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VEGETATION MEDIATED THE IMPACTS OF POSTGLACIAL CLIMATIC CHANGE ON FIRE REGIMES IN THE SOUTHCENTRAL BROOKS RANGE, ALASKA

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1 Running head: Postglacial fire history in the Brooks Range

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5 VEGETATION MEDIATED THE IMPACTS OF POSTGLACIAL CLIMATIC CHANGE ON FIRE REGIMES IN THE
6 SOUTHCENTRAL BROOKS RANGE, ALASKA

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1 ABSTRACT

2 We examine direct and indirect impacts of millennial-scale climatic change on fire regimes in the
3 southcentral Brooks Range, Alaska, using four lake-sediment records and existing paleoclimate
4 interpretations. New techniques are introduced to identify charcoal peaks semi-objectively and
5 detect statistical differences in fire regimes. Peaks in charcoal accumulation rates (CHARs)
6 provide estimates of fire return intervals (FRIs) which are compared between vegetation zones
7 described by fossil pollen and stomata. Climatic warming from ca 15-9 ka BP (calendar years
8 before CE 1950) coincides with shifts in vegetation from herb tundra to shrub tundra to
9 deciduous woodlands, all novel species assemblages relative to modern vegetation. Two sites
10 cover this period and show increased CHARs and decreased FRIs with the transition from herb
11 to shrub tundra ca 13.3-14.3 ka BP. Short FRIs in the *Betula*-dominated shrub tundra (mean [m]
12 FRI 144 yr; 95% CI 119-170) primarily reflect the effects of flammable, continuous fuels on the
13 fire regime. FRIs increased significantly with the transition to *Populus*-dominated deciduous
14 woodlands ca 10.5 ka BP (mFRI 251 yr [158-352]), despite evidence of warmer- and drier-than-
15 present summers. We attribute reduced fire activity under these conditions to low flammability
16 of deciduous fuels. Three sites record the mid to late Holocene, when cooler and moister
17 conditions allowed *Picea glauca* forest-tundra and *P. mariana* boreal forests to establish ca 8 and
18 5.5 ka BP. Forest-tundra FRIs did not differ significantly from the previous period (mFRIs range
19 from 131-238 yr), but FRIs decreased with the transition to boreal forest (mFRI 145 yr [129-
20 163]). Overall, fire-regime shifts in the study area showed greater correspondence with
21 vegetation characteristics than with inferred climate, and we conclude that vegetation mediated
22 the impacts of millennial-scale climatic change on fire regimes by modifying landscape

1 flammability. Our findings emphasize the importance of biological-physical feedbacks in
2 determining the response of arctic and subarctic ecosystems to past, and by inference, future
3 climatic change.

4 **Keywords:** Alaska; arctic; boreal forest; charcoal analysis; climatic change; deciduous
5 woodland; fire history; pollen analysis; shrub tundra; tundra.

6 INTRODUCTION

7 Recent warming in northern high latitudes (Overpeck et al. 1997, Serreze et al. 2000) has
8 initiated a variety of changes in vegetation and fire regimes, including population expansion and
9 increased growth of trees and shrubs (Lloyd 2005, Tape et al. 2006) and increased area burned
10 across boreal forests (Kasischke and Turetsky 2006, Soja et al. 2007). As climate warms over the
11 next century (ACIA 2004), annual area burned in boreal forests is predicted to continue
12 increasing (Rupp et al. 2000, Calef et al. 2005), in some cases by more than 100% (Flannigan et
13 al. 2005). The response of fire regimes to climatic change in these regions will ultimately depend
14 upon feedbacks between climate and vegetation that determine landscape flammability at
15 multiple temporal scales.

16 Numerous studies in North American boreal forests document the importance of direct
17 climatic controls on fire regimes. At annual time scales, area burned in recent decades has been
18 tightly linked to warm, dry weather and frequent lightning (Johnson 1992, Kasischke et al. 2002,
19 Duffy et al. 2005). Paleoecological studies support these climate-fire relationships over
20 millennial time scales and illustrate that fire frequencies have varied with changes in relative
21 moisture throughout the late Holocene (Carcaillet et al. 2001, Lynch et al. 2002, Lynch et al.

1 2004b). However, climatic influences on fire regimes are also mediated by vegetation. Area
2 burned across interior Alaska, for example, is positively correlated with tree cover (Kasischke et
3 al. 2002), and the probability of fire in many boreal forests varies with stand age, a determinant
4 of fuel abundance (Yarie 1981, Lynch et al. 2002). In addition, modeling studies predict
5 increased burning in boreal Alaska simply in response to increased black spruce (*Picea mariana*
6 Mill. BSP.) densities (Rupp et al. 2002).

7 We use a paleoecological approach to examine the relationships between climate,
8 vegetation, and fire regimes in the southcentral Brooks Range, Alaska (Fig. 1), where millennial-
9 scale climate and vegetation histories are well known based several decades of research in the
10 region (Anderson et al. 2004). Our goal is to document fire history to understand how millennial-
11 scale climatic changes have interacted with vegetation change to influence fire regimes over the
12 past 15,000 years. We use macroscopic charcoal from lake sediments to reconstruct fire
13 occurrence and statistically compare fire return intervals (FRIs, the time between consecutive
14 fires) between vegetation zones inferred from fossil pollen, stomata stratigraphy, and modern
15 analog analysis. If climatic variations were the dominant control of fire regimes, changes in fire
16 occurrence between vegetation zones should be consistent with direct climate-fire relationships
17 and relatively independent of vegetation characteristics (e.g. Carcaillet et al. 2001). In contrast, if
18 vegetation change was the dominant control of fire regimes, changes in fire occurrence between
19 vegetation zones should be consistent with the role that fuels play in determining landscape
20 flammability (e.g. Lynch et al. 2002), but possibly unexpected given the direct effects of climate
21 change on fire regimes. In addition to testing these two alternative hypothesis, by documenting
22 fire regimes in novel vegetation assemblages that covered the study region during late glaciation

1 and the early Holocene (c. 14.0-9.0 k ybp; e.g. Anderson et al. 1989, Edwards et al. 2005), our
2 study provides examples of how direct and indirect impacts of climatic change may shape future
3 fire regimes in arctic and boreal ecosystems.

4 STUDY LAKES AND REGIONAL SETTING

5 We examined sediment cores from four lakes along a 120 km east-west transect in the
6 foothills of the southcentral Brooks Range (Table 1, Fig. 1). Modern climate in the study region
7 is continental. January and July mean maximum temperatures in Bettles (Fig. 1) are -20°C and
8 21°C, respectively; mean annual precipitation is 36 cm, with 55% falling between June and
9 September (Western Regional Climate Center, 1951-2005 observations¹). Forests and woodlands
10 dominate lowlands and hill slopes in the study region, with *Picea mariana* in wet muskegs, *P.*
11 *glauca* (Moench) Voss. and *Populus balsamifera* Mill. along riparian areas, and *P. glauca*,
12 *Betula papyrifera* Marsh. and *Populus tremuloides* Michx. on uplands and warm, south-facing
13 slopes (Nowacki et al. 2000). *Salix* spp., *Betula glandulosa* Michx., and *Alnus* spp. form shrub
14 communities in non-forested areas, (Nowacki et al. 2000). Fire is the primary disturbance agent
15 in the region, with an estimated fire rotation period of 175 yr (based on observations from 1950-
16 2001 from the Kobuk Ridges and Valleys Ecoregion; Kasischke et al. 2002).

17 We cored small (2-15 ha), relatively deep (7.0-11.6 m) lakes (Table 1) surrounded by
18 discontinuous *P. mariana*-dominated forest. Recent fires burned to the edge of Ruppert Lake
19 (RP) in CE 1991 (15,357 ha), to 1 and 3 km east of Code Lake (CO) in CE 1959 (788 ha) and
20 1949 (2456 ha), and to 5 km west and 1 km southwest of Wild Tussock Lake (WK) in CE 1997
21 (9750 ha) and 1991 (6390 ha; Alaska Fire Service 2004; Fig. 1).

¹ Data available online: <http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?akbett>

METHODS

Lake sediments

Sediments were collected from the center of each lake with two parallel, overlapping 8-cm diameter cores in summer 2001 (CO), 2002 (RP), or 2003 (XI, WK) using a modified Livingstone piston corer (Wright et al. 1984). Surface sediments (< ca 50 cm) were collected with a polycarbonate tube and the top 10-20 cm sliced at 0.5-1.0 cm in the field. All cores had intermittent laminae, and stratigraphic markers were used to develop continuous records from overlapping segments of adjacent cores. Cores were sliced at 0.25 to 0.50 cm intervals, and 1 cm³ subsamples were prepared at varying intervals for pollen and stomata analysis according to PALE (1994), except that samples were not subjected to a coarse sieve (Carlson 2003). Pollen was counted at 400-1000 x magnification to a terrestrial pollen sum > 300 (mean = 398, s.d. = 107) and displayed as percentages of total terrestrial pollen. In samples bracketing the *Picea* pollen rise ca 5.5 ka BP (Brubaker et al. 1983), (1) stomata searches were conducted to an equivalent pollen sum of 2000 grains (Carlson 2003) and *Picea* stomata were identified based on comparisons with an Alaskan reference collection and Hansen (1994), and (2) *Picea* pollen grains were classified as *P. mariana* or *P. glauca* based on morphological measurements on ca 30 *Picea* pollen grains per sample (Appendix A). For charcoal identification, 3-5 cm³ subsamples were taken from contiguous core slices and prepared following Higuera et al. (2005). Charcoal was identified at 10-40 x magnification based on color, morphology, and texture. Charcoal concentrations (pieces cm⁻³) were multiplied by the estimated sedimentation rate (cm yr⁻¹) to obtain the charcoal accumulation rate (CHAR; pieces cm⁻² yr⁻¹) of each sample.

