DRAFT LETTER

Dear

Please find attached an article for submission to GEB. There has been much debate recently about the role played by northern "refugia" (particularly of boreal trees): their role in post-glacial recolonization, what this means for estimates of migration speed, and indeed whether they actually existed at all. It is sometimes assumed that the observation of an isolated geographic population in a past landscape with generally inhospitable environmental conditions signifies a refugium. This definition requires that population to expand subsequently, but many isolated populations may be relicts bound for extinction. This is particularly probable at the end of glacial cycle, when rapid environmental change and a preceding period of genetic stress combine to challenge such populations. Much of the contemporary debate in biogeography omits the recent thinking on the genetic constraints faced by small populations, both relictual and founder.

This article compares two northern regions that share a dominant boreal genus (*Picea*): northwest North America and Scandinavia. They are two of the most intensively studied northern regions palaeecologically and show similar histories of *Picea*. We create parallel data syntheses for the regions and then present a new conceptual model that includes genetic constraints and reconciles the various (and apparently conflicting) patterns in the fossil data.

The text is well under 5000 words. The reference list is slightly over the advised length. I have found it hard to reduce it further given our need to reference several disparate lines of study plus critical site records.

Yours sincerely

Did genetic constraints limit post-glacial boreal tree expansion out of northern "refugia"?

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ABSTRACT

Aim To compare spatio-temporal patterns of late-Quaternary pollen and macrofossils for spruce (*Picea*) in two sub-continental regions in order to evaluate i) the contested idea that small populations survived through the last glacial period *in situ*, despite largely inhospitable conditions, ii) the linked implication that pollen does not accurately reflect vegetation across large regions over millennia, and iii) whether it is possible that such populations, if present, gave rise to extensive northern forests, thus changing conventional notions of tree species' responses to climate change at a continental scale.

Location Alaska/north-west Canada (ANWC) and Scandinavia.

Methods Mapped comparison of pollen, macrofossil and other fossil occurrences for *Picea*.

Results Mapped pollen data show strikingly similar E-W expansion patterns. Both regions have spatially disparate fossil evidence of presence preceding the major increase in pollen values taken to indicate expansion to forest dominance. Both regions harbour unique regional haplotypes, but these are uncommon to rare. In Alaska, data suggest late-glacial and early-Holocene *Picea* presence then subsequent extinction on the Bering Land Bridge. There is little evidence for the proposition that small glacial or late-glacial populations expanded rapidly with the onset of warmer conditions to form forest cover over large areas, except possibly in far north-west Canada.

Main conclusions Much current speculation about northern glacial-age tree populations fails to take evolution into account. Genetic theory indicates the potential for fragmented populations to respond evolutionarily to large climate changes is probably far less than usually assumed. Combined palynological and genetic data indicate the origin of extensive Holocene *Picea* populations in ANWC and Scandinavia was probably by large-scale immigration. Relictual tree populations were likely present during the glacial period, but they were probably genetically impoverished and extinction-prone, having been under strong selection pressure and genetically isolated. This disadvantaged them in any response to the rapidly changing conditions of deglaciation. On balance, fossil data, contemporary ecology, and genetic theory all argue against a model of widespread, *in-situ* expansion of *Picea* from putative northern refugia.

KEY WORDS: Refugial population, relictual population, *Picea*, evolution, climate change, Scandinavia, ANWC, Late Quaternary

INTRODUCTION

The role of northern refugia (Stewart *et al.*., 2009) as sources of post-glacial recolonization is highly topical; it has triggered a potential shift of emphasis from long-distance migration to *in-situ* expansion in determining spatial responses of species to climate change. If northern species survived in and expanded from small northern refugia (until recently "cryptic" but now increasingly discovered) this may alter our views of how recolonization of space occurs and also the rates at which species have been estimated to disperse over landscapes; this in turn affects the operation of niche models and other predictions of response to future climate change (Birks & Willis, 2008). The late-Quaternary history of such refugial populations would undoubtedly have unfolded differently depending upon the organism (e.g., small mammals vs. trees). Here we focus on trees, specifically spruce (*Picea* spp.), as there is an abundant fossil record for many tree species and their history is often used as a model for biogeographic and ecological thinking (e.g. Mclachlan *et al.*, 2005; Magri, 2008)

Records of continental-scale, directional, time-transgressive increases of forest tree taxa to relatively high pollen values (typically 5-15% or more) are interpreted as the gradual expansion of a large population from a distant region (Davis, 1981; Ritchie & MacDonald, 1986; Giesecke & Bennett, 2004). This expansion is usually taken to signify the achievement of a dominant role in forest composition. For Norway spruce (*Picea abies* L) such large-scale, sustained records of increase (Giesecke & Bennett, 2004) are now seen to conflict with the observations in Scandinavia of isolated, early occurrences of spruce macrofossils, e.g., Kullman (2002, 2008 and references therein), Oberg & Kullman (2011), Paus *et al.*. (2011). Most recently, ancient environmental DNA evidence of spruce has been reported for the LGM (NW coastal Norway) and the early Holocene (southern Scandes; Parducci *et al.*. 2012a), but this has been contested (cf. Birks *et al.*. 2012, Parducci *et al.*. 2012b). In ANWC, the assumption that *Picea* was eliminated in the LGM (Hopkins *et al.*., 1981) has been replaced, as more data have been obtained, by a view that survival of Picea through the LGM was likely (Brubaker *et al.*, 2005).

These observations fuel the notion of refugial populations as sources of post-glacial expansion, but this in turn should lead to the question of whether it is biologically *likely* that such small populations gave rise to Holocene populations. Further, unless palynological theory is seriously wrong, we need to reconcile the pollen and plant macrofossil data.

