Canadian Journal of Forest Research
Revue canadienne de recherche forestière

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Journal:	<i>Canadian Journal of Forest Research</i>
Manuscript ID	cjfr-2016-0399.R2
Manuscript Type:	Article
Date Submitted by the Author:	09-Jun-2017
Complete List of Authors:	Ellis, Todd; Western Washington University, Environmental Studies Flower, Aquila; Western Washington University, Department of Environmental Studies
Keyword:	dendrochronology, dendroecology, drought, Pacific Northwest, western spruce budworm
Is the invited manuscript for consideration in a Special Issue? :	N/A

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**A multcentury dendrochronological reconstruction of western spruce budworm outbreaks
in the Okanogan Highlands, northeastern Washington**

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ABSTRACT

The western spruce budworm (*Choristoneura occidentalis* Freeman) is recognized as the most ecologically- and economically-damaging defoliator in western North America. Synchronous western spruce budworm outbreaks can occur over much of a host species' range, causing widespread limb and tree mortality, regeneration delays, and reduction in tree growth rates. Observational outbreak records in northern Washington State extend back only to the mid-twentieth century, limiting our understanding of this species' long-term population dynamics. In this study, we used dendrochronological methods to reconstruct multi-century outbreak records at four sites in the Okanogan Highlands of northeastern Washington State. We assessed long-term changes in outbreak patterns and tested moisture availability as a potential driving factor of western spruce budworm population dynamics. Outbreak synchrony was found to increase after the late 19th century, especially for high-intensity outbreaks, possibly due to anthropogenic factors. Moisture availability records show that outbreaks tend to occur at the end of droughts. As the variability of climate conditions is projected to increase, trending towards warm and dry summer conditions, the intensity and frequency of high-intensity western spruce budworm outbreaks may increase as well.

Key words: dendrochronology, dendroecology, drought, Pacific Northwest, western spruce budworm

1. INTRODUCTION

Western spruce budworm (*Choristoneura occidentalis occidentalis* Freeman) is recognized as an ecologically- and economically-significant defoliating insect in western North America (Fellin and Dewey 1982; Jenkins 2015). Regionally synchronous, decade-long outbreaks over large areas lead to widespread ecological resource impacts. However, the causal mechanisms driving this species' outbreak patterns and population dynamics remain under-explored, with results often pointing to contradictory mechanisms. An understanding of the western spruce budworm's (WSB) population dynamics is necessary to understand ecosystem dynamics, predict climate change effects, and mitigate ecological and resource management impacts. Multi-century records are needed to establish accurate outbreak histories and shed light on climatic drivers of WSB's outbreak dynamics. While observational records of WSB activity are only available back to the mid-20th century, variations in the width of annual tree rings can serve as a proxy record of WSB defoliation. Dendrochronological records have been used to reconstruct multi-century histories of WSB outbreak dynamics in the American Southwest (Swetnam and Lynch 1993), central Rocky Mountains (Ryerson et al. 2003), and the Pacific Northwest, including British Columbia (BC), Montana, Idaho, and Oregon (Swetnam et al. 1995; Flower et al. 2014a; Axelson et al. 2015). A prominent gap in the spatial coverage of these outbreak records exists in northern Washington State. In this paper, we present a dendrochronological reconstruction of WSB outbreaks in Washington State's Okanogan Highlands region.

The WSB consumes host foliage with a preference for current-year buds, staminate flowers, and developing cones, causing reduction in growth rates, regeneration delays, and limb and tree mortality after several years of repeated defoliation (Alfaro et al. 1982; Fellin and

Dewey 1982). Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and true firs (*Abies* spp.) are the WSB's principal host species (Fellin and Dewey 1982). Host stands undergoing an outbreak suffer a loss of biomass, increased rates of topkill, stem deformities, and tree mortality, especially of saplings and seedlings (Fellin and Dewey 1982; MacLauchlan et al. 2006), and may have increased susceptibility to subsequent insect outbreaks and pathogens (Alfaro et al. 1982). Repeated outbreaks ultimately modify the composition and structure of forests, redistributing the biomass and resources of susceptible host stands by removing photosynthetic tissue and reducing the local carbohydrate supplies necessary for continued growth (Alfaro et al. 1982). For example, Alfaro et al. (1982)'s study found that four outbreaks over roughly 85 years reduced the stand's potential radial growth by about 12%, with mortality rates ranging from 4.5% among mature trees with a dominant canopy position to 39% among suppressed understory trees.

In the Pacific Northwest, WSB infestations are frequent in many coniferous stands, with insect populations often continuously present at low endemic levels (Fellin and Dewey 1982; Wickman 1992). Radial growth impacts from WSB outbreak defoliation tend to last, on average, between 11 and 15 years (Lynch 2007). Aerial survey records suggest even shorter intervals of WSB outbreaks, lasting as few as one to two years in some regions (USDA Forest Service 2014). Quiescent period durations also vary across impacted regions, with an average of 32 to 40 years between outbreaks (Swetnam et al. 1995; Lynch 2007).

WSB outbreaks tend to occur synchronously over large areas of the primary host species' range (Ryerson et al. 2003; Flower et al. 2014a; Flower 2016). Large regions of synchronous or near-synchronous WSB outbreaks are usually attributed to one or more of the following factors: adult moth dispersal, exogenous stochastic factors such as climate, or trophic interactions with similarly-synchronous or mobile populations (Peltonen et al. 2002). Dispersal capabilities

strongly influence synchrony of population fluctuations at finer spatial scales (i.e., under 200 km), whereas climatic controls may be more a more important driver of synchrony at coarse spatial scales, though the mechanisms behind observed patterns of synchrony are still not well understood (Peltonen et al. 2002).

Over the course of the 20th century, some regions have shown increasing outbreak synchrony, severity, and/or intensity, possibly as a result of human impact (Swetnam and Lynch 1993; Swetnam et al. 1995; Ryerson et al. 2003; Campbell et al. 2006; Flower et al. 2014a; 2014b). The expansion of the extent and predominance of WSB's host species (both Douglas-fir and true firs) due to historical human impacts (Hessburg et al. 1994; Keane et al. 2002) may be linked to these changing outbreak dynamics. Selective harvesting of competing species, fire exclusion, and livestock grazing are thought to have favored the establishment of WSB's host species (Wickman 1992).