Chronologies

Sediment chronologies for each site were based on ^{210}Pb dates for the upper 10-20 cm (using the CRS model; Binford 1990) and/or on AMS ^{14}C ages of concentrated charcoal from charcoal peaks, concentrated *Picea* pollen, or terrestrial macrofossils for deeper sediments. Chronologies were developed individually for the ^{210}Pb and ^{14}C portions of each core using a weighted cubic smoothing spline in Matlab (The MathWorks, Inc.) taking into account the number and uncertainty of age estimates. The number of age estimates in a chronology determined the smoothing parameter for each spline, such that a larger number of ages for a given time interval resulted in a more flexible spline. The uncertainty of each age estimate (i.e. two standard deviations) was used to weight the influence of each age in the age-depth model (cf. Telford et al. 2004). Finally, confidence intervals for the age-depth model, reflecting the combined uncertainty of all age estimates in a model, were derived from 1000 bootstrapped chronologies. For each bootstrapped chronology, each age used to develop the chronology was selected randomly based on the probably distribution of the ^{210}Pb or calibrated ^{14}C date. The final chronology represents the median age at each depth from the 1000 bootstrapped chronologies.

Analysis of pollen and stomata data

Pollen zone boundaries were delineated primarily by visual inspection of pollen percentages of major tree, shrub, and herb taxa and correspond to vegetation types previously recognized in the region (Anderson and Brubaker 1994). In addition, we used a modern analog analysis based on squared-chord distances (SCD) and receiver operating characteristic curves to quantify the probability that fossil pollen assemblages resembled modern pollen assemblages

1 from North American Arctic Tundra, Boreal Forest, and Forest-tundra biomes (Appendix A).
2 The arrival of *P. mariana* and development of the modern boreal forest was estimated via (1)
3 *Picea* stomata presence/absence (RP and WK), (2) discriminant analysis (RP and WK) of *Picea*
4 grains, and (3) modern analog analysis (Appendix A).

5 *Statistical treatment of charcoal records*

6 To assess whether CHARs differed between past biomes, we compared CHAR
7 distributions between pollen zones in each lake using a two-sample Kolmogorov-Smirnov (K-S)
8 test (e.g. Clark 1990, Lynch et al. 2002). Prior to subsequent analyses, which emphasize finer
9 temporal variation in CHARs, we interpolated CHARs to 15-yr time steps ($C_{interpolated}$),
10 approximating the mean sampling resolution at all sites (Table 1). This step reduces biases due to
11 variable sample resolution within and between records.

12 We inferred the timing of “local” fire occurrence by decomposing charcoal records (e.g.
13 Clark et al. 1996) and identifying “large”, distinct charcoal peaks based on a standard set of
14 threshold criteria applied to each record. Consistent with empirical and theoretical studies
15 (Lynch et al. 2004a, Higuera et al. 2007), we use the term “local” to refer to distances within
16 approximately 500-1000 m of each lake, corresponding to an area of ca 100-300 ha (1-3 km²).
17 We assume that low-frequency variations in CHARs, $C_{background}$, reflect changes in the rate of
18 total charcoal production, secondary charcoal transport, and sediment mixing (Clark et al. 1996,
19 Higuera et al. 2007). We subtracted $C_{background}$ from $C_{interpolated}$ to obtain a residual series, C_{peak}
20 (i.e. $C_{peak} = C_{interpolated} - C_{background}$), which contains high-frequency variability around the long-

1 term trend described by $C_{background}$ (e.g. Clark et al. 1996).² Prior decomposition methods have
2 assumed a constant relationship between C_{peak} and $C_{background}$ and applied a globally-defined
3 threshold values to C_{peak} series to identify peaks that reflect the occurrence of one or more local
4 fires. In our records, however, the variability of C_{peak} around $C_{background}$ changes through time
5 (Appendix A). Thus, we developed a locally-defined threshold that identifies charcoal peaks
6 based on local variability around each sample. Specifically, we used a Gaussian mixture model
7 to separate C_{peak} values within each overlapping 500-yr portion of a record into two components:
8 (1) C_{noise} , variations around $C_{background}$ that reflect natural and analytical effects (e.g. sediment
9 mixing, sediment sampling), and (2) C_{fire} , variations exceeding variability in the C_{noise}
10 distribution, assumed to reflect local fire events (Gavin et al. 2006). The threshold separating
11 C_{fire} from C_{noise} should occur in the upper range of the C_{noise} population. Thus, to identify C_{fire}
12 samples in any 500-yr portion of the record we considered three possible threshold values
13 corresponding to the 95th, 99th, and 99.9th percentile of the C_{noise} population. We present results
14 from all three criteria but discuss only those using the 99th percentile criterion. Finally, all peaks
15 identified via these methods were screened to test whether variations between a “peak” and the
16 smallest “non-peak” sample within the previous 5 samples (i.e. 75 yr) differed statistically based
17 on the size of the original charcoal counts (Gavin et al. 2006; Appendix A). This screening
18 eliminates “peaks” during periods of low charcoal accumulation (e.g. < 5 pieces per sample)
19 when the variation in low charcoal counts cannot be confidently separated from noise. Our

² We estimated low-frequency trends by calculating a 500-yr moving median across each record and then smoothing this series with a locally-weighted regression using a 500-yr window.

1 methods are described in detail in Appendix A and are contained within the publicly-available
2 program *CharAnalysis*³.

3 In addition, as an indication of the suitability of charcoal records for peak identification,
4 we calculated a signal-to-noise index (*SNI*) for each sample, SNI_i , describing the variance within
5 the C_{fire} distribution (i.e. signal) relative to the total variance in C_{peak} in the 500 years surrounding

6 that sample: $SNI_i = \frac{\text{var}(C_{fire})}{[\text{var}(C_{noise}) + \text{var}(C_{fire})]}$ The SNI varies from 0-1, with high values

7 representing large separation between charcoal peaks and non-peaks, and values close to 0
8 representing little separation between peaks and non peaks.

9 *Quantifying and detecting difference in fire regimes*

10 We infer aspects of past fire regimes based on the magnitude and temporal pattern of
11 identified charcoal peaks. Peak magnitude, the number of charcoal pieces from all samples
12 defining a peak (i.e. all samples above the threshold value; pieces cm^{-2} peak⁻¹), is measure of
13 total charcoal deposition per fire (Whitlock et al. 2006). Charcoal deposition for a given fire
14 should vary depending on fire size, fire location, and fuel consumption (Higuera et al. 2007).
15 Systematic changes in peak magnitude thus reflect variability in fuel consumption, as variability
16 due to fire size and fire location is accounted for as multiple fires are sampled.

17 We used the distribution of FRIs within each pollen zone to characterize the FRIs of each
18 vegetation type. FRI distributions were described by the mean FRI (mFRI), and if a pollen zone
19 had > 5 FRIs (> 6 fires), a two-parameter Weibull model was fit to FRIs using maximum
20 likelihood techniques (in Matlab, The Mathworks Inc.; Clark 1989, Johnson and Gutsell 1994).

³ *CharAnalysis* was written by PEH and is available at <http://CharAnalysis.googlepages.com>

1 Goodness-of-fit for each Weibull model was tested with a one-sample K-S test (Zar 1999) and
2 Weibull models are not reported unless $p > 0.10$ (i.e. there is $> 10\%$ chance that the empirical
3 distribution is not different from the Weibull model; Johnson and Gutsell 1994). 95% confidence
4 intervals for Weibull parameters and mFRI were estimated based on 1000 bootstrapped samples
5 from each distribution. We tested two null hypotheses using a likelihood-ratio test (LRT)⁴ based
6 on estimates of the Weibull b and c parameters (Appendix A): (1) FRI did not differ between
7 pollen zones within a given site, and (2) FRI did not differ between sites within a given pollen
8 zone. We rejected the null hypothesis if $p \leq 0.05$. If FRI distributions within a single vegetation
9 zone were statistically similar across sites (i.e. hypothesis 2 was not rejected), we pooled FRI to
10 form a composite record representing FRI from across the study area (i.e. 2-3 sites). With the
11 pooled FRI we performed the same between-zone comparisons as with individual records. Due
12 to the increased sample size in the composite records, this procedure yields greater statistical
13 power for detecting differences between fire regimes in different vegetation zones. Because in
14 most cases comparisons between zones at individual sites were similar to results for the pooled
15 data (although not always significant), we focus our discussion on results from the pooled data.

16 RESULTS

17 *Chronologies and sedimentation rates*

18 The RP and XI records are older (14 and 15.5 ka) than the CO and WK records (7.5 and
19 7.8 ka; Fig. 2). All age models since 8 ka BP are well constrained and generally pass through the

⁴ By utilizing both parameters of the Weibull distribution, the LRT provides a more powerful method for detecting difference in FRI distributions than possible by interpreting confidence intervals around mFRI and estimated Weibull parameters (e.g. Clark 1990, Lynch et al. 2002) or by using the non-parametric K-S test (Lynch et al. 2002, Anderson et al. 2006, Gavin et al. 2006).

