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Glacial Survival of Boreal Trees in Northern Scandinavia

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It is commonly believed that trees were absent in Scandinavia during the last glaciation and first recolonized the Scandinavian Peninsula with the retreat of its ice sheet some 9000 years ago. Here, we show the presence of a rare mitochondrial DNA haplotype of spruce that appears unique to Scandinavia and with its highest frequency to the west—an area believed to sustain ice-free refugia during most of the last ice age. We further show the survival of DNA from this haplotype in lake sediments and pollen of Trøndelag in central Norway dating back ~10,300 years and chloroplast DNA of pine and spruce in lake sediments adjacent to the ice-free Andøya refugium in northwestern Norway as early as ~22,000 and 17,700 years ago, respectively. Our findings imply that conifer trees survived in ice-free refugia of Scandinavia during the last glaciation, challenging current views on survival and spread of trees as a response to climate changes.

Understanding rates of tree migration and resilience to climate change is important for explaining both the distribution of single species and anticipating how ecosystems may respond to ongoing climate changes. Although trees are among the plants best able to disperse widely, and thus able to track their niches as climate changes (1), their rate of spread is debated (2–4). Strong paleoecological and genetic evidence supports the observation that most temperate and boreal plant species survived the glacial periods in south and east European ice-free macrorefugia and recolonized northern areas when

the ice retreated at the end of the Late Weichselian (Wisconsinian) and the beginning of the Holocene (5).

Several recent studies using fossil and genetic data indicate the presence of populations of boreal trees in the tundra of recent cold stages in Alaska (6), Yukon (7), Siberia (8), and Estonia (9). However, it remains controversial whether finds of spruce (*Picea*) and pine (*Pinus*) megafossils in the mountains of central Scandinavia dated to ~13,500 calibrated years before the present (cal. yr B.P.) (11,700 ¹⁴C yr B.P.) (10) indicate the presence of these tree taxa within the limits of the Scandinavian Ice Sheet (SIS) (Fig. 1A). If they did survive here, glacial tree locations were much farther north than generally accepted (11, 12). Previous estimates of potential Last Glacial Maximum (LGM) tree distributions using species distribution modeling have shown that boreal trees were much more widespread on the exposed North Sea continental shelf than thought (13). However, analyses of sedimentary pollen from central Scandinavia yield limited evidence to support the refugia hypothesis in this region (14), but near the tree limit there may be little or no pollen production (15).

Here, we extend traditional paleoecological methods with analyses of modern and ancient DNA (aDNA) to examine whether trees existed in Scandinavia at the LGM. We used mitochondrial DNA (mtDNA) analyses (16) to investigate whether modern Scandinavian Norway spruce (*Picea abies*) might be descended from ancient populations deriving from putative northern glacial locations. We sampled more than 100 forest stands across the contemporary European range of the species (the majority coming from the northern range) (Fig. 1B and table S1) and tested 11 variable noncoding regions. In spruce, mtDNA is maternally inherited (17) and shows a slow mutation rate in plants compared to the nuclear

and chloroplast genomes (18). This may result in strong genetic differentiation among modern populations underlined by the genetic signature of the glacial locations.

Sequencing analysis showed a deletion of 21 base pairs (bp) in the 141 bp constitutive of the mh05 fragment, yielding two haplotypes (Fig. 1B and table S4). Haplotype A was found only in populations within Scandinavia, with the highest frequency in the western regions and a decreasing frequency toward the east. A second haplotype B was also observed in Scandinavia. Haplotype B can be considered ancestral to A because of its complete sequence similarity with the two sister species, Siberian spruce (*Picea obovata*) and white spruce (*Picea glauca*), and with the outgroup species Scots pine (*Pinus sylvestris*) (16). Haplotype B is fixed in all populations outside Scandinavia—including trees sampled from the southern European range of spruce in Germany, Switzerland, Serbia, Italy, and Austria (table S1).

