Wetland succession in a permafrost collapse: interactions between fire and thermokarst

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Wetland succession in a permafrost collapse: interactions between fire and thermokarst

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Abstract

To determine the influence of fire and thermokarst in a boreal landscape, we investigated ~600 years of vegetation succession from peat cores within and adjacent to a permafrost collapse feature on the Tanana River Floodplain of Interior Alaska. Radioisotope dating, diatom assemblages, plant macrofossils, charcoal fragments, and carbon and nitrogen content of the peat profile indicate that succession proceeded from a terrestrial forest to a sedge-dominated wetland over 100 years ago and to a *Sphagnum*-dominated bog in approximately 1970. The shift from sedge to *Sphagnum*, and a decrease in the detrended tree-ring width index of black spruce trees adjacent to the collapse coincided with an increase in the growing season temperature record from Fairbanks. The concurrent wetland succession and reduced growth of black spruce trees indicates a non-linear ecosystem-level response to a change in regional climate. In 2001, fire was observed coincident with permafrost collapse and resulted in lateral expansion of the bog. These observations and the peat profile suggest that future warming and/or increased fire disturbance could promote permafrost degradation and bog expansion, and increase carbon storage in the collapse; however, the development of drought conditions could reduce the success of black spruce and *Sphagnum*, decreasing long-term ecosystem carbon storage in the adjacent landscape.

1 Introduction

The spatial patterns of vegetation in the low lying flood plains of interior Alaska are controlled by disturbances such as fire, permafrost degradation, flooding, and drainage. In particular, permafrost degradation is altering ecosystem structure and therefore, the capacity of northern wetlands to store carbon (Camill et al., 2001; Turetsky et al., 2002a). Because approximately one-quarter of the world's soil carbon is currently sequestered in boreal peatlands (Gorham, 1991; Apps et al., 1993; Turunen et al., 2002), degradation of permafrost could result in significant carbon emissions. Both carbon

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accumulation and methane emissions have been shown to increase in peatlands underlain by degrading permafrost as water tables increase and nutrients are released by the thawing soils (Robinson and Moore, 2000; Turetsky et al., 2000; Vitt et al., 2000; Camill et al., 2001; Turetsky et al., 2007). Permafrost thaw can also result in water body drainage (Yoshikawa et al., 2003; Jorgenson and Osterkamp, 2005; Riordan et al., 2006) potentially exposing wetlands to aerobic decomposition and carbon release. Future carbon accumulation in permafrost peatlands will depend not only on plant and microbial responses to a warming climate, but on vegetation succession driven by fire and permafrost thaw.

Permafrost degradation observed over the last half century has altered ecosystem structure in boreal peatlands (Vitt et al., 2000; Camill et al., 2001; Jorgenson et al., 2001; Turetsky et al., 2002b; Christensen et al., 2004). In upland ecosystems permafrost thaw has resulted in patterned ground and thermokarst pits (Osterkamp et al., 2000). In lowland ecosystems the loss of ice-rich permafrost has caused the conversion of forests to wetlands (Osterkamp et al., 2000; Jorgenson et al., 2001; Jorgenson and Osterkamp, 2005). Though air temperature influences the soil thermal regime, other factors such as ground ice content, soil texture, topography, slope, aspect, hydrology, winter snow fall and fire interact to determine rates of permafrost degradation (Osterkamp and Romanovsky, 1999; Jorgenson and Osterkamp, 2005). Discontinuous permafrost in Alaska is particularly sensitive to climate warming (Swanson, 1996) and warming of ground-ice has been observed at sites across the Interior (Osterkamp and Romanovsky, 1999). Since 1949, permafrost collapse has increased by 21% on the Tanana Floodplain of Interior Alaska (Jorgenson et al., 2001). It is projected that by the end of the next century, permafrost could be eliminated from this landscape (Jorgenson et al., 2001).

Climate models project that the western boreal forest will experience significant warming over the next century (Stocks et al., 1998). Historical data indicate that between 1950 and 2000 annual surface temperatures in Interior Alaska have warmed by approximately 2°C (Keyser et al., 2000); however, during this period no clear trend in

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growing season precipitation has occurred (Keyser et al., 2000; Serreze et al., 2000). Warmer temperatures will increase evaporation and evapotranspiration; and therefore, peatlands are project to experience drier conditions in the future (Wrona et al., 2004). Projected changes in temperature and precipitation could alter disturbance regimes. Warmer and drier summers could result in an increase in the frequency and severity of stand-replacing fires (Harden et al., 2000), and the extent of permafrost degradation (Jorgenson et al., 2001; Camill, 2005). These changes in the disturbance regime could have an even larger effect on the release of greenhouse gas emissions than direct physiological responses of plants and microbes to a warming climate (Chapin et al., 2000).

To understand the interactions between fire and thermokarst on wetland succession, we examined a *Sphagnum*-dominated permafrost collapse in a fire-scarred *Picea mariana* (black spruce) forest. We used paleoecological methods, namely diatom taxonomic shifts through a pedogenic sequence, to understand the mechanisms of collapse vegetation succession. The aims of this study were to: 1) investigate the interactions between fire and expansion of the permafrost collapse, 2) document wetland succession in this collapse feature, and 3) quantify the influence of these disturbances on carbon storage. We hypothesize that fire initiated collapse expansion at this site. The loss of transpiration, decrease in summer albedo, and decrease in organic matter thickness after fire can trigger permafrost degradation (Jorgenson et al., 2001; Yoshikawa et al., 2003). Though, fire has been linked with permafrost degradation in the peatlands of Western Canada, most studies identify climate warming as the dominant trigger of collapse in the boreal zone (Thie, 1974; Zoltai, 1993; Kuhry, 1994; Camill and Clark, 2000; Jorgenson et al., 2001). Furthermore, the connections between climate, fire, and fire induced thaw have been little studied because we are still developing the best techniques to address these complex ecological interactions. We believe that paleo-indicators including diatoms and testate amoeba are powerful tools for ecological and biogeochemical studies, with which we can begin to understand the controls over succession and better predict spatial patterning in boreal wetlands.

