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RESEARCH ARTICLE

Valleys of fire: historical fire regimes of forest-grassland ecotones across the montane landscape of the Valles Caldera National Preserve, New Mexico, USA

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Abstract
Context Montane grasslands and forest-grassland ecotones are unique and dynamic components of many landscapes, but the processes that regulate their dynamics are difficult to observe over ecologically relevant time spans.
Objectives We aimed to demonstrate the efficacy of using grassland-forest ecotone trees to reconstruct spatial and temporal properties of the historical fire regime in a complex landscape of montane forests and adjacent grasslands.
Methods We sampled and crossdated fire-scarred trees along ecotones and compared variations in historical fire occurrence within and among nine adjoining *valle* basins in a 10,158 ha landscape. We analyzed fire year extensiveness, climate regulation, and the occurrence of consecutive fire years.
Results The resulting tree-ring record covers 1240–2005 AD, with 296 trees recording 125 replicated fire years during the analysis period 1601–1902 AD. Mean fire intervals for all events recorded on two or more trees ranged from 4.7 to 13.6 years in individual *valles*, and a mean of 2.4 ± 1.7 (SD) years at the landscape scale. Between 1660 and 1902, extensive fires occurring in six or more *valles* occurred 15 times, on average at ~ 17-year intervals; 29 moderately widespread fires (3–5 *valles*) occurred during this period, at 8.7 year intervals on average. Widespread events occurred in years with a significantly lower Palmer Drought Severity Index (PDSI) preceded by years of significantly positive PDSI, indicating conditions favorable for fine fuel production. Spatial reconstruction of fire extent revealed

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multiple occurrences of consecutive-year fires burning non-overlapping areas, associated with persistent low PDSI anomalies preceded by positive conditions in antecedent years.
Conclusions A landscape spatiotemporal approach to reconstructing fire regimes of montane forest-grassland complexes provides a valuable baseline for guiding prescribed and natural fire management at large spatial scales.

Keywords Contingent causation · Dendroecology · Fire-climate · Fire scars · Forest-grassland ecotone · Fuel dynamics · Landscape fire · Spatial reconstruction · Top-down/bottom-up regulation

Introduction

Fire is a fundamental ecosystem process in forests and grasslands in the southern Rocky Mountains and the American Southwest (Weaver 1951; Kaib et al. 1999; Veblen 2000; Swetnam and Baisan 2003; Ford et al. 2004; Grissino-Mayer et al. 2004). Fire creates and maintains diverse vegetation mosaics of plant communities, species populations, and size and age distributions across the landscape (Miller and Urban 2000; Keeley et al. 2009; Hagmann et al. 2014; Heyerdahl et al. 2018). Due to differential adaptations to fire among plant functional groups, fire also plays a central role in mediating competition between herbaceous and woody plants (Van Langevelde et al. 2003; Beckage et al. 2009; Nano and Clarke 2010). As a consequence, fire is a key factor in the maintenance of landscape mosaics of grasslands, meadows, and seral stands, as well as determining the characteristic stand structure and composition of ponderosa pine, mixed-conifer, and spruce-fir landscapes (Koerner and Collins 2014; Margolis 2014; O'Connor et al. 2014).

Historical landscape-level spatial patterns of fire occurrence and the frequency of past fire events are critical to understanding the long-term ecological role of fire in montane ecosystems (Heyerdahl et al. 2001; Margolis 2014; Coop et al. 2016; O'Connor et al. 2017). While analyses of vegetation change due to fire extent and frequency are relatively straightforward using recent (twentieth century) fire records (Morgan et al. 2001; Rollins et al. 2002; Fairfax et al. 2015), modern landscapes are generally heavily managed, and their fire regimes may be modified by a wide range of management actions. To obtain a longer temporal perspective on landscape processes, tree-ring analysis of fire-scarred trees allows reconstruction of fire regimes over many centuries prior to documentary records of fire events (Agee 1993; Swetnam et al. 1999; Falk et al. 2011; Guiterman et al. 2017). Such information has contributed substantially to development of modern fire management policy and strategies in ecosystem restoration and management plans on both public and private forested landscapes (Allen et al. 2002; Keeley et al. 2009; Stephens et al. 2013).

Unlike forests, pre-settlement data on fire extent and frequency in grassland ecosystems are generally lacking, due to the absence of woody trees and shrubs that can record the year of fire exposure via fire scars and annual growth rings (Smith and Schussman 2007). Definitive measures of grassland fire return intervals and extent have been based on recent (twentieth century) documented occurrences, while estimates of pre-settlement grassland fire return intervals are based primarily on vegetation recovery times following burning. For example, semi-arid grasslands in the American Southwest have estimated historical fire return intervals of 5–15 years in ungrazed areas with sufficient fine fuels to carry fires (Johnsen 1962; Wright and Bailey 1982; McPherson 1995; Parmenter 2008). However, if high densities of livestock have removed most of the herbaceous fuels, then arid-land grassland may burn only two to three times per century on any given site (Parmenter 2008). In addition, roads can act as barriers to grassland fire spread, artificially increasing fire return intervals for grass-dominated rangelands. These factors confound natural fire occurrences and behavior, limiting current knowledge of the historical role of fire in Southwestern and southern Rocky Mountain grasslands. Hence, an alternative method for estimating pre-settlement grassland fire return intervals would provide valuable information for ecologists and land managers charged with understanding and restoring complex landscapes to their natural fire regimes.

In southwestern North America, montane grasslands occur across a wide range of elevations, from high elevation alpine and subalpine environments to lower elevations associated with ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson var. *scopulorum* Engelm) and piñon-juniper ecosystems along the 4830 km Rocky Mountain cordillera (Risser 1995;

Bogan et al. 1998; Finch 2004; League and Veblen 2006; Vankat 2013). In the Jemez Mountains of northern New Mexico, a locus of substantial research on montane grasslands (Allen 1984, 1989; Muldavin and Tonne 2003; Coop and Givnish 2007a, b, 2008; Suazo et al. 2018), grassland communities are embedded in broader landscape matrices of mixed conifer and ponderosa pine forests at elevations of 2600 m to ,500 m. Montane grasslands range in size from small islands of a few hectares within forests up to large expanses of thousands of hectares (Fig. 1).

Along with microclimate and soils, fire is a major influence on the creation and maintenance of montane grasslands, playing a particularly important role in maintaining the boundary between forest and adjacent grassland communities (Arno and Gruell 1983; Allen 1989; Brown and Sieg 1999; Ford et al. 2004; Coop and Givnish 2007a, b). The ecotonal community between grassland and adjacent forest is a dynamic zone where competition between grasses and trees is mediated by the relative (in)tolerance to fire of woody plant seedlings and grasses, respectively (Risser 1995; Myster 2012). Prior to the introduction of large-scale grazing by Euro-American settlers, frequent (mean fire intervals 5–15 year) surface fires maintained open stand structures on south-facing ecotones by killing most tree seedlings while permitting grasses and occasional trees to survive (Kaib et al. 1996, 1999; Brown and Sieg 1999). Fire thus maintained the forest-grassland ecotone by limiting tree encroachment into montane grasslands, while encouraging dominant grass growth. In swales and extensive low-lying *valles* (a Spanish word for grass-covered valleys), cold air drainage, frosts, and wet soils in valley basins may have inhibited successful tree seedling establishment, giving graminoid plants additional competitive advantage and maintaining these communities essentially free of trees (Peet 2000; Coop and Givnish 2007a,2008; Vankat 2013). Forest-grassland ecotones also can function as corridors for fire spread, due to the optimal combination of fine fuel mass, continuity, and

Fig. 1 Montane grasslands of the Valles Caldera, New Mexico, USA. The landscape is characterized by large, extensive grasslands surrounded by ecotones with mixed-conifer and ponderosa pine forests. Episodic surface fires burn through groves of trees in the ecotone, leaving a record in the form of scars in living trees. Images provided by JJ Dewar (upper right), TW Swetnam (lower), RR Parmenter (upper left)

packing ratio (Conver et al. 2018), which would further favor grass dominance.

In most dry forests and savannahs in southwestern North America, fire frequency is regulated primarily by fine fuel production. The seasonally dry climate generally offers a climatic window favorable for combustion, and in many areas (including the Jemez Mountains) lightning ignitions are abundant and thus generally not limiting (Allen 2002). In these ecosystems, Superposed Epoch Analysis (SEA) reveals consistently that widespread fire years are conditioned not only by fire-year conditions of drought and temperature, but also by one or more preceding years of cooler, wetter weather favorable for fine fuel production (Swetnam and Betancourt 1998; Stephens et al. 2003; Brown and Wu 2005; Brown et al. 2008; Swetnam et al. 2016; Margolis et al. 2017). In forested systems, herbaceous and foliar fuels may require several years following fire to accumulate sufficient biomass to carry a spreading fire, but in grasslands fuel recovery can occur much more rapidly, often within a year (Uresk et al. 1980; Hunter and Omi 2006; Suazo et al. 2018). Under historical conditions (i.e., prior to fire suppression) some fires may have carried over as smoldering combustion of ground fuels through a dry winter and then re-ignited in warmer conditions the following spring; alternatively, sequential fire years could represent independent ignition events by lightning or humans. In either case, forest-grassland ecotones and adjacent grasslands could experience spreading fires in consecutive years. This has not been widely observed in forested ecosystems, but we hypothesized that consecutive years with widespread fire could occur more frequently in a landscape with extensive forest ecotones with dry grasslands.

