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Using Paleolandscape Modeling to Investigate the Impact of Native American–Set Fires on Pre-Columbian Forests in the Southern Sierra Nevada, California, USA

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Ethnographic accounts document widespread use of low-intensity surface fires by California's Native Americans to manage terrestrial resources, yet the effects of such practices on forest composition and structure remain largely unknown. Although numerous paleoenvironmental studies debate whether proxy interpretations indicate climatic or anthropogenic drivers of landscape change, available data sources (e.g., pollen, charcoal) are generally insufficient to resolve anthropogenic impacts and do not allow for hypothesis testing. We use a modeling approach with LANDIS-II, a spatially explicit forest succession and disturbance model, to test whether the addition of Native American–set surface fires was necessary to approximate vegetation change as reconstructed from fossil pollen. We use an existing 1,600-year pollen and charcoal record from Holey Meadow, Sequoia National Forest, California, as the empirical data set to which we compared modeled results of climatic and anthropogenic fire regimes. We found that the addition of anthropogenic burning best approximated fossil pollen–reconstructed vegetation change, particularly during periods of prolonged cooler, wetter periods coinciding with greater regional Native American activity (1550–1050 and 750–100 cal yr BP). For lightning-caused wildfires to statistically approximate the pollen record required at least twenty times more ignitions and 870 percent more area burned annually during the Little Ice Age (750–100 cal yr BP) than observed during the modern period (AD 1985–2006), a level of natural fire increase we consider highly improbable. These results demonstrate that (1) anthropogenic burning was likely an important cause of pre-Columbian forest structure at the site and (2) dynamic landscape models provide a valuable method for testing hypotheses of paleoenvironmental change. *Key Words: anthropogenic burning, landscape modeling, Native Americans, paleoecology, Sierra Nevada.*

民族志记述，记载了美国加州原住民广泛使用低密度表火来管理陆地资源，但此般实践对于森林组成与结构的影响却仍鲜为人知。仅管众多的古环境研究，争论代理解释到底意味着气候或人为趋力改变了地景，但一般而言，可取得的数据来源 (例如花粉、木炭) 却不足以分辨人为的影响，并且无法提供假说检验。我们运用 LANDIS-II 的模式化方法——一个在空间上精确的森林连续与扰乱模型——检验趋近从花粉化石重建的植被变迁时，是否需增加美国原住民施放的表火。我们运用加州红杉国家森林的欧立草原既有的一千六百年花粉与木炭纪录，作为我们比较气候和人为火动态的模式化结果之经验数据集。我们发现，增加人为燃烧，可最佳地趋近花粉化石重建的植被变迁，特别是在与美国原住民较大的区域活动符合的长期较为湿冷的时期 (距今 1550-1050 年以及 750-100 年)。闪电所引发的野火，若要在统计上逼近花粉纪录，则小冰期 (距今 750至100 年) 每年至少需较现代时期 (西元 1985-2006 年) 所观察到的高出二十倍的着火和多出百分之八百七十的燃烧面积——一种我们认为高度不可能的自然火灾增加程度。这些研究证实，(1) 人为焚烧很可能是该地形成前哥伦比亚时期森林结构的重要导因，以及 (2) 动态地景模式提供了检测古环境变迁假说的宝贵方法。 *关键词： 人为焚烧，地景模式化，美国原住民，古生态学，内华达山脉。*

En relatos etnográficos se documenta el uso generalizado de incendios superficiales de baja intensidad de los nativos americanos para el manejo de recursos terrestres, pero los efectos de tales prácticas sobre la composición y estructura de los bosques siguen en gran medida desconocidos. Aunque numerosos estudios paleoambientales debaten si las interpretaciones proxy indican controles climáticos o antropogénicos en el cambio del paisaje, las fuentes de datos disponibles (e.g., polen, carbón vegetal) generalmente son insuficientes para resolver los impactos antropogénicos y no permiten poner las hipótesis a prueba. Usamos un enfoque de modelado con

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LANDIS-II, un modelo de sucesión y disturbio forestal espacialmente explícito para determinar si la adición de incendios superficiales provocados por nativos americanos era necesaria para aproximarnos al cambio de vegetación que resulta de la reconstrucción a partir de polen fósil. Usamos un registro existente de polen y carbón vegetal de 1.600 años de Holey Meadow, en el Bosque Nacional de Sequoias, California, como el conjunto de datos empíricos con el cual comparamos los resultados modelados de los regímenes de fuegos climáticos y antropogénicos. Encontramos que la adición de la quema antropogénica se acercaba mejor al cambio de vegetación reconstruido con base en polen fósil, en particular durante períodos más fríos y más húmedos prolongados que coinciden con una mayor actividad regional de nativos americanos (1550–1050 y 750–100 años cal AP). Para que los incendios forestales causados por rayos se aproximaran estadísticamente al registro con polen se requería durante la Pequeña Edad del Hielo (750–100 años cal AP) por lo menos veinte veces más encendidos del fuego y 870 por ciento más área quemada anualmente de lo observado durante el período moderno (1985–2006 DC), un nivel de incremento de los incendios que nosotros consideramos altamente improbable. Estos resultados demuestran que (1) los incendios antropogénicos probablemente fueron una causa importante de la estructura forestal precolombina en el sitio, y (2) los modelos dinámicos del paisaje proveen un método valioso para probar hipótesis de cambio paleoambiental. *Palabras clave: modelado del paisaje, nativos americanos, paleoecología, quemas antropogénicas, Sierra Nevada.*

Indigenous people have modified the physical landscape across North America for millennia, altering vegetation composition and fire frequency via land use practices such as agriculture, land clearing, and burning (Kroeber 1925, 1959; Voeglin 1938; Gayton 1948; Vankat 1977; Anderson and Moratto 1996; Lightfoot and Parrish 2009). The magnitude of the ecological footprint that Native Americans had on altering pre-Columbian ecosystems is strongly debated (Lewis 1973; Minnich 1988; Denevan 1992; A. J. Parker 2002; Vale 2002; Whitlock and Knox 2002; Bowerman and Clark 2011; Klimaszewski-Patterson 2016). Although evidence for prehistoric human impacts can be readily identified through the presence of crop plants such as maize (Bouey 1979; Rue 1987; Piperno 1994; Mazurkiewicz-Zapałowicz and Okuniewska-Nowaczyk 2015), Native Americans in the Western United States, particularly present-day California, were not farmers. They were hunter-gatherers and proto-agriculturalists, managing native vegetation for desirable types such as oaks (*Quercus* spp.), willows (Cupresaceae), sedge (Cypresaceae), and berries through horticultural techniques including coppicing, selective harvesting, and burning (Gayton 1925, 1948; Kroeber 1959; Moratto 1984; Basgall 1987; Anderson 2005). Geographers interested in reconstructing the impact of nonagriculturalist native Californians on the landscape must also contend with wildfires being a natural part of the summer dry California ecosystem. The challenge becomes distinguishing changes in forest structure caused by an increase in human-set fires from changes caused by an increase in climate-driven fires.

Ethnographic accounts from California document the regular use of surface fire as a low-cost tool to clear brush, drive game, and increase natural resource yields (Dincauze 2000; Fowler 2008). In the forests of the Sierra Nevada, fire was employed at intervals of one to several years, typically in autumn after one or two rains, to increase the following year's food production (Bean and Lawton 1973; Lewis 1973; Anderson and Moratto 1996). Many native crop-yielding trees (e.g., *Quercus*) in the Sierra Nevada of California are fire adapted and shade intolerant. Using fire as a tool, Native Americans could have influenced forest structure by promoting preferred species; therefore, it is reasonable that at the time of European contact, the Sierran forest structure was an artifact of human activity and not simply the result of ecologic response to climate. Although some have argued that climate has been the dominant control on vegetation dynamics throughout the Sierra Nevada (Parker 2002), with localized impacts following an elevational gradient from unambiguously humanized at low elevations to unarguably pristine at high elevations (Vale 2002), archeological evidence shows no such gradient (Gassaway 2005, 2009; Morgan 2009). Instead, the number of archeological sites remains constant or increases with elevation, suggesting widespread Native American occupation.

