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The distribution of late-Quaternary woody taxa in northern Eurasia: evidence from a new macrofossil database

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ABSTRACT

We present a database of late-Quaternary plant macrofossil records for northern Eurasia (from 23° to 180°E and 46° to 76°N) comprising 281 localities, over 2300 samples and over 13,000 individual records. Samples are individually radiocarbon dated or are assigned ages via age models fitted to sequences of calibrated radiocarbon dates within a section. Tree species characteristic of modern northern forests (e.g. *Picea*, *Larix*, tree-*Betula*) are recorded at least intermittently from prior to the last glacial maximum (LGM), through the LGM and Lateglacial, to the Holocene, and some records locate trees close to the limits of the Scandinavian ice sheet, supporting the hypothesis that some taxa persisted in northern refugia during the last glacial cycle. Northern trees show differing spatio-temporal patterns across Siberia: deciduous trees were widespread in the Lateglacial, with individuals occurring across much of their contemporary ranges, while evergreen conifers expanded northwards to their range limits in the Holocene.

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1. Introduction

Determining the distribution of woody taxa in Eurasia during the cold-stages of the Quaternary is important for understanding present-day patterns in tree populations of Northern Europe, for example, species richness (e.g. Svenning and Skov, 2007) and genetic diversity (e.g. Petit et al., 2003), which are linked to response

rates and dispersal dynamics of woody species to intervals of climate change (e.g. Pearson, 2006). Furthermore, reliable records of the location of trees during the Lateglacial and Holocene are important for understanding northern treeline dynamics. It is expected that high-latitude regions will be especially sensitive to future climate change (IPCC, 2007). Past behaviour of treeline is of considerable interest because it is a large-scale climate-related feature. Its position, if reliably determined, provides a useful benchmark for assessing the performance of climate models and earth-system models in simulating past climate changes in the northern high latitudes (e.g. Edwards et al., 2000; Wohlfarth et al., 2004).

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A clear understanding of where woody taxa were located during the last glacial maximum (LGM) has been hampered by lack of detailed records that can provide a reliable record of evidence of *in situ* populations. Originally it was proposed, based on fossil pollen records, that woody taxa were located in refugia in the three southern peninsulas of Europe (Huntley and Birks, 1983; Bennett et al., 1991; Willis, 1994). This viewpoint still persists in many interpretations of contemporary patterns (see, for example, Svenning and Skov, 2007). A contrasting view is that many woody taxa, especially those with traits that equip them to survive the cold conditions of the full glacial, persisted further north, i.e. north of 40°, and even up to the edge of the ice sheet (see Willis and van Andel, 2004; Bhagwat and Willis, 2008; Birks and Willis, 2008). These interpretations, however, are based predominantly on macrofossil charcoal remains and genetic evidence (Lascoux et al., 2004) rather than pollen. Since pollen productivity can become greatly reduced under cooler temperatures and lower atmospheric CO₂ (Jackson and Williams, 2004; Feurdean et al., 2007), using pollen as a proxy to reconstruct vegetation under such conditions can be unreliable (but see Brubaker et al., 2005).

Late-Quaternary plant macrofossil data can complement pollen data in defining, with some certainty, the local occurrence of plant species. As such they contribute greatly to our understanding of questions concerning vegetation–climate dynamics: changes in the distribution of taxa, rates of migration, and variations in treeline position in response to climate change. The utility of a plant macrofossil database has been demonstrated for North America (Jackson et al., 1997, 2000) indicating, for example, that at the end of the LGM and during the Lateglacial in the eastern United States there was a much more northerly distribution of trees, including temperate genera, than had been predicted from the pollen record. Such findings have led to reassessments of migration rates of woody taxa in response to climate change (Clark, 2004; McLachlan et al., 2005). Macrofossil data have been published for Mongolia (Gunin et al., 1999), although the majority of the dates are based upon *Larix* wood that is <5 kyr cal BP in age. In addition, the newly established European Macrofossil Database developed at the University of Bonn (unpublished at time of going to press) has the

potential to complement the work described here. However, to date, there has been no major published compilation of plant macrofossils for northern Eurasia, as there has been for North America, although it acknowledged that a wealth of macrofossil data for this region exists as published (e.g. Kremenetski et al., 1998b; MacDonald et al., 2000a) and unpublished records.

In this paper we describe a new plant macrofossil database for northern Eurasia. Most records span the time interval 25–0 kyr cal BP although a few are dated >25 kyr cal BP. We briefly discuss its potential contribution to the study of late-Quaternary vegetation dynamics, focusing on preliminary results relating to (a) northern full-glacial refugia of woody taxa and (b) Lateglacial latitudinal treeline patterns. This paper is necessarily limited in its exploration of the full potential of the assembled data, and we encourage other investigators to explore the database further.

2. Regional setting

The study area, hereafter described as northern Eurasia, extends from ca 46 to 76°N and from 23 to 180°E and includes sites in the Former Soviet Union (Russia, Kazakhstan, Ukraine, Estonia, Latvia, Belarus, and Lithuania) and one site in Finland (Fig. 1).

Northern Eurasia includes two-thirds of the Northern Hemisphere high-latitude land mass (~20% of the global land mass) and it is, therefore, a region which is critical to our understanding of past global climate. The region is characterized by a continental climate, with very low winter temperatures and high summer temperatures and aridity in the southern and interior regions. The general decrease in precipitation towards the southwest and the north–south gradient in solar radiation are responsible for distinct regional vegetation patterns. The southwest is particularly dry and is largely characterized by desert or steppe vegetation. The boreal forest (or taiga) occupies the largest part of the land area and is characterized by *Abies*, *Picea* and *Pinus*; *Larix* dominates in the forests to the east. Beyond the northern treeline the vegetation is zoned latitudinally from shrub-dominated tundra, to erect dwarf-shrub tundra and prostrate dwarf-shrub tundra. Islands in the Barents Sea with cold moist climates are characterized by sparse

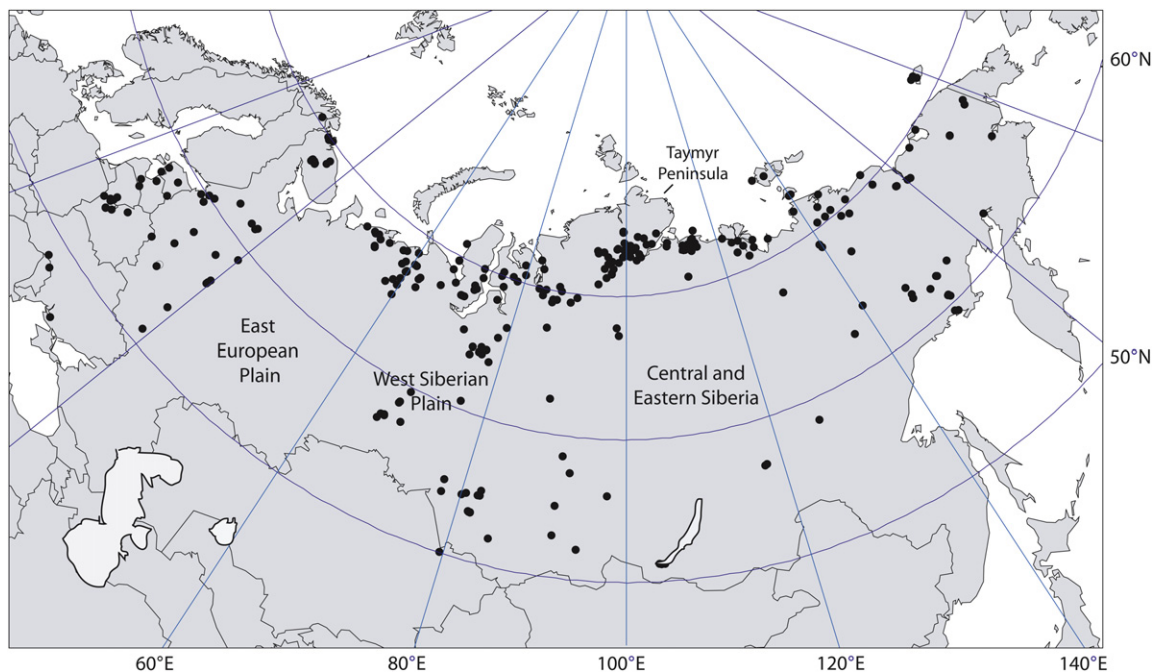


Fig. 1. Map indicating location of sites in the macrofossil database and geographical regions and locations referred to in the text.

Table 1
Taxonomy, synonyms and growth form of woody taxa in the database.

Original taxonomic identification	Revised taxonomy	Authority	Growth form
<i>Abies</i> sp.	<i>Abies</i> sp.	ITIS	Tree
<i>Abies sibirica</i>	<i>Abies sibirica</i> Ledeb.	Tropicos	Tree
<i>Alnus</i>	<i>Alnus</i> sp.	ITIS	Ambiguous
<i>Duschekia fruticosa</i>	<i>Alnus fruticosa</i> Rupr.	Tropicos	Shrub
<i>Alnus fruticosa</i>	<i>Alnus fruticosa</i> Rupr.	Tropicos	Shrub
<i>Alnus glutinosa</i>	<i>Alnus glutinosa</i> (L.) Gaertn.	ITIS	Tree
<i>Alnus incana</i>	<i>Alnus incana</i> (L.) Moench	ITIS	Ambiguous
<i>Betula</i>	<i>Betula</i>	ITIS	Ambiguous
<i>Betula</i> sp.	<i>Betula</i> sp.	ITIS	Ambiguous
<i>Betula</i> tree	<i>Betula</i> sp. (tree macrofossil)	HB	Tree
<i>Betula</i> sp. (tree macrofossil)	<i>Betula</i> sp (tree macrofossil)	HB	Tree
Tree type <i>Betula</i> seed	<i>Betula</i> sp. (tree macrofossil)	HB	Tree
Tree type <i>Betula</i> catkin scale	<i>Betula</i> sp. (tree macrofossil)	HB	Tree
Pieces of <i>Betula</i> leaves	<i>Betula</i> sp.	ITIS	Ambiguous
<i>Betule</i> bark	<i>Betula</i> sp.	ITIS	Ambiguous
<i>Betula</i> bud scale	<i>Betula</i> sp.	ITIS	Ambiguous
<i>Betula</i> sp. Seed	<i>Betula</i> sp.	ITIS	Ambiguous
<i>Betula</i> sp. Catkin scale	<i>Betula</i> sp.	ITIS	Ambiguous
<i>Betula</i> sp. bud scale	<i>Betula</i> sp.	ITIS	Ambiguous
<i>Betula</i> sp.	<i>Betula</i> sp.	ITIS	Ambiguous
<i>Betula</i> sp.s	<i>Betula</i> sp.	ITIS	Ambiguous
<i>Betula</i> bark	<i>Betula</i> sp.	ITIS	Ambiguous
<i>Betula</i> sp. seed	<i>Betula</i> sp.	ITIS	Ambiguous
<i>Betula alba</i>	<i>Betula pubescens</i> Ehrh.	ITIS	Tree
<i>Betula</i> sect. <i>Albae</i>	<i>Betula</i> sect. <i>Albae</i>	ITIS/HB	Tree
<i>Betula alba</i> ssp. <i>tortuosa</i>	<i>Betula pubescens</i> ssp. <i>tortuosa</i> (Ledeb.) Nyman	ITIS	Tree
<i>Betula</i> sect. <i>Costatae</i>	<i>Betula</i> sect. <i>Costatae</i>	Tropicos/HB	Tree
<i>Betula divaricata</i>	<i>Betula divaricata</i> Ledeb.	Tropicos	Shrub
<i>Betula exilis</i>	<i>Betula nana</i> L.	ITIS	Shrub
<i>Betula fruticosa</i>	<i>Betula fruticosa</i> Pall.	Tropicos	Shrub
<i>Betula</i> cf. <i>fruticosa</i>	<i>Betula</i> cf. <i>fruticosa</i>	Tropicos	Shrub
<i>Betula</i> sect. <i>Fruticosa</i>	<i>Betula</i> sect. <i>Fruticosa</i>	Tropicos/HB	Shrub
<i>Betula humilis</i>	<i>Betula humilis</i> Marshall	Tropicos	Shrub
<i>Betula</i> (<i>nana</i>) sp.	<i>Betula nana</i> L.	ITIS	Shrub
<i>Betula nana</i>	<i>Betula nana</i> L.	ITIS	Shrub
<i>Betula</i> sect. <i>Nana</i>	<i>Betula</i> sect. <i>Nanae</i>	ITIS	Shrub
<i>Betula</i> sect. <i>Nanae</i>	<i>Betula</i> sect. <i>Nanae</i>	ITIS	Shrub
<i>Betula nana</i> ssp. <i>nana</i>	<i>Betula nana</i> ssp. <i>nana</i>	Tropicos	Shrub
<i>Betula pendula</i>	<i>Betula pendula</i> Roth	ITIS	Tree
<i>Betula platyphylla</i>	<i>Betula platyphylla</i> Sukatschef	ITIS	Tree
<i>Betula pubescens</i>	<i>Betula pubescens</i> Ehrh.	ITIS	Tree
<i>Betula</i> cf. <i>pubescens</i>	<i>Betula</i> cf. <i>pubescens</i>	ITIS	Tree
Betulaceae sp.	Betulaceae	ITIS	Ambiguous
<i>Larix</i> sp.	<i>Larix</i> sp.	ITIS	Tree
<i>Larix gmelini</i>	<i>Larix gmelinii</i> (Rupr.) Kuzen.	Tropicos	Tree
<i>Larix sibirica</i>	<i>Larix sibirica</i> Ledeb.	Tropicos	Tree
<i>Picea</i>	<i>Picea</i> sp.	ITIS	Tree
<i>Picea abies</i>	<i>Picea abies</i> (L.) Karst.	ITIS	Tree
<i>Picea exelsa</i>	<i>Picea abies</i> (L.) Karst.	ITIS	Tree
<i>Picea obovata</i>	<i>Picea obovata</i> Ledeb.	Tropicos	Tree
<i>Pinus</i> sp.	<i>Pinus</i> sp.	ITIS	Ambiguous
Pinaceae	Pinaceae	ITIS	Ambiguous
Pinaceae gen.	Pinaceae	ITIS	Ambiguous
<i>Pinus pumila</i>	<i>Pinus pumila</i> (Pall.) Regel	Tropicos	Shrub
<i>Pinus sibirica</i>	<i>Pinus sibirica</i> Du Tour	Tropicos	Tree
<i>Pinus sylvestris</i>	<i>Pinus sylvestris</i> L.	ITIS	Tree
<i>Populus suaveolens</i>	<i>Populus suaveolens</i> Fisch.	Tropicos	Tree
<i>Populus tremula</i>	<i>Populus tremula</i> L.	ITIS	Tree
<i>Salix</i>	<i>Salix</i>	ITIS	Ambiguous
<i>Salix</i> sp.	<i>Salix</i> sp.	ITIS	Ambiguous
<i>Salix</i> sp. Vegetative remains	<i>Salix</i> sp.	ITIS	Ambiguous
<i>Salix</i> ex gr. herbaceaL.	<i>Salix herbacea</i> -type	ITIS	Shrub
<i>Salix herbacea</i> L.	<i>Salix herbacea</i> L.	ITIS	Shrub
<i>Salix nummularia</i>	<i>Salix nummularia</i> Anderss.	ITIS	Shrub
<i>Salix polaris</i>	<i>Salix polaris</i> Wahlenb.	ITIS	Shrub
<i>Salix</i> cf. <i>pulchra</i>	<i>Salix</i> cf. <i>pulchra</i>	ITIS	Shrub
<i>Salix rosmarinifolia</i>	<i>Salix rosmarinifolia</i> L.	Tropicos	Shrub
<i>Salix rotundifolia</i> Trenty	<i>Salix rotundifolia</i> Trautv.	ITIS	Shrub

