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Fire legacies, heterogeneity, and the importance of mixed-severity fire in ponderosa pine savannas

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A B S T R A C T

Globally, savanna ecosystems are shifting outside of “safe operating spaces” due to removal of their primary self-reinforcing feedback—fire—and subsequent erosion of disturbance legacies. Restoring savannas will require reinstating fire feedbacks. But knowledge gaps in the nature of historic fire regimes and how mechanisms such as time-since-fire and fire severity interact to produce disturbance legacies hinders development of ecologically relevant restoration targets. A theory-based approach for determining restoration targets is to compare structures produced by time-since-fire/fire severity interactions to structures that fostered animal communities that historically inhabited savannas. Here, we use a space-for-time substitution to quantify interactive effects of time-since-fire and fire severity on vegetation structures related to known animal community habitat preferences by surveying sites in 10-year-old and 27-year-old mixed-severity fires that occurred in an eastern ponderosa pine (*Pinus ponderosa*) savanna where fire was excluded since European settlement. Our specific objectives are to 1), quantify the relative strengths and interactive effects of time-since-fire and a full fire severity gradient on multivariate vegetation structure across landscape patches and 2), assess relationships between multivariate vegetation structures and time-since-fire/fire severity classes across landscape patches. We used a stratified random design to distribute 112 sampling plots by fire severity (unburned, low, moderate, and high) and time-since-fire (10 years and 27 years) and measured stand structure, tree cavity characteristics, and coarse woody debris. The interaction of time-since-fire and fire severity drove structure complexity for 27 years post-fire, but fire severity explained > 14 times the amount of variation in structure than time-since-fire alone. A full fire severity gradient (low-, moderate-, and high-severities) and structural changes within patches that experienced different fire severities generated sufficient patch-level heterogeneity to foster animal communities historically native to eastern ponderosa pine savannas. Structures generated by low fire severity alone, which is a common goal of fire management in easternmost ponderosa pine savannas, did not reflect sufficient structural complexity to support the diversity of endemic animal species. This indicates information legacies (i.e., represented by the distribution of species traits in a community) were shaped by mixed severity fire regimes, which provides further support for the scientific premise that management goals seeking to minimize variation in fire regimes (e.g., low intensity and low-severity fires only) is less able to support a full array of biodiversity. Rather, mixed-severity fire is an important driver of structural heterogeneity, fosters diverse information legacies, and enhances ponderosa pine savanna resilience to extreme fire.

1. Introduction

Savannas are among the most threatened ecosystems globally due to human suppression of savannas’ primary self-reinforcing feedback—fire (Stevens et al., 2017). Decoupling fire from savannas often shifts them out of “safe operating space” via the erosion of disturbance legacies—the material legacies (structures and communities that survive disturbances) and information legacies (species’ adaptations to disturbance regimes that manifest as the distribution of species’ traits) that support self-reinforcing feedbacks (Archer et al., 2017; Johnstone et al., 2016). Restoring savanna ecosystems therefore requires re-coupling fire with these systems in such a way that regenerates disturbance

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legacies that can maintain self-reinforcing feedbacks (Beckage et al., 2011; Bowman and Legge, 2016). Disturbance legacies are hypothesized to be necessary for biodiversity and emerge from the interaction of spatial heterogeneity in fire effects on vegetation (i.e., variation in fire severity across landscapes) (Johnstone et al., 2016; Keyser et al., 2008; Passovoy and Fulé, 2006) and subsequent temporal changes in post-fire vegetation response (i.e., time-since-fire). But how time-since-fire and fire severity gradients interact to create disturbance legacies necessary to restore self-reinforcing feedbacks remains unclear (Bowman et al., 2016), and this has led to considerable debate concerning effective restoration targets for savannas (Allen et al., 2002; Baker, 2018a; Williams and Baker, 2012).

This issue is exemplified in North American ponderosa pine (*Pinus ponderosa*) savannas. Decades of debate has centered on the nature of historic fire regimes that created disturbance legacies capable of maintaining self-reinforcing feedbacks in savannas (Bradstock et al., 2005; Driscoll et al., 2010; Twidwell et al., 2013). Some studies support fire regimes characterized by high frequency (i.e., short time-since-fire) and low-severity, whereas others support a wider range of fire frequencies and fire severity gradients (Covington and Moore, 1994; Hagmann et al., 2013; Odion et al., 2014; Wendtland and Dodd, 1992). Further complicating this debate are regional differences in ponderosa pine savannas varying from ponderosa woodlands embedded within larger forest ecosystems in the West to ponderosa savannas on the easternmost portion of their range embedded within grassland matrices (Allen et al., 2002; Brown and Sieg, 1999; Hagmann et al., 2013). Most of these studies use structural data (i.e., material legacies) such as fire scars, tree demographics, remotely sensed vegetation cover, and forest-savanna landscape responses to fire as evidence to support their respective claims; yet this evidence has led to contrasting findings throughout the literature (Baker, 2018b; Odion et al., 2016; Stephens et al., 2015; Stevens et al., 2016). As the implementation of different fire regimes will likely lead to disparate restoration outcomes, not to mention how outcomes could vary between regions, determining how time-since-fire and fire severity interact to create appropriate disturbance legacies is all the more crucial to restoring ponderosa pine savannas.

