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Landscape Ecol (2010) 25:1561–1573
DOI 10.1007/s10980-010-9527-5

RESEARCH ARTICLE

Using a stochastic model and cross-scale analysis to evaluate controls on historical low-severity fire regimes

Maureen C. Kennedy · Donald McKenzie

Received: 30 April 2010 / Accepted: 17 August 2010 / Published online: 28 August 2010
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Abstract Fire-scarred trees provide a deep temporal record of historical fire activity, but identifying the mechanisms therein that controlled landscape fire patterns is not straightforward. We use a spatially correlated metric for fire co-occurrence between pairs of trees (the Sorensen distance variogram), with output from a neutral model for fire history, to infer the relative strength of top-down vs. bottom-up controls on historical fire regimes. An inverse modeling procedure finds combinations of neutral-model parameters that produce Sorensen distance variograms with statistical properties similar to those observed from two landscapes in eastern Washington, USA, with contrasting topography. We find the most parsimonious model structure that is able to replicate the observed patterns and the parameters of this model provide surrogates for the predominance of top-down vs. bottom-up controls. Simulations with relatively low spread probability produce irregular fire perimeters and variograms similar to those from the topographically complex landscape. With higher spread probabilities fires exhibit regular perimeters and variograms similar to those from the simpler landscape. We demonstrate that cross-scale properties of the fire-scar record, even without historical fuels and weather data, document how complex topography creates strong bottom-up controls on fire spread. This control is weaker in simpler topography, and may be compromised in a future climate with more severe weather events.

Keywords Fire history · Sorensen distance · Neutral model · Top-down vs. bottom-up controls · Scaling

Electronic supplementary material The online version of this article (doi:10.1007/s10980-010-9527-5) contains supplementary material, which is available to authorized users

M. C. Kennedy (✉)
School of Forest Resources, College of the Environment, University of Washington, Box 352100, Seattle, WA 98195-2100, USA
e-mail: mkenn@u.washington.edu

D. McKenzie
Pacific Wildland Fire Sciences Lab, US Forest Service, 400 N 34th Street, Suite 201, Seattle, WA 98103, USA
e-mail: dmck@u.washington.edu

Introduction

The faithful reconstruction of historical (pre-1900) fire regimes is a difficult, yet essential task to inform ecosystem management and restoration. In low-severity fire regimes trees are not killed, but they may be damaged and scarred by a fire. The scars on these *recorder trees* (trees that have one or more fire scars) can be cross-referenced to provide a deep temporal record of fire activity (Kilgore and Taylor 1979; Heyerdahl et al. 2001; Hessl et al. 2004) that is unique to low-severity fire regimes. Fire-history reconstructions in general rely on aggregate measures such as mean fire-free intervals or fire rotations and mean fire size. Such measures mask variability among individual fires that are inherent in fire regimes, but are used by default because spatially explicit data on individual fire-scarred trees are rarely recorded. It is difficult to infer from fire-history data the sizes of past fires and there is little or no record of the mechanisms that may have generated individual fires such as the quantity and condition of fuels or the weather conditions. Therefore the replication of individual fire events is not a goal of our research, rather we focus on the larger-scale characteristics of the historical fire regime.

The interpretation of patterns observed in fire history depends on the scale of analysis (Lertzman et al. 1998; McKenzie et al. 2006; Falk et al. 2007; Kellogg et al. 2008), particularly with respect to distinguishing bottom-up (e.g., fine-scale changes in topography and in fuels) vs. top-down (e.g., climate) controls (Lertzman et al. 1998; Kellogg et al. 2008) that may have influenced the spatial pattern of fires that characterize the fire regimes at a given location. Understanding the relative importance of these processes is important from the perspective of fire management if we are to effectively manipulate bottom-up controls on fire spread. Evaluating fine-scale controls on fire history in a spatially explicit manner requires an extensive database of fire-scarred trees that preserves their spatial point pattern across the landscape (Falk 2004; Kellogg et al. 2008). Connecting the spatially explicit pattern of recorder tree scarring to processes that generate global properties of fire history regimes requires a simulation study, because no direct record of these historical processes remains.

Landscape ecologists use neutral models to generate null hypotheses for pattern-process interactions (Gardner and Urban 2007). Neutral theory has specific implications in community, population, and evolutionary biology (e.g., genetic drift-Kimura 1983), yet underlying these models is the null proposition that complex system patterns are the consequence of simple stochastic processes. If the patterns cannot be replicated with the neutral model, a more mechanistic explanation is necessary. We seek to find the level of model complexity justified for the observed system (With and King 1997). The neutral model is akin to a null hypothesis for drivers of system patterns that separates intrinsic stochastic processes from forcing functions-in a fire model these forcing functions are the effects of climate, fuel loadings, topography, and management (Gardner and Urban 2007). This method is valuable for conducting inference in ecological systems such as historical fire regimes or other retrospective studies (e.g., Parsons et al. 2007; Weisberg et al. 2008), where controls or even replicate observations are lacking.

McKenzie et al. (2006) created a neutral model to provide a mechanism for the scarring of recorder trees (i.e., a tree on a landscape that has produced a fire scar) in order to evaluate the effect of scale on aggregate measures of fire history. In their neutral model fire spread is not simulated, rather a random fire size is drawn from a probability distribution and a circular fire perimeter of that size is drawn at a random location on the simulated landscape. Any recorder trees within the random fire perimeter are scaned with some probability. Such a model does not replicate individual fire events or fire behavior (Finney 2004) and it does not attempt to simulate frequency distributions of fire sizes (Drossel and Schwabl 1992).

Scaling laws in fire regimes may provide evidence that drivers of landscape pattern change across scales (Falk et al. 2007; McKenzie and Kennedy in press). Fire frequency changes systematically with the scale of observation (McKenzie et al. 2006; Falk et al. 2007), and frequency distributions of fire sizes exhibit equally consistent scaling (Millington et al. 2006). Kellogg et al. (2008) showed that a measure of dissimilarity (Sorensen' s distance-Legendre and Legendre 1998) between time series of fire-scar dates reflected topographic controls on fire when analyzed analogously to a variogram. These "Sorensen's distance variograms" (hereafter SD variograms) had shorter ranges and less variability when computed on fire-scar records in watersheds with complex topography (Kellogg et al. 2008). This implies a strong spatial dependence and thereby bottom-up control in landscapes with complex topography. Their analysis did not, however, enable a comparison of the spatial pattern of fires in the various landscapes as characterized by the SD variograms. What are the consequences of fine-scale control in complex landscapes?

