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Paleoclimatic implications of glacial and postglacial refugia for Pinus pumila in western Beringia

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Title: Paleoclimatic implications of glacial and postglacial refugia for Pinus pumila in western Beringia

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Abstract: Palynological results from Julietta Lake currently provide the most direct evidence to support the existence of a glacial refugium for Pinus pumila in mountains of southwestern Beringia. Both percentages and accumulation rates indicate the evergreen shrub survived until at least ~19,000 14C yr B.P. in the Upper Kolyma region. Percentage data suggest numbers dwindled into the late glaciation, whereas pollen accumulation rates point towards a more rapid demise shortly after ~19,000 14C yr B.P. Pinus pumila did not re-establish in any great numbers until ~8100 14C yr B.P., despite the local presence ~9800 14C yr B.P. of Larix dahurica, which shares similar summer temperature requirements. The postglacial thermal maximum (in Beringia ~11,000-9000 14C yr B.P.) provided Pinus pumila shrubs with equally harsh albeit different conditions for survival than those present during the LGM. Regional records indicate that in this time of maximum warmth Pinus pumila likely sheltered in a second, lower-elevation refugium. Paleoclimatic models and modern ecology suggest that shifts in the nature of seasonal transitions and not only seasonal extremes have played important roles in the history of Pinus pumila over the last ~21,000 14C yr B.P.

Introduction

Pinus pumila (Pall.) Regel (Japanese stone pine) is a main component of modern forest and tundra of northeastern Asia (Kremenetski et al., 2000). In Russia, the shrub is found from eastern Chukotka to the Lena basin and southward to Lake Baikal and the Kuril Islands. *Pinus pumila* endures more frigid winters than other *Pinus* taxa, because its prostrate habit during the cold season allows for burial of its branches within deep snow-cover, thereby protecting the evergreen leaves from winter desiccation. *Pinus pumila* requires moderately warm summers, with its northern limit approximating the 12°C mean July isotherm (Andreev, 1980; Kozhevnikov, 1981). Thus, paleo-records of *Pinus pumila* are somewhat unique paleoenvironmental tools in that the data can be used for inferring conditions during both warm and cool seasons. *Pinus pumila* pollen also differs from other *Pinus* species in that its large grains are not carried long distances by wind, thus simplifying interpretations of the fossil record (Lozhkin et al., 2001).

Kremenetski et al. (2000) postulated that the adaptive strategies of *Pinus pumila* allowed it to survive the last glacial maximum (LGM; ~24,000 to 12,500 ^{14}C yr B.P.) throughout much of its modern range, including areas of northern China, Korea, Japan, eastern Siberia, and the Russian Far East. They cited the early Holocene appearance of *Pinus pumila* pollen in records from such widely separated areas as Lake Baikal, the Lena River valley, Sakhalin Island, and Kamchatka as indirect evidence of *Pinus pumila* expansion from multiple refugia within Russia. They further noted that the vegetation history of northeastern Siberia (western Beringia, WB) differed, with the earliest Holocene plant communities lacking *Pinus pumila.* This pattern implies a later migration of the shrub into far northeast Asia from distant LGM populations. In contrast, Brubaker et al. (2005), using mapped pollen percentages, proposed that Beringia was an important locality where boreal trees and shrubs, including *Pinus pumila,* survived long intervals of adverse glacial climates in cryptic refugia. Their argument for the presence of a *Pinus pumila* refugium in WB is one of the least strong for all described taxa. Although multiple LGM and late-glacial (LG; 12,500-10,000 ^{14}C yr B.P.) sites in this study contain *Pinus pumila* pollen, only Lesnoye Lake (96 m a.s.l.; Anderson et al. 1997a; Fig. 1) consistently has >5% *Pinus* Haploxylon pollen, a presence/absence threshold suggested by modern pollen studies (Lozhkin et al., 2001). Using this latter criterion, the percentage data imply that *Pinus pumila* survived during the LGM only at lower elevations. However, the spatial distribution of LG through early Holocene records with trace to 10% *Pinus pumila* pollen does suggest the northern Priokhot'ye-Upper Kolyma region as a possible refugium (Brubaker et al., 2005).

Shilo et al. (2007) reported a sediment record from Julietta Lake (61°20.25'N, 153° 93.33'E, 880 m a.s.l.; Fig. 1), located in the mountainous Kilgan Massif which separates the Okhotsk Sea coast from the Upper Kolyma drainage. The Julietta core contains a pollen assemblage with typical LGM contributors, but it also displays unusually high percentages of *Pinus pumila* pollen (Fig. 2). These high pollen percentages persist into the LG, when they decrease to trace amounts. To date, the Shilo et al. (2007) study provides the strongest evidence for the continued presence of *Pinus pumila* in WB throughout the LGM, but the absence of radiocarbon dates prior to ~12,200 BP limit the certainty of this conclusion. Additional radiocarbon dates from Julietta Lake, reported herein, support the idea that *Pinus pumila* did survive in this area during glacial times. However, the modified chronology suggests a somewhat different late LGM-LG vegetation history. We present these new results and discuss the implications of *Pinus pumila* ecology and history for interpreting WB paleoclimates.

