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Understory vegetation indicates historic fire regimes in ponderosa pine-dominated ecosystems in the Colorado Front Range

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Abstract

Question: Can current understory vegetation composition across an elevation gradient of *Pinus ponderosa*-dominated forests be used to identify areas that, prior to 20th century fire suppression, were characterized by different fire frequencies and severities (i.e., historic fire regimes)?

Location: *P. ponderosa*-dominated forests in the montane zone of the northern Colorado Front Range, Boulder and Larimer Counties, Colorado, USA.

Methods: Understory species composition and stand characteristics were sampled at 43 sites with previously determined fire histories. Indicator species analyses and indirect ordination were used to determine: (1) if stands within a particular historic fire regime had similar understory compositions, and (2) if understory vegetation was associated with the same environmental gradients that influence fire regime. Classification and regression tree analysis was used to ascertain which species could predict fire regimes.

Results: Indicator species analysis identified 34 understory species as significant indicators of three distinct historic fire regimes along an elevation gradient from low- to high-elevation *P. ponderosa* forests. A predictive model derived from a classification tree identified five species as reliable predictors of fire regime.

Conclusions: *P. ponderosa*-dominated forests shaped by three distinct historic fire regimes have significantly different floristic composition, and current understory compositions can be used as reliable indicators of historical differences in past fire frequency and severity. The feasibility demonstrated in the current study using current understory vegetation properties to detect different historic fire regimes, should be examined in other fire-prone forest ecosystems.

Keywords: CART; fire regime; fire severity; floristic association; indirect ordination; NMS; *Pinus ponderosa*.

Nomenclature: Harrington, (1954).

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Introduction

Across numerous ecosystems, such as *Pinus ponderosa* forests in North America, which range from western Canada to central Mexico (Critchfield & Little 1966), fire has been a key disturbance that historically shaped ecosystem structure (Peet 2000). In the northern Front Range of Colorado, prior to permanent Euro-American settlement and associated land-use changes of the late 19th century, *P. ponderosa*-dominated forests experienced a range of historic fire regimes (Veblen & Lorenz 1986; Mast et al. 1998; Brown et al. 1999; Veblen et al. 2000; Kaufmann et al. 2001; Ehle & Baker 2003; Sherriff 2004; Sherriff & Veblen 2006, 2007). Low elevation, xeric sites were characterized mainly by a regime of higher frequency but low severity fires, whereas higher elevations were characterized by a variable severity (also known as mixed severity) regime including some relatively long fire intervals and some high severity fires; in the former fire intensity typically was too low to kill large trees, but in the latter many fires were of sufficient intensity to kill large a proportion of the canopy trees (Veblen & Lorenz 1986; Brown et al. 1999; Kaufmann et al. 2000; Ehle & Baker 2003; Sherriff & Veblen 2006, 2007). Due to the spatial variability of historic fire regimes even within the same cover type (i.e., *P. ponderosa*), and the current management focus on restoring historic fire regimes and fuel structures (Healthy Forest Restoration Act 2003), an ability to efficiently and accurately predict historic fire regimes is highly desirable. Therefore, the aim of the current study was to determine if the attributes (floristic composition and species abundance) of the current understory vegetation can identify variation in historic fire regime in the *P. ponderosa*-dominated forests of the northern Front Range.

Although understory species have long been used as indicators of site quality and potential natural vegetation (Daubenmire 1943; Marr 1961; Mueller-Dombois & Ellenberg 1974; Frey 1978; Pfister & Arno 1980), understory vegetation has not previously been used as a tool for assessing historic fire regimes. The over-arching hypothesis of the current study is that the abiotic factors controlling understory composition along an elevation gradient should also predict site productivity and hence fuel structures that, in turn, influence fire severity and frequency. Previous research showed that present cover type (i.e., based on degree of dominance by *P. ponderosa* and other tree species) was not a reliable indicator of historic fire regime (Sherriff 2004; Sherriff & Veblen 2007). However, variation in understory composition within stands currently dominated by *P. ponderosa* potentially reflects relatively stable abiotic site factors (mostly elevation and topography) that also determine site productivity (Pfister & Arno 1980) and potentially, historic fuel types and fire regimes. For the *P. ponderosa*-dominated cover type of the Colorado Front Range, between-stand variations in the presence and abundance of herb and shrub species have long been used as indicators of spatial variation in abiotic site factors (Peet 1981; Hess & Alexander 1986). We expect that the same abiotic factors (e.g., temperature, topography, soil moisture) that influence understory vegetation composition also influence site productivity and stand structure attributes that determine fuel loads, and therefore, fire regime. Furthermore, abiotic variables have not changed significantly over the time period of interest (i.e., ca. 1700 AD to present). It is assumed that the magnitude of any climate variability since ca. 1700 AD (i.e., the time scale considered in the historic fire regime concept; Sherriff 2004) has not been significant enough to invalidate the spatial association of current understory composition and historic fire regimes.

The overall aim of this study was to determine if ponderosa pine forest stands with different historic fire regimes are associated with characteristic understory plant species cover and abundance across environmental gradients in the northern Colorado Front Range. The specific objective was to determine understory composition at sites of known historic fire regime, as evidenced in Sherriff (2004), and compare understory composition for three types of historical fire regime: (1) low-severity, (2) moderate-severity, and (3) high-severity fire regimes; the latter two comprise the variable-severity fire regime defined by Sherriff & Veblen (2007) (Table 1).

Methods

Study area

The 60 875-ha study area extends from ca. 1800 to 2800 m in the montane zone on the eastern slope of the northern Colorado Front Range (Fig. 1). The highly continental climate of the Front Range includes a trend towards higher precipitation with increasing elevation. At 1639 m, the mean annual precipitation is 480 mm and the mean annual temperature is 10.6°C (Boulder Station, 1897-2004, Colorado Climate Center). At 2576 m, the mean annual precipitation is 530 mm and the mean annual temperature is 4.8°C (Allenspark Station, 1948-1994, Colorado Climate Center). Soils are derived from Precambrian granites and similar schists and gneisses, which are generally rocky and poorly developed (Peet 2000).