1 95% confidence interval of ^{14}C or ^{210}Pb dates (Fig. 2). At RP we rejected two ^{14}C dates on
2 concentrated pollen (19.02 and 29.50 cm) because they are ca 500-1000 yr older than ages
3 defined by five other ^{14}C dates on charcoal in sediments spanning the same core depths (10 and
4 60 cm; Fig. 2; Appendix B). At RP and XI, age models > 8 ka BP are less well constrained, and
5 predicted ages do not always intersect the uncertainty of ^{14}C dates (e.g. RP; Fig. 2). Given these
6 results and the sensitivity of CHARs to sedimentation rates, we evaluated whether different
7 choices of age-depth relationships altered the general features of the CHAR series at these sites.
8 We developed 5-7 alternative age-depth relationships by excluding individual dates and
9 changing the age-depth model criteria. In no case did the overall nature of the CHAR records
10 change.

11 Sedimentation rates ranged from 0.017 to 0.040 cm yr^{-1} (Table 1, Fig. 2). They vary little
12 in the CO and WK records, but are higher prior to ca 8 and 11 ka BP at RP and XI, respectively
13 (Fig. 2). The mean sample resolution at each site is ~ 15 yr sample^{-1} (Table 1), varying from < 5
14 to ca 50 yr sample^{-1} (Fig. 2). Slow sedimentation resulted in low sample resolution at XI from
15 8.0-0 ka BP (> 50 yr sample^{-1}).

16 *Peak identification in charcoal records*

17 . The median signal-to-noise index (SNI) for all records where peak analysis was
18 interpreted exceeds 0.80 (Table 1). This is well above the median SNI expected from records
19 without a peak signal (e.g. 0.15 for red noise; Appendix A) and indicates good separation
20 between peak and non-peak values. We do not interpret peak analysis results at XI from 8.0-0 ka
21 BP because the SNI in this period is consistently $\ll 0.5$ (data not shown). The sensitivity of
22 charcoal peak identification to different threshold criteria varies between pollen zones (Fig. 3;

1 Appendix B) and between sites (Fig. 4) but characterizations of FRI distributions are generally
2 robust to all three threshold criteria (data not shown).

3 Comparisons between known fire events and the most recent charcoal peaks at RP, CO,
4 and WK support the assumption that identified charcoal peaks detect fires within (and not
5 beyond) 1 km of these lakes. The CE 1991 (-41 yr BP) fire that burned to the edge of RP is
6 represented by an identified peak centered at -39 BP, while the most recent peaks identified at
7 CO (69 yr BP) and WK (38 yr BP) both occur before the start of fire observation in CE 1950 (0
8 yr BP); thus the fires that burned to ca 1, 3, and 5 km from these lakes were undetected.

9 *Pollen, stomata, and charcoal records*

10 *Herb Tundra Zone: 14.0-13.3 (RP), 15.5-14.3 (XI) ka BP* – This zone is characterized by
11 Cyperaceae (>25%), *Salix* (ca 25%), Poaceae (ca 15%), and *Artemisia* (ca 10%) pollen, with
12 relatively high percentages of *Pediastrum* algal cell nets (> 25%; Fig. 3; Appendix B). Although
13 SCDs are lowest for comparisons with Arctic Tundra (ca 0.2), the probability-of-analog (< 20%)
14 indicates little similarity with modern tundra (Fig 3; Appendix B). CHARs are low at both sites
15 (medians = 0.00-0.01 pieces cm⁻² yr⁻¹; Appendix B). The presence of only one identified
16 charcoal peak (at RP; Fig. 4) precludes the analysis of fire regimes but suggests long FRIs in this
17 zone.

18 *Shrub Tundra Zone, 13.3-10.3 (RP), 14.3-10.3 (XI) ka BP* -- Increased *Betula* pollen (*B.*
19 *glandulosa* and/or *B. nana*; Anderson and Brubaker, 1994) to > 60% marks the transition from
20 herb to shrub tundra (Fig. 3; Appendix B). SCDs (ca 0.2) continue to indicate a low similarity of
21 fossil to modern pollen assemblages from all modern biomes (probability of analog < 20%; Fig.
22 3; Appendix B). CHARs increase at the onset of this zone (medians = 0.02-0.05 pieces cm⁻² yr⁻¹

1 1), and CHAR distributions are distinct from those in the Herb Tundra Zone ($p \ll 0.01$;
2 Appendix B). Maximum peak magnitudes exceed $5 \text{ pieces cm}^{-2} \text{ peak}^{-1}$ (Fig. 4). Fire regimes at
3 RP and XI are characterized by mFRIs (95% CI) of 137 (107-171) and 150 (113-189) yr,
4 respectively (Table 2; Fig. 5), with no difference in FRI distributions between sites (Fig. 5;
5 Appendix B). The mFRI (95% CI) of the pooled record is 144 (119-170) yr (Fig. 6).

6 *Deciduous Woodland Zone, 10.3-8.5 (RP), 10.3-8.0 (XI) ka BP* – This zone is
7 characterized by increased *Populus* pollen percentages (inferred as *P. balsamifera*, Anderson and
8 Brubaker, 1994; 10-20%; Fig. 3; Appendix B). SCDs are the highest for the entire record (> 0.3),
9 and no analogs exist with modern North America pollen spectra (probability of analog < 0.2 ; Fig.
10 3; Appendix B). CHARs decrease (medians = $0.01\text{-}0.02 \text{ pieces cm}^{-2} \text{ yr}^{-1}$) and distributions are
11 distinct from those in the Shrub Tundra Zone ($p < 0.01$; Appendix B). Peak magnitudes decrease
12 to $< 5 \text{ pieces cm}^{-2} \text{ peak}^{-1}$ (Fig. 4). mFRIs (95% CI) at RP and XI are 223 (90-390) and 293 (225-
13 360) yr, respectively (Table 2; Fig. 5). Because XI recorded only four FRIs (Table 3, Fig. 5), we
14 deemed mFRIs between RP and XI sufficiently close to pool data from within this zone. The
15 mFRI (95% CI) of the composite record is 251 (158-352) yr, significantly different from the
16 composite record of the Shrub Tundra Zone ($p = 0.03$; Fig. 6; Appendix B).

17 *Forest-tundra Zone, 8.5-5.5 (RP), 8.0-5.5 (XI), 7.5-5.5 (CO), 7.8-5.5 (WK) ka BP* --
18 Decreases in *Populus* ($< 10\%$) and increases in *Picea* ($\geq 1\%$) pollen percentages mark the onset
19 of the Forest-tundra Zone (Fig. 3; Appendix B). *Alnus* pollen percentages increase from trace
20 amounts to $> 50\%$ starting around 7.25-7.50 ka BP (Fig 3; Appendix B), coinciding with the start
21 of the CO and WK records (Appendix B). With the rise in *Alnus* pollen, SCD values decrease for
22 comparisons to modern Boreal Forest and Forest Tundra (< 0.1), and probability-of-analog for
23 these biomes increase to $> 30\text{-}40\%$ (Fig. 3; Appendix B). Discriminant analysis of *Picea* pollen

1 at RP and WK (Appendix B) plus previous research (Brubaker et al. 1983) indicate the near
2 exclusive presence of *P. glauca* in this zone.

3 CHARs at XI (median = 0.03 pieces cm⁻² yr⁻¹) are higher than in all previous zones (p <
4 0.01), while CHARs at RP were intermediate between the Herb Tundra (p < 0.01) and Shrub
5 Tundra zones (p < 0.01; medians = 0.02-0.03 pieces cm⁻² yr⁻¹; Appendix B). Charcoal peak
6 magnitude is similar to the previous zone at RP, and generally remains below 5 pieces cm⁻² peak⁻¹
7 at all sites (Fig. 4). mFRIs (95% CI) for RP, CO, and WK are 238 (158-324), 210 (145-277),
8 and 131 (95-172) yr, respectively. Except for RP vs. WK (p = 0.04), FRI distributions do not
9 differ among sites (Fig. 5; Appendix B). Given the statistical difference between RP and WK, the
10 composite FRI distribution only includes FRIs from RP and CO. The composite records has a
11 mFRI (95% CI) of 227 (173-282) yr, similar to the composite record from the Deciduous
12 Woodland Zone, but significantly longer than the composite records from the Shrub Tundra
13 Zone (p = 0.02; Fig. 6; Appendix B).

14 *Boreal Forest Zone, 5.5 ka BP - present (RP, XI, CO, WK) -- Picea pollen percentages*
15 increase to > 10% at all sites between 6 and 4 ka BP (Fig. 3; Appendix B). With the rise in *Picea*
16 pollen, all sites show an increase in the probability-of-analog with the modern Boreal Forest
17 biome (> 75%) and lower probabilities for modern Forest-tundra (< ca 70%; Fig. 3; Appendix
18 B). The first presence of *Picea* stomata ca 5.0 ka BP (RP; Fig. 3) and 5.4 ka BP (WK; Appendix
19 B) coincides with the transition from Forest-tundra to Boreal Forest inferred from the modern
20 analog analysis (Fig. 3; Appendix B). *Picea* pollen morphology from RP and WK (Appendix B)
21 and previous research (Brubaker et al. 1983) indicate an increase of *P. mariana* at this time
22 (Appendix B). While the beginning of this zone arguably differs across sites (e.g. RP vs. CO and

1 WK; Fig. 3, Appendix B), our results do not change when all sites are analyzed with a starting
2 date of 5.0 vs. 5.5 ka BP (data not shown). We use 5.5 ka BP at all sites for simplicity.

