Received: 28 March 2019 | Revised: 2 July 2019 | Accepted: 3 July 2019

DOI: 10.1111/jvs.12796

RESEARCH ARTICLE

Journal of Vegetation Science IAVS

Fire severity and changing composition of forest understory plant communities

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Funding information
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Co-ordinating Editor: John Morgan

Abstract

Questions: Gradients of fire severity in dry conifer forests can be associated with variation in understory floristic composition. Recent work in dry conifer forests in California, USA, has suggested that more severely burned stands contain more thermophilic taxa (those associated with warmer and drier conditions), and that forest disturbance may therefore accelerate floristic shifts already underway due to climate change. However, it remains unknown how rapidly thermophilic taxa shifts occur following disturbance, how long such shifts are likely to persist, and how different thermophilic post-disturbance communities are from pre-disturbance communities.

Location: Colorado Front Range, USA.

Methods: We investigated these questions using a unique 15-year vegetation plot dataset that captures pre- and post-fire understory community composition across a gradient of fire severity in dry conifer forests, classifying taxa using the biogeographic affinity concept.

Results: Thermophilization (defined here as a decrease in the ratio of cool-mesic taxa to warm-xeric taxa, based on biogeographic affinity of paleobotanical lineages) was observed as early as one year post-fire for all fire severity classes, but was stronger at sites that burned at higher severity. The ratio of cool-mesic to warm-xeric taxa recovered to pre-fire levels within 10 years in stands that burned at low severity, but not in stands that burned at moderate or high severity. The process of thermophilization after high-severity fire appears to be driven primarily by the gain of warm-xeric taxa that were absent before the fire, but losses of cool-mesic taxa, which did not return during the duration of the study, also played a role.

Conclusions: Decreases in canopy cover appear to be a main contributor to understory thermophilization. Fine-scale heterogeneity in post-fire forest structure is likely an important driver of floristic diversity, creating the microclimatic variation necessary to maintain floristic refugia for species mal-adapted to increasingly warm and dry conditions.

KEYWORDS

biodiversity, biogeographic affinity, Colorado, dry conifer forests, fire, Hayman Fire, thermophilization, understory

1 | INTRODUCTION

Generalizable patterns of plant community responses to disturbance can be difficult to discern, in part because plant communities are composed of many species that have diverse adaptations to disturbance (Grime, 1977). Species niches are often conserved through evolutionary time (Ackerly, 2003), and environmental conditions present at the time of a particular clade's diversification are likely related to the contemporary niche space where those clades occur (Ackerly, 2009). Therefore, lineages of similar biogeographic affinities (appearances in the paleobotanical record at a similar place and time) may be more likely to have relatively similar response to environmental conditions, including those induced by disturbance (Harrison & Grace, 2007).

In forests, canopy cover is a primary driver of understory species composition (Hart & Chen, 2006). Canopy cover mediates the understory microclimate; for instance, canopy disturbance can cause increases in understory temperature, wind speed and transpirational demand (Ma, Concilio, Oakley, North, & Chen, 2010). Alterations to canopy cover and the understory microclimate can in turn create conditions that favor certain understory plant species, including species that can tolerate the increased temperatures and water stress that sometimes accompany canopy removal (Ma et al., 2010). Particularly in climatically drier forests, warmer and more water-stressed microclimates in the post-disturbance landscape can cause increases in species adapted to warmer, more xeric conditions and decreases in species with affinities for cooler, more mesic conditions, a phenomenon that has been termed "thermophilization" (Gottfried et al., 2012). In general, species that decline after disturbance tend to have biogeographic affinities for higher latitudes, while species that increase after disturbance tend to be species with more equatorial biogeographic affinities (De Frenne et al., 2013; Stevens, Safford, Harrison, & Latimer, 2015).

Forest canopy disturbance, particularly from high-severity fire that removes an entire tree canopy within a given area, can lead to dramatic and rapid understory plant community shifts, potentially accelerating the shifts in vegetation expected with climate warming (Miller & Safford, 2019; Stevens et al., 2015). This rapid thermophilization via disturbance is distinct from gradual climate warming and forest cover reductions, which can lead to varying degrees of protracted understory plant community thermophilization (De Frenne et al., 2013; Gottfried et al., 2012). And while general changes in understory community composition associated with fire have been observed for at least 20–30 years post-fire in conifer forests (Coop, Massatti, & Schoettle, 2010; Romme, Whitby, Tinker, & Turner, 2016; Webster & Halpern, 2010), it remains unknown how long post-fire thermophilization might persist, although post-fire successional trajectories likely play a role (Stevens, Collins, Miller, North, & Stephens, 2017). Further, although fire has been shown to cause shifts towards plant communities with a greater proportion of warm-xeric species, it is unknown whether this pattern is driven by gains of such species, losses of cool-mesic species, or both (Stevens et al., 2015). Long-term landscape-scale extirpations of cool-mesic species could represent biodiversity losses of substantial conservation concern.

Ongoing increases in fire severity, and particularly the increasing incidence of uncharacteristically large, spatially contiguous patches of high-severity fire in dry conifer forests of some regions (Singleton, Thode, Sánchez Meador, & Iniguez, 2019; Stevens et al., 2017), have raised concern that forest stands burning at high severity over large areas may lack the resilience to return to a forested condition, because the dominant species require seeds produced by living trees in order to regenerate (Johnstone et al., 2016). The time required for mature trees to reestablish and create the heterogeneous understory microclimate likely associated with historical forest conditions (Dodson & Peterson, 2010) is unknown in many forest types. Longitudinal studies of post-fire understory communities are rare, but when present they offer the opportunity to document the resilience of understory communities to different degrees of disturbance severity over time.