The distinct geographic distribution of haplotypes A and B is in agreement with classical patterns of population expansion out of at least two different locations after the LGM. As haplotype B is fixed outside Scandinavia, it appears to have dispersed after deglaciation from areas east or south of the Late Weichselian ice sheet, most likely from the Russian refugial areas, as indicated by earlier fossil (19) and molecular data (20). In contrast, haplotype A appears to have dispersed from western Scandinavia, as it is absent from the rest of the European range. Reconstructions of the distribution and flow patterns of the SIS suggest the presence of ice-free corridors along the Atlantic coastal areas of north Scandinavia and the Kola Peninsula during most of the Middle and Late Weichselian, except for relatively short intervals during the LGM between 22,000 and 20,000 cal. yr B.P. and 18,000 and 16,000 cal. yr B.P. (Fig. 1A). The origin of haplotype A must, however, predate the LGM, as simple models with constant population size and exponential growth show that the fixation of a mitochondrial mutation requires a minimum number of 200,000 years in spruce populations [~5000 generations; (16)], excluding, therefore, a Holocene founder event from the east followed by subsequent expansion across northern Scandinavia. Alleles can also surf to high frequency at the edge of a colonization process, although in such circumstances we would expect to see a decreasing level of nuclear genetic diversity with increasing genetic distance from the Russian glacial origin. Instead, nuclear genetic diversity in Norway spruce is largely maintained from the Russian refugial areas to Scandinavia (21). A western origin of haplotype A is supported also by modern molecular analysis based on nuclear microsatellites that identified in the northern European range of Norway spruce a cluster of populations from central Scandinavia (21). Such differentiation had not previously been found in the *nad1* region of the slower-evolving mtDNA genome,

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but all populations from the northern European range share a similar old and ancestral *nad1* mtDNA variant (20).

A likely explanation for the distribution patterns of haplotypes A and B is that scattered populations carrying A survived the LGM in microenvironmentally favorable pockets in western Norway, where proximity to the relatively temperate conditions of the Atlantic Ocean may have favored survival during glacial times. After climate warming, colonization of Scandinavia started first from local western stands that initially expanded slowly and eventually mixed with populations arriving from the east. Rapidly rising sea levels and complex glaciated terrain probably contributed to the scattered populations on the Atlantic coast remaining isolated and becoming fixed for haplotype A. As spruce can persist for hundreds of years by vegetative propagation under unfavorable conditions (22), it is possible that these trees produced no pollen, leaving no trace in the palynological record.

To test whether spruce trees carrying haplotype A are indeed early Scandinavian survivors, we used aDNA extracted from lake sediments (23, 24) from the Trøndelag region (63°N; central Norway) and on the island of Andøya (69°N; northern Norway). Such environmental aDNA (25) is shown to be local in origin and provides a proxy for plant paleo-community reconstruction that exhibits more similarity to macrofossils than to pollen records (26, 27). We also extracted and

analyzed aDNA from the oldest spruce pollen found in the Trøndelag core [6300 cal. yr B.P.; (16)]. We could not recover mtDNA from the deepest Andøya samples, likely due to the relatively low-copy number of mtDNA compared to chloroplast DNA (cpDNA) in plant tissues (see below). In contrast, we detected the spruce mtDNA haplotype A from the deepest samples at Trøndelag dating to 10,300 and 6500 cal. yr B.P. and from spruce pollen 6300 years old (Fig. 2 and table S5A).

These early occurrences of haplotype A in Trøndelag indicate that spruce was already present in the region during the early Holocene, much earlier than the first wave of colonization inferred from pollen analyses (~3000 cal. yr B.P.) (19). Our data are reinforced by a recent report of late-glacial and early-Holocene pollen and stomata of *Pinus* and *Picea* in the Dovre mountains in central Norway, which also indicate local presence of the two taxa (28).