3 CHARs increase to their highest levels in most records (median CHARs = 0.05-0.11
4 pieces $\text{cm}^{-2} \text{yr}^{-1}$; Fig. 4; Appendix B), although the period of increase varies by ca 500 to 1000 yr
5 (CO, WK vs. RP; Fig. 4). mFRIs (95% CI) at RP, CO, and WK are 171 (135-216), 135 (113-
6 160) and 135 (113-157) yr, respectively (Table 2; Fig. 5), and FRI distributions do not differ
7 between sites (Fig. 5; Appendix B). The mFRI (95% CI) of the composite FRI distribution is 145
8 (129-163) yr; significantly shorter than mFRI in the composite record from the Forest-tundra and
9 Deciduous Woodland Zones but similar to the composite record from the Shrub Tundra Zone
10 (Fig. 6; Appendix B)⁵.

11 DISCUSSION

12 *Interpreting sediment charcoal records and detecting changes in fire regimes*

13 We introduce three general tools that facilitate the interpretation of fire history from
14 sediment-charcoal records. First, the signal-to-noise index provides a semi-objective way to
15 judge if a record is appropriate for peak analysis. For example, while > 0.8 in most records, SNIs
16 were consistently < 0.5 for the 8-0 ka BP in the Xindi Lake record (data not shown), indicating
17 that this section was not suitable for peak identification. Second, our use of a Gaussian mixture
18 model to determine threshold values for peak identification allowed us to treat all charcoal
19 records with one set of objectively-determined criteria. These criteria are consistent with a

⁵ To test the sensitivity our results to FRIs from WK, we constructed a pooled record for the Boreal Forest Zone that excluded WK. Significant differences remained when comparing the pooled Forest-tundra and Boreal Forest zones ($p = 0.047$), but not when comparing pooled Deciduous Woodland and Boreal Forest zones ($p = 0.072$).

1 mechanistic model of the origin of charcoal records (Higuera et al. 2007) and have the
2 advantage of being established *a priori*. Further, because thresholds are defined locally, this
3 approach is appropriate for records with changing variability in charcoal accumulation and is
4 insensitive to variety of analytical choices (e.g. transforming charcoal data, defining C_{peak} via
5 ratios vs. residuals; P.E. Higuera unpublished data). Our approach was generally successful, as
6 the 99th-percentile criterion accurately identified known fires within 1 km of each lake, although
7 a robust calibration requires a large dataset of known fires. Third, using the likelihood ratio test
8 and pooling FRIs from multiple records greatly improved the ability to detect changes in fire
9 regimes with long return intervals. In stand-replacing fire regimes with long and variable FRIs,
10 individual records can detect only large or long-lasting changes in mFRIs (e.g. > 30-50% change
11 over millennial time scales). Pooling data from several sites increased the sample size of FRIs
12 and allowed the detection of statistical differences between pollen zones that was not possible
13 using single records. This approach assumes that fire regimes are homogenous across sites and
14 within time periods. We used between-site comparisons to evaluate the assumption of
15 homogenous fire regimes, leading to the elimination of sites with statistically different records
16 from the pooled data (i.e. WK within the Forest-tundra Zone)

17 *Late-glacial and Holocene fire regimes: patterns and inferred controls*

18 *Herb Tundra Zone* -- Though spanning a brief period of this zone, charcoal records
19 suggest that fire was rare in the late-glacial herb tundra. Both climate and vegetation likely
20 reduced the probability of fire. Summers were cooler and drier than present (Anderson and
21 Brubaker 1994, Edwards et al. 2001, Anderson et al. 2004), with cold temperatures implying
22 limited convection necessary for lightning ignition. The discontinuous herbaceous and low-shrub

1 vegetation would have reduced fire spread if/when ignitions occurred. While species
2 composition differed from modern tundra, the structure of vegetation in this zone may have been
3 similar to present high-arctic tundra, where a cold and dry climate results in discontinuous
4 vascular plant cover (Walker et al. 2005) that supports few fires (Kasischke et al. 2002).

5 *Shrub Tundra Zone* -- Fire activity increased markedly with the transition from herb to
6 shrub tundra ca 13.3-14.3 ka BP, resulting in a mFRI (144 yr [119-170]; Fig. 6) statistically
7 similar to those characterizing Alaskan boreal forests (Kasischke et al. 2002, Lynch et al. 2002;
8 this study). This finding is surprising relative to modern tundra, since only 3% of Alaskan tundra
9 burned between 1950 and 2004 (Alaska Fire Service 2004, Walker et al. 2005) and even the most
10 flammable Alaskan tundra region, the Seward Peninsula (Fig. 1), has an estimated fire rotation
11 period (analogous to a mFRI) of 270 yr (Kasischke et al. 2002).

12 Changes in both climate and vegetation favored frequent fires. Increased summer
13 temperature from the Herb Tundra Zone and drier-than-present conditions (Anderson and
14 Brubaker 1994, Abbott et al. 2000, Edwards et al. 2001, Anderson et al. 2004) would have
15 favored fire ignition and spread. However, since temperatures remained cooler-than-present for
16 most of the Shrub Tundra Zone, it is unlikely that temperature was the major driver of higher fire
17 frequencies. The coincidence of increased CHARs and larger CHAR peaks with the expansion of
18 shrub *Betula* (*B. glandulosa* and *B. nana*; Anderson and Brubaker 1994) suggests that the
19 development of shrub tundra itself facilitated greater burning. *B. glandulosa*, with its small
20 diameters and highly resinous stems (Dugle 1966), burns readily on modern landscapes (de
21 Groot and Wein 2004), and high shrub densities would have provided the continuous flammable
22 fuels necessary for fire spread. In addition, rapid revegetation following fire (de Groot and Wein

1 1999) would have facilitated short FRIs. Although FRIs were statistically similar to those in
2 the Boreal Forest Zone (Fig. 5, 6), the lower overall CHARs and peak magnitudes (Fig. 4;
3 Appendix B) in the Shrub Tundra Zone suggest that fuel loads were lower than in modern boreal
4 forests.

5 *Deciduous Woodland Zone* – With the development of deciduous woodlands ca 10.5 ka
6 BP, fires became less common (mFRI 251 yr [158-352], Fig. 6) and produced little charcoal
7 (Fig. 4; Appendix B), implying that both climate and vegetation were less conducive to burning.
8 However, given regional evidence that summers that were $> 2^{\circ}$ C warmer and 25-40% drier than
9 present (Edwards et al. 2001, Anderson et al. 2004, Kaufman et al. 2004), one would predict an
10 increase rather than decrease in fire activity during this period. Though inconsistent with
11 direction of climatic change, a decline in fire would be expected given the lower flammability of
12 deciduous vegetation. As in the modern boreal forest, deciduous trees in the past (both *Populus*
13 and *Betula*; Edwards et al. 2005) would have acted as fire breaks, reducing fire spread across the
14 landscape (Johnson 1992, Cumming 2001, Hely et al. 2001). Our findings contrast with those of
15 Anderson et al. (2006), who infer that fires were common (mFRI of 77 yr, +/- 49 s.d.) when
16 *Populus* pollen was abundant at Paradox Lake (Fig. 1), Kenai Peninsula, Alaska (8.5-10.7 ka
17 BP). Although climatic difference between the Kenai Peninsula and Brooks Range may have
18 resulted in different ignition rates and moisture levels, it is difficult to reconcile the short FRIs at
19 Paradox Lake with the low flammability of the deciduous vegetation and the finding of low
20 CHARs in this portion of the Paradox Lake record.

21 *Forest-tundra Zone* -- Fire return intervals decreased slightly, but not significantly, with the
22 establishment of *P. glauca* in the mid-Holocene (mFRI 227 yr [173-282]; Fig. 6). Summer

1 temperatures cooled and relative moisture increased in this zone (but remained drier than
2 present; Abbott et al. 2000, Anderson et al. 2001, Edwards et al. 2001). Pollen and stomata data
3 suggest that the vegetation resembled modern treeline, with *P. glauca* trees or stands dispersed
4 within a landscape of *Betula* shrubs (Fig. 3; Appendix B). Although temperature and moisture
5 trends would have reduced fire activity compared to the previous period, the unchanging mFRI
6 suggest that these climatic effects were balanced by the increase in landscape flammability
7 resulting from the replacement of *Populus* with *P. glauca*. In addition increased CHARs and
8 peak magnitudes in this zone (Fig. 4; Appendix B) suggest greater biomass burning per fire due
9 to increased fuel loads. Unlike other zones, fire regimes varied across the study region, with
10 significantly higher fire activity in the east (WK) compared to the west (RP; Fig. 5). Pollen
11 records do not indicate a gradient in vegetation that would account for this pattern (Appendix B),
12 and thus the shorter FRIs at WK suggest a gradient in climatic controls of fire during this period.
13 Unfortunately, evaluating this possibility is difficult with existing paleoclimate records. Overall,
14 mFRI of this zone are at the lower end estimated fire rotation periods in modern forest-tundra
15 (180-1000+ yr; Payette et al. 1989, Kasischke et al. 2002), possibly reflecting the generally
16 warmer, drier climatic conditions during the Forest-tundra Zone compared to modern (Anderson
17 et al. 2004).