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2   Methods

2.1   Study area

This study was conducted in a permafrost collapse scar (64° N. 38.448′, 148° W. 20.009′, 132 m elevation) southwest of the Bonanza Creek experimental forest on the Tanana River floodplain in Interior Alaska (Fig. 1). Variable vegetation, hydrology, and topography from legacies of flooding, fire and thermokarst have created a complex landscape mosaic (Jorgenson et al., 2001). The study site is in an area of the Tanana Floodplain that is not subject to groundwater upwelling (Jorgenson et al., 2001); therefore, these wetlands are best characterized as ombotrophic bogs or poor fens, receiving the majority of their water and nutrients from atmospheric sources (personal communication J. Bubier, August 2001, Mount Holyoke University and M. Turetsky, Michigan State University, 2004). Water level in wells (2 m screen depth) did not correlate significantly with river stage (National Water Information System, USGS) in the two years of this study (linear regression, inverse transformation, p-value=0.540), suggesting that this site is isolated from the active floodplain of the Tanana River (Myers-Smith, 2005).

In June 2001 an extensive fire, known as the Survey-Line fire, occurred in the study area. We first visited the study site in July 2001, a month following the fire, and a transect was established from the center of a permafrost collapse peatland feature into the surrounding burned area (Fig. 2). The periphery of the collapse feature had undergone a 6 m lateral expansion by 2002. We surveyed the site on 5 August 2004, using a Topcon GTS 220 Series All-Weather Total Station (Topcon America Corporation, Paramus, NJ, USA), and found the area of the collapse to be 175 by 75 m with a surface depression of up to 0.5 m (Fig. 2).

In 2004, three ecological zones with distinct vegetation assemblages were observed along the transect, and were characterized as the bog, moat and burn. The bog was considered to be the *Sphagnum* mat, the moat, the area of recent soil subsidence, and the burn, the adjacent burned forest. The dominant vegetation types in the bog

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were *Sphagnum* spp. (primarily *S. riparium* with increased *S. squarrosum* towards the margins of the collapse), *Carex* spp. (primarily *C. canescens*, *C. aquatilis*, and *C. rostrata*) and *Eriophorum angustifolium*. The average growth of the *Sphagnum* mat measured along the transect from the edge to the centre of the permafrost collapse

5   was 2.5±1.2 cm (±SE, *n*=19). The moat was dominated by *Eriophorum vaginatum* tussocks and *Carex* spp. Standing water was present in the moat throughout both the growing seasons of 2003 and 2004, allowing for the growth of aquatic vegetation. Prior to the Survey-Line Fire, the burn was a low-lying open-canopy *Picea mariana* forest with an understory of tussock vegetation. After the 2001 fire, the dominant vegetation

10 types were *Eriophorum vaginatum* tussocks, Grass spp., *Betula* spp., *Salix* spp., *Potentilla palustris*, *Ledum groenlandicum*, *Vaccinium uliginosum*, *Vaccinium vitis-idaea* and *Chamaedaphne calyculata*.

The bog, moat and burn zones had unique soil profiles (Fig. 2b). The bog organic layer was 0.5 m thick and the active layer was >2 m. The moat was the lowest portion

15 of the transect, with an above surface water table for much of the growing season. The organic matter thickness was highly variable (2–40 cm) in the burn because of tussock-hollow microtopography, patchy fuel consumption, and variable soil subsidence patterns. The maximum thaw depth in the burn was ~80 cm.

2.2 Active layer depth

20 To monitor changes in thaw depth, we pushed a 120 cm or 200 cm fiberglass frost probe into the soil until impenetrable ground was reached. The length of the probe inserted into the earth was considered to be the depth to frozen soil. We conducted three replicate measurements of the active layer every 3 m along both sides of the transect at each visit to the site (every one to two weeks throughout the growing season).

2.3 Soil coring

In March of 2003 we drilled three 7.7 cm diameter-cores using a gasoline-powered permafrost corer from the center of the bog (0 m), the moat (12 m) and within the burn (27 m). Minimal rotation or deformation of soil layers and sediments occurred, because coring was conducted during winter when ambient temperatures were below freezing. Cores were stored frozen, until we sectioned the core into 2 cm depth increments using a radial saw. We then oven-dried the soil samples at 50–65°C and ground them in a tumbling ball mill for 2–5 min, until a homogeneous powder. These soil samples were analyzed for %C and %N using a Carlo Erba EA1108 CHNS analyzer (CE Instruments, Milan, Italy) and a COSTECH ECS 4010 CHNS-O analyzer (Costech Analytical Technologies Inc., Valencia, CA, USA). Sample standard errors were ±0.01% for nitrogen, ±0.45% for carbon. We counted charcoal layers in the cores and estimated charcoal deposition by emptying dried samples of a known volume and depth (on mean 4.5 cm^3) over a 10 cm×10 cm grid and counting macroscopic charcoal fragments (greater than 0.05 mm in diameter) in each cm grid cell. Due to limited sample size, we did not measure total charcoal abundance in the core.

2.4 Core dating

To estimate the age of peat deposits we utilized AMS radio carbon, ^{210}Pb and ^{137}Cs isotopic dating techniques (Oldfield et al., 1995; Turetsky et al., 2004). *Sphagnum* fruiting bodies, charcoal and bulk peat samples from the center of the bog were analyzed for ^{14}C using accelerator mass spectrometry (Table 1; AMS, 1.5 SDH.1 Pelletron Accelerator, National Electrostatics Corporation, Middleton, Wisconsin, USA) at the Lawrence Livermore National Laboratory Center for AMS (LLNLCAMS) and the UC Irvine W. M. Keck Carbon Cycle AMS facility (KCCAMS). Peat samples from 2, 8, 20, and 24–54 cm-depths were analyzed for ^{137}Cs, total ^{210}Pb and ^{226}Ra activity by gamma spectrometery at the USGS Sediment Radioisotope Laboratory in Menlo Park (Fuller et al., 1999).