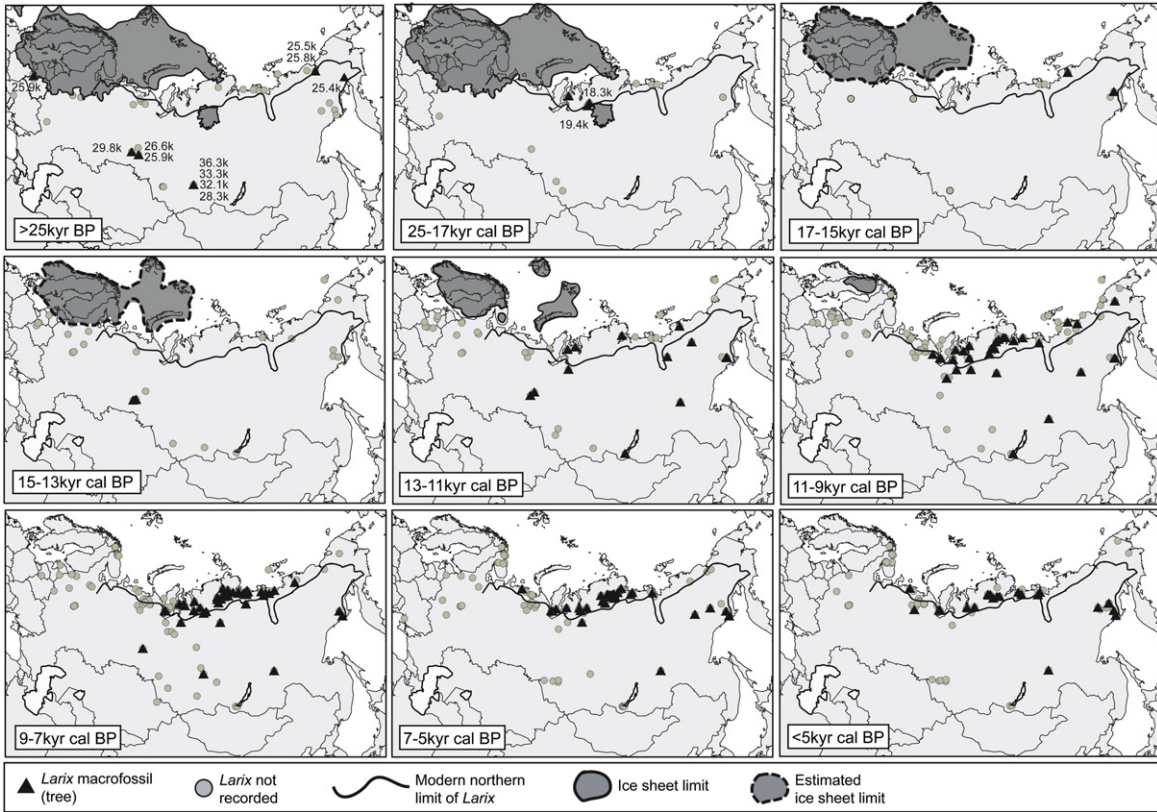


Fig. 2. Distribution of *Larix* macrofossils. Grey circles show location of sites where macrofossil data exist for a time slice but where *Larix* is not recorded. The solid line represents the modern northern limit of *Larix* sp.

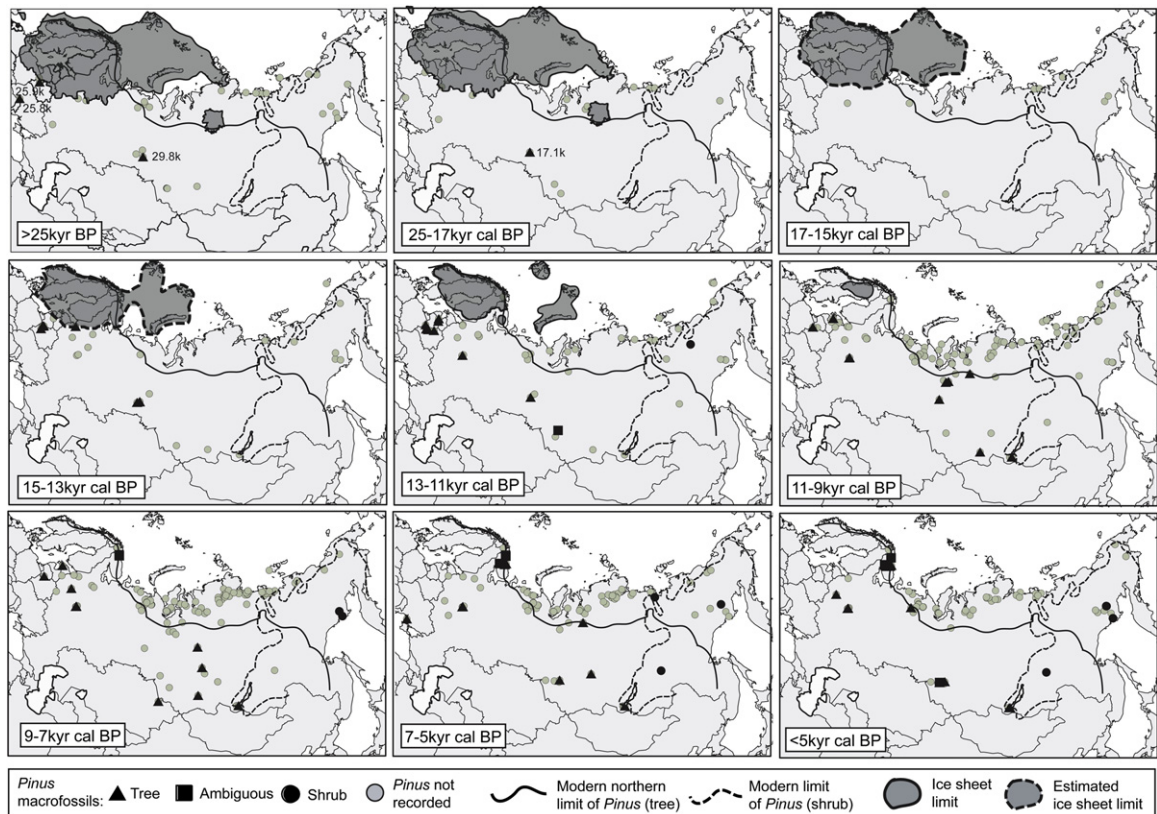


Fig. 3. Distribution of *Pinus* macrofossils. Grey circles show location of sites where macrofossil data exist for a time slice but where *Pinus* is not recorded. The solid line represents the modern northern limit for *Pinus* trees and the dashed line represents the western and northern limit for *Pinus* shrubs.

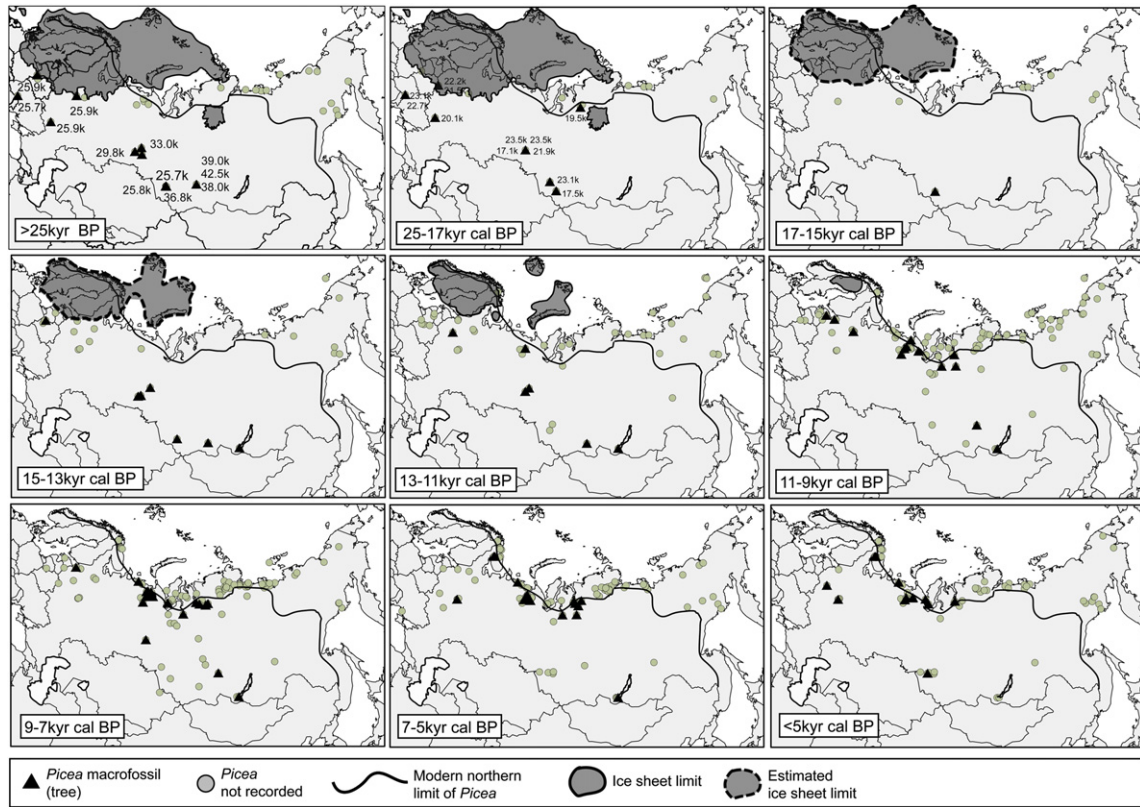


Fig. 4. Distribution of *Picea* macrofossils. Grey circles show location of sites where macrofossil data exist for a time slice but where *Picea* is not recorded. The solid line represents the modern northern limit of *Picea* sp.