In this paper we apply the biogeographic affinity concept to document thermophilization within a unique longitudinal study of vascular understory vegetation spanning 15 years around the Hayman Fire, a large fire that occurred in dry conifer forests of the Colorado Rocky Mountains, USA (Abella & Fornwalt, 2015; Fornwalt, Kaufmann, & Stohlgren, 2010). While previous research in the Sierra Nevada, California, USA (Stevens et al., 2015) has documented stronger thermophilization following high-severity fire compared with low-severity fire or forest thinning, this process has not been examined for longer than three years post-fire, nor has the relative contribution of extinction and colonization to the thermophilization process been examined, due to the rarity of pre-disturbance data. We examine temporal trends in biogeographic affinity of the understory vegetation community on the Hayman Fire to ask (a) whether the short-term thermophilization caused by high-severity fire occurs in dry conifer forests of the Rocky Mountains to a similar extent as in the Sierra Nevada; (b) how long understory thermophilization persists following disturbance of different severities; and (c) whether thermophilization is driven primarily by the extinction of cool-mesic affinity taxa, the colonization of warm-xeric affinity taxa, or both. By investigating these previously unaddressed questions, we hope to increase our understanding of the resilience of understory vegetation to gradients in disturbance severity over time.

2 | METHODS

2.1 | Study site

Our study was conducted at a 400-ha site in the Pike National Forest (39.14° N, 105.24° W), approximately 60 km southwest of Denver, CO, USA (Figure 1). Elevations at the site range from about 2,300 to 2,500 m. The climate is warm and dry — over the 1996–2012 study period, average January temperature was about −4°C, average July temperature was about 17°C, and average annual precipitation was about 320 mm (Appendix S1; Asherin, 2016). Soils, derived from Pikes Peak granite, are poorly developed. Historical fire intervals

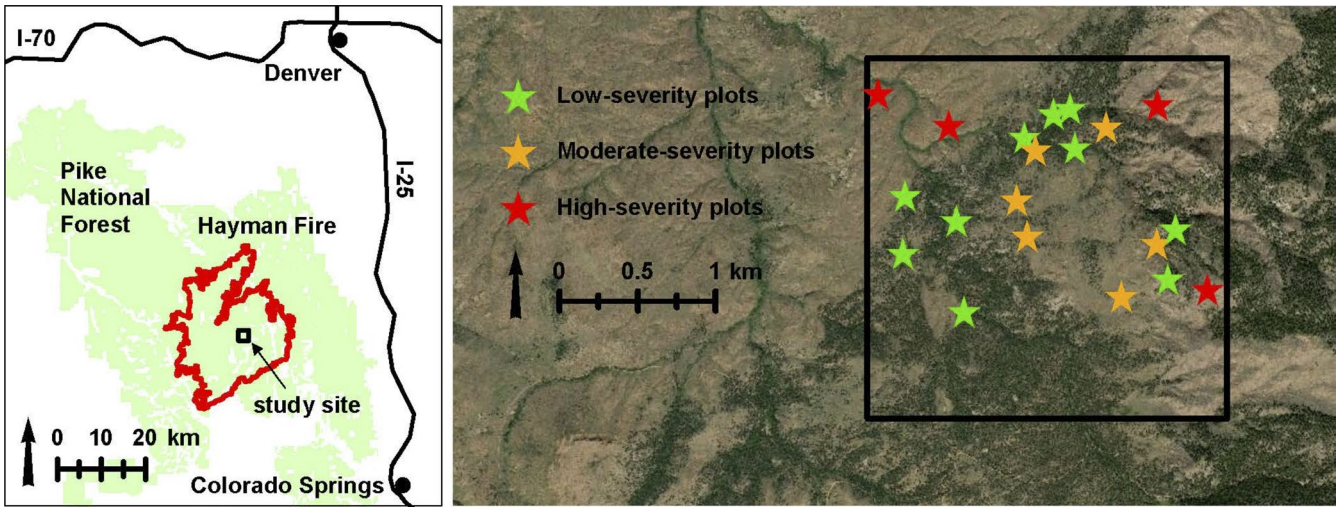

FIGURE 1 Location of the 400-ha study site within the 2002 Hayman Fire, Colorado, USA (left). Location and severity of the 20 upland 0.1-ha plots within the study site (right). Post-fire aerial imagery is shown in the background (imagery sources: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community). This figure was adapted from Fornwalt et al. (2018) [Colour figure can be viewed at wileyonlinelibrary.com]

for individual *Pinus ponderosa–Pseudotsuga menziesii* forest stands at and surrounding the site varied from very short (≤10 years) to very long (>100 years) (Brown, Kaufmann, Shepperd, 1999). Historical fires likely included patches of high-severity fire effects within a matrix of lower-severity fire effects (Brown et al. 1999), with high-severity patches likely not exceeding about 100 ha (Romme, Veblen, Kaufmann, Sherriff, & Regan, 2003). This site experienced few wildfires beginning in the late 1800s, coincident with Euro-American settlement and associated land-use activities including fire suppression, livestock grazing, and logging.

In 2002, the study site burned in the Hayman Fire. This fire was ignited on 8 June, and ultimately burned more than 52,000 ha (Graham 2003). Heavy and continuous fuels, low relative humidity, and strong and gusty winds enabled the fire to burn approximately 24,000 ha on 9 June, largely as a contiguous high-severity fire. While historical fires sometimes created high-severity patches, the patches created on this day appear to be of a size that is unprecedented over at least the last two to four centuries (Fornwalt et al., 2016). Less extreme weather arrived on 10 June, enabling the fire to burn more heterogeneously until it was contained on 2 July. Our study site is situated in the transitional zone between these two fire behavior patterns.

