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Natural and historical variability in fluvial processes, beaver activity, and climate in the Greater Yellowstone Ecosystem

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ABSTRACT: Two centuries of human activities in the Greater Yellowstone Ecosystem (GYE) have strongly influenced beaver activity on small streams, raising questions about the suitability of the historical (Euro-American) period for establishing stream reference conditions. We used beaver-pond deposits as proxy records of beaver occupation to compare historical beaver activity to that throughout the Holocene. Forty-nine carbon-14 (^{14}C) ages on beaver-pond deposits from Grand Teton National Park indicate that beaver activity was episodic, where multi-century periods lacking dated beaver-pond deposits have similar timing to those previously documented in Yellowstone National Park. These gaps in the sequence of dated deposits coincide with episodes of severe, prolonged drought, e.g. within the Medieval Climatic Anomaly 1000–600 cal yr BP, when small streams likely became ephemeral. In contrast, many beaver-pond deposits date to 500–100 cal yr BP, corresponding to the colder, effectively wetter Little Ice Age. Abundant historical beaver activity in the early 1900s is coincident with a climate cooler and wetter than present and more abundant willow and aspen, but also regulation of beaver trapping and the removal of wolves (the beaver's main predator), all favorable for expanded beaver populations. Reduced beaver populations after the 1920s, particularly in the northern Yellowstone winter range, are in part a response to elk overbrowsing of willow and aspen that later stemmed from wolf extirpation. Beaver populations on small streams were also impacted by low streamflows during severe droughts in the 1930s and late 1980s to present. Thus, both abundant beaver in the 1920s and reduced beaver activity at present reflect the combined influence of management practices and climate, and underscore the limitations of the early historical period for defining reference conditions. The Holocene record of beaver activity prior to Euro-American activities provides a better indication of the natural range of variability in beaver-influenced small stream systems of the GYE. Copyright © 2012 John Wiley & Sons, Ltd.

KEYWORDS: Greater Yellowstone Ecosystem; fluvial geomorphology; beaver; *Castor canadensis*; climate change

Introduction

The Greater Yellowstone Ecosystem (GYE, Figure 1) is considered one of the most pristine temperate ecosystems on Earth (Keiter and Boyce, 1991), which may lead to the assumption that GYE stream systems have remained largely free from human impacts. By the early 1800 s, however, GYE stream systems were already subjected to intensive beaver trapping for the European market (Schullery and Whittlesey, 1992). The loss of beaver and associated beaver dam abandonment can cause channel incision, water table lowering, and loss of riparian habitat (Pollock *et al.*, 2003; Butler and Malanson, 2005; Green and Westbrook, 2009). Therefore, reductions in GYE beaver populations may have strongly altered stream ecosystems shortly after the arrival of Europeans.

Dramatic variations in beaver abundance within the Euro-American period have prompted a debate over the ecologically appropriate density of beaver in the GYE (Yellowstone National Park, 1997, and references cited therein). Beaver were abundant throughout the GYE in the early 1900s (Warren, 1926; Skinner, 1927; Seton, 1929). In comparison, beaver populations are generally reduced at present, particularly in the elk winter range in northern Yellowstone National Park (YNP), where 1st to 4th order streams have been essentially devoid of beaver for at least 55 years (Jonas, 1955; Smith, 2003). Elk populations increased following the elimination of wolves in the early 1900s, and consequent overbrowsing of willows and aspen has been cited as the cause of widespread beaver dam abandonment in northern YNP through reduction of beaver food and dam-building resources (Chadde and Kay, 1991). In turn, some infer that beaver dam abandonment initiated widespread channel incision on small streams, with ensuing loss of riparian habitat and conversion of the landscape from a beaver-meadow state to an elk-grassland state (Chadde and Kay, 1991; Wolf *et al.*, 2007). While the abundant beaver populations of the early 1900s have been considered representative of appropriate ecological conditions (Wagner *et al.*, 1995; Wolf *et al.*, 2007), defining reference states for beaver populations, streams, and riparian ecosystems is complicated by over 200 years of Euro-American resource use and management

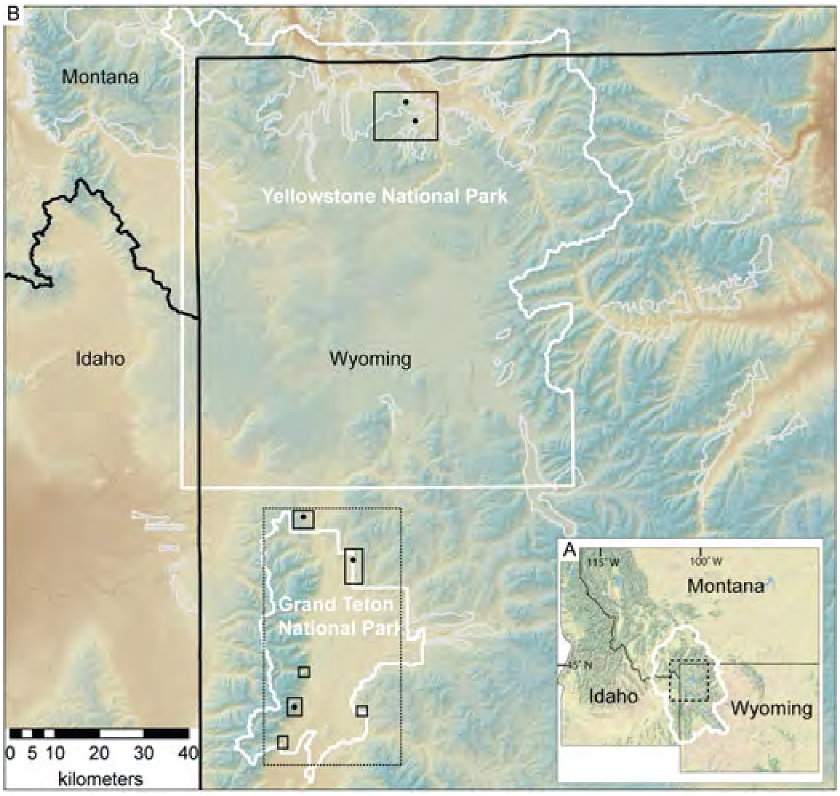

Figure 1. (A) Inset map showing location of the Greater Yellowstone Ecosystem (GYE, white line) in the central Rocky Mountains, USA. Dotted black line indicates area of map B. (B) Map showing general study locations (black boxes) in Grand Teton National Park (GTNP; white line) and the location of streams studied by Persico and Meyer (2009) in northern Yellowstone National Park (YNP, white line). Elevations range from 1550 m to 4200 m in the region. Thick black lines show state boundaries. Thin grey lines indicate elk winter range (US Fish and Wildlife Service – Mountain Prairie Region, 2005). Black dots show the location of coarse fluvial gravel deposits. Dotted black line indicates extent of map in Figure 2, which shows all streams studied in GTNP. This figure is available in colour online at wileyonlinelibrary.com/journal/espl

activities. Thus, the historical period (here defined as the time of Euro-American written and photographic records) may not be suitable for defining reference conditions and natural variability in GYE stream ecosystems. A longer-term record of beaver and associated stream dynamics prior to Euro-American impacts is desirable to characterize the natural range in variability.

Analysis of the long-term record of beaver activity is also necessary to assess relationships between climate variability and GYE stream system behavior, including potential climatic effects on beaver activity. The early historical record falls within a period of relatively cool and wet conditions known as the Little Ice Age (LIA, 600–50 cal yr BP; Meyer *et al.*, 1995; Cook *et al.*, 2004; Jacobs and Whitlock, 2008). Episodes of severe and prolonged drought have also punctuated late Holocene time, which may have forced a larger range of natural variability in stream ecosystems than that experienced in the historical reference period of the 1800 s and early 1900s. Severe and prolonged drought can have major impacts on streamflows (Graumlich *et al.*, 2003; Persico and Meyer, 2009), riparian and aquatic ecology (Lake, 2000; McMenamin *et al.*, 2008; Debinski *et al.*, 2010), and forest-fire severity and associated stream impacts (Meyer *et al.*, 1995; Legleiter *et al.*, 2003). In northern YNP, Persico and Meyer (2009) used information on both historical and Holocene beaver activity to infer that beaver occupation of small streams was limited by reduced streamflows in episodes of severe and widespread drought. If beaver activity is reduced in small streams across the GYE during such regional droughts, then the drought-associated gaps in the Holocene record of beaver activity in northern YNP should also be apparent in Grand Teton National Park (GTNP, in the southern part of the GYE). Alternatively, streams in GTNP are fed by generally greater snowpacks, thus baseflows and beaver occupation may be less sensitive to regional drought.

In the present study, we expand the record of Holocene beaver activity to small streams in GTNP in order to examine relationships with regional climate change and the northern YNP record of Persico and Meyer (2009). If long-term changes in beaver activity are substantially different between these study areas, then local geomorphic, hydrologic, and vegetative conditions are likely the most important controls on beaver occupation. In contrast, similarities in the timing of beaver-pond sedimentation and stream behavior throughout the GYE would imply that climatic controls can override local factors. Regardless, projections for increased temperatures and regional drought severity due to global warming (IPCC, 2007; Dai, 2011) underscore the need to better understand how GYE stream ecosystems respond to drought.

In this study, we also expand upon the methods developed by Persico and Meyer (2009) to identify beaver-pond sediments, using laboratory analyses of sediment organic content, carbon/nitrogen (C/N) ratios, $\delta^{13}C$, and $\delta^{15}N$. Ultimately, we use geomorphic, stratigraphic, and paleoenvironmental data over the Holocene (the 11 700 years since the nominal end of the last glaciation) to elucidate the natural range of variability in beaver-influenced small stream systems throughout the GYE. We then compare the Holocene record to beaver activity and stream-system changes over the historical period in the GYE, allowing an evaluation of the effects of human impacts, management activities, and climate change on beaver populations.

Background

The hydrologic, geomorphic, and ecological effects of beaver dams on streams have been well documented, as reviewed by Naiman *et al*. (1988) and Gurnell (1998). Beaver dams reduce flow velocities (Butler and Malanson, 1995; Westbrook *et al*., 2006) and promote fine-grained sediment deposition (Butler and Malanson, 1995; McCullough *et al*., 2005; Pollock *et al*., 2007). Beaver dams also elevate floodplain water tables and expand riparian areas (Westbrook *et al*., 2006). The creation of beaver ponds can increase species richness (Wright *et al*., 2002), for example, by creating different benthic macroinvertebrate assemblages than those on undammed stream reaches (Margolis *et al*., 2001). Beaver ponds can also promote increased plant (Johnston, 1994) and vertebrate diversity (Pollock *et al*., 1995), and help to sustain rich and abundant bird communities in semi-arid landscapes (Cooke and Zack, 2008).

Historical beaver activity and populations in the GYE

Beaver populations in the GYE have undergone substantial fluctuations in the past 200 years. At the time of European arrival in North America, beavers (*Castor canadensis*) were generally abundant throughout North America, likely including the GYE (Seton, 1929; Haines, 1965; Naiman *et al*., 1988), though population estimates there are unavailable (Yellowstone National Park, 1997). The expansion of the fur trade into the Rocky Mountains in the early 1800 s resulted in intensive beaver trapping throughout the Yellowstone region. Limited reports by fur trappers suggest that beavers were plentiful in the GYE in the early and middle 1800 s (Haines, 1965), but local overtrapping of beaver is also mentioned (Schullery and Whittlesey, 1992). By 1900, beaver populations were lowered to near extinction over most of North America (Naiman *et al*., 1988). Population declines in the GYE were apparently not as extreme, but trapping had significantly reduced populations by the 1870 s (Yellowstone National Park, 1997).

At the same time, greatly reduced demand for beaver pelts in Europe led to a collapse of the fur trade around 1870 (Clayton, 1966). This likely allowed GYE beaver populations to begin recovery, aided by prohibition of trapping in the YNP in 1883, and a Wyoming state closed-season on beaver trapping that began in 1897. The eradication of wolves in the GYE by the early 1900s may also have contributed to beaver population increases (Yellowstone National Park, 1997), as the short-term effect of wolf extirpation would be the elimination of the beaver's primary predator (Warren, 1926). Beaver recovery was supported by abundant aspen and willow, stemming in part from an aspen 'birth storm' in the late 1880 s, and a probable decrease in beaver use of this vegetation during the intensive trapping of preceding decades (Romme *et al*., 1995; Yellowstone National Park, 1997).

Beaver populations reached sufficiently high levels in the 1920s that YNP managers, worried that beaver would destroy aspen stands, employed Edward Warren in 1921–1923 to study beaver activity in northern YNP. Warren's (1926) study documented abundant beaver along streams near Tower Junction in northern YNP, but was limited to that area. Estimates of the park-wide beaver population in YNP during the 1920s vary widely, from 800 to over 10 000, and the census methods were not recorded (Yellowstone National Park, 1997).

Despite the lack of accurate population data, qualitative observations indicate that GYE beaver populations declined substantially sometime between 1930 and 1950. The decline of beaver was particularly severe in northern YNP, where all 17 sites where Warren (1926) identified beaver activity had been abandoned by 1950 (Jonas, 1955). Jonas (1955) documented stream reaches elsewhere in YNP that had been recently abandoned by beaver, indicating a marked reduction in numbers after the 1920s (Smith *et al*., 1996). During the same period, beaver were noted to be absent on many streams in GTNP where evidence of prior damming was observed, and so were widely re-introduced (Wyoming Game and Fish Commission, 1950).

Beaver extirpation by *c*. 1950 over much of northern YNP has been attributed to wolf eradication, which left few effective predators of elk (Chadde and Kay, 1991), so that expanding elk populations overbrowsed willow and aspen, leaving insufficient food or dam-building materials for beaver. The loss of beaver has been further linked to reduced riparian vegetation and widespread channel incision along small streams in northern YNP (Chadde and Kay, 1991; Wolf *et al*., 2007; Bilyeu *et al*., 2008), as when beaver dams are abandoned and breached, the lowered base level may result in downcutting and an associated decline of floodplain water tables (Butler and Malanson, 2005; Green and Westbrook, 2009).

Efforts to produce reliable estimates of GYE beaver populations began in the late 1900s. A 1973–1976 survey of beaver in GTNP found 103 active beaver colonies (Collins, 1976). Although not directly comparable, more recent beaver surveys in GTNP documented 126 bank burrows or lodges along the 137 km of streams surveyed, but only 33% displayed signs of current activity (Gribb, 2004). Aerial surveys of beaver began in YNP in 1988 and documented 71 active colonies (Smith and Tyers, 2008). In 1996, 49 beaver colonies were identified within YNP, increasing to 85 in 2003, but Smith and Tyers (2008) attribute this increase primarily to improved efficiency of the census methods. They also speculate that a further increase in colonies to 127 in 2007 occurred in part because drought allowed beaver to move into larger streams such as Slough Creek in northern YNP, where lowered peak streamflows allowed dams to survive snowmelt runoff. While the new Slough Creek occupation contributed to a notable increase in total northern YNP beaver colonies, they remained essentially absent from small streams in that area, with only one site of occupation documented on Elk Creek (Smith *et al*., 1996; Smith, 2003; Smith and Tyers, 2008).