A theory-based approach for determining attributes of disturbance legacies necessary for ecological restoration targets is to compare structures produced by time-since-fire/fire severity interactions to known historic savanna information legacies. Such an approach compares the results of the interaction of time-since-fire and fire severity to structures necessary for fostering animal communities that historically inhabited savannas (Bowman and Legge, 2016; Johnstone et al., 2016; Jones and Davidson, 2016; Swan et al., 2018). In fire-dependent systems like savannas, many floral and faunal adaptations and/or life history requirements encapsulate disturbance regime information (i.e., information legacies) (Hutto et al., 2016; Johnstone et al., 2016; Pausas and Parr, 2018). Post-fire structural characteristics govern habitat suitability for a wide range of taxa (Table 1) (Hutto et al., 2016; Keele et al., 2019; Spies et al., 2012; Taillie et al., 2018), supporting the premise that biodiversity in savanna systems is linked to structural heterogeneity resulting from fire (Bradstock et al., 2005; Fuhlendorf et al., 2017; Kelly et al., 2015; Swanson et al., 2011). Many species depend on post-fire habitat structures that only exist within a narrow temporal window post-fire or within specific ranges of fire severity (Hutto et al., 2008; Hutto and Patterson, 2016; Woinarski et al., 2010). Globally, there are more and more examples of species declines due to loss of savanna habitat; that is, loss of specific habitat structures that likely emerge from the interaction of time-since-fire and fire severity (Conway et al., 2010; Huntzinger, 2003; Means, 2006; Valentine et al., 2014; Webb et al., 2005). Restoration efforts can take advantage of this link between animal habitat requirements and structural complexity generated by the time-since-fire/fire severity interaction to set restoration targets based on historic savanna animal habitat requirements (Doherty et al., 2017; Jones and Davidson, 2016).

Although an information legacy approach for developing savanna restoration targets can harness the many studies investigating relationships between species and fire-dependent structures (especially in ponderosa pine systems), how the interaction of time-since-fire and fire severity gradients create necessary structures remains unclear (Bowman et al., 2016; Driscoll et al., 2010). Species-habitat research has traditionally focused on temporal aspects, especially on simple binary "burned-unburned" classifications and less-so on time-since-fire, and far less research has been conducted on fire severity (Fuhlendorf et al., 2009; Geary et al., 2019). As temporal and spatial aspects of fire are inextricable in real landscapes, isolating either one will produce reduced estimates of structural complexity necessary to restore self-reinforcing feedbacks (Bowman et al., 2016; Roberts et al., 2019; Smucker et al., 2005). To illustrate, species requiring park-like habitat resulting from low-severity fire tend to respond negatively to fires of higher intensities regardless of time-since-fire (Andersen et al., 2005; Margolis and Malevich, 2016; Yates et al., 2009). Likewise, some species require structures resulting from a single severity level (e.g., snags produced by high-severity fire) but only within a narrow window of time-since-fire (Dunham et al., 2007; Hossack et al., 2013; Saab et al., 2007; Tingley et al., 2018). These examples illustrate the complexity of even single species' post-fire structural requirements and support the need to understand how the interaction between time-since-fire and fire severity generates post-fire structures (Kelly et al., 2015; Lindenmayer et al., 2014; Taillie et al., 2018).

Here, we use a space-for-time substitution to determine how time-since-fire and fire severity interact to produce post-fire structural complexity in a ponderosa pine savanna. We do this from an information legacy perspective—collecting post-fire structural data important for myriad animal species' habitat requirements (Table 1). Specifically, we 1) quantify the relative strengths and interactive effects of time-since-fire and a full fire severity gradient on multivariate vegetation structure across landscape patches and 2), assess relationships between multivariate vegetation structures and time-since-fire/fire severity classes across landscape patches. We conducted our study in the Nebraska Pine Ridge—a region historically dominated by ponderosa pine savanna but which became afforested following European settlement and fire suppression eras (Donovan et al., 2019; Roberts et al., 2019). We use two mixed-severity fires that occurred 27 and 10 years prior to sampling for the space-for-time substitution. To compare resulting structures to savanna information legacies, we used known structural habitat preferences from an array of well-studied taxa historically native to the Pine Ridge (Table 1).

2. Materials and methods

2.1. Study site description

The Pine Ridge is an escarpment in northwestern Nebraska, USA. A semi-arid region, the Pine Ridge rises > 100 m above the surrounding plains and is characterized by rocky ridges, vertical slopes, and deep canyons with an average elevation of 1,219 m. The Pine Ridge has an average annual rainfall of about 43 cm, a mean high temperature of 16.3 degrees Celsius, and an annual low temperature of about 1 degrees Celsius at an average elevation of 1,000 m (Schneider et al., 2011). An ecotonal region, the Pine Ridge is characterized by ponderosa pine and other Rocky Mountain species embedded within and interspersed with mixed grass prairie (Table 1) (Johnsgard, 2005).

We assessed two large mixed-severity wildfires that occurred on the Pine Ridge: The Fort Robinson fire of 1989 burned approximately 20,000 ha, and the Dawes and Sioux County Complex fire of 2006 burned approximately 27,000 ha. The two fires are separated by approximately 40 km. Approximately 1330 ha of the Fort Robinson fire are classified as high-severity, 3604 ha as moderate-severity, and 5971 ha as low-severity within the fire perimeter. The Dawes Complex fire has approximately 508 ha classified as high-severity fire, 4008 ha

Table 1
Habitat structures and associated species from multiple taxa native to the Pine Ridge region of Nebraska, USA. Rows highlighted in gray indicate Nebraska Tier 1 threatened species native to the Pine Ridge (Schneider et al., 2011).

