

1 **Constraints on post-glacial boreal tree expansion out of far-northern**
2 **refugia**

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18 **ABSTRACT**

19 **Aim** To use a variety of data sources to infer how northern boreal trees recovered their range
20 upon deglaciation and/or Holocene warming.

21 **Location** Scandinavia, Alaska/north-west Canada (eastern Beringia).

22 **Methods** Mapped fossil occurrences for *Picea* (spruce) assessed against available
23 palaeoenvironmental and phylogeographic information.

24 **Results** Scandinavia — Last glacial maximum (LGM) evidence of *Picea* is confined to one
25 DNA record, but late-glacial and early-Holocene records include scattered macrofossils.
26 Holocene pollen data show a clear east-west increase to high values. A haplotype unique to
27 the Scandinavian Peninsula is recognised.

28 Eastern Beringia —Pre- and post-LGM macrofossils occur, but the LGM fossil record
29 comprises only scattered low pollen values. Early-Holocene pollen values increase markedly
30 ~11 cal yr BP (NW Canada) and ~10 kcal yr BP (central Alaska). Also at this time three sites
31 on the Bering Land Bridge indicate presence of *Picea* where it is now absent. Several unique
32 regional haplotypes are recorded; while most are rare, one is common in some modern
33 populations.

34 **Main conclusions** Small *Picea* populations probably occurred in pre-Holocene Scandinavia,
35 but pollen patterns argue against immediate expansion with the onset of warmer conditions.
36 Despite relatively weak fossil evidence, refugial populations are also probable in eastern
37 Beringia, particularly given the extent of unglaciated terrain. Post-glacial pollen patterns are
38 more nuanced, suggesting two spatially and temporally distinct expansions, one possibly
39 consistent with a unique central Alaskan haplotype, and subsequent westerly “filling-in”. The
40 presence of macrofossils and/or neutral markers does not require that current northern
41 populations are derived primarily from refugial ones, particularly where pollen patterns show

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42 delayed directional expansion of large populations through time. Refugial populations initially
43 responded weakly to major post-glacial environmental change; if subject to genetic isolation
44 and strong selection pressure they may have had little potential to do otherwise, instead being
45 largely replaced by in-migrating populations with greater genetic diversity.

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49 **KEY WORDS:** Refugial population, relictual population, *Picea*, evolution, climate change,

50 Scandinavia, Alaska, eastern Beringia, Late Quaternary

51 **INTRODUCTION**

52 The role of northern refugia as sources of post-glacial recolonization is highly topical
53 (Stewart *et al.*, 2009; Tzedakis *et al.*, 2013); it has triggered a potential shift of emphasis from
54 long-distance migration to *in-situ* expansion in determining spatial responses of species to
55 climate change. Survival and expansion of species from small northern refugia may alter our
56 views of how recolonization of space occurs, and also ideas about rates at which species can
57 disperse over landscapes. This in turn affects the operation of niche models and other
58 projections of response to future climate change (Birks & Willis, 2008; Svenning *et al.*,
59 2008). The fates of refugial populations undoubtedly unfold differently depending upon the
60 life-history of the organism: small mammals have vastly different life histories than trees, for
61 example. Trees, however, are an important long-term study system because of the abundant
62 fossil record for many species, and because their history is often used as a model for
63 biogeographic thinking (e.g. Mclachlan *et al.*, 2005; Magri, 2008), and it is tree-species
64 refugia we address here.

65 Good palaeoecological records of late-Quaternary tree species exist in Europe and
66 North America. Continental-scale, directional, time-transgressive increases of forest tree
67 pollen to relatively high values (values are taxon-dependent) are usually interpreted as
68 migration of a large population from a distant region (e.g., Davis, 1981; Giesecke & Bennett,
69 2004) and comprise two linked processes: the dispersal of individuals into new spaces (and
70 establishment of small founder populations), and population expansion, typically signifying
71 the achievement of a dominant role in forest composition (Giesecke 2005a). On the other
72 hand, persistent, low pollen values could be due to long-range pollen transport or to small
73 local populations, and they are ambiguous without other information (Brubaker *et al.*, 2005).
74 Macrofossils (wood, needles) provide clear evidence of presence of trees, but their generally
75 sporadic and localized occurrence says little about population size. A key question is the

76 extent to which refugial populations later expanded with climatic amelioration, as opposed to
77 being overtaken by larger in-migrating populations. An examination of macrofossil finds in
78 the context of large-scale pollen patterns can address this question.

79 While it is acknowledged that a range of ecological and genetic constraints to survival
80 and expansion may be experienced by contemporary small populations and founder
81 populations (Lande, 1988; Geisecke, 2005a), there currently seems to be quite broad
82 acceptance that Pleistocene refugial populations can be transformed into widespread
83 Holocene forest cover—that is, presence alone somehow assures later expansion (e.g.,
84 Feurdean *et al.*, 2013). The concept of a biological “refugium” implies the ability of refugial
85 species to expand at a later time, but various properties of a population can compromise that
86 ability (rendering the population an extinction-prone “relict”). Recently, properties such as
87 demographic status and evolutionary trajectory have been discussed by Bennett & Provan
88 (2008) and Hampe & Jump (2011); Hampe & Petit (2005) and Davis *et al.*, (2005) have
89 pointed out the important role of evolution in the migration of large populations. These
90 considerations deserve further attention, given the increasing focus on refugia.

91 In this study we explore the palaeoecological evidence for small refugial (or relictual)
92 populations and large-scale migration of the genus *Picea* (spruce) using a comparative
93 approach in two contrasting sub-continental regions, and we discuss the likely evolutionary
94 implications of observed patterns. *Picea* is a widespread genus, being dominant in the boreal
95 forest of both northern Europe and northern North America and featuring in a large number
96 of palaeoecological records. The patterns of post-glacial spruce colonization to its north-
97 western limits in both regions (Scandinavia and Alaska-northwest Canada [eastern Beringia],
98 respectively), as shown by broad-scale pollen mapping (e.g., Giesecke & Bennett 2004;
99 Brubaker *et al.*, 2005, respectively), occurred over many millennia. The glacial histories of
100 the two regions are strikingly different, however, Scandinavia having been widely glaciated

101 while large portions of northern and central eastern Beringia remained ice-free. Here we
102 compare the pollen and macrofossil patterns that are now available for both regions, taking
103 into account data on neutral genetic markers. Through a consideration of the major
104 environmental changes occurring with global deglaciation and the evolutionary processes
105 affecting both small, isolated populations in sub-optimal habitats and large-scale in-
106 migration, we present a conceptual model that attempts to reconcile current data.

107

108 **Geographic regions, study species and late-Quaternary history**

109 *Scandinavia* (*P. abies* [L.]Karst.)