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2.5 Diatoms

Diatoms have been shown to be a useful indicator of peatland succession, local hydrology, and fire disturbance (Kienel et al., 1999; Moser et al., 2000; Rühland et al., 2000) and can be more sensitive to changes in water chemistry than the commonly
5 used peat indicators such as pollen and macrofossil analysis (Rühland et al., 2000). In this study, we employed diatom analysis to indicate changes in pH and nutrients in the aquatic environment. To survey the diatom community, we processed three cores sampled every 2 cm by depth from the bog, moat and burn using methods described by the Queen's University Paleoecological Environmental Assessment and Research
10 Laboratory (PEARL) and personal communications (Kathleen Rühland, John P. Smol, John Barron, and Morgan Peterson). We digested the dried material, consisting of organic matter with varying amounts of sediment, in Kjeldahl digestion tubes in a heating block. We used 50:50 solution by molecular weight of concentrated H_2SO_4 and HNO_3 and digested for 3 days at 95°C or until the disappearance of all organic matter.
15 We diluted the resulting solution with deionized water to a neutral pH. We mounted the samples using the Pleurax high refractive index mounting medium (prepared by W. Dailey, University of Pennsylvania). To determine the prevalence of the different diatoms, we counted 400 valves (or for one sparse sample, four slides) for each sample. Partial diatoms were only counted when more than half of the valve remained
20 and the genus was clearly distinguishable. We identified samples according to Foged (1981), Krammer and Lange-Bertalot (1986–1991), and personal communications with K. Rühland and M. Peterson. All diatom valves were keyed out to genus, and when possible species were identified, we refer to these taxa together (genus and species) as diatom categories (see Fig. 7).

25 ## 2.6 Dendrochronology

We used dendrochronology to link the below ground data to above ground observations of the response of this system to collapse. Tree-ring analysis provides a record of

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the response of the black spruce trees to changing climate and ongoing thermokarst, allowing for speculation about the response of this landscape to future climate change. We harvested twenty-one fire-killed tree cross-sections from the margin of the collapse and in the surrounding burn in the growing season of 2004 (Wilmking and Myers-Smith, 2007). We measured ring width (sliding stage, Velmex Inc., Bloomfield, NY, USA, resolution: 0.001 mm) for two radial transects of the tree cross-sections, which showed the least amount of compression wood. To build site chronologies, we first crossdated tree ring series with the program Cofecha (Richard Holmes, Laboratory of Tree Ring Research, University of Arizona) and adjusted possible dating errors and then standardized ring-widths with the program ARSTAN using traditional negative exponential or straight line fits (Richard Holmes, Laboratory of Tree Ring Research, University of Arizona) to remove the age-related variation in growth rate. These site chronologies were used for climate-growth correlations with temperature and precipitation data from a composite of climate data from the University Experiment Station (1906–1947) and Fairbanks International Airport (1948–2000) (Wilmking et al., 2004). In addition, we recorded the presence and amount of compression-wood for each year in the disk, an indicator of leaning which is interpreted to be related to frost-heaving and permafrost collapse (Camill and Clark, 1998).

2.7 Statistical analysis and data reporting

We determined diatom-delineated zones using constrained cluster analysis by information content (CONIIC) by the program Psimpoll 3.01 (K. D. Bennett, Uppsala University). We performed regressions and ANOVAs in JMP IN 5.1.2 (SAS Institute Inc., Cary, NC, USA). Field and analytical data are reported for all sites and samples in http://www.lter.uaf.edu/studies/search.cfm listed under the investigator Isla Myers-Smith. Archive samples are stored at U.S. Geological Survey at Menlo Park.

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3 Results

3.1 Age estimates

Ages as a function of depth were estimated for the top 54 cm of the bog core from radioisotope profiles with correction for compaction within the core (Table 2). We de-
veloped three age estimate models. Two mass accumulation rates (MAR, g/cm^2/yr) derived from unsupported ^{210}Pb are the constant flux-constant accumulation rate (CF-CS) and the constant rate of supply (CRS) methods (Appleby and Oldfield, 1992). The CF-CS MAR is derived from the slope of the ln (unsupported ^{210}Pb) versus cumulative dry mass. The CRS method (CRS) assumes a constant rate of supply of unsupported
^{210}Pb and calculates the MAR of each successive layer by creating a ratio of the un-supported ^{210}Pb activity (decays per minute (dpm)/cm^2) below the layer to the total integrated activity to derive the age of the layer. The ^{137}Cs-MAR is derived by assigning dates of 1964 to the peak activity in ^{137}Cs (34 cm) and 1952 to the depth of first occurrence of measurable ^{137}Cs 1952 assuming a constant mass accumulation rate
at this depth range (Fuller et al., 1999). The radiocarbon age estimates for the sylvic (tree derived) peat samples in the bog core are 335 ybp at 56 cm, 475 ybp at 58 cm, and 585 ybp for a piece of charcoal at 56 cm depth. The age estimate for a sedge peat sample from 54 cm in the bog core is 245 years before present (ybp).

3.2 Core stratigraphy

Stratigraphic analyzes of the sediment cores from the center of the bog and moat, include records of carbon, nitrogen, charcoal, soil density, and vegetation assemblage (Figs. 3 and 4). Soil bulk density and the percent nitrogen were variable with depth through both cores; however, following peaks in charcoal deposits, greater bulk density corresponded with lower C:N.

We found three distinct organic matter substrates in the core from the center of the bog: sylvic peat from 53–59 cm, sedge-dominated peat from 27–53 cm, and *Sphag-*

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num-dominated peat from 0–27 cm (Fig. 3). We identified four organic matter substrates in the moat core: sylvic peat from 33–41 cm, sedge-dominated peat from 25–33 cm, *Sphagnum*-dominated peat from 9–25 cm and a return to sedge-dominated peat from 0–8 cm (Fig. 4). Diatom assemblages were very well preserved in the peat sediments in the top 48 cm of the bog core, and the top 44 cm of the moat core; however, at the base of both cores diatoms were sparse, many of the valves were broken and sediment obscured the slides. The diatom assemblages for the bog core delineated with CONIIC into three zones that agreed loosely with the three substrates: sylvic, sedge-dominated, and *Sphagnum*-dominated peat (Fig. 5); however, in the moat core the patterns are less clear (Fig. 6).

