



Fire season and time since fire determine arbuscular mycorrhizal fungal trait responses to fire

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Abstract

Background and aims Arbuscular mycorrhizal (AM) fungi are common mutualists in grassland and savanna systems that are adapted to recurrent fire disturbance. This long-term adaptation to fire means that AM fungi display disturbance associated traits which should be useful for understanding environmental and seasonal effects on AM fungal community assembly.

Methods In this work, we evaluated how fire effects on AM fungal spore traits and community composition vary with fire season (Fall vs. Spring) and time since fire. We tested this by analyzing AM fungal spore traits (e.g., colorimetric, sporulation, and size) from a fire regime experiment.

Results Immediately following Fall and Spring fires, spore pigmentation darkened (became less hyaline);

however, this trait response was not linked to fire driven changes in spore community composition and likely implies a plastic spore pigmentation response to fire. Six months after Fall fires, spores in burned plots were lower in volume, produced less color rich pigment, and had higher sporulation rates, and these differences in spore traits were associated with shifts in AM fungal spore communities demonstrating environmental filtering.

Conclusion Fire drove plastic and longer-term changes in AM fungal spore traits and community assembly that varied with fire season (stronger effects in Fall) and time since fire. This demonstrates the utility of applying trait-based approaches to microbial community assembly, and the importance of considering changes in community assembly across time.

Keywords Traits · Mycorrhizae · Disturbance · Fire · Grasslands · Seasonality

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Introduction

Mycorrhizal fungi are common mutualists of land plants that influence ecosystems through their roles in productivity and nutrient cycles (Smith and Read 2010). Since biological function is often closely associated with community composition (Forrester and Bauhus 2016; Maciá-Vicente et al. 2023), studying the processes that influence mycorrhizal community assembly can improve our understanding of

mycorrhizal ecology and responses to environmental change. Global patterns in mycorrhizal communities suggest that combinations of biotic and abiotic filters, as well as variation in their interactions through time, are strong determinants of community assembly (Kivlin et al. 2011; Bahram et al. 2015; Powell and Bennett 2016; Vályi et al. 2016). However, it is often difficult to quantify the relative importance of community assembly filters without the inclusion of biological traits which can be difficult to obtain for microbes (Green et al. 2008). Yet Arbuscular mycorrhizal (AM) fungal spores have easily observable traits and present an excellent system for leveraging trait-based methods to answer questions about community assembly (Chagnon et al. 2013; Chaudhary et al. 2020; Zanne et al. 2020; Hopkins and Bennett 2023).

Biological traits provide insight into how organisms interact with abiotic and biotic aspects of their environment, and how these aspects and interactions vary through time. This makes traits useful for measuring the relative importance of community assembly filters on AM fungal spores. For example, aerial dispersal ability has been linked to small spore ornamentation and size (Chaudhary et al. 2020), climate and aridity to melanin content (Deveautour et al. 2020), and disturbance to pigmentation (Hopkins and Bennett 2023). Further, AM fungal communities undergo natural seasonal shifts in composition (Lugo et al. 2003; Santos-Gonzalez et al. 2007; Dumbrell et al. 2011; Maitra et al. 2019) that allow for assessment of seasonal variation in AM fungal spore traits and their interactions with plant hosts. The clear relationship between AM fungal spore traits and environmental conditions both informs our understanding of mycorrhizal ecology, and allows us to test how traits mediate environmental influence on AM fungal spore communities.

AM fungi display significant interspecies variation in spore traits that can be linked to environmental variation (Chagnon et al. 2013; van der Heyde et al. 2017; Powell and Rillig 2018). This variation in spore traits is useful not only for distinguishing between AM fungal taxa (Powell et al. 2009; INVAM 2022), but also identifying which trait responses to fire are plastic or temporary responses, and which trait responses can be linked to changes in community assembly (e.g., environmental filtering; Hopkins and Bennett 2023). Despite phylogenetic conservatism in

many spore traits (Pringle and Bever 2002; Oehl et al. 2005; Powell et al. 2009), variation in spore traits has been linked to disturbance specific responses and can help explain changes in community assembly (van der Heyde et al. 2017). For example, increases in aridity explain variation in spore melanin synthesis in Australian AM fungal spore communities (Deveautour et al. 2020), differences in ability to colonize host root space are predictive of coexistence and community composition in old field systems (Maherali and Klironomos 2012), and fire and grazing associated filtering on spore pigmentation and volume influence community composition in tallgrass prairie systems (Hopkins and Bennett 2023). Spore volume may be an important determinant of fire survival, since smaller spores have smaller surface areas, which will absorb less heat energy during fire (Bejan and Kraus 2003). Protective pigmentation is of particular interest as it is known to provide resistance to heat and other fire associated stressors amongst other fire tolerant microbes (Gessler et al. 2014; Cordero and Casadevall 2017; Rajamani et al. 2021). The use of traits to understand AM fungal spore community assembly can further benefit from the inclusion of disturbance-based methods that allow for assessment of seasonal changes in communities.

Disturbance drives both initial and ongoing changes to environmental filters on AM fungal spore community dynamics. Fire in particular is useful for understanding AM fungal community assembly, as many AM systems require recurrent fire for their maintenance (e.g., prairies and savannas; Beckage et al. 2009; Ford 2010). This long-term adaptation to fire means that AM fungal spores display a suite of disturbance associated traits like protective pigmentation and fire associated life-history strategies that are informative of ongoing selective processes operating on AM fungal communities (Lenoir et al. 2016; Deveautour et al. 2020; Hopkins and Bennett 2023). Fire is also useful for evaluating seasonal variation in AM fungal spore communities, as fire causes immediate heat-related mortality of mycorrhizae (Klopatek et al. 1988; Hamman et al. 2007), and drives persisting increases in UV exposure (Certini 2005), soil drying (MacDonald and Huffman 2004; Pereira et al. 2018), soil pH changes (Verma and Jayakumar 2012), and oxidative stress (Sigmund et al. 2021) that can influence community assembly over longer time intervals. Further, modifying the time of fire

can inform how mycorrhizal community assembly is modified by seasonal differences in assembly filters (Santos-Gonzalez et al. 2007). Specifically, fire that occurs during times of higher sporulation (i.e., Fall; Smith & Read 2010) may have stronger effects on community assembly relative to fire at other times of year. By assessing how fire and timing of fire influence AM fungal spore traits and community composition, the underlying processes that structure AM fungal spore communities can be better understood.

