local adaptations (Hewitt, 2004). These patterns of diversification are supported by higher genetic distinctiveness of Arctic plants in

former refugial regions (Eidesen et al., 2013) and intraspecific genetic lineages reflecting isolation in multiple refugia (Abbott & Comes, 2004; Alsos et al., 2005; Ehrich et al., 2008; Eidesen, Alsos, et al., 2007; Eidesen, Carlsen, et al., 2007; Eidesen et al., 2015; Skrede et al., 2006).

Historical secondary contact between divergent populations has also generated Arctic diversity (Petit et al., 2003; Tsuda et al., 2017). As climatic and environmental conditions became suitable for certain taxa, expansion from refugia would have led to increased connectivity and genetic admixture between divergent populations (Hewitt, 2000; Petit et al., 2003). This is supported by a decline in Arctic plant species richness and genetic diversity with distance from refugial areas (reflecting population expansion), except in regions of probable secondary contact between previously isolated populations (Pellissier et al., 2016; L. Stewart et al., 2016). Signatures of secondary contact are often thought to reflect postglacial migration, but admixture during glacials has also been inferred for cold-adapted species like reindeer/caribou (Polfus et al., 2017; Taylor et al., 2021).

In the Quaternary, the geographical distribution, abundance, and associated genetic structure of Arctic species has been influenced by a complex interplay of isolation and secondary contact resulting from intermittent biogeographical barriers caused by changes in ice sheets, climate, and sea level. For example, connectivity between Eurasia and America would have been influenced by the intermittent emergence of the Bering Land Bridge during glacials (Edwards et al., 2018; Elias & Brigham-Grette, 2013; Salis et al., 2022; Vershinina et al., 2021). Geographical features such as mountains and rivers also appear to be important for Arctic biogeography, since genetic boundaries are found at the Kolyma River, the Lena River, and the Ural Mountains in Eurasia, and at the Mackenzie River in North America for many species (Eidesen et al., 2013; Hewitt, 2004).

1.3.2 Sea ice: past and present

In addition to Quaternary climate fluctuations, sea ice has shaped the biogeography of Arctic species. First present in the Arctic Ocean some 47 million years ago (mya), sea ice became a perennial feature around 13-14 mya (Polyak et al., 2010). Pliocene cooling around 3-4 mya led to sea ice expansion, until conditions similar to today were reached at the onset of the Quaternary, 2.6 mya (Knies et al., 2014). Thick, permanent pack ice was a feature of

most of the Quaternary glacial periods, but the ocean may have been ice-free during some interglacials (Polyak et al., 2010). As a long-term and persistent feature of the Arctic, eleven species of marine mammals evolved with or adapted to this unique habitat (Kovacs et al., 2011).

Sea ice has long been an important habitat and dispersal agent for many Arctic species, and a major geographic barrier for others (Alsos et al., 2007; Gajewski, 2015; Macias-Fauria & Post, 2018a). Sea ice variability over time has therefore influenced species' ranges, gene flow, and interactions with other taxa (Post et al., 2013). The role of glacial and postglacial sea ice fluctuations in shaping marine mammal evolutionary and population history is well-studied (Alter et al., 2012; Borge et al., 2007; Foote et al., 2013; Louis et al., 2020; McLeod et al., 2012; Skovrind et al., 2021). However, this thesis focuses on the ways that sea ice and other climatic processes have shaped the biogeography of terrestrial species.

Postglacial sea ice was likely important in shaping the present distributions and diversity of Arctic plants by enabling dispersal between landmasses and the colonisation of islands (Alsos et al., 2005, 2007; Eidesen et al., 2013; Gajewski, 2015; Johansen & Hytteborn, 2001). Open waters in the Arctic Ocean act as a barrier for plants (Hoffmann, 2012), but numerous vectors can aid long-distance dispersal of propagules and seeds, including driftwood transported by multiyear ice and drifting sea ice itself (Alsos et al., 2015). For example, sea ice likely enabled postglacial colonisation of Svalbard, as sea ice cover was more prevalent along most likely dispersal routes (based on genetic source regions) at times of assumed first colonization compared to other routes (Alsos et al., 2016).

The role of sea ice in shaping terrestrial mammal biogeography during the Quaternary is less well-known, despite its current role in dispersal and connectivity. Dispersal over sea ice helps maintain population connectivity and genetic diversity for Arctic foxes (*Vulpes lagopus*) (Carmichael et al., 2007; Geffen et al., 2007), polar bears (*Ursus maritimus*) (Kutschera et al., 2016), grey wolves (*Canis lupus*), and reindeer/caribou (*Rangifer tarandus*) in High Arctic archipelagos (Carmichael et al., 2008; Jenkins et al., 2016, 2018; Peeters et al., 2019). However, sea ice cover has not yet been linked to postglacial dispersal of terrestrial mammals onto ice-free Arctic islands.

1.4 Using genetics to infer species responses to past (and future) climate change

Analysing the spatial structure of modern-day genetic variation is a well-established tool to infer processes that influenced species' evolutionary histories (Abbott & Brochmann, 2003; Hickerson et al., 2010). Geographic patterns in genetic variation reflect evolutionary relationships that include signatures of past demography (Phillips et al., 2013). Historical population processes include range expansions and contractions, migration and gene flow, and population growth and decline (Epps & Keyghobadi, 2015; Mellows et al., 2012). Potential impacts of past climate change on species are therefore detectable in the genetics of modern populations (Norén et al., 2009). Previous work has shown that the modern genetic variation in Arctic biota reflects past climate change as well as the current environment (O'Corry-Crowe, 2008; Pellissier et al., 2016; Stewart et al., 2016).

The impacts of Quaternary climate change on past and present Arctic biodiversity have previously been studied with integrated research in paleoecology, paleogenomics, paleoclimatology, and macroecology (Fordham et al., 2014, 2020; Gavin et al., 2014; Lorenzen et al., 2011). The response of Arctic biota to past climate change is a complicated picture of bottlenecks, range shifts, population expansions, and postglacial dispersal and secondary contact (Hardy et al., 2011; Stewart et al., 2010). DNA sequences from contemporary populations have been informative for determining glacial-postglacial population size changes and dispersal of Arctic terrestrial and marine species (Hansen et al., 2018; Kozma et al., 2016; Louis et al., 2020; Skovrind et al., 2021; Taylor et al., 2021; Westbury et al., 2022).

Fossils and ancient DNA (DNA isolated from fossils and ancient sediments) provide an extremely useful window into species and ecosystem responses to past climate change (Alsos et al., 2020; Hofreiter, 2008; Kjær et al., 2022; Mourier et al., 2012; Parducci et al., 2017; Willerslev et al., 2003). However, contemporary genetic variation not only provides insights into past demographic trajectories and responses, but also influences how species will respond to ongoing and future climate change. The ability of species to adapt to and potentially evolve in response to environmental change depends on sufficient genetic variation (Alsos et al., 2012; Davis et al., 2005). Populations with higher genetic diversity may indicate regions with increased adaptive potential (Pauls et al., 2013). Future changes

are contingent on contemporary genetic variation that is determined - in part - by historical processes.

Furthermore, understanding how Arctic biota responded to past climate and environmental fluctuations may help to infer how species will respond to future climate change and inform conservation practices (Fordham et al., 2020). Insights into population history can be used to assess future extinction risk and model the future demography of populations in relation to terrestrial environmental changes and sea ice loss (O’Corry-Crowe, 2008; Pauls et al., 2013).

1.5 Focal taxonomic groups: ecology and phylogeography

1.5.1 Reindeer/Caribou (*Rangifer tarandus* L.)

Reindeer are the most numerous and widespread large herbivore in the Arctic and consequently have large effects on other species, tundra vegetation composition, and ecosystem functioning (Olofsson & Post, 2018; Spiegel et al., 2023). However, many reindeer populations are undergoing a multi-decadal decline, often driven by anthropogenic activities and landscape changes (Gunn, 2016). Smaller, fragmented populations have reduced genetic viability and are vulnerable to other pressures such as climate change, and extinction (Caughley, 1994; Schlaepfer et al., 2018). Population connectivity is crucial to maintain population numbers, genetic variation, and adaptive capacity in the face of environmental change (Torda & Quigley, 2022).

In several Arctic regions, sea ice maintains population connectivity of reindeer by enabling crossings between land masses (Jenkins et al., 2016; Miller et al., 2005; Poole et al., 2010). Loss of population connectivity following contemporary sea ice decline has been documented in the Canadian Arctic and Svalbard Archipelagos (Jenkins et al., 2018; Peeters et al., 2019), yet the historical role of sea ice in population connectivity is understudied. We need to study longer-term responses to natural sea ice variability to gain an increased understanding of ongoing sea ice reduction.

Modern and ancient DNA have been used to model historical reindeer population dynamics in relation to late Quaternary climate change (Lorenzen et al., 2011; Polfus et al., 2017; Taylor et al., 2021; Yannic et al., 2014). Major population expansions may have occurred at the start of the last glacial period (Taylor et al., 2021) and during the Last Glacial Maximum

(LGM) (Lorenzen et al., 2011; Weldenegodguad et al., 2020), during which reindeer were probably more widely distributed than they are today (Lorenzen et al., 2011). In North America, physical separation by ice sheets resulted in two lineages, detectable in mitochondrial DNA, where similar ecotypes evolved convergently (Polfus et al., 2017). One lineage had a distribution spanning Eurasia and Beringia, and the North American lineage was distributed south of the North American ice sheets (Klüttsch et al., 2012; McDevitt et al., 2009; Weckworth et al., 2012; Yannic et al., 2014). The two lineages experienced secondary contact and admixture after the North American ice sheets retreated during the postglacial period (Klüttsch et al., 2016) and may have also admixed when an ice-free corridor between the Cordilleran Ice sheet to the west and the Laurentide Ice Sheet to the east was present during the last glacial (Taylor et al., 2021).

There is conflicting genetic evidence as to whether the smaller-bodied reindeer of the High Arctic islands dispersed in the postglacial period from Beringian and other continental lineages (Flagstad & Røed, 2003; Gravlund et al., 1998; Kvie et al., 2016; Røed, 2005) or evolved in-situ in High-Arctic refugia (Eger et al., 2009; Klüttsch et al., 2017). The timing of High Arctic island (re)colonisation events is therefore uncertain. Dispersal during warmer periods with higher sea levels and ice-free High Arctic land masses would necessitate sea ice.

1.5.2 The dwarf birches (*Betula nana* L. and *Betula glandulosa* Michx.)

The dwarf birches are abundant circumpolar tundra deciduous shrub species (de Groot et al., 1997) that are implicated in the ongoing vegetation greening trends (see **Section 1.1**) in Alaska (*B. glandulosa* and *B. nana*), Arctic Canada (*B. glandulosa*), Arctic Russia, and the European Arctic (*B. nana*) (Andruko et al., 2020; Fraser et al., 2014; Lantz et al., 2013; Larking et al., 2021; Moffat et al., 2016; Myers-Smith et al., 2011; Tape et al., 2006; Tremblay et al., 2012). Examining how the dwarf birches responded to past episodes of climate change can inform the long-term ecological and evolutionary consequences of shrub expansion.

Pollen and macrofossil records and sedimentary DNA (sedaDNA) have formed the basis of our understanding that dwarf birches responded to Quaternary climate change through range contractions and expansions from refugia (Bigelow et al., 2003; Binney et al., 2017;

Birks, 2008; Clarke et al., 2020; Crump et al., 2019, 2021). Contemporary genetic data provides insights on population-level processes of individual genetic lineages (Pauls et al., 2013). Panarctic contemporary genetic variation in *B. nana* reflects Quaternary refugial isolation on a large scale, and postglacial migration history on a finer scale (Eidesen et al., 2015). Beringia was a key refugium and has been proposed by Eidesen et al. (2015) as the potential location of the ancestral population. During the LGM, the species appears to have been present south and southeast of the Eurasian ice sheet and in a west Siberian refugium (Eidesen et al., 2015).

Genetic structure also shows secondary contact between divergent refugial lineages during postglacial expansion (Eidesen et al., 2015). *Betula nana* underwent a degree of hybridisation during postglacial dispersal with the tree birches *B. pendula* Roth. and *B. pubescens* Ehrh., but with gene flow mostly from *B. nana* to *B. pubescens* (Karlsdóttir et al., 2009; Palmé et al., 2004; Thórsson et al., 2010; Wang et al., 2014; Zohren et al., 2016). The postglacial dynamics of *B. nana* are relatively well-constrained (Eidesen et al., 2015), but the genetics and phylogeography of *B. glandulosa* are understudied. The Quaternary history of both species, including the response to pre-LGM climate fluctuations, has not been explored with genetic data.

Elucidating how past climate change structured the genetic variation of dwarf birches has direct applications for inferring ongoing responses to present climate change. The long-term adaptive capacity of plants to climate change depends upon sufficient genetic variation (Pauls et al., 2013; Savolainen et al., 2007). Genetically diverse shrub populations, shaped by past climate change, may be better able to adapt to the environmental factors driving heterogeneous shrub expansion and greening trends (Gamm et al., 2018; Jump & Peñuelas, 2005; Myers-Smith et al., 2020; Phoenix & Bjerke, 2016). However, the role of genetic variation in the response of the dwarf birches to climate, and their adaptive potential, have not been studied (Henry et al., 2022). Investigating the relationship between the genetic diversity of tundra vegetation and Arctic shrub expansion could provide key insight on the response of Arctic tundra ecosystems to ongoing climate change.

1.6 Aims and objectives

The aim of the thesis is to infer responses of two important taxa in the Arctic tundra (reindeer – *Rangifer tarandus* L. – and the dwarf birches - *Betula nana* L. and *Betula glandulosa* Michx.) to Quaternary climate change using a phylogeographic approach based on contemporary genetic structure and diversity, to improve our understanding of ecological and evolutionary responses of Arctic biota to past climate change. Specifically, the research aims were structured into three research objectives.

Objective 1: How did Quaternary climate variability shape the evolution, population history, and subsequent contemporary genetic structure of Arctic island reindeer?

I compared reindeer population history with late Quaternary sea ice and ice sheet changes to determine the long-term role of sea ice in inter-island dispersal and population connectivity. I compiled published mitochondrial DNA datasets of island reindeer and their continental neighbours in North America (Canadian Arctic Archipelago and Greenland) and Eurasia (Svalbard and the Barents Sea area). Using a coalescent-based approximate Bayesian computation (ABC) modelling approach (Beaumont, 2010; Beaumont et al., 2002; Collin et al., 2021), I tested likely evolutionary scenarios. From the scenario that best matched the genetic data, I estimated timings of population divergence (representing island colonisation and isolation) and admixture (representing extensive inter-island migration). Population events were compared with sea ice extent derived from paleoclimate models, and regional proxy-based sea ice data, where available, together with past ice sheet extent and sea level. Fossil-based estimates of island colonisation were used as an independent evaluation tool.

I hypothesised that population events would coincide with deglaciation and sea ice availability but expected that the population histories and the role of sea ice in the two island systems would differ because of different geographies, deglaciation, and sea ice histories. The best supported model suggested postglacial dispersal onto deglaciated Arctic islands from continental refugia, with modelled divergence times agreeing with fossil data. Sea ice availability broadly coincided with population events, with differing impacts in the two geographically different systems. The compiled evidence suggested that ice sheet retreat, sea ice concentration, and ocean currents are associated with postglacial reindeer history and genetic structure in Arctic islands.

Objective 2: How did Quaternary climate fluctuations influence the evolution, population history, and subsequent contemporary genetic structure of the dwarf birches?

Using a novel, next-generation sequence dataset, I modelled the panarctic Quaternary evolutionary and population history of the dwarf birches to gain insight into how climatic fluctuations have affected their evolutionary relationships and population history. Using methods similar to those in *Objective 1*, I tested likely evolutionary scenarios and estimated population parameters from the best supported model. I compared dates of population divergence (representing population isolation) and admixture (representing secondary contact between populations) with the configuration of ice sheets at each time period, obtained from published reconstructions. I used published pollen, macrofossil, and sedaDNA records to independently evaluate the events.

I expected that inter- and intraspecific divergence and admixture would be associated with the major glacial cycles, yet as a relatively thermophilic Arctic species, the standard model of glacial isolation and interglacial expansion may not apply. The best supported model suggested a Mid-Quaternary origin of the dwarf birch species complex in response to global cooling. Population events were associated with major climatic transitions, with interactions between ice sheet changes, climatic conditions in ice-free areas, and geographical constraints likely resulting in a complex population history.

Objective 3: Do Arctic vegetation greening and shrub expansion trends reflect genetic legacies of past climate change in the dwarf birches?

Finally, I used the ongoing Arctic vegetation greening and shrub expansion trend (see **Section 1.1**) as an opportunity to test whether the impacts of past climate change on the genetic structure of the dwarf birches may be influencing their response to contemporary climate change. Using the same genetic dataset as *Objective 2*, I tested the association between population-level genetic diversity, genetic admixture, time since ice retreat, and regional greening trends of the Arctic tundra and sub-Arctic boreal areas as measured by remote sensing. I also tested the influence of contemporary climatic variables which have previously been used to explain greening trends.

I expected that greening would be greater in less recently glaciated regions with higher dwarf birch genetic diversity and genetic admixture, and that these factors would help

explain variance in greening trends. Although there were correlations between greening magnitude and genetic diversity, I found that the most important variables in a Random Forest regression model for predicting vegetation greening trends included genetic admixture, and to a lesser extent landscape age. Temperature and moisture-related variables were also key, similar to previous studies of shrub expansion (Mekonnen et al., 2021; Myers-Smith, Elmendorf, et al., 2015; Myers-Smith & Hik, 2018) and greening (Berner et al., 2020). By modelling the relative importance of these factors, I was able to determine that the legacy of past climate change and species population history is an important but previously neglected component of tundra vegetation greening trends.

1.7 Thesis structure

The above objectives are addressed in three research articles, forming three chapters, with additional background and synthesis chapters. This chapter (**Chapter 1**) introduces the background and motivation behind the work and states aims and objectives. **Chapter 2** describes the methods used in data collection and analysis; the dwarf birch DNA extraction protocol I developed is in **Appendix A**. **Chapters 3, 4, and 5** present the three studies (*Objectives 1, 2, and 3, respectively*) in the form of research articles. **Chapter 6** synthesises the results and conclusions of the three research articles, discusses implications of the research, and identifies future research directions.

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Chapter 2: Data and Methods



Photo: Maria Dance

2.1 Overview

This chapter describes the approach and rationale behind the data and methods used in this thesis, as well as any methodological details not covered in the research chapters (**Figure 1**). Data and methods were informed by the literature outlined in **Chapter 1**. I provide background on the types of genetic data used for this research and outline the phylogeographic and demographic modelling approaches used in **Chapters 3** and **4**. **Chapter 5** focuses on the contemporary genetic variation of dwarf birch, so genetic diversity metrics are discussed. I then outline the paleoclimate and paleoenvironmental data sources used to compare the Quaternary population dynamics of the target taxonomic groups to past climate change. Finally, an overview of the contemporary vegetation greening and climatic and environmental datasets and methods used in **Chapter 5** is presented. Further descriptions of the methodology of each research study are within each respective chapter (**Chapters 3, 4, and 5**).

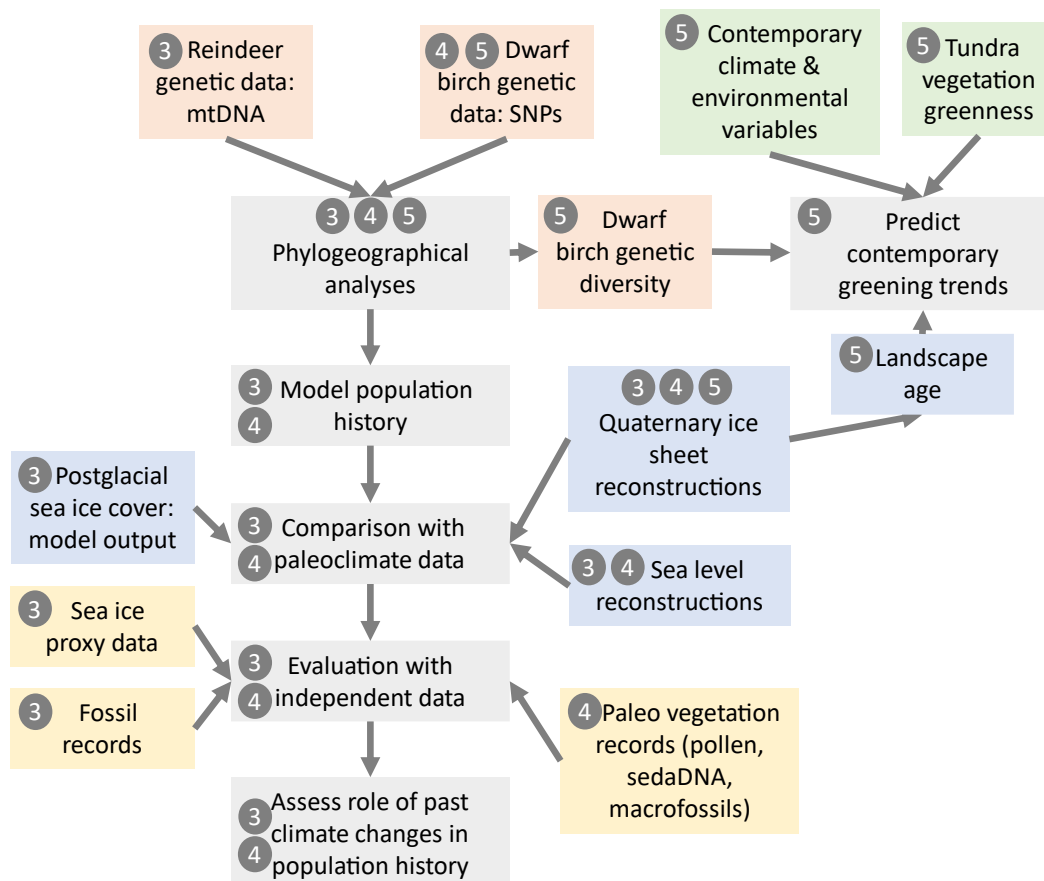


Figure 2.1. Overview of data and methods used in the thesis. Numbers refer to relevant chapters.

2.2 Genetic data (used in all research papers)

This thesis investigates the responses of two Arctic taxa (reindeer/caribou – *Rangifer tarandus* L. – and the dwarf birches - *Betula nana* L. and *Betula glandulosa* Michx.) to Quaternary environmental change using a phylogeographical approach. Inferring historical patterns and process from the geographical distribution of contemporary genetic variation forms the basis of the field of phylogeography (Avice, 2000; Hickerson et al., 2010). A consideration of appropriate genetic markers to infer Quaternary population histories and address the aims and objectives of this thesis was therefore required.

Phylogeographic datasets have evolved with the development of new molecular markers: from short nuclear or organelle sequences (mitochondrial - mtDNA and chloroplast - cpDNA), to nuclear markers such as microsatellites and Amplified Fragment Length Polymorphism (AFLP) markers, and more recently genome-wide markers (Single Nucleotide Polymorphisms, SNPs) and whole genomes (Edwards et al., 2015; Garrick et al., 2015; Morris & Shaw, 2018). As datasets have changed, a shift in phylogeographic methods from descriptive gene trees and haplotype networks to demographic model-based statistical inference using demographic models has occurred (Beaumont et al., 2010; Edwards et al., 2015).

The genetic relationships between populations and past demographic processes can be studied across a range of timescales thanks to differing marker mutation rates (I. J. Wang, 2010). Markers with higher mutation rates such as microsatellites are useful for detecting present-day demographic and population connectivity patterns, or relatedness among recently diverged conspecific populations (Freeland, 2020; Selkoe & Toonen, 2006). More slowly mutating markers such as mtDNA and cpDNA sequences are suited to studying less recent events such as inter- and intraspecific divergence times (Hung et al., 2016; Wang, 2010), and the slowest — short nuclear sequences — the most distant past (Zimmer & Wen, 2015; Zink & Barrowclough, 2008). SNPs are thought to be informative over broad timescales (Edwards et al., 2015; Garrick et al., 2015) and have been used to study the Quaternary population history of various Arctic species (Cronin et al., 2014; Hansen et al., 2018; Shafer et al., 2015).

Variable mutation rates also mean that species and population divergence time estimates are marker-dependent (Epps & Keyghobadi, 2015; Kadereit & Abbott, 2021). Combining different

marker types can provide insights into the evolutionary forces shaping population history (Garrick et al., 2015). For example, a more detailed understanding of *B. nana* phylogeography has been obtained by comparing cpDNA and AFLP markers (Eidesen et al., 2015). Similarly, late Quaternary divergence times of Canadian Arctic reindeer have been compared using microsatellites and mtDNA (Klüttsch et al., 2017). However, regional microsatellite datasets are difficult to combine and standardise across studies (Freeman et al., 2006).

Another consideration for marker choice is that estimates of genetic relationships and demographic parameters improve as the number of genomic sites (loci) per individual increases, particularly for more recent timescales (Arbogast et al., 2002; Garrick et al., 2015; Robinson et al., 2014). Different regions of the genome have different genealogical histories due to recombination, selection, and drift, so using only one locus can cause high sampling error (Selkoe & Toonen, 2006) and large uncertainties when inferring demographic histories (Beichman et al., 2018). Organelle sequences are single locus markers, whereas AFLP and microsatellite markers are multi-locus. SNPs are biallelic markers that differ by a single nucleotide between individuals and occur at a high frequency throughout the genome, enabling the sampling of thousands of loci (Kirk & Freeland, 2011).

For this research, contemporary genetic variation was required that would contain information on inter- and intraspecific divergences and admixture events that may have been shaped by past climate and environmental changes during the Quaternary. For reindeer, microsatellite data have been shown to reflect recent landscape features and population size (Serrouya et al., 2012; Yannic et al., 2014), while mtDNA variation reflects historical patterns of Quaternary and postglacial colonisation and fragmentation (Cronin et al., 2005; Eger et al., 2009; Flagstad & Røed, 2003; Weckworth et al., 2012; Yannic et al., 2014). Short cpDNA sequences, nuclear sequences, AFLPs, and microsatellite nuclear markers have been widely used in studying the Quaternary phylogeography of the dwarf birch species *B. nana* (Alsos et al., 2002; Dabrowska et al., 2006; Eidesen, 2007; Eidesen et al., 2015; Jadwiszczak et al., 2012; Palmé et al., 2004; Thórsson et al., 2010; Wang et al., 2014). However, variation in cpDNA tends not to show clear species delineation for the *Betula* genus (Eidesen et al., 2015; Maliouchenko et al., 2007) because of extensive hybridisation and introgression (Palmé et al., 2004; Thomson et al., 2015; Thórsson et al., 2010). Hybridisation complicates genetic signatures of refugial isolation and postglacial migration. Biparentally inherited nuclear

markers may improve species delineation because higher intraspecific gene flow through pollen may reduce the signal of introgressed alleles (Alsos et al., 2002; Tsuda et al., 2017).

Genome-wide SNPs are not yet widely available for reindeer, and whole genomes have only been obtained for some populations (Taylor et al., 2021); **Chapter 3** therefore compiles published mtDNA datasets across the High Arctic islands and neighbouring continental populations: see **Chapter 3** for details on the datasets. For *B. nana*, genome-wide SNPs had previously only been sequenced for British and some Scandinavian populations (Borrell et al., 2018; Wang et al., 2013; Zohren et al., 2016) and the genetic structure of *B. glandulosa* has not been explored. A newly sequenced dataset of multiple unlinked SNPs was produced in this DPhil and analysed in **Chapters 4** and **5**, providing a deeper understanding of genetic relationships among the dwarf birches (*B. nana* L. and *B. glandulosa* Michx.) than is possible using a single gene or locus (Tsuda et al., 2017).

A panarctic dwarf birch SNP dataset was obtained by compiling samples collected from sites across the range of the species. I developed and optimised a new DNA extraction protocol for dwarf birch and extracted DNA from 250 individuals across 49 sites. DNA was sequenced using restriction site-associated sequencing (RADSeq), a next-generation sequencing (NGS) approach that is widely used to generate SNPs for phylogeographic analysis of non-model organisms (Andrews et al., 2016; Vaux et al 2022). Sequenced reads were processed and aligned to a *B. nana* reference genome (Wang et al., 2013), and SNPs were genotyped and filtered. For details on the sampling method see **Appendix S1** of **Chapter 4**, and for details on the DNA extraction protocol see **Appendix A**, and for sequencing and bioinformatic processing details see **Chapter 4**. The genetic analyses in **Chapter 4** and **Chapter 5** were conducted in parallel using the same set of sequenced reads, but with different bioinformatic pipelines to suit the differing aims and objectives of each study.

2.3 Phylogeographic methods (all research papers) and demographic modelling (Chapters 3 & 4)

To infer how Quaternary climate variability shaped the evolution and population history of reindeer (**Chapter 3**) and the dwarf birches (**Chapter 4**), I compared population history with paleoclimate and paleoenvironmental data – see **Section 4**. Population history was inferred from the best supported scenarios of evolutionary history which were created using

phylogeographic exploratory analyses and demographic modelling of contemporary genetic variation (**Figure 2**). Phylogeographic exploratory analyses were also conducted in **Chapter 5** to analyse the contemporary genetic variation of the dwarf birches in relation to environmental changes past and present.

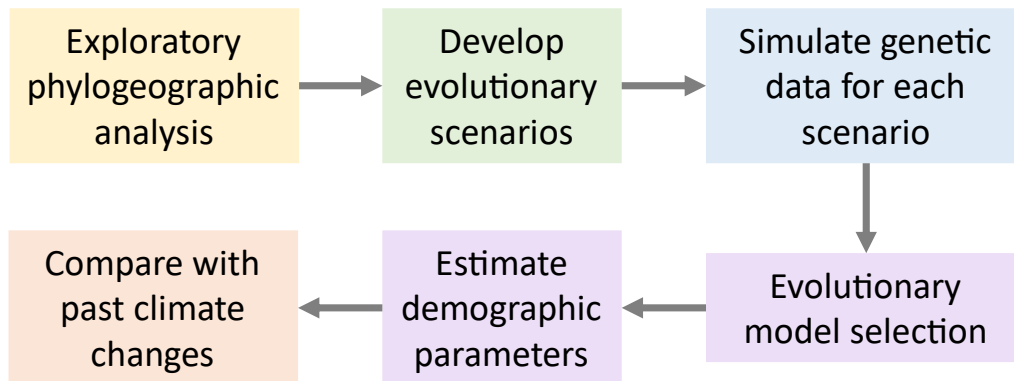


Figure 2.2. Summary of analysis workflow for Chapters 3 and 4.

To ensure thorough exploration of the genetic data, multiple methods were used in each study. Ordination techniques such as principal component analysis (PCA) and metric multidimensional scaling (mMDS), as well as clustering techniques such as K-means clustering and unweighted pair group method with arithmetic mean (UPGMA) were used to assess genetic (dis)similarity among individuals, the presence of distinct genetic populations, and their relationships with other populations. Since these methods do not assume an underlying evolutionary model (Jombart et al., 2009), different evolutionary histories could result in similar patterns, so distances among individuals cannot be directly equated with demographic processes (Loog, 2021). These methods are useful exploratory tools to help build hypotheses of population history.

For PCA, each locus is treated as an independent variable, and genetic variation among individuals is reduced to the main axes of variation—or principal components—using the covariance matrix (Loog, 2021). PCA was therefore suitable for reducing the complexity of thousands of SNPs which were analysed in **Chapters 4** and **5** and was implemented using the adegenet v 2.1.3 R package (Jombart, 2008). As mitochondrial DNA constitutes a single effective locus due to lack of recombination (Avise, 1991), distances between individuals and populations in **Chapter 3** could be better summarised using non-evolutionary Euclidean distance matrices, which can be visualised with MDS or hierarchical clustering. MDS seeks the

best approximation of the matrix of distances in reduced spatial dimensions, and like PCA, produces a set of uncorrelated axes to summarise the variability in the dataset. MDS was implemented using the `cmdscale` v. 4.0.3 function (R Development Core Team, 2022). For hierarchical clustering, UPGMA was used to construct dendrograms — simple branching relationships based on distance between populations — using the `hclust` function v. 4.0.3 (R Development Core Team, 2022). To identify the number of genetic clusters present in both the UPGMA and the MDS, K-Means clustering was performed on both the distance matrices and the MDS dissimilarity coordinates (R Development Core Team, 2022).

For the SNP data in **Chapter 4**, model-based clustering methods such as ADMIXTURE (Alexander et al., 2009; Alexander & Lange, 2011), RADpainter and fineRADstructure (Malinsky et al., 2018) were used to identify the number of genetically distinct populations and potential historical admixture events. Genetic admixture occurs when previously isolated populations interbreed and offspring inherit a mixture of alleles from different ancestral populations (Skotte et al., 2013). These methods are therefore useful for detecting potential ancestral genetic lineages generated by refugial isolation and secondary contact, which could be expected for the dwarf birches during Quaternary climate fluctuations (Abbott, 2008; Eidesen et al., 2015; Hofreiter & Stewart, 2009). These clustering methods were not applied to reindeer mitochondrial data in **Chapter 3** as these methods rely on multilocus genetic data.

ADMIXTURE models the probability of the observed genotypes using ancestry proportions and population allele frequencies. Maximum likelihood ancestry coefficients are estimated as the parameters of this statistical model, which indicate the proportion of an individual's alleles that come from K hypothesized ancestral populations. In **Chapter 4** separate analyses were performed for the global dataset and for regional subsets to identify hierarchical population structures. RADpainter and fineRADstructure were used in **Chapter 4** and can identify global population structure and local population structure simultaneously using linkage structure within haplotypes constructed from SNPs, in contrast to ADMIXTURE that uses one SNP per locus. Haplotypes are used to find the most recent coalescence (common ancestry) between individuals, from which a coancestry matrix summarising nearest neighbour haplotype relationships is derived. The matrix is ordered according to a tree-like structure of population relationships produced by the fineRADstructure Markov Chain Monte Carlo (MCMC) clustering algorithm (Malinsky et al., 2018). This helps to visualise whether

individuals are more closely related to individuals from other populations than to individuals within their own population, indicating gene flow and admixture between populations.

To model demographic history in **Chapters 3** and **4** I developed likely scenarios of population divergence and admixture using a) population genetic structure mapped using model-free and model-based clustering methods (see above), and b) phylogeographical inferences from relevant literature. These are common approaches, since an otherwise intractable number of models would need to be tested (Stone et al., 2017).

Scenarios were tested using coalescent modelling (Kingman, 1982; Wakeley & Sargsyan, 2009) of the genetic data for both reindeer (**Chapter 3**) and the dwarf birches (**Chapter 4**). The coalescent model is a mathematical model that describes the rate at which genetic lineages coalesce (i.e., join to form a common ancestor) in the past, forming a genealogy of the loci. The rate of coalescence depends on the demographic history (specifically, the effective population size) of the population at each time step in the past. Therefore, the likelihood of a given demographic scenario given the data (each genealogy) can be calculated (Navascués et al., 2017). An alternative to integrating over all possible genealogies is to use a likelihood-free approach, known as approximate Bayesian computation (ABC) (Beaumont et al., 2002, reviewed in Beaumont et al., 2010; Bertorelle et al., 2010; Csilléry et al., 2010).

In ABC, thousands of different genealogies are simulated by drawing parameter values from prior distributions under a given evolutionary scenario. ABC then evaluates the similarity between the simulated data and the observed genetic data using the distance between simulated and observed summary statistics. Simulations close to the observed data are selected (often using rejection sampling or linear regression methods) and their parameter values are used to generate posterior probability distributions of parameters of interest such as divergence times, admixture rates, and population sizes (Beaumont, 2010; Cornuet et al., 2014). In the same way, multiple demographic scenarios can be tested against each other by comparing model posterior probabilities and selecting the model with the highest probability (Bertorelle et al., 2010).

ABC can accommodate complex scenarios, large amounts of data, and various genetic marker types, and so was suitable for both the mtDNA of **Chapter 3** and the SNPs of **Chapter 4** (Csilléry et al., 2010; Lopes & Beaumont, 2010; Robinson et al 2014). I used the software DIYABC

Random Forest v1.0 (Collin et al., 2021; Cornuet et al., 2014), which improves upon conventional ABC approaches by using Random Forest supervised machine learning (SML) algorithms for scenario choice (classification model) and parameter estimation (regression model). SML methods improve some of the limitations of the ABC framework, such as the selection of large numbers of suitable summary statistics and the intensive computational requirements for NGS data (Bertorelle et al., 2010; Collin et al., 2021).

SML methods use training data—a set of data with explanatory variables (input) and known response values (output)—and learn the relationship between the two, to predict the response values of new data. The training data in ABC are the simulated datasets, with each dataset summarised by a feature vector (i.e., the gene genealogy and genetic variation are summarised by summary statistics and multivariate axes of variation). The output of the training data is known because each simulated dataset is generated under a particular demographic scenario and with certain parameter values. From learning the relationship between the feature vectors and the output, RF aggregates predictions of the demographic scenario (classification trees) or parameter values (regression trees) for the observed data, making a “random forest” of predictions that collectively have high predictive power. The scenario with the highest classification vote (the number of times a scenario is selected in the forest of n trees) is the scenario best suited to the observed dataset among those scenarios compared. The posterior probability of the model is calculated in a separate Random Forest regression step (Collin et al., 2021).

ABC loses power to differentiate between scenarios as the number of models in the comparison set increases (Carstens et al., 2013; Pelletier & Carstens, 2014). I therefore used a multi-tiered or hierarchical ABC approach, where small sets of scenarios were continually tested and improved, refining prior ranges to reduce model error rates and increase overlap between simulated and observed data. The best performing scenarios from different model sets were then tested against each other (Chen & Lou, 2019; Espíndola et al., 2016; Hyseni & Garrick, 2019; Stone et al., 2017). I selected the best-performing scenarios for each taxa using posterior probabilities and visual assessment of overlap between simulated and observed data projected on linear discriminant analysis (LDA) axes obtained by identifying the linear combinations of variables which best explain the different classes of data (Collin et al., 2021).

Population divergence and admixture time parameters were estimated from the observed data using the simulated data generated under the preferred model.

Population event times were estimated as the median number of generations with 95% confidence intervals to capture model uncertainty, which were then converted to calendar years estimates using the generation times for each species. Reindeer have variously been estimated to have a generation time length of 4-9 years (COSWIC, 2015; Eger et al., 2009; Gunn, 2016; McDevitt et al., 2009; Pacifici et al., 2013; Røed et al., 2014). In **Chapter 3** I chose an intermediate generation time of 7 years (Klütsch et al., 2017; Polfus et al., 2017). Inferring generation time is more difficult in woody plant species such as the dwarf birches due to their longevity, generational overlap, and variable age of maturity depending on environmental conditions (Tsuda et al., 2017). A generation time of 10 years was previously estimated for *B. nana* based on the calibration of a modelled British-Scandinavian population divergence with corresponding first occurrence in Britain according to pollen records (Borrell, 2016). Further exploration of pollen records in the Neotoma database suggested an earlier first occurrence, and therefore 14 years as an alternative generation time (Bartley, 2019; Bartley & Morgan, 1990; Fyfe et al., 2009; Giesecke et al., 2014; Williams et al., 2018). Therefore, in **Chapter 4** I estimated parameter timings using both generation time estimates.

Complex histories with repeated waves of isolation, divergence, and expansion with admixture make it more difficult to accurately determine the evolutionary histories of individual populations (Feng et al., 2022). Furthermore, DIYABC assumes admixture occurs as discrete unidirectional or bidirectional events (Collin et al., 2021; Cornuet et al., 2014), which could be a simplification of true population history. Inferences made about population history should therefore be interpreted with caution (Thomé & Carstens, 2016). See **Chapters 3** and **4** for more details on population history scenario development, testing, and parameter estimation.

2.4 Paleoclimate and paleoenvironmental data (used in all research papers)

To infer how Quaternary climate variability shaped the evolution and population history of reindeer (**Chapter 3**) and the dwarf birches (**Chapter 4**), I compared the timing of population events inferred with coalescent modelling – see **Section 3** – with paleoclimate and

paleoenvironmental data. Paleoclimate data was also used in **Chapter 5**, to investigate the relationship between the time since Quaternary ice sheet retreat and a) dwarf birches' genetic diversity and b) contemporary high latitude vegetation greening trends.

Chapter 3 focussed on the role of postglacial sea ice and ice sheet changes on reindeer dispersal and island colonisation in the High Arctic. I compared reindeer population histories in the North American Arctic islands (NAII) and the Barents Sea islands (BSI) with sea ice cover and published ice sheet chronologies (Dalton et al., 2020; Hughes et al., 2016; Winsborrow et al., 2023). Biogenic and geochemical proxies from marine sediment cores and shoreline records are typically used to reconstruct past sea ice dynamics (Belt, 2019; de Vernal et al., 2013; Polyak et al., 2010), but regional differences in taxonomy and preservation make panarctic comparisons difficult (de Vernal et al., 2013, 2020; Hole & Macias-Fauria, 2017). **Chapter 3** therefore used sea ice concentration estimates derived from paleoclimate models (Goosse et al., 2013) to enable inter-regional comparisons, while published regional sea ice proxy reconstructions were used to evaluate the modelled sea ice cover with independent data from within each region (Briner et al., 2016; Hörner et al., 2017; Jennings et al., 2011; Pieńkowski et al., 2021). Sea ice models can adequately reproduce mean ice extent in summer and winter when compared with observational and proxy data, but there are some discrepancies with summer ice extent in the early Holocene (Goosse et al., 2013).

Modelled sea ice concentration was derived from simulations of the global HadCM3 coupled atmosphere-ocean generalised circulation model (Singarayer et al., 2017; Valdes et al., 2017). A detailed description of the model is available in **Chapter 3** and in Valdes et al. (2017). When compared with observational datasets, the model represents accurately many aspects of the climate system on regional scales, including sea surface temperatures and ocean circulation, but tends to generate higher ocean salinities in the Kara Sea and north of Russia and reduced salinities in Hudson Bay compared to observations (Valdes et al., 2017). Although the sea ice model is relatively simple, it is better at reconstructing Southern Ocean sea ice extent during the Last Glacial Maximum (LGM) than more complex models, when compared to proxy data (Roche et al., 2012).

Daily sea ice concentration values from the model were output as monthly and annual climatological means for discrete simulation snapshots at a temporal resolution of one thousand years and a spatial resolution of 1.25°. Sea ice data were extracted at the closest

time step to each modelled population event from the geographical areas where reindeer crossing likely occurred for each event. The geographic position of the inferred event was calculated as the centroid between the modern locations of the populations involved in the event, which assumes a certain degree of stability in distributions. Sea ice concentration was estimated for the region around these locations, with varying radii depending on the size of the potential crossing over the sea. Estimated population event times were plotted against annual and monthly mean sea ice concentrations.

Estimated divergence times were also compared with the pattern and timing of ice sheet retreat over the relevant regions and islands, using time slice reconstructions of ice margins based on recent syntheses of published dates from geological and geomorphological records. Reconstructions were available from 25-6 thousand years ago (ka) (at 0.1-0.7 ka intervals) for the Laurentide and Innuitian ice sheets in North America (Dalton et al., 2022). Reconstructions of the Eurasian Ice Sheet were available from 25-10 ka (1 ka intervals) (Hughes et al., 2016; Winsborrow et al., 2023). Several sources of spatial and temporal uncertainty exist in ice sheet reconstructions as a result of compiling incomplete and sometimes conflicting information from diverse sources (Hughes et al., 2016). While recognising this uncertainty, qualitative comparisons with species demographic history use the most credible or best estimate of ice extent.

Chapter 4 focused on the impact of Quaternary glacial cycles, specifically ice sheet changes, on the isolation and mixture of dwarf birch populations. Similarly to **Chapter 3**, the spatiotemporal correspondence between population events and ice sheet dynamics were qualitatively examined. Global and regional published ice sheet reconstructions were used (Batchelor et al., 2019; Dalton et al., 2020, 2022; Winsborrow et al., 2023). Best estimates of ice sheet coverage at dated time intervals were derived from a combination of empirical data (geochronological, stratigraphic, geomorphological) and numerical data (modelling output). The global reconstruction consisted of 17 time slices spanning the pre-Quaternary ~3.6 million years ago to the LGM, with higher uncertainties in ice sheet coverage in the early Quaternary and in regions such as northeast Asia. Higher temporal resolution reconstructions were available from 115-25 ka (5 ka intervals) for the Laurentide and Innuitian ice sheets in North America (Dalton et al., 2020), although reconstructions were more loosely constrained prior

to 45 ka (Dalton et al., 2022). Higher resolution reconstructions of the Eurasian Ice Sheet were available from 40-25 ka (four intervals) (Hughes et al., 2016).

As dwarf birch populations span Eurasia and America, the Beringian Land Bridge (BLB) may have influenced dispersal and population connectivity. Therefore, I obtained estimated dates of BLB emergences based on geophysical and sediment records and geochemical proxies (Farmer et al., 2023; Jakobsson et al., 2017; Kender et al., 2018). I also compared Svalbard dwarf birch colonisation date to the first occurrence on Svalbard inferred from plant remains in sedimentary DNA (sedaDNA) (Alsos et al., 2016).

Chapter 5 aimed to determine if the impact of Quaternary climate change on the genetic structure of the dwarf birches may influence their response to contemporary climate change. To test the impact of past glaciations on contemporary genetic diversity and shrub expansion, I used the same ice sheet reconstructions employed in **Chapters 3** and **4** to estimate landscape age: that is, the length of time since a dwarf birch sampling site been covered by an ice sheet, and thus potentially available for plant colonisation (Raynolds & Walker, 2009). Previous studies have assessed landscape age in the Arctic in relation to tundra vegetation characteristics (Raynolds & Walker, 2009) and plant species richness and genetic diversity (Stewart et al., 2016).

2.5 Genetic diversity metrics (used in Chapter 5)

To explore the genetic legacy of Quaternary climate change on the response of the dwarf birches to current climate change, in **Chapter 5** I examined the links between past climate change, genetic diversity, and the ongoing trend of tundra shrub expansion. I compared variables relating to past climate change (landscape age and genetic diversity in the form of allelic richness, gene diversity, and genetic admixture proportion) with vegetation greening trends, a proxy for shrub expansion (see **Section 6**).

Chapter 5 used the SNP data sequenced in **Chapter 4**. I computed two complementary genetic diversity measures that contain distinct information about past population changes and the future evolutionary potential of a population:

Population allelic richness (allelic richness hereafter) refers to the number of alleles per locus and can be interpreted as a population's long-term potential for evolutionary

adaptation and persistence (Caballero & García-Dorado, 2013; Greenbaum et al., 2014). Allelic richness can generally be expected to be highest in glacial refugia areas and decline as distance from refugia increases, because cumulative founding events lead to allele losses as populations expand their distributions (Comps et al., 2001; Hewitt, 1996). Allelic richness can also increase in areas of historical population admixture, as it is dependent on effective population size (Widmer & Lexer, 2001; Petit et al 2003).

Population-level expected heterozygosity, also known as *gene diversity* (*gene diversity* hereafter), can be defined as the probability that an individual will possess two different alleles (be heterozygous) at a given locus, under Hardy-Weinberg equilibrium (Catchen et al., 2013). It reflects the additive genetic variance available to individuals in a population and thus is important for short-term responses to selection and evolutionary potential (Caballero & García-Dorado, 2013; Hoffmann et al 2017; Ørsted et al 2017). Gene diversity is expected to decline with distance from glacial refugia (Hewitt, 1996), but not as strongly as allelic richness declines in founding populations that have undergone bottlenecks (Comps et al., 2001). Gene diversity is also expected to increase in areas where populations from different refugia mix because a greater proportion of heterozygotes often occurs as the result of contributions of multiple ancestral groups (Boca et al., 2020; Petit et al., 2003).

As a result of losses during DNA extraction and post-sequencing bioinformatics processing, some sampling locations contained fewer than 5-6 individuals. Sample size can affect calculations of genetic diversity (Pruett & Winker, 2008), although this may be mitigated by using a large number of SNPs (Nazareno et al., 2017). Allelic richness was corrected for different sample sizes using a rarefaction method where the number of alleles expected in the smallest sample size were estimated (Foulley & Ollivier, 2006). Gene diversity is more robust to sampling size differences (Barrandeguy & García, 2021; Schmidt et al., 2021).

Finally, a measure of genetic variation that reflects the specific influence of past admixture events was also used: *ADMIXTURE ancestry coefficients* (*admixture proportion* hereafter), which indicate the proportion of an individual's alleles that comes from each ancestral population (Alexander et al., 2009). Admixture proportion was used to derive estimates of mean population admixture proportion and calculated for each individual as the sum of the

coefficients of the secondary ancestral groups (i.e., groups with an admixture coefficient of < 0.5 in an individual), so that admixture proportion could vary between 0 and 0.49. From this, mean population-level admixture proportion was then calculated.

2.6 Measuring vegetation greening trends (used in Chapter 5)

The “greening of the Arctic” refers to the recent multidecadal increase in tundra aboveground biomass as detected in remote sensing measurements of surface reflectance (Jia et al., 2003; Myneni et al., 1997; Zhou et al., 2001), which is part of a generalised greening trend observed in the northern hemisphere high latitudes (de Jong et al., 2012; Nemani et al., 2003; Piao et al., 2020). Tundra greening is associated with the expansion of deciduous shrubs (see **Introduction**), and the dwarf birches are one of the main taxonomic groups implicated in this shrub expansion or “shrubification” (Mekonnen et al., 2021). These greening trends are seen in calibrated, ground-truthed, and atmospherically corrected surface reflectance values captured by space-borne sensors, and are expressed and quantified using satellite-derived vegetation indices and are widely used as a proxy for shrub expansion in the Arctic (Mekonnen et al., 2021).

The Enhanced Vegetation Index (EVI) is a proxy for plant canopy structure (Huete et al., 2002; Jiang et al. 2008) and changes in the value of this index have been linked to increases in low and tall deciduous shrub cover in the Arctic (Chen et al., 2021; Seider et al., 2022). Increases in summer Normalised Difference Vegetation Index (NDVI), a measure of vegetation photosynthetic activity, have been directly linked with increased plant productivity and aboveground biomass, particularly for deciduous shrubs (Mekonnen et al., 2021; Reynolds et al., 2012). Using vegetation indices enables a panarctic comparison across regions where ground-based monitoring is scarce (Berner et al., 2018; Bjorkman et al., 2018).

In **Chapter 5** I used Landsat satellite imagery to derive spectral vegetation indices, as the spatial resolution (30 meter resolution) is higher than other publicly available satellite imagery. This resolution is relevant to the scale at which ecological processes occur, meaning that ecological changes should be captured in a realistic way (Berner et al., 2020). The lsatTS R package v1.1.0 (Berner et al., 2023) was used to export and process 30 m resolution Landsat satellite surface reflectance measurements for June-August from 2002-2021 from Google Earth Engine (Gorelick et al., 2017). Two vegetation indices: NDVI and two band Enhanced

Vegetation Index (EVI2) (Jiang et al., 2008) - were calculated using a site-specific phenological modelling approach to account for missing data (Berner et al., 2023). Preliminary analyses established that the relationships between greening trends and genetic and climate variables were similar regardless of the vegetation index used. In further analyses, EVI2 was used as it is more sensitive than NDVI to factors relevant for deciduous shrub growth, such as canopy structure and soil moisture (Chen et al., 2021). Furthermore, NDVI has been shown to saturate at high levels of photosynthetic activity (Myers-Smith et al., 2020), and so may underrepresent the magnitude of tundra greening.

2.7 Comparing genetic diversity, climate, and vegetation greening (used in Chapter 5)

Assessing the relationship between vegetation greening and genetic diversity in **Chapter 5** requires integrating data which may vary across different spatial scales. Genetic diversity was calculated from individuals sampled at specific sampling sites, while vegetation indices were available at 30 m resolution across the whole tundra landscape. To detect the spatial scale where variation in greening and genetic diversity corresponded, I performed preliminary analyses testing greening trends across a range of spatial grains, from local (~100 m radius) to more regional scales (25 km and 50 km radius) and identified 50 km as a suitable working spatial grain in this study. Furthermore, a previous analysis that assessed environmental drivers of tundra greening used 50 km pixel sizes (Berner et al., 2020).

A landcover mask was applied to filter tundra and high latitude treeless vegetation (see **Chapter 5** for details), and 100 pixels from Landsat satellite surface reflectance measurements were randomly sampled within a 50 km radius around each dwarf birch sampling site. EVI2 was calculated from surface reflectance and averaged for each sampling site. Regional trends in yearly maximum summer EVI2 ($EVI2_{max}$) spanning the last two decades were calculated using an existing rigorous protocol of time series statistical methods (Berner et al., 2020). Trends in seasonal air and soil temperatures, and soil moisture, were also calculated in a 50km radius around each dwarf birch sampling site to account for potential climatic controls on greening. These climate data came from a diverse range of sources - for details on the datasets used see **Chapter 5**.

Random Forest classification and regression models have previously been used to assess which environmental factors determine the direction and magnitude of tundra greening trends (Berner et al., 2020; Chen et al., 2021; Seider et al., 2022). Unlike those panarctic analyses, which employed thousands of data points extracted from timeseries of remote sensing imagery, my research focused on a limited number of locations where dwarf birch genetic diversity was calculated. Given the continuous nature of greening trends and the limited number of sites considered in my analysis ($n = 43$), I applied Random Forest regression models to assess the relative contribution of factors relating to past and present climate and change and genetic diversity in explaining variance in greening trends (Chen et al., 2021). See **Chapter 5** for details on the processing and analysis of vegetation greening trends, and the random forest modelling approach.

2.8 References

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Chapter 3:

Retracing the response of reindeer to postglacial climate change in Arctic islands

Maria Dance¹, Erin E. Saupe², Marc Macias-Fauria¹

¹School of Geography and the Environment, University of Oxford, Oxford, UK; ²Department of Earth Sciences, University of Oxford, Oxford, UK



Photo: Maria Dance

3.1 Chapter statement

This study addresses the first objective of the thesis, combining genetic data, coalescent modelling, and paleoclimate data to infer the impact of late Quaternary sea ice changes on the evolution and population history of Reindeer/Caribou (*Rangifer tarandus* L.), the most numerous and widespread terrestrial large herbivore of the Arctic tundra. Sea ice is crucial for maintaining connectivity between reindeer populations in the islands of the High Arctic but the role of sea ice in enabling postglacial dispersal and connectivity is understudied.

Building on previously phylogeographical studies of reindeer, we compile published records of mitochondrial sequences to compare Quaternary population histories across different island systems and analyse the role of past sea ice and ice sheet changes in shaping reindeer population history for the first time. We use well-established and robust methods to test hypotheses of evolutionary history, from which we compare estimated postglacial population events (~18-4 thousand years ago) with model-derived estimates of sea ice cover and reconstructed ice sheet changes, using proxy-based sea ice estimates as an independent evaluation tool.

This paper was presented at the INSTAAR Arctic Workshop conference in June 2022 and has been submitted as a primary research article to *Global Ecology and Biogeography*.

3.2 Author contributions

MD conceptualised the study and designed the research with input from MMF and EES. MD performed genetic data curation and EES performed sea ice data curation. MD performed all data analyses with input on sea ice data processing from EES. MD drafted the article with input from MMF and EES. All authors contributed to manuscript commenting and editing.

3.3 Abstract

Aim: Reindeer/Caribou (*Rangifer tarandus*) play a key role in Arctic ecosystems as the most numerous and widespread large herbivore but are currently in decline. Sea ice is vital for maintaining genetic connectivity of contemporary populations in Arctic island systems, yet the historical role of sea ice in shaping reindeer biogeography is understudied. Here we study the timing of reindeer dispersal to Arctic islands and the role of sea ice changes and ice sheet retreat in their dispersal dynamics. We test whether island populations dispersed in the Holocene or were isolated in separate locations during the last glacial period, as has been proposed previously.

Location: Arctic island systems (North American Arctic islands and Barents Sea islands)

Major taxa studied: Mammals: reindeer/caribou (*Rangifer tarandus*)

Methods: We compiled published datasets of mitochondrial DNA sequences for *R. tarandus* which informed scenarios of population history. These scenarios were evaluated in a coalescent-based approximate Bayesian computation (ABC) modelling framework to test hypotheses of Arctic island (re)colonisation and to determine timings of population divergence and admixture. Modelled population events were compared with modelled and proxy-based paleo-sea ice cover and published ice sheet chronologies.

Results: The coalescent-based analyses support Holocene dispersal of reindeer onto deglaciated Arctic islands from continental glacial locations. The degree of population admixture and the relationship between sea ice and population dynamics differed depending on regional geography and climate history. North American populations responded to deglaciation and reflected favourable sea ice conditions with frequent dispersal throughout the Holocene. The Svalbard and West Greenland population divergence times lagged island deglaciation but broadly align with fossil-based estimates of island colonisation, suggesting dispersal limitation due to sea ice conditions, potentially modulated by ocean currents and corresponding sea ice drifting routes.

Main conclusions: Our study sheds light on the Late Quaternary history of Arctic island reindeer and suggests that ice sheet retreat, sea ice cover, and ocean currents were likely important in shaping present-day population genetic patterns. Regional differences in

postglacial dynamics suggest that dispersal during contemporary climate change may vary regionally and depend upon the decreasing connectivity provided by sea ice.

Keywords: Approximate Bayesian computation, caribou, glacial refugia, ice sheets, phylogeography, postglacial dispersal, Quaternary, *Rangifer tarandus*, reindeer, sea ice

3.4 Introduction

Reindeer/Caribou (*Rangifer tarandus* L.) are the most numerous and widespread large herbivore in the Arctic and consequently have large effects on other species, tundra vegetation composition, and ecosystem functioning (Olofsson & Post, 2018). An overall 40% decline in population numbers has been inferred across the Arctic over the last three decades, often driven by anthropogenic activities and landscape changes (Gunn, 2016). Reindeer/caribou's range includes the many High Arctic island systems of North America and the Barents/Kara Seas (COSEWIC, 2011; Gunn et al., 2010; Mizin et al., 2018; Pedersen et al., 2019). There, the long-term viability and genetic variation of such smaller, fragmented, and isolated populations is reduced as a result of restricted gene flow and increased genetic drift and inbreeding (Petersen et al., 2010; Schlaepfer et al., 2018). Population connectivity is important to maintain population numbers, genetic variation, and subsequent adaptive capability in the face of environmental change (Mallory & Boyce, 2018; Torda & Quigley, 2022).

In the Arctic, sea ice is vital for maintaining reindeer population connectivity by enabling crossings between islands (Jenkins et al., 2016; Miller et al., 2005; Mizin et al., 2018; Peeters et al., 2019; Poole et al., 2010). Reindeer in the Canadian Arctic Archipelago (CAA) currently require an estimated 75-90% sea ice cover to make seasonal migrations (Mallory & Boyce, 2018; Poole et al., 2010). Regional differences in connectivity exist as a result of geographical distance and varying sea ice conditions. In the CAA reindeer regularly cross over sea ice as part of seasonal migrations and sporadic dispersal (Miller et al., 2005; Poole et al., 2010) as inter-island distances can be as narrow as 2-20 km and ice cover has been consistently seasonally present. Crossings between the CAA and Greenland are much rarer, although documented (COSWIC, 2015; A. D. M. Taylor, 2005), despite sea ice bridges previously connecting Greenland and Ellesmere Island on an annual basis (Moore et al., 2021).

Within the Svalbard archipelago, reindeer genetic structure shows that connectivity between islands depends on sea ice (Peeters et al., 2019), even though sea ice is more variable in time and space than in the CAA due to inflow of warm Atlantic water by the West Spitsbergen Current. Variable ice cover and large distances between land masses in the Barents Sea further limits opportunities for gene flow between islands and the mainland. Svalbard lies approximately 400 km from the Franz Josef Land archipelago, and 770 km from the islands of Novaya Zemlya (itself separated from the Russian mainland by the 56 km wide Kara Strait). Only a few sightings of reindeer migrating between the mainland and within Barents Sea islands have ever been recorded or inferred (Hoel, 1916; Kvie et al., 2016; Lønø, 1959). Loss of population connectivity following contemporary sea ice decline has been documented using genetic data in both the Canadian Arctic and Svalbard archipelagos, where continued sea ice loss is expected (Jenkins et al., 2018; Mallory & Boyce, 2018; Peeters et al., 2019).

Understanding how past sea ice changes influenced population dispersal to and connectivity within the Arctic islands would give insights into the evolutionary consequences of continued sea ice loss. Changes in population isolation and connectivity due to sea ice and climatic changes are detectable in contemporary geographic patterns of genetic diversity (Mellows et al., 2012; Norén et al., 2009). However, genetic data have not been used to assess the role of sea ice in enabling reindeer dispersal to Arctic islands, and colonisation history and the relationships between populations and subspecies remain unclear (Mizin et al., 2018).

The taxonomic and evolutionary relationships between Arctic island reindeer populations are complex, with small-bodied, large-bodied, and intermediate forms. The evolutionary origin of small-bodied reindeer has long been debated (Flagstad & Røed, 2003; Gravlund et al., 1998; Hoel, 1916; Lønø, 1959; Røed et al., 1986). The Svalbard (*R. tarandus platyrhynchus*) and North American (*R. t. pearyi*) species were thought to have a monophyletic origin based on their shared ecotype and early molecular studies (Røed et al., 1986). However, mitochondrial sequences suggest that the sub-species evolved convergently from different source populations: *R. t. pearyi* from a Euro-Beringian lineage in North America, and *R. t. platyrhynchus* from a Euro-Beringian lineage in Eurasia (Gravlund et al., 1998). The Euro-Beringian lineage likely spent the last glacial period in the ice-free parts of Eurasia, including the ice-free Beringian region which spanned from the Verkhoyansk mountains in Eastern Russia to the Mackenzie River in North America (Elias & Brigham-Grette, 2013; Hultén, 1937).

Svalbard reindeer are thought to have colonised from the Russian mainland via Novaya Zemlya and Franz Josef Land on the basis of strong genetic connections between island populations, and with the Russian mainland (Kvie et al., 2016). North American small-bodied reindeer have been proposed to have colonised islands in the postglacial period from a Beringean glacial location shared with mainland reindeer (Flagstad & Røed, 2003). Others have proposed that these reindeer were isolated in a separate High Arctic glacial refugium (i.e. a spatially restricted distribution in an isolated ice-free region), and then mixed to some degree with mainland reindeer in the postglacial period (Eger et al., 2009; Klütsch et al., 2017).

Constrained time estimates of island colonisation are needed to determine the potential roles of Quaternary ice sheet and sea ice changes in shaping reindeer population history. Estimates of population divergence and admixture time estimated from coalescent models can help infer the biogeographic barriers and corridors that shaped species' Late Quaternary histories (Hansen et al., 2018; Robinson et al., 2014; Sousa et al., 2012). Such timings have been previously estimated with genetic data only for the CAA (Klütsch et al., 2017), with fossil data currently the primary frame of reference in the Barents Sea islands (Forman et al., 2000; van der Knaap, 1989). A regional comparison of the role of sea ice in shaping population history requires a common framework.

Here we reconstruct and compare reindeer population histories in two Arctic island systems (North American Arctic Islands, NAAI and Barents Sea Islands, BSI) using available mitochondrial data and approximate Bayesian computation (ABC). Coalescent methods linking genetic diversity with population demographic history (Kingman, 1982; Marchi et al., 2021) have been previously used to infer the impacts of Quaternary climate change on reindeer (Eger et al., 2009; Klütsch et al., 2017; Lorenzen et al., 2011; Polfus et al., 2017; Taylor et al., 2021; Yannic et al., 2014), but not across different Arctic island systems. Specifically, we compare evolutionary scenarios to test whether island populations (i) were in a common location with mainland populations during the Last Glacial Maximum (LGM) and dispersed postglacially, or (ii) were isolated prior to the LGM in separate High Arctic refugia and came into contact with mainland populations during the LGM or the postglacial period.

Using the best-supported scenarios, we compare timings of population divergence and admixture with modelled sea ice cover, proxy-based sea ice reconstructions, and ice sheet retreat to infer the likely drivers of dispersal. We hypothesise that island colonisation

coincided with the emergence of newly available land after ice sheet retreat, provided that sea ice cover was sufficient for dispersal. We further hypothesise that the colonisation of the two island systems differed as a result of different geographies, deglaciation, and sea ice histories. Specifically, we expect more secondary contact and population admixture within the NAAI, with admixture occurring in periods of sufficient sea ice cover, and population divergences occurring during reduced sea ice cover as populations previously connected by sea ice became isolated. In the BSI, we expect stepwise dispersal with fewer opportunities for secondary contact, with divergence corresponding to island colonisation as founding populations were separated from source populations by long-distance dispersal over sea ice. Population divergence is therefore expected to be associated with sufficient sea ice cover in the Barents Sea. Testing these hypotheses is important for developing our understanding of the long-term ecological and evolutionary impacts of past climate change on reindeer, and the potential impacts of an increasingly ice-free Arctic on the population connectivity and long-term persistence of ice-influenced species.

3.5 Materials and methods

3.5.1 Species

Several recognised subspecies of *R. tarandus* inhabit the Arctic islands. The two extant small-bodied species, *R. tarandus platyrhynchus* (Vrolik, 1829) and *R. t. pearyi* (Allen, 1902) occur in Svalbard and in the Canadian Arctic Archipelago (CAA), respectively. Small-bodied reindeer described as *R. t. eogroenlandicus* (Degerbøl 1957; Meldgaard 1986) inhabited East Greenland but were extirpated around 1900 and were considered genetically and morphologically close to *R. t. pearyi* (Gravlund et al., 1998). *Rangifer t. platyrhynchus* and *R. t. pearyi* are specialised for the High Arctic environment and share similar morphologies of small body size, short legs and muzzle, and paler, longer winter fur than their mainland neighbours.

In North America, large-bodied reindeer (*R. t. groenlandicus*) occur on Baffin Island and West Greenland, as well as on the subarctic continental tundra (COSEWIC, 2011; McFarlane et al., 2016; Meldgaard, 1986). The Dolphin-Union herd in the CAA is currently designated as an intermediate form *R. t. groenlandicus* $\times$ *pearyi* (COSEWIC, 2011). In the Eurasian Arctic, large-bodied reindeer on Novaya Zemlya are variously recognised as the subspecies *R. t. pearsoni*

(Lydekker, 1903; Kvie et al., 2016; Mizin et al., 2018). Reindeer were also formerly present on the Franz Josef Land archipelago during the Holocene, with fossils dated to between 6.4-1.3 ka (Forman et al., 2000).

3.5.2 Genetic data

We used 524 mitochondrial control region (CR) sequences from across the Arctic from ten previously published datasets (Eger et al., 2009; Flagstad & Røed, 2003; Gravlund et al., 1998; Kuhn et al., 2010; Kvie et al., 2016; Letts et al., 2012; Petersen et al., 2010; Røed et al., 2008, 2020; Weckworth et al., 2012). Information on these studies is included in **Table S3.1**. In reindeer, the rapidly evolving mitochondrial control region has been found to be suitable for exploring intraspecific genetic relationships (Eger et al., 2009; Gravlund et al., 1998). Sequences were obtained from NCBI GenBank (Sayers et al., 2022), and haplotype-level sequences were converted to individual-level sequences with a corresponding population identification using study metadata. Ancient DNA, sequences from domesticated herds, and potentially domestically-introgressed wild populations were excluded, except for the key population of Novaya Zemlya, where possible introgression from domestic reindeer has been suggested (Mizin et al., 2018).

Sequences were aligned using default parameters in the ClustalOmega multiple alignment algorithm and msa package v 1.22.0 (Bodenhofer et al., 2015; Sievers et al., 2011). Sequences from the Gravlund (1998) dataset were manually corrected by adding an insertion of 1bp in length at position 220. Sequences were trimmed to the same length to minimise problems with lower quality read ends, to remove missing data, and because ABC software cannot handle indel mutations (Collin et al., 2021). Sequences were trimmed to 134 bp to retain the maximum number of sequences possible. Basic genetic summaries and pairwise F_{st} measures (Nei's G_{st} , Hedrick's G'_{st} , and Jost's D) were calculated using hierfstat v 0.5-7 and mmod v 1.3.3 R packages, respectively (Goudet et al., 2022; Winter, 2012). Haplotypes were extracted and mapped using the pegas v 0.14 R package (Paradis, 2010).

We divided genetic data into two regions: the North American Arctic islands (NAAI) and the Barents Sea islands (BSI), retaining island populations and neighbouring mainland populations. Where sampling location coordinates were not readily available, sampling location was inferred using locality metadata and georeferenced using the Google Geocoding

API in the ggmap v 3.0.0 package in R v 4.0.3 (Kahle & Wickham, 2013; R Development Core Team, 2022). Sequences from eastern Russia were included in the BSI dataset to test whether the Svalbard population arose from the Beringean glacial lineage or whether it diverged earlier, and occurred in a separate glacial location (Kvie et al., 2016). The North American lineage — that spend the LGM south of the North American ice sheets — was excluded from the analysis as the large genetic distance from the Beringean group made it more difficult to distinguish fine-scale regional phylogeographic patterns (Kuhn et al., 2010; Yannic et al., 2014).

3.5.3 Population genetic structure

Each individual genetic sample had been previously associated with a population, herd, or locality based on sampling location. For demographic modelling, using pre-defined populations (e.g., based on geographical proximity) is problematic because genetic variation in *Rangifer tarandus* often does not reflect present-day subspecies designations, geographical populations, or ecotypes (Polfus et al., 2017; Serrouya et al., 2012; Weckworth et al., 2012). Arbitrary assignment to populations can lead to more genetic variation and structure within populations than between populations, making genetic data simulation using coalescent modelling difficult.

To visualise the multivariate genetic dissimilarity between original populations, we used metric multidimensional scaling (mMDS) of distance matrices within the cmdscale v. 4.0.3 function (R Development Core Team, 2022). To determine the number of distinct genetic populations, we used exploratory clustering approaches without assumptions on the underlying evolutionary model (Jombart et al., 2009). Non-evolutionary Euclidean distance matrices were calculated using the adegenet v 2.1.3 R package (Edward's distance) (Jombart, 2008) and dendrograms constructed using the unweighted pair group method with arithmetic mean (UPGMA) hierarchical clustering method, implemented with the hclust function v. 4.0.3 (R Development Core Team, 2022). Various agglomeration methods were tested and the method with the highest correlation between original distances and resulting tree-based distances chosen ("average method"). UPGMA dendrograms were plotted using the dendextend v 1.14.0 package (Galili et al., 2023).

K-means clustering was performed on both the distance matrices and the mMDS dissimilarity coordinates and overlaid on a) the UPGMA dendrogram to compare groupings obtained by the different clustering methods (Galili et al., 2023), and b) the mMDS ordination plot to identify genetic clusters (R Development Core Team, 2022). K-means clustering assigned each observation to the cluster with the nearest mean. The optimal number of clusters (K) was estimated by both (i) examining plots of within-group variance at each value of K and selecting the highest value of K beyond which the variance did not markedly decline (Elbow method), and (ii) determining how well each object lies within its cluster for different values of K, using the average silhouette method in the cluster v 2.1.4 R package (Maechler et al., 2022).

3.5.4 Development of demographic modelling scenarios

We used the aforementioned clustering methods to inform population groups and relationships in evolutionary scenarios that represented a different hypothesis of population history. Initial pre-selection of plausible evolutionary scenarios is practical, given the prohibitively high number of potential demographic scenarios for multiple populations, and given the risk of multiple testing or overfitting when performing many analyses or testing complex models (Borrell et al., 2018).

For each scenario, the following parameters were specified: (i) population groups, (ii) topology, which is the branching relationships among populations and corresponding sequence of population events (population divergence, admixture, and bottlenecks), (iii) prior time ranges for population events, (iv) prior ranges for the effective population sizes (N_e) of modern populations and bottleneck magnitude, and (v) genetic data characteristics, including mutation rate and mutation model.

We grouped evolutionary scenarios into sets of models that could be tested against each other because they had the same population groups. Within each model set, scenarios differed in their topology or parameter prior ranges. The optimal number of genetic clusters identified in K-means clustering was used as a starting point for the population groupings. As the model sets were tested, new model sets were made where populations were split further or combined on the basis of F statistics to minimise within-population genetic structure and maximise between-population differences.

Scenarios of a single glacial population with postglacial divergence were tested against scenarios with earlier divergence and separate glacial locations (Klüttsch et al., 2017; Kvie et al., 2016). For the NAAI, we also tested a scenario of interglacial island population divergence and mainland admixture in the Last Glacial Maximum, followed by postglacial dispersal. We developed and tested 54 scenarios grouped in 19 model sets for the NAAI, and 30 scenarios grouped in 17 model sets for the BSI. See Tables **S2-S4** for details on model sets, scenarios, and their prior specifications.

3.5.5 Testing evolutionary scenarios

We used approximate Bayesian computation (ABC) to test our evolutionary scenarios (Beaumont, 2010; Cornuet et al., 2014). Within each model set, genetic data were simulated under the different evolutionary scenarios using a population genetic simulator, summarised by a large set of statistics, which were then compared to the observed genetic data statistics. Specifically, the software package DIYABC Random Forest v1.0 was used for ABC analyses in combination with supervised machine learning based on Random Forests (RF) (Collin et al., 2021) for model selection and parameter estimation. Using RF models is computationally efficient, addresses potential ABC limitations, and outperforms other ABC methods for analysis of multiple complex scenario, while using a smaller numbers of simulated datasets (Collin et al., 2021). For each model set, we generated 100,000 simulated genetic datasets, drawing parameter values from the prior distributions. The number of trees for model selection and parameter estimation was fixed to 500 to ensure stable estimation of the global error rate. Otherwise, default software parameters were used.

For each model set, we assessed overlap between 1000 genetic datasets simulated under each scenario with the observed genetic dataset on the first two axes of a principal component analysis (PCA). Visual assessment of dataset overlap identified poorly specified scenarios and helped to refine prior ranges for new model sets. When observed and simulated datasets overlapped, scenarios were tested against each other using RF model classification. The best-performing models were selected based on model error rates and on visual assessment of overlap between simulated and observed data when projected on linear discriminant analysis (LDA) axes. LDA also indicated the degree to which it was possible for RF classification to discriminate among scenarios within a model set.

The best-performing scenarios were iteratively improved and tested until a final set of models was produced in which local model error rate was reduced to approximately 20% or less (Table 1, Collin et al., 2021), complete overlap occurred between simulated and observed data, and posterior probabilities were above 65% (Collin et al., 2021). See **Tables S3.5** and **S3.6** for detailed DIYABC specifications of the scenarios in the final model set and **Figures S3.1** and **S3.2** for LDAs of observed versus simulated data for each scenario.

