

Rapid changes in functional trait expression and decomposition following high severity fire and experimental warming

Ethan M. Taber^{*}, Rachel M. Mitchell

School of Natural Resources and the Environment, University of Arizona, 1064 E Lowell St, Tucson, AZ 85721, USA

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ABSTRACT

Uncharacteristically severe wildfires are occurring at higher frequency, across larger spatial extents, and in new seasons in many parts of the globe. At the same time, climate change is elevating temperatures and altering precipitation patterns. High severity fires have the potential to produce shifts in ecosystem type and function in communities that are adapted to low severity fire via changes in community composition, functional trait values, and nutrient cycling processes. However, interactive effects between climate warming and fire severity on community composition, trait values, and ecosystem functioning are rarely studied and poorly understood. We assessed the impact of experimental warming via open top warming chambers across a burn severity gradient on the understory plant community of a Ponderosa pine (*Pinus ponderosa*) forest in northern Arizona, USA. Specifically, we examined community composition, three plant functional traits (specific leaf area (SLA), leaf dry matter content (LDMC), and plant height) and one ecosystem function (decomposition rate) in the first post-fire growing season. High burn severity produced significant shifts in community composition. The combination of experimental warming and high burn severity significantly decreased community weighted mean LDMC and plant height, and increased decomposition rate. Our study demonstrates significant and rapid responses of community composition, trait expression, and ecosystem function in response to burn severity, experimental warming, and their interaction. This suggests that ecosystems experiencing atypically severe fire under future climate and wildfire conditions may recover in fundamentally different ways than in the past, favoring a different suite of species and traits, with altered ecosystem function.

1. Introduction

In many regions of the world, wildfires are occurring in new seasons (Liu et al., 2021), over larger spatial extents (Canadell et al., 2021; Dennison et al., 2014), and at higher frequency and severity (Jones et al., 2022; Knox and Clarke, 2012; Prichard et al., 2017). Simultaneously, ambient temperature is increasing as a result of anthropogenic warming (Arias et al., 2021). Interactions between fire severity, especially uncharacteristically high severity fire, and increased ambient temperature may drive changes in recovery and succession in plant communities following wildfire via changes in species composition and trait expression (Anderson-Teixeira et al., 2013; Liang and Hurteau, 2023; Poulos et al., 2020). In addition, these novel abiotic conditions may interact with changes in plant composition and trait expression to alter key ecosystem functions such as decomposition (Chuckran et al., 2020; Kazakou et al., 2006; Knelman et al., 2017), which has the potential to feedback onto community assembly processes, favoring new

species assemblages and altering successional trajectories. Understanding how warming and fire severity interact to shape plant communities and ecosystem functions is key to predicting recovery and successional trajectories in the future.

Biotic communities, their species and traits, are a legacy of historic climate and disturbance regimes (the frequency, timing, size and severity of disturbance) and are strong drivers of key ecosystem functions. On a global scale, increasing frequency and intensity of disturbance has been demonstrated to reduce plant diversity and homogenize functional traits in persisting species (Ames et al., 2016; Bond and Keeley, 2005; Cavender-Bares and Reich, 2012; Diaz et al., 2007; Jung et al., 2010; MacDougall et al., 2013). Wildfire frequency and proportion of area burned at high severity have both increased in many parts of the world (Balch et al., 2017; Pechony and Shindell, 2010; Prichard et al., 2017) and these alterations have had measurable consequences for species composition (Bowman et al., 2014; Fairman et al., 2017) due to species loss and turnover and shifts in functional trait expression in

^{*} Corresponding author.

E-mail address: ethantaber@arizona.edu (E.M. Taber).

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response to fire (Ames et al., 2016; Mitchell et al., 2020). Increased fire activity is expected to select for families and species best adapted to coping with fire (Bond and Keeley, 2005; Cavender-Bares and Reich, 2012) and thus to reduce both species and trait diversity at the ecosystem level (Myers et al., 2015). The combined impacts of shifting climate, altered disturbance, and changed vegetation communities may drive hysteretic change in ecosystems (Johnstone et al., 2016).

Understory communities of dry western North American forests are typically well adapted to historic disturbance regimes (frequent, low-severity wildfire) and exhibit functional traits and life-history strategies that confer resilience to these disturbances at the species, community, and ecosystem level (Johnstone et al., 2016). Wildfire was the primary disturbance that shaped ecosystem dynamics in forests of the southwestern United States before EuroAmerican settlement (Covington and Moore, 1994; Swetnam and Baisan, 1996) and *Pinus ponderosa* forests of northern Arizona were characterized by an open, park-like stand structure, perennial grass dominance of the understory, and frequent, low-severity grass-fuel surface fires with an average return interval of 5 to 25 years (Covington and Moore, 1994; Friederici, 2004; Fulé et al., 1997; Swetnam and Baisan, 1996).

More than a century of land use changes—including fire suppression—have excluded fire from much of this region to the present day, increasing overstory density, biomass, and fuel continuity, leading to increased wildfire risk across the west (Hurteau et al., 2014; Walker et al., 2018). Simultaneously, climate change is shifting temperatures and precipitation directionally, with higher temperatures and reduced and more variable precipitation across the western US (Allen et al., 2015; Karl et al., 2009; Williams et al., 2013; Zhang et al., 2021), which has altered fire seasonality, and increased fire frequency and the proportion of high severity fire across the region (Hurteau et al., 2014). These changes in disturbance regimes and shifts in climate limit the species that are able to establish and persist (Munson et al., 2011; Pausas and Keeley, 2009), alter how those species express functional traits (Ames et al., 2016; Bjorkman et al., 2018; Descombes et al., 2020; McGill et al., 2006; Mitchell et al., 2020; Peng et al., 2020), and may directly affect ecosystem functions like decomposition (Brennan et al., 2009; Chuckran et al., 2020; Knelman et al., 2017).