The concept of a biological "refugium" implies the ability of refugial species to expand at a later time. Various properties of a population can compromise that ability to re-expand, such as its demography and evolutionary trajectory, as discussed, for example, by

Bennett & Provan (2008) and Hampe & Jump (2011). Furthermore Davis & Shaw (2001), Hampe & Petit (2005) and Davis *et al*. (2005) have pointed out the important role of evolution in the migration of large populations. In this study we explore the palaeoecological aspects of small refugial (or relictual) populations and large-scale migration using a comparative approach with the same genus, *Picea* (spruce), on two continents, and we discuss the likely evolutionary implications of observed patterns.

Picea is a widespread genus, being a dominant in the boreal forest of both northern Europe and northern North America. The patterns of post-glacial spruce colonization to its north-western limits in both regions (Scandinavia and ANWC, respectively), as shown by broad-scale pollen mapping (e.g., Ritchie, 1984; Giesecke & Bennett 2004), are superficially similar and occurred over many millennia, although the glacial histories of the two regions are strikingly different, Scandinavia having been widely glaciated while large portions of northern and central ANWC remained ice-free. From a comparison of the pollen, macrofossil and genetic patterns for both regions and a consideration of the evolutionary processes affecting both small, isolated populations in sub-optimal habitats and large-scale in-migration, we develop a hypothesis that largely reconciles available palaeoecological and genetic data.

METHODS

Fossil mapping

In order to compare the North American and Scandinavian records we synthesized spatio-temporal patterns for spruce in ANWC in ARC-GIS using a modification of the pollen threshold approach used by Giesecke & Bennett (2004) for Scandinavia (see below). We also mapped available macrofossil data for ANWC and Scandinavia. We used 70 dated pollen records from public databases and published data (SI). Most records have calibrated radiocarbon ages assigned by authors via age models. Radiocarbon date calibration approaches vary, but not to the extent that emergent patterns would be significantly affected, as we use 1000-yr time-slices, or greater, for this mapping. For older, single uncalibrated dates (e.g., those reported for some spruce macrofossils) we used CalPal-2007online (Danzeglocke *et al.,* 2013).

For mapping pollen thresholds we omitted sites with very few samples and sites with otherwise questionable data (e.g. inadequate or unclear dating), as inferred from the information provided in the relevant publication. Our previous experience of pollen mapping at this scale suggests that it makes little difference to broad-scale patterns whether the millennium mean or a single value within a time-slice is plotted. Here we map just a single value for each time slice, that nearest the time-slice date. Shapefiles for ANWC Alaska (coordinate system UTM Zone 6N) included site locations for *Picea* values from 15,000 yr BP-present. We mapped 5% pollen values, as 5% is great enough to avoid the randomness of occurrence inherent in a very low value such as 1% but less constrained than 10%, which is not always exceeded in forested landscapes in ANWC. This mapping value provided an appropriate comparison with the Scandinavian patterns shown by Gieseke & Bennett (2004). The Inverse Distance Weighting (IDW) tool in Arc-GIS was used to create a raster surface. A treeline shapefile was created by georeferencing an existing map representation of the treeline and digitising the outline.

Geographic regions and study species

Scandinavia (P. abies L.)

Today boreal forest covers much of the Scandinavian Peninsula except alpine areas (Moen 1998). A strong W-E gradient of increasing continentality influences vegetation composition. *Picea abies* prefers high-nutrient, moist soils and requires January mean temperatures of -1.0°C (Giesecke & Bennett 2004). Its range extends from NW Scandinavia to the mountains of central Europe and eastward to Russia.

Scandinavia was extensively glaciated in the LGM but a few areas remained intermittently ice-free (Wohlfarth *et al.*., 2008). Rapid deglaciation was complete by ~9 kyr BP. Pollen maps show northern regions of Europe were colonized from the south and east during the Holocene; the Scandinavian Peninsula was possibly colonized via east-west (trans-Baltic) and northern routes (Giesecke & Bennett, 2004); high values of *Picea* pollen are only achieved in the mid to late Holocene over much of the region (Fig. 1).

For several decades, Kullman and associates (see Kullman, 2008 and references therein and Oberg & Kullman, 2011) have reported finds of wood of *Picea* and other tree taxa across Scandinavia, which date variously from the LGM, Late Glacial or early Holocene. In southern Sweden, contemporary krummholz spruce clones are closely associated with woody remains, the oldest dating to ~12 ka; some of these appear to be extremely long-lived relictual individuals (Oberg & Kullman, 2011). The argument for *in-situ* survival and/or early colonization of Scandinavia is based largely on such finds. A *Picea* stoma dated indirectly to >11 ka from central Norway (Paus *et al.*., 2011), and finds of cpDNA attributed to *Picea* from lake sediments dated to ~17.7 ka in northwest Norway (Parducci *et al.*., 2012a) provide further evidence of spruce survival in the North (but see Birks *et al.*, [2012] cf. Parducci *et al.*, 2012b; see Fig.1)

Genetically, there is a deep split between northern (Russian-Scandinavian) and central European spruce populations (Tollesfrud, 2008). From a comparison of microsatellite and mtDNA data, Tollesfrud *et al.* (2009) conclude that individuals derived from the northern European population entered Scandinavia via both a southern (trans-Baltic) and a northern (north Finland) route, which is mirrored in the pollen-based Holocene migration patterns (Fig. 1; Giesecke & Bennett, 2004). A widespread northern haplotype occurs throughout the range and is present east and south of the Baltic, whereas a localized haplotype occurs only in NW Norway, indicating persistence of a separate population in the north, possibly over one or more glacial cycles (Parducci *et al.*, 2012a). Intriguingly, the "Norwegian" haplotype is present in pollen dated to ~10.3 ka from a lake in central Norway, near to one of the documented finds of ancient spruce wood (Parducci *et al.*, 2012a)

It is curious that of the two sub-continental regions, Scandinavia was far more heavily and extensively glaciated, and yet more finds of early spruce (and other tree) material are reported here. This is, perhaps, one reason for the more heated discussion surrounding spruce survival in Europe than in N America (Kullman, 2002; Birks *et al.*., 2005; Parducci *et al.*, 2012a; Birks *et al.*., 2012; Parducci *et al.*., 2012b).