3.5.6 Population history parameter estimation

The most plausible evolutionary scenario with the highest posterior probability was selected from each final model set and divergence, admixture, and bottleneck time parameters were estimated (**Figure 3.1** and **Figure 3.2**). We conducted independent RF models for each parameter of interest. The training sets included over 30,000 datasets per scenario for parameter estimation (100,000 datasets per model set divided by the number of scenarios per model set). Point estimates and 95% credible intervals were calculated along with global and local accuracy metrics. Estimates were converted from number of generations to calendar years assuming a generation time of seven years (Klüttsch et al., 2017; Polfus et al., 2017).

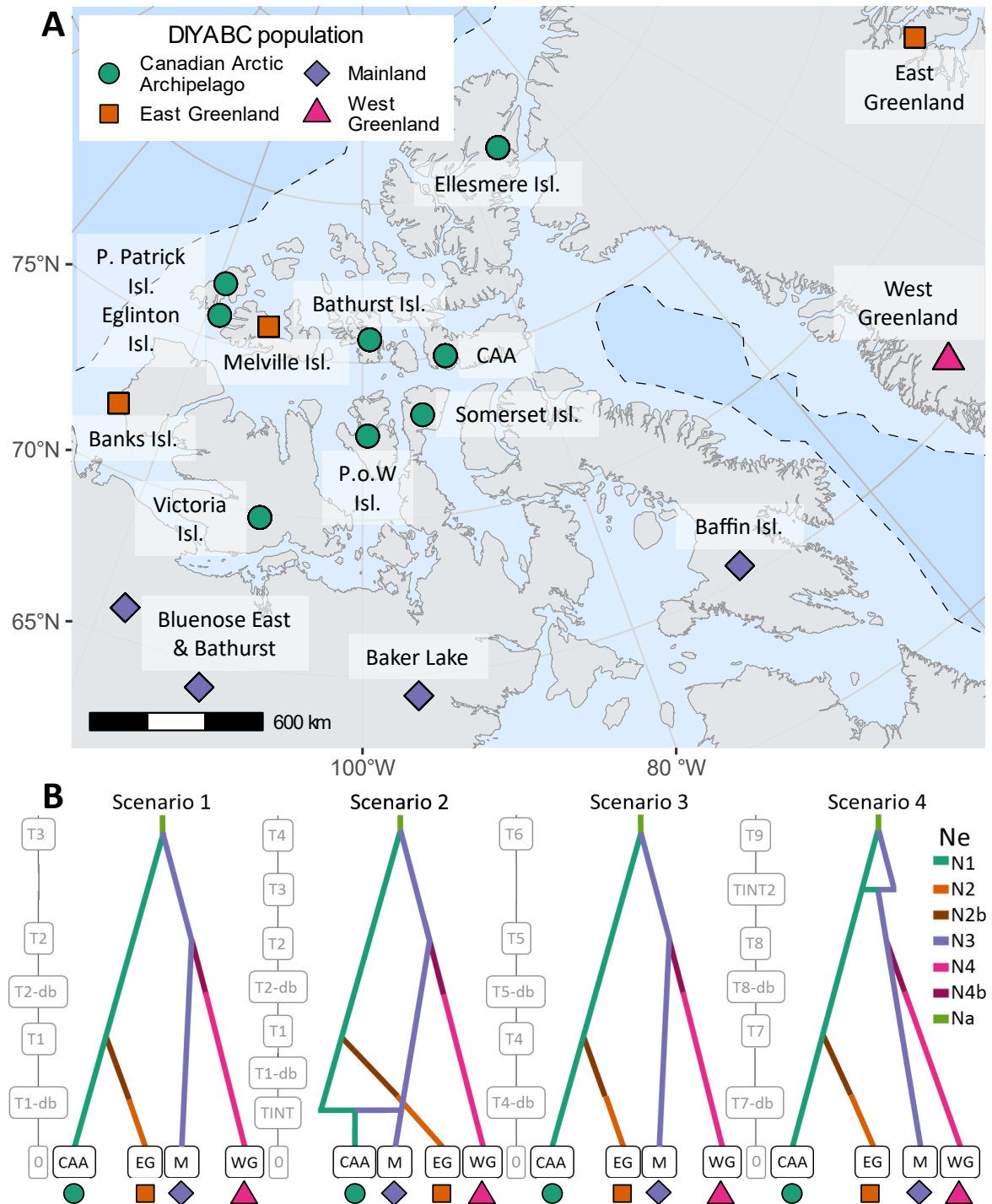


Figure 3.1. *Rangifer tarandus* in the North American Arctic Island system and final four evolutionary scenarios. Map of approximate geographic sampling locations for *R. tarandus* (A), colour-coded by the population groupings used for demographic analysis. Dotted line indicates the best estimate of LGM ice sheet extent (Batchelor et al., 2019). P. Patrick Isl. = Prince Patrick Island. P.o.W Isl. = Prince of Wales Island. (B) Evolutionary scenarios of the final model set tested with DIYABC RF (Collin et al., 2021). Scenario two was the preferred model (0.706 posterior probability). N_e is the haploid effective population size of each population, with population bottlenecks in East Greenland (N2b) and West Greenland (N4b) after divergence from ancestral populations.

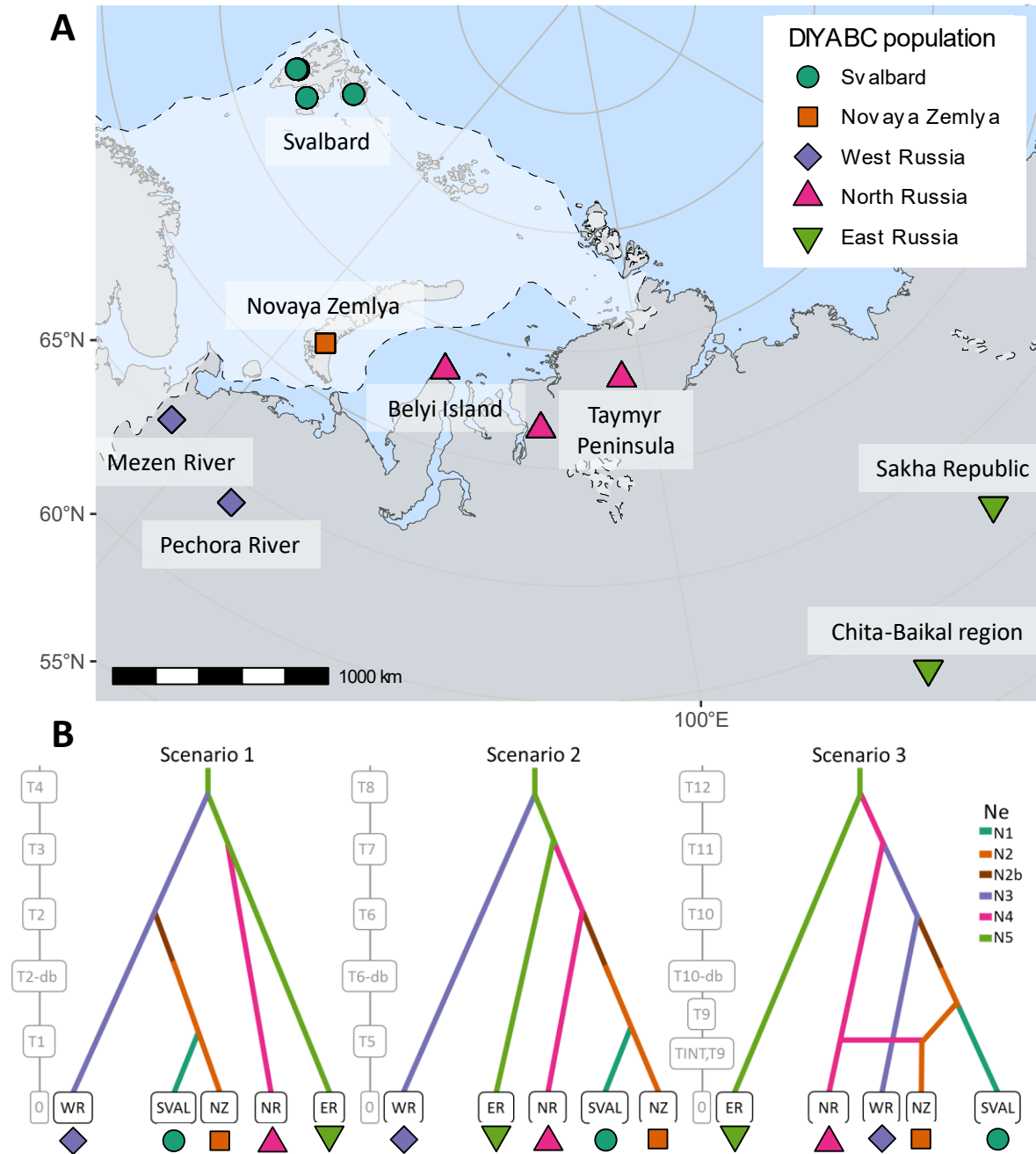


Figure 3.2. *Rangifer tarandus* in the Barents Sea Island system and final evolutionary scenarios. Map of approximate geographic sampling locations for *R. tarandus* (A), colour-coded by population groupings used for demographic analysis. Dotted line indicates the best estimate of LGM ice sheet extent (Batchelor et al., 2019). (B) Evolutionary scenarios of the final model set tested with DIYABC RF (Collin et al., 2021). Scenario three was the preferred model (0.980 posterior probability). N_e refers to haploid effective population size of each population, with population bottleneck (N2b) in the Novaya Zemlya ancestral population after divergence from ancestral populations.

3.5.6 Comparison with paleo sea ice data

Modelled sea ice concentration was used to assess whether estimated times of divergence and admixture corresponded to changes in sea ice cover in corresponding sea regions which may have supported reindeer crossings. Estimated population event times were compared with monthly and annual mean, maximum (March) and minimum (September) sea ice concentrations at the closest time step to determine temporal congruence with sea ice changes, and whether sea ice concentrations were sufficient to enable crossings (Mallory & Boyce, 2018; Poole et al., 2010).

Where available, published regional sea ice reconstructions derived from proxies were used as an independent comparison to model data (Briner et al., 2016; Hörner et al., 2017; Jennings et al., 2011; Pieńkowski et al., 2013, 2021). Estimated divergence times were also compared with the pattern and timing of ice sheet retreat over the relevant regions, using time slice reconstructions of ice margins at 1 thousand year (ka) resolution based on recent syntheses of published dates from geological and geomorphological records (Dalton et al., 2020; Hughes et al., 2016; Winsborrow et al., 2023).

Paleo-sea ice concentration was estimated from simulations using the global HadCM3 coupled atmosphere-ocean generalised circulation model (Singarayer et al., 2017; Valdes et al., 2017). The ocean component of the model has a horizontal resolution of $1.25^\circ \times 1.25^\circ$ and 20 vertical levels, with sea ice calculated as a zero-layer model on top of the ocean grid. The sea ice model uses a thermodynamic scheme and contains parameterizations of ice drift and leads. Sea ice cover is the fraction of the grid cell area covered by sea ice, which can take values up to 0.995, corresponding to a concentration measure of 99.5%. A detailed description of sea ice parameterisation is available in Valdes et al. (2017). When compared with observational datasets, the model accurately represents many aspects of the climate system on regional scales, including sea surface temperatures and ocean circulation (Valdes et al., 2017). For the paleoclimate model, sea-ice cover compares well with estimates of ice extent from microfossil data in regions with available data (Roche et al., 2012; Singarayer & Valdes, 2010). The simulations use the ICE-5G glacial ice sheet model (Peltier, 2004), which includes detailed evolution of ice sheet thickness, extent, and continental isostatic rebound from the LGM to the present at 500-year intervals. From this, total continental elevation, ice sheet extent, and land sea mask for each time interval were obtained.

Daily sea ice concentration values were summarised as monthly and annual climatological means for discrete snapshot simulations at the highest available resolution of one thousand years. Large sea ice changes can occur on sub-millennial timescales (Kinnard et al., 2011; Saini et al., 2020), but changes in sea ice that persist on millennial timescales are suitable for comparison with demographic history events as it can take many generations for a change in population structure or connectivity to be evident in the genetic structure (Epps & Keyghobadi, 2015). Furthermore, millennial-scale increases in sea ice cover provide more opportunities for rare and random long-distance dispersal of reindeer to islands across sea ice (Gillespie et al., 2012; Jordano, 2017).

We focused on the Last Glacial Maximum to the preindustrial period (~21-0 ka) as our best-supported demographic models suggested postglacial dispersal to islands. We projected sea ice data to the North Pole Lambert Azimuthal Equal Area projection (EPSG 3575) at 30 km resolution, centred at 100° W longitude for the NAAI model and 90° E longitude for the BSI model. Spatial data processing was conducted using the raster v 3.4-5 (Hijmans et al., 2023) and sp v 1.4-5 R packages (Pebesma et al., 2023).

To obtain estimates of sea ice concentration that were spatially and biologically relevant to the inferred population events, we extracted sea ice cover from geographical areas representative of likely reindeer crossing regions. Each DIYABC population usually consisted of several herds and was therefore spread over space. To estimate the overall geographic position of these populations, we calculated the centroid between herds using the rgeos v 0.5-5 R package (Bivand et al., 2023). Then, for each population event, we calculated geographic position as the centroid between populations involved in the event. To reduce the influence of selecting an arbitrary centroid as a proxy for a relevant spatial region we sampled 100 random points within a 100 km radius of the calculated centroid. For each of the 100 random points, we extracted sea ice concentration estimates from grid cells within a set radius: the NAAI model used 1000-1500 km radii to encompass all likely crossing regions within the Canadian Arctic Archipelago and Greenland. The BSI system has clear and geographically separated potential crossing regions with sea areas of different sizes, so sea ice was calculated separately for different regions: a 300 km radius to encompass a direct Svalbard-Novaya Zemlya crossing region, a 300 km radius between Novaya Zemlya and Franz Joseph Land, a 200 km radius between Franz Josef Land and Svalbard, and a 500 km radius

between Northern Russia and Novaya Zemlya. Mean and standard deviation of sea ice concentration were summarised across grid cells within each radius.

3.6 Results

3.6.1 Population genetic structure

Sixty-four unique haplotypes were identified across the regions from 42 segregating sites in the 134 bp mitochondrial CR sequences, with 27 haplotypes present in the NAAI and 42 haplotypes present in the BSI. The Svalbard, West Greenland, and East Greenland sampling populations had the lowest gene diversities and allelic richness compared to the rest of populations within each region; see **Tables S3.10** and **S3.11** for genetic summary statistics of original sampling populations.

In the North American Arctic Islands, NAAI, UPGMA and K-means clustering of the Euclidean distance matrices identified two genetic clusters (**Figure S3.3**). The Canadian Arctic Archipelago (CAA) populations formed one large cluster which included East Greenland and Baffin Island. The mainland populations of Baker Lake, Bluenose East, and Bathurst formed another cluster together with West Greenland (**Figure S3.3**). K-means clustering of the mMDS dissimilarity coordinates identified three clusters. The third cluster consisted of Banks Island, Melville Island, and East Greenland, while Baffin Island was grouped with the mainland populations (**Figure S3.4**).

In the BSI, UPGMA and K-means clustering approaches both identified four main genetic clusters (**Figure S3.5, S3.6**). In the UPGMA, Svalbard and Novaya Zemlya were grouped with the Pechora River in western Russia, the western Russian Mezen River population was distinct, and the eastern Russian and northern Russian populations also formed separate clusters. Four K-means clusters were also present in the mMDS ordination plot, but the western Russian Pechora River clustered together with the Mezen River (**Figure S3.6**).

3.6.2 Demographic history

3.6.2.1 North American Arctic Islands

The final set of NAAI models contained four populations. Scenario two (**Figure 3.1**) had the highest posterior probability (0.706). The best supported model suggested population divergence between the Canadian Arctic Archipelago (CAA) and the Mainland populations in

the early Holocene 10.6 ka (CI 5.15-13.6 ka), coinciding with the retreat of the Laurentide ice sheet and parts of the western CAA becoming ice free (Dalton et al., 2020). In this best-supported scenario, the East Greenland population was grouped with the geographically disjunct Banks and Melville Islands. These populations clustered together in the UPGMA and had low pairwise F_{ST} values, indicating that they were not genetically differentiated (**Table S3.10**). This pattern was likely affected by the presence of only one haplotype in East Greenland, which was shared with Banks Island and Melville Islands, in addition to some other populations from the CAA. The model suggests the East Greenland population diverged from the CAA population at 6.4 ka (CI 2.25-10.7 ka).

The West Greenland - Mainland population divergence was estimated at 6.3 ka (CI 2.16-10.07 ka). A potential sea dispersal route from the deglaciated coasts of Baffin Island to deglaciated coasts of West Greenland was available from ~8.5 ka (Dalton et al., 2020). Baffin Island was included in the Mainland group as Baffin Island reindeer grouped with Baker Lake reindeer in the mMDS and had a low pairwise F_{ST} value (**Table S3.12**), indicating the populations were not genetically differentiated. Scenario two also included an introgression (unidirectional admixture) event from the Mainland population into the CAA population (2.7 ka, CI 1.11-6.40 ka); see **Table S3.8** for all parameter estimates.

3.6.2.2 Barents Sea Islands

The final set of BSI scenarios contained five populations (**Figure 3.2**). Scenario three had the highest posterior probability (0.98) and showed populations diverging from an ancestral East Russian population during the last glacial period (64.2 ka, CI 26.47-95.34 ka; see **Table S3.9** for all time parameter estimates). Although the southern island of Novaya Zemlya was likely ice free by 18 ka (Hughes et al., 2016), the Novaya Zemlya population did not diverge from mainland populations until 11.7 ka (CI 5.61-19.54 ka). Similarly, the Svalbard - Novaya Zemlya divergence was estimated at 5.7 ka (CI 2.90-10.26 ka; Figure 2), considerably after ice sheet retreat from Svalbard coasts at 12 ka and from Franz Joseph Land by 10 ka (Hughes et al., 2016). In scenario three, the Novaya Zemlya population experienced an introgression event from the North Russian population dated at 3.3 ka (CI 2.06-6.90ka), which was supported by the lower genetic differentiation between Novaya Zemlya and the Taymyr Peninsula compared to Svalbard (**Table S3.13**).

3.6.3 Comparing demographic history and postglacial environmental changes

3.6.3.1 North American Arctic Islands

In the NAAI system, modelled sea ice cover declined from near-perennial cover in the early postglacial period (indicated by $\geq 50\%$ sea ice cover in summer months, **Figures S3.7 and S3.8**), to more seasonal and variable sea ice cover from the onset of the Holocene (12-11ka). During the Holocene, September sea ice fell below 50% across the NAAI (**Figure 3.3, 3.4**), and was mostly absent in Baffin Bay and the Davis Strait (**Figure 3.4B**) where sea ice concentration typically decreased from $>85\%$ in May to $<50\%$ by July (**Figure S3.8B**). Sea ice cover was greater and summer breakup later in the CAA channels and the Arctic Ocean (**Figure 3.4D**, with sea ice concentration typically decreasing from $\sim 90\%$ in May to $<50\%$ by August (**Figure S3.7**).

Sedimentary core analyses suggest land ice sheet retreat and a commencement of a marine environment within the channels of the CAA ~ 10.8 ka (Pieńkowski et al., 2013). Our paleoclimate model data did not show modern land configuration until 6 ka due to limited spatial resolution, resulting in absence of sea ice data for some CAA channels (**Figure 3.4A, 3.4C**). Proxy reconstructions show that the Nares Strait between East Greenland and Ellesmere island was inundated before 9 ka, and the Barrow Strait was inundated prior to 7.8 ka (Briner et al., 2013).

Two population divergences in the NAAI occurred during or following periods of modelled annual and summer sea ice decline, although spring sea ice cover remained above 90% (**Figure 3.3**). Postglacial divergence of the island populations from the mainland at 10.6 ka (CI 5.15-13.6 ka) occurred during large declines in modelled annual sea ice cover from 91.1% (SD 3.20%) to 67.1% (SD 9.10%) and in September sea ice cover from 91.5% (SD 5.11%) to 45.1% (SD 13.4%) from 13-10 ka (**Figure 3.3B**). Sea ice cover therefore fell below the 75% minimum threshold for crossing (Mallory & Boyce, 2018; Poole et al., 2010) during the autumn months (**Figure S3.7**). Proxy data from the mid-CAA indicates a transitional period of ice sheet retreat and gradual replacement by marine conditions around this time (Pieńkowski et al., 2012).

The East Greenland - CAA divergence at 6.4 ka (CI 225-10.7 ka) occurred during a period of reduced modelled sea ice cover. September sea ice cover was below 50% and therefore not sufficient for supporting crossing during the autumn (**Figure 3.3D**). Proxy-based

reconstructions suggest reduced sea ice cover from 9-6 ka in the Nares Strait that separates Ellesmere Island from Greenland, followed by increased sea ice cover from 6 ka (Briner et al., 2016; Jennings et al., 2011). An earlier general increase in CAA sea ice cover from ~7 ka until 6 ka (Briner et al., 2016) is not reflected in modelled sea ice cover (**Figure 3.3B**). The West Greenland - Mainland divergence at 6.3 ka (CI 2.16-10.07 ka) occurred during a period of stable but low ice cover with ice-free summers and annual concentrations below the 75% threshold. However, March sea ice concentration was close to 100%. (**Figure 3.4B**). Proxy-based reconstructions in northern Baffin Bay suggest an increase in sea ice cover from 6.4-5.8 ka (Saini et al., 2022) or 5.5 ka (Briner et al., 2016), surrounding the modelled West Greenland reindeer divergence time.

The CAA-Mainland admixture event at 2.7 ka (CI 1.11-6.40 ka) was coeval with a small increase in modelled September ice cover from 20.6% (SD 27%) to 28.4% (SD 30.7%) and in other autumn months (**Figure 3.4D, S3.8D**).

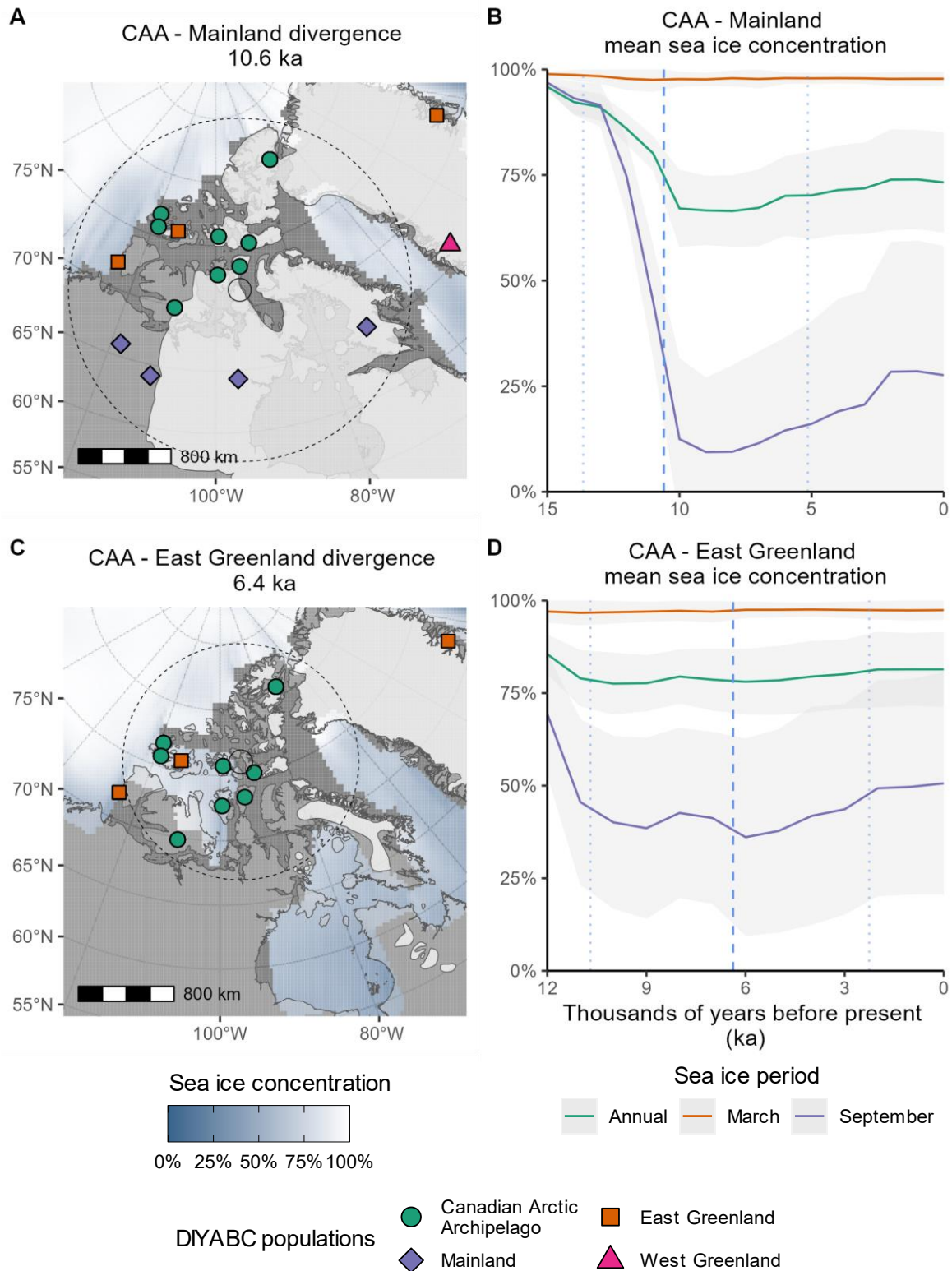


Figure 3.3. Reindeer population divergence events and modelled sea ice changes in the North American Arctic Islands (NAAI). (A, C): Demographic events mapped with relevant present-day populations, modern land extent (light grey), a snapshot of modelled mean sea ice concentration (blue - white) and land extent (dark grey) at 11 ka (A) and 6 ka (C) (Singarayer et al., 2017; Valdes et al., 2017), and reconstructed ice sheets at 10.3 ka (A) and 6.4 ka (C) – the closest time steps to the corresponding population events (Dalton et al., 2020). Divergence time estimates are the median parameter estimates from the most plausible

evolutionary model (scenario two). The geographic centroid between two populations (solid circle), within which 100 random samples of modelled sea ice concentration at different radii (dotted circle) were extracted and averaged (one radius shown for clarity). (**B, D**): Modelled sea ice concentration with associated standard deviations in 1 ka intervals. Demographic event times (dashed lines) with associated 95% credible intervals (dotted lines).

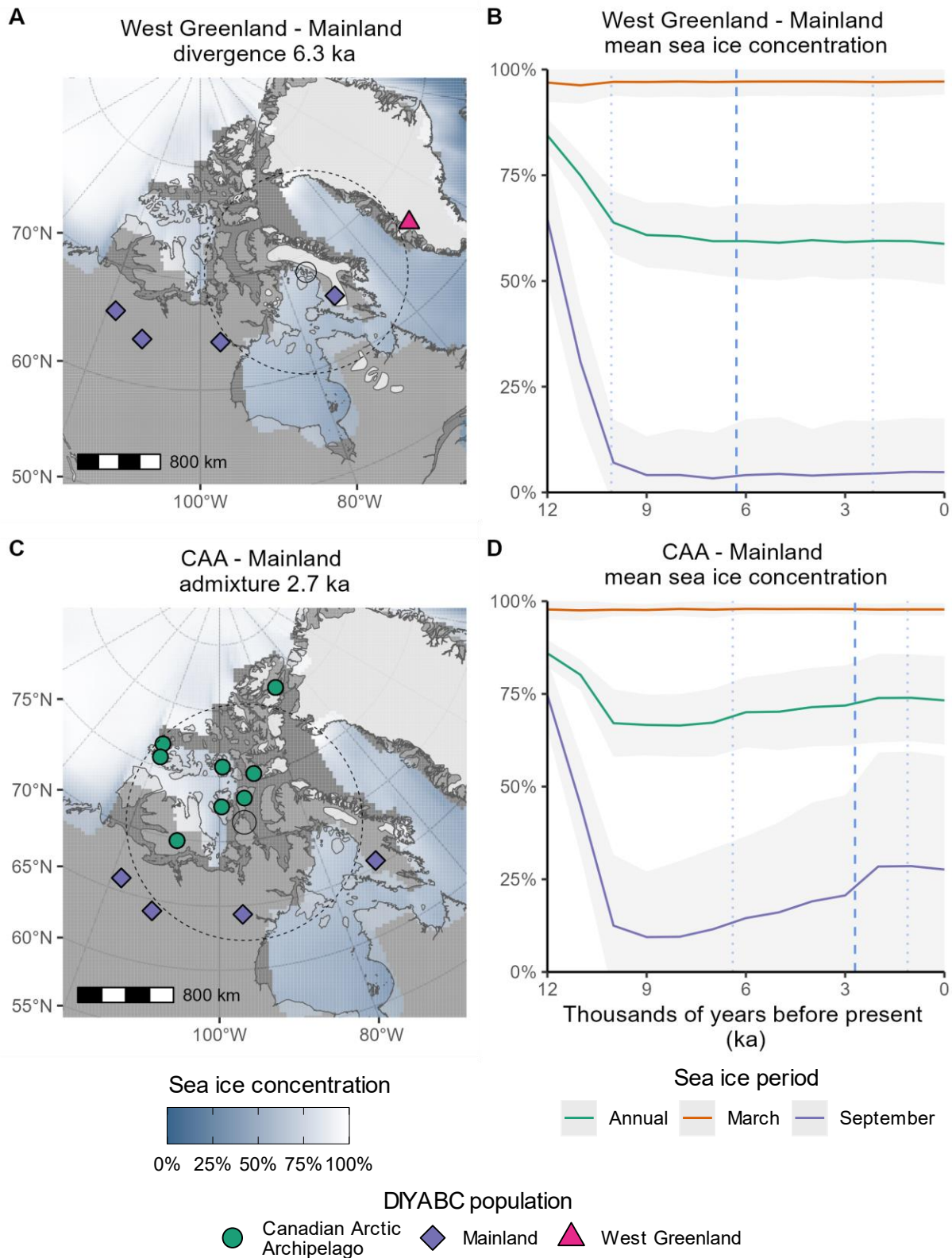


Figure 3.4. Reindeer population divergence and admixture events, and modelled sea ice changes in the North American Arctic Islands (NAAI). (A, C): Demographic events mapped with relevant present-day populations, modern land extent (light grey), a snapshot of modelled mean sea ice concentration (blue - white) and land extent (dark grey) at 6 ka (A) and 3 ka (C) (Singarayer et al., 2017; Valdes et al., 2017), and reconstructed ice sheets at 6 ka (A) and 3 ka (C) – the closest time steps to the corresponding population events (Dalton et al.,

2020). Divergence time estimates are the median parameter estimates from the most plausible evolutionary model (scenario two). The geographic centroid between two populations (solid circle), within which 100 random samples of modelled sea ice concentration at different radii (dotted circle) were extracted and averaged (one radius shown for clarity). **(A)** Divergence and **(C)** admixture time estimates mapped with relevant present-day populations. **(B, D)**: Modelled sea ice concentration with associated standard deviations in 1 ka time intervals. Timing of demographic events (dashed lines) with associated 95% credible intervals (dotted lines).

3.6.3.2 Barents Sea Islands

The Barents Sea was free from ground ice sheets by ~14 ka according to proxy-based ice sheet reconstructions (Hughes et al., 2016), and by 11-12 ka according to modelled sea ice data (**Figure 3.5**). No sea ice data were available for the period when Novaya Zemlya reindeer diverged from the West Russian reindeer 11.7 ka (CI 5.61-19.54 ka), as the sea ice model suggests complete ground ice sheet coverage in the area, although proxy-based ice sheet reconstructions suggest that ice sheets retreated from this potential crossing region by 16 ka (Hughes et al., 2016).

After an early Holocene decline in sea ice cover (largely driven by declines in summer sea ice, **Figure S3.9**), sea ice concentration remained relatively stable throughout the Holocene and was higher in the Barents Sea potential crossing regions (for the Svalbard-Novaya Zemlya population divergence) compared with the Kara Sea and Kara Strait (potential crossing region for the Novaya Zemlya - North Russia admixture) (**Figures 3.5, 3.6**). Similarly to the NAAI, March mean sea ice cover remained consistently above 90% in the Barents Sea during the Holocene, annual cover remained approximately 75%, while mean September sea ice cover remained below 50%. The northern Barents Sea (potential Franz Joseph Land - Svalbard crossing route) saw a more marked decline in mean September sea ice cover during the Holocene from 43.5% (SD 21.09) to 17.4% (SD 9.77), while the other crossing regions had fluctuating September sea ice with no consistent decline (**Figures 3.5, 3.6**).

Mean annual sea ice cover in the mid-Barents Sea (direct Novaya Zemlya - Svalbard crossing route) increased from 11 ka and peaked at 76.7% (SD 4.54) by 8 ka (**Figure 3.5B**). By 7 ka, mean annual sea ice concentration declined to 71.9% (SD 5.18). Sea ice cover in the eastern Barents Sea (Novaya Zemlya - Franz Josef Land crossing region) displayed similar dynamics (**Figure 3.5D**). In contrast, mean annual sea ice cover in the northern Barents Sea (Franz Josef Land - Svalbard crossing region) was relatively stable at ~76% from 8 to 6 ka (**Figure 3.5F**).

Proxy reconstructions support modelled spring sea ice cover persisting in the in the northern Barents Sea (Pieńkowski et al., 2021), with spring and summer sea ice present between Franz Josef Land and Nordaustlandet throughout the Holocene (Berben et al., 2017). However, the IP₂₅ proxy-based estimates of spring sea ice concentrations are consistently lower than our model-derived estimates, falling below 50% from ~12 to 8 ka during the main deglaciation of Svalbard, before increasing to ~60% by 6 ka (Berben et al., 2017; Pieńkowski et al., 2021), close to the modelled divergence time of Svalbard reindeer at 5.7 ka (CI 2.90-10.26 ka). Therefore, our modelled Svalbard - Novaya Zemlya population divergence was associated with annual modelled sea ice cover ~75% which approximates the threshold sufficient for supporting contemporary reindeer crossings in the CAA (Mallory & Boyce, 2018; Poole et al., 2010), and also a period of increased sea ice cover — although less than the 75% threshold — according to the proxy reconstructions.

Modelled annual sea ice cover was mostly stable — although < 75% — throughout the Holocene in the potential crossing region for the Novaya Zemlya - North Russia admixture event, which occurred at 3.3 ka (CI 2.06-6.90 ka) (**Figure 3.6**). Proxy reconstructions for the southern Kara Sea show more variable sea ice cover, with reduced sea ice cover from 5.6 ka until centennial-scale cycles of intense sea ice cover emerged at 3 ka (Hörner et al., 2017).

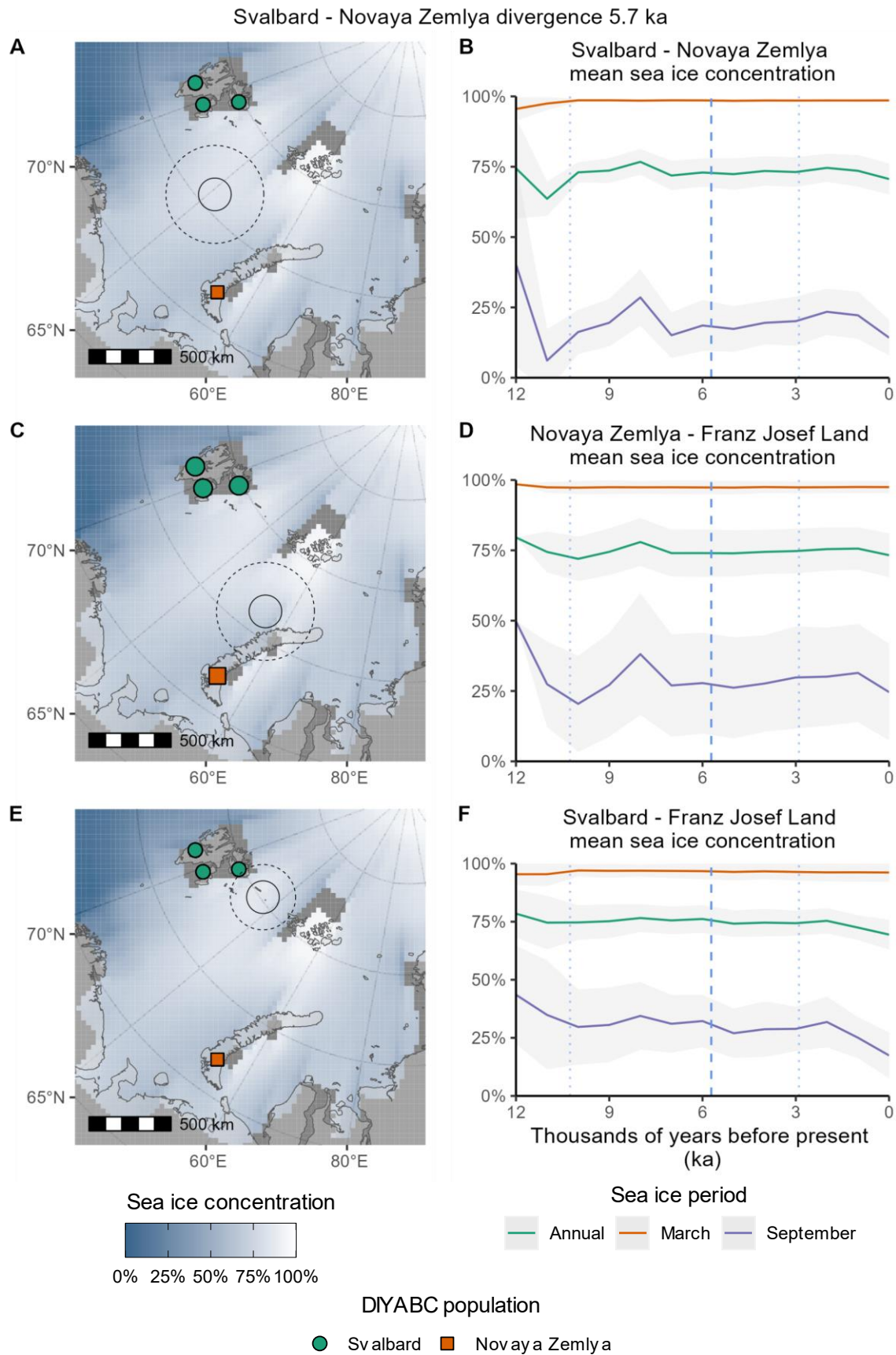


Figure 3.5. Svalbard and Novaya Zemlya reindeer population divergence and sea ice changes in the Barents Sea Islands system (BSI). (A, C, E): Demographic events mapped with relevant

present-day populations, modern land extent (light grey), a snapshot of modelled mean sea ice concentration (blue - white) and land extent (dark grey) at 6 ka (Singarayer et al., 2017; Valdes et al., 2017). Divergence time estimates are the median parameter estimates from the most plausible evolutionary model (scenario three). The geographic centroid between two populations (solid circle), within which 100 random samples of modelled sea ice concentration at different radii (dotted circle) were extracted and averaged (one radius shown for clarity). Three sea ice analyses were conducted to account for (A) a mid-Barents Sea crossing, and (C, E) a stepping-stone scenario with Franz Joseph Land as an intermediate step. (B, D, F): Modelled sea ice concentration with associated standard deviations in 1 ka intervals. Estimated population divergence time (dashed lines) with associated 95% credible intervals (dotted lines).

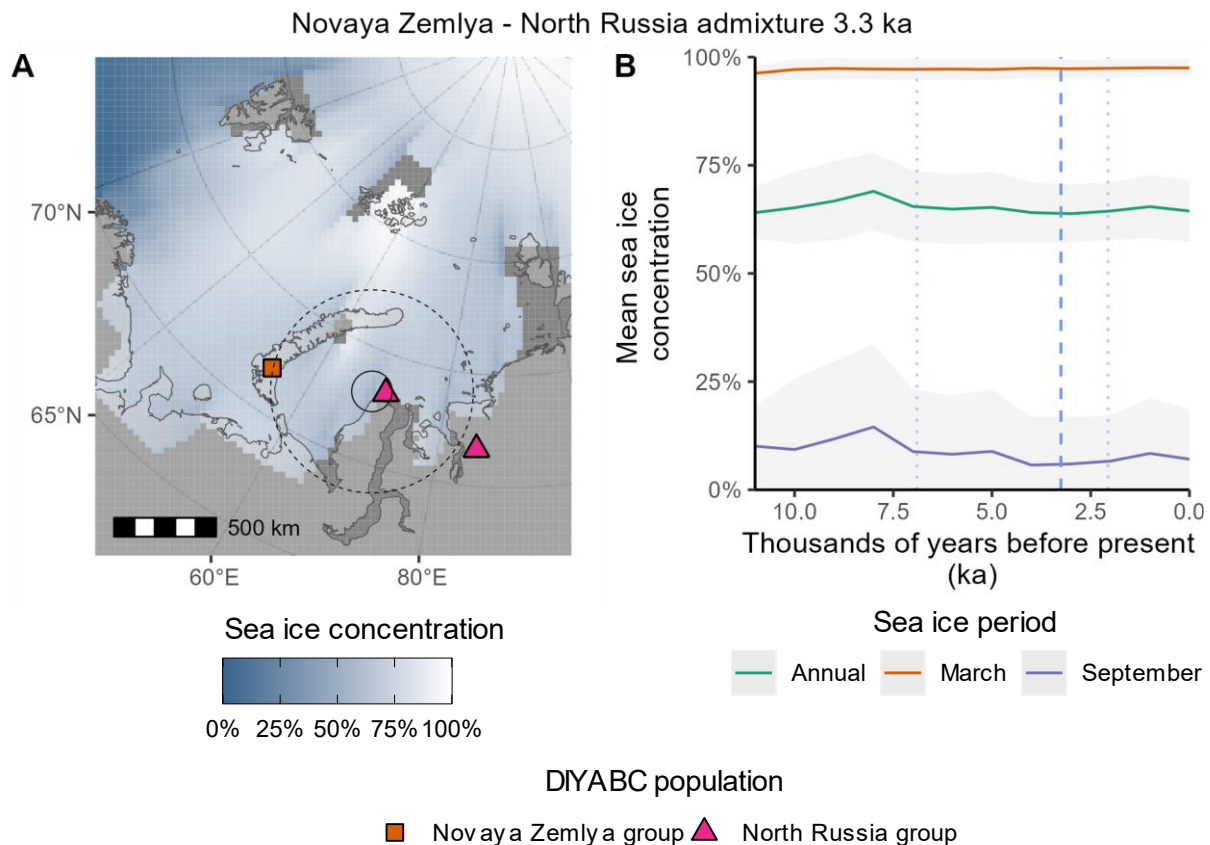


Figure 3.6. Novaya-Zemlya and mainland reindeer population admixture and modelled sea ice changes in the Barents Sea Islands system (BSI). (A): Demographic event mapped with relevant present-day populations, modern land extent (light grey), a snapshot of modelled mean sea ice concentration (blue - white) and land extent (dark grey) at 3 ka (Singarayer et al., 2017; Valdes et al., 2017). Divergence time estimates are the median parameter estimates from the most plausible evolutionary model (scenario three). The geographic centroid between two populations (solid circle), within which 100 random samples of modelled sea ice concentration at different radii (dotted circle) were extracted and averaged (one radius shown for clarity). (B): Regional modelled sea ice concentration with associated standard deviations in 1 ka intervals. Estimated admixture time (dashed line) with associated 95% credible intervals (dotted lines). Note that sea ice estimates include the most likely crossing point between Novaya Zemlya and the mainland, but also extend over a wider area of the Kara Sea.

3.7 Discussion

Our results show a complex Late Quaternary history for Arctic island reindeer, with Holocene dispersal to deglaciated islands followed by a degree of secondary contact with mainland populations. The divergence time of the NAAI island populations from the mainland coincided with ice sheet retreat from western islands, but the West Greenland divergence and the BSI Novaya Zemlya and Svalbard population divergences occurred thousands of years after deglaciated land was available, implicating other factors such as sea ice in determining the postglacial history of Arctic island reindeer.

3.7.1 Holocene divergence times: comparison with fossil record

BSI. Divergence times in our models align with fossil evidence of postglacial island colonisation by reindeer. Svalbard could have sustained a substantial reindeer population during the warmer climate conditions in the early to mid-Holocene (9-6 ka) (Forman et al., 2000), yet previous estimates of reindeer arrival on Svalbard were 6.7-5 ka based on subfossil faecal pellets in peat profiles (van der Knaap, 1989). Our modelled Svalbard – Novaya Zemlya divergence date of 5.7 ka (CI 2.90-10.26) is within this timeframe. Franz Josef Land has been proposed as a stepping stone for Svalbard reindeer due to Holocene fossils dated to 6.4 ka (Forman et al., 2000) and shared haplotypes with Svalbard in associated ancient DNA (Kvie et al., 2016). Apart from resulting from parameter uncertainty, the time lag between fossil presence and genetic divergence could result from these particular individuals not contributing to the gene pool of the contemporary Svalbard population which we sampled. Alternatively, they could result from delays in the change in connectivity being evident in the genetic structure after the colonisation event (Epps & Keyghobadi., 2015). Future ABC analyses that include ancient samples from Franz Josef Land would help refine colonisation times of Franz Joseph Land and Svalbard.

NAAI. For the NAAI, the earliest fossil occurrence of reindeer in West Greenland is at ~5.8 ka (Bennike, 1997), which is similar to our modelled divergence time of 6.3 ka (CI 2.16-10.07 ka). Our model supports a divergence between the geographically disjunct population of East Greenland and Banks/Melville Islands with the other CAA populations at 6.4 ka (CI 2.25-10.70 ka), which is substantially after the first Holocene appearance of fossils in North Greenland at ~7.98 ka (Bennike, 1997), although more similar to the first appearance of reindeer in East

Greenland ~6.2 ka (Bennike, 1997). This discrepancy may be because our analysis did not resolve East Greenland as a separate population from Banks/ Melville Islands, and so the divergence date may reflect a later split between Banks/Melville Islands and the CAA, rather than the initial colonisation of Greenland.

3.7.2 High Arctic refugium or postglacial dispersal

Our results do not support a High Arctic glacial refugium — i.e. the persistence of small populations in an isolated ice-free region — for island reindeer in either region. Instead, the ancestral populations of contemporary NAAI reindeer probably spent the last glacial period in a common Beringian location with mainland populations. Our BSI model suggested the possibility of at least two glacial populations in Eurasia, with reindeer in North and West Russia (from which the island reindeer are descended) apparently isolated from eastern Russian populations in a separate location.

BSI. The results from the BSI model agree with previous genetic work that suggested Svalbard was colonised from Russia via Novaya Zemlya during the postglacial period (Gravlund et al., 1998; Kvie et al., 2016). Recently, a new genetic study of Svalbard reindeer has suggested a colonisation date ca. 6-8 ka (Dusseux et al., 2023). The lower end of this colonisation estimate is similar to our median divergence date of 5.7 ka (CI 2.90-10.26), despite the use of nuclear genomes which have a different mutation rate, and the use of a different assumed generation time of six years.

However, we did not find evidence for a common Beringean glacial location in East Siberia, as was proposed previously (Flagstad & Røed, 2003; Kvie et al., 2016), but instead found that North and West Russian populations may have been isolated in a separate location. These populations were less genetically differentiated from each other than from the East Russian populations (Table S11), but we cannot rule out a scenario in which Russian populations formed a continuous glacial population, with reindeer from Fennoscandia coming into postglacial contact with West and North Russian populations and contributing to genetic distinctiveness from East Russia (Baranova et al., 2012; Røed, 2005). Therefore, the genetic relationships of the Russian reindeer should be examined further with whole genomic markers to resolve the question of multiple glacial locations.

NAAI. Our *NAAI* results contrast with coalescent-based modelling studies that proposed the existence of one or more High Arctic glacial refugia in the CAA (Eger et al., 2009; Klütsch et al., 2017). However, the presence of a High Arctic refugium during the Last Glacial Maximum (LGM, ~ 21 kyr BP) large enough to support reindeer populations has largely been discredited based on updated compilations of ice sheet chronologies, which show complete ice coverage of the hypothetical refugium on Banks Island (Dalton et al., 2022). Ice-free areas were present in the CAA during the last glacial period until 30-25 ka (Dalton et al., 2022), and thus small-bodied island reindeer in the CAA could have been separated from the mainland for much of the glacial period, moving south and mixing with mainland populations before the LGM, then moving northwards around 11 ka. However, this model was not supported in our analysis. Regardless, ice-free areas in the CAA may not have been capable of sustaining a reindeer population if conditions were too dry and cold for sufficient forage biomass, as has been suggested for Greenland (Gravlund et al., 1998).

3.7.3 Regional postglacial reindeer history and sea ice dynamics

Postglacial dispersal likely occurred in a stepwise fashion for both regions, as evidenced by the closer genetic relationships with decreasing geographic distance. The best-supported models in both regions included some form of secondary contact and genetic admixture between populations that were separated earlier in the postglacial period. These events occurred later in the Holocene, during a cooling period in the Arctic (Briner et al., 2016).

3.7.3.1 Sea ice concentration

NAAI. On the basis of sea ice-mediated genetic connectivity in the *NAAI* (Jenkins et al., 2016), we expected population divergences in the *NAAI* to be associated with reduced sea ice concentration, reflecting reduced inter-population connectivity, rather than island colonisation events. Accordingly, we found that postglacial divergences of island populations such as the CAA population and the East Greenland population were associated with periods of lower modelled sea ice cover, with annual or autumn averages typically below 75%. The East Greenland divergence was also associated with a decline in proxy-based sea ice cover (Briner et al., 2016; Jennings et al., 2011). Reindeer in the CAA currently require an estimated 75-90% sea ice cover to make seasonal migrations (Mallory & Boyce, 2018; Poole et al., 2010), which occur from April to June and from September to November (Jenkins et al., 2016).

Modelled sea ice reductions coinciding with divergences were strongest between June and October, with sea ice cover only remaining above 75% from October/November through to May. A reduction in the length of the migration season could have reduced spatiotemporal overlap between groups at autumnal rutting grounds (Dauphiné & McClure, 1974), leading to reproductive isolation and genetic divergence.

However, an increase in proxy-based sea ice cover coinciding with our modelled West Greenland divergence time suggests the relationship between population dynamics and sea ice cover may be different for this more isolated landmass in the NAAI, where long-distance dispersal may have played a role in colonisation of West Greenland.

The best supported NAAI scenario included dispersal and gene flow from the mainland to the CAA at 2.7 ka (CI 1.11-6.40 ka). This event could have taken the form of individuals from the Mainland population contributing to the gene pool of herds such as the Dolphin-Union herd on Victoria island, which is recognised as an intermediate subspecies *R. t. groenlandicus x pearyi* (COSEWIC, 2011). Furthermore, analysis of microsatellite data found evidence of historical gene flow between the Dolphin-Union and mainland herds (Mcfarlane et al., 2016). Alternatively, admixture may have occurred on Baffin Island as the placement of Baffin Island within the CAA or the Mainland genetic clusters varied depending on clustering method used. Victoria Island and Baffin Island are only separated from the mainland by narrow, ice-rich channels. Although proxy reconstructions suggest increased ice cover in eastern CAA commencing prior to the admixture event (Briner et al., 2016), we found no associated increase in modelled sea ice concentration which would be expected to promote extensive dispersal and admixture.

BSI. We expected a signal of high or increased sea ice cover linked to population divergence, representing long-distance dispersal and island colonisation. Sea ice reconstructions indicate low spring sea ice cover in the northern Barents sea between 12-8 ka (Berben et al., 2017; Pieńkowski et al., 2021). The large time interval between the Svalbard deglaciation (12-10 ka) and estimated Svalbard population divergence at 5.7 ka (CI 2.90-10.26 ka) indicates that the founders of the contemporary Svalbard population were not able to disperse to Svalbard earlier. This lag may be due to unfavourable sea ice conditions from 8-6 ka, since an increase in proxy-based spring sea ice concentration occurred around our modelled Svalbard divergence time (Berben et al., 2017; Pieńkowski et al., 2021). The lag could also be a result

of unsuccessful earlier colonisations, or result of the random and rare nature of long-distance dispersal (Gillespie et al., 2012; Jordano, 2017). Finally, favourable ocean currents and sea ice drift velocities may have also been required for successful long-distance dispersal to Svalbard (see section 3.7.3.2).

The best supported BSI model did not contain admixture events between distant island populations but did contain an admixture event between Novaya Zemlya and the North Russian population in the late Holocene. It is not surprising that the Novaya Zemlya population should be genetically close to mainland reindeer due to the relatively short (56 km) distance separating these two regions. Yet there was no associated increase in modelled sea ice cover in the Kara Sea or the Kara Strait that separates Novaya Zemlya from the mainland, and proxy-based records in the southern Kara Sea suggest lower sea ice cover compared with other periods in the Holocene (Hörner et al., 2017).

3.7.3.2 Sea ice drift

Sea ice drift speed and direction, determined by ocean currents and wind patterns, are likely as important as extensive sea ice cover in enabling long-distance dispersal (Johansen & Hytteborn, 2001; Kwok et al., 2013).

BSI. The Transpolar Drift (TPD) is a major surface ocean current running along the Siberian coast that transports drift ice westwards (Hole & Macias-Fauria, 2017). The TPD has been a long-term but variable feature of the Arctic Ocean since the opening of the Bering Strait ~11 ka (Bartlein et al., 2015; Hole et al., 2021). Ocean currents move sea ice up to several kilometres per day (Kaur et al., 2018) and so increase the effective distance that animals travelling in the same direction can cover with no additional energetic cost. Driftwood-based proxies suggest an enhanced TPD from approximately 7 ka and increasingly severe ice conditions from ~6 ka (Hole & Macias-Fauria, 2017), corresponding to the period close to our modelled Svalbard divergence. An enhanced TPD with greater ice drift velocities may have favoured reindeer dispersal westwards from Franz Joseph Land to Svalbard by reducing crossing time for the 300-400 km distance. Furthermore, the strong westerly drift may have prevented reindeer from returning to Franz Joseph Land, which, along with worsening climate conditions in the Neoglacial, may explain the absence of reindeer fossils after 1.3 ka (Forman et al., 2000).

NAAI. In the *NAAI*, the West Greenland population divergence similarly appears to represent a scenario of long-distance dispersal. It is unlikely that western Greenland was reached from the CAA via the Nares Strait and North Greenland, as ice sheets extended to the sea in this region throughout the Holocene (Dalton et al., 2020). The genetic data and best supported evolutionary scenario suggest a crossing from Baffin Island over the Davies Strait: 300 km across at its narrowest point. An increase in proxy-based sea ice cover occurred around the modelled reindeer divergence date, but no associated increases in modelled sea ice cover were evident. Favourable ocean currents and sea ice drift direction may have also been important. However, proxy records suggest a strengthened southerly West Greenland current from 7.3-6.2 ka (Ouellet-Bernier et al., 2014) which may have reduced the probability of ice transport across from the Baffin Island area.

3.7.3.3 Sea ice and long-distance dispersal of reindeer

The lack of a consistent sea ice signal preceding reindeer population admixture and island colonisation contrasts with previous evidence of increased sea ice along likely dispersal routes to Arctic islands coinciding with Holocene first occurrences of plant species (Alsos et al., 2016). Long distance dispersal of reindeer to islands across sea ice could be more rare and random and therefore difficult to associate with large-scale sea ice trends (Gillespie et al., 2012; Jordano, 2017). Reindeer regularly make short sea ice crossings in the Canadian Arctic, within Svalbard, and the New Siberian islands (Jenkins et al., 2016; Mizin et al., 2018; Peeters et al., 2019; Poole et al., 2010) but are less well-adapted for long-duration, long-distance crossings. However, dispersal over longer distances in the CAA (~300-400 km) are occasionally recorded (Miller et al., 2005).

There are also historical accounts of the sporadic movement of individual reindeer from Novaya Zemlya to Svalbard. A large male was shot in Sassendalen, Svalbard, in October 1911 and its antler was found to be tagged in a way that was associated with Nenets reindeer herders of Novaya Zemlya (Hoel, 1916; Lønø, 1959). Dispersal between Novaya Zemlya and Svalbard was constrained between antler regrowth (approximately May) and sea ice annual minimum extent (August/September) in what was reportedly a year with particularly extensive ice coverage in Svalbard (Lønø, 1959). A crossing of over 700km as the crow flies, or longer via Franz Joseph Land, was likely achieved within a few months. These anecdotes support the hypothesis that long-distance migrations over ice are possible, if rare.

3.8 Conclusions

This study sheds light on the glacial and postglacial history of the Arctic island reindeer and suggests sea ice played a role in shaping present population genetic patterns. Geographical and climatic differences between the North American Arctic islands and the Barents Sea islands contributed to different postglacial reindeer dynamics. Unlike the isolated archipelagos of the BSI, reduced genetic structure and modelled admixture events in the NAAI suggests that populations were connected to some degree throughout the Holocene via dispersal across narrow, but ice-rich ocean passages (Mallory & Boyce, 2018). Linked to this, we found evidence of low sea ice cover coinciding with genetic divergence between populations in the CAA, with late spring and autumn sea ice cover likely important in promoting connectivity. Despite a lack of a consistent sea ice signal preceding reindeer population admixture and island colonisation, proxy-based evidence suggests that increases in spring sea ice cover and favourable ocean currents enabled dispersal to Franz Joseph Land and Svalbard.

Postglacial and early Holocene divergences in the NAAI appear to follow retreating ice sheets. Yet both the West Greenland and Svalbard populations, which required the longest on-sea migration, diverged long after ice-free areas in their present-day ranges were available, suggesting dispersal limitation due to unfavourable sea ice conditions. However, time lags could also result from low probability of rare long-distance dispersal events, difficulties in detection given the coarse temporal resolution of the sea ice data, or uncertainty in the timing of demographic events resulting from the resolution of the genetic data.

The difference in historic population connectivity in each region has implications for the persistence of reindeer under future climate change. Seasonal land-fast ice cover is predicted to persist to some extent in the CAA (Newton et al., 2021), enabling some connectivity and potentially some movement of individuals from the southern CAA and mainland Canada (Mallory & Boyce, 2018). The Svalbard reindeer are much more geographically isolated than their counterparts in the CAA, both in terms of geographic distance from the mainland, and in terms of sea ice connectivity. The maximum spring sea ice extent in the Barents Sea is projected to move north of Svalbard under ongoing climate change (Dörr et al., 2021; Shu et al., 2021), so Svalbard will not be connected to any land masses in the future, however

ephemerally. Therefore, the dispersal of reindeer to newly available habitats may vary regionally and depend upon the increasingly reduced connectivity provided by sea ice, especially over larger distances.

3.9 Acknowledgements

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3.10 Data accessibility and benefit-sharing

Genetic data were derived from published datasets (DOIs in **Table S1**). Accession numbers are in the online supplementary material. Due to third party restrictions sea ice data are available upon request from the authors.

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3.12 Retracing the response of reindeer to postglacial climate change in Arctic islands: Supplementary information

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S3.1 Genetic datasets

Table S3.1. Details of published genetic data (mitochondrial control region) used in the analysis.

Publication	Publication title	Publication DOI	Number of populations	Number of individuals	Spatial coverage
Gravlund et al., 1998	Polyphyletic Origin of the Small-Bodied, High-Arctic Subspecies of Tundra Reindeer (<i>Rangifer tarandus</i>)	10.1006/mp ev.1998.0525	8	98	Circumpolar
Flagstad & Røed, 2003	Refugial Origins of Reindeer (<i>Rangifer tarandus</i> L.) Inferred from Mitochondrial Dna Sequences	10.1111/j.0014-3820.2003.tb01557.x	7	89	Circumpolar
Røed et al., 2008	Genetic analyses reveal independent domestication origins of Eurasian reindeer	10.1098/rspb.2008.0332	4	125	Palearctic
Eger et al., 2009	Genetic diversity and history of Peary caribou (<i>Rangifer tarandus</i>) in North	https://www.academia.edu/44005159/	9	90	American Arctic

	America	PROCEEDINGS_FROM_THE_CARIBOU_GENETICS_AND_RELATIONSHIPS_WORKSHOP			
Kuhn et al., 2010	Modern and ancient DNA reveal recent partial replacement of caribou in the southwest Yukon	10.1111/j.1365-294X.2010.04565.x	4	17	American Arctic
Petersen et al., 2010	Bottlenecks, isolation, and life at the northern range limit: Peary caribou on Ellesmere Island, Canada	10.1644/09-MAMM-A-231.1	1	121	CAA
Letts et al., 2012	Ancient DNA Reveals Genetic Continuity in Mountain Woodland Caribou of the Mackenzie and Selwyn Mountains, Northwest Territories, Canada	10.14430/arctic4186	5	38	American Arctic
Weckworth et al., 2012	Reconstruction of caribou evolutionary history in Western North America and its implications for conservation	10.1111/j.1365-294X.2012.05621.x	36	711	American Arctic
Kvie et al., 2016	Colonizing the High Arctic: Mitochondrial DNA Reveals Common Origin of Eurasian Archipelagic Reindeer (<i>Rangifer tarandus</i>)	10.1371/journal.pone.0165237	6	92	Barents region / Western Siberia
Røed et al., 2020	Temporal and structural genetic variation in reindeer (<i>Rangifer tarandus</i>)	10.1002/ecs3.6314	1	36	Western Siberia

	associated with the pastoral transition in northwest Siberia				

S3.2 Evolutionary scenario development and model testing

Table S3.2. DIYABC RF model specification common to all scenarios.

Priors	Characteristics	Source
Contemporary population size (Haploid effective population size (N_e))	Uniform distributions centred around census population sizes and estimates	(BQCMB, 2014; Cuyler, 2010, p. 20; Davison, 2016; Department of Environment, Government of Nunavut, 2013; Gunn, 2016; Kaluskar et al., 2020; Klütsch et al., 2017; Mizin et al., 2018; Pedersen et al., 2019; Poole et al., 2010; Wek'èezhii Renewable Resources Board, 2023)
Admixture rate r_a (how the lineages of admixed population are distributed among the parental population)	Uniform prior distribution bounded between 0.1 and 0.75 (NAAI) and 0.01 and 0.5 (BSI)	Evidence of admixture between Victoria island and mainland in NAAI (Mcfarlane et al., 2016) and guidelines in DIYABC RF manual (Collin et al., 2021)
Divergence/admixture time	Uniform distributions of plausible broad ranges: (i) Holocene - present day (x to x generations/years) (ii) Postglacial from LGM 24,000 years BP - present day (iii) Last glacial period from 100,000 years BP - present day	NA
Bottleneck duration	100-1000 years (14-140 generations) after the relevant divergence time	NA
Bottleneck size (Haploid population size (N_e) during bottleneck)	5-500	NA
DNA mutational model	HKY nucleotide substitution model with gamma-distributed rate heterogeneity (unless otherwise specified)	Previous studies of reindeer mitochondrial markers (Eger et al., 2009; Flagstad & Røed, 2003; Kuhn et al., 2010; Letts et al., 2012; Røed et al., 2020)

DNA mean mutation rate	1×10^{-6} - 1×10^{-8} per site per generation (unless otherwise specified)	(Eger et al., 2009; Flagstad & Røed, 2003; Kvie et al., 2016; Yannic et al., 2014)

Table S3.3. Evolutionary scenarios tested with DIYABC RF for the North American Arctic Islands (NAAI) region. Populations: CAA = Canadian Arctic Archipelago, EG = East Greenland, BAFF = Baffin Island, M = Mainland, DU = Dolphin-Union herd, WG = West Greenland, VIC = Victoria Island. Model sets tested against each other using Random Forest model classification with DIYABC RF when the simulated datasets from the training set and from the observed dataset overlapped on the first two axes of a principal component analysis (PCA), as recommended in the DIYABC RF manual (Prior scenario checks; Collin et al., 2021). Model choice refers to the overlap between observed and simulated data for each scenario on linear discriminant analysis (LDA) axes. Model posterior error corresponds to prediction quality exactly at the position of the observed dataset, with lower values indicating lower error rates and therefore higher prediction quality. Posterior probability reflects the most plausible, or “best model” within the tested model set.

Model set	Population groups	Scenario number	Key events	Source	Details	Prior scenario checks (PCA)	Model choice (LDA)	Model posterior error	Posterior probability
NAAI24 (10,000 datasets)	Pop 1: CAA Pop 2: EG Pop 3: M (including BAFF) Pop 4: WG	24.1	Holocene divergence	Gravlund et al., 1998; Flagstad et al., 2003		Scenario 1 and 2 closest to observed data. Scenarios 3 and 4 not distinct.	Observed data sits in between simulated data from scenario 1 and scenario 2	0.200	0.712
		24.2	Holocene divergence with CAA-M admixture	Mcfarlane et al., 2016	Gene flow from CAA into mainland			0.0942	
		24.3	High Arctic refugium for CAA: interglacial/glacial divergence	Eger et al., 2009; Klüstch et al., 2017				0.270	
		24.2	High Arctic refugium for CAA: interglacial/glacial divergence and LGM admixture	Eger et al., 2009; Klüstch et al., 2017	Gene flow from CAA into Mainland into CAA during LGM			0.252	
NAAI26 (10,000 datasets)	Pop 1: CAA Pop 2: EG Pop 3: Mainland Pop 4: WG Pop 5: BAFF	26.1	Holocene divergence	Gravlund et al., 1998; Flagstad et al., 2003	BAFF most closely related to M	Scenarios 1 and 2 on either end of spread of scenario 3 simulated datasets. Observed data not closely overlapping simulated data.	Observed data not closely overlapping simulated data, closest to scenario 1 and 3.	0.196	0.593
		26.2	Holocene divergence	Gravlund et al., 1998; Flagstad et al., 2003	BAFF most closely related to CAA			0.201	

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		10b.3	Holocene divergence with CAA-M admixture	Gravlund et al., 1998; Flagstad et al., 2003	BAFF formed from admixture between CAA and M			0.289	
NAAI27a (10,000 datasets)	Pop 1: CAA Pop 2: EG Pop3: M Pop4: WG Pop 5: VIC	27.1	Holocene divergence	Gravlund et al., 1998; Flagstad et al., 2003	VIC most closely related to M	Scenarios 3 and 4 not distinct, scenario 2 and scenario 1 at opposite ends of spread of scenarios 3 and 4. Observed data not closely overlapping simulated data.	Observed data closest to simulated data in scenarios 3 and 4.	0.320	
		27.2	Holocene divergence	Gravlund et al., 1998; Flagstad et al., 2003	VIC most closely related to CAA			0.314	
		27.3	Holocene divergence	Gravlund et al., 1998; Flagstad et al., 2003; McFarlane et al., 2016	VIC formed from admixture between CAA and M			0.560	
		27.4	Holocene divergence	McFarlane et al., 2016	VIC separate population most closely related to CAA, introgression into VI from M			0.589	0.444
NAAI27b (10,000 datasets)	Pop 1: CAA Pop 2: EG Pop3: M Pop4: WG Pop 5: VIC	27b.1	Holocene divergence		Models the same as 27a without scenario 4	Scenarios 1 and 2 distinct. Observed data closest to scenario 3.	Observed data overlapping simulated data in scenario 3.	0.198	
		27b.2	Holocene divergence					0.217	
		27b.3	Holocene divergence					0.295	0.493
NAAI27c (10,000 datasets)	Pop 1: CAA Pop 2: EG Pop3: M Pop4: WG Pop 5: VIC	27c.1	Holocene divergence		Models the same as 27b except with broader admixture and VIC Ne priors	Scenarios 1 and 2 distinct. Observed data closest to scenario 3.	Observed data overlapping simulated data in scenario 3.	0.159	
		27c.2	Holocene divergence					0.172	
		27c.3	Holocene divergence					0.262	0.586

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NAA27d (10,000 datasets)	Pop 1: CAA Pop 2: EG Pop3: M Pop4: WG Pop 5: VIC	27d.1			Models the same as 27c except with broader admixture and VIC Ne priors, and additional founding population Ne parameter in 27d.3.	Scenarios 1 and 2 distinct. Observed data closest to scenario 3.	Observed data overlapping simulated data in scenario 3.	0.152	
		27d.2						0.162	
		27d.3						0.232	0.623
NAAI27e (100,000 datasets)	Pop 1: CAA Pop 2: EG Pop3: M Pop4: WG Pop 5: VIC	27e.1			Models the same as 27c except with separate ancestral Ne parameter.	Scenarios 1 and 2 distinct. Observed data closest to scenario 3.	Observed data overlapping simulated data in scenario 3.	0.152	
		27e.2						0.161	
		27e.3	.					0.231	0.603
NAAI25b (100,000 datasets)	Pop 1: CAA Pop 2: EG Pop 3: M (including BAFF) Pop 4: WG	25b.1	Holocene divergence	Gravlund et al., 1998; Flagstad et al., 2003	Same as NAAI25a except for scenario 2 where gene flow direction changed.	Observed data overlapping simulated data in scenarios 1 and 2. Scenarios 3 and 4 far from data and not distinct from each other.	Observed data overlapping simulated data in scenarios 1 and 2.	0.346	
		25b.2	Holocene divergence with CAA-M admixture	Mcfarlane et al., 2016	Gene flow from M into CAA			0.202	0.614
		25b.3	High Arctic refugium for CAA: interglacial/glacial divergence	Eger et al., 2009; Klüstch et al., 2017				0.301	
		25b.4	High Arctic refugium for CAA: interglacial/glacial divergence and LGM admixture	Eger et al., 2009; Klüstch et al., 2017	Gene flow from CAA into Mainland into CAA during LGM			0.285	
NAAI25c	Pop 1: CAA Pop 2: EG Pop3: EM/BAFF Pop4: WG Pop 5: WM	25c.1			Same as NAAI25b except admixture parameter restricted between 0.1 and 0.75 as uninformative prior.	Observed data overlapping simulated data in scenarios 1 and 2. Scenarios 3 and 4 far from data and not distinct from	Observed data overlapping simulated data in scenarios 1 and 2.	0.325	
		25c.2						0.176	0.651
		25c.3						0.287	

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		25c.4				each other.		0.268	
NAAI25d	Pop 1: CAA Pop 2: EG Pop3: EM/BAFF Pop4: WG Pop 5: WM	25d.1			Same as NAAI25b except with additional ancestral Ne parameter	Observed data overlapping simulated data in scenarios 1 and 2.	Observed data overlapping simulated data in scenarios 1 and 2.	0.365	
		25.2				Scenarios 3 and 4 far from data and not distinct from each other.		0.216	0.706
		25.3						0.336	
		25.4						0.342	

Table S3.4. Scenarios tested for the Barents Sea Islands (BSI) region. Populations: SVAL = Svalbard, NR = northern Russia, WR = western Russia, NZ = Novaya Zemlya, ER = Eastern Russia. Model sets tested against each other using Random Forest model classification with DIYABC RF when the simulated datasets from the training set and from the observed dataset overlapped on the first two axes of a principal component analysis (PCA), as recommended in the DIYABC manual (Prior scenario checks). Model choice refers to the overlap between observed and simulated data for each scenario on linear discriminant analysis (LDA) axes. Model posterior error corresponds to prediction quality exactly at the position of the observed dataset, with lower values indicating lower error rates and therefore higher prediction quality. Posterior probability reflects the most plausible, or “best model” within the tested model set.