We tested how fire influenced AM fungal spore traits to drive changes in community assembly and incorporated variation in fire season and time since fire. Specifically, we sampled AM fungal spore communities following Spring and Fall fires in a tall-grass prairie fire manipulation experiment. Spore communities were quantified, and colorimetric, size, and sporulation traits were measured. This enabled us to test three questions (Fig. 1): 1) do fire effects on AM fungal spore traits and communities vary based on fire season, 2) do fire effects on AM fungal traits change with time since fire, and 3) are fire effects on AM fungal spore community composition mediated by spore traits? We hypothesized that fire would be associated with disturbance related spore traits and that this effect would be modified by fire season. We further hypothesized that fire effects on spore traits would change with time since fire, and that trait responses to fire would be correlated with changes in AM fungal spore community composition. We predicted that fire would select for darker colored

pigmentation that provides resistance to fire temperatures, and that smaller volume spores would be more likely to survive fire due to their smaller surface area. We also predicted that fire's influence on spore traits and community assembly would be stronger following Fall fire, since sporulation is higher in the Fall (relative to Spring).

Materials and methods

Study system This work was conducted at a tall-grass prairie restoration (4400 m²) at the Perennial Agriculture Project Field Station near Lawrence, KS, USA (39° 0' 6.9156" N, 95° 19' 10.4376" W; Fig. 2). This region has a 5–6 month long growing season between April and September, with an average annual rainfall of 900–1000 mm primarily between March and August. Prior to restoration the site was an old field system (10+ years since last planting) dominated by *Bromus inermis*. To prepare the site for restoration, the field was burned in March 2021, glyphosate herbicide was applied in March and April of 2021, and the field was rototilled and harrowed. Forty, five m² square plots were established with buffer zones of 5 m between plots. The plots were then planted with a regionally collected seed from Hamilton Native Outpost (Elk Creek, MO). Briefly, the seed mix contained a diverse mixture of native grasses, forbs, and legumes including: *Schizachyrium scoparium*, *Bouteloua curtipendula*, *Panicum*

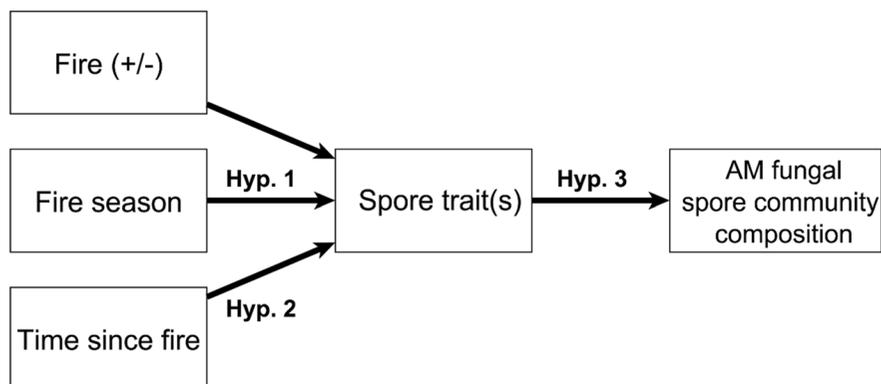


Fig. 1 Hypothesized pathways for fire season and time since fire effects on AM fungal spore traits and spore community composition. We hypothesized that AM fungal spore trait and spore community responses would vary between fire season

(Hyp. 1), and that fire effects on spore traits would vary with time since fire (Hyp. 2). We also hypothesized that fire effects on AM fungal spore community composition would be mediated by fire effects on spore traits (Hyp. 3)

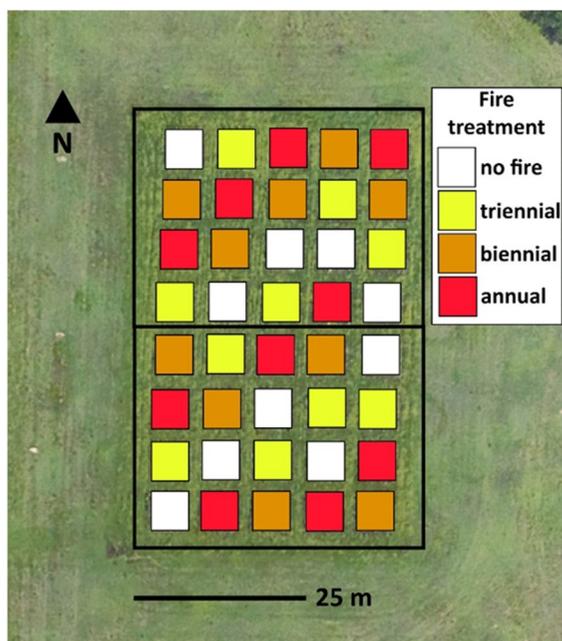


Fig. 2 Map of experimental site and fire treatment details. The site is divided into a northern (Spring fire) and southern (Fall fire) unit, with plots oriented slightly to the NE to ensure all plots are on level terrain. Each 5×5 m² plot is burned based on a three-year fire cycle (see figure legend) using a drip torch, with 5 m mowed buffers between plots. During October 2021, all Fall burn unit plots except for the no fire plots (white squares) burned. During April 2022, all Spring unit plots except for the no fire plots burned. During October 2022, only the annual burn plots (red squares) burned in the Fall burn unit

capillare, *Rudbeckia hirta*, *Liatris pycnostachya*, *Echinacea pallida*, *Solidago nemoralis*, *Coreopsis grandiflora*, *C. tinctoria*, and *Chamaecrista fasciculata*. Three *S. scoparium* nurse plants inoculated with locally collected AM fungi (Mycobloom LLC; Lawrence, Kansas) were planted in the center of each plot arranged in a column, oriented North/South, with spatial separation of 1 m between plants. Mycobloom inocula contains: *Glomus candidum*, *Funneliformis mosseae*, *Cetranspora pellucida*, *Claroideoglomus lamellosum*, *Acaulospora spinosa*, *Racocetra fulgida*, *Rhizophagus irregularis*, *Gigaspora margarita*, *C. candidum*, *G. mortonii*, and *Septoglomus constrictum*. AM fungal spore cultures were originally identified in partnership with the International Culture Collection of Vesicular Arbuscular Mycorrhizal and original sequence data is available through GenBank (INVAM 2022). These nurse plants allowed us to control for host species-based differences in AM

