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commentary

Tree refugia and slow forest development in response to post-LGM warming in North-Eastern European Russia

Though the Postglacial period counts its thousands of years, it was not indefinitely long, and few plants that merely scatter their seed could advance more than a yard in a year [...]. The oak, to gain its present most northerly position in North Britain after being driven out by the cold, probably had to travel fully six hundred miles, and this without external aid would take something like a million years. (Clement Reid 1899, p. 25)

Driven by an urge to understand how the composition of the British flora arose, Clement Reid was puzzled by the discrepancy between the apparent low dispersal capacity of big seeded trees and the high postglacial migration rates deduced from fossil evidence. Possible explanations resolving Reid's paradox, as it was later termed, were fast migration by long-distance dispersal events or glacial survival of small scattered populations at sheltered sites further north than evidenced by the fossil record (Reid 1899, Skellam 1951). More than 100 years have passed since the early writings of Reid, but two questions leading from his thoughts are still debated: *How far north did tree species survive the Last Glacial Maximum (LGM, ca. 21 kya)? How fast did tree species spread and thus current forest structure develop during post-LGM warming?*

A new paleoecological study by Välranta et al. (2011, *Journal of Biogeography*) provides, in addition to several other recent studies (e.g., Binney et al. 2009, Heikkilä et al. 2009), insight into these unresolved questions. Välranta et al. (2011) summarized macrofossil and stomata records from five sites at the late-glacial–early Holocene transition at the European Russian arctic tree line; an area east of the margin of the Scandinavian ice sheet and west of the Ural Mountains (Fig. 1). Their data evidenced the presence of Norway spruce (*Picea abies*) and tree birch (*Betula pendula/pubescens*) during the early Holocene (11,500–10,000 cal. yr BP) at all five sites. At one site, two radiocarbon dates even suggested the presence of these taxa up to 1000 yrs prior to the beginning of the Holocene. Historical biogeogra-

phy, however, depends on reliable chronologies of fossil records. Ideally, each site should have a well established chronology based on an adequate number of radiocarbon dated fragile and precisely identified terrestrial plant remains that show no signs of redeposition. In this respect, the chronologies of Välranta et al. (2011) were not optimal and the late-glacial presence of *P. abies* and tree *Betula* can be questioned, but their early Holocene records were well documented. Hence, the smoking gun, i.e., direct palaeoecological proof of LGM-populations, might be evasive, but scattered glacial and widespread early Holocene fossil records indeed reflect consistent patterns of early expansions in North-Eastern European Russia. Furthermore, independent climate reconstructions are crucial when evaluating the possible LGM survival of boreal tree populations so far north. Glacier-based climate models do indeed indicate relatively modest LGM temperature depressions in the arctic Ural Mountains (Allen et al. 2008). This might have facilitated survival of trees. Besides, the ability to produce krummholz forms (Öberg & Kullman 2011) or other strategies for non-reproductive persistence through millennia (Bhagwat & Willis 2008) may have been decisive. Nevertheless, as concluded by Välranta et al. (2011), it certainly seems likely that postglacial development of high-latitude forests occurred through expansion of local tree populations rather than through re-colonisation from distant southern refugia.

Using molecular markers, recent phylogeographic studies for both *P. abies* and *Betula* support glacial survival in north-eastern Europe (Maliouchenko et al. 2007, Tollefsrud et al. 2008). For example, *P. abies* shows distinct gene pools of similar within-population genetic diversity for northern and central-southern Europe (Tollefsrud et al. 2008): a pattern that supports west expansion from such north-eastern refugia and not re-colonisation of northern Europe from the south. For decades, pollen data have suggested early

Holocene north-eastern expansion of *P. abies* and tree *Betula* (e.g., Huntley & Birks 1983, Lang 1994). This notion is now supported and extended by the results of Välranta et al. (2011) together with other recent macrofossil evidence (Fig. 1), models of suitable climate conditions (e.g. Svenning et al. 2008), and insight from phylogeographic studies (Maliouchenko et al. 2007, Tollefsrud et al. 2008).