110 Nomenclature follows the Integrated Taxonomic Information System (www.itis.gov). Dates
111 and ages are reported as calibrated radiocarbon years before present unless otherwise
112 indicated. Today boreal forest covers much of the Scandinavian Peninsula except alpine
113 areas. A strong W-E gradient of increasing continentality influences vegetation composition.
114 *Picea abies* prefers high-nutrient, moist soils, and its current range limits coincide with
115 January mean temperatures of less than -1.0°C (Giesecke & Bennett 2004). Its range
116 extends from NW Scandinavia to the mountains of central Europe and eastward to Russia.

117 Spruce populations were present during Marine Isotope Stage (MIS) 3 (which began
118 >50 kyr BP and ended at the LGM) in ice-free areas of the Scandinavian Peninsula (Helmens
119 & Engels, 2010). Scandinavia was extensively glaciated during the last glacial maximum
120 (LGM; informally used here as ~ 25 -15 kyr BP to fit Beringian climate history). A few areas
121 remained intermittently ice-free and mountain tops likely became ice-free early (Wohlfarth *et*
122 *al.*, 2008; Giesecke 2005b and references therein). *In-situ* survival and/or colonization
123 during the Late Glacial/LGM is argued from two dated macrofossil finds (see Table 1) and
124 from other less secure data: a *Picea* stoma dated indirectly to >11 ka from central Norway

125 (Paus *et al.*, 2011), and cpDNA identified as *Picea* from lake sediments dated to ~17.7 ka in
126 northwest Norway (Parducci *et al.*, 2012a).

127 Rapid deglaciation occurred, being complete by ~9-7 kyr BP (Wohlfarth *et al.*,
128 2008). Pollen maps show northern regions of Europe were colonized from the south and east
129 during the Holocene; the Scandinavian Peninsula was possibly colonized via east-west (trans-
130 Baltic) and northern routes (Giesecke & Bennett, 2004); high values of *Picea* pollen are only
131 achieved in the mid to late Holocene over much of the region (Fig. 1). In contrast, Kullman
132 (2002, 2008) and Oberg and Kullman (2011, and references therein) report finds of fossil
133 wood across Scandinavia, the oldest of late-glacial age, but most of early-Holocene age
134 (Table 1).

135 Genetically, there is a deep split between northern (Russian-Scandinavian) and central
136 European spruce populations (Tollesfrud *et al.*, 2008). From a comparison of microsatellite
137 and mtDNA data, Tollesfrud *et al.*, (2009) conclude that individuals derived from the
138 northern European population entered Scandinavia via both a southern (trans-Baltic) and a
139 northern (north Finland) route, which is mirrored in the pollen-based Holocene migration
140 patterns (Fig. 1; Giesecke & Bennett, 2004). A widespread northern haplotype occurs
141 throughout the range and is present east and south of the Baltic, whereas a more localized
142 haplotype occurs only in western Scandinavia. Intriguingly, this haplotype is present in
143 pollen dated to ~6 ka BP from a lake in central Norway, near to one of the documented finds
144 of early-Holocene spruce wood (Parducci *et al.*, 2012a). Of the two sub-continental regions,
145 Scandinavia was far more heavily and extensively glaciated, and yet early-Holocene finds of
146 spruce (and other tree) macrofossil material are quite widely reported. This is, perhaps, one
147 reason for the more heated discussion surrounding spruce survival in Scandinavia (e.g.,
148 Kullman, 2002; Birks *et al.*, 2005; Geisecke, 2005b) than in unglaciated northwest North
149 America

150

151 *Eastern Beringia (Picea glauca [Moench] Voss and P. mariana [Mill.] Britton, Sterns and*
152 *Poggenb)*

153 Eastern Beringia is characterized by a cold continental climate, and the western coastal zone
154 is markedly less maritime than equivalent latitudes in Norway. Boreal forest in eastern
155 Beringia mainly lies between the southern Cordillera and the northern Brooks Range and its
156 eastward extensions. It is dominated by *Picea glauca* (white spruce) and *P. mariana* (black
157 spruce). Both species have continuous ranges east to the Atlantic seaboard. *Picea glauca*
158 tends to occupy warmer, better-drained parts of the landscape. Growth within parts of its
159 current range is limited by low summer moisture levels (Barber *et al.*, 2000). Most records
160 indicate that *P. glauca* was the first species to expand in the region during the Holocene, and
161 it is usually the treeline species today. *Picea mariana* became widely established in the mid
162 Holocene 5-8 kyr ago (Anderson *et al.*, 2004).

163 Large parts of the region were unglaciated in the last glacial cycle. MIS 3 in eastern
164 Beringia was a long phase during which warmth and moisture levels were intermediate
165 between LGM and interglacial conditions (Hopkins, 1982). LGM conditions were dry and
166 the vegetation largely treeless (Hopkins 1982; Anderson *et al.*, 2004). Lower sea levels
167 exposed the continental shelves of the Bering and Chukchi Seas and linked Alaska with
168 eastern Siberia. The Cordilleran and Laurentide Ice Sheets isolated eastern Beringia from the
169 rest of unglaciated North America. Exactly when the “ice-free corridor” opened as the
170 Laurentide and Cordilleran ice sheets parted is still a matter of some conjecture: it probably
171 opened between 13.5 and 12.5 kyr BP (Dyke, 2004). Strong summer warming occurred in the
172 Late Glacial and early Holocene (Kaufman *et al.*, 2004) and in eastern areas the late-glacial
173 period was characterized by low levels of effective moisture (Barber & Finney 2000). Post-
174 glacial sea-level rise subsequently severed the land connection and restored the Bering Strait.

175 The history of boreal forest taxa has been studied less intensively than in Scandinavia,
176 partly due to the large size and inaccessibility of the region. Macrofossil finds of boreal tree
177 taxa are relatively rare (Hopkins *et al.*, 1981), and a lack of macrofossils from LGM time led
178 initially to the assumption that *Picea* was eliminated from the region. This view is starting to
179 change as more data have become available (see below).

180 A survey of modern cpDNA variation in Alaskan *P. glauca* by Anderson *et al.*,
181 (2006) showed high variation, the authors arguing for the presence of refugial populations
182 that may have been largely undetected palaeoecologically (i.e., cryptic refugia).
183 Subsequently, using microsatellites to reassess the patterns, Anderson *et al.*, (2011) found
184 evidence of likely refugial populations, possibly focussed in north-central Alaska, and one
185 haplotype prominent in modern populations in this area. They interpret genetic patterns as
186 indicating mixing and bidirectional gene flow towards and from the east, but they also
187 detected lower heterozygosity levels in Alaskan populations and conclude that inbreeding and
188 bottlenecks may have occurred.