2.2 | Data collection and analyses

Vascular understory plant composition at the study site was first assessed in 1996/1997, 5–6 years before the Hayman Fire, in 20 upland 0.1-ha plots, where uplands were dominated by dry conifer forest vegetation distinct from riparian vegetation plots that were sampled but not analyzed in this study (Fornwalt, Kaufmann, Huckaby, & Stohlgren, 2009; Fornwalt, Kaufmann, Huckaby, Stoker, & Stohlgren, 2003). Six plots were sampled in 1996 and fourteen plots were sampled in 1997. We did not detect differences among pre-fire sampling years in eventual fire severity ($\chi^2 = 1.27$, $df = 2$, $p = 0.53$) or in the pre-fire ratio of our two floristic groups described below ($t = 0$, $df = 18$, $p = 0.998$), so for simplicity hereafter we ascribe all pre-fire sampling to 1997. Composition was assessed by recording the identities of all taxa in the plots. All graminoids, forbs, and shrubs were included in our surveys, but trees were not. Unknown taxa were collected for later identification. While most taxa were ultimately identified to the species level (varieties and subspecies were not distinguished), some taxa were only identified to the genus level because key morphological characteristics were not sufficiently developed. *Carex* spp., *Chenopodium* spp., *Fragaria* spp., *Rosa* spp., and *Solidago* spp. were often identified only to genus, and so for consistency we included them solely at this level. A small proportion of taxa could not be identified to at least the genus level, and were disregarded herein. Nomenclature follows The PLANTS Database (USDA NRCS, 2018).

Measurements were conducted following the Hayman Fire in 2003, 2004, 2005, 2006, 2007, and 2012 (1, 2, 3, 4, 5, and 10 years post-fire), using the same methodologies described above (Abella & Fornwalt, 2015; Fornwalt & Kaufmann, 2014; Fornwalt et al., 2010). Furthermore, direct fire effects on the overstorey and forest floor were assessed in 2003 in order to assign each plot a fire severity. Plots where ≤50% of the pre-fire live overstorey trees were killed and where tree crown and organic surface material consumption were generally slight were categorized as burning with low severity (i.e., burned by light surface fire; ten plots). This 50% threshold was used to accommodate mortality of the smallest size class (0–10 cm DBH); mortality of all trees >10 cm DBH in the low-severity plots did not exceed 20%, a more typical low-severity threshold, and accordingly basal area mortality in the low-severity plots was very low at <12% (Fornwalt, Stevens-Rumann, & Collins, 2018). Moderate-severity plots experienced >50% mortality of live overstorey trees and had modest tree crown and organic surface material consumption (i.e., burned by moderate to severe

surface fire; six plots). High-severity plots experienced 100% live overstorey tree mortality and complete or nearly complete tree crown and organic surface material consumption (i.e., burned by severe crown fire; four plots).

The three burn severity classes and the sampling year were our primary predictor variables for our analyses of plant community composition (see below), but because pre-fire environmental factors can influence burn severity, we also tested how such factors varied with burn severity class. Data on overstorey tree structure, ground cover, and topography were collected in 1996/1997 (Fornwalt et al., 2003, 2009; Kaufmann, Regan, & Brown, 2000). Overstorey measurements included species, diameter at breast height, total height, and live or dead status for all trees >1.4 m tall. From these data, we calculated live stand density (trees per ha) and live basal area (m^2 per ha). We also used these data and the Central Rockies Variant of the Forest Vegetation Simulator (FVS) to estimate percent canopy cover (Dixon, 2002, p. 226; Keyser & Dixon, 2008). Ground cover measurements included percent bare soil cover, litter and duff cover, and wood cover, which were recorded for 10 systematically located 1-m^2 subplots per plot and averaged. Topography measurements included elevation, slope and aspect. Aspect was categorized for analysis as southwest if it was between 135° and 315°, reflecting a more xeric exposure, otherwise it was categorized as northeast. We tested for differences among the three eventual burn severity classes for the following pre-fire environmental variables: elevation, aspect, slope, percent bare soil cover, litter and duff cover and coarse woody debris cover, live tree density, live tree basal area, and live tree canopy cover. We used pairwise *t* tests to compare the classes for all variables except aspect, where we used a χ^2 test to determine whether the distribution of a categorical aspect variable differed among burn severity classes.

To assess understory plant community composition over time and across the fire severity gradient, we categorized all understory taxa by their biogeographic affinity. The biogeographic affinity classifications describe the time period and geographic origin of distinct plant lineages in the fossil record (Raven & Axelrod, 1978), an approach developed for the California flora (Harrison & Grace, 2007) that we applied to our dataset. Biogeographic affinity describes the general location and associated climate where distinct evolutionary lineages (often at the genus level) first appear in the fossil record (Raven & Axelrod, 1978). For the purposes of our simplified classification of Raven and Axelrod's (1978) original work, we distinguish the "cool-mesic" biogeographic affinity, largely comprising genera that diversified during the early Tertiary (ca. 56–34 Ma) at higher latitudes in North America during relatively wetter conditions ("Arcto-Tertiary" flora in Raven & Axelrod, 1978), from the "warm-xeric" biogeographic affinity, largely comprising genera that diversified during the later Tertiary (ca 23–1.8 Ma) at lower latitudes in North America, particularly in the southwestern US and Mexico, during relatively drier conditions (Stevens et al., 2015). Our warm-xeric group includes three distinct groups classified by Raven and Axelrod (1978) as "Madro-Tertiary" (semiarid climate), "California Floristic Province" (mediterranean climate), and "Warm Temperate Desert" (arid climate) in origin (Harrison & Grace, 2007).

Our dataset contained 188 unique taxa, of which 171 were identified to the species level and 17 to the genus level. Of these 188 unique taxa, 166 were native to the continental USA, and of the 166 native taxa, we were able assign 154 (93%) to a biogeographic affinity. Of the 154 classified taxa, 63 (41%) were species that had exact matches to species in previous California-based datasets where biogeographic affinities had already been classified (Harrison & Grace, 2007; Raven & Axelrod, 1978; Stevens et al., 2015), and 64 (42%) belonged to genera in these datasets that Raven and Axelrod (1978) classified at the genus level (we assumed the same genus-level classification held in Colorado). We classified the remaining 27 taxa (17%) using the biogeographic affinities of close relatives based on existing phylogenies and associations with plant families that had a single classification in the Raven and Axelrod (1978) scheme, or by identifying taxonomic name changes. We could not confidently classify 12 (7%) of the 166 native taxa.

