Fire catalyzed rapid ecological change in lowland coniferous forests of the Pacific Northwest over the past 14,000 years

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Abstract. Disturbance can catalyze rapid ecological change by causing widespread mortality and initiating successional pathways, and during times of climate change, disturbance may contribute to ecosystem state changes by initiating a new successional pathway. In the Pacific Northwest of North America (PNW), disturbance by wildfires strongly shapes the composition and structure of lowland forests, but understanding the role of fire over periods of climate change is challenging, because fire-return intervals are long (e.g., millennia) and the coniferous trees dominating these forests can live for many centuries. We developed stand-scale paleorecords of vegetation and fire that span nearly the past 14,000 yr to study how fire was associated with state changes and rapid dynamics in forest vegetation at the stand scale (1-3 ha). We studied forest history with sediment cores from small hollow sites in the Marckworth State Forest, located ~1 km apart in the Tsuga heterophylla Zone in the Puget Lowland ecoregion of western Washington, USA. The median rate of change in pollen/spore assemblages was similar between sites (0.12 and 0.14% per year), but at both sites, rates of change increased significantly following fire events (ranging up to 1% per year, with a median of 0.28 and 0.38%, P < 0.003). During times of low climate velocity, forest composition was resilient to fires, which initiated successional pathways leading back to the dominant vegetation type. In contrast, during times of high climate variability and velocity (e.g., the early Holocene) forests were not resilient to fires, which triggered large-scale state changes. These records provide clear evidence that disturbance, in the form of an individual fire event, can be an important catalyst for rapid state changes, accelerating vegetation shifts in response to large-scale climate change.

Key words: charcoal; fire history; fire regime; Pacific Northwest; paleoecology; pollen analysis; rapid ecological change; state change; Tsuga heterophylla Zone.

INTRODUCTION

Understanding how shifting climate and changing disturbance regimes will interact, and whether the interaction will result in an ecological state change, is a critical research priority (Turner 2010, Johnstone et al. 2016). Disturbance initiates rapid ecological change by causing widespread mortality and, under relatively stable conditions, initiating successional pathways that lead back to pre-disturbance vegetation. During times of directional climate change, the context in which ecosystems recover from disturbance has shifted, and a new successional pathway can be initiated to catalyze a state change in vegetation (Johnstone et al. 2010, 2016). Evidence for such vegetation transformations exists (e.g., Allen and Breshears 1998, Savage et al. 2013), but is relatively rare. Instead, ecophysiological and demographic stabilizing processes are thought to promote inertia and reinforce ecological resilience even as a change in the disturbance regime interacts with climate change (Lloret

Manuscript received 4 November 2016; revised 2 May 2017; accepted 5 May 2017. Corresponding Editor: Donald R. Strong ⁴ E-mail: crausbay@gmail.com

et al. 2012). Ecosystems with long-lived organisms, such as in coniferous forests, experience particularly strong inertia to rapid state changes (Lloret et al. 2012).

Temperate coniferous forests globally have experienced rapid increases in the fire season length in recent decades (Jolly et al. 2015), and statistical modeling of the future suggests that average area burned in Pacific Northwest of North America (PNW) forests will double or triple by the late 21st century (Littell et al. 2010, Sheehan et al. 2015). But, understanding the implications of changing fire activity within a context of directional climate change is especially challenging, particularly in lowland forests of the PNW, where fire return intervals (FRIs) are on the order of centuries to millennia (Agee 1993), and the dominant tree species can live up to 1,000 yr (Hermann and Lavender 1990). The time scale of these fire regimes and mechanisms of forest change are well beyond the scope of studies on the contemporary landscape, and long-term empirical studies are needed to understand the resilience of lowland coniferous forests during times of environmental change (e.g., Johnstone et al. 2016).

Paleorecords provide the necessary temporal extent to study the role of fire in forests with long-lived species and infrequent burning. In the PNW, many paleoecological records began soon after the initial retreat of the Cordilleran Ice Sheet c. 14,000 yr ago. After deglaciation, pollen records from lake sediment show that regional (>100 ha) vegetation experienced several state changes (i.e., persistent changes in dominant vegetation) that are generally attributed to large-scale alteration in the climate system and a high velocity of climate change (e.g., Loarie et al. 2009, Dobrowski et al. 2013) during the early Holocene (Whitlock 1992, Sea and Whitlock 1995, Brown and Hebda 2003). Sediment records from small forest hollows (i.e., potholes or kettles formed from the melting of buried glacial ice) provide a detailed chronicle of forest composition at the spatial resolution of a forest stand (1-3 ha, Calcote 1998), and smallhollow charcoal records offer evidence of high-severity fire events at a spatial resolution <1 ha (Higuera et al. 2005). By capturing individual fire events and standscale vegetation responses during times of both rapid climate change and relative climate stability, smallhollow records offer a unique picture of how ecosystems respond to disturbance against a background of extrinsic climatic controls.

Here we study the role of fire in stand-scale vegetation dynamics since deglaciation in the Puget Lowland ecoregion (Bailey 1995) of western Washington, USA, an area characterized by long-lived coniferous forests and long FRIs. We present 13,560 yr-long records from small forest hollow sediments offering high to moderate spatial resolution for two sites to ask: (1) how did the well-documented and widespread state changes in regional vegetation unfold at the stand scale, and (2) what role did fire play, if any, in initiating these stand-level state changes? If fire served as an important intrinsic driver of rapid vegetation state change in the past, the patterns and inferred mechanisms would provide important precedence for how fires could catalyze the ecological state changes expected with ongoing climate change in the future.