Extensive tree-ring studies of historic surface fire regimes in ponderosa pine forests of southwestern North America document the widespread cessation of frequent, low-intensity surface fires by ca. AD 1900 across the region (Swetnam et al. 2001, 2016). Similar fire regime changes likely also occurred in adjoining and intermixed montane grasslands, although direct evidence is limited (but see Allen 1989; Kaib et al. 1999). Research on montane grasslands in the Jemez Mountains has found substantial post-1900 encroachment of coniferous trees into these varied grassland ecosystems, driven primarily by fire regimes altered by historic overgrazing by domestic livestock (sheep, cattle) and direct fire suppression (Allen 1984, 1989; Swetnam et al. 1999; Coop and Givnish 2007a, b) Knowledge of the ecological role of fire as a natural disturbance in high-elevation montane grasslands and adjoining forests is thus essential to support modern ecosystem management, particularly efforts to restore more natural fire regimes to maintain historic forest-grassland dynamics.

In this paper, we demonstrate the efficacy of using grassland-forest ecotone trees for recording the frequency and landscape pattern of historical ecotonal and adjacent grassland fires. We reconstructed the historical fire regime (AD 1601–1902) of montane valley forest-grassland ecotones of the Valles Caldera National Preserve (VALL) in the Jemez Mountains, New Mexico USA. We used these data to analyze spatial and temporal landscape-scale properties of the historical fire regime at multiple spatial scales, from single *valles* to the entire Valles Caldera complex. We also employed this high-resolution reconstruction of the ecotonal fire history to identify spatial and temporal controls on the fire regime in widespread and non-fire years, including the ability of this large landscape to support widespread fires in consecutive years. The insights derived from long-term reconstructions have potential application to large-scale ecosystem management in these unique systems.

Methods

Study Area and past land use

The Valles Caldera National Preserve (VALL), 35°50′ – 36° 00′ N, 106° 24′ – 106° 37′ W) occupies 35,976 ha in the Jemez Mountains of north-central New Mexico, USA. The Preserve is bounded primarily by the Santa Fe National Forest, with shorter boundaries in the southeast and northeast with Bandelier National Monument and Santa Clara Pueblo respectively, and Jemez Pueblo to the southwest (Fig. 2).

VALL is centered on the Valles Caldera geological landform in the heart of the Jemez Mountains, a 24 km-wide basin created by the collapse of a pair of underlying magma chambers following a series of volcanic eruptions 1.6 and 1.25 million years ago (Heiken et al. 1990; Goff 2009). The Valles Caldera evolved further through subsequent eruptions along the caldera ring-fracture zone, the rise of a large central resurgent dome (Redondo Peak), and the development of glacial-period lakes within the caldera basins (Fawcett et al. 2011). These processes resulted in a landscape of forested domes that arc from the east to the west in the northern portion of the caldera, surrounded by extensive basin-bottom grasslands within the circular caldera rim. Mountain slopes are comprised of ignimbrite and rhyolite rock types with primarily mountain soils (Andisol, Alfisol, and Inceptisol soil orders) derived from volcanic rock and gravel (Smith and Bailey 1963; Nyhan et al. 1978; Muldavin and Tonne 2003; Hibner et al. 2010). The caldera basins are underlain with mostly Mollisols (grassland soils), derived from alluvial and lacustrine sediments (Muldavin and Tonne 2003; Hibner et al. 2010).

The nearest long-term weather information for the VALL comes from stations at Los Alamos (35°52′ N, 106°21′ W, 2243 m) to the east, and Wolf Canyon (35° 57′ N, 106° 45′ W, 2506 m) to the west of VALL. Mean annual precipitation (1954–2004) at the Wolf Canyon weather station is 576 mm. The regional climate is semi-arid continental: dry conditions prevail during May and June ($\sim$ 6% and $\sim$ 5% of total annual precipitation, respectively), followed by frequent rains during the July–September North American Monsoon period, which accounts for 60% of annual precipitation (Sheppard et al. 2002; Touchan et al. 2011). Precipitation during the winter months is largely from snowfall delivered by synoptic-scale low pressure systems (Sheppard et al. 2002). The varied elevation, topography, and soils of the VALL modulate the influence of climate in this region, resulting in diverse vegetation (Muldavin and Tonne 2003).

The Valles Caldera includes a variety of habitat types and plant communities, including upper and lower montane grasslands, wet meadows, riparian areas, ponderosa pine woodlands, mixed-conifer forests, and wet and dry mesic spruce-fir, with aspen stands found at middle and upper elevations (Fig. 2; Muldavin and Tonne 2003). Mixed forests are distributed widely on the volcanic domes and

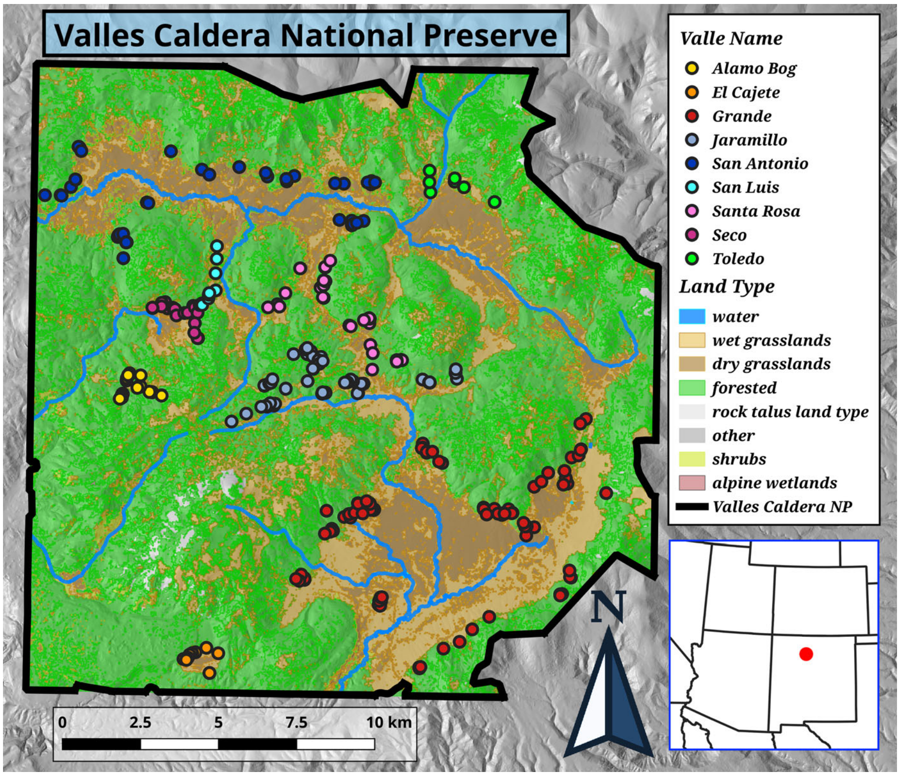

Fig. 2 Locations of fire-scarred trees sampled in ecotones of the Valles Caldera study area in New Mexico, USA. Symbol colors indicate the *valle* in which each sample was located (upper legend). Background colors indicate dominant vegetation types (lower legend) acquired from Muldavin et al. (2006). Terrain derived from PALSAR Radiometric Terrain Corrected High-Resolution Dataset (ASF DAAC 2006). Inset: geographic location of study area; red circle indicates location of study area

surrounding caldera rim, interspersed with upper montane grasslands on dry south-facing upper slopes.

Montane valley grasslands dominate the expansive lower elevations of the *valles*, forming an interconnected network of grasslands covering approximately 10,158 ha of the Preserve (Fig. 2). At mean elevations between 2628 and 2727 m, these valley bottoms support largely treeless meadows fringed with ponderosa pine and mixed conifer forests (Allen 1984, 1989; Muldavin and Tonne 2003). These grasslands are dominated by native bunchgrasses, sedges, and forbs, with wetter meadow vegetation found along drainages (Muldavin and Tonne 2003; Coop and Givnish 2007a).

Forest-grassland ecotonal communities occur along the boundaries between the treeless lower montane grasslands in the caldera basins and the closed forests on the slopes of the adjoining domes and caldera rim mountains (Figs. 1, 2). Forest-grassland ecotones include lifeforms and species from both adjacent forest and grassland communities.[1] Montane grassland ecotonal herbaceous communities are dominated by native bunchgrasses including Thurber fescue (*Festuca thurberi* Vasey), Parry's oatgrass (*Danthonia parryi* Scribn.), Arizona fescue (*Festuca arizonica* Vasey), and pine dropseed (*Blepharoneuron tricholepsis* (Torr.) Nash), along with the non-native Kentucky bluegrass (*Poa pratensis* L.) and diverse sedges and forbs. Ecotone forests on southerly aspects are dominated by ponderosa pine (*Pinus ponderosa*), with intermixed southwestern white pine (*Pinus strobiformis* Engelm.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. glauca (Beissn.) Franco), while north-facing *valle* borders typically are mixed-conifer forest dominated by Colorado blue spruce (*Picea pungens* Engelm.), aspen (*Populus tremuloides* Michx.), and Douglas-fir (Muldavin and Tonne 2003).