The vegetation pattern of the Front Range is strongly influenced by topographic position, with greater moisture availability at higher elevation (Peet 1981). The montane ponderosa pine zone extends from approximately 1800 to 2850 m and is largely defined by the distribution of *P. ponderosa*. In the lower montane zone (1800-2350 m), forests vary from open park-like stands of *P. ponderosa* with abundant grass and herbaceous cover at the plains–grassland ecotone, to dense stands mixed with *Pseudotsuga menziesii* (Douglas-fir) at more mesic sites and on north-facing slopes. In the upper montane zone, from 2350 to 2850 m, topographic

Table 1. The mean fire intervals and stand age characteristics that delineate each fire regime category. Adapted from Sherriff (2004).

Fire regime	Number of sample sites	Mean fire interval (years)	% live trees established pre-fire scar date	% live trees established during post-fire recruitment period
Low severity	8	<30	≥ 40	<20
Moderate severity	16	$\geq$ 30-40	<70	$\geq$ 20-70
High severity	19	>40	<20	>70

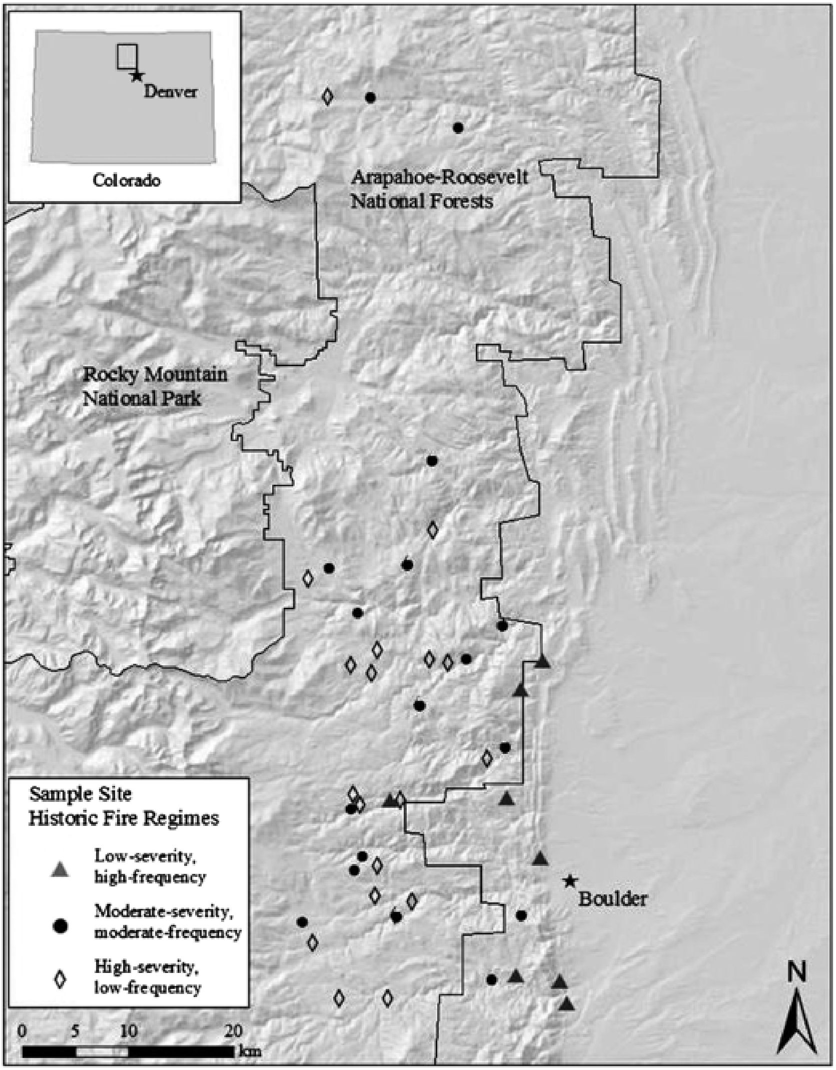

Fig. 1. Map of the 43 sites sampled for understory vegetation distributed within the three historic fire regimes (Sherriff 2004): low-severity fire regime (▲; $n = 8$), moderate-severity fire regime (•; $n = 17$), and high-severity fire regime (◇ ; $n = 18$).

position becomes increasingly important, with dense mixed stands of *P. ponderosa* and *P. menziesii* on north-facing slopes, and less dense pure stands of *P. ponderosa* on south-facing slopes. Above 2350 m, the abundance of grass and herbaceous cover declines greatly within dense stands of *P. ponderosa* and *P. menziesii*.

Although other cover types dominated by *Populus tremuloides* (quaking aspen), *Pinus flexilis* (limber pine), and/or *Pinus contorta* (lodgepole pine) occur frequently in the upper montane zone (Marr 1961; Peet 1988; Kaufmann et al. 2006), they do not occur in the lower montane zone, and the historic fire regimes and edaphic conditions in these cover types are often dissimilar to those of the *P. ponderosa* cover type. Therefore, sample sites for this study were limited to *P. ponderosa*-dominated stands. The area of frequent but low-severity historic fires occurs mainly from 1950 to 2200 m, and the area of variable-severity fire regime (including a significant component of high-severity fires) occurs from ca. 2200 to 2800 m in the *P. ponderosa* zone (Sherriff & Veblen 2006, 2007).