Climatic changes may have also played a role in these changing WSB outbreak dynamics, and climatic variables are thought to be a primary driving force of WSB population dynamics (Campbell 1993; Swetnam and Lynch 1993; Flower et al. 2014a). Fluctuations in moisture availability are seen as the most important variable in effecting changes to WSB population dynamics, with reduced moisture availability, and thus reduced needle moisture content, linked to enhanced larval survival, growth, and reproductive rates (Clancy 1991; Campbell 1993). In particular, the combination of increased moisture availability following drought conditions may improve both the quality and quantity of the WSB's preferred foliage during spring emergence (Flower et al. 2014a; Flower 2016). Previous studies have reported inconsistent relationships between WSB outbreaks and climatic conditions, suggesting that the WSB's response to climate variables may be regionally variable. For instance, Swetnam and

Lynch (1993) found that high spring precipitation was an influencing factor in outbreak timing in Colorado, while Flower et al. (2014a) found an increase in moisture stress was necessary in initiating outbreaks in Oregon, Idaho, and Montana. The potential range of the WSB includes a variety of climatic zones, with controlling climatic variables likely differing based on local- and regional-level climate. Local records are thus needed to assess climatic influences on WSB population dynamics in understudied areas such as northern Washington State.

The development of multi-century reconstructions contributes to the development of forest management strategies that can cope with the economic and ecological impacts of defoliating insects (Shepherd 1994). The purpose of this study is to uncover the Okanogan Highlands landscape's history of WSB outbreaks, connecting an important geographic gap to surrounding reconstructed outbreak records (e.g., Flower et al. 2014a; Axelson et al. 2015). We characterize the frequency, periodicity, levels of synchrony, and intensity of the landscape's outbreak history. Using these data with historical and reconstructed climate records, we enhance our understanding of how moisture availability influences the WSB's population dynamics and how changing climatic conditions may alter future WSB outbreak patterns.

2. MATERIALS AND METHODS

2.1 Study Area

We collected samples at six sites in the Okanogan Highlands of Okanogan National Forest in August and October 2014 (Fig. 1). The Okanogan Highlands are characterized by an arid, shrub-steppe environment, with vegetation dominated by Douglas-fir, with lesser amounts of ponderosa pine (*Pinus ponderosa* Douglas ex P. and C. Lawson), western larch (*Larix occidentalis* Nutt.), and grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.; McNab and Avers 1994). Elevations at our sites ranged between 1000 and 1600 m. The geological setting of most

study sites was gneiss bedrock, with the easternmost host site identified as basalt (Lasmanis and Cheney 1994). Using ClimateWNA's 30-year climate normals for 1981–2010, our site records report average temperatures between from -6.2°C to 15.8°C in the coldest and warmest months, respectively; average annual precipitation was recorded as 451 mm (± 62 mm), with 175 mm (± 5.2 mm) occurring during summer months (Wang et al. 2012).

2.2 Sampling Strategy

We collected samples at paired host and non-host sites. Samples collected at non-host sites were used to create a control chronology. This approach allowed us to isolate the defoliation signal contained in host tree-ring chronologies. We chose Douglas-fir as a host species due to its wide range in the Okanogan Highlands and its susceptibility to WSB outbreaks (Mason et al. 1997). We chose ponderosa pine as our non-host species. Douglas-fir and ponderosa pine have overlapping geographic ranges and similar responses to climate (Watson & Luckman 2002; Chen et al. 2010), but ponderosa pine is rarely defoliated by the WSB (Fellin and Dewey 1982).

We selected potential study areas with a history of frequent WSB outbreaks based on annual USFS Insect and Disease Survey data dating back to 1947 (Williams and Birdsey 2003; USDA Forest Service 2014). Within those potential study areas, we selected specific study sites using satellite imagery and in-situ evidence. We selectively targeted sites separated by significant topographic features such as mountains or valleys to insure adequate spatial coverage. We targeted stands with multi-century records, with the oldest trees ideally dating to at least 300 years (Table 1). We avoided host and non-host stands with extensive recent disturbances such as logging or fire damage.

We extracted two increment cores per tree. We avoided reaction-wood by coring parallel to the slope contour at 1.3 meters above ground, except where impossible due to difficult

topography. We sampled 15–20 trees from each of our four host stands for a total of 69 trees (Table 1). Within sites, we selectively-sampled based on visual assessment, using criteria that included old-age cues such as flattened tops, spiral-grained bark, large lower limbs, and the diameter at breast height being at least 40 cm. We avoided samples that included any indication of significant damage (e.g., fire scars) that could potentially distort the growth patterns.

For non-host stands, we sampled between six and 17 trees from three sites to maximize the visible impacts of defoliation (Table 1). To produce the longest possible record, we collected non-host samples with the intention of creating a single landscape-wide chronology for use with each host site. Monospecific non-host stands were preferentially targeted to avoid any growth release from species affected by defoliation or competition (Swetnam et al. 1995). Old-growth ponderosa pine stands are, however, aggressively-maintained by the USFS, who selectively harvests young growth around older pine trees (Nash, personal correspondence 2014). Because of these issues, the age of non-host stands superseded the importance of monospecificity and we include six trees from our Turner Lake site despite the presence of Douglas-fir.

2.3 Sample preparation and laboratory analysis

We prepared our samples using standard dendrochronological techniques (Speer 2010). We dried and glued core samples to wooden core mounts before surfacing with 120-, 220-, 320-, 400-, and 600-grit sandpaper. We first visually crossdated each sample from the bark inwards using a microscope. We then scanned and measured to the nearest 0.001 mm using Cybis' CooRecorder and CDendro software (Larsson and Larsson 2014). We used CDendro to visually identify known outbreak periods (Swetnam et al. 1995), and create master chronologies for each host and non-host site. CDendro allowed for the creation of a master chronology to be used with any sample measurements, minimizing the errors caused by our visual interpretation (Larsson

and Larsson 2014). We statistically crossdated our ring-width chronologies using the R package *dplR* (Bunn 2008; R Core Team 2013).

