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A Holocene record of vegetation change and mountain pine beetle outbreaks at Lake of the Woods, Montana, USA

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Abstract.—Recent mountain pine beetle (*Dendroctonus ponderosae*) outbreaks have been characterized as unprecedented largely in the absence of information about their occurrence prior to historical documentation. The ability to reconstruct presettlement outbreaks from sediment cores requires the identification and validation of appropriate proxies. In this paper, we provide a Holocene record of vegetation change indicating putative mountain pine beetle outbreaks in a lodgepole pine (*Pinus contorta*)/mixed-conifer forest at Lake of the Woods, Montana. Using a normalized difference pollen index, we positively identified postsettlement mountain pine beetle outbreaks, which served as calibration points for identifying other outbreaks through the Holocene. The Lake of the Woods record indicates that vegetation change was being driven primarily by precipitation and that the multiple reconstructed contemporary and presettlement mountain pine beetle outbreaks occurred during periods when the forest composition was dominated primarily by *Pinus* spp. The occurrence of one of these outbreaks at ~8200 cal yr BP is coincident with 2 other records from the Northern Rockies, suggesting a large regional outbreak at this time.

Resumen.—Los recientes brotes de escarabajos del pino de montaña (*Dendroctonus ponderosae*) se han caracterizado por no tener precedentes, en gran medida por la ausencia de información sobre su aparición antes de la documentación histórica. La capacidad de reconstruir brotes previos a los asentamientos, a partir de núcleos de sedimentos requiere la identificación y validación de indicadores apropiados. En este trabajo, proporcionamos un registro del cambio de la vegetación durante el Holoceno que indica posibles brotes del escarabajo del pino de montaña en un bosque de pino lodgepole (*Pinus contorta*) y de coníferas mixtas en Lake of the Woods, Montana. Utilizando un índice de diferencia de polen normalizado, identificamos positivamente brotes de escarabajos del pino de montaña posteriores al asentamiento, que sirvieron como puntos de calibración para identificar otros brotes a lo largo del Holoceno. El registro obtenido de Lake of the Woods indica que el cambio de la vegetación fue promovido principalmente por las precipitaciones y que los múltiples brotes de escarabajos del pino de montaña reconstruidos, contemporáneos y anteriores al asentamiento, se produjeron durante períodos en los que la composición del bosque estaba dominada principalmente por *Pinus* spp. La aparición de uno de estos brotes en ~8200 cal yr BP es consistente con otros dos registros en las Rocosas del Norte, lo que sugiere un gran brote regional durante esta época.

The scientific community and general public are increasingly interested and aware of the impacts of mountain pine beetle (MPB; *Dendroctonus ponderosae,* Coleoptera: Curculionidae, Scolytinae) in pine (*Pinus* spp.) forests of western North America. The heightened visibility of MPB is due to the many large-scale outbreaks that have occurred in recent decades (Aukema et al. 2006, Meddens et al. 2012, Hicke et al. 2016). Widespread tree mortality has disrupted the function and provision of many critical ecosystem services (Morris et al. 2017, Cottrell et al. 2020).

Recent studies have largely focused on climate as a primary driver of MPB outbreaks (e.g., Sambaraju et al. 2012, Buotte et al. 2016, Bentz et al. 2019). However, a growing body of forest ecology literature seeks to quantify the complex interactions among fire, climate, MPB outbreaks, and natural resource management activities (Jenkins et al. 2008, 2014, Klutsch et al. 2009, Kulakowski and Jarvis 2011, Simard

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et al. 2011, Hicke et al. 2012). A limit to existing research is that it has focused only on known outbreaks that have been observed during the last ~100 years (Waller 2013). Yet, there is a growing need to contextualize these disturbances over longer timescales (Brunelle et al. 2008, Morris et al. 2015b). Currently, few effective approaches for developing long-term histories are available. Dendrochronological approaches have been used to identify the timing of past beetle mortality events in some landscapes (e.g., Perkins and Swetnam 1996, Larson and Kipfmueller 2010) by collecting and dating the last annual ring developed by a tree before it was killed by beetles. Dendrochronological approaches to reconstructing past outbreaks are limited, however, by the rate of decay or degradation of killed trees, and their persistence on the landscape over time. To improve our understanding of MPB outbreak recurrence and fire and climate interactions, longer temporal records are needed.

Paleoenvironmental reconstructions from lake sediment records are an important approach that can provide detailed information about the interactions of climate, disturbance regimes, and ecosystem composition over centennial to millennial timescales (Willis et al. 2010). Such studies are increasingly recognized for their importance in landscape management to track changes in ecosystem services, conserve biodiversity, bolster ecological resilience, and develop restoration strategies (Jeffers et al. 2015, Davies et al. 2018, Słowiński et al. 2019). Recent paleoecological research has concentrated on understanding the relationships among fire, climate, and bark beetle outbreaks (both MPB and spruce beetle, *Dendroctonus rufipennis* (Kirby, 1937) (Coleoptera: Curculionidae, Scolytinae) over longer time periods in the western United States (Brunelle et al. 2008, Gage 2008, Watt 2008, Morris et al. 2010, 2015b, Watt and Brunelle 2020). This growing body of literature, which is focused on the reconstruction of bark beetle disturbances, is important for several reasons. First, these records provide ecological information that predates the arrival of European influence in western North America. Prior to this era, human impacts are thought to be relatively minimal compared to present-day impacts (Jenkins et al. 2014). Second, reconstructing successive disturbance events over longer timescales permits quantification of the drivers and potential interactions of fire and MPB outbreaks on forest succession and dynamics. Third, by reconstructing multiple disturbances, researchers can better understand the ecological impacts of single events, multiple events, and the legacy of disturbance regimes over much longer timescales (McLauchlan et al. 2013).