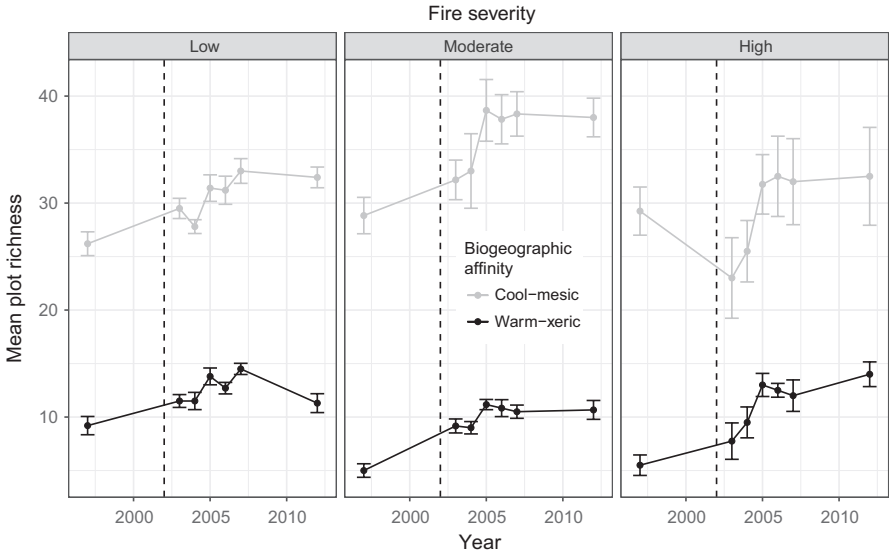

FIGURE 2 Mean plot-level richness (number of taxa per 0.1-ha plot) by biogeographic affinity and fire severity. Error bars represent one standard error around the plot-level mean. Dashed vertical line indicates the year of the Hayman Fire

We assessed trends over time in the richness (per 0.1-ha plot) and proportion of understory taxa belonging to the cool-mesic versus warm-xeric floristic groups, as well as the effects of fire severity on these trends. We used linear mixed-effects models that assigned a random intercept for plot, thereby accounting for repeated sampling of the same plots over time by allowing a given plot to have higher or lower overall values of the response variables, using the R package lme4 (Bates, Maechler, Bolker, & Walker, 2013). We evaluated the significance of these trends using the Kenward–Rogers approximation to estimate degrees of freedom in the mixed-effects models, and then compared the *t* statistic for the relevant fixed-effect coefficient in the model against a *t* distribution for the given degrees of freedom via the R package pbkrtest (Halekoh & Højsgaard, 2014).

We also estimated extinctions and colonizations of each unique taxon at the plot level over the 15-year duration of this study. We were particularly interested in qualitatively comparing extinctions and colonizations that were "permanent" for the duration of the study (i.e., persisting at least 10 years post-fire). We defined a permanent extinction as a taxon that was present in the pre-fire census in 1997, and was absent from the final post-fire census in 2012 from the same plot. The year of the permanent extinction was defined as the first year a taxon was absent in a plot between 2003 (the first post-fire census) and 2007 (the fifth post-fire census), inclusive. We defined a permanent colonization similarly, where a taxon was absent from a given plot in 1997 and present in 2012. The year of permanent colonization was defined as the first year a taxon was present in a plot between 2003 and 2007, inclusive. We recognize that we use the term "permanent" to only refer to changes evident in the last sampling year (2012), and that subsequent changes in these individual taxa may have occurred.

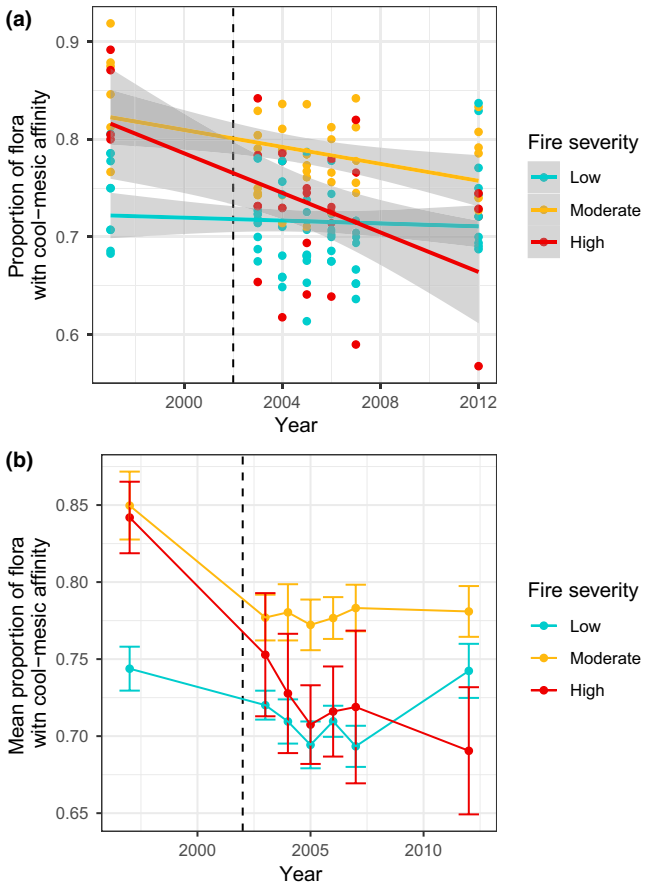

FIGURE 3 Change over time in proportion of total plot richness (number of taxa per 0.1-ha plot) in the cool-mesic group (vs warm-xeric group, the two groups summing to 1) by fire severity class. We show linear trend (a) and annual mean trend at the plot level (b). Error bars in (b) represent one standard error around the plot-level mean. Dashed vertical line indicates the year of the Hayman Fire [Colour figure can be viewed at wileyonlinelibrary.com]

