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Research article

Using neutral models to identify constraints on low-severity fire regimes*

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Abstract

Climate, topography, fuel loadings, and human activities all affect spatial and temporal patterns of fire occurrence. Because fire is modeled as a stochastic process, for which each fire history is only one realization, a simulation approach is necessary to understand baseline variability, thereby identifying constraints, or forcing functions, that affect fire regimes. With a suitable neutral model, characteristics of natural fire regimes estimated from fire history data can be compared to a "null hypothesis". We generated random landscapes of fire-scarred trees via a point process with sequential spatial inhibition. Random ignition points, fire sizes, and fire years were drawn from uniform and exponential family probability distributions. We compared two characteristics of neutral fire regimes to those from five watersheds in eastern Washington that have experienced low-severity fire. Composite fire intervals (CFIs) at multiple spatial scales displayed similar monotonic decreases with increasing sample area in neutral vs. real landscapes, although patterns of residuals from statistical models differed. In contrast, parameters of the Weibull distribution associated with temporal trends in fire hazard exhibited different forms of scale dependence in real vs. simulated data. Clear patterns in neutral landscapes suggest that deviations from them in empirical data represent real constraints on fire regimes (e.g., topography, fuels). As with any null model, however, neutral fire-regime models need to be carefully tuned to avoid confounding these constraints with artifacts of modeling. Neutral models show promise for investigating low-severity fire regimes to separate intrinsic properties of stochastic processes from the effects of climate, fuel loadings, topography, and management.

Introduction

Fire-history reconstructions provide the empirical basis for fine- and coarse-scale modeling of fire regimes and for informed management and restoration of ecosystems (Landres et al. 1999; Schmoldt et al. 1999; Swetnam et al. 1999; McKenzie et al. 2004). Reconstructions use different methods, depending on objectives, the nature of the fire regimes being studied, and the spatial and temporal scales of analysis (Clark 1990; Agee 1993; Heyerdahl et al. 1995; Lynch et al. 2003; Prichard 2003). Estimates of fire frequency from different methods are often combined for modeling and management (Agee 1993; Heyerdahl et al. 1995; McKenzie et at. 2000). For example, two metrics often associated with high-severity or stand-replacing fire-the "fire cycle" and "natural fire rotation" - explicitly measure area burned over time as a proportion of the total study area, but only record a subset of fire-free intervals experienced on the landscape, because stand-replacing fires destroy evidence of previous events. In contrast, fire-scarred trees contain a record of multiple fire events and the associated fire-free intervals in low severity fire regimes, but estimates of area burned at a point in time must be indirect and estimates of fire interval may be scale dependent (McKenzie et al. 2000; Falk and Swetnam 2003). Although the statistical properties of the different methods can be compared, estimates of "fire frequency" are not always equivalent (Li 2002).

Dry low-elevation forest ecosystems of the western United States allow methods of the second type, for which living trees provide a long-term record of low-severity fire from fire scars (Everett et al. 2000; Grissino-Mayer and Swetnam 2000; Veblen et al. 2000; Heyerdahl et al. 2001). Fire-history reconstructions are sensitive to the area sampled, because too small an area may miss fires entirely, whereas too large an area may record separate fire events as one (Agee 1993; Heyerdahl et al. 1995; Baker and Ehle 2001). Research is needed to quantify how fire regime statistics change across spatial scales and how these changes may differ in different ecosystems. These statistics, particularly fire return interval, or fire frequency, are widely used in management but estimates of both means and variances are sensitive to the area over which they are sampled (McKenzie et al. 2000, Falk and Swetnam 2003).

Understanding the spatial scales over which controls on fire regimes operate is essential both for effective ecosystem management and for anticipating how fire might respond to climatic change or land use. Climatic controls are most evident at regional scales, at which synchronous fire events are associated with drought or quasi-periodic patterns such as ENSO or PDO (Swetnam and Betancourt 1990; Grissino-Mayer et al. 2004; Hessl et al. 2004). Topography controls fire spread and therefore the synchrony of fire events at watershed scales or smaller, depending on the steepness and complexity of terrain (Taylor and Skinner 2003; Kellogg 2004). Patterns of fuel accumulation associated with time-since-fire, particularly in the era of active fire suppression, are linked with typical fire sizes, i.e. landscape patches of discrete fuel ages should be of the same size as past fires. Given that the scales at which these controls operate are different, and that each one varies with ecosystem type and fire regime, analyses would ideally be conducted at multiple scales to the extent that quality and spatial extent of data permit it. The neutral modeling approach we adopt here is motivated by the need to distinguish a signal (from such a control) from background variability at multiple scales.

Neutral models

In formal experiments, in which a null hypothesis is tested against an alternative, `controls' and `treatments' are ideally identical except for the treatment effect. If this effect is statistically significant, the null hypothesis is rejected. "Neutral models" in community and landscape ecology generalize the concept of a null hypothesis to an array of patterns and processes that capture relevant details of a system but eliminate the constraints or mechanisms of interest (Caswell 1976; Kimura 1983; Gardner and O'Neill 1991; Gotelli and Graves 1996; Hubble 2001). When a complex process (e.g., landscape disturbance or community assembly) is being studied, the identification of the appropriate neutral model is difficult, and much controversy exists in the literature (e.g., Weiher and Keddy 1999).

Neutral models have been used in landscape ecology to study species co-occurrence (Milne 1992; Palmer 1992), formation of ecotones Milne et al. 1996), metapopulation models and conservation (With 1997), and connectivity and disturbance spread (Green 1994; Keitt et al. 1997). In this paper, we present a neutral model of low-severity fire regimes-those for which the fire history is preserved via fire scars on living trees. The model was designed to capture the stochastic properties of fire regimes; fire sizes, fire-free intervals, and fire locations are considered to be random variables. We examine two statistical properties of the neutral model: how estimates of fire frequency change with changing sample areas, and how temporal trends in the hazard of burning change with area and number of trees sampled. To estimate the hazard of burning, we borrow from survival analysis (Hosmer and Lemeshow 1999), wherein the probability distributions in the exponential family are linked to a "hazard function" that quantifies the instantaneous probability of an event - a death, or in our case a fire - given survival to that point (Grissino-Mayer 1999). Better understanding of the first property, as a global or local scaling law, could lead to more robust comparisons of fire frequency among ecosystems, and understanding the second will permit more robust identification of key constraints on fire at specific spatial scales. We compare the null properties to the same statistical properties on real landscapes, using five watersheds in eastern Washington, USA, that have experienced low-severity fires. We make qualitative inferences about the usefulness of pursuing this method for identifying constraints on fire regimes.

