FIRE, FUNGI, AND FLORA: DESCRIBING THE RELATIONSHIP BETWEEN PRESCRIBED BURNS, FUNGAL COMMUNITIES, AND UNDERSTORY PLANTS IN SOUTHERN WILLAMETTE VALLEY OAK SAVANNA

by

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Oak savannas are an endangered habitat type once prevalent in the southern Willamette valley. Of high conservation concern today, these ecosystems are increasingly subject to the influences of prescribed or unprescribed fire; however, few studies have examined functional plant-fungal community responses to fire in similar habitats. Therefore, this study seeks to answer the following questions: (1.) How do oak savanna understory plants—generally, and in specific functional groups (introduced and perennial species)—vary with prescribed burn treatment? (2.) How do oak savanna soil fungi— generally, and in specific functional groups (ectomycorrhizae, pathogens, pyrophiles, and saprotrophs)—vary with prescribed burn treatment? (3.) How does the presence/absence of oak savanna fungal sporocarps vary with prescribed burn treatment? To these ends, vegetation, soil, and sporocarp data were collected from four oak savanna localities in the southern Willamette valley, each with both burned and unburned sites. Plant and fungal response to fire depended on functional group; after burning, introduced plants were more successful than native plants, and pathogens and saprotrophs were more successful than other fungal guilds. Fungal sporocarps revealed high biodiversity at both burned and unburned sites, leading to the classification of over 120 additional fungal taxa missed in the soil cores. Overall, my findings help to qualify the reintroduction of fire as a management tool and as a natural phenomenon.

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Introduction

Oak Savanna: Endangered Habitat

While contemporary depictions of western Oregon's ecology tend to home in on its iconic towering Douglas fir stands—forests and plantations of which have largely persisted in land cover, if not in habitat quality, through over a century and a half of intense regional development—western Oregon was historically a mosaic of diverse ecosystems, home to a vast, complex network of habitats and organisms. One such historically and ecologically significant habitat type was the oak savanna. These unique, mid-successional ecosystems are often described as ecotones between open prairie and oak woodland (Kipfmueller & Hepola, 2007) and characterized by prairie-like understories and sparse canopies of old-growth oaks. In the Willamette valley, oak savannas proved particularly valuable for hunting and foraging—amongst the most important of the First Foods they provided were deer and camas—and were thus expertly maintained by Indigenous managers, who found they could sustain a successional 'sweet spot' by conducting prescribed burns every 3–5 years (Grand & Berger, 2024).

Throughout the 1850s—early into Euro-Americans settlers' colonization of western Oregon—federal General Land Office surveyors delineated over 245,000 hectares of oak savanna in western Oregon's Willamette valley. According to their measurements, oak savanna was the ecoregion's third-most extensive vegetative class at the time, comprising 18.2% of the valley's natural landscapes (Christy & Alverson, 2011). It is also known that Euro-American contact caused Indigenous populations to decline precipitously throughout the 18th century (Liebmann, 2021), potentially leaving fewer Indigenous land managers to conduct the prescribed burns necessary to maintain savannas; thus, analysts estimate that fully pre-colonial oak

savannas may have spanned up to 440,000 hectares before the 18th century, constituting as much as 32.5% of the valley's total land cover (Christy & Alverson, 2011). Following Euro-American colonization, however, oak savanna rapidly disappeared, a phenomenon mostly attributed to the settlers' fierce fire-suppression and land-use practices. Now, in the 21st century, oak savanna is estimated to occupy less than 1% of its historic range—most of which is now woodland or farmland—and is considered severely endangered (Day, 2005; Ingersoll & Wilson, 1991; Noss & Scott, 1995).

Today, Oregon's remaining oak savannas are dominated by graminoid and forb taxa (many of which are introduced), have few shrubs, and lie below canopies punctuated by scattered stands of old-growth *Quercus garryana* trees (Hamman et al., 2011). Sometimes, they are joined by *Quercus kelloggii*, which reach the northernmost end of their natural range near Eugene, Oregon. In areas that are not burned frequently, other hardwoods (e.g., *Prunus sp.*) and conifers (e.g., *Psuedotsuga menziesii*) begin to encroach (Towle, 1982). Such encroachment was historically kept at bay by Indigenous prescribed burning, the absence of which has led to progressive oak habitat loss, as oaks are shade-intolerant trees. Thus, over the past 150 years, as Euro-American land management doctrines have superseded Indigenous ones and transformed ecological conditions, they have devastated the Willamette valley's *Quercus garryana* (Christy & Alverson, 2011) and the ecological niches these trees create.

Here, it is worth noting that these phenomena are not unique to western Oregon's Willamette valley alone: the loss of oak savanna habitat is felt across the nation. To the south, California's San Francisco Estuary Institute (2008) reported that "rangeland 'improvement' (clearing), agriculture and urban development in California" supplanted more than 525,000 hectares of oak woodland and savanna between 1945–1973. Hundreds of miles away, the

Midwest was once home to as many as 13,000,000 hectares of oak savanna; today, little more than 2,600 hectares of high-quality habitat remain. This marks a 99.98% overall reduction in Midwestern oak savanna range since colonial settlement (Nuzzo, 1986)—an even greater relative decline than on the West Coast. Sprawling, diverse oak savannas are also found in the American Southwest (McClaran & McPherson, 1999), and though oak savanna is not commonly described on the East Coast, here ecologists refer to the presence of "open oak forests" with as few as 50 trees per hectare before Euro-American colonization (Hanberry et al., 2018). Therefore, the dramatic loss of oak savanna over the past several centuries is not merely regional but a resounding national concern (Figure 1).

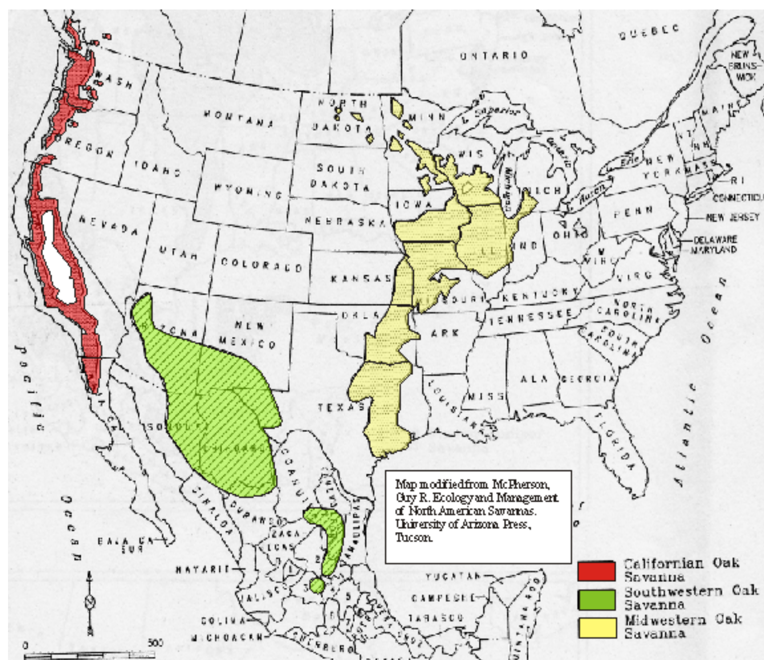

Figure 1. Historic range map attributed to McPherson (1997) depicting extent of contemporary regional oak savanna habitat prior to Euro-American settlement.

Beyond these dramatic historic habitat contractions, the future of American oak savannas is also unclear. There is reason to believe that oak savanna conservation and restoration is an endeavor worth investing in, especially as anthropogenic climate change and development lead

to increasing biodiversity loss, habitat fragmentation, and wildfire—to which, some studies suggest, arid habitats like oak savanna might be more resistant (Brandt et al., 2014). However, other research models scenarios in which West-Coast oak savannas contract to nearly half of their current range and shift northward (Kueppers et al., 2005). As we strive to answer these questions and examine these complex, important habitats more closely, there is a strong case to be made for focusing on the roles played by not only plants but also resident fungi, whose intricate symbiotic webs span mutualism, parasitism, and decomposition, shaping ecosystems like oak savannas in ways we are only beginning to comprehend.

Fungi: Savanna Symbiotes

In oak savannas, as in virtually all ecosystems on Earth, fungi play significant ecological roles. Oaks like *Quercus garryana* are known for forming ectomycorrhizal partnerships: symbiotic relationships wherein trees share and exchange key nutrients with fungal symbionts anchored to the surface of their roots (Morris et al., 2008). Prior studies of Oregon oak savannas' underground communities have found dozens of species of ectomycorrhizae living on *Quercus garryana* root tips (Valentine et al., 2002). Many of these ectomycorrhizal species produce above-ground sporocarps, making them unique to other locally common mycorrhizal clades that are restricted to below-ground reproduction—truffles (Frank et al., 2006; Frank et al., 2008).

A review of the literature more generally indicates that, while the role of ectomycorrhizae in savanna soils remain poorly described and understood, the few studies that have been conducted in these habitats thus far have yielded some of the richest ectomycorrhizal communities ever discovered (Authier et al., 2022). One study that sampled the roots of British Columbia *Quercus garryana* populations found 47 unique ectomycorrhizal taxa; notably, only 20% were assigned to known species (Berch et al., 2023). Another study of oak-fungal

interactions in the Sierra-Nevada foothills of California found incredible richness—140 ectomycorrhizal species—in an oak woodland (Morris et al., 2008). However, oak woodland studies cannot be expected to explain oak savanna dynamics directly: a study conducted in Minnesota found that oak savanna fungal communities, while just as highly diverse, were notably unique to those of their denser oak-woodland counterparts (Dickie et al., 2009).

These dynamics are important to understand. Experiments show that the formation of mycorrhizae is associated with a variety of biological benefits—including increases to primary root length, aboveground biomass, net photosynthesis, quantum yield, water synthesis, and photosynthetic pigmentation—in oak species (Slama et al., 2023). In this way, mycorrhizal networks can impart a biological advantage that is increasingly critical for oaks, especially as oak savanna habitat faces increasing anthropogenic and climatic pressures (Kueppers et al., 2005).

Beyond mycorrhizae, other fungal functional groups fulfill a variety of ecological roles on Oregon oak savanna, with habits ranging from saprotrophic to pathogenic (Wilson & Carroll, 1994). Despite their symbiotic significance, the majority of these fungal species have still not been studied or described; as fungi are highly cryptic organisms (Olson, 2022), the biology and ecology underpinning the specific ecosystem services they provide remains poorly understood. To date, the fungal kingdom has been markedly understudied compared to the plant kingdom. Presently, 148,000 fungal species have been identified, but it is estimated that more than 90% of fungal taxa continue to elude formal scientific recognition; modeling suggests that the true number of fungal species on Earth likely lies between 2.2 and 3.8 million (Cheek et al., 2020).

As climate change and its impacts construct increasingly stark realities for ecologists and policymakers alike, leveraging field research to increase understanding of fungal taxa and how

they respond to disturbance may prove pivotal in the race to mitigate climate impacts. A recent estimate states that mycorrhizal fungi serve as a sink for over one-third of global CO_2 emissions (Hawkins et al., 2023), providing another clear rationale for the inclusion of fungal associates in conservation-oriented research and policy moving forward. In the age of the Holocene, however, no ecosystem is in a truly steady state (Ellis, 2015). In attempts to study these organisms, any applied research project should examine them within the context of current and future localized impacts to their habitats; in the southern Willamette valley, this means accounting for the returning and growing presence of fire.