fungal communities. Following planting, fire regimes manipulating fire frequency and season were established in October 2021. Fire frequency treatments are based on three-year intervals with annual ($n=10$), biennial ($n=10$), triennial ($n=10$), and no fire control treatments ($n=10$). In this study, only burn and no burn comparisons were possible as the first three-year fire cycle had not been completed. The twenty plots in the northern portion of the restoration are burned in April (Spring fire treatment) while the twenty plots in the southern portion are burned in October (Fall fire treatment). Fire season treatments were separated into two blocks rather than randomly placed because 1) AM fungal spore communities at this site were found to be similar across the northern and southern units prior to fire (Supplementary Section S1: Table S1, Figure S1), 2) planned a priori comparisons specifically test fire effects within rather than across burn season, 3) to minimize loss of seasonal treatments if burns get out of control, and 4) keep fires within a smaller, more manageable area during prescribed burns. Each plot is burned individually using a drip torch by first igniting backing fires along the leeward side, then front fires along the windward side. Fire typically burn for 5–10 min producing whitish-gray ash, with fuel combustion estimated at 75–80%. In October 2021 all plots in the Fall burn block except for the “no burn” plots were burned. In April 2022 all plots in the Spring burn block except the “no burn” plots were burned. In October 2022 only the annual plots in the Fall burn section burned.

Field sampling Soils were collected from every plot ($n=40$) in April and October of 2022 immediately (<24 h.) and six months after seasonal fires. At each sampling time 100 mL of soil was collected near the base of one *S. scoparium* nurse plant (including roots and rhizosphere soil) in the center of each plot using a hand trowel to a depth of 10 cm. Soils were stored in sterile Whirl-Paks® (Nasco Sampling; Madison, WI). Sampling equipment was cleaned between plots using soapy water & EtOH, and soils were stored in a 4 °C refrigerator within one hour of collection. This produced 80 total samples with 40 from the Spring burn plots (immediate post-fire: burned (b)=15, no burn (nb)=5; six months post-fire: b=15, nb=5) and 40 from the Fall burn plots (immediately post-fire: b=5, nb=15; six months post-fire: b=15, nb=5).

Spore community and trait analyses Soil samples were stored at 4 °C for two weeks to promote AM fungal sporulation (INVAM 2023). Spores were then extracted from soil samples (100 mL each) using 2 mm and 38 µm sieves, followed by centrifugation in 60% sucrose solution and filtration into sterile water with a 38 µm sieve.

AM fungal spore communities were quantified using a Nikon SMZ800N dissection scope (Nikon; Tokyo, Japan) at 30X. For illumination, the microscope's base lamp and a ring light were used (TreochtFUN; China) to ensure that all photos were taken under the same light conditions. Spores were sorted into morphotypes based on color, size, and interior lipid contents, then putatively identified using INVAM species descriptions and comparison with taxa included in MycoBloom's inocula mixture (INVAM 2022; Supplementary Section S2). Species were counted based on morphology (counts = sporulation) and checked for viability by assessing cell wall integrity and internal lipid contents by crushing (if necessary). For trait analyses, pictures of each spore were taken using a Nikon DS-Fi3 microscope mounted camera at 30X under the same light conditions. NIS-Elements AR 5.02.01 software was then used to measure the radius, volume, luminance, saturation, hue, mean red, mean green, and mean blue, for each spore. Pictures were calibrated in µm and colorimetric variables (red–green–blue; RGB model) were measured from pixels in overlaid regions of interest on each spore. Trait variable equations developed in Hanbury 2003 are included below.

$$\text{spore volume } (\mu\text{m}^3) = \frac{4}{3}\pi r^3; r = \text{radius}$$

$$\text{saturation} = \max(R, G, B) - \min(R, G, B)$$

$$\text{luminance} = (0.216 * R) + (0.7152 * G) + (0.0722 * B)$$

Hue (H) was calculated using the following equations:

$$H' = \arccos \left[\frac{R - \frac{1}{2}G - \frac{1}{2}B}{(R^2 - G^2 - B^2 - RG - RB - BG)^{0.5}} \right]$$

$$H = \begin{cases} 360^\circ - H' & \text{if } B > G \\ H' & \text{if } B < G \end{cases}$$

Saturation is the purity of a spore's color (0 = white, 255 = pure color). Luminance describes how bright or dark a spore's color is (0 = black, 255 = white). Hue refers to spore color on a 0° to 360° color wheel. Traits were recorded for every spore ($n=1305$) and averaged at the community (plot) level.

Statistics All analyses were conducted in R version 4.2.2 (R Core Team 2022). We tested how fire, season of fire, and time since fire influenced AM fungal spore community composition using principle coordinates analyses (PCoA) and permutational multivariate analysis of variance (PERMANOVA) with the Vegan package (Oksanen et al. 2022). Bray–Curtis dissimilarity matrices and PCoAs for AM fungal spore communities were created with the `vegdist()` and `prcomp()` functions. After ordination, PERMANOVAs and beta-dispersion analyses were used to test for seasonal variation in AM fungal community responses to fire using the `adonis2()` and `betadisper()` functions. The PERMANOVA model included terms for fire, fire season, and sampling time, as well as plot row (nested in fire season block) and column terms that controlled for location effects. Further, the model also contained a three-way interaction between fire, fire season, and sampling time. Post-hoc comparisons testing how fire's effect (presence/absence) on AM fungi varied within fire season (Spring/Fall fire) based on time since fire (immediate post, six months post) were evaluated using the `pairwise.adonis2()` function in the `pairwiseAdonis` package (Martinez Arbizu 2020).