Plant functional trait values reflect a trade-off between ‘fast’ growth strategies that maximize resource acquisition, and ‘slow’ growth strategies that maximize resource conservation (Reich et al., 1999; Reich, 2014; Wright et al., 2004). Fast growth traits—including tall growth forms, high specific leaf area (SLA) and low leaf dry matter content (LDMC)—confer an advantage within high-resource environments, while slow growth traits—including shorter growth forms, low SLA, and high LDMC—allow for resource conservation in low resource environments. At the community level, wildfire that is more frequent or severe than historical norms can cause changes to understory plant communities not only via biodiversity loss (Richter et al., 2019) but also through changes in plant functional trait (PFT) expression (Ames et al., 2016; Enright et al., 2014; Kumordzi et al., 2019). For example, in longleaf pine forests of the southeastern United States, increased fire frequency produced directional changes in understory community leaf traits, with more frequently burned plots exhibiting more conservative leaf traits (Ames et al., 2016; Mitchell et al., 2020). In grasslands of Spain, increased fire severity has been shown to significantly alter plot-level leaf traits, although the direction of change varies according to climatic conditions. More mesic locations that experienced high severity fire shifted toward fast-growth traits, while more xeric locations favored conservative traits after similar burn severity (Fernández-García et al., 2020; Huerta et al., 2021). This interaction between climate and fire severity on community-level plant traits suggests that future vegetation community and ecosystem recovery after wildfire could be strongly shaped by changes in prevailing climate, leading to new successional trajectories.

Understanding the variability in plant traits at the species level can also provide information about which species or functional groups may

be able to persist through environmental shifts (Heilmeyer, 2019). While PFTs can provide mechanistic insight into ecosystem processes (Lavorel and Grigulis, 2012), it is important that researchers select proper traits to measure to avoid redundancy. Many PFTs within an individual may be correlated, and these redundant measurements will likely not produce results worth the effort to make them (Laughlin, 2014). Both SLA (leaf area/leaf dry mass) and LDMC (leaf dry mass/leaf fresh mass) have been demonstrated to respond to both warming and fire frequency and severity (Ames et al., 2016; Huerta et al., 2021; Mitchell et al., 2020; te Beest et al., 2021). Plant height is linked to competitive ability through increased light interception (Keddy et al., 1989; Westoby et al., 2002) and fecundity (Laughlin et al., 2010), and has been shown to decrease at the community level in response to increasing levels of disturbance intensity and stress (Herben et al., 2016; Sonnier et al., 2010). In a Brazilian Cerrado (savannah) landscape, fire-mediated canopy openness has been shown to affect SLA of understory species, with more open canopies associated with species with lower SLA values (Dantas et al., 2013). Similarly, experimental climate warming produces shifts in trait expression, including increased SLA in French subalpine graminoids (Debouk et al., 2015), decreased SLA in Arctic tundra shrubs (Hudson et al., 2011), decreased SLA and increased height in European temperate deciduous forest understory species (Govaert et al., 2021), increased LDMC in Afromontane grasses (te Beest et al., 2021), and both increased and decreased height in Arctic forbs and graminoids (Baruah et al., 2017).

In order to understand how burn severity and climate warming interact to shape understory plant community recovery and ecosystem function, we employed experimental warming in the first year following wildfire across a burn severity gradient ranging from unburned to high severity in a *P. ponderosa* understory community. We asked the following questions: how are 1) plant community composition; 2) plant functional trait expression (specifically SLA, LDMC, and plant height) across species; and 3) decomposition rates affected by burn severity, warming, and their interaction?

2. Materials and methods

2.1. Study area

This study was conducted within and immediately adjacent to the perimeter of the 2019 Museum Fire, located approximately 1.6 km north of Flagstaff, Arizona USA (35.263 latitude, −111.639 longitude). This fire burned in late July of 2019, with a total of 793.6 ha burned. The Museum Fire was characterized by interspersed patches of varying severity, with very low, low, moderate, and high severity patches present (USDA Forest Service, 2019). No post-fire seeding treatments were implemented on the research site (Jacob Dahlin, USDA Forest Service, personal communication). The fire occurred on a site with dominant overstory vegetation consisting of *Pinus ponderosa*, with patches of *Quercus gambelii* and *Juniperus deppeana*, and interspersed individuals of *Pinus strobus* and *Pseudotsuga menziesii*. Elevations within the fire site range from approximately 2240 m to approximately 2760 m above sea level. For this study, research plots were monumented at lower elevations within this range, from 2251 m to 2328 m. All plots were located on slopes with a southeasterly aspect, with slopes between 20 and 30°. Soils are based on mixed igneous parent material, with both Alfisol and Mollisol soil orders.

Annual precipitation averages 55.52 cm (National Weather Service, 2021), with a bimodal precipitation seasonality. An average of 28 % of annual precipitation falls in winter, while 34 % occurs in summer due to the southwestern monsoon (Hereford, 2007). The year in which this study was conducted (2020) was the driest year on record for our study site, with total precipitation >31 cm below the historical average, which included the driest summer monsoon season (June 15–Sept. 15) on record (16.58 cm below average). Additionally, 2020 was the 5th warmest year on record, with an annual mean temperature 1.11 °C above the

historical average (National Weather Service, 2021).