3 | RESULTS

Richness of the cool-mesic floristic group was consistently higher than richness of the warm-xeric floristic group, across all years (before and after the Hayman Fire) and all fire severities (Figure 2; $t = 38.7$, $df = 109$, $p < 0.001$). Within the cool-mesic floristic group, richness increased in the first year after low- and moderate-severity burns and stayed higher than pre-fire levels up to 10 years after fire, with a plateau in richness occurring between roughly four and 10 years post-fire (Figure 2). However, the north-temperate floristic group experienced a decrease in richness in the first year after high-severity fire, which persisted for two years before increasing rapidly in year three and reaching a similar plateau as in the low- and moderate-severity plots. The increase in cool-mesic richness over time was significant for low-severity plots ($t = 5.9$, $df = 59$, $p < 0.001$) and for moderate-severity plots ($t = 5.7$, $df = 35$, $p < 0.001$), and marginally significant for high-severity plots ($t = 1.8$, $df = 23$, $p = 0.08$), which had high variance due to a small sample size but nonetheless was robust to the removal of one plot with a very low ratio of cool-mesic to warm-xeric taxa ($t = 2.0$, $df = 17$, $p = 0.06$ without the outlier). The warm-xeric floristic group, conversely, saw an immediate increase in richness one year post-fire for all three fire severities (Figure 2; for low, moderate and high severity, respectively: $t = 3.2, 5.6, 6.0$; $df = 59, 35, 23$; all $p < 0.001$).

Consistent with the strong temporal increase in the richness of warm-xeric taxa in high-severity stands and the lack of significant temporal increase in cool-mesic taxa in high-severity stands, we observed greater thermophilization (a decrease in the ratio of cool-mesic to warm-xeric taxa) over time in stands that burned at higher severity (Figure 3a). Specifically, the relative proportion of cool-mesic taxa decreased strongly and significantly in high-severity plots over the 15-year duration of this study ($t = 5.3$, $df = 23$, $p < 0.001$; $t = 3.9$, $df = 17$, $p = 0.001$ without the outlier identified above). The decrease in the proportion of cool-mesic taxa in the moderate severity plots was also significant ($t = 3.47$, $df = 35$, $p = 0.001$), while there was no significant trend in the low-severity plots (Figure 3a; $t = 0.79$, $df = 59$, $p = 0.43$). The high-severity and moderate-severity plots had similar decreases in the proportion of cool-mesic taxa in the year immediately following the fire, but the decrease in this proportion continued in high-severity plots while it stabilized in moderate-severity plots (Figure 3b), despite both severity classes having nearly identical proportions of

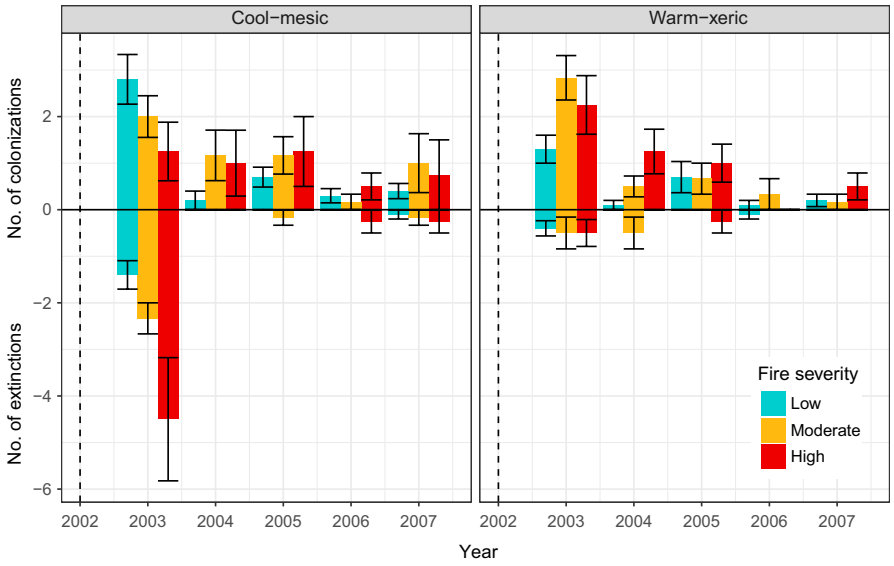

FIGURE 4 Mean number of permanent extinctions (negative bars) and colonizations (positive bars) per 0.1-ha plot over the five years post-fire, for cool-mesic taxa (left panel) and warm-xeric taxa (right panel). Error bars represent one standard error around the plot-level mean. Permanent extinctions are counted as taxa that were present in the pre-fire inventory at a given plot, were not present for the first time in the inventory of a given post-fire year, and did not re-appear by the final census in 2012. Permanent colonizations are counted as taxa that were absent in the pre-fire inventory at a given plot, appeared for the first time in a given post-fire year, and remained present in the plot during the final census in 2012. Dashed vertical line indicates the year of the Hayman Fire [Colour figure can be viewed at wileyonlinelibrary.com]

cool-mesic taxa prior to the fire. The lack of a significant linear trend in the low-severity plots was due to the recovery in the proportion of cool-mesic taxa in these plots to pre-fire levels within 10 years of the fire (Figure 3b), although the proportion of cool-mesic taxa started at a lower level in plots that burned at low severity.