Field sampling

We sampled understory vegetation plots within 43 of the 54 sites sampled by Veblen et al. (2000) and Sherriff (2004) for fire history and stand age structure. For simplicity, we refer to each fire regime in terms of its predominant severity class, although each fire regime represents a combination of characteristic severity and frequency (mean fire interval) (Table 1). Eight sample sites were located within the low-severity fire regime, all of which were located within the lower montane zone. Of the 17 sites in the moderate-severity fire regime, six were located in the lower montane zone, and 11 in the upper montane zone. All but one of the 18 sites in the high-severity fire regime were in the upper montane zone. In total, 15 sample sites were located in the lower montane elevation zone, and 28 in the upper montane elevation zone. Given the potential for recent fires and other disturbances to influence understory composition, sample sites that had been burned or were disturbed by mining or other land-use practices within the past ca. 50 years were excluded. Each site was sampled with eight 50×2 m belt transects placed in a stratified–random manner (Mueller-Dombois & Ellenberg 1974). Transects were oriented perpendicular to the slope.

Overstory and understory vascular plant species data and substrate type were recorded in five 2-m^2 microplots placed every 10 m along the length of each belt transect. Vegetation <2 m in height was considered understory. Saplings over 2 m in height were considered part of the forest canopy and recorded as overstory. We estimated percentage canopy cover of all overstory and understory species visually, and assigned each species one of six Braun-Blanquet cover–abundance scores (+ = <1%, 1 = 1-5%, 2 = 6-25%, 3 = 26-50%, 4 = 51-75%, 5 = >75%, Mueller-Dombois & Ellenberg 1974). The presence of additional species within the belt transect not captured in the microplots was recorded for calculation of species richness, which was used as a stand variable in the secondary matrix in the ordination (see below). Substrate type was recorded as fine organic litter, rock, bare mineral soil, coarse woody debris, or tree boles.

Data processing and analysis

We employed non-metric multidimensional scaling (NMS), an indirect ordination technique, to graphically arrange sites according to floristic similarity. We independently correlated the arrangement of sample sites in species space with environmental/stand variables (PC-ORD v. 4; McCune & Mefford 1999). NMS is a robust multivariate ordination technique for identifying gradients important in structuring community data across broad spatial scales (McCune & Mefford 1999; Urban et al. 2002). After ordination of the sites based on species abundances, NMS independently assesses the relationship of the environmental variables to the structure of the community data, providing an assessment of relationships between community data and environmental variables (Kruskal & Wish 1978; Clarke 1993). We chose two dimensions using the Sørensen relative distance measure and followed analytical recommendations of McCune & Grace (2002) related to stress value, stability criterion, and number of iterations.

In the ordination analysis, the primary data matrix was composed of the abundance values of 93 genus/species (taxa). Six understory vascular plants could only be positively identified to genus; all understory vascular plants are herein defined as “species” for simplicity. We converted Braun-Blanquet cover–abundance scores to the mean percentage cover in each class (+ = 0.5%, 1 = 2.5%, etc.; Podani 2006). We averaged the percentage cover values of each species across all 40 microplots per site to obtain the average percentage cover of each species in a study site. Then, we calculated a synthetic abundance value (Whittaker 1967) by summing the relative percentage canopy cover and percentage frequency values of each species, which expresses the species overall significance or conspicuousness in a site more effectively than either value can independently. Species with an abundance value <5 or that occurred in fewer than three sample sites were defined as rare and eliminated from the data matrix, leaving a total of 93 species for analysis in the primary data matrix.

The secondary matrix was composed of 21 environmental and stand variables, which were composed of data collected at the time of field sampling, information obtained from Sherriff (2004), and additional vegetation composition and site characteristics calculated from the collected and available data. The 14 variables that comprise data collected at the time of understory sampling were total percentage cover of overstory trees, fine organic litter depth (cm), cover of fine organic litter, dead wood, bare mineral soil, rock, and live tree boles (expressed as abundance value), and cover of overstory tree species *Pinus ponderosa*, *Pseudotsuga menziesii*, *Pinus contorta, Populus tremuloides, Pinus flexilis*, *Juniperus scopulorum*, and *Picea engelmanii* (where the abundance value of each tree species was calculated as a separate variable). The four variables that comprise data obtained from Sherriff (2004) were slope, aspect, elevation, and fire regime. Site aspect azimuths were assigned to one of four classes, 1 for north (316°-45°), 2 for east (46°-135°), 3 for west (226°-315°), and 4 for south (135°-225°), and fire regime was recorded numerically as 1 (low severity), 2 (moderate severity), or 3 (high severity).

The three variables that comprise data calculated from either collected or previously obtained data were species richness, total cover of live understory (expressed as abundance value), and potential solar radiation. We calculated potential solar radiation using cosine-transformed aspect (azimuth), slope (in degrees), and latitude (McCune & Keon 2002).

Pearson correlation coefficients (r) calculated for each species, and the environmental/stand variables in relation to primary ordination axes were used to assess the variation in floristic composition along environmental gradients (Kent & Coker 1992), and specifically, variation in fire regime. A power table was used to determine the cutoff for statistically significant r-values based on a sample size of 43 sites. An r of 0.3 ($r^2 = 0.09$) indicates a power (p) of 0.05, and an r-value of 0.393 ($r^2 = 0.154$) indicates a power (p) of 0.01 (Siegle 2006).

We also performed a multi-response permutation procedure (MRPP) to test whether the sites grouped by pre-defined fire regime categories were more floristically similar than expected due to chance. A rank-transformed Sørensen distance measure was used because it is less sensitive to outliers, reduces the loss of sensitivity of distance measures in heterogeneous datasets, and is analogous in theory to NMS (McCune & Grace 2002). The chance-corrected within-group agreement (A) and probability (p) of smaller or equal Δ were calculated using the default weighting formula (McCune & Mefford 1999), in which Δ is the measure of similarity represented by the weighted mean within-group distance (McCune & Grace 2002).