Fire, fire season, and time since fire effects on AM fungal spore traits and sporulation at the species and community level were assessed using type III multivariate analysis of variance (MANOVA). The community level MANOVA included spore color saturation, luminance, and volume (natural log transformed) as response variables, fixed effect terms for fire, fire season block, sampling time, their interaction, as well as terms for site row (nested in fire season) and column that controlled for locational effects. Note that spore traits were checked for collinearity (correlation > |0.8|) prior to analysis. The MANOVA for sporulation was identical to the community level traits MANOVA, except it contained spore abundance and AM fungal morphotype richness as response variables. The morphotype level traits MANOVAs

were identical to the community level model; however, separate models were created for each morphotype due to seasonal differences in sporulation (e.g., present in Spring & Fall, only Fall, only Spring). To assess morphotype level sporulation and richness responses to experimental treatments, generalized linear mixed effect models (GLMERs) with poisson link functions that included fixed effect terms for fire, fire season block, sampling time, and their interaction, as well as random effect terms for site row (nested in fire season block) and site column were used. For morphotypes present only in the Fall or Spring, the MANOVA and GLMER models did not contain the sampling time term. Due to low sporulation of some morphotypes, sporulation and trait responses to experimental treatment could only be assessed for fourteen and six of the morphotypes respectively. MANOVA and GLMER models were first created using the base MANOVA() and lme4 package's GLMER() functions (Bates et al. 2015), then the joint_tests() function from the emmeans package was used to apply type III tests (Lenth 2018). Following significant “fire (\pm) x fire season block x sampling time” terms for the MANOVA and GLMERs, custom a priori contrasts testing the effect of fire on AM fungal spore traits (species and community level) immediately and six months after Fall and Spring fires were tested using the emmeans() and contrast() functions. All MANOVA and GLMER model residuals were checked for deviations from model assumptions.

We then used structural equation modeling (SEM; lavaan package, Rosseel 2012) to test how fire effects on AM fungal spore traits and community composition varied based on fire season and time since fire (Fig. 1 Hypotheses 1, 2, and 3). Tables S1 and S2 in Supplementary Section S3 provide variable descriptions as well as the initial model structure used as starting point for each model (four total; Fall: immediate & six months-post; Spring: immediate & six months-post). It was necessary to individual models for each time point as categorical interaction terms are not supported by SEM (e.g., fire x time since fire). To control for this, each model began with the same structure linking fire (presence/absence) to AM fungal spore community composition (denoted by PCoA axes 1 & 2) through the measured AM fungal spore traits (Supplementary Section S3: Table S2) and model fitting procedures only allowed for removal of poorly supported paths rather than path additions.

All trait variables were scaled prior to analysis with the scale() function, and upon model convergence fit measures and parsimony were used to assess model fit via the fitmeasures() function. Model fitting started with a highly saturated, based model (Supplementary Section S3: Table S2) and poorly supported paths were iteratively parsed (e.g., $R^2 < 0.1$, $p > 0.75$, $p > 0.5$) until fit statistics indicated adequate model fit (i.e., CFI > 0.95 and NNFI > 0.9). See Supplementary Section S4 for more model fitting details.

Results

AM fungal spore community composition varies with fire and sampling time AM fungal spore communities and sporulation varied based on season, fire time, and with time since fire. In total 2,121 individual spores comprising nineteen AM fungal morphotypes were identified in the Fall and Spring, with nine unique morphotypes in the Spring, four unique morphotypes in the Fall, and six morphotypes found during both sampling times. AM fungal spore communities displayed seasonal differences in composition between the Spring and Fall ($F_{1,62} = 17.4$, $p = 0.001$, $R^2 = 17\%$; Table 1), and this effect was modified by fire ($F_{1,62} = 3.09$, $p = 0.004$, $R^2 = 3\%$). Specifically, changes in AM fungal spore community composition were observed immediately following Fall, but not Spring fires ($p = 0.02$; Fig. 3, Supplementary Section S4: Table S4). The observed variation in AM fungal spore community composition was driven by changes in sporulation rather than morphotype richness or differences in beta-dispersion ($F_{7,72} = 1.86$, $p > 0.05$), with higher spore densities in the Fall ($F_{3,53} = 3.7$, $p = 0.02$; Supplementary Section S4: Tables S1, S2). AM fungal sporulation was also influenced by fire; however, this response varied between morphotypes. *Glomus* sp. 3, spore densities increased immediately ($p = 0.0009$; Supplementary Section S4: Tables S4, S5) and six months after ($p = 0.0005$) fall fire, whereas *C. pellucida* ($p < 0.0001$), *Glomus* sp. 3 ($p < 0.0001$), *Gigaspora* sp. 1 ($p < 0.0001$), and *Paraglomus* sp. 3 ($p = 0.0001$) increased sporulation six months after Spring fire. In summary, fire associated changes in spore communities were driven by species-specific, fire driven

Table 1 PERMANOVA results for fire and sampling time effects on AM fungal community composition

Term	d.f	Sum Sqs	R ²	F	P
column	4	0.92	0.04	1.08	0.34
row (nested in season block)	6	1.7	0.08	1.33	0.08
fire (±)	1	0.39	0.02	1.8	0.06
sampling time	1	3.7	0.17	17.3	0.001***
fire x season block	1	0.16	0.01	0.74	0.68
fire x sampling time	1	0.66	0.03	3.09	0.004**
season x sampling time	1	0.32	0.02	1.50	0.15
fire x season block x sampling time	1	0.24	0.01	1.14	0.32
residual	62	13.22	0.61		
total	79	21.50	1.00		