ANWC (Picea glauca (Moench) Voss and P. mariana (Mill.) Britt., Sterns and Pogg.

ANWC is characterized by a cold continental climate; the western coastal zone is markedly less maritime than equivalent latitudes in Norway. Boreal forest in ANWC lies between the southern Cordillera and the northerly Brooks Range and its eastward extensions and is dominated by *Picea glauca* (white spruce) and *P. mariana* (black spruce). Both species have continuous ranges east to the Atlantic seaboard. *P. glauca* tends to occupy warmer, better-drained parts of the landscape (Viereck *et al.*, 1992). Its growth within its current range is limited by low summer moisture levels (Barber *et al.*, 2000). Most records indicate that *P. glauca* was the first species to expand in the region, and we focus on the ecology and palaeoecology of this species.

Large parts of the region were unglaciated in the last glacial cycle, particularly during Marine Isotope Stage (MIS) 2 (the last glacial maximum, LGM); conditions were dry, the vegetation largely treeless (Hopkins 1982). Lower sea levels in glacial periods exposed the continental shelves of the Bering and Chukchi Seas and linked Alaska with eastern Siberia. Ice sheets isolated ANWC from the rest of unglaciated North America during the LGM, which is here defined as ~25-15 kyr BP, because 15 kyr BP marks the onset of deglacial change in nearly all terrestrial records in the region. The history of the “ice-free corridor” that must have opened as the Laurentide and Cordilleran ice sheets parted is still only partially known. The corridor probably opened between 13.5 and 12.5 kyr BP (Dyke, 2004). Major warming occurred in the Late Glacial and early Holocene (Elias, 2001; Kaufman *et al.,* 2004). Post-glacial sea-level rise subsequently severed the land connection and restored the Bering Strait. Spruce colonizing the east of the region in the early Holocene was *P. glauca*; *P. mariana* became widely established in the mid Holocene 6-8 kyr BP (Ritchie, 1984; Brubaker *et al.,* 2005).

The history of boreal forest taxa has been studied less intensively than in Scandinavia, partly due to the size and inaccessibility of the region. Macrofossil finds of boreal tree taxa are relatively rare (Hopkins *et al*., 1981). However, new records of *Picea* (spruce) in the Yukon dating to just prior to the LGM (Zazula 2006) and to the early Holocene in far western Alaska beyond current range limits (Wetterich *et al*., 2012), together with low but persistent levels of spruce pollen at many sites (Brubaker *et a*.., 2005), drive a growing conjecture that small populations of spruce existed during full-glacial and late-glacial time.

A survey of modern cpDNA variation in Alaskan *P. glauca* by Anderson *et al.* (2006) showed high variation, the authors arguing for the presence of refugial populations that may have been largely undetected palaeoecologically (i.e., cryptic refugia). Subsequently, using microsatellites to reassess the patterns, Anderson *et al.* (2011) found evidence of likely refugial populations, possibly focussed in north-central Alaska, and also evidence of considerable genetic mixing. Refugial population genetic structure appears characterized by drift, whereas in-migrating populations indicate gene flow, suggesting that early-established or survivor populations were unable to expand far beyond their areas of origin and/or incoming populations from outside Alaska supplanted them in subsequent millennia.

RESULTS

Picea history in ANWC: synthesis

>50-15 k yr BP

MIS 3 in ANWC (which began >50kyr BP and is thus out of range of radiocarbon dating, and ended ~25 k yr BP) was a long phase during which warmth and moisture levels were intermediate between LGM and interglacial conditions (Hopkins, 1982). This climate regime should have supported tree growth in lowland areas, and, while there are relatively few MIS-

3 localities, macrofossils and pollen records indicate that both species of spruce were present in the region; the youngest recorded pre-LGM macrofossils are dated to ~25 kyr BP (Figs. 2a and 2b).

In contrast LGM records show little evidence of high spruce pollen values, except for values of >5% recorded intermittently at three sites in the eastern part of the region, although low values are recorded at more sites (see Brubaker *et al.*, 2005). There are no reliably dated macrofossil records (Fig 2c).

15 kyr BP – present

As there are too few sites recording pollen to use the threshold mapping approach prior to 15 kyr BP, the mapping begins at this time slice. Threshold-based trends for 5% spruce pollen (Fig. 3) show a general E-W expansion. This smoothed pattern suggests an overall spread from Canada into Alaska during the Late Glacial and early Holocene and the slowing of westward spread in the mid-Holocene, as reported by earlier syntheses (e.g., Ritchie, 1984).

The earliest reliable post-LGM macrofossil records are from the far east of the region and date to ~13.3 and ~11 ka (Fig . 4); two older dates on spruce macrofossils from the same area are treated as probably redeposited by Hopkins *et al.* (1981). With the youngest pre-LGM macrofossil records also recorded in the east (Fig 2b), a geographic focus for possible spruce survival may have been northwest Canada and eastern interior Alaska. Phylogenetic data from the MacKenzie Delta region may prove informative in this regard. However, both the oldest macrofossils and broad-scale multi-millennial pollen patterns (Figs 3 and4) are also just as consistent with dispersal from the south east through the ice-free corridor, although extremely fast migration rates are implied.

In the far west of the region, pollen of *Picea* is recorded during late-glacial (~13-11 kyr BP) from St. Paul Island on the Bering Land Bridge (Colinvaux, 1981; not included in the GIS mapping but see Fig. 4). The radiocarbon dating is not definitive, but the better dated later part of this record (with high pollen influx values) strongly indicates the presence of spruce near the site ~13 cal yr BP. Also in western Alaska, a white spruce twig AMS-dated to ~9200 cal yr BP has been reported from thaw-lake deposits on northern Seward Peninsula by Wetterich *et al.* (2012). Thus spruce populations may have been present on the land bridge and in adjacent areas of western Alaska at the beginning of the Holocene, and therefore also during the LGM, as the area is distant from any putative source populations. Even today this region lies beyond the range of either Alaskan spruce species (Fig. 3), and the nearest population of the East Asian species, *Picea obovata*, lies far to the west.