We used the *dplR* package to detrend raw measurements for host and non-host sites using a 100-year cubic smoothing spline (Bunn 2008). Since WSB growth impacts are inherently autocorrelative due to the decadal-plus temporal fingerprint of WSB outbreaks, we chose not to remove autocorrelation from our host site chronologies. This method of standardization ensures decadal impacts like WSB outbreaks will be maintained, while correcting for year-to-year age-related growth trends (Cook 1985). Resultant ring-width indices were averaged together by tree, and used to create mean site chronologies for host and non-host sites. A principal components analysis was run on the standard and residual (i.e., prewhitened using autoregressive modeling) non-host chronologies to extract the common signal shared by the non-host trees. We chose the first principal component of our three standard non-host master chronologies for our outbreak reconstructions because it explained the highest shared variance (81%) and correlated most strongly with our host chronologies.

2.4 Outbreak Reconstructions

We visually compared ring-width measurements with historical USFS records of known outbreak periods within the Okanogan Highlands (USDA Forest Service 2014), as well as nearby dendrochronological reconstructed outbreak dates (e.g., Campbell et al. 2006). Like crossdating, this visual comparison provided us with a first step to identifying periods of growth suppression at tree-level. Outbreaks are often visible as long-term growth suppression periods in the host tree chronologies that are not apparent in the landscape's non-host chronology. To statistically-reconstruct outbreak records, we first subtracted climatic noise from each host tree using the equation:

192 [1] $Corrected\ Index = I_{ht} - \frac{\sigma_h}{\sigma_n}(I_{nt} - \bar{I}_n)$

193 where I_h is the host trees' ring-width index for each individual year (t), σ_h and σ_n are the standard
 194 deviations of the individual host tree series and the landscape-wide non-host series' common
 195 period, I_n is the non-host control index for each year (t), and $\bar{I}_n$ is the mean for the non-host index
 196 for the common period. The output of this equation created a new value for each year of growth
 197 across host trees, where positive or negative values represent growth above or below the
 198 expected growth from climatic factors alone (Nash et al. 1975; Swetnam et al. 1985). Similarities
 199 between the corrected site indices during their shared common periods (1719–2014 for three
 200 sites, 1796–2014 for all four) were checked using Pearson's correlation coefficients.

201 To develop an appropriate set of criteria for identifying WSB outbreaks, we normalized
 202 the corrected tree series and identified outbreak-length periods of low growth. We did not record
 203 non-consecutive years of positive growth as outbreak interruptions, as non-consecutive positive
 204 growth years are common within outbreak periods (Swetnam et al. 1995). Minimum thresholds
 205 for WSB outbreak length vary by region, typically ranging between four to eight years of
 206 sustained below-average growth, with at least one year of growth at least 1.28 standard
 207 deviations below the long-term mean ring width (Swetnam et al. 1995). Another defoliating
 208 insect, the Douglas-fir tussock moth (*Orgyia pseudotsugata* McDunnough), can create similar
 209 outbreak patterns in Douglas-fir ring width records, but their outbreaks only last up to three years
 210 (Brubaker 1978), which makes four-year outbreak durations the shortest desirable outbreak
 211 length for separating the WSB signal from similar defoliating insects (Swetnam et al. 1995;
 212 Mason et al. 1997). We tested a minimum outbreak duration criterion of between four and eight
 213 years against observational outbreak records and chose four years as the most reflective of

historical outbreaks. A minimum growth reduction severity criterion of 1.28 standard deviations below the long-term mean was used for all reconstructions. Outbreak periods were identified based on these criteria for each individual tree, resulting in an annually resolved binary record of outbreak or non-outbreak conditions.

We standardized the binary, tree-level outbreak data into the percentage of a site's sample population reporting infestation year-to-year. Since outbreak reconstructions tend to regularly report some level of tree infestation reflecting endemic WSB populations, small-scale population changes, or background noise, we explored multiple outbreak intensity thresholds for each site between 30–80% of sampled trees reporting infestation. We compared the resultant outbreak time series with historical air and ground survey records (McComb 1979; Westfall and Ebata 2014; Jenkins 2015; Mehmél, personal correspondence 2015), with which a 40% threshold best identified the start of moderate outbreak conditions. Additionally, we used thresholds of 60% and 80% to identify high and very high outbreak intensities, respectively, which could gauge how intensity patterns have changed over the entire time series for each host site. The resultant corrected chronology provides measures of intensity, synchrony (the co-occurrence of outbreaks across our sites), and duration (the length of time when growth was below the corrected indices' potential growth) of outbreak disturbances within and between stands. We defined landscape-wide outbreaks as periods in which at least two of our four sites recorded coincident outbreaks for a minimum of two consecutive years.

2.5 Statistical Analysis

2.5.1 Outbreak Characteristics

We averaged outbreak duration and intensity for site and landscape-wide outbreak records, and checked for temporal changes by dividing both duration and intensity data into two

similar-sized groups: Before 1870 and after 1869. This separation would also roughly coincide with the introduction of forestry practices like harvesting in the Washington Territory (Chiang and Reese 2002). As historical records prior to 1970 either aren't reliable or don't exist for our study area, this breakpoint provides a loose representation for when Euro-American settlers' influences may have begun affecting regional outbreak patterns (Johnson and Ross 2008). We conducted ANOVA on stand-level normalized corrected indices to test for differences between Douglas-fir's growth response during and outside of outbreak conditions. Based on the results of the Shapiro-Wilk normality test, which indicated a non-normal distribution, we chose to use a Kruskal-Wallis nonparametric ANOVA.

2.5.2 Outbreak Synchrony Among Sites

We assessed the level of synchrony between stand-level outbreak histories (i.e., the percent of each site's trees recording an outbreak) using Pearson's correlation coefficients. Despite the high autocorrelation inherent in synchrony records, which makes estimation of statistical significance unreliable, the correlation coefficients can be used as an approximate index of sites' outbreak synchrony over time (Buonaccorsi et al. 2001). This simple analysis was conducted on the percent of each site's sampled trees recording outbreaks over both of our common periods (i.e., 1719–2014 and 1796–2014).

We used a modified one-dimensional Ripley's K-function (Gavin et al. 2006) to test whether discrete outbreak events were independent of one another over increasing bidirectional temporal lags. Years of outbreak occurrences, initiations, and cessations for our three oldest sites' common period were input into K1D v1.2 software (Gavin 2010). The youngest site, SMD, was removed from this method to retain as much of our landscape's record as possible without sacrificing too much of our sample size (Table 1). This method checks for co-occurrence of

outbreak events between any of the sites over increasingly long temporal windows until the bidirectional window is half the length of the total record length, with the resultant K and L functions providing a measure of outbreak synchrony or asynchrony over increasing temporal scales. To test for statistical significance, we ran 1000 simulations with a .95 confidence envelope using a circular randomization, with random year data added to all site records. We also separated the 1719 common period around the 1870 breakpoint for all three of our intensity thresholds – i.e., moderate (40%), high (60%), and very high (80%). This gives us a rough estimation of how site interactions may have changed before and after major human impacts began affecting the region.