Study area

We studied forest history at sites in the Marckworth State Forest, located in the Puget Lowland ecoregion (Bailey 1995) and the Tsuga heterophylla Zone described by Franklin and Dyrness (1998; Fig. 1). The modern climate in the Puget Lowland is characterized by warm, dry summers, and mild, wet winters. Average summer and winter temperature from a nearby climate station in Startup, WA (12 km to the northeast of our sites) is 17 and 5°C respectively; total annual precipitation is 1,860 mm, with an average annual snowfall of 660 mm (1981-2010, NOAA). The Puget Lowland ecoregion is densely populated, and it is estimated that only 5% of the pre-Euroamerican habitat remains, with much of that heavily altered (DellaSalla et al. 2001). Prior to commercial logging in c. CE 1860 and 1935 (personal communication, Paul Footen, Washington Department of Natural Resources, March 2016), the study area was dominated by coast Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco var. menziesii), western hemlock (Tsuga heterophylla (Raf.) Sarg.), and western redcedar (Thuja plicata Donn ex D. Don). Among these dominant species, Douglas-fir is the most able to persist with fire,



FIG. 1. Study area and regional setting. (A) Map of Washington State, USA, and the Pacific Northwest showing the Marckworth Forest study area and other paleorecords referenced in the text. (B) The Marckworth Forest study area and location of three small forest hollows used in this study. Circles around each site represent the approximate spatial scale represented by the charcoal (50-m radius; Higuera et al. 2005) and pollen/spores (100-m radius; Calcote 1998, Sugimura et al. 2008) records. Imagery from Google Earth; note that contour intervals in (B) are in feet.

regenerating after-stand replacing fires, and with mature trees surviving low-intensities fire due to thick bark. Post-fire successional patterns are diverse, however, and western hemlock can also be an early seral invader at moist sites, even after high-severity fires (Agee 1993, Higuera et al. 2005). Across most of the *Tsuga heterophylla* Zone, western hemlock is the climax dominant species (Agee 1993), although Douglas-fir remains a major component of these forests, given its lifespan of up to 1,000 yr (Hermann and Lavender 1990). Hardwood species are uncommon, except after disturbances and in riparian areas, and include red alder (*Alnus rubra* Bong.) and bigleaf maple (*Acer macrophyllum* Pursh).

METHODS

Small hollow sediment sampling

We analyzed sediment cores from three small forest hollows in Marckworth State Forest: MW1B (47.7690°, -121.8111°); MW13 (47.7722°, -121. 8253°); and MW14 (47.7710°, -121.8270). MW13 and MW14 are separated by <200 m and were amalgamated for our analysis (see next paragraph); MW1B is 1.1 km away. Forest hollows were <5 m in diameter and sediment collection and sampling generally followed previously described methods (Higuera et al. 2005, Sugimura et al. 2008). Hollows were selected from nearly 50 candidate sites that were visited and probed with a thin rod to assess sediment depth and potential impacts of recent disturbances. We cored six hollows and conducted basic sediment description, charcoal analysis, and radiocarbon dating of the basal sediments to address suitability for analysis. Small hollow cores were collected in the summer of 2001, using a 7.62-cm diameter, 100-cm long Gavin sampler (Gavin et al. 2003) modified with a detachable head to facilitate extrusion using a pulley system. Cores were extruded and described in the field, wrapped in polyvinylidene chloride film (Saran WrapTM) and aluminum foil, and transported in polyvinyl chloride (PVC) tubes. In the lab, we split the sediment cores longitudinally into working and archive portions, and we described the macroscopic structure and microscopic components of the sedimentary matrix based on Schnurrenberger et al. (2003). The working portion was sectioned contiguously at 0.25 cm increments using a custom-made sampling device and samples were stored in Whirl-Pak® bags. Archive portions and bags of 0.25-cm subsamples were stored at $\approx 3^{\circ}$ C at the University of Washington's Quaternary Research Center.

We present two records here. The MW1B sediment sequence consists of a single drive and the MW13+14 sediment sequence is an amalgam of drives from two hollows (MW13 and MW14) separated by <200 m (Fig. 1B). These two hollows are close enough to each other that they are likely sampling the same vegetation and fire history (Fig. 1B), making an amalgamation possible. Drives were spliced together to avoid core sections that were clearly mixed, due to disturbed sediments or angled stratigraphy. Drives were spliced together based on alignment of (1) the Mazama ash, a large volcanic ash deposit created by the explosive eruption of Mount Mazama that ultimately formed Crater Lake in Oregon, USA (2) stratigraphy of laminations, and (3) stratigraphy of charcoal counts. We use MW14A for the entire sediment sequence above the Mazama ash (0-58.0 cm), and two drives from MW13 for the sediment sequence below the Mazama ash (58.0-122.8 cm). Based on a comparison of the lithology from multiple drives in MW13, we recognized that some sediment was lost just below the Mazama ash in MW13B. We estimated this loss to be between 3.75 and 4.75 cm, by comparing laminations and the thickness of the Mazama ash between MW13A and MW13B. We developed age models using estimates of 3.75, 4.25, and 4.75 cm of sediment loss, and our results were robust to any selection; we present results using the middle estimate.

Chronologies are based on Accelerator Mass Spectrometer (AMS) 14C ages of terrestrial macrofossils, purified pollen/spore concentrates, and the identification of the Mazama ash (7627 calibrated years before present [CE 1950, hereafter BP]) based on color, texture, smear slide analysis, and a calibrated radiocarbon date of 7.659 BP at the basal contact of the ash in MW13+14 (Table 1). For MW1B, the age of the Mazama ash was prescribed to the top layer of deposition, and the thickness (3 cm) was removed from the age-depth model. Macrofossils were treated with an acid-base-acid procedure (Oswald et al. 2005) and pollen/spores were concentrated using heavy liquid methods (Sugimura et al. 2008) before being submitted to the Lawrence Livermore National Laboratory's Center for Accelerator Mass Spectrometry (CAMS) for radiocarbon measurements. Radiocarbon ages were calibrated using the IntCal 09 dataset in CALIB v6.1.0 (Reimer et al. 2004) and age models were developed using the MCAgeDepth program in Matlab, which applies a weighted cubic smoothing spline function with confidence intervals estimated through Monte Carlo methods (following Higuera et al. 2009).