Research Questions: Oak Savanna, Fungi, and Fire

In summary, little is currently known about the Willamette valley's oak savannas, and less still is known about the fungal populations that reside within it. However, some prior research in closely related fields—alongside the localized management context for this study—provides the basis for some of the methods, assumptions, and research questions for this project.

With awareness about the immensity of to-date oak savanna losses and investment in active conservation gradually growing, land managers are increasingly turning to previously shelved Indigenous Knowledge to help frame their work. Around the turn of the 21st century, prescribed fire began to resurge in popularity as a tool for managing habitats on Euro-American-controlled land. In the southern Willamette valley today—from Mount Pisgah to Coburg Ridge, Willamette Confluence Preserve to See-Sil—many public and private landowners alike are now regularly conducting control-burns, seeking to restore oak savanna and support its ecological benefits. Thus, as natural resource managers strive to reintroduce prescribed-fire land-management techniques to the Willamette valley—and as unprescribed wildfires simultaneously intensify in the region due to climate change—new questions emerge as to what impactful, little-

understood biological responses and processes might occur in the wake of re-burning these now-transformed oak savannas (Hamman et al., 2011), and what impacts might touch both their plant and fungal communities.

In Minnesota, a study comparing plant diversity of unburned oak woodland and frequently burned oak savanna found higher species and phylogenetic richness in the oak savanna, but more species with acquisitive leaf traits—or higher leaf area—in the oak woodland (Cavender-Bares & Reich, 2012). A second study found that understory woody plant cover was highest in unburned woodlands, grass cover was positively correlated with fire frequency, and forb cover was highest at sites burned 4–7 times per decade (Peterson et al., 2007). Additionally, a study of southern Willamette valley prairie—an adjacent habitat type—suggested that grassland fires may help native plants compete against introduced ones (Roy et al., 2014). However, a broader conceptual analysis on the reintroduction of prescribed burning to the West Coast asserts that fire may not play the same role in the altered western landscapes of today, arguing that land managers "may be forced to choose between restoring 'natural' fire regimes or altering fire regimes to favor communities of native species" (Keeley, 2006) and demonstrating that prescribed burning to eliminate introduced plants has had questionable success, especially when target species are disturbance-dependent annuals (Brambila et al., 2022). There is a lack of on-the-ground published research regarding the success of prescribed burning on altered southern Willamette valley oak savannas.

Meanwhile, in North Carolina oak-pine forest, a study showed that moderate to severe burning decreased fungal diversity; fires also resulted in significant shifts in the remaining fungal communities, increasing Ascomycota dominance and concurrently decreasing Basidiomycota and Zygomycota dominance in response to burning (Huffman & Madritch, 2018). However, the

body of research is notably heterogeneous on this issue. Other studies highlight benefits of fire for pyrophilous fungal diversity, review prospects and challenges in modeling overall fungal responses to fire (Fox et al., 2022), report both fire-driven diversity reductions and subsequent rebounds in mycorrhizal communities (Dove et al., 2017), and find more sporocarps on burned than unburned prairies—with some implications for similar oak savanna habitats (Roy et al., 2023). Overall, generalizability and definitive conclusions remain elusive, given the breadth of the problem and the diversity of the study organisms.

Thus, evident gaps in the current state of research on mycorrhizal oak fungi remain. Few to no studies (a) have been conducted within the Willamette valley, (b) focus on oak savanna rather than on oak woodland (c) intensively audit fungal diversity, and (d) examine the effects of fire on plant and fungal functional groups. Certainly, no studies have been undertaken in all four topic areas at once, though there are nearby prairie studies to draw on (e.g., Brambila et al., 2022; Roy et al., 2014; Roy et al., 2023). Therefore, the present research—a study of how plant and fungal communities vary in response to fire on the Willamette valley oak savanna—seeks to fill this gap. The research questions were as follows:

1. How do oak savanna understory plants—generally, and in specific functional groups (introduced and perennial species)—vary with prescribed burn treatment?
2. How do oak savanna soil fungi— generally, and in specific functional groups (ectomycorrhizae, pathogens, pyrophiles, and saprotrophs)—vary with prescribed burn treatment?
3. How does the presence/absence of oak savanna fungal sporocarps vary with prescribed burn treatment?

While this research, like the studies that preceded it, will not provide universal generalizability in its findings, it aims to supplement and extend current understandings of fire-plant-fungal dynamics in modern oak savannas.

Methods

Site Selection

This study used a burn chronosequence model to understand how plant and fungal communities responded to varying burned and unburned conditions. Four oak-savanna localities in the southern Willamette Valley—each with unburned and burned field sites from varying years (Table 1)—were sampled for fungal data. A subset of the field sites (PIS_2023, PIS_2019, and PIS_CTRL) were also sampled for plant data. All sites belonged to a cohort that was previously selected and permitted for truffle surveys by Heather Dawson with the University of Oregon's Roy Lab.

Table 1. Metadata for each of the field sites: treatment, locality, latitude, longitude (decimal degree coordinates, World Geodetic System 1984), aspect, and elevation (meters).

Field Site	Treatment	Locality	Latitude	Longitude	Aspect	Elevation
CBG_2022	Burned 2022	Coburg Ridge Preserve	44.100698	-123.01092	SE	270
CBG_CTRL	Unburned	Coburg Ridge Preserve	44.090241	-123.01325	SE	155
PIS_2023	Burned 2023	Howard Buford Recreation Area	43.995023	-122.95203	SE	197
PIS_2019	Burned 2019	Howard Buford Recreation Area	43.996184	-122.94761	SE	200
PIS_CTRL	Unburned	Howard Buford Recreation Area	43.998016	-122.95626	SE	253
SSL_2018	Burned 2018	See-Sil Savanna	44.078292	-123.24982	None	117
SSL_CTRL	Unburned	See-Sil Savanna	44.078992	-123.24617	None	118

WCP_2023	Burned 2023	Willamette Confluence Preserve	44.021289	-122.97911	NW	178
WCP_CTRL	Unburned	Willamette Confluence Preserve	44.018667	-122.98068	NW	180

All localities included both a site with recent prescribed fire (within the past seven years) and a site that had not been burned in its recorded history. While records on fire intensity were not available, it was reported that prescribed burns were conducted after sites were cleared of excess undergrowth and fall rains had onset to minimize intensity; loss of control in the urban-wildland interface is strenuously avoided by fire crews (H. Dawson, personal communication, 2025). Within each locality, 3-acre sites were delineated for the burned and unburned conditions. At each site, 9 mature oak trees were flagged for understory plant surveys and soil fungal sampling. By targeting trees throughout the site, this protocol aimed to accurately represent the overall diversity of the oak-associated soil fungi and plants found throughout the localities.

Matched-pair plots were selected to be as similar as possible, given the high variability and low availability of suitable oak-savanna habitat. Similarity criteria included oak tree maturity and number, absence of other ectomycorrhizal tree species, landscape aspect, and site proximity to minimize differences in community composition. The unburned site for one locality (SSL_CTRL) did not meet all similarity criteria, as the unburned areas in the See-Sil Savanna more closely resemble oak woodland than oak savanna—largely because burning is the primary means of preventing savanna-woodland succession. Thus, in SSL_CTRL, tree density was higher than in the burned plot, and scattered *Pseudotsuga menziesii* and *Corylus cornuta* trees were uniquely present.

Data Collection

Understory Plants

At Mount Pisgah, which contained three of the field sites—PIS_2023, PIS_2019, and PIS_CTRL—I conducted vegetation surveys in June 2024. I plotted m^2 quadrats at the north and south dripline of each of the 9 flagged *Quercus garryana* trees, with the goal of collecting vegetation data for the same micro–community from which the soil fungal samples would represent. For each quadrat, I created a plant list to estimate vegetative cover and species richness.

Plants that could not immediately be identified to the species level were identified to the most specific taxon practically possible and given distinct reference names. If there were any trees closer to the quadrat than the flagged *Quercus garryana*, these were also noted and identified to the most specific taxa possible.

Soil Fungi

Soil cores were sampled by Heather Dawson from the 9 flagged oaks at each of the same field sites in May 2024. The 20-by-2.5-cm soil cores were collected by pounding pre-cut, sterilized PVC pipes into the ground. 4 soil cores were collected radially from the dripline around each target tree—1 in each cardinal direction. The north and south cores were then isolated for plant-community comparison. Heather Dawson collected and processed the soil samples; I used these data, with permission, to compare with my plant and sporocarp data.

Fungal Sporocarps

I surveyed each field site 3 times: once each in May, October, and November 2024. The surveys were conducted in a semi-systematic manner: I walked a rough grid of each site for a

duration of 75 minutes. To reduce temporal variation, I completed monthly surveys for each site within a 1-week time span, and I surveyed matched-pair burned and unburned plots consecutively on the same day.

I photographed all detected sporocarps from above, below, and in profile onsite and collected fresh tissue (when possible, the entire sporocarp) from unrecognized fungal species for short-term storage in a tackle box. I also completed a detailed survey slip for each unrecognized specimen, including site, date, habit, and a specimen number.

To ensure the best possible representation of sporocarp fruiting patterns at oak-savanna sites—especially given the incredible rarity with which some fungal taxa are observed fruiting—I leveraged existing data sources to supplement my research. I used the website iNaturalist, a crowdsourced species-identification and occurrence-recording tool, to access peer-collected data. My goal was to synthesize all research-grade iNaturalist observations that fell within the bounds of any of the oak-savanna sites.

To gather this data, I created a new iNaturalist project: "Macrofungi of Southern Willamette Valley Oak Savannas." Then, I uploaded Keyhole Markup Language (KML) files delineating the geographic extent of each of the oak-savanna sites to iNaturalist, creating a new place page for each and setting the project to gather all fungal observations whose location tags fell within any of these places. Finally, I filtered the data to "research-grade," ensuring that all specimens I added to my dataset had a species-level designation confirmed by at least 2 iNaturalist users; this helped to avoid the misidentification of cryptic fungal species. This project was set to collect new data through mid-May 2025, at which point the data was exported to a datasheet for analysis.

Part of PIS_2019 was reburned in late summer 2024; thereafter, all fungal sporocarps collected in the reburned portion were coded as PIS_2024.

Data Processing

Understory Plants

Plant lists were entered into an electronic datasheet capturing taxon, site, and percent cover at each intersection. Plants that were absent at any given site were designated by 0s at that intersection.

Soil Fungi

Taxa identifications for soil fungi were obtained by DNA-sequencing the nuclear ribosomal internal transcribed spacer (ITS) region—a highly conserved, non-coding section of the genome. The ITS region has been fairly universally accepted as a standard barcode marker for fungi because it consistently displays high interspecific, low intraspecific variability (Baldwin et al., 1995; Schoch et al., 2012). The protocol for soil sequencing, designed by Heather Dawson, was as follows:

1. Deposit PVC pipe—which contains field-collected soil cores—into a sterile Whirl-Pak bag. Store at -20º C.
2. Thaw the Whirl-Pak bag. Remove the PVC pipe, leaving the soil contents behind.
3. Hand-homogenize the soil by gently crushing, mixing, and swirling the contents of the bag.
4. Take a 0.25-g soil sample for DNA extraction. Weigh the soil by adding small quantities of material to a zeroed-out scale equipped with a plastic boat until the desired value is reached.
5. Extract the soilDNA using the DNeasy PowerSoil Pro Kit (Qiagen, Hilden, Germany), following manufacturer instructions.

