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The late Pleistocene and Holocene history of *Pinus koraiensis* (Korean Pine) in the south of the Russian Far East based on palynological data

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ABSTRACT. This paper reviews the distribution of *Pinus koraiensis* in the south of the Russian Far East in the past based on palynological and chronological data. The aim is to determine the chronological timing of the spatial migration of *Pinus koraiensis* and to correlate it with climate fluctuations explaining the changes of the geographical range of *Pinus koraiensis* in the south of the Russian Far East during the Marine Isotope Stages MIS 5 (127 000–71 000 BP), MIS 3 (57 000 BP – 28 000 cal BP), MIS 2 (28 000–11 700 cal BP), and MIS 1 (11 700 cal BP – to present). The consideration of the obtained pollen fossil data suggests that the range of *Pinus koraiensis* was in the south of the Russian Far East during MIS 5, as it was proved based on significant pollen grain percentage in the sediments of this age. *Pinus koraiensis* was widespread along with *Pinus densiflora*, *Quercus*, *Ulmus*, *Juglans*, *Carpinus*, and *Phellodendron*. During MIS 3, *Pinus koraiensis* was a component of birch-fir and birch-broadleaved forests. In MIS 2, *Pinus koraiensis* disappeared from the vegetation of this region. In the early Holocene, *Pinus koraiensis* expanded its range northward and again appeared in the vegetation of the south of the Russian Far East. Soon enough, it became one of the leading components in spruce-fir forests with *Quercus* and *Ulmus*. The increase in its proportion in the vegetation in the Holocene coincided mostly with the periods of warming climate from 11 700 to 11 500 cal BP, from 10 100 to 9300 cal BP, from 8800 to 5300 cal BP, from 4700 to 3500 cal BP, and from 2600 to 1800 cal BP. In the present case, the most diverse vegetation with *Pinus koraiensis* was typical of the Holocene optimum of the south of the Russian Far East from 8800 to 5300 cal BP.

KEYWORDS: pollen, *Pinus koraiensis*, spatial and temporal migration of plants, south of the Russian Far East, late Pleistocene, Holocene

INTRODUCTION

Climatic changes during the late Pleistocene and the Holocene resulted in large-scale plant migrations (Birks, 1986; Lang, 1994). A notable migration is that of *Pinus koraiensis* (Korean Pine), one of the main forest-forming species in the south of the Russian Far East, the region where primary forests have been preserved (Krestov, 2003).

The south of the Russian Far East is located in the contact zone of the Amur, Manchurian and North China floristic provinces, where plants characteristic of boreal and warm-temperate zones are common (Komarov, 1949). Therefore, this is a key area for studies on plant migration due to shifting of their distribution ranges caused by fluctuations of climate and environmental changes during the late Pleistocene and the Holocene.

Though the evolution of vegetation in the south of the Russian Far East during the late Pleistocene and the Holocene has been investigated in considerable detail (Alekseyev and Golubeva, 1980; Golubeva and Karaulova, 1983; Korotky, 2002; Pavlyutkin

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and Belyanina, 2002; Mikishin et al., 2008; Razjigaeva et al., 2016; Anderson et al., 2017; Belyanin and Belyanina, 2018), the spatial and temporal migration of plants in the region have not been sufficiently understood so far.

The above is true in particular for the spatial dynamics of *Pinus koraiensis* in MIS 5 (127 000–71 000 BP, MIS 3 (57 000 BP – 28 000 cal BP), MIS 2 (28 000–11 700 cal BP), and MIS 1 (11 700 cal BP – to present). Most likely, it may be attributed to some gaps in the pollen records. Slight changes in the ranges of plants resulting from low-amplitude and short-term climatic fluctuations are difficult to record. Besides, the sediments of the late Pleistocene and early Holocene lie deep from the Earth's surface. All the above interferes considerably with reconstructing paleo-environments and forecasting the evolution of the vegetation in the south of the Russian Far East (Zhang et al., 2014).

Previously, palaeobotanical data were obtained that allowed the reconstruction of the history of *Pinus koraiensis* in the south of the Russian Far East during MIS 1 (11 700 cal BP – to present) (Belyanin and Belyanina, 2019). However, epochs MIS 5 (127 000–71 000 BP), MIS 3 (57 000 BP – 28 000 cal BP), and MIS 2 (28 000–11 700 cal BP) remained outside the field of studies. Recently, palynological data have been obtained and analysed contributing to the more detailed reconstruction of the history of *Pinus koraiensis* in the south of the Russian Far East during the epochs mentioned above.

The present work aims to reconstruct the distribution of *Pinus koraiensis* in the south of the Russian Far East in respect of vegetation history, a geographical range, dispersal, and migration during MIS 5 (127 000–71 000 BP), MIS 3 (57 000 BP – 28 000 cal BP), MIS 2 (28 000–11 700 cal BP), and MIS 1 (11 700 cal BP – to present) to gain better understanding of its past distribution, and also to predict the future distribution of *Pinus koraiensis*, taking into account the changing climate and environment.

ENVIRONMENTAL SETTING

The climate of the south of the Russian Far East is mainly controlled by the East Asian monsoon (Drozdov et al., 1989). Continental climate influence increases from the coast to inland. During the winter season, dry and cold winds blow towards the southeast from the Asian continent. In the summer season warm and humid winds come from the ocean. Mean temperatures in July and in January are ranging from 18°C to 20°C, and from −12°C to −21°C, respectively.

The average annual precipitation is between 550 and 920 mm and the most of it falls in summer. The relief of the eastern part of the south of the Russian Far East is mountainous, with average heights of the hills up to 600 m. The lowland sites are located in the coastal zone of the Sea of Japan, and the Pre-Khanka Plain, and the Ussuri River Valley.

THE GEOGRAPHICAL DISTRIBUTION AND ECOLOGY OF *PINUS KORAIENSIS*

The occurrence of *Pinus koraiensis* mostly depends on the climate (Solovyev, 1958). The leading factors, which determine the

Table 1. The extreme and optimum values of the most important climatic parameters, which determine the range of *Pinus koraiensis* in the south of the Russian Far East (Kolesnikov, 1954)

Parameter of climate	Physical characteristics		
	minimum	maximum	optimum
Mean annual temperature [°C]	0	+6	–
Extreme values of daily temperature [°C]	−50	+40	–
Number of months in a year with mean temperature 0°C	6	8	7
Growing period [days]	150	200	170–180
Degree day temperatures [°C]	100	170	120–150
Sum of the temperatures in the vegetative period	2600	>3200	–
Mean annual precipitation [mm]	500	1000	600–700
Extreme values of mean annual rainfall in individual years [mm]	320	>1200	–
Mean annual relative air humidity as recorded at 13 p.m. [%]	60	72	<70
Mean relative air humidity as recorded at 13 p.m. of the most rainy month (July or August) [%]	68	91	75
Mean relative air humidity as recorded at 13 p.m. of the driest month in the growing period (April or May) [%]	41	45	–

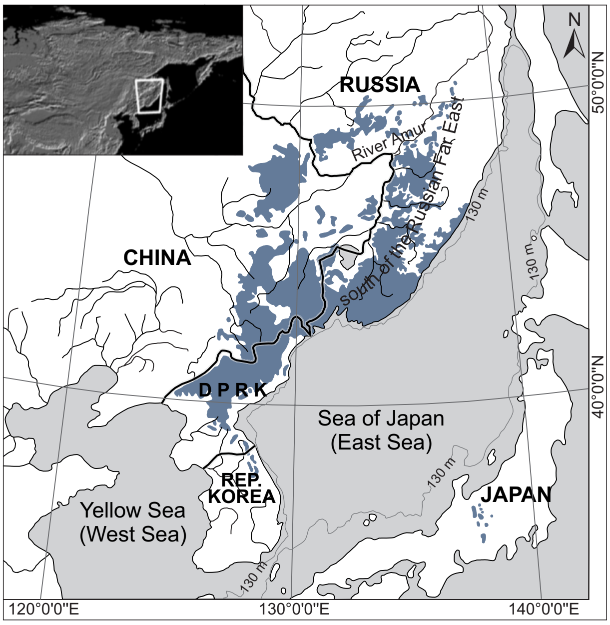

Fig. 1. The geographical distribution of *Pinus koraiensis* (Critchfield and Little, 1966; Krestov et al., 2006)

composition and structure of a mixed forest with *Pinus koraiensis* are as follows: the maximum temperature of the warmest month, the mean temperature of the warmest quarter of a year and the total precipitation of the wettest month (Zhang et al., 2014). The extreme and optimum values of the most important climatic parameters, which determine the range of *Pinus koraiensis* in the south of the Russian Far East are given in Table 1 (Kolesnikov, 1954).

Pinus koraiensis is a typical element of the vegetation in the East Asia mountain ecosystem of the Sikhote-Alin, Wanda, and Manchurian-Korean Mountains, Changbai Plateau, and the Maliy Khingan Ridge (Kolesnikov, 1954, 1956; Nakamura and Krestov, 2005). On the Islands of Japan, it is found in some locations in the Central and Southern Japanese Alps (Honshu Isl.), as well as on Shikoku Island (Ohwi, 1965) (Fig. 1). However, the most favourable climatic conditions for its growth exist between latitudes 41°N and 49°N in North Korea and northeastern China (Kolesnikov, 1954; Urusov, 1999).

In the south of the Russian Far East, the greatest part of the *Pinus koraiensis* range covers the Amur River drainage basin and a smaller part does the coast of the Sea of Japan. In this range *Pinus koraiensis* is mostly confined to the altitudes between 200 and 900 m a.s.l.

IDENTIFICATION OF THE *PINUS KORAIENSIS* POLLEN

In the modern vegetation of the south of the Russian Far East, genus *Pinus* is represented by two subgenera – *Pinus* subgen. *Haploxylon* (*Strobus*) and *Pinus* subgen. *Diploxylon*. *Pinus* subgen. *Haploxylon* includes two species – *Pinus koraiensis* and *Pinus pumila*, and *Pinus* subgen. *Diploxylon* is represented by one species – *Pinus densiflora*.

Fossil pollen of these species is found in the Pleistocene and Holocene sediments in the south of the Russian Far East. To distinguish between the fossil pollen of *Pinus koraiensis*, *Pinus pumila*, and *Pinus densiflora*, several pollen grains were selected from each uneven-aged palynological assemblage with a similar structure of palynospectra. After acetolysis, they were placed in glycerol jelly. Using an Axio Scope.A1 optical microscope and an AxioCam ICc1 camera (Carl Zeiss), five parameters of pollen grains were measured: ∑ (pollen length with sacci), A (pollen body length), B (pollen width), C (length of saccus), D (width of saccus) in an equatorial view (Fig. 2).