Field procedures

We used fire-scarred trees as the primary source of evidence to document and analyze spatial and temporal patterns of historical fires in the VALL. Provided that the rings are correctly crossdated, fire scars provide annually accurate point records of fire as a landscape process (Dieterich and Swetnam 1984; Falk et al. 2011; Farris et al. 2010, 2013).

In order to obtain a multi-century record of surface fires in the montane grassland, we located and collected fire scars from scarred trees along the surrounding grassland-forest ecotones of the major *valles* of the VALL (Fig. 2). Our sampling strategy was to obtain a representative sample from georeferenced fire-scarred trees along these ecotones to allow reconstruction of long-term spatial inventories of fire events at multiple scales from individual ecotonal areas to landscape levels (Heyerdahl et al. 2001). Fire-scarred specimens were sampled by searching systematically along the grassland-ecotones around the major montane grassland basins (*valles*) and smaller linear areas of grassland (Farris et al. 2013). The majority of field sampling was conducted in 2007–2008; we incorporated previously collected material by the co-authors, including 23 fire-scarred tree samples collected around the forest-grassland ecotone near Alamo Bog (Allen et al. 2008).

Crews searched extensively over two field seasons prior to sampling of fire-scarred old wood, including snags, down logs and stumps, and live trees with morphological signs of age including thick and twisted trunks, large drooping branches, flat-topped canopies, and other characters in order to capture a long temporal record. While selecting samples, we made a concerted effort to locate remnant dead wood in order to minimize the cutting of living trees and to extend fire chronologies as far into the past as possible, including old stumps from early logging operations that had harvested easily accessible ecotone trees (Balmat 2004). Wherever possible, we sampled fire-scarred trees in clusters of at least two nearby trees to improve the reliability of the fire record from a given locality (Dieterich 1980), to account for degradation of scars on older trees (Arno and Sneck 1976; Kilgore and Taylor 1979) and to improve the likelihood of dating fires to the exact calendar year (Swetnam and Baisan 1996). If there was an abundance of materials available for sampling, we selected trees with the maximum number of well-preserved scars in combination with old specimens to ensure the longest and most complete temporal record (Farris et al. 2013). We also sampled some younger trees or those with scars closer to the outer growth margin in order to capture the record of more recent fires.

[1] Taxonomy follows Dick-Peddie et al. (1993) and Muldavin and Tonne (2003). Plant authorities verified at USDA PLANTS Database (USDA NRCS 2020).

Once suitable fire-scarred trees were located, we used a chain saw to remove partial or full sections from snags, logs, stumps, and living trees. Wherever possible, we cut wedge sections from the face of fire scars in order to preserve standing trees and snags (Arno and Sneck 1976; Heyerdahl and McKay 2008). For each sample and for the surrounding area, we recorded specimen number, species, number of visible scars, scar condition, tree diameter, condition class, site topography, and stand conditions. All samples were field-referenced with handheld GPS. In cases where trees had fallen, GPS points were recorded closest to the estimated rooting point.

Laboratory procedures

In the laboratory, samples were re-assembled and stabilized, prepared for analysis by trimming excess wood, and then sanded with a series of progressively finer sanding abrasives (from 40 to 400 grit) until cell structure was clearly visible using a 10 × binocular microscope. Each cross section was examined and crossdated employing standard crossdating techniques (Dieterich and Swetnam 1984; Speer 2010) to determine the calendar year of each fire event recorded on the landscape. Other characteristics noted for each sample included the clarity of the fire scar within a dated ring, relative within-ring scar position where discernable, and the presence of other features that could be fire-related, including resin ducts, growth releases or suppressions, and other injuries (Swetnam et al. 2009; Arbellay et al. 2014; Guiterman et al. 2015; Smith et al. 2016). Two dendrochronologists crossdated each sample independently to ensure the accuracy of fire scar dates and ring chronologies.

We defined a tree to be in recording status after the date of an initial fire scar. Recording trees are fire-scarred individuals with an open wound (not covered by bark) and fully intact (*i.e.* sample margin not burned away or eroded) for a series of annual rings (Swetnam and Baisan 2003; Van Horne and Fulé 2006; Falk et al. 2011). Only recording periods were used from each sample in calculation of fire regime statistics.

Analytical procedures

Individual trees generally produce an incomplete fire record because not every fire wounds every tree, and because evidence of past fire exposure may have been lost (e.g. from weathering of old stumps and snags, or consumption in subsequent fires). To compensate for this incompleteness in the fire record, we compiled composite fire records (CFR) for years with at least two fire-scarred trees in each *valle*, which has been shown to produce the most reliable and replicable local fire chronology (Dieterich 1980; Falk et al. 2007, 2011; Farris et al. 2010).

Within- and among-valle contrasts

Fire chronologies were composited at different spatial scales to assess changes in fire regimes at multiple scales (Falk et al. 2007, 2011). Fire dates were entered into a database, then graphed and analyzed utilizing the Fire History Analysis and Exploration System (FHAES) (https://www.frames.gov/partner-sites/fhaes/fhaes-home/) software package to perform statistical analyses and developing graphical presentations of fire history (Brewer et al. 2017). Additional analyses were conducted in the *burnR* analysis platform (Malevich et al. 2018). Site-level chronologies were compiled into nine *valle* chronologies and then joined together to create a landscape fire chronology for the study area as a whole. These multi-scale composites of the fire record enabled us to assess the frequency, relative extent and the synchrony of fire events across multiple spatial scales in the entire VALL landscape.

We used the number of *valles* recording fire as an index of landscape spatial extensiveness of fire years. We define widespread fire years as those in which fire was present in 6–9 *valles*, moderate fire years as years with 3–5 *valles* recording fire, local fire years as years with fire in 1–2 *valles*, and non-fire years when fire was not recorded anywhere in the VALL.

Descriptors of the fire regime

We employed percentage-scarred based filters to identify widespread fire years for statistical analysis within *valles* (Swetnam and Baisan 2003). Composite fire chronologies at each scale were analyzed at different levels of filtering: 1) all fire scars recorded on all potential recorders (no filter), 2) fires recorded on at least 10% of potential recorders, and 3) fire recorded on at least 25% of potential recorders. We limited these analyses to the period with sufficient sample size and geographic dispersion, prior to the anthropogenic alteration of the landscape fire regime in the early 1900s.

For each scale of fire (widespread, moderate, local, no fire) and level of filtering, we determined the mean fire interval (MFI) and Weibull median probability interval (WMPI) for each sampled site and each *valle* for the period of record. MFI is defined as the average interval in years between fire dates in a composite fire chronology (Falk et al. 2007). Fire interval data are generally positively skewed because of an unbounded upper boundary to the maximum interval while the minimum interval is limited to one year (Grissino-Mayer 1999; Falk et al. 2007). Thus, we also modeled central tendency using the median (i.e., the 50% exceedance probability) of a fitted Weibull distribution, which provides a more robust fit to asymmetric fire interval distributions (Grissino-Mayer 1999; Falk and Swetnam 2003). We computed upper and lower bounds to 75% of the probability density of the fitted Weibull distribution as a measure of the most common range of fire intervals.

Scaling theory (Falk and Swetnam 2003; Falk et al. 2007) predicts shorter fire intervals when fire records are aggregated over larger areas. We regressed MFI and WMPI for each level of filtering (all fires, 10% and 25% of recording trees respectively) against *valle* area, and calculated the scaling exponent and proportion of variance explained by a power law function.

Fire-climate analyses

Relationships between historical climate and fire activity were calculated using historical summer Palmer Drought Severity Index (PDSI). PDSI values were obtained from the North American Drought Atlas (Cook and Krusic 2004) grid point nearest the VALL (Point 119, 107.5° W, 37.5° N) for the analysis period, 1601–1902. PDSI is a commonly used drought index in the United States, based upon the most influential time-varying factors that regulate plant growth, including precipitation, air temperature, and soil moisture (Palmer 1965; NOAA 2011). PDSI values typically range from − 6.0 and + 6.0; negative values indicate periods of drought stress, whereas positive values indicate periods more favorable for plant growth. We adopted the drought severity classifications of the US Drought Monitor (Miskus 2008) defining moderate drought conditions as PDSI − 2.0 to − 2.9, severe drought conditions as PDSI − 3.0 to − 3.9, and extreme drought conditions for PDSI values < − 4.0.

We employed superposed epoch analysis (SEA) (Baisan and Swetnam 1990; Swetnam and Betancourt 1992; Grissino-Mayer and Swetnam 2000) implemented in FHAES to determine lagged inter-year fire-climate relationships. SEA compares the average climate condition during, before and after event (fire) years. Monte Carlo simulations (1000 runs) were used to estimate confidence intervals around the observed mean values. We calculated PDSI in all fire years superposed, as well as a moving time window for 6 years prior and four years after. These event-year and lagged PDSI values were compared to an average of climate conditions for the period of analysis. We conducted separate analyses for widespread, moderate, local, and non-fire years and for percentage-scarred classes in order to assess variation in climatic conditions during, before, and after fire years of differing areal extent.