2.5.3 Climate-Outbreak Associations

We conducted a Pearson’s cross-correlation analysis on both standard and residual host and non-host chronologies against landscape-wide instrumental and reconstructed climate records to determine if the chronologies expressed the similar climate responses necessary for outbreak reconstructions (Speer 2010). Our climate records included both historical (1895–2014; NOAA 2015) and reconstructed (1685–2003; Cook et al. 2004) Palmer Drought Severity Indices (PDSI; Palmer 1965). PDSI records provide a measure of summer (i.e., between June and August) moisture stress based on soil type, precipitation, and temperature (Palmer 1965). Cook et al.’s (2004) multi-century, gridded PDSI reconstruction network is available for 2.5° by 2.5° gridcells, with our landscape’s data drawn from grid 43 (Cook et al. 2004). In addition to PDSI data, we used historical precipitation data for water years (i.e., previous October to current September) and growing years (April to September of the current year) for the Okanogan Big Bend (Climate Division 7) area (NOAA 2015).

To identify climatic conditions associated with WSB outbreak initiations and cessations,

we used superposed epoch analysis to identify patterns of climatic conditions associated with outbreak initiation and cessation dates. Superposed epoch analysis uses event years (i.e., outbreak initiation and cessation dates) with time series data and designated temporal lags to test for significant departures from the mean (Grissino-Mayer 2001). We defined initiation dates as the first of two or more consecutive outbreak years following a gap of at least two years without recorded outbreaks, and cessation dates as the first of at least three years of non-outbreak conditions following an outbreak. However, we acknowledge that these dates are approximate, as there may be a lag of up to three years between the actual date of outbreak initiations or cessations and the onset of resulting radial growth impacts (Alfaro et al. 1982). We quantified climate anomalies using both historical and reconstructed climate records for an eleven-year window centered on outbreak events. Statistical significance was assessed with 1000 Monte Carlo simulations using *dplR* (Bunn 2008). To assess longer-term patterns of climate associated with outbreaks, we conducted paired, two-sample t-tests to test for differences between PDSI data associated with outbreak conditions against non-outbreak conditions.

3 RESULTS

3.1 *Dendrochronological characteristics and Outbreak histories*

A total of 69 host trees and 32 non-host trees were sampled over our six sites. Our landscape-wide non-host chronology dated to 1685. Host site records with at least two trees started between 1685 and 1796 (Table 1). Interseries correlation (Pearson's r ; $p < 0.01$ for all pairs) for our host sites ranged between 0.650 and 0.780, while non-host sites ranged between 0.627 and 0.760. Correlation coefficients (Pearson's r) between both our host and non-host chronologies and climate data supported the use of our sites for outbreak reconstructions (Table 2). All of our host site residual chronologies, as well as our landscape-wide residual non-host

chronology, reported significant ($p < 0.05$), positive relationships with reconstructed and historical PDSI, as well as water-year precipitation for the current and preceding year. The relationship with temperature returned less significance, although the average July temperature had a significant, negative relationship with all but our non-host chronology (Table 2).

Outbreak durations, based on sites with at least 40% of their sampled trees reporting outbreak conditions, ranged from two to 19 years across sites, with mean site-level outbreak durations ranging between 8.6 (± 3.9) and 10.7 (± 5.8) years by site (Table 3). Quiescent periods lasted between four and 52 years, with site means ranging between 11.4 (± 7.5) and 20.0 (± 10.1) years. The average for the landscape-wide outbreak duration and quiescent period length was 8.3 (± 4.3) and 13.3 (± 11.0) years, respectively. The Kruskal-Wallis ANOVA analysis suggested stand-level corrected indices during and between outbreaks are significantly different (Table 3). All four of our sites showed changes between the early (1685–1869) and modern (1870–2014) periods, with more years reporting outbreaks in the modern period.

3.2 Inter-site outbreak synchrony

During the 330 years covered by our landscape-wide reconstruction (1685–2014), all reporting sites experienced identical outbreak conditions (either outbreak or non-outbreak) during 184 individual years (55.8% of years in the common period). There were a total of 16 landscape-wide outbreaks (i.e., periods in which at least two sites shared concurrent outbreak conditions) covering 130 years (39.4%) of the total 330 years. Outbreak and non-outbreak conditions tended to occur synchronously or near-synchronously (Fig. 2), with synchrony increasing after 1869. Using our moderate intensity threshold, the early period included 43.8% of landscape-wide outbreak years (i.e., years with outbreaks at two or more sites), and the modern period 56.2%. Based on the moderate outbreak threshold, there has been little to no change in

outbreak synchrony since the start of the reconstruction. However, analysis using higher intensity thresholds revealed an increase in high-intensity, synchronous outbreaks in the modern period (Table 4). Using our very high intensity threshold, all landscape-wide synchronous outbreaks occurred after 1869 (1938, 1992, and 2010). For our three oldest sites, very high intensity outbreaks occurred in 0% to 5.9% of the total early period years, and between 6.9% and 14.5% of the modern period years.

Pearson's correlation of outbreak histories also revealed a pattern of synchrony. The average inter-site correlation for the three oldest sites' outbreak histories (i.e., MPD, TMD and VLD) was 0.60, while all four sites yielded a correlation of 0.71. The Tunk Mountain Douglas-fir (TMD) reduces both periods' correlations likely due to a unique period of asynchronous, stand-specific outbreaks during the mid-19th century also recorded in nearby outbreak reconstructions (Fig. 2; Campbell et al. 2006; Axelson et al. 2015).

The modified one-dimensional K-statistic for all outbreak years was statistically significant ($p < 0.05$) for up to 11 years for our three sites dating to 1719 (Fig. 3). Initiation and cessation dates for the 1719 common period showed significant temporal synchrony over windows up to six and nine years, respectively, with a higher degree of synchrony for initiation events than cessation dates or all outbreak years (Fig. 4). In the early period (1719–1869), no significant synchrony was found for outbreaks using our high and very high outbreak intensities (Fig. 3). All outbreak intensities reported between up to nine to 24 years of synchrony for the late period records (1870–2014).