Study area, methods, and chronology

Julietta Lake is located in the light coniferous *Larix dahurica*-lichen forest that dominates much of far northeast Asia. *Betula middendorffii* and shrub *Salix* currently grow along the shore and in isolated thickets near the lake. Ericales (e.g., *Vaccinium uliginosum, V. vitis-ideae, Arctostaphylos, Empetrum*) occupy slightly better drained sites. *Pinus pumila, Duschekia fruticosa* (hereafter referred to as shrub *Alnus* to keep parallel to pollen nomenclature), and shrub *Betula* occur most abundantly at lower to mid-elevations in the nearby mountains. *Larix* forms open forest in the valley, occupying neighboring slopes and occasionally extending to ridge tops.

The lake basin is ~450 m long by ~250 m wide with a maximum water depth of ~6.35 m. The Kilgan Massif consists of Jurassic marine claystone and siltstone of the Verkhoyansk complex and late Cretaceous igneous deposits of the Okhotsk Volcanic belt (Shilo, 1970). The glacial history of the Julietta area is poorly known, but the terrain shows clear influence of what is likely Late Pleistocene glacial activity.

A 443-cm-long sediment core was raised from the center of Julietta Lake using a modified Livingstone piston sampler (Wright et al., 1984). Palynological samples were prepared following standard laboratory techniques (PALE, 1994). Pollen zones, which follow Shilo et al. (2007), were determined qualitatively based on variations in percentages of the major taxa. Because of lithological changes (Table 1), we applied a linear interpolation age-model to determine a chronology for the Julietta sediments. Age assignments are based on six radiocarbon dates and the Elikchan-KO tephra (Table 2).

We use the ~21,200 ^{14}C yr B.P. date (440-443 cm) for age modeling, presuming it more likely correct than the ~24,500 ^{14}C yr B.P. date; the reversal probably reflects redeposited material in the 315-317 cm core segment. All ages used in this paper are in ^{14}C yr B.P. Calibrated ages, which were obtained with CALIB 5.0 (2 σ range; http://calib.qub.ac.uk/calib/), are provided for the ^{14}C dates and the Elikchan tephra (Table 1; Stuiver and Reimer, 1993)

In an interpolated age-model, sedimentation rates, and thus pollen accumulation rates (PARs), are sensitive to the location of radiocarbon dates. For example, the most dramatic change in Julietta PARs occurs at ~250 cm and may simply reflect the presence of a radiocarbon date at 250-252 cm. This level also marks a shift from organic-rich (246-278 cm) to finely laminated silts (202-246 cm). The sediment change is consistent with a late-LGM environmental deterioration, resulting in a shift to sparse tundra and thus lower PARs. Additional dates at 218-219 and 199-201 cm (laminated silts) yield similar sedimentation rates, suggesting low PARs are not solely a function of date placement at 250 cm. Furthermore, increases in PARs during the LG are gradual and span several sedimentation-rate intervals. Maximum total PARs and increased Holocene *Pinus* PARs are all independent of radiocarbon date placement. With the exception of zone Ju1, we believe that shifts in PARS are not a function of the selected age model but more likely represent paleovegetation changes. The sandy layer at the bottom of the core corresponds to zone Ju1, where PARs for the major taxa are reduced and percentages are often variable. We choose to not interpret this basal zone as depositional changes may be the main factor influencing the pollen spectra.

History of *Pinus pumila* and other woody taxa near Julietta Lake

In most respects, the LGM assemblage from Julietta Lake (zones Ju2-Ju4; Fig. 2a) is characteristic of glacial records across WB, containing significant percentages of Cyperaceae, Poaceae, and *Artemisia* pollen and *Selaginella rupestris* spores (Lozhkin et al., 1993). However, *Pinus pumila* (*Pinus* subgen. Haploxylon) pollen percentages are unusually high between ~20,900 and 11,700 yr B.P. (zones Ju2-Ju5) and suggest that the evergreen shrub was important on the local landscape, most likely growing on lower slopes of nearby mountains or in scattered thickets near the lake (Shilo et al., 2007). Evidence for the presence of shrub *Betula* and *Alnus,* typical associates of *Pinus pumila* in modern tundra, is more ambiguous for the LGM, because their percentages are sufficiently low as to possibly represent long-distance transport (Lozhkin, 2001, 2002; Lozhkin et al., 2002; Anderson et al., 2002a, 2002b). Increases in *Betula* pollen percentages indicate that the shrub was well established at Julietta by ~12,400 yr BP and with *Pinus pumila* formed an unusual tundra association (zone Ju5; Shilo et al., 2007). The evergreen shrub declined ~11,700 yr BP being replaced by deciduous shrub tundra (first *Betula* (zone Ju6), then *Betula-Alnus* (lower zone Ju7)) from ~11,700- 9800 yr BP and finally *Larix* forest with a rich deciduous understory (upper zone Ju7). *Pinus pumila* reenters the landscape at ~8200 yr BP, marking the establishment of modern plant communities (zones Ju8-Ju9).

