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Drivers and trends in landscape patterns of stand-replacing fire in forests of the US Northern Rocky Mountains (1984–2010)

Brian J. Harvey · Daniel C. Donato · Monica G. Turner

Abstract

Context Resilience in fire-prone forests is strongly affected by landscape burn-severity patterns, in part by governing propagule availability around stand-replacing patches in which all or most vegetation is killed. However, little is known about drivers of landscape patterns of stand-replacing fire, or whether such patterns are changing during an era of increased wildfire activity.

Objectives (a) Identify key direct/indirect drivers of landscape patterns of stand-replacing fire (e.g., size, shape of patches), (b) test for temporal trends in these patterns, and (c) anticipate thresholds beyond which landscape patterns of burn severity may change fundamentally.

Methods We applied structural equation modeling to satellite burn-severity maps of fires in the US Northern Rocky Mountains (1984–2010) to test for direct and indirect (via influence on fire size and proportion stand-replacing) effects of climate/weather, vegetation, and topography on landscape patterns of stand-replacing fire. We also tested for temporal trends in landscape patterns.

Results Landscape patterns of stand-replacing fire were strongly controlled by fire size and proportion stand-replacing, which were, in turn, controlled by climate/weather and vegetation/topography, respectively. From 1984 to 2010, the proportion of stand-replacing fire within burn perimeters increased from 0.22 to 0.27. Trends for other landscape metrics were not significant, but may respond to further increases proportion stand-replacing fire.

Conclusions Fires from 1984 to 2010 exhibited tremendous heterogeneity in landscape patterns of stand-replacing fire, likely promoting resilience in burned areas. If trends continue on the current trajectory, however, fires may produce larger and simpler shaped patches of stand-replacing fire with more burned area far from seed sources.

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Introduction

Fire is the dominant natural disturbance in many coniferous forests worldwide (Attiwill 1994), where biota are adapted to a characteristic fire regime [frequency, size, and magnitude/severity of fires (Pickett and White 1985; Turner et al. 1998)]. Increased wildfire activity over the last several decades in temperate and boreal regions (Flannigan et al. 2009) has led to heightened concern that forest resilience [the capacity to tolerate disturbance without shifting to a qualitatively different ecosystem state (Walker et al. 2004)] may be compromised by climate-driven changes to historical fire regimes (Gauthier et al. 2015; Millar and Stephenson 2015; Trumbore et al. 2015). Western US coniferous forests, for example, have experienced a steady rise in the annual area burned and number of large wildfires (Westerling et al. 2006; Morgan et al. 2008; Littell et al. 2009; Dennison et al. 2014), and regionally variable increases in burn severity [(the degree of ecological change caused by fire, typically measured by the amount of vegetation killed by fire (Keeley 2009)] (e.g., Miller et al. 2009; Dillon et al. 2011).

In addition to the frequency, size, and severity of wildfires, a key mechanism of ecological resilience in fire-prone forests is the spatial, or landscape, pattern of burn severity within a fire perimeter. The mosaic of severely burned, lightly burned, and unburned forest patches sets the trajectory of succession (Turner et al. 1994, 1997), ultimately driving the configuration of forest structure (Romme 1982), carbon storage (Turner et al. 2004; Kashian et al. 2006; Meigs et al. 2011), and wildlife habitat (Boyce et al. 2003) for decades to centuries. This mosaic is particularly important around patches that burn as stand-replacing fire, where severe fire kills most or all pre-fire vegetation. In such areas, the size, shape, and spatial arrangement of stand-replacing patches determine key landscape features such as the distance to seed sources, which in turn controls the rate of vegetation recolonization and tree re-establishment (Donato et al. 2009; Kemp et al. 2015; Harvey et al. 2016). The importance of heterogeneity and spatial pattern is well established in disturbance ecology (Schoennagel et al. 2008; Turner et al. 2013); however significant gaps remain in understanding what determines landscape patterns of burn severity, or whether landscape patterns of stand-replacing fire are changing as wildfire activity increases.

If landscape patterns of stand-replacing fire are controlled by the same factors that drive fire occurrence and size, these patterns may also be expected to change over a period of increasing fire activity. Such a change would likely result in burned landscapes that are characterized by larger, simpler shaped (e.g., lower edge to area ratio) patches of stand-replacing fire. In general, wildfire occurrence and size are controlled by three primary factors: climate/weather, vegetation, and topography. Climate conditions affect the flammability of vegetation, and together with weather during a fire, control whether an ignition will result in the initiation and spread of fire. Thus, climate and weather are key drivers of fire occurrence and fire size (Westerling et al. 2006; Littell et al. 2009; Dennison et al. 2014). Vegetation (living and dead) provides fuel needed for ignition, and can further constrain or promote fire spread and size via amount, configuration, and connectivity (e.g., Rollins et al. 2002; Falk et al. 2007). Topography can impose constraints on fire spread in topographically complex landscapes, whereas relatively smooth topographic surfaces over large extents can facilitate fire spread (e.g., Rollins et al. 2002; Falk et al. 2007). In addition to fire size/occurrence, studies have assessed effects of these key drivers on burn severity at fine scales (i.e., plot or image pixel) using data from satellites (e.g., Holden et al. 2009; Miller et al. 2009; Dillon et al. 2011; Wu et al. 2013; Prichard and Kennedy 2014) or field measurements (e.g., Harvey et al. 2013; Andrus et al. 2016). However, little is known about how, or if, these drivers affect landscape patterns of stand-replacing fire within the perimeter of a fire.

Landscape patterns of stand-replacing fire may respond to climate/weather, vegetation, and topography directly and in ways similar to other measures of fire activity. Alternatively, landscape patterns should also be influenced by fire size and proportion of stand-replacing fire, with configuration metrics (e.g., patch size and core area) possibly exhibiting threshold-like behavior once critical proportions associated with spatial connectivity are reached (Gardner et al. 1987; Gustafson and Parker 1992). Theoretical studies using simulated landscapes have identified thresholds in proportion occupied (termed P_{crit}) that mark sharp discontinuities in configuration metrics, but such thresholds have not been evaluated using empirical data on wildfire burn-severity patterns. Improved understanding of the mechanisms that control spatial

patterns of burn severity requires tracking metrics over space and time, and testing direct and indirect relationships between landscape patterns and potential drivers.

In this study, we examined drivers and trends in landscape patterns of stand-replacing fire in the US Northern Rocky Mountains, a large fire-prone forested ecoregion with recent increases in fire activity (Morgan et al. 2008; Dennison et al. 2014). Like many other temperate and boreal coniferous forest regions worldwide, fire activity is projected to increase in the future (Westerling et al. 2011; Moritz et al. 2012; Flannigan et al. 2013). Using a field-validated burn-severity atlas (Harvey 2015) and existing geospatial datasets for other biophysical variables, we asked the following questions: (1) What are the dominant controls of landscape patterns of stand-replacing fire? (2) Have landscape patterns of stand-replacing fire changed from 1984 to 2010? Using results from these two questions, we also explore where thresholds in landscape patterns of burn severity (e.g., P_{crit}) may be crossed in the future, given current trends. We expected landscape patterns of stand-replacing fire to be strongly controlled by fire size and proportion stand-replacing fire, which in turn, are controlled by a combination of climate/weather, vegetation, and topography (Schoennagel et al. 2004). As such, we expected landscape patterns of stand-replacing fire to change over time, characterized by an increase in the proportion, average patch size, and amount of core area of stand-replacing fire, and by a decrease in shape complexity (edge-to-area ratio) of stand-replacing burn patches.