An indicator species analysis (ISA) was also performed to reveal if any species were strongly correlated with a particular fire regime group. An indicator value for each species was calculated with PC-ORD by multiplying concentration of abundance and fidelity of occurrence. A p-value associated with each indicator value is given to express the probability of randomly obtaining a higher indicator value (McCune & Grace 2002), which indicates statistical significance of an indicator value even if it is considerably lower than 100. The indicator values from randomly reassigned fire regime groups and the P-values were obtained from a Monte Carlo test of significance of observed maximum indicator values of species against 1000 randomized permutations of fire regime groups.

Classification and regression trees (CARTs)

Initial ordinations revealed that (1) sample sites with the same fire regime clustered together in ordination space according to species composition, (2) the three *a priori* fire regime groups differed significantly from one another, and (3) specific understory species are significant indicators of the different fire regimes. Consequently, we used a CART to investigate the potential utility of understory composition in predicting historical fire regimes (JMP v.6, SAS Institute Inc.). To create the CART, historic fire regime was the dependent variable and understory species were the independent (predictor) variables. Abiotic environmental variables were not included in this model to explicitly test the predictive capacity of understory species. The CART divides the data into progressively smaller, more homogeneous subgroups of the dependent categorical variable (fire regime) based on species abundance. Each group split increases the homogeneity of the sub-group and r^2 value. Ten consecutive runs of a five-fold cross validation estimated the predictive power and accuracy of the model.

Results

Vegetation community composition

One hundred seventy-three understory species were identified in the vegetation microplots: 106 forbs, 33 graminoids, 27 woody shrubs or subshrubs, six tree species, and one fern species. Abundance and frequency of exotic species and seedling trees were relatively low in all sites. Sites with the low-severity fire regime had an overstory dominated by *P. ponderosa*, *Artemisia ludoviciana* was the most abundant forb species, and (herein from highest to lowest abundance) *Carex* spp., *Bromus tectorum*, *Elymus lanceolata*, and *Andropogon gerardii* were the most abundant graminoid species. Sites in the moderate-severity fire regime had *P. ponderosa* overstory with occasionally co-dominant *J. scopulorum* and *P. menziesii*. These sites commonly had an abundant shrub understory composed of *Cercocarpus montanus*, *Purshia tridentata, Artemisia frigida*, *Rhus trilobata*, and/or *Ribes cereum*. In contrast to the lower elevation sites, high-elevation sites in the moderate-severity fire regime had fewer graminoids and a more variable overstory composition. The sample sites in the high-severity fire regime had variable overstory species compositions, although *P. contorta* and *P. tremuloides* were more abundant in this fire regime than the other fire regimes. These sites had the highest overall abundance value of shrub species *Purshia tridentata*, *Juniperus communis*, and *Arctostaphylos uva-ursi*. Common forb species in these stands were *Antennaria* spp., *Sedum lanceolatum*, *Thermopsis divaricarpa*, and *Packera fendleri*.

Ordination

Axis 1 accounted for 72% of the variation among sites and Axis 2 accounted for 14.4% of the variation, resulting in a total of 86.4% of the variance captured by the ordination (Fig. 2). The three site clusters that represent aggregations of fire regime groups are arranged along Axis 1. This suggests that sites within the same fire regime have floristic compositions that are distinct from sites within other fire regimes. The low-severity fire regime is the most homogeneous cluster. The moderate-severity fire regime appears to be floristically distinct from the other two fire regimes, but is less homogeneous and more widely dispersed in ordination space than the other two fire regimes, which demonstrates the complexity of this fire regime, and the greater difficulty in clearly delimiting it. The cluster of high-severity fire regime sites is farthest from the low-severity fire regime sites in ordination space.

Fifty-five species have a significant ($P \leq 0.05$) correlation with Axis 1. *A. uva-ursi*, *A. ludoviciana*, *Heterotheca villosa*, and *J. communis* have the highest correlation values, each with $r^2 > 0.50$ ($P < 0.01$) (Table 2). Twenty-four species have a significant correlation with Axis 2 ($P \leq 0.05$) (Table 3). *Campanula rotundifolia*, *Purshia tridentata*, and *Ribes cereum* have the highest correlation values, each with $r^2 > 0.30$ ($P < 0.01$).

With Axis 1, species richness is strongly negatively correlated ($r^2 = 0.63$, $P < 0.01$) and *P. contorta* overstory is positively correlated ($r^2 = 0.35$, $P < 0.01$). Elevation is strongly positively correlated ($r^2 = 0.54$, $P < 0.01$) and slope angle is negatively correlated ($r^2 = 0.28$, $P < 0.01$), suggesting that site arrangement along Axis 1 can be attributed to a combination of floristic and environmental variables (Table 4). Percentage cover of bare ground is positively correlated with Axis 2, while tree bole and litter are negatively correlated, each accounting for over 20% of the variance in Axis 2 ($P < 0.01$) (Table 5).

