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Multi-scale controls of historical forest-fire regimes: new insights from fire-scar networks

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Anticipating future forest-fire regimes under changing climate requires that scientists and natural resource managers understand the factors that control fire across space and time. Fire scars – proxy records of fires, formed in the growth rings of long-lived trees – provide an annually accurate window into past low-severity fire regimes. In western North America, networks of the fire-scar records spanning centuries to millennia now include hundreds to thousands of trees sampled across hundreds to many thousands of hectares. Development of these local and regional fire-scar networks has created a new data type for ecologists interested in landscape and climate regulation of ecosystem processes – which, for example, may help to explain why forest fires are widespread during certain years but not others. These data also offer crucial reference information on fire as a dynamic landscape process for use in ecosystem management, especially when managing for forest structure and resilience to climate change.

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Fire is a fundamental Earth-system process, linking ecosystems, biogeochemical cycles, and climate variability (Bowman *et al*. 2009). Understanding what controls fire regimes – the aggregate properties of multiple fires characteristic to an ecosystem – is of growing importance as the size and severity of forest wildfires increase in many regions. Regional to global climatic variability has been a primary driver of fire-regime variability for millennia (Swetnam and Anderson 2008; Whitlock *et al*. 2010), including the 20th century (Littell *et al*. 2009). Recent warming in some regions and ecosystems and at some elevations is at least partly responsible for the increase in the number and size of wildfires (Westerling *et al*. 2006).

In a nutshell:

- Tree-ring fire history networks provide accurate, high-resolution records spanning temporal scales from seasons to centuries and spatial scales from landscapes to continents
- Variations in fire synchrony across scales reflect interactions between local and regional controls of fire regimes, including physical, biological, and human factors
- Understanding past and present fire regimes and their controls allows ecologists and managers to anticipate future fire regimes as forests and climate change

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Fire regimes are also driven by relatively fine-scale, local conditions, particularly the spatial and temporal distributions of flammable fuels and ignitions as determined by complex interactions between physical and ecological processes. These controls frame a central challenge in understanding fire regimes: some dynamics are driven primarily by regional climate, others primarily by local ecology and/or humans, and still others – perhaps most commonly – by combinations of these factors. Furthermore, human influences on both fire regimes and climate have expanded from local to regional and even to global scales. Therefore, to understand how fire regimes vary, we need to understand the effects of physical, ecological, and human factors across multiple scales of time and space (Parisien and Moritz 2009; Turner 2010).

Fire is a spatial and temporal process, driven by controls acting across a range of scales. Scale considerations are central in the development of modern ecology (Ricklefs 1987; Turner 2010) and consequently in fire science as well. Although understanding of fire as a landscape process is progressing (McKenzie *et al*. 2011), long time series of linked ecological pattern and process data are rare, especially records spanning a century or longer across landscapes and regions. Fire-history studies are beginning to provide the necessary data for investigation of past and present fire regimes across these broader scales of space and time. One example is the recent proliferation of sedimentary charcoal-based fire histories that are now providing insights into changes in fire regimes and biomass burning at continental and millennial scales (Gavin *et al*. 2007; Marlon *et al*. 2008).

At fine scales, when and where fires start depend largely on the distribution and properties of fuels and ignitions.

Panel 1. The fire-scar record

Ecologists have long recognized the potential for fire scars to date past fires. Clements (1910) and Leopold (1924) observed fire scars on trees and understood that they captured the record of an ecological process. Pioneering work by Weaver (1943) and Arno (1976) in the inland Northwest, Kilgore (1973) in the Sierra Nevada, and Dieterich and Swetnam (1984) in the southwestern US developed the techniques for reconstructing past fires from fire scars.

Using dendrochronological methods, researchers can date fire scars to their exact calendar year and map their locations precisely (Figure 1). During surface fires, heated combustion gases interact with fine surface fuels to create a region of persistent high temperatures, usually on the uphill side of a tree (Gutsell and Johnson 1996); smoldering surface fuels contribute additional heat flux to the tree base and roots after passage of the flaming front. Heat penetrating the bark kills part of the vascular cambium (the layer of actively dividing cells between wood and bark tissues responsible for the annual increase in tree diameter), causing a lesion – a fire scar – where further radial growth cannot occur. In following years, the tree compartmentalizes the lesion, producing woundwood that scars more readily in a subsequent fire than the remaining bole because it has thinner bark. Some species also partition the wound with protective resins; where these flammable resins exude onto the surface, they increase the likelihood of subsequent scarring (Figure 1a). Repeated scarring before the cambium can fully reestablish produces a cavity surrounded by woundwood ribs, termed a "catface" (Figure 1b).

In a carefully sanded cross section, xylem cells are visible under moderate magnification (Figure 1c). To identify the correct calendar year of formation for each ring, dendrochronologists apply a pattern-matching process known as "crossdating", which identifies and corrects for growth anomalies such as false or absent rings. Fire scars are clearly visible in cross section and can generally be dated to their exact year of occurrence by determining the date of the annual ring in which they occur, even if the tree was dead when sampled (Figure 1d).

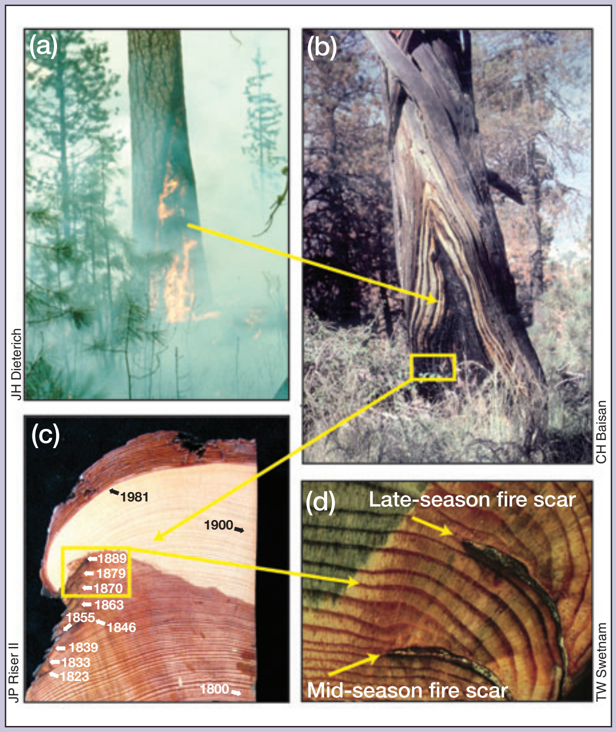

Figure 1. *Reconstruction of historical fires begins with processes such as low-severity surface fire that (a) scars a living tree, (b) often several times during its lifetime. (c) When crossdated, scars can provide accurate records of multiple fires with annual resolution. (d) Scars appear as growth lesions occurring in a specific growth-year ring when viewed in cross section.*

Once a fire has ignited, its rate and direction of spread are controlled by local fuel conditions, weather, and topography. These fine-scale, *bottom-up* controls modify fire physics and behavior, and consequently effects on vegetation and soils. Thus, most fires create mosaics of fire severity, a signature of bottom-up regulation (see www.mtbs.gov for modern trends in burn severity in the US; Table 1). This heterogeneity affects a wide range of ecosystem components, such as wildlife habitat, soil, and hydrology, and ecological processes, such as forest dynamics, carbon sequestration, and insect outbreaks, as well as influencing subsequent fires (Collins and Stephens 2008; Turner 2010).