Holocene beaver effects on northern YNP streams

Persico and Meyer (2009) examined fluvial morphology and Holocene stream sediments, including beaver-pond deposits, along the full length of six small streams and their tributaries within the elk winter range of northern YNP. Three of these were streams where Warren (1926) mapped beaver activity in the 1920s. In the ~29% of the total stream length suitable for beaver habitation, fine-grained and organic-rich beaver-related deposits constituted 58% of the thickness of Holocene floodplain sediments, highlighting the long-term influence of beaver damming on the stream and riparian environment. However, relatively high stream power in steeper reaches and likely other environmental factors prevented beaver damming or beaver-pond sediment preservation along the majority of the study stream length.

Rapid deposition of 1 to 2 m of fine-grained sediment is commonly observed in modern beaver ponds (e.g. Butler and Malanson, 1995; McCullough *et al*., 2005). These short-term observations have been extrapolated to suggest that over thousands of years, beaver damming has created broad, flat, gently graded valley floors by filling of valleys with a sequence of stacked beaver-pond sediments (Ruedemann and Schoonmaker, 1938; Rutten, 1967). This interpretation has also been applied to the small streams of northern YNP (Wolf *et al.*, 2007). However, Persico and Meyer (2009) observed that the total thickness of observed Holocene beaver-pond deposits there is less than 2 m in all reaches, except in ponded glacial scour depressions that would undergo aggradation even without beaver damming. In addition, exposed glacial erratics and early Holocene deposits within 2 m of the current stream elevation in beaver-affected reaches indicate that beaver activity has only locally produced a maximum of a few meters of post-glacial valley filling in reaches suitable for damming. In addition, whereas some reaches have undergone incision following historic beaver-dam abandonment, others remain unincised, and some reaches feature carbon-14 (^{14}C)-dated terraces demonstrating Holocene downcutting prior to the historic loss of beaver. Nonetheless, in some favorable reaches of these small northern Yellowstone streams, the long-term effects of beaver damming have helped to create nearly planar floodplain surfaces underlain by relatively thick fine-grained sediment. Where not abandoned by incision, these wet 'beaver meadows' provide expanded and productive riparian habitat.

Study Area and Controls on Beaver Occupation

The GYE encompasses approximately 57 000 km^2 in Wyoming, Montana, and Idaho (Figure 1) and has a high degree of biological diversity for a temperate ecosystem, including abundant large mammals. The largely intact assemblage of species stems in part from an environment that is relatively free from anthropogenic disturbances (Keiter and Boyce, 1991). The GYE thus represents a special case in the Rocky Mountain region due to the connectedness of ecosystem structure over a very large area, making it well-suited to assess historical variations in beaver abundance.

Our study sites in the GYE encompass a range of elevation, climate, basin size, channel gradient, and vegetation, enabling us to consider the relative roles of Holocene climate variability and local environmental factors in controlling beaver activity. In GTNP, elevations range from 2000 to 2300 m above sea level at study sites, generally higher than in those in northern YNP (1700–2100 m). Mean annual precipitation in GTNP ranges from 533 mm (Moose, 1970 m elevation) to 762 mm (Flagg Ranch, 2100 m), greater than in northern YNP (374 mm at Mammoth, 1900 m elevation). In higher elevations of the GYE, maximum precipitation occurs as snowfall during the winter months, and the study stream hydrographs are dominated by snowmelt during May and June.

Stream discharge and gradient exert a significant control on beaver dam distribution (see references in Gurnell, 1998), thus in steep mountainous terrain as in much of the GYE, beaver occupation is restricted by geomorphic factors. Generally, beaver dam abundance declines as streams become wider and steeper (Retzer *et al.*, 1956; Howard and Larson, 1985; Beier and Barrett, 1987; Suzuki and McComb, 1998; Pollock *et al.*, 2007). In northern YNP, Persico and Meyer (2009) observed that beaver dams locations mapped by Warren (1926) fell below a maximum channel slope threshold that declined with increasing basin area (a proxy for discharge). Holocene beaver-pond sediments were not deposited or preserved above a similar but lower threshold, indicating that high stream power (a function of discharge times slope) limits the ability of beaver to maintain dams. This is consistent with Smith and Tyers' (2008) observation that most modern YNP beaver dams lie on reaches with a slope of $< 0{\cdot}04$, although Warren (1926) mapped dams on small streams with gradient as much as 0·1. Similar stream power controls on modern beaver pond locations were also documented in the Stillaguamish River basin, Washington (Pollock *et al.*, 2004). Low and variable streamflows also have the potential to impact beaver dam building. In Wyoming, the conversion of a formerly ephemeral stream to perennial flow resulted in a large increase in beaver damming (Wolff *et al.*, 1989), whereas beaver abundance declined significantly on two Swedish rivers when hydroelectric plants created highly variable winter stream discharge (Curry-Lindahl, 1967). Ecological modeling further suggests that perennial water sources are necessary to maintain beaver populations along streams (Wright *et al.*, 2004).

Food resources also play a role in the location of beaver dams. In the GYE, beaver favor quaking aspen (*Populus tremuloides*), willow (*Salix* spp.), cottonwood (*Populus* spp.), and alder (*Alnus* spp.), however, they have also utilized lodgepole pine (*Pinus contorta*), Douglas-fir (*Pseudotsuga menziesii*), and sagebrush (*Artemisia* spp.) when their preferred food becomes unavailable (Warren, 1926; Collins, 1976; Smith *et al.*, 1996; Persico and Meyer, 2009). Beaver have been observed to exhaust their own food supplies, particularly when dependent on aspen and similar vegetation that is larger and slower to regenerate than willow (Beier and Barrett, 1987). Willow is thus an important and more reliable food and dam building material for beaver in widespread environments (Baker and Hill, 2003), Currently, the height, density, and patch size of willow is significantly greater in GTNP compared to northern YNP (Olechnowski and Debinski, 2008). Elk browsing in northern Yellowstone caused a major reduction in willow height after the eradication of wolves in the early 1900s (Chadde and Kay, 1991; Wolf *et al.*, 2007). However, pollen from GYE lake sediments indicates that over the late Holocene, willow has been generally more abundant in GTNP than in northern YNP, where it was never plentiful (Whitlock, 1993; Whitlock and Bartlein, 1993; Jacobs and Whitlock, 2008).

Beaver dam density and longevity are highly variable and often directly related to food and water availability (Gurnell, 1998). The lifetime of beaver dams ranges from only a single season, e.g. where they are commonly removed by floods, up to several decades where food and water conditions are favorable (Howard and Larson, 1985; Butler and Malanson, 1995). On Lost Creek in northern Yellowstone, Seton (1929) noted that beaver colonies present in 1897 were declining by 1904, with complete abandonment by 1912. During the period of beaver abundance in northern YNP in the 1920s, Warren (1926) documented colonies in decline and recently abandoned dams, in addition to newly established colonies. Beaver are also able to spread rapidly through a stream network; in the Truckee River basin in the Sierra Nevada, California, beaver introduced in 1938–1946 saturated the environment in less than 40 years and even colonized steep reaches that were largely lacking in preferred foods (Beier and Barrett, 1987). In these areas of marginal habitat, beaver caused local aspen extinction and apparently abandoned them within a few years as well. Overall, these observations illustrate the dynamic character of beaver populations, especially in areas of limited food and water resources. All of these studies involve populations affected to at least some extent by trapping and management activities, however, such that natural variability in the absence of such human impacts is uncertain.

In GTNP, streams of suitable size and gradient for beaver damming lie within a landscape strongly influenced by late Pleistocene glaciation, and occupy valleys cut in bedrock, glaciofluvial deposits, and till. Several of the study streams drain relatively small basins along the Teton Range front, where active faulting and down-dropping of the Jackson Hole basin has helped to produce relatively low stream gradients adjacent to the steep mountain front (Pierce and Good, 1992). Granite Creek, White Grass Creek (an unnamed creek above the White Grass Ranch), Beaver Creek, and an unnamed tributary below

Moose Pond are incised in end moraine complexes at the foot of the Teton Range, or in outwash fill terraces of the southern Yellowstone icecap outlet glacier farther to the east. The remaining study streams, Arizona Creek, Bailey Creek, and Glade Creek drain the Pinyon Peak Highlands northeast of Jackson Hole. These streams flow through fine-grained sediments deposited in Jackson Lake or deltas that built into the lake during the late Pleistocene (Pierce and Good, 1992). The study streams have basin areas ranging from 0·5 to 40 km^2, channel widths ranging from 1 to 7 m, and channel gradients ranging from 0·004 to 0·019. Channel sinuosity is generally low, but reaches with sinuosity up to 2·4 are found along Arizona and Glade Creeks, which flow through relatively wide former glacial outwash channels. Discontinuous fill-cut terraces are present along Arizona Creek, Bailey Creek, and Glade Creek. These terraces are associated with relatively coarse-grained pebble and cobble gravel deposits.

Methods

Field identification and sampling of sediments

We identified terrace and floodplain sediments with clear evidence for beaver-related sedimentation in GTNP to compare with Holocene beaver activity in the previously studied northern part of YNP (Persico and Meyer, 2009) (Figures 1 and 2). Identification and field descriptions of beaver pond and fluvial sediments, including in terrace deposits, were undertaken between August 2007 and September 2009, along with collection of ^{14}C and sediment samples. Geomorphic evidence of past beaver activity was used to locate stratigraphic sections, in particular traces of abandoned dams. Persico and Meyer (2009) found that abandoned beaver dams are expressed on terraces and floodplains as berms ~0·3–1·5 m high and up to 50 m long that are approximately perpendicular to the valley axis. Berms are often somewhat curved or sinuous, and typically have more relief on the down-gradient face due to sediment infilling upstream of the dam. When infilling above dams reaches the dam crest, a ramp-like morphology is observed across the floodplain. Thus both floodplain morphology and stratigraphy were used to identify beaver-pond sediments in GTNP (Figures 3 and 4). Most sections were natural exposures in stream cutbanks, but four pits and two auger holes were excavated at six additional sites.

Beaver-pond deposits have distinctive sedimentologic features that facilitate their identification in fluvial stratigraphy (McCulloch and Hopkins, 1966; Dalquest *et al.*, 1990; Baker *et al.*, 1996; Persico and Meyer, 2009). Beaver-pond deposits were often located in the field by their association with relict beaver dams, as the geomorphic expression of relict dams can persist on floodplains or terraces for thousands of years (Persico and Meyer, 2009). We focused on deposits a short distance upstream (1–5 m) of abandoned dam crests, where sediments are most likely to accumulate to maximum thickness in deep, low-velocity water, and have the greatest contrast in texture and structure with fluvial sediments in free-flowing environments. Beaver pond sediments at Moose Pond (section 3) were described ~15 m above the dam crest because of ponding of water behind the relict dam (Figure 3). Each stratigraphic section with beaver-pond deposits is separated by a berm or ramp, or long distances, thus each section likely represents a separate relict beaver pond. Beaver-pond deposits usually appear as fine-grained sedimentary units that are thicker and more organic-rich than typical overbank deposits. They are darker in color because of abundant organic material, and often contain abundant large woody fragments, some of which are beaver-chewed. Low-energy flows in beaver ponds may produce thin beds and laminations, sometimes with layers of fine organic fragments including twigs, cones, bark, and charcoal, but bioturbation commonly disrupts these structures. Soil textural classification (Birkeland, 1999) was used to describe beaver-pond sediments, as this allows more accurate classification of sand–silt–clay mixtures than standard fluvial sediment size classes (cf. Folk, 1954). Sediment samples were collected at the same location and within the same beaver-pond deposit as ^{14}C samples for each beaver-pond deposit, and from representative overbank deposits from each stream for further laboratory analysis.

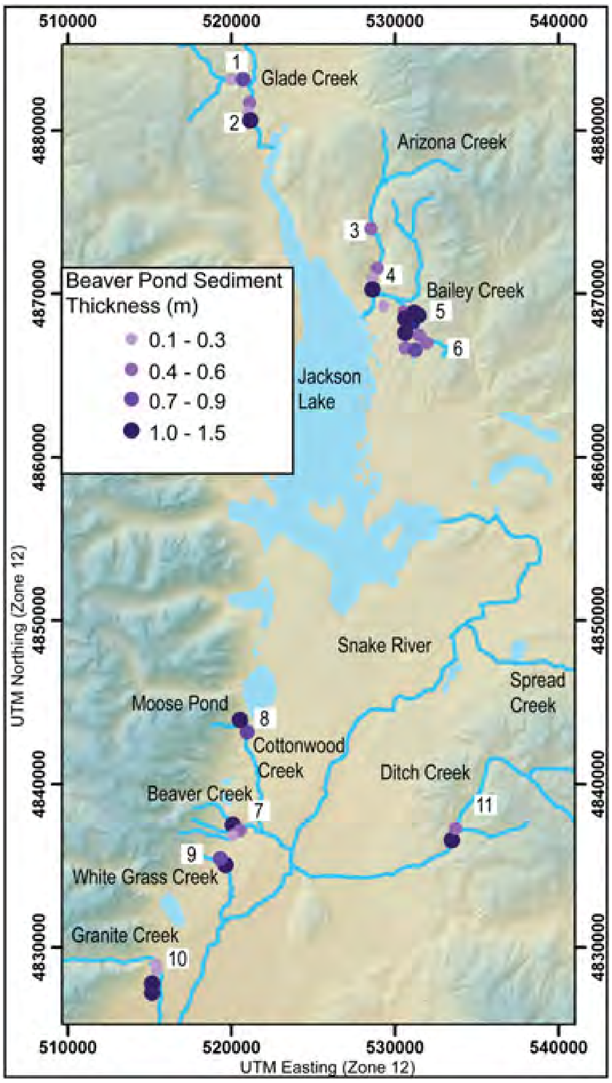

Figure 2. Location of study streams in GTNP. Numbers indicate study reaches where stratigraphic sections were described (Table I) and radiocarbon samples obtained (Table II); solid circles indicate the general location of individual stratigraphic sections in each reach. Color of solid circles indicates thickness of beaver-pond deposits at each stratigraphic section; in sections with multiple beaver-pond deposits, the summed total thickness is shown. This figure is available in colour online at wileyonlinelibrary.com/journal/espl

Laboratory analysis of beaver-pond sediments

In the current study, we expand upon the field-based criteria described earlier to develop further diagnostic characteristics for identifying beaver-pond sediments. We performed laboratory analyses of organic carbon content, C/N ratio, $\delta^{13}C$, and $\delta^{15}N$ of beaver-pond and overbank sediments (Table I). As beaver ponds are low-energy environments where beaver bring

