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Abstract

Context:
The proportion of fire area that experienced stand-replacing fire effects is an important attribute of individual fires and fire regimes in forests. It has been used to group forest types into characteristic fire regimes. However, relying on proportion alone ignores important spatial characteristics of stand-replacing patches, which can have a strong influence on post-fire vegetation dynamics.

Objectives:
We propose a new more ecologically relevant approach for characterizing spatial patterns of stand-replacing patches to account for potential limitation of conifer seed dispersal.

Methods:
We applied a simple modified logistic function to describe the relationship between the proportion of total stand-replacing patch area and an interior buffer distance on stand-replacing patches.

Results:
This approach robustly distinguishes among different spatial configurations of stand-replacing area in both theoretical and actual fires, and does so uniquely from commonly used descriptors of spatial configuration.

Conclusions:
Our function can be calculated for multiple fires over a given area, allowing for meaningful ecological comparisons of stand-replacing effects among different fires and regions.

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SHORT COMMUNICATION

Alternative characterization of forest fire regimes: incorporating spatial patterns

Brandon M. Collins · Jens T. Stevens · Jay D. Miller · Scott L. Stephens · Peter M. Brown · Malcolm North

Abstract

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Keywords Stand replacing patches · High severity · Fire severity · Fire ecology

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Introduction

Fire effects on vegetation can vary considerably within individual wildland fires, owing to underlying variability in fuel (vegetation) and topography throughout many landscapes, and to fluctuations in weather at the time of burning. The term fire severity is often used to capture these effects, which is generally defined as the amount of dominant vegetation killed or consumed by fire. In forests, understanding spatial patterns of fire severity is critical because overstory tree mortality can lead to a cascade of related ecological effects (Swanson et al. 2011). Fire-caused tree mortality is a binary process (a tree is either killed or not), but the nature of fire spread dictates that trees are often killed in contiguous patches of varying sizes (van Wagtendonk 2006), termed "stand-replacing". The proportion of a given burned area that experienced stand-replacing effects is often used to distinguish among individual fires or characteristic fire regimes. Low-severity, moderate- (or mixed-) severity, and high-severity is a readily used classification of fires and fire regimes, with various thresholds of stand-replacing effects delineating the classes (Agee 1998; Schoennagel et al. 2004).

Dendroecological reconstructions have provided a majority of the information from which historical fire regimes have been inferred (Fulé et al. 1997; Swetnam et al. 1999; Taylor 2004). These studies do well at characterizing the two extremes of historical fire regimes in forests: frequent, generally non-lethal surface fires (i.e., low severity), versus infrequent, generally lethal crown fires (i.e., high severity). Example forest types with these respective fire regimes include southwestern U.S. ponderosa pine (*Pinus ponderosa*) and Rocky Mountain lodgepole pine (*Pinus contorta*) (Schoennagel et al. 2004). However, the historical fire regime for many conifer-dominated forest types is somewhere in between these two extremes. These forests are described as historically having a mixed severity fire regime (Perry et al. 2011; Hessburg et al. 2016). Forest types characterized as mixed severity historically had structures that were maintained by low severity fire (i.e., large, widely spaced trees) intermixed with discrete vegetation patches created by high severity, or stand-replacing fire (i.e., shrubs, dense tree regeneration) (Agee 1998; Hessburg et al. 2016).

The most widely used definition of a mixed severity fire is 20–70% overstory tree mortality summed over a given fire area (Agee 1993; Perry et al. 2011). There are two major concerns with this definition. First, the range in overstory mortality across a single fire is so broad that most fires in forested landscapes fit within this range (Miller et al. 2012; Cansler and McKenzie 2014; Harvey et al. 2016), hence it is not very precise for distinguishing among fires (Brown et al. 2008; Perry et al. 2011). Second, a simple summing of overstory mortality across an entire fire ignores important spatial characteristics of overstory mortality. These spatial characteristics can have a strong influence on post-fire vegetation dynamics in conifer-dominated forests mainly owing to limitations in seed dispersal (e.g., Kemp et al. 2016). As such, quantifying these patterns is critical for understanding ecosystem responses following stand-replacing fire. In this paper we propose a new more ecologically relevant approach for describing spatial patterns of stand-replacing fire effects, which will improve the characterization of fire effects for individual fires and fire regimes. Our intent is to refine the current characterization of fire regimes, rather than replace it.

Scale and "percent stand-replacing"

The widely used definitions for binning individual fires based on percent overstory mortality (e.g., <20, 20–70, >70%; Agee 1993) have also been used to distinguish among fire regime types. Odion et al. (2014) suggested that low/moderate severity fire regimes are characterized by <20% overstory mortality, while mixed severity fire regimes have patches in all three overstory mortality levels. However, as with the classification for individual fires there is ambiguity in how spatial patterns of mortality may differ among fire regime types. Agee (1998) posited that low, mixed (referred to as moderate), and high severity fire regimes all had patches of stand-replacing fire, but differed in characteristic patch sizes and patch edge. This has been corroborated by Brown et al. (2008), which demonstrated that small stand-replacing patches occurred even in a low severity fire regime, albeit infrequently.