MPB and several other *Dendroctonus* spp. are native to western North America, have coevolved with conifer forests, and act as important drivers of ecosystem processes (Logan and Powell 2001, Fettig et al. 2007, Axelson et al. 2018). *Dendroctonus* beetles mostly complete their life cycle under the bark of host trees, except when adults emerge to select new potential hosts (Bentz et al. 2010). Endemic MPB populations are usually present in pine forests, causing mortality of relatively few trees (Gibson et al. 2009). At epidemic population levels, MPB can kill many thousands of individual trees across a landscape (Williams 2006, Raffa et al. 2008).

Climate is an important driver of the severity and synchrony of recent bark beetle outbreaks (Raffa et al. 2008, Bentz et al. 2010). A warming climate system directly affects bark beetles in 2 important ways. First, as poikilotherms, bark beetles are able to develop more quickly during periods of sustained warmth (Bentz and Powell 2014). Second, cold-induced mortality tends to decrease in response to ameliorating winter temperatures (Bentz et al. 2010, Weed et al. 2015). Warming trends also indirectly promote outbreaks through drought (Kolb et al. 2016). Attacked trees are capable of repelling colonizing beetles by flushing entry wounds with resin, but moisture stress can diminish the ability of trees to respond with defensive compounds (Anderegg et al. 2015). Stand structure and composition are also important determinants of outbreak severity. For example, monotypic, single-age lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) stands that result from logging, stand-replacing fires, and fire suppression may enhance landscape risk to high-severity outbreaks (Fettig et al. 2007), but the lack of long-term records makes it difficult to confirm this assessment (Brunelle et al. 2008).

Only 2 paleoecological records have recovered fossil MPB remains from lake sediment cores (Brunelle et al. 2008), which are suggestive of past bark beetle disturbances. Reports from modern, high-severity outbreaks have documented substantial accumulations of beetle carcasses in the littoral zone of high-elevation lakes (Schmid and Frye 1977), lending support for linking the recovery of beetle remains in lake sediments with outbreaks. However, multiple studies conducted in beetle-affected watersheds have not been able to reproduce these results, calling into question the validity of using only beetle remains to reconstruct outbreaks (Morris et al. 2015a).

Some recent work suggests that preserved insect remains may still have potential for reconstructing forest insect disturbances. For example, Navarro et al. (2017) reconstructed spruce budworm (*Choristoneura fumiferana* Clemens) outbreaks using wing scales recovered from lake sediments. The lack of subfossil beetle remains reported by Morris et al. (2015a) could be due to taphonomic or phenologic controls. Specifically, bark beetles spend a relatively brief time outside of the tree (compared to spruce budworm), which may result in few opportunities for remains to enter depositional environments (Morris et al. 2015a). Due to these and other potential limitations, pollen and biogeochemical indicators have also been analyzed to track bark beetle outbreaks in conifer forests (Morris et al. 2010, 2013, 2015b, Morris and Brunelle 2012).

Pollen has been recognized as a key proxy for reconstructing insect and pathogen disturbances in lake sediment records (e.g., Allison et al. 1986, Stivrins et al. 2017). Recent work has used changes in host/non-host pollen abundances to calculate a normalized difference pollen index (NDPI) that tracks vegetation change associated with bark beetle outbreaks (Morris and Brunelle 2012). In subalpine spruce-fir forests, only Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) is impacted by spruce beetle, while subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) is unaffected by the beetle. The decline in spruce pollen and the reciprocal increase in fir pollen is statistically significant and shifts by a factor of 2:1 in response to a severe outbreak with >90% spruce mortality (Morris et al. 2013). Watt and Brunelle (2020) analyzed the potential for calculating host to non-host NDPI to detect MPB disturbances in a pine ecosystem. Despite the dominance of pine pollen (>80%) in these systems, Watt and Brunelle (2020) confirmed in a calibration study that severe MPB outbreaks were detectable by calculating the NDPI.

Here, we present an application of the NDPI to a pollen record collected from a lake site surrounded by a pine/mixed-conifer forest. This study also provides a Holocene record of vegetation change and fire history, and contributes to our understanding of a putative regional MPB outbreak (Brunelle et al. 2008) that occurred in the northern Rocky Mountains likely in response to the 8200 cal yr BP climate event (Alley et al. 1997). This paleoecological reconstruction enables us to assess the role of MPB in the context of long-term vegetation and climate dynamics.

SITE DESCRIPTION

Lake of the Woods (45°34.940′N, 113° 14.111′W) is located in the western Pioneer Mountains (Fig. 1) at an elevation of 2575 m. The Pioneer Mountains are situated on the eastern side of the Northern Rocky Mountains, in central western Montana, USA, on the Beaverhead National Forest. The Pioneer Mountains span an elevational gradient from 1600 to 2850 m above sea level (Cooper et al. 1999), and Lake of the Woods occurs at an elevation of 2575 m. The northwestern margin of Lake of the Woods is steeply sloped with a small inlet that feeds the lake from a small pond higher in elevation. The maximum water depth was determined to be 9 m in July 2009. Vegetation composition in the watershed consisted of a mixed-conifer forest type composed of whitebark pine (*Pinus albicaulis* Engelm.), lodgepole pine, Engelmann spruce, and subalpine fir. Understory vegetation included grouse whortleberry (*Vaccinium scoparium* Leiberg ex Coville), silky lupine (*Lupinus sericeus* var. *sericeus* Pursh), and bear grass (*Xerophyllum tenax* [Pursh] Nutt.). The west side of the lake is bound by a steep sloping ridge, and the east side is relatively flat and currently has a camping area. A severe MPB outbreak recently (2008–2015) occurred in the watershed, and there was evidence of a severe outbreak earlier in the twentieth century (1920s and 1930s) (Fig. 2) (Margoles 2011, Jenne and Egan 2019).