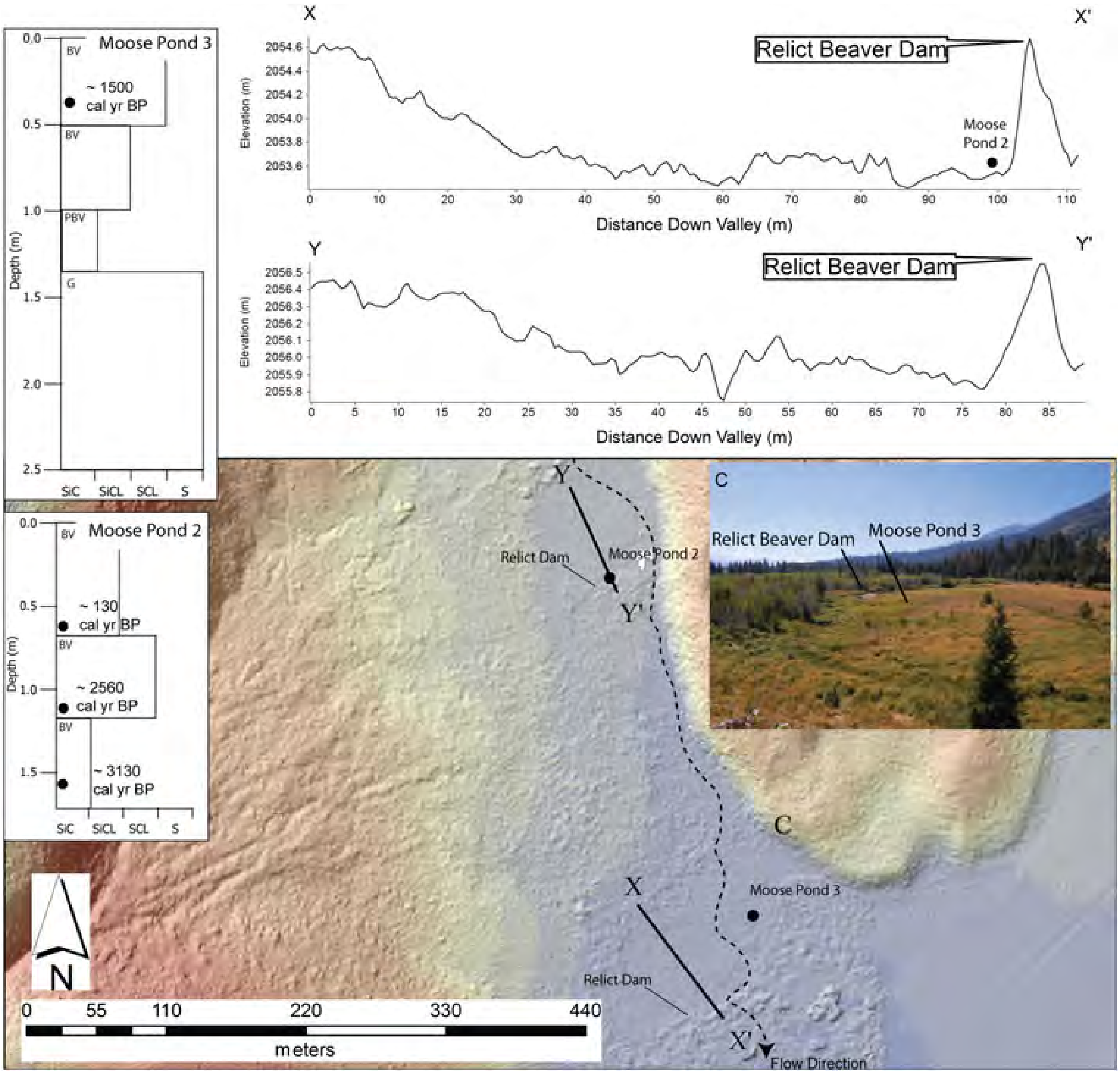

Figure 3. Beaver-pond sediments and relict beaver dam morphology along the unnamed south-flowing stream (dotted line) that drains Moose Pond (not pictured). Longitudinal profiles *X–X′* and *Y–Y′* (black lines) are derived from LiDAR topography. Stratigraphic sections are derived from augering at locations labeled Moose Pond 2 and 3 (Table I). Sediment texture: SiC = silty clay, SiCL = silty clay loam, SCL = sandy clay loam, S = sand. Deposit type: BV = beaver-pond deposit, PBV = probable beaver-pond deposit, G = gleyed gravel with no organic material. Calibrated radiocarbon ages of samples at solid black circles are shown as the weighted mean of the calibrated probability distribution (Telford *et al*., 2004) and are approximate; see Table II for 1σ uncertainty ranges. Photograph C was taken from location C looking south at the relict beaver dam downstream of Moose Pond 3. This figure is available in colour online at wileyonlinelibrary.com/journal/espl

in abundant terrestrial organic material (Naiman *et al*., 1986), we hypothesize that along with high overall organic content, pond sediments will have high C/N ratios, high $\delta^{13}C$, and high $\delta^{15}N$ compared to overbank sediments unaffected by beaver activity. These differences are the result of the distinct depositional environment created by beaver damming, where ponded water, introduction of plant materials by beaver, and lower dissolved oxygen conditions allow for greater deposition and preservation of terrestrial organic material than in a typical montane floodplain setting unaffected by beaver. Processes that would generate these C and N characteristics are considered further in the Discussion section. Organic content was estimated using loss on ignition (LOI) for 65 samples (2–3 g per sample) of (1) all pond deposits identified in GTNP, (2) representative fine-grained overbank deposits in GTNP, (3) deposits of the largest YNP beaver pond mapped by Warren in the 1920s (Chadde and Kay, 1991; Wolf *et al*., 2007), and (4) two locations where Persico and Meyer (2009) identified unambiguous beaver-pond deposits in YNP. Samples were dried at 90 °C for 24 hours, heated for four hours at 550 °C, and weight loss was used to calculate organic content (Dean, 1974). Measurements of C/N ratio, $\delta^{13}C$, and $\delta^{15}N$ were determined by mass spectrometry on 48 samples (5–25 mg per sample) from GTNP, including a subset of beaver-pond deposits and a subset of the representative fine-grained overbank deposits. Samples were first sieved to include only material < 1 mm in diameter and carbonate was removed from sediments using HCl. The $\delta^{15}N$ concentration of some beaver pond and overbank sediments could not be determined due to the overall low organic content of samples.

Dating of beaver-pond and fluvial sediments

The timing of sediment deposition was estimated using ^{14}C analyses of organic material within beaver-pond and fluvial overbank deposits. Carbon-14 ages of organic material in sediments may be older than the deposit itself if it is reworked from

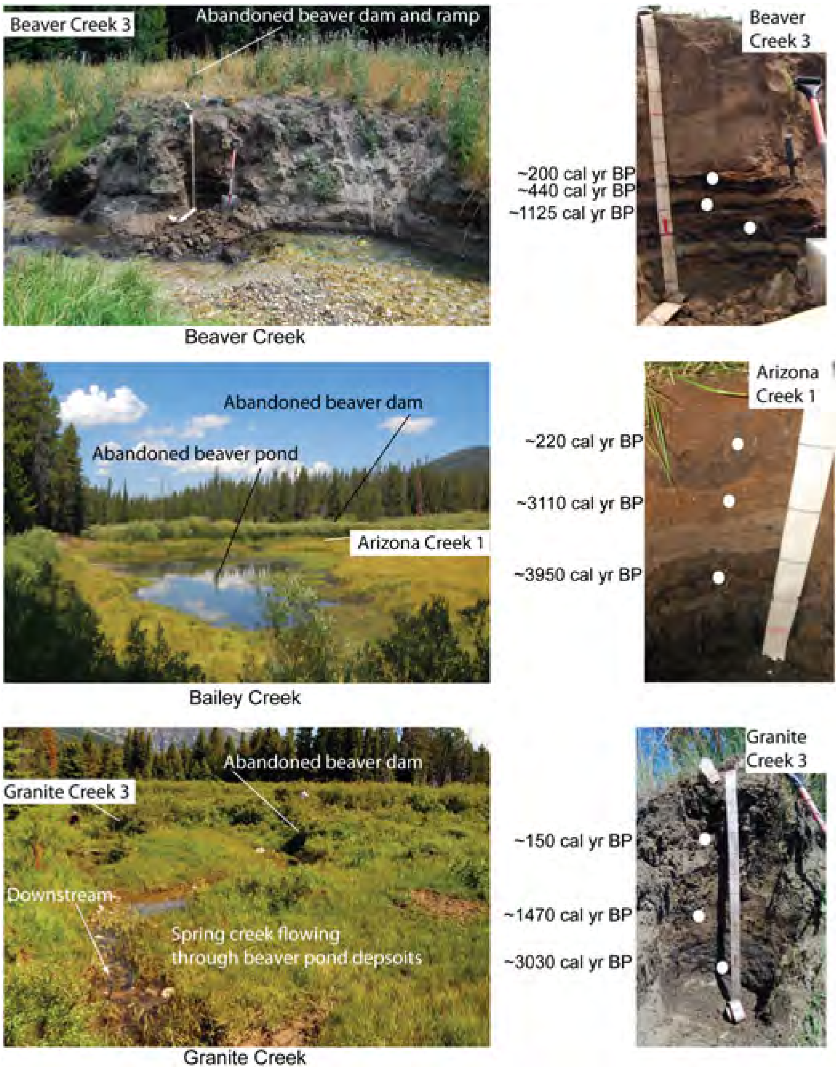

Figure 4. Examples of the surface expression of relict beaver dams and beaver-pond sediments along Beaver Creek, Bailey Creek, and Granite Creek, GTNP. Divisions on measuring tape in the stratigraphic sections are 10 cm. Solid white circles indicate location of calibrated radiocarbon ages, shown as weighted mean age as in Figure 3. Beaver-pond sediments are finer-grained and more organic-rich than fine-grained overbank sediments on these streams.

older deposits, or if the time of growth of the material predates the time of deposition (e.g. wood from the interior of a centuries-old tree). To minimize such ^{14}C dating errors, accelerator mass spectrometry (AMS) analyses of angular single fragments of easily degradable material such as twigs and cones and the outer rings of larger wood samples were used whenever available. Highly bioturbated sediment near floodplain and terrace surfaces was avoided when sampling organic materials. Where multiple radiocarbon ages were obtained from a single beaver-pond deposit, the youngest age was used because it likely has the smallest age error. For simplicity when reporting individual ^{14}C ages in this paper, the weighted mean of the calibrated probability distribution, rounded to the nearest decade (e.g. ~550 cal yr BP), is used as the best central point approximation of the true age (Telford *et al.*, 2004). Uncertainties associated with analytical error and calendar age calibration are shown by the calibrated 1σ ranges in Table II.

To examine the timing of beaver-pond sedimentation during the Holocene, individual calibrated calendar-year probability distributions of each ^{14}C age were summed for all pond sediments in GTNP. The height and form of the calibrated probability distribution of an individual ^{14}C age is influenced by temporal variations in the production of ^{14}C in the atmosphere. For example, a decrease in the atmospheric $^{14}C/^{12}C$ ratio makes younger samples have an apparent older age and produces a plateau in the calibration curve, which distributes the calibrated probability distribution over a broader time range. Conversely, increasing atmospheric $^{14}C/^{12}C$ produces a steep calibration curve and concentrates the probability distribution into a shorter time interval, generating a narrow probability peak. Therefore, a correction was applied to lessen these calibration effects on the summation of calibrated beaver-pond deposit ages, in particular to reduce false probability spikes. A simulated set of ^{14}C ages was generated for each ^{14}C year from 0 to 4000 ^{14}C yr BP. A calibrated probability distribution was produced for each of these ^{14}C ages using a typical analytical uncertainty associated with AMS dating ($1\sigma = 30$ ^{14}C yr). A summation of all 4000 simulated probability distributions was then calculated, where peaks in this synthetic cumulative probability distribution indicate a higher probability of calendar year ages solely because of variations in the atmospheric $^{14}C/^{12}C$ ratio over time. The summation curve of calibrated beaver-pond age ^{14}C distributions was then divided by the simulated probability distribution curve (cf. Macklin *et al.*, 2005). The resulting curve minimizes the enhancement of probability peaks caused by fluctuations in ^{14}C production through time.

Basin characteristics

Basin characteristics of stream reaches with evidence for beaver-pond sedimentation were extracted using ArcGIS 9.2.

Table I. Beaver-pond and overbank sediment characteristics.

Stratigraphic section/ stream reach[a]	^{14}C Sample code	Age (cal yr BP)[b]	Texture[c]	Color[d]	Organic content (%)	$\delta^{15}N$	$\delta^{13}C$	C/N	Sedimentary features[e]	Surface expression	Thickness (m)	Total thickness of section (m)	Pecentage of total[f]
Beaver-pond sediments													
Arizona Creek 1/6	ariz1_674	218	L	10YR 3/2	1·8	6·17	–24·93	10·0	bt bcs	berm	0·3	0·8	33
Arizona Creek 1/6	Ariz1_670	3116	CL	10YR 4/2	2·1	4·71	–24·00	12·3	l	berm	0·1	0·8	13
Arizona Creek 1/6	Ariz1_673	3945	SiCL	10YR 4/3	1·6	3·97	–24·18	10·6	l	berm	0·4	0·8	53
Arizona Creek 3/6	Ariz3_675	2791	SiCL	10YR 3/1	3·9	2·66	–25·72	15·9	bt bcs	berm	0·7	0·7	100
Arizona Creek 6/4	ariz6_6128	PB	SL	2·5Y 5/3	1·6	0·96	–25·49	24·6	l bcs	none	1·0	1·0	100
Arizona Creek 7/4	ariz7_6144	1598	SL	10YR 5/3	0·7	small[g]	–24·97	27·3	bcs	none[h]	0·3	2·3	14
Arizona Creek 12/4	ariz12_6156	1612	CL	2·5Y 4/2	0·4	small	–24·73	25·6	bcs	none	0·3	1·6	19
Arizona Creek 15/3	ariz15_6164	154	SiCL	2·5Y 4/2	3·0	–0·72	–25·28	24·1	bcs	none	0·5	1·7	29
Bailey Creek 4/5	bail4_6114	PB	SCL	10YR 3/2	NT[i]	NT	NT	NT	l awd	berm	0·3	0·5	60
Bailey Creek 5/5	bail5_6116	PB	SiC	2·5Y 5/3	1·3	5·64	–23·43	10·9	l awd	berm	0·3	0·3	100
Bailey Creek 7/5	bail7_6118	312	SL	2·5Y 5/3	NT	NT	NT	NT	bcs	berm	1·0	1·0	100
Bailey Creek 8/5	bail8_6119(2)	2939	SCL	10YR 6/2	1·9	2·59	–26·30	19·2	l	berm	0·8	1·2	67
Bailey Creek 8/5	bail8_6118a	3171	SCL	10YR 6/2	1·3	1·39	–26·01	12·8	l	berm	0·4	1·2	33
Bailey Creek 10/5	bail10_7015	7795	L	10YR 2/2	8·2	NT	NT	NT	bcs	berm	1·0	1·6	63
Bailey Creek 11/5	bail11_7021	380	CL	10YR 6/2	2·0	2·11	–24·26	16·0	bcs	berm	0·7	0·8	88
Bailey Creek 11/5	bail11_7022	387	SCL	10YR 3/2	NT	NT	NT	NT	bt bcs	berm	0·1	0·8	13
Bailey Creek 12/5	bail12_7023	PB	SCL	10YR 3/2	NT	NT	NT	NT	bt bcs	berm	0·5	0·5	100
Bailey Creek 14/5	bail14_7025	323	CL	10YR 6/3	2·2	2·54	–26·67	13·8	bt bcs	berm	0·5	0·5	100
Beaver Creek 1/7	beaver1_678	1615	SiCL	10YR 4/2	2·0	4·57	–26·10	10·9	l	berm	0·3	1·1	27
Beaver Creek 1/7	beaver1_675a	5955	L	2·5Y 5/2	0·6	small	–23·62	10·1	l	berm	0·1	1·1	9
Beaver Creek 1a/7	BV-1-07_0·5	1366	SiCL	10YR 5/2	NT	NT	NT	NT	bt bcs	berm	0·5	1·5	33
Beaver Creek 2a/7	BV-2-07-018	331	CL	10YR 3/2	1·0	NT	NT	NT	bt	berm	1·0	1·0	100
Beaver Creek 3/7	beaver3_685	206	SiC	10YR 3/2	0·8	small	–25·83	11·9	l awd	ramp	0·6	1·3	46
Beaver Creek 3/7	beaver3_684	436	SiC	10YR 4/3	4·0	small	–26·64	12·2	l awd	ramp	0·1	1·3	8
Beaver Creek 4a/7	BV-4-07-023	3776	CL	10YR 4/2	1·2	NT	NT	NT	l	ramp	0·2	1·5	13
Beaver Creek 4a/7	BV-4-07-025	133	L	10YR 5/2	1·6	0·93	–24·97	19·6	l	ramp	0·3	1·5	17
Ditch Creek 1/11	ditch1_7027	PB	L	10YR 5/3	1·0	0·80	–25·06	16·7	bcs	berm	0·5	0·5	100
Ditch Creek 2/11	ditch2_7028	142	SiCL	2·5Y 6/2	1·3	0·17	–25·53	15·4	bcs	berm	0·8	1·5	53
Ditch Creek 2/11	ditch2_7029	145	SiCL	2·5Y 6/3	NT	NT	NT	NT	bcs	berm	0·5	1·5	33
Glade Creek 16/1	glade16_6170	499	L	10YR 4/2	3·4	2·62	–26·49	19·3	bt bcs	berm	0·9	0·9	100
Glade Creek 2/1	GC-2-07-033	370	L	10YR 5/2	NT	NT	NT	NT	bt bcs	berm	0·6	0·9	67
Glade Creek 2/2	GC-2-07-34	PB	L	10YR 5/3	NT	NT	NT	NT	bt bcs	berm	0·3	0·9	33
Glade Creek 18/2	glade18_7019	1103	CL	10YR 5/3	1·8	1·98	–26·38	15·5	bt bcs	berm	1·0	1·0	100
Glade Creek 19/2	glade19_7020	117	L	10YR 5/2	NT	NT	NT	NT	bt bcs	berm	0·5	0·5	100
Granite Creek 1/10	Grani1_659	PB	SiCL	10YR 5/1	1·4	2·46	–25·24	15·5	awd bt	berm	0·6	1·5	40
Granite Creek 1/10	Grani1_658	161	SCL	10YR 5/3	2·0	2·84	–18·31	19·0	awd	berm	0·3	1·5	20
Granite Creek 1/10	Grani1_655	388	L	10YR 5/3	0·3	2·80	–22·81	16·7	awd	berm	0·3	1·5	20
Granite Creek 3/10	Grani3_667	148	SiL	10YR 4/3	4·6	3·86	–24·23	14·3	l awd	berm	0·8	1·4	57
Granite Creek 3/10	Grani3_664	1465	SiCL	10YR 5/3	1·4	5·73	–23·42	9·9	l awd	berm	0·2	1·4	14
Granite Creek 3/10	Grani3_663	3031	SiL	10YR 4/3	2·0	5·24	–24·81	12·8	l awd	berm	0·2	1·4	14
Granite Creek 6/10	grani6_6139	355	SiL	2·5Y 6/3	1·1	3·53	–23·51	10·4	awd	berm	0·2	0·8	25
Granite Creek 8/10	grani8_6142	125	SiL	10YR 5/3	2·1	0·07	–21·67	16·2	bt awd	berm	0·3	0·3	100