Based on the obtained values, the biometric characteristics – β, δ, γ were calculated and the angles between the axes of symmetry of the air sacs of the pollen grains of *Pinus koraiensis*, *Pinus pumila,* and *Pinus densiflora* were determined. The biometric parameters obtained using the method of Monoszon-Smolina (1949) were compared with the biometric characteristics of recent pollen grains (Tab. 2). This made the identification of the pollen of these species possible. A total of 58 pollen grains have been analysed.

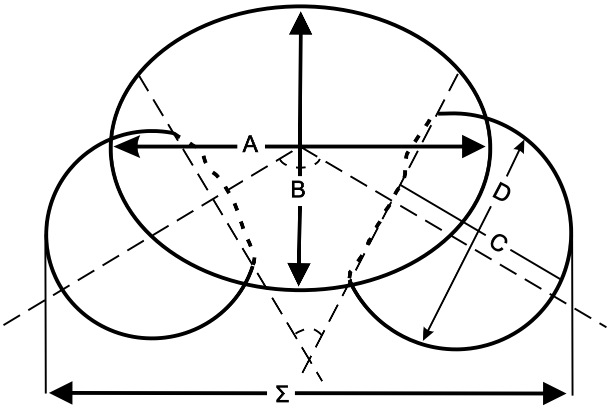

Fig. 2. Schematic representation of *Pinus* pollen grain indicating the positions of five parameters measured. ∑ – pollen length with sacci, A – pollen body length, B – pollen width, C – length of saccus, D – width of saccus

Table 2. Distinctive biometric characteristics of the pollen of *Pinus koraiensis*, *P. pumila*, and *P. densiflora* (Monoszon-Smolina, 1949)

Species	Total pollen grain size Σ, µm	Index β = A/B	Index δ = B/D	Index γ = A/D	The angle between the axes of symmetry of the air sacs
Pinus koraiensis	69.0–90.0 (on average 80.6)	1.03–1.44 (dominated 1.2–1.4)	0.8–1.5 (dominated 1.15–1.35)	1.2–1.9 (dominated 1.5–1.8)	104°–124° (dominated <120°)
Pinus pumila	72.0–99.0 (on average 86.2)	1.13–1.33 (dominated 1.2–1.3)	0.9–1.29 (dominated 1.05–1.2)	1.1–1.62 (dominated 1.2–1.5)	127°–149° (dominated >135°)
Pinus densiflora	60–78 (on average 69.9)	1.2–1.5 (dominated 1.25–1.35)	1.11–1.63 (dominated 1.25–1.5)	1.53–2.13 (dominated 1.6–1.9)	135°–160° (dominated >140°)

When identifying these species, the morphological features of pollen and sculptural patterns of pollen grains were also taken into account. The air sacs of *Pinus koraiensis* and *Pinus pumila* are spheroidal. Their upper part is located 1/3 higher than the middle line of the body of the pollen grain. The air sacs of *Pinus koraiensis* are large and distinct, with closed walls (Monoszon-Smolina, 1949). Their outlines are continuous in polar projection (Song et al., 2012). The diameter of the air sacs of *Pinus koraiensis* on the ventral side is almost the same as that of the body. Their structure is a uniform coarse mesh, through which a finer mesh appears. Exine has a fine, almost punctual structure, more distinct on the upper side of the body. The height of the exine above the line of sac attachment in *Pinus koraiensis* reaches a greater value than in *Pinus pumila* (Litvintseva, 1975; Monoszon-Smolina, 1949).

An important morphological feature of *Pinus pumila* pollen is large bumps (3.0–4.0 µm) at the base of the sacks, while *Pinus koraiensis* has simple waviness. The mesh structure of the pollen sacs of *Pinus pumila* is formed by the alternation of large and small cells. The length of the pollen sac is the same for one and other species, but its width in *Pinus koraiensis* is greater (Monoszon-Smolina, 1949; Litvintseva, 1975).

A distinctive feature of the pollen of another representative of the genus *Pinus*, the species of *Pinus densiflora*, is the location and the shape of the air sacs. The air sacs are located below the midline of the body of the pollen grain, which has a uniformly thickened exine. When considering the pollen grain in the lateral position, the air sacs have the form of three overlapping circles. On the ventral side, the boundaries of attachment of air sacs are sharply drawn together. The angle between the axes of their symmetry varies between 135° and 160° (with the predominance of an angle >140°), which is much more than that of *Pinus pumila* and *Pinus koraiensis*. The exine of the body is somewhat thicker on the dorsal side. It is represented by a small pattern evenly covering the entire surface (Monoszon-Smolina, 1949; Litvintseva, 1975). The air sacs of *Pinus densiflora* are discontinuous in polar projection with the outline of the body, so that the pollen grains appear to be composed of three separate oval parts (Song et al., 2012). Pollen of *Pinus densiflora* is characterised by a lighter color and transparency (Monoszon-Smolina, 1949).

MATERIALS AND METHODS

To reconstruct the late Pleistocene and Holocene history of *Pinus koraiensis* in the south of the Russian Far East, previously published paleobotanical materials (Korotky et al., 1980; Pavlyutkin et al., 1984; Korotky, 2002; Pavlyutkin and Belyanina, 2002; Bazarova et al., 2008; Mikishin et al., 2008; Anderson et al., 2017; Belyanin and Belyanina, 2018, 2020; Belyanin et al., 2018, 2019) were combined with new laboratory data on *Pinus koraiensis* fossil pollen data and chronological data on MIS 5 (127 000–71 000 BP), MIS 3 (57 000 BP – 28 000 cal BP), MIS 2 (28 000–11 700 cal BP) and MIS 1 (11 700 cal BP – to present). A significant part of *Pinus koraiensis* fossil pollen and chronological data was obtained, collected, and analysed from the NFE, CFE, and SFE ecological zones in the region (Tab. 3). Since the age of MIS 4 (71 000–57 000 BP) sediments is beyond radiocarbon dating and the pollen records of this age are absent in the south of the Russian Far East, we cannot reconstruct the history of *Pinus koraiensis* during MIS 4.

COLLECTION, PREPARATION OF THE SEDIMENT SAMPLES AND PALYNOLOGICAL ANALYSIS

New *Pinus koraiensis* fossil pollen data and chronological data were obtained from cross-sections 9 119, 6 159, 1 706–1 and 6 022. Sediments samples were taken at intervals of 5–10 cm. Fossil pollen particles were extracted from the sediments using standard methods, which included treatment with 10% KOH, separation of minerals with a solution of KJ and CdJ2 (2.2 g/cm^3), after which the samples were acetolysed and mounted in glycerol jelly (Pokrovskaya, 1950). Pollen and spores in glycerin jelly were identified,

Table 3. Geographic coordinates of the cross-sections and cores, their, elevation, and source of publication

Cores and Cross-sections	Subregion	No. on Fig. 3	Location	Altitude [m a.s.l.]	Reference to publication source
Core 33	SFE	1	43°31′43.43″N 131°52′40.55″E	5	Pavlyutkin and Belyanina, 2002
Core 11	SFE	2	42°50′45.08″N 133°00′11.04″E	2	Pavlyutkin and Belyanina, 2002
Core 10	NFE	3	48°14′33.11″N 138°29′44.45″E	1 320	Korotky, 2002
Cross-section 6 204	NFE	4	46°28′38.55″N 134°12′07.24″E	58	Belyanin and Belyanina, 2018
Core Lake Karasie	SFE	5	42°39′28.26″N 130°58′30.29″E	0.2 (water depth 1.5 m)	Anderson et al., 2017
Cross-section Tikhangoy Bay	SFE	6	43°50′28.49″N 132°47′04.12″E	4	Korotky, 2002
Cross-section Ovrazhnyii-2	CFE	7	43°15′45.29″N 138°33′08.58″E	20	Korotky, 2002
Cross-section Akulinin	NFE	8	47°03′51.57″N 134°34′28.01″E	10	Korotky, 2002
Cross-section 6 205	NFE	9	46°29′38.57″N 134°29′07.29″E	64	Belyanin and Belyanina, 2018
Cross-section 6 276	CFE	10	44°57′30.02″N 133°08′03.08″E	70	Belyanin and Belyanina, 2020
Core 579	CFE	11	44°52′44.02″N 132°39′48.24″E	67 (water depth 1.5 m)	Belyanin and Belyanina, 2012
Cross-section c	SFE	12	42°57′06.46″N 133°10′28.44″E	35	Korotky, 2002
Core 508	CFE	13	44°51′16.08″N 133°02′47.23″E	78	Belyanin and Belyanina, 2020
Cross-section 9 119	SFE	14	44°20′07.29″N 132°36′05.49″E	22	unpublished
Core 9	SFE	15	42°52′06.31″N 133°00′15.02″E	2	Pavlyutkin and Belyanina, 2002
Cross-section 1 438	CFE	16	44°20′07.09″N 132°36′05.18″E	75	Korotky et al., 1980
Core 272	SFE	17	42°42′02.25″N 130°56′31.08″E	5	Mikishin et al., 2008
Cross-section Bolotisty Stream	NFE	18	48°53′59.02″N 137°15′22.15″E	512	Belyanin et al., 2018
Cross-section 4 005	SFE	19	43°51′32.30″N 131°27′55.12″E	5	Pavlyutkin and Belyanina, 2002
Cross-section 6 010	NFE	20	46°39′01.19″N 134°24′17.06″E	63	Belyanin and Belyanina, 2018
Cross-section Kazachka River	SFE	21	43°51′32.13″N 131°27′55.62″E	82	Pavlyutkin et al., 1984
Cross-section 6 159	CFE	22	44°49′17.34″N 133°03′54.00″E	75	unpublished
Cross-section 6 056	NFE	23	46°33′33.24″N 134°10′43.71″E	63	Belyanin and Belyanina, 2018
Core Lake Utinoye	SFE	24	43°22′34.07″N 131°45′17.62″E	0.3 (water depth 3.5 m)	Anderson et al., 2017
Cross-section 1 706-1	SFE	25	43°25′13.99″N 132°11′34.56″E	1.8	unpublished
Cross-section 9 031a	SFE	26	42°50′45.02″N 133°00′11.01″E	2	Pavlyutkin and Belyanina, 2002
Cross-section 1 504	NFE	27	47°02′05.09″N 138°35′44.03″E	6	Korotky, 2002
Cross-section 1 508-1	SFE	28	42°22′49.05″N 130°45′17.00″E	2.8	Belyanin et al., 2018
Cross-section 6 022	NFE	29	46°37′82.89″N 134°29′48.24″E	58	unpublished
Cross-section Kiya	NFE	30	47°55′232.59″N 134°55′23.54″E	53	Bazarova et al., 2008

photographed and counted using an optical microscope Axio Scope.A1 and camera AxioCam ICc1(Carl Zeiss). At least 250 pollen grains of arboreal, dwarf shrubs, and herb were counted in each sample. Identifications of pollen grains were made with the aid of pollen atlases (Nakamura, 1980; Pokrovskaya, 1950). Proportion of each pollen taxon was calculated in percent of the pollen sum arboreal taxa, dwarf shrubs and herbs. Latin names are given according to Plants of the World Online (POWO, 2019). The results of the palynological analysis are plotted in diagrams using the software Tilia v. 2–0–41 (Grimm, 2004).