Habitat Structure	Specifics	Taxon	Species	Citation
Cavity height	high height	Bird	*Melanerpes erythrocephalus*	Sedgwick and Knopf, 1990
Cavity height	high height	Bird	*Falco sparverius*	Sedgwick and Knopf, 1990
Cavity height	low height	Bird	*Troglodytes aedon*	Sedgwick and Knopf, 1990
Cavity height	low height	Bird	*Poecile atricapillus*	Sedgwick and Knopf, 1990
Cavity size	large cavity size	Bird	*Falco sparverius*	Sedgwick and Knopf, 1990
Cavity size	moderate cavity size	Bird	*Melanerpes erythrocephalus*	Sedgwick and Knopf, 1990
Cavity size	small cavity size	Bird	*Troglodytes aedon*	Sedgwick and Knopf, 1990
Cavity size	small cavity size	Bird	*Poecile atricapillus*	Sedgwick and Knopf, 1990
Coarse woody debris	high cover	Large mammal	*Felix concolor*	Bull, 2002
Coarse woody debris	high cover	Small mammal	*Sorex cinereus*	Fauteux et al., 2012
Coarse woody debris	high-moderate cover	Insect	*Lasioglossum* sp.	Burkle et al., 2019
Coarse woody debris	high-moderate cover	Insect	*Osmia* sp.	Burkle et al., 2019
Coarse woody debris	high-moderate cover	Insect	*Megachile* sp.	Burkle et al., 2019
Coarse woody debris	high-moderate cover	Insect	*Bombus* sp.	Burkle et al., 2019; Galbraith et al., 2019
Coarse woody debris	high-moderate cover	Insect	*Halictus* sp.	Galbraith et al., 2019
Coarse woody debris	high-moderate cover	Mammal	*Vulpes vulpes*	Bull, 2002
Coarse woody debris	high-moderate cover	Mammal	*Mustela* sp.	Bull, 2002; McComb, 2003
Coarse woody debris	high-moderate cover	Mammal	*Lynx rufus*	Bull, 2002
Coarse woody debris	late decay stage	Small mammal	*Sorex cinereus*	Fauteux et al., 2012
Coarse woody debris	low cover	Reptile	*Phrynosoma hernandesi*	Mathies and Martin, 2008
Coarse woody debris	low cover	Small mammal	*Sciurus niger*	Loeb, 1999
Coarse woody debris	low-moderate cover	Reptile	*Terrapene ornata ornata*	Converse et al., 2002
Coarse woody debris	low-moderate cover	Reptile	*Crotalus viridis*	David et al., 2000
DBH	large tree diameter	Bird	*Melanerpes erythrocephalus*	Vierling and Lentile, 2006
DBH	larger tree diameter	Bat	*Eptesicus fuscus*	Arnett and Hayes, 2009
DBH	larger tree diameter	Bat	*Myotis volans*	Arnett and Hayes, 2009
DBH	larger tree diameter	Bird	*Picodes villosus*	Covert-Bratland et al., 2006
DBH	low-medium tree diameters	Bird	*Vireo bellii*	James, 1971
DBH	smaller tree diameter	Bird	*Buteo regalis*	Bechard et al., 1990
Snag decay	early to mid-decay stage	Bat	*Myotis volans*	Arnett and Hayes, 2009
Snag decay	early to mid-decay stage	Bat	*Myotis thysanodes*	Weller and Zabel, 2001
Snag decay	late decay stage	Bird	*Melanerpes lewis*	Linder and Anderson, 1998
Snag density	high density	Bat	*Myotis thysanodes*	Weller and Zabel, 2001
Snag density	high-moderate density	Bird	*Melanerpes erythrocephalus*	Sedgwick and Knopf, 1990; Vierling and Lentile, 2006
Snag density	low density	Bird	*Picodes villosus*	Covert-Bratland et al., 2006
Tree density	high density	Bird	*Seiurus aurocapilla*	Smith and Shugart, 1987
Tree density	high-moderate density	Small mammal	*Tamiasciurus hudsonicus*	Bayne and Hobson, 2000
Tree density	moderate-low density	Amphibian	*Lithobates pipiens*	Blomquist and Hunter, 2009; Popescu et al., 2012
Tree density	moderate-low density	Bird	*Gymnorhinus cyanocephalus*	Goguen and Mathews, 1998; Rosenstock and Charles Van Riper, 2001
Tree density	moderate-low density	Insect	*Bombus* sp.	Galbraith et al., 2019
Tree density	moderate-low density	Insect	*Halictus* sp.	Galbraith et al., 2019
Tree density	low density	Large mammal	*Ovis canadensis*	Shannon et al., 1975
Tree density	low density	Large mammal	*Odocoileus hemionus*	Altendorf et al., 2001
Tree density	low density, grassland	Bird	*Vireo bellii*	James, 1971
Tree density	low density, grassland	Bird	*Spizella breweri*	Noson et al., 2006
Tree density	low density, grassland	Bird	*Buteo regalis*	Gilmer and Stewart, 1983
Tree density	low density, grassland	Insect	*Erynnis martialis*	Scott and Epstein, 1987; Nelson and Epstein, 1998
Tree density	low density, grassland	Insect	*Speyeria idalia*	Collinge et al., 2003
Tree density	low density, grassland	Insect	*Phyciodes batesii*	Shuey et al., 1987
Tree density	low-density, grassland	Reptile	*Phrynosoma hernandesi*	Dibner et al., 2017

classified as moderate-severity fire, and 5762 ha classified as low-severity within the fire perimeter. Fort Robinson received no post-fire management, and the Dawes Complex received post-fire salvage logging and tree planting only in isolated sites (which were avoided during site selection).