Spatial analysis of the VALL fire history record

We reconstructed spatial and temporal patterns of historical fires using a combination of dendroecological and Geographic Information System (GIS) methods. We compiled tree location data into a geospatial database and assigned each sample to the *valle* in which it is located. Topography was derived from the PALSAR Radiometric Terrain Corrected High-resolution data set (ASF DAAC 2006). Vegetation layers were derived from Muldavin et al. (2006). All data layers were imported into QGIS (QGIS Development Team (2020) in NAD[2] 1983 projection, UTM[3] Zone 13 N. To highlight points (trees) on the landscape recording fire in each year of the record, we added a binary fire (1) / no-fire (0) attribute to each point for each year of record. Trees not in recording status for a given year were coded -1 and excluded from mapping for that particular year. These data were used to generate fire maps for each year in the period of record.

[2] North American Datum.

[3] Universal Transverse Mercator.

Results

Sample depth and period of analysis

Fire-scarred samples from the forest-grassland ecotones in the VALL contained an abundant and well-preserved fire scar record. We crossdated 2,361 fire scars from 296 trees recording 234 fire years covering the 766-year period AD 1240–2005 (the earliest and latest dated tree rings, respectively) (Table 1). Most (90%) of these trees were dead when sampled by chainsaw (i.e. stumps, logs, or snags); the remainder were taken as partial cross sections from living trees (Table S1). Most samples (79%) were ponderosa pine, southwestern white pine (8%), or Douglas-fir (1%); 12% of samples (all from dead trees) were not identifiable to species. The 302-year period from AD 1601 through 1902 met sample depth criteria for individual *valles* prior to the period of fire exclusion due to extensive livestock grazing. Within this period, we dated 2,321 fire scars to 204 fire years (66% of all years), of which 129 (63%) were recorded by two or more trees in the VALL landscape.

Fire chronologies and fire return intervals

We developed fire chronologies for each *valle* (Figure S1a–i), as well as a composite VALL-wide fire chronology summarizing fire history in all nine *valles* for the period 1601–1902 (Fig. 3).

The spatial extent of areas that burned historically in the VALL ranged from small fires that burned around the base of a cluster of trees in a single *valle* (Fig. 1) to widespread fire years that burned across the entire study area (Fig. 4). Between 1684 and 1902 when at least 8 of the 9 *valles* were recording fire, widespread fires years (recorded in six or more *valles*) burned across the landscape in 15 years (17.6% of fire years; range of intervals 1 to 27 years, mean interval 14.6 years; Fig. 5). There were 29 moderate fire years (3–5 of the nine *valles*, 29.4% of fire years) during the analysis period, occurring every 8.8 years on average (fire intervals 1 to 28 years). Local fire years (1–2 *valles*) occurred 45 times (52.9% of fire years), on average every 4.9 years (fire intervals 1 to 20 years). Fire regimes in all *valles* underwent a major shift post-1896, with declining local fires and no widespread events after this time (Figure S1a–i).

Fire frequency of the reconstructed fire regime indicated differing patterns of spatiotemporal variability among the nine *valles*. Mean fire intervals (MFI) for all fires, regardless of size, scarring at least two trees in individual *valles* ranged from 4.7 to 13.6 years (WMPI 3.9–11.6 years) (Table 2). MFI for all fire dates recorded by two or more trees at the VALL landscape scale was 2.4 ± 1.7 SD years (WMPI 2.2 years). Lower exceedance intervals (Weibull probability density $\leq$ 12.5%) ranged from 1.2 to 4.8 years (mean = 2.9 years) in individual *valles*, and 0.8 years for VALL as a whole. The upper exceedance probability intervals (i.e., the 12.5% longest intervals in the probability distribution) were 8.8–26.6 years (mean = 15.8 years) at the *valle* scale, 4.4 years for the entire VALL. Seventy-five percent of all fire intervals fell within these bounds.

Intervals between fires scarring a larger proportion of recording trees (10% and 25%) were longer, as fires scarring only a few trees were eliminated at each scale. For fire years when at least 10% of recording trees were scarred, MFI_{10} ($WMPI_{10}$) values were 5.3–10.3 (4.7–9.2) years at the *valle* scale, and 6.0 ± 5.0 SD (4.9) years at the landscape scale (Table S2). For fire years when at least 25% of recording trees were scarred, MFI_{25} ($WMPI_{25}$) intervals respectively were 7.7–13.7 (5.5–12.4) years at the *valle* scale and 13.0 ± 10.9 SD (9.9) years at the landscape scale (Table S3). Lower exceedance intervals for fires recorded by $\geq$ 10% of trees were 1.6–3.3 years (mean of *valles* = 2.1 years; VALL = 1.3), and 1.2–4.6 years (mean of *valles* = 3.4 years; VALL = 2.3 years) among fires recorded by $\geq$ 25% of trees. Upper exceedance probabilities for fires recorded by $\geq$ 10% of trees were 9.3–18.3 years (mean of *valles* = 13.3 years; VALL = 11.6), and 13.8–24.0 years (mean of *valles* = 18.9 years; VALL = 25.7 years) for fires recorded by $\geq$ 25% of trees (Tables S2 and S3). As above, 75% of fire intervals fell between these values.

Regardless of the measure of central tendency, the largest *valles* (Grande, San Antonio, Jaramillo, Santa Rosa) had the shortest fire intervals for all fires (mean of MFI 5.4 years), while mean fire intervals in the smaller *valles* (Alamo, San Luis, El Cajete, Seco), were more than twice as long (mean MFI 11.8 years; Table 2, Figure S3). Consistent with theory, *valle* area influenced fire return intervals strongly, accounting for 80% of variation in MFI among *valles* (WMPI 85%;

Table 1 Sample size, tree-ring record, and fire history records for individual *valles* and the entire Valles Caldera National Preserve (VALL) study area

Valle name (code)	# Trees dated	# Samples dated	# Rings dated	Earliest year	Last year	# Fire scars dated	Earliest year	Latest year
Alamo Bog (AB)	23	23	5037	1412	2002	125	1422	1899
El Cajete (VEC)	11	15	2111	1640	1997	95	1650	1904
Grande (VG)	103	115	23,357	1418	2005	701	1530	1992
Jaramillo (VJ)	48	63	10,882	1517	2005	455	1573	1992
San Antonio (VSA)	44	54	10,630	1526	2005	380	1542	1969
San Luis (VSL)	11	13	2102	1614	1960	95	1684	1908
Santa Rosa (VSR)	31	39	7139	1240	2005	327	1248	1971
Seco (VSC)	18	24	3595	1484	2005	137	1586	1929
Toledo (VT)	7	9	1274	1660	1965	46	1729	1901
VALL	296	355	66,127	1240	2005	2361	1248	1992

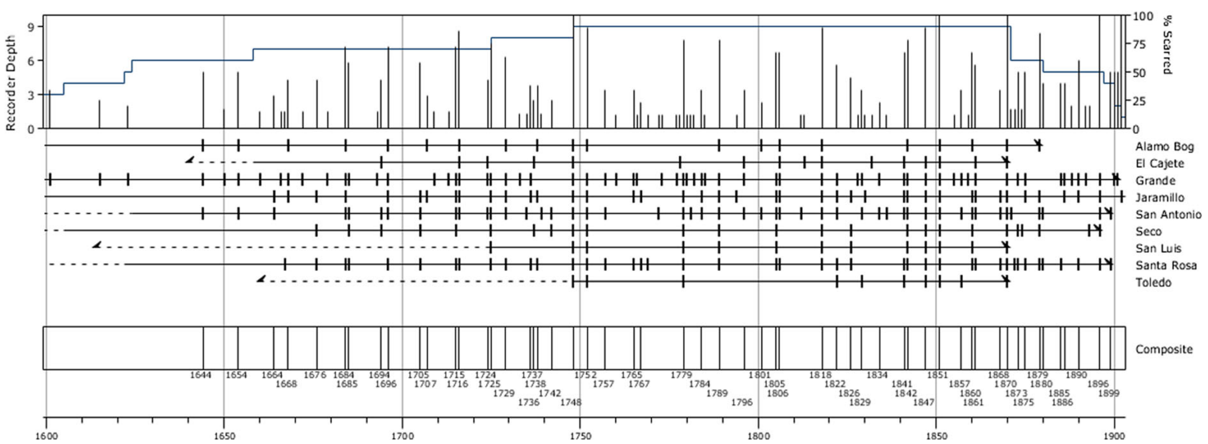

Fig. 3 Master fire history timeline for reconstructed fires in the period of analysis 1601–1902 for the Valles Caldera, New Mexico. Horizontal series are composite fire records for each major *valle*; vertical lines indicate years in which ≥ 2 trees recorded fire. The composite panel (bottom) indicates all fire years meeting that condition recorded by at least one *valle*. The upper panel indicates sample depth (number of valles in recording status, continuous line) and percent of recording trees among all sites scarred (histogram bars) by year. Locations: Alamo Bog (ALAMO), Valles El Cajete (VEC), Grande (VG), Jaramillo (VJ), San Antonio (VSA), Seco (VSC), San Luis (VSLD), Santa Rosa (VSR), Toledo (VTW). Dashed lines indicate…

Table S4). Valle area explained a smaller proportion of variance in fires affecting ≥ 10% and ≥ 25% of trees.