Given that the overall impact and extent of native fire practices is uncertain (Martin and Sapsis 1992; Allen 2002; Vale 2002; Lightfoot and Lopez 2013; Taylor et al. 2006), the fundamental questions become (1) can we identify past changes in forest vegetation composition that can be attributed to human activities, (2) can we distinguish that change from the concurrent influence of a changing climate, and (3) was the scale of this change sufficiently great to have altered pre-Columbian ecosystems? The steady increase of wildfires in the West in recent decades has become a critical land-use management issue

(Westerling 2006) and developing a better understanding of the long-term interaction among humans, climate, and forest structure plays an important role in future fire management. Fire is an efficient, if controversial, tool in forest management to reduce fuel accumulations that lead to destructive crown fires. Recent calls for policy reforms that promote more prescribed fires (North et al. 2015) suggest that gaining a better understanding of the forest structure created by Native Americans could help guide future fire policy.

Recent evidence has demonstrated that in the historical period (1776–present), fires increased in the Sierra Nevada following population decline of Native Americans after disease was introduced by Spanish settlers (Taylor et al. 2016), suggesting that human land use practices constrained the fire–climate relationship. Distinguishing human-caused change from climatically caused change has not been attempted for the prehistoric period. Paleoecology is a historical, empirical science that, by its very nature, does not allow for experimentation, only replication. Interpretation of data relies on some qualitative assessment and hypotheses of driving ecological forces. It is possible, however, to quantitatively compare predicted outcomes of competing, alternative hypotheses against empirical data using simulation approaches. Dynamic landscape change modeling (Solomon et al. 1980; Pastor and Post 1985; C. Miller and Urban 1999; Shugart 2002; Mladenoff 2004) allows analysis of pattern–process relationships via individual processes (e.g., succession, fire) interacting over space and time. Using a dynamic modeling approach allows us to experiment with various climatic and ecological conditions at different spatial and temporal scales. This approach allows us to quantitatively determine the relative importance of different fire regimes (climatic vs. Native American–influenced) by comparing modeled results against empirical paleoenvironmental records.

In this article, we develop novel methods to quantify the relative importance of anthropogenic versus climatic impact on vegetation change among nonagricultural societies during the prehistorical period and examine the spatial extent of these impacts across the landscape. We predict that an anthropogenic signal will be most pronounced during climatically wet periods when lightning-caused wildfires would be reduced and human-set fires would be necessary to maintain open woodlands. We use forest landscape models to explore the hypothesis that the addition of Native American–set fires is necessary to approximate the paleoenvironmental record of forest change. Our goal is to approximate the frequency, type, and extent of fire ignition necessary to approximate observed trends in forest composition. We pose two main hypotheses:

> H1. Climate and climatically induced fires approximate observed paleovegetation dynamics.
>
> H2. The addition of Native American–set fires to climatically driven fires is needed to approximate observed paleovegetation dynamics.

We examine the suggestion that Native Americans would have set more surface fires during archaeological periods of resource intensification and land use. Again, we test two hypotheses:

> H2-A. Set fires are necessary during all prolonged wet periods (pre-Medieval climate anomaly [MCA], 1550–1050 cal yr BP, and Little Ice Age [LIA], 750–100 cal yr BP; Klimaszewski-Patterson 2016).
>
> H2-L. Set fires are only necessary during the LIA (750–100 cal yr BP), when archaeological literature indicates a higher population density and more intense resource exploitation than in previous periods.

By using retrospective modeling to explore the importance of Native American–set fires in pre-Columbian ecosystems, this research has broad impacts on understanding how people might have purposely altered forest structure for multiple centuries prior to the introduction of modern forest management practices. This transformative approach adds an experimental method (landscape modeling) to a nonexperimental method (pollen and charcoal analysis) to enable hypothesis testing of multiple scenarios for past environmental change, thus improving our ability to distinguish the relative impacts of climatic and anthropogenic changes on past landscapes.

Study Area

Holey Meadow (HLY; 35° 57.3′ N, 118° 36.9′ W; elevation 1,945 m; Figure 1) is a sedge (Cyperaceae)-dominated perennially wet meadow in the southern Sierra Nevada, located within a montane conifer forest in Sequoia National Forest (Klimaszewski-Patterson and Mensing 2016). Dominant plant species of the meadow and adjacent forest include California black oak (*Quercus kelloggii*), Jeffrey pine (*Pinus jeffreyii*), ponderosa pine (*P. ponderosa*), white fir (*Abies concolor*), incense-cedar (*Calocedrus decurrens*), giant sequoia (*Sequoiadendron giganteum*), willow (*Salix* spp.), sedges (Cyperaceae), and grasses (Poaceae). Other taxa include canyon

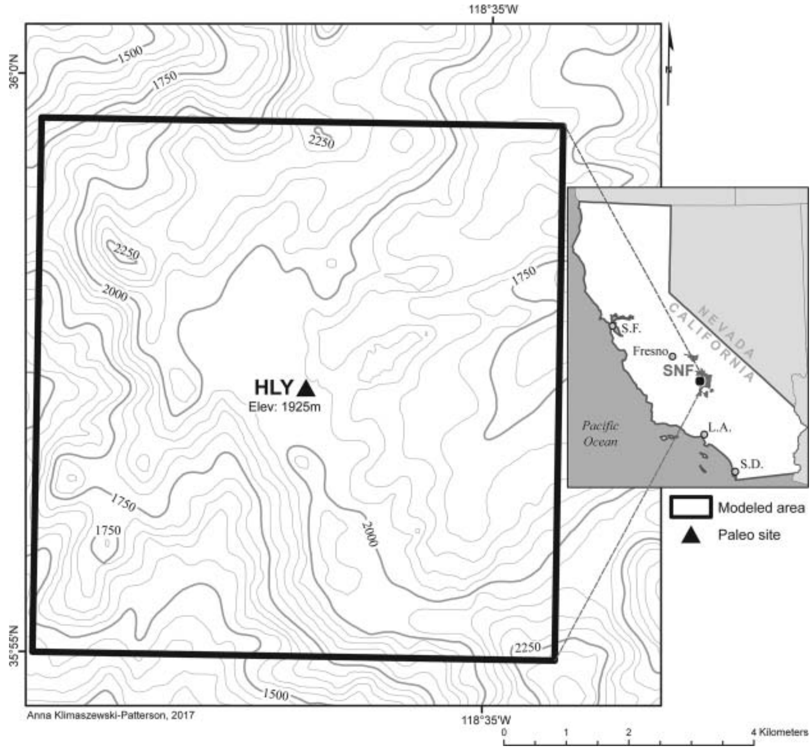

Figure 1. Extent of modeled study area within Sequoia National Forest in relation to paleoecologic site Holey Meadow. HLY = Holey Meadow; SNF = Sequoia National Forest.

live oak (*Q. chrysolepis*), interior live oak (*Q. wislizeni*), sugar pine (*P. lambertiana*), lodgepole pine (*P. contorta*), red fir (*A. magnifica*), western juniper (*Juniperus occidentalis*), chamise (*Adenostoma fasciculum*), mountain mahogany (*Cercocarpus montanus*), and other members of the rose family (Rosaceae).

Most precipitation comes between October and April in association with Pacific frontal systems (Millar et al. 2006), although summer afternoon thunderstorms are common. Lightning-caused fires peak between June and September, with June (31 percent) and September (19 percent) having the highest percentage (Vankat 1985; van Wagtendonk and Cayan 2008).

Fire is a natural disturbance in California's Sierra Nevada forests (Swetnam 1993; Brunelle and Anderson 2003). Multimillennial fire histories reconstructed from *Sequoiadendron giganteum* indicate periods of regionally synchronous fire events across the central and southern Sierra Nevada (Swetnam 1993; Swetnam et al. 2009). Reconstructions revealed decadal to centennial associations with summer temperatures, where cooler temperatures were associated with reduced fire frequency and warmer, drier conditions with higher fire frequency (Swetnam 1993; Swetnam et al. 2009).

Methods

Vegetation Response Index

We use a 1,600-year pollen-derived vegetation response index (pVRI) from HLY as an observed record of subcentennial (~50-year interval) paleoenvironmental change (Klimaszewski-Patterson and Mensing 2016). The pVRI is calculated as a ratio between the pollen percentages of two easily identified common pollen types with different ecologies, fir (*Abies*; shade tolerant, fire sensitive) and *Quercus* (shade intolerant, fire adapted). A positive pVRI (more *Abies*) is expected during cooler, wetter conditions with fewer fires (e.g., LIA 750–100 cal yr BP) and a negative pVRI (more *Quercus*) during warmer, drier conditions (e.g., MCA 1050–750 cal yr BP; Graumlich 1993; Stine 1994; Bowerman and Clark 2011) when natural fires are more likely (Higgins, Bond, and Trollope 2000; Peterson and Reich 2001; Bond and Keeley 2005). Shade-intolerant, fire-adapted taxa such as *Quercus* were important to Native American subsistence economies (Lewis 1973; Jordan 2003); therefore, a negative pVRI during climatically cool, wet periods would be interpreted as an anthropogenic signal (Figure 2; see Klimaszewski-Patterson and Mensing 2016).