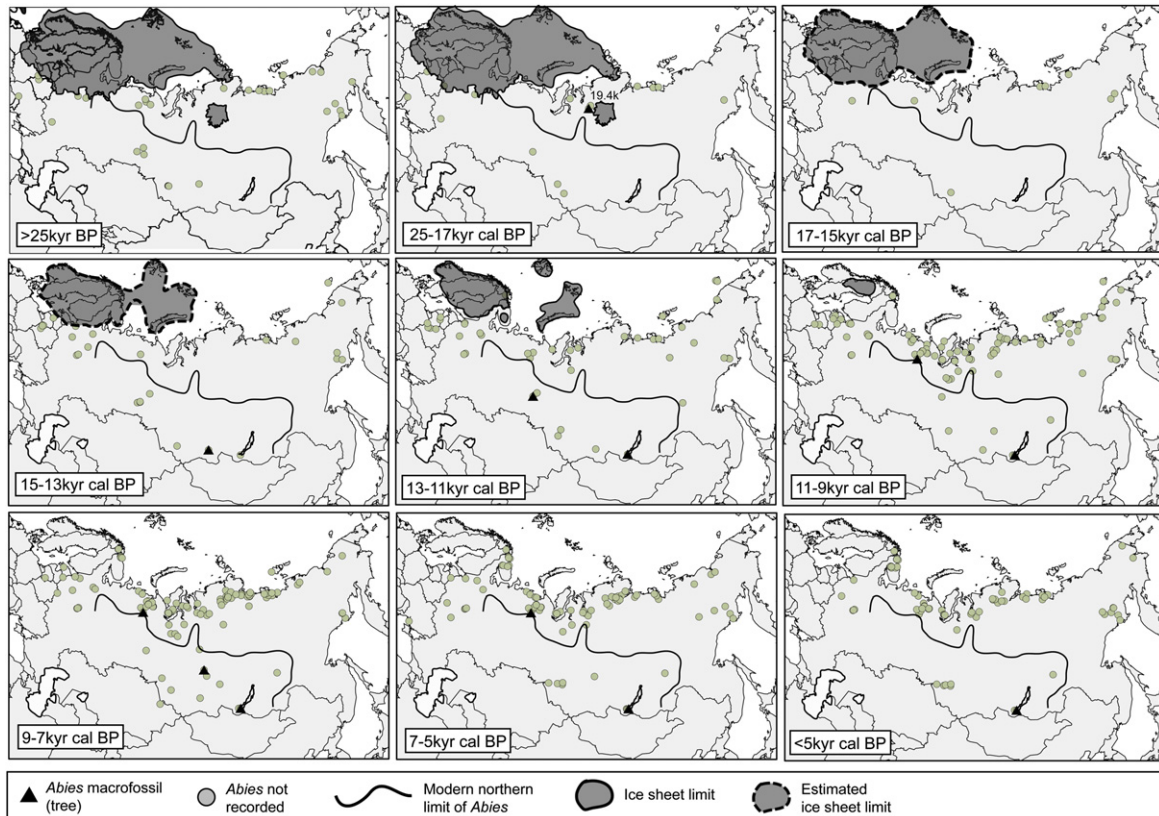


Fig. 5. Distribution of *Abies* macrofossils. Grey circles show location of sites where macrofossil data exist for a time slice but where *Abies* is not recorded. The solid line represents the modern northern limit of *Abies* sp.

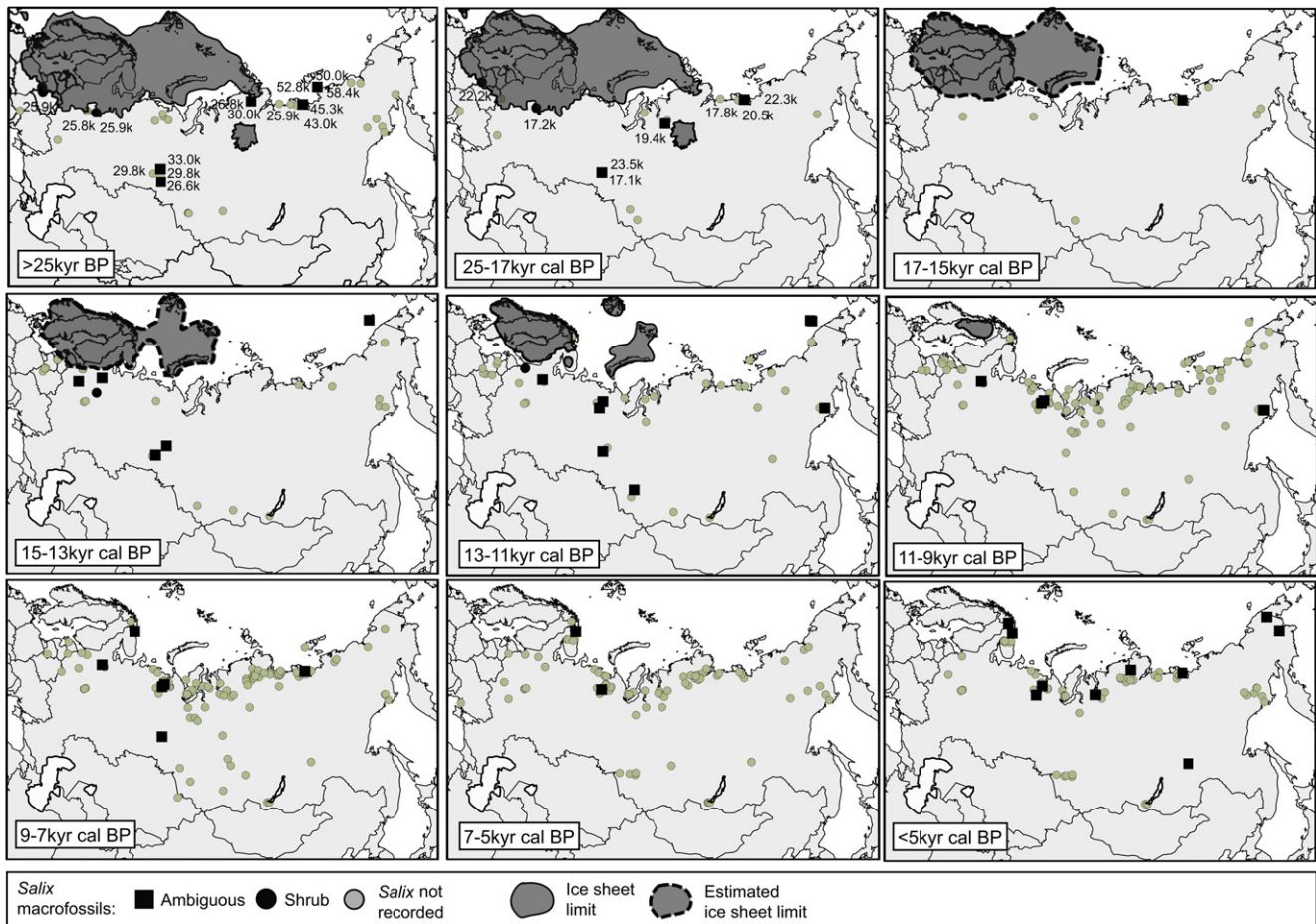


Fig. 6. Distribution of *Salix* macrofossils. Grey circles show location of sites where macrofossil data exist for a time slice but where *Salix* is not recorded.

herbaceous tundra dominated by cushion plants (Walker et al., 2002). The boreal and arctic zones are characterized by extensive wetlands. For a more detailed description of the environments and vegetation of northern Eurasia see Tarasov et al. (2007).

3. Materials and methods

Following Jackson et al. (1997), our database includes macroscopic plant parts, ranging in size from logs and stumps of trees to fruits and seeds and derived from a range of depositional environments. Most samples were retrieved from the sediments of small lakes, mires, or a range of deposits in exposed sections along river courses: most often palaeosol or peat layers, occasionally fluvial sediments. Data came either from the published literature or from unpublished material contributed by co-authors during a workshop held in March 2007 with the specific aim of constructing the database. Information was either transferred from extant databases, or entered newly from laboratory notes or unpublished files into spreadsheets and thence to the new database.

The database will be publicly available from the University of Oxford (<http://www.geog.ox.ac.uk/research/biodiversity/lel/NEMD.html>) with ghost sites located on the IGBP-PAGES and QUEST websites.

3.1. Database

The database uses Microsoft Access (2003) and is based upon a Site-Entity-Sample structure, similar to that used by the European

Pollen Database (<http://www.europeanpollendatabase.net/>). Each Site is defined by name and spatial coordinates, and a site may comprise one or more Entities. An Entity can represent a sediment core or individual samples such as stumps or logs. The Sample Table includes a calibrated age assigned for each sample (where possible) with notes for further explanation. The Dating Info Table includes information on radiocarbon samples and the calibrated ages assigned to the radiocarbon dates. If the dates are from a stratigraphic sequence, an age model was constructed outside the database (details below).

Metadata such as basin size, catchment area and site type (for example whether the site is a lake or a peat deposit) are all linked within the database to the Site and Entity Tables. Information on the type of macrofossil organ is recorded (138 different organ descriptions available) and type of quantification (for example: presence/absence, 5-point abundance scale, etc.). Electronic Appendix A contains a complete site list, with spatial coordinates and bibliographic reference/author details.

3.2. Taxonomy

The taxonomy was checked against a currently accepted taxonomic list (Integrated Taxonomic Information System [<http://www.itis.gov/>]) and others such as TROPICOS, Kew and iPIK as necessary. Where appropriate, regional nomenclature was changed to conform to these lists, for example, *Duschekia fruticosa* is renamed *Alnus fruticosa*. However, the original taxonomic identifications are preserved within the database alongside the revised names (if

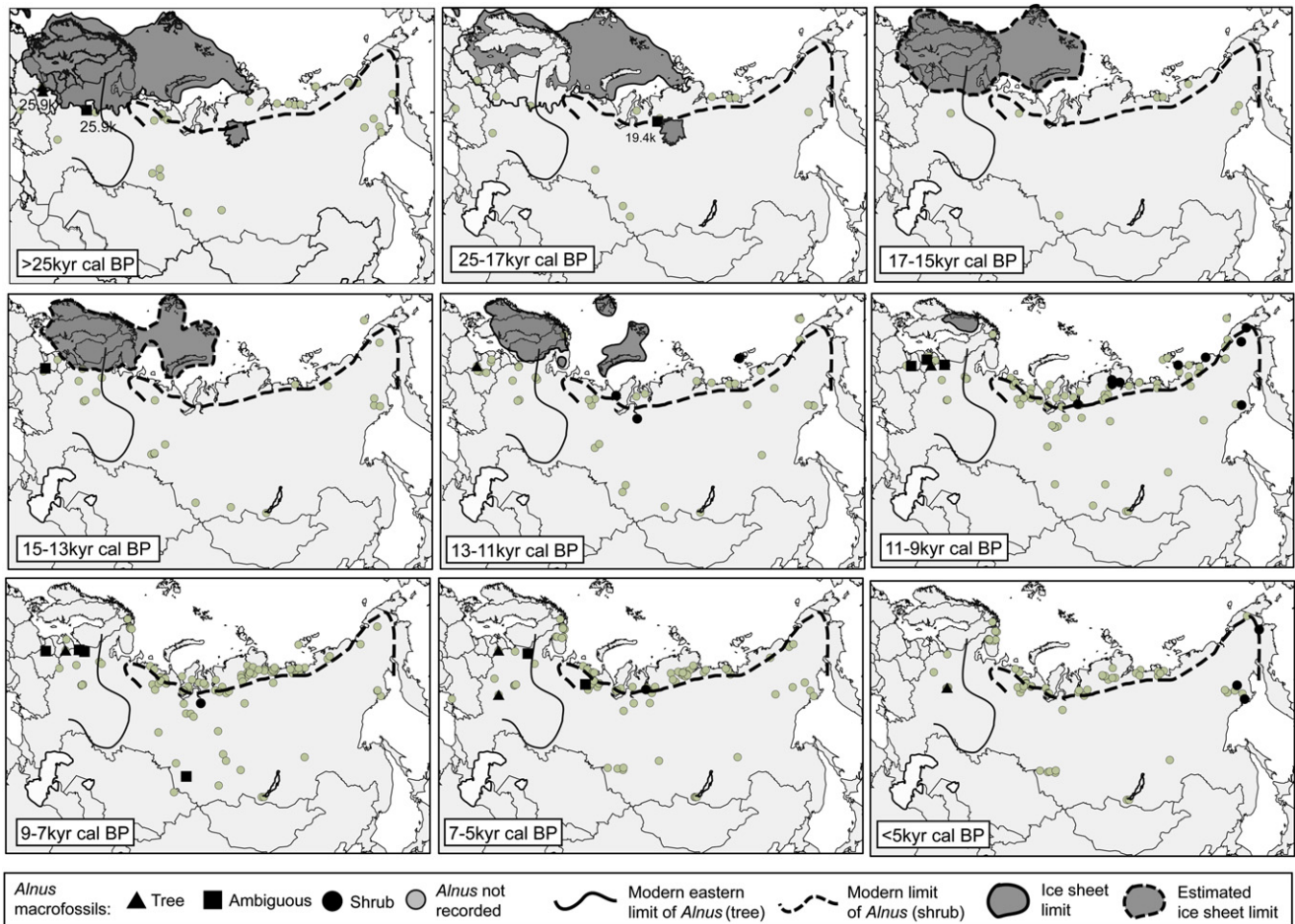


Fig. 7. Distribution of *Alnus* macrofossils. Grey circles show location of sites where macrofossil data exist for a time slice but where *Alnus* is not recorded. The solid line represents the modern eastern limit for *Alnus* trees and the dashed line represents the northern limit for *Alnus* shrubs.

applicable) to track any changes made. Table 1 lists the woody taxa identified in the database, including synonyms. The qualifiers “type” and “cf” are used, respectively, if a macrofossil could not be used to distinguish among two or more species or if the identification was uncertain, for example, because of poor preservation.

3.3. Calibration and age-depth modelling

Samples were either individually ^{14}C -dated or were located within dated sections, for which age models were constructed and ages assigned by interpolation. Age-depth models were constructed as follows. Radiocarbon dates were calibrated using the IntCal04 calibration curve (Reimer et al., 2004) and standard calibration methods (see Stuiver and Reimer, 1993). The midpoints of the 1-standard deviation calibrated ranges were taken as point estimates for the dated levels. Radiocarbon ages older than IntCal04 (>21 kyr ^{14}C BP) and less than 25 kyr ^{14}C BP were calibrated using the Fairbanks curve (Fairbanks et al., 2005). Ages greater than 25 kyr ^{14}C BP were not calibrated and are reported in radiocarbon years (years BP).