Methods

Study area

Our study area was the Northern Rockies ecoregion, encompassing EPA level III ecoregions 15, 16, 17, and 41, stretching from northwestern Wyoming to northeastern Washington through eastern Idaho and western Montana (Fig. 1). The ecoregion is over 30 million hectares (ha), of which 22,400,343 ha (74 %) is forest or woodland. Subalpine forests occupy the highest elevations (∼1500 to 3000 m) and are dominated by subalpine fir (*Abies lasiocarpa*), Engelmann spruce

(*Picea engelmannii*), lodgepole pine (*Pinus contorta* var. *latifolia*), and whitebark pine (*Pinus albicaulis*). Subalpine forests account for 45 % of the total forested area in the ecoregion (Appendix of ESM), and are characterized by infrequent, high-severity wildfires (Schoennagel et al. 2004; Baker 2009). Mid-montane forests are situated at intermediate elevations (∼750 to 2500 m) and are dominated by Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), western larch (*Larix occidentalis*), ponderosa pine (*Pinus ponderosa*), limber pine (*Pinus flexilis*), and quaking aspen (*Populus tremuloides*). Mid-montane forests account for 53 % of the total forested area in the ecoregion (Appendix 1), and the historical fire regime is mixed severity (Schoennagel et al. 2004; Baker 2009). Low-montane woodlands (∼500 to 1500 m elevation) are dominated by ponderosa pine, limber pine, and western juniper (*Juniperus occidentalis*), account for 3 % of the total forested area in the ecoregion (Appendix 1 of ESM), and are typified by a high-frequency and low-severity fire regime (Schoennagel et al. 2004; Baker 2009).

Burn severity data and metrics of landscape patterns of stand-replacing fire

Satellite burn-severity data at 30-m resolution were acquired from the Monitoring Trends in Burn Severity database (Eidenshink et al. 2007; www.mtbs.gov) for all fires that occurred between 1984 and 2010 and had a perimeter within (or at least intersected) the boundary of the study area (Fig. 1). Fires were retained for analysis if they met the following conditions: >50 % of the area within the fire perimeter was forest/woodland vegetation; fire size was ≥250 ha; and the fire was not a prescribed fire. Fires were excluded from the study if either the pre- or post-fire satellite image was obstructed by the scanner line correction (SLC) failure on the Landsat 7 satellite, as spatial pattern analysis is not possible with large swaths of missing data. After excluding 68 fires based on these criteria, the final dataset contained 668 fires, encompassing 3,366,328 ha. The Relative differenced Normalized Burn Ratio (RdNBR) was used as the measure of burn severity; RdNBR accounts for differences in pre-fire vegetation biomass among locations and is therefore best suited for regional studies across different forest types (Miller and Thode 2007;
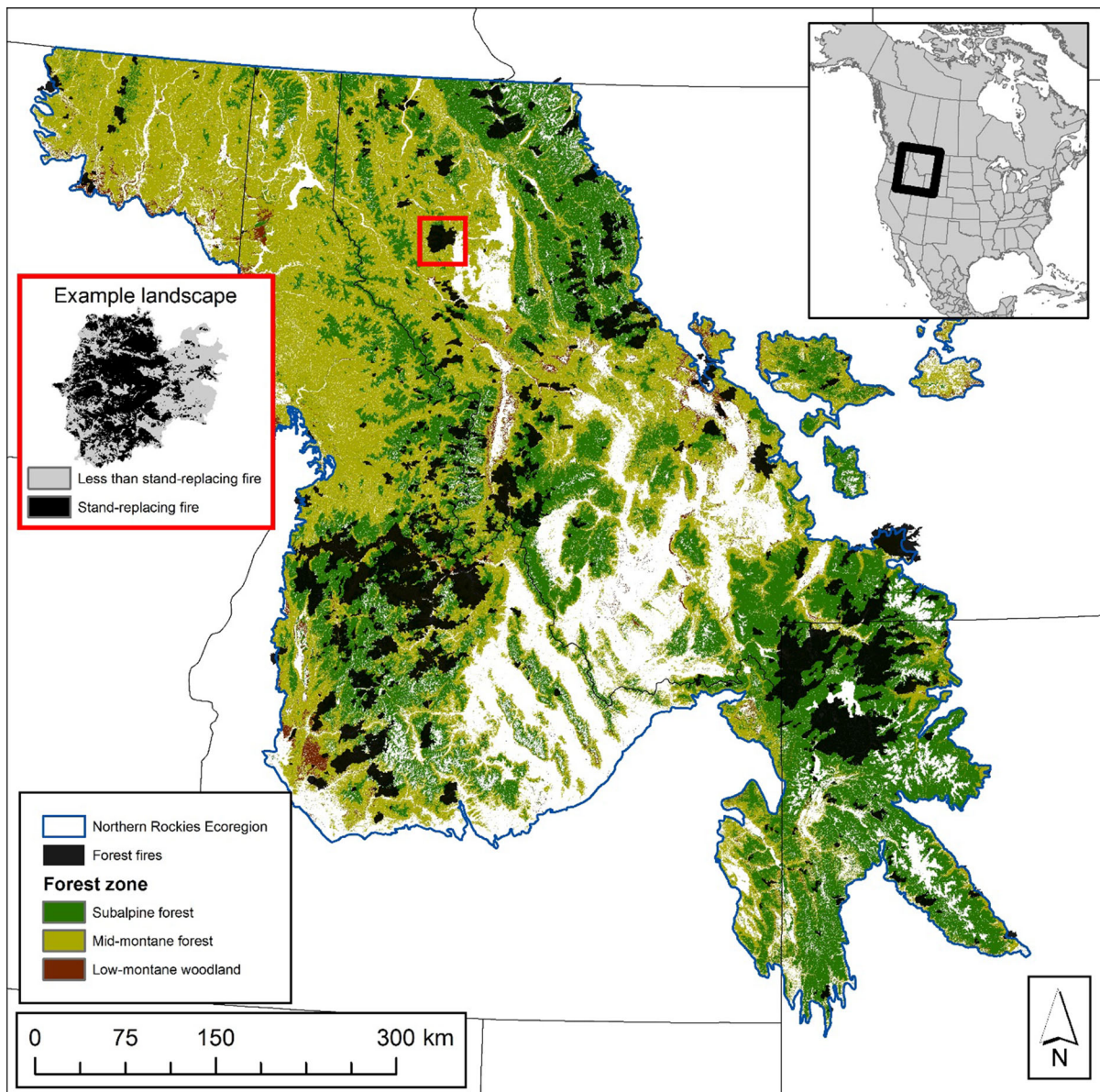
Fig. 1 Northern Rockies study area with all forest fires that were included in this study. *Right inset* shows regional location in North America. *Left inset* shows one example burned landscape (out of 688 total) with two classes: less than stand-replacing fire and stand-replacing fire

Dillon et al. 2011; Cansler and McKenzie 2012). By comparing differences between the near- and mid-infrared reflectance values in pre and post-fire Landsat satellite images, RdNBR represents a continuous index of burn severity across an entire burned landscape; higher RdNBR values equate to greater burn severity.