PARs suggest a slightly different vegetation history, particularly for *Pinus pumila* (Fig. 2b). *Pinus* PARs in LGM zones Ju2-Ju3, although not as great as in zones Ju8-Ju9 (i.e., modern vegetation), approximate or surpass recent samples from high shrub *Pinus pumila-Alnus* tundra of southern Chukotka (~100-200 grains cm^2 yr^{-1} Gytgykai Lake; Lozhkin et al., 1998) or higher elevation *Larix-Pinus pumila* forests in the Upper Kolyma region (<250 grains cm^2 yr^{-1} Goluboye and Elgennya; Lozhkin et al., 1996, 1997b, 2000). Although comparing PARs among varying basin types must be done with caution (Seppä and Hicks, 2006), the fact that the Julietta values are of equal or greater magnitude than samples where *Pinus pumila* is known to be an important landscape component strongly suggests that this shrub was present locally at least until ~19,000 yr B.P. and possibly grew in significant numbers from ~20,900-19,100 (412.5-252.5 cm of zone Ju3). *Alnus* and to a lesser extent *Betula* PARs in zones Ju2-Ju3 are generally lower than in the recent Julietta spectra, which represents a modern vegetation where shrubs are not as abundant as in lower elevations within the region. The PARs indicate the shrubs likely were absent (*Alnus)* or quite rare (*Betula*) during this portion of the LGM. In contrast, *Salix* and Ericales PARs are relatively high, suggesting these deciduous shrubs were probably present near Julietta Lake.

The decreases in PARs of *Pinus pumila* and deciduous shrubs after ~19,000 B.P. (zone Ju4) probably reflect a real decline in abundances of woody taxa. Values are sufficiently low that *Pinus pumila, Alnus*, and *Betula* were probably absent near Julietta, or if present, the survivors were few in number and restricted to the most protected microenvironments. Conditions perhaps deteriorated so greatly that herbaceous vegetation was also negatively impacted, as suggested in reduced graminoids and total PARs. The change in sediment type within the core further argues for adverse conditions for the local vegetation.

Betula percentages rise progressively after ~12,400 yr B.P. (zone Ju6), but PARs suggest the shrub was not abundant until ~11,900-11,200 yr B.P. Both percentages and PARs indicate expansions of shrub *Alnus* at ~10,800-10,500 yr B.P. (180.5-176.5 cm of zone Ju7) and *Larix* at ~9800 yr B.P. (167 cm). *Salix* pollen, although occurring in minor amounts, has relatively high percentages into lower zone Ju7 (~10,500 yr B.P.) and high PARs in zones Ju7-Ju8 (~10,800-7000 yr BP), perhaps suggesting greater abundances than during the early LGM. The growth form of *Salix* cannot be differentiated by pollen morphology, nor can it be separated from *Chosenia*, a tree within the Salicaceae. However, the *Salix* pollen values may represent the first postglacial incursion of deciduous trees into the Julietta area, which would be consistent with regional trends (see next section). Maximum total PARs occur ~9100-8100 yr B.P. (157.5-143 cm of zones Ju7-Ju8; total PARs increase ~11,000 yr B.P.), perhaps an indication of favorable growing conditions for all woody taxa, except *Pinus pumila*. The virtual absence of *Pinus* pollen in zone Ju7 and low amounts in zone Ju6 lend further support that *Pinus pumila* was extirpated from the landscape during the late LGM and the LG. With increases in percentages and PARs of *Pinus pumila* at ~8100 yr B.P. (143 cm of zone Ju8), the modern plant communities (zone Ju9, ~6900 yr B.P. to present) were established, marking a hiatus of ~11,000 (PAR) to 2600 (percentages) years for *Pinus pumila* near Julietta Lake.

Regional vegetation trends and paleoclimatic implications

The Julietta pollen record suggests: 1) a more moderate and a more severe interval within the LGM; 2) a gradual increase in summer temperature and precipitation beginning ~12,400 yr B.P. that perhaps culminated in a thermal maximum from ~11,000 to 8100 yr B.P.; and 3) an increase in snow fall and possible decrease in summer temperature at ~8100 yr B.P. Because the *Pinus pumila* record from Julietta is unique in WB, the above paleoclimate inferences may reflect local idiosyncrasies related to the mountainous terrain rather than wide-ranging changes reflecting climatic variations. To evaluate the local vs. extra local signal, we consider the Julietta history in light of previously defined, regional paleoenvironmental changes from the LGM to the early Holocene. We then discuss paleoclimatic implications of the *Pinus pumila* history.