$p \leq 0.1$; * $p \leq 0.05$;
** $p \leq 0.01$; *** $p \leq 0.0001$

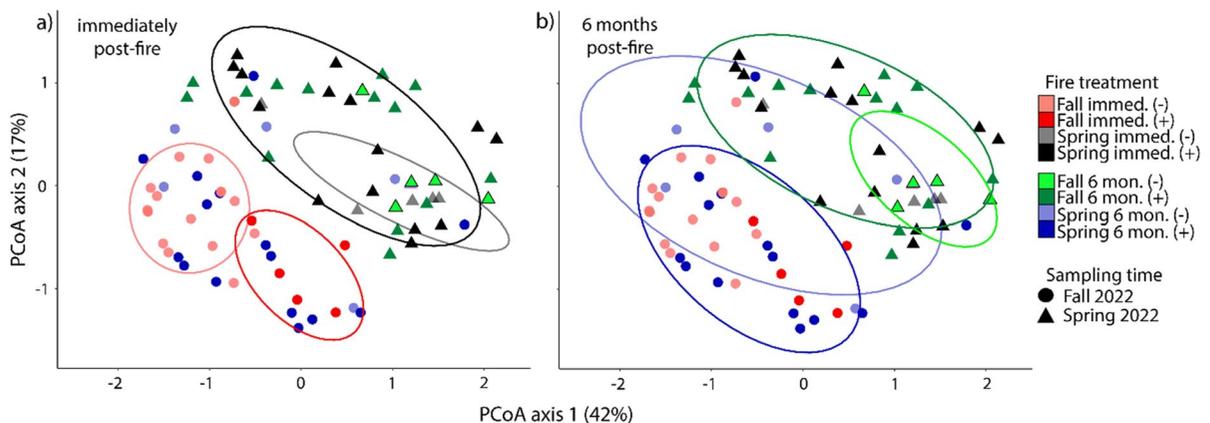


Fig. 3 Fire season and time since fire effects on arbuscular mycorrhizal (AM) fungal community composition. The panels display identical ordinations of AM fungal spore communities with ellipses (75% CI) marking (a) immediate and (b) six months post-fire spore communities. Note that the “+” or “-

” in the figure legend represent the occurrence or absence of fire respectfully. Fall, but not Spring fire drove (a) immediate changes in AM fungal community composition (red vs. pink points); however, (b) fire effects on community composition decreased six months after fire

increases in sporulation that were dependent on fire season and time since fire.

Fire drives changes in spore traits at the community level Fire driven filtering on AM fungal traits varied with fire season and time since fire. AM fungal spore traits responded to fire ($F_{6,53}=2.76$, $p=0.02$; Fig. 4, Supplementary Section S4: Tables S6, S7), but these responses were only observed following Fall fire. Immediately after Fall fires, average spore color luminance decreased ($p=0.03$; i.e., the color darkened; Fig. 4b); however, this was not observed six months after Fall fires. Six months after Fall fire, average spore color saturation ($p=0.04$; i.e., less color-pure pigmentation; Fig. 4a) and volume

($p=0.02$; Fig. 4c) were lower relative to no burn plots. AM fungal spore traits did not display community level responses to Spring fires. To summarize, AM fungal spores initially darkened in response to Fall fire, and color saturation and spore volumes decreased six months after fire.

Fire driven changes in spore traits varies between AM fungal morphotypes Fire driven filtering on AM fungal spore traits varied between morphotypes. Spore color luminance decreased (i.e., darkened; Fig. 5, Supplementary Section S4: Tables S8, S9) immediately following fire for *Gigaspora* sp. 1 (Spring fire; $p=0.0001$), *C. pellucida* (Fall fire; $p=0.0001$), and *Paraglomus* sp. 1 (Fall fire; $p=0.03$).

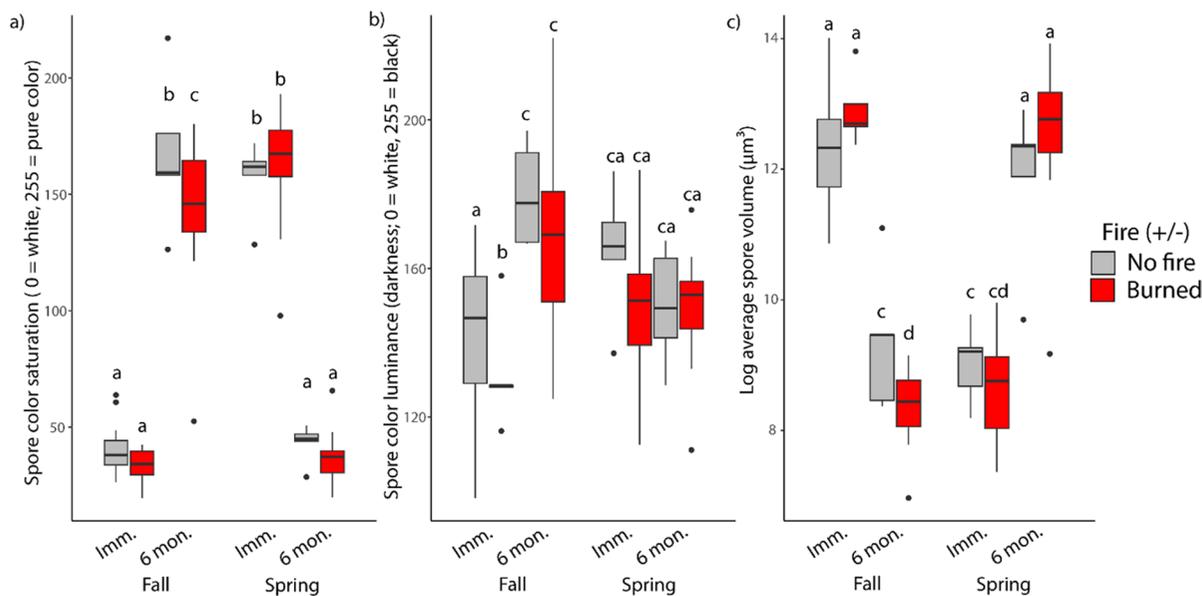


Fig. 4 Fire season and time since fire effects on community level AM fungal spore traits. Lower case letters represent differences between burned (red) and no burn (grey) treatments. Error bars represent the mean ± one SE. Relative to no burn

plots, AM fungal spores in burned plots had (a) lower color saturation (more white pigmentation) 6 months after Fall fire, (b) lower luminance (darker color) immediately after Fall fire, and (c) smaller volumes 6 months after Fall fire

Fig. 5 MANOVA results for fire season and time since fire effects on species level AM fungal spore traits. Red and blue boxes represent significantly higher (red) and lower (blue) trait values in burned vs. no burn plots. Dashes denote seasonal dependent sporulation that prevented analyses in both Fall and Spring

Trait	Fire season	Time since fire	<i>Gigaspora</i> sp. 1	<i>C. pellucida</i>	<i>Glomus</i> sp. 3	<i>Acaulospora</i> sp. 3	<i>Paraglomus</i> sp. 1
saturation	Fall	immediate				-	
		6 months					-
	Spring	immediate					-
		6 months					-
luminance	Fall	immediate				-	
		6 months					-
	Spring	immediate					-
		6 months					-
volume	Fall	immediate				-	
		6 months					-
	Spring	immediate					-
		6 months					-
spore abundance	Fall	immediate					-
		6 months					-
	Spring	6 months					-