Model set	Pop groups	Model	Key events	Source	Notes	Prior checks (PCA)	Model choice (LDA)	Class error	Posterior probability of preferred scenario
BSI1	Pop 1: SVAL Pop 2: NR/WR/NZ Pop3: ER	1.1	All divergence times from present to interglacial (100 kyr BP)		BSI1-3 focus on placement of NZ in topology and potentially multiple refugia	Simulated data overlap observed data	NA (no models to compare)	NA	NA
BSI2	Pop 1: SVAL Pop 2: NR/WR Pop3: NZ Pop 4: ER	2.1	All divergence times from present to interglacial		Potentially multiple refugia	Simulated data overlap observed data	NA (no models to compare)	NA	NA
BSI3	Pop 1: SVAL/NZ Pop 2: NR/WR Pop3: ER	3.1	All divergence times from present to interglacial		Potentially multiple refugia	Simulated data overlap observed data	NA (no models to compare)	NA	NA

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BSI1a	Pop 1: SVAL/NZ Pop 2: WR Pop3: NR/ER	1a.1	All divergences constrained to last glacial maximum (LGM).	Flagstad & Røed, 2003; Kvie et al., 2016	NZ grouped with SVAL. BSI1a-3a focussed on placement of NZ and effect of excluding ER. Shared Beringian refugia	Simulated data close to but not overlapping observed data	NA (no models to compare)	NA	NA
BSI1b	Pop 1: SVAL/NZ Pop 2: WR Pop3: NR	1b.1	All divergences constrained to last glacial maximum (LGM).	Flagstad & Røed, 2003; Kvie et al., 2016	NZ grouped with SVAL. ER excluded. Shared Beringian refugia	Simulated data overlap observed data	NA (no models to compare)	NA	NA
BSI2a	Pop 1: SVAL Pop 2: WR/NZ Pop3: NR/ER	2a.1	All divergences constrained to last glacial maximum (LGM)	Flagstad & Røed, 2003	NZ grouped with WR. Shared Beringian refugia	Simulated data overlap observed data	NA (no models to compare)	NA	NA
BSI2b	Pop 1: SVAL Pop 2: WR/NZ Pop3: NR	2b.1	All divergences constrained to last glacial maximum (LGM)	Flagstad & Røed, 2003	ER excluded. Shared Beringian refugia	Simulated data overlap observed data	NA (no models to compare)	NA	NA
BSI3a	Pop 1: SVAL Pop 2: NZ Pop3: WR Pop 4: NR/ER	3a.1	SVAL-NZ divergence in Holocene. NZ-mainland divergence up to LGM.	Kvie et al., 2016	BSI3a & 3b have narrower divergence time priors. Potentially two refugia	Simulated data overlap observed data. Scenarios not distinct.	Simulated data overlaps observed data Scenario 1 has two peaks.	0.28	NA
		3a.2	SVAL-NZ divergence in mid Holocene. NZ-mainland divergence in Holocene		Narrower divergence time priors. Potentially two refugia			0.34	0.639
BSI3b	Pop 1: SVAL Pop 2: NZ Pop3: WR Pop 4: NR	3b.1	SVAL-NZ divergence in Holocene. NZ-mainland divergence up to LGM.	Kvie et al., 2016	ER excluded. NR and WR have negative Fst. Potentially two refugia	Simulated data overlap observed data. Scenarios not distinct.	NA (due to negative FST)	NA	NA
		3b.2	SVAL-NZ divergence in mid Holocene. NZ-mainland divergence in Holocene		Narrower divergence time priors. Potentially two refugia			NA	NA
BSI4	Pop 1: SVAL Pop 2: NZ Pop3: WR Pop4: NR Pop 5: ER	4.1	SVAL-NZ divergence in mid Holocene. NZ-mainland divergence constrained up to LGM	Kvie et al., 2016	NR and WR have negative Fst. Potentially two refugia	Simulated data overlap observed data. Scenarios not distinct.	Simulated data overlaps observed data but closer to scenario 2 peak	0.33	NA
		4.2	SVAL-NZ divergence in mid Holocene. NZ-mainland		Broader priors. Island populations			0.33	0.619

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			divergence constrained up to interglacial (100 kyr BP)		potentially in separate refugium.				
BSI4a	Pop 1: SVAL Pop 2: NZ Pop3: WR Pop4: NR Pop 5: ER	4a.1	SVAL-NZ divergence in mid Holocene. NZ-mainland divergence constrained up to LGM	Kvie et al., 2016	Same as BSI4.1 but with faster mutation rate (1x10 ⁻⁸ -1x10 ⁻⁵). 2022_11_16	Simulated data overlap observed data. Scenarios not distinct.	Simulated data overlaps observed data.	0.32	0.592
		4a.2	SVAL-NZ divergence in mid Holocene. NZ-mainland divergence constrained up to interglacial (100 kyr BP)		Same as BSI4.2 but with faster mutation rate (1x10 ⁻⁸ -1x10 ⁻⁵). 2022_11_16			0.28	NA
BSI4b	Pop 1: SVAL Pop 2: NZ Pop3: WR Pop4: NR Pop 5: ER	4b.1	All divergence times from present to interglacial (100 kyr BP)		Same as BSI4.1 but with broader time priors. Potentially multiple refugia.	Simulated data overlap observed data. Scenarios not distinct.	Missing files - will rerun		
		4b.2	All divergence times from present to interglacial (100 kyr BP)		Same as BSI4.2 but with broader time priors. Potentially multiple refugia.				
BSI4c	Pop 1: SVAL Pop 2: NZ Pop3: WR Pop4: NR Pop 5: ER	4c.1	SVAL-NZ divergence in mid Holocene. NZ-mainland divergence constrained up to LGM	Kvie et al., 2016	Same as BSI4 but exclude River Mezen population. No negative Fst values anymore. Potentially two refugia.	Simulated data overlap observed data. Scenarios not distinct.	Simulated data overlaps observed data but bimodal distributions	0.37	0.599
		4c.2	SVAL-NZ divergence in mid Holocene. NZ-mainland divergence constrained up to interglacial.	PCoA; Fst	Island populations potentially in separate refugium.			0.3	NA
BSI4d	Pop 1: SVAL Pop 2: NZ Pop3: WR Pop4: NR Pop 5: ER	4d.1	SVAL-NZ divergence in mid Holocene. NZ-mainland divergence constrained up to LGM	UPGMA; Kvie et al., 2016	Same as scenario BSI4c.1. River Mezen population excluded. Potentially two refugia.		Only simulated data from scenario 1 overlaps observed data	0.074	0.78

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		4d.2	SVAL-NZ divergence in mid Holocene. NZ-mainland divergence constrained up to LGM. SVAL more recently diverged from NR than WR.	PCoA; Fst	River Mezen population excluded. Potentially two refugia.			0.091	NA
BSI2	Pop 1: SVAL Pop 2: WR Pop3: NZ Pop 4: NR/ER	2.1	SVAL divergence constrained up to LGM. NZ-mainland divergence constrained up to interglacial.	UPGMA; Kvie et al., 2016	Potentially multiple refugia.		Simulated data overlaps observed data but closer to scenario 2 peak	0.15	NA
		2.2	Island populations diverge in Holocene. Mainland populations diverge post-LGM.	UPGMA; Kvie et al., 2016; Flagstad & Røed, 2003	One Beringean refugium.			0.18	0.695
BSI5	Pop 1: SVAL Pop 2: NZ Pop3: WR Pop4: NR Pop 5: ER	5.1	SVAL-NZ divergence in mid Holocene. NZ-mainland divergence constrained up to LGM	UPGMA; Kvie et al., 2016	Same as 4d.1. River Mezen population excluded. Potentially two refugia.		Simulated data from scenarios 3 and 4 overlap observed data completely. Scenarios 3 and 4 not distinguishable	0.25	NA
		5.2	SVAL-NZ divergence in mid Holocene. NZ-mainland divergence constrained up to LGM. SVAL more recently diverged from NR than WR.	PCoA; Fst	Same as 4d.2. River Mezen population excluded. Potentially two refugia.			0.27	NA
		5.3	NR more recently diverged from WR than ER. SVAL-NZ divergence in mid Holocene. NZ-mainland divergence constrained up to LGM	Fst	River Mezen population excluded. Potentially two refugia.			0.51	NA
		5.4	NR more recently diverged from WR than ER; introgression from NR to NZ after SVAL divergence	Fst; PCoA	River Mezen population excluded. Potentially two refugia.			0.51	0.723
BSI6	Pop 1: SVAL Pop 2: NZ Pop3: WR Pop4: NR	6.1	SVAL-NZ divergence in mid Holocene. NZ-mainland divergence constrained up to LGM		Same as 5.1	Scenarios distinct and observed data closest to	Simulated data from scenario 3 overlap observed data.	0.15	NA

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	Pop 5: ER	6.2	SVAL more recently diverged from NR than WR.		Same as 5.2	scenario 3.		0.17	NA
		6.3	NR more recently diverged from WR than ER; introgression from NR to NZ after SVAL divergence		Same as 5.4			0.15	0.980

Table S3.5. DIYABC RF model specifications of final North American Arctic Islands (NAII) model set.

Priors	Scenario 1	Scenario 2	Scenario 3	Scenario 4
Population size priors	CAA N1 N UN[5000,15000,0.0,0.0] EG N2 N UN[1500,12500,0.0,0.0] M N3 N UN[400000,540000,0.0,0.0] WG N4 N UN[3500,4500,0.0,0.0] Ancestral NA N UN[5000,500000,0,0]			
Bottleneck size	N2b N UN[5,500,0.0,0.0] N4b N UN[5,500,0.0,0.0]			
Bottleneck duration	db T UN[14,142,0.0,0.0] db2 T UN[14,142,0.0,0.0]			
Admixture rate	r2 A UN[0.1,0.75,0,0] r3 A UN[0.1,0.75,0,0]			
Conditions	T3>T2, T3>T1, T2>TINT, T1>TINT, T6>T5, T6>T4, TINT2>T8, TINT2>T7, T9>TINT2			
Locus description	<M> [S] G1 134			
Mutation priors	group G1 [S] MEANMU UN[1.00E-8,1.00E-6,5E-9,2] GAMMU GA[1.00E-8,1.00E-6,Mean_u,2] MEANK1 UN[0.050,20,10,2] GAMK1 GA[0.050,20,Mean_k1,2] MEANK2 UN[0.050,20,10,2] GAMK2 GA[0.050,20,Mean_k2,2] MODEL HKY 10 2.00			
Topology	N1 N2 N3 N4 0 sample 1 0 sample 2 0 sample 3 0 sample 4 T1-db VarNe 2 N2b T1 merge 1 2 T2-db2 VarNe 4 N4b T2 merge 3 4 T3 merge 3 1 T3 varNe 3 Na	N1 N2 N3 N4 N1 N6 0 sample 1 0 sample 2 0 sample 3 0 sample 4 TINT split 1 5 6 r2 TINT merge 3 6 T1-db VarNe 2 N2b T1 merge 5 2 T2-db2 VarNe 4 N4b T2 merge 3 4 T3 merge 3 5 T3 varNe 3 Na	N1 N2 N3 N4 0 sample 1 0 sample 2 0 sample 3 0 sample 4 T4-db VarNe 2 N2b T4 merge 1 2 T5-db2 VarNe 4 N4b T5 merge 3 4 T6 merge 3 1 T6 varNe 3 NA	N1 N2 N3 N4 N3 N6 0 sample 1 0 sample 2 0 sample 3 0 sample 4 T7-db VarNe 2 N2b T7 merge 1 2 T8-db2 VarNe 4 N4b T8 merge 3 4 TINT2 split 3 5 6 r3 TINT2 merge 1 6 T9 merge 5 1 T9 varNe 5 NA
Historical	T1 T	T1 T	T4 T	T7 T

parameter priors	UN[142,1599,0.0,0.0] T2 T UN[142,1500,0.0,0.0] T3 T UN[142,2000,0.0,0.0]	UN[142,1599,0.0,0.0] T2 T UN[142,1500,0.0,0.0] T3 T UN[142,2000,0.0,0.0] TINT T UN[142,1500,0.0,0.0]	UN[142,1500,0.0,0.0] T5 T UN[142,1500,0.0,0.0] T7 T UN[142,2000,0.0,0.0] T6 T UN[142,3429,0.0,0.0] TINT T UN[142,1500,0.0,0.0]	UN[142,1500,0.0,0.0] T8 T UN[142,1500,0.0,0.0] TINT2 T UN[3000,14300,0.0,0.0] T9 T UN[4300,14300,0.0,0.0]

Table S3.6. DIYABC RF model specification for the final Barents Sea Islands (BSI) model set.

Priors	Scenario 1	Scenario 2	Scenario 3
Population size priors	N1 N UN[6000,16000,0,0] N2 N UN[1250,3750,0,0] N3 N UN[2500,25000,0,0] N4 N UN[50000,500000,0,0] N5 N UN[50000,500000,0,0]		
Bottleneck size	N2b N UN[5,500,0,0] N7b N UN[5,500,0,0]		
Bottleneck duration	db T UN[14,142,0,0]		
Admixture rate	r2 A UN[0.01,0.5,0,0]		
Conditions	t2>t1, t3>t2, t4>t3, t6>t5, t7>t6, t8>t7, t9>TINT, t10>t9, t11>t10, t12>t11		
Locus description	<M> [S] G1 134		
Mutation priors	group G1 [S] MEANMU UN[1e-08,1e-06,0,0] GAMMU GA[1e-08,1e-06,Mean_u,2] MEANK1 UN[0.05,20,0,0] GAMK1 GA[0.05,20,Mean_k1,2] MEANK2 UN[0.05,20,10,2] GAMK2 GA[0.05,20,Mean_k2,2] MODEL HKY 10 2		
Topology	N1 N2 N3 N4 N5 0 sample 1 0 sample 2	N1 N2 N3 N4 N5 0 sample 1 0 sample 2	N1 N2 N3 N4 N5 N2 N2 0 sample 1 0 sample 2

	0 sample 3 0 sample 4 0 sample 5 t1 merge 2 1 t2-db VarNe 2 N2b t2 merge 3 2 t3 merge 5 4 t4 merge 5 3	0 sample 3 0 sample 4 0 sample 5 t5 merge 2 1 t6-db VarNe 2 N2b t6 merge 4 2 t7 merge 5 4 t8 merge 5 3	0 sample 3 0 sample 4 0 sample 5 TINT split 2 6 7 r2 TINT merge 4 6 t9 merge 7 1 t10-db VarNe 7 N7b t10 merge 3 7 t11 merge 4 3 t12 merge 5 4
Historical parameter priors	t1 T UN[280,1570,0,0] t2 T UN[280,3400,0,0] t3 T UN[285,14300,0,0] t4 T UN[285,14400,0,0]	t5 T UN[280,1570,0,0] t6 T UN[280,3400,0,0] t7 T UN[285,14300,0,0] t8 T UN[285,14400,0,0]	t9 T UN[280,1570,0,0] t10 T UN[280,3400,0,0] t11 T UN[280,3400,0,0] t12 T UN[280,14300,0,0] TINT T UN[280,1570,0,0]

S3.3 Output from DIYABC RF model choice for final model sets

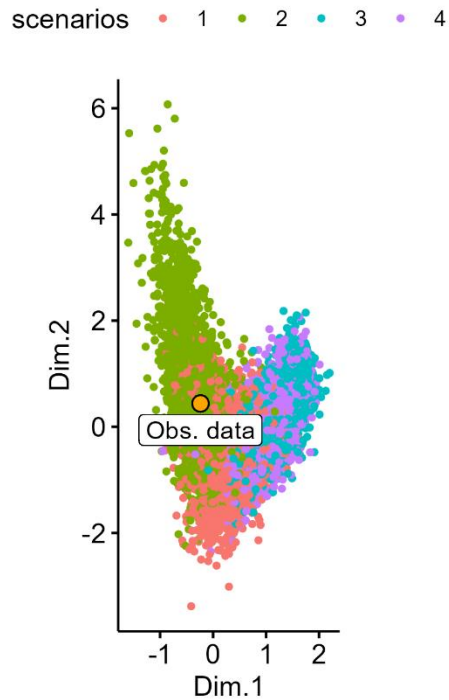


Figure S3.1. Projection of North American Arctic Islands (NAII) simulated datasets from the final model set on the first two axes of a Linear Discriminant Analysis. The location of the observed genetic data set is indicated by the yellow circle.

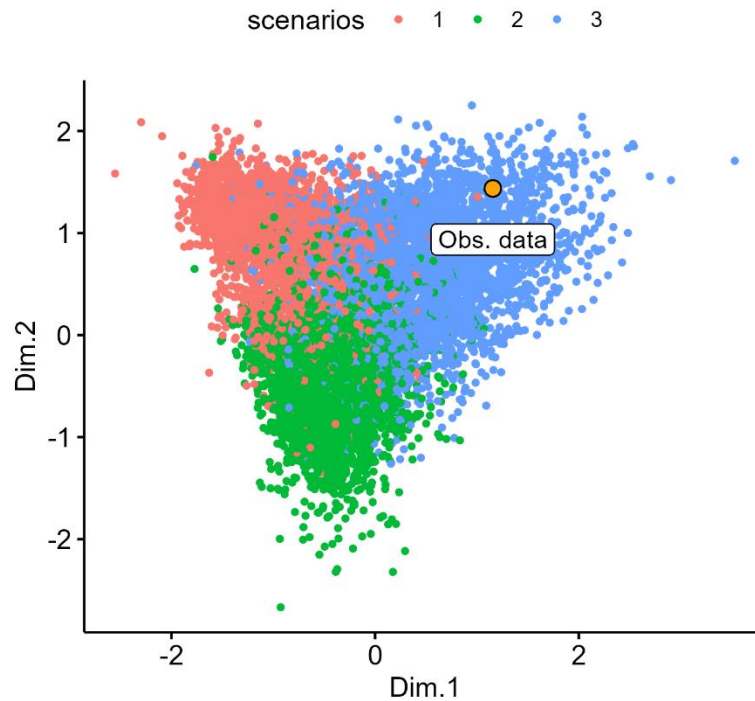


Figure S3.2. Projection of Barents Sea Islands (BSI) simulated datasets from the final model set on the first two axes of a Linear Discriminant Analysis. The location of the observed genetic data set is indicated by the yellow circle.

Table S3.7. Model error rates for the final DIYABC RF model sets. Global (prior) and scenario-specific error rates and RF classification votes for model choice for the final scenario set for the North American Arctic Islands model (NAAI) and the Barents Sea Islands model (BSI).

	NAAI model				BSI model		
	Scenario 1	Scenario 2	Scenario 3	Scenario 4	Scenario 1	Scenario 2	Scenario 3
Prior error rate	0.317	0.317	0.317	0.317	0.157	0.157	0.157
Votes	162	330	4	4	3	6	491
Class error rate	0.365	0.216	0.336	0.342	0.152	0.171	0.148

S3.4 Parameter estimates from final DIYABC RF models

Table S3.8. Parameter estimates for North American Arctic Islands (NAAI) model scenario 2. Estimates for the timing of population events in calendar years before present, assuming a reindeer generation time of seven years.

Time parameter	Event type	Populations	Median estimate (years)	95% CI (years)
TINT	introgression	M into CAA	2703	1113-6398
T1	divergence	CAA EG	6377	2254-10696
T2	divergence	M WG	6286	2163-10066
T3	divergence	CAA M	10591	5145-13643
db	Bottleneck duration	EG	322	119-847
db2	Bottleneck duration	WG	294	112-819
T2-db	End of bottleneck	WG	5992	1344-9954
T1-db	End of bottleneck	EG	6055	2153-10577

Table S3.9. Parameter estimates for Barents Sea Islands model scenario 3. Estimates for the timing of population events in calendar years before present, assuming a reindeer generation time of seven years.

Time parameter	Event type	Populations	Median estimate (years)	95% CI (years)
TINT	Introgression	NR into NZ	3255	2058-6902
T9	Divergence	SVAL NZ	5719	2898-10262
T10	Divergence	NZ WR	11662	5607-19537
T11	Divergence	WR NR	17864	10213-23268
T12	Divergence	NR ER	64246	26467-95354
db	Bottleneck duration	NZ	623	168-999
T10-db	End of bottleneck	NZ	11039	4641-19369

S3.5 Population genetic clustering results

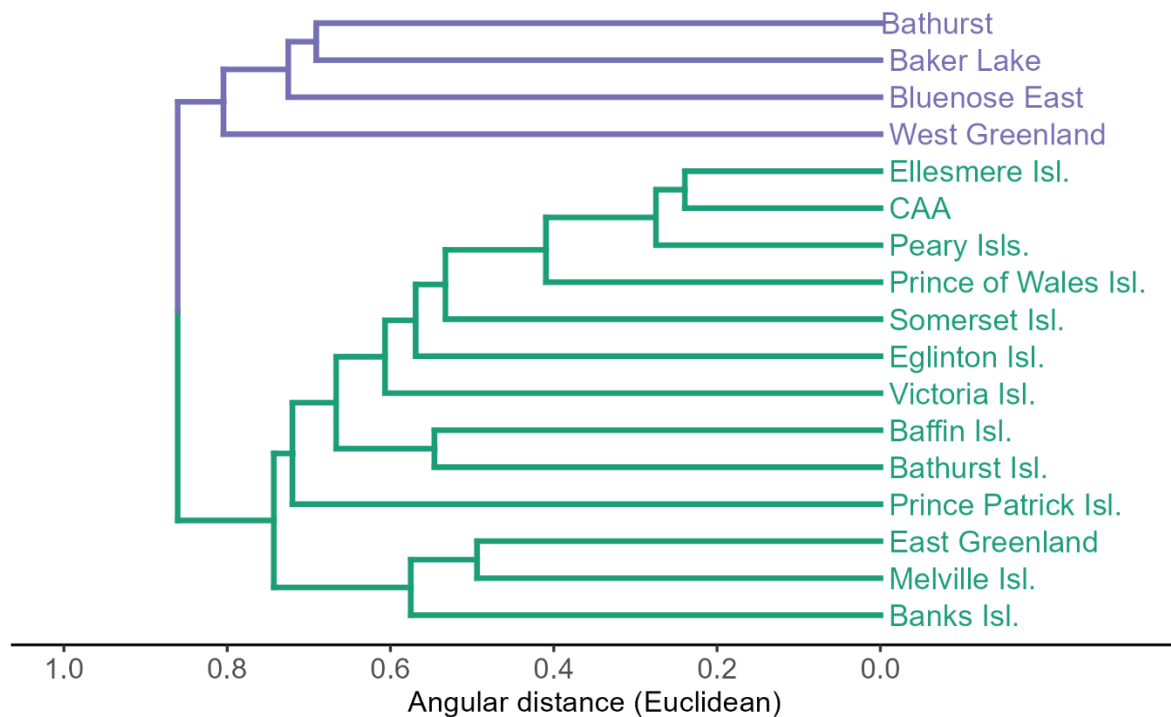


Figure S3.3. Hierarchical population genetic clustering of the North American Arctic Islands (NAII) and neighbouring mainland populations. Dendrogram of NAAI original sampling populations based on a UPGMA hierarchical clustering method where populations that are genetically closer to each other cluster together. Colours represent the optimal K-means clusters (K=2) identified using the average silhouette method on the Euclidean distance matrix of mitochondrial sequence data (n = 311).

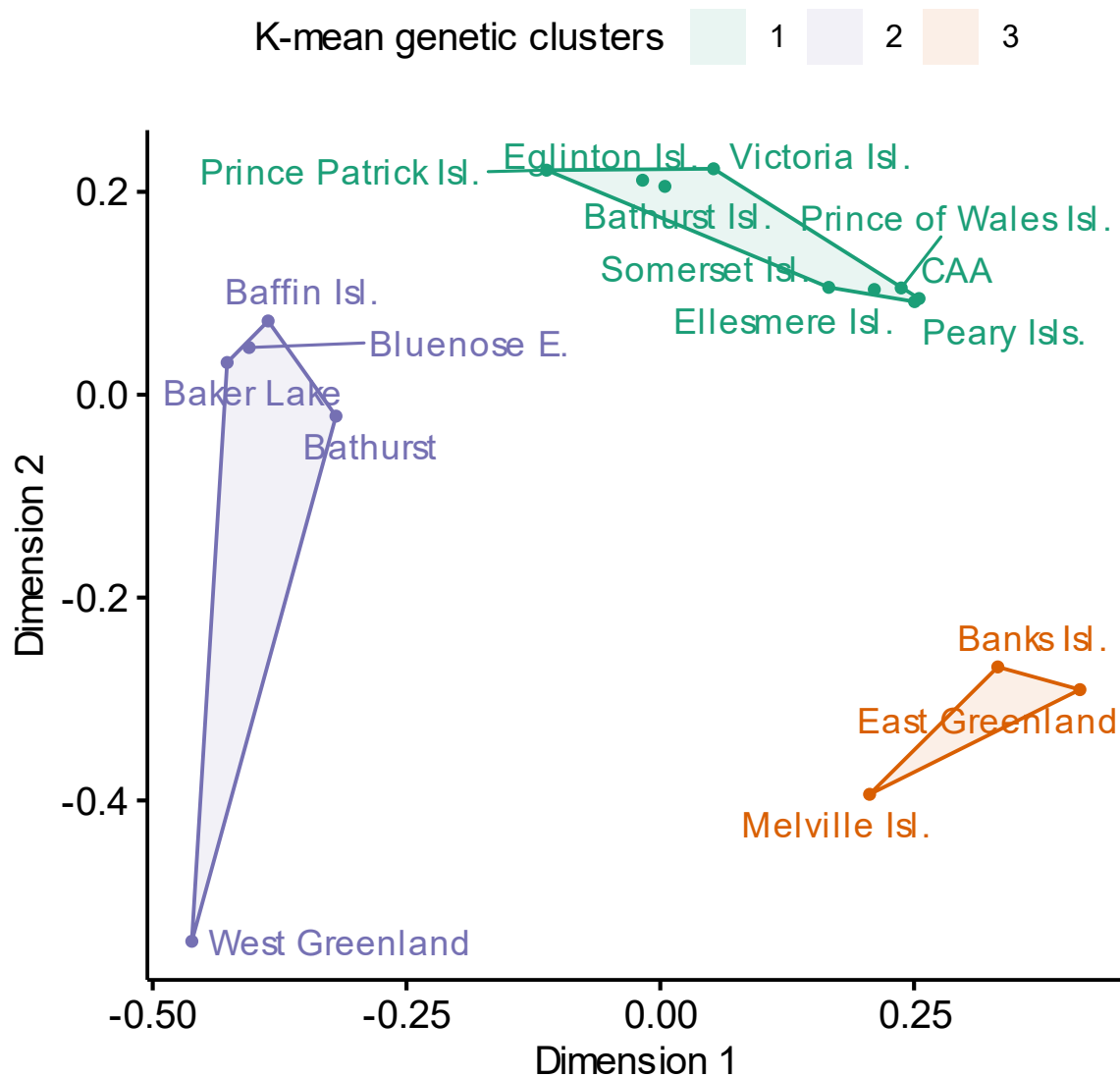


Figure S3.4. Population genetic clustering of the North American Arctic Islands (NAII) and neighbouring mainland populations. Ordination plot of metric multidimensional scaling (mMDS) of NAII original sampling populations. mMDS represents distances between populations with the lowest possible dimensional space; populations closer together are more similar than those further apart. Colours represent the optimal K-means clusters (K=3) identified using the average silhouette method on the Euclidean distance matrix of the mMDS coordinates (n = 311).

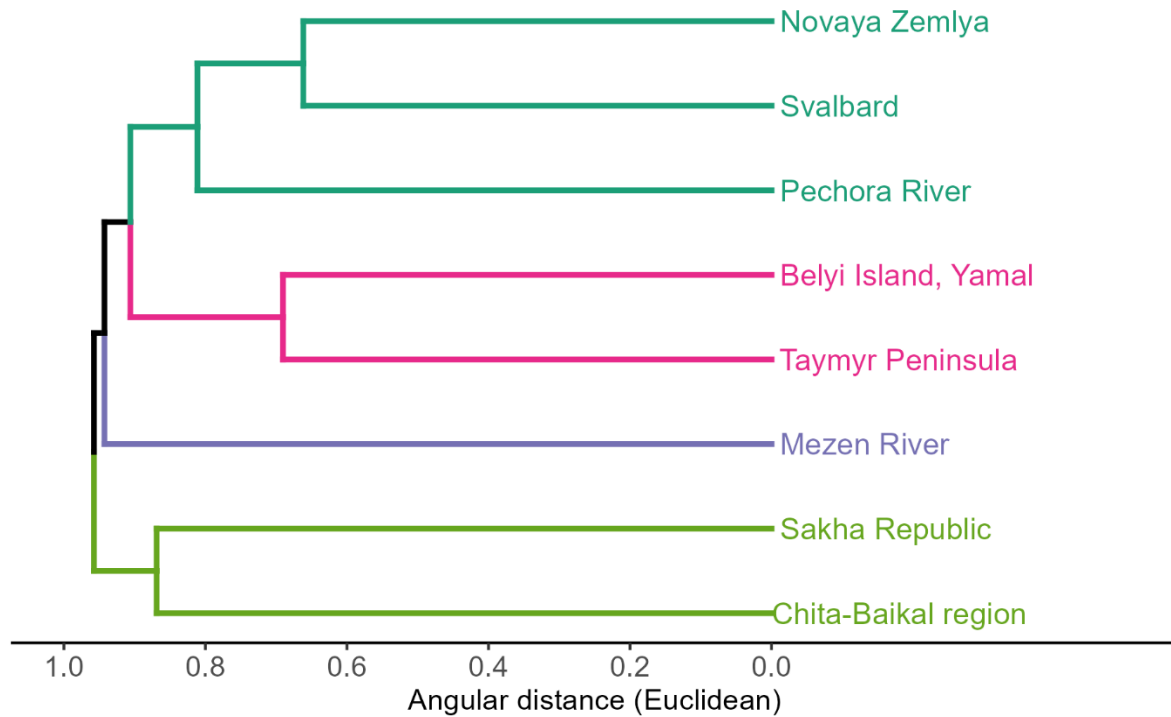


Figure S3.5. Hierarchical population genetic clustering of the Barents Sea Islands (BSI) and neighbouring mainland populations. Dendrogram of BSI original sampling populations based on a UPGMA hierarchical clustering method where populations that are genetically closer to each other cluster together. Colours represent the optimal K-means clusters (K=4) identified using the average silhouette method on the Euclidean distance matrix of mitochondrial sequence data (n = 213).

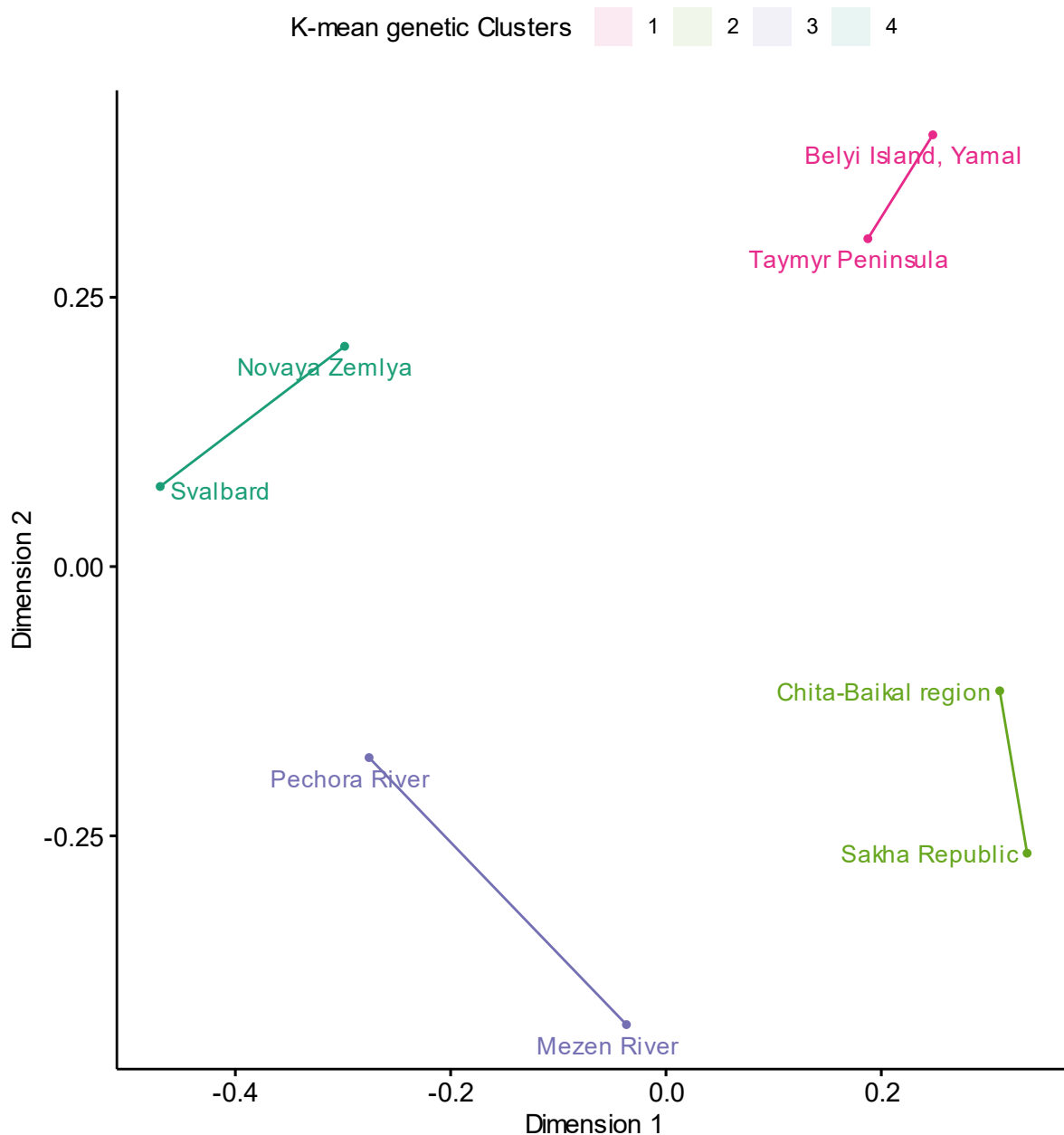


Figure S3.6. Population genetic clustering of the Barents Sea Islands (BSI) and neighbouring mainland populations. Ordination plot of metric multidimensional scaling (mMDS) of BSI original sampling populations. mMDS represents distances between populations with the lowest possible dimensional space; populations closer together are more similar than those further apart. Colours represent the optimal K-means clusters (K=4) identified using the average silhouette method on the Euclidean distance matrix of the mMDS coordinates (n = 213).

S3.6 Genetic summary statistics of sampling populations

Table S3.10. Genetic summary statistics of the North American Arctic island populations used in the study. Populations are given as the original population, herd, or locality based on sampling locality or region that was used in the original datasets/publications.

Population name	Number of individuals	Number of haplotypes	Rarefied allelic richness	Gene diversity
Banks Island	32	11	3.26	0.693
Bathurst Island	10	4	3.21	0.683
Baffin Island	13	6	3.64	0.708
Prince Patrick Island	3	3	5.00	0.750
Melville Island	7	4	3.21	0.678
Victoria Island	16	4	3.53	0.704
Eglinton Island	6	9	3.35	0.717
Prince of Wales Island	7	2	2.77	0.643
Somerset Island	3	3	4.00	0.750
Peary Islands	12	4	3.44	0.686
West Greenland	14	1	1.98	0.50
CAA	15	4	3.17	0.683
Baker Lake	8	6	4.30	0.732
East Greenland	4	1	2.00	0.50
Ellesmere Island	121	3	2.98	0.666
Bathurst	20	12	3.98	0.734
Bluenose East	20	11	3.98	0.728

Table S3.11. Genetic summary statistics of the Barents Sea Island populations used in the study. Populations are given as the original population, herd, or locality based on sampling locality or region that was used in the original datasets/publications.

Population name	Number of individuals	Number of haplotypes	Rarefied allelic richness	Gene diversity
Svalbard	58	2	3.00	0.627
Taymyr Peninsula	59	26	7.46	0.739
Novaya Zemlya, Yuzhny Island	18	3	3.81	0.642
Pechora River	13	9	7.22	0.740
Mezen River	14	6	5.86	0.695
Belyi Island, Yamal Nenets	21	6	5.41	0.704
Lake Chitta Region	10	5	5	0.667

Sakha Republic	20	6	6.01	0.662

Table S3.12. Genetic differentiation (Pairwise Nei's G_{ST} [Nei, 1973]) between North American Arctic Island populations used in the study. Populations are given as the original population, herd, or locality based on sampling locality or region that was used in the original datasets/publications.

	Banks Island	Bathurst Island	Baffin Island	Prince Patrick	Melville Island	Victoria Island	Eglinton Island	Prince of Wales Isl.	Somerset Island	Peary Islands	West Greenland	CAA	Baker Lake	East Greenland	Ellesmere Island	Bathurst	Bluenose
Banks Island	0.000	0.113	0.124	0.088	0.006	0.110	0.101	0.074	0.047	0.031	0.446	0.029	0.104	0.167	0.055	0.076	0.102
Bathurst Island	0.113	0.000	0.014	0.057	0.125	0.004	0.013	0.046	0.015	0.033	0.487	0.036	0.043	0.377	0.073	0.050	0.040
Baffin Island	0.124	0.014	0.000	0.043	0.139	0.027	0.020	0.113	0.043	0.072	0.359	0.073	0.019	0.410	0.092	0.025	0.015
Prince Patrick Island	0.088	0.057	0.043	0.000	0.135	0.045	0.024	0.133	0.053	0.051	0.459	0.046	0.046	0.439	0.023	0.022	0.026
Melville Island	0.006	0.125	0.139	0.135	0.000	0.132	0.132	0.063	0.054	0.037	0.452	0.041	0.125	0.116	0.087	0.104	0.120
Victoria Island	0.110	0.004	0.027	0.045	0.132	0.000	0.007	0.048	0.010	0.031	0.477	0.033	0.046	0.383	0.068	0.045	0.029
Eglinton Island	0.101	0.013	0.020	0.024	0.132	0.007	0.000	0.080	0.024	0.043	0.433	0.038	0.032	0.386	0.060	0.029	0.017
Prince of Wales Island	0.074	0.046	0.113	0.133	0.063	0.048	0.080	0.000	0.008	-0.001	0.589	0.007	0.123	0.224	0.084	0.116	0.106
Somerset Island	0.047	0.015	0.043	0.053	0.054	0.010	0.024	0.008	0.000	-0.001	0.459	0.003	0.046	0.262	0.051	0.040	0.035
Peary Islands	0.031	0.033	0.072	0.051	0.037	0.031	0.043	-0.001	-0.001	0.000	0.477	-0.014	0.076	0.222	0.019	0.060	0.064
West Greenland	0.446	0.487	0.359	0.459	0.452	0.477	0.433	0.589	0.459	0.477	0.000	0.477	0.344	1.000	0.498	0.325	0.320
CAA	0.029	0.036	0.073	0.046	0.041	0.033	0.038	0.007	0.003	-0.014	0.477	0.000	0.077	0.235	0.013	0.059	0.065
Baker Lake	0.104	0.043	0.019	0.046	0.125	0.046	0.032	0.123	0.046	0.076	0.344	0.077	0.000	0.381	0.095	0.019	0.014
East Greenland	0.167	0.377	0.410	0.439	0.116	0.383	0.386	0.224	0.262	0.222	1.000	0.235	0.381	0.000	0.348	0.350	0.370

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Ellesmere Island	0.055	0.073	0.092	0.023	0.087	0.068	0.060	0.084	0.051	0.019	0.498	0.013	0.095	0.348	0.000	0.065	0.083
Bathurst	0.076	0.050	0.025	0.022	0.104	0.045	0.029	0.116	0.040	0.060	0.325	0.059	0.019	0.350	0.065	0.000	0.014
Bluenose East	0.102	0.040	0.015	0.026	0.120	0.029	0.017	0.106	0.035	0.064	0.320	0.065	0.014	0.370	0.083	0.014	0.000

Table S3.13. Genetic differentiation (Pairwise Nei's G_{ST} [Nei, 1973]) between Barents Sea Island (BSI) populations used in the study. Populations are given as the original population, herd, or locality based on sampling locality or region that was used in the original datasets/publications.

	Belyi Island, Yamal	Chita-Baikal Region	Mezen River	Novaya Zemlya	Pechora River	Sakha Republic	Svalbard	Taymyr Peninsula
Belyi Island, Yamal	0	0.157	0.126	0.166	0.078	0.17	0.214	0.034
Chita-Baikal Region	0.157	0	0.182	0.243	0.125	0.201	0.277	0.108
Mezen River	0.126	0.182	0	0.207	0.061	0.185	0.230	0.079
Novaya Zemlya	0.166	0.243	0.207	0	0.102	0.258	0.129	0.117
Pechora River	0.078	0.125	0.061	0.102	0	0.131	0.133	0.027
Sakha Republic	0.170	0.201	0.185	0.258	0.131	0	0.281	0.114
Svalbard	0.214	0.277	0.230	0.129	0.133	0.281	0	0.155
Taymyr Peninsula	0.034	0.108	0.079	0.117	0.027	0.114	0.155	0

S3.7 Genetic summary statistics of DIYABC model populations

Table S3.14. Genetic summary statistics of the North American Arctic Island (NAAI) DIYABC populations used in the study. Populations refer to those used in the final model set.

Population name	Number of individuals	Number of haplotypes	Rarefied allelic richness	Gene diversity
Canadian Arctic Archipelago	193	14	4.84	0.680
East Greenland	43	13	5.65	0.678
Mainland	61	24	7.98	0.725
West Greenland	14	1	2.00	0.50

Table S3.15. Genetic summary statistics of the Barents Sea Islands (BSI) DIYABC populations used in the study. Populations refer to those used in the final model set.

Population name	Number of individuals	Number of haplotypes	Rarefied allelic richness	Gene diversity
Svalbard	58	1	4.84	0.627
Novaya Zemlya	18	3	5.65	0.642
Western Russia	27	13	7.49	0.726
Northern Russia	80	27	2.00	0.734
Eastern Russia	30	10	2.00	0.696

Table S3.16. Genetic differentiation (Pairwise Nei's G_{ST} [Nei, 1973]) between North American Arctic Island (NAII) DIYABC populations used in the study. Populations refer to those used in the final model set.

	Canadian Arctic Archipelago	East Greenland	Mainland	West Greenland
Canadian Arctic Archipelago	0	0.062	0.051	0.465
East Greenland	0.062	0	0.107	0.466
Mainland	0.051	0.107	0	0.316
West Greenland	0.465	0.466	0.316	0

Table S3.17. Genetic differentiation (Pairwise Nei's G_{ST} [Nei, 1973]) between Barents Sea Island (BSI) DIYABC populations used in the study. Populations refer to those used in the final model set.

	Svalbard	Novaya Zemlya	Western Russia	Northern Russia	Eastern Russia
Svalbard	0	0.129	0.163	0.162	0.224

Novaya Zemlya	0.129	0	0.137	0.121	0.199
Western Russia	0.163	0.137	0	0.044	0.094
Northern Russia	0.162	0.121	0.044	0	0.076
Eastern Russia	0.224	0.199	0.094	0.076	0

S3.8 Figures: reindeer population events and modelled sea ice change

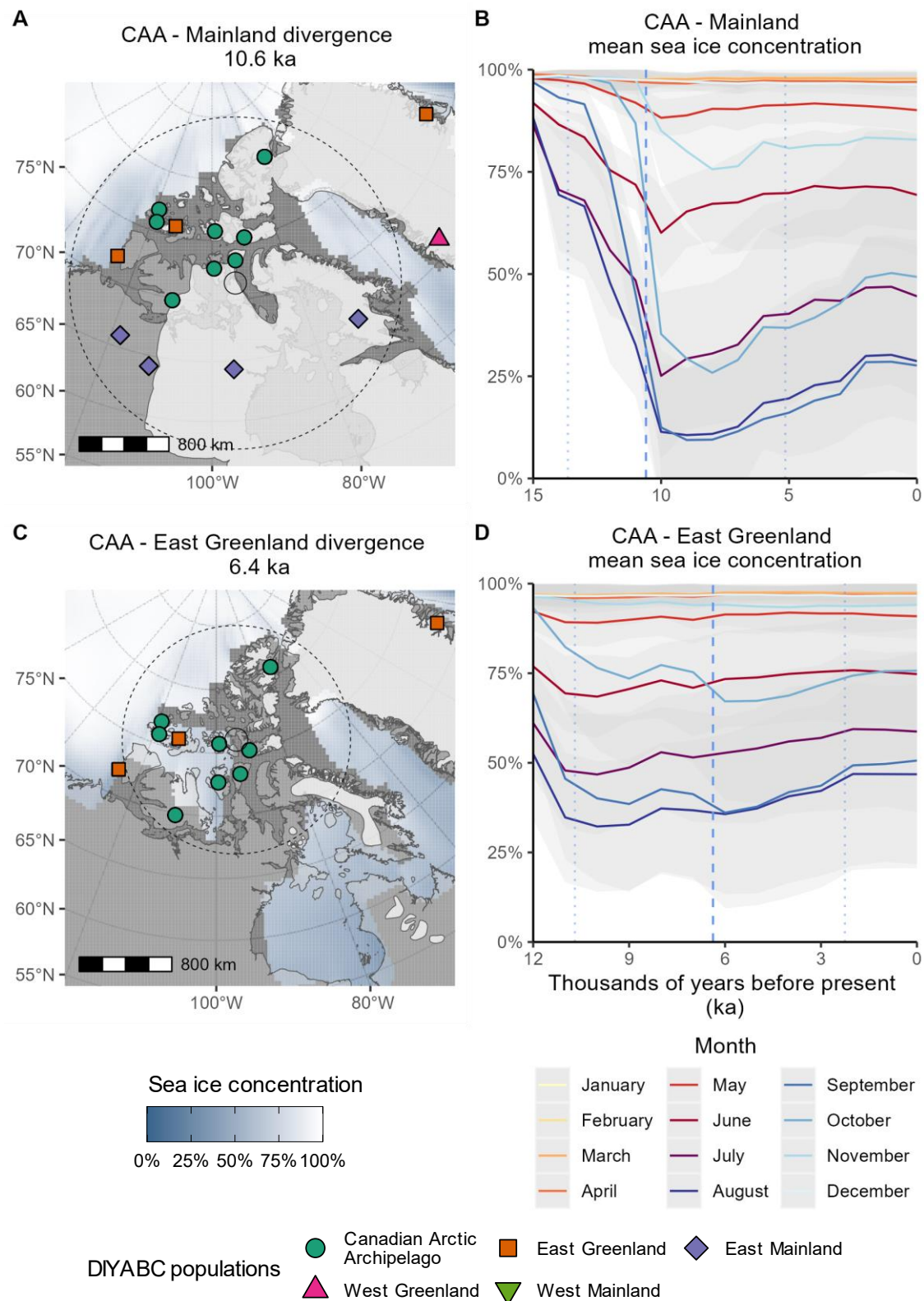


Figure S3.7. Holocene reindeer population divergence events and modelled sea ice changes in the North American Arctic Islands (NAAI). (A, C): Demographic events mapped with relevant present-day populations, modern land extent (light grey), a snapshot of

modelled mean sea ice concentration (blue - white) and land extent (dark grey) at 11 ka (**A**) and 6 ka (**C**) (Singarayer et al., 2017; Valdes et al., 2017), and reconstructed ice sheets at 10.3 ka (**A**) and 6.4 ka (**C**) – the closest time steps to the corresponding population events (Dalton et al., 2020). Divergence time estimates are the median parameter estimates from the most plausible evolutionary model (scenario two). The geographic centroid between two populations (solid circle), within which 100 random samples of modelled sea ice concentration at different radii (dotted circle) were extracted and averaged (one radius shown for clarity). (**B**, **D**): Modelled sea ice concentration with associated standard deviations in 1 ka intervals. Demographic event times (dashed lines) with associated 95% credible intervals (dotted lines).

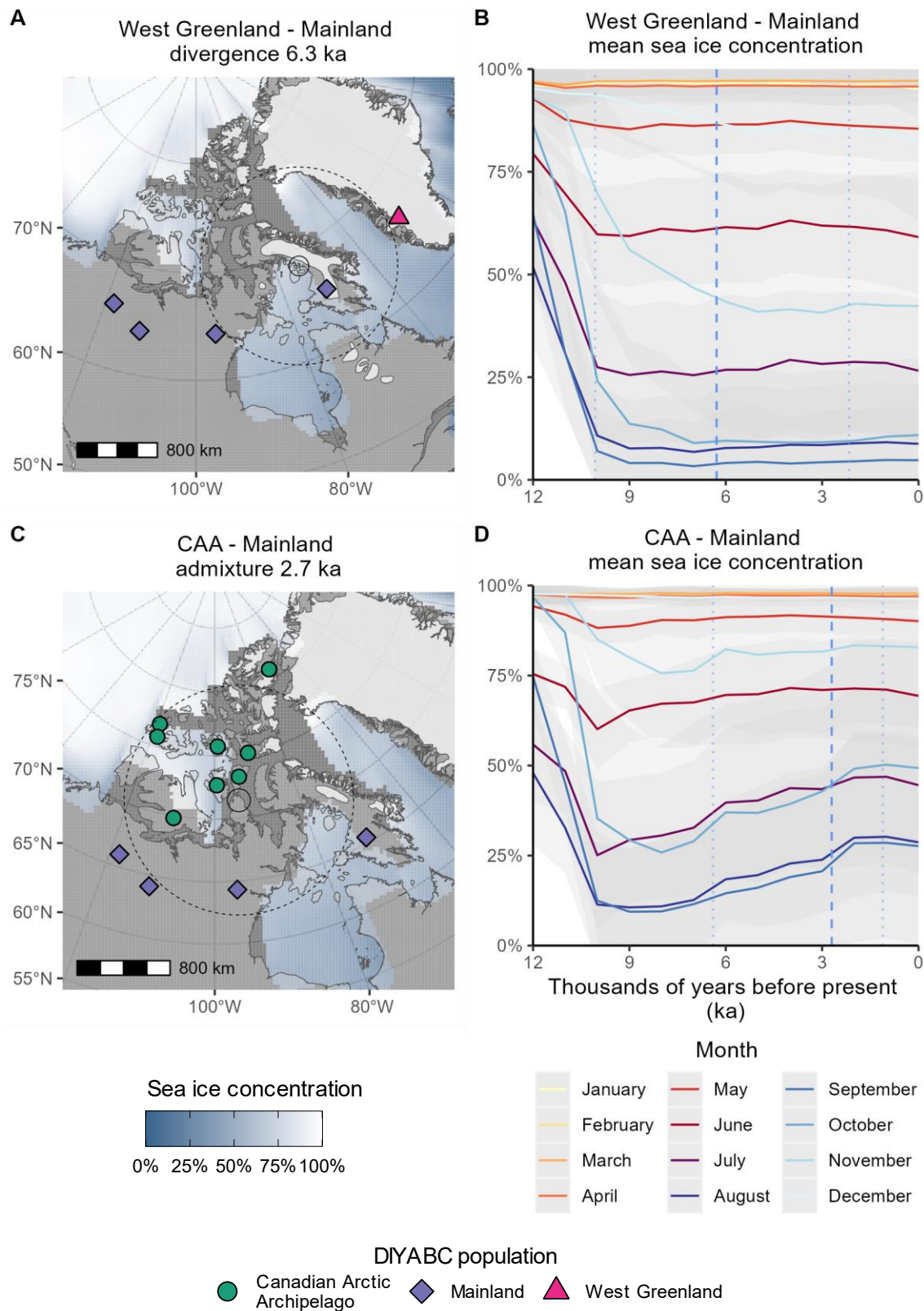


Figure S3.8. Holocene reindeer population divergence, admixture, and modelled sea ice changes in the North American Arctic Islands (NAAI). (A, C): Demographic events mapped with relevant present-day populations, modern land extent (light grey), a snapshot of modelled mean sea ice concentration (blue - white) and land extent (dark grey) at 6 ka (A) and 3 ka (C) (Singarayer et al., 2017; Valdes et al., 2017), and reconstructed ice sheets at 6

ka (**A**) and 3 ka (**C**) – the closest time steps to the corresponding population events (Dalton et al., 2020). Divergence time estimates are the median parameter estimates from the most plausible evolutionary model (scenario two). The geographic centroid between two populations (solid circle), within which 100 random samples of modelled sea ice concentration at different radii (dotted circle) were extracted and averaged (one radius shown for clarity). (**A**) Divergence and (**C**) admixture time estimates mapped with relevant present-day populations. (**B, D**) Modelled sea ice concentration with associated standard deviations in 1 ka time intervals. Timing of demographic events (dashed lines) with associated 95% credible intervals (dotted lines).

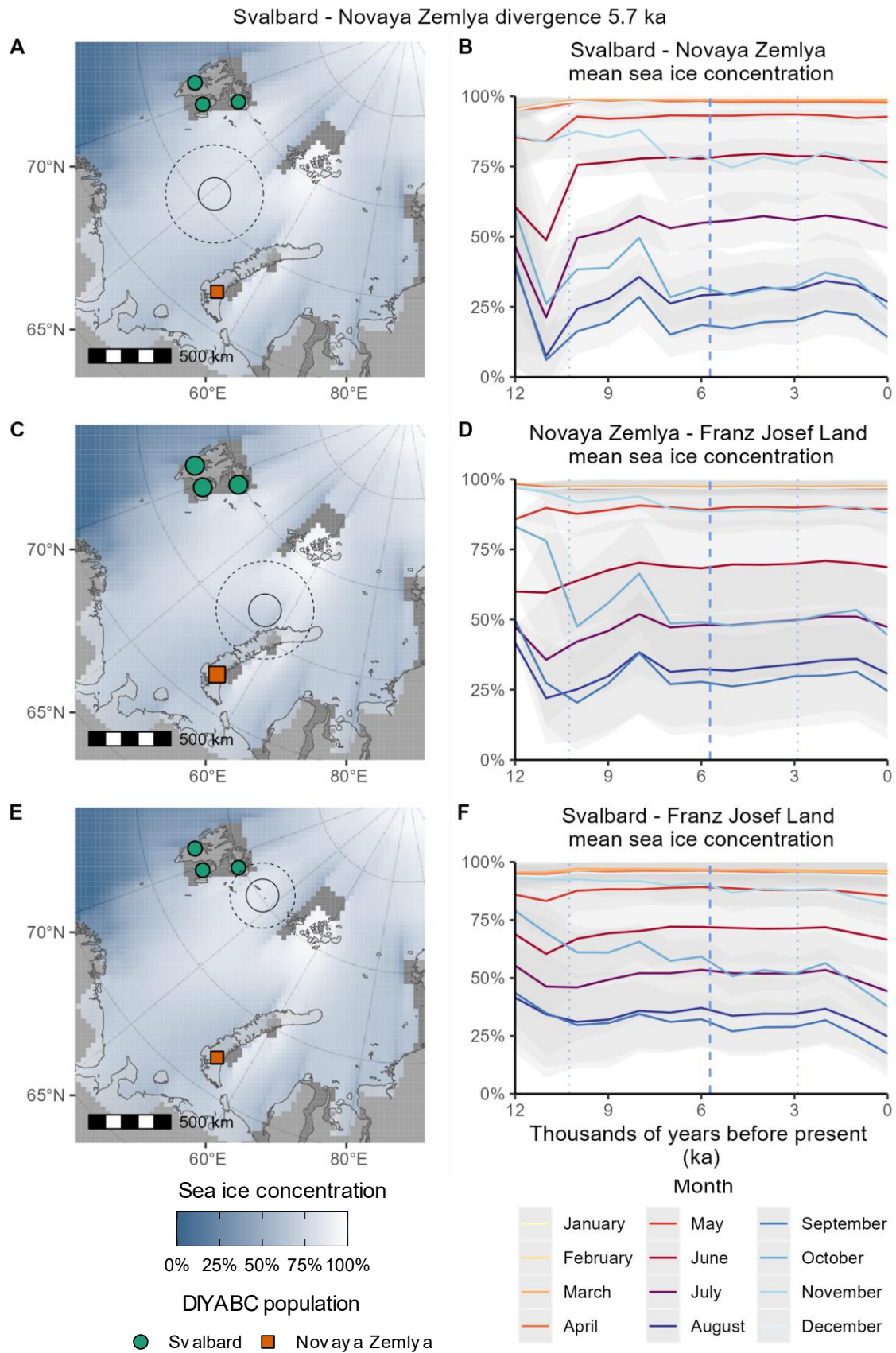


Figure S3.9. Holocene Svalbard and Novaya Zemlya reindeer population divergence and modelled sea ice changes in the Barents Sea Islands system (BSI). (A, C, E): Demographic

events mapped with relevant present-day populations, modern land extent (light grey), a snapshot of modelled mean sea ice concentration (blue - white) and land extent (dark grey) at 6 ka (Singarayer et al., 2017; Valdes et al., 2017). Divergence time estimates are the median parameter estimates from the most plausible evolutionary model (scenario three). The geographic centroid between two populations (solid circle), within which 100 random samples of modelled sea ice concentration at different radii (dotted circle) were extracted and averaged (one radius shown for clarity). Three sea ice analyses were conducted to account for (A) a mid-Barents Sea crossing, and (C, E) a stepping-stone scenario with Franz Joseph Land as an intermediate step. (B, D, F): Modelled sea ice concentration with associated standard deviations in 1 ka intervals. Estimated population divergence time (dashed lines) with associated 95% credible intervals (dotted lines).

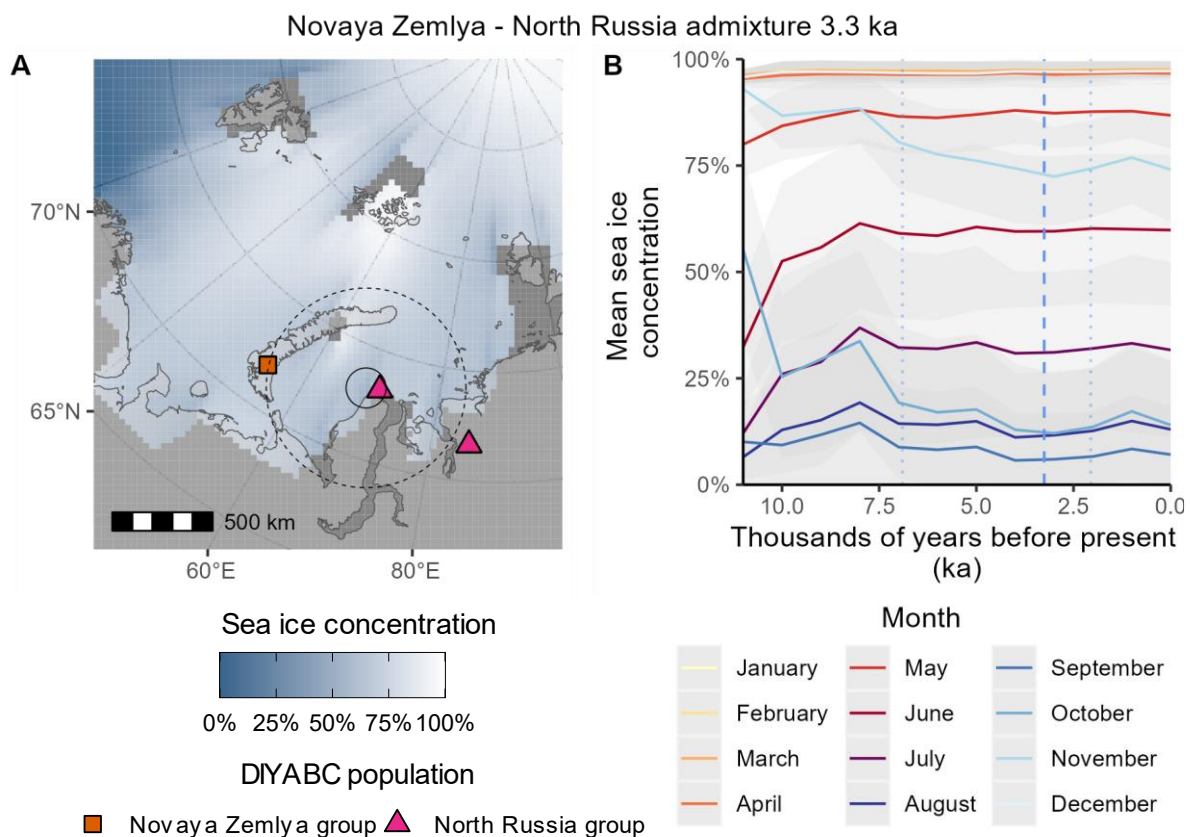


Figure S3.10. Holocene Novaya-Zemlya and mainland reindeer population admixture and sea ice changes in the Barents Sea Islands system (BSI). (A): Demographic event mapped with relevant present-day populations, modern land extent (light grey), a snapshot of modelled mean sea ice concentration (blue - white) and land extent (dark grey) at 3 ka (Singarayer et al., 2017; Valdes et al., 2017). Divergence time estimates are the median parameter estimates from the most plausible evolutionary model (scenario three). The geographic centroid between two populations (solid circle), within which 100 random samples of modelled sea ice concentration at different radii (dotted circle) were extracted and averaged (one radius shown for clarity). (B): Regional modelled sea ice concentration with associated standard deviations in 1 ka intervals. Estimated admixture time (dashed line) with associated 95% credible intervals (dotted lines). Note that sea ice estimates include the most likely crossing point between Novaya Zemlya and the mainland, but also extend over a wider area of the Kara Sea.

S3.9 References

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Chapter 4:

Molecular footprints of Quaternary climate fluctuations in the circumpolar tundra shrub dwarf birch

Maria Dance^{1,2}, Erin E. Saupe³, James Borrell⁴, Pernille Bronken Eidesen^{2,5}, Daniel Ackerman^{6*}, Jakob Assmann^{7*}, Bruce C. Forbes^{8*}, Marina Gurskaya^{9*}, Toke T. Høye^{10*}, Stein R. Karlsen^{11*}, Timo Kumpula^{12*}, Mariusz Lamentowicz^{13*}, Michael M. Loranty^{14*}, Isla Myers-Smith^{7*}, Janet Prevéy^{15*}, Christian Rixen^{15,16*}, Gabriela Schaepman-Strub^{17*}, Michał Słowiński^{18*}, Sandra Słowiński^{19*}, Aleksandr Sokolov^{20*}, James D. M. Speed^{21*}, Marcus Spiegel^{1*}, Martin Wilmking^{22*}, Marc Macias-Fauria¹



¹School of Geography and the Environment, University of Oxford, Oxford, UK; ²The University Centre in Svalbard, Longyearbyen, Norway; ³ Department of Earth Sciences, University of Oxford, Oxford, UK; ⁴Royal Botanic Gardens, Kew, London, UK; ⁵University of Oslo, Oslo, Norway; ⁶University of Minnesota, Minneapolis, USA; ⁷The University of Edinburgh, Edinburgh, UK; ⁸Arctic Centre, University of Lapland, Rovaniemi, Finland; ⁹Institute of Plant and Animal Ecology, UB RAS, Yekaterinburg, Russia; ¹⁰Department of Ecoscience, Aarhus University, Aarhus, Denmark; ¹¹Northern Research Institute NORUT, Tromsø, Norway;

¹²University of Eastern Finland, Kuopio, Finland; ¹³Adam Mickiewicz University, Poznań, Poland; ¹⁴Department of Geography, Colgate University NY, New York, USA; ¹⁵WSL Institute for Snow and Avalanche Research, SLF, Davos, Switzerland; ¹⁶Climate Change, Extremes and Natural Hazards in Alpine Regions Research Center CERC, Davos, Switzerland; ¹⁷Department of Evolutionary Biology and Environmental Studies, University of Zurich, Switzerland; ¹⁸Institute of Geography and Spatial Organization Polish Academy of Sciences (IGSO PAS), Warsaw, Poland; ¹⁹Stanisław Leszczycki Institute of Geography and Spatial Organization Polish Academy of Sciences (IGSO PAS), Warsaw, Poland; ²⁰Arctic Research Station of the Institute of Plant and Animal Ecology, UB RAS, Labytnangi, Russia; ²¹Department of Natural History, NTNU University Museum, Norwegian University of Science and Technology, Trondheim, Norway; ²²Institute of Botany and Landscape Ecology, University of Greifswald, Greifswald, Germany.

*Shrub Hub data contributors.

4.1 Chapter statement

As in **Chapter 3**, this study combines genetic data, coalescent modelling, and paleoenvironmental data to model the impact of Quaternary climate change on the evolution and population history of a key Arctic taxon. However, the focus moves from reindeer (*Rangifer tarandus* L.) to a dominant tundra shrub, the dwarf birches (*Betula nana* L. and *Betula glandulosa* Michx.), which constitute a key food source for terrestrial herbivores such as reindeer and are a common component of tundra vegetation. The spatial scope of this study widens from the High Arctic archipelagos to encompass the panarctic range of the dwarf birches. The focus also shifts from the role of sea ice and ice sheet dynamics shaping dispersal during the postglacial (21,000 years ago - present), to the role of glacial ice sheet fluctuations on dwarf birch population isolation and mixing with a temporal scope reaching deeper into the past to encompass the entire Quaternary glaciation (2.6 million years ago - present).

Whereas the previous chapter employed published mitochondrial DNA sequences, this study generated a novel genetic dataset with genome-wide Single Nucleotide Polymorphism (SNP) markers. This study builds on a previous phylogeographical study of the dwarf birches that used Amplified Length Polymorphism (AFLP) and chloroplast markers (Eidesen et al., 2015). Using SNPs offers the potential to extract more information on species genetic diversity, and therefore demographic history and unresolved evolutionary relationships.

This study is the first to use next-generation sequence data in concert with a coalescent-based approximate Bayesian computation (ABC) approach for a circumpolar Arctic plant species (Borrell et al., 2018; Chen & Lou, 2019; Ikeda et al., 2017). This chapter has been submitted as a primary research article to Molecular Ecology.

4.2 Author contributions

MD conceptualised the study and designed the research with input from MMF and PBE. MMF designed and coordinated data collection. DA, JA, BCF, MG, TTH, SRK, TK, ML, MML, IMS, JP, CR, GSS, MS, SS, AS, JDMS, MSp, and MW contributed to data collection. JB advised on DNA extraction, sequencing, and demographic modelling approaches. MD performed DNA extraction, data processing, and all data analyses. MD drafted the article with input from MMF and EES. All authors contributed to manuscript commenting and editing.

4.3 Abstract

The Arctic tundra biome is undergoing rapid shrub expansion (“shrubification”) in response to anthropogenic climate change. Quaternary glacial cycles previously caused substantial shifts in Arctic vegetation, with changes in species’ distributions, abundance, and connectivity. These climatic changes have left lasting impacts on the genetic structure of modern populations. Examining how shrubs responded to past episodes of climate change using genetic data can inform the long-term ecological and evolutionary consequences of shrub expansion today.

Here we test scenarios of Quaternary population history of the dwarf birches (*Betula nana* and *Betula glandulosa*) using informative SNP markers obtained from RAD sequencing (RADseq) and coalescent modelling in an approximate Bayesian Computation framework. We compare the timings of estimated population events with recently published ice sheet reconstructions and other paleoenvironmental information to untangle the impacts of alternating cold and warm periods on the phylogeography of the dwarf birches.

Our best supported model suggested that *B. nana* and *B. glandulosa* diverged in the Mid-Pleistocene Transition as glaciations intensified and ice sheets expanded. We found support for a complex Quaternary history of inter- and intraspecific divergences and admixtures, with secondary contact occurring during both periods of expanding and retreating ice sheets. We identify two distinct genetic groups in *B. glandulosa* for the first time, which likely reflect glacial isolation north and south of the North American ice sheets.

Our results suggest that the modern genetic structure of the dwarf birches was shaped by glacial cycles in diverse ways, with transitions in climate and interactions between ice sheets changes, climate, and environmental conditions likely influencing population history. Tundra shrubs such as the dwarf birches may have had more nuanced responses to past climatic changes than phylogeographic analyses have often suggested, with implications for future eco-evolutionary responses to anthropogenic climate change.

Keywords: *Betula nana*, *Betula glandulosa*, demographic history, dwarf birch, dwarf shrub, phylogeography, Pleistocene, Quaternary, refugia, tundra shrub

4.4 Introduction

Climate warming is contributing to changes in tundra vegetation composition, particularly shrub expansion (“shrubification”) (Mekonnen et al., 2021; Myers-Smith et al., 2011). Shrub expansion has and will have Arctic-wide impacts on vegetation communities, tundra ecosystems, surface energy and carbon balance, and potentially global climate feedbacks (Mekonnen et al., 2021). A greater understanding of the response of shrubs to past climate change beyond the short recent observational period will inform our understanding of long-term responses of Arctic shrubs and wider ecosystems to contemporary climate change.

Arctic tundra shrubs have responded to climate change over the past ~3 million years through changes in their distribution and abundance, as evidenced in the palaeoecological record (Anderson & Brubaker, 1994; Andreev et al., 2014; Bigelow et al., 2003; Crump et al., 2019; Fewster et al., 2023; Kullman, 1995; Meucci et al., 2021). The modern Arctic tundra biome formed during the transition from warmer Neogene climates to the onset of Quaternary glaciations in the Northern Hemisphere ~3-2.5 million years ago (Brochmann & Brysting, 2008; Miller et al., 2010). This transition resulted in new selective pressures and opportunities for speciation and diversification for tundra shrubs (Brochmann & Brysting, 2008; Davis & Shaw, 2001; Kadereit & Abbott, 2021), which were already present (Andreev et al., 2014; Bennike & Böcher, 1990). The dynamic glaciation history of the Quaternary (Miller et al., 2010) subsequently caused large vegetation shifts (Birks, 2008).

The impacts of Quaternary glacial cycles on Arctic plants are often generalised as ice sheet expansion causing species’ ranges to retract to climatically suitable land areas (refugia), leading to isolation in smaller populations and intraspecific divergence (Bennett & Provan, 2008; Hewitt, 2000; Hultén, 1937). This model is supported by higher genetic distinctiveness in former refugial regions (Eidesen et al., 2013). Fossil, molecular, and phytogeographical evidence shows that the Beringian region (stretching from the Verkhoyansk mountains in Eastern Russia to the Mackenzie River in North America) was an important refugium for shrubs such as the dwarf birches (Bigelow et al., 2003; Brubaker et al., 2005; Eidesen et al., 2015) and Arctic plants in general (Abbott & Brochmann, 2003; Brochmann & Brysting, 2008; Hewitt, 2004; Hultén, 1937; Weider & Hobæk, 2000; Westergaard et al., 2010).

Conversely, ice retreat in interglacials caused population expansion from refugia into ice-free areas as climatic and environmental conditions became suitable, leading to increased connectivity and genetic admixture between divergent populations (Hewitt, 2000; Petit et al., 2003). This model is supported by a decline in plant species richness and genetic diversity with distance from glacial refugia (reflecting population expansion), except in regions of likely secondary contact between previously isolated populations (Pellissier et al., 2016; Stewart et al., 2016). The phylogeographic structure of several shrub species suggests repeated differentiation into intraspecific lineages and intraspecific hybridization, likely in response to intermittent isolation and secondary contact in the Quaternary (Alsos et al., 2005; Ehrich et al., 2008; Eidesen, Alsos, et al., 2007; Eidesen, Carlsen, et al., 2007; Skrede et al., 2006).

However, the phylogeographic history of tundra shrub responses to glacial-interglacial cycles is likely more complex than the model of isolation in glacial refugia and enhanced connectivity in interglacials. During ice sheet expansion and associated fall in sea levels (Elias & Brigham-Grette, 2013), spatially separated populations may come back into contact as climatically suitable areas become more restricted, leading to admixture in refugia (Edwards et al 2018; Taylor et al., 2021). Likewise, during ice retreat, dispersal on continental-scales and sea level rise could increase isolation between populations at range limits (Slatkin, 1985).

Furthermore, ice-free regions do not necessarily permit unlimited dispersal and connectivity. Dry and cold conditions across many parts of northern Eurasia during glacial periods restricted the range of shrub tundra (Bigelow et al., 2003; Miller et al., 2010) and may have reduced population connectivity between refugia (Kienast et al., 2001, 2005). On the other hand, the northward expansion of boreal forest during interglacials reduced the spatial extent of the tundra biome (H. Binney et al., 2017), creating potential “interglacial refugia” (Bennett & Provan, 2008). Unsuitable climatic and biotic conditions for tundra shrubs in ice-free areas may therefore have been an effective biogeographic barrier contributing to population isolation.

Here we focus on *Betula nana* (L.) and *Betula glandulosa* (Michx.) (dwarf birches), widespread and ecologically important shrubs of the Arctic tundra (de Groot et al., 1997). As deciduous shrubs, they have been prominent in the multidecadal increases in aboveground biomass observed in the Arctic as a response to ongoing climate change (Elmendorf et al., 2012; Mekonnen et al., 2021; Myers-Smith et al., 2011; Sturm et al., 2001).

The response of the dwarf birches to past climate change has been investigated using Amplified Length Polymorphism (AFLP) and plastid markers to infer refugial locations and spatial patterns of postglacial dispersal and secondary contact (Palmé et al., 2004; Eidesen et al., 2015). However, determining the potential climatic conditions (i.e., interglacial *versus* glacial) responsible for shaping genetic variation is challenging without divergence time estimates (Taberlet et al., 1998). Furthermore, the timescale of glacial cycles is finer than the temporal resolution that can be inferred from short phylogeographic genetic markers (Carstens & Knowles, 2007). Therefore, much of the Quaternary history of the dwarf birches and associated paleoclimatic drivers remains unresolved.

As a species complex with hybridisation and introgression (Eidesen et al., 2015), examining a new range-wide genetic dataset will help resolve evolutionary relationships (Tsuda et al., 2017). We use coalescent modelling to link modern genetic structure with population demographic history in the Quaternary (Beichman et al., 2018; Kingman, 1982; Marchi et al., 2021; Wakeley & Hey, 1997). Approximate Bayesian computation (ABC)-based analyses (Beaumont, 2010; Bertorelle et al., 2010) enables testing alternative demographic scenarios by comparing genetic data simulated under competing models with observed genetic data. This method has been used to infer postglacial range shifts and historical population fragmentation of *B. nana* in Britain (Borrell et al., 2018) and has been used to infer the Quaternary histories of organisms including Arctic plants (Ikeda et al., 2017) and tree birches (Chen & Lou, 2019; Salojärvi et al., 2017; Tsuda et al., 2015, 2017).

Using estimated divergence and admixture times, we assessed the role of Quaternary climate change on the population history of the dwarf birches by comparing modelled population events to reconstructed ice sheet and sea level changes. We disentangle the effects of ice sheet changes, suitable climatic conditions, and geography on the isolation and mixing of dwarf birches during the Quaternary and the subsequent impact on modern genetic structure.

4.5 Materials and methods

4.5.1 Species

This study examines the genetic diversity of two dwarf birch species: *Betula nana* L. and *Betula glandulosa* Michx. *Betula nana* (diploid with $2n = 28$) is a shrub native to Arctic and boreal

regions with a circumpolar distribution. A characteristic plant of peat bog and tundra environments, it is monoecious, wind-pollinated, wind-dispersed, and has a prostrate or upright growth habit up to 1 metre in height (de Groot et al., 1997; Jadwiszczak et al., 2012). *B. nana* is found outside its core range in southerly populations that are glacial relicts (Eidesen et al., 2015; Hultén et al., 1986; Jadwiszczak et al., 2012). *Betula nana* is sometimes divided into two subspecies, with *B. nana* subsp. *nana* (Sukaczew) Hult. in western Eurasia and Greenland, and *B. nana* subsp. *exilis* (Sukaczew) Hult. in eastern Eurasia and northwest North America, with ranges overlapping in western Siberia (Elven et al., 2011). A strictly Beringean subspecies that occurs within the larger range of subsp. *exilis*, *Betula perfiljevii*, was described by Vassiljev (1966) but is otherwise taxonomically included within subsp. *exilis* (Elven et al., 2011).

Betula glandulosa (Michx.) is closely related to *B. nana* and occurs across Alaska and Canada to Baffin Island and southern Greenland (de Groot et al., 1997). *Betula glandulosa*'s range also extends south through the Rocky Mountains and the Cascade Range, with small populations in mountainous regions of eastern North America (Furrow, 2004). *Betula glandulosa* has similar habitat preferences to *B. nana* but is less cold tolerant (Eidesen et al., 2015). The species grows as tall, upright shrubs (up to 3 metres in height) in the core of its range but *B. glandulosa* and *B. nana* both become lower and more prostrate with smaller leaves in harsher environmental conditions and at their northern range limits (de Groot et al., 1997).

Introgression and hybridisation within the *Betula* genus have resulted in high morphological variability within and among species (Tsuda et al., 2017), making taxonomic and phylogenetic inferences difficult (Järvinen et al., 2004; Li et al., 2005, 2007). There is disagreement on whether *B. nana* subsp. *exilis* and *B. glandulosa* should be considered distinct species or combined as *B. glandulosa* (Ashburner & McAllister, 2013; de Groot et al., 1997). *Betula. nana* subsp. *exilis* and *B. glandulosa* hybridise and form intermediates in areas of range overlap but form distinct entities elsewhere in their ranges (Furrow, 2004). *Betula. glandulosa* and *B. nana* subsp. *nana* also hybridise in southern Greenland (Furrow, 2004).

4.5.2 Sampling

Dwarf birch samples (*B. nana* and *B. glandulosa*) were collected during the growing season between 2015 and 2021. Identification of individual dwarf birch plants can be difficult, as a

genetic individual can extend over many metres due to vegetative reproduction. This is common at northern range limits where climate currently limits sexual reproduction (Alsos et al., 2002; de Groot et al., 1997). To avoid resampling clonal or cryptic individuals, samples were collected over an approximately 200 m² area with a minimum distance of 10 metres between sampled individuals in continuous growth and 5 metres when growth was in distinct patches. See **Appendix S4.1** for more detail on sample collection and storage. To fill geographical sampling gaps, 42 silica-dried specimens from 7 sites that were also sequenced in Eidesen et al. (2015) were obtained with the permission of the NHMO DNA Bank of the Natural History Museum, University of Oslo. For each NHMO site, samples were collected 25 m apart along a 250 m transect.