The LGM

Marine and terrestrial investigations indicate that Okhotsk Sea surface and adjacent land temperatures in more southerly areas of the Russian Far East were not stable during the LGM, with particularly cool intervals ~24,000-21,700 yr B.P. and ~19,500-15,700 yr B.P. (Gorbarenko et al. 2004). Palynological and glacial data from eastern Beringia (EB) also suggest a moderation in LGM conditions ~22,000-20,000 yr B.P. (Cwynar, 1982; Porter et al., 1983; Anderson, 1985). Although Julietta does not span the entire Late Pleistocene, nearby records from Elikchan-4 (810 m a.s.l.) and Alut (480 m a.s.l.) lakes (Fig. 1), which are >25,000 yr B.P., indicate a dramatic decline in shrub communities ~24,000 yr B.P. (Lozhkin and Anderson, 1996; Anderson et al., 1998; Anderson and Lozhkin, 2001). *Pinus* pollen percentages at these sites are generally 5% or less, suggesting that *Pinus pumila*, an important component of interstadial (MIS3 equivalent) vegetation in the Upper Kolyma-northern Priokhot'ye region, was likely absent or greatly reduced during the LGM. A return to relatively milder conditions ~21,700 yr B.P., as suggested by Gorbarenko et al. (2004), is not evident at Elikchan-4 and only hinted at with a slight increase in *Betula* pollen at Alut Lake. In contrast, high percentages and PARs indicate the presence of *Pinus pumila* near Julietta Lake at least for a short interval ~20,900-19,100 yr B.P., with a population decline beginning approximately at the start of the second cool interval. With the exception of *Salix*, PARs from Julietta indicate deciduous shrubs were likely absent (*Alnus*) or rare (*Betula*) during this brief ~1800 yr period.

The Late Glaciation - Early Holocene

The widespread establishment of *Betula* shrub tundra ~12,500-12,000 yr B.P. is the first indication of postglacial climatic amelioration in WB, and is marked by a rapid shift from cool, dry herb-dominated communities to more moderate shrub *Betula* tundra (Lozhkin et al., 1993; Anderson and Lozhkin, 2002). While percentages increase ~12,400 yr B.P. at Julietta, PARs indicate that shrub *Betula* was not common until ~11,900-11,200 yr B.P., perhaps reflecting the lake's higher elevation and/or distance from possible refugial valley populations (Brubaker et al., 2005). A similar gradual expansion has been noted recently at Elikchan-4 Lake (Kokorowski et al., 2008).

Between ~11,000-9000 yr B.P., Edwards et al. (2005) suggested that Beringia was occupied by an unusual vegetation type, one dominated by deciduous forests in lowland sites and deciduous shrub (possibly high shrub) tundra at higher elevations. Regional patterns in pollen and plant macrofossils indicate summers were warmer and drier than present. The establishment of shrub *Alnus* (~10,800-10,500 yr B.P.) and *Larix* (~9800 yr B.P.) near Julietta reflects these warming conditions, allowing movement probably from lower elevations to the Kilgan Massif. However, evidence at Julietta for warmer and/or drier conditions than present, as opposed to a warming trend, is more indirect. *Salix* PARs, while variable, reach maxima beginning ~11,000 yr B.P. The PARs perhaps reflect the presence of tree *Salix* or *Chosenia* at higher elevation and/or increased local occurrences of shrub *Salix* (possibly high growth form). If the PARs indicate optimum warmth, then the *Salix* PARs suggest the continuation of early Holocene conditions until

~7000 B.P. In as much as total PARs reflect vegetation "abundance" or "density" and that, in turn, indicates a climatic response to warm summers, maximum PARs at Julietta occur ~9100 to 8000 yr B.P. This latter period corresponds to times in northern WB where woody taxa grew beyond modern latitudinal range limits and/or displayed high growth forms (Lozhkin, 1993; Edwards et al., 2005; Shilo et al., 2008). Thus, it seems a PGTM may have persisted longer in WB (~11,000 to 8000-7000 yr B.P.) than in EB (~11,000-9000 yr B.P.).

Implications for paleoclimatic interpretations

Although Brubaker et al. (2005) argued for the survival of *Pinus pumila* during the LGM, this conclusion was based largely on patterns of postglacial expansion seen in pollen percentage maps. The Julietta record provides more direct evidence for the presence of viable *Pinus pumila* populations at least during a portion of the LGM. The shrub's persistence at higher elevations suggests that the complex topography of southwestern Beringia provided microenvironments that were sufficiently protected to allow for survival in a cryptic refugium. Given that *Pinus pumila* requires a sufficient snow cover to protect its leaves, sheltered mountain localities may better provide that cool-season protection than in lower-elevation, windswept valleys.

Perhaps even more interesting than the refugium's high-elevation location is the absence of shrub *Alnus* and absence or rarity of shrub *Betula* during times when *Pinus pumila* persisted. Yet modern distributions of shrub *Alnus* and *Pinus pumila* are quite similar, although today shrub *Betula* extends farther north and east into cooler tundra settings in WB. If summer temperature and/or effective moisture played a critical role in determining presence/absence during the LGM, then all shrubs should have survived near

Julietta. Seasonal transitions and feedbacks rather than simply summer or growing season conditions may have favored the evergreen shrub over *Betula* and *Alnus*. For example, Bartlein et al. (1998) examined surface energy-water balance processes in Beringia at 21,000 cal yr B.P. (~18,000 yr ^{14}C B.P.) to assess possible reasons for mismatches between atmospheric general circulation model (AGCM) simulations and paleodata. In this exercise, they noted a positive snow-depth anomaly in WB that was statistically significant from June through February (present but not significant from March-May). Although conditions are summarized for greater WB and for maximum glacial conditions, the possibility of persistent snow cover through summer, fall, and winter might have restricted deciduous shrub growth in the Julietta area by impacting the length of snow-free or growing season. The growing season perhaps was too short for *Betula* and *Alnus* to flower and leaf out. *Pinus pumila*, as an evergreen, had an advantage in this situation, possibly further enhanced by its ability to quickly become upright with the beginnings of snow melt. Additionally, Bartlein et al. (1998) noted that positive summer snow depths resulted in negative surface-air temperature anomalies that exceeded simulated air mass temperatures, suggesting a further cooling in summer temperatures that could have additional negative impact on shrub *Betula* and *Alnus*.