189

190 **METHODS**

191 **Mapping of eastern Beringia fossil data**

192 In order to compare North American patterns with those already established for Scandinavia,
193 we synthesized spatio-temporal patterns for spruce in eastern Beringia in ARC-GIS using the
194 pollen threshold approach of Giesecke & Bennett (2004) for Scandinavia (see below). We
195 used 71 dated pollen records collated from public databases plus 20 records either digitized
196 from published data or taken from our own unpublished sites (Table S1). Only samples dated
197 to $\leq 15,000$ yr BP were used, and sites with only one reported sample were omitted (see Table
198 S-1). Most records had calibrated radiocarbon ages. Radiocarbon date calibration approaches
199 vary among authors, but not to the extent that emergent patterns would be significantly

200 affected in 1000-yr time-slices. To calibrate other records, typically single dates on
201 macrofossils, we used CalPal-2007online (Danzeglocke *et al.*, 2013). Where sites in the
202 database were older studies (pre-AMS dating) and had been re-studied with an AMS
203 chronology we used the newer study (Table S-1).

204 Threshold maps were made for the first occurrence of *Picea* pollen at the 1, 5 and
205 10% levels and pollen-percent. A threshold was crossed or a contour value attained if one or
206 more samples in a time-slice had the appropriate pollen value. Shapefiles for eastern Beringia
207 (coordinate system UTM Zone 6N) included site locations for *Picea* values from 15,000 yr
208 BP-present. We mapped percent pollen values using Inverse Distance Weighting (IDW) tool
209 in Arc-GIS to create a raster surface in exactly the same manner as Geisecke and Bennett
210 (2004). A treeline shapefile was created by georeferencing an existing map representation of
211 the treeline and digitising the outline.

212 The threshold algorithm has limitations when applied to eastern Beringia data.
213 Records show that in NW Canada the treeline advanced and then retreated, and at other sites
214 there are early increases to high *Picea* values and later declines. With this approach an
215 advance/increase can be seen but not a retreat/decrease. Furthermore, in western and northern
216 Alaska, a few points influence contours over wide areas. We therefore also plotted a series of
217 time-slice maps from 15 kyr BP to present showing contours for the following ranges of
218 pollen values: >1%<5%; >5%<20%; >20%. The maps include changing coastline and ice-
219 sheet extent based on Manley (2002) and Dyke *et al.*, (2003), respectively, and they enable
220 reductions in pollen values to be plotted spatially. Finally, we collated reported macrofossil
221 data for the region.

222

223 **RESULTS**

224 ***Picea* history in eastern Beringia: synthesis**

225 >50-15 kyr BP

226 The MIS-3 climate regime should have supported tree growth at least in lowland areas (see
227 above), and while there are relatively few MIS-3 localities, macrofossils and pollen records
228 indicate that both species of spruce were present in the region (Table 2; Figs. 2a and 2b). The
229 youngest recorded pre-LGM macrofossils are dated to ~25 ka BP (Zazula *et al.*, 2006). In
230 contrast, except for values of >5% recorded infrequently at two sites in interior Alaska,
231 LGM records show little evidence of high spruce pollen values, although low values (mostly
232 <2%) are recorded at over 30 sites (see Brubaker *et al.*, 2005; Fig. 2c). There are no reliably
233 dated LGM macrofossil records.

234

235 15 kyr BP – present

236 The earliest reliable post-LGM macrofossil records are from the far east of the region
237 and date to ~13.3 and ~11 ka (Table 2; Fig. 3d); two older dates (16.3 and 19.1 ka) for spruce
238 macrofossils from the same area are considered by Hopkins *et al.*, (1981) as unreliable and
239 the macrofossils as probably redeposited. Two macrofossil records in central Alaska date to
240 10.9 and 10.3 ka, though the older is not a direct date on the fossil (Weber *et al.*, 1981). In
241 western Alaska, a white spruce twig AMS-dated to ~9200 ka has been reported from thaw-
242 lake deposits on northern Seward Peninsula by Wetterich *et al.*, (2012). Today this region lies
243 beyond the range spruce, although spruce currently grows on the southeastern Seward
244 Peninsula (Fig. 3). In addition, Fig.2d shows two *Picea* pollen records (~13 kyr old) in far
245 western Alaska (Colinvaux 1981; Hunt *et al.*, 2013).

246 The GIS mapping begins at 15 kyr BP as there are too few sites prior to this to use the
247 threshold mapping approach (Fig.3a-c). The 10% pollen limits approximate to the modern
248 limits of spruce in the region, which agrees with previous observations (Anderson and
249 Brubaker, 1994). It is important to bear in mind the maps are not migration or distribution

250 maps; they merely summarize the available information on spatial patterns of initial
251 population increase. Southwest Alaska lacks sites, and in this area the age contours are
252 somewhat distorted by the GIS algorithm. It is clear, however, that thresholds are passed later
253 in western Alaska, and here a majority of sites do not pass the 10% threshold at any time.

254 Values of 1% are attained 15-12 kyr BP in NW Canada and interior Alaska and in
255 much of the rest of the region except the far west by 9-8 kyr BP. Single sites form “bulls-
256 eyes” giving the impression of widespread distribution (see also Brubaker *et al.*, 2005). The
257 5% and 10% maps feature smoother patterns and highlight two regions of relatively early
258 increase: northwest Canada (lower Mackenzie region) and interior Alaska—these
259 approximate to the areas where early macrofossils are recorded. At 5% and 10%, only sites
260 in NW Canada pass the threshold before 10 kyr BP, and sites in central interior Alaska pass it
261 between 10 and 8 kyr BP. In Figs. 3a-c, the star marks St Paul Island (Colinvaux 1981); here
262 *Picea* values of as high as 20% are recorded during the period 12,350-10,700 yr BP (the site
263 was included: compared with exclusion, inclusion affects the 1% map slightly, but there is
264 no discernable effect on the 5% and 10% maps).

265 The pollen contour maps (Fig. 4) show early (13-12 kyr BP) pollen values >5% in
266 NW Canada, possibly before the ice-free corridor is fully open, and values of >1% over much
267 of eastern Alaska. At 10 kyr BP the values are between 5 and 20% over eastern half of the
268 region, with the >20% area only in the far NW of the region. Between 10 and 7 kyr BP pollen
269 values decrease in NW Canada, while values >20% occur in the eastern interior of the study
270 area. After 7 kyr BP pollen values gradually increase westward. The spatial development of
271 the >20% contour likely reflects the mid- and late-Holocene increase and westward
272 expansion of the second species of spruce, *Picea mariana*.

