



Spatiotemporal dynamics of *Pinus densiflora* in the south of the Russian Far East during the Late Pleistocene and the Holocene by pollen records

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ABSTRACT

The aim of the present work is to reconstruct the distribution of *Pinus densiflora* Siebold & Zucc. in the south of the Russian Far East (SRFE) during the Late Pleistocene (MIS 2) and the Holocene based by pollen records and chronological data. We found that *P. densiflora* did not grow in SRFE under cold and dry climate of the MIS 2. Warming in the Early Holocene caused the expansion of *P. densiflora* to the region. Under maximum warming during the Middle Holocene, *P. densiflora* range reached the Central Subregion of the SRFE. The cooling at the beginning of the Late Holocene caused the decrease of *P. densiflora* distribution in the SRFE. Under subsequent warming during the second half of the Late Holocene, *Pinus densiflora* has taken again a dominant position in the Southern and the Central subregions in the SRFE. During the last two centuries, *P. densiflora* range in the region began to degrade, due to the anthropogenic influence.

Keywords: *Pinus densiflora*, spore-pollen analysis, radiocarbon dating, of the south of the Russian Far East, climatic changes, Late Pleistocene, Holocene

РЕЗЮМЕ

Белянин П.С., Белянина Н.И. Пространственно-временная динамика *Pinus densiflora* на юге Дальнего Востока России с позднего плейстоцена по пыльцевым летописям. Целью настоящей работы является реконструировать распространение *Pinus densiflora* Siebold & Zucc. на юге Дальнего Востока России в позднем плейстоцене (МИС 2) и голоцене на основе пыльцевых летописей и хронологических данных. Анализ таксономической структуры пыльцевых летописей показал, что *P. densiflora* не произрастала на юге Дальнего Востока России в условиях холодного и сухого климата МИС 2. Потепление в раннем голоцене вызвало миграцию *P. densiflora* на юг Дальнего Востока России. При максимальном потеплении в среднем голоцене ареал *P. densiflora* достиг Центральной области юга Дальнего Востока России. Похолодание в начале позднего голоцена привело к сокращению распространения *P. densiflora* в регионе. При последующем потеплении во второй половине позднего голоцена *P. densiflora* вновь заняла господствующее положение в Южной и Центральной областях юга Дальнего Востока России. В течение последних двух столетий ареал *P. densiflora* в регионе начал деградировать из-за антропогенного воздействия.

Ключевые слова: *Pinus densiflora*, спорово-пыльцевой анализ, радиоуглеродное датирование, юг Дальнего Востока России, климатические изменения, поздний плейстоцен, голоцен

The process of space-time migration of plants is interesting, but not completely studied question of the evolution of the Earth's vegetation. That process is a characteristic consequence of the direct and natural response of vegetation to climatic fluctuations, which have been superimposed by an anthropogenic influence in recent millennia (Wang & Feng 1991). Climate has a far-reaching effect on the configuration of plant ranges and is a key determinant of their spatial distribution (Wu et al. 2009). Under climatic fluctuations, there is a noticeable shift in the horizontal and altitudinal boundaries of plant ranges, which causes significant changes in the species composition of vegetation (Shin et al. 2021). Even low-amplitude climatic fluctuations cause significant spatial migrations of plants, which are most noticeable and pronounced near the boundaries of their ranges.

One of such regions is the south of the Russian Far East located in the north of Sino-Japanese floristic region, the richest one by the species of the Holarctic area. It in-

cludes 20 endemic families and higher representation of the endemic species (Good 1974). In this region the ranges' plants of the tropical, subtropical, and temperate zones of East Asia are overlapped with the areals of the elements of the flora of Eastern Siberia. Some plants of the flora of this region grow around the northern borders of their geographical ranges, under extreme climatic conditions for growth (Nakamura & Krestov 2005). *Pinus densiflora* Siebold & Zucc. is one of them. Therefore, this is a key region for studying the influence of climatic fluctuations on the spatiotemporal migrations of plants in the past.

The pollen records are effective in such detecting changes at the margin of vegetation zones or species distribution limits which are particularly sensitive even to minor climate fluctuations. Pollen analysis is accuracy and allow the ability to correlate paleobotanical results with other regions, the relative ease of obtaining data, and stable calculation of results. Even of a small amount of radiocarbon-dated pollen records, they allow reliable results that make it possible to

reconstruct geographical distribution of plants in the past. Therefore, such studies are important to understand the response of plants to likely climate changes in the future.

Analysis of the taxonomical structure of the pollen records made it possible to reconstruct the history and dynamic of major tree species in most regions of the Earth during the Late Pleistocene and the Holocene (e.g., Birks 1989, Velichko 2009, 2012, Chung et al. 2010, Helmens 2014, Binney et al. 2017). Obtained paleobotanical data is evidenced, that the global restructuring of the vegetation cover occurred under numerous climatic fluctuations during the Last Glacial Epoch (Marine Isotope Stage (MIS) 2) and in the Interglacial Epoch – the Holocene. This process also influenced the basins of the rivers of the Sea East basin. Due to the fluctuations of temperature, humidity and the changes of the monsoon circulation (Yi & Kim 2010) extensive restructuring of the vegetation cover also occurred in the south of the Russian Far East (Belyanin & Belyanina 2012, 2018, Korotky 2002). However, the spatiotemporal plants migrations in this region in past is still are almost unexplored. Only in the recent years, the spatial migrations in the south of the Russian Far East of one of the representatives of the genus *Pinus* – *Pinus koraiensis* Siebold & Zucc. were reconstructed (Belyanin & Belyanina 2019, 2021). Apparently, the scanty of such data is due to the poor development of paleobotanical research in this region.

The present work aims to reconstruct the time-spatial distribution of *Pinus densiflora* in the south of the Russian Far East during the Late Pleistocene (MIS 2) and the Holocene in respect of vegetation history, geographical range, dispersal, and migration to gain a better understanding of the features distribution of this species in past taking into account the changing climate and environment.

MATERIAL AND METHODS

Study area

The south of the Russian Far East is the study area (Fig. 1A). This is the way how the region is traditionally called in Northeastern Asia. It lies between 42°18'N and 50°07'N and 130°57'E and 140°52'E. In the east it is washed by the Sea of Japan (East Sea) and borders with China, North Korea, and Japan (Fig. 1B).

Climatic settings

The south of the Russian Far East is located in the cold temperate and cool temperate climatic zones in the Northeastern Asia. The climate of this area is characterized by Kira's warmth index exceeding 45 (Grishin 1995). Summer precipitation exceeds that of winter precipitation. Precipitation always exceeds evaporation.

Climate of this area is mainly controlled by the East Asian monsoon. It is characterized by prominent seasonality, due to the seasonal migration of the monsoon front across these regions (Nakagawa et al. 2006). As the seasonal temperature variability on the continent is greater than that in the ocean, the temperature gradient between the two air masses creates a surface-air pressure gradient that seasonally changes its direction, forcing NW surface cold winds

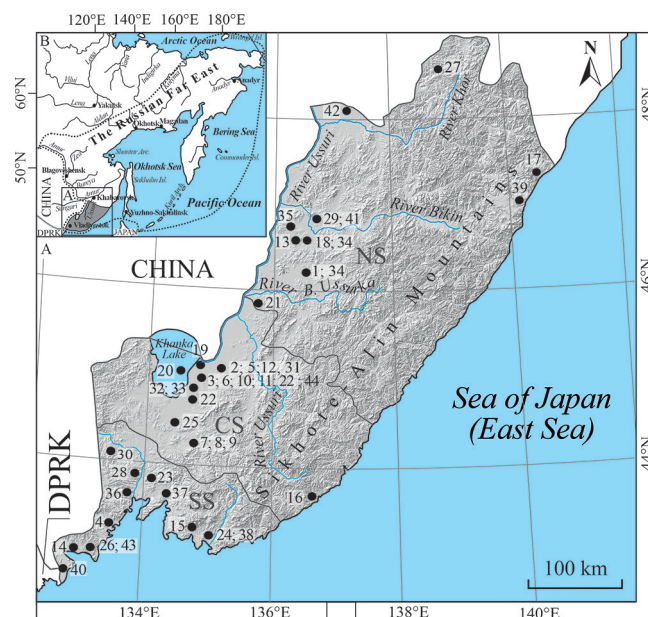


Figure 1 Overview maps showing (A) the location (inset) of the study region (the south of the Russian Far East) in Northeastern Asia and (B) location of studied pollen records (see Table 2 for site names per number). The digital elevation model is based on 90-m-resolution Shuttle Radar Topography Mission (SRTM) v4.1 data (Jarvis et al. 2008). SS – the Southern Subregion, CS – the Central Subregion; NS – the Northern Subregion

in winter and SE warm and humid winds in summer (Fig. 2). In winter, from December to February, it is cold and dry, due to the establishment of the strong Siberian anticyclone in Siberia and Tibetan Plateau. Meanwhile, summer, from June to August, is hot and wet, with frequent heavy rains (An 2000, Nakagawa et al. 2006, Yancheva et al. 2007). Mean temperatures in July and in January are ranging from 18°C to 20°C, and from -12°C to -21°C, respectively. Precipitation is relatively high (mean, 750 mm), and about 70 % of annual precipitation falls in summer, especially from June to August (Federal 2023).

Pinus densiflora

Geographical range of *P. densiflora* mainly lies in the ranges 32–45.3°N and 114–141°E (Fig. 3), within China (Shandong, Jiangsu, Eastern and Southern Heilongjiang, Northeastern Jiangsu, SE Jilin, Liaoning, Eastern and Northern Shandong), Japan (Southern Hokkaido, Honshu, Shikoku, Kyushu), South and North Korea (Critchfield & Little 1966).