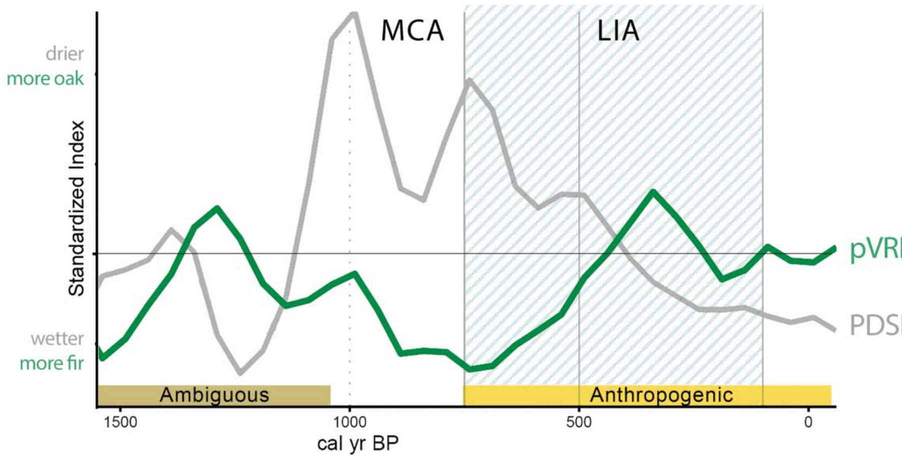

Figure 2. Observed reconstructions of vegetation (pollen-derived vegetation response index; green) and drought (Palmer Drought Severity Index fifty-year spline; gray) from Holey Meadow showing 1,600 years of change. Adapted from Klimaszewski-Patterson and Mensing (2016). MCA = Medieval climate anomaly; LIA = Little Ice Age; pVRI = pollen-derived vegetation index; PDSI = Palmer Drought Severity Index. (Color figure available online.)

Landscape Modeling Area

To model dynamic, spatially explicit paleolandscapes, we used two models: LANDIS-II, a stochastic forest succession model (Scheller and Mladenoff 2004; Scheller et al. 2007), and PnET-II, a process-based model (Xi and Xu 2010) that adds climate variations into LANDIS-II. The modeling area is a four-kilometer radius around HLY converted to a square raster (Figure 2), yielding a modeled area of 69.92 km^2 (6,992 hectares). This area is large enough to capture long-term fire dynamics and heterogeneous burn severity mosaics, while still reasonable for pollen transport distances. Pollen transport distances are derived from laboratory testing or modeled simulations under controlled conditions (Sugita 1993; Calcote 1995; Hjelle and Sugita 2011). Prior work showed that *Quercus* pollen sourced 4,000 m can represent up to 50 percent beyond source distance (Sugita 1993). Comparing modeled and empirical pollen data in semiopen terrain in western Norway, Hjelle and Sugita (2011) found relevant source area pollen to be within 1,100 m. Our study area, however, has more than double the wind speeds (Scheller et al. 2011; Syphard et al. 2011) used by Hjelle and Sugita, which increases potential pollen transport distance. Our four-kilometer modeled area is reasonable with respect to pollen transport and is also consistent with proposed foraging distances of Native Americans (Bettinger, Malhi, and McCarthy 1997; Morgan 2008). This extent represents the area most likely to have been affected by anthropogenic fire and other cultural practices.

Because climate has varied substantially over the last 1,600 years, it is inappropriate to assume static conditions; therefore, we created paleoclimatic proxies to approximate annual variability in the system using relationships between modern and paleo analogs.

Creating Monthly Paleoclimatic Records for PnET-II

PnET-II requires monthly temperature (T) and precipitation (P), which we infered from modern analogs. The North America Drought Atlas (NADA; Cook et al. 1999; Cook et al. 2004, 2008; Herweijer et al. 2007), a gridded network of drought reconstructions based on annual tree-ring chronologies, provides reconstructed Palmer Drought Severity Index (PDSI) values for the last 2,000 years (through AD 2003) at a 2.5° × 2.5° spatial resolution. The PDSI is widely used in ecological studies and climatic reconstructions (Swetnam et al. 1998; Fry and Stephens 2006; Gustafson and Sturtevant 2012). We used modern (1895–2015) monthly PDSI, T, and P values from the Western Regional Climate Center (WRCC) and paleo PDSI (pPDSI) for the period from 1550 to –63 cal yr BP (AD 400–2003) from the NADA to create a relational join. We identified the closest annual modern PDSI (mPDSI) analog per pPDSI year and then assigned the monthly T and P data for that year in the modern data to the pPDSI year from the tree-ring record. In cases where more than one mPDSI value was closest to the pPDSI value, a random mPDSI year was programmatically selected and assigned.

We recognize there are limitations in using PDSI to reconstruct climate and that different T and P combinations can result in similar annual PDSIs. Using modern to paleo analogs, however, provides the best data available to us at this time, and we used these best efforts to reasonably approximate annual variability in the system. Prior sensitivity testing found that running the LANDIS-II model with constant climate yielded no changes in forest structure during prehistoric periods of known climatic change (e.g., MCA and LIA). Instead, the forest steadily converted to fir dominance. Using our derived T and P reconstructions generated a more open-canopy forest during the MCA and a more closed-canopy forest during the LIA, as expected from models of climate-driven forest succession, and provided a more reasonable baseline data set. Further, although changes in monthly T and P are ecologically important to plant growth on an annual scale, disturbance through the quantity and type of fire had the greatest effect on forest structure in the model.

Process-Based Vegetation Modeling: PnET-II

PnET-II for LANDIS-II is a process-based model that simulates effects of changing climate conditions on forest ecosystem processes, ecophysiology, and establishment (Xi and Xu 2010). Inputs included our derived monthly paleoclimate data, atmospheric carbon dioxide (CO_2) from Antarctic Law Dome ice core reconstructions (Etheridge et al. 1996; Etheridge et al. 1998; MacFarling Meure 2004; Ferretti et al. 2005; MacFarling Meure et al. 2006), standard monthly photosynthetically active radiation (PAR) values, seven ecoregion physiographic parameters as defined by Syphard et al. (2011) within the study area, and species parameters as defined in the literature (Table 1). The final output included paleoclimate-derived species establishment parameters (SEP), annual net primary productivity (ANPP), and maximum biomass annually for each species by ecoregion that were then input into the LANDIS-II landscape model to generate climate change scenarios.

Landscape-Scale Modeling

LANDIS-II is a stochastic, raster-based model designed to simulate spatial interactions among succession, natural disturbances, and forest management (Scheller et al. 2007). The model simulates individual tree and shrub species based on their life history traits, including longevity, fire tolerance, shade tolerance, resprouting ability, age of maturity, seed dispersal distance, and reproduction following fire. Trees are modeled as species and age cohorts, allowing multiple cohorts within a single site (grid cell). LANDIS-II is appropriate for this study because of the interaction focus between fire and vegetation at an interannual time scale over long periods of time. This allows us to explore the effects of various fire regimes on the landscape and how species respond to climate and disturbance. Eleven scenarios (fifty-year aggregate time steps averaged over twenty replicates) were explored, each with a one-hectare cell resolution for a 6,992-hectare study area. Each simulation

Table 1. Data and source for modeling inputs used in this study

Data type	Source
Climate parameters	
Paleoclimate (PDSI)	NADA
Modern climate analogs (PDSI, T, P)	WRCC
PnET-II parameters	
Climate parameters	This study; Etheridge et al. (1996); Etheridge et al. (1998); MacFarling Meure (2004); Ferretti et al. (2005); MacFarling Meure et al. (2006)
Vegetation parameters	Radtke et al. (2001); Wythers et al. (2005); Midgley et al. (2010); Wythers, Reich, and Bradford (2013)
Ecoregion	Syphard et al. (2011)
LANDIS-II parameters	
Landscape (slope and upslope)	Syphard et al. (2011)
Ecoregions	Syphard et al. (2011)
Initial communities	Syphard et al. (2011)
Species life history	Syphard et al. (2011)
Biomass succession (ANPP, SEP, maximum biomass)	This study (PnET output)
Fire regions (baseline)	Modified from Syphard et al. (2011) to exclude wildland–urban interface
Fire regions (anthropogenic)	This study
Fire weather	Syphard et al. (2011)
Fire regime	Syphard et al. (2011, natural) and this study
Fuel type	Syphard et al. (2011)
Harvest regions	This study (based on anthropogenic fire regions)
Harvest parameters	Syphard et al. (2011) and this study

Note: PDSI = Palmer Drought Severity Index; NADA = North America Drought Atlas; WRCC = Western Regional Climate Center; T = temperature; P = precipitation; ANPP = annual net primary productivity; SEP = paleoclimate-derived species establishment parameters.

represents a different combination of climatic or anthropogenically influenced fire regimes.