Spore color saturation responses to fire were highly variable between morphotypes. *Gigaspora* sp. 1 spores had higher saturation six months after Fall fire ($p=0.002$) and lower saturation immediately after Spring fire ($p<0.0001$). *C. pellucida* saturation

values increased immediately after Spring ($p=0.007$) and Fall ($p=0.01$) fires, but were lower six months after Fall fire ($p=0.02$). *Glomus* sp. 3 and *Acaulospora* sp. 2 saturation values increased immediately after spring fire ($p=0.0006$, $p=0.007$). Spore volume

responses to fire also varied between morphotypes. Immediately after fire spore volumes for *C. pellucida* spore increased (Fall fire; $p=0.001$), *Glomus* sp. 3 decreased (Fall fire; $p=0.002$) and *Acaulospora* sp. 3 increased (Spring fire; $p=0.0002$). Six months after Fall fire, *Acaulospora* sp. 2 volumes were lower relative to no burn plots. In summary, AM fungal spores generally displayed an immediate darkening response to fire and fire season, as well as pigmentation (i.e., color saturation) and size (i.e., volumes) responses that varied between morphotypes.

Fire regime influences AM fungal community composition through spore traits Fire driven changes in spore traits modified AM fungal community composition, and this effect varied with fire

season and time since fire (Supplementary Section S5: Tables S1-S5). In the following paragraphs, numbers in parentheses represent standardized regression coefficients that allow for direct comparison of SEM pathways. Final model fit indices available in Table S16. Fall (-0.28; Fig. 6a) and Spring (-0.17; Fig. 7a) fires drove immediate decreases in spore luminance; however, these changes did not influence AM fungal spore community composition. Fall fires immediately altered AM fungal community composition through direct, unmeasured pathways (PCoA1: 0.78, PCoA2: -0.17), but Spring fires did not have a similar impact.

Six months after Fall fires (Fig. 6b), fire associated changes in spore traits was associated with changes in community composition. Specifically, spores in

Fig. 6 Fall fire SEM diagram relating fire effects on AM fungal spore traits to changes in AM fungal community composition. Path coefficients are standardized regression coefficients that allow for direct comparison of path strengths. Red and black arrows denote negative and positive interactions respectively. Fire drove (a) immediate changes in AM fungal community composition through direct, unmeasured paths. (b) Six months post-fire however, filtering on spore traits was correlated with observed differences in community composition

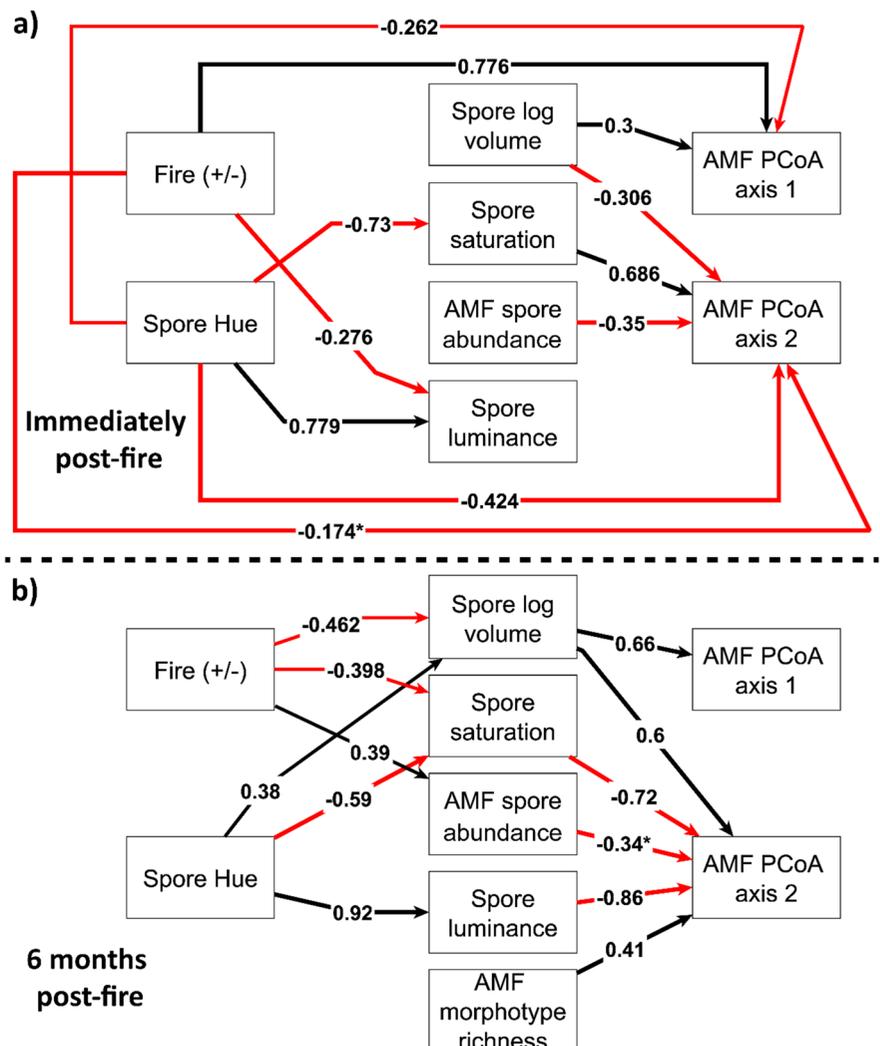
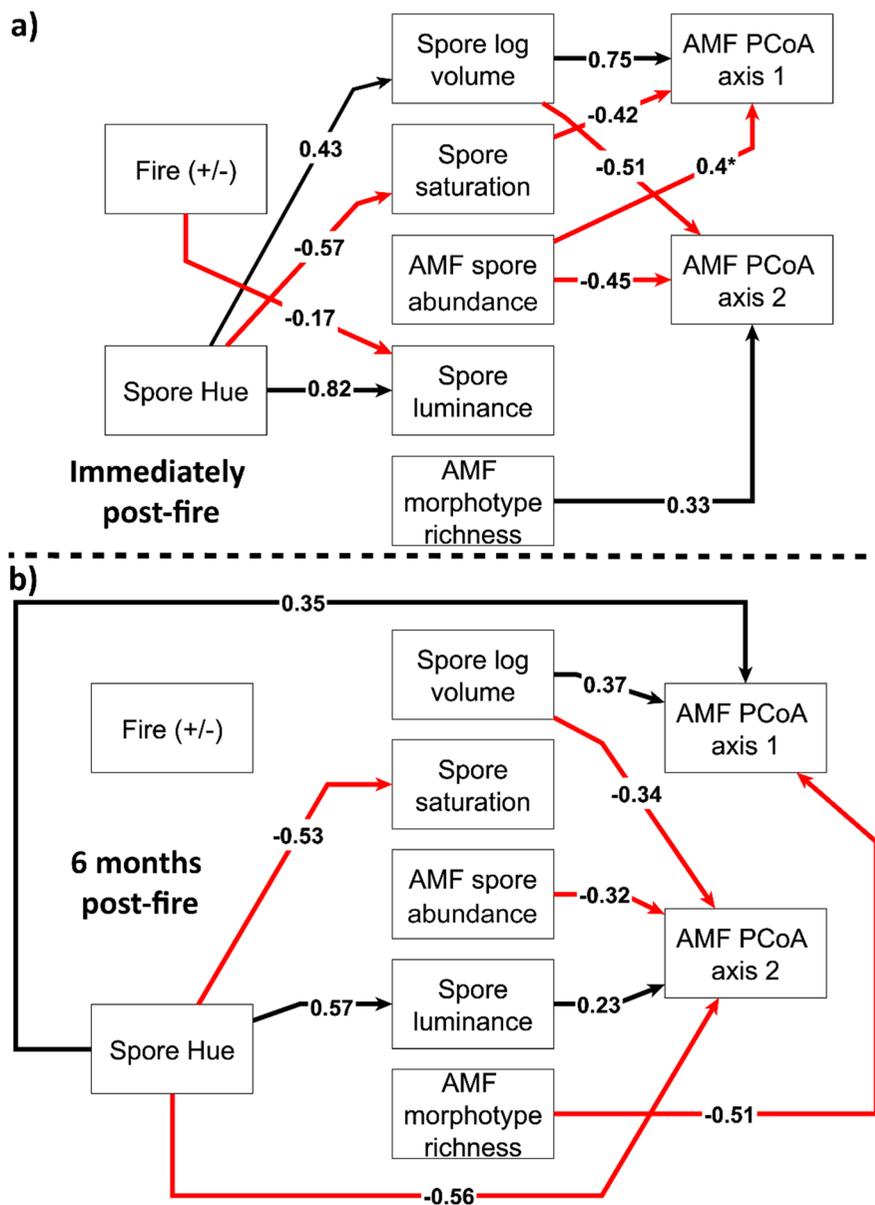