The southern limit of *P. densiflora* is on Jeju Island in South Korea at about 33°20'N. The northern limit of *P. densiflora* is on the south of the Russian Far East. This species forms there plant communities which are rare for the flora of Russia (Krestov et al. 2006, Krestov & Verkholat 2003).

Botanical description. *Pinus densiflora*, Korean Red pine or Red Japanese pine, is the member of the family Pinaceae, genus *Pinus*, subgenus *Diploxylon*. This is an evergreen coniferous tree. It reaches 30 m in height, with a trunk diameter of up to 1.5 m. Its needle leaves are 8–12 cm long, with two per a fascicle. The cones are 4–7 cm long (Urusov et al. 2007).

Ecology. *Pinus densiflora* is an endemic species of Eastern Asia. It is encountered in the subtropical, temperate, and sub-boreal climate zones in the Eastern Asia (Kremenetski et al. 1998). That species is one of the main forest-forming species in the area of transition from oceanic to monsoonal-continental climate (Krestov & Verkholat 2003).

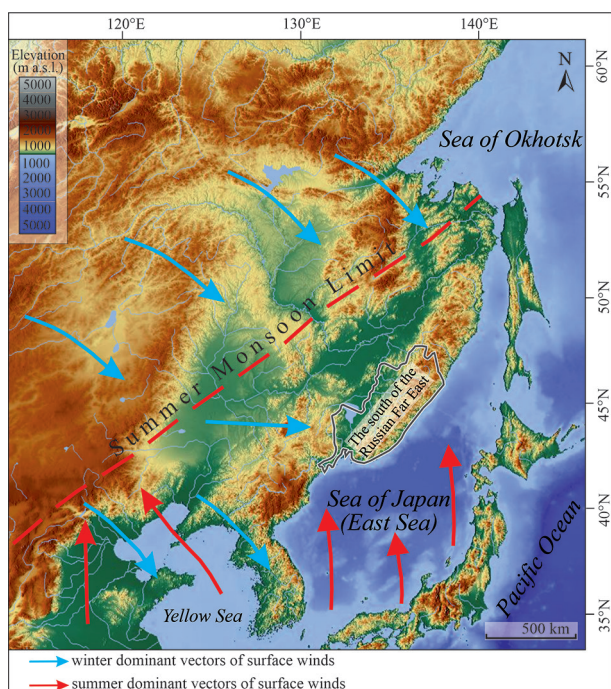


Figure 2 Seasonal changes in the wind system of the East Asian monsoon area (modified from Yi 2011)

Pinus densiflora is very light-demanding, frost- and drought-resistant and requires active temperatures between 2300 and 3600°, with an annual rainfall between 900 and 2000 (4000) mm (Fig. 4) (Urusov et al. 2007). Its seedlings are particularly light-demanding. An average annual temperature between 7.5 and 18.7°C is necessary for their growth (Nakamura & Krestov 2005). Its cold hardiness limit is between -23.3°C and -28.8°C under prolonged frosts (Bannister & Neuner 2001). This species does not stand prolonged soil freezing of the open, wind-blown and waterlogged places (Usenko 2009).

The major climatic factors affecting the geographical distribution of *P. densiflora* are the precipitation of the warmest quarter of the year (650–800 mm), temperature seasonality (900–1050°C), mean annual temperature (10–13°C) and mean temperature of the wettest quarter (23–24°C) (Duan et al. 2022) (Table 1).

Slightly acidic soil on the well-drained sand or gravel is the most favorable soil type for *P. densiflora* granite debris eroded by storm waters during the monsoon in summer and by water from melting snow in spring (Lee 1995). *Pinus densiflora* with such a wide range of tolerance is normally encountered on the thin and infertile soils of rock outcroppings, weathered rocks, ridge tops, and the sandy or pebble shores of streams. It also can grow well in disturbed soils along both mountain slopes and bases after forest thinning or brush removal near human settlements (Lee 1976, Toyohara 1981, 1984). *Pinus densiflora* is an excellent pioneer species for secondary succession, and, thus, is crucial for reforestation and soil and water conservation (Lee 2002).

Habitats of *P. densiflora* in the south of the Russian Far East tend to the coastal and mountainous areas. If in the south of the Korean Peninsula it sometimes reaches 2300 m a.s.l. (Ohwi 1965, Farjon 2010), then in the south of the Far East, the upper altitudinal limit of its distribution does not exceed 600–700 m a.s.l. Near the northern limit range *P. densiflora* grows in groves, which are represented by single trees among broadleaved and conifer-broadleaved forests, and the shrub thickets. It grows mainly in southern, well-insolated, dry treeless slopes, rocks and tops of the rocky ridges (Urusov et al. 2007). On the Pre-Khanka Plain and on the coast of



Figure 3 The modern geographical distribution of *Pinus densiflora* Siebold et Zucc. (Critchfield & Little 1966). 1 – the outlines of modern range of *P. densiflora*, 2 – the south of the Russian Far East, 3 – the main settlements, 4 – the main rivers

the Peter the Great Bay *P. densiflora* grows on sandy soils (Krestov & Verkholat 2003, Kharkevich & Kachura 1981). On gentle slopes, *P. densiflora* can not compete with other tree species at all and is replaced by them.

Approach

To reconstruct time-spatial distribution of *P. densiflora* in the south of the Russian Far East during the Late Pleistocene and Holocene, we analyzed of taxonomical structure of new and previously published pollen records and radiocarbon data (Table 2) (Alexeyev & Golubeva 1980, Korotky et al. 1980, Pavlyutkin et al. 1984, Korotky 2002, Pavlyutkin & Belyanina 2002, Bazarova et al. 2008, Mikishin et al. 2008, Belyanin & Belyanina 2012, 2018, 2020, Belyanin et al. 2018, 2019, Anderson et al. 2017). The sites of pollen dataset collection are divided into three subregions according to their climatic characteristics and geographical positions – the Southern, the Central, and the Northern subregions of the south of the Russian Far East (see Fig. 1A).

Table 1. The rate of climatic factors contribution for the growth of *Pinus densiflora* (Duan et al. 2022).

Climatic factors	Contribution (%)
Mean Annual Temperature (°C)	6.6
Isothermality	5.1
Temperature Seasonality (standard deviation × 100) (C of V)	13.9
Mean Temperature of the Wettest Quarter (°C)	5.6
Mean Temperature of the Driest Quarter (°C)	0.2
Precipitation of the Wettest Month (mm)	0.9
Precipitation of the Warmest Quarter (mm)	67.7

Table 2. Radiocarbon dates.