6. Use the fungal-specific primers ITS1F and ITS2 (Gardes and Bruns, 1993; White et al., 1990), modified with heterogeneity spacers and Illumina TruSeq barcode stubs, to amplify the ITS1 region in polymerase chain reactions (PCR).

7. To initiate PCR amplification, mix a 20-uL solution with GoTaq® Green Master Mix.

8. During the amplification process, set the reaction conditions for the solution to an initial 1-minute denaturation at 94 ºC. Next, cycle the solution between 45 seconds at 94ºC, 60 seconds at 54 ºC, and 90 seconds at 72ºC 30 times. Finally, hold the solution at 72ºC for 10 minutes.

9. Perform a second round of PCR to facilitate the attachment of unique multiplexed barcodes, repeating 12 times instead of 30.

10. Visualize the products on a 1% agarose gel via electrophoresis. Then, quantify the products using Quant-iT PicoGreen (ThermoFisher, Waltham, MA) on a SpectraMax M5E Microplate Reader (Molecular Devices, San Jose, California) and pool at equimolar concentrations. Lastly, purify the pools using Mag-Bind TotalPure NGS Magnetic Cleanup Beads (Omega Bio-tek, Norcross, Georgia) at 0.85X for amplicon size selection

11. Deliver the purified libraries to be sequenced on an Illumina MiSeq system.

12. Generate amplicon sequence variant (ASV) datasheet—including automatically generated fungal taxa assignments—using the CliMush Bioinformatics Pipeline (Delevich, 2025).

During soil fungi processing, Heather Dawson performed steps 1–2 and 5–12 of the above protocol (H. Dawson, personal communication, 2025). I performed steps 3–4.

Fungal Sporocarps

To obtain species identifications for fungal sporocarps, their DNA was extracted for sequencing, also of the ITS region. The protocol for preparing sporocarps is based on the work of M. Smith, H. Dawson, R. Vilgalys, and B. Roy (personal communication, 2025) as follows:

1. Store the fresh sporocarp, with its identifying survey slip, under refrigeration for up to 48 hours following in-field collection; within this window, begin processing the tissue.

2. With sanitized forceps, carefully remove a pinpoint amount of tissue from the spore-bearing region—if present—of the fresh sporocarp.

3. Place the tissue into a test-tube containing alkaline-buffer solution.

4. Using the forceps, grind the submerged tissue against the bottom of the test-tube to accelerate the cell disruption process; lysing the cell walls and membranes promotes the release of genetic material into the buffer solution (Mobley, 2024).

5. Seal and label the test-tube; store below freezing, occasionally allowing to thaw and refreeze to further accelerate cell disruption and enhance DNA extraction efficiency (Xin et al., 2021).

6. In the meantime, using a food dehydrator, completely dry the remainder of the sporocarp, along with its identifying survey slip. Once the sporocarp is dry, package it in an air-tight, zip-lock bag for long-term storage.

7. Thaw the test-tube, adding primers ITS1catta (ACCWGCGGARGGATCATTA; Tedersoo & Anslan, 2019) and LR5 (TCCTGAGGGAAACTTCG; Hopple and Vilgalys, 1994) with 5-nucleotide padding sequences and combinatorial 16-nucleotide dual-indexed barcodes for multiplexing. These primers assist with targeting the ~1600-base-pair region extending from the end of the small subunit (SSU) through ~1000-base-pairs of the large subunit (LSU) region, including the full internal transcribed spacer (ITS) region, which is the gold standard for fungal DNA barcoding (Fajarningsih, 2016).

8. To initiate PCR amplification, mix a 25-µL solution with 12.5 µL GoTaq® Green Master Mix, 0.4 µL 2% bovine serum albumin, 1 µL unique primer-barcode pairs, 0.8 µL DNA template, and 10.3 µL nuclease-free water.

9. During the amplification process, set the reaction conditions for the solution to an initial 2-minute denaturation at 95ºC. Next, cycle the solution between 30 seconds at 95ºC, 30 seconds at 51ºC, and 90 seconds at 72ºC 30 times. Finally, hold the solution at 72ºC for 7 minutes.

10. Visualize the products on 1% agarose gel via electrophoresis. Then, pool the products according to band brightness, following Runnel et al. (2022). Lastly, purify the pools using Omega Mag-Bind® TotalPure NGS Beads at 0.8X to remove small DNA fragments.

11. Deliver the purified libraries to be SMRT sequenced on a PacBio Sequel II system.

12. Process circular consensus sequences with read-quality scores of at least 40 using the CliMush Bioinformatics Pipeline (Delevich, 2025) with tools from VSEARCH (Rognes et al., 2016).

13. In Geneious Prime, use the MAFFT Alignment (Katoh & Standley, 2013) and Find Motifs tools to locate and orient de-replicated ITS sequences.

14. Using BLAST® (National Center for Biotechnology Information, 2025), compare new ITS sequences to existing sequences in the GenBank® nucleotide database. Make the species identification after reviewing the taxonomic diagram in BLAST® Tree View and filtering search results by percent identity. Salem-Bango et al. (2023) indicate a similarity cutoff of 98.5% as "the international consensus" for fungal species identification—i.e., they expect that fungi of the same species will share at least 98.5% of their ITS DNA—I round up to 99%.

15. If needed, search the literature for phylogenies and recent taxonomic work, as there is no mechanism to correct names in GenBank®, so the names can be wrong (Berch et al., 2023; Bidartando, 2008). If the sequence has no close species matches—as is the case for several of my sporocarps—seek a provisional name for the unique taxon.

During fungal sporocarp processing, Heather Dawson performed steps 6–11 of the above protocol (H. Dawson, personal communication, 2025). I performed steps 1–5 and 12–14.

In some cases, a secondary means of obtaining species identifications for the fungal sporocarps was necessary. In these instances, I documented microscopic characters for a subset of the sporocarps, adhering to the following protocol:

1. Rehydrate the dried sporocarp in isopropyl alcohol for several minutes.

2. With a sharp razor blade, cut a thin, aqueduct-shaped slice of tissue from the sporocarp, capturing a cross-section of the gills/pores and cap, if present. If no gills/pores and cap are present, ensure that the thin slice captures tissue from the sporocarp's spore-bearing region.

3. Mount the tissue slice in Melzer's Reagent or KOH on a glass slide.

4. Under a microscope, bring the tissue into focus under low magnification. Gradually increase to 40x and/or 100x (oil immersion) magnification.

5. Bring important microscopic features—including spores, basidia, and any other variable or unusual structures—into focus. Calibrate a scale bar for each scene.

6. Photograph and save all key features using the AmScope Version x64 application.

7. Use one or more fungal dichotomous keys to make the species identification, referring to the photographs of the microscopic features alongside other materials, including photos of the fresh sporocarp and notes about the environmental context.

When microscopy was necessary for fungal sporocarp identification, I performed steps 1–7 of the above protocol.

Data Analysis

All plant and fungal community data were analyzed in R. The base source code was written Haley Burrill with the University of Oregon's Roy Lab and subsequently adapted and modified by me. A Pearson correlation was used to assess any correlation between the species evenness, richness, and % cover of the overall understory plant community and the species evenness and richness of the overall soil fungal community.

Understory Plants

Cover data were used to calculate species evenness (Shannon-Weiner and base R diversity function), species richness, and Bray-Curtis dissimilarity between samples using the "vegdist" function in the "vegan" package (Oksanen et al., 2019). Generalized Linear Models (GLMs) were used to examine the dependent variables of plant species evenness, richness, and % cover in a statistical model that included burn condition (burned or not, hereafter BC), with the year of burn treatment nested within burn (hereafter BY). To account for variation in locality, the oak tree from which the samples were taken was numbered and used as a covariate. To analyze differences in vegetation cover composition between burned and unburned sites, a PERMANOVA was run using "adonis2" in "vegan," with the dependent variable Bray-Curtis dissimilarity of plant cover. As in the GLM, the PERMANOVA model included the main effect of burn treatment—BY nested within BC—and the tree from which the samples were taken was used as a covariate. To visualize differences between treatments, Bray-Curtis dissimilarity was used to calculate non-metric multi-dimensional scaling (NMDS) graphs.

Soil Fungi

The fungal soil sequencing Amplicon Sequence Variant (ASV) datasheet was used to calculate relative abundance, evenness, and richness of fungal ASVs. GLMs were used to measure the response of each fungal group to each burn treatment; again, BY was nested within BC, and the tree from which the samples were taken as a covariate. Robust Aitchison dissimilarity was calculated by first-center-log-ratio-transforming the ASV datasheet, then calculating Aitchison dissimilarity using "vegdist" in "vegan." Finally, "adonis2" was used once more to measure the fungal community response to the same model as with the univariate test.

Results

The Pearson correlation tests indicated that species evenness, richness, and % cover of the overall understory plant community were not significantly statistically correlated with the species evenness and richness of the overall soil fungal community.

Understory Plants

Description

Overall, there were at least 84 understory plant taxa at PIS_2023, PIS_2019, and PIS_CTRL (Figure 2). The most dominant plant species was the native shrub *Toxicodendron diversilobum.*

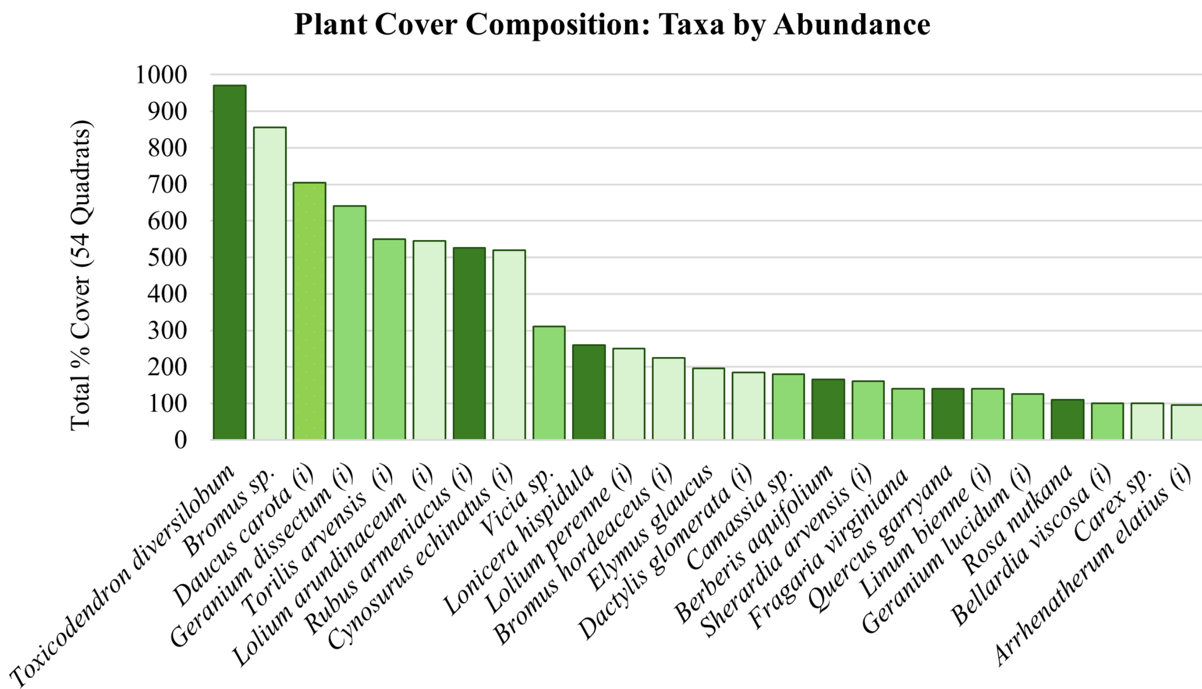

Figure 2. Total % cover of 25 most abundant understory taxa surveyed at PIS_2023, PIS_2019, and PIS_ctrl, summed across all 54 quadrats.