Charcoal and pollen/spore analysis

For charcoal analysis, subsamples of 3 cm³ were taken at intervals of 0.25–0.50 cm, disaggregated in a 10% sodium metaphosphate solution for 72 h, and gently washed with distilled water through 500 and 150 µm sieves. To aid in charcoal identification, samples were bleached with 8% hydrogen peroxide solution for 8 h, and sieved again with distilled water (Rhodes 1998). Charcoal pieces were counted with a stereomicroscope at 10–40× magnification, and we combined counts from both size classes for our analysis, because this yields the most accurate information on past fire occurrence in our study region (Higuera et al. 2005). Charcoal concentrations (# cm⁻³) were converted to charcoal accumulations rates (CHAR, # cm⁻² yr⁻¹) based on sediment

Sample depth (cm)	Laboratory ID [†]	Material dated	¹⁴ C age
MW1B			
11.00-11.25	CAMS 93663	Concentrated pollen	430 ± 35
24.75-25.00	CAMS 91404	Concentrated pollen	3510 ± 40
32.00-32.30	CAMS 91397	Concentrated pollen	4430 ± 40
40.59-40.82	CAMS 91403	Concentrated pollen	5885 ± 40
62.60-63.80	CAMS 93664	Concentrated pollen	$5330 \pm 60 \ddagger$
MW13+14		-	
23.50-23.75	CAMS 91399	Concentrated pollen	1545 ± 45
42.05-42.32	CAMS 91398	Concentrated pollen	4070 ± 40
51.25-51.50	CAMS 91405	Concentrated pollen	$3390 \pm 130 \ddagger$
61.74-61.99	CAMS 84912	Concentrated pollen	$6825\pm40\$$
72.50-72.75	CAMS 84913	Concentrated pollen	8045 ± 45
91.00-91.25	CAMS 84914	Concentrated pollen	10075 ± 40
102.25-102.50	CAMS 84916	Concentrated pollen	11135 ± 40
122.50-122.80	CAMS 84917	Alnus seeds	11590 ± 90

TABLE 1. Accelerator Mass Spectrometry ¹⁴C ages from sediment sequences recovered from two small forest hollows in the Puget Sound lowlands.

[†]CAMS: Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory.

[‡]Dates excluded from age model.

[§]Date was used only to identify the Mazama ash and was also excluded from the age model.

accumulation rates (cm yr^{-1}) from each age-depth model.

For pollen/spore analysis, sediment subsamples of 1 cm³ were taken at intervals of 0.25–1.00 cm and prepared following standard digestion methods, including acetolysis and the addition of an exotic spike (Lycopodium spores) to facilitate estimating pollen concentrations (Faegri and Iversen 1975). Pollen/spore residues were mounted in silicone oil and all pollen and fern spores were quantified at $400-1,000 \times$ to an average sum of 342 (median = 323, range = 211-977) terrestrial pollen grains and fern spores. Terrestrial pollen and spore percentages from plants growing in the upland, terrestrial environment were then calculated from raw counts after unknown pollen, indeterminate pollen, and wetland taxa (Poaceae, Cyperaceae, Typhaceae, Nuphar, Menvanthes, Spirea, Sparganium, and Lysichiton) were excluded from the sum. We include Poaceae in wetland taxa because in this region there are multiple species of Poaceae that are either wetland obligates, or are more likely to occur in wetlands vs. uplands. When paleorecords come from wetlands with the potential to support Poaceae, the inclusion of Poaceae in the sum can lead to misinterpretation (Bush 2002). However, removing Poaceae from the sum levies no cost in interpreting pollen assemblages in some systems (Crausbay and Hotchkiss 2012). To estimate pollen/spore accumulation rates (grains or spores $cm^{-2} yr^{-1}$), we multiplied estimated concentrations (grains or spores cm⁻³) by sediment accumulation rates (cm yr^{-1}).

Statistical treatment of charcoal and pollen/spore data

The goal of charcoal analysis was to identify peaks in the CHAR series that most likely represented high-severity fires burning within 0-50 m from the edge of each hollow ("local"). Based on a calibration study comparing tree-ring dated fire events to CHAR in small hollow sediment in similar forests in the region (Higuera et al. 2005), we defined a single threshold value for each record to identify CHAR peaks likely arising from local fire occurrence. Specifically, we defined "background" CHAR in each record as the series-wide median, and defined the threshold value as 1.70 times the background value. This threshold falls in the middle of the range of "optimum threshold values" identified by Higuera et al. (2005; i.e., 1.63–1.75). Following Higuera et al. (2005), to be identified as a peak, CHARs had to exceed the site-specific threshold for at least three consecutive samples.

The goals of pollen/spore analysis were to quantify the nature and timing of vegetation change from centennial through millennial time scales, highlighting both distinct, persistent vegetation assemblages and rapid change following fire events. We used four methods to accomplish these goals. First, to identify centuries to millennia with distinct pollen/spore spectra (i.e. "zones," which represent different vegetation states), we used a stratigraphically-constrained hierarchical agglomerative clustering (using the freeware program PAST⁵). This cluster analysis was based on a Bray-Curtis distance measure (Gotelli and Ellison 2004) 2w/(a + b), where a and b are the numbers of taxa in each of two samples and w is the number of taxa common to both samples, and an unweighted pair-group average (UPGMA) algorithm, where clusters were joined based on the average distance between all members in the two groups. The results of this analysis delineate statistically distinct pollen/spore zones.