2.2. Site selection

To sample fire severity gradients in each fire, we used remotely sensed fire severity maps collected from the Monitoring Trends in Burn Severity project (MTBS) (Eidenshink et al., 2007). MTBS uses pre- and post- fire satellite imagery to identify shifts in vegetation reflectance indicative of fire severity. Within each fire perimeter (Ft. Robinson fire, Dawes Complex fire), we distributed sampling quadrats of 30 × 30 m (pixel size of MTBS data) in a stratified-random fashion across unburned, low, moderate and high fire severity patches. To ensure quadrats did not overlap differing fire severity classes, we placed quadrats in burned patches that were a minimum of 60 m in width, with quadrats placed in the center of the fire severity patch. Quadrats were spaced ≥ 100 m apart to avoid pseudo-replication amongst quadrats within each fire perimeter. In total, we collected data from 13, 15, 14, and 12 quadrats in unburned, low-severity, moderate-severity, and high-severity patches, respectively, in the Dawes Complex fire, and we collected data from 14, 15, 15, and 14 quadrats in unburned, low-severity, moderate-severity, and high-severity patches, respectively, in the Fort Robinson fire. We ensured that no areas that had received post-fire management (tree planting, salvage logging) were included in sampling—which led to some quadrats being excluded from analyses after-the-fact and the differential number of samples by site and severity class.

2.3. Data collection

To estimate structural characteristics at each 30 × 30 m sampling quadrat, we collected vegetation structural data known to correspond with an array of animals historically native to our study site (Table 1).

Thus, we recorded tree stand structure, tree cavity characteristics, and coarse woody debris characteristics. For tree stand structure, we recorded tree density, tree diameter at breast height (DBH), and snag decay classes. Specifically, for every live tree and self-supporting snag ≥ 1.4 m in height in the quadrat, we recorded the species, DBH, and snag decay class. We used a standard five level classification for decay classes: decay class 1 indicates intact twigs and bark, class 2 indicates a main pole and some bark, class 3 indicates a broken top and most of the bark gone, class 4 indicates exposed heartwood, rotting, no bark, and class 5 indicates rotten snags with no branches or top pole and most of the heartwood is exposed (Spellman, 2011).

To measure tree cavity characteristics, we surveyed all live trees and snags in the quadrat for cavities. We defined cavities as holes in live trees or snags > 1 inch. in diameter that entered into the heartwood (Kunz et al., 2003). We used binoculars to search for cavities systematically from all sides of each tree in the quadrat. For each cavity we found on each tree, we recorded tree cavity height, tree cavity width. We used rangefinders to estimate cavity height.

We estimated coarse woody debris (CWD) characteristics by measuring CWD cover and decay class. We measured coarse woody debris cover along 30 m transects, where orientation was randomly selected (north/south or east/west). We defined CWD to be downed woody debris > 10 cm in diameter (Woldendorp et al., 2004). Additionally, we classified the decay class of each piece of debris using decay classification similar to snags, with decay class 1 being round, with branches, twigs and foliage (if applicable) to decay class 5 with a semi-round structure, possibly in multiple pieces, with the heartwood exposed and decaying (Woldendorp et al., 2004).

2.4. Statistical analysis

2.4.1. Relative strengths of time-since-fire and fire severity

We determined the relative and interactive strengths of time-since-fire and fire severity on structure by comparing observed multivariate structure (i.e., tree stand structure, tree cavity characteristics, and coarse woody debris characteristics) across a gradient of burn severities and across two fire ages (27-year-old Fort Robinson fire, 10-year-old Dawes Complex fire). We conducted a Hellinger transformation on all structure variables to account for rare structures (Legendre and Gallagher, 2001).

Prior to analysis, we used permutational multivariate analysis of variance (PERMANOVA) on Hellinger-transformed variables to compare unburned patches in both the Fort Robinson and Dawes Complex sites to test for differences in current structure that could indicate differences in structure pre-fire at the patch scale (Anderson and Walsh, 2013). Finding no significant difference between unburned patches ($F = 0.880$, $P = 0.460$), we considered our space-for-time substitution acceptable.

We then used PERMANOVA to quantify the relative strengths and interactive effects of fire severity and time-since-fire, on structural variables (Anderson, 2014). We compared relative strengths of time-since-fire, fire severity, and interactive effects by comparing R^2 outputs for each (Anderson and Walsh, 2013).

2.4.2. Relationship between time-since-fire/fire severity and structures

To identify distinct structural assemblages produced by the interaction of time-since-fire and fire severity, we grouped multivariate structure data by each time-since-fire and fire severity combinations (e.g., 10-year-old fire and low-severity, 10-year-old fire and moderate-severity, etc.) and then conducted multiple comparisons on each combinations using PERMANOVA. Importantly, because we used a space-for-time substitution to compare time-since-fire/fire severity combinations, our study design cannot completely avoid pseudo-replication. However, we mitigated for inflated significance by using false discovery rates (FDR) to adjust p-values for multiple comparisons. We then used adjusted p-values to determine which time-since-fire/fire severity classes had distinct ($P < 0.05$) and or similar ($P \geq 0.05$) structural assemblages relative to each other.

Finally, we determined how individual structural variables related to time-since-fire and fire severity via redundancy analysis (RDA). We used all Hellinger-transformed data from all sites as the multivariate response matrix. We used interactions between nominal times-since-fire/fire severities (e.g., “10 years X low-severity”, “27 years X high-severity”). Because these predictors are nominal and linearly dependent (i.e., coded as 0 or 1) and because our objective is to understand habitat associations between time-since-fire and fire severity classes, we excluded “unburned” as a predictor. To visually interpret RDA output, we plotted species scores, site scores, and arrows to indicate the relative strength and association between predictor variables. We performed all analyses in the “vegan” R package (Oksanen et al., 2018; Team, 2018).