Using statistical relationships between RdNBR and field measurements of fire-caused tree mortality from 371 plots distributed throughout the Northern Rockies (Harvey 2015), each RdNBR burn-severity map was reclassified into two classes: stand-replacing fire, and less than stand-replacing fire. Stand-replacing fire was defined as 90–95 % (midpoint 92.5 %) of pre-fire live

tree basal area killed by fire. After reclassifying each burn-severity map, a 3×3 majority filter was applied to minimize the influence of single-pixel patches.

Four metrics were used to characterize landscape patterns of stand-replacing fire in each burned landscape (a landscape was considered to be the area encompassed by the burn perimeter of each fire, $n = 668$). First, we calculated the proportion within each fire perimeter that was stand-replacing. Second, we calculated the area-weighted mean patch size and edge-to-area ratio for stand-replacing burn patches, measuring patch size and shape, respectively. Area-weighted means were chosen over arithmetic means because area-weighted means more accurately represent the 'average' location in a landscape by weighting larger patches more, as a randomly selected location in a landscape has a greater probability of coming from a large patch. Finally, we calculated total core area (defined as locations within stand-replacing burn patches that were ≥ 150 m from the patch edge). This distance was selected because it exceeds the probable dispersal distance for ~ 90 % of seed from most wind-dispersed conifers in the Northern Rockies (Greene and Johnson 1996). Fire size, although not a focal response variable in our analyses, was needed in our analysis (see below); therefore the total size of each fire (in ha) was also recorded as an intermediate variable for each fire, or burned landscape. Spatial pattern metrics were calculated in FRAGSTATS v4 (McGarigal et al. 2012). All patches were defined using the 8-neighbor rule (McGarigal et al. 2012).

Predictor variables

Because analyses were conducted at the sampling unit of each individual fire, values of predictor variables were averaged for the area within each fire perimeter (i.e., burned landscape). Climate and weather data for each fire were assigned using a 12×12 km gridded hydro-climatic dataset for the region (Westerling et al. 2011). To represent the climate conditions leading up to each fire, we used cumulative moisture deficit (potential evapotranspiration–actual evapotranspiration, mm) for the water year (Oct.–Sept.) up to the month when the fire started. For weather conditions during each fire, we used the moisture deficit (mm) for the month(s) when the fire was burning. Moisture deficit is an effective predictor of fire characteristics because it integrates temperature and precipitation, and correlates positively with area burned

(Westerling et al. 2011; Abatzoglou and Kolden 2013) and pixel-scale burn severity (Dillon et al. 2011) in the N. Rockies. Preliminary analyses also indicated that moisture deficit was more strongly correlated with response variables than other hydroclimatic variables (e.g., temperature, precipitation, snow water equivalent). Climate and weather values for each fire were assigned by extracting the area-weighted mean for all (or portions of) grid cells within the fire perimeter, and assigning that single value of each variable to the fire. Values were then normalized to departures from average conditions for each fire location by rescaling raw values to $\pm$SD from mean values between 1981 and 2010.

For vegetation, each fire was assigned a forest zone based on the forest type (subalpine forest, montane forest, low-montane woodland, Appendix of ESM) that comprised the greatest area within the fire perimeter. Forest zone data were obtained at 30-m resolution, using the environmental site potential (ESP) mapped by the LANDFIRE vegetation mapping project (Rollins 2009), which uses consistent mapping techniques across land ownership boundaries. Similar to other studies (e.g., Dillon et al. 2011), we used ESP instead of data on existing vegetation, because ESP represents the vegetation that a site is capable of supporting based on physical conditions (e.g., climate and substrate). Alternatively, existing-vegetation data are often recorded at a single point in time and could be affected by prior disturbance (e.g., displaying early seral forests as non-forest vegetation), therefore confounding analyses. Topographic complexity for each fire was assigned by calculating a topographic roughness index of the area within the fire perimeter, which is the ratio of the total surface area to the flat planar area within the perimeter of a fire; higher values indicate greater topographic complexity (Jenness 2004). Topographic data were obtained from 30-m resolution (1 arc second) digital elevation models downloaded from the USGS National Elevation Dataset (http://seamless.usgs.gov). Mean elevation of each fire was not used because it was strongly correlated, and therefore redundant with, forest zone. The effect of elevation on vegetation also varies by latitude; subalpine forests can range from as low as ~ 1500 m at the northern end of our study region to as high as ~ 3000 m at the southern end. In sum, using elevation as a proxy for vegetation and climate was not needed because we already included these variables directly.
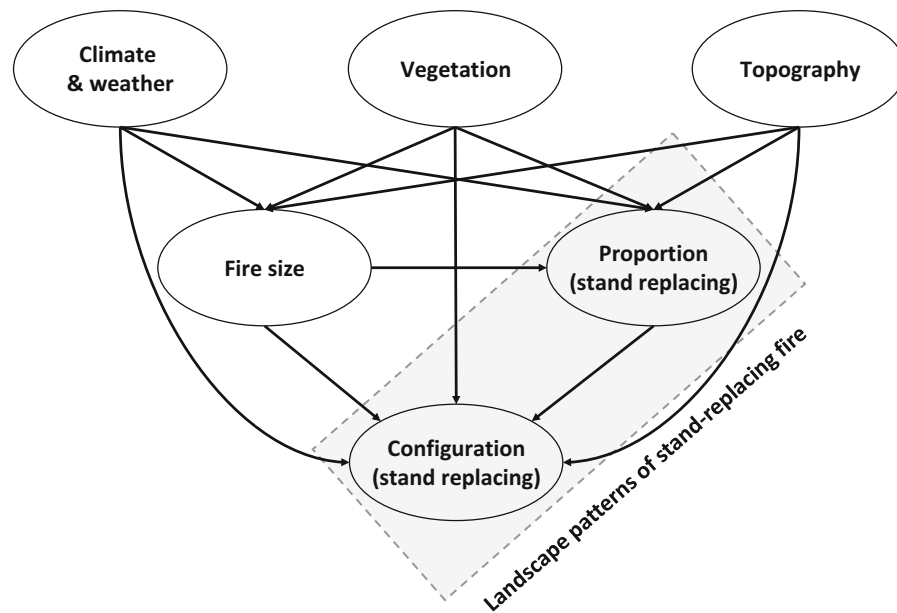
Fig. 2 Structural equation conceptual meta-model for influences of climate/weather, vegetation, and topography, on fire size and landscape patterns of stand-replacing fire [amount (proportion) and configuration of stand-replacing fire]

Analyses

All analyses were conducted at the scale of the individual fire (i.e., landscape, $n = 668$), which is the scale to which all predictor and response variables were assigned or averaged as appropriate. Using each fire as a replicate landscape, we used a combination of structural equation modeling (SEM) and correlation analyses to investigate the controls on our metrics of landscape patterns of stand-replacing fire. Structural equation modeling was used to test the relative strengths of direct controls of climate/weather, vegetation and topography on each landscape metric, as well as the indirect controls of these factors via their effects on fire size and proportion stand-replacing fire. The ability to test multiple cause-effect hypotheses in complex networks of variables in large observational datasets (Grace 2006) makes SEM is well suited to studying controls on burn-severity patterns (Grace and Keeley 2006).