⁵ Available online: http://folk.uio.no/ohammer/past/index.html

Second, to highlight the nature of vegetation change among pollen/spore zones, we used global nonparametric multidimensional scaling (NMS), based on a pooled analysis using pollen/spore spectra from both sites (using PC--ORD[™] 6.0, MjM Software Designs, Gleneden Beach, OR, USA). NMS is a multivariate ordination technique that reduces variability in multi- (k) dimensional space to fewer orthogonal dimensions (axes) through an iterative process (i.e., 500 iterations, 50% randomized runs, with instability criterion of 1.0×10^{-7}). Beginning with two dimensions, additional dimensions are added only if they reduced the final "stress" (a goodness-of-fit measure) by 5% or more. Final stress was lower than that for 95% of the randomized runs (i.e., P < 0.05 for the Monte Carlo test). Ordinations were based on the Bray-Curtis distance measure. The relationship between taxon abundance and axis scores was assessed with Pearson's correlation, and we highlight taxa with $r^2 > 0.3$ on either axis.

Third, to quantify the rate of compositional change in the pollen/spore spectra over multi-decadal to centennial time scales, we conducted rate-of-change analysis. As above, we used the Bray-Curtis distance measure to quantify the dissimilarity between all adjacent pollen/spore spectra in each record. We divided the resulting value (which is bounded between 0 and 1) by the time elapsed between samples (yr), and multiplied by 100, to obtain a metric that can be interpreted as % change over time (% per yr). We used a Wilcoxon rank-sum test to compare the series-wide median rate-of-change value between records, and the rate-of-change values associated with fire events (i.e. the maximum value within ± 1 sample of a charcoal peak) to those unassociated with fire events.

Finally, to describe the nature of centennial-scale vegetation change following fire events, we used a compositing analysis (aka "Superposed Epoch Analysis") to summarize the average response (across both sites) of major tree taxa to fire events (i.e., *Pseudotsuga, Tsuga*, Cupressaceae, and *Alnus*). Specifically, for each fire event, we conducted analysis on the first-differences of the pollen percentage time series highlighting the postfire sample with the highest rate-of-change value. The composite record reflects the average difference after all fires from ~ 8,200 BP to just before Euro-American logging, taken to represent "modern" pollen assemblages. To facilitate this analysis, pollen data were interpolated to constant 100-yr intervals, approximating the median interval between samples in each record (i.e., 102 in MW13+14 and 93 yr in MW1B). Statistical significance was estimated by repeating this analysis with 10,000 bootstrapped samples of random events (with replacement), and using the 2.5th and 97.5th percentiles from the resulting composites to define 95% confidence intervals. This analysis assumes that pollen records at each site represents an independent sample of post-fire vegetation change, although most fires likely burned both sites (see *Results*).

RESULTS

Lithology

The sediment sequence from MW1B is 63.8 cm long with a deposition of the Mazama ash at 46.0-49.0 cm. The sediments consist primarily of organic-rich diatomaceous silty clays with occasional woody and organic components >1 mm dispersed throughout. Black, charcoal-dominated laminations occur sporadically from 20 cm depth to the base of the core (excluding the Mazama ash). The sediment sequence from MW13+14 is 122.8 cm long with a deposition of the Mazama ash at 58.0-62.3 cm. The sediments above the Mazama ash consist primarily of organic-rich diatomaceous silty clays with occasional woody and organic components >1 mm dispersed throughout. Below the Mazama ash, from 62.3-82.3 cm, several black, charcoal-dominated laminations alternate with light, diatom-dominated laminations (laminations are not annual). From 100.0-122.8 cm, the sediment consists primarily of organic, diatomaceous, mineral-rich silts.

Chronologies and sample resolution

In combination with the Mazama ash, six ¹⁴C dates constrain the MW13+14 record and indicate a basal age of 13,560 BP, while four ¹⁴C dates constrain the MW1B record and indicate a basal age of 10,180 BP (Table 1, Appendix S1: Fig. S1). In both records, a single ¹⁴C date (ca. 51 cm for MW13+14 and 63 cm for MW1B) was excluded from the chronology, given significantly younger ages compared to dates above the sample. The

TABLE 2. Vegetation and fire history over the past ~14,000 yr in the Puget Lowland based on two stand-scale paleorecords from forest hollows in Marckworth State Forest.

Zone	Age range (cal. yr BP)	Dominant pollen/spores	N FRI, MW13+14	N FRI, MW1B
1	200-modern	Alnus and other disturbance types	1	1
2	8,210-200	Cupressaceae and Tsuga	4	6
3	11,280-8,210	Pseudotsuga and Pteridium	2	1
4	11,680–11,280	Picea and Abies	1	NA
5	13,560-11,680	Pinus and Alnus	0	NA

Notes: Mean fire return intervals (FRIs) were calculated from MW13+14 for zones 3–4 combined, and from MW1B for zones 2. Sample size (*n*) refers to FRIs, not number of fires.

pollen/spore records at each site provide centennial-scale resolution, with a mean (standard deviation) sampling interval of 93 (64) and 98 (43) years at MW13+14 and MW1B, respectively. Charcoal records provide multi-decadal scale resolution, with mean (standard deviation) sampling intervals of 44 (41) and 49 (24) yr at MW13+14 and MW1B, respectively. This resolution suggests a minimum detectable mean fire return interval of ca. 165–250 yr (i.e., ≈ 3.3 –5.0× sample interval; Clark 1988, Higuera et al. 2007).