18 *Boreal Forest Zone* – A decrease in mFRI at two of the three study sites coincided with
19 the development of *P. mariana*-dominated forests ca 5.5 ka BP (Table 2, Fig. 5), resulting in a
20 pooled mFRI of 145 yr (129-163; Fig. 6). The absence of decreased FRIs at WK can be
21 attributed to the significantly lower FRIs in the previous zone at this site (as described above).
22 Peak magnitudes and/or CHARs reach their maxima at all sites (Fig. 4; Appendix B), suggesting

1 greater charcoal production per fire, probably due to the abundant fine fuels of *P. mariana* and
2 increased conifer densities (Johnson 1992). Several lines of evidence indicate that effective
3 moisture increased to near-modern levels by ca 5 ka BP and that temperatures continued to cool
4 into the late Holocene (5-0 ka BP; Ellis and Calkin 1984, Evison et al. 1998, Abbott et al. 2000,
5 Anderson et al. 2001, Anderson et al. 2004). Since these climatic changes should reduce fire
6 ignition and spread, the increase in fire activity was likely due to increased landscape
7 flammability associated with greater conifer density and the flammable fuels of *P. mariana*. This
8 interpretation is consistent with several other Holocene fire-history studies from boreal Alaska
9 (Dune, Low, Moose and Chokosna lakes, Fig. 1; Lynch et al. 2002, Lynch et al. 2004b, Hu et al.
10 2006) and with modeling studies showing higher fire frequencies with increased *P. mariana*
11 abundance (Rupp et al. 2002). However, these findings contrast with the Paradox Lake record
12 (Anderson et al. 2006), which indicates that FRIs increased from 81 (+/- 41 s.d.) to 130 (+/- 66
13 s.d.) yr with *P. mariana* arrival ca 4.6 ka BP. Thus although the FRIs for the boreal forest period
14 are similar to the central Brooks Range, the direction of change differed. Perhaps the low density
15 of *P. mariana* at Paradox Lake (Anderson et al. 2006) did not cause a large enough increase in
16 landscape flammability to override the effects of cooler, moister climatic conditions on fire
17 regimes.

18 *Vegetation mediates the impacts of climatic change on fire regimes*

19 Despite numerous examples that millennial-scale climatic changes have driven variations
20 in Holocene fire regimes (e.g. Clark 1988, Millspaugh et al. 2000, Carcaillet et al. 2001, Gavin et
21 al. 2006), paleoecological records from central Brooks Range indicate that climatic change was
22 not the primary cause of many fire regime shifts. A major theme of fire-history records from this

1 region is that fuel characteristics and abundance amplified or dampened the direct effects of
2 millennial-scale climatic changes (Hu et al. 2006). For example, in response to climatic warming
3 during late glaciation and the early Holocene, vegetation shifted from herb tundra to *Betula*-
4 dominated shrub tundra (Anderson et al. 2004; Fig. 3). While warming likely facilitated
5 increased burning, the evidence of cooler-than-present summers implies that fuels were of
6 greater influence in creating fire frequencies similar to those in modern boreal forests (Fig. 6).

7 A more unexpected outcome of vegetation change occurs when vegetation negates the
8 direct effect of climate by changing the probability of fire in the opposite direction of climatic
9 change. We infer two examples of this effect. First, in the mid-to-late Holocene, a cooler and
10 wetter climate reduced the probability of fire, but an increase of *P. mariana* and overall conifer
11 densities increased vegetation flammability. The net result of these shifts in vegetation and
12 climate was greater fire activity (Fig. 5-6), with the positive effect of fuels overshadowing the
13 negative effect of climate on fire occurrence. Second, despite warmer-than-present summers
14 during the early Holocene, fire activity decreased when deciduous woodlands expanded into
15 shrub tundra (Fig. 6). In this case, the low flammability of deciduous trees had a greater
16 influence than increased temperatures on the probability of fire. Overall, the postglacial fire
17 history of the southcentral Brooks Range emphasizes the central role of fuels to past and, by
18 inference, to future fire regimes.

19 *Implications for global change in arctic and subarctic ecosystems*

20 Fire regimes in past herb tundra, shrub tundra, and deciduous woodlands reflect the
21 effects of climates and vegetation biomes that do not have counterparts on the modern landscape

1 (i.e. no analog climate and vegetation, Anderson et al. 1989, Bartlein et al. 1991, Williams and
2 Jackson 2007, Appendix B). Given the potential for novel vegetation and climate in the future
3 (Edwards et al. 2005, Williams and Jackson 2007), our results have implications for anticipating
4 future fire regimes in arctic and subarctic ecosystems.

5 Our finding that vegetation mediated the impacts of climate change emphasizes the
6 importance of biological-physical feedbacks in past arctic and subarctic ecosystems. While direct
7 linkages between climate and fire may predict future fire regimes at annual to decadal time
8 scales (Kasischke et al. 2002, Lynch et al. 2004b, Duffy et al. 2005), the paleo-record highlights
9 that feedbacks between climate, vegetation, and fire can override direct climatic effects at multi-
10 decadal to centennial time scales. For example, in boreal forests the direct effect of future
11 climatic warming should be to increase area burned, with a secondary effect of replacing
12 coniferous with deciduous forest types (Rupp et al. 2000, Calef et al. 2005, Flannigan et al. 2005,
13 Johnstone and Chapin 2006). Our finding of few fires during the warmer-than-present Deciduous
14 Woodland Zone implies that future increases in burning could lower the probability of
15 subsequent fires by favoring successional forests with less flammable, deciduous fuels. If
16 deciduous stands are maintained across the landscape via gap-phase replacement (Cumming et
17 al. 2000, Johnstone and Chapin 2006), this negative feedback mechanism could result in fires
18 being less frequent than would be predicted by climate's direct effect on area burned.

19 The importance of biological-physical feedbacks is also highlighted by high fire
20 frequencies in past shrub tundra. Our records provide a clear precedence that shrub-dominated
21 tundra can sustain higher fire frequencies than present-day tundra. Thus, the future expansion of
22 tundra shrubs (Tape et al. 2006, Walker et al. 2006) coupled with decreased effective moisture

1 (ACIA 2004) could enhance circumarctic burning and initiate feedbacks with the climate
2 system. Recent studies of modern tundra fires suggest the possibility for both short and long term
3 impacts of increased tundra burning ranging from increased summer soil temperatures and
4 moisture levels (Liljedahl et al. 2007) to the release ancient soil carbon from increased
5 permafrost thawing and organic-layer consumption (Racine et al. 2006, Liljedahl et al. 2007).
6 Given the concern over the fate of terrestrial carbon in tundra and other high-latitude ecosystems
7 (Zimov et al. 1999, Chapin et al. 2000, Mack et al. 2004, Weintraub and Schimel 2005), the
8 evidence of fires in early Holocene tundra should motivate research into the controls of tundra
9 fire regimes and linkages between tundra burning and the climate system.

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Vj ku'y qtmnr gthqto gf 'kp'r ctv'wvf gt 'yj g'cwur legu'qh'yj g'WUOF gr ctvo gpv'qh'Gpgti { 'd { 'Ney tgpeg"

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1

TABLES

2 **Table 1.** Lake locations, characteristics, and record quality.

Lake Name (unofficial)	N Latitude	W Longitude	Elevation (m asl)	Surface area (ha)	Depth at coring Site (m)	Age of record (ka)	Mean sedimentation rate +/- s.d. (cm yr ⁻¹)	Mean resolution +/- s.d. (yr sample ⁻¹)	Median signal-to- noise index
Ruppert	67°04'16"	154°14'45"	230	3	7.0	14.0	0.040 ± 0.023	13 ± 6	0.88
Xindi	67°06'42"	152°29'30"	240	7	10.6	15.5	0.025 ± 0.016	32† ± 24	0.71†
Code	67°09'29"	151°51'40"	250	2	7.0	7.5	0.017 ± 0.003	16 ± 3	0.83
Wild Tussock	67°07'40"	151°22'55"	290	15	11.6	8.0	0.019 ± 0.001	14 ± 5	0.84

† mean (s.d.) sample resolution and the signal-to-noise index for the section of core used for charocal peak identification was 23 (13) yrs, and 0.83, respectively.

1 **Table 2.** Fire regime statistics for each site, stratified by pollen-defined vegetation zone.
 2 Parentheses enclose 95% confidence intervals estimated by 1000 bootstrapped samples of the
 3 FRI distributions. “N_{FRI}” is the number of fire return intervals in each zone (the total number of
 4 fires in a zone, minus one).