Although stand-replacing patches are recognized as a component within all three fire regime types there is no consistent approach for describing how stand-replacing area is distributed spatially. Patch sizes,

129 shapes, and distribution throughout a fire (or across a
130 landscape) can vary considerably, which can result in
131 significantly different long-term ecological effects.
132 This is particularly relevant in forest types dominated
133 by tree species that lack direct mechanisms for
134 establishment following stand-replacing fire (e.g.,
135 vegetative re-sprouting or seed stored in serotinous
136 cones). In these forest types tree regeneration follow-
137 ing stand-replacing fire is dependent on seed dispersal
138 from surviving trees. For example, ponderosa pine has
139 relatively heavy seed that generally does not disperse
140 far from surviving trees, which can severely limit tree
141 regeneration into large stand-replacing patches
142 (Chambers et al. 2016). However, an individual fire
143 with small, widely scattered stand-replacing patches
144 would be expected to have ample seed available for
145 tree regeneration (Kemp et al. 2016). These potential
146 differences in forest recovery based on spatial patterns
147 of stand-replacing patches may not be as relevant in
148 areas with moderate to high levels of serotiny (e.g.,
149 Rocky mountain lodgepole pine; Turner et al. 1997).

150 Most evaluations of contemporary fire severity rely
151 on classifications of Landsat pixels by the change in
152 vegetation reflectivity before and after fires (e.g.,
153 relative differenced Normalized Burn Ratio-RdNBR;
154 Miller and Thode 2007). Using these satellite data
155 calibrated to field plots, it is possible to assign
156 categorical classifications of low, moderate and high
157 severity fire *at the 30-m pixel scale*. Independent plot
158 data sampled immediately before and one-year fol-
159 lowing wildfire demonstrate that a commonly used
160 classification of RdNBR into low, moderate, and high
161 severity (see thresholds in Miller and Thode 2007)
162 corresponds with the following tree basal area mor-
163 tality levels: 0–20, 25–70, and >95% based on
164 interquartile ranges, respectively (Lydersen et al.
165 2016). Although the range in mortality associated
166 with moderate severity at the pixel scale is fairly
167 consistent with the previously used definition of
168 "mixed-severity" (20–70% mortality summed across
169 an entire fire), fires where a majority of the area is
170 mapped as moderate severity are exceedingly rare
171 (Miller and Quayle 2015). A more frequently observed
172 pattern is that "mixed-severity" fires have some
173 substantial (>20%) proportion of their area mapped
174 as contiguous stand-replacing patches, amongst a
175 matrix of low or moderate severity effects. It should
176 be noted that even in boreal and subalpine forest types
177 characterized by high severity fire regimes,

178 contemporary fires very rarely have more than 70%
179 of their area mapped as stand-replacing (Harvey et al.
180 2016).

181 These patterns suggest that a defining characteristic
182 of fire regimes is not whether average percentages of
183 overstory mortality within a fire fit in the commonly
184 used classes (<20, 20–70, >70%), but rather it is the
185 size and shape of contiguous stand-replacing patches.
186 To illustrate this, we examined two recent fires in the
187 northern Sierra Nevada (Fig. 1). The 2012 Chips Fire
188 in the Plumas National Forest burned with a modest
189 overall proportion of stand-replacing fire (22%). Note,
190 we used the "≥90% basal area change" threshold
191 described by Miller and Quayle (Miller and Quayle
192 2015), which is very similar to the high severity
193 threshold described by Miller and Thode (2007). Both
194 of these fire severity categories are consistent with
195 stand-replacing effects (Miller and Quayle 2015;
196 Lydersen et al. 2016). This proportion of stand-
197 replacing fire was very similar to the 2008 Cub
198 Complex Fire (20%), which occurred 10 km north-
199 west of the Chips Fire. The patterns of stand-replacing
200 patches, however, were distinct. Forty-three percent of
201 the stand-replacing area in the Chips Fire was
202 aggregated in contiguous patches that were larger
203 than 250 ha, while for the Cub Complex only 24% was
204 in the >250 ha class (Fig. 1). Furthermore, stand-
205 replacing area was relatively evenly distributed among
206 patch size classes for the Cub Complex, but heavily
207 skewed for the Chips Fire (Fig. 1).