3.3 Climatic influences on outbreaks

Outbreak initiation dates were preceded by between two and five warm-dry years at all sites, with initiation dates tending to occur in cooler, wetter years (Fig. 5). While no site reported

statistically-significant cool-wet years in the five years following an initiation event, all sites still showed a shift towards cool-wet conditions. Our landscape-scale outbreak record (1685–2014) shows a statistically-significant warm-dry anomaly in the second year preceding initiation events (Fig. 6). Paired, two-sample t-tests revealed significantly ($t = 2.83$, $p = 0.01$) cooler/wetter conditions during outbreak years (mean PDSI = 0.51) than during non-outbreak years (mean PDSI = -0.26).

We identified a tendency for shifts from cool-wet to warm-dry conditions during outbreak cessation years (Fig. 5). Between three and four sites reported cool-wet conditions in each of the five years preceding outbreak cessation dates, with two sites reporting at least one significant year of cool-wet conditions. The landscape-wide outbreak record shows the same pattern, with cool-wet conditions shifting to warm-dry conditions one year prior to cessation dates.

We saw the same patterns for historical PDSI data (1895–2014) from climate station records (Fig. 5). All sites reported warm-dry conditions for at least three years preceding outbreak initiations, with one site reporting significance for three years. Following outbreak initiations, all sites reported cool-wet periods for at least two years, with three sites reporting significant cool-wet conditions. Three sites reported warm-dry conditions during outbreak initiation events. All sites reported warm-dry conditions at least once in the two years following outbreak initiations, with one instance of significance. The landscape-wide outbreak record exhibits a statistically significant pattern of warm-dry conditions two years prior to initiation events, with significant cool-wet periods between three and five years after initiation dates (Fig. 6). All four of our sites and the landscape-wide outbreak record showed between one and four significant years of cool-wet conditions prior to cessation dates using the historical PDSI data,

with no sites returning significant conditions following cessation dates (Fig. 6).

4 Discussion

4.1 *Outbreak histories*

We were able to successfully reconstruct 330 years of WSB outbreak history for the Okanogan Highlands. Our reconstructed outbreak dates closely match those recorded in historical documents and aerial survey reports. Since accurate historical records for our study area are only available after the 1970s, nearby historical records for southern BC were used alongside our landscape's records to check against our outbreak reconstructions. Harris et al. (1985) used historical records to identify WSB outbreaks either as hectares affected, percent of trees infested, or severity of impact (e.g., existence of topkill) in the Canadian Cascade Range for the 1923–1930, 1943–1958, and 1977–1983 periods, with all but the earliest outbreak period not reflected in our data. WSB defoliation and population data were not recorded for the region between 1931 and 1942, possibly explaining the discrepancy between our reconstructions and historical records. The three most recent outbreaks (1975–1983, 1990–2001, 2009–present) concur with the USFS insect survey data and other WSB outbreak studies from the Pacific Northwest (USDA Forest Service 1977; McComb 1979; Alfaro et al. 2014; USDA Forest Service 2014; Axelson et al. 2015). Some inconsistencies between aerial survey records and our reconstructed outbreak dates may be due in part to inconsistent quality control and accuracy in identifying insect outbreaks via aerial survey (Johnson and Ross 2008).

Climate-growth analysis showed that the annual radial growth rates of both host and non-host trees were significantly limited by moisture stress (Table 2). Similar to Chen et al. (2010), we found positive correlation between our trees' radial growth and precipitation values, as well as negative correlation with temperature values. This suggests that warm, dry conditions inhibit

radial growth rates similarly in both ponderosa pine and Douglas-fir, while cool, wet conditions promote radial growth rates. The similarity in the climate-growth responses of the two species supports our use of ponderosa pine as a proxy for climatic variability in the construction of our corrected indices.

Douglas-fir dwarf mistletoe (*Arceuthobium douglasii* Engelm.) was prevalent in 11 of our sampled trees from MPD and VLD, but no associated radial growth anomaly could be identified (Hadfield et al. 2000). External signs of severe Douglas-fir dwarf mistletoe infection are known to overlap with signs of long-term WSB infestation, but radial growth impacts are unrelated (Hadfield et al. 2000). The 1975–1983 landscape-wide outbreak shows no lag between our reconstruction and historical records for the initiation year, which may be the result of signal contamination by Douglas-fir tussock moth's landscape-wide 1970–1974 outbreak (Mehmel, personal correspondence 2014). The Douglas-fir tussock moth impacts trees' growth response similarly to the WSB, which could replace the lag between outbreak initiation and trees' growth response we expect to see with WSB outbreaks (Brubaker 1978). Such overlaps are rare but always a potential issue with WSB studies, and this is the only known case in our study site of overlapping Douglas-fir tussock moth and WSB outbreak records overlapping. Since the relationship between our reconstructed outbreak history and moisture availability follows other studies (e.g., Swetnam and Lynch 1993; Flower et al. 2014a), we can safely assume the Douglas-fir tussock moth's influence on our reconstructions is minimal, but we acknowledge that a more conservative interpretation of our record would be that this is a history of defoliation events in general.

Our outbreak reconstructions resulted in outbreak patterns similar to those seen in nearby regions. The landscape's average outbreak duration of 8.3 years roughly matches nearby studies

in the Pacific Northwest (Campbell et al. 2006: 12 years; Flower et al. 2014a: 12 years; Alfaro et al. 2014: 7 years; Axelson et al. 2015: 11.2 years), while the landscape's quiescent period of 13.3 years was the lowest among nearby studies, which ranged between 15 to 64.2 years.

4.2 Inter-site outbreak synchrony and driving factors

Our reconstructions show that WSB outbreaks have been occurring synchronously in the region back to at least 1685. The landscape-wide outbreak records showed 16 instances of synchronous outbreaks occurring between 1685 and 2014. Similar to other studies, our region has seen an increase in outbreak synchrony, but not duration or frequency after the 19th century (Ryerson et al. 2003; Alfaro et al. 2014). The increase in outbreak synchrony is likely related to anthropogenic climate change and changing land-use regimes. Climate change over the 20th century has promoted climatic variability and aridity (Cook et al. 2004), with warming temperatures, regardless of changes to moisture availability, effecting an increase in the moisture stress response of trees during summer months (Coops and Waring 2011). Changing land-use regimes have increased forest homogenization by favoring expansion and increased density of the WSB's host tree species through practices such as fire exclusion and logging (Swetnam and Lynch 1993; Wickman 1992; Swetnam et al. 1995; Hessburg et al. 1994; Keane et al. 2002; Maclauchlan and Brooks 2009).