Climate variation at interannual to centennial (and longer) time scales tends to have the opposite effect, by synchronizing regional and sub-continental fire occurrence. Climate thus acts as a *top-down* control, the signature of which is synchronous fire occurrence among sites beyond the reach of a single spreading fire, in contrast to the patchy landscape patterns created by bottom-up regulation (Table 1). Understanding the interplay of bottom-up and top-down controls on fire is thus central to understanding fire as an ecosystem process, and to managing fire in the presence of rapid changes in land use and climate (Heyerdahl *et al.* 2001; Falk *et al.* 2007).

Fire history can be reconstructed from a variety of proxies, including forest stand ages and their landscape distribution (Heinselman 1973; Margolis and Balmat 2009). Here, we focus on dendrochronologically crossdated fire-scar networks from low- and mixed-severity fire regimes (Panel 1). The high temporal (to season) and spatial (to tree level) resolution of such records offers unique opportunities for multi-scale ecological analyses. Using examples from recent publications, we demonstrate how these high-resolution temporal data can be linked in a spatially explicit framework to provide new insights into fire regimes. We also discuss questions of interpretation and inference, as well as knowledge gaps, and we examine how these emerging networks are proving useful to land managers.

The North American fire-scar network

In much of North America, contemporary fires reflect a century or more of human-driven fire exclusion and landscape change. Fortunately, fire scars on trees record spatial and temporal patterns of fires that predate this time of great change in some forest types (Panel 2). Most fire scars form on trees in forests that historically sustained

Table 1. Fire regimes are governed by the interaction of top-down and bottom-up factors operating over a range of spatial and temporal scales

	Top-down regulation	*Bottom-up regulation*
Signature	Persistent annual synchrony of fire- and non-fire years at regional or broader scales	Spatial heterogeneity in fire occurrence, extent, or severity across areas with similar climate
Drivers	Interannual to millennial climate variation	Temporal or spatial variation in fuels (amount, condition, and distribution), ignition sources, topography, weather, and barriers to fire spread
Mechanism	Variations in temperature and moisture associated with regional droughts and pluvials (wet periods) regulate fuel production and flammability; succession and vegetation types govern fire regime	Variation in factors that control ignition and fire behavior leads to variation in fire timing, spread, and effects; post-fire landscape legacies
Typical scale	$> 10^4$ ha	10^{-4}–10^4 ha

primarily low-severity fires, although trees also scar along the perimeter of forest patches that burned with high severity (ie where all trees were killed) or in low-severity burn patches within landscape mosaics of varying burn severity (Kipfmueller and Kupfer 2005; Margolis and Balmat 2009).

Networks of fire-scarred trees can be analyzed across a wide range of spatial scales (Figure 2). Local-scale studies may focus on fire seasonality, episodes of tree mortality, and fire as a driver of stand demography. In other studies, trees are sampled to explore variation across environmental gradients, such as elevation, vegetation, and microclimate, leading to inferences about bottom-up drivers of fire regimes (Brown *et al.* 2001; Heyerdahl *et al.* 2001; Fulé *et al.* 2003; Sherriff and Veblen 2007; Margolis and Balmat 2009).

As local fire histories have proliferated across North America, they have been combined into broader-scale networks that are proving especially useful for understanding regional variation in top-down drivers of fire occurrence over time, including large-scale climate patterns, such as the El Niño–Southern Oscillation (ENSO), the Pacific Decadal Oscillation (PDO), the Atlantic Multidecadal Oscillation (AMO; Swetnam and Betancourt 1998; Kitzberger *et al.* 2007), and the Pacific North American (PNA) pattern (Trouet and Taylor 2010). These broad-scale fire–climate analyses are novel in that they provide a view of how fire responds to low-frequency climatic variation that cannot be explored with relatively short modern instrumental climate records (Figure 2).

Regional to continental fire-scar networks are expanding as dendrochronologists build chronologies in Europe, Asia, and South America (see Web-only materials). A driving rationale for this work is to understand broad-scale interactions between climate, fire, human activities, and carbon dynamics. The International Multiproxy Paleofire Database (IMPD) was created to facilitate the analysis of such networks through public archiving of fire chronologies, and now holds more than 400 fire-scar records (WebPanel 1). We have compiled more than 460 additional crossdated fire-scar chronologies from western

Panel 2. Interpretation and inference in fire history

Like all paleoecological records, fire scars require careful interpretation. The presence of a scar indicates heat energy sufficient to wound but not kill the tree – for example, by killing roots, cambium, or crown (Panel 1). Thus, a fire scar, like many ecological legacies, is context-dependent evidence that forms only under a prescribed range of physical and biological conditions. The same may be said of most paleoecological evidence; for instance, stand origin cohorts and sediment charcoal records predominantly reflect high-severity, stand-replacing fires.

The *lack* of a scar, however, is more uncertain evidence. Fire-scar formation and retention depend on fine-scale variation in bark thickness, heat load at the time of a fire, and subsequent events that may consume scars from earlier fires (Gutsell and Johnson 1996; Stephens *et al.* 2010). Thus, whereas a scar is affirmative evidence of fire, the absence of a scar does not necessarily prove the absence of fire, at least at the scale of an individual tree.

This simple asymmetry has generated an ongoing debate about interpretation of and inference from the fire-scar record (Baker and Ehle 2001). Spatial scale is central to this discussion. For example, what do point records of scarred trees tell us about the behavior of fire across larger landscapes? Do areas with fire scars differ from other parts of the landscape? Can we infer properties of mixed- and high-severity fire regimes, or in mosaics of varying severity, from the fire scars that form along their perimeters?

Although uncertainties remain, recent work has demonstrated that fire-scar networks accurately record the occurrence, extent, and frequency of historical low- and mixed-severity fire occurrence. Intensive studies have examined a complete site census of fire-scarred material, testing whether differences in sample selection affected the interpretation of fire-regime characteristics (Van Horne and Fulé 2006). Studies combining fire-spread modeling and fire atlases with fire-scar evidence have corroborated the historical and modern records (Fulé *et al.* 2003; Farris *et al.* 2010). Better understanding of the observed variability in scar formation across real landscapes (Stephens *et al.* 2010) is helping to elucidate some of the mechanisms of fire-scar formation.