When possible, section surfaces (e.g. water–sediment interface, top of modern soil or peat profile) were assumed to be of recent age (AD 2000) and used as an extra data point in regressions. In most cases we used linear interpolation between the data points as age-depth model (Bennett, 1994). Whenever linear interpolation resulted in obviously wrong models (e.g. negative accumulation

rates), we used linear regression instead. For a few records we extrapolated beyond the data points in circumstances where, for example, there is only one radiocarbon date but the data collector is confident the surface is modern (i.e. –50 cal BP) and the section is continuous. Caution should be taken when interpreting these extrapolated ages. Electronic Appendix B provides details of all radiocarbon dates included in the database, their calibration, whether an age model has been constructed and if age estimates for samples have been achieved through extrapolation.

3.4. Geographic location of samples and nature of sediments

Macrofossil finds are dependent upon their depositional context (Jackson et al., 1997; Birks, 2003). In northern Eurasia, much of the dated material is derived from stable surfaces such as palaeosols or accumulations of peat, rather than from detrital deposits or alluvium. However, a few samples have radiocarbon ages and/or assemblages that seem unusual when compared with other samples close in age and location and when viewed in the light of other palaeoecological information. Typically, such samples have dates that were derived from bulk material of fluvial origin that contained macrofossils within it; these are treated with caution.

Landscape position is also critical in the interpretation of macrofossil assemblages because of their generally local origin. Occasionally, wood remains, including *in situ* stumps, have been found in upland situations (e.g. Kullman, 1998, 2003; Krivonogov,

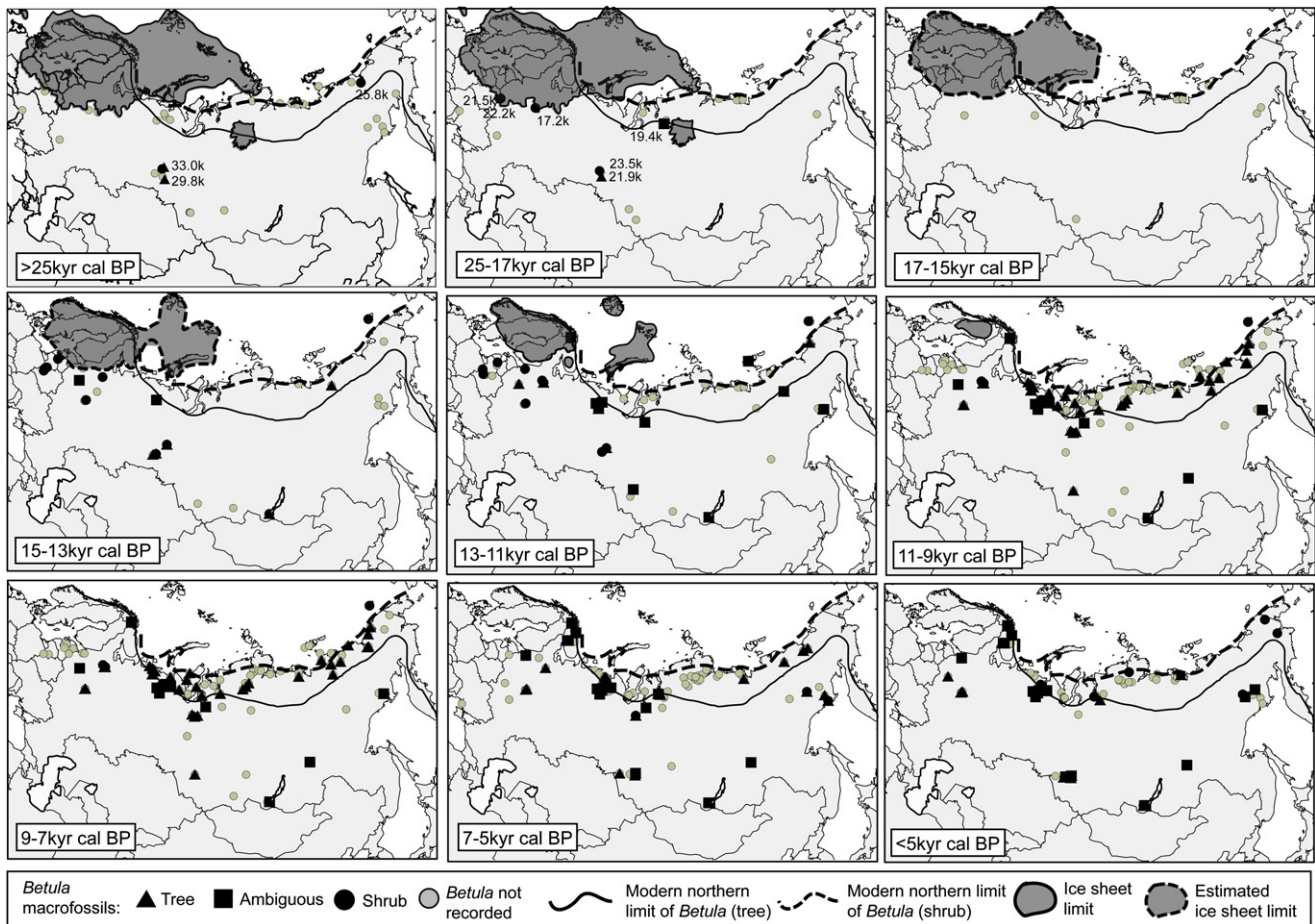


Fig. 8. Distribution of *Betula* macrofossils. Grey circles show location of sites where macrofossil data exist for a time slice but where *Betula* is not recorded. The solid line represents the modern northern limit for *Betula* trees and the dashed line represents the northern limit for *Betula* shrubs.

2001), but more typically wood and other plant remains are derived from river valleys, mires, and lakes, which bias the record towards lowland, mesic situations. Knowledge of depositional context and landscape position of fossil sites is thus critical, particularly for the LGM, when conditions across northern Eurasia were considerably more arid than today (Tarasov et al., 2000). It may be that trees and shrubs occupied climatically unusual azonal environments, and such a pattern would have different implications for both the nature of LGM vegetation in general and Holocene patterns of species expansion. The database also, therefore, contains information on the geography of the collections and their depositional context, as these are essential to an accurate interpretation of the data. We used a 3-type categorization for reporting the 'position on the landscape' of the fossil or deposit. The categories are, i) deposits/fossils located in or near a river floodplain; ii) deposits/fossils located on an interfluvium (region of higher land between two rivers that are part of the same drainage system) or iii) deposits/fossils located within a lowland lake-dominated plain; this refers to large, predominantly flat landscapes of northern Siberia.

The deposits themselves were usually described as i) terrestrial, which refers to peat (cored or sampled from exposures), loess and palaeosols, and material retrieved from yedoma (ice-rich and often rapidly accumulated silty sediments of northern Siberia (Romanovskii et al., 2000)); ii) lacustrine, which includes sediments of extant lakes and ancient lake deposits revealed in exposures; or iii) fluvial/alluvial. Virtually all exposures are natural, cut by river action or lying along the coast.

3.5. Mapping

Pollen data have typically been mapped at 1000-year time slices (e.g. Huntley and Birks, 1983; Giesecke and Bennett, 2001; Williams et al., 2004), as this temporal scale resolves patterns of (postulated) migration and changes in taxon distributions. Macrofossil data are scarcer in time and space. Jackson et al. (1997) chose to map macrofossils at 3000-year intervals using a 2000-year window in the pre-Holocene period and a 1000-year window in the Holocene. The region represented in the northern Eurasian database is far larger and the records are more scattered in time and space than in their eastern North America study. For many taxa such mapping intervals would be inappropriate. In this paper, we focus on key woody taxa that are relevant to the issues of glacial refugia and treeline dynamics, and these are organized into two kinds of time-window: i) those of variable length that represent periods of relative climate uniformity (25–17 kyr cal BP, the LGM; <5 kyr cal BP, the late Holocene) or that are poorly represented by samples (>25 kyr B.P.), and ii) 2000-year intervals that cover the climatically dynamic deglacial period and the first half of the Holocene. Sample ages are binned into 2000-year periods without reference to the error on the calibrated age estimate. In the case of structurally variable taxa, ambiguous and unambiguous samples were mapped separately. For example, samples assigned to *Betula pubescens* and *Betula fruticosa* are tree and shrub species, respectively, but those assigned to *Betula* and *Betula* sp. are structurally ambiguous. Table 1 indicates how morphology was assigned to taxa.

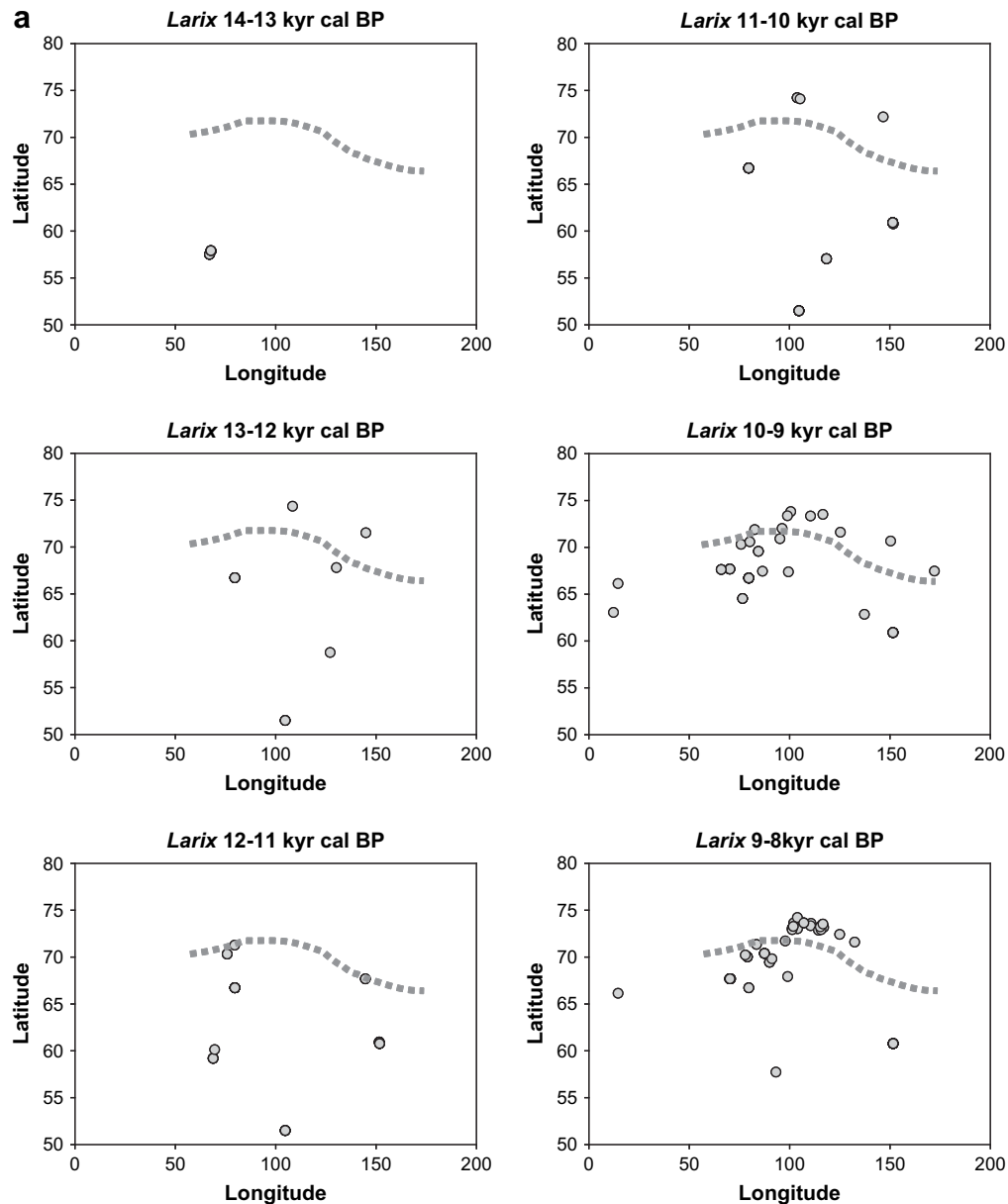


Fig. 9. Lateglacial and early-Holocene tree distributions. The dotmap series show records for *Larix* (9a), tree-*Betula* (9b), *Pinus* (9c) and *Picea* (9d). The dashed lines indicate the modern range limits for each taxon.

The maps are produced in ArcGIS 9 using a World Equidistant Conic projection. The ice limits for >25 kyr BP, the LGM (25–17 kyr cal BP), the Lateglacial (15–13 kyr cal BP), the Younger Dryas (13–11 kyr cal BP) and the early Holocene (11–9 kyr cal BP) are based upon those proposed by Ehlers and Gibbard (2004) and implemented in the GIS using masks created by Jürgen Ehlers. The ice limits for 17–15 ka cal BP and 15–13 ka cal BP have been estimated by the authors and are presented only as a guide for comparison with the presence of macrofossils.