Boreholes, cores & cross-sections names	Site No.	Depth, m	Dated material	Laboratory number	¹⁴ C Age, BP	Calibrated age range, cal BP	References
Borehole 526	10	9.10–9.15	wood	Ki–3621	43400±190	45 928–45 572	unpublished
core Lake Karasie	14	3.24–3.23	seeds, wood, moss stem	CAMS # 71 813	35 610±510	41 206–40 248	Anderson et al. 2017
cross-section 6205	18	10.60–10.57	wood	Ki–3370	34 500±250	39 930–39 382	Belyanin & Belyanina 2018
cross-section 9119	23	1.61–1.58	wood	Ki–2236	30 000±600	35 143–33 873	unpublished
cross-section Akulinin	17	1.30–1.28	peat	Ki–2904	29 430±475	34 458–33 338	Korotky 2002
cross-section 6204	13	9.14–9.10	wood	Ki–3275	27 750±150	31 809–31 509	Belyanin & Belyanina 2018
cross-section Tikhangu Bay	15	12.67–12.60	wood	Ki–2904	27 000±1500	33 615–30 029	Korotky 2002
borehole 613	2	2.60–2.55	wood, plant detritus	Ki–2383	22 890±350	28 087–27 343	unpublished
cross-section Akulinin	17	3.35–3.30	peat	MAG–341	22 700±80	27 222–26 886	Korotky 2002
borehole 313	1	9.06–9.01	wood	Ki–2758	22 330±210	26 672–26 399	unpublished
cross-section River Vinogradnaya	43	3.00–2.92	peat	GIN–745	22 200±500	27 020–26 058	Alexeyev & Golubeva 1980
cross-section 4037	3	3.10–3.07	wood	Ki–2359	21520±320	21 480–21 200	unpublished
cross-section 6276	19	1.00–0.94	wood	Ki–2174	18 580±225	22 774–22 302	unpublished
cross-section 6205	18	6.90–6.85	wood	Ki–3293	17 990±200	22 135–21 571	Belyanin & Belyanina 2018
borehole 579	20	5.22–5.19	humified loam	Ki–2166	17 840±200	21 946–21 356	Belyanin & Belyanina 2012
cross-section 4118	44	3.00–2.96	wood	Ki–2164	17 830±200	21 934–21 344	unpublished
borehole 526	10	4.91–4.88	plant detritus	Ki–2751	17 640±70	21 275–21 047	unpublished
cross-section 4110	5	2.20–2.14	wood	Ki–2378	17 740±280	21 895–21 143	unpublished
core Lake Karasie	14	1.66–1.63	seeds, wood, tree moss	CAMS # 73 291	17 160±40	20 793–20 629	Anderson et al. 2017
borehole 620	6	5.90–5.83	wood	Ki–2183	15 930±210	19 482–19 010	unpublished
cross-section 6205	18	5.73–5.69	wood	Ki–3 294	14 800±100	18 225–17 981	Belyanin & Belyanina 2018
cross-section 9134	8	1.90–1.86	wood	Ki–4038	13 980±110	17 171–16 813	unpublished
borehole 526	10	7.30–7.23	wood	Ki–2751	13 290±60	16 075–15 865	unpublished
cross-section 6205	18	3.64–3.61	wood	Ki–3298	12 300±100	14 594–14 098	Belyanin & Belyanina 2018
cross-section Pravyi Bereg	4	2.60–2.52	vegetative detritus & shrub twigs	Tka–13 007	12 240±160	14 610–13 974	Mikishin et al. 2008
borehole 313	1	3.50–3.44	wood	Ki–2750	12 090±90	14 024–14 024	unpublished
cross-section 6213	11	1.50–1.46	wood	Ki–2370	11 920±170	14 025–13 585	unpublished
cross-section 6204	13	3.10–3.06	wood	Ki–3343	11 270±80	13 242–13 102	Belyanin & Belyanina 2018
borehole 328	34	1.61–1.64	wood	Ki–3674	11 040±40	13 039–12 911	unpublished
cross-section 9139	9	6.00–5.94	wood	Ki–2363	10 120±140	12 008–11 430	unpublished
cross-section 9132	7	0.92–0.89	plant detritus	Ki–4058	9950±65	11 889–11 635	unpublished
borehole 508	22	4.50–4.43	wood	Ki–2171	9680±130	11 529–11 294	Belyanin & Belyanina 2020
cross-section 4074	12	2.12–2.07	wood	Ki–2140	9600±110	11 098–10 774	unpublished
cross-section 9119	23	2.14–2.10	wood	Ki–2235	9250±70	10 516–10 332	unpublished
cross-section 9119	23	1.61–1.58	wood	Ki–2234	8960±80	10 184–9930	unpublished
borehole 9	24	6.51–6.48	plant detritus	Ki–3688	8900±60	10 136–9902	Pavlyutkin & Belyanina 2002
cross-section Creek Bolotisty	27	3.20–3.14	peat	LU–8138	8620±90	9745–9501	Belyanin et al. 2018
cross-section 1438	25	1.70–1.65	wood	MAG–332	8180±80	9267–9025	Korotky et al. 1980
cross-section 272	26	1.96–1.90	wood	SOAN–7179	7995±45	8995–8767	Mikishin et al. 2008
borehole 335	21	1.81–1.75	plant detritus	Ki–2953	7950±50	8919–8705	unpublished
core Lake Karasie	14	1.40–1.37	seeds, wood, charcoal	CAMS # 73 290	7550±40	8415–8319	Belyanin et al. 2019
cross-section 4005	28	2.40–2.37	plant detritus	Ki–2365	7240±120	8193–7975	Pavlyutkin & Belyanina 2002
cross-section 4049	32	2.30–2.24	plant detritus	Ki–2374	7160±140	8127–7835	unpublished
borehole 526	10	3.80–3.83	plant detritus	Ki–2751	7050±40	7929–7835	unpublished
cross-section 6010	29	1.70–1.66	plant detritus	Ki–3269	6660±70	7590–7472	Belyanin & Belyanina 2018
cross-section 272	26	1.75–1.68	wood	SOAN–7181	6555±40	7510–7420	Mikishin et al. 2008
cross-section 4005	28	2.20–2.15	plant detritus	Ki–2159	6530±75	7514–7364	Pavlyutkin & Belyanina 2002
cross-section 6056	35	2.92–2.88	plant detritus	Ki–3256	6090±70	7068–6852	Belyanin & Belyanina 2018
cross-section River Kazachka	30	0.95–0.98	wood	DVGU–TIG–28	6035±94	7018–6762	Pavlyutkin et al. 1984
cross-section 4074	12	1.72–1.68	plant detritus	Ki–2 139	5800±50	6665–6533	unpublished
borehole 328	34	3.11–3.08	wood	Ki–3 672	5650±40	6517–6353	unpublished
cross-section 6159	31	3.05–2.97	wood	Ki–2141	5360±75	6231–6043	unpublished
cross-section 6205	18	0.80–0.76	peat	Ki–3372	5120±80	5960–5746	Belyanin & Belyanina 2018
core Lake Karasie	14	1.04–1.03	seeds, charcoal	CAMS # 71 814	5050±40	5876–5748	Belyanin et al. 2019
core Lake Utinoye	14	4.71–4.68	wood, charcoal	CAMS # 73 295	5000±80	5834–5646	Belyanin et al. 2019
core Lake Karasie	14	0.77–0.74	seeds	CAMS # 74 346	4890±40	5675–5583	Belyanin et al. 2019
cross-section 1706–1	37	1.89–1.86	buried soil	LU–8780	4650±110	5529–5207	Belyanin et al. 2021
cross-section 4005	28	2.12–2.07	peat	Ki–3679	4 600±60	5444–5188	Pavlyutkin & Belyanina 2002
Pravyi Bereg	4	2.00 – 1.90	peat	SOAN–3938	5125±45	5963–5789	Mikishin et al. 2008
core Lake Karasie	14	0.67–0.60	seeds	CAMS–73288	4300±40	4914–4812	Belyanin et al. 2019
Pravyi Bereg	4	1.39–1.35	peat	SOAN–3937	4225±50	4819–4661	Mikishin et al. 2008
cross-section 9031a	38	2.43–2.39	wood	Ki–3686	4210±60	4865–4570	Pavlyutkin & Belyanina 2002
cross-section Tikhangu Bay	15	1.25–1.20	peat	TIG–DVGU–51	4195±50	4815–4641	Korotky 2002
cross-section 4053	33	2.30–2.26	wood	Ki–2135	4130±60	4776–4568	unpublished

Table 2. Continued.

Boreholes, cores & cross-sections names	Site No.	Depth, m	Dated material	Laboratory number	¹⁴ C Age, BP	Calibrated age range, cal BP	References
core Lake Utinoe	36	3.47–3.45	wood	CAMS # 76 800	3920±40	4419–4285	Belyanin et al. 2019
core Lake Karasie	14	0.45–0.43	seeds	CAMS # 74 344	3870±40	4372–4226	Belyanin et al. 2019
borehole 328	34	1.61–1.64	wood	Ki–3 673	3820±40	4293–4137	unpublished
cross-section 6159	31	2.31–2.27	plant detritus	Ki–2 142	3620±40	3971–3891	unpublished
cross-section Ovrazhnyii–2	16	2.10–2.00	wood	TIG–41	3490±90	3883–3639	Korotky 2002
cross-section Pravyi Bereg	4	1.15–1.00	peat	SOAN–5 054	3715±60	3465–3325	Mikishin et al. 2008
cross-section 1706–1	37	0.73–0.70	buried soil	LU–8 779	3020±100	3330–3070	Belyanin et al. 2021
cross-section 4118	44	2.54–2.51	wood	Ki–2 181	2750±40	2886–2788	unpublished
cross-section 1504	39	2.80–2.70	wood	MAG–244	2770±60	2322–2162	Korotky 2002
core Lake Utinoe	36	2.23–2.21	plant detritus	CAMS # 76 799	2510±60	2236–2040	Belyanin et al. 2019
cross-section 1508–1	40	2.88–2.73	buried soil	LU–7961	2460±100	2665–2413	Belyanin et al. 2019
cross-section 6022	41	1.60–1.57	plant detritus	Ki–3 270	2350±40	2454–2298	unpublished
cross-section Pravyi Bereg	4	0.65–0.60	peat	SOAN–3935	2275±45	2308–2176	Mikishin et al. 2008
cross-section Ovrazhnyii–2	16	1.05–0.95	wood	TIG–1966	2220±60	2298–2144	Korotky 2002
cross-section 4005	28	1.80–1.77	wood	Ki –3678	1930±40	1907–1791	Pavlyutkin & Belyanina 2002
cross-section 1508–1	40	1.52–1.44	buried soil	LU–7960	1930±100	1983–1729	Belyanin et al. 2019
core Lake Utinoe	36	1.30–1.27	wood	CAMS # 76 798	1810±60	1787–1631	
cross-section 4074	12	0.59–0.55	wood	Ki–2169	1550±80	1519–1363	unpublished
cross-section 6159	31	3.10–2.97	plant detritus	Ki–2143	1480±40	1395–1319	unpublished
cross-section 4118	44	1.20–1.22	wood	Ki–1460	1460±45	1381–1309	unpublished
cross-section Tikhangu Bay	15	0.55–0.50	peat	SOAN–136	1375±75	1361–1213	Korotky 2002
cross-section 1508–1	40	0.65–0.57	buried soil	LU–7959	1360±60	1337–1217	Belyanin et al. 2019
cross-section Pravyi Bereg	4	0.3–0.25	peat	SOAN–3934	640±40	669–539	Mikishin et al. 2008

Collection, preparation of the sediment samples and palynological analysis

New pollen and chronological data were obtained from cross-sections 4037, 6276, 4118, 9134, 6213, 328, 9139, 9132, 4074, 9119, and boreholes 335, 526, and 620. 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/cm³), after which the samples were mounted in glycerol jelly (Pokrovskaya 1966). Pollen and spores in glycerol jelly were identified and counted using an optical microscope Axio Scope A1 at ×400 magnification. Proportion of each pollen taxon was calculated in percent of the pollen sum arboreal taxa, dwarf shrubs and herbs. Proportion of plant groups (trees and shrubs – AP, herbs, grass, and dwarf shrubs – NAP, spores – SP) was calculated in percent of the total amount of microfossils. At least 250 pollen grains of arboreal and dwarf shrubs plants were counted in each sample. Identifications of pollen grains were made with the aid of pollen atlases (Pokrovskaya 1950, Nakamura 1980). Latin names are given according to Plants of the World Online (POWO 2023). 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 *P. densiflora* pollen records is based on results of radiocarbon dating of eighty seven samples of peat, wood, plant detritus, buried soil, seeds, moss stem and humified loam. They were dated by radiocarbon method in the Laboratory of Geochronology, Saint-Petersburg State University; in the Lawrence Livermore Center of Accelerated Mass-Spectrometry of the National Laboratory, Department of Energy, the University of California; in the

Laboratory of Radiocarbon Dating, University Museum, University of Tokyo and in the Institute of Geological Sciences of National Academy of Sciences, Kiev. Obtained radiocarbon dates were calibrated using OxCal 4.4 with the "IntCal 20" calibration curve (Ramsey 2017, Reimer et al. 2020) (see Table 2).