273

274

275 **DISCUSSION**

276 Are the eastern Beringia data and maps reliable? They are based on fewer sites than those of
277 Giesecke and Bennett (2004) and thus noisier. The GIS algorithm has limitations, notably
278 that isolated sites exert undue influence on space around them. This is particularly noticeable
279 in SW Alaska, where sites are scarce over a large area. Nevertheless, the maps function to
280 summarize broad spatio-temporal trends in spruce population increase. In particular, both
281 sets of maps show directional trends most clearly at the 10% pollen threshold, which is
282 consistent with the presence of closed spruce forest, and in both cases is in a broadly east-
283 west direction.

284 Some Beringian studies report bulk-sediment ages, which can be older than AMS
285 ages at the same level due to incorporation of old carbon from catchments (Abbott and
286 Stafford, 1999). Where possible we checked records with bulk dates against new (repeat)
287 studies. For example, the notable early spruce rise at Hanging Lake, NW Canada (Cwynar
288 1982) is retained in the AMS chronology of Kurek *et al.*, (2009).

289

290 **Comparison of patterns of palaeodata in Scandinavia and eastern Beringia**

291 A comparison of the two regions reveals both similarities and differences. In Scandinavia the
292 expansion of populations follows a clear east-west trajectory over millennia. In eastern
293 Beringia there are early focussed expansions in the far northeast and central regions, a
294 subsequent filling-in of higher values in these areas, then a more clearly directional westward
295 expansion in the later Holocene.

296 Nevertheless, in Scandinavia, scattered macrofossil localities record spruce presence
297 in places and at times that complicate a simple model of time-transgressive in-migration that
298 might be inferred from large-scale pollen patterns alone. There is a significant temporal gap
299 between the earliest dated macrofossils, which indicate that small populations of spruce were

300 already present, and the later, time-transgressive pollen expansion. This disparity led
301 Kullman (2008) to suggest that pollen records need to be re-evaluated. Do low counts
302 conventionally referred to long-distance transport indicate local presence? More
303 provocatively, is the pollen record incapable of reflecting more widespread populations? Low
304 (or no) pollen production is possible under sub-optimal growth conditions (Hicks, 2006), but
305 this is not likely to be the case when large, widespread populations are present as, by
306 definition, these indicate suitable conditions for reproduction. Thus palynological theory
307 suggests the most parsimonious explanation for the pollen and macrofossil observations is
308 that the Scandinavian early post-glacial period was characterized by small, scattered
309 populations that persisted in sub-optimal conditions at the onset of the interglacial climatic
310 regime. Some of these populations may possibly have been LGM survivors, others probably
311 represent founder events preceding Holocene expansion (Geisecke and Bennett 2004;
312 Kullman 2008).

313 In eastern Beringia both species of spruce were present until the LGM. Low levels of
314 spruce pollen at a majority of sites in ice-free parts of the region dated to the LGM suggest
315 small populations of one or both species (not determined) may have persisted. If so, given a
316 climate substantially more arid than present (Hopkins 1982), trees probably only occurred in
317 highly favourable azonal sites, for example, on or at the base of south-facing slopes, which
318 generated sufficient growing degree-days but where soil conditions were relatively moist,
319 such as drainage gullies or river floodplains. As such, the region would have contained
320 refugia that were scattered and possibly ephemeral (in the case of dynamic floodplain
321 surfaces).

322 A simple in-migration model is even less well supported in eastern Beringia, where
323 spruce was arguably present in the lower Mackenzie region prior to the opening of the
324 northern portion of the ice-free corridor (Figs. 3 and 4). The existence of *in-situ* survivors is

325 indirectly supported by the fact that the youngest pre-LGM macrofossil records are recorded
326 in the east (Table 2; Fig. 2b), where the earliest rise in pollen values is seen. However, both
327 the oldest post-LGM macrofossils, dated to ~13.0 ka, (Table 2; Fig. 2d) and broad-scale
328 multi-millennial pollen patterns are also consistent—just—with dispersal from the south east
329 through the opening ice-free corridor, assuming extremely fast migration. As of yet, genetic
330 data that might address this dilemma are not reported for this region.

331 The maps also show populations increasing relatively early (at ~10 kyr BP) in the
332 Alaskan interior. This expansion is noticeably later than that in NW Canada and could be
333 explained by either dispersal from the east preceded by founder events (compare Fig.1 and
334 Fig.3) or *in situ* expansion of extant populations. Genetic studies indicate the probable
335 occurrence of local ancestral populations in eastern Beringia, although strong Holocene gene
336 flow has also occurred, and the occurrence of these local haplotypes in central Alaska lends
337 support to the latter explanation (Anderson *et al.*, 2006; 2011).

338 In the far west of eastern Beringia, pollen of *Picea* is recorded during late-glacial
339 (~13-11 kyr BP) from St. Paul Island on the Bering Land Bridge (Colinvaux, 1981; Figs. 2
340 and 3). The ages are based on bulk sediment dates and thus slightly questionable, but the
341 better dated later part of this record (with high pollen influx values) strongly suggests the
342 presence of spruce at the site ~13 cal yr BP. Hunt *et al.*, (2013) report *Picea* pollen (1-4%)
343 dating to ~13,000 cal yr BP from the southern Seward Peninsula (Fig. 2); this is associated
344 with *Larix* pollen (up to 10%), which would signal the nearby presence of larch trees, as larch
345 pollen is poorly dispersed. Further to the north is the record of a single *Picea glauca* needle
346 AMS-dated to ~9 ka (Wetterich *et al.*, 2011; Fig. 2d). Thus spruce may have survived on
347 portions of the land bridge and then extirpated during the transgression (the slowly westward
348 advancing treeline now lies to the east; see Fig. 3).

349

350 **The role of post-glacial environmental constraints**

351 The late-glacial and early-Holocene periods saw major climate change at high latitudes
352 (Miller *et al.*, 2010). In both regions summer temperatures increased and maximum
353 temperatures were probably warmer than present, but cold springs linked to enhanced early-
354 Holocene seasonality (Miller *et al.*, 2010; Kaufman *et al.*, 2004), low effective moisture
355 (Barber & Finney 2000), and thin snow cover could all have constrained spruce growth
356 (Huntley, 1988; Giesecke & Bennett, 2004; Brubaker *et al.*, 2005).

357 Holocene sea-level rise likely contributed to the physical and/or climatological demise
358 of any spruce populations in offshore locations and along the modern coasts of both regions.
359 In Norway, rising eustatic sea-level outpaced isostatic rebound and led to rapid submergence
360 of narrow coastal shelves. Had populations occurred on the shelves (see Parducci *et al.*,
361 2012), they would in all likelihood have been rapidly extirpated. In western Alaska, the
362 Bering Sea transgression covered shallow shelves far more slowly (Figure 4). Eventually,
363 though, coasts and islands in a region increasingly dominated by the expanding cold ocean
364 would have experienced cooling in the growing season (Wetterich *et al.*, 2011). For example,
365 according to the pace of transgression (Manley 2002), the land area of St. Paul Island was
366 rapidly reduced and fragmented at the time *Picea* disappeared from the pollen record (see
367 Fig. 4). Thus, sub-optimal environmental conditions alone may have played a role in delaying
368 spruce population expansion. When genetic constraints are added, the likelihood of expansion
369 from small populations is lessened further.