3. Results

3.1. Relative effects of time-since-fire and fire severity

Structures were significantly influenced by fire severity ($F_{3,111} = 30.243$, $P = 0.001$; subscript indicates degrees of freedom used by fire severity [i.e., number of severity classes – 1] and total degrees of freedom, respectively), time-since-fire ($F_{1,111} = 7.130$, $P = 0.004$), and the interaction between fire severity and time-since-fire ($F_{3,111} = 3.456$, $P = 0.007$; Fig. 2). Fire severity ($R^2 = 0.428$) explained > 14 times more variance in structure than time-since-fire ($R^2 = 0.034$). In total, fire severity, time-since-fire, and the interaction of time-since-fire and fire severity explained > 51% of variance in habitat structure.

3.2. Relationship between time-since-fire/fire severity and structures

Multiple comparisons revealed four distinct structural assemblages across all fire severity/time-since-fire combinations (Table 2; Fig. 1). Unburned patches significantly differed from all burned areas (Table 2; Fig. 1). Low-severity patches 10 years post-fire, moderate-severity patches 10 years post-fire, and low-severity patches 27 years post-fire were all similar, but they differed from all other fire severity/time-since-fire combinations (Table 2; Fig. 1). High-severity patches 10 years post-fire differed from all other fire severity/time-since-fire combinations (Table 2; Fig. 1). Finally, moderate-severity patches 27 years post-fire and high-severity patches 27 years post-fire were similar, but they differed from all other fire severity/time-since-fire combinations (Table 2; Fig. 1).

RDA constraints explained 16.9% of variance, and the first (79.3%) and second (10.2%) RDA axes explained approximately 90% of constrained variance (Fig. 2). RDA axis 1 mainly captured differences in fire severity, and RDA 2 captured differences in time-since-fire as well as differences in severity (Fig. 2). RDA 1 showed high and moderate-severity structural assemblages were more similar that low-severity structural assemblages (Fig. 2). And, as expected, RDA 2 predominately showed similar time-since-fire had similar structural assemblages (Fig. 2). The predictive strengths of all fire severity/time-since-fire interactions were relatively even—except for moderate-severity at 27 years-since-fire that was a weak predictor and almost completely mirrored the effects of high-severity patches at 27 years-since-fire (Fig. 2). Because RDA 1 (representing fire severity largely) explained much more of the constrained variance than RDA 2 (time-since-fire), the following paragraphs are organized by fire severity, then time-since-fire by fire severity.

Overall, high and moderate fire severity patches were positively associated with numbers of late decay-stage (3 – 5) snags, cavity size, CWD cover, amount of late (3 – 5) decay-stage CWD, and CWD width (Figs. 1, 2). High and moderate severities were negatively associated with tree diameter, overall tree density, and number of early decay-stage snags (Figs. 1, 2). CWD cover was closely associated (positively)

Table 2
Multiple comparisons of vegetation structure variables by fire severity and time-since-fire. Multiple comparisons were conducted with PERMANOVA, and P-values reflect adjustments for multiple comparisons using false discovery rate. Grey rows indicate comparisons that significantly differed. Vegetation structure was collected in the Pine Ridge of Nebraska, USA, summer 2016.

Comparison	F-value	P-value (adjusted)
10-year, High – 10-year, Low	3.68	0.031
10-year, High – 10-year, Moderate	2.82	0.044
10-year, High – 10-year, Unburned	29.65	0.002
10-year, High – 27-year, High	11.28	0.002
10-year, High – 27-year, Low	4.07	0.031
10-year, High – 27-year, Moderate	9.91	0.002
10-year, High – 27-year, Unburned	38.67	0.002
10-year, Low – 10-year, Moderate	1.13	0.323
10-year, Low – 10-year, Unburned	23.48	0.002
10-year, Low – 27-year, High	16.60	0.002
10-year, Low – 27-year, Low	2.25	0.120
10-year, Low – 27-year, Moderate	10.78	0.003
10-year, Low – 27-year, Unburned	29.98	0.002
10-year, Moderate – 10-year, Unburned	25.65	0.002
10-year, Moderate – 27-year, High	11.61	0.002
10-year, Moderate – 27-year, Low	1.72	0.185
10-year, Moderate – 27-year, Moderate	7.31	0.002
10-year, Moderate – 27-year, Unburned	32.17	0.002
10-year, Unburned – 27-year, High	53.42	0.002
10-year, Unburned – 27-year, Low	8.88	0.003
10-year, Unburned – 27-year, Moderate	43.32	0.002
10-year, Unburned – 27-year, Unburned	0.88	0.460
27-year, High – 27-year, Low	8.01	0.004
27-year, High – 27-year, Moderate	2.50	0.090
27-year, High – 27-year, Unburned	72.65	0.002
27-year, Low – 27-year, Moderate	3.94	0.039
27-year, Low – 27-year, Unburned	11.26	0.002
27-year, Moderate – 27-year, Unburned	57.92	0.002

with high-severity patches at 10 years following fire. However, CWD width was most closely and positively associated with moderate-severity patches at 10 years following fire (Figs. 1, 2). Cavity size and number of late decay-stage snags were most closely, albeit relatively weakly, associated with both high and moderate-severity patches at 27 years following fire (Figs. 1, 2).

Low-severity patches were positively associated with amount of early (1 – 2) decay-stage CWD, snag densities, cavity heights, mean and range (standard deviation) in tree diameters, and overall (live tree and snag) tree densities (Figs. 1, 2). Low-severity patches at 10 years-since-fire were weakly positively associated with range of tree diameters and CWD width, but these patches were weakly negatively associated with number of late decay-stage snags, amount of early decay-stage CWD, cavity size, and cavity height (Figs. 1, 2). Low-severity patches at 27 years-since-fire were positively associated with amount of early decay-stage CWD, snag density, cavity height (Figs. 1, 2).