DISCUSSION

A comparison of late-Quaternary spruce data from two continents shows strong similarities at a general level: establishment of dominant populations as represented by high pollen values following a roughly east-west trajectory over millennia, and scattered localities recording spruce presence in places and at times that contradict a simple model of time-transgressive in-migration. In both regions genetic studies indicate the likelihood of ancestral populations originating in the region, but strong Holocene gene flow has also occurred. Pollen production is unlikely to have been reduced (and thus pollen records confounded) by lower atmospheric CO_2, because the major post-glacial CO_2 rise preceded the major pollen increases (Rose *et al.*., 2010).

In ANWC both species of spruce were present until the LGM. Subsequently small populations of spruce may have persisted, but probably only in highly favourable azonal sites (for example, on or at the base of south-facing slopes that generated sufficient GDD but where soil conditions were relatively moist, such as in drainage gullies and on river floodplains), the region comprising a broad and exceedingly diffuse refugium (sensu Ashcroft 2010), Far to the west, it appears likely that spruce had been growing on the southern Bering land bridge (from fossil evidence dated to ~13-11 ka) and on the Seward Peninsula at ~9 ka—both localities being beyond modern range limits—but here spruce faded completely in the early Holocene and never recovered.

Populations of *Picea glauca* in the MacKenzie delta region evidenced by macrofossils as old as ~13.0 ka expanded earlier than any others in the region. They may have been derived from an early migration from the south, or they might have been *in-situ* survivors that subsequently mixed with in-migrating populations. It is also possible that *in situ* expansion of extant populations occurred in the Alaskan interior ~10, kyr BP, where Anderson *et al.* (2006) report rare haplotypes, but current genetic data provide no support that these populations were ultimately widely successful (Anderson *et al.*, 2011). Taken together, the data suggest that some spruce populations survived until the end of the glacial period but left little contribution to the distribution or genetic composition of current populations.

In Scandinavia, there is a significant temporal gap between the earliest dated macrofossils, which indicate that small populations of spruce were already present, and the later, time-transgressive pollen expansion. This disparity has led Kullman (2008) to suggest that pollen records need to be re-evaluated, particularly the implications of low counts conventionally referred to long-distance transport. While low (or no) pollen production is possible under sub-optimal growth conditions (Hicks, 2006), this is not likely to be the case when large, widespread populations are present as, by definition, these indicate suitable conditions for reproduction. Thus palynological theory suggests the most parsimonious explanation for the observations is that the Scandinavian early post-glacial period was characterized by small, scattered populations that persisted in sub-optimal conditions at the onset of the interglacial climatic regime. As suggested by Kullman (2008), some of these populations may have been LGM survivors while others may represent founder events preceding Holocene expansion.

The role of post-glacial environmental constraints

Previous explanations for apparently conflicting fossil data (which in Scandinavia also involves species other than spruce, e.g. Kullman, 1998) have focussed on Late-glacial and early-Holocene conditions that might have restricted the growth of tree species. This period (referred to here as deglaciation for brevity and representing ~15-8 kyr BP) saw dramatic climate change in both regions. While precipitation increased, summer temperatures increased rapidly by several degrees (Elias, 2001; Atkinson *et al.*, 1987), which likely maintained low potential evapotranspiration-precipitation ratios). Summer temperatures were evidently warm enough for spruce growth (Elias, 2001; Lemdahl, 1991), but enhanced seasonality (Miller *et al.*, 2010; Kaufman *et al.*, 2004) linked to cold springs, relatively high moisture deficits, and thin snow cover have all been suggested as constraints on spruce growth, based on contemporary observations (Huntley, 1988; Giesecke & Bennett, 2004; Hogg & Schwartz, 1997; Barber *et al.*, 2000). In ANWC, strong seasonality and low spring-summer moisture availability likely favoured deciduous over evergreen growth forms until ~10,000 yr BP when rising effective moisture levels coincided with the expansion of spruce in the interior (Abbott *et al.*, 2000). We can conclude, based on local and regional modern habitat preferences, that the onset of a warmer climate would not necessarily have improved the growth opportunities of surviving spruce populations.

Both regions share a geographic position at the western edge of a continental land mass and were affected by large-scale changes in coastline and ocean circulation that occurred with deglaciation. Currently submerged shelves and unglaciated areas that are now coastal but were once more continental were possible LGM locations for both Scandinavian and North American spruce populations (Kelly *et al.*, 2010; Parducci *et al.*, 2012a; Colinvaux, 1981; Wetterich *et al.*, 2011). In Norway, rising eustatic sea-level brought rapid submergence of land due to the slower pace of isostatic rebound. In western Alaska, the Bering Sea transgression covered shallow shelves far more slowly and afforded a possibility for fossil deposition in terrestrial locations. Eventually, though, coasts and islands in region increasingly dominated by the expanding cold ocean would have experienced summer cooling (Wetterich *et al.*, 2011). Thus Holocene sea-level rise likely contributed to the physical and/or climatological demise of any spruce populations in offshore locations and along the modern coasts of both regions.

The fate of populations surviving long periods in diffuse northern refugia – evolutionary and phenotypic constraints

Are the above explanations sufficient? There remains the fact that as Holocene climate became moister and less seasonal as the Holocene progressed (e.g. Bartlein *et al.*, 1992) the pollen data indicate a gradual E-W spread of spruce, not a pattern of spread from small foci across the modern range. If survivor populations consisted of more than a few trees at a very few sites, they should have expanded rapidly and contributed substantially to the eventual Holocene repopulation of spruce in the northern boreal forest in the study regions. However, the genetic evidence indicates they did not, at least if we infer that the local endemic haplotypes predominated in Alaska in the past, as appears to be the case in Scandinavia. A possible, overlooked factor in this dynamic is genetic constraint. Davis *et al.*, (2005) expressed surprise that so little attention is given to the potential (or lack thereof) for taxa to adapt to Quaternary climate change. As with founder populations, relict populations are liable to genetic and demographic constraints related to isolation and small population size (Lande 1988; Hampe & Jump 2011). In contrast, large migrating populations have a deep reservoir of genetic variation, and this can facilitate rapid evolutionary response to changing environments (Davis *et al.*, 2005). How would such constraints act on populations surviving a glacial-interglacial cycle?