3.3 Bog core zone 1

Zone 1 (53–59 cm) consisted of charred sylvic peat and well decomposed sedges. Bulk density in this region of the core was high (0.1–$1.1\,\mathrm{g\,cm^{-3}}$) and C:N ratios were low (11–28). The diatom species *Pinnularia* spp., *Hantzschia amphioxys var. major*, *Eunotia praerupta*, *Navicula amphibola*, *Stauroneis phoenicenteron* were present in low densities at the bottom of the sedge-dominated portion of the core. The diatom assemblages in zone 1 were similar to that at 4 cm depth in the terrestrial soil core from the adjacent burned forest (Fig. 5) and conspicuous (∼0.5 millimetres in diameter) charcoal pieces were found in the sylvic peat deposits. A peak of charcoal was found at 46 cm depth just prior to the transition to the second diatom zone.

3.4 Bog core zone 2

Zone 2 (27–53 cm) was composed of sedge-dominated peat. Bulk densities were less in this portion of the core (0.06–$0.09\,\mathrm{g\,cm^{-3}}$); however, C:N ratios remained low (22–29). The diatom species *Gomphonema* spp., *Cymbella ventricosa var. groenlandica*, *Navicula tripunctata var. arctica*, and *Nitzchia* spp. were common in this middle portion of the bog core. A peak of *E. rhomboidea*, *Tabellaria flocculosa* (girdle bands),

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and *E. faba* at 42 cm coincided with a peak in % nitrogen. *E. tenella*, *C. ventricosa*, *N. tripunctata*, *Pinnularia* spp., and *E. flexuosa* peak at 36 cm which corresponded to another peak in density and % nitrogen. Estimated carbon accumulation averaged 171 g C m^{-2} y^{-1} (or 6 mm y^{-1}) for this sedge-dominated zone.

3.5 Bog core zone 3

Zone 3 (0–27 cm) was made up of primarily *Sphagnum*-dominated peat. In this portion of the transect bulk densities were lowest (0.06–0.02 g cm^{-3}) and C:N ratios were highest (27–84). Three peaks in charcoal abundance were found during this zone of the core (Fig. 3). A shift in the diatom assemblage was initiated 6 cm beneath the shift to *Sphagnum*-domination at 33 cm (Fig. 5) in the macrofossil record. In the uppermost *Sphagnum*-dominated portion of the core (zone 3), *Eunotia rhomboidea*, *E. nymanniana*, *E. glacialis*, and *Navicula subtilissima* were prevalent. Peaks in specific diatom abundance (Fig. 5) often correlated with specific physical and chemical characteristics of the core. For example, the abundance of *E. nymanniana* responded positively to charcoal deposits and tracked bulk density (cross correlation, r=0.62, p-value<0.003, d=−1; Figs. 3 and 5). Estimated carbon accumulation averaged 172 g C m^{-2} y^{-1} (or 11 mm y^{-1}) for the *Sphagnum* dominated portion of the core.

3.6 Dendrochronology

For the period from 1930 to 2000, we found a negative relationship between growing season air temperature and the detrended tree-ring width index for black spruce in the terrestrial portion of the landscape (Fig. 7; Wilmking and Myers-Smith, 2007). The tree ring width index for trees growing in the wetter environment at the margins of the collapse feature showed weaker relationship with temperature (linear regression, R^2=0.04, P=0.11). Compression-wood was observed in 14 of the 21 trees sampled.

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4 Conclusions

Diatom assemblages, plant macrofossils and soil chemistry in the earliest organic soil layers from both bog and moat cores indicate that a terrestrial forest pre-dated the initiation of the collapse around 200 years ago. The %C, %N, C:N, and density in the organic matter above the mineral horizon was similar in all of the cores from the transect, and woody peat and charcoal were found at the base of both the bog and moat cores. The diatom assemblage above the sylvic peat layer in the bog and moat cores were analogous to assemblages observed in modern soils from the terrestrial portion of the transect. This assemblage of alkaliphilous to pH neutral, salt tolerant, and mesotraphentic to eutraphentic (tolerant of nutrient enrichment) taxa of diatoms (*Pinnularia* spp., *Navicula amphibola*, *Stauroneis phoenicenteron*) and the aerophilic diatom taxon *Hantzschia amphioxys var. major* indicate less acidic, nutrient rich soil (Van Dam et al., 1994).

Dating of the transition from (burned) sylvic organic matter to sedge-dominated peat terrestrial layers in the bog and moat cores suggest that the collapse formed over 200 years ago (Figs. 3 and 5) from a landscape similar to the present-day black spruce forest. During the initial collapse, the sedge-dominated zone (zone 2) was colonized by circum-neutral, mesotraphentic (indifferent to trophic conditions) and epiphytic (growing on plants, rather than planktonic) diatom species. This is consistent with a more nutrient rich environment found in sedge-dominated ecosystems today (Rühland et al., 2000). The dominant vegetation, diatom assemblage, and peat chemistry changed in zone 2 (between 26 and 32 cm depth in the core). The shift in the diatom assemblage occurred around 1969±15 yrs and predated the shift from sedge to *Sphagnum* peat and C:N ratio that occurred around 1978±13 yrs. Diatoms in Siberia have previously been shown to respond first to changes in peatland chemistry and then secondarily to changes in bryophytes (Rühland et al., 2000). In our study, the shift in diatom assemblage may be in response to the shift in temperature in the Fairbanks region (Fig. 7), which seemed to be part of a synoptic scale shift to warm and dry conditions since

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1974 (Barber et al., 2004). Since a sedge-dominated wetland is consistent with wetter, more nutrient rich conditions (Zoltai, 1995), the change to *Sphagnum*-domination suggests that conditions became drier, more acidic and/or more nutrient poor in the collapse perhaps as a result of consecutive warm growing seasons in the late 1970s.

5 Diatom assemblages and peat macrofossils in the most recent zone of the bog core (zone 3) indicate that the peatland collapse has become an acidic ombrotrophic bog. This *Sphagnum*-dominated portion of the core contained predominantly acidophilous (mainly occurring below pH 7) *Eunotia* spp, and a peak in the acidobiontic (optimal occurrence at pH 5.5; Van Dam et al., 1994) species *Navicula subtilissima* at 14 cm,

10 suggesting a period of low pH during the recent history of the bog environment.