Vegetation history

Pollen/spore percentages and influx values for major taxa are well correlated at both sites (0.57 < r < 0.97, P < 0.05, Appendix S1: Figs. S2, S3) and we therefore report analyses based upon pollen percentages only. Five vegetation zones were defined by the stratigraphically constrained cluster analysis (Table 2, Appendix S1: Figs. S4, S5), and were also clearly delineated in ordination space (Fig. 2). The two-dimensional NMS ordination explains 95% of the variation in pollen/spore assemblages, with 80% explained by axis 1 alone (Fig. 2). Zones are characterized by significant patterns in the abundance and frequency of dominant taxa (Fig. 2), and each zone transition denotes a state change in pollen/spore assemblages.

Pollen/spore assemblages were relatively stable throughout Zone 5, which occurred from the beginning of the record at 13,560 BP through the Younger Dryas Chronozone (YDC, 12,900–11,600 BP) and ended at

11,680 BP. Pollen/spore assemblages from Zone 5 suggest an open, Pinus-dominated (likely P. contorta, lodgepole pine) forest with some Alnus (likely A. viridis subsp. sinuata, a high elevation shrub) (Fig. 3A). Zone 4 began essentially at the termination of the YDC and lasted for only 400 yr from 11,680-11,280 BP. In Zone 4, Pinus pollen declined rapidly, suggesting the abrupt end of lodgepole pine forests, and a dynamic, transitional forest followed, with an increase in Picea, Abies, and Pseudotsuga pollen, followed by an increase in Tsuga pollen (Fig. 3A). At the beginning of Zone 3 at 11,280 BP, the rapid and sustained increase of Pseudotsuga pollen (interpreted as and hereafter Pseudotsuga menziesii, Douglas-fir) and Pteridium spores (interpreted as and hereafter Pteridium aquilinum, bracken fern) occurred, suggesting an open Douglas-fir forest. Zone 3 also included Spirea and other wetland taxa and these taxa remained dominant until 8,210 BP (Fig. 3A, E, Appendix S1: Figs. S4, S5). The rapid changes that occurred between Zones 3-5 are clearly delineated along NMS axis 2, which explains 15% of the total variation in composition (Figs. 2A, 3A, B).

Zone 2 begins at 8,210 BP when Cupressaceae pollen (presumably *Thuja plicata*, western redcedar) increased and became dominant, while *Tsuga* pollen (interpreted as and hereafter *Tsuga heterophylla*, western hemlock) increased in abundance and bracken fern and wetland taxa declined sharply (Fig. 3A, E, Appendix S1: Figs. S4, S5). The sharp transition from Zone 3 to Zone 2 at 8,210 BP largely defines NMS axis 1, which explains 80% of the variation in composition. Zones 3–5 (late



FIG. 2. Non-metric multidimensional scaling (NMS) ordination. NMS analysis explains 95% of the variation in the combined MW13+14 and MW1B pollen/spore data set. Taxa highly correlated with each axis are shown, with the associated r^2 in parentheses. Symbology represents vegetation zones defined by stratigraphically constrained cluster analysis (See Appendix S1: Figs. S4, S5).

glacial to early Holocene) are on the positive end of NMS axis 1, and Zones 1 and 2 (mid Holocene to present times) are on the negative end (Figs. 2, 3B, F). Zone 2 persisted for several thousand years, until 200 BP, and during this period there were short-lived, rapid successional changes associated with fire, with western redcedar and Douglas-fir declining, and western hemlock and *Alnus* (presumably *A. rubra*, red alder) increasing (Fig. 3A, E, Appendix S1: Figs. S4, S5). From 200 BP until today, a dramatic increase in red alder and other disturbance indicators co-occur with logging and define Zone 1. Assemblages from Zone 1 are clearly differentiated on NMS axis 1 by a shift to more positive values (Fig. 2).

Fire history

Charcoal peak analysis identified a total of eight fire events at each site, with one event (at MW 13+14) occurring prior to the time period represented by both records (10,180 BP). Within the common period, the timing of six fire events was coincident between sites (i.e., within the confidence intervals on age estimates), and three fire events were unique to a single site (Fig. 3D, H). One fire event at 9,800 BP was uniquely identified in MW13+14, and two fire events were uniquely identified at MW1B, between 3,300-2,600 BP (Fig. 3D, H). The absence of distinct peaks in the MW13+14 record between 3,300-2,600 BP combined with high background charcoal accumulation rates (CHAR) from c. 1,500-3,000 BP suggest potentially missing CHAR peaks, due to mixing in the sediments over this section. The pollen/spore stratigraphy in MW13+14 is likewise less variable (relative to MW1B) during this period, consistent with an interpretation of increased sediment mixing (e.g., Fig. 3). In contrast, the sediment sequence around 9,800 BP in MW1B does not have high background CHAR or other clear evidence of sediment mixing. Overall, the coincident timing of fire events strongly suggests that most fires burned both sites, with the possible exception of the fire event at 9,800 BP.

Individual fire-event return intervals (FRIs) varied from 450–4,330 yr; if the putative missing fire events at MW13+14 is included, then this maximum FRI is reduced to 2,200 yr. No fire events were detected prior to 11,500 BP, and only one fire event was detected in Zone 4, immediately prior to the transition to Zone 3. Two fire events were detected between 11,280 and 8,210 BP (Zone 3; Fig. 3D) at MW13+14, yielding a single 1,250-yr FRI. Only one fire event at MW1B precluded measuring FRIs in Zone 3 (Fig. 3H). From 8,210-200 BP (Zone 2), the average FRI at each site was statistically similar: 1,883 yr (95% CI 591–4,329, n = 3) and 1,129 yr (705–1746, n = 5) at MW13+14 and MW1B, respectively (Table 2). Given likely undetected fires at MW13+14, we consider the mean FRI from MW1B as the more accurate estimate. Zone 1 includes a single fire event at each site, which we interpret to be associated with logging in the 19th century.