Any small, pre-Holocene populations were probably derived from the previous period of widespread forest cover during the last interglaciation ~125 kyr BP. Subsequent environmental conditions fluctuated but generally worsened for spruce (reduced GDD, increased aridity, and, particularly in Scandinavia, displacement to periglacial locations by ice advance). Populations left behind on favourable sites as the forest fragmented would have initially maintained genetic interchange and replacement of individuals. The period represented by MIS4-2 was punctuated by warm intervals lasting from a few centuries to several thousand years, particularly during MIS 3 (Miller *et al.*, 2010), which would have allowed some population some population recovery/expansion.

Because the trend of climate conditions became more hostile for spruce as time went on most populations would have become smaller and some eventually extinct. In Beringia, the coldest and driest period (and the most inimical to spruce), and, in Scandinavia, the greatest expansion of the ice sheet, came at the end of the glacial period, ~25-15 kyr BP. Remaining small and isolated populations would have lost genetic variation through genetic drift (random loss of alleles through inter-generational sampling "error") and undergone stringent selection that would also have further reduced genetic variation, for example, in conditions far from the climate optimum for the species, traits such as a low photosynthetic temperature optimum would have been favoured. Narrow selective optima may also have led to lower phenotypic plasticity and loss of the genetic basis for future plasticity (Scheiner, 1993; Wagner *et al.,* 1997). This loss of plasticity would have reduced the opportunities for genetic assimilation in a strongly altered environment (the potential for genetic evolution to maintain a successful phenotype that arose from initial plasticity in face of new conditions; see Lande, 2009). In addition, recently developed genetic models have shown that fragmented populations occupying disparate environments have limited capacity to exchange beneficial genes successfully because of genetic correlation (linkage disequilibria) of those genes with genes that are beneficial in the "mother" environment but deleterious in the dispersal environment. Hence there is a much reduced potential for fragmented populations to respond evolutionarily to changing climatic conditions than is usually assumed. Furthermore, these models also show that, due to divergent local adaptation, small, fragmented sub-populations occupying disjunct, heterogeneous environments, but subject to gene flow, are at risk of demographic collapse with rapid climate change (Schiffers *et al.*, 2013). On the other hand, populations migrating into the study regions from eastern Europe/western Russia or western Canada would have contained far more genetic variation and phenotypic plasticity, allowing a more rapid and effective evolutionary response to selection, including through genetic assimilation (Lande, 2009). Gene exchange subsequently occurred enough that regional haplotypes are still observable in modern populations, albeit in low proportions, as recorded by contemporary genetic studies (see above). However, given the arguments above, it is unlikely the genetically constrained relictual populations would have led to early-Holocene forest expansions; this is consistent with the observed pollen patterns.

CONCLUSION

It seems likely that the difference in evolutionary response to major climate changes shown by small populations compared with large ones, particularly for organisms with long generation times such as trees, is currently greatly underestimated, and inferences about past processes based observed characteristics of modern populations may be misleading. New genomic approaches to analysing contemporary populations and the ability to extract mitochondrial DNA from fossil material such as pollen may help further distinguish among the roles of refugial, relictual and founder populations in the response of late-Quaternary trees to climate change.

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SUPPORTING INFORMATION

SI: Map of sites used in the ANWC pollen mapping

BIOSKETCHES

Mary Edwards is interested in, among other things, the biogeography, ecology and palaeoecology of northern regions and is currently fascinated by the heated debate surrounding the implications of northern refugia.

Scott Elias

Scott Armbruster

Figure captions

Fig. 1. *Picea* pollen and macrofossil data for Scandinavia. 1(a) a contour map of the first rise of *Picea* pollen to the 5% level (after Giesecke and Bennett 2004 and reproduced with permission of the publishers). 1(b), the locations of the earliest reported non-pollen evidence of *Picea* in Scandinavia: A - Kullman 2002 (wood or cone); B and C - Oberg and Kullman 2011 (wood or cone); D - Paus *et al.*. 2011 (stoma); E – Parducci *et al.* 2012 (sediment DNA).

Fig. 2. Dated *Picea* macrofossil records from Alaska Yukon, plus early pollen records. 2a, records for 50-35 ka; 2b, records for 35-24 ka; 2c, records for 24-15 ka; circles are pollen sites (see key for pollen values). Triangles are macrofossil sites from Hopkins *et al.,* (1981 and Zazula *et al.,* (2006).

Fig. 3. A contour map based on the first rise of *Picea* pollen to the 5% level for 15 ka BP to present for ANWC. Small black circles denote sites used in the mapping. Triangles indicate sites with *Picea* records but omitted from mapping (see methods).

Fig. 4. Late-glacial and early-Holocene Picea macrofossils from ANWC (triangles). A Sleet Lake (Spear, 1993); B Twin Lakes (Hopkins *et al*. 1981); C Whitefish Lake (Hopkins *et al.,* 1981); D Tangle Lakes (Hopkins *et al.,* 1981); E Canyon Creek (date on soil not macrofossil; Weber *et al*.,); F Kitluk Pingo (Wetterich *et al.,* 2012). The filled circle represents a local *Picea* pollen signal from Calaloq Lake (Colinvaux, 1981)