Composition

The PERMANOVA indicated that both the interaction of burn condition (BC)—the state of being burned or unburned—with burn year (BY) and tree-plot—the particular oak tree whose understory was sampled—were statistically explanatory of variation in understory plant community composition. BC (Figure 3A) and BY (Figure 3B) together—though not individually significant—explained about 15.4% of the variation in community composition ($p = 0.001$), and tree-plot explained another 3.5% of the variation ($p = 0.009$).

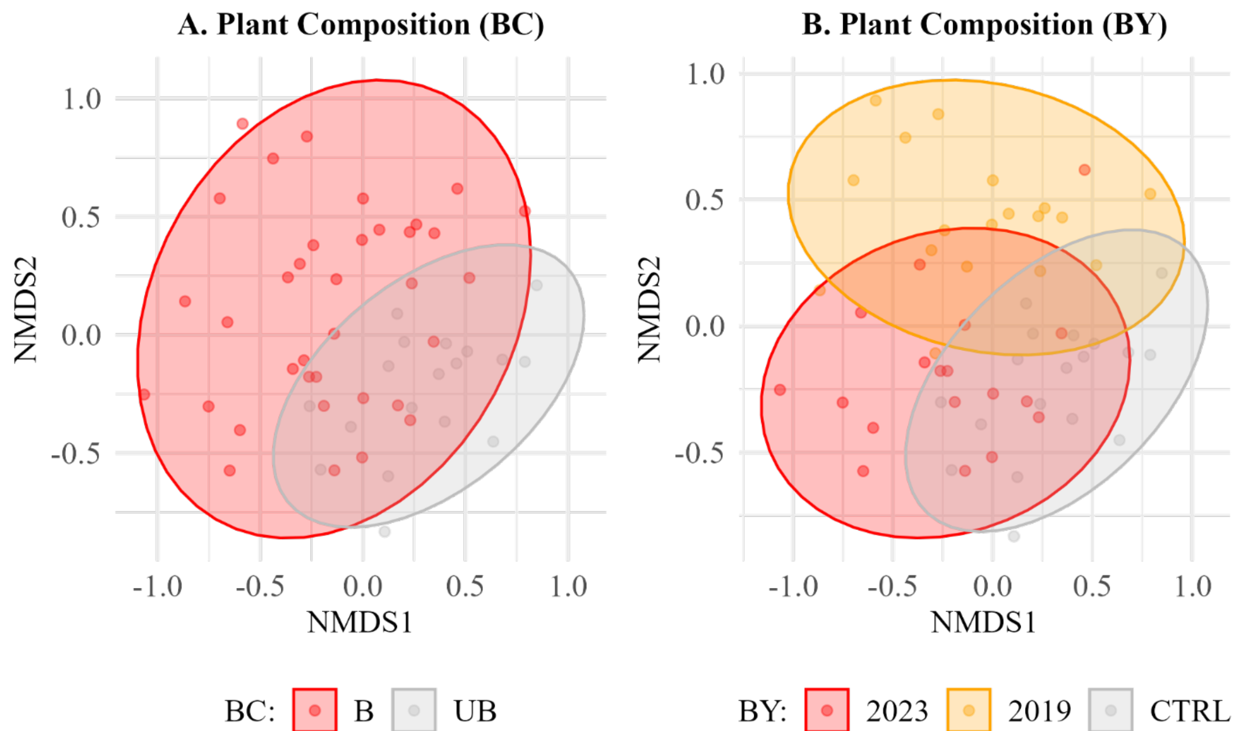

Figure 3. Comparison of overall understory plant community composition by oak savanna BC (A) and BY (B). Overlapping areas signify similarity in community composition; areas without overlap indicate dissimilarity.

Diversity and Abundance

In the overall understory plant community, the Poisson GLM indicated no significant difference in species evenness or richness across BC and BY; the mean ($\bar{x}$) species richness was

x̄ = 12.000 in plots with BY-2023, x̄ = 14.000 in BY-2019, and x̄ = 11.667 in the control (Figure 4). There was, however, a significant increase in % plant cover for BY-2023 ($p = 0.006$) and a significant tree-plot correlation ($p = 0.014$); the mean % cover was x̄ = 204.17% in plots with BY-2023, x̄ = 156.94% with BY-2019, and x̄ = 169.44% in the control (Figure 4).

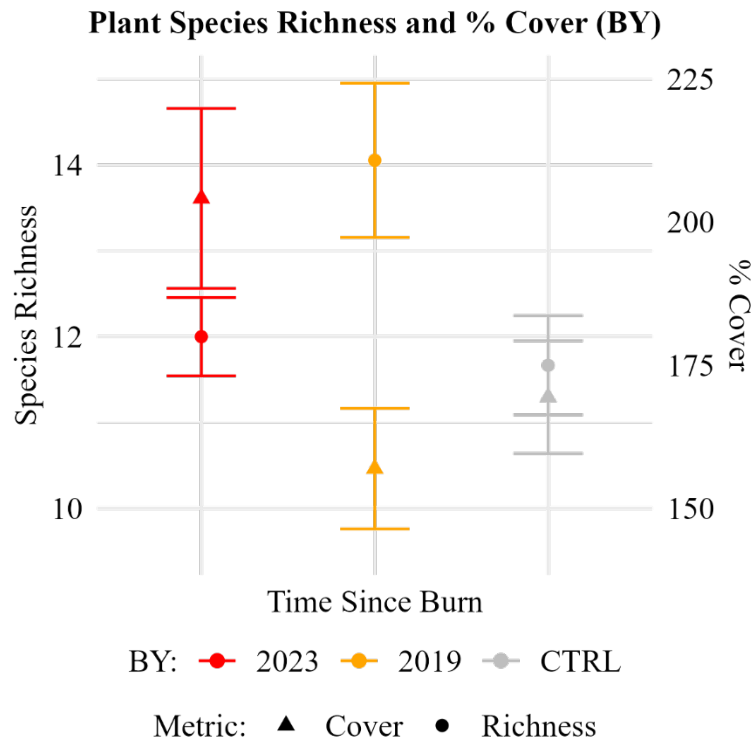

Figure 4. Comparison of overall plant species richness and % cover between oak savannas burned in 2023 and 2019 and unburned oak savannas.

When comparing subsets of the understory plant community—annual and perennial species—a stronger pattern emerged. Plant species evenness and richness did not depend on either BC or BY, but there was significantly higher perennial plant species richness for the interaction of BC-burned with BY-2019 ($p < 0.001$). The mean annual species richness was x̄ = 5.056 in plots with BY-2023, x̄ = 3.944 with BY-2019, and x̄ = 4.556 in the control (Figure 5A); the mean perennial species richness was x̄ = 4.833 in plots with BY-2023, x̄ = 8.500 with BY-2019, and x̄ = 5.500 in the control (Figure 5B). For annual plants, there was also a significant decrease in mean % cover

for BC-unburned (p = 0.002), a significant increase in % cover for BY-2023 (p < 0.001), and a significant tree-plot correlation (p = 0.008); for perennial plants, there was a significant decrease in mean % cover for BY-2023 (p = 0.00291). The mean annual % cover was x̄ = 86.111% in plots with BY-2023, x̄ = 26.944% with BY-2019, and x̄ = 57.500% in the control (Figure 5A); the mean perennial % cover was x̄ = 68.056% in plots with BY-2023, x̄ = 109.17% with BY-2019, and x̄ = 86.389% in the control (Figure 5B).

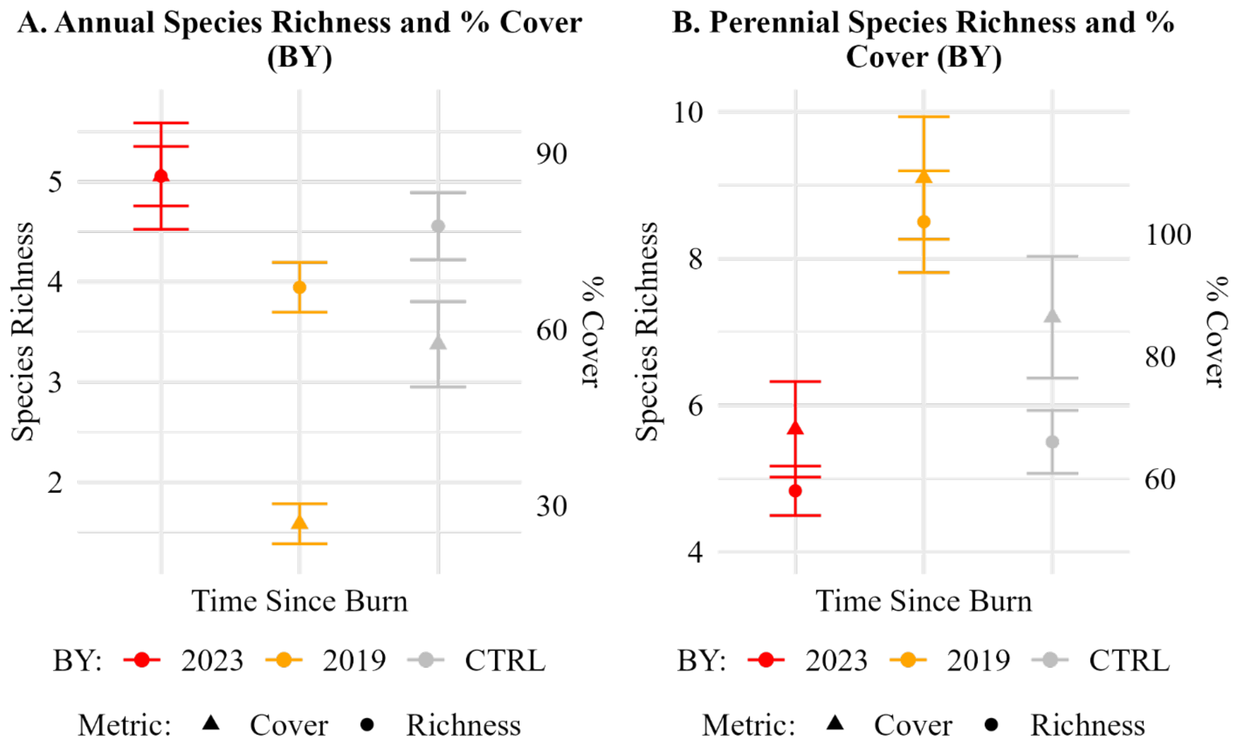

Figure 5. Comparison of annual (A) and perennial (B) plant species richness and % cover between oak savannas burned in 2023 and 2019 and unburned oak savannas.