Methods

Fire history data

The fire-history data are from montane forest ecosystems in eastern Washington, USA. Everett et al. (2000) produced a detailed, spatially explicit dataset of fire history data from 1701 fire-scarred trees, collected in five study sites (3116-12747 ha) extending from the Okanogan Wenatchee National Forest in central Washington to the Colville National Forest in northeastern Washington (Figure I). These study sites extend along a 300-km northeast to southwest transect across the Okanogan Highlands and down the east side of the Cascade Range. The fire-history sites are

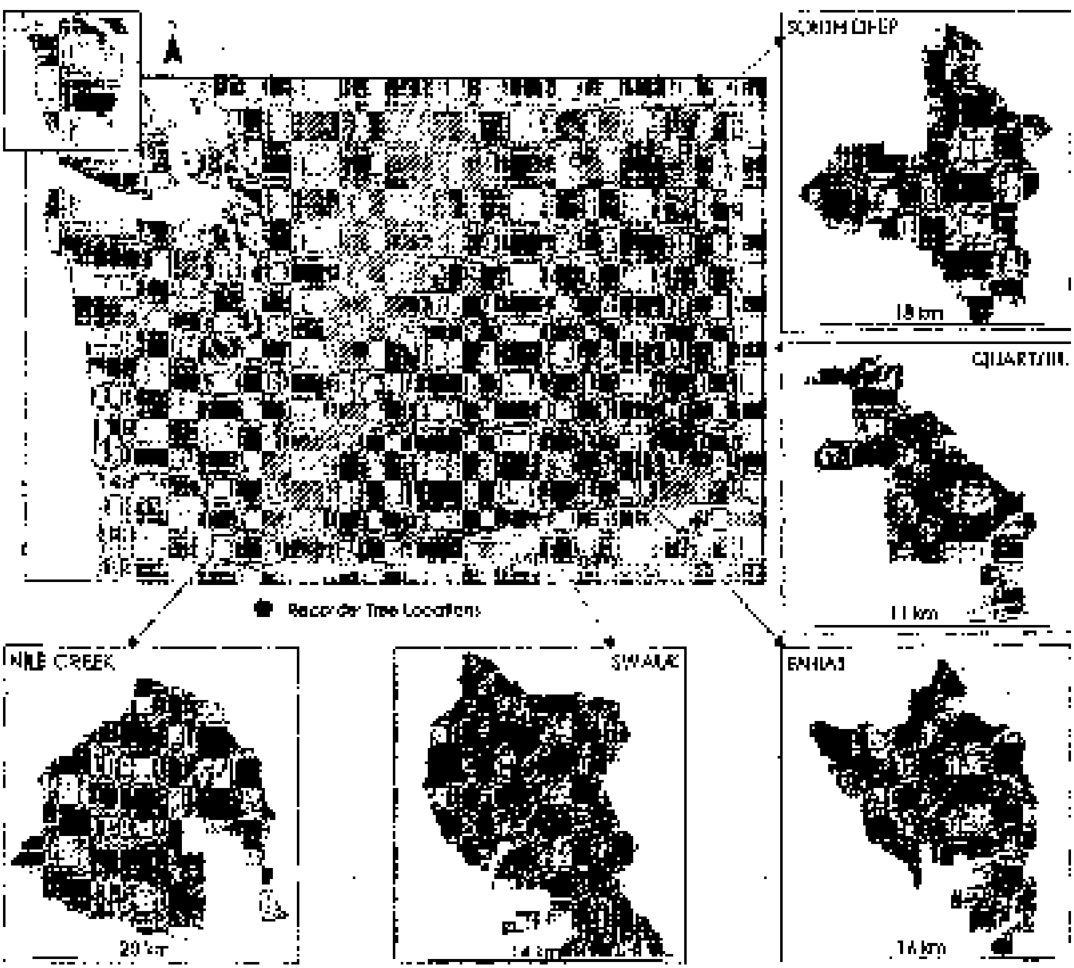

Figure I. Study sites in eastern Washington, USA - the five real watersheds used to compare to the neutral model.

Table I. Location, area, sample sizes and analysis time frame of fire scarred trees at each of the five sites.

Site	Location		Fire scars				
	Lat. (N)	Lon. (W)	Sampled area (ha)	Trees	No. fire scars	First scar	Last scar
Entiat River	47°48'	120'20'	12747	490	3904	1530	1988
Nile Creek	46°52'	121°05'	3237	234	2314	1367	1970
Swauk Creek	47°15'	120°38'	11088	667	7048	1257	1942
South Deep	48°45'	117°40'	12019	168	680	1399	1986
Quartzite	48°17'	117°37'	3116	142	1300	1384	1989
Total			42207	1701	15246		

located within forests dominated by ponderosa pine *(Pinus ponderosa* Douglas ex C. Lawson). Ponderosa pine forests in Washington typically occur between 600-1200 m elevation, with Douglas-fir *(Pseudotsuga menziesii* [Mirb.] Franco), grand fir *(Abies grandis* [Douglas ex D. Don] Lindl.), western larch *(Larix occidentalis Nutt.)* and lodgepole pine *(Pinus contorta* Douglas ex Loudon) at higher elevations and grassland or sagebrush *(Artemisia tridentata Nun.)* at lower elevations.

Lightning is the primary ignition source in the Northwest, though not so common as in other parts of the western United States (Rorig and Ferguson 1999). The eastern portion of the study area receives more cloud-to-ground lightning than the western portion, but these strikes are more likely to be associated with precipitation than those occurring in the western part, and consequently produce fewer ignitions (Rorig and Ferguson 1999). Native Americans_ first settled the inland Pacific Northwest approximately 13,000 years ago (Robbins 1999), and may have also been an ignition source, burning low elevation ponderosa pine forest and grasslands, prior to the major population and cultural changes of the early 1900s (Robbins and Wolf 1994; Boyd 1999; Robbins 1999; Ross 1999).

In 1878, the Northern Pacific Railroad forbade native burning (Ross 1999), and in 1908 the US Forest Service began a program of fire suppression (Pyne 2001), which probably became fully effective around the mid-20th century. Other disturbances - cattle and sheep grazing and selective logging of ponderosa pine forests - increased after the 1880s (Galbraith and Anderson 1991, Robbins and Wolf 1994). Approximately 50% of the fire scar samples in this study were collected from stumps remaining following logging (Hessl et al. 2004).

This dataset, a spatially distributed network of geo-referenced, crossdated fire scar chronologies, is ideal for spatial and temporal analysis of regional surface-fire history. **In** particular, its spatial structure allows for analysis at multiple spatial scales (Hessl et al. 2004; Kellogg 2004). To date, chronologies have been developed for five study sites (Figure 1). Within each site, all fire-scarred trees were mapped, and a spatially stratified random sample of high-quality trees (with a large number of scars) was collected (Table 1)-Hessl et al. (2004) provide a detailed description of sampling methods.

Composite fire intervals for the watersheds (counting only fires that scarred > 10% of the trees) range from 5-10 year, and the Weibull median probability interval (WMPI) for these same fires ranges from 4 to 7 year (Table 2, Hessl et al. 2004). The frequency of occurrence of a fire somewhere in the watershed (possibly fewer than 10% of trees scarred), however, ranges from just under 2-5 year.