370

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

373 The conceptual model developed below assesses how genetic constraints interacting with a
374 changing environment may explain the observed patterns. The focus is more on eastern

Genetic constraints on post-glacial boreal tree expansion

375 Beringia, where the physical and biological chances of LGM survival were greater, but
376 comparisons are made where appropriate with Scandinavia. Genetic constraint is an
377 overlooked factor in discussions of Holocene repopulation dynamics. Davis *et al.*, (2005)
378 expressed surprise that so little attention is given to the potential (or lack thereof) for taxa to
379 adapt to Quaternary climate change. As with founder populations, relict populations are liable
380 to genetic and demographic constraints related to isolation and small population size (Lande
381 1988; Hampe & Jump 2011). In contrast, large migrating populations have a deep reservoir
382 of genetic variation, and this can facilitate rapid evolutionary response to changing
383 environments (Davis *et al.*, 2005).

384 How would genetic constraints act on populations surviving a glacial-interglacial
385 cycle? Any small, pre-Holocene populations were probably derived from the previous period
386 of widespread forest cover during the last interglaciation ~125 kyr BP. Subsequent
387 environmental conditions fluctuated but generally worsened for spruce (reduced growing-
388 degree days, increased aridity, and, particularly in Scandinavia, displacement to periglacial
389 locations by ice advance). Populations left behind on favourable sites as the forest
390 fragmented would have initially maintained genetic interchange and replacement of
391 individuals. The earlier part of the last glacial cycle was punctuated by warm intervals
392 lasting from a few centuries to several thousand years, particularly during MIS 3 (Miller *et*
393 *al.*, 2010), which would have allowed some population recovery/expansion.

394 Climate conditions tended to become more hostile for trees as time went on, and most
395 populations would have become smaller, some eventually extinct. In Beringia, this process
396 culminated in the LGM, the coldest, driest interval (and thus the most inimical to spruce). As
397 populations became small and isolated, they would have lost genetic variation, and hence
398 evolutionary potential, through genetic drift (i.e., the loss of alleles at random because too
399 few offspring are produced in each generation to “sample” all the genetic diversity of the

400 previous generation). Small, isolated populations would also have experienced stringent
401 selection that would have further reduced genetic variation. For example, in conditions far
402 from the climate optimum for the species, shifts in traits characterizing photosynthesis and
403 water use may have been favoured, and the capacity for efficient photosynthesis under more
404 typical climatic conditions may have been lost (i.e., evolutionary specialization). In addition,
405 narrow selective optima may also have led to reduced expression of phenotypic plasticity and
406 eventually, in combination with drift and selection, loss of the genetic basis for future
407 plasticity (Scheiner, 1993; Wagner *et al.*, 1997), reducing the capacity for individuals in the
408 population to adjust physiologically to changing climate. This loss of plasticity would also
409 have reduced the opportunities for genetic assimilation in a strongly altered environment (i.e.,
410 it reduced the potential for genetic evolution to maintain a successful phenotype that might
411 arise from initial plasticity in face of new conditions; see Lande, 2009).

412 In addition, recently developed genetic models have shown that fragmented
413 populations occupying disparate environments have limited capacity to exchange beneficial
414 genes successfully. This is because of genetic correlations (linkage disequilibria) between the
415 genes that are beneficial for the dispersed populations and genes that are beneficial in the
416 “mother” environment but deleterious for the dispersed populations (Schiffers *et al.*, 2013).
417 Hence there is a much reduced potential for fragmented populations to respond evolutionarily
418 to changing climatic conditions than is usually assumed. Furthermore, these models also
419 show that, due to divergent local adaptation, small, fragmented sub-populations occupying
420 disjunct, heterogeneous environments, but subject to gene flow, are at risk of demographic
421 collapse with rapid climate change (Schiffers *et al.*, 2013).

422 In contrast, larger populations migrating into the study regions from further east
423 would have contained far more genetic variation and phenotypic plasticity, allowing a more
424 rapid and effective phenotypic and evolutionary responses to selection, including via genetic

425 assimilation (Lande, 2009). In such a case, sufficient gene exchange would have occurred
426 subsequently for regional haplotypes to still be observable in modern populations, albeit in
427 low proportions, as recorded by contemporary genetic studies (see above). However, given
428 the arguments above, it is unlikely that genetically constrained relictual populations would
429 have generated all the observed forest expansion in Beringia, at least not without considerable
430 gene flow from in-migrating populations.

431 In Scandinavia, the greatest expansion of the ice sheet came at the end of the glacial
432 period, ~25-15 kyr BP, generating a strong spatial constraint on the size of any surviving
433 populations. Similar genetic constraints would have applied to these populations. It is
434 possible that spatial and temporal dynamism of the ice sheet allowed northern populations
435 present in MIS-3 to persist surprisingly long and even contribute to the Holocene gene pool.
436 If so, it is unlikely they were centrally ancestral to the modern forest, because both the
437 genetics and the pollen-based east-west pattern of expansion are strongly consistent with the
438 spread of a large in-migrating population from central Europe.

439

440 **CONCLUSION**

441 It seems likely that the differences in evolutionary response to major climate changes shown
442 by small populations compared with large ones, particularly for organisms with long
443 generation times such as trees, are currently greatly underestimated, and inferences about past
444 processes of population expansion based on observed characteristics of modern populations
445 plus the occurrence of macrofossils may be misleading. New genomic approaches to
446 analysing contemporary populations and the ability to extract mitochondrial DNA from fossil
447 material such as pollen may help further distinguish among the roles of refugial, relictual and
448 founder populations in the response of late-Quaternary trees to climate change. Meanwhile,

449 caution is desirable when making inferences about the role of small, refugial populations in
450 large-scale range expansions.

451

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453 We thank Mark Dover of the Southampton Cartographic Unit for GIS analysis and creation
454 of Figures 3 and 4. We are greatly indebted to Thomas Giesecke for the originals of Figure 1
455 and his thoughtful reviews of earlier versions of this article. Inger Alsos also provided helpful
456 comments on the manuscript.

457

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614 Additional references to data sources may be found at the end of Appendix S1 at [[URL](#)]

615

616 SUPPORTING INFORMATION

617 Appendix S1. List of sites used in the eastern Beringia pollen mapping and related references.

618

619

620 BIOSKETCHES

Genetic constraints on post-glacial boreal tree expansion

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

624

625 **Scott Armbruster** is interested in the evolutionary genetics and ecology of
626 plant adaptation to the biotic environment and in the role of microclimatic
627 heterogeneity and competition in plant-community assembly.