METHODS

Two sediment cores were collected from Lake of the Woods in July 2009 (LoW-10-A)

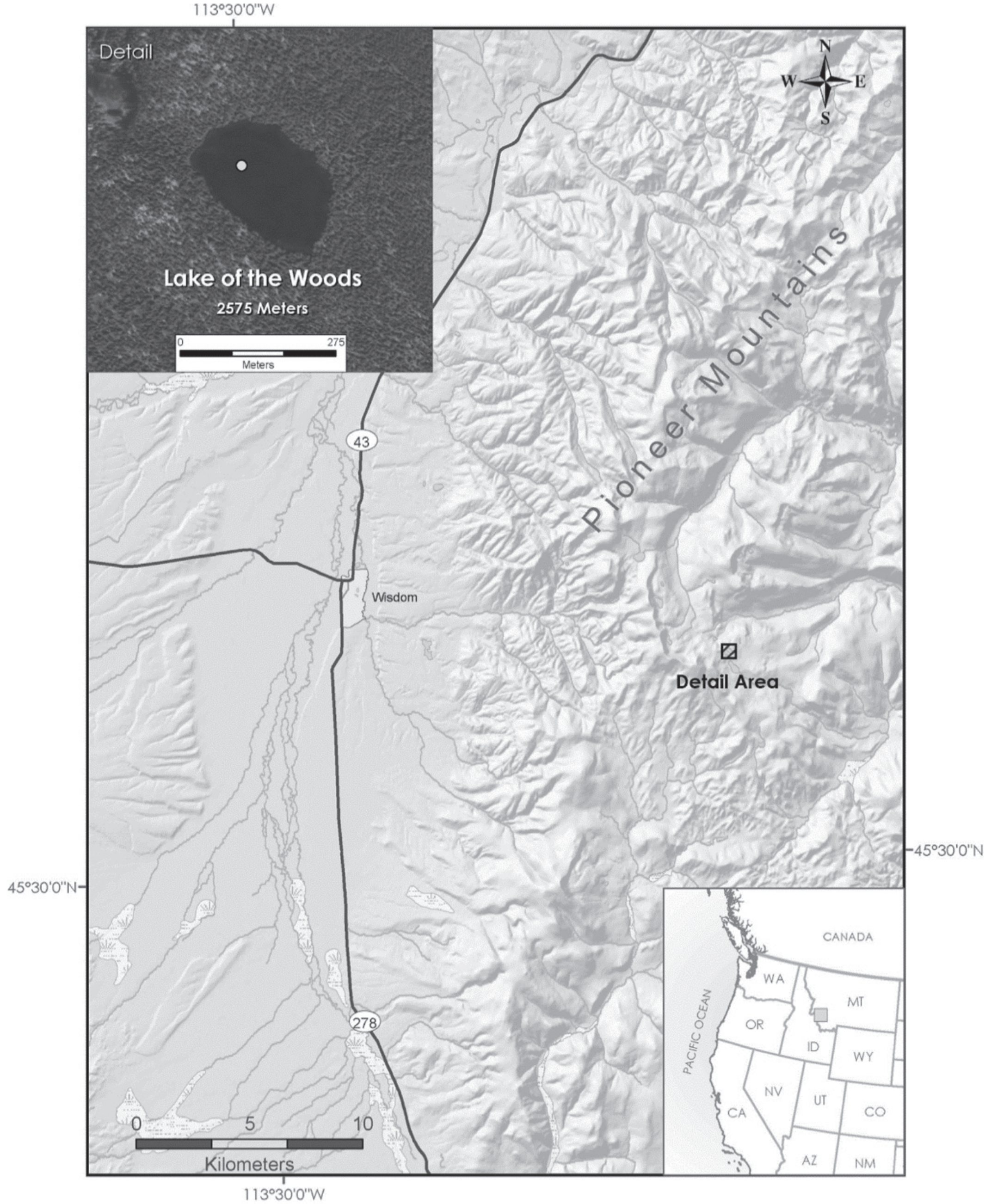

Fig. 1. Detailed location of Lake of the Woods, Montana, USA, at 2575 m elevation.

and September 2010 (LoW-09-C) using Klein and Livingstone coring devices, respectively. Sediments from LoW-10-A were subsampled at 1-cm intervals in the field and then placed in labeled whirl bags and stored in a cooler during fieldwork. LoW-09-C was wrapped in plastic wrap and aluminum foil and placed in a core box for transport to the Records of Environment and Disturbance (RED) Lab at the University of Utah. In the lab, the LoW-09-C core was subsampled into 1-cm increments and then placed in whirl bags.