The SEM framework was applied in several steps. First, we constructed a structural equation meta-model, which represents the general hypothesized relationships among climate/weather, vegetation, topography, and fire size and landscape patterns of stand-replacing fire (Fig. 2). Second, we developed

parameterized SEMs for each metric of the configuration of stand-replacing fire: patch size (Fig. 3a); patch shape (Fig. 3b); and total core area (Fig. 3c). Each of these parameterized SEMs included fire size and proportion stand-replacing fire as response variables of interest, and also as potential predictors of stand-replacing burn configuration. For predictor variables, each model contained one composite latent variable (climate & weather), which was represented by cumulative (climate) and current (weather) moisture deficit. Vegetation and topography were latent variables represented by forest zone and topographic roughness index, respectively.

Beginning with the full meta-model (Fig. 2), each model was trimmed by removing non-significant ($P > 0.05$) paths (linear relationships between variables). Model comparison between trimmed and full models was conducted using AICc in the lavaan.modavg.R package (Byrnes 2012), ensuring that removing non-significant terms did not reduce model performance. Models were trimmed until all non-significant paths were removed and/or removing additional terms no longer improved model AICc. Each predictor and response variable was standardized to ±SD from the mean of that variable in the dataset, allowing for direct comparison of effect sizes among

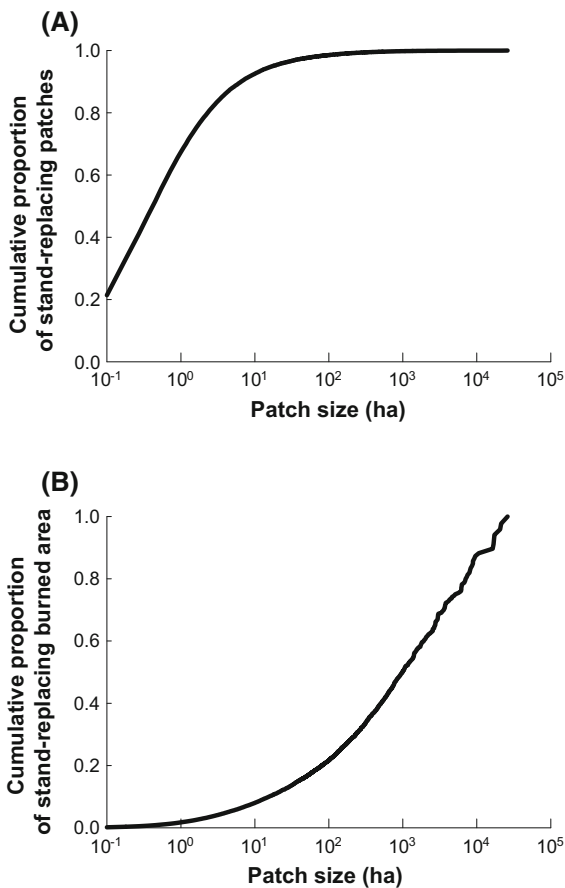**(A)**

(B)

Fig. 3 Cumulative frequency distribution of number of stand-replacing patches (**a**) and stand-replacing burned area (**b**) as a function of increasing patch size for all patches in all fires (1984–2010). X-axis is $\log_{10}$ scale

different variables in the model. Forest zone, as the only ordinal categorical variable, was recoded as the following (subalpine forests = 3; mid-montane forests = 2; and low-montane woodlands = 1) and then transformed to ±SD from the mean forest zone. All SEM models were analyzed using the lavaan package (Rosseel 2012) in (R Development Core Team 2012). To aid interpretation of relationships among predictor variables (climate/weather, vegetation, and topography) and each of the metrics for landscape patterns of stand-replacing fire, we also tested correlations (Spearman's *rho*) in the raw units of each variable and presented results in scatter plots (bar graphs for forest zone).

To test for trends in landscape patterns of stand-replacing fire over time (1984–2010), we used linear regression with year as the predictor variable of interest, and included a term for fire size (to control for the effects of landscape size) before testing for changes in configuration. Drawing on landscape ecological theory regarding critical thresholds in proportion occupied within landscapes (Gardner et al. 1987; Gustafson and Parker 1992), we also tested for evidence of thresholds in the effect of proportion stand-replacing fire (P_{crit}) on two key configuration metrics: patch size and core area of stand-replacing fire. To perform this test, we used only fires near the median fire size to hold fire size relatively constant (as landscape extent can affect both patch size and core area) and obtain a large enough sample.

Prior to all analyses (SEM and regression), area measures (fire size, patch size, patch shape, core area) were $\log_{10}$ transformed and proportion data were logit transformed. Reported values are means (±1SE) unless otherwise noted.

Results

Number of fires, burned area, and patches of stand-replacing fire

From 1984 to 2010, a total of 668 forest fires larger than 250 ha were recorded, burning 3,366,328 ha in total and accounting for ~15 % of the total forested area in the Northern Rockies (Table 1; Fig. 1). Across all fires accounting for the total burned area, 34 % (1,152,636 ha) burned as stand-replacing fire, accounting for ~5 % of the total forested area in the Northern Rockies. Of the total area burned, 9 % (286,506 ha) was core area within stand-replacing patches (i.e., greater than 150 m from the nearest stand-replacing patch edge), accounting for ~1 % of the total forested area in the Northern Rockies. Individual patches of stand-replacing fire ranged from smaller than 0.1 ha to larger than 25,000 ha. More than half of all patches were smaller than 0.5 ha, and more than two thirds of all patches were smaller than 1 ha (Fig. 3a); however, the summed area burned as stand-replacing fire in patches smaller than 1 ha accounted for only 1.7 % of the total area in stand-replacing fire (Fig. 3b). Conversely, greater than 75 % of the total area of stand-replacing fire was in patches

Table 1 Summary statistics for the number of fires, area burned, fire size, and landscape patterns of stand-replacing fire by each forest zone and for all fires combined across forest zones

	Low-montane woodlands	Montane forests	Subalpine forests	Total (all forest types combined) Min–max	Mean (SE)	Median
Ecoregion-level statistics (all fires)						
Number of fires	20	295	353	n/a	n/a	n/a
Total area burned	42,160	1,400,428	1,923,740	n/a	n/a	n/a
Fire-level statistics (per fire)						
Fire size, ha, mean (SE)	2108 (619)	4747 (661)	5450 (1064)	260–229,048	5039 (634)	
Fire size, ha, median	890	1343	1316			1312
Stand-replacing fire within perimeter						
Total area, ha, mean (SE)	502 (273)	1200 (204)	2234 (436)	0–113,393	1726 (248)	344
Percent, mean (SE)	14 (3)	20 (1)	38 (1)	0–83	29 (1)	28
Patch size, ha, area wtd. mean (SE)	115 (62)	354 (70)	677 (83)	0–14,652	517 (54)	106
Edge:area, m/ha, area wtd. mean (SE)	443 (61)	302 (13)	174 (4)	44–1333	239 (7)	190
Core area, ha, mean (SE)	67 (48)	245 (55)	603 (148)	0–44,277	429 (82)	28

Values are means (SE) unless otherwise noted. All fires ($n = 668$)

larger than 100 ha, and nearly 50 % was in patches larger than 1000 ha (Fig. 3b).