Fig. 7 Spring fire SEM diagram relating fire effects on AM fungal spore traits to changes in AM fungal community composition. Path coefficients are standardized regression coefficients that allow for direct comparison of path strengths. Red and black arrows denote negative and positive interactions respectively. While fire was associated with an (a) immediate darkening of AM fungal spores, spring fire did not influence AM fungal community composition (a) immediately or (b) six months after fire



burned plots had smaller average volumes (-0.46), lower color saturation values (-0.4), and higher spore densities (0.39), and these difference were correlated with changes in AM fungal community composition (PCoA1: -0.3, PCoA2: -0.12). Similar effects were not observed six months after Spring fires (Fig. 7b). In summary, fire altered AM fungal spore community composition through effects on spore traits, but this effect varied with fire season and time since fire.

Discussion

Fire drove both plastic trait responses (i.e., trait responses not linked to community composition) and longer-term filtering (i.e., trait responses linked to community composition) on AM fungal spore traits that influenced AM fungal spore community assembly; however, this effect varied with fire season and time since fire. Spores immediately darkened (lower

color luminance) in response to Fall and Spring fires, however fire-associated changes in spore community composition were only observed after Fall fires. While this plastic, darkening response disappeared by six months, spores in Fall burned plots displayed long-term changes in coloration (less color rich pigmentation), volume (lower), and spore abundance (higher), and this variation was associated with changes in AM fungal spore community composition (i.e., environmental filtering). The observed changes in spore traits in this study reflects spore responses in other Tallgrass Prairie systems where AM fungal spore communities displayed similar pigmentation responses to fire (Hopkins and Bennett 2023). While fire did alter AM fungal spore community composition through changes in spore traits, this effect took time to develop, demonstrating the importance of considering seasonal variation in community assembly.

Variation in fire's effect on AM fungal spore traits and community composition across time shows that AM fungal spore community assembly has a clear seasonal component. Fire's effect on AM fungal spore communities differed based on fire season, with only Fall fire driving changes in spore traits and community assembly. This seasonal effect may have been caused by higher average sporulation in the Fall, which would correspond with known differences in AM fungal sporulation between the growing season (Spring–Summer) and when plants senesce for the year (Fall; Smith and Read 2010). Fall fires that correspond with seasonal peaks in sporulation likely have greater impacts on AM fungal spores than fires in the Spring when sporulation is lower. If reductions in sporulation associated with Fall fires persist into the following Spring, then this could harm AM fungal dependent plant taxa and explain reduced mycorrhizal colonization in burned environments (Dove and Hart 2017). The nature of fire's effect on AM fungal community assembly also varied with time since fire. Immediately after fire, fire influenced community assembly through direct, non-trait linked pathways, potentially related to fire driven changes in soil conditions and host-plant mortality. Since spore abundance and morphotype richness were not influenced by fire at this time point, this suggests that changes in community composition were related to species turnover rather than mortality. Fire does not always kill AM fungal spores in grassland ecosystems (Klopatek