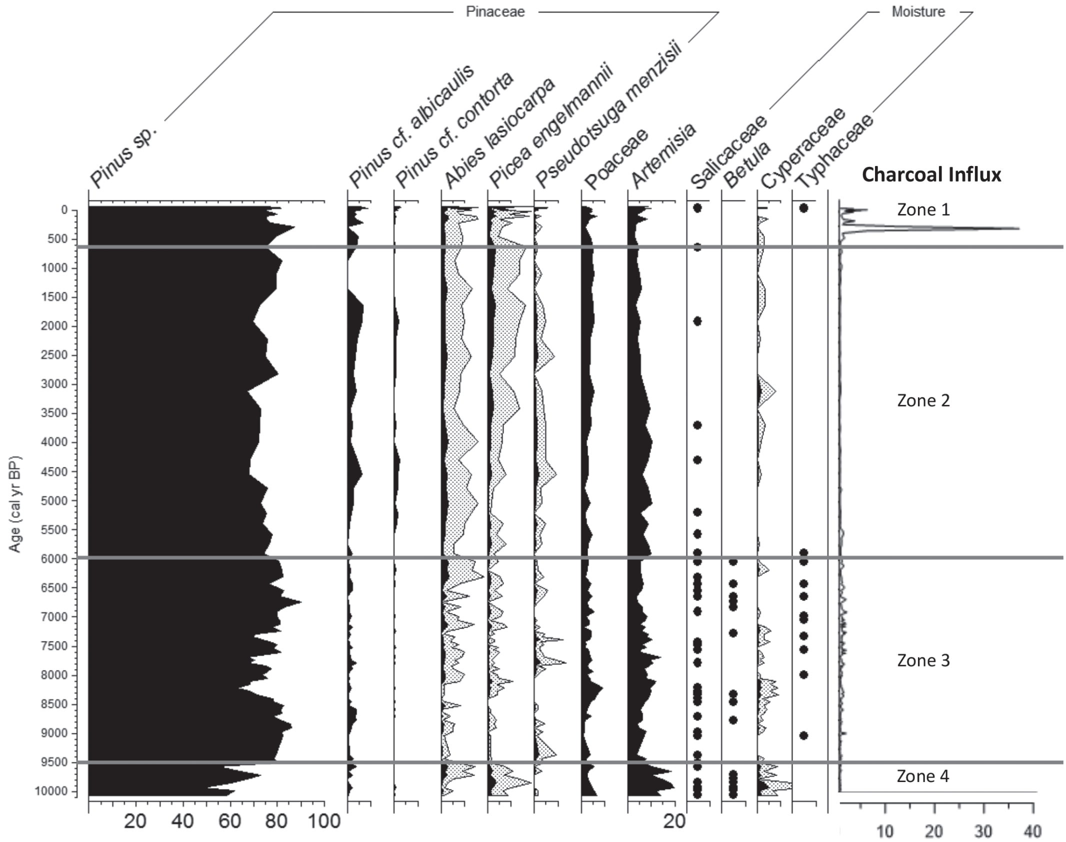

Fig. 2. Lake of the Woods Holocene pollen data presented in percentages (major tick marks at intervals of 10 percentage points, minor tick marks at intervals of 5 percentage points). Shaded curves over solid represent a 5× exaggeration to show detail. Dots indicate presence of rare pollen types. The zones are indicated on the right-hand side of the figure. On the right are the charcoal data plotted as influx.

The top 40 cm (LoW-10-A) was submitted for plutonium dating (Pu-239/240) and sent to the Ketterer lab at Northern Arizona University (Ketterer et al. 2004). Two charcoal particles from the depth of 92 cm (Low-09-C 92 cm and LoW-10-A 92 cm) and one schultzed[1] pollen sample (Kapp et al. 2000) from 340 cm were submitted to the Center for Applied Isotope Studies (Table 1) for radiocarbon (C^{14}) analysis. The Mazama tephra layer was identified at 223 cm depth and used as an age marker (7684 cal yr BP; Zdanowicz et al. 1999) in calculating the age-depth model (Table 1).

The Lake of the Woods chronology was produced from 2 overlapping sediment cores (LoW-09-C and LoW-10-A) that totaled 380 cm in length (Table 1). LoW-09-C was 288 cm long (92 to 380 cm) and LoW-10-A was composed of 120 cm of sediment (1–120 cm). Two samples were dated using radiocarbon from a depth of 92 cm—one from LoW-10-A and one from LoW-09-C. Both samples dated to the same radiocarbon age with the same error range (Table 1). The decision to use the depth of 92 cm to join the short (LoW-10-A) and long core (LoW-09-C) was based on the identical dates at this depth, and therefore samples from 1 to 92 cm were from LoW-10-A and samples from 93 cm to 380 cm were from LoW-09-C.

The resulting age model was generated in CLAM (Blaauw 2010) using a smoothing spline with a smoother of 0.2 and a goodness-of-fit equal to 9.8. The smoothing spline was the best choice for the number of available dates

[1]Pollen extractions for radiocarbon analysis were processed using a dilute Schultze solution of 10% $KClO_3$ and 35% HNO_3 (Gray 1965).

TABLE 1. Age reported at 1 cm was the year the core was collected, and age reported at 14 cm represented the Plutonium peak identified by Mike Ketterer at Northern Arizona University, Flagstaff, Arizona (Ketterer et al. 2004, Ketterer and Szechenyi 2008). Age at depth 223 cm was Mazama Ash tephra (Zdanowicz et al. 1999). Cal yr BP refers to calibrated years before present. ^{14}C refers to uncalibrated radiocarbon dates.