The substantial decrease in the proportion of cool-mesic taxa in high-severity plots over time (Figure 3) was driven by a continued increase in the warm-xeric richness, which by 2012 was higher than in the low-severity plots despite having lower richness than the low-severity plots prior to the fire (Figure 2). In general, it was more common for novel warm-xeric taxa to colonize after the fire than for previously present warm-xeric taxa to go extinct (Figure 4; Table 1), with this colonization process more pronounced in moderate and high-severity plots than in low-severity plots. While "permanent extinctions" (i.e., taxa present pre-fire failing to recover within 10 years of the fire in these stands; Table 2) were uncommon among warm-xeric taxa, they were much more common in cool-mesic taxa, particularly in the first year after the fire (Figure 4). Permanent extinctions of cool-mesic taxa were also much more common in high-severity plots than in low-severity plots, with moderate-severity plots having an intermediate level of permanent extinctions (Figure 4), although it is possible that some of the extinctions occurred before the fire.

Evidence from plot environmental data suggests that the temporal trend toward increased thermophilization at higher severities was largely driven by changes in forest structure. The plots in the three severity classes did not differ significantly from each other in elevation, aspect or slope (Appendix S2), and yet exhibited strong differences in post-fire floristic pathways (e.g., Figure 3). Furthermore, differences in pre-fire forest structure may have been related to differences in eventual fire severity and in pre-fire plant community composition. In particular, plots that eventually burned at low severity had a tendency to have increased bare ground cover and reduced litter cover, tree density, basal area and canopy cover compared to plots that eventually burned at moderate or high severity, although these differences were rarely significant (Appendix S2) and differences in weather also likely played a strong role in eventual fire severity (Fornwalt et al., 2018). However, notably, the considerable variation in the pre-fire ratio of cool-mesic to warm-xeric taxa (Figure 3a) is well explained by variation in pre-fire canopy cover, with higher canopy cover plots associated with significantly higher ratios of cool-mesic to warm-xeric taxa (Figure 5).

4 | DISCUSSION

Increasingly severe fire effects in Colorado's Hayman Fire were associated with increasingly pronounced shifts in understory plant composition in comparison to pre-fire communities (Figures 3,4). Specifically, we found strong evidence of greater thermophilization over time with greater fire severity, indicated by shifts in the community from taxa with cool-mesic biogeographic affinities towards taxa with warm-xeric biogeographic affinities. While shifts towards warm-xeric understory taxa with increasing disturbance severity have been documented previously within three years of fire in California (Stevens et al., 2015), we show for the first time that, in Colorado, colonizing warm-xeric taxa are largely observed within the first year after fire, representing a marked departure from pre-fire

TABLE 1 List of taxa permanently colonizing during the first year post-fire (subsequent colonizations not shown), with cool-mesic (n = 22) and warm-xeric (n=16) biogeographic affinities

	Number of plots colonized, by severity class			
Scientific name	High	Moderate	Low	Biogeographic affinity
Allium cernuum	0	1	2	Cool-mesic
Androsace septentrionalis	1	2	1	Cool-mesic
Antennaria parvifolia	0	0	1	Cool-mesic
Arabis fendleri	1	0	2	Cool-mesic
Artemisia ludoviciana	0	0	1	Cool-mesic
Campanula rotundifolia	1	0	1	Cool-mesic
Elymus elymoides	0	0	2	Cool-mesic
Erigeron subtrinervis	0	2	0	Cool-mesic
Erysimum capitatum	0	1	2	Cool-mesic
Heterotheca villosa	0	1	0	Cool-mesic
Packera fendleri	1	0	3	Cool-mesic
Penstemon glaber	0	2	3	Cool-mesic
Penstemon virens	0	1	0	Cool-mesic
Poa fendleriana	0	1	0	Cool-mesic
Potentilla hippiana	0	1	1	Cool-mesic
Ribes cereum	0	0	1	Cool-mesic
Rubus deliciosus	0	0	1	Cool-mesic
Scutellaria brittonii	0	0	1	Cool-mesic
Silene scouleri	0	0	1	Cool-mesic
Solidago	1	0	2	Cool-mesic
Symphoricarpos albus	0	0	1	Cool-mesic
Townsendia grandiflora	0	0	2	Cool-mesic
Aliciella pinnatifida	0	0	1	Warm-xeric
Bahia dissecta	0	3	1	Warm-xeric
Cercocarpus montanus	0	0	1	Warm-xeric
Chamerion angustifolium	0	1	0	Warm-xeric
Chenopodium	4	3	3	Warm-xeric
Conyza canadensis	0	1	0	Warm-xeric
Cryptantha virgata	1	0	1	Warm-xeric
Eriogonum alatum	1	2	0	Warm-xeric
Ipomopsis aggregata	0	1	1	Warm-xeric
Machaeranthera bigelovii	0	2	1	Warm-xeric
Pediocactus simpsonii	0	0	1	Warm-xeric
Phacelia heterophylla	2	4	3	Warm-xeric
Yucca glauca	1	0	0	Warm-xeric
Pediocactus simpsonii	0	1	0	Warm-xeric
Verbena	0	0	1	Warm-xeric

Note: Number of plots is indicated by severity class, out of a possible total of ten low-severity plots, six moderate-severity plots, and four high-severity plots.

plant community composition. We also show that these taxa can persist for at least 10 years post-fire.