The Julietta data suggest that *Pinus pumila* was likely absent (PAR) or rare (percentages) from the Kilgan Massif between ~19,000 and 8100 yr B.P. The loss of *Pinus* during the latter portion of the LGM could reflect: 1) regionally drier winters and possibly somewhat cooler summers associated with intensification of the Aleutian Low (Kutzbach et al., 1998; Mock et al., 1998); or 2) local changes (e.g., slight shifts in wind patterns or storm tracks) that altered depth or duration of snow cover. By the LG, differences in seasonal insolation were becoming marked with simulated summer temperatures over Beringia having warmed significantly (16,000 cal yr B.P. model; ~13,400 yr BP) and with cold dry winters continuing into the early Holocene (14,000 and 11,000 cal yr B.P. models; Kutzbach et al., 1998; Bartlein et al., 1998). The widespread expansion of shrub *Betula* ~12,500 yr B.P. reflects this summer warming. *Larix* (~12,000-11,000 yr B.P.) and *Alnus* (~12,000 yr B.P.) pollen maps illustrate the slightly later expansion of these taxa in the Upper Kolyma region (Brubaker et al., 2005; Lozhkin et al., 1993). If conditions were warmer than present by ~13,400 yr B.P., as suggested by the model simulations, then low effective moisture and not summer temperature alone was probably the main factor limiting spread of these taxa to the Kilgan Massif (see also Edwards and Barker, 1994; Mann et al., 2002). The presence of *Larix* near the lake indicates that summer temperatures were at least 12°C, a temperature adequate for *Pinus pumila* growth. However, the regional absence or rarity of *Pinus pumila* at this time implies an inadequacy of snow cover, even in near-coastal uplands like the Kilgan Massif. Modeling experiments have shown that in the Arctic increased summer radiation results in: 1) warmer surface temperatures from fall to spring (Gallimore and Kutzbach, 1995); and 2) reduced sea-ice coverage and thickness that consequently led to fall-winter warming (Kutzbach and Gallimore, 1988; Mitchell et al., 1988; Kutzbach et al., 1991). These mechanisms and feedbacks could account for a reduced snow cover that would be detrimental for *Pinus pumila* growth during the LG into the early Holocene.

Shrub *Betula*, shrub *Alnus*, and *Larix* have delayed arrivals near Julietta as compared to regional trends. *Pinus pumila,* however, appeared on the Kilgan Massif at ~8000 yr B.P., the time the shrub was spreading rapidly throughout areas of WB

(Anderson and Lozhkin, 2002; Brubaker et al., 2005) . After ~9000 yr B.P., summer insolation, the main driver in the postglacial thermal maximum (PGTM) of Beringia (Bartlein et al., 1998), was declining as was seasonality, but both were still significantly greater than present at the time of *Pinus pumila* expansion (Kutzbach et al., 1998). Changes in boundary conditions between 8000 and 9000 yr B.P. are not so great as to expect major changes in the regional climate of WB. However, some fundamental characteristic of the climate must have changed, allowing for the widespread expansion of *Pinus pumila* in WB. In contrast, such a climatic threshold evidently was surpassed earlier in the Holocene in other areas of Siberia, such as Lake Baikal, the Lena basin, Sakhalin, and Kamchatka, where *Pinus pumila* was a consistent part of the Holocene pollen spectra (Kremenetski et al., 2000). Although this mechanism is unclear at this time, it may well have to do with seasonal transitions rather than July or January extremes.

Conclusions

While recent biogeographical and genetic studies have revitalized interests in northern plant refugia (see Brubaker et al., 2005), they not surprisingly have focused on the survival of modern individuals or communities under full-glacial conditions. The Julietta record adds to this discussion in several ways. Firstly, it provides the most direct evidence to date for a *Pinus pumila* refugium in WB, at least for a portion of the LGM if PAR interpretations are correct or throughout this interval if percentages are more reliable. Secondly, the extirpation of *Pinus pumila* at Julietta by the late LGM or early LG combined with mapped pollen data (Brubaker et al., 2005) suggest the presence of a second *Pinus pumila* refugium. This one likely occurred at lower elevations during the

LG into the earliest Holocene (PGTM in Beringia). Both the PGTM and the LGM provided equally harsh albeit different conditions for the survival of this evergreen shrub. Paleoclimatic modeling experiments and understanding of modern ecology suggest that shifts in the nature of seasonal transitions and not only seasonal extremes have played important roles in the history of *Pinus pumila* over the last glacial-interglacial cycle. The Julietta record also adds to the building database for WB that indicates, like in EB, modern communities did not survive full-glacial conditions intact but rather the main boreal taxa responded individualistically to the changing climates of the LG and early Holocene.