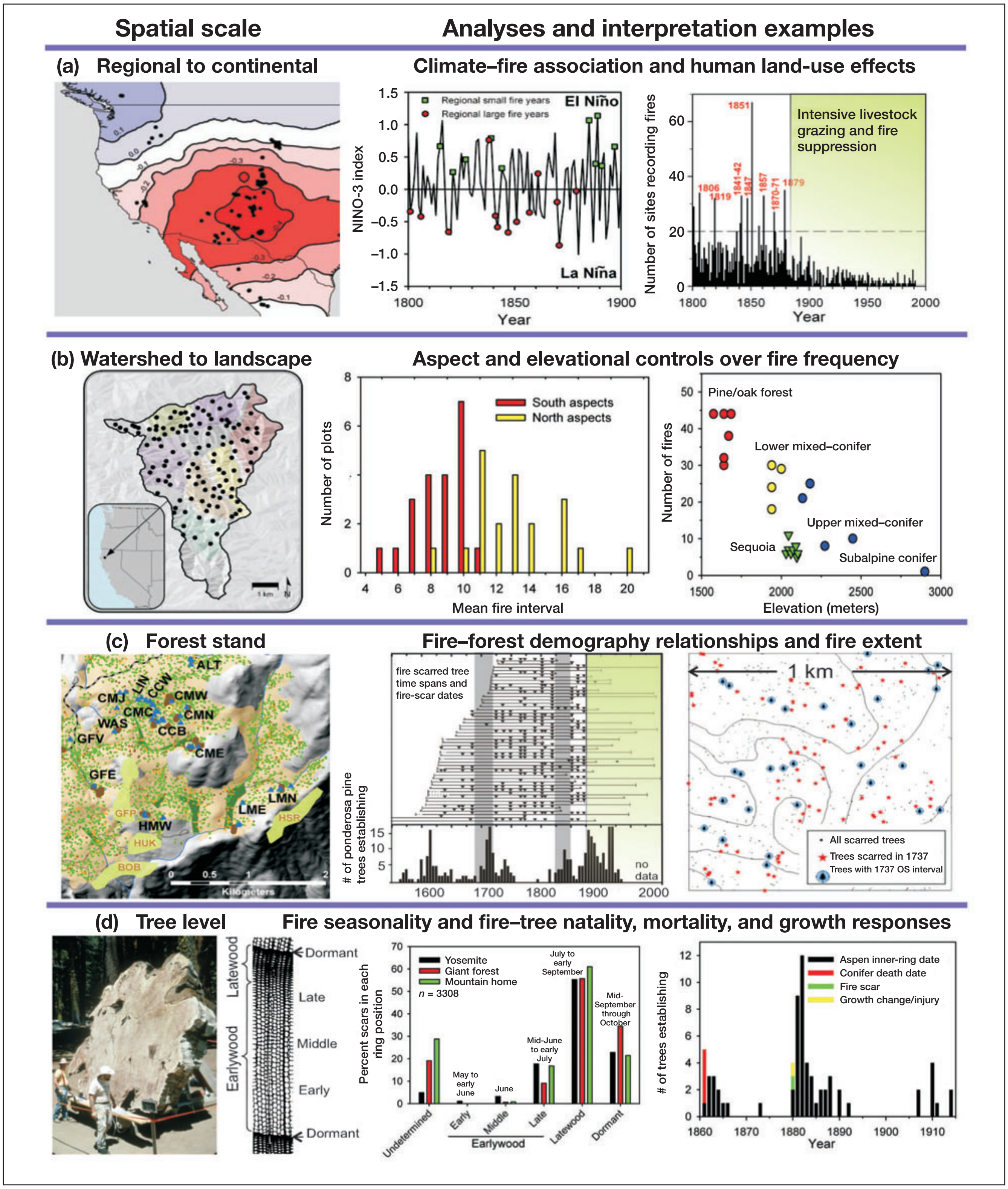

Figure 2. *Fire-scar networks can be created and analyzed at a range of spatial scales, from trees and stands to subcontinents, revealing different patterns and processes at different scales. (a) At regional to subcontinental scales, extensive fire-history networks are analyzed in aggregate to identify widespread fire–climate associations and human land-use effects. (b) Watershed and landscape networks can be used to explore topographic controls, such as aspect and elevation, on fire regimes. (c) At forest-stand scales, fire-scarred trees and tree ages can be sampled systematically or randomly to investigate fire–forest demography relations and patterns of synchrony related to fire spread. (d) Studies of individual trees can identify the seasonality of historical low-severity fires, tree-ring growth responses (releases and suppressions), and dates of tree recruitment or death. See WebPanel 3 for more detailed descriptions and references.*

North America that are not yet archived in the IMPD (Figure 3).

■ Ecological insights from multi-scale fire-scar networks

These new multi-scale fire-history networks provide unprecedented opportunities to examine how climate, vegetation, and topography influence low- and mixed-severity fire regimes over space and time (Kellogg *et al.* 2008). The potential strength of these inferences derives from the increased statistical power that comes from sampling a large number of extensively distributed sites, and from the distribution of samples and plots along biophysical gradients at multiple scales. Below, we focus on three areas of broad interest to ecologists, in which analysis of multi-scale fire-scar networks has enabled substantial scientific progress.

Mapping historical fires

Fire-scar networks can yield basic information about when and where fires occurred (Swetnam *et al.* 2011). Fire perimeters reconstructed from scars correspond well to those mapped from direct observation and from remotely derived data, confirming their reliability as recorders of past fires.

For example, Farris *et al.* (2010) compared fire dates and perimeters reconstructed from systematically sampled fire scars with dozens of historical fires that were mapped independently over a 64-year period by foresters and surveyors in a 2780-ha area of the Rincon Mountains of southern Arizona. Fire scars recorded a complete inventory of all independently mapped fires larger than 100 ha, and even detected some fires that were not mapped (Figure 4). When applied to the patterns of pre-20th-century fire scars, their interpolation method reveals the perimeters of historical fires for which there are no maps. Similarly, Hessl *et al.* (2007) used a network of fire-scarred trees in eastern Washington State to test spatial algorithms for interpolating point data to landscape scales, demonstrating that fire-scar networks can be used to reconstruct perimeters and heterogeneity in burn patterns (Figure 5).

Fire-scar networks can also yield estimates of the extent of large historical fires. In some landscapes, fire-scar networks may not capture every small fire, but they reliably capture large fires, which generally account for most of the area burned. This information could help resolve a current debate about whether contemporary fires are larger and/or more severe than historical fires. Fire-scar networks show that low-severity fires in many dry forests and woodlands burned large areas, often hundreds of square kilometers. The tree-ring record illustrates clearly that in many low- and mid-elevation forests these fires did not cause widespread overstory tree mortality, indicating that they were primarily of low severity (Brown and Wu 2005; Brown *et al.* 2008; Scholl and Taylor 2010). Low-severity fires are rarely so extensive in North America today, except in parts of northern Mexico and in some large wilderness areas, because fires of this kind occur under fuel and weather conditions that make them relatively easy to suppress.