2.2. Plot establishment

Plots were established in May of 2020, 10 months following the fire. Plot establishment was delayed due to permitting issues with the USDA Forest Service caused by the COVID-19 pandemic. We established sixty 4 × 4 m research plots across the burn severity gradient, with twenty of these research plots located within unburned (abbreviated ‘U’), low (abbreviated ‘L’), and high (abbreviated ‘H’) burn severities. Unburned plots were located immediately outside of the burn perimeter and no further than 470 m from the edge of the fire perimeter. Burn severity classifications for these research plots were initially derived from the USDA Burned Area Emergency Response (BAER) map, which is based on Burned Area Reflectance Classification remote sensing data that has been verified by field crews (Noll and Malis-Clark, 2020; Parsons et al., 2010). BAER classifications are based on relative change in soil organic matter and soil structure due to fire (Keeley, 2009). We confirmed burn severity classifications for each plot by visually assessing first order fire severity effects in May 2020 including vegetation cover within plots, the presence of bare mineral soil within plots, and overstory mortality within an approximately 25 m radius of the center of each research plot. Indicators of high severity areas included > 50 % bare mineral soil and > 90 % overstory mortality. Indicators of low severity included extant understory vegetation, low bole scorch height, and < 50 % overstory mortality. Each research plot was subdivided into two 1 m² sampling plots located 1 m apart, with one treatment plot randomly assigned as a control (n = 60), and the other subjected to warming (n = 60) via an open-top warming chamber (Fig. S1). This generated 20 treatment plots in each of 6 severity*treatment classes (unburned*control, “UC”; unburned*warmed, “UW”; low-severity*control, “LC”; low-severity*warmed, “LW”; high-severity*control, “HC”; high-severity*warmed, “HW”) for a total of 120 plots. This design allowed us to test the impacts of fire severity, warming, and their interaction independently.

2.3. Open-top warming chambers (OTCs)

Open-top warming chambers (OTCs) were used to simulate predicted warming due to climate change in the next ~ 50 years (Garfin et al., 2014; Kunkel et al., 2013). Warming chambers were based on modified versions of designs from the International Tundra Experiment (Marion, 1993). The chambers are 1.5 m × 1.5 m in area, with a square footprint and 60 cm vertical side walls constructed from 10 mil string-reinforced clear poly sheeting, attached to rebar stake corners (Fig. S1). Open-top chambers were installed in the first week of June 2020 and all vegetation measurements within chambers were taken between 90 and 150 days after chamber installation. Temperature data was collected in both the control (‘C’) and warmed (‘W’) treatments for 30 days after OTC installation, using HOBO UA-001-08 data loggers (Onset; Bourne, Massachusetts USA) set at ground level. Loggers were installed in all 120 sampling plots. Loggers within warming chambers were placed ~ 30 cm from a corner of the chamber, toward the center of the plot. Loggers for control plots were placed adjacent to the corner of each control plot, over 2 m from the warming chambers (Fig. S1). Logger data showed an average daytime temperature (defined as the period between 0800 and 2000 MST) of 29.134 °C for warmed plots and 28.055 °C for control plots, with OTCs producing an average of 1.079 °C of daytime warming, mimicking anticipated warming by 2050 (Garfin et al., 2014; Kunkel et al., 2013). Temperature data was only collected during the first month of the experiment, as the loggers were on temporary loan to the authors.

2.4. Data collection

2.4.1. Community composition

Collection of community composition data took place in September

2020 (~90 days after OTC installation). Percent cover for vegetation and substrates were visually assessed using a modified Daubenmire method (Daubenmire, 1959). Individuals were identified to the species-level with the exception of two visually similar *Muhlenbergia* species (*M. montana* and *M. virescens*), which were combined into one taxon for analysis (*Muhlenbergia* spp.), and one *Penstemon* species which could not be identified to the species level. Both vegetation and substrate cover were estimated to the nearest 0.25 % (estimates below 0.25 % were recorded as “trace”). All nomenclature follows the USDA NRCS Plants Database (<https://plants.usda.gov/>) accessed in 2020.

2.4.2. Plant traits

Trait data was collected in Fall of 2020 prior to senescence (between 100 and 150 days after OTC installation). SLA (cm² g⁻¹), LDMC (g g⁻¹), and height (mm) were collected for species accounting for > 85 % of total cover within each burn severity category. All measurements followed standardized collection protocols (Cornelissen et al., 2003; Garnier et al., 2001; Pérez-Harguindeguy et al., 2013). Measurements on individuals were collected regardless of sun exposure, slope, or aspect, but only mature, healthy leaves were measured. Height was measured for 20–25 individuals per species within each severity*treatment class (n = 332 individuals). For species with <20 individuals within a severity*treatment class, height was recorded for all individuals present (Table S1). To measure SLA and LDMC, one leaf sample was taken from individuals of each species within each severity*treatment class (n = 645 leaves). Samples for each species were pooled across severity*treatment classes, as many species occurred on limited numbers of plots within a given severity*treatment class. For species with <20 individuals within a severity*treatment class, we collected between 3 and 10 leaves from an individual, aiming for a total of 20 leaves per species per severity*treatment class (minimum 10 leaves; Table S1). Leaf area for all samples was determined using a CID-203 leaf area meter (CID Bio-Science; Camas, Washington USA). All fresh samples were rehydrated by placing petioles in distilled water for at least 6 h before being scanned and weighed following Garnier et al. (2001). After leaf area and fresh mass were measured, leaf samples were dried at 70 °C for 72 h, then reweighed. SLA and LDMC were then calculated from the area and mass data for each sample.