The younger substrates and return of sedges in the profile of the moat core suggests lateral expansion of the collapse and terrestrialization of the peatland over time. The shorter organic profile of the moat core and single charcoal peak indicate that the sylvic organic matter in this core is younger than in the bog core. In addition to younger sub-

15 strate, the moat core showed less clear changes in diatom assemblages with depth. Acidophilious diatoms were found throughout the core and alkaliphilious diatoms were present at depth and near the surface of the core. The eutraphentic *Stauroneis phoeni-centeron* and aerophilic *Hantzschia amphioxys var. major* were counted at 8 cm depth in the core. The presence of these diatom species indicate a terrestrial influence in the

20 recent history of the bog and is coincident with a return of sedge-dominated substrate in the moat core.

The charcoal peaks observed in the core indicate that fire is a frequent disturbance in this ecosystem. We attribute the charcoal peak at 12 cm in the bog core and 20 cm in the moat core to ash deposits from the Survey-line fire of 2001. The ages inferred

25 from the radioisotope profiles indicate that the two charcoal peaks at 20–22 cm and 28–30 cm depth in the bog core are likely fallout from historic regional fires that did not directly affect the forest stand adjacent to the permafrost collapse. The charcoal peak at 46 cm depth could indicate a localized fire; however, the dating is uncertain. The maximum ages of the trees (182, 172 and 169 years old) in the adjacent black spruce

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indicate that the last stand-replacing fire would have been prior to 1821.

Diatom assemblages changed directly following charcoal peaks, suggesting that the algal community is sensitive to charcoal deposition and changes in pH. The increase in *Eunotia nymanniana* (optimal occurrence at pH of 6.1; Weckström et al., 1997) after charcoal peaks may indicate a response to increasing pH caused by the flush of nutrients from charcoal deposition. Ash remaining after the fire and leaching of ammonia can increase the soil pH (Smithwick et al., 2006). This change to soil water chemistry can persist for multiple growing seasons after fire (Certini, 2005). Diatom responses to fire were documented in a core from Siberia in which Rühland et al. (2000) attributed the assemblage shifts to changes in silt influx from the recently denuded catchment. Decreases in bulk density and increases in C:N in the bog also indicate a response of the wetland vegetation to nutrient flux from charcoal deposits.

4.1 Mechanism of collapse

At our study site in the three growing seasons following the 2001 fire, we observed a 6 m lateral expansion of the collapse. The ^{210}Pb and ^{137}Cs dating models indicate that the initial collapse initiation occurred before 1900. Given a black spruce forest with a thin active layer growing over ice-rich permafrost, we propose the following sequence. After burning of the forest, an initial collapse is formed as a result of permafrost thaw. The lowered landscape, now partially submerged in thaw water, is then colonized by wetland vegetation such as sedges and *Sphagnum*. Subsequent fire events in the adjacent forest lead to lateral expansion of the collapse. As the collapse expands, wetland vegetation colonizes the newly subsided margins. Fire initiation of permafrost thaw, however, is not the only trigger of collapse and wetland expansion. The presence of compression-wood in the growth rings of trees at the margin of the collapse feature suggests ground movement, which could be evidence of subsidence since the last stand-replacing fire. While results from this study supports the hypothesis that fire is an important driver of collapse initiation and growth in this ecosystem after isolation from the active floodplain, permafrost degradation and wetland succession likely proceed in

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the recovery periods between fires.

4.2 Future trajectories

Since carbon accumulation is greater in permafrost collapse scars than in other peat features, future climate warming could lead to increased collapse and peat expansion and greater carbon storage (Camill and Clark, 1998; Robinson and Moore, 2000). If, however, pervasive drying of wetlands occurs, increased storage may be offset by greater aerobic decomposition (Hilbert et al., 2000) or vegetation shifts (Payette and Delwaide, 2004). Carbon accumulation rates estimated in this study, $172\,\mathrm{gC\,m^{-2}\,y^{-1}}$ (or $11\,\mathrm{mm\,y^{-1}}$) for the *Sphagnum* dominated portion of the core, are significantly higher than that reported for a similar *Sphagnum riparium* collapse feature in Western Canada of $25.6\,\mathrm{gC\,m^{-2}\,y^{-1}}$ or $1.56\,\mathrm{mm\,y^{-1}}$ (Robinson and Moore, 2000), and for boreal peat-lands in general of $21\,\mathrm{gC\,m^{-2}\,y^{-1}}$ (Clymo et al., 1998). This young collapse should continue to accumulate carbon unless future warming or permafrost degradation results in drainage of the wetland.

We attribute the negative relationship between growing season air temperature and the detrended tree-ring width index for black spruce growing in the terrestrial portion of the study site (Fig. 7; Wilmking and Myers-Smith, 2007) to drought-inhibited growth. Although this poorly drained forest seems an unlikely candidate to experience significant plant drought stress, the combination of root systems limited by a shallow active layer and rapid fluctuations in the water table may lead to periods of reduced water availability (Dang and Lieffers, 1989). Annual growth in Western Canadian black spruce stands has previously be shown to be negatively correlated with temperature and positively correlated with precipitation (Dang and Lieffers, 1989; Brooks et al., 1998). In Interior Alaskan white spruce (*Picea glauca*) tree-ring width, C13 and maximum latewood density was shown to be an indicator of tree growth response to temperature-induced drought stress (Barber et al., 2000). In our study, the observed decreased black spruce growth in warmer growing seasons may indicate reduced success of this forest type with climate warming.

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The spatial mosaic of the Tanana Floodplain landscape is formed by fire, permafrost degradation and vegetation succession. If drought conditions do not increase in Interior Alaska, this system will likely continue on a trajectory of fire mediated collapse and bog expansion. An expansion of wetland could increase carbon storage and methane
⁵ emissions in this landscape (Turetsky et al., 2000; Vitt et al., 2000; Camill et al., 2001; Myers-Smith, 2005). Results from this study indicate that both the succession from a sedge- to a *Sphagnum*-dominated wetland and the decrease in the detrended tree-ring width index of black spruce trees surrounding the collapse were coincident with a climate shift (Fig. 7). This stepwise increase in summer temperature in Interior Alaska
¹⁰ in the late 1970's has been attributed to a regime change in the Pacific Decadal Oscillation (Mantua et al., 1997). Since it is suspected that carbon accumulation is more strongly controlled by vegetation succession than responding directly to climate (Camill et al., 2001), future vegetation succession away from *Sphagnum* and sedge species could lead to reduced carbon storage in this ecosystem, particularly if decomposition
¹⁵ is not nitrogen limited (Mack et al., 2004). A significantly drier climate or the initiation of subsurface drainage, however, could also trigger a return to terrestrial vegetation in the collapse and potentially prevent the regeneration of black spruce in the forest after fire, resulting in the development of a novel ecological state such as a steppe-like community (Chapin et al., 2004).