4.5.3 DNA extraction

Extracting high-quality DNA from dwarf birch is difficult due to a high concentration of secondary compounds such as polysaccharides and phenolics/polyphenols in leaves (Wang et al., 2013). We developed a new DNA extraction protocol to address this issue, which we used to extract total genomic DNA from dried leaves (see **Thesis Appendix A**). Sample quality was assessed using 1% gel electrophoresis, and DNA purity and concentration were assessed using a Qubit with dsDNA BR assay kits Fluorometer (Life Technologies Corporation, Carisbad, CA). Approximately 26% of samples were rejected due to degraded DNA, which mostly came from populations with senesced or limited starting material. In all, 244 samples from 48 populations passed quality control and DNA concentrations were normalised to 20 ng/μl. A subset of samples with sufficient DNA were duplicated (between 1-3 duplicates per sample) to increase sequencing coverage, resulting in 376 DNA extracts in total.

4.5.4 RAD sequencing and bioinformatics

DNA extracts were submitted to FLORAGENEX (Beaverton, Oregon) for RAD library preparation and sequencing. Previous RAD sequencing of *Betula nana* used the cleavage enzyme *Pst*I, which has approximately 70,954 cut sites in the draft genome (Borrell et al., 2018; Wang et al., 2013). Here we used the cleavage enzyme *Sbf*I, which produces a subset of the same cut sites since it has a 2 bp longer recognition sequence. One library was prepared per sample, with unique 10-base barcodes ligated via adaptors to *Sbf*I digested genomic DNA. To ensure consistency in the loci sequenced across samples and to reduce the number of

missing genotypes downstream, fragments between 300 and 500 bp were selected and amplified with PCR. After library QA/QC, libraries were pooled and fragments were sequenced across four lanes of an Illumina NovaSeq 6000 platform with single-end 1 x 100 bp chemistry. Each plate also contained one blank control in differing locations in case of problems with plate identification, and one internal control.

Raw libraries were checked for errors using fastqc (Andrews, 2010). Libraries were demultiplexed and barcode sequences checked for errors using the process_radtags module of Stacks v 2.60 (Catchen et al., 2011, 2013; Rochette et al., 2019). A quality threshold phred score of 10 was used in sliding windows of 15% of the length of the read (19.8 bp in a 131 bp alignment) (Rochette et al., 2019). Reads from duplicated samples from the same original individual were combined. The sequencing depth coverage for each individual and population was assessed; four individuals with fewer than 300,000 reads and two individuals with more than 4 million reads were removed from the analysis. Reads were aligned to a reference *B. nana* genome (Wang et al., 2013, ENA accession number GCA_000327005) using Bowtie2 v2.5 with sensitive and end-to-end parameters (Langmead & Salzberg, 2012). Reference-based SNP calling was performed using the gstacks module of Stacks, which uses a sliding window algorithm to detect RAD loci across all populations, detect SNPs, and then genotype each individual. Preliminary analyses indicated that four sampling sites were hybrids with unknown birch species, so these were excluded from further analyses and genotype calling and filtering steps were repeated without them (**Appendix S4.2**).

The Populations module of Stacks was used to filter loci. Initial filtering suggested that a large number of SNPs were specific to certain sampling locations. Therefore, filtering was performed for regional subsets of the data to maximise the number of SNPs: a) the global dataset, b) North American sampling sites, c) Eurasian sampling sites, and d) western Eurasian sampling sites. To further retain a maximal number of SNPs, a two-stage filtering step was created (**Appendix S4.3**). To minimise missing data, population filters were applied. Loci were retained that were present in 70% of individuals within a population, or present in 70% of individuals across populations. SNPs with a minor allele frequency (MAF) <0.01 were excluded to remove uninformative markers. SNPs were output as a) files with phased haplotypes with multiple SNPs per locus, and b) as files retaining only the first SNP per locus as downstream analyses required unlinked SNPs. Gene diversity was extracted from Stacks populations output

(a) while rarefied allelic richness (corrected for sample size) was calculated from output (b) using the hierfstat package v 0.5-7 in R v 4.0.3 (R Development Core Team, 2022).

To meet assumptions of principal component analysis (PCA) and ADMIXTURE analyses (Alexander et al., 2009; Alexander & Lange, 2011), SNPs were filtered to remove loci in Linkage Disequilibrium (LD). Parameters for filtering were determined by calculating the average LD across intervals in the genome in 100 kb bins using PLINK v1.9 (Chang et al., 2015; Purcell & Chang, 2022) and haplotype variant call format files (VCFs). Visual inspection of the results identified a window size of 33 kb where LD decayed to a background rate of 0.1. VCF files were then filtered in windows of 33 kb sliding by 10 kb with a threshold of correlation coefficient (r^2) > 0.2. LD-filtered SNPs were converted to DIYABC (Collin et al., 2021; Cornuet et al., 2014) SNP input format using custom R scripts.

4.5.5 Population genetic structure

We used the software ADMIXTURE v 1.3.0 (Alexander et al., 2009; Alexander & Lange, 2011) to infer the number of ancestral populations and to identify potential historical admixture events. Genetic admixture occurs when previously isolated populations interbreed, and offspring inherit a mixture of alleles from different ancestral populations (Skotte et al., 2013). ADMIXTURE outputs maximum likelihood estimates of ancestry coefficients that indicate the proportion of an individual's alleles that come from K hypothesized ancestral populations (Alexander et al., 2009). We conducted ADMIXTURE analyses on plink files of the global dataset and for each regional subset using default parameters after replacing chromosome names with "0". We tested a range of 2-7 possible ancestral populations (K); the K with the lowest cross-validation error was chosen. We plotted individual population assignment probabilities in ggplot2 (Wickham, 2016) in R v 4.0.3 (R Development Core Team, 2022), which was used to identify main ancestral groupings and admixed populations.

We also examined global and regional population structure using RADPAINTER and fineRADstructure (Malinsky et al., 2018). These tools can identify global population structure and local population structure simultaneously using linkage structure within each haplotype derived from RADseq data, compared with methods that use one SNP per locus such as ADMIXTURE. Haplotypes are used to find the most recent coalescence (common ancestry)

between individuals, from which a coancestry matrix summarising nearest neighbour haplotype relationships is derived. The matrix is ordered according to a tree-like structure of population relationships produced by the fineRADstructure Markov chain Monte Carlo (MCMC) clustering algorithm. This helps visualise whether individuals are more closely related to individuals from other populations than to individuals within their own population: suggesting gene flow and admixture between populations. The coancestry matrix was calculated using RADpainter and default parameters. Individuals were assigned to populations with fineRADstructure with 100,000 burn in iterations and 100,000 sample iterations, and 1000 thin interval in the output file. A population tree was built with fineRADstructure with 10,000 burn in iterations.

We examined genetic variation among individuals with a PCA of the single unlinked SNP dataset using the adegenet package v2.1.3 (Jombart, 2008; Jombart & Ahmed, 2011) in R v 4.0.3 (R Development Core Team, 2022). PCA summarises genetic variation among individuals using linear combinations of the SNPs, which can identify genetic clines.

4.5.6 Development of demographic modelling scenarios

The aim of our demographic modelling was to infer the timing of splits and the timing and degree of admixture between populations, to understand when the modern genetic structure of the dwarf birches was generated. We used approximate Bayesian computation (ABC) to test evolutionary scenarios (Beaumont, 2010; Cornuet et al., 2014). Testing all potential scenarios with more than three populations and possible admixture events can become intractable and carries risks of multiple testing or overfitting (Borrell et al., 2018). Therefore, we used a hierarchical approach where simpler models were tested and improved using a subset of the data, before the best scenarios from each simpler model set were combined into a final panarctic model set (Chen & Lou, 2019). These model sets were as follows:

1. Global models exploring the divergences of the three main genetic groups (Nana, Exilis, and Glandulosa), excluding individuals identified as admixed.
2. Regional models for Eurasia and America including intraspecific divergences and admixture events.
3. Global models combining scenarios from the regional models, with additional population events between the Eurasia and America.

DIYABC populations were defined based on ancestral populations inferred from ADMIXTURE results (see **Appendix S4.5** for population assignment method). To differentiate between taxonomic species and ancestral/DIYABC populations, subspecies were referred to in italics, while ancestral/DIYABC populations were in regular text and capitalised. Scenarios were developed based on the population genetic structuring analyses and were also informed by glacial and postglacial histories of *B. nana* inferred from previous phylogeographical analysis (Eidesen et al., 2015). For each scenario, the following parameters were specified: (i) populations, (ii) topology (including divergence, admixture, and bottleneck events), (iii) prior time ranges for events, and (iv) prior ranges for effective population sizes (N_e) and bottleneck magnitude. Secondary contact events were coded as discrete periods of unidirectional (introgression) or bidirectional gene flow (admixture) between populations. MAF was set to 0.25. See **Appendix S4.6 (Figures S5-S22)** for details on model sets and scenarios and **Table S4.4** for model specification of the final global model used for parameter estimation.

4.5.7 Testing demographic scenarios

Within each model set, genetic data were simulated under the different evolutionary scenarios using a population genetic simulator, summarised by a large set of statistics, which were then compared to the observed genetic data statistics. We used DIYABC Random Forest v1.0 for ABC analyses in combination with supervised machine learning based on Random Forests (RF) (Collin et al., 2021) for model classification (model selection) and parameter estimation. For each model set, we generated 10,000 simulated genetic datasets, drawing parameter values from the prior distributions. The number of trees for model selection and parameter estimation was fixed to 500 to ensure stable estimation of the global error rate. Otherwise, default software parameters were used.

For each model set, scenarios were evaluated using Random Forest classification. The best-performing scenarios were selected based on model error rates and on visual assessment of overlap between simulated and observed data when projected on linear discriminant analysis (LDA) axes. LDA also indicated how well RF classification could discriminate among scenarios within a model set and identified poorly specified scenarios and helped to refine prior ranges for new iterations of the model sets. The best-performing scenarios were iteratively improved and tested until a final set of models was produced in which local model error rate was

reduced to approximately 20% or less (see Table 1 Collin et al., 2021), complete overlap occurred between simulated and observed data, and posterior probabilities were above 65% (Collin et al., 2021). See **Appendix S4.6** for LDA projections, **Table S4.5** for model error rates, and **Table S4.6** for posterior probabilities of all model sets.

4.5.8 Population history parameter estimation

The most plausible evolutionary scenario with the highest posterior probability was selected from the final global model set, and divergence and admixture time parameters were estimated. We conducted independent RF treatments for each parameter of interest. The training sets included ~25,000 datasets per scenario for parameter estimation (100,000 datasets/four scenarios). Point estimates and 95% credible intervals were calculated along with global and local accuracy metrics.

Estimates were converted from number of generations to calendar years, assuming a generation time between 10 and 14 years (Borrell et al., 2018). Inferring generation time is challenging in woody plant species such as the dwarf birches due to their longevity, vegetative reproduction, generational overlap, and variable age of maturity depending on environmental conditions (Tsuda et al., 2017). An average generation time was approximated using the colonisation date of first occurrence of *Betula* pollen in Scotland inferred from the pollen record from the Neotoma database (Bartley, 2019; Bartley & Morgan, 1990; Fyfe et al., 2009; Giesecke et al., 2014; Williams et al., 2018), which was divided by the number of generations estimated for a Scandinavian-British population divergence in a previous study of *B. nana* demographic history using RADseq data (Borrell et al., 2018).

Calculating generation time using pollen records could be affected by lower-resolution time scales and uncertainties in colonisation timing due to long-distance dispersal of pollen (Parducci et al., 2015). However, there are also uncertainties in estimating generation time directly from observations because of vegetative growth and reduced sexual reproduction in unfavourable environments (de Groot, 1997), leading to difficulties in estimating age of first seed reproduction, i.e. generation time. For example, based on ring-width analysis, one study in northeast Siberia found that dwarf birch ramets (clones/individuals belonging to the same genet, or genetic parent individual) were typically established 20 - 50 years ago (Li et al., 2015), while another study found stems up to 147 years of age in Greenland (Miller, 1975). Genet

turnover is likely also slower than mean ramet turnover, leading to a potentially much longer generation time.

SNPs do not require mutation model parameterisation (Collin et al., 2021), but this means that population event timings are not calibrated by mutation parameters. Ratios of time divided by effective population size can therefore be estimated, although point estimates and confidence intervals are more difficult to interpret biologically. Consequently, raw parameters are often used (Bernos et al., 2023; Huanel et al., 2022; Kozhar et al., 2022; McDevitt et al., 2022; Pless et al., 2022; Senczuk et al., 2021; Strumia et al., 2021). We estimated both types of parameters and found local posterior RMSE estimates to be lower in raw parameters. hence, results from raw parameters are presented.

4.5.9 Comparison with paleoclimate and paleoenvironmental data

Median estimates of the timing of key demographic events from the best performing model were compared to global and regional Quaternary ice sheet reconstructions to infer spatiotemporal correspondence with potential climatic drivers (Batchelor et al., 2019; Dalton et al., 2020, 2022; Hughes et al., 2016). Best estimates of ice sheet coverage at dated time intervals were derived from empirical (geochronological, stratigraphic, geomorphological) and numerical data (modelling output). The global reconstruction consisted of 17 time slices spanning the pre-Quaternary ~3.2 million years ago (mya) to the Last Glacial Maximum (LGM), with ice sheet coverage in the early Quaternary and in regions such as northeast Asia less well-constrained. Higher temporal resolution reconstructions were available from 115-25 thousand years ago (ka) (5 ka intervals) and 25-6 ka (0.1-0.7 ka intervals) for the Laurentide and Innuitian ice sheets in North America (Dalton et al., 2020, 2022), although reconstructions were more loosely constrained prior to 45 ka (Dalton et al., 2022). Reconstructions of the Eurasian Ice Sheet were available from 25-10 ka (10 ka intervals) and 40-25 ka (four intervals) (Hughes et al., 2016).

As dwarf birch populations span Eurasia and America, the Beringian Land Bridge (BLB) may have influenced dispersal and population connectivity. Therefore, we obtained estimated dates of BLB Quaternary emergences based on geophysical and sediment records and geochemical proxies (Farmer et al., 2023; Jakobsson et al., 2017; Kender et al., 2018). We also

compared the Svalbard divergence date to dates of first occurrence of *B. nana* in Svalbard inferred from sedimentary DNA (sedaDNA) (Alsos et al., 2016).

4.6 Results

4.6.1 RADseq SNP discovery

A total of 419,484,325 reads were generated from four single-end Illumina HiSeq lanes, of which 91.33% passed quality controls. After merging duplicates, six individuals were removed due to anomalously low or high coverage. The number of reads per individual ranged from 351,332 to 3,596,943, with a mean of 1,126,061. Across all individuals, 87.7% of reads successfully mapped to the *B. nana* reference genome, with 71.7% retained with a mapping quality > 10. We genotyped 218 individuals from 43 sampling sites (**Figure 4.1**). Mean effective per-sample coverage after gstacks was 346 x (min 99.7, max 1031). For the final global dataset, a threshold of 70% presence and a MAF of 0.01 resulted in 2180 loci. 74.5% of loci were phased into haplotypes and contained 7528 variant sites, of which 3830 were unlinked. The single SNP dataset contained 1744 variant sites of which 1041 were unlinked.

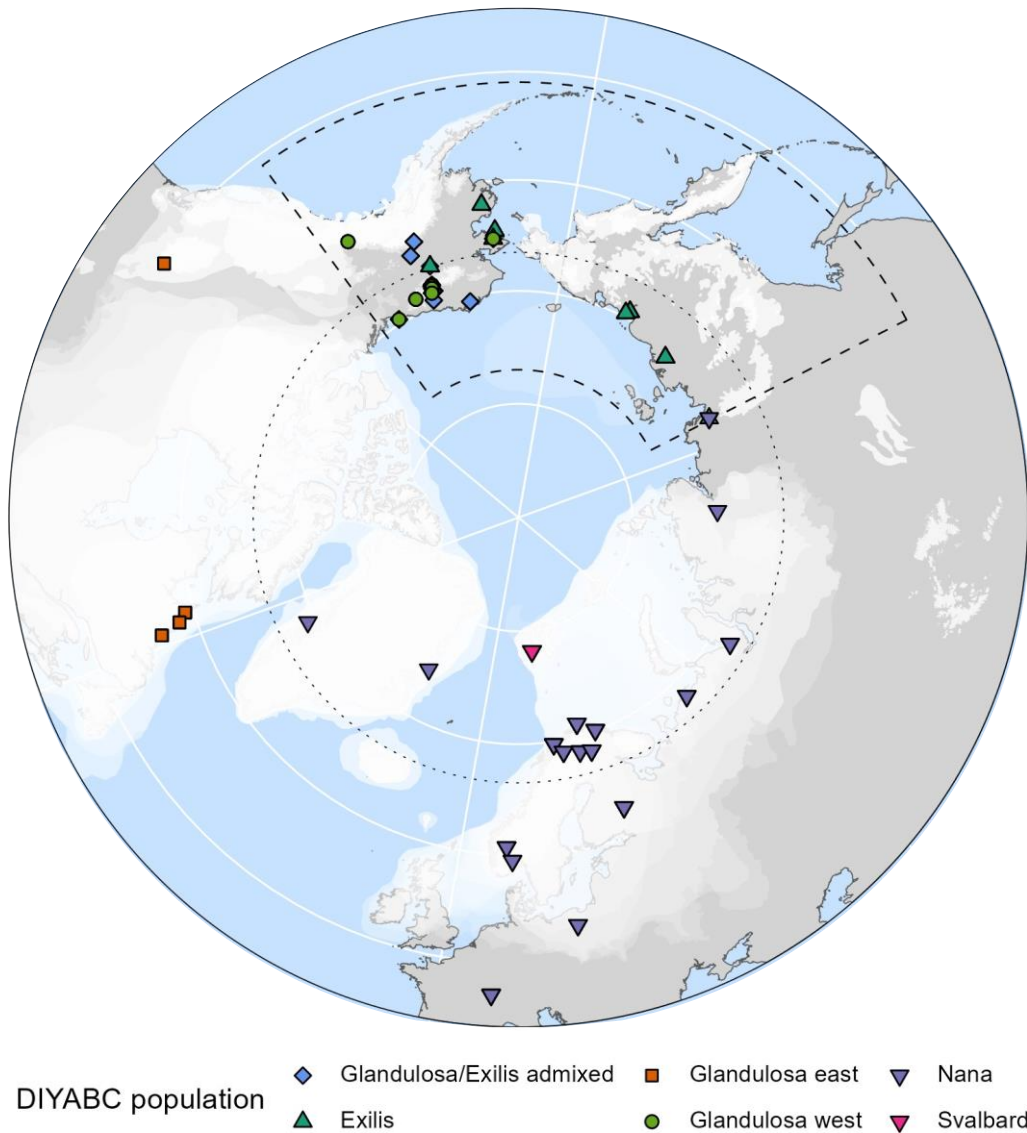


Figure 4.1. Dwarf birch sampling sites and Quaternary ice sheet history. Map of dwarf birch sampling sites ($n=43$) coloured according to populations used in approximate Bayesian computation (ABC) modelling with DIYABC RF (Collin 2021). Two populations that were geographically overlapping in the River Lena area were assigned to different populations: Exilis and Glandulosa. Populations were assigned using ancestral group coefficients from ADMIXTURE analysis. To differentiate between taxonomic species and DIYABC populations, subspecies are referred to in *italics*, while DIYABC populations in regular text are capitalised. Ice sheet “intensity” plotted in white shows relative amount of time that regions were covered by ice sheets during the Quaternary. Intensity was produced by overlaying best-estimated ice sheet reconstructions (Batchelor et al., 2019; Dalton et al., 2020, 2022; Hughes et al., 2016). The earliest period (1.78 - 2.6 million years ago) is omitted because of the broad timespans and high uncertainty of these reconstructions (Batchelor et al 2019). The refugium of Beringia (Hultén, 1937) is outlined with a dotted line. See **Figure S4.2** for a detailed map of Alaskan populations.

4.6.2 Global and regional population genetic structure

Global ADMIXTURE and RADPAINTER analyses identified three ancestral populations, corresponding to *B. glandulosa* in North America and two *B. nana* populations. One *B. nana* population occurred in western Eurasia and another in eastern Eurasia and Alaska (**Figure 4.2A, 4.3, 4.4**). This is congruent with previous phylogeographical and taxonomic work identifying eastern and western *B. nana* groups, corresponding to two often recognised subspecies: *B. nana* ssp. *nana* (Suk.) Hult. and *B. nana* ssp. *exilis* (Suk.) Hult. (Eidesen et al., 2015; Elven et al., 2011; Hultén et al., 1986). Hereafter, the three ancestral populations are referred to as “Glandulosa”, “Nana”, and “Exilis”. Nana and Glandulosa were genetically distinct, but many individuals in dwarf birch populations in Alaska were admixed between Exilis and Glandulosa (**Figure 4.2A**) and shared closer co-ancestry with individuals from other populations, suggesting extensive hybridisation has occurred (**Figure 4.3**).

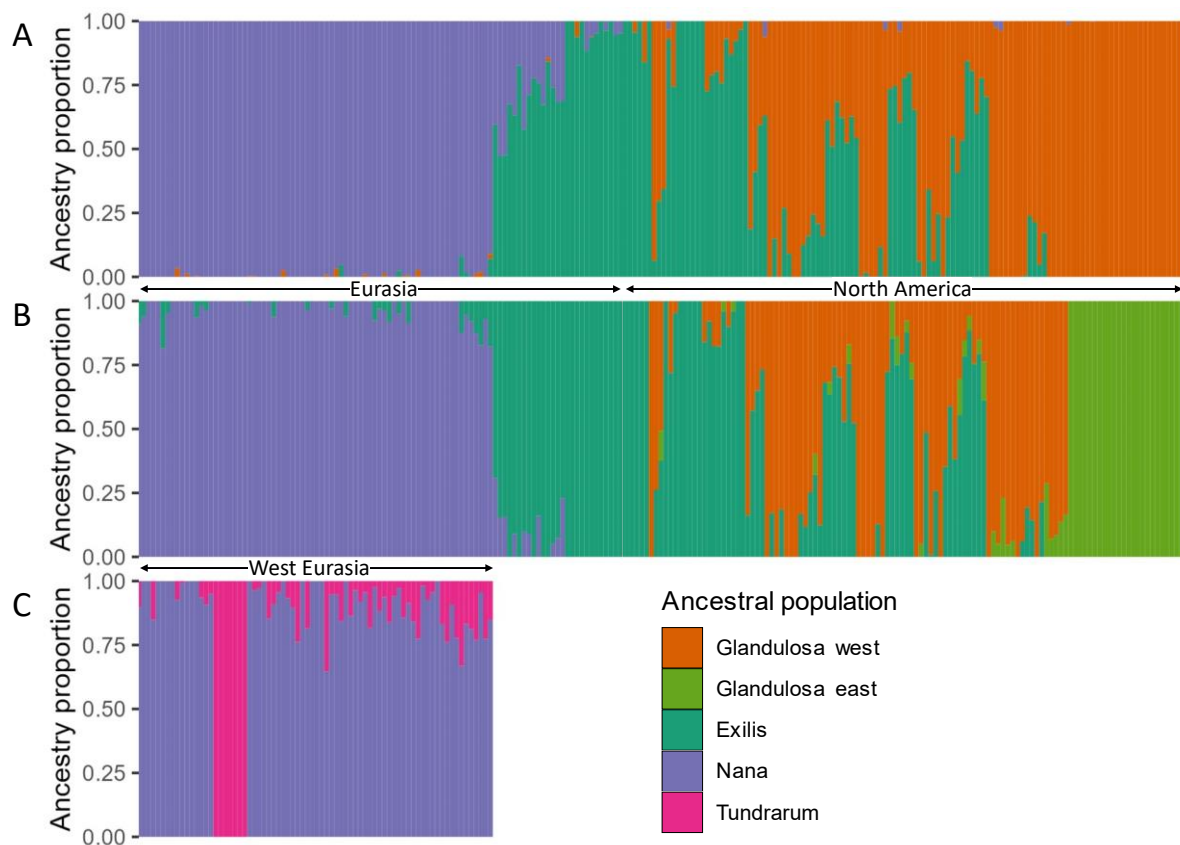


Figure 4.2. Dwarf birch ancestry proportions inferred from hierarchical ADMIXTURE analysis (Alexander et al 2008; 2011). Ancestry proportions are displayed for each individual and arranged by longitude. Colours represent the optimal number (lowest cross validation error) of proposed ancestral populations (K). Separate analyses were run for (A) the global dataset

with 1041 SNPs ($K = 3$), (B) Eurasia with 1072 SNPs ($K = 2$), America with 864 SNPs ($K = 3$), and (C) western Eurasia with 1040 SNPs ($K = 2$).

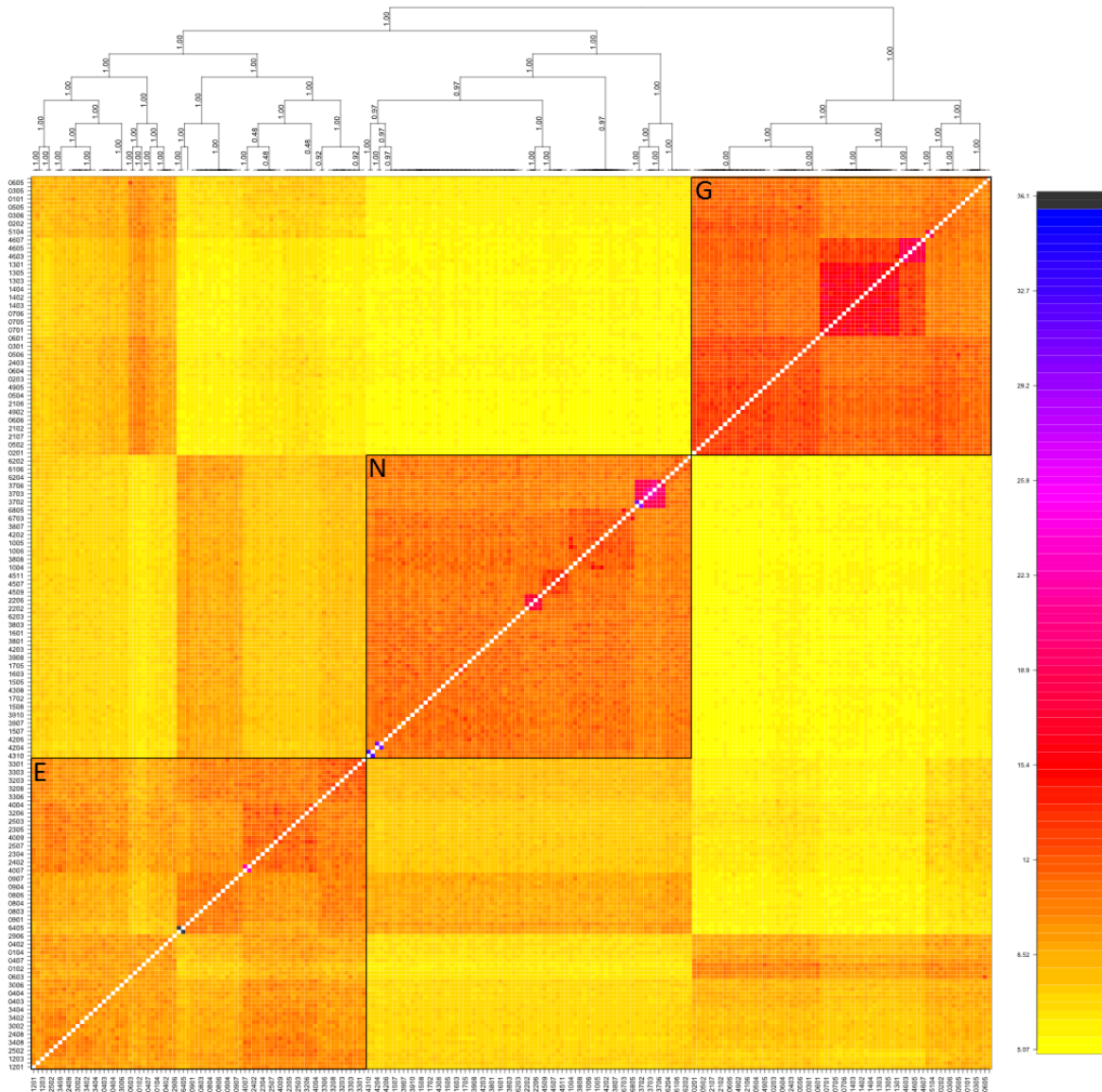


Figure 4.3. Global dwarf birch population genetic structure inferred from RADPainter. Coancestry matrix summarising nearest neighbour haplotype relationships between 218 individuals inferred from linkage structure derived from 3830 SNPs. Red and yellow cell colours indicate a higher and lower degree of coancestry, respectively. Matrix clustered according to fineRADstructure population relationships using a Markov chain Monte Carlo (MCMC) clustering algorithm. Discrete blocks of high coancestry represent a population where individuals are genetically indistinguishable from each other and different from other populations, while interpopulation coancestry indicates interpopulation gene flow and admixture (Malinsky et al., 2018). Regional RADPainter analyses were also conducted (**Figures S4.2, S4.3**). Proposed genetic groups marked with letters: E = Exilis, N = Nana, G = Glandulosa.

The first axis in the PCA which summarised linear combinations of SNP genetic variation showed Exilis and Glandulosa individuals arranged along a cline of genetic differentiation, with individuals in some sites in southwest Alaska more similar to those in sites in the Russian Far East than those in other sites in Alaska. In comparison, Nana and Exilis were genetically distinct except for two individuals (**Figure 4.4**). However, in the ADMIXTURE plot apparent gene flow from Nana to Exilis was also visible in a cline of admixed populations from the Lena River eastwards to the Kolyma River (**Figure 4.2A**).

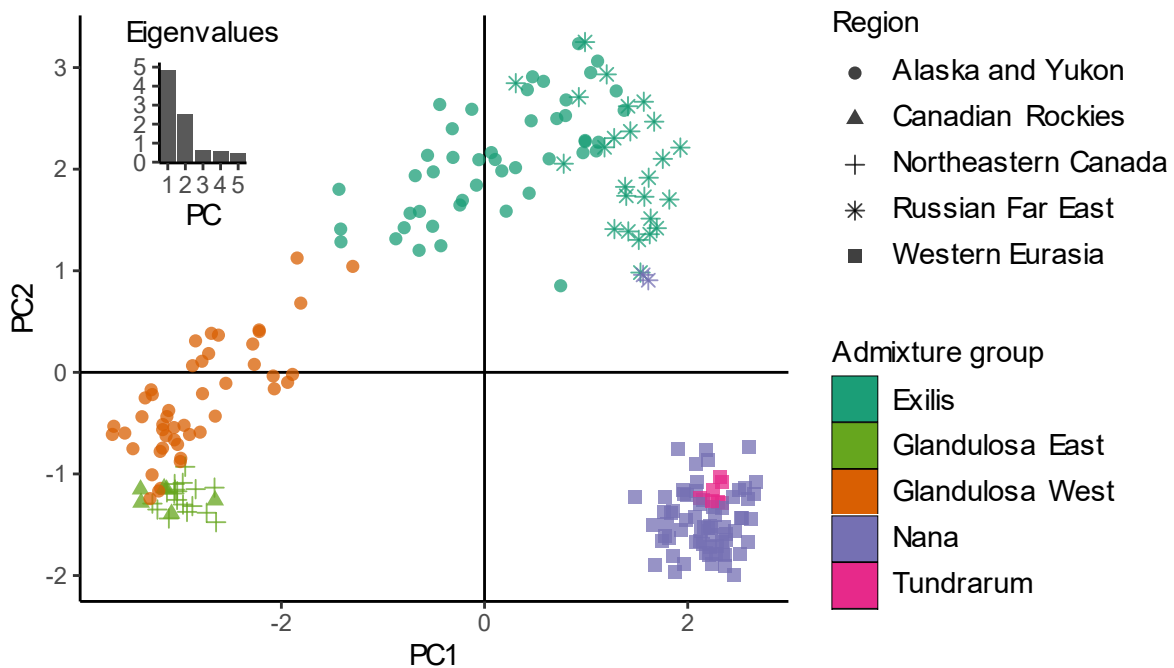


Figure 4.4. Ordination plot summarising genetic variation in SNPs among dwarf birch individuals ($n = 218$). Principal component analysis (PCA) with colours corresponding to ADMIXTURE ancestral groups and shapes corresponding to sampling region. The first two PCs summarising linear combinations of genetic variation (1001 SNPs) are plotted (with 21.5% of variance explained), with a scree plot of eigenvalues for each principal component (inset).

Finer-scale population structure was evident in the regional ADMIXTURE and RADPAINTER results. The regional North American results suggested two ancestral Glandulosa populations: a western Glandulosa group in present-day Alaska and the Yukon, and an eastern Glandulosa group consisting of two distinct populations in the Canadian Rockies and Labrador (**Figure 4.2B**, **Figure S4.3**). The eastern group may be distributed across continental Canada, as populations sampled from Yellowknife, NWT (excluded from further analyses due to potential

hybridisation with another *Betula* species) appeared to contain eastern Glandulosa ancestry. A small proportion of ancestry from eastern Glandulosa was present in eastern Alaskan populations that were predominantly western Glandulosa (**Figure 4.2B**).

The Eurasian ADMIXTURE analysis suggested differing patterns for Nana–Exilis admixture. Admixed populations occurred in the Taimyr Peninsula east of the Lena River, while admixture eastwards extended only to the Yana-Indigirka Lowlands. This transition corresponds to a previously inferred area of range overlap (Hultén et al., 1986). However, ADMIXTURE analysis of western Eurasian populations suggested that Exilis ancestry in western Eurasia consisted of another ancestral population that tended to increase in proportion from northeast Fennoscandia towards eastwards western Siberia (**Figure 4.2C**). This population likely corresponds to a west Siberian group identified in previous genetic analyses (Alsos et al., 2007; Eidesen et al., 2015) and described as *Betula nana* var. *tundrarum* Perfil. (Elven et al., 2011). The Svalbard population was dominated by this group (**Figure 4.2C**), which is referred to as “Tundrarum” hereafter. Previous analyses have identified the Svalbard population as genetically most similar to northwest Russian and west Siberian populations (Alsos et al., 2007; Eidesen et al., 2015). Central European refugial populations in the Alps and Poland formed distinct groups (**Figure S4.4**), and southern Norway and Greenland grouped together, similar to a distinct Atlantic *B. nana* subgroup identified with AFLP data (Eidesen et al., 2015).

4.6.3 Demographic history

The final set of global models contained six populations (Exilis, Nana, Svalbard, Glandulosa west, Glandulosa east, and Glandulosa west/Exilis admixed, and one unsampled Tundrarum population) (**Figure S4.18**). In the DIYABC RF analysis, scenario 1 had the highest probability (**Figure 4.5**) and was characterised by admixture and introgression events in Eurasia and North America. The Exilis group was the ancestral population, from which Glandulosa, and later Nana, split. Alternative models with Glandulosa as the ancestral population had lower posterior probability (**Table S4.6**), and a model with Nana as ancestral had simulated data in disagreement from observed data (**Figure S4.22**). Estimates of recent population events were better-constrained than population events occurring earlier in time (**Table S4.7**, **Figure S4.24**). Population sizes were estimated between ~100,000 - 200,000, except for Svalbard, with an estimated population size of ~1000 (**Table S4.8**).

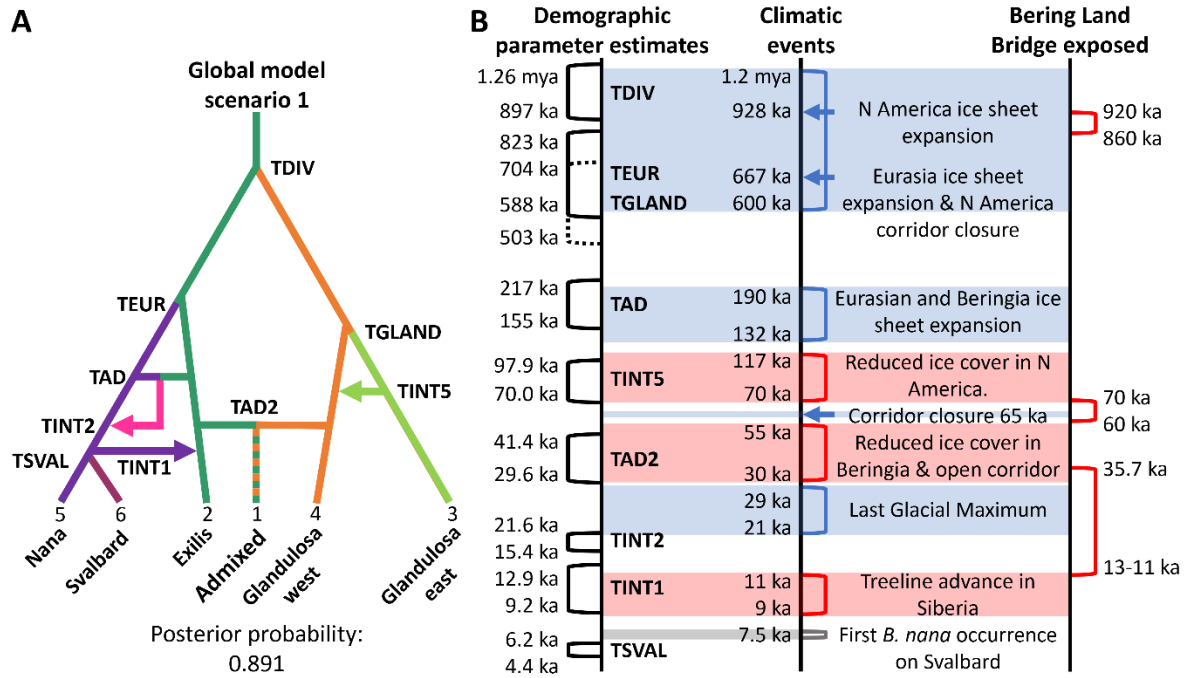


Figure 4.5. Quaternary demographic model of dwarf birch with corresponding climatic and environmental changes. (A) Tree depicting the best supported scenario according to DIYABC RF model choice with a posterior probability of 0.891. Lineage colours correspond to the DIYABC populations Nana, Svalbard, Exilis, Admixed, Glandulosa west, and Glandulosa east, as in Figure 1. (B) The timing of population events from the best supported scenario compared with climatic and environmental changes in the Quaternary inferred from the literature. Population events given as a range between the median estimates calculated using different generation times (10 - 14 years); see Table S4.7 for 95% confidence intervals. Note that time is not to scale.

4.6.4 Comparing demographic history and Quaternary environmental changes

The best supported scenario suggested divergence between Exilis and Glandulosa populations 897 thousand years ago (ka) (median with 10 year generation time, CI 806 ka – 1.15 mya) to 1.2 million years ago (mya) (median with 14 year generation time, CI 1.13 mya – 1.60 mya), coinciding with intensification of glacial conditions during the Mid Pleistocene Transition (1.2 mya – 600 ka). Extensive ice sheets were present in North America from ~928 ka, with a corridor between eastern and western ice sheets (Batchelor et al., 2019).

Divergence between Exilis and Nana populations estimated from 588 ka (CI 278 – 937 ka) to 823 ka (CI 389 ka – 1.31 mya) encompassed varied climate conditions and multiple glacial cycles. A major expansion of northwest Eurasian ice sheets likely capable of separating

Eurasian dwarf birch populations did not occur until 677 ka, when ice sheets also expanded in the uplands of west Beringia; present-day Russia (Batchelor et al., 2019). Divergence between east and west *Glandulosa* populations was estimated between 503 ka (CI 158 – 857 ka) and 704 ka (CI 221 ka – 1.20 mya). The ice-free corridor between the Cordilleran and Laurentide ice sheets was closed between 677 ka and 429 ka (Batchelor et al., 2019), potentially isolating the east *Glandulosa* ancestral population of contemporary southern and eastern Canadian populations from Beringia.

Admixture between *Exilis* and *Nana* populations estimated between 155 ka (CI 97 – 231 ka) and 217 ka (CI 135 – 324 ka) coincided with expansion of ice sheets in northwest Eurasia and western Beringia (Batchelor et al., 2019). The Barents-Kara ice sheet reached its maximum Pleistocene extent over continental Siberia ~190-132 ka, at a time of extensive glaciation in the west Beringian uplands (Batchelor et al., 2019). This admixture was supported over scenarios without admixture and scenarios with unidirectional gene flow from *Exilis* to *Nana* (**Figure S4.7, Figure S4.8**). This admixture event resulted in an unsampled *Tundrarum* population, which remained isolated in a separate refugium until the postglacial period. The existence of this distinct admixed group located in a separate west Siberian refugium, and the source of present-day west Siberian populations, was previously hypothesised based on AFLP markers (Eidesen et al., 2015) and is supported by dwarf birch pollen in Lake Taymyr during the LGM (Andreev et al., 2002).

The best supported scenario also estimated that gene flow occurred from the east to west *Glandulosa* population between 70.0 ka (CI 28.2 – 151.5 ka) and 97.9 ka (39.5 – 212 ka), coinciding with a period of much reduced ice cover in North America, potentially allowing connectivity between continental America and Beringia (Dalton et al., 2022). Admixture between *Exilis* and the west *Glandulosa* populations estimated between 29.6 ka (CI 6.47 – 56.2 ka) and 41.4 ka (CI 9.06 – 91.2 ka) coincided with an opening of the ice corridor between the Cordilleran and Laurentide ice sheets and ice sheet retreat from the Yukon and Brooks Range ~55-30 ka (Batchelor et al., 2019; Dalton et al., 2020). During this period (Marine Interstadial 3), conditions in Beringia were similar to the present, with temperatures 1-2°C lower and spruce forest present in interior Alaska and the Yukon (Miller et al., 2010).

The *Tundrarum*-*Nana* admixture estimated between 15.4 (CI 6.06 – 23.2 ka) and 21.6 ka (CI 8.48 – 32.44 ka) coincided with the initial retreat of the Eurasian Ice Sheet complex after the

LGM (~21-23 ka in Eurasia) (Hughes et al., 2016), suggesting secondary contact between populations during range expansions. *Betula nana* macrofossils were present in periglacial sites along the edges of the Eurasian ice sheet during this time period, with *Betula* macrofossils occurring in the Taymyr Peninsula from 19.4 ka (Binney et al., 2009) and *Betula* sedaDNA in the Polar Urals from ~15 ka onwards (Bjune et al., 2022; Clarke et al., 2020). Gene flow from Nana to Exilis was estimated to have occurred in the early Holocene between 9.2 ka (CI 1.43 – 20.0 ka) and 12.9 ka (CI 2.00 – 27.9 ka) and may represent eastward Nana expansion to the Lena River and beyond, where some contemporary Exilis populations contain ancestry (**Figure 4.2**).

The Svalbard population in the best supported model was derived from the Nana population after the Nana-Tundrarum admixture event, supporting previous genetic data which found Svalbard was predominantly colonised from northwestern Russia (Alsos et al., 2007, 2015). The divergence was estimated to occur in the mid-Holocene between 4.4 ka (CI 0.908 – 7.04 ka) and 6.2 ka (CI 1.27 – 9.86). The first occurrence of *B. nana* in Svalbard inferred from sedaDNA is at 7.5 ka, during a period of milder and wetter conditions (Bilt et al., 2019; Mangerud & Svendsen, 2018; Voldstad et al., 2020) which seem to have been suitable for colonisation, establishment, and population growth beyond the restricted distribution in which *B. nana* is found in Svalbard today (Alsos et al., 2002, 2016).

Pollen records suggest that *B. nana* underwent range contraction and population bottlenecks during the late Holocene cooling in Svalbard (Alsos et al., 2015, 2016; Birkeland et al., 2017). Our models were unable to differentiate between scenarios with and without a late Holocene population bottleneck (**model set 8.5: Figure S4.9, Figure S4.10, Table S4.6**). However, a strong population bottleneck and associated loss in genetic variation (Nei et al., 1975) can cause a more recent apparent coalescence of lineages compared with neutral expectations (Gattepaille et al., 2013). Previous studies have found low genetic diversity in Svalbard populations (Alsos et al., 2002; 2007; Eidesen et al., 2015), and in our study Svalbard population genetic diversity was relatively low compared to the global means, although possibly inflated as we grouped two populations several kilometres apart (**Table S4.3**). The population divergence date may therefore reflect the climate-related bottleneck, rather than initial colonisation.

4.7 Discussion

Our best supported coalescent model indicate the temporal correspondence of multiple population divergences and admixture events with climatic and ice sheet changes. This suggests that glacial cycles may have influenced dwarf birch population dynamics. However, the response of the dwarf birches to past climate change appears to be more complex than a simple glacial isolation-interglacial expansion population history, with climate conditions in ice-free areas influencing distribution and associated population connectivity during both glacials and interglacials.

4.7.1 The Mid-Pleistocene origin of the dwarf birch species complex

Our best demographic model supported a divergence between *B. nana* and *B. glandulosa* in the Mid-Pleistocene between 897 ka (CI 806 ka – 1.15 mya) and 1.26 mya (CI 1.13 – 1.60 mya). Macrofossil and pollen records with *B. nana*-type morphology in North Greenland and northeast Russia ~3-2.6 mya show a dwarf birch taxon with a widespread Arctic distribution before the onset of Quaternary glaciations, and a marked increase in pollen abundance with the expansion of the tundra biome ~2.7 mya (Andreev et al., 2014; Bennike & Böcher, 1990). Thus, the onset of glaciations provided new opportunities for dwarf birch expansion, although glacial cycle intensification in the Mid-Pleistocene transition (1.2 mya - 600 ka), with a drastic increase in North American ice sheet cover from ~900 ka, likely isolated dwarf birch in two lineages south and north of the ice sheets, leading to allopatric speciation between *B. nana* and *B. glandulosa*.

Alternatively, *B. nana* may have expanded eastwards into Eurasia with a potential exposure of the Bering Land Bridge between ~920-860 ka (Kender et al., 2018). Regardless, Beringia was the likely source for Pleistocene diversification, as the amphiberian Exilis was ancestral in the best supported model. A Beringian origin of the current dwarf birches was previously suggested based on a shared ancestral pDNA haplotype between *B. nana*, *B. glandulosa*, and *B. pubescens* that is dominant in Beringia. Previous phylogeographic work has also indicated that Beringia was an important source of early Pleistocene dispersals and colonisations for many Arctic plants (Abbott et al., 2000; Abbott & Comes, 2004; Alsos et al., 2005; Eidesen, 2007; Hultén, 1937). The genetic similarities we identified between the Russian Far East and

southwest Alaska further support the importance of the Beringian region as a glacial refugium for dwarf birch (Eidesen et al., 2015).

Intraspecific divergences within *B. nana* and *B. glandulosa* are also estimated to have occurred during the Mid-Pleistocene, from 823-588 ka. Within *B. nana*, the Nana and Exilis populations may have diverged due to westward expansion by Nana into ice-free Eurasian areas, subsequent separation due to expanding ice sheets ~677 ka, and unsuitable climate conditions in ice-free areas (Batchelor et al., 2019). Similarly, closure of the corridor between the Cordilleran and Laurentide ice sheets ~677 ka may have isolated *B. glandulosa* in two separate areas until at least 429 ka (Batchelor et al., 2019), leading to the two distinct genetic groups identified in our study. Continental dwarf birch divergences in the Quaternary therefore appear to be linked to isolation following climate deterioration.

The taxonomy and evolutionary relationships of the dwarf birches have long been unclear (Ashburner & McAllister, 2013; Elven et al., 2011; Hultén et al., 1986). The presence of two major ancestral dwarf birch populations (Exilis and Glandulosa) in North America is counter to recent taxonomic work where *B. nana* ssp. *exilis* is referred to as *B. glandulosa* (Ashburner & McAllister, 2013), although high levels of genetic admixture identified between the two groups in Alaska is in line with the morphological continuum that is observed between the two species in this region (Furrow, 2004).

4.7.2 The complex role of ice sheets in the Quaternary

Unlike population isolation and divergence events, secondary contact and admixture events appear to coincide with both periods of ice sheet retreat and expansion. Admixture between the two Glandulosa groups occurred during a period of much reduced ice cover in North America, suggesting a northwards range shift of the eastern Glandulosa group resulting in secondary contact between the two Glandulosa groups. Similarly, admixture between Exilis and the western Glandulosa group coincided with the reopening of the north-south ice-free corridor and ice sheet retreat within Beringia prior to the LGM (Batchelor et al., 2019), with the west Glandulosa group likely remaining in Beringia during the LGM.

The re-emergence of the Bering Land Bridge from 35.7 ka onwards (Farmer et al., 2023) may have increased population connectivity between Exilis and Glandulosa and within Exilis. Since modern Exilis populations in southwest Alaska are genetically closer to individuals in the

Russian Far East than to other *Exilis* populations in Alaska, intermittent connectivity of the Bering Land Bridge in the Pleistocene appears to have been sufficient to maintain gene flow across Beringia during the Quaternary.

There is a general increasing pattern of *Exilis*/*Glandulosa* admixture eastwards in Alaska: from pure *Exilis* in the unglaciated southwest to *Glandulosa* dominating in the Brooks Range and the Yukon that were glaciated during the LGM (Dalton et al., 2022). Based on these patterns, *B. glandulosa* appears to have been more adept at postglacial colonisation of ice-free land. However, uneven sampling distribution and uncertainties in the LGM locations of *Exilis* and *Glandulosa* genetic groups in Beringia mean that these patterns are difficult to verify. The spatial distribution of *Exilis* and *Glandulosa* in Alaska is indicative of other Arctic plant species where divergent genetic groups co-occur within Alaska (Abbott & Comes, 2004; Jorgensen et al., 2003). It was suggested that these patterns result from different sub-refugia within Beringia (Abbott & Comes, 2004). Systematic sampling across Alaska targeting both *B. nana* and *B. glandulosa* may shed further light on these patterns.

The timing of admixture events between *B. nana* populations in the postglacial period follows the pattern of range expansion from refugia and secondary contact during warmer periods. Previous phylogeographical analysis suggested that *B. nana* in western Eurasia was isolated both south of the Eurasian ice sheet and east in western Siberia (Eidesen et al., 2015), which is supported by our data.

Contrary to other admixture events that occurred during warmer periods, the *Exilis*-*Nana* admixture event was estimated between 154 ka (CI 97 – 231 ka) and 216 ka (CI 136 – 323 ka), during the maximum Quaternary coverage of ice sheets over Siberia and the west Beringian uplands (Batchelor et al., 2019). Ice sheet expansion may have increased the likelihood of secondary contact between geographically separated populations, similarly to caribou glacial introgression events during the last glacial cycle in North America (Taylor et al., 2021). *Nana* and *Exilis* populations may have come into contact by contracting towards the Lena River and Beringean coastal lowlands, where the modern population genetic structure suggests that postglacial admixture between *Nana* and *Exilis* also occurred. Alternatively, the two populations may have both expanded into areas that are currently taiga and so come into contact.

Secondary contact and admixture during both ice retreat and expansion indicates a complex relationship between dwarf birch population dynamics and climate variability. Admixture occurs during periods of climatic transition, rather than during a particular absolute climate state, similarly to admixture events between polar bears (*Ursus maritimus* L.) and brown bears (*Ursus arctos* L.) (Wang et al., 2022).

4.7.3 Dwarf birch as a thermophilous Arctic shrub: population connectivity in ice-free areas

Intermittent connectivity and barriers caused by ice sheets were likely not the only factor affecting the population dynamics of the dwarf birches during the Quaternary. Unsuitable abiotic conditions can be an effective barrier to population establishment (Soberón & Nakamura, 2009). For relatively thermophilic Arctic taxa such as the dwarf birches (Alsos et al., 2002; Crump et al., 2019), cold and dry climatic conditions may have formed as an effective barrier as ice sheets. Although large parts of the north Eurasian continent were not glaciated during glacial periods (Batchelor et al., 2019), a treeless tundra-steppe ecosystem of forbs and graminoids likely dominated, although the prevailing flora is still debated (Clarke et al., 2020 and refs within). Shrubs appear to have been a rare component of this vegetation (Ager & Phillips, 2008; Andreev et al., 2002; Bigelow et al., 2003; Binney et al., 2017; Binney et al., 2009; Müller et al., 2009), suggesting these unglaciated areas may have been too cold and dry to sustain large communities of shrubs and enable connectivity between refugial areas in western Eurasia and Beringia (Anderson & Lozhkin, 2015; Kienast et al., 2001, 2005).

However, ice-free areas in the Eurasian and North American high latitudes during warmer interglacial periods may have also been unsuitable for dwarf birch. For example, tree birches occurred far north of their contemporary limit across northern Eurasia from 11-9 ka (Binney et al., 2009), and the consequently reduced area of tundra habitat may have restricted the distribution of dwarf birch and led to population isolation (Stewart et al., 2010). The postglacial northward retreat of dwarf birch left behind small populations at more southerly latitudes (de Groot et al., 1997; Eidesen et al., 2015; Hultén et al., 1986; Jadwiszczak et al., 2012; Wang et al., 2014). These glacial relict populations (Hampe & Jump, 2011) persist in locally suitable conditions — cryptic refugia — (Stewart et al., 2010), such as cooler mountainous areas. Similarly, remnants of more northerly early Holocene distributions in the

form of clonal populations in Svalbard and Baffin Island—areas currently too cold for sexual reproduction and seed set—shows the species can be isolated by unsuitable climatic conditions (Alsos et al., 2002; Engelskjøn et al., 2003; Hermanutz et al., 1989).

The varying effects of Quaternary glacial cycles on the population dynamics of the dwarf birches shows that the species do not fit the glacial refugial isolation and postglacial expansion model of temperate tree species, often assumed for a wide range of taxa (Hewitt, 2000). Nor do they fit the model of a “true Arctic” species, such as *Dryas octopetala* (L.), that expanded its range in glacials and contracted its range in interglacials (Bennett & Provan, 2008). The dwarf birches instead behave as intermediate taxa, thermophilous from an Arctic (tundra) point of view, but cold-adapted from a boreal/temperate perspective.

Finally, sources of uncertainty exist, both in the climatic data and ice sheet reconstructions (Batchelor et al., 2019; Miller et al., 2010), and in the time estimates derived from coalescent modelling. The challenges of estimating the generation time of the dwarf birches discussed in section 4.5.8. leads to uncertainty in time estimates in number of calendar years. Estimates from two generation times helped to capture some of this uncertainty. The use of known dates of population events inferred from fossil pollen, macrofossil, and sedaDNA records to calibrate population events could help address this issue (Borrell et al., 2018; Tsuda et al., 2017). These sources of uncertainty lead to wide confidence intervals of demographic events. Wider confidence intervals in the earlier Quaternary period population events in our model tended to become narrower in more recent time periods, with confidence intervals calculated from the two generation times overlapping nearly completely. This is similar to the greater uncertainty present in ice sheet reconstructions earlier in the Quaternary period (Batchelor et al., 2019). Therefore, as with any analysis of demographic history and past climate change, our model of the demographic history of the dwarf birches and association with large-scale environmental changes should be interpreted with caution, particularly in the early Quaternary period.

4.8 Conclusions

We inferred the Quaternary population history of the dwarf birches, key Arctic tundra shrubs, by testing alternative evolutionary scenarios. The correspondence between the timing of population events and major ice sheet changes suggests a complex response of the dwarf

birches to past climate change, with ice sheets acting alternately as a barrier or an enabler of population mixing. Early Quaternary inter- and intraspecific divergences appear to be associated with climatic deterioration and extensive ice sheet coverage, suggesting isolation in separate refugia. Later admixture events between these divergent lineages occur during periods of climatic transition and are independent of absolute climate state. Rapid variability between climatic extremes was therefore a key feature that drove the generation of genetic diversity in the Quaternary (Brochmann & Brysting, 2008).

Evidence from the pollen records of the last glacial period and from the distribution of the dwarf birches in the current interglacial suggests that the climate and ecological conditions in ice-free areas are also likely important mediators of population connectivity. Dwarf birches do not appear to follow a simple refugial isolation-postglacial expansion model, which raises further questions about their eco-evolutionary responses to present and future climate change (Mekonnen et al., 2021).

Taking the uncertainties inherent in the reconstruction and modelling of past populations and *lgclimate* into account, the correspondence of multiple population events with multiple climatic events is indicative of an important role of the Quaternary glacial cycles in influencing the evolution and population dynamics of the dwarf birches.

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4.10 Data accessibility and benefit-sharing

The genetic data for this study have been deposited in the European Nucleotide Archive (ENA) at EMBL-EBI under accession number PRJEB67938. Data derived from NHMO samples are published for non-commercial use only. Utilization by third parties for purposes other than non-commercial scientific research may infringe the conditions under which the genetic

resources were originally accessed and should not be undertaken without contacting the corresponding author of the paper and/or seeking permission from the original provider of the genetic material.

Data were obtained from the Neotoma Paleoecology Database (<http://www.neotomadb.org>) and its constituent database the European Pollen Database. The work of data contributors, data stewards, and the Neotoma community is gratefully acknowledged.

The ice sheet data that support the findings of this study are available at identifiers [10.17605/OSF.IO/7JEN3](https://doi.org/10.17605/OSF.IO/7JEN3), <https://doi.org/10.1016/j.quascirev.2020.106223>, <https://doi.org/10.1016/j.earscirev.2021.103875>.

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4.12 Molecular footprints of Quaternary climate fluctuations in the circumpolar tundra shrub dwarf birch: Supplementary information

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Appendix S4.1: Sampling and storage details

Where possible, individuals were sampled along three transects of approximately 100 metres in length. Transects were evenly spaced across the area with a minimum distance of 10 metres between the transects. Twig and leaf samples were collected from up to 30 individuals. GPS coordinates were obtained for each site. Samples were dried in silica gel, drying ovens, or air-dried, and stored in plastic zip lock bags, or paper bags/envelopes. Samples were shipped to the UK and stored in a 4-8°C cold room until processing in 2021. Sixty sites were selected for DNA extraction on the basis of tissue quantity and quality. For each NHMO DNA bank site, samples were collected 25 meters apart along a 250 metre transect and dried in silica gel.

Table S4.1. Dwarf birch sampling site collection metadata. Sites which were used in the Eidesen et al. (2015) study are marked with * and for these populations the Site ID column includes the population name from the original study. Samples for these populations were provided with permission of the NHMO DNA Bank at the Natural History Museum, University of Oslo. Sample IDs available from the author (mariaemilyd@gmail.com) upon request.

Site ID	Taxon (field ID)	Country	Region	Locality	Collection year	Collector	Latitude (decimal degrees)	Longitude (decimal degrees)	Number of individuals sequenced	Used in analysis
BN01	<i>B. nana</i>	USA	Alaska	Itkillik	2015	DA	68.6422	-149.64	4	Y
BN02	<i>B. nana</i>	USA	Alaska	Chandalar	2015	DA	68.0678	-149.599	6	Y
BN03	<i>B. nana</i>	USA	Alaska	Dalton Mountain	2015	DA	68.1719	-149.44	6	Y
BN04	<i>B. nana</i>	USA	Alaska	Kuparuk River	2015	DA	68.6486	-149.403	7	Y
BN05	<i>B. nana</i>	USA	Alaska	Roche Mountonee	2015	DA	68.3747	-149.313	6	Y
BN06	<i>B. nana</i>	USA	Alaska	Bunny Haven	2015	DA	68.7657	-148.9	6	Y
BN07	<i>B. nana</i>	Canada	Labrador	Komaktorvik River	2015	DM; LH	59.204	-64.0985	6	Y
BN08	<i>B. nana</i>	Russia	Sakha	Kytalyk1	2015	GSS; RS	70.8284	147.4703	6	Y
BN09	<i>B. nana</i>	Russia	Sakha	Kytalyk2	2015	GSS; RS	70.831	147.4746	6	Y
BN10	<i>B. nana</i>	Norway	Viken	Hol	2015	JDMS	60.7052	7.9355	6	Y
BN12	<i>B. nana</i>	USA	USA	Atqasuk	2015	JP; SW	70.4833	-157.417	4	Y
BN13	<i>B. nana</i>	Canada	Labrador	Torngats Basecamp	2015	LH	58.4581	-62.8087	6	Y
BN14	<i>B. nana</i>	Canada	Labrador	Nain	2015	LH	56.5439	-61.6993	6	Y
BN15	<i>B. nana</i>	Finland	Lapland	Näkkälä	2015	MMF	68.641	24.7725	5	Y
BN16	<i>B. nana</i>	Norway	Finnmark	Nordkapp	2015	MMF	71.1087	25.7973	6	Y
BN17	<i>B. nana</i>	Finland	Lapland	Saariselkä	2015	MMF	68.4352	27.4351	6	Y
BN18	<i>B. humilis</i>	Russia	Urals	Nurgush Mountain	2015	MG; MW	54.8296	59.1588	6	Y

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BN21	<i>B. nana</i>	USA	Alaska	East Fork Chandalar River	2015	MW	68.71	-144.825	6	Y
BN22	<i>B. nana</i>	Poland	Kujawsko-Pomorskie	Linje	2015	MS	53.1876	18.3096	4	N
BN23	<i>B. nana</i>	USA	Alaska	Nome	2015	ML	64.508	-165.297	5	Y
BN24	<i>B. nana</i>	USA	Alaska	Kuzitin	2015	ML	65.2293	-164.827	6	Y
BN25	<i>B. nana</i>	USA	Alaska	Old Man	2015	ML	66.4501	-150.619	5	Y
BN29	<i>B. nana</i>	USA	Alaska	SAG	2015	ML	69.4254	-148.697	3	Y
BN30	<i>B. nana</i>	USA	Alaska	Fox	2015	ML	64.9506	-147.618	6	Y
BN31	<i>B. nana subsp exilis</i>	Russia	Sakha	Chersky	2015	ML	68.7521	161.4686	6	N
BN32	<i>B. nana subsp exilis</i>	Russia	Sakha	Krutaya Drisva	2015	ML	69.3452	161.5314	6	Y
BN33	<i>B. nana subsp exilis</i>	Russia	Sakha	Ambarchik	2015	ML	69.6215	162.3131	6	Y
BN34	<i>B. nana</i>	USA	Alaska	Healy	2015	ML	63.8782	-149.253	6	Y
BN37	<i>B. nana</i>	Svalbard	Norway	Endalen & Janssonhaugen	2015	SRK	78.1868	15.7632	7	Y
BN38	<i>B. nana</i>	Norway	Troms	Kvaløya	2015	SRK	69.759	18.8524	6	Y
BN39	<i>B. nana</i>	Norway	Finmark	Vadsø	2015	SRK	70.0712	29.8731	5	Y
BN40	<i>B. nana</i>	USA	Alaska	St. Mary's	2015	SN	62.0555	-163.259	6	Y
BN42	<i>B. nana ?</i>	Finland	Lapland	Kilpisjärvi	2015	TK	68.9441	20.9116	6	Y
BN43	<i>B. nana</i>	Finland	Karjala	Joensuu	2015	TK	62.6691	30.017	6	Y
BN44	<i>B. nana</i>	Norway	Telemark	Lifjeld	2015	TTH	59.486	8.998	2	Y
BN45	<i>B. nana</i>	Switzerland	Neuchâtel	Les Ponts-de-Martel	2015	CR	46.9842	6.7167	6	Y
BN46	<i>B.</i>	Canada	British	Og Lake	2015	MMF	50.9516	-115.635	6	Y

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	<i>glandulosa</i>		Columbia							
BN47	<i>B. nana</i>	Russia	Sakha	Rodinka Mountain	2016	TK	68.7337	161.5375	6	N
BN49	<i>B. glandulosa</i>	Canada	Yukon Territories	Kluane - Pika Valley	2015	JA	61.22145	-138.286	6	Y
BN51	<i>B. nana</i>	Canada	Yukon Territories	QHI - Hawk Valley	2015	JA	69.58539	-138.922	6	Y
BN54	<i>B. glandulosa</i>	Canada	Northwest Territories	Yellowknife - Bog	2015	HT	62.45721	-114.533	5	N
BN55	<i>B. glandulosa</i>	Canada	Northwest Territories	Yellowknife - Site 2	2015	HT	62.69975	-116.131	3	N
BN61	<i>B. nana</i>	Russia	Yamal	Erkuta Tundra Monitoring site	2021	MSp	68.239	69.142	4	Y
BN62* AK-3213	<i>B. nana</i>	Russia	Nenetsky AO	Malozemel'skaya tundra. Nenetskaya Gryada, Korovinskaya Guba; 5.5-8 km W Cape Seduysky Nos, c. 0-3 km W to NW the shore	2004	DE	68.336	53.3	3	Y
BN63* AK-3506	<i>B. nana</i>	Russia	Taimyrsky AO	Ary-Mas nature reserve, (c. 50-60 km NNW Khatanga), right riverside of Novaya, along the river and up	2004	PS; AT	72.46444	101.8636	1	Y

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				to c. 3 km S of river						
BN64* AK-3885	<i>B. nana</i> <i>subsp</i> <i>exilis</i>	Russia	Yakutia	Lena R. west bank: Chekurovka village, surroundings of settlement	2004	HS; RE	71.04833	127.5233	3	Y
BN67* AK-1241	<i>B. nana</i>	Greenland	Qeqertarsuaq (Disko), Qeqertalik	5-10 km from Arctic Station (coordinates are for station)	2003	BJG; GB	69.25	-53.5667	1	Y
BN68* AK-125	<i>B. nana</i>	Greenland	Zackenberg	South of the landingstrip close to "Kjovedammen" and "Teltdammen".	2002	KA	74.46667	-20.55	1	Y

Appendix S4.2: Hybrid populations

Initial analyses identified four sampling locations as potential hybrid populations with additional, unidentified *Betula* species: two *B. glandulosa* sampling locations near Yellowknife, NWT (BN54, BN55) and two *B. nana* sampling locations near Chersky, Sakha Republic (BN37, BN41). Collection metadata had indicated that these individuals may be hybrids due to their large morphology. Furthermore, populations had a substantial proportion of missing SNP data (~25% compared with ~5% in other populations). Finally, ADMIXTURE (Alexander et al., 2009; Alexander & Lange, 2011) analyses including individuals from the similar species *B. humilis* Schrank. indicated four ancestral groups (K=4), with the four sampling sites containing a substantial proportion of ancestry from the same ancestral group as *B. humilis* (**Figure S4.1**). As these sites were spread across two continents outside the range of *B. humilis*, we hypothesised that different birch species were likely contributing to the hybridisation process in each location, and that the ADMIXTURE results identified these groups as the most divergent from others so grouped them together. SNP genotyping and filtering steps was repeated without these sampling sites as they would have reduced the number of SNPs genotyped and filtered, and they were excluded from further analyses.

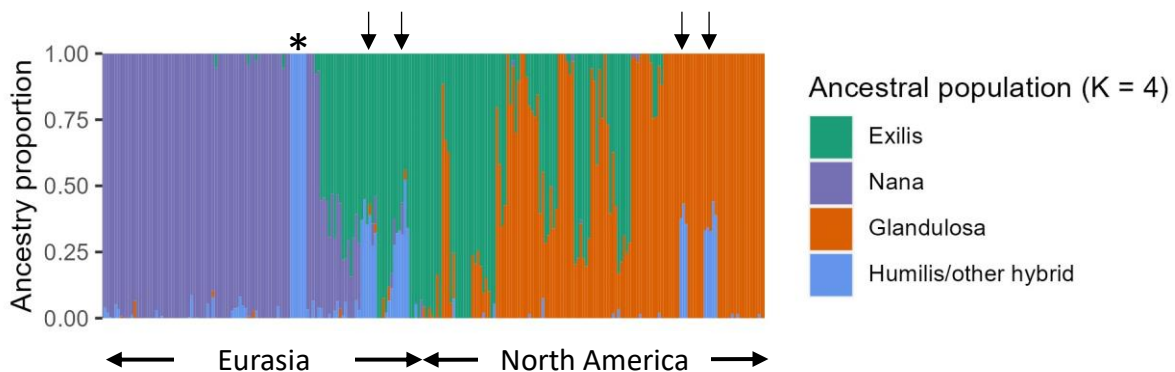


Figure S4.1. Population genetic structure inferred from ADMIXTURE analysis including potential hybrid populations (Alexander et al., 2009; 2011). Colour corresponds to the optimal number (lowest cross validation error) of proposed ancestral groups (K), with each dwarf birch individual plotted by longitude, represented by bars with total ancestry proportions. *Betula humilis* population (BN18) marked with asterisk (*). Potential hybrid populations marked with arrows, from left to right: BN31, BN47, BN54, BN55.

Appendix S4.3: Two-stage SNP filtering

First stage

Loci were filtered with sampling locations treated as populations, except for the two Svalbard populations as they were both within the Adventdalen area (~13 km distant) which were merged due to the low number of samples per population. To minimise missing data, population filters were applied. Loci were retained that were present in 70% of individuals within a population, or present in 70% of individuals across populations. SNPs with a minor allele frequency (MAF) of <0.01 (SNPs where >99% of individuals share the same allele) were excluded to remove uninformative markers. The Populations module of Stacks v2.60

(Catchen et al., 2011, 2013; Rochette et al., 2019) can output phased haplotypes with multiple SNPs per locus, from which population estimates of expected heterozygosity (gene diversity) were extracted. Populations output was also exported taking the first SNP per locus as downstream analyses (ADMIXTURE, PCA) required unlinked alleles, from which rarefied allelic richness was extracted using hierfstat (Goudet et al., 2022) in R v 4.0.3 (R Development Core Team, 2022). To meet assumptions of PCA and ADMIXTURE analyses (Alexander et al., 2009; Alexander & Lange, 2011) the SNPs were filtered further to remove loci that were in Linkage Disequilibrium with nearby loci. SNPs were output as VCFs and converted to plink (bed) files (Chang et al., 2015; Purcell & Chang, 2022).

Second stage

We used the software ADMIXTURE v 1.3.0 (Alexander et al., 2009; Alexander & Lange, 2011) to redefine input populations for a second run of the Populations module of stacks. We conducted ADMIXTURE analyses on the plink files of the global dataset and for each regional subset of the dataset. ADMIXTURE does not accept non-human chromosome names, so chromosome names were replaced with “0” in the first column of each bed file. ADMIXTURE was run with default parameters. We tested a range of 2-7 possible ancestral populations (K); the K with the lowest cross-validation error was chosen as the optimal value. We equated the number of ancestral populations K with the number of genetically distinct populations. New population maps for the Populations module were created based on the assignment to ancestral populations. Individuals were considered part of a population if they had >50% assignment probability. The Populations module was repeated, with population filters on the new populations. Genetic summary statistics were calculated by population as before. LD filtering was repeated as before and SNPS output as VCFs and converted to plink (bed) files. The two-stage filtering resulted in a 4-16% increase in SNPs (**Table S2**).

Table S4.2. Results of two-stage SNP filtering using Stacks v2.60 populations module (Catchen et al., 2011, 2013; Rochette et al., 2019). Loci were subject to population filters, but not every locus had a variant site (SNP), hence the drop in number. Percentage increase refers to the increase in variant sites obtained from filtering stage two relative to filtering stage one. LD = Linkage disequilibrium.

Dataset	Output	# loci		# variant sites post filters		% increase	# variant sites in LD		% increase
		Pre-filters	Post-filters	Filtering stage 1	Filtering stage 2		Filtering stage 1	Filtering stage 2	
America	First SNP per locus	53349	2165	1697	1721	1.41	834	864	3.60
America	Multiple SNPS	53349	2165	6301	6615	4.98	2564	2698	5.23

Eurasia	First SNP per locus	53349	2222	1778	1888	6.19	991	1072	8.17
Eurasia	Multiple SNPS	53349	2222	7232	7945	9.86	3295	3624	9.98
Western Eurasia	First SNP per locus	53349	2245	1747	1917	9.73	946	1040	9.94
Western Eurasia	Multiple SNPS	53349	2245	6185	7164	15.8	2551	2953	15.76
Global	First SNP per locus	53349	2180	1724	1744	1.16	1001	1041	4.00
Global	Multiple SNPS	53349	2180	7528	7858	4.38	3642	3830	5.16

Appendix S4.4: Population genetic structure and diversity

Table S4.3. Genetic diversity of dwarf birch sampling sites. Gene diversity (Expected heterozygosity) was calculated using 7232 variant sites whereas rarefied allelic richness which was calculated using 1724 variant sites. Mean global gene diversity was 0.091 (SD 0.0196) and mean rarefied allelic richness was and 1.10 (SD 0.0177).