2.4.3. Quantifying decomposition

Decomposition rates were determined using the Tea Bag Index (TBI; Keuskamp et al. 2013). This technique provides an easy method of measuring decomposition using readily available organic materials of uniform composition and mass. We buried one bag of Lipton green tea (Sencha exclusive collection, EAN 8714100770542) and one bag of Lipton rooibos tea (Lipton Herbal infusion Rooibos – Rooibos and hibiscus: EAN 87 22700 18843 8) in each treatment plot, with each tea bag buried in its own 8 cm deep hole (Keuskamp et al., 2013), in early July 2020. After ~ 90 days, the bags were unburied, cleaned of soil particles, and dried for 48 h at 70 °C. The bags were then weighed and compared to an average original tea weight for each tea type. Average original tea weight was determined by weighing the contents of 20 unburied tea bags with batch numbers that corresponded to those buried. Stabilization factors and decomposition rates were then determined using the equations provided by Keuskamp et al. (2013).

A small number of tea bags used in the experiment contained very small holes upon exhumation due to the coarse texture of soils at the site. Power analysis using *G*Power* 3.1.9.4 (Faul et al., 2009) determined that a minimum of 11 tea bag pairs were needed for each burn severity*treatment class in order to achieve an effect size (f) of 0.4, with an alpha error probability of 0.05 and power of 0.8. All severity*treatment classes met the minimum required number of usable tea bags, with the exception of one class (low severity*warmed), which contained 9 pairs of tea bags without holes. For this class, tea bag holes were measured and the two tea bags with the smallest holes (maximum hole size 2 mm) were included in analysis to meet minimum power requirements for ANOVA.

2.5. Statistical analyses

All analyses were conducted using R version 4.2.2 (R Core Team 2022).

2.5.1. Community composition

Percent cover for vegetation was standardized using Wisconsin double standardization (McCune and Grace, 2002). Standardized abundance values were then used in all analyses involving abundance. Differences in composition according to severity and treatment were analyzed using PERMANOVA (Anderson, 2017, 2001) within the *vegan* package (Oksanen et al., 2022), Non-metric Dimensional Scaling (NMDS), and Indicator Species Analysis (ISA; Bakker 2008) using the *Indval* function in the *labdsv* package (Roberts, 2019).

2.5.2. Plant functional traits

Community weighted mean (CWM) PFT values were calculated for SLA, LDMC, and height using the *dbFD* function in the *FD* package in R (Laliberté et al., 2014). Generalized linear mixed models (GLMMs) were used to assess whether CWM trait values differed according to burn severity, warming treatment, and their interaction. Mixed effects models were fitted using the *lme4* (Bates et al., 2015) and *glmmTMB* (Brooks et al., 2017) packages. Distributions for mixed effects models were selected using the *descdist* function in the *fitdistrplus* package (Delignette-Muller and Dutang, 2015). Residual plots were employed to ensure that model assumptions had been met (Zuur et al., 2009). Akaike's information criterion (AIC) was used to select the most parsimonious model from candidate models (Akaike, 1987). In instances where AIC differed between candidate models by < 2, the simpler model (i.e. fewer fixed effects) was chosen. Model fit was assessed using marginal and conditional R^2 values (Nakagawa and Schielzeth, 2013) using the *r2* function in the *performance* package (Lüdtke et al., 2021). Model forms are displayed in Table 1.

2.5.2.1. Specific leaf area. SLA was modeled using a GLMM fitted to CWM SLA as the response variable, with severity as a fixed effect. Plot was treated as a random effect, and a Gaussian distribution with the identity link function was applied. Three outliers were indicated using Rosner's outlier test and were not included in analysis.

2.5.2.2. Leaf dry matter content. LDMC was modeled using a GLMM with a beta distribution and logit link. We used severity, warming, and their interaction as fixed effects, plot as a random effect, and CWM LDMC as the response variable.

2.5.2.3. Plant height. CWM plant height was modeled using a GLMM with a Gaussian distribution and identity link. Severity, warming treatment, and their interaction were included as fixed effects, with plot as a random effect and CWM height as the response variable. Three outliers were identified using Rosner's outlier test and were not included in analysis.

2.5.3. Decomposition

Decomposition rates (k) determined by the Tea Bag Index were compared across severity, treatment, and their interaction using a GLMM with beta distribution and logit link. Model fitting and selection followed the same protocols used for functional traits described above. Severity, warming treatment, and their interaction were included as fixed effects, with plot as a random effect and decomposition rate (k) as the response variable (Table 1).

3. Results

3.1. Community composition

Unburned locations were dominated by two perennial bunchgrass taxa (*Muhlenbergia* spp. and *Piptochaetium pringlei*: 31 % and 58 % of vegetative cover, respectively). Low severity locations were also dominated by perennial bunchgrasses (*Muhlenbergia* spp., and *Piptochaetium pringlei*: 35 % and 22 % of vegetative cover, respectively). High severity plots consisted of a more even mixture of graminoids, forbs, and woody species (*Muhlenbergia* spp. and *Elymus elymoides*: 17 % and 13 % of vegetative cover, respectively; *Solanum triflorum*, *Lotus wrightii*, and *Oenothera elata*: 15 %, 10 %, and 5 %, respectively; *Quercus gambelii* and *Ceanothus fendleri*: 18 % and 6 %, respectively).