et al. 1988; Hamman et al. 2007) due to the insulative properties of soil (Massman 2012; Pingree and Kobziar 2019). Despite the lower severity of grassland fires (relative to forest fires; Whelan 1995), the instantaneous responses of AM fungal spore traits to fire in this system suggest that temperature effects of grassland fire (often exceeding 40 °C) are strong enough to influence AM fungal spore communities. When coupled with taxa dependent responses to disturbance (Hart et al. 2016; van der Heyde et al. 2017), this can explain the observed changes in spore communities. Six months after Fall fires, fire affected community assembly through changes in sporulation (higher), spore volume (lower), and color saturation (less color rich pigmentation). Sporulation allows fungi to survive stressful conditions (Peay et al. 2009; Taudière et al. 2017), and pigmentation can provide protection against high temperatures and harmful reactive oxygen species (Gessler et al. 2014; Rajamani et al. 2021), while smaller spore volumes can help prevent heat transfer during fire (Bejan and Kraus 2003). This suggests that fire-associated changes to the soil environment like increased UV exposure, soil heating, and oxidative stress drove the observed changes in community assembly (Certini 2005; Pereira et al. 2018; Magaña-Hernández et al. 2020; Sigmund et al. 2021). While more work is required to test the links between fire associated stressors and community assembly, the connections between fire and AM fungal spore traits provide valuable insight into the ecology and natural history of AM fungi.

Linking fire disturbance to AM fungal spore traits helped uncover community wide and species-specific responses to community assembly filters. First, AM fungal spores reliably darkened (luminance decrease) immediately after fire, relative to other spore traits, though this effect was not linked to changes in community composition and disappeared after six months. This suggests that changes in spore luminance may represent a protective, plastic response to fire (Hopkins and Bennett 2023). Fire effects on spore volume and saturation following Fall fire however, persisted at least six months and were correlated with community composition. Since AM fungal volume is a meaningful metric of fitness and heritable across generations (Bever et al. 1996; Bever 2002; Hopkins et al. 2023), fire effects on spore volume may represent true selection. Since AM fungal spore trait and community responses to prairie fires have also been

demonstrated to influence host resource allocation in *Schizachyrium scoparium* (Hopkins and Bennett 2023), this suggests that fire associated filtering on AM fungal spore traits may also drive changes in plant-AM fungal interactions.

Fire effects on spore traits also displayed considerable inter-species variation. The spores of larger taxa like *C. pellucida* had higher volumes in burned plots, whereas spore volumes of smaller taxa (e.g., *Glomus* sp. 3 and *Acaulospora* sp. 3) tended to be lower in burned plots. Since the sporulation of both smaller and larger spored taxa was often higher in burned plots, this suggests spore heat resistance mechanisms may vary based on spore size. For example, larger taxa may rely on heat resistant internal lipids and fluid cells (Balogh et al. 2013), while smaller spores resist changes in temperature by having smaller surface areas (Bejan and Kraus 2003). More work is required to see if changes in spore color saturation persist across generations. Fire effects on spore color saturation also displayed considerable inter-species variation, with yellow-hyaline and brown spores showing increased color saturation (more color rich pigmentation) and hyaline spores decreased saturation (less color rich pigmentation) after fire. This indicates that while spores with higher pigmentation levels (i.e., less hyaline; *Glomus* sp. 3 and *Paraglomus* sp. 1) are favored by fire, the nature of this response varies based on initial spore hue. Since there is overlap in the protections provided by fungal pigments (Gessler et al. 2014; Villa et al. 2022), it may be that the ability to synthesize pigment is more important than the pigment color in regard to fire. Utilizing trait-based approaches provided invaluable insight into the importance of community assembly filters on AM fungi.

Measuring trait responses to fire allowed us to assess the relative importance of different community assembly filters. Specifically, fire effects on spore color saturation and volume were stronger determinants of community composition than sporulation associated pathways. This effect may be due to strong phylogenetic conservatism in sporulation that prevents filtering on this trait (Pringle and Bever 2002; Oehl et al. 2009). Alternatively, pigmentation and cell volume provide protection against an array of fire associated stressors making them better targets for fire associated filtering (Gessler et al. 2014; van der Heyde et al. 2017;

Hopkins and Bennett 2023). The relative importance of fire effects on spore traits and community assembly also varied with time, and were strongest six months after fire. This change in spore traits takes time to develop, and may be augmented by repeated disturbance during key life history stages (Daubemire 1968; Brewer and Platt 1994; Platt et al. 2015). Changes in fire effects across time also suggest that the relative importance of different disturbance associated traits may be dependent on season. For example, during fire the ability to form heat resistant spores may be a key trait (Peay et al. 2009; Glassman et al. 2016; Pulido-Chavez et al. 2023), but as time since fire increases stress tolerance may be more important (Pereira et al. 2018). If AM fungal taxa possess traits that allow them to transition from surviving fire into tolerating harsh post-fire conditions, this could allow them to take advantage of reduced competition after fire and explain post-fire changes in community assembly. By examining AM fungal spore trait responses to disturbance, we were able to assess how community assembly processes change with time.

In conclusion, fire driven changes in AM fungal spore traits influences AM fungal spore community assembly, and this process is dynamic with time. This work is the first to consider how seasonal variation in spore traits mediates mycorrhizal community assembly, and builds on prior work linking mycorrhizal traits to life history and community assembly (Powell et al. 2009; Maherali & Klironomos 2012; Chagnon et al. 2013; Chaudhary et al. 2020; Deveautour et al. 2020; Hopkins and Bennett 2023). By using the disturbance-traits framework we were able to assess key components of seasonal variation in mycorrhizal community assembly dynamics. Future work should test the importance of other disturbance associated stressors and traits in community assembly (e.g., oxidative stress, UV exposure, melanin synthesis, reactive oxygen resistance, and lipid content), improve our molecular and trait-based understanding of AM fungal species-specific response to fire, as well as how environmental filtering of traits varies with climate. To conclude, trait-based approaches provide not only new insights into the processes that underly community assembly, but also help predict how changes in communities influence ecosystems as a whole.

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Author contributions All authors developed and designed all experiments. Jacob R. Hopkins and Thomas P. McKenna established the field site and managed Spring and Fall prescribed burns. Jacob R. Hopkins and Thomas P. McKenna performed the field portion of the research. Jacob R. Hopkins performed the traits portion of the research and analyzed all data. All authors wrote the manuscript.

Data availability The datasets generated during the current study are available in the Dryad repository, <https://datadryad.org/stash/share/wYru5MRmn-VFjQbzIFy5tqiulZbwvz0wxxTesp2V87k>.

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