208 The potential impact of these different distributions
209 of stand-replacing patch area on post-fire vegetation
210 dynamics is significant. Large, contiguous and
211 roundly-shaped patches of tree mortality have much
212 more "core" area, which is the amount of stand-
213 replacing area that remains greater than a given
214 distance in from the patch edge (Cansler and McKen-
215 zie 2014). Smaller or elongated patches, on the other
216 hand, have greater proportions of edge, and lesser
217 distances-to-patch edge. For the Chips Fire, 33% of
218 the stand-replacing patch area is >120 m from patch
219 edges, compared to 17% for the Cub Complex
220 (Figure S1). The significance of the 120 m threshold
221 is that it exceeds the likely distance of seed dispersal
222 for even the tallest mixed conifer trees in this area
223 (McDonald 1980; Clark et al. 1999). This means that a
224 considerable amount of the stand-replacing area in the
225 Chips Fire will likely be void of natural conifer
226 regeneration for an extended period of time (Collins
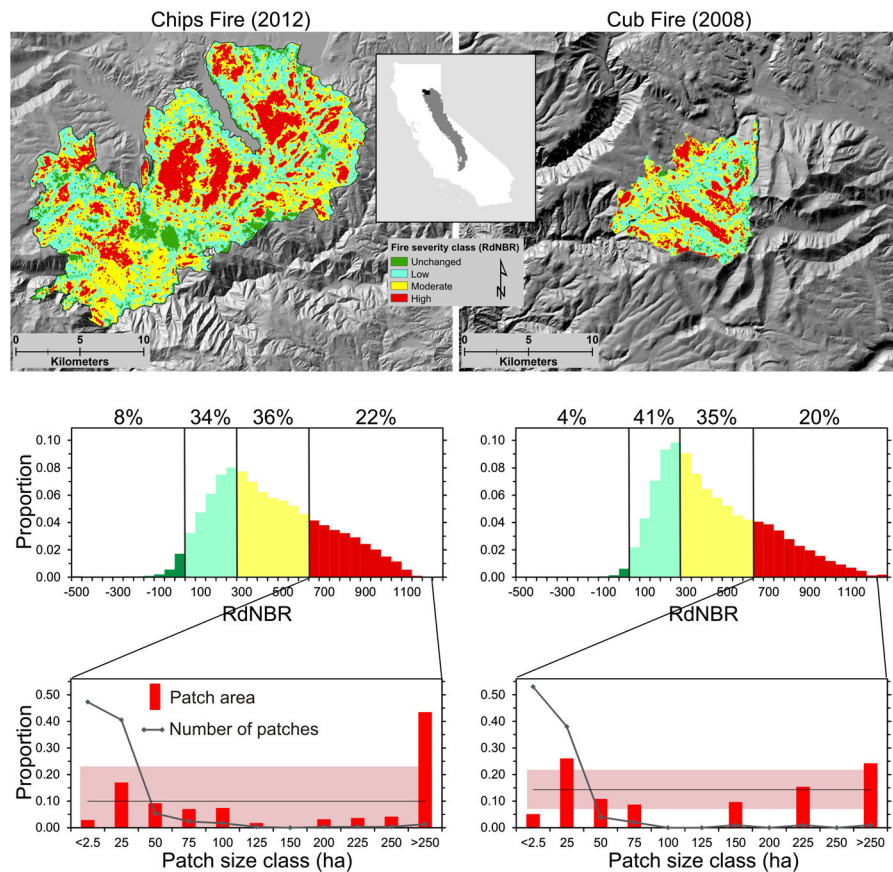
Fig. 1 Contrasting spatial patterns of fires that burned with "mixed" severity in the Sierra Nevada, USA (*top*). Fire severity classes are based on the relative differenced normalized burn ratio (RdNBR) using threshold values from Miller and Thode (2007). RdNBR histograms of all 30 m pixels within fire perimeters (*middle*) are colored by the same fire severity class thresholds, with total percentages for each class reported above. Distributions of both proportional stand-replacing patch area

and number of stand-replacing patches (*bottom*) pertain to the "high" severity class alone. Patches were delineated using the same methods described in Collins and Stephens (2010). *The shaded bands* in these distributions indicate the mean proportion (*horizontal gray line*) of total patch area ±1 SD. Means and standard deviations were calculated using all non-zero patch size class proportions

and Roller 2013). While these different patterns may be related to the disparity in overall fire sizes (Chips: 30,898 ha; Cub: 7940 ha), they emphasize the importance in not only examining overall proportions of stand-replacing effects, but also examining patch sizes and the distribution of area among patch size classes.

Alternate characterization of fire effects

Building on the ideas discussed previously, we sought to develop a more robust method for characterizing spatial distributions of stand-replacing patch area. Our intent was to derive a quantitative measure of these

distributions that did not rely on binning data into patch-size classes (Fig. 1) or distance-to-patch-edge classes (Fig. S1), to allow for robust comparisons between individual fires or sets of fires. We constructed a mathematical model to describe the relationship between stand-replacing patch area and distance from patch edge. Rather than simply plotting distributions of stand-replacing area by patch size class, we sought a more process-based characterization of these very different configurations. Given the importance of seed dispersal from live trees (outside of stand-replacing patches) in many conifer-dominated forests, we focused on distance-to-patch-edge as an important variable influencing post-fire vegetation

dynamics. The concept of "core patch area" is one approach that can address this. However, core patch area is a binary classification that depends on a single distance threshold. We extend this concept to describe the continuous relationship between the proportion of total stand-replacing patch area and an interior buffer distance applied to stand-replacing patches. The proportion of original stand-replacing area remaining within a given internal buffer distance is necessarily bounded between 1 and 0 inclusive, equaling 1 when the internal buffer distance is zero (as all the original patch area remains), and equaling 0 when the internal buffer distance is equal to the maximum distance to edge within the largest patch. This relationship can be approximated for multiple irregularly shaped patches by a modified logistic function:

$$P \sim \frac{1}{10^{SDC \times Dist}} \tag{1}$$

where P is the proportion of the total original stand-replacing area, $Dist$ is the internal buffer distance (m), and SDC a free parameter that describes the shape of the relationship which we call the *stand-replacing decay coefficient*. Larger values of SDC describe a more rapidly decaying proportional patch area, while smaller values of SDC describe more slowly decaying proportional patch area.