Total vegetative cover between severity*treatment classes was highly variable. Mean raw vegetative cover values are as follows: UC, 10.27 %; UW, 21.7 %; LC, 16.53 %; LW, 20.01 %; HC, 5.23 %; HW, 9.49 %. When plots with no vegetation (mainly in HC and HW) were removed from analysis, mean cover values between treatments were considerably more similar: UC, 10.27 %; UW, 21.7 %; LC, 17.4 %; LW, 20.01 %; HC,

Table 1

Model forms, effects, results and R^2 values for all GLMMs used. Bold text indicates significance at $\alpha = 0.05$. All models included plot as a random effect.

Response Variable	Model	Model family/link	Fixed effect	Estimates	SE	P	$R^2(m)$	$R^2(c)$
CWM SLA	Severity	Gaussian/identity	Intercept	113.613	1.442	<2e-16	0.112	0.28
			SeverityL	-1.404	2.061	0.49979		
			SeverityH	-7.586	2.323	0.00194		
CWM LDMC	Severity × Treatment	beta/logit	Intercept	0.02108	0.0709	0.76618	0.573	0.976
			SeverityL	-0.04752	0.10141	0.63936		
			SeverityH	-0.19027	0.11542	0.09925		
			TreatmentW	0.06298	0.08559	0.4618		
			SeverityL:TreatmentW	-0.05316	0.12189	0.66277		
			SeverityH:TreatmentW	-0.45725	0.14434	0.00154		
CWM Height	Severity × Treatment	Gaussian/identity	Intercept	278.244	9.812	<2e-16	0.404	0.43
			SeverityL	-4.653	14.058	0.7414		
			SeverityH	-48.783	16.021	0.00302		
			TreatmentW	10.13	13.571	0.46026		
			SeverityL:TreatmentW	2.404	19.759	0.90381		
			SeverityH:TreatmentW	-61.85	22.289	0.00774		
Decomposition rate (k)	Severity × Treatment	beta/logit	Intercept	-5.32628	0.15584	<2e-16	0.23	0.467
			SeverityL	0.2365	0.20068	0.2386		
			SeverityH	0.27704	0.21045	0.188		
			TreatmentW	-0.22837	0.20574	0.267		
			SeverityL:TreatmentW	-0.02969	0.28024	0.9156		
			SeverityH:TreatmentW	0.5884	0.26588	0.0269		

8.45 %; HW, 15.03 %. ANOVA of square root transformed cover data with zero-cover plots removed revealed significant differences according to severity ($F(2,98) = [4.613]$, $p = 0.012$), with significantly higher average cover in low severity plots compared to high severity ($p = 0.010$).

PERMANOVA revealed that vegetation cover and composition vary by burn severity ($F(2,101) = [5.910]$, $p = 0.001$), but no significant treatment or severity*treatment effects were detected (Table 2). NMDS plots demonstrated differences in vegetation composition between high severity plots and others, with substantial overlap between unburned and low severity locations (Fig. 1). Follow-up analysis with *beta.disper*—a multivariate analogue of Levene's test—and *permutest.betadisper*—a permutation-based test of multivariate homogeneity of group dispersions—revealed higher beta diversity within the high severity treatment than observed in other severities ($F(2,101) = [10.934]$, $p < 0.003$).

Indicator Species Analysis demonstrated that three species are significant indicators of various severity, and severity*treatment classes. *Ceanothus fendleri* ($IndVal = 0.3284$, $p = 0.002$) is strongly associated with high severity locations, *Piptochaetium pringlei* ($IndVal = 0.5815$, $p = 0.001$) with unburned locations, and the legume *Lotus wrightii* ($IndVal = 0.3333$, $p = 0.001$) is strongly associated with high severity*warm plots (Table S2). No species were identified as significant indicators of low burn severity.

abundances (Wisconsin double-standardized; 999 permutations) in response to severity, warming treatment and their interaction (significant factors/ P values in bold).

3.2. Community-level trait responses

In our generalized linear mixed model for SLA, high burn severity had a negative effect on CWM values ($t = -3.266$, $p = 0.002$; Fig. 2a, Table 2) compared to unburned locations. Fixed effects alone (R^2_{marginal}) explained 11.2 % of variance in the model, while fixed effects plus random effects ($R^2_{\text{conditional}}$) explained 28 % of variance.

In our GLMM for LDMC, the interaction of high burn severity and experimental warming had a negative effect on CWM values ($z = -3.168$, $p = 0.002$; Fig. 2b, Table 2), with HW plots exhibiting negative change in LDMC of larger magnitude than all other severity*treatment combinations compared to unburned control plots. Fixed effects alone (R^2_{marginal}) explained 57.3 % of variance in the model, while fixed effects plus random effects ($R^2_{\text{conditional}}$) explained 97.6 % of variance.

In our GLMM for plant height, high burn severity had a negative effect on CWM values ($t = -3.045$, $p = 0.003$; Fig. 2c, Table 2) compared to unburned locations. Additionally, the interaction of high severity and experimental warming was significant ($t = -2.775$, $p = 0.008$; Fig. 2c, Table 2). Fixed effects alone (R^2_{marginal}) explained 40.4 % of variance in the model, while fixed effects plus random effects ($R^2_{\text{conditional}}$) explained 43 % of variance.