Simulation model

The `neutral' landscape consisted of a square grid with unitless *X* and *Y* coordinates (range 0-1), in emulation of a watershed. We located 200 points randomly to represent trees that could record fires. Sequential spatial inhibition (Ripley 1987) was used to ensure that no two trees overlapped. A 200-year fire history was simulated for two watershed-scale mean fire-return intervals (MFRIs), 2 and 5 year. These numbers represent the average interval between the occurrence of fire somewhere in the watershed, and correspond roughly to the range of the equivalent statistic for the five real watersheds (1.4-5.0 year). Time steps (years until

Table 2. Composite fire interval statistics (in years) for the period 1701-1900 defined as years in which ?10% of trees recorded scars (minimum of 2 trees).

Watershed	No. fire intervals	WMPI	Mean interval	SD	Min interval	Max interval
Entiat River	32	5	6	4	1	16
Nile Creek	30	6	6	4	1	18
Swauk Creek	25	7	8	7	1	33
South Deep	20	7	10	9	1	31
Quartzite	41	4	5	4	1	17

the next fire) were drawn from an exponential distribution with mean = MFRI, and rounded to the nearest integer, until their sum was > 200. The exponential distribution was used because it is `memory free' (Ross 1988; Johnson and Gutsell 1994), thereby representing a neutral landscape with no time dependence of fire probabilities. At each time step, a fire was simulated as a circle with its center located randomly in the central 90% of the watershed. Mean fire sizes were defined within a range of proportions of the total area of the watershed, between 0.1 and 0.4, with steps of 0.05. For each round of simulations, the size of each fire was drawn from a gamma distribution, with shape parameter = 2 (a right-skewed distribution) and mean equal to the mean fire size. Use of the gamma distribution instead of, for example, the negative exponential or one generated by a power-law (Malamud et al. 1998), reduced the number of very small fires, particularly those scarring only one `tree' whose counterparts on real landscapes might easily be missed. Simulations were conducted in Splus 6 for Windows (Insightful 2002).

Composite fire records

The coordinates of each recorder tree were noted, and a data matrix created (200 rows = years, 200 columns = trees) to hold the "fire history" of the simulated watershed. We then simulated fire-history reconstructions within the watershed, using a `neutral' method whereby for each iteration, one tree from the interior of the watershed (defined as >.0.1 units from the edge) was randomly selected as a starting location. We made this partial correction for edge effects here and an analogous one in the analysis of the real watersheds (see below), to approximate artifacts of limited sampling areas in the collection of fire-history data, e.g., restrictions' on plot sizes in sample design mean that only a proportion of the scars from some fires will be identified. Using this `tree' as a center, we computed composite fire intervals (CFIs) for circular areas composing proportions of the watershed from 0.15 to 0.45 (at intervals of 0.01), by identifying all tree locations within the search radius associated with these proportions. We refer to the search radius as a proxy for sample area because an analogous method was used in analyzing the real watersheds (below). *The event-area relationship,* a well known example of which is the species-area curve (Rosenzweig 1995; Falk 2004), is a model, often parametric, of how a quantity changes with the area over which it is sampled. We fit each time series of fire-free intervals to the two-parameter Weibull distribution (Evans et al. 1993; Grissino-Mayer 1995), using numerical maximum likelihood. For each search radius, 20 replicate CFIs, corresponding to different starting locations, were computed.

Two features of the Weibull distribution make it well suited to modeling both high-severity (Clark 1989; Johnson and Gutsell 1994) and low-severity (Grissino-Mayer 1999) fire regimes. The Weibull median probability interval (WMPI-Grissino-Mayer 1995) is a robust measure of central tendency, and the shape parameter and its associated hazard function allow changes in the hazard of burning over time to be estimated. For each of the composite fire records (20 replicates x 50 search radii), we computed the WMPI and the Weibull shape parameter, the latter as a surrogate for the slope of the hazard function (Clark 1989, Johnson and Gutsell 1994). For each search radius, the mean of 20 replicates was stored.

We applied the same iterative process to the fire history record for the five watersheds, but restricted sample years to the period 1701-1900. By 1700 most sampled trees had already recorded one fire, and before 1900 fire exclusion had not drastically changed fire frequency (Hessl et at. 2004).

We created a set of composite fire records (100 replicates x 30 search radii) similar to that for the simulated watershed, wherein any fire-scarred tree defined a time series of fire years, using this 200-year fire record.

Each fire record was weighted to reduce the bias expected by edge effects (due to search radii extending outside the often irregular watershed boundaries), by downweighting observations near the edge of the sample area in the following way. A convex hull (Barnett 1976) was generated around the outside of each watershed, and a buffer was created around the hull, equal in width to the mean nearest-neighbor distance between fire-scarred trees. Thus, buffer widths were different for each watershed. The weight assigned to each fire record was (Edge.dist/Search.radius)^{hi2}, where Edge.dist is the distance from the starting location to the outside of the buffer, and Search.radius is the search radius for that record (as in the neutral model simulations). All replicates in the resampling whose search areas were completely inside the buffer were thus given a weight of 1. These weights were used to compute weighted means of WMPI and Weibull shape parameters at each search radius in each watershed.

The slope of the hazard function, defined by the Weibull shape parameter, is theoretically zero if the hazard of burning is constant over time and the shape parameter = 1. A simple bootstrap procedure (Efron and Tibshirani 1993) was employed to determine whether the 95% lower confidence bound of estimates of the shape parameter was below 1.0, thereby indicating that the slope of the hazard function was not significantly different from zero. Computational resources limited us to 100 resamples, however, whereas 1000 would have been minimum and 10000 preferable (Efron and Tibshirani 1993; Davison and Hinckley 1997), so we do not report p-values here.

After examining scatterplots and various nonlinear models, we fit simple log-linear regressions to quantify the relationship between search radius and WMPI for the neutral model and for each of the five watersheds. For the five watersheds we used weighted means of WMPI (see above), and examined models for goodness-of-fit and patterns in the residuals. We compared these empirical estimates of WMPI and shape parameters, and how they changed with changing spatial scale, to simulated estimates. The exploratory analysis presented here was designed to provide insight as to whether the neutral model is a useful concept that can be applied to inferences about constraints (for example, fuels, topography, climate, or land use) on low-severity fire regimes. Formal statistical tests and extrapolation to other geographic areas will be the subject of future research.

Results

Scaling relationships for the estimated fire-free intervals (WMPI) between simulated (neutral) and real watersheds are clearly similar in shape, although the slope terms decrease as mean fire size increases (Figures 2, 3, and 4). In all cases a log-linear model best predicted the relationship between the search radius, (proportional to the square root of sample area in a firehistory study), and WMPI, with R^2 between 0.923 and 0.969 for simulated data (Figures 2 and 3) and between 0.882 and 0.985 for real data (Figure 4). When the watershed-scale MFRI is 2 year in simulated data, mean WMPI at the smallest search radius (representing approximately 10% of the watershed) ranges from 9 year for simulated mean fire sizes of 0.15 of the watershed area, to 5 year for a simulated size of 0.35. For watershed-scale means of 5 year, mean WMPI at the smallest search radius ranged between 23 year (fire size = 0.15 of watershed) down to 12 year (fire size = 0.35 of watershed). As search radii increased mean WMPI decreased, as expected, toward the `watershed' MFRI (2-5 year).