Depth (cm)	Core	Lab number	Material	Age (^{14}C yr BP)	Age (Cal yr BP)
1	LoW-10-A	Surface			−60 (AD 2010)
14	LoW-10-A	Pu peak	Bulk Sediment		−13 (AD 1963)
92	LoW-10-A	CAIS7907	Needle	3739 ± 20	4044
92	LoW-09-C	CAIS7906	Needle	3840 ± 25	4044
223	LoW-09-C	Zdanowicz et al. (1999)	Mazama Ash	6845 ± 45	7684
340	LoW-09-C	CAIS8669	Pollen	8410 ± 30	9444

and incorporated all dates. Interpolation to the bottom depth of the core indicated that the LoW record represented the last ~10,000 cal yr BP. The Lake of the Woods record was very highly resolved, varying over the course of the record from 3 years/cm in the recent portion of the record to an average of ~25 years/cm over the early and middle Holocene segments.

Plant macrofossils and charcoal were identified and counted at 1-cm intervals for both Lake of the Woods cores (LoW-10-A and Low-09-C) after the sediment was sieved through 2 nested sieves (125 and 250 microns). Macroscopic charcoal was used to reconstruct local fire episodes in the watershed, using conventional methods (Whitlock and Larsen 2002, Brunelle and Anderson 2003, Brunelle et al. 2005). CharAnalysis software (Higuera et al. 2007) was not used because the charcoal data set did not meet sufficient minimum criteria to warrant further analysis (Kelly et al. 2011) due to the low charcoal counts at this site. Plant and insect macrofossils were scarce and therefore not included in the analysis.

Pollen data from the Lake of the Woods cores were used to determine both local and regional vegetation change over time associated with climate variability and disturbance. Standard procedures for pollen extraction and identification were followed (Fægri et al. 1989), and 1 cm^3 was processed at every 1 cm from 1 to 24 cm depth, then every other centimeter from 24 to 48 cm, and then every 4 cm from 48 to 380 cm. This sampling resolution provides a continuous record of vegetation change. Tilia software was used for analyzing and plotting pollen counts, and data are reported in percentages of total pollen (Grimm 1987).

To track the reciprocal shift between host and nonhost conifers associated with an MPB outbreak, the NDPI—i.e., NDPI = [pine − (spruce + fir)]/[pine + (spruce + fir)]—was calculated and plotted over time. Morris and Brunelle (2012) found a distinct change in the NDPI of spruce and fir between nonoutbreak and outbreak years. Watt and Brunelle (2020) determined that this same method could be applied in lodgepole pine–dominated forests to detect MPB outbreaks. Watt and Brunelle (2020) used historic records, such as U.S. Forest Service reports and documents, to constrain the years during which an outbreak occurred. For Lake of the Woods, we confirmed the timing of a late 1920s MPB outbreak with historic documents (Jenne and Egan 2019) and dendrochronological dating of dead pines remaining in the watershed (Fig. 2) (Margoles 2011).

To reduce the complexity of a multitaxon record into fewer uncorrelated indices that were representative of the different potential vegetation communities (Ter Braak and Prentice 1988), we used principal component analysis (PCA) to identify statistically distinctive taxa, represented by significant principal components, and we quantified temporal trends in pollen composition. In this environment, the spectrum of *Artemisia* to Poaceae likely represented the amount of effective moisture (Williams et al. 2006), and we interpret PC2 as an index of available moisture. The results of the PCA analysis suggested that the dominant signal in the pollen data (PC1) is driven by variations in pine abundance, which account for a large proportion of the variance (83%). Given this, we instead focus on the second PCA axis (PC2), which was associated with variations in *Artemisia* spp. and Poaceae. Williams et al. (2006) provide pollen-based climate envelopes for a suite of taxa. When examining the climate

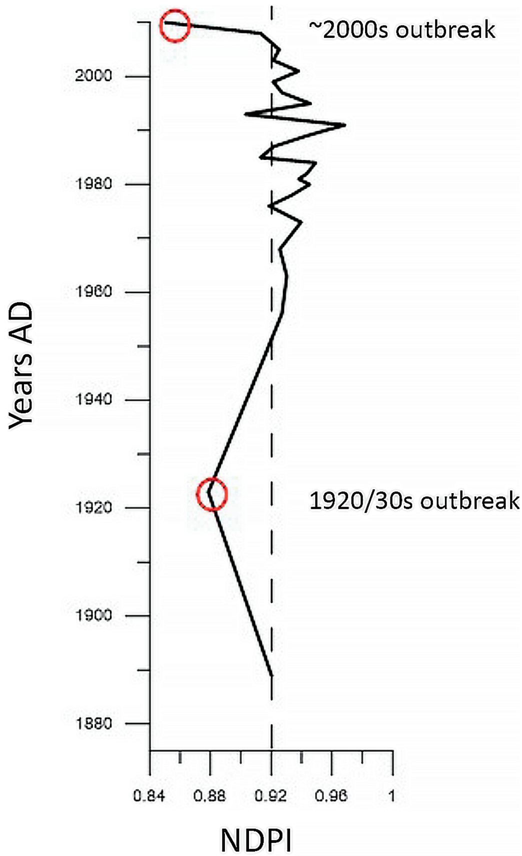

Fig. 3. Normalized difference pollen index (NDPI) of pine to spruce + fir plotted over time for the last 150 years (cal yr BP). Red circles indicate the timing of the 2 known MPB outbreaks in the postsettlement time period.

envelopes for *Artemisia* and Poaceae, the difference is mainly characterized by the amount of annual precipitation they require and their moisture indices. A comparison (ratio) of these 2 taxa was used as a proxy for effective moisture over the Lake of the Woods record.