The neutral model of McKenzie et al. (2006) restricts fires to circular perimeters, which does not allow for variability in the spatial structure of simulated fires. We propose that a neutral model for fire history that expands that of McKenzie et al. (2006) with an additional fire spread parameter, can guide interpretation of patterns within and among SD variograms. This analysis can thereby help to evaluate possible controls on fire-regime properties and to guide where future efforts in the study of fire regimes should be focused. We use a spatially explicit fire history database from eastern Washington, USA (Everett et al. 2000). Following Kellogg et al. (2008), we expect different patterns associated with topographic complexity. Furthermore, we expect that interpretation of the parameters in this neutral model can parsimoniously characterize the relative importance of top-down vs. bottom-up controls (e.g., Lertzman et al. 1998) on historical low-severity fire. If successful, we can infer that patterns in fire-history data across topographically diverse landscapes can be explained by changes in key parameters governing simple stochastic processes. The underlying drivers of these patterns would thereby be accessible to retrospective simulation studies and this can guide future studies in these landscapes.

Methods

Study location

Everett et al. (2000) sampled fire-scarred trees in sites extending from the Okanogan Wenatchee National Forest in central Washington to the Colville National Forest in northeastern Washington. 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. These sites are located within forests dominated by ponderosa pine (pinus ponderosa Douglas ex C. Lawson). Kellogg et al. (2008) characterized the topographic complexity of the fire history sites by calculating the fractal dimension of each site, such that sites with higher fractal dimension have more complex topography. We choose the fire scar records from the years 1700-1900 for two of these sites, Swauk Creek and Twentymile (Fig. 1), for comparison to neutral model results. These two sites represent the strongest contrast in topographic complexity as identified by Kellogg et al. (2008), whereas we can expect that they experience similar regional climate throughout their record. Swauk Creek was characterized by the highest fractal dimension and hence the most complex topography, while Twentymile was characterized by the lowest fractal dimension and the simplest topography among the fire history sites (Kellogg et al. 2008). The contrast between Twentymile and Swauk Creek is useful because we can infer that differences in response between the two sites are likely due to their different topographic complexity.

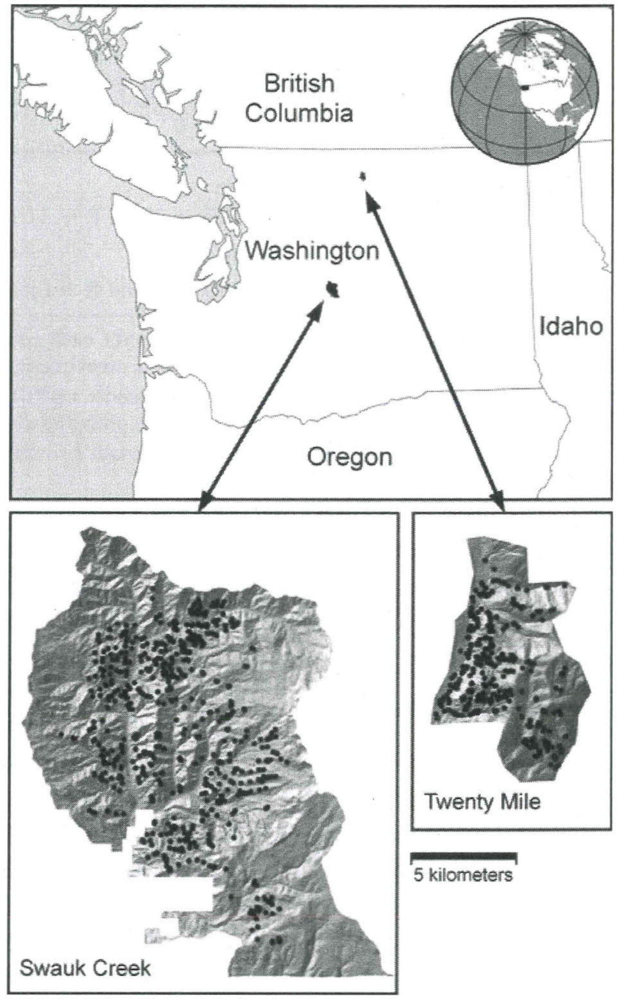

Fig. 1 Two fire history study sites, east of the crest of the Cascade Range, Washington, USA. **a** Watershed locations, **b** inserts display hill *shaded* topography with *dots* representing the locations of recorder trees

A spatially correlated metric for fire history

The georeferenced fire history data of Everett et al. (2000) allow us to compare fire histories of pairs of recorder trees using the Sorensen distance. The Sorensen distance is 1-the Sorensen coefficient (Table 1), which is a multivariate measure of

Table 1 Frequency table to summarize the fire history of two recorder trees, A and B, where A = 1 denotes A is scarred in a given year, and B = 1 denotes B is also scarred in that year

	A = 1	A = 0
B = 1	n_{11}	n_{01}
	P(A = 1 and B = 1)*k	P(A = 0 and B = 1)*k
B = 0	n_{10}	n_{00}
	P(A = 1 and B = 0)*k	P(A = 0 and B = 0)*k

Each value nxx counts the number of realizations for each cell (e.g., nll is the tally of the number of years both trees record the same fire). Adapted from Legendre and Legendre (1998). The second line in each cell of the table gives a probabilistic expression for the expected number in that cell, and k is the number of fires in the fire history

similarity commonly used in analyses of species and community composition (Legendre and Legendre 1998). The Sorensen distance between any two recorder trees is calculated as (Table 1)

$$SD = 1 - 2n_{11}/(2n_{11} + n_{10} + n_{01}), \quad (1)$$

where n_{ll} is the count of joint presences (both trees record a fire), n_{l0} is the count of fires recorded by the first tree in the pair not recorded by the second, and n_{0l} is the count of fires recorded by the second tree in the pair not recorded by the first.

Kellogg et al. (2008) plotted the SD between time series of fire-scars in pairs of recorder trees against Euclidean distance between each pair in what they term a Sorensen variogram (hereafter SD variogram). Changes in the shape of the SD variogram would be related to changes in the spatial structure of fire spread. We use the SD variogram to evaluate how neutral model outputs vary with changes in neutral model parameters. We compare the neutral model SD variograms to the observed SD variograms for Swauk Creek and Twentymile.