On four watersheds (Nile Creek, Swauk Creek, Entiat River, Quartzite), the smallest search radius at which parameters could be estimated for the Weibull distribution was 40 m, due to limits in the maximum likelihood algorithm. At this search radius, estimated WMPI at the smallest search radius ranges from 7 year on Entiat River to nearly 14 year on Swauk Creek (Figure 4). At search radii >_800 m, estimated WMPIs are essentially the same as the whole-watershed statistics (all fires). Because of the paucity of fires at South Deep and associated small sample size, Weibull parameters could not be estimated at search radii smaller than 400 m, at which mean WMPI is 12.5.

Patterns in residuals are similar between the neutral model and the two watersheds with the highest R^2, Quartzite and South Deep (Figure 4).

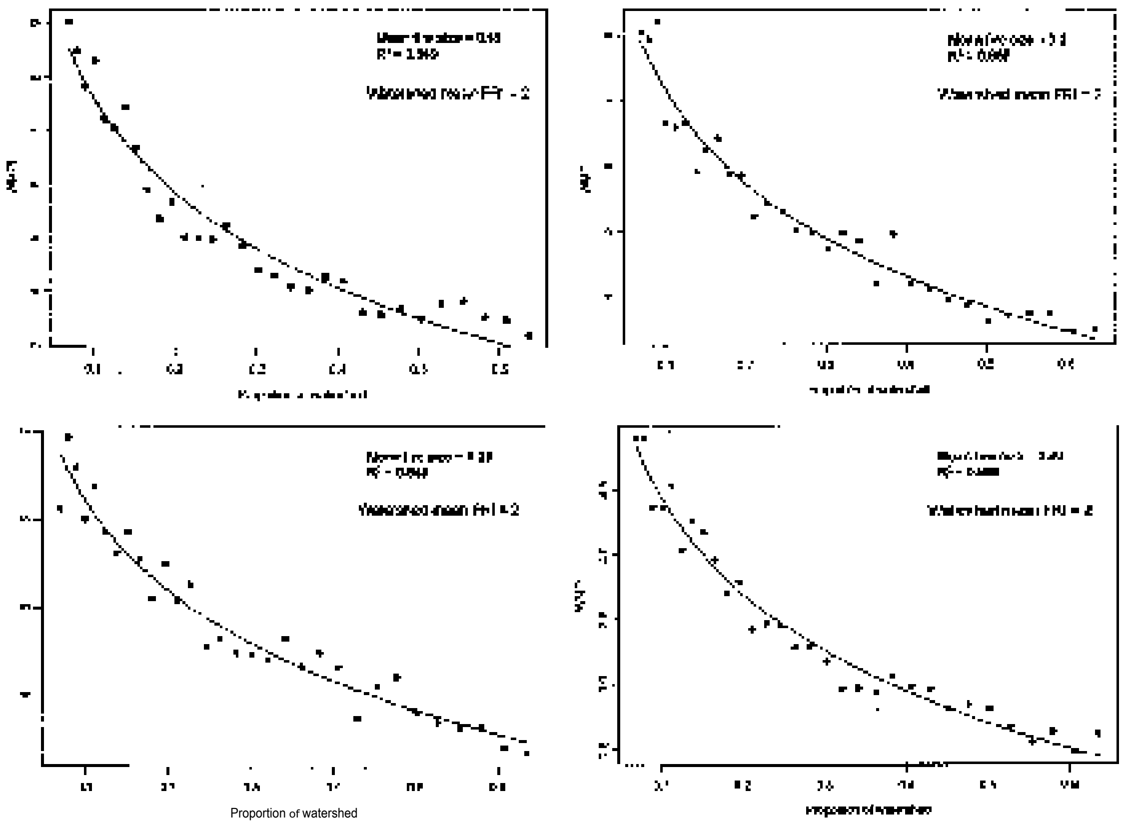

Figure 2. Scaling relations for WMPI, as functions of search radius and log-linear regressions from the neutral model WMPI, associated with different simulated fire sizes and watershed-scale mean fire-return interval = 2 year. Each data point represents the mean of 20 replicates.

In contrast, residuals for Nile Creek, Swauk Creek, and Entiat River are strongly patterned, with those in the middle range of the predictor variable (search radius) consistently falling below the regression line, suggesting the need for a more complex model than the simple log-linear relationship used here.

Estimates of the Weibull shape parameter differ substantially between simulated and real watersheds, both in mean value and trends over increasing search radii. For simulated watersheds, mean estimates are between 1.10 and 1.45 for a variety of mean fire sizes (0.1 to 0.4 of watershed) and search radii (0.15 to 0.45) (Figure 5). Search radii associated with less than 0.15 of watershed area contained too few fires to fit the Weibull distribution and estimate shape parameters successfully. In contrast, shape parameter estimates in two of the real watersheds (Nile Creek and Swauk Creek) show a sharp decline over the smaller search radii and little change over larger search radii (Figure 6). Shape parameter estimates for Entiat River increase slightly with search radius, though more than in the other watersheds, except for two outliers at the smallest radii that are in the middle of the small range (Figure 6). Estimates for Quartzite decrease nearly monotonically until ca. 600 m, and are consistently higher than for the other watersheds. Estimates for South Deep cannot be easily compared to those from the other watersheds, because of the lack of parameter estimates for small search radii.

Discussion

Results from the neutral model suggest that non-linear scaling laws may be an intrinsic property of