For the native and introduced subsets of plant species, another pattern emerged. Again, there was no significant difference in species evenness across BC and BY. There was, however, a significant decrease in native species richness in the interaction of BC-burned with BY-2023 (p = 0.009). The mean native species richness was x̄ = 2.167 in plots with BY-2023, x̄ = 4.556 with BY-2019, and x̄ = 3.778 in the control (Figure 6A); the mean introduced species richness was x̄

= 4.833 in plots with BY-2023, x̄ = 8.500 with BY-2019, and x̄ = 5.500 in the control (Figure 6B). Additionally, for native plants, there was a significant decrease in % cover for BY-2023 ($p = 0.009$); for introduced plants, there was a significant increase in % cover for BY-2023 ($p = 0.002$) and a significant tree-plot correlation ($p = 0.013$). The mean native % cover was x̄ = 28.889% in plots with BY-2023, x̄ = 56.111% with BY-2019, and x̄ = 54.722% in the control (Figure 6A); the mean introduced % cover was x̄ = 151.11% in plots with BY-2023, x̄ = 96.111% with BY-2019, and x̄ = 101.94% in the control (Figure 6B).

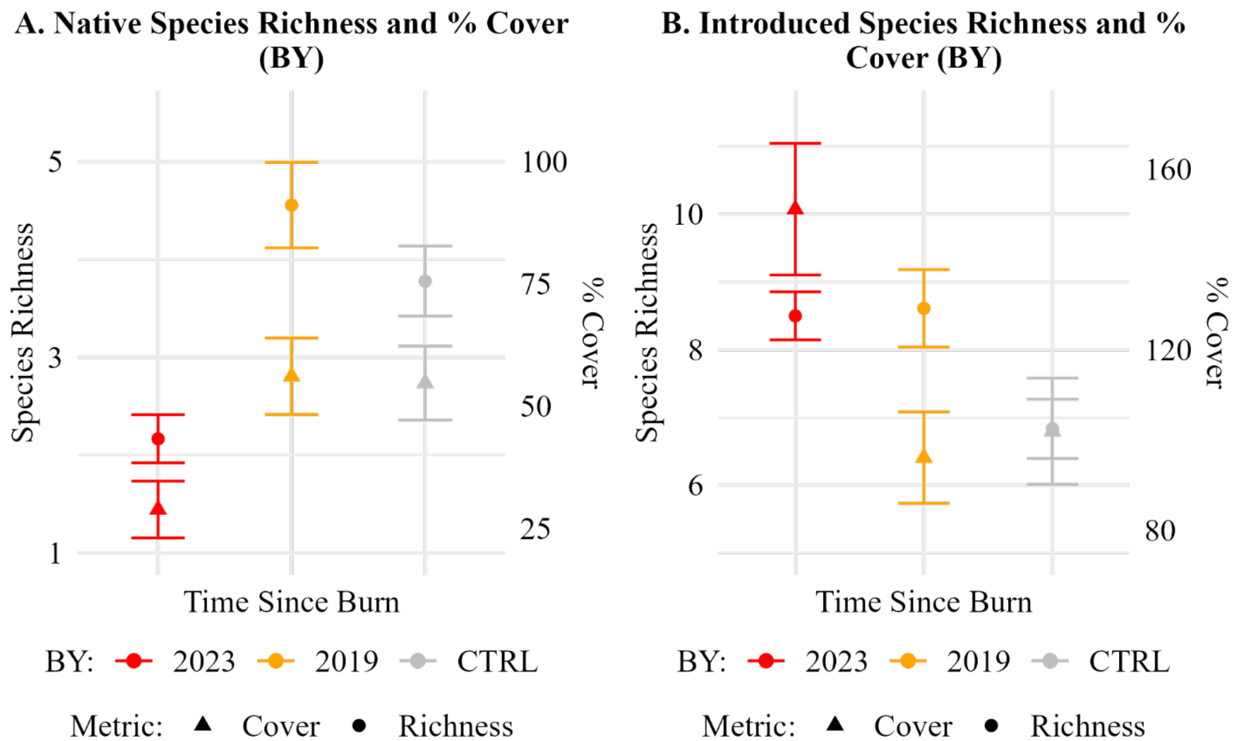

Figure 6. Comparison of native (A) and introduced (B) plant species richness and % cover between oak savannas burned in 2023 and 2019 and unburned oak savannas.

Soil Fungi

Composition

The PERMANOVA indicated that the interaction of BC with BY was statistically explanatory of variation in overall soil fungal community composition. BC (Figure 7A) and BY (Figure 7B) together—though not individually significant—explained about 4.2% of the variation in overall fungal composition (p = 0.005).

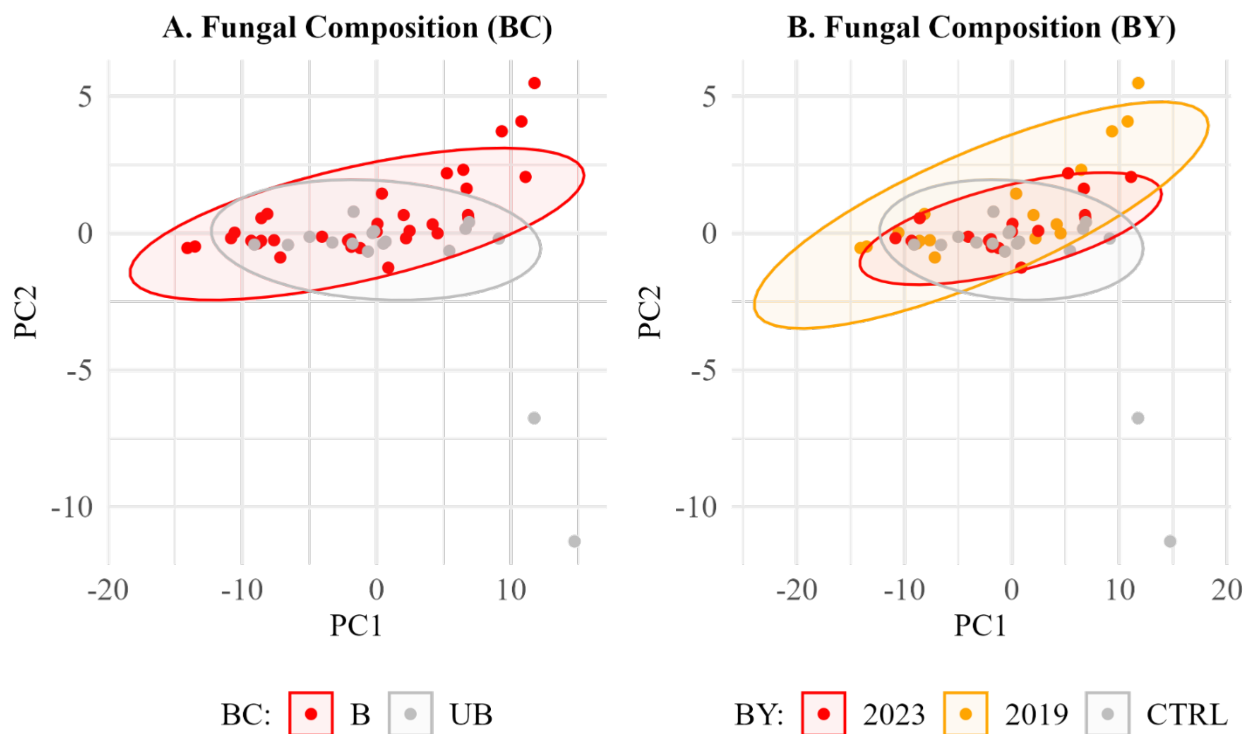

Figure 7. Comparison of soil fungal community composition by oak savanna burn condition (A) and burn year (B). Overlapping areas signify similarity in community composition; areas without overlap indicate dissimilarity.

In the saprotrophic soil fungi subset, the interaction of BC with BY was also statistically explanatory of variation in community composition (Figure 8). BC and BY together—though not individually significant—explained about 4.2% of the variation in saprotroph composition (p = 0.041).

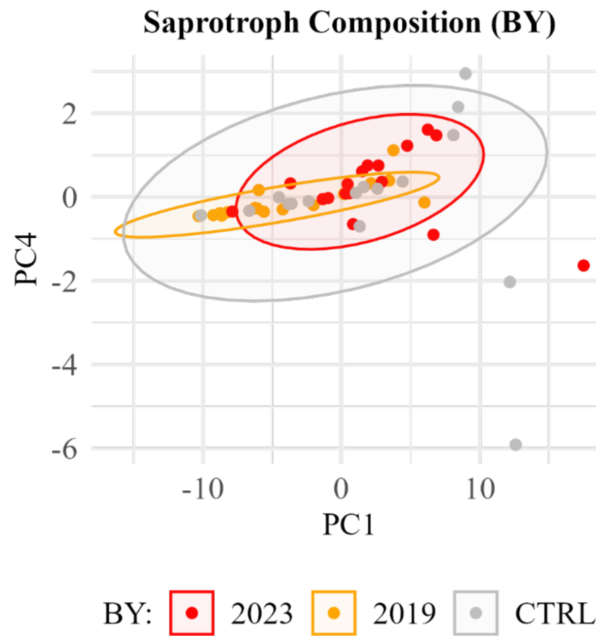

Figure 8. Comparison of saprotrophic soil fungal community composition by oak savanna BY. Overlapping areas signify similarity in community composition; areas without overlap indicate dissimilarity.

Further, BC and BY together—though individually insignificant—explained about 4.5% of the variation in ectomycorrhizae composition (p = 0.054; Figure 9A) and about 8.2% of the variation in pathogenic composition (p = 0.051; Figure 9B).