3.3. Decomposition

In our GLMM for decomposition rate (k), the interaction of high burn severity and experimental warming had a positive effect on k ($z = 2.21$, $p = 0.027$; Fig. 3, Table 2), with HW exhibiting increases in

decomposition rates of larger magnitude than all other severity*treatment combinations compared to unburned control plots. Fixed effects alone (R^2_{marginal}) explained 23 % of variance in the model, while fixed effects plus random effects ($R^2_{\text{conditional}}$) explained 46.7 % of variance.

4. Discussion

Fires in the American southwest are occurring in new seasons, with larger proportions of high burn severity, while climate change has increased mean annual temperatures across the American southwest. How these changes will interact to shape community composition, functional trait expression, and ecosystem function following wildfire are critically important for understanding and predicting successional trajectories in the future. We found that there were significant independent and interactive effects of fire severity and experimental warming on community composition, plant trait expression across species, and rates of a key ecosystem function, decomposition, in the first post-fire growing season and following short-term (~90–150 days) experimental warming. Our results suggest that fire recovery under future climatic conditions may exhibit different functional trait expression and altered ecosystem function, which may contribute to novel successional trajectories and species assemblages.

Community composition was not significantly impacted by burn severity*warming interactions, but severity alone did shape community composition. Indicator Species Analysis found that *Ceanothus fendleri* is strongly associated with locations that burned at high severity within this study site ($IndVal = 0.328$, $p = 0.002$). This nitrogen-fixing shrub species (Story, 1974) typically resprouts after fire and its seeds are dependent on heat to germinate (Huffman and Moore, 2004). Nitrogen fixation by dense post-fire stands of *Ceanothus* species in semi-arid forests can return larger amounts of N to the soil than were depleted by fire (Johnson and Curtis, 2001) and *Ceanothus* can rapidly dominate high severity burn areas, out-competing potential colonizers and tree seedlings (Bohlman et al., 2016; Welch et al., 2016). Furthermore, relatively deep-rooted woody species such as *C. fendleri* can drive conversion of grass-dominated communities to shrub-dominated understories, as they are able to access water at greater soil depths and out-compete shallow rooted native grasses, and this conversion is enhanced by increased aridity (Berdugo et al., 2022). Such priority effects can not only shape species composition but can influence ecosystem functions like decomposition and primary productivity through changes in composition and trait expression (Dickie et al., 2012; Körner et al., 2008). Areas that are adapted to high frequency/low severity fires, like our study system, are likely to see such shifts in composition following fires that are outside their historical range of variation (Miller and Safford, 2020), which has the potential to drive a shift from forested ecosystems to non-forest shrublands (Richter et al., 2019). The increased occurrence and abundance of *C. fendleri* in high severity areas suggests that such an alternate trajectory may already be underway in these areas of our study site.

In contrast with community composition, we did observe significant interacting effects of fire severity and experimental warming on CWMs of key functional traits. We observed a significant severity*treatment interaction for CWM values of LDMC. LDMC is strongly correlated with maximum relative growth rate (RGR_{max}) and decomposition potential (K_{pot}), and low LDMC values are an indicator of rapid growth and decomposability (Kazakou et al., 2006). Further, LDMC has been negatively correlated with aboveground net primary productivity (ANP) (Polley et al., 2022), indicating higher ANP in HW plots. Our finding of low LDMC in the most disturbed (HW) locations corresponds with the fast-economics “ruderal syndrome” commonly seen in highly disturbed ecosystems and in the first stages of succession (Grime, 1977). Increased production of highly decomposable litter may change rates of nutrient cycling, altering successional trajectories over time as soil nutrient levels increase. However, our study examined rapid and short-term responses of this system to warming and fire. Thus, further research will be required to determine the temporal duration of these effects, and

Table 2

Results of PERMANOVA based on Bray-Curtis dissimilarities of relative species abundances. Bold text indicates significance at $\alpha = 0.05$.

Factor	DF	Sum of Squares	R^2	F	P
Severity	2	4.18	0.10455	5.9097	0.001
Treatment	1	0.278	0.00695	0.7859	0.659
Severity $\times$ Treatment	2	0.865	0.02163	1.2229	0.173
Residual	98	34.657	0.86686		
Total	103	39.979	1		

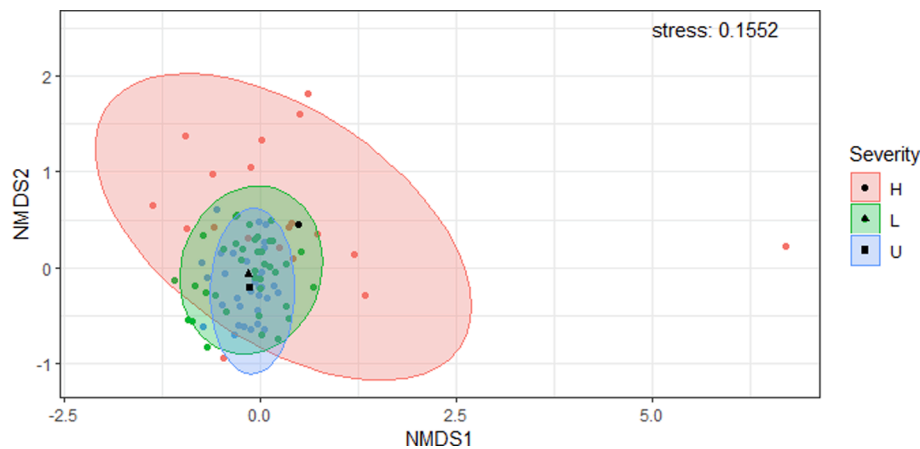


Fig. 1. Non-metric multidimensional scaling (NMDS) ordination of plots which contained vegetation. Ellipses represent 95 % confidence levels and black points represent group centroids for each severity classes.

whether decomposition rates and soil nutrients are impacted by changed leaf traits over time.