Neutral model description

The purpose of using the neutral model is to find the simplest representation of the system that is able to replicate observed patterns. The neutral model is initialized with a homogeneous rectangular raster landscape with a user-specified number of cells and cell resolution (we use grids of 100 x 100 cells, each cell is assigned a width of 90 m). In the simulation, all random numbers are generated from algorithms adapted from Press et al. (2003). Figure 2 shows the spread of a fire from a single ignition point across three iterations in the neutral model.

The number of fires that are simulated for a fire history depends on the mean fire return interval (u_{fri}; McKenzie et al. 2006), which is used as the rate parameter in a random draw of a fire return interval from an exponential distribution. A series of fire return intervals are randomly drawn and sumined until the first fire interval is drawn at which the cumulative fire return >200 years. The length of this series is the number of fires for the fire history; i.e., as the mean fire return interval decreases, the number of fires that occur over 200 years increases. In all simulations the u_{fri} is 3 years, roughly corresponding to that from the eastern Washington watersheds. In keeping with the simplest possible representation, there is also no memory of past fires in the neutral model; the spread of one fire does, not affect the

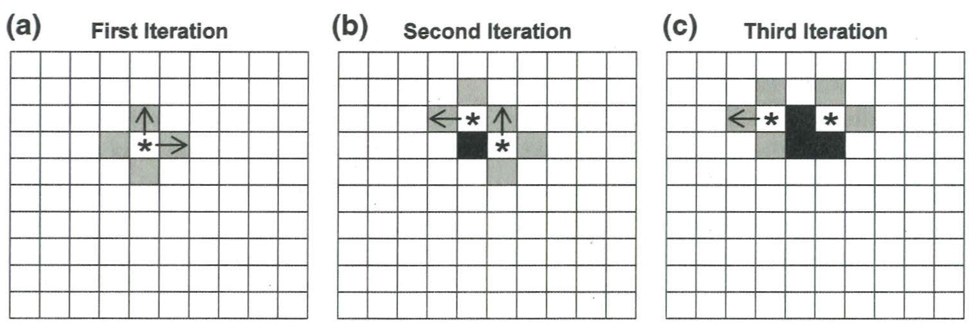

Fig. 2 Fire spread in the neutral model though three iterations (a-c) on a small landscape (for illustration only-neutral model is designed for larger landscapes). * denotes a cell that is actively spreading fires to neighbors, *black* denotes a burned cell that is no longer spreading fire, and *grey* denotes cells that are being tested for fire spread. *Black arrows* indicate the direction of successful fire spread for each iteration (a random process) for this example. In the neutral model these cells would contain a random pattern of recorder trees that would be tested independently for scarring in pixels that experience fire

spread of subsequent fires (see Supplementary material S2).

For each fire in the history a random ignition point is chosen, with every pixel within a 5-cell buffer having an equal chance to be the ignition point. There is no explicit time step in the fire spread algorithm, rather fire spread proceeds along successive iterations until a stopping point is reached.

In the neutral model we separate a top-down constraint on fire size from a bottom-up control on fire spread. We define a top-down constraint on the fire size distribution by the target size of the fire, which is drawn from a gamma probability distribution whose mean is the specified mean fire size (u_{size}). The fire size is defined as the maximum proportion of pixels burned in the landscape for the single fire, and can be interpreted as the duration of conditions conducive to fire spread. This parameter is the simplest possible representation of a top-down control on fire history, and it subsumes more complicated processes believed to act as top-down controls, principally climate. By using this single parameter the model assumes that the more complicated factors are stationary across the fire history and can be summarized by a mean fire size. The use of this parameter does not mean that fire sizes are constant across the fire history-they are variable around the mean value. For example, 1 year the random fire size might be relatively large, which would correspond to a year in the history for which the climate and prevailing weather is conducive to a large fire. If a single parameter is found to be inadequate to replicate observed patterns, then this parameter might be disaggregated to a more complicated representation of top-down controls on fire spread.

The bottom-up control on fire spread is defined by a single spread probability that is assigned to every pixel in the landscape (P_{spread}). This is the probability the fire spreads to a given pixel from a neighboring burning pixel (no diagonal neighbors) and can be interpreted as the likelihood a pixel that neighbors a burning pixel also has the conditions that enable fire spread. This is a more complicated representation of fire spread than that presented by McKenzie et al. (2006), where fires are assumed to occupy a circular perimeter of a random fire size. The P_{spread} parameter subsumes possible bottom-up controls on fire spread, including fuels, memory of past fires, local weather patterns, topography, etc. The model assumes that across a fire history these more complicated bottom-up controls on fire spread are stationary processes that can be summarized by a mean value, in contrast to their very specific roles in replicating individual fires. Simulations show that varying the P_{spread} parameter across the landscape does not change the shape of the SD variogram (Supplementary S2) and that it is the mean value that drives the shape of the SD variogram. The use of a single value for P_{spread} does not imply that fire spread is constant across the fire history, only that the mean process is stationary; the path of each individual simulated fire is the cumulative result of a random process. If a single parameter for fire spread were found to be inadequate to replicate observed patterns, then P_{spread} might be disaggregated to a more complicated representation of bottom-up controls on fire spread, including an explicit representation of fuels and memory of past fires.

As the current fire spreads it is evaluated against three possible stopping rules each iteration. Fire spread is terminated if: (1) all tests of fire spread fail in a given iteration; (2) if the fire has spread to all four of the landscape borders; or (3) if the proportion of pixels burned is > the randomly assigned fire size for the current fire. Once fire spread is terminated, the landscape is reset to its pre-burned condition and the next fire in the fire history is initialized at its random ignition point. This process is repeated until all fires in the fire history have been spread.