Age-depth modeling

To construct the continuous chronology of sediments from cross-sections, cores, and boreholes which have more than two radiocarbon dates (the cores from the lakes Karasie and Utinoe; boreholes 313, 328, 613, and 526; cross-sections Pravyi Bereg, 1508, 4005, 4037, 4053, 4074, 4118, 6159, 6204, 6205, 6276, and 9119), we used an age-depth models constructed using the Bacon program (Blaauw & Christen 2011) in R (R Core Team 2017). Using the age-depth modeling method allowed us to test the calendar ages of the calibrated radiocarbon dates and their probability density functions by a repeated random sampling method

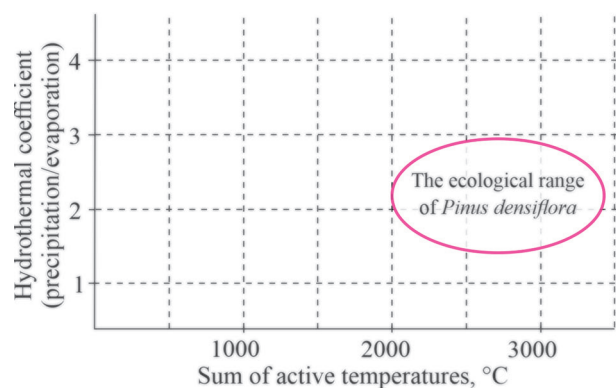


Figure 4 The The thermal and humid ecological range of *Pinus densiflora* (Urusov et al. 2007)

(Blaauw & Christen 2011, Telford et al. 2004). It allowed, it was found that the obtained calendar ages were monotonic in depth and had positive accumulation rates (Lacourse & Gajewski 2020; Trachsel & Telford 2017).

Correlation of paleobotanical data

Palaeobotanical data were correlated using the General Stratigraphic Scale of the Quaternary System (Borisov 2013) and according to Marine isotope stages (MIS) (Bassinot et al. 1994). Time subdivision of the Holocene was given according 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). Little climatic changes are identified based on the regional stratigraphic scale for the Russian Far East (Korotky et al. 1980, Korotky 2002).

RESULTS

According to the age-depth models (Fig. 5) the studied sediments accumulated during the Late Pleistocene MIS 2 and the Holocene. The basal age of the sediments columns being estimated between at 43.0–2.9 ka cal BP. The age models indicates large changes in sediments accumulation rates in some columns. This is due to the change in natural conditions during the sedimentation of sediments and the differentiation of geomorphological conditions. Studied sediments monotonic in depth and had positive accumulation rates.

Changes in *Pinus densiflora* pollen abundance in the pollen records

The Late Pleistocene (MIS 2) sediments from cal BP 33.5 to 11.7 ka cal BP. Sediments were not detected in any studied core, borehole and cross-section from the south of the Russian Far East.

The Early Holocene sediments from 11.7 to 8.2 ka cal BP. Fossil pollen grains of *P. densiflora* in the sediments of the Early Holocene age were found only in the southernmost of the south of the Russian Far East (the Southern Subregion) (Plate I). They are recorded in the sediments of all cores, boreholes, and cross-sections. *Pinus densiflora* percentage of its pollen is rather high; it ranges from 1.6 to 21.7 % (approximately 4.6 % on average). The most complete and longest pollen records in the Southern Subregion were obtained from sediment cores of lakes Karasie (Fig. 6) and Utinoe. The highest percentage of *P. densiflora* pollen is noted in the cross-section 272 at a depth of 1.90–1.95 m. In the Central Subregion, for example a pollen percentage diagram for cross-section 4 118 (Fig. 7) and Northern Subregion, for example a pollen percentage diagram for cross-section 6 205 (Fig. 8), the *P. densiflora* pollen fossil in the sediments of the Early Holocene age was not detected.

The Middle Holocene sediments from 8.2 to 4.2 ka cal BP. Fossil pollen of *P. densiflora* was found in the mid-Holocene Thermal Maximum sediments from all cores, boreholes and cross-sections of the Southern Subregion and also in most of them in the Central Subregion of the south of the Russian Far East (see Fig. 6 & 7). Its highest percentage, from 1.8 to 10 % (approximately 3.2 % on average),

is recorded in the Southern Subregion. To the north, in the Central Subregion, its percentage decreases, it ranges from 2.3 to 3.8 % (approximately 1.6 % on average). *Pinus densiflora* fossil pollen in the Middle Holocene sediments in the northernmost (the Northern Subregion) of the south of the Russian Far East was not found (see Fig. 8).

The Late Holocene sediments from 4.2 ka cal BP to the present. Fossil pollen of *P. densiflora* Late Holocene age was mainly found in the southernmost of the south of the Russian Far East (the Southern Subregion) (see Fig. 6) and in some areas of the southern sector of the Central Subregion. Their percentages are ranging from 1.8 to 25.9 % (approximately 8.5 % on average). The highest percentage of *P. densiflora* pollen is noted in the cross-section 1 508 at a depths of 1.9 and 2.7 m. In the Central Subregion its percentage to an average value is relatively low, approximately 0.8 % (it is varying from 0 to 2.3 %). *Pinus densiflora* fossil pollen from the sediments in the northernmost (the Northern Subregion) of the south of the Russian Far East was not found (see Fig. 7).

DISCUSSION

The obtained of pollen dataset as compared with the paleogeographic data for adjacent areas of East Asia, allow us to determine the time of appearance of *P. densiflora* in the vegetation of the south of the Russian Far East after the end of the cold epoch MIS 2 and reconstruct of its dynamics during the Holocene.

The Late Pleistocene MIS 2 (from 33.5 to 11.7 ka cal BP)

The pollen records obtained in the study indicate that during MIS 2 *P. densiflora* did not grow in the south of the Russian Far East. This is evidenced by the lack of its pollen in the pollen assemblages from the MIS 2 age sediments. The pollen of boreal plants – *Alnus* sp., *A. alnobetula*, *Betula glandulosa*, *B. pubescens*, *Larix*, *Picea*, *Pinus pumila*, and forbs dominates in the obtained of pollen assemblages. This testifies to a wide distribution of cold-resistant mosaic steppe communities and sparse forest-tundra forests with sphagnum bogs in the region. *Pinus densiflora* is not found in the present plant formations with such floristic composition and cannot grow in such harsh climatic conditions as these tree plants (Urusov et al. 2004).

At the present, similar plant formations in the south of the Russian Far East are confined to mountain slopes above 1500 m or are located much to the north, outside the region. Such a composition of vegetation evidences that the regional flora was similar to that of the forest-tundra belt, for which average annual temperatures that do not exceed -9 ... -3°C are common. Under such harsh conditions, *P. densiflora* cannot grow. Thus, the temperate-boreal mixed forests with *P. densiflora* disappeared absolutely during the MIS 2 in the south of the Russian Far East. Similar vegetation changes were taking place in adjacent areas, in the Northeast China (Stebich et al. 2009, Binney et al. 2017, Li et al. 2019). In Eastern China cold-deciduous forests, cool-temperate evergreen needle leaf forests, cool mixed forests, warm-temperate evergreen broadleaf, and mixed forests also displaced to the south by 300–1000 km. Many plants in