Zones were determined visually by identifying distinctive shifts in the NDPI and the significant principal components. A constrained cluster analysis program (CONISS) (Grimm 1987) was applied to pollen percentages but was not used in determining zones because the pollen percentage data did not adequately identify the main vegetation shifts due to the regional dominance of pine in the record. For the purpose of comparing the MPB outbreaks of the late 1920s and early 2000s as a calibration for the rest of the record, Zone 1 was considered to be representative of the late Holocene, and subsequent zones were defined in chronological order back in time.

RESULTS

Pollen percentages at Lake of the Woods were dominated by pine (often greater than 85%) and were not used for further interpretation (Fig. 2). The NDPI identified the documented (historical documents) 1920s and 2000s outbreaks (Fig. 3). The results showed an increase of spruce + fir coupled with an associated decrease in pine, which suggested that pine mortality resulted from a disturbance agent that was not universally impacting other conifers (i.e., MPB outbreak as opposed to fire).

The first 2 PCA axes (i.e., PC1, PC2) accounted for 83% and 6% of the total variance in the pollen data, respectively. However, the trends shown on these axes did not correlate with the NDPI trends (R^2 = 0.0159), which suggested that the largest changes in forest composition were forced by environmental factors other than MPB impacts. Pine was most strongly associated with the first PC axis (PC1), and the trend matched the changes in pine abundance. Given the strength of this association, we did not use PC1 for further interpretation. The second axis (PC2; Fig. 4) was associated with sagebrush (*Artemisia* spp.) and grass (Poaceae). The correlation coefficient is −0.992 for pine and PC1 and −0.878 for *Artemisia*/Poaceae and PC2. Both are highly significant ($P < 0.05$).

Zone 1: Late Holocene (650 cal yr BP to present)

Zone 1 comprised the last 650 years. Zone 1 was particularly important to this analysis because 2 MPB outbreaks occurred during this period (e.g., late 1920s and early 2000s), which were mandatory for further interpretation of NDPI (see below) (Fig. 3). The largest charcoal peak (36.4 particles/cm^2 per year) occurred at ca. 280 cal yr BP. When this peak was removed from the time series average, the charcoal influx averaged 1.9 particles/cm^2 per year. Overall, charcoal influx was higher during this time period than during the rest of the Holocene. The pollen percentage data did not show any conspicuous changes over this time period, except immediately following a fire event at ca. 280 cal yr

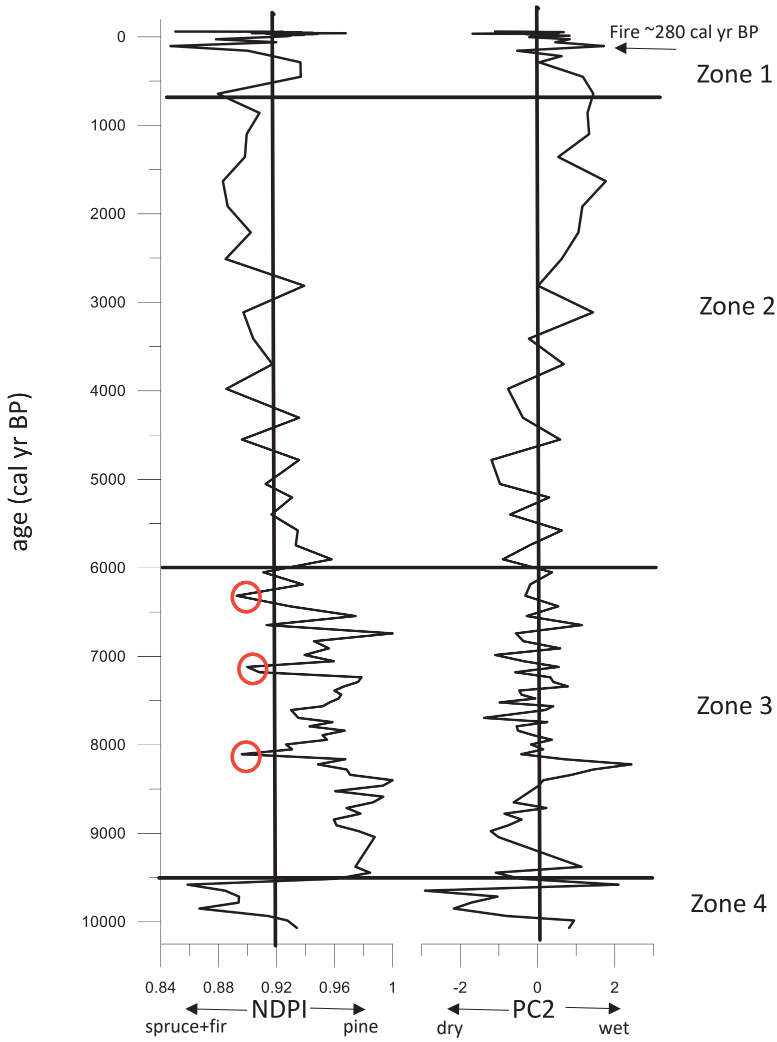

Fig. 4. Normalized difference pollen index (NDPI) of pine to spruce + fir plotted over time (cal yr BP). Black lines separate zones 1–4, and an arrow indicates the timing of the large fire that occurred at ca. 280 cal yr BP. Red circles indicate the timing of the 3 putative MPB outbreaks in the early Holocene. Principal component 2 (PC2) is plotted over time (cal yr BP).