AQ1 To illustrate this relationship, we generated four hypothetical scenarios of stand-replacing patches with identical areas and proportions of the landscape (Fig. 2a–d). Each scenario had 1000 ha of area in stand-replacing patches, but scenario A had 1024 circular patches of 0.98 ha each, scenario B had 100 patches of 10 ha each, scenario C had 9 patches of 111.11 ha each, and scenario D had 1 patch of 1000 ha. We buffered each patch internally in 10-m increments and recalculated P at each interval, and then estimated SDC for each scenario using non-linear least squares estimation in R. The fitted values of SDC were 0.0219, 0.0068, 0.0020, and 0.0006 for scenarios A–D, respectively. This translates to predictions of the original stand-replacing area greater than 120 m from the patch edge of <0.01, 15, 58 and 85% for scenarios A-D, respectively. SDC does not capture the complete loss of stand-replacing area with a large enough distance because the modified logistic function does not go to zero, but it is a very good approximation of the rate of loss of stand-replacing area with increasing distance from edge, which is the value of ecological

importance. In addition, SDC appears to distinguish among the configurations with intermediate sized patches (Fig. 2b, c), with corresponding intermediate SDC values (Fig. 2e). The interpretation of these different distributions is that flatter curves depict greater proportions of stand-replacing area at larger distances from "green" forest edge. A similar example varying patch shape from elongated to round would display a similar difference in distributions, where rounder shapes or simpler patch edges that have larger distances to forest edge would have flatter curves than would more elongated patches or patches with more complex edges (Fig. 3).

We applied this approach to two actual wildfires. Because of the potential influence of total fire size on stand-replacing proportion and patch sizes (Cansler and McKenzie 2014) we chose a pair of similarly sized fires (~5000 ha) to compare stand-replacing area at different distances to patch edge. These fires, the 1987 East Fire and the 2008 Caribou Fire, occurred in the Klamath region of northwestern California, and had similar proportions of stand-replacing area (~20%—Fig. 4a, b). Unlike our hypothetical fires (Figs. 2, 3) both of these fires exhibited a range of patch sizes and shapes, so it was uncertain how well the univariate decay function would capture actual patterns of stand-replacing patches. Plots of both observed and fitted (using Eq. 1) stand-replacing proportions as a function of interior distance were quite consistent (Fig. 4c), suggesting this decay function could be applied to actual fires. The two example fires had noticeably different decay curves, with the East Fire having a much longer and flatter shape (Fig. 4c). This shape reflects the disproportionate amount of area in large stand-replacing patches observed for the East Fire (Fig. 4a) relative to the Caribou Fire (Fig. 4b). In the absence of post-fire vegetation management these two fires would be expected to have noticeably different landscape vegetation recovery and successional patterns, i.e., more coarse-grained or homogenous patterns for the East Fire. This reduction in fine-scale heterogeneity can significantly simplify post-burn conditions, reducing microclimate, habitat, and species diversity (Stevens et al. 2015). It may also entrench alternate disturbance patterns as large stand-replacing burn patches, which can develop into relatively continuous "fuelbeds" of woody shrubs interspersed with heavy concentrations dead wood, are

Fig. 2 Four hypothetical stand-replacing patch configurations for the same total fire area (3600 ha) and stand-replacing area (1000 ha or 28% of total fire area). Patch sizes were ~1 ha (**a**), 10 ha (**b**), ~111 ha (**c**) and 1000 ha (**d**). Panel **e** illustrates how stand-replacing area in these different configurations is distributed as a function of patch interior buffer distance, i.e., moving further towards the interior of patches. *Points* indicate observed proportions for a given distance, while solid lines are the proportions predicted by Eq. 1 fit to the point data. The stand-replacing decay coefficient (SDC) is reported for each configuration
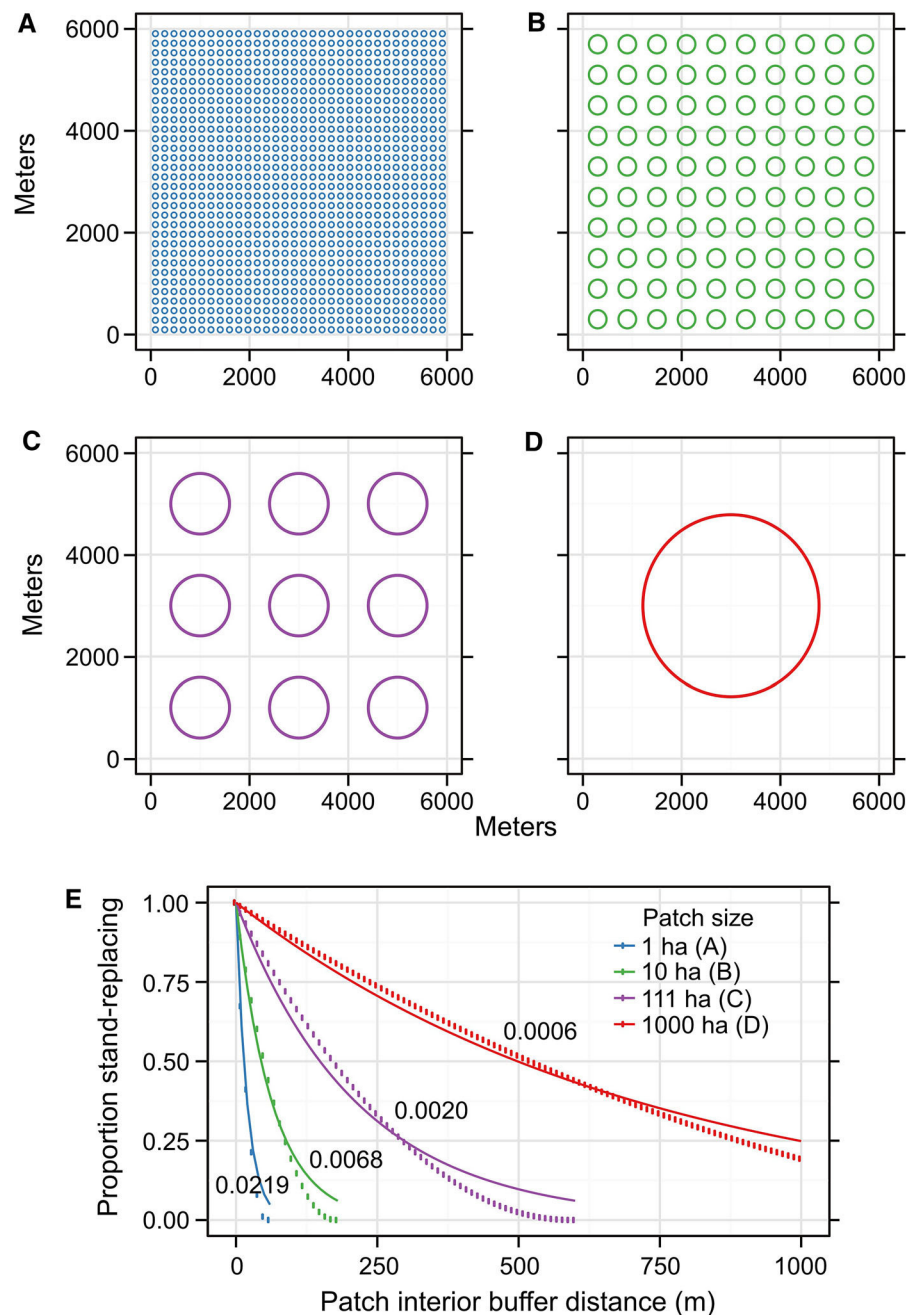
prone to re-burn at high severity when wildfire returns (Coppoletta et al. 2016).