At our sites, a highly asynchronous period of site-specific outbreaks occurred between 1820–1870, during which only one site (TMD) was impacted by outbreaks. This asynchronous period is also reported by nearby records (Harris et al. 1985; Campbell et al. 2006; Axelson et al. 2015), and may be at least partially attributable to alternating regimes of warm and cool sea surface temperatures driven by the Pacific Decadal Oscillation teleconnections between 1840–1923 affecting local climate variables like PDSI (Gedalof and Smith 2001; Campbell et al.

444 2006).

445 Higher-intensity outbreaks at both site- and landscape-levels were more frequent in the
446 last century than in previous centuries. The degree of synchrony tended to increase with the
447 intensity threshold used, particularly when looking at outbreaks that occurred during the late
448 period (1870–2014). This clustering of synchronous events towards the 20th century suggests the
449 patterns of synchrony we see in the full records (i.e., 1719–2014) for high and very high
450 intensities may not accurately reflect the clustered pattern, due to the method of randomization
451 built into the K1D software being less effective at finding patterns with increasingly-clustered
452 temporal events (Gavin, personal communication 2016). The highest-tested intensity threshold
453 had no landscape-wide outbreak events prior to the 20th century, making the degree of frequency
454 and synchrony in the late period unprecedented. Three landscape-wide outbreaks of very high
455 intensity occurred among our sites, and all of them in the last century (during the 1940s, 1990s,
456 and 2010s), strongly suggesting anthropogenic impacts such as climate change or land-use
457 practices play a primary role.

458 The drivers of synchronous insect outbreaks are not fully understood, but there is support
459 for the role of both fine-scale (i.e., up to 200 km, but strongest up to 100 km) dispersal abilities
460 and exogenous, abiotic stochastic factors in driving WSB and similar insect outbreak synchrony
461 (Peltonen et al. 2002; Liebhold et al. 2004). WSB and similar moths have been found capable of
462 flying hundreds of km in above-canopy winds (Greenbank et al. 1980; Campbell 1993), and
463 synchrony of outbreak records is highest among sites less than 100–200 km apart (Peltonen et al.
464 2002), suggesting a moderate dispersal ability constrained by geography such as mountainous
465 terrain. Since our sites were all within 50 km of one another, it could be assumed that dispersal
466 plays a role in our outbreak synchrony. Dispersal abilities are likely influenced by local land-use

histories, as well, which have promoted the expansion and growth of Douglas-fir over non-host species like ponderosa pine since the late 19th century. Coupled with fire exclusion, this has led to an increase in host range and canopy density (Swetnam and Lynch 1993; Maclauchlan and Brooks 2009). This homogenization of host forests could also increase dispersal abilities over smaller areas with limited topographic barriers like the Okanogan Highlands, potentially leading to higher population densities during outbreak conditions (Willhite and Stock 1983). Another potential factor, the influence of trophic interactions on WSB populations, has been underexplored in research, but is assumed as similarly limited to local area due to the mobility of insectivores nearly mirroring prey dispersal abilities (Peltonen et al. 2002).

The Moran theorem proposes that the spatial and temporal autocorrelation of abiotic, exogenous factors help to synchronize biotic populations over a landscape (Moran 1953). Regional climatic stochasticity has been found to be the dominant influence synchronizing many insect species' population dynamics, particularly over larger spatial scales (Peltonen et al. 2002; Swetnam and Lynch 1993; Flower et al. 2014a). Flower (2016) linked widespread synchrony of WSB outbreaks with fluctuations in moisture availability. Synchrony across the scale of the landscape we analyzed could be due to either dispersal or climatic controls, or, most likely, a combination of the two. However, our outbreak history is strikingly similar to outbreak records at other sites across much of western North America. We found that all of our outbreak records between 1700 and 1990 coincide with synchronous outbreaks recorded in three to six other regions (central British Columbia, southern Colorado, northern New Mexico, Idaho, Oregon, and/or Montana). Specifically the landscape-wide outbreaks that occurred during 1715-1717, 1742-1752, 1760-1768, 1775-1777, 1785-1797, 1809-1814, 1819-1829, 1871-1883, 1892-1898, 1901-1910, 1938-1956, 1960-1963, and 1975-1983 all fall within time periods of widespread,

synchronous outbreaks (Flower 2016). This scale of synchrony suggests that climate, which varies over a similarly large geographic scale, plays a role in the synchronization of WSB outbreaks.

4.3 Outbreaks and climatic variability

WSB outbreak initiation dates show a distinct trend of transitioning climate from warm-dry conditions to cool-wet conditions: All four of our sites showed strong warm-dry conditions in two or more years immediately prior to initiation events (Fig. 5). During and after initiation dates, climate tended towards cool-wet conditions. This pattern of cool-wet climate conditions during outbreak conditions has been identified by other dendrochronological studies (Swetnam and Lynch 1993; Swetnam et al. 1995; Ryerson et al. 2003; Flower et al. 2014a). Since a variable lag of one to three years for both initiation and cessation dates usually exists between the actual time of an infestation's initiation / cessation and a tree's radial growth impacts (Alfaro et al. 1982; Swetnam et al. 1995; Mason et al. 1997), this suggests that the warm-dry years prior to an outbreak initiation represent the climatic conditions driving WSB outbreak initiations, and the subsequent transition to cool-wet conditions are necessary to sustain outbreak-level populations. This is consistent with previous studies that linked warm-dry conditions to outbreak initiation timing (Hard et al. 1980; Thomson et al. 1984; Campbell 1993; Flower et al. 2014a).

The transitional climate conditions we found associated with outbreak initiations supports the nonlinear pulsed plant stress hypothesis (Huberty and Denno 2004; Mody et al. 2009), in which temporal variability in moisture stress was proposed as crucial for initiating and subsequently sustaining insect outbreaks. Moderate drought stress has been found to favor WSB and similar herbivorous insects' growth and reproductive rates, as well as larval survival, by increasing foliar concentrations of nitrogen, sugars, and other favorable compounds (Mattson

and Haack 1987; Campbell 1993). These changes to foliage composition prior to transitioning climate conditions would benefit the growth and survival of WSB during larval stages by favoring the species' diet during moderate drought stress, and subsequently allowing for increased needle production and decreased needle toughness during sustained cool-wet conditions (Gower et al. 1992). This relationship can, however, reverse with prolonged outbreak conditions or increasing outbreak severity (Mattson and Haack 1987; Campbell 1993; Hubert and Denno 2004). Our results indicate the non-linear relationships described by the pulsed plant hypothesis as the strongest explanation for WSB outbreak dynamics over multi-century records.