Rapid vegetation change after fire

The rate-of-change in pollen/spore assemblages showed similar medians across both sites (MW13+14 = 0.14% yr⁻¹ and MW1B = 0.12% yr⁻¹; P = 0.145, Wilcoxon rank-sum test; horizontal line in Fig. 3C, G). Rates of change rose above the median at various times throughout each record, extending up to ~1% yr⁻¹ in both records, and these peaks were generally associated with identified CHAR peaks (vertical lines in Fig. 3D, H). The median rate-of-change within ± 1 sample of identified CHAR peaks was significantly higher than series-wide medians at MW13+14 (0.38% yr⁻¹, P = 0.003) and MW1B (0.28% yr⁻¹, P < 0.001, Wilcoxon rank-sum test).

In Zones 3–4 the rapid changes after two of three fire events (c. 11,380 and 8,500 BP), during a time of species expansion and rapid climate change, culminated in establishment of new vegetation types. In contrast, the average response of major tree taxa to fire events in Zone 2 (8,210–200 BP) was characterized by significant increases in pollen percentages of western hemlock and red alder and significant decreases in western redcedar (Fig. 4), but with an eventual return of pollen across all taxa to pre-fire levels. Douglas-fir decreased slightly, but was not significantly different from random when averaged across all fire events. The direction and significance of post-fire changes did not differ when we repeated this analysis including the two most recent, logging-related fires (data not shown).

DISCUSSION

Our study provides records of stand-level vegetation dynamics and fire history from a temperate coniferous forest, capturing nearly 14,000 yr of environmental change. This combined history highlights high-severity fire as an important mechanism of vegetation change, with two distinct modes of post-fire forest dynamics. Over the mid- to late-Holocene when climate was relatively stationary, forest composition was resilient to infrequent high-severity fires, with fire mainly initiating successional changes resulting in the re-establishment of pre-fire vegetation. In contrast, during periods of high climate velocity in the early and mid-Holocene, forests were not resilient to fire. Instead, fire was followed by state changes in the dominant vegetation type, revealing how fire can catalyze climate-driven vegetation change. These records highlight the potential for large, infrequent disturbances to initiate rapid ecological state changes during periods of high climate velocity.

Regional and stand-scale vegetation change

The pattern and timing of vegetation changes in our study area are broadly consistent with many regional records, suggesting large-scale climate change as the ultimate driver. Across the PNW, paleorecords including ours indicate open, pine-dominated (presumably lodgepole pine) forests for up to 2,000 yr after the initial



FIG. 3. Vegetation and fire history. (A, E) Pollen and spore percentages of select taxa (ordered from top to bottom as in the legend), with vegetation zones noted (as in Fig. 2, Appendix S1: Figs. S4, S5; (B, F) NMS axis scores over time; (C, G) rate-of-change time series, with series-wide median values indicated by the horizontal line; and (D, H) charcoal accumulation rates, threshold values (horizontal line), and identified peaks from each site (vertical dashed lines). For comparison, the dates of fire events from MW13+14 are shown by squares and MW1B by circles on both plots. The vertical solid line crossing all panels denotes the timing of the Mazama ash, and vertical dashed lines denote fire events. YDC = Younger Dryas Chronozone.

retreat of the Cordilleran Ice Sheet c. 14,000 BP (Whitlock 1992, Brown and Hebda 2003, Gavin and Brubaker 2015). Between 12,000–9,000 BP, forests across the region became more closed and more diverse with the expansion of spruce (Sitka, Engelmann), hemlock (western, mountain), Pacific silver fir, Douglas-fir, and alder.



FIG. 3. Continued.

These late glacial pollen assemblages are mixtures of lowland and montane species with both dry and mesic site requirements (Barnosky 1985, Cwynar 1987, Brubaker 1991, Whitlock 1992, Gavin and Brubaker 2015), and have few or no analogs in today's forests, yet are consistently seen in regional-scale paleorecords across the PNW. Our small-hollow records provide more nuance to this "no-analog" forest composition. We see Sitka spruce, Pacific silver fir, Douglas-fir, and alder expand rapidly in our study area c. 11,680 BP, suggesting



FIG. 4. Composite pollen response to fire events from 8,200 to 200 BP (Zone 2). Mean change represents the difference between post-fire samples with the highest rate-of-change (Fig. 3C, G), and the proceeding sample. Error bars represent 95% confidence intervals generated from 10,000 bootstrapped samples of randomly selected sample pairs; error bars overlapping 0 suggest no significant post-fire change.

that trees presently common at low elevations (Sitka spruce) did co-occur, at the stand scale, with trees currently restricted to higher elevations (Pacific silver fir). This combination of species does occur in some cool, moist climates of northern British Columbia today, but it was much more widespread in the late glacial. However, our records suggest the presumed mixture of dry (Douglas-fir) and mesic (alder) species did not occur at the scale of individual forest stands, based on Alnus pollen percentages below the value suggesting local presence (e.g., c. 30%, Sugimura et al. 2008). Our results suggest these species likely occupied different landscape positions, with alder in riparian habitats and Douglas-fir in more upland habitats. By 10,000 yr ago Douglas-fir became dominant across much of the region, along with bracken fern, grasses, and red alder, and we see this distinct vegetation shift in our stand-scale record at 11,280 BP. Regionally, the first analogs to modern forests of the Tsuga heterophylla Zone appear between 5,000-8,000 vr ago, depending on latitude, when western hemlock and western redcedar increased markedly (Brown and Hebda 2003, Walsh et al. 2008). Both of our stand-scale records show this distinct vegetation shift ~8,210 BP. This forest type persisted for more than 8,000 yr and declined only ~200 BP at our sites, with the advent of logging that culminated in the rise of vegetation dominated by red alder and other disturbance-related taxa.