Moose Pond 2/8	moose2_688	2560	SiCL	10YR 7/2	2·2	1·72	–23·65	16·3	awd bt	berm	0·3	1·7	18
Moose Pond 2/8	moose2_690	3125	LS	10YR 6/2	1·1	small	–26·39	20·4	awd bt	berm	1·0	1·7	59
Moose Pond 2/8	moose2_692	132	L	10YR 5/2	1·7	1·34	–25·82	16·5	awd bt	berm	0·4	1·7	24
Moose Pond 3/8	moose3_695	1500	SiL	10YR 4/2	5·6	2·48	–23·98	16·4	awd bt	berm	1·1	2·5	44
Whitegrass Creek 2/9	white1_6102	9708	LS	10YR 3/1	4·4	2·96	–22·28	20·3	l awd	berm	0·1	1·2	8
White Grass Creek 2/9	white2_6103	11229	L	2·5Y 3/1	4·6	1·82	–26·86	17·9	l awd	berm	0·7	1·2	58
White Grass Creek 3/9	white3_6109	5749	SiCL	10YR 6/3	2·8	1·29	–28·50	19·0	l awd	berm	1·1	1·5	70
Overbank sediments													
Arizona Creek 4/4	^{14}C sample not collected	—	S	2·5Y 5/3	1·8	small	NT	NT	m	NA	0·8	2·0	40
Arizona Creek 8/3	^{14}C sample not collected	—	S	2·5Y 6/3	0·3	small	–23·92	12·6	l	NA	0·5	1·3	38
Arizona Creek 9/3	^{14}C sample not collected	—	S	2·5Y 6/2	NT	1·17	–24·82	8·2	l	NA	0·6	1·8	33
Arizona Creek 9/3	^{14}C sample not collected	—	S	2·5Y 5/1	0·2	small	–21·59	17·5	l	NA	0·7	1·8	39
Arizona Creek 10/4	^{14}C sample not collected	—	S	2·5Y 6/2	0·8	small	–27·20	8·5	m	NA	0·4	1·6	25
Arizona Creek 11/4	^{14}C sample not collected	—	S	2·5Y 5/3	0·6	small	NT	NT	m	NA	0·2	0·5	40
Arizona Creek 12/3	^{14}C sample not collected	—	S	2·5Y 6/5	0·4	small	–24·73	25·6	m	NA	0·3	1·4	21
Arizona Creek 12/3	^{14}C sample not collected	—	S	2·5Y 5/3	0·2	small	–25·24	8·7	l	NA	0·4	1·4	29
Arizona Creek 12/3	^{14}C sample not collected	—	S	2·5Y 5/3	0·3	small	–24·77	7·4	m	NA	0·4	1·4	29
Arizona Creek 13/4	^{14}C sample not collected	—	S	2·5Y 6/2	0·3	small	–22·90	11·1	m	NA	0·2	1·7	12
Arizona Creek 13/4	^{14}C sample not collected	—	S	2·5Y 6/3	1·1	2·41	–25·24	8·7	l	NA	0·5	1·7	29
Bailey Creek 1/5	^{14}C sample not collected	—	S	10YR 5/3	0·5	NT	NT	NT	m	NA	0·5	1·3	38
Bailey Creek 2/5	^{14}C sample not collected	—	S	2·5Y 4/2	1·0	NT	NT	NT	m	NA	0·5	0·5	100
Bailey Creek 3/5	bail3_6111(1)	2563	S	2·5Y 5/3	NT	4·20	–25·24	13·3	l	NA	0·4	1·1	36
Bailey Creek 3/5	^{14}C sample not collected	—	S	10YR 4/2	1·0	NT	NT	NT	m	NA	0·4	1·1	36
Beaver Creek 1/7	LPGTBV-4-07-21	5139	S	2·5Y 4/2	0·8	NT	NT	NT	l	NA	0·4	1·1	36
Beaver Creek 1/7	LPGTBV-4-08-22	2580	S	10YR 4/4	0·6	3·60	–26·15	12·9	m	NA	0·2	1·1	18
Beaver Creek 3/7	beaver3_683	1029	S	10YR 4/3	0·8	NT	NT	NT	m	NA	0·3	1·3	23
Glade Creek 14/2	^{14}C sample not collected	—	S	2·5Y 5/4	0·4	NT	NT	NT	m	NA	0·5	1·0	50
Granite Creek 2/10	^{14}C sample not collected	—	S	2·5Y 5/2	1·3	NT	NT	NT	l	NA	0·5	0·5	100
Granite Creek 5/10	grani5_6138	1621	CL	2·5Y 5/2	1·6	NT	NT	NT	m	NA	0·5	0·5	100
Granite Creek 6/10	^{14}C sample not collected	—	CL	2·5Y 5/2	1·5	NT	NT	NT	m	NA	0·1	0·7	14
Moose Pond 3/8	^{14}C sample not collected	—	S	2·5Y 7/1	0·1	NT	NT	NT	m	NA	0·5	2·5	20
Moose Pond 3/8	^{14}C sample not collected	—	S	2·5Y 4/2	1·1	NT	NT	NT	m	NA	0·4	2·5	16

[a]Location of stream reach where stratigraphic section is located on Figure 2.
[b]Radiocarbon dates in pond sediment shown as weighted mean calibrated age. PB = 'post-bomb' age, i·e·, $\delta^{14}C$ values show that they contain excess ^{14}C from above-ground nuclear weapons testing and must be younger than 1955.
[c]Texture of sand fraction where SiCL = silt clay loam, LS = loamy sand, SL = sandy loam, CL = clay loam, SiL = silty loam, S = sand.
[d]Munsell dry color values of the sediment.
[e]Sedimentary features used to identify beaver-related sediments: bt = bitoturbated, bcs = beaver-chewed sticks, l = laminations, awd = abundant woody detritus, m = massive·
[f]Thickness of the beaver pond sediment as a percentage of the total thickness of the section
[g]Sample does not contain enough nitrogen to measure $\delta^{15}N$.
[h]No surface expression of beaver damming.
[i]NT = not tested.

Table II. Radiocarbon samples, ^{14}C and calibrated ages and interpretation.

Sample name	Loc. #[a]	Lab. #[b]	UTM coordinates (Zone 12)		Material[c]	^{14}C Age ± 1σ[d]		Calibrated 1σ age ranges (cal yr BP)[e]	Weighted mean cal. age[f]	Interp.[g]
			Easting	Northing						
ariz1_674_lodge	6	88902	530981	4866415	swf, dph	230	38	–1–10, 150–174, 177–185, 272–307	218	BV
Ariz1_670_0.52	6	84265	530981	4866415	swf, dph	2948	65	3004–3210	3116	BV
Ariz1_673_0.7–0.75	6	84266	530981	4866415	mcf, no ID	3625	67	3844–3992, 4040–4073	3945	BV
Ariz3_675_0.65	6	84267	531022	4866325	swf, dph	2677	36	2751–2793, 2828–2840	2791	BV
ariz6_6128_0.95	4	84281	528703	4871205	swf, pine	PB	na	na	na	BV
ariz7_6144_1.68	4	84653	528807	4871302	swf, softwood	1685	35	1541–1616, 1676–1685	1598	BV
ariz12_6156_1.4	3	84686	528910	4871534	scf, pine	1788	38	1552–1625, 1669–1688	1612	BV
ariz15_6164_1.33	3	84660	528970	4873228	swf, dph	164	34	–1–29, 139–153, 168–221, 258–283	154	BV
bail4_6114_0.28	5	88906	529679	4869982	swf	PB	na	na	na	BV
bail5_6116_0.2	5	88907	529400	4869984	swf	PB	na	na	na	BV
bail7_6118_0.7	5	84278	529386	4869981	swf, true fir	268	62	152–170, 281–334, 349–438, 449–451	312	BV
bail8_6119(2)_0.8	5	84685	529199	4870026	scf, pine	2829	41	2870–2977, 2983–2987	2939	BV
bail8_6118a_1.05	5	84303	529199	4870026	swf, true fir	2985	38	3080–3093, 3107–3128, 3139–3241	3171	BV
bail10_7015_0.7–0.8	5	88919	530726	4868817	swf, dph	6962	46	7724–7844	7795	BV
bail11_7021_0.55–0.65	5	88924	530065	4869740	swf, pine	305	33	305–330, 359–368, 372–429	380	BV
bail11_7022_0.6–0.65	5	88925	530065	4869740	swf, dph	321	34	310–332, 354–434	387	BV
bail12_7023_dam	5	88926	530077	486974	swf, dph	PB	na	na	na	BV
bail14_7025_0.5	5	88928	529592	4869943	swf, dph	265	33	157–165, 285–317, 395–423	323	BV
bail14_7026_0.45–0.55[h]	5	88929	529592	4869943	swf, dph	330	58	314–337, 348–457	389	BV
beaver1_678_0.51	7	88903	520728	4837469	scf, no ID	1702	41	1552–1628, 1659–1660, 1665–1691	1615	BV
beaver1_675a_1.1	7	84305	520728	4837469	scf, pine	5190	42	5912–5950, 5963–5989	5955	BV
LPGTBV-1-07-17_0.5	7	84675	520576	4837365	swf, softwood	1478	37	1329–1396	1366	BV
LPGTBV-2-07-018-0.75	7	84674	520215	4837471	swf, dph	268	34	157–165,285–319, 393–425	331	BV
beaver3_685_0.69	7	84270	520133	4836687	swf, softwood	225	33	–1–8, 150–172, 277–305	206	BV
beaver3_684_0.77	7	84672	520133	4836687	swf, dph	396	37	334–345, 438–506	436	BV
LPGTBV-4-07-023-1.27	7	84682	520117	4836597	swf, true fir	3504	44	3718–3835	3776	BV
LPGTBV-4-07-025-0.65	7	84678	520117	4836597	swf, dph	110	37	–2, 28–43, 58–139, 221–259	133	BV
ditch1_7027_0.4	11	88931	534878	4839102	swf, dph	PB	na	na	na	BV
ditch2_7028_1	11	88932	534855	4839085	swf, dph	136	44	–2 to –1, 68–118, 131–150, 175–176, 186–230, 244–270	142	BV
ditch2_7029_1.5	11	88933	534855	4839085	swf, dph	140	55	–2–1, 8–35, 10–117, 131–150, 244–248, 250–275	145	BV
glade16_6170_0.85	1	84667	520149	4883660	swf, dph	453	38	493–529	499	BV
LPGTGC-2-07-033-0.65	1	84692	520830	4883019	swf, no id	316	70	305–340, 347–460	370	BV
LPGTGC-2-07-34-0.30	1	88934	520830	4883019	swf, dph	PB	na	na	na	BV
glade18_7019_0.7–0.8	2	88922	521507	4880295	swf, pine	1179	39	1060–1146, 1157–1170	1103	BV
glade19_7020_0.5	2	88923	521509	4880194	swf, dph	63	33	–5 to –2, 34–71, 116–134, 228–252	117	BV
Grani1_659_0.4	10	84260	515778	4828086	swf, dph	PB	na	na	na	BV
Grani1_658_0.58–0.63	10	84259	515778	4828086	swf, dph	178	33	–1–21, 144–154, 166–216, 266–284	161	BV
Grani1_655_1.25	10	84258	515778	4828086	swf, dph	323	33	312–333, 352–435	388	BV
Grani3_667_0.47	10	84263	515656	4828346	swf, dph	151	49	–2–0, 5–33, 73–100, 102–114, 136–152, 169–225, 253–281	148	BV
Grani3_664_0.93	10	84262	515656	4828346	scf, softwood	1577	34	1415–1469, 1482–1517	1465	BV
Grani3_663_1.15	10	84261	515656	4828346	scf, softwood	2892	36	2961–3074	3031	BV
grani6_6139_0.78	10	84651	515543	4828682	scf, no ID	279	34	289–321, 378–427	355	BV