DATING

The chronology of the *Pinus koraiensis* pollen records is based on radiocarbon dates. Four samples of wood, plant detritus, and buried soil were dated using the radiocarbon method in the Laboratory of Geochronology, St Petersburg State University (Kh.A. Arslanov and F.B. Maksimov) and in the Institute of Geological Sciences of National Academy of Sciences of Ukraine (N.N. Kovalyukh). Radiocarbon ages within the sensitivity of the radiocarbon method were calibrated using OxCal 4.4 with the «IntCal 20» calibration curve (Bronk Ramsey, 2017; Reimer et al., 2020) (Tab. 4).

Palaeobotanical data were correlated using the General Stratigraphic Scale of the Quaternary System (Borisov, 2009). The age division of the Pleistocene is given in accordance with Marine Isotope Stages (MIS) (Bassinot et al., 1994). The subdivision of the Holocene was related to the stratigraphic scheme of the Quaternary suggested by the Sub-Commission on Quaternary Stratigraphy and by the INTIMATE Working Group (Walker et al., 2012). Small climatic changes are identified based on the regional stratigraphic scale for the Russian Far East (Korotky et al., 1980; Korotky, 2002).

MAPPING

A map of *Pinus koraiensis* fossil pollen distribution in MIS 5, MIS 3, MIS 2, and MIS 1 (see Fig. 1) was produced by plotting the locations where *Pinus koraiensis* fossil pollen was reported. Geographical locations of the pollen data collection sites are divided into three groups based on their geographical positions in three subregions: north (NFE), central (CFE), and south (SFE). ArcGIS version 10.5 and Corel Draw version 20 were employed to produce the past distribution map of *Pinus koraiensis*.

RESULTS

PINUS KORAIENSIS POLLEN IN THE SEDIMENTS OF MIS 5 (127 000–71 000 BP)

According to the published palaeobotanical data on MIS 5 by Pavlyutkin and Belyanina (2002), *Pinus koraiensis* pollen fossils are found in the sediments of the Partizanskaya River floodplain, in core 11, in the SFE subregion (Fig. 3) (107 000 ± 4500 BP and 85 500 ± 2000 BP) and in the lower reaches of the Razdolnaya River, SFE, in core 33 SFE (80 600 ± 2900 BP), in the south of the Russian Far East. In the pollen assemblages the pollen of the broadleaved species such as *Quercus*, *Ulmus*, *Carpinus*, *Tilia*, and *Syringa* dominates. This indicates that *Pinus koraiensis* grew in the forests with a diverse composition (Fig. 4).

PINUS KORAIENSIS POLLEN IN THE SEDIMENTS OF MIS 3 (57 000 BP – 28 000 cal BP)

According to palaebotanical reports from the south of the Russian Far East related to MIS 3, *Pinus koraiensis* fossil pollen was found at the Kontrovod River Basin in cross-section 6 204, NFE (>54 000 BP, 40 329–39 199 cal BP and 31 977–31 273 cal BP) (Belyanin and Belyanina, 2018), at the Opasnaya River Valley in core 10 and in cross-section Akulinin, NFE (46 100–45 005 cal BP and 45 476–42 221 cal BP, respectively) (Korotky, 2002), at the Neprimetnaya Bay in cross-section Ovrazhnyii-2, CFE (35 317–33 918 cal BP) (Korotky, 2002), at the Opasnaya River Valley in cross-section Akulinin, NFE (34 892–32 771 cal BP) (Korotky, 2002) and in the cross-section of the Tikhangoy Bay, SFE (35 464–28 587 cal BP) (Korotky, 2002). A large proportion of *Pinus koraiensis* fossil pollen with 12% in a pollen assemblage was obtained from the bottom sediments of Lake Karasie, SFE (41 014–40 563 cal BP (Anderson et al., 2017).

PINUS KORAIENSIS POLLEN IN THE SEDIMENTS OF MIS 2 (28 000–11 700 cal BP)

During MIS 2, *Pinus koraiensis* fossil has not been found at the lower reaches of the Kontrovod River in cross-section 6 205, NFE (22 368–21 292 cal BP, 18 269–17 849 cal BP and 14 867–14 039 cal BP) (Belyanin and Belyanina, 2018), near Novorusanovka Village, in cross-section 6 276, CFE (22 974–22 105 cal BP), at the Opasnaya River Valley in cross-section Akulinin, NFE (27 262–26 918 cal BP) (Korotky, 2002) and on the Pre-Khanka Plain, in core 579, CFE (22 169–21 021 cal BP (Belyanin and Belyanina, 2012) (Fig. 5). Nevertheless, the rare *Pinus koraiensis* fossil pollen has been recorded in the south of the Russian Far East at the lower reaches of the Partizanskaya River, in cross-section Unashi, SFE (21 403–20 670 cal BP and 13 601–13 156 cal BP) (Korotky, 2002) and in the core of Lake Karasie, SFE (20 856–20 558 cal BP) (Anderson et al., 2017).

Table 4. Radiocarbon and Uranium series dates (Korotky et al., 1980; Pavlyutkin et al., 1984; Korotky, 2002; Pavlyutkin and Belyanina, 2002; Bazarova et al., 2008; Mikishin et al., 2008; Anderson et al., 2017; Belyanin and Belyanina, 2018, 2020; Belyanin et al., 2018, 2019)

Cores and Cross-sections	No on Fig. 3	Depth [m]	Dated material	Laboratory number	^{14}C age, BP	Calibrated age range, cal BP (probability)
Core 11	1	16.5	quartz	K – 173	107 000±4 500	–
Core 11	1	14.9	quartz	K – 172	85 500±2 000	–
Core 33	2	9.1	quartz	K – 171	80 600±2 900	–
Cross-section 6 204	4	12.6	wood	Ki – 3 371	>54 000	–
Core 10	3	4.2	peat	Ki – 2 403	46 200±280	46 100–45 005 (95.4%)
Cross-section Akulinin	8	5.1–5.0	wood	Ki – 1 849	40 040±1 200	45 476–42 221 (95.4%)
Core Lake Karasie	5	3.24–3.23	wood, seeds, tree moss	CAMS # 71 813	35 610±40	41 014–40 563 (95.4%)
Cross-section 6 204	4	10.6	wood	Ki – 3 370	34 500±250	40 329–39 199 (95.4%)
Cross-section Ovrazhnyii – 2	7	3.9–3.8	wood	SOAN – 627	30 070±370	35 317–33 918 (95.4%)
Cross-section Akulinin	8	3.65–3.6	peat	TIG – DVGU – 17	29 430±475	34 892–32 771 (92.9%) 32 602–32 277 (2.5%)
Cross-section 6 204	4	9.1	wood	Ki – 3 275	27 750±150	31 977–31 273 (95.4%)
Cross-section Tikhangoy Bay	6	12.5	wood	Ki – 2 904	27 000±1500	35 464–28 587 (95.4%)
Cross-section Akulinin	8	3.35–3.3	peat	MAG – 341	22 700±80	27 262–26 918 (88.7%) 26 707–26 600 (4.7%) 26 541–26 485 (2.0%)
Cross-section 6 276	10	1.0	wood	Ki – 2 174	18 580±225	22 974–22 105 (95.4%)
Cross-section 6 205	9	6.9	wood	Ki – 3 293	17 990±200	22 368–21 292 (95.4%)
Core 579	11	5.2	humified loam	Ki – 2 166	17 840±200	22 169–21 021 (95.4%)
Cross-section Unashi	12	3.3–3.4	wood	Ki – 2 917	17 400±125	21 403–20 670 (95.4%)
Core Lake Karasie	5	1.66–1.63	seeds, wood, tree moss	CAMS # 73 291	17 160±40	20 856–20 558 (95.4%)
Cross-section 6 205	9	5.7	wood	Ki – 3 294	14 800±100	18 269–17 849 (95.4%)
Cross-section 6 205	9	3.6	wood	Ki – 3 298	12 300±100	14 867–14 039 (95.4%)
Cross-section Unashi	12	2.4–2.3	wood	SOAN – 288	11 500±130	13 601–13 156 (94.3%) 13 142–13 119 (1.2%)
Core 508	13	4.5	wood	Ki – 2 171	9 680±130	11 391–11 378 (0.4%) 11 337–10 652 (94.3%) 10 621–10 594 (0.8%)
Cross-section 6 205	9	1.8	wood	Ki – 3 293	9 270±60	10 642–10 637 (0.4%) 10 582–10 253 (95.0%)
Cross-section 9 119	14	2.1	wood	–	9 250±70	10 581–10 245 (95.4%)
Cross-section 9 119	12	1.6	wood	–	8 960±80	10 247–9 884 (90.0%) 9 865–9 775 (5.4%)
Core 9	15	6.5	plant detritus	Ki – 3 688	8 900±60	10 205–9 767 (95.4%)
Cross-section Bolotisty Stream	18	3.2	peat	LU – 81 38	8 620±90	9 900–9 462 (95.4%)
Cross-section 1 438	16	1.7	wood	MAG – 332	8 180±80	9 425–8 968 (95.4%)
Core 272	17	1.95–1.9	wood	SOAN – 7 179	7 995±45	9 005–8 698 (92.0%) 8 672–8 649 (3.5%)
Core Lake Karasie	5	1.40–1.37	seeds, wood, charcoal	CAMS # 73 290	7 550±40	8 420–8 309 (86.6%) 8 260–8 210 (8.9%)
Cross-section 4 005	19	2.4	plant detritus	Ki – 2 365	7 240±120	8 091–8 188 (95.4%)
Cross-section 6 010	20	1.7	plant detritus	Ki – 3 269	6 660±70	7 660–7 636 (3.7%) 7 622–7 427 (91.8%)
Cross-section 4 005	19	2.2	plant detritus	Ki – 2 159	6 530±75	7 427–7 156 (92.5%) 7 111–7 072 (2.4%) 7 041–7 031 (0.5%)
Cross-section 6 056	23	2.9	plant detritus	Ki – 3 256	6 090±70	6 786–7 162 (95.4%)
Cross-section 6 159	22	3.1	wood	Ki – 2 141	5 360±75	6 293–5 991 (93.1%) (5 965–5 945) (2.3%)
Cross-section 6 205	9	0.8	peat	Ki – 3 372	5 120±80	6 170–6 150 (1.0%) 6 112–6 081 (2.2%) 6 009–6 564 (91.5%) 5 622–5 607 (0.8%)
Core Lake Karasie	5	1.04–1.03	seeds, charcoal	CAMS # 71 814	5 050±40	5 907–5 710 (91.4%) 5 686–5 662 (4.1%)