Short-term warming in other systems has been found to produce community shifts toward species with higher SLA (Debouk et al., 2015), but we detected no such shift under warming treatments in this experiment. Instead we found that, in contrast to other studies in dry western forests (Huerta et al., 2021; Stevens et al., 2015), high-severity plots exhibited lower CWM SLA than low or unburned plots. High SLA is generally correlated with early successional and fast-growing species (Garnier et al. 2004) while low SLA is correlated with slow growth and stress tolerance (Reich et al., 1997). Areas that burn at high severity often experience warmer post-fire conditions than adjacent locations with extant canopy cover (Haffey et al., 2018; Meyer et al., 2001) and our high severity plots had reduced canopy cover due to near total canopy mortality. Furthermore our plots were measured during an unusually dry period (<44 % of average annual precipitation; the driest year on record; National Weather Service 2021). Although high severity plots which contained vegetation had lower mean vegetative cover than low severity and unburned classes (11.61 %, 18.74 %, and 15.99 % respectively), this unusually stressful post-fire environment may have favored the survival and growth of more stress tolerant species, or a shift toward more stress tolerant leaves within species.

High SLA is typically coupled with low LDMC (Garnier et al., 2001), in line with the acquisitive vs. conservative strategies described by the leaf economic spectrum (Wright et al., 2004). However, our observation of both lower CWM SLA and LDMC in high severity locations runs counter to this general trend. This is likely due to the influence of a few species with relatively thick, high-water content leaves that occurred at high cover at a few of our plots (specifically *Solanum triflorum*, *Lotus wrightii*, *Oenothera elata*) and almost exclusively within high severity locations. This finding suggests that, in high stress post-fire environments, species that are able to rapidly acquire limited soil moisture and retain it within their tissues may have a competitive advantage. The lack of monsoonal rainfall in the year of this study likely favored these drought-tolerant plants. As year-to-year precipitation in this region is expected to become more variable (Zhang et al., 2021), community trait expression during post-fire recovery may likewise vary and diverge from common global trends because of stochastic weather conditions.

High burn severity influenced a significant decrease in CWM values for plant height compared to low severity and unburned plots. Further, this trend was exacerbated by experimental warming. A shorter growth form is associated with a conservative growth strategy, and is common in ecosystems where light is not a limiting factor such as savannahs (Maracahipes et al., 2018). High severity locations experienced near total overstory mortality, increasing understory light availability in these areas. Additionally, increasing environmental stress has been

shown to decrease CWM plant height in early successional herbaceous communities in southern Quebec (Sonnier et al., 2010), and experimental warming has produced significant shifts toward decreased intraspecific height in some Arctic species (Baruah et al., 2017). The decrease in CWM height we detected in HW compared to HC plots may be a reaction to higher drought stress induced by warming in this treatment class.

Taken together, the PFT trends we observed indicate that warmer conditions following high severity fire result in a faster growing understory that rapidly acquires resources, invests less energy in vertical growth, and stores resources within tissues as a means of stress tolerance. *Solanum triflorum* and *Oenothera elata*, described above, typify this syndrome. These two species, each averaging <15 cm in height, accounted for over 20 % of total vegetative cover within high severity locations, and occurred solely on warmed plots in our study. The potential impact of atypical, extremely dry conditions on the counterintuitive trait syndrome we observed in HW plots should not be overlooked and warrants further investigation into the combined effects of variable precipitation, climate warming, and burn severity.

We found a significant severity*treatment effect for decomposition rate after only ~ 90 days of warming. These findings suggest that rates of one key ecosystem function, decomposition, were accelerated following high severity fire and warmer conditions. This change is likely to alter soil nutrient levels and may impact successional trajectories in this ecosystem in the future by favoring faster growing or highly competitive species over more conservative species. Indeed, the decreased CWM LDMC we observed within this treatment may be indicative of such a shift already underway within the first post-fire year. Although we found no significant compositional difference between HC and HW plots, increased growth rate—as indicated in our study by lower LDMC in HW plots—can contribute to priority effects through increased reproduction and population growth, leading to alternative transient or stable states (Fukami, 2015). Rapid growth of early successional species under warmer conditions may have the potential to alter successional trajectories by strengthening the importance of priority effects.

A high abundance of ruderal species in the years immediately following high severity fire has been linked to type conversion from forested to non-forested ecosystems in the southwestern U.S. (Coop et al., 2016), and such fire-induced ruderal systems can increase reburn potential and persist after future reburns, reinforcing the formation of alternative stable states (Coop et al., 2016; Keeley and Brennan, 2012). It is unclear whether our high severity plots represent a long-term change in successional trajectory, or a short-term change in plant composition in the earliest stages of fire recovery. The long-term stability of post-fire type conversion in the southwestern U.S. is not fully understood, but stability of converted areas will likely be bolstered by