Applications of this approach

To further investigate the applicability of this new metric, we calculated the SDC for 477 fires that burned in California between 1984 and 2015. This included most California fires >80 ha with mapped fire severity that were predominantly forested, regardless of the managing agency. The resulting values of SDC were approximately normally distributed after a log transformation (Fig. 5a), which appears to clearly distinguish the few select fires that have extremely small SDCs and thus a higher proportion of their stand-

Fig. 3 Three hypothetical stand-replacing patch shapes for the same total fire area (3600 ha) and stand-replacing area (1000 ha or 28% of total fire area): *circle* (**a**), ellipse (**b**), and irregular ellipse (**c**). Panel (**d**) illustrates how stand-replacing area in these different configurations is distributed as a function of patch interior buffer distance. *Points* indicate observed proportions for a given distance, while *solid lines* are the proportions predicted by Eq. 1 fit to the point data. The stand-replacing decay coefficient (SDC) is reported for each configuration
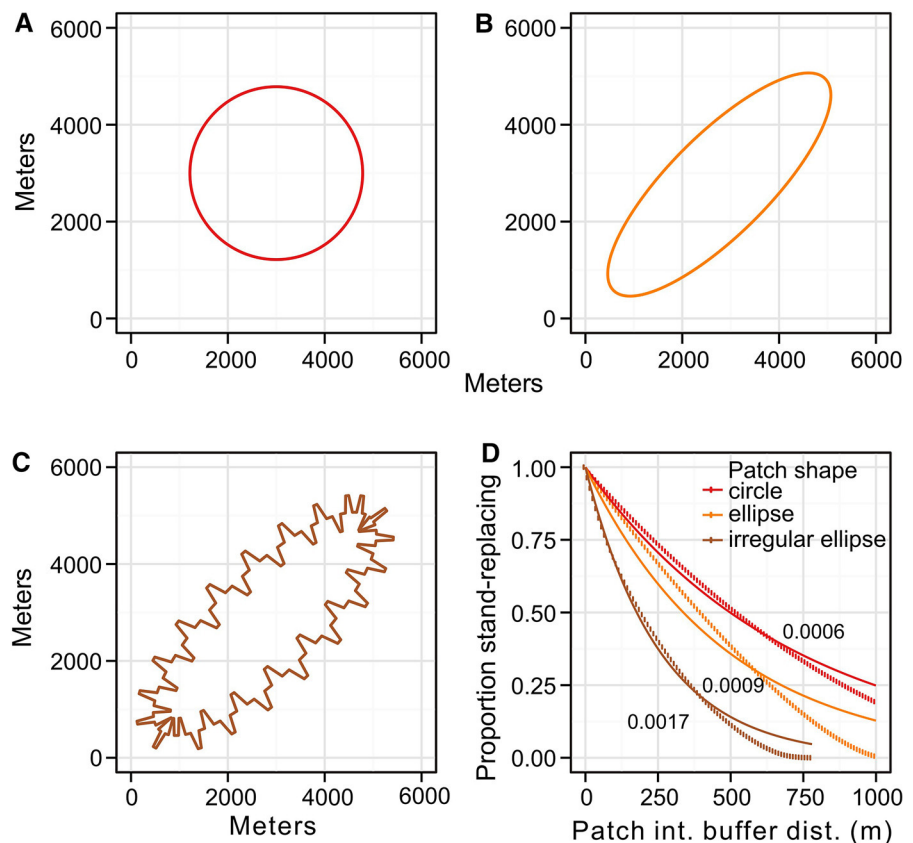