628 **Scott Elias** is principally interested in Quaternary insect fossils, with a focus on the regions
629 on both sides of the Bering Strait, and in the integration of insect-based climate
630 reconstructions with other proxy data.

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645 **Table 1**

Genetic constraints on post-glacial boreal tree expansion

646 *Picea* macrofossil records from Scandinavia.

647

Site Name	Date (cal yr (BP))	Date ¹⁴C yr BP	Source publication
Mt Åreskutan		11,020±90	Kullman (2002)
Mt Åreskutan		10,250±90	Kullman (2002)
Mt Åreskutan		8640±60	Kullman (2002)
Southern Swedish Scandes	9540 – 9320	8450 ± 60	Oberg and Kullman (2011)
Southern Swedish Scandes	9530 – 9380	8490 ± 70	Oberg and Kullman (2011)
Southern Swedish Scandes	9720 – 9520	8630 ± 60	Oberg and Kullman (2011)
Southern Swedish Scandes	9120 – 8660	8050 ± 70	Oberg and Kullman (2011)
Southern Swedish Scandes	9270 – 9000	8140 ± 60	Oberg and Kullman (2011)

648

649

650 **Table 2**651 *Picea* macrofossil records from eastern Beringia. The sites are shown on Fig. 2. Sites labelled

652 (4) on map (b) are located close together. *Original dates that were calibrated for this study.

653 **Sleet Lake date is an estimate only, derived from digitizing the pollen/macrofossil diagram

654 and assigning an arbitrary error to the estimated radiocarbon age that was calibrated.

Site Name	Date cal yr BP	Date ¹⁴ C yr BP	Location on Fig.2	Source publication
Isabella Basin	38,994 ± 2843*	34900±2950	(a) 1	Hopkins <i>et al.</i> , (1981)
Mayo Village	42697 ± 1024	38100±1330	(a) 2	Zazula <i>et al.</i> , (2006)
Bluefish River	29328 ± 469	24530±180	(b) 3	Zazula <i>et al.</i> , (2006)
Quartz Creek	30846 ± 386; 30891 ± 362	25800±240; 25800±240	(b) 4	Zazula <i>et al.</i> , (2006)
Last Chance Creek	31122 ± 364	26280±210	(b) 4 (overlaid)	Zazula <i>et al.</i> , (2006)
Sixtymile River	31009 ± 388	26080±300	(b) 4 (overlaid)	Zazula <i>et al.</i> , (2006)
Mayo Village	33587 ± 555	29600±300	(b) 4 (overlaid)	Zazula <i>et al.</i> , (2006)
Twin Lakes	13391 ± 181*	11500±160	(d) 6	Hopkins <i>et al.</i> , (1981)
Sleet Lake**	11025 ± 166	9700±100	(d) 5	Spear (1993)
Whitefish Lake	10849 ± 241	9530±170	(d) 7	Hopkins <i>et al.</i> , (1981)
Canyon Creek	10965±207	9640±155	(d) 8	Weber <i>et al.</i> , (1981)
Tangle Lakes	10304 ± 88	9100±80	(d) 9	Hopkins <i>et al.</i> , (1981)
Kitluk Pingo	9012-9562	8250±100	(d) 10	Wetterich <i>et al.</i> , (2011)

655

656 **Figure Captions**

657 Figure 1. Three maps of the time of first expansion of pollen percentages of *Picea abies* to a
658 threshold value. Maps (a-c) are for 1%, 5% and 10% thresholds, respectively. Dots, squares
659 and triangles mark sites used in the interpolations (see Giesecke & Bennett [2004] for
660 complete details). Dark line marks the limits of *P. abies*. Figure reproduced, with permission,
661 from Giesecke and Bennett (2004).

662

663 Figure 2. Pollen (circles) and macrofossil records (triangles) of *Picea* in eastern Beringia.
664 (a) – records from mid marine isotope stage 3 (MIS-3), 50-35 kyr BP; (b) – records from late
665 MIS-3, 35-24 kyr BP; (c) – records from the last glacial maximum (LGM), 24-15 kyr BP; (d)
666 – late-glacial and early-Holocene macrofossils (15-9 kyr BP). Numbers in triangles refer to
667 macrofossil site details provided in Table 2. Site 4 (Fig. 2b) represents four different localities
668 in the same area. The filled circles in (d) represent *Picea* pollen values from Calalooq Lake, St.
669 Paul Island (Colinvaux, 1981) and southern Seward Peninsula (Hunt et al., 2013). On (a)
670 “SP” denotes the Seward Peninsula and “LM” the lower Mackenzie region, as mentioned in
671 the text.

672

673 Figure 3. The times at which pollen values of 1%, 5%, and 10% are reached in eastern
674 Beringia is shown by maps a-c, respectively. Black dots are sites that reach the threshold;
675 white dots are sites not reaching the threshold (note in Fig. 3c these have a light grey tone to
676 help distinguish against background). Current *Picea* distribution is shown by the solid line.
677 The star indicates St. Paul Island (Colinvaux, 1981).