4. Discussion

A full fire severity gradient (low, moderate, and high-severity classes) generated sufficient patch-level structural heterogeneity to foster animal communities historically native to eastern ponderosa pine savannas (Table 1). Eastern ponderosa pine savanna information legacies are strongly associated with mixed-severity fire regimes; this provides further support for the scientific premise that management goals seeking to minimize variation in fire regimes (e.g., low intensity and low-severity fires only) are unable to provide the suite of necessary structures required for restoring or conserving biological diversity (Hutto et al., 2016; Johnstone et al., 2016; Odion et al., 2014; Pausas and Parr, 2018; Roberts et al., 2019; Galbraith et al., 2019). Further, individual structures and structural assemblages persisted for differential times-since-fire and/or only emerged after certain times-since-fire; but all these structural patterns were predicated on the specific fire

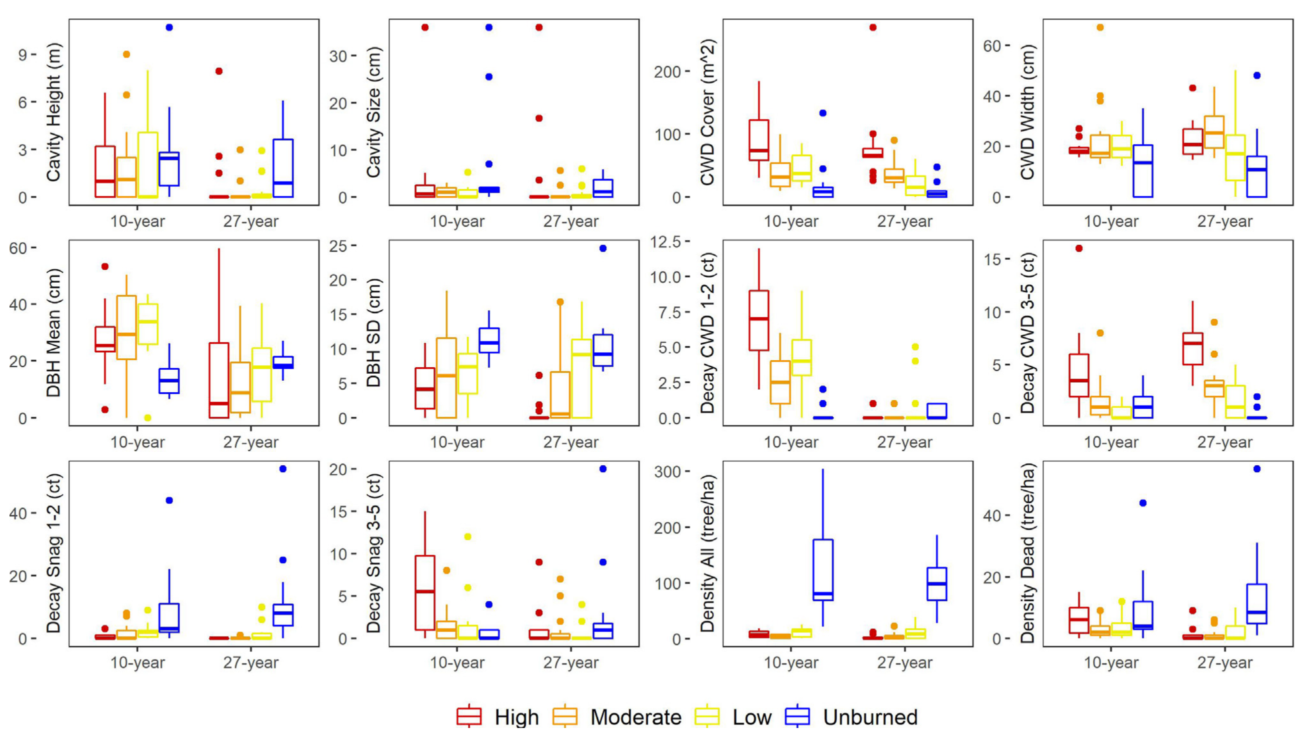

Fig. 1. Box plots of vegetation structure data observed across fire severities (colors) and time-since-fire (10-year-old Dawes Complex fire, 27-year-old Fort Robinson fire) in the Pine Ridge region of Nebraska, USA, summer 2016 (Density All = live and dead tree density; Density Dead = dead tree density; Decay 1–2 = number of dead trees in decay classes 1 and 2; Decay 3–5 = number of dead trees in decay classes 3, 4, and 5; Cavity Size = average cavity size; Cavity Height = average cavity height; coarse woody debris Cover = estimated area covered by coarse woody debris; coarse woody debris 1–2 = number of pieces of coarse woody debris in decay classes 1 and 2; coarse woody debris 3–5 = number of pieces of coarse woody debris in decay classes 3, 4, and 5; DBH Mean = average diameter at breast height for all trees; DBH SD = standard deviation of diameter at breast height for all trees).