²⁰ Paleo-ecological records are powerful techniques for inferring past climate (Blackford, 2000). With uncertain future scenarios for this landscape, we must continue to expand paleo-ecological studies utilizing all tools available including diatoms, testate amoeba, stable and radio isotopes. By refining our understanding of the influence of the disturbance regime over succession and spatial patterning, we can continue to
²⁵ improve projections of ecological feedbacks to climate change in boreal wetlands.

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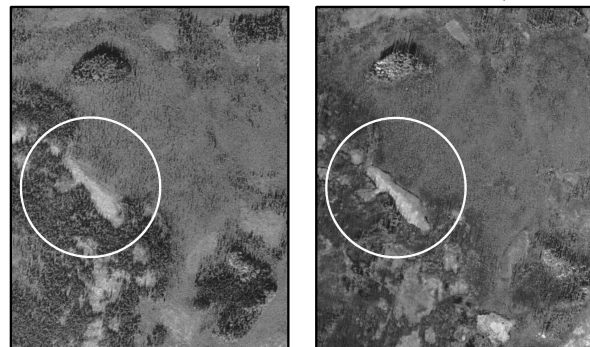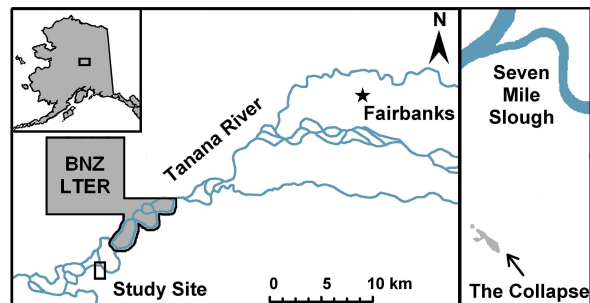| Abstract | Introduction |
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Table 1. Sample results for ^{14}C activity by accelerator mass spectrometry including samples from transects on the north (BBC1) and south (BBC2) sides of the collapse. The sample material included peat fruiting bodies (fb), bulk peat (bp), and charcoal (c). Analyzes were conducted at the Lawrence Livermore National Laboratory Center for AMS (LLNL) or the UC Irvine W. M. Keck Carbon Cycle AMS facility (KC).

Transect Name	Smpl. ID	Anal. Loc.	Depth (cm)	Smpl. Mat.	δ13C (‰)	δ14C (‰)	14C age (BP)
BBC1	TFBC 26.20	LLNL	20	fb	−25	187.5±5.3	< modern
BBC1	TFBC 26.34	LLNL	34	fb	−25	187.5±7.8	< modern
BBC1	TFBC 26.40	LLNL	40	fb	−25	−18.0±4.4	145±40
BBC1	TFBC 26.54	KC	54	bp	−26.7±0.15	−36.3±1.8	245±20
BBC1	TFBC 26.56	LLNL	56	bp	−25	−34.5±8.2	280±70
BBC1	TFBC 26.56	KC	56	bp	−26.6±0.15	−47.1±1.6	335±15
BBC1	TFBC 26.56	LLNL	56	c	−25	−70.1±4.1	585±40
BBC1	TFBC 26.58	KC	58	bp	−27.2±0.15	−63.7±1.7	475±15
BBC1	TFBC 2.60	KC	60	bp	−27.2±0.15	−27.1±1.6	165±15
BBC1	TFBC 1.65	KC	65	bp	−27.2±0.15	−39.3±1.6	270±15
BBC2	TFBC2 6.75	KC	75	bp	–	–	505±40
BBC2	TFBC2 5.77	KC	77	bp	–	–	80±40

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Table 2. Sample results for ^{137}Cs and ^{210}Pb (mean ± SE), the isotope derived age model, and estimated carbon accumulation for the bog core. The supported ^{210}Pb activity, defined by the ^{226}Ra activity, was determined on each interval by subtracting the ^{226}Ra activity, defined as the average of the measured ^{214}Pb and ^{214}Bi, from total ^{210}Pb. In many intervals no correction was made because the measured ^{226}Ra was less than the detection limit (0.3 dpm/g).

Depth (cm)	^{137}Cs (pCi/gm)	^{210}Pb Total	Sup. Act. ^{226}Ra	Unsup. ^{210}Pb	Age Model	C Acc. (kgC m^{-2})
2	0.26±0.26	8.48±4.41	<0.3	8.48±4.41	2003±0	0.2
8	0.16±0.11	9.32±1.76	0.55±0.39	8.77±1.47	1999±2	0.8
10	0.15±0.13	5.61±2.20	<0.3	5.61±2.20	1998±3	1.1
12	0.24±0.13	4.68±2.20	0.41±0.47	4.27±1.64	1996±4	1.4
14	0.12±0.14	9.06±2.38	0.70±0.54	8.37±1.71	1994±5	1.7
16	<0.07	8.97±2.87	0.71±0.67	8.27±1.88	1992±6	2.0
20	0.40±0.13	8.20±2.11	0.41±0.47	7.79±2.16	1987±8	2.9
24	0.31±0.07	5.16±1.08	<0.3	5.16±1.08	1981±11	3.8
26	0.51±0.08	4.10±1.15	<0.3	4.10±1.15	1979±12	4.3
28	0.62±0.08	4.97±1.14	<0.3	4.97±1.14	1976±14	4.7
30	1.66±0.10	4.48±1.89	<0.3	4.48±1.89	1974±14	5.0
32	2.75±0.12	5.48±1.33	<0.3	5.48±1.33	1971±15	5.5
34	2.78±0.10	8.11±1.16	<0.3	8.11±1.16	1967±15	6.1
36	1.46±0.08	5.48±1.09	<0.3	5.48±1.09	1964±17	6.6
38	2.03±0.09	5.59±1.12	<0.3	5.59±1.12	1961±18	7.1
40	1.66±0.10	6.52±1.35	<0.3	6.52±1.35	1958±19	7.6
42	0.95±0.10	4.30±1.52	<0.3	4.30±1.52	1954±21	8.3
44	1.08±0.09	3.70±1.31	<0.3	3.70±1.31	1950±22	9.1
46	1.08±0.08	2.06±1.12	<0.3	2.06±1.12	1945±24	9.8
48	1.19±0.07	2.84±1.05	<0.3	2.84±1.05	1941±26	10.7
50	1.29±0.09	4.36±1.24	<0.3	4.36±1.24	1935±29	11.7
52	0.27±0.03	1.98±0.52	1.16±0.12	0.81±0.53	1915±52	13.0
54	<0.07	1.48±0.41	0.86±0.09	0.62±0.42	1889±85	14.2