The plant community shifts we observed are likely associated with changes in the microclimate with increasing disturbance severity (North, Oakley, Fiegener, Gray, & Barbour, 2005). The warm-xeric biogeographic affinity is generally associated with a greater functional tolerance for water stress (Harrison & Grace, 2007; Stevens et al., 2015), corresponding to the increasing canopy openness, understory temperatures, wind speeds, and evapotranspirational demand increase created by canopy tree mortality (Ma et al., 2010). Thus, the microclimatic shifts associated with high-severity fire are likely filtering the regional species pool to favor an understory

TABLE 2 List of taxa going permanently extinct during the first year post-fire (subsequent extinctions not shown), with cool-mesic (n = 29) and warm-xeric (n=9) biogeographic affinities

Scientific name	Number of plots extinct, by severity class			Biogeographic affinity
	High	Moderate	Low	
Achnatherum scribneri	1	0	0	Cool-mesic
Arenaria hookeri	0	1	0	Cool-mesic
Campanula rotundifolia	1	0	0	Cool-mesic
Castilleja integra	1	0	0	Cool-mesic
Clematis columbiana	1	0	0	Cool-mesic
Crepis	1	0	0	Cool-mesic
Elymus trachycaulus	0	1	1	Cool-mesic
Erigeron compositus	1	0	0	Cool-mesic
Festuca saximontana	0	1	0	Cool-mesic
Fragaria	1	0	1	Cool-mesic
Gentiana	0	0	1	Cool-mesic
Hesperostipa comata	0	0	1	Cool-mesic
Heuchera parvifolia	1	0	0	Cool-mesic
Hieracium fendleri	1	0	0	Cool-mesic
Juniperus communis	3	3	4	Cool-mesic
Leucocrinum montanum	0	1	0	Cool-mesic
Leucopoa kingii	1	1	0	Cool-mesic
Oxytropis	0	0	1	Cool-mesic
Poa	1	0	0	Cool-mesic
Poa annua	0	1	0	Cool-mesic
Poa reflexa	1	2	0	Cool-mesic
Potentilla hippiana	1	0	1	Cool-mesic
Ribes inerme	0	0	1	Cool-mesic
Rosa	0	1	1	Cool-mesic
Rubus deliciosus	1	1	0	Cool-mesic
Sedum lanceolatum	1	0	0	Cool-mesic
Senecio	0	0	1	Cool-mesic
Solidago	0	0	1	Cool-mesic
Symphoricarpos albus	0	1	0	Cool-mesic
Astragalus parryi	0	1	0	Warm-xeric
Blepharoneuron tricholepis	1	0	0	Warm-xeric
Bouteloua gracilis	0	0	1	Warm-xeric
Collomia linearis	0	0	1	Warm-xeric
Cryptantha virgata	1	0	0	Warm-xeric
Gayophytum diffusum	0	0	1	Warm-xeric
Oenothera caespitosa	0	1	0	Warm-xeric
Pediocactus simpsonii	0	1	0	Warm-xeric
Verbena	0	0	1	Warm-xeric

Note: Number of plots is indicated by severity class, out of a possible total of ten low-severity plots, six moderate-severity plots, and four high-severity plots.

flora associated with warmer, drier conditions. A component of this warm-xeric flora may also be adapted to surface disturbance, and indeed we saw a shift towards the warm-xeric flora following low-severity burning where the canopy was minimally affected. In low-severity stands, however, the ratio of cool-mesic to warm-xeric taxa returned to pre-burn levels within 10 years, while it remained low in moderate- and high-severity stands relative to pre-fire levels, and comparable to low-severity stands in absolute terms (Figure 3). The strong and persistent thermophilization observed in stands that experienced moderate- and especially high-severity fire suggests

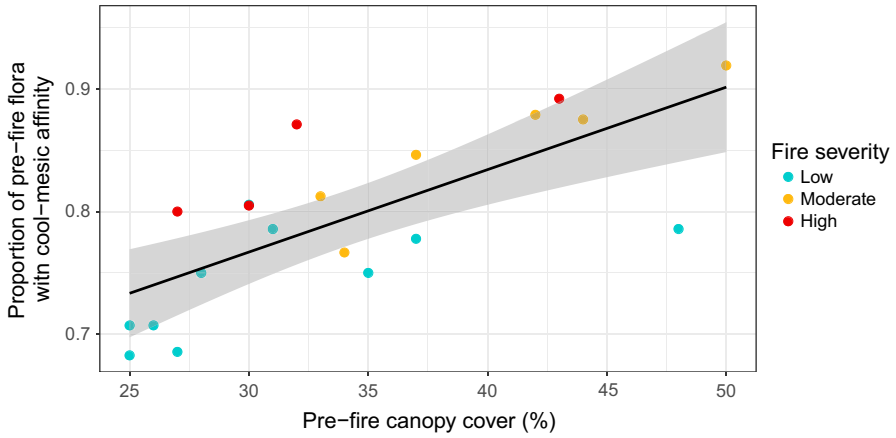

FIGURE 5 Effects of pre-fire canopy cover on the proportion of pre-fire understory flora in the cool-mesic category (vs. the warm-xeric category). Relative pre-fire richness of cool-mesic flora was significantly and positively related to pre-fire canopy cover, both over all plots and over eventual low-severity plots only [Colour figure can be viewed at wileyonlinelibrary.com]

that canopy removal by fire contributed to the strong differences in post-fire communities among severity classes. Recent research also suggests that altered microclimates caused by high-severity fire in dry forests may lead to long-term diversity losses of lichens, another taxonomic group that is characteristic of cooler, more mesic environments (Miller, Root, & Safford, 2018).

Interestingly, the ratio of cool-mesic to warm-xeric taxa in 1997, prior to the 2002 Hayman Fire, was actually higher in stands that subsequently burned at moderate and high severity compared to low-severity stands (Figure 3). While there was no clear evidence that pre-fire stand density or basal area were greater in stands that eventually burned at moderate or high severity compared to low severity (Appendix S2), we found that higher pre-fire canopy cover was strongly associated with an understory dominated by cool-mesic taxa (Figure 5), consistent with previous research suggesting that variation in microclimates created by forest structure is largely responsible for understory thermophilization (De Frenne et al., 2013; Stevens et al., 2015).