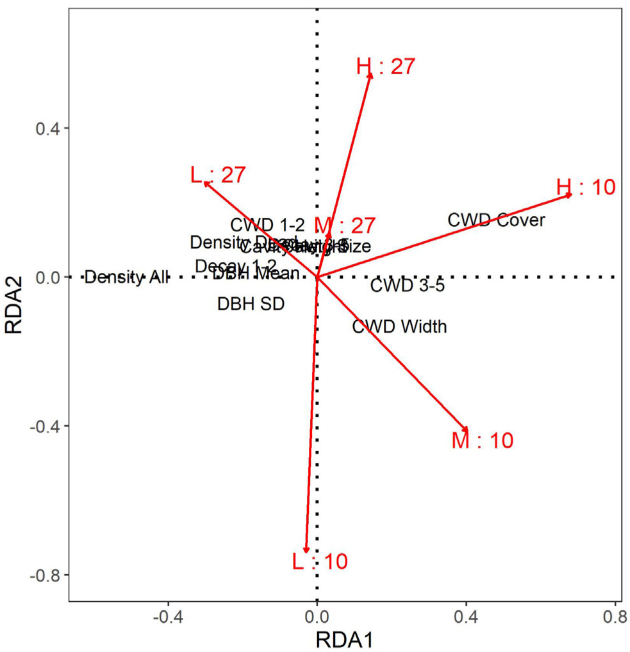

Fig. 2. Biplot from redundancy analysis assessing the relationship between vegetation structure and the interaction of time-since-fire and fire severity from two wildfires in the Pine Ridge region of Nebraska, USA. Red arrows indicate the strength of the interaction term, and red text with fire severity (high = H, moderate = M, low = L) and time-since-fire (10 = 10-year-old Dawes Complex wildfire, 27 = 27-year-old Fort Robinson wildfire) indicating the interaction term associated with each arrow. Black text elements are the "species" scores for the structure variables measured in 30 m^2 plots (Density All = live and dead tree density; Density Dead = dead tree density; Decay 1–2 = number of dead trees in decay classes 1 and 2; Decay 3–5 = number of dead trees in decay classes 3, 4, and 5; Cavity Size = average cavity size; Cavity Height = average cavity height; coarse woody debris Cover = estimated area covered by coarse woody debris; coarse woody debris 1–2 = number of pieces of coarse woody debris in decay classes 1 and 2; coarse woody debris 3–5 = number of pieces of coarse woody debris in decay classes 3, 4, and 5; DBH Mean = average diameter at breast height for all trees; DBH SD = standard deviation of diameter at breast height for all trees). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

severity associated with a given patch in the burned landscape. It follows that, historically, mixed-severity fires must have occurred with sufficient frequency in eastern ponderosa pine savannas to create the patch-level structural complexity to host historic communities that form and dissipate on short (e.g., over *years* in the case of bee communities) to long (e.g., over *decades* in the case of bird communities) time scales (Bowman et al., 2016; He et al., 2019; Hutto et al., 2008; Pausas and Parr, 2018; Taillie et al., 2018; Galbraith et al., 2019; Burkle et al., 2019). Thus, we provide indirect support that mixed-severity fire historically shaped disturbance (information) legacies in eastern ponderosa pine savannas, and more broadly, we add to the growing body of literature that supports the importance of mixed-severity fires in maintaining ponderosa pine savannas (Baker, 2015; Hutto et al., 2016; Ingalsbee, 2017; Keele et al., 2019; Odion et al., 2014, 2016; Roberts et al., 2019).

Time-since-fire alone was a poor predictor of the structural heterogeneity that emerged following fire (Hutto and Patterson, 2016; Swan et al., 2018). For example, among burnt patches, two distinct structural assemblages emerged at 10 years-since-fire: low and moderate-severity patches together comprised a distinct structural assemblage, and high-severity patches comprised a distinct structural assemblage. At 27 years-since-fire, low-severity patches retained their distinct structural assemblages, but moderate-severity patch structure shifted, becoming more similar to high-severity patches and forming a new distinct structural assemblage. Similarly, individual structures such as snag density, CWD cover, and decay classes of snags and CWD were more clearly explained by changes amongst patches that experienced different fire severities than just time-since-fire. Our results corroborate and add complexity to previous studies that only examined temporal dynamics of post-fire structures using fire as a binary process (burned vs. unburned) (Passovoy and Fulé, 2006) or that considered fire severity but only for a few years post-fire (Keyser et al., 2008).

Patches associated with moderate and high fire severity exhibited the most complex structural changes over time. Over 17 years (10–27 years-since-fire) in our space for time substitution, low-severity patch structures remained relatively constant, although low-severity patch structures such as snag density, amount of early decay-stage CWD, and number of snags at late decay-stages did shift subtly in those 17 years. In contrast, high-severity patches at 10 years-since-fire provided the clearest example of emergence and fading of a distinct structural assemblage in a discrete temporal range. Further, two specific structures–CWD cover and amount of late decay-stage CWD–were associated most closely with this ephemeral structural assemblage. Moderate-severity patches also exhibited complex behaviors, switching from similarity with low-severity patches at 10 years-since-fire to similarity to high-severity patches at 27 years-since-fire. However, moderate-severity patches at 10 years-since-fire were unique in their strong positive association with a specific structure–CWD width–and they were the most strongly negatively associated with structures associated with low-severity patches. This suggests that either moderate fire severity creates distinct structural assemblages that emerge and fade within a narrower temporal window than our study could detect (Fontaine and Kennedy, 2012; Hutto and Patterson, 2016; Tingley et al., 2018) or that current categorical severity designations (i.e., low, moderate, and high) are not optimal for quantifying fire severities' roles in structuring systems.