Fire-climate relationships

Fire occurrence in the VALL was related significantly to climate variation at both inter-annual and decadal time scales (Fig. 6). Of the 22 fire years during the analysis period that were recorded in two-thirds or more *valles*, 20 (91%) occurred in years with PDSI below the mean for the period; 13 (59%) occurred during moderate to extreme drought conditions (PDSI ≤ 2), including four years (18%) characterized as extreme drought conditions (PDSI ≤ 4). Only two (9%) widespread fire years (1725 and 1841) occurred

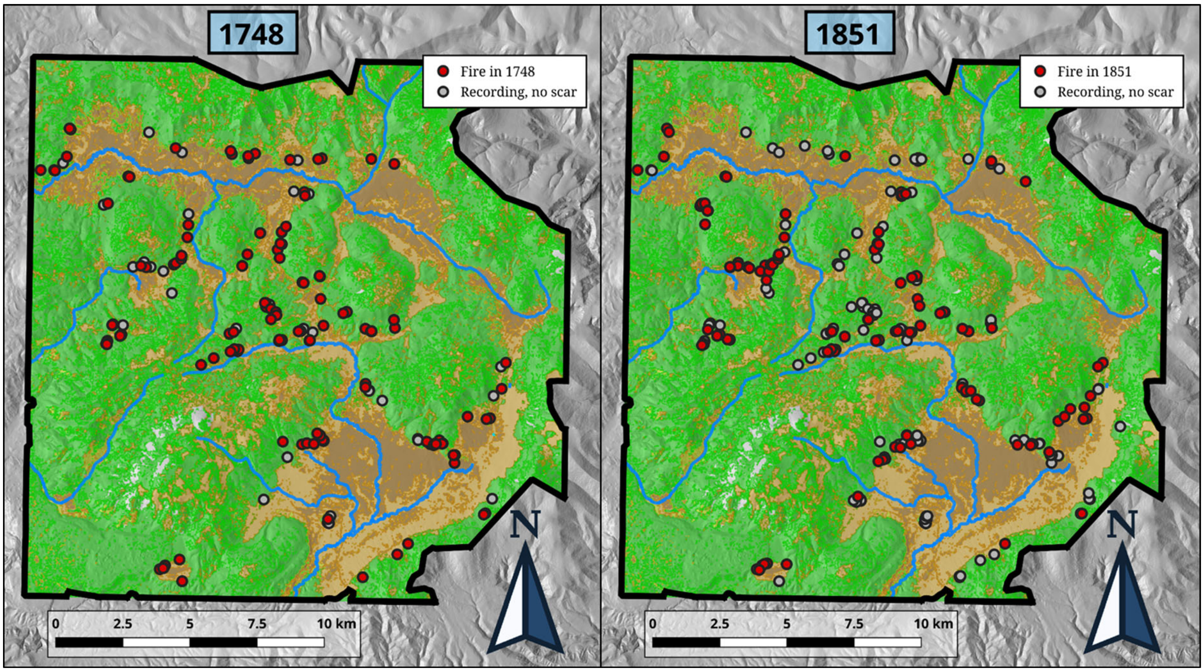

Fig. 4 Landscape maps of two years of widespread fire occurrence in the Valles Caldera, New Mexico, USA 1748 and 1851 (69.7% and 43.0% of recording trees scarred, respectively) in all nine *valles*

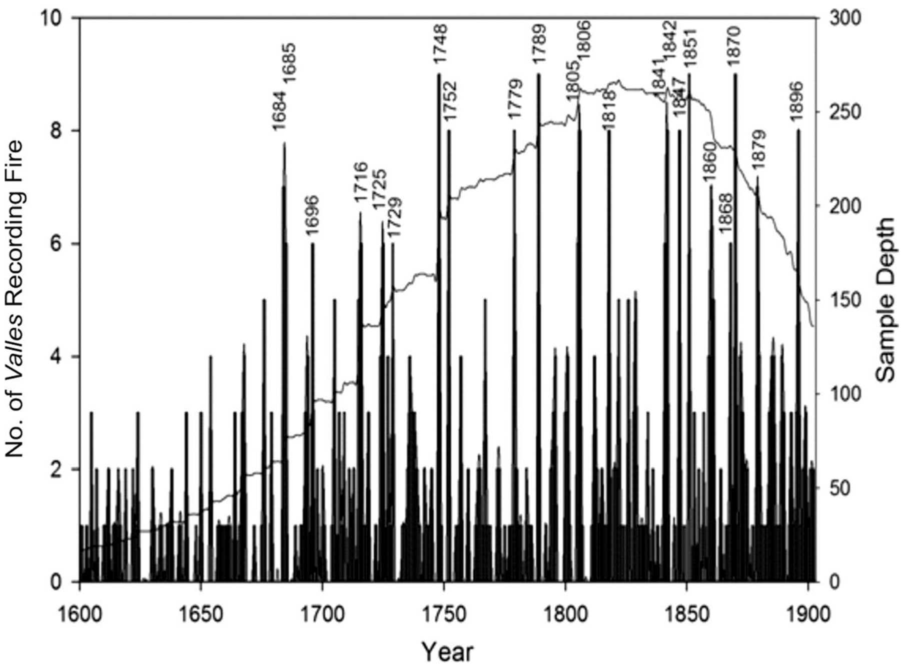

Fig. 5 Fire occurrence time series for the Valles Caldera, New Mexico 1601–1902. Left axis indicates the number of *valles* recording fire in each year (vertical bars); right axis indicates sample depth (total number of recording trees by year, continuous line). The 22 most widespread fire years are indicated

Table 2 Summary fire history statistics for fire-scarred trees in the period of analysis, 1601–1902

Valle	No. of fire intervals	MFI	SD	WMPI	Lower ex. Interval	Upper ex. interval	Maximum interval
Alamo Bog	19	12.37	7.30	11.55	4.83	20.67	37
El Cajete	15	11.73	6.97	10.96	4.57	19.64	30
Grande	64	4.69	3.80	3.93	1.16	8.84	21
Jaramillo	40	5.95	3.47	5.44	2.16	10.08	13
San Antonio	47	5.43	4.09	4.62	1.44	10.05	20
San Luis	12	12.08	7.32	11.21	4.58	20.36	27
Santa Rosa	41	5.66	4.05	4.81	1.51	10.44	16
Seco	24	9.17	5.61	8.36	3.26	15.67	27
Toledo	9	13.56	13.18	10.82	2.81	26.61	43
Mean of valles	30	8.96	6.20	7.97	2.94	15.82	26.0
VALL	124	2.43	1.71	2.15	0.75	4.36	8

Statistics are for all fire years in which at least two trees in recording status in each site were scarred. Minimum fire intervals were 1 year in all *valles*. Units of all columns to right of "number of fire intervals" are years. Lower and upper exceedance intervals bracket 75% of recorded fire intervals; 12.5% of intervals are shorter (longer) than the lower (upper) exceedance interval

VALL are composite statistics for the study area fire record as a whole, *MFI* mean fire interval, *SD* standard deviation, *WMPI* Weibull Median Probability Interval

years with above-mean PDSI. Thus, most widespread fire years occurred during drought years, but not all drought years produced widespread fires, indicating a contingent relationship between drought and fire (Fig. 7).

Superposed epoch analysis indicates that fire year drought conditions were related significantly ($p < 0.01$) to the occurrence of widespread (6–9 *valles*) fire years in the VALL (Fig. 8.a). There is also strong support for the occurrence of antecedent moist years preceding widespread fire years: in the three years prior to the year of a widespread fire event, PDSI values were generally positive, and were significant ($p < 0.01$) two years prior to the fire year.

Moderate fire years (3–5 *valles*) were also significantly ($p < 0.01$) associated with negative (dry) conditions during the year of a fire event (Fig. 8b). Moderate fire years were not preceded by significantly moist or dry antecedent years, indicating a potential constraint in fine fuel production. Local fire years (1–2 *valles*) occurred predominantly during neutral conditions and were preceded by at least six dry years, with consistent statistically significant ($p < 0.05$) dry conditions in the fourth year prior to a fire event (Fig. 8.c). Years in which no fires burned on the landscape occurred when conditions were significantly wetter ($p < 0.01$), and the preceding years drier and warmer than average, with consistent statistically significant ($p < 0.05$) dry conditions in the year prior (Fig. 8d), indicating a combination of fire year conditions less favorable for spreading fire, including fuel limitation from antecedent years.

Consecutive fire years

During the analysis period 1601–1902, 19 (35%) of the 55 fire years recorded in at least two *valles* were part of sequential fire years, in which fire occurred in consecutive years in VALL (Fig. 3, composite plot). In ten (53%) of these cases, consecutive fire events included at least one widespread fire while the other fire was either widespread or moderate; we refer to these hereafter as widespread consecutive fire years (Figs. 9 and S2). The remaining nine (47%) consecutive fire years were comprised of two moderate fire events, or one widespread fire and one localized fire year, one moderate fire and one localized fire year, or two localized fire years, referred to hereafter as moderate consecutive fire years. Only one out of 296 recording trees incurred a scar in both years of any pair of consecutive fire years (1779–1780).