Sampling site ID	Locality	Number of individuals	Gene diversity (He)	Rarefied Allelic Richness (Ar)
BN01	Itkillik	3.89	0.116	1.133
BN02	Chandalar	5.89	0.095	1.1
BN03	Dalton Mountain	5.82	0.104	1.112
BN04	Kuparuk River	6.74	0.122	1.134
BN05	Roche Mountonee	5.9	0.087	1.089
BN06	Bunny Haven	5.9	0.101	1.108
BN07	Komaktorvik River	5.88	0.081	1.08
BN08	Kytalyk1	5.85	0.103	1.107
BN09	Kytalyk2	5.82	0.105	1.107
BN10	Hol	5.88	0.091	1.102
BN12	Atqasuk	3.83	0.107	1.128
BN13	Torngats Basecamp	5.89	0.075	1.076
BN14	Nain	5.85	0.079	1.079
BN15	Näkkälä	4.89	0.097	1.106
BN16	Nordkapp	5.83	0.097	1.105
BN17	Saariselkä	5.85	0.097	1.102
BN21	East Fork Chandalar River	5.9	0.083	1.088

BN22	Linje	3.94	0.078	1.084
BN23	Nome	4.8	0.098	1.107
BN24	Kuzitin	5.82	0.126	1.139
BN25	Old Man	4.88	0.103	1.116
BN29	SAG	3	0.103	1.126
BN30	Fox	5.84	0.119	1.13
BN32	Krutaya Drisva	5.87	0.104	1.109
BN33	Ambarchik	5.88	0.097	1.104
BN34	Healy	5.78	0.119	1.134
BN37	Endalen & Janssonhaugen	6.81	0.079	1.082
BN38	Kvaløya	5.84	0.096	1.102
BN39	Vadsø	4.84	0.092	1.099
BN40	St. Mary's	5.84	0.089	1.1
BN42	Kilpisjärvi	5.9	0.096	1.102
BN43	Joensuu	5.91	0.085	1.091
BN44	Lifjeld	2	0.067	1.084
BN45	Les Ponts-de-Martel	5.91	0.09	1.101
BN46	Og Lake	5.93	0.064	1.068
BN49	Kluane - Pika Valley	4.9	0.08	1.084
BN51	QHI - Hawk Valley	5.9	0.091	1.099
BN61	Erkuta Tundra Monitoring site	3	0.092	1.111
BN62	Malozemelskaya tundra. Nenetskaya Gryada, Korovinskaya Guba; 5.5-8 km W Cape Seduysky Nos, c. 0-3 km W to NW the shore	3	0.084	1.098
BN63	Ary-Mas nature reserve, (c. 50-60 km NNW Khatanga), right riverside of Novaya, along the river and up to c. 3 km S of river	1	0.05	1.104
BN64	Lena R. west bank: Chekurovka village, surroundings of settlement	3	0.082	1.092
BN67	5-10 km from Arctic Station (coordinates are for station)	1	0.039	1.078
BN68	South of the landingstrip close to "Kjovedammen" and "Teltdammen".	1	0.034	1.074

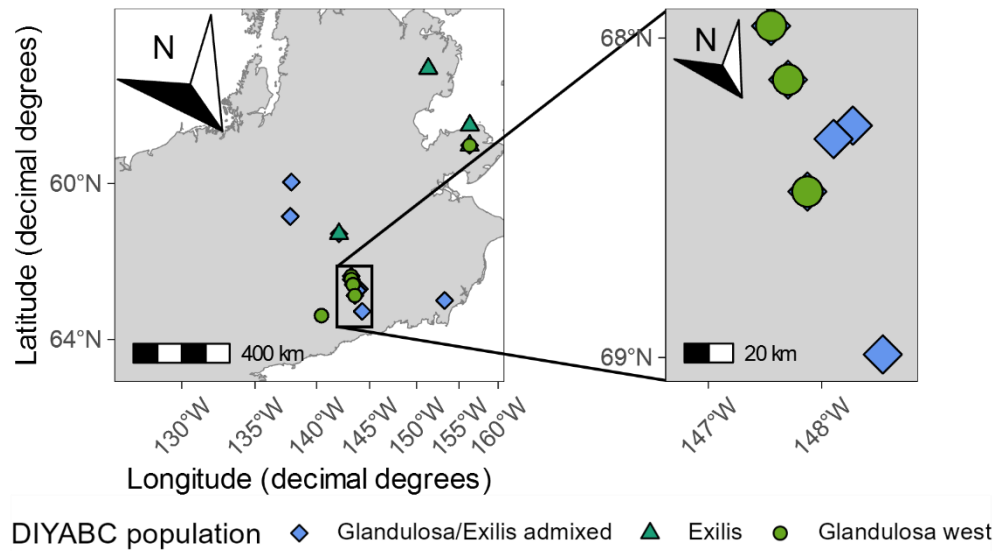


Figure S4.2. Alaskan dwarf birch sampling sites. Sites coloured according to populations used in Approximate Bayesian computation (ABC) modelling with DIYABC RF (Collin et al., 2021). Populations were assigned using ancestral group coefficients from ADMIXTURE analysis.

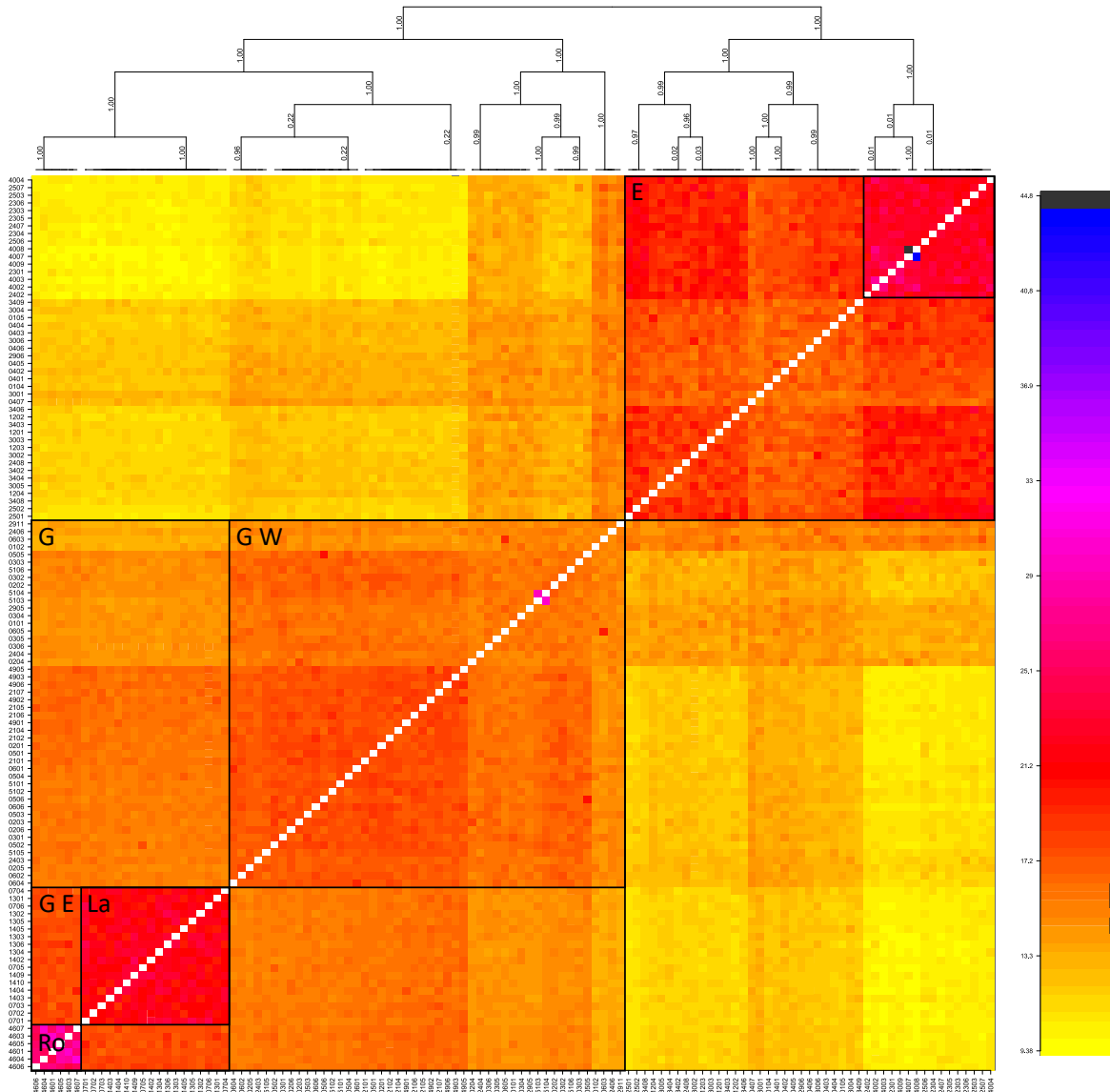


Figure S4.3. North American dwarf birch population genetic structure inferred from RADPainter. Coancestry matrix summarising nearest neighbour haplotype relationships between 117 individuals inferred from linkage structure derived from 2698 SNPs. The colour of each cell corresponds to the degree of coancestry, with red and yellow indicating a higher and lesser degree of coancestry, respectively. The matrix is clustered according to fineRADstructure population relationships using a Markov chain Monte Carlo (MCMC) clustering algorithm. The presence of discrete blocks of higher coancestry represents a genetic population where individuals are genetically indistinguishable from each other and different from other populations, while higher coancestry between different populations indicates gene flow and admixture between populations (Malinsky et al., 2018). Letters represent possible populations: E = Exilis, G = Glandulosa, GW = Glandulosa west, GE = Glandulosa east, La= Labrador, Ro = Rocky mountains.

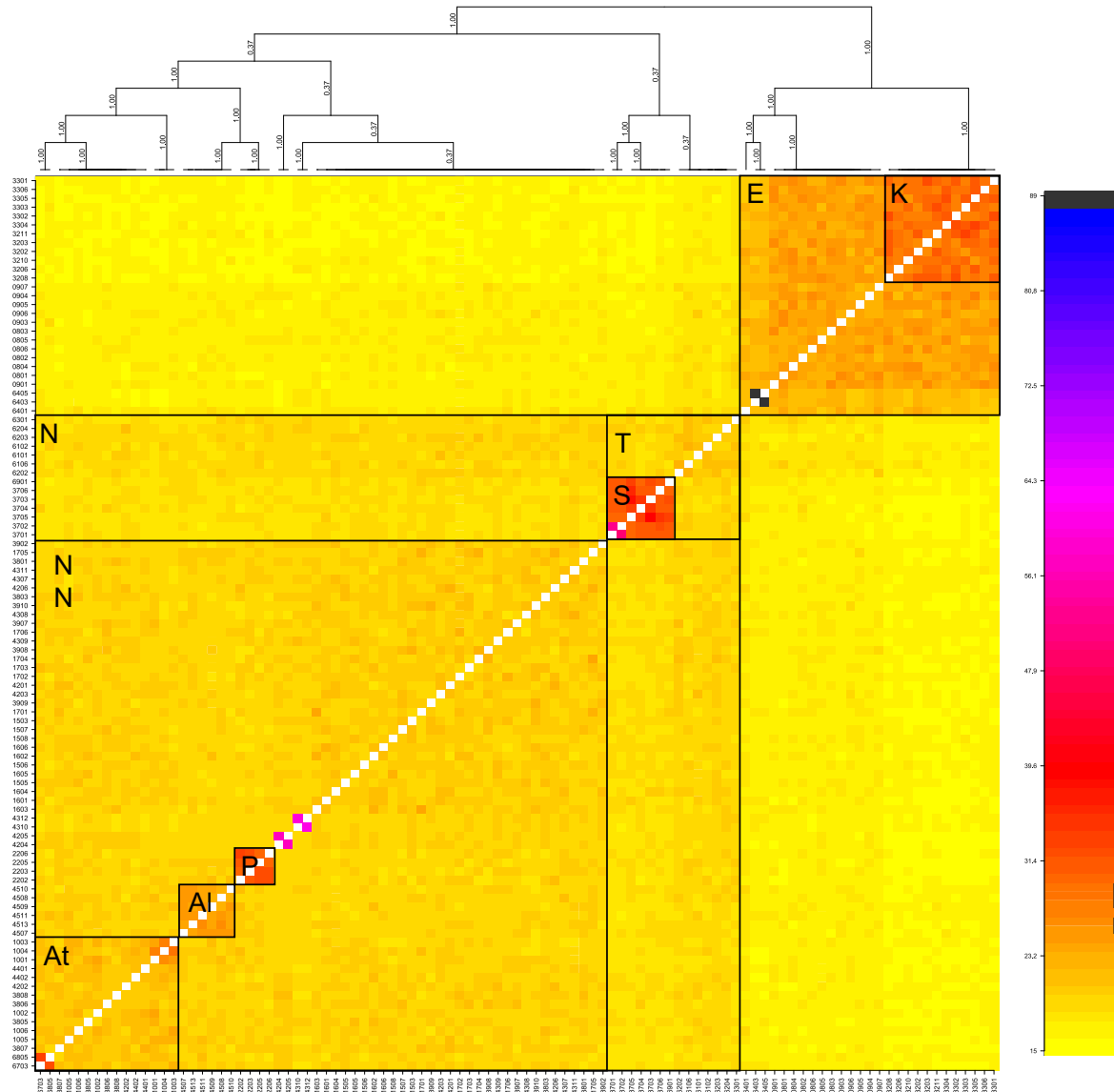


Figure S4.4. Eurasian dwarf birch population genetic structure inferred from RADPainter. Coancestry matrix summarising nearest neighbour haplotype relationships between 101 individuals inferred from linkage structure derived from 3624 SNPs. The colour of each cell corresponds to the degree of coancestry, with red and yellow indicating a higher and lesser degree of coancestry, respectively. The matrix is clustered according to fineRADstructure population relationships using a Markov chain Monte Carlo (MCMC) clustering algorithm. The presence of discrete blocks of higher coancestry represents a genetic population where individuals are genetically indistinguishable from each other and different from other populations, while higher coancestry between different populations indicates gene flow and admixture between populations (Malinsky et al., 2018). Letters represent possible populations: N = Nana, E = Exilis, NN = Nana subsp. nana, K = Kolyma River, T = Tundrarum, S = Svalbard, At = Atlantic, Al = Alps, P = Poland.

Appendix S4.5: Population assignment for demographic modelling

Populations were assigned using ancestry coefficients from the regional ADMIXTURE analyses:

Species divergence model: three main populations were identified in the global ADMIXTURE analysis (Exilis, Nana, Glandulosa). Admixture between populations can affect patterns of relatedness between groups and divergence time estimates, so only individuals with >95% ancestry proportion from a single population were retained for these models.

American models: three main populations were identified in the ADMIXTURE analysis (Exilis, Glandulosa west and Glandulosa east). The extensive admixture between exilis and Glandulosa west in present-day Alaskan populations was interpreted as potentially a longer period of range overlap and gene flow between exilis and glandulosa in Beringia. DIYABC can include discrete admixture and introgression events but not continuous gene flow (Collin et al., 2021; Cornuet et al., 2014). Therefore we treated the admixed populations as one effective population, with an admixture date representing the time when the admixture between exilis and glandulosa west began. Individuals with >95% ancestry proportion were assigned to the relevant population. Individuals with >5% and < 95% exilis were assigned to the “admixed population”.

Eurasian models: Two populations were identified in the ADMIXTURE analysis (Exilis and Nana), with an additional population identified in the west Eurasian ADMIXTURE analysis that delineated the Svalbard population and was also introgressed into the Nana group, particularly in northeast Scandinavia and northwest Russia. This was suggestive of the “west Siberian group” previously hypothesised to be formed as a result of admixture between Exilis and Nana in west Siberia, and then isolated in a later glacial period to result in a genetically distinctive west Siberian population (Eidesen et al., 2015), sometimes recognised taxonomically as *Betula nana* L. ssp. *tundrarum* (Perfil.) Á.Löve & D.Löve (Elven et al., 2011). As the ancestry proportion of this population never exceeded 50% excepting in Svalbard, the west Siberian population was coded into model scenarios as an unsampled “ghost” population. Individuals with >50% exilis or nana proportion were assigned to exilis or nana, respectively. The Svalbard individuals were assigned to a unique population.

Global models: The global model used the same population groupings as the regional models, meaning that Eurasian individuals that were >50% exilis and American individuals that were >95% exilis were combined in an exilis population. Population genetic structure analyses found Exilis populations in eastern Russia and western Alaska to be very little differentiated, supporting grouping in one population.

Appendix S4.6: Model set scenario details and DIYABC RF (Collin et al., 2021) model choice output

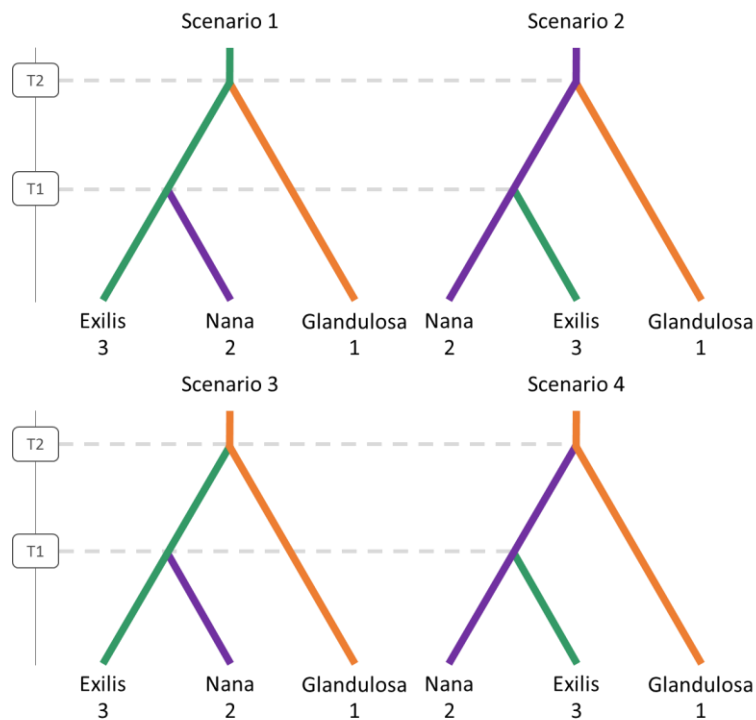


Figure S4.5. Global species divergence model (model set 4).

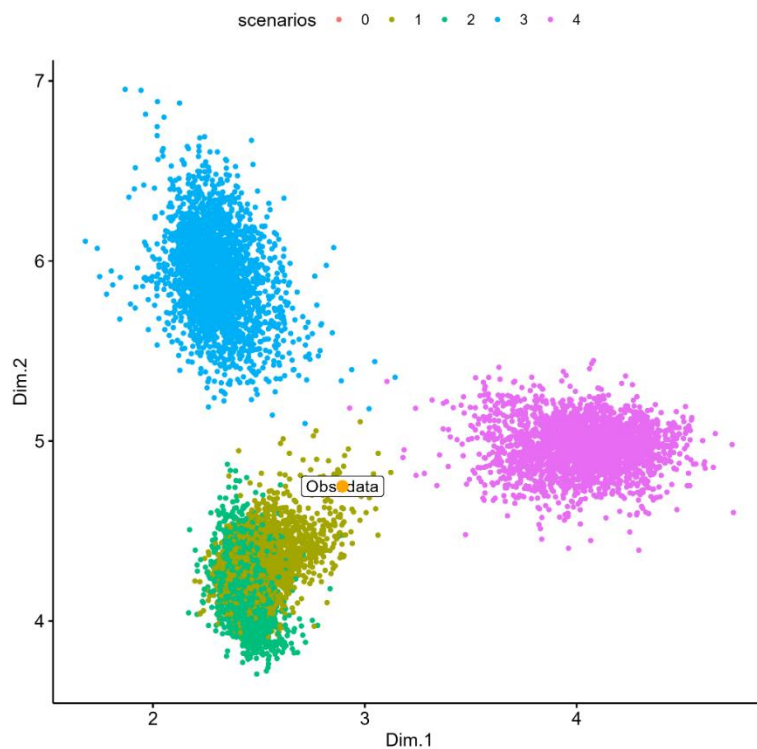


Figure S4.6. Projection of simulated datasets of global species divergence model (model set 4) on the first two axes of a Linear Discriminant Analysis. The location of the observed genetic data is indicated by the yellow circle. 10,000 datasets were used for model choice.

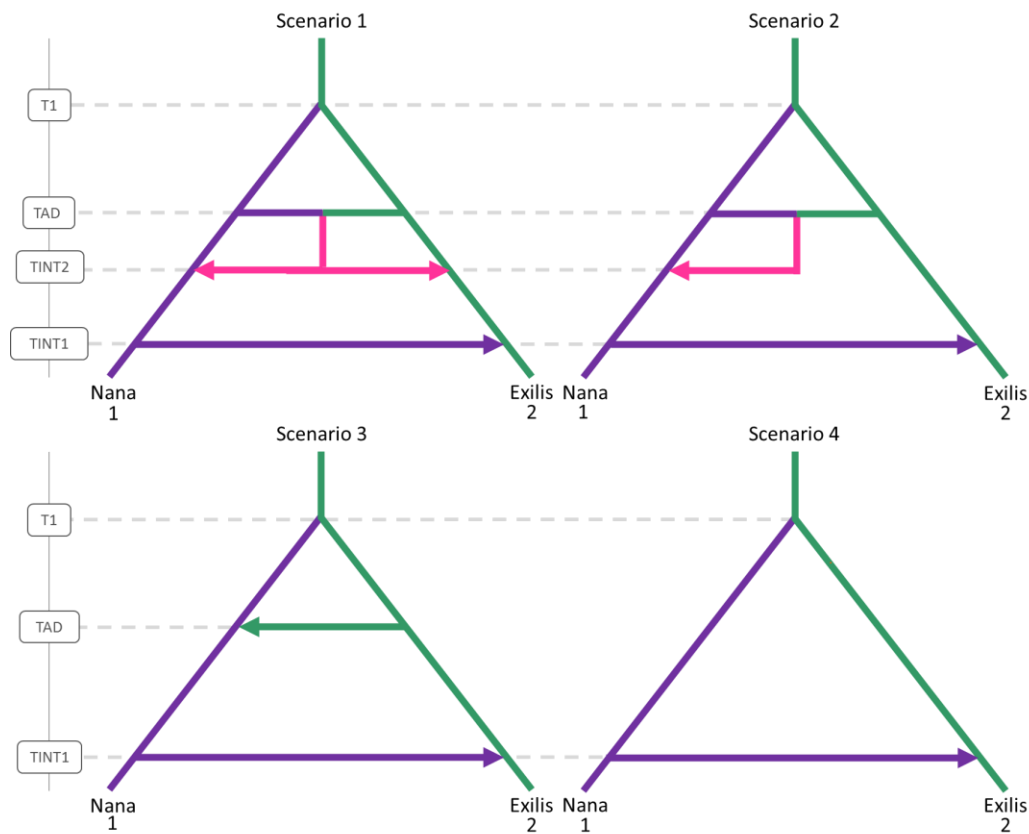


Figure S4.7. Eurasia model without Svalbard (model set 8.3).

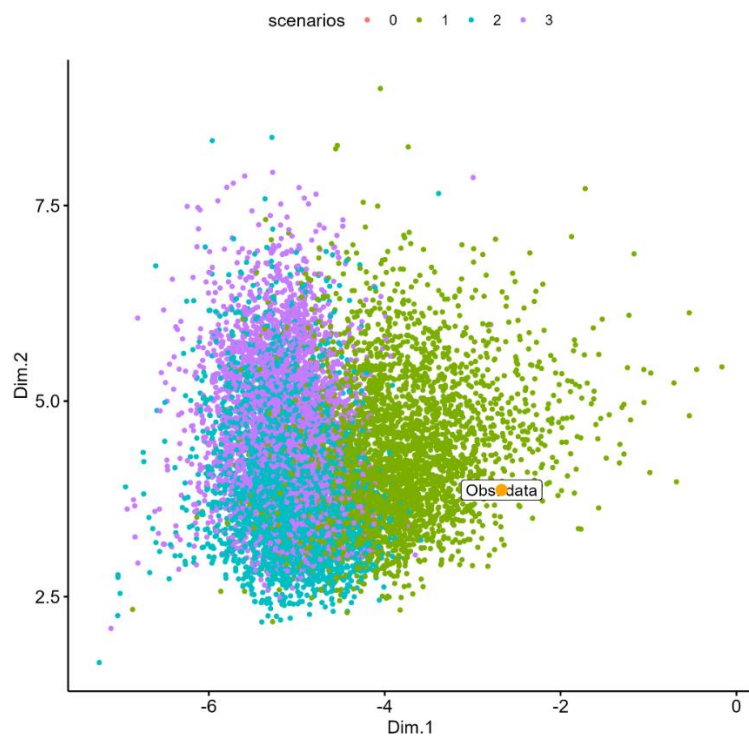


Figure S4.8. Projection of simulated datasets of Eurasian model without Svalbard (model set 8.3) on the first two axes of a Linear Discriminant Analysis. The location of the observed genetic data is indicated by the yellow circle. 10,000 datasets were used for model choice.

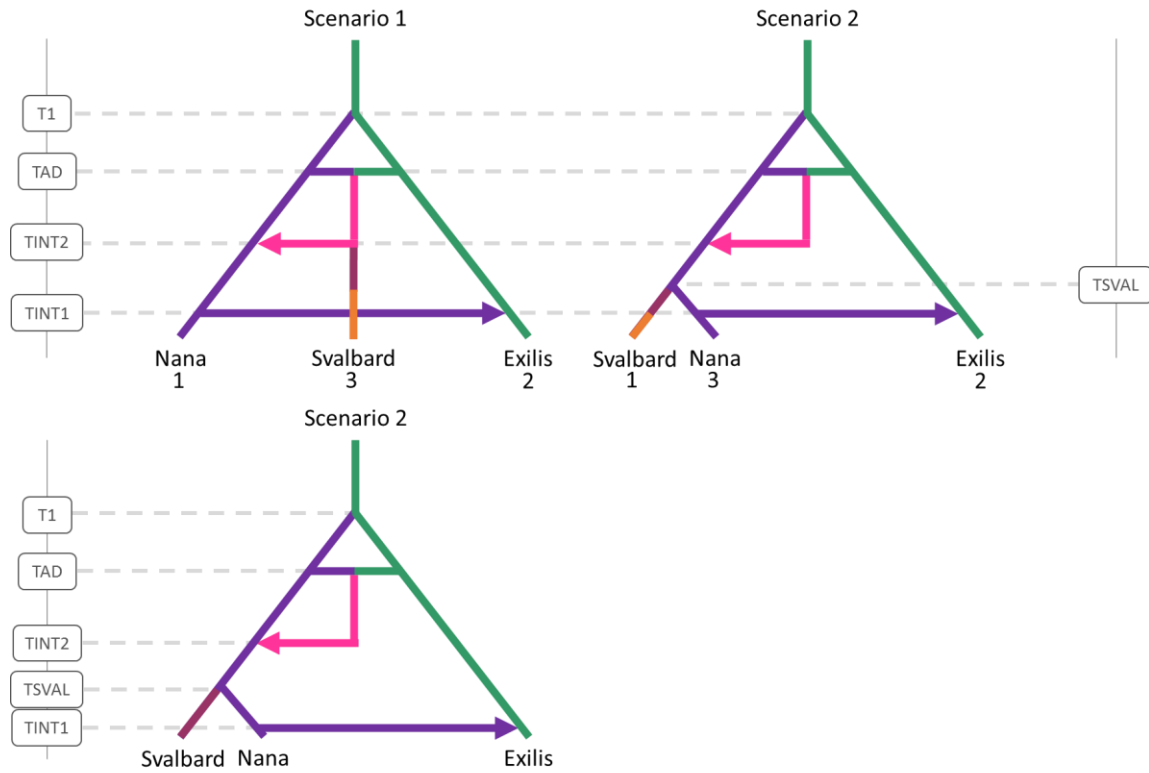


Figure S4.9. Eurasia model with Svalbard: model sets 9 (3 scenarios) and 10 (Scenario 1 and 3 only).

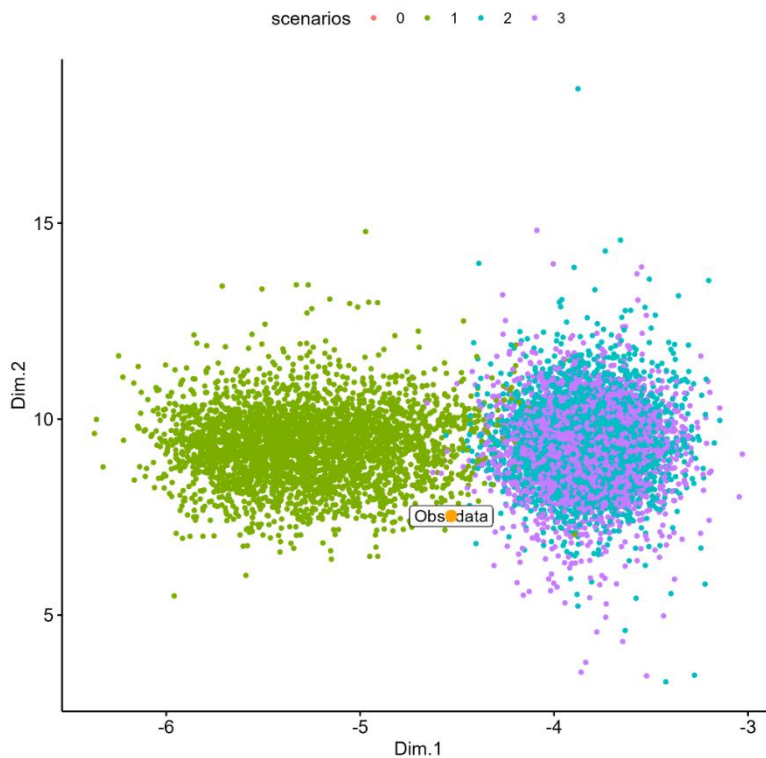


Figure S4.10. Projection of simulated datasets of Eurasian model with Svalbard (model set 9) on the first two axes of a Linear Discriminant Analysis. The location of the observed genetic data is indicated by the yellow circle. 10,000 datasets were used for model choice.

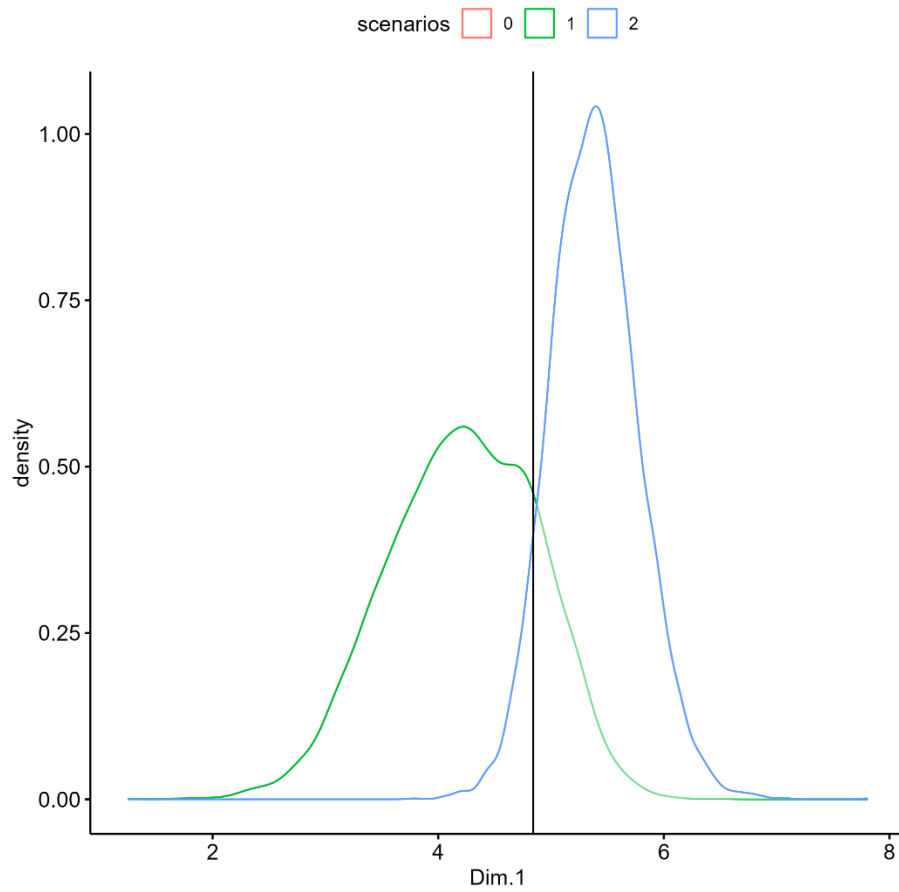


Figure S4.11. Projection of simulated datasets of Eurasian model without Svalbard (model set 10) on the first axis of a Linear Discriminant Analysis. The location of the observed genetic data is indicated by the solid black line. 10,000 datasets were used for model choice.

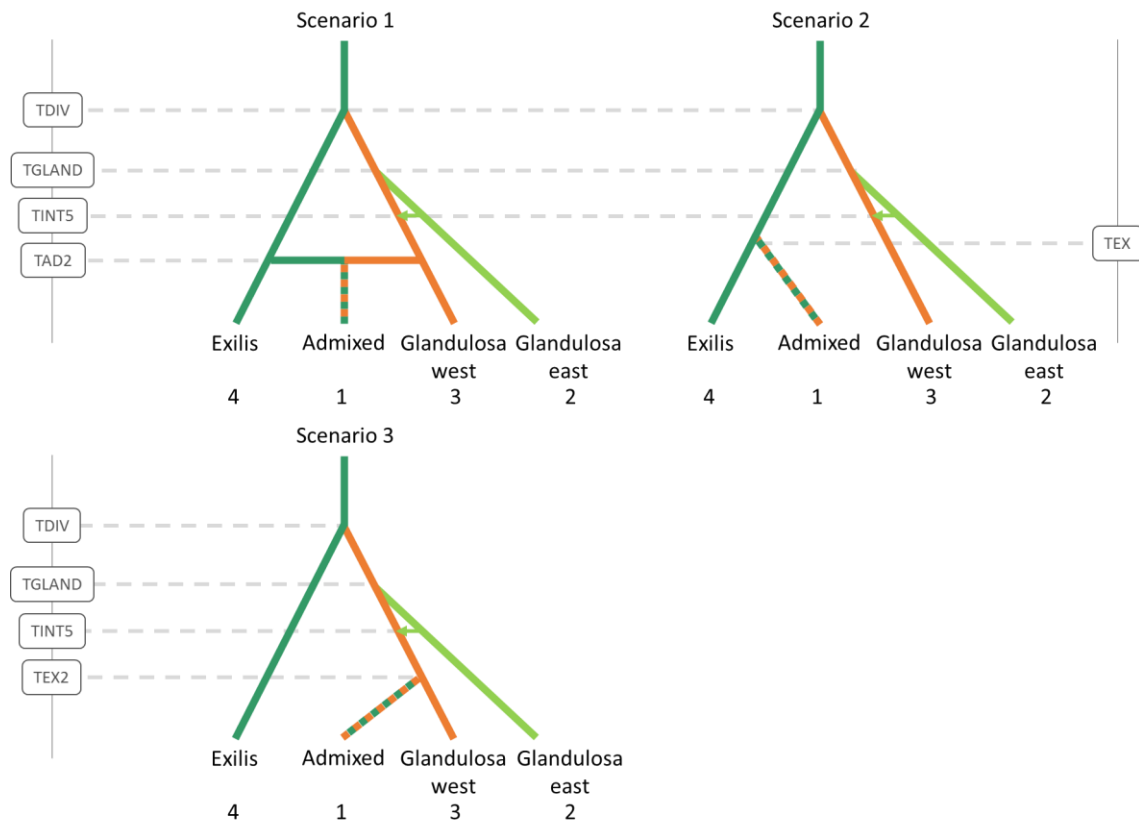


Figure S4.12. North American model (model set 14.1).

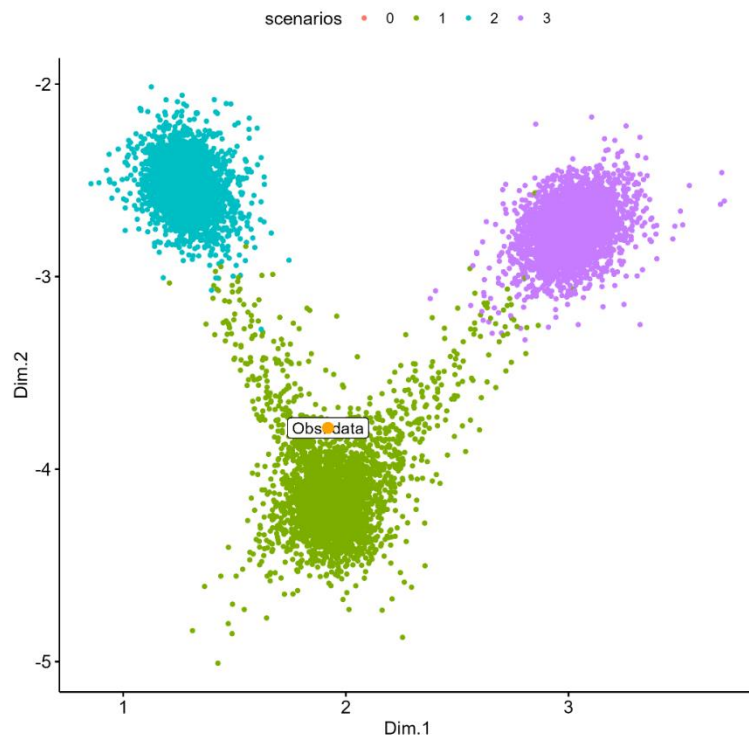


Figure S4.13. Projection of simulated datasets of North American model (model set 14.1) on the first two axes of a Linear Discriminant Analysis. The location of the observed genetic data is indicated by the yellow circle. 10,000 datasets were used for model choice.

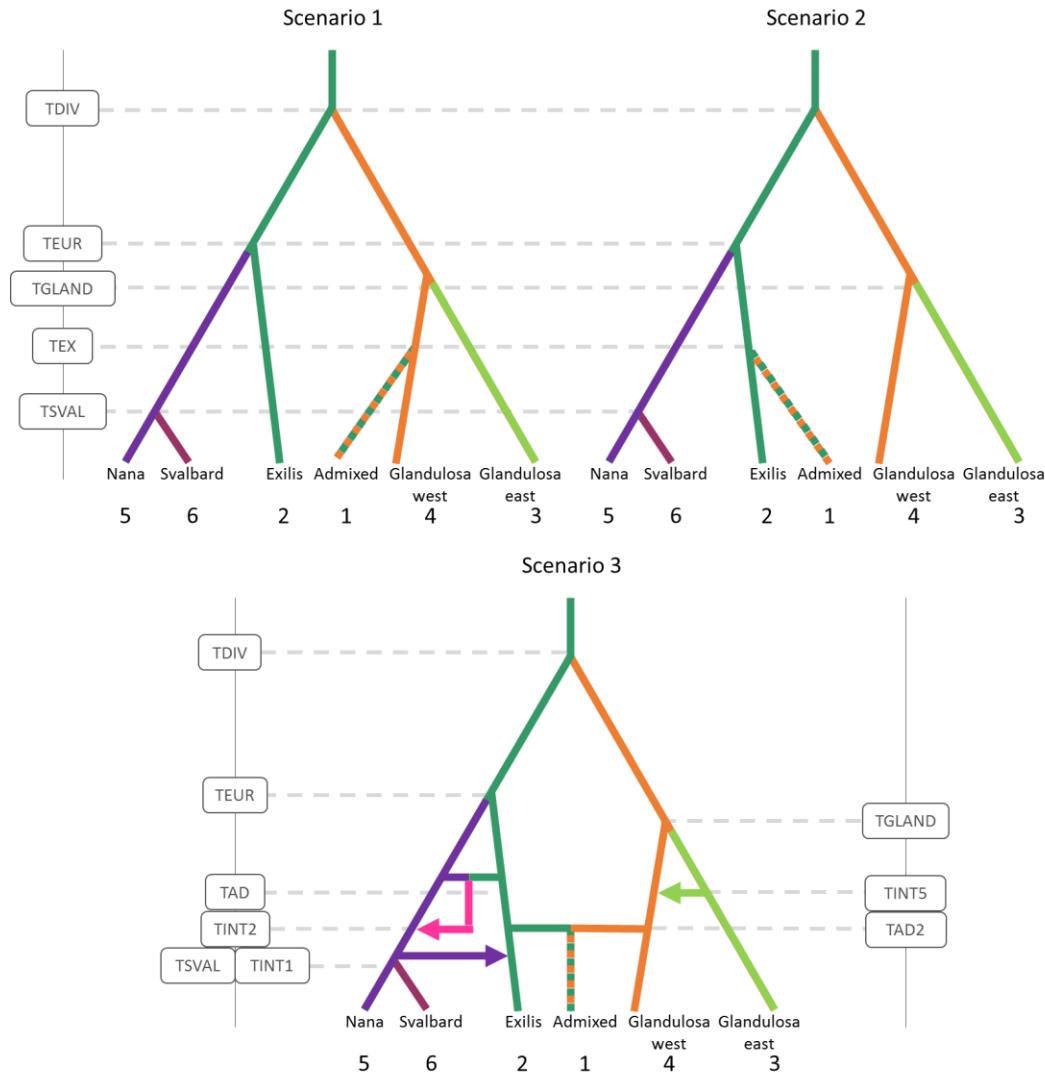


Figure S4.14. Global model (model set 20).

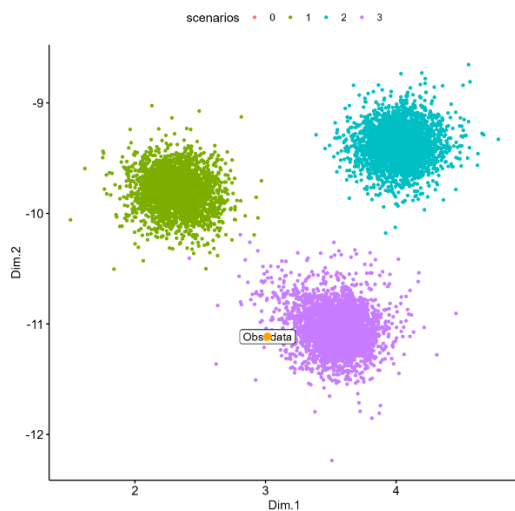


Figure S4.15. Projection of simulated datasets of global model (model set 20) on the first two axes of a Linear Discriminant Analysis. The location of the observed genetic data is indicated by the yellow circle. 10,000 datasets were used for model choice.

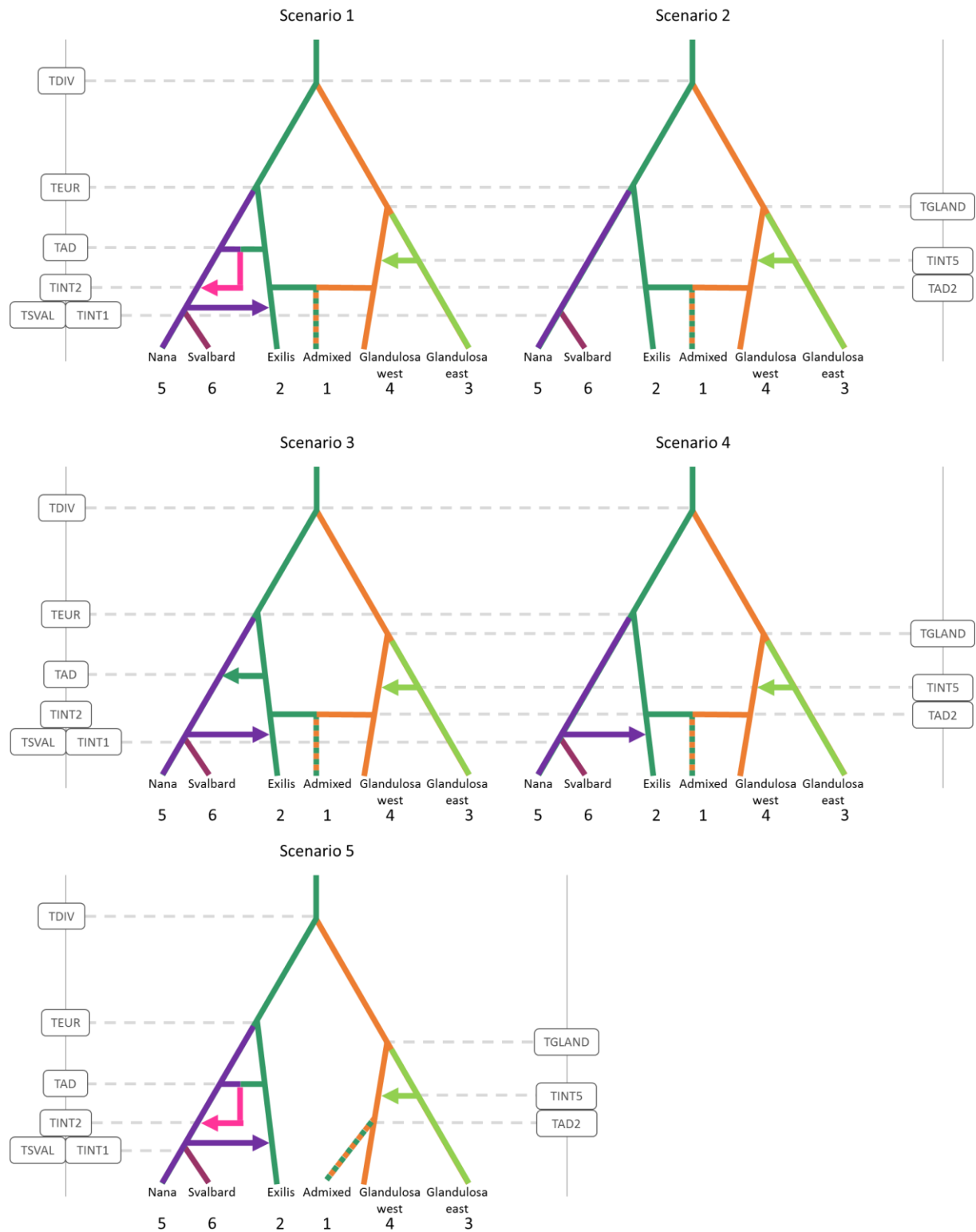


Figure S4.16. Global model (model set 21).

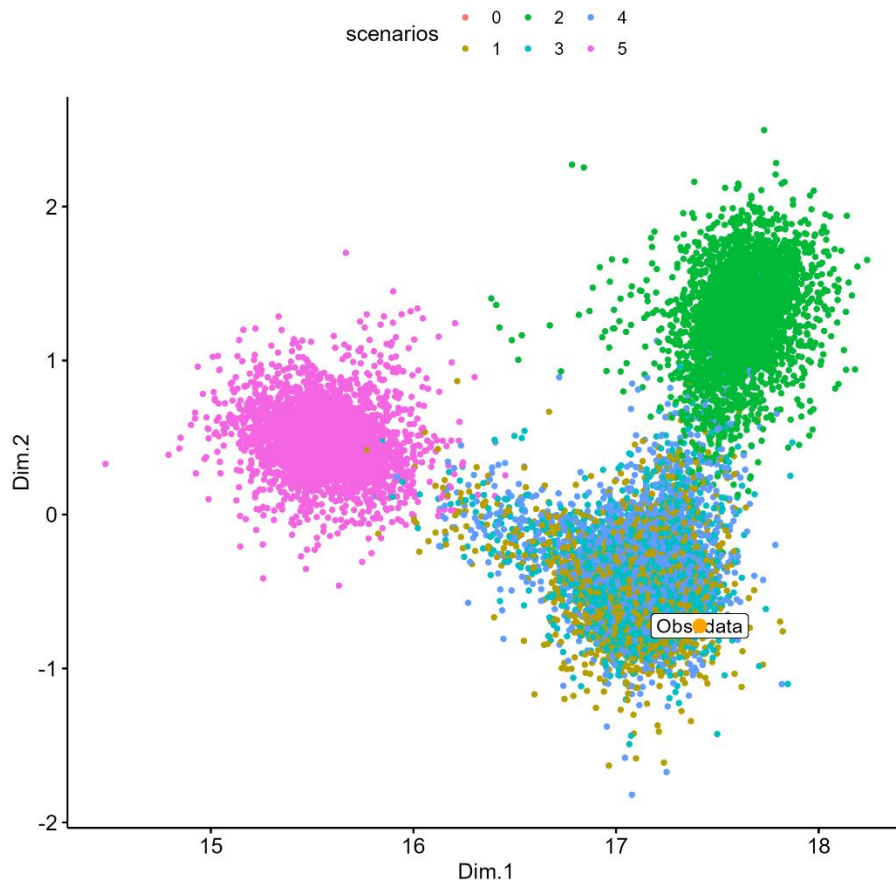


Figure S4.17. Projection of simulated datasets of global model (model set 21) on the first two axes of a Linear Discriminant Analysis. The location of the observed genetic data is indicated by the yellow circle. 16,500 datasets were used for model choice.

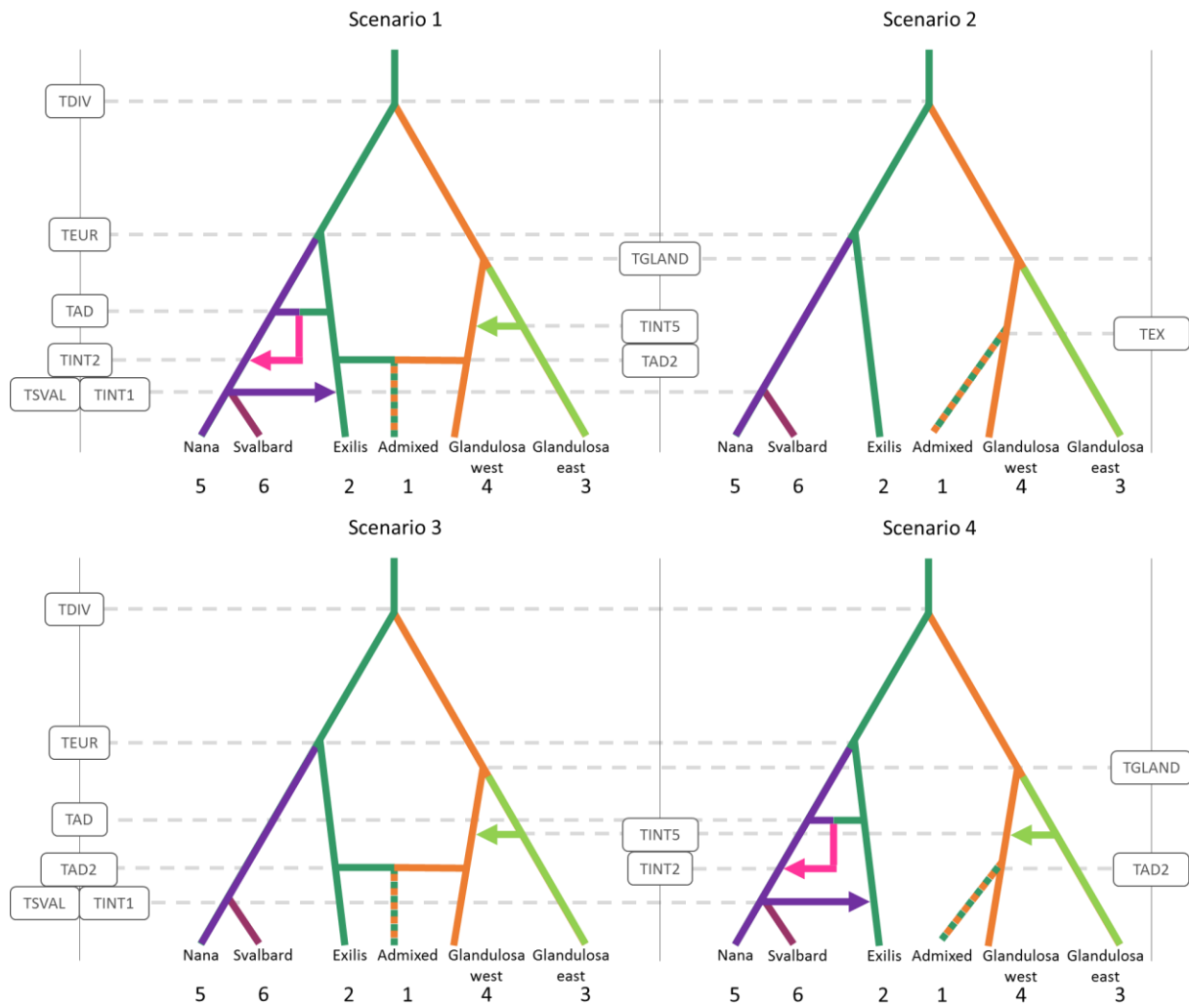


Figure S4.18. Global model (model set 22) with Exilis as ancestral population.

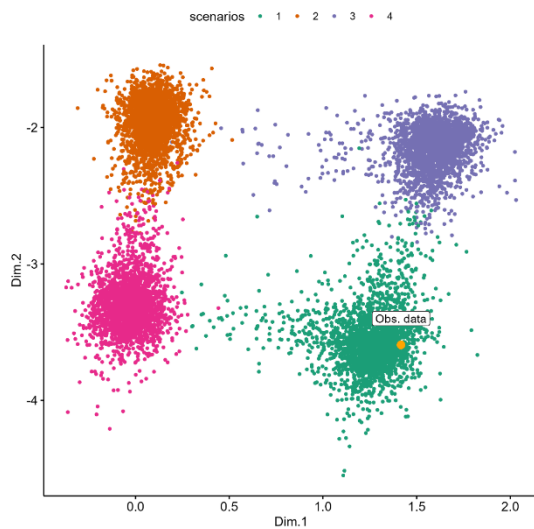


Figure S4.19. Projection of simulated datasets of global model (model set 22) on the first two axes of a Linear Discriminant Analysis. 100,000 datasets were used for model choice but only a random 10,000 subsample are plotted. The location of the observed genetic data is indicated by the yellow circle.

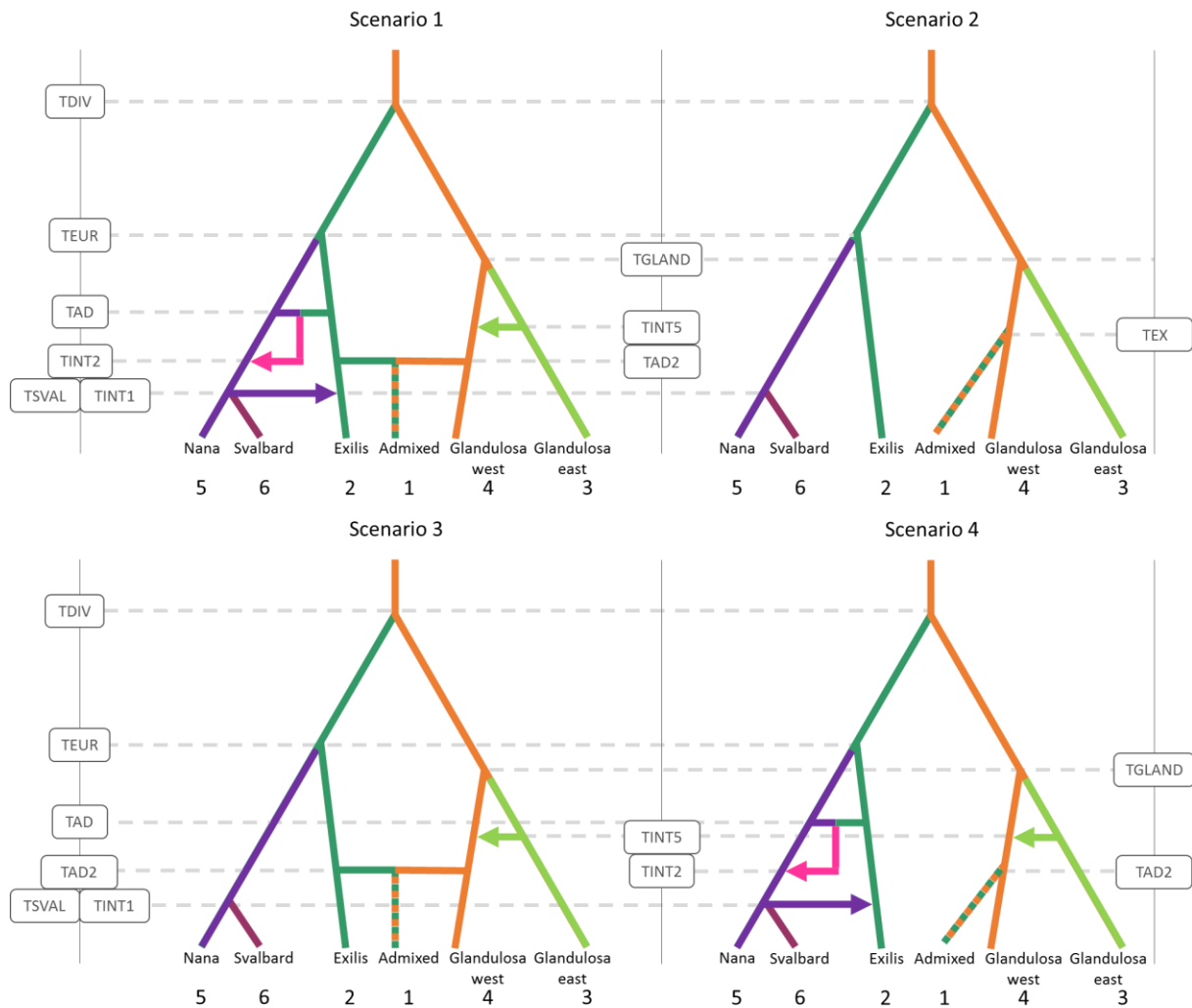


Figure S4.20. Global model (model set 23) with Glandulosa as ancestral population.

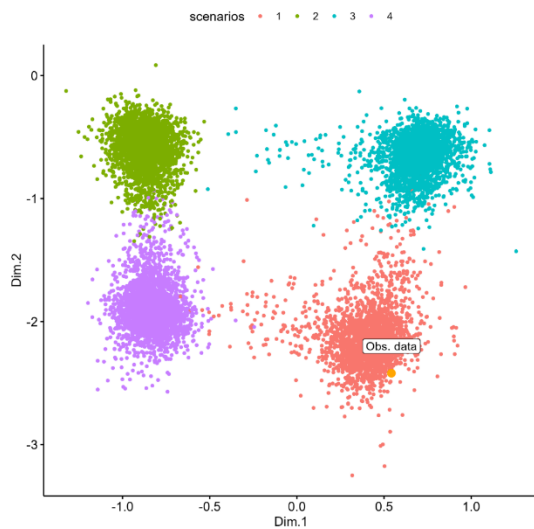


Figure S4.21. Projection of simulated datasets of global model (model set 23) on the first two axes of a Linear Discriminant Analysis. 100,000 datasets were used for model choice but only a random 10,000 subsample are plotted. The location of the observed genetic data is indicated by the yellow circle.

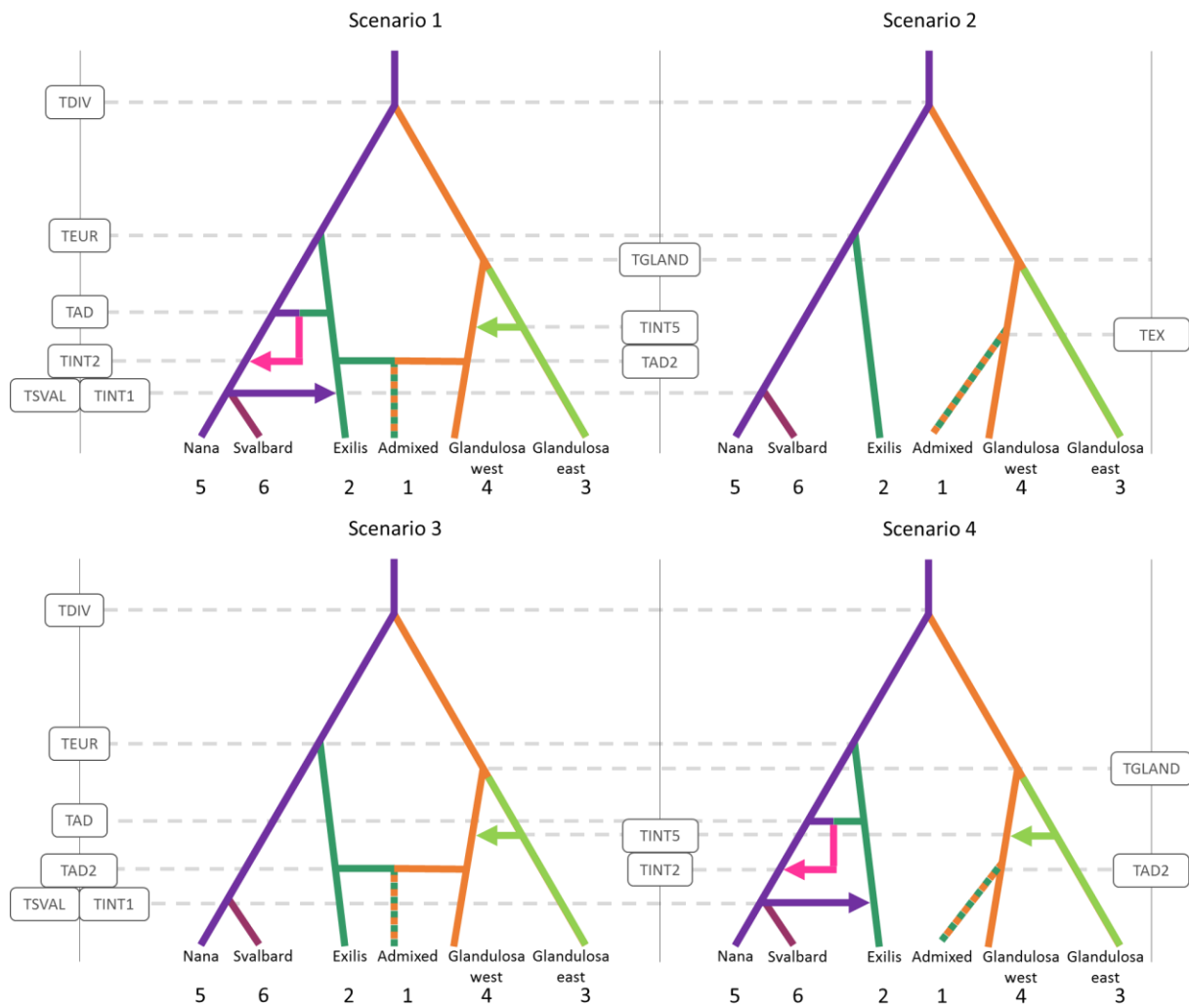


Figure S4.22. Global model (model set 24) with Nana as ancestral population.

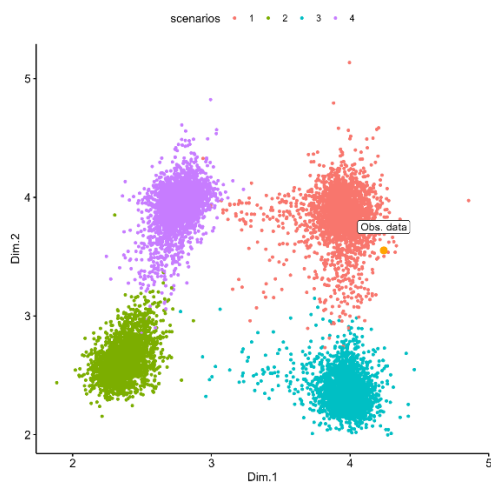


Figure S4.23. Projection of simulated datasets of global model (model set 24) on the first two axes of a Linear Discriminant Analysis. 100,000 datasets were used for model choice but only a random 10,000 subsample are plotted. The location of the observed genetic data is indicated by the yellow circle.

Table S4.4. DIYABC RF (Collin et al., 2021) model specifications for the final global model (model set 22) used for parameter estimates. Model specifications form part of the DIYABC header input file.

Priors	Scenario 1	Scenario 2	Scenario 3	Scenario 4
Population size	N1 N UN[10000,150000,0,0] N2 N UN[1000,75000,0,0] N3 N UN[10000,60000,0,0] N4 N UN[10000,150000,0,0] N5 N UN[5000,100000,0,0] N6 N UN[27,750,0,0] N7 N UN[1000,100000,0,0]			
Conditions	TINT2>TINT1, TINT2>TSVAL, TAD2>TINT1, TAD>TSVAL, TAD>TINT2, TAD>TAD2, TEUR>TAD, TEUR>TINT1, TEUR>TSVAL, TEUR>TAD2, TINT5>TAD2, TGLAND>TINT5, TGLAND>TEX, TDIV>TEUR, TDIV>TGLAND			
Locus description	543 <A> G1 from 1			
Topology	scenario 1 [0.25] (21) N1 N2 N3 N4 N5 N6 N2 N5 N7 N7 N4 N3 N5 0 sample 1 0 sample 2 0 sample 3 0 sample 4 0 sample 5 0 sample 6 TSVAL merge 5 6 TINT1 split 2 13 7 r1 TINT1 merge 5 13 TINT2 split 5 8 9 r2 TINT2 merge 10 9 TAD2 split 1 7 4 r3	scenario 2 [0.25] (11) N1 N2 N3 N4 N5 N6 0 sample 1 0 sample 2 0 sample 3 0 sample 4 0 sample 5 0 sample 6 TSVAL merge 5 6 TEX merge 4 1 TEUR merge 2 5 TGLAND merge 4 3 TDIV merge 2 4	scenario 3 [0.25] (14) N1 N2 N3 N4 N5 N6 N4 N3 0 sample 1 0 sample 2 0 sample 3 0 sample 4 0 sample 5 0 sample 6 TSVAL merge 5 6 TAD2 split 1 2 4 r3 TEUR merge 2 5 TINT5 split 4 8 7 r5 TINT5 merge 3 7 TGLAND merge 8 3 TDIV merge 2 8	scenario 4 [0.25] (20) N1 N2 N3 N4 N5 N6 N2 N5 N7 N7 N4 N3 N5 0 sample 1 0 sample 2 0 sample 3 0 sample 4 0 sample 5 0 sample 6 TSVAL merge 5 6 TINT1 split 2 13 7 r1 TINT1 merge 5 13 TAD2 merge 4 1 TINT2 split 5 8 9 r2 TINT2 merge 10 9

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	TAD split 10 8 7 r4 TEUR merge 7 8 TINT5 split 4 11 12 r5 TINT5 merge 3 12 TGLAND merge 11 3 TDIV merge 7 11			TAD split 10 8 7 r4 TEUR merge 7 8 TINT5 split 4 11 12 r5 TINT5 merge 3 12 TGLAND merge 11 3 TDIV merge 7 11
Admixture priors	r1 A UN[0.01,0.99,0,0] r2 A UN[0.01,0.99,0,0] r3 A UN[0.01,0.99,0,0] r4 A UN[0.01,0.99,0,0] r5 A UN[0.01,0.99,0,0]			
Event parameter priors	TSVAL T UN[10,2000,0,0] TINT1 T UN[10,2400,0,0] TINT2 T UN[10,2400,0,0] TAD2 T UN[10,9000,0,0] TAD T UN[9000,24000,0,0] TEUR T UN[25000,100000,0,0] TINT5 T UN[100,20000,0,0] TGLAND T UN[10000,90000,0,0] TDIV T UN[80000,200000,0,0] TEX T UN[10,10000,0,0]			

Table S4.5. Model error rates for DIYABC RF (Collin et al., 2021) model sets.

Model set	Prior error rate			Model 1	Model 2	Model 3	Model 4		Class error
Species divergence: 4.3	0.0371	predicted	model 1	2249	112	0	0		0.0474
		predicted	model 2	258	2414	0	0		0.0966
		predicted	model 3	0	0	2496	1		0.0004
		predicted	model 4	0	0	0	2470		0
				model 1	model 2	model 3			class error
Eurasia without Svalbard: 8.5	Prior error rate	predicted	model 1	2875	226	151			0.116
	0.2838	predicted	model 2	274	2129	938			0.363
		predicted	model 3	267	982	2158			0.367
Eurasia with Svalbard: 9				model 1	model 2	model 3			class error
	Prior error rate	predicted	model 1	3327	9	12			0.006272
	0.3299	predicted	model 2	20	1640	1586			0.495
		predicted	model 3	8	1664	1734			0.491
Eurasia with Svalbard 10.1	Prior error rate			model 1	model 2				class error
	0.0982	predicted	model 1	4277	297				0.0649
		predicted	model 2	685	4741				0.126
North America: 14.1	Prior error rate			model 1	model 2	model 3			class error
	0.003	predicted	model 1	3315	1	1			0.0006
		predicted	model 2	12	3343	0			0.00358
		predicted	model 3	16	0	3312			0.00481
Global model:	Prior error rate			model 1	model 2	model 3			class error

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20									
	0.0001	predicted	model 1	3244	0	1			0.00031
		predicted	model 2	0	3356	0			0
		predicted	model 3	0	0	3399			0
Global model: 21	Prior error rate			model 1	model 2	model 3	model 4	model 5	class error
	0.193333	predicted	model 1	1886	5	810	176	0	0.345
		predicted	model 2	23	3243	29	67	1	0.0357
		predicted	model 3	948	9	2109	313	0	0.376
		predicted	model 4	373	0	344	2753	0	0.207
		predicted	model 5	38	5	25	24	3319	0.027
Global model: 22	Prior error rate		1	model 1	model 2	model 3	model 4		class error
	0.00406	predicted	model 1	24698	0	39	1		0.00162
		predicted	model 2	0	25011	24	78		0.00406
		predicted	model 3	115	0	25042	0		0.00457
		predicted	model 4	104	45	0	24843		0.00596
Global model: 23	Prior error rate		1	model 1	model 2	model 3	model 4		class error
	0.00432	predicted	model 1	24743	0	27	5		0.00162
		predicted	model 2	0	24921	22	99		0.00406
		predicted	model 3	107	0	24987	0		0.00457
		predicted	model 4	107	64	1	24917		0.00596
Global model: 24	Prior error rate		1	model 1	model 2	model 3	model 4		class error
	0.0039	predicted	model 1	24617	0	27	4		0.00126
		predicted	model 2	0	24919	37	77		0.00455
		predicted	model 3	98	1	24845	0		0.00397
		predicted	model 4	92	51	3	25229		0.00575

Table S4.6. Posterior probabilities of DIYABC RF (Collin et al., 2021) model sets. Model choice conducted with 10,000-100,000 datasets depending on the model, 500 trees, minimum node size of 1, n summary statistics, n axes of summary statistics LDA linear combination (1 - number of scenarios), and 5 noise variables.

Model set	Votes model 1	Votes model 2	Votes model 3	Votes model 4	Votes model 5	Selected model	Posterior probability
Species divergence: 4.3	186	180	110	24	NA	1	0.77
Eurasia without Svalbard: 8.5	480	15	5	NA	NA	1	0.994
Eurasia with Svalbard: 9	162	114	224	NA	NA	3	0.541
Eurasia with Svalbard: 10.1	245	255	NA	NA	NA	2	0.772
North America: 14.1	476	8	16	NA	NA	1	0.98
Global model: 20	9	24	467	NA	NA	3	1
Global model: 21	262	11	169	58	0	1	0.55
Global model: 22	439	0	53	8	NA	1	0.891
Global model: 23	449	0	48	3	NA	1	0.869
Global model: 24	457	0	41	2	NA	1	0.896

Appendix S4.7: DIYABC RF (Collin et al., 2021) parameter estimates

Table S4.7. Time parameter estimates for the best supported scenario in global model set 22. Estimates were based on 24,917 simulated datasets from scenario 1, with minimum node size of 5, 572 summary statistics, n axes of summary statistics in PLS linear combination, 5 noise variables, and with 1000 out-of-band samples used as a test. Estimates are given in generations and years with (a) 10-year generation time and (b) 14-year generation time. 95% confidence intervals and local posterior root-mean-square error (RMSE) have the same units as the variable, and local posterior Normalised RMSE (RMSE divided by the median parameter estimate) is unitless.

Event	Event type	Description	Median generations	Years (10)	95% CI		Years (14)	95% CI		RMSE	NRMSE
TSVAL	divergence	Svalbard and Nana	444	4,440	908	7,040	6,216	1,272	9,856	192.756	0.434
TINT1	introgression	Nana to Exilis	923	9,230	1,430	19,960	12,922	2,002	27,944	481.909	0.522
TINT2	introgression	Tundrarum to Nana	1,544	15,440	6,060	23,170	21,616	8,484	32,438	493.066	0.319
TAD2	admixture	Exilis and Glandulosa west	2,959	29,590	6,474	65,150	41,426	9,064	91,210	1227.015	0.415
TINT5	introgression	Glandulosa east to Glandulosa west	6,996	69,960	28,215	151,450	97,944	39,501	212,030	2464.674	0.352
TAD	admixture	Nana and Exilis	15,486	154,860	97,133	231,160	216,804	135,987	323,624	4540.784	0.293
TGLAND	divergence	Glandulosa east and Glandulosa	50,292	502,921	157,700	856,896	704,089	220,780	1,199,654	22295.23	0.443

		west									
TEUR	divergence	Nana and Exilis	58,837	588,367	278,050	937,323	823,714	389,270	1,312,252	20703.545	0.352
TDIV	divergence	Glandulosa and Exilis	89,750	897,497	806,395	1,145,920	1,256,496	1,128,953	1,604,288	10689.464	0.119

Table S4.8. Population size parameter estimates for the best supported scenario in global model set 22. Effective haploid population size (N_e) is 1/2 of effective population size as *Betula nana* and *Betula glandulosa* are diploid. 95% confidence intervals and local posterior root-mean-square error (RMSE) have the same units as the variable, and local posterior Normalised RMSE (RMSE divided by the median parameter estimate) is unitless.

Parameter	Population	Median (haploid)	95% CI (haploid)		Median (diploid)	95% CI (diploid)		RMSE	NRMSE
N1	Admixed	99461	30759	147742	198922	61518	295484	35543.650	0.357
N2	Exilis	59243	31197	73615	118486	62395	147229	9446.427	0.160
N3	Glandulosa east	47584	26518	59346	95167	53037	118691	6147.911	0.129
N4	Glandulosa west	104968	54350	145876	209936	108700	291752	25627.353	0.244
N5	Nana	71105	33705	97611	142210	67409	195223	17051.889	0.240
N6	Svalbard	503	93	726	1006	186	1452	235.398	0.470
N7	Tundrarum	65395	21738	97806	130789	43476	195612	24533.653	0.375

Table S4.9. Ratio of time/population size parameter estimates for the best supported scenario in global model set 22. Estimates were based on 24,917 simulated datasets from scenario 1, with minimum node size of 5, 572 summary statistics, n axes of summary statistics in PLS linear combination, 5 noise variables, and with 1000 out-of-band samples used as a test. 95% confidence intervals and local posterior root-mean-square error (RMSE) have the same units as the variable, and local posterior Normalised RMSE (RMSE divided by the median parameter estimate) is unitless.

Event	Event type	Description	Median estimate	95% CI		RMSE	NRMSE
TSVAL/N6	divergence	Svalbard and Nana	0.786	0.605	1.03	0.120	0.15248
TINT1/N2	introgression	Nana to Exilis	0.0195	0.00221	0.0688	0.00836	0.42983
TINT2/N5	introgression	Tundrarum to Nana	0.0349	0.0126	0.215	0.0780	2.23640
TAD2/N1	admixture	Exilis and Glandulosa west	0.0268	0.00721	0.0731	0.0136	0.50861
TINT5/N4	introgression	Glandulosa east to Glandulosa west	0.0888	0.0304	0.251	0.0470	0.52887
TAD/N7	admixture	Nana and Exilis	0.355	0.136	6.09	1.145	3.22868
TGLAND/N3	divergence	Glandulosa east and Glandulosa west	0.972	0.283	2.23	0.558	0.57346
TEUR/N5	divergence	Nana and Exilis	1.153	0.441	5.086	1.457	1.26338
TDIV/N4	divergence	Glandulosa and Exilis	0.867	0.594	1.604	0.113	0.13039

Table S4.10. Admixture rate parameter estimates for the best supported scenario in global model set 22. 95% confidence intervals and local posterior root-mean-square error (RMSE) have the same units as the variable, and local posterior Normalised RMSE (RMSE divided by the median parameter estimate) is unitless.