4. Results

There are 281 sites and 684 entities in the database with records for 2317 samples and over 13,000 individual plant macrofossils (see Fig. 1 for locations of the sites). In this paper we focus on the preliminary patterns to emerge from the records of woody taxa, namely the conifers *Larix*, *Pinus* and *Picea*, and *Abies* (Figs. 2–5) and

the hardwoods and shrubs *Salix*, *Alnus* and *Betula* (Figs. 6–8). We also differentiate between the form (tree and shrub) where data are available. The northern limits of *Larix*, *Picea*, *Abies* (tree form) and *Pinus*, *Picea*, *Alnus* and *Betula* (both tree and shrub forms) are also indicated on the figures (after Hultén and Fries, 1986; Kremenetski et al., 1998a,b). For each time slice, the pale grey circles indicate locations of sites where macrofossils are recorded for this time period but the records do not include the taxon under consideration.

4.1. The conifers

In general, the late-Holocene macrofossil distributions of the conifers map well on to current distributions. The following descriptions are taxonomic specific patterns identified from the figures.

Larix (larch): *Larix* sp. (tree), *Larix gmelini* (tree), *Larix sibirica* (tree).

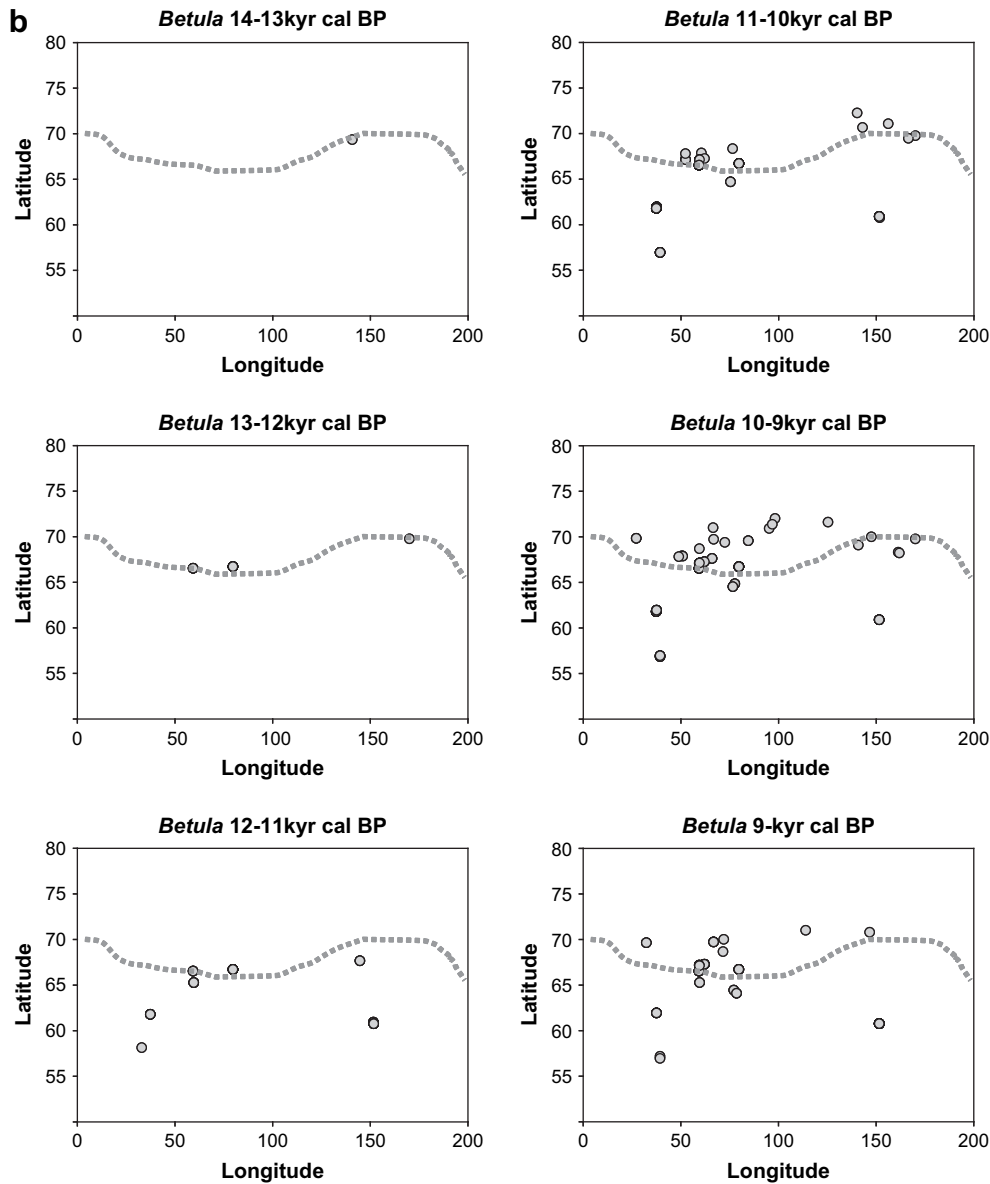


Fig. 9. (continued).

The earliest records of *Larix* in the database (Fig. 2) occur between ~25 and 36 kyr BP and cover a wide geographical range. During the LGM *Larix* macrofossils are reported only from the Taymyr Peninsula and beyond the current northern treeline. More macrofossils are dated to between 13 and 11 kyr cal BP, particularly along the northern coastline. In the early-Holocene *Larix* is widely distributed and well represented in northern regions with a subsequent reduction in the northern limit of *Larix* macrofossils during the past 5000 years.

Pinus (pine): *Pinus* sp. (ambiguous), *Pinus sibirica* (tree), *Pinus sylvestris* (tree) *Pinus pumila* (shrub).

There is macrofossil evidence for the presence of pine in the pre-LGM (>25 kyr BP) (Fig. 3). Sites are in the southern West Siberian Plain and from the Ukraine and Belarus; the latter were relatively close to the maximum extent of the ice sheet. No *Pinus* macrofossils of LGM age have been found (although there is one macrofossil dated to 17.1 kyr cal BP). However, macrofossil evidence indicates that *Pinus* occurred early in the Holocene in northern Finland.

Picea (spruce): *Picea abies* (tree), *Picea obovata* (tree), *Picea* sp. (tree)

Macrofossil remains of *Picea* dating to prior to the LGM are found at a number of sites at the southern edge of the West Siberian Plain and on the East European Plain (Fig. 4). There is also evidence for the presence of *Picea* at a number of sites during the LGM, including some very close to the edge of the ice sheet at its maximum extent. By the early-Holocene, the distribution of *Picea* has reached its northern and eastern limits.

Abies (fir): *Abies sibirica* (tree), *Abies* sp. (tree)

Abies macrofossils are poorly represented in the database and it is difficult to draw any conclusions from the macrofossil evidence alone (Fig. 5). There is one sample of *Abies* during the LGM time slice (19.4 kyr cal BP) and only a sparse record of macrofossil occurrences is apparent from 15 kyr cal BP to present; the majority of these are in more southerly locations.

4.2. Hardwoods and shrubs

Salix (willow): *Salix herbacea* (shrub), *Salix nummularia* (shrub), *Salix polaris* (shrub), *Salix rosmarinifolia* (shrub), *Salix rotundifolia* (shrub), *Salix* sp. (ambiguous).

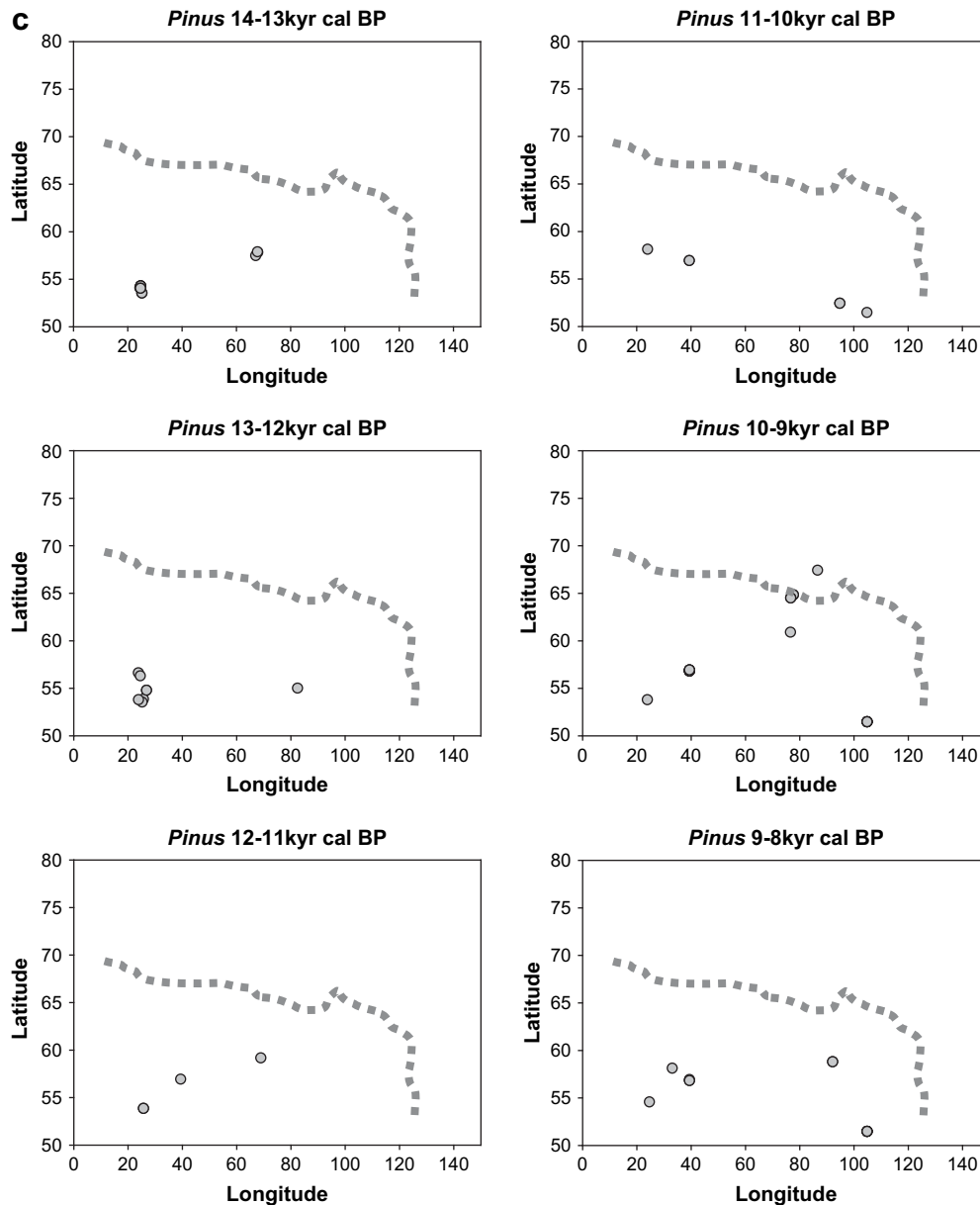


Fig. 9. (continued).

Leaves of the large shrub taxon *S. rosmarinifolia* dating between c. 33 kyr BP and 26 kyr BP have been identified from the southern West Siberian plain (Fig. 6). The remaining macrofossils in subsequent time slices are mainly identified to genus level and are therefore ambiguous in their growth form or they are shrubs. There is, however, an almost continuous record of *Salix* across the region from before the LGM to the present.

Populus (poplar): *Populus suaveolens* (tree), *Populus tremula* (tree) (taxon not mapped).

No records of poplar macrofossils date to the LGM, and the subsequent relatively sparse macrofossil record between 13 kyr cal BP to present is difficult to interpret other than indicating Lateglacial/Holocene presence in Eurasia.

Alnus (alder): *Alnus* sp. (ambiguous), *A. fruticosa* (shrub), *Alnus glutinosa* (tree), *Alnus incana* (ambiguous).

For the period >25 kyr cal BP two macrofossils of *A. glutinosa* are reported from Belarus (both c. 25.9 kyr cal BP) and one sample of *A. incana* (25.9 kyr cal BP) (Fig. 7). During the LGM an *Alnus* sp. fossil

from west of the Putorana Plateau is dated to 19.4 kyr cal BP. There is also evidence for the shrub *A. fruticosa* and for the presence of the tree *A. glutinosa* in Belarus during the period 13–11 kyr cal BP. During the early-Holocene there was a significant increase in the occurrence of shrub *Alnus* macrofossils, particularly along the northern coastline after ~10 kyr cal BP.