replacing area far from the nearest patch edge. Not surprisingly, fires that are larger and have a higher proportion of stand-replacing effects tend to have smaller SDCs (Fig. 5b, c). It is possible to interpret this inverse relationship between fire size/percent stand-replacing and SDC as simple scale dependence in the SDC metric (Wu et al. 2002). However, the fact that both of these variables tend to be positively associated with stand-replacing patch size (Miller et al. 2009; Harvey et al. 2016) suggests that SDC is capturing a real phenomenon (distance to edge) that is affected by the scale of stand-replacing effects and is not an artifact of scale dependence. For any given fire size or percent stand-replacing area, there are still a wide range of potential SDC values. This illustrates potentially profound ecological differences among "mixed-severity" fires that might otherwise be considered very similar if just percent stand-replacing were used as the relevant variable. Thus, SDC may be a reasonable integration of both of these variables, but it also contains additional information that is highly relevant to quantifying fire effects in many conifer-

dominated forest ecosystems (e.g., distance to seed source).

To investigate the relationship between SDC and other spatial statistics, we calculated two metrics of patch complexity typically used in the FRAGSTATS software package (McGarigal et al. 2002). Specifically, we calculated the area-weighted mean shape index (AWMSI; essentially the perimeter-to-area ratio weighted towards larger patches) and the area-weighted mean patch fractal dimension (AWMPFD). These two metrics provide information on patch complexity, while remaining fairly insensitive to the spatial grain or extent of the landscape (Wu et al. 2002). We found a correlation between SDC and AWMSI (on a log scale), but not between SDC and AWMPFD (Fig. S2). However, the relationship between SDC and AWMSI is less consistent for more simply shaped patches (lower AWMSI); for instance, two fires with a similar ln(AWMSI) of −4.6 can have quite different SDC values, such as ln(SDC) = −5.28 for the 2008 Venture fire and ln(SDC) = −6.19 for the 2015 Castle fire (Fig. S2). This small difference in

Fig. 4 Stand-replacing area for two example wildfires that occurred in the Klamath region, northwestern California, USA (**a**, **b**). Both fires have similar total area (4643 and 5319 ha) and stand-replacing proportions (20%), but different spatial distribution of stand-replacing area. These different patterns are captured by the plots showing how stand-replacing area is distributed as a function of interior buffer distance (**c**). *Points* indicate observed proportions for a given distance, while *solid lines* are the proportions predicted by Eq. 1 fit to the point data. The stand-replacing decay coefficient (SDC) is reported for each fire
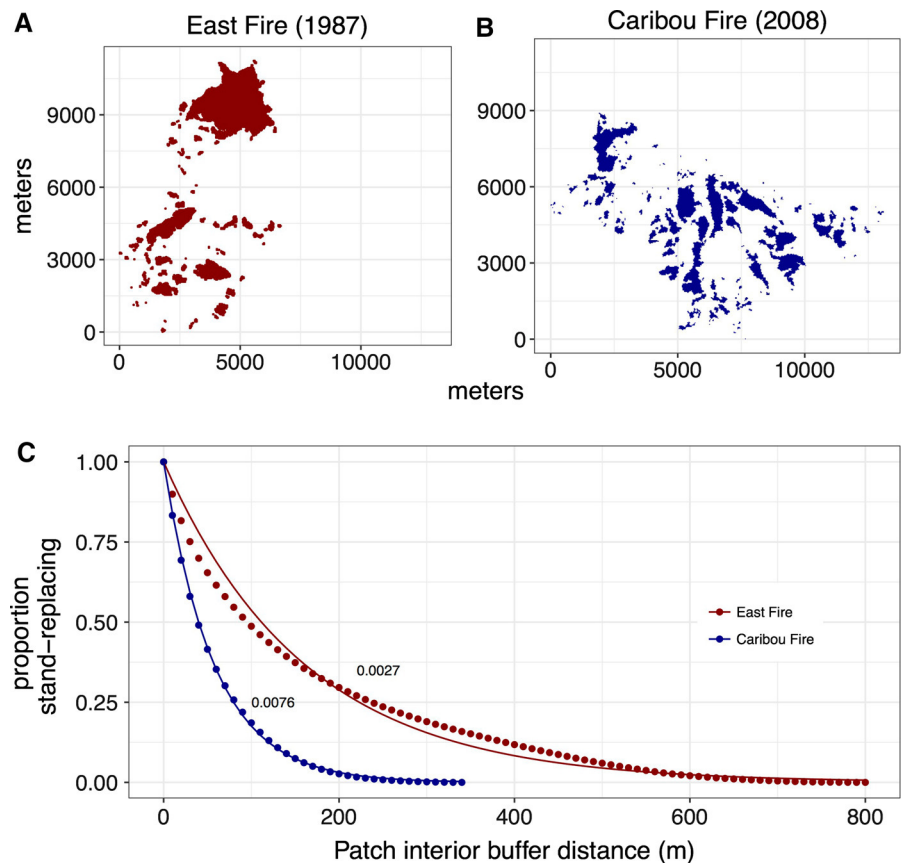
Fig. 5 Distribution of the natural logarithm of the stand-replacing decay coefficient (lnSDC) estimated for 477 fires in California between 1984 and 2015 (**a**). Plots of SDC as a function of the log of the fire size (**b**) and percent stand-replacing (**c**) are also shown. The four colored lines correspond to the colors and patch configurations in Fig. 2. *Smaller values* of lnSDC indicate fires with much of their stand-replacing area far from the patch edge
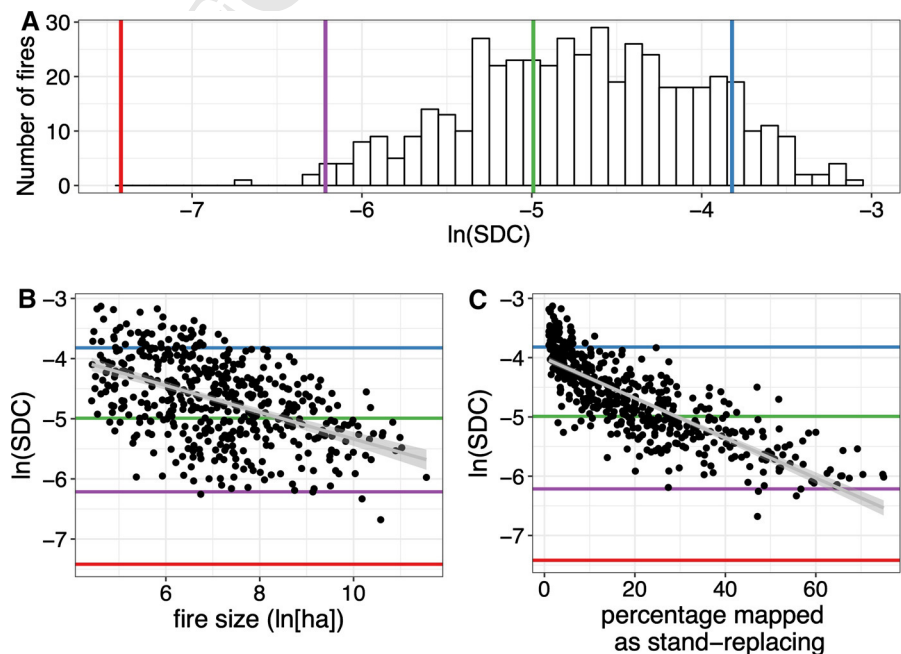
SDC ($\sim$ 0.005 vs. 0.002) is equivalent to the difference between a fire with approximately 20 ha circular stand-replacing patches and a fire with approximately 100 ha circular stand-replacing patches (Fig. 2). Thus, although there is some overlap between SDC and existing patch complexity metrics, SDC appears to better differentiate ecologically relevant patterns of fire severity as they relate to tree regeneration following stand-replacing fire.