5

Site	Zone	N _{FRI}	Fire-history parameter (95% CI)		
			Mean fire return interval (yr)	Weibull <i>b</i> parameter (yr)	Weibull <i>c</i> parameter (unitless)
Ruppert	Shrub Tundra	20	137 (107 - 171)	151 (116 - 191)	1.84 (1.43 - 3.35)
Ruppert	Deciduous Woodland	6	223 (90 - 390)	229 (94 - 429)	1.16 (0.90 - 3.11)
Ruppert	Forest-tundra	12	238 (158 - 324)	262 (172 - 360)	1.63 (1.30 - 2.75)
Ruppert	Boreal Forest	31	171 (135 - 216)	188 (147 - 239)	1.53 (1.31 - 2.06)
Xindi	Shrub Tundra	24	150 (113 - 189)	164 (122 - 207)	1.68 (1.45 - 2.25)
Xindi	Deciduous Woodland	4	293 (225 - 360)	Weibull model not fit (< 5 FRIs)	
Code	Forest-tundra	8	210 (145 - 277)	235 (162 - 302)	2.39 (1.78 - 5.2)
Code	Boreal Forest	39	135 (113 - 160)	150 (123 - 178)	1.85 (1.52 - 2.60)
Wild Tussock	Forest-tundra	16	131 (95 - 172)	145 (104 - 191)	1.66 (1.38 - 2.5)
Wild Tussock	Boreal Forest	39	135 (113 - 157)	149 (123 - 174)	1.96 (1.61 - 2.75)

FIGURE LEGENDS

1
2 **Figure 1.** Location of lakes in this study and others discussed in the text (1, Dune Lake; 2, Low
3 Lake; 3, Moose Lake; 4, Chokosna Lake; 5, Paradox Lake). Grey polygons are areas that have
4 burned between CE 1950-2003 (Alaska Fire Service 2004), and the dashed line on the lower map
5 is the southern border of Gates of the Arctic National Park. The black dots and larger circles
6 identifying each lake on the bottom map have 1 and 2 km radii, representing the approximate
7 spatial scale of each fire history record.

8 **Figure 2.** Age-depth models for each site with the resulting sedimentation rates and sample
9 resolution, with 95% confidence intervals. At RP, temporal resolution changes from ca 25 to 10
10 yr sample⁻¹ at 2.2 ka BP because sampling intervals change from 0.5 to 0.25 cm. *see Results for
11 explanation.

12 **Figure 3.** Pollen and spore percentages of selected taxa; total pollen accumulation rate (PAR);
13 squared chord distance (SCD) and probability of analog values for comparisons between fossil
14 samples and those from modern Boreal Forest, Forest-tundra, and Arctic Tundra vegetation
15 zones; and charcoal accumulation rate (CHAR) for Ruppert Lake. Filled (empty) circles on *Picea*
16 panel represent *Picea* stomata presence (absence). Triangles below lower horizontal axis
17 represent the location of ¹⁴C or ²¹⁰Pb dates. See Appendix B for same figures for Xindi, Code,
18 and Wild Tussock lakes.

19 **Figure 4.** (i) $C_{interpolated}$ (black) and $C_{background}$ (grey) series; (ii) C_{peak} series with the values
20 identifying noise-related variability (positive and negative grey lines) and peaks identified with
21 each threshold criterion. The 99th percentile criterion used for interpretation is represented with
22 '+', and the 95th and 99.9th percentile results are represented with '.'. (iii) Pollen-inferred

1 vegetation zone and peak magnitude for all CHAR values exceeding the positive threshold
2 value in (ii). Note, peak magnitude values not corresponding to “+” symbols in (ii) are those that
3 did not pass the minimum-count screening (see Methods for details), and “+” symbols in (ii)
4 with no apparent peak magnitude value correspond to very small peak magnitudes.

5 **Figure 5.** Distribution of FRIs and fitted Weibull models for each vegetation zone (columns) at
6 each site (rows). Results from statistical comparisons are summarized by “=”, not different ($p >$
7 0.05), or “ \neq ”, different ($p \leq 0.05$) . Appendix B contains p-values for all comparisons.

8 **Figure 6.** Results from the analysis of pooled FRIs: distributions of FRIs, fitted Weibull models,
9 Weibull b and c parameters (95% CI), mean fire return intervals (mFRI; 95% CI), and number of
10 FRIs in each vegetation zone. Results from statistical comparisons are summarized as in Fig. 5
11 and presented in Appendix B. NOTE: Wild Tussock Lake (WK) is not included in the pooled
12 record for the Forest-tundra Zone because of statistical differences between WK and Ruppert
13 Lake (RP) during this period (Fig. 5; Appendix B).