Drivers of fire size and landscape patterns of stand-replacing fire

Fire size was a strong predictor of landscape patterns of stand-replacing fire (Fig. 4, top row), and was, in turn, strongly controlled by climate/weather. Fire size increased with cumulative moisture deficit at the time when the fire started ($r_s = 0.25$, $P < 0.001$) and moisture deficit during the month(s) of the fire ($r_s = 0.24$, $P < 0.001$), and decreased with topographic roughness ($r_s = -0.09, P = 0.03$). Fire size did not differ among forest zones ($P = 0.38$, one-way ANOVA). The effect of climate/weather on fire size was >4× stronger than the effect of topography on fire size (Fig. 5a–c).

Proportion of stand-replacing fire was greatest for fires occurring in subalpine forests (0.38 ± 0.01), did not differ between fires in mid-montane forests (0.20 ± 0.01) and low-montane woodlands (0.11 ± 0.03), and decreased with topographic roughness (Fig. 4e, f). Proportion stand-replacing fire also

increased with fire size (Fig. 4a), and therefore was indirectly affected by climate/weather; however there was no direct link between climate/weather and proportion stand-replacing (Fig. 5a). The effect of vegetation on proportion stand-replacing was nearly 2× stronger than the effect of topography and nearly 3× stronger than the effect of fire size (Fig. 5a–c).

Mean patch size of stand-replacing fire and total core area within stand-replacing patches were most strongly and positively correlated with fire size and proportion stand replacing (Fig. 4g–h, s–t). Correlations were weaker with other variables, but mean patch size and total core area increased with both measures of moisture deficit, increased from low-montane woodlands to subalpine forests, and decreased with topographic roughness (Figs. 4i–l, t–x, Fig. 5c). Significant direct drivers of patch size were fire size, proportion stand replacing, climate/weather, and vegetation. The effect of proportion stand replacing on patch size was nearly 2× stronger than the effect of fire size (Fig. 5a). Direct effects of climate/weather and vegetation on mean patch size were comparatively minor, with effect sizes >10× smaller than proportion stand replacing or fire size (Fig. 5a).

Therefore, climate/weather, vegetation, and topography were indirect drivers of patch size through their effects on fire size and proportion stand-replacing fire. For total core area, effects of fire size and proportion stand-replacing were similar, and after accounting for both variables, no other direct relationships between predictor variables and total core area remained in the SEM model (Fig. 5c).

Mean patch shape complexity of stand-replacing fire was correlated with all predictor variables, but the direction of effects was opposite to those for mean patch size (Fig. 4m–r). Patch shape complexity (edge:area) decreased with fire size and proportion stand-replacing, decreased with both measures of moisture deficit, decreased from low-montane woodlands to subalpine forests, and increased with topographic roughness (Fig. 4m–r). Proportion stand-replacing fire was by far the strongest driver of patch shape complexity, with effects $>7\times$ stronger than other drivers (Fig. 5b). Significant direct effects of fire size and climate/weather remained in the SEM model.

Temporal trends and thresholds in landscape patterns of stand-replacing fire

Over time, proportion stand-replacing fire increased from 0.22 to 0.27 (Fig. 6a). Trends were suggestive of an increase in patch size, decrease in patch shape complexity, and increase in total core area; however slopes were not significantly different from zero ($0.11 < P < 0.14$, Fig. 6b–d). Holding fire size constant by using only fires near the median fire size (all fires between 1000 and 1500 ha; median fire size was 1312 ha), the increase in proportion stand replacing from 0.22 to 0.27 we detected from 1984 to 2010 does not strongly affect spatial metrics such as mean patch size or total core area (Fig. 7, within the dashed zone). However, increases in proportion beyond this zone are characterized by steep increases in patch size and core area (Fig. 7, to the right of the dashed zone), indicating that contemporary landscape patterns of stand-replacing fire are approaching P_{crit}.

Discussion

Landscape patterns of stand-replacing fire can influence resilience in fire-prone forests, and understanding how increases in fire activity will affect such landscape patterns is critical for ecosystem management and conservation planning (Turner et al. 2013). To our knowledge, this is the first study to quantify landscape patterns of stand-replacing fire, test relationships with drivers, and evaluate trends over time for fires across an entire ecoregion. Our use of structural equation modeling provides insight into the complex relationships among controls of landscape patterns in burn severity. Our results demonstrate that controls on landscape patterns of stand-replacing fire are variable, and relationships between those drivers and patterns differ in important ways from relationships between drivers and fire size. However, the strong controls of fire size and proportion stand-replacing fire on the configuration of stand-replacing fire (patch size, shape and core area) suggest that predictions of larger fires in the future have important implications for spatial patterns of burn severity.

Fire size and proportion stand-replacing were controlled by different drivers

The strong control of moisture deficit on fire size reported in this study supports the understanding that fire occurrence, area burned, and fire size are strongly driven by broad-scale climate and weather conditions. At regional to continental scales, similar findings have been reported for relationships between integrated measures of drought and annual total area burned (Morgan et al. 2008; Abatzoglou and Kolden 2013) and annual number of large (>400 ha) wildfires (Westerling et al. 2006). Climate and weather have been shown to control the size of individual fires in other regions such as California (Miller et al. 2009) and across all fires in the western US (Riley et al. 2013). At within-fire scales, short periods (hours to days) of hot, dry, and windy conditions also control area burned (Turner et al. 1994; Thompson and Spies 2009; Harvey et al. 2014a; Andrus et al. 2016).