Interannual climate variation, especially climate in the second year, strongly influenced the occurrence of consecutive year fire events (Fig. 10). The first year of

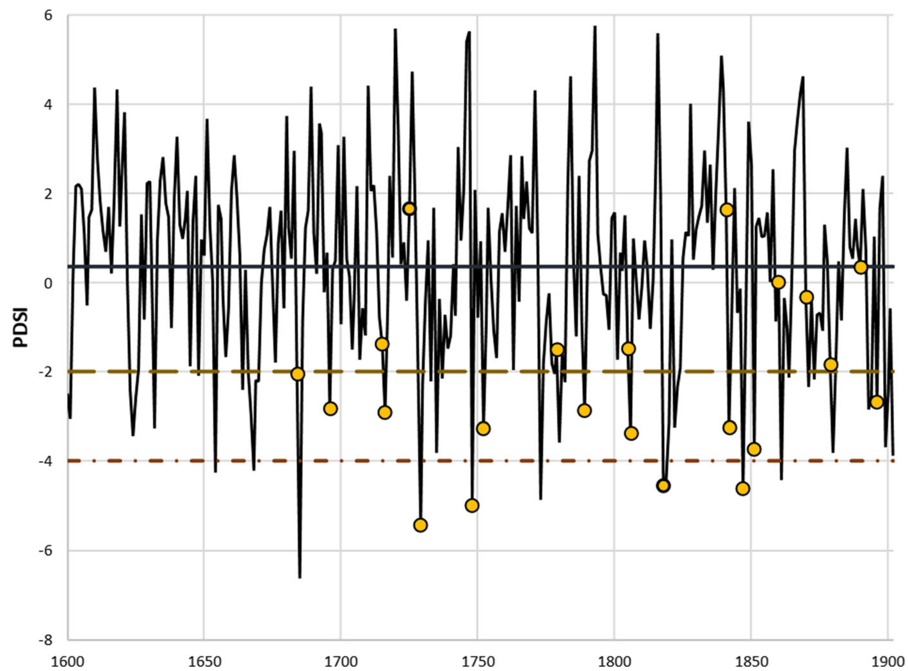

Fig. 6 Time series of widespread fire years (colored circles) in the Valles Caldera as a function of Palmer Drought Severity Index (PDSI), 1601–1902. Colored circles indicate the 22 most widespread fire years during the analysis period. Solid line indicates mean PDSI during the analysis period (0.3570). Long-dash and short-dash lines indicate PDSI = − 2.0 and − 4.0, corresponding to thresholds of moderate and extreme droughts respectively (US Drought Monitor, Miskus 2008)

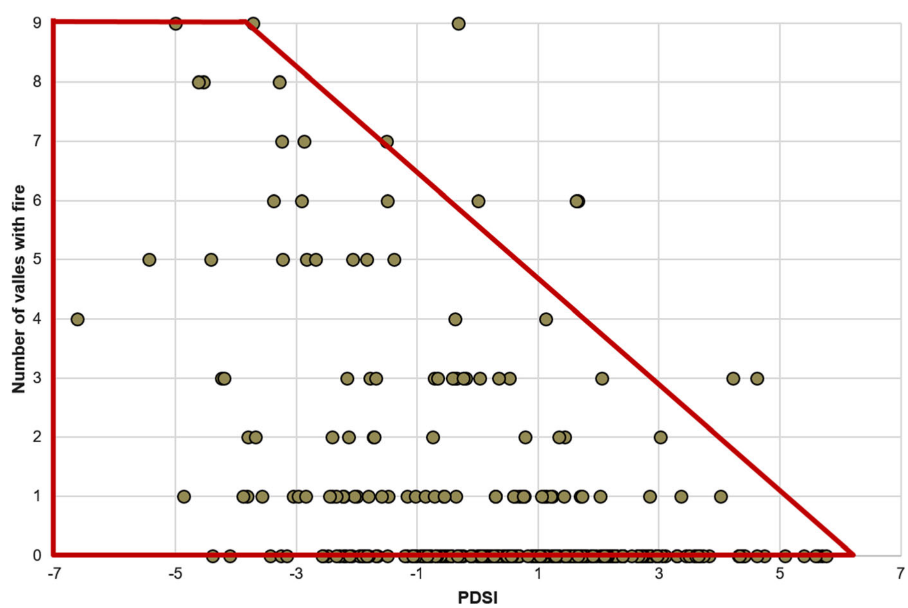

Fig. 7 Contingency diagram of fire extent as a function of PDSI. Each dot is a year in the analysis period. The red polygon indicates a contingent fire occurrence pattern: no widespread fires occurred in years of high positive PDSI, but there is wide variation in fire extent during years of negative PDSI, indicating the influence of other factors

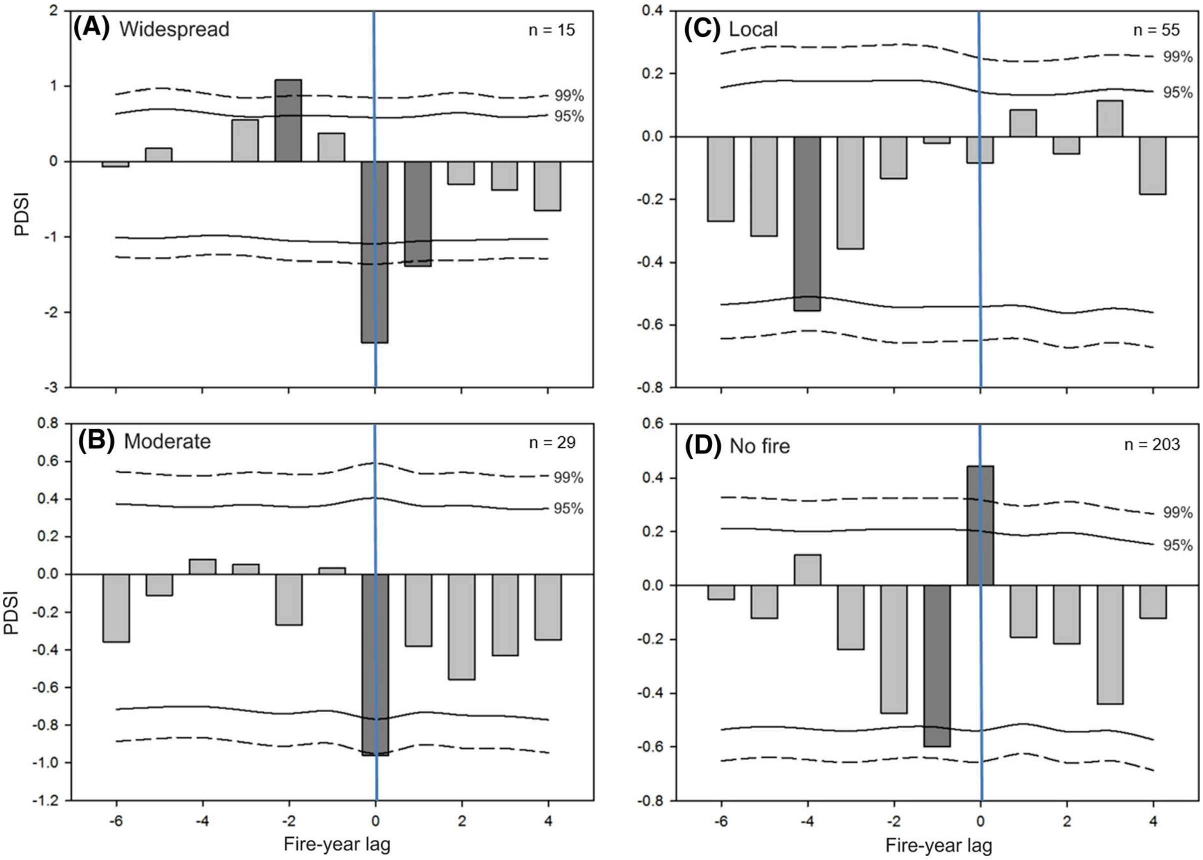

Fig. 8 Superposed epoch analysis (SEA) comparing the lagged responses of the number of *valles* recording fire events to the Palmer Drought Severity Index (PDSI) during **a** widespread, **b** moderate, **c** local, and d non-fire years. Vertical line indicates the fire year. Solid and dashed horizontal lines indicate the 95% and 99% confidence intervals, respectively, in annual variability in PDSI (see text for details). Dark-shaded bars indicate years in which PDSI significantly ($p < 0.05$) exceeds the confidence interval. N = number of fire years by category

widespread consecutive fire years tended to be slightly drier than normal (-1.4 PDSI), and antecedent years were wetter than average (0.6–1.1 PDSI) although not statistically significantly so ($p > 0.05$). The second year in consecutive fire year pairs was significantly dry (mean $-$ 2.0 PDSI, $p < 0.01$), as were widespread consecutive fire years (mean -3.5 PDSI, $p < 0.01$) (Fig. 10).