MRPP and indicator species analysis (ISA)

MRPP showed that the sample sites in each of the three fire regime categories are floristically more similar than expected due to chance. A rank-transformed distance matrix showed that chance-corrected within-group agreement (*A*) was 0.1636. The probability of smaller or equal average distance (Δ) with random grouping (*P*) was 0.0001. When the moderate-severity and high-severity fire regimes were combined into one category (variable severity),

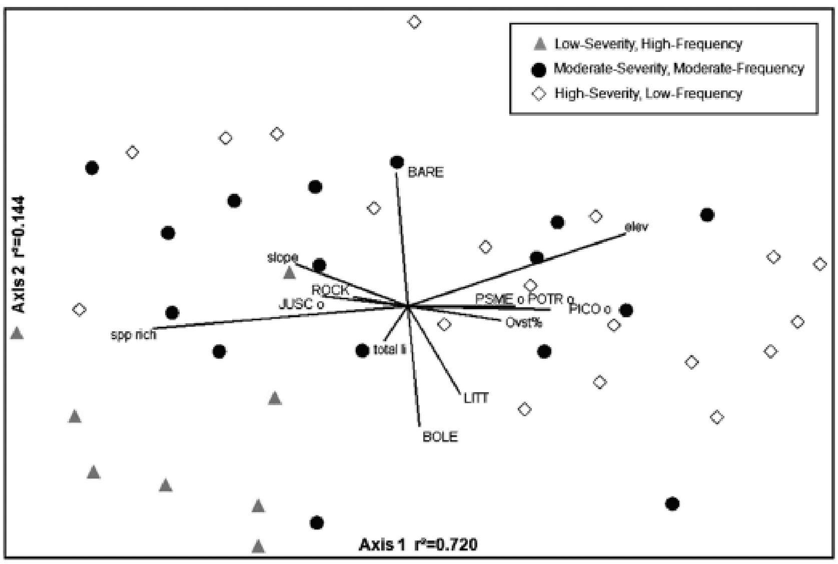

Fig. 2. NMS ordination of understory composition of 43 sample sites and groupings of sample sites according to historic fire regime types with joint plot overlay. Symbols for historic fire regimes are: (1) low-severity fire regime (▲), (2) moderate-severity fire regime (•), and (3) high-severity fire regime (◇). Strength and direction of correlations of environmental and stand variables (see Tables 4 and 5 for codes), with Axes 1 and 2 represented by straight lines, where only significant correlations with either axis ($P \leq 0.05$) are shown.

Table 2. Results of NMS ordination showing the 55 taxa with abundance values that were significantly correlated with Axis 1 ($P \leq 0.05$). *Non-native species. †Most likely *P. compressa* or *P. pratensis*, but characteristics for positive identification not present.

Primary matrix: species				
Significant correlations with Axis 1				
Taxa	Code	r	r^2	P
Arctostaphylos uva-ursi	ARUV	0.78	0.61	< 0.01
Artemisia ludoviciana	ARLU	– 0.77	0.59	< 0.01
Heterotheca villosa	HEVI	– 0.75	0.56	< 0.01
Juniperus communis	JUCO	0.73	0.53	< 0.01
Elymus lanceolata	ELLA	– 0.68	0.46	< 0.01
Opuntia polyacantha	OPPO	– 0.67	0.44	< 0.01
Helianthus pumilus	HEPU	– 0.66	0.44	< 0.01
Scutellaria brittonii	SCBR	– 0.63	0.40	< 0.01
Tradescantia occidentalis	TROC	– 0.63	0.40	< 0.01
Artemisia frigida	ARFR	– 0.59	0.34	< 0.01
*Bromus tectorum**	BRTE	– 0.58	0.34	< 0.01
Stipa comata	STCO	– 0.58	0.34	< 0.01
Bouteoula gracilis	BOGR	– 0.57	0.33	< 0.01
Grindelia squarrosa	GRSQ	– 0.57	0.32	< 0.01
Populus tremuloides – seedling	POTR	0.53	0.29	< 0.01
Sedum lanceolatum	SELA	0.53	0.28	< 0.01
Aster porteri	ASPO	– 0.52	0.27	< 0.01
Erigeron colomexicanus	ERCO1	– 0.50	0.25	< 0.01
Eriogonum umbellatum	ERUM	– 0.49	0.24	< 0.01
*Capsella bursa-pastoris**	CABU	– 0.49	0.24	< 0.01
Linum genistifolium	LIGE	– 0.47	0.22	< 0.01
Rubus deliciosus	RUDE	– 0.46	0.21	< 0.01
Thermopsis divaricarpa	THDI	0.46	0.21	< 0.01
*Tragopogon dubius**	TRDU	– 0.45	0.20	< 0.01
Muhlenbergia montana	MUMO	– 0.45	0.20	< 0.01
Padus virginiana	PAVI	– 0.44	0.20	< 0.01
Packera fendleri	PAFE	0.44	0.20	< 0.01
*Ambrosia trifida**	AMTR	– 0.44	0.19	< 0.01
Poa spp.*	POSP	– 0.44	0.19	< 0.01
Solidago spp.	SOSP	0.43	0.19	< 0.01
Chenopodium fremontii	CHFR	– 0.41	0.17	< 0.01
Rhus trilobata	RHTR	– 0.41	0.17	< 0.01
Allium cernum	ALCE	– 0.41	0.16	< 0.01
Ribes cereum	RICE	– 0.40	0.16	< 0.01
Erigeron compositus	ERCO2	0.40	0.16	0.01
Yucca glabra	YUGL	– 0.39	0.15	0.01
Leucocrinum montanum	LEMO1	– 0.39	0.15	0.05
Cerastium strictum	CEST	– 0.39	0.15	0.05
Andropogon gerardii	ANGE	– 0.38	0.15	0.05
Bromus lenatipes	BRLE	– 0.38	0.14	0.05
Lesquerella montana	LEMO2	– 0.37	0.14	0.05
Pinus contorta – seedling	PICOs	0.37	0.14	0.05
Pinus flexilis – seedling	PIFLs	0.37	0.14	0.05
Geranium caespitosum	GECA	– 0.35	0.12	0.05
*Poa compressa**	POCO	– 0.34	0.11	0.05
Symphoricarpos rotundifolius	SYRO	– 0.33	0.11	0.05
Rosa woodsii	ROWO	0.33	0.11	0.05
Antennaria spp.	ANSP	0.33	0.11	0.05
Potentilla fissa	POFI	0.33	0.11	0.05
Festuca saximontana	FESA	0.31	0.10	0.05
Penstemon virens	PEVI	0.31	0.10	0.05
Pinus ponderosa – seedling	PIPO s	0.31	0.09	0.05
Erysimum captiatum	ERCA	– 0.30	0.09	0.05
Lathyrus eucosmus	LAEU	– 0.30	0.09	0.05
Purshia tridentata	PUTR	– 0.30	0.09	0.05

Table 3. Results of NMS ordination showing the 24 taxa with abundance values that were significantly correlated with Axis 2 ($P \leq 0.05$).