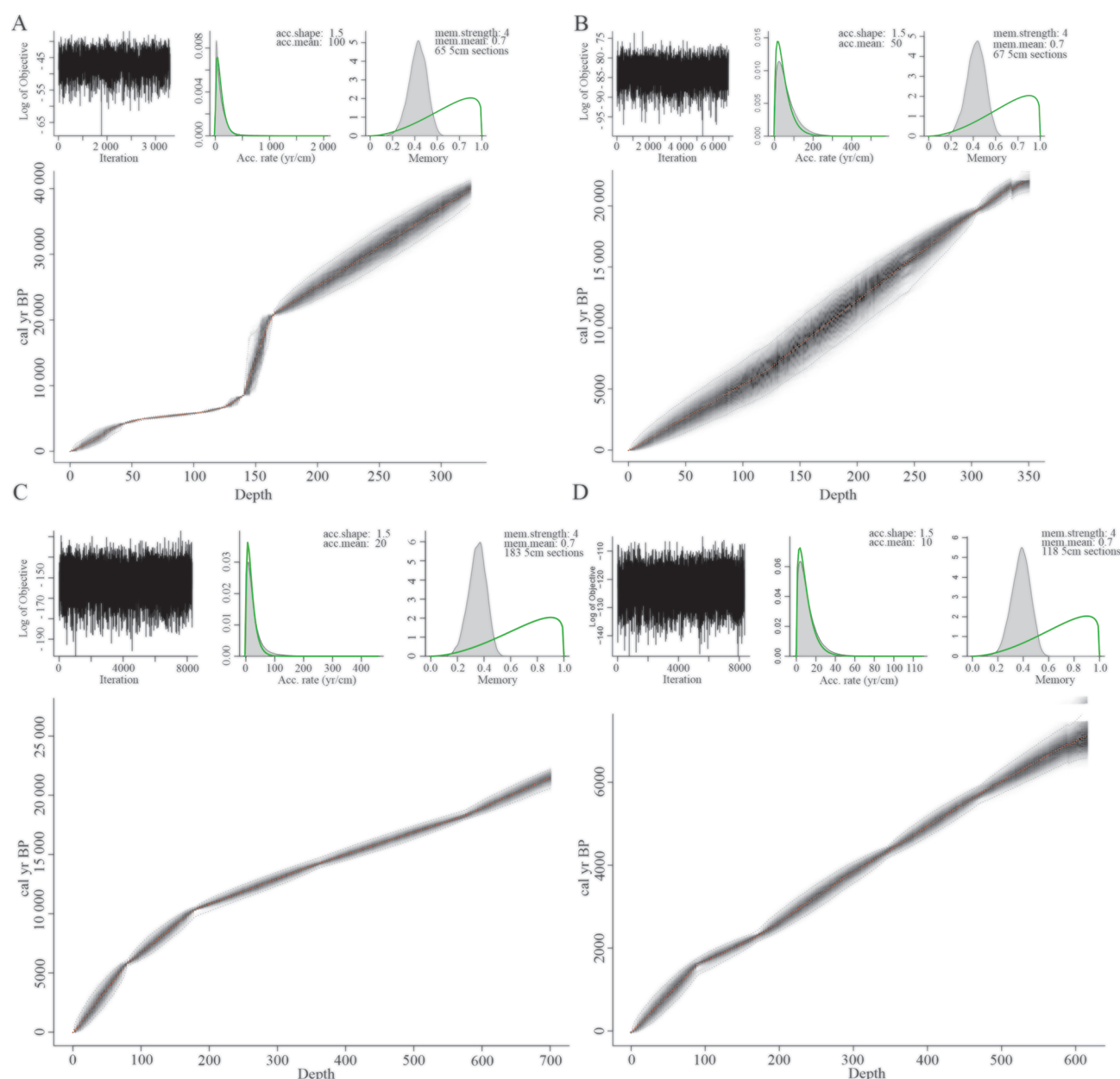


Figure 5 Age-depth models for the some studied the most representative of sediments columns. Core Lake Karasie (A), cross-sections 6205 (C) and 4118 (B) and core Lake Utinoye (D), plotted using Bacon (Blaauw & Christen 2011)

the Eastern Asia migrated to the south (Tsukada 1984, Yi & Kim 2010, Chung et al. 2010). Evergreen vegetation in Eurasia retreated to the equator (Ni et al. 2010).

The main factors limiting *P. densiflora* regeneration and distribution are the low temperatures during development of its shoots and the relative sensitivity of seedlings to destruction by frost. However, probably, not only low temperatures, but also aridity were the limiting factors for the survival of *P. densiflora* during the MIS 2 (Kremenetski et al. 1998). The weakening of the East Asian summer monsoon in response to changes in insolation in the Northern Hemisphere (Cosford et al. 2010) led to the formation of drier climate in the south of the Russian Far East during the MIS 2. This caused the lack of moisture for the growth of *P. densiflora*. Although this species grows well under high solar radiation (Koyama 1943), the initial stage of its establishment is more sensitive to the availability of soil

moisture than to solar radiation (Oosting & Kramer 1946). Therefore, the drier climate, combined with extremely low temperatures during the growing season, is another factor preventing the spread of *P. densiflora* in the south of the Russian Far East during the MIS 2.

However, phylogeographic investigations evidenced that the population of *P. densiflora* during the MIS 2 in Northeast China and the Korean Peninsula experienced a strong decline, but did not completely disappear. Apparently, this species can survive in the refuges formed by the complex mountainous terrain and mild microenvironment of the central part of the Japanese Archipelago and the north of the Korean Peninsula, where the cold and dry climate did not have a strong adverse effect on it (Bai et al. 2010, Qiu et al. 2011). Small populations of *P. densiflora* could also survive in the refuges, on the alluvial lowlands and plains in North Korea and the northeast of China even during



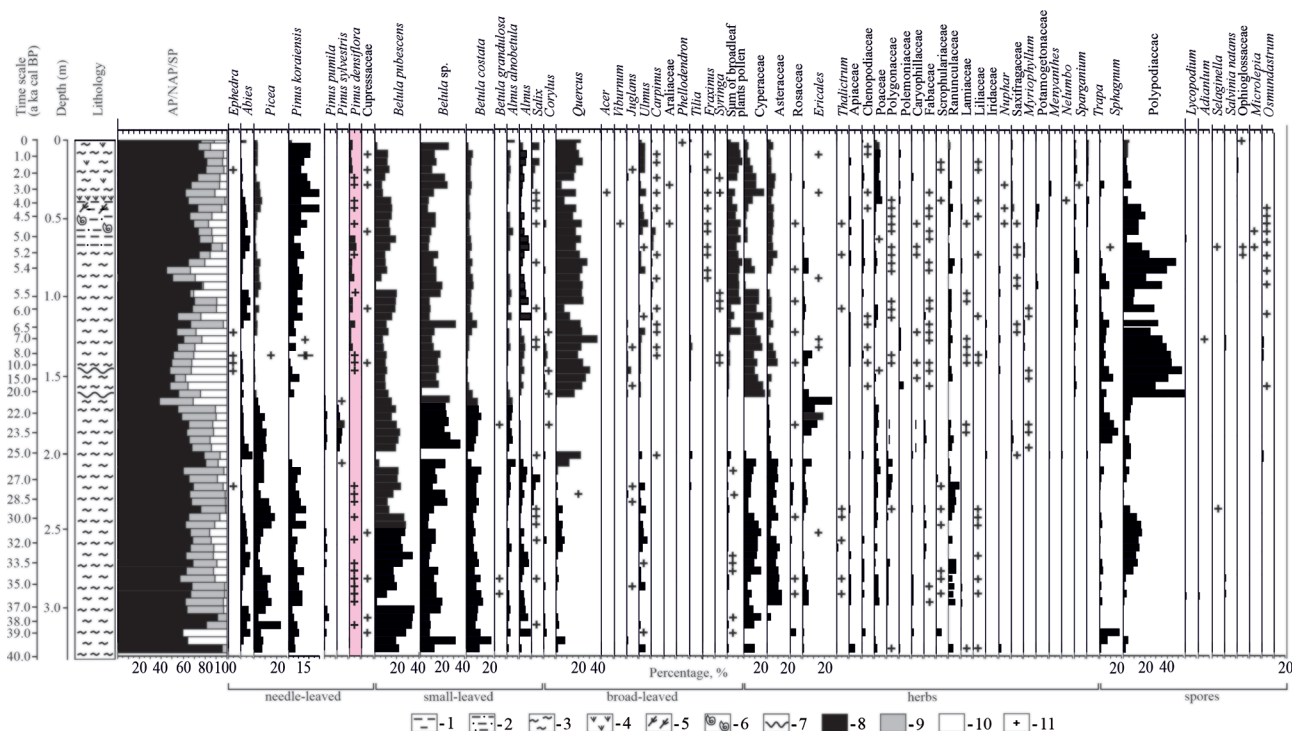


Figure 6. A pollen percentage diagram of Late Pleistocene-Holocene sediments from core Lake Karasie (the Southern Subregion), plotted using Tilia (version 2.0.41) (Grim 2004). 1 – loam, 2 – sandy loam, 3 – silt, 4 – peat, 5 – plant remains, 6 – clam shells, 7 – gap in the sedimentation. Relationship between plant groups: 7 – trees and shrubs, 8 – herbs and dwarf shrubs, 9 – spores, 10 – the taxa present in the assemblage in amounts less than 2 %

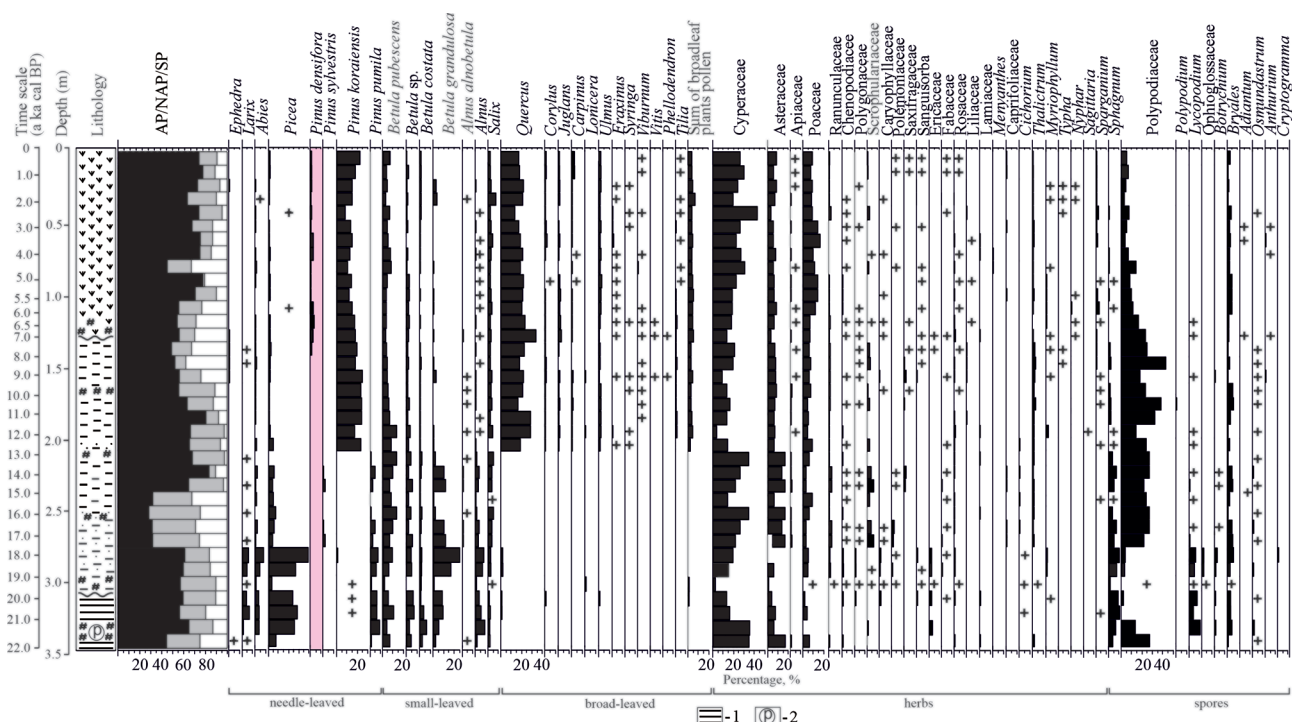


Figure 7. A pollen percentage diagram of Late Pleistocene-Holocene sediments from cross-section 4118 in the Sorochevka River Valley (the Central Subregion), plotted using Tilia (version 2.0.41) (Grim 2004). 1 – clay, 2 – vivianite. For explanation see Fig. 6