BP when pine percentages decreased and sagebrush and grass percentages increased.

The NDPI indicated that there was more pine during Zone 1 and that it decreased immediately following the charcoal peak at ca. 280 cal yr BP. The recent part of the record revealed the largest amplitude of variability, with the largest shift from spruce + fir to pine than at any other time during the Holocene (with the exception of Zone 4, when forest composition was different from Zone 1, see below). PC2 indicated that during the late Holocene there was more grass than sagebrush, and it recorded several high-amplitude shifts between sagebrush and grass over time (Fig. 4).

Zone 2: Middle Holocene (6000 to 650 cal yr BP)

Charcoal influx was lower during the middle Holocene than during the late Holocene and averaged 0.16 particles/cm^2 per year. Pollen percentages were static during the middle-Holocene and revealed no distinct shifts (Fig. 2).

The NDPI of pine : spruce + fir showed a gradual trend from more pine toward more spruce and fir (Fig. 4). PC2 indicated a gradual shift from sagebrush to grass throughout this time period (Fig. 4).

Zone 3: Early Holocene (9500 to 6000 cal yr BP)

Charcoal influx increased during the early Holocene to 0.43 particles/cm^2 per year. Pollen percentages for the early Holocene showed a decrease in pine from Zone 2 to an average of 80%, with an increase in sagebrush to 5%–10%. At ca. 8200 cal yr BP, pine decreased to ~60% and sagebrush and grass increased to 12% and 10%, respectively (Fig. 2). Following this shift, pine rebounded to an average of 80%, and sagebrush and grass decreased to ~5%. Figure 4 reports a largely pine-dominated system with 3 distinct excursions to increased spruce + fir at 6300, 7000, and 8200 cal yr BP. PC2 showed a similar forest composition to Zone 1 (650 cal yr BP to present), with consistent reciprocal shifts between sagebrush dominance and grass dominance throughout this period.

Zone 4: Postglacial (10,200 to 9500 cal yr BP)

During the late glacial period, charcoal influx was low, averaging 0.14 particles/cm^2 per year. Pollen percentages showed the lowest percentage of pine for the entire record during this time period (50%–70%) and the highest percentage of sagebrush (15%–20%) (Fig. 2).

The NDPI indicated a period of greater spruce and fir abundance during the late glacial (0.92) (Fig. 4). PC2 showed several shifts between more grass and more sagebrush, one at the very beginning of the record and a second at ca. 9600 cal yr BP, although sagebrush generally dominated during the late glacial period (Fig. 4).

DISCUSSION

This study provides a Holocene record of environmental change from a small watershed in the Northern Rocky Mountains that characterizes the role that climate, MPB, and fire play in modifying ecosystem composition. This study uses NDPI to track recent MPB disturbance and a PCA to identify shifts in vegetation composition driven by variations in effective moisture. A main goal of this research was to further test the ability of the NDPI to identify MPB outbreaks in a longer sedimentary record (e.g., Watt and Brunelle, 2020).

In the Lake of the Woods watershed, there is visual evidence of recent MPB activity in the down and dead trees surrounding the lake (dead pines with beetle galleries). In addition, historical records documented MPB in the study area and elsewhere in the northern Rockies in the 1920s and 1930s AD. The dendrochronological record for the Lake of the Woods watershed also supported the identification of 2 MPB outbreaks in the 20th century (Margoles 2011, Jenne and Egan 2019).

Zone 1: Late Holocene (650 cal yr BP to present)

Zone 1 begins with the postsettlement period. This zone contains the highest charcoal influx values in the entire record, which is the only evidence of a major fire found in the entire record (Fig. 2). Forest age structure information collected within the basin also suggests that whitebark and lodgepole pine regenerated at around the same time as the peak in charcoal around 280 cal yr BP. A tree-ring study from the area also identified this event as a local fire (Margoles 2011), supporting our interpretation that this fire event occurred within the watershed. Several complex and interacting factors, such as anthropogenic climate change, grazing, mining, and fire suppression, likely affected vegetation composition over the recent past.

PC2 (Fig. 4) indicates that precipitation is driving shifts in forest composition during the late Holocene period, with wetter conditions in the early part of this period and a trend toward drier conditions later in the period, but with substantial variation, suggesting a dynamic precipitation pattern. The NDPI for Zone 1 identifies 2 time periods where there is a distinct shift from pine to spruce + fir (Figs. 3, 4). These shifts align with MPB outbreaks reconstructed from dendrochronological records at this site (Margoles 2011). This corroborates the assertion that our approach to reconstructing MPB outbreaks using NDPI has utility in mixed-conifer forests.

Zone 2: Middle Holocene (6000 to 650 cal yr BP)

The charcoal record indicates low fire activity based on the lack of charcoal over the remainder of the record (Fig. 2), similar to the findings reported from Montana for this same time period (Power et al. 2011). PC2 indicates a long-term shift in vegetation from sagebrush dominance to grass dominance at this time, which suggests a shift from drier to wetter conditions (Fig. 4). The decrease in charcoal abundance and increase in mesic taxa also suggest that vegetation change was driven primarily by climate, with disturbance playing a smaller role.

The NDPI data for the middle Holocene (Zone 2) indicate a vegetation shift from a pine-dominated forest to a mixed-conifer forest through the increase in spruce and fir likely caused by increased precipitation and little fire activity (Fig. 4). The wet climate and the abundance of spruce and fir in this zone would have likely created enough discontinuity among the pines to limit the ability of MPB to reach watershed-scale outbreaks during this time.