We found that fire size was also controlled by topography, though to a lesser degree than by climate/weather. Decreasing fire size with greater topographic roughness indicates that complex topography constrains fire size, in contrast to dry ponderosa pine forests of the southwestern US where the probability of large fires increases in topographically complex locations (Dickson et al. 2006). This difference could be due to divergent primary controls of fire regimes
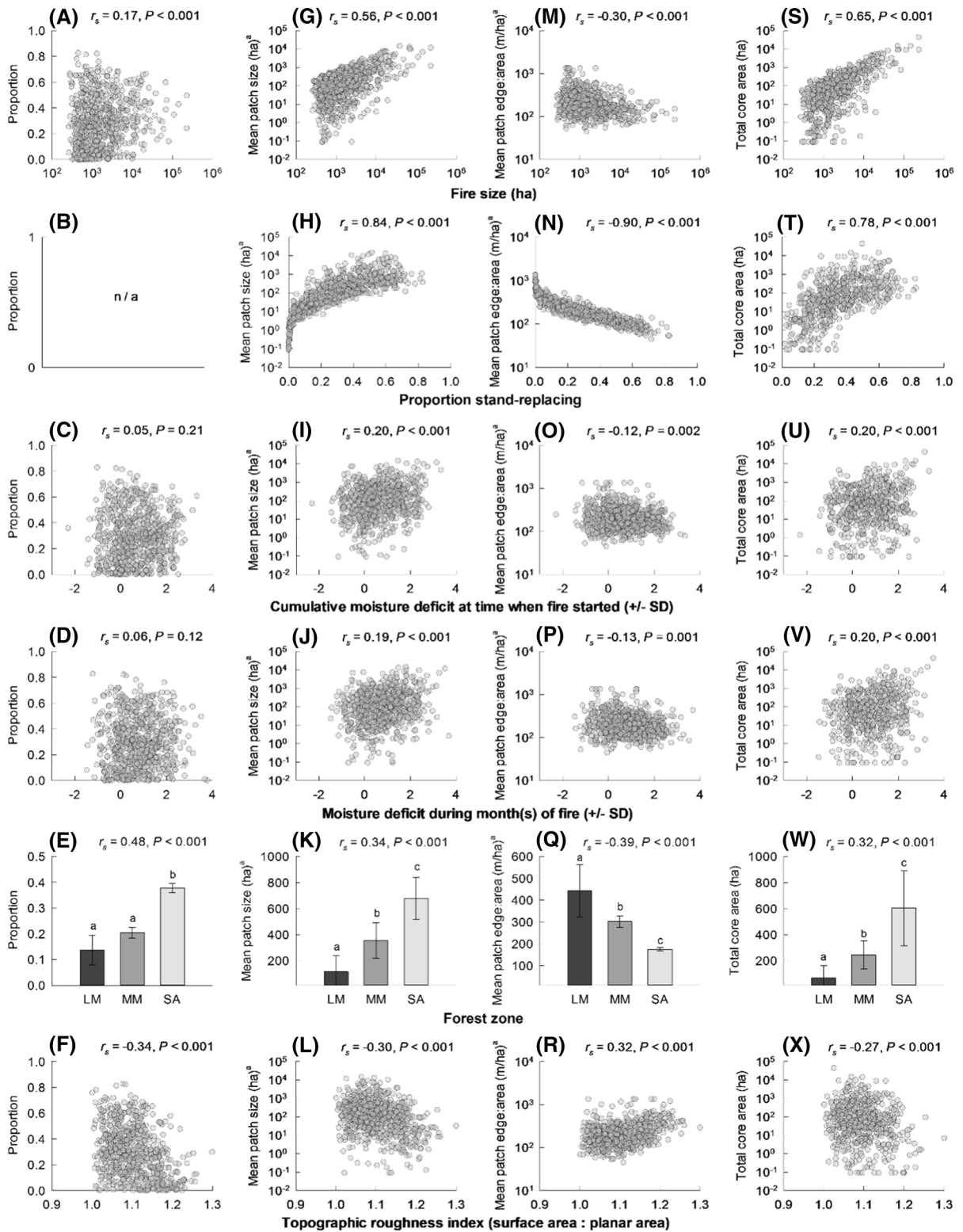
◀ **Fig. 4** Bivariate relationships between each metric of landscape patterns of stand-replacing fire (*left to right*) and predictor variables of fire size, proportion stand replacing, climate, weather, vegetation, and topography (*top to bottom*). *Error bars* (*E*, *K*, *Q* and *W*) represent 95 % confidence intervals

between the warmer-drier US southwest (where fire is generally limited by vegetation accumulation) and the cooler-wetter US Northern Rockies (where fire is generally limited by suitable climate/weather

conditions, and vegetation is typically abundant) (Schoennagel et al. 2004). We found no relationship between fire size and vegetation; thus topography may impose a more important constraint on fire size in systems where vegetation is generally not limiting.

The proportion of stand-replacing fire was controlled primarily by vegetation and topography, and less so by climate/weather through indirect effects on fire size. Our results at the unit of individual fire events support conclusions from studies conducted at fine
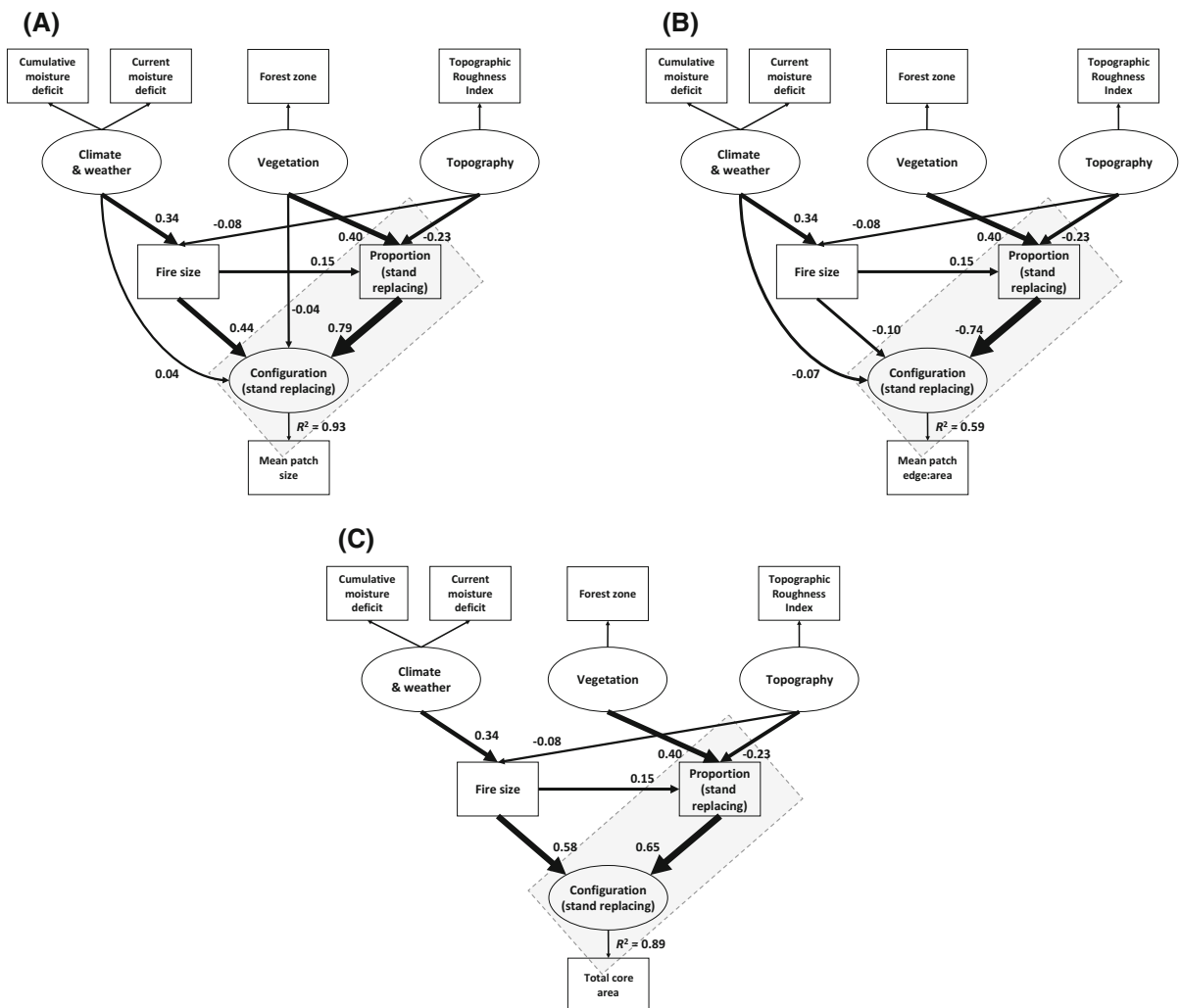