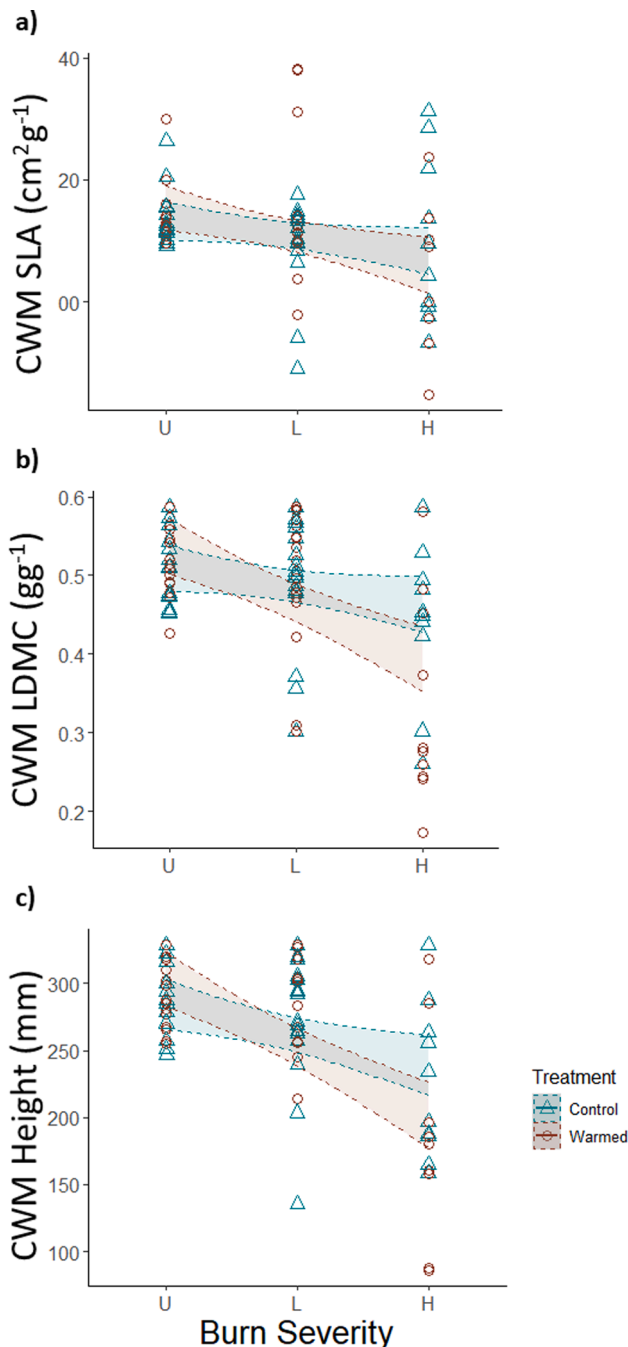


Fig. 2. Effect of burn severity and experimental warming treatment on community weighted mean (CWM) values of specific leaf area (SLA; a), leaf dry matter content (LDMC; b), and plant height (c). Blue and red symbols represent plot-level CWM values for unwarmed and warmed plots, respectively. Error bars represent means $\pm$ standard error.

subsequent disturbance (Falk et al., 2022; Roccaforte et al., 2012). If warmer conditions following high severity fire are indeed contributing to ruderal dominance during post-fire succession, reburning of such sites will likely support the stability of non-forest states.

5. Conclusions

Our results indicate that *Pinus ponderosa* forest understories subjected to atypically high burn severity and experimental climate warming exhibit altered CWM trait expression and accelerated decomposition rates. These changes have the potential to change successional

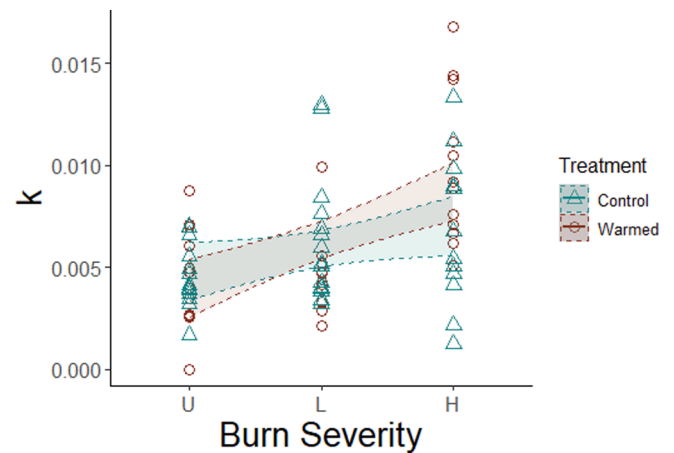


Fig. 3. Effect of burn severity and experimental warming treatment on decomposition rate (k). Blue and red symbols represent plot-level k values for unwarmed and warmed plots, respectively. Error bars represent means $\pm$ standard error.

trajectories and alter understory composition, structure, and ecosystem functioning over time. Ongoing management efforts to return these forests to historical stand densities are the best insurance against high severity fire and maintenance of understory biodiversity into the future. In our study, the largest changes to ecosystem function associated with warming occurred in high severity plots. As the proportion of high severity wildfire increases in this region, it is likely that the trends observed in our study will become more prevalent in the southwestern US.

The year in which this study took place was the fifth warmest and single driest year on record for our study area (National Weather Service, 2021). These unusual but increasingly typical weather conditions likely had an effect on post-fire regeneration and the variables measured in this study. However, as the southwestern United States is predicted to become warmer and drier under future climate change (Diffenbaugh and Ashfaq, 2010; Garfin et al., 2014), the weather conditions during the study likely more accurately represent projected climatic conditions in this region. Future research should focus on quantifying the duration of the trends observed in this study to better understand ecosystem trajectories under climate change and in response to interannual variation in weather.

Data availability

Data will be made available upon request.

CRediT authorship contribution statement

Ethan Taber: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization, Funding acquisition. **Rachel M. Mitchell:** Conceptualization, Methodology, Investigation, Resources, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2023.121019>.

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