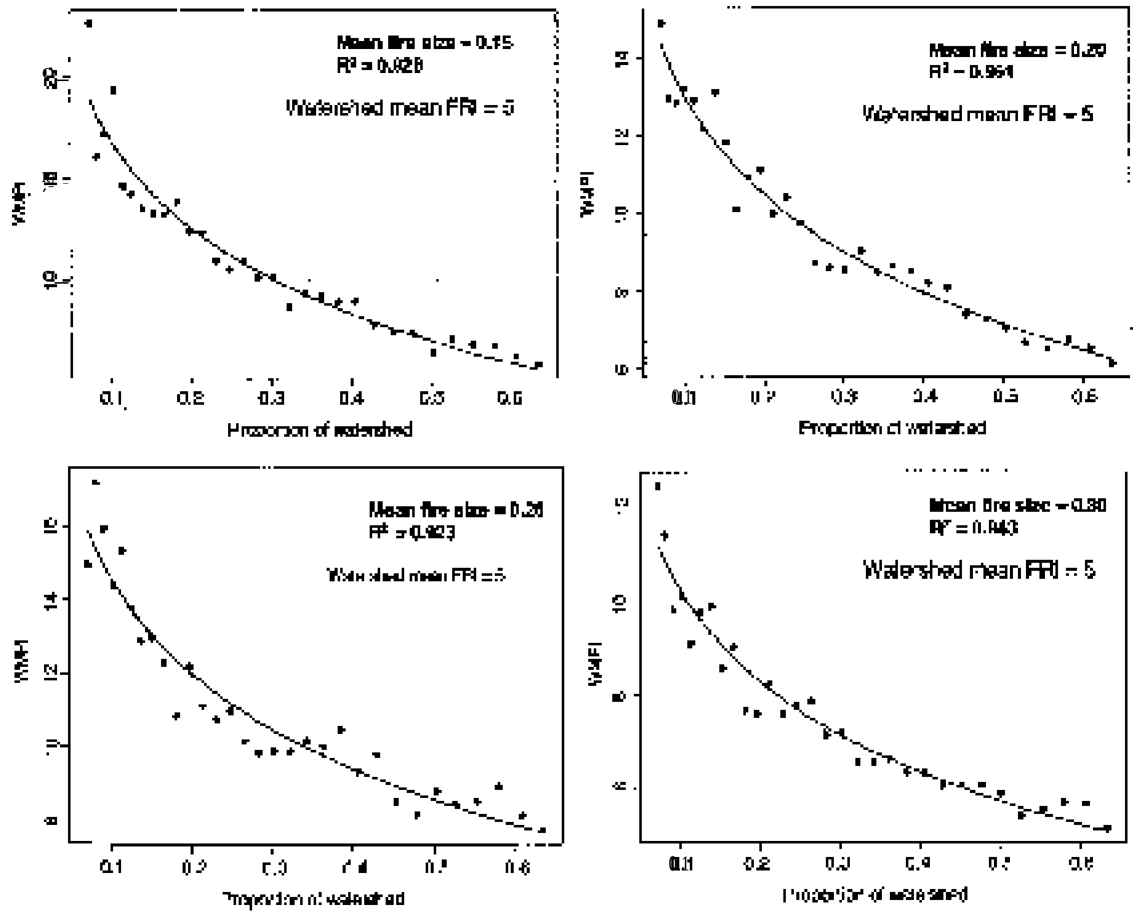

Figure 3. Scaling relations for WMPI as function of search radius and log-linear regressions from the neutral model WMPI, associated with different simulated fire sizes and watershed-scale mean fire-return interval = 5 year. Each data point represents the mean of 20 replicates.

the spatial relationships among points subject to low-severity fire. The log-linear relationship holds for a variety of mean fire sizes and fire frequencies, and is mathematically analogous to an event-area relationship that is linear in log-log space (Falk and Swetnam 2003; Falk 2004).

The scaling laws appear to hold generally in the composite fire record for our sites in eastern Washington, despite the variety of fire sizes and the relatively complex, dissected topography. Residuals from the three watersheds with (relatively) noisier models show a distinct pattern, however, of consistently negative residuals at intermediate values. These are an artifact of unusually long fire-free intervals associated with small search radii, which `bend' the regression line upward at small values of the predictor. These extreme values appear despite the robust nature of WMPI, which is less sensitive to outliers than a simple mean. Long fire-free intervals experienced by small areas within watersheds may indicate refugia from frequent fire that exist because of topographic or other biophysical anomalies (Camp et al. 1997) and can be important for the life histories of competing tree species (Clark 1996).

On the other hand, extremely long fire-free intervals may be partly due to the spatially random resampling within irregular watershed boundaries. Locally clustered point patterns of sampled trees could cause the same phenomenon because data can be missed if their spatial pattern (sizes of fires

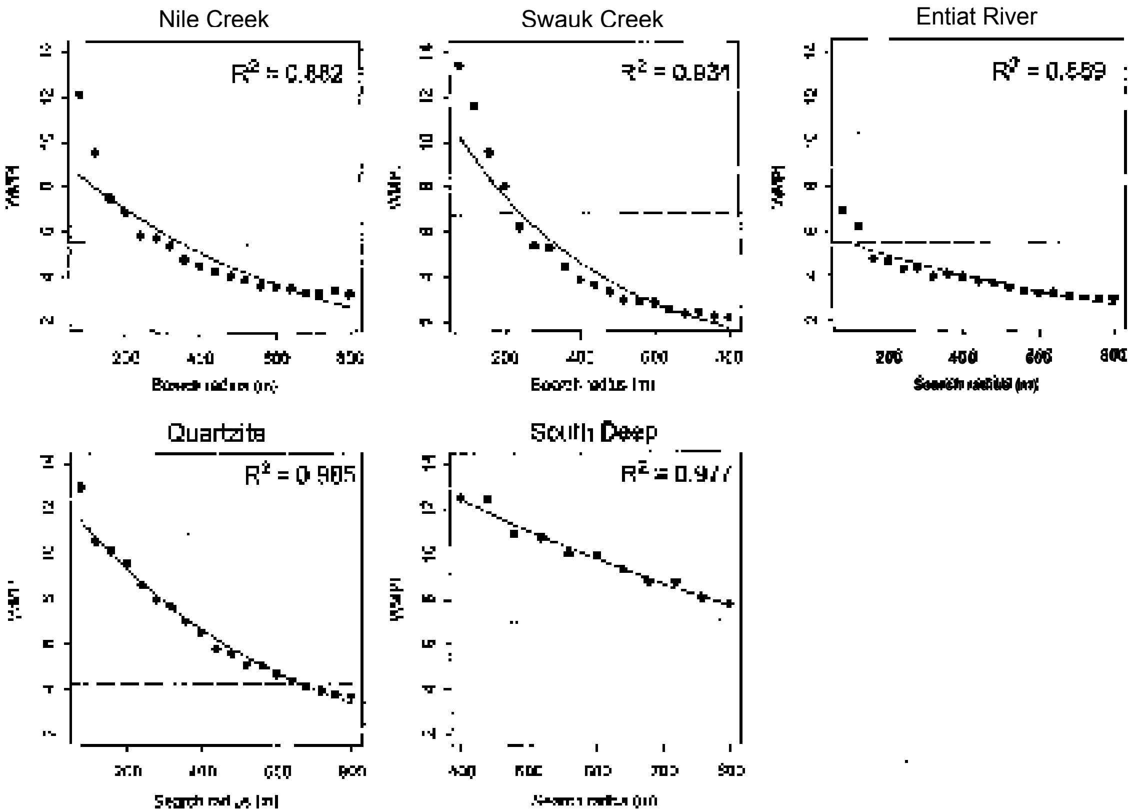

Figure 4. WMPI scale dependence in the five watersheds from eastern Washington. Horizontal lines mark the value for WMPI from the composite records of fires that scarred ?l0% of recorder trees (Hessl et al. 2004) in each watershed. The intersection of the lines may be associated with a modal fire size (see text). Each data point represents the mean of 20 replicates.