Our approach of plotting stand-replacing proportions as a function of interior distance offers a relatively simple way to capture complex patterns of fire effects. The decay curves and associated SDC can be calculated for individual fires and summarized for multiple fires over a given area. This allows for meaningful quantitative comparisons between individual fires and among regions. Furthermore, patterns of individual fires or aggregations of fires can be assessed relative to desired land management outcomes. For example, if management objectives call for establishment of some proportion (say 10%) of stand-replacing area to be maintained in a longer-term early seral condition, then a SDC of 0.0083 could be used as a target threshold (based upon a 120 m distance from the edge of high severity patches that estimates the distance to the nearest seed source). Given the ecological importance of mapping and quantifying stand-replacing patches, it is imperative to use appropriate thresholds (e.g., >95% basal area mortality) for classifying burn severity imagery that are based on empirical data. Although methods for mapping and classifying burn severity using remotely sensed imagery are imperfect, high severity fire effects clearly have the lowest misclassification rate (Miller and Quayle 2015) and the smallest range in actual tree mortality (Lydersen et al. 2016). Establishing robust thresholds in regions that currently do not have them should be a high priority.

While we have focused on western US conifer forests, our approach may have broader application to other forest types. An important ecological effect of fires on forest succession is the amount of burn area that is beyond the seed dispersal distance of the nearest tree survivors. This distance will vary with tree species and dispersal mechanisms, and is information that can be used to set the relevant buffer distance (i.e., D in Eq. 1), adapting the SDC calculation to different forest types. Large stand-replacing patches may take much longer to restore mature forest conditions and

against a background of changing climate, may be more prone to vegetation community shifts. Such abrupt shifts were likely rare in forests historically associated with frequent fire. The size and shape of high-severity patches should be considered when measuring fire effects because they can have significant long-term effects on vegetation succession and ecosystem resilience.

References

Agee JK (1993) Fire ecology of Pacific Northwest forests. Island Press, Washington DC

Agee JK (1998) The landscape ecology of Western forest fire regimes. Northwest Sci 72:24–34

Brown PM, Wienk CL, Symstad AJ (2008) Fire and forest history at Mount Rushmore. Ecol Appl 18:1984–1999

Cansler CA, McKenzie D (2014) Climate, fire size, and biophysical setting control fire severity and spatial pattern in the northern Cascade Range, USA. Ecol Appl 24:1037–1056

Chambers ME, Fornwalt PJ, Malone SL, Battaglia MA (2016) Patterns of conifer regeneration following high severity wildfire in ponderosa pine—dominated forests of the Colorado Front Range. For Ecol Manag 378:57–67

Clark JS, Silman M, Kern R, Macklin E, HilleRisLambers J (1999) Seed dispersal near and far: patterns across temperate and tropical forests. Ecology 80:1475–1494