Significant correlations with Axis 2				
Taxa	Code	r	r^2	p
Campanula rotundifolia	CARO	– 0.64	0.41	< 0.01
Purshia tridentata	PUTR	0.60	0.36	< 0.01
Ribes cereum	RICE	0.58	0.34	< 0.01
*Poa compressa**	POCO	– 0.53	0.28	< 0.01
Artemisia frigida	ARFR	0.53	0.28	< 0.01
Allium cernum	ALCE	– 0.48	0.23	< 0.01
Poa spp.*	POSP	– 0.48	0.23	< 0.01
*Tragopogon dubius**	TRDU	– 0.46	0.21	< 0.01
Cerastium strictum	CEST	– 0.44	0.20	< 0.01
*Taraxacum officinale**	TAOF	– 0.41	0.17	< 0.01
Jamesia americana	JAAM	0.41	0.17	< 0.01
Geranium caespitosum	GECA	0.40	0.16	0.01
*Alyssum parviflorum**	ALPA	– 0.39	0.15	0.05
Danthonia paryii	DAPA	– 0.38	0.15	0.05
Liatris punctata	LIPU	– 0.38	0.14	0.05
*Ambrosia trifida**	AMTR	– 0.38	0.14	0.05
Andropogon gerardii	ANGE	– 0.37	0.14	0.05
Carex spp.	CASP	– 0.36	0.13	0.05
*Bromus tectorum**	BRTE	– 0.35	0.12	0.05
Achillea millefolium	ACMI	– 0.35	0.12	0.05
Muhlenbergia montana	MUMO	0.34	0.11	0.05
Erigeron colomexicanus	ERCO1	– 0.32	0.10	0.05
Grindelia squarrosa	GRSQ	– 0.32	0.10	0.05
Lathyrus eucosmus	LAEU	– 0.31	0.09	0.05

Table 4. Results of NMS ordination showing the 10 environmental and stand variables that are significantly correlated with Axis 1 ($P \leq 0.05$). ROCK, LITT, PICO o, POTR o, JUSC o, and PSME o were analyzed with abundance values.

Secondary matrix: stand characteristics				
Significant correlations with Axis 1				
Variable	Graph code	r	r^2	P
Species richness	spp rich	– 0.80	0.63	< 0.01
Elevation	elev	0.74	0.54	< 0.01
Pinus contorta overstory cover	PICO o	0.59	0.35	< 0.01
Slope	slope	– 0.53	0.28	< 0.01
Populus tremuloides overstory cover	POTR o	0.52	0.27	< 0.01
Overstory percentage cover	Ovst%	0.48	0.23	< 0.01
Juniperus scopulorum overstory cover	JUSC o	– 0.46	0.21	< 0.01
Pseudotsuga mensizii overstory cover	PSME o	0.41	0.17	< 0.01
Rock cover	ROCK	– 0.37	0.13	0.05
Fine organic litter cover	LITT	0.36	0.13	0.05
Total live understory cover	total li	0.30	0.09	0.05

the chance-corrected within-group agreement (A) decreased to 0.1214, which indicates less, although still statistically significant, fire regime group homogeneity. The probability of smaller or equal Δ increases to 0.0002, which is slightly less significant than the three fire regime group analysis.

Table 5. Results of NMS ordination showing the five environmental and stand variables that are significantly correlated with Axis 2 ($P \leq 0.05$). Total cover of BARE, BOLE, and LITT were analyzed with abundance values.

Significant correlations with Axis 2				
Variable	Graph code	r	r^2	P
Bare mineral soil cover	BARE	0.58	0.33	<0.01
Live tree bole cover	BOLE	– 0.55	0.30	<0.01
Fine organic litter cover	LITT	– 0.47	0.22	<0.01
Elevation	elev	0.43	0.18	<0.01
Slope	slope	0.33	0.11	0.05

ISA of the three fire regimes revealed that 35 of the 93 genus/species in the primary data matrix indicate a particular fire regime ($P \leq 0.05$). Twenty-eight species are indicators of the high-frequency fire regime, five species are indicators of the low-frequency fire regime, and two species are indicators of the moderate-frequency fire regime (Table 6). There were 32 significant indicator species when two fire regime categories were analyzed (results not shown).

CART analysis

The CART showed that the understory indicator species split into six branches that accounted for 69% of the variance in the model and predicted the three different fire regimes relatively well (Fig. 3). This model independently grouped 75% of the low-severity sites, 50% of the moderate-severity sites, and 73.68% of the high-severity sites. The first split divided the low-severity fire regime from the other two fire regimes, with an abundance value >7.83 for the annual composite, *Grindelia squarrosa*. A subsequent branching indicated that six sites in the low-severity fire regime also had an abundance value <32.06 for *Artemisia frigida*, a native perennial forb. A homogeneous group of eight high-severity fire regime sites was predicted by an abundance value <5.18 of the native perennial forb *Harbouria trachypleura*. High-severity fire regime sites that had an abundance value >5.18 of *H. trachypleura* also had an abundance value >7.78 of the native perennial *Packera fendleri*. The majority of the moderate-severity sites had an abundance value <7.78 of *P. fendleri*, and a homogeneous group of moderate-severity sites also had an abundance value >8.80 of the native perennial grass *Muhlenbergia montana*. Ten runs of a five-fold cross validation of the model calculated an r^2 value of 0.499 for the randomization test, indicating statistically significant results.