Plate I. Selected pollen grains of *Pinus densiflora* in the Holocene sediment from the south of the Russian Far East. Photographed using an camera AxioCam ICc1 (Carl Zeiss) (photos by P. Belyanin). Cross-sections: 1 – 508 (sample depth: 360–365 cm); 2 – 1706–1 (sample depth: 80–90 cm); 3 – 1706–1 (sample depth: 90–100 cm); 4 – 4005 (sample depth: 240–250 cm); 5 – 9031a (sample depth: 230–240 cm); 6 – 9119 (sample depth: 120–125 cm); 7 – 9119 (sample depth: 155–160 cm); 8 – 4074 (sample depth: 180–185 cm); 9 – 6159 (sample depth: 90–55 cm); 10 – 6159 (sample depth: 230–235 cm); 11 – River Kazachka (sample depth: 95–100 cm). Cores: 12 – Lake Utinoye (sample depth: 465–470 cm); 13 and 14 – Lake Karasie (sample depth: 60–70 cm); 14 – Lake Karasie (sample depth: 110–115 cm)

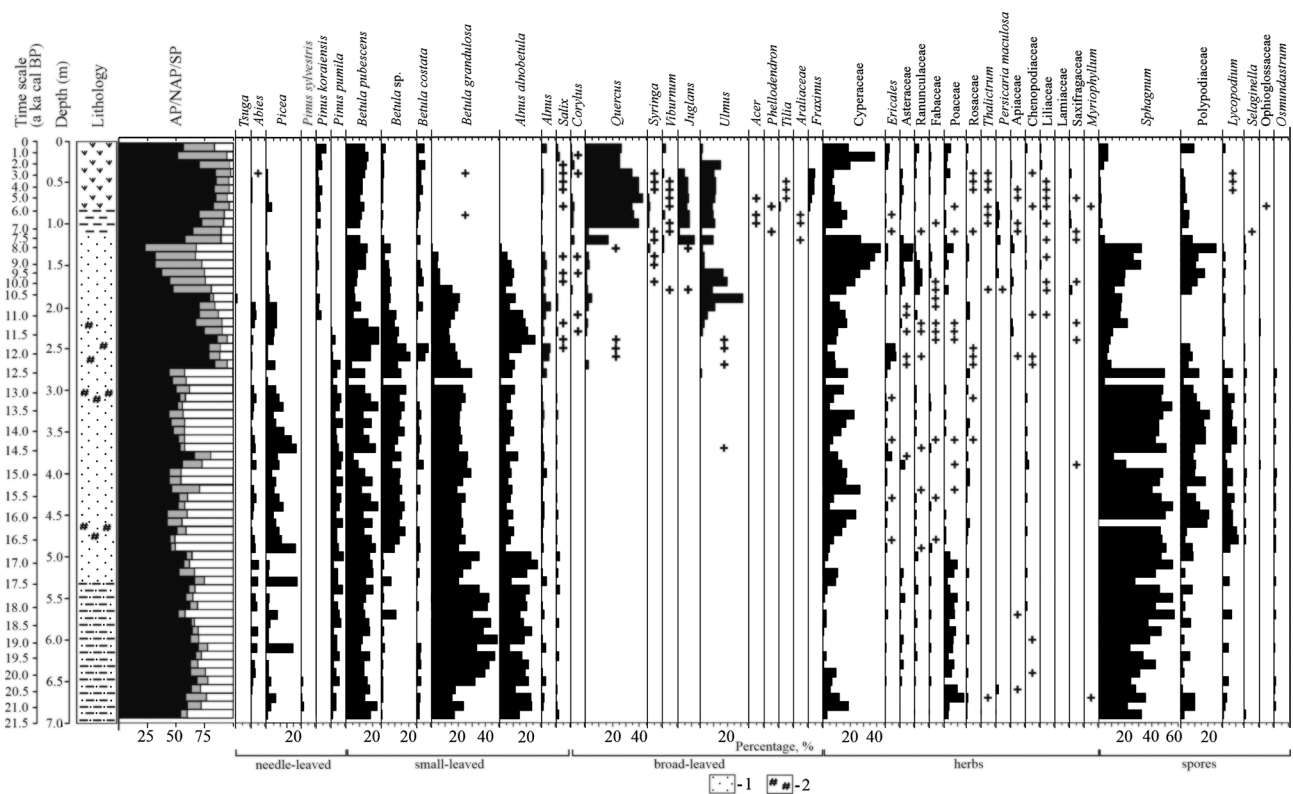


Figure 8. A pollen percentage diagram of Late Pleistocene-Holocene sediments from cross-section 6205 in the Bikin River Valley (the Northern Subregion), plotted using Tilia (version 2.0.41) (Grim 2004). 1 – sand, 2 – wood. For explanation see Fig. 6

the coldest and driest phase of the MIS 2 (Kremenetski et al. 1998).

The northern limit of the main range of *P. densiflora* during the MIS 2 crossed the south of the Korean Peninsula and the Shikoku and Kyushu islands, where the climate remained favorable for the growth of this species. Numerous dated pollen records and finds of macrofossil remained indicate that *P. densiflora* was a main component of coniferous and mixed forests, which prevailed in the southern part of the Korean Peninsula and the Southern Japanese islands during the MIS 2 (Tsukada 1983, 1984, Yi & Kim 2010).

The southward shift of the *P. densiflora* range during MIS 2 is also indicated by the results of the MaxEnt Modeling to Estimate the Impact of Climate Factors on Distribution of *P. densiflora*. This data showed that under strong cooling during the MIS 2, the suitable habitat area by climatic parameters for distribution of *P. densiflora* in the East Asia decreased to 2.68×10^6 km (Duan et al. 2022). As the results of the pollen analysis showed in the south of the Russian Far East, this species was completely disappeared (Fig. 9).

Centroid of the *P. densiflora* habitat during the MIS 2 was located close to the Shandong Peninsula (Duan et al. 2022) which lies to the east, in the same latitudes with the central part of the Korean Peninsula. At the present time, the Shandong Peninsula and the Korean Peninsula are separated by ~ 250 km water area of the shallow Yellow Sea. However, during the MIS 2 the Yellow Sea level was dropped about by 145 m. A vast accumulative plain was formed in its place (Park et al. 1994). As a result, the Shandong Peninsula was connected to the Korean Peninsula by a land bridge (Badejo et al. 2015, Park et al. 1994). Therefore, apparently,

the Shandong Peninsula and the Korean Peninsula were a unified range of *P. densiflora* in the coldest epoch of MIS 2.

The mainland and Japanese island ranges of *P. densiflora*, even during the Last Glacial Maximum under a significant sea level fall, remained geographically separated only by a narrow strait between the East China Sea and the Japan Sea (East Sea). Its width did not exceed 20 km (Park et al. 2000).

Despite the fact that the width of the strait was relatively little, it is unlikely that birds could carry *P. densiflora* seeds through it (Yamashita 1989). Therefore, it seems that the very south of the Korean Peninsula was the main source of northward migration of *P. densiflora* during the Early Holocene warming.

The Early Holocene (from 11.7 to 8.2 ka cal BP)

The rapid warming that began around 11.7 ka cal BP marked the start of the current interglacial, the Holocene. Despite the significant increase of heat supply at the beginning of the Early Holocene, the average annual temperatures in the south of the Russian Far East during 11.7–11.5 ka cal BP were 3–4° below than the modern ones, i.e. July temperatures by 2°, January temperatures by 4–5°, and precipitation fell by 50 mm less (Kuzmina et al. 1987, Korotky et al. 1996). Average annual temperatures in the Southern Subregion were about 1.5°C, in the Central Subregion about 0°C, and in the Northern Subregion about -3.0°C.