Betula (birch): *Betula* sp. (ambiguous), *Betula* cf *fruticosa* (shrub), *Betula divaricata* (shrub), *B. fruticosa* (shrub), *Betula humilis* (shrub), *Betula nana* (shrub), *Betula nana* ssp. *nana* (shrub), *Betula* sect. *Nanae* (shrub), *Betula* sect. *Fruticosa* (shrub), *Betula pendula* (tree), *Betula platyphylla* (tree), *B. pubescens* (tree), *Betula* sect. *Costatae* (tree), *Betula pubescens* ssp. *tortuosa* (tree)

Although macrofossils of *Betula* are relatively common in the database, many are identified only to genus level and therefore are plotted as having an ambiguous growth form (Fig. 8). The oldest *Betula* macrofossils are from western Siberia and include the earliest occurrence of the tree form of birch (*B. pubescens*) (c. 33.0 kyr cal BP). During the LGM *B. nana* was located close to the Scandinavian ice

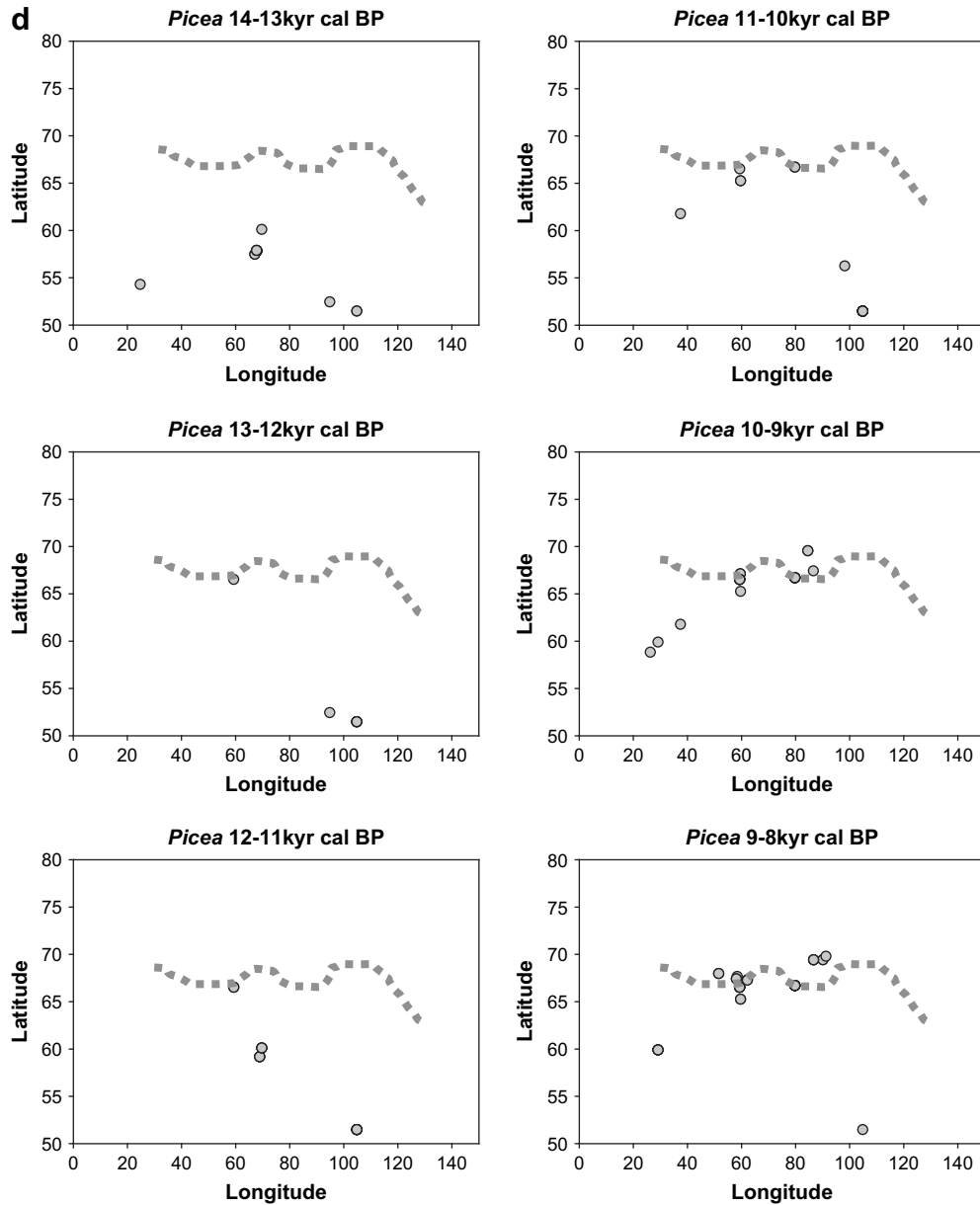


Fig. 9. (continued).

sheet (c. 22 kyr cal BP) but there is a marked absence of any *Betula* macrofossils for the period 17–15 kyr cal BP. *Betula* fossils of early-Holocene age are common along the northern coastline, some of which are attributable to tree forms and beyond today's treeline.

4.3. Treeline dynamics

When the temporal records of *Larix*, *Betula*, *Pinus*, and *Picea* are plotted against latitudinal and longitudinal distribution in

1000-year time slices (Fig. 9a–d), variable patterns are evident. From ~13 kyr cal BP (Fig. 9a) *Larix* is recorded across its current range and, notably, beyond modern treeline. Tree-*Betula* records suggest its presence at its northern limit by 13 kyr cal BP, and they show a major expansion beyond current limits between 11 and 8 kyr cal BP (Fig. 9b; see also discussion in Kremenetski et al., 1998b). In contrast, all records of *Pinus* (Fig. 9c) are located considerably south and west of its present limits until ~10 kyr cal BP. *Picea* (Fig. 9d) is recorded at its current limit at one locality at

Table 2
Landscape position of Entities in the database.

	Terrestrial (peat, palaeosols, material retrieved from yedoma)	Lacustrine (extant and ancient lakes)	Fluvial/alluvial	Unclear	Total	% of total
In or near a river floodplain	131	4	23	0	158	55.44%
Interfluvial	35	2	1	0	36	12.63%
Lowland lake plain	44	28	3	0	75	26.32%
Unclear	15	1	0	0	16	5.61%

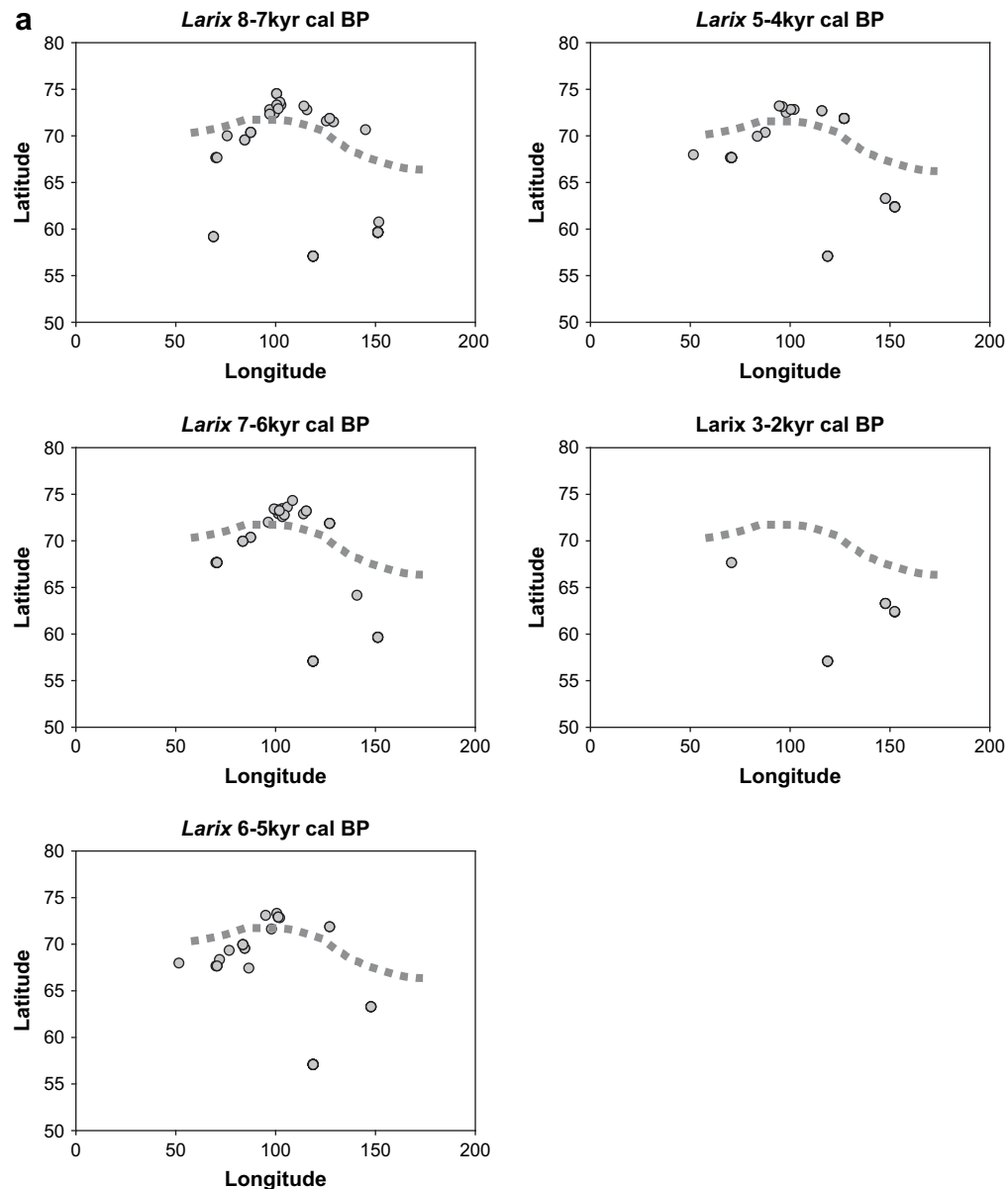


Fig. 10. Late-Holocene tree distributions for *Larix* (10a), tree-*Betula* (10b), *Pinus* (10c) and *Picea* (10d). The dashed lines indicate the modern range limits for each taxon.

13–11 kyr cal BP, although the overall pattern suggests expansion northward to beyond its current limits in the early Holocene.

5. Discussion

5.1. Depositional contexts of the macrofossils

Examination of the different landscape positions of Entities in the database (Table 2) reveals that ~55% are from floodplain deposits or close to flood plains. Many localities from northern Siberia are located in flat lowlands with many small meandering streams and thaw lakes, or other types of lakes, these comprise ~26%. Approximately 13% of sites are listed as upland or on interfluvies. For ~6% of sites there is insufficient information to determine their landscape position. There is, therefore, some bias in the record towards lowland and river-valley locations. This may partly reflect more collections from river systems, but there is also a temporal pattern to site locations (see below).

Fig. 11 shows a breakdown of the samples with woody taxa into the landscape position of the site and the type of deposit using the same time slices as for the taxon maps. For the period >25 kyr BP, 69% of tree macrofossil samples are located on interfluvies and 28% are in or near a river floodplain. This predominance of interfluvie sites for the period >25 kyr cal BP reflects collections largely from yedoma complexes. During the LGM (25–17 kyr cal BP), all the samples of trees are from samples located in or near a river floodplain. For the period 17–15 kyr cal BP, there are only four tree macrofossils, of which three are located in or near a river floodplain and one is of unknown position. For subsequent time slices all types of landscape position are represented in the samples. Late-Holocene distribution patterns map well onto the areas where these taxa currently dominate the boreal forest: *Larix* and *P. pumila* in eastern Siberia, and *Picea* and *Pinus* in Europe and Western Siberia. However, for the period 25–17 kyr cal BP, a dominance of river-valley locations might suggest trees persisted in ‘cryptic refugia’ (e.g. Stewart and

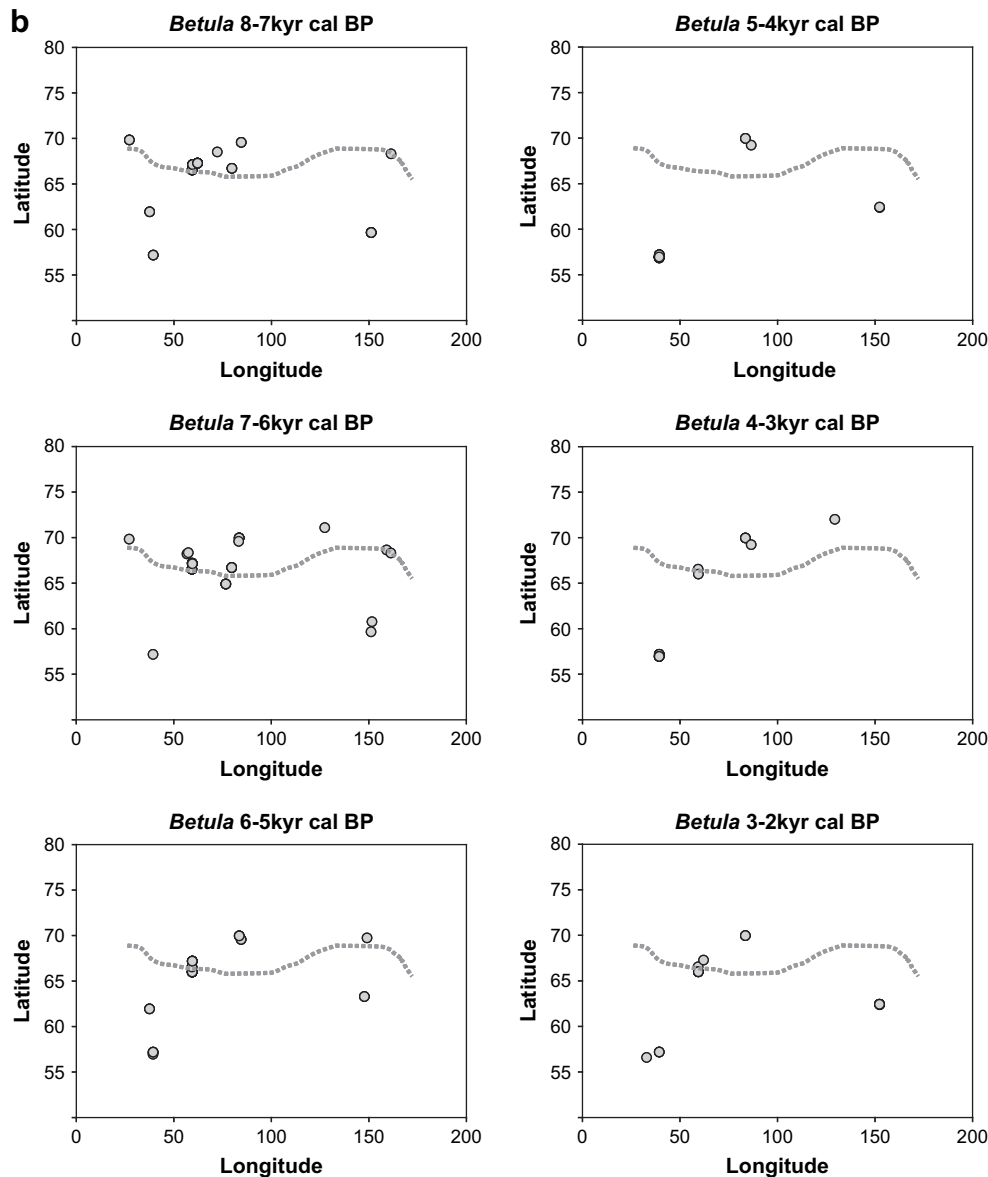


Fig. 10. (continued).