Table 6. Results of ISA. Thirty-four taxa were identified as significant ($P<0.05$) indicators of a particular fire regime group. *Non-native species.

Taxa	Group indicated	Observed indicator value	Indicator value from randomized groups	P
Grindelia squarrosa	Low severity	78.9	22.6	0.001
Stipa comata	Low severity	68.0	21.0	0.001
*Bromus tectorum**	Low severity	67.3	23.5	0.001
Erigeron colomexicanus	Low severity	64.3	15.9	0.001
Andropogon gerardii	Low severity	62.5	11.8	0.001
*Poa compressa**	Low severity	59.6	12.7	0.001
Opuntia polyacantha	Low severity	57.0	20.6	0.001
Aster porteri	Low severity	57.2	28.0	0.002
*Tragopogon dubius**	Low severity	54.7	13.8	0.002
Allium cernum	Low severity	61.7	24.9	0.003
*Ambrosia trifida**	Low severity	45.5	12.8	0.003
Liatris punctata	Low severity	37.5	9.4	0.003
Psoralidium tenuiflorum	Low severity	37.5	9.4	0.003
Yucca glabra	Low severity	39.5	14.1	0.005
Cerastium strictum	Low severity	44.5	19.0	0.006
*Taraxacum officinale**	Low severity	32.3	11.6	0.008
Lathyrus eucosmus	Low severity	37.5	9.6	0.009
Padus virginiana	Low severity	36.3	14.8	0.010
Danthonia parryii	Low severity	33.2	11.0	0.012
Leucocrinum montanum	Low severity	33.4	14.2	0.013
Artemisia ludoviciana	Low severity	44.6	36.2	0.014
Elymus lanceolata	Low severity	45.8	26.9	0.015
Tradescantia occidentalis	Low severity	33.1	16.1	0.021
Poa spp.*	Low severity	42.4	23.7	0.024
Helianthus pumilus	Low severity	38.3	19.7	0.024
Rhus trilobata	Low severity	27.0	11.4	0.039
Mertensia lanceolata	Low severity	42.5	28.4	0.043
Geranium caespitosum	Moderate severity	49.3	32.4	0.013
*Verbascum thapsus**	Moderate severity	23.5	10.3	0.036
Juniperus communis	High severity	52.4	27.7	0.003
Packera fendleri	High severity	54.6	25.7	0.004
Erigeron compositus	High severity	38.1	16.7	0.010
Arctostaphylos uva-ursi	High severity	48.2	31.7	0.022
Solidago spp.	High severity	45.2	31.8	0.038

Discussion

Indirect ordination

The 43 sample sites are clustered into three fire regime categories, and arranged along Axis 1, which is strongly positively correlated with elevation and negatively correlated with species richness (Fig. 2, Table 4). The low-severity fire regime group is most conspicuously clustered, which is consistent with the previous finding that among the abiotic variables, historic fire regime is most strongly correlated with elevation (Sherriff 2004; Sherriff & Veblen 2007). The correlation of overstory cover of *P. contorta*, *P. menziesii*, and *P. tremuloides* with Axis 1 can generally be attributed to higher elevation. *P. ponderosa* does not appear as an environmental correlate because it was abundant in all sample sites, and consequently had no discriminating value. While it is expected that overall overstory cover and overstory cover of certain species will be higher in high-severity fire regimes, where abundant fuel would promote crown fires, the NMS results suggest that species richness and elevation have stronger associations with fire regime.

Although an important component of the moisture–topography gradient, potential solar radiation (derived from transformed aspect) did not have a significant correlation with either axis. This result may reflect the under-representation of north-facing slopes in the original field sampling of fire scars. Few north-facing slopes were sampled in previous supporting fire history studies because *P. ponderosa* is usually not dominant on moist, more shaded aspects (e.g., Veblen et al. 2000; Sherriff 2004; Sherriff & Veblen 2006, 2007).

MRPP and ISA

MRPP showed that the groups of sites in each fire regime category were significantly dissimilar floristically from one another. Thus, understory composition can be used to distinguish among the three historic fire regimes.

ISA revealed 34 different species as significant indicators of fire regime (Table 6). Only six species had an indicator value greater than 60. As a whole, the species in this study did not have high indicator values for two reasons. First, many species had abundance values that were too low to infer statistical significance, and second, many species occurred in a large proportion of the total sample sites, resulting in low group fidelity.

Most of the indicator species were associated with the low-severity fire regime. This was expected since the NMS ordination showed that this fire regime is the least widely distributed in ordination space (Fig. 2). Many of the species that indicated a low-severity fire regime were grasses and annual forbs in the Asteraceae. The tendency of graminoids and annual forbs to have high abundances in low-severity fire regimes is consistent with associations of vegetation to shorter fire intervals in other *P. ponderosa* ecosystems in the western US (Laughlin et al. 2005).

Shrub indicator species were generally only found at higher elevations, where most high-severity, low frequency fires occur (Marr 1961; Peet 1981; Sherriff 2004; Sherriff & Veblen 2006, 2007). The two herbaceous species that indicated the moderate-severity fire regime were the native annual forb *Geranium caespitosum* and the exotic biennial forb *Verbascum thapsus*. Given that many of the moderate-frequency fire regime stands occurred on steep slopes with relatively high percentage cover of bare ground (Fig. 2, Table 5), we expected the presence of annual or biennial obligate seeders (versus perennial species or resprouters) in the sites with more bare ground, where these forb species generally establish in higher abundances (Wang & Kemball 2005).