Table 4. Continued

Cores and Cross-sections	No on Fig. 3	Depth [m]	Dated material	Laboratory number	^{14}C age, BP	Calibrated age range, cal BP (probability)
Core Lake Utinoye	24	4.71–4.68	wood, charcoal	CAMS # 73 295	5 000±80	5 905–5 595 (95.4%)
Core Lake Karasie	5	0.77–0.74	seeds	CAMS # 74 346	4 890±40	5 722–5 580 (93.0%) 5 503–5 489 (2.5%)
Cross-section 1 706-1	25	1.89–1.86	buried soil	LU – 8 780	4 650±110	5 593–5 040 (94.7%) 5 002–4 895 (0.8%)
Cross-section Kazachka	21	1.2	wood	DVGU – TIG – 29	4 472±75	5 311–4951 (86.4%) 4 944–4 875 (9.0%)
Core Lake Karasie	5	0.67–0.60	seeds	CAMS # 73 288	4 300±40	4 974–4 823 (94.8%) 4 744–4 736 (0.7%)
Cross-section 9 031a	26	2.4	wood	Ki – 3686	4 210±60	4 865–4 570 (94.2%) 4 550–4 533 (1.3%)
Cross-section Tikhangoy Bay	6	1.25–1.20	peat	TIG – DVGU – 51	4 195±50	4 850–4 577 (95.4%)
Cross-section 1 504	27	3.8–3.7	peat	Ki – 1 455	4 000±60	4 796–4 761 (3.0%) 4 693–4 679 (0.8%) 4 643–4 635 (0.4%) 4 626–4 288 (90.1%) 4 272–4 251 (1.2%)
Core Lake Utinoye	24	3.47–3.45	wood	CAMS # 76 800	3 920±40	4 515–4 480 (4.5%) 4 444–4 235 (90.4%) 4 195–4 188 (0.5%)
Core Lake Karasie	5	0.45–0.43	seeds	CAMS # 74 344	3 870±40	4 414–4 224 (82.5%) 4 205–4 155 (13.0%)
Cross-section Kiya	30	0.95	peat	(SOAN – 4 752)	3 720±100	4 405–3 836 (95.4%)
Cross-section Ovrazhnyii – 2	7	2.1–2.0	wood	TIG – 41	3 490±90	4 060–4 052 (0.4%) 3 985–3 549 (92.9%) 3 535–3 492 (2.2%)
Cross-section 1 706 – 1	25	0.73–0.7	buried soil	LU – 8 779	3 020±100	3 447–2 950 (95.4%)
Cross-section 1 504	27	2.8–2.7	wood	MAG – 244	2 770±60	3 054–3 048 (0.4%) 3 027–3 019 (0.6%) 3 004–2 755 (94.5%)
Core Lake Utinoye	24	2.23–2.21	plant detritus	CAMS # 76 799	2 510±60	2 744–2 410 (93.1%) 2 388–2 369 (2.4%)
Cross-section 1 508 – 1	28	2.88–2.73	buried soil	LU – 7 961	2 460±100	2 755–2 335 (95.4%)
Cross-section 6 022	29	1.6	plant detritus	Ki – 3 270	2 350±40	2 674–2 655 (1.7%) 2 612–2 600 (1.2%) 2 495–2 308 (90.9%) 2 225–2 210 (1.0%) 2 193–2 183 (0.7%)
Cross-section Ovrazhnyii – 2	7	1.05–0.95	wood	TIG – 1 966	2 220±60	2 340–2 051 (94.8%) 2 015–2 009 (0.7%)
Cross-section 4 005	19	1.8	wood	Ki – 3 678	1 930±40	1 979–1 967 (1.6%) 1 943–1 737 (93.8%)
Cross-section 1 508 – 1	28	1.52–1.44	buried soil	LU – 7 960	1 930±100	1 979–1 967 (1.6%) 1 943–1 737 (93.8%)
Borehole Lake Utinoye	24	1.30–1.27	wood, leaves	CAMS # 76 798	1 810±60	1 865–1 856 (1.0%) 1 833–1 549 (94.5%)
Cross-section Ovrazhnyii – 2	7	0.65–0.6	peat	SOAN – 554	1 450±50	1 413–1 283 (95.4%)
Cross-section Tikhangoy Bay	6	0.55–0.5	peat	SOAN – 136	1 375±75	1 407–1 172 (90.9%) 1 164–1 121 (3.8%) 1 093–1 079 (0.8%)
Cross-section 1 508 – 1	28	0.65–0.57	buried soil	LU – 7 959	1 360±60	1 376–1 174 (95.4%) 1 158–1 150 (0.7%) 1 139–1 131 (0.6%)

PINUS KORAIENSIS POLLEN IN THE SEDIMENTS OF MIS 1

(11 700 cal BP – to present)

The Holocene in the south of the Russian Far East is subdivided into three time zones, 11 700–8200 cal BP (early Holocene), 8200–4200 cal BP (middle Holocene), and 4200 cal BP to the present (late Holocene), based on pollen data (Korotky, 2002).

From 11 700 to 8200 cal BP, *Pinus koraiensis* pollen fossil has been found at the lower reaches of the Sorochevka River, in core 508,

Fig. 3. Locations and ages in the *Pinus koraiensis* fossil record in the southern part of the Russian Far East (Korotky et al., 1980; Pavlyutkin et al., 1984; Korotky, 2002; Pavlyutkin and Belyanina, 2002; Bazarova et al., 2008; Mikishin et al., 2008; Anderson et al., 2017; Belyanin and Belyanina, 2018, 2020; Belyanin et al., 2018, 2019). Numbers 1–30 – locations of cores and sections. Time intervals: **A**. MIS 5 (127 000–71 000 BP); **B**. MIS 3 (57 000 BP–28 000 cal BP); **C**. MIS 2 (28 000–11 700 cal BP); MIS 1: **D**. The early Holocene (11 700–8200 cal BP); **E**. The middle Holocene (8200–4200 cal BP); **F**. The late Holocene (4200 cal BP to the present). For the designation of cross-sections and cores on the map, see Table 3

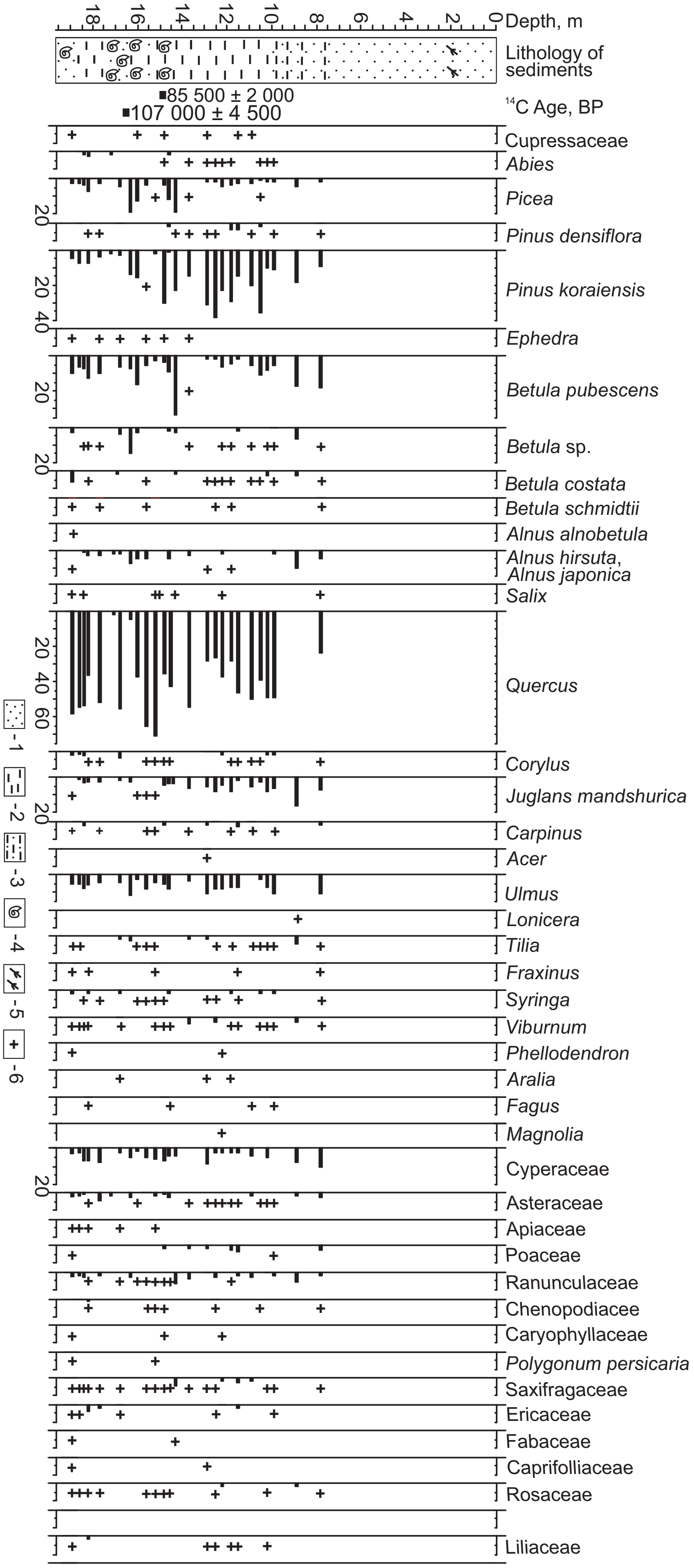

Fig. 4. Palynological diagram from core 11 in the floodplain of the Partizanskaya River. 1 – sand, 2 – loam, 3 – sandy loam, 4 – marine shells, 5 – plant detritus, 6 – taxa present in the assemblage in amounts less than 3% (Pavlyutkin and Belyanina, 2002)