Cessation dates, like initiation dates, are expected to show a one- to three-year lag between years of outbreak conditions and a tree's return to normal growth conditions during the recorded cessation date (Swetnam et al. 1995; Mason et al. 1997). This suggests that the five years of sustained cool-wet conditions recorded at our sites should represent the conditions in which outbreak-level WSB populations crashed (Fig. 5). Cessation dates with defoliating species like WSB are typically attributed to a loss of food from sustained overpopulation and trophic interactions with natural predators, parasites, or pathogens (Nealis 2015). As available needles become more sparse or difficult to mine, the WSB population density inevitably dips, while predators, parasitoids, and pathogens that prey on WSB are able to maintain population densities and increasingly contribute to WSB population losses (Nealis 2015). Despite also showing a transitioning climate around cessation dates, the transition to warm-dry conditions after cessation would not have a causal relationship with the WSB's population crashes. However, since our superposed epoch analysis consistently reported cool-wet conditions at three to four of our sites over five years prior to cessation dates, it's likely that long-term maintenance of cool-wet conditions plays a role in WSB population crashes via climatic effects on trophic interactions,

food loss, emergence- and budburst-timing, and physically damaging local weather conditions (Fellin and Dewey 1982; Campbell 1993).

5. CONCLUSION

WSB outbreaks have been occurring synchronously in the Okanogan Highlands since at least 1685. Outbreak synchrony across the landscape has increased in the late period (1870-2014). Although moderate-intensity outbreaks only increased in synchrony, high- and very high-intensity outbreaks saw drastic increases in both frequency and synchrony between the early (pre-1870) and late (post-1869) periods. It is probable that these changes were influenced by changing land-use regimes initiated by western expansion in the 19th century, with impacts like forest homogenization and fire exclusion favoring the expansion of WSB's host species, and thus increasing the likelihood of frequent, widespread WSB outbreaks.

Our superposed epoch analyses found strong relationships between landscape- and site-level outbreak histories and moisture availability using both dendroclimatic and observational climate records. Outbreak initiation dates showed a relationship with multiple, consecutive years of low moisture availability in the years preceding initiation events, and consecutive years of high moisture availability during and after initiation years. Cessation dates, on the other hand, showed a strong relationship with high moisture availability during the five years preceding recorded cessation dates. The temporal variability in moisture availability occurring during and around outbreak events supports the pulsed plant stress hypothesis in explaining WSB outbreak dynamics: High moisture stress encourages increases in WSB populations and dispersal rates, and a shift to low moisture stress is necessary to maintain the inflated outbreak-level populations.

The results of our study suggest that a complex combination of climate change, land-use patterns, and disturbances such as fires will continue affecting WSB outbreak dynamics in

coming centuries, and continued study is needed to better understand how this complex interplay of exogenous factors will direct WSB populations. Regional and global climate models project a continuing rise in temperatures over the 21st century, while precipitation may be impacted by stronger seasonality, including drier summers (Mote and Salathé 2010). These projected changes will likely increase the frequency of drought conditions necessary for initiating WSB outbreaks. It is also possible that the increase in drought conditions could hamper WSB outbreaks if drought conditions are sustained over too many consecutive years, or occur too frequently, since the climatic reversal warm-dry to consecutive cool-wet conditions appears necessary in sustaining outbreak-level WSB populations. Changes to land-use practices over the next century should also impact the occurrence of WSB outbreaks. A potential increase in forest fire occurrences with a changing climate could lead to changes in the landscape's biomass available to WSB populations, leading to indirect effects on WSB dynamics (Flower et al. 2014b). Additionally, changing climate may drive shifts in the distribution of the WSB's host populations over coming centuries.

ACKNOWLEDGEMENTS

We would like to thank Paul Nash of the USFS for his assistance in locating study sites essential for our study. We are also grateful to Connie Mehmel of the USFS for her knowledge of the study area's management history. Dr. Daniel Gavin of the University of Oregon also provided important feedback on our statistical methods. Drs. Andy Bunn and Michael Medler of Western Washington University provided important feedback and guidance during the course of the project. Lastly, this project would not have been possible without the field and lab assistance of Marissa Bhatnagar, Branden Rishel, Christopher Zemp, Venice Wong, Ryan Schumacher, Shelby Van Arnam, Demian Estrada, Derek Huling, and Dustin Gleaves.

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TABLES

Table 1

Site and chronology characteristics for our four host (Douglas-fir) sites and three non-host (ponderosa pine) sites in the Okanogan Highlands.

Site	Latitude	Longitude	Elevation (m)	# of trees	DBH* (cm)	Oldest record	EPS [†] (Pearson)	Interseries <i>r</i> (Pearson)
<i>host (Douglas-fir)</i>								
MPD	48.786	-119.243	1359	16	86.1 (±16.8)	1685	0.933	0.686
SMD	48.561	-119.172	1379	18	70.7 (±15.4)	1796	0.943	0.780
TMD	48.552	-119.225	1599	20	75.0 (±14.5)	1685	0.936	0.650
VLD	48.825	-118.927	1286	15	92.5 (±21.5)	1719	0.965	0.760
<i>non-host (ponderosa pine)</i>								
DCP	48.528	-119.029	1003	17	66.2 (±8.1)	1685	0.942	0.627
TLP	48.672	-118.981	1334	6	66.3 (±13.3)	1685	0.847	0.720
VLP	48.824	-118.927	1274	9	95.3 (±24.9)	1685	0.936	0.760

* Diameter at breast height, which represents the measured diameter of a tree at breast height. Numbers in parentheses represent standard deviations.

[†] Expressed population signal, which is an estimation of how well a limited chronology represents an area’s true chronology.

Table 2

Cross-correlation (Pearson's r ; $p < 0.05$ except where noted) values of residual host (Douglas-fir) chronologies and the landscape's non-host (ponderosa pine) chronology against reconstructed (1685-2003) and historical (1895-2014) climate data for the Okanogan Highlands.