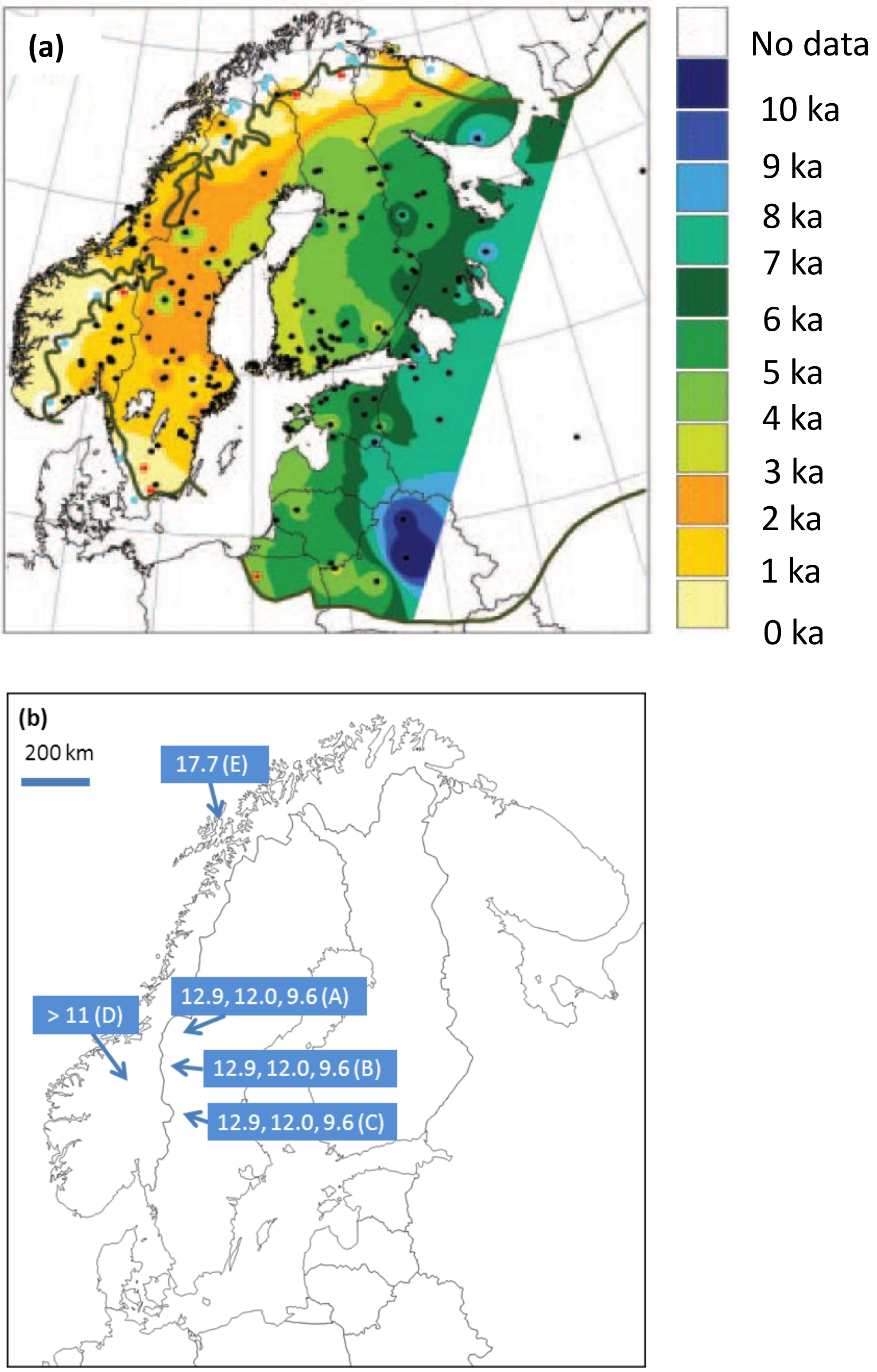

(a)
No data
10 ka
9 ka
8 ka
7 ka
6 ka
5 ka
4 ka
3 ka
2 ka
1 ka
0 ka
(b)
200 km
17.7 (E)
12.9, 12.0, 9.6 (A)
> 11 (D)
12.9, 12.0, 9.6 (B)
12.9, 12.0, 9.6 (C)