A spatial point pattern of recorder trees (trees available to be scarred and hence record the fire) is also overlain on the landscape, simulated as a Poisson pattern of complete spatial randomness (CSR; Diggle 1983) with a specified intensity (we use a mean of 400 trees, similar to that across the fire history sites; Kellogg et al. 2008). These trees only serve to record (with a scar) the occurrence of fire-fuels are not included in the process of fire spread. When the fire spreads to a given pixel, all recorder trees within the pixel are tested for scarring against a scar probability (P_{scar}) that is applied homogeneously across the point process of recorder trees. Recorder trees are tested once for scarring in the iteration that fire spreads to the relevant pixel. Scarring is independent fire to fire and tree to tree in a given fire history. As with the other major parameters (u_{size} and P_{spread}), P_{scar} is the simplest possible representation of recorder tree scarring, subsuming more complicated processes

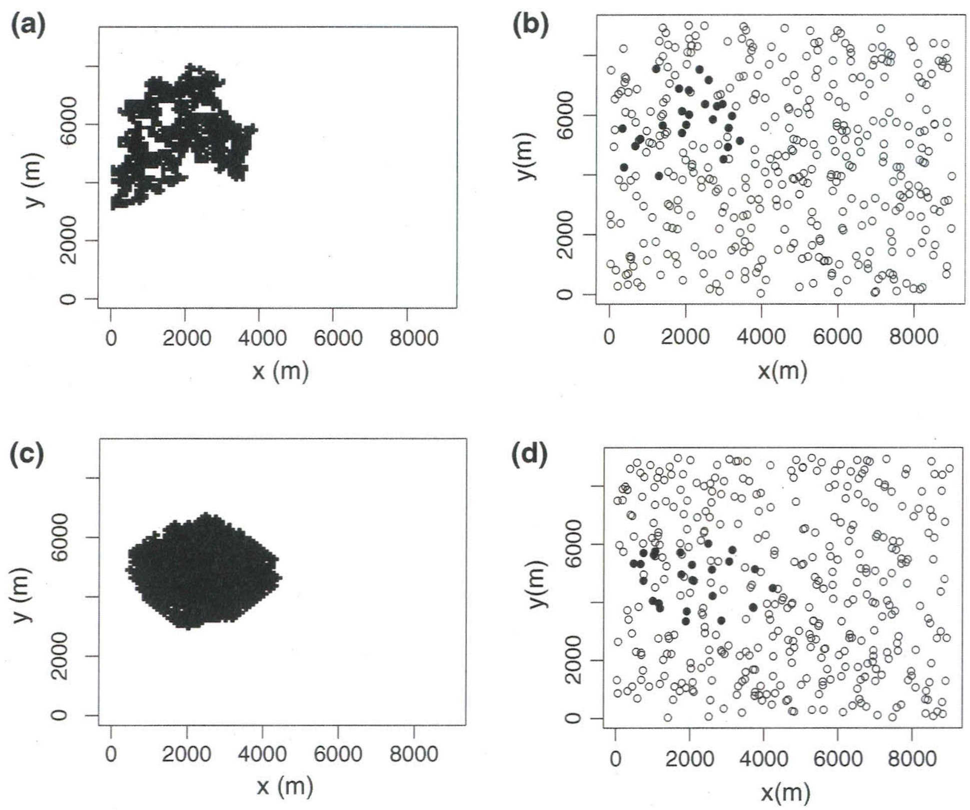

Fig. 3 **a** Single realization of fire spread on a 100 × 100 pixel landscape (90 m resolution) with $p_{spread} = 0.49$ and $p_{scar} = 0.5$, with a fire size of 1127 pixels burned (0.1127 in proportion). **b** The *solid circles* in the point pattern of recorder trees show those that were scarred by the fire in (a). c, d contrast that with $p_{spread} = 0.75$ and $p_{scar} = 0.5$ with a fire size of 1301 pixels burned (0.1301 in proportion)

such as the damage caused by a previous fire. If this is seen to be inadequate to replicate observed patterns, then a more complicated representation would be justified.

The model returns the fire history of each recorder tree, which reflects the spatial structure of each fire in the set of fires and is comparable to observed fire history data sets. To aid interpretation of the P_{spread} parameter we compare maps of individual fires and the corresponding scarring patterns for $p_{spread} = 0.49$ and $p_{spread} = 0.75$ ($\mu_{size} = 0.15$; $p_{scar} = 0.50$; Fig. 3).

Interpretation of the SD variogram

In order to use the neutral model to explain what differentiates the SD variograms observed at the fire history sites, we consider whether the value of Sorensen's distance between two trees could be predicted by probability features of the neutral model. To derive an expression to predict SD for a given pair of recorder trees, we take each component of Eq. 1 in turn. The value of n_{11} is number of fires recorded by both trees in the pair, which depends on two events: they must both be in a burned pixel and they must both be scarred. We define A_{fire} to mean that tree A is in a burned pixel, and B_{fire} to mean that tree B is in a burned pixel. The probability that both trees A and B are in a burned pixel and they both scar is $P(A_{fire})*P(B_{fire}/A_{fire})*P^2_{scar}$(Appendix 1 in Supplementary material 4), i.e., the probability both trees in a pair are both in a burned pixel for a fire event is the probability the first tree is in a burned pixel times the probability the second is in a burned pixel given that the first already is (by Bayes theorem). For the case that both trees are in a burned pixel, the probability they both scar is the product of their scar probabilities (P^2_{scar}) because scarring is independent within the fire. We would expect the value of n_{11} to be the number of fires *(k)* times this probability.

There is a single probability to be calculated for both n_{01} and n_{10}: $P(A = 1 \text{ and } B = 0) = P(A = 0$

and B = 1). There are two possibilities for tree A to be scarred in a given fire while tree B is not scarred (A = 1 and B = 0). (i) A is in a burned pixel (A_{fire}) while B is not ($B_{not\_in\_fire}$)and A is scarred, which is $P(A_{fire})*P(B_{not\_in\_fire\_}{}^{I}A_{fire})*P_{scar}= P(A_{fire})*[1 - P(BfireIAfire)]*Pscar$(ii) A and B are both in burned pixels, and A is scarred while B is not, which is $P(A_{fire})*P(B_{fire}{}^{I}A_{fire})*P_{scar}*(1 - P_{scar})$· The probability tree A is scarred and tree B is not scarred is the sum of these probabilities (i and ii), and we would expect the value of n_{01} and n_{10} to each be the number of fires *(k)* times this probability. We can then combine these elements and propose an expression for the expected value of Sorensen distance for a pair of trees a given distance apart (E(SD)):

$$E(\mathrm{SD}) = 1 - \frac{k * 2P(A_{\mathrm{fire}})P(B_{\mathrm{fire}}|A_{\mathrm{fire}})p^2_{\mathrm{scar}}}{k * 2P(A_{\mathrm{fire}})P(B_{\mathrm{fire}}|A_{\mathrm{fire}})p^2_{\mathrm{scar}} + k * 2P(A_{\mathrm{fire}})p_{\mathrm{scar}}[1 - P(B_{\mathrm{fire}}|A_{\mathrm{fire}})p_{\mathrm{scar}}]}, \quad (2)$$

which reduces to (Appendix 1 in Supplementary material 4):

$$1 - P(B_{\mathrm{fire}}|A_{\mathrm{fire}}) * p_{\mathrm{scar}}. \quad (3)$$

This derivation implies that the shape of the SD variogram can be directly predicted by the probability a recorder tree that experiences fire is scarred and the probability a second recorder tree in a pair experiences fire given the first has.