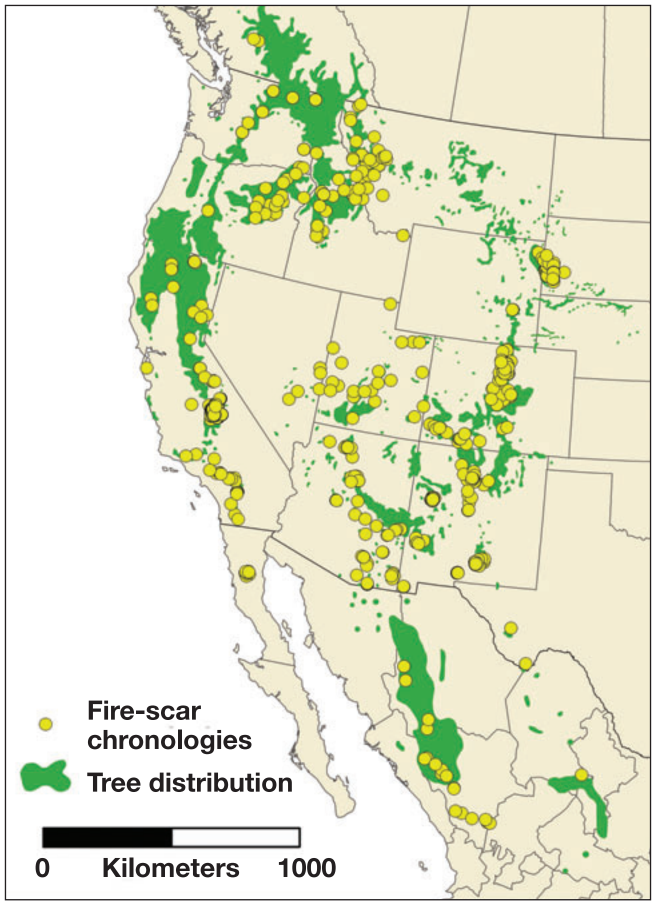

Figure 3. *The fire-scar network for western North America includes 415 fire chronologies recorded in the International Multiproxy Paleofire Database and an additional 468 fire chronologies not archived in this database. Tree distribution in the map base layer is the range of giant sequoia (*Sequoiadendron giganteum*), ponderosa, and related pines in Mexico, species that are well represented in the fire-scar record.*

Bottom-up controls of fire regimes

Topographic variation influences the local distribution of plant communities and, together with vegetation, forms the dominant bottom-up control of forest wildland fires (Taylor 2000; Heyerdahl *et al.* 2001; Table 1). For example, aspect and elevation strongly affect solar insolation (exposure to sunlight), which in turn controls dominant vegetation types as well as the amount and moisture content of fuel, and the period during which fuels are dry enough to burn (the fire season). Fuel type and fuel moisture content also vary with elevation, in response to variations in temperature and evaporation rate during the fire season. Dry surface fuels, consisting of long-needled litter and cured grasses in low-elevation forests of ponderosa (*Pinus pon-*

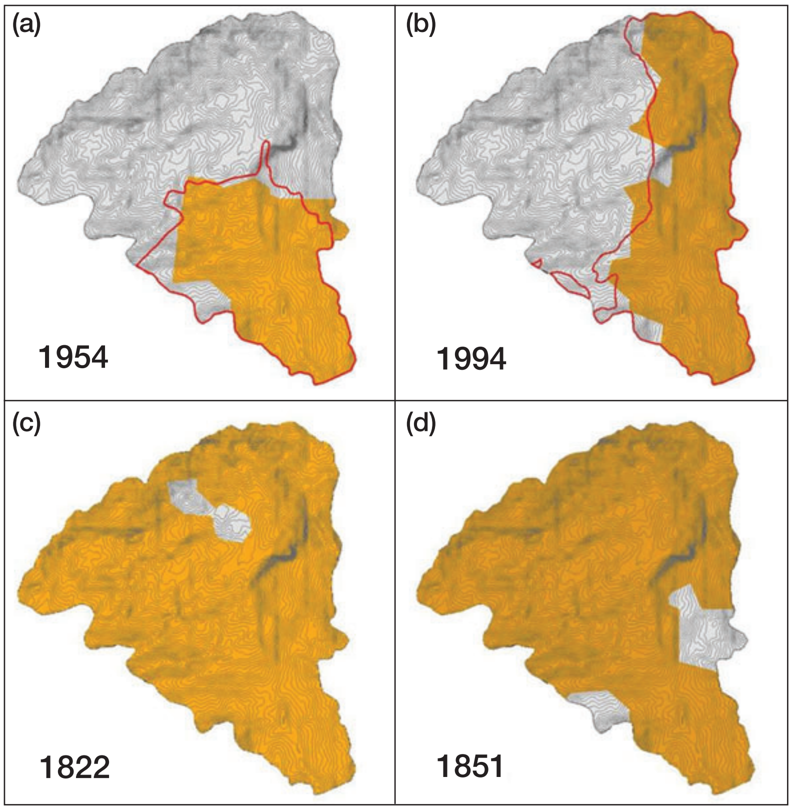

Figure 4. *Fire perimeters in the Rincon Mountains, Arizona, reconstructed from a 2780-ha fire-scar network. (a and b): Shaded polygons represent fire areas in 1954 and 1994 reconstructed from fire scars; red outline indicates National Park Service-mapped fire perimeters. (c and d): Shaded polygons represent fire areas for 1822 and 1851, reconstructed from fire scars based on the same interpolation algorithm. Derived from Farris* et al. *(2010).*

derosa) or other pines, tend to facilitate fire spread. By contrast, in mesic high-elevation mixed-conifer (*Pinus*, *Pseudotsuga*, and *Abies* spp) and spruce-fir (*Picea* and *Abies* spp) forests, higher fuel moisture and denser surface fuel beds derived from short-needled species inhibit fire spread except under extreme weather conditions.

Spatial fire-scar networks reveal how historical fire regimes reflected the biophysical template across which they burned (Heyerdahl *et al.* 2001; Taylor and Skinner 2003; Heyerdahl *et al.* 2007; Sherriff and Veblen 2007). Studies in Grand Canyon National Park and the Arizona Sky Islands show that contrasting north and south aspects led to a mixture of fire frequencies and severities in close proximity (Fulé *et al.* 2003; Iniguez *et al.* 2008; Figure 2b). In Sequoia and Kings Canyon National Parks (Caprio 2004), fire frequency varied with aspect at lower, drier elevations, but not at higher elevations where temperatures are lower and fuel moisture content is higher, regardless of aspect.

Interactions of top-down and bottom-up controls

Fire-scar networks can identify interactions of top-down and bottom-up controls of fire regimes. Some studies examine the interplay of top-down and bottom-up controls by sampling a regional network of local grids. In eastern Oregon and Washington State, Heyerdahl *et al.* (2001) found that top-down and bottom-up controls interacted to regulate fire occurrence: a latitudinal climate gradient produced earlier and more frequent fires to the south, consistent with a warmer and drier climate there as compared with sites to the north. Fire frequency also varied with aspect – a bottom-up control – but only in watersheds with steep terrain and strong topographic barriers to fire spread.