The complex vegetation responses to the interaction of time-since-fire and fire severity has important implications for ecological restoration. In this study system, and across much of the distribution of ponderosa pine savannas and woodlands, ecological restoration efforts tied to wildland fire management, timber management, and wildlife conservation, still seek to constrain fire and minimize its frequency, intensity, and severity (Dellasala et al., 2004; Donato et al., 2006; Hutto et al., 2016; Twidwell et al., 2019). Effectively, such approaches would mimic the vegetation responses to a single severity class (e.g., low-severity) in this study. Minimizing variation in fire severity creates structurally depauperate landscapes (Bowman et al., 2016; Hutto, 2008). The result is high structural similarity between patches and high spatiotemporal synchrony in structure across the landscape (Fontaine and Kennedy, 2012; Hutto et al., 2016; Keele et al., 2019; Taillie et al., 2018). However, endangered mammals and insects such as *Ovis canadensis* and *Speyeria idalia* prefer very low tree density; taxa such as *Sorex cinereus* use high CWD cover; the bee genera *Bombus* and *Halictus* strongly associate with ephemeral flushes of flowers generated by high tree mortality from moderate-high fire severities; and the endangered bat *Myotis thysanodes* tends to use late decay stage snags (Table 1). The result of minimizing fire severity is a simpler or more spatiotemporally homogenous landscape that does not support the full array of biodiversity present in the historic ponderosa pine community (Donovan et al., 2019; Saab et al., 2007), and tends to result in more problematic wildfire conditions and more extreme wildfire events (Dellasala et al., 2004; Donato et al., 2006). These outcomes are the opposite of savanna restoration goals (Allen et al., 2002; Bowman and Legge, 2016; Hutto et al., 2016).

5. Conclusions

Given the strength of fire severity as a driver of habitat structure over multiple decades, biodiversity assessments, species-specific research, and management should move beyond only considering simplistic fire characteristics and instead move toward incorporating both fire severity and time-since-fire into models and decisions. Currently, most species-habitat relationship research in fire-dependent systems only considers a binary burnt/unburnt classification or time-since-fire (e.g., Fuhlendorf et al., 2009; Geary et al., 2019). Clearly, burned vs unburned and time-since-fire relate to many species-specific patterns: elk (*Cervus canadensis*) select newly-burnt areas with increased forage availability (Roberts et al., 2017), black-backed woodpeckers only utilize newly-burnt forest patches for breeding (Saracco et al., 2011; Tingley et al., 2018). However, we show that fire severity, time-since-fire, and the interaction of fire severity and time-since-fire explain a majority of habitat structural characteristics for decades post-fire. For example, in our study, we found fire severity influenced tree and snag characteristics that are highly related to multiple bat species' habitat preferences. Big brown bats (*Eptesicus fuscus*) roosting preferences are highly related to snag diameter (Arnett and Hayes, 2009). Fringed myotis (*Myotis thysanodes*) and long-legged myotis (*Myotis volans*) strongly prefer early-mid decay stage snags for roosting habitat (Baker and Lacki, 2006; Weller and Zabel, 2001), and the threatened northern long-eared bat (*Myotis septentrionalis*) select for burnt sites with very particular coarse woody debris cover and decay stage as well as high snag densities (Arnett and Hayes, 2009). This, along with the ease in obtaining remotely-sensed fire severity data (Eidenshink et al., 2007), suggests that fire severity and its interaction with time-since-fire merit use as surrogates for specific habitat structures as well as serving as covariates in habitat selection or species distribution modeling (Buchalski et al., 2013; Chia et al., 2015; Fontaine and Kennedy, 2012).

Our results support using mixed-severity fire to restore ponderosa pine savanna in such a way that fosters diverse information legacies that were shaped by and helped perpetuate ponderosa pine savannas historically (Hutto et al., 2016; Johnstone et al., 2016; Pausas and Parr, 2018; Roberts et al., 2019). At a minimum, we demonstrate the array of structural heterogeneity that eastern ponderosa pine savanna restoration efforts should not ignore (Bowman and Legge, 2016; Odion et al., 2014). Although studies will continue exploring the particulars of "how much" and "how often" mixed-severity fire should be applied to restore self-reinforcing feedbacks in ponderosa pine savannas, historic evidence from ponderosa pine savannas similar to our study site suggests mixed-severity fires occurred as often as every 15 – 30 years (Sieg, 1997; Wendtland and Dodd, 1992). Additionally, there is a growing number of successful passive and active approaches to implementing mixed-severity fire to restore savanna structure and function. For passive restoration, resilience theory suggests that allowing naturally-occurring mixed-severity fires to burn without human interference (in sparsely-populated areas) can passively restore and maintain savannas (McWethy et al., 2019). For example, Larson et al. (2013) demonstrate how latent resilience to fire in unlogged, fire-excluded ponderosa pine systems (similar conditions to our study system) allows repeated mixed-severity wildfires to passively restore ponderosa pine woodlands and savannas. For active restoration, studies in North America (Twidwell et al., 2013; Twidwell et al., 2016) and South Africa (Smit et al., 2016) show repeatedly implementing prescribed high-intensity fires can restore savanna structure and function. Alongside these studies, our findings support moving beyond using fire suppression, pre-fire tree thinning, or post-fire salvage logging to constrain future fires to low intensities with the goal of preventing so-called "catastrophic" state transitions in ponderosa pine systems (Donovan et al., 2019; Twidwell et al., 2019).

CRediT authorship contribution statement

Caleb P. Roberts: Conceptualization, Methodology, Data curation, Formal analysis, Project administration, Visualization, Writing - review and editing. **Victoria M. Donovan:** Conceptualization, Methodology, Data curation, Formal analysis, Project administration, Visualization, Writing - review and editing. **Sarah Nodskov:** Conceptualization, Methodology, Data curation, Formal analysis, Project administration, Visualization, Writing - review and editing. **Emma Keele:** Conceptualization, Data curation, Visualization, Writing - review and editing. **Craig R. Allen:** Methodology, Resources, Funding acquisition, Writing - review & editing. **David Wedin:** Resources, Funding acquisition, Writing - review & editing. **Dirac Twidwell:** Conceptualization, Resources, Funding acquisition, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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