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Fig. 1. Location of the study site in Interior Alaska, a permafrost collapse scar (64° N. 38.448′, 148° W. 20.009′, 132 m elevation) southwest of the Bonanza Creek experimental forest on the Tanana River floodplain in Interior Alaska. Images show the collapse scar prior to and after the Survey-line Fire burned through the study site in late June 2001.
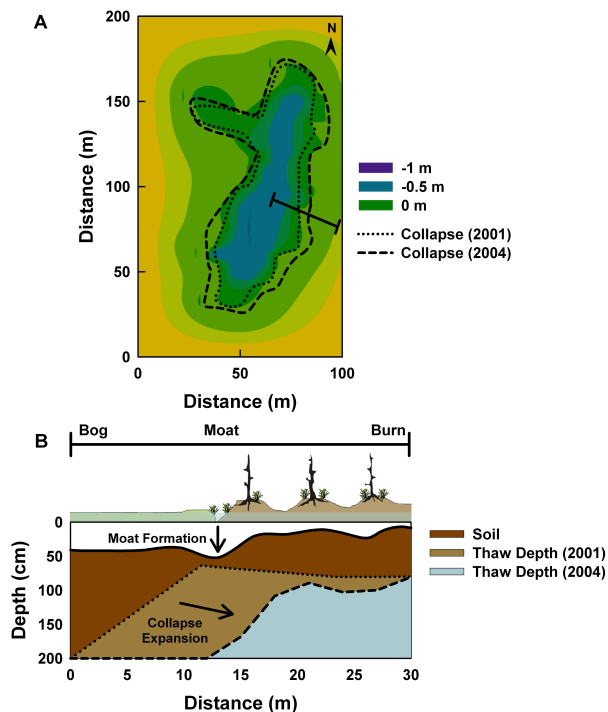
Fig. 2. Collapse expansion since the 2001 fire, illustrating the spatial extent of the collapse **(A)**. The extent of the collapse in 2001 is indicated by the dotted line and in 2004 is indicated by the dashed line. Cross section of transect from center of bog to burn zone illustrating lateral subsidence and moat formation **(B)**. The soil surface topography is indicated by the shades of colour in plot A and by the bold solid line in plot B. Frozen ground is represented by the pale blue polygon and the ground that has thawed since the fire is indicated by the light brown polygon. Cores were sampled along the transect at 0 m in the centre of the bog, 12 m in the moat, and 27 m in the burned forest.

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Fig. 3. Stratigraphy of a core from the center of the bog indicating charcoal remains, soil bulk density, %C, %N, and C:N. Dotted lines correspond to the diatom zones (Fig. 5).

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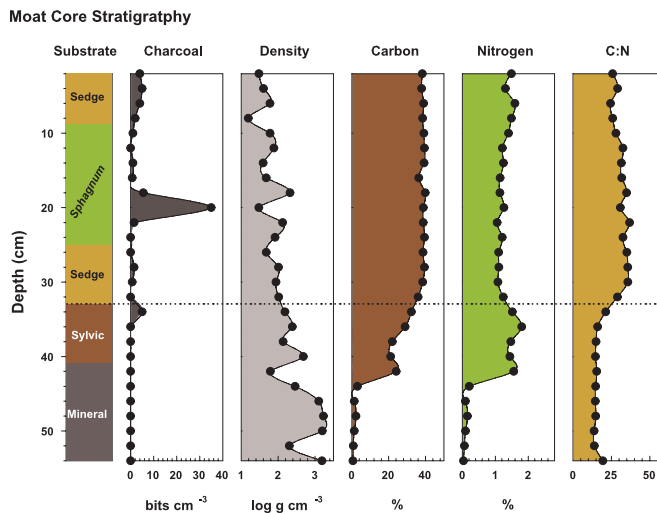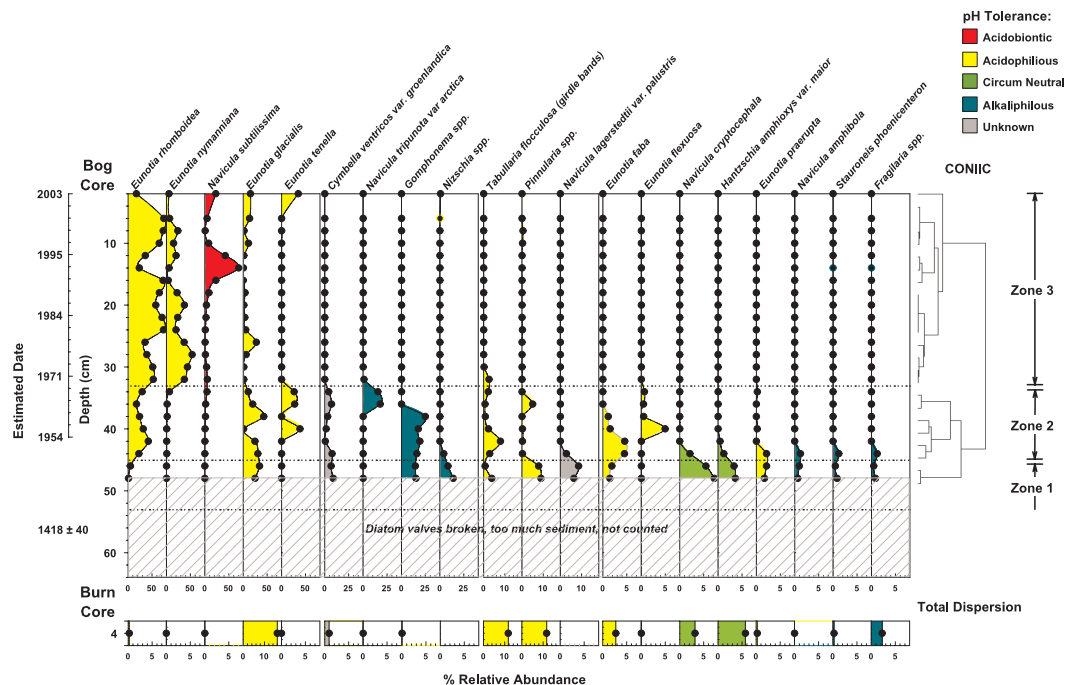
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Fig. 4. Stratigraphy of a core from the moat portion of the transect indicating charcoal remains, soil density, %C, %N, and C:N. Dotted line corresponds to the transition from terrestrial organic matter to sedge-dominated peat.