In northern California, Taylor and Skinner (2003) identified persistent similarities in fire chronologies within landscape compartments (ie spatially coherent areas separated by features such as ridges, streams, and aspect changes; Figure 2b). These bottom-up controls served as filters to fire spread, rather than absolute barriers: during years of extreme drought, top-down controls created weather and fuel conditions that overrode bottom-up controls, allowing fires to cross barriers that impeded fire spread under more moderate conditions and spread among landscape compartments.

Recent studies of large landscapes where modern fires burn freely, as well as fire-history studies, reveal fire's self-limiting properties across scales (Scholl and Taylor 2010; Collins and Stephens 2008). Reconstructing fire perimeters from fire-scar networks in successive years has shown that each fire modifies the fuel environment for subsequent events, for a period of time that varies with productivity and changes in climate. These fuel mosaics influence the behavior of subsequent fires and provide a window into how fire and vegetation interacted before the fuel environment was modified by intensive management.

Applications to ecosystem management

Fire history has long guided ecosystem management in the American West. Weaver (1943) based his recommendations for prescribed burning at the Colville and White Mountain Apache reservations in Washington State and Arizona on insights gained from studies of fire scars. Subsequent reconstruction of fire regimes in southwestern forests confirmed the historical pattern of high-frequency, low-severity surface fires – a point of considerable contention in the early 20th century, when many land managers still considered fire to be an anomalous and unnatural process.

Spatial fire-scar networks provide managers and scientists with insights into how fire functions in ecosystems lacking the pervasive effects of fire suppression, livestock grazing, and logging that influence modern fires. For example, in Sequoia and Kings Canyon National Park, decades of fire-history research "provided a firm justification and basis for the development of the Parks' prescribed and natural fire management programs" (NPS 2010). This included studies of topographic and climatic controls of fire regimes, departures from historical fire intervals, and landscape patterns of fire severity derived from park-wide fire-scar networks (Caprio 2004).

Fire severity

A key concern in contemporary forest management is the severity and extent of fires. Managers can use fire history as a "best available science" standard to evaluate contemporary fires. Because fire scars form only under certain combinations of fire behavior and tree properties (Panel 1), spatial fire-scar networks can be used to bracket the historical range of variability in fire severity in some forest types. Recent landscape studies in ponderosa pine and Sierran dry mixed-conifer forests (Brown and Wu 2005; Brown *et al.* 2008; Scholl and Taylor 2010) have combined fire scars and tree demography to demonstrate differences in past fire regimes as compared with the extensive high-severity fires that currently burn these forests. Other studies, conducted at higher elevations or along elevation gradients, have found a continuum of fire severity, with frequent surface fires at low elevations and infrequent stand-replacing events in higher elevation forests (Sherriff and Veblen 2007; Margolis and Balmat 2009). The Sequoia and Kings Canyon National Parks Fire Management Plan (NPS 2010) used maps of historical fire regimes, based on fire-history research, to guide management treatments at sites across gradients of elevation and vegetation.

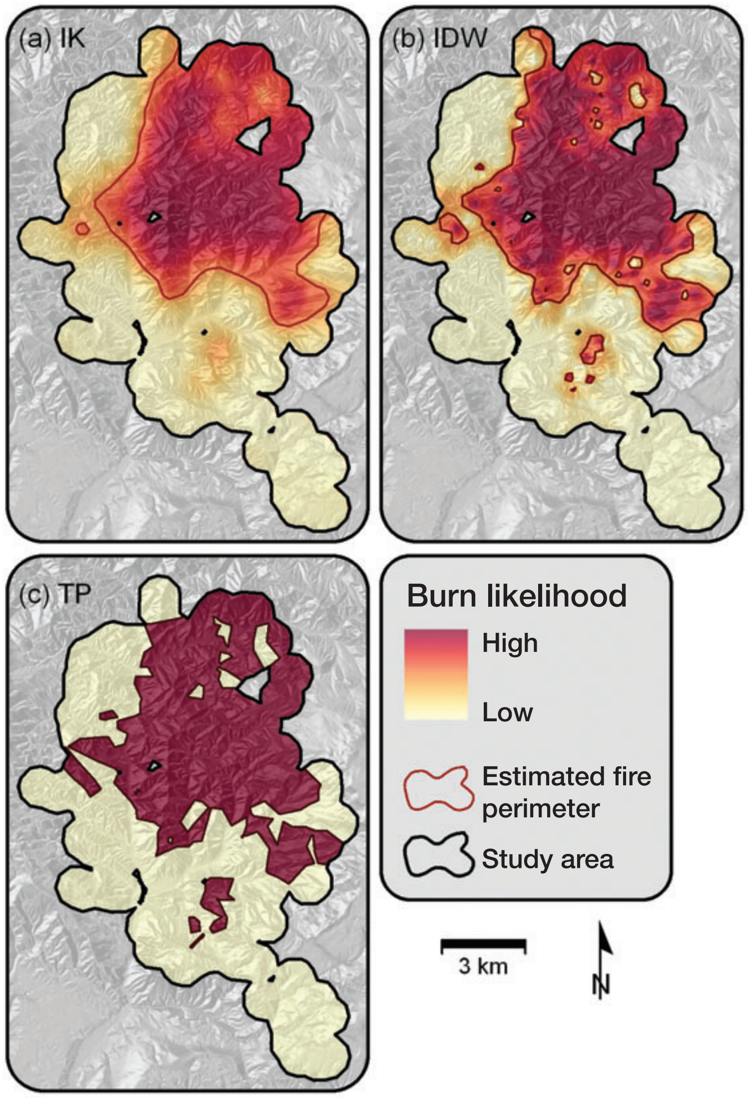

Figure 5. *Reconstructed burned likelihood for 1895 in the Swauk Creek watershed, eastern Washington State, through (a) indicator kriging (IK), (b) inverse distance weighting (IDW), and (c) Theissen polygons (TP). Red, orange, and yellow indicate higher likelihood that an area burned (Hessl* et al. *2007).*

Fire size

The spatial distribution of historical fires also provides a reference by which ecosystem managers can assess fire management in specific vegetation types. In Lassen Volcanic National Park in northern California, most large fires burned historically in the ponderosa-pine and mixed-conifer belts, but not in red-fir (*Abies magnifica*) forests at higher elevations, suggesting that fuel type and increasing moisture levels (snow line) along an elevation gradient limited the upslope spread of fire (Taylor 2000). Historical fires were, on average, 20 times the size of contemporary prescribed burns, indicating that the spatial scale of contemporary management burns did not fully represent the historical fire regime. This led to a shift by park managers toward larger burns and use of topographic features such as stream courses, ridge tops, and lava flows to create natural fire compartments (NPS 2005).