Simulation to verify interpretation of the SD variogram

We use simulation to verify whether the value of SD expected from the neutral model probability structure (Eq. 3) is able to predict the shape of simulated SD variograms. Given Eq. 3 above, the shape of the SD variogram can be partitioned into two components: the P_{scar} parameter and the probability a second tree in a pair experiences a fire given the first has. We use fire histories simulated from the neutral model to estimate $P(B_{fire}{}^{I}A_{fire})$ for each pair of trees in the simulated point pattern (Supplementary S1) in order to evaluate how the conditional probability changes with distance. We repeat the simulation for two values of P_{scar}(0.5 and 0.75) with ,u_{size}= 0.15 and P_{spread}= 0.49 for both simulations. If Eq. 3 is correct, then the shape of $P(B_{fire}{}^{I}A_{fire})$ should not change with P_{scar} and the value of SD should be predicted by the value of $P(B_{fire}{}^{I}A_{fire})$ multiplied by P_{scar}.

To characterize the shape of the relationship between $P(B_{fire}{}^{I}A_{fire})$ with the distance between trees A and B we evaluated the fit of three candidate curves: exponential, 2-coefficient power, 3-coefficient power (Supplementary S1). The 3-coefficient power curve had the lowest AIC value and was chosen as the best fit.

$$P(B_{\mathrm{fire}}|A_{\mathrm{fire}}) = b_0 - b_1 d^{b_2}, \quad (4)$$

where d is the distance between trees A and Band b_0, b_1 and b_2 are non-linear regression coefficients. For all non-linear least-squares regression fits we us the nls function in the R statistical package (R Development Core Team 2009).

The fit of the 3-coefficient power function has consequences for the value of E(SD). If we substitute Eq. 4 for $P(B_{fire}{}^{I}A_{fire})$ in Eq. 3, we get a new expression for E(SD):

$$\begin{aligned} E(\mathrm{SD}) &= 1 - p_{\mathrm{scar}}\left(b_0 - b_1 d^{b_2}\right) \\ &= 1 - p_{\mathrm{scar}} b_0 + p_{\mathrm{scar}} b_1 d^{b_2} \end{aligned} \quad (5)$$

SD would thereby depend on the shape of the relationship between $P(B_{fire}{}^{I}A_{fire})$ with distance, in conjunction with the value of Pscar.

It is clear from Eq. 3 how the value of P_{scar} modifies the shape of the SD variogram, but the effects of $P_{spread}$and ,usizeare not as obvious. Any effect $P_{spread}$and ,usizewould have on the shape of the SD variogram would be manifested through changing the shape of $P(B_{fire}{}^{I}A_{fire})$ (Eq. 3). We conduct a sensitivity analysis of Pspreadand ,usizeby performing a set of five simulations each at three levels of Pspread (0.49, 0.65, 0.75) in combination with increasing u_{size}(0.05, 0.06, 0.07, 0.08, 0.09, 0.10, 0.11, 0.12, 0.15, 0.20, 0.25,0.5). For the purpose of the sensitivity analysis we set P_{scar} to 0.5, knowing that the value of P_{scar} modifies the SD variogram in a predictable manner (Eq. 3), and in order to isolate the effects of P_{spread} and u_{size}. We estimate the coefficients b_o, b_1 and b_2 (Eq. 4) for the relationship between $P(B_{fire}{}^{I}A_{fire})$ and the distance between trees A and B for every combination of Pspreadand u_{size}. All statistical tests were conducted using the R statistical package (R Development Core Team 2009). For illustration we plot example curves of $P(B_{fire}{}^{I}A_{fire})$ at each of the spread probabilities (0.49, 0.65, 0.75) at three of the u_{size} values (0.05, 0.25, 0.50). The full results of the sensitivity analysis can be found in Supplementary material (Figs. S2.4-S2.6).

Comparison of simulated SD variogram to observed

We can use the relationship in Eq. 3 to aid interpretation and fitting to the observed SD variograms. One consequence of Eq. 3 is that we can estimate a value of P_{scar} for a given SD variogram. When $P(B_{fire}{}^{I}A_{fire})$ approaches 1, then the value of SD is predicted to be 1 - P_{scar}. If we assume that at the smallest distance bin the $P(B_{fire}{}^{I}A_{fire})$ is essentially zero, then we can estimate P_{scar} as 1 minus the value of SD in the smallest distance bin. We can then estimate the coefficients b_o, b_1, and b_2 (Eq. 5) for the observed SD variogram by setting P_{scar} at the previously estimated value. This enables us to back-engineer the relationship $P(B_{fire}{}^{I}A_{fire})$ for the observed fire histories and compare those curves to the simulated set. We fit the value of P_{scan} then estimate b_o, b_1, and b_2 for both the Swauk Creek and Twentymile SD variograms.

We then used the coefficient values estimated for each of the 36 parameter combinations evaluated in the sensitivity analysis (three levels of P_{spread}* 12 levels of u_{size}) to find the combination that best corresponds to the observed SD variograms. The parameter combination that resulted in a model realization with the lowest residual sum of squares (RSS) relative to each observed pattern was recorded. The SD variogram predicted for that realization is overlain on each observed pattern to visually compare the fit between simulated and observed.

Results

Interpretation of the SD variogram

There is a surprisingly simple expression for the expected value of SD for a pair of trees (Eq 3). This indicates that the relationship between Sorensen distance and geographic distance relies on the probability a second tree is in a burned pixel given the first one is ($P(B_{fire}{}^{I}A_{fire})$) and how that changes with distance, as well as the probability a tree in a burned pixel is scarred (P_{scar}). The value of $P(B_{fire}{}^{I}A_{fire})$ is equivalent to the probability the two pixels occupied by each tree in the pair experiences fire, which is a result of the spatial structure of the fire.