1

2 Figure 1.

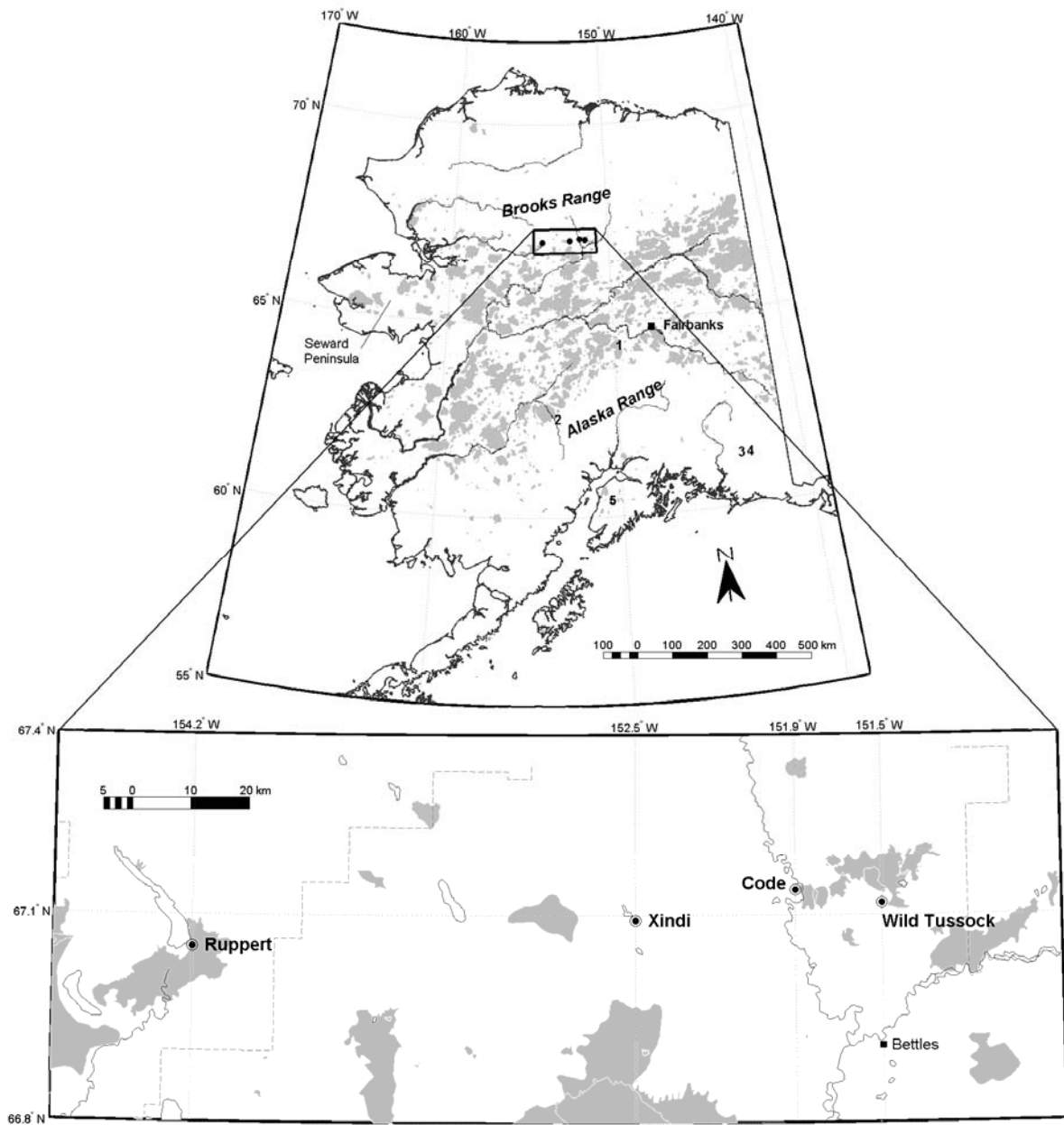
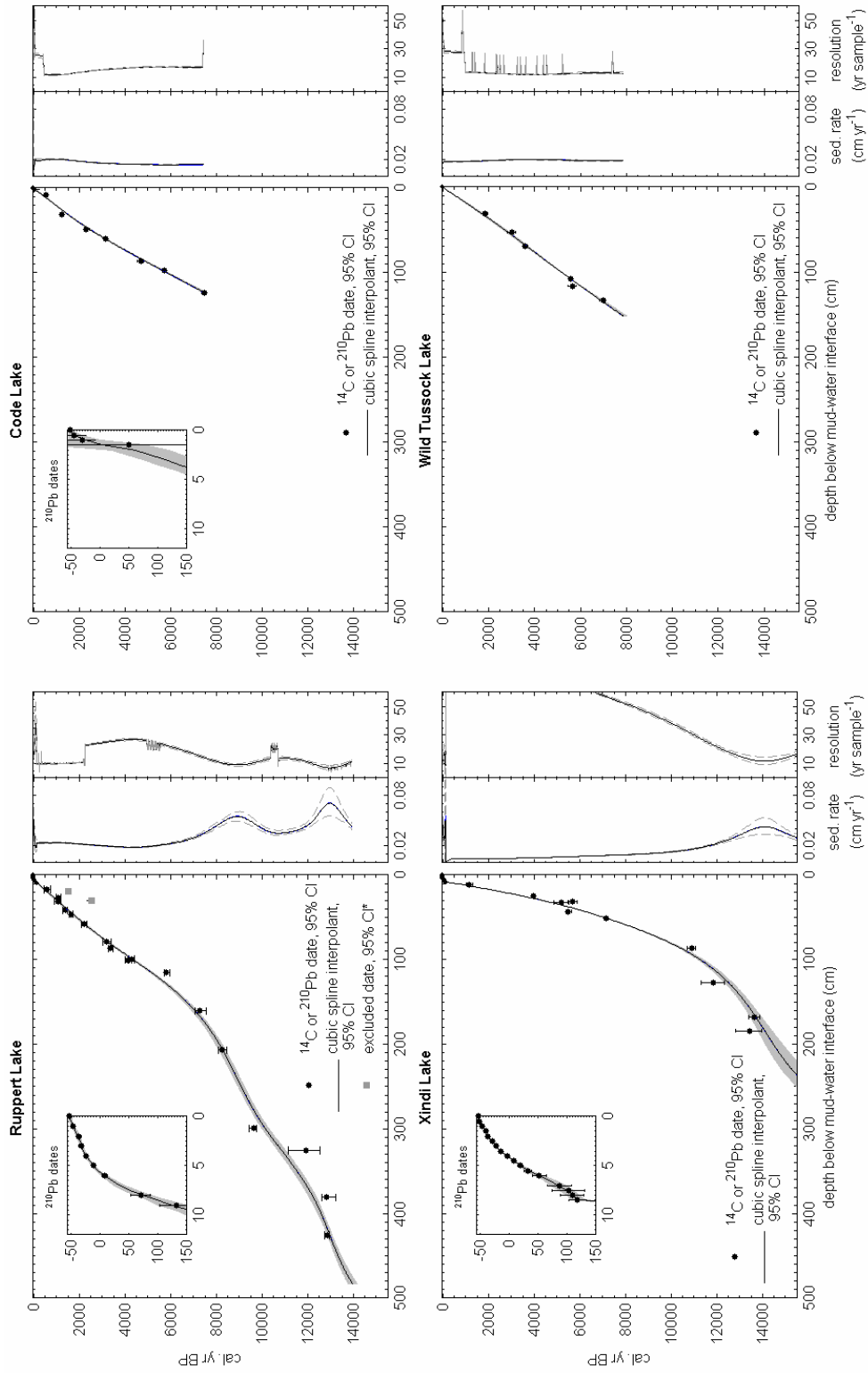
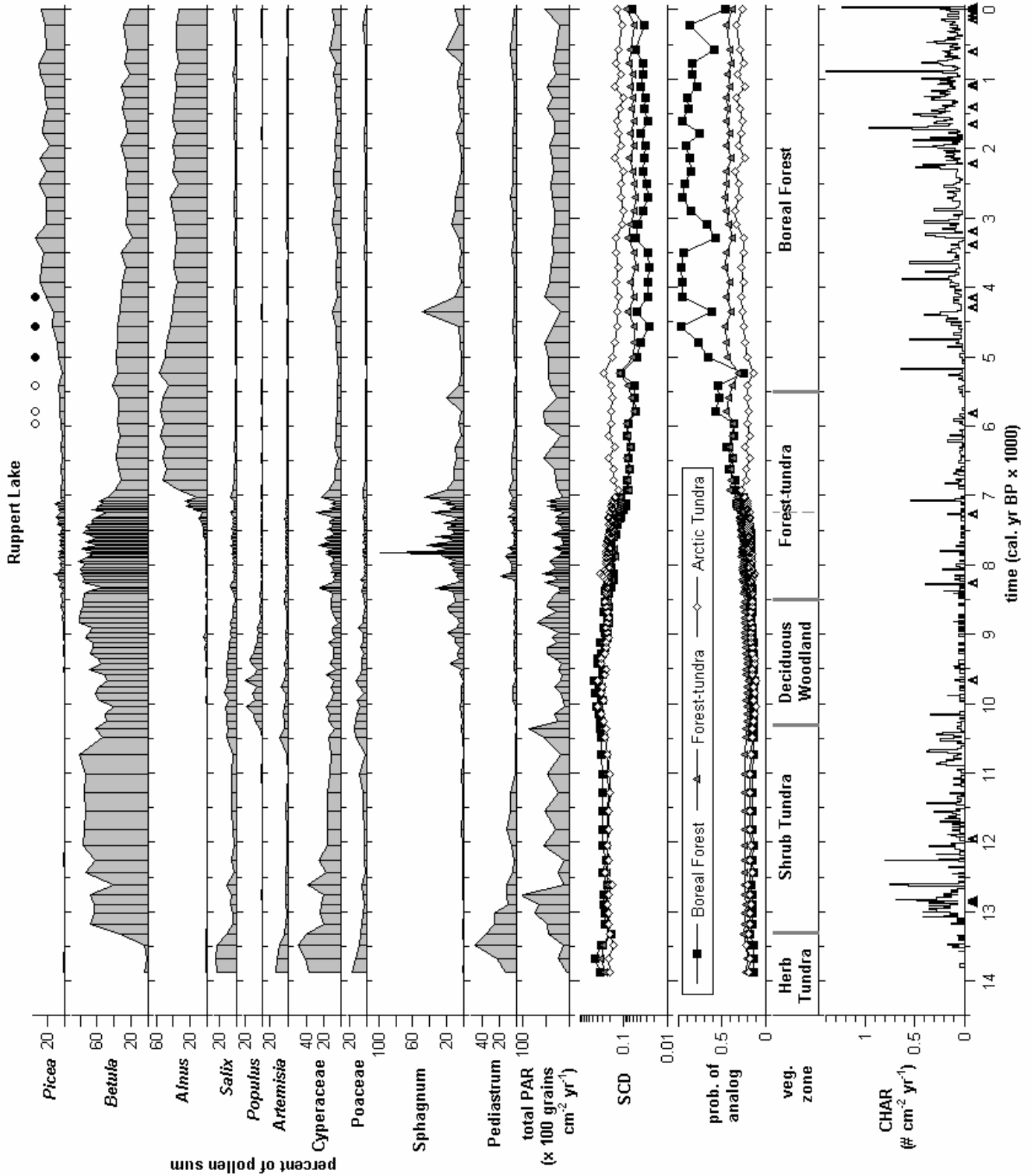


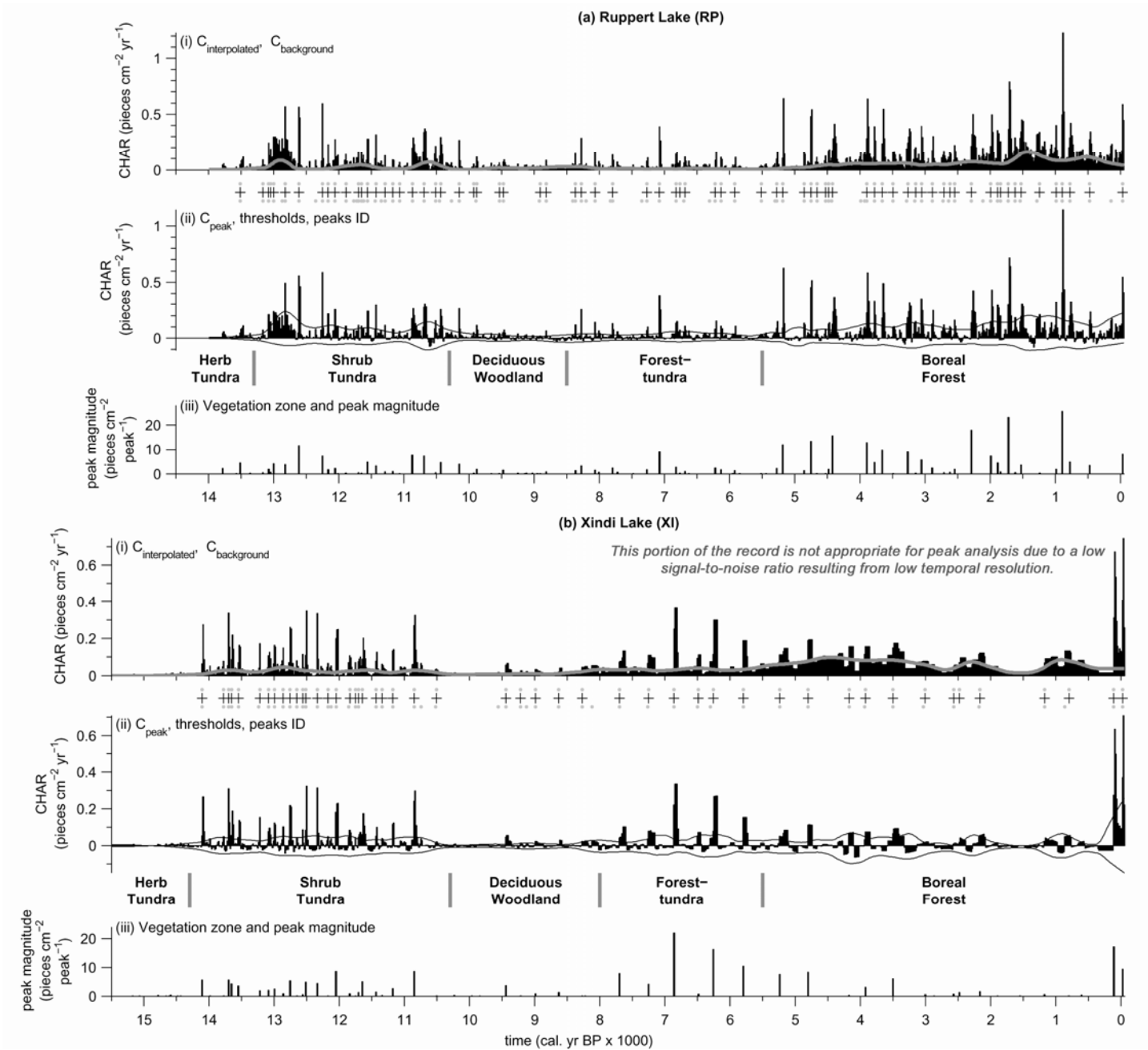
Figure 2.