Collins BM, Roller GB (2013) Early forest dynamics in stand-replacing fire patches in the northern Sierra Nevada, California, USA. Landscape Ecol 28:1801–1813

Coppoletta M, Merriam KE, Collins BM (2016) Post-fire vegetation and fuel development influences fire severity patterns in reburns. Ecol Appl 26:686–699

Fulé PZ, Covington WW, Moore MM (1997) Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. Ecol Appl 7:895–908

Harvey BJ, Donato DC, Turner MG (2016) Drivers and trends in landscape patterns of stand-replacing fire in forests of the US Northern Rocky Mountains (1984–2010). Landscape Ecol 31(10):2367–2383

Hessburg PF, Spies TA, Perry DA, Skinner CN, Taylor AH, Brown PM, Stephens SL, Larson AJ, Churchill DJ, Povak NA, Singleton PH, McComb B, Zielinski WJ, Collins BM, Salter RB, Keane JJ, Franklin JF, Riegel G (2016) Tamm review: management of mixed-severity fire regime forests in Oregon, Washington, and Northern California. For Ecol Manag 366:221–250

507 Kemp KB, Higuera PE, Morgan P (2016) Fire legacies impact
508   conifer regeneration across environmental gradients in the
509   U.S. northern Rockies. Landscape Ecol 31:619–636
510 Lydersen JM, Collins BM, Miller JD, Fry DL, Stephens SL
511   (2016) Relating fire-caused change in forest structure to
512   remotely sensed estimates of fire severity. Fire Ecol
513   12:99–116
514 McDonald PM (1980) Seed dissemination in small clearcuttings
515   in north-central California. General Technical Report
516   PSW-150. U.S. Department of Agriculture, Forest Service,
517   Pacific Southwest Forest and Range Experiment Station,
518   Berkeley, CA, USA, p 5
519 McGarigal K, Cushman SA, Neel MC, Ene E (2002) FRAG-
520   STATS v3: spatial pattern analysis program for categorical
521   and continuous maps. University of Massachusetts,
522   Amherst
523 Miller JD, Quayle B (2015) Calibration and validation of
524   immediate post-fire satellite derived data to three severity
525   metrics. Fire Ecol 11:12–30
526 Miller JD, Thode AE (2007) Quantifying burn severity in a
527   heterogeneous landscape with a relative version of the delta
528   Normalized Burn Ratio (dNBR). Remote Sens Environ
529   109:66–80
530 Miller JD, Safford HD, Crimmins M, Thode AE (2009) Quan-
531   titative evidence for increasing forest fire severity in the
532   Sierra Nevada and southern Cascade Mountains, California
533   and Nevada, USA. Ecosystems 12:16–32
534 Miller JD, Collins BM, Lutz JA, Stephens SL, van Wagtendonk
535   JW, Yasuda DA (2012) Differences in wildfires among
536   ecoregions and land management agencies in the Sierra
537   Nevada region, California, USA. Ecosphere 3:80
538 Odion DC, Hanson CT, Arsenault A, Baker WL, DellaSala DA,
539   Hutto RL, Klenner W, Moritz MA, Sherriff RL, Veblen
540   TT, Williams MA (2014) Examining historical and current
541   mixed-severity fire regimes in ponderosa pine and mixed-

542 conifer forests of western North America. PLoS ONE
543   9:e87852
544 Perry DA, Hessburg PF, Skinner CN, Spies TA, Stephens SL,
545   Taylor AH, Franklin JF, McComb B, Riegel G (2011) The
546   ecology of mixed severity fire regimes in Washington,
547   Oregon, and Northern California. For Ecol Manag
548   262:703–717
549 Schoennagel T, Veblen TT, Romme WH (2004) The interaction
550   of fire, fuels, and climate across Rocky Mountain forests.
551   Bioscience 54:661–676
552 Stevens JT, Safford HD, Harrison S, Latimer AM (2015) Forest
553   disturbance accelerates thermophilization of understory
554   plant communities. J Ecology 103:1253–1263
555 Swanson ME, Franklin JF, Beschta RL, Crisafulli CM, Dellasala
556   DA, Hutto RL, Lindenmayer DB, Swanson FJ (2011) The
557   forgotten stage of forest succession: early-successional
558   ecosystems on forest sites. Front Ecol Environ 9:117–125
559 Swetnam TW, Allen CD, Betancourt JL (1999) Applied his-
560   torical ecology: using the past to manage for the future.
561   Ecol Appl 9:1189–1206
562 Taylor AH (2004) Identifying forest reference conditions on
563   early cut-over lands, Lake Tahoe Basin, USA. Ecol Appl
564   14:1903–1920
565 Turner MG, Romme WH, Gardner RH, Hargrove WW (1997)
566   Effects of fire size and pattern on early succession in
567   Yellowstone National Park. Ecol Monogr 67:411–433
568 van Wagtendonk JW (2006) Fire as a physical process. In:
569   Sugihara NG, van Wagtendonk JW, Shaffer KE, Fites-
570   Kaufman JA, Thode AE (eds) Fire in California's ecosys-
571   tems. University of California Press, Berkeley, pp 38–57
572 Wu J, Shen W, Sun W, Tueller PT (2002) Empirical patterns of
573   the effects of changing scale on landscape metrics. Land-
574   scape Ecol 17:761–782

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