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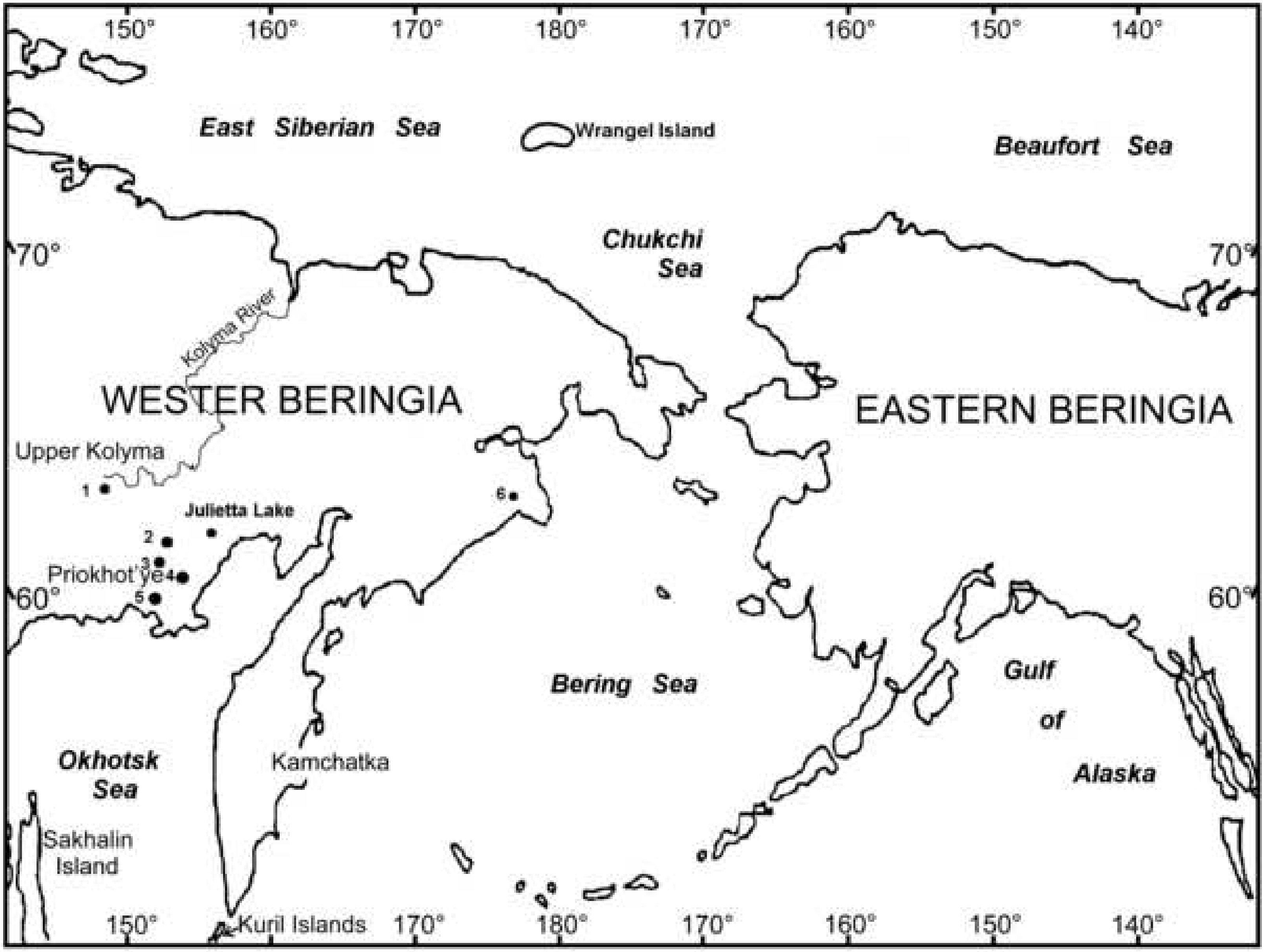