Simulation to verify interpretation of SD variogram

The value of $P(B_{fire}{}^{I}A_{fire})$ clearly declines non-linearly with distance (d; Fig. 4a) and is well fit by the 3-coefficient power curve. When we calculate expected SD values given the combination of $P(B_{fire}{}^{I}A_{fire})$ and the value of P_{scar} (as in Eq. 3) the expected value of SD (lines in Fig. 4b) closely follows the simulated values (points in Fig. 4b). As expected, the shape of the $P(B_{fire}{}^{I}A_{fire})$ curve does not change with P_{scar} (Fig. 4), and the SD variogram shifts with P_{scar} in a manner that is predicted by Eq.3.

There is no obvious reason to expect the fit to $P(B_{fire}{}^{I}A_{fire})$ and the value of P_{scar} to translate directly to SD (points in the variogram were generated from neutral model results, and not from any of the above derivations), and we assume agreement in the fits supports the derivation of E(SD). This also shows that a higher value of P_{scar} results in an SD variogram that is shifted lower on the y-axis, implying greater similarity in fire history if the value of P_{scar} is higher.

The sensitivity analysis shows that the relationship of $P(B_{fire}{}^{I}A_{fire})$ does change with both u_{size} and P_{spread} (Fig. 5). The estimates of the coefficients (b_0, b_1, b_2) of the 3-coefficient power function vary with the value of u_{size} and P_{spread} (Supplementary S2 Figs. S2.4-S2.6), which is reflected in a change in the curve $P(B_{fire}{}^{I}A_{fire})$ with distance. For a given P_{spread}, the probability a second tree in a pair experiences a fire given the first has is higher with increasing u_{size} (Fig. Sa, b, c). This change in $P(B_{fire}{}^{I}A_{fire})$ is more

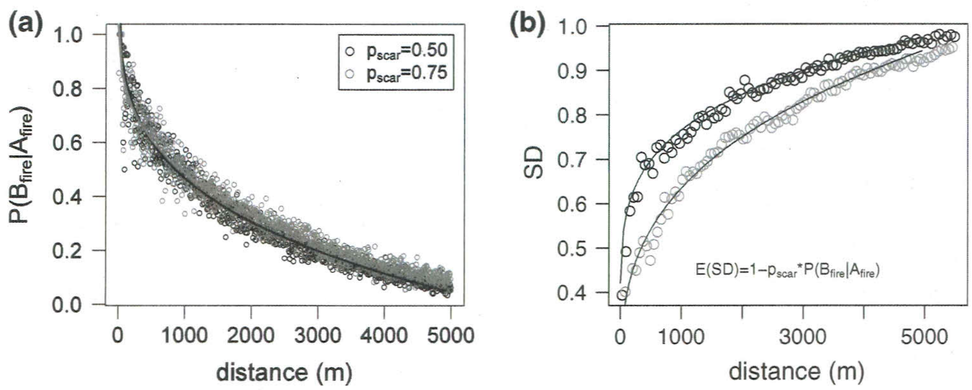

Fig. 4 **a** The 3-coefficient curve (Eq. 4) fits the relationship between $P(B_{fire}|A_{fire})$ and distance well, and the relationship is independent of p_{scar} ($\mu_{size} = 0.15$, $p_{spread} = 0.49$). **b** The fit to $P(B_{fire}|A_{fire})$ is used to predict E(SD) with distance, and when compared to simulated values the predicted curve fits well. It also changes with p_{scar} in a manner consistent with Eq. 3

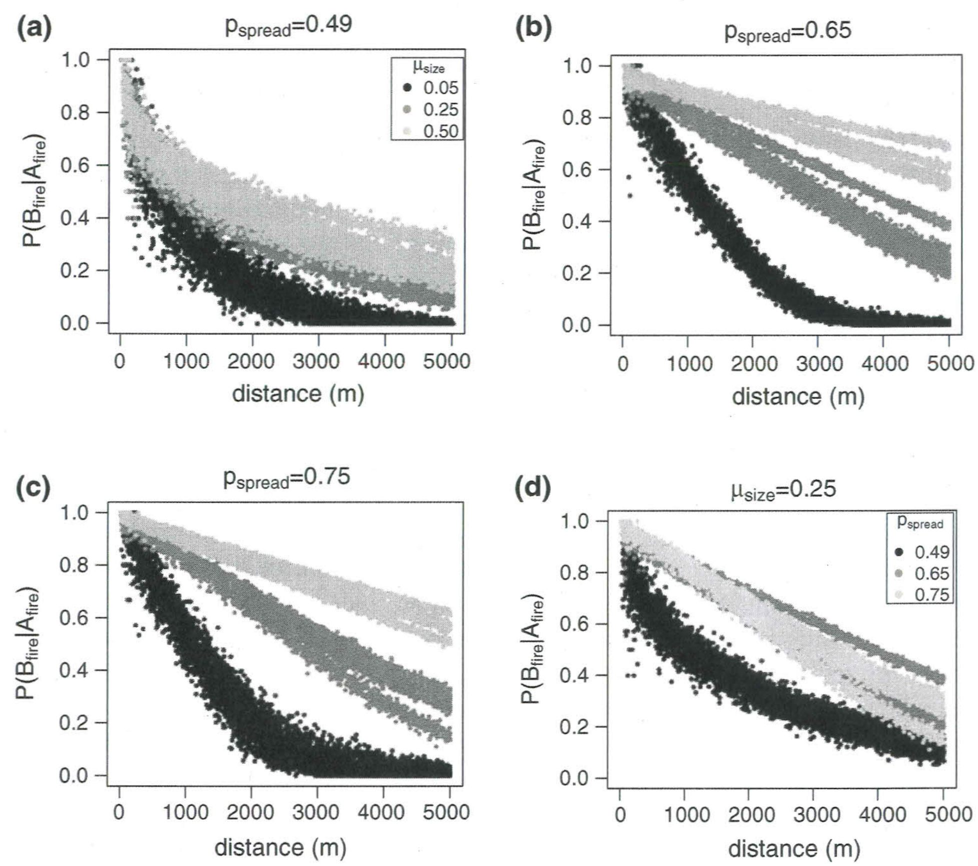

Fig. 5 The probability a second tree in a pair experiences fire given the first has ($P(B_{fire}|A_{fire})$) declines with the distance between the trees in the pair. The shape of that decline for a given value of p_{spread} changes with μ_{size} **a** $p_{spread} = 0.49$; **b** $p_{spread} = 0.65$; **c** $p_{spread} = 0.75$. **d** For a given value of μ_{size} the shape of the curve changes with p_{spread}

pronounced for the higher values of Pspread' At a given value of I[size the P(BfireIAfire) curves for $P_{spread} = 0.65$ and 0.75 are shifted higher on the y-axis relative to $P_{spread} = 0.49$ (Fig. 5d), which is more pronounced with increasing u_{size}. The $P(B_{fire}{}^{I}A_{fire})$ curves are almost indistinguishable for $P_{spread} = 0.65$ and 0.75, and the relationship between $P(B_{fire}{}^{I}A_{fire})$ with distance becomes more linear (b_2 approaches 1), reflecting the more regular fire shapes characterized by higher P_{spread} (Fig. 3).