We used the Biomass Succession extension version 3.2 (Scheller and Mladenoff 2004); inputs include paleoclimate-derived annual SEP, ANPP, and maximum biomass (described earlier) and initial communities (Figures 3 and 4). Species parameters, ecoregion parameters, biomass succession parameters, and ecoregions are from Syphard et al. (2011).

Fire regimes and fuels respond to vegetation feedbacks arising from changes in species biomass. This interaction is modeled by using the Dynamic Fire System (DFS; Sturtevant et al. 2009) and Dynamic Biomass Fuels System (DBFS; Syphard et al. 2011) extensions. DBFS classifies cells into season-independent fuel types that affect fire frequency, size, and severity (Syphard et al. 2007). DFS uses these values, along with the expected number of ignitions per year, to simulate fire ignition, initiation, severity, and spread to adjacent cells depending on weather and topography (Sturtevant et al. 2009). DFS parameters are from Syphard et al. (2011) and stratified by elevation (Figure 5A). The number of ignitions varies over time by modeled scenarios.

We used the Base Harvest module to simulate surface fires because DFS simulates mixed-severity crown fires and does not model low-mortality surface fires. The Base Harvest module has been used by other studies to simulate low-severity surface fires including prescribed burn treatments (Sturtevant, Gustafson, and He 2004; Scheller et al. 2011; Syphard et al. 2011). We used this module to simulate surface fires, allowing for a scaled, age-dependent reduction in younger fire-sensitive trees while maintaining older trees of fire-resistant species.

For scenarios that involve surface fires, we applied climatically adjusted ignitions (Scenario H1-C1 later) first, followed by surface fire of the remaining stands with stand ages of at least thirty years. Stochastic survival of younger cohorts was simulated by allowing a mortality for up to 70 percent of a 30-hectare patch. If a patch did not meet the minimum stand age requirement, it was bypassed.

It is estimated that 2 to 5 million hectares (6–16 percent) of prehistoric California burned annually as a result of climate and human influences, with a state-wide average of 13 percent (Martin and Sapsis 1992; Stephens, Martin, and Clinton 2007). We allowed a conservative 6 percent annual maximum of total study area to burn because the southern Sierra Nevada forests are thought to have had some of the lowest pre-Columbian population densities in the state (Kroeber 1925; Baumhoff 1963).

Similar to the wildland–urban interface concept (Radeloff et al. 2005), we introduce the concept of a wildland–habitation interface (WHI), an area of increased likelihood of fires set by Native Americans. We generated 500-m buffers around all recorded archaeological sites in the study area under the assumption that

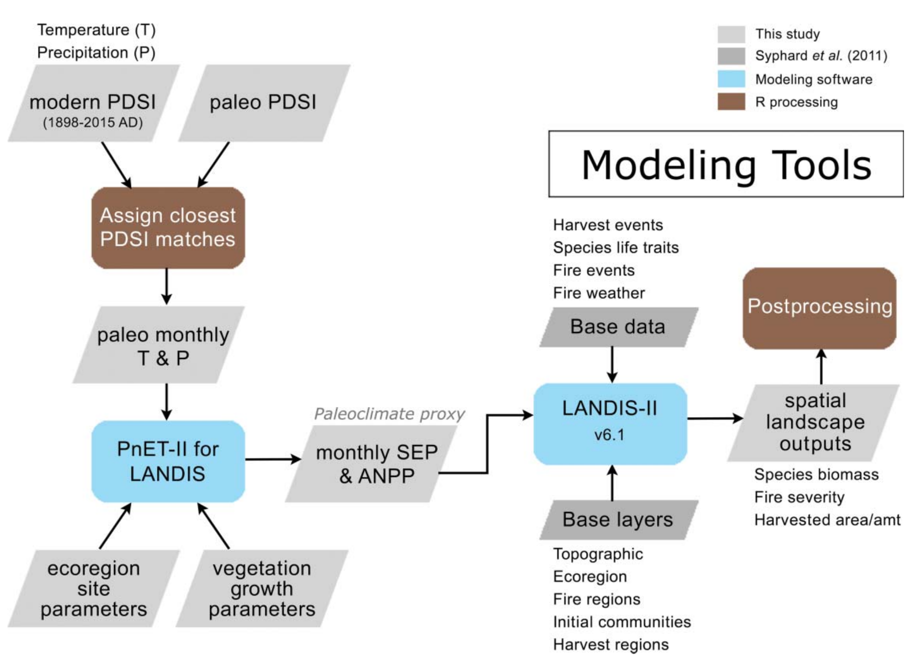

Figure 3. Overview flowchart demonstrating modeling inputs and flow. PDSI = Palmer Drought Severity Index; SEP = paleoclimate-derived species establishment parameters; ANPP = annual net primary productivity. (Color figure available online.)

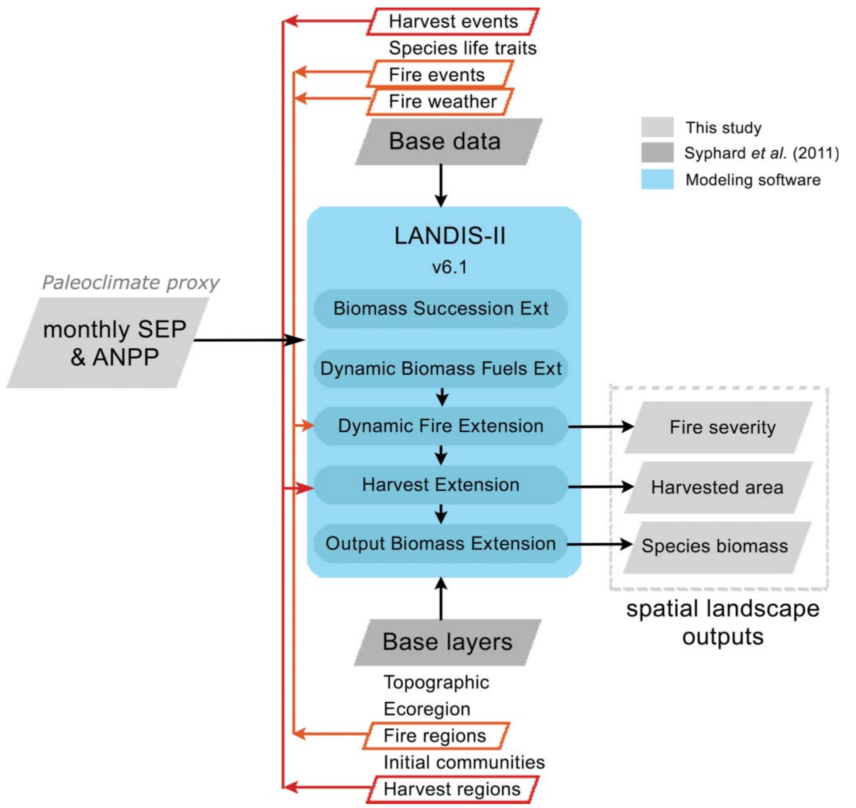

Figure 4. Overview flowchart of LANDIS-II inputs and extensions. Items outlined in red indicate variable inputs. SEP = paleoclimate-derived species establishment parameters; ANPP = annual net primary productivity. (Color figure available online.)

Native Americans would have set fires more consistently near areas of recorded use (Figure 5B).

Our modeling allows for three different burn modes:

1. Climatically caused lightning ignitions that could result in mixed-severity fires that kill stand and age cohorts. Even the lowest fire severity results in mortality of grown trees (e.g., <80-year-old *Quercus* and <120-year-old *Abies*). We refer to these as *wildfires*.
2. Using the harvest module to simulate surface fires that affect young, fire-susceptible cohorts. When applied in a stochastic manner, we refer to these as *wild surface fires*.