Fig. 1

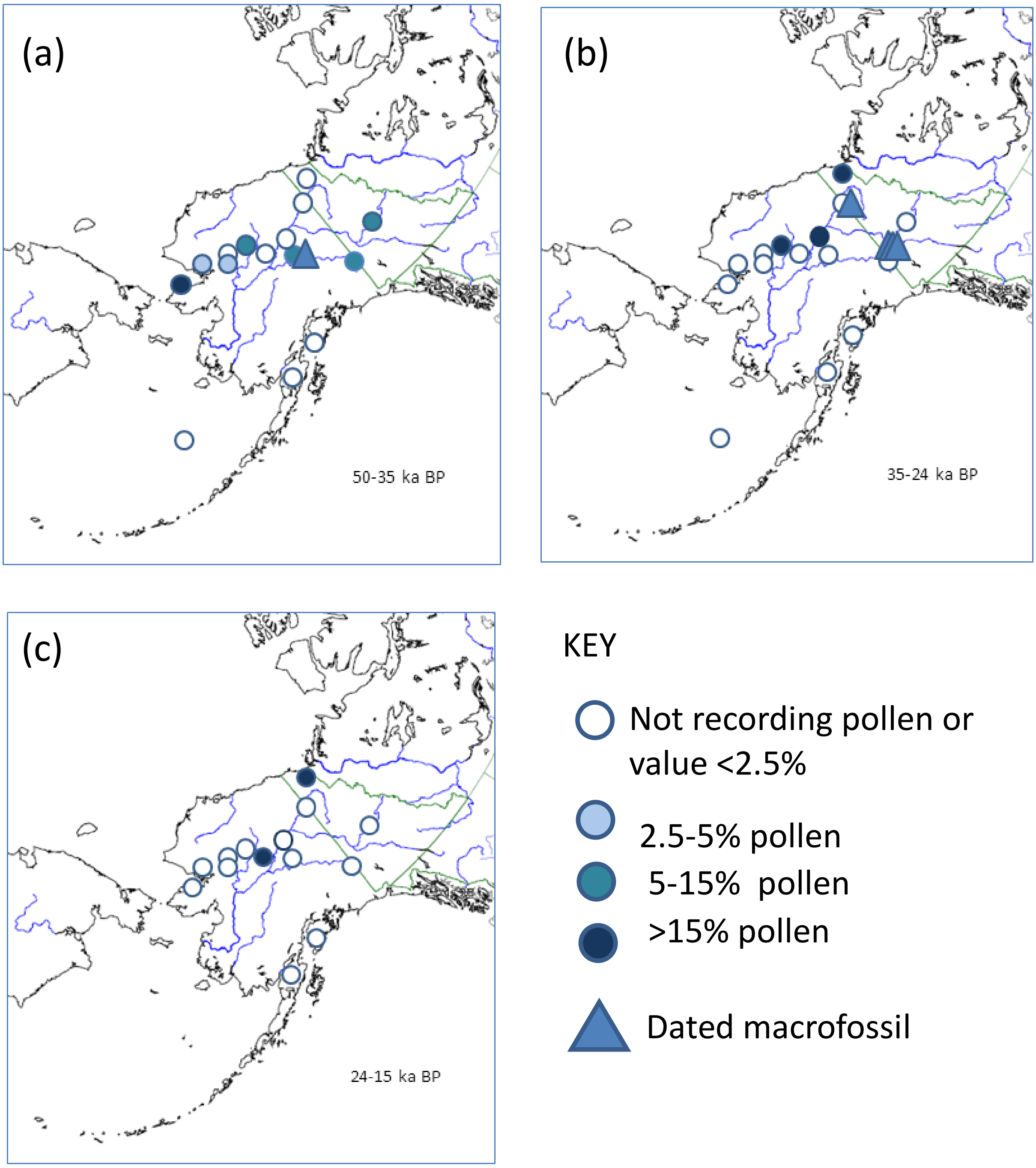
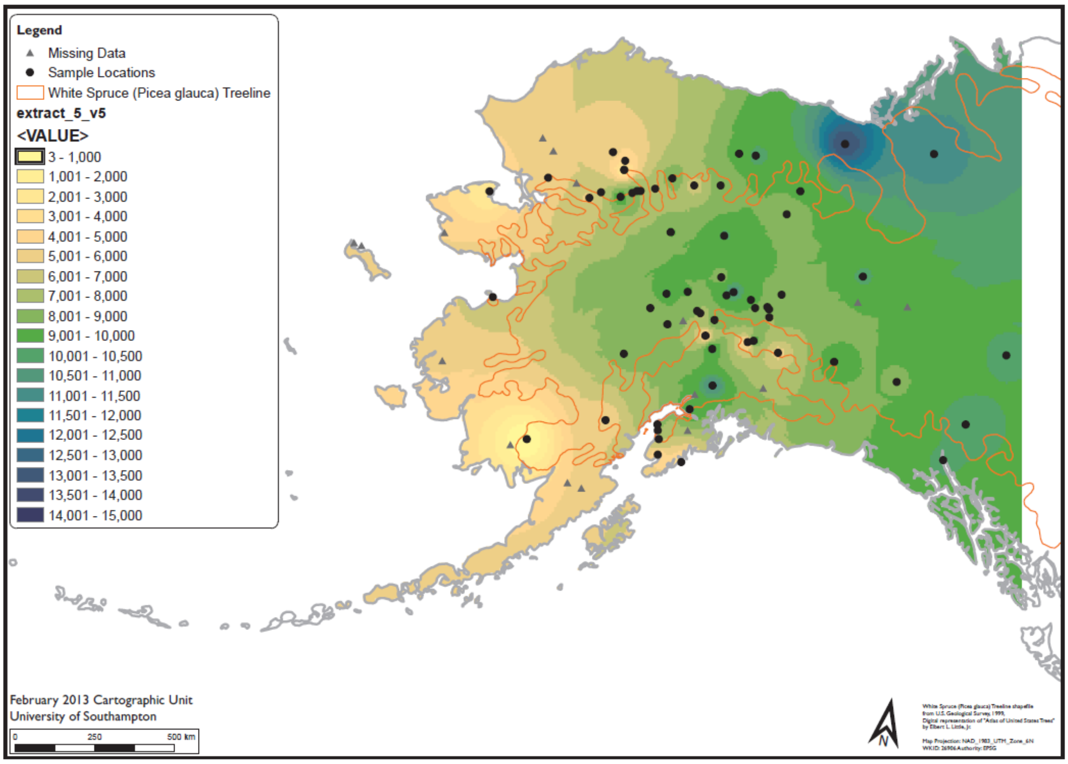

(a)
50-35 ka BP
(b)
35-24 ka BP
(c)
24-15 ka BP
KEY
Not recording pollen or value <2.5%
2.5-5% pollen
5-15% pollen
>15% pollen
Dated macrofossil

Fig. 2


Legend
Missing Data
Sample Locations
White Spruce (Picea glauca) Treeline
extract_5_v5
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1,001 - 2,000
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3,001 - 4,000
4,001 - 5,000
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7,001 - 8,000
8,001 - 9,000
9,001 - 10,000
10,001 - 10,500
10,501 - 11,000
11,001 - 11,500
11,501 - 12,000
12,001 - 12,500
12,501 - 13,000
13,001 - 13,500
13,501 - 14,000
14,001 - 15,000
February 2013 Cartographic Unit
University of Southampton
0
250
500 km
N