grani8_6142_0.3	10	84652	515665	4828630	swf, true fir	83	34	–4–2, 33–73, 79–80, 99–106, 114–136, 224–254	125	BV
moose2_688_B8	8	84271	520853	4843898	swf, softwood	2473	35	2471–2480, 2483–2545, 2560–2617, 2634–2702	2560	BV
moose2_690_B6	8	84272	520853	4843898	swf, softwood	2954	36	3070–3168, 3178–3201	3125	BV
moose2_692_B3	8	84273	520853	4843898	swf, dph	111	33	–2–1, 30–42, 59–139, 221–259	132	BV
moose3_695_B1-2	8	84274	520974	4843653	swf, softwood	1622	35	1418–1466, 1509–1557	1500	BV
white1_6102_1.2	9	84275	519344	4835597	swf, softwood	8729	48	9562–9572, 9584–9590, 9595–9765	9708	BV
white2_6103_0.75	9	88905	519344	4835597	swf, softwood	5000	41	5659–5749, 5829–5855	5749	BV
white3_6109_1.05	9	84276	519356	4835644	swf, pine	9812	52	11197–11251	11229	BV
ariz4_6124_4.3	3	84280	528661	487115	mcf, no ID	10120	110	11409–11434, 11477–11486, 11491–11552, 11600–11979	11721	FGF/T
ariz8_6148_1.14	3	84654	528802	4871293	swf, true fir	2152	36	2064–2083, 2106–2158, 2172–2176, 2248–2300	2169	CGGF
ariz10_6152_0.6	3	84658	528444	4874676	scf, no ID	2001	42	1898–1914, 1919–1993	1955	CGGF
bail3_6111(1)_0.9	5	84684	529937	4869891	scf, pine	2479	40	2487–2618, 2633–2645, 2651–2705	2563	FGO
bail6_6117_0.4	5	84277	529453	4869880	scf, pine	3545	37	3729–3747, 3767–3792, 3824–3891	3824	CGO
LPGTBV-4-07-22-1.35	7	84676	520117	4836597	scf, no ID	4490	140	4892–4898, 4910–4926, 4960–5313	5139	FGO
bail13_7024_0.61	5	88927	530093	4869715	scf, no ID	2438	37	2362–2492, 2601–2608, 2641–2679	2512	FGO
LPGTBV-3-07-021-0.75	7	84677	520229	483745	scf, true fir	2503	47	2492–2602, 2607–2641, 2678–2720	2580	FGO
beaver2_679_0.7	7	84268	520707	4837449	scf, pine	1122	34	978–1039, 1043–1059	1026	CGGF
beaver3_683_0.87	7	84269	520133	4836687	swf, softwood	1125	34	978–1039, 1043–1060	1029	FGO
glade10_6130_0.41	2	84282	521304	4882255	scf, softwood	7733	68	8447–8561, 8568–8581	8514	FGO
glade11_6131_3.5	2	84283	521621	4880706	swf, dph	11701	83	13447–13653	13553	FGF/T
glade11_6133_1	2	84284	521621	4880706	scf, no id	6010	100	6733–6989	6870	FGF/T
glade14_6137_1.3	2	84650	521225	4880666	swf, dph	896	49	741–802, 810–829, 859–904	821	CGGF
Grani4_668_0.48	10	84264	515610	4828475	scf, no ID	3484	58	3691–3835	3757	CGGF
grani5_6138_0.21	10	84662	515122	4829328	scf, true fir	1709	35	1562–1625, 1658–1662, 1665–1691	1621	FGO
Tow2_629_0.82	YNP[i]	84645	547055	4970149	scf, no ID	1073	35	934–986, 1032–1050	990	CGGF
Tow2_631_0.47	YNP	84251	547055	4970149	scf, douglas fir	619	33	557–571, 579–605, 625–652	600	FGO
Tow3_633_0.73	YNP	84647	547048	4970115	scf, no id	2471	37	2469–2546, 2560–2617, 2634–2702	2556	CGGF

[a]Location identified in Figure 2.
[b]Sample number assigned at dating laboratory. All samples have AA prefix indicating NSF – Arizona Accelerator Facility of Isotope Dating.
[c]Material dated: swf = single wood fragment, mcf = multiple charcoal fragments, scf = single charcoal fragment, dph = diffuse porous hardwood, no ID = sample was too small for identification.
[d]Age $\pm 1\sigma$ = conventional radiocarbon age and analytical standard deviation (yr BP). PB = 'post-bomb' age, contains excess ^{14}C from above-ground nuclear weapons testing and must be younger than 1955.
[e]Calibrated calendar ages, given in format: minimum and maximum 1σ calibrated age ranges where endpoints of 1σ calibrated age ranges are calculated from intercepts of (^{14}C age +1σ) and (^{14}C age – 1σ) with calibration curve INTCAL04 (Stuiver and Reimer, 1993).
[f]Weighted average of calibrated probability distribution.
[g]Interpretation = Interpretation of depositional environment: BV = beaver-pond sediment; FGO = fine-grained overbank sediment; FGF/T = fine-grained fan or terrace sediment; CGGF = coarse-grained fluvial gravel.
[h]Age not included in probability summation curves to avoid duplication of an event.
[i]Sample is from Yellowstone National Park (YNP).

Channels were digitized from the blue lines on US Geological Survey (USGS) topographic maps, which by field inspection are reasonably accurate representations of channel location and sinuosity. The topographic maps were used to determine channel gradient between 12·2 m contour intervals for each stream reach where beaver-pond deposits were identified. Contributing basin areas were calculated from USGS 10-m digital elevation models (DEMs).

Holocene and historical climate analysis

The Palmer Drought Severity Index (PDSI) was used to assess how historical climate variability compares to late Holocene climate variability. The PDSI is an effective measure of long-term drought that estimates dryness, standardized for a given area, using temperature and precipitation (Palmer, 1965). Measured August PDSI values from 1895 to 2010 were averaged for Wyoming climate divisions 1 and 2 (http://www.ncdc.noaa.gov/temp-and-precip/drought/historical-palmers.php), which contain the study sites and much of the GYE, to determine the historical variability of drought. Average yearly PDSI values reconstructed from tree rings were used to assess drought variability in the late Holocene (Cook *et al.*, 2004). Ten-year moving averages of the reconstructed PDSI were created for the past 2000 years in northern Wyoming (grid point 100: 110 W, 45 N).

Results

Distribution of beaver-pond deposits

Beaver-pond deposits were identified on at least some reaches of all streams surveyed in GTNP. Berms associated with relict beaver dams were identified at all beaver-pond deposit stratigraphic sections except on Arizona Creek, where beaver-pond sediments were identified by beaver-chewed sticks in unusually thick fine-grained deposits. In addition to the study streams, evidence for recent beaver damming was observed along Cottonwood Creek and Spread Creek (Figure 1); however, no clear evidence exists for beaver-related deposition along these larger, gravelly channels. Along reaches with evidence for beaver-related deposition, stream gradients ranged from 0·1 to 0·001 (Figure 5). All of these reaches plot below the power-law threshold for pond deposit preservation observed in northern YNP (Persico and Meyer, 2009).

Individual pond deposit units ranged in thickness from 0·1 to 1·1 m (mean = 0·5 m, Figure 2) and make up 76% of the total thickness of stratigraphic sections (Table I). At Moose Pond, a low-gradient, moraine-dammed tributary of Cottonwood Creek, Holocene beaver-related sedimentation totals 1·7 m in thickness (Figures 2 and 3). Directly beneath the beaver-pond sediments are gleyed, poorly sorted sand and gravel with no visible organic material. On the Granite Creek floodplain, berm locations indicate damming of a spring-fed tributary, but no evidence of beaver damming exists on the relatively large, steep main channel of Granite Creek itself (study reach 10, Figure 2). This reach of Granite Creek plots near the maximum slope-area threshold for beaver-related sedimentation developed in northern YNP (Persico and Meyer, 2009). As its drainage basin is much steeper and receives significantly more winter precipitation than streams in northern YNP, Granite Creek likely has greater discharge per unit contributing area and falls above the stream-power threshold for beaver-related sedimentation.

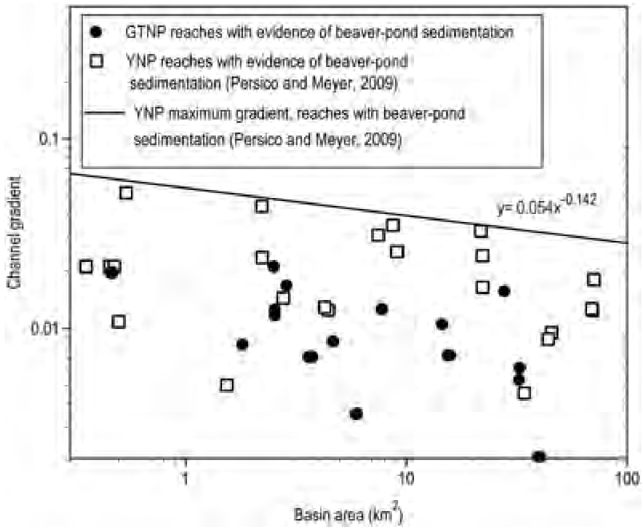

Figure 5. Plot of channel gradient as a function of contributing basin area for stream reaches with Holocene beaver-pond sedimentation in GTNP and YNP (Persico and Meyer, 2009). All reaches with documented beaver-pond sedimentation in GTNP plot below the maximum gradient threshold for beaver-pond sediment preservation defined in YNP. Reaches that plot above the threshold line are not shown, but are common in both GTNP and YNP and lack evidence of beaver-pond sedimentation.

Sediment characteristics

Field descriptions of beaver-pond sediments from GTNP show that they are similar to those in northern Yellowstone (Persico and Meyer, 2009). Pond deposit textures in GTNP range from loamy sand to clay loam (Table I). Beaver-pond sediments are generally more poorly sorted and contain a greater percentage of clay than typical fluvial sediments of streams of this size in the study area, as also documented by Wolf *et al.* (2007). Fine-grained overbank deposits are generally weakly laminated and bedded to massive silty sand, with less clay (< 20%) than beaver-pond sediments (up to 45%). Fine-grained overbank deposits often contain small amounts of charcoal, but are lighter in color and less organic-rich than beaver-pond deposits, except where A horizons overprint them. Pebbles and cobbles are sometimes incorporated into otherwise fine-grained pond deposits, especially near relict dams, because beaver often use these coarser sediments in dam construction (Gurnell, 1998).

Organic carbon content of beaver-pond sediments in GTNP ranges from 0·3 to 8·2% (Table I and Figure 6). The mean organic content of beaver-pond deposits is 2·2%, which is significantly greater than the 0·7% mean organic content of overbank deposits ($T = 3{\cdot}22$, $p < 0{\cdot}001$). The Holocene beaver-pond deposits sampled in northern Yellowstone have a mean organic content of 2·7%, similar to those in GTNP, though this is quite variable among deposits. The $\delta^{13}C$ composition of all sediments is similar at around –24·8‰, indicating that not surprisingly, C3 plants that comprise GYE terrestrial woody vegetation are the principal source of organic matter stored in overbank and beaver-pond sediments. We hypothesized that beaver-pond sediments may have higher $\delta^{15}N$ values because organisms at higher trophic levels may be incorporated in deposits; however, no obvious differences exist between the $\delta^{15}N$ compositions of beaver-pond and overbank deposits, likely because any higher trophic-level organisms in beaver-pond deposits have a small total mass. Beaver-pond deposits have higher average C/N ratios than overbank sediments

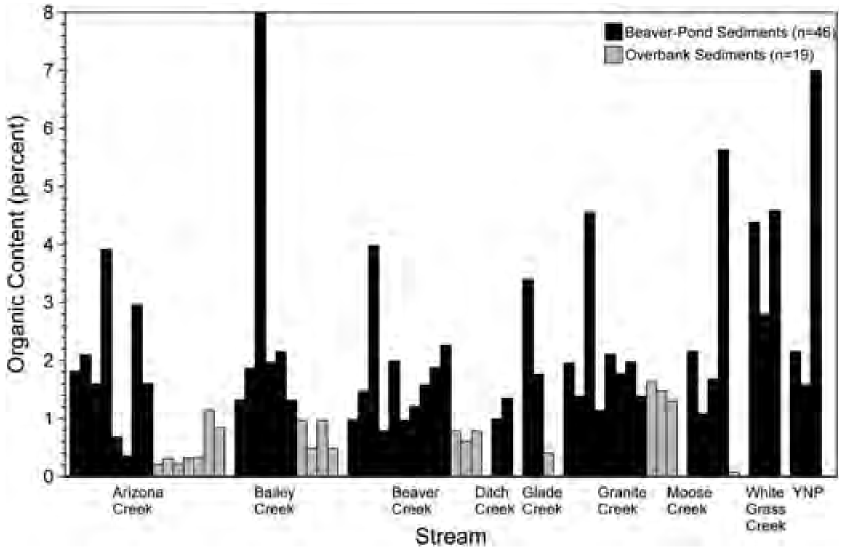

Figure 6. Organic carbon content of beaver pond and overbank deposits in GTNP, and three sites in northern YNP, by percent of total sediment mass. Beaver-pond sediments have a significantly greater mean organic content (2·2%) than overbank sediments (0·7%).

[beaver-pond mean = 16·1, standard deviation (SD) = 4·6; overbank deposits: mean = 11·9, SD = 4·6]. These means are statistically different ($T = 2{\cdot}8$, $p = 0{\cdot}003$).

Dating of beaver-pond deposits

Forty-nine beaver-pond deposits were ^{14}C-dated in GTNP (Table I). Six of the dated samples were of 'post-bomb' age, i.e. δ^{14}C values show that they contain excess ^{14}C from above-ground nuclear weapons testing and must be younger than 1950. The summed calibrated probability distributions for the remaining 43 ^{14}C ages are illustrated in Figure 7 as a proxy for relative changes in beaver activity within the Holocene. As in northern YNP (Persico and Meyer, 2009), we find that multiple ^{14}C dates from the same beaver pond deposit in GTNP have ages that are statistically indistinguishable within the dating errors (Table II). This generally supports the accuracy of the ^{14}C ages, and indicates that sediment accumulated rapidly in individual ponds that had a maximum lifetime less than a few hundred years. Calibrated ^{14}C ages for late Holocene beaver-pond deposits tend to cluster within three time periods in the late Holocene: 0–500, 1000–1700, and 2500–4200 cal yr BP (Figure 7).

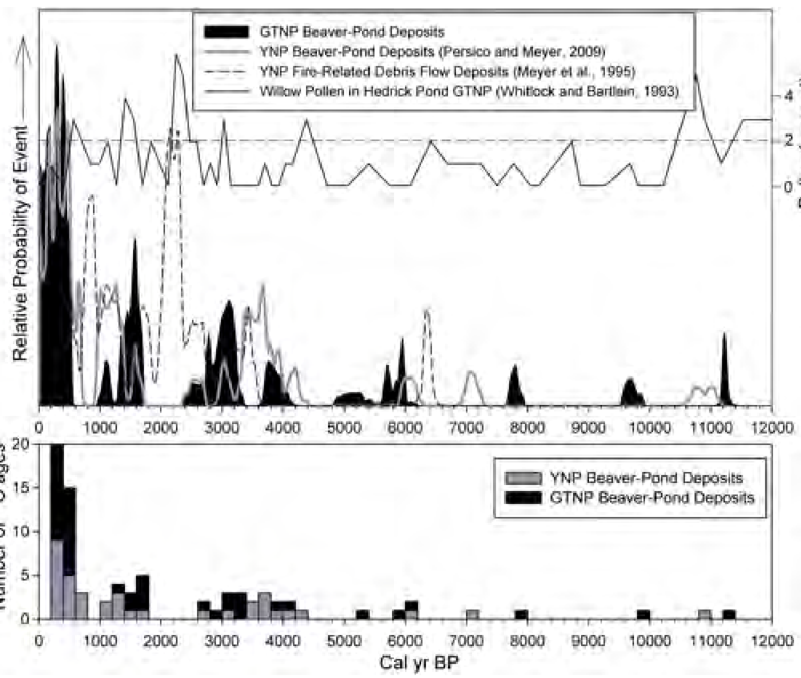

Figure 7. Chronology of ^{14}C-dated beaver-pond sedimentation in GTNP and YNP. Relative probability curves are derived by summing calibrated probability distributions for individual ^{14}C ages, where each age distribution has unit probability, reducing calibration artifacts as described in the text, and then smoothing the summation using a 70-yr running mean. Histogram shows the number of ages in each data set contributing to probability curves, placing the weighted mean of calibrated age distributions in 200-yr age classes. North-eastern Yellowstone fire-related debris flows are alluvial-fan deposits in high-relief terrain, inferred to indicate severe fires from extreme droughts (Meyer *et al.*, 1995); these debris-flow deposits are not found along the lower-relief beaver study drainages of Persico and Meyer (2009). The decline in frequency of ^{14}C dates with increasing age in beaver-pond and debris-flow deposits is in large part due to limited exposure and removal by erosion of older sediments.