Comparing observed SD variograms to simulated

The 3-coefficient function (Eqs. 4, 5) fits both observed SD variograms well, and exhibits different estimates of the coefficients between the two sites

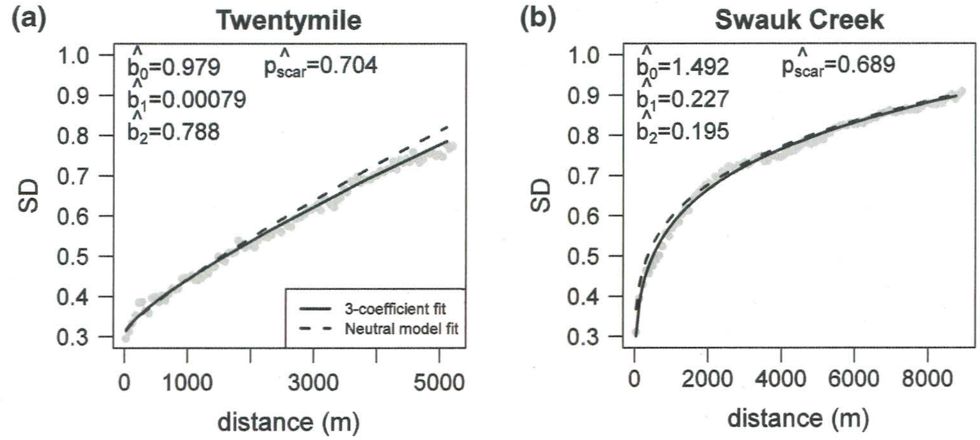

Fig. 6 Observed SD variograms (*points*) for two fire history sites described previously (in Kellogg et al. 2008), but here fit to Eq. 5 (*solid lines*). *Dashed lines* show the SD variogram fit to a neutral model simulation in the sensitivity analysis that most closely follows the observed SD variogram. **a** Twentymile with low topographic complexity matches a neutral model realization with $p_{spread} = 0.65$ and $\mu_{size} = 0.25$. **b** Swauk Creek with higher topographic complexity matches a neutral model realization with $p_{spread} = 0.49$ and $\mu_{size} = 0.5$. The two sites have a similar estimated value for p_{scar}, but the shapes of their variograms clearly differ, reflected in the estimates of the 3-coefficient power function

(Fig. 6). The neutral model parameter combination in the sensitivity analysis that is able to best match each observed variogram also differs between the two sites The realization from the sensitivity analysis that best fits the observed Twentymile pattern ($P_{scar}= 0.704$) corresponds to $P_{spread} = 0.65$ and $u_{size} = 0.25$, whereas the realization from the sensitivity analysis that best fits the Swauk Creek pattern ($P_{scar} = 0.689$) corresponds to $P_{spread} = 0.49$ and $u_{size} = 0.5$.

Discussion

The neutral model for fire history provides a simple framework for understanding spatial patterns in low-severity fire regimes and how they change across scales, which is a major topic of fire-history research (Falk et al. 2007). We were able to reproduce the spatial auto-correlation structure of fire regimes on two contrasting landscapes, using a combination of simulations and statistical modelling. Classical geo-statistical techniques can provide descriptive comparisons among spatial patterns of fire, but their parameters (nugget, sill, range) are difficult to interpret with respect to the mechanisms of fire occurrence and spread (Kellogg et al. 2008). We derived a probabilistic interpretation of the value of SD between two trees a given distance apart, which depends on the probability the second tree (B) in a pair experiences a fire given the first (A) has ($P(B_{fire} I A_{fire})$) and on the probability a tree that experiences the fire is scarred (P_{scar}). The $P(B_{fire} I A_{fire})$ is the component of the SD variogram that represents the spatial pattern of fire spread that is independent of the value of P_{scar}. The $P(B_{fire} I A_{fire})$ decreases with the distance between the two trees, and the shape of the curve that defines that decrease depends on the pattern of fire spread (P_{spread}) and on the mean fire size (u_{size}; Fig. 5). These neutral model parameters are thereby identifiable by the shape of the SD variogram, and enable neutral model simulations to be tuned to produce realizations of fire history that mirror those on observed landscapes.

Top-down and bottom-up controls on fire spread are not either-or propositions, as both contribute to some degree to patterns in fire histories (Parisien et al. 2010), but their relative importance in a given system may vary. Quantifying the three neutral model parameters and comparing simulations to observed patterns allows us to extend the inferences in Kellogg et al. (2008) about the relative contribution of top-down and bottom-up controls on historical fire regimes. Those authors theorized that intuitively, climatic controls (top-down) should be dominant in landscapes with relatively simple topography and less heterogeneity in fine-scale barriers to fire spread. The interpretation of the parameters P_{spread} and u_{size} in the neutral model as aggregate representatives of bottom-up and top-down controls, and how those are able to reproduce observed fire history patterns, allows us to characterize the simulated spatial structures of fires that correspond to the fire histories of landscapes in similar regions with varying topographic complexity. This analysis does not inform the controls on the spread of individual fire events, which are more detailed and complicated than possible to incorporate into a fire history simulation. Rather we evaluate the control of global fire regime properties as expressed in the SD variogram.