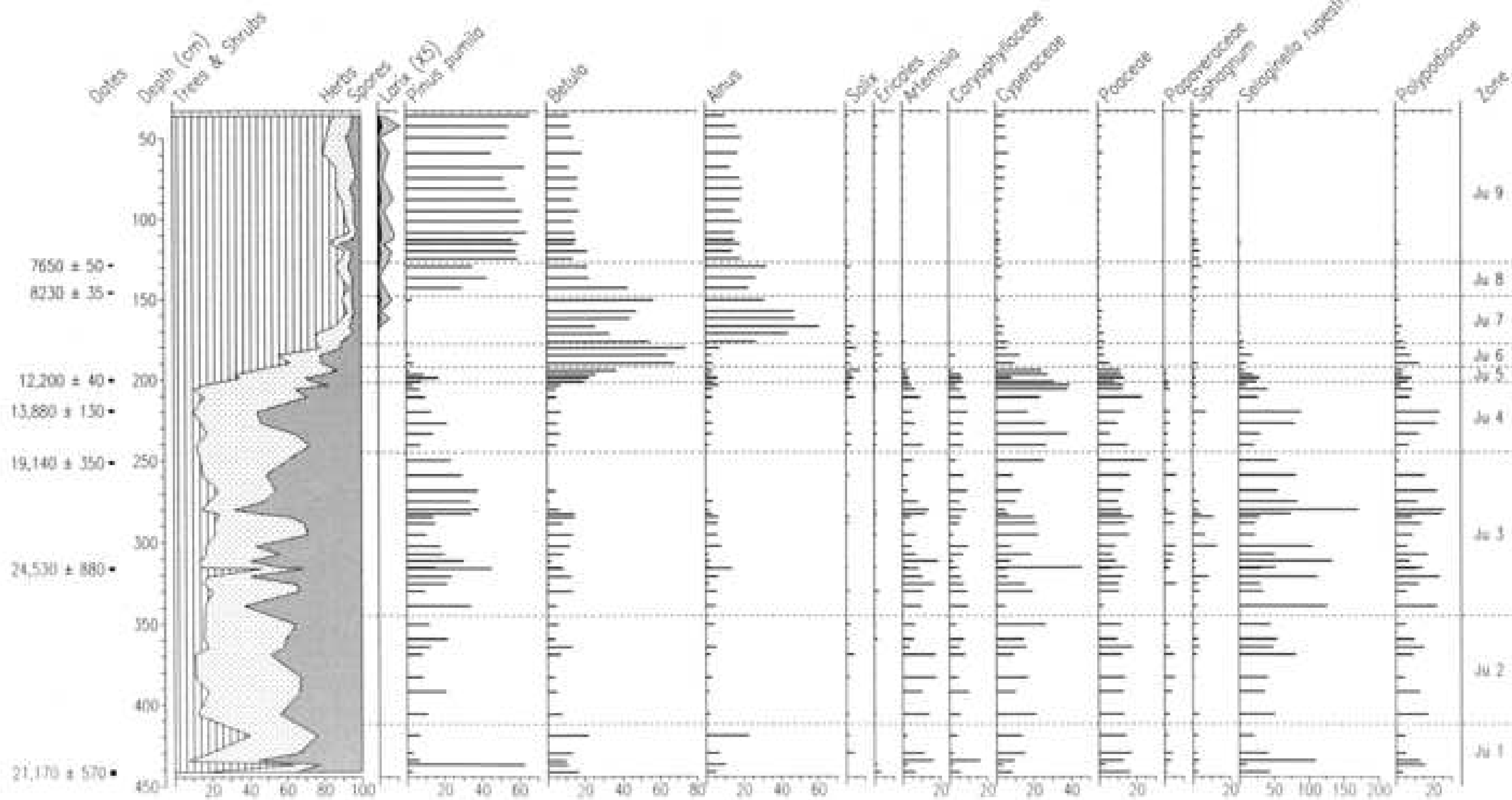
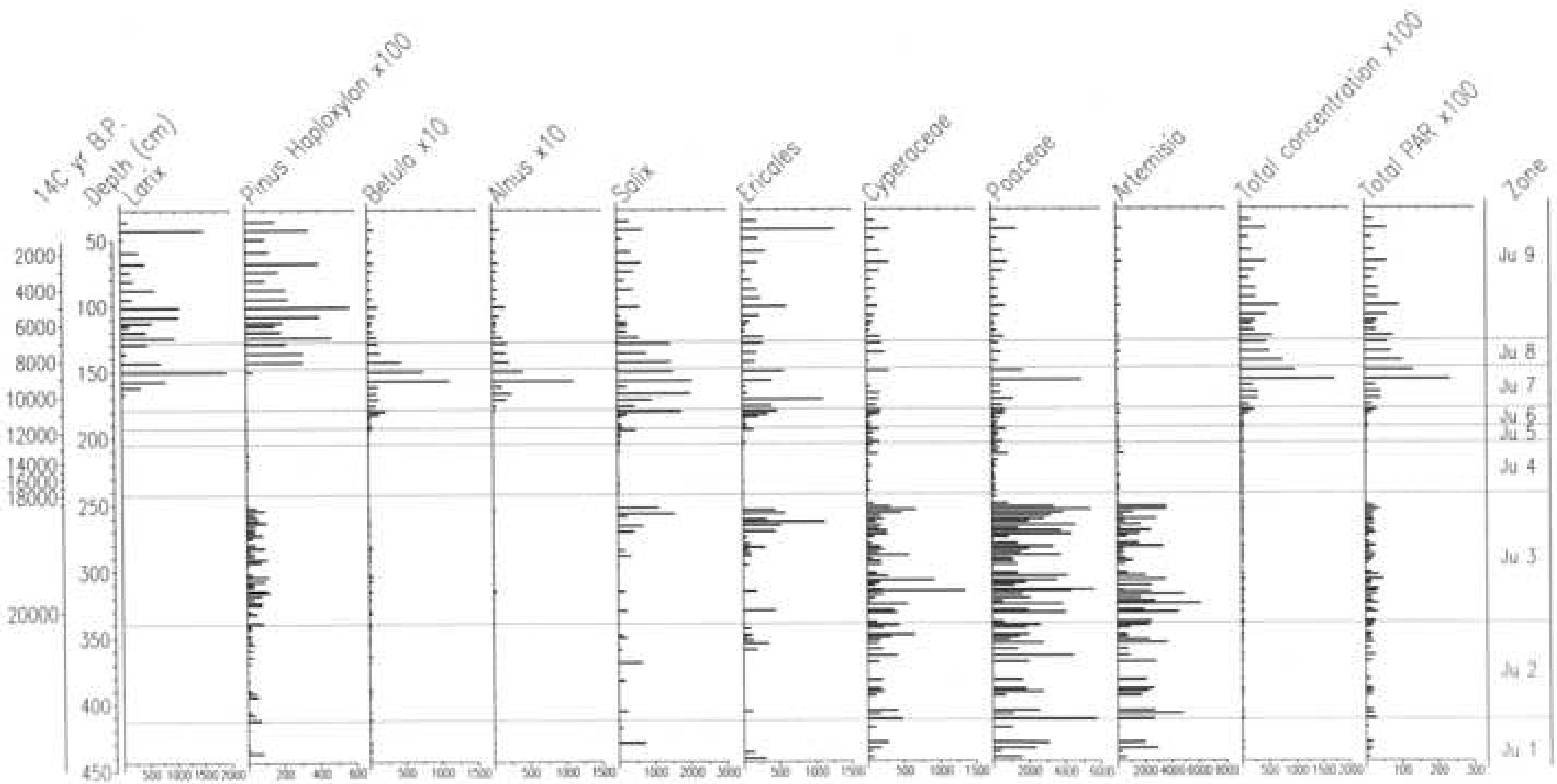