The role of climate

Despite more than a century of land-use change, the top-down climate drivers of historical fire documented in the fire-scar record still operate today (Morgan *et al.* 2008; Littell *et al.* 2009). Consequently, understanding how climate variability – such as periods of extended, multi-year drought – has controlled fire regimes in the past can inform scientists and managers about the drivers of modern fires. Spatial fire-scar networks also provide a long-term perspective for understanding the climatic conditions that lead to regional fire years – conditions that most climate projections indicate will become more common in the future.

Understanding the interactions of top-down and bottom-up controls allows fire-scar networks to complement other spatial arrays of biophysical data, leading to a broad range of ecological inferences across landscapes and regions. The fire-scar network can be coupled with tree-ring width, sediment charcoal, and other proxies to allow reconstruction of area burned and carbon dynamics over centennial to millennial time scales (Girardin 2007; Whitlock *et al*. 2010). The growth of spatial fire-scar networks around the world (Veblen *et al*. 2003; Yocom *et al*. 2010) promises to reveal new insights about fire as a keystone ecological process in the Earth system.

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■ References

Arno SF. 1976. The historical role of fire on the Bitterroot National Forest. Research Paper INT-187. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station.

Baker WL and Ehle D. 2001. Uncertainty in surface-fire history: the case of ponderosa pine forests in the western United States. *Can J Forest Res* **31**: 1205–26.

Bowman D, Balch JK, Artaxo P, *et al*. 2009. Fire in the Earth system. *Science* **324**: 481–84.

Brown PM, Kaye MW, Huckaby LS, and Baisan CH. 2001. Fire history along environmental gradients in the Sacramento Mountains, New Mexico: influences of local patterns and regional processes. *Ecoscience* **8**: 115–26.

Brown PM, Weink CL, and Symstad AJ. 2008. Fire and forest history at Mount Rushmore. *Ecol Appl* **18**: 1984–99.

Brown PM and Wu R. 2005. Climate and disturbance forcing of episodic tree recruitment in a southwestern ponderosa pine landscape. *Ecology* **86**: 3030–38.

Caprio AC. 2004. Temporal and Spatial Dynamics of Pre-Euroamerican Fire at a Watershed Scale, Sequoia and Kings Canyon National Parks. Proceedings of the Conference on Fire Management: Emerging Policies and New Paradigms. 16–19 Nov 1999, San Diego, CA. In: Sugihara NG, Morales ME, and Morales TJ (Eds). *Misc Pub No 2*, Association for Fire Ecology.

Clements FE. 1910. The life history of lodgepole burn forests. Bulletin 79. Washington, DC: USDA Forest Service.

Collins BM and Stephens SL. 2008. Fire scarring patterns in Sierra Nevada wilderness areas burned by multiple wildland fire use fires. *Fire Ecol* **3**: 53–67.

Dieterich JH and Swetnam TW. 1984. Dendrochronology of a fire-scarred ponderosa pine. *Forest Sci* **30**: 238–47.

Falk DA, Miller C, McKenzie D, and Black AE. 2007. Cross-scale analysis of fire regimes. *Ecosystems* **10**: 809–23.

Farris CA, Baisan CH, Falk DA, *et al*. 2010. Spatial and temporal corroboration of fire-scar based fire history reconstructions in a frequently burned ponderosa pine forest in southern Arizona. *Ecol Appl* **20**: 1598–1614.

Fulé PZ, Heinlein TA, Covington WW, and Moore MM. 2003. Assessing fire regimes on Grand Canyon landscapes with fire-scar and fire-record data. *Int J Wildland Fire* **12**: 129–45.

Gavin DG, Hallett DJ, Hu FS, *et al*. 2007. Forest fire and climate change in western North America: insights from sediment charcoal records. *Front Ecol Environ* **5**: 499–506.

Girardin MP. 2007. Interannual to decadal changes in area burned in Canada from 1781 to 1982 and the relationship to Northern Hemisphere land temperatures. *Global Ecol Biogeogr* **16**: 557–66.

Gutsell SL and Johnson EA. 1996. How fire scars are formed: coupling a disturbance process to its ecological effect. *Can J Forest Res* **26**: 166–74.

Heinselman ML. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. *Quaternary Res* **3**: 329–82.

Hessl A, Miller J, Kernan J, *et al*. 2007. Mapping paleo-fire boundaries from binary point data: comparing interpolation methods. *Prof Geogr* **59**: 87–104.

Heyerdahl EK, Brubaker LB, and Agee JK. 2001. Spatial controls of historical fire regimes: a multi-scale example from the Interior West, USA. *Ecology* **82**: 660–78.

Heyerdahl EK, Lertzman KP, and Karpuk S. 2007. Local-scale controls of a low-severity fire regime (1750–1950), southern British Columbia, Canada. *Ecoscience* **14**: 40–47.

Iniguez JM, Swetnam TW, and Yool SR. 2008. Topography affected landscape fire history patterns in southern Arizona, USA. *Forest Ecol Manag* **256**: 295–303.

Kellogg LB, McKenzie D, Peterson DL, and Hessl AE. 2008. Spatial models for inferring topographic controls on historical low-severity fire in the eastern Cascade Range of Washington, USA. *Landscape Ecol* **23**: 227–40.

Kilgore BM. 1973. The ecological role of fire in Sierran conifer forests: its application to national park management. *Quaternary Res* **3**: 496–513.

Kipfmueller KF and Kupfer JA. 2005. Complexity of successional pathways in subalpine forests of the Selway-Bitterroot Wilderness Area. *Ann Assoc Am Geogr* **95**: 495–510.

Kitzberger T, Brown PM, Heyerdahl EK, *et al*. 2007. Contingent Pacific–Atlantic Ocean influence on multi-century wildfire synchrony over western North America. *P Natl Acad Sci USA* **104**: 543–48.

Leopold A. 1924. Grass, brush, timber, and fire in Southern Arizona. *J Forest* **22**: 1–10.

Littell JS, McKenzie D, Peterson DL, and Westerling AL. 2009. Climate and wildfire area burned in western US ecoprovinces, 1916–2003. *Ecol Appl* **19**: 1003–21.

Margolis EQ and Balmat J. 2009. Fire history and fire–climate relationships along a fire regime gradient in the Santa Fe Municipal Watershed, NM, USA. *Forest Ecol Manag* **258**: 2416–30.

Marlon JR, Bartlein PJ, Carcaillet C, *et al*. 2008. Climate and human influences on global biomass burning over the past two millennia. *Nat Geosci* **1**: 697–702.

McKenzie D, Miller C, and Falk DA (Eds). 2011. The landscape ecology of fire. Dordrecht, The Netherlands: Springer.

Morgan P, Heyerdahl EK, and Gibson CE. 2008. Multi-season climate synchronized forest fires throughout the 20th century, northern Rockies, USA. *Ecology* **89**: 717–28.

NPS (National Park Service). 2005. Lassen Volcanic National Park, Wildland Fire Management Plan. Washington, DC: US Department of Interior. www.nps.gov/lavo/parkmgmt/index.htm. Viewed 19 Apr 2011.