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Fig. 5. The percent relative abundance of key diatom species/genera assemblages for the bog core. Diatom-delineated zones were determined using constrained cluster analysis by information content (CONIIC). We consider the first diatom zone to begin at 53 cm where the sedge-dominated substrate begins; however, diatoms were not counted below 48 cm due to a high proportion of broken valves, residual organic matter and inorganic sediment on the slides. The diatom taxa are presented from most dominant to least dominant from left to right across the figure, the color of the area under each curve corresponds to the pH tolerance of each diatom (see legend). The abundance of diatom species in the terrestrial soil core at 4 cm is included below the bog core data.
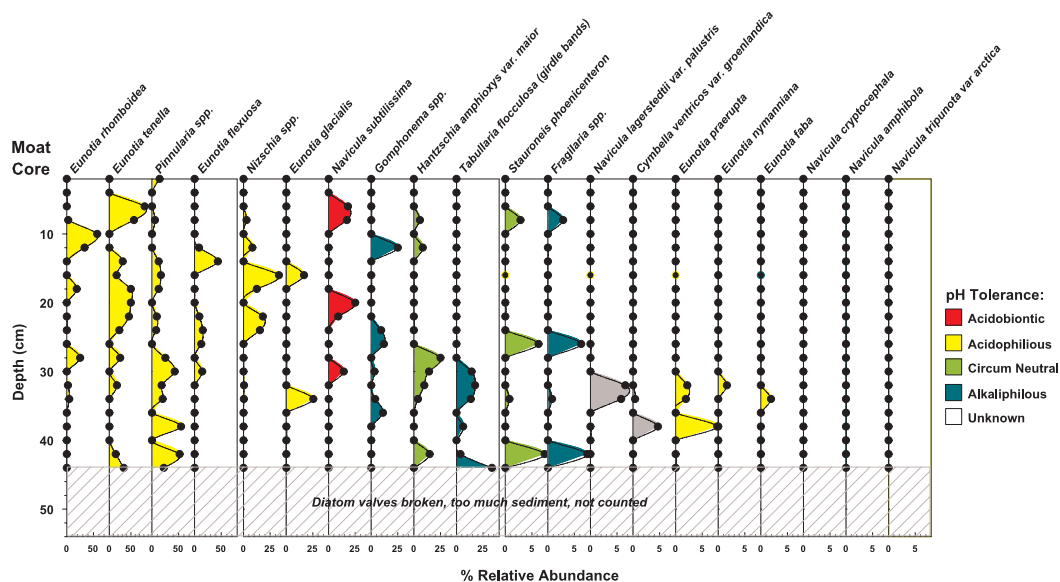
Fig. 6. The percent relative abundance of key diatom species/genera assemblages for the moat core. Diatoms were not counted below 44 cm due to sparse diatom densities, a high proportion of broken valves, residual organic matter and inorganic sediment on the slides. The diatom taxa are presented from most dominant to least dominant from left to right across the figure, the color of the area under each curve corresponds to the pH tolerance of each diatom (see legend).
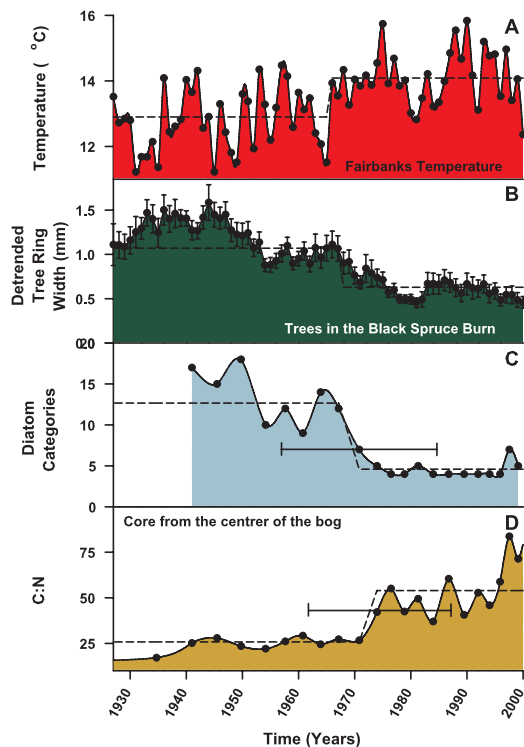
Fig. 7. Growing season temperature (May, June, July and August) from a composite of University Experiment Station (1906–1947) and Fairbanks International Airport (1948–2000) from Wilmking et al. (2004) **(A)**, detrended tree-ring width index for black spruce trees in the ecosystem surrounding the collapse (mean±SE , *n*=11, **(B)**; Wilmking and Myers-Smith, 2007), number of diatom categories (diatom genus or species; error bar indicates the error in the age estimate at 1965, **(C)**, and the ratio of carbon to nitrogen (error bar indicates the error in the age estimate at 1965, **(D)**. Dashed lines indicate the shift in each of the data sets.

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