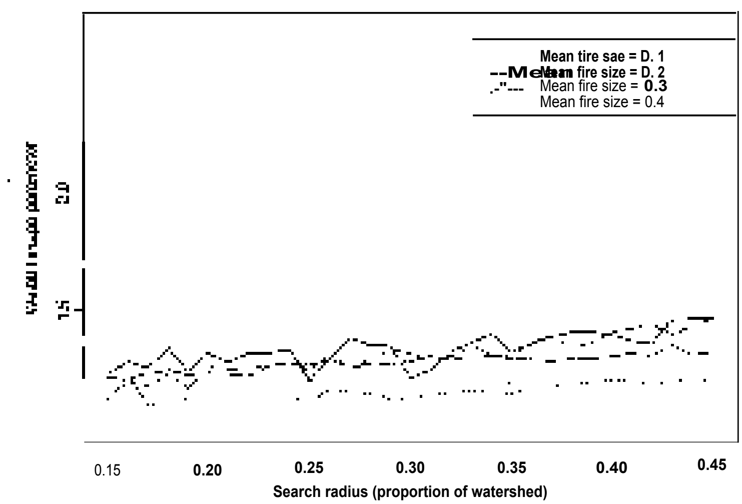

Figure S. Trends in Weibull shape parameters as functions of scale on neutral landscapes, for different mean fire sizes. Each data point represents the mean of 20 replicates.

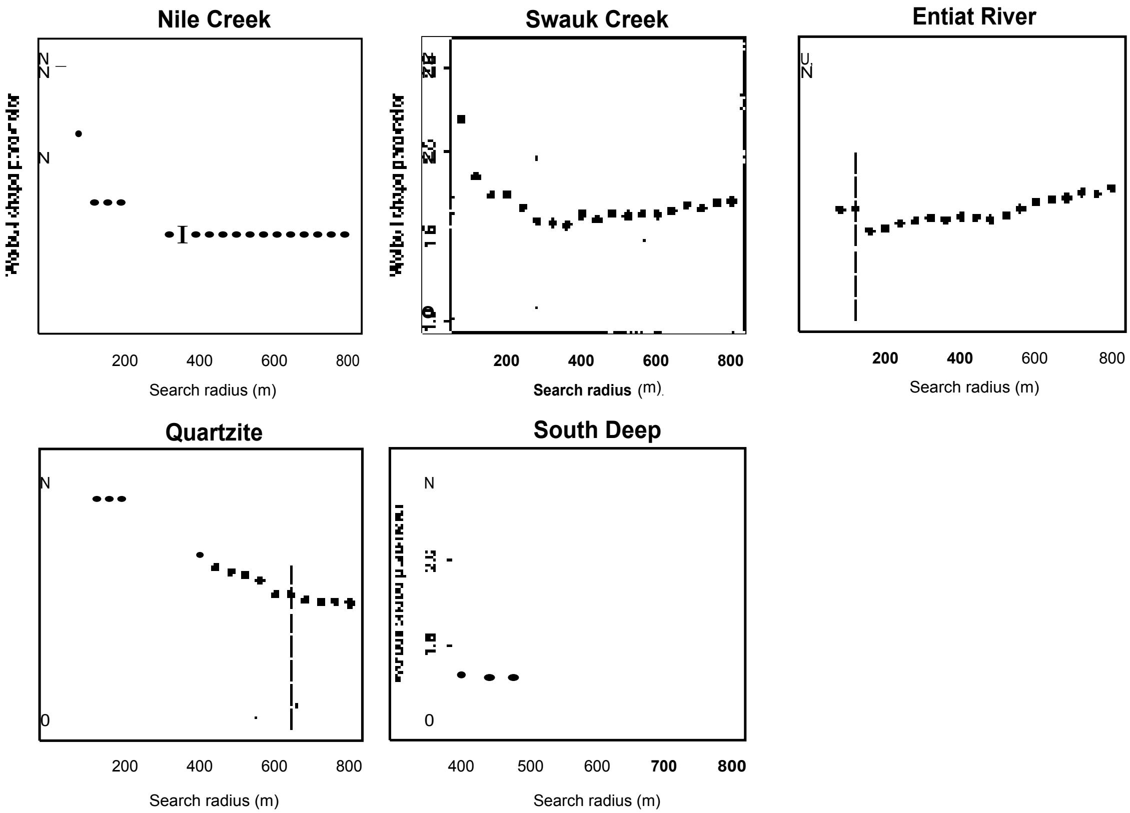

Figure 6. Weibull shape parameters as functions of scale on the five watersheds. The vertical line marks the search radius at which the shape parameter crosses 1.6, the value provisionally associated with a lower 95% confidence bound (see text). Each data point represents the mean of 20 replicates.

in this case) varies proportionally to the sampling resolution (Legendre et al. 2002).

Given that fire regimes vary over seemingly homogeneous landscapes (e.g., Baker 1989), and that topography and other landscape features appear to provide strong constraints on fire regimes on some landscapes (Taylor and Skinner 2003; Kellogg 2004), more research is needed in a range of low-severity fire regimes before a global scaling law can be said to apply to the event-area relationship. For example, how do fire-size distributions affect the model form (loglinear or other) and parameter estimates (Malamud et al. 1998, Reed and McKelvey 2002)? Such a scaling law would permit more robust comparisons of fire frequency among ecosystems because it would adjust for both different sample sizes and sample areas (Falk 2004).

Changes in the shape parameter are surrogates for changes in the slope of the hazard function (Clark 1989, Johnson and Gutsell 1994). In the neutral model, the shape parameters increased gradually with increases in search radius (Figure 5), although changes were slight and probably not statistically significant. However, similar behavior for a variety of simulated fire sizes suggests that this gradual increase may be an intrinsic property of the stochastic process being modeled, and needs to be distinguished from any processes of interest when the neutral model is compared with real data.

In contrast, in Swauk Creek and Nile Creek the shape parameters drop quickly with increasing spatial scale, up to 240 and 350 m search radii, respectively, then begin a gradual ascent (Swauk Creek) similar to those in the neutral model, although values are higher (ca. 1.5-1.8 in Swauk vs. a maximum of 1.45 for neutral model). The rapid drop corresponds to a change from increasing hazard of burning over time to constant hazard. Taking Swauk Creek as an example, we infer that a constraint on fires in rapid succession is operating on the landscape up to, on average, an area of 18 ha ($[240\ m]^2 * n/10^4\ m^2\ ha^{-1}$), and that the increasing hazard function over time at this scale is a reflection of it. Beyond this search radius (240 m), the shape parameter behaves similarly to that from the neutral model. In similar landscapes to these watersheds, composite fire records from study areas of different sizes, for example 10 ha vs. 40 ha, could therefore yield very different interpretations about the mechanisms influencing fire history. Baker (1989) observed that different statistical models were appropriate for different-sized study areas in a landscape with high-severity fire. Key processes controlling fire frequency may change, or at least appear different, when data are collected and analyzed at different spatial scales.