Discussion

Fire is a keystone landscape process in montane ponderosa pine and mixed-conifer ecotones and adjacent grasslands of southwestern North America. Spreading surface fires occurred throughout our focal period of historical record from 1601–1902 (99/302 years, 33%), with considerable variability in frequency and extent in space and time (Figs. 3 and 5). This period of widespread fires ended with interruption of significant surface fires in the 1890s by changes in land use, especially the advent of intensive landscape-wide livestock grazing with associated reductions of grass cover and increased soil exposure that decreased connectivity of fine surface fuels and constrained surface fire spread, followed by active fire suppression (Allen 1989, 2007; Touchan et al. 1996; Swetnam et al. 2016). The lack of fire activity subsequent to the late 1800s reflects the impacts of changing land use, as the VALL area was colonized by EuroAmerican settlers and converted to large-scale, intensive production grazing (Allen 2002; Martin 2003; Swetnam et al. 2016), and is not

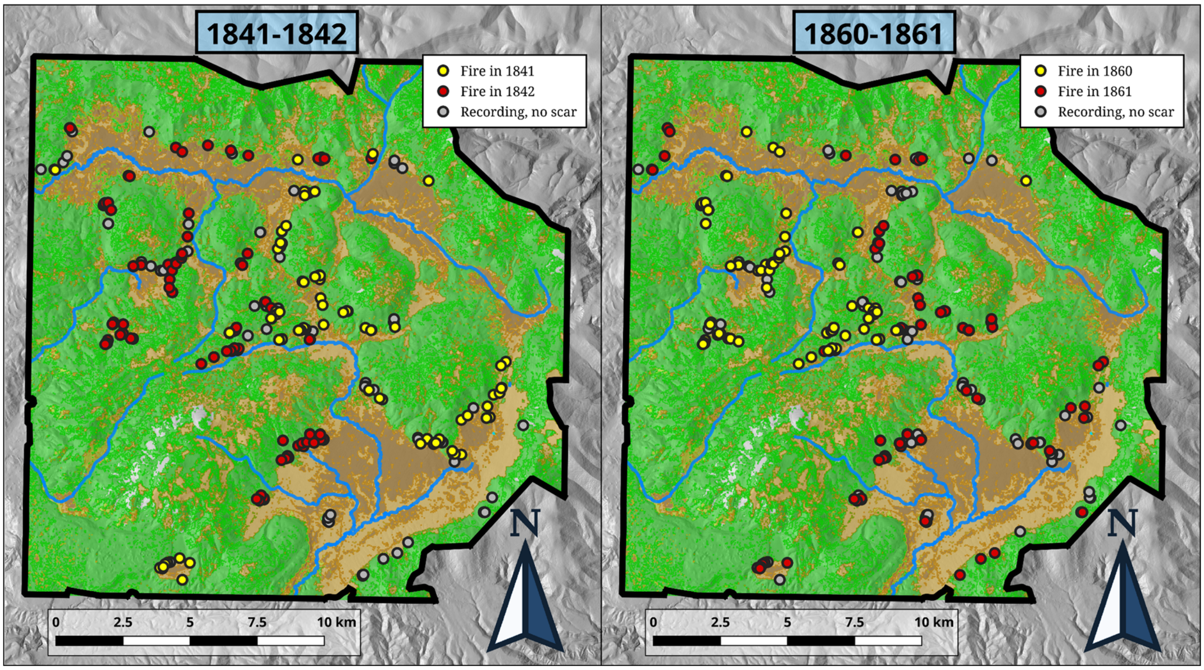

Fig. 9 Widespread consecutive fire years in the Valles Caldera, New Mexico, USA, 1841–1842 (left) and 1860–1861 (right). In each panel, yellow dots indicate trees scarred in the first year, red in the second year. Grey dots are trees in recording status that did not indicate fire in either year

attributable to a change in the climate regime (Fulé et al. 2012).

The VALL fire record reveals 40 moderate to widespread fire years (18% of years, affecting ≥ 3 *valles*) during the 219-years period of strongest spatial record, 1684–1902 (Fig. 3). Many of the notable large fire years in the Valles Caldera and surrounding Jemez Mountains (Allen 1989; Touchan et al. 1996; Allen et al. 2008) coincide with extensive fire years throughout the Southwest (Swetnam and Baisan 1996, 2003). For example, 1748 is documented to be the largest single regional fire year recorded on fire-scarred samples in the Southwest over the past 3 centuries (Swetnam and Betancourt 1998; Diaz and Swetnam 2013; Swetnam et al. 2016); in this year fire was correspondingly widespread at the landscape scale in VALL (Fig. 4). Other regional fire years (1684–1685, 1694, 1696, 1715–1716, 1724–1725, 1729, 1738, 1752, 1765, 1789, 1806, 1841–1842, 1847, 1851, 1857, 1861, 1870, 1879, 1896) were also years of widespread fire in the VALL (Swetnam and Brown 2010).

Fire-scar records in the VALL provide evidence of other years of relatively small fires recorded in local patches of scarred trees. These years may reflect single ignitions from lightning storms or humans, or areas in which vegetation/fuels were not conducive for fire to spread to other stands and adjacent *valles*. During other fire years, the record shows clusters of fire-scarred trees separated by intervening trees that show no record of fire. This spatial pattern likely is a result of multiple ignitions that often result from dry lightning storms in the American Southwest (Allen 2002), or patchy fire spread patterns at landscape scales (Conver et al. 2018).

The apparent reduced frequency of multi-*valle* (extensive) fire events before the mid-1600s is consistent with findings from a Jemez Mountains-wide study of fire event synchrony (Swetnam et al. 2016). That study also showed a higher frequency of small fire events (i.e., fires recorded by only 1 tree) before the mid-1600s than after. Interannual fire-climate associations were weak or statistically non-significant prior to *ca*. 1680, but after 1680 the commonly observed pattern of wet prior years and dry fire event years was evident and significant ($p < 0.05$). Before the mid-1600s the Jemez Puebloan people practiced extensive farming, hunting, timber

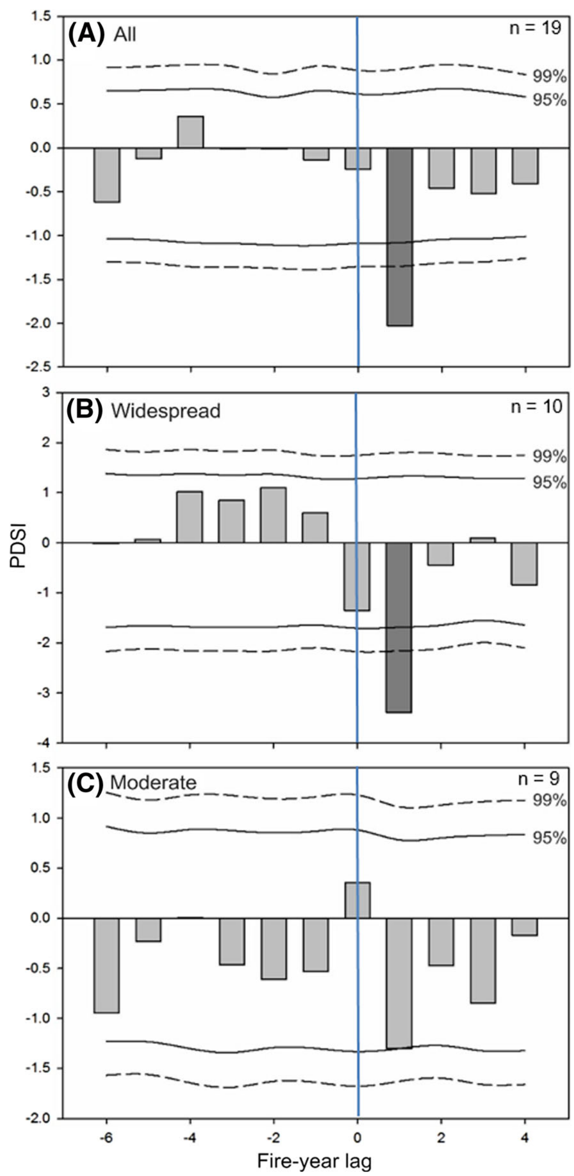

Fig. 10 Superposed epoch analysis comparing the Palmer Drought Severity Index (PDSI) for selected consecutive fire years. **a** All sequential fire year pairs, **b** widespread fire year pairs, and **c** moderate fire year pairs. Vertical line indicates the fire year. Solid and dashed horizontal lines indicate the 95% and 99% confidence intervals, respectively, in annual variability in the Palmer Drought Severity Index (PDSI). Dark-shaded bars indicate years in which PDSI significantly ($p < 0.05$) exceeds the confidence interval. N = number of years by category. In each panel, 0 is the first year of the sequential pair, and 1 is the second

harvesting for building structures, fuelwood gathering for domestic fires, and use of fire for manipulating vegetation. These land uses occurred especially on the extensive plateau, mesas, and canyons to the south of the *valles*. Hence, the observed changing patterns of fire synchrony (extent) and fire-climate associations were interpreted as likely due to the depopulation of the southern Jemez Plateau during the early 1600s to late 1600s Spanish colonial period, and consequent land-use and fire ignition/fuels changes (Liebmann et al. 2016; Swetnam et al. 2016).

At both the site and landscape scales, the length of time between fires varied in the VALL, in part as a function of *valle* area (Table 2; Figure S3). In the VALL landscape as a whole prior to 1900, spreading fire occurred somewhere within the area approximately every two to three years (MFI 2.4 years, WMPI 2.2 years), with widespread surface fires occurring at decadal intervals. These fire intervals are consistent with other studies of fire regimes in the ponderosa pine forest-grassland ecotone (Brown and Sieg 1996; Kaib et al. 1996, 1999). A significant proportion of variation in fire intervals (80–85% for all fires) among *valles* is explained by differences in area (Figure S1; Table S4), reflecting a universal scaling law in fire regimes (Falk and Swetnam 2003; Falk et al. 2007; Farris et al. 2010). As sample area increases, the rate of encountering widespread fires declines (already captured in the record), and the record of smaller events eventually saturates; this explains why area explains less interval variance among widespread fires. Fire interval estimates should be reported explicitly to scale whenever comparisons are made among study areas.