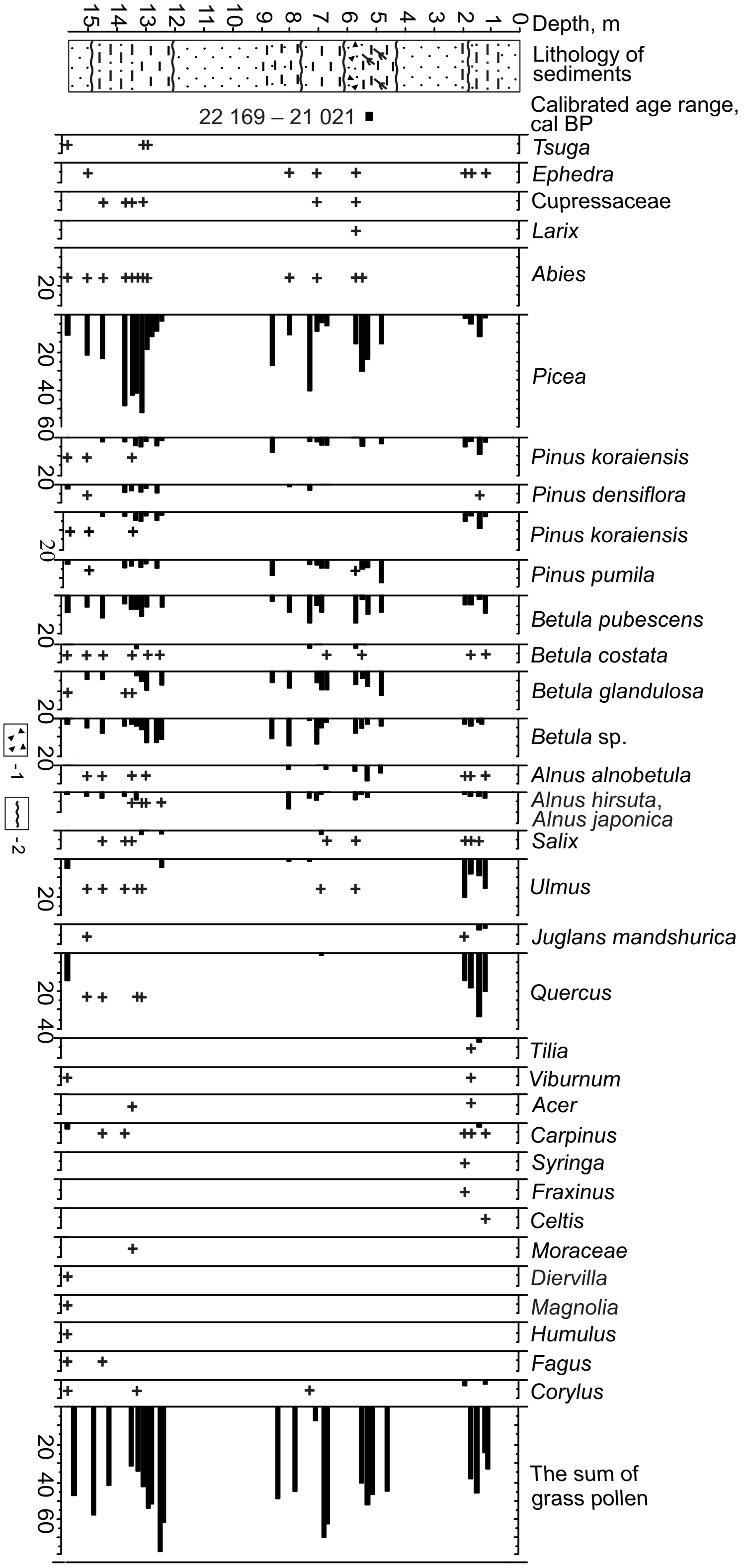

Fig. 5. Palynological diagram from core 579 from the bottom sediments of Lake Khanka. 1 – gravel, 2 – gap in the sediments. For explanation see Fig. 4 (Belyanin and Belyanina, 2012)

CFE (11 337–10 652 cal BP) (Belyanin and Belyanina, 2020) (Fig. 6), at the lower reaches of the Kontrovod River, in cross-section 6 205, NFE 10 582–10 253 cal BP), at the mouth of the Popovka River, in cross-section 9 119, SFE (10 581–10 245 cal BP and 10 247–9884 cal BP), at the mouth of the Partizanskaya River, in core 9, SFE (10 205–9767 cal BP) (Pavlyutkin and Belyanina, 2002), at the Bolotisty Stream, NFE (9900–9462 cal BP) (Belyanin et al., 2018), at the lower reaches of the Chernigovka River, in cross-section 1 438, CFE (9425–8968

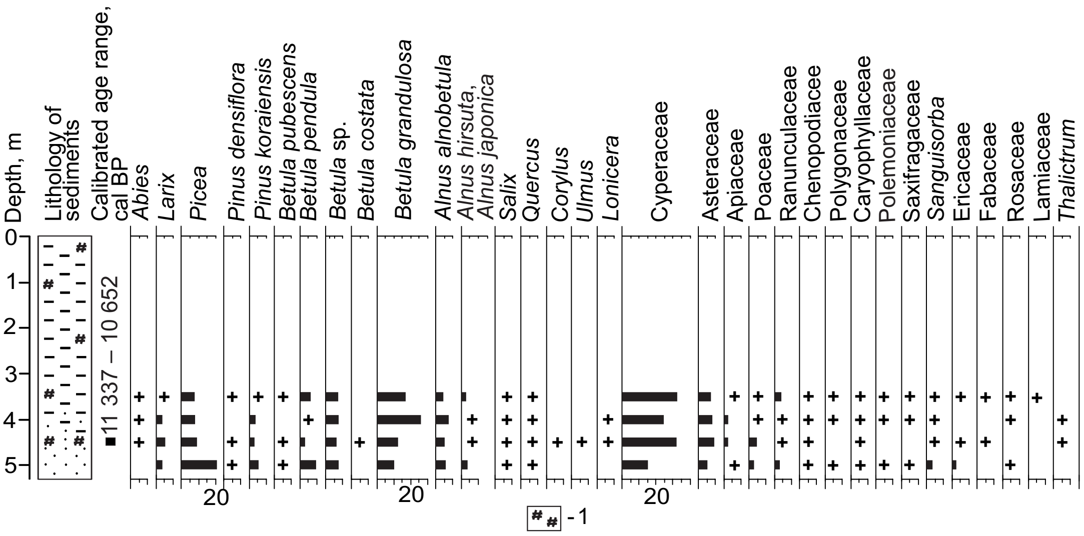

Fig. 6. Palynological diagram from core 508 in the floodplain of the Sorochevka River 1 – wood. For explanation see Fig. 4 (Belyanin and Belyanina, 2020)

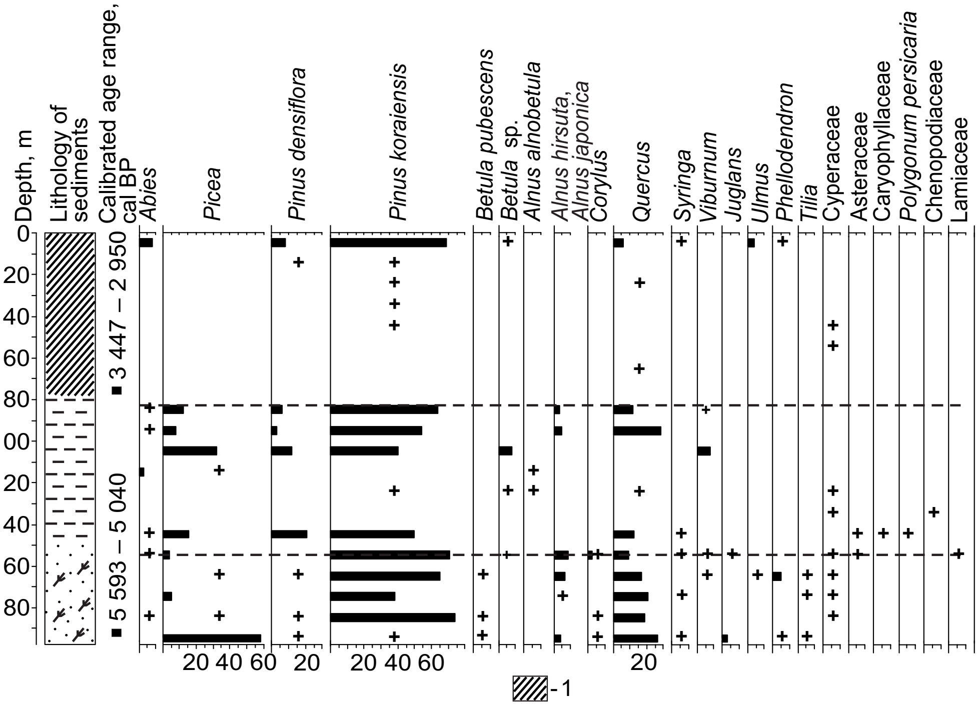

Fig. 7. Palynological diagram from cross-section 1 706–1 in the floodplain of the Knevichanka River. 1 – soil. For explanation see Fig. 4

cal BP) (Korotky et al., 1980), at the mouth of the Vinogradnaya River, in core 272, SFE (9005–8698 cal BP) (Mikishin et al., 2008) and in the core of Lake Karasie, SFE (8420–8309 cal BP) (Anderson et al., 2017).