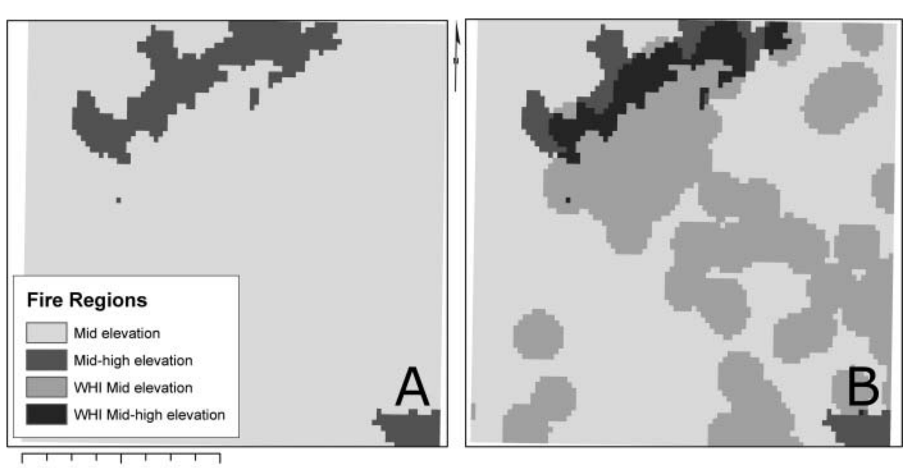

Figure 5. (A) Fire regions used to determine the number of lightning ignitions. (B) Anthropogenic burning in wildland–habitation interface areas. WHI = wildland–habitation interface.

3. Using the harvest module to simulate targeted placement of surface fires, with a greater proportion of surface fire within the WHI. We refer to this as *anthropogenic burning*.

All LANDIS-II modeling runs begin at 1550 cal yr BP using modern vegetation communities. The first 500 years are excluded from analysis as a modeling "burn-in" period, allowing for at least one full successional cycle to develop climatic and response conditions of forest community distribution. Previous work has created conversion factors from biomass to pollen percentage (Lotter and Kienast 1990; Keller et al. 2002) to allow for comparison between modeled and pollen-derived analogs. Both *Quercus* and *Abies* have a conversion factor of 1.0 and, as such, were unmodified in our analysis.

Modeling Scenarios (H1: Wildfires)

The following six scenarios (Table 2) test Hypothesis 1, that modeled predictors of forest composition derived from wildfires alone can approximate observed paleovegetation dynamics. Each scenario number is prefaced by a "C" for "climatic fire." These scenarios test how much wildfire is necessary to approximate pVRI and whether the amount appears plausible. Each scenario is based on a multiplier of PDSI-adjusted lightning ignitions (baseline), where H1-C1 is the baseline value, H1-C10 is ten times the number of ignitions, and so on.

Scenario H1-C1: Baseline Reconstructed Wildfire

A recent study in the Lake Tahoe basin of the Sierra Nevada demonstrated that the number of lightning-caused wildfires from 1986 to 2009 had a positive linear relationship with both climatic water deficit (CWD) and lightning density (Yang et al. 2015). Because both PDSI and CWD are estimates of drought stress, we assumed a similar linear relationship between lightning ignitions and PDSI. We applied a smooth-spline PDSI multiplier at each fifty-year time step to create climatic PDSI-adjusted ignition values. In the southern Sierra Nevada, mid elevations (MID) have a higher observed fire frequency than slightly higher (MID-HIGH) elevations. To account for this in the model, we used observed ignition values by fire region from Syphard et al. (2011). Daily fire weather (Syphard et al. 2011), which is randomly assigned by LANDIS-II from weather records, remained unchanged.

Scenarios H1-C10, C20, C40: Increased Lightning Ignitions from 750 to 100 Cal Yr BP

We increased the number of potential lightning ignitions to determine how much more fire beyond the baseline was necessary to approximate the reconstructed pVRI values (Figure 1). Initial testing found that increasing the number of ignitions through the MCA resulted in conversion of the area to oak woodland, which is not representative of either the observed record or historic accounts. Therefore, baseline ignition values were used from model initiation through the MCA (Scenario H1-C1 data) and then increased during the LIA, the period during which the pVRI showed an open forest despite a cooler, wetter climate. At 100 cal yr BP, the period when European American activities are known to have reduced fires in the region (Vankat and Major 1978), we returned the number of ignitions to observed modern values.

Table 2. Parameters for the amount of lightning ignitions, by temporal period and scenario

	cal yr BP	1550–750		750–100		100–AD 2011	
		Fire type		Fire type		Fire type	
		Wildfire	Surface	Wildfire	Surface	Wildfire	Surface
H1 scenarios	C1	Baseline	—	Baseline	—	Baseline	—
	C10	Baseline	—	Baseline * 10	—	Baseline	—
	C20	Baseline	—	Baseline * 20	—	Baseline	—
	C40	Baseline	—	Baseline * 40	—	Baseline	—
	C1(s6)	Baseline	6% (30%)	Baseline	6% (30%)	Baseline	6% (30%)
	C10(s6)	Baseline * 10	6% (30%)	Baseline * 10	6% (30%)	Baseline * 10	6% (30%)

Note: Baseline represents the amount of climatically adjusted ignitions. Baseline * multiplier (e.g., 10) indicates the amount of increase for that period (e.g., ten times the number of ignitions). Surface fire values represent up to the amount of area burned annually (and by five-year time step).

The value at the end of the scenario name corresponds with the multiplier increase of ignitions modeled. We increased the number of ignitions over baseline values tenfold in Scenario H1-C10, twentyfold in Scenario H1-C20, and fortyfold in Scenario H1-C40.

Scenarios H1-C1(s6) and C10(s6): Wildfires + Wild Surface Fires

These two scenarios further test wildfires by adding wild surface fires. We used the same wildfire parameters as earlier (H1-C1 and H1-C10), adding wild surface fires over the entire modeling duration. Wild surface fires could bring the total amount of annual area burned up to 6 percent.

Modeling Scenarios (H2: Wildfires + Anthropogenic Burning)

Scenario H2-A: Wildfires + Anthropogenic Burning from 1550 to 1050 and 750 to 100 Cal Yr BP (LIA)

This scenario tests the hypothesis (H2-A) that anthropogenic burning during both periods of prolonged wetter climate (1550–1050 and 750–100 cal yr BP) is necessary to approximate the fossil pollen record. Anthropogenic burning during the MCA was excluded for two reasons: (1) because Native American populations are thought to have either declined or dispersed widely during this time (Lewis 1973; Jones et al. 1999; Hull 2005) and (2) because climate would have created favorable conditions for common food taxa. Previous studies have shown a regional increase in fire during the MCA (Swetnam 1993; Swetnam et al. 2009); therefore, it might have been unnecessary for Native Americans to use additional fire as a resource intensification tool, particularly if population density was lower. Anthropogenic burning within the WHI is doubled (20 percent MID and 12 percent MID-HIGH; Table 3) over base fire region values (10 percent and 6 percent, respectively) under the assumption that Native Americans would have burned more extensively or intensively in areas near archaeological sites. The removal of anthropogenic burning at 100 cal yr BP coincides with the establishment of Sequoia National Forest, the resettlement of Native Americans to the Tule River Indian Reservation, and fire suppression policies (Vankat and Major 1978).

Scenario H2-L: Wildfires + Anthropogenic Burning from 750 to 100 Cal Yr BP (LIA).

This scenario tests the hypothesis (H2-L) that anthropogenic burning was only necessary during the LIA, a period of greater Native American population density and resource intensification compared to all prior periods. Parameters are identical to H2-A but with anthropogenic burning only during the LIA.

Paleoclimate Evaluation of Modeling Outputs

We used the existing pVRI from HLY (Klimaszewski-Patterson and Mensing 2016) as the observation set against which modeled scenarios were compared (Figure 2). We used the relationship in simulated biomass between *Abies concolor* and *Quercus kelloggii* to create a modeled VRI analog (mVRI) for comparison to the observed pVRI. A conversion factor from biomass to pollen percentage of 1.0 was used for both taxa (Lotter and Kienast 1990; Keller et al. 2002) to allow for comparison between analogs.