Zone 3: Early Holocene (9500 to 6000 cal yr BP)

The early Holocene fire record shows a higher level of charcoal influx from Zone 2, which suggests more fire activity (Fig. 2). Fire activity can be related to fuels and/or conditions of effective moisture. In Zone 3, the PC2 axis shows little trend but instead alternates shifts between sagebrush dominance and grass dominance, suggesting shifts between more and less effective moisture around a steady long-term mean. These shifts between greater and lesser amounts of fine fuels and the associated shifts between wetter and drier climate would have facilitated the occurrence of small understory fires and thus charcoal abundance (Fig. 4).

The NDPI data for zone 3 indicate that there were fewer spruce and fir trees in the forest and that the canopy was largely dominated by pine (Fig. 4). However, there are 3 points (ca. 6300, 7000, and 8200 cal yr BP) when the NDPI indicates a greater dominance of spruce and fir relative to pine, which is similar to the values observed during the known late-Holocene MPB outbreaks discussed in Watt and Brunelle (2020). These 3 excursions are not coincident with a fire, so the vegetation is not responding successionally. The excursions are all consistent with the NDPI signal of the MPB outbreak in the 1920s and 1930s and the 2000 outbreak at this site itself. The combination of the pine-dominated forest composition (which is necessary for a large-scale MPB outbreak) along with the similarity of the excursions to other known outbreaks is strongly suggestive of MPB outbreaks in the Lake of the Woods watershed during those times.

The 3 excursions to increased spruce-fir abundance are similar in magnitude and duration. None are associated with peaks in charcoal and so are not ecological responses to fire. Further evidence that these 3 times represent MPB outbreaks is the coincidence of the excursion at 8200 cal yr BP with fossil beetle evidence of an MPB outbreak at 2 other sites in the Northern Rocky Mountains (Brunelle et al. 2008). The event at 8200 cal yr BP has been identified as one of the most abrupt climate changes to have occurred during the last 10,000 years, and it occurred in 2 phases, with a distinct cold event separated by a brief warm period (Morrill and Jacobsen 2005). The 8200-year event was likely caused by the final collapse of the Laurentide Ice Sheet, which delivered pulses of cold freshwater to the northern Atlantic Ocean that disrupted thermohaline circulation (Clarke et al. 2004). Brunelle et al. (2008) attributed the outbreak at ~8200 cal yr BP to the increased food value of the phloem during the brief warm period. The temporal correspondence of these 2 lines of evidence for an outbreak at ~8200 cal yr BP indicates that regional MPB outbreaks are not unique to the twentieth and twenty-first centuries; however, they were likely associated with extreme climate conditions.

Zone 4: Postglacial (10,200 to 9500 cal yr BP)

Based on the pollen percentage data, the postglacial time period represents the lowest percentage of conifer pollen in the record, suggesting less abundant and/or low flammability of arboreal fuels, which is accompanied by low charcoal influx. The record indicates small, infrequent fires during the late glacial period (Fig. 2), which is consistent with low fuel abundance as reported in other paleoecological reconstructions from the northern Rocky Mountains (Brunelle et al. 2005, Power et al. 2011).

The postglacial vegetation community was an open parkland with the highest sagebrush pollen percentages (~20%) (Fig. 2) and the lowest pine percentages observed in the record.

PC2 also indicates dry conditions associated with a parkland environment, and more sagebrush than at any other time in the Holocene (Fig. 4). The NDPI data (Fig. 4) indicated relatively more spruce and fir than the Holocene average. Therefore, with fewer pines and more sagebrush on the landscape, the vegetation surrounding Lake of the Woods would have been less susceptible to a severe MPB outbreak.

CONCLUSION

Here we used a paleoecological record from Lake of the Woods to reconstruct the vegetation, fire history, and potential timing of MPB disturbance events during the last 10,000 years. To reconstruct MPB outbreaks, we compared recently observed changes in vegetation (i.e., changes in response to MPB outbreaks during the late 1920s and early 1930s and during the 2000s) to pollen time-series data that span the Holocene. By applying the NDPI method presented in Watt and Brunelle (2020) to a longer temporal record, we were able to identify 3 putative MPB outbreaks in the early Holocene as well as extract more details of the drivers of forest composition change. Our research supports previous studies and provides additional evidence for a regional MPB disturbance event in the Northern Rocky Mountains around 8200 cal yr BP. Extending this analysis to additional Holocene records would help us to determine whether similar patterns are evident in other conifer forests in western North America.

The long-term trends presented in the pollen percentages, NDPI, and PC2 data indicate that precipitation may be the dominant long-term driver of forest composition at Lake of the Woods, with disturbance playing a secondary and shorter-term role. The majority of the vegetation shifts are associated with changes in effective moisture, including the shift from a more parkland setting at the beginning of the record to the trends in forest composition associated with trends in PC2 over the remainder of the Holocene.

We acknowledge the limitations of the standard pollen percentage analysis in pine forests in demonstrating the utility of using NDPI to identify periods of potential MPB disturbance events in the past when beetle remains are not preserved. Our results indicate that the NDPI method can identify the reciprocal shifts in vegetation that follow mortality of canopy-dominant pine resulting from MPB disturbance events. While the PCA did not identify MPB disturbance events, it did identify broad trends in vegetation composition, which were an indicator of effective moisture. In combination, these 2 indicators suggest the drivers of forest composition change and therefore offer a framework for other studies in the region.

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