Lister, 2001), where growing conditions were locally more sheltered and/or moister than typical for the time.

5.2. Lateglacial refugia and migration rates

Results from this macrofossil database clearly demonstrate the existence of some woody taxa during the full glacial in Northern Europe and Eurasia, including *Picea*, *Larix*, *Pinus*, *Alnus* and *Betula*. A number of previous fossil and genetic studies have suggested the possibility of these taxa being located in refugia in the periglacial zone of central and eastern Europe. Grichuk (1984) suggests that a complex of tundra, steppe and forests of *Larix*, *Pinus* and *Betula* existed very close to the edge of the Scandinavian ice sheet and extended far into eastern Siberia. Similarly, Frenzel et al. (1992) proposes that scattered refugial populations of boreal coniferous and deciduous trees existed in southern and central Siberia during the LGM. Brubaker et al. (2005) examined pollen evidence for the presence of boreal trees during the LGM in Beringia (NE Siberia and NW North America). They conclude that the postglacial migration

rates for some of the taxa may have previously been over-estimated and that small populations of boreal trees and shrubs may have had existed in small refugial populations during the LGM. Tarasov et al. (2007) quantitatively reconstruct tree cover density using pollen data from the LGM in northern Asia. The reconstructions are based upon the observed agreement between modern pollen data and remotely sensed tree cover estimates and indicate relatively low tree cover density during the LGM but not the complete absence of trees.

Each taxon is briefly discussed in turn below.

5.2.1. *Larix*

While there are only scattered records for *Larix* from the LGM and just prior to the LGM, the pattern is still northerly, suggesting the *in situ* survival of *Larix* in northern regions throughout the glacial maximum (Fig. 2). This concurs with earlier work by Anderson et al. (2002) and Brubaker et al. (2005), who, from mapped pollen data, concluded that *Larix* persisted in eastern Siberia since the LGM.

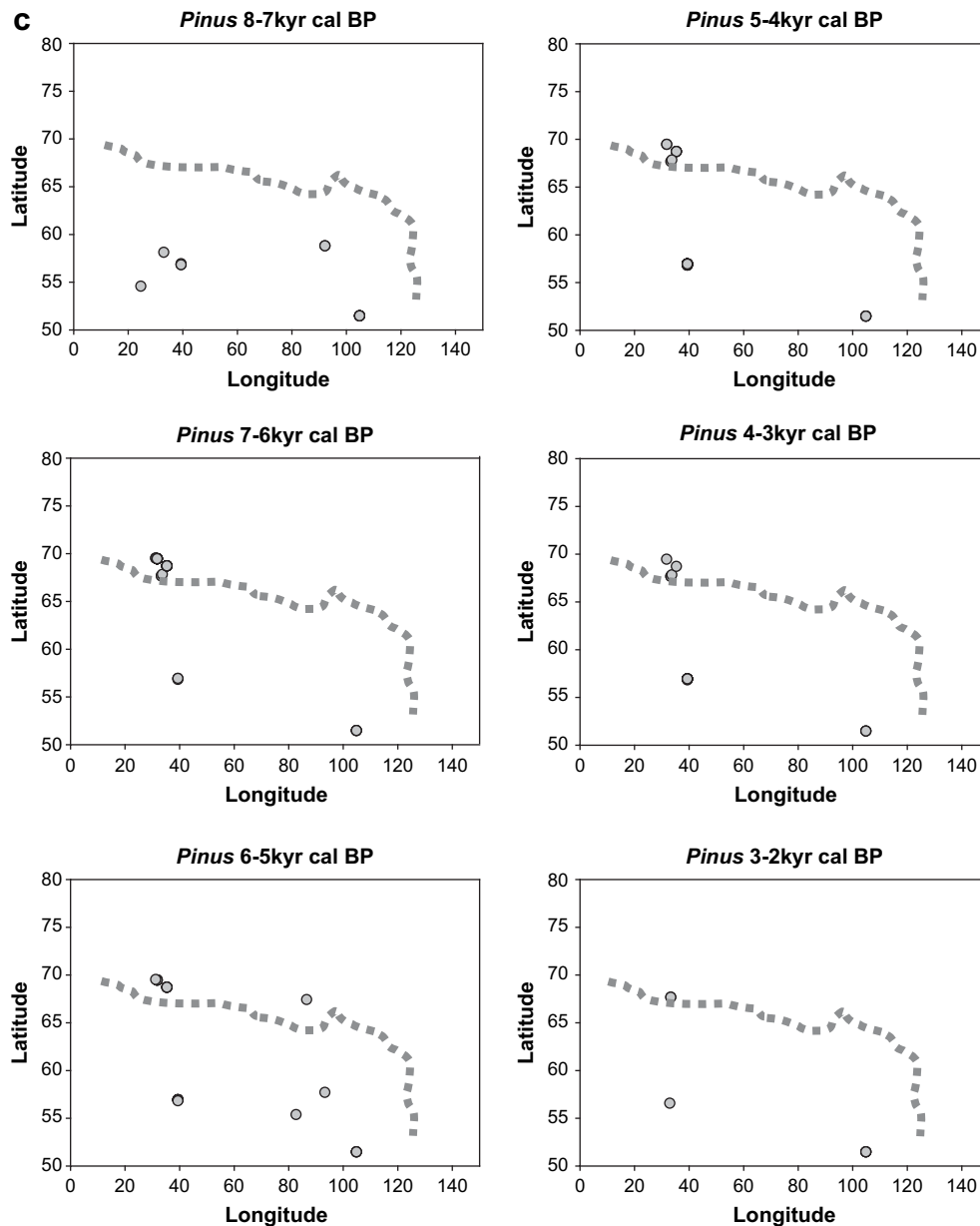


Fig. 10. (continued).

5.2.2. *Pinus*

Pinus is recorded in the database at scattered localities in Europe and southwest Siberia prior to the LGM, in southwest Siberia during the LGM and again in Europe and southwest Siberia during the Lateglacial (~15–13 kyr cal BP) (Fig. 3). This result is in agreement with evidence for the presence of *Pinus* pollen in many LGM pollen records in central, eastern and northern Europe (for a review, see Willis et al., 1998). However, due to the long-distance dispersal and prolific production of this pollen type, their full-glacial northerly extent has until now remained unclear. Recent evidence of early postglacial fossil stomata in Scotland, 1600 and 600 years prior to the arrival times indicated by traditional palynological methods has indicated the possibility of northerly European refugia (Froyd, 2005). Also, work by Cheddadi et al. (2006), who used an extensive dataset of pollen and macrofossil remains of *P. sylvestris* in combination with genetic evidence and a vegetation model to simulate the extent of the potential refugia during the last glacial period, proposed glacial refugia around the

Iberian peninsula and Italy, as well as in the Hungarian Plain and the Danube area (cf Willis et al., 2000; Willis and van Andel, 2004). In the east Carpathian area, charcoal remains also attest to pine stands along the Pruth and Dniester rivers (Dambon and Haesaerts, 2002; Haesaerts et al., 1998; Haesaerts et al., 2003). Genetic work on the phylogeography of the Eurasian pine shoot beetle *Tomicus piniperda*, a species that is presently a pest in pine stands in Eurasia, also shows a clear genetic differentiation between populations found presently in southern Europe and those in western Russia (Ritzerow et al., 2004). From this study, the authors conclude that Western Russia was probably an important full-glacial refugial locality for these beetles, and presumably for the trees associated with them. Our results would support this interpretation.

5.2.3. *Picea*

A review of the European distribution of *Picea* by Ravazzi (2002) led him to propose that the full-glacial refugia of *Picea* sp. were in

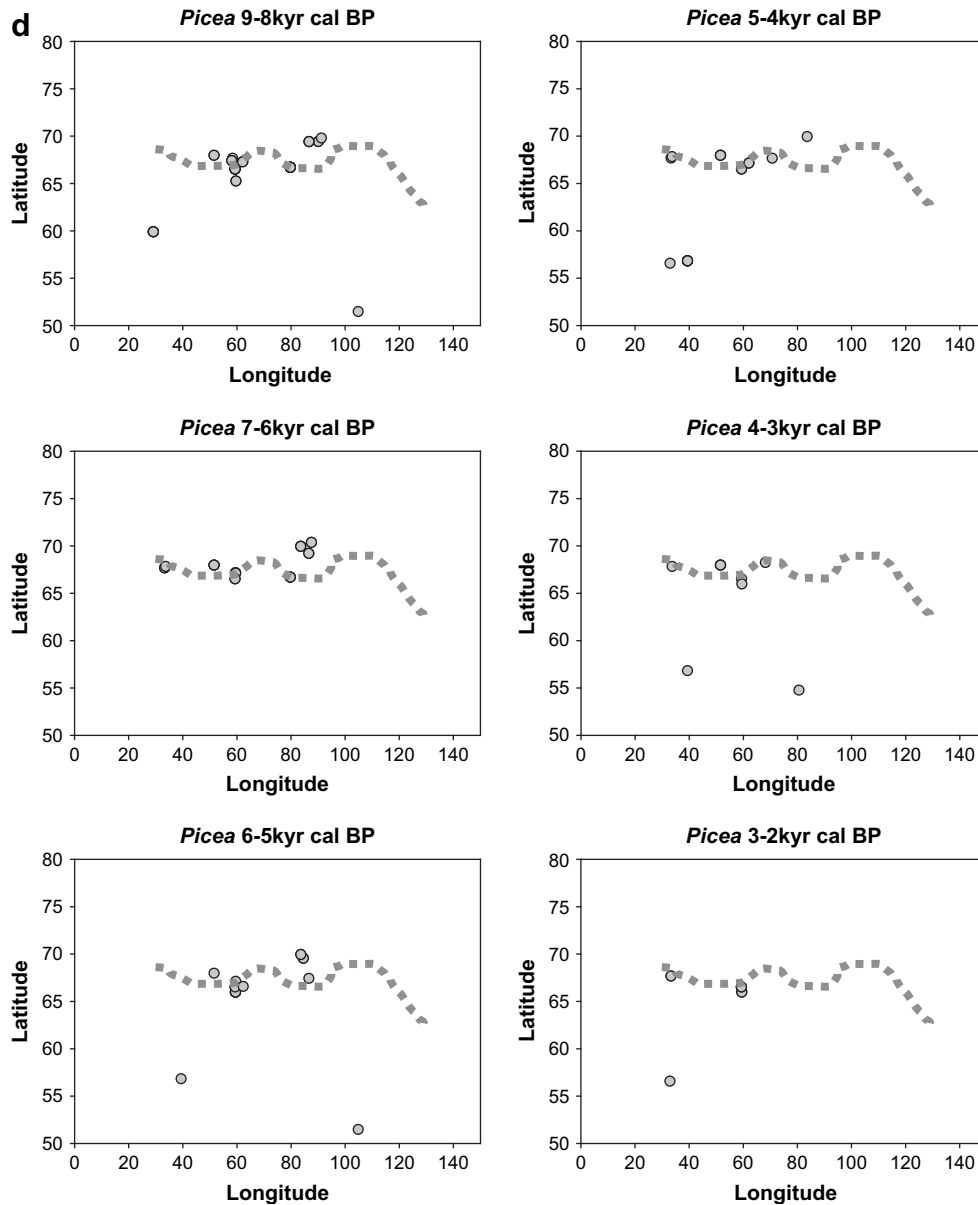


Fig. 10. (continued).

central and eastern Europe. Charcoal and wood remains of *Picea* sp. ranging between 42.5 kyr BP and 26 kyr BP have also been recorded from central Siberian loess deposits and multi-layered organic deposits along the Yenisei river (Haesaerts et al., 2005). There have also been early postglacial macrofossil finds of *Picea* in Scandinavia (Kullman, 2005; but see also Birks et al., 2005). The compiled data provide compelling evidence for widely distributed occurrences of *Picea* through Eurasia before and during the LGM (Fig. 4).