We used both Pearson's r and Spearman's rho (ρ) two-tailed tests to statistically evaluate changes in pVRI and mVRI from 1050 to 100 cal yr BP. We excluded 100 cal yr BP to present because forest structure has been highly

Table 3. Overall patch area to apply 70% prescription burn annually by fire region, by temporal period and scenario (H2). Up to 6 percent of the overall study area may burn annually through a combination of wildfire and surface fires.

cal yr BP		1550–1000				750–100 (LIA)			
		Fire region				Fire region			
		Mid	Mid + WHI	Mid-high	Mid-high +WHI	Mid	Mid + WHI	Mid-high	Mid-high +WHI
H2 scenarios	A	10%	20%	6%	12%	10%	20%	6%	12%
	L	—	—	—	—	10%	20%	6%	12%

Note: LIA = Little Ice Age; WHI = wildland–habitation interface.

manipulated in the study area since 96 cal yr BP (1854) through European settlement, fire suppression, silvicultural practices, and exclusion of Native American influences (Silcox 1910; Kilgore 1973; Franklin and Fralish 2002; Ramirez et al. 2010; Gassaway 2011).

Results

Climatic Wildfires

A significant increase in modeled lightning ignitions (at least twentyfold; H1-C20 and H1-C40; Table 4), with no wild surface fire component, was necessary to statistically approximate trends in the paleoenvironmental record (Table 5). Modeled output for Scenario H1-C1 (baseline) matched climatic trends between PDSI and percent area burned (Table 4) but did not approximate trends in pVRI (Figure 6A), with negative statistical correlations over the entire period ($r/\rho = -0.55/-0.64$; p values = 0.01/0.004; Table 5). The area burned was highest in the MCA (27 percent average) and decreased throughout the LIA (from 28 to 4 percent, 14 percent average) as expected based on climate. Increasing the number of lightning ignitions in Scenarios H1-C10 (tenfold) through H1-C40 (fortyfold) caused a nonlinear increase in the number of modeled fire events and hectares burned. A greater number of fire events did not result in a linear increase of area burned. Changes in the area burned over baseline expectations became apparent once the number of lightning ignitions increased at least

Table 4. Number of lightning-caused wildfires and percentage study area burned by wildfires per cumulative fifty years, by scenario (averaged)

	Wildfires												Anthropogenic burning			
	H1-C1		H1-C10		H1-C20		H1-C40		H1-C1(s6)		H1-C10(s6)		H2-A		H2-L	
Scenario	Baseline		10-fold		20-fold		40-fold		Baseline + wild surface fire		10-fold + wild surface fire		1550–1000; 750–100 cal yr BP		750–100 cal yr BP (LIA)	
Cal yr BP	#	%	#	%	#	%	#	%	#	%	#	%	#	%	#	%
1050	10	24	9	18	9	23	9	35	11	39	78	85	**10**	**28**	10	29
1000	11	37	11	38	10	36	11	41	13	29	92	74	**11**	**37**	11	37
950	10	34	8	31	8	17	8	24	10	27	66	54	**9**	**33**	9	41
900	7	22	7	22	7	21	6	34	7	29	58	46	**8**	**33**	6	28
850	6	24	5	28	5	16	6	16	7	17	47	38	**6**	**15**	5	19
800	9	19	10	35	8	24	10	47	10	30	68	60	**10**	**31**	9	18
750	11	28	76	28	**154**	**48**	**277**	**81**	10	40	88	67	**10**	**24**	**12**	**41**
700	9	17	71	35	**138**	**40**	**243**	**59**	8	21	65	57	**8**	**24**	**10**	**23**
650	6	19	52	18	**102**	**40**	**193**	**58**	6	25	63	51	**8**	**15**	**6**	**17**
600	5	18	55	22	**103**	**33**	**190**	**46**	7	23	46	43	**6**	**17**	**6**	**9**
550	6	18	52	23	**96**	**38**	**193**	**44**	7	16	47	49	**7**	**16**	**7**	**22**
500	6	14	50	18	**98**	**34**	**190**	**46**	7	15	47	50	**7**	**20**	**5**	**20**
450	6	14	54	20	**103**	**38**	**191**	**44**	7	16	46	46	**7**	**17**	**7**	**28**
400	5	21	33	19	**71**	**27**	**139**	**38**	6	19	46	40	**5**	**11**	**5**	**13**
350	5	8	38	15	**75**	**29**	**135**	**35**	5	14	50	52	**6**	**20**	**5**	**19**
300	2	10	27	9	**56**	**19**	**113**	**33**	1	6	32	35	**2**	**2**	**2**	**7**
250	2	12	30	10	**56**	**22**	**112**	**32**	2	5	34	39	**2**	**7**	**2**	**4**
200	2	5	29	8	**57**	**18**	**114**	**38**	2	4	36	53	**1**	**4**	**2**	**4**
150	1	4	30	9	**56**	**22**	**111**	**31**	2	8	34	40	**2**	**14**	**2**	**12**
100	3	5	3	8	2	5	2	6	3	11	26	33	3	6	3	4
50	2	3	2	7	2	4	4	8	3	8	27	47	3	5	3	9
0	2	4	3	10	3	6	3	7	3	9	28	37	3	17	3	14

Note: Gray cells represent years with ignition increases over baseline conditions (e.g., 10-fold, 20-fold, 40-fold). Values shown in bold represent positive statistically significant correlations between modeled vegetation response index and pollen-derived vegetation response index. Values shown in italics are years with the application of surface fires (either wild surface fires or anthropogenic burning). All surface fires (H1-C1(s6), H1-C10(s6), H2-A, and H2-L) are excluded from area burned. LIA = Little Ice Age.

Table 5. Correlation values between mVRI and pVRI values, by scenario, for the analyzed period (1050–100 cal yr BP; 900–1850)

	Climatic fires						Anthropogenic burning	
	H1-C1	H1-C10	H1-C20	H1-C40	H1-C1(s6)	H1-C10(s6)	H2-A	H2-L
Scenario	Climatic	10-fold	20-fold	40-fold	Climatic + 6% surface	10-fold + 6% surface	1550–1000; 750–100 cal yr BP	750–100 cal yr BP
MCA								
r/p value	***−0.87/0.03***	***−0.88/0.02***	***−0.82/0.04***	***−0.87/0.03***	***−0.81/0.05***	***−0.73/0.19***	**0.98./ 0.001**	***−0.86/0.03***
ρ/p value	***−0.88/0.03***	***−0.94/0.02***	***−0.77/0.10***	***−0.86/0.03***	***−0.89/0.03***	***−0.76/0.08***	**0.99/<0.001**	***−0.89/0.03***
LIA								
r/p value	*−0.45/0.1*	*−0.38/0.20*	**0.89/<0.001**	**0.89/<0.001**	*−0.35/0.25*	*N/A*	**0.59/0.03**	**0.69/0.009**
ρ/p value	***−0.58/0.04***	***−0.61/0.03***	**0.91/0.0**	**0.93/0.0**	***−0.58/0.04***	*N/A*	**0.51/0.07**	**0.53/0.07**
All								
r/p value	***−0.55/0.01***	*−0.36/0.13*	**0.43/0.06**	**0.54/0.02**	*−0.25/0.30*	0.06/0.81	**0.61/0.005**	0.38/0.11
ρ/p value	***−0.64/0.004***	***−0.62/0.005***	**0.67/0.002**	**0.67/0.002**	***−0.43/0.07***	0.16/0.51	**0.61/0.005**	**0.48/0.04**

Note: Values shown in bold indicate statistically significant correlations. Gray shaded values shown in italics indicate negative correlations. Climatic fire scenarios H2-C1 to H1-C40 include lightning-caused wildfires only. H1-C1(s6) and H1-C10(s6) include lightning-caused wildfires and 6 percent study area burned by surface fires throughout the entire modeling run. Anthropogenic burning scenarios include baseline wildfires plus 6 percent study area burned annually through Native American–set fires during specific periods. H2-A represents burning during both prolonged wet periods (1550–1000 and 750–100 cal yr BP). H2-L has burning only during the LIA, when population densities were greatest. During this simulation, *Abies* becomes locally extinct and there is no variance in mVRI. mVRI = modeled vegetation response index; pVRI = pollen-derived vegetation index; MCA = Medieval climate anomaly; LIA = Little Ice Age; N/A = not applicable.