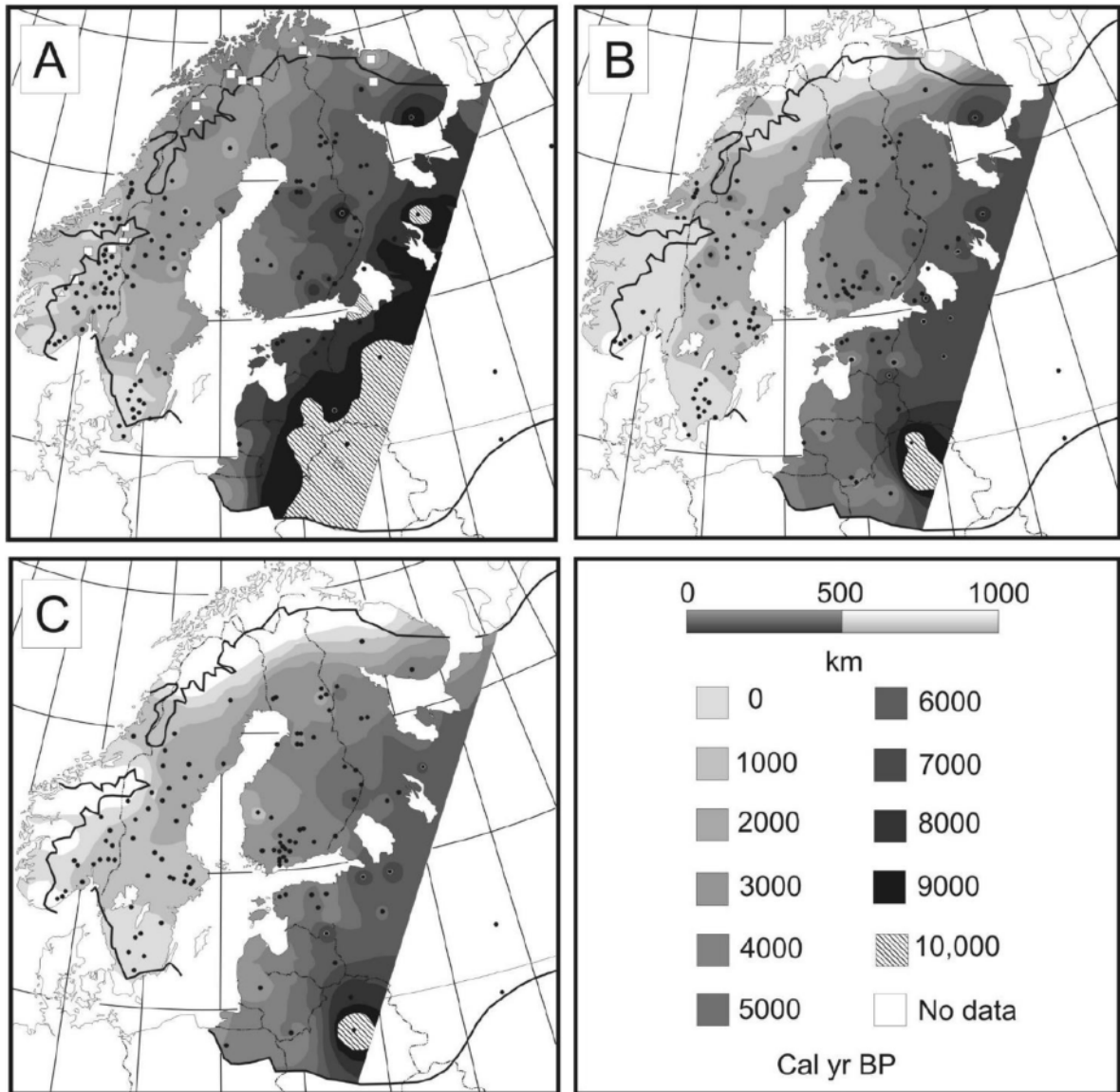
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679 Figure 4. Eight maps for 1000-yr time slices showing contours for the following pollen
680 percentage ranges: >1-5; >5<20; and >20. The format enables both increases and declines in

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681 pollen abundance over time to be visualized. Also shown: the Bering Sea post-glacial
682 transgression after Manley (2002) and extent of ice sheets after Dyke *et al.*, (2003).
683

684 **Figure 1**



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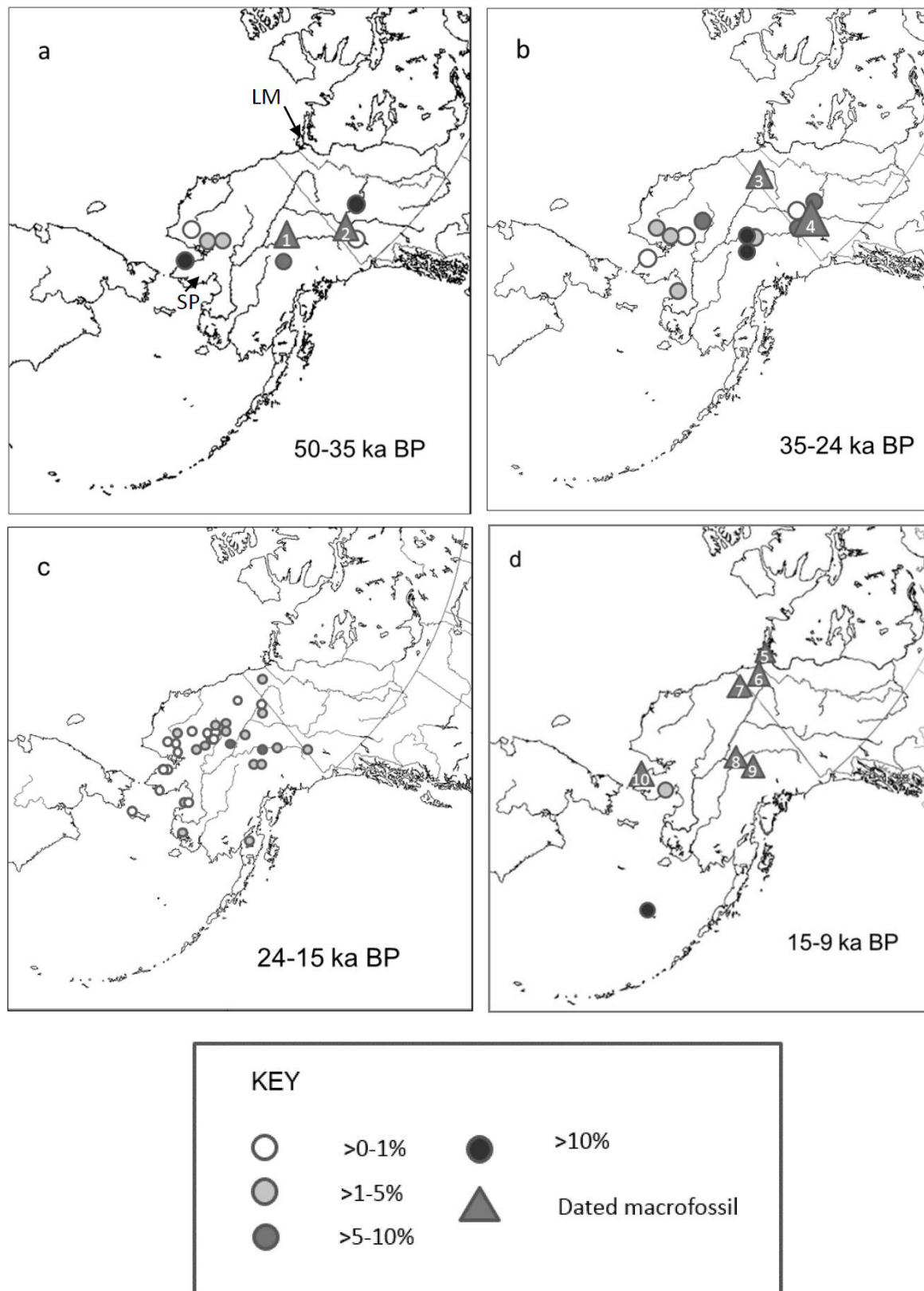
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694 **Figure 2**