Later, between 11.5 and 10.5 ka cal BP, the temperature dropped again becoming 6–8° below than the present one. The average annual temperatures in July and May dropped by 4–5° and 8–10°, respectively. Precipitation fell 100–150 mm less than at the present (Kuzmina et al. 1987). Average annual temperatures in the Southern Subregion

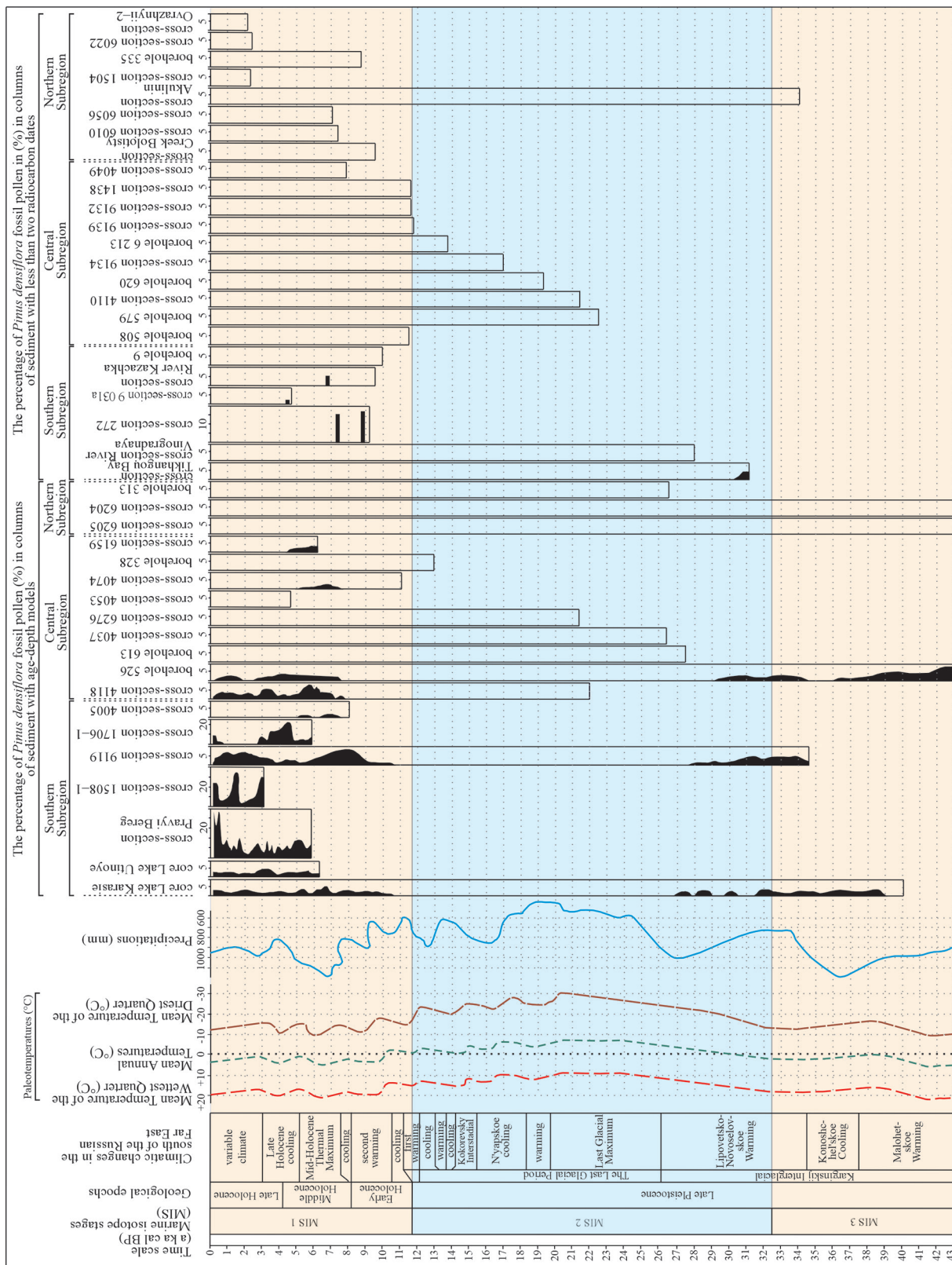


Figure 9. The ratio of the main paleoclimatic trends (after Kind 1974, Khotinsky 1977, Korotky et al. 1996 & Kuzmina 1987) and percentage of *Pinus densiflora* fossil pollen (%) in the studied of sediment columns

were about -1.5°C , in the Central Subregion about -3.5°C , and in the Northern Subregion around -7.0°C . Obviously, that *P. densiflora*, cannot grow in such cold climate. This is also evidenced by the absence of its pollen in the sediments of the beginning of the Early Holocene in the south of the Russian Far East. Forest-tundra formations with birch-larch sparse forests and dwarf birch communities still

dominated in the vegetation on the plains. Birch-elm forests were spread on the warmer southern slopes.

The subsequent warming interrupted by slight coolings continued between 10.1–9.3 ka cal BP. Average annual temperatures in July have become $1\text{--}2^{\circ}$ higher than the modern ones, and January temperatures – by $0.5\text{--}1^{\circ}$. Precipitation fell about the same as it is today (Kuzmina et al. 1987). In

the Southern Subregion the average annual temperatures were about 7.5°C, in the Central Subregion – about 5.0°C, and in the Northern Subregion – about 2.0°C.

A significant increase of temperatures and strengthening of the Asian summer monsoon (Cosford et al. 2008, Yi 2011) caused a shift of the range of *P. densiflora* to the north. According to pollen records, at that time, range of this species has reached and covered the southernmost of the south of the Russian Far East – its Southern Subregion. It is proved by the appearance of its pollen in the sediments from the Southern Subregion, among the pollen of broad-leaved plants primarily *Ulmus*, *Quercus mongolica* and *Pinus koraiensis* (see Fig. 6).

However, despite warmer climate than the present one, the range of *P. densiflora* did not shift further north and did not reach the Central Subregion of the south of the Russian Far East. This is confirmed by the lack of its pollen from the sediments of the Central and Northern subregions of the south of the Russian Far East, which are characterized by more continental climate (i.e. the Khanka Plain and the basin of the Ussuri River) (see Fig. 7 & 8).

Apparently, the climate in these subregions, has not yet become favorable for the distribution of this species. Pollen data from the northeast China evidence that *P. densiflora* also grew in the region during the Early Holocene. Its expansion also took place from south to north (Ren & Zhang 1998). Also, one of the cold-tolerant coniferous species – *Pinus koraiensis* revealed similar spatial-temporal dynamics, i.e. the shift northward to the south of the Russian Far East during the Early Holocene (Belyanin & Belyanina 2021)

The Middle Holocene (from 8.2 to 4.2 ka cal BP)

The most significant climate warming for the whole postglacial period began since 8.2 ka cal BP. It correlates with the thermal maximum of the middle Holocene in many regions of the Earth (Igarashi 2013, Razjigaeva et al. 2013, 2021, Borisova 2014). During this epoch the average global temperatures were 0.7–1°C higher than the present ones (Velichko 2012). The temperature in the south of the Russian Far East was 2° higher than today, and the amount of precipitation fell by 50–100 mm more (Kuzmina et al. 1987, Korotky et al. 1996). A maximum of the climate warming in this region occurred during 6.8–5.3 ka cal BP (Khotinsky 1977, Mikishin et al. 2019). At that time the mean annual temperature in the Southern Subregion in the south of the Russian Far East increased to 7.8°C, in the Central subdivision to 5.7°C and in the Northern Subregion to 2.5°C.

The significant rise of temperatures led to the shift of broad-leaved and evergreen needle-leaved plants ranges northward by 200–400 km (Khotinsky 1977). Obtained pollen records indicate that *P. densiflora* range expanded notably its distribution in the south of the Russian Far East. This is evidenced by an geographical expanded of sites, where detected of *P. densiflora* fossil pollen. Besides the Southern subregions it was also detected in the Middle Holocene sediments from the Central of the south of the Russian Far East.

Regional vegetation was more diversified by species composition compared with those of the present days. It is was represented by *Pinus koraiensis*, *Abies*, *Quercus*, *Ulmus*,

Carpinus, *Fraxinus*, *Syringa*, and other broad-leaved trees. *Pinus densiflora* is was one of the main components of forests.

The constant presence of *P. densiflora* pollen in the pollen assemblages from all studied cross-sections, cores and boreholes from the Central and Southern subregions in the south of the Russian Far East indicate that the Middle Holocene climate was milder and stable than during the Early Holocene. Therefore, *P. densiflora* was able to successfully grow with deciduous and coniferous plants and its range continued to shift north. Warmer temperatures promoted migration of *P. densiflora* up the slopes. *Pinus densiflora* has reached the continental areas with drier and colder climate, i.e. on the inland (subcontinental) slopes of the Sikhote-Alin and Manchurian-Korean Mountains. Apparently, the climatic conditions during the mid-Holocene Thermal Maximum in the southernmost part of the Russian Far East were close to the modern ones on the Korean Peninsula, about 39°N. As a result of the shift of the plants ranges to the north, in the south of the Russian Far East there grew more species from the modern flora of the Korean Peninsula and Northeast China than at present.

It should be also noted that pollen records for the Middle Holocene obtained from the south of the Russian Far East are in good agreement with those for other regions of the Eastern Asia and Eastern Siberia. For example, between 6.8 and 6.0 ka cal BP in the Baikal basin there was an expansion of another species of genus *Pinus* – *Pinus sylvestris* (Kobe et al. 2020). Besides, the pollen records from the Northeast China show that the cool temperate boreal forest shifted to the north from its southern boundary by about 2° of latitude (Yafeng et al. 1993). The northern limit of tropical forests in Eastern China shifted ~100 km northwards during the mid-Holocene, the northern limit of broadleaved evergreen forests shifted 300–400 km north and the northern limit of temperate deciduous forests shifted ~ 800 km further north relative to the present position (Yu et al. 2000). Forests also extended further westwards into the continental interior, invading on non-forest areas in the East Asia. The north shift of vegetation zones during the mid-Holocene Thermal Maximum reflects an increase in plant-available moisture during the growing season (Sun & Weng 1992, Ren & Zhang 1998).

The obtained paleobotanical data are in good agreement with the results of the MaxEnt Modeling to Estimate the Impact of Climate Factors on Distribution of *P. densiflora*. According to this modeling, the centroid of potential geographical distribution of *P. densiflora* habitat in the Middle Holocene was in Jiangsu Province (33°59'N 118°E), China. Compared with the current position, under the warmer and humid climate of the mid-Holocene Thermal Maximum its position increased by 1.36° of north latitude to the north. *Pinus densiflora* range has reduced in the southeast, and expanded slightly in the northeast direction (Duan et al. 2022), i.e. in south of the Russian Far East.