Dating of terrace deposits

Discontinuous fill-cut terraces are present along Arizona Creek, Bailey Creek, and Glade Creek, the three largest GTNP study streams. Two sandy fill-cut terraces are preserved on Arizona Creek. The higher terrace (~2·5 m above the modern floodplain) is inset in fine-grained alluvial fan deposits of reworked deltaic material. The terrace deposit associated with this surface contains no macroscopic organic material and thus was not directly dated. However, a ^{14}C age of ~11 720 cal yr BP from the older alluvial fan deposits provides a broad maximum limiting age near the Pleistocene-Holocene boundary for the inset terrace deposit (Table II). The lower inset terrace varies from 1 to 2 m above the modern Arizona Creek floodplain. The terrace sediments contain beaver-pond deposits, and multiple ^{14}C ages place deposition between 2200 and 1500 cal yr BP. Along Bailey Creek, a single terrace is preserved ~2 m above the modern floodplain. Two ^{14}C ages bracket the terrace deposits to between 2750 and 2350 cal yr BP. Glade Creek terrace deposits are inset about 3·0 m above the modern floodplain in latest Pleistocene fine-grained paraglacial deposits, here dating to ~13 550 cal yr BP (Table II).

Unusually coarse gravelly deposits are associated with these post-glacial terraces in GTNP and also in YNP (Figure 1). These deposits are dominated by clasts of pebble to coarse cobble size that are minor to absent in either beaver-pond or overbank sediments, and often contain abundant charcoal. The coarse gravels contain little unburned organic material and have less than 5% clay. In GTNP, such deposits along Glade Creek and Arizona Creek are coarser than typical overbank deposits and modern stream channel gravel, and exceed 1 m in thickness. They were deposited ~820 cal yr BP on Glade Creek and ~2170 cal yr BP on Arizona Creek. Along Tower Creek in YNP, the terrace deposits have variable sediment sizes from sand to cobbles, similar to modern channel sediments, but contain abundant charcoal fragments and charcoal lenses, and were deposited ~600, ~990, and ~2560 cal yr BP (Table II). The deposits in GTNP and YNP have the form of both incised channel fills and sheet-like deposits with no distinct channel boundaries. The thickness, coarse variable sediment size, and charcoal content suggest that they were deposited during large flash floods following severe forest fires (Meyer *et al.*, 1995; Legleiter *et al.*, 2003).

Late Holocene and historical PDSI variability

Ten-year mean PDSI values reconstructed from tree rings for the past two thousand years in the GYE region (Cook *et al.*, 2004) have less variability than yearly historical values, as high year-to-year changes are averaged out (Figure 8). Nonetheless, 10-yr averages equal to moderate to severe drought in the PDSI classification appear in the record. The driest 10-yr period occurred from 802 to 793 cal yr BP during the Medieval Climatic Anomaly (MCA, ~1050–650 cal yr BP), with a mean PDSI value of –2·8, below the first percentile (Figure 8). In contrast, PDSI values derived from the 1895 to 2010 instrumental record show that during the period of documented beaver abundance in the 1920s, the 10-yr average is 0·9 (86th percentile); for the 10-yr period centered on the year 1912, the mean PDSI is 2·9

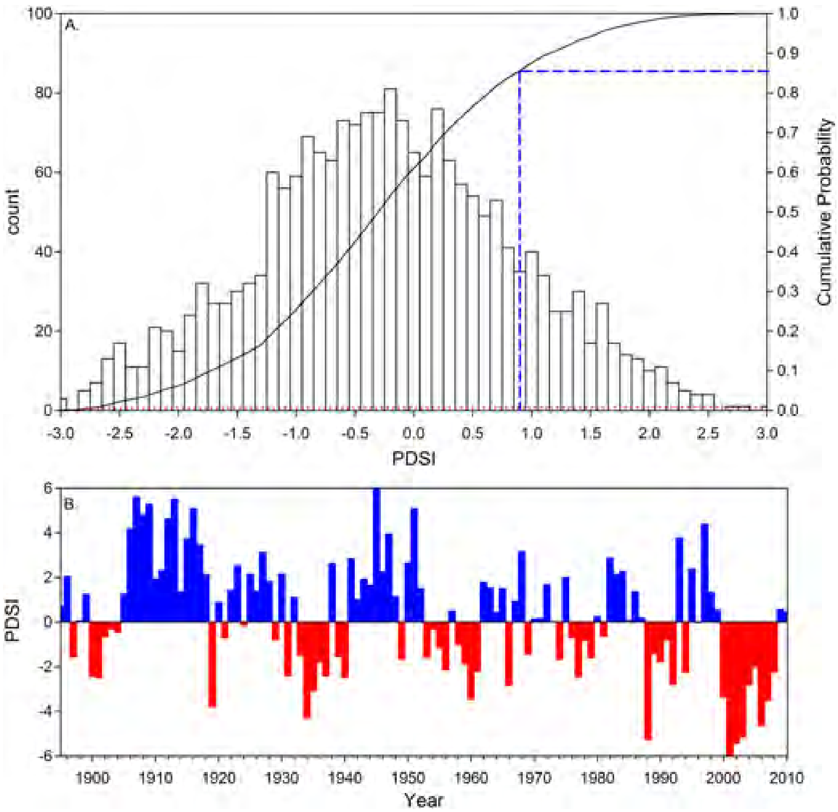

Figure 8. (A) Histogram of 10-yr averages of reconstructed PDSI values from tree-ring records in the western USA from 5 to 1993 CE (1945– –43 cal yr BP) for grid point 110 W, 45 N (Cook *et al.*, 2004). During the 1920s when beaver were abundant, the mean PDSI value was 0·9 (blue dashed line, 86th percentile) indicating unusually wet conditions. The most severe 10-yr drought during the Medieval Climatic Anomaly (802–793 cal yr BP) has a mean PDSI of –2·8 (red dotted line, < first percentile). (B) August mean PDSI values for 1895 to 2010 derived from Wyoming climate divisions 1 and 2. High PDSI values from 1904 to 1918 illustrate the wet period contemporaneous with abundant beaver in the GYE. Low PDSI values during the 1930s and 1950s–early 1960s indicate severe drought associated with a decline in beaver activity in the GYE. Note the most severe and prolonged drought of the record in the 2000s, when some small GYE streams that hosted beaver in the 1920s were observed to have ephemeral flow (Figure 10). This figure is available in colour online at wileyonlinelibrary.com/journal/espl

(99th percentile), highlighting the early 1900s as a prolonged, unusually wet interval.

Since the 1920s, periods of multiyear moderate to severe drought are the most notable features of the GYE instrumental climate record (Figure 8; Balling *et al.*, 1992; McMenamin *et al.*, 2008). In the 1930s 'Dust Bowl' drought, the driest 10-year mean PDSI was –1·6, and in the 1950s it was –1·2. The driest 10-yr mean PDSI in the shorter late 1980s–early 1990 drought was –0·4, although 1988, the year of the widespread and severe Yellowstone fires, featured the lowest summer (June–July–August) mean PDSI value of the instrumental record to that date (–6·0; Balling *et al.*, 1992). The severity of the 2000s drought even in a long-term context is clearly demonstrated by a 10-yr mean PDSI of –3·5. From 2001 to 2008, summer mean PDSI consistently fell between –2 and –6, and in Wyoming Climate Division 1 (Yellowstone Drainage, comprising northern YNP), monthly PDSI was between –6·0 and –9·7 indicating extreme drought in 63 of 96 total months.

Discussion

Interpretation of the records of GYE beaver-pond sedimentation, fluvial processes, climate variability, and human activity is organized into five subsections, beginning with beaver-pond sediment characteristics, and the role of beaver activity in overall Holocene sedimentation and valley-floor aggradation and incision. The last three subsections explore relationships between beaver activity, climate, stream processes, and human impacts, considering the range in variability within the Holocene as compared to that within the Euro-American historical period.

Organic content and C/N ratios of beaver-pond sediments

Organic content in Holocene beaver-pond sediments in GTNP is similar to that of unambiguous beaver-pond sediments documented by Persico and Meyer (2009) in northern YNP (Figure 6). GTNP beaver-pond sediments also have similar organic content to that measured by Wolf *et al.* (2007) in Holocene beaver-pond sediments in northern YNP and in active beaver ponds where beaver have been re-introduced north of the park. These similarities suggest that the observed range of organic content (0·3–8·2%) is representative of Holocene beaver-pond sediments on relatively high-energy small streams in the GYE. However, it is substantially less than in active ponds in Glacier National Park, where organic matter accounted for up to 50% of beaver-pond deposits (Butler and Malanson, 1995). The relatively low organic content of Holocene pond sediments in the GYE likely results from decay of organic material over centuries to millennia, especially in unsaturated, oxygenated settings, and may also result from less efficient trapping of organic material by beaver dams in the relatively high-gradient streams of the GYE. Nonetheless, GYE beaver-pond sediments are generally more organic-rich than overbank deposits (Figure 6) indicating that high organic content is a useful diagnostic criterion, and that beaver damming increases long-term storage of organic matter in terrace and floodplain deposits.

Beaver-pond deposits have a higher nitrogen content than fine-grained overbank deposits (means = 0·63% and 0·18% of the total sample mass, respectively, statistically significant, $T = 2{\cdot}46$, $p < 0{\cdot}02$). Because algae has more nitrogen than terrestrial organic matter, C/N ratios sometimes reflect the relative amounts of algae and terrestrial organic matter in water-lain sediments (Meyers, 1994). However, in the subset of samples analyzed for C/N ratios by mass spectrometry, beaver-pond deposits have much greater carbon than fine-grained overbank deposits (means = 9·02% and 1·33%, respectively; statistically significant: $T = 2{\cdot}99$, $p < 0{\cdot}01$). Mean total carbon content for this subset of samples is greater than those determined by LOI because they were sieved to < 1 mm in diameter, and organic material is concentrated in this fine fraction. The greater variation in carbon relative to nitrogen variation results in control of C/N ratios dominantly by carbon content, and higher C/N ratios in beaver-pond deposits. Although beaver ponds likely contain more algal organic material than is generated in a free-flowing channel (Naiman *et al.*, 1986), it is very likely overwhelmed by the abundant terrestrial organic material brought into ponds by beaver for both food and dam building. The relatively high C/N ratios of all beaver-pond sediments also indicate long-term storage of terrestrial organic matter. These data are preliminary, but suggest that C/N ratios in conjunction with organic content may be helpful in identification of beaver-pond sediments in similar fluvial environments.

Beaver-pond sediments and their role in Holocene fluvial sedimentation

Individual beaver-pond deposits in GTNP average 0·5 m in thickness, and at all sites total less than 2 m thick (Table I; Figure 2). The individual deposit thickness of Holocene beaver-related sediments in GTNP is consistent with northern YNP, where pond sediments average 0·5 m in thickness, and only 3 of 35 documented pond deposits are thicker than 1·0 m (Persico and Meyer, 2009). Net Holocene beaver-related sediment thickness in GTNP is not much greater than the measured depth of fine sediment in 26 modern beaver ponds in GTNP, which is between 0·08 and 0·33 m (Gribb, 2007). The thickest pond deposits in the GYE are in very low-gradient reaches resulting from glaciation, such as the moraine-dammed reach below Moose Pond (Figure 3), or the glacially scoured depressions in northern YNP (Persico and Meyer, 2009). Similarly, beaver in the Colorado Front Range have taken advantage of low-gradient moraine-dammed reaches (Ives, 1942; Kramer *et al.*, 2011), where dams can flood large areas and be maintained more readily than on steeper channels.

In stratigraphic sections where beaver activity was documented in GTNP, beaver-pond deposits make up 76% of the total sediment thickness, compared to 58% in YNP (Table I, Persico and Meyer, 2009). In a moraine-dammed valley in the Colorado Front Range, beaver-pond sediments comprise 30–50% of the total Holocene sediment volume, which consists of deposits 1–6 m deep (Kramer *et al.*, 2011; Polvi and Wohl, 2012). These values are not directly comparable, however, because we measured vertical thickness of deposits, not sediment volumes, and our data are derived from a variety of stream environments. Nonetheless, both studies demonstrate that beaver-pond deposits are an important component of Holocene floodplain sedimentation, particularly in relatively low-gradient glacially modified reaches. In northern YNP, lower-gradient reaches provide important beaver and riparian habitat, but the majority of the small-stream network consists of steeper reaches without evidence for beaver-related sedimentation (Persico and Meyer, 2009), highlighting the reach-specific nature of beaver influence on streams.

The limited net depth of beaver-pond sediments indicates that despite significant beaver-related sedimentation, net Holocene aggradation (i.e. vertical rise in stream channel level) due to beaver damming has been small and localized in the GYE, and has not in itself resulted in major valley filling, widening, or widespread smoothing of valley floors (cf. Ruedemann and Schoonmaker, 1938; Rutten, 1967). This is likely the result of (1) erosion of beaver-pond sediments by channel incision with dam failure or after abandonment, (2) erosion by lateral channel migration and floods, (3) intermittent beaver occupancy on any given stream reach during the Holocene, (4) increasing instability as relief increases between aggrading dammed reaches and undammed reaches below, and (5) the overall tendency of many stream reaches to incise over post-glacial time, especially during the late Holocene (Meyer *et al*., 1995; Persico and Meyer, 2009). Many GYE streams underwent major aggradation with glacial and paraglacial sediments in the latest Pleistocene (Pierce and Good, 1992), and typically, these streams have later downcut through these deposits within the Holocene (Meyer *et al*., 1995). As documented on Glade Creek and Arizona Creek in GTNP, early Holocene-latest Pleistocene paraglacial alluvial fan deposits grade to ~4 m above the current stream channel, with subsequent Holocene incision along these streams. At White Grass Creek, the position of ~11 000 cal yr BP beaver-pond deposits indicates net incision of about ~1·0 m since the early Holocene (Table I). Late Holocene terraces on Bailey Creek, Arizona Creek, and Glade Creek indicate that these streams have incised since ~2000 years ago. These examples of net incision in GTNP are also consistent with streams in northern YNP that commonly display Holocene terraces (Meyer *et al*., 1995; Persico and Meyer, 2009). There are, however, unincised reaches of the GTNP study streams that contain extensive 'beaver meadows', including along the low-gradient tributary of Bailey Creek that drains Arizona Lake, and the tributary of Cottonwood Creek that drains Moose Pond. These relatively wide, fine-grained, wet floodplains are in part the result of late Holocene beaver damming, along with glacial erosion and deposition that generated the initial broad, low-gradient valley reaches.