Predictive model based on CART analysis

The CART analysis was exploratory in nature and conducted to test the potential utility of understory species in a predictive model. Using the 93 understory species from the primary data matrix, the hierarchical diagram showed that the sampling sites were divided into six splits of homogeneous species groups; accounting for 69% of the variability in the model (Fig. 3). Some of the results were not consistent with the NMS and ISA results. *Harbouria trachypleura* was not significantly correlated with either axis in the NMS analysis, nor was it a significant indicator species. In addition, many species that were more highly significant indicator species, such as *J. communis*, did not appear in the CART model. These differences result from CART groupings by overall group homogeneity, rather than group abundance and fidelity in ISA.

The advantage of the CART analysis is that the results are easily interpretable, applicable in the field, and any combination of species can be explored as predictor variables. For example, land managers can easily apply this method using the species most relevant to them, such as invasive exotic species. An accurate dichotomous key produced from the CART could be used in the field for a variety of purposes (Urban et al. 2002), such as determining historic forest conditions for ecological restoration, or prioritizing fuels mitigation prior to management implementation. Easily identifiable indicators of fire regime are also helpful in determining fire hazard in the wildland–urban interface, which in turn helps inform risk mitigation

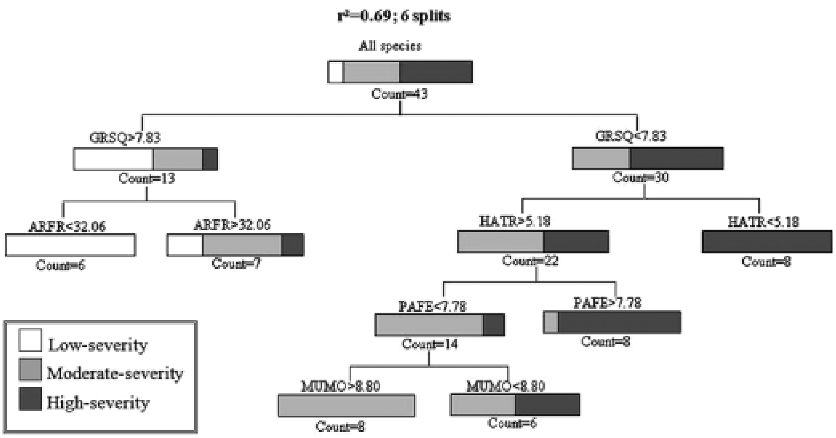

Fig. 3. Classification and regression tree predicting historic fire regime with understory species. The six split CART accounts for 69% of the variance in the model. The four-letter species code comprises the first two letters of the genus and the first two letters of the species; ARFR = *Artemisia frigida* GRSQ = *Grindelia squarrosa*, HATR = *Harbouria trachypleura*, MUMO = *Muhlenbergia montana*, and PAFE = *Packera fendleri*.

strategies. Although a five-fold cross-validation of the computer-generated model shows statistically significant results ($r^2 = 0.499$), additional field sampling and trials of training data against test data are needed to verify the accuracy and utility of this model.

Methodological considerations

The relatively short time period over which the field sampling took place limits the scope of this study. The results of this study do not account for year-to-year variation in the relative abundances of understory species. Climate variability at a decadal or multi-decadal time scale can potentially alter fire behavior and understory composition along the environmental gradients studied. Additionally, closer examination of soil depth, texture, moisture, and nutrient content could provide important information about the role of edaphic gradients in determining species composition.

The sites sampled in the present study were limited to areas that have not experienced recent fires, logging, or grazing. Therefore, short-term responses and compounding effects on understory vegetation as a result of these disturbances could not be determined by the present study. Such disturbances could create confounding results in other studies.

In more recent supporting studies, Sherriff & Veblen (2006, 2007) combined the moderate-severity and the high-severity fire regime into one group, called variable-severity fire regime, which reflects the overall importance of higher-severity fires in shaping stand structures in lower montane forests, in contrast to the low-severity fire regime (Sherriff 2004; Kaufmann et al. 2006; Sherriff & Veblen 2006, 2007). In addition to the three fire regime analyses, MRPP and ISA analyses were run with the two fire regime categories used by Sherriff & Veblen (2006, 2007) for the purpose of revealing the floristic discreteness of the fire regimes. Results from the two fire regime analyses are not presented because they were identical to or less statistically significant than the three fire regime analyses. Two additional CART analyses using the 34 indicator species and the 55 species associated with Axis 1 were also performed (results not shown), and both had lower r^2 values.

Conclusions and management implications

The sample sites in each of the three historic fire regimes (high-severity, low-frequency; moderate-severity, moderate-frequency; and high-severity, low-frequency fires) sampled in this study of *P. ponderosa* ecosystems differ significantly in their understory vegetation composition. Forest stands with different fire regimes are floristically less similar than expected, despite the overall homogeneity of the dominant overstory trees. The results of this study provide compelling evidence that understory vegetation and historic fire regimes have similar distributions along the elevation and topographic–moisture gradients of the montane zone of the northern Front Range, with some species serving as useful indicators of fire regime type. We believe the underlying explanation for the prediction of *past* fire regimes from *current* understory composition is the dependence of both of these dependent variables on the same abiotic factors that co-vary along the elevation and topographic-moisture gradient (*sensu* Peet 2000).

In a management context, the current study provides a relatively simple, efficient way of retrodicting past fire regimes. At sites not altered by recent fire or other significant disturbance, the predictive model described here allows the use of understory species as a means of retrodicting historic fire regimes in *P. ponderosa*-dominated ecosystems in the northern Front Range of Colorado. Groupings of species that distinguish three historic fire regimes could be cross-walked to units in vegetation classifications commonly used by land managers in the central Rocky Mountains. Thus, by using the understory species associated with the different historic fire regimes in the current study, it is feasible to obtain historic fire regime information from existing understory data in commonly used vegetation classifications. We suggest that in many fire-prone forest ecosystems, understory composition could be a useful tool in the context of evaluating departures from historic fire regime conditions and potential goals for ecological restoration.

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