Regional and stand-scale fire history

Our study provides a rare glimpse into the post-glacial fire history of a Puget Lowland forest, highlighting a pattern of infrequent but regular burning since the early Holocene (i.e., Zone 4, 11,680 BP). Within Douglas-fir dominated forests of the early Holocene (i.e., Zone 3 from 11,280-8,210 BP) and Douglas-fir, western hemlock, and western redcedar forests of the late Holocene (i.e., Zone 2 from 8,210 BP to 19th century land clearance), fires impacted stands nearly every millennium. While the average return intervals at these sites are an order of magnitude longer than in many fire-prone forests in western North America (Johnson 1992, Agee 1993, Baker 2009), they are only slightly longer than the lifespan of the tree species characterizing these forests for most of the Holocene (e.g., up to 1,000 yr; Hermann and Lavender 1990). Thus, despite periods of over a millennium without high-severity fires, forest structure and species composition was still strongly shaped by fire activity, providing an important example of the legacy that large-scale disturbances can have in forest ecosystems (Agee 1993, Franklin et al. 2002, Turner 2010).

Interestingly, the long average fire return intervals of 1,100–1,400 yr at our sites (Table 2) show no evidence of shifting fire regimes over time, although the concept of a (shifting) fire regime loses value when return intervals are longer than time scales of climate variability (Agee 1993, Gavin et al. 2003). These patterns contrast with regional records with evidence of more frequent burning in general, and higher fire frequencies in the early Holocene (Long et al. 1998, Brown and Hebda 2003, Hallett et al. 2003, Prichard et al. 2009, Gavin et al. 2013, Walsh et al. 2015). Our records suggest that high fuel moisture consistently limited biomass burning (Krawchuk and Moritz 2011) throughout the Holocene. If Puget Lowland forest fire regimes varied in response to Holocene climate change, the response is subtle enough to require more than two local-scale records to detect (Kelly et al. 2013, Calder et al. 2015).

The charcoal records also reveal the spatial extent of past burning, with most inferred fires showing evidence of impacting both sites (just over 1 km apart; Figs. 1B, 3D, H). Combined with evidence of rapid vegetation change over the decades following fire events (Figs. 3C, G, 4), these records suggest that fires were likely of "high" or "mixed" severity - killing canopy trees and opening space on the forest floor to initiate new tree cohorts (Keeley 2009). The only limited evidence of varying fire severity in these records is the lower CHAR values associated with charcoal peaks prior to 8,210 BP, suggesting less biomass burning per fire event. Lower-severity fires are consistent with the more open vegetation suggested by the abundance of bracken fern spores, the higher abundance of Douglas-fir pollen (Fig. 3), and interpretations of lower-severity fires in early Holocene Douglas-fir forests on the Olympic Peninsula (175 km west of our sites, Gavin et al. 2013). Given evidence of disturbancerelated taxa and that ~50% of low-severity fires go undetected in small-hollow charcoal records (Higuera et al. 2005), it is likely that low-severity fires affected our sites more often than suggested by charcoal peaks alone.

The history of very low frequency and high severity fires over the mid and late Holocene (i.e., Zone 2) at our sites fills an important gap in our knowledge of fire regimes characterizing Pacific Northwest forests. In lowland moist forests dominated by Tsuga heterophylla, tree-ring based fire history records are rarely long enough to document multiple fire events on a single site (Agee 1993, Gavin et al. 2003). Our estimate of an 1,100-yr or longer mean fire return interval helps refine coarser estimates for moist Tsuga heterophylla forests of the Oregon Coast Range, Olympic Mountains, and Washington Cascades, which range from 750 to 3500 yr, based on modern age classes or extrapolating 20th-century fire-climate conditions (Agee and Flewelling 1983, Agee 1993). Fire-free intervals of >1,000 yr are also consistent with studies from wetter costal temperate rainforest on Vancouver Islands, Canada (i.e., more than twice as much precipitation annually), where median time-since-fire values vary from centuries to just under 2,000 yr across most landforms (Gavin et al. 2003, Hoffman et al. 2016). In addition, post-fire vegetation change at our sites over the past 8,210 yr, characterized by a distinct post-fire increase of Tsuga pollen percentages (Fig. 4), is also consistent with observations and predictions of post-fire dominance of hemlock in moist forests of the Tsuga heterophylla Zone (Huff 1984, cited in Agee 1993). Specifically, when fire return intervals exceed 700-1,000 yr, Huff (1984, cited in Agee 1993) predicted that western hemlock would be the primary seed source for post-fire regeneration.