NPS (National Park Service). 2010. Sequoia and Kings Canyon National Parks Fire and Fuels Management Plan. Washington,

DC: US Department of Interior. www.nps.gov/seki/nature science/fic_ffmp.htm. Viewed 19 Apr 2011.
Parisien M-A and Moritz MA. 2009. Environmental controls on the distribution of wildfire at multiple spatial scales. *Ecol Monogr* **79**: 127–54.
Ricklefs RE. 1987. Community diversity: relative roles of local and regional processes. *Science* **235**: 167–71.
Scholl AE and Taylor AH. 2010. Fire regimes, forest change, and self-organization in an old-growth mixed-conifer forest. Yosemite National Park, USA. *Ecol Appl* **20**: 362–80.
Sherriff RL and Veblen TT. 2007. A spatially-explicit reconstruction of historical fire occurrence in the ponderosa pine zone of the Colorado Front Range. *Ecosystems* **10**: 311–23.
Stephens SL, Fry DL, Collins BM, *et al.* 2010. Fire-scar formation in Jeffrey pine–mixed conifer forests in the Sierra San Pedro Mártir, Mexico. *Can J Forest Res* **40**: 1497–505.
Swetnam TL, Falk DA, Hessl A, and Farris C. 2011. Reconstructing landscape pattern of historic fires and fire regimes. In: McKenzie D, Miller C, and Falk DA (Eds). Landscape ecology of fire. Dordrecht, The Netherlands: Springer.
Swetnam TW and Anderson RS. 2008. Fire climatology in the western United States: introduction to special issue. *Int J Wildland Fire* **17**: 1–7.
Swetnam TW and Betancourt JL. 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *J Climate* **11**: 3128–47.
Taylor AH. 2000. Fire regimes and forest changes in mid and upper montane forests of the southern Cascades, Lassen Volcanic National Park, California, USA. *J Biogeogr* **27**: 87–104.
Taylor AH and Skinner CN. 2003. Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. *Ecol Appl* **13**: 704–19.
Trouet V and Taylor AH. 2010. Multicentury variability in the Pacific North American circulation pattern reconstructed from tree rings. *Clim Dynam* **35**: 953–63.
Turner MG. 2010. Disturbance and landscape dynamics in a changing world. *Ecology* **91**: 2833–49.
Van Horne ML and Fulé PZ. 2006. Comparing methods of reconstructing fire history using fire scars in a southwestern United States ponderosa pine forest. *Can J Forest Res* **36**: 855–67.
Veblen TT, Kitzberger T, Raffaele E, and Lorenz DC. 2003. Fire history and vegetation changes in northern Patagonia, Argentina. In: Veblen TT, Baker WL, Montenegro G, and Swetnam TW (Eds). 2003. Fire and climatic change in temperate ecosystems of the western Americas. New York, NY: Springer-Verlag.
Weaver H. 1943. Fire as an ecological and silvicultural factor in the ponderosa pine region of the Pacific Slope. *J Forest* **41**: 7–15.
Westerling AL, Hidalgo HG, Cayan DR, and Swetnam TW. 2006. Warming and earlier spring increase western US forest wildfire activity. *Science* **313**: 940–43.
Whitlock C, Higuera PE, McWethy DB, and Briles CE. 2010. Paleoecological perspectives on fire ecology: revisiting the fire-regime concept. *The Open Ecology Journal* **3**: 6–23.
Yocom L, Fulé PZ, Brown PM, *et al.* 2010. El Niño-Southern Oscillation effect on a fire regime in northeastern Mexico has shifted over time. *Ecology* **91**: 1660–71.

WebPanel 1. The International Multiproxy Paleofire Database (IMPD)

The IMPD, established in 2003, is a free public online database of fire-history chronologies, based on tree-ring and charcoal proxies and their associated metadata (www.ncdc.noaa.gov/paleo/impd/paleofire.html). The IMPD is managed by the National Oceanic and Atmospheric Administration (NOAA) Paleoclimatology Program and hosted by the NOAA World Data Center for Paleoclimatology, and represents the collective efforts of the international research community. IMPD archives both tree-ring (fire scars and the establishment dates of post-fire cohorts of trees) and charcoal proxy records of fire from around the world, although the collection is currently dominated by data from North America. All data are contributed in standard formats. Associated metadata are also available, and user-friendly tools for accessing the data are being developed. There are currently 415 fire-scar chronologies archived with the IMPD, along with 51 studies based on charcoal.

WebPanel 2. Additional considerations in inference from the tree-ring record

All paleoecological evidence requires careful interpretation, and fire scars are no exception (Johnson and Gutsell 1994). For instance, in addition to variation in landscape burn patterns, variation among tree species introduces other variables that can influence the formation of fire scars. Life-history strategies and architecture of trees (eg high crowns and thick bark versus low crowns and thin bark) interact with fire behavior to affect survivorship and scarring rates (Fall and Lertzman 1999). Mature individuals of thick-barked species (eg *Pinus ponderosa, Pseudotsuga menziesii, Sequoiadendron giganteum*) may sustain little or no cambial damage in a very low-intensity fire, whereas trees that are younger or belong to thinner-barked species (eg *Pinus contorta*) may be killed outright. Some thick-barked species may contain scars that are not visible as an exterior wound (Van Horne and Fulé 2006; Lombardo *et al*. 2009). Surviving a fire is a species- and size-dependent process: small trees are more likely to be killed outright than to survive with scars if the canopy base height is lower than flame or scorch height (Gutsell and Johnson 1996). These considerations influence the interpretation of fire severity and landscape patterns of fire occurrence.

Fire can link landscapes across vegetation and fire-regime types. Studies in Colorado and New Mexico have combined fire-scar data with stand origin dates to reconstruct fire history along elevation gradients from pine- and mixed-conifer stands to subalpine forests (Sherriff and Veblen 2006; Sibold and Veblen 2006; Margolis and Balmat 2009). These studies document trends of increasing fire severity with elevation. Interestingly, years in which more severe fires occurred are commonly also reflected in the fire-scar record of surface and mixed-severity fire regimes at lower elevations (Margolis *et al.* 2007). These results suggest the expression of interacting, bottom-up controls across landscape gradients within a context of top-down climatic regulation.

Gradient studies require careful interpretation if recording species are not equally distributed over the gradient. For example, if scarred trees are found only in a certain elevation range in a study area, or only on some aspects, then estimates of fire interval and frequency could be influenced by these landscape differences in species distributions. Most fire-history studies are designed to take this into account by limiting the scale of inference. Studies that combine fire scars with other lines of evidence, such as tree death and post-fire recruitment dates, are especially valuable for providing convergent estimates of fire years and extent (Margolis *et al*. 2007; Brown *et al*. 2008; Margolis and Balmat 2009).