Parameter	Description	Median	95% CI		RMSE	NRMSE
r1	Proportion of Exilis genes from Nana	0.159	0.0414	0.386	0.178	1.12
r2	Proportion of Nana genes from Tundrarum	0.584	0.0772	0.922	0.297	0.509
r3	Proportion of Glandulosa genes from Exilis	0.512	0.363	0.640	0.0225	0.0439
r4	Proportion of Tundrarum genes from Nana	0.463	0.0397	0.843	0.297	0.641
1-r5	Proportion of Glandulosa west genes from Glandulosa West (as opposed to Glandulosa east)	0.663	0.0958	0.960	0.0347	0.0523

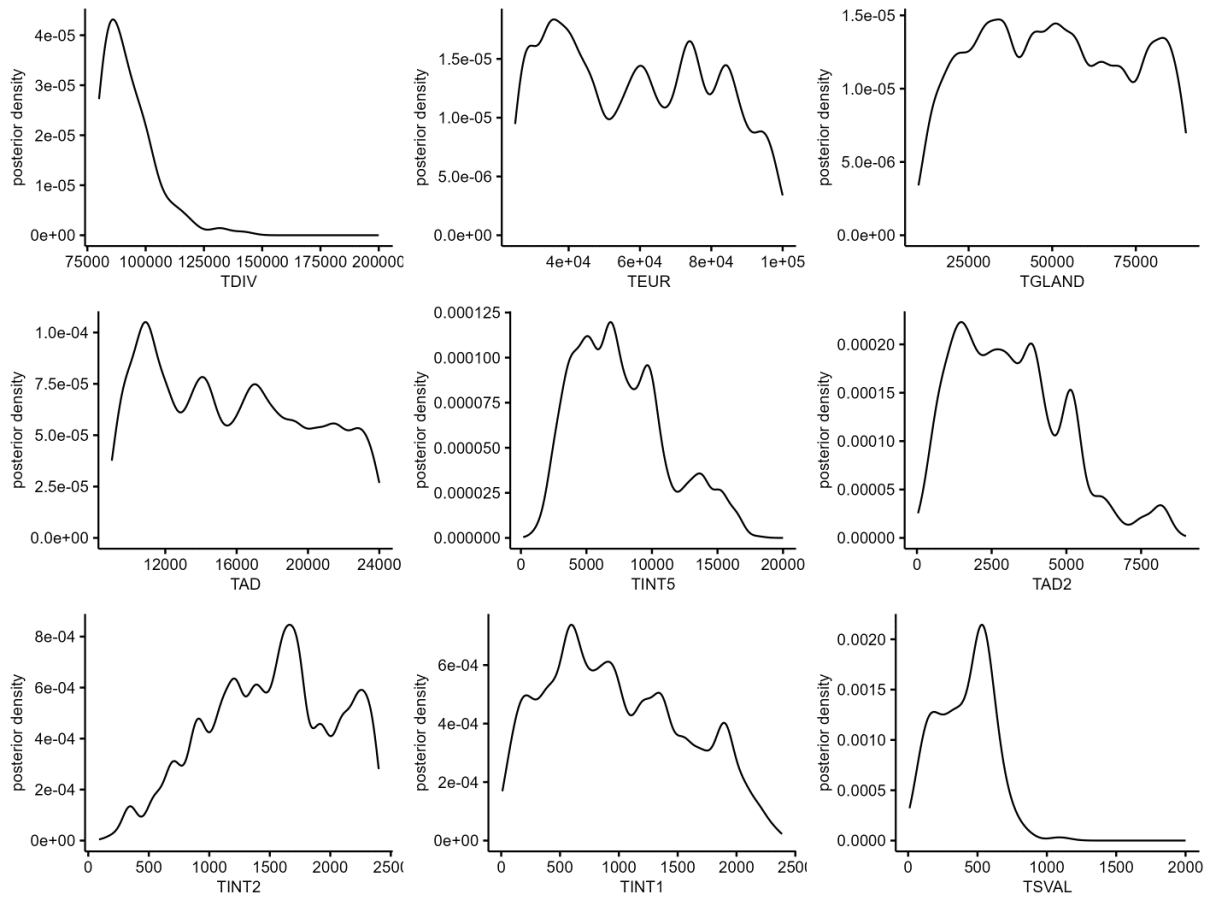


Figure S4.24. Posterior probability distributions for time parameters from the best supported scenario in global model set 22. Time given in number of generations.

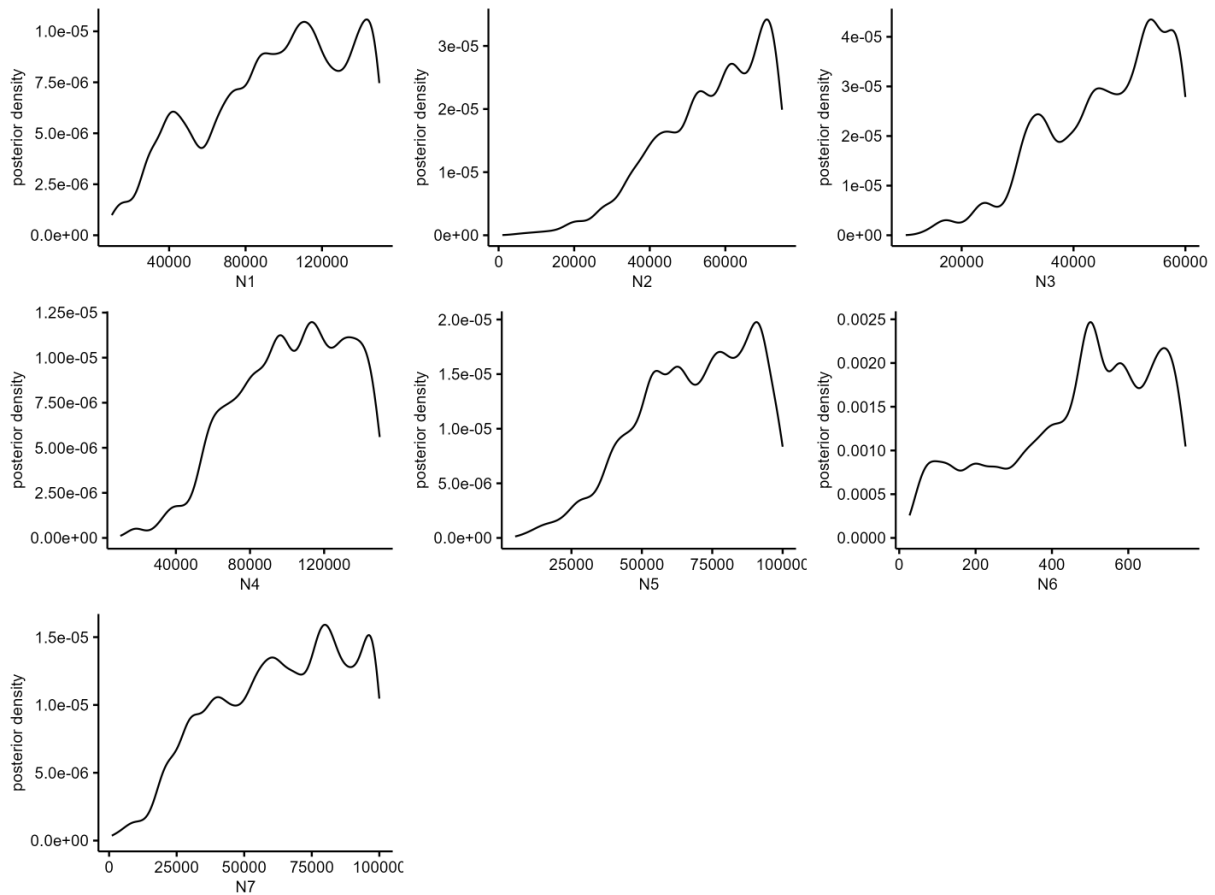


Figure S4.25. Posterior probability distributions for population size parameters from the best supported scenario in global model set 22. The parameters are effective haploid population size (N_e): 1/2 of effective population size as *Betula nana* and *Betula glandulosa* are diploid.

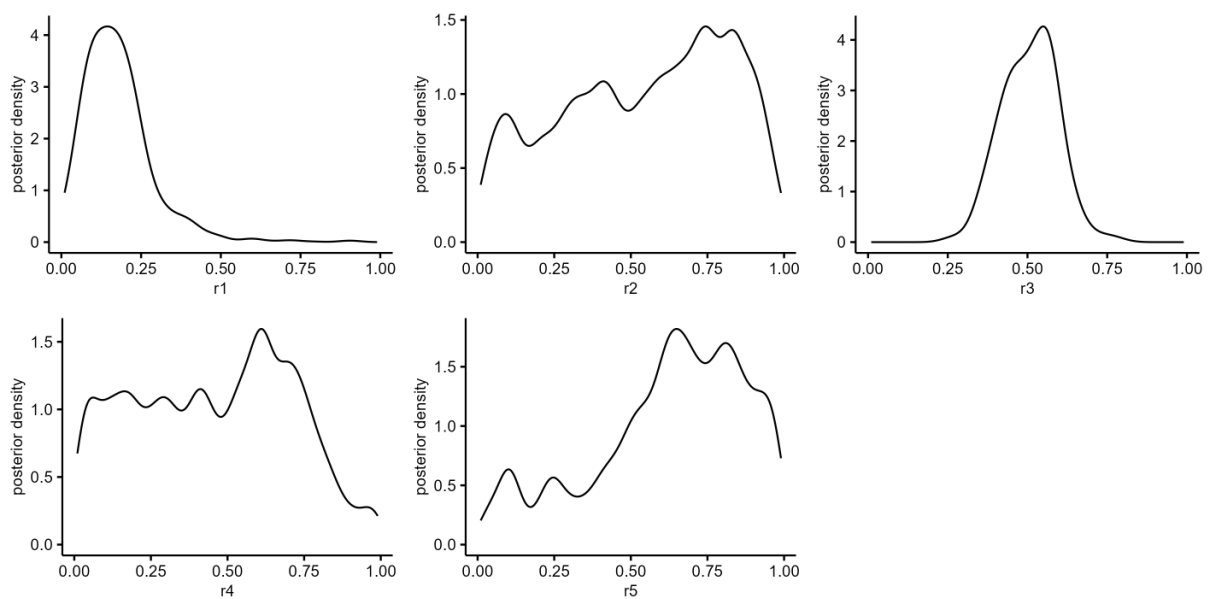


Figure S4.26. Posterior probability distributions for admixture rate parameters from the best supported scenario in global model set 22.

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Chapter 5:

Arctic greening patterns reflect genetic legacies of glacial refugia and past climate change

Maria Dance^{1,2}, James Borrell³, Logan T Berner⁴, Pernille Bronken Eidesen^{2,5}, Daniel Ackerman^{6*}, Jakob Assmann^{7*}, Bruce C. Forbes^{8*}, Marina Gurskaya^{9*}, Toke T. Høye^{10*}, Stein R. Karlsen^{11*}, Timo Kumpula^{12*}, Mariusz Lamentowicz^{13*}, Michael M Loranty^{14*}, Isla Myers-Smith^{7*}, Janet Prevéy^{15*}, Christian Rixen^{15,16*}, Gabriela Schaepman-Strub^{17*}, Michał Słowiński^{18*}, Sandra Słowiński^{19*}, Aleksandr Sokolov^{20*}, James D M Speed^{21*}, Marcus Spiegel^{1*}, Martin Wilmking^{22*}, Marc Macias-Fauria¹



Photo: Marc Macias-Fauria

¹School of Geography and the Environment, University of Oxford, Oxford, UK; ²The University Centre in Svalbard; ³Royal Botanic Gardens, Kew, London, UK; ⁴Northern Arizona University, Flagstaff, Arizona, USA; ⁵University of Oslo, Oslo, Norway. ⁶University of Minnesota, Minneapolis, USA; ⁷The University of Edinburgh, Edinburgh, UK; ⁸Arctic Centre, University of Lapland, Rovaniemi, Finland; ⁹Institute of Plant and Animal Ecology, UB RAS, Yekaterinburg, Russia; ¹⁰Department of Ecoscience, Aarhus University, Aarhus, Denmark; ¹¹Northern Research Institute NORUT, Tromsø, Norway; ¹²University of Eastern Finland, Kuopio, Finland; ¹³Adam Mickiewicz University, Poznań, Poland; ¹⁴Department of Geography, Colgate University NY, New York, USA; ¹⁵WSL Institute for Snow and Avalanche Research, SLF, Davos,

Switzerland; ¹⁶Climate Change, Extremes and Natural Hazards in Alpine Regions Research Center CERC, Davos, Switzerland; ¹⁷Department of Evolutionary Biology and Environmental Studies, University of Zurich, Switzerland; ¹⁸Institute of Geography and Spatial Organization Polish Academy of Sciences (IGSO PAS), Warsaw, Poland; ¹⁹Stanisław Leszczycki Institute of Geography and Spatial Organization Polish Academy of Sciences (IGSO PAS), Warsaw, Poland; ²⁰Arctic Research Station of the Institute of Plant and Animal Ecology, UB RAS, Labytnangi, Russia; ²¹Department of Natural History, NTNU University Museum, Norwegian University of Science and Technology, Trondheim, Norway; ²²Institute of Botany and Landscape Ecology, University of Greifswald, Greifswald, Germany.

*Shrub Hub data contributors.

5.1 Chapter statement

Chapter 5 addresses the third objective of the thesis, to test whether the impacts of Quaternary climate change on the modern genetic structure of the dwarf birches, explored in in **Chapter 4**, may be influencing their response to contemporary climate change. The analyses in **Chapter 4** and **Chapter 5** were conducted in parallel so results are presented independently before being synthesised in **Chapter 6**. This chapter examines contemporary Arctic shrub expansion and associated high latitude vegetation greening trend, in which the dwarf birches are implicated, as an opportunity to test this objective.

The study has its foundation in the well-established research field investigating Arctic greening, a major contemporary environmental change that is occurring on a panarctic scale. We use an exploratory and novel approach to address unresolved predictors of greening trends. Previous research has focussed on extrinsic potential drivers of greening such as contemporary environmental conditions and recent changes (Mekonnen et al., 2021), with a more limited focus on the role of historical conditions (Chen et al 2021; Ropars et al., 2015a, Reynolds & Walker 2009). The role of intrinsic biological factors in explaining heterogeneity in trends is underexplored, although the ability of plant traits to predict shrub responses to climate change has been tested (Garcia-Criado et al 2023).

This study is the first to examine greening trends in relation to the genetic structure of an ecologically dominant Arctic shrub species using a novel genetic dataset. The goal is to determine how the impacts of past climate change on contemporary genetic structure may shape adaptation and resilience of Arctic tundra shrubs to anthropogenic climate change. This paper was presented at the Arctic Science Summit Week conference in February 2023, and has been submitted as a primary research article to *Global Change Biology*.

5.2 Author contributions

MD and MMF designed the research. MMF designed and coordinated data collection. DA, JA, BCF, MG, TTH, SRK, TK, ML, MML, IMS, JP, CR, GSS, MS, SS, AS, JDMS, MSp, and MW contributed to data collection. JB advised on DNA extraction, sequencing, and bioinformatics. LB processed the greening data and provided code templates. MD performed DNA extraction and genetic data processing. MD performed data analyses and drafted the article with input from MMF. All authors contributed to manuscript commenting and editing.

5.3 Abstract

Arctic shrubs are expanding, and the tundra is greening in response to climate warming. However, spatiotemporal heterogeneity in trends suggests an interplay of extrinsic and intrinsic drivers. The adaptive capacity of Arctic shrubs to climate change depends on genetic variation, in turn shaped by past climate change. Yet the influence of genetic variation on the greening trend is unknown. We examine whether contemporary greening trends are influenced by genetic legacies of glacial refugia and postglacial dispersal, as exemplified by the dwarf birches, a major component of tundra vegetation and greening.

We analysed the range-wide genetic diversity and admixture of the dwarf birch species *Betula nana* (L.) and *Betula glandulosa* (Michx.) using a newly compiled next-generation sequenced RADSeq genetic data set from 43 sites throughout the Arctic. We compared site-level genetic diversity, admixture, and time since deglaciation with Landsat-derived EVI2 greening trends. We predicted the magnitude of greening using Random Forest regression modelling to test the importance of genetic characteristics in relation to environmental controls.

We found significant greening trends at 51.2% of our study sites over the last two decades, while only 9.3% of sites showed significant browning. The magnitude of greening was greater in sites with genetically diverse dwarf birch populations and with genetic material from multiple ancestral groups. The magnitude of greening was also greater in landscapes that were not glaciated during the last glacial cycle. These variables improved models and made a substantial contribution to explaining variance in greening trends. Recent increases in mean annual temperature and soil moisture were overall the most important environmental factors for explaining greening magnitude, in agreement with previous literature.

Our results suggest that factors related to past climate change are linked to tundra greening alongside contemporary climatic change. The importance of landscape age and dwarf birch genetic diversity — particularly admixture — point to the influence of glacial refugia and historical population mixing on the magnitude of vegetation greening. Overall, we show that the tundra greening response to contemporary climate change is modulated by late Quaternary legacies.

Keywords: Arctic, *Betula*, dwarf birch, EVI, glaciation, intraspecific genetic diversity, Quaternary climate change, RADSeq, shrub expansion, tundra greening

5.4 Introduction

Climate warming is contributing to shrub expansion (“shrubification”) in the Arctic tundra (Elmendorf et al., 2012; Mekonnen et al., 2021; Myers-Smith et al., 2011; Sturm et al., 2001). The dwarf birches – *Betula nana* (L.) and *Betula glandulosa* (Michx.) – are ecologically important tundra shrubs that comprise a substantial portion of the regional vegetation (de Groot et al., 1997). The dwarf birches are implicated in shrub expansion across the Arctic (Andruko et al., 2020; Fraser et al., 2014; Lantz et al., 2013; Larking et al., 2021; Moffat et al., 2016; Tape et al., 2006; Tremblay et al., 2012), which is supported by their strong positive recruitment and growth responses under experimental warming and associated nutrient increases (Chapin et al., 1995; Milbau et al., 2009; Shaver et al., 2001).

Satellite-derived vegetation indices are useful proxies for Arctic shrubification (Forbes et al., 2010; Mekonnen et al., 2021). The overall increase in Arctic tundra aboveground biomass in recent decades has left a clear signal in vegetation indices derived from remote sensing imagery, termed “the greening of the Arctic” (Jia et al., 2003; Myneni et al., 1997; Zhou et al., 2001). Normalised Difference Vegetation Index (NDVI), a measure of vegetation greenness related to photosynthetic activity, has been shown to relate to tundra plant productivity and aboveground biomass through comparison with field measurements of gross primary productivity (Street et al., 2007) biomass harvests (Berner et al., 2018; Reynolds et al. 2012), and shrub ring chronologies (Blok et al., 2012; Macias-Fauria et al., 2012; Ropars et al., 2015b; Weijers et al., 2018; Berner et al., 2020). An increase in summer NDVI has been directly linked to increased aboveground biomass of deciduous shrubs using repeat aerial photography (Fraser et al., 2014; Frost et al., 2014) and shrub ring width chronologies (Andreu-Hayles et al., 2020; Forbes et al., 2010; Ropars et al., 2015b). Increases in the Enhanced Vegetation Index (EVI), which is related to canopy structure as well as photosynthetic activity, (Huete et al., 2002; Kushida et al., 2015), have been linked to increased shrub cover in the Canadian Arctic (Chen et al., 2021; Seider et al., 2022). Vegetation indices enable systematic comparisons across Arctic regions with little – but essential – ground-based monitoring (Berner et al., 2020; Bjorkman et al., 2018).

Tundra greening is a circumpolar phenomenon with local to regional heterogeneity (Berner et al., 2020; Myers-Smith et al., 2020). Greening is more widespread in the Low Arctic than

High Arctic (Berner et al., 2020; Chen et al., 2021; Lantz et al., 2010), and is particularly common at the tundra-taiga transition (Myers-Smith et al., 2020). On a panarctic scale, summer and winter air and soil temperatures, moderated by moisture availability, are important for increased shrub growth (Hollesen et al., 2015; Myers-Smith et al., 2015; Myers-Smith & Hik, 2018) and tundra greening (Berner et al., 2020; Chen et al., 2021; Seider et al., 2022). On local to regional scales, hydrology, topography, disturbance, herbivory, and nutrient availability are also important (Mekonnen et al., 2021). Over the last decade, the link between greening and temperature appears to have weakened (Keenan & Riley, 2018; Piao et al., 2020) as temperature correlations with vegetation growth have declined, particularly in the Low Arctic (Elmendorf et al., 2012; Lantz et al., 2013; Myers-Smith & Hik, 2018). This suggests other controlling factors (Martin et al., 2017).

Variation in shrub growth may be linked to intrinsic differences within and between species as well as extrinsic environmental factors (Shao et al., 2019). Long-lived woody plants have evolved a high level of tolerance to a range of environmental conditions, with individuals displaying phenotypic plasticity, i.e., the ability to alter traits in response to environmental change without changing genotype (Gratani, 2014; Nicotra et al., 2010). The expansion of the dwarf birches may be linked to their growth plasticity, as well as their high reproductive potential due to clonal growth, long-distance dispersal ability, and mycorrhizal networks (Bret-Harte et al., 2001; Deslippe et al., 2011; Deslippe & Simard, 2011; Ropars & Boudreau, 2012; Weis & Hermanutz, 1988).

However, differences in predicted growth and range shifts of tundra shrubs under climate change do not appear to be consistently explained by differences in traits (García Criado et al., 2023), although species with greater trait variation may undergo larger range shifts (García Criado et al., 2023). Trait variation is also linked to genetic variation (Csilléry et al., 2020; Karbstein et al., 2020; Waitt & Levin, 1998). High genetic diversity may increase plasticity (Falk & Holsinger, 1991) which has a genetic basis (Karbstein et al., 2020), and therefore influence species short-term responses to environmental change. High genetic variation is also essential for long-term adaptation to climate change (Alberto et al., 2013; Caballero & García-Dorado, 2013; Davis et al., 2005; Hoffmann & Sgrò, 2011; Pauls et al., 2013). Genetic variation may therefore be an underappreciated and unexplored factor in the response of tundra shrubs to climate change.

Arctic plant genetic variation has been strongly shaped by past climate change (Abbott, 2008; Abbott & Brochmann, 2003). Species geographical ranges underwent drastic contractions and expansions in response to Quaternary glaciations (~2.6 million years ago to the present) (Birks, 2008). Pollen and sedimentary DNA records show that dwarf birch occurred north of its current range during warmer interglacials (Anderson & Brubaker, 1994; Crump et al., 2021; Fewster et al., 2023; Kullman, 1995; Meucci et al., 2021) and that its range was restricted during glacials (Bigelow et al., 2003; Binney et al., 2017). These distributional changes caused repeated genetic isolation and mixing between populations (Hofreiter & Stewart, 2009), leaving lasting impacts on the contemporary genetic variation of dwarf birch (Eidesen et al., 2015) and other arctic plants (Brochmann & Brysting, 2008; Davis & Shaw, 2001; Hewitt, 2004; Kadereit & Abbott, 2021).

Large unglaciated regions such as Beringia (Hultén, 1937) were important refugial areas for many Arctic species including dwarf birch (Abbott, 2008; Eidesen et al., 2015; Stewart et al., 2010). Beringia spanned an area from the Mackenzie River in North America to the Lena River in Russia (**Figure 5.1**). Contemporary populations in these oldest regions tend to contain the highest genetic diversity and distinctiveness (Eidesen et al., 2013; Stewart et al., 2016). As ice sheets retreated and populations expanded, successive founder events decreased genetic diversity with distance from refugia (Hewitt, 1996; Ibrahim et al., 1996; Pellissier et al., 2016). However, population expansion also led to contact between populations from different refugia (Hewitt, 2000; Petit et al., 2003), resulting in admixed populations with higher genetic diversity (Eidesen et al., 2015; Hewitt, 2004).

Arctic shrub populations with higher genetic diversity likely have increased adaptive potential to respond to ongoing and future climate change (Pauls et al., 2013; Savolainen et al., 2007). Yet the influence of genetic variation on shrubification and associated greening trends is unknown. In this study we quantify genetic diversity of the dwarf birches *Betula nana* and *Betula glandulosa* using new genetic data. We examine whether high latitude greening trends are influenced by genetic legacies of glacial refugia and postglacial dispersal by comparing Landsat-derived EVI2 greening trends with genetic diversity and admixture, and time since landscape deglaciation (“landscape age”) for 43 sites across the panarctic. We use a Random Forest regression modelling framework to predict the magnitude of greening and test the importance of genetic characteristics in relation to other environmental controls.

We hypothesise that stronger tundra greening trends are associated with increased dwarf birch genetic diversity and admixture and with landscapes less recently glaciated, and we test this hypothesis by examining the contribution of these features to explaining variance in greening trends. We further expect differences in greening trends for sites dominated by different dwarf birch taxa, since regional differences in herbivore regulation of dwarf birch expansion have been predicted due to possible taxon-specific differences in palatability (Christie et al., 2015; Lindén et al., 2022). Testing these hypotheses will develop our understanding of how legacies of Quaternary climate change in the genetic composition of Arctic shrubs impact their response to contemporary climate change.

5.5 Materials and methods

5.5.1 The dwarf shrubs

We examined the genetic diversity of two characteristic Arctic and boreal shrubs of peat bog and tundra environments: the dwarf birches *Betula nana* (L.) and *Betula glandulosa* (Michx.). *Betula nana* has a near-circumpolar distribution and a prostrate or upright growth habit up to ~1m in height (de Groot et al., 1997). *Betula nana* is sometimes divided into two subspecies, with *B. nana* subsp. *nana* (Sukaczew) Hult. in western Eurasia and Greenland, and *B. nana* subsp. *exilis* (Sukaczew) Hult. in eastern Eurasia and northwest North America, with ranges overlapping in western Siberia (Elven et al., 2011). *B. glandulosa* (Michaux.) is a closely related species occurring only in North America. It has similar habitat preferences but is less cold tolerant, and usually grows up to 2.5-3 m in height at the core of its range (de Groot et al., 1997). *Betula nana* subsp. *exilis* and *B. glandulosa* hybridise and form intermediates in areas of range overlap but form distinct entities elsewhere in their ranges (Furlow, 2004).

5.5.2 Genetic data

5.5.2.1 Plant sampling and DNA extraction

Samples were collected from sites across the species ranges during the growing season from 2015-2021. See **Appendix S5.1** for detail on sample collection and storage. Extracting high-quality DNA from dwarf birch is challenging due to high concentrations of secondary compounds such as polysaccharides and phenolics/polyphenols in leaves (Wang et al., 2013). Total genomic DNA was extracted from dried leaves following a new protocol (see **Thesis**

Appendix A), with 244 samples from 47 populations passing the quality control process after extraction (**Figure 5.1; Table S5.1**).

5.5.2.2 RAD sequencing and genotyping

DNA extracts were submitted to FLORAGENEX (Beaverton, Oregon) for RAD (Restriction site-associated) library preparation and sequencing (RADseq). Sequenced reads were demultiplexed and analysed for quality assurance and control using the process_radtags module of Stacks v 2.60 software (Catchen et al., 2011, 2013; Rochette et al., 2019) and fastqc software (Andrews, 2010). Reads were aligned to a reference *B. nana* genome (Wang et al 2013), ENA accession number GCA_000327005 using Bowtie2 v2.5 (Langmead & Salzberg, 2012).

Reference-based Single Nucleotide Polymorphism (SNP) genotyping was performed using the gstacks module of Stacks v 2.60. The populations module of Stacks v 2.60 was used to filter loci. Loci were retained that were present in 70% of individuals within a sampling site, or present in 70% of individuals across sampling sites. SNPs with a Minor Allele Frequency (MAF) of <0.01 were excluded to remove uninformative markers. We retained one SNP per locus as downstream analyses of population genetic structure required unlinked alleles. The output was filtered further to remove loci that were correlated with other loci for PCA and ADMIXTURE ((Alexander et al., 2009; Alexander & Lange, 2011) analyses. See **Appendix S5.2** for details on RAD sequencing and genotyping.

5.5.2.3 Genetic diversity

Rarefied population allelic richness (the number of alleles per locus corrected for sample size, “allelic richness” hereafter) is a genetic diversity measure that contains information about the genetic variability and long-term evolutionary potential of a population (Caballero & García-Dorado, 2013; Greenbaum et al., 2014). Population-level expected heterozygosity, also known as gene diversity, is the probability that an individual will possess two different alleles at a given locus, under Hardy-Weinberg equilibrium (Catchen et al., 2013). It reflects available genetic variability in a population and therefore short-term evolutionary potential (Caballero & García-Dorado, 2013; Hoffmann et al., 2017; Ørsted et al., 2019). Allelic richness is expected to decline with increasing distance from glacial refugia as multiple population founder events lead to allele losses (Comps et al., 2001; Hewitt, 1996). Less steep declines are expected in

gene diversity, which is less sensitive to bottlenecks (Comps et al., 2001). Both measures of genetic diversity are expected to increase in areas where populations from different refugia mix (Boca et al., 2020; Petit et al., 2003; Widmer & Lexer, 2001).

Allelic richness was calculated using the hierfstat package v 0.5-7 in R v 4.0.3 (R Development Core Team, 2022). Gene diversity was extracted from the Stacks populations output using variant sites only. Relationships between these indices of genetic diversity and latitude were assessed using non-parametric Spearman's Rank Correlation tests, which allow for potential non-linear relationships, implemented in the `stat_cor()` function in the R package `ggpubr` v 0.4.0 (Kassambara, 2023).

5.5.2.4 Population genetic structure and admixture

We analysed the genetic structure of each subspecies to determine whether subspecies contributed to explaining variation in greening trends. Given potential hybridisation and morphological similarity between *B. nana exilis* and *B. glandulosa* in areas of range overlap, we assessed genetic similarity between subspecies as identified in the field and identified individuals whose genetic structure did not match their field taxonomic identification. We assessed genetic similarity with principal component analysis (PCA) of the SNP data with the `ade4` package v2.1.3 (Jombart, 2008).

To identify possible *B. nana* subsp. *exilis* and *B. glandulosa* hybrid populations, we used the software ADMIXTURE v 1.3.0 (Alexander et al., 2009; Alexander & Lange, 2011). Genetic admixture occurs when previously isolated and genetically distinct populations interbreed, and offspring inherit a mixture of alleles from different ancestral populations (Skotte et al., 2013). Hybridisation usually refers specifically to admixture between different species (Eidesen et al., 2015). As ADMIXTURE infers the number of ancestral populations and shows which sampling sites contain more than one ancestral population, it is useful for detecting hybridisation and admixture. ADMIXTURE outputs maximum likelihood estimates of ancestry coefficients that indicate the proportion of an individual's alleles that come from K hypothesized ancestral populations (Alexander & Lange, 2011). We tested a range of 2-5 possible ancestral populations (K); the K with the lowest cross-validation error was chosen as the optimal value. We plotted population assignment probabilities for each individual using

the ancestry fractions output files in ggplot2 (Wickham, 2016) in R v 4.0.3 (R Development Core Team, 2022) (See **Appendix S5.3** for further details).

We reclassified individuals by predominant ADMIXTURE ancestral population (genetic group). We equated the number of ancestral populations with the number of genetically distinct groups. Individuals were reassigned to a genetic group if they had >50% assignment probability (ancestral coefficient > 0.5) to that corresponding ancestral population. Sampling sites containing individuals from more than one genetic group and where individuals also contained more than 10% assignment probability to another genetic group were classified as “hybrid” sites. To differentiate between taxonomic species and genetic groups, subspecies are referred to in italics, while genetic groups are in regular text and capitalised.

Genetic diversity metrics were recalculated by genetic group. ADMIXTURE ancestry coefficients were also used to derive estimates of genetic admixture proportion — the proportion of genetic material in individuals arising from admixture — for each sample site. Individual admixture proportion was calculated as the sum of the coefficients of the secondary ancestral groups (i.e. groups with an admixture coefficient of < 0.5 in an individual), so that admixture proportion could vary between 0 and 0.49. Mean admixture proportion was calculated by averaging individual admixture proportions occurring at a site.

We tested for significant differences in genetic diversity between the genetic groups with one-way analysis of variance (ANOVA) tests and compared differences between the group means with a post hoc Tukey test. Non-parametric Kruskal-Wallis rank sum tests were used when the variance of samples was non-equal. All statistical analyses were implemented in the stats R package v 4.0.3 (R Development Core Team, 2022).

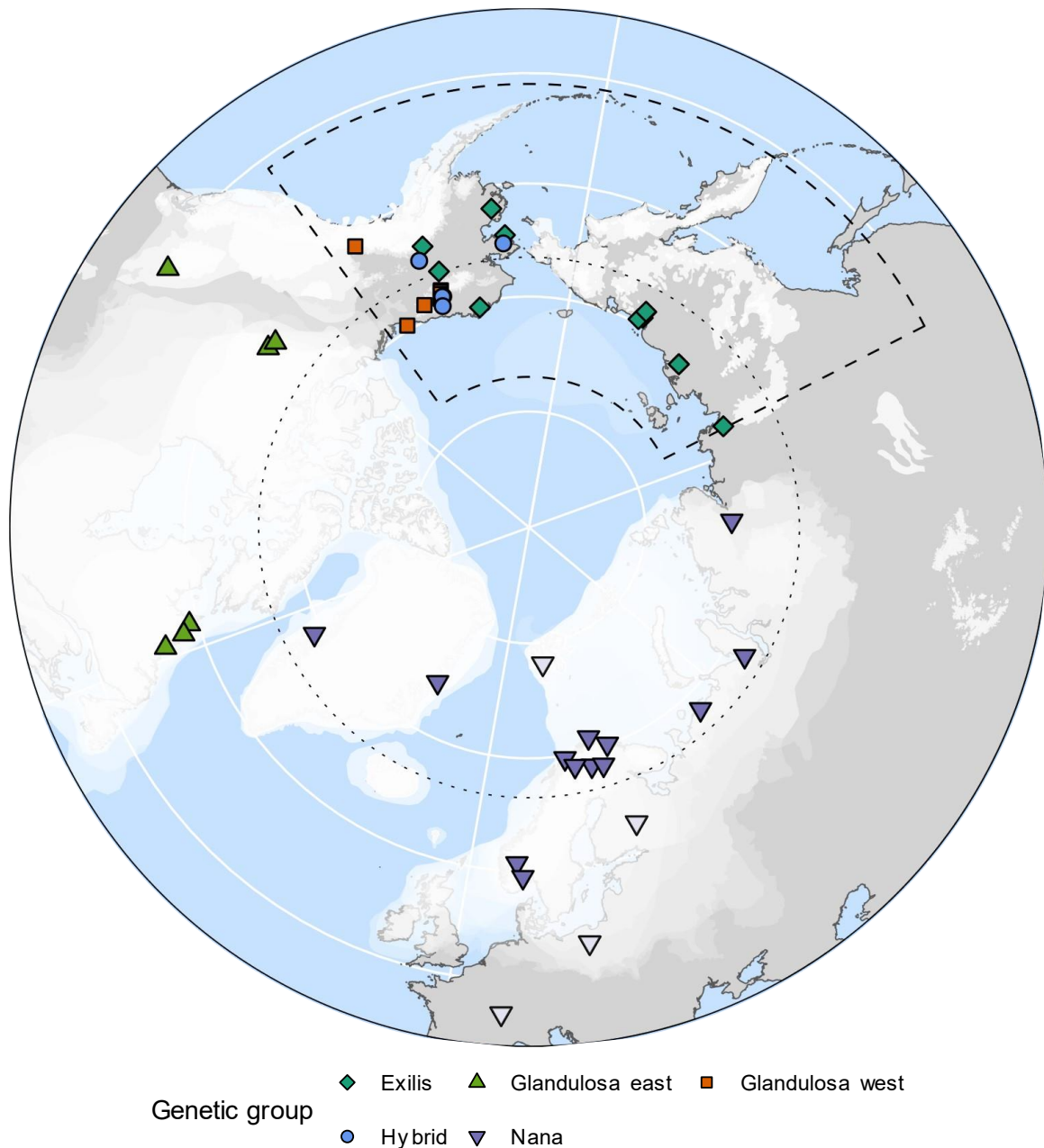


Figure 5.1. Map of dwarf birch sampling sites sequenced for DNA with associated genetic groups. Sites coloured according to genetic group (see **Section 6.1** in Results). Individuals were assigned to genetic groups based on >50% ancestry proportion in the corresponding ADMIXTURE (Alexander et al., 2009; Alexander & Lange, 2011) ancestral population. Sampling sites containing individuals from more than one genetic group, and where individuals were completely admixed genetically, were classified as “hybrid” genetic groups. See **Figure S5.1** for a detailed Alaska map. Four sampling sites that were not used in the greening analysis due to lack of Landsat data or unsuitable regional landcover are shaded in grey. Ice sheet intensity plotted in white shows relative amount of time that regions were covered by ice sheets during the Quaternary glacial period. Intensity was produced by overlaying best-estimated ice sheet reconstructions (Batchelor et al., 2019; Dalton et al., 2020, 2022; Hughes et al., 2016). The earliest period (1.78 - 2.6 million years ago) is omitted because of the broad timespans and high uncertainty of these reconstructions (Batchelor et al., 2019). The Arctic circle (66°33'N) is plotted as a dotted line and Beringia is plotted as a dashed polygon.

5.5.3 Remote sensing data

5.5.3.1 Landsat vegetation index time series

We estimated annual maximum vegetation greenness (NDVI_{max} and EVI2_{max}) around each sampling site using Landsat surface reflectance measurements from 2002 to 2021. To identify tundra and other treeless vegetation around each sampling site, we used the natural non-forest land cover classes from the ESA WorldCover 2021 v200 data set (Zanaga et al., 2022), which we clipped to north of 45°N and majority projected to Bering Sea Albers Equal Area at 30 m resolution. We excluded three dwarf birch sampling sites from the greening analysis because they occurred in temperate lowlands that were not representative of tundra vegetation, and one site because Landsat data were not available (**Table S1**). For each sampling site, we created 100 random sample points in tundra vegetation within a 50 km buffer. For every random sample point, we then exported from the Landsat Collection 2 archive on Google Earth Engine (Gorelick et al., 2017) all Landsat 5, 7, and 8 surface reflectance measurements acquired June through August during those two decades. We exported and processed the Landsat data using the LandsatTS package v1.1.0 for R (Berner et al., 2023).

We removed reflectance measurements affected by clouds, shadows, and surface water using quality assurance flags, and performed additional quality assurance, then derived spectral vegetation indices including NDVI (Rouse et al., 1974) and EVI2 (Jiang et al., 2008). While both are indicators of potential photosynthetic activity, EVI2 is less prone than NDVI to saturation in dense vegetation (Jiang et al., 2008). There are systematic differences in NDVI and EVI2 among Landsat 5, 7, and 8 (Berner & Goetz, 2022), so we cross-calibrated the spectral indices from Landsat 5 and 8 with Landsat 7 using polynomial regression models fit to a large sample of Landsat pixels from across northern lands (Berner et al. 2023). To remove barren sample points, we filtered out those with average summer NDVI < 0.15, which corresponds to tundra aboveground biomass of approximately 50 g m⁻² (Berner et al., 2018). We derived annual estimates of NDVI_{max} and EVI2_{max} using site-specific phenological modelling that reduces the impact of uneven data in the Landsat record (Berner et al., 2020). While targeting 100 random pixels, each sampling site ultimately had suitable Landsat time series for between 21 and 100 (median = 93) sample points. An overall time series of annual EVI2_{max} was calculated for each dwarf birch sampling site by averaging EVI2_{max} across all available pixels using

Tukey's Biweight Robust Mean implemented in the dplR package v 1.7.4 for R (Bunn et al., 2022).

5.5.3.2 Landsat greening trends

EVI2_{max} anomalies and trends were calculated from 2002-2021 due to incomplete Landsat panarctic coverage prior to 2002. Using the zyp R package v 0.10.1.1 (Bronaugh & Werner, 2019), the presence of a monotonic trend in the time series was assessed using a rank-based Mann-Kendall trend test, and the slope of each time series was determined using a non-parametric Theil–Sen slope estimator to account for temporal autocorrelation (Berner et al., 2020). Trends were calculated for each dwarf birch site and across sites. We classified sites with a positive trend ($\alpha=0.10$) as greening and a negative trend ($\alpha=0.10$) as browning (Berner et al., 2020). We examined the distribution of greening trends for each genetic group, tested if the slope of the greening trend varied by group with one-way analysis of variance (ANOVA) tests, and compared differences between group means with a post hoc Tukey test, implemented in the R stats package v 4.0.3 (R Development Core Team, 2022). Greening trends were available for 43 out of 47 dwarf birch sampling sites (**Table S5.3**).

5.5.4 Environmental data sets

5.5.4.1 Landscape age

The length of time since the most recent glacial ice sheet retreat from a given point in the landscape is an indicator of how long the landscape has been available for plant colonisation and plant community development (Raynolds & Walker, 2009). Landscape age was calculated for each dwarf birch sampling site using reconstructions of ice margins based on recent syntheses of published dates from geological and geomorphological records, and numerical modelling (Batchelor et al., 2019; Dalton et al., 2020, 2022; Hughes et al., 2016). Seventeen time slices were available from the onset of the Quaternary (2.6 million years ago) to the Last Glacial Maximum (LGM) (Batchelor et al., 2019). Higher temporal resolution data were available from 115-25 thousand years ago (ka) (at 5 ka intervals) and from 25-6ka (at 0.1-0.7 ka intervals) for the Laurentide and Innuitian ice sheets in North America (Dalton et al., 2020, 2022), and from 25-10 ka (1 ka intervals) for the Eurasian Ice Sheet (Hughes et al., 2016). Shapefiles of ice margins at each time slice were used to plot the position of sampling sites in relation to ice sheets over time. Landscape age was calculated as the time encompassed

between the last time that a sampling site became ice-free in the last 2.6 million years and the present, based on the date and position of the closest ice sheet margin.

5.5.4.2 Environmental timeseries (period 2002-2021)

We obtained time series of additional climatic and environmental variables which may influence greening trends from 2002-2021 (see Introduction).

Summer air temperature. Recent changes in summer temperatures were characterised with annual cumulative summer heat load, i.e. summer warmth index (SWI), calculated as the annual sum of mean monthly air temperatures above 0°C. Two data sets with different spatial resolutions were used: ARCLIM v 2 (Rantanen et al., 2023) SWI at 0.1 x 0.1° resolution and Climate Research Unit gridded Time Series (CRU TS) v 4.06 (Harris et al., 2020) mean monthly temperatures at 0.5 x 0.5° resolution.

To assess inter-annual covariation between SWI and greening anomalies, we compared EVI2_{max} and SWI anomalies at each sampling site using Spearman's Rank Correlation tests. As the strength of correlation could be influenced by underlying trends in both time series, and greening may depend on temperatures in the previous growing season, we assessed correspondence for each site using current and 2-year average SWI, and after linearly detrending the SWI and greening time series by taking the residuals from a linear model of anomalies against year.

Soil moisture. Annual estimates of minimum summer soil moisture were calculated from mean monthly soil moisture at 0.042° resolution from the TerraClimate 2022 data set (Abatzoglou et al., 2018).

Soil temperature. Annual permafrost ground temperature (1 m depth) at 0.927 km resolution was obtained from the ESA Permafrost Climate Change Initiative v3.0 (Obu et al., 2021). Mean annual air temperatures (MAT) were also extracted from the ARCLIM data set to help account for warming outside the growing season.

Regional time series of climate variables for each dwarf birch site were calculated by extracting and averaging annual values within a 50km radius around the site coordinates using the extract function in the raster R package (Hijmans et al., 2023). An average pixel size of 50km was previously used for assessing predictors of Landsat greening trends (Berner et al.,

2020), and a radius of 50km was also expected to match the spatial scale of the genetic data, based on the genetic similarity and geographic distance between sampling sites in the PCA (**Figure 5.2**). To assess recent changes in climate variables, we calculated the slope of each time series using a non-parametric Theil–Sen slope estimator to account for temporal autocorrelation (Berner et al., 2020), as well as calculating total change across the period of interest (slope multiplied by number of years).

5.5.4.3 Time-invariant environmental data

Finally, we considered other potentially explanatory variables for which we obtained a time-invariant value. These are:

Elevation. Elevation data were extracted in a 50 km radius of each dwarf birch site from AWS Open Data Terrain Tiles using the *elevatr* R package v 0.4.5 (Hollister et al., 2023) to account for the influence of topography on greening (Chen et al., 2021). Data were extracted at two spatial resolutions: 152 m and 38 m resolution at 60°N. Topographic heterogeneity was calculated as the standard deviation of elevation around each dwarf birch site.

Bioclimatic subzones. To examine regional differences in greening trends, we extracted bioclimatic subzones of the Arctic according to the Circumpolar Arctic Vegetation Map (CAVM) (Conservation of Arctic Flora and Fauna, 2013; Raynolds et al., 2019) for each dwarf birch site.

Biome type. Biome type was extracted from WWF terrestrial ecoregions (Olson et al., 2001) using the *st_intersection* function from the *sf* R package v 0.9-7 (Pebesma, 2018) for sites outside the CAVM area. Sites outside the CAVM area that were assigned the WWF tundra biome were classed as *oroarctic* (Virtanen et al., 2015).

See **Table S5.4** for more details on environmental data sets.

5.5.5 Assessing variables associated with greening trends

The association between regional greening trends, genetic variables, and landscape age was first assessed using Spearman’s Rank Correlation tests (Berner et al., 2020). We constructed Random Forest (RF) regression models to evaluate the ability of genetic variables, landscape age, and contemporary climatic and environmental variables to predict the magnitude of

EVI2_{max} trends (the trend slopes) at dwarf birch sites. RF regression models are a supervised machine learning technique based on regression trees. Repeated sampling of data with replacement was used to derive many sample subsets (bootstrap samples). Each subset was used to train a different tree, which were then combined (bootstrap aggregated, or bagging) into an ensemble random forest model. The ensemble forest model then predicted the slope of EVI2_{max} trends based on unseen values of predictor variables, specifically, out-of-bag predictions of the original dataset.

Timeseries predictors included total change in SWI, MAT, minimum summer soil moisture, and annual soil temperatures from 2002-2021. Trend model intercept values (i.e., start year values) of climate variables were also used. Additional predictors included landscape age, bioclimatic zone/biome, topographic heterogeneity, and genetic group. Unique local factors were accounted for by including site identity, latitude, and longitude as predictors. Highly correlated variables ($r > 0.75$) were screened by computing pairwise correlations and removing the variable with the highest average absolute correlation. To test the importance of genetics and past climate change in relation to contemporary environmental controls, we also constructed models with only the genetic and landscape age variables.

Random Forest models were repeatedly fitted to optimise model error (root mean square error, RMSE) by varying the number of variables assessed at each node of the trees. The model with the lowest RMSE was selected and reassessed by predicting EVI2_{max} trend slope magnitude using the original training data ($n = 43$). The number of trees was selected based on the best fit model with highest variance explained.

Variable importance for predicting EVI2_{max} trends was ranked based on a) the percentage increase in MSE when variable values were randomly permuted, or effectively absent, from the model, and b) the increase in node purity caused by the variable. Partial dependence plots visualising the marginal effect of variables on the predicted EVI2_{max} slope were used to evaluate how greening trends varied across the range of each individual variable when all other variables were held constant. Model construction and evaluation were conducted using functions from the randomForest v 4.6-10 (Breiman et al., 2022) caret v 6.0-94 (Kuhn et al., 2023) and pdp v 0.8.1 (Greenwell, 2022) R packages.

5.6 Results

5.6.1 Dwarf birch population genetic diversity and landscape age

238 individuals from 47 dwarf birch sampling sites were sequenced and genotyped (**Table S5.1**). Two ancestral populations (genetic groups) largely corresponding to the recognised dwarf birch subspecies *B. nana* subsp. *nana*, *B. nana* subsp. *exilis*, and two ancestral populations within *B. glandulosa* were identified in the genetic data (Glandulosa west and east; **Figure 5.2A**). For 14 sample sites, field species identification did not match their ancestral population/genetic group (**Table S5.2**). The Glandulosa and Nana groups were most genetically differentiated according to PCA and pairwise F_{ST} , with the two Glandulosa groups least differentiated (**Figure 5.2B**; **Table S5.5**). Extensive genetic admixture appears to have occurred historically between the Nana and Exilis groups, and the Exilis and Glandulosa west groups (**Figure 5.2A**). Individuals dominated by both Exilis and Glandulosa west occurred in five sampling sites, where individuals were completely admixed genetically (“hybrid” populations) (**Table S5.2**; **Figure 5.1**). The genetic groups differed significantly in their gene diversity (ANOVA $F_{(4, 42)} = 17.89$, $p < 0.001$), rarefied allelic richness (ANOVA $F_{(4, 42)} = 17.89$, $p < 0.001$), and degree of genetic admixture ($H_2 = 32.617$, $p < 0.001$). Genetic diversity and admixture were highest in the Exilis-Glandulosa west sampling sites, and lowest in the Glandulosa east sampling sites (**Figure S5.3**; **Table S5.6**).

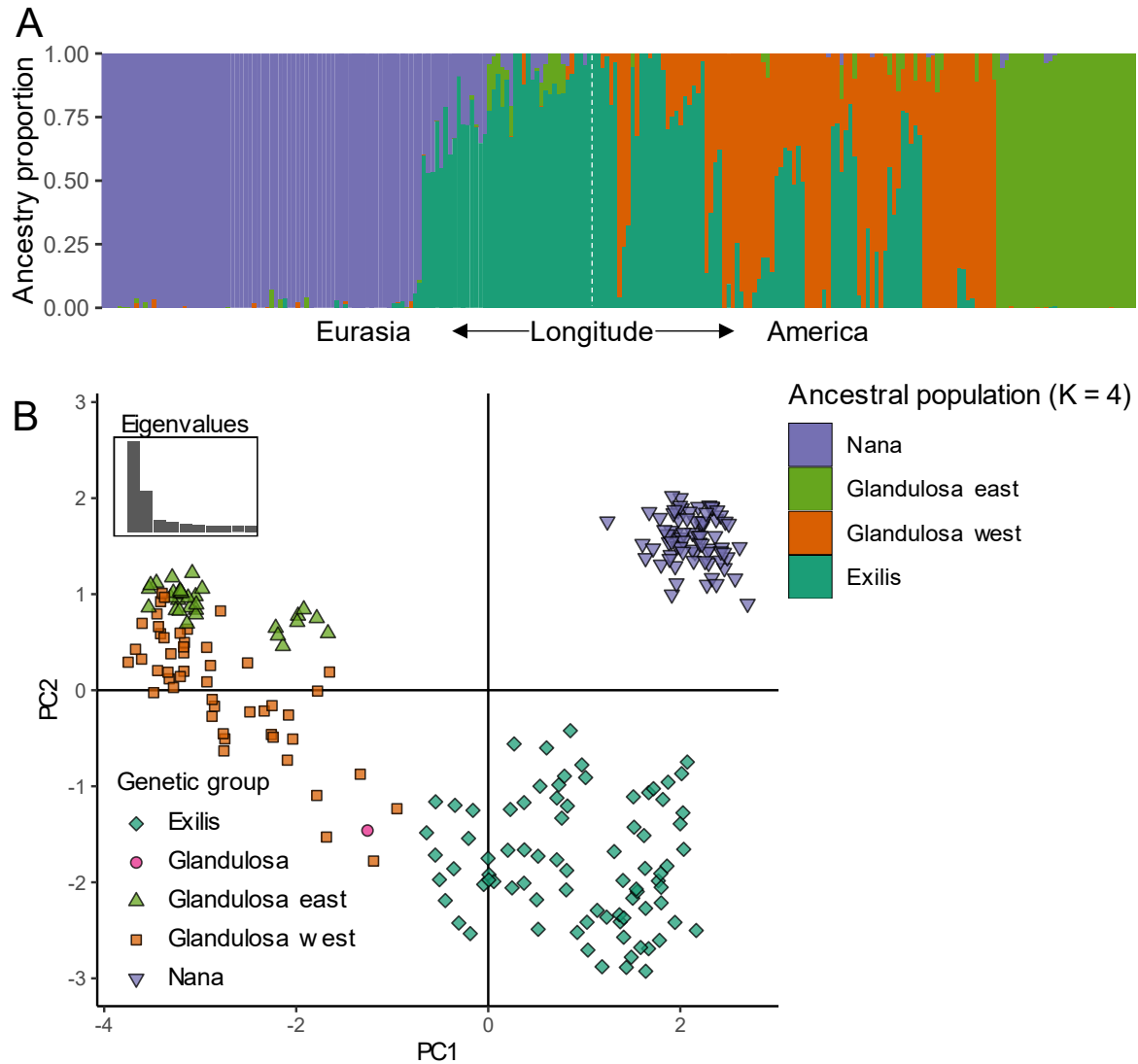


Figure 5.2. Population genetic structure of the dwarf birches. (A) Population genetic structure inferred from ADMIXTURE analysis (Alexander et al., 2009; Alexander & Lange, 2011). Colour corresponds to four hypothesised ancestral populations, with each dwarf birch individual plotted along longitude (x-axis), represented by bars with total ancestry proportions (y-axis). White dotted line indicates the division between Eurasian and American samples with the Bering Strait. (B) PCA of genetic variation among dwarf birch individuals coloured according to genetic groups. The sum of the variances explained by the first two principal components (PCs) was 22.1% and are plotted in an ordination plot, with an inset scree plot of eigenvalues for the first five PCs. Individuals were assigned to genetic groups based on >50% ancestry proportion in the corresponding ADMIXTURE ancestral population in (A). One individual was nearly equally admixed between both glandulosa groups and exilis and was assigned to a Glandulosa group. Taxonomic subspecies are in *italics*, while genetic groups are in regular text and capitalised.

Genetic diversity measures were highest at intermediate latitudes, with a significant positive Spearman's correlation between latitude and genetic admixture proportion (**Figure S5.4**). The greatest range and highest levels of genetic diversity occurred in Alaska west of 140°W in North America, corresponding with the eastern Beringian region (**Figure S5.5**). Both gene diversity and allelic richness were correlated with admixture proportion ($r_{s(45)} = 0.7$, $p < 0.01$ and $r_{s(45)} = 0.83$, $p < 0.01$, respectively), with the largest increases in genetic diversity occurring between 0-10% genetic admixture proportion, with smaller increases in genetic diversity at higher admixture values (**Figure S5.6**).

The landscape age of dwarf birch sampling sites varied from 6.5 thousand years (ka) to 2.6 million years (mya), i.e., not glaciated in the Quaternary period. All genetic diversity measures were significantly higher in sites that were unglaciated (landscape age ≥ 2.6 mya) compared to glaciated sites (< 2.6 mya) (**Figure S5.7**). In landscapes that were glaciated during the Last Glacial Maximum (LGM), admixture proportion was greater in older landscapes ($r_{s(26)} = 0.4$, $p = 0.034$), but gene diversity and admixture were not significantly correlated with landscape age (**Figure S5.7**). For detailed comparisons of sample site genetic diversity see **Table S5.2**.

5.6.2 Greening trends

Landsat-derived regional (i.e., robustly averaged over up to 100 suitable pixels within a 50 km radius) tundra greening trends were available for 43 dwarf birch sampling sites (**Table S5.3**). There was an overall 7.88% increase in $EVI2_{max}$ from 2002-2021 (slope 0.001 yr^{-1} [CI 0.097-0.00172], $p < 0.001$). A substantial proportion of dwarf birch sampling sites (51.2%) showed significant positive $EVI2_{max}$ trends (vegetation greening), whereas 9.3% of sites showed significant negative trends (vegetation browning) and the remaining 39.5% of sites exhibited no significant trends. Greening trends varied by bioclimatic zone/biome and by genetic group (**Figure 5.3**). The slope of the greening trend was significantly different between genetic groups (ANOVA $F(4, 38) = 3.56$, $p = 0.015$) driven by the difference between the Hybrid and *Glandulosa* East groups (post hoc Tukey test $p = 0.0093$) (**Figure S5.8**).

Summer warming has previously been found to be an important component of panarctic tundra greening (Berner et al., 2020). In this study, annual mean $EVI2_{max}$ anomalies were significantly positively correlated with SWI anomalies from 2002-2021 ($r_{s(41)} = 0.57$, $p = 0.0094$; **Figure S5.9**). Correlations were significant and positive at 30.3% of sites, and were

weaker, but still positive, when detrended and two-year averaged SWI time series were used (**Figure S5.10**). Positive EVI2_{max} -SWI correlations occurred both in greening sites and in sites that had no significant trends (**Figure S5.10**).

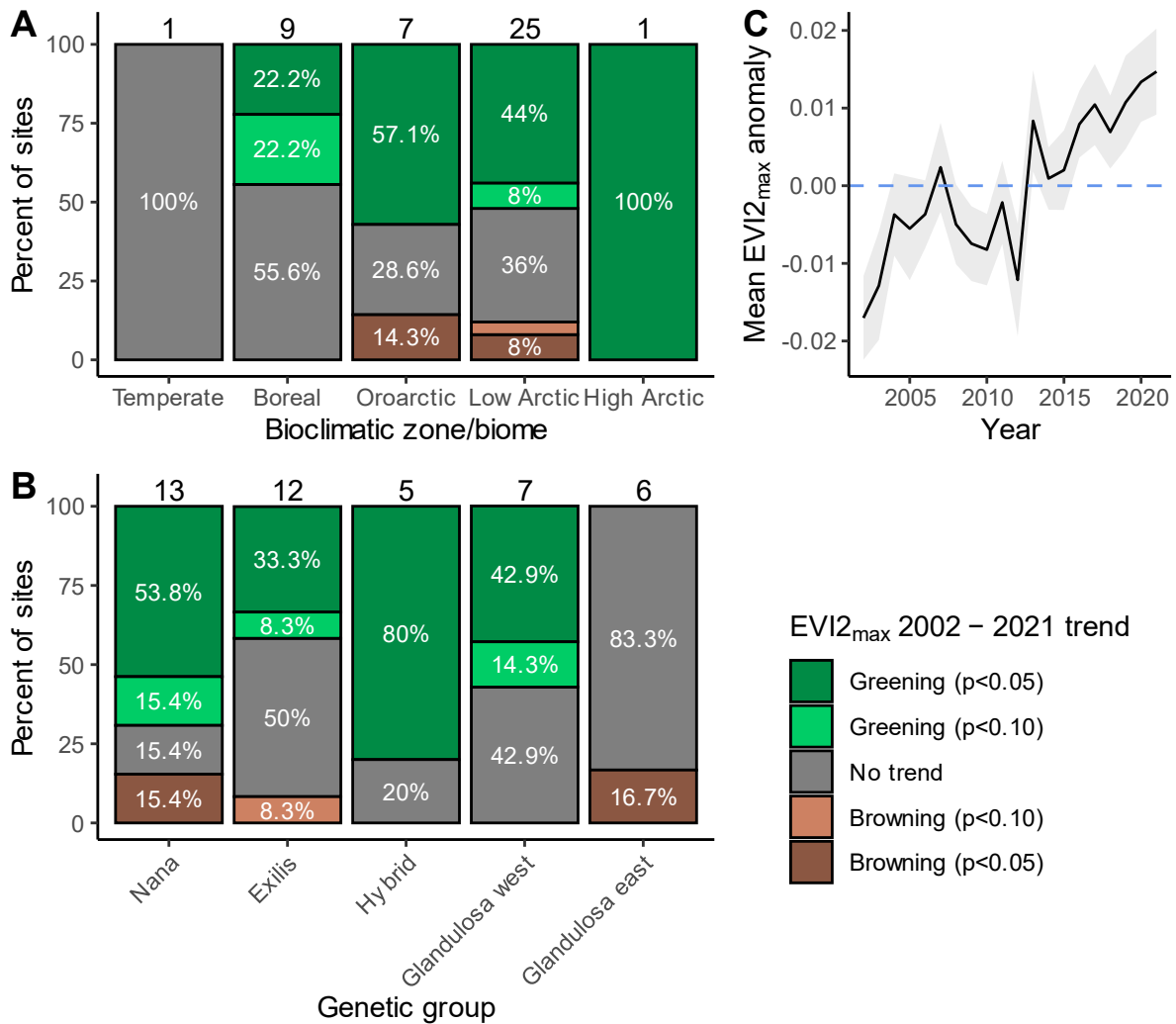


Figure 5.3. Greening trends for dwarf birch sampling sites. EVI2_{max} trends categorised for each dwarf birch sampling site for **(A)** bioclimatic zones/biomes and **(B)** dwarf birch genetic groups. Number of sites per group above bars. **(C)** Change in EVI2_{max} anomalies from 2002–2021 across all dwarf birch sampling sites (n=43). Dotted line indicates the period mean, and error bands depict 95% confidence intervals. “Greening” indicates a significant positive trend ($\alpha=0.10$), “browning” indicates a significant negative trend ($\alpha=0.10$).

Greening trends were significantly positively associated with all three genetic variables ($R = 0.4 - 0.45$; **Figure 5.4**) and were marginally greater in sites that were unglaciated (landscape age ≥ 2.6 million years) compared to glaciated sites (< 2.6 million years) ($T_{(31)} = 1.977$, $p = 0.057$) (**Figure 5.4**). However, there was no significant positive association between greening and landscape age for sites that were glaciated during the Last Glacial Maximum (postglacial landscapes) (**Figure S5.11**).

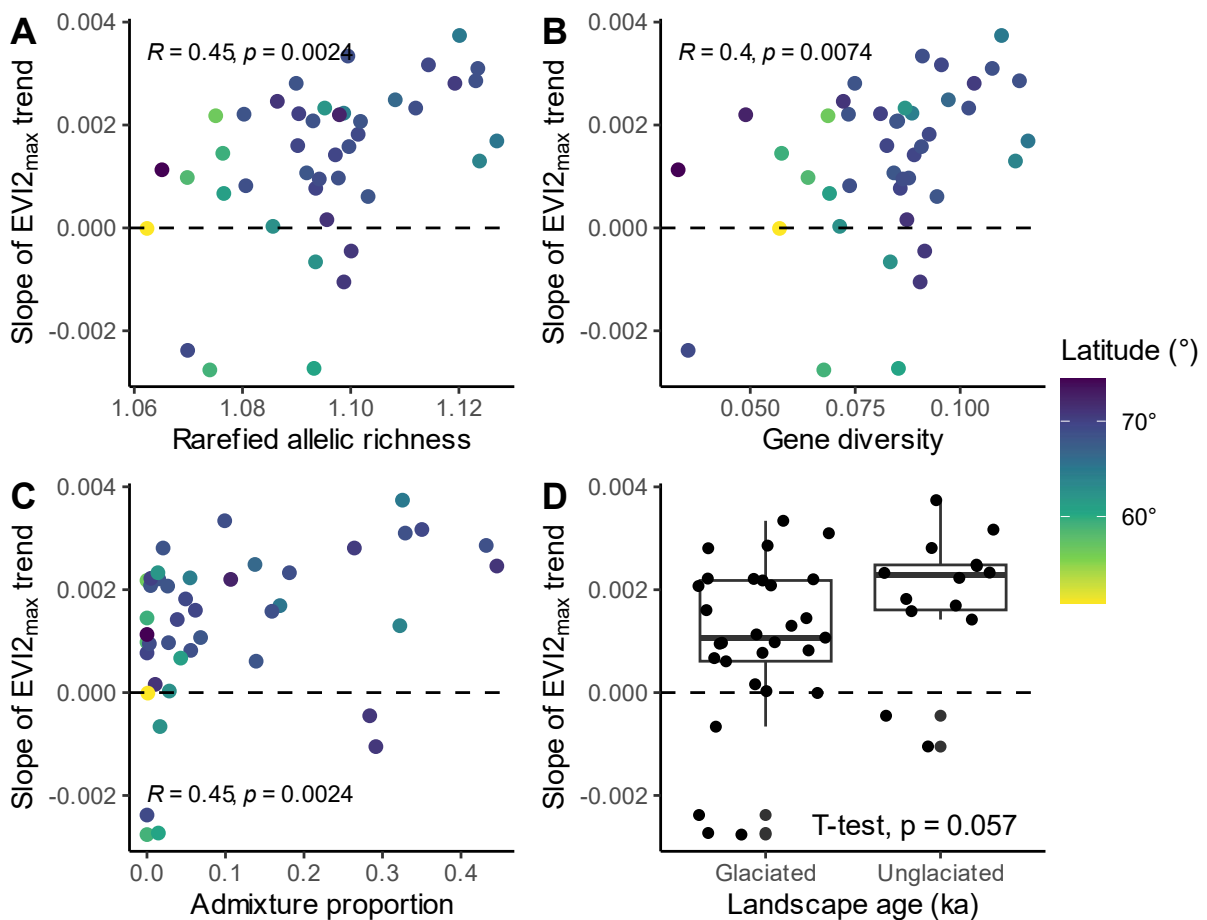


Figure 5.4. The relationship between greening trends and dwarf birch site genetic diversity and landscape age. Slope of EVI2_{max} trends from 2002-2021 and corresponding rarefied allelic richness (A), gene diversity (B), and admixture proportion (C) at dwarf birch sampling sites with Spearman's correlation coefficients (R) and associated p values (p). Colours represent latitude of sample sites. (D) Comparison of EVI2_{max} trends at sites that were glaciated (landscape age < 2.6 million years) and unglaciated (landscape age ≥ 2.6 million years) in the Quaternary period with associated T-test p values (p). Sites above the dotted line indicate a positive EVI2_{max} trend, sites below the dotted line indicate a negative trend.

5.6.3 Random Forest regression model

The final model contained twelve predictors, which explained 31.6% of the variance in greening trends based on out-of-bag predictions of the original dataset, with a RMSE of 0.00126. Some predictors were removed from the dataset due to mean absolute pairwise correlations of > 0.75 with other variables. Gene diversity was highly correlated with allelic richness (pair-wise absolute correlation = 0.90), but allelic richness was kept in the final model. Models with allelic richness explained more variance in greening trends than those with gene diversity, potentially because gene diversity was more highly correlated with admixture according to other correlation measures (Figure S6).

Likewise, soil temperature change was chosen over 2002 soil temperature (correlation - 0.837), SWI variables from the ARCLIM dataset were chosen over the CRU TS SWI dataset (2002 SWI correlation 0.916 and total change correlation 0.83), and topographic heterogeneity (the standard deviation of elevation) calculated at $\sim 150\text{m}$ resolution was chosen over topographic heterogeneity calculated at $\sim 38\text{m}$ resolution (correlation 0.999). The addition of site-specific factors such as site ID, latitude, and longitude, did not improve the variance explained by the model.

The most important variables were mean annual temperature (MAT) change, soil moisture 2002 value and total change, soil temperature change, admixture proportion, SWI 2002 value, and topographic heterogeneity. Allelic richness and landscape age were more informative than bioclimatic zone and genetic group. Change in mean annual temperature (MAT) had the greatest impact on the accuracy of the regression model (**Figure S5.12**). The partial dependence plot for MAT showed that the magnitude of greening was greatest in areas where the MAT had risen $>1^{\circ}\text{C}$ during the twenty-year study period (**Figure 5.5**). The partial dependence plot also showed that greening was greatest in the areas with the largest increases in soil moisture. Greening was also greatest in soils which had warmed $>3^{\circ}\text{C}$, in sites that were drier and warmer to start with, in sites with over 30% dwarf birch genetic admixture, and in areas of low to moderate topographic heterogeneity.

An additional model was run without MAT to focus on the relative importance of the other explanatory variables, which explained 16.5% of the variance in greening trends, with a RMSE of 0.00139. In comparison, a model including only allelic richness, admixture proportion, and

landscape age explained 7.8% of the variance. When only MAT was excluded, the most important variables according to RMSE were soil temperature change, landscape age, admixture proportion, SWI 2002 change, and soil moisture variables. Allelic richness was among the most important variables according to its contribution to node purity (**Figure 5.6**). The partial dependence plot for landscape age showed that the magnitude was greatest in areas which had not been glaciated during the entirety of the last glacial period (landscape age > 100 ka). For allelic richness, the magnitude of greening was greater as allelic richness increased (**Figure S5.13**).

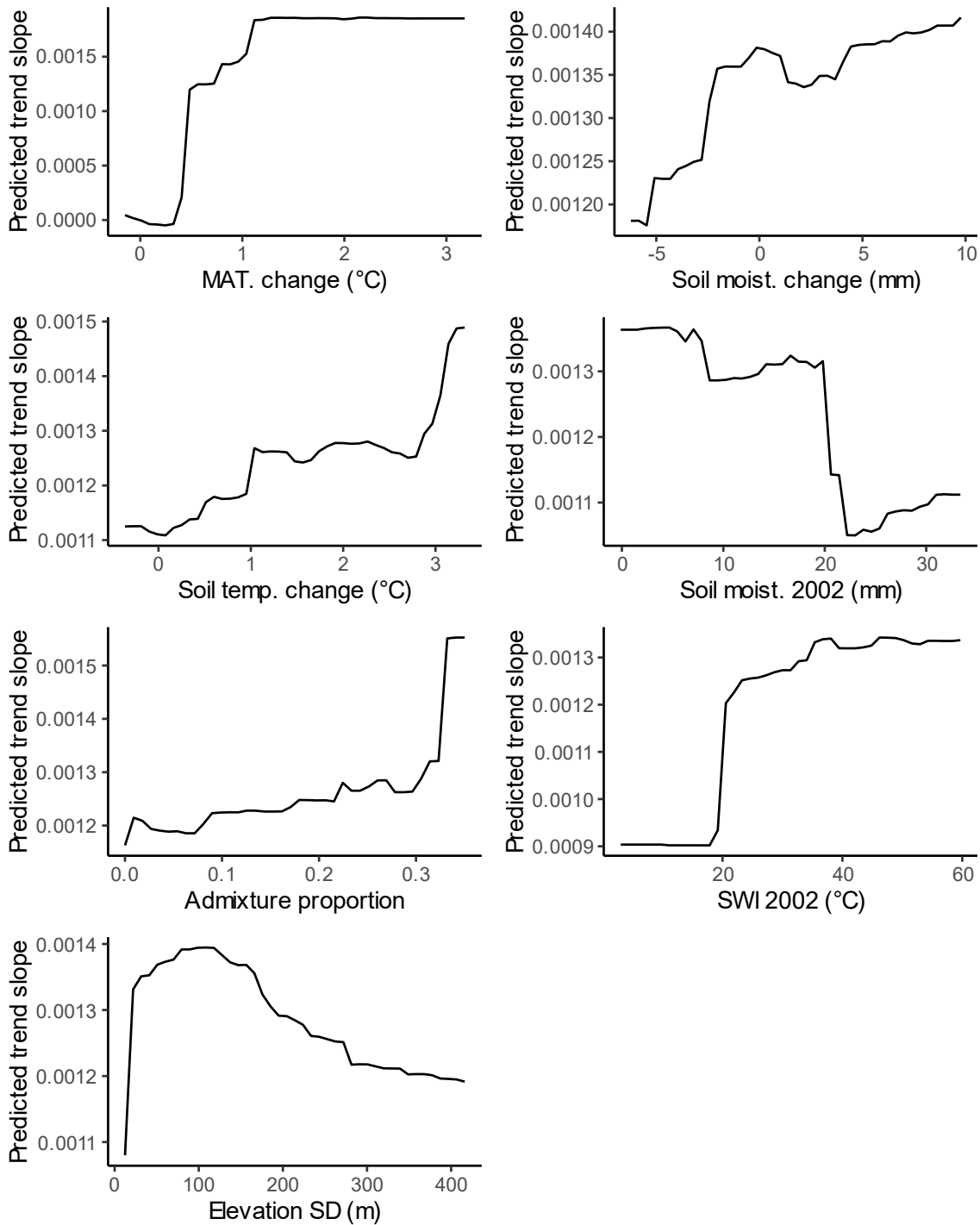


Figure 5.5. Partial dependence plots for the most important variables determined by Random Forest regression model. Variables were ranked based on the percentage increase in RMSE and increases in node purity when variable values were randomly permuted. The Y axis shows the average $EVI2_{max}$ trend slope predicted at different levels of a given explanatory variable across models, with other variables held constant. The model explained 31.6% of variance in greening trends based on out-of-bag predictions of the original dataset (RMSE 0.00126).

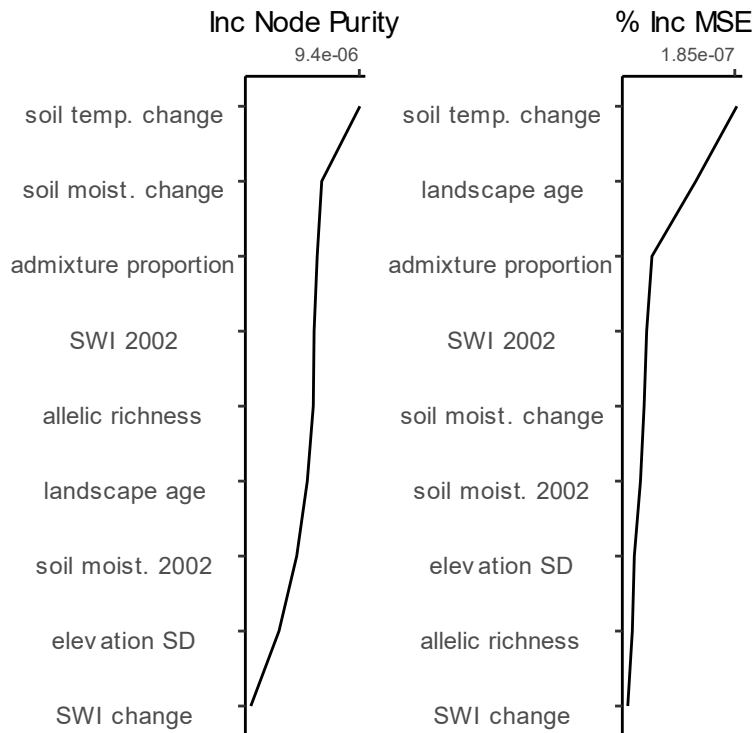


Figure 5.6. Variable importance in Random Forest Regression model predicting magnitude of greening trends, excluding mean annual temperature (MAT). Variables ranked according to the increase in node purity, and percentage increase in MSE, when they are randomly permuted. Without MAT, the model explained 16.5% of variance in greening trends based on out-of-bag predictions of the original dataset (RMSE 0.00139).

5.7 Discussion

Our analysis showed that changes in tundra greenness during recent decades were related to glaciation history and the genetic variability of dwarf birch, a key Arctic tundra shrub implicated in current vegetation greening trends. We assessed changes in tundra greenness from 2002 to 2021 using Landsat EVI2_{max} and found significant greening at about half of sampling sites, browning at about 10% of sampling sites, and no systematic change in vegetation greenness at the remaining sampling sites. These frequencies and the spatial patterns of tundra greenness trends are broadly consistent with prior studies that evaluated changes across the Arctic using satellite measurements of NDVI or EVI (Ropars et al., 2015a; Park et al., 2016; Berner et al., 2020; Mekonnen et al., 2021). While confirming that soil temperature and moisture are important predictors of tundra greening (Berner et al., 2020; Mekonnen et al., 2023), we further demonstrate that tundra greening occurred most rapidly not only at sampling sites with the most genetically mixed dwarf birch populations, but also at sampling sites that were unglaciated during the Quaternary period. Links between the strength of tundra greening trends and genetic signatures of glacial refugia and historical population mixing suggests that the response of dwarf birch to past climate change may in turn affect responses to contemporary climate change.