For example, in an earlier paper we identified climatic constraints operating on fire regimes in these same five watersheds at broad (whole watersheds and multiple watersheds) spatial scales (Hessl et al. 2004). In contrast, an obvious candidate for the small-scale constraint on historical fire frequency in the Swauk Creek and Nile Creek watersheds is buildup of fine fuels after fire. Time is required for a spatially continuous fuelbed, and therefore sufficient potential fire spread for trees to record fire, to accrue. When viewed at scales much greater than 18 ha, this constraint on fire occurrence is no longer observed, whereas climatic controls become more apparent (Hessl et al. 2004). The 18-ha threshold would appear to be a surrogate for a modal, or characteristic fire size, in that it defines the spatial extent over which the constraint of fuel buildup can be observed. When the search radius becomes much greater than typical fire size, it would be expected to include multiple fires, burning different patches over time, and thus confounding the fuel constraint. No such change occurs in the neutral landscape as either fire size or search radius changes, because there is no fuel constraint. This 18 ha area $(240\ m)^2$ corresponds closely to the intersection of the event-area curve and the mean interval between fires that scar > 10% of recorder trees in Swauk Creek (Figure 4).

A similar inference could be made for Quartzite, wherein the fine-fuel constraint represented in the hazard function declines, by comparison, but still applies out to the 800 m cutoff for search radius, suggesting that the modal fire size is substantially larger than in the watersheds to the west (Entiat River, Swauk Creek, Nile Creek). Quartzite, unlike the other watersheds, recorded several very large fires in the 1800s (> 50% of recorder trees - Hessl et al. 2004), and an increasing proportion of large fires during that century, for which the most recorder trees exist. Our resampling design captured the associated scaling relation in the hazard function. The lack of an apparent threshold on the Entiat River, which displays patterns similar to those in the neutral model, may reflect the preponderance of relatively small fires (those scarring fewer than 10% of trees - Hessl et al. 2004), so that if a threshold search radius did exist the associated area would be too small to detect with our methods because of limits on parameter estimation.

The threshold for change in behavior of the hazard function tracks changes in characteristic fire size, but only on landscapes on which a mechanism exists that controls fire recurrence (not neutral landscapes). Constraints on fire size, then, are associated with how temporal patterns of susceptibility to repeated fires change across spatial scale. Along with the other results from this exercise - the log-linear models of WMPI as a function of search radius (and fire size) - patterns in the hazard function suggest that on both neutral landscapes and watersheds in eastern Washington, scaling relationships among factors controlling fire regimes are evident. If proven to be robust on a variety of landscapes, particularly those on which topography provides strong constraints on fire spread, these scaling relationships could be very useful for predicting characteristics of fire regimes for which extensive, spatially explicit data are not available.

Conclusions

Neutral models hold promise for understanding complex behavior in low-severity fire regimes. Each fire-history record is just one of many potential realizations (Lertzman et al. 1998). Because fire-history reconstructions are made with finite resources, each can discover only an incomplete sample of even the one realization that it observes (Baker and Ehle 2001). A template is needed that faithfully reproduces aggregate statistical properties of fire regimes, against which specific realizations, i.e., landscape fire regimes, can be compared to distinguish their individual properties (for example, constraints on fire size and frequency).

In this paper, we begin to explore the ways in which neutral models can help distinguish these individual properties on real landscapes from the `neutral' background. More research is needed as to what to include in the neutral background. For example, some fire-history reconstructions develop collector's curves (a fire-history analog of the species-area curve) to determine the first point in time at which a representative sample of the total population of recorder trees has recorded at least one fire (Falk 2004; Hessl et al. 2004). Should a neutral model incorporate an increasing population of trees over time? Similarly, researchers commonly include only significant fire events (greater than a certain percentage of recorder trees scarred) when analyzing the association between fire occurrence and fuel or climatic constraints (Swetnam and Betancourt 1990; Grissino-Mayer 1995; Heyerdahl et al. 2001; Hessl et al. 2004). How would neutral model behavior differ with these additional attributes? Finally, more comparisons with data from real landscapes are needed, both to test the usefulness of the concept and to identify consistent patterns, if any, in scaling relationships and departures from `neutrality' in real fire regimes.

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References

Agee J.K. 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington DC.

Baker W.L. 1989. Effect of scale and spatial heterogeneity on fire-interval distributions. Can. J. Forest Res. 19: 700-706.

Baker W.L. 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: 1205-1226.

Barnett V. 1976. The ordering of multivariate data. J. Roy. Stat. Soc. Series A 139: 318-354.

Boyd R. 1999. Introduction. In: Boyd R. (eds), Indians, Fire, and the Land in the Pacific Northwest. Oregon State University Press, Corvallis, Oregon, USA, pp. 1-30.

Camp A., Oliver C., Hessburg P. and Everett R.L. 1997. Predicting late-successional fire refugia pre-dating European settlement in the Wenatchee Mountains. Forest Ecol. Manage. 95: 63-77.

Caswell H. 1976. Community structure: a neutral model analysis. Ecol. Monogr. 46: 327-354.

Clark J.S. 1989. Ecological disturbance as a renewal process: theory and application to fire history. Oikos 56: 17-30.

Clark J.S. 1990. Fire and climate change during the last 750 year in northwestern Minnesota. Ecol. Monogr. 60: 135-159.

Clark J. 1996. Testing disturbance theory with long-term data: alternative life-history solutions to the distribution of events. Am. Nat. 148: 976-996.

Davison A.C. and Hinckley D.V. 1997. Bootstrap Methods and their Application. Cambridge University Press, Cambridge, UK.

Efron B. and Tibshirani R.J. 1993. An Introduction to the Bootstrap. Chapman and Hall, New York, USA.

Evans M., Hastings N. and Peacock B. 1993. Statistical Distributions. Wiley and Sons, New York, USA.

Everett R.L., Schellhaas R., Keenum D., Spurbeck D. and Ohlson P. 2000. Fire history in the ponderosa pine/Douglas-fir forests on the east slope of the Washington Cascades. Forest Ecol. Manage. 129: 207-225.

Falk D.A. and Swetnam T.W. 2003. Scaling rules and probability models for surface fire regimes in ponderosa pine forests. In: Omi P.N. and Joyce L.A. (eds), Fire, Fuel Treatments, and Ecological Restoration: Conference Proceedings, 2002 16-15 April, Fort Collins, Colorado. USDA Forest Service Proceedings RMRS-P-29, Rocky Mountain Research Station, Fort Collins Colorado USA.

Falk D.A. 2004. Scaling Rules for Fire Regimes. Ph.D. dissertation, Department of Ecology and Evolutionary Biology, Laboratory of Tree-Ring Research, University of Arizona, Tucson, AZ, USA.

Galbraith W.A. and Anderson E.W. 1991. Grazing history of the Northwest. Rangelands 13: 213-218.

Gardner R.H. and O'Neill R.V. 1991. Neutral models for landscape analysis, Chapter 11. In: Turner M.G. and Gardner R.H. (eds), Quantitative Methods in Landscape Ecology. Springer-Verlag, New York, USA.

Gotelli N.J. and Graves G.R. 1996. Null Models in Ecology. Smithsonian Books, NY.

Green D.G. 1994. Connectivity and complexity in landscapes and ecosystems. Pacific Conserv. Biol. 1: 194-200.

Grissino-Mayer H.D. 1995. Tree-Ring Reconstructions of Climate and Fire History at El Malpais National Monument, New Mexico. Ph.D. dissertation, University of Arizona, Tucson, Arizona, USA.