Fig. 5 Diagram of structural equation model for mean patch size (**a**) mean patch shape (**b**), and total core area (**c**) of stand-replacing fire. Observed variables are represented by *rectangles* and latent variables are represented by ovals. All pathways in Fig. 2 were tested for each model; non-significant relationships ($P > 0.05$) were removed from each model. Significant

relationships ($P \leq 0.05$) between model variables are represented by *solid lines* that vary in width corresponding to standardized-coefficient size (also labeled with the coefficient next to each significant path). Total variance explained for the response variable is presented at the bottom of each figure (R^2). All models included each fire as a replicate landscape ($n = 668$)
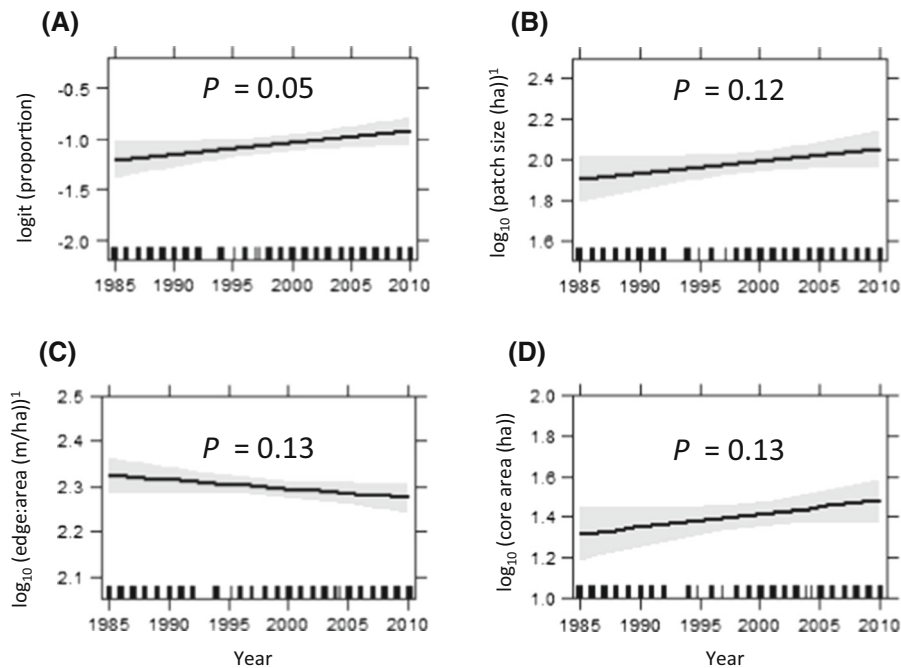
Fig. 6 Temporal trends for each metric of landscape patterns of stand-replacing fire. Plots depict the effect of year holding fire size constant at the mean fire size (5,039 ha). The *dark line* represents the mean and shaded areas are 95 % confidence intervals. Each *short vertical line* along the x-axis represents one of the fires included in this study (total $n = 668$ fires). [1]Area-weighted to best represent an average location of stand-replacing fire, rather than weighting patches of all sizes equally
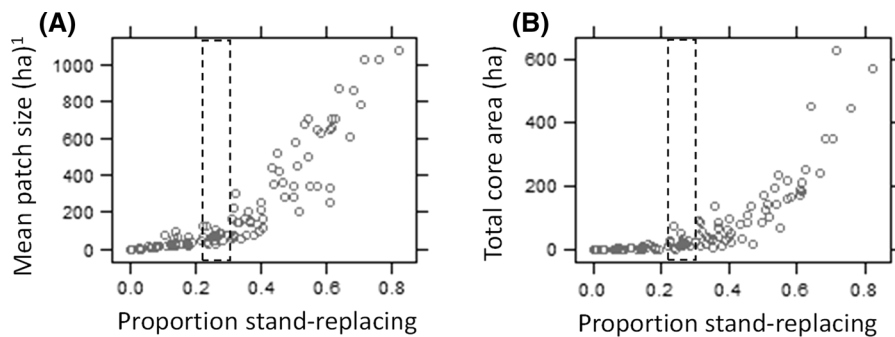

Fig. 7 Effects of proportion stand-replacing fire on mean patch size (**a**) and total core area (**b**), holding fire size constant between 1000 and 1500 ha (median fire size was 1312 ha). The area between the *dashed lines* illustrates the amount of change in proportion stand replacing observed from 1984 to 2010 (.22 to .27), beyond which sharp non-linear increase in both patch size and total core area are observed. [1]Area-weighted to best represent an average location of stand-replacing fire, rather than weighting patches of all sizes equally

(e.g., 30-m pixel-scale, Birch et al. 2015) and coarse spatial scales (e.g., the entire Northern Rockies ecoregion, Dillon et al. 2011), reinforcing the notion that drivers of burn severity are more complex than the broad-scale climate/weather drivers of fire size. Weather/climate can have strong direct effects on burn severity at the scale of an individual forest stand (Harvey et al. 2014b) and detectable effects at the

scale of 30-m pixels (Birch et al. 2015). Our findings in this study suggest that these effects of daily weather conditions, when averaged over the duration (e.g., monthly) and extent (e.g., tens of km) of an entire fire event, are not as strong as vegetation and topography are for directly controlling the proportion of a fire that is stand-replacing. This difference is likely due to the spatial (e.g., several km) and temporal resolution (e.g.

monthly) of weather data for each fire event we used, intended to align with our analysis at the scale of individual fire events rather than with individual pixels or different time periods within fires. Future work could test relationships between higher temporal resolution weather data and individual patches of stand-replacing fire, if such data on time of burning and localized weather were available across all fires. Our finding that fire size increased with more extreme climate/weather (increased moisture deficit), and proportion stand-replacing increased with fire size, supports findings in the Cascade Mountains (Cansler and McKenzie 2014), and suggests that the effects of climate/weather on burn severity are mediated through effects on fire size.

Configuration of stand-replacing fire was strongly controlled by fire size and proportion

As expected from well-developed theory in landscape ecology (e.g., Gardner et al. 1987), we found the configuration of stand-replacing fire to be strongly controlled by fire size and proportion of stand-replacing fire. The relative importance of fire size and proportion stand-replacing differed among configuration metrics, lending insight into mechanisms that generate landscape patterns of burn severity. The size of stand-replacing burn patches was most strongly affected by proportion stand replacing, which was in turn primarily driven by vegetation and topography, indicating strong indirect control of vegetation and topography on stand-replacing burn patch size. The direct and indirect (via fire size) links between patch size and climate/weather suggest that climate and weather may override constraints imposed by vegetation and topography under extreme conditions (Turner and Romme 1994; Bessie and Johnson 1995). In contrast, the shape of stand-replacing burn patches was almost entirely driven by proportion stand-replacing fire, and therefore strongly affected indirectly by vegetation and topography rather than climate/weather. Greater sensitivity to these fine-scale constraints suggests that vegetation arrangement and variable topography can produce patches with complex shapes, but those patches may be quite large. The amount of core area within stand-replacing burn patches was almost equally controlled by fire size and proportion stand-replacing, indicating that climate/weather, vegetation, and topography all play

important roles. Compared to the weaker effect of fire size on the size and shape of stand-replacing patches, the stronger effect of fire size on total core area makes sense, as core area should be tightly constrained by fire size (i.e., small fires must inherently contain a small amount of core area, if any; conversely only large fires possess the potential for large amounts of core area).