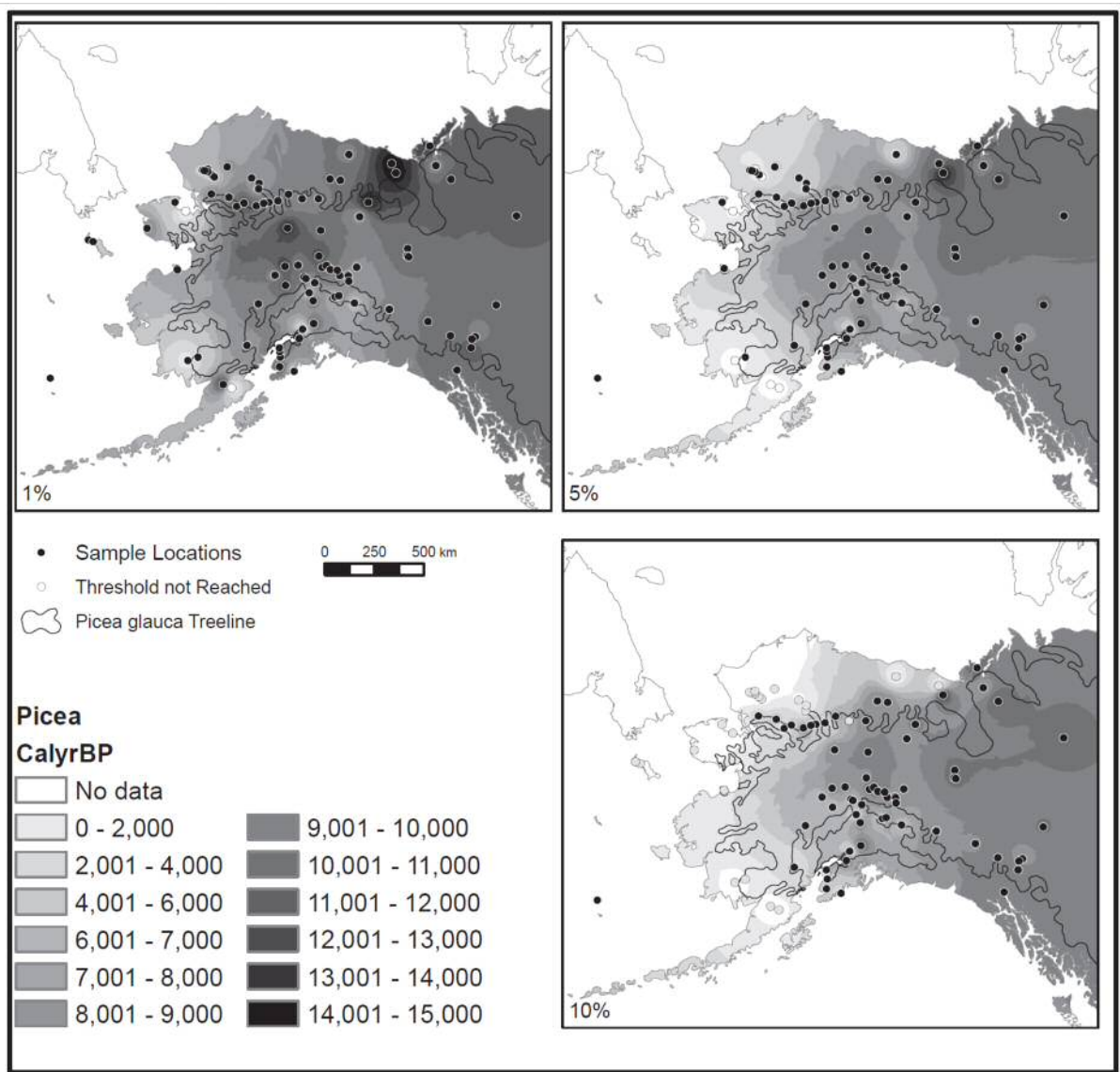


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697 **Figure 3**

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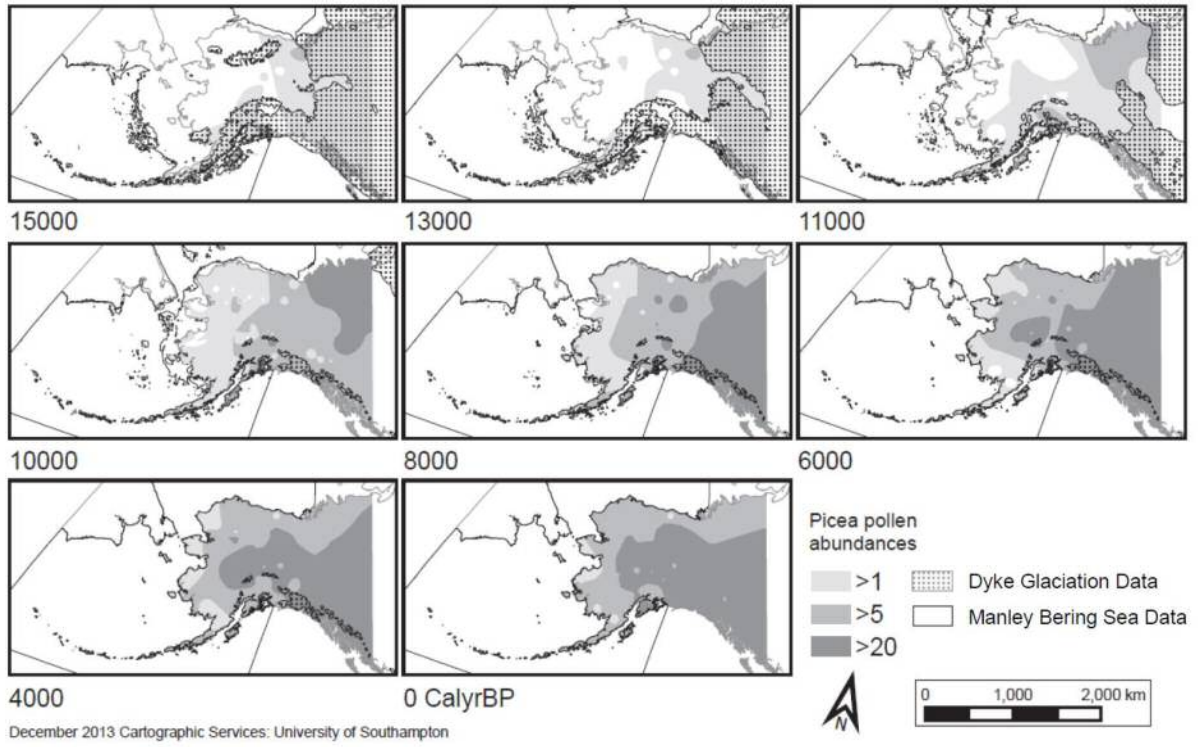
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703 **Figure 4**



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