Twentymile is a site of relatively low topographic complexity, and its SD variogram corresponds to simulated fire histories with higher P_{spread} (Fig. 6a). Fires in a simulated history with a higher value of P_{spread} have a more regular shape and lower perimeter:area ratio (Fig. 3c; Supplementary S3). We interpret this to correspond to a landscape with weak local bottom-up control on fire spread, i.e., the fire spreads uniformly over a fixed area, encountering minor barriers. These simulated fires would continue to spread if not for an extra stopping rule, which in the neutral model is u_{size} (a top-down constraint). This is not to say that bottom-up controls do not exist on this landscape, rather that such controls are less important than in topographically complex landscapes.

In contrast to Twentymile, Swauk Creek is a site of relatively high topographic complexity. The shape of its SD variogram corresponds to a simulated fire history with a lower P_{spread} value (Fig. 6b). Fires in these simulated histories have relatively irregular fire shapes (Fig. 3a) and a higher perimeter:area ratio (Supplementary S3). Simulated fires are more likely to stop (from repeated application of P_{spread}) before they reach the targeted fire size u_{size}. This is interpreted to correspond to strong local bottom-up control on fire spread, with highly variable conditions across the landscape associated with the varying topography. We reiterate that top-down and bottom-up controls are not either-or propositions. On these topographically complex landscapes top-down controls obviously influence fire regimes, it is just that bottom-up controls are relatively more important for sites with greater topographic complexity.

Fire spread is a stochastic process in the neutral model, and lower P_{spread} emulates the cumulative effects of fire spread's encountering barriers. This can be interpreted as the chance a neighbor of a burned cell is also ignitable. In a landscape with topography that varies at fine scales, the bottom-up controls on fire spread such as fuel abundance, fuel moisture, fuel recovery after fire, and fuel type are also expected to vary at relatively fine scales. These may represent barriers to fire spread, and correspond to a low value of P_{spread}. In a topographically simple landscape neighboring cells are more likely to have similar fuel characteristics and the chance of encountering a barrier is lower. This corresponds to a higher P_{spread}. Note that these inferences are made on aggregate measures of bottom-up and top-down controls (P_{spread} and u_{size}) and no inference is made on what specific components of those larger classes of control dominate in these landscapes. These results should be used to design future studies that are able to identify the components of top-down and bottom-up controls that act on the scales that our simulation results imply.

Neutral models for fire history: strengths and relevance

It could be argued that our results are mainly phenomenological and a more rigorous analysis would involve mechanistic simulations of fire spread. We agree that such an approach would be informative but there are two problems with it, one mainly technical and the other more methodological. First, mechanistic fire spread simulations require data that are not and will never be available-historical fuel abundance and spatial pattern. Fire-spread models are difficult enough to implement even on contemporary landscapes (Keane and Finney 2003, Cushman et al. 2007); the further difficulty of reconstructing historical fuels and patterns of fuel recovery after fire makes such an approach intractable. Second, the relative parsimony of the neutral model is invaluable in an analytical environment subject to cumulative errors from multiple parameters (McKenzie et al. 1996; Gardner and Urban 2007). Here we have found simulated results consistent with the observed spatial structure of fire regimes with simulations uniquely identified by the values of three model parameters (P_{spread}, u_{size}, P_{scar}).

The overriding goal of the neutral model is to find the model with the minimum level of complexity that is able to replicate observed patterns. The three neutral model parameters are surrogates for multiple physical and biological processes. They do not provide explicit mechanistic inferences about each individual process as would a landscape simulation model that represents each separately. Such detail would be uninformative in our current context, which is to identify different controls associated with spatially correlated properties of fire regimes represented in the SD variograms. Additional parameters that might be more biologically meaningful in themselves (such as including the legacy of past fires to modify P_{spread}; Supplementary S2) would simply accommodate and perhaps distort each other (analogous to collinear variables in regression) to achieve the same match to observations that we accomplish with three parameters (Turley and Ford 2009). Almost certainly we would encounter the problem of non-uniqueness, such that multiple model structures are able to fit the data equally well without evidence to choose among them. This makes inferences for those parameters questionable and we would lose the parsimony of the current neutral model. The mean value of P_{spread} drives the observed patterns, and we have no evidence to assign a root cause to that mean value. As with any modeling exercise, our results can only point toward a possible explanation for congruence between simulation results and observed patterns. Our conclusions should guide further study in the relevant spatial scales of bottom-up and top-down controls on fire spread, and how those are mediated by the local topography of a landscape and to identify the root causes of the differences in mean P_{spread} between the landscapes.

Our results reveal one way in which spatially explicit fire-history data can inform our understanding of multi scale controls on landscape fire (Falk et al. 2007). Our analysis is limited to low-severity fire regimes because it is for these systems that spatially rich fire history data are available. This dovetails with the inherent advantages of historical data in low-severity fire regimes-a deep temporal record and an absence of pervasive human influence-to suggest that we may have scientific leverage to at least propose some implications for broad-scale management of fire-prone landscapes, particularly in a warming world in areas that are now delicately balanced between top-down and bottom-up controls.

With fire-climate models predicting broad-scale increases in fire extent (Gedalof et al. 2005; Westerling and Bryant 2008; Littell et al. 2009), fine-scale controls could become less effective at constraining fire spread. This may lead to more homogeneous spatial patterns with larger burned patches even in topographically complex landscapes, i.e., similar to those in our models in which P_{spread} is relatively high. Notwithstanding the above, there may be opportunities to effectively decrease P_{spread} across landscapes. Topography is essentially constant, but the spatial configuration of fuels is subject to management (Finney 2001; Peterson and Johnson 2007). Judicious placement of fuel treatments could conceivably function as if reducing P_{spread} to maintain fine-scale environmental controls on fire and their associated benefits for fire management; i.e., mimic the variability in fuel conditions implied by rapid changes in topography.

We are unlikely to experience analogues to historical environmental conditions in the foreseeable future. Nevertheless, thoughtful inferences from historical patterns can still inform both future modelling exercises (including, we hope, those that further advance the work we have presented here) and decisions about adaptation and management of fire-prone landscapes in a time of rapid global change (Swetnam et al. 1999; Millar et al. 2007).

Acknowledgments We dedicate this paper to the memory of Lara-Karena Kellogg, whose earlier work in modeling the spatial structure of fire-scar records has inspired ours. We thank David L. Peterson, Ashley Steel, Carol Miller and two anonymous reviewers for comments that improved an earlier draft of this manuscript. Robert Norheim produced the map for Fig. 1. Research was supported by the Pacific Northwest Research Station, USDA Forest Service.

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