From 8 200 to 4 200 cal BP, *Pinus koraiensis* pollen fossil has been reported from many sites, such as the lower reaches of the Razdolnaya River, in cross-section 4 005, SFE (8091–8188 cal BP and 7427–7156 cal BP), SFE (Pavlyutkin and Belyanina, 2002), at the lower reaches of the Alchan River in cross-section 6 010 (7622–7427 cal BP), NFE (Belyanin and Belyanina, 2018), at the lower reaches of the Burlitovka River in cross-section 6 056 (6786–7162 cal BP), NFE (Belyanin and Belyanina, 2018), at the Sorochevka River Valley in cross-section 6 159 (6293–5991 cal BP), at the lower reaches of the Kontrovod River in cross-section 6 205 (6009–6564 cal BP), NFE (Belyanin and Belyanina, 2018), NFE, in Lake Karasie (5907–5710 cal BP, 5722–5580 cal BP, 4850–4938 cal BP, 4974–4823 cal BP and 4414–4224 cal BP), SFE (Anderson et al.,

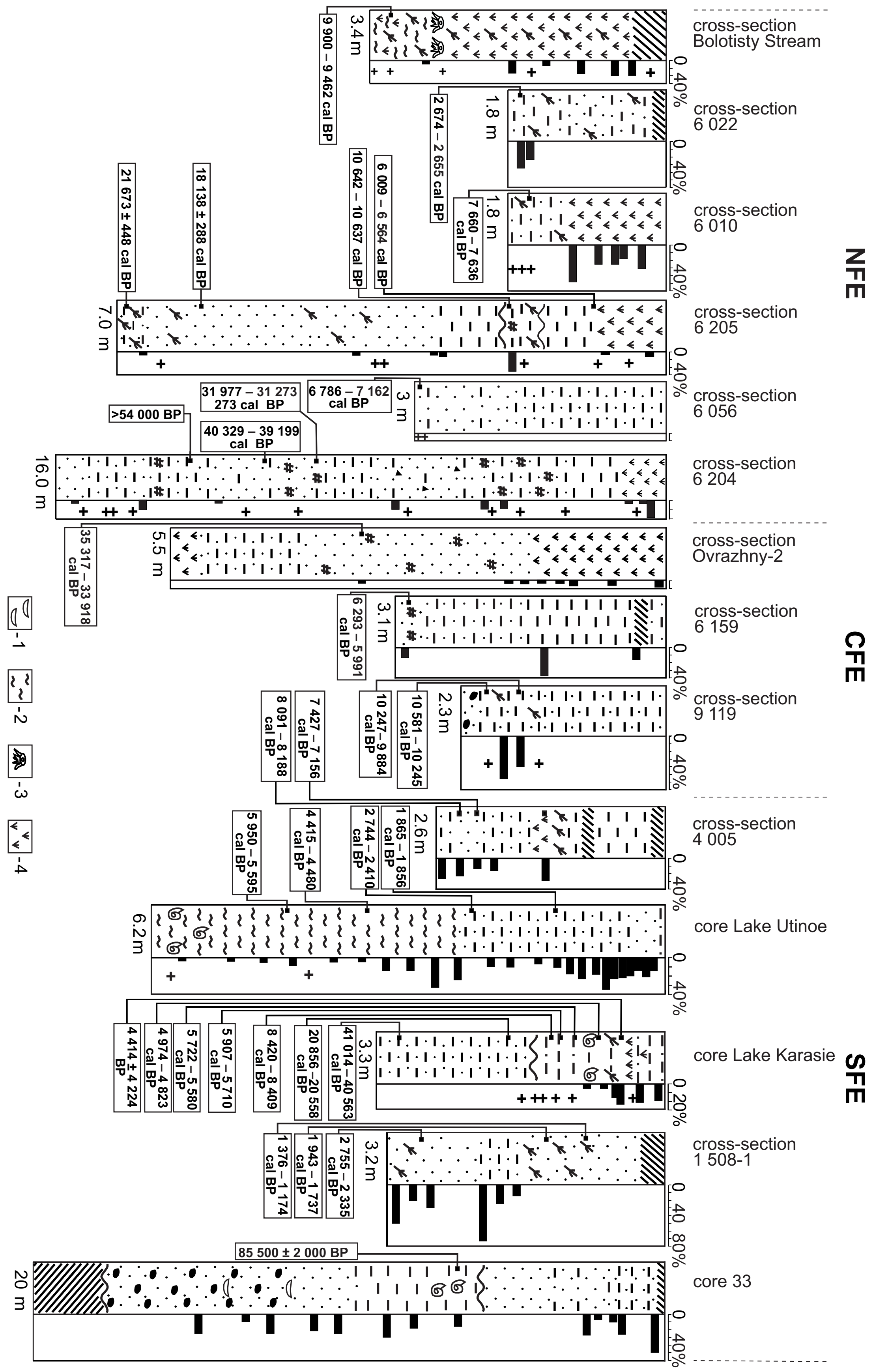

Fig. 8. The presence of *Pinus koraiensis* pollen in assemblages in MIS 5 (127 000–71 000 BP), MIS 3 (57 000 BP–28 000 cal BP), MIS 2 (28 000–11 700 cal BP), and MIS 1 – early Holocene (11 700–8200 cal BP), middle Holocene (8200–4200 cal BP) and late Holocene (4200 cal BP to the present) sediments in the south of the Russian Far East. 1 – shell detritus, 2 – mud, 3 – stump horizon, 4 – peat. For explanation see Figs 4, 5, 6, 7 (Pavlyutkin and Belyanina, 2002; Mikishin et al., 2008; Anderson et al., 2017; Belyanin et al., 2018; Belyanin and Belyanina, 2018, 2020)

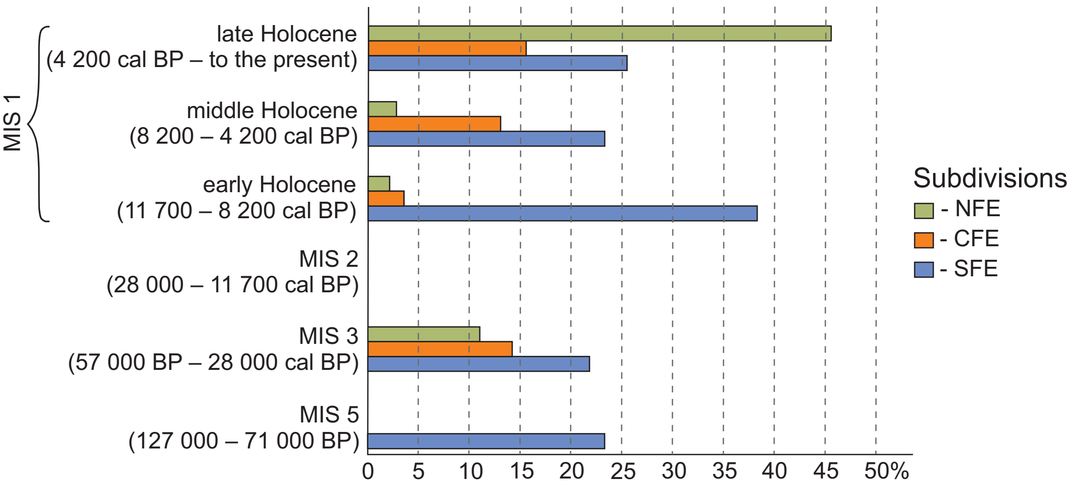

Fig. 9. Average percentage of *Pinus koraiensis* fossil pollen in each division in the south of the Russian Far East in MIS 5 (127 000–71 000 BP), MIS 3 (57 000 BP – 28 000 cal BP), MIS 2 (28 000–11 700 cal BP), and MIS 1 – early Holocene (11 700–8200 cal BP), middle Holocene (8200–4200 cal BP) and late Holocene (4200 cal BP to the present) (Korotky et al., 1980; Pavlyutkin et al., 1984; Korotky, 2002; Pavlyutkin and Belyanina, 2002; Bazarova et al., 2008; Mikishin et al., 2008; Anderson et al., 2017; Belyanin and Belyanina, 2018, 2020; Belyanin et al., 2018, 2019)

2017), at Lake Utinoe (5905–5595 cal BP and 4444–4235 cal BP), SFE (Anderson et al., 2017), at the Knevichanka River Valley in cross-section 1 706–1 (5593–5040 cal BP), SFE (Fig. 7), on the floodplain of the Partizanskaya River in cross-section 9 031a (4865–4570 cal BP), SFE (Pavlyutkin and Belyanina, 2002), at the mouth of the Venyukovka River in cross-section 1 5041 504, NFE (4626–4288 cal BP) (Korotky, 2002), in the valley of the Kazachka River in the Kazachka cross-section (5311–4951 cal BP), CFE (Pavlyutkin et al., 1984), and in the cross-section of the Tikhangou Bay (4850–4577 cal BP), SFE (Korotky, 2002).

From 4200 cal BP to the present day, *Pinus koraiensis* pollen fossil has been encountered at the interfluve of the Khor and Kiya rivers, in Kiya cross-section, NFE (4405–3836 cal BP) (Bazarova et al., 2008), at the Neprimetnaya Bay in cross-section Ovrazhnyii-2 (3985–3549 cal BP, 2340–2051 cal BP and 1413–1283 cal BP) (Korotky, 2002), at the Knevichanka River Valley, in cross-section 1 706–1, SFE (3447–2950 cal BP), at the mouth of the Venyukovka River in cross-section 1 504, NFE (3004–2755 cal BP) (Korotky, 2002), in Lake Utinoye, SFE (2744–2410 cal BP and 1833–1549 cal BP) (Anderson et al., 2017), at the mouth of Tumen River in cross-section 1 508–1, SFE (2755–2335 cal BP, 1943–1737 cal BP, 1376–1174 cal BP, and 1220–1340 cal BP) (Belyanin et al., 2019), at the lower reaches of the Alchan River, in cross-section 6 022, NFE (2495–2308 cal BP), at the lower reaches of the Razdolnaya River, in cross-section 4 005, SFE (1943–1737 cal BP) (Pavlyutkin and Belyanina, 2002), and in the cross-section of the Tikhangoy Bay, SFE (1 407–1 172) (Korotky, 2002).

DISCUSSION

The available palynological and chronological data (Tab. 4) allow us to reconstruct the changes in the distribution of *Pinus koraiensis* in the south of the Russian Far East during MIS 5 (127 000–71 000 BP), MIS 3 (57 000 BP –28 000 cal BP), MIS 2 (28 000–11 700 cal BP), and MIS 1 (11 700 cal BP – to present).

As a result of average annual temperatures increasing by 1.7–2.0°C in MIS 5 compared with the present values in the south of the Russian Far East (Velichko, 2012), a significant change occurred in the structure of vegetation, including a noticeable displacement of the range of *Pinus koraiensis* to the north. Although the number of MIS 5 samples is limited, its palynological record is abundant with *Pinus koraiensis* pollen fossil (Pavlyutkin and Belyanina, 2002). According to this pollen record, *Pinus koraiensis* dominated in the vegetation of MIS 5 in the south of the Russian Far East (Figs 8, 9). In that time, the mixed forests with *Pinus koraiensis*, *Pinus densiflora, Quercus*, *Ulmus*, *Juglans*, *Carpinus*, *Phellodendron*, *Tilia*, Cupressaceae families, and other broad-leaved plants dominated in the region.

In the south of the Russian Far East the period of MIS 3 refers to Chernoruch’inskii

Stage by the regional scheme (Korotky, 2002). This period is characterised by small climatic fluctuations in the region. According to pollen reports (Korotky, 2002; Anderson et al., 2017; Belyanin and Belyanina, 2018), *Pinus koraiensis* grew in birch-fir forests in subregions SFE and CFE in the south of the Russian Far East during MIS 3. In SFE, it was the dominant species in birch-deciduous forests.