WebPanel 3. Detailed sources for Figure 2

(a) Data from fire-scar networks can be combined at regional to subcontinental scales for comparison with broad-scale patterns of climate variation and land use. Map of western North America showing iso-correlation lines of site-level fire occurrence (first component of a rotated principal components analysis of annual percentage of trees scarred in 238 fire-history sites) with independent tree-ring width reconstructions of Palmer Drought Severity Index, for the period 1550–1924 AD (Kitzberger *et al.* 2007). Middle: time series of NINO-3, an index of the El Niño–Southern Oscillation reconstructed from tree-ring width, with the largest (red circles) and smallest (green squares) late 19th-century fire years in the southwestern US superimposed (Swetnam and Brown 2010). Right: time series of the total number of sites recording fire (out of 120) in the southwestern US, with widespread fire years and the period of extensive grazing indicated (Swetnam and Brown 2011).

(b) At watershed and landscape scales, fire-scar records may be obtained from spatially distributed plots or stands representing different aspects, slopes, elevations, overstory composition, or other physical or ecological variables. Left: map of Hayfork Watershed, Klamath Mountains, CA, showing spatially coherent fire-date patterns within a network of sites partitioned by multivariate analysis (Taylor and Skinner 2003). Middle: the distribution of mean fire intervals from plot composites located systematically on northerly versus southerly aspects at similar elevations in the Santa Catalina Mountains, AZ (Iniquez *et al.* 2008). Right: number of fire years (1700–1900 AD) within plots on south-facing slopes along an elevational gradient in Sequoia and Kings Canyon National Park, CA (Caprio 2004).

(c) Fire-scarred trees and tree ages can be sampled systematically or randomly within stands, and at this scale, patterns of synchrony may be used to infer patterns of fire spread. Combined analyses of tree recruitment and mortality, along with fire-scar spatiotemporal patterns, can be used to assess fire–forest demography relations. Left: a portion of the Giant Forest (CA) stem map of giant sequoia trees (small green and brown dots), with fire-scarred tree sample locations indicated by large blue and brown symbols and three-letter codes (Swetnam *et al*. 2009). Middle: simultaneous analyses of fire-scar-based fire history and tree demography from the San Juan Mountains, CO. Horizontal black lines are individual fire-scarred trees, arrowheads are fire dates; the number of ponderosa-pine trees recruiting into the stand (black bars) indicates that recruitment episodes occurred during periods of lower fire frequency, including the post-1900 period of fire exclusion (Brown and Wu 2005). Right: stem map of 1246 fire-scarred trees in a complete census of 1km^2 in Centennial Forest, near Flagstaff, AZ (Van Horne and Fulé 2006). OS indicates trees that were alive but not previously scarred in 1737.

(d) Studies of individual trees based on detailed microscopic analyses of fire scars and other injuries can identify the seasonality of historical low-severity fires, tree growth responses (abrupt increases or decreases in tree-ring width), and dates of tree recruitment or death. Left: a giant sequoia cross section located in Giant Forest, CA. This tree has an inner ring date of 259 BCE and a cutting date of 1950 CE, and contains 84 fire scars and an additional 41 fire event indicators, such as post-fire growth changes (Swetnam *et al*. 2009). Middle: seasonal position of fire scars within annual rings from 3308 fire scars in three groves of giant sequoia (Swetnam *et al.* unpublished). Right: a combined record of aspen and conifer tree recruitment dates, tree-ring growth changes, and fire-scar dates used to reconstruct fire history in a high-elevation stand-replacing fire regime, Sangre de Cristo Mountains, NM (Margolis *et al*. 2007).

WebReferences

Brown PM, Heyerdahl EK, Kitchen SG, and Weber MH. 2008. Climate effects on historical fires (1630–1900) in Utah. *Int J Wildland Fire* **17**: 28–39.

Brown PM and Wu R. 2005. Climate and disturbance forcing of episodic tree recruitment in a southwestern ponderosa pine landscape. *Ecology* **86**: 3030–38.

Caprio AC. 2004. Temporal and spatial dynamics of pre-Euroamerican fire at a watershed scale, Sequoia and Kings Canyon National Parks. Proceedings of the Conference on Fire Management: Emerging Policies and New Paradigms. 16–19 Nov 1999, San Diego, CA. Sugihara NG, Morales ME, and Morales TJ (Eds). *Misc Pub No 2*, Association for Fire Ecology.

Fall GJ and Lertzman KP. 1999. An interactive tutorial on fire frequency analysis (Version 3.0). *Bull Ecol Soc Am* **80**: 174–78.

Gutsell SL and Johnson EA. 1996. How fire scars are formed: coupling a disturbance process to its ecological effect. *Can J Forest Res* **26**: 166–74.

Iniguez JM, Swetnam TW, and Yool SR. 2008. Topography affected landscape fire history patterns in southern Arizona, USA. *Forest Ecol Manag* **256**: 295–303.

Johnson EA and Gutsell SL. 1994. Fire frequency, models, and interpretations. *Adv Ecol Res* **25**: 239–87.

Kitzberger T, Brown PM, Heyerdahl EK, *et al.* 2007. Contingent Pacific–Atlantic Ocean influence on multi-century wildfire synchrony over western North America. *P Natl Acad Sci USA* **104**: 543–48.

Lombardo KJ, Swetnam TW, Baisan CB, and Borchert MI. 2009. Using bigcone Douglas-fir fire scars and tree rings to reconstruct interior chaparral fire history. *Fire Ecol* **5**; doi:10.4996/fireecology.0503035.

Margolis EQ and Balmat J. 2009. Fire history and fire–climate relationships along a fire regime gradient in the Santa Fe Municipal Watershed, NM, USA. *Forest Ecol Manag* **258**: 2416–30.

Margolis EQ, Swetnam TW, and Allen CD. 2007. A stand-replacing fire history in upper montane forests of the southern Rocky Mountains. *Can J Forest Res* **37**: 2227–41.

Sherriff RL and Veblen TT. 2006. Ecological effects of changes in fire regimes in *Pinus ponderosa* ecosystems in the Colorado Front Range. *J Veg Sci* **17**: 705–18.

Sibold J and Veblen TT. 2006. Relationships of subalpine forest fires in the Colorado Front Range with interannual and multidecadal-scale climatic variation. *J Biogeogr* **33**: 833–42.

Swetnam TW, Baisan CH, Caprio AC, *et al.* 2009. Multi-millennia fire history of the Giant Forest, Sequoia National Park, USA. *Fire Ecol* **5**: 117–47.

Swetnam TW and Brown PM. 2011. Climatic inferences from dendroecological reconstructions. In: Hughes MK, Swetnam TW, and Diaz HF (Eds). Dendroclimatology: progress and prospects. New York, NY: Springer Verlag.

Taylor AH and Skinner CN. 2003. Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. *Ecol Appl* **13**: 704–19.

Van Horne ML and Fulé PZ. 2006. Comparing methods of reconstructing fire history using fire scars in a southwestern United States ponderosa pine forest. *Can J Forest Res* **36**: 855–67.