Natural range in variability

Beaver-pond deposit ages are distributed throughout the Holocene, but the bulk of dated deposition occurred within the last 4200 years (Figure 7). A decline in the number of dated deposits with increasing age is common to many ^{14}C chronologies of discrete geomorphic events, and is caused by both lack of exposure and erosion of older deposits (Schumm, 1991; Meyer *et al*., 1995; Persico and Meyer, 2009). Beaver-pond sedimentation in the early and middle Holocene is thus more difficult to assess in relation to climatic and environmental controls. In the early Holocene (~11 000 cal yr BP), willow pollen increased markedly in GYE pond sediments (Whitlock *et al*., 1995), potentially because deglaciated valley floors can be quickly colonized by willow (Nakatsubo *et al*., 2010). It may be speculated that increased willow abundance following deglaciation favored early Holocene beaver colonization in the GYE, but we have insufficient exposure of early Holocene sediments to test this. Seventeen stratigraphic sections in the GYE contain deposits of middle Holocene age, but only four beaver-pond deposit ages fall between 9500 and 4200 cal yr BP (Table II, Persico and Meyer, 2009). This suggests that beaver activity may have been limited by prolonged warmer and drier conditions in the middle Holocene (Whitlock and Bartlein, 1993; Shuman *et al*., 2009).

As in northern YNP, the majority of beaver-pond sedimentation in GTNP occurred after 4200 cal yr BP, and 89% of ^{14}C ages from both areas are younger than this date. Although the prevalence of beaver-pond deposits dating within the last 4200 years is at least partly an artifact of better preservation and exposure of younger sediments, it may also reflect an increase in beaver activity with the onset of generally cooler, wetter conditions of the late Holocene Neoglacial period. This climatic change is indicated by expansion of glaciers in GTNP (Mahaney and Spence, 1990) and the Rocky Mountain region in general (Luckman *et al*., 1993), along with an increase in spruce, fir, and pine in the southern GYE (Whitlock and Bartlein, 1993) and episodes of extensive lateral migration of stream channels in northern YNP (Meyer *et al*., 1995). During the Neoglacial, increased discharges and fewer ephemeral flows would have favored beaver populations in small GYE streams (Wolff *et al*., 1989).

Two noteworthy gaps appear in the record of beaver-pond sedimentation in GTNP, at 2400–1700 and 1000–500 cal yr BP (Figure 9). The absence of dated beaver-pond deposits cannot be interpreted as evidence for a total lack of beaver on the study streams during these intervals. However, beaver continuously bring new wood into ponds in the form of food caches and dam-building material, so that new ^{14}C-dateable material is introduced whenever beaver are present. Thus, the lack of dated pond deposits suggests that beaver activity on small streams is at least significantly decreased during these times. These gaps are contemporaneous with hiatuses in the beaver-pond record in northern YNP (Persico and Meyer, 2009), increased charcoal accumulation rates in lakes of the GYE (Millspaugh *et al*., 2000; Jacobs and Whitlock, 2008), low δ^{18}O values in Crevice Lake in northern YNP that reflect warm dry winters (Whitlock *et al*., 2008), and heightened fire-related debris-flow activity in north-eastern YNP, consistent with severe drought and warmer temperatures (Meyer *et al*., 1995).

The gap in dated beaver-pond deposits from 1000 to 600 cal yr BP coincides with the MCA, a time of widespread drought and high climatic variability in the GYE and the western United States (Meyer *et al*., 1995; Stine, 1998; Whitlock *et al*., 2003; Cook *et al*., 2004). Using PDSI values reconstructed by Cook *et al*. (2004) for northern Wyoming during the severe MCA droughts, Persico (2012) estimated average August discharge along stream reaches with documented Holocene beaver activity. The estimates indicate that during the MCA droughts, these streams experienced low and variable summer baseflow, with ephemeral summer flows in the smaller drainages. As conversion of ephemeral flows to perennial discharge is documented to increase beaver damming (Wolff *et al*., 1989), reduction of discharge to ephemeral flows likely limits the ability of beaver to maintain ponds. This inference is supported by the observation that some small northern YNP streams that supported beaver in the 1920s were ephemeral during recent summer droughts and have been entirely abandoned by beaver (Figure 10; Persico and Meyer, 2009). Decreased willow abundance in GTNP during the MCA (Jacobs and Whitlock, 2008) may also have limited beaver occupation (Figure 9).

During severe and prolonged droughts in the late Holocene, beaver-pond sedimentation on small streams was reduced concurrently in GTNP and YNP, as shown by similar gaps in both ^{14}C chronologies. Beaver-pond deposits are absent within these intervals even in stratigraphic sections with pond deposits that both pre-date and post-date the gap (Figure 4, Persico and Meyer, 2009). This concordance of records indicates that the generally greater GTNP precipitation and riparian vegetation relative to northern YNP was not sufficient to sustain beaver colonies and associated pond sedimentation on small GTNP streams during severe drought.

In severe or prolonged droughts, beaver may abandon small streams for more reliable flows and riparian habitat in higher-order reaches in the stream network. During severe drought in the 2000s, beaver population counts in Yellowstone showed an increase mainly along Slough Creek (Smith and Tyers, 2008). With a basin area of ~275 to 600 km^2 in its YNP reaches, Slough Creek is a much larger stream than those we studied elsewhere in the GYE, although it contains relatively low-gradient reaches between resistant bedrock knickpoints in its stepped glacial valley (Meyer, 2001). Smith and Tyers

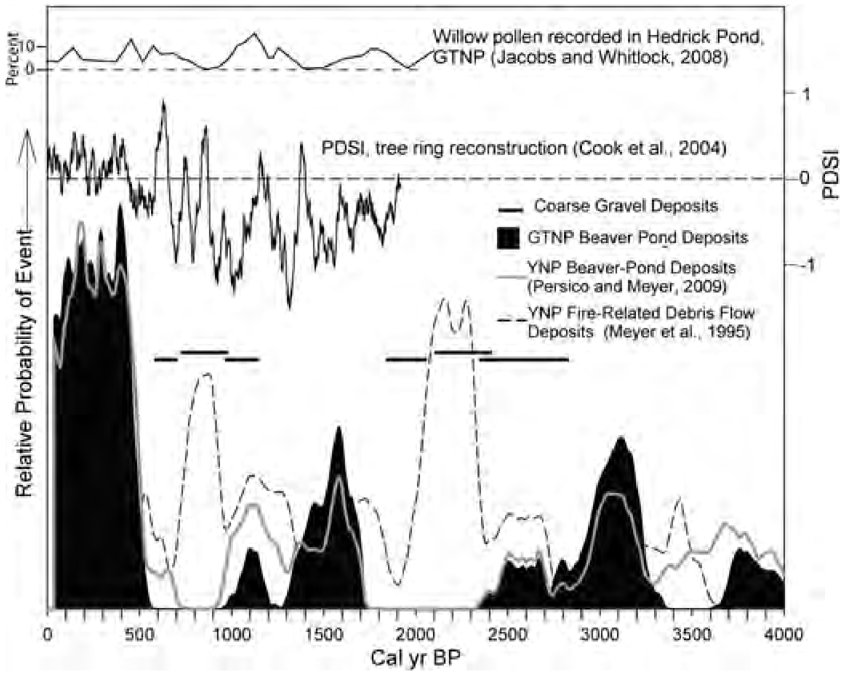

Figure 9. Chronology of GYE beaver-pond deposits for the past 4000 years. The relative probability summation is constructed as in Figure 7. Black horizontal lines show the 2σ calibrated age ranges for coarse gravel deposits inferred to represent fire-related flash floods on the streams of this study. Major peaks in north-eastern YNP fire-related debris flows *c.* 850 and 2100 cal yr BP (see Figure 7) correspond to minima in beaver-pond sedimentation, and the deposition of coarse gravel in both GTNP and YNP. Palmer Drought Severity Index (PDSI) reconstruction for grid point 110 W, 45 N from tree-ring records in the western USA was smoothed using a 70-yr running mean; negative values indicate drought. Sampling of willow pollen in late Holocene Hedrick Pond sediments by Jacobs and Whitlock (2008) is at greater resolution (~100 years) than that of Whitlock and Bartlein (1993) shown in Figure 7.

(2008) hypothesized that drought-reduced discharges enabled beaver to build new dams on Slough Creek and other larger streams where dams were not previously observed, because high peak flows during normal years would have removed them. During droughts within the MCA, discharge in larger streams was probably reduced for prolonged periods (Persico, 2012), such that a decline in beaver damming on small streams may have been accompanied by an increase in damming on larger streams. Beaver also inhabit burrows in banks of larger streams and rivers (Gurnell, 1998), which likely acted as refugia during prolonged severe drought. However, as low-order channels make up the great majority of stream length in the network, drought-related reductions to beaver habitat and associated riparian area along small streams represent a substantial and widespread impact in the GYE.

During the MCA and other intervals of severe late Holocene drought (e.g. ~2100 cal yr BP), thick channel fills and sheets of gravel were deposited along streams in both GTNP and YNP (Figure 9). The coarse sediments often contain abundant charcoal and at least in part are the result of large flash floods following severe forest fires, which increased markedly in the MCA (Meyer *et al.*, 1995). Charcoal is often not deposited with coarse sediment in fire-related floods on larger streams, however, so direct evidence for such floods may be lacking in some deposits. Channel incision is also associated with post-fire floods (Legleiter *et al.*, 2003). Rapid snowmelt and rain-on-snow events are likely more common in warmer climates in the GYE, and may also have promoted extreme flooding in the MCA (Meyer, 2001). Regardless of the specific cause of flooding, the thick gravelly deposits suggest that large flash floods and unstable channels may also have inhibited the ability of beaver to maintain dams during associated severe drought episodes. These large floods may also have flushed out stored pond sediment (Butler and Malanson, 2005).

Sustained periods of increased temperatures and scant precipitation, as during the megadroughts of the MCA, can have significant effect on ecosystems (e.g. Debinski *et al.*, 2010) that may persist longer than the climate event itself (Elias, 2003). During the driest intervals in the MCA, ephemeral streamflows, lowered water tables, and decreased snowpacks allowing greater winter elk browsing pressure may have combined to suppress willow and aspen. This vegetation may have recovered slowly, so that even though annual precipitation increased markedly from 675 to 600 cal yr BP (Gray *et al.*, 2007), no increase in GYE beaver activity is evident until about 500–450 cal yr BP. Although less pronounced than in the MCA, drought *c.* 600–500 cal yr BP (Meyer *et al.*, 1995; Cook *et al.*, 2004) may also have retarded riparian vegetation and beaver recovery. As sustained increases in precipitation can also be strong drivers of ecosystem change (Brown and Wu, 2005), a pronounced wet episode around 500–400 cal yr BP (Whitlock *et al.*, 2008) may have led to the initiation of large cohorts of willow and aspen (Gray *et al.*, 2007), and along with increased streamflows, contributed to the resurgence in beaver activity (Figure 9).

During the LIA (500–50 cal yr BP) in the GYE, climate variability was reduced significantly, with much less severe droughts relative to the MCA (Cook *et al.*, 2004). A cooler and effectively wetter LIA climate is indicated by decreased incidence of severe fire, floodplain widening on larger northern YNP streams, and multiple paleoclimatic proxies in lake sediment records (Meyer *et al.*, 1995; Whitlock *et al.*, 2008; Jacobs and Whitlock, 2008). This period is associated with abundant dated beaver-pond sedimentation in the GYE (Figure 9). Three peaks in beaver-pond sedimentation in GTNP occur at ~200, 300, and 400 cal yr BP, and match well with peaks in beaver-pond sedimentation in YNP (Figure 9). There is no obvious connection, however, between smaller changes in PDSI, willow and aspen pollen abundance, and beaver-pond sedimentation during this period (Figure 9). Nonetheless, the high frequency of beaver pond ages in the LIA may reflect optimal conditions for beaver, when streamflows were generally higher and climate variability was reduced relative to the MCA.

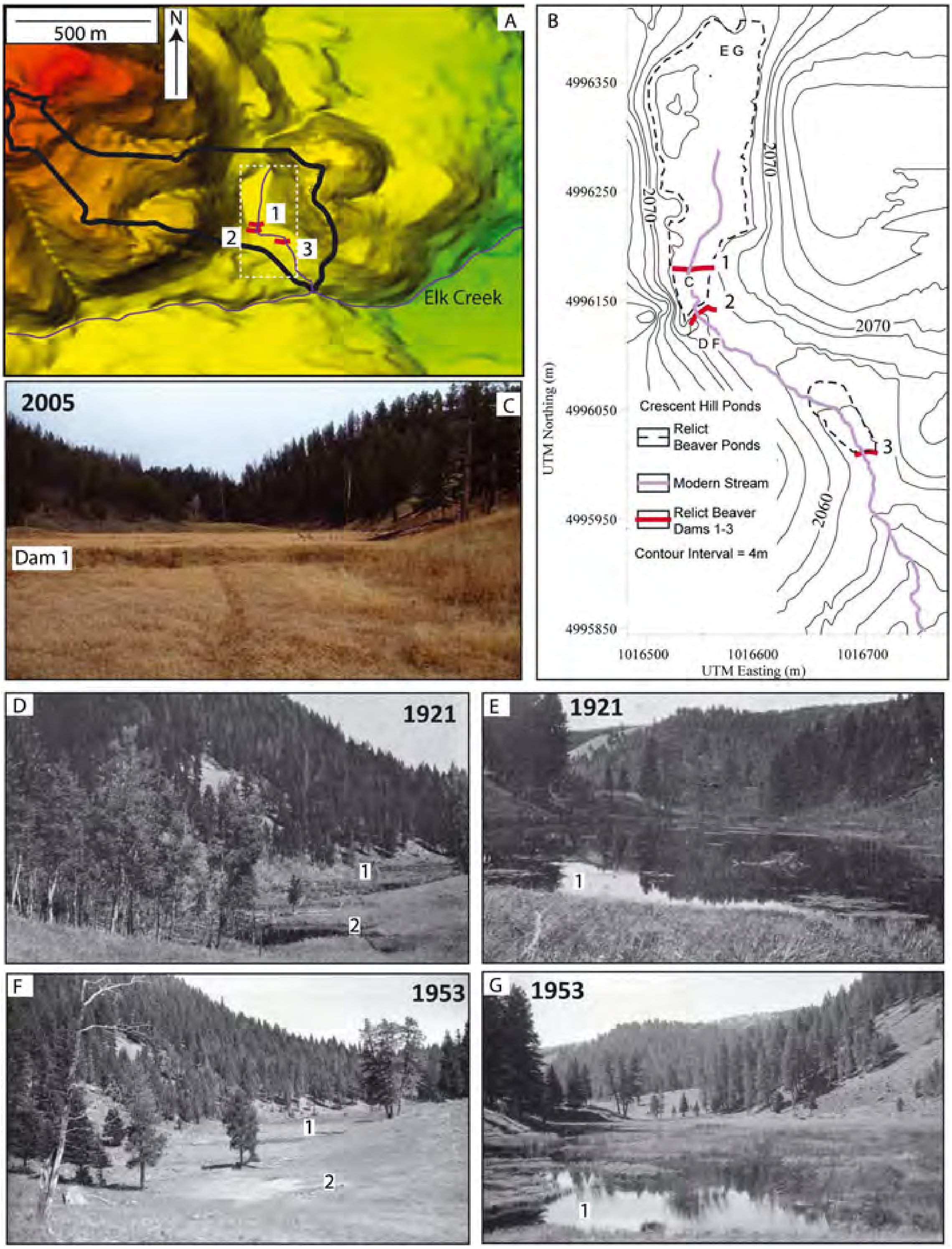

Figure 10. (A) Digital shaded relief map showing beaver dams (red lines 1–3) mapped by Warren (1926) during the 1920s near Crescent Hill in northern YNP, along an unnamed tributary of Elk Creek (purple line). Elevations range from about 1950 to 2380 m; warmer colors indicate higher elevations. Black line shows the small 0·1 km^2 drainage basin for the tributary. Dotted white line shows the location of topographic map B. (B) Location of active beaver dams 1–3 in 1921; 1 and 2 are shown in photographs D and E from Warren (1926). These dams were abandoned by 1953 (photographs F and G from Jonas, 1955). The location of photographs C, D, E, F, and G are also shown. (C) Photograph showing dry, vegetated stream channel below dam 1 in 2005. The stream is fed by springs emerging from a talus slope immediately west of pond 1, so no beaver ponds could exist above this area. No flow was observed in the stream below dam 1 during the summer months of 2004, 2005, and 2006, concurrent with severe regional drought. No willow or aspen currently exist along the channel. This figure is available in colour online at wileyonlinelibrary.com/journal/espl