150°
160°
170°
180°
170°
160°
150°
140°
East Siberian Sea
Wrangel Island
Beaufort Sea
Chukchi Sea
70°
70°
Kolyma River
WESTER BERINGIA
EASTERN BERINGIA
Upper Kolyma
1
Julietta Lake
6
2
3
Priokhot'ye
4
5
60°
60°
Bering Sea
Gulf of Alaska
Okhotsk Sea
Kamchatka
Sakhalin Island
Kuril Islands
150°
170°
180°
170°
160°
150°
140°



Dates
Depth (cm)
Trees & Shrubs
Herbs
Spores
Larix (X5)
Pinus pumila
Betula
Alnus
Salix
Ericales
Artemisia
Caryophyllaceae
Cyperaceae
Poaceae
Papaveraceae
Sphagnum
Selaginella rupestris
Polypodiaceae
Zone
7650 ± 50
8230 ± 35
12,200 ± 40
13,880 ± 130
19,140 ± 350
24,530 ± 880
21,170 ± 570
Ju 9
Ju 8
Ju 7
Ju 6
Ju 5
Ju 4
Ju 3
Ju 2
Ju 1



14C yr B.P.
Depth (cm)
Larix
Pinus Haploxylon x100
Betula x10
Alnus x10
Salix
Ericales
Cyperaceae
Poaceae
Artemisia
Total concentration x100
Total PAR x100
Zone
Ju 9
Ju 8
Ju 7
Ju 6
Ju 5
Ju 4
Ju 3
Ju 2
Ju 1

FIGURE CAPTIONS

Fig. 1. Map of Beringia with location of Julietta and other lake sites mentioned in the text: 1) Elgennya Lake; 2) Goluboye Lake; 3) Elikchan-4 Lake; 4) Lesnoye Lake; 5) Alut Lake; and 6) Gytgykai Lake.

Fig. 2. Diagrams of percentage (A) and pollen accumulation rates (B) for the main taxa from Julietta Lake. Subsum values shown on the left side of the percentage diagram are based on the total of arboreal and nonarboreal pollen and spores. Individual taxa percentages use a pollen sum of arboreal and nonarboreal pollen minus Cyperaceae. Note scale changes in PAR diagram.

Table 1

Sedimentology of the Julietta core

Core depth (cm)	Sediment type
0-116	Organic-rich silt
116-128.6	Laminated silt
128.6-128.8	Tephra
128.8-168	Silt
168-202	Laminated silt with organics
202-246	Finely laminated silts
246-278	Organic-rich layered silts
278-340	Finely laminated silts
340-375	Clay
375-411	Laminated clay
411-433	Sand

Table 2

Radiocarbon, calibrated, and tephra ages for Julietta Lake

CAMS #	Sample depth (cm)	Age (^{14}C yr BP)	Age (cal yr BP) 2σ range	Material dated
103338	145-145.5	8230 ± 35	9032-9058	woody fragment
103339	199-201	12,200 ± 40	13,940-14,176	woody fragments; aquatic moss
128576	218-220	13,880 ± 130	16.075-17,006	bulk sediment
128577	250-252	19,140 ± 350	22,046-23,815	bulk sediment
128578	315-317	24,530 ± 880	Beyond calibration range	bulk sediment
128579	440-443	21,170 ± 570	24,124-25,980	bulk sediment
Elikchan/KO tephra	128.6-128.8	7650 ± 50	8467-8477	tephra