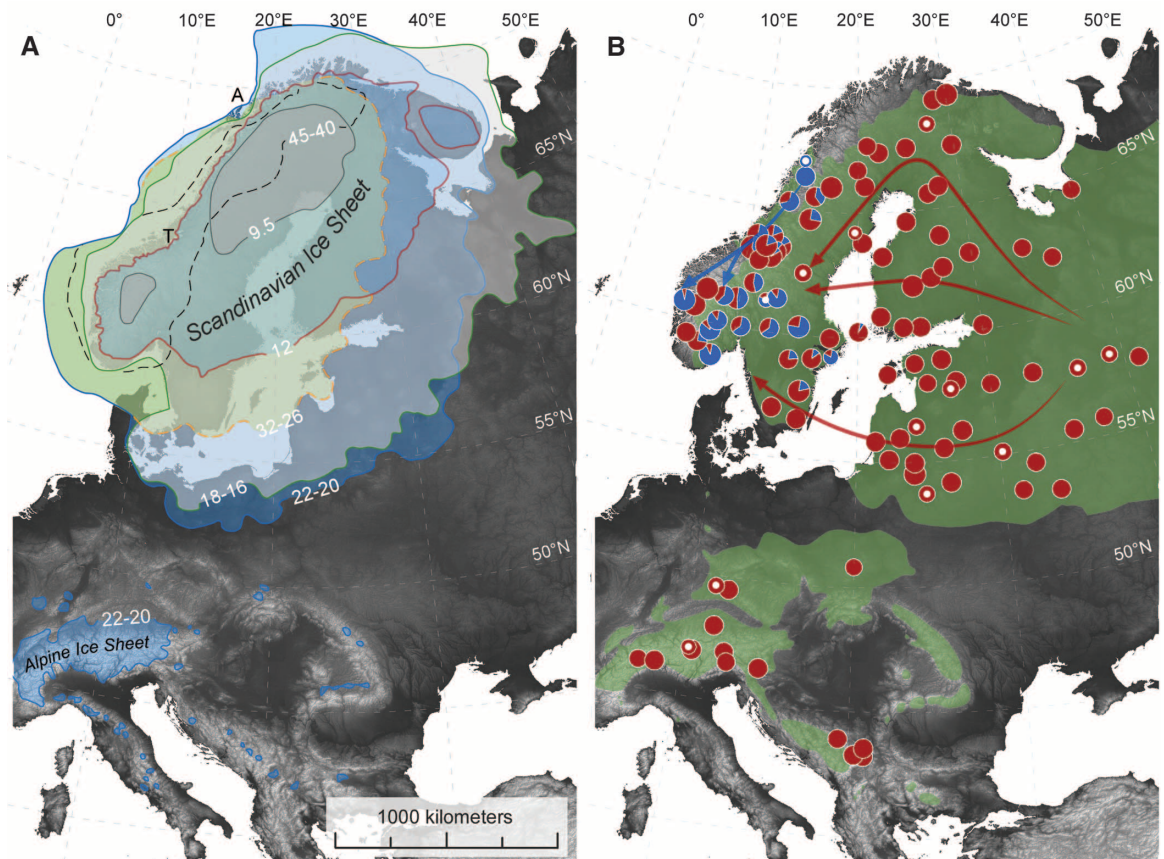
To further test where, and for how long, spruce trees might have survived in Scandinavia, we focused our studies at Andøya (Fig. 1A). This island is particular with regards to Late Weichselian and Holocene paleoenvironments, due to its long, continuous lacustrine sedimentary records, its early deglaciation at ~26,000 cal. yr B.P. (29), and its location only a few hundred kilometers north of the modern northern limit of spruce haplotype A. Thus, at a time when almost the whole of Scandinavia was covered by ice, Andøya's

northern tip harbored a nunatak ecosystem [see (29–31)]. Previous work on the early vegetation history of Andøya is based on pollen records, and to a lesser extent on macrofossils (32). Here, we combined macrofossil and aDNA analyses of lake sediments to assess past local vegetation (16, 33) to amplify short fragments of cpDNA [generally <100 bp; thus, shorter than the mtDNA mh05 fragment (16)]. Chloroplast DNA is also more common than mtDNA in many plant tissues (34, 35), increasing the chances of DNA survival and detection in older sediments.