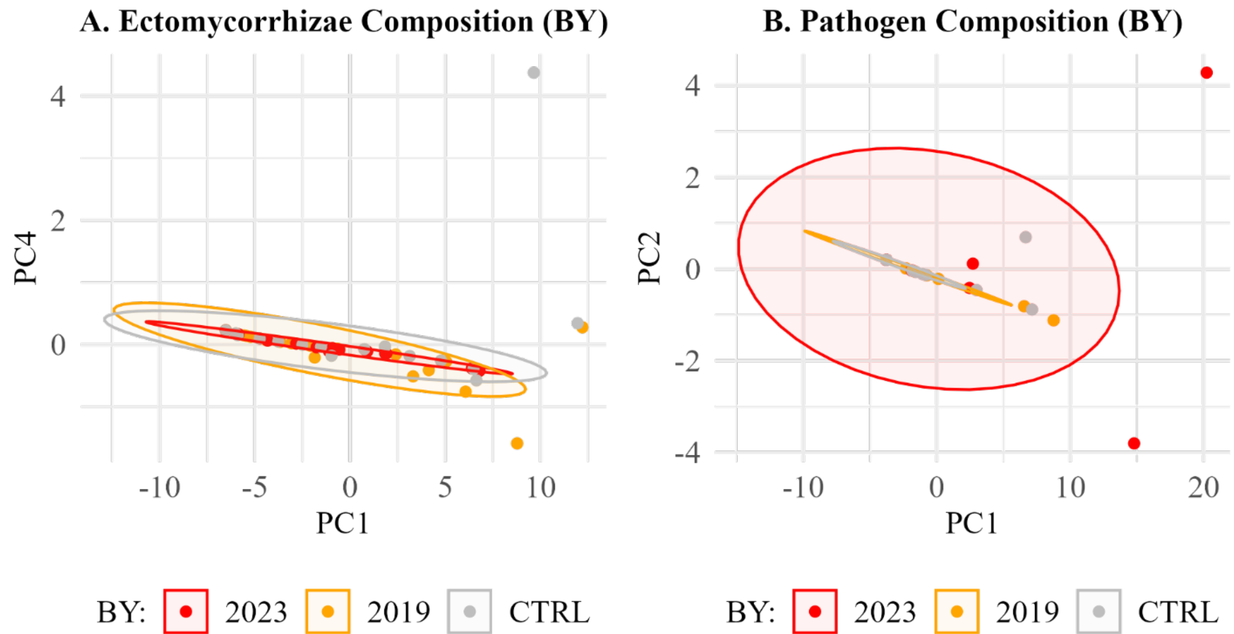

Figure 9. Comparison of soil fungal community composition by oak savanna BY for ectomycorrhizae (A) and pathogens (B). Overlapping areas signify similarity in community composition; areas without overlap indicate dissimilarity.

Diversity and Cover

In the overall soil fungal community, the Poisson GLM indicated no significant difference in species evenness across burn conditions and burn years. However, it did report a significant decrease in overall fungal species richness for the interaction of BC-burned with BY-2023 ($p = 0.039$) and BY-2019 ($p < 0.001$). Additionally, tree-plot was a significant driver of fungal species richness ($p = 0.005$). The mean fungal species richness was $\bar{x} = 6507.9$, 95% CI [5459.2, 7556.6] in plots with BY-2023; $\bar{x} = 6132.5$, 95% CI [4863.0, 7401.9] with BY-2019; and $\bar{x} = 7815.9$, 95% CI [6315.7, 9316.1] in the control (Figure 10).

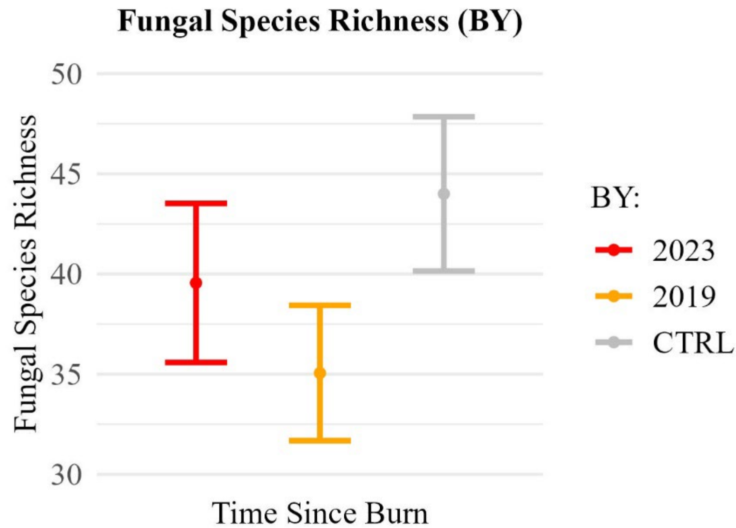

Figure 10. Comparison of overall soil fungal species richness between oak savannas burned in 2023 and 2019 and unburned oak savannas.

In the ectomycorrhizal soil fungal subset, a similar trend appeared: there was a significant decrease in ectomycorrhizae species abundance for the interaction of BC-burned with BY-2023 ($p < 0.001$) and BY-2019 ($p = 0.016$). Additionally, tree-plot was a significant driver of ectomycorrhizae species abundance ($p < 0.001$). The mean ectomycorrhizae species abundance was $\bar{x} = 293.89$, 95% CI [139.79, 447.99] in burned plots with BY-2023; $\bar{x} = 1058.7$, 95% CI [548.67, 1568.7] with BY-2019; and $\bar{x} = 1085.1$, 95% CI [620.29, 1549.8] in the control (Figure 11).

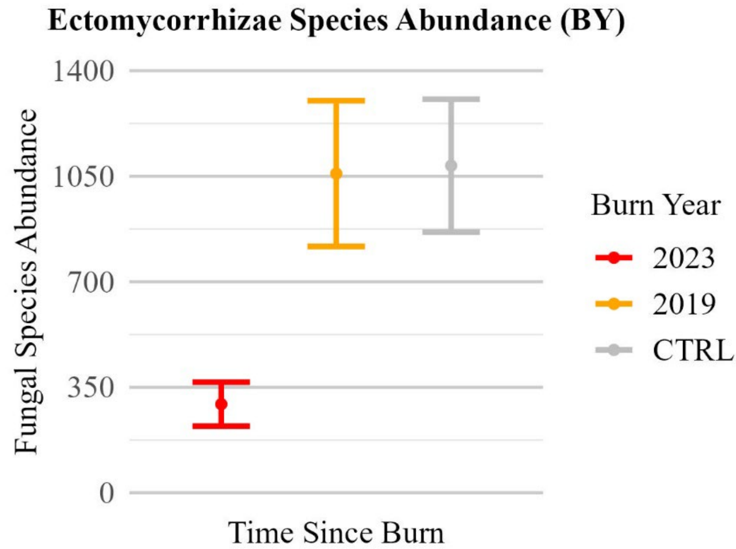

Figure 11. Comparison of ectomycorrhizal soil fungal species abundance between oak savannas burned in 2023 and 2019 and unburned oak savannas.

In the pyrophilous soil fungi subset, the opposite trend appeared. There was a significant increase in pyrophile species abundance for the interaction of BC-burned with BY-2023 ($p < 0.001$) and BY-2019 ($p < 0.001$). Additionally, tree-plot was a significant driver of pyrophile species abundance ($p < 0.001$). The mean pyrophile species abundance was $\bar{x} = 53.444$, 95% CI [-23.998, 130.89] in burned plots with BY-2023; $\bar{x} = 55.889$, 95% CI [-8.3991, 120.18] with BY-2019; and $\bar{x} = 16.722$, 95% CI [-18.559, 52.003] in the control (Figure 12).

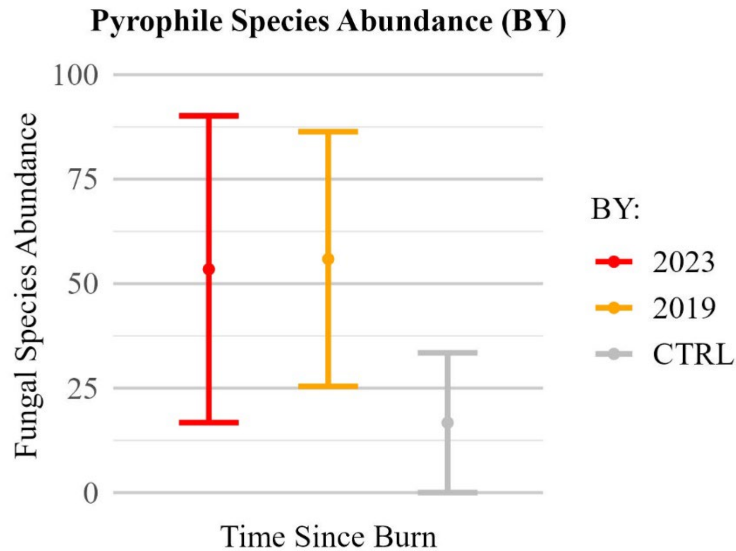

Figure 12. Comparison of pyrophilous soil fungal species abundance between oak savannas burned in 2023 and 2019 and unburned oak savannas.

In the pathogenic and saprotrophic soil fungi subsets, a third trend appeared. There was a significant increase in pathogen and saprotroph species abundance for the interaction of BC-burned with BY-2023 ($p < 0.001$) but a significant decrease in pathogen and saprotroph species abundance for the interaction of BC-burned with BY-2019 ($p < 0.001$). Additionally, tree-plot was a significant driver of pathogen and saprotroph species abundance ($p < 0.001$). The mean pathogen species abundance was $\bar{x} = 257.78$, 95% CI [24.865, 490.69] in burned plots with BY-2023; $\bar{x} = 64.333$, 95% CI [11.962, 116.70] with BY-2019; and $\bar{x} = 161.89$, 95% CI [39.291, 284.49] in the control (Figure 13A). The mean saprotroph species abundance was $\bar{x} = 1864.5$, 95% CI [1270.8, 2458.2] in burned plots with BY-2023; $\bar{x} = 1198.4$, 95% CI [835.65, 1561.2] with BY-2019; and $\bar{x} = 1631.9$, 95% CI [1129.6, 2134.2] in the control (Figure 13B).

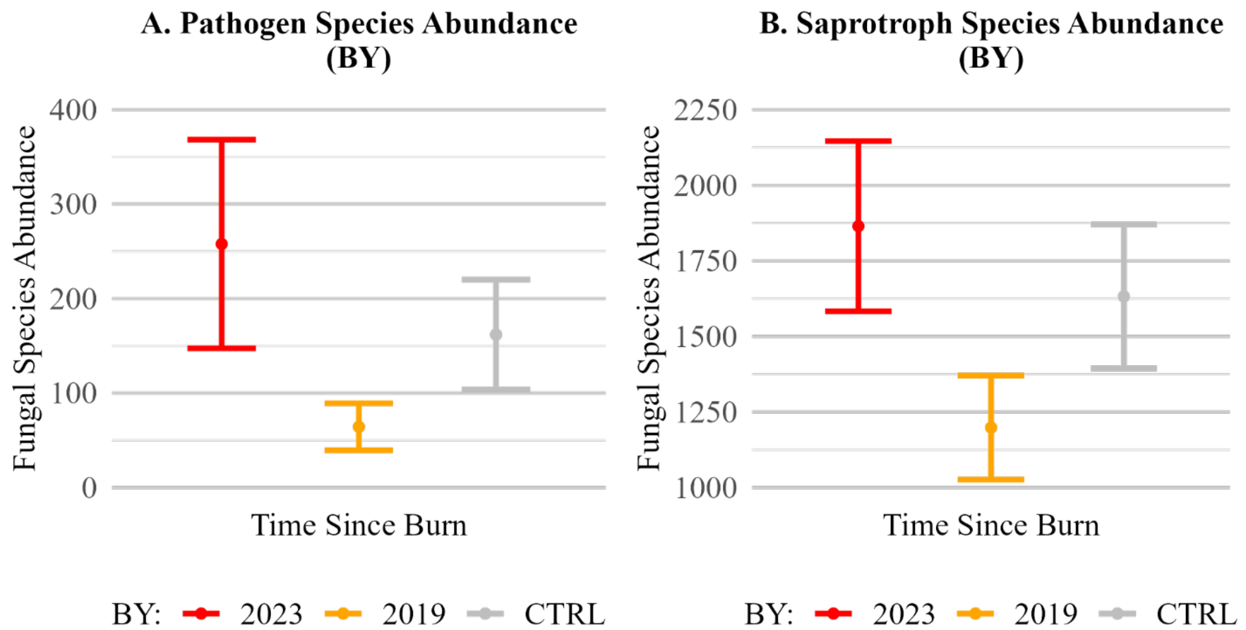

Figure 13. Comparison of pathogenic (A) and saprotrophic (B) soil fungal species abundance between oak savannas burned in 2023 and 2019 and unburned oak savannas.