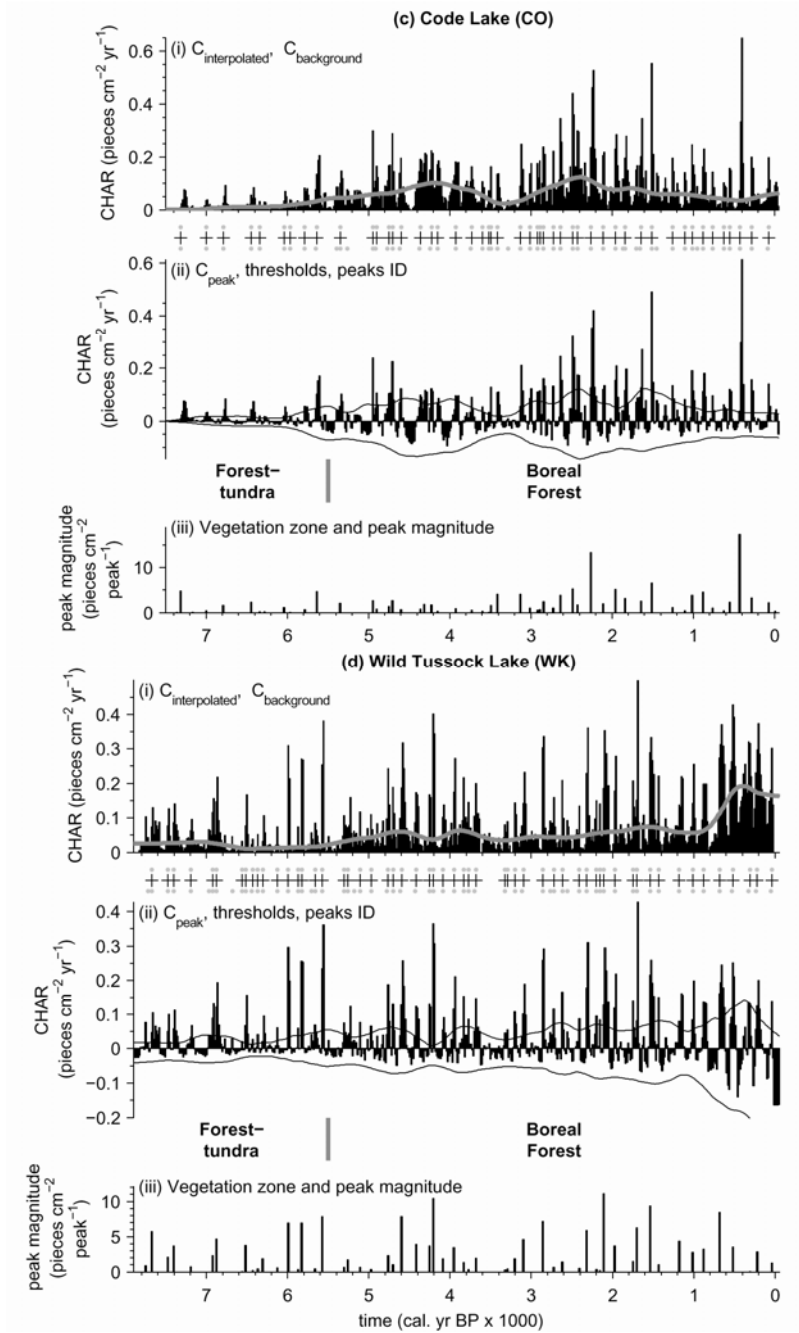
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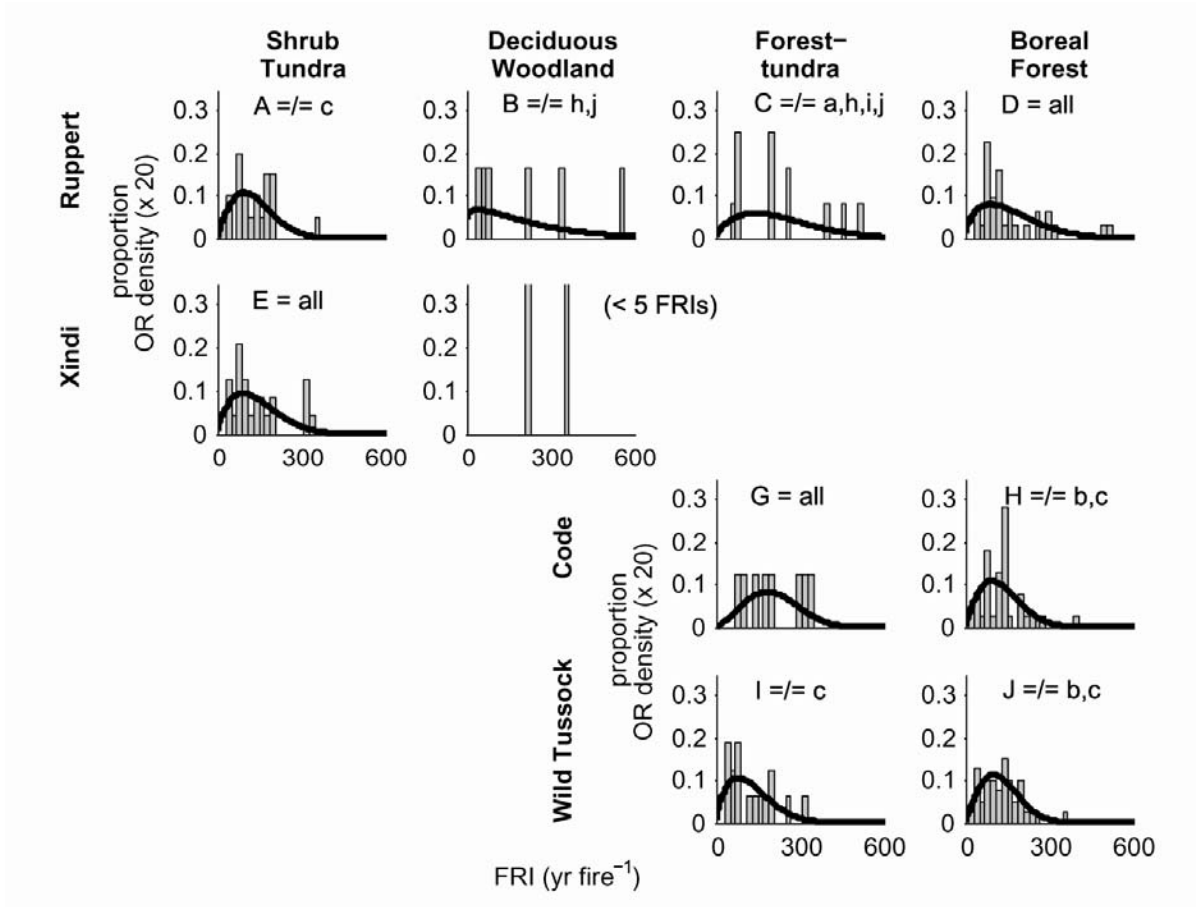
1 Figure 4.



1 Figure 4 – continued.

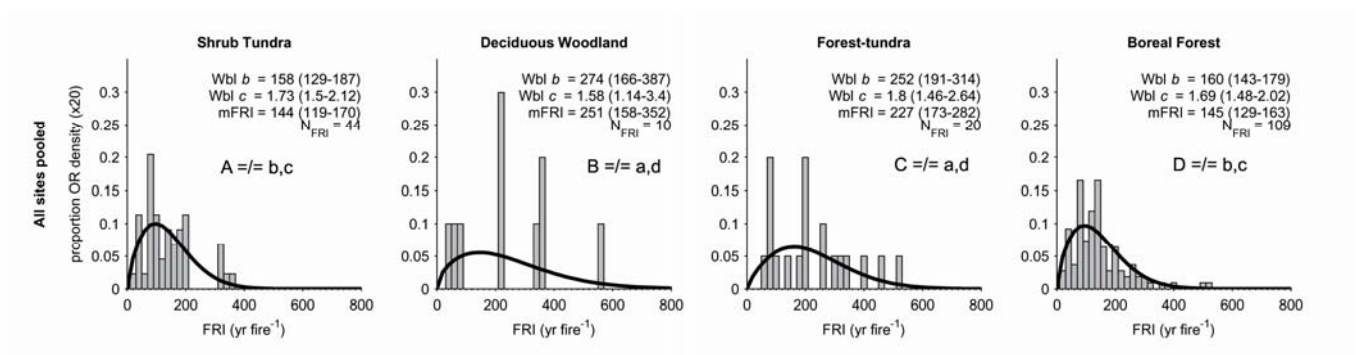


1 Figure 5.



2

1 Figure 6.



2