Fire as a catalyst of rapid ecological change

We detected significantly rapid vegetation change after most fire events in the Marckworth small-hollow records, suggesting that fire has been the primary catalyst of rapid change at the stand scale in lowland PNW forests. Fire also initiated three out of four state changes in these temperate coniferous forests since deglaciation. The rapid expansion of Douglas-fir and bracken fern (Zone 3, 11,280 BP) that ended the "no-analog" forests of Zone 4 was the first fire-catalyzed vegetation state change in the Marckworth forest. Douglas-fir was wellsuited to the warm, dry climates of this time, and it germinates and establishes best on mineral seed beds after fire (Uchytil 1991). Similarly, a high-severity fire was associated with a rapid transition between Douglas-fir and western redcedar at 8,210 BP, just as summers were becoming wetter and climate boundary conditions were increasingly like modern conditions. Western redcedar is well suited to the warmer wetter climate of the mid and late Holocene, and it readily establishes on post-fire bare mineral soil seedbeds through wind-dispersed seeds (Feller 1982). The most recent state change occurred abruptly only 200 yr ago, after fire and logging, which arguably could have induced this state change alone, without fire as a catalyst. In contrast to these state changes, after the distinct arrival of western redcedar, post-fire vegetation changes were still rapid, but were largely successional, with the dominant

vegetation type consistently resilient to the six wildfires from 8,210–200 BP.

These two modes of forest dynamics suggest that in this temperate coniferous forest, fire catalyzes rapid state changes in vegetation during times of high climate velocity, whereas forest composition is resilient to high-severity fires when climate velocity is low. The velocity of climate change in North America was high from the late glacial until about 7,000 yr ago (Ordonez and Williams 2013). This time period was characterized by multiple rapid warming events (Williams et al. 2011), profound changes in summer insolation due to differences in Earth's orbital parameters, and reorganization of atmospheric patterns after the collapse of continental ice sheets. In contrast, after about 7,000 yr ago, the velocity of climate change decreased relative to the late glacial and early Holocene, and climate boundary conditions were similar to today. Paleorecords from the Olympic Mountains show a strikingly similar pattern of forest history, with two modes of forest dynamics: before 7,000 yr ago, species turnover was rapid and associated with fire, while after 7,000 yr ago, species turnover was slower (Gavin et al. 2013). Like our study, Gavin et al. (2013) suggest that after 7,000 yr ago state changes generally did not occur after fire in the Olympic Mountains, attributed to low variability in climate over this period. The hypothesis of faster species turnover due to greater climate variability and velocity before 7,000 yr ago also has support in eastern North America (Ordonez and Williams 2013), where rapid state changes during the late glacial and early Holocene were likely the result of extrinsic climatic forcing (Ordonez and Williams 2013). In contrast, state changes in the PNW during this period (this study, Gavin et al. 2013) appear to be driven by a mix of extrinsic and intrinsic factors, with evidence for fire catalyzing nearly every large-scale state change in vegetation.

The catalyzing role of fire at times of high climate velocity arises because fire accelerates population turnover when climatic conditions are unfavorable for seedling establishment of dominant species (Brubaker 1986). Given long-lived tree species, mature forests without disturbance can exist for decades to centuries after climate has become inhospitable for regeneration, resulting in considerable inertia in response to climate change (i.e., "the storage effect," Chesson and Warner 1981). Large, stand-replacing disturbances like these highseverity fires create a pulse of mortality that eliminates these lagging effects, catalyzing changes in species composition that would otherwise take many decades to centuries to unfold. Over the entire post-glacial period, regional-scale state changes in vegetation were associated with high-severity fire in our stand-scale records, save one - the arrival of Abies and Picea at the terminus of the YDC. The end of the Younger Dryas was a time of unprecedented climate velocity (Williams et al. 2011), and although the observed vegetation state change may have occurred through rapid competitive replacement alone, we cannot rule out high-severity disturbance that

induced mortality, such as drought, as a contributing mechanism (e.g., Lloret et al. 2012). Overall, our data suggest that vegetation state changes can be triggered by a combination of high-severity disturbance that synchronize mortality, and alternative successional pathways that arise and persist due to directional climate change. The strong similarity of dynamics between our two sites suggests these results are representative of processes affecting long-lived forests at the stand-scale. These inferred mechanisms have broad relevance, to any ecosystem where high-severity disturbances are possible, and three criteria are met: the life span of the dominant species exceed the time scale of climate change; mature individuals can persist through climate conditions under which germination of the same species is unlikely; and propagules are available from species that are better suited to post-disturbance climate.

Implications for the future

Our records highlight how individual high-severity fires can initiate rapid ecological state changes at local, stand-level spatial scales, when they occur in the context of directional climate change. These persistent state changes in vegetation at the stand scale (e.g., the shift from Douglas-fir to western redcedar dominated forests in the mid-Holocene) were almost certainly associated with changes in other ecosystem properties, including carbon and nutrient cycling (e.g., Franklin et al. 2002, Hudiburg et al. 2013). Given a 21st Century where many ecosystems are expected to experience rapid climate changes (IPCC 2014), favoring alternative species assemblages and altered fire regimes (Littell et al. 2010, Bell et al. 2014, Sheehan et al. 2015, Parks et al. 2016, Batllori et al. 2017), our paleoecological records suggest that stand-scale vegetation may quickly transform after a single fire event. As such, managers of coniferous forests with long-lived species will likely be faced with the choice of accommodating this transformation, actively resisting post-fire vegetation transformation, or directing change toward specific desired conditions based on new management goals that account for new or anticipated climate conditions (Fisichelli et al. 2015).

ACKNOWLEDGMENTS

We thank Jason Smith and Ethan Cuduback for field and lab work, Gregor Schuurman for charcoal counting, Wendy Sugimura for help throughout this project, and Tom Brown for assistance in AMS dating. Comments from Dan Gavin, Aaron Ramirez, Brett Dickson, and two reviewers improved this manuscript. Funding was provided by NSF grant 9873692 to LBB and DGS. Pollen and charcoal data presented here are publicly available thorough the Dryad Digital Repository (www.dryad.org) doi:10.5061/dryad.8h5d8.

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SUPPORTING INFORMATION

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.8h5d8