Fungal Sporocarps

A variety of taxonomically distinct fungal sporocarps fruited across the 9 field sites (n = 138); these observations are documented below (Table 2). Amongst the sporocarp observations, the mean species richness was $\bar{x} = 17.6$ for BC-B and $\bar{x} = 21.25$ for BC-UB; the mean abundance was $\bar{x} = 36.6$ for BC-B and $\bar{x} = 44.25$ for BC-UB. Saprotrophs were the most commonly found fungal guild (n = 77), followed by pathogens/parasites (n = 32) and mycorrhizal fungi (n = 25).

Table 2. Fungal sporocarps observed fruiting at each oak savanna site; 1 indicates species presence, 0 indicates species absence, underlining signifies correlation with a soil-sample analog, and * signifies a research-grade iNaturalist observation without DNA sequencing done. Ecology is mycorrhizal (M), pathogenic/parasitic (P), or saprotrophic (S). Green boxes mark sporocarp-soil same-site analogs; gold boxes mark sporocarp-soil same-locality analogs.

Sporocarp Taxon	**Ecology**	**CBG_2022**	**CBG_CTRL**	**PIS_2024**	**PIS_2023**	**PIS_2019**	**PIS_CTRL**	**SSL_2018**	**SSL_CTRL**	**WCP_2023**	**WCP_CTRL**
Adustoporia sinuosa	P	0	0	0	0	1	0	0	0	0	0
Agaricus xanthodermus	S	1	1	0	0	0	0	0	0	0	0
Aleuria aurantia	M/S	1*	0	0	0	0	0	0	0	0	0
Amanita muscaria	M	0	0	0	0	0	0	1	0	0	0
Amanita phalloides	M	0	0	0	0	0	0	<u>0</u>	<u>1</u>	0	0
Amyloporia xantha	S	0	0	0	0	1	0	0	0	0	0
Armillaria sp.	P	0	0	0	0	0	0	1	0	0	0
Ascocoryne sarcoides	S	0	1	0	0	0	0	0	0	0	0
Athelia arachnoidea	P	0	<u>0</u>	0	<u>1</u>	<u>0</u>	<u>0</u>	0	0	0	<u>0</u>
Bolbitius reticulatus	S	0	0	0	0	0	0	0	1	0	0
Bolbitius titubans	S	0	1	0	0	0	0	0	0	0	0
Boletus edulis	M	0	0	0	0	0	0	1	0	0	0
Calocera cornea	S	0	0	0	0	0	0	1	0	0	0
Cantharellus californicus	M	0	0	0	0	0	0	1	0	0	0
Ceriporia sp. 'CA-02'	S	0	0	0	0	0	0	0	0	1	0
Ceriporia reticulata	S	<u>0</u>	<u>0</u>	0	0	1	<u>0</u>	<u>0</u>	<u>0</u>	0	0
Chalciporus piperatus	M	0	0	0	0	0	0	<u>1</u>	<u>0</u>	0	0

Sporocarp Taxon	Ecology	CBG_2022	CBG_CTRL	PIS_2024	PIS_2023	PIS_2019	PIS_CTRL	SSL_2018	SSL_CTRL	WCP_2023	WCP_CTRL
Chlorociboria aeruginascens	S	0	0	0	0	0	0	0	1	0	0
Clarireedia bennettii	P	0	0	0	0	0	0	0	0	1	0
Clavariadelphus occidentalis	M	0	0	0	0	0	0	1	0	0	0
Collybia sp. 'KMS-01'	--	0	0	0	0	0	0	0	0	0	1
Collybia 'rivulosa-PNW-07'	S	0	0	0	0	0	1	0	0	1	0
Conocybe sp. 'ON-01'	--	0	1	0	0	0	0	0	0	0	0
Coprinopsis lagopus	S	0	1	0	0	0	0	0	0	0	0
Coprinellus sp. 'radians-IN-03'	S	0	1	0	0	0	0	0	0	0	0
Corticium roseum	P	0	0	0	0	0	0	0	0	1	0
Cortinarius albofragrans	--	0	0	0	0	0	0	0	1	0	0
Craterellus calicornucopioides	M	0	0	0	0	0	0	0	1	0	0
Crepidotus sp. 'KMS-01'	--	0	0	0	0	0	0	0	0	1	1
Crustomyces subabruptus	P/S	0	0	0	0	0	0	0	1	0	0
Dendrocollybia racemosa	P/S	0	0	0	0	0	0	0	1	0	0
Diplocarpa sp. 'PNW-02'	--	0	0	0	0	0	0	0	0	1	0
Ductifera sucina	--	0	0	0	1	0	0	0	0	0	0
Exidia glandulosa	P/S	0	1	0	0	0	0	0	0	0	0
Flagelloscypha sp. 'KMS-01'	--	1	0	0	0	0	0	0	0	0	0
Fomitopsis quercina	S	1	0	0	0	0	0	1	1	0	0
Fomitiporia punctata	P/S	0	1*	0	0	0	0	0	0	0	0
Fuscoporia ferrea	P/S	0	1	0	1	0	1	0	1	0	0

Sporocarp Taxon	Ecology	CBG_2022	CBG_CTRL	PIS_2024	PIS_2023	PIS_2019	PIS_CTRL	SSL_2018	SSL_CTRL	WCP_2023	WCP_CTRL
Galerina badipes	S	0	0	0	0	0	0	0	0	1	0
Galerina sp.	S	0	0	0	0	0	0	0	1	0	1
Galerina castaneipes	S	0	1	0	0	0	0	0	0	0	0
Galerina marginata	S	0	0	0	0	0	0	0	1*	0	0
Galerina nigripes	S	0	0	0	0	0	0	0	0	0	1
Galerina semilanceata	S	0	0	0	0	0	0	0	0	1	1
Gloeoporus dichrous	S	1	0	0	0	0	0	0	0	1	0
Gloeoporus sp. 'dichrous-CA-01'	--	0	0	0	0	1	0	0	0	0	0
Guepiniopsis alpina	S	0	0	0	0	0	0	0	1*	0	0
Gymnopus dryophilus	P/S	0	1	0	0	0	0	0	0	0	0
Gymnopus longisterigmaticus	--	0	0	0	0	0	0	0	1	0	0
Gymnopus sp. 'PNW-11'	--	0	1	0	0	0	0	0	0	0	0
Hebeloma sacchariolens	M	0	0	0	0	0	0	0	0	0	1
Hyalorbilia sp.	P/S	0	0	0	0	0	0	0	0	0	1
Hygrocybe sp. 'singeri-CA-01'	--	0	0	0	0	0	0	1	0	0	0
Hygrophorus eburneus	M	0	0	0	0	0	1*	0	0	0	0
Hygrophorus sp. 'eburneus-CA-01'	--	0	0	1	0	0	0	0	0	0	0
Hygrophorus roseobrunneus	M	0	0	1	0	0	0	0	0	0	0
Hypholoma fasciculare	S	0	0	0	0	0	0	1	1	0	1
Hypomyces aurantius	P	0	0	0	0	0	0	0	1	0	0
Hypomyces sp. 'KMS-01'	--	0	0	0	0	0	0	1	0	0	0

Sporocarp Taxon	Ecology	CBG_2022	CBG_CTRL	PIS_2024	PIS_2023	PIS_2019	PIS_CTRL	SSL_2018	SSL_CTRL	WCP_2023	WCP_CTRL
Inocybe sp. 'CA09'	M	0	0	0	0	0	0	0	1	0	0
Inocybe sp. 'geophylla-PNW-06'	M	0	0	0	0	0	0	1	0	0	0
Inocybe sp. 'KMS-01'	M	0	0	0	0	0	0	1	0	0	0
Laccaria laccata	M	0	0	0	0	0	0	0	1	0	0
Lachnum sp. 'virgineum-PNW-02'	--	1	0	0	0	0	0	0	0	0	0
Lactarius sp. 'acrid orange'	M	0	0	0	0	0	0	0	0	0	1
Lactarius argillaceifolius	M	0	0	0	0	0	0	1	0	0	0
Lactarius sp. 'IN-09'	M	0	0	0	0	0	0	0	1	0	0
Marasmius plicatulus	S	0	0	0	0	0	0	0	0	0	1
Melanogaster natsii	--	0	0	0	0	0	0	0	1	0	0
Merulius tremellosus	S	0	0	0	0	0	0	0	1	0	1
Mollisia sp. 'CA-01'	P/S	0	0	0	1	0	0	0	0	0	0
Mollisia oblonga	P/S	1	0	0	1	0	0	0	0	0	0
Mycena sp. 'acicula-CA-01'	S	1	0	0	0	0	0	0	0	0	0
Mycena citrinomarginata	S	0	0	0	0	0	0	0	0	1	0
Mycena cf. sp. 'filopes-PNW12'	S	0	1	0	0	0	0	0	0	0	1
Mycena galericulata	S	1	1	0	0	0	0	0	1	1	1
Mycena haematopus	S	0	1	0	0	0	0	0	0	0	0
Mycena meliigena	S	0	0	0	0	0	0	0	0	0	1
Mycena murina	S	0	0	0	0	0	1	0	0	0	0
Mycena subcana	S	0	0	0	0	0	0	0	0	1	1

Sporocarp Taxon	Ecology	CBG_2022	CBG_CTRL	PIS_2024	PIS_2023	PIS_2019	PIS_CTRL	SSL_2018	SSL_CTRL	WCP_2023	WCP_CTRL
Mycena vitilis	S	0	1	0	0	0	0	0	0	0	0
Myxarium sp. 'CA-01'	P/S	0	0	0	0	0	1	0	0	0	0
Naematelia aurantia	P	0	0	0	0	1	0	1	0	0	0
Orbilia sp. 'PNW-03'	--	0	0	0	0	0	1	0	0	0	0
Panaeolus acuminatus	S	0	1	0	0	0	0	0	0	1	0
Panellus stipticus	S	0	1	0	0	0	0	0	0	0	0
Panus conchatus	S	0	0	0	0	1	0	0	0	0	0
Parasola 'neoplicatilis-PNW-01'	S	1	1	0	0	0	0	0	0	0	0
Peniophora sp.	P/S	1	0	0	0	0	0	0	0	0	0
Peniophorella sp. 'KMS-01'	--	0	0	0	1	0	0	0	0	0	0
Peniophorella pubera	--	0	0	0	0	0	0	1	0	0	0
Phanerochaete livescens	--	0	0	0	0	0	0	0	0	0	1
Phlebia sp. 'acanthocystis-CA-01'	--	0	0	0	0	0	0	0	1	0	0
Phlebia rufa	P/S	0	0	0	0	1	1	0	0	1	0
Phloeomana hiemalis	P/S	0	0	0	0	0	0	0	0	1	1
Phloeomana speirea	P/S	0	0	0	0	0	0	0	1	1	1
Pholiota brunnescens	--	1	0	0	0	0	0	0	0	0	0
Picipes tubaeformis	S	1	1	0	0	0	0	0	0	0	1
Pluteus sp. 'CA-01'	S	1	0	0	0	0	0	0	0	0	0
Pluteus exilis	S	1	1	0	0	0	0	0	0	0	1
Pluteus sp. 'thomsonii-PNW-04'	S	0	0	0	0	0	0	0	0	1	1