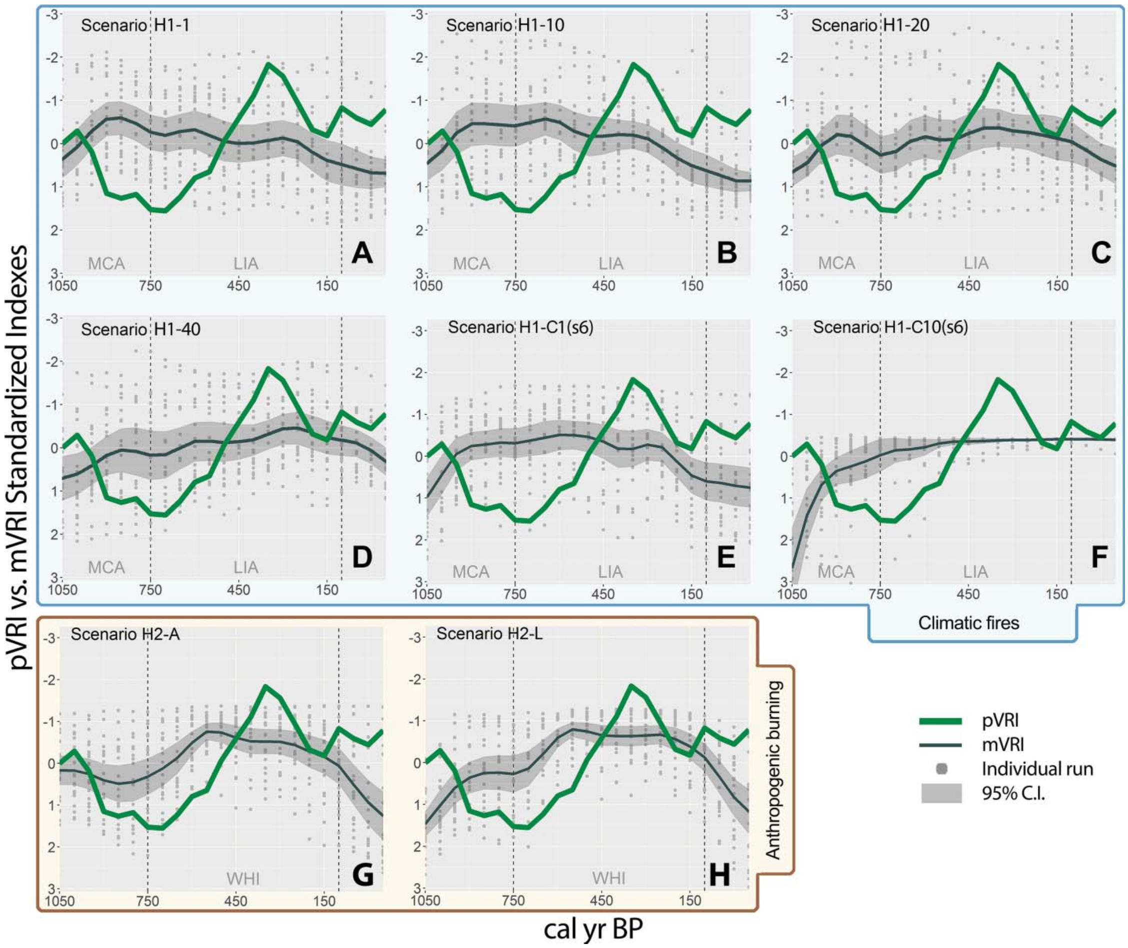

Figure 6. Standardized mVRI vs. pVRI values. Thick green line represents fifty-year splined pVRI values to which mVRI is compared. Dark line represents the standardized average mVRI, gray dots mVRI per run, and gray band a 95 percent confidence interval MCA = Medieval Climate Anomaly; LIA = Little Ice AgeWHI = wildland-habitation interface; pVRI = pollen-derived vegetation response index; mVRI = modeled vegetation response index; C.I. = confidence interval. (Color figure available online.)

twentyfold (Scenario H1-C20). Scenarios H1-C20 and H1-C40 (Figure 6C, 6D) showed strong positive statistical correlations with pVRI over the entire record ($r/\rho =$ 0.43/0.66, p values = 0.06/0.002; and $r/\rho = 0.54/0.67$, p values = 0.02/0.002), especially during the LIA. These latter scenarios require a minimum increase of 215 percent area burned by wildfires over the baseline PDSI-adjusted values, which are our expectations of the past. This equates to a minimum of 870 percent more area burned annually for the last 1,100 years by mixed-severity wildfires (Table 6) over observed calibrated conditions from 1985 to 2006 (Syphard et al. 2011).

The addition of wild surface fires allowing for up to 6 percent total of the study area to burn annually resulted in unexpectedly strongly negative correlations between mVRI and pVRI values (Table 5; Figures 6E, 6F).

Table 6. Increase in area burned from 750–100 cal yr BP as a result of only lightning-caused wildfires

	H1-C1	H1-C10	H1-C20	H1-C40
	Scenario			
	Climatic	10-fold	20-fold	40-fold
Over climatically adjusted (Scenario H1-C1)	—	125%	215%	310%
Over modern conditions (no PDSI adjustment)	400%	500%	870%	1,245%

Note: Only scenarios H1-C20 and H1-C40 are statistically significant, indicating that at least 870 percent more area would have needed to burn annually over the last 800 years than has been observed in the modern period. PDSI = Palmer Drought Severity Index.

Scenario H1-C1(s6) (baseline wildfires + wild surface fires) had a negative correlation throughout the record ($r/\rho = -0.25/-0.43$, p values $= 0.30/0.07$), with a strongly significant negative correlation during the MCA ($r/\rho = -0.81/-0.89$, p values $= 0.05/0.03$) and LIA ($r/\rho = -0.35/-0.58$, p values $= 0.25/0.04$). Increasing lightning ignitions tenfold (H1-C10(s6)) while maintaining 6 percent wild surface fires caused *Abies* to become locally extinct by 500 cal yr BP (Figure 6F). As a result, the correlations between mVRI and pVRI were not significant for H1-C10(s6) ($r/\rho = 0.06/0.16$, p values $= 0.81/0.51$).

Wildfires + Anthropogenic Burning

The addition of anthropogenic burning best approximated overall pVRI, especially when burning occurred during both wetter periods (Scenario H2-A, Figure 6G and Table 5; $r/\rho = 0.61$, p values $= 0.005$). Further, burning during both wet periods stabilized the general trend in amount of area burned, with total hectares burned annually consistently decreasing over time (Table 4). This trend is consistent with modern land management practices and expectations, where prescribed fire is implemented with the purpose of reducing the extent of wildfires through removal of fine fuels and reduced fuel loads. Although the scenario of anthropogenic burning only during the LIA (H2-L) was moderately effective at approximating overall pVRI ($r/\rho = 0.38/0.48$; p values $= 0.11/0.04$; Figure 6H), it did not explain MCA paleovegetation ($r/\rho = -0.86/-0.89$, p values $= 0.03/0.03$), further supporting a pattern of anthropogenic burning preceding the MCA (Scenario H2-A).

The "natural" background amount of hectares burned as a result of wildfires was highest in the warmer, drier MCA and decreased throughout the cooler, wetter LIA as expected based on climate. This result is supported by the sedimentary charcoal record at HLY, which Klimaszewski-Patterson and Mensing (2016) found to correspond with variation in PDSI and representative of a regional fire regime. The number of wildfires and hectares burned was comparable to the baseline climate scenario H1-C1.

Discussion

Fires at HLY were simulated through (1) climatic, lightning-caused, mixed-severity wildfires (Scenarios H1-C1 to C40) and (2) the addition of patchy, frequent surface fires that kill off primarily the youngest cohort (one to ten years old; H1-C1(s6) H1-C10(s6), both H2 scenarios). The H2 scenario results (wildfires with the addition of anthropogenic burning) were more consistent with observed paleoecologic reconstructions (Figure 6) than wildfires alone (H1 scenarios).

Model Support for the Anthropogenic Fire Hypothesis

Scenarios of lightning-set wildfires plus Native American–set surface fires most successfully approximate the paleoecologic data from HLY (Table 5, Figure 6G, H). Burning up to 6 percent of the total area annually through the addition of anthropogenic burning during all prolonged wet periods (Scenario H2-A) had the strongest statistical correlations. This strongly suggests that Native American–set fires, in addition to lightning-set wildfires, were necessary to develop pre-MCA conditions and that a substantial reduction in surface fires during the MCA and reintroduction of anthropogenic burning during the LIA was required to develop the pVRI observed at HLY.