Results from both macrofossil and cpDNA analyses indicate the presence of a polar desert or open pioneer vegetation community from ~22,000 cal. yr B.P. (fig. S3). Tundra herb diversity increased with a climatic warming around 15,000 cal. yr B.P., and there were further increases and changes in diversity in the Holocene, including the establishment of boreal species such as rowan (*Sorbus aucuparia*), generally reflecting previous vegetation reconstructions [see (29–31)]. The most notable result was the finding of DNA of pine (*Pinus* sp.) in sediments dating to ~22,000 and ~19,200 cal. yr B.P., and spruce (*Picea* sp.) in sediments dating to ~17,700 cal. yr B.P. (Fig. 2 and fig. S3).

There is little knowledge about aDNA taphonomy and the processes that may deliver plant DNA to lake sediments. However, it is likely that tree aDNA at Andøya and Trøndelag reflects contemporaneous plant biomass derived

Fig. 1. (A) Reconstructions of stages in the development of the Scandinavian Ice Sheet 45,000 to 9500 cal. yr B.P. compiled from a range of sources (16) A, Andøya; T, Trøndelag. (B) Geographical distribution of mitochondrial mh05 haplotypes A (dark blue circles) and B (red circles) in Norway spruce populations. Size of the circles is proportional to population size (centered white dots indicate populations with $N < 10$; table S1). Arrows suggest postglacial movements of the two haplotypes after the LGM. The olive shading shows the natural range of Norway spruce.



from the lake catchment. Seeds, needles, and bud scales can indeed be blown or washed over substantial distances, especially in open ice-covered landscapes, but the long-distance proportion deposited into an Arctic lake appears very small compared to that of any local component. Additionally, during the early Holocene, the shortest distance to any known pine or spruce locality from Andøya makes any long-distance transportation of macrofossils highly unlikely. The degree of vertical migration or leaching of DNA through the sediments is also of concern, as periodic downward percolation of water can move DNA in porous, granular sediments of cave profiles (36). Lake sediments, however, are permanently saturated, and vertical percolation of liquids does not occur while organic compounds are immobilized in the sediment matrix (23). Other processes must be also considered, such as DNA derived from nonlocal pollen (i.e., from long-distance transport) and reworking of older organic material. However, no pollen grains of spruce or pine were found in the Andøya samples in question [investigated explicitly microscopically (16)]. Additionally, the possibility of a pollen source for our amplifications is unlikely as pollen grains contain small amounts of DNA, which are difficult

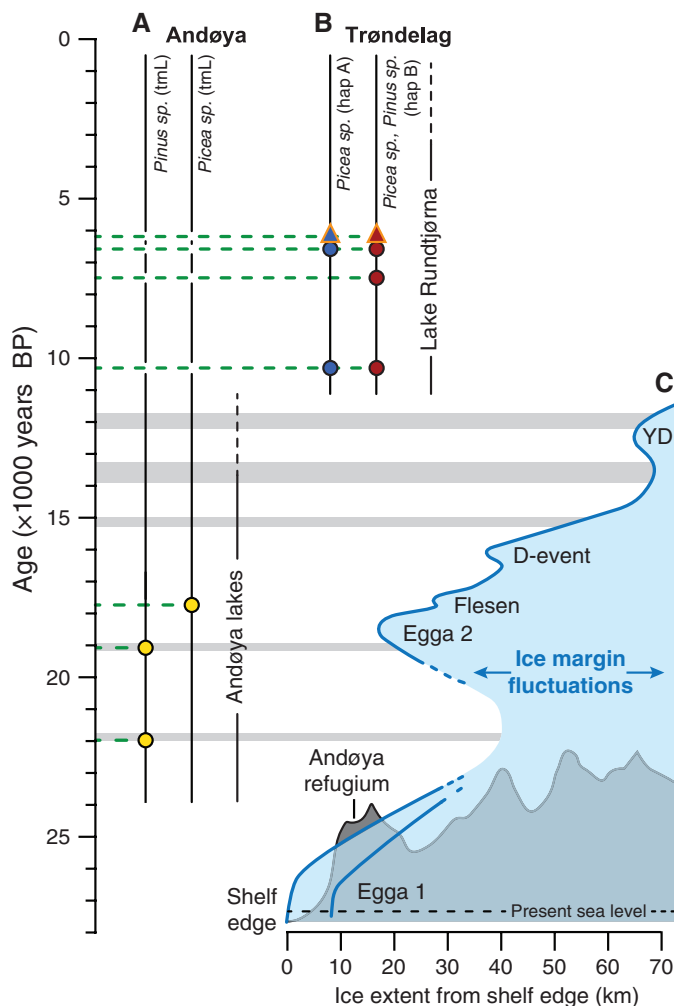
to amplify (37). Also, at Trøndelag in an attempt to use the generic *trnL* primers, we failed to recover pine and spruce DNA from horizons where such pollen was present (16). For Andøya, reworking (e.g., of interglacial or interstadial material) is also unlikely even though ice-free conditions prevailed before LGM. Although Quaternary terrestrial deposits containing Eemian material have been reported 120 km farther north (16), none are known from Andøya itself, and pollen stratigraphies do not indicate that reworking is prevalent (29–31).