Of the three explanatory factors (climate/weather, vegetation, topography) examined in our study, vegetation exhibited the strongest relationships with response variables, indicating that landscape patterns of stand-replacing fire differ in important ways among forest zones. Each metric of landscape pattern differed among at least one of the forest zones (Fig. 4e, k, q, w), illustrating clear and quantitative differences among fire regimes previously described qualitatively (Schoennagel et al. 2004; Baker 2009). These findings can inform efforts to characterize fire heterogeneity across space, improving the ability of managers to quantify ranges of variability in these patterns in various forest zones (e.g., Hessburg et al. 2007; Belote 2015). For example, our study demonstrates that subalpine forests in the US Northern Rockies are characterized by more stand-replacing fire that is spatially aggregated in larger and more simple-shaped patches than mid-montane or lower elevation forests and woodlands, and the numbers provided can help define when a particular fire is inside or outside the range of what may be considered "normal" for each forest zone. However, just as important as the difference in means among forest zones is variability within each forest zone. For example, area-weighted mean patch sizes for stand-replacing fire in mid-montane forests and subalpine forests were 354 and 677 ha, respectively. Including 95 % confidence intervals in these estimates demonstrates that mean patch sizes for any given fire could be anywhere from 217 to 491 ha in mid-montane forests and 515–839 ha in subalpine forests. Such ranges of variability at the fire level (with even greater ranges of variability at the level of individual patches) demonstrate that, although subalpine forests are well-known as stand-replacing fire regimes, stand-replacing fire also constitutes a substantial portion of contemporary mixed-severity fire regimes in mid-montane forests (Halofsky et al. 2011; Perry et al. 2011). Using dendroecological data and/or historical photographs to place the contemporary fire patterns we describe in a broader historical (i.e., pre-dating the era of satellite data) context

remains a research priority (e.g., Hessburg et al. 2007; Sherriff et al. 2014).

Temporal trends: slow, linear change, or approaching thresholds?

Our findings suggest that over time, landscape patterns of stand-replacing fire are changing during an era of increasing wildfire activity, and future changes may be accelerated. Proportion stand-replacing was the only metric to show a significant ($P \leq 0.05$) increase over time, but trends for other measures were suggestive ($P \leq 0.15$) of hypothesized shifts toward larger, simpler-shaped patches with more total core area. Moreover, several metrics were driven in part by proportion stand-replacing fire, making it reasonable to expect concomitant changes in patch size, shape, and core area. Randomized data on simulated landscapes (Gardner et al. 1987) and empirical data presented in our study (Fig. 7) suggest that once fires are characterized by proportion stand-replacing fire exceeding ~ 0.35, patch sizes and total core area are likely to increase non-linearly.

Whether or not average future fires will reach P_{crit} in the proportion of the fire that is stand replacing therefore becomes an important question, and relationships between drivers (climate/weather, vegetation, and topography) and landscape patterns of stand-replacing fire we report in this study can lend insight for expectations. Climate in the Northern Rockies is expected to warm over the next century, with average annual moisture deficits by 2075 regularly exceeding the most extreme on record (Westerling et al. 2011). Shorter term weather conditions that drive large fires have also increased in recent decades, and are expected to continue increasing in frequency and duration (Jolly et al. 2015). Therefore, the climate/weather driver of burn-severity patterns will likely increase in the future. In contrast, vegetation may become more limited in the future if increased fire activity results in reduced forest cover or biomass, initiating negative feedbacks on fire activity. For example, areas that have re-burned within the last ~ 30 years in the Northern Rockies have shown evidence that the spread (Parks et al. 2015) and burn severity (Parks et al. 2014; Harvey et al. 2016a) of the second fire can be, for a time, limited by vegetation recovery from the first fire. Therefore, the vegetation that drives spatial patterns of burn severity may decrease in the future, leading to an increase in the

importance of vegetation limits on landscape patterns of fire. Topography, on the other hand, is relatively static, and will continue to constraint fire size and burn severity, perhaps increasing in relative importance with future changes to the other two drivers. Understanding how the controls of landscape patterns of stand-replacing fire change through time is therefore critical to predicting whether trends will continue in the directions we report.

Landscape patterns of stand-replacing fire: implications for forest resilience

Heterogeneity in disturbance patterns has an important influence on forest resilience, and the findings from our study hold important implications for current and future forests. Large patches of stand-replacing fire are characteristic of many forest fires in the US Northern Rockies. For example, the 1988 Yellowstone Fires produced the three largest stand-replacing burn patches in our dataset–each larger than 20,000 ha in total and containing more than 8000 ha of core area. Forest regeneration following the 1988 Yellowstone Fires demonstrated enormous resilience to such large patches of stand-replacing fire (Romme et al. 2011), as even in the large fires of 1988 the majority of severely burned area was within 200 m of surviving trees (Turner et al. 1994). In our study, greater than 90 % of the >3 million ha burned between 1984 and 2010 in the Northern Rockies was within 150 m of forests that did not burn as stand-replacing fire (and thus presumably provide a seed source). These findings suggest that burn-severity heterogeneity maintained so far during a period of increasing fire activity is likely sufficient for seed dispersal into most stand-replacing burned areas (Kemp et al. 2015; Harvey et al. 2016b). However, if fire size continues to increase (Morgan et al. 2014) and trends continue on trajectories illustrated in Fig. 6, they will carry important consequences for future composition and structure of forests in the Northern Rockies.

Fires with larger, simpler shaped patches, and more core area far from seed sources will likely favor tree species that don't rely on dispersal into burned patches, but instead possess mechanisms for in situ post-fire regeneration. For example, post-fire tree seedling establishment of serotinous lodgepole pine is not affected by burn patch size or distance to seed source (Turner et al. 1997; Kemp et al. 2015; Harvey et al.

2016b). Similarly, quaking aspen can colonize large burned patches, owing to the ability to re-sprout from underground root structures and disperse light-weight seeds over several kilometers (Turner et al. 2003). In contrast, species that rely on dispersal from surviving individuals (i.e., outside the stand-replacing burn patch) such as Engelmann spruce or Douglas-fir, exhibit exponential declines in post-fire seedling establishment with increasing distances to seed sources (Kemp et al. 2015; Harvey et al. 2016b) and will likely experience declines in post-fire seedling establishment if stand-replacing patch size and total core area increase. Collectively, trends in burn-severity patterns continuing along the trajectory we present may result in post-fire landscapes that are dominated by species such as lodgepole pine and quaking aspen, with decreases in overall tree density (Harvey et al. 2016b).

Our study illustrates that drivers of landscape patterns of stand-replacing fire differ from drivers of overall fire activity, but fire size and proportion stand-replacing fire strongly control the configuration of stand-replacing fire. Therefore, increases in fire activity in the US Northern Rockies will likely be associated with larger patches of stand-replacing fire that are simpler in shape. The framework applied here (e.g., structural equation modeling, testing for thresholds in P_{crit}) may be helpful in other fire-prone systems, where forecasting thresholds in disturbance activity can aide in anticipating consequences for forest resilience.

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