Fire frequencies observed in this system are broadly comparable to those observed in forest-grassland ecotones elsewhere in western North America. Kaib et al (1996, 1999) found fire intervals of 4–12 years in grasslands and ecotones elsewhere in the Southwest along the edges of open areas or meadows where conditions encourage herbaceous growth, similar to the ecosystem studied here. In a mesic mixed-severity ecotone in west central British Columbia, Canada, Harvey et al. (2017) found a mean MFI of 23.5 ± 15.2 years among 27 plots; widespread fires (25% of recording trees) occurred on average every 17.5 years; grassland-proximate fires were recorded on average every 9.1 years. In the Palouse prairie-forest ecotone in eastern Washington, USA, Morgan et al. (2020) found frequent (5–8 years) fire intervals at sites ranging in size from 2–28 ha. In these and other cases, frequent fire plays a key role in regulating spatiotemporal dynamics of the forest-grassland boundary.

Fire-climate relationships

Widespread fires in the VALL showed a strong and significant relationship ($p < 0.01$) to dry conditions preceded by years of wet conditions (Fig. 8a). Interannual variability in growing season conditions (as reflected in PDSI) during the year of a fire event influenced fire extent by regulating live and dead fuel moistures during fire season (Fig. 6). Moist/cool conditions during prior years, which hinder fire spread during those years, also promote production of fine fuels, thus preconditioning the landscape for the subsequent fire seasons (Swetnam and Baisan 1996; Swetnam and Betancourt 1998; Brown et al. 2001; Margolis et al. 2017). In contrast to closed-forest ecosystems, the fuels in VALL ecotones are dominated by perennial bunchgrasses that can recover fuel mass and continuity quickly (Suazo et al. 2018), and are thus ready to reburn sooner than adjacent forests, as evidenced by short return intervals. In contrast, non-fire years were often associated with wet conditions (Fig. 8d), and were often both preceded and followed by unusually dry conditions. In these years, spreading fires were probably inhibited both by cool and wet conditions in the potential fire year, and by an insufficient fuel base for an extensive fire, either because of lower productivity in those years, or because fires had occurred during those previous drier years. This evidence suggests that climate variability is important in both the production and conditioning of fine fuels in the ecotone (Nippert et al. 2006; Fig. 8).

Close examination of our results indicates that PDSI is a constraint on fire in the VALL, but not an absolute driver (Figs. 6, 7). In years of high positive (wet/cool) PDSI, widespread fires were rare because high fuel moisture inhibits the physics of combustion and thus fire spread. In contrast, during negative (warm/dry) PDSI years, fire can range from local to widespread; widespread fires occurred in some but not all *valles* even during years with strongly negative PDSI. In fact, non-fire years (0 *valles* recording fire) occurred across the full range of PDSI ($-$ 4.2 to $+$ 4.5) as did years when fire occurred in a single *valle*. Only in the few years with extreme negative PDSI ($\leq$ 4.5) were widespread fires the majority response. Thus, we conclude that fire occurrence is contingent upon drought conditions in the fire year and antecedent years, but these conditions alone are not sufficient for widespread fire to occur. This contingent relationship indicates interactions of top-down (climate) and bottom-up (such as ignitions, fuel conditions, short-term weather, local topography) factors in regulating fire extent: top-down regulation is a necessary but not sufficient condition for a landscape fire event (McKenzie et al. 2011; O'Connor et al. 2017; Yocom Kent et al. 2017).

Consecutive fire years

Consecutive fire years were a regular and relatively frequent occurrence in the historical fire regime of the VALL. In many consecutive fire year pairs, the two years generally burned over different areas of the VALL landscape (Figs. 9 and S2), whereas in other pairs of fire years, fire spread across the VALL landscape in a patchy mosaic.

The montane forest-grassland ecotones of the VALL include continuous fine fuels (mainly grasses) with high potential for frequent and extensive fire activity (Conver et al. 2018). Suazo et al. (2018) found that grass biomass in VALL recovers quickly after fire and maintains sufficient fuel mass to carry fire in most years. Decomposition studies conducted by one member of our group (RR Pamenter) on VALL of the three dominant grass species (Parry oat grass, Arizona fescue and Kentucky bluegrass) showed that dried grass blades lost only 25–35% of their dry mass over the first winter (November to April; unpublished data, RR Parmenter, 2006–2008). In those studies, after a full year (November to November), 40–60% of the dry biomass remained; thus, on average, approximately two-thirds of the current summer's grass biomass was available the following spring for burning, along with up to half of the growth from the two previous summers. This persistence of fine fuels would account for the rapid recovery of fire spread potential.

In the majority of cases (8/10 pairs), PDSI for the second year in a consecutive-year pair was lower (drier) than that of the first year, whether the fires were widespread or localized (Fig. 10). For consecutive fire pairs in which at least one year was a widespread fire year ($\geq$ 6 *valles*), SEA indicated 2–5 antecedent wet years (nonsignficant, suggesting the influence of herbaceous fuel production. Consecutive years in which at least one was a moderate fire year were generally preceded by several years of drought. This indicates that while climatic conditions might favor fires in these years, there may have been insufficient fine fuels to support widespread fires. Fine fuel dynamics thus provide a mechanism for regulating consecutive fire years at landscape scales, creating a self-organizing landscape dynamic (Parks et al. 2015; Margolis et al. 2017; Suazo et al. 2018).

Management implications

Forest-grassland ecotones can provide unique windows into the essential dynamics of adjoining grassland fire regimes (Myster 2012). The widespread removal of wildland fire from diverse ecosystems in the Southwest has left many forests and grasslands overly dense with flammable vegetation. Ecologists and managers recognize the loss of variability in natural processes such as fire from fire-adapted landscapes, with equally undesirable consequences to biodiversity and sustainable ecosystems (Valles Caldera Trust 2003). Exclusion of fire in forest-grassland ecotones contributed to ingression of forest into the *valles* of the VALL during the twentieth century (Coop and Givnish 2007b). The area of upper montane grasslands on south-facing mountain slopes of the caldera rim and resurgent domes in the VALL decreased by 55% between 1935 and 1981 through tree invasion as a result of intensive grazing and active fire suppression since the 1800′s (Allen 1989; Swetnam et al. 1999), although recent fire episodes may reverse this trend.

In grasslands and forest-grassland ecotones of the VALL, surface fires burned frequently prior to Euro-American establishment of permanent settlements in and around the Jemez Mountains. These frequent, low-intensity fires promoted the growth of grasses and herbaceous plants in the understory and enabled large, open ponderosa pine and mixed-conifer stands to persist by effectively preventing the survival of higher densities of seedlings. These recurrent fires also helped to maintain the ecotonal boundary between forests and grasslands by constraining the spread of woody species into the adjacent grassland ecosystems (Coop and Givnish 2007b; Conver et al. 2018).

Our reconstruction of historical fire regimes along the grassland-forest ecotone provides an ecological reference for land managers planning restorative actions in forests and grasslands, by using pre-fire-suppression fire regimes as a benchmark for current programs of prescribed and natural fire management (Valles Caldera Trust 2003; Keeley et al 2009). Surface or mixed severity fires within individual *valles* at intervals of 3 to 12 years, and widespread fires in ecotones throughout the VALL every nine to 14 years, with fire occurring somewhere in the Valles Caldera ecotonal zone on average every two years, would approximate the spatiotemporal properties of the historically natural fire regime (Table 2; Fig. 3). While these intervals are not necessarily a complete prescription for ecologically-based fire management, they provide a guide for fire frequency and scale that would approximate the natural background process (Falk 2006).

The high frequency of fires documented in this research could be reinstituted in the forest-grassland ecotone through planned burning, which is the intentional combustion of fuels under conditions specified and approved through a management plan. Planned burning, coupled with managing natural lightning-ignited fires instead of mandatory suppression, can reduce surface fuel loads, stimulate nitrogen availability, increase herbaceous productivity and reduce the density of pine and mixed-conifer seedlings, and in this way begin to re-establish the historic ecotonal community (Harrington and Sackett 1990; Stephens et al. 2013; Shive et al. 2013; Coop et al. 2016).

After more than a century of fire suppression and livestock grazing, fire has begun to return to forests and grasslands of the Valles Caldera. Since 1977, a series of large wildfires has burned much of the eastern Jemez Mountains, including large areas of the Valles Caldera in 2000, 2011, and 2013. These fires have caused extensive tree mortality over large contiguous high-severity patches, creating potentially novel landscape configurations and extensive ecological, hydrologic and geomorphic consequences (Coop et al. 2016; Orem and Pelletier 2016). Combined strategies of thinning, manual fuel removal and planned or managed burning are likely to benefit restoration of grasslands, forests, and ecotones to conditions that will provide resilience in an era of rapidly changing fire regimes and climate.

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