The Late Holocene (from 4.2 ka cal BP to the present)

The global cooling, that began at the transition from the Middle Holocene to the Early Holocene about 4.2 ka cal BP,

led to a decrease in average annual temperatures in the south of the Russian Far East. The average annual temperature was 2° below the modern one, and the temperature in July and January was 1–2° below (Kuzmina et al. 1987, Korotky et al. 1996). In the Southern Subregion the temperature fell to about 3.8°C, in the Central Subregion it decreased to about 1.8°C, and in the Northern Subregion – to about -1.5°C. The amount of precipitation fell approximately as much as now.

Under such cold natural conditions, it became not only difficult for the *P. densiflora* to grow, but also to compete with other tree plants. Therefore, a reduction of *P. densiflora* distribution occurred in the regional vegetation. In the mountain ecosystems, in particular on the north-facing slopes, *P. densiflora* with broadleaved species was partially replaced by *Abies*, *Pinus koraiensis*, *Alnus*, *Betula pubescens*, and other more cold-tolerant trees. At the same time the distribution of other more cool-tolerant trees, such as *Betula glandulosa*, *Alnus alnobetula*, *Alnus*, *Ulmus*, *Larix*, *Picea* increased.

The subsequent cooling accompanied by the increase of dryness of the climate (Korotky 2002) led also to a decrease in the role of *P. densiflora* in the vegetation of the south of the Russian Far East and the lowering of its altitudinal range limit. The general trend towards cooling was interrupted by short-term warming from 4.7 to 3.0 ka cal BP and from 2.6 to 1.8 ka cal BP (Korotky 2002). The obtained pollen records show that during this warming *P. densiflora* was a codominant species in the plant formations with *Pinus koraiensis*, *Abies*, *Quercus*, *Ulmus*, *Carpinus*, *Fraxinus*, *Syringa*, and other thermophilic trees.

Thus, unstable climate (Korotky 2002) and gradually decreasing heat supply during the Late Holocene led to the multidirectional fluctuations of the *P. densiflora* role in the regional vegetation. But, at the same time, *P. densiflora* was constantly present in the vegetation of the south of the Russian Far East.

During the Late Holocene similar processes took place in Eastern Siberia – in the Lake Baikal region from 4.0 to 3.7 ka cal BP, when this region was widely covered by the *Pinus sylvestris* forests (Kobe et al. 2020). Besides, expansion of the representatives of genus *Pinus*, has changed strongly vegetation in the northeast China about 4.7 ka cal BP (Sun & Weng 1992).

Abiotic factors, such as climatic, are not the only factors that should be considered if one tries to understand dynamics of *P. densiflora* in the past. Deforestation, grazing and agriculture processes triggered by human activity also seem to have been decisive in the evolution of vegetation during the historical time in the south of the Russian Far East. They all have led to strong disturbances with decisive effects on the modern state of vegetation. The regression of forests since the Late Holocene is noted all around the south of the Russian Far East.

Apparently, an anthropogenic impact began to influence the distribution of *P. densiflora* in the south of the Russian Far East since ~ 5.0 ka cal BP. Pollen records and the archaeological reconstructions evidence clearance and burning the taiga forests for new pastoral and/or wood cutting used for construction of log houses. Light-

demanding *Phellodendron* thickets and a forest-steppe with *Betula pubescens* and Asteraceae began to dominate in the valley vegetation. A partial change from a mixed broad-leaved forest with *P. densiflora* to a semi-open forest and steppe-parklands took place. As a result *P. densiflora* which is very sensitive to human disturbance, was replaced by the communities of the fire-resilient and re-sprouted plants. The time of proliferation of Neolithic settlements matches that of forest decline in the south of the Russian Far East (Chlachula et al. 2015).

In the Middle Ages, the human activity of the Dzhezhen (Juchen, Jurchen) population between 500 and 700 cal BP has led to a significant decrease in the areas of forests due to their clearing for agricultural lands. Since then the region has remained relatively populated, and regular fires have supported the development of vegetation without needle-leaved species (Nakamura & Krestov 2005). For the last 250 years in the south of the Russian Far East most fires have occurred under human activities (Sheingauz 1996).

However, still in the 18th century *P. densiflora* was widespread in the forests of the region. According to botanical descriptions of this region by A.F. Budishchev during the expedition in 1860, *P. densiflora* grew both in continuous massifs in the Pre-Khanka Basin and in the isolated localities in the central ridges of the Southern Sikhote-Alin. The richest *P. densiflora* forests grew in the interfluvium of the Ilistaya and Arsenyevka Rivers, in the mountains west of the Ilistaya River valley, and on the whole western coast of Khanka Lake (the Central Subregion) (Budishchev 2016).

Due to a strong increase in fires and clearings in the south of the Russian Far East since the 1890s, the *P. densiflora* range in this region was reduced by more than 100 times to the 1930s (Urusov et al. 2004). Today broad-leaved forests with *P. densiflora* in the south of the Russian Far East covered an area of about only 123 km² (Petropavlovsky et al. 1985). The main impact factors to the decrease of *P. densiflora* distribution in the region are extensive felling, fires, strong winds, and the proliferation of insect pests (Ivanov & Shashenok 2018). They led to the transformation of vast areas of the deciduous forests with *P. densiflora* and *Pinus koraiensis* to simpler re-sprouted forests and scrubs-herbs thickets which were mainly represented by thickets of shrubs *Lezpedeza bicolor*, *Corylus sieboldiana* and by forests with *Quercus mongolica*, *Q. dentata*, *Tilia amurensis*, *Betula pubescens*, *Larix dahurica*, *Populus tremula* and forb meadows.

However, despite the fact that fires typically destroy trees of *P. densiflora*, this species can quickly attain dominance after a severe fire under favorable climate and environment. Probably, due to a such regeneration potential, *P. densiflora* is a good example of a species that can be facilitated by human impact. For example, this process takes place in Japan, where *P. densiflora* was an uncommon species before about 2.6 ka cal BP when severe fires were frequent. However, this species becomes prominent in the pollen record at about the time that agriculture becomes widespread. Its spread in Japan is strongly correlated with the rise of agriculture (Agee 1998, Kremenetsi et al. 1998).

Nevertheless, that example is not correct for the south of the Russian Far East. The reason for this is frequent an-

nual fires in this region, in which therefore, undergrowth of *P. densiflora* regularly burns. Also, due regular fires under monsoon climate, a thick sod is formed that prevents from the germination of its seeds. Additionally, pathogenic fungi can breed in the humus layer under the sod after the fires. They infect the trees of *P. densiflora* weakened by fires. Therefore, the anthropogenic impact did not have a favorable effect on the range of *P. densiflora* in the south of the Far East, as it did in Korea and Japan.

CONCLUSIONS

Analysis of the taxonomic structure of pollen allowed us to reconstruct the spatial and temporal distribution of *P. densiflora* in the southern Far East in the Late Pleistocene (MIS 2) and Holocene. The data obtained showed that *P. densiflora* did not occur in the south of the Russian Far East under conditions of cold and dry climate during the MIS 2. At that time, the regional vegetation was dominated by more cold-tolerant plants characteristic of the forest-tundra zone. The range of *P. densiflora* was located to the south. Rapid global warming, which marked the beginning of the early Holocene, intensified the spatial migration of plants. More heat-loving plants began to migrate to continental ecosystems of the southern Russian Far East from the Korean Peninsula and Northeast China. Due to the mild climate in the Holocene, the heat-loving species *P. densiflora* became the dominant vegetation element in the southern part of the southern Russian Far East. Its range, synchronously with the increase in temperature and humidity, shifted northward and reached the southern subregion of the southern part of the Russian Far East about 10.5 thousand years ago. At that time, the formation of modern vegetation began there. However, the range of *P. densiflora* at that time had not yet reached the Central subregion of the southern Far East. Apparently, the climate of this subregion has not yet become favorable for the spread of this species. At the beginning of the middle Holocene thermal maximum, the range of *P. densiflora* shifted even further northward and reached the Central Subregion of the southern Russian Far East, which is characterized by a colder and drier climate. The vegetation of the region was characterized by a more diverse species composition compared to the modern one. However, even under the most favorable natural conditions of that time, *P. densiflora* could not reach the Northern sub-area of the southern Far East, where the climate was much drier and colder than in the Southern and Central sub-areas. *Pinus densiflora*, characterized by a narrow ecological and physiological amplitude in the conditions of cold temperate and cool temperate climatic belts in the south of the Far East, limited its distribution mainly to the southern part of this region. The cooling that occurred at the beginning of the late Holocene again reduced the distribution of *P. densiflora* in the southern Far East. Its range shifted to the south. However, *P. densiflora* survived in the southern subregion of the southern Far East. Apparently, it occupied well isolated slopes of southern exposure.

Natural conditions as a result of warming in the second half of the late Holocene, interrupted by short episodes of cooling, determined the formation of the modern vegeta-

tion structure of the southern Russian Far East. The *P. densiflora* range shifted northward again. Broad-leaved forests with *P. densiflora* and *Pinus koraiensis* became dominant in the ecosystems of the Southern and Central subregions.

Over the last two centuries, vegetation in the southern Russian Far East has begun to degrade rapidly due to intensive anthropogenic impact. As a result of logging and fires, significant areas of broad-leaved forests with *P. densiflora* have been replaced by overmature forests and shrub thickets. Therefore, at present, *P. densiflora* does not form a continuous range in the south of the Russian Far East. Despite this, it has largely preserved its primary outlines in this region.

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