Assessment of beaver activity in the 1900s with ^{14}C is complicated by the large relative magnitude of analytical errors, very large calibration uncertainties, and the spike in atmospheric ^{14}C concentrations from nuclear weapons testing in mid-century. However, some significance may lie in the observation that six ^{14}C ages in GTNP are 'post-bomb' dates younger than 1950 (Table II), whereas only two ages are younger than 1950 in northern YNP (Persico and Meyer, 2009), despite similar sampling methods and total sample numbers. The greater number of post-bomb dates in GTNP may reflect beaver re-introduction there in the early 1950s (Collins, 1976), which was not conducted in YNP. GTNP may also have been more favorable to beaver occupation throughout the 1900s, because of greater tall willow conducive to beaver dam building (Olechnowski and Debinski, 2008), and little elk winter range within the park (Figure 1). The contrast in beaver activity between the parks probably increased in the middle to late 1900s because of elk overbrowsing in northern YNP (Chadde and Kay, 1991), and other factors as discussed later.

Historical range in variability

Many aspects of the historical record show that beaver activity in the GYE has been impacted by both humans and climate since the onset of Euro-American activities in the region. Beaver populations were likely high at the start of the 1800 s, but were quickly reduced by trapping during the height of the fur trade in the early to mid-1800 s. By the end of the 1800 s, beaver populations had been depressed enough to warrant regulation of beaver trapping by the state of Wyoming, and beaver trapping was prohibited in YNP in 1883. Also, we infer that the extirpation of wolves, the beaver's main predator, initially contributed to the beaver resurgence in the early 1900s. We have observed that a number of ponds mapped by Warren (1926) in the 1920s and others in northern YNP were unusually small, and thus provided little protection from predators. Prior suppression of beaver populations by trapping may also have allowed regrowth of willows and aspen along streams, and regardless of the cause, a major episode of aspen regeneration occurred in northern YNP *c.* 1870–1880 (Romme *et al.*, 1995; Yellowstone National Park, 1997). Natural environmental changes almost certainly played a role in beaver recovery as well, especially markedly increased streamflows during the early 1900s (Graumlich *et al.*, 2003). Thus, by the 1920s, a combination of factors including the absence of wolf predation, limited beaver trapping, high streamflows, and abundant willow and aspen likely stimulated a dramatic expansion of beaver populations. This inference is supported by documented beaver dams on many small, steep stream reaches with limited evidence for prior occupation (Warren, 1926; Persico and Meyer, 2009). Beaver expansion apparently extended into marginal habitat in the 1920s; e.g. Warren (1926) observed a substantial beaver colony on a very small spring-fed tributary of Elk Creek in northern YNP near Crescent Hill (Figure 10), where beaver were using Douglas-fir bark for food because they had exhausted the readily available willow and aspen.

The cause of beaver extirpation from small northern YNP streams by the early 1950s has been the subject of prolonged debate. Some researchers have suggested that YNP policy of natural regulation (and in particular, the banning of human reduction of elk in the park) resulted in highly elevated elk populations, given the absence of wolves. In this view, the overwhelming factor in the decline of beaver was elk overbrowsing, which dramatically decreased the beaver's food and dam building resources (Chadde and Kay, 1991; Wolf *et al.*, 2007). However, as with the high beaver populations of the 1920s, it is likely that multiple factors were involved in the subsequent major decline of beaver. The impetus for Warren's (1926) study was the observation that beaver themselves were depleting aspen along streams in the Northern Range. Marginal beaver habitat where aspen is the primary food resource may be particularly susceptible to beaver extirpation, as aspen regeneration is much slower than willow regeneration (Beier and Barrett, 1987). As discussed earlier, both human and natural factors were involved in producing abnormally high beaver populations in the 1920s, which along with elk browsing contributed to aspen and possibly willow decline. During the 1950s, substantially reduced beaver activity relative to the 1920s was observed throughout YNP (Jonas, 1955), not just in the northern elk winter range where the effects of browsing were most prominent. Beaver decline in the mid-1900s extended to streams in GTNP (Wyoming Game and Fish Commission, 1950), which contains little elk winter range (Figure 1). The end of the early twentieth century wet interval and onset of the 1930s 'Dust Bowl' drought likely contributed to decreased beaver populations in the GYE, particularly outside of elk winter range.

Droughts of the late 1980s–early 1990s and in the 2000s have also limited streamflows and reduced the area of potential beaver habitat in the GYE. At the Crescent Hill location where several active beaver dams were documented by Warren (1926) in the 1920s, we noted that not only were beaver absent, but stream channels were entirely dry during severe summer drought in the 2000s (Figure 10). We have observed that flow in five other small, spring-fed tributaries of Elk Creek, Blacktail Deer Creek, Soda Butte Creek, and Slough Creek in northern YNP has turned ephemeral during recent summers, despite evidence along these streams for late Holocene and historic beaver damming and willow communities in the late 1800 s–early 1900s (Warren, 1926; Chadde and Kay, 1991). The source of streamflow in springs just upstream of the former beaver ponds means that the discharge reduction cannot be attributed to loss of water storage in beaver ponds upstream, and underscores the impacts of severe drought on these small streams and associated riparian habitat.

Historical versus natural range in variability

The Holocene record indicates that climatic variations altered fluvial processes and produced significant changes in beaver activity on small streams in the GYE (Table III). Dated terraces along Arizona Creek, Bailey Creek, Glade Creek, and several streams in northern YNP (Persico and Meyer, 2009) indicate episodic channel incision in the late Holocene, prior to the historical period. Thus, not all stream incision is related to historical beaver dam abandonment (cf. Wolf *et al.*, 2007). During the MCA, incised paleochannels and floodplains filled with unusually coarse sand and gravel, indicating a dramatic change in stream behavior, likely in part a result of extreme post-fire floods (Meyer *et al.*, 1995). Also during the MCA, severe droughts caused some small streams to become ephemeral (Persico, 2012) and beaver-pond sedimentation was minimal. Even during historical times, some climate variations have been large in a centennial to millennial context. For example, the early 1900s pluvial episode was among the wettest periods in the past 500 years (Cook *et al.*, 2011); in contrast, during the 'Dust Bowl' drought of the 1930s, stream discharge on the Yellowstone River was reduced to its lowest level in 300 years (Graumlich *et al.*, 2003). Severe droughts beginning in the late 1980s and early 2000s were also significant, even in the context of late Holocene drought variability (Balling *et al.*, 1992; McMenamin *et al.*, 2008; Persico, 2012). Along with the loss of flow in small streams that formerly held beaver colonies, the ~2001–2008 drought caused drying of a number of kettle ponds in northern Yellowstone, with associated loss of wetlands habitat and amphibians (McMenamin *et al.*, 2008). The historical droughts were not as prolonged as some megadroughts of the MCA, e.g. during the 50-year period from 925 to 875 cal year BP, the GYE region experienced only six years when the PDSI was above 1, and from 900 to 915 cal yr BP, the region experienced 13 years of continuous moderate to extreme drought (Cook *et al.*, 2004). Overall, historic climatic variations were substantial, yet they were also concurrent with major human influences on beaver, including intensive beaver trapping, wolf extirpation, and subsequent elk overbrowsing,

Table III. Factors favorable and unfavorable to beaver on small streams within key periods in the late Holocene.

	950–1450	1450–1900	1800–1900	1900–1930	1930–present
Anthropogenic					
Factors favorable to beaver	Elk harvest by Native Americans(?)	Elk harvest by Native Americans(?)	Beaver trapping declining over the mid- to late 1800s[a]	Regulated or banned beaver trapping, especially within National Parks; wolf extirpated so little predation of beaver[b]	Regulated or banned beaver trapping, beaver re-introduction in some areas outside YNP[d]
Factors unfavorable to beaver	Potential beaver harvest by Native Americans(?)	Potential beaver harvest by Native Americans(?)	Extensive beaver trapping by Europeans and Native Americans, especially in the early 1800s[a]	Wolf extirpation and hunting regulations promote increasing competition with elk for food resources, particularly in northern YNP winter range[,c,d]	Greatly increased competition with elk for food resources, particularly in elk winter range[c]
Climatic					
Factors favorable to beaver		Colder, effectively wetter climate of Little Ice Age[e]	Colder, effectively wetter climate of Little Ice Age[e]	Early 1900s pluvial, anomalously wet conditions[e]	
Factors unfavorable to beaver	Severe multidecadal droughts associated with the Medieval Climatic Anomaly[e]		Minor warming and mild drought episodes in late 1800s[e]		Strong warming trend and severe drought in the 1930s, 1950s, late 1980s–early 1990s, and especially 2000s[f]
Environmental					
Factors favorable to beaver		Perennial summer stream flows; relative willow abundance[j]	High perennial summer stream flows; abundant willow; aspen available and increasing with ‘ birthstorm’ *c.* 1870–1880[j]	High perennial summer stream flows; abundant aspen following birthstorm; abundant willow; no wolf predation[c]	No wolf predation until 1995, local increase of willows after 1995[m]
Factors unfavorable to beaver	Ephemeral streamflow during droughts, extreme forest fire-related floods, potentially decreased willow and aspen abundance[h,i]			Decreasing willow and aspen abundance[l]	Ephemeral stream flow during drought years, extreme forest fire-related floods, decreasing willow and aspen abundance[h]

[a]Schullery and Whittlesey, 1992;
[b]Collins, 1976;
[c]Chadde and Kay, 1991;
[d]Smith and Tyers, 2008;
[e]Cook *et al.*, 2004;
[f]Balling *et al.*, 1992;
[g]Graumlich *et al.*, 2003;
[h]Persico, 2012;
[i]Meyer *et al.*, 1995;
[j]Riparian vegetation conditions are unclear prior to beginning of photographic records in the 1870 s;
[k]Romme *et al.*, 1995;
[l]Warren, 1926;
[m]Wolf *et al.*, 2007.

making it difficult to entirely disentangle human and climatic effects (Table III).

Substantial Euro-American impacts from economic activities and management indicate that no single historical period such as the 1920s is representative of typical natural conditions in GYE streams, even though some researchers have suggested it as an appropriate reference period for YNP beaver activity (Chadde and Kay, 1991; Wagner *et al.*, 1995). In the future, humans will very likely influence beaver and stream habitats in the GYE through anthropogenic warming of climate as well. In the 1920s, the 10-yr average PDSI value was in the 86th percentile of values for the past 2000 years (Figure 8), highlighting the unusually wet conditions that produced high streamflows, even in a millennial context. In contrast, future streamflows in the GYE are likely to fall to opposite extremes at times compared with the 1920s, as regional models predict an increased probability of severe and prolonged drought in the coming century (Dai, 2011). Thus, it is probable that a greater number of small streams will become ephemeral and unsuitable for beaver colonization, as has already been observed in northern Yellowstone (Figure 10; Persico and Meyer, 2009), producing a landscape-scale reduction in riparian habitat.

Conclusions

Beaver-pond deposits in GTNP average 0·5 m in thickness and account for the majority of Holocene fluvial sedimentation at sites with evidence for beaver activity. The net thickness of less than 2 m of most beaver-related sedimentation indicates that beaver damming has not forced major valley aggradation, and along a number of streams, beaver-related sedimentation has occurred within the context of overall net Holocene incision of late Pleistocene and early Holocene deposits. However, the long-term influence of beaver is clearly evident in relatively thick, organic-rich fine-grained sediments along many small streams, and deposition of beaver-pond deposits accounts for 76% and 58% of Holocene sediments in stream reaches conducive to damming in YNP and GTNP, respectively. Clearly, beaver are important agents in promoting long-term fine sediment and organic material storage, greater wetted areas along small streams, and the growth of riparian vegetation.

Dated beaver-pond sediments span the entire Holocene, but a significant increase in beaver-pond sedimentation is evident in both GTNP and YNP *c.* 4200 cal yr BP. In both areas as well, gaps in beaver-pond sedimentation occurred between 2400–1700 and 1000–600 cal yr BP during periods of severe regional drought. During the MCA ~1050–650 cal yr BP, severe multidecadal droughts lowered stream baseflows and may have decreased riparian vegetation, which along with episodic large floods, limited the potential for beaver occupation on small streams. Abundant beaver-pond sedimentation 500–50 cal yr BP during the LIA reflects higher and more consistent streamflows and likely greater riparian vegetation growth, optimal for beaver.

Large beaver populations in the 1920s are likely the result of several human-caused and natural factors, including reduced beaver predation after eradication of wolves, regulation of beaver trapping, unusually wet conditions, regrowth of riparian vegetation during the preceding period of beaver trapping, and a marked increase in aspen regeneration. The decline of beaver that began before 1950 and which has largely persisted to today was promoted by overbrowsing of food resources by elk, particularly within the northern YNP winter range, in part a longer-term consequence of wolf extirpation. However, the loss of beaver is also likely related to food resource depletion by elevated beaver populations in the 1920s and episodes of prolonged and severe drought that began in the 1930s, and which have dominated GYE climate over the late twentieth century to present.

No period within historical times provides an appropriate reference period for natural variability in beaver and stream conditions in the GYE, as human activities have had a large effect on beaver throughout this period. In some periods, management actions combined with climate variations to enhance beaver populations, as in the 1920s, and in other periods, to suppress them, as from the 1930s to present. Natural variability is much better expressed over pre-historic late Holocene time, when climatic controls on beaver activity are very clear. In particular, long-lasting and severe droughts produced concurrent gaps in the late Holocene record of dated beaver-pond sedimentation across the GYE. These gaps likely represent greatly lowered populations along small streams due to reduced and ephemeral streamflows. Severe droughts of the late twentieth century to present have also had negative impacts on flows and beaver on low-order streams throughout the GYE, as they did during the late Holocene droughts. The prospect of increasing temperatures and prolonged, severe drought in the future indicates that further reductions in small-stream beaver habitat are likely. Although beaver may move to larger streams as flows decline, the loss of beaver-enhanced riparian areas on small streams would result in widespread reductions to some of the most diverse and productive habitat of the GYE landscape.

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