5.7.1 Greening trend heterogeneity

We found consistent and significant positive trends in maximum summer EVI2 (EVI2_{max}) across sampling sites over the last two decades, in agreement with previous studies of Arctic tundra NDVI and EVI trends (Berner et al., 2020; Chen et al., 2021; Park et al., 2016; Seider et al., 2022). Despite this overall greening trend, many sites exhibited no greening trend, with a small proportion of browning sites, similar to previous panarctic analyses of Landsat NDVI trends (Berner et al., 2020; Mekonnen et al., 2021). The spatially heterogeneous greening trends in our analysis are consistent with other studies of the Arctic tundra (Larking et al., 2021; Nill et al., 2022; Ropars et al., 2015a).

5.7.2 Climate variables and greening trends

The most important variables for predicting the magnitude of greening trends were climate variables related to temperature and moisture trends; however, the magnitude strength of

the greening trends was positively correlated with all measures of dwarf birch genetic diversity. Sampling sites with the strongest greening trends were initially warmer and experienced the greatest increases in soil and air annual temperatures, and soil moisture. This is consistent with findings that shrub expansion is affected by summer and winter temperature and moderated by moisture availability (Mekonnen et al., 2021; Myers-Smith et al., 2015; Myers-Smith & Hik, 2018).

Mean annual temperature (MAT) was the most important variable in the regression model, and when removed, the amount of variance explained by the predictors declined by nearly 50%. In contrast, change in summer warmth index (SWI) did not appear to drive the magnitude of greening, despite being correlated with $EVI2_{max}$ at over 30% of sites. This suggests that productivity and greening were sensitive to temperatures outside the growing season at the dwarf birch sampling sites, so that considering temperatures both in summer and outside of summer was necessary to capture the temperature-sensitivity of the tundra greening trends. This contrasts with recent work which found summer warmth to be the main determinant of the direction of Arctic greening trends (Berner et al., 2020) but agrees with studies that found MAT and winter temperatures to be important variables for predicting dwarf birch response to climate change in species distribution models (Seider et al., 2022).

Winter biological processes may influence tundra greening, with conditions outside the main growing season having been shown to affect influence birch secondary growth during recent decades in Greenland (Hollesen et al., 2015). Secondary growth increased as winter and spring warming led to earlier snowmelt, warmer soils that drain earlier, and subsequently a longer growing season. However, the effect of manipulated winter and spring temperatures on dwarf birch growth in northern Sweden appears to be more limited (Krab et al., 2018). As the Arctic becomes wetter and warmer (Boisvert & Stroeve, 2015; Druckenmiller et al., 2022), conditions for dwarf birch and other shrubs might improve if accompanied by deeper snow and earlier spring snow melt (Wipf & Rixen, 2010).

5.7.3 The influence of genetic diversity and landscape age on greening

Admixture proportion - the proportion of genetic material in an individual arising from admixture - was consistently one of the most important variables in the Random Forest regression model. The magnitude of greening increased with a higher proportion of

admixture, most notably at the highest levels of admixture (30-40%). Landscape age was one of the most important variables when MAT was removed from the RF regression model, suggesting that MAT and landscape age were competing for explained variance. Admixture proportion and allelic richness also increased in importance. Greening magnitude rapidly peaked in landscapes ~100 ka or older, suggesting that the largest differences in greening were between sites which were glaciated at some point during the last glacial cycle (115 ka - 11.7 ka), and those which were not glaciated.

Genetic diversity at dwarf birch sampling sites was also closely associated with landscape age, with the highest genetic diversity in sites that were unglaciated during the Quaternary. Genetic diversity was highest in Beringia and declined in more recently glaciated sites, similar to other Arctic plants (Eidesen et al., 2013; Pellissier et al., 2016; Stewart et al., 2016). Beringia was mostly unglaciated during the Quaternary and was ice-free in the last glacial period (115 ka - 11.7 ka) (Batchelor et al., 2019; Dalton et al., 2022). Pollen and macrofossil records and phylogeographical work show that Beringia was an important refugium for dwarf birch (Bigelow et al., 2003; Binney et al., 2017; Brubaker et al., 2005; Eidesen et al., 2015).

Genetic admixture proportion was also higher in unglaciated regions on average, although there was a notable increase in admixture proportion in postglacial sites 13-14 ka old. Admixture events in former refugial areas therefore appear to be as important for generating dwarf birch genetic diversity as secondary contact and admixture between expanding populations in formerly glaciated areas (Petit et al., 2003). Regions where dwarf birch genetic lineages have undergone secondary contact may show enhanced greening in response to climate change because intraspecific gene flow can provide a mechanism to escape limited adaptive potential from low standing genetic variation (Borrell, 2016; Hamilton & Miller, 2016). In contrast, shrubs in sites with low genetic diversity and young landscape age could have a more limited adaptive response to climate change (Savolainen et al., 2007), thereby limiting the overall magnitude of tundra greening in those areas.

Genetic diversity was highest in regions that were unglaciated throughout the Quaternary, yet the largest impact of landscape age on greening occurs in landscapes that were unglaciated in the last glacial cycle, ~ 115 ka. This suggests that landscape age-related factors influence greening independently of dwarf birch genetic diversity. Soil development and corresponding nutrient availability increases with postglacial landscape age (Evans &

Cameron, 1979; Stevens & Walker, 1970), which may allow dwarf birch in older landscapes to respond more positively to warming through increased shrub growth (Bret-Harte et al., 2001; Chapin et al., 1995; Mekonnen et al., 2021). The poor relationship between landscape age and greening magnitude when constrained to the current interglacial suggests that the role of processes of glacial soil erosion and postglacial soil formation in facilitating climate-driven increases in plant productivity might be important at timescales longer than tens of thousands of years.

The relationship between dwarf birch genetic diversity and landscape age, and the independent contributions of genetic admixture, allelic richness, and landscape age in explaining variance in $EVI2_{max}$ trends in the RF regression model, suggest that large glacial refugia such as Beringia and the postglacial dynamics of shrub migration have shaped present-day shrub genetic diversity and greening trends.

5.7.4 Dwarf birch subspecies and greening trends

We hypothesised that spatial heterogeneity in greening trends could be attributed to different dwarf birch sub-species but did not find any support for this hypothesis. We detected two main genetic groups for *B. nana*: an eastern group largely corresponding to the Beringean subspecies *exilis*, and a western group largely corresponding to the western Eurasian and Atlantic subspecies *nana*. Similarly, *B. glandulosa* consisted of two main groups corresponding to eastern and western populations. We detected extensive genetic admixture between the *Exilis* and *Glandulosa* groups in their area of range overlap, supporting morphological evidence of *B. nana* subsp. *exilis* and *B. glandulosa* hybridisation (Furlow, 2004). Despite substantial differences in genetic diversity and admixture in the genetic subgroups of the species, differences in the magnitude of greening between genetic groups were small and genetic group was not an important predictor in the RF model. Sites with extensive *Exilis*-*Glandulosa* admixture (“hybrid” populations) had the highest genetic diversity and greening magnitude, suggesting that the presence of hybridisation, and the resulting increase in genetic diversity, may be more important than taxon identity for influencing greening trends. Dwarf birch species hybridise with other *Betula* shrub and tree species not included in this study (Furlow, 2004; Karlsdóttir et al., 2009; Palmé et al., 2004; Thórsson et al., 2010; Wang et al., 2014; Zohren et al., 2016), which could potentially impact the genetic

structure of the dwarf birches. However, we did not detect elevated genetic diversity in Europe that would indicate hybridisation with *Betula pubescens* (Eidesen et al., 2015). The previous research chapter identified four populations in Siberia and North America which potentially contained genetic material from other shrub *Betula* species, but the admixture proportions in these populations (3-18%) is lower than the >30% admixture rates that are associated with the highest greening trends in the partial dependence plots of the regression model.

Interspecific differences in herbivore palatability between the different dwarf birch taxa have been hypothesised to lead to divergent shrubification patterns (Christie et al., 2015). *B. nana* subsp. *exilis* and *B. glandulosa* are considered less palatable than *B. nana* subsp. *nana* (Bryant et al., 2014). Although biogeographical patterns in anti-herbivore defence compounds correspond loosely to these subspecies, there is also much intraspecific variation (Lindén et al., 2022). Contrary to expectations, the sites with Glandulosa genetic groups did not show a greater magnitude of greening or a higher number of greening sites compared to the sites with the presumably more palatable Nana genetic group. Therefore, shrubification differences arising from species palatability and herbivore pressure do not appear to be critical in driving greening trends.

5.7.5 Explained and unexplained variance

Genetic and environmental predictors together explained 31.6% of the variance in greening trends of our 43 sites in the RF model. A study spanning an 800,000 km² area in the western Canadian Arctic tundra found biophysical variables such as elevation, slope, and landcover, explained 48.4% of variance in EVI trends for 80,000 sample points (Landsat pixels) (Chen et al., 2021). However, topographic variability, represented by the standard deviation of elevation, was not a good predictor of greening magnitude in our study. In a panarctic study of NDVI_{max} greening trends, environmental variables including SWI trends predicted greening trend class in an RF classification model with 55.4% (CI 53.1,57.5) accuracy (Berner et al., 2020). We aimed to account for potential unaccounted-for variables that may influence greening on regional and local scales by including latitude, longitude, and site name as predictors in the RF model, which did not improve model performance.

The lower variance explained by the RF regression model in our study may be related to the limited number of sampling sites ($n = 43$), and the very different types of data incorporated into the model. For instance, we used satellite-observed tundra greening data as a proxy for shrub expansion, which we linked to dwarf birch genetic data sampled on a local scale. Based on preliminary analysis of population genetic structure, we match the expected regional footprint of the genetic data to satellite measurements by analysing Landsat EVI2_{max} time series from tundra land cover types within a 50km radius of each sampling site. Nevertheless, satellite measurements of vegetation greenness are strongly scale-dependent (Myers-Smith et al., 2020), which could contribute to the unexplained variance in our RF modelling. In addition, and like previous studies (Berner et al., 2020; Chen et al., 2021; Nill et al., 2022; Park et al., 2016; Seider et al., 2022), climate data was variously derived from station data, model reanalysis, and remote sensing. Therefore, the consistent signal between genetic diversity and greening is indicative of a persistent link between the genetic diversity of tundra shrubs and increases in productivity and greening.

The presence of shrubs and vegetation other than the dwarf birches could also contribute to unexplained variance in greening trends. We assumed that dwarf birch presence at the sampling sites would relate to greening trends as previous studies have linked dwarf birch shrub expansion and tundra greening trends (Andruko et al., 2020; Fraser et al., 2014; Lantz et al., 2013; Larking et al., 2021; Moffat et al., 2016; Tape et al., 2006; Tremblay et al., 2012). *Salix* and *Alnus* shrubs are also circumpolar tundra shrubs which are also implicated in shrubification (Myers-Smith et al., 2011; Lantz et al., 2013; Frost & Epstein, 2014) and Arctic greening trends (Fraser et al., 2014; Frost et al., 2014). Varying shrub species composition may affect vegetation indices (Myers-Smith et al., 2020) and therefore the relationship between greening trends and potential drivers. On the other hand, *Betula* shrubs may be representative of shrub species as shrub and tree growth in Siberian tundra has been shown to be correlated across species (Forbes et al., 2010). Furthermore, patterns of covariation in Arctic plant diversity across space (Eidesen et al., 2013) and landscape age (Stewart et al., 2016) suggest that species experienced similar glacial histories and responses to past climate change, although variable genetic structure in *Alnus*, *Salix*, and *Betula* can occur in particular locations (Meucci et al., 2021). An increased understanding of *Betula* dominance at each sample site would help eliminate noise due to varying species composition.

5.8 Conclusions

Here, we demonstrate for the first time that there are consistent links between the strength of tundra greening trends as measured by $EVI2_{max}$, glacial history as represented by landscape age, and the genetic variation of dwarf birch, a key Arctic tundra shrub implicated in current tundra greening trends. Temperature and moisture changes over the last twenty years are important predictors of tundra greening trends, consistent with previous studies of remotely-sense tundra greening and shrub expansion. Conditions outside of the growing season appear to be important determinants of greening, consistent with studies of dwarf birch growth responses to climate.

The close association between genetic diversity and landscape age suggests that the role of genetic diversity in greening is in part driven by historical processes and could be due to the influence of glacial refugia and postglacial climate change. The important independent contribution of genetic diversity, particularly in the form of admixture, to explaining greening trends illustrates that genetic diversity is not simply a proxy for landscape age.

Our results suggest that factors related to past climate change drive are linked to tundra greening alongside contemporary climatic change. Specifically, the importance of landscape age, allelic richness, and dwarf birch genetic admixture point to glacial refugia and postglacial population mixing influencing the magnitude of greening. Overall, we show that the tundra greening response to contemporary climate change is likely modulated by Late Quaternary legacies.

The relationship between greening trends and genetic diversity suggests that Arctic shrub expansion may be an adaptive response to climate change, and that future evolutionary potential may be constrained or modulated by genetic legacies of past climate change. Genetic diversity can predict the evolutionary responses of specific genetic loci linked to climate change (Bertin et al., 2020), but further investigation of the genetic-environment associations of loci potentially under selection could further inform the evolutionary basis of shrubification and the future adaptive potential of dwarf birch.

5.9 Acknowledgements

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5.10 Data and code availability statement

The genetic data for this study have been deposited in the European Nucleotide Archive (ENA) at EMBL-EBI under accession number PRJEB67938.

The data that support the findings of this study were derived from the following resources available in the public domain:

The United States Geologic Survey Landsat 5, 7, and 8 Surface Reflectance data are available from [Google Earth Engine](#). The ESA WorldCover 2021 data are available from <https://esa-worldcover.org/en/data-access>. The CRU TS4.06: Climatic Research Unit (CRU) Time Series (TS) version 4.01 data are available from the Center for Environmental Data Analysis, <https://catalogue.ceda.ac.uk/uuid/e0b4e1e56c1c4460b796073a31366980>. The TerraClimate data are available from the University Corporation for Atmospheric Research, http://thredds.northwestknowledge.net:8080/thredds/catalog/TERRACLIMATE_ALL/data/catalog.html. The ESA Climate Change Initiative Permafrost and ground temperature data are available from the Center for Environmental Data Analysis with identifier <https://dx.doi.org/10.5285/c7590fe40d8e44169d511c70a60ccbcc>. The Bioclimatic atlas of the terrestrial Arctic (ARCLIM) is available on figshare with identifier <https://doi.org/10.6084/m9.figshare.c.6216368.v2>. The Digital Elevation Model data are available from [Amazon Web Services Terrain Tiles](#) via the [elevatr](#) R package. See Table S5.4 for a full list of DEM sources. The Arctic Bioclimatic zones are available from the Arctic Biodiversity Data Service Catalogue, <https://geo.abds.is/geonetwork/srv/eng/catalog.search#/metadata/f0eb86a7-e408-4138-9432-dedb991f13d1>. The WFF Terrestrial ecoregions are available from <https://www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world>. The ice sheet data are available at identifiers [10.17605/OSF.IO/7JEN3](https://doi.org/10.17605/OSF.IO/7JEN3), <https://doi.org/10.1016/j.quascirev.2020.106223>, <https://doi.org/10.1016/j.earscirev.2021.103875>.

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5.12 Arctic greening patterns reflect genetic legacies of glacial refugia and past climate change: Supplementary information

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Appendix S5.1: Plant sampling and storage

Dwarf birch (*Betula nana* L. and *Betula glandulosa* Michx.) samples were collected across the species ranges during the growing season between 2015 and 2021. Identifying individual plants can be difficult, as a genetic individual can extend over many metres due to clonal reproduction. This is common at northern range limits where climate limits sexual reproduction, and these plants may be remnants of previous sexually reproducing populations (Alsos et al., 2002; de Groot et al., 1997; Engelskjøn et al., 2003; Hermanutz et al., 1989). To avoid resampling clonal or cryptic individuals, individuals were sampled at least 10 metres apart in continuous growth and 5 metres apart when growth was in distinct patches. Where possible, individuals were sampled along three transects of approximately 100 metres in length. Transects were evenly spaced across the area with a minimum distance of 10 metres between the transects. Twig and leaf samples were collected from up to 30 individuals. GPS coordinates were obtained for each site.

Samples were dried in silica gel, drying ovens, or air-dried, and stored in plastic zip lock bags, or paper bags/envelopes. Samples were shipped to the UK and stored in a 4-8°C cold room until processing in 2021. Sixty sites were selected for DNA extraction on the basis of tissue quantity and quality. To fill geographical sampling gaps, 42 silica-dried specimens from seven populations were obtained with the permission of the NHMO DNA Bank of the Natural History Museum, University of Oslo. For each of these populations, samples were collected 25 metres apart along a 250 metre transect.

Appendix S5.2: DNA sequencing and genotyping

Sample quality was assessed using 1% gel electrophoresis, and DNA purity and concentration were assessed using a Qubit with dsDNA BR assay kits Fluorometer (Life Technologies Corporation, Carisbad, CA). Approximately 26% of samples were rejected due to degraded DNA which mostly came from populations with senesced or limited starting material. In all, 244 samples from 48 populations passed quality control and DNA concentrations were normalised to 20 ng/μl. A subset of samples with sufficient DNA were duplicated (between 1-3 duplicates per sample) to increase sequencing coverage, resulting in 376 DNA extracts in total.

DNA extracts were submitted to FLORAGENEX (Beaverton, Oregon) for RAD library preparation and sequencing. Restriction-site associated DNA sequencing (RADSeq) is a form of reduced representation sequencing and is widely used for generating genome-wide single nucleotide polymorphisms (SNPs) for population genomic analyses in non-model organisms such as *Betula* species (Borrell et al., 2018; Ding et al., 2021; Zohren et al., 2016). Previous RAD sequencing of *Betula nana* used the cleavage enzyme *PstI* which has approximately 70,954 cut sites in the draft genome (Borrell et al., 2018; Wang et al., 2013). Here we used the cleavage enzyme *Sfbl*, which produces a subset of the same cut sites, since it has a 2 bp longer recognition sequence. One library was prepared per sample, with unique 10-base barcodes ligated via adaptors to *Sfbl* digested genomic DNA. To ensure consistency in the loci sequenced across samples and to reduce the number of missing genotypes downstream, fragments between 300 and 500 bp were selected and amplified with PCR. After library QA/QC, libraries were pooled and fragments were sequenced across four lanes of an Illumina NovaSeq 6000 platform with single-end 1 x 100 bp chemistry. Each plate also contained one blank control in differing locations in case of problems with plate identification, and one internal control.

A total of 419,484,325 reads were generated from one single-end Illumina HiSeq lane, of which 91.33% passed quality controls. Raw libraries were checked for errors using fastqc (Andrews, 2010). Libraries were demultiplexed and barcode sequences checked for errors using the process_radtags module of Stacks v 2.60 (Catchen et al., 2013; Catchen et al., 2011; Rochette et al., 2019). A quality threshold phred score of 10 was used in sliding windows of 15% of the length of the read (19.8 bp in a 131 bp alignment) (Rochette et al., 2019). Reads from duplicated samples from the same original individual were combined. Six individuals were removed due to anomalously low or high coverage. The number of reads per individual ranged from 351,332 to 3,596,943, with a mean of 1,126,061. Reads were aligned to a reference *Betula nana* genome ((Wang et al., 2013) ENA accession number GCA_000327005) using Bowtie2 v2.5 with sensitive and end-to-end parameters (Langmead & Salzberg, 2012). Across all individuals, 87.7% of reads successfully mapped to the *B. nana* reference genome, with 71.7% retained with a mapping quality > 10.

Reference-based SNP calling was performed using the *gstacks* module of *Stacks* v 2.60, which uses a sliding window algorithm to detect RAD loci across all populations, detect SNPs, and then genotype each individual. Reads with a mapping quality score of less than 10 were removed (Rochette et al., 2019). Mean effective per-sample coverage after *gstacks* was 346 x (min 99.7, max 1031). The *Populations* module of *Stacks* was used to filter loci to minimise missing data. Loci were retained that were present in 70% of individuals within a population, or present in 70% of individuals across populations. SNPs with a minor allele frequency (MAF) of <0.01 were excluded to remove uninformative markers, resulting in 1,930 loci containing 7,998 SNPs. The first SNP per locus was kept as downstream analyses (ADMIXTURE, PCA, allelic richness) required unlinked SNPs, leaving 1,766 SNPs (variant sites).

To meet assumptions of PCA and ADMIXTURE analyses (Alexander et al., 2009; Alexander & Lange, 2011), SNPs were filtered to remove loci in Linkage Disequilibrium (LD). Parameters for filtering were determined by calculating the average LD across intervals in the genome in 100 kb bins using PLINK v1.9 (Chang et al., 2015; Purcell & Chang, 2022) and haplotype VCFs. Visual inspection of the results identified a window size of 33 kbp where LD decayed to a background rate of 0.1. VCF files were then filtered in windows of 33 kbp sliding by 10 kbp with a threshold of correlation coefficient (r^2) > 0.2. A subset of 1,1063 loci remained after LD filtering.

Appendix S5.3: Genetic diversity and genetic clustering

Extensive hybridisation and introgression within the *Betula* genus have resulted in high morphological variability within and among species (Palme et al., 2004; Thomson et al., 2015; Thórsson et al., 2010; Tsuda et al., 2017), making taxonomic identification and phylogenetic inferences difficult (Järvinen et al., 2004; Li et al., 2005, 2007; Maliouchenko et al., 2007). *B. nana* subsp. *exilis* and *B. glandulosa* hybridise and form intermediates in areas of range overlap but form distinct entities elsewhere in their ranges (Furrow, 2004). There is therefore disagreement on whether *B. nana* subsp. *exilis* and *B. glandulosa* should be considered distinct species or combined as *B. glandulosa* (Ashburner & McAllister, 2013; de Groot et al., 1997). *B. glandulosa* and *B. nana* subsp. *nana* also hybridise in southern Greenland (Furrow, 2004).

Given potential hybridisation between *B. nana* subsp. *exilis* and *B. glandulosa* in North American sampling locations, we examined the genetic similarity and overlap between subspecies identified during sample collection with Principal Component Analysis using the *adegenet* package v2.1.3 (Jombart, 2008; Jombart & Ahmed, 2011) in R v 4.0.3 (R Development Core Team, 2022). PCA summarises genetic variation among individuals using linear combinations of the alleles, which can identify genetic clines indicating admixture, and identify individuals whose genetic structure does not match their taxonomic identification. Taxonomic groups identified in the field were not clearly clustered in a

multidimensional genetic space (i.e., they were not genetically distinct; **Figure S2**): the first PC axis in the PCA showed individuals identified as *B. nana* and *B. glandulosa* arranged along a cline of genetic differentiation with considerable overlap, suggesting possible species misidentification or the existence of hybrids. The second PC axis showed the existence of at least two genetically distinct groups of sampling sites which separated sampling sites in western Eurasia from Eastern Eurasia and America (**Figure S2**).

To identify possible *B. nana* subsp. *exilis* and *B. glandulosa* hybrid populations, we used the software ADMIXTURE v 1.3.0 (Alexander et al., 2009; Alexander & Lange, 2011). ADMIXTURE does not accept chromosome names that are not human chromosomes, so chromosome names were replaced with “0” in the first column of each bed file. ADMIXTURE was run with default parameters. We tested a range of 2-5 possible ancestral populations (K); the K with the lowest cross-validation error was chosen as the optimal value. We plotted population assignment probabilities for each individual using the ancestry fractions output files in ggplot2 (Wickham, 2016) in R v 4.0.3 (R Development Core Team, 2022).

We equated the number of ancestral populations with the number of genetically distinct populations. Individuals reassigned to a genetic population if they had >50% assignment probability. Genetic diversity metrics were recalculated by genetic group. The populations module of Stacks v 2.60 (Catchen et al., 2013; Catchen et al., 2011; Rochette et al., 2019) was repeated, with population filters based on the new populations. Genetic summary statistics were calculated by population as before. Pairwise Analysis of Molecular Variance F_{ST} estimates (Weir, 1990) were also output from the populations module of Stacks.

ADMIXTURE maximum likelihood estimates of ancestry coefficients were used to derive estimates of mean genetic admixture for each sample site. Individual admixture proportion was calculated as the sum of the coefficients of the secondary ancestral groups (i.e. groups with an admixture coefficient of < 0.5 in an individual), so that admixture proportion could vary between 0 and 0.49. Mean admixture proportion was calculated by averaging individual admixture proportions occurring at a site.

We tested for significant differences in genetic diversity between the genetic clusters with one-way analysis of variance (ANOVA) tests and compared differences between the subspecies means with a post hoc Tukey test. Non-parametric Kruskal-Wallis rank sum tests were used when the variance of samples was non-equal. All statistical analyses were implemented in the stats R package v 4.0.3 (R Development Core Team, 2022).

Appendix S5.4: Supplementary figures

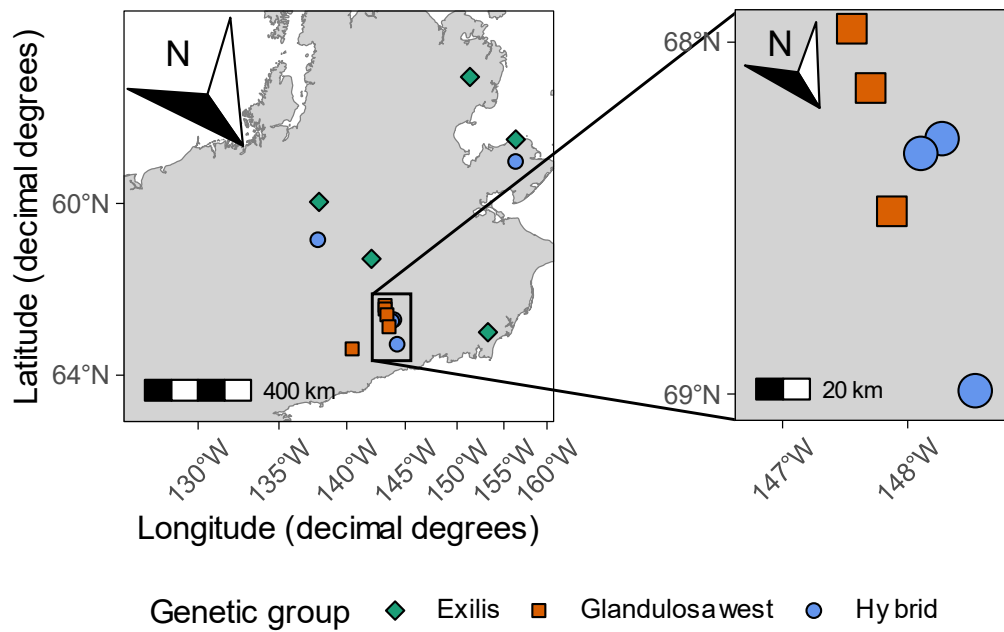


Figure S5.1. Alaskan dwarf birch sampling sites. Individuals were assigned to genetic groups based on >50% ancestry proportion in the corresponding ADMIXTURE (Alexander et al., 2009; 2011) ancestral population. Sampling sites containing individuals from more than one genetic group, and where individuals were completely admixed genetically were classified as “hybrid” genetic groups.

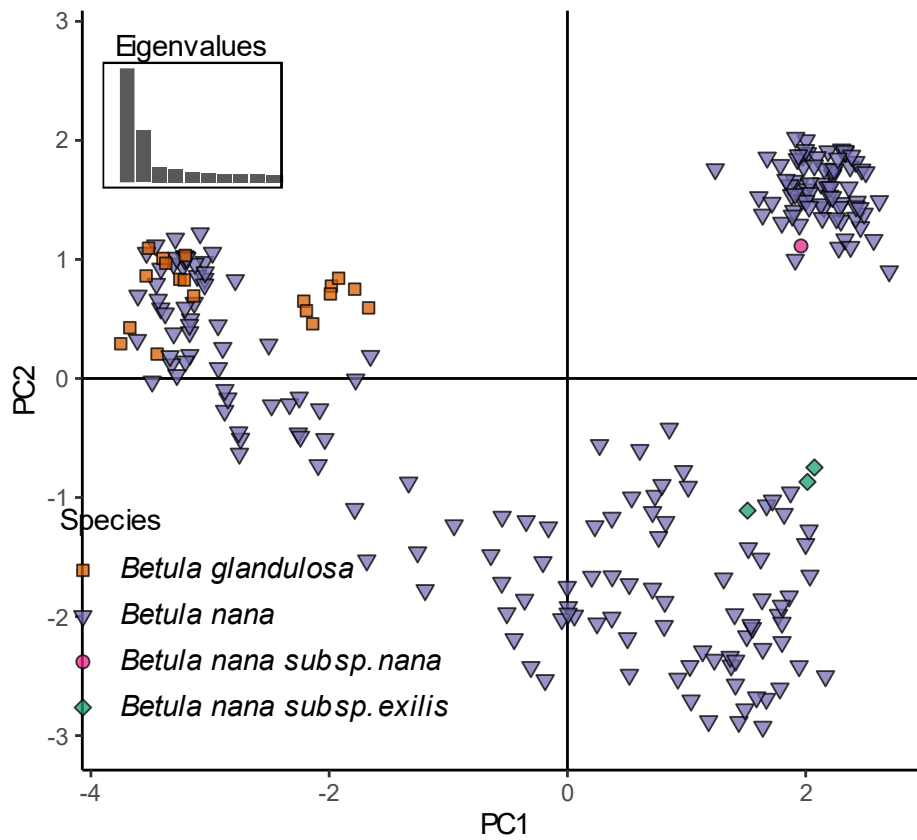


Figure S5.2. Principal Component analysis (PCA) of genetic variation among dwarf birch individuals coloured according to field species identification. The sum of the variances explained by the first two principal components (PCs) was 22.1% and are plotted in an ordination plot, with an inset scree plot of eigenvalues for the first five PCs.

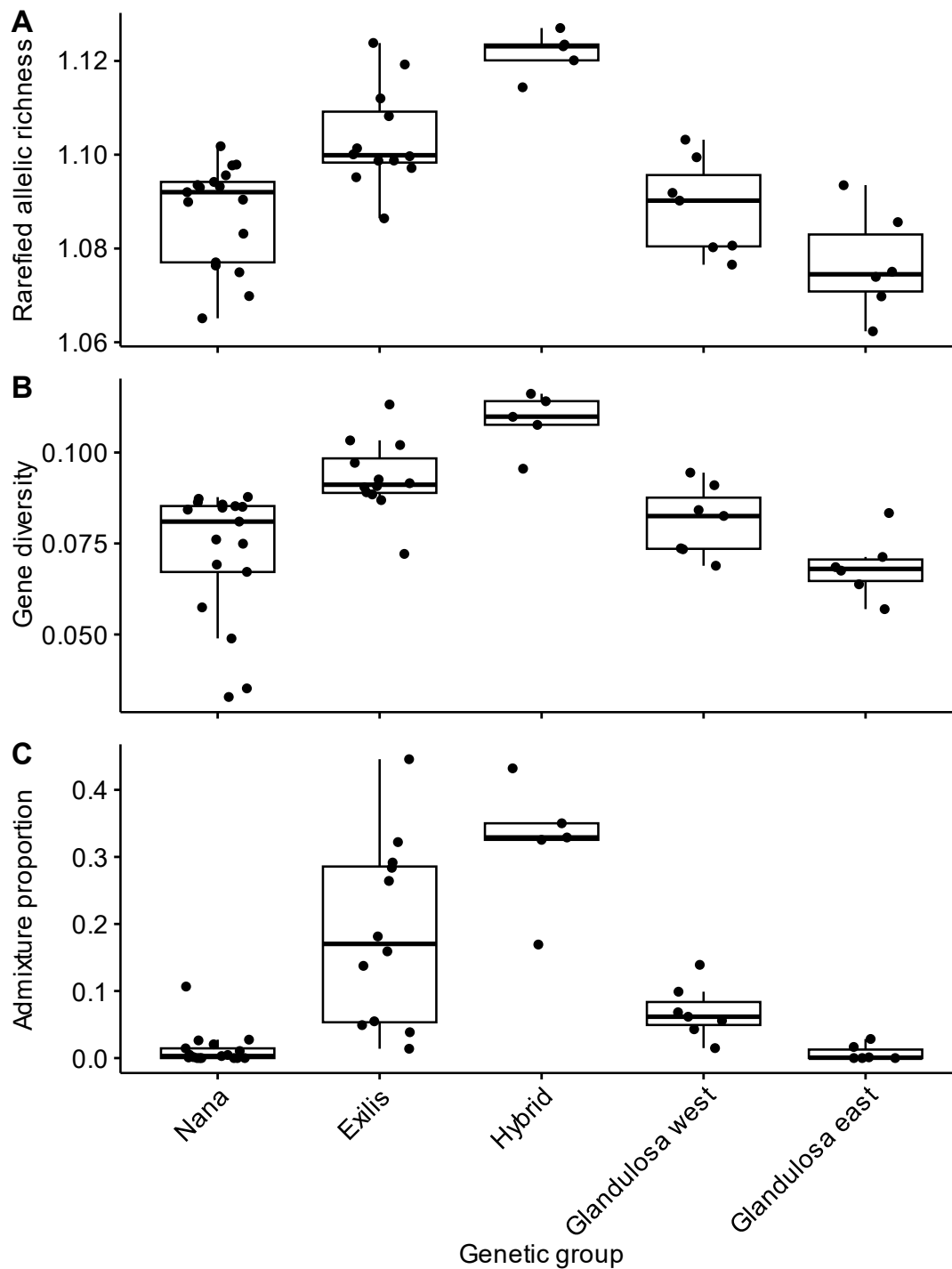


Figure S5.3. Dwarf birch sampling site genetic differences according to dwarf birch genetic groups. (Rarefied allelic richness (A), gene diversity (B), admixture proportion (C). Individuals were assigned to a genetic groups (ADMIXTURE ancestral population) based on >50% assignment probability to a group. Some sampling sites contained individuals from more than one genetic group, and where individuals were completely admixed genetically (“hybrid” populations).

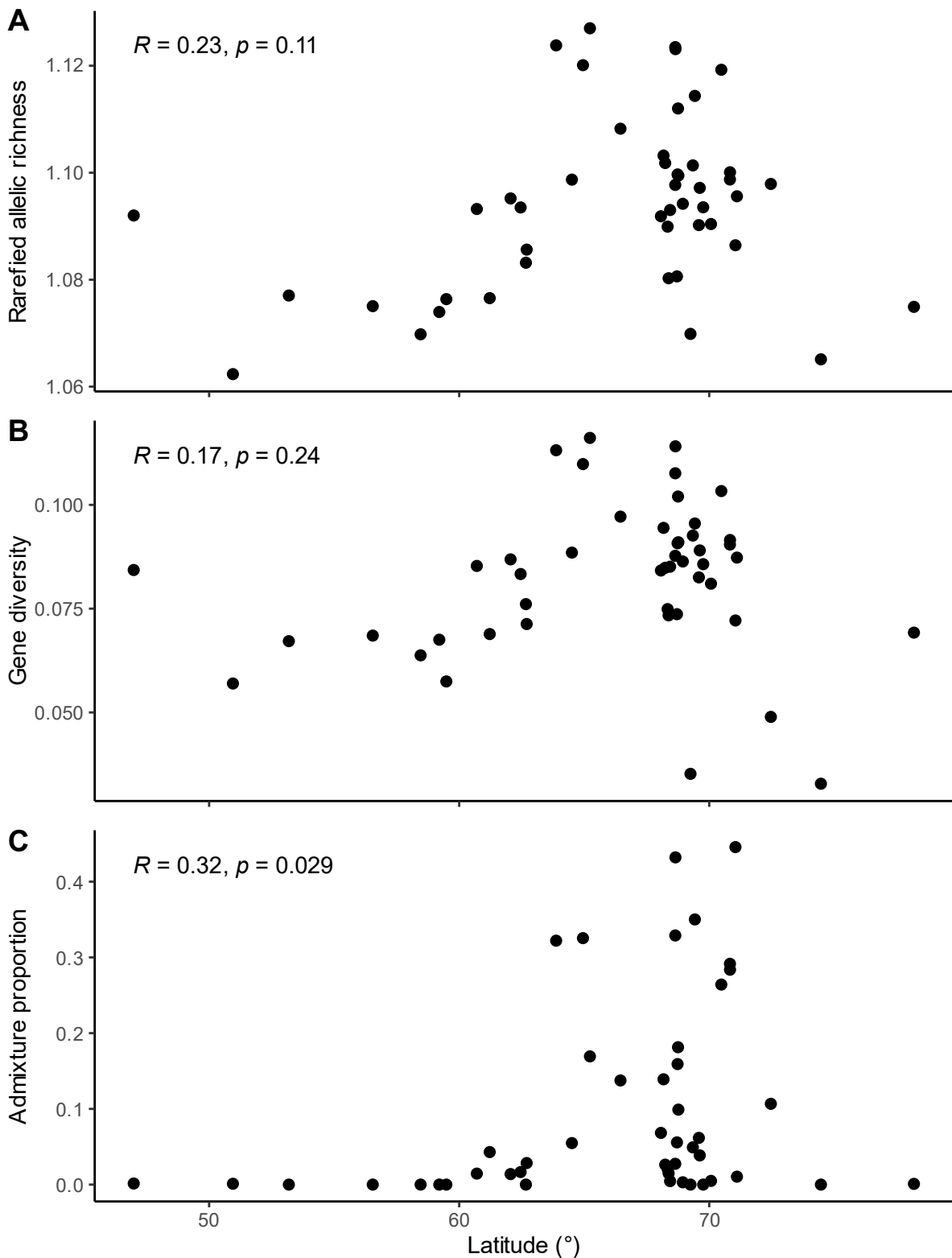


Figure S5.4. Population genetic diversity of dwarf birch and latitude. Relationship between genetic diversity and latitude for each dwarf birch sampling site with Spearman's correlation coefficients (R) and associated p values (p). Rarefied allelic richness (**A**), gene diversity (**B**), and admixture proportion (**C**).

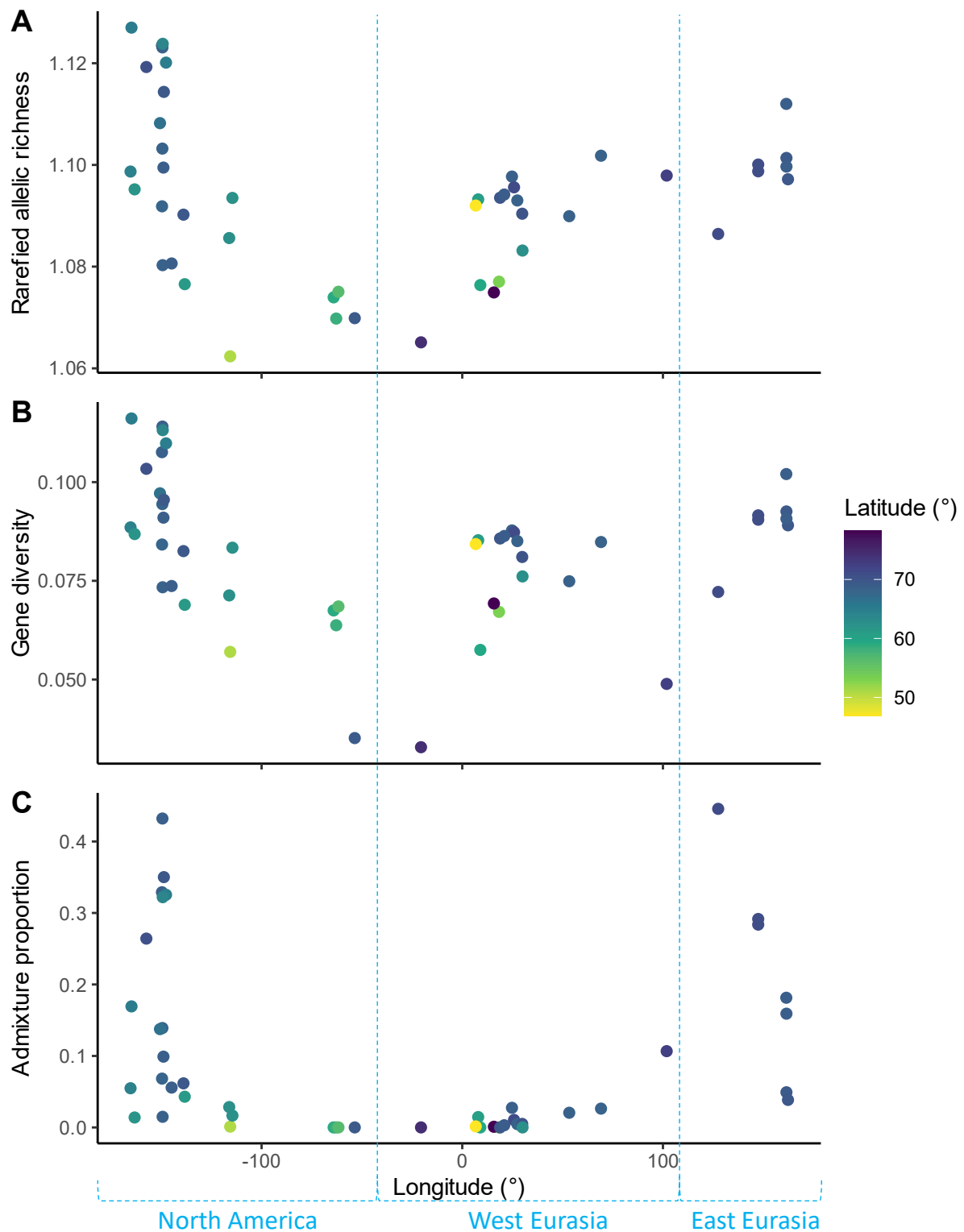


Figure S5.5. Variation in dwarf birch genetic diversity across geographical space. Rarefied allelic richness (A), gene diversity (B), genetic admixture proportion (C), across longitude (decimal degrees) for each dwarf birch sampling site. Point colour corresponds to latitude. North America encompasses the western Greenland sampling site while the eastern Greenland sampling site is included in West Eurasia.

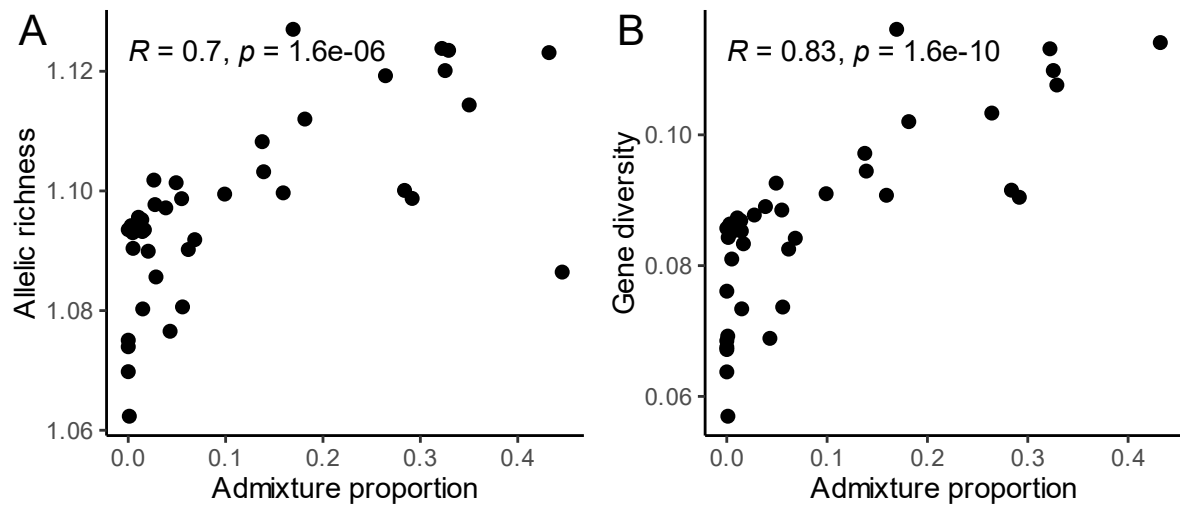


Figure S5.6. Relationships between dwarf birch sampling site genetic diversity and admixture. Rarefied allelic richness (A) and Gene diversity (B) with Spearman's correlation coefficients (R) and associated p values (p).

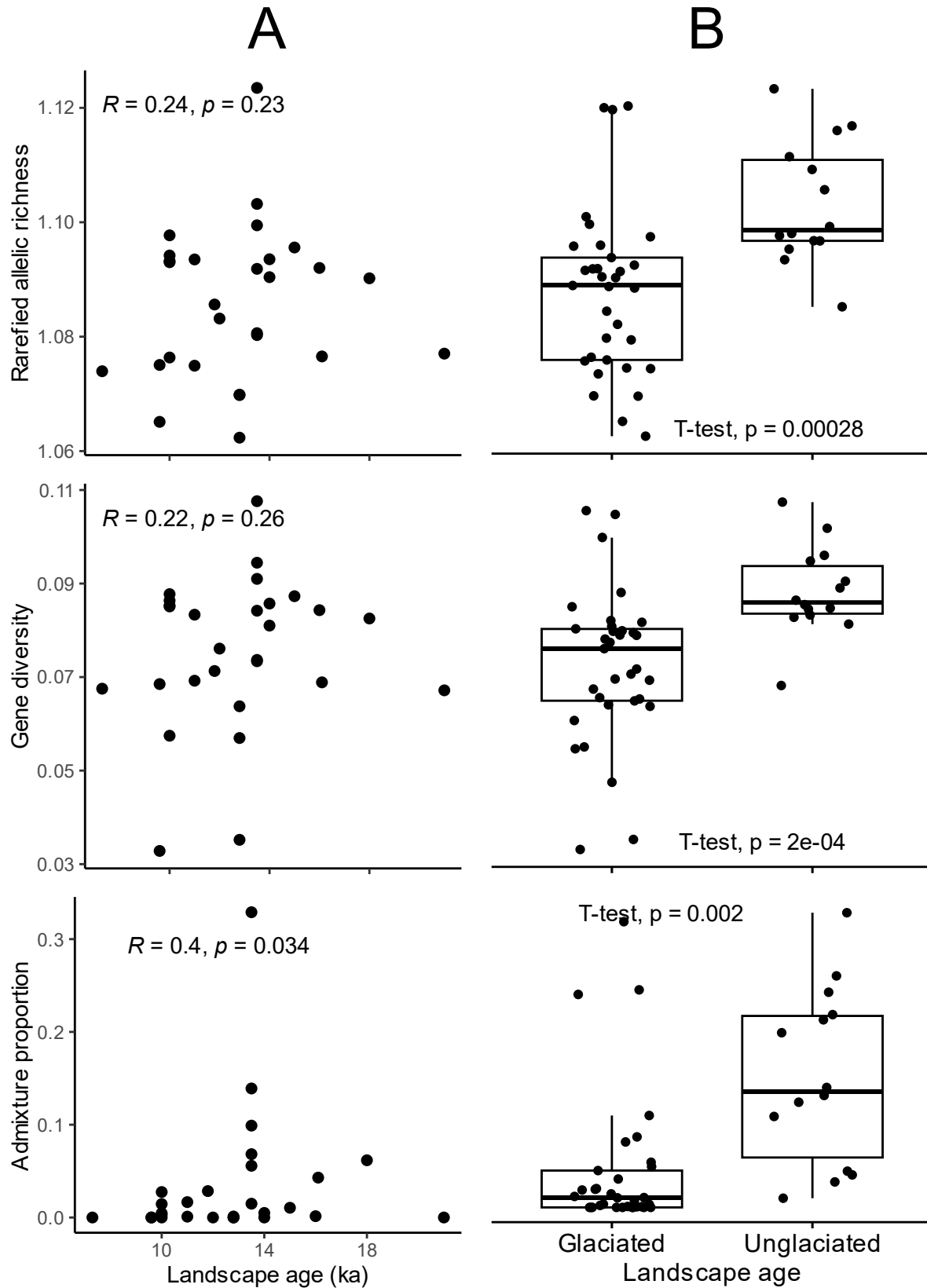


Figure S5.7. Relationship between dwarf birch sampling site genetic diversity and landscape age. (A) comparison of sites that were glaciated during the Last Glacial Maximum (postglacial landscapes) with Spearman's correlation coefficients (R) and associated p values

(p), and **(B)** comparison of sites that were glaciated (landscape age < 2.6 million years) and unglaciated (landscape age $\geq$ 2.6 million years) in the Quaternary period with associated T test p values (p). Landscape ages compiled from reconstructed Quaternary ice sheet margins (Batchelor et al., 2019; Dalton et al., 2020, 2022; Hughes et al., 2016).

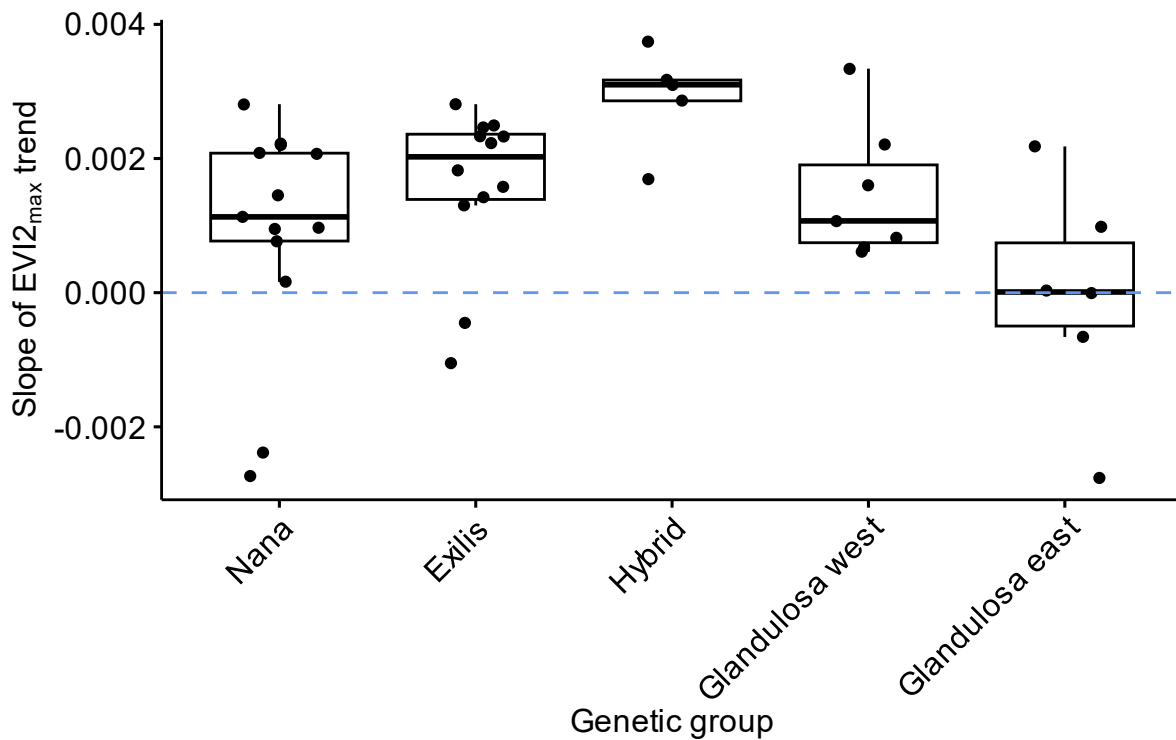


Figure S5.8. Differences in EVI2_{max} greening trends for dwarf birch genetic groups. EVI2_{max} calculated from spectral reflectances of a sample of 30m resolution Landsat pixels, filtered for treeless landcover, in a 50km radius of each dwarf birch sampling site. The slope of each greening time series was determined using a non-parametric Theil–Sen slope estimator. Sites above the dotted line indicate a positive trend, sites below the dotted line indicate a negative trend. Individuals were assigned to genetic groups based on >50% ancestry proportion of the corresponding ADMIXTURE ancestral population. Some sampling sites contained individuals from more than one genetic group, and where individuals were completely admixed genetically (“hybrid” populations).

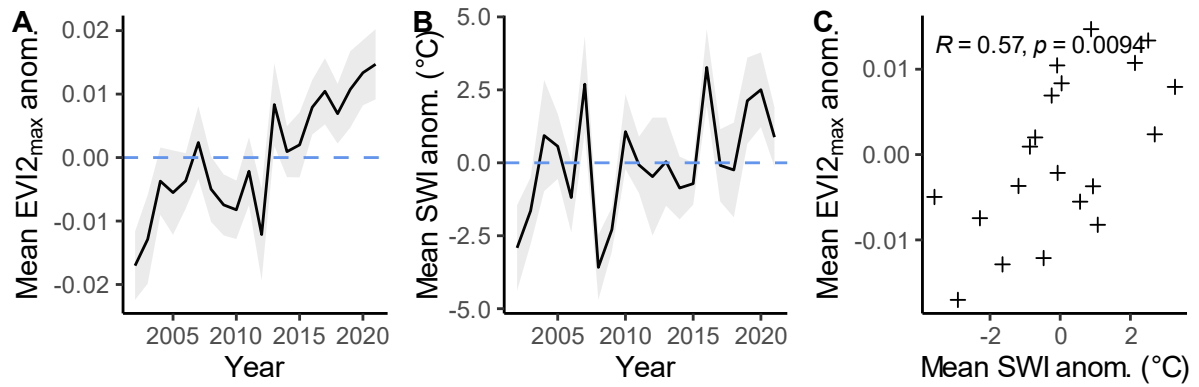


Figure S5.9. Annual greening and summer warmth anomalies across dwarf birch sites from 2002-2021. EVI2_{max} anomalies (A), summer warmth index (SWI) anomalies (B), and (C) EVI2_{max}-SWI anomaly correlations across sites with Spearman's correlation coefficient (R) and associated p value (p). Dotted line indicates the period mean, and error bands depict 95% confidence intervals.

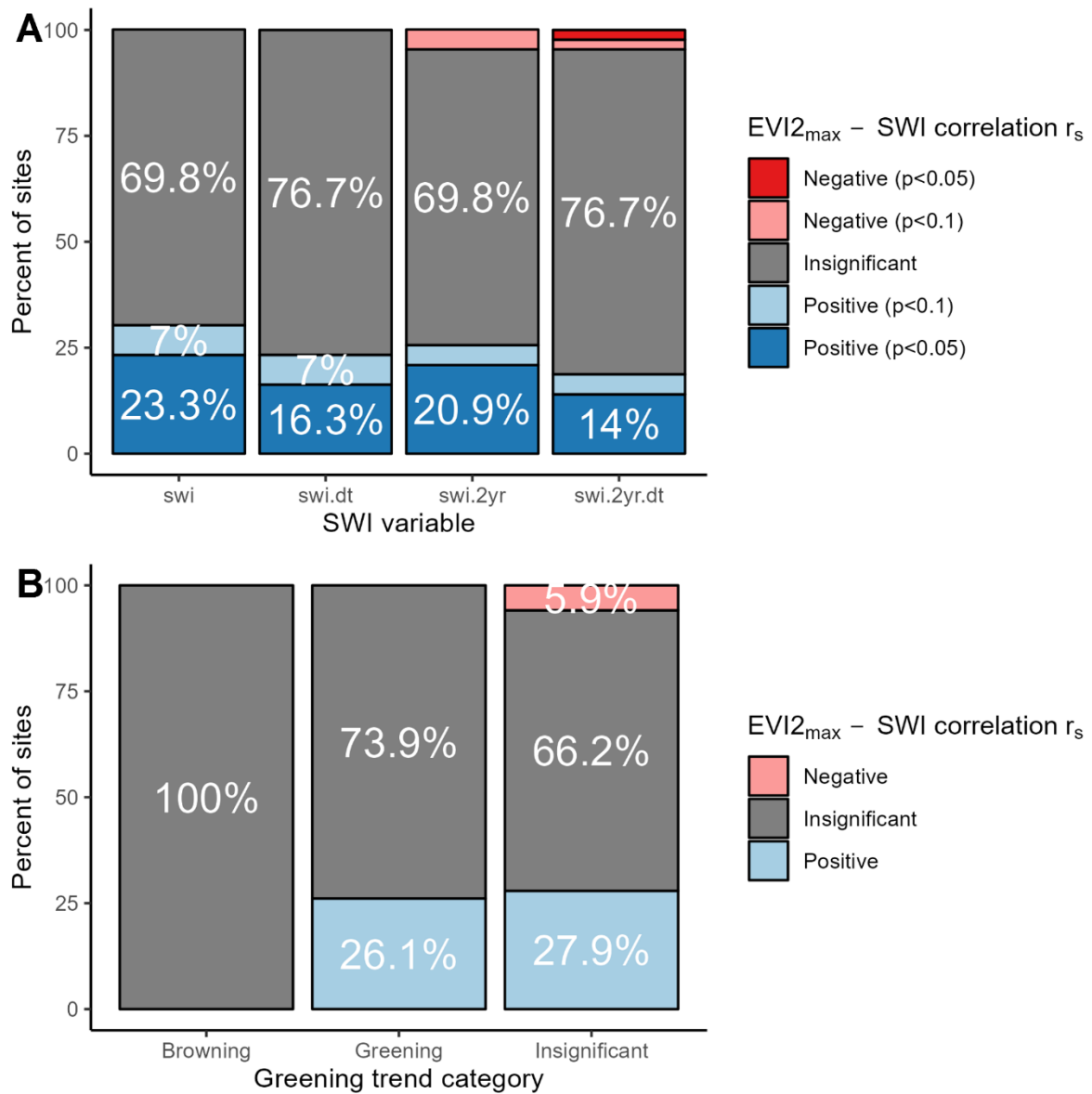


Figure S5.10. Correlations between annual greening and summer warmth anomalies at dwarf birch sites from 2002-2021. Correlations between EVI2_{max} and summer warmth index (SWI), detrended SWI, two-year average SWI, and detrended two-year average SWI (**A**): EVI2_{max}-SWI correlations split by greening trend category (**B**): The slope of each EVI2_{max} and SWI time series was determined using a non-parametric Theil–Sen slope estimator and the significance of trends evaluated with a rank-based Mann–Kendall trend test. “Greening” indicates a significant positive trend, “browning” indicates a significant negative trend.

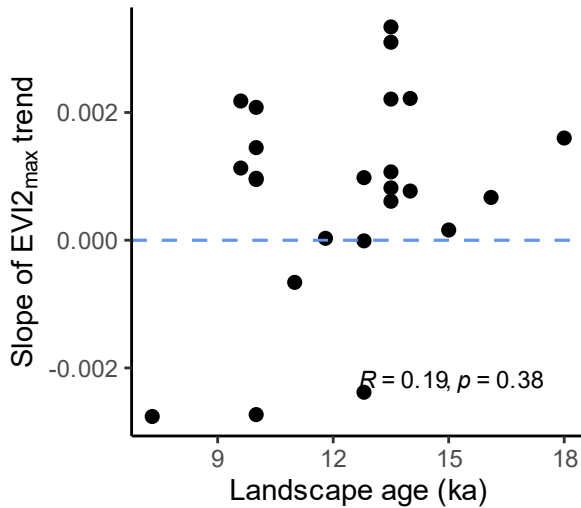


Figure S5.11. The relationship between dwarf birch sampling site greening trends and landscape age. Slope of EVI2_{max} trends from 2002-2021 and corresponding landscape ages of sites that were glaciated during the Last Glacial Maximum (postglacial landscapes), with Spearman's correlation coefficient (R) and associated p value (p). Sites above the dotted line indicate a positive trend, sites below the dotted line indicate a negative trend.

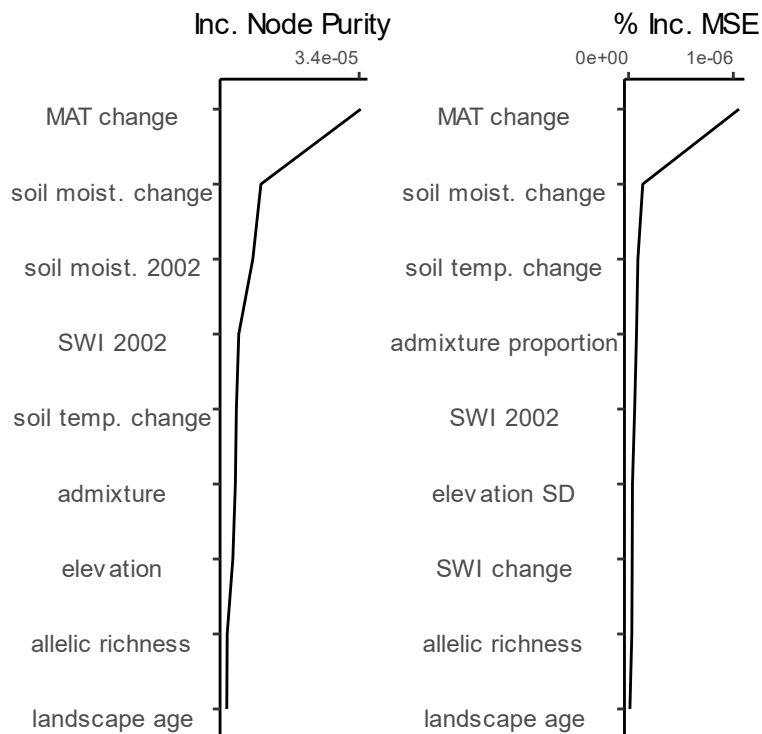


Figure S5.12. Variable importance in Random Forest Regression model predicting magnitude of greening trends. Variables ranked according to the increase in node purity, and percentage increase in MSE, when they are randomly permuted. The model explained 31.6% of variance in greening trends based on out-of-bag predictions of the original dataset (RMSE 0.00126).

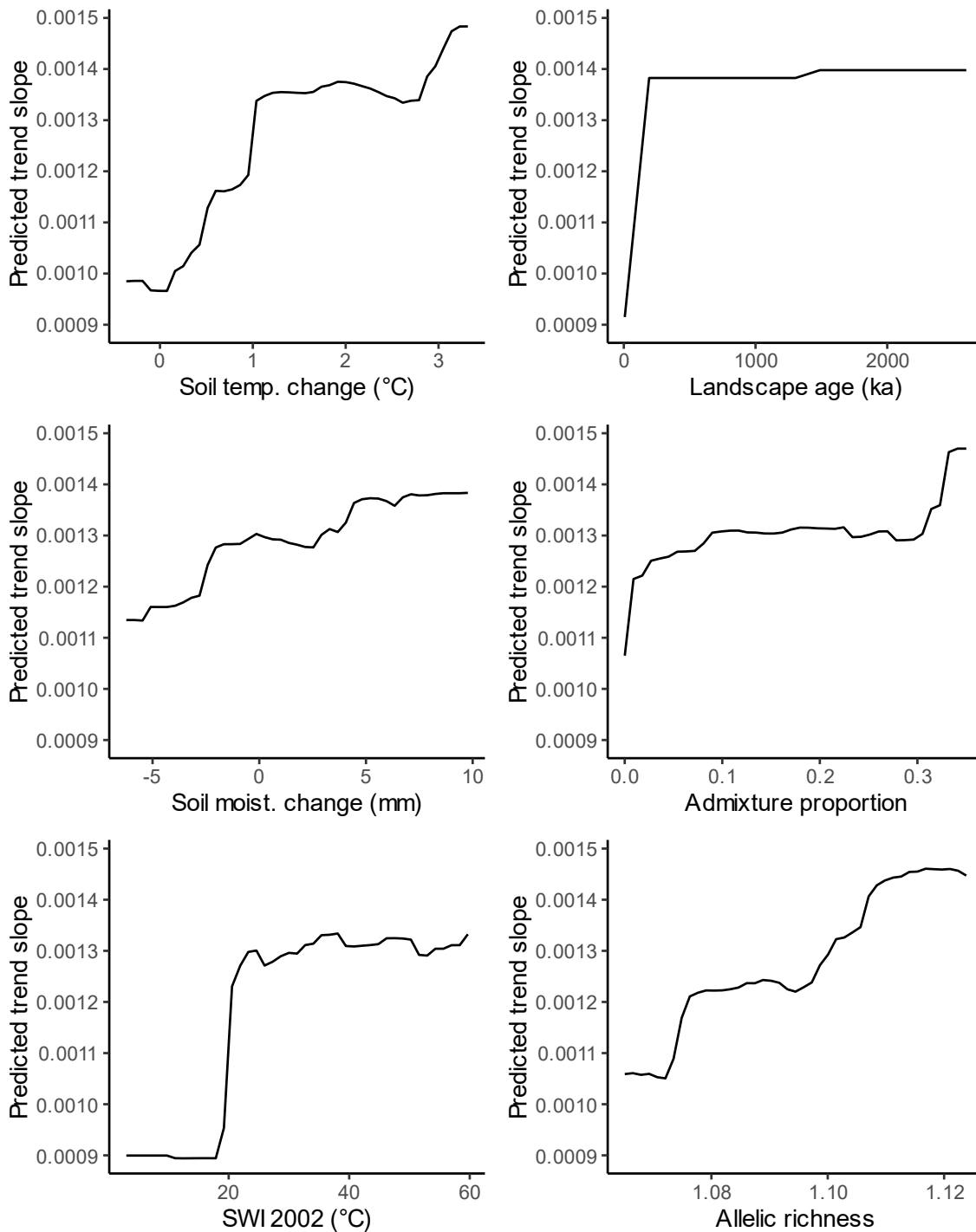


Figure S5.13. Partial dependence plots for the most important variables determined by Random Forest regression model without Mean Annual Temperature change. The Y axis shows the average $EV_{12_{max}}$ trend slope predicted at different levels of a given explanatory variable across models, with other variables held constant. The model explained 16.5% of variance in greening trends based on out-of-bag predictions of the original dataset (RMSE 0.00139).

Appendix S5.5: Supplementary tables

Table S5.1. Dwarf birch sampling site metadata. Samples from sites BN62 to BN68 were provided with permission of the NHMO DNA Bank at the Natural History Museum, University of Oslo. Sample IDs available from the author (mariaemilyd@gmail.com) upon request.

Sampling site ID	Taxon (field ID)	Country	Region	Locality	Collection year	Collector	Latitude (decimal degrees)	Longitude (decimal degrees)	Number of individuals sequenced	Bioclimatic zone
BN01	<i>B. nana</i>	USA	Alaska	Itkillik	2015	DA	68.6422	-149.64	4	E
BN02	<i>B. nana</i>	USA	Alaska	Chandalar	2015	DA	68.0678	-149.599	6	E
BN03	<i>B. nana</i>	USA	Alaska	Dalton Mountain	2015	DA	68.1719	-149.44	6	E
BN04	<i>B. nana</i>	USA	Alaska	Kuparuk River	2015	DA	68.6486	-149.403	7	E
BN05	<i>B. nana</i>	USA	Alaska	Roche Mountonee	2015	DA	68.3747	-149.313	6	E
BN06	<i>B. nana</i>	USA	Alaska	Bunny Haven	2015	DA	68.7657	-148.9	6	E
BN07	<i>B. nana</i>	Canada	Labrador	Komaktorvik River	2015	DM; LH	59.204	-64.0985	6	E
BN08	<i>B. nana</i>	Russia	Sakha	Kytalyk1	2015	GSS; RS	70.8284	147.4703	6	E
BN09	<i>B. nana</i>	Russia	Sakha	Kytalyk2	2015	GSS; RS	70.831	147.4746	6	E
BN10	<i>B. nana</i>	Norway	Viken	Hol	2015	JDMS	60.7052	7.9355	6	Oro-Arctic tundra
BN12	<i>B. nana</i>	USA	USA	Atqasuk	2015	JP; SW	70.4833	-157.417	4	D
BN13	<i>B. nana</i>	Canada	Labrador	Torngats Basecamp	2015	LH	58.4581	-62.8087	6	E
BN14	<i>B. nana</i>	Canada	Labrador	Nain	2015	LH	56.5439	-61.6993	6	Boreal
BN15	<i>B. nana</i>	Finland	Lapland	Näkkälä	2015	MMF	68.641	24.7725	5	Boreal

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BN16	<i>B. nana</i>	Norway	Finnmark	Nordkapp	2015	MMF	71.1087	25.7973	6	E
BN17	<i>B. nana</i>	Finland	Lapland	Saariselkä	2015	MMF	68.4352	27.4351	6	Boreal
BN21	<i>B. nana</i>	USA	Alaska	East Fork Chandalar River	2015	MW	68.71	-144.825	6	E
BN22*	<i>B. nana</i>	Poland	Kujawsko-Pomorskie	Linje	2015	MS	53.1876	18.3096	4	Temperate
BN23	<i>B. nana</i>	USA	Alaska	Nome	2015	ML	64.508	-165.297	5	E
BN24	<i>B. nana</i>	USA	Alaska	Kuzitin	2015	ML	65.2293	-164.827	6	E
BN25	<i>B. nana</i>	USA	Alaska	Old Man	2015	ML	66.4501	-150.619	5	Oro-Arctic
BN29	<i>B. nana</i>	USA	Alaska	SAG	2015	ML	69.4254	-148.697	3	E
BN30	<i>B. nana</i>	USA	Alaska	Fox	2015	ML	64.9506	-147.618	6	Boreal
BN31	<i>B. nana</i> subsp. <i>exilis</i>	Russia	Sakha	Chersky	2015	ML	68.7521	161.4686	6	Boreal
BN32	<i>B. nana</i> subsp. <i>exilis</i>	Russia	Sakha	Krutaya Drisva	2015	ML	69.3452	161.5314	6	E
BN33	<i>B. nana</i> subsp. <i>exilis</i>	Russia	Sakha	Ambarchik	2015	ML	69.6215	162.3131	6	D
BN34	<i>B. nana</i>	USA	Alaska	Healy	2015	ML	63.8782	-149.253	6	Oro-Arctic
BN37	<i>B. nana</i>	Svalbard	Norway	Endalen	2015	SRK	78.1868	15.7632	7	C
BN38	<i>B. nana</i>	Norway	Troms	Kvaløya	2015	SRK	69.759	18.8524	6	Oro-Arctic
BN39	<i>B. nana</i>	Norway	Finmark	Vadsø	2015	SRK	70.0712	29.8731	5	Oro-Arctic
BN40	<i>B. nana</i>	USA	Alaska	St. Mary's	2015	SN	62.0555	-163.259	6	E
BN42	<i>B. nana</i> ?	Finland	Lapland	Kilpisjärvi	2015	TK	68.9441	20.9116	6	Oro-Arctic
BN43*	<i>B. nana</i>	Finland	Karjala	Joensuu	2015	TK	62.6691	30.017	6	
BN44	<i>B. nana</i>	Norway	Telemark	Lifjeld	2015	TTH	59.486	8.998	2	Boreal
BN45*	<i>B. nana</i>	Switzerland	Neuchâtel	Les Ponts-de-Martel	2015	CR	46.9842	6.7167	6	

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BN46	<i>B. glandulosa</i>	Canada	British Columbia	Og Lake	2015	MMF	50.9516	-115.635	6	Temperate conifer
BN47	<i>B. nana</i>	Russia	Sakha	Rodinka Mountain	2016	TK	68.7337	161.5375	6	Boreal
BN49	<i>B. glandulosa</i>	Canada	Yukon Territories	Kluane - Pika Valley	2015	JA	61.22145	-138.286	6	Oro-Arctic
BN51	<i>B. nana</i>	Canada	Yukon Territories	QHI - Hawk Valley	2015	JA	69.58539	-138.922	6	D
BN54	<i>B. glandulosa</i>	Canada	Northwest Territories	Yellowknife - Bog	2015	HT	62.45721	-114.533	5	Boreal
BN55	<i>B. glandulosa</i>	Canada	Northwest Territories	Yellowknife - Site 2	2015	HT	62.69975	-116.131	3	Boreal
BN61	<i>B. nana</i>	Russia	Yamal	Erkuta Tundra Monitoring site	2021	M Sp	68.239	69.142	4	E
BN62	<i>B. nana</i>	Russia	Nenetsky AO	Malozemelskaya tundra. Nenetskaya Gryada, Korovinskaya Guba; 5.5-8 km W Cape Seduysky Nos, c. 0-3 km W to NW the shore	2004	DE	68.336	53.3	3	E
BN63	<i>B. nana</i>	Russia	Taimyrsky AO	Ary-Mas nature reserve, (c. 50-60 km NNW Khatanga), right riverside of Novaya, along	2004	PS; AT	72.46444	101.8636	1	E

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				the river and up to c. 3 km S of river						
BN64	<i>B. nana</i> subsp. <i>exilis</i>	Russia	Yakutia	Lena R. west bank: Chekurovka village, surroundings of settlement	2004	HS; RE	71.04833	127.5233	3	E
BN67	<i>B. nana</i>	Greenland	Disko, Qeqertalik	5-10 km fra Arktisk Stasjon (koordinater er for stasjonen)	2003	BJG; GB	69.25	-53.5667	1	D
BN68	<i>B. nana</i>	Greenland	Zackenberg	South of the landingstrip close to "Kjovedammen" and "Teltdammen".	2002	KA	74.46667	-20.55	1	C

* Sites excluded from tundra greening analysis as lowland temperate sites.

Table S5.2. Genetic groups and genetic diversity of dwarf birch sampling sites. Individuals were assigned part of a genetic group (ADMIXTURE ancestral population) if they had >50% assignment probability to that group. Some sampling sites contained individuals from more than one genetic group, and where individuals were completely admixed genetically (“hybrid” populations).