Apparently, the small amount of data obtained on *Pinus koraiensis* pollen in the region during MIS 5 (127 000–71 000 BP) and MIS 3 (57 000 BP–28 000 cal BP) is associated with, among other things, a long period of aerobic conditions, which led to a significant depletion of the taxonomic composition of fossil pollen. Contact with oxygen might have also fostered the bacterial and fungal degradation of sporopollenin (Elsik, 1971; Havinga, 1971). Moreover, the alternation of wet and dry cycles, which are common for several types of soils, can cause mechanical damage to pollen grains, presumably due to flexing with repeated shrinking and swelling (Campbell, 1994).

Cooling of the climate in MIS 2 caused a decline of plant diversity in the south of the Russian Far East and forced the migration of *Pinus koraiensis* southward where better climate and habitat conditions were found. The abundant pollen record obtained from the sediments, proved that during MIS 2 *Pinus koraiensis* disappeared from the south of the Russian Far East. Principal pollen taxa (Korotky, 2002; Anderson et al., 2017; Belyanin and Belyanina, 2018) suggest that the annual mean temperatures of about 5°C were colder than nowadays, and annual mean precipitation was less than at present. This is consistent with the climatic stratigraphic scheme of the south of the Russian Far East (Korotky et al., 1980; Korotky, 2002).

Most of the *Pinus koraiensis* range during MIS 2 was confined to the south of the Korean Peninsula (Kong et al., 2014) and covered Honshu, Shikoku, and Kyushu, islands of Japan (Miki, 1956; Aizawa et al., 2012), as lower sea level separated them from the continent in a narrow strait (Tsukada, 1984; Ohshima, 1990; Igarashi, 1993; Dobson and Kawamura, 1998; Nakamura and Krestov, 2005).

A common range of *Pinus koraiensis* on the Korean Peninsula, Northeast China, and Japan Islands is confirmed by the results of *Pinus koraiensis* phylogeographic studies. The cpDNA variation indicates that there was no difference between the populations on the Asian continent and those in the Japanese archipelago. Continental populations do not show mtDNA diversity, despite the current extensive range and large populations of the species. Despite that *Pinus koraiensis* is seldom encountered in Japan, the Japanese populations show greater levels of mtDNA diversity. Higher mtDNA diversity (Aizawa et al., 2012) and numerous remains of *Pinus koraiensis* macrofossils recovered at various sites in Japan and dated to the Pleistocene (Miki, 1956) suggest that the Japanese Archipelago once served as a refuge to a much larger *Pinus koraiensis* population with a more extensive range than today. The presence of the single mtDNA haplotype of *Pinus koraiensis* on the Asian continent suggests that the present populations could have expanded from a single refuge population after MIS 2 (Aizawa et al., 2012).

Dated pollen records from northeast China indicate that *Pinus koraiensis* was an important component of coniferous forests, which prevailed in the region before MIS 2. During MIS 2, *Pinus koraiensis* populations in the region underwent great reductions in the range, but they did not disappear completely. Small populations survived in the refuge, which was located on alluvial lowlands and plains, and in mountain ranges during the cold and dry MIS 2 (Kremenetski et al., 1998).

This decline of *Pinus koraiensis* is consistent with climatic and palaeobotanical data. The maps drawn for MIS 2 indicate that temperate-boreal mixed forests in northeast China, which were overlapped by modern forests dominated with *Pinus koraiensis* disappeared completely during MIS 2 (Harrison et al., 2001; Qiu et al., 2011).

Probably, not only low temperatures, but also aridity (Kremenetski et al., 1998) was the limiting factor for the survival of *Pinus koraiensis* during MIS 2. During MIS 2, the East Asian summer monsoon weakened and then intensified in response to the changes in insolation in the northern hemisphere (Cosford et al., 2010). In this case, during the coldest periods of MIS 2, which in the south of the Russian Far East were recorded from 25 300 to 19 300 cal BP, from 14 700 to 13 300 cal BP and from 12 700 to 11 700 cal BP (Korotky, 2002), the range of *Pinus koraiensis* could be preserved in the refuge in the Changbai Mountains and in the Xiaoxingan Ridge (Bai et al., 2010; Qiu et al., 2011). Apparently, *Pinus koraiensis* migrated from these refuge areas to the south of the Russian Far East during warming in early Holocene (Korotky, 2002).

At the same time, it should be noted that during maximum cooling of MIS 2 from 25 300 to 19 300 cal BP (Korotky, 2002), the northern border of coniferous-deciduous forests, in which *Pinus koraiensis* is the main edificator, was located at about 30° N on the Asian continent, and at about 35° N on the islands of Japan. The pollen of *Pinus koraiensis* could not be transferred from the refuge in the Changbai Mountains and Xiaoxingan Range (Bao et al., 2015) to the south of the Russian Far East, since most of it is deposited from pollen rain within 58 km of the source (Ledig, 1998). The above refuges are located at a distance of 200 and 600 km from the south of the Russian Far East, respectively. Taken into account the period of time, which passed since MIS 2 and the rate at which *Pinus koraiensis* can expand its range, it is possible that the modern population in the south of the Russian Far East could have originated from an isolated group of the trees in the Changbai Mountain region (Aizawa et al., 2012).

The migration of *Pinus koraiensis*, the wingless seeds of which cannot be carried by wind (Lanner, 1998) takes place mainly with the help of animals. Nutcracker (*Nucifraga caryocatactes*) is the most important distributing agent, and it can carry a single seed per trip up to 100 *Pinus koraiensis* nuts (Omelko and Omelko, 2017) for a distance of up to 15 km (Formozov, 1976; Mattes, 1985; Hutchins et al., 1996). The Eurasian nuthatch (*Sitta europaea*) can carry a single seed per trip for distances less than 50 m, but it needs nutcrackers to open the cones and to expose the seeds before they can get the seeds and sometimes they take seeds from the soil (Hutchins et al., 1996). Manchurian squirrel (*Sciurus vulgaris mantchuricus*) transfers the nuts for a distance of about 0.6 km (Miyaki, 1987). At the same time, the migration of *Pinus koraiensis* is often limited by the available seed sources, and this would be particularly true for new species encroaching into existing forest vegetation (Iverson et al., 2004).

The beginning of the Holocene at 11 700 cal BP (Walker et al., 2012) was marked by a sharp warming that resulted in conspicuous changes in the structure of the vegetation. *Pinus koraiensis* responded relatively quickly to the changing environment. Significant warming caused the active migration of *Pinus koraiensis* from the refuge in the Changbai Mountains and in the Xiaoxingan Range (Bai et al., 2010; Qiu et al., 2011) to the south of the Russian Far East. According to the palynological data obtained from the south of the Russian Far East (Pavlyutkin et al., 1984; Korotky, 2002; Pavlyutkin and Belyanina, 2002; Mikishin et al., 2008; Anderson et al. 2017; Belyanin et al., 2018; Belyanin and Belyanina, 2018, 2020), dark coniferous (spruce and fir) forests, very diverse in structure, were widespread in the region in the early Holocene. Such vegetation provides good conditions for the growth of *Pinus koraiensis*. In contrast, another cold tolerant species of *Pinus* subgen. *Haploxylon* – *Pinus pumila* cannot grow under the canopy of a closed forest. This species is photophilous and can hardly compete with other trees and shrubs in the shade under the canopy of a closed forest (Kabanov, 1977). Therefore, under the conditions of the onset of warming, *Pinus pumila* was forced to retreat to the north and to the upper belt of the mountains.

During early Holocene (from 11 700 to 8200 cal BP), *Pinus koraiensis* was widespread in the south of the Russian Far East. Significant percentage of *Pinus koraiensis* in the pollen assemblages can indicate that the climate of the early Holocene was milder than in MIS 2, and a stable climatic condition was maintained at the beginning of MIS 1.

Nevertheless, in the early Holocene the presence of *Pinus koraiensis* in the forests of the NFE subdivision was still insignificant. *Pinus koraiensis* grew mainly together with *Betula glandulosa*, *Betula pubescens*, *Alnus alnobetula, Alnus hirsuta, Ulmus davidiana*, *Larix gmelinii, Picea jezoensis* and *Picea koraiensis*. The broadleaved species, such as *Ulmus davidiana* and *Quercus mongolica* were seldom encountered in this subregion (Belyanin and Belyanina, 2018). In the CFE subdivision *Pinus koraiensis* was codominant in the vegetation among *Picea jezoensis*, *Larix gmelinii*, *Abies nephrolepis*, *Betula glandulosa*, *Betula pubescens*, *Quercus mongolica*, *Corylus heterophylla, Ulmus laciniata* and *Ulmus davidiana*. In the SFE subdivision *Pinus koraiensis* became one of the main forest-forming species in the forests with *Quercus mongolica*, *Ulmus* *laciniata*, *Ulmus davidiana*, *Juglans mandshurica*, *Carpinus cordata*, *Tilia amurensis*, *Tilia mandshurica*, *Fraxinus mandshurica*, *Corylus heterophylla*, *Abies holophylla*, *Abies nephrolepis*, *Picea koraiensis* and *Picea jezoensis*. This is strongly confirmed by the pollen records where the proportion of the *Pinus koraiensis* pollen in the SFE subdivision is notably greater than in the sediments from the NFE and CFE subdivisions (Pavlyutkin et al., 1984; Mikishin et al., 2008; Anderson et al., 2017).

The higher proportion of *Pinus koraiensis* in the early Holocene pollen records documented in the SFE subdivision suggests that this species migrated to the south of the Russian Far East from the Korean Peninsula, where the climate was more favourable for the growth of *Pinus koraiensis* even at the beginning of MIS 2 (Kong et al., 2014). The displacement of the *Pinus koraiensis* range to the north in the early Holocene might indicate that the climate in the early Holocene was milder than in MIS 2, and a more stable climatic condition was maintained. This interval corresponds to the time of coniferous – broadleaved forest recovery in the south of the Russian Far East after the MIS 2 epoch had come to its end. Vegetation of the region obtained gradually its modern appearance. Pollen data for northeast China also show that *Pinus koraiensis* grew in the region in the early Holocene, expanding outwards concentrically from the Changbai Mountain region (Ren and Zhang, 1998).

Pollen records for the early Holocene obtained from the south of the Russian Far East are also in good agreement with those in the Lake Baikal region, where the expansion of other species of *Pinus* subgen. *Haploxylon* – species *Pinus sibirica* (Siberian stone pine) began ~11 000 cal BP (Bezrukova et al., 2005). These facts correspond well with evidence on the change of global climate and environment amelioration at that time (Korotky, 2002; Anderson et al., 2017; Belyanin et al., 2018) that led to essential changes in the structure of vegetation.