Site	PDSI* (Cook)	PDSI* (NOAA)	WYP†	Previous year's WYP†	GYT‡	Previous year's GYT‡	Mean July temperature
MPD §	0.40	0.39	0.37	0.24	-0.08	-0.06	-0.22
SMD §	0.42	0.48	0.42	0.29	-0.13	-0.06	-0.18
TMD §	0.33	0.27	0.22	0.33	-0.36	-0.13	-0.22
VLD §	0.47	0.46	0.40	0.27	-0.13	-0.03	-0.24
Landscape non-host	0.56	0.53	0.53	0.28	-0.09	-0.11 [§]	-0.12

* Summer (June to August) Palmer Drought Severity Index, provided either by Cook et al. (2004) as climatic reconstructions (1685-2003), or NOAA's historical records (1895-2014)..

† Water-year (previous October to current September) precipitation.

‡ Growing-year (April to September) temperature.

§ Host sites Mount Phoebe (MPD) and Tunk Mountain (TMD) reflect the full reconstructed PDSI record (1685-2003). Sneed Mountain (SMD) covers only 1796-2003, and Virginia-Lily (VLD) covers 1719-2003.

^{||} Value does not represent a significant ($p < 0.05$) relationship.

Table 3

Outbreak statistics for our four Douglas-fir host sites (MPD, SMD, TMD, and VLD), and our landscape-wide outbreak record in the Okanogan Highlands. Numbers in parentheses represent standard deviation.

Site	# of outbreaks	Mean outbreak length (years)	Mean quiescent period (years) *	% of record with outbreak conditions	Outbreak and non-outbreak ANOVA †
MPD	15	8.6 (±3.9)	14.5 (±11.4)	38.2	97.85 $p < 0.01$
SMD	8	9.1 (±4.5)	20.0 (±10.1)	32.4	67.24 $p < 0.01$
TMD	17	8.9 (±4.3)	11.4 (±7.5)	44.6	109.85 $p < 0.01$
VLD	11	10.7 (±5.8)	16.0 (±13.6)	38.2	83.67 $p < 0.01$
Landscape-wide ‡	16	8.3 (±4.3)	13.3 (±11.0)	39.4	112.24 $p < 0.01$

* Mean quiescent period represents the average period of time between outbreak cessations and subsequent outbreak initiations.

† Kruskal-Wallis ANOVA conducted on corrected indices during outbreak conditions against non-outbreak conditions. Numbers represent chi-square and p -values.

‡ Landscape-wide outbreak record represents times where two or more sites reported concurrent outbreaks (1685-2014).

Table 4

Percent of outbreak years occurring in the early (1685–1869) and modern (1870–2014) periods using moderate (40% of trees), high (60% of trees), and very high (80% of trees) outbreak intensity thresholds. MPD, SMD, TMD, and VLD represent our four Douglas-fir host sites in the Okanogan Highlands, and the landscape-wide record represents time when two or more sites reported outbreak conditions.

Site	Moderate		High		Very high	
	Early	Late	Early	Late	Early	Late
MPD	34.1	43.4	21.6	23.4	5.9	14.5
SMD	20.3	38.6	8.1	22.1	0.0	6.9
TMD	41.6	48.3	6.5	26.9	2.2	11.7
VLD	33.8	42.8	13.9	22.1	2.6	13.1
<i>Landscape-wide</i>	30.8	50.3	9.7	28.3	0.0	14.5

Note: Percents shown are the total number of years within each period's length. Each of our four sites are represented, as well as the landscape-wide outbreak history with at least two sites reporting outbreaks concurrently. SMD (1796–2014) and VLD (1719–2014) do not represent equal measures of time between early and modern periods. Landscape-wide outbreaks record represents times where two or more sites reported concurrent outbreaks (1685–2014).

FIGURE CAPTIONS

Fig. 1

Location of host (Douglas-fir) and non-host (ponderosa pine) sites within the Okanogan Highlands. Significant local features include the highest peak, Mount Bonaparte, immediately east of site MPD, and the Aeneas Valley dividing our southern sites from our northern locations. Shaded region on the inset map represents distribution of Douglas-fir, provided by Little (1971). Digital elevation model courtesy of the U.S. Geological Survey.

Fig. 2

Percent of trees recording an outbreak at our four Douglas-fir host sites. Solid black lines represent an 8-year moving average of the percent of trees returning outbreak records, and the dashed line represents the unfiltered outbreak records. The two dotted straight lines indicate two of our outbreak intensity levels, wherein our sites have at least 40% (moderate) and 80% (very high) of the sampled trees reporting outbreak conditions

Fig. 3

Modified Ripley's K-function calculated for all outbreak years (1719–2014) in the Okanagan Highlands using moderate (40% of sampled trees reporting outbreak conditions), high (60%), and very high (80%) outbreak intensities. The top image represents all years of data. The middle and bottom images separate the outbreak years between early (1719–1869) and late (1870–2014) periods. Note the change to the y-axis due to the decreased sample sizes for very high-intensity outbreaks.

Fig. 4

Modified Ripley's K-function for moderate outbreak initiation dates and cessation dates. All dates were taken from our three host Douglas-fir sites dating to 1719 to include as much of the record with as many of our sites as we could. Y-axis represents a level of synchrony (positive) or asynchrony (negative) calculated using the temporal window (one to 30 years) shown on the x-axis, with the shaded region representing the confidence interval (95%).

Fig. 5

Summary of superposed epoch analysis summary of our four host Douglas-fir sites' initiation (first year of outbreak) and cessation (first year of non-outbreak conditions following an outbreak) dates using Cook et al.'s (2004) PDSI reconstructions (1685–2003) and historical (1895–2014; NOAA 2015) PDSI records. Ascending bars represent number of sites with positive PDSI anomaly, descending bars represent number of sites with a negative PDSI anomaly. Instances of high significance are noted by dark grey (90%) and black (95%) shading.

Fig. 6

Superposed epoch analysis using the landscape-wide outbreak initiation and cessation dates for the Okanogan Highlands. We used Cook et al.'s (2004) PDSI reconstructions (1685–2003) and historical (1895–2014; NOAA 2015) PDSI records. Ascending and descending bars represent positive and negative departures from the mean, respectively. Instances of high significance

(95%) are noted by black shading.

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