5.2.4. *Alnus* and *Betula*

These are two taxa that often appear in full-glacial pollen diagrams but are usually attributed to long-distance dispersal, reworking or in the case of *Betula*, of shrub forms which today characterise arctic vegetation. However, both types have an interesting genetic structure of present-day populations in Europe. Work by King and Ferris (1998) on *A. glutinosa*, for example, indicates highly structured haplotypes in European populations with a distinctive central and northeastern European type. They

conclude that this was probably indicative of full-glacial refugial isolation in the Carpathian Mountains. Similarly Palme et al. (2003) found that present-day populations of *B. pendula* have a distinctive haplotype structure with five genetic boundaries across Europe including genetically differentiated eastern and western European populations. They conclude that these two regions were repopulated in the early postglacial from populations surviving in refugia in central Europe and that populations in the Iberian Peninsula and in Italy did not take part in the postglacial recolonization of Europe (Palme et al., 2003).

While there are no LGM samples of *A. glutinosa* (Fig. 7), the macrofossil data indicate a presence of *Betula* sp. during the LGM further north than predicted by the genetic evidence: its remains are reported from several places in Siberia between 18 and 11 kyr cal BP as well as pre-LGM. There are also numerous *Betula* fossils apparent along the northern coastline in the early postglacial, and some of these are tree form (Fig. 8) suggesting either very fast postglacial dispersal rates or *in situ* refugia.

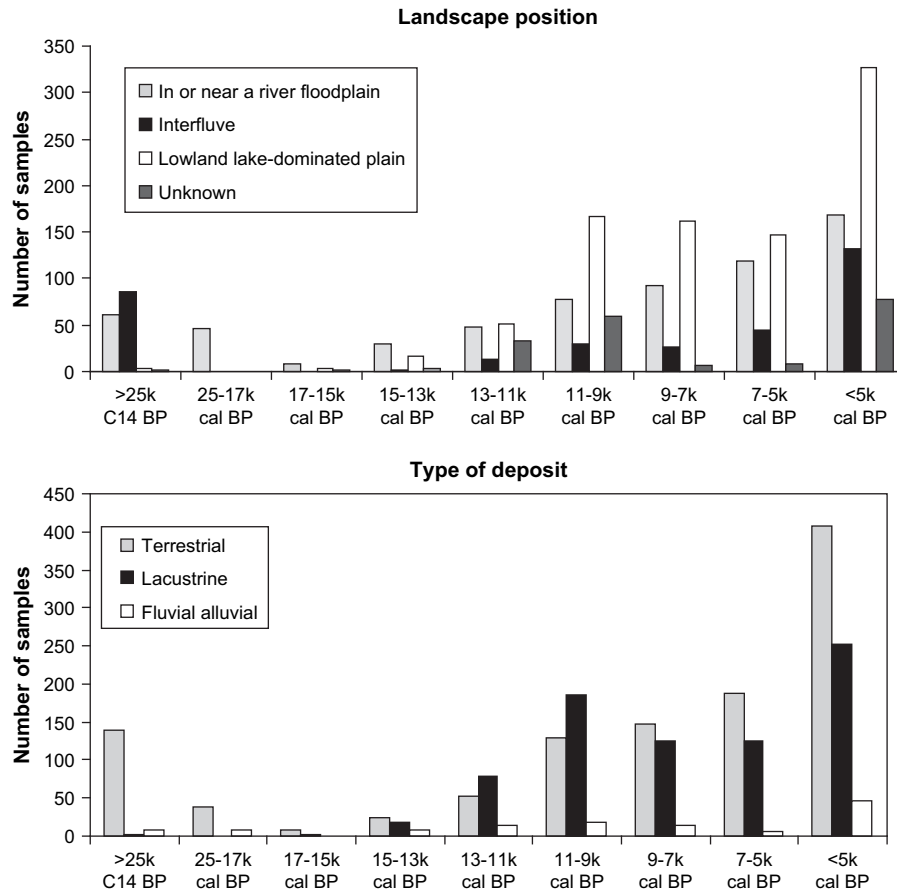


Fig. 11. Comparison of the number of samples for each time slice in terms of a) the position of the site on the landscape and b) the depositional context.

5.3. Lateglacial latitudinal treeline dynamics

The spatial and temporal patterns of forest spread in the Lateglacial and early Holocene inform us about a number of critical issues: tree-species dispersal rates (e.g. Ritchie and MacDonald, 1986; Brewer et al., 2002; McLachlan et al., 2005) the role of refugia as centres of spread and sources of modern genetic diversity (e.g. Brubaker et al., 2005; Anderson et al., 2006; Cheddadi et al., 2006; Bennett and Provan, 2008; Provan and Bennett, 2008); the interaction of climatic controls and tree structural–functional characteristics and hence land-cover characteristics (e.g. Edwards et al., 2005); the interaction of global and regional forcing in driving a heterogeneous circumpolar vegetation response to postglacial warming (e.g. Kaufman et al., 2004; Wohlfarth et al., 2004). The position of the Holocene northern boreal treeline is generally taken to be controlled by growing-degree days, which in turn are governed by hemispheric-scale climate controls (see Prentice et al., 1992; Kaplan et al., 2003); this bioclimatic relationship therefore means that broad-scale reconstructions of treeline position also provide useful benchmarks for evaluating paleoclimate simulations (Edwards et al., 2000; Bigelow et al., 2003; Wohlfarth et al., 2004). Previous pollen- and macrofossil-based studies indicate latitudinal and altitudinal shifts of treeline and overall tree distribution patterns during the Late Quaternary (e.g. Hyvärinen, 1975; Ritchie et al., 1983; Lamb, 1984; Payette and Gagnon, 1985; Lozhkin et al., 1993; MacDonald et al., 1993; Anderson et al., 1997; Tarasov et al., 1998; Kremenetski et al., 1998a,b; Edwards et al., 2000; MacDonald et al., 2000a; CAPE project members, 2001; Andreev et al., 2002, 2009; Bigelow et al., 2003). Such dynamics reflect differences in

climate, physiography and species' ecology and patterns vary among regions.

There are constraints upon pollen-based treeline reconstructions because the relationship between pollen patterns and the treeline position varies with the pollen productivity and dispersal characteristics of treeline species. Thus for high pollen producers, such as many *Pinus* species (though not *P. pumila*: PMA and AVL, personal observation), there is an over-representation of tree pollen beyond treeline. Conversely, under-represented taxa such as *Larix* may not be detected in pollen records even when present in the vegetation. Macrofossils, on the other hand, provide precise spatial information on the past location of trees and can enhance spatio-temporal reconstructions of the past treeline (see MacDonald et al., 2000b; Edwards et al., 2005).

Previous studies using macrofossils to reconstruct past treeline include work by Kremenetski et al. (1998b) and MacDonald et al. (2000a) who collated wood macrofossils and used them to reconstruct broad-scale Siberian treeline dynamics and to examine the pattern and timing of treeline extension beyond current limits, with a focus on western and central Siberia. MacDonald et al. (2000a) equated the oldest reported fossils in their dataset to initiation of forest development 10–9 kyr BP (~12–11 kyr cal BP) and suggested that the treeline behaved synchronously in the Holocene as a result of hemispheric-scale climate forcing. Results from our new database which also includes data from far eastern Siberia, confirm the trends identified (Kremenetski et al., 1998a,b; MacDonald et al., 2000a) but also reveal further details showing that different species exhibit different spatial and temporal patterns.

The deciduous trees *Larix* and *Betula* (Fig. 9a and b respectively) appear to have been able to exist at or beyond their postglacial limits earlier than the evergreen conifers, particularly *Pinus* (Fig. 9c). The form of the *Larix* expansion, at least as indicated by the plots, is rapid extension to beyond its current limits and, possibly, subsequent infilling, although the low number of records makes interpretations of density tentative. Two possible reasons for the early, northerly distribution of deciduous trees are related to different aspects of climate and their interaction with tree function. In the Lateglacial, early summer insolation values were high and generated summer warmth that could have been conducive to tree growth, but the growing season was short (Edwards et al., 2006). Extreme seasonality also characterized this period; thus winters were most likely colder than present. Enhanced continentality due to the exposed Siberian shelf (Bauch et al., 2001), more extensive sea-ice and lower sea surface temperatures (SSTs) (Bartlein et al., 1992) would have exacerbated these extremes. It is also likely that effective moisture was lower; this has been demonstrated for Alaska by Abbott et al. (2000), Barber and Finney (2000), and Barber et al. (2000). These conditions would have likely stressed evergreen conifers to a greater extent than deciduous trees (e.g. Opik and Rolfe, 2005).

Between 10 and 8 kyr cal BP all records suggest a major infilling of the northern forest and *Picea* (Fig. 9d) and *Pinus* (Fig. 9c) rapidly extended their distributions beyond current limits. Extra-limital distributions occur across the whole Eurasian region and all tree-line species (*Betula*, *Picea*, *Pinus*, *Larix*) likely reflect a major environmental change. Given the above arguments, a reduction in seasonality and/or increase in moisture availability may have been involved. There are insufficient macrofossil data to record the dynamics of *P. pumila* in eastern Siberia, but pollen records from the region indicate an expansion of this species beginning at this time (see Lozhkin et al., 1993; Anderson et al., 1997; Kremenetski et al., 1998a; Brubaker et al., 2005).

Deciduous broadleaf taxa that have a largely ambiguous growth form in fossil samples, such as *Salix* and *Alnus*, appear in Eastern Siberia as large woody remains (tree-sized) in the Lateglacial and early postglacial (Edwards et al., 2005). *Salix* remains are recorded at ~11–12 kyr cal BP from northern coast exposures, where now no such large deciduous woody taxa occur (Fig. 6). The largest *A. fruticosa* records from the modern coast region, which is now occupied by herb tundra or prostrate shrub tundra, are dated slightly later, at ~9.5 kyr cal BP; *Alnus* is also reported from the New Siberian Islands (Kaplina and Lozhkin, 1982; Andreev et al., 2009) and is showing a northward extension into central Siberia in the early Holocene (Kremenetski et al., 1998b). Finds of *Betula* logs and other large woody fossils are reported at coastal sites in Russian expedition logbooks from the early 20th century (AVL, personal observation). These finds or similar ones were later dated and fall predominantly in the period ~10.5–8 kyr cal BP. There is also a good macrofossil record of a northern extension of tree-*Betula* in central Siberia (Kremenetski et al., 1998b).

Overall, the record shows that both deciduous and evergreen taxa grew beyond their northern limits in the early Holocene, and that deciduous taxa were an important component of the earliest boreal forest to establish across Siberia. Edwards et al. (2005) have pointed out that a land cover dominated by shrubs the size of small trees is functionally a deciduous forest cover, although through pollen patterns alone, such areas would be classified as tundra.

A late-Holocene retreat of the treeline is also evident in the records (Fig. 10a–d). Kremenetski et al. (1998b) and MacDonald et al. (2000a) describe the boreal forest limit retreating to its present position between 4 and 3 kyr cal BP, the retreat being roughly synchronous across northern Russia. This pattern shows clearly in the *Picea* data (Fig. 10d). In eastern Siberia, *Larix* (Fig. 10a)

retreated marginally from its most northern limits after ~7 kyr cal BP. After this its distribution remained stable, beyond current limits. Like *Picea*, records show it only fell back to its current limits at ~3 kyr cal BP. *Pinus*, on the other hand (Fig. 10c), shows its more expanded distribution in the later Holocene (especially in the west, MacDonald et al., 2000b). Records are insufficient to detect patterns of fragmentation as shown for Quebec by Payette and Gagnon (1985). However, the expansion of wetlands (Smith et al., 2004; MacDonald et al., 2006) must have created forest–wetland mosaics over large regions of northern Siberia as the Holocene progressed, and such changes in forest openness (see Williams et al., 2004) would have implications for the surface energy balance.

6. Conclusions

The Eurasian plant macrofossil database provides new insights into late-Quaternary biogeography and the dynamics of northern tree species in relation to climate change. A key finding from the emergent patterns is that northern refugia most likely existed for some tree species, confirming in several cases other lines of evidence for the persistence for northerly populations. This should stimulate further investigation of new and existing macrofossil and pollen evidence.

Furthermore, the existence of refugial populations of woody taxa further north than previously proposed has interesting implications regarding postglacial migration rates. In Europe, traditional pollen-based estimates of postglacial migration rates usually assume migration from southerly refugia with migration rate estimates of up to 1–2 km year⁻¹ (Huntley and Birks, 1983). However, it is possible that if species had northerly refugial populations, they may have achieved postglacial expansion from local, isolated populations, rather than via long-distance dispersal. For such species, postglacial migration rates may be greatly over-estimated and the ability of the species to track future climate change via dispersal overstated. Similarly, the migration of taxa northwards with increased global temperatures is not entirely comparable with the early Holocene. Today, the landscape north of the treeline is often covered with thick organic soils which hinder the establishment of many of the woody taxa whereas in the early Holocene much of the landscape would have been covered with mineral soils (MacDonald et al., 2008).

We have discussed here only part of the data contained within the database and invite further perusal of the records. Further, the database is open to new additions; many data remain to be reported and archived and have the potential to clarify further the biogeography of this extensive and under-studied region of the northern hemisphere.

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Appendix A. Supplementary information

Sites in the database, spatial co-ordinates and bibliographic reference/author details.

Appendix B. Supplementary information

Radiocarbon samples and dates, calibrated dates and use of age model.

Appendix. Supplementary information

Supplementary information associated with this article can be found, in the online version, at doi: [doi:10.1016/j.quascirev.2009.04.016](https://doi.org/10.1016/j.quascirev.2009.04.016).

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