In the climatic scenarios, wildfires (H1-C1 to C40) needed to annually burn at least 215 percent more of the study area on average over baseline conditions (870 percent over modern observed conditions; Table 6) to achieve a forest composition statistically similar to that observed in the pollen record, while still providing a poor match to the reconstructed pattern of forest change (Figures 6B, 6C, 6D). Although such a fire regime is obtainable within the model, these scenarios are unrealistic and inconsistent with fire history reconstructions (Taylor et al. 2016). There is no plausible climatic driver for increasing the necessary amount of area burned during the cooler LIA period for which regional fire history studies report reduced fire occurrence (Swetnam et al. 2009). It is more plausible that Native Americans set low-intensity fires (H_2) targeting the youngest cohorts following natural stand-replacing wildfires, thus maintaining the more open forest environment observed in the pollen record.

To create a model more consistent with local and regional fire scar data (Kilgore and Taylor 1979; Warner 1980; Swetnam et al. 2009; Taylor et al. 2016), climatic scenarios with the addition of lightning-caused surface fires (H1-C1(s6) and H1-C10 (s6)) were modeled; however, these were also unsuccessful in approximating paleovegetation response (Figures 6E, 6F). Statistically, the addition of consistent surface fires was considerably less effective at approximating the pollen record than modeling increases only in wildfires. This could be due to the indiscriminant nature of where surface fires occurred on the modeled landscape, as opposed to a greater percentage of anthropogenic burning occurring in a WHI area (H2).

Further, a reduction in surface fires is needed during the MCA to prevent the model from producing a local extinction of *Abies*. The inconsistencies between the expected pattern and that which is observed in pollen and fire records do not support an increase in lightning-caused wildfires alone as a likely explanation for observed paleovegetation dynamics.

Climate scenario H1-C1(s6) and anthropogenic scenario H2-A are the most similar in their use of a combination of wildfire and surface fires; however, the difference in their ability to approximate the fossil pollen record (Figures 6E, 6G) demonstrates the importance of the timing and spatial location of surface fires. Where H1-C1(s6) had a significant negative correlation with the pVRI (Table 5, Figure 6E) due to stochastic wild surface fires over the entire area and time period, the targeted placement of anthropogenic burning in H2-A, both temporally (when there is evidence for regional Native American activity) and spatially (within WHI areas), had the strongest relationship with pVRI (Table 5, Figure 6G).

Results from Native American–set fire scenarios (H2) are consistent with fire scar and sedimentary charcoal records. Swetnam (1994, 2009) regionally observed short periods of increased fire frequency around 350 and 250 cal yr BP. This increase in fire frequency coincides with a slight increase in average modeled area burned around 400 and 250 cal yr BP in H1-C1 and all H2 scenarios. Periods of increased spatial high-intensity fires (background lightning-caused wildfires) are also associated with increased charcoal production at HLY (Klimaszewski-Patterson and Mensing 2016). Decreases in the number of modeled wildfires after 1650 coincided with both land management expectations from prescribed burns and with decreased charcoal production and increased *Quercus* pollen in the observed record.

Additional Considerations

The southern Sierra Nevada is a landscape defined by fire (C. Miller and Urban 1999; Flannigan, Stocks, and Wotton 2000; J. D. Miller et al. 2009). Plants have traits such as resprouting (e.g., *Quercus kelloggii*, *Q. chrysolepis*), thick bark and self-pruning (e.g., *Pinus ponderosa*, *P. jeffreyi*), and serotiny (e.g., *Sequoiadendron giganteum*, *P. contorta*). The changes in VRI seen in our record, however, could possibly be associated with other forms of disturbance, such as insect or pathogen outbreaks.

Outbreaks of insects such as the bark beetle are common in coniferous forests of the Western United States, and there is a significant link between drought and outbreaks (Dobbertin et al. 2007; Fettig et al. 2007). Warmer conditions and resource competition create suitable conditions for infestations, tending to increase tree mortality under already stressful conditions. The LIA is expected to be a period of less stress for vegetation than the MCA, though. Therefore, insect outbreaks should be decreased during the LIA and are a less likely explanation for a more open canopy during the LIA than MCA.

The relationship between relative modeled biomass and observed pollen percentages is necessarily imprecise; however, previous paleolandscape modeling studies in Europe have successfully compared modeled biomass and pollen percentages (Keller et al. 2002; Heiri et al. 2006; Colombaroli et al. 2010). These studies differed in their analysis by either using a pollen/biomass dissimilarity index per iteration (Keller et al. 2002), treeline elevation (Heiri et al. 2006), or generalized additive models for species response curves (Colombaroli et al. 2010). The pollen/biomass dissimilarity index (Keller et al. 2002) is similar in principle to our mVRI/pVRI comparisons. Where they identify differences between all modeled and observed taxa, we explore an identified relationship in VRI between key taxa to test an existing paleoenvironmental interpretation.

The model is further limited in that it relies heavily on calibrations from modern observations, including vegetation, climate, fire frequency, and fire weather. Although we have done our best to mitigate these issues (e.g., by discarding the first 500 years from analysis), uncertainty remains. The generalizability of modern fire history (size and frequency) is limited because of fire suppression policies.

Arguments for a climate-driven fire regime rely on the predominance of lightning strikes and ignitions, but spatial variability in lightning strike frequency in the Sierra Nevada is only moderately associated with the frequency of lightning-caused fires, with climate and topography playing a greater role (Yang et al. 2015). Lightning-caused wildfires in the drier Sierra San Pedro Mártir of Baja California, which might be more representative of pre-suppression California's mixed conifer forests, have forty times more lightning strikes than wildfire events (Minnich et al. 1993; Minnich et al.

2000). These fires are typically small but have ranged up to 6,400 hectares. Increase in wildfire size is interpreted as more closely associated with fuel accumulation than lightning strike saturation.

Fires in the Sierra Nevada can persist for extended periods as smoldering, banked fires that our model does not capture (Caprio and Swetnam 1995). These banked fires can result from less frequent ignitions and could burn a larger area. We attempt to account for this behavior by testing both the saturation of lightning ignitions (H1-C10 to H1-C40) and by including indiscriminant surface fires that occur throughout the duration of the modeling period (H1-C(s6) and H1-C10(s6)). The amount of area annually burned would still need to average 870 percent more than modern to approximate changes observed in the paleoenvironmental record and would need a reduction of surface fires to occur during the MCA.

Conclusions

Forest landscape models can be used to test hypotheses about which forces caused environmental change in the past as expressed in the paleoenvironmental record (Heiri et al. 2006; Colombaroli et al. 2010; Berland, Shuman, and Manson 2011). We find modeling support for the conclusions made by Klimaszewski-Patterson and Mensing (2016) that the area surrounding Holey Meadow in Sequoia National Forest is most likely anthropogenically influenced through the use of low-intensity fires by Native Americans following natural stand-replacing wildfires, maintaining a more open forest environment.

The importance of Native American–set fires in pre-Columbian ecosystems needs to be further explored, both empirically and experimentally. This approach could allow us to investigate what role Native American use of fire played in increasing or decreasing forest resilience to climate change. Our modeling results suggest that pre-Columbian forest structure was a result of the use of fire by Native Americans, interacting with climate influences. This has two significant implications for paleoecology and forest management: (1) In California for the late Holocene, the use of pollen alone for reconstructing climate is not appropriate because pollen signals might represent anthropogenic impacts and (2) if prehistorical information is to be used to set targets for forest restoration (Cissel, Swanson, and Weisberg 1999; Swetnam, Allen, and Betancourt 1999; Keane et al. 2009), the role of anthropogenic burning could have strong implications for management strategies. Changes in Native American populations have been shown to control Sierra Nevada fire activity and affect fire–climate relationships (Taylor et al. 2016). Calls for reforms in forest management suggest that the use of fire is the least expensive, although still controversial, method for reducing fuel buildup that leads to high-severity crown fires (North et al. 2015). If a goal is to create open forests with frequent surface fires, then the processes can be consistent with traditional Native American cultural lifeways. Native Americans are key stakeholders in the use of fire to increase biodiversity and enhance resources and it might be useful to reexamine land use management strategies with Native American practices in mind (Anderson 1999, 2005; Fry and Stephens 2006).

This research demonstrates the ability to use a landscape dynamics model to explore alternative hypotheses about past climate–fire–vegetation interactions. Using spatially explicit simulation models to extend spatially implicit paleo records can be a powerful way to extend our knowledge of past landscape dynamics and forest response to changing climate and fire regimes.

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