Sporocarp Taxon	Ecology	CBG_2022	CBG_CTRL	PIS_2024	PIS_2023	PIS_2019	PIS_CTRL	SSL_2018	SSL_CTRL	WCP_2023	WCP_CTRL
Psathyrella longipes	S	1	0	0	0	0	0	0	0	0	0
Psathyrella microrhiza	--	0	1	0	0	0	0	0	0	1	1
Psathyrella piluliformis	S	1	0	0	0	0	0	0	0	0	0
Pseudoclitocybe cyathiformis	S	0	0	0	0	1	0	0	0	0	0
Pseudoclitocybe sp. 'CA-01'	--	1	0	0	0	0	0	0	0	0	0
Rhodonia placenta	P/S	0	0	0	0	1	0	0	0	0	0
Russula sp. 'albidula-CA-01'	M	0	0	0	0	0	0	0	1	0	0
Russula sp. 'basifurcata-PNW-01'	M	0	0	0	0	0	0	0	1	0	0
Russula 'brevipes-CA-02'	M	0	0	0	0	0	0	0	1	0	0
Rutstroemia sp. 'CA-01'	--	1	0	0	0	0	0	0	0	0	0
Sarcodontia uda	S	0	1	0	0	1	0	0	0	1	0
Schizophyllum commune	P	1*	1	0	1*	1*	0	0	0	0	0
Scleroderma areolatum	M/S	1	0	0	0	0	0	0	0	0	0
Scutellinia sp.	--	1	0	0	0	0	0	0	0	0	0
Scutellinia scutellata	S	0	0	0	0	0	0	0	0	1	0
Sidera sp. 'CA-01'	P/S	0	0	0	1	0	0	0	0	0	0
Simocybe haustellaris	S	0	0	0	0	0	1	0	0	0	0
Simocybe serrulata	P/S	0	0	0	0	0	1	0	0	0	0
Sistotrema brinkmannii	P/S	0	0	0	1	0	0	0	0	0	0
Sistotremastrum niveocremeum	--	0	0	0	0	0	1	0	0	0	0
Steccherinum bourdotii	P/S	0	0	0	0	0	1	0	0	0	0

Sporocarp Taxon	Ecology	CBG_2022	CBG_CTRL	PIS_2024	PIS_2023	PIS_2019	PIS_CTRL	SSL_2018	SSL_CTRL	WCP_2023	WCP_CTRL
Steccherinum sp. 'CA-05'	--	0	0	0	0	0	1	0	0	0	0
Stereum hirsutum	S	0	0	0	0	1	0	0	0	0	0
Stereum ochraceoflavum	P/S	0	0	0	0	1	0	0	0	0	0
Stropharia ambigua	S	0	0	0	0	0	0	0	1	0	0
Suillus caerulescens	M	0	0	0	0	0	0	1	1	0	0
Trametes betulina	S	1	0	0	0	0	0	0	0	0	0
Trametes versicolor	S	0	1*	0	0	1	0	0	0	0	1
Tricholoma sp. 'saponaceum-PNW-05'	M	0	0	0	0	0	0	1	0	0	0
Tubaria sp. 'IN-01'	--	0	0	0	0	0	0	0	0	1	0
Tyromyces chioneus	S	0	0	0	0	0	0	1	0	0	0
Xenasma sp. 'CA-01'	S	0	0	0	1	0	0	0	0	0	0
Xerocomellus mendocinensis	M	0	0	0	0	0	0	1	0	0	0
Xylodon sp.	P/S	0	0	0	1	0	0	0	1	0	0
Xylodon sp. 'CA-01'	P/S	0	0	0	1	0	0	0	0	0	0
Xylodon quercinus	P/S	1	0	0	0	0	0	0	0	0	0
Xylodon sp. 'rimosissimus-CA-01'	P/S	0	0	0	1	0	0	0	0	0	0
Total		22	24	2	12	13	11	20	27	21	23

Further, of all the sporocarp taxa observed (n = 138), only a handful (n = 15) could be matched to a soil analog at the same site, and—increasing the coarseness—only an additional few taxa (n = 8) could be matched to a soil analog at the same locality. Conversely, however, there were even more sporocarp taxa (n = 458) found in the soil that were not observed fruiting at any of the field sites.

Discussion

Across the sampled oak savannas, the condition of being burned or not (BC) and burn year (BY) affected both overall understory plant and overall soil fungal composition—in agreement with the previously reviewed literature, which found significant fire-mediated effects in plant and fungal community structure and identity—although plant and fungal metrics did not appear to be internally correlated. This lack of correlation fails to provide field-based support for the results of a pot-based experiment by Shen et al. (2021), which found soil fungal diversity to be significantly and positively correlated with plant diversity—joining a cohort of global studies with similar findings (e.g., Prober et al., 2015; Tedersoo et al., 2014)—demonstrating the significant role that experimental/site-level conditions can play in shaping research outcomes.

More specifically, however, the overall plant community saw a significant increase in % cover in BY-2023, indicating that plants can generally both recover and expand within just one season of control-burning; however, these changes did not appear to be persistent, as demonstrated by the (not significantly) lower % cover in BY-2019, even as compared to the control. Here, it is worth noting that not all plants responded equally: perennial plants saw decreased % cover in BY-2023 but increased species richness in BC-burned:BY-2019. Meanwhile, annual plants saw decreased % cover in BC-unburned and increased % cover in BY-2023. This is likely explained by the general tendency for annual plants to grow more quickly and perennial plants to grow more slowly (Lambers et al., 1998); if the fire is of a high enough intensity enough to prevent perennials from re-sprouting from the same root crowns, then they will likely take several years to catch up to or surpass annuals post-burn.

Concerningly, native plants saw decreases in species richness and % cover for BC-burned:BY-2023 and BY-2023, respectively; simultaneously, introduced species % cover

increased for BY-2023. This trend falls in line with similar evidence from other habitat types, such as a study from the western Colorado desert, which found that annual plant richness was lowest and invasive annual grass cover was highest in stands burned more than once, though this burning was wild rather than prescribed (Steers & Allen, 2012). However, a more recent study analyzing introduced grasses in the Great Basin region responds that fire suppression may not be a warranted response to all such cases of invasion, considering that the majority of annual grass invasions have occurred evenly with or without the presence of fire (Smith et al., 2023). By prescribed or unprescribed burn, however, oak savannas are again becoming landscapes that are increasingly interfacing with fire, and research shows that native species richness is an important prerequisite to a habitat's ability to stabilize and resist invasions (Brambila et al., 2022; MacDougall, 2005).

On the fungal side, overall richness declined for BC-burned:BY-2023, in agreement with much of the existing literature but in deviation from the work of Glassman et al. (2023), who found that fungal richness did not decline following the prescribed burning of a California prairie. A similar trend was also true of ectomycorrhizae, which saw decreased abundance in BY-2023 and in BY-2019, with implications, especially in the short-term, for plant survival and condition. In this instance, the finding agreed with Glassman et al. (2023), who reported a negative effect of prescribed burning on fungal abundance. However, from my sites, the ectomycorrhizal abundance in BY-2019 was more than three times higher than that in BY-2023 and only a few dozen short of that in BY-CTRL, suggesting that ectomycorrhizal communities can make a near-full recovery within a couple years of a prescribed burn. As expected, and as indicated by Fox et al. (2022), pyrophilous fungi abundance was higher in both BY-2023 and BY-2019 than in BY-CTRL. These pyrophilous species are known to populate burned areas and

create mycelial mats that help reduce soil erosion (Filialuna & Cripps, 2021), serving important roles in the successional process; many are also mycorrhizal, supporting the reestablishment of the plants they form connections with (Hughes et al., 2020).

Pathogens and saprotrophs both saw increases in abundance for BC-burned:BY-2023 and decreases in abundance for BC-burned:BY-2019. This trend may be explained by wounded and weakened plants becoming more readily infected by pathogens, and the decomposition of killed plants in the year immediately following a burn, but a drop-off several years later as these food sources are exhausted and healthy, new plants take their place. After enough time passing since the burn, pathogen and saprotroph abundance seems to level out to an intermediate value again, as indicated by the abundance values in BY-CTRL. In both cases, these fungi and fire play important roles in selecting for healthy, diverse plant populations (Termorshuizen, 2016) and recycling nutrients into the soil for future use (Dighton, 2007).

While sporocarps did not represent the full diversity of soil fungi present at the oak savanna sites, the inverse was also true: in many cases, fungal sporocarps collected were not detected in the soil analyses. Further, the sporocarps were diverse amongst themselves, representing several potentially new fungal genetic variants and taxa and including some taxa that have not been seen since they were originally described. Additionally, the ectomycorrhizal fungus *Cantharellus californicus*—which has always been described as endemic to the state of California, with one subpopulation recognized in Corvallis (Siegel, 2022)—was for the first time found in the Eugene area, on a burned oak savanna (SSL_2018), highlighting the surprising biodiversity these ecosystems can foster. In this way, the collection and analysis of sporocarps remains an effective and relevant means of paving the way to the mapping of new or unexpected

species in understudied oak-savanna habitats, and it can be used in conjunction with soil sequencing to paint a more holistic picture of the fungal diversity of a locality.

Limitations

Several limitations to this study are worth noting. First, the understory plant and soil fungal comparisons—based exclusively on data collected at PIS_2023, PIS_2019, and PIS_ctrl—only had one site for each of the treatments. As such, this portion of the analysis was not replicated across multiple localities, limiting the study's ability to accurately generalize these treatment effects. Second, the soil cores were collected in the spring only, while fungal sporocarps were collected in both the spring and the fall; fall soil cores may have yielded richer taxonomic data, especially given that seasonality in soil-fungal community composition has been observed in other oak habitats (Voříšková et al., 2014). Finally, the soil sequencing pipeline had limited success in assigning species names to DNA sequences; of n = 9863 total sequences, only n = 2099 were assigned at the species level. While this flaw is in itself a finding, as compared against the results of the fungal sporocarp observations, it also indicates that the fungal community subsets from the preceding section are likely under-representative of their full extent in the soil cores.

Conclusions

Overall, this study puts forth several valuable lessons to understanding oak savanna biodiversity and advising the reintroduction of prescribed fire on these landscapes. First, plant response to fire is dependent on functional group, and effective restoration efforts must consider the potential for increased introduced species establishment following fire; other techniques, such as sowing the seeds of fast-establishing native plants immediately after fire, may be necessary to ensure desirable outcomes (Brambila et al., 2022). Future research should seek to

understand what, if any, the short-term effects of declining ectomycorrhizal species abundance are for oaks and their understories. Finally, these sporocarp collections and sequencing efforts—and, hopefully, the addition of more in future studies—will assist with the ongoing endeavor to describe new fungal species and map fungal diversity across West-Coast oak savannas.

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