Coupling our findings with the results of previous megafossil-based analyses (10), the overall evidence for presence of conifer trees in Scandinavia during the last glaciation seems the only explanation for our observations. Although we cannot yet resolve whether this evidence reflects local survival of trees from previous warm periods, or an early spread of trees as land became ice-free, these findings have considerable conservation implications, particularly in relation with the ability of spruce to survive under changing climates. Although long-term survival does not exclude long-distance dispersal, such northerly spruce distributions provide a case study of a species capacity to persist locally in a marginal

environment during the LGM and expand rapidly under more favorable conditions to develop dispersed populations over a broad area, and expand yet again under even more favorable conditions to form dense and widespread populations. The identification of these genetic resources is also of great importance to breeding programs interested in identifying spruce provenances with traits related to flexibility to survive under changing climatic conditions.

Northern glacial distributions of trees also indicate that tree populations can be undetected in pollen assemblages for millennia, which has cascading implications for pollen-based inference of species invasion and migration patterns and rates. The latter may well have been lower for conifer trees than estimated from classical palynological studies. This should be taken into account when modeling future vegetational changes due to global warming. Finally, if tree populations survived one of the most severe glacial periods (LGM), and by inference even previous ones, this extends the history of trees in these locations back to before the last glacial–interglacial period. Such persistence highlights the importance of extending ecological and genetic studies in forest trees to longer time scales, in order to properly explain the evolutionary processes that shaped the modern distribution and genetic patterns of tree taxa.

Fig. 2. Temporal occurrence of boreal trees at Andøya (A) and Trøndelag (B) based on fossils, aDNA from sediments (circles), and aDNA from pollen (triangles) data. (C) Ice sheet fluctuations across northwestern Norway 27,000 to 10,000 years ago. LGM (Egga 1) glacier extent went beyond the examined Andøya lakes, reaching the west coast of the island (38) or alternatively 10 km farther west at the shelf edge (39). Re-advances (Egga 2, Flesen D-event, Younger Dryas) left lakes unglaciated. Possible location for the Andøya refugium is indicated. Horizontal gray scaled lines indicate +10°C, as reconstructed by Alm (29).



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(UAA) intron for plant identification using degraded template DNA. These patents only restrict commercial applications and have no impact on the use of this locus by academic researchers. The *trnL* DNA sequences can be found at the European Nucleotide Archive with the study accession no. ERP001153. The mtDNA sequences can be found at the European Molecular Biology Laboratory database with the accession no. HE652882-HE653002.