Grissino-Mayer H.D. 1999. Modelling fire interval data from the American Southwest with the Weibull distribution. Int. J. Wildland Fire 9: 37-50.

Grissino-Mayer H.D., Romme W.H., Floyd-Hanna M.L. and Hanna D. 2004. Climatic and human influences on fire regimes of the southern San Juan Mountains, Colorado, USA. Ecology 85: 1708-1724.

Grissino-Mayer H.D. and Swetnam T.W. 2000. Century-scale climate forcing of fire regimes in the American Southwest. The Holocene 10: 213-220.

Hess] A.E., McKenzie D. and Schellhaas R. 2004. Drought and Pacific Decadal Oscillation linked to fire occurrence in the inland Pacific Northwest. Ecol. Appl. 14: 425-442.

Heyerdahl E.K., Berry D. and Agee J.K. 1995. Fire history database of the western United States. EPA Office of Research and Development: Report EPA/600/R-96/081, Washington, DC, USA.

Heyerdahl E.K, Brubaker L.B. and Agee J.K. 2001. Spatial controls of historical fire regimes: a multiscale example from the Interior West, USA. Ecology 82: 660-678.

Hosmer D.W.Jr. and Lemeshow S. 1999. Appl. Survival Anal. Wiley and Sons, NY.

Hubble S.P. 2001. A Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton, New Jersey, USA.

Insightful, Inc. 2002. Splus 6 for Windows. Seattle, Washington, USA.

Johnson E.A. and Gutsell S.L. 1994. Fire frequency models, methods, and interpretations. Adv. EcoL Res. 25: 239-287.

Keitt T.H., Urban D.L. and Milne B.T. 1997. Detecting critical scales in fragmented landscapes. Conserv. Ecol. http://www.consecol.org/ voll/issl/art4.

Kellogg L-K.B. 2004. Quantifying Spatial Structures Associated with Low-Severity Fire Regimes in the Eastern Cascade Mountains of Washington State, USA. Master's Thesis, University of Washington, Seattle, WA, USA.

Kimura M. 1983. The Neutral Theory of Molecular Evolution. Cambridge University Press, Cambridge, UK.

Landres P., Morgan P. and Swanson F.J. 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecol. Appl. 9: 1179-1188.

Legendre P., Dale M.R.T., Fortin M-J., Gurevitch J., Hohn M. and Myers D. 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. Ecography 25: 601-615.

Lertzman K.; Fall J. and Dorner B. 1998. Three kinds of heterogeneity in fire regimes: at the crossroads of fire history and landscape ecology. Northwest Sci. 72: 4-23.

Li C. 2002. Estimation of fire frequency and fire cycle: a computational perspective. Ecol. Model. 154: 103-120.

Lynch J.A., Clark J.S., Bigelow N.H., Edwards M.E. and Finney B.P. 2003. Geographic and temporal variations in fire history in boreal ecosystems of Alaska. J. Geophys. Res. 107, 8152, doi:10.1029/2001JD000332, 2002.

Malamud B.D.; Morein G. and Turcotte D.L. 1998. Forest fires: an example of self-organized critical behavior. Science 281: 1840-1842.

McKenzie D., Peterson D.L. and Agee J.K. 2000. Fire frequency in the Columbia River Basin: building regional models from fire history data. Ecol. Appl. 10: 1497-1516.

McKenzie D., Prichard Si., Hess! A.E. and Peterson D.L. 2004. Empirical approaches to modelling wildland fire: methods and applications to landscape simulation. Chapter 7 In: Perera A.J. and Buse L. (eds), Emulating Natural Forest Landscape Disturbances. Columbia University Press, New York USA.

Milne B.T. 1992. Spatial aggregation and neutral models in fractal landscapes. Am. Nat. 139: 32-57.

Milne B.T., Johnson A.R., Keitt T.H., Hatfield C.A., Hraber D.J. and Hraber P.T. 1996. Detection of critical densities associated with pinon-juniper woodland ecotones. Ecology 77: 805-821.

Palmer M.W. 1992. The coexistence of species in fractal landscapes. Am. Nat. 139: 375-397.

Prichard S.J. 2003.Spatial and Temporal Dynamics of Fire and Forest Succession in a Mountain Watershed, North Cascades National Park. **Ph.D.** Dissertation, University of Washington, Seattle, Washington, USA.

Pyne S.J. 2001. Year of the Fires: The Story of the Great Fires of 1910. Viking Press, New York, USA.

Reed W.J. and McKelvey K.S. 2002. Power-law behavior and parametric models for the size distribution of forest fires. Ecol. Model. 150: 239-254.

Ripley B.D. 1987. Stochastic Simulation. Wiley and Sons, New York, USA.

Robbins W.G. 1999. Landscape and environment: ecological change in the intermontane Northwest. In: Boyd R. (eds), Indians, Fire, and the Landin the Pacific Northwest. Oregon State University Press, Corvallis, Oregon, USA, pp. 219-237.

Robbins W.G. and Wolf D.W. 1994. Landscape and the Intermontane Northwest: An Environmental History. USDA Forest Service General Technical Report PNW-GTR-319, Pacific Northwest Research Station, Corvallis, Oregon, USA.

Rorig M.L. and Ferguson S.A. 1999. Characteristics of lightning and wildland fire ignition in the Pacific Northwest. J. Appl. Meteorol. 38: 1565-1575.

Rosenzweig M.L. 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge, UK.

Ross S. 1988. A First Course in Probability. Macmillan, New York, NY.

Ross J.A. 1999. Proto-historical and historical Spokane _prescribed burning and stewardship of resource areas. In Boyd R. (eds), Indians, Fire, and the Land in the Pacific Northwest. Oregon State University Press, Corvallis, Oregon, USA, pp. 1-30.

Schmoldt D.L., Peterson D.L., Keane R.E., Lenihan J.M., McKenzie D., Weise D.R. and Sandberg D.V. 1999. Assessing the Effects of Fire Disturbance on Ecosystems: A Scientific Agenda for Research and Management. USDA Forest Service General Technical Report PNW-GTR-455. Pacific Northwest Research Station, Portland, Oregon, USA.

Swetnam T.W. and Betancourt J.L. 1990. Fire-Southern Oscillation relations in the southwestern United States. Science 249: 1017-1020.

Swetnam T.W., Allen C.D. and Betancourt J.L. 1999. Applied historical ecology: using the past to manage for the future. Ecol. Appl. 9: 1189-1206.

Taylor A.H. and Skinner C.N. 2003. Spatial and temporal patterns of historical fire regimes and forest structure in the Klamath Mountains. Ecol. Appi. 13: 704-719.
Veblen T.T., Kitzberger T. and Donnegan J. 2000. Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado Front Range. Ecol. Appl. 10: 1178-1195.
Weiher E. and Keddy P. 1999. Ecological Assembly Rules: Perspectives, Advances, Retreats. Cambridge University Press, Cambridge, UK.
With K.A. 1997. The application of neutral landscape models in conservation biology. Conserv. Biol. 11: 1069-1080.