The three lines of evidence (paleoecological, modelling, and phylogeographical) highlight that the traditional view of Central Europe (including the Russian Plain) as mainly treeless at the LGM needs revision: the ice-free European Russian Plain but also sheltered valleys in the Ural Mountains possibly acted as LGM refugia for boreal tree species serving as sources for colonisation during post-LGM times. Evidence for glacial survival of temperate tree species, however, is still restricted to southern and more rarely, Central Europe north of the Alps (e.g., Bhagwat & Willis 2008, Svenning et al. 2008).

The implications of these results for our understanding of postglacial migration rates remain unclear. While evidence of more northern refugia might help explaining Reid's paradox for some species, the role of long-distance dispersal

during migration and for initiating early Holocene populations still remains undecided. Some recent paleoecological evidence suggests rapid responses of species to Quaternary climate warming (Öberg & Kullman 2011) while others suggest migrational lags (cf. Willis et al. 2010). Interestingly, even with survival of tree species as far north as suggested by Välranta et al. (2011), forest development was indicated with lags of 800 to 3000 years. Slow soil reactions due to relaxation of permafrost severity but also many other factors may have led to such considerable time-lags (Välranta et al. 2011).

In summary, the study of Välranta et al. (2011) consolidates our understanding that north-eastern tree refugia contributed importantly in the rapid re-colonization of northern Europe but also highlights that forest development was rather slow even though these northern nuclei existed. We conclude that in order to understand the spread of boreal tree and other plant species with post-LGM warming, the areas of the Russian plain and Ural need special attention.

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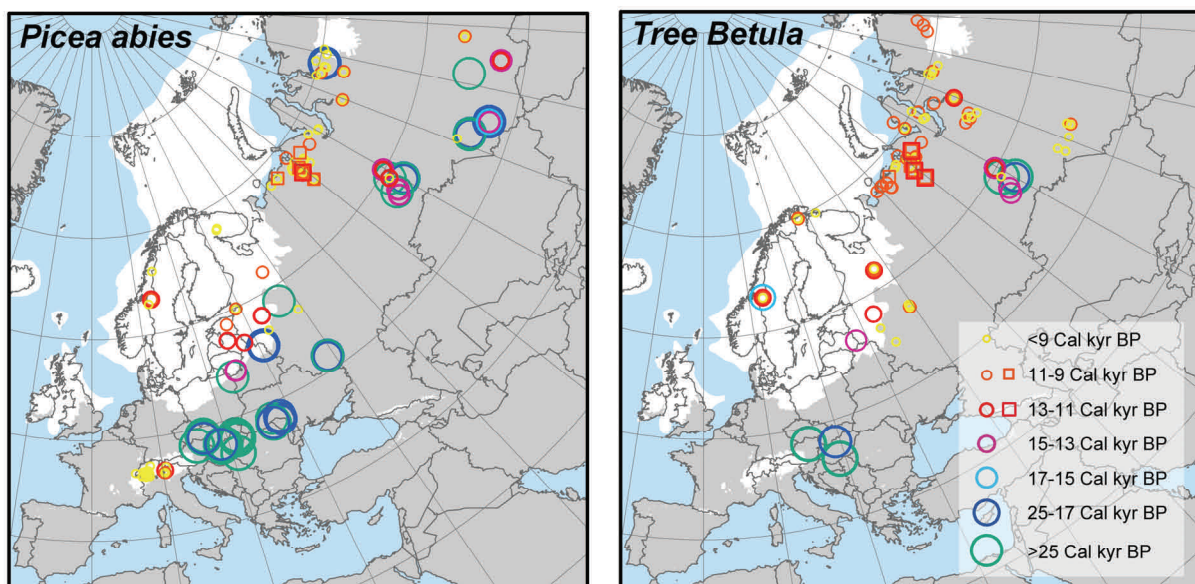


Figure 1. Distribution of macrofossil and stomata records for *Picea* and tree *Betula* in Eurasia. The macrofossil records from Välranta et al. (2011) are indicated with squares. Additional data were compiled from the Northern Eurasian Macrofossil Database (Binney et al. 2009), the European Pollen Database (<http://europeanpollendatabase.net/data/>), Heikkilä et al. (2009), Koff (unpublished), and Willis & Van Andel (2004). The LGM ice sheet extent follows Ehlers & Gibbard (2004). Data were compiled with focus on late-glacial–early Holocene records in Eastern Europe and Eurasia but cannot be claimed to be complete.

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