The transition from the early Holocene (from 11 700 to 8200 cal BP) to the middle Holocene (from 8200 to 4200 cal BP) was marked by a short-term cooling at about 8200 cal BP (Korotky, 2002) that resulted in *Pinus koraiensis* being replaced in part by conifers plants more tolerant to cold. In the mountain ecosystems, in particular on the north-facing slopes, *Pinus koraiensis* together with broadleaved species gave the way to fir and spruce. But the presence of *Pinus koraiensis* remained considerable in the SFE and CFE subdivisions.

According to the data published by A.A. Velichko (2012), global temperatures in the Holocene optimum were 0.7–1°C higher than those today. Probably, in the south of the Russian Far East the rise in the average annual temperature could have been as great as 3–5°C and the amount of precipitations was between 900–1600 mm / year (Mikishin et al., 2019). A maximum in climate warming from 8600 to 5500 cal BP (Korotky et al., 1980; Korotky, 2002) led to the shift of broadleaved plants and some ranges of coniferous plants northward by 200–400 km (Khotinsky, 1977).

As a result of the rise of mean annual temperatures, *Pinus koraiensis* increased notably its presence in the south of the Russian Far East (Belyanin and Belyanina, 2019). Its fossil pollen was recorded in each subregion in the south of the Russian Far East. Plant formations were more diversified in species composition compared with those of present days. It should be noted that in a drier climate in the adjacent mountains in northeastern China, near Lake Sihaylongwan, *Pinus koraiensis* began to spread from ~6600 cal BP, where it became one of the main forest-forming species at ~5200 cal BP (Stebich et al., 2015), and in the Lake Qingbohu (Jingbo) region *Pinus koraiensis* began to spread from 5400 cal BP (Li et al., 2011). Similar processes are known to have taken place in the Lake Baikal region where *Pinus sibirica* was one of the chief forest-forming species at ~6800 cal BP (Danko et al., 2009).

Cooling, which started at the transition from the middle Holocene to the early Holocene about 4200 cal BP, resulted in a competition between *Pinus koraiensis* and species more tolerant to cold like *Picea jezoensis* and *Abies nephrolepis* that led to a reduction of *Pinus koraiensis* in the vegetation. The general trend towards cooling was interrupted by short-term warning from 4700 to 3500 cal BP (Korotky, 2002). It was marked by an increase in the role of *Pinus koraiensis* in the vegetation. It was a codominant species in the plant formations with *Pinus densiflora*, *Abies holophylla*, *Abies nephrolepis*, *Quercus mongolica*, *Ulmus laciniata, Ulmus davidiana, Carpinus cordata*, *Fraxinus mandshurica*, *Syringa*, and other warm-tolerant trees. The subsequent cooling periods from 11 500 to

10 100 cal BP, from 9300 to 8800 cal BP, from 5300 to 4700 cal BP, from 3300 to 2600 cal BP, and from 700 to 100 cal BP (Korotky, 2002) led to a decrease in the role of *Pinus koraiensis* in the vegetation, which had been largely replaced by *Abies* and *Picea*, along with the lowering of its altitudinal range (tree line).

Similar processes took place in the Lake Baikal region from 2600 to 2000 cal BP, when forests with Siberian stone pine gained substantial territories in the area (Bezrukova et al., 2013). Another short-term warming from 1700 to 700 cal BP (Korotky, 2002) led to the expansion of *Pinus koraiensis* and broadleaved plants in the south of the Russian Far East. It seems likely that *Pinus densiflora*, *Betula pubescens*, *Betula costata*, *Abies holophylla*, *Carpinus cordata*, and some other plants were present as codominant (Belyanin and Belyanina, 2012, 2018; Belyanin et al., 2019).

Spatial fluctuations of the *Pinus koraiensis* range occurred in the late Holocene (from 4200 cal BP to the present day) against the background of an unstable climate and gradually decreasing heat supply (Wanner et al., 2008). Palynological data (Pavlyutkin et al., 1984; Korotky, 2002; Pavlyutkin and Belyanina, 2002; Bazarova et al., 2008; Mikishin et al., 2008; Anderson et al., 2017; Belyanin and Belyanina, 2018, 2020) suggest some wave-like fluctuations of the proportion of *Pinus koraiensis* in the vegetation.

Apparently, an anthropogenic impact began to influence the distribution of *Pinus koraiensis* in the south of the Russian Far East in the Neolithic epoch. Pollen data in the Iman River valley, the NFE subdivision in the south of the Russian Far East, indicate significant vegetation changes during the periods of occupation at 5000 cal BP and 4000 cal BP. They reflect fire clearance of taiga forests for new pastoral lands and/or wood cutting used for archaeologically documented log houses (Chlachula et al., 2015).

In the cultural layers, corresponding to the Almazinka Culture (4580–3530 cal BP) and the Dal'nyy Kut Culture (2910–2410 cal BP), progressive valley vegetation associated with the dominance of light-demanding *Phellodendron* thickets and a forest-steppe with *Betula pubescens* and Asteraceae, respectively have been found. A change from a mixed broadleaved forest with *Pinus koraiensis* to a semi-open forest and steppe-parklands also took place. The latter was interpreted as a result of a direct anthropogenic impact on the pristine vegetation (Chlachula et al., 2015).

At the beginning of the 1890s AD the south of the Russian Far East was populated by the Russians. According to the records of that time, broadleaved-*Pinus koraiensis* forests in the south of the Russian Far East covered an area of about 65 000 km^2 (Petropavlovsky et al., 1985). By today, the size of such areas has decreased by 33 000 km^2 (Petropavlovsky et al., 1985; Nakamura and Krestov, 2005). Extensive felling, fires, strong winds, the proliferation of insect pests contributing to the change of deciduous forests with *Pinus koraiensis* into simpler secondary plantations are the main reasons for the decrease of forest areas (Ivanov and Shashenok, 2018). The area formerly covered with broadleaved-*Pinus koraiensis* forests is now occupied by secondary *Betula pubescens*, *Larix dahurica*, *Populus tremula* forests formed mainly after logging and/or single fires, also by secondary *Quercus mongolica* forests (12 000 km^2) formed after logging and regularly repeated fires, especially around settlements, and by near agricultural lands (about 15 000 km^2) (Nakamura and Krestov, 2005). At the same time, the remaining primary forests with *Pinus koraiensis* continue to experience the extreme stress caused by a growing anthropogenic pressure and sharp climate changes.

The maps of potential vegetation (Kolesnikov, 1954, 1956) and bioclimatic indices (Grishin, 1995) suggest the possibility of a wide distribution of broadleaved forests with *Pinus koraiensis* at the edaphically suitable sites in the south of the Russian Far East. However, the area of this vegetation type is much smaller both in China and in the south of the Russian Far East (Petropavlovsky et al., 1985).

Human activity of the Dzhurzhen (Juchen, Jurchen) population between 500 and 700 cal BP has led to a decrease in the areas of forests due to clearing for agricultural lands. Since then the region has remained relatively densely populated, and regular fires have supported the development of vegetation without conifers (Nakamura and Krestov, 2005). In the south of the Russian Far East most fires have originated from human activities for the last 250 years (Sheingauz, 1996).

Using gap models, earlier studies predicted the change of forests under a warming climate in the region of Northeast China adjacent to the south of the Russian Far East. They predict drastic changes in the major forest types, where dominant species became extinct or were replaced within a relatively short period of time by species, which adapted better to new climate conditions. For example, the extinction of *Pinus koraiensis* within 80 years, followed by the complete dominance of *Quercus mongolica* was predicted in *Pinus koraiensis*-hardwood forests (Zhao et al., 1998; Hao et al., 2001).

The results of modelling the response of a forest ecosystem to warming of the climate, taking into account the spatial effects in north-eastern China, show some recovery of *Pinus koraiensis* from the levels of low abundance due to cutting. But it is recovered to substantially lower abundance compared with the predicted current climatic scenario. Simulations with a warming climate scenario indicate that the abundance of *Pinus koraiensis* in north-eastern China will be 10% by 2290 AD compared to the 44.5% under the current climate. At the same time, oak abundance in forests increases steadily from 20% at 1990 AD to almost 40% by 2290 AD. Modelled proportions are 7% for maple, 3% for elm and basswood, and 2% for aspen by 2290 AD (He et al., 2005).

According to one of the scenarios of climate change in the future (model CMIP5, phase five of the Coupled Model Inter-comparison Project), the global temperature averaged from 2041 to 2050 AD is projected likely to exceed 2°C but unlikely to exceed 4°C above the global temperature averaged from 1850 to 1900 AD (Stocker et al., 2013). Recent CMIP5 scenarios also predicted that not only surface air temperatures but also precipitation in north-east China between 2071 and 2100 AD would be higher than those between 1986 and 2005 AD (Xu and Xu, 2012).

Based on the predicted averages of rainfall and temperature and a new model HadCM2 for 2 030, predictions were made on the future distributions of *Pinus koraiensis*. The result shows that the southern boundary of the potential distribution area of *Pinus koraiensis* would have a northward shift of 0.1° to 0.6° in latitude, and the northern boundary would have a northward shift from 0.3° to 0.5°. Other parts of the distribution region remain roughly the same. The area of potential distribution of *Pinus koraiensis* would increase by 3.4% of the total distribution area compared with the area before climate change (Xu and Yan, 2001).

CONCLUSIONS

Palynological and chronostratigraphic data obtained in the course of our studies provided the grounds to determine the chronological timing of the spatial migration of *Pinus koraiensis* and to correlate it with the climate fluctuations explaining the changes of the geographical range of *Pinus koraiensis* in the south of the Russian Far East during MIS 5 (127 000–71 000 BP), MIS 3 (57 000 BP–28 000 cal BP), MIS 2 (28 000–11 700 cal BP), and MIS 1 (11 700 cal BP–to present). During MIS 5 and MIS 3, *Pinus koraiensis* was widely spread in the south of the Russian Far East. Under cold climate in MIS 2, *Pinus koraiensis* disappeared from the regional vegetation. At the transition from MIS 2 to MIS 1 the range of *Pinus koraiensis* expanded northwards. The species became the principal component of the vegetation in the south of the Russian Far East. The increase in its proportion in the vegetation in the Holocene coincided mostly with the periods of climate warming from 11 700 to 11 500 cal BP, from 10 100 to 9300 cal BP, from 8800 to 5300 cal BP, from 4700 to 3500 cal BP, and from 2600 to 1800 cal BP. In this case, the most diversified vegetation with *Pinus koraiensis* was typical of the Holocene optimum of the south of the Russian Far East from 8800 to 5300 cal BP.

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