Sampling site ID	Taxon (field ID)	Genetic group	Rarefied allelic richness	Gene diversity	Admixture proportion mean	Admixture proportion SD	Used in greening analysis
BN01	<i>B. nana</i>	Exilis/ Glandulosa west	1.12	0.108	0.329	0.132	Y
BN02	<i>B. nana</i>	Glandulosa west	1.09	0.0842	0.068	0.099	Y
BN03	<i>B. nana</i>	Glandulosa west	1.10	0.0945	0.139	0.107	Y
BN04	<i>B. nana</i>	Exilis/ Glandulosa west	1.12	0.114	0.432	0.058	Y
BN05	<i>B. nana</i>	Glandulosa west	1.08	0.0734	0.0149	0.0286	Y
BN06	<i>B. nana</i>	Glandulosa west	1.10	0.0910	0.099	0.132	Y
BN07	<i>B. nana</i>	Glandulosa east	1.07	0.0675	0.000	0.000	Y
BN08	<i>B. nana</i>	Exilis	1.10	0.0905	0.292	0.132	Y
BN09	<i>B. nana</i>	Exilis	1.10	0.0915	0.284	0.0570	Y
BN10	<i>B. nana</i>	Nana	1.09	0.0853	0.0145	0.0166	Y
BN12	<i>B. nana</i>	Exilis	1.12	0.103	0.264	0.0331	Y
BN13	<i>B. nana</i>	Glandulosa east	1.07	0.0638	0.000	0.000	Y
BN14	<i>B. nana</i>	Glandulosa	1.08	0.0685	0.000	0.000	Y

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		east					
BN15	<i>B. nana</i>	Nana	1.10	0.0877	0.0275	0.0289	Y
BN16	<i>B. nana</i>	Nana	1.10	0.0873	0.0105	0.0172	Y
BN17	<i>B. nana</i>	Nana	1.09	0.0851	0.00462	0.0112	Y
BN21	<i>B. nana</i>	Glandulosa west	1.08	0.0737	0.0557	0.0649	Y
BN22*	<i>B. nana</i>	Nana	1.08	0.0672	0.000	0.0000	N
BN23	<i>B. nana</i>	Exilis	1.10	0.0885	0.0548	0.0860	Y
BN24	<i>B. nana</i>	Exilis/ Glandulosa west	1.13	0.116	0.169	0.142	Y
BN25	<i>B. nana</i>	Exilis	1.11	0.0972	0.138	0.0665	Y
BN29	<i>B. nana</i>	Exilis/ Glandulosa west	1.11	0.0955	0.350	0.1065	Y
BN30	<i>B. nana</i>	Exilis/ Glandulosa	1.12	0.110	0.325	0.113	Y
BN31	<i>B. nana</i> subsp. <i>exilis</i>	Exilis	1.11	0.102	0.181	0.0922	Y
BN32	<i>B. nana</i> subsp. <i>exilis</i>	Exilis	1.10	0.0926	0.0492	0.0566	Y
BN33	<i>B. nana</i> subsp. <i>exilis</i>	Exilis	1.10	0.089	0.0385	0.0463	Y
BN34	<i>B. nana</i>	Exilis	1.12	0.113	0.322	0.0965	Y
BN37	<i>B. nana</i>	Nana	1.07	0.0692	0.000944	0.0024	Y
BN38	<i>B. nana</i>	Nana	1.09	0.0857	0.000	0.0000	Y
BN39	<i>B. nana</i>	Nana	1.09	0.0810	0.00494	0.0110	Y
BN40	<i>B. nana</i>	Exilis	1.10	0.0869	0.0139	0.0262	Y
BN42	<i>B. nana</i> ?	Nana	1.094	0.0864	0.0030	0.0074	Y
BN43*	<i>B. nana</i>	Nana	1.08	0.0761	0.000	0.000	N

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BN44	<i>B. nana</i>	Nana	1.08	0.0575	0.000	0.000	Y
BN45*	<i>B. nana</i>	Nana	1.09	0.0843	0.00145	0.00224	N
BN46	<i>B. glandulosa</i>	Glandulosa east	1.06	0.0570	0.00110	0.00262	Y
BN47	<i>B. nana</i>	Exilis	1.10	0.0908	0.159	0.0294	Y
BN49	<i>B. glandulosa</i>	Glandulosa west	1.08	0.0689	0.0430	0.0589	Y
BN51	<i>B. nana</i>	Glandulosa west	1.09	0.0825	0.0617	0.0719	Y
BN54	<i>B. glandulosa</i>	Glandulosa east	1.09	0.0833	0.0166	0.0177	Y
BN55	<i>B. glandulosa</i>	Glandulosa east	1.09	0.0713	0.0285	0.0299	Y
BN61	<i>B. nana</i>	Nana	1.10	0.0848	0.0263	0.0280	Y
BN62	<i>B. nana</i>	Nana	1.09	0.0749	0.0205	0.00446	Y
BN63	<i>B. nana</i>	Nana	1.10	0.0489	0.107	NA	Y
BN64	<i>B. nana</i> subsp. <i>exilis</i>	Exilis	1.09	0.0722	0.446	0.0391	Y
BN67	<i>B. nana</i>	Nana	1.07	0.0352	0.000	NA	Y
BN68	<i>B. nana</i>	Nana	1.07	0.0328	0.000	NA	Y

* Sites excluded from tundra greening analysis as lowland temperate sites.

Table S5.3. Comparison of full genetics dataset and subset of sites that were used in the tundra greening analysis.

	Full dataset	Subset dataset
Number of sampling sites	47	43
<i>B. nana</i> subsp. <i>nana</i> sites	17	13
<i>B. nana</i> subsp. <i>exilis</i> sites	12	12
<i>B. glandulosa</i> sites	13	13
<i>B. nana</i> subsp. <i>exilis</i> - <i>B. glandulosa</i> hybrid sites	5	5
Number of individuals	238	215
Mean individuals per site	5.11 (min = 1, max = 7)	5.0 (min = 1, max = 7)

Table S5.4. Summary of environmental datasets used with random forest models to predict Landsat EVI2_{max} trends from 2002-2021 at each dwarf birch sampling site.

Environmental variable	Derived variable	Dataset	Sources	Publication	Version	Spatial resolution	Period	Cadence
Landscape age	Landscape age	Shapefiles of ice sheet chronologies	Geological and geomorphological records and numerical modelling	(Batchelor et al., 2019; Dalton et al., 2020, 2022; Hughes et al., 2016)			2.6 million years ago - 6,000 years ago	Single time
Summer warmth index (°C)	Summer warmth index (°C)	ARCLIM: Bioclimatic atlas of the terrestrial Arctic	ERA5-Land climate model reanalysis	(Rantanen et al., 2023)	2	0.1 x 0.1 °	2002-2021	Annual
Mean monthly air temperature (°C)	Summer Warmth Index (°C)	CRU TS: Climatic Research Unit (University of East Anglia) and Met Office	Interpolation from weather station observations	(Harris et al., 2020)	4.06	0.5 x 0.5 °	2002-2021	Annual
Monthly soil moisture (mm)	Minimum summer (June July August) soil moisture (mm)	TerraClimate	Soil moisture output from water balance model based on climatically aided interpolated variables from WorldClim, CRU TS v 4.0, and JRA-55 datasets	(Abatzoglou et al., 2018)	2022	0.042 x 0.042 °	2002-2021	Annual
Mean annual ground temperature 1m depth (K)	Mean annual soil temperature 1m depth	ESA Permafrost Climate Change Initiative (Permafrost_cci):	Remotely sensed (MODIS) land surface temperature input into permafrost model CryoGrid CCI.	(Obu et al., 2021)	3	926.63 m	2002-2019	Annual

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	(°C)	Permafrost Ground Temperature for the Northern Hemisphere, v3.0	Temperature input prior to 2003 derived from downscaled and bias corrected ERA5-Land climate model reanalysis.					
Mean annual air temperature (K)	Mean annual air temperature (°C)	ARCLIM: Bioclimatic atlas of the terrestrial Arctic	ERA5-Land climate model reanalysis	(Rantanen et al., 2023)	2	0.1 x 0.1 °	2002-2021	Annual
Digital Elevation model (m)	Standard deviation of elevation (m)	AWS Open Data Terrain Tiles via elevatr R package.	(1) 152m resolution: SRTM, CDEM in Canada, EUDem in Europe, with GMTED in high latitudes above 60°* (2) 38m resolution: CDEM in Canada, ArcticDEM in latitudes above 60°, Kartverket in Norway†	(Hollister et al., 2023)	v 0.4.5	(1) 152m (2) 38m at 60°N		Single time
Arctic bioclimatic zones	Bioclimatic zone/biome	Bioclimatic subzones of the Arctic territory according to the CAVM		(Conservation of Arctic Flora and Fauna, 2013)				Single time
Ecoregion	Bioclimatic zone/biome	Ecoregions from: WWF Terrestrial Ecoregions		(Olson et al., 2001)				Single time

* GMTED2010 and SRTM data courtesy of the U.S. Geological Survey. Canadian Digital Elevation Model (CDEM) contains information licensed under the Open Government Licence – Canada. EU-DEM Produced using Copernicus data and information funded by the European Union - EU-DEM layers.

†Norway terrain data © Kartverket. ArcticDEM DEM(s) were created from DigitalGlobe, Inc., imagery and funded under National Science Foundation awards 1043681, 1559691, and 1542736.

Table S5.5: Pairwise genetic differentiation (AMOVA F_{ST}) for genetic groups (ADMIXTURE ancestral population).

	Nana	Exilis	Glandulosa west	Glandulosa east
Nana	0	0.0454	0.117	0.133
Exilis		0	0.0724	0.0830
Glandulosa west			0	0.0333
Glandulosa East				0

Table S5.6: Genetic diversity of sampling sites according to genetic group (ADMIXTURE ancestral population).

Genetic group	No. sampling sites	Rarefied allelic richness		Gene diversity		Admixture proportion	
		Mean	SD	Mean	SD	Mean	SD
Nana	17	1.09	0.0109	0.0723	0.0182	0.0130	0.00925
Exilis	12	1.10	0.0106	0.0931	0.0102	0.187	0.0634
Glandulosa west	7	1.09	0.0102	0.0812	0.00959	0.0688	0.0804
Glandulosa east	6	1.08	0.0112	0.0686	0.00877	0.00771	0.00837
Hybrid	5	1.12	0.00473	0.109	0.00807	0.321	0.110

S5.6 References

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Chapter 6: Synthesis and conclusion

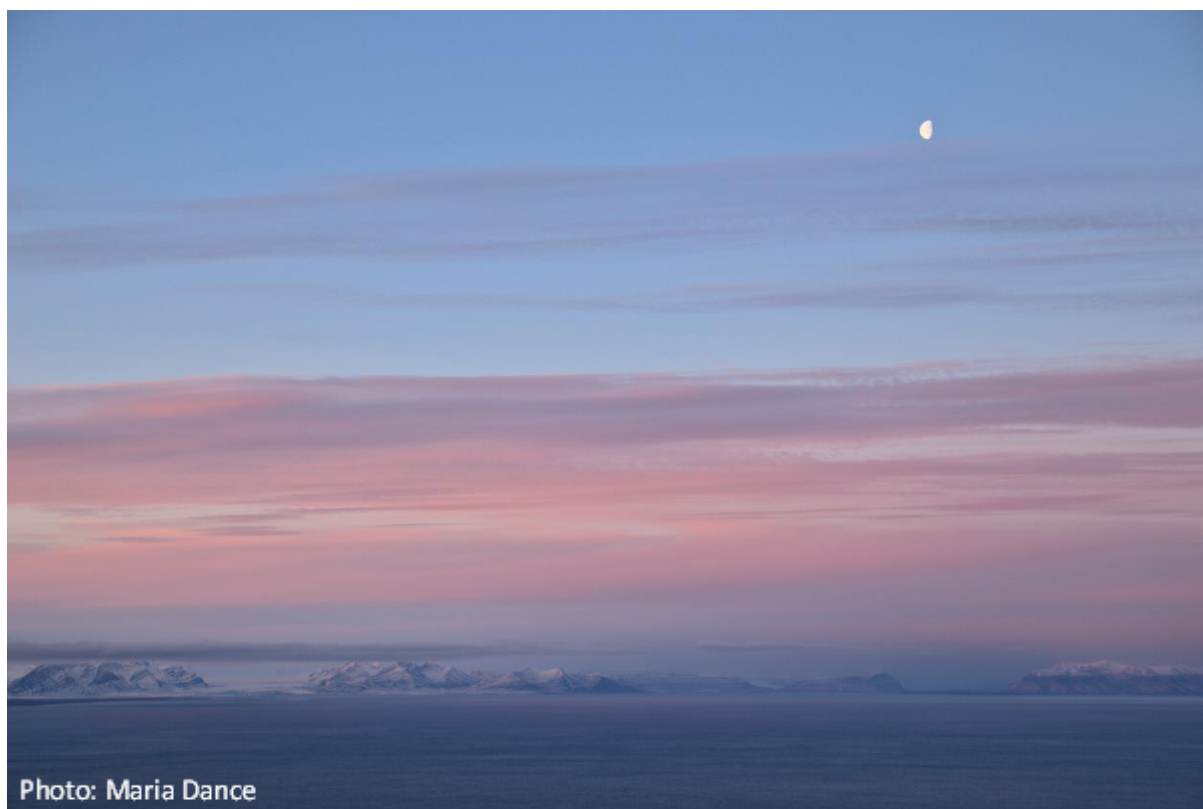


Photo: Maria Dance

6.1 Summary

This thesis used genetics as a tool to infer past ecological and evolutionary responses of Arctic biota to climate change, and how this genetic legacy may impact responses to ongoing climate change. To address this aim, I focused on two ecologically important panarctic taxa and used a phylogeographic approach based on contemporary genetic structure and diversity. I used coalescent modelling with an approximate Bayesian computation (ABC) framework to test hypotheses on the Quaternary demographic histories of the study taxa and compared the timing of derived population events with paleoenvironmental data. I then compared the genetic structure of modern dwarf birch populations with ongoing environmental change in the Arctic to infer the continuing genetic legacy of past climate change. This synthesis chapter brings together the main results from the three research papers and considers emergent themes and future directions arising from this research.

In **Chapter 3** I examined the role of postglacial sea ice and ice sheet changes in modulating reindeer/caribou (*Rangifer tarandus* L.) colonisation and connectivity in the Arctic islands. I determined that ice sheet retreat, sea ice concentration, and ocean currents were likely important in shaping postglacial dispersal and subsequent evolution and population history of Arctic island reindeer (*Rangifer tarandus* L.). This study was the first to compare late Quaternary reindeer dynamics across different Arctic regions using ABC combined with sea ice data and ice sheet chronologies.

In **Chapter 4** I used the richer genetic information that can be derived from genome-wide markers to evaluate how Quaternary climate fluctuations impacted the evolution and population history of the dwarf birch complex (*Betula nana* L. and *Betula glandulosa* Michx.). I found that climatic transitions in the Quaternary — as indicated by ice sheet expansion and retreat — appear to have been associated with population history in complex ways, with interactions between ice sheet changes, climate, and other environmental conditions. This research was the first to study the phylogeographic structure of *B. glandulosa* and to use next-generation sequence data and the ABC approach to study the circumpolar range of an Arctic plant species (Borrell et al., 2018; Chen & Lou, 2019; Ikeda et al., 2017).

Building on the insights on the impact of Quaternary climate change on the genetic structure of dwarf birches, in **Chapter 5** I assessed whether these historical influences on genetic structure affect the response of the dwarf birches to contemporary climate change. I found that recent greening trends in tundra vegetation reflect dwarf birch genetic diversity and landscape history, in addition to climate trends. The genetic diversity generated by historical admixture between different populations was particularly important for predicting the magnitude of greening. This study is a novel comparison of contemporary greening trends with the genetic structure of one of the shrub species complexes underlying these trends.

6.2 Main findings

6.2.1 Species evolution and population history shaped by Quaternary climate change

Reindeer and dwarf birch histories appear to have been shaped by the rapid and large climatic changes of the postglacial period (reindeer) and Quaternary glaciations (dwarf birch).

Arctic island reindeer showed a complex late Quaternary history, with Holocene dispersal to deglaciated islands followed by a degree of secondary contact with mainland populations. Secondary contact between island and mainland populations has been identified previously with genetic data (McFarlane et al., 2016). My models found that island reindeer diverged from separate mainland populations during the postglacial period, in agreement with some phylogeographic studies (Flagstad & Røed, 2003; Gravlund et al., 1998; Kvie et al., 2016), but in contrast to others that suggested a High Arctic refugium for the Canadian Arctic (Eger et al., 2009; Klütsch et al., 2017). My models also suggested multiple glacial locations for Eurasian reindeer instead of a common Beringean location, as previously hypothesised (Flagstad & Røed, 2003; Kvie et al., 2016). These results imply that the small-bodied reindeer ecotype evolved convergently in response to common selection pressures as reindeer colonised the High Arctic islands in the postglacial period (*R. tarandus* subsp. *pearyi* in Canada and *R. tarandus* subsp. *platyrhynchus* in Svalbard).

Unlike the relatively recent evolutionary history of Arctic island reindeer, my results show that the dwarf birch species complex arose earlier in the Quaternary, similar to other Arctic

species radiations (Kadereit & Abbott, 2021). Speciation occurred during cooling and ice sheet expansion associated with the Mid-Pleistocene transition (Herbert, 2023; Miller et al., 2010), with subsequent intraspecific divergence and secondary contact occurring during climatic transitions between glacial cycles, leading to multiple genetic lineages, such as those found in many Arctic plants (Abbott & Comes, 2004; Alsos et al., 2005; Ehrich et al., 2008; Eidesen et al., 2007a; Eidesen et al., 2007b; Skrede et al., 2006). Postglacial dispersal and admixture were also evident in the genetic structure of the dwarf birches, as has been found previously with other genetic markers (Eidesen et al., 2015).

The timing of modelled population genetic divergences and admixture events — representing decreases and increases in population connectivity, respectively — often coincided with changes in ice sheet coverage (both species) and sea ice cover (reindeer). The divergence time of the North American island reindeer from mainland populations coincided with ice sheet retreat. Yet the divergences of island populations that were more geographically distant from source populations (West Greenland and Svalbard) occurred thousands of years after deglaciated land was available, as did the first fossil occurrences, suggesting dispersal limitation.

Postglacial reindeer population divergences in North America occurred during periods of reduced modelled and proxy-based sea ice cover. Given the reduced genetic structure we found in North America and the contemporary connectivity of those populations due to sea ice (Jenkins et al., 2016, 2018), we hypothesised that population divergences represent geographical separation due to loss of connectivity, rather than initial island colonisation as in the Barents Sea islands. In the Barents Sea islands, population divergence and island colonisation coincided with increases in proxy-based sea ice cover and favourable currents, suggesting that long-distance dispersal (LDD) via sea ice was important for colonisation of Svalbard.

As with reindeer, we found that postglacial dispersal in the dwarf birch — inferred from postglacial admixture between genetic lineages — occurred after new land was available for colonisation after ice sheet retreat. However, earlier in the Quaternary, ice sheets might have acted as either a barrier or an enabler of population mixing. The modelled *B. nana* and *B. glandulosa* divergence dates coincided with glacial cycle intensification in the Mid-Pleistocene transition and significant expansion of the North American ice sheets, suggesting

allopatric speciation arising from isolation in separate refugia. Intraspecific divergences were also associated with ice sheet expansion — and likely refugial isolation — but later admixture events between these lineages coincided with both periods of ice sheet retreat and expansion (see next section).

6.2.2 Species responses to past climate are context specific

The results of both **Chapters 3** and **4** highlight that species' responses to Quaternary climate fluctuations were complex, with similar climatic processes resulting in different population effects depending on regional and temporal context.

Geographical and climatic differences between the North American Arctic islands and the Barents Sea islands have contributed to different postglacial reindeer dynamics. Unlike the isolated archipelagos of the Barents Sea, North American island populations were likely connected to some degree throughout the Holocene via dispersal across ice-rich, narrow ocean passages, thus giving rise to population admixture (Mallory & Boyce, 2018). Linked to this, we found evidence of multiple sea ice reductions coinciding with genetic divergence among populations in the CAA and admixture between populations. Conversely, in the geographically isolated archipelagos of the Barents Sea, colonisation was more dependent on rare LDD events, as indicated by the increases in proxy-based sea ice cover and favourable currents coinciding with population divergence. Sea ice therefore promoted extensive connectivity in one region but functioned as a (probably unidirectional due to the dominating ocean currents) LDD agent in the other.

Similarly to reindeer and sea ice, the relationship between Quaternary ice sheet changes and dwarf birch population history was context dependent. Ice sheets have variously functioned as a barrier or enabler of population mixing over time. Our model indicated that dwarf birch admixture events occurred during periods of ice sheet expansion as well as interglacial and postglacial ice sheet retreat. As has been previously found for Quaternary admixture events in other Arctic species (Taylor et al., 2021; Wang et al., 2022), dwarf birch admixture occurred during periods of climatic transition, independent of absolute climatic state.

Environmental conditions in ice-free areas also likely contributed to the complex relationship between dwarf birch demographic history and ice sheet changes. The pollen, macrofossil,

and sedimentary DNA (sedaDNA) records that I evaluated alongside the phylogeographic history indicate that unsuitable climatic and biotic conditions may have been an effective biogeographic barrier contributing to population isolation in the Quaternary. Dry and cold ice-free areas in glacials and expanded boreal forest during the warmest interglacials both seem to have restricted the distribution of shrub tundra (Bigelow et al., 2003; Binney et al., 2017) and may have reduced population connectivity between dwarf birch populations (Bennett & Provan, 2008; Kienast et al., 2001, 2005).

The dwarf birches did not, therefore, appear to follow a simple refugial isolation-interglacial expansion and admixture model, originally applied for temperate tree species (Hewitt, 2000). They also do not fit the model of a “true Arctic” species, such as *Dryas octopetala* (L.), which appears to have expanded its range in glacials and contracted its range in interglacials (Bennett & Provan, 2008). The dwarf birches instead may have behaved as an intermediate taxon, thermophilous from an Arctic (tundra) point of view, but cold-adapted from a boreal/temperate perspective. This resulted in a complex relationship between dwarf birch population dynamics and climate variability, with rapid transitions between climatic extremes seemingly key for generating genetic diversity in the Quaternary.

Our results illustrate that the impact of Quaternary climate change could be unexpectedly complex, and that the incorporation of additional paleoenvironmental and biological information is often necessary to understand these species’ responses to past climate change.

6.2.3 Common source regions and colonisation of Svalbard

Modelling Quaternary population history of reindeer and the dwarf birches highlighted a common source region and likely colonisation route from northwest Russia for the Svalbard populations of both taxa.

As in previous work that used subsets of the same genetic dataset, we found the Svalbard reindeer are genetically most similar to northwest Russian populations (Gravlund et al., 1998; Kvie et al., 2016), although we did not include Norwegian populations, which have some genetic similarities (Gravlund et al., 1998). Our best-supported demographic model included an ancestral Novaya Zemlya and Svalbard population diverging from the northwest Russian populations, supporting this colonisation route as previously hypothesised (Kvie et

al., 2016). In addition, our results add an additional line of evidence for constraining the time of colonisation of Svalbard as they are similar to times inferred from published fossil data (Forman et al., 2000; van der Knaap, 1989) and genetic data (Dussex et al., 2023).

As with reindeer, we found that the Svalbard dwarf birch population was also genetically most similar to populations in northwestern Russia and west Siberia, in agreement with previous literature (Eidesen et al., 2007a; Eidesen et al., 2015). The Svalbard population has previously been assigned to the same subspecies, *Betula nana* var. *tundrarum* Perfil. (Elven et al., 2011) based on closer morphological similarities with populations in northwest Russia than those in Norway. Our best supported demographic model contained a divergence between the Svalbard population and a mainland *B. nana* population originating from admixture between the European and west Siberian genetic groups, reinforcing the hypothesis that Svalbard was colonised predominantly from north-western Russia (Alsos et al., 2007, 2015).

Our Svalbard divergence date for *B. nana* occurred 1-3 thousand years after previously published estimates of the first occurrence on Svalbard using sedaDNA records (Alsos, et al., 2016b). As discussed in **Chapter 4**, a potential late Holocene climate-related bottleneck and subsequently low genetic diversity means that our population divergence date may reflect the bottleneck time, rather than initial colonisation.

Northwestern Russia is not the closest continental landmass to Svalbard, yet it is the most likely source region for dwarf birch and reindeer based on our results and previous research. By comparing population divergence dates with sea ice cover and currents, we provided the first indication that long-distance dispersal (LDD) over sea ice was a likely way that reindeer reached Svalbard from the Russian mainland. Proxy-based reconstructions suggest our modelled reindeer Svalbard divergence time coincides with increased ice in the potential crossing region between Franz-Josef Land and Svalbard (Pieńkowski et al., 2021; Berben et al., 2017), and an enhanced Transpolar Drift (TPD) current from Russia to Svalbard (Hole & Macias-Fauria, 2017), suggesting colonisation via Franz Josef Land. These results support previous fossil and ancient DNA evidence that suggested Franz Josef Land as a potential stepping stone (Forman et al., 2000; Kvie et al., 2016). Furthermore, the absence of reindeer fossils on Franz Josef Land after 1.3 ka (Forman et al., 2000) suggests local extinction in

response to worsening climate conditions in the Neoglacial period, similarly to the range contractions of *B. nana* experienced on Svalbard during this time (Alsos et al., 2016b).

Sea ice drift speed and direction, determined by ocean currents and wind patterns, are likely as important as extensive sea ice cover in enabling LDD (Johansen & Hytteborn, 2001; Kwok et al., 2013). An enhanced TPD with greater ice drift velocities may have favoured reindeer dispersal westwards from Franz Joseph Land to Svalbard by reducing the transport time required to cross the 300 to 400 km distance, as the likelihood of survival without food during a long crossing is probably low. Unlike reindeer, dwarf birch propagule survival across long distances is more probable. *B. nana* would also have reached Svalbard through LDD, via wind or sea ice vectors (Alsos et al., 2007). Long distance dispersal followed by successful establishment was likely rare, but AFLP data suggest that at least 7-11 successful establishments were required to generate the diversity seen in *B. nana* in Svalbard (Alsos et al., 2007, 2015). We did not compare our Svalbard divergence dates with sea ice information due to divergence time and bottleneck uncertainties, but previous work found increased sea ice along likely dispersal routes coinciding with the Svalbard colonisation times of plant species including dwarf birch (Alsos et al., 2016a). In summary, mid-Holocene LDD over sea ice may explain the commonalities in Svalbard source regions and colonisation routes by reindeer and dwarf birch.

6.2.4 The legacy of past climate on genetic diversity and adaptive potential

The phylogeographical results illustrate that Quaternary climate change have impacted contemporary genetic variation through their effects on population history. The link between past climate and population history is further visible in the consistent relationships between dwarf birch contemporary genetic diversity and the length of time since an area has been deglaciated in **Chapter 5**, with landscapes that were unglaciated in the Quaternary —i.e., likely refugia — exhibiting significantly higher genetic diversity and genetic admixture.

Contemporary genetic variation is the basis for long-term adaptation to environmental change (Pauls et al., 2013; Savolainen et al., 2007). Climate warming is contributing to shrub expansion (“shrubification”) of species such as the dwarf birches in the Arctic tundra (Elmendorf et al., 2012; Mekonnen et al., 2021; Myers-Smith et al., 2011; Sturm et al., 2001), which is visible in remotely sensed data as a vegetation greening signal (Jia et al., 2003;

Mekonnen et al., 2021; Myneni et al., 1997; Zhou et al., 2001). Genetically diverse dwarf birch populations may be better able to tolerate and adapt to potentially important limiting factors driving heterogeneous tundra greening trends, such as nutrient depletion, competition, and drought stress (Gamm et al., 2018; Phoenix & Bjerke, 2016), because of greater standing genetic variation (Jump & Peñuelas, 2005). Subsequently, regions with higher genetic diversity and large shrub populations could be expected to be more likely to show increased productivity in a greening signal if dispersal and establishment are also favourable (Alberto et al., 2013; Savolainen et al., 2007).

In **Chapter 5** we found correlations between all measures of dwarf birch genetic diversity and tundra greening magnitude. Although climate variables explained the most variance in greening trends, genetic admixture proportion — that is, the proportion of an individual's genetic material that is modelled to arise from more than one ancestral population — was also one of the most important variables for predicting greening trends in a Random Forest regression model. Greening was highest in sites with substantial admixture — >30% — between the Exilis and Glandulosa west genetic groups and between the Exilis and Nana genetic groups. We can infer that this admixture reflects the impact of past climate change on dwarf birch population history, since the best-supported demographic model in **Chapter 4** dated the admixture event between Exilis and Glandulosa during the last glacial period and the admixture event between Exilis and Nana early in the postglacial period.

The most important facet of genetic diversity in explaining greening trends therefore appears to be genetic admixture. Admixture or introgression through interspecific hybridisation, may contribute adaptive genetic material, for example through larger variation in fitness-related traits (Arnold & Martin, 2009; Palmé et al., 2004). This process could allow populations to immediately escape from low standing genetic variation, and so adapt more quickly to climate change (Hamilton & Miller, 2016; Suarez-Gonzalez et al., 2016). The relationship between greening and genetic admixture suggests the dwarf birches are potentially adapting to climate change via adaptive historical introgression, as admixture has provided a ready source of genetic diversity (J. Borrell, 2016).

Allelic richness also helped explain the variance in greening trends in the RF models, but gene diversity was not an important variable in the RF model. This may be because gene diversity was more highly correlated with admixture proportion, and so explained less

independent variance in greening trends. Gene diversity has previously been found to be higher in regions of population secondary contact and admixture (Boca et al., 2020) than in refugial areas (Petit et al., 2003), whereas allelic richness is expected to be highest in glacial refugia (Comps et al., 2001; Hewitt, 1996), although it increases in admixture zones too (Widmer & Lexer, 2001; Petit et al., 2003). The independent contribution of allelic richness to explaining variance in greening trends suggests a relationship between glacial refugia and greening independent of historical admixture events.

We found that dwarf birch genetic diversity and genetic admixture were lowest in relatively recently deglaciated and colonised areas (such as Labrador and Greenland), often at the northern edge of the species thermal tolerances (such as East Greenland and Svalbard). Successive founder events and/or LDD mean that these populations were likely founded by a small number of individuals (Alsos et al., 2007, 2015; Hewitt, 1996, 2000), reducing intrapopulation genetic diversity (Birkeland et al., 2017). Low genetic diversity (and in some cases small population size) could limit the adaptive response of dwarf birch to climate change in these areas (Savolainen et al., 2007), potentially leading to reduced shrub expansion and associated tundra greening.

These results illustrate that genetic legacies of past climate change influence how dwarf shrubs are responding to current climate change, with regions with greater allelic richness, and those containing populations descended from glacial and postglacial admixture events exhibiting the greatest greening trends. The adaptive potential of tundra shrubs may be elevated in regions of higher allelic richness and where historical admixture has taken place.

6.3 Future perspectives

The significant role of past climate in shaping the ecology and evolution of Arctic species has implications for how these species will respond to current and future climate change. For reindeer, regional differences in the effects of postglacial sea ice changes on dispersal suggest that dispersal during contemporary climate change may vary regionally and depend upon the decreasing connectivity provided by vanishing sea ice, especially over larger distances.

For example, the Svalbard reindeer are much more geographically isolated than their counterparts in the Canadian Arctic Archipelago (CAA), both in terms of geographic distance from their nearest mainland reindeer populations, and in terms of sea ice connectivity. The maximum spring sea ice extent in the Barents Sea is projected to move north of Svalbard under ongoing climate change (Dörr et al., 2021; Shu et al., 2021), so Svalbard will likely not be connected by sea ice to any land masses in the future, however ephemerally. Furthermore, the ongoing loss of sea ice within fjords and straits will reduce population connectivity and impact species viability within Svalbard (Adakudlu et al., 2019; Peeters et al., 2019). In contrast, seasonal land-fast ice cover is predicted to persist to some extent in the CAA (Newton et al., 2021), enabling some connectivity and potentially some movement of individuals from the southern CAA and mainland Canada (Mallory & Boyce, 2018). The impact of a warming climate on sea ice loss and subsequently reindeer connectivity will vary in various parts of the reindeer distribution, highlighting the importance of considering regional context in assessment of the future of species in the Arctic.

The genetic legacy of past climate change is associated with tundra greening, suggesting that genetic variation may already contribute to the response of dwarf birch species to current climate change. Although the dwarf birches appear to have high dispersal ability (Alsos et al., 2002; Meucci et al., 2021), supported by northward range shifts in interglacials (Crump et al., 2021), there is limited evidence of ongoing northward range expansion in Arctic shrubs in response to climate change (Myers-Smith et al., 2015; Myers-Smith & Hik, 2018). Increased density of birch (Ropars & Boudreau, 2012) across the low Arctic and subarctic without significant range expansion also indicates that dispersal limitation can cause temporal lags between warming and range expansion (Seider et al., 2022; Svenning & Sandel, 2013). Along with sedimentary DNA evidence of shrub range expansion lagging postglacial climate warming (Crump et al., 2019), this suggests that in-situ responses to climate change in the form of phenotypic plasticity and genetic adaptation will remain crucial.

Although the range of dwarf birch is predicted to expand locally with warming (Seider et al., 2022), the effects of warming on a panarctic scale are unclear, with some predictions of range reduction (Alsos et al., 2012) as boreal biomes shift northwards (Berner & Goetz, 2022), and others suggesting the range of shrub tundra will increase (Reji Chacko et al., 2023). Range reductions could reduce genetic diversity and future adaptive potential (Pauls

et al., 2013), although dwarf birch may be less affected due to its dispersal and outcrossing adaptations, which help maintain genetic diversity (Alsos et al., 2012, 2015; Hamrick & Godt, 1997; Thiel-Egenter et al., 2009).

Comparisons between modelled population history using contemporary genetic variation and reconstructed and modelled Quaternary climate change have proven useful in indicating the role of past climate in shaping species biogeographic and demographic histories. However, complementary approaches could lead to further insights.

Ancient DNA would improve reconstructions of demographic history as it provides a direct snapshot of the genetic diversity, and hence demography, of a taxon at a particular time and place (Fordham et al., 2014; Hofreiter, 2008; Mourier et al., 2012). For tundra vegetation, sedaDNA holds promise for improving the limitations of reconstructing historical vegetation dynamics with pollen records (Edwards et al., 1991; Niemeyer et al., 2017; Parducci et al., 2015, 2017; Pedersen et al., 2013; Sønstebo et al., 2010). sedaDNA has been used to show that dwarf birch expanded its range northwards during the last interglacial and postglacial periods on Baffin Island (Crump et al., 2019, 2021), and to infer first occurrences and presumed colonisation dates in the postglacial period (Alsos et al., 2016a; Crump et al., 2019). Since it is challenging to equate the modern distribution of genetic lineages with the location of past populations, combining the phylogeographic analysis in **Chapter 4** with sedaDNA could help verify the spatiotemporal location of dwarf birch genetic lineages during past climate change: for example, refugial locations during the LGM.

The use of reindeer ancient DNA is limited by its uneven spatial and temporal distribution in the Arctic, with limited coverage in the island populations relevant to this research (Lorenzen et al., 2011). An ongoing research project is sampling ancient DNA in Svalbard with the aim of reconstructing the timeline for environmental adaptation on Svalbard¹.

In this research, comparisons between population history and paleoclimatic data were largely qualitative due to the complexity and associated uncertainties of the population parameters generated by modelling simulated genetic data. Ice sheet reconstructions and models also have inherent uncertainties (Batchelor et al., 2019; Goosse et al., 2013; Miller et

¹ ColdRein <https://tinyurl.com/4us5dwkc>

al., 2010). Incorporating hindcast species distribution models or habitat suitability maps would further the aims of directly comparing paleoclimatic changes with species histories. Methods that integrate SDMs with genetic data have shown how climate and environmental processes have shaped the movement of genetic lineages through space and time (Brown & Knowles, 2012; Carstens & Knowles, 2007; Chan et al., 2011; Knowles et al., 2007; Metcalf et al., 2014). The models are also useful for projecting species responses to future climate change scenarios (Alsos et al., 2009; Brown et al., 2016; Louis et al., 2020; Skovrind et al., 2021; Yannic et al., 2014).

Finally, the relationship between greening trends and genetic diversity in **Chapter 5** suggests that Arctic shrub expansion may be an adaptive response to climate change, but future evolutionary potential may be constrained by genetic legacies of past climate change. Previous research has found that genome-wide genetic diversity can predict evolutionary responses of loci linked to climate change (Bertin et al., 2020), but further investigation of the genetic-environment associations of loci potentially under selection (Tóth et al., 2023) could further inform the evolutionary basis of shrubification and the future adaptive potential of the dwarf birches to climate change.

6.4 Conclusion

The comparison of the genetic structure and phylogeography of two ecologically important Arctic taxa — reindeer and the dwarf birches — with Quaternary paleoclimatic changes has shown that postglacial climate change and glacial cycles are associated with their evolution and population history. Climatic cycles variously drove population isolation and connectivity, as represented by genetic divergence and admixture. The impacts of these processes included driving allopatric speciation, generating diverse genetic lineages in different regions, enabling dispersal into deglaciated areas, and restoring connectivity between divergent lineages. Species responses to climate fluctuations were complex, with similar climatic processes likely resulting in different population effects depending on geographical and temporal context. Finally, Arctic species responses to past climate change may impact their future population dynamics and evolution by influencing their contemporary genetic structure and adaptive potential, as illustrated by the link between the population history and genetic structure of the dwarf birches, and their response to ongoing climate change in

the form of tundra vegetation greening. Reconstructing past species dynamics in relation to paleoclimatic changes is thus necessary to help us understand the long-term ecological and evolutionary impacts of environmental change, past, present, and future.

6.5 References

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Appendix A: Developing a non-toxic DNA extraction protocol from dwarf birch herbarium specimens for next-generation sequencing

A new effective method for high-quality DNA isolation from dried leaves of *Betula* species suitable for next-generation sequencing (NGS).



Photo: William Hartz

A.1 Rationale

A.1.1 Challenges of DNA extraction from *Betula* species for next generation sequencing

To address the aims and objectives of the second and third research papers in this thesis (**Chapters 4 and 5**), DNA from the dwarf birch species *Betula nana* L. and *Betula glandulosa* Michx. suitable for next-generation sequencing (NGS) was required. However, extracting high-quality DNA from dwarf birch is difficult due to a high concentration of secondary compounds such as polysaccharides and phenolics/polyphenols in leaves (Wang et al., 2013).

DNA has been extracted from *B. nana* leaf tissue using commercial kits for analyses involving Amplified Fragment Length Polymorphism (AFLPs) and chloroplast markers (Alsos et al., 2007; Eidesen et al., 2015; Järvinen et al., 2004). Commercial kits were also used on 6 silica-dried and herbarium *B. nana* samples for shallow pass shotgun sequencing (“genome skimming”), resulting in 6 partial chloroplast assemblies and 3 nuclear ribosomal DNA assemblies (Alsos et al., 2020). For these applications DNA yield and concentration can be relatively low (e.g. 250 ng, or 5 ng/μL).

However, large amounts genomic DNA are required for many next-generation sequencing applications (Mavrodiev et al., 2021) such as RADseq (Andrews et al., 2016). The DNA must be high quality, uncontaminated, and high molecular weight. One challenge is secondary compounds which are difficult to remove from DNA extracts as they co-precipitate or bind with the DNA (Mavrodiev et al., 2021). Contaminants inhibit enzymes and chemical processes in DNA extraction and NGS library preparation (Barbier et al., 2019; Porebski et al., 1997; Sahu et al., 2012). They also prevent use of DNA for PCR, restriction digests, or sequencing through inhibition of polymerases and endonucleases (Healey et al., 2014). Another challenge is that tough plant cell walls usually require mechanical disruption to free cell contents, which can fracture the DNA into smaller fragments (Mavrodiev et al., 2021).

A.1.2 Dwarf birch tissue for DNA extraction

Previous DNA extractions for RADseq analyses have found more success with fresh cambium tissue than with leaf tissue (Wang et al., 2013). However, for the present study DNA extraction tests using cambial material were unsuccessful: possibly due to the age variable preservation of the material (DNA concentration mean = 2.52 ng/μl, SD = 4.38, n = 47). In addition, removing cambium from the thin stems of a dwarf shrub is laborious compared to a mature tree. Therefore, DNA was extracted from dried leaf tissue. Mature leaves of plants have higher quantities of secondary compounds (Sahu et al., 2012). In the present study leaves were often mature and some were undergoing senescence at time of harvest due to constraints in the sampling periods. For each individual, 20 mg of the youngest and greenest leaves without visible fungal or herbivore damage were removed from each sample, placed in a 2ml Eppendorf collection tube with a 3 mm tungsten bead, and flash-frozen in liquid nitrogen before further storage at -70°C.

A.1.3 DNA extraction protocols for recalcitrant plant species

A CTAB method DNA extraction protocol was first described in 1987 (Doyle & Doyle, 1987). Since then, various CTAB-based extraction protocols have been devised for plant species with a high concentration of secondary compounds such as temperate and tropical woody species (Healey et al., 2014; Inglis et al., 2018; Mavrodiev et al., 2021; Porebski et al., 1997; Sahu et al., 2012; Souza et al., 2012). CTAB-based protocols can be labour-intensive and lengthy compared to commercial extraction kits. On the other hand, the high cost of commercial kits can be prohibitive (Inglis et al., 2018). Some protocols combine elements of CTAB protocols with commercial post-extraction clean up kits (Tibbits et al., 2006). Some CTAB protocols use phenol, a toxic and hazardous chemical to separate DNA from cellular molecules and debris (Cheng et al., 2003; Porebski et al., 1997). Other protocols are phenol-free, but use toxic chloroform to separate components (Healey et al., 2014; Inglis et al., 2018; Mavrodiev et al., 2021; Souza et al., 2012; Tibbits et al., 2006), or β -mercaptoethanol to remove polyphenols (Sahu et al., 2012). In addition, many protocols are optimised for fresh leaf samples which require instant freezing with liquid nitrogen. That is often not feasible when sampling is constrained by budget or when samples are collected in remote location, as in the case of this thesis.

I aimed to find a protocol that could produce large quantities of high-quality genomic DNA from dried dwarf birch samples, that would be suitable for NGS such as restriction-site associated sequencing (RADSeq). A second objective was to avoid use of toxic and carcinogenic chemicals where possible, therefore a range of protocols were tested without the use of phenol, chloroform, and β -mercaptoethanol.

A.2 Methods

A.2.1 Testing protocols

For all tests and extractions, flash-frozen tissues were disrupted using a TissueLyzer (with adaptors pre-cooled to -80°C) at 28 Herz for 1 minute, plate alignment was rotated 180° , and samples disrupted for a further 1 minute. Silica-dried leaf tissue from *Bistorta vivipara* L., a High Arctic and alpine perennial herb, was used as a control. To conserve material 5-10 mg of tissue was used when testing protocols. Product quality and DNA degradation were assessed by electrophoresis on a 1% TAE agarose gel, stained with ethidium bromide, viewed under UV light. DNA concentration was assessed using a Qubit Fluorometer with dsDNA BR assay kits (Life Technologies Corporation, Carisbad, CA). Contamination from secondary compounds were assessed using the ratio of absorbance at 260 and 280 nm (A260/A280 ratio for proteins), and at 260 and 230 nm (A260/A230 for polysaccharides including phenols). Purity ratios were calculated using a NanoDrop™ One Microvolume UV-Vis Spectrophotometer (Thermo Scientific, Waltham, MA, USA).

Protocol A: commercial plant DNA extraction kit

Commercial plant kits have been used to successfully extract *B. nana* DNA of lower concentration and yield for methods other than RAD-seq (Alsos et al., 2007, 2020; Eidesen et al., 2015). Therefore a commercial extraction kit (Qiagen DNeasy Plant Mini Kit) was used to

test samples that I had previously successfully extracted DNA from and sequenced with Sanger sequencing using primers based on chloroplast regions *trnS-trnBW* and *trnQ-rps16*. However, preliminary testing of these samples alongside a geographically widespread samples of other *B. nana* and *B. glandulosa* individuals resulted in negligible yields of DNA from both dried cambium and leaf material (DNA concentration mean 2.41 ng/μL, SD 2.54, n 22). Therefore, alternative CTAB-based protocols were tested.

Protocol B: Phenol-chloroform-free CTAB-SDS protocol (Barbier et al., 2019)

The Barbier et al. (2019) protocol yielded DNA concentrations below the 20 ng/μL threshold required by the RAD-seq company (mean = 7.46 ng/μL, SD = 8.43), with purity ratios also far below acceptable limits (A260/Q280 mean 1.41, SD 0.287; A260/Q230 mean 0.515, SD 0.212). After precipitation, DNA pellets were discoloured greenish-brown, and often a dark green pellet of co-precipitated secondary compounds was visible. In contrast, more DNA was obtained from *Bistorta vivipara* (L.) extracts (32.6 ng/μL, n = 1) although purity ratios were below acceptable limits (A260/A280 1.18; A260/A230 0.6).

Protocol C: Phenol-chloroform-free CTAB-SDS protocol with Wang et al. (2013) modifications

Therefore, modifications from a CTAB protocol originally devised for fresh cambium material from *B. nana* by Wang et al. (2013) were incorporated: an initial sample wash in TNE buffer; doubling CTAB buffer volume from 400μl to 800μl; addition of proteinase K; increasing the CTAB incubation temperature from 37°C to 65°C; increasing isopropanol incubation time from 15 minutes to 1 hour; additional 95% ethanol precipitation; and suspending the DNA pellet in TE buffer instead of water.

This protocol yielded much improved but still highly variable DNA concentrations (mean 28.8 ng/μL, SD 15.2) and protein purity ratios (mean 1.59, SD 0.21), but polysaccharide purity ratios were largely still below the acceptable limit (mean 0.80, SD 0.34). For *Bistorta vivipara*, DNA yield decreased (concentration 15.2 ng/μL, n = 1) although purity ratios were improved (A260/A280 1.97; A260/A230 2.79).

Protocol D: Phenol-chloroform-free CTAB-SDS protocol with Wang et al. (2013) modifications & sorbitol wash (Inglis et al., 2018)

To improve low polysaccharide purity ratios in protocol C, a sorbitol wash adapted from Souza et al. (2012) and Inglis et al. (2018), but without toxic β-mercaptoethanol, was added to the protocol. Nucleic acids are kept out of solution in a sorbitol buffer while prewashes reduce or remove polyphenols before they can covalently bind to the DNA and remove polysaccharides before they can be co-precipitated with DNA (Inglis et al., 2018). A sorbitol buffer was added to the ground tissue, centrifuged, and the resulting mucilaginous liquid pipetted off. However, polysaccharide purity ratios did not improve (mean 1.21, SD 0.61).

Protocol E: Phenol-chloroform-free CTAB-SDS protocol with: Wang et al. (2013) modifications, sorbitol wash (Inglis et al., 2018) and commercial spin columns

Finally, silica membrane spin columns for DNA (Qiagen DNeasy Plant Mini Kit) were added to protocol D in place of a second alcohol precipitation step in order to remove all secondary compound contamination from the DNA extracts. The spin columns in protocol E improved protein and polysaccharide purity ratios to within acceptable limits (A260/280 mean 1.84, SD 0.07; A260/230 mean 2.17, SD 0.67). For *Bistorta vivipara*, DNA concentration was higher but also variable (mean 54.08 ng/μL, SD 34.7), and purity ratios were within acceptable limits (A260/A280 mean 1.8, SD 0.046; A260/A230 mean 2.21, SD 0.324).

A.2.2 Sequencing

Protocol E was chosen to extract DNA from dwarf birch samples for sequencing based on superior DNA quality and quantity. Sample quality was assessed using 1% gel electrophoresis, and DNA purity and concentration were assessed using a Qubit with dsDNA BR assay kits Fluorometer (Life Technologies Corporation, Carisbad, CA). Approximately 26% of samples were rejected due to degraded DNA which mostly came from populations with senesced or limited starting material. In all, 244 samples from 48 populations passed quality control and DNA concentrations were normalised to 20 ng/μL. A subset of samples with sufficient DNA were duplicated (between 1-3 duplicates per sample) to increase sequencing coverage, resulting in 376 DNA extracts in total.

DNA extracts were submitted to FLORAGENEX (Beaverton, Oregon) for RAD library preparation and sequencing. Previous RAD sequencing (RADseq) of *Betula nana* used the cleavage enzyme *PstI* which has approximately 70,954 cut sites in the draft genome (Borrell et al., 2018; Wang et al., 2013). For this analysis the cleavage enzyme *SfbI* was used which produces a subset of the same cut sites, as it has a 2 bp longer recognition sequence. One library was prepared per sample, with unique 10-base barcodes ligated via adaptors to *SfbI* digested genomic DNA. To ensure consistency in the loci sequenced across samples and to reduce the number of missing genotypes downstream, fragments between 300 and 500 bp were selected, amplified with PCR. After library QA/QC, libraries were pooled and fragments were sequenced across four lanes of an Illumina NovaSeq 6000 platform with single-end 1 x 100 bp chemistry. Each plate also contained one blank control in differing locations in case of problems with plate identification, and one internal control.

A.2.3 Bioinformatics

Raw libraries were checked for errors using fastqc (Andrews, 2010). Libraries were demultiplexed and barcode sequences checked for errors using the process_radtags module of Stacks v 2.60 (Catchen et al., 2011, 2013; Rochette et al., 2019). A quality threshold phred score of 10 was used in sliding windows of 15% of the length of the read (19.8 bp in a 131 bp alignment) (Rochette et al., 2019). Reads from duplicated samples from the same original individual were combined. Four individuals with coverage below 300,000 reads and two individuals with coverage over 4,000,000 reads were excluded. The sequencing depth coverage for each individual and population was assessed. Reads were aligned to a reference

Betula nana genome (Wang et al., 2013, ENA accession number GCA_000327005) using Bowtie2 v2.5 with sensitive and end-to-end parameters (Langmead & Salzberg, 2012). Reference-based SNP calling was performed using the gstacks module of Stacks v 2.60, which uses a sliding window algorithm to detect RAD loci across all populations, detect SNPs, and then genotype each individual. The Populations module of Stacks v 2.60 was used to filter loci.

A.3 Results and discussion

A.3.1 DNA extraction

From the new protocol E which I developed and optimised, DNA concentrations of up to 134 ng/μL and corresponding yield of 670 μg per gram of leaf material were obtained. Mean yield was 169 μg/g for 10mg starting leaf tissue, 262 μg/g for 20 mg leaf tissue, and 279 μg/g for 30 mg leaf tissue¹.

The spin columns in protocol E dramatically improved protein and polysaccharide purity ratios to within widely considered acceptable limits (A260/280 mean 1.84, SD 0.07; A260/230 mean 2.17, SD 0.67), indicating high purity (**Figures A1; A2**). This suggests the extracts were sufficiently free of proteins and polyphenolics/polysaccharides, respectively. Protocol E was the only protocol tested with acceptable polysaccharide purity ratios and had comparable protein purity ratios to the commercial kit (**Figures A1; A2**).

Many sequencing companies require normalised DNA concentrations of 20 ng/μl for NGS, which requires at least 20 ng/μL to be produced during extractions. Mean DNA concentration was sufficient (25.3 ng/μL) although variable (SD 16.1) (**Figure A3**). Samples which did not meet the DNA quality and quantity requirements were rejected (26% of extracts), which mostly came from populations with poor quality (e.g. senesced) starting material. In all, 244 samples passed quality control from 48 populations. DNA concentration was similar to other CTAB-based protocols that were tested, and both were consistently higher than results obtained from the commercial kit (**Figure A3**).

Low-level DNA degradation of dwarf birch samples was detected by agarose gel electrophoresis (indicated by smearing below the DNA band). As level of degradation was sample-dependent yet was consistently present in all protocols tested, I think it reflects the compromised quality of some of the starting material, rather than damage occurring during the protocols. For example, some material was dried at high temperatures (60-70°C) which results in double stranded DNA breaks and other structural modifications, fragmenting the DNA (Inglis et al., 2018). Many steps were taken in the protocol to minimise degradation during extraction, such as cooling with liquid nitrogen and ice, and minimising mechanical shearing.

¹ Yield was estimated from the Qubit ssDNA BR Assay Kit (Thermo Scientific) readings considering the DNA resuspension volume for each single preparation starting from 20-25 mg of tissue.

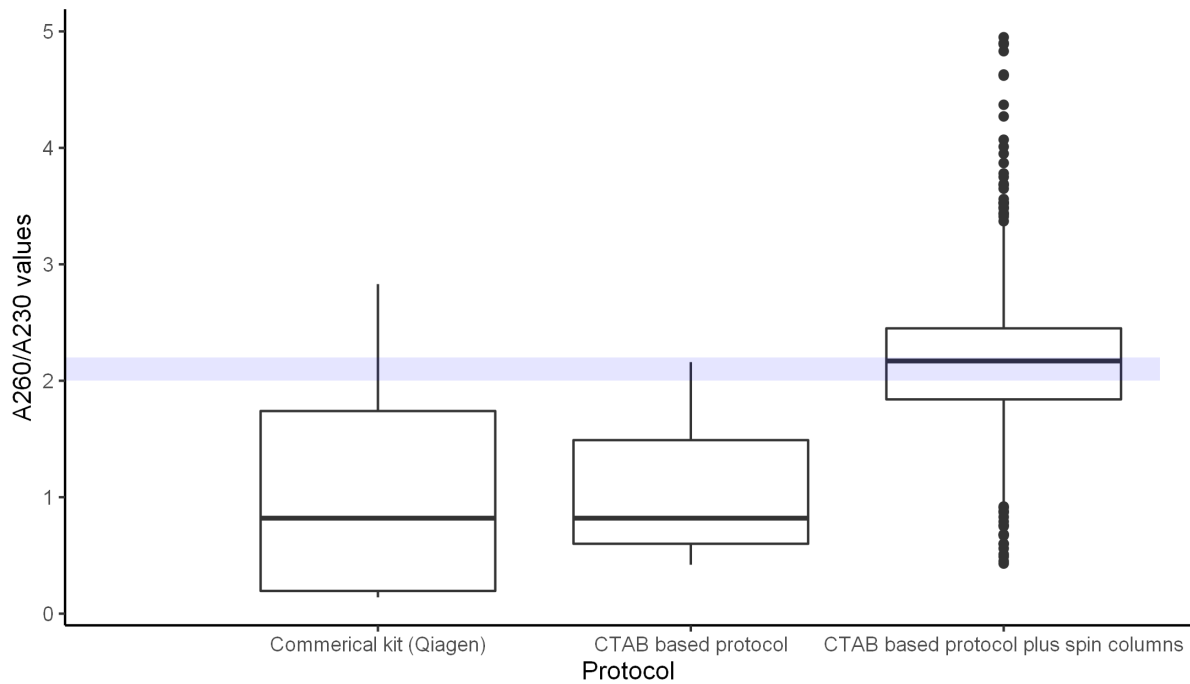


Figure A1. Polysaccharide contamination in DNA extracts measured across DNA extraction protocols. Ratio of absorbance at A260 and A230 nm indicates degree of polysaccharide contamination. Blue line indicates a broadly accepted minimum threshold and range required for downstream use of DNA. Results are presented for protocol A (“Commercial kit”) and protocol E (“CTAB based protocol plus spin columns”). Results were combined for protocols B-D (“CTAB based protocol”) for ease of comparison with protocol E.

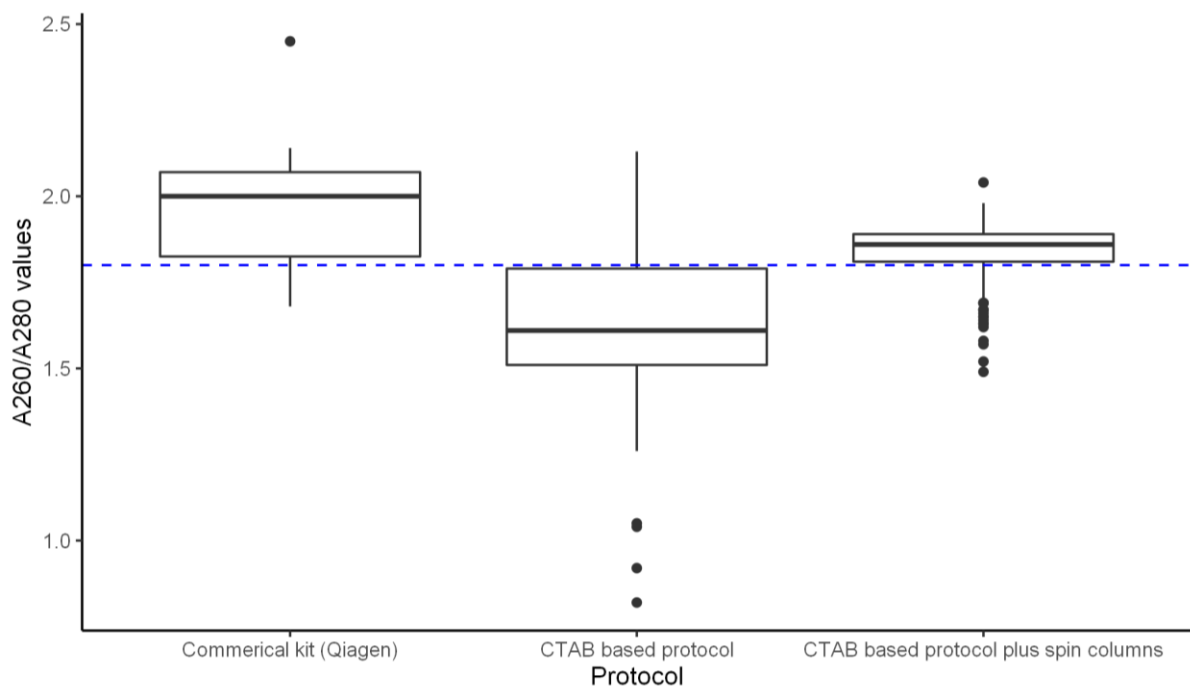


Figure A2. Protein contamination in DNA extracts measured across DNA extraction protocols. Ratio of absorbance at A260 and A280 nm indicates degree of protein contamination. Dashed line indicates a ratio of 1.8, a broadly accepted minimum threshold required for downstream use of DNA.

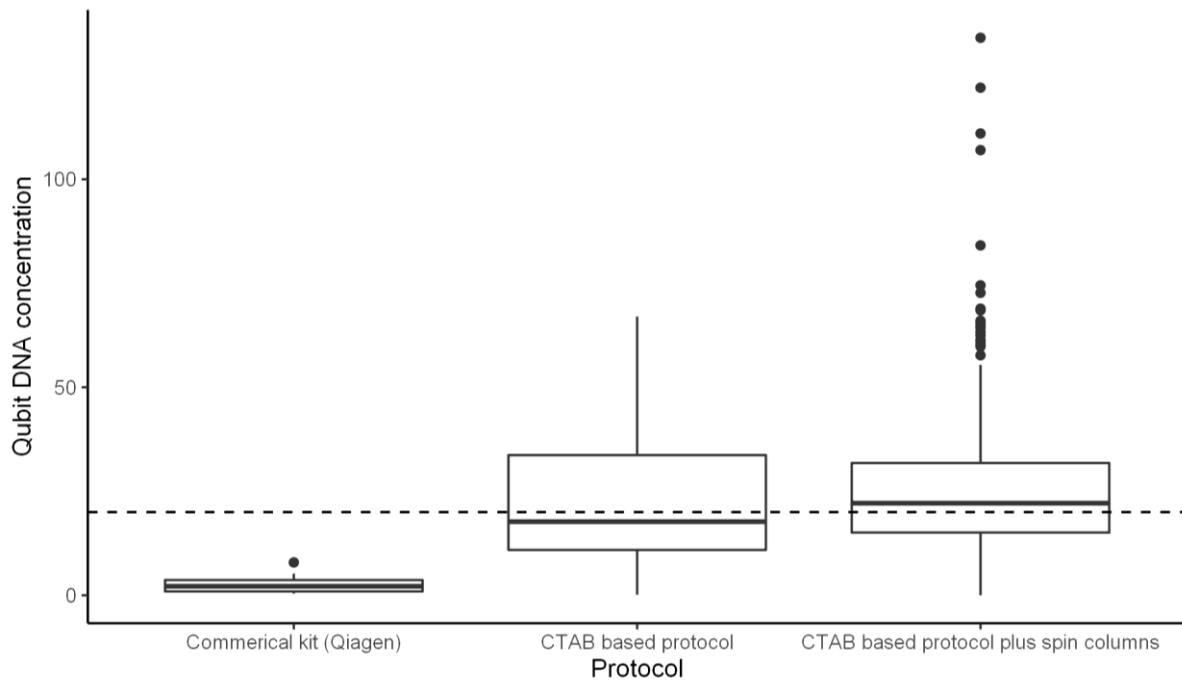


Figure A3. DNA concentration measured across DNA extraction protocols. Dashed line indicates 20 ng/μL: minimum threshold requirement for RAD-seq library preparation input.

A.3.2 Sequencing

A total of 419,484,325 reads were generated from one single-end Illumina HiSeq lane, of which 91.33% passed quality controls. The number of reads per individual ranged from 351,332 to 3,596,943, with a mean of 1,126,061. 87.7% of reads successfully mapped to the *B. nana* reference genome (Wang et al., 2013), with 71.7% retained with a mapping quality > 10. In **Chapter 4**, mean effective per-sample coverage after gstacks was 346 x (min 99.7, max 1031). For the final dataset used in **Chapter 4**, a threshold of 70% presence and a MAF of 0.01 resulted in 2,180 loci. 74.5% of loci were phased into haplotypes and contained 7528 variant sites (SNPs). For the final dataset used in **Chapter 5** filtering resulted in 1,930 loci containing 7,998 SNPs. These constituted ample loci to conduct population genetics and phylogeographic analyses of the dwarf birches to address the aims of this thesis.

A.4 Conclusions

Protocol E produced large quantities of high-quality genomic DNA, free of contaminant secondary compounds. It consistently outperformed other tested protocols when all three quality and quantity metrics (DNA concentration, polysaccharide purity ratios, and protein purity ratios) were considered. The extraction protocol produced high-quality sequencing data suitable for population genomics analysis, phylogeographic analyses, and other NGS applications. Protocol E is a CTAB-based protocol with reduced toxicity compared to other published protocols for woody species.

The addition of spin columns in the protocol was conceived independently from Mavrodiev et al. (2021), a CTAB protocol with chloroform and spin columns that yields 5-75 μg of DNA per gram of plant material for various plant species, in comparison with our mean yields of

169-279 µg DNA per gram of dried leaf material. Our protocol could be useful in other studies of *Betula* species and in other woody plant species with high levels of secondary compounds: particularly in instances when fresh material is not available, and material is older and dried (i.e. herbarium specimens).

A.5 Protocol: CTAB and SDS protocol, modified from Barbier et al. (2019), with additions from Wang et. al. (2013) and Qiagen DNeasy Plant Mini Kit.

Summary: We created an efficient and cheap protocol that can produce large quantities of high-quality genomic DNA from dried dwarf birch samples, and so is suitable for samples collected in remote field campaigns. The DNA produced is of sufficient quality and quantity for next generation sequencing such as restriction site-associated sequencing (RADSeq). The protocol also avoids use of toxic and carcinogenic chemicals (Phenol-chloroform and 2-mercaptoethanol) commonly used in extraction protocols.

Duration: The full protocol takes approximately 9 hours for 24 samples (plus additional optional overnight incubation), with 2 consecutive hours unsupervised time. Although approximately double the time required for a commercial kit extraction, the protocol is relatively fast for a CTAB-based method, where one extraction can otherwise take 2-4 days. The protocol could in theory be used for high-throughput processing of 96 well cluster tube arrays if appropriate centrifuge and rotor are available, but it has not been tested. Care would be needed to ensure DNA pellets are not accidentally discarded.

Reagents

- 1 M Tris hydrochloride (Tris-HCl) buffer, pH 8.0 (1 M Tris-HCl pH3.0-5.0, adjust to pH 8.0 using 10N NaOH, fill to final volume with deionised H₂O)
- 0.5 M Ethylenediaminetetraacetic acid (EDTA) buffer, pH 8.0 (0.5 M EDTA, adjust to pH 8 using 10N NaOH, fill to final volume with deionised H₂O)
- Sorbitol buffer (Inglis et al. 2018) (0.35 M sorbitol, 100 mM of 1M TRIS-HCl buffer pH8, 5 mM EDTA buffer, Polyvinylpyrrolidone (PVP40) 1% w/v (weight by volume, i.e. the mass per 100 ml solution), fill to final volume with deionised H₂O)
- Cetrimonium bromide (CTAB) buffer (Barbier et al. 2019) (CTAB 2% w/v, 1.4 M NaCl, 0.5 M EDTA buffer pH 8, 1 M TRIS-HCl buffer pH 8, PVP40 2% w/v, fill to final volume with deionised H₂O)
- TE buffer (10 mM of 1 M TRIS-HCl buffer pH 8.0, 1 mM of 0.5 M EDTA buffer)
- NaCl solution (5 M NaCl, fill to final volume with deionised H₂O)
- Isopropanol (100%)
- Ethanol (70%, fill to final volume with deionised H₂O)
- AW1, AW2, and AE buffers from DNeasy Plant Mini Kit (catalogue no. 69104; QIAGEN, Hilden, Germany). See protocol for generic alternatives.
- Proteinase K (any brand)
- RNase A (any brand)
- SDS (sodium dodecyl sulfate, 10% w/v)

Equipment and consumables

- 2ml tubes for freezing and grinding stages (Safe-Lock Tubes 2.0mL, catalogue no. 0030120230; Eppendorf, Hamburg, Germany). Alternatives include cryotubes to withstand low temperatures.
- 3mm Tungsten beads
- Liquid nitrogen
 - N.B Use of liquid N is optional if plants are dried. We retained the liquid N step to minimise further DNA degradation as it was suspected that samples could have been subject to degradation resulting from collection or storage conditions. A less costly alternative to liquid N would be to carefully freeze and store tissue at -80°C, when possible, then disrupt with a) a bead mill, or b) grind with a prechilled mortar and pestle (Sahu et al., 2012). As sample heating occurs during disruption with a bead mill, refreezing the samples for 30 minutes between cycles may reduce DNA degradation.
- Bead mill (TissueLyser II and adaptor set 2 x 24; catalogue no.s 85300, 69982; QIAGEN, Hilden, Germany)
- Vortex mixer
- Heating block (water bath can also be used)
- Microcentrifuge (5425 R, catalogue no.5406000569; Eppendorf, Hamburg, Germany)
- White spin columns from DNeasy Plant Mini Kit (catalogue no. 69104; QIAGEN, Hilden, Germany). Less costly alternatives include EconoSpin All-In-One Silica Membrane Mini Spin Column (catalogue no. 1920-050/250; Epoch Life Sciences, Missouri City, Texas, USA), as used by Mavrodiev et al. (2021).
- Open bore pipettes for later stages in the extraction protocol, to prevent damage and shearing of DNA during pipetting.

Equipment used for DNA quantification and quality assessment:

- Spectrophotometer (Nanodrop One, catalogue no. ND-ONE-W; Thermo Scientific, Waltham, Massachusetts, United States)
- Fluorometer (Qubit 4 Fluorometer, dsDNA Broad Range Assay kit, and assay tubes; Catalogue no.s Q33226, Q32850, and Q32856; Invitrogen, Waltham, Massachusetts, USA)
- Gel electrophoresis apparatus with 1% TAE agarose gel, ethidium bromide, and UV light box
- DNA ladders: FastRuler High Range DNA Ladder (catalogue no. SM1123; Thermo Scientific Waltham, Massachusetts, United States), GeneRuler 1 kb DNA Ladder (catalogue no. SM0311; Thermo Scientific Waltham, Massachusetts, United States)

Protocol

Part I: Tissue disruption and sorbitol wash

1. Place 20 mg of dried leaf tissue in a 2ml tube or cryotube with a 3mm tungsten bead. 100-150 mg may be required for fresh tissue. Flash-freeze with liquid nitrogen for 2 minutes and transfer to -80°C freezer for storage.
2. Use TissueLyser adaptors that have been stored at -80°C. Disrupt tissues in TissueLyser at 28 hertz for 1 minute. Rotate alignment of plates 180° and disrupt for a further 1 minute.

- a. N.B keeping the sample and equipment as cold as possible reduces nuclease activity and chance of DNA degradation. Browning of tissue during extraction indicates DNA degradation (Sahu et al., 2012)
 - b. N.B if tubes crack during disruption, use stronger cryotubes or lower frequency (e.g. 23 hertz). We found that if tubes were not stored at -80°C overnight, but used immediately after liquid nitrogen step, 2ml SafeLock Eppendorf tubes cracked.
3. To remove polysaccharides, add 1 ml Sorbitol buffer. Briefly vortex samples and inspect to confirm suspension of powdered material.
 - a. N.B Ensure all tissue powder is in contact with liquid using pipette tips.
 - b. N.B Store samples on ice until CTAB and proteinase K are added.
4. Centrifuge tubes at 5,000 x g (relative centrifugal force) for 5 minutes at room temperature (RT).
5. Carefully uptake supernatant with pipette
 - c. N.B repeat sorbitol addition and centrifuge steps if the supernatant from the first wash is viscous, turbid, or dark in colour (Inglis et al., 2018).
6. Turn on heat block to 65°C.

Part II: Cell lysis and phase separation

7. Add 800 µL CTAB buffer and 20µL proteinase K and mix by inversion.
 - a. N.B minimise mechanical damage of DNA by inverting rather than vortexing the DNA from this stage.
8. Incubate at 65°C for 1 hr. Mix by inversion every 15 mins.
 - a. N.B An incubation temperature of 65°C irreversibly denatures nucleases.
 - b. N.B the beads in the tubes help with the macerating process, ensuring the plant material is in contact with the buffer.
9. Add 50 µL of SDS 10% and mix by inversion.
 - a. N.B SDS precipitates with CTAB-polysaccharide complexes, making the sample cloudy.
10. Centrifuge at 20,000 x g for 15 minutes at RT. Turn on heating block to 37°C and cool plates in running water if necessary.
 - a. N.B Centrifugation and pelleting of un-lysed leaf material and tissue debris reduces the continued leeching of leaf phenolics into solution.
11. Remove carefully from the centrifuge, uptake, and transfer 600 µL of the liquid phase into a new 2 ml tube.
 - a. CTAB/SDS complexes will form a semi-solid film at the surface, so push the pipette tip past this to uptake the liquid below (but also avoid uptake of the cell debris pellet at the bottom of the tube).
12. Add 4µL RNase A and incubate at 37°C for 30 minutes.
13. Centrifuge at 20,000 x g for 15 minutes at RT.
14. Uptake and transfer 600 µL of supernatant from each sample into new 2ml tube. Avoid uptake of any remaining pelleted material at the bottom.

Part III: Nucleic acid precipitation and elution

15. Add 420 µL (0.7 x volume) of pre-cooled (-20°C) isopropanol and 300µL (half volume) pre-cooled 5M NaCl solution and mix by inversion.

- a. N.B NaCl promotes precipitation by neutralising the charge on the nucleic acid backbone, while polysaccharides stay in solution.
- b. N.B lower temperatures promotes better pellet formation of nucleic acids.
- 16. Leave tubes at -20°C for 1 hour.
 - a. N.B the 1 hour incubation time should not be exceeded as NaCl will eventually precipitate, preventing the DNA pellet from forming during centrifugation (Healey et al., 2014).
- 17. Centrifuge at 20,000 x g for 1 hour at 4°C.
- 18. Remove isopropanol carefully with pipette, avoiding the pellet which will be glassy and difficult to see at this point.
- 19. Add 700 µL pre-cooled (-20°C) 70% ethanol and mix by inversion.
 - a. N.B Ethanol removes excess salt from previous step, while polysaccharides, phenols, and proteins remain soluble.
- 20. Centrifuge at 20,000 x g for 15 mins at 4°C.
- 21. Remove ethanol carefully with pipette, centrifuge briefly (1 minute), and remove remaining ethanol.
 - a. N.B. Additional ethanol wash, centrifuge, and removal step with 100% ethanol can be added here if not using spin columns. Ensure that all the ethanol is removed before proceeding to the next step, e.g. by air-drying the samples for some minutes.
- 22. Add 200 µL pre-warmed TE buffer. Gently pipette the solution up and down to resuspend the pellet but avoid uptake of pellet.
- 23. Incubate samples at 65°C for 20 minutes.
 - a. N.B. This speeds up the resuspension and redissolving of the pellet. Leaving samples overnight at 4°C or RT will ensure the pellet has completely redissolved before further stages.

Part IV: Further DNA separation and purification using spin columns.

If purity ratios of the DNA extracts determined using a spectrophotometer are unacceptable ($A_{260}/A_{280} < 1.8$, $A_{260}/A_{230} < 2$), an additional stage using silica membrane spin columns to purify the DNA and remove polysaccharide contamination can be carried out. An indication whether this is necessary is the colour of the DNA pellet after step (17). If the DNA pellet is not pure white but discoloured yellow or green then the spin column step is necessary. Polysaccharide contamination in the extracted DNA solution after step (18) will be indicated by a viscous, glue-like solution (Porebski et al., 1997; Souza et al., 2012) that is difficult to pipette. Note that spin columns may reduce the yield of DNA (Healey et al 2014). The spin columns may be sufficient so that alcohol precipitation is not necessary, as in Mavrodiev et al (2021), but this was not tested.

- 24. Add 250µl (1.5 x volume) of buffer AW1 (or an alternative high-salt TNE buffer; TRIS-HCL, NaCl, and EDTA). Mix by pipetting.
 - a. N.B The buffer promotes DNA binding to the spin column by maintaining pH at an optimal level.
 - b. N.B. Using wide bore tips may reduce DNA shearing.
- 25. Pipette all liquid into spin columns placed in collection tubes.
- 26. Centrifuge at 6000 x g for 1 minute at RT. Discard flow through and collection tube, keeping spin column.

27. Place spin column in new collection tube. Add 500 μ L AW2 (or similar ethanol-containing wash solution).
28. Centrifuge at 6000 x g for 1 minute at RT. Discard flow through.
 - a. N.B DNA remains bound to the membrane while contaminants are washed away.
29. Add another 500 μ L AW2 and centrifuge at 20,000 x g for 2 minutes. Discard flowthrough.
30. Remove spin column carefully, ensuring flowthrough does not touch spin column. Transfer to new 2ml tube.
31. Add 50 μ L AE¹ (or TE buffer; 10 mM Tris-HCl pH 9 and 0.5 mM EDTA pH 9). Incubate for 5 minutes at RT.
32. Centrifuge at 6,000 x g for 1 minute at RT.
33. Repeat steps (27) and (28) and then remove spin column and store DNA samples at 4°C, or at -20°C for longer storage periods.

Notes on reagents and extraction conditions

- CTAB is a cationic detergent that captures lipids of cell membranes, frees contents of inner cell, and promotes separation of proteins and polysaccharides from nucleic acids. At high ionic strength (i.e. when the buffer contains higher concentrations of CTAB and NaCl), CTAB bind to polysaccharides and forms complexes which are removed. CTAB also denatures proteins and enzymes including deoxyribonuclease DNase which degrades DNA (Heikrujam et al., 2020).
- NaCl in the CTAB buffer prevents formation of CTAB-nucleic acid complexes. Note that lower salt concentrations (<0.5 M) DNA is insoluble, while at higher salt concentrations polysaccharides are insoluble (Sahu et al., 2012).
- EDTA chelates divalent cations which are used as cofactors for nucleases, thus reducing the activity of nucleases which could degrade the DNA (Heikrujam et al., 2020).
- Using a TRIS-HCl buffer at pH 8.0 helps maintains extraction pH at a level which promotes DNA stability and reduces DNA degradation (Heikrujam et al., 2020).
- PVP 40 prevent polyphenols present in plant tissue from oxidising and binding to DNA (indicated by a browning of the extracts), reducing the likelihood of polyphenols co-precipitating with DNA and making downstream processing difficult and reducing DNA stability (Heikrujam et al., 2020; Sahu et al., 2012).
- SDS is a detergent which helps digest the cell membrane and the release of more nucleic acids, while separating proteins from nucleic acids (Barbier et al., 2019).

A6. References

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