Fig. 3

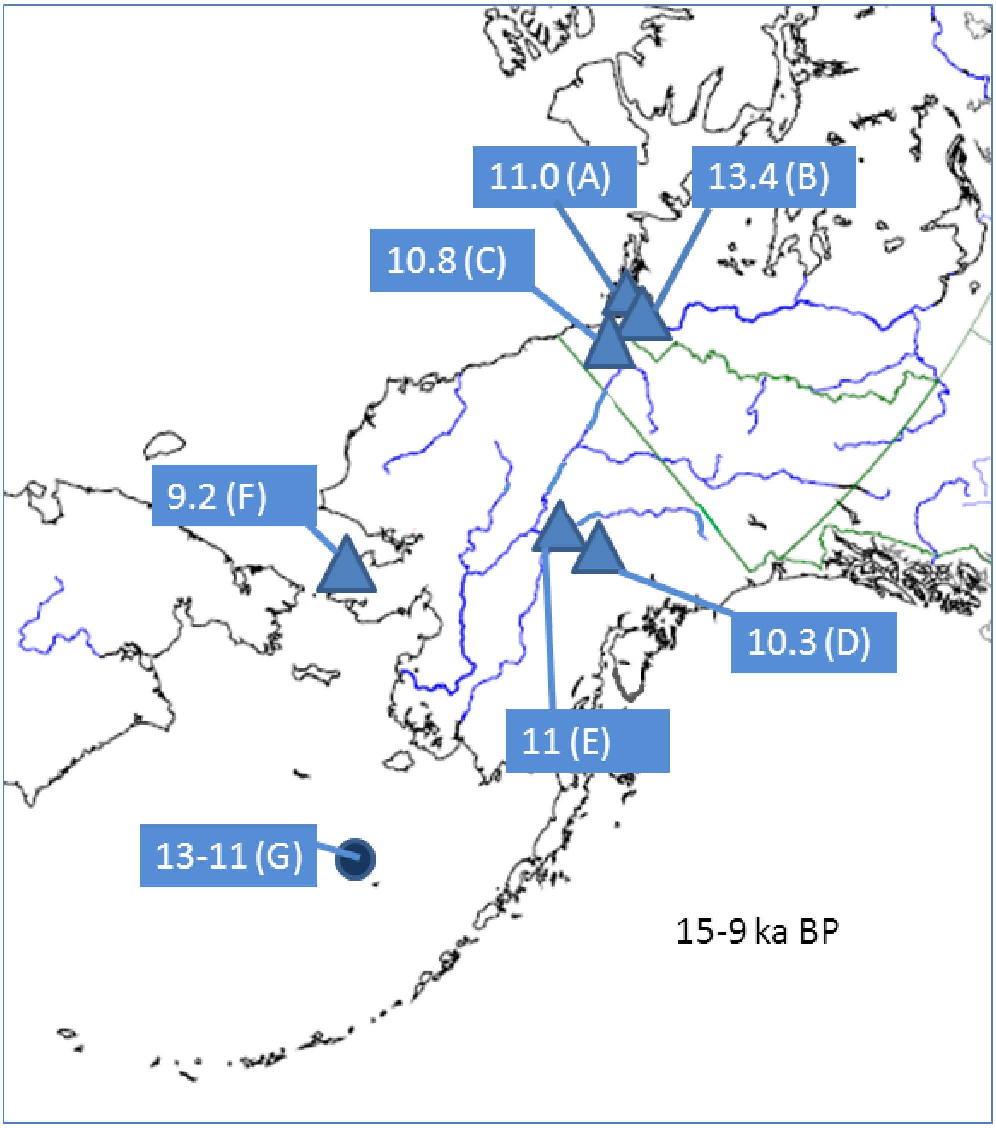
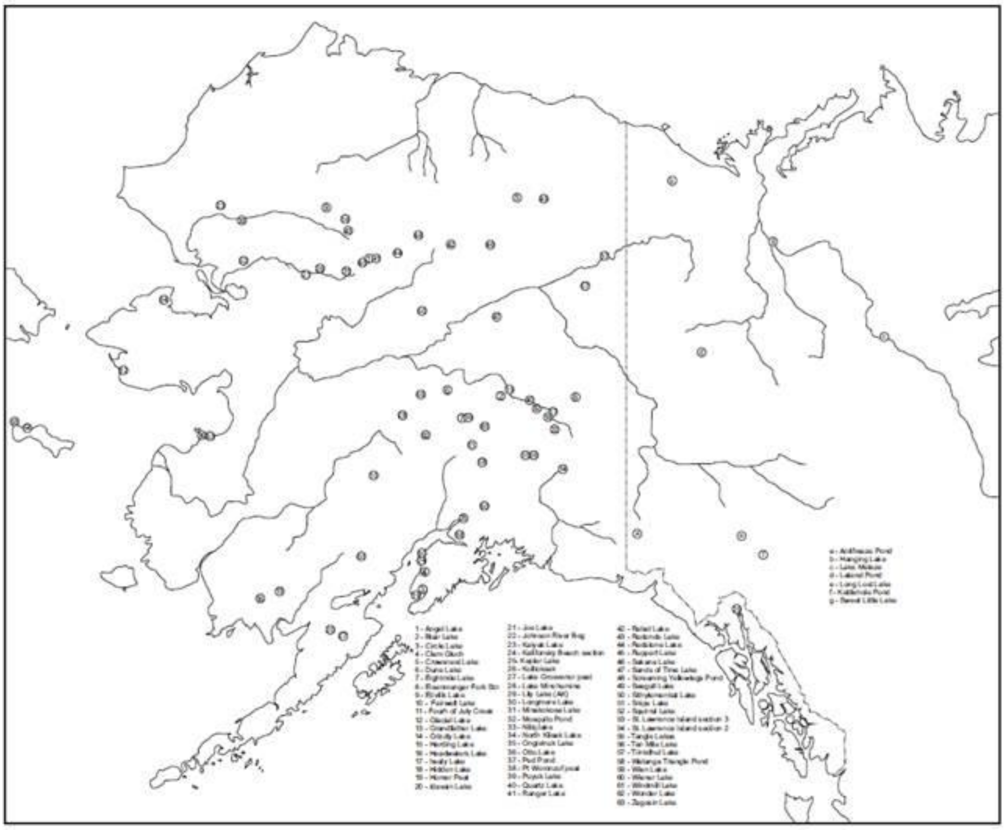


Fig. 4



Supporting Information: map