Supporting Online Material

www.sciencemag.org/cgi/content/full/335/6072/1083/DC1
Materials and Methods

SOM Text

Figs. S1 to S5

Tables S1 to S5

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Founder Effects Persist Despite Adaptive Differentiation: A Field Experiment with Lizards

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The extent to which random processes such as founder events contribute to evolutionary divergence is a long-standing controversy in evolutionary biology. To determine the respective contributions of founder effects and natural selection, we conducted an experiment in which brown anole (*Anolis sagrei*) lizard populations were established on seven small islands in the Bahamas, from male-female pairs randomly drawn from the same large-island source. These founding events generated significant among-island genetic and morphological differences that persisted throughout the course of the experiment despite all populations adapting in the predicted direction—shorter hindlimbs—in response to the narrower vegetation on the small islands. Thus, using a replicated experiment in nature, we showed that both founder effects and natural selection jointly determine trait values in these populations.

Island populations are renowned for their extent of divergence from each other and from mainland source populations (1, 2). Mayr (3, 4) argued that these differences are often triggered by random sampling when island populations are founded by a few colonizing individuals. The resultant founder effects—changes in the genetic and phenotypic composition of a population due to founding by a small number of individuals—have been proposed as an important cause of evolutionary divergence and even speciation for the past half-century (3–6). However, an alternative explanation is that island environments differ from each other and from the source locality, and these ecological differences result in divergent natural selection (7–9). The evolutionary significance of founder effects also has been

questioned because their imprint may be short-lived if populations perish because of a lack of genetic variation or because of demographic stochasticity, or if natural selection overwhelms their effects (10, 11). Data from nature are lacking because founder events are rarely observed [but see (12)], and thus their effects must be inferred post hoc; yet laboratory studies indicate that even in the presence of natural selection, genetic drift induced by founder effects or population bottlenecks can contribute to patterns of phenotypic divergence [e.g., (13, 14)]. We report an experimental study of founder effects in a natural system of a Caribbean lizard, demonstrating that morphological divergence caused by the founder effect persists even as populations adapt to their new environments.

Some have argued that marked phenotypic change from a single founder event is very unlikely (11) and that genetic drift in general plays little part in morphological evolution (15). Moreover, others note that evidence from recent introductions suggests that adaptation is a more common cause of trait evolution than drift (16–18). Yet most concede that documenting these random sampling events in nature is exceedingly difficult (11, 15, 19–21). Without knowledge of founder

attributes and repeated sampling of colonized islands, the relative contributions of founder effects, population bottlenecks, natural selection, and gene flow to evolutionary divergence are impossible to disentangle (19–21).

We capitalized on the extensive knowledge of how *Anolis* lizards adapt to their environment, combined with the opportunity to use small islands in the Bahamas, recently cleared of lizards by a hurricane, as experimental units in a natural setting. Our focus was on limb length and the extent to which lizard populations would adapt to the novel environments on these small and scrubby islands. Extensive comparative and experimental research supports an adaptive explanation for the positive relationship between hindlimb length and perch diameter (i.e., the width of the cross section of the substrate that a lizard perches on, such as a branch or trunk) that is found among populations of anoles. Functional studies show a clear biomechanical basis: Lizards with relatively longer hindlimbs run faster on broad substrates, whereas lizards with shorter limbs for a given body size move more adeptly on narrow surfaces. Such performance probably aids in capturing prey, defending territories, and escaping from predators. Indeed, field studies in this system show that hindlimb length is under selection, favoring longer hindlimbs to run faster when exposed to terrestrial predators and shorter hindlimbs after lizards become arboreal and shift to narrower perches [reviewed in (22)].

To assess the relative importance of founder effects versus natural selection, we introduced lizards to replicate islands to which we predicted they were not well adapted because of differences in structural habitat from their source, thereby simulating founding events and altering the selective regime for limb length. Specifically, founding propagules were established on small experimental islands, all of which are sparsely vegetated and covered primarily with short, narrow-diameter vegetation as compared to the more forested habitat of the lizards' source area on a nearby larger island (Fig. 1 and figs. S1 and S2). Our prediction is that if natural selection is the dominant force, then we would expect all populations to evolve shorter hindlimbs as they adapt to using narrower

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