This study provides insight into the relative stability of plant communities in dry conifer forests in the first decade following low-severity burning. Communities in low-severity burns appear more resistant to disturbance than those in high-severity burns over time, in that they exhibit less change in composition, and more resilient, in that they move toward their pre-disturbance composition relatively quickly, at least with respect to the ratio of the two biogeographic groups (Figure 3). These trends in understory thermophilization are consistent with our expectation that low- and moderate-severity burns (at the sub-hectare scale) are associated with greater structural resilience in dry forests (Stevens, Safford, & Latimer, 2014) where understory structure and tree regeneration are dependent on a local component of surviving trees. Critically, the heterogeneity in understory microclimate and species composition is facilitated by the fine-scale (i.e., sub-hectare, individual tree scale) heterogeneity of canopy cover occurring within stands with low- and moderate-severity disturbance at that scale (Dodson & Peterson, 2010; Stevens et al., 2015). Post-fire canopy heterogeneity within low- and moderate-severity stands (which retained some canopy cover in our study, unlike high-severity plots) appears to be important for the greater persistence of cool-mesic lineages in post-fire stands, via the creation of microclimatic refugia within warm and dry conifer forests (Blomdahl, Kolden, Meddens, & Lutz, 2019; Rapacciuolo et al., 2014). Supporting this inference, we showed that extinctions of cool-mesic lineages were most pronounced in high-severity burned areas (Figure 4), which had complete canopy removal at the plot scale. Although our post-fire timeframe of 10 years may limit our ability to infer longer-term community dynamics, we believe that the changes we observed in canopy structure and understory diversity should persist for the near future due in large part to the slow growth rates of surviving and establishing trees (Fornwalt et al., 2018; Malone et al., 2018).

The strength of our conclusions is somewhat limited by the relatively small sample size of plots due to the opportunistic nature of our study, particularly in high-severity stands which predictably had high variance in understory data (e.g., Figure 2). However, despite this small sample size we still detected significantly greater thermophilization in high-severity burn classes compared with low- and moderate-severity classes (Figures 2,3). Our analyses of temporal trends in understory vegetation are strengthened by the inclusion of pre-fire understory data, which are uncommon (Fornwalt & Kaufmann, 2014), and multiple lines of evidence support the importance of the overstorey canopy in driving understory thermophilization (e.g., Figure 5). Alternatively, the thermophilization observed over time could be attributable to generally below-average precipitation during the post-fire years in this region (Appendix S1), but we did not observe this trend in low-severity plots despite their experiencing the same drying trend (Figure 3), again suggesting that canopy loss is the primary driver of change. It is also possible that plots that eventually burned at high severity had a greater abundance of warm-xeric taxa in the surrounding landscape and this was the main driver of thermophilization. We think this is less likely than a canopy-driven explanation, because these high-severity plots had the highest pre-fire proportion of cool-mesic taxa (Figures 2,3) and generally higher pre-fire canopy cover Figure 5).

The plant biogeographic affinity classifications pioneered by Raven and Axelrod (1978) has proven to be a useful framework for understanding California plant communities, and this study suggests the framework may also be applicable to other locales in western North America. Although Raven and Axelrod's (1978) floristic classifications rely on the historical concept of geofloras, which pre-date contemporary phylogenetic methods, numerous quantitative studies lend credence to their classifications. For example, woody cool-mesic plants have been shown

to have significantly larger seeds and lower specific leaf area than woody warm-xeric plants (Ackerly, 2003). Raven and Axelrod's classifications have also been shown to reflect contemporary plant distributions among ecoregions in California (Ackerly, 2009; Harrison & Grace, 2007), and there is evidence that cool-mesic species have declined more over recent decades under climate change (Damschen, Harrison, & Grace, 2010). In this study, the extinctions of cool-mesic taxa after fire occur across numerous disparate phylogenetic lineages (e.g., Poales, Lamiales, Rosales, and Asterales; Table 2), highlighting that patterns we observed do not seem to be caused by the chance vulnerabilities of a few taxa to fire. Future research should further elucidate mechanisms linking plant community shifts to fire severity through studies of functional traits and quantitative community phylogenetic patterns.

Our findings suggest that management activities that reduce fire severity could contribute to the conservation of plant diversity in dry conifer forests. Many such forests are increasingly experiencing uncharacteristically extensive high-severity fire (Singleton et al., 2019; Stevens et al., 2017), due at least in part to increased forest density and homogeneity following a century of fire suppression, livestock grazing, and logging (Battaglia et al., 2018; Safford & Stevens, 2017). Restoration and fuels reduction treatments that create more open and heterogeneous forest conditions have been shown to reduce fire-caused tree mortality, even under extreme weather conditions (Fulé, Crouse, Roccaforte, & Kalies, 2012; Safford, Stevens, Merriam, Meyer, & Latimer, 2012). By conserving living trees in the footprint of future fires, such heterogeneous treatments should also conserve cooler, more mesic microclimatic conditions, and the cool-mesic taxa that are adapted to them (Stevens et al., 2015).

ACKNOWLEDGEMENTS

The initial conception of this manuscript occurred at the Natural Areas Conference, Davis, CA, 2016. We thank Susan Harrison and Brian Anacker for compiling and sharing initial classifications from the Raven and Axelrod (1978) monograph.

AUTHOR CONTRIBUTIONS

JTS and PJF conceived of the study. PJF provided the data. JTS analyzed the data. JTS, JEDM, and PJF wrote the manuscript.

DATA AVAILABILITY STATEMENT

Final data and R code used to generate the manuscript are publicly available via the USDA Forest Service archive at https://doi.org/10.2737/rds-2019-0031.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Variation in annual site precipitation from 1995-2012
Appendix S2. Comparison of environmental conditions across plots of different burn severity

How to cite this article: Stevens JT, Miller JED, Fornwalt PJ. Fire severity and changing composition of forest understory plant communities. *J Veg Sci*. 2019;30:1099–1109. https://doi.org/10.1111/jvs.12796